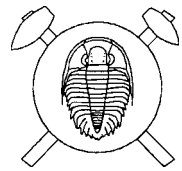
# Secondary shell deposits in a new plectonotid gastropod genus (Bellerophontoidea, Mollusca) from the Early Devonian of Bohemia



## Sekundární schránkové uloženiny u nového plectonotidního gastropodového rodu (Bellerophontoidea, Mollusca) ze spodního devonu Čech (Czech summary)

*(2 text-figs)*

JIŘÍ FRÝDA

*Czech Geological Survey, Klárov 3, 118 21 Praha 1, Czech Republic, fryda@cgu.cz*

Secondary shell deposits are described in a new plectonotid genus, *Blodgettinotus*, from the *Boucotonotus-Palaeozygopleura* Community of the Prague Basin (Bohemia). The new taxon was found in the uppermost part of the Třebotov Limestone (Daleje-Třebotov Formation; late Emsian, late Early Devonian). The genera *Boucotonotus* and *Blodgettinotus* share some shell characters and are placed in a new tribe Boucotonotini of the subfamily Plectonotinae. The occurrence of secondary shell deposits in bellerophontiform molluscs is discussed. It is suggested that they were developed independently in several groups of these molluscs; thus, this feature has limited significance for their suprageneric classification.

*Key words:* Paleozoic, Devonian, Gastropoda, Bellerophontoidea, secondary shell deposists, Prague Basin

## Introduction

The higher classification of a bellerophontiform molluscs, one of the most frequently discussed group of the Paleozoic molluscs, is still problematic (see Yochelson 1967, Horný 1992, Peel 1991a,b, Wahlman 1992, and Frýda 1999a for review). Unusual attention in this molluscan group has been caused by their key-position in evolutionary models describing phylogenetic relationships between the classes Monoplacophora and Gastropoda. Knight (1952) considered bellerophontoideans to be torted gastropods forming an intermediate group between isostrophic monoplacophorans and pleurotomarioidean archaeogastropods. On the other hand, Yochelson (1967, 1984) suggested that bellerophontoideans may be derived from pleurotomarioidean archaeogastropods and their shells are secondarily symmetrical. In addition, Rollins and Batten (1968) suggested that the bellerophontiform and pleurotomarioidean gastropods originated independently from monoplacophorans several times during the Cambrian, Ordovician and Devonian, and thus gastropods represent a polyphyletic group. Recently Bandel and Geldmacher (1996) recalled Naef's (1911) almost forgotten hypothesis considering bellerophontiform molluscs (=Amphigastropoda) to represent gastropods in which the torsion of the soft body occurred during the early benthic stage, resulting in a bilaterally symmetrical shell. This model seems to be evidenced by the discovery of a non-archaogastropod protoconch type in *Bellerophon* (Frýda 1998, 1999a). In contrast to all the above mentioned models, Runnegar and Pojeta (1974) suggested that all bellerophontoideans are isostrophic monoplacophorans. Recent data of the protoconch morphology in the bellerophontiform molluscs (Dzik 1978, 1981; Horný 1993; Frýda 1998a, 1999a, c) suggest that they may represent a polyphyletic group. To sum up, the bellerophontiform molluscs are very important group(s) for our understanding of the early evolution of Mollusca, but the still poor knowledge of these molluscs has provided sufficient space for many, often contradictory, speculations. In this short paper, an occurrence of secondary shell deposits in a plectonotid bellerophontoidean is described for the first time. All the herein described specimens are deposited in the collection of Jiří Frýda, Czech Geological Survey, Prague.

## Systematic part

Subclass A m p h i g a s t r o p o d a
Superfamily B e l l e r o p h o n t o i d e a M'Coy, 1851
Family B u c a n i i d a e Ulrich and Scofield, 1897

R e m a r k s : Recently Wahlman (1992) discussed the suprageneric classification of bellerophontoidean molluscs in detail and he again raised the Bucaniidae to family rank as their authors, Ulrich and Scofield (1897), had done. Koken (1925) considered this group to be only a subfamily of the Bellerophontidae. This opinion was later followed by Knight et al. (1960) and Horný (1963). Wahlman (1992) recognized four subfamilies within the Bucaniidae: Bucaniinae Ulrich and Scofield, 1897, Salpingostomatinae Koken, 1925, Plectonotinae Boucot and Yochelson, 1966, and his new subfamily Undulabucaniinae. Wahlman considered the family Tropidodiscidae to be the most primitive family of all of the slit-bearing families. The family Bucaniidae was derived, according to him, from tropidodiscid ancestors. The members of Plectonotinae are considered to be more advanced Bucaniidae. Wahlman (1992) represents the last detailed study of the suprageneric classification of bellerophontoidean molluscs and this classification is also followed here. For this reason the subfamily Plectonotinae Boucot and Yochelson, 1966 is here also placed within the family Bucaniidae. However, the family-level classification of the bellerophontoidean molluscs is still not stable and a new

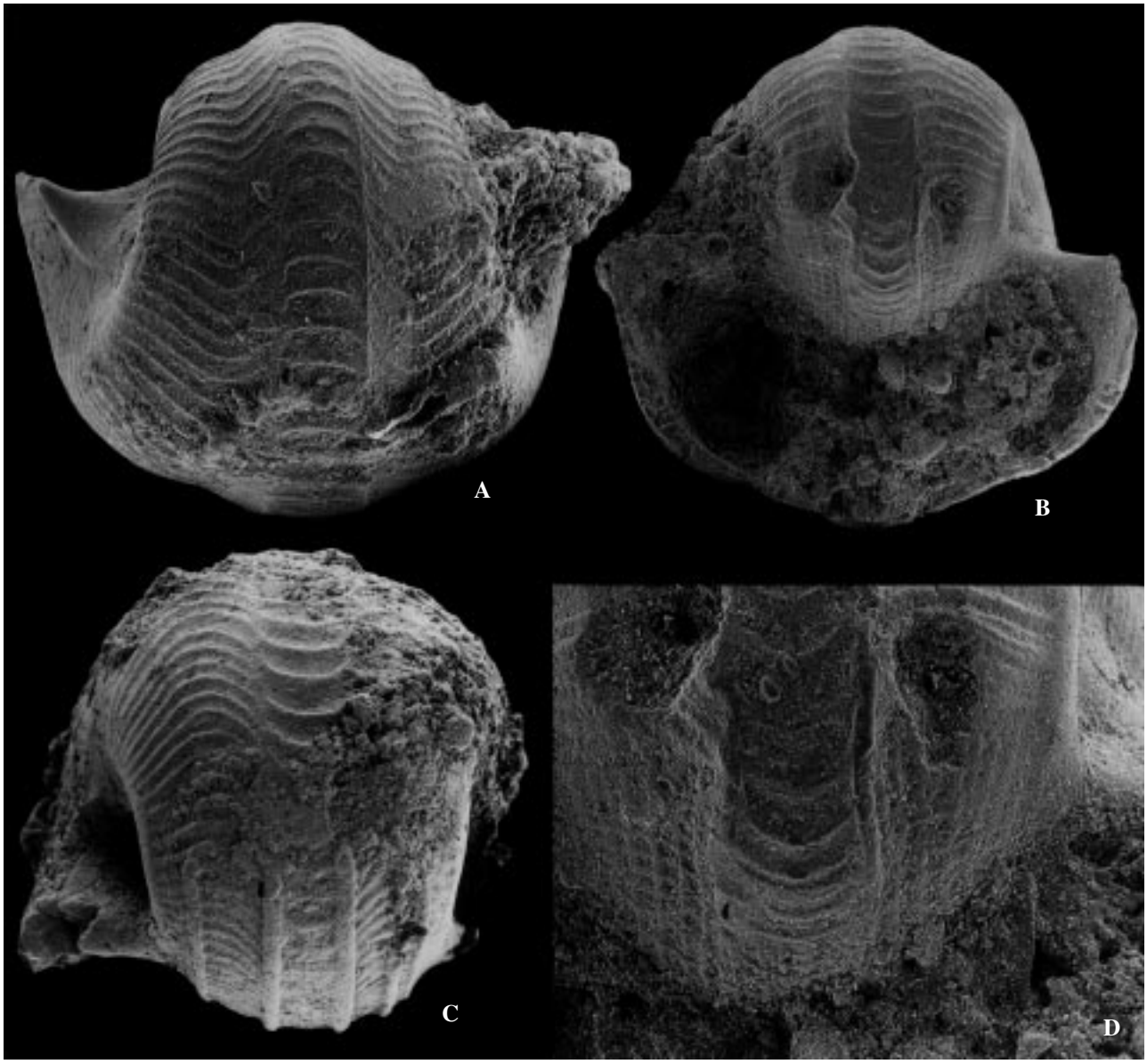



Fig. 1. *Blodgettinotus ornatus* sp. nov. from the uppermost part of the Třebotov Limestone (Daleje-Třebotov Formation; late Emsian, late Early Devonian). A – dorsal view of holotype showing a trilobate dorsum in juvenile whorl, x45, B – apertural view of holotype, parietal region covered by inductural shell deposits, x40, C – paratype A, dorsal view showing inductural shell deposits of *Euphemites*–type, x32, D – detail view of figure 1B, x92.

detailed revision is necessary which will also consider much new data published during last ten years. The shell characters of some plectonotids like those placed here in the new tribe Boucotonotini seem to be closer to members of the Bellerophontidae than to the Bucaniidae. However, the higher position of the subfamily Plectonotinae is not the subject of this study and remains opened for future studies.

Subfamily P l e c t o n o t i n a e Boucot and Yochelson, 1966
Tribe B o u c o t o n o t i n i nov.

T y p e g e n u s : *Boucotonotus* Frýda and Manda, 1997
D i a g n o s i s : Members of Plectonotinae ornamented by distinct collabral ribs; aperture bearing an anteriorly concave sinus at the lateral shell lobe; collabral ribs and lunulae regularly spaced; umbilicus narrow or filled by secondary shell deposits.
R e m a r k s : Boucot and Saul (in Saul – Boucot – Finks 1963) transferred the genus *Plectonotus* from the family Sinuitidae to the Bellerophontidae because they found a true slit and selenizone in *Plectonotus fraternus* (Reed 1908) from the Devonian of Ghana. Horný (1963) on the basis this discovery also placed *Plectonotus* near the genus *Tetranota* within the subfamily Bucaniinae. The selenizone was later discovered also in the type species of *Plectonotus*, *Plectonotus derbyi* Clarke, 1899 (Boucot 1965; Peel 1974; Boucot et al. 1986). Boucot and Yochelson (1966) established a new subfamily Plectonotinae for "moderately large slit-bearing bellerophontid gastropods


Fig. 2. A–C. *Boucotonotus mareki* from the uppermost part of the Třebotov Limestone (Daleje-Třebotov Formation, late Emsian, late Early Devonian). A – dorsal view showing the distinct, regularly spaced collabral ribs and lunulae, CGU JF 148, x38. B – abapertural view of the same shell, x35, C – lateral view showing a periumbilical smooth ridge formed by the secondary shell deposits, CGU JF 148, x27. D – *Blodgettinotus ornatus* sp. nov., holotype, lateral view showing coinductural and inductural shell deposits, x33.

having a prominent raised median lobe that forms a trilobed cross section". According to these authors *Plectonotus* Clarke, 1899 represents the only known genus of this subfamily. Peel (1974) redescribed the genus *Tritonophon* Öpik, 1953, which is based on *Kokenospira* (*Tritonophon*) *trimetra* Öpik, 1953. This author placed in *Tritonophon* most of the forms earlier assigned to *Plectonotus trilobatus* (Sowerby in Murchison, 1839). The genus *Tritonophon* Opik, 1953 according to Peel (1974) is distinguished from the genus *Plectonotus* Clarke, 1899 by "its more pronounced trilobation producing a narrow and strongly vaulted median lobe". Boucot et al. (1986) established the subgenus *Plectonotus* (*Plectonotoides*), based on the relatively small Lower Devonian species, *Plectonotus gaspensis* Clarke, 1908. Wahlman (1992) transferred the Ordovician genus *Tetranota* to the subfamily Plectonotinae and noted its similarity to genus *Kokenospira* of the subfamily Bucaniinae. Frýda and Manda (1997) introduced a new taxon *Boucotonotus* as a subgenus of *Plectonotus*, but they noted that it may represent a separate genus because of its unusual shell features. In contrast to species of *Plectonotus* (*Plectonotus*) and *Plectonotus* (*Plectonotoides*), the aperture of *Boucotonotus* bears an anteriorly concave sinus at the lateral shell lobe. In addition, it differs from *Plectonotus* (*Plectonotus*), *Plectonotus* (*Plectonotoides*), and *Tritonophon* by its distinct collabral ornamentation of both the shell and selenizone. The shells of *Blodgettinotus* gen. nov. bear the same shell characters (i.e., distinct collabral ribs; aperture bearing an anteriorly concave sinus at the lateral shell lobe) as *Boucotonotus*, which are unknown amongst other plectonotids. For this reason, *Boucotonotus* is considered here to be a separate genus related to *Blodgettinotus* gen. nov. Both genera share the above mentioned shell features, but having a different dorsum in the adult shell (see below) and are placed here in a new

tribe Boucotonotini to emphasize their closer phylogenetic connection within the Plectonotinae. Boucotonotini show some shell characters (very narrow or closed umbilicus, globose adult shell of *Blodgettinotus*) which are closer to members of the Bellerophontidae than to the Bucaniidae. On the other hand, Plectonotini nom. nov., including *Plectonotus* (*Plectonotus*), *Plectonotus* (*Plectonotoides*), *Tritonophon*, and *Tetranota*, are considered to be more primitive Plectonotinae. The above mentioned data, however, suggests that this problem needs more detailed study, as does the whole suprageneric classification of bellerophontoidean molluscs.

Included genera:
*Boucotonotus* Frýda and Manda, 1997
*Blodgettinotus* gen. nov.

### *Blodgettinotus* gen. nov.

Type species: *Blodgettinotus ornatus* gen. et sp. nov.; late Emsian (late Early Devonian); Prague Basin, Bohemia.
Etymology: *Blodgettinotus*, in honour of the American paleontologist Robert B. Blodgett who has contributed much to our knowledge of Devonian gastropods.

Diagnosis: Small plectonotid shell ornamented by distinct collabral ribs; dorsum of juvenile whorls distinctly trilobate with selenizone occupying the full width of the upper surface of the median lobe; dorsum of later (adult) whorl rounded; selenizone ornamentation consisting of distinct lunulae; collabral ribs and lunulae regularly spaced; umbilici covered by coinductural shell deposits; inner lip in adult whorl covered by inductural shell deposits with reticulate ornamentation; inductural deposits form several spiral ribs of Euphemites-type in gerontic shells.

Comparison: *Blodgettinotus* gen. n. is closest to *Boucotonotus* Frýda and Manda, 1997 among all bellerophontoidean genera. The former genus may be distinguished from the latter by shape of its dorsum and presence of characteristic inductural deposits in the adult shell, as well as by a slightly wider shell. The dorsum of the gerontic whorl in all species of *Boucotonotus* is distinctly trilobate (see Horný 1963, Pl. 28, Figs 1, 3; Frýda – Manda 1997, Pl. 1, Fig. 6; herein Fig. 2A, B) but it is rounded in *Blodgettinotus* gen. nov. In addition, the adult shells of the latter genus is partly covered by inductural shell deposits forming a characteristic ornamentation (Figs 1A–D, 2D), in contrast to *Boucotonotus* in which only a smooth periumbilical ridge (Fig. 2C) formed probably by coinductural shell deposits was found. This smooth periumbilical ridge is also found in *Blodgettinotus* gen. n. (Fig. 2D).

The new genus *Blodgettinotus* may be easily distinguished from species of *Plectonotus* (*Plectonotus*) Clarke, 1899 and *Plectonotus* (*Plectonotoides*) Boucot, Rohr, Gray, Faria and Colbath, 1986 by its distinct shell ornamentation, the shape of its aperture and adult dorsum. The shell of *Blodgettinotus* is ornamented by distinct, regularly spaced collabral ribs and its selenizone by regularly spaced lunulae (Figs 1A–D, 2D). The shells of species belonging to the subgenera *Plectonotus* (*Plectonotus*) and *Plectonotus* (*Plectonotoides*) are smooth, with only growth lines developed on their shell surface. In some species of the subgenus *Plectonotus* (*Plectonotoides*), such as *Plectonotus* (*Plectonotoides*) *boucoti* Peel, 1974 and *Plectonotus* (*Plectonotoides*) *cherylae* Peel, 1974 (see also Peel 1991, fig. 14), the shell is ornamented by very fine spiral lirae. A similar type of shell ornamentation is also developed in some species of *Tritonophon* Öpik, 1953 (Peel 1974). The aperture of *Blodgettinotus* bearing an anteriorly concave sinus at the both lateral shell lobes is similar to that in *Boucotonotus*. This character also differentiates *Bouconotus* and *Blodgettinotus* from *Plectonotus* Clarke, 1899 and *Tritonophon* Öpik, 1953.

Species included: Only the type species *Blodgettinotus ornatus* gen. et sp. nov. is hitherto known.

### *Blodgettinotus ornatus* sp. nov.

Text-figs 1A–D, 2D

Holotype: Specimen ČGÚ JF 770, figured here as Figs 1A, B, D, 2D.
Paratype: Specimen ČGÚ JF 771, figured here as Fig. 1C.
Type horizon: The uppermost part of the Třebotov Limestone, Daleje-Třebotov Formation; late Emsian, late Early Devonian.
Type locality: Holyně near Prague, central Bohemia.
Etymology: *ornatus* (Lat.), bearing ornament.

Diagnosis: Because of monotypy, see that of genus.
Description: Bellerophontid with bilaterally symmetrical shell having height/width ratio slightly less than 1; early whorls distinctly trilobate (Fig. 1A) but gerontic whorl rounded (Fig. 1C); relatively wide selenizone occupying the full width of the upper surface of the median lobe in juvenile shell whorls; selenizone width about 1/5 of dorsum width; flat central lobe low, separated from the lateral lobes by very shallow furrow on each side; lateral lobes gently arched; umbilici covered by smooth coinductural deposits; anterior margin of the aperture with narrow sinus having in its middle a wide slit; width of the sinus about 1/2 of dorsum width; flat selenizone generated by slit forms the upper surface of the median lobe; apertural margin runs from the selenizone obliquelly forwards, at position of interlobe furrow it abruptly turns backwards and then curves smoothly towards circumbilical region to form an anteriorly concave, shallow sinus at the lateral shell lobe (Fig. 1A); shell ornamented by distinct collabral ribs; selenizone ornamentation consisting of distinct lunulae; collabral ribs and lunulae regularly spaced and their distance about 1/3 of selenizone width (Fig. 1A–C); inner lip of adult whorl covered by inductural shell deposits with reticulate ornamentation (Fig. 1D); the distance between the spiral threads, as well as that between the radial threads forming the reticulate ornamentation is the same and equal to about 1/4 of selenizone width; smooth periumbilical ridge separating dorsolateral and circumbilical regions projects about 1/4 of a volution from the aperture (Fig. 2D); this

rounded ridge is formed by coinductural shell deposits; in the most adult whorl inductural deposits form several spiral ribs of *Euphemites*-type (Fig. 1C); shell structure and protoconch unknown.

R e m a r k s: *Blodgettinotus ornatus* sp. nov. is rare and only two complete shell are hitherto known from its type locality.

**Secondary shell deposits in bellerophontiform molluscs**

Secondary shell deposits are secreted on the surface of gastropod shells by flaps of their mantle and also occur in several groups of the bellerophontiform molluscs. The Carboniferous-Permian members of the family Euphemitidae Knight, 1956, represent a typical group of such bellerophontiform molluscs. Secondary shell deposits entirely cover the outer surface of their shells. The shell structure of the representatives of this family has been studied and interpreted by many authors (Weller 1930; Moore 1941; Yochelson 1960; McClintock 1967; Harper – Rollins 1985; etc.). Moore (1941) described secondary shell deposits in *Euphemites* Warthin, 1930, in detail and used the terms "inductura", "perinductura" and "coinductura". The inductura is a secondary shell layer extending from the inner side of the aperture over the parietal region, columellar lip, and part or all of the outer shell surface. In *Euphemites*, Moore (1941) used the term inductura for layers on the outer shell surface bearing numerous spiral costae. This author concluded that the inductura had been secreted by a forward-growing posterior flap of the mantle. The perinductura is a secondary shell layer secreted by the mantle flap and reflected back over the outer apertural lip. This shell layer obscures the growth lines and is the innermost of three outer shell layers. In *Euphemites*, the perinductura is the layer on the outer shell surface and is either smooth and unornamented or bears nodes or nodose ridges. The coinductura is a secondary shell layer extending over the inner lip within the aperture and covering only a small part of the inductura. Yochelson (1960) suggested that the coinductura was secreted by the same part of the mantle as the inductura, in contrast with Moore's (1941) opinion that there was no obvious correlation between the coinductura and inductura.

Horný (1962, 1963) described a new euphemitid genus, *Paleuphemites*, shells of which bear well developed secondary shell deposits but only in the parietal and umbilical regions. This genus is based on *Paleuphemites petrboki* Horný, 1962 from the Dvorce-Prokop Limestone of Praha Formation (Pragian, middle Early Devonian) of the Prague Basin. *Paleuphemites petrboki* was interpreted as the oldest representative of the family Euphemitidae. The shells of the latter species have an inner lip covered by parietal inductura generating longitudinal (spiral) ribs forming a reticulate ornamentation with intersecting collabral ribs (see Horný 1963, fig. 14). According to this author, in the gerontic shells of *Paleuphemites petrboki* the inductural deposits are formed by heavy callus instead of ribs (see Horný 1963, fig. 15). The reticulate ornamentation of the inductural deposits in *Blodgettinotus ornatus* sp. nov. is very similar to that in *Paleuphemites petrboki* (compare Horný 1963, Pl. XLIII, fig. 1 and herein Figs 1B, D). Also a change of morphology of the inductural shell deposits in gerontic shells is a character shared by both genera.

Secondary shell deposits limited to the parietal region and portions of the umbilical region were also previously described in some representatives of the family Sinuitidae [e. g., *Sinuites cancellatus* (Hall 1847), *Sinuites granistriatus* (Ulrich 1897), and *Sinuites (Strangulites) strangulatus* (Perner 1903)] (see Knight 1941; Horný 1990; Wahlman 1992). Frýda and Marco (1996) described a Middle Ordovician species of genus *Hispanosinuites, Hispanosinuites peeli*, the shell of which is entirely covered by secondary shell deposits. This genus of their new subfamily Hispanosinuitinae was interpreted as a member of a highly specialized phylogenetic lineage separated from the morphological range of the genus *Sinuites* during the Early Ordovician. Similar secondary shell deposits were described in "*Sinuites*" by Horný (1996). Rollins (1966) described thick, padlike parietal deposits in the Devonian genus *Ptomatis*. Recently, highly ornamented secondary shell deposits were found in genus *Branzovodiscus* Frýda, 1999, which was tentatively placed in the subfamily Bucanellinae of the Sinuitidae because of its resemblance with genus *Sinuitina* Knight, 1945 in terms of its general shell shape as well as of its helmet-shaped dorsum (subgenus *Sinuitina* (*Sinuitina*)). The genus *Sinuitina* was placed in the subfamily Bucanellinae by Knight et al. (1960). However, the shell morphology of *Sinuitina* and *Branzovodiscus* seems to be far from that of the type genus *Bucanella* Meek, 1871. The ripple-like pattern of slightly irregular ribs in the middle of dorsum of *Sinuitina* (*Globosinuitina*) Frýda, 1998 may also be the result of perinductural secondary shell deposits.

The occurrence of secondary shell deposits limited to the parietal region was noted by Wahlman (1992) also in the genera *Bucania* and *Salpingostoma* belonging to the family Bucaniidae, as well as in genus *Carinariopsis* of the family Carinaropsidae. Secondary shell deposits are also known among members of the subfamily Bellerophontinae such as *Bellerophon* and *Kodymites*. These deposits are typically smooth, without any ornamentation and they are restricted only to the inner lip and/or they fill the umbilici. Secondary shell deposits of similar morphology also occurs in the genera *Cymbularia* Koken, 1896, *Prosoptychus* Perner, 1903, and *Coelocyclus* Perner, 1903, belonging to the subfamily Cymbularinae Horný, 1963.

Wahlman (1992) discussed the functional significance of the secondary shell deposits in bellerophontiform molluscs. According to him, these deposits serve two functions. First, they add weight to the part of the shell that lies on the central portion of the foot and so help to stabilize the shell under higher energy conditions. Mo-

dification of the design of the parietal shell region is considered to be a second reason for the development of secondary shell deposits. However, the considerable variability in terms of the shape, position and ornamentation of the secondary shell deposits in the bellerophontiform molluscs suggests that these deposits were developed for many different reasons.

## Conclusions

The above short overview clearly shows that secondary shell deposits occurs in many groups of almost all known families of the Bellerophontoidea. This shell feature was probably independently developed for several different reasons. The significance of secondary shell deposits for the suprageneric classification of the bellerophontoidean molluscs seems to be limited. Also, the evolutionary relationships of bellerophontoideans with such deposits are probably much more complicated than were suggested by Frýda and Marco (1996). The herein described occurrence of the secondary shell deposits in *Blodgettinotus ornatus* sp. nov. belonging to the subfamily Plectonotinae is a further contribution to our knowledge of this shell feature in bellerophontoidean molluscs.

*Acknowledgments.* This publication is based on the work sponsored by the U. S. – Czechoslovak Science and Technology Joint Fund in cooperation with the Czech Geological Survey and U. S. Geological Survey under Project Number 95057. I also wish to acknowledge Robert B. Blodgett (Corvallis, Oregon) and Dave M. Rohr (Alpine, Texas) for improving language and for their helpful, critical reviews of this paper.

*Submitted October 1, 1999*

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## Sekundární schránkové uloženiny u nového plectonotidního gastropodového rodu (Bellerophontoidea, Mollusca) ze spodního devonu Čech

Sekundární schránkové uloženiny jsou popsány u nového plectonotidního rodu *Blodgettinotus* z gastropodového společenstva *Boucotonotus-Palaeozygopleura* pražské pánve. Tento taxon byl nalezen v nejvyšší části třebotovských vápenců (dalejsko-třebotovské souvrství, pozdní ems, nejvyšší spodní devon). Na základě zjištění některých společných znaků jsou rody *Boucotonotus* a *Blodgettinotus* umístěny do nového tribu Boucotonotini patřící do podčeledi Plectonotinae. Je diskutován výskyt sekundárních schránkových uloženin u bellerophontoformních měkkýšů. Tyto uloženiny se pravděpodobně vyvinuly nezávisle v různých skupinách těchto měkkýšů a mají tedy omezený význam pro jejich klasifikaci.