Acta Musei Nationalis Pragae, Series B, Historia Naturalis, 61 (1–2): 53–76 issued June 2005
Sborník Národního muzea, Serie B, Přírodní vědy, 61 (1–2): 53–76

MUSCLE SCARS, SYSTEMATICS AND MODE OF LIFE OF THE SILURIAN FAMILY DRAHOMIRIDAE (MOLLUSCA, TERGOMYA)

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Horný, R. J. (2005): Muscle scars, systematics and mode of life of the Silurian Family Drahomiridae (Mollusca, Tergomya). – Acta Mus. Nat. Pragae, Ser. B, Hist. Nat., 61 (1-2): 53–76. Praha. ISSN 0036-5343.

Abstract. The Silurian tryblidioidean Family Drahomiridae, established as a subfamily by Knight and Yochelson (1958), was defined as to contain low spoon-shaped shells with seven pairs of muscle scars in the dorsal area. Originally it contained the genus *Drahomira* BARRANDE in PERNER, 1903. In 1995, Horný added a related genus, *Pragamira*. During the new investigation of additional material, the genus *Archaeopraga* HORNÝ, 1963 was studied in detail and its lateral scars were ascertained also in the genera *Drahomira* and *Pragamira*. Moreover, the typical drahomirid muscle scar pattern was found also in two additional specimens of *Archaeopraga pinnaeformis* (PERNER, 1903). The Family Archaeopragidae HORNÝ, 1963 is thus synonomous with the Family Drahomiridae which contains tryblidioidean genera with mostly seven sets of dorsal paired muscle scars and two long, large, lateral pedal muscle scars. The lateral scars are interpreted as a musculature assuring balance, necessary for the mode of life on shells of dead orthoconic nautiloids and may be analogous to the horseshoe-shaped scars in the archinacellid gastropods.

■ Mollusca, Tergomya, Tryblidiidae, Drahomiridae, *Drahomira*, *Pragamira*, *Archaeopraga*, internal shell morphology, muscle scars, systematics, mode of life, Silurian, Barrandian Area, Bohemia, Czech Republic

Received March 29, 2005

Introduction

Like the majority of Lower Palaeozoic "monoplacophorans" (tergomyans of present usage), the Silurian *Drahomira* BARRANDE in PERNER, 1903 has an unsettled history. It was first observed by Joachim Barrande during the second half of the 19th century, certainly about 1880, when he prepared plates for the 4th volume (Gastéropodes) of his Système silurien du centre de la Bohême. His first illustration of a drahomirid mollusc appeared in 1881 in the 6th volume (Acéphalés). On plate 212, figs VI/3–5, he figured and named *Mytilus buridani* BARRANDE, 1881; of the three figured specimens, one belongs to *Pragamira perlonga* (HORNÝ, 1963) (figs 1, 2) and one to *Archaeopraga pinnaeformis* (PERNER, 1903) (figs 3–5). Only one specimen is a bivalve (figs VI/6, 7). Regrettably, Barrande did not recognize the marked muscle scars in the large specimen but mentioned a calcite vein crossing the fossil (Text-fig. 1).

Barrande's first conscious illustration of *Drahomira*, followed with a name and probably also a label, probably originated shortly after 1880 when he finished bivalves and started to prepare gastropods for the 4th volume. Here he figured two specimens on plate 104. According to Perner (1903), they represented one species, named by Barrande *Drahomira glaseri* after Mrs Glaser, who lent him a plaster cast of a specimen from her private collection (the correct spelling of the specific name should be, therefore, *Drahomira glaserae*). This plaster cast, at present together with the original specimen, is placed in a rounded drug box, bearing Barrande's inscription "drahomira Glaseri Barr. Pl. 104 – " (Text-fig. 2). After Barrande's death, it has been housed in the Barrande's collection in the Department of Palaeontology, National Museum, Prague.

The first description of *Drahomira glaserae* was published by Perner (as *Tryblidium glaseri*) in 1903. The Barrande's plate 104 was issued in 1907 within the second tome of Vol. IV – Gastéropodes. Perner described three species, based on three specimens: *Tryblidium glaseri* BARR. sp., *T. rugatum* PERNER, and *T. barrandei* PERNER. According to Perner 1903, *T. barrandei* was the second specimen originally representing Barrande's species *D. glaseri*. Perner had not accepted Barrande's generic name *Drahomira*, but published it in a footnote on p. 23 ("Barrande a donné à deux de ces formes le nom de *Drahomira Glaseri* sur les etiquettes et les explications provisoires des figures."). The third species described by Perner was *T. rugatum*, based also on a single specimen. In 1938 A. Říha published an old find of an indeterminate small Ordovician internal mould of a tryblidiid shell, labelled by Perner as *Tryblidium* sp. Comparing it with all three existing Silurian tryblidiids described by Perner, he respected Perner's determination and still used the generic name *Tryblidium* LINDSTRÖM, 1880.

J. B. Knight (1952) listed for the first time the genus *Drahomira* among the genera of the Subfamily Tryblidiinae PILSBRY, 1899. At that time, he interpreted the tryblidiids as members of the gastropod Subclass Isopleura, consisting of Families Tryblidiidae PILSBRY, 1899 and Archinacellidae KNIGHT, 1952. In his paper, he commented *Drahomira* in a footnote on p. 47: '*Drahomira* is a name published, but not adopted, by Perner, 1903 (p. 23, footnote) for *Tryblidium glaseri* Barrande in Perner, 1903 (p. 23), genotype by

monotypy. This name was overlooked by me in the preparation of "Paleozoic Gastropod Genotypes" (Knight 1941). Seemingly it is the valid name for a distinct genus of this family.' Following this paper, Horný (1956) redescribed the genus *Drahomira* as a gastropod, with all three species.

Only a year later Lemche (1957) described a living representative of monoplacophorans (tergomyans of present usage), *Neopilina* LEMCHE, 1957. This phenomenal event was followed by fundamental changes in the systematics of gastropods and their presumed ancestors. The first outcome of this impact was expressed in the paper by Knight and Yochelson (1958). The monoplacophoran Order Tryblidiida LEMCHE, 1957 embraced Families Palaeacmaeidae GRABAU et SHIMER, 1909 and Tryblidiidae PILSBRY, 1899. The Family Tryblidiidae was divided into five subfamilies, one of them being Drahomirinae KNIGHT et YOCHELSON, 1958 with the diagnosis: "Aperture elongate; shell spoon-shaped; with seven pairs of muscle scars; muscle scars mostly simple and elongate, normal to margin of aperture." This conception of the genus and subfamily were accepted in the Treatise on Invertebrate Paleontology, part Monoplacophora (Knight and Yochelson 1960) as well as by Horný (1963a), who extended his descriptions of 1956. In 1963b he published various data concerning palaeobiology and ontogeny of *Drahomira* species, and described a new species, *D. perlonga* HORNÝ, 1963. In 1995 Horný established the genus *Pragamira*, based on this species. The genus *Drahomira* was illustrated in several papers, but without any description or comments [e.g. Wingstrand (1985), Prokop (1989), Král et *al.* (1998), Košťák (2004)].

The present paper summarizes all finds of drahomirids known to the author. The majority of them are deposited in the collections of the National Museum, Prague. These specimens have been derived from the collection of Barrande (5 specimens) and the collections of the Museum, including specimens found by Bláha, R. Horný, R. Růžička and V. Turek. The best specimens were carefully collected by J. Kříž during his investigation of bivalves of the Požáry Formation, now deposited in the collections of the National Museum and the Czech Geological Survey, Prague. One specimen comes from the collection of J. Marek (Charles University, Prague).

Following this revision, the Silurian genus *Drahomira* comprises two species: rare *D. kriziana* sp. n., found in the Kopanina Formation (Ludlow, Gorstian), and *D. glaserae* (including *D. barrandei* and *D. rugata*), distributed in several localities of the Požáry Formation (Přídolí). The genus *Pragamira* with one species, *P. perlonga*, occurs rarely in the Požáry Formation, similarly to *Archaeopraga* HORNÝ, 1963, also with one species, *A. pinnaeformis*. Various statements concerning stratigraphy occur in older literature. Perner (1903) erroneously indicated F_1 (Lower Devonian, Lochkovian of present usage) for *Tryblidium glaseri* and *T. barrandei*, and Knight and Yochelson (1958) quoted Ordovician for *Drahomira*.

The most important asset of this paper, besides the detailed internal shell morphology, is an ascertainment that the genus *Archaeopraga* belongs to the Class Tergomya, and the Family Archaeopragidae HORNÝ, 1963 is synonomous with the Family Drahomiridae. Except for the two large lateral muscle scars, it has six pairs of scars morphologically close to those of *Drahomira*. The genus *Pragamira* has also similar large lateral scars. This fact is interpreted here as a result of adaptation to life on shells of dead orthoconic nautiloids, accompanying all finds of these tergomyans. Origin and phylogeny of drahomirids and their Ordovician ancestors remain unknown.

Specimens indicated with L are housed in the collections of the Department of Palaeontology, National Museum, Prague; those with prefix YA are deposited in the collections of the Czech Geological Survey, Prague.

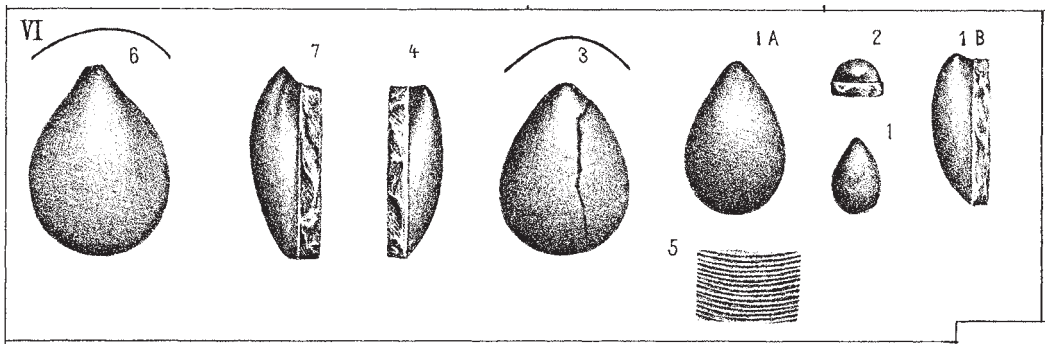
Systematic palaeontology

Class **Tergomya** HORNÝ, 1965
Order **Tryblidiida** LEMCHE, 1957

Superfamily **Tryblidioidea** PILSBRY in ZITTEL-EASTMAN, 1899
Family **Drahomiridae** KNIGHT et YOCHELSON, 1958, emend. (syn. Archaeopragidae HORNÝ, 1963)

Diagnosis (emend.). Shell spoon-shaped, aperture oval; apex above the anterior part of apertural margin or just overhanging; aperture planar, without brim; outer shell sculpture consists of concentric growth lines, often combined with inconspicuous radial structures, sometimes present even on internal surface; inner surface of apex with two symmetrical muscle scars on top; a pair of rounded, compound cephalic scars, posteriorly followed by mottled radular scars; five to six sets of bilaterally symmetrical dorsal scars, mostly simple and elongate, with the exception of the last pair normal to margin of aperture; the last pair often modified; two large lateral scars or granular zones located between the dorsal scars and the margin of aperture.

Discussion. The drahomirids, distributed in the Silurian of the Perunica microcontinent, are a specialized group of tryblidioideans fixed on the biofacies, in which dark grey cephalopod limestones were deposited. Adaptation to probably almost stationary mode of life on arched, dead cephalopod shells caused relevant changes of internal shell morphology, notably the origin of large lateral pedal muscles. This feature, not homologic with the apico-lateral scars of some archinacellids, distinguishes the drahomirids from all so far discovered fossil and living tryblidioidean tergomyans. An additional characteristic and unique feature are the two apical scars, probably serving an identical purpose in early post-larval stage. Also the rounded scars of the first anterior pair, probably composed of 2 elements in close juxtaposition, are quite different from any similarly positioned tryblidiid scars. However it is probable that *Drahomira* had eight pairs of retractors like typical tryblidians. The absence of the diaphragm scar, well developed e.g. in



Text-fig. 1. Barrande's illustration of *Mytilus buridani* BARRANDE, 1881; Pl. 212, case VI, figs 1-7: 1-2 = *Pragamira perlonga* (HORNÝ, 1963), 3-5 = *Archaeopraga pinnaeformis* (PERNER, 1903); 6, 7 = a bivalve.

Pilina [Lemche and Wingstrand (1959), Peel (1977)] is notable, however not unique among the tryblidioideans. For these reasons I accept the family level of the Subfamily Drahomirinae as used by Wahlman (1992).

Genera. *Drahomira* BARRANDE in PERNER, 1903, *Pragamira* HORNÝ, 1995, *Archaeopraga* HORNÝ, 1963.

Distribution. Silurian, Barrandian Area, Czech Republic.

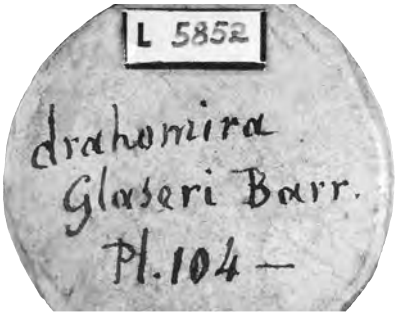
Drahomira BARRANDE in PERNER, 1903, emend.

Type species: *Tryblidium glaseri* BARRANDE in PERNER, 1903. Silurian, Ludlow, Gorstian, Kopanina Formation; Barrandian Area, Czech Republic.

Diagnosis. Genus of the Family Drahomiridae. Shell with apex above the anterior part of the apertural margin; a pair of rounded composite cephalic scars (A), followed by radular scars; six sets of bilaterally symmetrical dorsal scars (B–G), mostly simple and elongate, with the exception of the last pair normal to margin of aperture; the last pair of irregular pustulose shape, located on a raised growth structure; two large lateral scars, sometimes weak or not observable, rarely substituted by a zone of numerous small grain-like scars.

Discussion. The Barrande's manuscript name *Drahomira* was first used but not adopted by Perner (1903) in a footnote on p. 23. Perner preferred the name *Tryblidium* LINDSTRÖM, 1880 which, at that time, encompassed also species with smooth shell, later separated in the genus *Pilina* by Koken and Perner (1925). Knight (1952) confirmed the validity of *Drahomira* and Knight and Yochelson (1958) established the Subfamily Drahomirinae on its basis. This standpoint was accepted in the Treatise (Knight and Yochelson 1960) and by Horný (1956, 1963a). In 1995, Horný separated the genus *Pragamira* HORNÝ, 1995 from *Drahomira*.

Species. *Drahomira glaserae* (BARRANDE in PERNER, 1903), *D. kriziana* sp. n.; Silurian, Ludlow and Přídolí, Czech Republic.

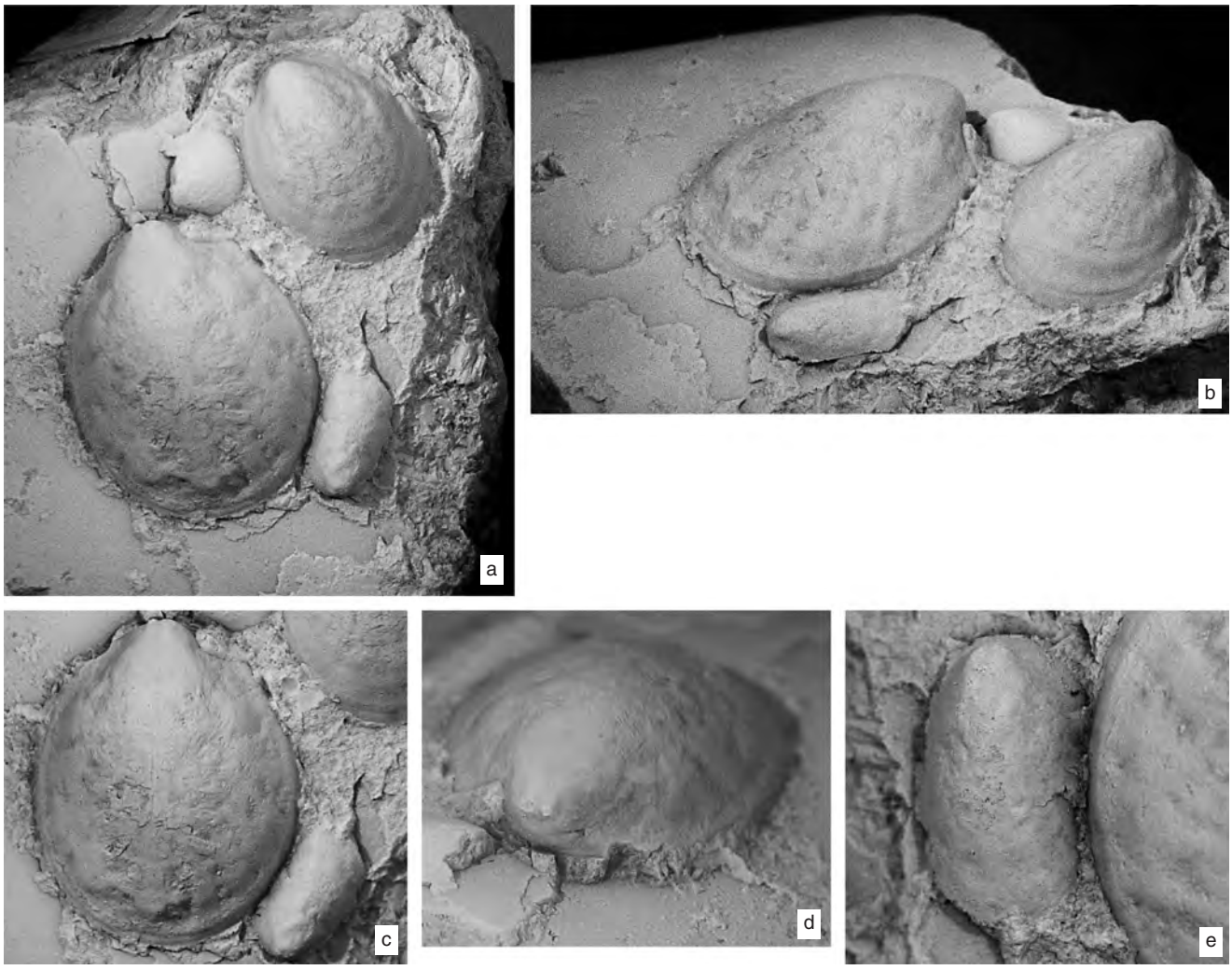


Text-fig. 2. An original box with Barrande's handwriting and the Museum catalogue number.

Drahomira glaserae (BARRANDE in PERNER, 1903), emend.

(Text-figs 3–15)

1903 *Tryblidium Glaseri* BARR. sp.; J. Perner, Gastéropodes, 1, p. 23, 24, Text-fig. 1a–c.
1903 *Tryblidium Barrandei* PERNER; J. Perner, *ibidem*, p. 25.
1903 *Tryblidium rugatum* PERNER; J. Perner, *ibidem*, p. 25, 26, Text-fig. 2a–e; pl. 5, figs 12–14.
1907 *Tryblidium Glaseri* BARR.; J. Perner, Gastéropodes, 2, expl. pl. 104, figs 21–23.
1907 *Tryblidium Barrandei* PERNER; J. Perner, *ibidem*, expl. pl. 104, figs 24–26.
1938 *Tryblidium glaseri* BARR.; A. Říha, Příspěvek k poznání etc., p. 4.
1938 *Tryblidium barrandei* PERNER; A. Říha, Příspěvek k poznání etc., p. 4.
1938 *Tryblidium rugatum* PERNER; A. Říha, Příspěvek k poznání etc., p. 4.
1952 *Tryblidium* (= *Drahomira*) *glaseri* BARRANDE in PERNER, 1903; J. B. Knight, Primitive fossil gastropods etc., p. 47.
1956 *Drahomíra glaseri* (BARRANDE in PERNER, 1903); R. Horný, Tryblidiinae PILSBRY etc., p. 80, 81, pl. 1, figs 1, 2, pl. 2, fig. 1.
1956 *Drahomíra rugata* (PERNER, 1903); R. Horný, *ibidem*, p.81–83, pl. I, figs 3, 4.
1956 *Drahomíra barrandei* (PERNER, 1903); R. Horný, *ibidem*, p. 99, pl. 1, figs 5, 6.
1960 *Drahomira glaseri* (PERNER, 1903); J. B. Knight and E. L. Yochelson, Monoplacophora, *in* Treatise etc., Part I, Mollusca 1, p. *I*77, fig. 48/3.
1963a *Drahomira glaseri* (PERNER, 1903); R. Horný, Lower Pa-



Text-fig. 3. *Drahomira glaserae*, L 5908. a, b - a group of immature specimens on a fragment of orthoconic nautiloid, × 3.8. Note the orientation of the two big specimens. c, d – dorsal and oblique apical views of the biggest specimen, × 4, × 5.5; e – dorsal view of the juvenile specimen, × 9.5. Požáry F., probably Praha-Slivenec.

leozoic Monoplacophora etc., p. 24, 25, Text-fig. 3, pl. 2, figs 1, 2.

1963a *Drahomira rugata* (PERNER, 1903); R. Horný, *ibidem*, p. 25, fig. 25, Text-fig. 4.

1963a *Drahomira barrandei* (PERNER, 1903); R. Horný, *ibidem*, p. 26, Text-fig. 5, pl. II, figs 6, 7.

1963b *Drahomira rugata* (PERNER, 1903); Horný, Nové nálezy etc., p. 79–84, Text-figs 1–4.

1988 *Drahomira rugata*; Turek *et al*., Fossils of the World, p. 161, fig. 2.

Holotype. NM L 5852, figured here on Text-figures 5, 6.

Stratum typicum. Silurian, Přídolí, Požáry Formation.

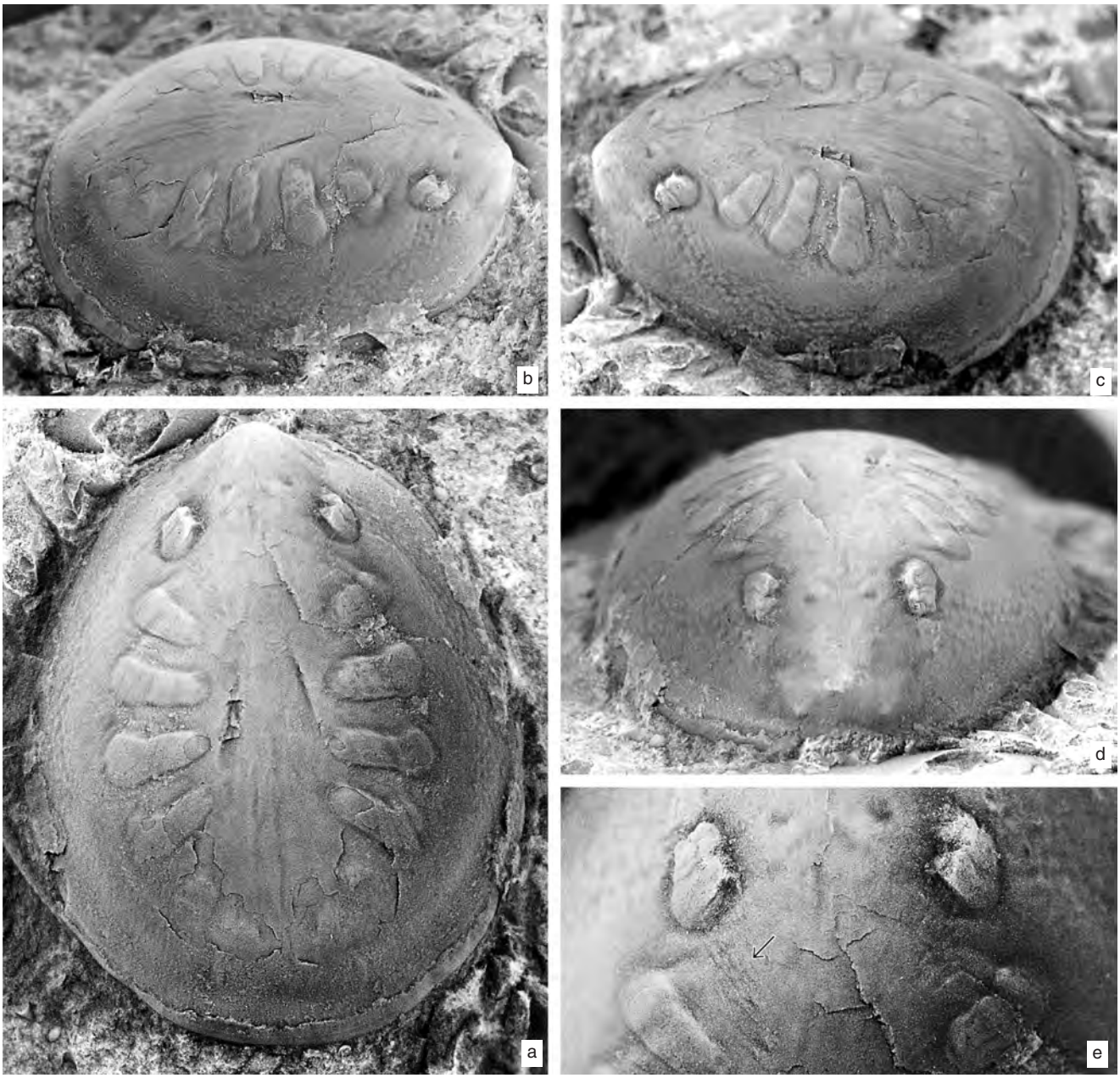
Type locality. Praha-Lochkov, Barrandian Area, Bohemia, Czech Republic.

Material. 22 specimens.

Diagnosis. Species of the genus *Drahomira* with low to arched shell, narrow apex, smooth or scarcely radially striated internal mould. Lateral scars weak or not observable, or substituted by a zone of granular surface connected with cephalic scars.

Description. The majority of specimens studied are preserved as internal moulds, some of them with counterparts or patches of shell. With the exception of specimen L 5853, which is preserved in calcareous shale, they come from dark, grey, bituminous cephalopod limestones with numerous fragments of orthoconic nautiloids. All of them were found in the Požáry Formation, mostly in localities Praha-Lochkov, Praha-Slivenec, Praha-Velká Chuchle, but several come from Karlštejn and one specimen was collected at the Lejškov hill near Suchomasty.

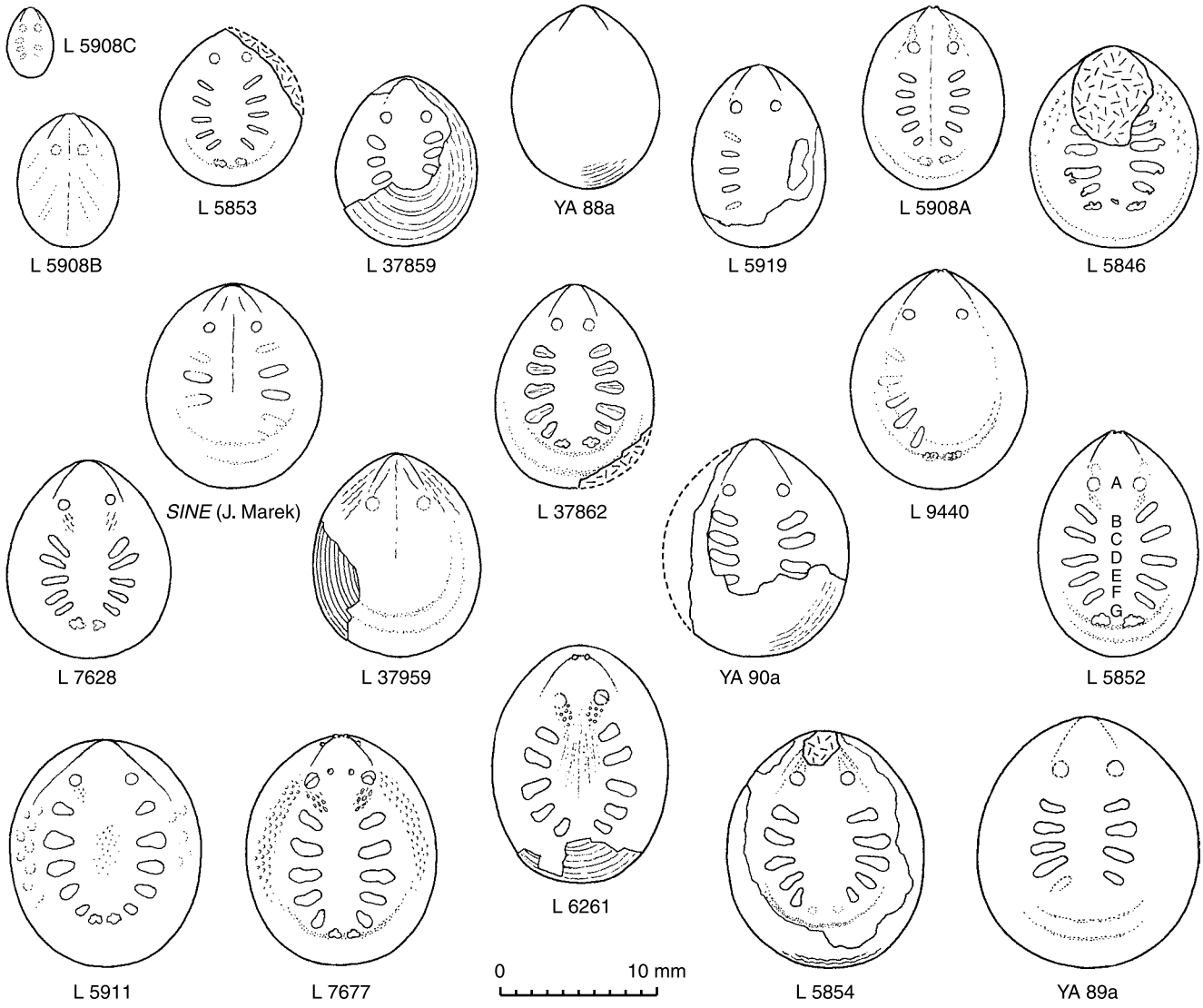
Shell morphology. The shell wall is 0.1–0.2 mm thick, in some specimens with lamellae of hypostracum adherent to the mould surface. External surface bears dense, mostly uneven concentric growth lines, rarely combined with very fine radial striae; as an exception, the otherwise simple growth lines are slightly waved in the posterior area in the specimen L 5854, which is the holotype of *D. rugata.* In general, the shell (observed on internal moulds) is spoon-shaped, shallowly convex between the apex and the posteri-



Text-fig. 4. ***Drahomira glaserae*****, L 7677. The best specimen. a – dorsal (× 6.5), b – right oblique lateral (× 5), c – left oblique lateral (× 5) views, both showing zones with granules; d – frontal view with well visible subapical scars, × 6.5; e – anterior area with radular scars (arrowed, × 10). Požáry F., Praha-Slivenec.**

or margin; a few specimens show a shallow, saddle-like depression separating the cephalic part. Shells show a great variability, which is due to probable stationary life on shells of orthoconic nautiloids lying on the bottom, what probably may have limited their width. The fully adult specimens show a tendency to widen even the anterior part of the shell. The l:w ratio fluctuates between 1.2 and 1.5. The apertural margin is planar, without emarginations. Apex (observed on moulds) is narrow, reaching, but not overhanging, the anterior part of apertural margin.

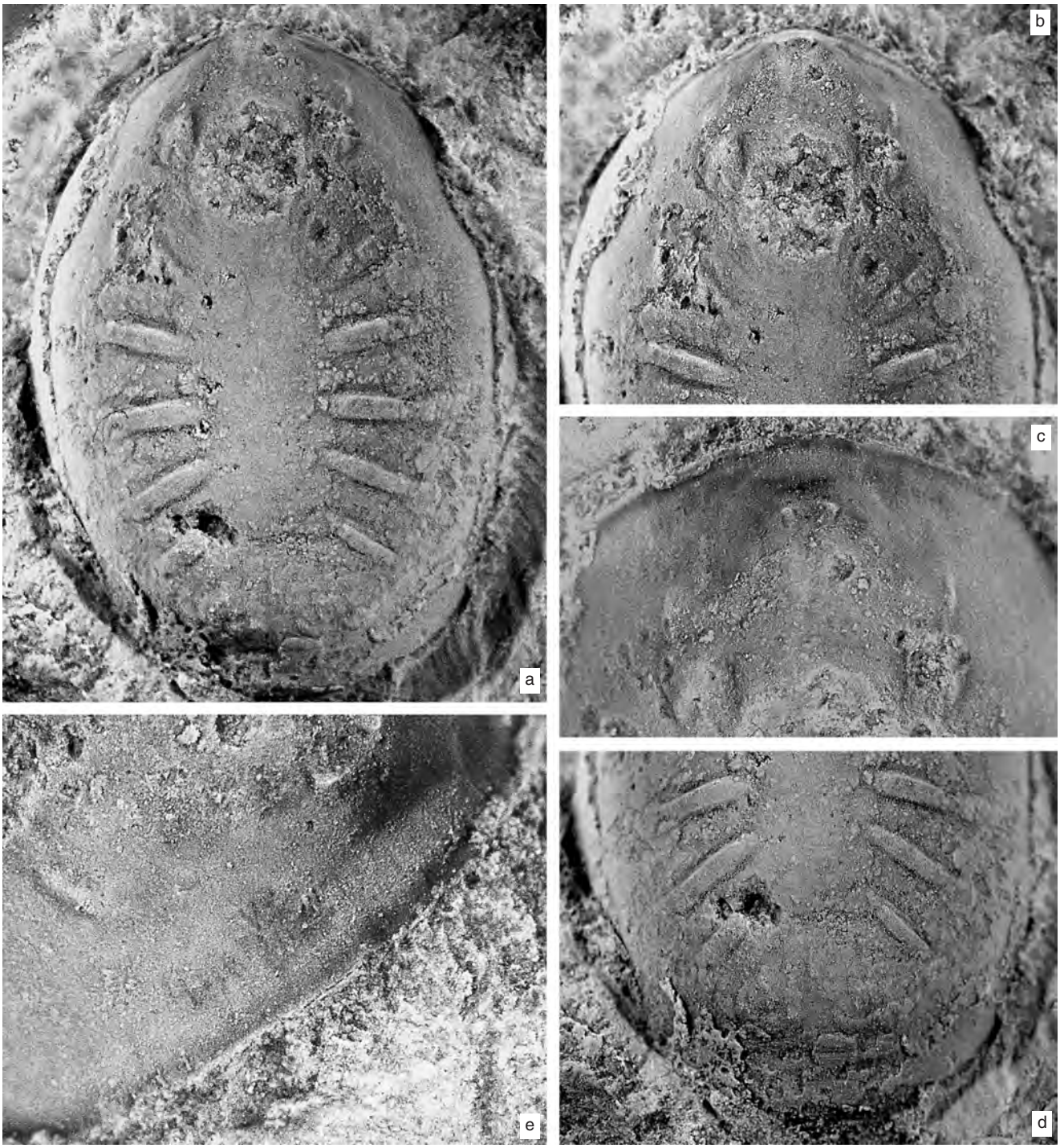
Muscle scars. The main muscle scars are arranged in seven pairs. The first, cephalic pair (A) contains two conspicuous, apparently rounded scars which, however, consist of two insertions in close juxtaposition, corresponding to various muscles. The dorsal scars, forming five pairs (B–F) are arranged radially toward the centre of shell. They are rather variable in shape (linear, elliptic, cuneate, or peanut-shaped) and depth; this probably depends on environmental conditions, age and mode and intensity of partial prediagenetic solution of the internal shell surface. The best preserved scars in fully adult specimens show rough surface and fine, irregular lines, probably junctions of insertions of muscle fibres. The last, posterior (G) pair consists of two rather different, pustulose scars, located on raised concentric elevation, closing the



Text-fig. 5. ***Drahomira glaserae*****. Line drawings of all specimens studied, arranged according to length (descriptions on p. 60–64).**

central scar pattern. Lateral scars developed in other drahomirids are in *D. glaserae* either not observable or substituted by a zone with granules running from the cephalic scars in latero-posterior direction along the lateral apertural margin; granulae may correspond to insertions of isolated muscle fibres. Characteristic are groups of microscars adjacent to the cephalic scars (A) and located between A and B scars. According to the shape and location, they can be compared with the mottled muscle scars in *Pilina unguis*, by Lemche and Wingstrand (1959, Fig. 133) and Wingstrand (1985) interpreted as the radular scars. These groups are usually radially oriented like the dorsal scars and probably were the cause of description of the so-called "tadpole tails" by Knight and Yochelson (1960) in the poorly preserved holotype of *D. glaserae* (Text-fig. 6). Shape of these minor scars is variable; this is probably also caused by individual conditions of almost stationary mode of life and variable *post mortem* and prediagenetic processes affecting the shell. Constantly present are the two frontal grain-like scars (probably not homologic with the protoconchal protuberance of *Pilina*), separated by axial groove sometimes running across the dorsum. These frontal scars resemble morphology of apex in *Bipulvina*, described from the Lower Ordovician of Missouri by Yochelson (1958). They may correspond to scars which may have served to provide stability of early shell after settling of pelagic larva on the surface of cephalopod shell.

The anterior part of the mould proximal to cephalic (A) scars bears a pair of small grain-like bilaterally symmetric subapical scars and a pair of pit-like depressions between the A scars which correspond to muscles of various functions in the cephalic area. They are best preserved in specimen L 7677 (Text-figs 4, 5). Pallial and branchial scars have not been ascertained. Remarkable is a quite frequent asymmetry of scars. The left and right sets of scars are often slightly shifted, the groups of radular scars are never bilaterally symmetric (which is also the case in *Pilina unguis* [LINDSTRÖM in ANGELIN and LINDSTRÖM, 1880] and *P. cheyennica* PEEL, 1977), and also the pairs of dorsal scars are asymmetric. Distance between the cephalic scars and the first dorsal pair of scars is variable, similarly as the

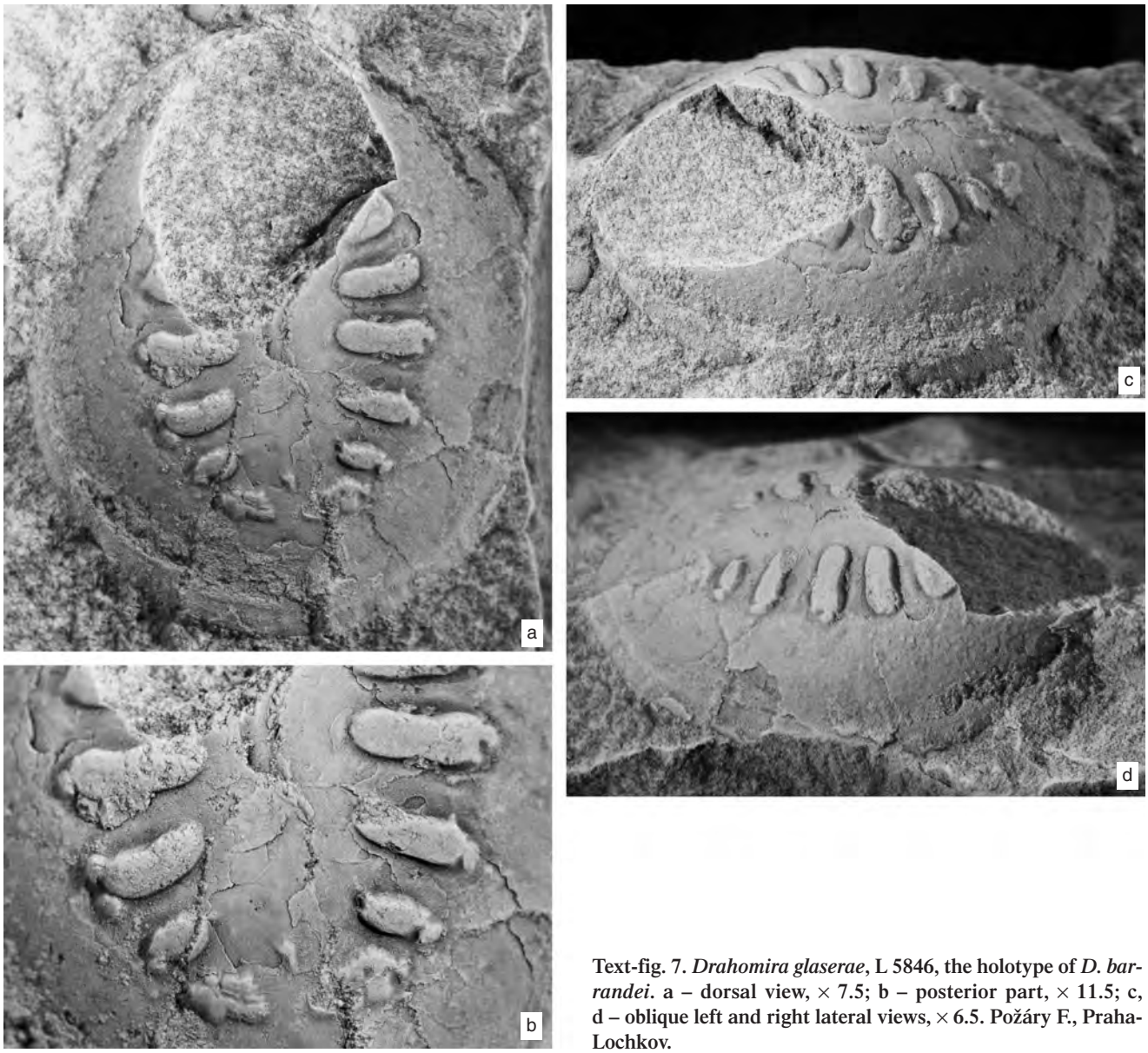


Text-fig. 6. ***Drahomira glaserae*****, L 5852, the holotype. a – dorsal view, × 7.5; b – anterior area, × 8; c – oblique anterior view, × 13; d – posterior area, × 8; e – anterolateral part of apertural margin below the apex with small scars which may be connected with pallium, × 23. Požáry F., Praha-Lochkov.**

distance between the last posterior pair and the posterior part of apertural margin.

Thanks to a unique find of four immature specimens on the surface of a large orthoconic nautiloid (Text-fig. 3), we have more data about the ontogeny of these molluscs. The smallest known specimen (L 5908C) is 4.5 mm long and 3.4 mm wide, and its preservation does not permit restoration of the morphology of scars. It seems that the rounded cephalic scars were developed but delimitation and location of individual dorsal scars is unclear. The second, bigger specimen (L 5908B), 8.4 mm long and 6.3 mm wide, has well developed cephalic scars, but other details are missing. The biggest specimen of the group (L 5908A), 11.5 mm long and 9.0 mm wide, has the cephalic, dorsal, and posterior scars already fully developed.

D i s c u s s i o n . As described by Perner (1903), the genus



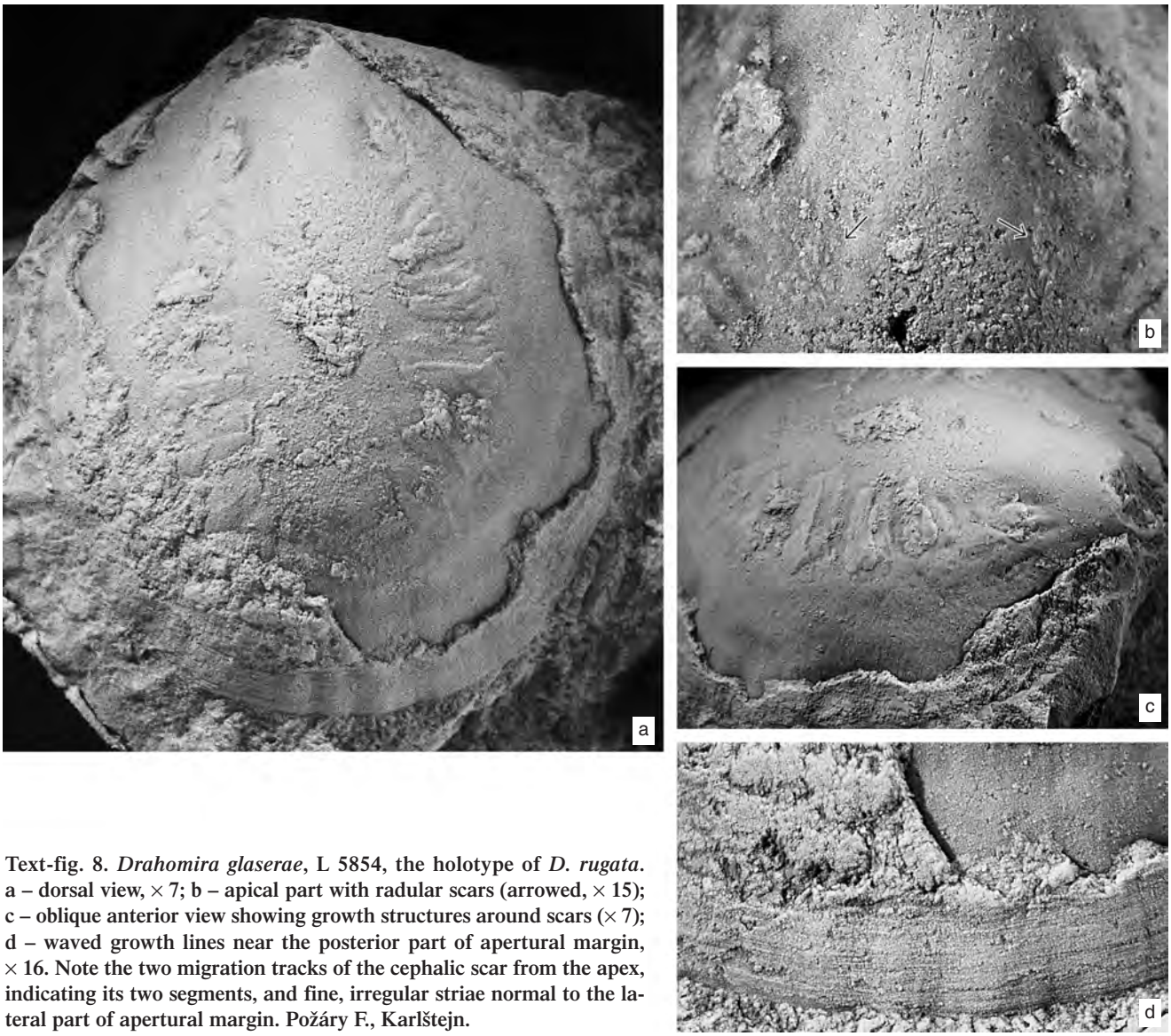
Text-fig. 7. ***Drahomira glaserae*****, L 5846, the holotype of** ***D. barrandei*****. a – dorsal view, × 7.5; b – posterior part, × 11.5; c, d – oblique left and right lateral views, × 6.5. Požáry F., Praha-Lochkov.**

Drahomira originally encompassed three species, *D. glaserae* (the type species), *D. rugata*, and *D. barrandei*, each represented by a single specimen. This scheme was accepted by Horný (1956, 1963a). Accumulation of a relatively large collection of these rare fossils resulted in a conclusion that we are most probably concerned with only one variable species. All three original "species" are connected by numerous "transition" forms, reflected particularly in shape and outline of the shell and muscle scars. The reason for such a large variability was undoubtedly the stationary mode of life on shells of dead orthoconic nautiloids. Similar situation is known among various cyrtonellids (Horný, paper in preparation), platyceratids (e.g. Linsley 1978, Horný 2000), and others. Determination of various finds of drahomiras was, therefore, rather subjective or impossible. For these reasons, the species *D. rugata* and *D. barrandei* have been relegated to the synonomy of the type species, *D. glaserae.* Taxonomy of the tryblidiids is more or less based on shape of the muscle scar pattern. It is a rare criterion among molluscs, and undoubtedly unsteady, influenced by individual disposals of the animal, environmental conditions, and chemical and diagenetic factors. Moreover, drahomirids offer no variable external shell sculpture available for this purpose.

Specimens studied (measurements in mm).

L 5908C, Text-figs 3, 5, Požáry F., probably Praha-Slivenec, coll. Musei; orig. Horný 1963b.
l. 4.5, w. 3.4, h. 1.5, l:w =1.3
Juvenile specimen, internal mould on surface of a large orthoconic nautiloid; scars A–D weak, others not observable. Outline of shell slightly restored.

L 5908B, Text-fig. 5, Požáry F., probably Praha-Slivenec, coll. Musei; orig. Horný 1963b.
l. 8.4, w. 6.3, h. 3.3, l:w =1.3
Juvenile specimen, internal mould on surface of a large orthoconic



Text-fig. 8. ***Drahomira glaserae*****, L 5854, the holotype of** ***D. rugata*****. a – dorsal view, × 7; b – apical part with radular scars (arrowed, × 15); c – oblique anterior view showing growth structures around scars (× 7); d – waved growth lines near the posterior part of apertural margin, × 16. Note the two migration tracks of the cephalic scar from the apex, indicating its two segments, and fine, irregular striae normal to the lateral part of apertural margin. Požáry F., Karlštejn.**

nautiloid; A scars weak, B–G invisible, weak posterior growth elevations, weak irregular radial grooves and "ribs", locally pores and small depressions.

L 5853, Text-fig. 5, Požáry F., Praha-Velká Chuchle, leg. Bláha.
l. 10.0, w. 9.3, h. 1.0 (strongly depressed), l:w =1.0. Strongly depressed, probably immature specimen in calcareous shale; B–F scars linear, G on posterior elevation.

L 37859, Text-fig. 5, Požáry F., Zone P. transgrediens, Praha-Slivenec, leg. J. Kříž.
l. 10.5, w. 8.8, h. 2.5, l:w =1.2
Juvenile specimen; shell partly exfoliated; internal mould with visible A scars and short ovate-linear, pigmented B–D scars; apical part swollen and slightly separated by a shallow saddle; external shell surface with fine growth threads.

YA 88, Text-figs 5,10, Požáry F., Zone P. transgrediens, Praha-Velká Chuchle, leg. J. Kříž
l. 11.3, w. 9.2, h. 3.1, l:w =1.2
Mature specimen, internal mould with roughly preserved surface; apex above the anterior part of apertural margin; muscle scars not observable; external shell surface with fine regular concentric lirae near the posterior part of apertural margin.

L 5919, Text-fig. 5, Požáry F., Praha-Lochkov, coll. Musei (Barrande?).
l. 11.4, w. 6.0, h. 3.5, l:w =1.2
Immature specimen, internal mould with patches of shell; dorsal scars B–F narrow, almost linear.

L 5908A, Text-fig. 5, Požáry F., probably Praha-Slivenec, coll. Musei; orig. Horný 1963b.
l. 11.5, w. 9.0, h. 3.3, l:w =1.3
Immature specimen, internal mould on surface of a large orthoconic nautiloid; A scars not well visible, with unclear adapically adjacent structures; grain-like frontal scars, B–F scars ovate, weak, short, G scars not well defined, preserved as a median bulge on the posterior growth elevation; mediodorsal furrow between the frontal scars and posterior elevation; lateral and posterior areas with irregular surface.

L 5846, Text-figs 5, 7, the holotype of *D. barrandei*. Požáry F., Praha-Lochkov, coll. Barrande.
l. 12.5, w. 10.5, h. 3.5, l:w =1.2

Text-fig. 9. *Drahomira glaserae*, **L 37862. Two dorsal views, × 5. a – whitened with ammonium chloride, b – not whitened to show pigmented muscle scars. Požáry Fm., Karlštejn.**

Text-fig. 10. *Drahomira glaserae*, **YA 88. Fine outer shell sculpture, about 10 inequal growth lines per mm, × 10. Požáry F., Praha-Velká Chuchle.**

Text-fig. 11. *Drahomira glaserae*, **L 6261. a – dorsal view, × 3.7; b – anterior part with radular scars (arrowed), × 7.4; c – posterior part with typical outer shell sculpture, × 13. Požáry F., Praha-Slivenec.**

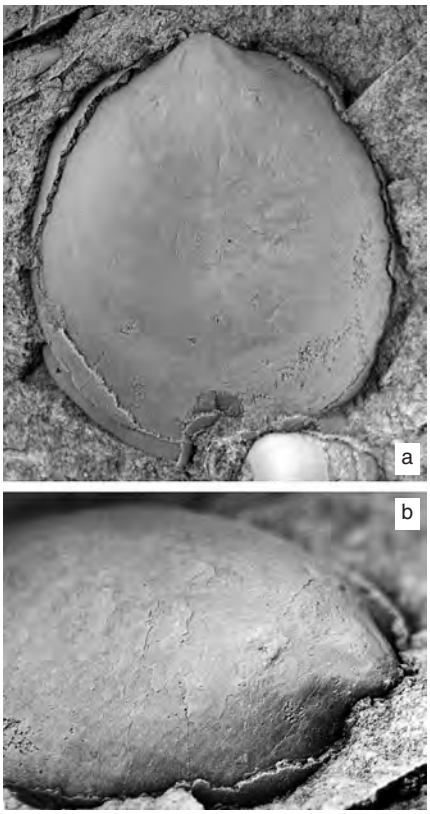
Adult specimen, incomplete internal mould (apical area with scars A and partly B lacking), scars strong, peanut-shaped, with rough surface, often simply indented in outer ends, a small additional scar between G scars; lateral sparsely granular scar zones connected with the A scars; apparent postero-lateral brim is probably due to syndiagenetic deformation.

L 7628, Text-figs 5, 15, Požáry F., Praha-Velká Chuchle, leg. R. Růžička.
l. 12.7, w. 10.2, h. 3.5 (depressed), l:w =1.2
Depressed and partly crushed adult specimen. Between the cephalic A scars and the dorsal B scars groups of small linear elements of radular scars by direction mimetizing the dorsal scars; B–F scars narrow, almost linear, left G scar larger. Weak impressions probably indicating lateral scars. Surface with thin lamellae of dark grey hypostracum.

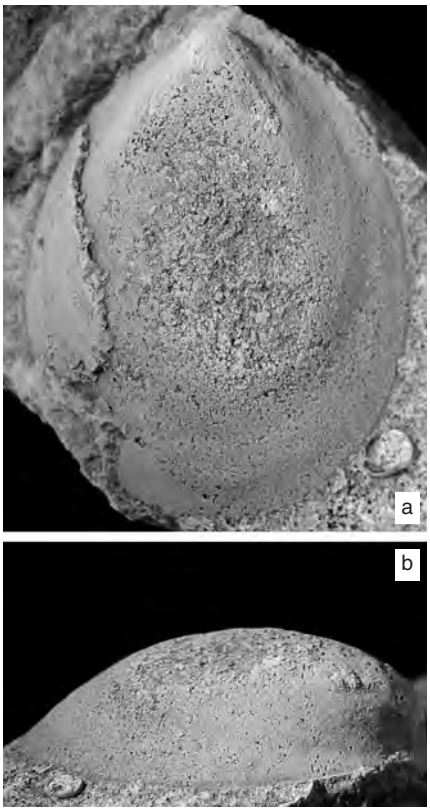
sine (J. Marek), Text-figs 5, 12, Požáry F., Praha-Lochkov, Mramorový lom, leg. J. Marek; orig. Král et *al*. (1998), Košťák (2004).
l. 12.7, w. 11.0, h. 4.5, l:w =1.2
Mature specimen, internal mould partly covered with lamellae of hypostracum and shell; two low ridges between the apex and A scars; shallow axial groove between A and B scars; B–D scars observable, linear; two posterior concentric elevations.

L 37959, Text-figs 5, 13, Požáry F., Suchomasty, Lejškov, leg. R. Horný.
l. 12.8, w. 10.6, h. 4.5, l:w =1.2
Mature specimen, internal mould with roughly preserved dorsal area; rounded A scars weak but present, low ridges between cephalic scars and the apex, a low scar in front of the cephalic scar from which thin wavy threads run posteriorly; dorsal scars n o t observable; two posterior concentric elevations; left side with patch of shell bearing dense, regular growth lines.

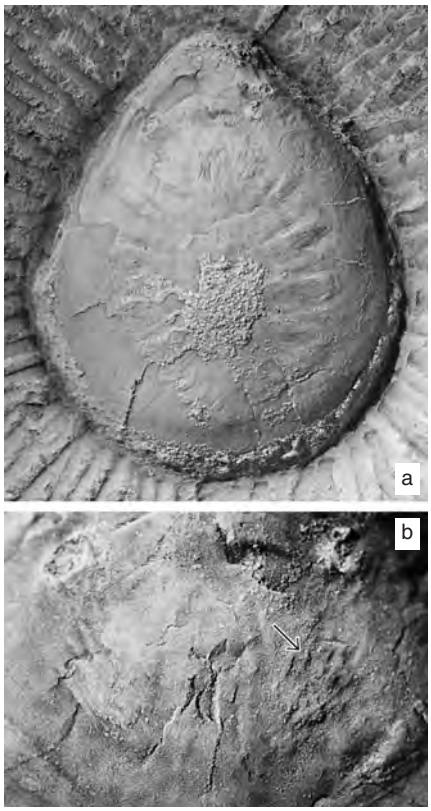
L 37862, Text-figs 5, 9, Požáry F., Zone P. transgrediens, Karlštejn – Třebaňská stráň, leg. R. Horný.
l. 13.0, w. 10.0, h. 3.2, l:w =1.3



Text-fig. 12. ***Drahomira glaserae*, *sine*** **(J. Marek). a – dorsal view, × 4; b – oblique apico-lateral view showing fine, irregular striae running from the apex, × 6. Požáry F., Praha-Lochkov.**



Text-fig. 13. ***Drahomira glaserae*, L 37959. a – dorsal view, × 5; b – right lateral view showing irregular striae running from the apex obliquelly across the mould to the lateral part of apertural margin, × 4. Požáry F., Suchomasty.**



Text-fig. 14. ***Drahomira glaserae*, L 7628. a – dorsal view, × 4.6; b – anterior part with radular scars (arrowed), × 11.5. Požáry F., Praha-Velká Chuchle.**

Mature specimen, incomplete internal mould damaged in anterior part, B–F scars irregularly cuneate, in central parts lineate and pigmented; scars B–F are slightly posteriorly tilted, G scars irregular, posterior concentric elevation close to the apertural margin.

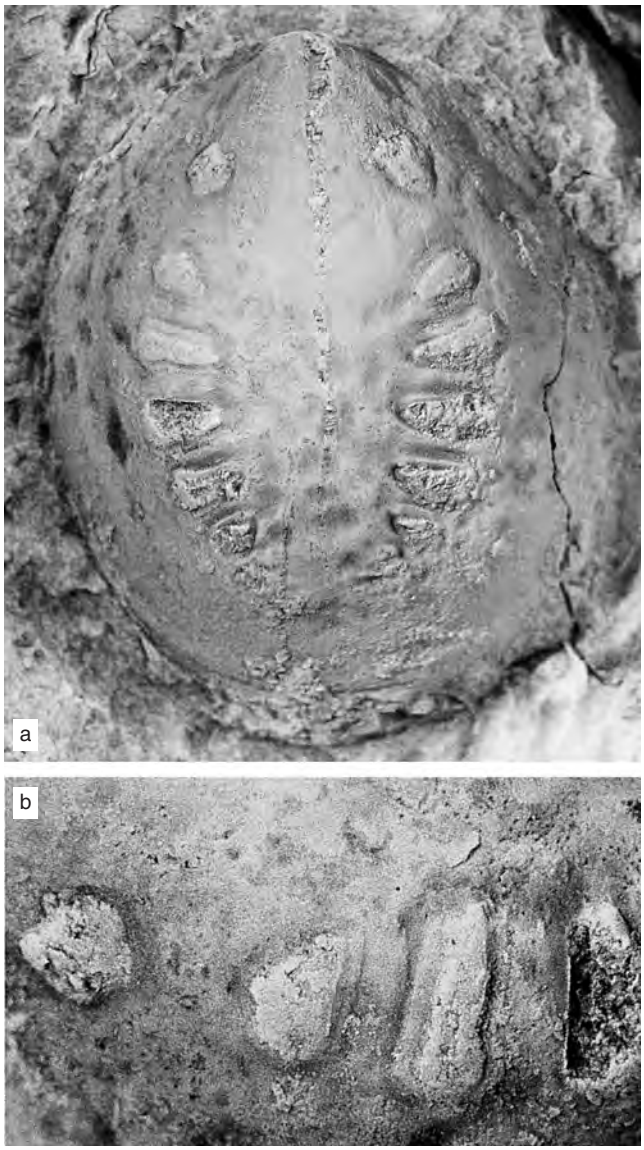
YA90, Text-fig. 5, Požáry F., Zone P. transgrediens, Praha-Velká Chuchle, leg. J. Kříž.
l. 13.5, w. 12.0, h. 4.5, l:w =1.1
Mature specimen with partly exfoliated shell, apex above anterior margin, A scars imperfectly preserved, B–D peanut-shaped, slightly bent, right and left sets of dorsal scars slightly asymmetric. External shell surface with fine concentric striae.

L 9440, Text-fig. 5, Požáry F., Zone P. transgrediens, Karlštejn–Spálený, plot of Mrs Rampas, leg. R. Horný.
l. 13.8, w. 11.2, h. 5.0, l:w =1.2
Internal mould with partly damaged dorsum; frontal scars broken off, apical part slightly separated by a shallow depression or saddle between A scars; low swellings lateral to A scars; a short, low ridge anterolateral to the right A scar; B–F scars cuneate linear, G scars on doubled concentric elevation running around the dorsum to the apex.

L 5852, Text-figs 5, 6, the holotype of *D. glaserae*, Požáry F., Praha-Lochkov, coll. Mrs Glaser/Barrande.
l. 14.0, w. 10.0, h. 4.5, l:w =1.4
Mature specimen, internal mould with postcephalic saddle-like depression, small scar anterolateral to right A, a pair of frontal grain-like scars; B–E scars linear, ray-like; A scars with unclear posterior depressed structures, possibly connected with radular scars and by direction mimetizing ray-like scars (“tadpole tails” of Knight and Yochelson 1960); pronounced posterior growth elevation with irregular G scars; right to the apex dendritic structures which may be connected with pallium (Text-fig. 6e).

L 5911, Text-figs 5, 15, Požáry F., Zone P. transgrediens, Praha-Slivenec, leg. J. Kříž; orig. Horný 1963b.
l. 14.3, w. 12.0, h. 5.2, l:w =1.3
Gerontic specimen, internal mould with asymmetric mirrored depressions adapical to A scars, large radular scars between A and B scars, peanut-form to cuneiform dorsal B–F scars; dorsal area with pores, irregular rounded depressions mainly on the dorsum and lateral sides, scarce grains on the right lateral side.

L 7677, Text-figs 4, 5, Požáry F., Zone P. transgrediens, Praha-Slivenec, leg. J. Kříž.
l 14.5, w 12.0, h 5.0, l:w =1.2
The best preserved, adult specimen, internal mould. Apical part slightly separated by a shallow depression, A scars composed of 2–3 segments, paired mirrored additional anterolateral scars and paired depressions, a pair of small pits near the median line, a pair of grain-like subapical scars, a pair of apical grain-like frontal scars, clusters of radular microscars between A and B by direction mimetizing the dorsal scars, lateral granular zones on first 3/5 of the shell length, running from the A scars; scars B–G peanut-form, G scars small, on growth elevation. A small area of locally preserved vermiculous structure is near the right posterolateral part of apertural margin.



Text-fig. 15. ***Drahomira glaserae*****, L 5911. a – dorsal view, × 6; b – oblique left lateral view showing details of muscle scars and minor pits in the dorsal area to the right, × 12. Požáry F., Praha-Slivenec.**

L 6261, Text-figs 5, 11, Požáry F., Zone P. transgrediens, Praha-Slivenec, leg. J. Kříž.
l. 15.0, w. 11.0, h. 4.4, l:w =1.4
Adult specimen, internal mould with a patch of shell in posterior region; apex shifted posteriorly, with frontal scars and asymmetric pits posterior to them; anterior part of shell slightly separated by a shallow saddle-like depression; groups of radular microscars between A and B scars, connected to A scars; dorsal scars B–F irregular cuneate; low, irregular depressions on the dorsum between D-F scars; in the centre of dorsum fine, partly radially arranged granulation somewhat similar to that in *Kosovina peeli* HORNÝ, 2004 (Horný 2004, Pl. 2, fig. 2).

L 5854, Text-figs 5, 8, the holotype of *D. rugata*. Požáry F., probably Zone P. transgrediens, Karlštejn, coll. Musei.
l. 15.0, w. 12.4, h. 4.5, l:w =1.2
Mature, incomplete specimen with apex broken off, internal mould with patches of shell along the margin; A scars with traces of migration from the apex, cluster of radular microscars posterior to the left A scar, B–F scars cuneate, mostly slightly bent, G scars almost invisible, concentric posterior elevation weak; dorsum transversely strongly arched; outer shell surface in the posterior area slightly wavy, with fine dense growth lines crossed with scarce, weak, fine radial threads.

YA 89, Text-fig. 5, Požáry F., Zone P. transgrediens, Praha-Velká Chuchle, leg. J. Kříž.
l. 15.5, w. 14.0, h. 5.0, l:w =1.1
Mature specimen, internal mould with a pathology depression in central part of the shell; unclear raised axial structure between A scars; additional scar anterolaterally close to the right A scar; scar B–E observable, cuneiform-linear; two posterior concentric elevations.

Drahomira kriziana sp. n.

(Text-figs 16–19)

1963b *Drahomira* aff. *rugata* (PERNER, 1903); R. Horný, Nové nálezy etc., p. 83, 84, Text-figs 5–7.

Holotype: Specimen NM L 6113, figured here on Text-figs 16, 17.

Stratum typicum: Silurian, Ludlow, Gorstian, Kopanina Formation, Zone C. colonus.

Type locality: Praha-Jinonice, Na břekvici; Barrandian Area, Bohemia, Czech Republic.

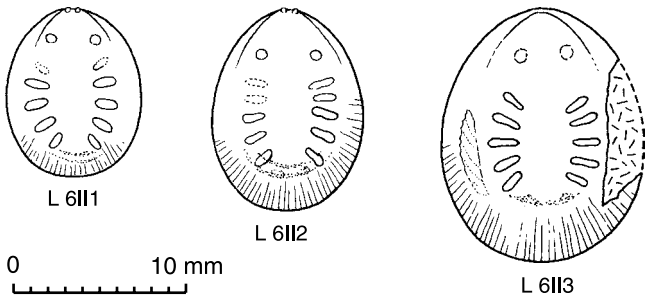
Derivatio nominis: In honour of Jiří Kříž, specialist in Lower Palaeozoic bivalves, who collected the majority of *Drahomira* specimens.

Material: three specimens and a fragment.

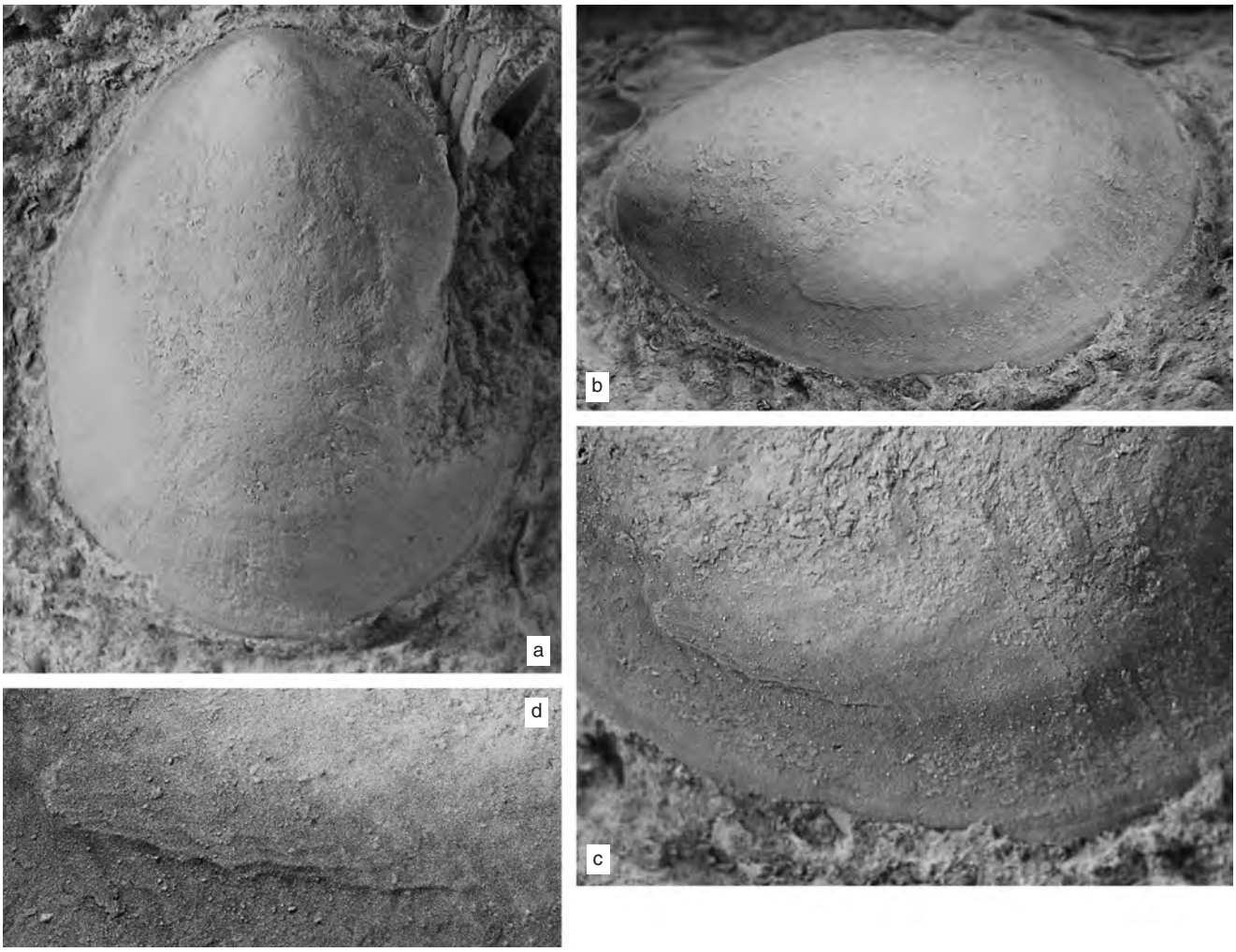
Diagnosis. Species of the genus *Drahomira* with low shell, wide and blunt apex, and densely radially striated posterior area of internal mould.

Description. All three described specimens are preserved as internal moulds in dark grey bituminous cephalopod limestone with numerous fragments of orthoconic nautiloids. They come from typical flat limestone concretions accumulated at the interface of grey shales and base of a local effusive body of basaltoids.

Shell morphology. Small patches of spoon-like shell adhere to counterparts; the shell is 0.1–0.2 mm thick and on the external surface bears weak, simple, inequal lines of growth (see Horný 1963b, fig. 7). The dorsum of internal moulds is shallowly convex between the apex and the posterior margin. The apertural margin is planar, without



Text-fig. 16. ***Drahomira kriziana.*** **Line drawings of all specimens studied, arranged according to length (descriptions on p. 65, 66).**



Text-fig. 17. ***Drahomira kriziana*****, L 6113, the holotype. a – dorsal view, × 6; b – oblique left lateral view, × 5.7; c – extent and surface of the lateral scar, × 10; d – enlarged anterior part of the lateral scar with oblique increments and waved adapertural margin, × 18. Kopanina F., Praha-Jinonice.**

emarginations. Apex of moulds is low, blunt, wide, located above or not reaching the anterior part of apertural margin. The surface of moulds bears dense, fine, radial ribs running from the apex, abundant particularly in the posterior area and present even on the surface of lateral and dorsal scars. Similar sculpture of internal mould is characteristic for the Ordovician *Bipulvina croftsae* YOCHELSON, 1958. These ribs are normal to the right lateral part of the apertural margin in specimen L 6112. The l:w ratio varies between 1.2 and 1.3.

Muscle scars. Two small frontal, grain-like scars are on the top of the mould of apex. The cephalic scars (A) are rounded, without observable details; radular scars between A and B have not been observed. The dorsal scars B–F are well developed, linear or narrowly elliptic, often finely black pigmented, arranged radially to the centre of the shell. The posterior scars G are not sharply delimited, located at the posterior, raised, concentric structure. Lateral scars are located at a swollen zone between the distal ends of dorsal scars and apertural margin. Best preserved, about 4 mm long and 0.8 mm wide, continuous scar with sharp lines of growth, is preserved on the left side of the holotype (Text-figs 6, 17).

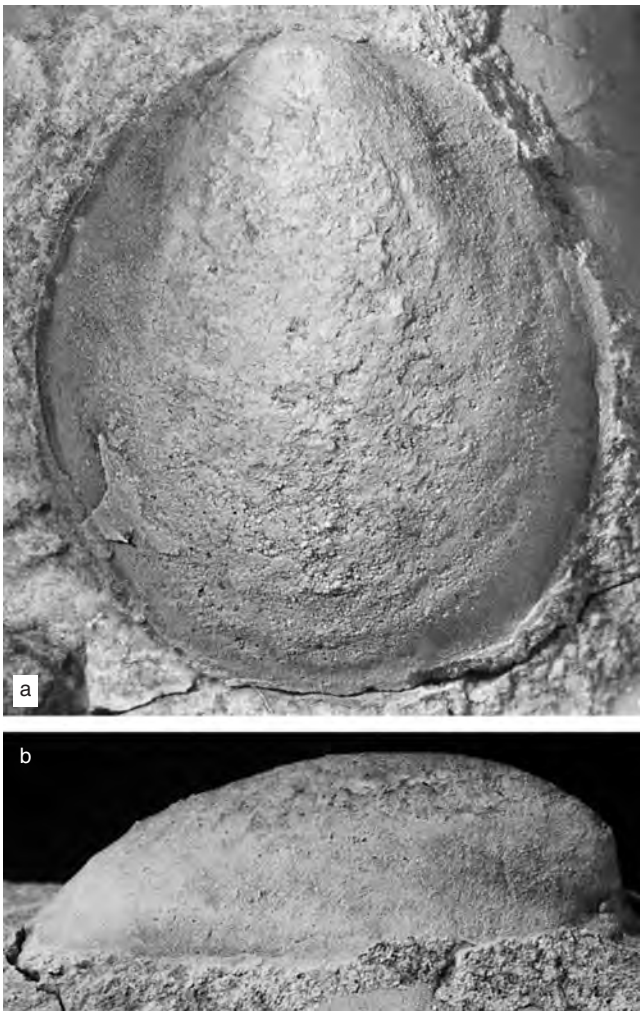
Discussion. Horný (1963b) held an opinion that this taxon was closely related to *D. rugata*. After the present study which enabled the comparison with more than 20 specimens of the Pridolian *D. glaserae* (which includes *D. rugata*), it is evident that this stratigraphically distant Gorstian taxon represents a separate species. It is distinguished chiefly by lower and wider apex, dense radial striation of the mould surface, and development of continuous lateral muscle scars.

Specimens studied (measurement in mm).

L 6111, Text-figs 16, 17, paratype of *D. kriziana*, Kopanina F., Zone C. colonus, Praha-Jinonice, leg. Horný and Kříž; orig. Horný (1963b). l. 9.5, w. 7.5, h. 3.5, l:w =1.3

Immature specimen, internal mould with weathered surface, apex low, wide, blunt, not overhanging the anterior part of apertural margin, frontal scars distinct, A scars weak, B–F scars narrowly elliptic with linear carbon pigmentation, G scars weak, located on doubled concentric elevation, close to the posterior margin; dense radial striation in posterior area.

L 6112, Text-figs 16, 18, paratype of *D. kriziana*, Kopanina F., Zone C. colonus, Praha-Jinonice, leg. Horný and Kříž; orig. Horný (1963b).



Text-fig. 18. ***Drahomira kriziana*****, L 6111. a, b – dorsal and right lateral views, × 9.3, × 8.5 . Kopanina F., Praha-Jinonice.**

l. 11.3, w. 8.6, h. 4.5, l:w =1.3
Probably immature specimen, internal mould, apex low, blunt, slightly overhanging, frontal scars distinct, B–F scars linear, the left F scar indistinct, posterior scars indistinct, dense radial striae in posterior area, raised narrow axial rib in posterior half of the shell, well developed posterior concentric elevation.

L 6113, Text-figs 16, 19, holotype of *D. kriziana*, Kopanina F., Zone C. colonus, Praha-Jinonice, leg. Horný and Kříž; orig. Horný (1963b).
l. 14,3, w. 11.5, h. 4.5, l:w =1.2
Mature specimen, incomplete internal mould, apex blunt, not reaching the anterior part of the apertural margin, frontal scars not preserved, A scars weak, with shallow anterolateral depressions, dorsal B–F scars linear, pigmented, G scars weak, located on concentric elevation; left lateral scar distinct, with adapertural increments, dense radial striation in posterior and lateral areas including the lateral scar, shallow circummarginal groove along the anterior part of the apertural margin.

Drahomiridae gen. et sp. indet.

(Text-figs 20, 21)

Description. Specimen L 37861. Small, flat, probably adult specimen, preserved as an internal mould. Apex is

Text-fig. 19. ***Drahomira kriziana*****, L 6112. Dorsal view, × 9. Kopanina F., Praha-Jinonice.**

low, positioned above the anterior part of apertural margin, and bears two grain-like frontal scars. Each cephalic A scar is substituted by a group of four small, inequal, linear-oblong, axially oriented scars. Posterolaterally from this group runs out fine striated structures, oriented to the lateral scar, which is, however, not preserved. The dorsal scars B–E are oblong, arranged radially to the centre of shell; the F pair consists of scars almost parallel to the axis, and the G scars are irregular, positioned on the posterior incremental structure. The lateral scars are not observable. The surface of the mould bears fine, sparse radial ribs. l. 9.0, w. 6.5, h. 2.5, l:w = 1.4.

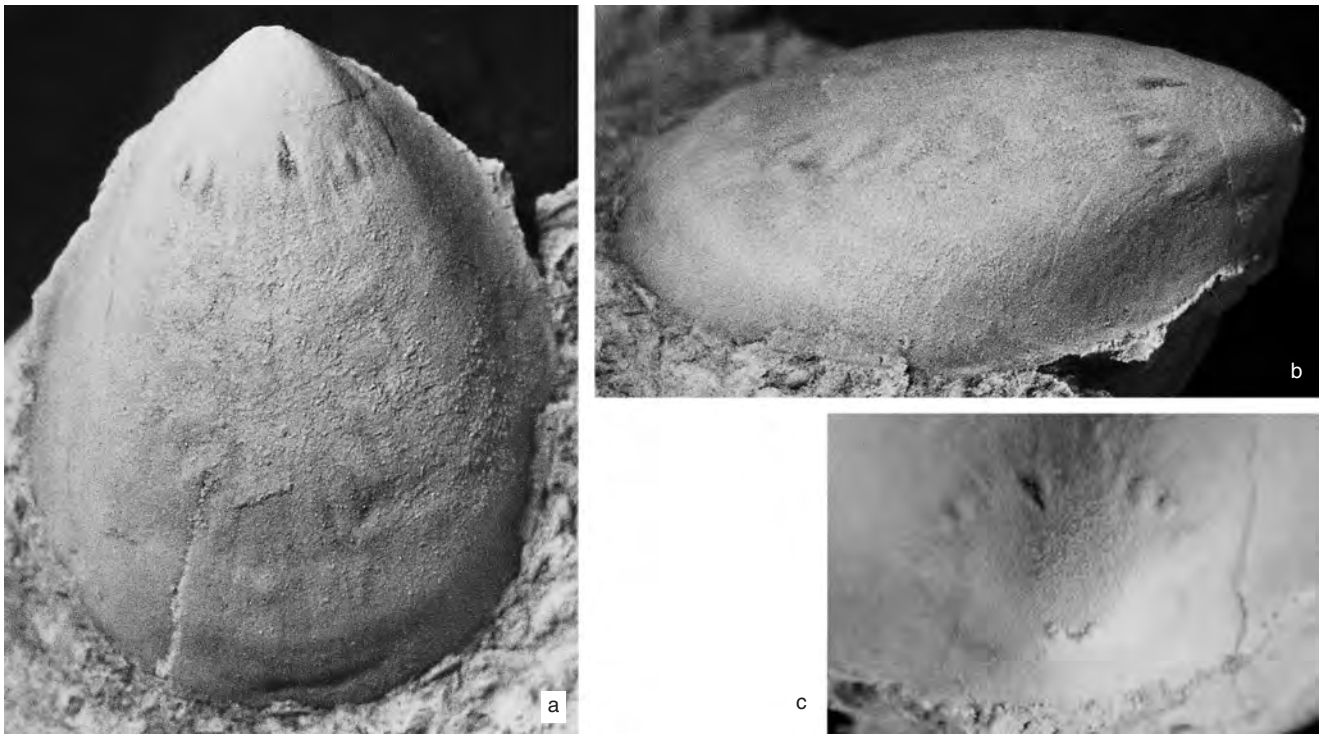
Morphology of the cephalic A scars is unique among all collected specimens of the family. The general shape of the shell is closer to *D. glaserae.*

The specimen was collected by J. Kříž in the basal parts of the Požáry Formation (Přídolí, graptolite Zones M. parultimus – M. ultimus), in the small collectors' quarry "Ortocerový lůmek", Praha-Lochkov.

Pragamira HORNÝ, 1995

Type species: *Drahomira perlonga* HORNÝ, 1963. Silurian, Přídolí, Požáry Formation; Barrandian Area, Bohemia, Czech Republic.

Diagnosis. Genus of the Family Drahomiridae. Shell small, narrow, apex overhanging the anterior part of apertural margin; posterior G scars elongate, parallel with the shell axis; lateral sides steep, swollen; lateral scars long, band-like, originating near the cephalic A scars and tapering posteriorly.



Text-fig. 20. Unidentified drahomirid, L 37861. a – dorsal view, × 10; b – oblique right lateral view, × 10; c – oblique frontal view, × 12. Požáry F., Praha-Lochkov.

Discussion. The holotype of *P. perlonga* and originally the only specimen available, is a well preserved internal mould but lacks the lateral scars. Following the main generic characters, four other specimens have been added, two of them with excellently preserved lateral scars. All have overhanging apices and steep lateral sides, posterior G scars are not observable. Radular scars have not been observed. More material is needed to clarify the relationship with *Drahomira* and the unidentified specimen L 37861.

Species. *Pragamira perlonga* HORNÝ, 1963; Silurian, Přídolí, Czech Republic.

Pragamira perlonga (HORNÝ, 1963)

(Text-figs 21–25)

1963b *Drahomira perlonga* HORNÝ; R. Horný, Nové nálezy etc., p. 84–87, Text-figs 8–10.

1995a *Pragamira perlonga* (HORNÝ, 1963); R. Horný, *Pragamira* etc., p. 61, 62, Text-fig. 1.

Holotype. Specimen L 37960, figured here on Text-figs 21, 22.

Stratum typicum. Silurian, Přídolí, Požáry Formation.

Type locality. Praha-Velká Chuchle, Barrandian Area, Bohemia, Czech Republic.

Material. 5 specimens.

Diagnosis. See the genus.

Description. All specimens are preserved as internal moulds in dark grey bituminous cephalopod limestone with numerous fragments of orthoconic nautiloids.

Shell morphology. The shell is small (9.2–11.0 mm), narrow (6.5–8.0 mm), spoon-shaped, l:w ratio = 1.3–1.5. Small patches of shell are preserved in specimens L 37860 and L 7675. The shell wall is 0.10–0.15 mm thick and on external surface bears weak, simple, inequal lines of growth. The dorsum of the internal mould is shallowly convex between the apex and the posterior part of apertural margin. The apex is narrow, overhanging the anterior part of apertural margin. Lateral sides are steep, almost perpendicular to plane of the aperture.

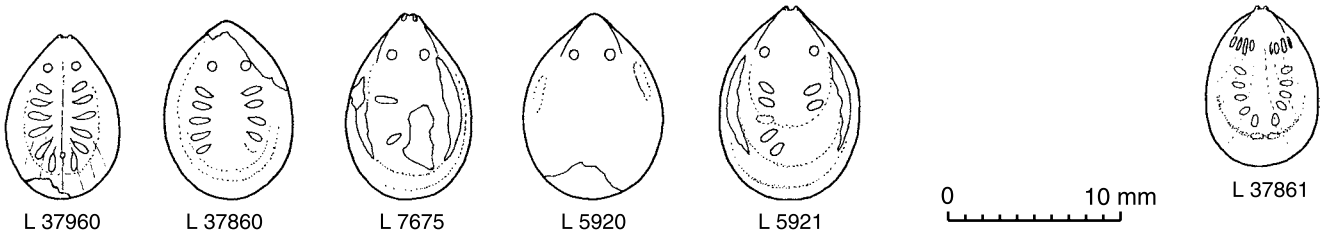
Muscle scars. The holotype, which is the best preserved specimen, shows all seven pairs of main retractor scars, arranged similarly as in *Drahomira.* The addorsal ends of the dorsal B–F scars are thin and bent anteriorly. The posterior G scars are elongate and parallel to the shell axis. Radular scars have not been ascertained. Lateral scars are located close to the distal ends of the dorsal scars.

Discussion. See the genus.

Specimens studied (measurement in mm).

L 37960, Text-figs 21, 22, the holotype of *P. perlonga*, Požáry F., Praha-Velká Chuchle, coll. Barrande; orig. Horný (1963b, 1995a).
l. 9.2, w 6.5, h 3.5, l:w = 1.4
Mature specimen, internal mould; well preserved frontal scars, D-G scars with thin, adapically bent internal ends, G scars elongate, parallel with axis, growth elevation well developed; median grain between the anterior ends of G at the long median rib; both lateral sides of shell slightly swollen; lateral scars not visible; the right and left sets of A–C scars asymmetric.

L 37860, Text-figs 21, 23, Požáry F., Zone P. transgrediens, Karlštejn – V Krabině, plot of the Pospíšil family, isolated limestone boulder in Quaternary deposit, leg. R. Horný.



Text-fig. 21. ***Pragamira perlonga*****. Line drawings of all specimens studied, arranged according to length (descriptions on p. 67, 68). The unidentified drahomirid L 37861 is added.**

l. 9.0, w. 7.2, h. 2.8, l:w = 1.3
Mature specimen, internal mould with patch of shell in anterior region; a low, slightly bent ridge anterolateral to the left A scar; shallow depressions between A and B scars, G scars not observable, lateral slopes below scars steep, posterior concentric elevation close to the scars. The specimen may belong to *Drahomira glaserae.*

L 7675, Text-figs 21, 24, syntype of *Mytilus buridani* BARRANDE, 1881, Požáry F., Praha-Lochkov, coll. Barrande.
l. 10.5, w. 7.0, h. 3.5, l:w = 1.5
Mature specimen, internal mould with patches of shell in posterodorsal area; frontal scars well preserved; dorsal scars poorly visible; well preserved large lateral scars; the central part of the dorsum partly crushed, probably syndiagenetically; the right cephalic scar overlain with a fragment of shell layer with radial structure; fragments of shell in posterodorsal area with fine concentric striae.

L 5920, Text-fig. 21, Požáry F., Praha-Lochkov, coll. Musei (Barrande?).
l. 10.5, w. cca 8.0, h. 3.6, l:w = 1.3
Mature specimen, internal mould with rough surface, dorsal muscle scars not observed; lateral sides almost perpendicular, swollen; residua of large lateral scars.

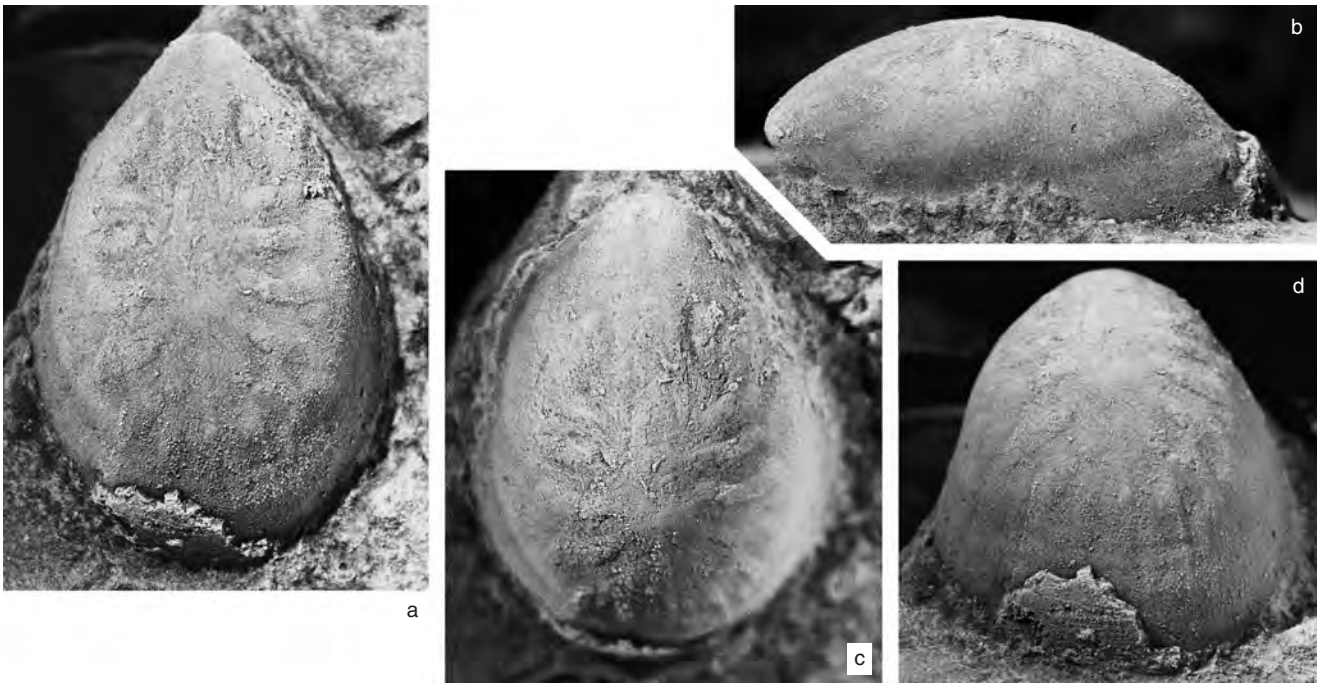
L 5921, Text-figs 21, 25, probably Požáry F., Praha-Lochkov, coll. Musei (Barrande?).
l. 11.0, w. 8.0, h. 4.0, l:w = 1.4
Mature specimen, internal mould; apex with two frontal scars; fine granulation posterior to A scars; shallow depressions in front of the cephalic scars, the left cephalic scar obliterated with hypostracum layer with radial ribs; elliptic to linear dorsal scars weak; long and well preserved lateral scars; two or three concentric growth structures.

Archaeopraga HORNÝ, 1963 (emend.)

Type species. *Helcionopsis pinnaeformis* PERNER, 1903. Silurian, Přídolí, Požáry Formation; Barrandian Area, Czech Republic.

Diagnosis (emend.). Genus of the Family Drahomiridae. Shell large, flat, with apex above the anterior part of apertural margin; protoconch rounded; a pair of composite cephalic scars, followed by radular scars; five sets of bilaterally symmetrical, elongate, flat scars; a pair of large, lateral scars.

Discussion. Perner (1903) placed this species, because of the radial rib-like structures on the internal mould

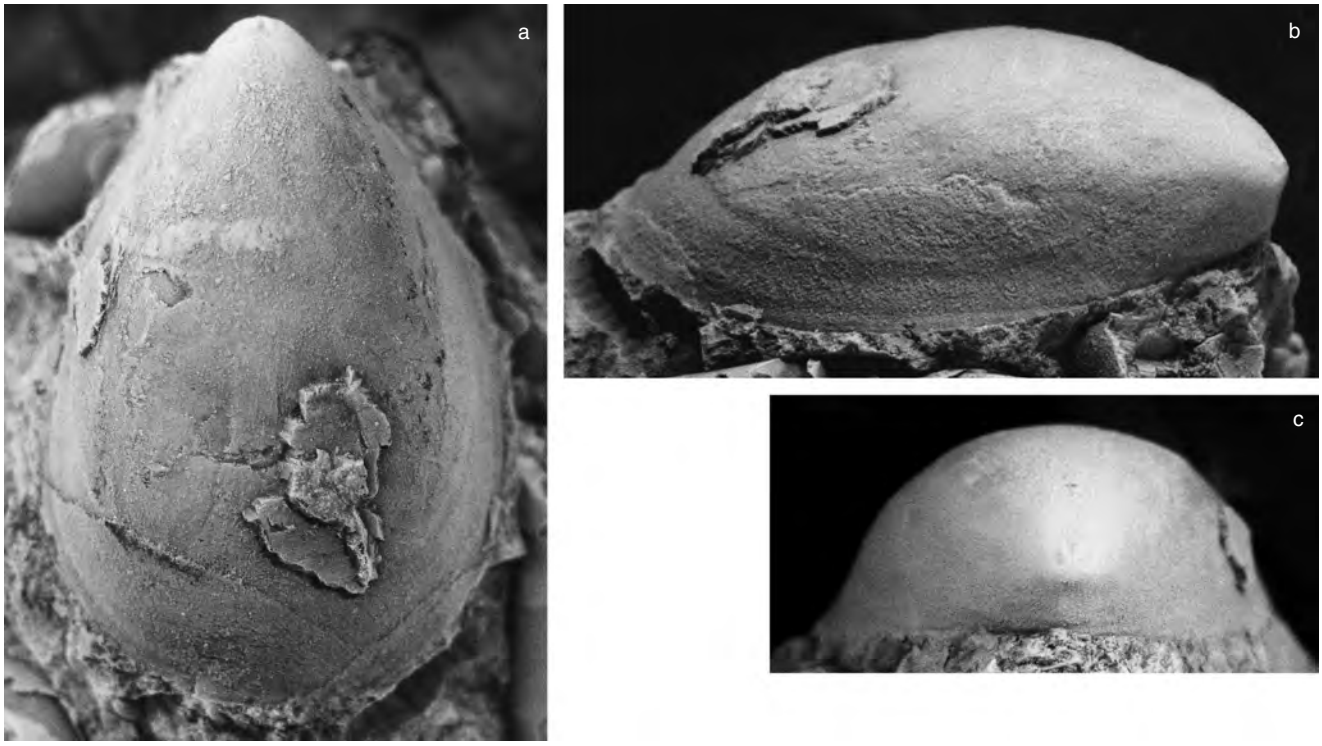


Text-fig. 22. ***Pragamira perlonga*****, L 37960, the holotype. a – dorsal view, × 7.4, b – left lateral view showing swollen lateral side, × 7; c – oblique apico-dorsal view, × 7.4; d – posterior view, × 7.4. Požáry F., Praha-Velká Chuchle.**

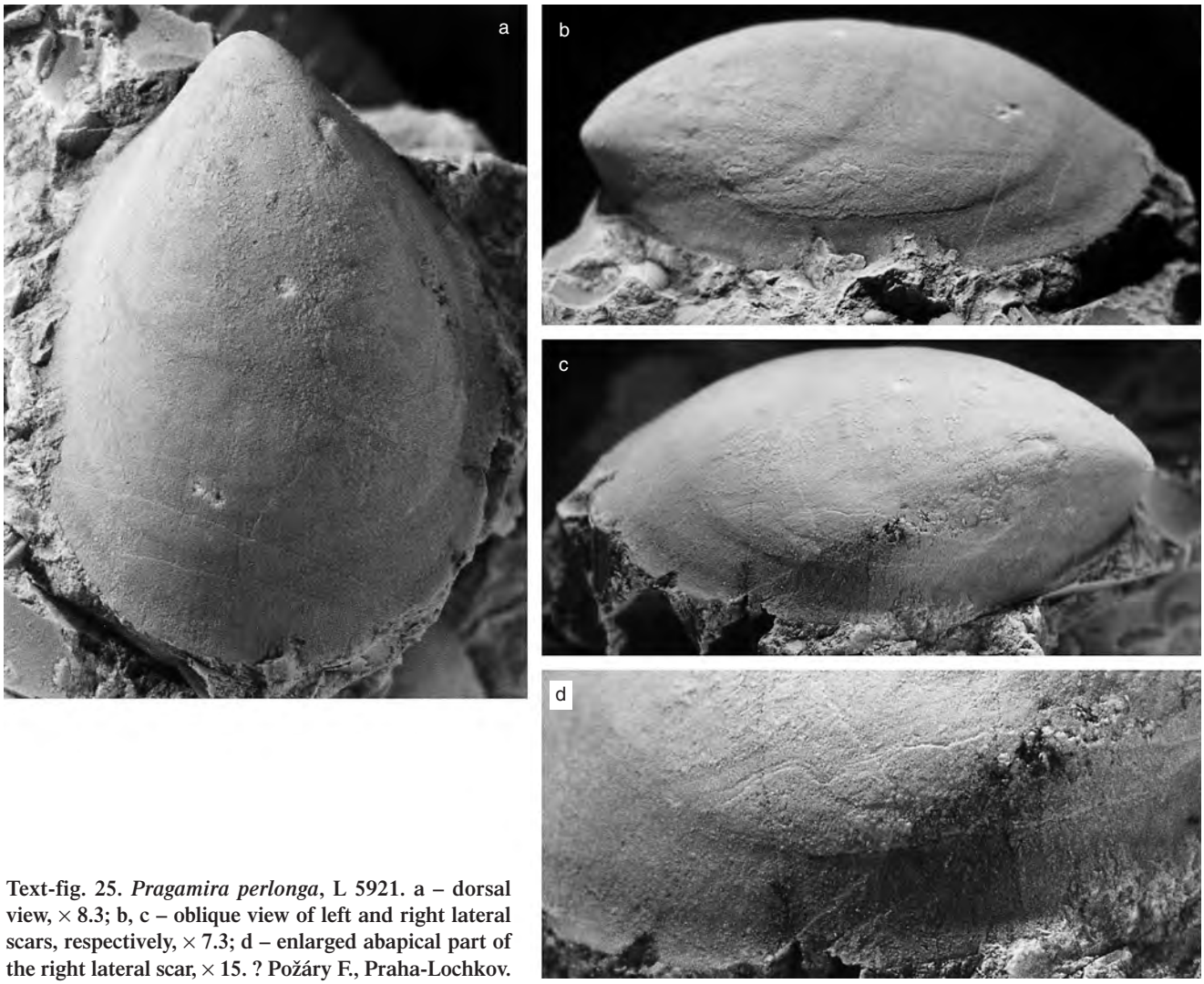
surface, in *Helcionopsis* ULRICH et SCOFIELD, 1897. On his Text-fig. 12 on p. 39 he figured this species as having seven small, rounded scars in the centre of the dorsum. Horný (1961, published in 1963a) did not find the specimen in the collections of the Department of Palaeontology, expressed doubts about the "scars" and the systematic position of this fossil and did not include it into his Lower Palaeozoic Monoplacophora. Fortunately in 1962 the supposedly lost specimen was found, and another specimen of this species was discovered in the old collections of the National Museum showing excellently preserved, large lateral muscle scars. Horný (1963c) interpreted this fossil as a new problematic genus of monoplacophoran molluscs and established a new monotypic genus *Archaeopraga* with a new Family Archaeopragidae. Yochelson (1967) regarded *Archaeopraga* as a monoplacophoran with a single pair of scars, and in 1978 commented this genus as a monoplacophoran with extremely reduced number of paired scars, which "one tends to ignore...". Starobogatov (1970) considered this genus to be a gastropod. Harper and Rollins (1982) regarded *Archaeopraga* a tergomyan monoplacophoran with fused muscles, resulting in a single pair of elongate scars. Peel and Horný (2000) speculated about *Archaeopraga* as a morphologically more advanced state than the Ordovician archinacellids; however they retained the Family Archaeopragidae to include this genus.

The two new specimens of *Archaeopraga pinnaeformis* (one of them even a syntype of Barrande's bivalve species *Mytilus buridani* BARRANDE, 1881) have, besides incomplete lateral scars, also drahomirid muscle scar pattern and

Text-fig. 23. ***Pragamira* cf.** ***perlonga*****, L 37860. Dorsal view of a specimen, which may be a small** ***D. glaserae*****, × 10.6. Požáry F., Karlštejn.**



Text-fig. 24. ***Pragamira perlonga*****, L 7675. a – dorsal view, × 9; b – oblique right view with well-preserved lateral muscle scar showing increments, × 9; c – frontal view showing steep lateral sides and frontal grain-like scars, × 9. Požáry F., Praha-Lochkov.**



Text-fig. 25. ***Pragamira perlonga*****, L 5921. a – dorsal view, × 8.3; b, c – oblique view of left and right lateral scars, respectively, × 7.3; d – enlarged abapical part of the right lateral scar, × 15. ? Požáry F., Praha-Lochkov.**

undoubtedly confirm the systematic position of *Archaeopraga* among the tergomyan molluscs. The lateral muscles of drahomirids are probably not homologic with the anterolateral muscles of *Archinacella* ULRICH et SCOFIELD, 1897, *Barrandicella* PEEL et HORNÝ, 1999 and other related genera. In these genera they may have functioned as retractors similarly as in the bellerophontoidean gastropods. In drahomirids they served to enhance clamping and balance on cephalopod shells. According to Peel and Horný (1999), similar reason can be advanced to explain the formation of horseshoe-shaped muscle scars in *Archinacella*, *Archinacellina* HORNÝ, 1961 and *Archinacellopsis* HORNÝ, 1995. Origin of the large muscles leaving long continuous scars in *Archaeopraga* is unclear and in tight connection with metameric tryblidioidean scars is paradoxical. Moreover, its position close to the shell periphery brings problems to restore the location of gills and space for water currents.

Species. *Archaeopraga pinnaeformis* (PERNER, 1903). Silurian, Přídolí, Czech Republic.

Archaeopraga pinnaeformis (PERNER, 1903)

(Text-figs 26–32)

1881 *Mytilus Buridani* BARR. (partim); J. Barrande, Systême silurien etc., 6, expl. Pl. 212, figs VI/3–5.

1903 *Helcionopsis pinnaeformis* PERNER; J. Perner, Gastéropodes, 1, p. 39, Text-fig. 12, Pl. 40, figs 21–22.

1963c *Archaeopraga pinnaeformis* (PERNER, 1903); R. Horný, A new problematic genus etc., p. 171–173, Pl. 144, Text-fig. 1.

1982 *Archaeopraga pinnaeformis* (PERNER); J. A. Harper and H. B. Rollins, Recognition of Monoplacophora etc., Text-fig. 1, p. 228.

1999 *Archaeopraga pinnaeformis* (PERNER, 1903); J. S. Peel and R. J. Horný, Muscle scars and systematic position etc., p. 112, Text-figs 13A, B.

Holotype. NM L 29423, figured here on Text-figs 27, 32.

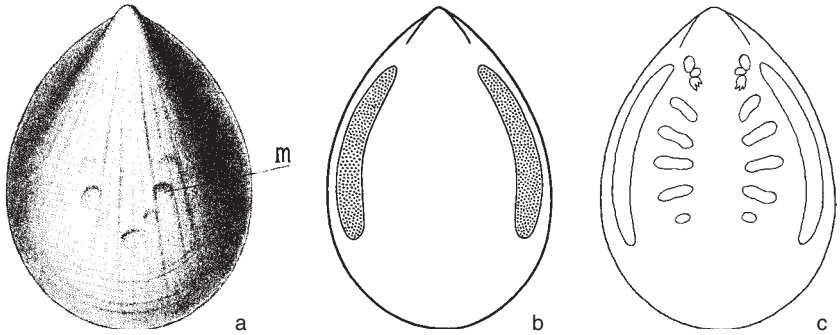
Stratum typicum. Silurian, Přídolí, Požáry Formation.

Type locality. Praha-Podolí, Dvorce, Barrandian Area, Bohemia, Czech Republic.

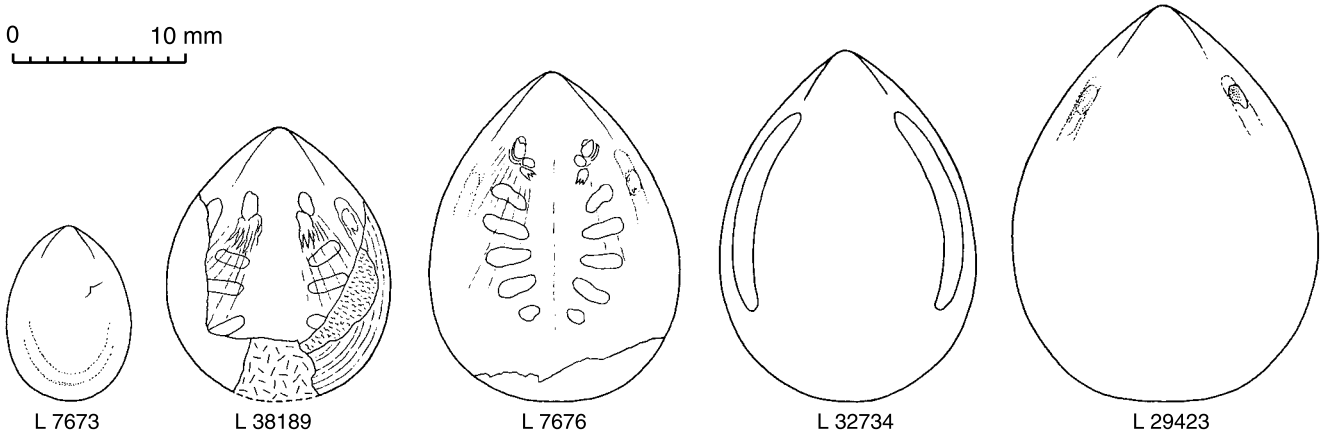
Material. 5 specimens.

Diagnosis. See the genus.

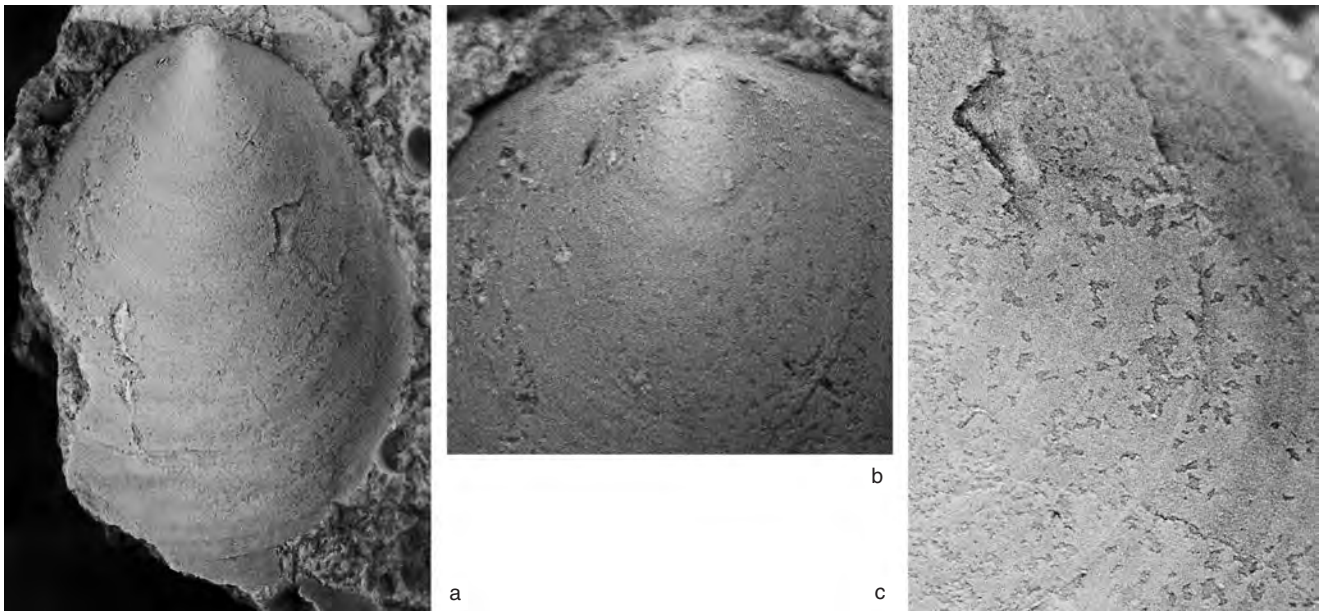
Description. All specimens come from dark grey bi-



Text-fig. 26. ***Archaeopraga pinnaeformis*****. a – figured by Perner 1903, fig.12, p. 39, with seven rounded dorsal muscle scars, after the holotype L 29423; b – figured by Horný 1963c, after the holotype and specimen L 32734; c – current restoration, after the holotype and specimens L 32734 and L 7676.**



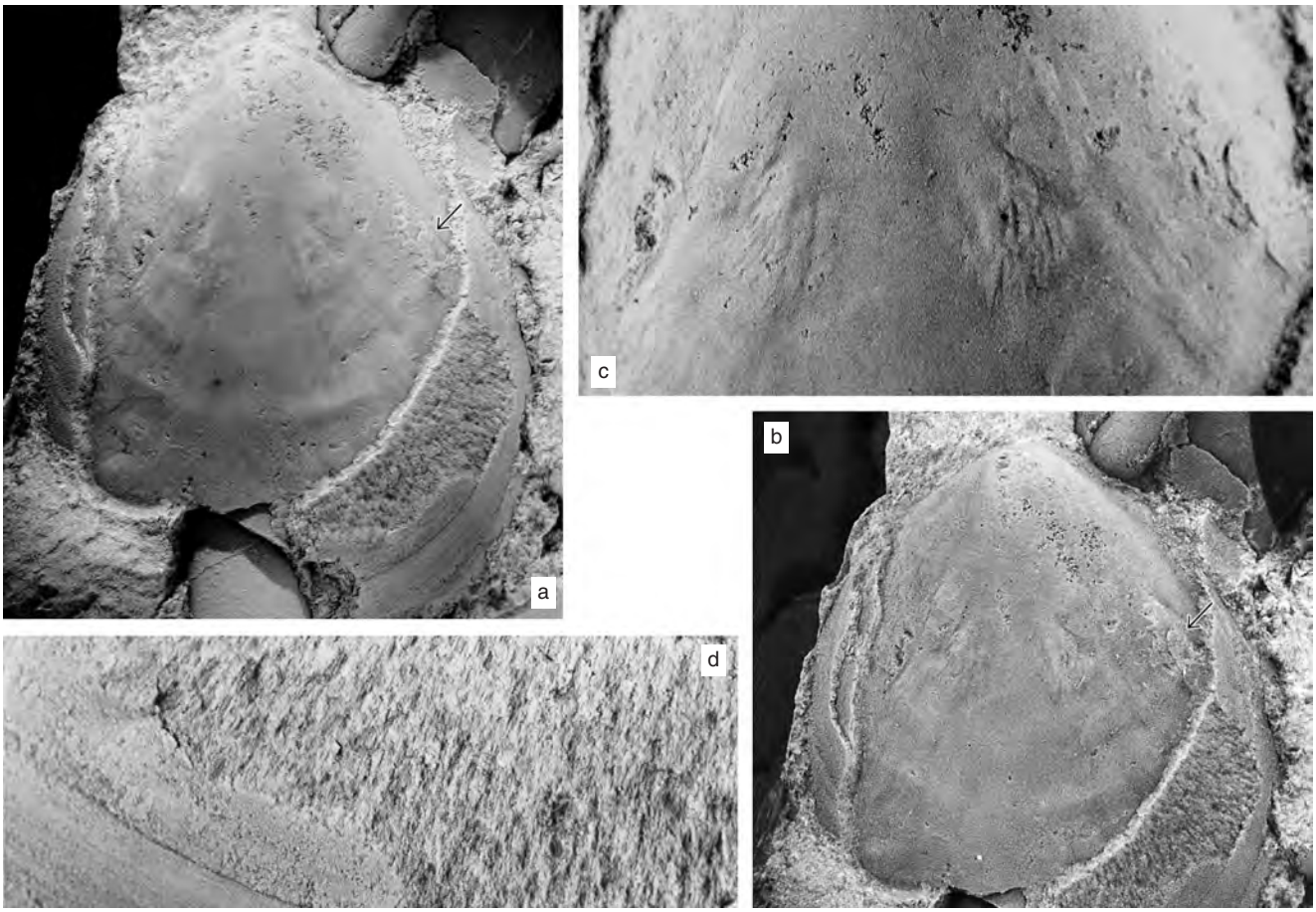
Text-fig. 27. ***Archaeopraga pinnaeformis*****. Line drawings of all specimens studied, arranged according to length (descriptions on p. 72–74).**



Text-fig. 28. ***Archaeopraga pinnaeformis*****, L 7673. a – dorsal view, × 6; b – apical area with protoconch, × 18; c – enlarged right area with a small, repaired, V-shaped marginal injury, × 15. Požáry F., Praha-Lochkov.**

tuminous cephalopod limestone with fragments of orthoconic nautiloids, bivalves and other benthic fauna.

Shell morphology. Shell is preserved in the juvenile specimen L 7673 and the adult specimen L 32734. Imperfectly preserved protoconch in L 7673 is spherical, about 0.8 mm across (Text-fig. 28b). External surface of the flat



Text-fig. 29. ***Archaeopraga pinnaeformis*****, L 38189. a, b – dorsal views in different lighting. A part of the right lateral scar arrowed, × 4.2; c – enlarged anterior area with cephalic and radular scars, × 8.5; d – two-layered shell with partly exposed fibrous structure, × 12. Požáry F., Praha-Lochkov.**

juvenile specimen bears fine, dense, inequal lines of growth, combined with even weaker radial structures. A small, V-shaped, repaired injury originated during the ontogeny in posterolateral part of the apertural margin. Shell wall of adult specimens is 0.4–0.5 mm thick. Shell of the adult specimen L 32734 is poorly preserved, probably recrystallized. A part of shell preserved in the posterolateral area of specimen L 38189 shows two layers, the inner with fine, radially arranged fibrous structure. The dorsum is almost flat between the apex and posterior apertural margin. The aperture margin is planar, without emarginations and without a brim. The apex is located above the anterior part of the apertural margin. The surface bears sparse, imperfectly defined radial ribs running from the apex. The l:w ratio (apart from the probably pathologic specimen L 38189) is 1.4.

Muscle scars. The top of the apex is either covered with shell or slightly damaged so that the frontal scars are not observable. The cephalic group of scars consists of several attachments including the radular scar. Only six pairs of dorsal scars were ascertained. The large lateral muscle scars are located along all sets of scars between their distal ends and the apertural margin. The specimen L 38189, shorter than the other four specimens, may have lived in specific conditions (limited size of a substrate?) and probably had even a smaller number of dorsal scars.

Specimens studied (measurement in mm).

L 7673, Text-figs 27, 28, probably basal parts of the Požáry F., Zones M. parultimus – M. ultimus, Praha-Lochkov, Orthoceras quarry; leg. V. Turek.

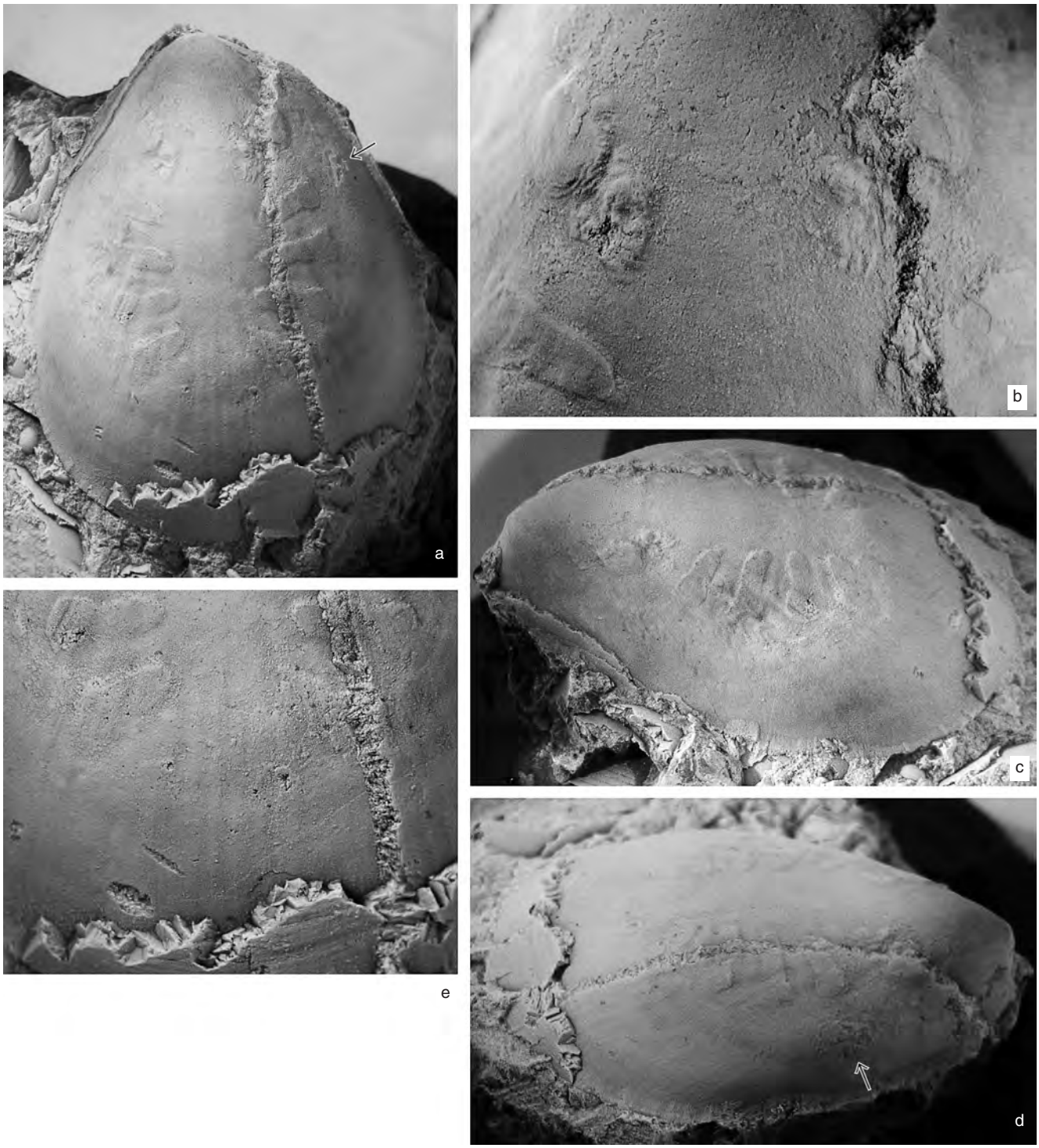
l. 12.6, w. 8.8, h. 2.0, l:w =1.4

Immature specimen with preserved shell; protoconch rounded, symmetrical, without visible sculpture, locally corroded, diameter about 0.8 mm; external shell sculpture with fine concentric lines, slight radial rib-like structures; local small V-shaped marginal injury during ontogeny in the right side; low concentric growth elevations in the posterior area.

L 38189, Text-figs 27, 29, Požáry F., probably Karlštejn, coll. Musei.

l. 19.4, w. 15.6, h. 4.5, l:w =1.2

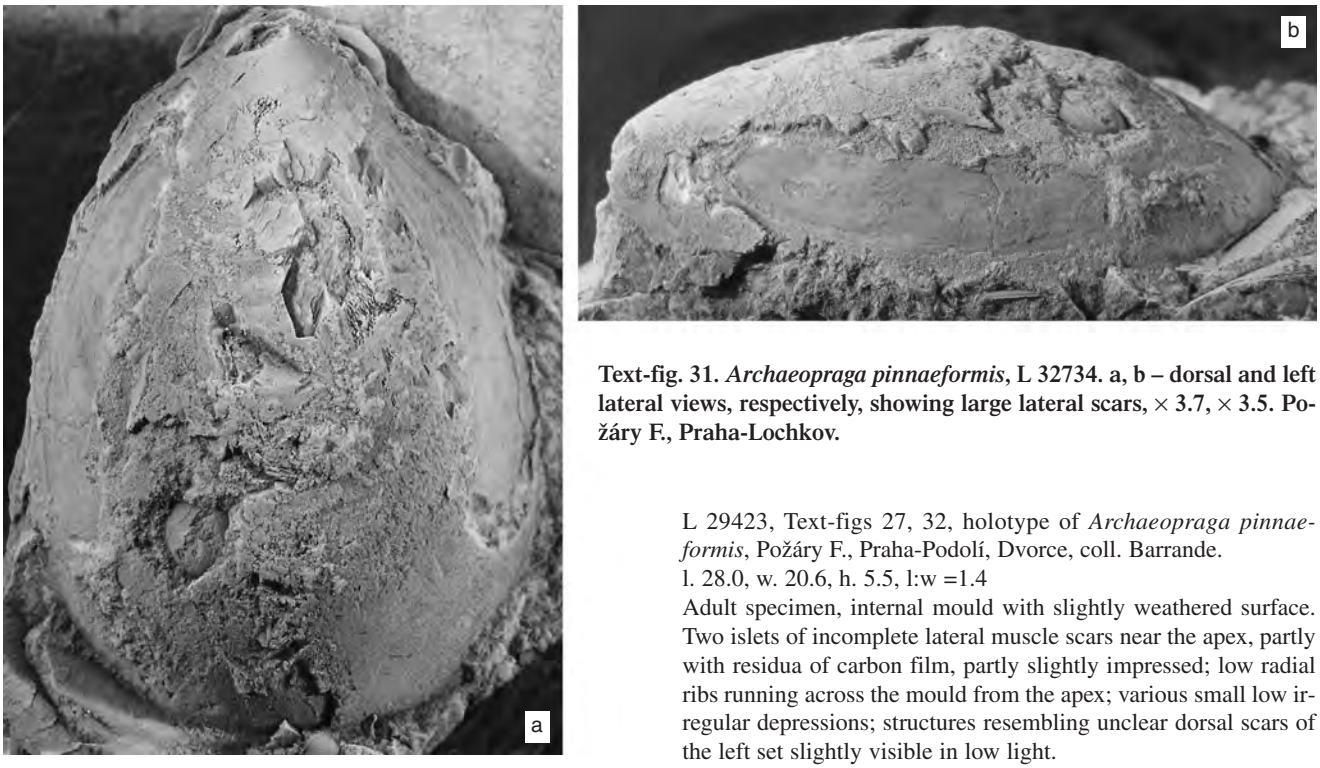
Incomplete adult specimen, probably pathologic, slightly shortened in posterior part, mostly preserved as internal mould; A scars consist of 2–3 segments, with branching structures in posterior direction, probably radular scars; B–D scars widely linear, flat, smooth, tilted posteriorly; scars F, G covered with shell; a small islet of lateral scar preserved on the right side; shell O.5 mm, two-layered, internal layer with conspicuous, radially arranged, fibrous structure; surface of the external layer with dense, fine, concentric growth lines, about 10–15 per mm.



Text-fig. 30. ***Archaeopraga pinnaeformis*****, L 7676. a – dorsal view with slighly visible lateral scar (arrowed), × 3,6; b – enlarged cephalic complex of scars including the radular scars, × 11; c, d – left and right oblique lateral views, respectively, showing a patch of right lateral scar, arrowed in d, × 3,6; e – posterior part with patch of shell, × 7,4. Požáry F., Praha-Lochkov.**

L 7676, Text-figs 27, 30, syntype of *Mytilus buridani* BARRANDE, 1881, Požáry F., Praha-Lochkov, coll. Barrande.
l. 23.0, w. 17.0 (restored), h. 4.2, l:w =1.4
Adult specimen, internal mould with patch of shell with inequal concentric growth lines; A scars of 2–3 segments, with branching structures in posterior direction, probably radular scars; B–G scars peanut-shaped, H scars not visible, two small fragments of lateral scars and weak impressions indicating their incomplete shape. The mould seems to be slightly dorsally postdiagenetically flattened, and is affected by a calcite vein (omitted in the drawing).

L 32734, Text-figs 27, 31, Požáry F., Praha-Lochkov, coll. Musei; orig. Horný (1963c), Peel and Horný (1999).
l. 25.2, w. 18.0, h. 4.7 (without shell thickness), l:w = 1.4



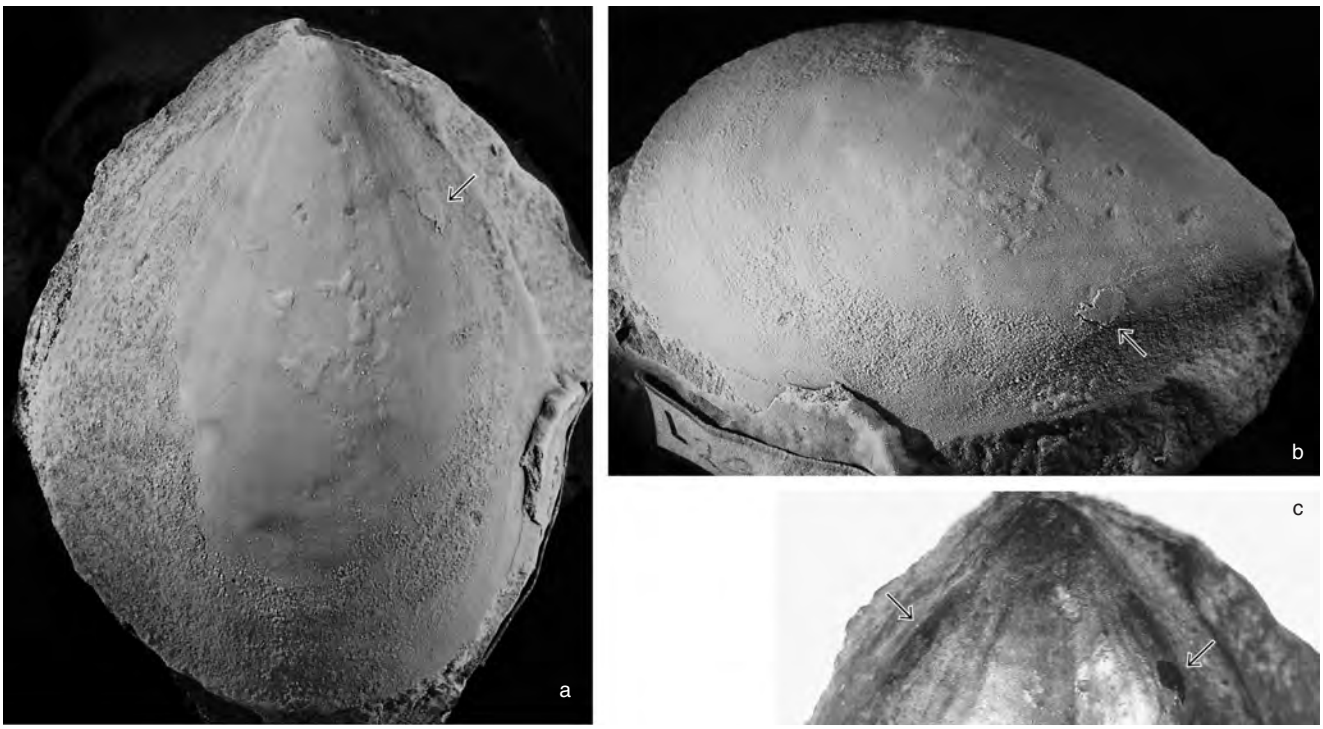
Text-fig. 31. ***Archaeopraga pinnaeformis*****, L 32734. a, b – dorsal and left lateral views, respectively, showing large lateral scars, × 3.7, × 3.5. Požáry F., Praha-Lochkov.**

L 29423, Text-figs 27, 32, holotype of *Archaeopraga pinnaeformis*, Požáry F., Praha-Podolí, Dvorce, coll. Barrande.
l. 28.0, w. 20.6, h. 5.5, l:w =1.4
Adult specimen, internal mould with slightly weathered surface. Two islets of incomplete lateral muscle scars near the apex, partly with residua of carbon film, partly slightly impressed; low radial ribs running across the mould from the apex; various small low irregular depressions; structures resembling unclear dorsal scars of the left set slightly visible in low light.

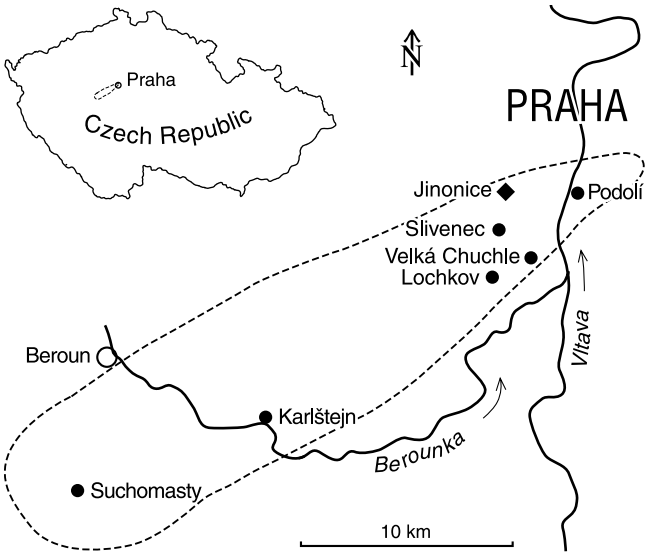
Adult specimen, shell preserved except for two large lateral muscle scars; A scars and dorsal B–G scars not exposed; lateral scars flat, 14.5 mm long and max. 3.7 mm wide, partly covered with carbon film with obliquely striated surface. Shell 0.4–0.5 mm thick.

Mode of life of drahomirid tergomyans

Drahomirid tergomyans are the only known group of tryblidioideans, adapted to life in specialized conditions of sedimentation of Silurian cephalopod limestones. These



Text-fig. 32. ***Archaeopraga pinnaeformis*****, L 29423, the holotype. a – dorsal view, ×3.2; b – oblique right latero-apical view showing small parts of the right lateral scar (arrowed), × 3.2; c – anterior part of the mould, not whitened to show pigmented remains of lateral scars (black, arrowed), × 3.2. Požáry F., Praha-Podolí, Dvorce.**



Text-fig. 33. Localities of drahomirid tryblidioideans in the Silurian of the Barrandian Area. Schematized; tectonics and overlying Devonian strata leaved out. ♦ – Kopanina Formation (Gorstian), ● – Požáry Formation (Přídolí).

limestones occur in several biostratigraphic levels in the Barrandian Area, representing assemblages characteristic for the environment below the wave base. The subparallel arrangement of shells gives evidence of water currents even near the bottom. This specific ecosystem has been studied from various aspects e.g. by Turek (1974, 1983), Ferretti and Kříž (1995), Kříž (1998, 1999). Several contributions have been applied to slow or stationary bivalves, crinoids, or gastropods, using empty shells of dead orthoconic and other cephalopods as a firm and elevated, and therefore better oxygenated ground in otherwise soft muddy bottom, namely by Turek (1974, 1983), Kříž (1979, 1999), Prokop and Turek (1984), Ferretti and Kříž (1995), Horný (2000). Rollins and Brezinski (1988) expected this strategy for platyceratids; see also Horný (2000). Already in 1963 Horný (1963b) published a find of four juvenile specimens of *Drahomira rugata* (= *D. glaserae*) *in situ* on the surface of a large orthocone. It is likely that drahomirids as inhabitants of single cephalopod shells were probably filter-feeders, rather then benthonic browsers or deposit feeders like *Pilina* or *Tryblidium* (Peel 1977, 1984).

Presence of species of the Family Drahomiridae has been undoubtedly ascertained in only two biostratigraphic levels, i.e. in the basal Ludlow (Gorstian) and throughout the Přídolí. Their acme in Přídolí (Požáry Formation) contrasts with their illogical absence in the upper Ludlow (Ludfordian, upper Kopanina Formation). According to the occurrence of the biofacies of Silurian cephalopod limestones in the Gondwana and Perunica basins (Ferretti and Kříž 1995, Kříž 1998, 1999), it is possible to expect finds of drahomirids also in extrabarrandian regions.

Drahomirid shells show no signs of transport. The functional morphology brings evidence of probably permanent stationary life on cephalopod shells. The apertural margin has no anterolateral emarginations, and the planar aperture with relatively sharp margin provided effective clamping to protect the soft body and avoid fouling of gills with mud. A unique feature among all known tryblidioideans – the large continuous lateral muscles – provided the shell stability on arched, rounded and smooth cephalopod shell. The shape of the drahomirid shell was also adapted to the dimensions of cephalopod, on which the pelagic larva settled. As shown by Peel (1977), tryblidians with elongate shells like *Pilina cheyennica* with length:width ratio = 1.5 were more mobile than their extant deep sea relatives (e.g. the Recent *Neopilina galatheae c.* 1). *Drahomira glaserae*, however, had a wide scope between 1.1 to 1.5 (prevailing value 1.2 to 1.4). The reason for this unusual state may have been rather in a limited space on mostly narrow cephalopod shell than a variable mobility; the drahomirids were probably not able to move easily over muddy depressions between cephalopod shells. In several cases the adult narrow shells, unable to increase the lateral sides, had a tendency to increase even the anterior part of the apertural margin (e.g. L 6261).

Acknowledgements

Financial support from the Ministry of Culture of the Czech Republic, project MK 00002327201, is gratefully acknowledged. Vojtěch Turek read and commented the manuscript, which was refereed by Rudolf J. Prokop. Petr Daneš kindly searched for mistakes in English. Jana Nedomová attentively helped with photography. The author thanks Jiří Kříž who collected several *Drahomira* specimens from the Požáry Formation and made them available for study. He also helped to determine age of several samples from older collections. Jaroslav Marek is thanked for stimulating discussions and the loan of his famous specimen. Petr Budil loaned the specimens deposited in the Czech Geological Survey, Prague.

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