

## A new Silurian gastropod from Bohemia with the operculum *in situ*

Nový český silurský gastropod s operkulem *in situ*  
(Czech summary)

(1 text-fig., 4 plates)

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A paucispiral operculum is described *in situ* in the gastropod *Tophicola linsleyi* gen. n., sp. n. from the Kopanina Formation (Silurian, early Ludlow) of Bohemia, confirming that shell coiling is dextral orthostrophic. Medial excavation of the columellar lip and bevelling of the apertural margin are morphological features of the shell in *T. linsleyi* which may be useful in inferring the presence of an operculum in other gastropods when, as is usual in the fossil record, this is not preserved in place.

**Key words:** Gastropoda, *Tophicola linsleyi* gen. et sp. n., dextral orthostrophic, paucispiral operculum *in situ*, apertural margin, Silurian, Bohemia

### Introduction

Most living prosobranch gastropods develop an operculum within the aperture but only infrequently is this structure mineralised and suitable for fossilisation (Yochelson 1979). Familiar to many at the present day is the thick, calcareous operculum ("cat's eye") developed in many turbinid trochoideans (see Hickman and McLean 1990 for a recent discussion of trochoidean opercula and relevant terminology). These turbinid opercula, readily isolated from the coiled gastropod shell following the death and decomposition of the animal, often form a conspicuous element in the shell beds on present day tropical beaches (Yochelson 1979).

Examples of isolated gastropod opercula are known from Early Ordovician and younger strata. They were recognised as such already by early workers, e.g. Billings (1865), from the Ordovician of Canada, and Lindström (1884), from the Silurian of Gotland, Sweden, but such opercula generally are not common fossils within the geological record. The unusual abundance of opercula of *Ceratopea*, however, within Laurentian carbonates deposited under restricted marine conditions during the early Ordovician has allowed establishment of a biostratigraphic scheme (see Yochelson 1979 for a summary and references).

Finds of Palaeozoic gastropods with the operculum *in situ* within the aperture are rare but a number of examples is described in the literature (e.g. Lindström 1884, Perner 1903-1911, Teller 1910, Knight 1941, Boucot et al. 1966, Yochelson and Linsley 1972, Yochelson and Wise 1972, Linsley 1978a, Gubanov and Yochelson 1994, Peel and Horný, in press). In the present paper we describe four specimens of a new gastropod genus with the operculum *in situ* from the Silurian of the Barrandian Area, central Bohemia. At-

tention is given to features of the coiled shell which seem to be associated with the operculum, in the hope that information about the presence or nature of the operculum in other taxa can be deduced from occurrences of the coiled shell alone.

### Gastropod opercula from Bohemia

Multispiral opercula of *Oriostoma* and *Beraunia* occur sporadically at different stratigraphic levels within the Silurian of Bohemia, sometimes also *in situ* within the gastropod shell (Perner 1903-1911, Knight 1941). One isolated operculum is known from the Lower Devonian (Pragian, Koněprusy Limestone). Barrande (in manuscript) believed this specimen to be a coiled shell, *Rotella confusa*, and it was described by Perner (1903, 1907) as a shell of *Pleuronotus? confusus* Barrande in Perner, 1903. Horný (1994) assigned the operculum to *Australonema cf. guillieri* (Oehlert, 1881).

Horný (1992) described an operculum *in situ* in *Tychobrahea aerumnans* Horný, 1992 from the Lower Devonian (Pragian, Dvorce-Prokop Limestone) of Bohemia. This species is of particular interest in representing the first identification of sinistral hyperstrophic coiling in a marine gastropod, an interpretation based on the comparison of coiling direction in the preserved operculum and the gastropod shell (Peel and Horný, in press). In contrast to *T. aerumnans*, the anticlockwise coiling of the outer surface of the operculum of *Tophicola linsleyi* indicates that the parent shell was dextral orthostrophically coiled, the dominant condition within shelled gastropods.

The present finds of shells with the operculum *in situ* come from poorly consolidated, calcareous, volcanic ash of the Kopanina Formation (Silurian, Ludlow, earliest Gorstian). In spite of the fact that shells of the

described species, *Tophicola linsleyi* gen. et sp. n., are very abundant, no isolated opercula have been found as yet in associated material.

Genus: *Tophicola* gen. n.

Type species: *Tophicola linsleyi* gen. et sp. n., typically from the Kopanina Formation (Silurian, Ludlow, earliest Gorstian) at Karlštejn, Czech Republic.

Derivation of name: Alluding to the habitation of an area influenced by volcanic ash; *tophus* (Lat.), volcanic ash.

Diagnosis: A dextral orthostrophic gastropod, turbiniform, with uniformly expanding rounded whorls which are anomphalous to narrowly phaneromphalous. The aperture is sub-tangential, thickened at the suture and along the columellar lip, the latter being excavated medially and carrying a low tooth-like extension into the interior. The operculum is calcareous, paucispiral, and coiled anti-clockwise when viewed externally.

Discussion: While the operculum of *Tophicola* is similar to that described in *Australonema* by Yochelson and Linsley (1972) and Gubanov and Yochelson (1994), the shells of the two genera are readily distinguished. In *Australonema* the whorls are strongly ornamented with abundant coarse spiral lirae, while spiral ornamentation in *Tophicola* is essentially restricted to the sub-sutural cord. In the absence of more widespread information concerning opercula in Palaeozoic gastropods, it is not possible to assess the relationship (if any) between *Australonema* and *Tophicola*. Spiral ornamentation also serves to delimit *Cyclonema* from *Tophicola*. The former genus frequently develops an excavated columellar lip (Thompson 1970) similar to that seen in *Tophicola*, suggesting that an operculum was present.

*Naticonema* has a spirally ornamented shell which expands more rapidly than that of *Tophicola*. Knight (1941) considered the columellar lip in the former genus to be excavated, but Thompson (1970) claimed it to be smooth with an umbilical depression. *Holopea* has a shell of similar proportions to *Tophicola* and also lacks ornamentation other than fine growth lines. It is distinguished from *Tophicola* by its simple columellar lip.

*Turbinilopsis* has a holopeiform shell not dissimilar to *Tophicola*, but the operculum is multispiral (Tyler 1965).

Assigned species: Only the type species, *T. linsleyi* sp. n. is currently assigned to *Tophicola*.

*Tophicola linsleyi* sp. n.

Pls I-IV

Holotype: Specimen figured here as Pl. I, figs 1, 2, Pl. IV, figs 4, 5. Praha, National Museum, L 29308.

Paratypes: L 29309 -L 29326 in the same collection. Stratum typicum: Silurian, Ludlow, earliest Gorstian, Kopanina Formation, graptolite zone C. *colonus*.

Locus typicus: Karlštejn, the abandoned quarries "Na rešných" ("Liščárna") near Mořina.

Derivation of name: For Robert M. Linsley.

Material: About 1000 specimens are available, but only those illustrated here retain an *in situ* operculum.

Diagnosis: See genus.

Description: The shell has the general appearance of *Holopea* Hall, 1847. The initial whorl(s) is separated by an internal septum or filled by a calcareous plug (Pl. II, figs 1, 2) and is usually lost or dissolved, seemingly also post-diagenetically, as reported in *Cyclonema* by Thompson (1970). The spire expands gradually such that the final whorl is not inflated, as it is in *Naticopsis*. The whorls are rounded, slightly adpressed with a sub-sutural cord, and sutures are shallow. The base is rounded, narrowly phaneromphalous or anomphalous. Ornamentation consists of fine slightly prosocline growth lines, but some specimens show traces of very fine spiral lines near the suture with the previous whorl. The shell wall is of moderate thickness, but thickened at the suture and on the base; it is thickest in the umbilical region; a cord-like elevation near the upper suture is pronounced in some specimens and serves to reinforce the shell at the juncture of the parietal and outer lips. The aperture is simple and almost tangential; the outer lip is slightly prosocline. The columellar lip is excavated with a lobe-like extension ("tooth") passing into a ramp as the parietal region is approached and then gradually into a thin parietal inductura. This "tooth" is absorbed during growth and does not form a columellar ridge. The junction of the columellar and outer lips is broadly rounded; the apertural margin is reinforced, with a narrow, acute, margin and conical sides enabling partial withdrawal of the operculum. A shallow apertural notch in the reinforced, adpressed, junction of the outer and parietal walls probably served as an exhalant channel.

The operculum is calcareous, paucispiral, expanding in an anti-clockwise direction; it is asymmetric, somewhat tear-shaped in plan and fits perfectly within the aperture. The growing edge of the operculum, parallel to the parietal lip of the coiled shell, has an angle of accretion of about 25 degrees. The outer surface shows the initial concave and smooth disc followed first by numerous narrow, but later more quickly expanding, volutions of the logarithmic spiral; there are numerous oblique and irregular growth increments and weak spiral lines. A partly broken operculum (Pl. III, figs 5, 6) shows broad, smooth, gradate clockwise volutions on the inner surface. The lateral margins of the operculum are not simple. The periphery lies on

a narrow ridge which is located slightly below the level of the outer (adapertural) surface; a narrow groove lies immediately adapertural of this ridge. Adapical (i.e. towards the interior surface of the operculum) of the peripheral ridge lies a broad concave groove, the adapical margin of which is rounded. The operculum is thinnest in the centre (0.4 mm) and has a maximum observed thickness of 0.9 mm.

### Discussion

The operculum of *Tophicola* is similar to that of *Australonema lilydalensis* (Etheridge, 1894) as described by Yochelson and Linsley (1972). The early volutions following the central concave disc are less rapidly expanding, however, and consequently more densely crowded than in *Australonema*, and the final two volutions are more rapidly expanding. This variation suggests a change in the rate of rotation of the operculum during ontogeny (Hickman and McLean 1990). The operculum of *Australonema lilydalensis* has simple, uniformly convex edges which contrast with the ridged and channeled margins of *Tophicola*.

Gubanov and Yochelson (1994) described an operculum of similar proportions *in situ* in *Australonema varvarae* from the Silurian (Wenlock) near Norilsk, northern Siberia. The operculum itself is poorly preserved and few features other than style of coiling can be discerned.

The morphology of the aperture in *Tophicola linsleyi* clearly indicates the presence of an operculum in the otherwise holopeiform shell. Thus, even without the operculum, *Tophicola* is readily distinguished from the thin-shelled holopeids by its re-inforced apertural margin and the excavated columellar lip. This lip carries a lobe-like extension into the aperture which narrows into a ridge-like ramp as the parietal area is approached, tapering across the parietal wall (Pl. II, fig. 8). These structures were gradually resorbed during growth. As discussed below, the lobe-like extension or "tooth" and the widened ramp served as a primitive articulation for the operculum (Hickman and McLean 1990) and is known from a number of other fossil gastropods.

*Tophicola linsleyi* has not been found from other similar localities or in different contemporary facies in the Barrandian area. It is necessary to recognise, however, that identification of this genus on material without a preserved aperture is difficult or impossible. A superficially similar species is known from the volcanic facies of the Liteň Formation (Wenlockian) at Barrande's locality Bubovice, described as *Holopea timida* Barrande in Perner, 1903. This latter species differs by deeper sutures, thicker, evenly thick shell wall, not excavated columellar lip and a simple apertural margin; it definitely belongs to another genus. Of the foreign materials, *Holopea transversa* Lindström, 1884, described on the basis of a single small shell by

Lindström (1884, Pl. 15, figs 59, 60) should be compared with *T. linsleyi* more closely.

### Mode of life

*Tophicola linsleyi* occurs abundantly in a transition layer, about 5 m thick, between almost unfossiliferous deposits of fine-grained volcanic ash and bioclastic crinoidal limestone. This layer contains several horizons of poorly consolidated calcareous deposits with variable amounts of volcanic ash with lapilli and volcanic glass. These strata contain local biostromes, the development of which was repeatedly influenced or even interrupted by the import of fine-grained volcanic ash from the nearby volcanic area. The autochthonous shallow-water fauna, often preserved *in situ*, contains calcareous sponges, stromatoporoids, rugose and tabulate corals, bryozoans, brachiopods, crinoids, bivalves, chitons, tergomyans, rare nautiloids, trilobites and locally large communities of gastropods, consisting of more than 60 species. Predominating genera are *Euomphalopterus*, *Tophicola*, and *Oriostoma*; thousands of specimens of *Euomphalopterus aliger* have been collected. Other typical and frequently found genera are *Boiotremus*, *Bellerophon*, *Kodymites*, *Liospira*, *Loxoplocus* (*Lophospira*), *Phanerotrema*, *Cataschisma*, *Platyconus*, *Trochonema* (*Eunema*), *Gyronema*, *Naticonema*, *Platyceras* (*Platyceras*), *P.* (*Orthonychia*), *Beraunia*, *Murchisonia* s. l., *Loxonema*, and *Subulites* (*Cyrtoospira*).

Excellent preservation and the mode of deposition indicate that most of the shells were not transported postmortally. High-spined species of *Loxonema* or *Murchisonia* s.l. are often found with preserved minute initial whorls and do not show breakage. Signs of repaired injuries of the apertural margin are rare. The communities contain both the adults and different stages of juveniles which might have perished during the periods of higher import of fine dispersed volcanic ash. All these observations indicate quiet, well aerated and, according to other fauna, rather shallow surroundings.

The main factor determining development of the communities was the import of fine periodically dispersed volcanic material. This presumption also agrees with the low percentage of the pleurotomariaceans which, with the exception of *Cataschisma*, never form larger populations. Dominating operculate species of *Oriostoma* and *Tophicola* were seemingly well adapted to these conditions. *Oriostoma*, *Beraunia* and *Euomphalopterus* are believed to be sedentary ciliary feeders (Linsley 1978b, c, Linsley, Yochelson and Rohr 1978, Peel 1984, Horný 1995). *Tophicola* with its heavy operculum in an otherwise thin-shelled conch could represent a similar adaptation. A thick operculum thus should not necessarily be just an antipredatory feature (Gubanov and Yochelson 1994).

The disproportion between the total number of

more than a thousand collected specimens of *T. linsleyi* and only four specimens with an operculum preserved *in situ* seems striking, but conforms with other descriptions of Palaeozoic gastropods with an *in situ* operculum (cf. Yochelson and Wise 1972; Peel and Horný, *in press*). The absence of isolated opercula of *T. linsleyi* is also noteworthy. They may have been dissolved after being separated from the shells (Yochelson and Linsley 1972) or even while still within the shell after the death of the animal (the paratype with a partly dissolved outer surface illustrated as Pl. I, fig. 7 and Pl. IV, fig. 6 could support this opinion). Isolated heavy opercula of the *Oriostoma* species are present but even these are rare in proportion to the very abundant shells.

Some specimens of *T. linsleyi* exhibit a pattern of small pits in the outer shell surface (Pl. II, fig. 3, Pl. IV, fig. 2). Similar structures have been described by Hoare et al. (1980) from specimens of the Carboniferous gastropod *Microdoma conicum* Meek et Worthen, 1867 from Ohio, U.S.A., and attributed to the activity of an unknown organism. Wahlman (1992) figured this pattern in *Sinuities granistriatus* (Ulrich in Ulrich et Scofield, 1897) from the Ordovician of Ohio, U. S. A., describing them as a sculpture of the parietal deposits (p. O114). We follow the opinion of Hoare et al. 1980.

### Opercular structures in the gastropod shell

The presence of an operculum is a feature of most adult prosobranch gastropods, although a lack of calcification commonly renders the operculum unsuited for preservation as a fossil. Opercula must also be presumed to have been present in most Palaeozoic gastropods, most of which are traditionally assigned to the Prosobranchia (cf. Knight et al. 1960). Records of fossil opercula *in situ* provide invaluable, but scarce, direct evidence about the distribution of opercula within the Gastropoda through geologic time. A more widespread source of information is provided by structures in the coiled shell which reflect the presence of an operculum, and the gastropods described here can be examined with this aim in mind (Text-fig. 1).

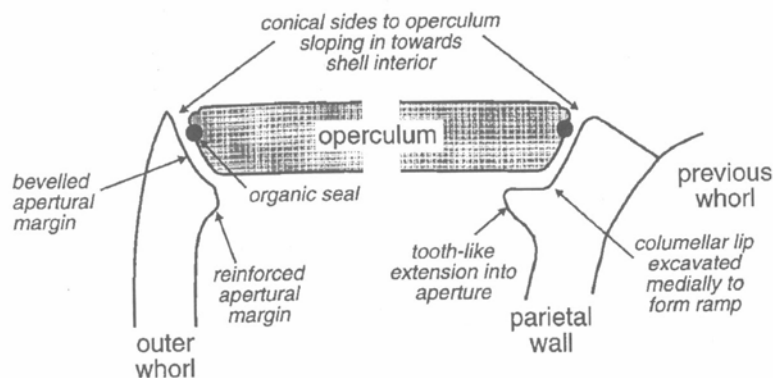


Fig. 1. Schematic section to illustrate features of the operculum and apertural margins in *Tophicola linsleyi*

The operculum in *Tophicola linsleyi* sits on a narrow shelf-like excavation in the columella which continues into the parietal region. A similar groove in the columellar lip was described in *Cyclonema* by Thompson (1970) who presumed that it may have functioned in conjunction with an operculum (which was presumably corneous in composition). A groove is also developed in *Littorinides*, *Naticopsis* (*Jedria*), *Damesia* and some other Neritacea also show well-developed excavation of the columella (Knight et al. 1960) and fossil forms with the operculum *in situ* have been described (Gordon and Yochelson 1982, Yochelson 1991).

The apertural margin along the outer lip in *T. linsleyi* is bevelled such that within the thickness of the shell wall, the margin slopes adapically in towards the shell interior from the acute outer margin. Thus, the apertural margin along the outer lip is excavated into a cone into which the conical operculum fits. A conical operculum has been described by Tyler (1965) in *Turbinilopsis anacarina* from the Devonian of Michigan and by Peel and Horný (*in press*) in *Tychobrahea aerumnans* from the Devonian of Bohemia. The conical effect in *T. linsleyi* is increased by a slight comarginal thickening, producing a corresponding channel on the surface of the internal mould (Pl. II, figs 5, 7-9).

The margin of the operculum in *Tophicola linsleyi* is not smoothly conical, as in *Tychobrahea aerumnans*, but is excavated into a median groove (Pl. III, fig. 6). The groove may have been filled with organic tissue which could have increased the effectiveness of the seal between the conical operculum and the bevelled apertural margins (Text-fig. 1). The outer lip in *T. linsleyi* also extended slightly beyond the plane of the outer surface of the operculum. Thus, in life, it was possible for the animal to open its operculum slightly along the outer lip without the operculum margin projecting beyond the apertural margin, while the shelf-like platform on the columellar lip still supported the operculum along that side. Such a pivot at the inner (=columellar) margin of the operculum would not be expected in gastropods where the operculum is located deep within the aperture, as in *Tychobrahea aerumnans* (Horný 1992, Peel and Horný *in press*). In *T. aerumnans*, slight forward movement of the entire operculum can be accommodated easily within the shell interior.

The whorl profile in *Tophicola linsleyi* corresponds closely to the internal shape of the aperture and the operculum. In *Tychobrahea aerumnans*, the whorl profile is often angular, with a clearly developed upper whorl surface. The internal shape of the aperture and the operculum itself, however, are almost circular. This contrast between a circular apertural shape and the angular whorl profile may provide a clue to the presence of a circular operculum and

a similar situation exists in *Liomphalus* (Yochelson and Linsley 1972; Linsley 1978a). The shape of many modern gastropod opercula, however, poorly reflects the shape of the aperture, although Knight et al. (1960) noted that most calcareous opercula conform with the shape of the aperture interior.

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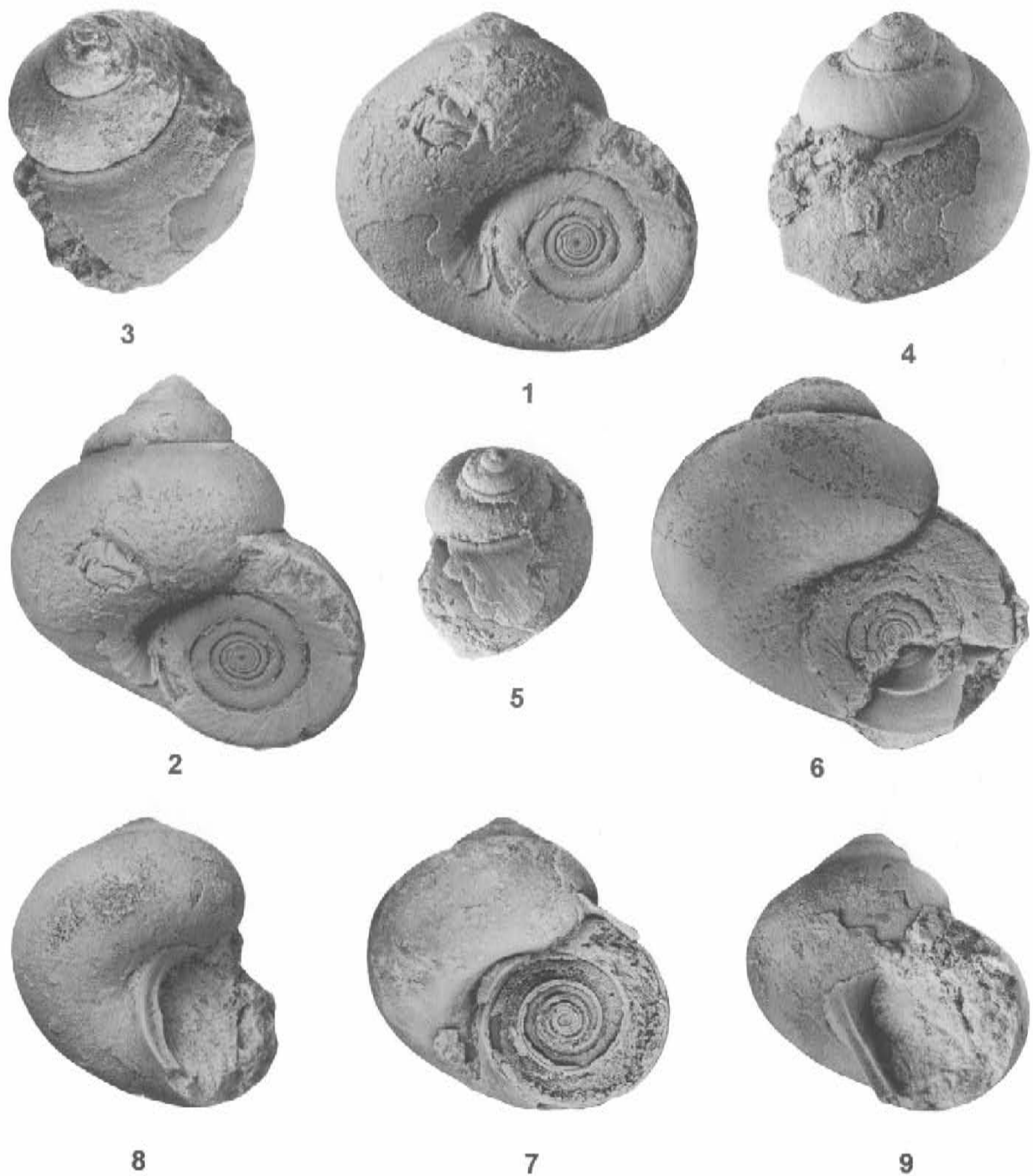
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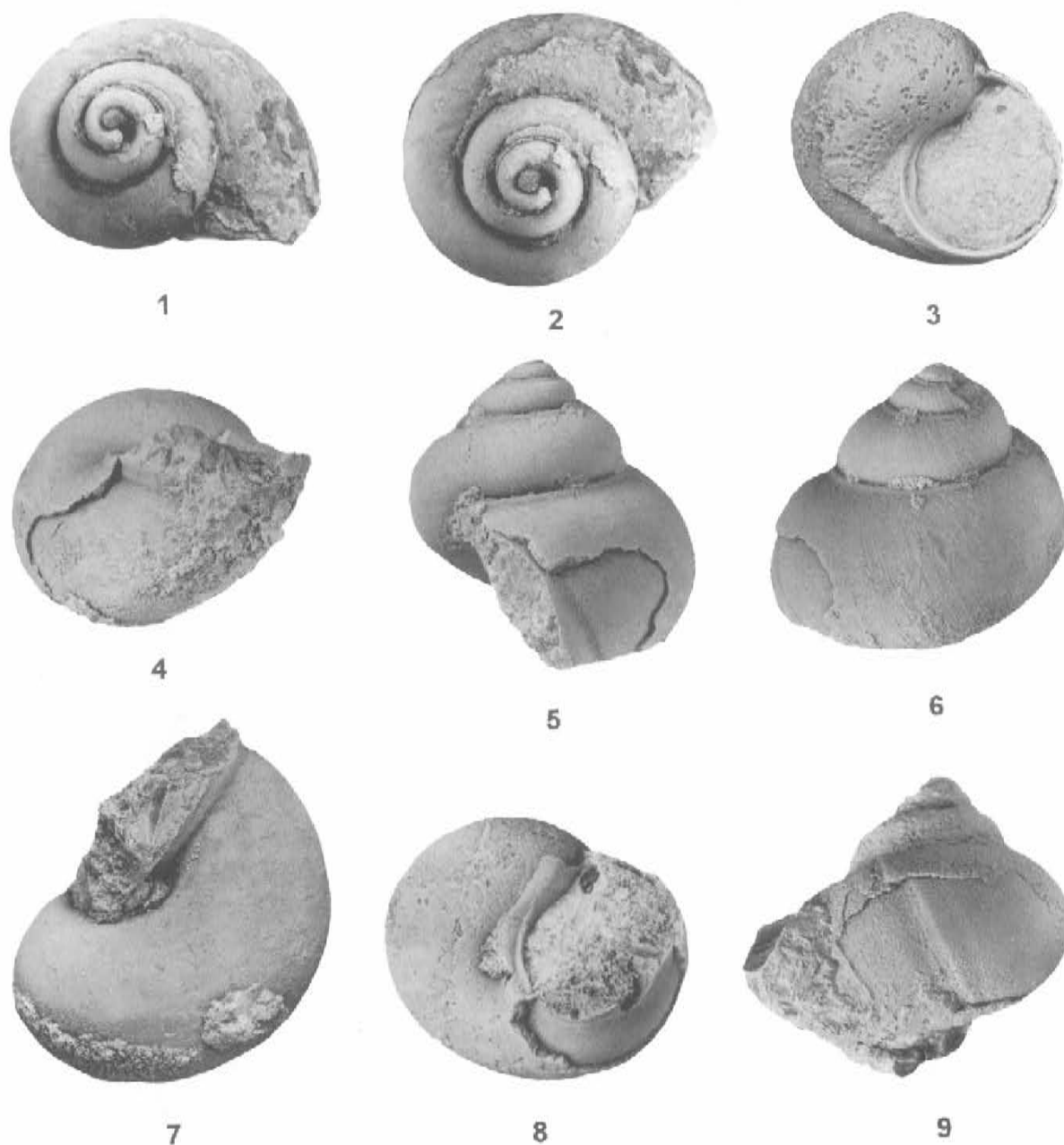
Ve vápnatých tufitických sedimentech bazálních poloh kopaninského souvrství u opuštěných lomů Na rešných u Karlštejna bylo nalezeno více než 1000 jedinců holopeiformního gastropoda, který je v této práci popsán jako nový rod a druh *Tophicola linsleyi* gen. et sp. n. Pouze čtyři jedinci mají zachováno paucispirální operkulum *in situ*, které dokazuje dextrálně ortostrofické vinutí ulity. Mimořádně příznivě zachované exempláře umožnily studovat doposud neznámé morfologické podrobnosti, zejména vyhloubení kolumelárního pysku s plochým výčnělkem a konické zešíkmení okraje apertury. Tyto znaky umožňují předpokládat existenci víčka i u fosilních druhů, u kterých doposud nebylo nalezeno *in situ*. Nepatrný počet nalezených jedinců s víčky *in situ* a nepřítomnost izolovaných víček na lokalitě odpovídají dřívějším zahraničním zjištěním o labilitě tohoto typu víček při fosilizačních pochodech.



*Tophicola linsleyi* gen. et sp. n.

1, 2 - holotype, L. 29308, x4, showing the operculum preserved *in situ*, viewed perpendicular to the axis of coiling (2) and perpendicular to the apertural plane (1). 3 - paratype, L. 29321, x4, showing weak spiral ornamentation near the upper suture. 4 - paratype, L. 29315, x4, with fine, almost straight, growth lines. Note the thin, two-layered shell. 5 - paratype, L. 29314, x3.5, showing fine growth lines passing the sub-sutural cord at the addressed suture. 6 - paratype, L. 29309, x4, with operculum partly broken away to show the counterpart of the internal surface. 7 - paratype, L. 29310, x4, showing the deeply corroded external surface of the operculum. Note the exhalant channel at the junction between the parietal and outer lips. 8 - paratype, L. 29313, x4, showing the excavated columella with the tooth-like extension into the aperture. 9 - paratype, L. 29317, x4, showing the ramp produced by the columellar excavation dying out at the parietal wall.

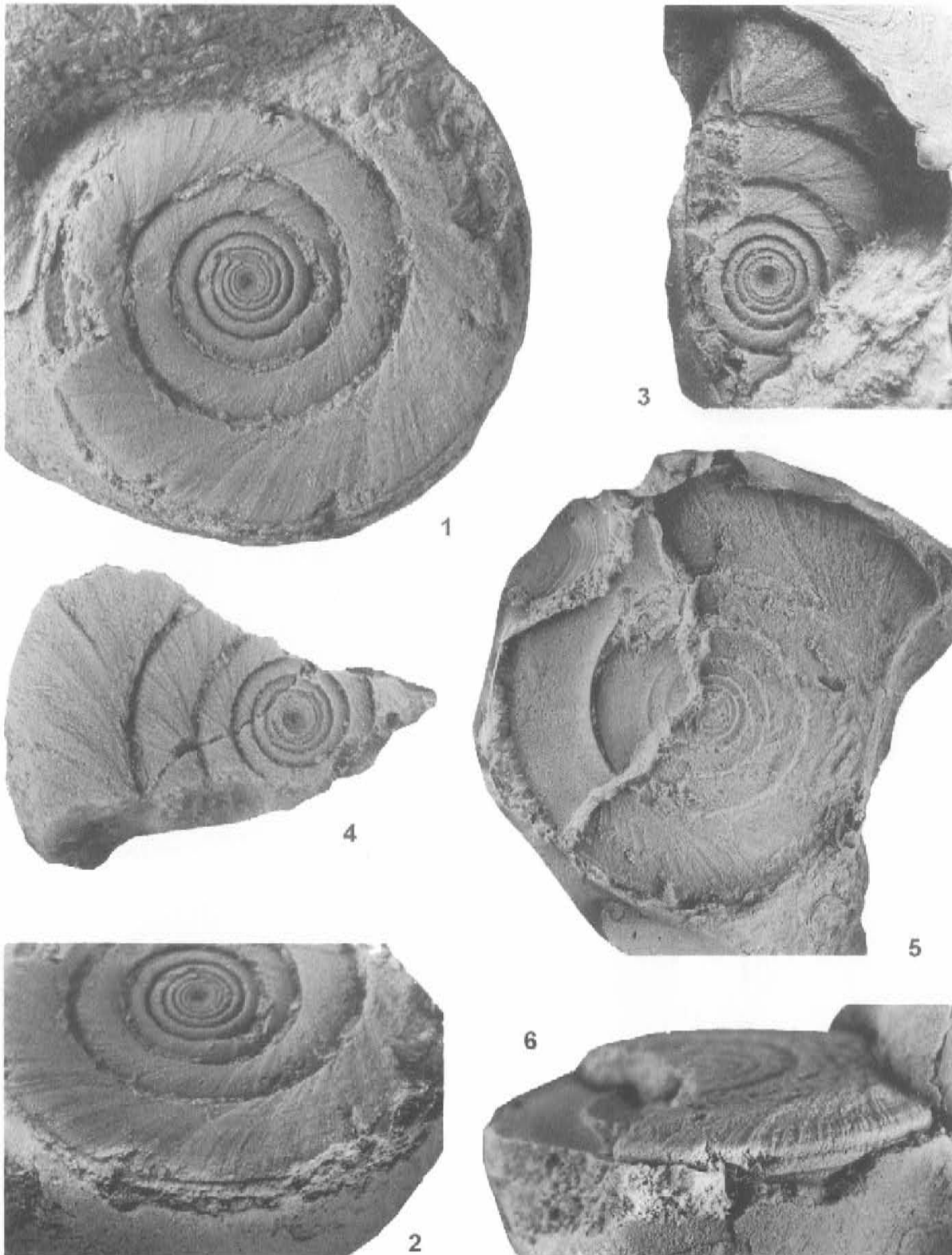
All specimens figured on Pls I-IV are deposited in the collections of the Department of Palaeontology, National Museum, Prague. Coated with ammonium chloride before photographing.



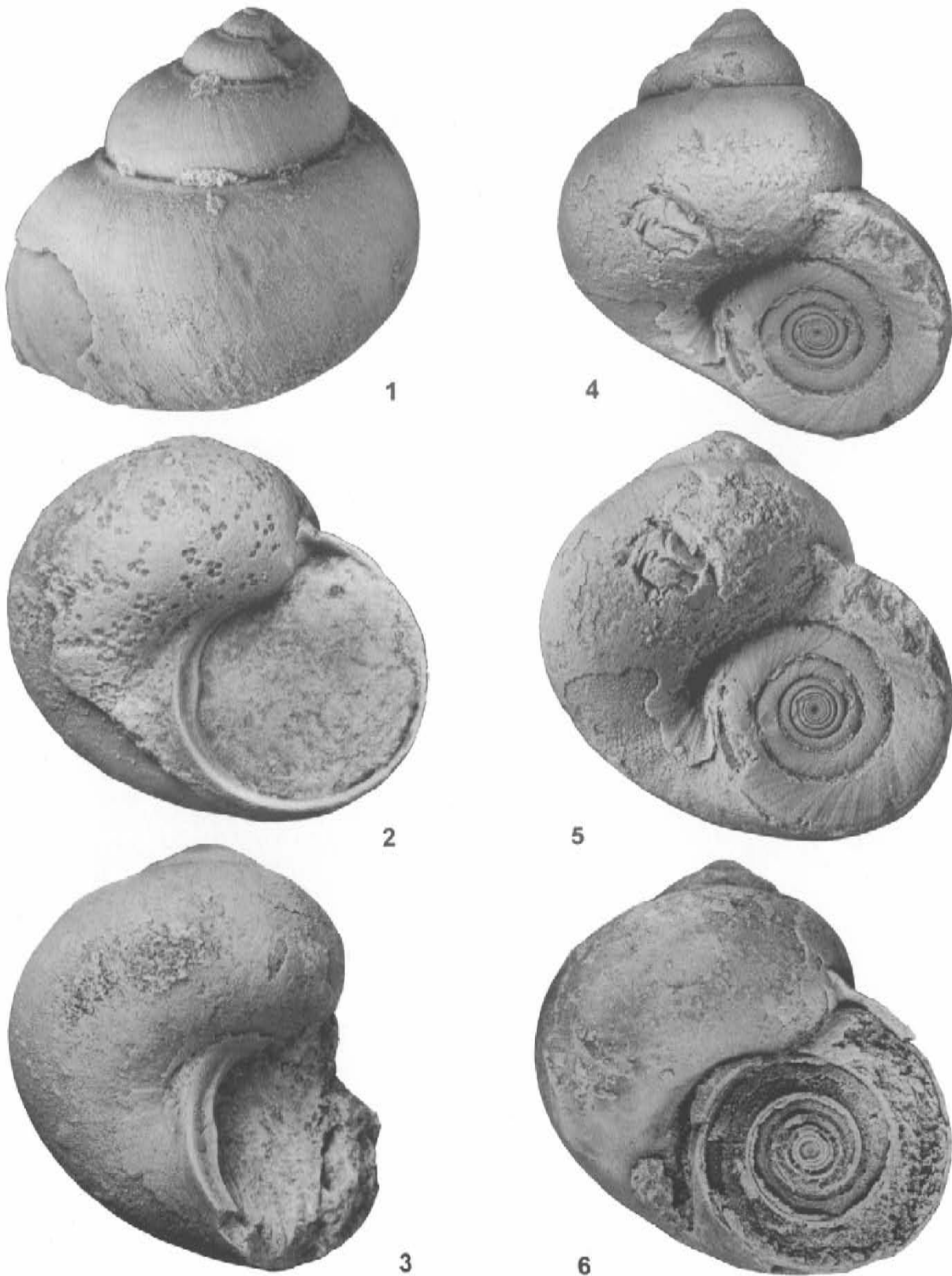
*Tophicola linsleyi* gen. et sp. n.

1, 2 - paratype, L 29326, x4, two views of the rounded apex of an internal mould terminated at an internal septum or plug. 3 - paratype, L 29312, x4, showing the well preserved thin apertural margin and the tooth-like extension of the columellar lip. Structures similar to the numerous pits visible on the lower whorl surface were ascribed to the activity of an unknown organism by Hoare et al. (1980). 4 - paratype, L 29325, oblique basal view showing the reinforcement of the shell wall in the columellar region, producing a constriction on the internal mould. Note the bevelled apertural margin, with acute peristome, forming a conical surface for reception of the operculum. 5, 6 - paratype, L 29323, x4, lateral views of a partly exfoliated specimen showing the reinforced apertural margin producing a constriction on the internal mould (5) and rare preservation of fine growth lines (6). Note the slightly adpressed whorls and minor injury in the central part of the final whorl. 7 - paratype, L 29322, x4, showing the reinforced apertural margin in the columellar region preserved as a constriction on the internal mould. 8 - paratype, L 29316, x 4, oblique basal view showing the ramp produced by median excavation of the columellar lip fading out into the parietal region. 9 - paratype, L 29324, x 4, partly exfoliated specimen showing a constriction on the internal mould produced by incomplete resorption of a reinforced aperture. The constriction marks a former, now abandoned, position of the operculum



*Tophicola linsleyi* gen. et sp. n.

1 - holotype, L 29308, x10, external surface of operculum *in situ* showing the anti-clockwise coiling and accretion structures ("growth lines") tangential to the spiral of earlier whorls. Note the concave nucleus forming the earliest and thinnest part of the operculum. 2 - holotype, L 29308, x10, oblique view of the opercular margin and external surface showing the narrow groove above the peripheral ridge. 3, 4 - paratype, L 29311, x 13, a fragment of an operculum (4) and a latex impression of its counterpart *in situ*, showing the concave nucleus. 5 - paratype, L 29309, x10, latex impression showing part of the smooth internal surface of the operculum *in situ*. Note that coiling is clockwise. 6 - paratype, L 29309, x10, oblique lateral view of an operculum located within the reinforced aperture. The operculum narrows towards the shell interior, being slightly conical in shape. Note the grooves above and below the circum-opercular peripheral ridge. The outer (= upper in figure) surface of the operculum is ornamented by sharp transverse accretion structures (growth lines) and less pronounced spiral ridges.



*Tophicola linsleyi* gen. et sp. n.

1 - paratype, L 29323, x5.5, showing the fine growth lines, slightly adpressed whorls and the minor injury in the central part of the final whorl. 2 - paratype, L 29312, x7, showing the well preserved thin apertural margin and the tooth-like extension of the columellar lip. Note the numerous pits visible on the whorl surface, probably a result of the activity of an unknown organism. 3 - paratype, L 29313, x5.5, showing the excavated columella with the tooth-like extension into the aperture. 4, 5 - holotype, L 29308, showing the operculum preserved *in situ*, viewed perpendicular to the axis of coiling (4, x4.5) and perpendicular to the apertural plane (5, x5). 6 - paratype, L 29310, x6, showing the deeply corroded operculum and the exhalant channel at the junction between the parietal and outer lips