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SEM pictures of holotype of *Papiliograptus retimarginatus* n. sp. Photo: Anna Kozłowska, Institute of Paleobiology Polish Academy of Sciences, Poland.

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ABSTRACT
Papiliograptus retimarginatus n. sp. is reported from the *praedeubeli/deubeli* Biozone, upper Homerian (Silurian) of the Bartoszyce IG-1 drill core of Poland, Baltica. It is the second species of the genus *Papiliograptus* Lenz & Kozłowska-Dawidziuk, 2002, belonging to the new retiolitid fauna of the recovery period after the *lundgreni* Extinction Event. Two characteristic features of the new retiolitid fauna are the development of a geniculum and singular or paired genicular structures. The new form has extremely wide, singular, reticulated genicular processes. It is suggested that these structures may have been an adaptation to prevent the planktonic colony from sinking in the water column.

KEY WORDS
Graptolithina,
Retiolitidae,
Silurian,
Baltica,
Papiliograptus,
genicular structures,
new species.

RÉSUMÉ
Papiliograptus retimarginatus *n. sp., un nouveau rétiolitidé (Graptolithina) de la biozone à* predeubeli/deubeli *(Homérien supérieur, Wenlock, Silurien), phase de récupération après l'événement d'extinction* lundgreni. On rapporte une nouvelle espèce de *Papiliograptus* Lenz & Kozłowska-Dawidziuk, 2002, la seconde appartenant à ce genre, de la biozone à *praedubeli/deubeli* (Silurien, Homérien supérieur) du forage de Bartoszyce IG-1 (Pologne, paléo-continent de Baltica). *Papiliograptus retimarginatus* n. sp. appartient à la faune de rétiolitidés s'étant reconstituée après l'extinction liée à l'événement *lundgreni*. Les membres de cette faune se caractérisent par le développement du géniculum et des structures géniculaires paires. Chez l'espèce décrite ici, les dimensions d'un processus géniculaire unique sont particulièrement grandes. De telles structures accessoires larges chez les rétiolitidés étaient des adaptations servant à empêcher l'engloutissement de la colonie au mode de vie planctonique dans la masse d'eau.

MOTS CLÉS
Graptolithina,
Retiolitidae,
Silurien,
Baltica,
Papiliograptus,
structures géniculaires,
espèce nouvelle.

INTRODUCTION

The planktonic graptolites evolved from benthic Cambrian ancestors, and flourished in the Ordovician and Silurian, becoming one of the most important components of the marine zoo-plankton around the world. They were colonial organisms living in a housing built of separate secreted tubes, the thecae, forming tubaria. The thecae were built by zooids, presumably similar to their recent relatives, the Pterobranchia (Kozłowski 1949; Mitchell *et al.* 2013). They presumably fed on micro-plankton, filtering it using a pair of lophophores, feathery arms, similar to those in their recent benthic relatives, the Pterobranchia.

One of the most interesting groups of biserial graptolites is the Silurian retiolitids. Their tubaria were built by strong rod-like bandaged lists and incrementally deposited continuous fusellar membranes, usually not preserved (Bates & Kirk 1992, 1997). The tubaria are unique also in possessing an outer layer, the ancora sleeve, being a prolongation of the ancora umbrella (Bates *et al.* 2005).

At least two lineages of retiolitids survived the *lundgreni* Extinction Event in the late Homerian, and subsequently re-diversified. The genera *Gothograptus* Frech, 1897 and *Semigothograptus* Kozłowska, 2016 show distinctly different tubarium constructions that can be followed from the *lundgreni* Biozone into the post-extinction interval and the later recovery phase, largely recognized by the re-diversification in the *praedeubeli/deubeli* Biozone (Kozłowska 2016; Štorch & Manda 2019). New characters were established, including a free nema, simple ancora umbrella, geniculum and variously developed paired and unpaired genicular processes. These features were common and characteristic of several species of *Spinograptus* Bouček & Münch, 1952 (Kozłowska-Dawidziuk 1997; Kozłowska-Dawidziuk *et al.* 2001).

The post-extinction faunas bearing retiolitid taxa have been described in some detail mostly from Arctic Canada (Lenz 1993; Lenz & Kozłowska-Dawidziuk 2002; Lenz *et al.* 2012) and from boreholes in the Baltic region, largely from Poland (Kozłowska-Dawidziuk *et al.* 2001; Kozłowska-Dawidziuk 2004).

The new species *Papiliograptus retimarginatus*, described in this paper, shows particularly wide genicular processes (Figs 1; 2A), suggesting an adaptation to a quiet environment. All these faunas provide a window into the recovery phase after the mid-Homerian extinction and the diversification in the upper Homerian.

MATERIAL AND METHODS

The material comes from the Bartoszyce IG-1 core, located in the eastern part of the Peribaltic Syneclise of the Polish part of the East European Platform, Baltica. This area was located in low latitudes during the Silurian (Porębska *et al.* 2004 [Fig. 1A]). The studied material comes from depths 1647.9 m and 1649.0 m lower part of the *praedeubeli/deubeli* Biozone (see Porębska *et al.* 2004).

The rock samples from the Bartoszyce IG-1 drill core were treated with 10-30% hydrochloric acid solution. A fine hair-brush was used to pick and transfer specimens. Sediment not dissolved was partly removed using 5-15% HF. The specimens were imaged with a Philips XL scanning electron microscope and light microscope.

The material is stored in glycerin in plastic containers or on SEM stubs. Specimens are deposited at the Institute of Paleobiology of the Polish Academy of Sciences, Poland under catalogue number ZPAL G.62.

A single juvenile specimen (MBg 1092; JM 59) from a glacial boulder, Hiddensee, Rügen Island, northern Germany was originally identified as *Retiolites* (*Plectograptus*) *retimarginatus* by Hermann Jaeger (Maletz 2010). The specimen is not included in the type series as it was obtained from a glacial erratic, but is important to understand the construction of the tubarium of this species.

The terminology for retiolitid graptolites follows Bates *et al.* (2005) and Lenz *et al.* (2018). The term tubarium is used in the paper, as well as in some of our former papers, instead of the former term rhabdosome, used in the new edition of the Treatise of Invertebrate Palaeontology (Maletz *et al.* 2014). This term is also used in all Pterobranchia (recent and fossil) terminology, instead of using the term rhabdosome for the fossil Pterobranchia and the term coenecium for the extant members (Maletz *et al.* 2014) to describe the organic housing.

Abbreviations

Institutional Abbreviations

MBg	Museum für Naturkunde, Hermann Jaeger collection, Berlin;
ZPAL	Institute of Paleobiology of the Polish Academy of Sciences, Warszawa.

SYSTEMATIC PALEONTOLOGY

Phylum HEMICHORDATA Bateson, 1885
Class PTEROBRANCHIA Lankester, 1877
Subclass Graptolithina Bronn, 1849
Superfamily Retiolitoidea Lapworth, 1873
Family Retiolitidae Lapworth, 1873
Subfamily *Retiolitinae* Lapworth, 1873

Genus *Papiliograptus* Lenz & Kozłowska-Dawidziuk, 2002

Type species. — *Papiliograptus papilio* Lenz & Kozłowska-Dawidziuk, 2002.

Diagnosis (modified from Lenz *et al.* 2018). — Retiolitine graptoloid; tubarium narrowing distally, but appendix unknown; pleural and mid-ventral lists present and well developed; ancora umbrella simple; dense reticulum with zigzag or almost horizontal coarser ancora sleeve lists; proximal lateral orifices large, circular to kidney shaped; thecal orifices deep; (butterfly-shaped) reticulate genicular processes; lists with pustules.

Species included. — *Papiliograptus papilio* Lenz & Kozłowska-Dawidziuk, 2002.

Papiliograptus retimarginatus n. sp.; *Papiliograptus*? *petilus* Lenz & Kozłowska-Dawidziuk, 2002.

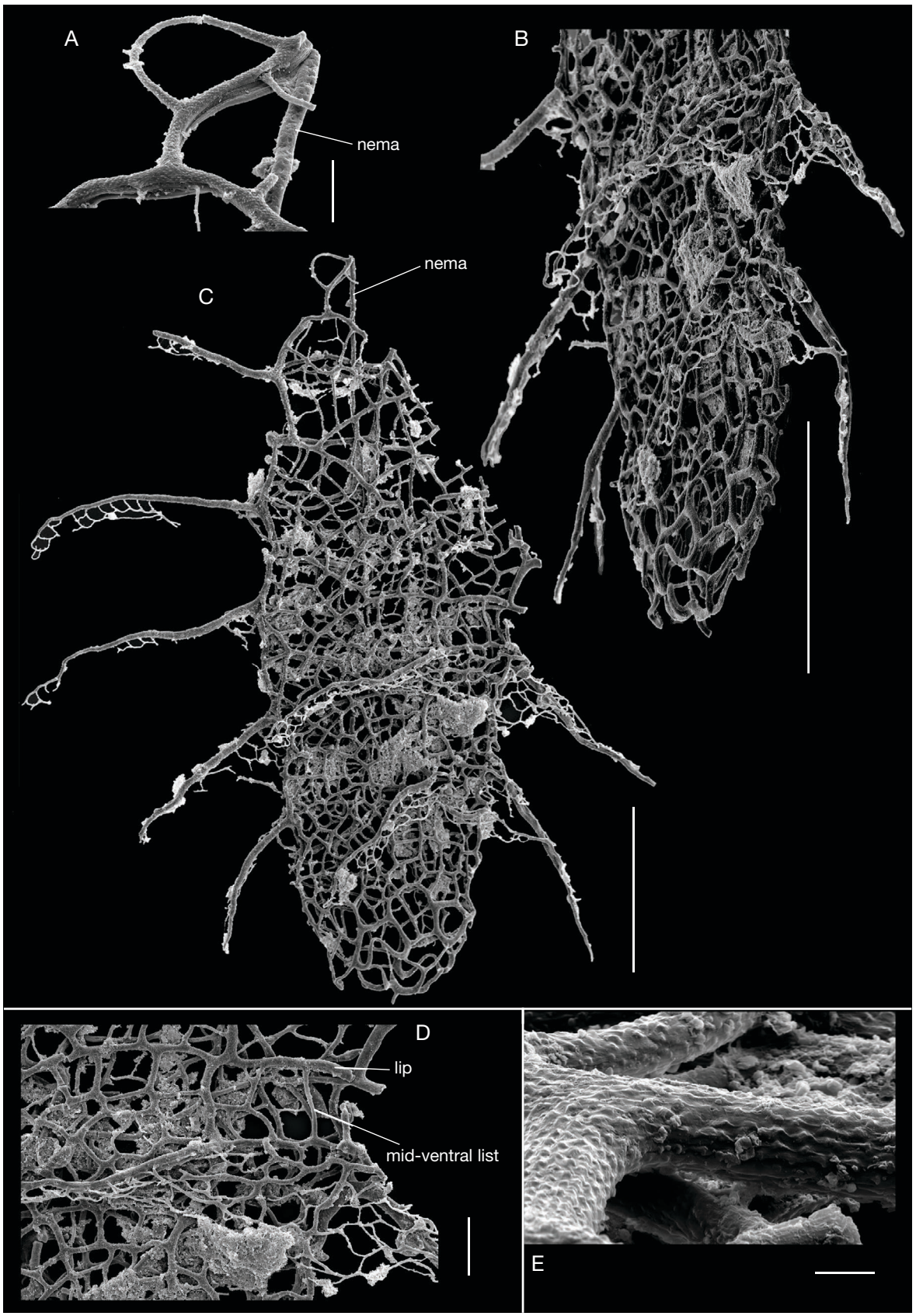

Fig. 1. — SEM pictures of holotype of *Papiliograptus retimarginatus* n. sp., ZPAL G.62/1, Bartoszyce IG-1 core, depth 1647.9 m, Poland. **A**, obverse view of distal end showing connection of nema with pleural list; **B**, oblique view showing ventral wall; **C**, ventro-lateral view of the obverse side of the specimen; **D**, enlargement of genicular structure of th1[2]; **E**, enlargement of lists above ancora umbrella showing distinctive pustules. Scale bars: A, 100 µm; B, C, 1 mm; D, 200 µm; E, 20 µm.

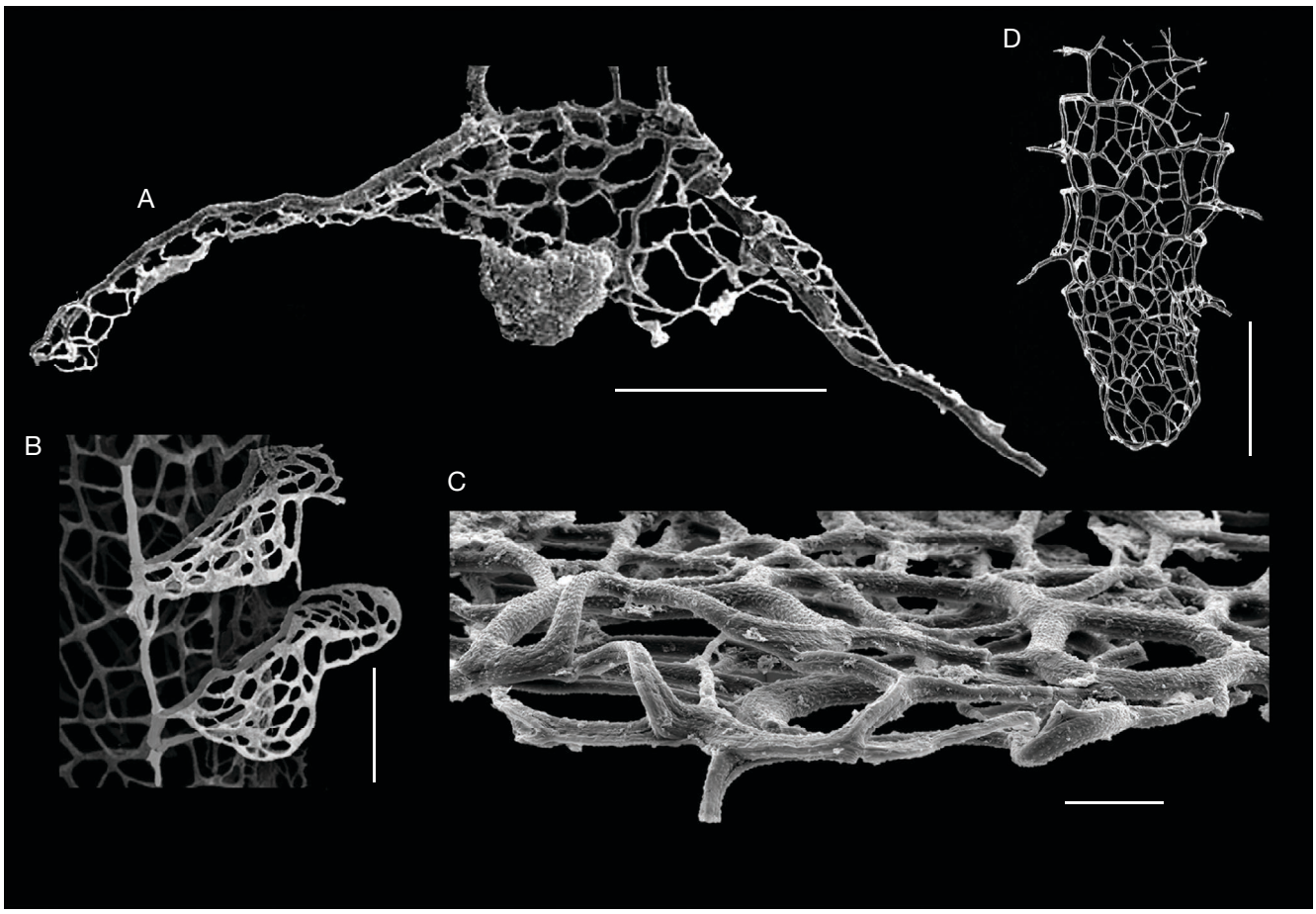

Fig. 2. — SEM pictures of some structures of *Papiliograptus retimarginatus* n. sp. and *Papiliograptus papilio* Lenz & Kozłowska-Dawidziuk, 2002: **A**, genicular structure of *Papiliograptus retimarginatus* n. sp., ZPAL G.62/1, Bartoszyce IG-1 core, depth 1647.9 m, Poland; **B**, genicular structures of *Papiliograptus papilio* Lenz & Kozłowska-Dawidziuk, 2002, Arctic Canada (based on Lenz & Kozłowska-Dawidziuk 2002); **C**, SEM picture of ancora umbrella, proximal view, *Papiliograptus retimarginatus* n. sp., holotype ZPAL G.62/1, Bartoszyce IG-1 core, depth 1647.9 m, Poland; **D**, *Papiliograptus retimarginatus* n. sp., juvenile, reverse view, MB.G 1092, Hiddensee, Mecklenburg-Vorpommern, Germany (based on Maletz *et al.* 2017, Fig. 12.9D). Scale bars: A, B, 500 µm; C, 100 µm; D, 1 mm.

Discussion

Papiliograptus? *petilus* from Arctic Canada occurs in the lower part of the *praedeubeli/deubeli* Biozone, like the new species. It is described from well-preserved specimens which all lack the proximal end. The best preserved specimen is a parallel-sided fragment with *c.* seven thecal pairs (Lenz & Kozłowska-Dawidziuk 2002: figs 11; 12). The material lacks any genicular additions and does not show any indication of distal narrowing of the tubarium. Thus, it may belong to any genus in which the nema is free inside the colony and the ancora sleeve walls possess comparable list constructions (e.g. *Baculograptus, Papiliograptus*).

Papiliograptus retimarginatus n. sp.
(Figs 1; 2A, C, D; 3)

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Retiolites (*Plectograptus*) *retimarginatus* – Jaeger (*nomen nudum*). — Maletz 2010: 503, fig. 1 (no description).

Papiliograptus retimarginatus – Maletz 2010: 505, fig. 2 (no description).

Papiliograptus papilio – Kozłowska & Radzevičius 2013: 14-15, figs 3, 4. — Kozłowska 2016: 539, fig. 4A.

Papiliograptus sp. — Maletz *et al.* 2017: 218, fig. 12.9D.

Holotype. — ZPAL G.62/1 is from depth 1647.9 m, Bartoszyce IG-1 core, Poland.

Diagnosis. — *Papiliograptus* with single genicular structure formed as long lateral lists, thinning distally and lacking a ventrally continuous (connecting) rim; delicate reticulum in the proximal part of the hoods, growing from geniculum and reaching sideways onto the preserved spiny extensions.

Etymology. — The name of the species *retimarginatus* is from the Latin: *reti* means reticulum; *marginatus* means having a border or margin. It is based on the reticulated margins of the elongated genicular processes of this taxon. The name is retained from the specimen of Hermann Jaeger, who called the taxon *Retiolites* (*Plectograptus*) *retimarginatus* in his notes with no year.

Locus typicus and *stratum typicum*. — Bartoszyce IG-1core, north eastern Poland; lower part of the *praedeubeli/deubeli* Biozone, upper Homerian, Wenlock, Silurian.

Material examined. — Several specimens from depths 1647.9 m and 1649.0 m, Bartoszyce IG-1core, mostly fragments, two specimens with proximal end. Paratype (ZPAL G.62/3-5) comes from

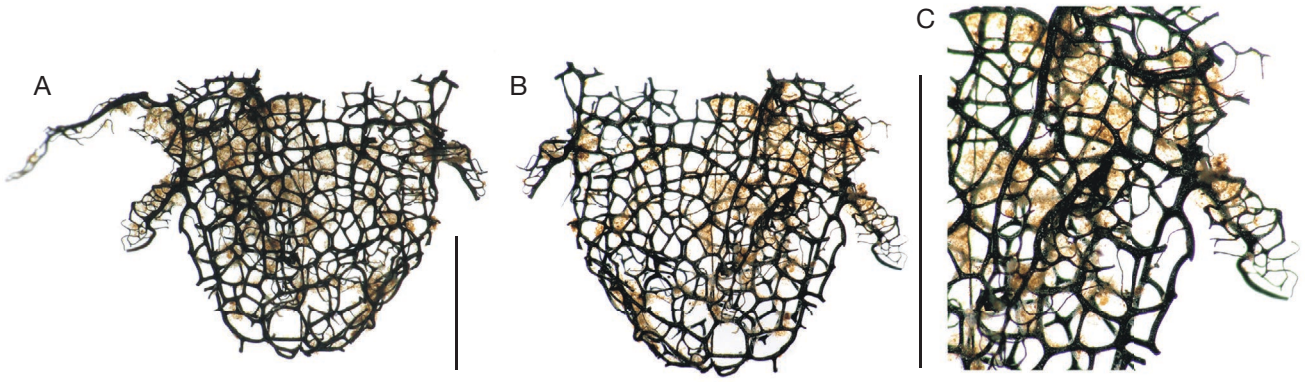

Fig. 3. — *Papiliograptus retimarginatus* n. sp., light photos of proximal part of mature tubarium, lateral view; paratype ZPAL G.62/2, Bartoszyce IG-1 core, depth 1649.0 m, Poland. **A**, **B**, whole specimen in obverse (A) and reverse (B) views; **C**, enlargement of genicular structure of th1[1] and partly th2[1], reverse view. Scale bars: 1 mm.

depth 1649.0 m. The material is associated with *Gothograptus auriculatus* Kozłowska, Bates, Zalasiewicz & Radzevičius, 2019; and *Colonograptus praedeubeli* Jaeger, 1990. A single juvenile specimen (MBg 1092; JM 59) comes from a glacial boulder, Hiddensee, Rügen Island, northern Germany.

Description

The holotype is a proximal fragment with about five pairs of thecae. The specimen is preserved on an SEM stub in obverse view and is nearly completely flattened, showing a slightly distorted and rotated lateral preservation with the ventral side of thecal series two shown completely, while the apertural orifices of thecal series one are covered and only the lateral genicular constructions are visible (Figs 1; 2A). The specimen has a maximum length of *c.* 4.5 mm.

The paratype specimen represents the proximal part of a tubarium in which only the first two thecal pairs are preserved and the genicular processes of th1[1] and 2[1] are well-developed (Fig. 3).

The tubarium widens slightly from the level of the ancora umbrella rim, which is the narrowest part of the colony. The approximate lateral width of the holotype tubarium, measured between the pleural lists below the lip of th1[1], is 0.7 mm and reaches 1.1 mm at the level of the lip of th3[2]. The 2TRD, two thecae repeat distance (Howe 1983) at th4[1] is 1.38 mm. The nema is free inside the tubarium, but appears to be connected to a rounded list, probably representing part of th6[1] in the holotype, which may indicate a finite growth of the colony. The length of the sicula cannot be determined from this specimen and has not been recognized in other material.

The ancora umbrella is formed from seven meshes and is fairly asymmetrical, as the paired ventro-lateral ancora umbrella lobes reach much higher on the th2[1] side. The rim of the ancora umbrella is strongly lobate and shows paired lobes on the ventro-lateral sides of both thecal series and two lobes on the lateral sides of the tubarium, which are distinctive in ventral view of well-preserved material, but difficult to see in the flattened type material.

The ancora umbrella is moderately deep, reaching a width of *c.* 0.8 mm on the obverse and reverse sides and a depth of *c.* 0.65 mm at the ventro-lateral lobes in the holotype, but as the specimen is flattened, this might not be accurate.

The single specimen from the Jaeger collection preserved in full relief is about 0.7 mm wide and *c.* 0.5 mm high. Drawing by Jaeger (Maletz 2010: fig. 1) shows the reverse side of the specimen and highlights the characteristic lateral, nearly vertical lobes of the ancora umbrella. The width across these lateral lobes of the ancora umbrella is 0.55 mm in the Jaeger specimen (Fig. 2D).

The shape of the proximal ventral orifice on the theca one series is approximately hexagonal on the holotype (Figs 1; 4). In the Jaeger specimen the proximal ventral orifice of the theca two series is tetragonal. The rounded proximal lateral orifices are located centrally on the lateral sides of the tubarium. They may appear as of kidney shape when the colony is flattened and the lateral lobes rotated upwards as in the holotype of the species. However, in the original three-dimensionally preserved material, they show a widely arched rim with a horizontal base.

The ancora sleeve is outlined on the ventral (thecal orifice) sides by pleural lists, the lateral apertural rods, genicular lists and thecal lips. The genicular lists are thinner than thecal lips, lateral apertural rods and pleural lists and in more distal thecae it is difficult to distinguish them from the reticulum of the genicular structure. The mid-ventral lists are relatively thin in the available material and appear to be constructed at a later stage of the colony development (Figs 1; 4). Thus, they appear to be incomplete in distal parts of the few available specimens and are difficult to differentiate from other lists on the ventral side of the tubarium.

The lateral walls of the ancora sleeve show a distinct dense meshwork of lists, showing an indistinct zigzag pattern of slightly wider main lists, while smaller meshes are aligned in curved rows. The single larger specimen from Lithuania appears to show a more regular zigzag pattern (Kozłowska & Radzevičius 2013; Kozłowska 2016: fig. 4A) in the medial and distal part of tubarium. The cortical bandages show the distinctive, regularly developed pustules on the surface.

The thecal orifices have a semi-rectangular shape and increase slightly in size and regularity towards the distal end. They bear

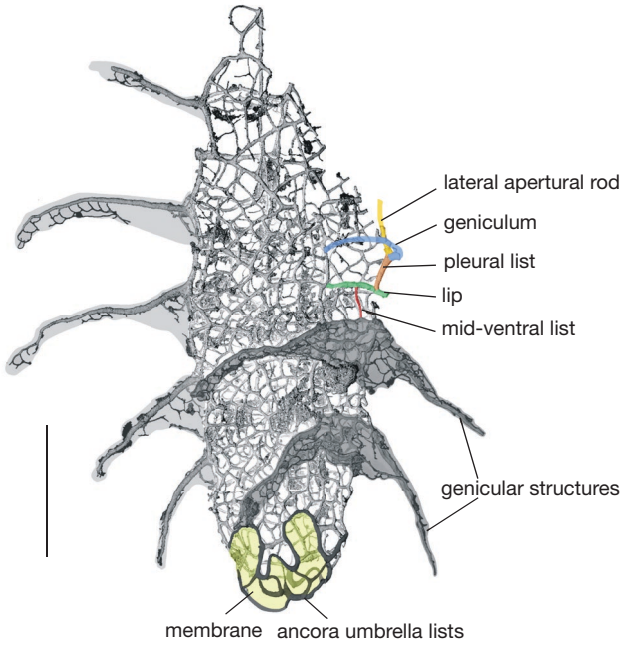

Fig. 4. — Reconstruction of holotype of *Papiliograptus retimarginatus* n. sp. with coloured main structures of tubarium. Note the large genicular structures. Scale bar: 1 mm.

paired, long and outwards directed genicular processes with seams on the inside, indicating the former presence of a non-preserved membrane. The membranes supported a delicate reticulum spreading along the spines and being widest in the centre. The genicular processes of *Papiliograptus retimarginatus* n. sp. represent some of the largest genicular constructions among retiolitids. The distance between the tips of the lateral lists of the genicular processes is about 1.8-2.0 mm in th1[2], about 2.5 mm in th2[2].

The genicular processes appear to start as "spiny" extensions from the genicular edges of the thecal orifices and the delicate reticulum developed along the genicular lists as well as these processes which grow out for a considerable distance. Strong, curved bounding lists then appear at the geniculum and spread on the inner side of the lateral genicular "spines" to form a meshwork of fine meshes. At most a maximum of two layers of meshes can be seen along the genicular processes, but it may be assumed that a much wider membrane was extending between the processes.

DISCUSSION

Occurrence of *Papiliograptus* species

Papiliograptus species appear to be restricted to Laurentia and Baltica, evolving during the post-*lundgreni* extinction interval, during the recovery phase of graptolite faunas. The type species *Papiliograptus papilio* Lenz & Kozłowska-Dawidziuk, 2002 is described from the Arctic Canada, Laurentia, from the middle part of the *praedeubeli/deubeli* Biozone (Lenz & Kozłowska-Dawidziuk 2002).

The second species of the genus, *Papiliograptus retimarginatus* n. sp. is described herein from Poland, East European Platform, Baltica, from the *praedeubeli/deubeli* Biozone.

Kozłowska & Radzevičius (2013) described *Papiliograptus papilio* from the lower part of the *praedeubeli* Biozone of the Šiupyliai-69 drill core of Lithuania, based upon a number of fragments and a single mature specimen. This specimen is comparable to *Papiliograptus retimarginatus* n. sp. in the development of the genicular extensions which have destroyed distal ends. We include this material in *Papiliograptus retimarginatus* n. sp. because the remnants of the genicular processes show big similarity of the construction to the new species. There are some fragments of the thicker "spiny" extensions and delicate reticulum between them.

A single immature specimen known from a North German glacial boulder, referred in manuscript notes to the *praedeubeli* Biozone by Jaeger, is regarded as *Papiliograptus retimarginatus* n. sp. However, the characteristic genicular structures are not well-developed and partly destroyed (Fig. 2D).

Porębska *et al.* (2004: fig. 3F) illustrated a single specimen with a proximal end and three pairs of thecae as *Papiliograptus papilio* (?) from the *praedeubeli* Biozone of Poland, East European Platform, Baltica.

Specimens identified on the range chart as *Papiliograptus papilio* from the base of the *praedeubeli* Biozone from Lithuania, East European Platform, Baltica (Radzevičius *et al.* 2014: fig. 2) have not been illustrated. Thus, their identity remains uncertain.

Genicular structures in *Papiliograptus* species

Papiliograptus papilio and *Papiliograptus retimarginatus* n. sp. can be differentiated easily by the shape and size of their respective genicular processes. The genicular hood of *Papiliograptus papilio* is a two-lobed single hood construction with a rounded rim on the geniculum of the thecae (Fig. 5B). The rim is continuous and composed of a delicate reticulum, not strong bordering lists as in *Papiliograptus retimarginatus* n. sp. This hood extends horizontally from the ventral wall of the tubarium or bends slightly downwards in the distal end at the rim.

A distinct lateral thickening as in the processes of *Papiliograptus retimarginatus* n. sp. is not developed in *Papiliograptus papilio*. They are much smaller and only slightly extend beyond the borders of the thecal orifices (Fig. 5). In *Papiliograptus retimarginatus* n. sp. the genicular constructions distinctively extend and two distinct thickened borders extend like paired spines outwards forming an obtuse angle with each other (Figs 2A; 5A). Proximally, a meshwork of curved bars made of cortical bandages forms a variably wide horizontal to sub-horizontal hood, but the mesh also reaches outwards along the "spines" for a considerable distance. The membranes supported a delicate reticulum spreading along the spines and being widest in the centre.

CONCLUSIONS

The genus *Papiliograptus*, composed of two species (*P. papilio* and *P. retimarginatus* n. sp.), occurs in two Silurian palaeocontinents,

Laurentia and Baltica. The type species of the genus occurs in Laurentia (Arctic Canada), whereas *Papiliograptus retimarginatus* n. sp. is endemic to Baltica (Poland, Lithuania and glacial erratics from Germany). The position of Baltica and Laurentia during the *praedeubeli/deubeli* and *praedeubeli* biozones was close to the equator, which suggests a warm water palaeo-realm for *Papiliograptus*. The fact that the genus *Papiliograptus* is known only from isolated material may suggest that the delicate meshwork of some tubaria can be overlooked on shale bedding surfaces from other regions.

Papiliograptus retimarginatus n. sp. has the largest genicular processes known in retiolitids. They were formed by strong lists and a network of thin lists, and a thin membrane spread between them. This confirms a trend to develop structures extending from the main part of the tubarium, characteristic of retiolitids which evolved during the recovery period after the *lundgreni* Extinction Event. In contrast, the gothograptids from pre- and immediately post the event have genicular structures covering the thecal openings, e.g. *Gothograptus obtectus* and *Gothograptus nassa* from the *dubius/nassa* Biozone.

Both fossil and recent holoplankton organisms have similar problems with opposing sinking in the water column. We have no direct knowledge of how extinct planktonic pterobranchs, the graptolites, would have behaved in the water column among other holoplanktonic organisms. Some indication of their life style is given by the shape and construction of their tubaria. The large extensions of *Papiliograptus retimarginatus* n. sp. formed a continuous surface which could be interpreted to have developed to retard sinking in quiet sea water, as in some present-day plankton. Recent holoplanktonic organisms have many kinds of mechanisms to reduce the rate at which they sink in the water column. In general, the shape of the body evolves to increase the surface area of such organisms. Many zooplankton have flattened and elongated appendages or lateral spines. For example, some marine planktonic polychaetes have many parapodia which are greatly expanded laterally; sometimes to about 20 pairs as in *Tomopteris nisseni* Rosa, 1908 (Fernández-Álamo 2000). In the case of some Euphausiacea (krill) (Crustacea) the extensions of the projecting parts of the body are antennae, several pairs of thoracic legs (pereiopods), swimming legs (pleopods), and externally visible gills (Miller & Hampton 1989).

The life strategy in the water column of the graptolites, the dominant Palaeozoic plankton, with their colonial organisation and wide variety of tubaria, is unique and unknown in the recent plankton.

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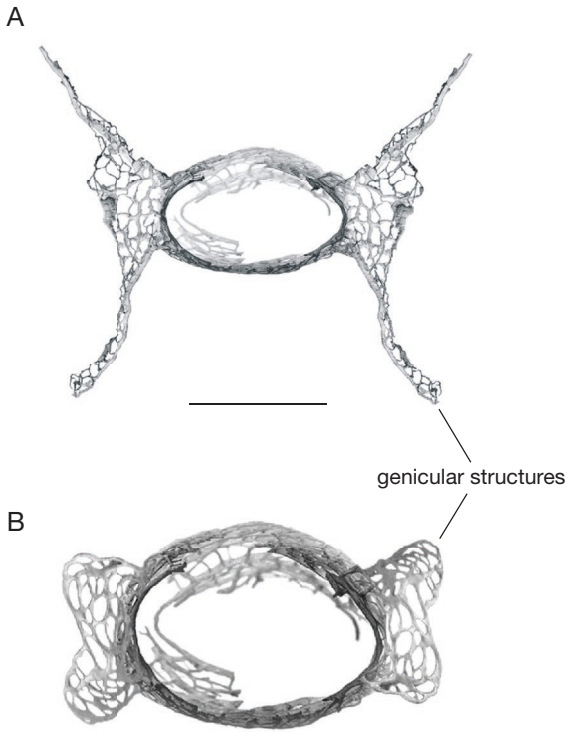

Fig. 5. — Schematic pictures comparing the genicular structures of *Papiliograptus retimarginatus* n. sp. (**A**) with those of *Papiliograptus papilio* Lenz & Kozłowska-Dawidziuk, 2002 (**B**). Illustrations are based on Fig. 2A and *Papiliograptus papilio* from Lenz & Kozłowska-Dawidziuk (2002: fig. 12. 2). Scale bar: 1 mm.

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