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ARTICLE



The Dala thumb: shell morphology and failed predation in *Pollicina cyathina* (Gastropoda) from the Ordovician of Dalarna, Sweden

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ABSTRACT

The distinctive, tall and slender cyrtoconic shell of the gastropod *Pollicina cyathina* Koken, 1897, originally established on a poorly preserved internal mould from the Middle Ordovician of the Dalarna region of central Sweden, is redescribed on the basis of additional material from several localities in the vicinity of Rättvik. Repaired injuries preserved in the fine comarginal growth lines of the archinacelloidean gastropod indicate failed durophagous predatory attacks. Unusual apical structures on an internal mould from Sjurberg probably result from closure of the earliest growth stages later in ontogeny.

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Gastropoda; systematics;
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The slowly expanding, slightly curved and bilaterally symmetrical mollusc *Pollicina* derives its name from the Latin “pollex” (genitive “pollicis”) meaning thumb and was proposed by Koken in Holzapfel (1895) for an Ordovician species originally described from the Ordovician of the St Petersburg region of Russia: *Pollicina corniculum* (Eichwald 1860). Rare specimens of the upright fossil are known from Ordovician limestones in the Siljan district, Dalarna (Fig. 1), where this “Dala thumb” was given the name *Pollicina cyathina* by Koken (1897, see also Koken & Perner 1925). The species epithet is probably a reflection of the similarity of the inverted shell form to the deep ladle or cup (Latin, “cyathus”) used as a measure to dispense wine in the ancient world. *Pollicina* has always been a troublesome mollusc. Originally considered to be a cephalopod (Eichwald 1842), it has been interpreted subsequently as a hyolith or pteropod (Eichwald 1860), a capuliform gastropod (Koken 1897; Koken & Perner 1925), a scaphopod-like mollusc (Starobogatov 1974; Kisselev 1994), a tergomyan monoplacophoran (Evans & Cope 2003) and a euomphaliform gastropod (Yochelson & Webers 2006). After redescribing the type species from Russia and related material from Estonia, Peel (2020) recognised the similarity to some tergomyans but assigned *Pollicina* to the archinacelloidean gastropods, a group of Palaeozoic patelliform gastropods, but not patellogastropods as defined by Lindberg (1986, 1988, 2008).

Koken & Perner (1925) recognised nine species of *Pollicina* from the Baltic Ordovician but only three of these are sufficiently well founded to be retained in the genus at this time. *Pollicina corniculum* (Eichwald 1860), the type species (Fig. 2B, F), was originally described from the St Petersburg region of Russia (Koken 1897) but it is known also from the United Kingdom (Evans & Cope 2003). Ursula Toom (written communication 13 January 2020) has brought to my attention a well preserved specimen of *Pollicina corniculum* from the Kunda Stage at Vihula (Vihula I outcrop) in northern Estonia. The specimen (GIT 693–4) is essentially complete, although the shell

has been exfoliated in the latest growth stage. It is well illustrated on the Geoscience Collections of Estonia website (<http://geocollections.info/specimen/161183>).

Pollicina crassistesta Koken, 1897 is an Estonian species (Fig. 2A, C–E) and together with *P. corniculum* it was recently redescribed by Peel (2020).

Pollicina cyathina Koken, 1897 from the Ordovician of Dalarna, central Sweden, is redescribed in the present paper on the basis of the holotype, a poorly preserved internal mould (Fig. 3G, H), and supplementary material showing shell ornamentation (Fig. 3A–D) together with unusual features of the shell interior (Fig. 4A–C). Repaired injuries preserved in growth ornamentation (Fig. 3A) indicate that *P. cyathina* was subject to durophagous predatory attacks which the specimen in question survived.

Systematic Palaeontology

Repositories. – CNIGRM, F.N. Chernyshev Central Geological Survey Research Museum, St Petersburg. ELM, Estonian Natural History Museum, Tallinn. GIT, Geological collections at Tallinn University of Technology. LO, palaeontological type collection, Department of Geology, Lund University. PMU, palaeontological type collections of the Museum of Evolution, Uppsala University. PSM, Museum of the Department of Historical Geology, St Petersburg State University. SMNH, Swedish Museum of Natural History, Stockholm.

FAMILY POLLICINIDAE PERNER in KOKEN & PERNER, 1925
Genus *Pollicina* Koken in Holzapfel, 1895

Type species. – *Cyrtolithes corniculum* Eichwald, 1860 from the Darriwilian Series, Kunda Stage of the St Petersburg region, Russia.

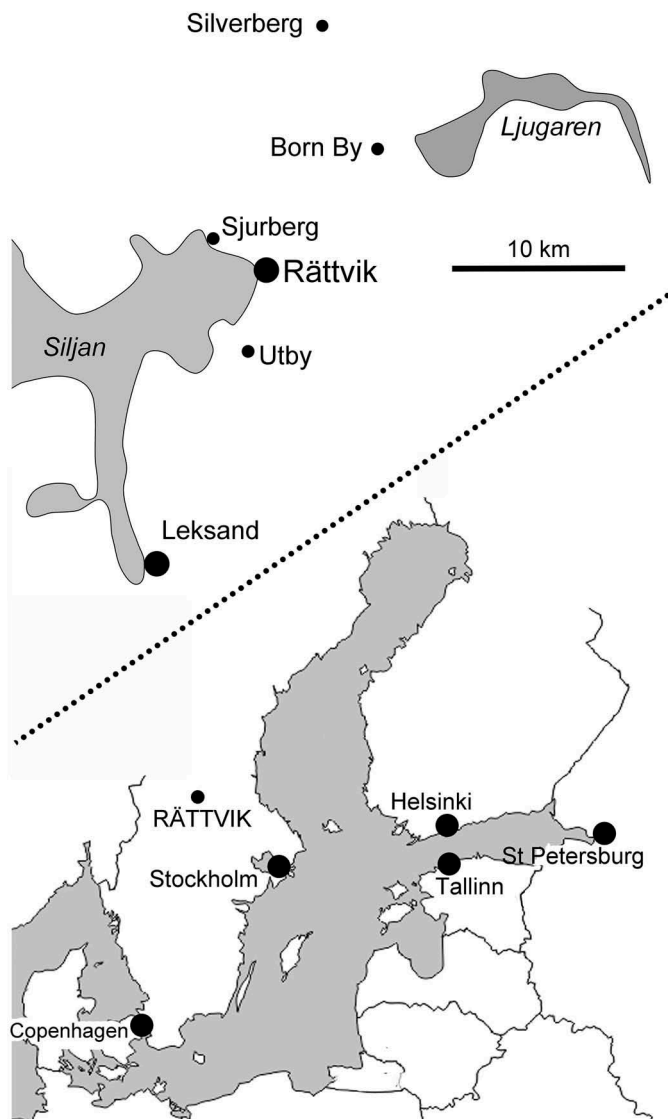


Figure 1. Localities for *Pollicina cyathina* Koken, 1897 in the Rättvik area of Dalarna, central Sweden.

Discussion. – Peel (2020) presented an emended diagnosis and described the type species on the basis of type and other material from Pulkova, St Petersburg, Russia, of Darriwilian (Kunda Stage) age. Specimens of *Pollicina corniculum* from Russia usually retain the shell (Fig. 2B). In contrast, almost all specimens of *P. crassitesta* Koken, 1897 from the Kunda Stage of Estonia are preserved as internal moulds (Peel 2020; Fig. 2A, D, E), although the lectotype retains patches of shell with ornamentation (Fig. 2A, C). Only one of ten examined specimens of *Pollicina* from Dalarna retains shell (Fig. 3A–D), but the four specimens described herein permit a redescription of *P. cyathina*. Specimens of other species are rare. *Pollicina conoidea* Koken in Koken & Perner, 1925 was transferred to *Pygmaeoonus conoideus* by Yochelson (1977). Peel (2020) excluded *P. ampliata* Koken in Koken & Perner, 1925 from *Pollicina*, while *P. acuta* and *P. brevis* are too poorly known for placement (Perner in Koken & Perner 1925; Peel 2020).

Scale measurements in the caption accompanying illustrations of the lectotype of *P. corniculum* by Kisselev (1994, fig. 1) indicated that the specimen is only 9 mm tall, less than half its

true height, although other measurements in Kisselev's (1994) Russian text appear to be correct. The incorrect specimen height was inadvertently restated by Evans & Cope (2003, p. 143).

Pollicina cyathina Koken,
1897 Figs. 3A–D, G, H; 4A–I

1897 *Pollicina cyathina* Koken, p. 198–199, fig. 38

1925 *Pollicina cyathina*; Koken & Perner, p. 227, pl. 38, figs. 6, 7

Holotype. – SMNH Mo 7767, the specimen figured in simple sketches by Koken (1897, fig. 38) and stated to be from Clason. Koken & Perner (1925, pl. 38, figs. 6, 7; Fig. 3G, H) illustrated a single specimen from the collections of the Swedish Natural History Museum, Stockholm, which is compatible with these sketches and also stated to be from Clason. This name is scrawled across the specimen label but most probably indicates the collector, I.G. Clason (1856–1930) of Rättvik. The specimen is from Born By [Borns By], about 10 km north-east of Rättvik, Dalarna (Fig. 1) and was collected during 1892 from the Lower Grey Orthoceras Limestone (Holen Limestone, Darriwilian Series, Kunda Stage; Ebbestad & Högström 2007).

Figured material. – LO 12 441t, internal mould, Utby, Dalarna; LO 12 442t, internal mould, Sjurberg, Dalarna. Lower Grey Orthoceras Limestone (Holen Limestone, Darriwilian Series, Kunda Stage; Ebbestad & Högström 2007). PMU 35717 from Rättvik, Dalarna.

Other material. – Incomplete internal moulds from Silverberg and Utby (Fig. 1) in the collections of the Swedish Natural History Museum, Stockholm.

Diagnosis. – Slender species of *Pollicina* with circular cross-section and ornamentation of fine comarginal growth lines.

Description. – The slowly expanding, bilaterally symmetrical, cyrtoconic shell curves through about 60 degrees, such that the apex of the tall shell overhangs the sub-apical margin. In lateral view (Figs. 3D, H; 4F, G) the maximum dimension of the aperture is about two fifths of the total height. The cross-section is almost circular (Fig. 3B, C). The apertural margin is orthocline and the internal mould periodically may be slightly constricted near the aperture (Fig. 4D). The shell is thick near the apex (Fig. 3C) but thins to an acute margin, feather edge, at the aperture (Fig. 3A, B). Ornamentation consists of fine growth lines (Fig. 3A–D). Internal moulds are generally smooth (Figs. 3G, H; 4F, G), without indications of transverse rugae, although a comarginal raised band of muscle scars (Peel 2020) may be prominent at about half to two thirds of the distance from the apex to the aperture in some of the unfigured material.

Discussion. – The lectotype is a large but poorly preserved internal mould with the apex broken away, although it appears rounded in lateral view in the illustrations due to weathering (Fig. 3G, H). It has the same curvature and circular cross-

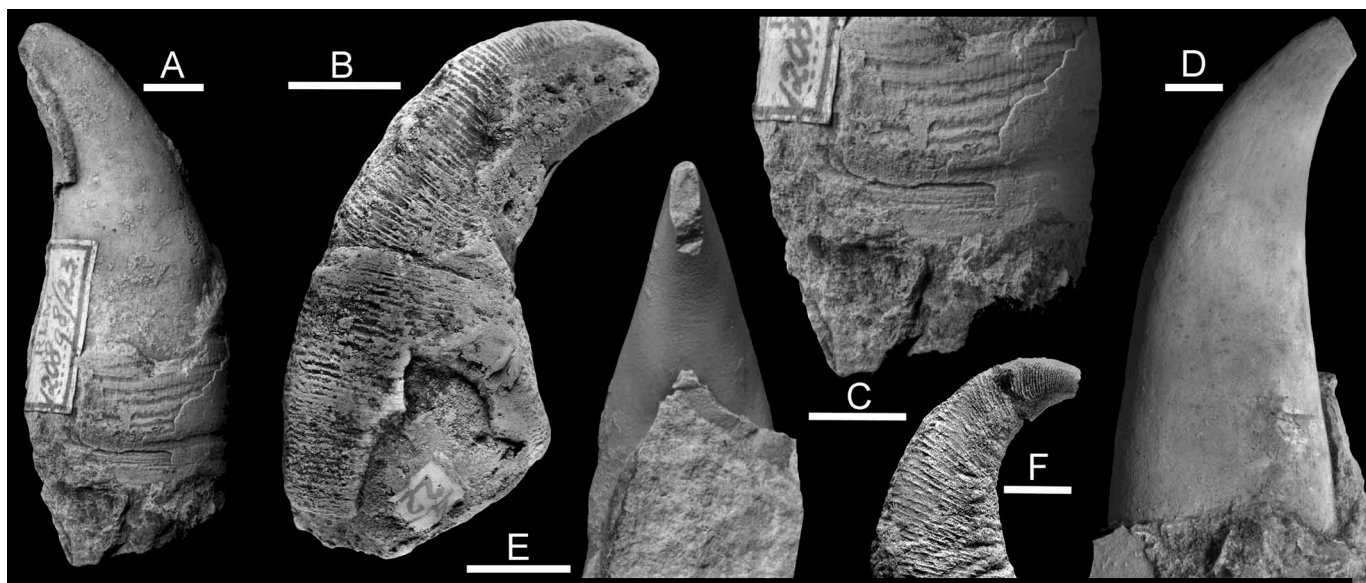


Figure 2. *Pollicina* from the Ordovician of Estonia and Russia. **A, C–E.** *Pollicina crassitesta* Koken, 1897, Ordovician, Darriwilian Series, Kunda Stage, Estonia. **A, C.** ELM g8:23 [1208g8/23], lectotype, largely exfoliated specimen in lateral view (A) with detail of ornamentation (C), original of Koken & Perner (1925, pl. 38, fig. 9), Domberg (= Toompea). **D, E.** ELM g8:7 [1208g8/7], paralectotype, internal mould in lateral (D) and sub-apical (E) views, Springthal (= Tondi), original of Koken & Perner (1925, pl. 38, figs. 1, 2). **B, F.** *Pollicina corniculum* Koken in Holzzapfel, 1895, Ordovician, Darriwilian Series, Kunda Stage, Pulkova [Pulkowa], St Petersburg. **B.** PSM 4/22, lectotype in lateral view. **F.** CNIGRM 15702 (200/10903), lateral view with deep scratches resulting from preparation on right side. Scale bars: 5 mm.

section as a broken specimen from Rättvik, which retains the shell with its ornamentation of fine comarginal growth lines (Fig. 3A–D). The broken apex demonstrates the almost circular cross-section of the shell interior even in early growth stages and stands in contrast to the strongly laterally compressed apex of *P. crassitesta* (Fig. 3E, F). However, the shell wall in the latter (indicated by arrows in Fig. 3E, F) is substantially thicker than in *P. cyathina*.

Koken (1897, p. 199) described but did not illustrate *Pollicina acuta* Koken, 1897 from the Lower Grey Orthoceras Limestone of Dalarna (Holen Limestone, Darriwilian Series, Kunda Stage; Ebbestad & Höglström 2007). Koken & Perner (1925, p. 228) noted that *P. acuta* Koken, 1897 was based on material from Dalarna, but Perner in Koken & Perner (1925) commented that the specimen before him did not agree with the original description and the name is not employed. The cross-section of *P. acuta* was stated to be elliptical even angulated, in the plane of symmetry while that of *P. cyathina* is circular. Both species were reported from Sjurberg (Fig. 1).

Pollicina corniculum usually has a more rapidly expanding shell than *P. cyathina* and lamellose growth lines (Fig. 2C). *Pollicina crassitesta* was illustrated by Koken (1897, p. 198) with a schematic drawing based on a specimen (Koken & Perner 1925, pl. 38, fig. 9) designated as the lectotype by Peel (2020; Fig. 2A, C). Internal moulds of *P. crassitesta* are similar in lateral profile to *P. cyathina*, although the latter may be more slender, but they are more rapidly expanding when viewed in the plane of symmetry (compare Fig. 3G with Fig. 4D). *Pollicina crassitesta* differs from *P. cyathina* in having an oval cross-section. In the earliest growth stages, the lateral surfaces of the internal mould in *P. crassitesta* are strongly flattened such that the length of the whorl cross-section is about twice its width (Fig. 2E), whereas the cross-section is almost circular in *P. cyathina* (Fig. 3C). The

ornamentation of *P. crassitesta* has spiral lirae not seen in *P. cyathina*.

Shell growth in *Pollicina*

Most specimens assigned to *Pollicina* by Koken (1897) and Koken & Perner (1925) are internal moulds without details of ornamentation and great care is required in making deductions based on such material. However, the shell exterior surface with ornamentation is usually preserved in the type species, *Pollicina corniculum* (Fig. 2B, F). The lectotype of *Pollicina crassitesta* (Fig. 2A, C) and one specimen of *P. cyathina* described herein (Fig. 3A–D) are rare specimens of their respective species which also retain shell, but information concerning shell at the apex is lacking in both.

The apex of *Pollicina corniculum* is bluntly rounded without discernible changes in the nature of the ornamentation (Fig. 2B, F). Evidence of septation or closure of the early parts of the shell is not known in 3-dimensionally preserved material of *P. corniculum* from East Baltica although Evans & Cope (2003) noted that an internal plug or septum was present in some, but not all, of available crushed specimens from the United Kingdom.

In general, the apex of *Pollicina crassitesta* is known only from internal moulds that show the strong laterally compressed form characteristic of the species (Peel 2020; Fig. 2D, E). However, where patches of shell material are preserved, it is evident that there has been very substantial thickening of the shell at the apex (Fig. 3E, F where arrows indicate the outer surface of the shell) leading to significant reduction in the volume of the shell interior at the apex. The lack of constrictions or discontinuities in the profile of the internal moulds indicates that this secondary thickening in the apical area passed imperceptibly into the normal shell growth as the

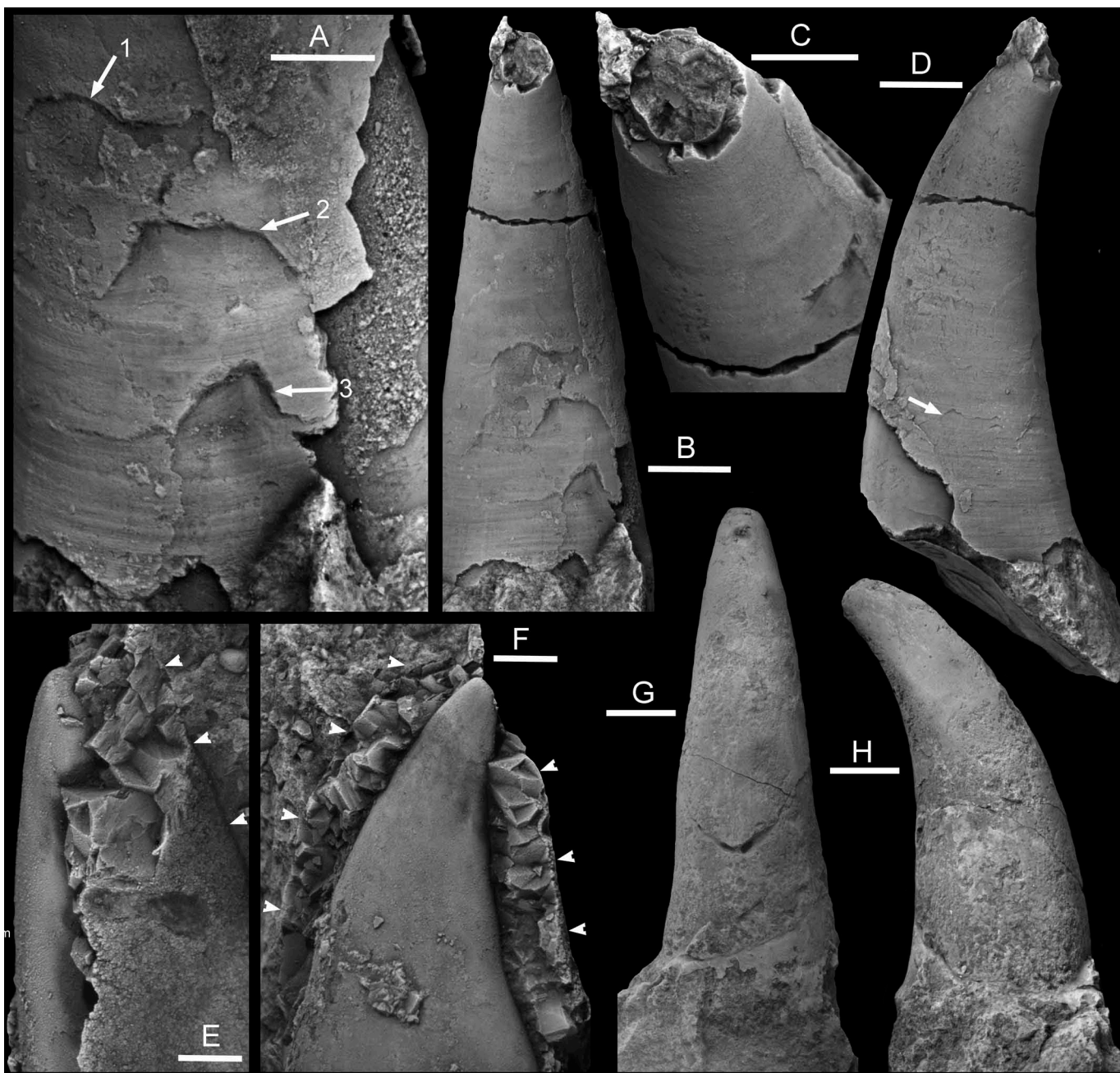


Figure 3. *Pollicina* from the Ordovician of Sweden and Estonia. **A–D, G, H.** *Pollicina cyathina* Koken, 1897, **A–D.** PMU 35717 from Rättvik, Dalarna. **A.** close up sub-apical surface showing fine comarginal growth lines on adaperturally tapering growth lamellae disturbed by penetrative fractures (arrows 1–3) repaired during life. **B.** view of sub-apical surface showing broken apex. **C.** detail of broken apex showing circular cross-section and thick shell. **D.** lateral view. **G, H.** SMNH Mo 7767, holotype by monotypy, original specimen of Koken & Perner (1925, pl. 38, figs. 6,7). Born [Borns] By, Rättvik, Dalarna. Lower Grey Orthoceras Limestone (Holen Limestone, Darriwilian Series, Kunda Stage; Ebbestad & Högström 2007). **E, F.** *Pollicina crassitesta* Koken, 1897, ELM 1201: g1:2664, Tallinn, Ordovician, Darriwilian Series, Kunda Stage, Estonia. **A.** slightly oblique view from perspective of sub-apical surface showing laterally flattened internal mould overlain by extremely thick shell (arrows mark lateral margin of shell). **F.** lateral view of internal mould and enveloping thick shell (arrows mark margin of shell on supra-apical surface). Scale bars: **A, C** (2 mm), **B, D** (4 mm), **E, F** (1 mm), **G, H** (5 mm).

aperture was approached. Thus, shell thickness at the apex may be the same as that around the aperture. A similar situation is evident in *P. cyathina* where the shell near the apex (Fig. 3B, C) is almost as thick as that in the latest preserved growth stage, but not as massively thickened as in *P. crassitesta*. At this latest stage, however, the shell in *P. cyathina* is clearly seen to have been built up from successive feather-edged lamellae (Fig. 3A).

Two internal moulds from the Törnquist Collection (Lund University), here assigned to *Pollicina cyathina*, are preserved

in black limestone and their smooth glossy surface retains no trace of adherent shell material (Fig. 4). Periodicity in growth of the largest specimen, possibly of a seasonal nature, is suggested by shallow constrictions in the lateral margins in sub-apical view (Fig. 4D, arrows). The apex in this specimen is uniformly and smoothly rounded with a weakly developed terminal node (Fig. 4D). In contrast, the internal mould of the smaller specimen narrows abruptly to a distinct node at the apex (Fig. 4C, G). In detail (Fig. 4A, B, H), this apical area is



Figure 4. *Pollicina cyathina* Koken, 1897 from Dalarna, Sweden, Ordovician, Darriwilian Series, Kunda Stage, Lower Grey Orthoceras Limestone (Holen Limestone; Ebbestad & Högström 2007). **A–C, G, H.** LO 12 441t, internal mould, Utby, Dalarna. **A, B.** views of smooth nodose tip. **C.** dorsal view of supra-apical surface showing pointed apex. **G.** lateral view showing pointed apex. **H.** detail of raised tip in lateral view. **D–F, I.** LO 12 442t, internal mould, Sjurberg. **D.** sub-apical surface showing apical node and periodic slight constrictions (arrows) of lateral profile during growth. **E.** supra-apical surface. **F.** lateral view. **I.** oblique lateral view of apex. Scale bars: **A, B, H** (1 mm), **C** (2mm), **D–G, I** (5 mm).

delimited in part from the later growth area by its smooth texture and a narrow comarginal groove (Fig. 4B). The apical node is transversely elongate and its upper surface is flattened, with acute edges suggestive of breakage.

The delimitation of the distinct apical portion of the internal mould may have several causes. It might represent the internal core of a small protoconch but it is not known how this was reflected, if at all, in the external morphology of the apex. A structure similar to the apical node is preserved on an internal mould of the tryblidioid tergomyan *Pilina cheyennica* Peel, 1977 from the Late Ordovician of Oklahoma, U.S.A. (Peel 1977, text-fig. 2A, B). A corresponding pit on the shell interior was illustrated by Lindström (1884, pl. 1, fig. 36) in *Pilina unguis* (Lindström in Angelin & Lindström 1880) and by

Angelin & Lindström (1880, pl. 10, fig. 9) in *Tryblidium reticulatum* Lindström in Angelin & Lindström, 1880 from the Silurian of Gotland, Sweden. A low conical species described from Gotland by (Lindström 1884, pl. 19, fig. 3) as *Palaeacmaea* (?) *solarium* Lindström, 1884 also preserves a distinct apical node on the internal mould; it is not a species of *Palaeacmaea* Hall & Whitfield, 1872 originally described from the Cambrian (Furongian) of the U.S.A. (Webers & Yochelson 1999). Recognition of a protoconch could be extended to also include the initial, smooth, conical section of the internal mould from which the apical node arises (Fig. 4A, B), but both interpretations fall if there was substantial ontogenetic thickening of the shell at the apex, as in *P. crassitesta*.

A more fanciful interpretation is that the node could represent a trace of the infilling of a siphuncle and that *Pollicina* is therefore a cephalopod. But there is scarcely room for camerae in the apical portion of the shell and this interpretation is dismissed. Kisselev (1994; see discussion in Peel 2020) did not record septa in the early sectioned portion of the lectotype of *Pollicina corniculum*, although they are present in some specimens figured by Evans & Cope (2003). Septa are of common occurrence in slowly expanding Palaeozoic gastropod shells (Yochelson 1971; Linsley 1978; Cook 1994; Peel 2019) and usually result from the closing off of narrow, unwanted, early growth stages as growth progresses. Internal thickening of the apical shell or the deposition of internal apical plugs may have a similar function, but can also serve to close off corroded early growth stages, or to strengthen weak, originally thin-shelled, early growth stages. The last case is supported by the similarity in shell thickness of the strengthened apex and the adult shell (Fig. 3F).

As regards cephalopods, however, it is the presence of a siphuncle penetrating the septa that defines a cephalopod and not the presence of septa alone (Teichert 1988; Peel 1991). Yochelson et al. (1973) proposed that the cephalopod siphuncle was developed from a strand of tissue that remained attached to the shell apex as the mollusc body mass migrated in its narrow shell towards the aperture with growth, with septa forming astride this remnant tissue. Adherents of this theory may find support in the apical node of *Pollicina cyathina* but this is a Middle Ordovician taxon, which bears little similarity in detail to the Cambrian (Furongian) ancestor of cephalopods proposed by Yochelson et al. (1973) and Webers & Yochelson (1989). A morphological comparison of the two was given by Peel (2020).

At the present day, the minute (1–2 mm) gastropod *Caecum* Fleming, 1813 has a tubular, slightly curved shell that is not dissimilar in curvature to *Pollicina*, but is parallel-sided (Bandel 1996). Its protoconch is usually trochospirally coiled and is decollated during ontogeny from the later, tubular, teleoconch at a septum that closes the apical extremity of the adult shell (de Folin 1868; Bandel 1996; Pizzini et al. 1998; Pastorino & Chiesa 2014). The septum is usually convex and often develops an adapically directed protruberance, termed the mucro, well illustrated by Pastorino & Chiesa (2014, figs. 7,8). Their illustrations show a transversely elongate mucro, with a flattened upper surface with angular edges that is morphologically similar to the apical node in *P. cyathina* (Fig. 4B). Pizzini et al. (1998, figs. 12–19) demonstrated that the septation and decollation process in *Caecum* involved the formation of two septa. An initial temporary convex septum is followed adaperturally by a second, mucronate, septum. Thus, the mucro occurs in the space between the two septa and may have contact with the temporary septum. The mucronate septum eventually forms the permanent septum following loss of the adapical temporary septum. While any taxonomic relationship between *Pollicina* and *Caecum* is obviously discounted, the morphological similarity of the mucro-bearing septa may indicate comparable mechanisms for the closing off of unwanted earlier portions of the shell. Septum formation in *Caecum* is followed by decollation of the protoconch, while in *Pollicina cyathina* it precedes closure of the apex by a septum or plug.

Peel (2020) concluded that the frequent displacement of the lamellose growing margin in *Pollicina corniculum* indicated a limpet-like mode of life, although such a tall shell form is not found in limpets at the present day (Vermeij 2017). Comparison can be made with the frequent development of tall, but irregular, clamping shells of *Orthonychia* Hall, 1843 amongst the anisostrophic platyceratoidean gastropods in the Silurian–Carboniferous (Perner 1903; Frýda et al. 2008, 2009; Peel 2020), although no taxonomic relationship is implied. The uniformly thick shell of *P. crassitesta* might support the limpet interpretation, suggesting life in a higher energy environment than *P. corniculum*, but the extreme height of the shell does not suggest stability under such conditions. A simple protective function seems inadequate in *P. cyathina* where the apex is relatively thick shelled (Fig. 3C) but the growing edge of the aperture is a feather-edge lamella susceptible to breakage (Fig. 3A). However, such an edge functions equally well as a seal against the substrate and may just indicate that soft parts never extended beyond the apertural margin (Peel 2020).

Many Cambrian (Furongian)–Early Ordovician molluscs develop tall shells (Stinchcomb & Echols 1966; Stinchcomb 1980, 1986; Stinchcomb & Angeli 2002; Webers & Yochelson 1989; Webers et al. 1992; Yochelson & Webers 2006) and Stinchcomb (1975) suggested association of some of these with sheltered sites within digitate stromatolites. At the present day, siliquariid gastropods live within sponges (Savazzi 1996; Pansini et al. 1999) but their irregularly uncoiled anisostrophic shells are dissimilar to the bilaterally symmetrical cones of *Pollicina*.

Shell breakage and repair

Numerous irregularities and dislocations were noted by Peel (2020) in the growth lines of *Pollicina corniculum* (Fig. 2B) but penetrative fractures of the margin or shell repairs were not observed. In contrast, the single available specimen of *Pollicina cyathina* with preserved shell shows a series of repaired injuries on the sub-apical surface (Fig. 3A, B). The regular pattern of fine growth lines is largely undisturbed on other surfaces with the exception of minor chipping (Fig. 3D, arrow). The apex of the specimen is missing, almost certainly broken away during collection: the rest of the specimen has been re-assembled from two broken pieces. The aperture is also broken, but there is some evidence that the sub-apical margin was broken prior to burial.

The fractures on the sub-apical surface are penetrative embayments into the apertural margin that have left scars with raised, scarp-like edges at their deepest, adapical, point. This relief is quickly lost laterally where traces of the breakage events are absent. Three major scars are visible (Fig. 3A, arrows 1–3), each infilled by subsequent shell growth. In each scar the thin growth lamella of the shell is seen to taper to an acute margin, which produces just a normal, fine growth line on the adjacent lateral surface. Growth lines in the shell filling the fractures are initially irregular but gradually return to their normal transverse pattern as the embayment is filled. Repaired injuries of this kind are well known in Palaeozoic molluscs (Vermeij et al. 1981; Peel

1984, 2015; Vermeij 1987, 2013; Ebbestad & Peel 1997; Horný 1997; Ebbestad 1998; Alexander & Dietl 2003; Lindström & Peel 2005; Ebbestad et al. 2009; Stafford et al. 2015) and may result from physical as well as biological agencies (Peel 2020).

On account of their depth, form and location, the three scars described here in *Pollicina cyathina* are readily interpreted as the result of non-lethal predatory attacks that have been repaired by subsequent shell growth (Fig. 3A, B). However, discrimination between physical and biological breakage is rarely clear cut (Stafford et al. 2015). The scars are unusual in that they form a series on the sub-apical surface of the shell while evidence of attacks is absent from other areas. It might be expected that if breakage was a result of physical agencies similar scars would be present on other parts of the feather-edge apertural margin, but this is not the case. Most of the remaining shell surface is characterised by very fine, undisturbed growth lines (Fig. 3C, D). However, on the basis of a single specimen it is not profitable to assess if this pattern is coincidental or if there is an underlying cause. The location of predatory attacks is often stimulated by features of shell morphology in the prey, e.g., focus on the apertural emargination in bellerophonitiform and pleurotomarioidean gastropods (Lindström 2003; Ebbestad et al. 2009), but could reflect features of the behaviour of either the prey or attacker, or a response to the reception of chemical signals from an exhalant current from the mantle cavity (Kohn 1961; Croll 1983; Sakata 1989; Villanueva et al. 2017).

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