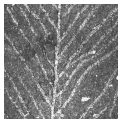
The Ordovician and Silurian benthic graptolite *Ptilograptus* Hall, 1865 (Graptolithina, Dendroidea)

Jörg Maletz & Juan Carlos Gutiérrez-Marco



The genus *Ptilograptus* is re-described from its type species and a revision of the included taxa is attempted. The genus is widely distributed from the Darriwilian (Middle Ordovician) to the Ludlow (Ludfordian) or even the Přídolí (upper Silurian), but its origin is uncertain and may be much earlier. The characteristic zigzag shaped first order stipes and alternating lateral second order stipes formed through monoprogressive branching are characteristic and are not shared with other dendroid genera. *Ptilograptus* is transferred from the Callograptidae to the Dendrograptidae based on its stipe and thecal development. Notes on the validity of all 41 described *Ptilograptus* species are provided, of which 18 species are accepted as valid and useful. • Key words: Ordovician, Silurian, graptolites, Dendroidea, *Ptilograptus*, taxonomy.

Maletz, J. & Gutiérrez-Marco, J.C. 2025. The Ordovician and Silurian benthic graptolite *Ptilograptus* Hall, 1865 (Graptolithina, Dendroidea). *Bulletin of Geosciences 100*(*X*), xxx–xxx (5 figures). Czech Geological Survey, Prague. ISSN 1214-1119. Manuscript received March 18, 2025; accepted in revised form July 29, 2025; published online September 14, 2025; issued Xxxxxxxx XX, 2025.

Jörg Maletz (corresponding author), Institute of Geology, Free University of Berlin, Malteserstrasse 74-100, Haus C005, 12249 Berlin, Germany; Yorge@zedat.fu-berlin.de • Juan Carlos Gutiérrez-Marco, Instituto de Geosciencias CSIC-UMC, and Área de Paleontología, Departamento GEODESPAL, Facultad de CC. Geológicas UCM, José AntonioNovais 12, 28040 Madrid, Spain; jcgrapto@geo.ucm.es

As is the case for many benthic dendroid graptoloids, numerous species, based often on small tubarium (an alternative term for rhabdosome) fragments, have been included in the genus *Ptilograptus*. Species are mostly based on minor differences in dimensions and features of the branching pattern, largely seen in the outlines of flattened specimens preserved on shale surfaces. This typical preservation of flattened colonies of graptolites hides most taxonomically important features of the originally three-dimensionally constructed tubaria. Also, the biostratigraphical age of the specimens appears to have been used in the introduction of new species. Thus, true understanding of the genus is hampered by lack of detailed information on tubarium construction, thecal style, intraspecific variation and biostratigraphical distribution of the available material. This was the reason for inclusion of *Ptilograptus* in the family Callograptidae by Maletz (2020, 2023), as the diagnosis of the genus does not provide any useful information.

Hall (1865) introduced the genus *Ptilograptus* for two new species (*P. plumosus* and *P. geinitzianus*) from the Ordovician of Quebec, Canada, based on the monoprogressive branching pattern (referring to the zigzag shaped main or first order stipes: Cooper & Fortey 1982, fig. 6d). Maletz *et al.* (2025) re-illustrated the two species for the first time and compared their tubarium shape with that of fossil and extant Hydrozoa and algae, but did not provide a detailed investigation of the thecal construction. Hopkinson, 1875 *in* Hopkinson & Lapworth (1875, p. 633) erected the family Ptilograptidae for the genus *Ptilograptus*, but did not provide any useful information for differentiation from other dendroid families. Schmidt (1940) separated species without a 'denticulate apertural margin' as *Ptilograptus* (*Ptilograptus*) from *Ptilograptus* (*Denticulograptus*) with 'denticulate apertural margin', a differentiation not accepted by Bulman (1955, 1970), who retained Ptilograptidae with its single genus in the order Dendroidea. Maletz (2020, 2023) accepted the synonymy of *Denticulograptus* and *Ptilograptus*, but referred *Ptilograpus* to the Callograptidae and discussed the presence of isolated metathecae and formation of twigs in the genus, but also stated in the diagnosis, that the thecal details and tubarium development of the genus are unknown. Zhang *et al.* (2009a) synonymized *Zigzagigraptus* with *Ptilograptus* based on the identical zigzag shape of the main (first order) stipes and the unbranched second order branches.

Tubarium construction

The true tubarium shape is poorly known for most *Ptilograptus* species. Interestingly, one of the best illustrations of a *Ptilograptus* colony was provided by Goeppert

(1860, pl. 36, fig. 14) for a specimen described as *Callithamnion Reussianum* (*Callithamnites Reussianus* in plate explanation), identified as an alga from Barrande's Étage E at Dlouhá hora south of Beroun, Czech Republic. The illustration (Fig. 1A) clearly shows the multiramous colony with numerous monoprogressively branching (zigzag shaped) first order stipes and unbranched second order stipes. Light dots on the stipes indicate what we now can interpret as thecal apertures. The specimen may represent the largest and most complete one described and illustrated for the genus so far. The illustrations of Hall (1865) of the type species of the genus, *Ptilograptus plumosus* (Fig. 1C), and of *Ptilograptus geinitzianus* (Fig. 1B), show fragments of colonies with a similar construction of first and second order stipes due to the monoprogressive branching. They represent, however, only small fragments of presumably much larger colonies, that were fragmented probably due to transport from shallow water to a much deeper water depositional environment. The transport is recognizable through the common association of benthic and planktic graptolites in the Ordovician shales, but also the massive conglomeratic layers largely incorporating limestone boulders bearing rich Cambrian trilobite faunas in the succession at Lévis, Quebec (Logan 1863, 1865; Rasetti 1946; Maletz 1997).

The basic concept of the monoprogressive development of the first order stipes in *Ptilograptus* was established from the early descriptions, even though details of the development and size of the colonies have not previously been described. Some new information is available now and will be discussed herein to stabilize the understanding of the genus and to document its biostratigraphical distribution.

Monoprogressive branching

The presence of a somewhat zigzag shaped main or first order stipe with alternating unbranched second order stipes is recognized as monoprogressive branching in graptolite taxonomy (Cooper & Fortey 1982). Maletz *et al.* (2014, revision *in* Maletz 2023) defined the term monoprogressive stating that at a dichotomy, only one of the resulting stipes will produce later dichotomies, while the second one will stay undivided. These undivided stipes are here identified as second order stipes to differentiate them from the first order stipes (main stipes) with their zigzag shape (Fig. 2).

Jaanusson (1965, fig. 4) illustrated the monoprogressive branching style for the Floian to Darriwilian (Lower to Middle Ordovician) genus *Goniograptus* (Fig. 2D), based on a single specimen preserved in partial relief. This example of *Goniograptus* shows that the zigzag shaped 'main stipes' produce a secondary unbranched stipe after only one additional monocalycal theca was formed. Every second theca on the first order stipe is a dicalycal theca (shown in black in Fig. 2D), producing a new secondary stipe and continuing the main stipe. The precise style of branching and stipe development has not been described, however, for most species and even genera referred to the Sigmagraptinae in which monoprogressive branching can be observed frequently (cf. *Praegoniograptus*, *Sigmagraptus*, *Yushanograptus*). In these sigmagraptine genera, there are no bithecae and the development differs in certain aspects from that of the dendroid triad budding style of *Ptilograptus*, in which autothecae and bithecae can be differentiated (Fig. 2C). Maletz (1992) provided a model for the triad budding of the Tremadocian planktic Anisograptidae with quadriradiate to biradiate proximal

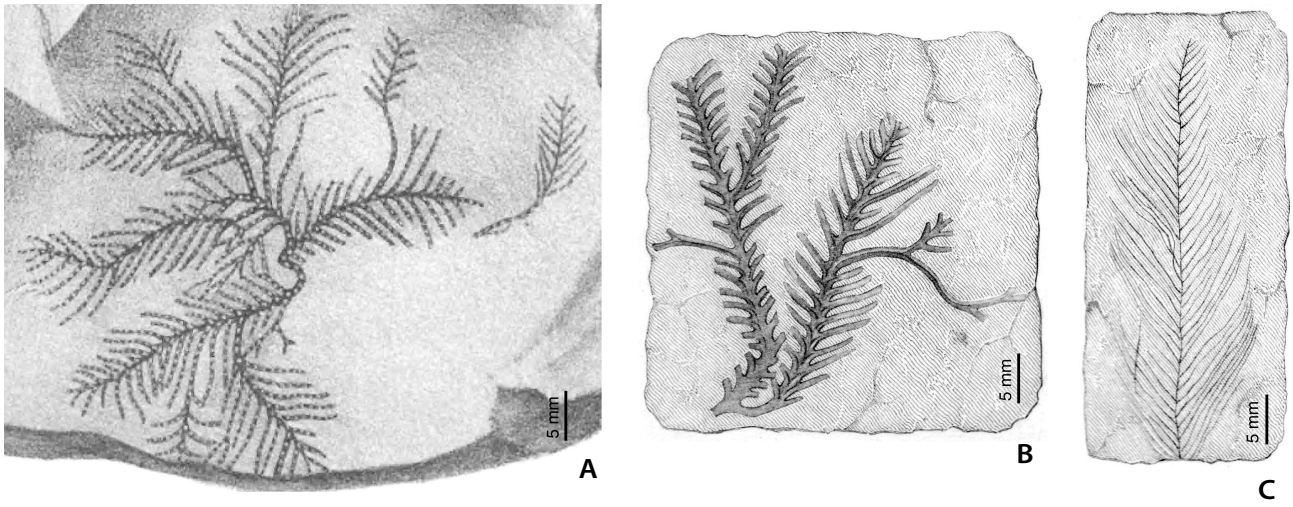


Figure 1. Tubarium construction. • A – *Callithamnion Reussianum* Goeppert, 1860, type (Goeppert 1860, pl. 36, fig. 14a). • B – *Ptilograptus geinitzianus* Hall, 1865 (Hall 1865, pl. 21, fig. 6). • C –*Ptilograptus plumosus* Hall, 1865 (Hall 1865, pl. 21, fig. 2).

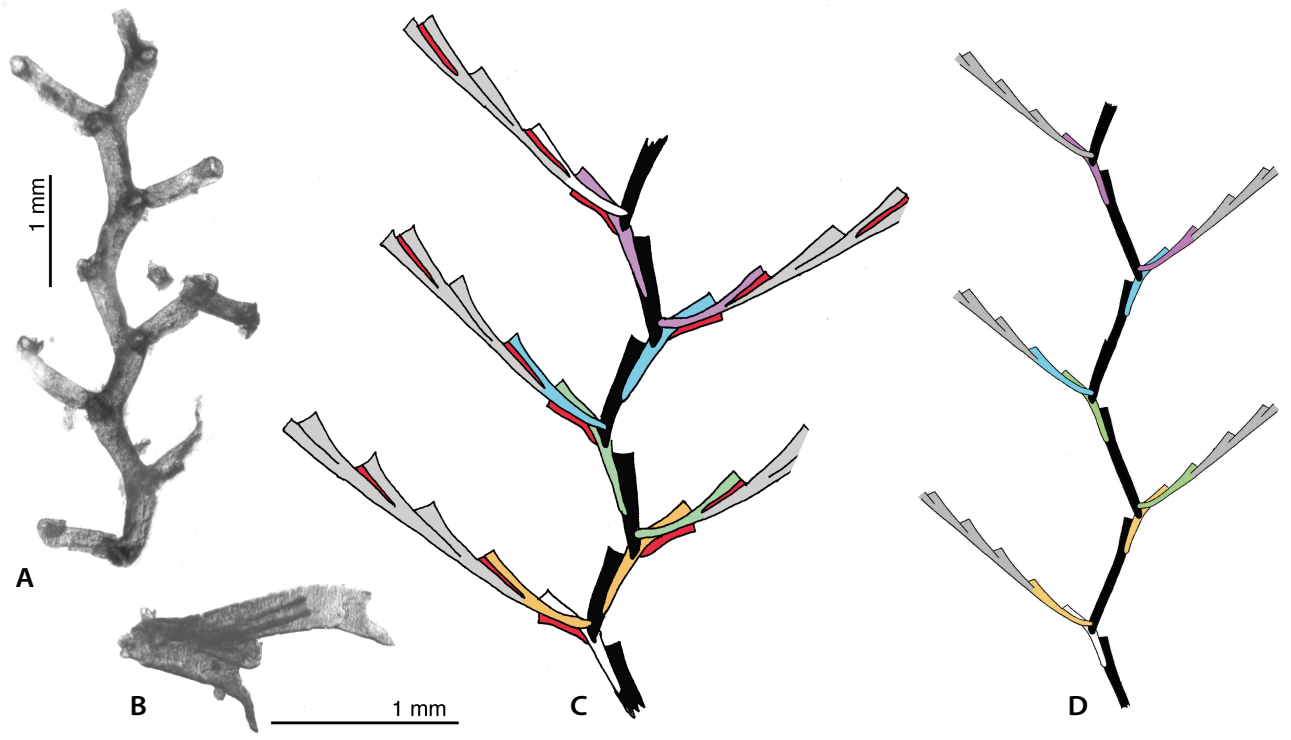


Figure 2. Monoprogressive branching. • A, B – *Ptilograptus* sp., Table Head Group, West Bay Centre Quarry, western Newfoundland, chemically isolated specimens. A – GSC 144530, WBC4.91.128b, thecal fragment showing apertural style. B – GSC 144531, WBC4.91.126a, dorsal view of stipe fragment. • C – reconstruction of dendroid branch with bithecae (in red), showing monoprogressive branching (details in text). • D – monoprogressive branching in the graptoloid genus *Goniograptus* (after Jaanusson 1965, fig. 4). The dicalycal thecae are shown in black with the two originating autothecae in matching colours. The bithecae are marked in red and the unbranched second order stipes in grey.

development. This model can also be used to understand the monoprogressive development of *Ptilograptus* (Fig. 2C), even though chemically isolated material or even three-dimensionally preserved specimens were not available at that time and only a few flattened fragments have been investigated (Fig. 2A).

Small chemically isolated fragments referred to *Ptilograptus* (Fig. 2A) show that each stipe partition of the main stipe bears a single theca before the stipe branches again. Unfortunately, details of the thecal differentiation and the presence of bithecae is not recognizable in the available flattened specimens, that otherwise compare well with the model (Fig. 2C). The model shows the dicalycal thecae in black with the two originating autothecae in matching colours. The bithecae are marked in red and the unbranched second order stipes in grey.

Thecal style

It is difficult to observe the thecal style in the type species *Ptilograptus plumosus* and in most other taxa, but a few specimens show the lateral preservation of the stipes. Only in these cases can the thecal style be investigated. The thecae are fairly slender, as can be seen in dorsal view, and the size of the stipes fits with the chemically isolated material of an undescribed species of *Ptilograptus* from the Table Head Group of eastern Canada (Fig. 2A). As all specimens are preserved in dorso-ventral view, the thecal apertures are not seen in lateral preservation. Fragments show thecae with distinct ventral apertural extensions (Fig. 2B) that are similar to the thecae found in *Ptilograptus acutus* Hopkinson, 1875 *in* Hopkinson & Lapworth (1875) and *Ptilograptus sibiricus* Obut & Sobolevskaya, 1967. The type specimen of *Ptilograptus acutus* shows a lateral preservation of some distal stipes with low inclined, pointed thecal apertures. This specimen from the Abereiddy Bay locality may however, be distorted tectonically and the thecal density is unreliable, as the example of *Didymograptus murchisoni* from the same locality shows (see Jenkins 1987, fig. 4).

The type specimen of *Ptilograptus geinitzianus* indicates low inclined thecae of a general dendroid type without extended rutelli (Fig. 1B; see description of species). The specimen is largely flattened and the wide stipes appear to show considerable cortical thickening as can be found in many dendroid graptolites (*cf.* Bates *et al.* 2011).

Biostratigraphy

Several taxa have been referred to *Ptilograptus*, but the inclusion of many is questionable, largely due to poor preservation or fragmentation of the material. Often only small fragments have been described and referred to new species without regard to possible intraspecific variation. The age and relationship of a number of species is also uncertain as will be discussed in the list of species included in the genus *Ptilograptus* herein. A number of species has been illustrated in Figure 3 to show the established biostratigraphical range of the genus.

The identity of *Ptilograptus yidouensis* Li, 1984 from the Tremadocian of China as a species of *Ptilograptus* is questioned. The specimens may represent fragments of *Acanthograptus sinensis* Hsü & Ma, 1948. *Ptilograptus patens* Ruedemann, 1947 (Fig. 3E) from western Newfoundland comes from an interval spanning the *Paratetragraptus approximatus* Biozone (basal Floian) to the *Levisograptus dentatus* Biozone (lower Darriwilian) (see Williams & Stevens 1988).

Hall (1865) described two different species from the Pointe de Lévis area and established on this material the genus *Ptilograptus* (Fig. 3A, B). The species show distinct differences in their dimensions and can easily be separated. Maletz *et al.* (2025) re-illustrated the material but did not describe it in detail. *Ptilograptus yui* Lin, 2002 *in* Mu *et al.* (2002) and *Ptilograptus yunnanensis* (Yu, 1962) originate from the Darriwilian, Middle Ordovician, Shihtien Formation, Baoshan, Yunnan Province, China (Zhang *et al.* 2009a, b) and thus, have a similar age to Hall's (1865) material from Quebec.

The Sandbian is the most diverse interval for *Ptilograptus* species. Ruedemann (1947) described a number of species from the Ottosee Shale of Tennessee (*P. alternans*, *P. delicatulus*, *P. rectus*, *P. sparsus*), of which *P. delicatulus* (Fig. 3J) and *P. rectus* are here accepted. All of these species, however, need to be revised. *Ptilograptus poctai* Ruedemann, 1908 (Fig. 3F) from the Upper Ordovician Normanskill Shale of Glenmont, Albany (New York, USA) was considered by Ruedemann to be intermediate between *Ptilograptus plumosus* and *P. geinitzianus*. A single fragment from the Pirgu Regional Stage of Estonia (upper Katian) was named *Ptilograptus pennatus* Obut & Rytzk, 1958 (Fig. 3H), a species similar to *P. geinitzianus* in its dimensions.

A few Silurian taxa have been erected, including *Ptilograptus venetus* Gortani, 1923 (Fig. 3K) from the Llandovery of the Carnic Alps, a typical example of the poor and fragmentary preservation typical of the genus. *Ptilograptus hartnageli* Ruedemann, 1908 (Fig. 3L) from the Llandovery of Cayuga County, New York State, USA, again was described from a single small fragment. Bouček (1957, fig. 65) illustrated a number of specimens from the upper Wenlock *Cyrtograptus radians* Biozone of the Czech Republic under this name, including somewhat larger, branching colonies. More often, however, material has been identified only as *Ptilograptus* sp. (cf. Ni 1978).

A few records originate from the Ludlow to possibly Přídolí (upper Silurian) and represent the youngest specimens of *Ptilograptus*. Nicholson (1868) illustrated a single specimen of his new species *Ptilograptus anglicus* (Fig. 3M) from Bow Bridge near Ludlow, possible of late Ludlow (?Ludfordian) age. It is characterized by relatively short second order stipes, thus differing from most other species included in the genus. The precise age of *Ptilograptus reussianus* (Goeppert, 1860) (Fig. 3N) is unclear (see under species remarks). If a Přídolí age could be confirmed, it represents the youngest known *Ptilograptus* species.

Systematic palaeontology

The systematics and taxonomy for the Graptolithina follow Maletz (2023). Higher level taxonomic units are not listed here.

Repositories. – The illustrated graptolite material is preserved in the type collections at the Australian Museum, Sydney, Australia (AMF); Natural History Museum, University of Tartu, Estonia (GIT); Geological Survey of Canada, Ottawa, Canada (GSC); Nanjing Institute for Geology and Palaeontology, Academia Sinica, Nanjing, China (NIGPAS); Sedgwick Museum of Earth Sciences, Cambridge, United Kingdom (SM); Geological Survey Museum, London, United Kingdom (GSM).

Family Dendrograptidae Roemer, 1897 *in* Frech (1897)

Genus *Ptilograptus* Hall, 1865

Ptilograptus Hall, 1865, p. 139 [**P. plumosus*; SD Miller (1889), p. 201; misspelled *Ptylograptus* in Spencer (1878), p. 462] [= *Stelechograptus* Ruedemann, 1947, p. 279 (type, *S. rectus*, OD), syn. Maletz (2020), p. 14]; [= *Denticulograptus* Schmidt, 1940, p. 122, ex *Ptilograptus* (*Denticulograptus*) Schmidt, 1940, p. 122 [type, *Ptilograptus acutus* Hopkinson, 1875 *in* Hopkinson & Lapworth (1875), p. 662, OD], syn. Bulman (1955), p. V36]; [= *Zigzagigraptus* Yu, 1962, p. 49 (type, *Z. yunnanensis*, OD), syn. by Zhang *et al.* (2009a), p. 311].

Type species. – *Ptilograptus plumosus* Hall, 1865 from the lower Darriwilian (*Levisograptus austrodentatus* to *L. dentatus* biozones), Middle Ordovician of Point Lévis, Québec, Canada.

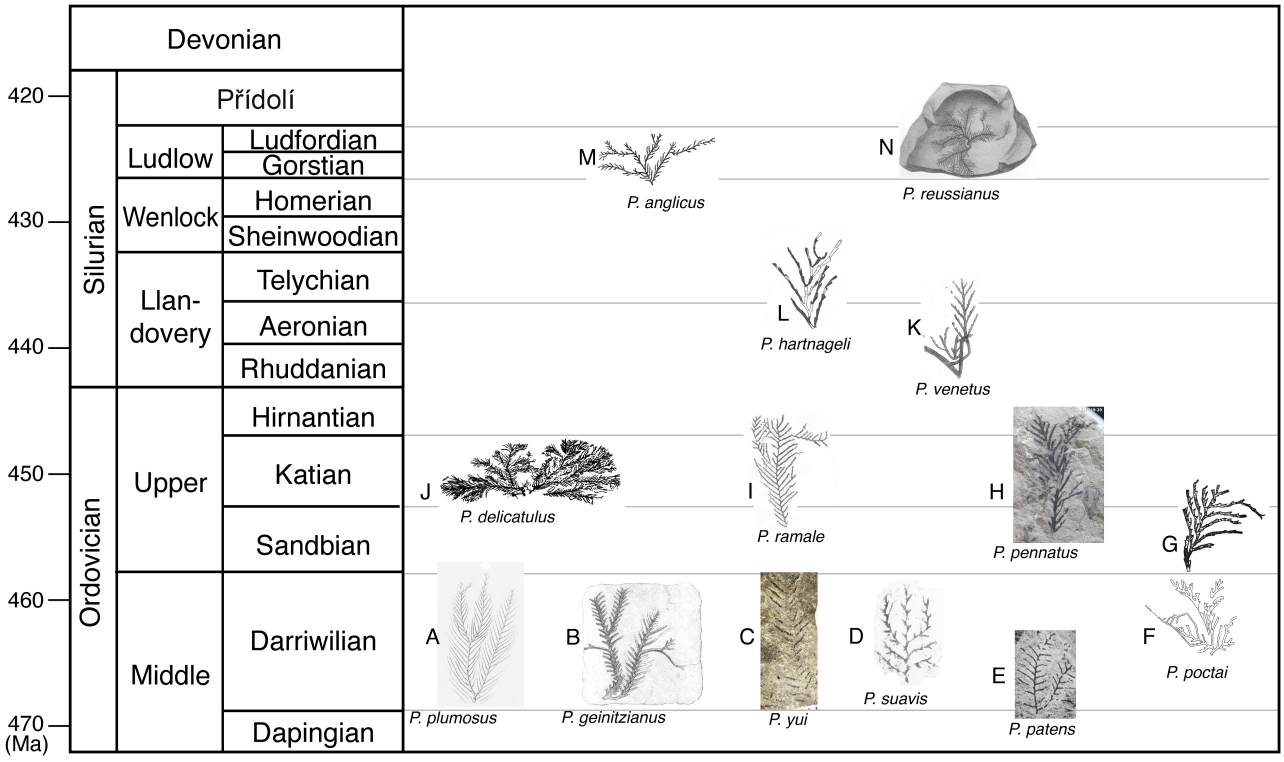


Figure 3. Biostratigraphical distribution of selected *Ptilograptus* species. A – (Hall 1865, pl. 21, fig. 3). B – (Hall 1865, pl. 21, fig. 6). C – (NIGP 14331, new, JM). D – (Počta 1894, pl. 1, fig. 23). E – (Ruedemann 1947, pl. 33, fig. 16). F – (Maletz 2023, fig. 151.7d; holotype of *P. yunnanensis*). G – (Ruedemann 1908, text-fig. 53). H – (*Fossilid.info*). I – (Počta 1894, pl. 2, fig. 28). J – (Ruedemann 1947, pl. 34, fig. 3). K – (Gortani 1923, pl. 1, fig. 1). L – (Ruedemann 1908, text-fig. 53). M – (Nicholson 1868, fig. 1). N – (Goeppert 1860, pl. 36, fig. 14a).

Diagnosis. – Multiramous dendrograptid with several orders of monoprogressive branches; thecal style with triad budding and simple, dendrograptid, non-isolated thecae, often bearing a distinct rutellum (revised from Maletz 2023, p. 246).

Remarks. – The diagnosis of the genus has been modified as it is now included in Dendrograptidae based on the denticulate thecae. Maletz (2023, p. 246) included the genus *Ptilograptus* in Callograptidae but stated that the thecal details and development are unknown, indicating an uncertainty of the inclusion in this family. New information now shows a 'dendrograptid' type of thecae, necessitating referral to Dendrograptidae. The investigation shows that there are no twigs as can be seen in Callograptidae, thus the diagnosis in the Treatise (Maletz 2023, p. 246) has to be revised and the genus excluded from Callograptidae. Branching appears to be dichotomous, monoprogressive in all species for which detailed information is available. The monoprogressive branching produces the zigzag shape of the main stipes with the unbranched secondary stipes, so characteristic for all species of the genus. This style has been termed 'feather-like' and found in at least three different groups: the graptolites, hydroids and algae (Maletz *et al.* 2025).

Very little is known about the detailed development of thecae and stipes as no isolated material has ever been described. Hall (1865) erected the genus *Ptilograptus* with two species, *Ptilograptus plumosus* and *Ptilograptus geinitzianus* from the lower Darriwilian of Point Lévis, Quebec, Canada, but the original illustrations did not show any thecal details. Ruedemann (1947, pls 33, 34) illustrated the denticulate thecae of a number of species.

Maletz (2020, 2023) synonymized the subgenus *Ptilograptus* (*Denticulograptus*) Schmidt (1940) with *Ptilograptus*, but did not provide additional information. The synonymy is here accepted, as the lack of the thecal denticles in *Ptilograptus* can easily be explained by the dorso-ventral preservation of the stipe, so that thecal apertures are not visible.

Occurrence. – Middle Ordovician (Darriwilian)–Silurian [Ludlow (?Ludfordian) to ?Přídolí]. The genus is distributed worldwide as can be seen from records from Canada, USA, South America (Argentina, ?Peru), Europe, China, Russia, Kyrgyzstan, North Africa (Morocco), and Australia. A number of specimens have been described in open nomenclature (mainly as *Ptilograptus* sp.) and are not discussed here.

***Ptilograptus plumosus* Hall, 1865**
Figures 1C, 3A, 4A–E

1865 *Ptilograptus plumosus* (n. s.); Hall, p. 140, pl. 21, figs 1–4.
1904 *Ptilograptus plumosus* Hall. – Ruedemann, p. 588, pl. 4, figs 14, 15.
1947 *Ptilograptus plumosus* Hall. – Ruedemann, p. 247, pl. 33, figs 1–8.
2020 *Ptilograptus plumosus* Hall. – Maletz, p. 14, fig. 7.7a.
2025 *Ptilograptus plumosus* Hall. – Maletz *et al.*, fig. 8a–c.

Type material. – Bolton (1960, p. 108) listed GSC 947, 947a, 947b as the syntypes of *Ptilograptus plumosus*. Maletz (2020, p. 14) selected GSC 947b (Fig. 4C) as the lectotype. The specimens are from the shales of the Quebec Group, Point Lévis, of early Darriwilian age (probably from the *Levisograptus austrodentatus* to *L. dentatus* biozones).

Diagnosis. – Dendroid graptolite with slender main or first order stipes; unbranched second order stipes originating in monoprogressive fashion from first order stipes; thecae widening towards the aperture, often with rutellum; proximal end unknown.

Description. – All available specimens are fragments, not showing the precise development of the colony. Thus, the shape of the colony is unknown. Complete colonies are obviously going to have been much larger than the available fragments. No additional material has ever been referred to this species.

The material shows the characteristic main stipes or first order stipes with monoprogressive development of secondary, unbranched stipes. One fragment shows three branching divisions (Fig. 4C: white arrows), in which the longest unbranched first order stipe on the right side of the fragment is about 35 mm long. This stipe shows that the second order stipes are successively shorter distally, indicating the growing end of the main stipe. The second first order stipe shows a branching division approximately at the position of the second order stipe 14 or 15. Another branching division is found after approximately the same distance, forming two next first order stipes, both originating on the same side. The first order stipes produce unbranched second order stipes, but it is unclear what defines the position of the branching of the first order stipes and whether there is a difference between first and second order stipes. The angle between the first and second order stipes is about 30–40°, but the second order stipes are slender and appear to have been fairly flexible.

The first order stipes are about 0.3–0.4 mm wide and, in some cases, preserved in low relief, indicating a possible strong cover with cortical material. They are fairly straight, but in some cases may show slight undulations, expressed more strongly through the alternating second order stipes. Indication of thecal style is rarely seen (Fig. 4D, arrows). The longest first order stipe is 45 mm long and does not show any branching. The second order stipes are up to 15 mm long and decrease in length towards the tip of the first order stipes indicating the growth pattern. They are 0.2–0.25 mm wide. Hall (1865, pl. 21, fig. 2) indicated in his illustrations, that the second order stipes are thinner towards their tips, but this is not visible in the specimens (Fig. 4).

Remarks. – Maletz *et al.* (2025) discussed the species and re-illustrated the type material of Hall (1865), but did not provide a description of the material. *Ptilograptus plumosus* has been illustrated in Mu *et al.* (2002, pl. 7, fig. 4) from China, but the illustration is too poor for verification. The specimen originated from the upper Tremadocian *Acanthograptus sinensis* Biozone and, thus, if correct would represent the oldest taxon of the genus. However, it is unlikely that it represents *Ptilograptus plumosus*.

***Ptilograptus geinitzianus* Hall, 1865**
Figures 1B; 3B; 5F, G, I

1865 *Ptilograptus geinitzianus* n. s.; Hall, p. 140, pl. 21, figs 5–8.
1947 *Ptilograptus geinitzianus* Hall. – Ruedemann, p. 246, pl. 33, figs 9–13.

Type material. – The syntypes are GSC 961, a, b (Bolton 1960, p. 140). Ruedemann (1947, pl. 33) illustrated GSC 961a as the holotype. As types were not designated by Hall (1865), Maletz *et al.* (2025) identified the specimen (GSC 961a) as the lectotype. The original labels used the name *Ptilograptus dumosus* for this species. The slabs bear other dendroid graptolites, possible biserials, *Tetragraptus* sp., *Pseudotrigonograptus* sp. and *Arienigraptus angulatus*. The rock is a laminated siltstone with black, finer shale intercalations in which the graptolites can be found. The specimens are from the shales of the Quebec Group, Point Lévis, of early Darriwilian age (probably from the *Levisograptus austrodentatus* to *L. dentatus* biozones).

Diagnosis. – Quite robust tubarium with thick cortical layer, no thecae visible in dorsal view; first order stipe shape with somewhat irregular zigzag development; secondary stipes slightly more slender, showing thecae in lateral view

Description. – The material consists of a few fragments not showing the tubarium shape and size. The specimens are either flattened or show low relief with most of the fusellum preserved as dark brown, somewhat silvery shiny

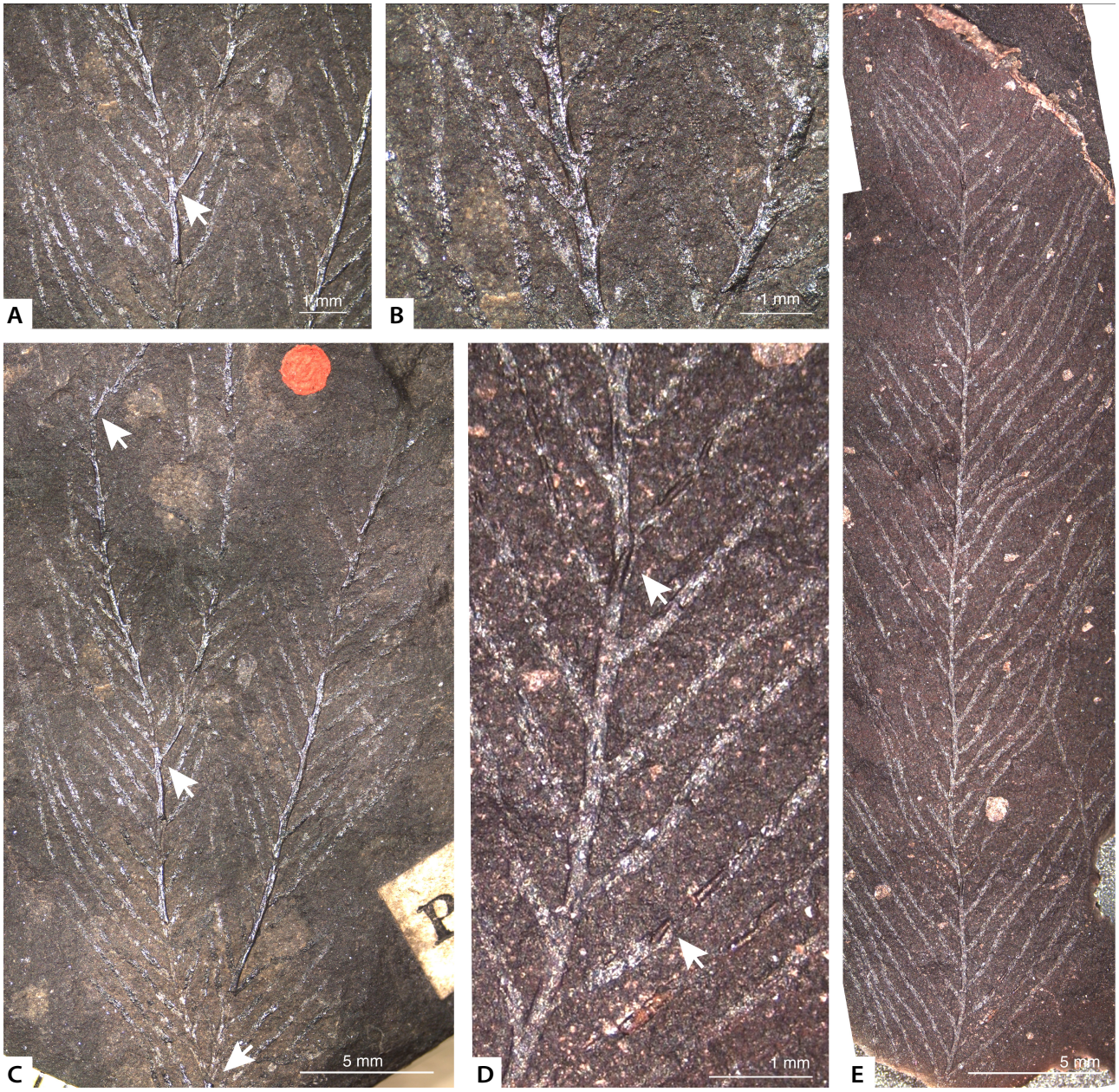


Figure 4. *Ptilograptus plumosus* Hall, 1865. A, B, C – GSC 947b, lectotype, arrows indicate branching division in primary stipes. D, E – GSC 947, paralectotype, long, unbranched primary stipe with numerous secondary stipes. White arrows indicate where slender thecal tubes are visible in dorsal view.

organic material. Whitish minerals cover parts of the stipes and are here interpreted as pressure shadow minerals. Fragments are up to 40 mm long with several branching divisions of the first order stipes. The specimens represent distal parts of the colonies as can be shown from the decrease in length of the second order stipes (Fig. 1B).

The first order stipes are 0.7–1.0 mm wide, but probably even wider in proximal ends. They branch at irregular distances dichotomously. Secondary stipes branch off on alternate sides at regular distances of *ca*. 1.0–1.2 mm, suggesting a monoprogressive branching pattern (Fig. 5F, G, I). The second order stipes are 0.6–0.7 mm wide in dorsoventral view and also in lateral view, when the thecal apertures are visible. The second order stipes are inclined at *ca*. 35–40° to the first order stipes. There are about 10 thecae in 10 mm (2TRD *ca*. 2 mm) at the distal ends of laterally preserved stipes (Fig. 5G). Fusellar construction is not visible in the material, most likely as the stipes may be covered by a considerable thickness of cortical material. Irregularly, second order stipes are modified to develop into first order stipes after a number of thecae are formed (Fig. 5G: white arrows). Then, suddenly, they start to

develop into slightly zigzag shaped first order stipes and branch monoprogressively forming new second order stipes. Dark lines in several places (Fig. 5G) indicate partially pyrite-filled thecal tubes or remains of the stolon system, but details are not available.

The length of the second order stipes is variable, reaching up to at least 8 mm, but maybe considerably more. One of the syntypes of Hall (1865) shows the variability of the dimensions (Fig. 1B). Most of the short second order stipes in this specimen may have been broken off, while others reach a considerable length. The longest second order stipe is 10 mm long. Several second order stipes transform into first order stipes after growing for a few mm before branching into alternately originating second order stipes again.

Remarks. – The species is more robust than any other described species of *Ptilograptus*. Thus, it should easily be recognized in the fossil record. The most similar taxon is the much younger *Ptilograptus reussianus* (Goeppert, 1860), known from a single, large colony. *Ptilograptus reussianus*, however, shows the monoprogressive branching with the zigzag shape of the first order stipes more clearly. A differentiation from the genus *Acanthograptus* can be made through the complex thecal overlap of tubular thecae in *Acanthograptus*, forming a wide and straight main stipe. Thus, *Acanthograptus* does not show the characteristic zigzag shape of the main stipes. Often, in this genus, the parallel-sided tubular thecal callograptid tubes can be discerned.

Distribution. – The species is known only from its type material, from the Darriwilian (Middle Ordovician) at Point Lévis, Quebec, Canada, collected by James Richardson (see Logan 1863). As GSC 961b bears a poor specimen of *Arienigraptus angulatus,* this slab may have originated from the *Levisograptus dentatus* Biozone (see Maletz, 1997, fig. 5). *Ptilograptus geinitzianus* was also illustrated from the Darriwilian (lower Dw1) of the Argentinian Precordillera (Brussa 1997a, fig. 8l; 1997b, fig. 3e and pl. 1, fig. b) through a single fragment of the zigzag main stipe (= *P.* cf. *geinitzianus* in Toro & Brussa 2003, p. 452, pl. 15, fig. 10). Due to the poor preservation, a verification of the identification as *Ptilograptus geinitzianus* is impossible, even though the specimen appears similarly robust.

Notes on other *Ptilograptus* species

The list includes all species referred to *Ptilograptus* either originally or later. They are listed here in alphabetical order. Species in bold letters are here accepted as valid species. Others may not belong to *Ptilograptus* or are synonyms of established species. Notes on their assignment are provided here. There are 41 listed species, of which at least 18 are accepted as belonging to the genus *Ptilograptus*, but some may turn out to be synonyms of others when revised. Fifteen species are based on small fragments and are considered unidentifiable at the species level. Another 8 species do not belong to the genus *Ptilograptus*.

***Ptilograptus acutus* Hopkinson, 1875** *in* Hopkinson & Lapworth (1875, p. 662, pl. 37, fig. 1a, b). SM A19220b, holotype (Fig. 5A, B). Middle Ordovician, Darriwilian, *Didymograptus murchisoni* Biozone. Abereiddy Bay, Wales, United Kingdom. *Ptilograptus acutus* is the type species of *Ptilograptus* (*Denticulograptus*) Schmidt, 1940. The only available specimen shows a low thecal inclination and no further thecal details. Branching is seen in one place indicating that this is a dendroid (Fig. 5A, B: left red arrow) and not a fragment of the Darriwilian planktic genus *Pterograptus*. The species has not been revised since its first description.

Ptilograptus alternans Ruedemann, 1947 (p. 244, pl. 34, figs 13, 14). Katian (Upper Ordovician), Ottosee Shale, Tennessee, USA. The species is based on the very poor illustrations of two specimens and is indeterminable.

***Ptilograptus anglicus* (Nicholson, 1868)** (p. 239, figs 1–3; originally as *Ptilograpsus*). GSM 10764, holotype (Fig. 3K). The specimens originate from Bow Bridge, near Ludlow (Nicholson, 1868), probably of late Ludlow (early Ludfordian) age. A nice, flattened specimen with pointed thecal apertures; showing several branching points and relatively short secondary branches, was illustrated. The description suggests that more than one specimen was available, but only one was illustrated.

Ptilograptus cristula Hopkinson, 1875 *in* Hopkinson & Lapworth (1875, p. 661, pl. 36, figs. 2a, b). Lower Arenig (= Floian), Uchaf Road, Ramsey Island, St. David's, Pembrokeshire, Wales. SM A17491a, b (counterparts), holotype (Fig. 5D). The thecae were described and illustrated as dendrograptid ('hydrothecae about 40 to the inch, narrowly cup-shaped in form, and with minute circular apertures'). The single specimen shows a main, slightly zigzag stem with secondary stipes that branch at various distances. Thus, the specimen may not represent a member of the genus *Ptilograptus*.

Ptilograptus daduhensis Mu, 1993 *in* Mu *et al.* (1993, p. 92, pl. 3, fig. 1) (ex *Zigzagigraptus*) (Fig. 3G). Upper Ordovician, Daduhe Formation, Sichuan, China. The specimen looks a lot like *Ptilograptus anglicus* with the short secondary stipes, but may be too poorly preserved for further identification.

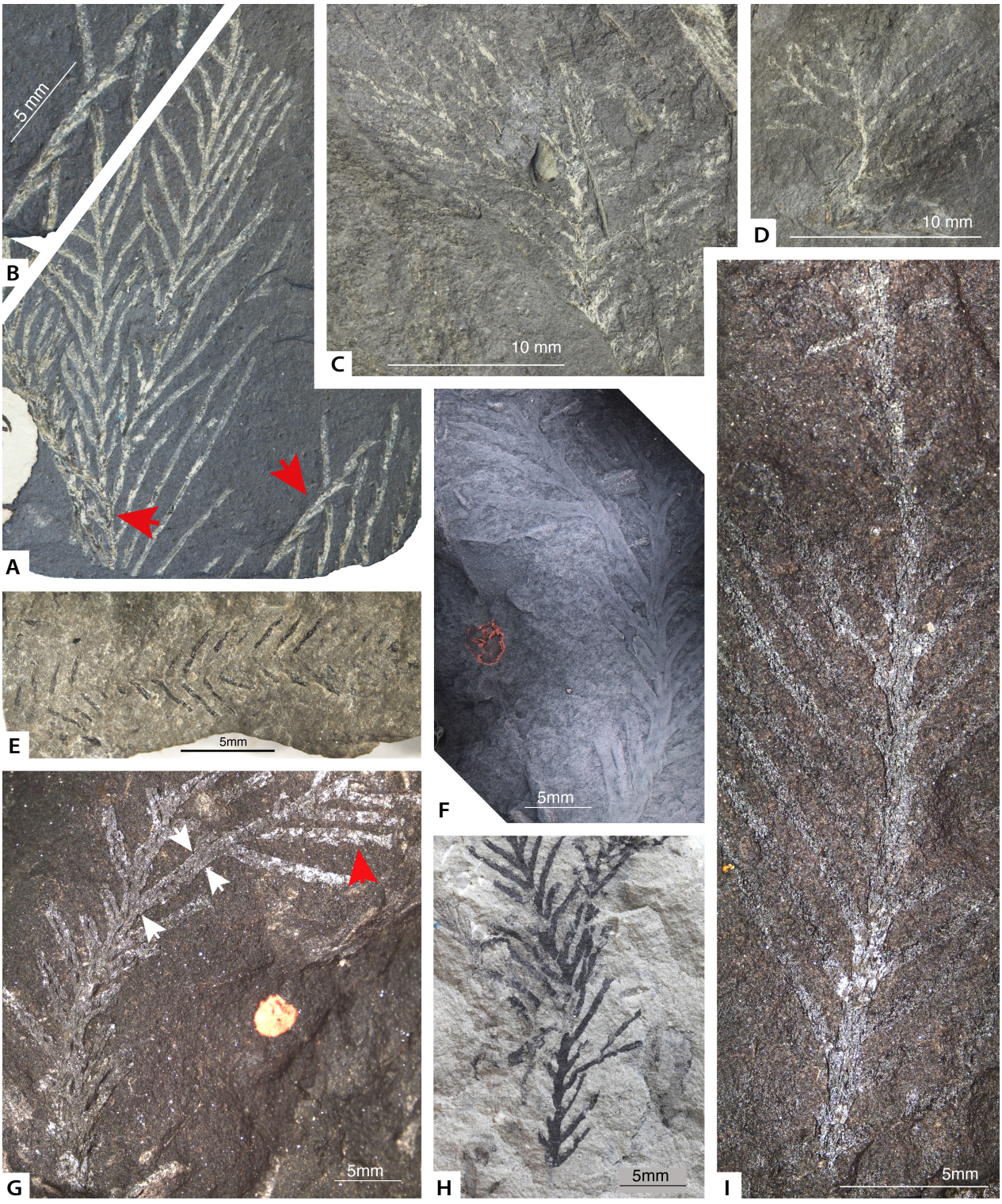


Figure 5. Additional *Ptilograptus* species. • A, B – *Ptilograptus acutus* Hopkinson, 1875 *in* Hopkinson & Lapworth (1875), SM A19220a, holotype, (B) shows thecal style in magnification, Middle Ordovician, Darriwilian, *Didymograptus murchisoni* Biozone. Abereiddy Bay, Wales, United Kingdom. • C – *Ptilograptus hicksii* Hopkinson, 1875 *in* Hopkinson & Lapworth (1875), SM A17492a, holotype, Floian, Ramsey Island, Wales, United Kingdom. • D – *Ptilograptus cristula* Hopkinson, 1875 *in* Hopkinson & Lapworth (1875), SM A17491a, b, holotype, Floian, Uchaf Road, Ramsey Island, St. David's, Pembrokeshire, Wales. • E– *Ptilograptus yui* Lin, 2002 *in* Mu *et al.* (2002), p. 51, pl. 7, fig. 8, NIGP 14331, holotype, Darriwilian, Middle Ordovician, Shihtien Formation, Baoshan, Yunnan Province, China. • F, G, I – *Ptilograptus geinitzianus* Hall, 1865, syntypes. F, G – GSC 961a, lectotype, specimen showing thecal style (red arrow in G), Middle Ordovician, Darriwilian, Point Levis, Quebec, Canada. I – GSC 961 (see Hall 1865, pl. 21, fig. 7). • H – *Ptilograptus pennatus* Obut & Rytzk, 1958, GIT 1119-20, Prigu Regional Stage (= upper Katian), Upper Ordovician, Kose 2323 borehole, Estonia.

Ptilograptus delicatulus **Ruedemann, 1947** (p. 245, pl. 34, figs 1–12) (Fig. 3H). Katian (Upper Ordovician), Ottosee Shale. Specimens are poorly illustrated, but show the characteristic monoprogressive branching. The holotype was also illustrated in Bulman (1970, fig. 20.1b). Leone *et al.* (1993, pl. 1, fig. 10) illustrated a single fragment from the Upper Ordovician (lower Katian) of Sardinia as *Ptilograptus* aff. *delicatulus* Ruedemann. The type specimens represent a delicate species of the genus, but need to be revised and redescribed. Zima (1973, pl. 2, figs 6, 7) described P. delicatulus from the Darriwilian of Central Asia. The specimens may represent *P. plumosus*, even though they are much older, thus indicating a relatively long biostratigraphical range of the species. Several specimens of *Ptilograptus* cf. *delicatulus* Ruedemann have been recorded and illustrated from the lower Darriwilian beds of the Argentine Precordillera (Sierra de La Invernada, Los Azules, and San Juan formations: Ortega 1987; Brussa 1997a, b; Toro & Brussa 2003). The first published illustration of a specimen from the La Invernada Formation (Brussa 1997a, fig. 8j) represents an unrecognizable species with remarkably fine stipes (0.2 mm or less), lacking thecal details and apparently displaying a non-zigzag main stipe. However, new material from the same locality (Brussa 1997b, p. 361, fig. 3a, c, f and pl. 1, figs a, c, d; Toro & Brussa 2003, p. 452, pl. 8, figs 1, 2) confirms the presence of the genus *Ptilograptus* in this section in rocks that had been previously attributed to the Dapingian but were reassigned by Albanesi & Ortega (2016) to the *Levisograptus austrodentatus* Biozone of the lower Darriwilian. The specimens show a probably zigzag main stipe with very slender secondary stipes bearing low inclined thecae. The specimens are completely flattened and details of the thecal development are not available. The early Darriwilian graptolite material from the upper San Juan and Los Azules formations of the Cerro Viejo section (Ortega 1987) remains unpublished and cannot be verified.

Ptilograptus discurrens Sherrard, 1956 (p. 89, pl. 8, fig. 12). Middle Telychian (Silurian), New South Wales, Australia; associated with *Monograptus* (now = *Torquigraptus*) *pragensis*, suggesting the *Monoclimacis griestoniensis* Biozone, and *Dictyonema*. The poor, small fragment illustrated, showing a zigzag main stipe and unbranched lateral stipes, is indeterminable.

Ptilograptus discurrens sherrardae Rickards & Wright, 1997 (p. 219, fig. 5b). AMF 91959. Silurian, Ludlow, Barnby Hills Shale, New South Wales, Australia. The single small fragment is indeterminable even to genus level.

Ptilograptus flexus Lin, 1978 *in* Wang & Zhao (1978, p. 602, pl. 195, fig. 1). The specimen comes from the Ningguoan Stage of the Lower Ordovician of SW China. According to Zhang *et al.* (2023, fig. 2), the Ninggkuoan can be correlated to the interval from the base of the Floian to the higher part of the Darriwilian, and thus does not provide a precise age. It is a small, indeterminable fragment, possibly showing monoprogressive branching.

Ptilograptus foliaceus Spencer, 1878 (p. 462, pl. 6, fig. 1). (ex *Ptylograpsus foliaceus*). Middle Silurian; Niagara Limestone, Hamilton, Ontario, Canada (probably the Lockport Dolomite: Brett *et al.* 1995, p. 8, fig. 5). We agree with Gurley's statement (*in* Bassler 1909, p. 17) that the species is based on a single indeterminable specimen, very poorly illustrated.

Ptilograptus? *gaspensis* Ruedemann, 1947 (p. 246, pl. 33, figs 19, 20). Ordovician, Port Daniels Series. The specimen is very slender with low thecal inclination and overlap apparently. It probably does not belong to *Ptilograptus*, but appears to be indeterminable.

Ptilograptus glomeratus Počta, 1894 (p. 203, pl. 6, figs 1–3). (d_3 from Trubín). Upper Darriwilian to upper Sandbian (Middle to Upper Ordovician), Dobrotivá to Vinice formations. Počta (1894) illustrated two specimens and a magnification of one, suggesting thecal tubes in dorsal view (Počta 1894, pl. 6, fig. 3). The monoprogressive branching suggests *Ptilograptus*. Kraft (1975) provided very poor line drawings lacking info on thecae. The lectotype was illustrated by Počta (1894, pl. 6, fig. 1) and Kraft (1975, pl. 13, fig. 6). The species is indeterminable as thecal details are not available in the type material. Gutiérrez-Marco *et al.* (2022) illustrated a few specimens from the Upper Ordovician (Sandbian 2 – Katian 2) Tafilalt Biota of Morocco as *Ptilograptus* aff. *glomeratus*. Several specimens of *Ptilograptus* ex gr. *glomeratus* were illustrated from the Middle Ordovician of China (Lin 1994, pl. 2, figs 5–7), but they are small, unrecognizable fragments. It is worth noting that the first forms attributed to the group were described as a variety of *Ptilogr. glomeratus*, now considered a separate species [see *Ptilograptus. sinicus* (Mu, 1955)]. Tokarev *et al.* (2018) also cited *Ptilograptus glomeratus* from the lower Hirnantian *Hedrograptus mirnyensis* (now *Metabolograptus extraordinarius*) Biozone of Salair, southern Siberia.

Ptilograptus hanyuanensis (Mu, 1993) *in* Mu *et al.* (1993), p. 92, pl. 3, fig. 3 (holotype), NIGP 56 582 (?), (English description on p. 323) (ex *Zigzagigraptus*). Upper Ordovician, Sichuan Province, China. The single small fragment with strongly zigzag stipe and very short second order stipes is indeterminable.

***Ptilograptus hartnageli* Ruedemann, 1908** (p. 149, pl. 1, fig. 9). (Fig. 3J). Clinton Shale, middle Telychian, Llandovery (Silurian), based on the presence of *Stimulograptus clintonensis* (see Loydell *et al.* 2007, fig. 10). The species is based on a single small fragment; details of thecae are uncertain. Bouček (1957, fig. 65) illustrated a number of specimens under this name showing the thecal style in more detail. This relatively nice material with larger, branching colonies shows some details of the stipes in relief. Bouček's (1957) material originated from the upper Wenlock *Cyrtograptus radians* Biozone, correlated with the *Cyrtograptus lundgreni* Biozone of the lower Homerian by Štorch (2023).

Ptilograptus hicksii Hopkinson, 1875 *in* Hopkinson & Lapworth (1875, p. 661, pl. 36, fig. 1a, b). Lower Arenig, Ramsey Island, Wales. Holotype SM A17492a, b (counterparts). (Fig. 5C). The locality also yielded specimens of *Arienigraptus stellus* (Hopkinson, 1875) *in* Hopkinson & Lapworth (1875), as revised by Jenkins (1982), suggesting a latest Dapingian to early Darriwilian age. The species is based on a single, poorly preserved specimen showing possibly monoprogressive branching. The specimen shows strong tectonic deformation and the presence of pressure shadow minerals. It is indeterminable at both genus and species level.

Ptilograptus mirus Ni, 1979 *in* Mu *et al.* (1979, p. 40, pl. 12, fig. 11). Lower Darriwilian, China. A single poor fragment with one possible branching, but no thecal details in the photo; thus the specimen is indeterminable.

***Ptilograptus patens* Ruedemann, 1947** (p. 246, pl. 33, fig. 16, 17). Green Point Shale, St. Paul's Inlet, western Newfoundland, Canada. A single, small fragment with one dichotomous branching and monoprogressive branching producing short secondary stipe; stipes loosely spaced, no thecal details (Fig. 3D). The age is uncertain as the St. Paul's Inlet locality bears strata from the *Paratetragraptus approximatus* Biozone (basal Floian) to the *Levisograptus dentatus* Biozone (lower Darriwilian) (see Williams & Stevens 1988).

***Ptilograptus pennatus* Obut & Rytzk, 1958** (p. 133, pl. 6, fig. 1, 1a) (Figs 3F, 5H). Pirgu Regional Stage, Estonia. According to Meidla *et al.* (2023, fig. 3) this is upper Katian. A single small fragment of a robust taxon, similar to *Ptilograptus geinitzianus*, has been illustrated.

***Ptilograptus poctai* Ruedemann, 1908** (p. 148, pl. 1, fig. 8, text-fig. 53) (Fig. 3E). Sandbian (Upper Ordovician, Normanskill Shale; Glenmont, Albany, New York, USA. The species is based on a single small fragment associated with *Dicranograptus nicholsoni diapason*. The thecae appear to show strong ventral extensions or rutelli. Ruedemann (1908, p. 148) considered the species to be intermediate between *Ptilograptus plumosus* and *Ptilograptus geinitzianus* in stipe thickness.

non *Ptilograptus*? *pribyli* Bouček, 1957 (p. 139, pl. 39, fig. 1, text-fig. 66). Přídolí (upper Silurian), Velká Chuchle, Czech Republic. The species is characterized by a strongly zigzag-shaped stem with long secondary stipes with smooth rims. These secondary stipes widen distally, suggesting that it is not a graptolite, nor belongs to a benthic encrusting taxon in which the 'secondary stipes' represent long thecal tubes as present in *Sphenoecium*. The species is here excluded from *Ptilograptus*.

***Ptilograptus ramale* Počta, 1894** (p. 203, pl. 2, figs 26–30). Middle Berounian (upper Sandbian), Upper Ordovician (Kraft *et al.* 2023), Vinice Formation, Czech Republic. The material includes a few small fragments showing monoprogressive branching. Thecal details are not available. Gutiérrez-Marco *et al.* (2022, p. 219) considered the species to be closely related to their *Ptilograptus* aff. *glomeratus*. The species is indeterminable at the moment, but the type material needs to be redescribed. The assignment to *Ptilograptus* is convincing from the original illustrations.

***Ptilograptus rectus* Ruedemann, 1947** (p. 279, pl. 42, fig. 9) (ex *Stelechograptus*). Katian (Upper Ordovician), Ottosee Shale, Tennessee, USA. The species is based on a poorly illustrated fragment with a main stem and alternating second order stipes, apparently forming a monoprogressive development. Maletz (2020) synonymized *Stelechograptus* with *Ptilograptus*.

***Ptilograptus reussianus* (Goeppert, 1860)** (p. 35, pl. 36, fig. 14a, b) (Figs 1A, 3L). According to Goeppert (1860), the specimen is from the upper Silurian Formation of Bohemia, from grey limestones of Barrande's Étage D at Dlouhá hora, SE of Beroun. '*The whole cluster of localities designated as Dlouhá hora (in the neighbourhood of Kosov Quarry) belong to the Kopanina Formation (Ludlow) or Požáry Formation (Pridoli)*' (pers. comm. Petr Štorch, March 2020). Thus, a precise locality and age cannot be provided, but a late Silurian age is likely for the specimen. The species may represent the youngest known member of the genus.

Ptilograptus rigidus Mu, 1993 *in* Mu *et al.* (1993, p. 91, pl. 3, figs 5–7) (English description on p. 323), Fig. 5 is holotype. Upper Katian (Ordovician), *Paraorthograptus uniformis* Biozone, China. The species may be a synonym of *Ptilograptus geinitzianus*. Especially the holotype (Mu

et al. 1993, pl. 3, fig. 5) is well preserved and shows the characteristic stipe width and monoprogressive branching of *P. geinitzianus*.

Ptilograptus scalaris Sherrard (1956, p. 89, pl. 8, fig. 11). New South Wales, Australia. Probably Sandbian, Upper Ordovician (*Climacograptus bicornis*, *Orthograptus calcaratus* and *Dicellograptus elegans* are associated). A single indeterminable fragment with denticulate thecae and spines; but these details are not visible in the poor photo.

***Ptilograptus sibiricus* Obut & Sobolevskaya, 1967** (p. 53, pl. 8, fig. 6; pl. 9, figs 2, 3; pl. 10, figs 1–8; pl. 11, figs 1–5). Ordovician, Norilsk Region, Siberia, Russia. The material consists of poorly preserved shale material, but also a few chemically isolated thecae showing ventral extensions in the form of rutelli or spines on partly isolated thecal apertures (Obut & Sobolevskaya 1967, pl. 11). It is, however, uncertain whether all specimens belong to the same taxon.

non *Ptilograptus sichuanensis* (Mu *et al.*, 1974) (p. 155, pl. 67, fig. 16) (ex *Zigzagigraptus*). NIGP 21398a, b. A single fragment has been illustrated (also by Mu *et al.* 2002, pl. 7, fig. 9). The specimen appears to show a stem with a number of dichotomous branchings, but not a clear monoprogressive branching of the stipes. Thus, this species is not regarded as representing *Ptilograptus*. Its fan-shaped tubarium could alternatively be identified as a species of the genus *Dendrograptus* with dense spacing of proximal branchings, but thecal details are not available.

***Ptilograptus sinicus* (Mu, 1955)** (p. 22; p. 53 – English text, pl. 8, figs 6–8) (ex *Ptilograptus glomeratus* var. *sinicus*). The specimens are from the Huloan, Middle Ordovician (now uppermost Darriwilian to lower Sandbian: Zhang *et al.* 2023, fig. 2), of North China. NIGP 7349, 7350a, b. Two small fragments have been illustrated, one of them also by Mu *et al.* (2002, pl. 7, fig. 7). They appear to represent *Ptilograptus*.

non *Ptilograptus sparsus* Ruedemann, 1947 (p. 248, pl. 33, figs 21–26). Katian (Upper Ordovician), Ottosee Shale, USA. Several poorly illustrated specimens with uncertain development. It appears that the thecae point alternately to the right and left sides. This is not *Ptilograptus*, but needs to be revised.

non *'Ptilograptus' spiculifolius* Lin (1992, p. 50, pl. 21, figs. 1–2; text-fig. 6). NIGP 68509, also figured by Mu *et al.* (2002, pl. 7, fig. 10). *Callograptus taizehoensis–Dictyonema flabelliforme orientale* Biozone, Tremadocian, Lower Ordovician, Yehli Formation, North China. The single specimen was referred as a possible alga to the genus *Plumalina* and is now named *Plumalina*? *spiculifolia* (Lin, 1992) (see Maletz *et al.* 2025).

***Ptilograptus suavis* Počta, 1894** (p. 204, pl. 1, figs 23–25) (Fig. 3C). Darriwilian (Middle Ordovician), Šárka Formation, Czech Republic. The species is based on two small fragments showing little detail in the poor illustrations. Počta (1894) referred the species only with reservation to *Ptilograptus*. Kraft *et al.* (2023, fig. 5) indicated the origin of the material from the Šárka Formation and illustrated a different specimen, indicating that it is a 'common species'. However, it has never been revised or redescribed. The zigzag main branches with monoprogressive secondary stipes support inclusion in *Ptilograptus*, even though there are no thecal details available.

non *Ptilograptus suecicus* Wiman, 1895 (p. 301, pl. 12, figs 11, 13). Katian (Upper Ordovician), Sweden. The stipes are complex with slender, parallel-sided thecal tubes and produce twigs as short extensions from the main stipes. There is no indication of the zigzag monoprogressive branching found in *Ptilograptus*. The species was referred to *Acanthograptus* by Ruedemann (1908) and its tubarium construction analyzed by Bulman (1937).

non *Ptilograptus tenusissimus* Ruedemann, 1904 (p. 591, pl. 4, fig. 13). Upper Floian (Lower Ordovician), *Didymograptellus bifidus* Biozone, Deepkill, New York. The species is based on a single very slender fragment and could be referred to *Plumalina*? *spiculifolia*. It should be excluded from *Ptilograptus*.

non *Ptilograptus tenuiramosus* Ruedemann, 1904 (listed *in* Ruedemann 1908, p. 132; most probably a misspelling of *Ptilograptus tenuissimus*).

***Ptilograptus thuringicus* Schmidt, 1940** (p. 123, pl. 1, figs 1–3). Katian (Upper Ordovician), Schmiedefeld Formation ('Oberer Erzhorizont'), Germany; see Kemnitz *et al.* (2017). One poor specimen is available, the type species of the subgenus *Denticulograptus* Schmidt, 1940 (syn. of *Ptilograptus*; see Maletz 2020, 2023). The specimen is too poor for a proper identification, but can be referred to *Ptilograptus*.

***Ptilograptus venetus* Gortani, 1923** (p. 8, pl. 1, fig. 3) (Fig. 3I). Llandovery (Silurian). Carnic Alps. The age is probably Aeronian, Llandovery, lower Silurian, based on the identification of *Pribylograptus argutus* (see Gortani 1923, p. 8). A single illustrated specimen shows a wider main stem with monoprogressive branching of stipes

showing simple, low inclined thecae without distinct rutelli.

non *Ptilograptus yidouensis* Li, 1984 (p. 446, pl. 178, figs 1–3); see also Mu *et al.* (2002, pl. 7, fig. 2). Upper Tremadocian, Lower Ordovician (*Acanthograptus sinensis* Biozone), South China. The very poor illustration of the small specimens do not provide enough information to determine the identity of the material. The shape makes it likely to represent fragments of *Acanthograptus sinensis* Hsü & Ma, 1948.

***Ptilograptus yui* Lin, 2002** *in* Mu *et al.* (2002, p. 51, pl. 7, fig. 8) (Fig. 5E). Darriwilian, Middle Ordovician, Shihtien Formation, Baoshan, Yunnan Province, China. NIGP 14331 (holotype). The species is based on a single poorly preserved fragment showing a main, somewhat zigzag shaped stem (imprint only) and partially preserved secondary stipes formed in a monoprogressive fashion, originally described as *Ptilograptus* aff. *plumosus* Yu, 1962. The tubarium is about 25 mm long. Branching of the main stipe is not present. Most parts of the fusellum are flaked off and only parts are preserved in the specimen. The secondary stipes are about 3 mm long and 0.2–0.25 mm wide. Towards the distal end, the secondary stipes are shorter. Details of the thecae are not available.

Ptilograptus yunnanensis (Yu, 1962) (p. 50, pl. 1, figs 1–4), ex *Zigzagigraptus.* NIGP 14329, 14330. Middle Ordovician, Darriwilian, Baoshan, Yunnan Province, China. Zhang *et al.* (2009a, b) described the fauna from the Shihtien Formation and referred the interval to the *Didymograptus artus* and *Didymograptus murchisoni* biozones. Zhang *et al.* (2009a, p. 311) synonymized the species with *Ptilograptus poctai* Ruedemann, 1908. The species shows several branchings on the main zigzag shaped stem indicating monoprogressive branching. Simple, inclined thecae are visible in certain places.

Acknowledgements

Jörg Maletz was supported by Deutsche Forschungsgemeinschaft project DFG 1269/10-1. This paper is a contribution to project PDI2021-125585NB-100 of the Spanish Ministry of Science, Innovation and Universities and Agencia Estatal de Investigación (to J.C.G.-M). It is a contribution to IGCP project 735 (Rocks and the Rise of Ordovician Life). Yuandong Zhang (NIGPAS, Nanjing, China) provided important information and publications on some Chinese species of the genus *Ptilograptus* and together with Xue-Jian Zhu (NIGPAS, Nanjing) provided access to additional graptolite material in the NIGPAS type collection. The paper benefited considerably from remarks by the Handling Editor David K. Loydell (Portsmouth, UK), by Lucy Muir (Cardiff, UK) and an anonymous reviewer.

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