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# THE MORPHOLOGY, PALEOECOLOGY AND SYSTEMATICS OF *NOTHIA EXCELSA* (GRZYBOWSKI), A DEEP-WATER AGGLUTINATED FORAMINIFER

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A b s t r a c t : A study of unusually well-preserved specimens from the upper surface of a turbidite sandstone layer indicates the tubular agglutinated foraminifer described by Grzybowski (1898) as *Dendrophrya excelsa* must be transferred to the genus *Nothia*. The autecology of this common species is interpreted as a surface-dwelling detritivore.

K e y w o r d s : Agglutinated foraminifera, *Nothia excelsa*, Paleogene, flysch, Carpathians.

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## INTRODUCTION

An increasingly popular method of paleoenvironmental analysis is to assign benthic foraminiferal species to morphogroups based on their life mode and feeding behaviour, which are then treated as a unit. The main assumption in morphogroup analysis is a close link between "form and function", i.e. that species possessing similar morphology also share a common microhabitat. Tubular agglutinated genera such as *Nothia, Rhabdammina, Hyperammina*, and *Bathysiphon*, are commonly placed in a single morphogroup (erect suspension feeders) even though individual species may have displayed differences in their autecology. Indeed, some modern tubular species have been observed to be suspension feeders (Altenbach *et al.*, 1988), while others utilize dissolved organic matter (Delaca *et al.* 1981). Still others from oligotrophic oceanic environments retain their waste products internally as stercomata, and may be "autotrophic" in a sense by utilizing commensal bacteria. Studies of tubular agglutinated foraminifera in their life position are therefore

necessary to determine their autecology, and in turn their position in the trophic structure of the benthic community.

Unfortunately, flysch-type agglutinated foraminifera are rarely observed in life position. However, on rare occasions the odd well-preserved specimen is found which is more valuable in terms of ecology and systematic zoology than all the millions of fragments observed in normal sample preparations. One such specimen was discovered in the village of Lipnica Mała during field work conducted on trace fossils from the lower Eocene Beloveža beds of the Carpathian flysch. This specimen represents a virtual "rosetta stone" giving us unique insight into the autecology and systematics of a well-known species from the Carpathian flysch – Józef Grzybowski's *Dendrophrya excelsa*.

## THE NATURE OF THE PROBLEM

In 1898, Józef Grzybowski published his classic monograph on the Paleogene foraminiferal assemblages from the western Galician oil fields. One of the first species described in this monograph is *"Dendrophrya excelsa"*, a small, branching tube that is common in the Upper Cretaceous and lower Paleogene throughout the Carpathians, western Tethys, and North Atlantic region. Grzybowski's collection at the Jagiellonian University houses numerous fragments 'of this species, all carefully preserved in small glass vials. Grzybowski (1898) assigned this form to the genus *Dendrophrya*, based on comparison of his specimens with those depicted in Brady's (1884) monograph of the HMS CHALLENGER Expedition. Grzybowski (1898, p. 272) remarked:

[...] This species is very similar to *Dendrophrya erecta* T. S. Wright (Brady, 1884, p. 239 pl. 27A, fig. 7-9) but differs from it markedly in size. I know it only from fragments, which are rather common and up to 2.5 mm in length and 0.6 to 1.0 mm in width, whereas Brady reports a length of 3.5 mm for the entire branched test in *Dendrophrya erecta*.

Grzybowski lamented not having complete specimens to work with, but such was the nature of the material at hand – his raw material consisted almost exclusively of drill cuttings.

In 90 years of subsequent micropaleontological investigations in the Carpathian flysch, *"Dendrophrya excelsa"* has been observed by authors too numerous to mention. Despite its wide distribution, no study has revealed anything more about its morphology other than isolated, sporadically branched fragments. However, an understanding of its morphology is crucial to the systematics of this species, since Brady himself (op cit., p. 237) described the genus *Dendrophrya* Strethill Wright as:

"test adherent, consisting of a sessile chamber with erect or spreading arms. Arms tubular, irregular, often branching; with apertures at the distal ends. "

Brady cited the observation of Dr. T. Strethill Wright that the genus *Dendrophrya* was originally set up to encompass "rhizopodous animals, found plenty on Sertularias, Flustras, Fuci, and stones in shallow water pools". Clearly, there is a disparity between the nearshore environment of seaweed

and rocky pools, and the deep-water fine, muddy substrate of the flysch basin. In the latter environmental setting, hard substrates are exceedingly rare, and sessile, attached organisms ought to be ecologically excluded. Why then is "*Dendrophrya excelsa*" so common in the Carpathian flysch?

In all the washed samples that we have analyzed from the Carpathian flysch and North Atlantic regions, we have never observed a fragment of this species suggesting the presence of a "hemispherical or cap-like expansion that may attach to hard substrate" or "basal chamber", which according Loeblich and Tappan (1988) characterizes the genus *Dendrophrya*. Nor do specimens display "successive branchlets of decreased diameter". All specimens, including exceedingly long and well-preserved forms obtained in acid residues from the Paleogene of the Scaglia Rossa in Italy, are simply straight or slightly bent tubes with rare dichotomous branches. Because specimens present in any washed residue are invariably fragmented, the true morphology of this species has until now remained an enigma.

## GEOLOGIC SETTING

Specimens examined in this study were collected from the Beloveža beds of the Polish Carpathians near the border with Czecho-Slovakia (Fig. 1). The sample locality is the bed of the Syhlec stream, a tributary of the Orawa River, in the village of Lipnica Mała. This was a key locality in the monograph "Trace fossils in the flysch of the Polish Carpathians" by Książkiewicz (1977), and is the subject of ongoing investigations by paleontologists at the Jagiellonian University. Field work undertaken in the outcrops by A. Uchman in 1988 (indicated as localities A and B in Figure 2) uncovered large fragments of tubular foraminifera in association with numerous trace fossils. The specimen illustrated in Plate 1 was found as a loose fragment in the stream bed. Subsequent attempts to trace the specimen to a precise sandstone bed in the outcrop have not been successful, but specimens of tubular foraminifera do occur on the upper and lower surfaces of several sandstone layers in the stream outcrops.

The Beloveža beds are developed in the middle part of the Magura nappe (the Bystrica subunit). These beds consist of thin-bedded, light-blue sandstones alternating with argillaceous or marly, green or grey-blue shales. In the lower part of the unit, red and green shales are present. Sandstones are finely laminated, and often rippled or weakly convoluted. Graded bedding is usually visible. The thickness of the Beloveža beds may exceed 300 m.

The age of the Beloveža beds has been determined as early Eocene, based on benthic and planktonic foraminifers. In the lower part of the unit, the microfaunal assemblage consists entirely of agglutinated foraminifera dominated by the genus *Glomospira*. This assemblage is the lateral equivalent of the distinctive *Glomospira* facies present in the lower Eocene of the Vienna

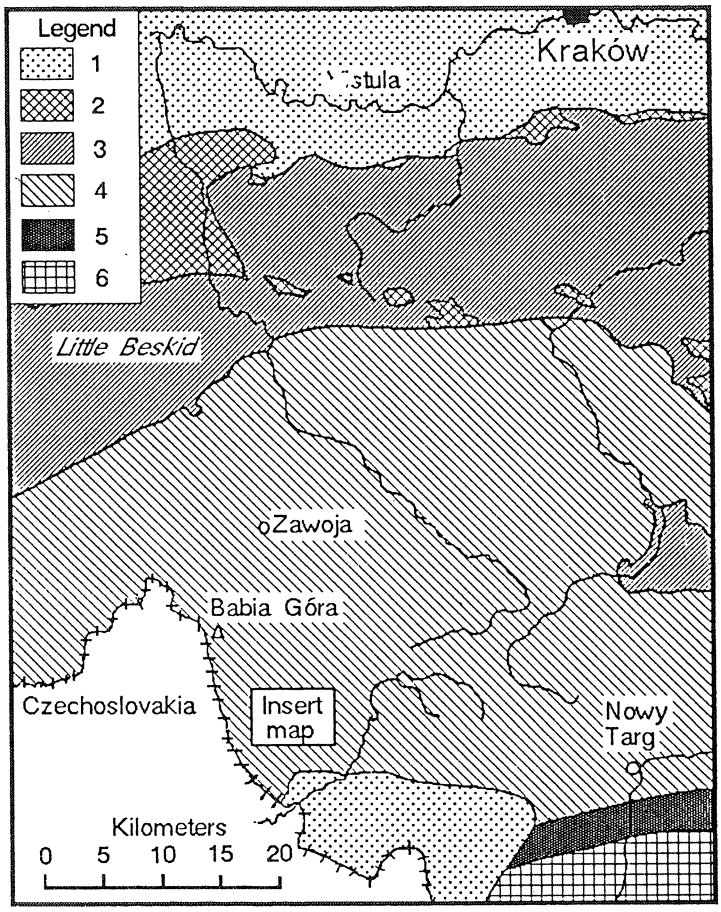


Fig. 1 Tectonic sketch map of the outer flysch zone in the western Carpathians in the area of Poland southwest of Kraków (modified from Geroch *et al.*, 1967). Numbers in the legend refer to the following sedimentary or tectonic units. *1* – Neogene clastic sediments of the Carpathian fore-basin and Orava depression, *2* – Subsilesian nappe and Mszana tectonic window; *3* – Silesian nappe; *4* – Magura nappe; *5* – Pieniny Klippen Belt; *6* – Inner zone of the Carpathians.

Woods flysch (Grün *et al.* 1964), in Switzerland (Winkler, 1984) and in the northern North Atlantic (Kaminski, 1988). Above the *Glomospira* facies, rare planktonic foraminifera belonging to the *Subbotina inaequispira* Zone (P9) of Berggren and Miller (1988) are present. The age, therefore, of the agglutinated *Glomospira* facies of the Beloveža beds is consistent with its age determined at other localities in the North Atlantic and western Tethys. Occasional nummulites, including the species *Nummulites planulatus* Lamark, *N. burdigallensis* de la Harpe, and *N. gallensis* Heim, have been found redeposited in the coarser sandstone layers (Bieda, 1959).

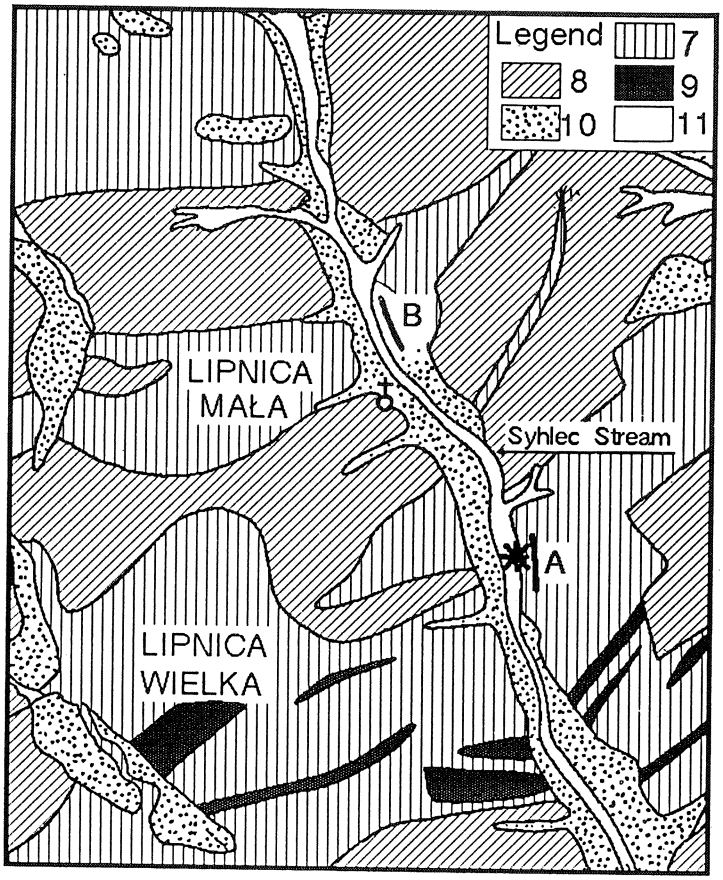


Fig. 2 Simplified portion of the "Geological Map of Babia Góra" by M. Książkiewicz showing the location of the outcrops in the Syhlec stream, near the village church in Lipnica Mała. Numbers in the legend refer to the following sedimentary units: *7* – Beloveza Beds (lower Eocene); *8* – Łącko marls (middle Eocene); *9* – variegated shales (lower Eocene); *10* – Quaternary deposits; *11* – alluvial deposits of the Syhlec stream. Scale: 1 cm = 0.5 km

The Beloveža beds harbour the most diversified trace fossil assemblage of the Carpathian flysch. Traces are present on both lower and upper surfaces of the sandstone beds. The ichnofaunal association (54 ichnogenera) of the Beloveža beds is rich in graphoglyptids (e.g. *Paleodictyon, Urohelminthoida, Megagrapton*). This association, as well as the associated microfauna, indicates well oxygenated sediments, somewhat oligotrophic conditions, and relative ecologic stability only occasionally interruped by turbidites (Uchman, 1992).

Foraminiferal assemblages from gray marly claystones collected in the Syhlec stream are only moderately diverse, and consist of a large proportion

of tubular agglutinated species, with a smaller proportion of calcareous benthic species and radiolarians. The accessory species in these samples include *Glomospira charoides* (Jones and Parker) and *Glomospira gordialis* (Jones and Parker), *Ammodiscus cretaceus* (Reuss), *Glomospira serpens* (Grzybowski), *Saccammina placenta* (Grzybowski), *Recurvoides* spp., *Paratrochamminoides* spp., *Haplophragmoides walteri* (Grzybowski), *Haplophragmoides* sp. cf. *H. kirki* (Wickenden), and rare *Nuttallides truempyi* (Nuttall). These assemblages of foraminifera indicate a middle to lower bathyal environment, and are typical of the middle part (mid-lower Eocene) of the Beloveža beds.

## THE SPECIMENS

The occurrence of long, well-preserved specimens of *Nothia excelsa* is only associated with infrequent beds, and appear to be related to the physical properties of the sediments. Long tests of *Nothia excelsa* are only developed on well-expressed interbedding surfaces, such as the top surfaces of sandstone layers. We suspect that these semi-consolidated surfaces offered a sufficiently firm substrate for the organism to live, as opposed to the soft-substrate environment represented by the pelagic mud.

Numerous fragments of tubular agglutinated foraminifers are found on the upper surface of the sandstone block illustrated in Plate 1. Specimens vary in length up to a maximum of about 40 mm. The tubes themselves are somewhat compressed and have rather uniform width (0.3 to 0.4 mm). They possess neither constrictions nor inflations, and do not decrease in diameter in any preferred direction. The branching is sparse, always dichotomous, and at irregular intervals. The length between branches averages 5 mm. The intervals between branches may be straight or gently curved, and the specimens are often broken at the point of branching. The tubes are eliptical in cross section, and may have slightly concave sides. Because of the compression of the test, the chamber lumen is only visible as an indistinct dark streak, which derives from its organic inner lining. The surface of the test is somewhat rough, which may be partially due to adventitious agglutinated grains adhering to its suface that are difficult to brush away. Sections of the tubes examined in polarized light show that the agglutinated material is comprised of about 90% quartz, with the remainder consisting of mica, and less commonly, feldspar. The intergranular cement is present in the form of chalcedony, illite, and iron compounds. The thickness of the wall varies from 0.06 to 0.08 mm. For comparison, specimens from washed samples collected from claystones in the Syhlec stream profiles are 0.2 to 0.5 mm in width, and the wall thickness varies from 0.06 to 0.15 mm.

**Comparison with other tubular forms:** The type specimens of *Dendrophrya excelsa* from the area of Krosno preserved in the Grzybowski Collection compare well with the specimens from Lipnica Mała. The dimensions

of the types (width and thickness) overlap with those described above, but Grzybowski's specimens possess a rather finely agglutinated wall. This may be attributed, however, to either differences in the available substrate or to later diagenesis.

The species *Psammatodendron dichotomicum* described by Neagu (1964) has a more robust tube, with the width varying from 0.9 to 1.1 mm, and the thickness of the wall between 0.16 and 0.19 mm. This species is similar in possessing sparse branching and in the nearly constant diameter of the tube.

## DISCUSSION

**Generic affiliation:** The first and foremost morphologic trait of our specimens from Lipnica Mała is the absence of any sign of a basal attachment or center of organization. This precludes classifying them in the genus *Dendrophrya*. Branched tubular agglutinated forms which lack a proloculus or basal attachment have been traditionally placed in the genus *Rhizammina* Brady, 1879. The definition of this genus, however, has been restricted to include only those forms which have a thin and flexible test wall comprised mainly of organic matter (Loeblich and Tappan, 1988). At least one species, *Rhizammina algaeformis* Brady, 1879, has been demonstrated to be a komokiacean (Cartwright *et al.*, 1989). Although isolated tubular fragments of *R. algaeformis* may be similar to our specimens in external appearance. Cartwright *et al.* (1989) have shown that the whole organism consists of a tangled clump of intertwined tubes several centimeters across. The stratigraphic distribution of *Rhizammina* has been reported as "Holocene" by Loeblich and Tappan (1988). Our fossil specimens from the Carpathian flysch and other localities in the North Atlantic and western Tethys have a relatively thick, monolamellar wall made up of silt-sized grains with some admixture of pelitic material. Specimens are generally straight, not laterally distorted, and therefore probably possessed a rigid wall. These features plus the lack of a proloculus indicate that the species *D. excelsa* Grzybowski belongs to neither *Dendrophrya* nor *Rhizammina*. Adherence to the current generic classification of Loeblich and Tappan (1988) requires this species to be transferred to the genus *Nothia* Pflaumann, 1964. This genus, which various authors have considered to be a synonym of *Rhizammina*, was originally set up to encompass branched forms described from the Cretaceous flysch deposits. Although the type species of *Nothia* (*N. grilli* Pflaumann, 1964) was described as having a bilamellar wall, the current definition of the genus given by Loeblich and Tappan does not exclude forms that have a single-layered wall.

**Ecology:** The specimens preserved on the rock slab display several anatomical features that argue for a sessile surface-dwelling organism, not one that is suited for an erect life position. Conventional wisdom dictates that any organism which lives erect on the substrate must possess a holdfast or anchor

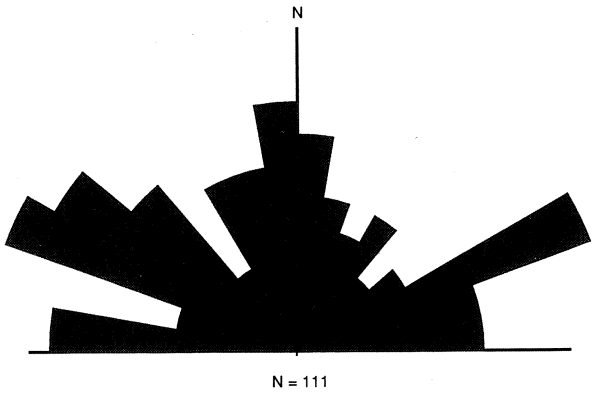


Fig. 3 Orientation of individual segments of the specimens in Plate 1, measured relative to an arbitrary reference line. The lack of a preferred orientation argues against post-mortem transport

itself in some other manner. Erect forms that live in muddy substrates, such as the modern species *Saccorhiza ramosa*, have an inflated proloculus anchored in the sediment, and a tubular part that is more massive at the base (e.g. Altenbach *et al.* 1988). The specimens of *N. excelsa* in Plate 1 display an irregular, almost meandering morphology that precludes an erect life style. The specimens are supported by the rigid sandstone bed, so any post-mortem deformation must have been minimal.

Another aspect of the specimens in Plate 1 that gives supporting evidence for a sessile life position, is the presence on the slab of a feeding trace belonging to the genus *Scolicia*. Two of the specimens were clearly disturbed by the feeding activity of a benthic metazoan. Moreover, when the orientation of individual segments are measured relative to an arbitrary reference line they display no preferred oriention (Fig. 3). Therefore, we interpret the specimens on the sandstone bed as being in their *in situ* life position.

The interpreted life position of *Nothia excelsa* has far-reaching implications for paleoecology. Until now, tubular agglutinated forms have generally been interpreted as sessile, suspension feeders, deriving their sustenance from particulate or in some cases, dissolved, organic matter (e.g. Delaca *et al.*, 1981). In what is now a classic study, Jones and Charnock (1985) presented a conceptually elegant ecological model that subdivides agglutinated foraminifera into four morphogroups based on inferred life position and feeding strategy. The relative proportions of different feeding-strategy groups were shown to vary as a function of water depth. Nearly all tubular forms were placed together in their "morphogroup A", interpreted as erect epifaunal suspension feeders. Subsequent investigations of modern deepsea agglutinated foraminifera collected in box cores have generally upheld this view. In a study of box cores from the west African margin, Altenbach *et al.* (1988) reported finding living, erect individuals of *Saccorhiza ramosa* with pseudopodal nets still extended into the water column. In studies of modern faunas from the

Panama Basin, one of us (MK) has observed rose-bengal stained individuals of *Dendrophrya* only in samples from the supernatant water of box core samples (probably suspended during the handling of the box core), and from the sediment surface layer. Jones and Charnock noted that some tubular forms, such as *Rhizammina* may be deposit feeders, and tentatively placed another tubular genus, *Hippocrepina*, in their "morphogroup B" which is the group of surface-dwelling detritivores. In our opinion, *Nothia excelsa* clearly belongs in "morphogroup B" of Jones and Charnock. Reassigning *D. excelsa* to the genus *Nothia*, thereby removes a quantitatively important constituent of the flysch-type fauna from the ranks of the suspension-feeding bottom community and places it among the detritivores.

**Acknowledgements**

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## Streszczenie

# MORFOLOGIA, PALEOEKOLOGIA I POZYCJA SYSTEMATYCZNA GŁĘBOKOWODNEJ OTWORNICY AGLUTYNUJĄCEJ *NOTHIA EXCELSA* (GRZYBOWSKI)

**Stanisław Geroch & Michael A. Kaminski**

Dobrze zachowane okazy rurkowatej otwornicy opisanej jako *Dendrophrya excelsa* Grzybowski (1898) znaleziono w warstwach beloweskich (Eocen) w miejscowości Lipnica Mała koło Jabłonki (fig. 1,2). Okazy sa rozmieszczone w pozycji przyżyciowej na górnej powierzchni ławicy drobnoziarnistego piaskowca. Rurki mają do 40 mm długości, 0,3-0,4 mm szerokości i rozwidlają się w odstępach średnio 5 mm. Odcinki między rozwidleniami są proste lub nieco zgięte. Przekroje rurek sa na ogół eliptyczne, a ich powierzchnia słabo szorstka. Aglutynowana ścianka o grubości 0,06 - 0,15 mm zawiera ok. 90% drobnego kwarcu, nieco miki i skalenia, oraz cement z chalcedonu, illitu, i związków Fe.

Powyższe cechy dobrze upodabniają znalezione okazy do typowych *D. excelsa* z okolicy Krosna, które są znane tylko z krótkich odłamków. *Psammatodendron dichotomicum* Neagu, 1964 opisany z senonu Rumunii na podstawie dobrze zachowanych okazów, odznacza się większą średnicą rurki (0,9 - 1,1 mm) i grubszą ścianką (016 - 019 mm), chociaż ma podobnie rozmieszczone rozwidlenia i stałą grubość ścianki.

Dotychczasowe zaszeregowanie rodzajowe *Dendrophrya excelsa* nie może być utrzymane, bo nie zauważono ani oznak "zakotwiczenia" okazów, ani

komory embrionalnej, co też wyklucza zaliczenie *D. excelsa* do rodzaju *Rhizammina*. Nawiązując do aktualnej klasyfikacji otwornic według Loeblich i Tappan (1988), słuszne wydaje się włączenie do rodzaju *Nothia* Pflaumann 1964, opisanego z osadów fliszowych senonu w Bawarii.

Nasze obserwacje dotyczące rozmieszczenia skorupek *N. excelsa* pozwalają nawiązać do proponowanego przez Jones i Charnock (1985) podziału otwornic aglutynujcych na 4 morfogrupy w zależnosci od pozycji przyżyciowej i sposobu odżywiania. Dotychczas na ogół większość współczesnych otwornic rurkowatych zaliczano do grupy A – form zakotwiczonych "sterczących" odżywiajcych się zawiesiną (morphogroup A – erect suspension feeders). Natomiast, *N. excelsa* można zaliczyć do grupy B, obejmującej formy płożące odżywiające się detrytusem organicznym.

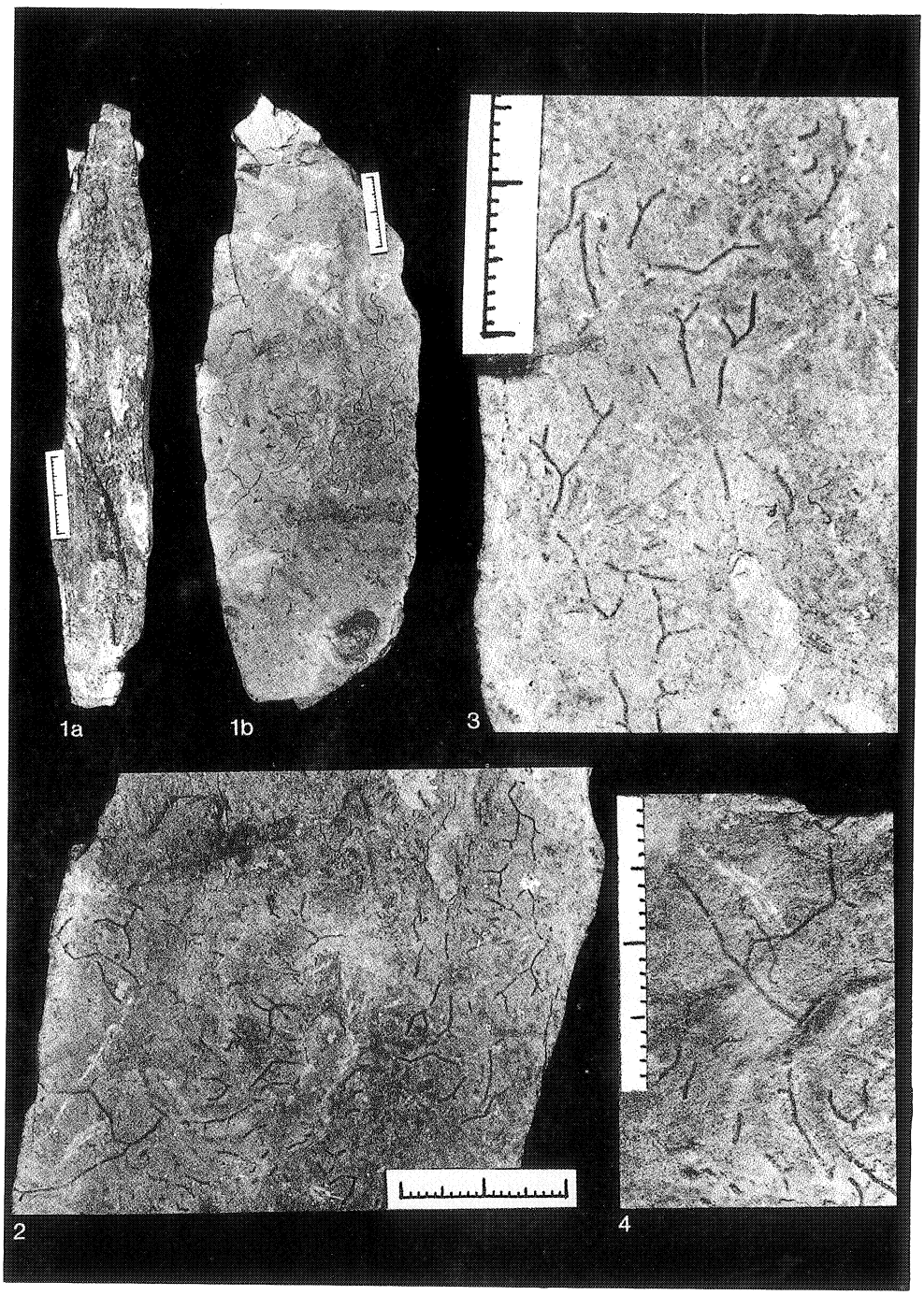
## EXPLANATIONS TO PLATES

### Plate I

1 — Complete specimen found in the Syhlec stream in the village of Lipnica Mała, Poland. a – edge view of the sandstone bed; b – upper surface of sandstone specimen. Scale bar is 2 cm
2 — Detail of central portion of specimen, showing randomly oriented complete specimens of *Nothia excelsa* on upper surface of sandstone
3-4 — Detail of specimens

### Plate II

1-4 — Specimens of *Nothia excelsa* collected *in situ* at outcrop "*B*" in the Syhlec stream (see Fig. 2 in text), x4
5a,b — Thin section of specimen from outcrop "*B*" in the Syhlec stream (see Fig 2 in text), a – transmitted light, b – crossed nichols, x130
6a,b — Thin section of specimen from the sandstone slab in plate I, showing the compressed chamber lumen. a – transmitted light, b – crossed nichols, x130
7 — SEM of specimen from the sandstone slab in plate I, x50
8 — SEM of specimen from the sandstone slab in plate I, x106
9 — Longitudinal thin section of specimen from the sandstone slab in plate I, transmitted light, x130
10-11 — Paratype specimens of "*Dendrophrya excelsa*" from the Grzybowski Colletion, x56. Specimens are from an exploration well in the Silesian Unit drilled in Krościenko, Poland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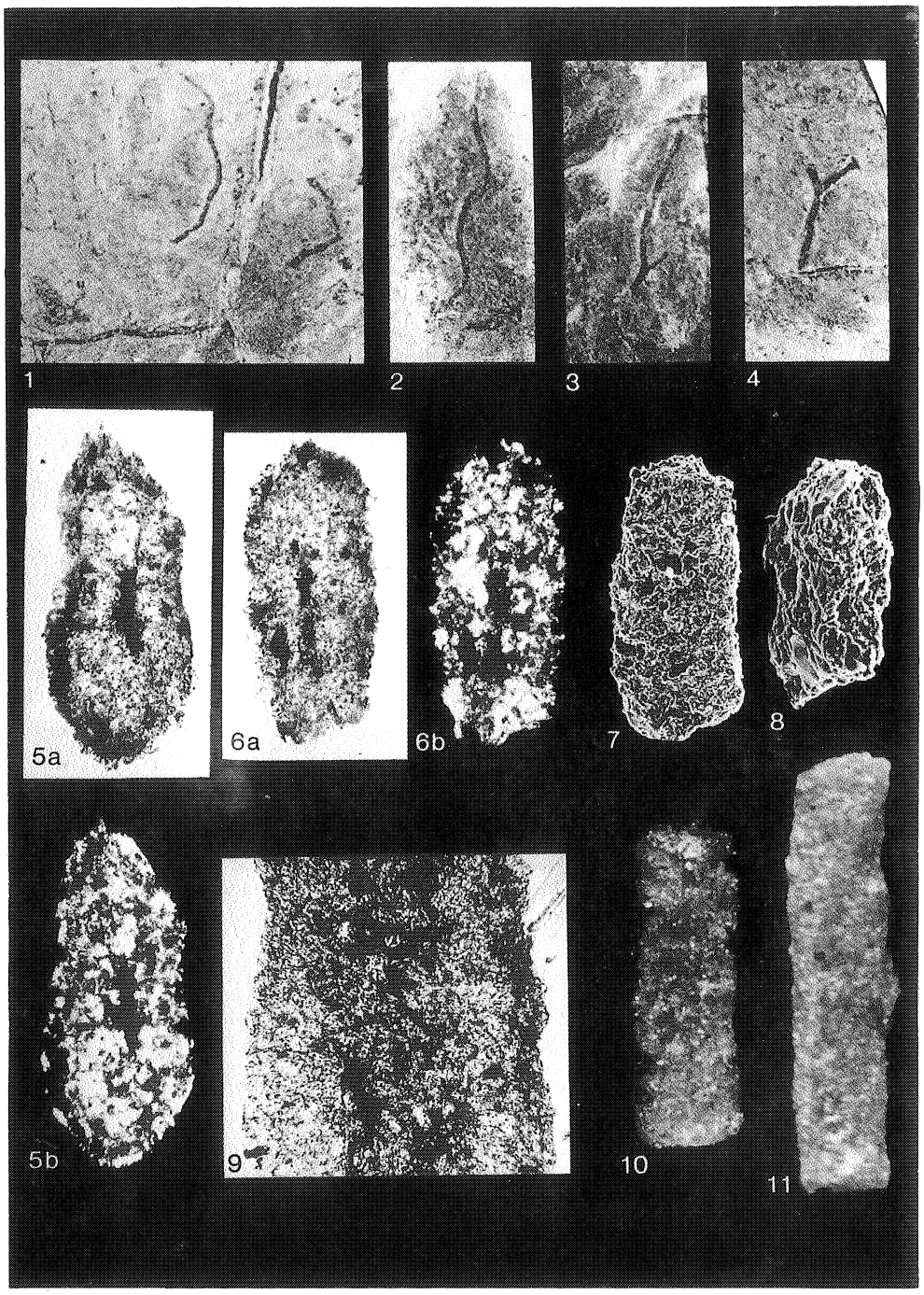
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