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# *Bohemograptus papilio* sp. nov. three-dimensionally preserved monograptid (Graptolithina) with an adaptation to retard sinking, from the Upper Silurian Poland

Bohemograptus papilio sp. nov., monograptidé (Graptolithina) conservé en trois dimensions avec une adaptation à un enfouissement ralenti, dans le Silurien supérieur de Pologne

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#### ABSTRACT

An unexpected new form of *Bohemograptus* with unusual morphological structure has been found in the upper part of the *Bohemograptus praecornutus* Biozone, Upper Ludlow of the Mielnik borehole, Poland. *Bohemograptus papilio* sp. nov. has the characteristic rhabdosome for *Bohemograptus*, in addition to extraordinary paired latero-dorsal additions, not comparable to any processes typical for *Bohemograptus* thecal openings. The new structure, a patagium, is located in the proximal part of the rhabdosome, and is built from main rods dividing repeatedly into thinner lists with significant remnants of membranes spread between them. Another new structure is the virgellarium, a membranous addition to the virgella. Membranes of the patagium and virgellarium are not built from microfusellar tissue as additions in other bohemograptids. It is suggested that the membranous additions were orientation devices, constructed to retard the sinking of the colony in the water column.

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# RÉSUMÉ

On rapporte la découverte d'une nouvelle forme du genre *Bohemograptus* dans la partie supérieure de la zone à *Bohemograptus praecornutus* (Ludlow supérieur) du forage Mielnik (Pologne). *Bohemograptus papilio* sp. nov. se caractérise par le rhabdosome caractéristique du genre, mais avec des extensions latéro-dorsales exceptionelles. Cette structure, non comparable avec des processus typiques des apertures thécales des *Bohemograptus*, appelée le patagium, se situe dans la partie proximale du rhabdosome ; elle se compose de quelques tiges principales se divisant plusieurs fois pour donner de plus minces filets avec d'importants restes de membranes étalées entre eux. Une autre structure nouvelle,

Abbreviations: ZPAL G, number of collection.

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le virgellarium, est une addition membraneuse à la virgelle. Les membranes du patagium et du virgellarium ne sont pas constituées de tissu microfusellaire, contrairement aux autres Bohêmograptidés. On suggère que la fonction des extensions en forme de membrane était d'orienter le mouvement de la colonie par rapport à l'eau, en réduisant la vitesse à laquelle la colonie tombe en profondeur.

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#### 1. Introduction

Nowadays, the Silurian is regarded as a period with one of the most unstable climates during the Paleozoic (Calner, 2008; Munnecke et al., 2010). It is rich in numbers of graptolite forms, which show their great ability to produce new forms and survive small or large environmental changes. The variety of planktonic graptolite forms indicates the number of ecological niches which they occupied in the variable environments (Kozłowski, 1971). The new form described in this paper seems to be some answer for the environmental changes.

Among many studies of Ludlow graptolites from around the world, those from the Polish part of the East European Platform, part of Baltica (Fig. 1), belong to one of the best studied faunas in the sense of morphological variation as well as evolution (Kozłowska-Dawidziuk, 1995, 2004; Urbanek, 1963, 1966, 1970, 1997). This is due to their presence in boreholes, and their excellent preservation giving the possibility of study in three dimensions. Comparison with graptolite faunas from elsewhere (Koren' and Sujarkova, 2004; Lenz and Kozłowska-Dawidziuk, 2004; Rickards et al., 1993; Rickards and Wright, 1999) is very important and provides further significant information.



**Fig. 1.** A structural map of East Poland, the west margin of the East European Platform, with location of the Mielnik borehole. Based on Teller, 1997.

**Fig. 1.** Carte structurale de l'Est de la Pologne : bordure occidentale de la Plate-forme est-européenne et localisation du forage Mielnik (à partir des données de Teller, 1997).

The subfamily Neocucullograptinae sensu Urbanek, 1970 represents a specialized group of species in which some of them developed extraordinary apertural processes located on apertural margins (Urbanek, 1970) (Fig. 2). Bohemograptus Přibyl, 1967, belonging to this subfamily, displays initially little variation and very slow morphological evolution. The genus is common in the Ludlow and started to radiate in Lower Ludfordian, directly after the leintwardinensis Event, which probably caused the extinction of many Ludlow graptolites, e.g. Lobograptus Urbanek, 1958. Bohemograptus has a narrow, small, ventrally curved rhabdosome with relatively simple thecae that widen distally. The ancestral form, Bohemograptus bohemicus (Barrande, 1850) does not have any apertural structures, in contrast to the later forms. The simple ancestral Bohemograptus forms survived up to the kozlowskii Biozone (Urbanek, 1997), possible at that time the Lau Event (Jeppsson and Aldridge, 2000) may have occurred.

During the "Bohemograptus proliferation zone" (acme zone) of Urbanek, 1970 there was an increase in variation within Bohemograptus populations. The most distinctive developments are the production of apertural additions, modifications of the sicula, and increases in size of rhabdosomes and in curvature. There are detailed observations of extremely well developed apertural structures at different astogenetic stages of isolated material from Poland (Urbanek, 1970) as well as of flattened forms from Kyrghizstan (Koren' and Sujarkova, 2004).

This article describes an unexpected morphological structure in isolated specimens of *Bohemograptus papilio* sp. nov., from the upper part of "*Bohemograptus* proliferation zone" (acme zone), in the *praecornutus* Biozone, of the Lower Ludfordian of Poland (Urbanek, 1970, pl.1). The new form has the typical bohemograptid rhabdosome added to which is a previously unrecognized structure, called herein the *patagium*, (Figs. 3 and 4). The new species has also the virgella divided irregularly with remnants of membranes between the branches, making a membranous virgellarium similar to the patagium but oriented vertically like the keel of a boat (Figs. 4 and 5). The structures with membranes were probably relatively large (Fig. 5).

The new membrane addition, the patagium of the *B. papilio* sp. nov., is regarded as an organ invented to retard or prevent the sinking of the colony in the water column. The reason was probably to keep the graptolite in a position, in the food-rich photic zone (Kozłowski, 1971).

Various types of alleged floating additions have been described, but only in flattened graptolites. However, the proximal organ described here is the first studied on isolated and 3D material. To sum up, the new form being an unexpected phenomenon shows the ability of graptolites



**Fig. 2.** *Bohemograptus tenuis* (Bouček, 1936), Poland, Mielnik borehole, *kozlowskii* biozone (A–D) and *auriculatus* biozone (G); proximal end of rhabdosome with two thecae (A), paired broad lobes forming velum (B, C), small paired apertural lobes (D), pseudomicrofusellar structure on virgella (G). *Bohemograptus cornutus* Urbanek, 1970, Poland, Mielnik borehole, *cornutus* Biozone (E, F), proximal part of rhabdosome with paired apertural apparatus on first theca (E), paired apertural apparatus on second theca (F). Scale B–D, F 0.5 mm, G–1 mm. Drawings from Urbanek, 1970 (A) pl. 24A, (B) pl. 21B<sub>2</sub>, (C) pl. 21A<sub>2</sub>, (D) pl. 14C<sub>2</sub>, (E) pl. 25A<sub>1</sub>, (F) 25B, (G) 22A<sub>4</sub>.

**Fig. 2.** Bohemograptus tenuis (Bouček, 1936), forage Mielnik, zones à *kozlowskii* (A-D) et à *auriculatus* (G); extrémité proximale du rhabdosome avec deux thèques (A), lobes pairs larges formant le voile (B, C), petits lobes aperturaux paires (D), structure pseudomicrofusellaire sur la virgelle (G). Bohemograptus cornutus Urbanek, 1970, forage Mielnik, zone à *cornutus* (E, F), partie proximale du rhabdosome avec un appareil apertural pair sur la première thèque (E), appareil apertural pair sur la seconde thèque (F). Scale B-D, F 0,5 mm, G–1 mm. Dessins d'après Urbanek (1970).

to produce new forms in the variable environments of the Silurian seas.

#### 2. Material and methods

The graptolites studied herein came from the Mielnik borehole, depth 915.6 m, upper part of the *Bohemograptus praecornutus* Biozone (Urbanek, 1970, Table 1). There are 25 specimens mostly fragments up to 4 thecae, 20 proximal ends with new structures, mostly broken. Other monograptids include several complete rhabdosomes and fragments of *Pristiograptus dubius* (Suess, 1851), *Monoclimacis* sp., *Prolinograptus packhami* Rickards and Wright, 1997, and remnants of some retiolitids.

The new form was isolated from rock following slow dissolution of the host carbonate in 1 to 10% HCl. A fine hairbrush was used to transfer specimens. The specimens, destined for a detailed examination were bleached in a mixture of potassium chlorate, nitric acid and water. After about a 10 to 15 hour bath, the specimens were washed in water to remove the remnants of acid and chlorine. The material is stored in glycerine in plastic containers, and on SEM stubs. The SEM pictures were made at the Institute of Paleobiology Polish Academy of Sciences, Warsaw, Poland with a Philips XL.

#### 3. Systematic palaeontology

Family Monograptidae Lapworth, 1873 Subfamily Neocucullograptinae, Urbanek, 1970 Genus Bohemograptus Přibyl, 1967 Type species *Graptolithus bohemicus* Barrande, 1850 *Bohemograptus papilio* sp. nov.

Etymology: *papilio* butterfly in Latin, referring to the shape of extraordinary proximal structures.

Holotype: Rhabdosome possessing three thecae and patagium ZPAL G.49/2, depth 915.6 m Mielnik borehole, Poland (Fig. 4A, B).

Diagnosis: A *Bohemograptus* with thin, gently curved rhabdosome. Sicula clearly curved, length up to 1.45 mm, possessing small dorsal apertural lobes. Two multiply divided rods with remnants of membranes, the patagium, located proximally on both sides of rhabdosome. Rods arising from the edge of interthecal septum between th1 and th2 or from the border between prosicula and metasicula. Membranous virgellarium situated vertically on virgella.

## 3.1. Material examined

ZPAL G.49/1-5 (20 proximal ends with patagium and virgellarium and several distal fragments).

# 3.2. Description

The longest rhabdosome with a sicula contains four thecae. The sicula is 1.45 mm long, clearly widening distally and displaying an obvious ventral curvature. The prosicula length is 0.6 to 0.7 mm. The prosicular apex is located about the level of th1<sup>1</sup> aperture. The metasicula has four to five annuli. Aperture of metasicula has distinctive, shovel-like dorsal process, slightly bifd with two wing-like outgrowths, typical for *Bohemograptus* (Urbanek, 1970, pl.



**Fig. 3.** Scanning electron microscope pictures of *Bohemograptus papilio* sp. nov., Poland, Mielnik borehole, depth 915.6 m, *Bohemograptus praecornutus* Biozone, ZPAL G. 49/1, fragment of proximal end of rhabdosome with prosicula, metasicula and fragments of two first thecae; dorsal view of specimen showing patagium (A), enlargement of the region with beginning of main rods of patagium (B), enlargement of second rod with fragments of membrane (C), distalo-lateral view of whole specimen (D), enlargement of the beginning of first rod (E), distalo-lateral view of specimen (F), lateral view of the side with second rod (G).

**Fig. 3.** Images MEB du *Bohemograptus papilio* sp. nov., du forage Mielnik, profondeur 915,6 m, zone à *Bohemograptus praecornutus*, spécimen ZPAL G. 49/1, fragment de l'extrémité proximale du rhabdosome avec la prosicule, la métasicule et les fragments des deux premières thèques ; vue dorsale montrant le patagium (A), grossissement de la région où commencent les tiges principales du patagium (B), grossissement de la seconde tige avec des fragments de membrane (C), vue distalo-latérale du spécimen entier (D), grossissement du commencement de la première tige (E), vue distalo-latérale du spécimen (F), vue latérale du côté avec la seconde tige (G).

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**Fig. 4.** *Bohemograptus papilio* sp. nov., Poland, Mielnik borehole, depth 915.6 m, *Bohemograptus praecornutus* Biozone. A-B proximal end of rhabdosome with three thecae, holotype, ZPAL G. 49/2, light photograph (A) and scanning electron photograph with broken off patagium (B). C proximal end of rhabdosome with one theca and beginning of second theca, light photograph, ZPAL G. 49/3. D fragment of patagium, light photograph, ZPAL G. 49/4. E-G scanning electron photograph of rhabdosome with one theca, broken patagium (arrowed), and preserved membranaceus virgellarium, ZPAL G. 49/5 (E), enlargement of virgellarium (F), enlargement of broken patagium, proximal-lateral view (G).

**Fig. 4.** Bohemograptus papilio sp. nov., forage Mielnik, profondeur 915,6 m, zone à Bohemograptus praecornutus. A-B extrêmité proximale du rhabdosome avec trois thèques, holotype ZPAL G. 49/2, photographie au microscopie optique (A) et au MEB avec le patagium cassé (B). C extrêmité proximale du rhabdosome avec une thèque et le commencement d'une seconde, microscopie optique, ZPAL G. 49/3. D fragment du patagium, microscopie optique, ZPAL G. 49/4. E-G photographies MEB du rhabdosome avec une thèque, patagium cassé (flèche), et le virgellarium en forme de membrane conservé, ZPAL G. 49/5 (E), grossissement du virgellarium (F), grossissement du patagium cassé, vue proximale-latérale (G).

25c). The metasicular aperture is 0.4 mm wide. The virgella has additional, thinner lists growing up ventrally from the edge of the metasicula (Fig. 4A–C, E), mostly preserved as remnants (Fig. 4A–C). The list divides into thinner lists,

between of which there is a membrane (Fig. 4E, F) or its remnants (Fig. 4A–C), all creating a virgellarium.

The first theca arises 0.4 mm from the aperture of the metasicula. It is distinctively curved, the prothecal



**Fig. 5.** Reconstruction of *Bohemograptus papilio* sp. nov. Most probably, the life position of the patagium was horizontal.

**Fig. 5.** Reconstitution du *Bohemograptus papilio* sp. nov. La position du patagium *in vivo* était le plus probablement horizontale.

part is 0.1 mm wide, whereas the distal part is 0.3 to 0.4 mm wide (Fig. 4A–E). The slightly elaborated apertural lip of first thecae has paired elevations situated laterally, and similar but smaller elaborations occur in the next thecae (Fig. 4A, B). The distance between thecal lips is 0.9 mm. The next thecae have a similar width of apertures (Fig. 4A).

On the dorsal part of the proximal end of the rhabdosome there are two dividing rods, projecting at an angle about 90<sup>0</sup> to the nema (Fig. 4C). It is clear that the first rod is growing from the distal part of the prosicula, on the border with the metasicula (Fig. 3A, B, F). The second is located on the other side of metasicula level and growing from the edge of interthecal septum between th1 and th2 (Fig. 3A, B, F). Between the lists of the structure called here the *patag*ium there are some membranes, preserved mostly only as ragged remnants (Fig. 3A-D). The membranes do not show any microfuselli or fuselli. There are distinctive seams on the lists (Fig. A, B, D, E). Sometimes there are very distinctive traces of membranes along the lists (Fig. 3A-C). The longest isolated, divided structure contains two rods, probably a fragment of a patagium or virgellarium, containing lists with small fragments of membranes, is 3.5 mm long.

As seen on isolated specimens studied with a light microscope and SEM, the patagium is only partly preserved (Figs. 3 and 4). One can observe the skeletal supporting rods, branching (bifurcating) many times, devoid of lumen (being solid). The membrane is preserved mostly as a web spread between bifurcating supporting rods or as remnants (ragged edges on the surface of rods) (Figs. 3 and 4).

#### 3.3. Remarks

The patagium and virgellarium membranes differ from membranes known in other bohemograptids (Urbanek, 1970) in the lack of any microfusellar structures. The other difference is in the location of the virgellarium. The virgellarium of the *Bohemograptus papilio* sp. nov. is located ventrally (Fig. 4 A–C, E) whereas that of the *Bohemograptus tenuis* is located dorsally (Fig. 2G, Urbanek, 1970, pl. 12A<sub>4</sub>).

# 4. Discussion

# 4.1. Two trends in morphological evolution in bohemograptids

The apertural processes of *Bohemograptus* from the proliferation zone are built from microfusellar tissue (Urbanek, 1970). There are two types of processes representing two trends in morphological evolution of bohemograptids. The first trend is that of horned bohemograptids, with paired ventro-lateral lappets in the form of gradually widening membranous fan-like structures, as in *Bohemograptus praecornutus* Urbanek, 1970 and *B. cornutus* Urbanek, 1970 (Fig. 2E,G). The most developed, large processes are observed in flattened forms from Altaj (Koren' and Sujarkova, 2004) in *B. cornutus*, and *B. decorus*.

The second trend leads to velum structures made of paired broad lobes or of a single addition forming the entire platform surrounding the thecal aperture as in *Bohemograptus tenuis* (Fig. 2B, C).

From the microfusellar additions, described in *Bohemograptus tenuis* (Urbanek, 1970, pl. 22), those in *B. decorus* differ in their proximal development. First, a short stalk is formed, and it later expands into the broadly circular structures (Koren' and Sujarkova, 2004, fig. 13J, N).

#### 4.2. Horned bohemograptids

Bohemograptus praecornutus Urbanek, 1970 and Bohemograptus cornutus Urbanek, 1970 represent two morphological stages of evolution. The former species represents an earlier morphological stage with microfusellar additions representing paired tape-like processes, while in the latter such processes are provided with a strong fan-like expansion (Fig. 2E, F). They are strongly developed, usually measuring 3 mm in length, but attaining in gerontic stages as much as 7 mm. Koren' and Sujarkova (2004) described a rhabdosome of B. cornutus with 40 thecae, of which the 30 most proximal displayed such fan-like processes. Due to the ventral curvature of the rhabdosome in bohemograptids its proximal part was literally crowded with mass of densely packed processes (Koren' and Sujarkova, 2004, fig. 15E). They doubtlessly provided a surface for various activities of the zooids which cannot be deduced from their structure, but probably were effective also in slowing the sinking of the colony.

Higher in the succession of the Kursala Formation (central Asia, Kyrghizstan), Koren' and Sujarkova (2004) described *Bohemograptus decorus*, a form similar to *B. cornutus*, but its tape-like processes on the apertures of the proximal thecae extend into what the authors call "balloon-like additions" (Koren' and Sujarkova, 2004, fig. 13J, N). The presence of a "concentric" substructure may indicate their microfusellar nature, but their real 3D shape needs further study. *B. decorus* is probably a product of evolution of a lineage parallel to that of *B. cornutus* and stemming from *B. b. tenuis*. *B. decorus* has a different morphology from *B. cornutus*. Its processes are rounded, paired balloon-like with a concentric structure. In both species the processes occur in proximal thecae, whereas the distal ones have even apertural margins.

#### 4.3. Velum and veliger morph

Much more advanced morphologically are forms with microfusellar additions forming paired processes, being entire instead of bilateral as additions described above, and in other cases displaying bilateral symmetry and representing paired broad lobes more or less advanced in size (Fig. 2B, C). This was considered by Urbanek (1970) as an extreme form of the microfusellar additions found in Bohemograptus tenuis in its higher zonal populations and termed collectively the velum. In each case microfusellar additions in proximal thecae are accompanied by some microfusellar structures on the aperture of the sicula and on the virgella (Fig. 2G). The annular variations of velum probably represent only a short episode of microevolution in Bohemograptus tenuis, and were not continued in later evolution as distinct trend, while their lobate form resembles microfusellar additions in Neolobograptus auriculatus Urbanek, 1970, which could appear by a modification of less advanced bilobate velum, but still display a sporadic occurrence and is subject to great variation. Later in their evolution, in Neocucullograptus, such incipient microfusellar lobes reappeared and were transformed into large and stable species-specific apertural lobes (Urbanek. 1970).

Instead of erecting a number of morphological species with very short stratigraphic ranges Urbanek (1970) suggested a hypothesis of genetic polymorphism in *B. tenuis* populations. This caused the presence at the same time of two morphs – the typical represented by rhabdosomes made only of fusellar tissue and the other capable of microfusellar additions of varied shape and called the "veliger" morph. Microfusellar derivatives in *B. tenuis* were strongly variable, but still retained the species specific features. The veliger morph, when deprived of its microfusellar additions, resembling a typical *B. tenuis*, may support the hypothesis of polymorphism (for a discussion see Urbanek, 1970). The veliger morphs have been described also in *Pristiograptus* from Morocco, *incipiens* Biozone (Rickards, 2001).

#### 4.4. Patagium

The colonial skeleton of *Bohemograptus papilio* sp. nov. consists of the rhabdosome proper, added to which is a

specialized structure the patagium, produced in addition to the standard monograptid rhabdosome. This term is borrowed from comparative anatomy to denote a membranous structure which is suggested to have served to impede sinking. The patagium in *B. papilio* sp. nov. grows latero-dorsally, in contrast to the ventral structures of other bohemograptids as well as all monograptids.

The structure reveals a distinct structural pattern: it is made of an attenuated membrane spread between a number of branches of skeletal supporting rods. The beginnings of the patagium are two single basal rods which started to grow from the end of the prosicula and the beginning of the first theca (Fig. 3).

During life the patagium would have formed a relatively large surface, probably functioning as a "water parachute" as an adaptation to prevent or slow sinking (Fig. 5: restoration of the rhabdosome with thecal and virgellar patagia). The patagium, through multiple bifurcations of supporting rods, outlines a roughly fan-shaped area.

#### 4.5. Virgellarium

In *B. papilio* sp. nov., the virgellarium is located vertically close to the edge of the metasicula (Fig. 4A–C, D). The shape of virgellarium cannot be safely established because of its partial state of preservation in the material studied, and is presented slightly conjecturally. The orientation of the virgellarium is vertical, as opposed to the latero-dorsally located patagium. Thus the purpose of it was probably some kind of keel in the water being orientation device.

A similar virgellarium, but located on the dorsal side of rhabdosome, and clearly built of microfusellar structure occurs in *Bohemograptus tenuis* (Fig. 2G, see Urbanek, 1970 [pl. 22, A<sub>4</sub>]).

# 5. Proximal membrane additions in other graptolites

There are many examples of proximal membranaceus structures in certain groups of graptolites. Unfortunately all of them are flattened so that their morphology, and relationship to the sicula or thecae are impossible to recognize. Some spectacular membrane constructions appear in multiramous mature forms such as Llandovery Cyrtograptus sp. (Lenz, 1974; Underwood, 1995) but the young stages of colonies with proximal structures are not known. The proximal structures appear especially in biserial graptolites like the Ordovician Climacograptus bicornis (Hall, 1847). Some of the biserial membrane structures are similar to the patagium of Bohemograptus papilio sp. nov. The most comparable structures seem to be in the Upper Ordovician species "Climacograptus" ensiformis Mu and Zhang, 1963 in Mu, 1963 (fig. 12) and "Climacograptus" papilio, Mu and Zhang, 1963 in Mu, 1963 (fig. 11d-f).

Other proximal structures are well known in Silurian, such as the Llandovery diplograptids illustrated in Koren' and Rickards (1996), or Štorch (2001). The additions are developed at the end of the virgella e.g. in *Petalolithus ovatoelongatus* (Kurck, 1882), *Pseudorthograptus obuti* (Rickards and Koren', 1974). In the early stages of development, the virgella is divided dichotomously, followed by the development of lists forming an ancora umbrella. Between the lists there is some type of membrane spreading similarly to a patagium but showing fusellar structures. The evolution of diplograptids forms with an umbrella was very successful, giving rise the unique group of graptolites, the retiolitids, in which a prolonged ancora evolved into an ancora sleeve (Bates, 1990). The ancora umbrella proximal device, recovered in 3D, would have increased the surface area of young forms and, as such, probably would have aided in the flotation of the organism.

There is only one recorded monograptid, "*Monograptus*" pala Moberg, 1892, in which proximal membranes have been recognised. "*M.*" pala, known only from flattened material, is illustrated with the membrane spread up to the 15<sup>th</sup> thecae on both sides of rhabdosome looking to the ventral side of rhabdosome or as one membrane on the lateral position of the flattened specimen (Bulman, 1964, fig. 6d, e).

# 6. Conclusion

Plankton organisms avoid or slow down sinking by increasing their surface area through the development of appendages, spines or body projections. This is an important adaptive trend in all plankton, both present and extinct. Bohemograptids also benefited from slowly sinking by a number of the apertural projections, and the patagium present in *Bohemograptus papilio* sp. nov. is interpreted as a highly specialized antisinking apparatus.

The nature of the unique proximal addition in monograptids is recognised for the first time thanks to the three dimensional specimens of the *Bohemograptus papilio* sp. nov., studied under SEM. It appeared that the first branch of the membranous patagium grew from the sicula, specifically at the border between the prosicula and metasicula. The second branch grew from the edge of the interthecal septum between th1 and th2.

The patagium seems to be some kind of a fin projecting at 90° to the nema in proximal part of rhabdosome and thus being horizontal, whereas the virgellarium is a vertical "keel".

The patagium and virgellarium are built of membranes stretched between the lists; there are no traces of microfuselli or fuselli in apertural additions as in other bohemograptids.

The development of a proximal apparatus that may have prevented from sinking in the Neocucullograptinae sensu Urbanek, 1970 and is demonstrated for the first time.

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