Phyletic Evolution and Iterative Speciation in the Persistent Pristiograptus dubius Lineage

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The paper focuses on patterns of the evolution of the simplest and longest-ranging (approximately 18 Ma) Silurian graptolite *Pristiograptus dubius*. The *Pristiograptus dubius* species group consists of the *P. dubius* stem lineage represented by a sequence of a number of subspecies displaying only small morphological changes as well as derivative species produced from the stem lineage by means of iterative speciation. This long raging graptolite lineage is the only one, apart of one retiolitid, which survived the most severe environmental event for graptolites, the *Cyrtograptus lundgreni* Event. Based on three-dimensional, isolated material two *P. dubius* groups taxa are distinguished. One group has an obtuse angle between the thecal lip and the succeeding thecal wall, the second group has a right or acute angle. Other characters differentiating *P. dubius* forms are: the shape of the apertural lips, differences in rhabdosome shape and size, and a different number of sicular rings. Sixteen species and subspecies of *Pristiograptus* from the East European Platform, Poland and Lithuania are discussed. Five new subspecies *P. dubius magnus*, *P. dubius paezerensis*, *P. dubius praelodenicensis*, *P. dubius postfrequens*, and *P. dubius postmagnus* are proposed.

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Introduction

Pristiograptus dubius (Suess, 1851) ranges from the *Monograptus riccartonensis* Biozone of the Wenlock to the *Monograptus perneri* Biozone of the Přidoli and thus is one of the longest-ranging graptolite taxa known (Fig. 1). Both thecae and rhabdosome are simple. The *Pristiograptus* stem lineage represents a type of evolution that shows numerous new lineages arising by means of iterative speciation (Urbanek 1998).

Přibyl (1943) first distinguished more than a dozen *Pristiograptus* species and subspecies, based on flattened material from the Czech Republic. The first detailed studies of isolated, three-dimensional *Pristiograptus dubius* forms were made by Urbanek (1953) who also reviewed some earlier papers and then followed by Urbanek (1959, 1997) and Walker (1953) based on Ludlow material from Poland and northern Germany, respectively. These studies noted the presence of thickening rings in the sicula. Urbanek's (1997, 1998) studies, additionally, gave a general view of the extraordinary evolution of the *P. dubius* group.

Jaeger (1959, 1991) also studied the *Pristiograptus* in Germany using isolated material. Rickards (1965) investigated pristiograptids from Northern England and from Australia (Rickards and Wright 1999), and an attempt at understanding the evolution of the *P. dubius* group was presented by Rickards and Wright (2003).

Holland et al. (1969) described a new species *P. jaegeri* Holland, Rickards, and Warren, 1969 from the upper Wenlock and lowermost Ludlow of Great Britain. More detailed studies of that important appearance and succession of *Pristiograptus* species after the *Cyrtograptus lundgreni* extinction Event were made by Ulst (in Gailite et al. 1967; Ulst 1974), based on material from Latvia. She described the diminutive *Pristiograptus parvus* Ulst, 1975, the only monograptid taxon to appear immediately after the most severe extinction event in graptolite history.

Pristiograptus taxa from the Llandovery to Ludlow interval of Lithuania were studied by Paškevičius (1974, 1979). The most recent revision of *P. dubius* morphotypes, based on isolated Wenlock material from Lithuania, was made by Radzevičius and Paškevičius (2000), and Radzevičius (2003, 2006, 2007).

The *Cyrtograptus lundgreni* Extinction Event was probably the only one to severely affect the evolution of *P. dubius* lineage. It survived other less severe events that extinguished many co-existing taxa. This exceptional survivability of *P. dubius* may probably be explained by eurybiotic nature of its

Fig. 1. Graptolite phylogenetic relationships between the iterative of *Pristiograptus dubius* group taxa species and subspecies from Poland and Lithuania and their stratigraphical ranges. For more data concerning iterative clades that branched off the stem lineage see Fig. 4. Generalized graptolites biozones (Koren' et al. 1996) correlated with biozones of Poland and Lithuania (Urbanek and Teller 1997; Radzevičius 2007). Abbreviations: *B.*, *Bohemograptus*; *Col.*, *Colonograptus*; *Cucullo.*, *Cucullograptus*; *Cyrto.*, *Cyrtograptus*; *d.*, *dubius*; *G.*, *Gothograptus*; *I.*, *Istrograptus*; *L.*, *Lobograptus*; *M.*, *Monograptus*; *Neocol.*, *Neocolonograptus*; *Neocucul.*, *Neocucullograptus*; *Neodiver.*, *Neodiversograptus*; *Neolob.*, *Neolobograptus*; *P.*, *Pristiograptus*; *S.*, *Saetograptus*; *Slov.*, *Slovinograptus*; *t.*, *transgrediens*; *U.*, *Uncinatograptus*.

adaptation and lack of specialization. This is why Jaeger (1991) called it "a generalist". The long period of existence of *P. dubius* is doubtlessly related to its ability to adapt to environmental changes, without responding by any considerable morphological change.

The purpose of this paper is an attempt to understand the evolution of *P. dubius* group and show its iterative character, extraordinary among graptolites. The paper describes the morphological changes and stratigraphic distribution of isolated *P. dubius* forms from Wenlock and Ludlow strata of Poland and Lithuania (Fig. 2).

This paper employs terminology (Fig. 3) from Urbanek (1997) and Radzevičius (2003).

Institutional abbreviations.—ZPAL G., Institute of Paleobiology, Polish Academy of Sciences; VU, collection of Vilnius University, Department of Geology and Mineralogy, Geological Museum.

Other abbreviations.—L, length; W, width; ß, the angle between the thecal lip and the free ventral wall of succeeding theca; λ, the angle between interthecal septum (thecal axis) and virgula; th, theca; th[1], first theca (Fig. 3); SEM, Scanning
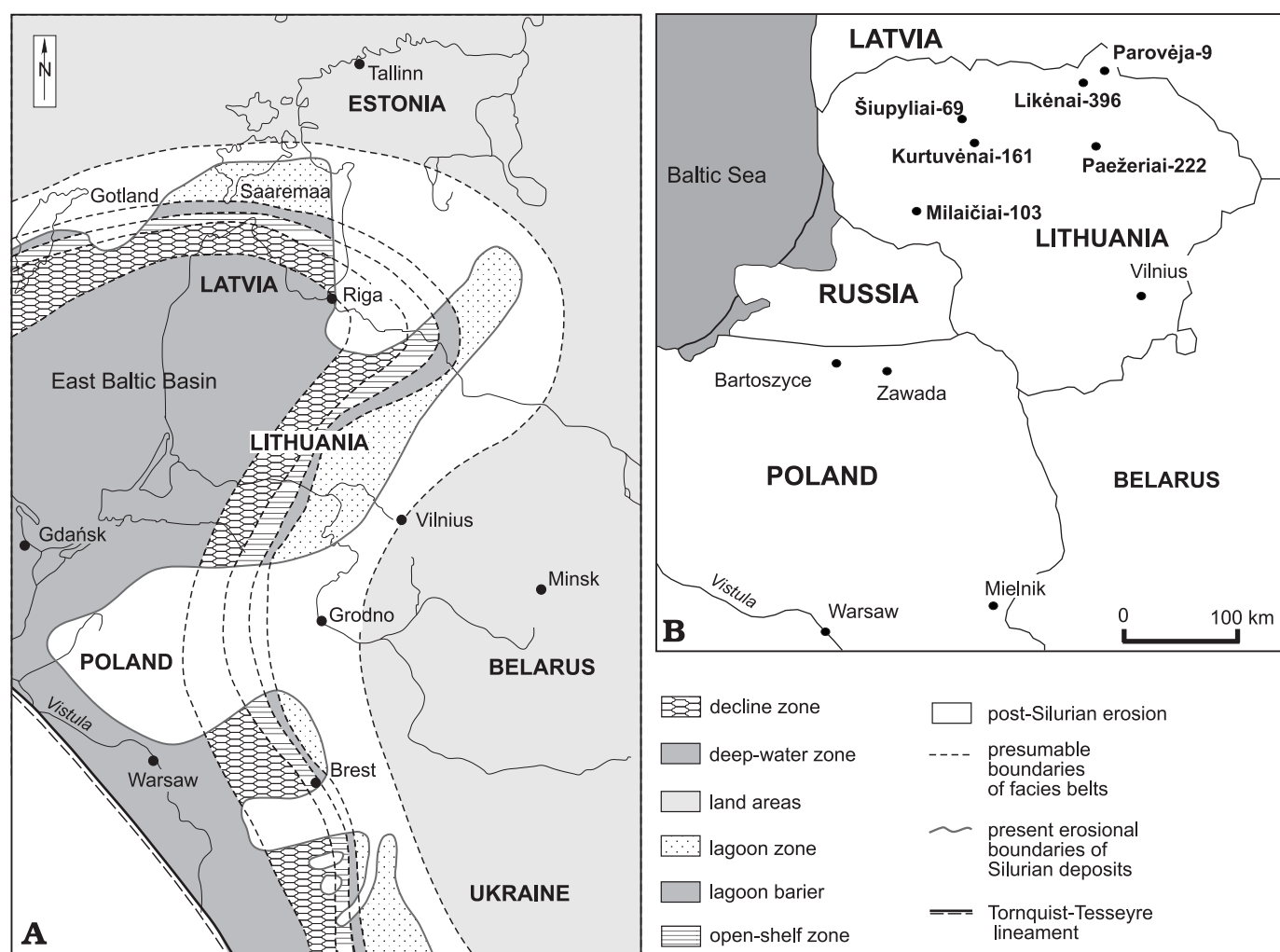
Fig. 2. Map of western margin of the East European Platform. **A**. Facies across the studied region (modified after Porębska et al. 2004). **B**. Location of the investigated boreholes in Lithuania and Poland.

Electron Microscope; K, borehole Kybartai; S, borehole Šiupyliai; P, borehole Paežeriai.

Evolution in the Silurian *Pristiograptus dubius* (Suess, 1851) species group

The *Pristiograptus dubius* species group consists of (i) the proper *P. dubius* stem lineage represented by an unbroken succession of *P. dubius* populations (chronodemes), displaying essentially a morphological near-stasis, and therefore showing only limited change through time, (ii) representatives of a numbers of phyletic lines which appeared as the result of early divergence immediately after the *P. dubius/ Gothograptus nassa* survival interval, as well as of a number (iii) of derivative species produced by means of iterative speciation from the stem lineage parental species, and displaying usually minor differences from it.

Phyletic evolution.—The concept of the stem lineage developed gradually. Urbanek (1997, 1998) and Rickards and Wright (2003) considered that a stem lineage is represented by a single species or even subspecies. Other observations suggested, however, a certain amount of variation between successive populations. Urbanek (1997) recognized a fluctuating variation expressed in the degree of robustness of the rhabdosome. A gracile morphotype is present in the Gorstian, represented by *P. dubius frequens* Jaekel, 1889, substituted at higher horizons (*Pseudomonoclimacis latilobus– Monograptus* [*Slovinograptus*] *balticus* biozones) by a much more robust morphotype, with taxa having strong virgula and thick virgella. A gracile morphotype, however, reappears again in higher horizons of the Ludfordian (*P. dubius welchae*).

Besides fluctuating morphological changes, Urbanek (1997) recognized a directional (anagenetic) trend in the number and placement of sicular rings (annuli). In the Gorstian, sicular rings vary in number (up to 8) and in position, while in the Ludfordian there are always 3 rings occupying the same position on the sicula (Fig. 1). Urbanek (1997) provisionally classified this latter form as *P. dubius* cf. *frequens*, relying on
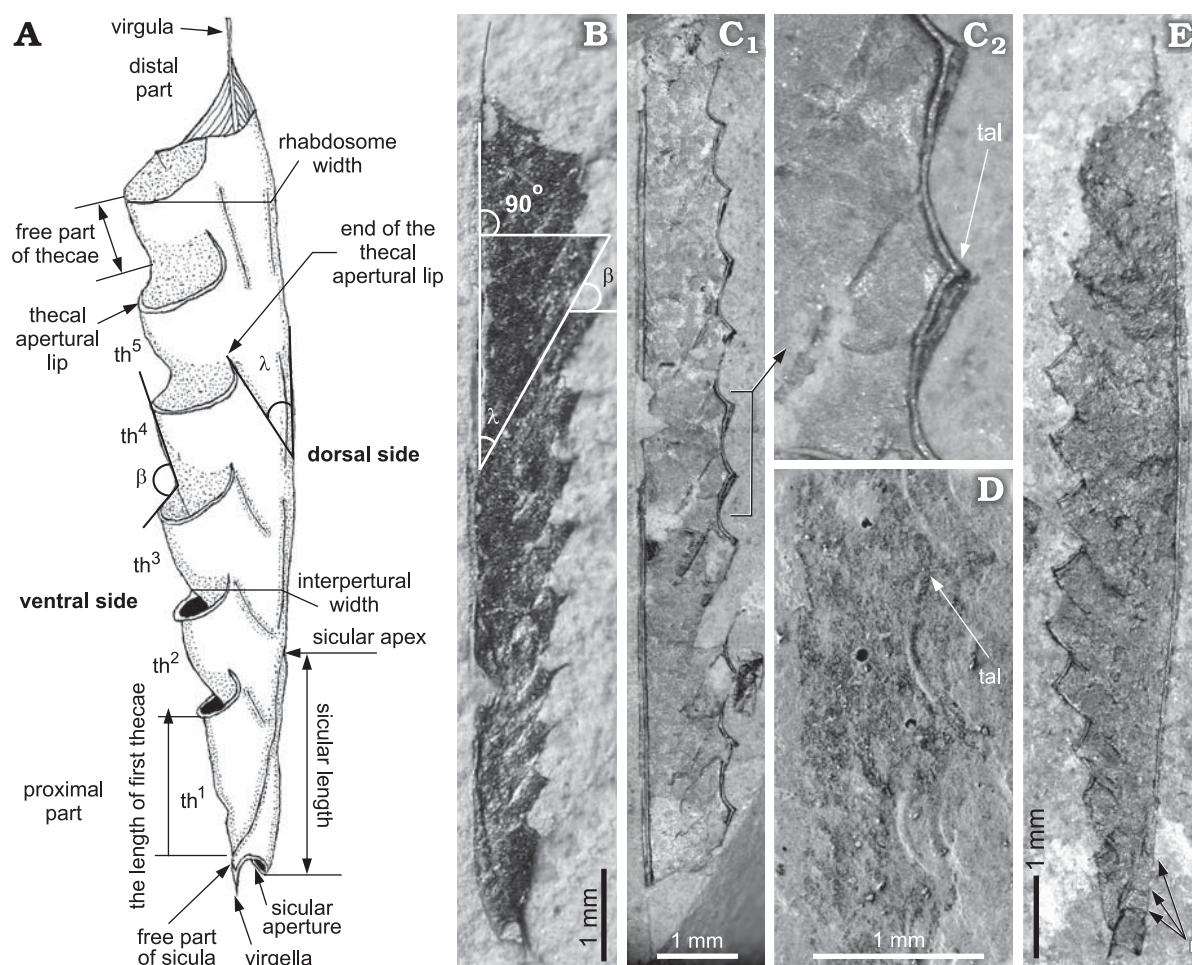
Fig. 3. Morphology of graptolite *Pristiograptus* rhabdosomes. **A**. Drawing of rhabdosome showing its characters (modified from Radzevičius 2003). **B–E**. Morphological features on flattened specimens. **B**. *Pristiograptus lodenicensis* Přibyl, 1948; VU-813, Likёnai-396 borehole, Lithuania, depth 589.5 m; *Cyrtograptus lundgreni* Biozone, Riga Formation. **C**. *Pristiograptus dubius magnus* subsp. nov., VU-835, Parovёja-9 borehole, Lithuania, depth 599.8 m; *Cyrtograptus perneri* Biozone, whole specimen (C₁), enlargement showing thecal apertural lip (C₂). **D**. *Pristiograptus dubius pseudodubius* (Bouček, 1932), fragment of rhabdosome, VU-A3-0047a; *C. lundgreni* Biozone, Żdanów outcrop, Sudetes, Poland. **E**. *Pristiograptus jaegeri* Holland, Rickards, and Warren, 1969; Vilkaviškis-131 borehole, depth 1073.2 m, VU-8004, *Colonograptus deubeli* Biozone. Abbreviations: ß, angle between thecal lip and wall of succeeding theca; λ, angle between interthecal septum (thecal axis) and virgule; r, sicula ring; th¹, first theca; tal, thecal apertural lip.

general similarity. In this paper, this form is distinguished as new subspecies *P. dubius postfrequens* subsp. nov.

Taking into account the stratigraphic range of the *P. dubius* lineage (from the *Monograptus crispus* Biozone of the Llandovery to the *Cyrtograptus perneri* Biozone of the Přidoli) and its duration (estimated by Jaeger 1991, as about 20 Ma, but in the light of currently available radiometric data the time span in question might be some 12 Ma), certain microevolution within the stem species seemed almost inevitable. This is also recently indicated by the studies of Radzevičius (2003) on chemically isolated material from deep boreholes of Lithuania and the Polish Lowland. He has suggested the following succession of subspecific variants within the initial portion of the stem lineage: *Pristiograptus dubius dubius–P. dubius pseudodubius–P. dubius parvus–P. dubius frequens–P. dubius postfrequens* subsp. nov. The succession of the remaining part of the stem lineage is still not recognized, the first of the mentioned subspecies being

probably preceded by the diminutive and little known Upper Llandovery *P. dubius initialis* (Kirste, 1919) (compare Jaeger 1991). As the study of *Pristiograptus* species has been proceeding piecemeal, particular taxa were differently ranked (as species or subspecies), but in the above list all are treated as subspecies of *P. dubius*, taking into account limited morphological differences and the presence of transient forms during its long evolution.

In Europe immediately following the *Cyrtograptus lundgreni* extinction event, the *P. dubius* lineage is represented solely by the dwarf subspecies *P. dubius parvus* (see above), while pristiograptids from the *P. dubius* group with a normal size of rhabdosome reappear above the *P. parvus* horizon and are represented by *P. dubius frequens* (see Jaeger 1991). However, in other regions of the world the situation is different. In Central Asia Koren' and Urbanek (1994) were unable to recognize *P. parvus* in their carefully measured sections. It is likely that immediately above the *C. lundgreni* extinction hori-

zon there, the retiolitid *Gothograptus nassa* (Holm, 1890) is associated with *P. dubius* of normal size. The same seems to be true for Arctic Canada (Lenz and Kozłowska-Dawidziuk 2002). It seems that in different, parts of the world the *P. dubius* lineage was represented in the early post-*C. lundgreni* time by coeval, vicarious subspecies, namely either by a dwarf variety *P. dubius parvus* or by normal-sized *P. dubius*. At present, these early post-*C. lundgreni* normal-sized representatives are insufficiently known morphologically and cannot be assigned taxonomically to any subspecies.

A special role in stratigraphy and phylogeny was played by the diminutive *P. dubius parvus*. However, the origin as well as the nature of this subspecies is disputed. According to Jaeger (1991) the dwarf variety was "always" present in *P. dubius* populations but because it was rare it remained unnoticed. However, under the stress conditions caused by environmental changes related to the *C. lundgreni* Event, this variety (probably a mutation) proved to be better adapted, in some parts of the world, than the normal forms with long rhabdosomes and underwent a rapid numerical increase, marking a distinct horizon (*P. parvus* Biozone). After the recovery of environmental conditions the dwarf mutation was replaced by populations showing a normal size of rhabdosome that had survived "somewhere".

Urbanek (1993) emphasized that *P. parvus* populations display characteristics that he has called the post-event syndrome, namely a monospecific mass occurrence as well as reduced size of rhabdosome, that he called the Lilliput effect. Dwarfism in particular could be interpreted as an ecophenetic reaction on general impoverishment of environmental conditions and at the same time the main cause of mass extinction. Biological causation of the post-Event syndrome is discussed in Urbanek (1993), while Twitchett (2007) discussed a wide occurrence of the Lilliput effect close to horizons of mass extinction at different stratigraphic settings. All authors agree that in Europe the dwarf variety *P. dubius parvus* was later replaced by *P. dubius frequens* representing the mainstream evolution and being soon followed by one of the greatest population and adaptive radiation bursts among graptolites (Koren' and Urbanek 1994). The status of *P. dubius parvus* is difficult to evaluate: it differs from standard iterative taxa of the *P. dubius* group, as it completely replaced the normal-sized form on a continental scale, making its first appearance immediately after a major biotic crisis. If we interpret the subnormal size of *P. parvus* as a result of the Lilliput effect, the range of its distribution might be interpreted as the area characterized by extreme environmental conditions. For these reasons we consider *P. dubius parvus* provisionally as a link in the evolution of the stem lineage taxa.

One of the products of the post-extinction big radiation was again the conservative *P. dubius* stem lineage, accompanied by the ancestors of a number of progressive lineages which split from the main stock of *P. dubius* as a result of early divergence. They exhibited a great evolutionary potential producing on the one hand cucullograptids, bohemograptids including the horned bohemograptids and, related to them, neo-cucullograptids as well as multiramous linograptids and on the other hand spinose monograptids (*Colonograptus, Saetograptus*) and specialized ones such as *Colonograptus deubeli* (Jaeger, 1959). At the same time the *Pristiograptus dubius* stem lineage emerged from an early divergences without greater morphological changes, representing a conservative morphotype, capable of further near-stasis. Great amounts of variation, needed as raw material for this diversification, were probably generated during the population burst, recorded taphonomically as mass abundances of graptolite remains (Koren' and Urbanek 1994) in the *Pristiograptus dubius/ Gothograptus nassa* Biozone.

Iterative and parapatric speciation.—Therefore one should distinguish taxa produced during the early divergence, from *Pristiograptus* species repeatedly produced from the stem lineage and termed by Rickards and Wright (2003) as an iterative species. This term was also applied by Koren' and Urbanek (1994: 150) and Urbanek (1998: 561–563). These species are derivatives of stem lineage taxa, and were produced at different times, either before or after the *P. dubius/G. nassa* Event. As a rule they are usually of short duration, differing only in a few characters from the parental stem species. In their careful revision of iterative species derived from the stem lineage Rickards and Wright (2003) have distinguished some 5 "robust" and 8 "gracile" ones.

A classical example of an iterative speciation process may be the appearance of incipient bilateral apertural lobes in *Neocolonograptus parultimus* (Jaeger, 1975) which were developed from the persistent stem lineage of *Pristiograptus dubius* in the early Přidoli (Urbanek 1997). Similar structures developed many times, heterochronously and independently from the stem lineage of *P. dubius* with straight apertural margins (Fig. 3). According to Urbanek (1998), within the early Ludlow to late Přidoli time span, these iterations occurred at least five times, producing in each case a short lateral clade which branched off the *P. dubius* stem lineage, namely: *Colonograptus praedeubeli–Saetograptus chimaera* clade A, *Pseudomonoclimacis latilobus* clade B, *P. d. labiatus* clade C, *Neocolonograptus parultimus–N. lochkovensis* clade D, and *Istrograptus transgrediens* clade E displaying isochronous parallelism to clade D. Apertural elaborations attain in each case a different degree of expressivity (Fig. 4), from gentle elevations of the apertural rim (weak expressivity), through distinct lateral lobes (moderate expressivity) to strongly developed lobes overhanging the aperture (strong expressivity). In fact, the first of these clades (Fig. 1) branched off so early that it may be considered also as one of the early divergent phyletic lines (compare Koren' and Urbanek 1994). Morphological effects of changes are also somewhat greater: lateral lappets being provided in terminal forms with an additional structure in the form of the spines (Fig. 4). In most cases the early representatives of particular clades reveal low expressivity of the newly introduced character, later being subject to gradual increase. But these are exceptions to the rule and some iterative species
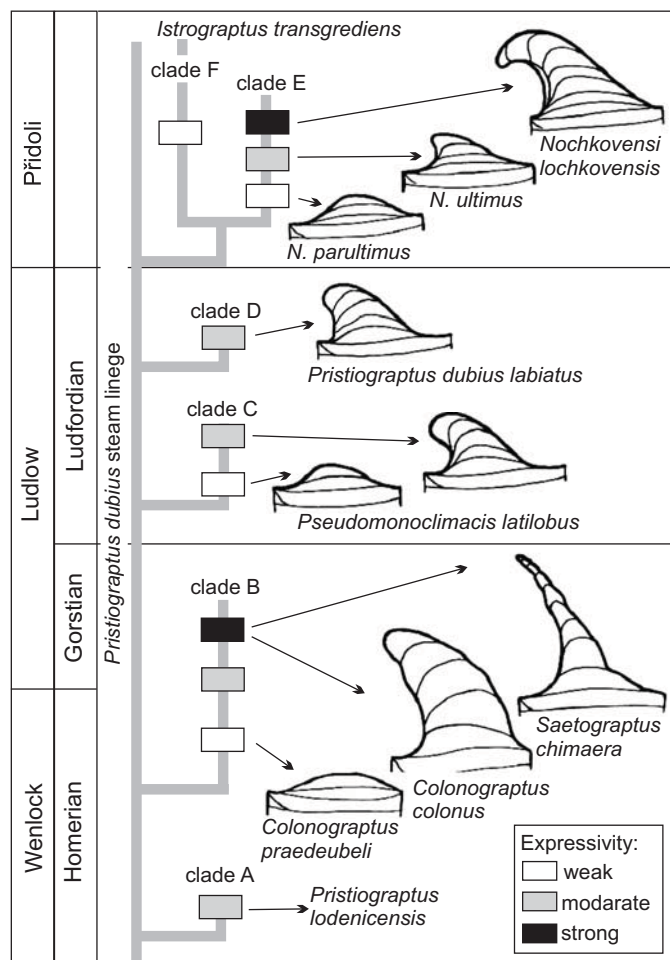
Fig. 4. The distribution and degree of expression of paired lateral apertural elevations or lobes within iterative clades that branched off the graptolite *Pristiograptus dubius* stem lineage (modified after Urbanek 1998).

display strong expressivity of new characters from the very beginning (Urbanek 1997).

Some iterative species reveal remarkable homeomorphy, as in the case of *Pristiograptus lodenicensis* Přibyl, 1948 from the upper Wenlock and *P. dubius labiatus* Urbanek, 1997 from the upper part of Ludfordian, which form almost

identical apertural elaborations (Fig. 4). Therefore as the *P. dubius* stem lineage shows no significant alteration of its evolutionary potential, producing remarkably similar iterative species separated by a few Ma, it seems that iterative speciation in each case involved only a small fraction of the existing parental gene system the vast majority remaining intact. The survival of parental species along with daughter species provides evidence that the evolutionary potential of the stem species, remains essentially unchanged (compare Koren' and Urbanek 1994; Urbanek 1998).

Therefore application of the "nodal principle" of cladistic taxonomy demanding that after each speciation the ancestral species should be given different binominals seems unjustified and undesirable in view of parsimony of nomenclature (see Urbanek 1996 for detailed discussion). An application of non-cladistic understanding of the relations between *P. dubius* stem species and iteratively derived species was suggested by Urbanek (1996, 1998). In this practice, the surviving ancestral species retains its previous name even after iterative speciation of a new species. This is justified by the mode of speciation used by an iterative species that does not break the cohesion of the ancestral lineage and involves only peripheral populations that later became isolated or semi-isolated as in the case of parapatric speciation.

Rickards and Wright (2003) mention as a remarkable fact that the stem taxon *P. dubius* always occurs in the same strata as species derived by iteration. They explain this co-occurrence by adaptation to different depth zones or hydrodynamic regime. The distribution of both species in question may be also related to a parapatric mode of speciation, considered by some zoogeographers as a common phenomenon in marine macrozooplankton (van der Spoel 1983). Iterative species, branching off the stem lineage, may be considered as probable examples of the parapatric mode of speciation.

An exceptional role of the *P. dubius* stem lineage, in the phylogeny of monograptids, relies on it being a persistent source of non-specialized morphologies, capable of easy specialization under suitable conditions. *P. dubius* as the stem species and all iterative species derived from it form a monophyletic group which may be called a genealogical do-

Fig. 5. SEM micrographs showing thecal lip variations in proximal thecae in graptolites *Pristiograptus* and *Colonograptus praedeubeli* (Jaeger, 1991). → **A**, **D**, **H**. Parovėja-9 borehole, Lithuania. **A**. *Pristiograptus dubius dubius* (Suess, 1851), VU S.P9-31, depth 644.8 m; *Monograptus riccartonensis* Biozone. **D**. *Pristiograptus* sp. sensu Radzevičius, 2003, VU S.P9-219, depth 595.4 m; *Cyrtograptus perneri* Biozone. **H**. *Pristiograptus lodenicensis* Přibyl, 1943, VU P.P9-4b, depth 561.9 m; *Cyrtograptus lundgreni* Biozone. **B**, **C**, **E–G**, **I**. Zawada borehole, Poland. **B**. *Pristiograptus dubius pseudodubius* (Bouček, 1932), ZPAL G.44/2, depth 1584.9–1590.6 m; *Cyrtograptus perneri* Biozone. **C**. *Pristiograptus dubius magnus* subsp. nov., ZPAL G.44/3, depth 1577.5–1582.5 m; *Cyrtograptus perneri* Biozone. **E**. *Pristiograptus sardous* (Gortani, 1922), ZPAL G..44/8, depth 1590.6–1597.7 m; *Cyrtograptus rigidus* Biozone. **F**, **G**. *Pristiograptus dubius paezerensis* subsp. nov.; *Cyrtograptus lundgreni* Biozone. **F**. ZPAL G.44/10, Zawada borehole, Poland, depth 1546.5–1552.7 m. **G**. ZPAL G.44/17, Bartoszyce borehole, Poland, depth 1663.2 m, mature rhabdosome. **I**. *Pristiograptus dubius praelodenicensis* subsp. nov., ZPAL G.44/6, depth 1546.5–1552.7 m; *Cyrtograptus lundgreni* Biozone. **J**. *Pristiograptus parvus* Ulst, 1974, VU P.K14-108, Kybartai-14 borehole, Lithuania, depth 1071.7 m; *Pristiograptus parvus* Biozone. **K**. *Pristiograptus virbalensis* Paškevičius, 1974, VU P.S87-71, Sutkai-87 borehole, Lithuania, depth 768.9 m; *Colonograptus praedeubeli* Biozone. **L**. *Colonograptus praedeubeli* (Jaeger, 1991), ZPAL G.44/23, Bartoszyce IG-1borehole, Poland, depth 1643.9 m; *Colonograptus praedeubeli* Biozone. **M**. *Pristiograptus dubius frequens* Jaekel, 1889, ZPAL G.44/30, Baltic erratic boulder S36, Gdańsk, Poland; *Lobograptus scanicus* Biozone. **N–R**. Mielnik-1 borehole, Poland. **N**. *Pristiograptus dubius tumescens* (Wood, 1900), ZPAL G.44/41, depth 892.2 m; *Lobograptus scanicus* Biozone. **O**. *Pristiograptus dubius postmagnus* subsp. nov., ZPAL G.44/50, depth 780.5 m; *Monograptus (Uncinatograptus) acer* Biozone. **P**. *Pristiograptus dubius welchae* Rickards, 1965, ZPAL G.44/47, depth 836.6 m; *Saetograptus leintwardinensis* Biozone. **Q**. *Pristiograptus dubius labiatus* Urbanek, 1997, ZPAL G.44/55, depth 753.3 m; *Monograptus (Uncinatograptus) spineus–Nocolonograptus parultimus* Interzone.
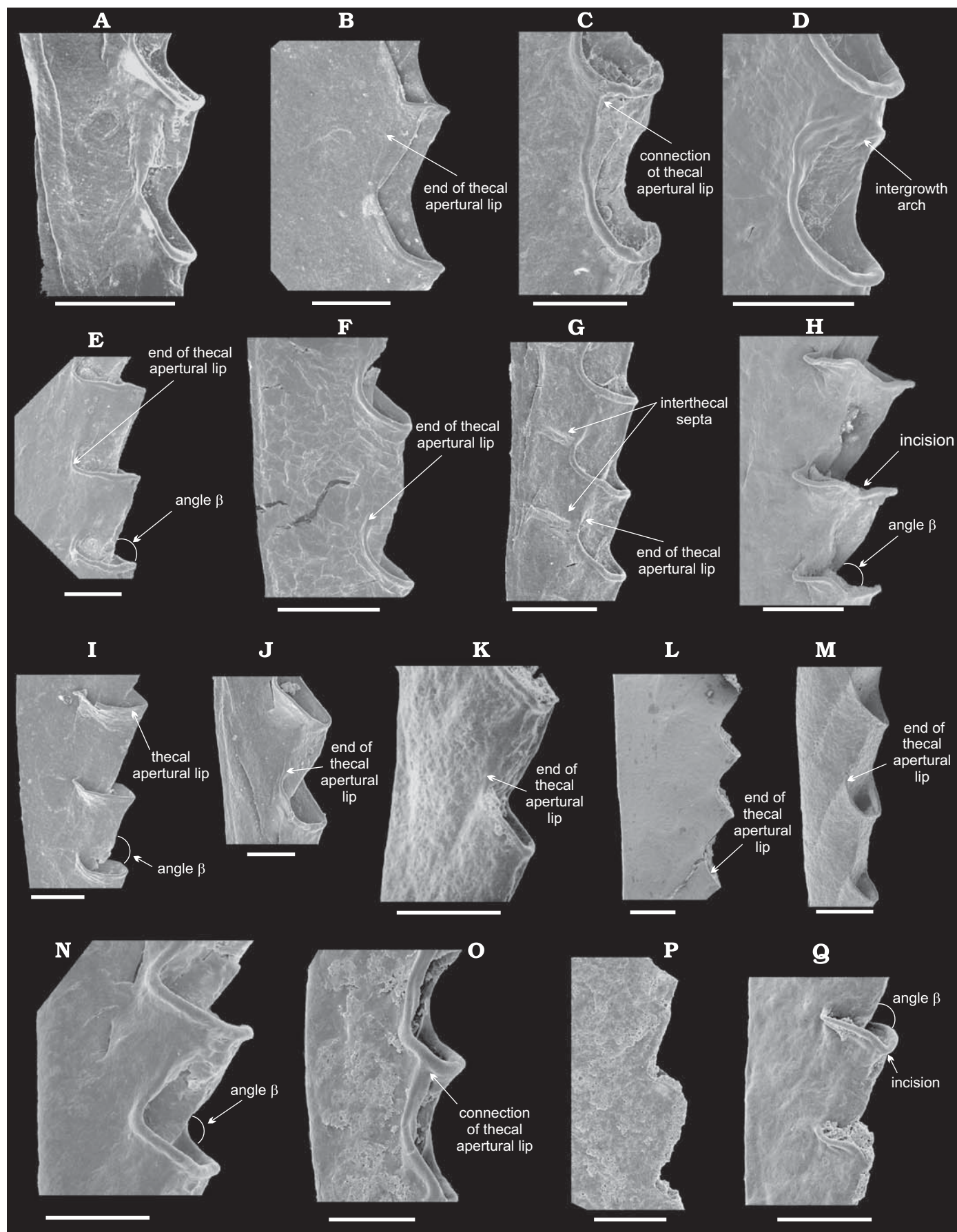
main. As defined by phylogenetic systematics, such domains are characterized by a proximity of their common ancestry and by similar apomorphic tendencies within its taxa or clades. This is shown by abundant (rampant) parallelism which involves repeatedly evolving characters in our case e.g., bilateral apertural lobes. The capacity to develop synapomorphies (derived shared characters) called the underlying synapomorphy by Saether (1979, 1983) and Sluys (1989) may be considered one of the most characteristic features of evolution within a genealogical domain. The *P. dubius* group provides a graphic example of such capacity.

Morphological variation in *Pristiograptus dubius* group

There are two important characters for distinguishing forms of *Pristiograptus dubius* group (Fig. 3). One is the angle β between the thecal apertural lip and the succeeding metathecal wall (β-angle), in which the variations in the angle permits splitting *Pristiograptus* into two main gonujroups. Another important feature is the shape of thecal apertural lip and its location to the ventral wall of the succeeding theca (the end of thecal apertural lip). The thecal apertural lip is a thickening around the aperture and may be linked to the development of the ectocortex. The end of the thecal apertural lip is regarded herein as a lateral margin of the thecal aperture. Its location is a very important taxonomic feature in distinguishing forms of the *P. dubius* group.

Our descriptions of species and subspecies are based on isolated material. Some species of *P. dubius* morphotypes are described from isolated material for the first time. The specific features e.g., the position of the thecal aperture end in *P. dubius* morphotype species and subspecies have never been documented, except some Wenlock taxa of *P. dubius* morphotype (Radzevičius and Paškevičius 2000; Radzevičius 2003). Width of 3D rhabdosomes is different than in the flattened ones. The problem is that the description of majority species and subspecies of *P. dubius* morphotypes is based on flattened

material what sometimes makes a difference comparing the description of 3D specimens. Thus the assignment of those isolated specimens to *P. dubius* morphotype species and subspecies is relative.

General features.—The widths of *P. dubius* morphotypes rhabdosomes vary, and the proximal end up to level of the fifth theca varies from straight to slightly ventrally curved. The rhabdosome widens gradually from 0.5 mm (e.g., *P. dubius shearsbyi* Rickards and Wright, 1999) to 0.8 mm (e.g., *P. sardous* [Gortani, 1922]), to 1.2 mm (e.g., *P. tumescens* [Wood, 1900]) at th^5.

Thecae are simple and cylindrical (Fig. 5). Thecal spacing ranges from 9–12 in 10 mm, the numbers varying whether measured in the proximal, medial and distal parts of rhabdosome. The thecae are inclined at angle λ varying between 25–35° (Fig. 4). The first theca is 1–1.2 mm long and 0.3 mm wide.

The sicula may be straight or weakly ventrally curved (Fig. 6), and its length varies from 1.3 mm in *P. dubius parvus* to 2.2 mm in *P. dubius postmagnus* subsp. nov. The width of the sicular aperture ranges from 0.2 mm (e.g., *P. dubius parvus*) to, most commonly, 0.3 mm. The aperture of the sicula is concave in lateral view. The apex of the sicula reaches the base of th^2 or th^3. The prosicula is 0.38–0.46 mm long. The metasicular length ranges from 1.41–1.48 mm. The width of the free part of sicula could be above 0.2 mm e.g., *P. dubius paezerensis* subsp. nov. (Fig. 6C, D, E).

The inclination of the thecal aperture to the sicular axis (angle ß) ranges from oblique to a right angle e.g., *P. dubius praelodenicensis* subsp. nov. In most of the *P. dubius* group species, angle ß is obtuse but may be a right angle in some forms e.g., *P. sardous*, *P. dubius praelodenicensis* subsp. nov., *P. dubius labiatus* Urbanek, 1997 and others (Fig. 5). The apertural lip can be narrow, or sometimes very thick as in *P. lodenicensis* Přibyl, 1943 (Fig. 5H).

The rim of the thecal lip may reach only as far as the middle part of the free ventral wall of the succeeding theca e.g., *P. dubius pseudodubius* (Bouček, 1932) (Fig. 5B), *P. dubius postfrequens* subsp. nov., or may be connected to the lip of

Fig. 6. SEM micrographs showing variations of proximal end in some graptolites *Pristiograptus* and *Colonograptus* forms. **A**, **B**. Zawada borehole, Poland. → **A**. *Pristiograptus dubius pseudodubius* (Bouček, 1932), ZPAL G.44/2, depth 1584.9–1590.6 m; *Cyrtograptus perneri* Biozone. **B**. *Pristiograptus sardous* (Gortani, 1922), ZPAL G.44/8, depth 1590.6–1597.7 m; *Cyrtograptus rigidus* Biozone. **C–E**. *Pristiograptus dubius paezerensis* subsp. nov.; *Cyrtograptus lundgreni* Biozone. **C**. ZPAL G.44/17, Bartoszyce borehole, Poland, depth 1663.2 m. **D**. ZPAL G.44/10, Zawada borehole, Poland, depth 1546.5–1552.7 m. **E**. VU P.P222-216, Paežeriai-222 borehole, Lithuania, depth 734.5 m. **F**. *Pristiograptus dubius praelodenicensis* subsp. nov., ZPAL G.44/6, depth 1546.5–1552.7 m; *Cyrtograptus lundgreni* Biozone. **G**, **H**. *Pristiograptus lodenicensis* Přibyl, 1943, Zawada borehole, Poland; *Cyrtograptus lundgreni* Biozone. **G**. ZPAL G.44/14, depth 1546.5–1552.7 m. **H**. ZPAL G.44/19, depth 1555.9–1562 m. **I–M**. *Pristiograptus virbalensis* group; *Colonograptus praedeubeli–C. deubeli* biozones. **I–L**. *Pristiograptus virbalensis* Paškevičius, 1974. **I–K**. Sudkai-87 borehole. **I**. VU P.S87-121a, depth 768.2 m. **J**. VU P.S87-121b, depth 768.2 m. **K**. VU P.S87-382, abnormal virgella, depth 877 m. **L**. ZPAL G.44/27, Bartoszyce borehole, depth 1642.4 m. **M**. *Pristiograptus auctus* Rickards, 1965, VU P.S87-362, Sutkai-87 borehole, 768.2 m depth; *Colonograptus deubeli* Biozone. **N**. *Pristiograptus dubius parvus* Ulst, 1974, VU P.K14-109, Kybartai-14 borehole, Lithuania, depth 1088.4 m, *Pristiograptus parvus* Biozone; th^1 with sicula (N$_1$), enlargement of sicula aperture (N$_2$). **O**, **P**. *Colonograptus praedeubeli* (Jaeger, 1991); *Colonograptus praedeubeli* Biozone. **O**. ZPAL G.44/21, Bartoszyce IG-1 borehole, Poland, depth 1646 m. **P**. VU K.PS87-134, Sutkai-87 borehole, Lithuania, depth 776 m. **Q**. *Colonograptus deubeli* (Jaeger, 1959), VU S.S69-61, Šiupyliai-69 borehole, Lithuania, depth 983 m; *Colonograptus deubeli* Biozone. **R**. *Pristiograptus dubius postfrequens* subsp. nov., ZPAL G.44/37, Mielnik-1 borehole, Poland, depth 716.3 m; *Monograptus (Uncinatograptus) spineus–Nocolonograptus parultimus* Interzone. **S**. *Pristiograptus dubius labiatus* Urbanek, 1997, ZPAL G.44/52, Mielnik-1 borehole, Poland, depth 753.3 m; *M. (U.) spineus–N. parultimus* Interzone. **T**. *Pristiograptus dubius welchae* Rickards, 1965, ZPAL G.44/44, Mielnik-1 borehole, Poland, depth 836.6 m; *Saetograptus leintwardinensis* Biozone.
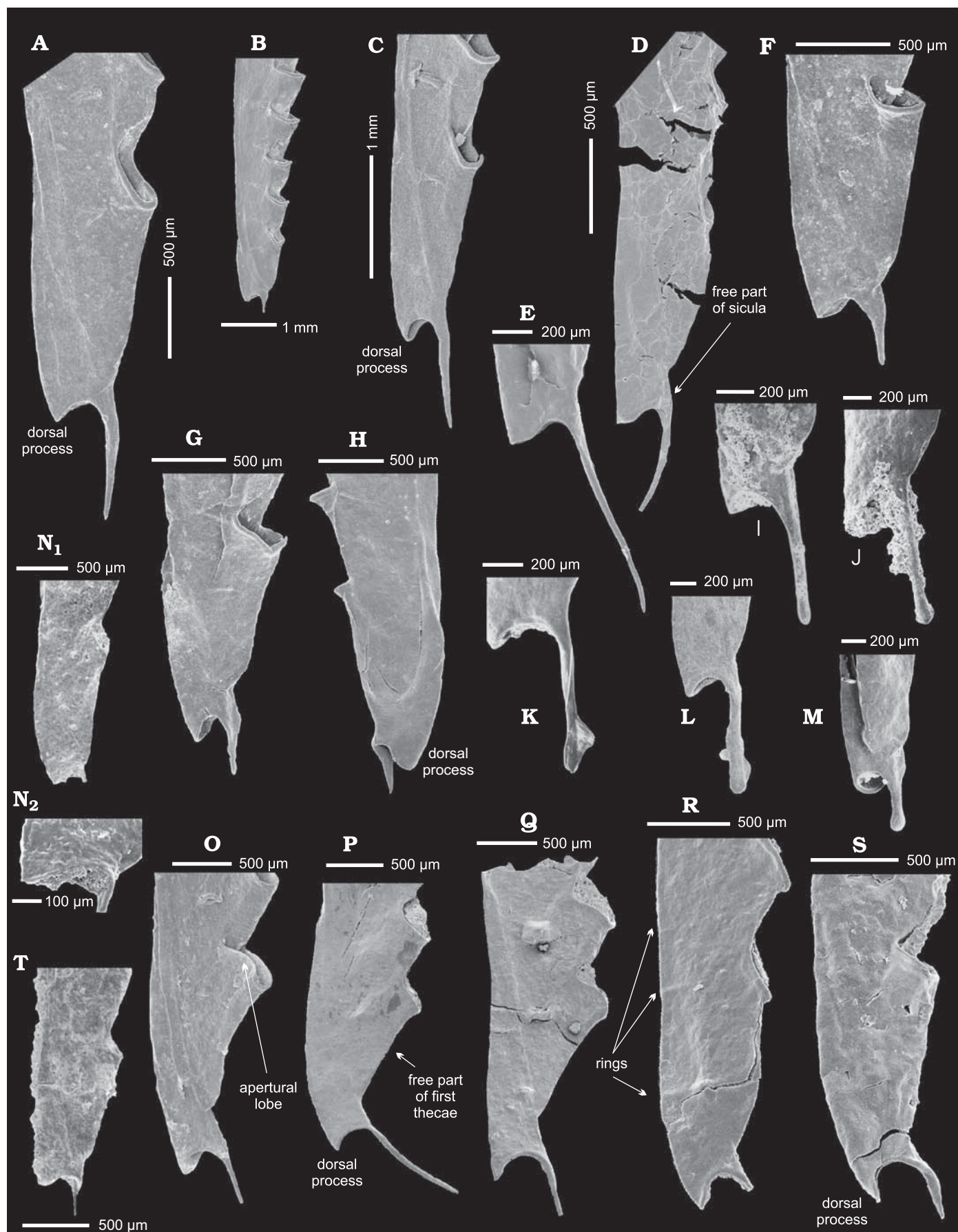
the succeeding theca e.g., *P. dubius magnus* subsp. nov. (Fig. 5C), *P. dubius postmagnus* subsp. nov. (Fig. 5O). The thecal lips can be simple e.g., *P. dubius dubius* (Fig. 5A), can have some depression e.g., *P. lodenicensis* (Fig. 5H) and made some intergrowth arch e.g., *Pristiograptus* sp. sensu Radzevičius 2003 (Fig. 5D).

Variation groups.—The investigation of all mentioned characters in *P. dubius* group permits the recognition of two main groups that differ in the angle ß (Fig. 3) between the apertural margin of the theca and the succeeding thecal wall.

The first, and main, *P. dubius* group contains forms with an obtuse angle ß. This group consists of *P. dubius dubius* (Suess, 1851) (Fig. 7A), *P. dubius pseudodubius* (Bouček, 1932) (Fig. 7C, D), *P. dubius magnus* subsp. nov. (Fig. 7E, F), *P. dubius paezerensis* subsp. nov. (Figs. 8F–I, 9A, B), *Pristiograptus* sp. sensu Radzevičius 2003 (Fig. 7B), *P. dubius* Ulst, 1974 (Fig. 10C, D), *P. dubius frequens* Jaekel, 1889 (Fig. 11A–C, F–H), *P. dubius* aff. *welshae* Rickards, 1965 (Fig. 12H–K), *P. dubius postmagnus* subsp. nov. (Fig. 13A–C), *P. dubius postfrequens* subsp. nov. (Fig. 11J, L), *P. dubius shearsbyi* Rickards and Wright, 1999 (Fig. 11D, E, I, K).

The second *P. dubius* group is characterized by possessing a right or acute angle ß. The species diversity is smaller, comprising only five forms: *P. sardous* (Gortani, 1922) (Fig. 8B, D), *P. dubius praelodenicensis* subsp. nov. (Fig. 8A, C, E), *P. tumescens* (Wood, 1900) (Fig. 12A–F), *P. dubius labiatus* Urbanek, 1997 (Fig. 13D–F), and *P. lodenicensis* Přibyl, 1943 (Fig. 10).

Other differences between the two main groups include the shape of the apertural lips, differences in rhabdosome shape and size, and a different number of sicular rings (annuli). Ludfordian species display sicula with a fixed 3-ring pattern (Urbanek 1997).

Material and methods

The Wenlock and Ludlow material described herein was derived from the East European Platform of Poland and Lithuania (Fig. 2). Our study is based on 3D specimens studied on light microscope and scanning electron microscope (SEM). Some characters are recognisable on well preserved flatten material (Fig. 3B–E). The Wenlock pristiograptids were recovered from boreholes Zawada IG-1 and Bartoszyce IG-1 of Poland, and Kurtuvėnai-161, Šiupyliai-69, Paežeriai-222, Likėnai-396, and Parovėja-9 boreholes of Lithuania. The Lud-

low material was collected from the Mielnik IG-1 borehole, Baltic erratic boulders from Jarosławiec of Poland, and the Milaičiai-103 borehole of Lithuania. The rocks were dissolved in 5–10% hydrochloric acid using standard techniques for graptolites. A fine hairbrush was used to pick and transfer specimens. The recovered material is stored in glycerine or on the SEM stubs in the Institute of Palaeobiology Polish Academy of Sciences, Warsaw, Poland (ZPAL G.), and in Vilnius University, Geological Museum, Lithuania. Photographs were made utilizing the SEM in the Geological Museum of Denmark, Copenhagen, and ZPAL.

Systematic palaeontology

Order Graptoloidea Lapworth, 1873

Family Monograptidae Lapworth, 1873

Subfamily Pristiograptinae Gürich, 1908

Genus *Pristiograptus* Jaekel, 1889

Type species: *Pristiograptus frequens* Jaekel, 1889, erratic boulders, North Germany, *Lobograptus scanicus* Biozone, Lower Ludlow.

Diagnosis.—Rhabdosome of variable length and curvature but usually almost straight; thecae are straight, simple tubes throughout length of rhabdosome, thecae have varying degrees of overlap and inclination; sicula small to large.

Remarks.—*Pristiograptus* rhabdosomes have a large variation of characters, that consequently gives a large "number" of species and subspecies.

Pristiograptus dubius dubius (Suess, 1851)

Figs. 5A, 7A.

1851 *Graptolithus dubius* sp. nov.; Suess 1851: 115, pl. 9: 5a, b.
1913 *Monograptus dubius* (Suess, 1850); Elles and Wood 1913: 376–378, text-fig. 247a, b.
1943 *Pristiograptus dubius dubius* (Suess, 1850); Přibyl 1943: 3–4, pl. 1: 4–6.
1952 *Pristiograptus dubius dubius* (Suess, 1850); Münch 1952: 85, pl. 18: 1.
1958 *Pristiograptus dubius dubius* (Suess, 1850); Přibyl 1958: 117.
2000 *Pristiograptus dubius dubius* (Suess, 1850); Radzevičius and Paškevičius 2000: 91–92, pl. 1: 2.

Material.—Ten fragments of rhabdosomes of different preservation from the Kurtuvėnai-161 (1420.5–1396.9 m) and Parovėja-9 boreholes (651.3–638 m), Lithuania.

Description.—The ß angle is obtuse. The thecal lips are distinct, not extending onto the ventral wall of the succeeding

Fig. 7. SEM micrographs of Sheinwoodian (Wenlock) graptolite *Pristiograptus* forms. **A**, **B**. Parovėja-9 borehole, Lithuania. **A**. *Pristiograptus dubius dubius* →
(Suess, 1851), VU S.P9-31, depth 644.8 m; *Monograptus riccartonensis* Biozone, general view of rhabdosome (A_1), th[4] apertural lip (A_2), apex of sicula and first theca apertural lip (A_3), mouth of sicula and virgella (A_4). **B**. *Pristiograptus* sp. sensu Radzevičius, 2003, VU S.P9-219, depth 595.4 m; *Cyrtograptus perneri* Biozone, general view of rhabdosome (B_1), connection of thecal apertural lip with succeeding theca apertural lip (B_2), intergrowth arch of th[1] (B_3), and intergrowth arch of th[3] (B_4), thick virgella and sicular apertural lip (B_5). **C**, **D**. *Pristiograptus dubius pseudodubius* (Bouček, 1932), Zawada borehole, Poland, depth 1584.9–1590.6 m; *Cyrtograptus perneri* Biozone. **C**. ZPAL G.44/1, general view of rhabdosome. **D**. ZPAL G.44/2, general view of rhabdosome (D_1), th[5] apertural lip (D_2), and th[1] with sicula (D_3). **E**, **F**. *Pristiograptus dubius magnus* subsp. nov., Zawada borehole, Poland. **E**. ZPAL G.44/3, depth 1577.5–1582.5 m; *Cyrtograptus perneri* Biozone, general view of rhabdosome (E_1), th[6] apertural lip (E_2), and th[1] with sicula (E_3). **F**. ZPAL G.44/4, depth 1590.6–1597.7 m, *Cyrtograptus rigidus* Biozone, general view of rhabdosome (F_1), th[4] apertural lip (F_2), and th[1] with sicula (F_3).
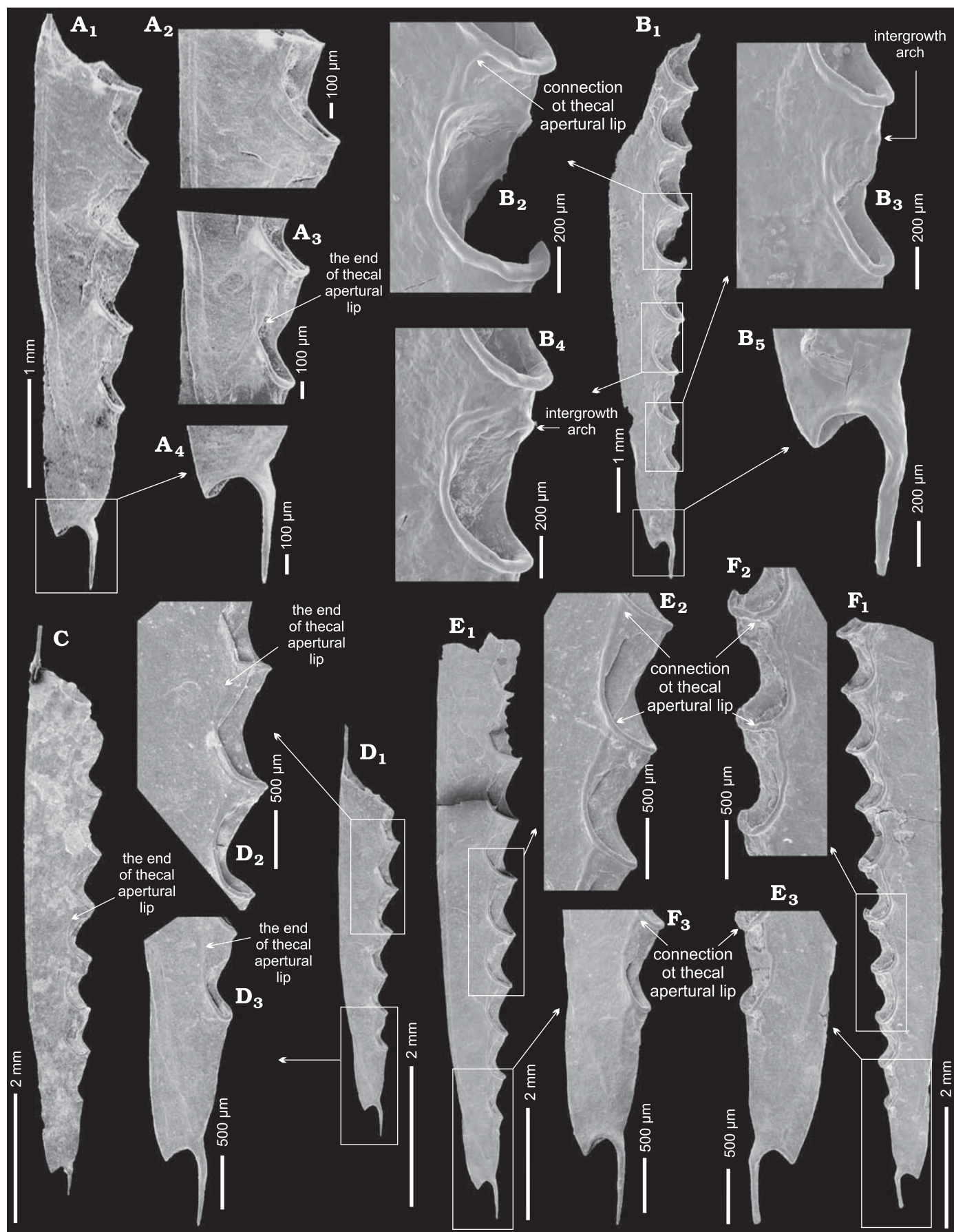
thecae and ending in the beginning of the ventral wall (Figs. 5A, 7A). No sicular rings are observed.

Discussion.—The type material of the *P. dubius* (Suess, 1851) is flattened and poorly illustrated. It has never been redescribed and refigured. Details of the *P. dubius dubius* rhabdosome structures are not visible at the type material. The *P. dubius* morphotype is considered to be *P. dubius dubius* subspecies, which thecal apertural lip not extending onto the ventral wall of succeeding thecae and ending at the beginning of the ventral wall and without sicular rings.

Stratigraphic and geographic range.—Lower Wenlock *Monograptus riccartonensis–M. antennularius* Biozones. *P. dubius dubius* is widespread, having been recorded from all continents.

Pristiograptus dubius pseudodubius (Bouček, 1932)

Figs. 5B, 6A, 7C, D.

1943 *Pristiograptus pseudodubius* (Bouček, 1932); Přibyl 1943: 8–9, pl. 1:. 1, 3.
1952 *Pristiograptus pseudodubius* (Bouček, 1932); Münch 1952: 86, pl. 18: 7.
1965 *Pristiograptus pseudodubius* (Bouček, 1932); Obut et al. 1965: 72, pl. 13: 2.
1965 *Pristiograptus pseudodubius* (Bouček, 1932); Rickards 1965: 260, pl. 29: 10, text-fig. 2I.
1967 *Pristiograptus pseudodubius* (Bouček, 1932); Gailite et al. 1967: 243–244, pl. 18: 8, 9, text-fig. 57.
1974 *Pristiograptus pseudodubius* (Bouček, 1932); Ulst 1974: 108–109, pl. 11: 1, pl. 12: 1, 2.
2000 *Pristiograptus pseudodubius* (Bouček, 1932); Radzevičius and Paškevičius 2000: 92–94, pl. 2: 1.

Material.— More then 200 rhabdosomes and fragments from Kurtuvėnai-161 (1351.9–1328.1 m), Likėnai-369 (630.0–582.1 m), and Parovėja-9 (621.5–588.6 m) boreholes, Lithuania and Zawada-1 borehole (1590.65–1584.9 m), Poland.

Description.—The ß angle is obtuse. The thecal apertural lip reaches only the middle of the free ventral wall of the succeeding theca (Figs. 5B, 7C, D). No sicular rings are observed.

Discussion.—The type material of *P. dubius pseudodubius* has been described from flattened material and detailed account of the structures of its rhabdosome are not visible. In this work *P. dubius pseudodubius* is considered to be as *dubius* morphotype with ß angle obtuse, which thecal apertural lip reaches only the middle of the free ventral wall of the succeeding theca.

Stratigraphic and geographic range.—Wenlock *Monograp-*

tus belophorus–Cyrtograptus lundgreni Biozones; *P. dubius pseudodubius* is widespread, known from all continents.

Pristiograptus dubius parvus Ulst, 1974

Figs. 5J, 6H, 10C, D.

1974 *Pristiograptus parvus* sp. nov.; Ulst 1974: 111–113, pl. 12: 43, pl. 11 : 5.
1991 *Pristiograptus dubius parvus* Ulst, 1974; Jaeger 1991: 316–318, pl. 25: 2–6, 8.
1996 *Pristiograptus dubius* "*parvus*" Ulst, 1974; Gutierrez-Marco et al. 1996: 660, pl. 1: 1–3.
1998 *Pristiograptus parvus* Ulst, 1974; Kozłowska-Dawidziuk et al. 1998: 99, pl. 1G.
1999 *Pristiograptus parvus* Ulst, 1974; Kozłowska-Dawidziuk 1999: 356, fig. 3a.
2000 *Pristiograptus parvus* Ulst, 1974; Radzevičius and Paškevičius 2000: 95–96, pl. II: 2, 3; pl. VI: F.
2001 *Pristiograptus parvus* Ulst, 1974; Kozłowska-Dawidziuk et al. 2001: 159–161, fig. 8: 11–13, fig. 9: 6–8.
2004 *Pristiograptus parvus* Ulst, 1974; Porębska et al. 2004: 276, fig. 3R.
2010 *Pristiograptus parvus* Ulst, 1974; Radzevičius et al. 2010: 56, fig. 3B, D.

Material.—About 100 rhabdosomes and fragments from the Kurtuvėnai-161 (1323.2–1321.1 m), Parovėja-9538 m), Šiupyliai-69 (1004–1000.8 m) boreholes, Lithuania and Bartoszyce IG-1 borehole (1660–1657.8 m), Poland.

Description.—The rhabdosome is straight, sometimes slightly curved to the ventral side, the ß angle is obtuse (Fig. 5J). The first theca begins at the level of the sicula aperture (Fig. 6H). *P. parvus* is like a small version of *P. dubius pseudodubius*.

Discussion.—The type of *P. parvus* Ulst, 1974 was described using non-isolated, flattened material. This species is specific having very small rhabdosome.

Stratigraphic and geographic range.—*P. parvus* Biozone, East European Platform (Poland, Latvia, Lithuania, Sweden), Czech Republic, Germany, Spain, Canada.

Pristiograptus dubius frequens Jaekel, 1889

Figs. 5M, 11A–C, F–H.

1943 *Pristiograptus frequens* Jaekel, 1889; Přibyl 1943: 24–25, pl. 3:13, text-fig 3A.
1991 *Monograptus dubius frequens* (Jaekel, 1889); Jaeger 1991: 314, fig. 25: 9, 11, 15.

Material.—More then 50 rhabdosomes and fragments from

Fig. 8. SEM micrographs of Sheinwoodian and Homerian (Wenlock) graptolite *Pristiograptus* forms. **A**, **C**, **E**. *Pristiograptus dubius praelodenicensis* → subsp. nov., Zawada borehole, Poland, depth 1546.5–1552.7 m; *Cyrtograptus lundgreni* Biozone. **A**. Holotype, ZPAL G.44/5, general view of rhabdosome (A[1]), proximal part of rhabdosome (A[2]), the end of th 2 apertural lip (A[3]), and aperture of sicula (A[4]). **C**. ZPAL G.44/6, general view of rhabdosome (C[1]), th[3] and th[4] apertures (C[2]), and sicula with th[1] (C[3]). **E**. ZPAL G.44/7, young rhabdosome. **B**, **D**. *Pristiograptus sardous* (Gortani, 1922), Zawada borehole, Poland, depth 1590.6–1597.7 m; *Cyrtograptus rigidus* Biozone. **B**. ZPAL G.44/8, general view of rhabdosome (B[1]) and th[6] lip (B[2]). **D**. ZPAL G.44/9, general view of rhabdosome. **F–I**. *Pristiograptus dubius paezerensis* subsp. nov.; *Cyrtograptus lundgreni* Biozone. **F**, **G**, **I**. Zawada borehole, Poland. **F**, **G**. Depth 1546.5–1552.7 m. **F**. ZPAL G.44/10, general view or rhabdosome (F[1]), enlargement with the end of th[2] lip (F[2]). **G**. ZPAL G.44/11, general view of rhabdosome (G[1]) and sicula with long virgella (G[2]). **I**. ZPAL G.44/12, depth 1555.9–1562 m, general view of rhabdosome. **H**. VU P.P222-216, Paežeriai-222 borehole, Lithuania, depth 734.5 m, general view of proximal part of a rhabdosome (H[1]), th[5] lip (H[2]), end of the th[2] lip (H[3]), and sicular aperture with dorsal process and long virgella (H[4]).
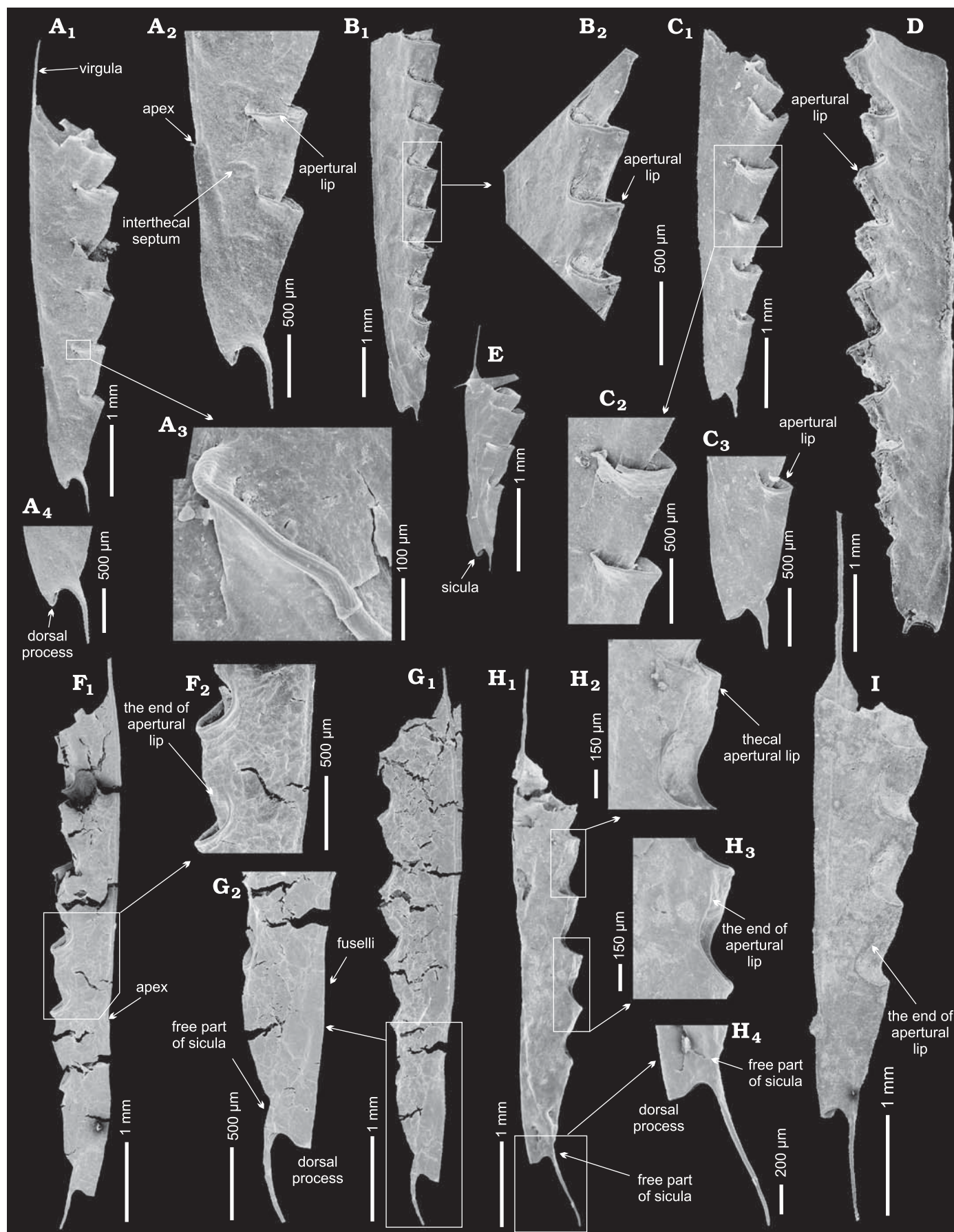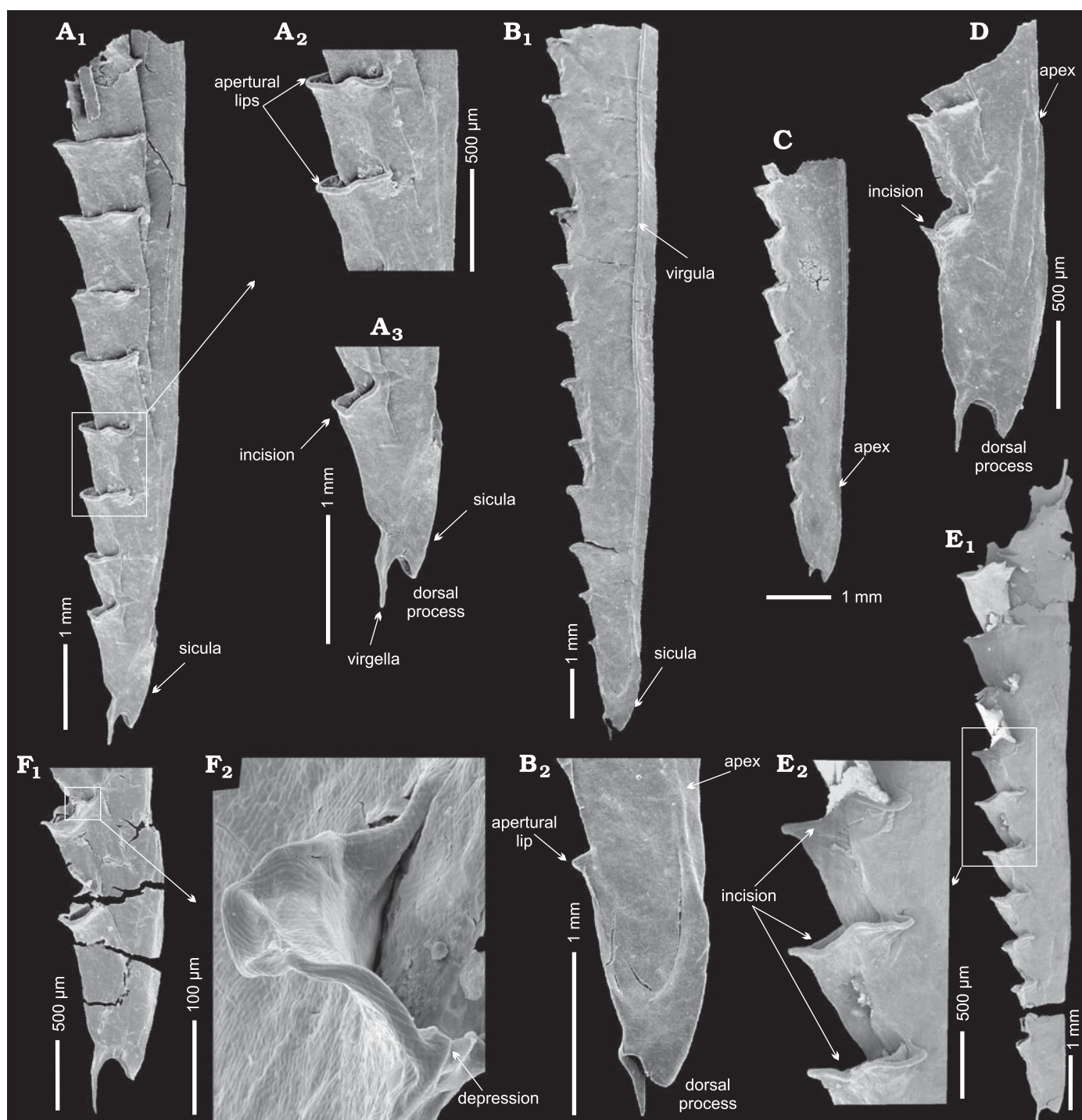
Fig. 9. SEM micrographs of the graptolite *Pristiograptus lodenicensis* Přibyl, 1943; *Cyrtograptus lundgreni* Biozone, Lower Homerian, Wenlock. **A–D**, **F**. Zawada borehole, Poland. **A–C**. Depth 1546.5–1552.7 m. **A**. ZPAL G. 44/13, general view of rhabdosome (A_1), lips of th^3 and th^4 (A_2), and th^1 with sicula (A_3). **B**. ZPAL G.44/14, general view of dorsal side of rhabdosome (B_1), proximal end (B_2). **C**. ZPAL G.44/15, general view of rhabdosome. **D**, **F**. Depth 1540–1546.5 m. **D**. ZPAL G.44/16, proximal end of rhabdosome. **F**. ZPAL G.44/17, proximal end of rhabdosome (F_1) and th^2 lip with cortical tissue "script" ("manta ray wing") (F_2). **E**. VU P.P9-4b, Parovėja-9 borehole, Lithuania, depth 561.9 m, general view of rhabdosome (E_1), depressions of thecal apertural lip (E_2).

erratic boulder (S36), Poland and Šiupyliai-69 (994.2–905.5 m), Kurtuvėnai-161 (1297.1–127.2 m) boreholes, Lithuania.

Description.—The rhabdosome is narrow and graceful. The proximal end is slightly curved ventrally as far th^5. The ß angle is obtuse. The thecal apertural lip is distinct, not extend-ing onto the ventral wall of the succeeding theca and ending in the beginning of the ventral wall. The number of sicular rings varies from 3 to 8 (Fig. 11A, B).

Remarks.—The genus *Pristiograptus* was erected by Jaekel (1889), designating *P. frequens* as its type species. Recent

studies reveal that the differences between *P. frequens* and *P. dubius* (Suess, 1851) are so small, that the former species should be considered as a subspecies of the last mentioned, and earlier established, species by Suess (1851) [compare Jaeger 1991, who used the name *Monograptus dubius frequens* (Jaekel, 1889)]. The difference between *P. dubius dubius* and *P. dubius frequens* is in absence of sicular rings in *P. dubius dubius* and their presence in *P. dubius frequens*.

Stratigraphic and geographic range.—*Colonograptus praedeubeli–Cucullograptus hemiaversus* Biozone. *P. dubius frequens* having been recorded from: Latvia, Lithuania, Poland, Czech Republic, and Germany.

Pristiograptus dubius postfrequens subsp. nov.

Figs. 6P, 11J, L.

Etymology: From Latin *post*, after; *frequens*, frequent.

Holotype: ZPAL G./24, isolated rhabdosome with sicula and thee thecae illustrated in Urbanek 1997: fig. 43D.

Type locality: Mielnik-1 borehole, depth 786.5 m, Poland.

Type horizon: Upper Ludlow, *Monograptus* (*Uncinatograptus*) *acer* Biozone.

Material.—About 50 rhabdosomes and some fragments from Mielnik-1 borehole (915–690 m), Poland and Milaičiai-103 borehole (1255–1210 m), Lithuania.

Diagnosis.—Thecal lip ends in the middle or above the free ventral wall of the succeeding theca. Sicula with three rings.

Description.—The rhabdosome is narrow and slightly curved ventrally at the proximal end. The rhabdosome widens gradually from 0.6 mm at th[1], to 0.7 mm at th[2], 0.8 mm at th[3]. Interapertural width is 0.5 mm at th[1], 0.6 mm at th[2], 0.7 mm at th[3]. There are 10–12 thecae in 10 mm. The ß angle is obtuse. Th[1] is 0.9 mm long and 0.3 mm wide. The free part of each theca is half of its whole length. The end of the thecal lip may continue up to the half length of the free part of succeeding thecae or above. The λ angle is 30°. Sicula length is 2.2 mm and width is 0.3 mm. The apex of the sicula reaches the base of th[3]. There are three sicular rings.

Discussion.—*P. dubius postfrequens* is similar to *P. dubius frequens*. The difference is in the number of sicula rings and in the position of the thecal apertural end. *P. dubius postfrequens* has fixed 3 sicular rings whereas in *P. dubius frequents* the number of sicular rings vary from 3 to 8. The end of the thecal lip of *P. dubius postfrequens* may continue up to the half length of the free part of succeeding theca or above, whereas the thecal apertural lip of *P. dubius frequens* is ending at the beginning of the ventral wall of succeeding theca.

Stratigraphic and geographic range.—*Saetograptus leintwardinensis–Monograptus* (*Uncinatograptus*) *spineus* Biozone, Poland and Lithuania.

Pristiograptus dubius magnus subsp. nov.

Figs. 5C, 7E, F.

2003 *Pristiograptus dubius* var. "A"; Radzevičius 2003: 6–7, figs. 5–7.
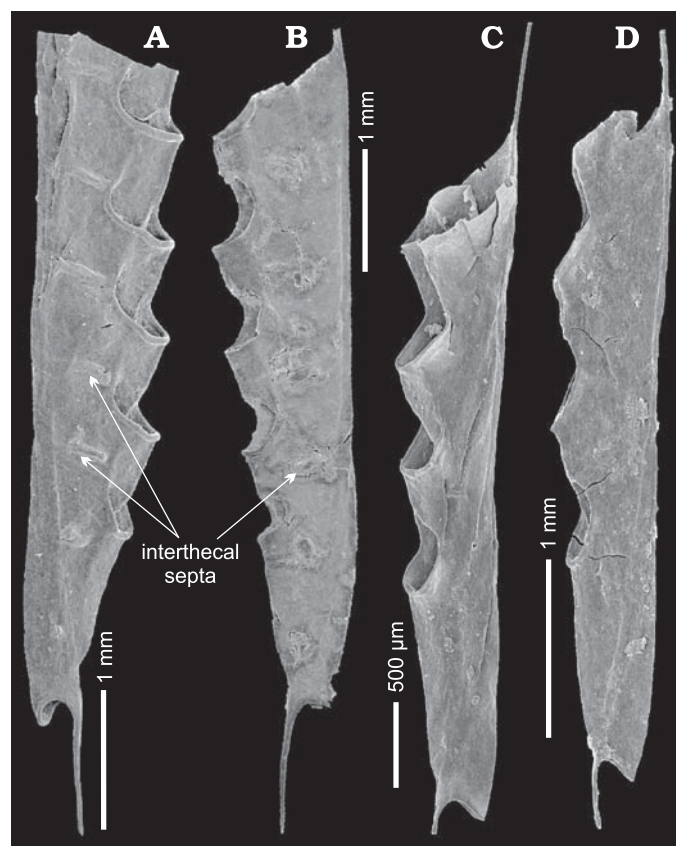2008 *Pristiograptus dubius* var. A Radzevičius, 2003; Radzevičius et al. 2008: 38, fig. 4C.

Fig. 10. SEM micrographs of two Homerian (Wenlock) graptolite *Pristiograptus* forms. **A**, **B**. *Pristiograptus dubius paezerensis* subsp. nov., mature rhabdosomes; *Cyrtograptus lundgreni* Biozone. **A**. ZPAL G.44/17, Bartoszyce IG-1 borehole, Poland, depth 1663.2 m. **B**. ZPAL G.44/19, Zawada borehole, Poland, depth 1555.9–1562 m. **C**, **D**. *Pristiograptus dubius parvus* Ulst, 1974 growing rhabdosomes, Bartoszyce IG-1 borehole, Poland, depth 1660.7 m; *Pristiograptus parvus* Biozone. **C**. ZPAL G.44/25. **D**. ZPAL G.44/26.

2010 *Pristiograptus dubius* var. A sensu Radzevičius, 2003: Loydell et al. 2010: 256, fig. 3s, t.

Etymology: From Latin *magnus*, great, grand.

Holotype: VU-9-220, isolated rhabdosome with with sicula and 11 thecae illustrated in Radzevičius 2003: fig. 5A.

Type locality: Parovėja-9 borehole, depth 605.25 m, Lithuania.

Type horizon: Lower Wenlock, *C. perneri* Biozone.

Material.—About 25 rhabdosomes and additional fragments from the Parovėja-9 borehole (605.25–590.5 m), Lithuania, depth and Zawada-1 borehole (1577.5–1582.5 m), Poland.

Diagnosis.—Thecal lips distinct and connected with those of succeeding thecae. No sicular rings.

Description.—The rhabdosome is robust and straight, although some specimens show ventral curvature proximally. L is >11.5 mm. The rhabdosome widens gradually from 0.8 mm at th[1], to 0.9 mm at th[2], 1 mm at th[3], and 1.2 mm at th[4]. W_{max} is 1.7 mm. The interapertural W is 0.55 mm at th[1], 0.65 mm at th[2], 0.85 mm at th[3], 0.95 mm at th[4], and 1.05 mm at th[5]. There are 10–11 thecae in 10 mm. The ß angle is obtuse. Th[1] is 1 mm long. The free part of each theca is half of

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its whole length. The thecal lips are distinct and connected with that of the succeeding thecae, except th^1 and th^2 although it may have been obscured in these thecae by overgrowth of cortical tissue. The lip connection is particularly distinctive in the medial and distal parts of the rhabdosome. The λ angle is 30°. The sicula is short and narrow, L is 1.8 mm and apertural W is 0.3 mm. The apex of the sicula reaches the base of th^3. The free part of the sicula is 0.3 mm long. The virgella is short, up to 0.6 mm. In one specimen there is a thickened protrusion in the middle part of the virgella. No sicular rings are observed.

Stratigraphic and geographic range.—Lower Wenlock, *C. perneri* Biozone, Poland and Lithuania.

Pristiograptus dubius paezerensis subsp. nov.
Figs. 5F, G, 6C, D, E, 8F–I, 9A, B.

2003 *Pristiograptus dubius* var. B; Radzevičius 2003: 7–8, figs. 8, 9.
2006 *Pristiograptus dubius* var. B; Radzevičius 2006: 337, fig. 4B.

Etymology: After Paežeriai village and borehole in Lithuania.

Holotype: VU-222-229, isolated rhabdosome with with sicula and five thecae illustrated in Radzevičius 2003: fig. 8A.

Type locality: Paežeriai-222 borehole, depth 730 m, Lithuania.

Type horizon: Upper Wenlock, *C. lundgreni* Biozone.

Material.—About 20 rhabdosomes and many fragments from boreholes: Paežeriai-222 (734.5–730 m), Likėnai-369 (577–605.9 m), Šiupyliai-69 (1007 m) boreholes, Lithuania and Zawada-1 (1546.5–1552.7 m), Bartoszyce IG-1 (1665.3–1663.2 m) boreholes, Poland.

Diagnosis.—Thecal lip distinct, extending onto the ventral wall of the succeeding theca up to the middle of the ventral wall, not reaching its apertural lip. First theca starts 0.3 mm above the sicular aperture. Long virgella. No sicular rings.

Description.—The rhabdosome is straight and narrow, L is >12.5 mm, W is 0.7 mm at th^1, 0.75 mm at th^2, 0.85 mm at th^3, 0.95 mm at th^4, and 1mm at th^5. W_{max} is 1.1 mm on th^6. The interapertural W is 0.5 mm at th^1, 0.6 mm at th^2, 0.75 mm at th^3, 0.8 mm at th^4, and 0.9 mm at th^5. There are 10–11 thecae in 10 mm. Thecae are cylindrical. The angle ß is obtuse. The free part of each theca is half of its entire length. The thecal lip is distinct, the end of thecal lip may continue up to the half length of the free part of succeeding thecae. The λ angle is 30°. The sicula L is 2 mm, apertural W is 0.35 mm. The apex of the sicula is at approximately at the level of the apertural lip of th^2. Th^1 arises 0.3 mm above the sicular aperture. The virgella is thin, L to 1.35 mm.

Remarks.—The thecal apertural lips are thick and distinctive and interthecal septa of astogenetically old rhabdosomes are very thick (Fig. 10A, B).

Stratigraphic and geographic range.—Upper Wenlock, *C. lundgreni* Biozone; Poland and Lithuania.

Pristiograptus sp. sensu Radzevičius, 2003
Figs. 5D, 7B.

2003 *Pristiograptus* sp.; Radzevičius 2003: 8–9, fig. 10.

Material.—One specimen, VU-9-219, from the Parovėja-9 borehole (595.4 m), Lithuania; rhabdosome with first 8 thecae and sicula.

Remarks.—The thecal lip is distinct, extending over the free part of the succeeding theca and additionally its ends are connected (Fig. 5D). This connection is clearly visible in the medial and distal parts of the rhabdosome. Th^1 and th^2 either do not have such thecal apertural lip connections or they are covered by cortical tissue. The lips of the distal thecae are bifurcated. An intergrowth arch is well developed especially in the proximal part of the rhabdosome. The distance between the thecal apertural lip connection on the succeeding theca and the origin of its bifurcation is 0.25 mm for th^1 and th^2, and 0.35 mm for th^3 to th^5. There are no sicular rings.

Stratigraphic and geographic range.—Wenlock, *C. perneri* Biozone, Lithuania.

Pristiograptus sardous (Gortani, 1922)
Figs. 5E, 6B, 8B, D.

1943 *Pristiograptus sardous sardous* (Gortani, 1922); Přibyl 1943: 14–15, pl. 1: 3, text-fig. 2C.
1943 *Monograptus sardous* Gortani, 1922; Přibyl 1943: pl. 8: 1, text-fig. 9.
1952 *Pristiograptus sardous* (Gortani, 1922); Münch 1952: 86, pl. 18: 10.

Material.—About 5 rhabdosomes from Zawada-1 borehole (1590.6–1597.7 m), Poland.

Description.—The apertural lips of symmetrically flattened thecae form an acute or right ß angle. Overall, thecal apertures are perpendicular to the rhabdosome axis in the medial and distal parts of the rhabdosome. The λ angle is 30°. There are no sicular rings.

Discussion.—The type material of *P. sardous* is flattened. *P. sardous* is *P. dubius* type *Pristiograptus* with wide proximal end of rhabdosome.

Fig. 11. SEM micrographs showing variations of proximal end of rhabdosomes in three *Pristiograptus dubius* subspecies of graptolites. **A–C**, **F–H**. *Pristiograptus dubius frequens* Jaekel, 1889, Baltic erratic boulder S36, Gdańsk, Poland; *Lobograptus scanicus* Biozone. **A**. ZPAL G.44/28, general view of rhabdosome (A_1) and proximal end (A_2). **B**. ZPAL G.44/29, lateral view of rhabdosome. **C**. ZPAL G.44/30, general view of rhabdosome. **F**. ZPAL G.44/31, proximal end of rhabdosome with sicular rings. **G**. ZPAL G.44/32, general view of rhabdosome (G_1) and proximal end (G_2). **H**. ZPAL G.44/33, ventral view of young rhabdosome. **D**, **E**, **I**, **K**. *Pristiograptus dubius shearsbyi* Rickards and Wright, 1999, Mielnik borehole, Poland, depth 688.8 m; *Neocolonograptus parultimus* Interzone. **D**. ZPAL G.44/27, proximal end of rhabdosome (D_2) and general view of rhabdosome (D_1). **E**. ZPAL G.44/34, general view of rhabdosome (E_1) and proximal end (E_2). **I**. ZPAL G.44/35, lateral view of medial part of rhabdosome (I_1) ventral view (I_2). **K**. ZPAL G.44/36, general view of rhabdosome (K_1) and sicula with two first thecae (K_2). **J**, **L**. *Pristiograptus dubius postfrequens* subsp. nov., Mielnik borehole, Poland; *Monograptus (Uncinatograptus) spineus–Neocolonograptus parultimus* Interzone. **J**. ZPAL G.44/37, depth 716.3 m, general view of rhabdosome (J_1) and proximal end (J_2). **L**. ZPAL G.44/38, depth 715.6 m, lateral view of young rhabdosome (L_1), and proximal end (L_2).
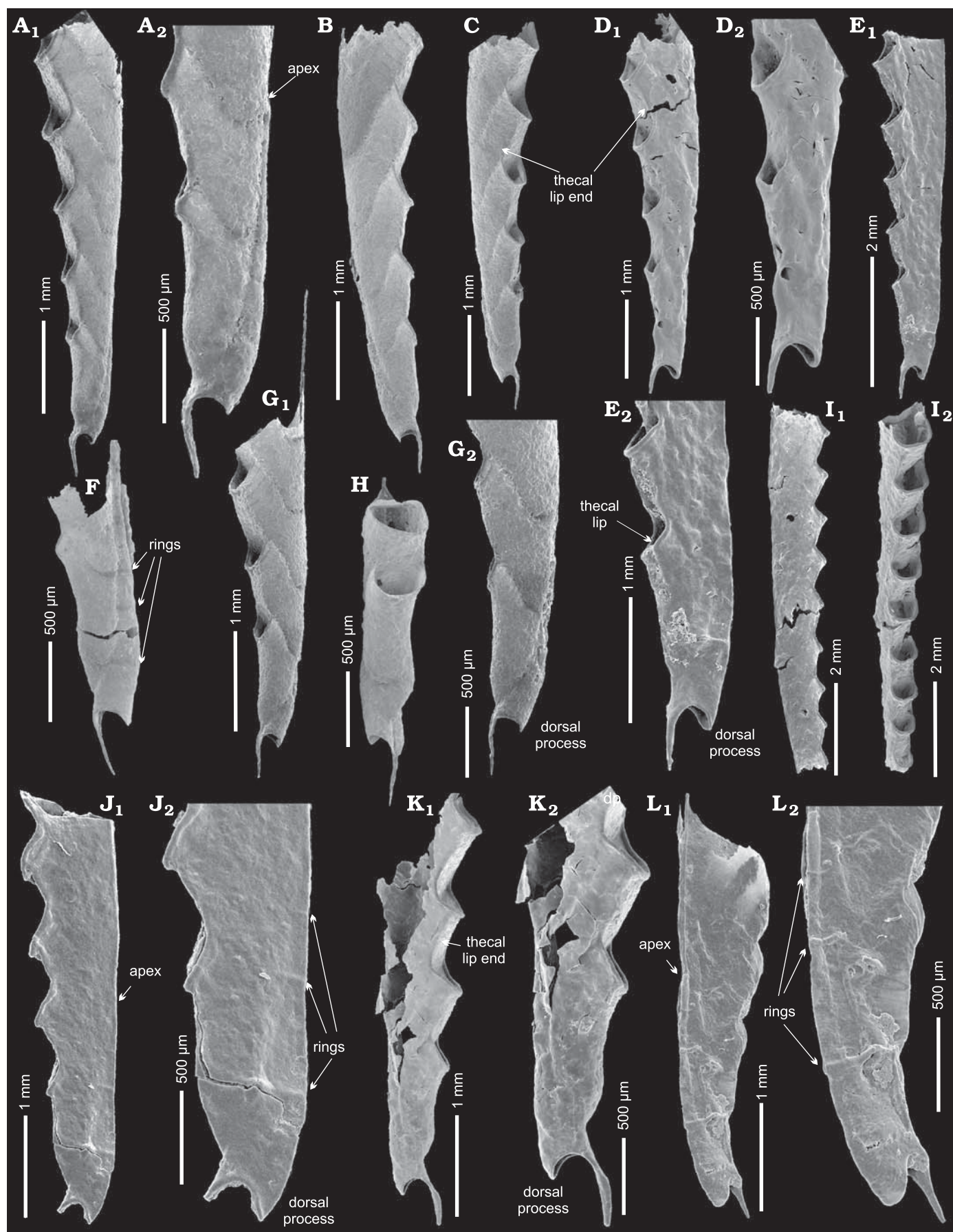
Stratigraphic and geographic range.—Wenlock *Cyrtograptus rigidus*, *Cyrtograptus perneri* biozones; Poland, Czech Republic, Italy.

Pristiograptus dubius praelodenicensis subsp. nov.

Figs. 5I, 6F, 8A, C, E.

Etymology: From Latin *prae*, before; supposedly *P. dubius praelodenicensis* is the ancestor of *P. lodenicensis*.

Holotype: ZPAL G.44/5, isolated rhabdosome with sicula and 6 thecae, Fig. 8A.

Type locality: Zawada IG-1 borehole, depth 1546.5–1552.7 m, Poland.

Type horizon: Upper Wenlock, *Cyrtograptus lundgreni* Biozone.

Material.—About 25 rhabdosomes and many fragments from Zawada IG-1 borehole (1546.5–1552.7 m), Poland.

Diagnosis.— ß angle acute. Thecal lips straight and perpendicular to the rhabdosome axis. No sicula rings.

Description.—The rhabdosome is narrow, the proximal end is slightly curved ventrally up to th^4 or th^5. L is more than 30 mm. W is 0.7 mm at th^1, 0.85 mm at th^2, 1 mm at th^3, 1.2 mm at th^4, and 1.2 mm at th^5 level. W_{max} is usually 1.5 mm. The interapertural W is 0.65 mm at th^1, 0.7 mm at th^2, 0.8.5 mm at th^3, 0.9 mm at th^4, and 1 mm at th^5. The ß angle is acute. The thecae are uniform. Thecal lips are perpendicular to the rhabdosomal axis. The th^1 L is 0.9–1 mm, W is 0.3 mm and overlaps th^2 for 1/3 to 1/2 of its length. The λ angle is 29–32°. The sicula is slightly curved ventrally, L is 1.5–2.0 mm, and W 0.25–0.3 mm at apertural level. The sicular apex is on a level between the middle and the top of th^2. No sicula rings.

Discussion.—*P. dubius praelodenicensis* subsp. nov. is similar to *P. lodenicensis* Přibyl, 1943 in having an acute to right β angle.

Stratigraphic and geographic range.—Upper Wenlock, *Cyrtograptus lundgreni* Biozone, Poland.

Pristiograptus lodenicensis Přibyl, 1943

Figs. 4B, 5H, 6G, 10.

1943 *Pristiograptus lodenicensis* sp. nov.; Přibyl 1943: 23–24, textfigs. C, D, J, K; pl. 3: 8–11.

1952 *Pristiograptus lodenicensis* Přibyl, 1943; Münch 1952: 91, pl. 20: 7.

1967 *Pristiograptus lodenicensis* Přibyl, 1943; Gailite et al. 1967: 244, text-fig. 58; pl. 29: 4, 5.

1974 *Pristiograptus lodenicensis* Přibyl, 1943; Ulst 1974: 115, pl. 13: 1, 2a, b, pl. 11: 7.

2000 *Pristiograptus lodenicensis* Přibyl, 1943; Radzevičius and Paškevičius 2000: 97–98, pl. 4: 1a–c, 2a–c, pl. 6D.

2003 *Pristiograptus lodenicensis* Přibyl, 1943; Radzevičius 2003: 10–11, figs. 11A–H, 12A–F.

2005 *Pristiograptus lodenicensis* Přibyl, 1943; Radzevičius and Paškevičius 2005: 165, pl. 2: F.

2006 *Pristiograptus lodenicensis* Přibyl, 1943; Radzevičius 2006: 337, fig. 4C–F.

Remarks.—The thecae are slightly curved, and widen towards their apertures. The ß angle is acute, and the λ angle is right. The thecal lips are symmetrically curved (Fig. 9A, E). The depressions and curvature of lips are variable in proximal and distal thecae. The lips maybe slightly or much curved, they may widen towards their ends, and may have small or large ventral incisions and curvatures close to their ends. In some specimens there are large symmetrical "stingray wing" structures located at the ends of lips (Fig. 9F). These structures may occur in a few thecae or all the thecae (Radzevičius 2006: fig. 4c–f). The thecal apertures are right angles to the rhabdosome axis. Similar thecae occur in *P. d. labiatus*, thus both forms are not typical members of *P. dubius* group. This type of theca is similar to those of *Istrograptus* Tsegelniuk, 1976 and *Neocolonograptus* Urbanek, 1997. This species is separated from the *lodenicencis* group (Radzevičius and Paškevičius 2000).

P. praelodenicensis is very similar to *P. lodenicensis* with thecae slightly curved, widening towards the aperture, which shows a small ventral depression. Thecae of *P. praelodenicensis* do not have such kind of depression.

Stratigraphic and geographic range.—Upper Wenlock *Cyrtograptus lundgreni* Biozone; Latvia, Lithuania, Poland, Czech Republic.

Pristiograptus tumescens (Wood, 1900)

Figs. 5N, 12A–F.

1916 *Monograptus tumescens* Wood, 1900; Elles and Wood 1910: 379–380, pl. 38: 12a–d.

1943b *Pristiograptus tumescens tumescens* (Wood, 1900); Přibyl 1943: 18–19.

Material.—More then 50 rhabdosomes and rhabdosomes fragments from Mielnik-1 borehole (976–896 m), Poland and Milaičiai-103 borehole (1269–1259 m), Lithuania.

Description.—The ß angle is obtuse or right. The thecal apertural lip reaches the middle part or above of the free ventral wall of the succeeding theca. The sicula has rings.

Stratigraphic and geographic range.—Ludlow *Cucullograptus hemiaversus*, *Saetograptus leintwardinensis* Biozones, East European Platform (Latvia, Lithuania, Poland), Czech Republic, Great Britain.

Fig. 12. SEM micrographs of graptolites *Pristiograptus tumescens* (Wood, 1900) and *P. dubius welchae* Rickards, 1965. **A–F**. *Pristiograptus tumescens* (Wood, 1900). **A–C**, **F**. Mielnik borehole, Poland. **A–C**. Depth 892.2 m; *Lobograptus scanicus* Biozone. **A**. ZPAL G.44/39, lateral view of rhabdosome. **B**. ZPAL G.44/40, whole rhabdosome (B_1), enlargement of th^3 lip (B_2), sicula with th^1 (B_3). **C**. ZPAL G.44/41, medial part of rhabdosome. **F**. ZPAL G.44/42, general view of rhabdosome. **D**, **E**. Milaičiai-103 borehole, Lithuania, depth 11267.5 m. **D**. VU S.M103-21X, lateral view of rhabdosome. **E**. VU S.M103-22X, lateral view of rhabdosome. **G–K**. *Pristiograptus dubius welchae* Rickards, 1965, Mielnik borehole, Poland, depth 836.6 m; *Saetograptus leintwardinensis* Biozone. **G**. ZPAL G.44/43, lateral view of rhabdosome (G_1) and sicula with th^1 (G_2). **H**. ZPAL G.44/44, young rhabdosome (H_1), sicula (H_2). **I**. ZPAL G.44/45, lateral view of rhabdosome (I_1), distal part (I_2), and aperture of sicula (I_3). **J**. ZPAL G.44/46, ventral view of distal end of rhabdosome. **K**. ZPAL G.44/47, lateral view of rhabdosome (K_1), th^3 (K_2), and sicula with th^1 (K_3).

Pristiograptus dubius welchae Rickards, 1965

Figs. 5P, 6Q, 12G–K.

1965 *Pristiograptus welchae* sp. nov.; Rickards 1965: 261, pl. 30: 6; text-fig. 2f.

Material.—About 20 rhabdosomes and rhabdosomes fragments from Mielnik-1 borehole (836.6 m), Poland.

Description.—The rhabdosome is very small, up to 5 mm long, narrow 0.7–1.2 mm, and slightly curved to the ventral side, sometimes straight. The ß angle is obtuse or right. The thecal lip is distinct, ending at the beginning of the free ventral wall of succeeding theca. The sicula has three rings.

Remark.—The *P. dubius welchae* is very similar to the Wenlock species *P. dubius parvus*, although *P. dubius parvus* does not have sicular rings.

Stratigraphic and geographic range.—*Saetograptus leintwardinensis–Neocucullograptus kozlowskii* Biozone, Poland; *Neodiversograptus nilssoni–Lobograptus scanicus* and *S. leintwardinensis* biozones of North England (Rickards 1965).

Pristiograptus dubius labiatus Urbanek, 1997

Figs. 5R, 6T, 13D–F.

1997 *Pristiograptus dubius labiatus* subsp. nov.; Urbanek 1997: 160–161, pl. 16: 1–11, text-fig. 44A–D.

Material.—20 rhabdosomes and many from Mielnik borehole (761.75–727.7 m), Poland.

Remarks.—The ß angle is acute and the thecal apertural lip is at a right angle to rhabdosomal axis. The thecal lip is distinct with an incision in its ventral side, similar to *P. lodenicensis* (Fig. 5H). The sicula has three rings.

Stratigraphic and geographic range.—*Monograptus* (*Slovinograptus*) *balticus–M.* (*Uncinatograptus*) *spineus* Biozone, Upper Ludlow, Poland.

Pristiograptus dubius postmagnus subsp. nov.

Figs. 5O, 13A–C.

Etymology: From Latin *post*, after; *magnus*, great, large.

Holotype: ZPAL G.44/48, rhabdosome with sicula and seven thecae, Fig. 13.

Type locality: Mielnik-1 borehole, depth 780.5 m, Poland.

Type horizon: Upper Ludlow, *M.* (*U.*) *acer* Biozone.

Material.—15 rhabdosomes and many fragments from Mielnik borehole (780.5 m), Poland.

Diagnosis.—Distinct thecal lips connecting with those of the succeeding thecae. Sicula with three rings.

Description.—The rhabdosome is robust and the proximal end is slightly curved ventrally up to th[5]. The longest rhabdosome L is more than 15 mm long. The rhabdosome W from 0.65 mm at th[1], to 0.8 mm at th[2], 9 mm at th[3], 1 mm at th[4], 1.1 mm at th[5], 1.2 mm at th[6]. The W_{max} is 1.3 mm. The interapertural width is 0.55 mm at th[1], 0.65 mm at th[2], 0.75 mm at th[3], 0.8 mm at th[4], and 0.9 mm at th[5]. There are 10–11 thecae in 10 mm. The ß angle is obtuse. Th[1] is 1mm long and 0.3

mm wide. The free part of each theca is half of its whole length. The thecal lips are distinct and connected with the lip of the succeeding thecae (Figs. 5O, 13A–C). The lip connection is particularly well developed in the medial and distal parts of the rhabdosome. The λ angle is 30°. The sicula is short and narrow. Its L is 1.8 mm and apertural W is 0.3 mm. The apex of the sicula reaches the base of th[3]. The sicula has three rings. The virgella is short, up to 0.5 mm.

Remarks.—*P. dubius postmagnus* subsp. nov. is similar to *P. dubius magnus* subsp. nov., in the connection of the lip with the succeeding thecal lip. In contrast to *P. dubius magnus* subsp. nov. it has sicular rings.

Stratigraphic and geographic range.—*M.* (*U.*) *acer* Biozone, Upper Ludlow, Poland.

Pristiograptus dubius shearsbyi Rickards and Wright, 1999

Fig. 11D, E, I, K.

1999 *Pristiograptus dubius shearsbyi* sp. nov.; Rickards and Wright 1999: 194, figs. 3J–P, 11A, B, 13B, E.

Material.—10 rhabdosomes, Mielnik-1 borehole (688.8 m), Poland.

Description.—The rhabdosome is narrow and proximally is either slightly curved ventrally or straight. The ß angle is obtuse. The thecal lips are distinct, not extending onto the free ventral wall of the succeeding thecae. The λ angle is 25°. The sicula L is 2 mm and W is 0.3 mm. The sicula has three rings.

Stratigraphic and geographic range.—*M.* (*U.*) *spineus–Neocolonograptus parultimus* Interzone, Australia and Poland.

Conclusions

The detailed investigation in SEM of three-dimensionally preserved Silurian graptolites chemically isolated from host rocks provides numerous new morphological information. This throws a new light on pattern of evolution of the longest ranging monograptid *Pristiograptus dubius* (Suess, 1851) and a number of closely related taxa, forming the *P. dubius* group taxa. The studied fauna comes mainly from boreholes of Poland and Lithuania which permits to trace their changes in a stratigraphic interval from *Monograptus riccartonensis* to *Neocolonograptus ultimus* Biozone.

The *P. dubius* group taxa is divided into two morphological groups differing in the angle between the thecal lip and the succeeding thecal wall, namely into the group with obtuse and acute angle. The *P. dubius* stem lineage taxa forming an unbroken sequence of closely related subspecies and displaying only minor morphological changes through time all belong to the first and main morphological group. These taxa represent a graphic example of phyletic evolution. The second morphological group is composed of iterative *P.*
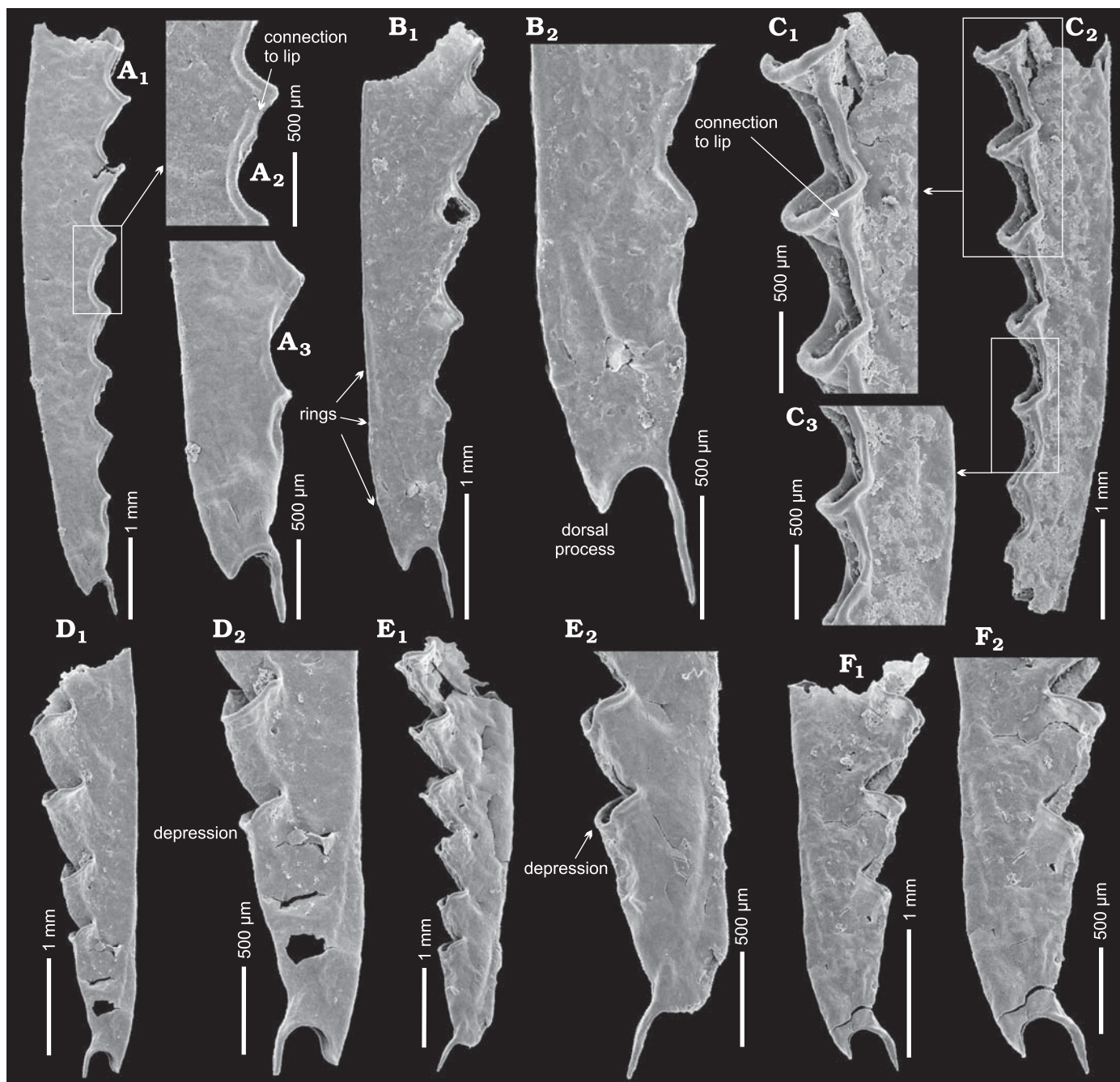
Fig. 13. SEM micrographs of Ludfordian graptolites *Pristiograptus dubius postmagnus* subsp. nov. and *Pristiograptus dubius labiatus* Urbanek, 1997. **A–C**. *Pristiograptus dubius postmagnus* subsp. nov., Mielnik-1 borehole, Poland, depth 780.5 m; *Monograptus (Uncinatograptus) acer* Biozone. **A**. ZPAL G.44/48, lateral view of rhabdosome (A_1), the thecal lip with connection to the succeeding theca (A_2), and proximal end of rhabdosome (A_3). **B**. ZPAL G.44/49, lateral view of rhabdosome sicula with rings (B_1) and proximal end of rhabdosome (B_2). **C**. ZPAL G.44/50, medial part of rhabdosome (C_2), enlargements showing connections to the succeeding thecae (C_1, C_3). **D–F**. *Pristiograptus dubius labiatus* Urbanek, 1997, Mielnik-1 borehole, Poland, depth 753.3 m; *Monograptus (Uncinatograptus) spineus–Neocolonograptus parultimus* Interzone. **D**. ZPAL G.44/51, general view of rhabdosome (D_1), sicula with two first thecae and depression on th[1] lip (D_2). **E**. ZPAL G.44/52, lateral view of rhabdosome (E_1) and proximal end of rhabdosome (E_2). **F**. ZPAL G.44/53, lateral view of rhabdosome (F_1) enlargement of proximal end (F_2).

dubius group taxa derived from the stem lineage by means of iterative speciation.

Examined phylogenetic relationship between fifteen species and subspecies derived from *P. dubius* reveals many examples of heterochronic parallelism which may indicate the preservation of evolutionary potential capable of multiple production of similar forms. The taxa give the stem lineage continuing at successive stratigraphic levels during the extremely long time span, approximately 18 Ma.

Significance of the presence of dwarfed form *P. dubius parvus*, the only monograptid taxon to appear immediately after the most severe extinction event in graptolite history,

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the *C. lundgreni* Event is discussed. We advanced the hypothesis that this taxon in question appeared as result of the so-called Lilliput effect (defined by Urbanek 1993), and probably represents a geographically vicarious form of *P. dubius* with the normal rhabdosome size. Thus we consider *P. dubius parvus* provisionally as a link in the evolution of the stem lineage taxa.

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