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A biogenic paradigm of shells of the clavatulid gastropods: the trace fossil *Clavatulicola evaephilus* ichnogen. et ichnosp.n. from the Middle Miocene localities Korytnica (Holy Cross Mountains, Poland) and Grund (Vienna Basin, Austria)

ABSTRACT: A peculiar paradigm of shells of the clavatulid gastropod (genus *Clavatula* LAMARCK, 1801, of the subfamily Clavatulinae, family Turridae) of Miocene age, and displayed by a pattern of furrows sculpturing preferentially the median part of the shell whorls (*i.e.*, the anal fasciole), is ascribed to the life activity of commensals to the live gastropods. This pattern, classified as an ichnofossil, taxonomically new, *Clavatulicola evaephilus* ichnogen. et ichnosp.n., bears its specific name referring to the clavatulid species *Clavatula evae* (HOERNES & AUINGER, 1891), upon whose shells it was first presented over a century ago from Grund in the Vienna Basin, Austria. Within rich gastropod assemblages from Korytnica in the Holy Cross Mountains, Central Poland, containing a dozen or so clavatulid species, the newly established ichnotaxon is confined exclusively to the four species, viz. *Clavatula evae* (100% of shells infested), *Cl. styriaca* (100%), *Cl. asperulata* (92%), and *Cl. suturalis* (72%), what indicates a very high host specifity of the ichnofossil-producing commensals. As the potential producers of the ichnofossil pattern briefly discussed are the folliculinid infusorians and the phoronids. An attention is paid to the occurrence of the newly established ichnotaxon in the Vienna Basin fromwhere it was presented solely from the locality Grund, the gastropod assemblage of which is closest to that of Korytnica in Poland.

INTRODUCTION

The aim of the paper is to present a unique shell paradigm revealed by some species of the gastropod genus *Clavatula* LAMARCK,

1801 (subfamily Clavatulinae, family Turridae) whose large-sized representatives are the most spectacular components of ubiquitous gastropod assemblages within a Middle Miocene sequence of the Korytnica Clays exposed along the southern slopes of the Holy Cross Mountains, Central Poland.

The Korytnica Clays, known also as the *Pleurotoma* Clays of Korytnica (*see* BAŁUK & RADWAŃSKI 1977, p. 96; BAŁUK 1997, p. 5) have subjected to the Authors' studies since thirty years (*see* review *in*: BAŁUK & RADWAŃSKI 1977; BAŁUK 1995, p. 161). To these reports the readers are addressed to acquaint with the paleogeographic setting and age of the Korytnica sequence developed (*cf.* RADWAŃSKI 1969) at time of the Middle Miocene transgression (Badenian stage in the Paratethys basins, close to the Langhian/Serravallian stage boundary of standard geochronologic scale).

During the research of numerous gastropods, totalling about 800 taxa (*see* BAŁUK 1975, 1995, 1997), various anomalies and damages in their shells were studied, and ascribed to the life activity of diverse endo- or epibionts, as well as of predators preying either upon the gastropods themselves, or upon the squatters of their emptied shells (*see* review *in*: BAŁUK 1995, p. 161; BAŁUK & RADWAŃSKI 1996, p. 282). Little attention has however been paid to the endo- and/or epibionts of shells of the live gastropods, and to which the term commensals could be applied. The present paper offers the first insight into such a biogenic relationship amongst the gastropods of the Korytnica Clays.

The identical shell paradigm in the clavatulid species has been recognized by the present authors also in illustrations of some clavatulid shells presented by HOERNES & AUINGER (1891) in their classical monograph of Miocene gastropods from the Vienna Basin and adjacent countries. This recognition extends the scope of the present paper, to discuss a matter of the host specifity of the still mysterious commensals, and of their environmental requirements.

THE SETTING OF THE PARADIGM

The studied shell paradigm, featuring the infested shells more or less wholly, is typical of only some of the *Clavatula* species occurring in the Korytnica sequence.

The genus *Clavatula* within the ubiquitous gastropod assemblages of the Korytnica sequence is represented by a dozen or so species, as

evidenced by the present-day state of its taxonomic recognition established long ago by FRIEDBERG (1912, 1928, 1938). To the truth, all these *Clavatula* species require a thorough revision that is intended to be the 4th Part of monographic descriptions of the Korytnica gastropods, prepared by the co-author of this paper (*cf.* BAŁUK 1975, 1995, 1997).

Apart from seven rare species, represented by one or several specimens, the more common are the four species:

Clavatula jouanneti (DESMOULINS, 1842) – 40 specimens collected,
Clavatula evae (HOERNES & AUINGER, 1891) – 45 specimens collected,
Clavatula styriaca (AUINGER *in* HILBER, 1879) – 60 specimens collected,
Clavatula camillae (HOERNES & AUINGER, 1891) – 250 specimens collected,

whose shells are numerically very subordinate to those of the three other species:

Clavatula laevigata (EICHWALD, 1853) – 760 specimens collected,
Clavatula asperulata (LAMARCK, 1822) – 1200 specimens collected.
Clavatula suturalis (ANDRZEJOWSKI, 1833) – 1400 specimens collected,

The studied shell paradigm is revealed by all the collected shells of the species

Clavatula evae (HOERNES & AUINGER, 1891)
and *Clavatula styriaca* (AUINGER *in* HILBER, 1879),

and by the majority of the shells of

Clavatula asperulata (LAMARCK, 1822) – 92% of total (1200)
Clavatula suturalis (ANDRZEJOWSKI, 1833) – 72% of total (1400).

On the contrary, the studied paradigm is totally absent from the shells of *Clavatula laevigata* [760 specimens inspected(!)], *Clavatula camillae*, *Clavatula jouanneti*, and all the herein unnamed rare species.

Moreover, the studied paradigm is completely absent from any other gastropod genera, other mollusks (bivalves, scaphopods, chitons), and other shelled invertebrates. This recognition allows to postulate a very high host specifity of the studied paradigm which is confined exclusively to the four, above-indicated species of the genus *Clavatula* LAMARCK, 1801, coming from the Korytnica Clays.

To clarify the taxonomy of the four indicated species, it is to announce herein, prior to their formal revision, that the species

Clavatula suturalis (ANDRZEJOWSKI, 1833) is understood the same as it was established by ANDRZEJOWSKI (1833), and not as it was treated by subsequent authors [that is as *Clavatula laevigata* (EICHWALD) by EICHWALD (1853), by FRIEDBERG (1912, 1928, 1938), and by the present authors in former papers (*e.g.* BAŁUK & RADWAŃSKI 1977, 1996); or *Clavatula susannae* (HOERNES & AUINGER) by HOERNES & AUINGER (1891)], whereas the three remaining species are treated the same as used by FRIEDBERG (1912, 1928, 1938).

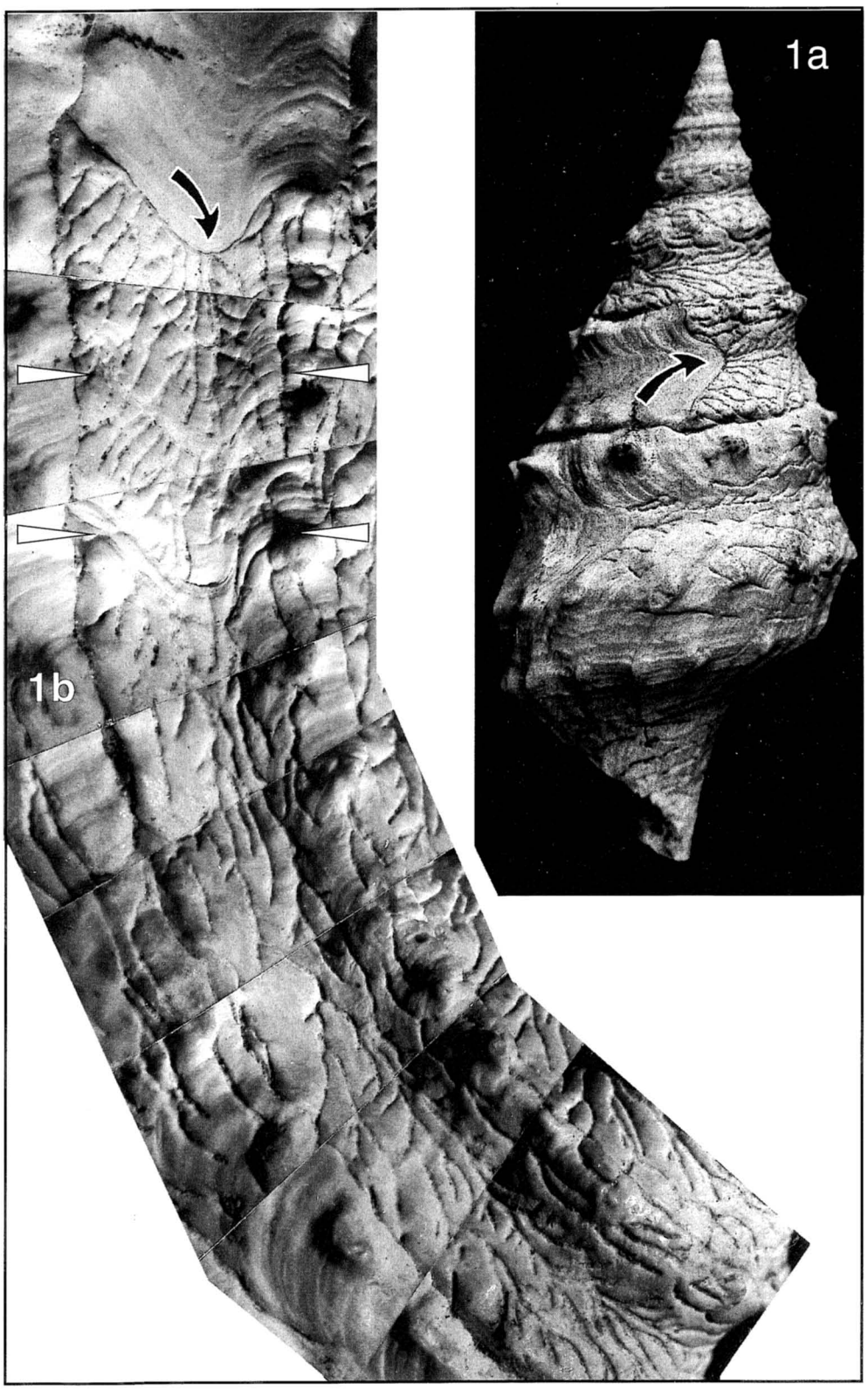
THE STRUCTURE OF THE PARADIGM

The recognized paradigm of the clavatulid shells from the Korytnica Clays (*see* Plates 1 – 4) covers more or less totally the whole surface of the shell whorls (*see* Pl. 1, Fig. 1a; Pl. 2, Fig. 1; *and* Pl. 3, Fig. 1). It realizes by a complex pattern of tiny furrows in the shell surface, and its particular furrows may either be relatively long, and more or less continuous (Pl. 1, Fig. 1b), or relatively shorter, and thus more or less discontinuous (Pl. 2, Fig. 2). The furrows, extended from the upper to the lower suture of the whorl (*see* Pl. 1, Fig. 1b *and* Pl. 2, Fig. 2), are convergent aperturally, and conjoining medially to the anal fasciole, that is the zone originating from the apertural notch typical of all the clavatulid shells (*see also* Pl. 2, Fig. 3 *and* Pl. 4, Fig. 1). The furrows, nearly hemispherical in outline (*see* Pl. 2, Fig. 3; Plate 3; Pl. 4, Figs 1-3), never bifurcate. The beginning of the furrows is well pronounced (*see* Pl. 2, Fig. 3), the same as the places where they take-off the shell surface (*see* Pl. 4, Fig. 2). Since the beginning, the diameter of the furrows is stable, ranging 0.145-0.2mm, and it is kept throughout the whole length of the furrow. The longest furrows, usually solitary (!), settled at the middle of the clavatulid anal fasciole, continue at

PLATE 1

1a — Overall view of the shell of *Clavatula suturalis* (ANDRZEJOWSKI, 1833) bearing a distinct pattern of the trace fossil, *Clavatulicola evaephilus* ichnogen. et ichnosp.n., represented by the **holotype**, abruptly truncated by a shell-growth break (*arrowed*) and scarcely re-appearing during further growth of the shell; × 3

1b — Panoramic close-up, to show the course and structure of the **holotype** of *Clavatulicola evaephilus* ichnogen. et ichnosp.n. in an older part of the same shell, before the shell-growth break (*arrowed*; compare Fig. 1a); the pattern, settled around the clavatulid anal fasciole, is composed of continuous furrows, interrupted or terminated at some growth lamellae of the gastropod shell (*leadered*); × 7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1b


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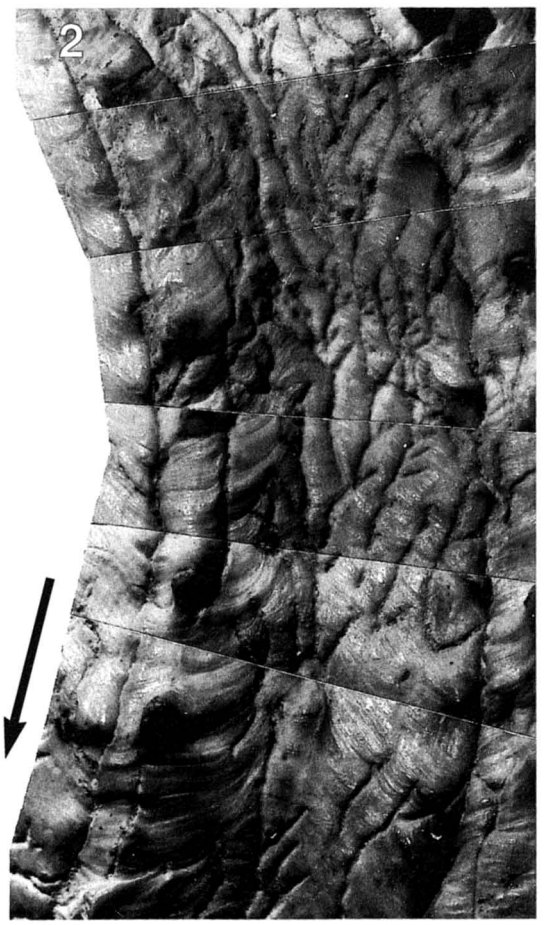
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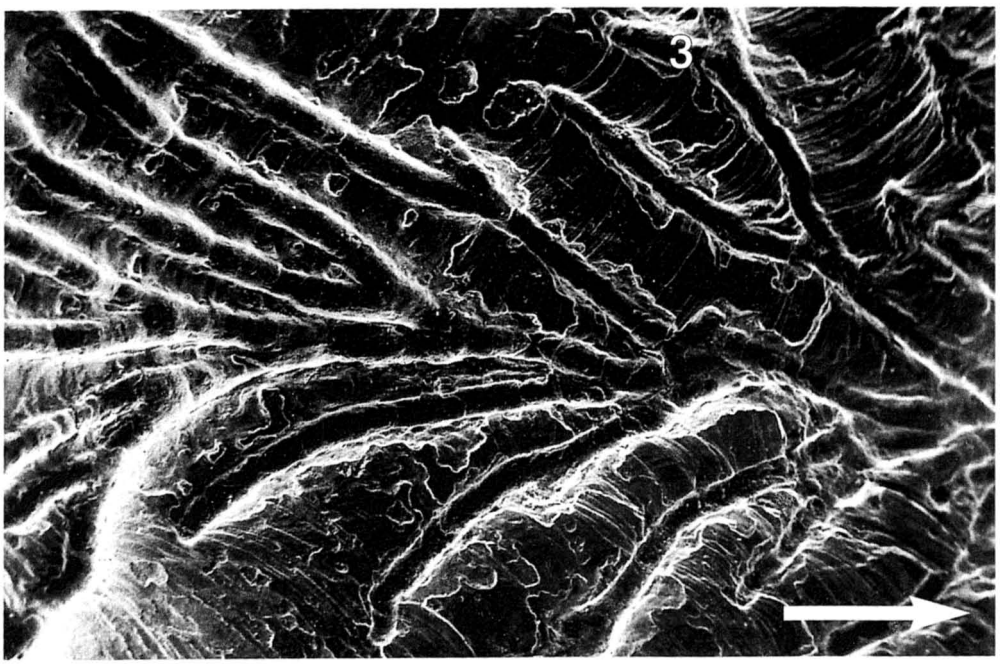
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a distance up to about 10mm (ranging 8-14mm), although extremely they may reach even 40mm (about 1½ whorls). In some clavatulid shells there appear two, more or less parallel furrows (0.2-0.3mm distant) within the anal fasciole, and they continue even alongwith 2 whorls.

Within the studied clavatulid shells the paradigm appears at very early stages of the shell growth, namely at the 4th whorl behind the protoconch; the clavatulid shells are then about 2mm in width, and 6mm in length, being as yet either almost smooth (as in young *Clavatula suturalis*), or already ornamented (as in young *Clavatula asperulata*).

The paradigm on a shell may appear either once, and be continuous downshell as far as the final aperture (Pl. 2, Fig. 1), or it is terminated by a shell-growth break (Pl. 4, Fig. 1), and may re-appear, even repeatedly afterwards (Pl. 1, Fig. 1a).

The shell-growth break in the clavatulid shells featured by the studied paradigm corresponds either to a temporary stop of the shell accretion (*see* Pl. 1, Fig. 1b), or to a damage of the shell margin, caused by predatory attacks, primarily of various crustaceans, the stomatopods including (*cf.* BAŁUK & RADWAŃSKI 1996). The re-appearing pattern originates usually at a distance from the shell-growth break (compare Figs 1a and 1b of Pl. 1).

To exemplify, in a group of 50 hazardly taken shells of *Clavatula suturalis* (ANDRZEJOWSKI, 1833), the studied pattern re-appeared, the most commonly, five times in 12 specimens, being maximally seven times in 3 specimens. The pattern appearing once in this studied group

PLATE 2

1 — Overall view of the shell of *Clavatula suturalis* (ANDRZEJOWSKI, 1833) bearing a distinct pattern of the trace fossil, *Clavatulicola evaephilus* ichnogen. et ichnosp.n., that developed alongwith the whole shell spire, down to the aperture, the base of the preceding whorl and siphonal canal including, where it became overgrown by the inner lip of the gastropod shell; × 2, arrow is aperture-directed

2 — Panoramic close-up of a fragment of another specimen of *Clavatula suturalis* (ANDRZEJOWSKI, 1833), to show the pattern of *Clavatulicola evaephilus* ichnogen. et ichnosp.n. composed of short, commonly discontinuous furrows; × 7, arrow is aperture-directed

3 — Close-up from another specimen of *Clavatula suturalis* (ANDRZEJOWSKI, 1833), to show the furrows of *Clavatulicola evaephilus* ichnogen. et ichnosp.n., to which the growth lamellae of the clavatulid shell are precisely adjusted; note, the settlement sites of furrows disturbing the normal course of growth lines; *SEM* × 62

of shells was found in 4 specimens, in which it continued through 1/4, 1 1/4, 4 1/4 and 6 whorls of teleoconch, respectively. The longest pattern, composed of six systems, continued alongwith 7 1/2 whorls.

The studied pattern is composed of various number of furrows which may either form a very dense design, or may appear very sparsely, even singly. In all these cases they are always convergent to the anal fasciole; if they occur singly, very rarely indeed, are inclined to that very fasciole. When more densely occurring, they embrace also the whorl base (Pl. 3, Fig. 1d), reaching even the siphonal canal at the final aperture (Pl. 2, Fig. 1).

Within the pattern, the particular furrows tend to be placed perpendicularly to the growth lines of clavatulid shells, whose growth lamellae become always very well adjusting to the course of furrows (*see* Pl. 2, Fig. 3 *and* Pl. 4, Figs 1-3), also in the case when a furrow terminates by itself, before reaching a growth stop or a damage of the clavatulid shell (*see* Pl. 4, Figs 1-2). On the other way, in many places the pattern is evidently overgrown by the successive whorls of the clavatulid shell (*see* Pl. 2, Fig. 1 *and* Pl. 3, Fig. 1d).

The latter recognitions clearly indicate that the studied pattern was acquired by the clavatulid shells when they were in their ontogenic growth during which the successive growth lamellae, also of the shell

PLATE 3

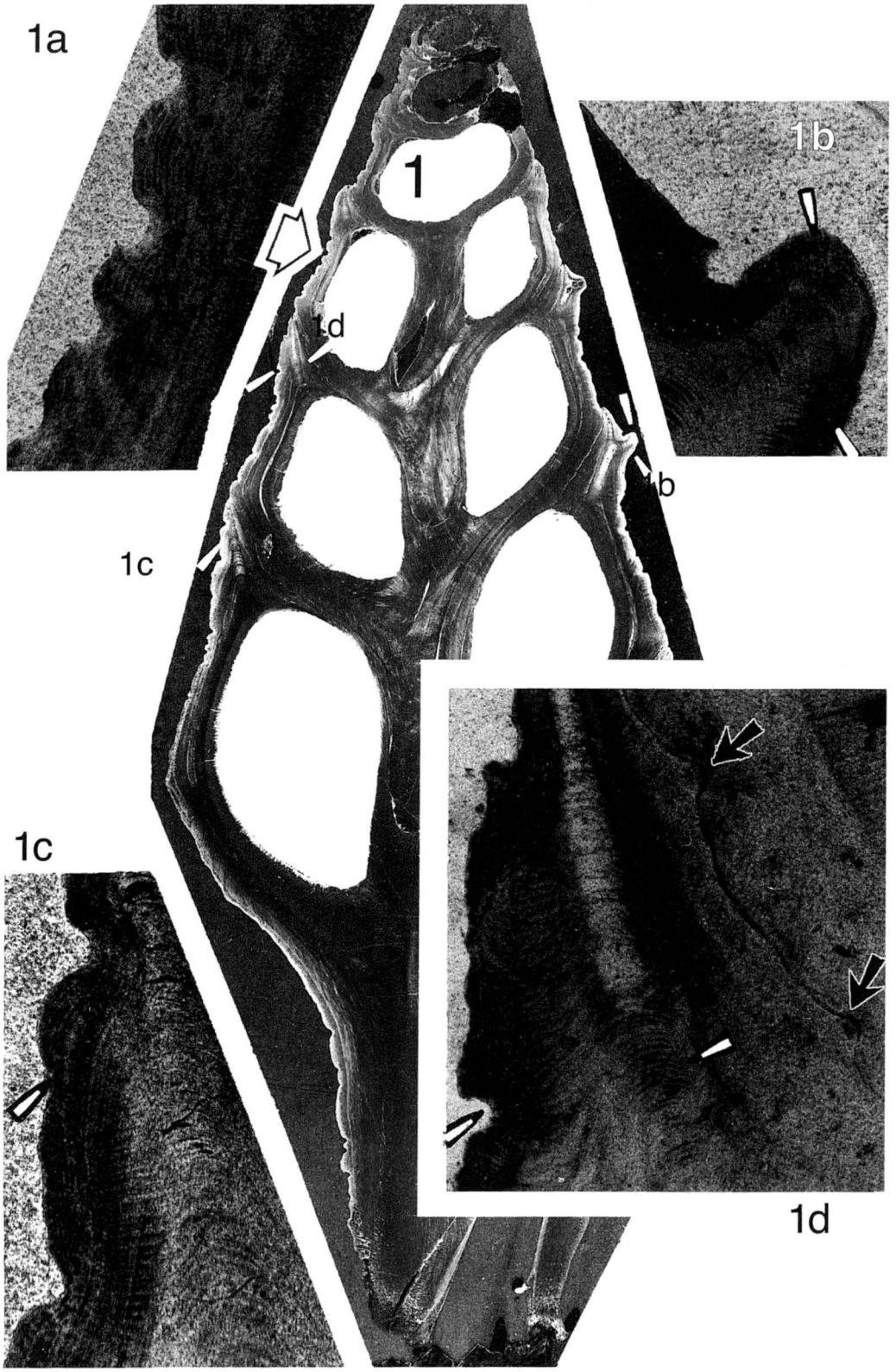
1 — Overall view of a thin section (taken × 5) of the clavatulid shell, *Clavatula suturalis* (ANDRZEJOWSKI, 1833), sculptured by the furrow pattern of the trace fossil *Clavatulicola evaephilus* ichnogen. et ichnosp.n., and its details (Figs 1a-1d; taken × 50), to show a relation of the studied trace fossil to the gastropod shell (note, the furrows developed also in the base of the last whorl); thin section is mounted in Canadian balsam

1a — Outer surface of the shell whorl, to show the growth lamellae of the clavatulid shell adjusted to the deeply seated furrows

1b — Outer surface of the shell whorl, to show the growth lamellae of the clavatulid shell adjusted to a deeply seated furrow neighboring a prickly node of the shell sculpture (reference leaders the same as in Fig. 1)

1c — Outer surface of the shell whorl (reference leaders the same as in Fig. 1), to show one shallow furrow (indicated by the leader) and two deeply seated furrows, to which the growth lamellae of the clavatulid shell are adjusted

1d — Section through the inner whorls of the clavatulid shell (reference leaders the same as in Fig. 1; the left one indicates a furrow on the outer surface of the shell), to show the two furrows on the base of the preceding whorl (*arrowed*), to which the growth lamellae of the successive whorl of the clavatulid shell are adjusted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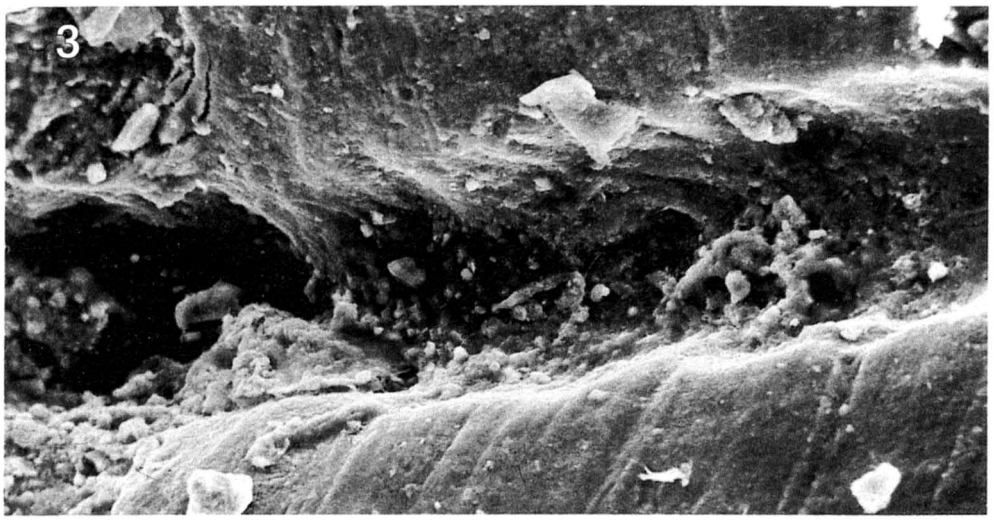
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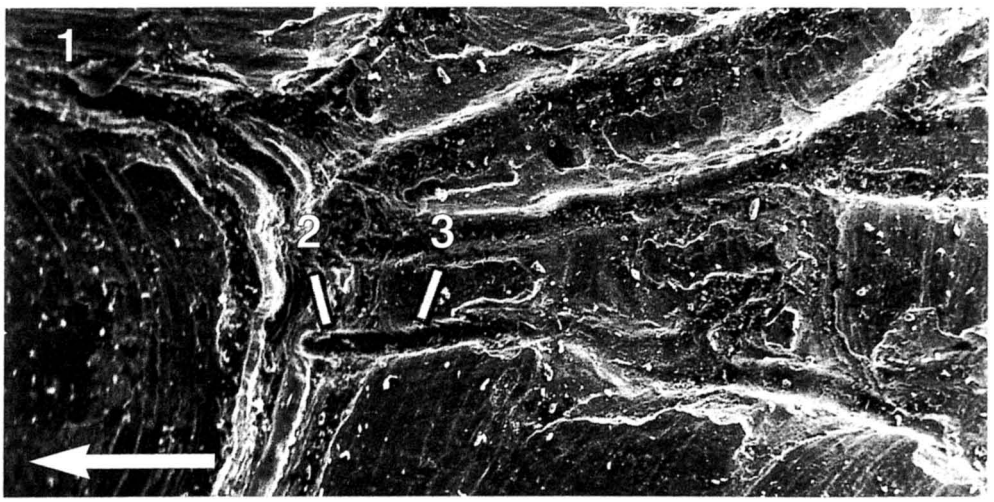
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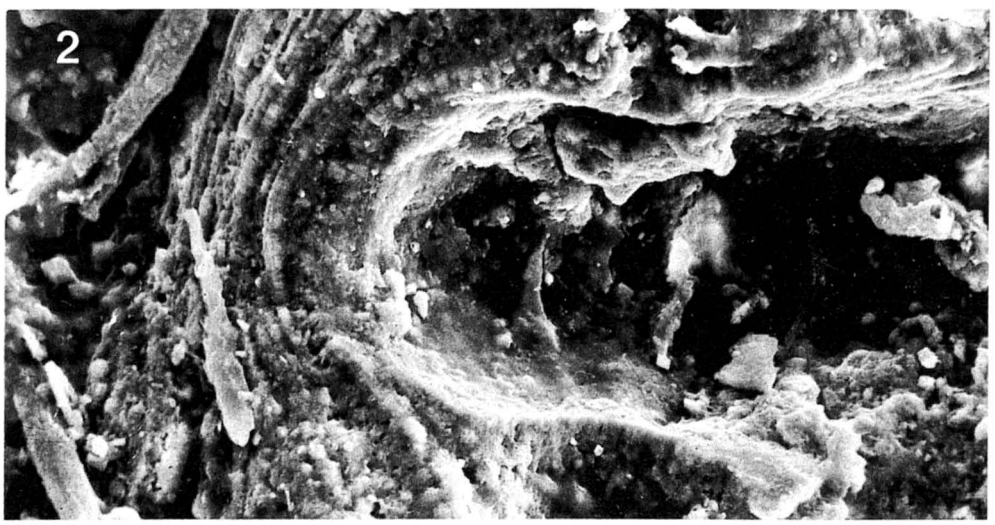
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sculpture (*e.g.*, prickly nodes, *see* Pl. 3, Fig. 1b), had to adjust to the objects firmly adhered to the outer wall surface of particular shells. In other words, the furrowed pattern featuring the shells was developing when the shell hosts, that is the clavatulid gastropods, were alive and were accreting their shells, on the outer surface of which the studied paradigm propagated coevally with the shell growth. A further attempt to consider the furrows being formed at life of clavatulid gastropods is that the furrows are intersected by the drillings of carnivorous gastropods, the naticids and muricids (*see* HOFFMAN & *al.* 1974), and by the injuries caused by the stomatopods (*see* BAŁUK & RADWAŃSKI 1996, especially Pl. 3, Fig. 13), which all prey upon the alive gastropods.

THE NATURE OF THE PARADIGM AND ITS CLASSIFICATION

The studied paradigm of shells of the clavatulid gastropods, as developed during the shell growth, must be ascribed to the objects existing coevally with the gastropod life. An orientation of the furrow patterns, precisely of particular furrows, towards the anal fasciole of the clavatulid shells, that is the zone along which the exhalant water current was propelling, speaks clearly about alive objects of animal nature, benefiting from that current. It is inferred that the animal creatures benefiting from the life function of the clavatulid gastropods did not cause any reliable suffering to the latter but, on the other way, their existence was controlled by the life activity of the gastropods. Consequently, it is apparent that the then-established biologic relationship was of commensal character. A systematic position of the inferred commensal cannot be however precisely stated.

PLATE 4

1 — Fragment of the clavatulid shell, *Clavatula suturalis* (ANDRZEJOWSKI, 1833), to show the terminations of some furrows (*see* Figs 2-3 of this Plate) of the trace fossil *Clavatulicola evaephilus* ichnogen. et ichnosp.n., erected at the growth-discontinuity band of the shell; *SEM* × 57, arrow is aperture-directed

2 — Close-up, to show the furrow at the erection site around which the adjusting growth lamellae of the clavatulid shell are closely spaced; *SEM* × 780

3 — Close-up, to show an older part of the same furrow to which the growth lamellae of the clavatulid shell are adjusted; *SEM* × 550

From the aforegoing, the studied biogenic paradigm is herein classified within the frames of the category of ichnofossils (trace fossils), produced by animals of an uncertain systematic position.

ICHNOTAXONOMY OF THE PARADIGM

Ichnogenus *Clavatulicola*, ichnogen.n.

DIAGNOSIS: A complex pattern of tiny furrows, hemicircular in outline, more or less continuously convergent medially and anteriorly to the anal fasciole of shells of the clavatulid gastropod upon which it develops obligatorily, and whose growth lamellae are adjusted to particular furrows of the pattern.

DERIVATION OF THE NAME: *Clavatulicola*, a neo-Latinized noun (masculine) – inhabitant of shells of the gastropod genus *Clavatula*.

TYPE SPECIES: *Clavatula evaephilus* ichnosp.n., the only ichnospecies assigned to the ichnogenus.

Ichnospecies *Clavatulicola evaephilus* ichnosp.n. (Plates 1 – 4)

HOLOTYPE: The pattern presented in Pl. 1, Fig. 1a-1b.

PARATYPES: The specimens illustrated in Pls 2-4.

TYPE LOCALITY: Korytnica, 24 km SSW of Kielce, southern slopes of the Holy Cross Mountains, Central Poland.

TYPE HORIZON: Middle Miocene (Badenian, corresponding to the Langhian/ Serravallian boundary interval).

DIAGNOSIS: The same as for the genus.

DERIVATION OF THE NAME: *evaephilus*, a neo-Latinized adjective, referring to the first illustration of the pattern, recognizable on shells of the species *Clavatula evae* (HOERNES & AUINGER, 1891), presented by HOERNES & AUINGER (1891, Pl. 44, Fig. 3a – adapertural view of the shell, and Fig. 3b – abapertural view of the shell).

DESCRIPTION, REMARKS, and OCCURRENCE – discussed in the preceding and subsequent sections of the present paper.

POTENTIAL PRODUCERS OF THE ICHNOFOSSIL

The commensals to the clavatulid gastropods, and which produced the ichnofossil pattern *Clavatulicola evaephilus* ichnogen. et

ichnosp.n., are to be characterized as tiny, strongly elongated, thus almost filiformis animals that lived gregariously. The pattern, composed of isolated furrows that do not bifurcate, indicates the solitary, not colonial invertebrates. As all the furrows cause a very precise adjustment of the gastropod shell lamellae, the commensal body is thought to have been either very solid, or coated with a not preservable (? non-mineralized) lining, likely an elongate case, or a tube. The more or less hemispherical section of the furrows shows the tubes having been more or less circular in outline. Particular furrow-producing individuals were able to erect their tubes, especially at any breaks in the gastropod shell growth (*see* Pl. 4, Fig. 2).

To the present authors' knowledge, of the potential producers of the studied ichnofossil pattern, the folliculinid infusorians (*see* HADZI 1938, 1951; MULISCH 1985; ERNST 1985) and/or the phoronids (*see* EMIG 1974) should preferably be taken into account, although none offer a significant analogy or, at least, morphologic similarity of traces they may leave upon the substrate they live upon.

THE PARADIGM IN THE CLAVATULID GASTROPODS FROM GRUND IN THE VIENNA BASIN

When checking-up illustrations of the clavatulid gastropods presented, in a form of lithographic engravings, by HOERNES & AUINGER (1891), it is easily recognizable that the studied shell paradigm, that is the newly established ichnofossil *Clavatulicola evaephilus* ichnogen. et ichnosp.n., does occur in some specimens of various species. The list of its occurrence on the host shells is following:

Clavatula evae (HOERNES & AUINGER, 1891) – *see* HOERNES & AUINGER (1891, Pl. 44, Figs 3a-3b and 4),

Clavatula antoniae (HOERNES & AUINGER, 1891) – *see* HOERNES & AUINGER (1891, Pl. 44, Fig. 6a-6b),

"intermediate forms" (*Uebergangsformen*) between *Clavatula asperulata* (LAMARCK) and *Clavatula rosaliae* (HOERNES & AUINGER, 1891) – *see* HOERNES & AUINGER (1891, Pl. 44, Figs 7-8),

"intermediate form" (*Uebergangsform*) between *Clavatula asperulata* (LAMARCK) and *Clavatula styriaca* (AUINGER *in* HILBER, 1879) – *see* HOERNES & AUINGER (1891, Pl. 44, Fig. 9).

Similarly as at Korytnica, the studied shell paradigm in the Vienna Basin is displayed only by some clavatulid species. Moreover, it is note-

worthy that all the clavatulids recognized as hosts of the studied paradigm in that Basin are coming from one locality, that is Grund (occurrence site: Guntersdorf).

[To note, all the clavatulid shells in the referenced monograph of HOERNES & AUINGER (1879-1891) were engraved by the same lithographer, Adalbert SWOBODA; it may therefore be thought that the sculptural details of the shells were pictured to the same extent of care on all the clavatulid species(!)].

FINAL REMARKS

A very high host specifity of the commensal-originated paradigm of shells, which is confined exclusively to the four (*Clavatula evae*, *Cl. styriaca*, *Cl. asperulata*, *Cl. suturalis*) of the total of fourteen clavatulid species from the Korytnica Clays, indicates that the paradigm-producing invertebrates were able to select precisely the hosts they settled upon. This was certainly involved by the food supplies from the water currents expelled by the gastropods. After larval settlement, further growth of the suggested suspension-feeding commensals was controlled by the growth of the gastropod, to the apertural notch of the outer lip of which the commensals became oriented. At the break in the gastropod shell growth the commensals could not survive and, consequently, they died. During a predatory attack upon the gastropod, and a partly damage of its shell, the commensals also became the victims. To note, at a longer break in the growth of a gastropod shell, caused by the decrease in the shell accretion due to unfavorable environmental and/or biologic (?teratologic) reasons, the commensals were erecting their tubes from the substratal shell (*see* Pl. 4, Figs 1-2), as if searching for another source of food.

A similar host-specifity of the studied paradigm recognized in the locality Grund in the Vienna Basin, and revealed by some clavatulid species, although as concerns their taxonomy treated differently by HOERNES & AUINGER (1891), may be interpreted either as confined to the gastropod species very closely related to those of Korytnica, or to a group of species of a similar food diet, that is expelling presumably a similar content of undigested particles. Moreover, still other factors of more general environmental provenance may be discussed (*e.g.*, bathymetry, bottom and photic conditions, co-occurrence of other biota), and which were controlling the content and structure of the whole gastropod assemblage at Grund. To note, of all gastropod assemblages known from the Vienna Basin and adjacent countries (*see* HOERNES & AUINGER 1879-1891), the

Grund assemblage is the closest to that from the Korytnica Clays (*see* BAŁUK 1997, p. 51).

A similar connotation as concerns the host specifity of the studied paradigm is also apparent for the locality Varovce in the Ukraine, wherefrom it was illustrated by ANDRZEJOWSKI (1833, Pl. 13, Fig. 5) on his *Clavatula suturalis*, precisely on the only figured specimen, that is the holotype of the species which is so heavily infested by that paradigm within the studied assemblage of the clavatulids at Korytnica.

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