

## SECONDARY SHELL DEPOSITS AND PRESUMED MODE OF LIFE IN *SINUITES* (MOLLUSCA, GASTROPODA)

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**Abstract.** Secondary shell deposits, covering parts of the shell exterior, their morphology, origin and function in relation to environmental conditions are described in two Lower Ordovician species of *Sinuities* from Bohemia. Fossilisation and weathering processes are regarded as important for the preservation and appearance of these structures. *Sinuities* is considered a semi-infaunal, ploughing and burrowing gastropod, probably an active predator feeding on infauna, inhabiting quiet-water muddy sediments.

■ *Sinuities*, secondary shell deposits, labro-umbilical ridge, labro-umbilical depression, inductura, subinductura, subinductural vallum, functional morphology, mode of life, systematics, Ordovician, Bohemia

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The Ordovician genus *Sinuities* KOKEN, 1896, a member of the Family Sinuitidae DALL in ZITTEL-EASTMAN, 1913, is one of the rare Lower Palaeozoic bellerophontacean gastropods with developed, preserved, and observed secondary shell deposits, covering variable extent of the shell exterior. *Euphemites* WARTHIN, 1930 has been studied in detail and its secondary shell deposits are well explained (Weller 1930, Moore 1941, Yochelson 1960, Harper and Rollins 1985). Similar deposits in *Sinuities* – although first observed, but not explained, in 1896 – are still imperfectly known.

In defining *Sinuities* in 1896 (type species, *Bellerophon bilobatus* J. de C. SOWERBY, 1839), Koken mentioned the wrinkled circumbilical structure as one of its generic diagnostic signs (“Nabelgegend mit nach vorn abgegrenzter Runzelschicht”, p. 392). In 1987, he figured *Sinuities rugulosus* (Fig. 4, p. 117) showing this structure which he described, but did not interpret, on p. 118 (“Die Seiten in der Nabelgegend mit deutlicher, feiner Runzelung, die in die Mündung tretende Rückenfläche grob und kraus gerunzelt”).

In the same year, Ulrich and Scofield (1897) established *Protowartha*, based on *Bellerophon cancellatus* HALL, 1847, later synonymized with *Sinuities* (Bassler 1915). They also mentioned the circumbilical structures as one of the diagnostic characters but, in contrast to Koken, they explained their origin (p. 848: “The inner lip forms a thin granulose deposit over the dorsum of the inner end of the last whorl and extends on each side around the umbilical region. This portion is covered with interrupted or inosculating lines”). In the description of *Protowartha granistriata* ULRICH in ULRICH et SCOFIELD, 1897 (p. 870), they speak about “what may be called a fourth layer”, which “seems to have been deposited by the inner mantle over the inner volutions, including the smaller half of the outer, while on each side it extends around the callous filling of the umbilicus”. Describing *P. cancellata* (HALL, 1847) (p. 872), they use the term “thin extensions of the callosity of the inner lip”, noting that these structures, absent dorsally on the inner whorls, are composed of a more durable substance than is the usual sculpture-bearing layer of the shell. In total, the secondary shell deposits have been described in four species, *P. granistriata*, *P. cancellata*, *P. sub-*

*compressa* ULRICH in ULRICH et SCOFIELD, 1897, and probably *P. concinna* ULRICH et SCOFIELD, 1897.

Reed (1920) reported 15 species of *Sinuities* from the British Ordovician strata without describing or discussing secondary shell deposits in any of them and omitting this feature from the generic diagnosis. Nevertheless, he mentioned (pp. 13, 14) three shell layers in *Sinuities soudleyensis* REED, 1920 (thin smooth outer layer; thicker second, ornamented layer; inner smooth layer). In *S. sphaeroidalis* REED, 1920 he described and figured (Pl. 3, fig. 13a) "granulated transverse lines, interlacing and forming a fine reticulation" (p. 16); these structures could be of inductural origin.

In 1925, J. Perner finally edited Koken's long delayed monograph. Besides the diagnosis, indicating the presence of secondary shell deposits (called "Runzelschicht"), Koken emphasized these structures in *S. rugulosus* ("Die starke Querfaltung der oberflächlichen Schalenlage, welche auf der Innenlippe entsteht, markirt sich im Schliff dur spitze Sägezähne, welche besonders bei *S. rugulosus* schon sehr früh auftreten und periodisch stärker und schwächer werden." (p. 37; fig. 9:2, p. 38). Describing *S. rugulosus* (p. 39), Koken also noted its possible origin ("Es ist nicht daran zu zweifeln, dass diese auffalende, auch bei anderen Arten wiederkehrende Sculptur von einem lappenförmige Forsatz gebildet wurde, der ventral gegen war, wenn man die Sinusseite dorsal nennt."). Besides *S. rugulosus*, the secondary shell deposits ("Runzelschicht") were mentioned in *S. vetustus* KOKEN, 1897, *S. gracilis* KOKEN, 1925, *S. bilobatus* (?), *S. angustus* (LINNARSON, 1879), and *S. nanus* (EICHWALD, 1861) (?). Koken's assumption that certain structures in the umbilical area of the internal mould of *S. ammonoides* KOKEN, 1897 (Pl. 18, fig. 16) indicate the presence of secondary shell deposits (p. 43) is misleading as these structures, in fact, represent a retractor muscle impression (see Peel 1976, 1986).

Knight (1941) redescribed and refigured *Protowarthia cancellata*, pointing out the secondary shell deposits ("umbilicus wanting or very small and plugged with callus; parietal inductura well developed but not strongly thickened, covering the dorsum of the previous whorl for some distance outside the aperture and extending into the umbilical depressions, the inductura carrying fine, wavy revolving lirae" - p. 279). Fig. 3a on Pl. 6 clearly shows this structure.

Secondary shell deposits have also been mentioned as one of the generic characters in the short diagnosis of *Sinuities* s. str. given in the Treatise (Knight et al. 1960). The text-figure 6a on p. 1176, representing here *S. (S.) bilobatus*, however, probably shows the deposits as developed in *S. cancellatus*. (As far as I can recollect, they have not been observed in true *S. bilobatus* as yet. The only available note about weak secondary deposits in this species is that of Koken 1925 (p. 42) and possibly concerns a related species.)

Wahlman (1992) mentioned thin, in many cases ornamented parietal deposits in his diagnosis of *Sinuities* (p. O110). Nevertheless, he did not discuss this important phenomenon in the chapter on functional morphology (p. O44). He described the secondary shell deposits in *Sinuities pervoluta* (ULRICH et SCOFIELD, 1897) (parietal deposits granistriate), *S. cancellatus* (parietal inductura thin, folding over venter of coil onto umbilical region, marked by fine, closely spaced growth lines, giving a faint cancellate appearance), *S. obesus* (ULRICH in ULRICH et SCOFIELD, 1897) (parietal deposits quite thin, ornamentation unknown), and *S. granistriatus* (parietal deposit fairly thin, with fine pitting. (This pitting, figured by Wahlman on Pl. 45, figs 1, 2, was formed by an unknown epifaunal element (probably alga?); it has been described by Hoare, Atwater, and Sparks 1980 in the Pennsylvanian gastropod *Microdoma conicum* MEEK et WORTHEN, 1867 from the Vanport marine unit of the Allegheny Group in Ohio. It has also been observed in a Silurian holopeiform gastropod from Bohemia by Horný and Peel (in press).)

In the same year, Horný (1992) noticed secondary shell deposits in *Sinuities* from Bohemia (p. 96, in Czech, p. 98, in English).

## Material

The first specimen of *Sinuities* from Bohemia in which the presence of secondary shell deposits was ascertained in 1988, comes from the collection of the late Ing. F. Hanuš (Hanus coll. No 381), deposited in the Department of Palaeontology, National Museum, Prague (cat.

No. L 30060). It is an immature specimen of *Sinuities reticulatus* PERNER, 1903, an internal mould with a counterpart, preserved in a small, atypical, flat, decalcified siliceous concretion, found in the Šárka Formation (Llanvirn) at Praha-Šárka. No traces of secondary shell deposits have been found on other specimens with preserved outer shell surface (about 160 external moulds or counterparts of internal moulds from different localities, mostly Osek near Rokycany and Praha-Šárka (see Horný 1992, p. 84)). In 1992, Ing. V. Peršín found a concretion in the Šárka Formation at Volduchy near Rokycany, containing several specimens of *Sinuities sowerbyi* PERNER, 1903 (L 30061). A counterpart of one of them shows the secondary shell deposits in the umbilical region. It is an exceedingly rare find, as there exist at least 600 specimens in the collections showing external shell surface (as in the previous species) but none of them with the secondary shell deposits (see Horný 1992, *ibidem*).

In 1993, Dr Jaroslav Kraft, CSc. from the West Bohemian Museum, Plzeň, arranged for me the loan of 15 mature and immature, but not juvenile, specimens of *Sinuities reticulatus* from the collection of different gastropods in concretions, gathered by Libor Novotný on the fields in the vicinity of Cheznovice near Rokycany. All of them come from weathered shales of the Šárka Formation. Additional material loaned for study in 1994, included similar material. Both lots together contained about 50 specimens of *Sinuities reticulatus*, of which 23 preserved traces of secondary shell deposits, and about 10 specimens of *S. sowerbyi*, 2 of them with these deposits. The 25 specimens studied have been deposited in the Museum of Dr B. Horák at Rokycany (Nos 65938 - 65962); the remaining part, seemingly containing further, more recently found specimens, is housed in the private collection of L. Novotný at Cheznovice.

## Preservation

All specimens studied come from small siliceous concretions derived from the Llanvirnian Šárka Formation. The specimen L 30060 (*S. reticulatus*) from Praha-Šárka is preserved as an internal mould with a counterpart, which shows a well preserved outer shell sculpture including the secondary shell deposits (Pl. 4, fig. 2). Similarly preserved is the specimen of *S. sowerbyi* from Volduchy (L 30061), in which the surfaces of the internal mould and its counterpart are slightly covered with limonite. The concretions originated as carbonate, seemingly calcareous, structures in fine clayey sediments, now represented by about 100 m thick sequence of blackish micaceous shales. During the diagenetic processes, the shell matrix, originally calcitic and aragonitic, has been dissolved. In cases where the dissolution took place early after burial of the shell, external moulds originated which are relatively common in majority of localities. Most common are finds of internal moulds with separated counterparts, showing a well preserved outer surface; the shell matrix was partly or entirely substituted with ankerite or pyrite during postdiagenetic processes, and these minerals have been subsequently often dissolved during the Quaternary weathering, leaving certain amount of limonite or gypsum in the otherwise empty space after the shell.

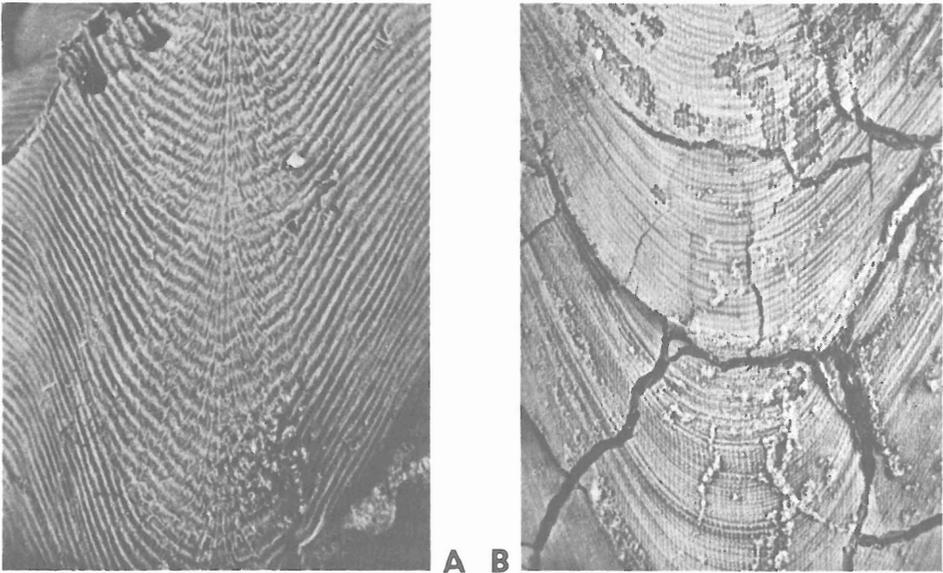
Quite different is the preservation of finds from Cheznovice. The specimens are partly exposed on the surface of small concretions, or represent concretions by themselves. As all layers of the shell matrix are totally substituted by silica, the substitution must have taken place early after the burial of the shell, before solution of the probably aragonitic, less stable secondary shell deposits. This unique kind of preservation presumes conditions influenced with silicic acid in that local area of the sea bottom.

Characteristic of some of these specimens is irregular corrugation or waving of the shell surface (Pl. 3, figs 1, 2; Pl. 7, figs 1 - 3), probably due to an enlargement of the shell wall volume surrounded by still plastic sediment. The material is not suitable for study in thin sections (Pl. 7, figs 1, 2).

## Secondary shell deposits in *Sinuities reticulatus* and *S. sowerbyi*

Ulrich and Scofield (1897) reported four shell layers in *Sinuities granistriatus* but, unfortunately, without a precise definition (see here on p. 89). Reed (1920) reported three layers of shell in *Sinuities soudleyensis*: inner smooth layer, second, thicker and ornamented layer,

and third, smooth outer layer. The description of these three layers, however, does not necessarily confirm the presence of unusual inductural deposits. Moore (1941) described three different secondary shell layers in *Euphemites*, later discussed by Yochelson 1960, Linsley 1978, and Harper and Rollins 1985. The lowermost, secreted by the anterior mantle flap, he called perinductura. The second layer, which he called inductura, is the well-known lirate layer typical for *Euphemites*, secreted by the posterior flap of the mantle. He considered this layer as homologous to the inductura (or callus, see Knight 1931), common in gastropods (see also Harper and Rollins 1985). The third layer, secreted over the lirate layer within and near the aperture, Moore called coinductura. Yochelson (1960) assumed that both the lirate inductura and the coinductura were secreted by the same part of the mantle (inductura during locomotion when fully extended, and coinductura when resting). Explaining this morphology, Harper and Rollins (1985) noted that the coinductura is “generally restricted to the area adjacent to and within the aperture, similar to the normal parietal inductura of other gastropods. Because of its position on the shell and its thickness, this layer on almost any other genus would have been called inductura” (p. 25). This observation is important for the terminology used here in *Sinuities*.



Text-fig. 1. Outer shell sculpture of the dorsal area in *Sinuities sowerbyi* (a, National Museum, L 29013,  $\times 10$ ), and *Sinuities reticulatus* (b, National Museum, L 29014,  $\times 8$ ). Latex impressions. Šárka Formation, Praha-Vokovice.

In the Bohemian *Sinuities reticulatus*, two layers of inductural deposits have been distinguished. The lower, carrying lirae and corrugation and obscuring a considerable part of the shell surface, has been secreted by the inner surface of the posterior flap of the mantle, directly over the uppermost shell layer. This deposit was thinnest aperturally, where the mantle flap probably periodically extended, and thickest near the parietal area of the aperture, constantly covered with the flap. The deposit is absent in the labro-umbilical depression. It is assumed that this layer is homologous to the lirate “inductura” of Moore in *Euphemites*. To avoid possible misunderstanding and to better distinguish the function, I use the term “subinductura”, which, etymologically, should express its position below the inductura proper.

Inductura, which is understood in accordance with Knight 1931, is probably synonymous to “coinductura” of Moore. It is a smooth, lamellar layer secreted by the general surface of the mantle over the subinductura, and filling the labro-umbilical depression. It has been

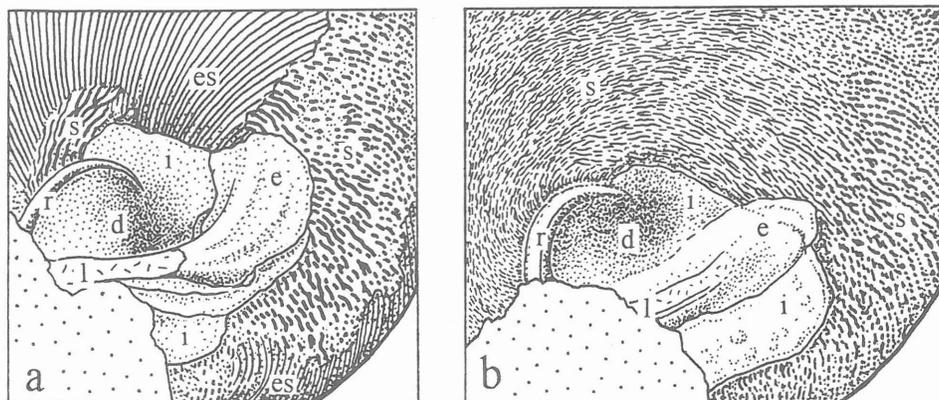
ascertained in large areas surrounding the bases of the columellar lips, and it also probably takes part in the construction of the umbilical ridge. It has not been found on the parietal area where it would be expected to cover the subinductural rugosities. The inductura must have been secreted either over the naked subinductural surface by a separate mantle fold, or, if we follow Yochelson's concept, by the posterior surface of the fold secreting the subinductura.

No perinductural deposits have been ascertained in the Bohemian species of *Sinuities*. The notice of Horný 1952 about remarkable perinductural deposits (p. 98) resulted from incomplete material and concerns the subinductura.

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The morphology and development of the secondary shell deposits cannot be explained without a description of the morphology of the umbilical area. The older descriptions (Koken 1897, 1925, Perner 1903, Reed 1920) indicate that the umbilicus in *Sinuities* is either narrow or wide (this concerns the condition of internal moulds), or plugged to a variable extent with callus. Knight (1941) observed in *Protowartha cancellata* that "umbilicus (is) wanting or very small and plugged with callus" (p. 279). Horný (1992) noticed "complicated apertural structures in the umbilical area" (p. 98) but did not describe them in detail, following the interior shell morphology. Ulrich and Scofield (1897) are the only authors who observed these structures correctly, as noted in their description of *Protowartha concinna*: "...the thickened base of the lip forms a small sharply defined and shallow umbilical depression..." (p. 874). The morphology of this umbilical depression is excellently preserved in the Bohemian specimens.

Near the umbilical area, at about 1/3-1/5 of its length (which is variable among different species), the lateral lip becomes excavated and bifurcates into two arms. The adapertural arm, bordering the internal whorl cavity, corresponds to the simple columellar labrum in other gastropods and smoothly joins the lateral wall of the early part of the final whorl. The second, abapertural arm, which I call the labro-umbilical ridge, joins the opposite wall of the umbilicus and runs down as a spiral ridge, decreasing towards the bottom of the plugged labro-umbilical depression. This ridge sharply limits the subinductural deposits towards the labro-umbilical depression. The concave labro-umbilical depression, bordered by the columellar labrum and the labro-umbilical ridge, has a shape of a slightly spirally twisted triangle, opened against the umbilical wall (Pl. 6, figs 1-3; Pl. 7, figs 1-3, Text-fig. 2). It is similar in both species studied, *S. reticulatus* and *S. sowerbyi*, and well illustrated by Ulrich and



Text-fig. 2. Umbilical area in *Sinuities reticulatus*. a - after MBHR 65948, Pl. 6, fig. 1; b - after MBHR 65960, Pl. 4, fig. 1. r - labro-umbilical ridge, d - labro-umbilical depression, l - columellar labrum, e - basal extension of the columellar labrum (with three rotated increments in 2a), es - external shell sculpture (spiral structures omitted), s - subinductura, i - inductura. Orig.

Scofield 1897 in *S. cancellatus* (Pl. 63, fig. 4). As it is possible to deduce from different figures, mostly those published by Ulrich and Scofield 1897, the length, width and depth of the depression is variable in various species. The surface of the labro-umbilical depression is smooth, covered with thin lamellae of inductural deposits, extending onto the lateral wall of the early part of the final whorl and surrounding the base of the columellar labrum. A somewhat similar labro-umbilical depression is developed in *Kodymites* HORNÝ, 1962 (Horný 1963, Pl. 40, fig. 2).

### *Sinuities reticulatus*

(Plates 1-7; Text-figs 1b, 2-4)

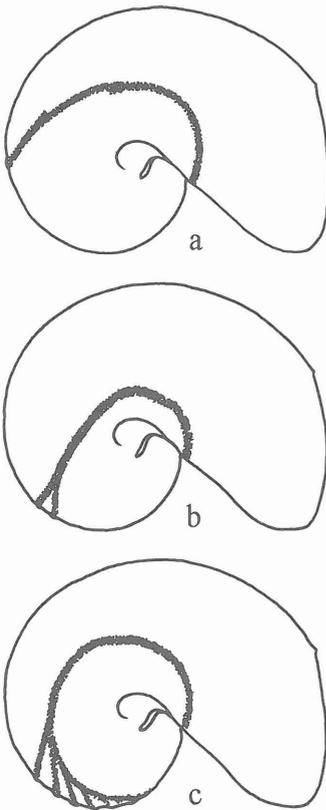
In *S. reticulatus*, the subinductura covers the dorsum of at least the first half of the final whorl, extending onto the lateral sides of the whorls, surrounding the umbilical area and sharply ending at the labro-umbilical ridge. It is thin (on average 0.1 mm) but originally continuously covering parts of the sculptured shell exterior (Pl. 4, fig. 1). Its surface consists of spiral, almost concentric, irregular wavy revolving lirae near the labro-umbilical depression, often with anastomoses, locally inflated, discontinuous or reduced to the ro of islets, probably emphasized by postmortem dissolution. The anterodorsally more distant structures, originally weaker, usually fade away and are often reduced to isolated islets (Pl. 4, fig. 2).

Being concentrically arranged, the structures approximately copy the spiral elements of the outer shell sculpture, however, being much less dense (about 6-10 lirae per 1 mm, 10-15 spiral lines of the outer shell sculpture per 1 mm in average).

In posterodorsal direction, approximately halfway between the umbilicus and the dorsum, the spiral subinductural lirae become more wavy, often irregularly bifurcating, disintegrate into wrinkled rows of granulose rugosities (slightly resembling the "pearling" of the deer antlers), and gradually getting the direction of the transverse elements of the outer shell sculpture (Pl. 4, fig. 1; Pl. 5, figs 1, 2, 4; Pl. 6, figs 1, 2). Finally they precisely copy the dorsal sinus by rows of isolated grains, emphasizing the transverse ribs, cut by the sharp spiral grooves of the proper shell surface (Pl. 5, fig. 2).

The subinductural deposits have not been observed in the adapertural part of the shell, including the lateral lobes. This does not mean, however, that these parts of the shell were really uncovered. Being the youngest and thinnest deposit, they may have been first to be completely dissolved. The last isolated patches of the typical granulose subinductural deposit have been ascertained about 2/5 of the final whorl back from the dorsal apertural emargination (Pl. 3, fig. 2).

A very peculiar morphological feature, previously undescribed, has been found in seven specimens of *S. reticulatus*. It is a thick, narrow dike, secreted over the subinductural deposits, obliquely across the shell (Pl. 1, 2, 3). Because of its shape, I call this structure subinductural vallum. It is almost symmetrical on both sides



Text-fig. 3. Variable shape of the subinductural vallum in *S. reticulatus*. a - specimen MBHR 65955, b - specimen MBHR 65952, c - specimen MBHR 65948. Orig.

of the shell, beginning at the lateral lip near the place where it bifurcates (i. e. where the whorl is widest), and almost perpendicular to it. Following roughly the subinductural structures, it runs along the sides of the shell, and crosses the dorsum forming there an arch, much wider than the dorsal sinus indicated by the collabral ribs. Adapturally, it usually limits the preserved extent of the subinductural deposits. The subinductural vallum is about 1.0 mm wide and maximum 0.5 mm thick, with a corroded surface, in some specimens discontinuous or absent as being partly or even entirely dissolved. It also locally extends over the granulose subinductural deposits in the dorsal area, forming flat, irregularly bordered crusts (Pl. 3, figs 1, 2). In the specimen L 65948 (Pl. 1, figs 3-6), at least six positions of the vallum are preserved in the dorsal area, indicating gradual widening of the dorsal arch in an adaptural direction. Although lying above the subinductura, the subinductural vallum is believed to have been secreted by the addorsal and forward edges of the posterior mantle flap in retracted position. In similar fashion to the dark bands in *Euphemites* (Weller 1930, Moore 1941, Yochelson 1960, Harper and Rollins 1985), the vallum probably indicates a relatively long-termed position of the mantle flap edge. It may also indicate the line of the deposit/water interface, which may have stimulated the secretion of the calcium carbonate deposit. As demonstrated by the specimen L 65955 (Pl. 3, fig. 2), small islets of subinductural deposit occur also outside the vallum (i. e. adapturally), where the mantle flap periodically extended. During the growth of the shell, the vallum deposits have been probably gradually resorbed. Location and shape of the vallum on the shell surface is variable among different specimens, being defined by variable extent of the subinductural deposits. Similar as its slightly inequilateral development, it may have been conditioned by individual factors of the animal.

#### *Sinuities sowerbyi*

(Plate 8, Text-fig. 1a)

As already noted previously, the labro-umbilical depression between the two labral arms is developed in the same way as in *S. reticulatus* (Pl. 8, figs 3, 6). Inductural deposits have been found in two specimens only, L 30061 (Volduchy near Rokycany) and MBHR 65939 (Cheznovice near Rokycany). In specimen L 30061 the subinductural deposits were studied on a latex impression. The deposits are preserved in close proximity to the labro-umbilical depression as fine, slightly waved, discontinuous lirae, perpendicularly joining the umbilical ridge and concentrically arranged around the centre of the shell, obliquely crossing the labral ribs of the shell surface (Pl. 8, figs 2, 5). They undoubtedly represent a small residue strongly affected by dissolution. The second, immature specimen, MBHR 65939, is preserved on the surface of a concretion. A rather small patch of subinductura is preserved only in the proximity of the umbilical area, as a few incontinuous lirae obliquely crossing the collabral ribs. Deposits of inductura, with the exception of the fillings within the labro-umbilical depression, have not been ascertained.

#### Mode of life of *Sinuities*

Not much attention has been paid to the mode of life of this genus by previous authors. Titus and Cameron (1976) reported *Sinuities* as common in lagoonal and nearshore shoal carbonate facies of the Trenton Group in eastern North America, similarly as did Titus (1982) who found it also in the foreshoal shallow shelf facies and in the offshore open shelf facies. Byers and Galvin (1979), analysing the shallow subtidal Rocklandian deposits of Wisconsin, found *Sinuities* to be the most abundant member of assemblages, considering it to be an algal-browsing archaeogastropod. Hurst (1979), describing the fauna of the Upper Caradocian Series in England, regarded *Sinuities* a characteristic element of the early diversification faunas succeeding a *Nuculites*-trilobite fauna that colonized barren fine-mud bottoms. He reported it from 8-13 depositional facies (offshore silt facies to deeper mud environments). Wahlman (1992), describing the Middle and Upper Ordovician symmetrical univalved molluscs from the Cincinnati arch region (U. S. A.), reported *Sinuities* to be most common in

shaly and silty rocks. Comparing it with *Cyrtolites* CONRAD, 1838, he found *Sinuities* to be more dominant in deeper water facies; as he stated, its shells are rarely encrusted, because of their smoother shell surface, of their occupation of more turbid environments, or some aspects of their mode of life (p. O29). He also found *Sinuities* with highly irregular apertural margins well adapted to the efficient channelling of water through the shell. He concluded, that *Sinuities* may have been a deposit feeder on soft bottoms.

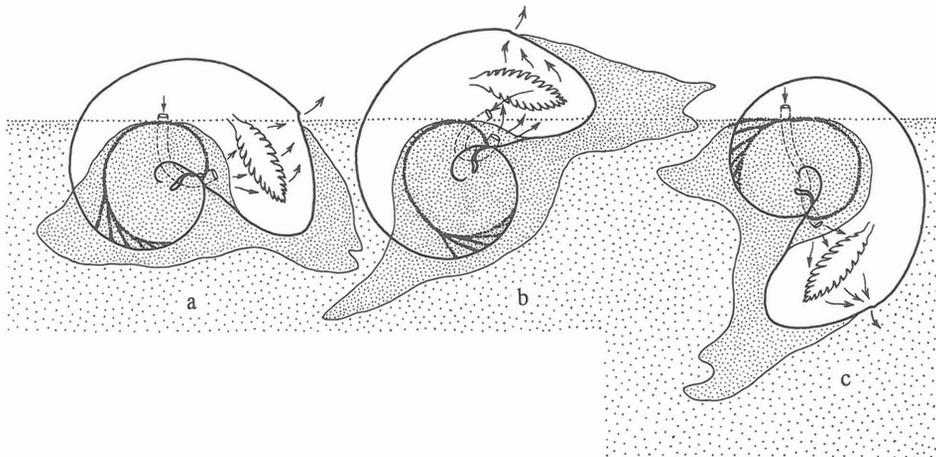
Horný (1992), describing the muscle scars in *S. reticulatus* and *S. sowerbyi* from the Barrandian area, published a few notes (p. 80) concerning preservation and mode of occurrence of the shells. He stated that in the majority of cases the shells were deposited in the soft sediment complete, with preserved apertures, and that they probably were buried early after death of the animal, without being transported. A groups of specimens oriented perpendicularly to the bedding plane, and roughly in one direction, could indicate a life assemblage (Horný 1992, p. 82, Text-fig. 2). Finds of bivalves (*Redonia bohémica* BARR.) with the valves *in situ*, lying in close proximity, may confirm this presumption. No shell repair has been ascertained, and the shells are never overgrown with epibionts.

Following the criteria diagnostic of a probable infaunal mode of life in bellerophontiform molluscs, formulated by Harper and Rollins 1985, and based on *Euphemites* and functionally related taxa, it is possible to find that most of them can be applied to *Sinuities*: 1 - lack of apertural flare, 3 - low rate of whorl expansion, 4 - semi-radial aperture (better radial in *Sinuities*), 5 - extensive secondary shell deposits, 9 - absence of shell breakage and repair, and 10 - associated lithologies indicative of penetrable substrates such as mudstones. Criteria which are not in agreement or agree only partially are: 2 - restricted aperture: aperture is not restricted in *Sinuities*; 6 - absence of extensive collabral ornament: most of *Sinuities* species have very fine collabral lines but there exist finely ribbed species; 7 - dorsolateral or umbilical furrows: absent in *Sinuities*; 8 - colour patterns indicative of mantle extension and retraction capabilities: unknown in *Sinuities* but the vallum is well developed. If compared with *Euphemites* and *Praematuratropis*, the shell of *Sinuities* is definitely less "internal": it is thin-shelled, light, superficially resembling some epibenthic bellerophontacean genera. It is probable, therefore, that adaptation of this genus to a semi-infaunal mode of life was not exclusive, and perhaps may have been a variable habit among different species.

Harper and Rollins (1985) have presented a detailed review of reasons which led to the conclusions that *Euphemites* and a few similar genera of gastropods lived as infaunal or semi-infaunal animals (see also Weller 1930, Moore 1941, Yochelson 1960, Rollins and al. 1971, Linsley 1978, Palmer 1980). The morphology of the aperture and the secondary shell deposits indicate that it had a large soft body, adapted for life on/in a soft substrate, and that its shell was, to variable extent, enveloped in mantle flaps.

The presence of mantle flaps is usually explained as a protection of the shell against sediment abrasion. This, however, could have hardly been the primary purpose in soft clayey surroundings. They may have also protected the shell against the chemical action of the substrate in cases where the periostracum was inadequately developed or absent, or the otherwise naked secondary deposits reinforced the shell against the pressure of deposits. A third, most probable reason, may have been connected with the function of the inhalant siphons. The mantle flap, covering the shell exterior around the umbilical area, may have originated to facilitate the function of the inhalant siphons. Being protected on the outside by the metapodium folds, the siphons thus lay between two folds of tissue, facilitating their movements (extension and swinging) during the animal's activity.

The probably large cephalopodal mass with a wide foot, adapted for effective burrowing or ploughing, and the mantle flap, probably periodically moving, were operated by large, deep and specially positioned muscles, characteristic for the sinuitids (see e. g. Peel 1980, 1991, Horný 1992, in press). The semi-infaunal mode of life also explains the large anterolateral lobes or shields, which protected the probably bipectinate ctenidia against the pressure of deposit and fouling. The more globose sinuitids with short lobes, like *Strangulites strangulatus* (BARRANDE in PERNER, 1903) or *Sylvestrosphaera lemchei* PEEL, 1980 may have been epibenthic, with no need of secondary shell deposits. The well-preserved specimens of *S. strangulatus* really seem to lack subinductura (Horný 1963, Pl. 5, fig. 4, and 1990, Pl. 2, fig. 2) but more material is necessary to prove this observation. Otherwise the extent of the secondary shell deposits probably depended on the mode of the animal's activity (similarly as in *Euphemites*: see Yochelson 1960, Harper and Rollins 1985, where it varies from species



Text-fig. 4. Suggested life positions of *Sinuites reticulatus*. a – resting and defence position, b – ploughing position, c – burrowing and hunting position. Note the inhalant siphons, gradually swinging across the whole extent of the subinductural deposits between the mantle flap and the metapodium fold during different life positions. As figured, the mantle flap is completely hidden below the metapodium fold, enveloping most of the shell. Orig.

to species (Harper and Rollins 1985, p. 25); similar situation can be expected in *Sinuites*). Several authors expressed a suggestion that bellerophonitiform molluscs with a globose, compact shell with narrow or closed umbilici may have lived as active predators (Linsley 1978, Peel 1984, Horný 1995), but Harper and Rollins 1985 argued that they have found no evidence to confirm this, speculating that *Euphemites* was a deposit feeder, similarly as did Wahlman (1992) in the case of *Sinuites*.

According to the functional morphology of *Sinuites*, it is suspected that it lived as a predator and not as a less active deposit feeder. Different species of this genus, some of them fairly common, like *S. reticulatus* or *S. sowerbyi*, which may have flourished, respectively, in large communities, inhabited quiet-water, mostly deeper, areas of the Ordovician seas, preferring soft, clayey or calcareous muddy bottom; they have never been found in sandy deposits in Bohemia. Here was the Llanvirnian sea characterised by rather diversified, predominantly epibenthic assemblages of *Euorthisina* Community, which corresponds to the benthic assemblage 3 of Boucot (Havlíček 1982) and approximately ranges to the transition from the *Cruziana* to the *Zoophycos* ichnofacies (Mikuláš 1991). It consists of many trilobites, ostracodes, hyoliths, bivalves, cephalopods, brachiopods, echinoderms, and others. Gastropods were not very abundant, but *Tropidodiscus* (*Peruniscus*) *pusillus* (BARRANDE in PERNER, 1903), also indicating quiet-water environments (Linsley 1978a), lived here in enormous large populations (perhaps as an algal foliage dweller – see Peel 1975, 1977, 1978). The shales and the concretions also contain trace fossils, indicating the presence of infauna (Chlu-páč and Kukul 1988, Mikuláš 1991, 1993, 1994, Horný 1992).

*Sinuites*, adapted for a semi-infaunal mode of life, must have had a reason for its muddy substrate preference. The most probable reason was food. As a predator, it may have been specialized – at least its species with long apertural lobes – to feed on infaunal invertebrates, dwelling in the surface layer of the soft muddy sediment.

Restoration of the positions of the living animal has been based on the following presumptions (Text-fig. 4).

a) the resting and defence position: the anal (dorsal) emargination is just above the sediment/water interface, enabling continuous outflow of desoxygenated water and faeces; the subinductural vallum is believed to originate at the sediment/water interface, and therefore the upper point of the resting position is limited by the vallum arch on the dorsal part of the whorl; inhalant siphons run up vertically across the umbilical area; the animal rests in

a position in which crowded shells are sometimes found in the concretions (see Horný 1992, Text-figs 2 and 4).

b) ploughing position: the animal rotates along the shell axis, so that the anal emargination is directed obliquely forwards or almost upwards, depending on the mode and speed of ploughing; in this position, the widest part of the shell is above the sediment, and the narrow part, covered by the posterior mantle flap and foot fold, penetrates the sediment; the siphons are directed obliquely forwards, detecting the water.

c) burrowing and hunting position: when detecting the prey, the animal rotates along the shell axis so that the lobes are directed downwards to reach the desirable depth and direction; in this position the animal can burrow and seek the prey; the siphons are probably inactive during these relatively short actions, but could also vertically stick up in the most posterior position.

Restoring *Euphemites*, Harper and Rollins 1985 paid great attention to the shape of the bellerophonacean foot and to locomotion on a soft substrate (McNair et al. 1981), but modified for the burrowing condition of *Euphemites*. Their final restoration of *Euphemites* offers inspiration for the interpretation of *Sinuities*, although there are dissimilarities determined by different shell morphology. *Sinuities* was probably also characterised by ciliary locomotion, typical for gastropods living on soft substrates, and perhaps even by “subsidiary locomotion produced by monotaxic muscular gliding, providing extra power needed for burrowing” (Harper and Rollins, p. 30).

A common problem for restorations of both genera is the inhalant siphons. In *Euphemites*, as well as in *Sinuities*, they are expected to have been located in the postero-lateral parts of the aperture. According to Harper and Rollins 1985, the inhalant siphons are “sticking up out of the umbilical area under the metapodium” (p. 32). This, of course, brings an exception to the Linsleys law of reentrants (1977; see also Berg-Madsen and Peel 1978, and Harper and Rollins 1982). Describing the functional morphology of *Sinuitopsis* and *Neocyrtolites* HORNÝ, 1965 (Horný 1991, 1993), I again supported the importance of this law for determination of the cyrtoneid tergomyans, and I still have no reason to renounce this conception. The anatomy inferred in *Euphemites* and *Sinuities* does not disclaim the validity of this law: it only shows how necessary is to evaluate the whole complex of morphological characters (in this connection see above all Peel 1974, 1976, 1980, 1986, 1991). Because of the mantle and epipodium folds, the inhalant re-entrants cannot be located anterolaterally or laterally along the labrum (as, for example, in *Plectonotus* CLARKE, 1899 (Peel 1974)). Their anterior position is, however, substituted by the flexible rolls of tissue, the inhalant siphons, operated by effective muscles enabling them to be oriented in the most beneficial direction (undoubtedly forward when the animal moves and tests the surroundings). The bifurcation of the labrum and the presence of the labro-umbilical depression are seemingly structures supporting the function of the inhalant siphons, the labro-umbilical depression being probably the place of insertion of the siphonal muscles.

## Systematic criteria

In the Treatise, Knight and al. (1960) recognized five genera within the Subfamily Sinuitinae: *Anconochilus* KNIGHT, 1947, *Sinuities* (*Sinuities*) KOKEN, 1896, *Sinuities* (*Sinuitopsis*) PERNER, 1903, *Ptomatis* CLARKE, 1899, and *Crenistriella* KNIGHT, 1945. Later have been added *Sinosinuities* YU, 1961, *Strangulites* HORNÝ, 1962, and *Sylvestrosphaera* PEEL, 1980. *Sinuitopsis* has been excluded from the Class Gastropoda by Horný (1991) and classed as a cyrtoneid tergomyan. The position of *Strangulites* remains unclear; Wahlman (1992) proposed to synonymize it with *Sinuities* but it may be emended if the absence of subinductural deposits is proved; *Sinosinuities* (Wu 1961) remains imperfectly known. According to Peel 1980, the Family Sinuitidae contains only three genera, the Ordovician *Sinuities* and *Strangulites*, and the Silurian *Sylvestrosphaera*. While *Strangulites* and *Sylvestrosphaera* are monotypic, *Sinuities* contains several tens of species, mostly distributed in Europe and North America. On the basis of external shell sculpture, species of *Sinuities* can be divided in two groups - species with simple collabral structures (like *S. bilobatus*) and those with both radial and collabral elements, forming a fine cancellate sculpture (like *S. cancellatus*). Born (1916) proposed to preserve the original name of Ulrich and Scofield 1897, *Protowarthia*,

for the second group, but his suggestion has not been followed. A wide variability exists in shell parameters, the shape of the dorsal sinus, and the length of the apertural lobes in both groups, but these have not been evaluated as yet. Horný (1992) noted slight differences in the shape of the retractor muscle scars in different species but was cautious to attribute to them any serious systematic meaning. Secondary shell deposits have been observed in at least nine species, possessing either transverse or cancellate sculpture. As the secondary shell deposits are generally rarely preserved, being too susceptible to dissolution, they can be also hardly useful as systematic criteria at the present state of knowledge.

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## Explanation of plates

All specimens were coated with ammonium chloride before photographing.

### Plate 1

*Sinuities reticulatus* PERNER, 1903

- 1, 2. Specimen MBHR 65955. 1 - Right side with well developed corrugate subinductural structures and a strong vallum. The part of the shell outside vallum is shaddowed (compare Pl. 3, figs 1, 2, and Pl. 7, fig. 2). 2 - Left side; subinductural structures are dissolved, the vallum is strongly corroded and therefore missing adeptural. Note the inductural deposits in the parietal area and the well-preserved labro-umbilical ridge (compare Pl. 7, figs 1, 3). Both  $\times 3$ .
- 3 - 6. Specimen MBHR 65948. 3 - right side with almost dissolved subinductural deposits but showing outer shell sculpture; 4 - left side with strong vallum, divided in several increments in the dorsal area. Subinductural deposits are almost dissolved but inductural deposits and the labro-umbilical ridge are well preserved (compare Pl. 7, figs 1, 3). 5 - oblique dorsal, and 6 - dorsal views showing the dorsal part of the vallum with several positions of a slightly asymmetrical dorsal arch. All  $\times 3$ .

### Plate 2

*Sinuities reticulatus* PERNER, 1903

- 1, 2. Specimen MBHR 65952. 1 - dorsal view, illustrating two positions of slightly asymmetrical dorsal vallum arch, much wider than the dorsal sinus (above). 2 - right side with a well-developed vallum and growth structures of the shell exterior, indicating the shape of the antero-lateral lobes. Both  $\times 3$ .
3. Specimen MBHR 65960. The best preserved specimen, left side showing the reticulate outer shell sculpture, transparently obscured by fine, thin subinductural deposits (compare Pl. 4, fig. 1 and Pl. 5, figs 1, 2).  $\times 4$ .
- 4 - 6. Specimen MBHR 65959. 4 - left side with traces of vallum and fine subinductural lirae, to the right of the umbilical area (compare Pl. 6, fig. 4). 5 - right side. 6 - dorsal view showing the vallum arch, passing to flat crusts down onto the younger parts of the whorl. All  $\times 2$ .

### Plate 3

*Sinuities reticulatus* PERNER, 1903

- 1, 2. Specimen MBHR 65955, right side (compare Pl. 1, fig. 1). 1 - oblique right dorso-lateral view, showing a thick vallum, passing to flat crusts, and corrugate subinductural deposits with anastomoses (adumbilical to the vallum). The smooth area between the corrugate deposits and the labro-umbilical depression is a weathered shell surface almost lacking its sculpture. Note the corrugate shell surface in the dorsal area (upper right). 2 - oblique right latero-dorsal view, showing large areas of a cancellate shell surface bearing islets of subinductural deposits with granulose rugosities adapertural to the vallum (black arrows), which are again covered by irregular crusts of flat vallum deposits (white arrows). Both  $\times 6.5$ .

### Plate 4

*Sinuities reticulatus* PERNER, 1903

1. Specimen MHBR 65960, left side (compare Pl. 2, fig. 3, and Pl. 5, figs 1, 2). A thin subinductural deposit covers partly visible transverse shell sculptures (above the umbilical area). Note the fine spiral anastomosing subinductural lirae surrounding the umbilical area, addorsal gradually deviated and desintegrated into granulose rugosities (to the right). The inductura, probably showing its original extent, covers the bottom of the labro-umbilical depression, delimited by the labro-umbilical ridge (black arrow) and the columellar labrum (white arrow). Note the irregular surface of the inductura, bearing pustulose rugosities, and the plate-like base of the columellar labrum, extending over the inductura onto the subinductural deposit (compare Text-fig. 2).  $\times 7$ .
2. Specimen L 30060, right side of a latex impression. Residue of partially dissolved subinductural deposits overlying the cancellate shell exterior. The oldest, strongest, subinductural deposits (to the left) cover the parietal parts of the final whorl, whilst the weakest, incontinuous traces correspond to the younger increments of subinductura. Note the sharp margin of the labro-umbilical ridge, on which the subinductural structures almost perpendicularly terminate.  $\times 9.5$ .

Figs 1 and 2 illustrate two kinds of preservation of the subinductural deposit; the first is rare and probably represents the original appearance of the deposit, whilst the second is more common, showing its gradual dissolution.

Plate 5

*Sinuities reticulatus* PERNER, 1903

- 1, 2. Specimen MBHR 65960 (compare Pl. 2, fig. 3, and Pl. 4, fig. 1). 1 - dorsal view of the final whorl near the parietal area, showing the subinductural deposit, copying the dorsal sinus by rows of granulose rugosities. 2 - latero-dorsal view, showing the transition between the spiral and transverse subinductural structures (to the right), strongly affected by dissolution. Both  $\times 7$ .
3. Specimen MBHR 65946, left side. Thin traces of deeply dissolved spiral subinductural structures, and a residue of the vallum (upper part of the figure). Note the transverse sculpture of the shell exterior in the background.  $\times 7$ .
4. Specimen MBHR 65957. A narrow patch of shell on the left side of an internal mould, with well-preserved thin spiral lirae of subinductura, addorsal deviated to join the transverse shell sculptures. Note the anastomoses, bifurcating lirae and disintegration of the structures in the dorsal area.  $\times 9$ .

Plate 6

*Sinuities reticulatus* PERNER, 1903

- 1, 2. Specimen MBHR 65948 (compare Pl. 1, figs 3 - 6). 1 - oblique left lateral view showing the labro-umbilical ridge, the labro-umbilical depression, the widened base of the columellar labrum, joining the inductura, and the inductura, overlapping the subinductural lirae, discontinuous in the area of transition between their spiral and transverse directions. 2 - the same, more dorso-lateral oriented view, showing the joint of the columellar labrum with the inductura; the plate-like base extends onto the subinductural deposits, similar as in Pl. 4, fig. 1. Note the periodical, rotated increments of the columellar labrum in both figures (compare Text-fig. 2).  $\times 7$ .
3. Specimen MBHR 65950, left lateral view, showing fine subinductural lirae with anastomoses, the discontinuous lirae between the spiral and transverse structures (to the left), the sharp labro-umbilical ridge limiting the subinductural structures towards the smooth labro-umbilical depression, and the base of the columellar labrum.  $\times 8$ .
4. Specimen MBHR 65959 (see Pl. 2, fig. 4). Thin, dense spiral subinductural lirae, addorsally passing to transverse structures (bottom).  $\times 6.5$ .

Plate 7

*Sinuities reticulatus* PERNER, 1903

- 1 - 3. Specimen MBHR 65955 (compare Pl. 1, figs 1, 2). 1 - left anterolateral view showing the labro-umbilical ridge, joining the apertural margin, the smooth labro-umbilical depression, and the inductural deposit, ostensibly directly overlapping the shell surface (the subinductural layer was dissolved). Note the pustulose, corrugate surface of the partly dissolved shell exterior. 2 - right anterolateral view showing preserved traces of subinductural deposits, quite strong to the right, overlain by the inductura. The columellar labrum is broken off on both sides and the recrystallized shell wall is well visible. 3 - oblique laterodorsal view. The smooth inductural deposit, covering the subinductura, ostensibly overlies the cancellate outer shell surface. All  $\times 7.5$ .
4. Specimen MBHR 65945. Left lateral view showing periphery of the labro-umbilical depression, irregularly plugged with inductural deposit, and the adjacent abapertural area mostly covered with subinductura. Note its fine, irregular spiral structure, locally decomposed in fine rugosities on the periphery (to the right), where it passes into the transversely arranged deposit of the dorsal area.  $\times 9$ .

Plate 8

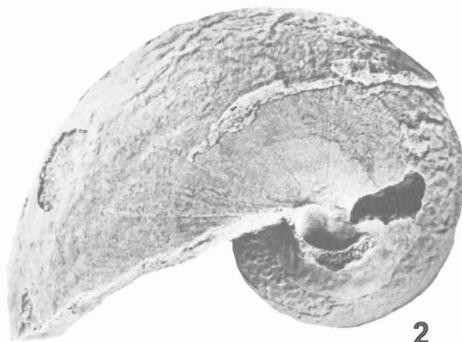
*Sinuities sowerbyi* PERNER, 1903

- 1 - 3. Specimen L 30061. 1 - a latex impression, illustrating the assemblage with *Tropidodiscus (Peruniscus) pusillus* (BARRANDE in PERNER, 1903).  $\times 3.5$ . 2 - right side, umbilical area with residue of subinductural deposits. The latero-umbilical ridge, columellar labrum and a part of the labro-umbilical depression are well visible.  $\times 9.5$ . 3 - oblique lateral view, showing the smooth latero-umbilical depression.  $\times 7$ .

- 4, 5. Specimen MBHR 65938. 4 - right side with transversely ribbed shell exterior,  $\times 5$ . 5 - umbilical area with a few spiral subinductural lirae cutting the ribs,  $\times 12$ .
6. Specimen MBHR 65939. Right side, umbilical area with the labro-umbilical ridge, labro-umbilical depression and the basal part of the columellar labrum, widened to a plate-like extension; the subinductural and inductural deposits are not preserved.  $\times 7$ .



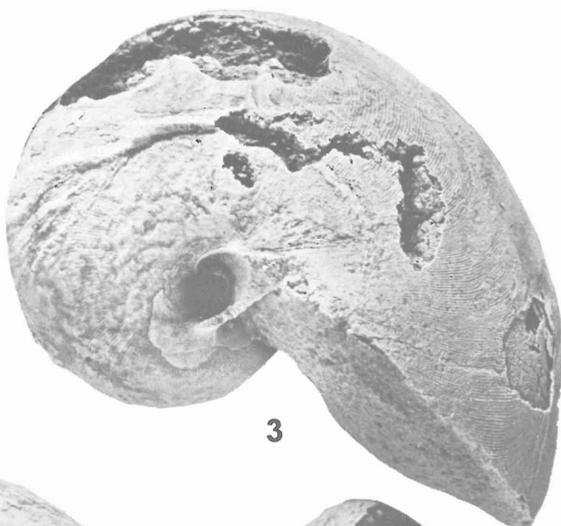
1



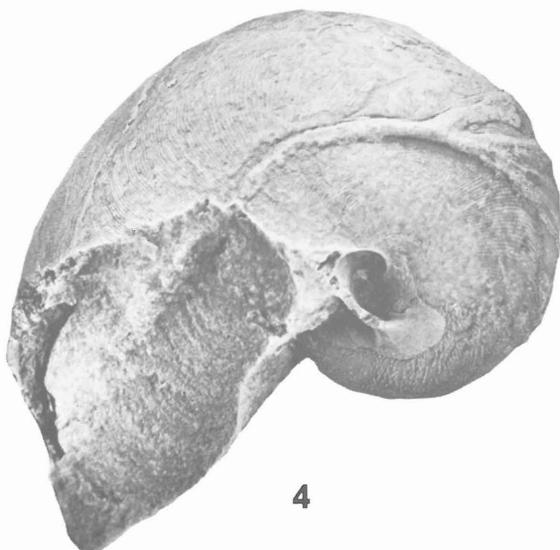
2



5



3



4



6

