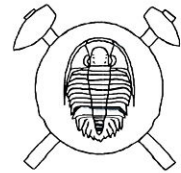


Muscle scars and systematic position of the Lower Palaeozoic limpets *Archinacella* and *Barrandicella* gen. n. (Mollusca)



Svalové vtisky a systematické postavení spodnopaleozoických rodů *Archinacella* a *Barrandicella* gen. n. (Mollusca) (Czech summary)

(15 text-figs)

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The new genus *Barrandicella* is proposed to commemorate the 200th anniversary of the birth of Joachim Barrande (1799–1883), with type species *Archinacella ovata* Barrande in Perner, 1903 from the Middle Ordovician (Darriwilian) of Bohemia. *Barrandicella* is interpreted as a gastropod (Mollusca) on the basis of a pair of well preserved muscle scars and associated tiny subsidiary scars located at the apex of the limpet shell. It lacks the dorsal band-like muscle scar characteristic of *Archinacella* and related genera but can be placed together with these in a revised Superfamily Archinacelloidea. No apparent link is perceived between the Archinacelloidea and the Patellogastropoda, currently widely viewed as the sister group of all other gastropods.

Key words: Mollusca, Gastropoda, Archinacelloidea, Patellogastropoda, *Barrandicella*, *Archinacella*, *Tergomya*, muscle scars, systematics, Ordovician, Bohemia

Introduction

Patellogastropod limpets are regarded as the most primitive living gastropods in current evolutionary models (Lindberg and Ponder 1996) and even as an archetype for the first gastropods (Haszprunar 1988). Yet the oldest certain patellogastropods are Triassic in age (Hedegaard et al. 1997) and the Palaeozoic record of limpet-like shells is sparse.

In this paper we review one of the most common Lower Palaeozoic cap-shaped molluscs, namely *Archinacella* Ulrich and Scofield, 1897, enquiring after possible ancient patellogastropods. Our stimulus is provided by recently discovered muscle scars in *Archinacella ovata* Barrande in Perner, 1903 from the Ordovician of Bohemia (Horný 1996) which is assigned to a new genus *Barrandicella*, named in honour of Joachim Barrande (1799–1883) on this 200th anniversary of his birth. *Archinacella* was originally described as a gastropod (Ulrich and Scofield 1897), since untorted molluscs of the Class Tergomya (formerly Monoplacophora) were not recognised at that time. The genus, however, has been interpreted variously as untorted (tergomyan) or torted (gastropod) but it is here considered to be a gastropod (Yochelson 1988; Peel 1990; Horný 1996).

Gastropod classification past and present

Classification of the Class Gastropoda (Cambrian–Recent) has been dominated for much of the century by the scheme presented by Thiele (1925, 1929) with the names of the three sub-classes reflecting primary organisation of the mantle cavity: Prosobranchia, Opisthobranchia and Pulmonata. The prosobranchs were subdivided into

the three orders Archaeogastropoda, Mesogastropoda and Stenoglossa but Wenz (1938–1944) replaced Stenoglossa with Neogastropoda when he fully integrated fossil gastropods into Thiele's Class Prosobranchia. Wenz (1938) recognised 11 superfamilies (6 extinct) of archaeogastropods, although the superfamilies Bellerophontoidea and Tryblidioidea were subsequently removed from the Prosobranchia to the Amphigastropoda (Wenz 1944, p. 1491; both here and below, original -acea terminations to superfamilies have been replaced by -oidea). The Superfamily Patelloidea, containing the familiar limpets of present day seas, was recognised from Triassic and younger strata.

The only published volume concerning gastropods within the *Treatise on Invertebrate Paleontology* is mainly concerned with Palaeozoic fossils, and these are referred dominantly to the prosobranch Order Archaeogastropoda. However, its authors followed Cox (1960) and grouped Mesogastropoda and Neogastropoda into a single Order Caenogastropoda (Knight et al. 1960). Knight et al. (1960) recognised 7 archaeogastropod suborders (16 superfamilies) and 5 superfamilies of uncertain position. Three of these suborders (Bellerophontina, Macluritina and Murchisoniina) are based exclusively on taxa now extinct, as are 15 superfamilies. This classification also includes superfamilies which some contemporary workers exclude from the Gastropoda (Bellerophontoidea and/or Helcionelloidea; see summaries in Peel 1991a and Runnegar 1996). The superfamilies Subulitoidea and Loxonematoidea were regarded as Caenogastropoda by Knight et al. (1960), although Wenz (1938–1944) had placed them as archaeogastropods. Knight et al. (1960) recognised Patelloidea tentatively from the Silurian, and with certainty from the Triassic.

Taylor and Sohl (1962) preferred Spengel's (1881) terms Streptoneura (= Prosobranchia) and Euthyneura (= Opisthobranchia + Pulmonata), but recognised only superfamilies, not sub-orders, within the orders of the Streptoneura.

During the last two decades, Thiele's classification has been subject to new enquiry, to some extent motivated by renewed interest in molluscan origins and evolution (e.g. Salvini-Plawen 1980). Noteworthy contributions include Golikov and Starobogatov (1975), Graham (1985), Salvini-Plawen (1980); Salvini-Plawen and Haszprunar (1987), Haszprunar (1988), Ponder (1988) and Ponder and Lindberg (1997). Reviews are presented by Haszprunar (1988), Fretter and Graham (1994) and Ponder and Lindberg (1996, 1997). A stabile picture is yet to emerge but some general agreement exists. Thus, Prosobranchia is recognised as paraphyletic and the constituent Archaeogastropoda and Mesogastropoda are seen as grades of evolution. Perhaps the most significant development is the suggestion that marine limpets related to *Patella* represent a lineage distinct from other archaeogastropods. This thesis is not entirely new, since limpets were delimited already by Troschel (1866, as Docoglossa) on account of their radular structure. It was more recently revived in a controversial paper by Golikov and Starobogatov (1975) and since then has been developed in a series of papers by Lindberg (1986, 1988a, b), author of the term Patellogastropoda. Ponder and Lindberg (1996) proposed that patellogastropods form a group (Eogastropoda) equivalent to the rest of gastropods (Orthogastropoda).

Inevitably, the status of extinct archaeogastropod groups recognised by Wenz (1938–1944) and Knight et al. (1960) remains largely unresolved in the newly emerging classifications whose perspective is from the present day, with little account taken of the fossil record. Several papers by McLean (1981, 1984, 1990) provide a notable example of attempts to address this problem, although with mixed results. The challenge is to fully integrate the fossil record into these modern schemes, both as a test of their validity and to provide a more complete model of gastropod evolution. Clearly, the living sample of gastropods represents just a fraction of the 500 million year history of the group. Nowhere is this need currently greater than in the case of the Patellogastropoda. While considered to be the sister group of all other gastropods (Lindberg 1988a; Haszprunar 1988; Ponder and Lindberg 1996, 1997), patellogastropods currently lack a convincing record through the Palaeozoic. In contrast, pleurotomariiform shells assignable to the Vetigastropoda and other orthogastropods (Ponder and Lindberg 1996) are known from the Late Cambrian (Knight et al. 1960). Correctly or incorrectly, this latter distribution favours models (e.g. Knight 1952, see review by Wahlman, 1992) which place pleurotomariiform shells (vetigastropods) in a more prominent ancestral evolutionary position than the patellogastropods. The dilemma is well-illustrated by Hedegaard et al. (1997, fig.

2) whose phylogenetic model of gastropod relationships infers ghost lineages (i.e., no unequivocal record) between the Early Cambrian and the Middle Triassic for Patellogastropoda and between Early Cambrian and Middle Devonian for Neritopsina. We might tentatively reduce the duration of these ghost lineages somewhat and even point out that the proposed record of Vetigastropoda before the Late Cambrian is ethereal. Nevertheless, the picture of a widely accepted (we do not offer dissent) phylogenetic model for gastropods based on morphological and molecular data from the modern world having such poor direct support from the abundant fossil record of gastropods is disturbing.

Haszprunar (1988) argued that the bilaterally symmetrical limpet shell of patellogastropods (as Docoglossa) is original and not derived from a coiled ancestor, as most others have assumed (Lindberg 1988a; Fretter and Graham 1994). Moreover, the archetype gastropod was considered to have had a limpet shell (Haszprunar 1988). The issue of shell symmetry of the earliest gastropods is also relevant to the status of the isostrophic Bellerophon-toidea where it has been argued that bilateral symmetry of the shell and muscle scars indicates a lack of torsion and non-gastropod affinity (Runnegar and Pojeta 1974; Runnegar and Jell 1976; Fretter and Graham 1994), although Haszprunar (1988) and others (e.g. Horný 1963b; Peel 1991a; Wahlman 1992) considered them to be gastropods.

Rapidly expanding, cap-shaped shells reminiscent of *Patella* occur widely, but infrequently, in Palaeozoic sediments and historically often have been referred to the Gastropoda. Some may be patellogastropods, although the status of many late Cambrian–early Ordovician forms described by Stinchcomb (1986) and Webers et al. (1992) is highly problematic. Reasonable claims exist that many of these shells are gastropods (e.g. Horný 1963a, b; Yochelson 1988; Peel 1990 concerning Ordovician–Silurian species) but the difficulty is to ascertain if these putative gastropods are true patellogastropods or independently evolved cap-shaped lineages. Hedegaard et al. (1997) noted that only shell microstructure provides unequivocal recognition of patellogastropods in the fossil record. While their extension of the range of undoubted patellogastropods from the Cretaceous to the Triassic added significantly to the known range of the group, some 300 million years of Earth history without proven remains of patellogastropods separate this earliest known record from the time of origin of the group postulated in current models (e.g. Hedegaard et al. 1997, fig. 2; Ponder and Lindberg 1996, 1997).

History of *Archinacella*

Archinacella is a familiar and widely distributed Ordovician genus. Nevertheless, its shell structure and internal shell morphology, and consequently its systematic position, remain unclear. Wahlman (1992) recorded 32 species of *Archinacella* from North America Ordovician

strata in the eastern half of the continent, discounting Cambrian and Silurian records of the genus. *Archinacella* is a characteristic, although not very common, component of the benthic fauna in the Lower–Upper Ordovician formations of Europe (Montagne Noire, Yochelson 1982; Bohemia, Perner 1903, Horný 1963a; England, J. S. Peel, unpublished observation; the Baltic area, Koken and Perner 1925, Yochelson 1963). Scarce finds have been reported from the Lower Ordovician of Greenland (Peel 1991a) and Asiatic Russia (Vostokova 1962).

After description by Ulrich and Scofield (1897) as a gastropod of the Family Patellidae, *Archinacella* was generally accepted as a member of this class for more than 50 years. Within the larger monographic studies, Perner (1903), Koken and Perner (1925) and Wenz (1938–1944) classified it within the same family. Knight (1941) redescribed the type species *A. powersi* Ulrich and Scofield, 1897 in detail, again as a gastropod, and later erected the gastropod Family Archinacellidae (Knight 1952). Nevertheless, Knight and Yochelson (1958) classified *Archinacella* as a monoplacophoran genus within the Family Archinacellidae of their new Order Archinacelloidea. The holotype of *A. powersi* was described as showing an unbroken ring-shaped muscle scar. This interpretation was continued in the *Treatise on Invertebrate Paleontology* (Knight et al. 1960). Three years later, Horný (1963a) used this classification in his revision of Bohemian Lower Palaeozoic forms, redescribing Barrande's Bohemian species of *Archinacella* as monoplacophorans and fully describing the previously established, related genus *Archinacellina* Horný, 1961. Yochelson (1963) reported two species of *Archinacella* from the Middle Ordovician of the Oslo region, classed as monoplacophorans.

Pchelintsev and Korobkov (1960), in the Russian treatise *Osnovy paleontologii*, classified *Archinacella* as a gastropod of the Family Tryblidiidae (Gastropoda, Isopleura) while Vostokova (1962) reported two species from the Lower Ordovician of the Siberian platform as gastropods of the Family Tryblidiidae (trybilidiids are now recognised as the central stock of the Class Tergomya, following Peel 1991a, b).

In establishing the monoplacophoran Subclasses Tergomya and Cyclomya, Horný (1965a, b) interpreted archinacelloid monoplacophorans as cyclomyans which developed a more or less complete ring of muscle scars, often fused to form a continuous band. Starobogatov (1970) pointed out the problem of location of the head when a continuous band-like muscle scar is present in the apical part of the shell and relocated Archinacellida from the Class Monoplacophora (abandoned by Peel 1991a, b in favour of the Class Tergomya) to the Gastropoda. He linked *Archinacella* with the Silurian *Archaeopruga* Horný, 1963, as tentatively assumed already by Horný (1965b). Starobogatov's interpretation was used in the classification proposed by Golikov and Starobogatov (1975), although Rosov (1975) placed *Archinacella* again among the monoplacophorans, deriving the orders

Archinacellida and Tryblidiida from the Order Kirengellida. Runnegar and Jell (1976) classed *Archinacella* within the Family Tryblidiidae, Order Tryblidiida, Class Monoplacophora. Harper and Rollins (1982) concluded that *Archinacella* and all other cyclomyan univalves were gastropods.

Yochelson (1977) re-described *Archinacella approximans* Koken and Perner, 1925 from the Upper Ordovician of Norway, together with two unnamed species, as monoplacophorans. He reported *Archinacella* cf. *A. ovata* from the Arenigian (Lower Ordovician) strata of the Montagne Noire of southern France, noting that in the absence of observable muscle scars the assignment to Monoplacophora is uncertain. "As currently used, *Archinacella* is something of a »wastebasket« that includes shells having the apex in a variety of positions." (Yochelson 1982, p. 54). Yu Wen (1987) mentioned *Archinacella*, *Archinacellina* Horný, 1961 and *Archinacellopsis* Horný, 1995 as the Ordovician descendants of his Lower Cambrian monoplacophoran genus *Truncatoconus* Yu, 1978.

Yochelson (1988) established *Floripatella*, claimed as the oldest known patellid gastropod, within the Family Archinacellidae (containing the genera *Archinacella* and *Floripatella*) within the Superfamily Patelloidea. He noted (p. 196) that "The family name is used for low shells varying in outline from nearly circular to elongate, which carry on their interior a horseshoe-shaped muscle scar and a single pair of muscle spots, each near one end of the horseshoe." This latter comment, however, concerns *Archinacella* (= *Archinacellopsis*) *patelliformis* (Hall, 1847) and not *Archinacella powersi*, which is the type species of *Archinacella*. Yochelson (1988, p. 199) argued that "If *Floripatella* is a gastropod, then *Archinacella* is also a gastropod."

Peel (1990) redescribed in detail *Tryblidium canadense* Whiteaves, 1884, establishing a new genus, *Guelphinacella*, on this rare species from the Silurian of Canada. Ulrich and Scofield (1887) had compared Whiteaves' species with *Archinacella powersi* when describing the musculature of *Archinacella*. Peel interpreted *Guelphinacella* as a gastropod, drawing comparisons with *Archinacella* and by making analogy between the sub-apical shell thickening of *Guelphinacella* and the inner shelf-like septum of carinaropsinid bellerophonitoidean gastropods. He noted that the band-like muscle scar in *A. powersi* was not continuous, but broken at the abapical margin. *Archinacella* and its relatives were considered to be gastropods by Peel (1991a, b).

Horný (1991) compared the muscle scar pattern of *Archinacella patelliformis* (Hall 1847) with that of *Sinuitopsis neglecta* Perner, 1903, obviously expressing his secret conviction that both genera belonged to the unsorted Tergomya. In 1995 (p. 8) he described the problematic *Solandangella* Horný, 1995 originally reported as *Archinacella*, suggesting that "none of the [listed] authors has brought together sufficient evidence to support their points of view, and that the archinacelloids still await stable systematic assignment."

Webers et al. (1992) questionably classified the Order Archinacelloidea within the Class Monoplacophora, noting the wide variety of morphologies within the order and casting doubt on its basic premise. They noted that the placement of *Archinacella* remains uncertain. Wahlman (1992) classified *Archinacella* as a monoplacophoran mollusc within the Family Archinacellidae of the Superfamily Archinacelloidea. He was sceptical about the validity of the large number of species of the genus described from the Ordovician of North America due to the high degree of intraspecific variability in the shell form of many monoplacophorans. Yochelson (1994) discussed *Archinacella* while re-describing *Macroscenella* Wilson, 1951, pointing out that the “easy view of the world was complicated when Horný (1963) described a Late Silurian patellacean” and “effectively ended when Yochelson (1988) described a Middle Ordovician patellacean, *Floripatella*, and therein also confirmed the assignment to Patellacea of another genus of the same age, *Archinacella*, which has been transferred back and forth between Patellacea and Monoplacophora” (Yochelson 1994, p. 1225). He affirmed his belief that genera which lack evidence of multiple pairs of muscles should be excluded from the Class Monoplacophora [equivalent to *Tergomya* of present usage].

In a preliminary account, Horný (1996) reported muscle scars in *Archinacella ovata* Barrande in Perner, 1903, concluding that the species, and probably the genus *Archinacella*, did not belong within the Class *Tergomya*.

Systematic palaeontology

Genus *Barrandicella* gen. n.

Type species. *Archinacella ovata* Barrande in Perner, 1903.

D i a g n o s i s. Archinacelliform, rather globose, univalve molluscs coiled through about one quarter to one third of a whorl with the prominent marginal apex interpreted as posterior. Sub-apical surface short, concave and steeply inclined or overhanging; supra-apical surface convex, rising from the apex to form the dorsal surface, prior to curving uniformly towards the interpreted anterior margin. Shell thin, with acute apertural margins. Ornamentation of comarginal growth lines which may be crossed by radial striations. A single large pair of muscle scars with granular texture is located immediately adjacent to the apex. Two or four tiny muscle scar occur on the apex between the principal scars.

D e s c r i p t i o n. As for the constituent species *Barrandicella ovata* (the type species) and *B. tarda*, described by Horný (1963a, pp. 26–30) and discussed below.

D i s c u s s i o n. On the original labels from about 1870–80, Barrande attributed his undescribed species “*ovata*” to the three living genera *Capulus*, *Patella* and *Crepidula*, with all three names appearing on the same label. Perner (1903), following Lindström (1884) and Ulrich and Scofield (1897), had a much easier position and his concept of *Archinacella* fully corresponded to the general interpretation at the beginning of this century. Barrande’s (in Perner 1903) species was revised by Horný (1963a) who pointed out its great variability, a comment echoed by Wahlman (1992) for North American species of *Archinacella*. The overall shell morphology of the Bohemian species fits quite well with the general shape of species of *Archinacella* but it is readily distinguished by the muscle scars which form the basis for delimiting *Barrandicella*.

In addition to the type species (Darriwilian), *Archinacella tarda* Perner, 1903 (Berounian) and a similar undescribed form from the intervening upper Darriwilian of Bohemia are referred to *Barrandicella*.

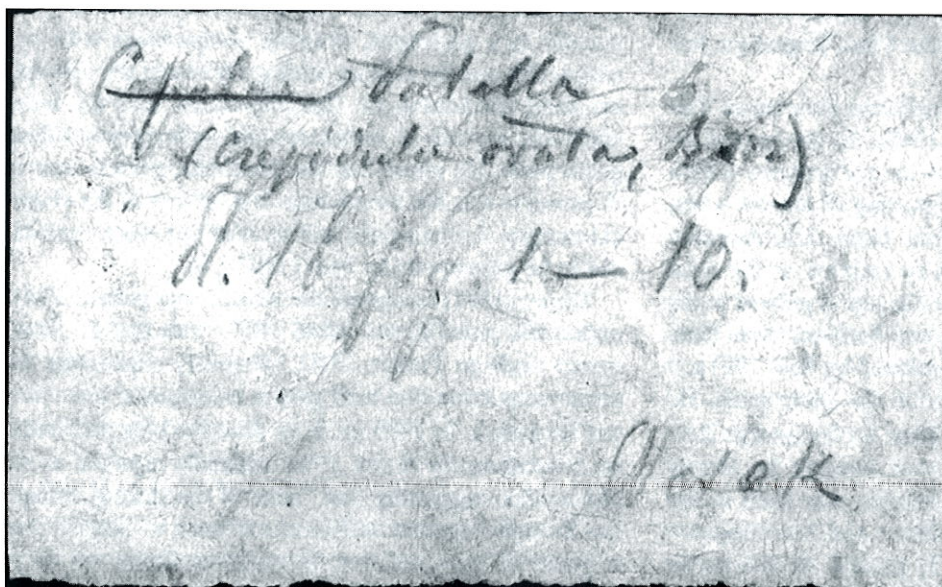


Fig. 1. Barrande’s label in pencil, showing his uncertainty about the generic assignment of his species *ovata*: *Capulus* [deleted], *Patella* (*Crepidula ovata*, Barr) Pl. 18 fig. 1–10. Wosek.

***Barrandicella ovata* (Barrande in Perner, 1903)**

Discussion. The shell morphology of this species was fully described by Horný (1963a, pp. 26–29), although one feature may be emphasised. The margin of the aperture in *Barrandicella ovata* as defined in the very thin shell is sharply angular, not rounded. This implies that the soft parts did not extend beyond the shell margin which is not surprising given the pattern of muscle scars described below. The supposed loop-like muscle scar which Horný (1963a) reported in *Barrandicella ovata* is not now considered to be present (see description of musculature below). Rather, the co-marginal structure is a shell morphological feature representing a growth pause or other event in the life history of the individual.

Archinacella sp. cf. *ovata* from the Arenigian strata of the Montagne Noire (Yochelson 1982) is undoubtedly very close to the Bohemian species, as is *A. stoermeri* Yochelson, 1963 from the Middle Ordovician of the Baltic Area (Yochelson 1963). *Archinacella*(?) cf. *A. elongata* (Cullison, 1944), illustrated by Peel (1991a) from the Lower Ordovician Poulsen Cliff Formation of Washington Land, western North Greenland, is similar to the “narrow forms” of *A. ovata*. Unfortunately, muscle scars which would confirm assignment to *Barrandicella* are not known in any of these species.

Barrandicella ovata (Barrande in Perner, 1903) occurs abundantly in the Darriwilian Šárka Formation of Bohemia and less frequently in the overlying Dobrotivá Formation. Horný (1963a) mentioned about 500 specimens available in different collections, but only about 300 specimens have been studied at the present time. Of these, about 200 are preserved in the Museum of Dr. B. Horák at Rokycany and about 100 are deposited in the Department of Palaeontology, National Museum, Prague.

***Barrandicella tarda* (Perner, 1903)**

Discussion. This species was fully described by Horný (1963a, pp. 29–30) but very fine radial striations (20–30 striae per mm) have now been observed in specimen NM L 31965 (Text-fig. 8D). *Barrandicella tarda* is distinguished from the type species by its thicker (0.10–0.15 mm), two-layered shell, more protruding apex and the fine radial ornamentation. The principal muscle scars show a similar location in both species.

Barrandicella tarda is a rare species (about 15 specimens known) which is distributed throughout the Berounian stage. The majority of finds come from the Zahořany Formation (Loděnice, Praha-Štěrboholy, Praha-Duběč).

Muscle scars in *Archinacella powersi*

Ulrich and Scofield (1897) figured one specimen of *Archinacella powersi*, consisting of both the internal and external moulds (Ulrich and Scofield 1897, pl. LXI,

figs 3–5, and fig. 1 on p. 820). This specimen was designated as the “holotype, seemingly by monotypy” by Knight (1941, p. 44). Both parts were re-figured by Knight (1941, pl. 1, figs a–g) and again by Peel (1990, figs 3 and 4). There is no doubt that the re-figured specimen is identical with Ulrich and Scofield’s specimen because of the peculiar preservation of the internal structures reflected on the shell surface which are visible both on the drawing given by Ulrich and Scofield 1897 (pl. LXI, fig. 4) and the photographs published by Knight (1941) and Peel (1990).

The problems of shape, preservation and configuration of muscle scars in the holotype of *Archinacella powersi* were discussed in detail by both the latter authors but with different conclusions. Thus, Knight (1941) suggested that the loop-like muscle scar was a broad band, much wider than originally suggested by Ulrich and Scofield (1897), while Peel (1990, fig. 4C) considered the lower margin of this broad band to represent the lower margin of the pallial cavity. The main difference in interpretations of the holotype concerns the three pairs of muscle scars which Ulrich and Scofield (1897) described in addition to the loop-like muscle scar. One of these pairs, the so-called rostral scars, consists of two small equilateral scars which Ulrich and Scofield (1897, fig. 1a; pl. LXI, fig. 5, denoted by A) observed one on each side of the apex of *A. powersi* within the loop-like scar. Just behind these rostral scars they indicated a narrow pair of scars (denoted by D) also within the loop. In a foot-note to the generic diagnosis (Ulrich and Scofield 1897, p. 828) they commented that they had “omitted from the generic diagnosis one feature that ought perhaps to have been included, namely, a pair of scars (?muscular) occurring one on each side of the apex. They lie on the outside of the usual muscular band and have been observed in two species, *A. powersi* and *A. (Tryblidium) canadensis* Whiteaves. The latter is a Guelph species and, as shown in Whiteaves’ figures (Pal. Foss., vol. iii, pl. v), has these scars more strongly impressed (in the cast) and further forward than they are in *A. powersi*.” These scars (denoted by B) are termed antero-laterals in the caption to their plate LXI, fig. 5.

The sub-apical area of Whiteaves’ species was re-described by Peel (1990, as *Guelphinacella canadense*). The structure depressed into the internal mould which Ulrich and Scofield (1897, p. 828) considered to be antero-lateral muscle scars was explained as an internal thickening of the shell, morphologically resembling the shelf-like parietal thickening formed within the aperture in some Palaeozoic representatives of the bellerophon-toidean Sub-family Carinaropsinae Ulrich and Scofield 1897. Ulrich and Scofield (1897) considered a pair of antero-lateral muscle scars to be present in *G. canadense* but Peel (1990) confirmed the observation of Whiteaves (1895) that the so-called scars represented the lateral terminations of a continuous sub-apical depression. Knight (1941) had previously dismissed the antero-lateral scars of *A. powersi* as fortuitous iron staining.

Peel (1990) did not discuss the rostral scars in *Archinacella powersi* since no equivalent structures are preserved in *Guelphinacella*. However, according to Knight (1941, p. 45), "The evidence for ... rostral scars is almost nonexistent".

The internal mould of the holotype of *Archinacella powersi* (Text-fig. 3) clearly displays the raised, horse-shoe-shaped muscle scar (C of Ulrich and Scofield 1897) which is located somewhat nearer to the mid-dorsum than to the apertural margin. The narrow band is stron-



Fig. 2. *Archinacella powersi* Ulrich et Scofield, 1897. Holotype USNM 135949, latex impression of external mould of the holotype: A – oblique dorsal, B – dorsal, C – abapico-dorsal, D – right lateral, E – oblique apico-dorsal, F – right dorsolateral, G – oblique right apico-dorsal views. Middle Ordovician, Platteville Limestone, Beloit, Wisconsin, U.S.A. All x2.

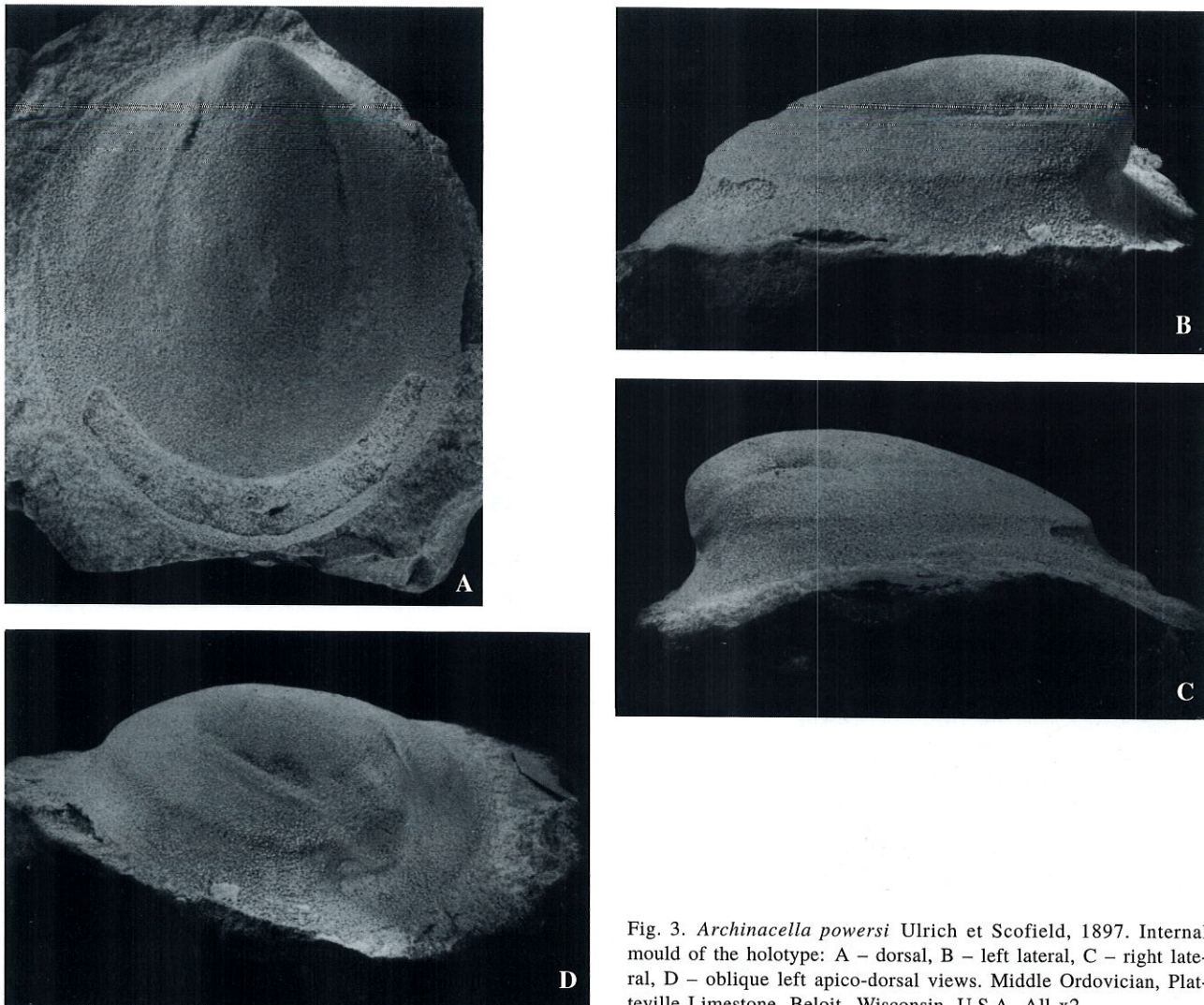


Fig. 3. *Archinacella powersi* Ulrich et Scofield, 1897. Internal mould of the holotype: A – dorsal, B – left lateral, C – right lateral, D – oblique left apico-dorsal views. Middle Ordovician, Platteville Limestone, Beloit, Wisconsin, U.S.A. All x2.

gly expressed in the adapical half of the shell where it dips below the apex, but it decreases in relief abapically and seems to terminate at about 60 % of the distance from the apex to the abapical margin. A comarginal, semicircular, zone of ill-defined minor irregularities joins the two prongs of the horseshoe, commencing prior to their terminations and lying outside (abapical) of the prongs. This semicircular zone is clearly visible in the illustrations of Ulrich and Scofield (1897, pl. XLI, fig. 5; fig. 1), although too strongly expressed and seemingly erroneously interpreted as a continuation of the horseshoe-shaped muscle scar. Halfway between the muscle scar and the apertural margin, a conspicuous angulation is produced by a sudden steepening of the dorsal surface of the internal mould (Text-fig. 3B–D). The zone demarcated by this angulation is clearly visible in the illustrations of Ulrich and Scofield as a paler grey colouration but was not discussed. Knight (1941) considered all the area between the horseshoe-shaped muscle scar and this angulation to represent a broad muscle attachment scar.

The structures interpreted as the narrow pair of scars (D) by Ulrich and Scofield are readily located on the internal mould as two elongate depressions located along

the upper margin of the horseshoe-shaped scar (dark spots in Text-fig. 2). Their margins are unclear and their negative relief indicates that they were raised on the shell interior, whereas the horseshoe-shaped scar was depressed into the shell surface. We have been unable to locate any structure reflecting the antero-lateral scars (B) on the internal mould. The supposed rostral scars, however, are based on a pair of oval structures with a smoother surface texture. They are scarcely visible and even more difficult to photograph, but the area between them is slightly depressed, producing a shadowed area in Text-fig. 2A, B, D–G. Based on this examination, it is possible to perceive similar textural features in the illustration given by Knight (1941, pl. 1, fig. 1b).

Interpretation of the external mould of the holotype of *Archinacella powersi* is based on a latex cast. It is a composite mould carrying impressions of the shell interior (muscle scars) diagenetically superimposed on the impression of the shell exterior. Structures are mainly discernible on account of their smooth surface texture when compared to the porous or granular texture of the peripheral areas of the shell. The latter appear dark in the photographs (Text-fig. 2A, B, D–G) whereas the smooth

areas appear pale. These differences seem to reflect variation in cementation or some differential diagenetic effect. Even so, they may still accurately reflect structures impressed on the shell interior. For comparison, it may be noted that internal moulds of *Bellerophon* preserved in limestone from the Lower Carboniferous of England often show differential shell recrystallisation in the area of the muscle scars when compared to the rest of the shell (J. S. Peel, unpublished observation).

The horseshoe-shaped muscle scar is clearly visible and directly comparable to its form on the internal mould. The area between the muscle scar and the co-marginal angulation visible on the internal mould is seen as

a smooth (pale) band with a rather uneven adaperatural margin; the dorsal surface steepens as the angulation is crossed (Text-fig. 3D). Much of the mid-dorsal area has the same texture and colour as the band, as also reproduced in Ulrich and Scofield's illustration. The rostral scars are similarly smooth (pale) and separated by a shallow median depression of darker, granular matrix (Text-fig. 2 A, B, D-G). Abapical of the rostral scars lies a pair of dark, granular, depressions representing the so-called narrow scars (D) of Ulrich and Scofield.

To summarise, the band-like muscle scar (C of Ulrich and Scofield 1897) is clearly visible in the form of a narrow horseshoe-shaped scar rather than the continuous

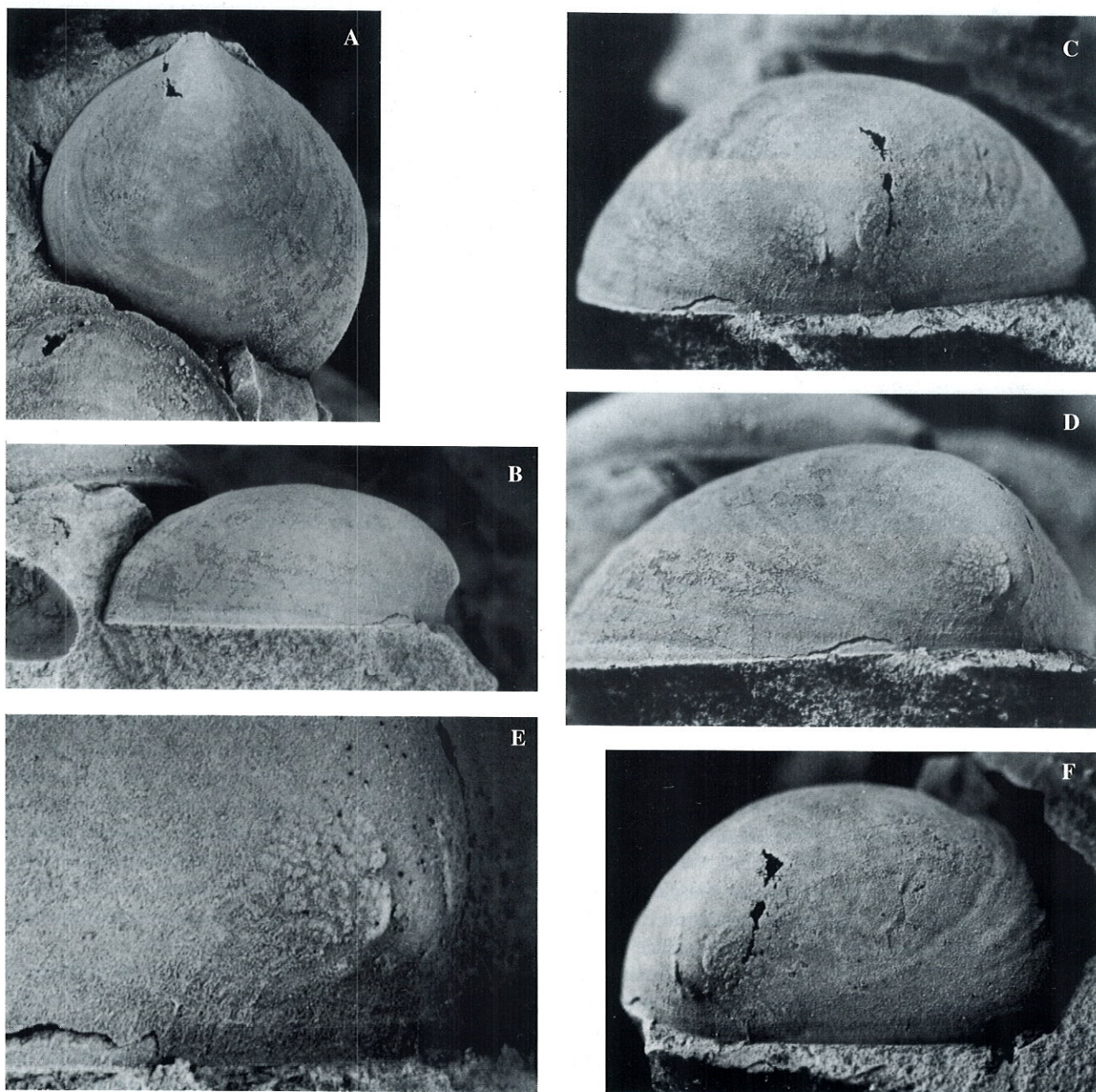


Fig. 4. *Barrandicella ovata* (Barrande in Perner, 1903), internal mould MBHR 4604, showing best preserved muscle attachment areas. A – dorsal, B – left lateral, C – apical, D, E – left apico-lateral, F – right apico-lateral views. Note the thin rib-like structures radiating from the scars towards the posterior margin of the shell. Middle Ordovician, Šárka Formation, Darriwilian (Llanvirnian). Osek near Rokycany, Bohemia. A, B x5, C, D, F x8, E x23.

loop suggested by Ulrich and Scofield or the broad band suggested by Knight (1941). The supposed rostral scars (A) can be recognised, although striations or other ornamentation on their surface to confirm their function as muscle scars are lacking. The antero-lateral scars (B) have not been recognised. The supposed narrow scars (D) represent depressions in the internal mould rather than the more usual raised muscle scars; they probably represent local thickening of the shell interior associated with the migrating margin of the horseshoe-shaped muscle scar.

Muscle scars in *Barrandicella ovata*

Four internal moulds of *Barrandicella ovata* from the Rokycany Museum (abbr. MBHR) and one from the National Museum, Prague (abbr. NM L) were found to carry a well-preserved pair of muscle scars in the latero-apical position, corresponding to the position and even to the shape of the rostral scars described in *Archinacella powersi* by Ulrich and Scofield (1897). All the specimens come from grey to black fine-grained siliceous concretions, and are preserved as internal moulds. They are derived from the Šárka Formation (Darriwilian) at the locality Osek near Rokycany.

Description. Specimen MBHR 4604 (Text-fig. 4) is an internal mould in which the abapical part is covered

with rock matrix. Estimated length 11.5 mm, width 10.0 mm. Each of the pair of tear-shaped muscle areas is located along the beak-like apex, including its most anterior part; the two scars are separated by a median zone 0.6 mm wide. The muscle scar areas are inequilateral and each consists of isolated grains which show a tendency to be more raised and coalescent along the median shell line. Each area consists of two main groups of grains. Two elongate grains lie on the subapical slope, in the direction of the main groups. When viewed from the apical margin (Text-fig. 4C), the right muscle scar area (interpreted as the post-torsional right scar) is smaller. The left muscle scar area is 1.1 mm long and 0.8 mm wide.

MBHR 14761b is an internal mould 12.7 mm long and 10.2 mm wide. The paired, tear-shaped muscle scar areas are almost equilateral, raised near the median shell line, without preserved granular texture. The median zone between the muscle scars is 1.0 mm wide; two asymmetrically positioned grains are located on the subapical slope. The right area is 0.8 mm long and 0.4 mm wide.

Specimen MBHR 20782 (Text-fig. 5) consists of four stacked individuals. The observed internal mould has no observable peripheral outline; its estimated length is 14.0 mm, width 12.0 mm. Muscle scar areas are displaced abapically, away from the apex, and consist of isolated grains, coalescent and raised along the median zone,

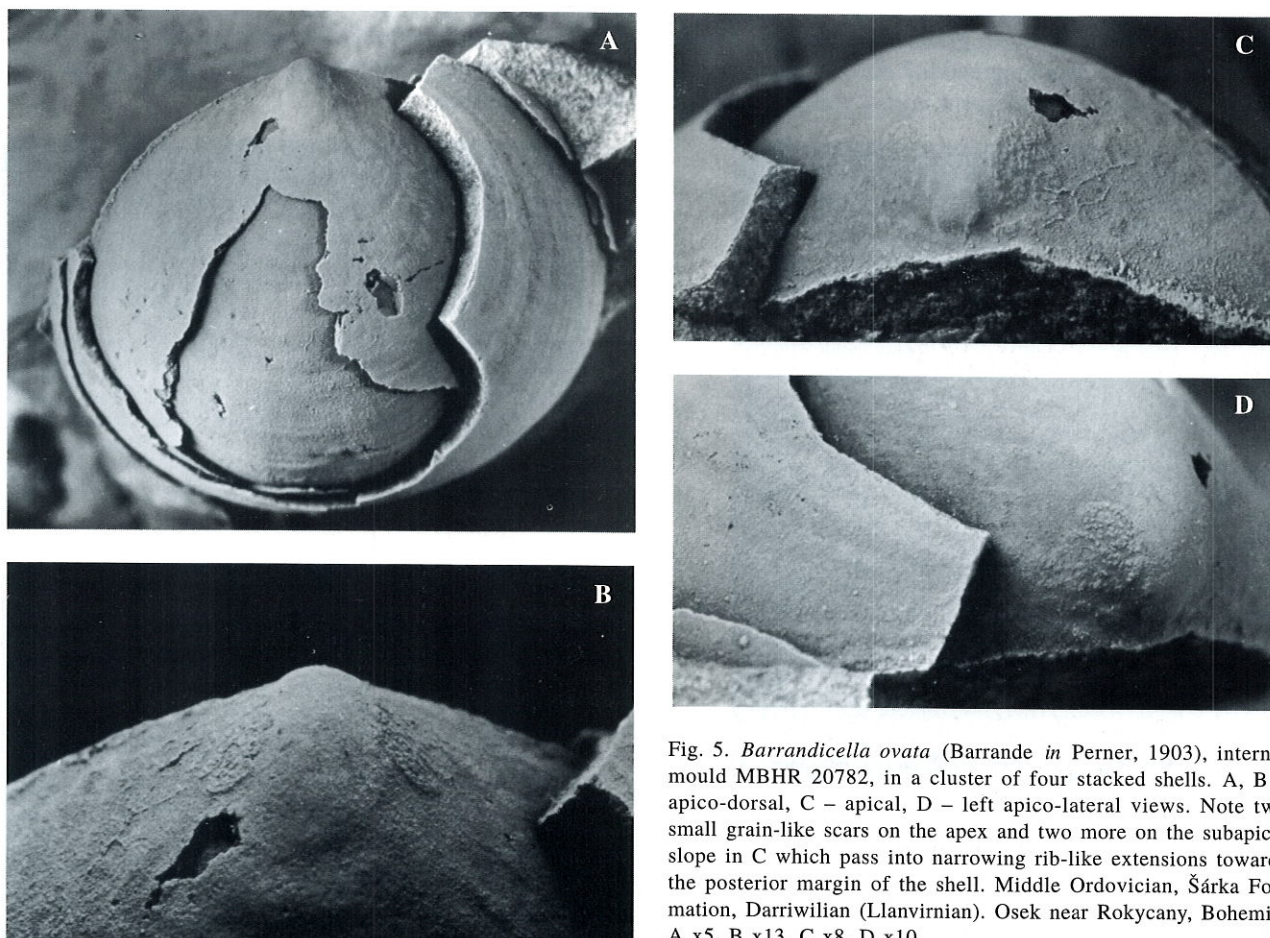


Fig. 5. *Barrandicella ovata* (Barrande in Perner, 1903), internal mould MBHR 20782, in a cluster of four stacked shells. A, B – apico-dorsal, C – apical, D – left apico-lateral views. Note two small grain-like scars on the apex and two more on the subapical slope in C which pass into narrowing rib-like extensions towards the posterior margin of the shell. Middle Ordovician, Šárka Formation, Darriwilian (Llanvirnian). Osek near Rokycany, Bohemia. A x5, B x13, C x8, D x10.

which is 1.0 mm wide. Two small grain-like scars are located on the apex and two more on the subapical slope pass into narrowing ribs towards the margin of the shell. The right muscle scar area is 1.1 mm long and 0.6 mm wide; the left is 1.3 mm long and 0.8 mm wide.

Specimen NM L 31757 (Text-fig. 6) is a well-preserved internal mould 15.0 mm long and 13.6 mm wide. Muscle scar areas are only slightly raised, 0.6 to 0.8 mm long and smooth, lacking the granular texture. They are equilateral and located along the apex; the subapical area is smooth. The median zone between the scars is 0.1 mm. Numerous fine short whisker-like swellings and threads radiate from the muscle scars lateral and down towards the margin of the shell (Text-fig. 5B). The surface of the internal mould bears irregular, flat, radial structures.

MBHR 14761a (Text-fig. 7) is the largest of the internal moulds in which muscle scars are preserved; it is associated with specimen 14761b in a single concretion. The mould is 17.6 mm long and 14.3 mm wide. The central part of the internal mould is deeply corroded so that another, juvenile specimen is visible beneath. The apical part of the shell is strongly deformed by a pathological condition which has caused reduction of the left apical side when viewed dorsally (this is the area to the left in Text-fig. 7C–E). The muscle scar areas are strongly asymmetric and inequilateral, raised along the median zone. The scar on the right, deformed, area, is 2.0 mm long and 1.1 mm wide; it is displaced abapically, and consists of several groups of coalescent grains. The left area, lateral to the apex, is 1.5 mm long and 0.7 mm wide, consisting of several groups of coalescent grains which are agglom-

erated into two groups. The median zone between the muscle scars is 0.9 mm wide. Two asymmetric grains are located on the top of the apex.

Remarks. In general, the tear-shaped, often inequilateral, muscle scar areas of *Barrandicella ovata* lie just lateral to the beak-like apex. Their location along the shell axis varies, and they are often located asymmetrically. The areas increase their size with increase in shell dimensions; the longest area measured 2.0 mm, the widest 1.1 mm. The surface of the muscle scar areas generally has a conspicuous raised granular texture, with individual grains corresponding to pits on the shell interior where the individual muscle fibres were inserted. Along the median zone (width 0.6–1 mm) between the muscle areas, the grains are more elevated and often coalescent, forming two or more groups. Two, rarely four, isolated grains are located on the apex or on the subapical slope, in one case (in specimen MBHR 20782) associated with aperturally radiating, narrowing threads.

The apical scars of *Barrandicella ovata* are slightly inequilateral and asymmetric, which contrasts with the otherwise symmetric shell, but not consistently so. However, whenever the scars are inequilateral it is the right (post-torsional) scar which is always smaller. No published records seem to exist of similar asymmetry within bellerophonitoidean gastropods but muscle scar asymmetry is recorded within the circum-dorsal scar patterns of cap-shaped tergomyans (e.g. *Pilina cheyennica* Peel, 1977) and helcionelloids (*Scenella* sp. of Rasetti 1954, see also Runnegar and Pojeta 1985), where it has little functional effect.



Fig. 6. *Barrandicella ovata* (Barrande in Perner, 1903), internal mould NM L 31757. A – dorsal, B – apical, C – right apico-lateral views. The muscle attachment areas are small and the surface of the mould bears numerous, weak, radial structures. Middle Ordovician, Šárka Formation, Darriwilian (Llanvirnian). Osek near Rokycany. All x5.

The structure of the scars is not marked by crescentic striations but consists of isolated or coalescent grains, corresponding to pits on the shell interior. However, crescentic striations of the kind well known in bellerophon-toidean gastropods (Peel 1972, 1982, Horný 1992, 1995c) indicate migration of the muscle attachment field. The location of the muscle scars very close to the apex in *B. ovata* probably indicates very little migration with growth, and, hence, the granular texture of the scars. The size of the grains within the muscle scars does not increase abapically but addorsally. Two or four small, asymmetric, accessory scars are located either on the apex or

on the subapical slope. These scars could hardly belong to effective clamping muscles in this location, and their specific function in the apical area of the shell is enigmatic. However, they may be extreme examples of the incomplete fusion of individual muscle bunches within the principle muscles indicated by the granular, locally coalesced, texture of the principal scars.

It is noteworthy that the radular muscle scars in the tergomyan *Pilina unguis* (Lindström, 1880) also have a pitted, if not granular texture. Furthermore, the tergomyans *Drahomira* Perner, 1903 and *Pragamira* Horný, 1995 show a pair of tiny tubercles (muscle scars?) on the

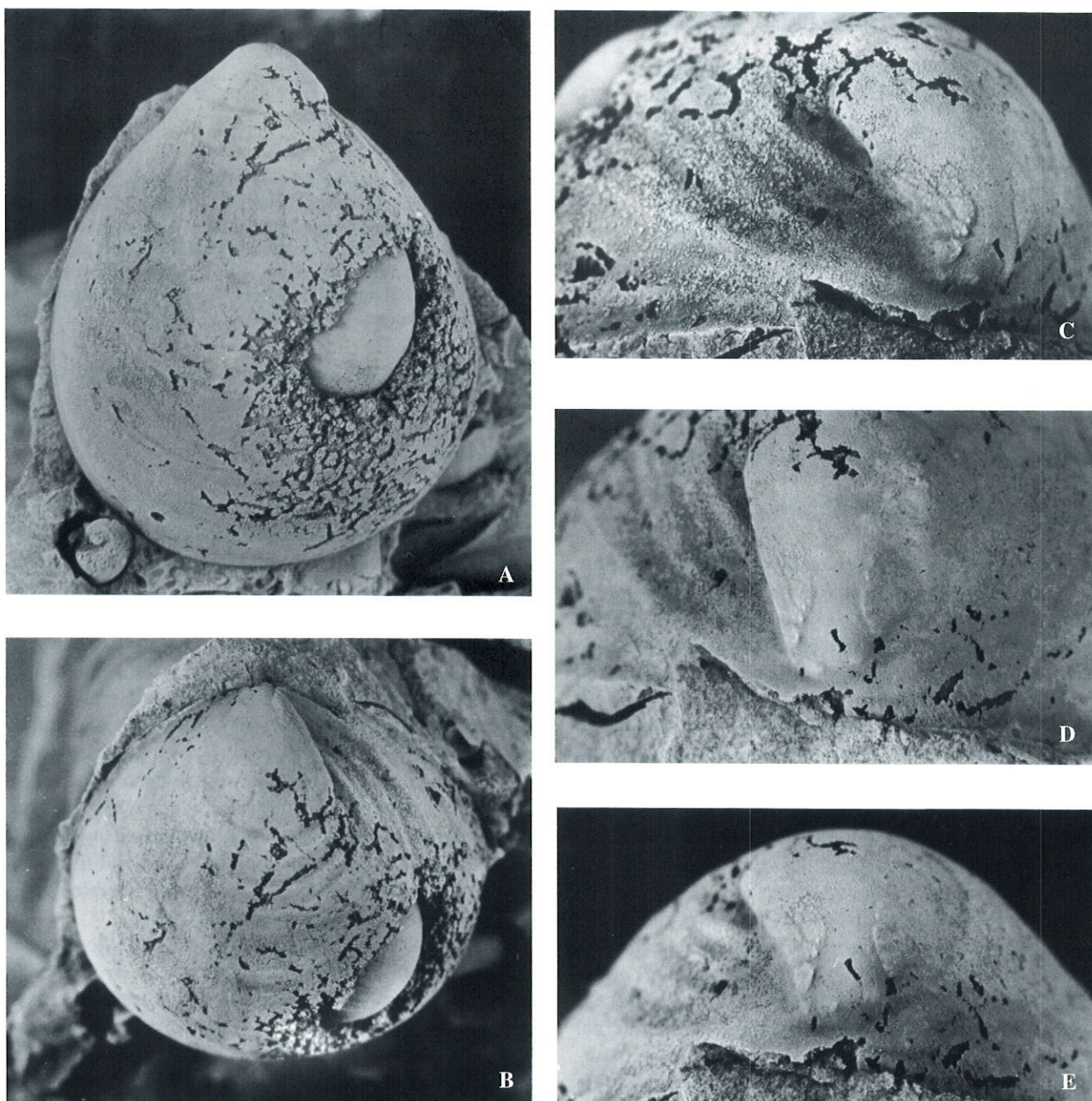


Fig. 7. *Barrandicella ovata* (Barrande in Perner, 1903), internal mould MBHR 14761a. A – dorsal, B – apico-dorsal, C – oblique apical, D – dorso-apical, E – apical views. Note the deep, repaired injury on the left side near the apex, which caused an asymmetry of the shell and an inaequilateral development of the muscle attachment areas. Middle Ordovician, Šárka Formation, Darriwilian (Llanvirnian). Osek near Rokycany, Bohemia. A, B x4.5, C, D, E x8.

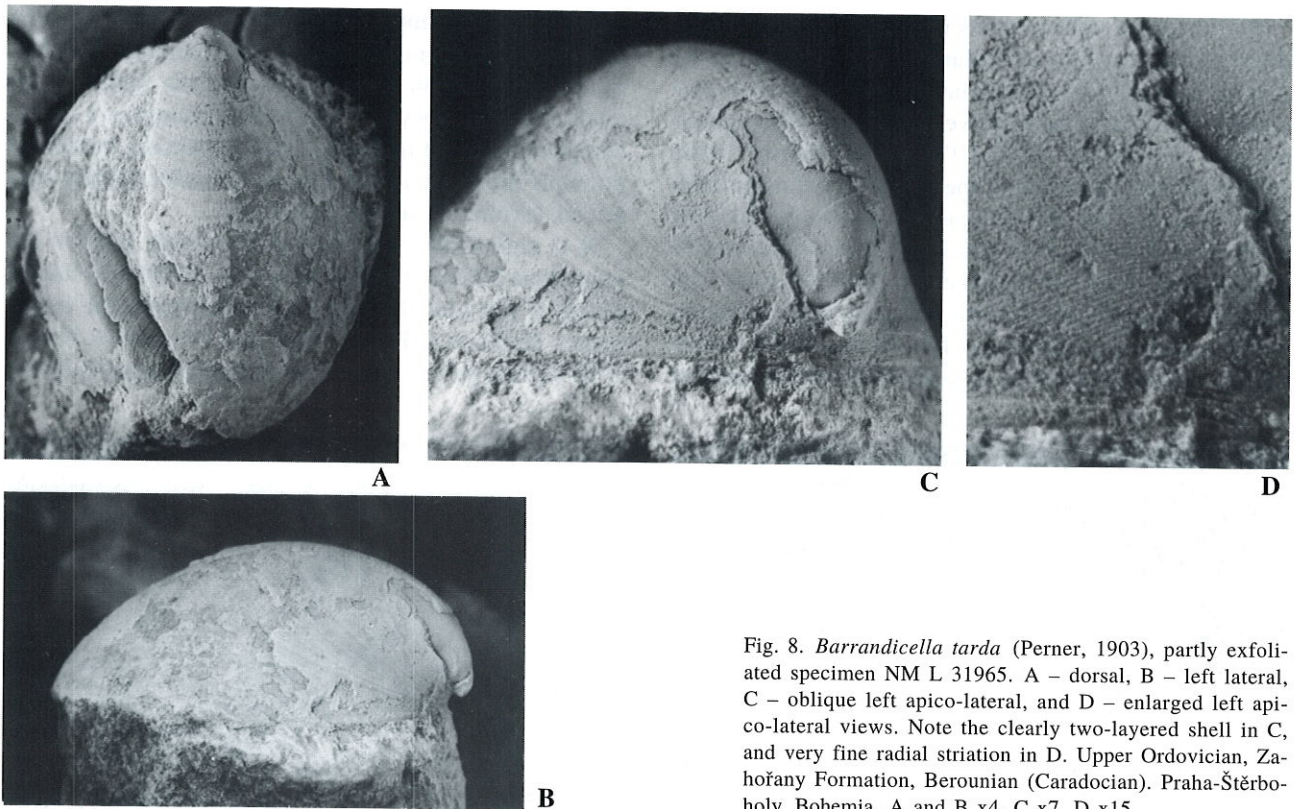


Fig. 8. *Barrandicella tarda* (Perner, 1903), partly exfoliated specimen NM L 31965. A – dorsal, B – left lateral, C – oblique left apico-lateral, and D – enlarged left apico-lateral views. Note the clearly two-layered shell in C, and very fine radial striation in D. Upper Ordovician, Zahořany Formation, Berounian (Caradocian). Praha-Štěrboholy, Bohemia. A and B x4, C x7, D x15.

internal mould of the shell at the apex which are reminiscent of the small accessory scars of *Barrandicella* (Horný 1963c, 1995a). The apex is posterior in the latter form, of course, but anterior in the tergomyans.

Muscle scars in *Barrandicella tarda*

Well preserved muscle scars in *Barrandicella tarda* are known from two specimens; three other specimens have poorly preserved scars. In specimen NM L 31965 the post-torsional left scar (length approximately 1.1 mm) is partly visible on the internal mould in an exfoliated patch at the apex (Text-fig. 8B, C), as is a single, left, minute apical scar. The principal muscle scar shows a similar location to *B. ovata* and in both species the apico-dorsal margin of the scars is raised on the internal mould. However, the granular texture of the attachment area in this specimen is not clearly visible due to a thin covering layer of internal shell. It is this specimen which shows fine striations on the shell surface.

The second specimen (NM L 31964, Text-fig. 9) has each principal attachment area composed of 5 detailed insertions which are arranged in rows (0.9 mm long) oriented parallel to the plane of symmetry. From each of these muscle insertions whisker-like swellings on the internal mould widen abapically, some bifurcating or even trifurcating. On average the swellings are 0.5 to 1 mm long, but on the right side the highest addorsal swelling is 3.5 mm long and directed obliquely antero-laterally. This swelling is reminiscent of the most adapical portion of the muscle band in *Archinacella* and *Archinacellina*. Otherwise, the attachment areas are equilateral. Two

small, inequilateral grain-like scars are located on the apex (Text-fig. 9B, C).

Discussion

Ulrich and Scofield (1897) described and figured a loop-like muscle scar in *Archinacella powersi* as a continuous narrow band curving distinctly down adapically so as to pass below the apex. Knight (1941) re-interpreted its position and width. Yochelson (1988, p. 196) stated that “the family name [Archinacellidae] is used for low shells varying in outline from nearly circular to elongate, which carry on their interior a horseshoe-shaped muscle scar and a single pair of muscle spots, each near one end of the horseshoe”. Peel (1990) recognised a horseshoe-shaped muscle scar which opened towards the abapical margin in the holotype of *A. powersi*, suggesting that the lower margin of the broad scar recognised by Knight (1941) might be the lower margin of the pallial cavity. He commented that weak structures were visible abapically between the prongs of the horseshoe.

Horný (1963a, p. 27), redescribing *Barrandicella ovata* (as *A. ovata*), followed the concept of *Archinacella* employed by earlier workers and recognised a continuous scar in this species: “...broad, sometimes obscure band-like muscle scar parallel with the growth structures, narrowing anteriorly and dying out near the apex; on the anterior [adapical] side of the shell very weak, but present. ... Muscular impression obscure, but on many specimens very well observable (see figs 9–10, pl. V). It is band-like, elevated, parallel with lines of growth, broad in the posterior and narrowing to the anterior region,

where unites with growth structures and becomes unclear (see fig. 7, pl. V). This band-like scar is a muscle scar because of the constant shape and position in many specimens observed." (Horný's use of posterior and anterior reflects his belief at that time that *Archinacella* was a tergomyan.) However, recent revision of internal moulds of *B. ovata* with potential band-like muscle scars led Horný (1996) to the conclusion that these structures are most probably connected with growth rather than shell muscu-

lature. The features reflected through the very thin shell to the internal shell surface may have originated at a similar ontogenic stage, possibly connected with specific living phases of the animal (e.g. resting phases, changes connected with sexual maturity, etc.). A similar statement has been made in the case of the presumed ring-shaped muscle scar in *Hypseloconus* by Webers et al. (1992, p. 198). Thus, *Barrandicella* differs from *Archinacella* in lacking the band-like, horseshoe-shaped, scar.

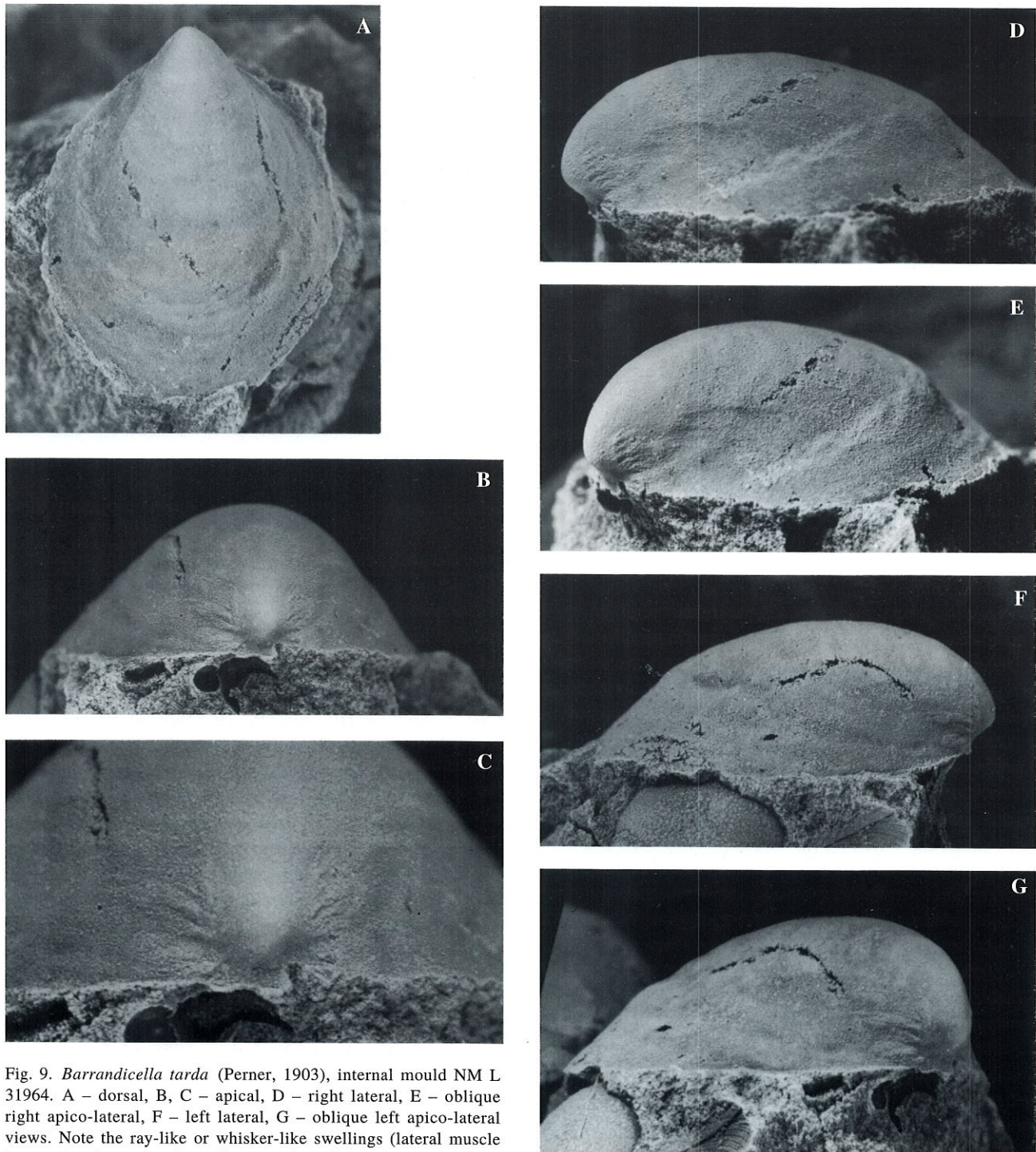


Fig. 9. *Barrandicella tarda* (Perner, 1903), internal mould NM L 31964. A - dorsal, B, C - apical, D - right lateral, E - oblique right apico-lateral, F - left lateral, G - oblique left apico-lateral views. Note the ray-like or whisker-like swellings (lateral muscle impressions) running from the scars lateral to the apex, and the long addorsal swelling in D, E, reminiscent of the most adapical portion of the muscle band in *Archinacella* and *Archinacellina*. Upper Ordovician, Zahořany Formation, Berounian (Caradocian). Praha - Dubeč. A x6, B, D-G x8, C x16.



Fig. 10. *Archinacellina modesta* (Barrande in Perner, 1903). Paralectotype NM L 5903. A – dorsal, B – right lateral, C – left lateral, D – apical, E – dorso-apical, F – oblique right apico-lateral views. Upper Ordovician, Králův Dvůr Formation, Královodvorian; Chodouň (Lejškov), Bohemia. All x5.

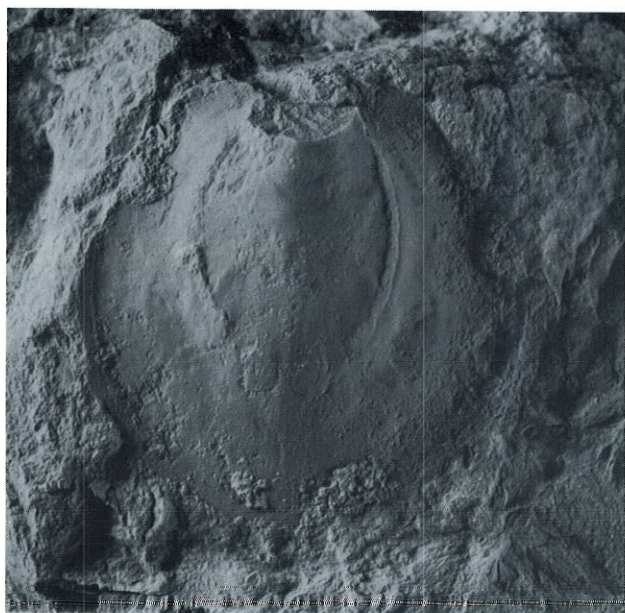


Fig. 11. *Archinacellopsis patelliformis* (Hall, 1847). Specimen U.S. NM 79216, dorsal view. Middle Ordovician, Black River Group, possibly Lowville Limestone; north of Watertown, New York, U.S.A. x3.

Two more archinacellids possess band-like muscle scars which are supposedly continuous below the apex. One is *Archinacella modesta* Barrande in Perner, 1903 from the Upper Ordovician of Bohemia, the type species of *Archinacellina* Horný, 1961, the other *Archinacella patelliformis* (Hall, 1847) from the Middle Ordovician of North America, the type species of *Archinacellopsis* Horný, 1995. Disregarding the question of whether or not these genera should be separated from *Archinacella*, *A. modesta* has a continuous ring in the abapical area, whilst *A. patelliformis* has an abapically discontinuous ring, with a pair of isolated, spot-like, rounded scars. Unfortunately, the apical parts of both specimens are damaged so that the course of the scar below the apex cannot be observed. In *A. patelliformis* the whole apical part is broken off (Knight and Yochelson 1958, pl. 5, fig. 4); in *A. modesta*, the apical part in the lectotype is partly broken off and partly corroded, while the scar is not discernible in the apical region in both paralectotypes. It should be noted that the muscle scar band, as figured by Ulrich and Scofield (1897) in *A. powersi*, is principally similar to that of *A. modesta*. In the latter (Text-fig. 10),

the band is most strongly delimited in the adapical half of the shell, with the abapical half being both weaker and irregular, with several equilateral swellings. This is reminiscent of *A. powersi*, although the continuity of the poorly preserved band in the abapical area is lacking.

Muscle scar evolution in archinacelloids

The recently discovered apico-lateral muscle scars of *Barrandicella* are seemingly largely equivalent to the rostral scars of *Archinacella powersi*. The horseshoe-shaped muscle scar band of *Archinacella*, *Archinacellina* and *Archinacellopsis* represents a development from the condition present in *Barrandicella*, aimed at increasing clamping efficiency. The scars in *Barrandicella* also resemble the tear-shaped scars of *Carinaropsis* Hall, 1847 which was interpreted as a bellerophonotoidean gastropod by Peel (1993). The comparison is strengthened by the analogy drawn by Peel (1990) between the sub-apical thickening in *Guelphinacella* (also incipient in *Archinacella powersi*) and the internal septum characteristic of *Carinaropsis*. Of particular note is the location of the muscle scars in both *Barrandicella* and *Carinaropsis* near the apex of the widely expanded shell. The muscle scars indicate that muscle attachment had not migrated dorsally with rapid expansion of the shell to form muscle attachment areas analogous to the horseshoe-shaped band seen in *Archinacella*, *Archinacellopsis* and *Archinacellina* and equivalent to the circum-dorsal band seen in recent patelliform gastropods. Also the granular character of the muscle scars in *Barrandicella* indicates a lack of translation of the muscle attachment scars. In *Carinaropsis*, clamping was aided by muscle contraction around a fulcrum provided by the massively strengthened internal septum (Peel 1993). No similar structure is present in the more globose *Barrandicella* and clamping must have been accomplished, however poorly, by linear muscle contraction oblique to the plane of the aperture.

Archaeopruga Horný, 1963 from the Upper Silurian of Bohemia is characterised by a single pair of large, elongate muscle scars located on the lateral areas of the spo-

on-shaped shell (Horný 1963d, pl. 144; Text-fig. 1) (Text-fig. 13 herein). Although originally described as a monoplacophoran and only member of the new Family *Archaeoprugidae* (Horný 1963d), *Archaeopruga* preserves a morphologically more advanced state than the much older *Barrandicella* since the muscle scars have migrated abapically to a lateral position near the aperture. This position and the increased size of the muscle scars (more than half the length of the 2–3 cm long shell) is clearly more in accord with a mode of life clamping against the substratum than is the case in *Barrandicella*. Interestingly, the adapical termination of the muscle scar in *Archaeopruga* shows slight curvature towards the dorsum which is reminiscent of the shape of the muscle scar band in *Archinacella* prior to passing underneath the apex. There is, however, no indication of a continuation of the scars beneath the apex in *Archaeopruga*.

The enlargement and lateral migration of the apico-lateral muscles in *Archaeopruga* enhance clamping of the shell against the substratum. The same explanation can be advanced to explain the formation of horseshoe-shaped muscle scars in *Archinacella*, *Archinacellina* and *Archinacellopsis*. In both cases, muscle contraction acts perpendicular to the plane of the aperture (substratum) and clamping efficiency is improved by distributing the muscle attachment area around the shell periphery. The mechanism of development of the continuous band below the apex is uncertain, and *Archaeopruga* as far as is known maintained separate lateral scars. It may be recalled, however, that muscle scars in *Barrandicella ovata* consist of isolated packets of muscle fibres with some attachment points even lying outside the main scar areas. Such a lack of tight fusion of the muscle fibres might have facilitated the re-distribution of muscle attachment seen in *Archinacella* and its near relatives.

Classification

The single pair of apico-lateral muscle scar areas indicates that *Barrandicella* is a gastropod. This finding supports the view expressed by Peel (1990) that a majority of recent authors interpret *Archinacella* as a gastropod,

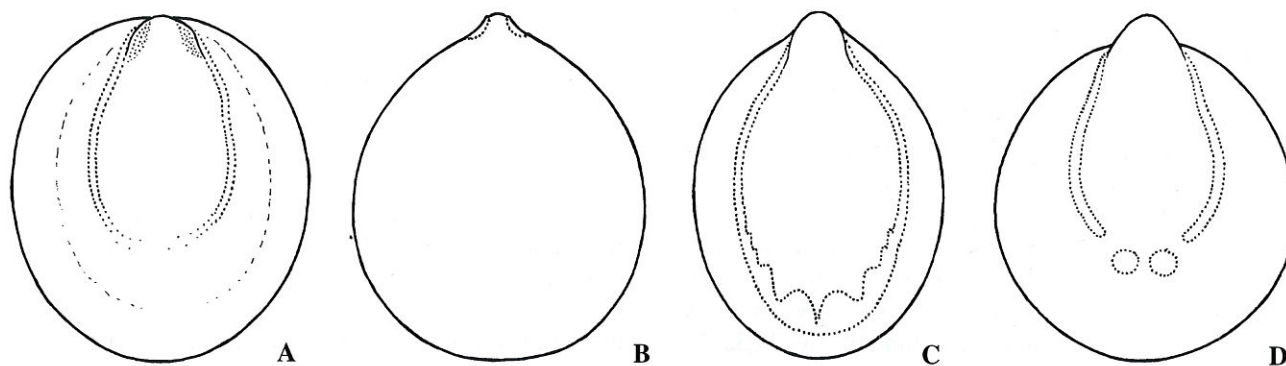


Fig. 12. Gross morphology of *Archinacella* (A), *Barrandicella* (B), *Archinacellina* (C), and *Archinacellopsis* (D). D after Knight et al. 1960.

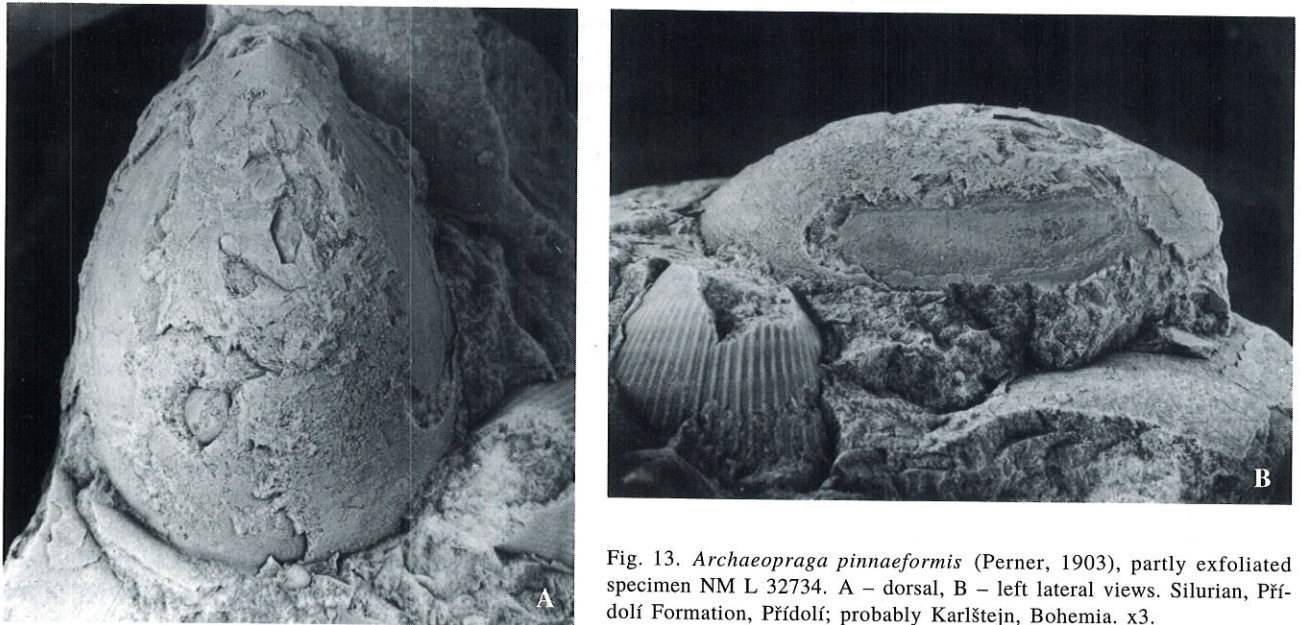


Fig. 13. *Archaeopruga pinnaeformis* (Perner, 1903), partly exfoliated specimen NM L 32734. A – dorsal, B – left lateral views. Silurian, Přídolí Formation, Přídolí; probably Karlštejn, Bohemia. x3.

although for different reasons. The pair of muscles presents a conclusive argument against the theory that *Archinacella* and its relatives are untorted Tergomya. In addition to the lack of multiple paired dorsal retractor muscle scars typical of tergomyans, both genera lack any indication of antero-lateral sinuses (Horný 1970a, b; Peel 1991a).

Without the discovery of paired apical muscle scars in *Barrandicella ovata*, it is unlikely that the rostral scars described in *Archinacella powersi* would be accepted as muscle scars. Indeed, as with the other smooth/pale areas visible in *Archinacella powersi*, they may still represent a diagenetic artefact. The muscle bands of *Archinacella powersi*, *Archinacellina modesta* and *Archinacellopsis patelliformis* are undoubtedly similar and preservational differences might explain the degree of expression of the abapical region of the band. *Archinacella powersi* is known only from a single specimen. Differentiation of the abapical prongs of such a scar into the pair of separate scars seen in *Archinacellopsis patelliformis* probably has little functional significance, although such an isolated pair might control the head or buccal mass, if the abapical margin is interpreted as anterior which is consistent with interpretation as a gastropod. Bundling of muscle fibres in recent *Patella* often produces a discontinuous muscle band, as noted already by Lindström (1884) when he compared the Silurian tergomyan *Tryblidium* to the recent limpet. A similar feature is also clearly visible in *Damilina* Horný, 1961 from the Silurian of Bohemia (Text-fig. 15).

As described above, the presence of the muscle band originally reported by Horný (1963a) in *Barrandicella ovata* is now rejected. However, it should be noted that the shell of *Archinacella* is very thin (Horný 1963a; Yochelson 1982; Wahlman 1992) and that thin shells often do not preserve readily identifiable scars. Thus, it could be argued that a muscle band in *B. ovata* may simply

have left no scar, although this is not easy to reconcile with the fine detail of muscle preservation in the apical region of *B. ovata*. While we acknowledge that new material may promote revision and result in synonymisation, we chose to recognise *Archinacella*, *Archinacellina* and *Archinacellopsis* as separate genera at this time, although we suspect that *Archinacellina* may prove to be a junior synonym of *Archinacella*. *Archinacella*, *Archinacellina*, *Archinacellopsis* and *Barrandicella* are placed together within the Family Archinacellidae of the Superfamily Archinacelloidea. *Marekicella* Horný, 1997 from the Berounian of Bohemia (Horný 1997) is strongly laterally compressed but displays similar curvature to *Barrandicella* and some suggestion of the internal structures seen in *B. tarda*; it is placed here with some confidence. *Guelphinacella* from the Silurian of North America is also tentatively placed in the Family Archinacellidae on account of its similarity to *Archinacella*, but its musculature is not known. The expansion of the Archinacellidae to include *Barrandicella* requires appropriate re-definition of the family and superfamily to include forms with a pair of apical muscles and no horse-shoe-shaped scar. The Family Archaeopragidae is retained to include *Archaeopruga*.

Archinacelloids as Palaeozoic patellogastropods

Despite wide current acceptance of patellogastropods as the sister group of all other gastropods, only Haszprunar (1988) among contemporary workers has proposed that the original gastropod shell was patelliform. Others (such as Lindberg 1988a, b; Fretter & Graham 1994) seek the origin of the limpet-like patellogastropods in an as yet unrecognised helically coiled group of gastropods, even though shell asymmetry is not evident during ontogeny in certain patellogastropod lineages (Haszprunar 1988). At which point (or points) patelliform patellogastro-

pod(s) diverged from the helical ancestor is not known. Given the extreme adaptability of gastropods and the wide occurrence of limpet-like shells in various groups at the present day, there is little reason to assume that only a single diversification of limpet-like shells took place within the patellogastropod clade. The description of a Triassic patellogastropod by Hedegaard et al. (1997) is based on information on shell structure not available through much of the Palaeozoic record, although additional discoveries can be expected from the Late Palaeozoic.

While archinacelloids are demonstrated to have been gastropods, little evidence has been presented to indicate that they were patellogastropods. Information on shell structure is not available, but even the strongly coiled form of the shell with its often overhanging apex is unlike Mesozoic–Recent patellogastropods. Archinacelloids represent a limpet experiment within the earlier Palaeozoic but their closer affinity is obscure. Their lack of shell asymmetry is inconclusive, not the least if modern symmetrical patellogastropods were ultimately derived from helical ancestors. The isostrophic coiling is shared with the bellerophontoid gastropods and the archinacelloid shell could have developed from a more strongly coiled, bellerophontiform, ancestor by dramatic increase in abapical expansion. The dorsal slit and parietal deposits characteristic of most bellerophontoids are lacking in archinacelloids, but this is to be expected from the widely expanded, limpet-like form. A slit is often redundant in bellerophontoids with widely expanded apertures



Fig. 14. *Floripatella rousseai* Yochelson, 1988, internal mould, holotype USNM 410165. Dorsal view. Middle Ordovician, Whiterockian, probably early Llanvirnian (Darriwilian). South flank of Fossil Mountain, Confusion Range, Ibex area, western Millard County, Utah, U.S.A. $\times 3.3$.

(Peel 1991a). The similarity of muscle scar patterns between *Barrandicella* and *Carinaropsis* noted above reflects similar acquisition of an expanded shell; the muscle scars themselves are quite different in detail. Moreover, the tendency for the post-torsional right muscle attachment scar in *Barrandicella ovata* to be slightly smaller than the left could support derivation from a helically coiled ancestor, although more data are required to confirm this observation. Thus, while Archinacelloidea is here recognised as a non-patellogastropod superfamily of archaeogastropod grade, its closer affiliations remain unresolved. Ironically, on account of the uncertainty, a relationship to the patellogastropod ancestral lineage can not be discounted!



Fig. 15. *Damilina subrotunda* (Barrande in Perner, 1903), internal mould, holotype NM L 5843. Dorsal view. Silurian, Kopani-na Formation, Ludlow, Ludfordian. Dlouhá hora near Beroun, Bohemia. $\times 4.6$.

Yochelson (1988) classed *Floripatella* (Text-fig. 14) within the Family Archinacellidae which he assigned to the Superfamily Patelloidea. This genus lacks the prominent marginal or overhanging apex characteristic of archinacellid genera, although Yochelson (1988) described a variety of forms within *F. rousseai*, varying from elongate with an excentric apex to circular with a central apex. *Floripatella* is more reminiscent of *Damilina* Horný, 1961 (Horný 1961, 1963a) and we transfer it to the Family Damilinidae Horný, 1963 which Horný (1963a) placed within the Superfamily Patelloidea. McLean (1990) assigned the late Palaeozoic limpet *Lepetopsis* Whitfield, 1882 to a new Family Lepetopsidae. He placed this family of fossil species together with the recently discovered deep ocean vent Family Neolepetopsidae in a Sub-order Lepetopsina of the Patellogastropoda, speculating that Palaeozoic patellogastropods may belong with this group rather than with the Sub-order Patellina.

While acknowledging the discrepancies in age (early Ordovician, Silurian, Carboniferous–Permian) between the three genera, we most tentatively place the Family Damilinidae alongside the Family Lepetopsidae within the Lepetopsina, fully aware of the speculation involved, to express our conviction that these forms are not related to the Archinacelloidea. They are superficially more patellogastropod-like in their morphology than archinacelloids but at our current stage of knowledge that is a challenge rather than a solution.

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Svalové vtisky a systematické postavení spodnopaleozoických rodů *Archinacella* a *Barrandicella* gen. n. (Mollusca)

Nový rod *Barrandicella* je navržen k uctění dvoustletého výročí narození Joachima Barranda (1799–1883), na základě druhu *Archinacella ovata* Barrande in Perner, 1903 ze středního ordoviku (darriwilu) Čech. *Barrandicella* je interpretována jako plž (Gastropoda), a to na základě páru dobře zachovaných svalových vtisků a přidružených pomocných vtisků umístěných na vrcholu příliskovité schránky. *Barrandicella* nemá vyvinutý dorsální pentlicovitý svalový vtisk, charakteristický pro rod *Archinacella* Ulrich et Scofield, 1897 a příbuzné rody, ale může s nimi být umístěna v revidované nadčeledi Archinacelloidea. Mezi nadčeledí Archinacelloidea a skupinou Patellogastropoda, v současné době považovanou za sesterskou skupinu všech ostatních plžů, neexistuje zřejmý spojovací článek. K rodu *Barrandicella* je kromě typického druhu zařazen i druh *Barrandicella tarda* (Perner, 1903) z barrandienského berounu, u kterého byly rovněž nalezeny vrcholové svalové vtisky a velmi jemná paprscitá skulptura povrchu schránek. Do čeledi Archinacellidae jsou kromě rodů *Archinacella* a *Barrandicella* včleněny rody *Archinacellina* Horný, 1961, *Archinacellopsis* Horný, 1995 a prozatímně i rody *Marekicella* Horný, 1997 a *Guelphinacella* Peel, 1990, u nichž nejsou svalové vtisky známy. Do patellogastropodní čeledi Damilinidae jsou zařazeny rody *Floripatella* Yochelson, 1988 a *Damilina* Horný, 1961. Rod *Archaeopruga* Horný, 1963 je ponechán v čeledi Archaeopragidae.