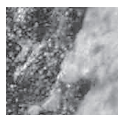


Lower Homerian (Silurian) *Pristiograptus* from the Zdanów section, Bardo Mountains (Sudetes, Poland) and their palaeobiogeographical implications

SIGITAS RADZEVIČIUS, PAWEŁ RACZYŃSKI & MISHA WHITTINGHAM



Pristiograptus dubius pseudodubius and *Pristiograptus lodenicensis* were collected from outcrops of black pelagic shales of the Zdanów section of the Bardo Mountains (Sudetes, Poland). The species are easily distinguished from one another in that *P. lodenicensis* has distinct lobate processes on its thecae, whereas those of *P. d. pseudodubius* are comparatively unornamented. Our findings indicate that the age of the Lower Graptolitic Shales in the Zdanów is the middle part of the *C. lundgreni* graptolite Biozone (lower Homerian, upper Wenlock). The presence of *P. d. pseudodubius* at this site adds another locality to its global range, while the presence and abundance of *P. lodenicensis* further indicates the restriction of the latter species to the Rheic palaeo-ocean. • Key words: Homerian, Silurian, Bardo Mountains, Sudetes, Poland, *Pristiograptus*, Graptoloidea.

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The genus *Pristiograptus* (Graptoloidea) has been recorded from the Llandovery to the upper Přídolí, but is most common in the Wenlock–Ludlow interval and is one of the longest ranging monograptid genera. The genus is characterized by cylindrical thecae without distinct apertural processes and a slightly curved or straight, simple rhabdosome (after Urbanek 1958). This conservative monograptid group survived all of the Wenlock–Ludlow biotic crises and radiated and prospered while populations of other monograptids decreased. After those biotic crises new genera of monograptids developed from *Pristiograptus* via speciation and adaptive radiation. The extinction of the *Pristiograptus* lineage was the penultimate “nail in the coffin” of monograptid evolution.

Jaekel (1889) erected the genus *Pristiograptus*. According to him, the rhabdosome of *Pristiograptus* is unbranched, is straight or a little curved, the thecae are cylindrical, inclined to rhabdosome axis, the thecal mouth opening free (the mouths of the thecae are not covered by any lid or hood) and, if present, apertural processes stand as spines at the lower edge of the mouth. Today, some of Jaekel’s *Pristiograptus* taxa are assigned to other genera [e.g. *Testograptus testis* (Barrande)]. Přibyl (1943) revised *Pristiograptus* based on material from Czechia and lit-

erature data, producing the first catalogue of the genus. Münch (1952) assembled his own summary of known graptolites, including *Pristiograptus*, and presented short descriptions and illustrations of all known taxa. This was later followed up by phylogenetic studies of *Pristiograptus* and related genera presented by Rickards & Wright (2003), Radzevičius (2003), Radzevičius *et al.* (2008), Urbanek *et al.* (2012) and Whittingham *et al.* (2020). In short, the taxa of *Pristiograptus* genera are well known and very important for graptolite evolution and palaeogeography.

Only one problematical species, *Pristiograptus frequens* Jaekel (described as having thecae of *colonus* type, as opposed to the unornamented thecae typical of *P. frequens*), has been recorded from the Zdanów outcrop (Malinowska 1955), although graptolites are common there. Surprisingly, there have been very few graptolite studies based on material from the Zdanów outcrop, despite graptolites from the lower Silurian to the lower Devonian in this section being very common in this section. The Zdanów outcrop is thus very important in the Sudetes region because of its considerable stratigraphical extent.

In this work two species of *Pristiograptus* are documented for the first time from the Sudetes Mountains. We

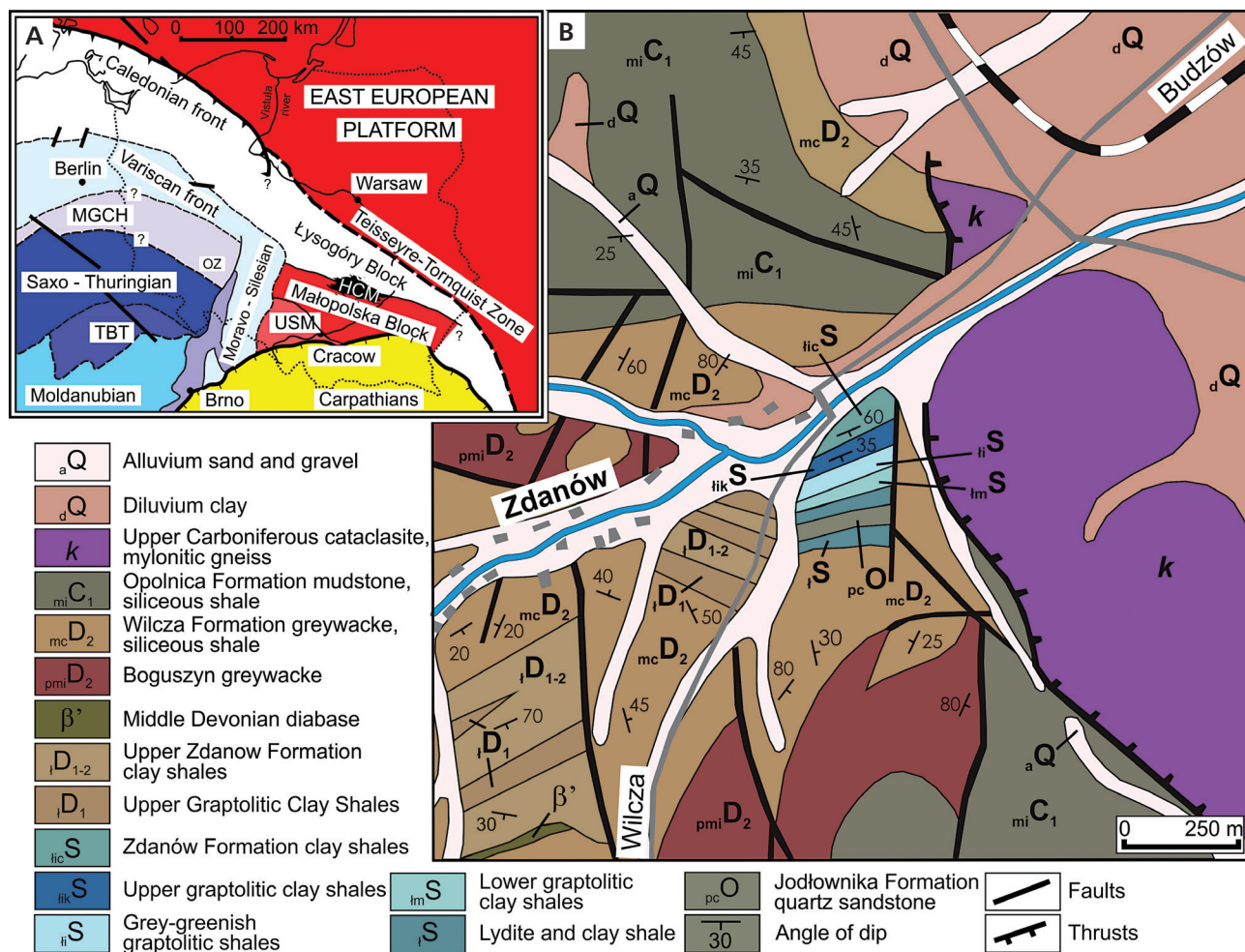


Figure 1. A – simplified structural map of central Europe (Belka *et al.* 2002). Abbreviations: HCM – The Holy Cross Mountains; MGCH – Mid German Crystalline High; OZ – Odra Zone; TBT – Tepla-Barrandian Terrane; USM – Upper Silesian Massif. • B – geological map of the Bardo Mountains with the Zdanów outcrop location (Oberc *et al.* 1994).

present detailed descriptions of flattened pristiograptids that enable a better understanding of the morphology of the taxa and expand our knowledge of the palaeogeographical range of these species of *Pristiograptus*.

Geological setting and material

The Bardo Mountains (Góry Bardzkie) are located in the Central Sudetes (Żelazniewicz & Aleksandrowski 2008) and assigned to the European Variscides Belt, which runs from Central Poland in the East to southern Portugal in the West (Mazur *et al.* 2006). The Central European Variscides Belt is subdivided into several zones (Fig. 1A). The Silurian sections of the Bardo Mountains are assigned to the Saxothuringian zone (Porębska & Sawłowicz 1997), part of the Armorican Terrane Assemblage (Franke 2000). The Armorican Terrane Assemblage is considered

to have been located in the southern part of the Rheic Ocean during the Silurian (Winchester *et al.* 2002).

There are several small Silurian outcrops in the Bardo Mountains. The most complete Silurian geological section is the Zdanów outcrop which is located on the road from Budzów to Wilcza (Fig. 1B) near Zdanów village (N 50° 33' 43.2", E 16° 39' 55.0").

Graptolites from the Zdanów outcrop have been known since the 19th century. Looking for resources of coal, Krug von Nidda (1853) described black shales with graptolites in the Zdanów area and documented *Graptolithus priodon* [= *Monograptus priodon* (Bronn)]. Frech (1897) described the new genus *Monoclimacis* and several other graptolites from Zdanów (in German Herzogswalde). Through graptolite biostratigraphy, Frech (1897) determined that the rocks of the Zdanów outcrop belonged to the Wenlock and Ludlow series. Dathe (1904) supposed that part of the Zdanów (the Zdanów

beds) outcrop was early Devonian in age. The first Silurian graptolite zonal scale for the Bardo Mountains was given by Dahlgrün & Finckh (1924). Hundt (1924) also confirmed that Ludlow age rocks crop out in Zdanów. Malinowska (1955) later investigated graptolites from the Llandovery–Ludlow interval in the Zdanów outcrop. She described more than 50 graptolite species and provided a detailed graptolite biozonation. Jaeger (1959) described the new graptolite species *Monograptus silesicus* and *Monograptus praehercynicus* based on material from Zdanów. Teller (1959, 1960) investigated graptolites from the Silurian–Devonian boundary interval. The graptolite stratigraphy, especially that of the uppermost Silurian and lowermost Devonian, was investigated by Porębska (1980a, 1982; Porębska & Sawłowicz 1997), and a short report on the local graptolites was given by Kurałowicz (1976).

The thickness of Silurian strata is about 50 m in Zdanów (Porębska 1980b, Wyżga 1987) and represents pelagic sediments. These are distinguished as the Lower Graptolitic Shales, the Green Shales and the Upper Graptolitic Shales (Wyżga 1987). The Silurian shales overlie the light-coloured sandstone and clay shales of the Upper Ordovician Jodłownik Beds (Chorowska & Oberc 1980). The lithology of all units is represented by lydites (radiolarian cherts), clay shales with tephra interbeds, and phosphatic nodules (Porębska & Koszowska 2001). The Lower Graptolitic Shales span the *Parakidograptus acuminatus*–*Lobograptus scanicus* biozones, the Green Shales the *Saetograptus leintwardinensis*–*Neocolonograptus ultimus* biozones, and the Upper Graptolitic Shales the *Monograptus transgrediens*–*Monograptus craigensis* biozones (Porębska & Sawłowicz 1997).

Our new material comes from the Lower Graptolitic Shales (Fig. 2). The graptolite finds from the *lundgreni* Biozone are solely in our collection due to limited collecting. *Monograptus flemingii* (Salter) (Fig. 3A) and *Testograptus testis* (Barrande) (Fig. 3B) have been identified together with *Pristiograptus dubius pseudodubius* (Bouček) and *Pristiograptus lodenicensis* Přibyl. *Testograptus testis* indicates the mid–upper *lundgreni* Biozone of the lower Homeric. *Monograptus flemingii* ranges from the *riccartonensis* Biozone to the topmost *lundgreni* Biozone and is a typical Wenlock monograptid.

Systematic palaeontology

The classification and morphological terminology of pristiograptids is after Urbanek *et al.* (2012) and two

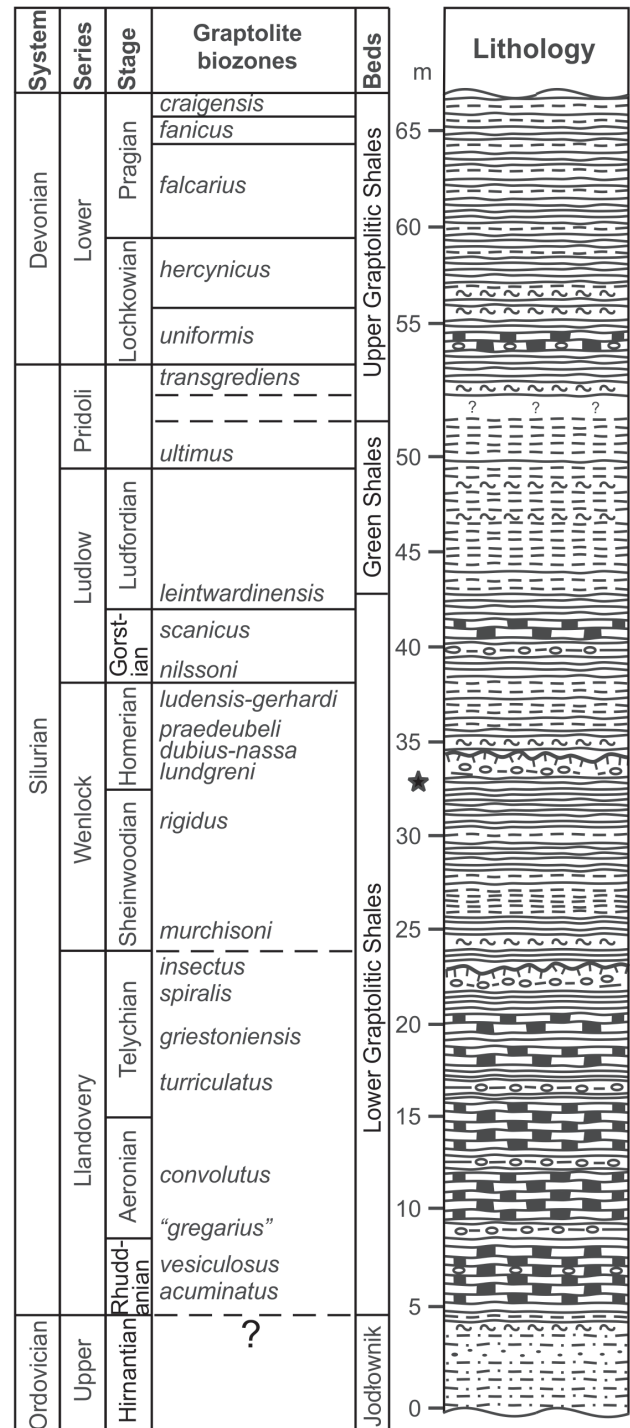


Figure 2. Silurian cross section of the Zdanów outcrop (Porębska & Koszowska 2001). The star marks the approximate sampling position.

thecae repeat distance (2TRD after Howe 1983). Material is stored at the Department of Geology and Mineralogy of Vilnius University.

Order Graptoloidea Lapworth, 1873
Family Monograptidae Lapworth, 1873
Subfamily Pristiograptinae Gürich, 1908

Genus *Pristiograptus* Jaekel, 1889

Type species. – *Pristiograptus frequens* Jaekel, 1889, from erratic boulders from Świebodzice (Freiburg Schlesien) and Nowa Sol (Neusalz on Oder) Lower Silesia (Poland), *Lobograptus scanicus* Biozone, lower Ludlow.

Diagnosis. – Rhabdosome variable in length, straight or gently curved. Thecae are straight, simple cylindrical, generally uniform throughout the rhabdosome, varying in degrees of inclination to the rhabdosome axis and amount of overlap. Aperture is without any distinct structures. Ventral wall quite straight with a clear thecal apertural lip.

Remarks. – Widely used diagnosis of *Pristiograptus* genus is incomplete and mostly corresponding to *Pristiograptus* of Wenlock–Přídolí interval. There are some strongly dorsal or ventral curved *Pristiograptus* species in the upper Aeronian and lower Telychian (Llandovery). The dorsally curved rhabdosome have *P. xiushanensis* NIGP (Loydell *et al.* 2015), *P. renaudi* (Philippot) (Štorch & Massa 2006). Loydell & Walasek (2020) describe *Pristiograptus paradoxus* with ventrally curved rhabdosome. *Pristiograptus* from Llandovery needed revision and perhaps will be placed in a separate genus in the future or the diagnosis of *Pristiograptus* will need to be revised. However, that problem will not be discussed herein.

Pristiograptus dubius pseudodubius (Bouček, 1932)

Figure 3C–E

- 1932 *Monograptus pseudodubius*; Bouček, pp. 1, 2, fig. 2e, f, pl. 8, fig. 3.
- 1943 *Pristiograptus pseudodubius* (Bouček). – Přibyl, pp. 8, 9, pl. 1, figs 1, 3.
- 1952 *Pristiograptus pseudodubius* (Bouček). – Münch, p. 86, pl. 18, fig. 7.
- 1965 *Pristiograptus pseudodubius* (Bouček). – Jaworowski, pl. 1, fig. 12, text-fig. 9.
- 1965 *Pristiograptus pseudodubius* (Bouček). – Obut *et al.*, p. 72, pl. 13, fig. 2.
- 1965 *Pristiograptus pseudodubius* (Bouček). – Rickards, p. 260, pl. 29, fig. 10, text-fig. 2i.
- 1967 *Pristiograptus pseudodubius* (Bouček). – Gailite *et al.*, pp. 243, 244, pl. 18, figs 8, 9, text-fig. 57.

- 1974 *Pristiograptus pseudodubius* (Bouček). – Ulst, pp. 108, 109, pl. 11, fig. 1, pl. 12, figs 1, 2.
- 1999 *Pristiograptus dubius* cf. *pseudodubius* (Bouček). – Zalasiewicz & Williams, fig. 9m.
- 2000 *Pristiograptus pseudodubius* (Bouček). – Radzevičius & Paškevičius, pp. 92–94, pl. 2, fig. 1.
- 2008 *Pristiograptus pseudodubius* (Bouček). – Sachanski *et al.*, p. 389, fig. 4.7.
- 2012 *Pristiograptus dubius pseudodubius* (Bouček). – Sachanski *et al.*, p. 872, pl. 2, fig. e.
- 2012 *Pristiograptus dubius pseudodubius* (Bouček). – Urbanek *et al.*, p. 600, figs 5b, 6a, 7c, d.

Material. – Four asymmetrical flattened rhabdosomes from the Zdanów outcrop, Bardo Mountains, Lower Silesia, Poland, the *lundgreni* Biozone, the Lower Graptolitic Shales, Homerian.

Description. – Rhabdosome is narrow and either straight or slightly ventrally curved. The width (W) of the rhabdosome gradually increases from 0.7 mm at th1, 0.75 mm at th2, 0.8 mm at th3, 1 mm at th4, 1.1 mm at th5. Value of W_{max} is 1.5 mm. The interapertural width is 0.55 mm at th1, 0.65 mm at th2, 0.75 mm at th3, 0.85 mm at th4, 0.9 mm at th5. The 2TRD measurements are 1.6–1.9 mm (th2), 1.7–2 mm (th3), 1.6–2 mm (th4), 1.9–2 mm (th5) and 2–2.5 mm in medially and distally. Thecae are cylindrical; apertures possess a pronounced lip which extends half way up the outer wall of the succeeding theca. The angle (β angle) between the thecal apertural lip and the succeeding metathecal wall is obtuse (Fig. 3D₂). No sicula are adequately preserved for measurement in any of the specimens.

Remarks. – *Pristiograptus d. pseudodubius* can be easily mistaken for other subspecies of *P. dubius*. Width of *P. d. dubius* (Suess) is 0.8 mm at th1, 1.0 mm at th2, 1.1 mm at th3, 1.25 mm at th4 and it is slightly greater than in *P. d. pseudodubius*. *Pristiograptus d. parvus* is smaller than *P. d. pseudodubius*. The rhabdosome of *P. d. parvus* widens from 0.6 mm at th1, 0.7 mm at th2, 0.8 mm at th3, 0.85 mm at th4. The rhabdosome of *P. d. parvus* is reduced in size as a result of so-called Lilliput effect (Urbanek *et al.* 2012).

The significant differences of *P. dubius* stem lineage subspecies are in the extension of the thecal apertural lip. The species sits directly above *P. d. dubius* stratigraphically, differing in morphology by the extension of the thecal apertural lip midway up the succeeding theca (Fig. 3C–E). *Pristiograptus d. dubius* has a thecal apertural lip ending at the beginning of the succeeding metathecal wall, and has a broader rhabdosome. The stratigraphically succeeding *P. d. parvus* Ulst bears even closer similarity to *P. d. pseudodubius*, also having a slender rhabdosome,

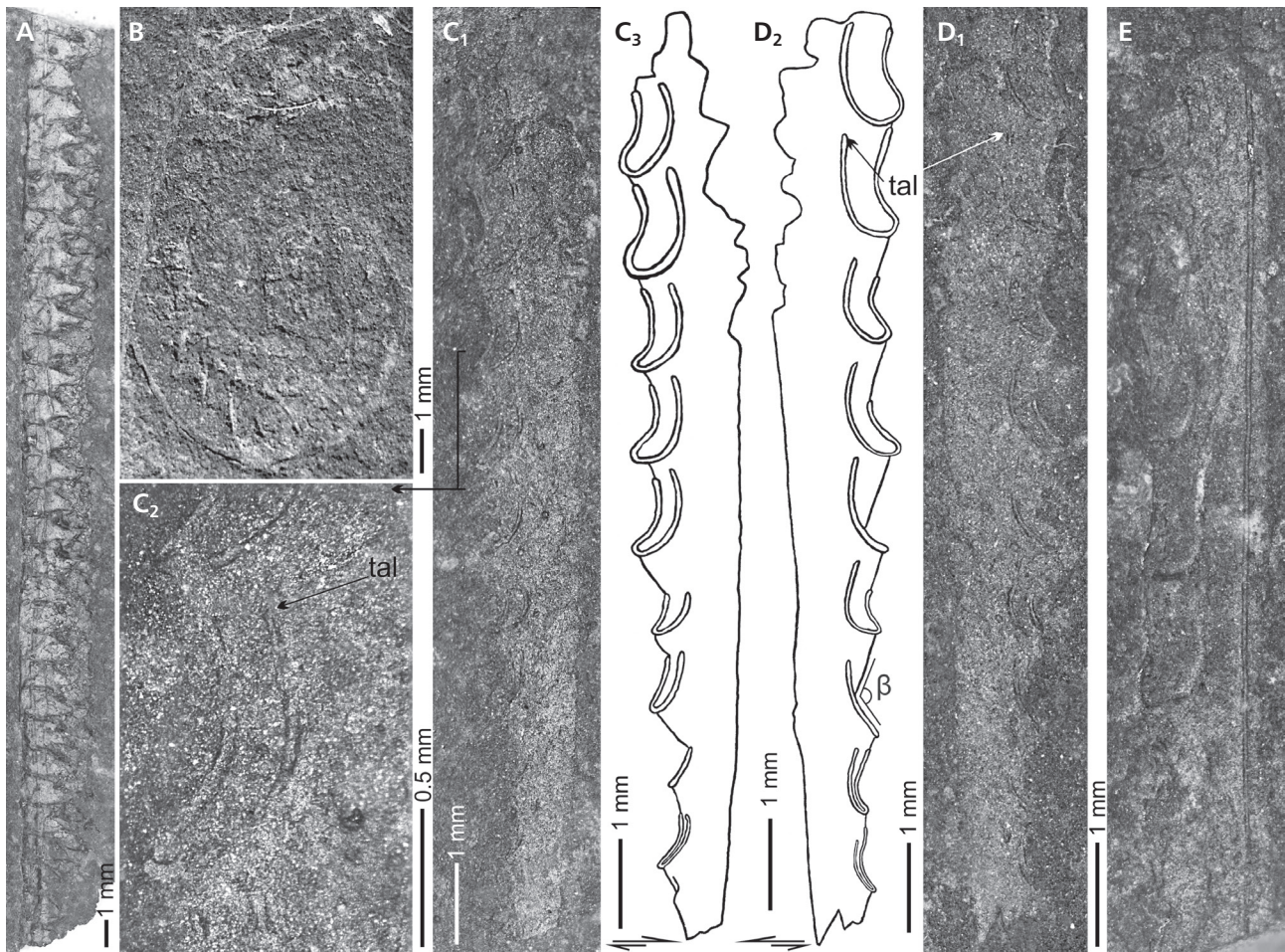


Figure 3. Graptolites from the Zdanów outcrop, the Bardo Mountains, Sudetes, South West Poland, Lower Graptolitic Shales, *lundgreni* Biozone, Homerian. • A – *Monograptus flemingii* (Salter), no. ZDW-A3-0055. • B – *Testograptus testis* (Barrande), no. ZDW-A3-0029. • C–E – *Pristiograptus dubius pseudodubius* (Bouček); C – no. ZDW-A3-07; C₁ – general view of rhabdosome; C₂ – thecae apertural lip (tal); C₃ – interpretive drawing of specimen; D – no. ZDW-A3-0020; D₁ – general view of rhabdosome; D₂ – interpretive drawing of specimen; E – medial part of rhabdosome. Abbreviation: tal – thecal apertural lip.

though generally even more so than *P. d. pseudodubius*. *P. d. parvus* lacks thecal lips extending onto the wall of the succeeding theca, further distinguishing the species. Despite these differences, the two have been treated as synonymous in the past (e.g. Rickards & Wright 2003).

The close morphological and stratigraphical relationship between the three above-mentioned taxa has resulted in the inference of their inclusion in the central *P. dubius* stem lineage (Urbanek *et al.* 2012, Whittingham *et al.* 2020). The inclusion of *P. d. dubius*, *P. d. pseudodubius* and *P. d. parvus* with that anagenic stem lineage supports their status as subspecies of *Pristiograptus dubius* under a lineage species concept (*sensu* de Quieroz 1998, 2007), as outlined and recommended by Whittingham *et al.* (2020).

Occurrence. – *Monograptus belophorus*–*Cyrtograptus lundgreni* biozones of the Wenlock. Range of geographical

distribution is broad, spanning Arctic Canada (Lenz & Kozłowska-Dawidziuk 2001, Lenz *et al.* 2012), Australia (Rickards & Sandford 1998), Czech Republic (Bouček 1932, Přibyl 1943), England (Rickards 1965), Ireland (Rickards *et al.* 1973, Doran 1974), Latvia (Ulst 1974), Libya (Štorch & Massa 2003), Lithuania (Radzevičius & Paškevičius 2000), Poland (Jaworowski 1965, Urbanek *et al.* 2012), Romania (Iordan 1992, Colțoi *et al.* 2016), Sardinia (Italy) (Štorch & Piras 2009) Serbia (Krstić *et al.* 2005), South China (Xu 1984), Turkey (Sachanski *et al.* 2008, 2012), Vietnam (Thanh *et al.* 2013) and Wales (Warren *et al.* 1984).

***Pristiograptus lodenicensis* Přibyl, 1943**

Figure 4

1943 *Pristiograptus lodenicensis*; Přibyl, pp. 23, 24, pl. 3, figs 8–11, text-figs c, d, j, k.

- 1952 *Pristiograptus lodenicensis* Přibyl. – Münch, p. 91, pl. 20, fig. 7.
- 1965 *Pristiograptus lodenicensis* Přibyl. – Jaworowski, pp. 522, 523, pl. 1, fig. 10, text-fig. 13.
- 1967 *Pristiograptus lodenicensis* Přibyl. – Gailite *et al.* p. 244, pl. 29, figs 4, 5, text-fig. 58.
- 1974 *Pristiograptus lodenicensis* Přibyl. – Ulst, p. 115, pl. 11, fig. 7, pl. 13, figs 1, 2.
- 2000 *Pristiograptus lodenicensis* Přibyl. – Radzevičius & Paškevičius, pp. 97, 98, pl. 4, fig. 1, 2, pl. 6d.
- 2003 *Pristiograptus lodenicensis* Přibyl. – Radzevičius, pp. 10, 11, figs 11a–h, 12a–f.
- 2005 *Pristiograptus lodenicensis* Přibyl. – Radzevičius & Paškevičius, p. 165, pl. 2, fig. f.
- 2006 *Pristiograptus lodenicensis* Přibyl. – Radzevičius, p. 337, fig. 4c–f.
- 2012 *Pristiograptus lodenicensis* Přibyl. – Urbanek *et al.* p. 606, figs 4b, 5h, 6g, 10.

Material. – More than ten flattened rhabdosomes, of proximal and medial parts, from the Zdanów outcrop, Bardo Mountains, Lower Silesia, Poland, the *lundgreni* Biozone, the Lower Graptolitic Shales, Homerian.

Description. – Rhabdosome is straight and broad. The width of the rhabdosome gradually increases from 0.75 mm at th1, 0.8 mm at th2, 0.95 mm at th3, 1.1 mm at th4, 1.25 mm at th5. Value of W_{max} is 1.8 mm. The interapertural width is 0.5 mm at th1, 0.6 mm at th2, 0.7 mm at th3, 0.8 mm at th4, 0.85 mm at th5, with W_{max} being 1.5 mm. The 2TRD measurements are 1.0–1.3 mm (th2), 1.1–1.4 mm (th3), 1.4–1.5 mm (th4), 1.4–1.5 mm (th5) and 1.7–2.0 mm in medially and distally. The β angle between the thecal apertural lips is right or acute (Fig. 4). The thecal apertural lip is narrow with symmetrical lateral elevations (e.g. Fig. 4C₁, F) or “manta ray wings” of cortical tissue and ventral incision (e.g. Fig. 4F). The development of the lateral elevations increases with astogeny. The sicula is ventrally curved, and bears a short virgella. The length of the sicula is 1.3 mm. The sicula apex reaches the aperture of the second theca.

Remarks. – These traits make *P. lodenicensis* easily identifiable, particularly in the *lundgreni* Biozone, and allowed us to place the previously unassigned *Pristiograptus* sp. 1 of Holland *et al.* (1969) in *P. lodenicensis* as the morphological characters, particularly those of thecal width, β angle, and apertural shape, all fit comfortably into the range of morphology seen in *P. lodenicensis* elsewhere (e.g. Urbanek *et al.* 2012).

The lateral elevations on the thecae of *P. lodenicensis* make this species easily distinguishable from other monograptids that occur in the *C. lundgreni* Biozone. Within this biozone *P. praelodenicensis* Urbanek *et al.*

from Poland bears closest resemblance to *P. lodenicensis*. It also possesses a right or acute β angle. However, *P. praelodenicensis* lacks thecal lateral elevations and has a narrower rhabdosome. Width of *P. praelodenicensis* is 0.7 mm at th1, 0.85 mm at th2, 1.0 mm at th3, 1.2 mm at th4. The similarity between *P. lodenicensis* and *P. praelodenicensis* caused Urbanek *et al.* (2012) to treat the latter as an ancestor taxon to the former, with *P. lodenicensis* speciating shortly after the origin of *P. praelodenicensis*.

The bilateral processes are more commonly found on the thecae of later Silurian monograptids, appearing with varying exaggeration in *Colonograptus*, *Saetograptus* and *Pristiograptus labiatus* Urbanek. In particular, the similarity between *P. lodenicensis* and *P. labiatus* has been used as an example of Rickards & Wright’s (2003) iterative speciation in the *Pristiograptus dubius* stem lineage (Urbanek *et al.* 2012). The possible origination of each of these lobate taxa from a central stem appears to challenge the notion of morphospace “progress” in graptolites put forth by Pearson (1998), at least in the case of the *P. dubius* stem lineage.

Also of interest in the morphology of *P. lodenicensis* is the shift seen in thecal morphology with progressing astogeny. This is a pattern not seen in other species of *Pristiograptus*, instead being more diagnostic of the thecae of *Colonograptus colonus* (Barrande) and *Saetograptus chimaera* (Barrande). The patterns seen herein are exemplary of the morphogenic gradients outlined in Urbanek & Uchmanski (1990) and Urbanek (2003). This would indicate that the same process may be at work in *P. lodenicensis*, with a diluting morphogen resulting in two separate astogenetic phases in the species.

Occurrence. – *Cyrtograptus lundgreni* Biozone of the lower Homerian, upper Wenlock. Ulst (1988) proposed distinguishing a *P. lodenicensis* Subzone in the middle part of *T. testis* Biozone (= middle part of *C. lundgreni* Biozone). *Pristiograptus lodenicensis* is known from Latvia (Gailite *et al.* 1967, Ulst 1974), Lithuania (Paškevičius 1983, Radzevičius & Paškevičius 2005), the Polish part of the East Europe platform (Jaworowski 1965, Urbanek *et al.* 2012), the Polish part of the Sudetes Mountains (this paper), Thuringia (Jaeger 1959, 1991), Czech Republic (Přibyl 1943) and England (Holland *et al.* 1969) and Wales (Warren *et al.* 1984).

Palaeobiogeography

The long-ranging *P. d. pseudodubius* had a particularly widespread distribution during the middle Wenlock (Fig. 5). It occurs in Latvia (Ulst 1974), Lithuania (Radzevičius & Paškevičius 2000) and northeastern Poland

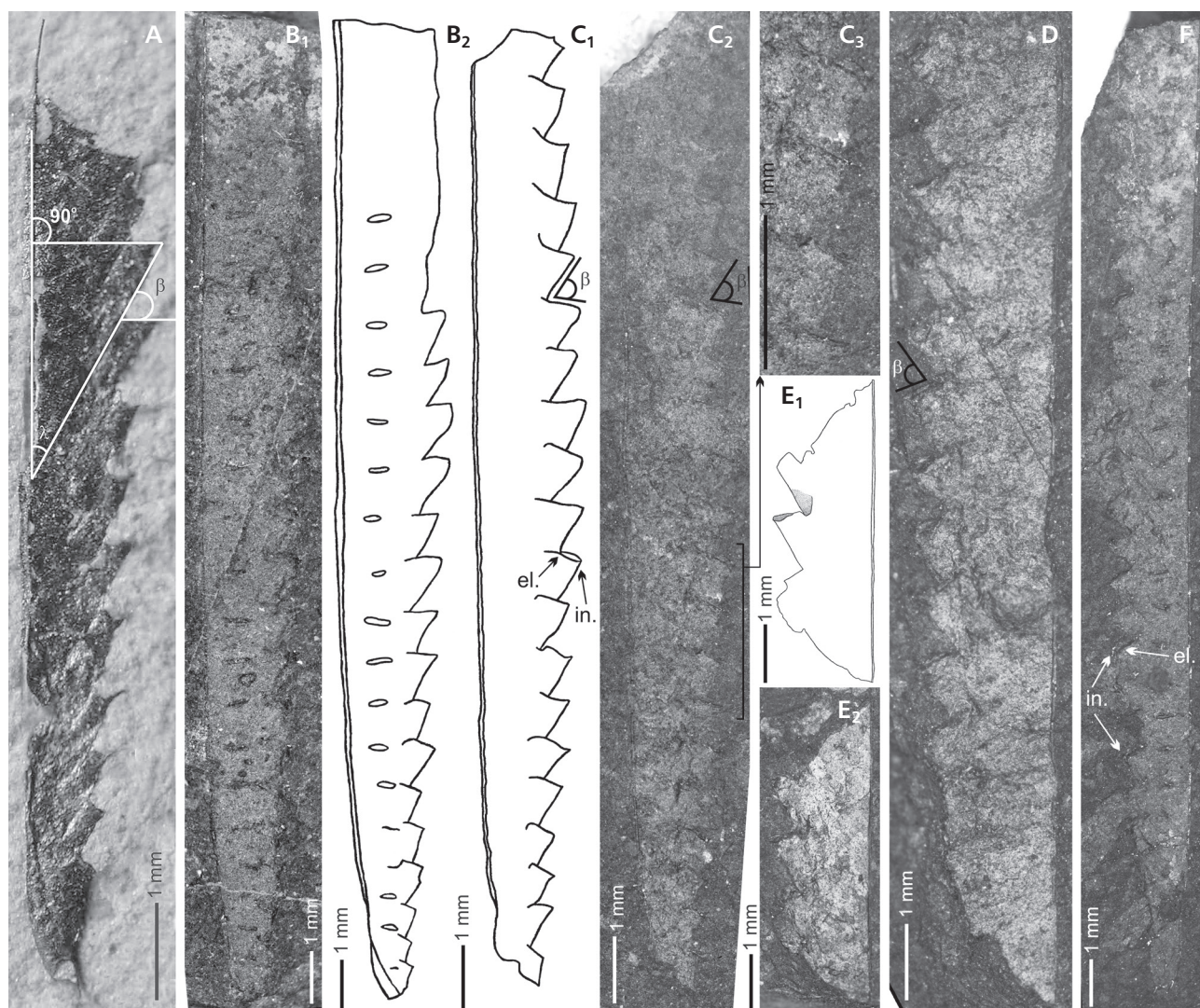


Figure 4. *Pristiograptus lodenicensis* Přibyl; A – no. VU-813 with the main morphological elements, Likėnai-396 borehole, Lithuania, depth 589.5 m, *lundgreni* Biozone, Riga Formation, Homeric; B – no. ZDW-A3-0030c, B₁ – general view of rhabdosome, B₂ – interpretive drawing of specimen; C – no. ZDW-A3-0053d, C₁ – interpretive drawing of specimen, C₂ – general view of rhabdosome, C₃ – the form of thecal apertural lips; D – no. ZDW-A3-0048, medial part of rhabdosome; E – no. ZDW-A3-0022b, E₁ – interpretive drawing of specimen, E₂ – general view of rhabdosome; F – no. ZDW-A3-0043. Abbreviations: el. – lateral elevations; in. – incision.

(Jaworowski 1965, Urbanek *et al.* 2012) on the east part of the palaeocontinent Baltica and is also known from Bornholm (Bjerreskov & Jørgensen 1983), another locality linked to Baltica. The species is documented from Northern England (Rickards 1965) and Denbighshire north-east Wales (Warren *et al.* 1984) part of the palaeocontinent Avalonia. There are also findings of *P. d. pseudodubius* near Balbriggan (Rickards *et al.* 1973) and Hollyford Slieve Phelim (Doran 1974) in Ireland. Both localities are a part of the Leinster Terrane (Chew & Stillman 2009) and linked to the Avalonian side of the Iapetus Ocean (Cocks *et al.* 2003).

Pristiograptus d. pseudodubius is known from Czechia, often referred to the Perunica Terrane (Bouček 1932, Přibyl

1943), the Bardo Mountains part of the Saxo-Thuringia Terrane (this paper) and from Sardinia (Štorch & Piras 2009), which was a part of the Iberia massif during the Silurian (Torsvik & Cocks 2016). However, the Perunica and Saxo-Thuringia terranes, as well as Sardinia, are the part of Armorican terrane assemblage (Servais & Sintubin 2009) which was located near Central Gondwana (Torsvik & Cocks 2011) on the opposite side of the Rheic Palaeo-ocean with respect to Baltica during the Wenlock (Fig. 5). *Pristiograptus d. pseudodubius* is found in Romania (Iordan 1992, Colțoi *et al.* 2016) and Serbia (Krstić *et al.* 2005), localities in the Moesia Terrane (Torsvik & Cocks 2004). The Moesia Terrane is located between the Saxo-Thuringian Terrane and Moesia, Istanbul, Pontides (Ruban

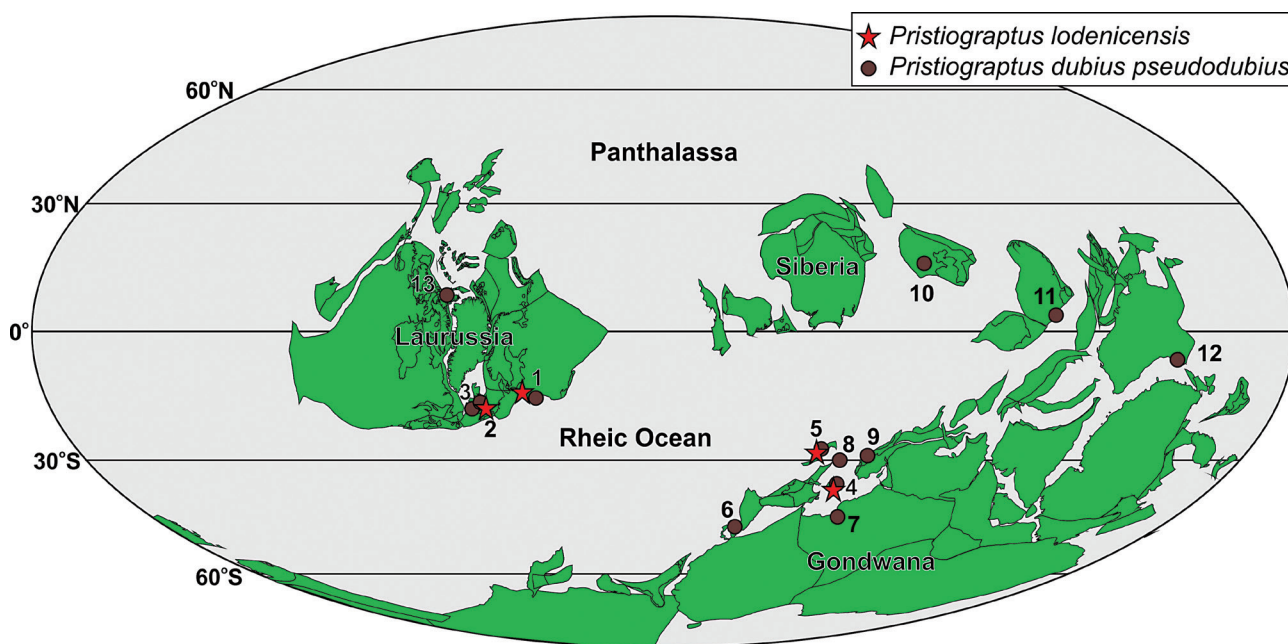


Figure 5. Late Wenlock palaeogeographical reconstruction (after Torsvik & Cocks 2013) and palaeobiogeographical distribution of *P. d. pseudodubius* and *P. lodenicensis*. Abbreviations: 1 – Baltica [Bornholm (Bjerreskov & Jørgensen 1983), Latvia (Ulst 1974), Lithuania (Radzevičius & Paškevičius 2000), Poland (Jaworowski 1965, Urbanek *et al.* 2012) part of the East Europe platform]; 2 – Avalonia [Northern England (Rickards 1965)]; 3 – the Avalonia side of the Iapetus Ocean [Ireland (Rickards *et al.* 1973, Doran 1974, Chew & Stillman 2009)]; 4 – the Perunica Terrane [Czech Republic (Bouček 1932, Přibyl 1943)]; 5 – the Saxo-Thuringia Terrane [Bardo Mountains Sudetes (this paper), Thuringia (Jaeger 1959, 1991)]; 6 – the Iberia massif [Sardinia (Štorch & Piras 2009)]; 7 – central Gondwana [Libya (Štorch & Massa 2003)]; 8 – the Moesia Terrane [Romania (Iordan, 1992, Colțoi *et al.* 2016) and Serbia (Krstić *et al.* 2005)]; 9 – the Pontides Unit [north Turkey (Sachanski *et al.* 2008, 2012)]; 10 – North China [China (Xu 1984)]; 11 – South China [China (Xu 1984), Vietnam (Thanh *et al.* 2013)]; 12 – East Gondwana [Central Victoria, East Australia (Rickards & Sandford 1998)]; 13 – Laurentia [Arctic Canada Cornwallis Island (Lenz & Kozłowska-Dawidziuk 2001, Lenz *et al.* 2012)].

et al. 2007) and was probably part of Armorican terrane assemblage. According to Sachanski *et al.* (2008, 2012), *P. d. pseudodubius* is known from north Turkey in part of the Pontides Unit (Torsvik & Cocks 2016), which was located near central Gondwana during middle Silurian (Torsvik & Cocks 2011). There is also a record of *P. d. pseudodubius* from Libya (Štorch & Massa 2003) which was part of central Gondwana (Fig. 5).

Pristiograptus d. pseudodubius is also recorded from the South and North China palaeocontinents (Xu 1984). Thanh *et al.* (2013) recorded *P. d. pseudodubius* from the Quang Ninh Zone of the Bac Bo Region in northeastern Vietnam, part of the South China Plate (Torsvik & Cocks 2013).

Pristiograptus d. pseudodubius has been described from central Victoria in East Australia (Rickards & Sandford 1998). East Australia makes up part of east Gondwana and was located near the equator during the middle Silurian (Torsvik & Cocks 2009).

There are very well documented graptolites including *P. dubius* (Lenz & Kozłowska-Dawidziuk 2001) and *P. dubius s.l.* (Lenz *et al.* 2012) from Wenlock of Arctic Canada, the part of Laurentia. Authors noted considerable

variations in the collected specimens, albeit all the material is assigned to a single *P. dubius* species (Lenz & Kozłowska-Dawidziuk 2001). Accordingly, it can be assumed that *P. d. pseudodubius* might be present in the Arctic Canada.

Pristiograptus lodenicensis, however, is known from very few locations and only from the middle part of the *lundgreni* Biozone. It is known from Baltica (Latvia, Lithuania and Poland) (Fig. 5). Holland *et al.* (1969) figured *Pristiograptus* sp. 1 with cortical tissue (text-fig. 1d) typical of *P. lodenicensis* and illustrated some specimens (pl. 130, figs 5, 6) with the horizontal thecal aperture lips that are typical for *P. lodenicensis* (Fig. 4A). Based on those illustrations, we recognize the existence of *P. lodenicensis* from the Ludlow district, Shropshire and Denbighshire north-east Wales (Warren *et al.* 1984), expanding the species' range to the Avalonia palaeocontinent.

There are also *P. lodenicensis* records from Thuringia (Jaeger 1959, 1991) and the Bardo Mountains of the Sudetes (this paper). Both locations are linked to the Saxo-Thuringian terrane which was located on the opposite side of the Rheic Palaeo-ocean during the Wenlock along with

the Perunica terrane from which *P. lodenicensis* is also known (Bouček 1932, Přibyl 1943).

Graptolites of the *lundgreni* Biozone have been studied in Arctic Canada the part of Laurentia (Lenz & Kozłowska-Dawidziuk 2001, Lenz et al. 2012) but *P. lodenicensis* was not documented. Present all data indicates that *P. lodenicensis* is characteristic for the the Rheic Palaeo-ocean.

Conclusion

In summary, the long-ranging *Pristiograptus d. pseudo-dubius* is known from the *riccartonensis* to *parvus* biozones and is widespread, from Laurussia to Central Gondwana and East Gondwana. *Pristiograptus lodenicensis* is known only from middle part of the *lundgreni* Biozone and is linked to the palaeogeographical province of the Rheic Palaeo-ocean. This difference in geographical range may be related to *P. lodenicensis*' proposed position as a short-ranged iterative branch off of the *P. dubius* stem lineage (Urbanek et al. 2012), with little opportunity to spread widely after speciation.

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