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The Lower Ordovician (Tremadocian to Floian) graptolite fauna of Hunneberg, Västergötland, Sweden

Jörg Maletz

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Cover picture: *Hunnegraptus copiosus* from Storeklev, Hunneberg (see Fig. 21F, G). The genus is named by Lindholm (1991) after the Hunneberg Mountain from which the species was described.

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by

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The Diabasbrottet section at Hunneberg, Västergötland, Sweden is the type section (GSSP) for the Floian Stage, the second stage of the Ordovician System. The base of the Floian is determined by the First Appearance Datum (FAD) of the graptolite species *Paratetragraptus approximatus*, appearing at the same level as the typically Scandinavian *Tetragraptus phyllograptoides*, allowing the level to be determined also where the index species is lacking. The section is correlated worldwide through the presence of its graptolite faunas, but also through the presence of conodonts of the *Paroistodus proteus* conodont zone. Research in the graptolite faunas of Hunneberg and surrounds began in the late 19th and early 20th century, but a detailed taxonomic treatment has not been undertaken hitherto. This is despite the biostratigraphic ranges of the main faunal elements being well known and used for the definition of the Diabasbrottet section as the Global Stratopype Section and Point (GSSP) for the Floian. The revision of the faunas documents the most complete and highly diverse graptolite faunas from the late Tremadocian to early Floian known worldwide and also indicates a considerable biogeographical faunal differentiation in this time interval. The faunal composition indicates higher latitude faunas with a number of cold-water endemic faunal elements.

New species are *Jishougraptus hunnebergensis* n. sp., *Tetragraptus gerhardi* n. sp., *Baltograptus novus* n. sp., *Baltograptus floianus* n. sp., and *Cymatograptus kristinae* n. sp. ☐ Ordovician, Graptolithina, Hunneberg, Västergötland, Sweden, Tøyen Shale Formation, biostratigraphy, palaeogeography, taxonomy.

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Introduction

The region of Västergötland in west-central Sweden (Fig. 1A) provides a unique opportunity for geologists to investigate the Lower Palaeozoic succession once covering large parts of Baltoscandia. This succession has subsequently been eroded and few remains are preserved. The main reason for the preservation of the remnants on the once extensive blanket of sediments covering the peneplained Precambrian basement (see Rudberg 1970; Lidmar-Bergström *et al.* 2017) is the intrusion of large volumes of magma during the late Palaeozoic rifting of the Oslo Graben and related structures. In Västergötland, this led to the formation of thick dolerite sills intruding the Palaeozoic succession at various levels and leaving up to 100 m thick layers of hard and resistant rocks, now covering and protecting the softer sedimentary rocks from erosion. At Hunneberg and Halleberg (Fig. 1B), the Permian dolerite sill is up to 100 m thick and forms steep slopes and often vertical cliffs around the mountains. The Palaeozoic sediments are preserved and accessible only at the foot of these cliffs and have been mined extensively in the 18th and 19th centuries, leaving large complexes of caves reaching many metres into the sedimentary strata, with wide pillars of sediments left to support the roof of the caves. Here, the sedimentary successions and the included fossil faunas can be investigated in great detail. The caves are largely found in the late Cambrian Alum Shale Formation, but at a number of localities, in the vertical walls below the dolerite sill, remnants of Ordovician sediments are preserved.

The scientific investigation of the geology of the Hunneberg and Halleberg region is connected to eminent earlier Swedish scientists like Nils Peter Angelin (1805–1876), Jonas Gustaf Oscar Linnarsson (1841–1881) and Anton Hilmer Westergård (1880–1968). Prior to this, Wilhelm Hisinger (1797) had investigated the sedimentary successions of Västergötland

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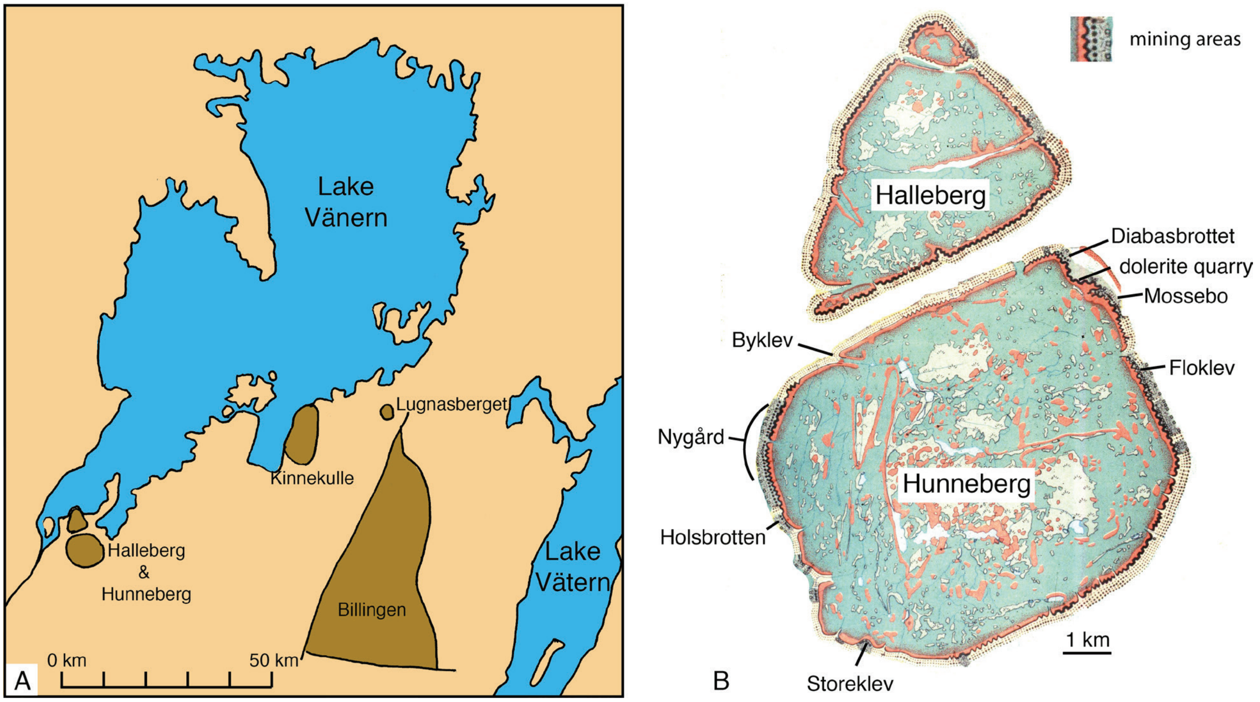

Fig. 1. **A**. Overview map of Västergötland, Sweden. **B**. Halleberg and Hunneberg, geomorphological map showing mining areas around the mountains associated with the fossil localities (map after Rudberg *et al.* 1976).

and had provided a generalized map and geological section through the lithological succession at Halleberg and Hunneberg. Angelin (1854) discussed the 'Regio Ceratopygorum' (*Ceratopyge* Region) from the Hunneberg Mountain and described some trilobites, probably from the vicinity of the modern Diabasbrottet section (cf. position of Mossebo locality *in* Hisinger 1797, pl. 2).

The detailed palaeontological investigation of the Hunneberg and Halleberg succession began later, when Törnquist (1901, 1904) described the Ordovician graptolite faunas. Moberg & Segerberg (1906), Westergård (1909, 1922, 1944) and Wallerius (1930) described the Cambrian to Lower Ordovician trilobite succession of southern Sweden and provided information also from the Hunneberg sections, but it is due to the precise work of Tjernvik (1956) that the upper Tremadocian to Floian (Lower Ordovician) trilobite faunas are now well known. The conodont studies of Lindström (1957), Andres (1981) and Löfgren (1993) are the only work done on microfossils.

Hunneberg in Västergotland became well known for its Lower Ordovician graptolite faunas, even though the faunas have rarely been treated taxonomically and quite a number of faunal elements remained undescribed, but can be found in many older collections (e.g. the Törnquist collection at Lund University; Swedish Museum of Natural History, Stockholm; Sveriges Geologiska Undersökning, Uppsala). Linnarsson (1869, pp. 6, 15) discussed the succession of Västergötland and mentioned the richness of graptolites in the 'Undre Graptolithskiffer' at Hunneberg, but at the time, these faunas were not treated systematically and no illustrations were provided. Linnarsson (1871a) described *Adelograptus tenellus* (Linnarsson, 1871) from the upper part of the Alum Shale Formation at Nygård on the western side of Hunneberg, but did not mention the younger graptolite faunas. Moberg (1892) described additional material from Nygård of the same species under a variety of names (revised by Maletz & Erdtmann 1987).

A few Lower Ordovician graptolites were described by Holm (1881), who introduced *Holograptus expansus* from the Phyllograptus Shale of Mossebo, a species now known to have come from the *Tetragraptus phyllograptoides* Biozone. Törnquist (1901, 1904) described the graptolite faunas of Hunneberg in some detail and erected a number of new species. At the same time, Strandmark (1902) described *Tetragraptus phyllograptoides* from Mossebo, based on material collected by Moberg, a species that had long been known under this name by Linnarsson 'in museo'. These were the only detailed studies of Hunneberg graptolites and the succession at Hunneberg has long been neglected until the discussion of the Hunnebergian Substage began (cf. Tjernvik 1956; Tjernvik & Johansson 1980), and Lindholm (1991a, b) described the *Kiaerograptus supremus* to *Hunnegraptus copiosus* biozones, now included in the late Tremadocian, from Västergötland, Scania and the Oslo Region of Norway. A number of graptolites have been described and illustrated in various publications (Erdtmann *et al.* 1987; Lindholm & Maletz 1989; Lindholm 1991a; Maletz *et al.* 1991; Maletz 1996a, 1996b), but this is the first comprehensive taxonomic revision of the graptolite faunas from Hunneberg.

Due to the search for a GSSP (Global Stratotype Section and Point) section for the base of the second stage of the Ordovician System, Maletz *et al.* (1995, 1996) proposed the Diabasbrottet section at Hunneberg (Fig. 2) as the international level for correlation, a proposal that was accepted and documented in detail by Bergström *et al.* (2004, 2006). Thus, the first appearance datum (FAD) of the graptolite *Paratetragraptus approximatus* in the Diabasbrottet section (Fig. 2C) became the accepted level for global correlation of the base of the time interval, now known as the Floian Stage of the Ordovician System. The level has the advantage to be equivalent to the base of the local Scandinavian *Tetragraptus phyllograptoides* Biozone, enabling the correlation of endemic and pandemic graptolite faunas in the Early Ordovician. Subsequently, Egenhoff & Maletz (2007, 2012) investigated the sedimentology and biosequence stratigraphy of the Hunneberg succession and provided a detailed sedimentological analysis of the lower Palaeozoic succession of the region. Egenhoff & Maletz (2007) also presented updated biostratigraphic range charts for a number of sections, but did not describe or illustrate the graptolite faunas.

Geological setting

Hunneberg and Halleberg (Figs 1B, 2A) represent the southwesternmost extension of the Precambrian peneplain of Västergötland with its typical table mountains formed from Permian dolerite sills overlying Palaeozoic sediments (Streng 1858; Törnebohm 1877a, b; Svedmark 1878; Merian 1885; Troedsson 1923; Mulder 1971). While the general succession and development of the Palaeozoic sediments and their geological setting were already known through the initial mapping projects of Sidenbladh (1870) and Lindström (1887), many details of the succession had been neglected by subsequent authors.

The peneplained Precambrian basement beneath the Hunneberg and Halleberg mountains is covered by a Cambrian to Lower Ordovician succession about 60 m in thickness, but only part of the strata is exposed in currently accessible outcrops. Thus, the exact thickness of some of the individual units is uncertain. The succession starts with the File Haidar Formation (Jensen & Ahlberg 1998; Nielsen & Schovsbo 2011), previously termed the Eophytonsandstein by Linnarsson (1871b) or the Fucoidsandstein by Lindström (1887). It attains a thickness of ca 24 m (Lindström 1887) and is poorly exposed. Trilobites in the File Haidar Formation show that it correlates with the Cambrian Series 2 (see Cederström *et al.* 2012). Nielsen & Schovsbo (2006, p. 70) recognized an unconformity at the top of the File Haidar Formation, identified as the Hawke Bay hiatus or regression (Bergström *et al.* 1982; Ahlberg 1998, fig. 14) and overlain by a sandy conglomerate (first noted by Hansen 1933 at Hunneberg) that forms the basal part of the Alum Shale Formation. The conglomerate is overlain by the Cambrian Alum Shale Formation of Middle to late Cambrian age (cf. Martinsson 1974; Ahlberg 1998). The succession spans the Cambrian Series 3 to the top of the Cambrian and appears to be incomplete in the Hunneberg area (Weidner *et al.* 2004; Nielsen & Schovsbo 2006). The upper part of the Furongian and the lowermost part of the Tremadocian (Ordovician) are missing, with the Bjårkåsholmen Formation directly overlying a thin, less than 0.5 m thick, massive glauconitic layer on top of the Furongian *Peltura minor* trilobite zone interval (Tjernvik 1956; Egenhoff & Maletz 2012). Thus, a number of trilobite zones are missing in the region (see Terfelt *et al.* 2008, 2011 and Nielsen *et al.* 2020 for Furongian trilobite zonation). Rasmussen *et al.* (2016) revised the upper Cambrian trilobite succession at Nygård and recognized the *Ctenopyge bisulcata* Zone of the *Peltura* Superzone as the youngest trilobite interval. The zone is correlated with the *Trilobagnostus holmi* agnostoid Zone of Terfelt *et al.* (2011), indicating a considerable gap of the succession in the upper Cambrian.

Andres (1981, 1988) discussed the record of upper Cambrian conodonts from Hunneberg. The precise origin of this material is uncertain, but Andres (1988, p. 109) stated that it orignated from the northern slope of Hunneberg, 400 m east of Nygård, ca 6 m below the base of the dolerite. His assignment to the *Agnostus pisiformis* Biozone must be wrong, as this taxon is found in the Guzhangian (Miaolingian or Cambrian Series 3). The succession described by Rasmussen *et al.* (2016, fig. 7) suggests that the material originated from the upper part of the *Olenus* Superzone, as the *Parabolina spinulosa* Biozone occurs at ca 5 m below the top of the Cambrian in the Nygård section. The Ordovician part of the succession at Nygård is less than 1 m thick (see Maletz 1987), but has not been described in detail.

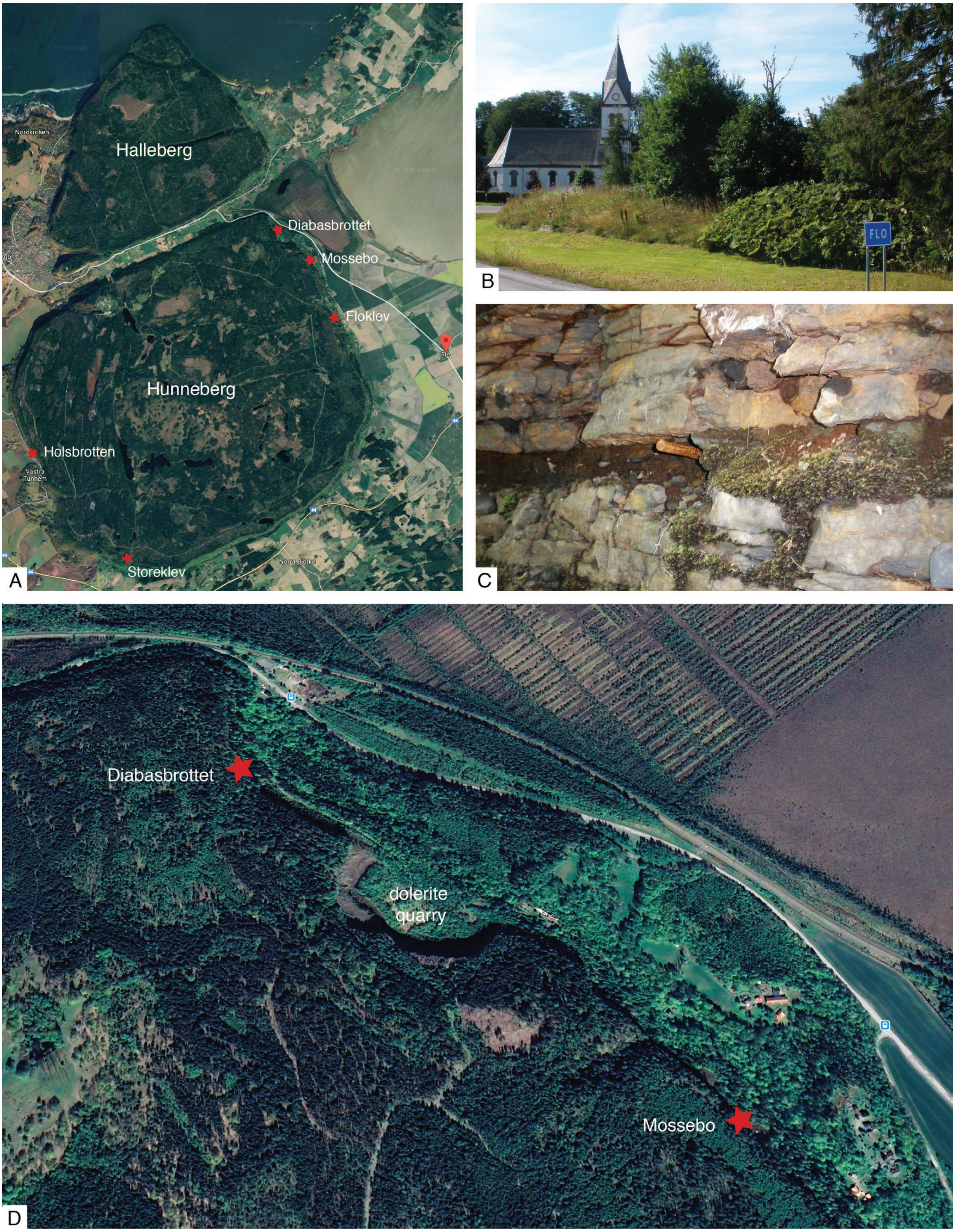

Fig. 2. **A**. Hunneberg and Halleberg (Google Earth Maps). **B**. View at the entrance to Flo, showing Flo Kyrka, Västergötland, Sweden, the name giver of the Floian Stage of the Ordovician System. **C**. The 'Golden Spike' at the GSSP level at Diabasbrottet (photo JM, 2011). **D**. Detailed map of the Diabasbrottet-Mossebo region (Lilla Mossebo & Stora Mossebo of Sidenbladh 1870).

Locality Information

The successions at Holsbrotten and Storeklev on the W slope of Hunneberg and the Diabasbrottet and Mossebo sections on the NE slope together represent the most complete successions of Lower Ordovician (lower Floian) graptolite faunas found in any exposure in southern Scandinavia. The strata are partly contact metamorphosed and preserved flat lying, but tectonically undisturbed on the Precambrian basement, protected from erosion by the cap of dolerite. The biostratigraphy of the Storeklev and Mossebo sections was first documented by Tjernvik (1956), who used trilobites for his biozonation of the late Tremadoc to early Arenig time interval (now the late Tremadocian to Floian).

Outcrops are present around Hunneberg and Halleberg virtually everywhere where old limestone quarries are present (Fig. 1B). Sidenbladh (1870) provided the best-known cross-section showing the connection between the successions of Hunneberg and Halleberg (Fig. 3). He documented the fault between the two table mountains, not known to Hisinger (1797), that produced a deep incision and estimated a displacement of more than 24 m. Modern estimates suggest about 30 m for the uplift (Martinsson 1974; Hall *et al.* 2019). The precise age of the fault is uncertain, but must be post-Silurian (Ahlin 1987) and must also be younger than the Permian intrusions as the situation of the Lilleskog Fault between Hunneberg and Halleberg indicates (see Lidmar-Bergström *et al.* 2017; Hall *et al.* 2019).

At Halleberg, exposures are generally found in the middle to upper Cambrian Alum Shale Formation, but non-fossiliferous black shales of possibly Tremadocian age are present at Skytteklev on the eastern margin of Halleberg (Maletz 1987). The Tøyen Shale Formation has not been reported from Halleberg, as the contact between the dolerite and the sedimentary rocks is at the level of the middle to upper Cambrian, as shown by Sidenbladh (1870) (Fig. 3). The individual sections around Hunneberg are easily correlated lithologically and biostratigraphically. Certain marker beds can be followed for hundreds of meters along the outcrops.

Storeklev

The locality Storeklev (N58°17'38"; E12°25'53.5") is the type locality of the Scandinavian Hunneberg stage of Tjernvik (1956). The trilobite faunas were described by Tjernvik (1956) who also discovered the important 'dichograptid horizon', later described to belong to the *Hunnegraptus copiosus* Biozone and found widely distributed in southern Scandinavia (Lindholm 1991a, b). Tjernvik (1956, p. 117) defined the base of his Hunneberg Group on the presence of the trilobite *Megistaspis* (*Ekeraspis*) *armata* in this section (Fig. 4).

The Tøyen Shale interval differs considerably from the localities on the NE corner of the mountain. Here the shale interval is much thicker and greyish green instead of black, but this color may be largely due to the contact metamorphism. Graptolites are uncommon and poorly preserved, but still identifiable even in the metamorphosed upper part of the succession. Individual limestone layers can be correlated with Mossebo and Diabasbrottet by their trilobite and conodont faunas (Tjernvik 1956; Maletz *et al.* 1996).

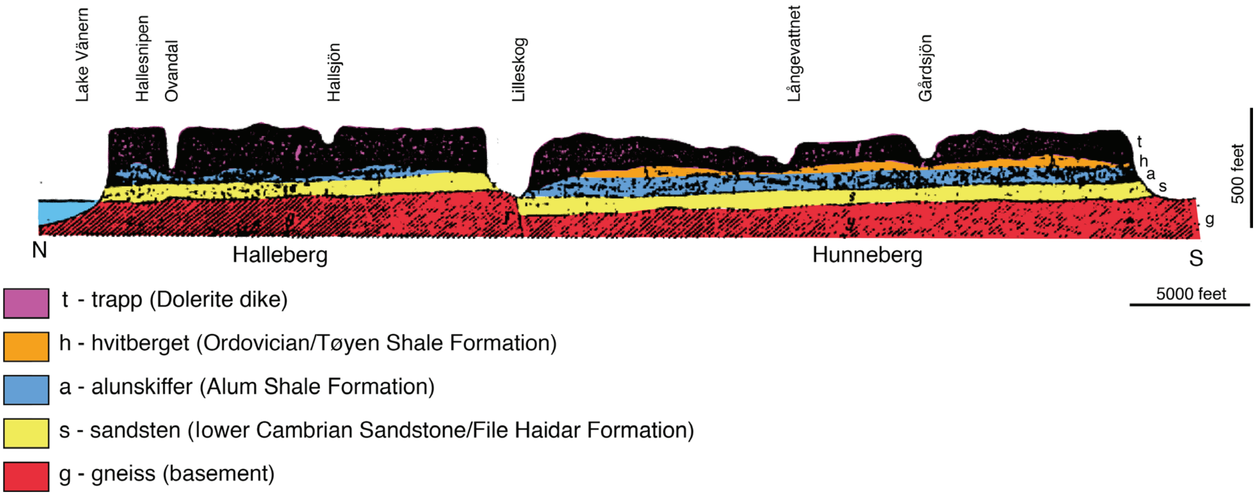

Fig. 3. Cross-section of Hunneberg, colored and modified after Sidenbladh (1870, fig. on p. 48). Scale in feet as originally indicated and not converted to meters.

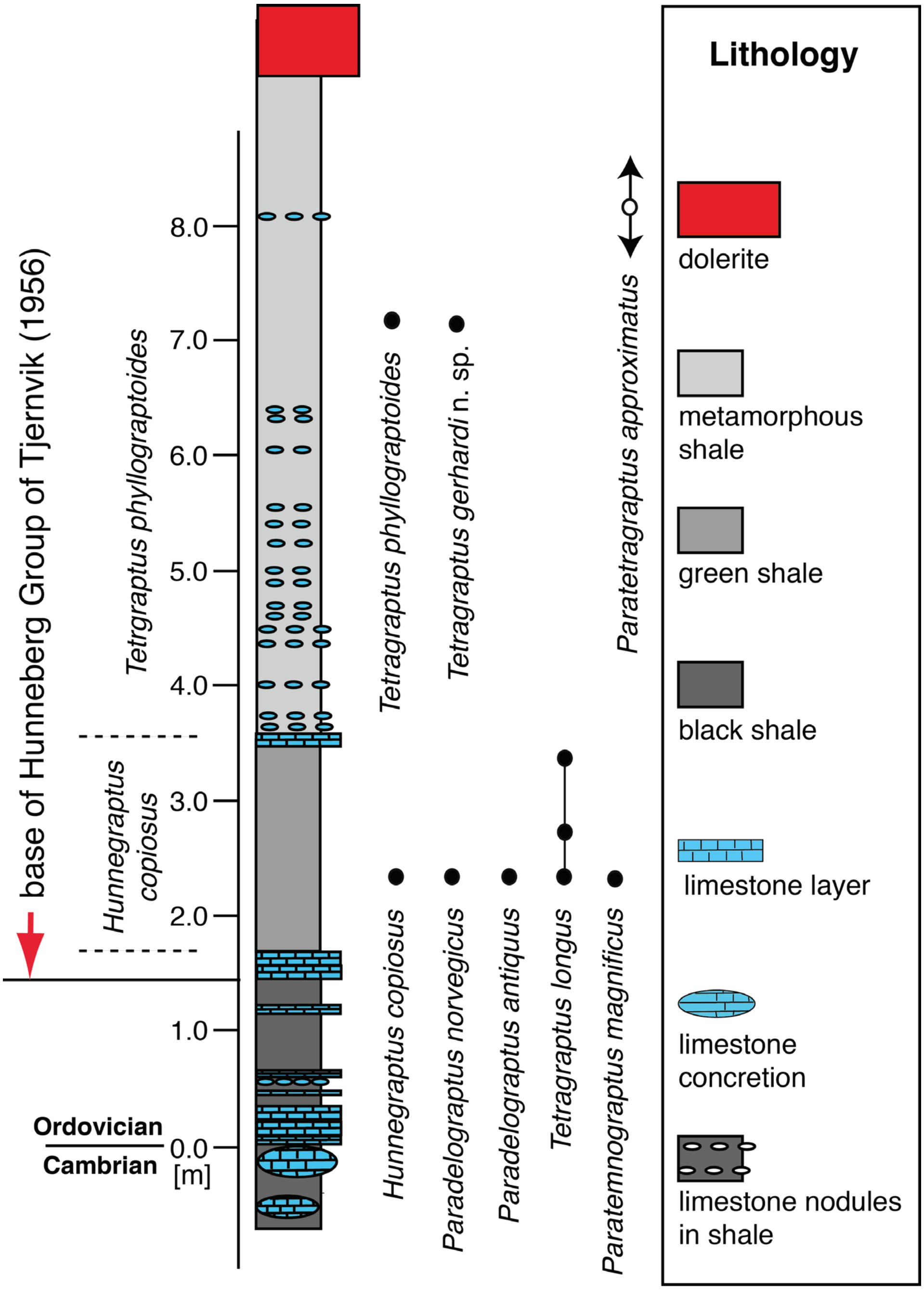

Fig. 4. The graptolite succession at Storeklev, based on Egenhoff & Maletz (2007). The base of the Hunneberg Group of Tjernvik (1956) is marked. Lithology explanations for Figures 4–7.

Tjernvik (1956) discovered the main layer with the *Hunnegraptus copiosus* Biozone fauna at Storeklev, but rare graptolites can be found at a number of levels of the whole approximately 2 m thick interval (Fig. 4). The *Hunnegraptus copiosus* Biozone fauna was found at only three localities in the Hunneberg area. It is present at Holsbrotten and Storeklev in green shales, but in a small pit a few tens of meters west of Storeklev, *Hunnegraptus copiosus* was discovered in an interval of black shales. The presence of *Tetragraptus phyllograptoides* and *Prothorthis hunnebergensis* indicate an increased thickness of the *Tetragraptus phyllograptoides* Biozone interval at Storeklev. *Paratetragraptus approximatus* was found on loose slabs in the higher part of the section, exposed above the cliff section in the forest, where it is associated with *Tetragraptus phyllograptoides*.

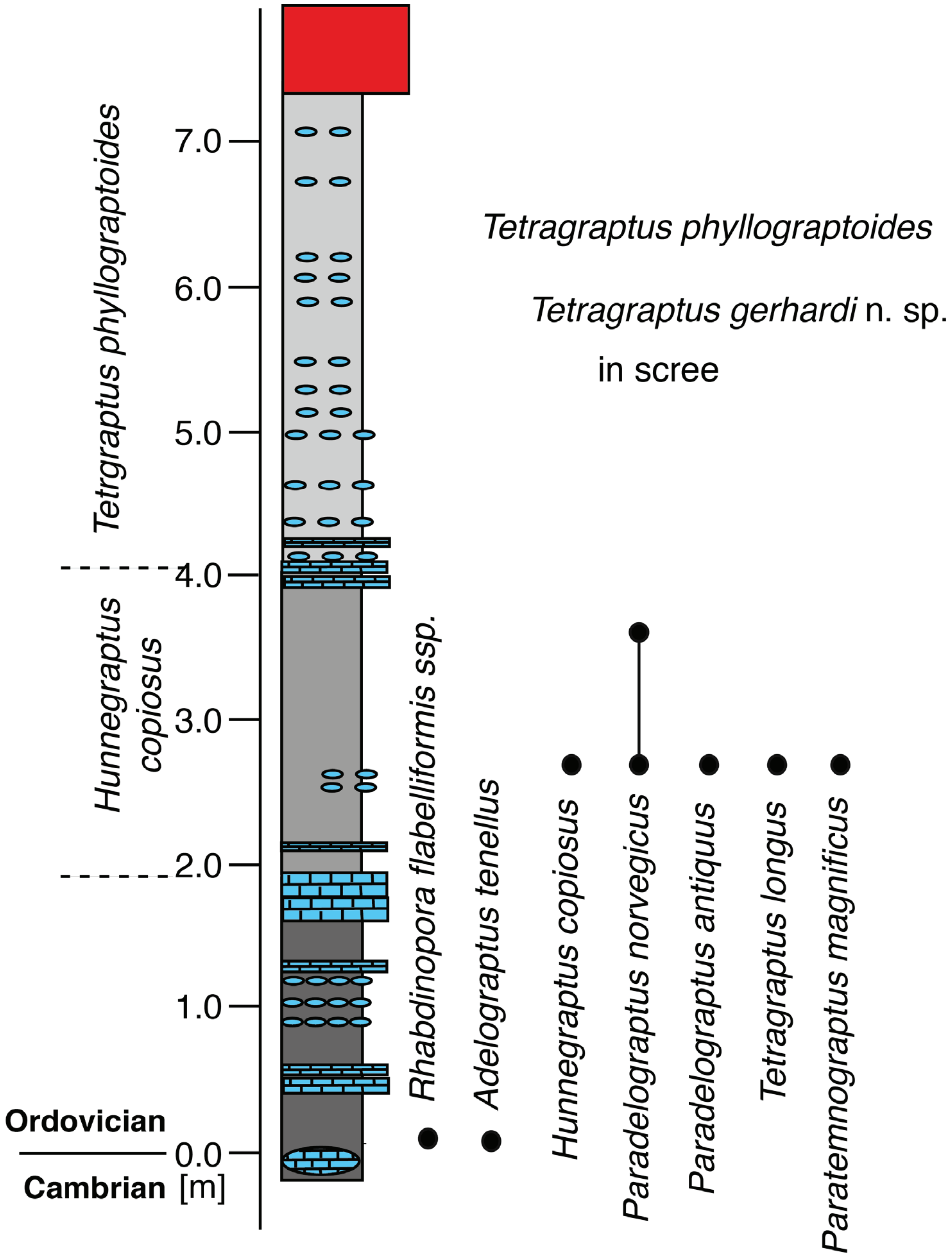

Fig. 5. The graptolite succession at Holsbrotten, based on Egenhoff & Maletz (2007).

Holsbrotten

The locality Holsbrotten (N58°19'12.9"; E12°23'42"), on the western side of Hunneberg (Fig. 2A) has a nearly identical lithology to the Storeklev locality. The succession ranges from the upper Cambrian *Peltura scarabaeoides* Trilobite Zone to the *Megistaspis* (*Paramegistaspis*) *planilimbata* Trilobite Zone (Fig. 5). Löfgren (1993) documented the conodont faunas from the section and from the comparable Prästeklev section a little further south. Graptolites are present at a few levels at Holsbrotten, but have not been described previously. Except for the main *Hunnegraptus copiosus* band, graptolites are rare and poorly preserved in the grey shales of the Tøyen Shale Formation and only a few specimens have been collected from the contact metamorphosed shales.

Tremadocian graptolites can be found in a thin band of shale at the base of the upper Alum Shale Formation (previously *Dictyonema* Shale). Numerous specimens of *Rhabdinopora flabelliformis* occur crowding a thin layer of shale. In other parts of the interval, few metres along strike, specimens of *Adelograptus tenellus* occur at roughly the same level. These graptolites, however, are extremely rare and mainly preserved as small fragments. *Rhabdinopora flabelliformis* and *Adelograptus tenellus* do not occur together and must have originated from different biostratigraphic and lithostratigraphic intervals (see Egenhoff & Maletz 2012, fig. 2).

Nygård

The Nygård locality on the western slope of Hunneberg, north of Holsbrotten, was first noted by Linnarsson (1869) and the graptolites were subsequently described by Linnarsson (1871a) as the first graptolites to be described and illustrated from Hunneberg. The precise origin of this material, however, is unknown, as there are a number of small pits along a long line of caves (Fig. 1B) on the western to northwestern slopes of the mountain, over a distance of more than two km, where Tremadocian graptolites can occasionally be found. Moberg (1892) described *Adelograptus tenellus* (Linnarsson, 1871a) from 'Skaktet No. 1 at Nygård' and added *Adelograptus hunnebergensis*, now a junior synonym (Maletz & Erdtmann 1987) from the same layers. Sidenbladh (1870, fig. 4) illustrated the highly uneven surface of the lower Tøyen Shale Formation (his unit hvitberget) under the dolerite in the area between Nygård and Holsbrotten.

Rasmussen *et al.* (2016) provided precise locality data for their Nygård section, but the location on their map does not fit the information and is much closer to the section here identified as Holsbrotten. Their succession at Nygård starts in the late Cambrian (Furongian) *Olenus* Superzone, overlain by the *Parabolina, Leptoblastus, Protopeltura* and *Peltura* superzones (Rasmussen *et al.* 2016). The *Ctenopyge bisulcata* Biozone is unconformably overlain by the Ordovician succession with *Adelograptus tenellus* or *Rhabdinopora flabelliformis*, indicating probably a time of erosion during the latest Cambrian time interval. The Ordovician strata usually only reach the *Megistaspis* (*Ekeraspis*) *armata* Biozone, and faunas of the Tøyen Shale are not preserved under the dolerite sill at this locality.

Diabasbrottet

The modern Diabasbrottet section (N58°21'47"; E12°29'46.5") (Fig. 6) is the GSSP (Global Stratotype section and Point) of the Floian Stage of the Ordovician System (Maletz *et al.* 1995, 1996; Bergström *et al.* 2004, 2006) at the NE edge of Hunneberg, an important international level for geological correlation. The section is adjacent to a now inactive quarry (Fig. 2D), in which the overlying dolerite was mined for road construction material and other purposes.

Based on the description in Sidenbladh (1870, p. 72) this locality is the old Lilla Mossebo, probably also identified as Mossebo by early graptolite workers (e.g. Holm 1881; Törnquist 1901, 1904). The dolerite sill described and illustrated by Sidenbladh (1870, fig. 10) is recognizable in the modern section (Fig. 6) and can be followed for some distance from the section to the NW, where it merges with the overlying massive dolerite cap. The lowermost levels of the succession at Diabasbrottet can be found in the mines below the vertical cliffs. These were made during the exploration for limestones in the upper Cambrian Alum Shales. The GSSP at the base of the Floian is positioned at the 2.10 m level in the section initially described and figured by Maletz *et al.* (1995, 1996), shown as the 0.0 m level here (Fig. 6). This level is directly above marker bed E (see Tjernvik 1956, fig. 5), yielding conodont faunas of the *Oelandodus elongatus–Acodus deltatus deltatus* Conodont Subzone of the *Paroistodus proteus* Conodont Zone. Directly above the limestone, the earliest specimens of *Paratetragraptus approximatus* and *Tetragraptus phyllograptoides* were discovered. The level can also be recognized by trilobites from marker bed E, which have yielded faunas of the *Megistaspis* (*Paramegistaspis*) *planilimbata* Trilobite Zone.

Figure 6 shows the ranges of all taxa found in the Diabasbrottet section. The range chart was modified from Egenhoff & Maletz (2007, fig. 3). Identifications of all species have been revised from the available collections. Information has been added from museum collections and approximate biostratigraphic occurrence is added, based on faunal assemblages. Thus, for example, the presence of *Holograptus expansus* in the higher part of the *Tetragraptus phyllograptoides* Biozone is shown, as the type specimen is associated with four-stiped *Tetragraptus amii* and *Cymatograptus demissus*. The youngest occurrence of this species is uncertain, as the available material consists of very large four-stiped specimens without further branching. These are referred to *Holograptus expansus* only with reservation. The presence of *Paratemnograptus magnificus* is based on the record of a single specimen showing the characteristic plaited overlap of thecae. It is associated with a faunal assemblage typical of the *Tetragraptus phyllograptoides* Biozone including its index species.

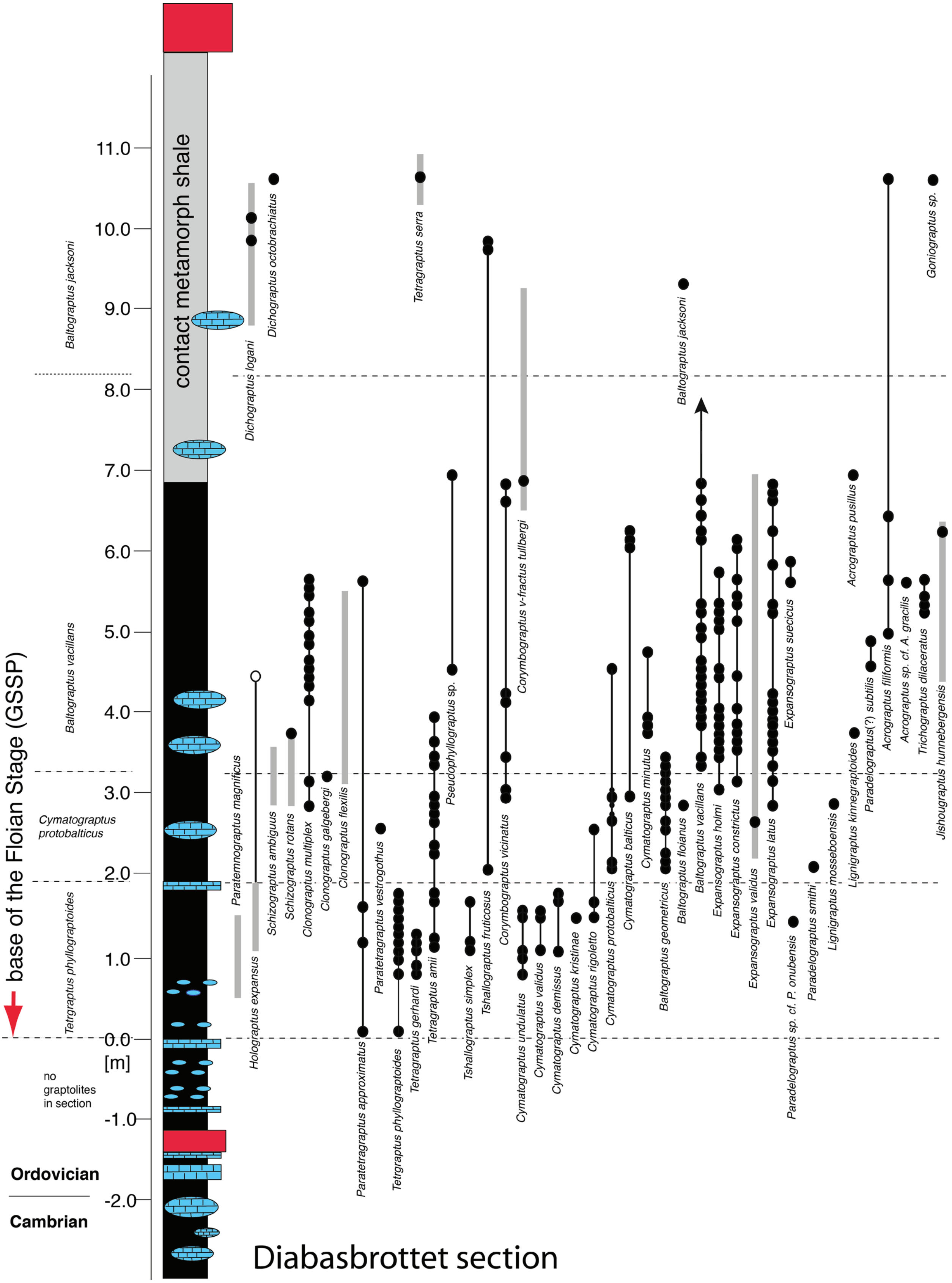

Fig. 6. The graptolite succession at Diabasbrottet, revised and corrected from Egenhoff & Maletz (2007). Grey bars indicate estimated species ranges of taxa not recognized during this investigation.

Mossebo

The modern outcrop Mossebo (cf. Maletz *et al.* 1996; Bergström *et al.* 2001) (N58°21'22.2"; E12°30'44") (Fig. 7) was shown as Stora Mossebo on the map of Sidenbladh (1870). A number of smaller exposures of the Lower Ordovician succession can be found poorly exposed to the SE of the Diabasbrottet quarry, where the base of the dolerite forms an uneven surface. Here the Ordovician succession is less extensively exposed and often only a few meters of strongly contact-metamorphosed shales are exposed, bearing a very poor graptolite fauna.

The modern Mossebo section was first described by Tjernvik (1956), who documented the trilobite fauna from the limestone layers in detail and regarded this section as one of his key sections. Löfgren (1993) described the conodont faunas from the limestone layers and differentiated a number of zones. There are minor differences in thickness of the individual shale layers from the nearby Diabasbrottet section, but all limestone intervals can be correlated easily. The metamorphism from the overlying dolerite sill is more pronounced than at Diabasbrottet and the graptolites are generally poorly preserved except for the *Tetragraptus phyllograptoides* Biozone fauna. Thus, the section has been less collected and many species found at Diabasbrottet have not been documented from the Mossebo section.

Another fairly complete succession through the upper Cambrian to Lower Ordovician, reaching the *Baltograptus vacillans* Biozone, can be found in the Floklev section of Maletz (1987) (Fig. 2A), but is not described herein, as it was not investigated in detail. Egenhoff & Maletz (2007, fig. 8) illustrated a tepee structure in the upper *Megistaspis* (*Paramegistaspis*) *planilimbata* limestone bed (bed F/G *in* Maletz *et al.* 1996) from this locality, quoted only as 'south of the locality Mossebo'. The section is to the south of the eastern road ascending to the top of the mountain.

Chronostratigraphy

The Ordovician chronostratigraphy has been modified considerably in recent decades and an internationally accepted subdivision of the Ordovician has been adopted, but quite a number of regional subdivisions exist (cf. Bergström *et al.* 2009). The regional chronostratigraphy of Baltica (see Cooper & Sadler 2012; Goldman *et al.* 2020) was mainly based on the Estonian sequence and was later also applied to the Swedish successions (e.g. Jaanusson & Strachan 1954; Nõlvak *et al.* 2006). Bergström *et al.* (2009) stated that there are few problems in applying the global chronostratigraphic classification to the Baltoscandic successions and that two of the global GSSPs are situated in Sweden. The Baltoscandian chronostratigraphic scheme has slowly been abandoned in Sweden (e.g. Maletz & Ahlberg 2011, 2018), but is still commonly used in the Baltic states (e.g. Goldman *et al.* 2015; Hints 2019). The use of the Hunnebergian and Billingenian should be replaced by the Floian as continued usage of the local stages names could lead to confusion, especially so as the regional Hunnebergian Stage and the international Floian Stage are defined in localities only a few kilometres apart. It is ironic that the Hunnebergian and Billingenian stages are still used in the East Baltic Basin, but not in the region in which they were originally defined. The Hunnebergian and Billingenian stages are here only used in their historical context. Nielsen *et al.* (2023, fig. 3) provided a revised regional stage classification for Scandinavia, in which the Ottenbyan is used and correlated with the upper Varangu and the Hunnebergian of the East Baltic region (Meidla *et al.* 2023, fig. 2), but kept the Billingenian for the upper Floian interval.

The Hunnebergian

Tjernvik (1956) introduced the Hunnebergian substage, based on the succession at Storeklev, SW Hunneberg (Fig. 4), where he found a fauna of 'undescribed dichograptids', now known as the *Hunnegraptus copiosus* Biozone fauna (Lindholm 1991a, b). Tjernvik (1956) understood the Hunneberg and Billingen groups to represent the lower Arenig of Sweden. Jaanusson (1960, table 3) introduced the Latorp Stage for the same interval in limestone facies and regarded the Hunnebergian and Billingenian intervals as substages. Lindholm (1991a) suggested introducing a Hunneberg Series between the Tremadoc and Arenig Series, following Erdtmann (1988) and differentiated a lower and upper Hunnebergian. She defined the interval through the use of conodonts, comprising the *Paroistodus proteus* and *Prioniodus elegans* conodont zones. Lindholm (1991b) provided a detailed discussion on the correlation of the Hunnebergian beginning with the *Sagenograptus murrayi* Graptolite Biozone. Cooper & Lindholm (1990, fig. 1) provided a worldwide correlation of Ordovician graptolite sequences and indicated the Hunnebergian to include the *Sagenograptus murrayi* to *Tetragraptus phyllograptoides* biozones. The Hunnebergian is overlain by the Billingenian including the *Cymatograptus balticus* to *Pseudophyllograptus angustifolius elongatus* biozones. The Hunnebergian thus starts in the late Tremadocian

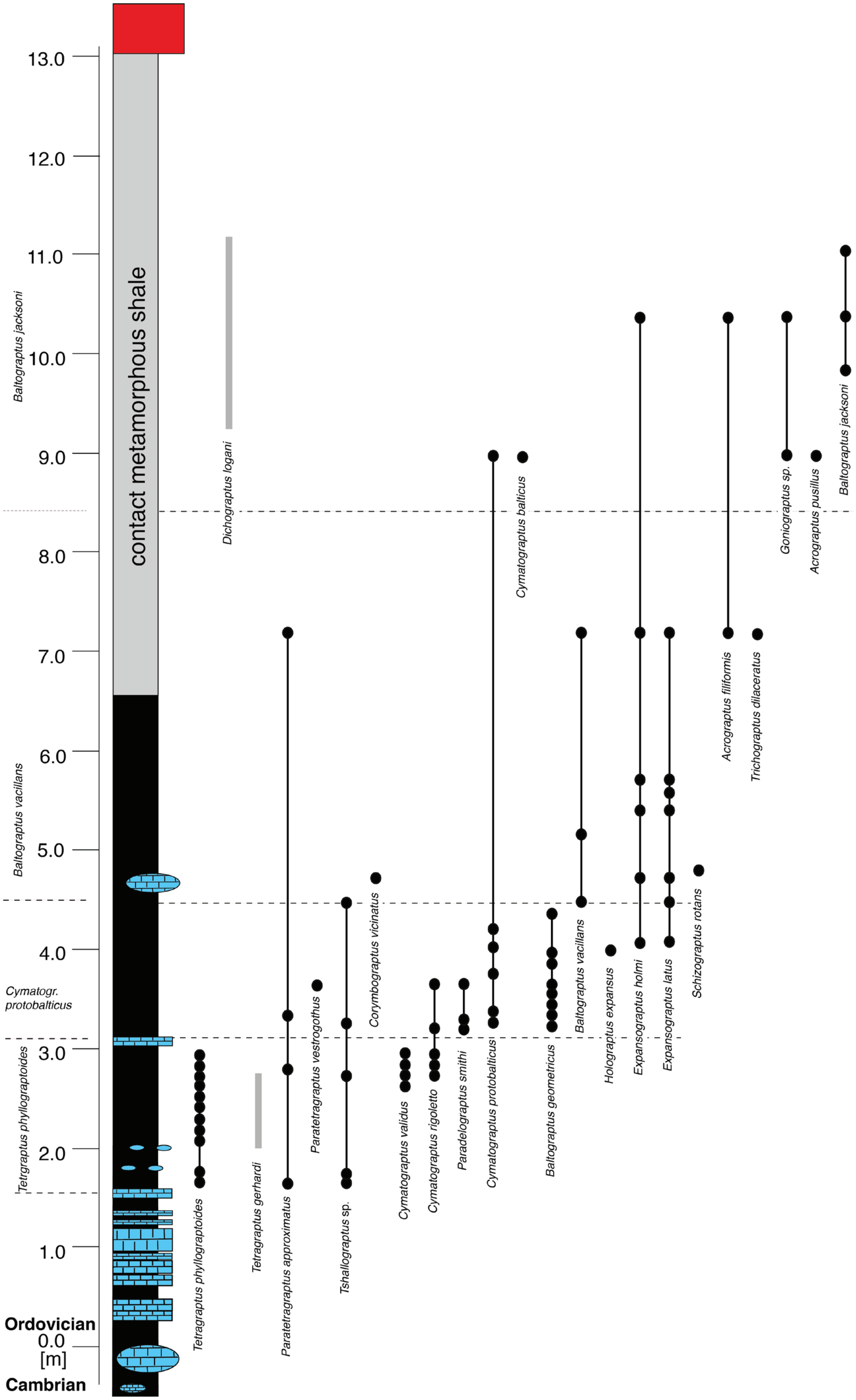

Fig. 7. The graptolite succession at Mossebo, based on Egenhoff & Maletz (2007).

and ranges into the early Floian of the modern global chronostratigraphy (Goldman *et al.* 2020). Bergström *et al.* (2009, fig. 1) erroneously correlated the Hunneberg and Billingen stages of Baltoscandia with the Floian of the international chronostratigraphy and indicated the presence of a GSSP at the base of the Hunneberg stage. They defined the base of the Billingen Group by the *Megalaspides dalecarlicus* trilobite zone and the *Pseudophyllograptus densus* graptolite Biozone (see Jaanusson 1960).

The Billingenian

Tjernvik (1956) introduced the Billingen Group based on the succession in Västergötland with the name derived from Billingen Mountain, and regarded the *Pseudophyllograptus densus* Biozone as its base. Tjernvik & Johansson (1980) introduced the Billingen substage and regarded the *Cymatograptus balticus* Biozone as its basal graptolite biozone. Lindholm (1991a, b) preferred to use the original definition of the Hunneberg and Billingen substages, however, while Maletz & Ahlberg (2018), in their discussion of the Tøyen Shale Formation in Scania, did not discuss the Hunnebergian and Billingenian stages at all. Based on the poor graptolite record and the lack of trilobites in the succession, it is not clear whether the Tøyen Shale Formation at Hunneberg reaches up into the Billingenian stage. If the definition of Tjernvik & Johansson (1980) is used, the uppermost part of the Hunneberg succession, including the *Cymatograptus balticus* bearing interval, would have to be included in the Billingenian.

Lithostratigraphy

Egenhoff & Maletz (2012) provided the latest interpretation of the upper Cambrian to Lower Ordovician lithostratigraphy of Hunneberg (Fig. 8). The authors clearly indicated the extensive gap and lithological condensation in the Cambrian–Ordovician boundary interval, where a number of trilobite and graptolite biozones are absent.

The Alum Shale Formation

The term Alum Shale has commonly been used in Scandinavia for the Cambrian succession of black shales with its typical 'Orsten Limestone', but is now understood to also include the lowermost Ordovician black shales. Buchardt *et al.* (1997) provided the

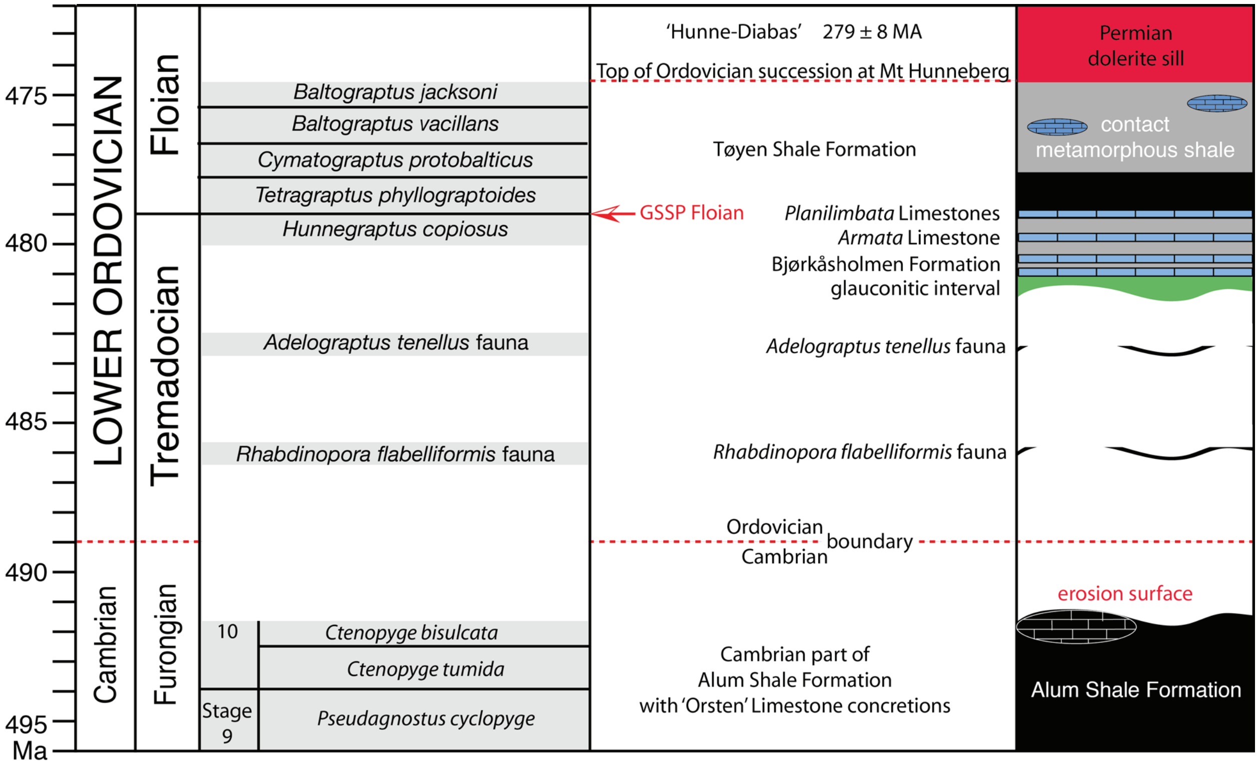

Fig. 8. Bio- and lithostratigraphy of Hunneberg (revised from Egenhoff & Maletz 2012). Lithological and biostratigraphical gaps in the succession shown in white.

formal definition of the Alum Shale Formation as currently used in the literature and designated a type section in the Gislövshammer-2 drill core of southeastern Scania. Nielsen & Buchardt (1994) described the successsion of the drill core in some detail. The definition of the Alum Shale Formation follows the suggestions of Gee (1972, 1987) and used by Andersson *et al.* (1985) and Vejbæk *et al.* (1994) to include the Ordovician alum shales of the *Dictyonema* and *Ceratopyge* shales with the Cambrian Alum shales in a single lithostratigraphic unit. Thus, the upper part of the Alum Shale Formation includes the continuation of the alum shale facies into the Ordovician and now includes the '*Dictyonema* Shale' and '*Ceratopyge* Shale' of earlier Scandinavian literature. The unit is noteable for the 'Orsten fauna' of small phosphatized arthropods (Müller 1982, 1983, 1985; Andres 1989; Maeda *et al.* 2011), but these faunas have not been discovered in the Hunneberg region so far.

The upper part of the Alum Shale Formation at Hunneberg bears thin layers of black shale with *Rhabdinopora* specimens or with monospecific faunas of *Adelograptus tenellus*, indicating a strong condensation (Fig. 8). The graptolites are quite fragmentary and have been discovered only at the western side of the mountain between the localities Nygård and Västra Tunhem/Holsbrotten. Their presence indicates that the uppermost part of the Alum Shale Formation at Hunneberg is Tremadocian in age, and also indicates a considerable gap in the succession, encompassing the upper Cambrian to basal Ordovician. These graptolites may have been preserved in pockets in the undulating surface of the late Cambrian erosion surface within the Alum Shale Formation.

The Bjørkåsholmen Formation

The Bjørkåsholmen Formation (formerly *Ceratopyge* Limestone) is a thin succession of limestones overlying the Alum Shale Formation (Fig. 8) and separates the Alum Shale Formation from the overlying Tøyen Shale Formation (Owen *et al.* 1990; Egenhoff *et al.* 2010). It is well known from the Hunneberg area (Tjernvik 1956; Egenhoff & Maletz 2012). The limestones bear a rich fauna of trilobites referable to the *Apatokephalus serratus* Biozone (Moberg & Segerberg 1906; Tjernvik 1956; Ebbestad 1999) and conodonts (Löfgren 1993), but other faunal elements have not been described. Graptolites are absent from the unit.

The Tøyen Shale Formation

Erdtmann (1965b) initially defined the Tøyen Shale Formation in a temporary tunnel section at Tøyen in the city of Oslo and differentiated the Hagastrand, Galgeberg and Slemmestad members. Owen *et al.* (1990) defined a neostratotype at Hagastrand in Asker, Oslo Region, but did not accept the Slemmestad Member and differentiated only a lower Hagastrand Member and an upper Galgeberg Member. The name Tøyen Shale Formation has also been used for equivalent lithologies in southern Sweden (e.g. Lindholm 1991a, b; Maletz & Ahlberg 2011; Egenhoff & Maletz 2012). Egenhoff *et al.* (2019) discussed the highly complex mudstone diagenesis of the Tøyen Shale Formation of Scania, southern Sweden. The authors recognized tempestite laminae and an abundance of trace fossils, indicating that the black shales might not have been deposited in anoxic conditions.

The base of the Tøyen Shale Formation is defined by the base of the unit overlying the Bjørkåsholmen Formation limestones (Owen *et al.* 1990) and appears to be abrupt in the Norwegian successions in the Oslo Region. Biostratigraphically, the correlation is difficult, as graptolites are generally not present in the Bjørkåsholmen Formation. Maletz *et al.* (2010) described the late Tremadocian graptolite faunas of the top of the Alum Shale Formation and referred the graptolites to the *Kiaerograptus kiaeri*/*Aorograptus victoriae* Biozone. Erdtmann (1965a) described *Kiaerograptus stoermeri* from a level directly above the main limestone of the Bjørkåsholmen Formation (then the *Ceratopyge* Limestone), shown as the *Kiaerograptus stoermeri* Biozone in Maletz *et al.* (2010). This interval may be regarded as the base of the Tøyen Shale Formation in the Oslo Region of Norway. It is followed by the *Kiaerograptus supremus* Biozone, which is usually regarded as the lowermost graptolite biozone of the Tøyen Shale Formation in southern Scandinavia (Lindholm 1991a, b; Maletz & Ahlberg 2018).

The Tøyen Shale Formation is quite variably developed in the localities of Hunneberg (Fig. 8), recognizable above the Bjørkåsholmen Formation limestones with its trilobite fauna of the *Apatokephalus serratus* Trilobite Biozone (Moberg & Segerberg 1906; Tjernvik 1956; Ebbestad 1999). It includes a number of limestone beds, the '*Armata*' and '*Planilimbata*' limestones, individual layers of carbonate, up to 10–12 cm thick, bearing moderately diverse Floian trilobite and conodont faunas (Tjernvik 1956; Löfgren 1993; Maletz *et al.* 1996). The '*Armata*' and 'lower *Planilimbata*' limestones are quite compact in the Mossebo–Diabasbrottet region and form a unit largely consisting of carbonates more than 1 m thick. Individual beds can be differentiated from the trilobite and conodont faunas. Thin shale beds may be present, but do not bear any recognizable faunas.

The lower part of the Tøyen Shale Formation is a carbonaceous mudstone to marlstone and can be differentiated from the typical Tøyen Shale Formation through its light color. This pale interval is identified as the Hagastrand Member of the Tøyen Shale Formation and is similar to the equivalent interval in the Oslo Region of Norway. It bears a graptolite fauna of the *Hunnegraptus copiosus* Biozone (Lindholm 1991a), from a single level and few localities at Hunneberg, but initially recognized by Tjernvik (1956) who discussed a 'large dichograptid' as the most important faunal element. Lindholm (1991a) described this taxon as *Hunnegraptus copiosus*. The Hagastrand Member is found only in the western outcrops at Storeklev, Nygård and Holsbrotten (Fig. 2), as the succession is more condensed in the eastern outcrops where little remains of shales of this lower interval, which appears to lack graptolites.

The overlying succession of black shales is rich in graptolites at many levels. These can be referred to several graptolite biozones (Egenhoff & Maletz 2007). The graptolites are well preserved and often found in full relief, filled by pyrite. The Tøyen Shale succession on the NE side of Hunneberg is up to ca 12 m thick, but the Hagastrand Member is not present and the graptolitic succession begins with the *Tetragraptus phyllograptoides* Biozone.

Maletz (2020a) discussed the preservation of graptolites in some detail and provided examples from the Hunneberg sections. The material shows the profound effects of contact metamorphism. Most of the graptolites are preserved as silvery shining fusellum, contrasting markedly from the black shale (see Bates *et al.* 2015). Material from the *Tetragraptus phyllograptoides* Biozone of Diabasbrottet shows the increasing coalification. Higher up in the succession, close to the contact with the dolerite sill, growth of metamorphic minerals has modified the sediment and the fusellum of the graptolites disappears. The baked shales are hard and their color is light grey to yellowish, with graptolites preserved as faint outlines when remains of the fusellum is preserved. Pyrite-filled tubaria are still evident but may no longer be identifiable.

Biostratigraphy

The graptolitic succession at Hunneberg (Figs 8, 9) is highly incomplete in the Lower Ordovician as is evident from the lithological succession (see Egenhoff & Maletz 2012). The early Tremadocian graptolite faunas occur at two levels with poorly preserved fragmented graptolites, whereas the late Cambrian to Early Ordovician lithological interval is characterized by erosion and reworking. Graptolite occurrences appear to be in erosional remnants preserved in small depressions between the more resistant 'orsten' limestone lenses. Thus, the basal Ordovician *Rhabdinopora flabelliformis* is found only in a very thin localized layer and its precise age in the rhabdinoporid succession of the Lower Ordovician (cf. Cooper *et al.* 1998; Maletz *et al.* 2017; Wang *et al.* 2019) cannot be determined. The succession is more complete only in the latest Tremadocian, where light grey silty shales of the Hagastrand Member of the Tøyen Shale Formation bear a fauna of the *Hunnegraptus copiosus* Biozone in a single layer at Storeklev and Holsbrotten/Västra Tunhem. A few additional specimens have been found scattered within the shale interval. The shales of the Hagastrand Member are overlain by the Floian succession of the Tøyen Shale Formation, represented by black shale of the Galgeberg Member. It shows a fairly complete graptolite succession, ranging into the *Baltograptus jacksoni* Biozone and is more widely distributed around the plateau mountain (Egenhoff & Maletz 2007), where four graptolite biozones can be differentiated.

The Rhabdinopora flabelliformis *fauna*

Graptolite faunas with *Rhabdinopora flabelliformis* have not previously been illustrated from Hunneberg. Neither Linnarsson (1869) nor Sidenbladh (1870) in the initial mapping mentioned the presence of the '*Dictyonema* Shale' at Hunneberg. However, Lindström (1887, p. 39) and Westergård (1909, p. 34) discussed the record of *Dictyonema flabelliforme* from Skaktet No. 1 near Nygård by the collector Gustaf von Schmalensee. Fearnsides (1907) mentioned this record, but stated that he was unable to find the species. Maletz (1987) illustrated a single fragment with its typical mesh from Nygård (actually Holsbrotten) on the western side of the mountain, confirming the presence of the *Rhabdinopora flabelliformis* interval. Due to the fragmentary preservation of the material, it is uncertain which part of the early Tremadocian succession is present. Cooper *et al.* (1998) and Cooper (1999) indicated the range of *Rhabdinopora flabelliformis* and its subspecies through the entire Lower Tremadocian, and ranging into the *Adelograptus* interval of the Upper Tremadocian.

The Adelograptus tenellus *fauna*

Linnarsson (1871) recognized the level with *Adelograptus tenellus* at Hunneberg, but referred it the Cambrian *Olenus* interval (*regio Olenorum*). Moberg (1892) described the species in some detail and added *Bryograptus*? *hunnebergensis* and *Bryograptus*? *sarmentosus* from the same level. Maletz & Erdtmann (1987) revised the material and considered the fauna to be based on a single, highly variable species. The authors considered the morphs distinguished by Moberg (1892) to be astogenetic variants of *Adelograptus tenellus*. Egenhoff & Maletz (2012) showed that the layer with *Adelograptus tenellus* is a part of the highly condensed Tremadocian succession at Hunneberg. *Adelograptus tenellus* may be from the basal part of the upper Tremadocian and is clearly younger than the *Rhabdinopora flabelliformis* fauna, but a precise biostratigraphic assignment of the interval is impossible from the poor record and Maletz & Erdtmann (1987) considered many records of the species in various regions as misidentifications.

The Hunnegraptus copiosus *Biozone*

Tjernvik (1956) first recognized the *Hunnegraptus copiosus* fauna from Hunneberg as a separate and special fauna. Lindholm (1991a, b) described it in some detail from southern Sweden and Norway. Initially known only from Storeklev at the south-western side of Hunneberg (Tjernvik 1956), it is now known from two localities at the western and south-western side of the mountain. Identical faunas occur at Storeklev and Holsbrotten/Västra Tunhem at a single level of the Hagastrand Member of the Tøyen Shale (Egenhoff & Maletz 2007, figs 5, 6). A few specimens of *Hunnegraptus copiosus* are also present in black shale at Nygård and specimens of *Paradelograptus norvegicus* and *Tetragraptus longus* have been discovered at other levels at Holsbrotten and Storeklev. Altogether, however, the Hagastrand Member is very poor in graptolites and the typical *Hunnegraptus copiosus* fauna is restricted to a single layer, less than 0.5 cm thick. Only at Storeklev is the Hagastrand Member overlain by graptolite-bearing shales of the *Tetragraptus phyllograptoides* Biozone (Egenhoff & Maletz 2007, fig. 6), providing the evidence for the correlation of the faunal succession around this table mountain.

The base of the Floian

The Floian Stage is based on the rocks overlying the GSSP at Diabasbrottet, one of the most important sections of the Hunneberg region. Maletz *et al.* (1995, 1996) proposed the First Appearance Datum (FAD) of *Paratetragraptus approximatus* in the section for the GSSP of the second stage of the Ordovician System and this was subsequently accepted by the International Commission on Stratigraphy. The name Floan Stage was initially proposed (Bergström *et al.* 2004, p. 271), but later changed to Floian Stage (Bergström *et al.* 2006). The GSSP of the Floian Stage is correlated with the first appearance of the graptolite *Tetragraptus phyllograptoides*, a common faunal element in cold-water faunas worldwide, thus useful for wider, global correlation of the *Paratetragraptus approximatus* Biozone across temperature gradients in the Early Ordovician.

Recently, Bergström *et al.* (2020) provided the first geochemical data for the GSSP section and identified a $\delta^{13}C$ excursion that correlated with biostratigraphic data. The authors interpreted their data to show the base of the Floian between the LTNICE and BFICE $\delta^{13}C$ excursions recognized in other regions. The work, thus provides new chemostratigraphic evidence for the worldwide correlation of the Diabasbrottet GSSP section in addition to the well established biostratigraphic correlation.

The Tetragraptus phyllograptoides *Biozone*

The *Paratetragraptus approximatus* Biozone was introduced by Maletz *et al.* (1996) in the discussion of the proposed GSSP at Diabasbrottet, but the local *Tetragraptus phyllograptoides* Biozone is preferred here as this index species is more common and is easily recognized. The *Paratetragraptus approximatus* Biozone is a widely used Lower Ordovician graptolite biozone (Berry 1992; Maletz 1999), but has rarely been used in Scandinavia in the past, even though the species has been reported from Sweden by Törnquist (1901) and was also found in the Oslo region of Norway by Monsen (1937). The biozonation of Monsen (1937) for the Oslo sequence was not based on observation of precise biostratigraphic ranges of the graptolite species, but largely on faunal associations. She named the *Tetragraptus phyllograptoides* and *Paratetragraptus approximatus* biozones as the lowermost graptolite zones of the Lower *Didymograptus* Shale. In the lower zone, the *Tetragraptus phyllograptoides* Zone, she also found specimens of *Sagenograptus murrayi*.

The base of the *Tetragraptus phyllograptoides* Biozone can be recognized in the Diabasbrottet and Mossebo sections (Figs 6, 7), where the species occurs together with *Paratetragraptus approximatus*. The connection to the underlying *Hunnegraptus copiosus* Biozone is documented from the Storeklev and Holsbrotten sections (Figs 4, 5), in which the *Hunnegraptus copiosus* Biozone was recognized in the greenish shales at the base of the Tøyen Shale Formation. *Tetragraptus phyllograptoides* and *Paratetragraptus approximatus* can be found in the higher part of the succession, here in strongly metamorphosed strata.

Paratetragraptus approximatus ranges through most of the succession in the Diabasbrottet section and the highest records are from the *Baltograptus vacillans* Biozone (Fig. 6). It is uncertain whether this is the top of its range in Västergötland, but the younger fossil record is very poor due to the contact metamorphism from the overlying dolerite sill. *Tetragraptus phyllograptoides* is restricted to the lower part of the *Paratetragraptus approximatus* interval. A number of two-stiped graptoloids are common in the lower part of the *Tetragraptus phyllograptoides* Biozone, including the highly characteristic *Cymatograptus undulatus* and a number of other species referred to the genus *Cymatograptus*. The two-stiped taxa may be the earliest didymograptids in the fossil record and demonstrate the diversification of *Cymatograptus* in the higher part of the *Tetragraptus phyllograptoides* Biozone. A single-stiped form also appears here, assigned to *Azygograptus* in the past but here identified as *Cymatograptus validus* (Törnquist, 1904).

Rare specimens of large dichograptids, including *Holograptus expansus* and *Paratemnograptus magnificus*, have been discovered in the *Tetragraptus phyllograptoides* Biozone. Horizontal to somewhat reclined and declined tetragraptids are common, including the highly characteristic three-stiped *Tetragraptus gerhardi* n. sp. *Tshallograptus simplex* may be regarded as a predecessor of the slightly younger *Tshallograptus fruticosus* and can be differentiated from *Tetragraptus* specimens in the same interval by a proportionally longer and more slender sicula.

The Cymatograptus protobalticus *Biozone*

Egenhoff & Maletz (2007) used the concept of the *Cymatograptus protobalticus* Biozone for the Hunneberg sections and the interval was subsequently defined by Maletz & Ahlberg (2011). The *Cymatograptus protobalticus* Biozone is defined by the first appearance of the index species in the Diabasbrottet section (Fig. 6), where it is associated with *Baltograptus geometricus*. The interval is widely distributed in southern Scandinavia and is easily recognizable through its graptolite fauna. The higher part of the zone is characterized by the appearance of *Expansograptus* species, while in the lower part only members of the genera *Cymatograptus* and *Baltograptus* are found. The species *Baltograptus geometricus* is the most common two-stiped graptoloid in the interval and ranges into the lowermost part of the *Baltograptus vacillans* Biozone. A number of multiramous members of the Dichograptidae and Sigmagraptidae have been discovered in the *Cymatograptus protobalticus* Biozone, but are usually uncommon.

The Baltograptus vacillans *Biozone*

Maletz & Ahlberg (2011) erected the *Baltograptus vacillans* Biozone that had been used informally by Egenhoff & Maletz (2007) for the Hunneberg succession. The base of the zone is defined by the first occurrence of its index species at Diabasbrottet (Fig. 6) that quickly becomes one of the most common members of the fauna. The zone shows a further increase in diversity of the Early Ordovician graptolite faunas and a number of new taxa appear in the interval. The *Baltograptus vacillans* Biozone is also characterized by a rich and diverse fauna of expansograptids. The intraspecific variation of these expansograptids has not yet been evaluated, but a number of taxa can be differentiated and more have been described from other regions in the world. The species of the genus *Expansograptus* are uncommon elements in the earlier zones, but here become the dominant faunal elements. The most common dichograptid is *Clonograptus multiplex*, but other species of the genus, as well as *Schizograptus* and the sigmagraptine *Trichograptus* are not uncommon in some layers. Slender two-stiped taxa that are here referred to the sigmagraptine genus *Acrograptus* are present in the higher part of the *Baltograptus vacillans* Biozone.

The Baltograptus jacksoni *Biozone*

Maletz & Ahlberg (2011) introduced the *Baltograptus* sp. cf. *Baltograptus deflexus* Biozone for the interval following the *Baltograptus vacillans* Biozone in the Lerhamn drill core of Scania. The base of the interval is recognized by the first appearance of truly deflexed *Baltograptus* specimens. As this taxon is now known as *Baltograptus jacksoni* (Rushton, 2011), the name of the zone has been changed to the *Baltograptus jacksoni* Biozone (Fig. 6). The base of the zone is difficult to define in the Diabasbrottet section, as the faunas of the interval are poorly preserved and largely destroyed through contact metamorphism. Only parts of the graptolite colonies that were filled with pyrite are preserved in the highest layers of the section and the apertural parts of the thecae are missing, so that the true shape and dimension of the tubaria is not recognizable. A few poorly preserved graptolites have been found in the highly contact metamorphosed shales, including a number of multiramous taxa. At a single level, specimens of the genus *Goniograptus* were found, a taxon that is extremely rare in Scandinavia.

Correlation with other fossil groups

Tjernvik (1956) documented the trilobite succession of the Bjørkåsholmen Formation and the '*Armata*' and '*Planilimbata*' limestones at Hunneberg and differentiated the various trilobite faunas (Fig. 9). Hoel (1999) revised the taxonomy of the *Megistaspis* species from the Oslo Region of Norway and these names are used herein also for species found in the Hunneberg succession in the correlation chart.

Löfgren (1993) described the conodonts based on large collections from a number of sections around Hunneberg and established a very detailed conodont biostratigraphy. The succession ranges from the late Tremadocian *Paltodus deltifer* Conodont Biozone to the Floian *Prioniodus elegans* Conodont Biozone. This work enables individual limestone beds to be correlated all around the mountain. Maletz *et al.* (1996) discussed the correlation of the graptolite, trilobite and conodont faunas of the Mossebo, Diabasbrottet and Storekelev sections in some detail (Fig. 9). Little can be added here for the interval around the GSSP level. The succession of the *Baltograptus vacillans* and *Baltograptus jacksoni* biozones does not include any limestones from which conodonts or trilobites have been collected.

The Hunneberg sequence has not been investigated for chitinozoans, acritarchs and brachiopods. Chitinozoans originated in the Early Ordovician (Grahn & Paris 2011) and a few specimens have been observed on shale surfaces at Diabasbrottet, but have not been described, so that only indirect regional correlation of the Hunneberg succession (Fig. 9) is made. Paris (1996) correlated the Early Ordovician chitinozoan biozonations worldwide and recognized a *Lagenochitina esthonica* Biozone covering most of the Hunnebergian and Billingenian of Baltica, correlatable to the upper Latorpian *Paroistodus proteus* to lower Volkhovian *Paroistodus originalis/Baltoniodus navis* conodont biozones. Webby *et al.* (2004) correlated the chitinozoan biozones of Baltoscandia and north Gondwana. The authors recognized a *Lagenochitina destombesi* Biozone, correlated with the *Paltodus deltifer* Conodont Biozone, and a very long *Euconochitina primitiva* Biozone ranging up to the base of the Darriwilian. Grahn & Nõlvak (2007b) discussed *Lagenochitina esthonica* from the *Hunnegraptus copiosus* Biozone of the Krapperup drillcore of Scania, southern Sweden and Grahn & Nõlvak (2007a) described chitinozoans from the Bjørkåsholmen Formation of the Oslo Region. Achab & Maletz (2021) discussed the biostratigraphic distribution of the *Euconochitina symmetrica* Zone that was formerly regarded as of basal Floian age (Achab 1980, 1986; Paris 1990) from the record at Lévis, Québec, Canada. It is now clear that the base of the *Euconochitina symmetrica* Zone is below the base of the Floian (Achab & Maletz 2021). Precise correlation of these Early Ordovician chitinozoan biozones (Fig. 9) is impossible at the moment.

Biostratigraphic correlation

Numerous graptolitic successions exist worldwide that bear some faunal elements found also at Hunneberg. As it is impossible to discuss them all, I concentrate on the major palaeogeographical regions

	Graptolites	**Trilobites**	**Conodonts**		**Chitinozoans**
Floian	*Baltograptus jacksoni*	*Megistaspis* (*Paramegistaspis*) sp. aff. *M.* (*P.*) *estonica*	*Prioniodus elegans*		*Eremochitina baculata*
	Baltograptus vacillans				
	Cymatograptus protobalticus				
	Tetragraptus phyllograptoides	*Megistaspis* (*Paramegistaspis*) *planilimbata*	*Paroistodus proteus*	*Oelandodus elongatus* - *A. d. deltatus*	*Euconochitina symmetrica*
Tremadocian	*Hunnegraptus copiosus*			*Paracordylodus gracilis*	
	Araneograptus murrayi	*Megistaspis* (*Ekeraspis*) *armata*		*Tripodus*	no data
				Drep. aff. D. amoenus	
	Kiaerograptus supremus?	*Apatokephalus serratus*	*Paltodus deltifer*		

Fig. 9. Correlation of graptolite, conodont and trilobite biostratigraphies (modified from Maletz *et al.* 1996).

in which Floian graptolite faunas are preserved and provide information for the biostratigraphic correlation of these successions. The correlation chart (Fig. 10) provides information on the general biostratigraphy of most regions, but I also discuss some scattered records that have been published more recently as I think it necessary to provide a more complete picture. These may not be shown on the correlation chart.

Tøyen Shale Formation

The graptolite biostratigraphy of the Tøyen Shale Formation has recently been described and correlated for Scania, southern Sweden in some detail (Maletz & Ahlberg 2018), but the succession at Hunneberg includes only the central part, from the latest Tremadocian to the mid-Floian (Fig. 10). The Scanian succession is much more complete than the Hunneberg one. It ranges from the late Tremadocian *Kiaerograptus supremus* Biozone to the *Levisograptus sinicus* Subzone of the *Levisograptus austrodentatus* Biozone and includes 14 biozones and subzones. It is known largely from a number of drillcores and has been pieced together from incomplete and tectonically disturbed successions. Late Floian to Dapingian graptolite faunas are known from other successions in Västergötland, but appear to be more strongly condensed.

The succession at Kinnekulle (Västergötland) is incompletely known. Graptolite faunas of the formation have been noted by Linnarsson (1866, 1869), indicating a thickness of the unit of ca 30 feet. Törnquist (1901, 1904) listed the zone of *Phyllograptus densus* from Martorps-klef, where the graptolites occur in thin black shales within a green shale unit. This material, however, was not illustrated, nor was *Didymograptus hirundo* in the upper part of the formation at Hällekis (Tjernvik 1956, fig. 14), which probably indicates a mid to late Dapingian age. Skoglund (1961) was the first to describe and illustrate graptolites from Kinnekulle. He erected the genus *Kinnegraptus* and described two species, *Kinnegraptus kinnekullensis* and *Kinnegraptus multiramosus* from chemically isolated material showing growth lines and further details of the development of the colonies. He listed a number of additional genus level taxa, but these were not described. Lindholm (1992) noted the presence of *Tetragraptus phyllograptoides* at Kinnekulle, but the material was never described and has not been found in the collections at Lunds University. The presence of the *Tetragraptus phyllograptoides* Biozone at Kinnekulle therefore, remains questionable.

The succession in Dalarna (Siljan impact) is poorly known and the faunas have not been described in detail. Törnquist (1876) described a section at Skattungbyn (later known as the Talubäcken section). Törnquist (1879, 1890) documented the graptolite fauna and erected a number of new species from the succession. Two of these, *Baltograptus minutus* (Törnquist, 1879) and *Pseudophyllograptus densus* (Törnquist, 1879), subsequently became index taxa for Floian graptolite biozones. Törnquist (1883) listed a number of taxa from the Tøyen Shale Formation of Dalarna and Warburg (1910) extended the list considerably. Skoglund (1968) indicated the presence of chemically isolatable graptolites at Skattungbyn. Maletz & Slovacek (2013) and Schulze (2018) provided the first descriptions of the material. Maletz (2023) described the remaining material from the Skoglund collection of isolated graptolites. There is no evidence so far for the presence of early Floian graptolites in Dalarna.

Graptolites from the Tøyen Shale Formation are present in Jämtland, central Sweden, but have rarely been discussed or illustrated, so that the completeness of the succession is unknown. Wiman (1893, p. 263) regarded the formation at Tossasen, Jämtland as the ‘classical area of the *Phyllograptus* Shale in Jämtland’ (see Bulman, 1950a, p. 389) and cited a number of taxa, but did not describe or illustrate them. Wiman (1899) suggested that the formation (Unterer Graptolithenschiefer) may be present everywhere in the region and listed a number of taxa, including *Tshallograptus fruticosus*. Bulman (1950a) described the well-preserved fauna and Maletz (2004) re-identifed the species described as *Holmograptus callotheca* by Bulman (1950a) with the mid-Floian *Maeandrograptus sinosus* Maletz, 2004. Tjernvik (1956) indicated the presence of graptolites in the Tøyen Shale Formation of Jämtland and even listed *Tetragraptus phyllograptoides* from Anderson Island in Lake Storsjön, providing evidence for the age of the base of the formation. Beckly & Maletz (1991, pl. 1, fig. 1) illustrated *Azygograptus ellesi* Monsen, 1937 from Nipan, Jämtland and Maletz (1994) illustrated a specimen of *Tshallograptus flagellifer* from the same locality. The presence of *Tshallograptus fruticosus*, *Pseudophyllograptus* and *Maeandrograptus sinosus* indicates that the higher part of the Floian or even the Dapingian may be present in the region.

Monsen (1937) described the graptolite fauna of the Tøyen Shale succession of Norway and erected numerous new species. She recognized the *Tetragraptus phyllograptoides* Biozone at the base of the unit and listed the *Phyllograptus angustifolius elongatus* Biozone as the youngest biozone of the region. The *Tetragraptus phyllograptoides* Biozone included specimens of *Dictyonema* cf. *D. murrayi* and *Dictyonema macgillivrayi* (now *Sagenograptus*) and *Tetragraptus* (now *Paratetragraptus*) *approximatus*. *P. approximatus*, together with *T. phyllograptoides*, ranges upwards into the *P. approximatus* Biozone, so that the two intervals correlate with the *Tetragraptus phyllograptoides* Biozone at Hunneberg. The overlying *Didymograptus validus* and *Didymograptus balticus* biozones can be correlated with the *Cymatograptus protobalticus* to *Baltograptus vacillans* biozones. It needs to be pointed out that the Monsen material was not collected from precise levels and the assignment to a certain biozone is based in many cases on the interpretation of the taxa present on the same slabs. Precise correlation of the Tøyen Shale Formation in the Oslo Region therefore remains difficult. Erdtmann (1965b) described a new section in the city of Oslo, but did not provide precise ranges of taxa and did not describe the faunas. Maletz (2011) discussed the late Floian to Dapingian succession of the Oslo region by using isograptid faunal elements. He recognized the *Isograptus mobergi* & *Maeandrograptus schmalenseei* Biozone as the youngest graptolite zone of the Tøyen Shale Formation below the Komstad Limestone.

Britain

The British standard succession (Fig. 10) is well known and has been revised most recently by Zalasiewicz *et al.* (2009). It appears to be fairly incomplete and has few faunal elements, so that biostratigrapically useful successions showing precise ranges and boundaries between the individual biozones are unknown. The late Tremadocian faunas are sparse and only the *Sagenograptus murrayi* Biozone is recognized in the Skiddaw Slates (Cooper *et al.* 1995), where specimens of *Sagenograptus* (previously *Araneograptus*: Maletz *et al.* 2017) are associated with possible didymograptids (Molyneux & Rushton 1988). A more precise identification of these is impossible due to their poor preservation and tectonic deformation. Cooper *et al.* (1995) identified the *Tetragraptus phyllograptoides* Biozone through the presence of *Cymatograptus protobalticus*, *Cymatograptus rigoletto* and *Clonograptus multiplex*, but this interval is here correlated with the *Cymatograptus protobalticus* Biozone (Fig. 10), as *Tetragraptus phyllograptoides* is not present and in any case would be found at a lower biostratigraphic horizon. A considerable biostratigraphic gap therefore occurs between the late Tremadocian and early Floian faunas, as no graptolite faunas of this interval have been found. *Paratetragraptus approximatus* occurs at Ballantrae, Scotland, associated with *Tshallograptus fruticosus* (Stone & Rushton, 1983), indicating probable correlation with the *Baltograptus vacillans* to *Baltograptus jacksoni* Biozone, as the *Paratetragraptus approximatus* Biozone does not include *Tshallograptus fruticosus*.

The *Corymbograptus varicosus* Biozone fauna of Zalasiewicz *et al.* (2009) can be correlated with the *Baltograptus jacksoni* Biozone (Rushton 2011). The base of the interval in Britain is not defined, but the fauna shows a higher diversity with the appearance of a number of new faunal elements. The *Expansograptus simulans* Biozone shows a high diversity and yields a number of characteristic faunal elements (e.g. *Azygograptus*, *Baltograptus minutus*), indicating a long late Floian to early Dapingian time interval (Fig. 10). Zalasiewicz *et al.* (2009) indicated that the interval straddles the Floian–Dapingian boundary. The overlying *Isograptus victoriae* Biozone is characterized by the index species, but the species is rare in the Lake District. The specimen illustrated by Zalasiewicz *et al.* (2009, fig. 66) may be *Isograptus rigidus* Maletz, 2011, known mainly from Scandinavia (Spjeldnaes 1953; Maletz 2011). The specimen was first illustrated as *Isograptus victoriae* by Fortey *et al.* (1990, fig. 6K).

Bohemo–Iberia (South Gondwana)

Gutiérrez-Marco *et al.* (2017) discussed the chronostratigraphy of the region and provided some general information on the faunal successions (Fig. 10). They did not, however, discuss the graptolite succession of the Tremadocian to Arenigian (Floian–Dapingian) interval in any detail. The lower Tremadocian interval with *Rhabdinopora* has been identified in a number of papers in North Africa. Legrand (1974) described the quadriradiate proximal development in intermediate forms of *Rhabdinopora socialis* from the Lower Ordovician of the Algerian Sahara and noted the presence of somewhat younger strata with *Adelograptus* (Legrand 1964a, b). Gutiérrez-Marco & Martin (2016) discussed the succession of the Tremadocian–Floian interval of southern Morocco and provided an overview of the faunas, including the important faunas of the Fezouata Biota. In general, the successions are fairly incomplete and the fossil record has to be pieced together from many localities. Thus, precise ranges have not been established for the faunas. Further study, however, may show that the graptolite sequence is more complete. Two specimens with subhorizontal, slender stipes have been identified as *Hunnegraptus copiosus* by Martin *et al.* (2016), but the identification remains in doubt until better material is available. Gutiérrez-Marco *et al.* (2016) discussed the *Hunnegraptus copiosus* Biozone of the

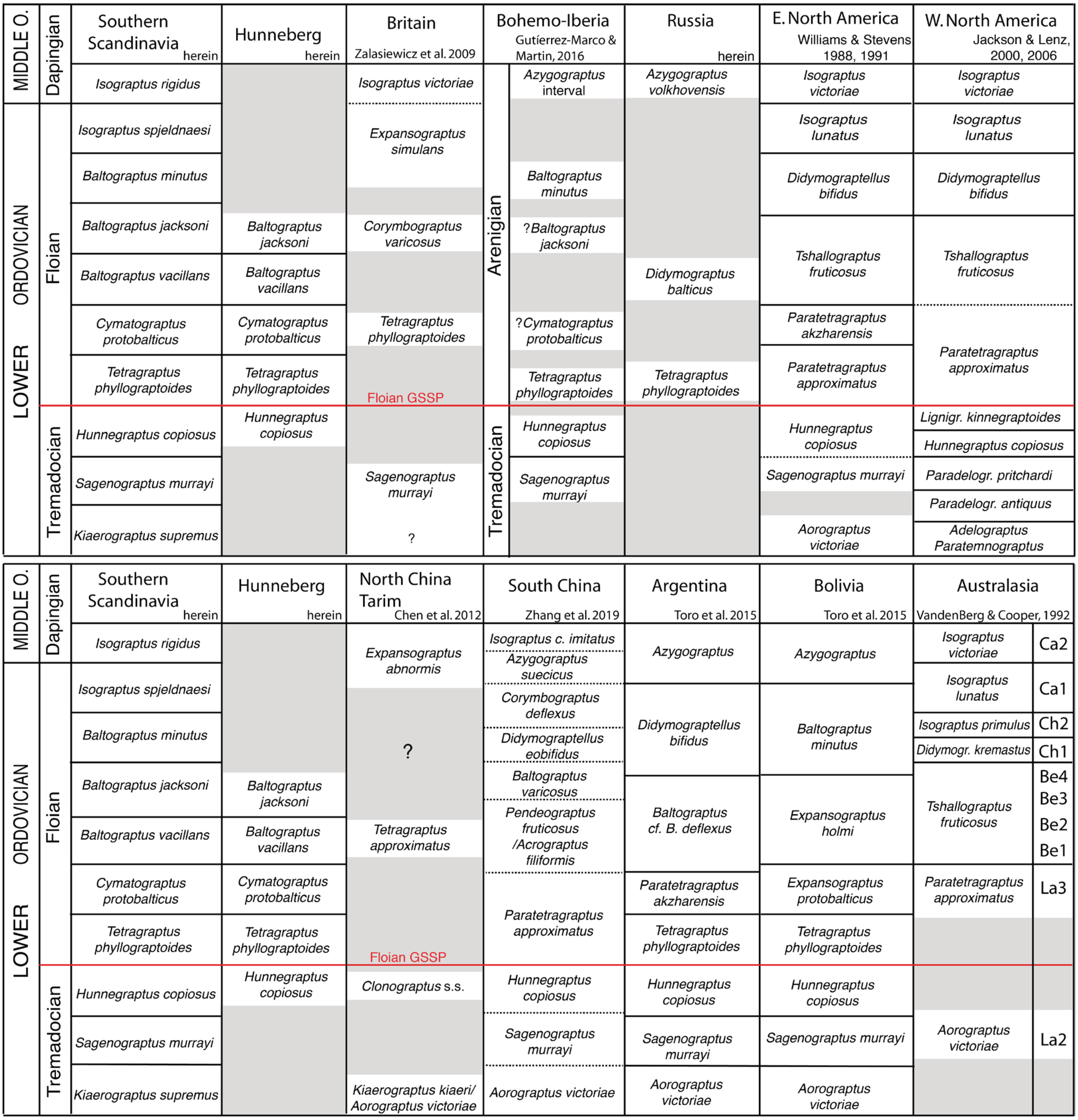

Fig. 10. International correlation of the Floian.

Fezouata lagerstätte, but did not illustrate the material. Gutiérrez-Marco & Martin (2016) inserted the *Tetragraptus phyllograptoides* Biozone in their scheme for a barren interval in the Fezouata Biota, even though the taxon has not been collected and the interval is known only from a single specimen of *Tetragraptus phyllograptoides* collected in the Sinclinal de Valle (Sevilla, Spain) (Gutiérrez-Marco *et al.* 1984). These authors also illustrated a poorly preserved specimen as *Cymatograptus* cf. *C. protobalticus* from Fezouata, representing the *Cymatograptus protobalticus* Biozone of Scandinavia. Deflexed and pendent *Baltograptus* specimens may represent the *Baltograptus jacksoni* to *Baltograptus minutus* biozones. An interval with *Azygograptus eivionicus* may represent the early Dapingian, but a more precise determination of the age of this interval is not possible. Typical examples of the presence and preservation of Lower Ordovician graptolite faunas of the Bohemo–Iberian area can be found in the Czech Republic (see Bouček 1973), but also include isolated records like *Azygograptus undulatus* in northern Spain (Gutiérrez-Marco & Rodriguez 1987).

Phillipot (1950) illustrated a deflexed didymograptid under the name *Didymograptus falco* Phillipot, 1950 from the French 'Massif Armoricain'. The species is here regarded as synonymous with *Baltograptus deflexus*. The illustrations in Phillipot (1950, p. 239) indicate considerable tectonic deformation of the material, making the identification difficult. This is also true for material considered as belonging to the *Didymograptus murchisoni* group (Phillipot, 1950, fig. 21). Other Early Ordovician graptolites were not illustrated.

Iran

Iran as part of Gondwana (cf. Ghorbani 2021) is not well known for the presence of early Ordovician graptolite faunas. Rushton *et al.* (2021) described small faunas from the *Rhabdinopora flabelliformis, Hunnegraptus copiosus* and *Cymatograptus protobalticus* biozones, including the widely distributed *Baltograptus geometricus*. The faunas indicate that the successions could be more complete and new records can be expected.

Russia (East European Platform)

Kaljo (1974) discussed the Tremadocian–Arenigian succession of the Peribaltic and Moscow syneclises and recognized the succession as similar to the one in southern Sweden. Following the *Clonograptus* cf. *tenellus* Biozone of late Tremadocian age is the *Paratetragraptus approximatus* + *Tetragraptus phyllograptoides* Biozone, overlain by the *Didymograptus balticus* Biozone and the *Phyllograptus densus* Biozone (probably correlating with the *Azygograptus volkhovensis* Biozone of Koren' *et al.* 2004). As the faunas were not illustrated, some doubt remains about the identity of the taxa and the biostratigraphic ranges (Fig. 10). The information was supported by the findings of Ulst (1976), but the fauna of the *Tetragraptus phyllograptoides* Biozone of this general region was first described and illustrated by Tolmacheva *et al.* (2001). The authors documented the *Tetragraptus phyllograptoides* Biozone of the St. Petersburg area. *Tetragraptus phyllograptoides* and *Didymograptus rigoletto* are found in the lower part of the interval, while *Tetragraptus phyllograptoides* is associated with *Cymatograptus* sp. cf. *C. protobalticus* in the higher part of the zone. Younger Floian graptolite faunas have not been found. Paškevičius (2011) discussed Floian–Dapingian graptolites from Lithuania, but the material has not been illustrated. Koren' *et al.* (2004) described the Dapingian succession of the St. Ptersburg region. The oldest faunal elements include *Azygograptus volkhovensis* Koren *et al.*, 2004, but the majority of the faunas are younger and can be referred to the *Pseudophyllograptus angustifolius elongatus* to *Expansograptus hirundo* biozones. The presence of *Azygograptus volkhovensis* may indicate an early Dapingian age, but a comparison with other species of *Azygograptus* is not possible and the species must be regarded as endemic at the moment.

North America

Williams & Stevens (1988) described the Lower Ordovician graptolites of the Cow Head Group of western Newfoundland (Fig. 10), the most complete succession known from North America. The faunas are documented in great detail and numerous species are described from chemically isolated material. The sequence begins with the late Tremadocian *Aorograptus victoriae* Biozone (Williams & Stevens 1991), followed by the early Floian *Paratetragraptus approximatus* Biozone. Maletz *et al.* (1996) discussed the presence of a biostratigraphic gap between these zones, based on the faunal succession at Hunneberg, covering the *Sagenograptus murrayi* to *Tetragraptus phyllograptoides* Biozone interval. A part of this gap may be closed in eastern North America by the *Sagenograptus murrayi* Biozone found in Québec (Hall 1865; Maletz 1997a). However, the *Hunnegraptus copiosus* Biozone may be missing. *Hunnegraptus novus* has been recognized in the succession of Texas (Maletz 2006) and *Hunnegraptus copiosus* has been described from northern Yukon by Jackson & Lenz (2003). The *Paratetragraptus approximatus* Biozone of the Cow Head Group bears a poor and low diversity fauna in which *Paratetragraptus approximatus* is the most important faunal element. Interestingly, *Cymatograptus* sp. cf. *Cymatograptus protobalticus* is present in the upper part of the interval, recorded as *Didymograptus* (*Expansograptus*) *latus* (Hall, 1907). It is the only species of *Cymatograptus* found in North America and indicates correlation with the *Cymatograptus protobalticus* Biozone of Scandinavia. The *Tetragraptus akzharensis* Biozone may correlate with the upper part of the *Cymatograptus protobalticus* Biozone and the *Baltograptus vacillans* Biozone because of the presence of the common *Expansograptus* specimens. The base of the *Tshallograptus fruticosus* Biozone is based on the FAD of its index species, but Williams & Stevens (1988) indicate that the species may have originated earlier. This fits with the occurrence of earlier *Tshallograptus* in the *Paratetragraptus approximatus* Biozone (see also VandenBerg 2017). Proximal ends of these may be impossible to distinguish from true *Tshallograptus fruticosus*. The overlying *Didymograptellus bifidus* Biozone should in general correlate with the *Baltograptus minutus* Biozone of Scandinavia. The correlation of the *Isograptus lunatus* and *Isograptus victoriae* biozones was discussed by Maletz (2010).

The succession in the western part of North America (Fig. 10) seems quite different, at least in the late Tremadocian. Jackson & Lenz (1999, 2000, 2003, 2006) described the late Tremadocian to Floian graptolites of the Yukon territory in some detail and established a quite detailed biostratigraphy. The *Psigraptus–Adelograptus* Biozone of Yukon (Jackson & Lenz 1999) can be correlated with the *Kiaerograptus kiaeri* Biozone based on the presence of *Ancoragraptus*, even though *Psigraptus* has never been discovered in Scandinavia. Jackson & Lenz (2000) differentiated a number of local biozones in the late Tremadocian based on species of the genus *Paradelograptus*. Jackson & Lenz (2003) made the first record of *Hunnegraptus copiosus* in Yukon and placed a *Hunnegraptus copiosus* Biozone below the *Lignigraptus kinnegraptoides* Biozone. Jackson & Lenz (2006) identified the *Paratetragraptus approximatus* Biozone followed by the *Tshallograptus fruticosus* Biozone in the Yukon sections. The faunas show a relatively low diversity of *Tetragraptus* and *Paradelograptus* species. *Expansograptus* appears in the lower part of the Lower Canyon of Peel River indicating the presence of an interval correlating with the *Tetragraptus phyllograptoides* or *Cymatograptus protobalticus* Biozone, while the higher part with its characteristic *Expansograptus* species may represent the *Baltograptus vacillans* Biozone or a higher interval. The *Tshallograptus fruticosus* Biozone is indicated by its index species associated with a number of new taxa appearing in this interval.

Vietnam

Very little is known of the graptolitic succession of Vietnam and few taxa have been listed from the region, but Ordovician to Devonian graptolite faunas have been mentioned from scattered outcrops in the region (see Van Phuc 2002; Thanh & Khuk 2011). Hung *et al.* (2017) described a poorly preserved Floian graptolite fauna including *Paratetragraptus approximatus, Expansograptus urbanus* and *Expansograptus abnormis* from the Dinh Ca Formation of NE Vietnam. The fauna shows a low diversity and few taxa are present. It was referred to a local *Tetragraptus quadribrachiatus* Biozone and may be correlated with the *Baltograptus vacillans* Biozone of Scandinavia due to the presence of the *Expansograptus* species. Rushton *et al.* (2018) described a similar small fauna of Floian age from the Than Sa Formation of NE Vietnam, bearing *Paratetragraptus approximatus* associated with a number of expansograptids. A slender declined species was identified as '*Didymograptus*' *sinensis*? Its poor preservation precludes a more precise identification, but the specimens may be a declined *Baltograptus* species intermediate between *Baltograptus geometricus* and *Baltograptus vacillans*. The material is certainly from a level above the *Tetragraptus phyllograptoides* Biozone, in which no horizontal *Expansograptus* species occur. The authors suggest a correlation with the Be1 of Australasia, even though *Tshallograptus fruticosus* is not present. Further graptolite records are not known from the region.

South China

Zhang *et al.* (2019) discussed the Ordovician time scale for China and provided the latest information on the graptolite biozonation of the region (Fig. 10). However, only some of the biostratigraphic intervals were discussed in the paper. Zhang *et al.* (2005) recognized the *Aorograptus victoriae, Acanthograptus sinensis* and *Hunnegraptus copiosus* biozones in the late Tremadocian of South China, with a gap between the *Aorograptus victoriae* and *Acanthograptus sinensis* biozones. Feng *et al.* (2009) revised the succession based on the Nanba section, Hunan Province, and recognized the *Adelograptus tenellus, Aorograptus victoriae, Araneograptus* (*now Sagenograptus*) *murrayi and Hunnegraptus copiosus* biozones in the late Tremadocian, followed by the basal Floian *Paratetragraptus approximatus* Biozone. Wang & Wang (2001) introduced the *Hunnegraptus copiosus–Clonograptus s.s.* Biozone to the succession of South China and Zhang *et al.* (2003, 2004) first recognized the genus *Hunnegraptus* in China. A number of small specimens have been identified as *Hunnegraptus novus* (Berry, 1960) and Feng *et al.* (2009) identified other juvenile specimens from the Nanba section as *Hunnegraptus copiosus*. Mature specimens of *Hunnegraptus copiosus* supporting the identification are unknown from China.

Zhang *et al.* (2019) provided an overview on the Floian succession with five biozones (Fig. 10), which were not discussed in detail. The basal Floian *Paratetragraptus approximatus* Biozone is widely distributed in South China and bears a diverse graptolite fauna of tetragraptids and dichograptids (see references in Chen *et al.* 1983). The lack of extensiform didymograptids (genus *Expansograptus*) in many faunas may indicate that the interval can be correlated with the *Tetragraptus phyllograptoides* to lower *Cymatograptus protobalticus* biozone interval of Scandinavia. The *Pendeograptus fruticosus–Acrograptus filiformis* Biozone can be correlated with the *Baltograptus vacillans* to *Baltograptus jacksoni* biozones as both index species are common here.

Zhang & Zhang (2014) described deflexed *Baltograptus* species from the *Baltograptus varicosus* Biozone of Eastern Yunnan, South China and correlated it with the mid-Floian *Tshallograptus fruticosus* to *Didymograptus eobifidus* Biozone of other regions of South China. The authors indicated the presence of a *Baltograptus deflexus* Biozone above the interval. The preservation of many specimens is quite good, even though the specimens are flattened and details of the proximal development are rarely visible. The material may originate from an equivalent of the *Baltograptus jacksoni* Biozone based on the presence of *Expansograptus similis* and *Expansograptus constrictus*, but a precise correlation is impossible, as these wide-stiped *Baltograptus* taxa are unknown from Scandinavia and may be endemic. However, wide-stiped deflexed taxa are also present in Argentina and Bolivia (see below). The *Didymograptellus eobifidus* Biozone can be correlated with the *Didymograptus bifidus* Biozone of North America or the *Didymograptellus kremastus* Biozone of Australasia.

North China

North China, including the Tarim region, has very little record of Lower Ordovician graptolite faunas (Fig. 10). Zhang & Erdtmann (2004) and Zhang *et al.* (2005) discussed the Tremadocian graptolite succession of North China, especially of Jilin Province, and introduced the *Aorograptus victoriae* Biozone above the *Psigraptus jacksoni* Biozone. The *Aorograptus victoriae* Biozone is recognized by the presence of the index species, associated with numerous dendroids. No other planktic graptoloids are present and a precise correlation of this interval is not possible. The higher part of the biozone is characterized by the genus *Kiaerograptus* and probably correlates with the *Bryograptus ramosus* to *Kiaerograptus kiaeri* biozones of Scandinavia (Maletz *et al.* 2010). The top of the biozone cannot be determined with certainty, leaving a gap in the late Tremadocian faunal succession. Zhang *et al.* (2019) named the latest Tremadocian as the *Clonograptus* s.s. Biozone, but did not discuss it.

Paratetragraptus approximatus has not been recognized in North China (Zhang *et al.* 2019), where the base of the Floian is therefore difficult to identify. Xu & Huang (1979) described the *Paratetragraptus approximatus* Biozone from Xinjiang, but the succession appears to be highly incomplete and the next younger fauna belongs to the late Dapingian *Oncograptus upsilon–Cardiograptus morsus* Biozone. The fauna of the *Paratetragraptus approximatus* Biozone includes a number of tetragraptids, clonograptids and expansograptids, some of them described as new species. The presence of the typical extensiform *Expansograptus holmi* may indicate correlation with the *Baltograptus vacillans* Biozone of Scandinavia.

Chen *et al.* (2012) indicated a considerable biostratigraphic gap in the eastern Tienshan Mountains, where the *Kiaerograptus kiaeri–Aorograptus victoriae* Biozone is folllowed by the *Expansograptus abnormis* Biozone of latest Floian to early Dapingian age in the Heituao Formation. Thus, the Floian and some of the Dapingian biozones are not present. Zhang *et al.* (2019) combined the succession of North China and Tarim and indicated the presence of the *Paratetragraptus approximatus* Biozone in the Liangchiashan Formation, but noted the next younger graptolite biozone as that of *Expansograptus abnormis* from the latest Floian (Fig. 10).

South America

The Early Ordovician graptolite faunas of South America can be referred to two distinct realms. Those of the Argentine Precordillera belong to the Pacific faunal realm, whereas the remaining South American faunas are of the the Atlantic faunal realm (Maletz & Ortega 1995). Goldman *et al.* (2013) preferred the terms high and low latitude realms instead of Atlantic and Pacific, as the latter refer to modern biogeography and Goldman's terms will be used herein. The presence of the *Didymograptellus bifidus* Biozone in a number of sections of the Eastern Cordillera and the Famatina Range of Argentina (Toro 1994, 1997a, b; Toro & Brussa 1997) may indicate a more differentiated picture, but a number of questions remain unresolved.

The Early Ordovician graptolite faunas of the eastern Cordillera of Argentina have been covered in numerous publications and only few of these are discussed here. *Paratetragraptus approximatus* has been reported from several localities in South America, especially from the Cordillera Oriental of Argentina (Martin *et al.* 1987), but it seems that the presence of *Tetragraptus phyllograptoides* is the most indicative evidence of the base of the Floian in South America. Moya *et al.* (1994) described a number of faunal associations from the eastern Cordillera of Argentina that range from the basal Tremadocian to the early Arenig

(Floian). Specimens identified as *Isograptus* sp. (Moya *et al.* 1994: pl. 4, figs 9, 10) and referred to the mid-Arenig *Isograptus* Biozone (assemblage 10) were supposedly among the youngest graptolites recorded from the region. However, they must be reassigned to *Tetragraptus phyllograptoides* of basal Floian age, as is the specimen (Moya *et al.* 1994, pl. 4, fig. 12) found in assemblage 11. Faunal assemblage 9 contains *Sagenograptus murrayi*, identified as *Dictyonema yaconense* by Moya *et al.* (1994). Moya *et al.* (1998) used graptolites of the *Tetragraptus phyllograptoides* Biozone to date the Tumbaya unconformity in the Eastern Cordillera of the Argentinian Andes. Ortega *et al.* (1998) described further graptolite faunas from the *Tetragraptus phyllograptoides* Biozone of the eastern Cordillera of Argentina.

Toro (1993, 1994, 1996, 1997a) initially documented the succession from the Eastern Cordillera in more detail and Toro *et al.* (2015) provided the most complete overview of the succession (Fig. 10), that is easily correlated with Scandinavia trough the presence of *Tetragraptus phyllograptoides* and the indicative *Baltograptus* species of the Floian. The presence of *Baltograptus turgidus* (Lee) and *Baltograptus kunmingensis* (Ni) in the *Baltograptus deflexus* Biozone of Bolivia is important for the correlation of this interval and the first time that these conspicuous faunal elements were described from outside China. The species of the *Baltograptus calidus* group (cf. Maletz 1994) were previously known only from southwest China, but not described from established successions. Toro (1999a, b) also described the peculiar *Baltograptus bolivianus* (Finney & Branisa, 1984) for the first time from Argentina. Toro (1994, 1997a) recognized the *Didymograptellus bifidus* zone faunas as the youngest faunas from the Eastern Cordillera. The presence of the low-latitude type *Didymograptellus bifidus* in this region of apparent high latitude faunas still needs to be explained. Further work has refined the biostratigraphy of the Eastern Cordillera (Toro & Vento 2013), showing the presence of the late Tremadocian *Hunnegraptus copiosus* Biozone (Toro & Brussa 2003; Toro *et al.* 2010) to the mid-Floian deflexed *Baltograptus* species (cf. Toro & Maletz 2007, 2008; Toro *et al.* 2011, 2015).

Toro (1997b) described two faunal associations from the La Alumbrera section in the Famatina range, but did not assign zonal names. The lower fauna includes a number of *Tetragraptus* species, of which *Tetragraptus phyllograptoides* is the most important one. The specimens are relatively slender, but appear otherwise typical of this species. The association with *Didymograptus* (*Expansograptus*) sp. (Toro 1997b, pl. 1, fig. 3) and *Tetragraptus akzharensis* might indicate that the fauna comes from a high level in the *Tetragraptus phyllograptoides* Biozone. The occurrence of *Tetragraptus phyllograptoides* here may be slightly younger than the Scandinavian occurrences. Toro & Brussa (1997) described slightly younger faunas of the *Baltograptus deflexus* and *Didymograptellus bifidus* biozones from the Saladillo River gorge. Unfortunately, there is no good succession of faunas between both zones. However, the presence of *Phyllograptus sensu stricto* and *Didymograptellus bifidus* clearly indicates the shift from high to low latitude region faunas in the higher part of the succession.

The Lower Ordovician graptolite faunas of southern Bolivia have also been studied more recently. Maletz *et al.* (1995, 1999) initially described the lower Ordovician graptolites from southern Bolivia and realized the similarity of the faunas to those of southern Scandinavia. Egenhoff (2000) discussed the sedimentology of the extremely thick succession of southern Bolivia and, with the biostratigraphical investigation and correlation by Maletz & Egenhoff (2001, 2003) and Egenhoff *et al.* (2004), was able to interpret the basin evolution based on the widely scattered and poorly preserved graptolite faunas. The faunas range from the basal Ordovician *Rhabdinopora flabelliformis* Biozone to the lower Dapingian interval with *Azygograptus lapworthi*. The index of the basal Floian *Paratetragraptus approximatus* has been reported from several localities (Maletz & Egenhoff 2001; Egenhoff *et al.* 2004) and is associated with *Tetragraptus phyllograptoides*. Altogether the succession was considered to be closely comparable to the Scandinavian successsion and many of the faunal elements suggested to be endemic for Scandinavia by Egenhoff & Maletz (2007) were recognized in the region. Toro & Maletz (2018) provided a current overview on the graptolite faunas of Bolivia, including also the upper Ordovician to Silurian faunas.

Australasia

The Lower Ordovician graptolite succession of Australasia (Fig. 10) has been revised by VandenBerg & Cooper (1992) and updated by Percival *et al.* (2011). It consists largely of a number of isolated levels with distinct graptolite faunas, but a precise and detailed biostratigraphic succession is not established. Thus, precise boundaries between the faunal associations cannot be provided. The late Tremadocian is represented by the *Aorograptus victoriae* Biozone (La2), an interval often identified as the *Sagenograptus murrayi* Biozone in other regions (Lindholm 1991a; Gutiérrez-Marco & Martin 2016) due to this more characteristic faunal element. The Floian *Paratetragraptus* *approximatus* Biozone (La3) is characterized by its index species and marks also the first occurrence of extensiform didymograptids (VandenBerg & Cooper 1992, p. 39). It might therefore be correlated with a level in the *Cymatograptus protobalticus* or even *Baltograptus vacillans* Biozone of Scandinavia, but not with the basal Floian, as in this interval no extensiform didymograptids have been discovered. The Bendigonian is differentiated into four intervals, based on the number of stipes in *Tshallograptus fruticosus* (VandenBerg & Cooper 1992; VandenBerg 2017). The differentiation is impossible to follow in most regions, however, but the whole interval may be correlated with the *Baltograptus vacillans* to *Baltograptus jacksoni* biozones of Hunneberg, in which specimens of *Tshallograptus fruticosus* are uncommon. The higher interval is not discussed herein, but it is noted that the lower Chewtonian (mid-Floian) of Australasia is now known as the *Didymograptellus kremastus* Biozone (VandenBerg 2018). *Didymograptellus kremastus* VandenBerg, 2018 is very similar to *Yutagraptus mantuanus*, but not to *Didymograptellus bifidus*, but the FAD of both taxa might have been at approximately the same level (see Maletz 2010, text-fig. 7). *Didymograptellus bifidus* is extremely rare in the Chewtonian of Australasia contrary to common understanding (VandenBerg 2018). *Didymograptus protobifidus* Elles, 1933 was previously used as the index for the lower Chewtonian, but considerable concerns exist about the identity of this species (see Williams & Stevens 1988) and its type material may have originated from the lower Darriwilian.

Systematic palaeontology

The taxonomy used herein is based on Maletz *et al.* (2009) and Maletz (2014) and in the various chapters of the revised Graptolite Treatise (Maletz *et al.* 2017, 2018a, b; Maletz, 2017b). Additional details are discussed when necessary. The synonymy lists are restricted to Scandinavian occurrences unless absolutely necessary for the understanding of the taxa, but may also cover some fairly unknown localities and regions.

Repository. – Most of the material used for this research was collected by the author during numerous visits to Hunneberg and have in part been used for a Diploma thesis (Maletz 1987). The main collection is now housed at the Museum für Naturkunde (MB.g) and at the Museum of Evolution, Palaeontological Institute, Uppsala University, Sweden (PMU). Additional material used during the research is in the collections of the Naturhistoriska Riksmuseet, Stockholm, Sweden (RM), the Geology Department at University of Lund, Sweden (LO), the collection of the Geologiska Undersökning, Uppsala, (SGU), the Geological Museum of Oslo, Norway (PMO) and the Melbourne Museum (Museums Victoria), Melbourne, Australia (NMV). Canadian material for comparison has been deposited at the Geological Survey of Canada, Ottawa (GSC). Material of the Tøyen section, Oslo, Norway (T) is preserved in the Erdtmann collection at the West Bohemian Museum in Plzeň (Pilsen), Czech Republic.

Order Graptoloidea Lapworth *in* Hopkinson & Lapworth, 1875

Diagnosis. – Graptolites united by the retention of the nematophorous sicula in the adult stage as the defining synapomorphy (Maletz *et al.* 2017a, p. 1).

Remarks. – The diagnosis is in accordance with the definition of Fortey & Cooper (1986), who were the first to define the Graptoloidea to include all planktic graptolites. The presence of bithecae has long been taken as an important character to differentiate the benthic Dendroidea from the planktic Graptoloidea, but many early planktic taxa of the Anisograptidae and even the Sigmagraptidae bear bithecae along the stipes or at least a sicular bitheca.

Suborder Graptodendroidina Mu & Lin *in* Lin, 1981

Diagnosis. – Quadriradiate to biradiate planktic, nematophorous graptolites with a triad budding system of the thecae; bithecae reduced or even lost in stratigraphically younger taxa; colonies multiramous to biramous, pendent to reclined; dissepiments present in some taxa; autothecae simple, widening tubes with or without short ventral rutellum; thecal apertures may be isolated; prosicula with distinct differentiation of conus and cauda; origin of th1^1 in the middle part of the conus; proximal end may possess one to three successive (proximal) dicalycal thecae with th1^2 as the first dicalycal theca; later dicalycal thecae adventitiously or regularly distributed (Maletz *et al.* 2017, p. 2).

Remarks. – Mu & Lin *in* Lin (1981) introduced the Graptodendroidina for planktic forms showing intermediate thecal features between the benthic Dendroidea and the planktic Graptoloidea, assembled in the family Anisograptidae. All taxa bear a nematophorous sicula and bithecae along the stipes, thus show typical dendroid characters combined with derived graptoloid characters. Fortey & Cooper (1986) redefined the Graptoloidea as including all planktic, nematophorous forms in the attempt to define a monophyletic unit, but stated that the bithecae were lost separately and independently in a number of lineages. It is here advocated to lessen the emphasis on the presence of bithecae and define upper level taxa based on proximal development types only. This interpretation lends considerable support to the independent loss of bithecae in a number of groups of planktic Graptolithina (see also Maletz *et al.* 2017, fig. 1).

Family Anisograptidae Bulman, 1950b

Diagnosis. – Planktic nematophorous, multiramous graptoloids with a triad budding system; colony shape ranges from reclined through horizontal to declined and bell-shaped or pendent; bithecae distinctly smaller than autothecae; bithecae initially regular, but in later taxa irregular and often reduced or absent; autothecae simple, widening tubes, sometimes aperturally isolated; ventral rutella common; dissepiments present in a few taxa; proximal development type isograptid, quadriradiate to biradiate, variably dextral or sinistral; maeandrograptid type proximal symmetry with inclined sicula; prosicula with distinct differentiation of conus and cauda; origin of first theca in median part of the conus; $\text{th}1^2$ is first dicalycal thecae, later dicalycal thecae adventitiously or regularly distributed (Maletz *et al.* 2017a, pp. 2, 3).

Remarks. – The family Anisograptidae are the earliest planktic graptoloids and are used in the sense of Maletz *et al.* (2017a). All members of the taxon bear at least a single sicular bitheca, but most members possess bithecae in alternating positions along the stipes. The identification of anisograptid taxa is often problematic, especially in flattened material, in which the bithecae cannot be observed. Anisograptidae appear to be restricted to the Tremadocian and are replaced by the Dichograptina and Sinograptina in the basal Floian. The transition is, however, poorly known and the Anisograptidae must be regarded as a paraphyletic taxon. Sadler *et al.* (2011, fig. 14) indicated a distinct extinction event within the clade of the Anisograptidae in the late Tremadocian, after which they recovered and survived into the late Floian. Maletz (2017a) considered this extinction event as a gap in the investigation of Tremadocian graptolite faunas, stating that late Tremadocian faunas are very poorly known.

Genus *Rhabdinopora* Eichwald, 1855

Type species. – *Gorgonia flabelliformis* Eichwald, 1840 from the Lower Tremadocian Türisalu Member of the Pakerort Stage of Paldiski, Osmussar, Estonia; subsequent designation (Bassler 1911, p. 348).

Diagnosis. – Pendent multiramous anisograptid with irregularly to regularly distributed dissepiments; proximal development quadriradiate (Maletz *et al.* 2017a, p. 6).

Remarks. – The genus *Rhabdinopora* Eichwald, 1855 and its type species *Rhabdinopora flabelliformis* (Eichwald, 1840) are among the most controversial taxa of the planktic graptolites. For a long time, benthic and planktic graptolites with the typical mesh of *Rhabdinopora flabelliformis* were included in the genus *Dictyonema*, before Erdtmann (1982) re-established the genus *Rhabdinopora* for the planktic taxa and separated the benthic species under the genus name *Dictyonema* Hall, 1851. Numerous species have been described under the name *Dictyonema*, largely based on tubarium fragments so that comparison is difficult. The number of synonyms is likely to be high. Maletz (2019) recognized the acanthograptid thecal style of *Dictyonema retiforme* (Hall, 1843), the type species of the genus *Dictyonema*, and transferred the genus to the Acanthograptidae (now Callograptidae: Maletz 2020b). Therefore, the supposed phylogenetic origin of *Rhabdinopora* from the genus *Dictyonema* (Erdtmann 1982) needs to be re-evaluated and late Cambrian dendroid taxa bearing a meshwork of stipes connected with dissepiments must be referred to another genus.

***Rhabdinopora flabelliformis* (Eichwald, 1840)**

Figure 11C

Remarks. – The species is not described here, as only poor fragments are available and the species is well known (cf. Cooper *et al.* 1998). The material cannot be referred to any of the described subspecies of *Rhabdinopora flabelliformis* and a precise age determination is therefore impossible. The dimensions of the meshes may indicate *Rhabdinopora flabelliformis* sensu stricto, but not one of the early forms, which have more densely spaced meshes (Cooper *et al.* 1998).

Distribution. – The species was found as fragments at Holsbrotten at the western side of Hunneberg. It occurs in a thin layer of black shale at the top of

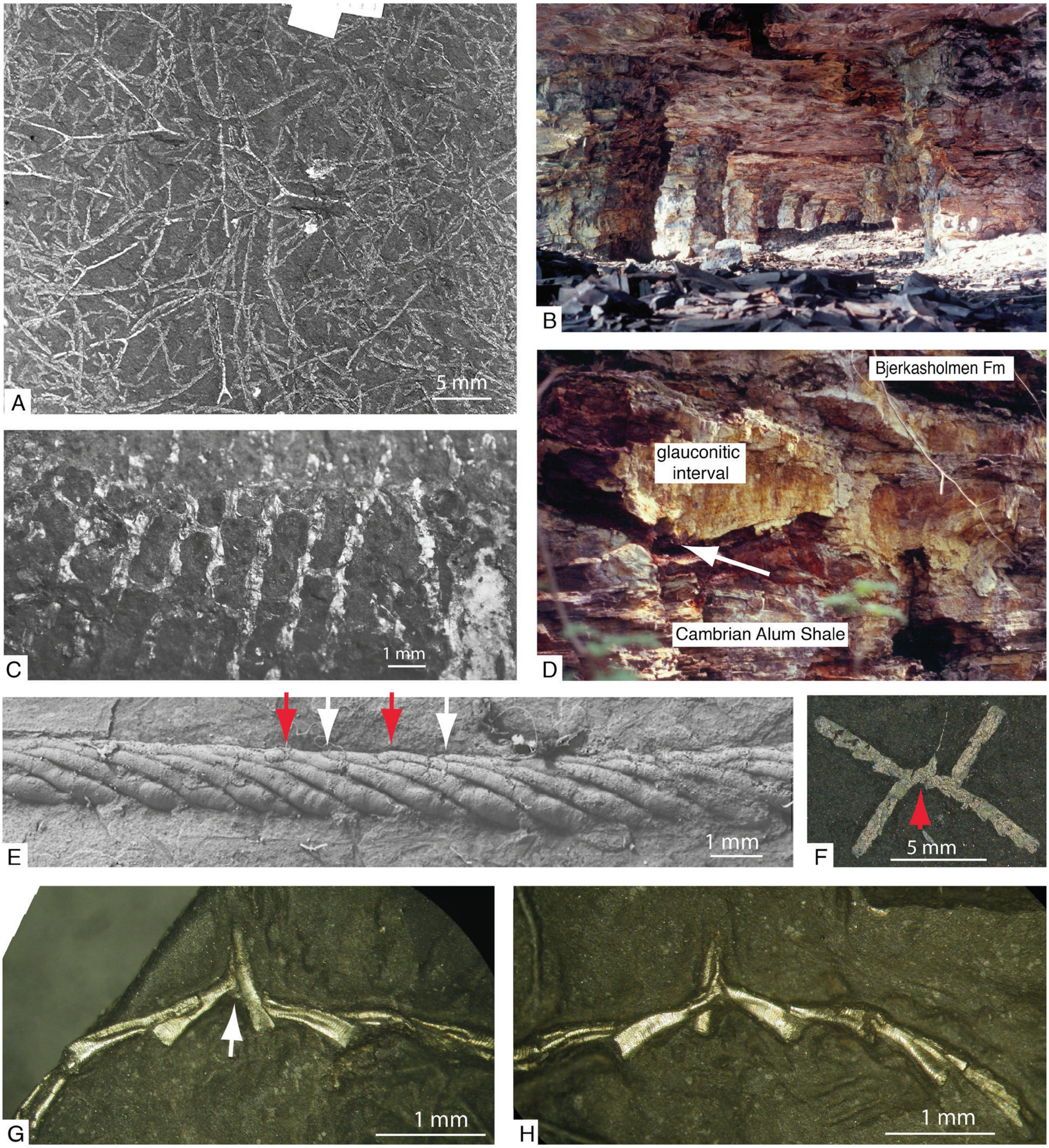

Fig. 11. Tremadocian graptolites at Hunneberg. **A**, **G**, **H**. *Adelograptus tenellus* (Linnarsson, 1871). **A**, neotype, SGU 4497a, Nygård, Skaktet No. 1, coll. von Schmalensee. **G**, LO 2257t, pyritic internal cast in reverse view, crossing canals broken off, white arrow indicates sicular bitheca, sinistral specimen (see Westergård, 1909, pl. 5, fig. 20). **H**. LO 2258t, pyritic internal cast in reverse view, dextral specimen (see Westergård, 1909, pl. 5, fig. 19). **B**. Holsbrotten caves showing Upper Cambrian (Furongian) succession, roof formed by Björkåsholmen limestones. **C**. *Rhabdinopora flabelliformis* s. l., MBg material, Holsbrotten, coll. J. Maletz. **D**. Location of *Rhabdinopora* layer (arrowed), Holsbrotten. **E, F**. *Paratemnograptus magnificus* (Pritchard, 1892). **E**. PMO 108.558, stipe fragment showing plaited overlap (white and red arrows), Slemmestad, Norway. **F**. NMVP 14368, holotype of *Tetragraptus decipiens* Hall, 1899b (Hall 1899b, pl. 17, fig. 14, 15) showing indication of sicular bitheca (arrow).

the Cambrian portion of the Alum Shale Formation (Fig. 11D). Linnarsson (1869) first recognized the '*Dictyonema* Shale' at Hunneberg, but this record was not mentioned by Sidenbladh (1870) in his description of the mapping of the Hunneberg area. Lindström (1887) noted that von Schmalensee collected *Dictyonema flabelliforme* at Skaktet No. 1 at Nygård. The species has not previously been illustrated from Hunneberg.

Genus *Adelograptus* Bulman, 1941

Type species. – *Bryograptus*? *hunnebergensis* Moberg, 1892, p. 92 (= *Dichograptus*? *tenellus* Linnarsson, 1871, p. 794: Maletz & Erdtmann 1987, p. 180) from the upper part of the Alum Shale Formation at Nygård, Hunneberg; original designation.

Diagnosis. – Biradiate anisograptid with horizontal to subhorizontal tubarium; distal dichotomies irregularly spaced; cortical overgrowth of proximal part of stipes in gerontic specimens; bithecae on alternate sides of stipes; slender, slowly widening thecae, often with short rutellum (Maletz *et al.* 2017a, p. 8).

Remarks. – The genus *Adelograptus* is in urgent need of revision as many late Tremadocian species, of which the detailed tubarium construction is unknown, have been included in it. Species with a sicular bitheca but lacking additional bithecae were referred to *Adelograptus* by Williams & Stevens (1991, p. 29). This would broaden the concept of the genus to the extent that even the genus *Hunnegraptus* could be interpreted as a synonym of *Adelograptus*. It is here preferred to include only species with a typical anisograptid proximal end with a biradiate development, showing an obliquely oriented sicula (cf. Maletz 1992a, 2014) and bithecate stipes.

Adelograptus tenellus (Linnarsson, 1869)

Figure 11A, G, H

1871 *Dichograptus*? *tenellus* n. sp. Linnarsson, p. 794, pl. 16, figs 13–15.
1892 *Bryograptus*? *hunnebergensis* n. sp. Moberg, p. 92, pl. 1, figs 5–7, ?8, 9. (see Maletz & Erdtmann 1987 for further info)

Remarks. – Maletz & Erdtmann (1987) redescribed this species in some detail and selected a neotype for the lost type material of Linnarsson. The neotype (Fig. 11A) is the largest and most complete of the specimens described and illustrated by Moberg (1892, pl. 2, fig. 1a, b) and has been regarded as typical of the species (see illustrations in Bulman 1970; Zalasiewicz *et al.* 2009). Details of the tubarium construction are not evident in this material and the presence of bithecae is uncertain. Maletz & Erdtmann (1987) listed synonyms of Scandinavian and British material, but did not include specimens from elsewhere. The authors regarded *Bryograptus*? *hunnebergensis* Moberg, 1892 as laterally preserved proximal ends and smaller specimens referrable to *Adelograptus tenellus* and identified *Bryograptus*? *sarmentosus* as mature specimens of *Adelograptus tenellus* with cortical overgrowth on the stipes.

Westergård (1909, pl. 5, figs 19, 20) illustrated two proximal ends of *Adelograptus tenellus*, preserved in pyrite in full relief from Jerrestad, Scania, southern Sweden (Fig. 11G, H). Maletz (2017a, 2020a) provided photos of the specimens that even show imprints of the fusellar construction on the internal cast. The material includes both dextral and sinistral specimens (cf. Maletz *et al.* 2016; Maletz 2021), identified as right- and left-handed specimens by Hutt (1974). The two illustrated specimens are on a single slab and show a sinistral (left-handed) specimen in which the crossing canal is broken off (Fig. 11G), but the apertural part of the sicular bitheca is visible (arrowed). In the dextral specimen (Fig. 11H) the crossing canals are preserved and the sicular bitheca is not visible.

Stubblefield (1929) and Hutt (1974) described *Adelograptus tenellus* in great detail from shale material and chemically isolated material collected in the Shineton Shales of Shropshire, but referred the material to *Clonograptus tenellus* (Linnarsson, 1871) and *Bryograptus hunnebergensis* Moberg, 1892. Maletz & Erdtmann (1987) synonymized the two taxa originating from the same locality and obviously being based on material from a single horizon. Hutt (1974) was unable to separate proximal ends of both species and differentiated larger specimens only by the angle between the two first-order stipes, measuring 145° in '*Adelograptus hunnebergensis*' and 110° in '*Clonograptus tenellus*'.

Gutiérrez-Marco & Martin (2016) illustrated a single specimen as '*Adelogratus*' *tenellus* from the eastern Anti-Atlas of Morocco and used this to introduce the '*Adelograptus*' *tenellus* Biozone to the Fezouata lagerstätte of the central Anti-Atlas, where this taxon has not been recognized. The identity of this material is unknown even though it appears generally similar to *Adelograptus tenellus*.

Legrand (1964b) described *Adelograptus bagueli* and *Adelograptus messaoudi* from the Tremadocian of the Algerian Sahara in some detail from chemically isolated material, showing a very similar development to the British material of *Adelograptus tenellus*. The two species appear to differ slightly from *Adelograptus tenellus*, but may represent a very similar biostratigraphic interval.

Occurrence. – *Adelograptus tenellus* is found between Nygård and Holsbrotten intermittedly at the top of the Cambrian portion of the Alum Shale Formation, but is rare. It covers the bed surfaces in dense layers and individual colonies are difficult to recognize. Due to its sporadic occurrence, the exact stratigraphic level of its appearance is uncertain. Material from the Shineton Shales of Shropshire (Stubblefield 1929; Hutt 1974), considered conspecific with the type material, is well preserved and Hutt (1974) described the development of the species in detail from chemically isolated material, showing the presence of bithecae on alternating sides along the stipes and the presence of a sicular bitheca. The exact biostratigraphic distribution of the species is unknown, as many slender multiramous taxa from the late Tremadocian may have been mistaken for it.

Genus *Paratemnograptus* Williams & Stevens, 1991

Type species. – *Paratemnograptus isolatus* Williams & Stevens, 1991 from the *Aorograptus victoriae* Biozone at The Ledge, Cow Head Peninsula, western Newfoundland, Canada (= *Clonograptus magnificus* Pritchard, 1892: Maletz *et al.* 2017a, p. 8); original designation.

Diagnosis. – Horizontal to subhorizontal, multiramous tubarium with biradiate development and tetragraptid foundation; sicular bitheca present; stipes with plaited overlap of thecae, but without bithecae (Maletz *et al.* 2017a, p. 8).

Species. – *Clonograptus magnificus* Pritchard, 1892; *Tetragraptus decipiens* Hall, 1899a; *Paratemnograptus isolatus* Williams & Stevens, 1991; *Kiaerograptus magnus* Williams & Stevens, 1991; *Clonograptus* (*Clonograptus*) *magnus* Lindholm, 1991a.

Remarks. – Williams & Stevens (1991) described *Paratemnograptus* based on isolated material and shale specimens from the upper Tremadocian of western Newfoundland. The single isolated stipe fragment (Williams & Stevens 1991, pl. 4, fig. 8) shows the plaited thecal overlap without bithecae. The proximal end bears a slender and long sicula with a distinct sicular bitheca. The proximal end differs considerably from that of *Clonograptus* (see Lindholm & Maletz 1989). The sicula is wider and shorter in *Clonograptus* and there is no sicular bitheca and plaited thecal structure on the stipes. Even though details of the proximal development are not known from the Scandinavian material, the plaited thecal overlap of the large tubarium is well displayed in a single specimen from the *Tetragraptus phyllograptoides* Biozone of Diabasbrottet (Lindholm & Maletz 1989, pl. 83, fig. 7).

Paratemnograptus magnificus (Pritchard, 1892)

Figures 11E, F, 22A

1892 *Temnograptus magnificus* n. sp. Pritchard, p. 56, pl. 6, figs 1–3.
1899a *Tetragraptus decipiens* n. sp. Hall, p. 168, pl. 17, figs 13–15; pl. 18, figs 16–19.
1989 *Clonograptus* (*Clonograptus*) sp. aff. *Clonograptus* (*Clonograptus*) *multiplex* (Nicholson, 1868); Lindholm & Maletz, p. 734, pl. 83, fig. 7; text-fig. 12.
1991a *Clonograptus* (*Clonograptus*) *magnus* sp. nov. Lindholm, p. 307, text-fig. 10A, C, D.
1991 *Paratemnograptus isolatus* sp. nov. Williams & Stevens, p. 19, pl. 1, figs 10–16, pl. 2, fig. 4, pl. 4, figs 1–8, text-fig. 10A–O.
1991 *Kiaerograptus magnus* sp. nov. Williams & Stevens, p. 16, pl. 1, figs 5–7, pl. 3, figs 4, 7, text-fig. 7I–P.
?2016 *Paratemnograptus magnificus* (Pritchard); Gutiérrez-Marco & Martin, fig. 4G (no description).
?2016 *Paratemnograptus magnificus* (Pritchard); Martin *et al.*, fig. 5I (no description).
?2020a *Paratemnograptus magnificus* (Pritchard, 1892); Maletz, fig. 10 L (no description).
2021 *Paratemnograptus magnificus* (Pritchard); Achab & Maletz, figs 4C–E (no description).

Type material. – The holotype is NMV 13400 from the ‘Lancefield quarry’ (NMV loc. PL 1144), allotment 56, Parish of Goldie, near Lancefield, Victoria. It is the largest graptolite known from Australia (A. H. M. VandenBerg pers. com. 2018) and was glued together from numerous fragments. Due to the varnish it is covered in, a photograph is impossible and the original drawing by Pritchard is still the best illustration of the specimen.

Remarks. – The single specimen (Fig. 22A) of this form from Hunneberg (SGU 5468) was collected by von Schmalensee in the ‘Mossebo Limestone Quarry’, north-west Hunneberg, Sweden. This locality is likely to have been close to the modern Diabasbrottet section. The specimen shows the typical ‘dendroid’ stipes with the plaited overlap of thecae, but has no bithecae (Lindholm & Maletz 1989). It is associated with a typical *Tetragraptus phyllograptoides* zone fauna (Lindholm & Maletz 1989) including *Tetragraptus phyllograptoides*, *Cymatograptus undulatus*, *Cymatograptus demissus* and *Tetragraptus amii*, clearly indicating its age is early Floian. The specimen thus is the youngest anisograptid known so far and the only specimen of *Paratemnograptus magnificus* from the *Tetragraptus phyllograptoides* Biozone.

Kiaerograptus magnus Williams & Stevens, 1991 appears to be based on juvenile specimens of *Paratemnograptus isolatus* Williams & Stevens, 1991 as the material of both taxa originated from the same locality and level. Lindholm (1991a) described *Clonograptus* (*Clonograptus*) *magnus* Lindholm, 1991a from a single complete specimen with eight stipes, and a number of stipe fragments. The specimen from the *Hunnegraptus copiosus* Biozone of Slemmestad, Norway is now considered to be *Paratemnograptus magnificus*, based on the robustness of the colony and the branching patterns. The material is similar to specimens identified as *Clonograptus (Clonograptus)* sp. aff. *C.* (*C.*) *multiplex* by Lindholm & Maletz (1989, fig. 12) from Slemmestad, Norway and Mossebo.

Maletz & Egenhoff (2001) discussed the identity of the large 'clonograptids' of Upper Tremadocian age and already suggested the synonymy of *Paratemnograptus isolatus* Williams & Stevens, 1991 and *Clonograptus magnificus* Pritchard, 1892. The authors also considered the species *Kiaerograptus magnus* Willliams & Stevens, 1991 to be juveniles of *Paratemnograptus magnificus*.

The thecal development is known from very few specimens preserved in relief. The specimen of Lindholm & Maletz (1989, pl. 83, fig. 7) shows a regular development of thecal origins on alternating sides (Fig. 11E), but the thecal apertures are not preserved and some diagenetic distortion trough flattening of the specimen must be expected. Williams & Stevens (1991, pl. 4, fig. 8) illustrated a stipe fragment of *Paratemnograptus isolatus* in partial relief that appears to lack bithecae and is comparable with the Hunneberg material. The Fezouata specimens from Morocco (Gutiérrez-Marco & Martin 2016; Martin *et al.* 2016) show the origin of two thecae on one side followed by one theca on the other side, suggesting a possibly more irregular development. However, the observation is based on short stipe fragments and it is uncertain whether this is representative. The specimens are here identified only tentatively as *Paratemnograptus magnificus*.

Occurrence. – *Paratemnograptus magnificus* is most probably a deep-water species as it is rarely found in shallow water regions. The best specimens come from the Lancefieldian (La2, *Aorograptus victoriae* Biozone) of Australia (VandenBerg & Cooper 1992), where it is fairly common. It is often found as juvenile specimens, generally identified in the past as *Tetragraptus decipiens* (Hall, 1899a). The holotype of this species clearly shows the sicular bitheca (Fig. 11F).

A single specimen from the Tøyen Shale of Norway originated from ca 0.5–1.0 m above the Bjørkåsholmen Formation at Slemmestad (*Hunnegraptus copiosus* Biozone: Lindholm & Maletz, 1989). Lindholm (1991a) described *Clonograptus* (*Clonograptus*) *magnus* from the same interval.

The few specimens that have been found in Scandinavia and Australia indicate a biostratigraphic range from the *Sagenograptus murrayi* Biozone to the *Tetragraptus phyllograptoides* Biozone. Gutiérrez-Marco & Martin (2016) indicated the presence of this species in the *Sagenograptus murrayi* and *Hunnegraptus copiosus* biozones of the Fezouata lagerstätte of Morocco, but illustrated only one small stipe fragment, preserved in relief, that shows the plaited overlap of the thecae.

Suborder Sinograptina Mu, 1957

Diagnosis. – Planktic graptoloids with multiramous to single-stiped, horizontal to subhorizontal tubarium; sicula often nearly parallel-sided and without rutellum, oriented perpendicular to stipes; proximal development isograptid, dextral or sinistral with distinct asymmetry of the crossing canals, lost in derived forms; artus-type development in derived taxa; origin of th1^1 in middle part of prosicula in early taxa, but generally in the lower part of prosicula, rarely in metasicula in younger ones; thecal style varies from simple dichograptid with gradually widening thecae to forms with distinctly differentiated pro-and metathecae; thecal elaborations such as prothecal folds, lateral apertural lappets, rutella or spines common; fusellum normal to strongly reduced and possibly lacking in some (Abrograptidae) (Maletz *et al.* 2018a, p. 1).

Remarks. – Maletz (2014) and Maletz *et al.* (2018a) differentiated a number of family level taxa in the Sinograptina. Of these, only the Kinnegraptidae includes members that are found in the Hunneberg Region.

Family Kinnegraptidae Mu, 1974

Diagnosis. – Multiramous to one-stiped, reclined to horizontal and pendent tubaria; colony biradiate with asymmetrical placing of first-order stipes; sicula parallel sided or nearly parallel sided with parallel-sided prosicula; proximal development isograptid, dextral or sinistral, or of artus-type development in derived taxa; origin of first theca in median part of prosicula in early taxa, in lower part of prosicula in younger ones; crossing canals more slender than in Dichograptina; thecae simple or with complex and elaborate apertures, slender and sometimes elongated (Maletz *et al.* 2018a, pp. 2, 3).

Remarks. – A number of family taxa have in the past been introduced that included taxa currently referred to the Sigmagraptidae (see Maletz *et al.*

2018a). However, the name of family rank should be the oldest valid name, which appears to be the family Kinnegraptidae Mu, 1974, which is therefore used herein.

The Azygograptidae Mu, 1950 is here regarded as a *nomen dubium*, as it included a heterogenous group of single-stiped taxa with multiple independent origins, based on colony shape in the sense of the polyphyletically defined initial taxa of the Graptolithina (e.g. *Didymograptus*, *Tetragraptus*) that alone is insufficient for defining groups of family rank. It appears impractical to combine a highly diverse group of graptoloids to this taxon and to use the family Azygograptidae Mu, 1950 for the clade here named the Kinnegraptidae.

Subfamily Sigmagraptinae Cooper & Fortey, 1982

Diagnosis (revised herein). – Multiramous to single-stiped, reclined to horizontal and pendent tubaria; colony biradiate with asymmetrical placing of first-order stipes; sicula parallel-sided or nearly parallel with parallel-sided prosicula; proximal development isograptid, dextral or sinistral, or of artus-type in derived taxa; origin of first theca in median part of prosicula in early taxa, in lower part of prosicula in younger ones; crossing canals more slender than in Dichograptina; thecae generally simple with straight or rutellate apertures.

Remarks. – Cooper & Fortey (1982) introduced the subfamily Sigmagraptinae, upgraded to family level rank by Fortey & Cooper (1986), but Williams & Stevens (1988) included it as a subfamily in the Sinograptidae. The Sigmagraptinae may be regarded as the base of the entire clade of the Sinograptina and ancestral to all derived Sinograptina, so that it may be understood as a paraphyletic taxon. The members of the Sigmagraptinae bear a slender parallel-sided sicula with a relatively large prosicula and a straight non-rutellate sicular aperture. The shape and dimensions of the sicula, the asymmetrical proximal development and the simple thecal style are interpreted as plesiomorphic characters retained from the Anisograptidae. Many derived sigmagraptines have a considerably extended rutellum on the sicula (ex. gr. *Goniograptus*: Williams & Stevens 1988; Maletz 2004), but this is not developed in early members of the subfamily.

Genus *Acrograptus* Tzaj, 1969

Types species. – *Didymograptus affinis* Nicholson, 1869 from the Tarn Moor Formation at Aik Beck, E of Ullswater, English Lake District, *Didymograptus artus* Biozone, Darriwilian; original designation.

Diagnosis. – Slender sigmagraptine with two horizontal to declined stipes; sicula small, triangular; proximal development artus-type; thecae slender and with low thecal overlap or with distally increasing overlap (Maletz *et al.* 2018a, p. 8).

Remarks. – Tzaj (1969) erected the genus *Acrograptus* essentially for slender two-stiped horizontal to declined species showing low thecal overlap and simple thecal apertures. This information provides little guidance for the identification of many Lower to Middle Ordovician species as the proximal shape and development appears to be quite variable and the genus must be regarded as a basket name for slender two-stiped taxa, but not as a useful taxonomic unit.

Tzaj (1969) listed 33 species under the genus name, including species now referred to the genera *Baltograptus, Cymatograptus, Holmograptus* and *Maeandrograptus*, even including the robust *Cymatograptus protobalticus*. Thus, there might be considerable doubt as to the taxonomic understanding and use of the genus. The definition here follows the common use as discussed by Cooper & Fortey (1982, 1986). The type species *Acrograptus affinis* (Nicholson, 1869) is from the Darriwilian of English Lake District and appears to show an artus-type proximal development (see Rushton 2000a; Maletz *et al.* 2018a, fig. 6.4) and is not comparable to older Floian to Dapingian species currently referred to the genus, often bearing an isograptid type proximal development. A revision of the genus is not possible here due to the limited number of taxa studied in this investigation.

Li *et al.* (2012) discussed the distribution of the genus *Acrograptus* in China and found most of the species discussed in their paper to be restricted to the Floian. The authors indicated a range of *Acrograptus gracilis* through the Dapingian and the upper Darriwilian *Pterograptus elegans* Biozone. The identity of most of their illustrated specimens, however, needs to be re-evaluated. The material referred to *Acrograptus affinis* (Li *et al.* 2012, fig. 4a–d) is from the late Floian, bears a long, highly inclined sicula and an isograptid proximal development and does certainly not belong to this species.

Acrograptus filiformis (Tullberg, 1880)

Figures 12A, B, 13C, D

1880 *Didymograptus filiformis* n. sp. Tullberg, p. 42, pl. 2, figs 8–11.

1901 *Didymograptus filiformis* Tullberg, 1880; Törnquist, p. 21, pl. 3, figs 6–9.
1937 *Didymograptus filiformis* Tullberg; Monsen, p. 122, pl. 2, figs 5, 12, 13, 18, 68, 72.
1990 *Acrograptus filiformis* (Tullberg, 1880); Bahlburg, Breitkreuz, Maletz, Moya & Salfity, pl. 2, fig. d.
1994 *Acrograptus filiformis* (Tullberg, 1880); Ortega & Suarez-Soruco, p. 238, pl. 3, fig. 1; text-fig. 8c–f, i.
1997 *Acrograptus filiformis* (Tullberg, 1880); Toro & Brussa, fig. 3I, j, n.
pars 2012 *Acrograptus filiformis* (Tullberg, 1880); Li, Feng, Wang & Chen, p. 1118, fig. 5k–m; ?fig. 5j.

Type material. – LO 350T, LO 351t, LO 352t, from the Tøyen Shale of Kiviks-Esperöd, Scania, Sweden. They are preserved as flattened films of thin, somewhat silvery fusellum in black shale. The specimens are associated with *Baltograptus vacillans*, indicating they are from the *Baltograptus vacillans* Biozone. The material is fairly poor and the specimens are difficult to see on the shale surfaces. They clearly show the very slender, declined stipes with thecae inclined at a low angle. The proximal development is impossible to see in the specimens, but the proximal ends show a distinct asymmetry of the divergence of the two stipes.

Material. – Numerous specimens from Diabasbrottet, associated with *Baltograptus vacillans* and a number of other taxa. The specimens are preserved in partial relief to completely flattend as silvery films of organic material.

Description. – The sicula is about 0.9–1.0 mm long and largely parallel-sided. The sicular aperture is about 0.2 mm wide. A short nema may be present in some specimens. The sicula is straight and oriented perpendicular to the stipes. The proximal development is isograptid, dextral with a highly asymmetrical divergence of the two stipes. Th1^1 originates high on the sicula, possibly in the prosicula, but this is uncertain because preservation is too poor to identify the beginning of the metasicula (Fig. 12A). Th1^1 bends away from the sicula about 0.3 mm above the sicular aperture. On the obverse side, the slender protheca of th2^1 is visible on the dorsal side of th1^1 (Fig. 12B) indicating the isograptid development. The thecae are slender, with an inclination of about 10° and a straight aperture perpendicular to the dorsal side of the stipes. The thecal overlap is about 0.3 mm, thus, less than 1/3 with a 2TRD of ca 2.1 mm. The stipes appear to be parallel-sided and about 0.3 mm wide. A distal widening was not observed, but the stipes are short in all investigated specimens and no specimens with more than 5–6 thecae on a stipe have been found.

Remarks. – The type material from Kiviks Esperöd in Scania, southern Sweden is poorly preserved, but most of the important characters of the species can be seen. It includes three specimens, of which the best preserved specimen, LO 350T (Fig. 13C), is here designated as the lectotype. It is a flattened proximal end and does not show more than the outline of the tubarium. *Acrograptus filiformis* is slender with widely spaced thecae with low overlap, making it easily identifiable even in poorly preserved material. The specimens described and illustrated by Törnquist (1901) from Diabasbrottet are preserved as moulds in partial relief and show the obverse and reverse sides (Fig. 12A, B). Latex casts of the specimens provide excellent information on the tubarium development, leaving no doubt that the Hunneberg material belongs to *Acrograptus filiformis*.

Occurrence. – *A. filiformis* is common in Scandinavia in the *Baltograptus vacillans* and *Baltograptus jacksoni* biozones. The species was also reported from the Oslo Region of Norway (Monsen 1937) and from Scania, Sweden (Tjernvik 1960; Lindholm 1981). Its exact range is uncertain as a similar, undescribed species with an artus-type development occurs in the upper Dapingian (Maletz & Ahlberg 2021, fig. 1i). Maletz (2023) described this form as *Acrograptus*(?) *artus*, based on material chemically isolated by Roland Skoglund.

Acrograptus filiformis is common in South America (Bahlburg *et al.* 1990; Ortega & Suarez-Socruco 1994; Toro & Brussa 1997) and has been cited from China (Mu *et al.* 2002). There are no references of this species from Australasia (see VandenBerg & Cooper 1992).

Acrograptus pusillus **(Tullberg, 1880)**

Figures 12C, D, 13A, B

1880 *Didymograptus pusillus* n. sp. Tullberg, p. 42, pl. 2, figs 12–14.
?1937 *Didymograptus* cf. *pusillus* Tullberg; Monsen, p. 129, pl. 2, figs 21, 50, 61, 65; pl. 9, fig. 4.
?1997a *Acrograptus* cf. *A. pusillus* (Tullberg, 1880); Toro, pl. 3, figs 11, 12.
2012 *Acrograptus pusillus* (Tullberg, 1880); Li, Feng, Wang & Chen, p. 1118, fig. 5b, g, h.
2021 ‘*Acrograptus*’ *pusillus* (Tullberg); Rushton, Ghobadi Pour, Popov, Jahangir & Amini p. 10, fig. 8a, b, f, g, ?fig. 8c–e.

Type material. – Two slabs with the two illustrated specimens from Kiviks Esperöd, Scania, southern Sweden. LO 348T (Tullberg 1880, figs 12, 13) is here designated the lectotype. Rushton *et al.* (2021, fig. 8f, g) illustrated the type material from drawings by Kristina Lindholm (Kävlinge, Sweden). The slab includes a number of poorly preserved specimens, of which one can be identified as the original for Tullbergs figure. Two poor proximal ends show

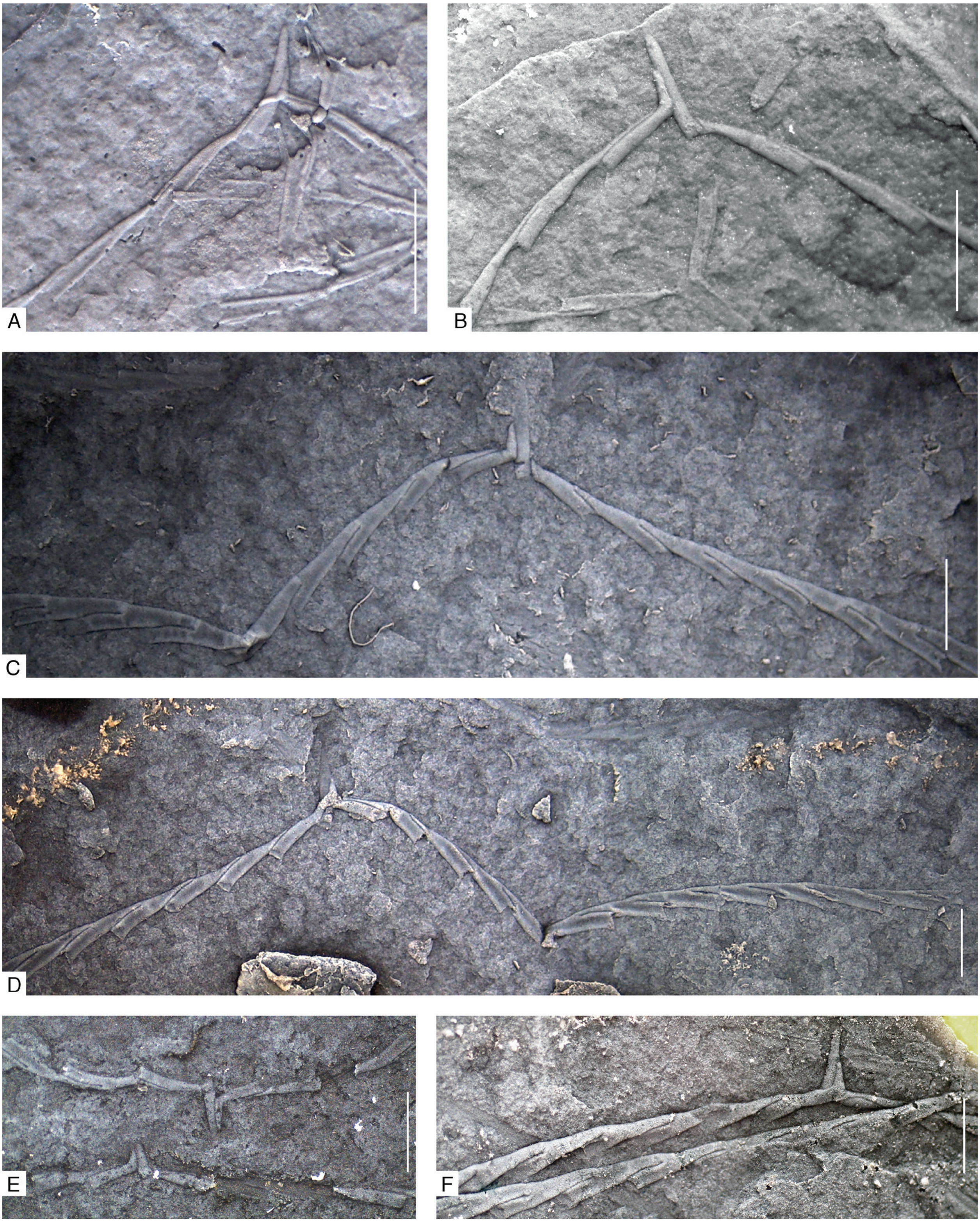

Fig. 12. *Acrograptus* specimens. **A**, **B**. *Acrograptus filiformis* (Tullberg, 1880). **A**, LO 1639t, Diabasbrottet, (Törnquist 1901, pl. 3, fig. 7), latex cast in reverse view. **B**, LO 1638t, Diabasbrottet, Törnquist, 1901 (pl. 3, fig. 7), latex cast in obverse view. **C**, **D**, *Acrograptus pusillus* (Tullberg, 1880), PMU 38391A, B, Diabasbrottet, coll. Moberg, latex casts in obverse (C) and reverse (D) views showing isograptid proximal development and thecal style. **E**, **F**. *Acrograptus* sp. cf. *Acrograptus gracilis* (Törnquist, 1890), Diabasbrottet, latex coated. **E**, PMU 38392/1, PMU 38392/2, two specimens in obverse view. **F**, PMU 38393/2, proximal end in reverse view, 'Mossebo', old collection, Lund. Scale indicates 1 mm in each photo.

parts of the proximal development (Fig. 13A, B). The slab also includes fragments of a slender *Acrograptus* or *Jishougraptus* specimen. The juvenile specimen on slab LO 349t is very poor and it is impossible to be certain that it is the basis for the illustration in Tullberg (1880, fig. 14). The slab also includes specimens of *Acrograptus filiformis*.

Material. – Several poor specimens from Diabasbrottet. Additional specimens collected and identified by Moberg were found in the collections at the Geology Department, Lund University (Fig. 12C, D). The species appears to be uncommon and only a few specimens have been identified.

Description. – The species is a slender, subhorizontal acrograptid with a prominent, parallel-sided sicula. The stipes are 0.3–0.35 mm wide and do not widen distally. The 2TRD is 1.6–1.7 mm in the proximal end, and none have stipes long enough to determine distal spacing. The sicula is 1.1–1.2 mm long and slender, measuring less than 0.2 mm across the aperture. The aperture is nearly straight, with just a minimal indication of a rutellum. The origin of th1^1 is 0.2–0.3 mm below the apex of the sicula, most probably in the lowermost part of the prosicula. The proximal development is isograptid, dextral, expressing a considerable asymmetry. The thecae are slender, with low inclination and an overlap of less than 50%.

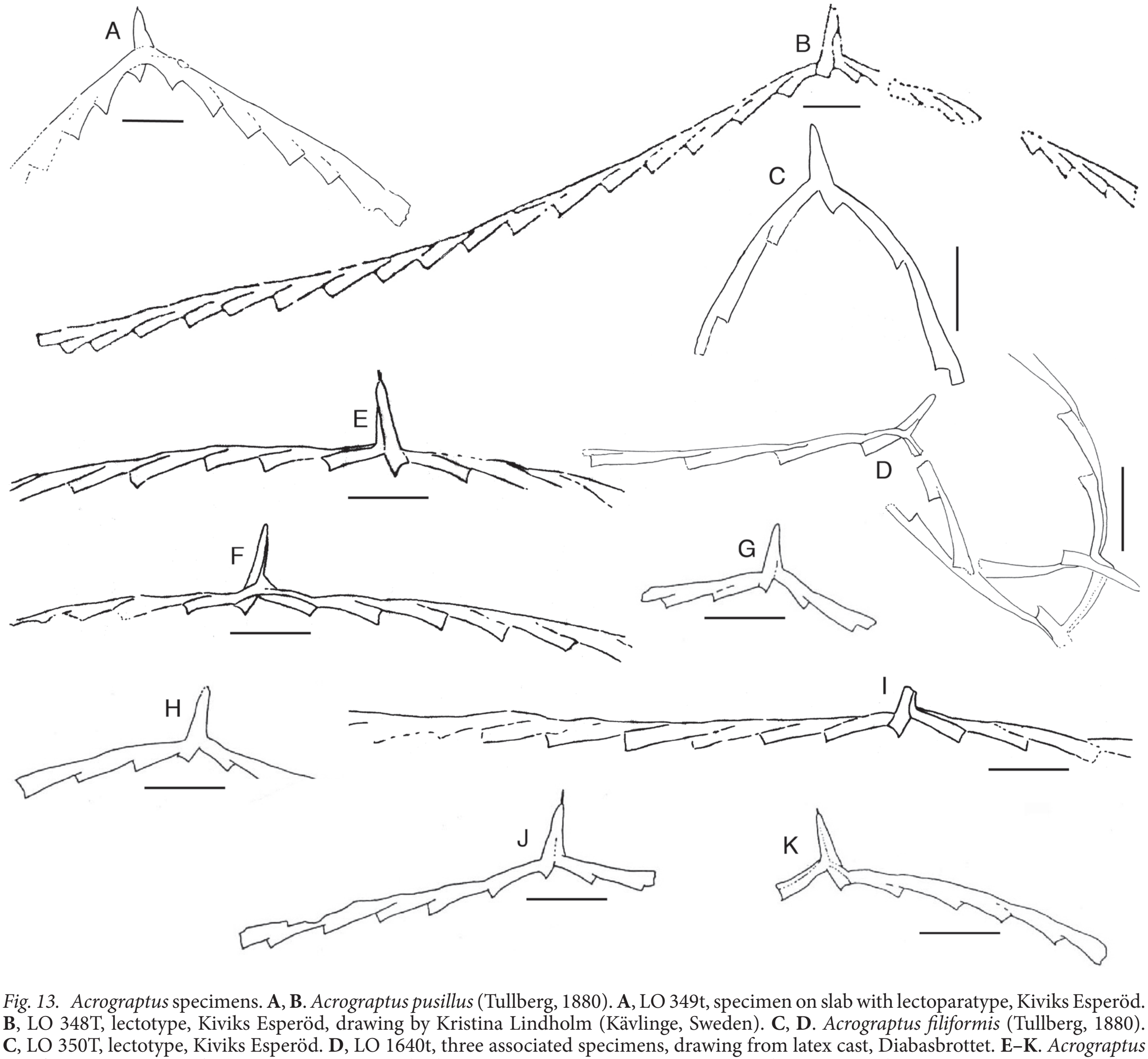

Fig. 13. Acrograptus specimens. **A**, **B**. *Acrograptus pusillus* (Tullberg, 1880). **A**, LO 349t, specimen on slab with lectoparatype, Kiviks Esperöd. **B**, LO 348T, lectotype, Kiviks Esperöd, drawing by Kristina Lindholm (Kävlinge, Sweden). **C**, **D**. *Acrograptus filiformis* (Tullberg, 1880). **C**, LO 350T, lectotype, Kiviks Esperöd. **D**, LO 1640t, three associated specimens, drawing from latex cast, Diabasbrottet. **E–K**. *Acrograptus* sp. cf. *Acrograptus gracilis* (Törnquist, 1890), Diabasbrottet at 4.6–4.7 m. **E**, PMU 38392a/3, latex cast in obverse view. **F**, PMU 38392b/3, latex cast in reverse view. **G**, MBg Di 894-130-2, Diabasbrottet at 5.6–5.7 m. **H**, MBg Di 894/130-3. **I**, PMU 38392a/2, mould, obverse view. **J**, PMU 38394/1. **K**, PMU 38394/2, Scale indicated by 1 mm long bar close to each specimen.

Remarks. – The species is variable in shape due to the slender, flexible stipes. The stipes may originally have been subhorizontal, but often more declined due to transport and other preservational aspects. It is one of the most slender early Ordovician species, but is here referred to *Acrograptus* as its proximal shape and development is not comparable to that of the species of the genus *Expansograptus*. The proximal end is highly asymmetrical and the first two thecae bend strongly sidewards. They also show a low thecal inclination and overlap. The type specimens of *Acrograptus pusillus* are similar to the relief specimen from Diabasbrottet (labeled Mossebo) (Fig. 12C, D), collected and identified by Moberg in 1892. The specimen is associated with *Baltograptus vacillans* and both counterparts are here illustrated. *Acrograptus pusillus* is more robust than *Acrograptus filiformis*, with wider stipes, more highly inclined thecae and shows a higher thecal overlap (ca 50%). The proximal end is also less asymmetrical and the crossing canal one is much wider.

Occurrence. – The species is rare in the *Baltograptus vacillans* Biozone of southern Scandinavia, but its exact biostratigraphic range is uncertain as it may easily have been overlooked in poorly preserved material. Monsen (1937) identified a number of slender *Acrograptus* specimens from the *Cymatograptus balticus* Biozone as *Didymograptus* cf. *D. pusillus* Tullberg. The material might belong to *Acrograptus pusillus*, but the poor preservation leaves identification uncertain.

Specimens identified as *Acrograptus* cf. *A. pusillus* (Tullberg, 1880) by Toro (1997a) from the *Baltograptus deflexus* Biozone of the Argentinian Cordillera Oriental appear to be more robust and may not belong to this species. Li *et al*. (2012) discussed the Chinese record of specimens identified as *Acrograptus pusillus*. The authors identified the species from the *Acrograptus filiformis* Biozone or its equivalent, the *Tshallograptus fruticosus* Biozone of China.

Acrograptus sp. cf. *Acrograptus gracilis* (Törnquist, 1890)

Figures 12E, F, 13E–K

cf. 1890 *Didymograptus gracilis* n. sp. Törnquist, p. 17, pl. 1, figs 9–12.

Material. – Numerous flattened and relief specimens from the *Baltograptus vacillans* Biozone at Diabasbrottet.

Description. – Slender, horizontal to subhorizontal acrograptid with a prominent, parallel-sided sicula. The sicula is obliquely oriented so that the stipes appear to originate nearly at the same level, giving a more or less symmetrical appearance. The sicula is 1.0–1.1 mm long and slender, measuring less than 0.2 mm across the aperture. The aperture is straight, without a rutellum. The sicula is inclined at about 5° to the horizontal stipes. The origin of th1^1 is 0.25–0.3 mm below the apex of the sicula, most probably in the lower part of the prosicula, but the prosicula cannot be distinguished. The proximal development is isograptid, dextral with crossing canal of th1^2 wider than the crossing canal of 2^1. The thecae are slender, slightly inclined with an overlap of less than 50%. The stipes are 0.3 mm wide and do not widen distally. The 2TRD is 1.6–1.7 mm in the proximal end. None have stipes long enough to determine distal spacing.

Remarks. – The species is variable in shape due to the slender, flexible stipes with thecae of low overlap. The specimens are generally similar to *Acrograptus gracilis* (Törnquist, 1890), but have different development of the sicula, which in *Acrograptus gracilis* shows a vertical sicula with asymmetrically oriented stipes and a partly free dorsal supra-apertural side of the sicula (Schulze 2018). *Acrograptus gracilis* has a prosicula, which makes up about 50% of the length of the sicula, and has thecae with very low overlap, slender prothecae and flared thecal apertures. The species is more slender than *Acrograptus pusillus* and also has nearly horizontal stipes. Details of the proximal development are known only from very few and often incompletely preserved relief specimens.

Occurrence. – The species is common in the Diabasbrottet section, where it associated with a diverse graptolite fauna. Formal naming awaits further information becoming available on its distribution and relationships to other taxa of *Acrograptus*.

Genus *Trichograptus* Nicholson, 1876

Type species. – *Dichograptus fragilis* Nicholson, 1869, from the *Didymograptus artus* Biozone (Darriwilian) of the upper Skiddaw Slates (Tarn Moor Formation) of the English Lake District at Thornship Beck (Cooper *et al*. 2004); original designation.

Diagnosis. – Horizontal to subhorizontal sigmagraptine with two curved main stipes; lateral second order stipes originating on one side of the main stipes through normal dichograptid, but lateral branching; proximal development isograptid, dextral, with distinct asymmetry of crossing canals; thecae simple dichograptid thecae with low overlap (Maletz *et al*. 2018a, p. 6).

Included species. – *Dichograptus fragilis* Nicholson, 1869; *Pterograptus* (?) *dilaceratus* Herrmann, 1885; *Trichograptus fergusoni* T. S. Hall, 1912; *Trichograptus crinitus* Törnquist, 1904; *Trichograptus immotus* Harris & Thomas, 1935; *Tetragraptus triograptides* Harris & Thomas, 1938a.

Remarks. – The type specimen of *Trichograptus fragilis* is flattened and does not provide much detail of the tubarium development (Rushton 2000c). It shows two main stipes with lateral branches originating from the ventral side of the main stipes at the apertures of the most proximal two or three thecae. The thecae are simple, gently inclined, showing little overlap. The sicula is either short (Rushton 2000c) or only partly preserved in the specimen. Based on these characters, the specimen clearly belongs to the genus *Trichograptus* and appears to be the youngest taxon of the genus. Nicholson (1869) described it from Thornship Beck, the same locality that also yielded *Nicholsonograptus fasciculatus* (see also Zalasiewicz *et al.* 2009). Skevington (1970, fig. 13e) illustrated a single specifically indeterminable stipe fragment as *Trichograptus fragilis* from the Skiddaw Slates of Westmorland.

The genus is a rare component of many Lower to Middle Ordovician graptolite faunas, but may be extremely common at certain levels (cf. Egenhoff & Maletz 2007, fig. 3). Species range from the early Floian (*Trichograptus dilaceratus*) to the mid-Darriwilian (*Trichograptus fragilis*).

Information on proximal development, thecal structure and branching is shown in the Lower Ordovician *Trichograptus dilaceratus* (Hermann, 1885) found at Hunneberg. This species is here used to understand the construction of the tubarium in the genus *Trichograptus*. Juveniles clearly show the characteristic somewhat asymmetrical proximal development of a sigmagraptine in relief and the isograptid proximal development, as well as the very slender crossing canals. Relief material of mature specimens shows the lateral origin of the second order stipes, but also the isograptid development and absence of cladial branching.

Trichograptus dilaceratus (Herrmann, 1885)

Figures 14A–G, 15A–G, I

1885	*Pterograptus* (?) *dilaceratus* n. sp. Herrmann, p. 69, fig. 7.
1904	*Trichograptus crinitus* (Moberg MS); Törnquist, p. 4, pl. 1, figs 5–7.
1912	*Trichograptus fergusoni* n. sp. Hall, p. 210, pl. 26, fig. 1.
1937	*Trichograptus dilaceratus* (Herrmann); Monsen, p. 200, pl. 5, figs 4, 13; pl. 14, figs 1, 7; pl. 16, fig. 3.
1991	*Trichograptus fergusoni* Hall, 1912; Rickards & Chapman, p. 93, pl. 34, figs a–c, e; text-figs 74, 75.
1996	*Trichograptus dilaceratus* (Herrmann, 1885); Rushton, p. 67, figs 4a–d, 6.
2008a	*Trichograptus fergusoni* Hall, 1912; VandenBerg, No. 2.26.
2012	*Trichograptus dilaceratus* (Herrmann, 1885); Vento, Toro & Maletz, p. 353, figs 5A, B, 6E.

Type material. – PMO 73.151 from the Tøyen Shale Formation at Galgeberg, Oslo, coll. Hermann, 1883 is the holotype of the species. The exact age of the specimen is uncertain, but it may originate from the *Baltograptus vacillans* Biozone. A photo of the holotype is available from the Geological Museum (PMO) database.

Törnquist (1904) described the species *Trichograptus crinitus* from the same interval at Hunneberg (LO 1701T, 1702t; both on one slab). The material was collected by Moberg in 1892 at Mossebo (modern Diabasbrottet). The slabs show a considerable development of metamorphic minerals, indicating its origin from closely to the contact of the dolerite sill.

Material. – Many specimens from Diabasbrottet and Mossebo (Egenhoff & Maletz 2007).

Description. – The proximal development of this species is characteristically asymmetrical, biradiate and is clearly isograptid. The length of the sicula reaches about 1.5–1.7 mm with a supradorsal part of ca 1.0 mm (Figs 14E–G, 15E–G). The free ventral side of the sicula is 0.3 mm long, whereas at the dorsal side the ventral side of stipe 2 touches the aperture. The prosicula is long and largely parallel-sided (Fig. 15G) with a rounded apex bearing indications of a nema. The origin of th1^1 is about 0. 4 mm below the apex of the sicula (Fig. 15G). The downward growing part of th1^1 is very slender (ca 0.04 mm wide) and the theca widens only more considerably after the outward bend to form stipe 1. Crossing canal one is about 0.15 mm wide, while crossing canal two is only 0.02–0.04 mm wide. Both separate from the sicula at slightly different levels forming a somewhat asymmetrical proximal end.

The thecae are slender and show an apertural inclination of about 22–26°. The thecal overlap appears to be less than 40%. The 2TRD is 3.0–3.2 mm in the proximal part of the second-order stipes and distal first-order stipes. The full length of the first-order stipes is at least 25 mm, but may be much longer in mature specimens. Fragments of lateral stipes are up to 40 mm long.

The first two thecae of the tubarium appear to have been horizontal to subhorizontal or slightly declined, but more distal portions of the tubarium show such variation that the original tubarium shape is uncertain (Fig. 14A, B). The lateral stipes are separated by a single theca (Fig. 14A, B), but it is unclear at what stage in the astogeny the insertion of the lateral branches occurs and whether there is a final number of lateral branches. At least four lateral branches occur on each first-order stipe in larger specimens.

The branching is dichotomous, shown conclusively in a few specimens preserved in partial relief (Fig. 15A, B) with the lateral branches bending strictly outwards from the main stipe. The dicalycal theca (thX; shown in yellow) grows along its precursor theca (thX^{-1}) for a very short distance and bends sideways at the previous thecal aperture (thX^{-2} aperture). ThX^{1} (orange), the first theca originating from dicalycal theca thX, originates approximately at this point and immediately grows to the top of thX^{-1} to continue the main stipe, while thX forms the beginning of the new stipe. The second theca originating form the dicalycal thX is thX^{2} (orange), formed much later in the development of thX and continues the newly formed stipe. The development follows the model proposed by Maletz (1992a) and the branching style of *Paradelograptus smithi* (Erdtmann *et al.* 1987, fig. 6). In the ventral preservation (Fig. 15I), the lateral branches appear to originate from the aperture of the previous theca and only in the dorsal view the dicalycal development can be observed.

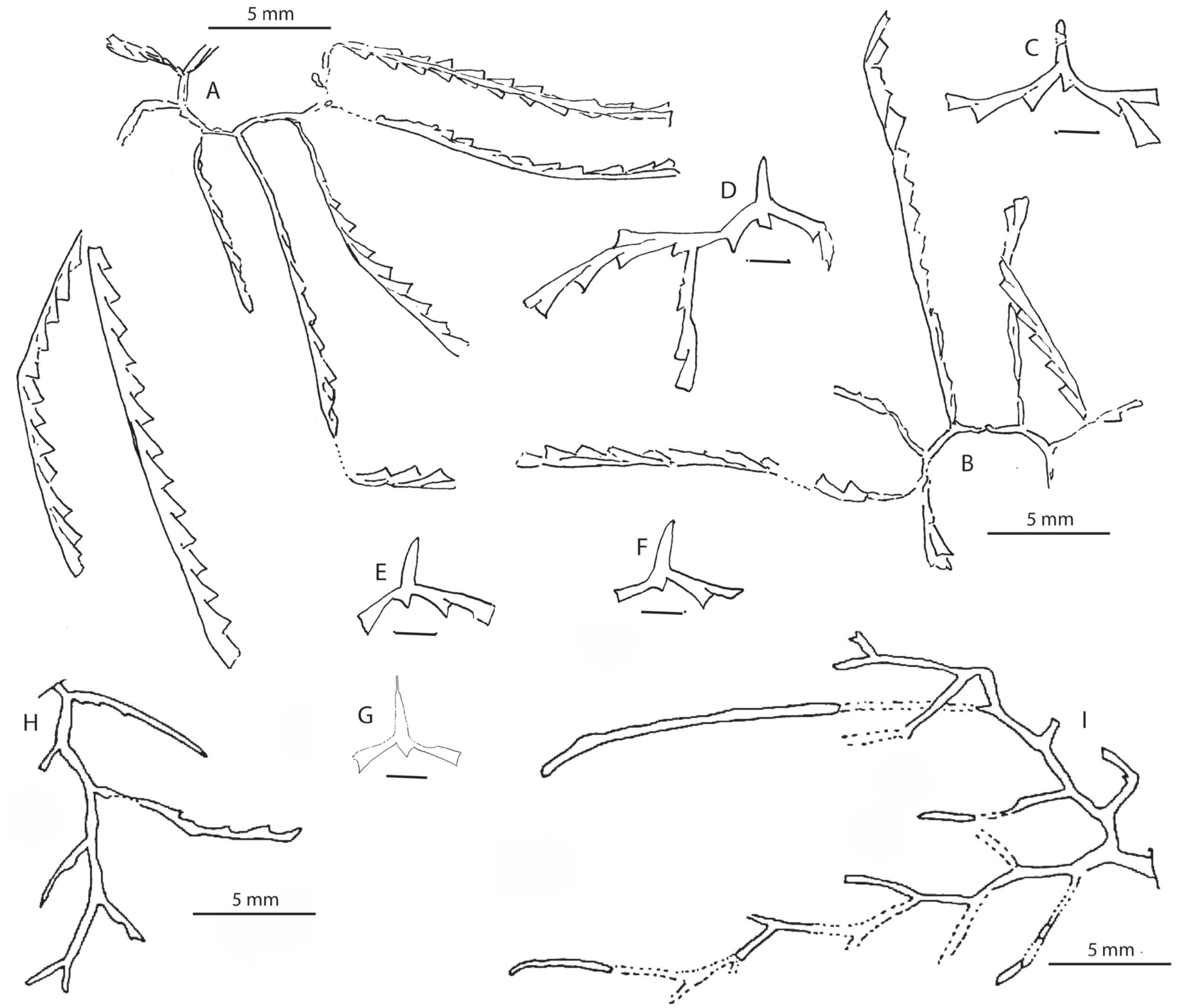

Fig. 14. **A–G**. *Trichograptus dilaceratus* (Herrmann, 1885). **A**, MBg Di 894/1291-1, large specimen in partial relief. **B**, MBg Di 894/1291-2, large specimen. **C**, MBg Di 894/130-1, juvenile with one lateral branch. **D**, MBg Di 894/1301-1, small specimen with lateral branches. **E**, MBg Di 894/1301-3, juvenile. **F**, MBg Di 894/130-5, juvenile. **G**, juvenile on slab with LO 1701T, 1702t, syntypes of *Trichograptus crinitus* (Törnquist 1904, pl. 1, figs 5–7). All specimens from Diabasbrottet at 5.6–5.7 m. **H–I**, *Goniograptus* sp. cf. *Goniograptus thureaui* (M'Coy, 1876), Diabasbrottet, MBg Di 13.50–14.50, Diabasbrottet, 8.1–9.1 m, both specimens on one slab. Scale bars are 1 mm, unless stated otherwise.

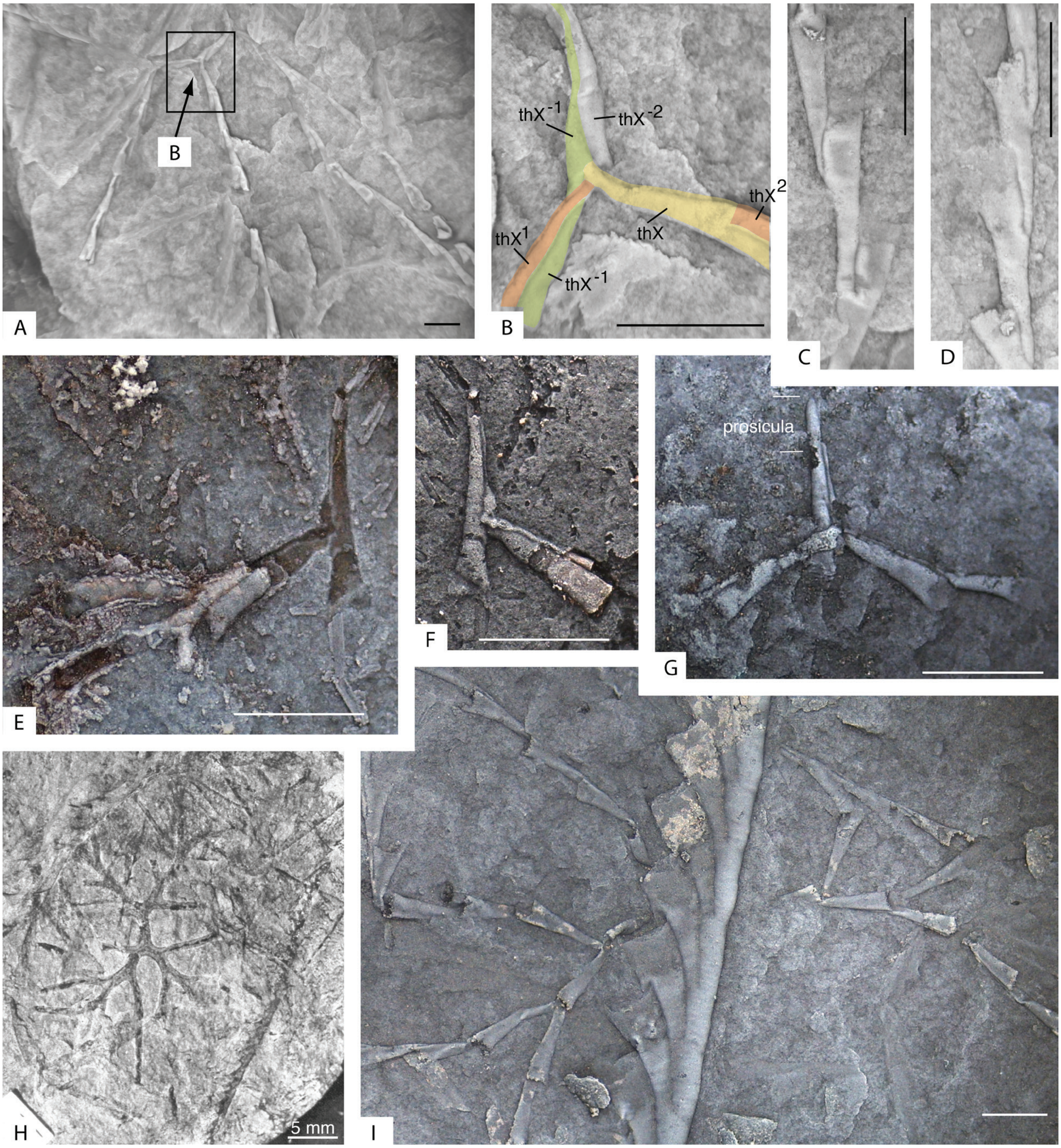

Fig. 15. **A–G, I**. *Trichograptus dilaceratus* (Herrmann, 1885). **A–D**, MBg Di 858/1, Diabasbrottet at 5.2–5.3 m, latex cast of specimens with enlargement of branching (**B**), indicated by arrow in (**A**) and thecal style (**C**, **D**). **E–G**. Diabasbrottet at 5.3–5.4 m, proximal ends, **E**, **F**, PMU 38395/1, **E**, mould of specimen showing branching on stipe 1. **F**, latex cast of same specimen, reverse view, th1^2 broken off, showing slender initial part of th2^1 on top of th1^1. **G**, PMU 38396/1, reverse view showing origin of first theca and both crossing canals. **I**, PMU 38394/3, Diabasbrottet at 5.6–5.7 m, latex cast of specimen in ventral (apertural view) showing lateral branches (arrows), a fragment of *Expansograptus holmi* crosses specimen. Scale bar indicates 1 mm in each photo. **H**, *Goniograptus* sp. cf. *Goniograptus thureaui* (M'Coy, 1876), PMU 38397a, Mossebo, flattened specimen showing monoprogressive branching.

Remarks. – A number of species of the genus *Trichograptus* have been described from the Lower Ordovician. They are mostly known from few poorly preserved flattened specimens and difficult to interpret. The tubarium shape and dimensions of *Trichograptus crinitus* Törnquist (1904) from the *Baltograptus vacillans* Biozone at Diabasbrottet, Hunneberg are identical to those of *Trichograptus dilaceratus* Herrmann (1885) and is clearly a junior synonym.

Trichograptus fergusoni (T. S. Hall, 1912) from the early Bendigonian (Be2) of Australia may also be identical to *Trichograptus dilaceratus*. Rickards & Chapman (1991) selected a lectoype for *Trichograptus fergusoni* and illustrated additional specimens. VandenBerg (2008a) illustrated the lectotype and provided precise measurements for the identification of the species. The specimen is here interpreted to be a juvenile specimen of *Trichograptus dilaceratus* with short stipes. The specimen shows the typical lateral origins of the second-order stipes from positions close to the thecal apertures of the first-order stipes. Additional specimens show much longer stipes. Rickards & Chapman (1991) mentioned stipes of more than 40 mm from the Bendigonian Be1 of Tarnagulla, Australia.

Occurrence. – *Trichograptus dilaceratus* is found in the *Baltogratus vacillans* Biozone at Hunneberg (Törnquist 1901, Egenhoff & Maletz 2007). Tjernvik (1960) reported the presence of this species from the *Didymograptus balticus* Biozone of the Flagabro drill core. The single fragment from the Lerhamn drillcore is from the *Baltograptus* sp. cf. *Baltograptus deflexus* Biozone (Maletz & Ahlberg, 2011). All data indicate that *Trichograptus dilaceratus* is limited to the *Baltograptus vacillans* to *Baltograptus jacksoni* biozones in the Lower Floian. Rushton (1996) illustrated specimens of *Trichograptus dilaceratus* from the Floian at Kilarea, Ireland, associated with *Expansograptus* sp. cf. *Expansograptus similis* and referred to the *Baltograptus varicosus* Biozone. The specimen is the only record of this species from Britain.

Genus *Goniograptus* M'Coy, 1876

Type species. – *Didymograpsus thureaui* M'Coy, 1876 from the Bendigonian (*Tshallograptus fruticosus* Biozone; Floian) of the Bendigo goldfield, Sandhurst, Victoria, Australia; original designation.

Diagnosis. – Sigmagraptines with two orders of progressive branching, followed by unlimited monoprogressive branching forming four zig-zag main stipes; proximal end isograptid, dextral; extended rutellum on sicula; thecae dichograptid with short rutella; moderate to high thecal overlap; thecal shape variable, from low inclined and considerably widening to high overlap and strong curvature towards aperture (Maletz *et al.* 2018a, p. 8).

Included species. – *Goniograptus alternans* Harris & Thomas, 1939; *Goniograptus guangdongensis* Zhao, 1978; *Goniograptus guangxiensis* Zhao, 1978; *Goniograptus macer* T. S. Hall, 1899a; *Goniograptus sculptus* Harris & Thomas, 1939; *Goniograptus speciosus* T. S. Hall, 1914; *Didymograpsus thureaui* M'Coy, 1876; *Goniograptus thureaui* var. *postremus* Ruedemann, 1904; *Goniograptus thureaui* var. *selwyni* Ami, 1889a, b; *Goniograptus thureaui* var. *inaequalis* Harris & Thomas, 1939; *Goniograptus tumidus* Harris & Thomas, 1939; *Goniograptus velatus* Harris & Thomas, 1939.

Remarks. – The monoprogressive branching typical of *Goniograptus* is easily recognizable from the fourth branching point onwards and is only shared with the genus *Sigmagraptus*. The latter genus has only two monoprogressive stipes, while *Goniograptus* usually has four. Williams & Stevens (1988) described an unusual development in a population of *Goniograptus*? cf. *D. speciosus* Hall, 1914 in which only three stipes with monoprogressive branches are present. A number of specimens from the *Isograptus maximus* Biozone of Cow Head South show this development. Thus, Williams & Stevens (1988) considered the development as an ecophenotypic variation and not based on an accident or injury of a single specimen due to pathological causes.

Species of the genus *Goniograptus* are widely distributed in Australasia (Hall 1899, 1914; Harris & Thomas 1939; M'Coy 1876; VandenBerg & Cooper 1992) and North America (Ami 1889a, b; Ruedemann 1904; Williams & Stevens 1988). *Goniograptus* was also described from the Zhangmuqu Formation of Jiangxi and in other regions of China (Zhao 1986). A few specimens of *Goniograptus* have been found in Scandinavia (Monsen 1937; Jaanusson 1965; Schmidt-Gündel 1994).

The genus *Goniograptus* is common from the Bendigonian to the Yapeenian in Australasia, but has not been found in the Darriwilian (Thomas 1960). Schmidt-Gündel (1994) illustrated specimens of *Goniograptus* from the Lo-Shale of Norway, possibly from an interval of Yapeenian to basal Darriwilian age. Maletz *et al.* (2018a) listed the biostratigraphic range from the *Tshallograptus fruticous* Biozone to the early Darriwilian *Levisograptus austrodentatus* Biozone. The biostratigraphic ranges of individual species are not well known and a detailed taxonomic and stratigraphic investigation is pending. The identity of some of the extensive Australasian material is particularly uncertain due to the poor preservation of the specimens and lack of understanding of the astogenetic changes of the specimens.

Rickards & Chapman (1991) revised the Bendigonian species of *Goniograptus* from Victoria, Australia and re-illustrated the type material. The authors also introduced the genus *Praegoniograptus* as an intermediate taxon to *Clonograptus*, in which not all of the stipes develop monoprogressively. The genus *Praegoniograptus* was based on two species, so far restricted to Victoria, Australia.

Goniograptus sp. cf. *Goniograptus thureaui* (M'Coy, 1876)

Figures 14H, I, 15H

Material. – Four specimens from Mossebo and Diabasbrottet.

Description. – The material is poorly preserved in metamorphosed black shale, but the outlines of the tubaria with their typical monopodial branching is clearly visible. The preservation is however too poor to show structural details. The length of the first-order stipes (the 'funicle') is about 4.5 mm; subsequent dichotomies are spaced 2.0 mm apart. At the proximal end the width of the stipes reaches about 1.5 mm and decreases to 0.8 mm distally. A better preserved specimen (Fig. 15H) shows a thin dark line in the center of the wide stipes, suggesting either a stolon system or the presence of a rim of cortical material on the sides of the stipes forming a buoyancy support. This overgrowth with cortical material prevents the identification of thecal shape and spacing.

Remarks. – The tubarium shape of the few specimens clearly indicates a member of the genus *Goniograptus*, but the preservation is too poor to identify the species with confidence.

Occurrence. – The specimens originate from the *Baltograptus jacksoni* Biozone at Diabasbrottet and Mossebo. Further Scandinavian material of *Goniograptus* is known from the Tøyen Shale Formation at Loke in Jämtland (Jaanusson 1965). The material is well preserved in relief and shows slender, thecae with low inclination. It might be a different species than the Hunneberg material. According to Jaanusson (1965) the associated fauna indicates that the material comes from the *Pseudophyllograptus densus* to *Pseudophyllograptus angustifolius elongatus* Biozones, thus is younger.

Monsen (1937, pl. 6, fig. 4) described a single fragment as *Goniograptus* aff. *G. palmatus* Harris & Keble, 1932 from the *Pseudophyllograptus angustifolius elongatus* Biozone of the Tøyen Shale Formation of Norway. *Goniograptus palmatus* occurs in the Chewtonian Ch2 of Castlemaine, Victoria, Australia and is the only species of the genus from which web structures are known. Monsen (1937) also illustrated a poor fragment from Galgeberg, Oslo as ?*Clonograptus norvegicus*, showing the monoprogressive branching of *Goniograptus* (Monsen, 1937, pl. 5, fig. 22). Thus, *Goniograptus* may be more widely distributed in Scandinavia, but has rarely been identified.

Genus *Jishougraptus* Geh, 1988

Type species. – *Jishougraptus mui* Geh, 1988 from the Floian to Dapingian of the Qiaotingzi Formation at Xiayanzhai, Hunan Province; original designation.

Diagnosis. – Sigmagraptines with a single deflexed stipe; dorsal stipe margin somewhat undulate but without pronounced prothecal folds; sicula often long and slender with th1^1 origin in middle part of metasicula or close to sicular aperture; thecae long and slender with high overlap and increasing overlap distally; apertural elaborations indistinct; thecae may be geniculate (Maletz *et al*. 2018a, p. 10).

Remarks. – The genus is based on single-stiped sigmagraptines with long and strongly overlaping thecae with simple to slightly elaborate thecal apertures. The type material of the genus, *Jishougraptus mui* Geh, 1988 (Fig. 16F, H), is associated with *Didymograptus* cf. *praenuntius* Törnquist, probably indicating a level in the Dapingian. Beckly & Maletz (1991) described well-preserved material of *Jishougraptus* from the *Pseudophyllograptus angustifolius elongatus* Biozone of the Tøyen Shale of the Oslo Region. The specimens are are considerably younger than the material discussed here and *Jishougraptus hunnebergensis* n. sp. is the oldest known *Jishougraptus* species. Constructional differences to other species are discussed below.

Jishougraptus hunnebergensis n. sp.

Figures 16A–E, 17D–L

Holotype. – Specimen (Figs 16A, 17J) on the back of LO 1589t (*Expansograptus holmi*; Törnquist, 1901, pl. 1, fig. 16), Mossebo.

Paratypes. – Specimens illustrated on Figures 16 and 17.

Remarks. – Several specimens from the Törnquist collection in the Geology Department at Lunds University. The material is labeled to originate from Mossebo, i.e. the modern locality of Diabasbrottet. The specimen on the back of LO 1589t (*Expansograptus holmi*; Törnquist, 1901, pl. 1, fig. 16) is selected as the

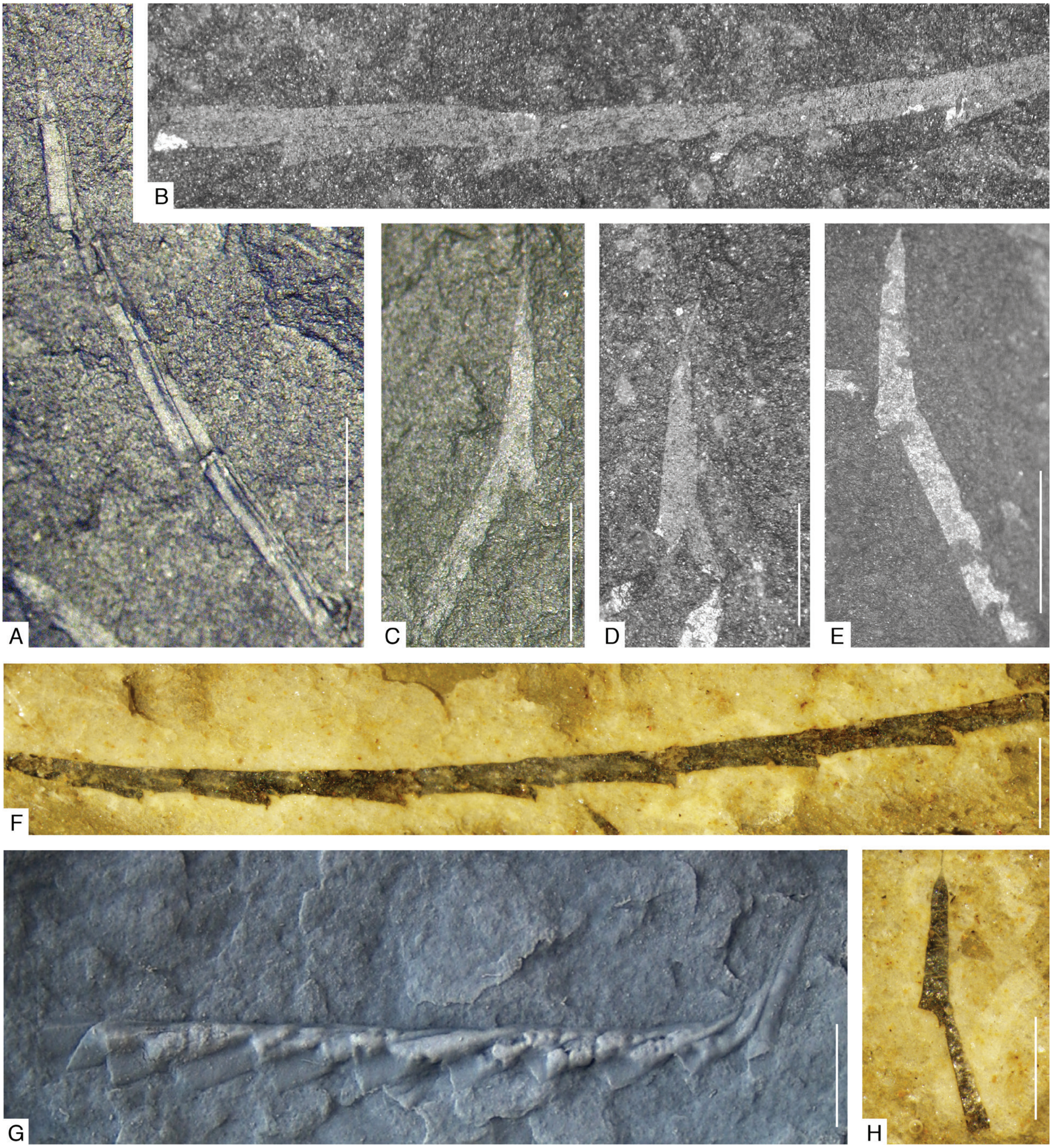

Fig. 16. Single stiped taxa. **A–E**. *Jishougraptus hunnebergensis* n. sp. **A**, specimen on slab with LO 1589t, latex cast of holotype, showing complete sicula and downward growth of th1. **B**, PMU 38398/1, flattened fragment showing thecal style. **C**, second specimen on slab with LO 1589t, small flattened specimen. **D**, PMU 38398/2, juvenile with complete sicula and part of th1, showing short nema. **E**, PMU 38398/3, proximal end of longer specimen. **F, H**. *Jishougraptus mui* Geh, 1988, type material. **F**, NIGP 104 481, holotype, stipe fragment. **H**, NIGP 104 475, proximal end showing shape of sicula and low origin of th1. **G**, *Cymatograptus validus* (Törnquist, 1901), MBg material, latex cast showing high origin of th1, Diabasbrottet at 1.4–1.5 m. Scale indicated by 1 mm long bar in each photo.

holotype, as it is preserved in partial relief and has a complete sicula (Figs 16A, 17J). The remaining illustrated specimens are regarded as paratype material. The exact level of the origin of this material is uncertain. However, the specimens are associated with *Baltograptus vacillans* (Fig. 17M) and *Expansograptus holmi* (Fig. 17N), indicating the *Baltograptus vacillans* Biozone. One stipe fragment is associated with the lectotype of *Acrograptus pusillus* (LO 348T), but is not figured here. The presence of patches of metamorphic minerals, typical of the higher part of the Diabasbrottet section on the slabs, supports the reference to this locality and level.

Diagnosis. – *Jishougraptus* with high origin of th1 on the sicula; thecae slender, with low inclination and considerable overlap, bearing simple, slightly outwardly inclined apertures and lacking geniculae.

Description. – The species has a single, strongly declined stipe making an initial angle of ca 70˚ with the sicula. Distally the stipe may show gentle dorsal curvature. The length of the stipe is uncertain as only small specimens with less than three complete thecae and fragments with no more than four thecae have been found.

The sicula is 1.2–1.4 mm long and straight for most of its length. The ventral side of the aperture forms a distinct rutellum that bends across the aperture (Fig. 16D, E). Therefore, the sicula appears to have a slight dorsal curvature, but the dorsal side of the sicula remains straight. The apex of the sicula is rounded and bears a short and slender nema. Due to the width of the rounded apex, the sicula is nearly parallel-sided, about 0.15–0.2 mm wide. The origin of th1 is about 0.2 mm below the apex of the sicula. The stipe is 0.4 mm wide across the thecal apertures and 0.2 mm below the thecal apertures. The thecae have an inclination of 2–3° and show a slight flare at the aperture. The apertures are simple, straight and somewhat inwardly inclined, but do not bear a noticeable rutellum. The 2TRD is about 3 mm in the longest fragment, but due to the shortness of the specimens, cannot be measured in most examples. The thecal overlap appears to be around 50%, but is visible clearly only in the holotype (Figs 16A, 17J) and in a single stipe fragment preserved in low relief (Fig. 17K).

Remarks. – A number of specimens are present in the Törnquist collection at Lund University and on

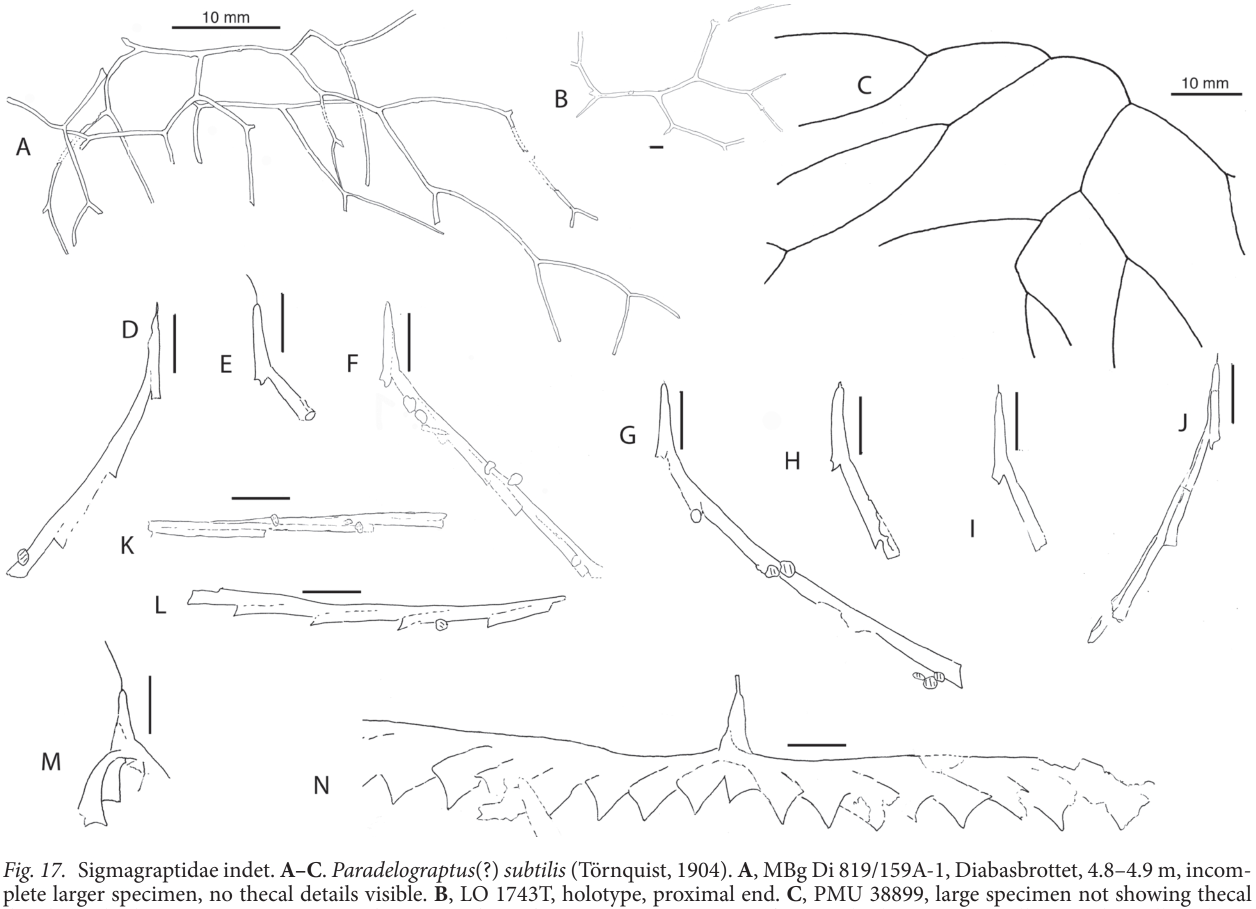

Fig. 17. Sigmagraptidae indet. **A–C**. *Paradelograptus*(?) *subtilis* (Törnquist, 1904). **A**, MBg Di 819/159A-1, Diabasbrottet, 4.8–4.9 m, incomplete larger specimen, no thecal details visible. **B**, LO 1743T, holotype, proximal end. **C**, PMU 38899, large specimen not showing thecal details, Diabasbrottet, 4.5–4.6 m. **D–L**. *Jishougraptus hunnebergensis* n. sp., specimens from Diabasbrottet (originally Mossebo, coll. Moberg, 1892). **D**, PMU 38398/1. **E**, PMU 38400/1. **F**, PMU 38401/1. Törnquist 1. **G**, PMU 38399/4. **H**, PMU 38400/2. **I**, PMU 38399/2. **J**, specimen on LO 1589t, holotype, low relief specimen showing origin of first theca and thecal overlap. **K**, PMU 38400/2, fragment showing thecal overlap. **L**, PMU 38398/1, fragment showing thecal apertures. **M**, *Baltograptus vacillans*, PMU 38401/2. **N**, *Expansograptus holmi* (Törnquist, 1901) PMU 38401/3. Scale bars 1 mm unless stated otherwise.

slabs bearing other species previously published by Törnquist (1901). The material of this species is fragmentary and incomplete, but shows a number of characters sufficiently different from other species of the genus *Jishougraptus*. This is important, as it is the oldest single-stiped sigmagraptine and the oldest material that may be referred to the genus *Jishougraptus*.

Jishougraptus hunnebergensis n. sp. differs from all other *Jishougraptus* species by the high origin of th1 on the sicula. In *Jishougraptus novus* Beckly & Maletz, 1991 the origin is halfway down the sicula. The sicula is also much longer in this species and the thecal style is more complex, with overlap increasing distally (Beckly & Maletz, 1991). *Jishougraptus mui* Ge, 1988 has a shorter sicula with no adpresssed downward growth of th1 and shows a slight geniculum at the thecal apertures (Fig. 16F, H). The slender thecae with low inclination and high overlap show slight apertural modification that is difficult to interpret from the flattened material (Fig. 16F).

Occurrence. – The species is known only from the *Baltograptus vacillans* Biozone at Diabasbrottet. It might have a wider distribution, but this record of a new species in old collections indicates that it can easily be overlooked.

Subfamily Kinnegraptinae Mu, 1974

(ex family Kinnegraptidae, Mu, 1974;
VandenBerg 2019, p. 11)

Diagnosis. – Tubarium multiramous to biramous, reflexed to horizontal to pendent, with or without irregularly spaced delayed dichotomies, nematophorous sicula with or without virgellar process, $th1^1$ diverging at higher level from metasicula than $th1^2$ resulting in variably asymmetrical appearance, with sicula often skewed towards stipe 1; sicula conical; thecae long and slender; metathecal walls often attenuated; sicular bithecae observed in well preserved specimens (VandenBerg 2019, p. 11).

Included genera. – *Kinnegraptus* Skoglund, 1961, *Prokinnegraptus* Mu, 1974, *Wuninograptus* Ni, 1981, *Paradelograptus* Erdtmann, Maletz & Gutiérrez-Marco, 1987, *Lignigraptus* VandenBerg, 2019, ?*Psenograptus* VandenBerg, 2019 (*nomen dubium*).

Remarks. – Mu (1974) defined the family Kinnegraptidae for a number of taxa with distinctly differentiated thecae and long apertural rutellae. The proximal end of the genus *Kinnegraptus*, however, differs little from earlier sigmagraptines. Slender kinnegraptines of the genus *Paradelograptus* occur first in the late Tremadocian (Jackson & Lenz 2000) and are not uncommon at Hunneberg in the *Hunnegraptus copiosus* Biozone and in younger strata. Maletz and others (2018a) did not use the Kinnegraptidae, but still separated the 'kinnegraptids' from the rest of the family Sigmagraptidae. VandenBerg (2019) used the Kinnegraptinae as a subfamily of the Sigmagraptidae Cooper & Fortey, 1982 and argued that the subfamily differs enough from the remaining sigmagraptids to warrant a separate taxonomic unit, the Kinnegraptinae.

The Prokinnegraptidae of Yu & Fang, 1979 was erected to incorporate only the genus *Prokinnegraptus* Mu, 1974, regarded as a member of an informal group by Maletz *et al.* (2018a: 'Kinnegraptidae of Mu, 1974'). There is no point to separate the genus from the rest of the Kinnegraptinae.

Distribution. – VandenBerg (2019, table 1) provided some general information on the biostratigraphic distribution of the Kinnegraptinae in Australasia. He noted that *Kinnegraptus kinnekullensis* has not been recognized in the region, but should possibly be found in the *Isograptus lunatus* Biozone (Castlemainian, Ca1). A considerable biostratigraphic gap occurs between this and the youngest kinnegraptine, the genus *Wuninograptus*, present in the late Darriwilian *Archiclimacograptus riddellensis* Biozone (Da4).

Genus *Paradelograptus* Erdtmann, Maletz & Gutiérrez-Marco, 1987

Type species. – *Paradelograptus onubensis* Erdtmann, Maletz & Gutiérrez-Marco, 1987 from the Upper Tremadocian (*Sagenograptus murrayi* Biozone) of the Barriga Shale, SW Spain; original designation.

Diagnosis. – Tubarium multiramous to biramous, horizontal to pendent, with or without irregularly spaced delayed dichotomies, nematophorous sicula, $th1^1$ diverging at higher level from metasicula than $th1^2$ resulting in characteristic asymmetrical appearance, with sicula skewed towards stipe 1; thecae long and slender; metathecal walls may be attenuated, thecal apertures simple or with denticulate apertures. (VandenBerg 2019, p. 11).

Included species. – VandenBerg (2019, p. 11) listed all species included in the genus and described the three new species *Paradelograptus maletzi* VandenBerg, 2019, *Paradelograptus orthae* VandenBerg, 2019 and *Paradelograptus cayleyi* VandenBerg, 2019.

Remarks. – Erdtmann *et al.* (1987) included the genus *Paradelograptus* in the Kinnegraptidae. Early specimens of the genus *Paradelograptus* come from the upper Tremadocian and show the simple, characteristic proximal development style of the Kinnegraptidae with highly asymmetrical stipe divergence.

The diagnosis of VandenBerg (2019, p. 11) differs in wording, not in characters from the diagnosis of Maletz *et al.* (2018a, p. 10). The proximal development of *Paradelograptus* has not been described in much detail so far and is difficult to recognize in the delicate and slender specimens. The development is isograptid, but can be dextral (Fig. 18C) or sinistral (Fig. 18A, B, D) as is shown by specimens of *Paradelograptus onubensis* from the *Kiaerograptus pritchardi* Biozone of Peel River Canyon, Yukon. The specimens show a slender, nearly parallel-sided sicula without a rutellum. Distinct dark slightly oblique bands in the upper part of the sicula may be evidence of the spiral line of the prosicula (Fig. 18A). If true, the origin of th1^1 is in the middle part of the prosicula in this form. Specimens of *Paradelograptus filiformis* from the Upper Tremadocian of eastern Newfoundland (Willliams & Clarke 1999) clearly show the moderately high prosicular origin of th1^1 clearly.

The obverse side shows a prominent left-handed or right-handed sicular bitheca (Fig. 18A, C), while the reverse side shows the origin of th1^2 (Fig. 18B). The thecae are distinctly differentiated with a slender, 0.05 mm wide prothecal portion and a gradually widening metathecal portion, reaching an apertural width of 0.2 mm. The metathecal expansion is produced at some distance from the aperture of the previous theca, forming very slender and fragile looking stipes. All specimens show an isograptid proximal development with considerable asymmetry of the stipe divergence.

The species of *Paradelograptus* are often difficult to differentiate in poorly preserved material. Therefore, they have not been determined to species level in all cases and may only be listed as *Paradelograptus* sp. in range charts.

Jackson & Lenz (2000) erected a *Paradelograptus kinnegraptoides* Biozone for Peel River, Yukon, Canada. The authors differentiated the *Paradelograptus antiquus*, *Paradelograptus pritchardi* and *Paradelograptus kinnegraptoides* Biozones in the late Tremadocian, indicating that species of the genus *Paradelograptus* are common in the Yukon sections. *Paradelograptus kinnegraptoides* has rarely been found in other regions and its biostratigraphical distribution is not well

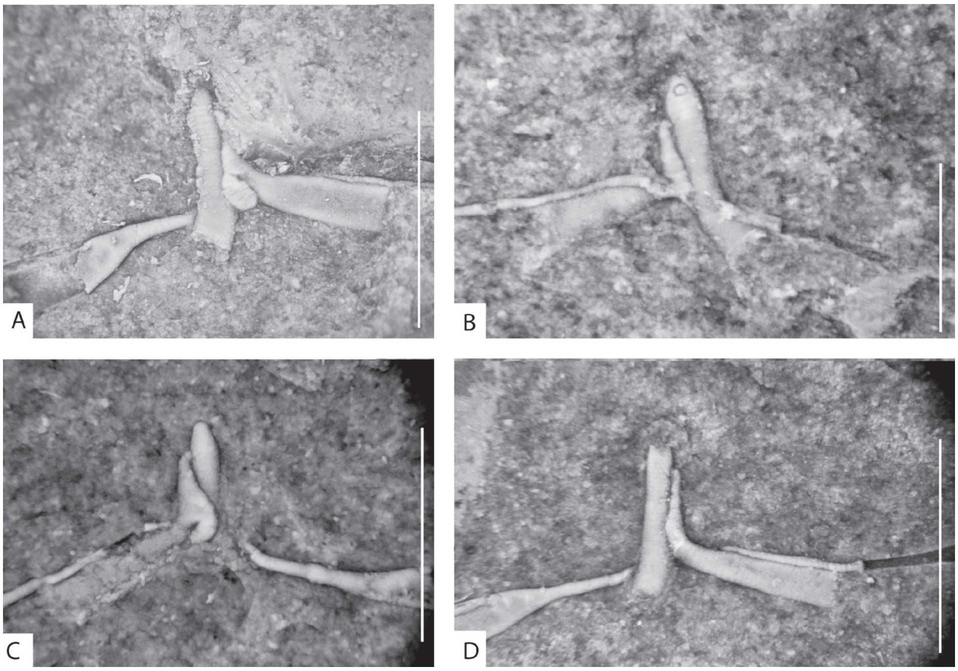

Fig. 18. Paradelograptus onubensis Erdtmann, Maletz & Gutierrez-Marco, 1987, proximal development. **A**, GSC 118739b, sinistral specimen, obverse view, showing prominent sicular bitheca and high prosicular origin of th1^1. **B**, GSC 118750, sinistral specimen in reverse view, part of crossing canal of th1^2 is missing. **C**, GSC 118754, dextral specimen in obverse view, showing sicular bitheca. **D**, GSC 118739, sinistral specimen in obverse view, sicular bitheca broken off. All specimens from Peel River, Yukon, Canada, probably from the *Sagenograptus murrayi* Biozone, first illustrated as drawings by Jackson & Lenz (2000). Scale is indicated by a 1 mm long bar in each photo.

known. The type material is considerably younger than the Yukon material. According to VandenBerg (2019) the species is not present in Victoria, Australia.

Occurrence. – According to VandenBerg (2019, p. 9) *Paradelograptus* species are restricted to the late Tremadocian in Australasia where they have been found only in the *Aorograptus victoriae* Biozone (La2). The Scandinavian material of *Paradelograptus* sp. cf. *P. onubensis* Erdtmann, Maletz & Gutiérrez-Marco, 1987, from the base of the *Paratetragraptus approximatus* Biozone (basal Floian), must be the youngest specimens of *Paradelograptus* or have to be referred to a different genus.

***Paradelograptus* sp. cf. *Paradelograptus antiquus* (Hall, 1899b)**

Figure 19J

cf. 1899b *Leptograptus antiquus* n. sp. Hall, p. 166, pl. 17, figs 5, 6.
cf. 1935 *Bryograptus*(?) *antiquus* var. *inusitatus* var. nov. Benson & Keble, p. 267, pl. 30, figs 17, 18.
non 1974 *Adelograptus antiquus* (Hall, 1899); Jackson, p. 41, text-fig. 2F–H.
cf. 1974 *Kiaerograptus* (?) cf. *pritchardi* (Hall, 1899); Jackson, p. 51, pl. 5, fig. 3; text-fig. 2A, C, D.
cf. 1979 *Adelograptus*? *antiquus* (Hall, 1899); Cooper, p. 51, pl. 2c–e; text-figs 17a–k, 18.
cf. 1979 *Kiaerograptus antiquus* (Hall, 1899); Cooper & Stewart, p. 791, text-fig. 8d, e.
1987 *Paradelograptus antiquus* (Hall, 1899); Erdtmann, Maletz & Gutiérrez-Marco, p. 122, figs 5G, 10C (? fig. 4).
cf. 2019 *Paradelograptus antiquus* (Hall, 1899); Vanden Berg, p. 11, figs 4–6A, 8A.

Diagnosis. – Slender *Paradelograptus* with two or three stipes, proximal habit horizontal to slightly declined, prosicula mitre-shaped with bluntly conical proximal end and tubular metasicula, with distinct bend towards antirutellar side, aperture slanted with acutely angled rutellum; th1^1 short, oriented approximately at right angle to sicula; other thecae long, with long threadlike prothecae and shorter triangular metathecae (VandenBerg 2019, p. 12).

Type material. – Lectotype NMV P14241 from Lancefield Quarry (NMV PL1144), Victoria, Australia (see VandenBerg 2019, p. 10 for details) (Fig. 19L), selected by Cooper (1979, p. 51).

Remarks. – Morris (1988, p. 65), in an unpublished thesis, described the lectotype of *Paradelograptus antiquus*. He measured six thecae in 10 mm, a fairly wide thecal spacing and noted a thecal length of ca 1.8 mm. The sicula is distinctly curved and has a length of 1 mm and an apertural width of 0.2 mm. Of the two proximal stipes, one stipe diverges distally but the ultimate number of stipes is not known and may be quite variable, depending on size of the specimens. The identity of this species is quite uncertain and many specimens identified under this name may not belong to the species, especially as the identifications are usually based on proximal fragments. The name is generally used to refer to late Tremadocian paradelograptids of any kind.

VandenBerg (2019) redescribed the species in great detail from Australian material. The Swedish material illustrated herein is based on a single, poorly preserved proximal end with short stipes from the *Hunnegraptus copiosus* Biozone of Storeklev. It has a sicula of about 1mm in length and a probably fairly irregular thecal spacing that is not easy to estimate from the poor preservation, but seems to be higher than in the Australian material of *Paradelograptus antiquus*. The stipes are more distinctly declined than typical *Paradelograptus antiquus* (Figs 19L, 20L, M), leaving some doubt about the identity of the specimen. Fragments possibly belonging to the same species can be found more commonly at this level, however.

Occurrence. – The Swedish specimen originated from the *Hunnegraptus copious* Biozone of Storeklev, thus is from an interval largely comparable to the Lancefieldian La2 (VandenBerg & Cooper 1992). The species appears to be restricted to the Australasian *Aorograptus victoriae* Biozone (= Lancefieldian La2).

***Paradelograptus* sp. cf. *Paradelograptus onubensis* Erdtmann, Maletz & Gutiérrez-Marco, 1987**

Figures 19G–I, ?K; 20B, C, E, F, K

1987 *Paradelograptus* sp. cf. *P. onubensis* n. sp. Erdtmann, Maletz & Gutiérrez-Marco, p. 117, figs 5k–m, 9C, D, 10E.

Material. – Several poor proximal ends from Diabasbrottet.

Diagnosis. – Small, probably multiramous paradelograptid with highly asymmetrical proximal end and long slender prothecae.

Description. – The sicula is 1.3–1.5 mm long, slender and 0.25–0.3 mm wide at the aperture. A short rutellum is visible at the aperture of the often curved sicula. A short nema, less than 0.5 mm in length, occurs in some specimens. The proximal end is highly asymmetrical with stipe 1 bending outwards from the middle of the sicula or even higher, while stipe 2 grows

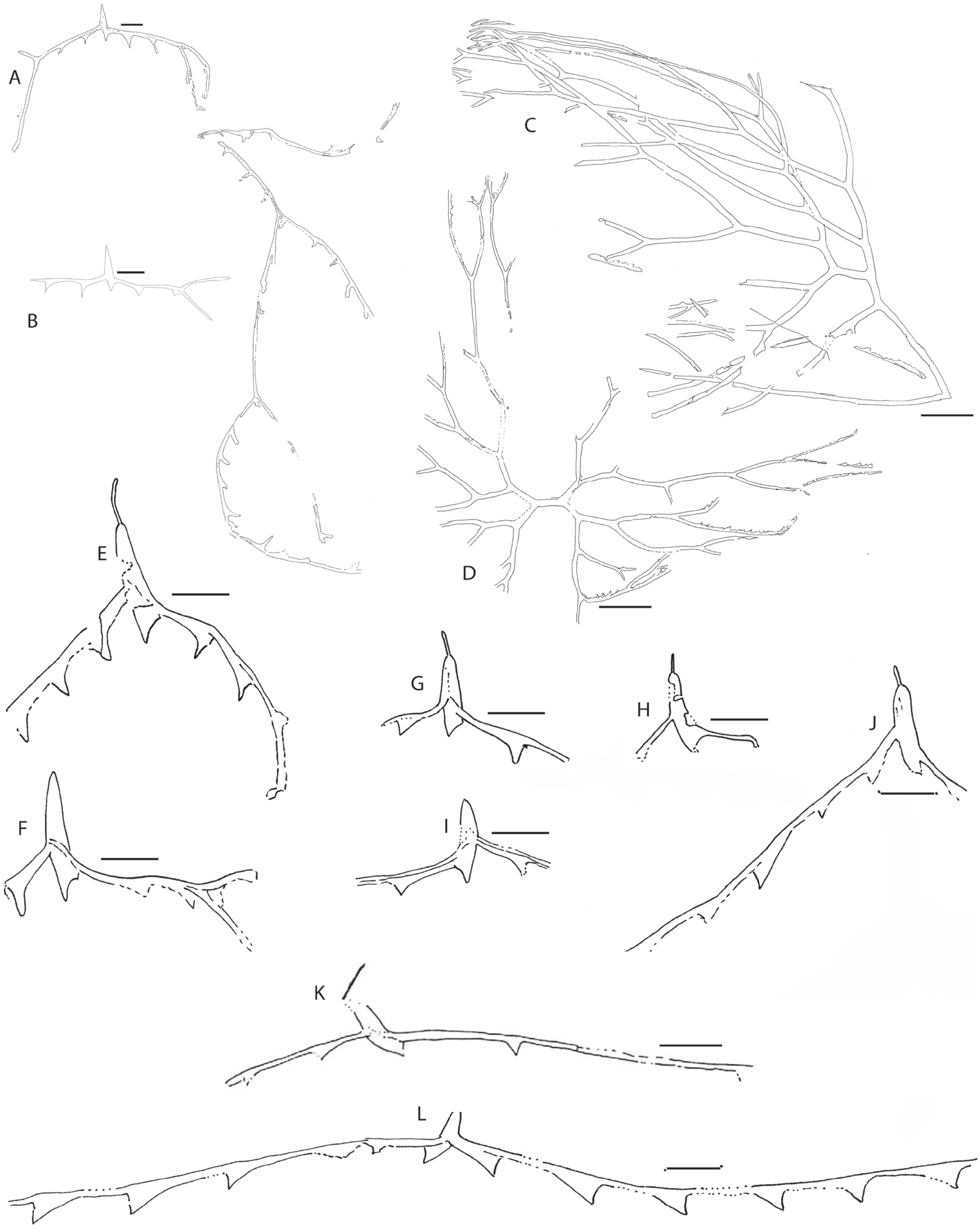

Fig. 19. Paradelograptus species. **A, B**. *Lignigraptus kinnegraptoides* (Erdtmann *et al.*, 1987), Diabasbrottet at 3.7–3.8 m. **A**, MBg Di 709/59B-1, holotype. **B**, MBg Di 709/59B-2, paratype. **C**, **D**. *Paradelograptus smithi* (Harris & Thomas, 1938a). **C**, MBg MO 400/225, Mossebo. **D**, MBg Di 543/26a, Diabasbrottet, 2.0–2.1 m. **E, F**. *Lignigraptus chapmani* (Keble & Harris, 1934). **E**, MBg Di 614/119, holotype of *Paradelograptus mossebоensis*, Diabasbrottet, 2.8–2.9 m. **F**, MBg S-HUN-MO/069a, proximal end, coll. Erdtmann. **G–I, ?K**. *Paradelograptus* sp. cf. *Paradelograptus onubensis* Erdtmann *et al.*, 1987, Diabasbrottet, 1.4–1.5 m. **G**, MBg Di 377/218B-1. **H**, MBg Di 477/218C-2. **I**, MBg Di 477-218A-3. **?K**, PMU 38402/1, Diabasbrottet, 1.7–1.8 m. **J**, *Paradelograptus* sp. cf. *Paradelograptus antiquus* (Hall, 1889), MBg Di Hun/S-2.18–2.3 m/058, Diabasbrottet, coll. Erdtmann. **L**, *Paradelograptus antiquus* (Hall, 1889), NMV P 19241, lectotype (from Cooper, 1979). Scale indicated by a 1 mm long bar close to each specimen.

from the dorsal side of the sicular aperture. The proximal thecae are about 1.4 mm long, with very slender prothecae and triangular metathecae, up to 0.4 mm long with an apertural width of 0.3 mm, measured excluding the extended rutella. None of the proximal ends show more than one or two thecae on a stipe, but longer fragments possibly belonging to the species are present, some showing dichotomous branching.

Remarks. – This species is known from a few proximal ends and distal fragments only found at a single level in the Diabasbrottet section. Thus, nothing can be learned from its biostratigrapical distribution. The Hunneberg material shows more extended thecal rutella and originates from the basal Floian, while typical *Paradelograptus onubensis* were found in the late Tremadocian *Sagenograptus murrayi* Biozone of the Barriga Shale of Spain (Erdtmann *et al.* 1987). Jackson & Lenz (2000) illustrated line drawings of a number of specimens from the *Sagenograptus murrayi* Biozone of Yukon, Canada as *Paradelograptus onubensis*. Their material is preserved in full relief and shows the proximal development in reverse and obverse views (Fig. 18A–D), including a prominent sicular bitheca.

A single proximal end with very slender and long thecae was found associated with *Tetragraptus amii* and *Tetragraptus phyllograptoides* (Fig. 19K) that differs from the rest of the material referred to this taxon. The thecal apertures are barely recognizable in the specimen.

Occurrence. – The taxon is found in the Diabasbrottet section in the 1.4–1.5 m level in the *Tetragraptus phyllograptoides* Biozone, associated with *Tetragraptus phyllograptoides* and *Cymatograptus undulatus*.

***Paradelograptus norvegicus* (Monsen, 1937)**

Figure 20I, J

pars 1937 *Clonograptus norvegicus* n. sp. Monsen, p. 198, pl. 5, fig. 22, pl. 20; non pl. 5, fig. 22 (=*Goniograptus* sp.).
1991a *Clonograptus* cf. *norvegicus* Monsen, 1937; Lindholm, p. 305, fig. 10F.
1991a *Paradelograptus tenuis* n. sp. Lindholm, p. 319, fig. 15A, B, D–F.
2016 *Paradelograptus norvegicus* (Monsen); Gutiérrez-Marco & Martin, fig. 3R–U (no description).
?2016 *Paradelograptus norvegicus* (Monsen); Martin *et al.*, fig. 5E (no description).

Type material. – Holotype PMO 59.509 from Grundvik, Asker, coll. Brøgger (Monsen, 1937, pl. 20). The second specimen of Monsen (1937, pl. 5, fig. 22) is PMO K 0110 from Galgeberg, Oslo. It is a fragment of *Goniograptus* as can be seen from the monoprogressive branching.

Diagnosis. – Large, multiramous species of *Paradelograptus* with extensive cortical overgrowth in mature and gerontic specimens.

Remarks. – Monsen (1937) described the species from a single gerontic specimen showing little detail of the thecal development and proximal construction. A number of smaller specimens from Storeklev show part of the thecal development and growth already illustrated by Lindholm (1991a) from Norwegian specimens.

Together with specimens described by Lindholm (1991a) from the *Hunnegraptus copiosus* Biozone of the Oslo Region in Norway, a better understanding of the species can be achieved. The specimens show an obliquely positioned sicula, thecae with considerable differentiation of pro- and metathecae and low thecal overlap. The first-order stipes appear to be short and formed from a single theca each, indicating possibly dicalycal thecae at th3^1 and th3^2. Distally, the position of dicalycal thecae is more variable and the colony forms a tubarium generally resembling a species of *Clonograptus*. However, the thecal style is quite different, with higher thecal overlap and simple, gradually widening thecae found in *Clonograptus* (cf. Lindholm & Maletz 1989).

Paradelograptus norvegicus closely resembles *Paradelograptus smithi* (Harris & Thomas, 1938a) but is of different age. *Paradelograptus norvegicus* appears in the *Hunnegraptus copiosus* Biozone, but *Paradelograptus smithi* is considerably younger, occurring in the *Cymatograptus protobalticus* Biozone. Until more is known about tubarium details of the two taxa, the two are kept separate.

Occurrence. – This robust species appears to be common in the *Hunnegraptus copiosus* Biozone at Storeklev and Holsbrotten. Most specimens do not show details of their thecal construction. The age of the type specimen is uncertain, as Monsen (1937, p. 200) stated it is probably from the *Pseudophyllograptus densus* Biozone, a statement questioned by Lindholm (1991a, p. 307). Lindholm (1991a) described *Clonograptus* cf. *C. norvegicus* from a level 0.5 m above the *Ceratopyge* Limestone (Bjørkåsholmen Formation) at Bødalen, Slemmestad, Oslo Region, Norway, which is within the *Hunnegraptus copiosus* Biozone.

Gutiérrez-Marco & Martin (2016) illustrated a number of robust multiramous specimens as *Paradelograptus norvegicus* from the *Sagenograptus murrayi* Biozone in the Fezouata Biota of Morocco.

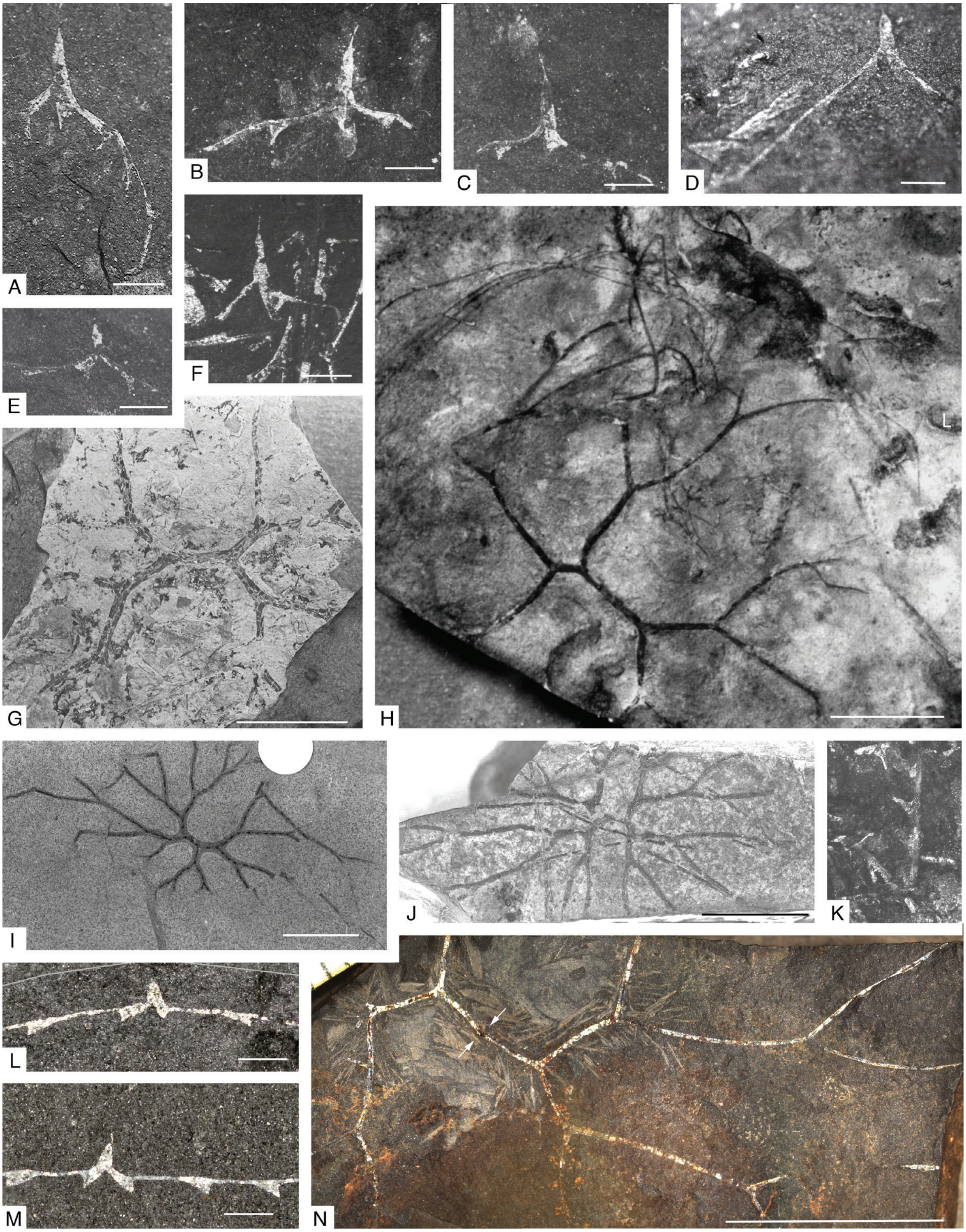

Fig. 20. Paradelograptus specimens, proximal ends. **A**. *Lignigraptus chapmani* (Keble & Harris, 1934), MBg Di 614/119, holotype of *Paradelograptus mosseboensis* Erdtmann, Maletz & Gutierrez-Marco, 1987, Diabasbrottet, 2.8–2.9 m. **B, C**, **E**, **F**, **?K**. *Paradelograptus* sp. cf. *Paradelograptus onubensis* Erdtmann, Maletz & Gutierrez-Marco, 1987, Diabasbrottet, 1.4–1.5 m. **B**, MBg Di 477/218C-2. **C**, MBg Di 477/218B-1. **E**, MBg Di 477/218A-3. **F**, MBg Di 477. **K**, MBg Di 477/218, thecal style. **D**, *Paradelograptus* sp. cf. *Paradelograptus antiquus* (Hall, 1899b), MBg Hun/S2.18–2.3 m/058, Storeklev. **G–H**. *Paradelograptus smithi* (Harris & Thomas, 1938a). **G**, MBg Di 543/26B, Diabasbrottet at 2.1–2.2 m, proximal end showing cortical cover. **H**, PMU 38403a, Mossebo at 3.1–3.2 m, large specimen showing poor preservation of distal stipes, no thecal details available. *Paradelograptus norvegicus* (Monsen, 1937). **I**, MBg TU 2303, Holsbrotten, complete specimen possibly showing stolon system. **J**, MBg ST, Storeklev. **L**, **M**. *Paradelograptus antiquus* (Hall, 1899b) (photos by A. H. M. VandenBerg). **L**, NMV P329383, poor proximal end. **M**, NMV P329462, proximal end. **N**. *Paradelograptus*(?) *subtilis* (Törnquist, 1904), PMU 38404, Diabasbrottet?, arrows indicate position of sicula, coll. Lindholm. Scale bars indicate 1 mm, 10 mm in **G–J**, **N**.

The specimens are similar to the Hunneberg material, bearing darker lines along the middle of the stipes that may be interpreted as a stolon system. The dorsoventral preservation, however, does not show the thecal construction.

Paradelograptus smithi (Harris & Thomas, 1938a)

Figures 19C, D, 20G, H

1938a *Clonograptus smithi* n. sp. Harris & Thomas, p. 73, pl. 1, fig. 9; pl. 4, fig. 8.
1987 *Paradelograptus smithi* (Harris & Thomas, 1938); Erdtmann, Maletz & Gutiérrez-Marco, p. 123, figs 6, 8A, B; 10D.

Type material. – GSV 41317, from locality 1, allotment 16A, near Campbelltown, 20 miles SW of Castlemaine, Victoria, Australia. The specimen originates from the 'Good Bed' (Harris & Thomas, 1938a, p. 70). Rickards & Chapman (1991, p. 31) indicated that the specimen is missing from the collection at Museums Victoria.

Diagnosis. – Large multiramous *Paradelograptus* species with robust tubarium and extensive cortical overgrowth in mature specimens; thecae with distinct differentiation of prothecae and metathecae, possessing strong rutella; details of proximal development unknown.

Remarks. – Erdtmann *et al.* (1987) described the Hunneberg material in detail and referred the interval at Hunneberg to the *Paratetragraptus approximatus* Biozone. Numerous specimens cover a single layer in the basal *Cymatograptus protobalticus* Biozone at Diabasbrottet and Mossebo. The species has previously been recorded only from Victoria, Australia and from the Hunneberg region of Sweden. VandenBerg & Cooper (1992) indicated its presence in the Lower Bendigonian (Be1) *Paratetragraptus approximatus* + *Tshallograptus fruticosus* Biozone, slightly younger than the Swedish material from the *Cymatograptus protobalticus* Biozone. VandenBerg (2019) did not discuss this species in his revision of the Victorian Kinnegraptinae.

Occurrence. – The species is common in a layer at 2.1–2.2 m above the base of the Floian, in the basal part of the *Cymatograptus protobalticus* Biozone at Diabasbrottet. It has not been discovered at other levels, but can be found at a similar level in the Mossebo section. Nothing is known on the further distribution in Scandinavia and the Australian record of Harris & Thomas (1938a) is the only evidence of a wider palaeobiogeographic distribution of the species.

Paradelograptus(?) *subtilis* (Törnquist, 1904)

Figures 17A–C, 20N

1904 *Clonograptus subtilis* n. sp. Törnquist, p. 11, pl. 2, figs 20, 21.
1937 *Clonograptus subtilis* Törnquist, 1904; Monsen, p. 196, pl. 14, fig. 6.

Type material. – Holotype LO 1734T from the Tøyen Shale Formation at Flagabro, Scania, from the *Didymograptus balticus* Biozone (Törnquist 1904).

Diagnosis. – Slender multiramous tubarium with thecae of low inclination and widely and iregularly spaced dichotomies; details of development unclear.

Description. – The type material consists of a single flattened specimen showing little detail of the thecal style (Fig. 17B). The stipes are slender, with at least four dichotomies, reaching a considerable size. The fragmentary specimen indicates that the colony attained a diameter of at least 30–40 mm. The stipes are initially ca 0.2 mm wide, and are more slender distally. The funicle is five mm long with the sicula approximately in the middle, forming a symmetrical proximal end. Length of stipe segments increases from ca 3 mm proximally to at least 10 mm distally at the third and fourth order and may be even longer in distal stipes. A maximum of seven orders of stipes has been observed (Fig. 17A), but specimens may have been larger. There are indications that the thecae may be slender, of low inclination and overlap, and without apertural modifications, but details are obscured.

Remarks. – Fragments of *Paradelograptus*(?) *subtilis* are abundant in the Hunneberg sections, but more complete colonies are extremely rare. A single larger specimen was found in the *Baltograptus vacillans* Biozone at Diabasbrottet (Fig. 17A), but even this specimen did not show any details of the thecal development. Until the development of the proximal end and the thecal style are verified, the species is only tentatively referred to the genus *Paradelograptus*.

VandenBerg (2019) described the genus *Psenograptus* for possible Kinnegraptinae with 'the absense of visible thecae' and identified *Psenograptus costermansi* VandenBerg, 2019 as type species. The genus *Psenograptus* is here regarded as a *nomen dubium*, as the taxon is impossible to identify even at the genus level due to the lack of characters (Maletz & Steiner 2021). Many fragments of *Paradelograptus*(?)

subtilis do not show thecal details and could thus be included in *Psenograptus*.

Genus *Lignigraptus* VandenBerg, 2019

Type species. – *Tetragraptus chapmani* Keble & Harris, 1934 from the *Paratetragraptus approximatus* Biozone of Victoria, Australia; original designation.

Diagnosis. – Kinnegraptines with th1[1] diverging at higher level from metasicula than th1[2], resulting in characteristic asymmetrical appearance, with sicula skewed towards stipe 1; thecae long and slender; metathecal walls may be attenuated, thecal apertures bearing elongate apertural apparatuses (glossae) (VandenBerg, 2019, p. 25).

Included species. – VandenBerg (2019, p. 27) listed all known species referred to this genus from Australasia, North America and Scandinavia, including three new taxa.

Remarks. – VandenBerg (2019) erected the genus for multiramous kinnegraptines with extended rutella, called glossae. The differentiation from the genus *Kinnegraptus* is based on the proximal end development, showing the characteristic asymmetrical origin and initial growth of the first-order stipes in *Lignigraptus*. The genus *Kinnegraptus* shows a stronger extension of the rutellum and a symmetrical origin and growth of the first thecal pair from the sicula (see VandenBerg 2019, fig. 1). The proximal development of *Wuninograptus* is poorly known from both the Chinese type material of *Wuninograptus quadribrachiatus* (VandenBerg 2019, fig. 3) and from the single Australian specimen (see VandenBerg 2019, fig. 47). Thus, a comparison between *Wuninograptus* and *Lignigraptus* cannot be made.

Distribution. – VandenBerg (2019) recognized several species of *Lignigraptus* in the early Floian, from the *Paratetragraptus approximatus* Biozone to the early Chewtonian *Didymograptellus kremastus* Biozone. The genus is here recognized for the first time in Scandinavia.

Lignigraptus chapmani (Keble & Harris, 1934)

Figures 19E, F, 20A

1934	*Tetragraptus chapmani* n. sp. Keble & Harris, p. 169, pl. 20, figs 3a, b.
1987	*Paradelograptus mosseboensis* n. sp. Erdtmann, Maletz & Gutiérrez-Marco, p. 120, figs 5H, I; 10B.
?1994	*Kinnegraptus* sp.; Moya, Malanca, Monteros & Cuerda, pl. 4, fig. 13.
1995	?*Paradelograptus* sp. Ortega & Rao, p. 309, pl. 1, fig. 4.
?1997b	*Paradelograptus* sp. Maletz, fig. 3i.
2000	*Paradelograptus mosseboensis* Erdtmann, Maletz & Gutiérrez-Marco, 1987; Jackson & Lenz, p. 1189, fig. 12A–E.
2019	*Lignigraptus chapmani* (Keble & Harris, 1934); VandenBerg, p. 27, figs 22–26, 29.

Type material. – Holotype NMV P14378 from ‘gully near junction of Kangaroo Creek and Lerderderg River, 2 miles below Blackwood (right bank)’ (VandenBerg 2019, figs 22, 23, 24A, D).

Type material of Paradelograptus mosseboensis. – MBg Di 614/119, holotype, Diabasbrottet section at 2.8–2.9 m above the base of the Floian. MBg S/HUN-MO/069a, b, paratype from Mossebo, exact level unknown. Erdtmann *et al.* (1987, p. 120) referred a number of additional fragments to the species.

Diagnosis. – Four-stiped *Lignigraptus* with declined funicle comprising 3–4 thecae on both stipes, secondary stipes long; sicula 1.6–2.1 mm long, provided with a short, sharply pointed rutellum, and a short nema (VandenBerg 2019, p. 27).

Remarks. – VandenBerg (2019) synonymized *Paradelograptus mosseboensis* with *Lignigraptus chapmani* (Keble & Harris, 1934). Erdtmann *et al.* (1987) described the species in all details available at the time as *Paradelograptus mosseboensis*, thus, the identity with *Lignigraptus chapmani* is probable. The species can be differentiated from other species from the same time interval by the size of the sicula, the declined first-order stipes and the more strongly developed apertural rutellae (glossae).

Jackson & Lenz (2000) recognized the species in the *Paratetragraptus approximatus* and *Tshallograptus fruticosus* biozones of Yukon, Canada. Their material showed that the species developed at least four distal stipes. *Kinnegraptus* sp. described by Moya *et al.* (1994) is similar to this species, but is difficult to identify from the single poorly preserved fragment. The specimen of *Paradelograptus* sp. of Ortega & Rao (1995) is too small to be certain about the specific identity. It consists of a sicula with the initial part of the first theca. The latter is very slender and the relationship to *Lignigraptus* is obvious.

Occurrence. – The species was found at 2.8–2.9 m in the Diabasbrottet section, in the *Cymatograptus protobalticus* Biozone, the interval correlatable with the higher part of the *Paratetragraptus approximatus* Biozone. A single specimen from the Mossebo section may have originated from a comparable level. VandenBerg (2019) indicated that *Lignigraptus chapmani* is from the *Paratetragraptus approximatus* Biozone of Victoria, Australia.

Lignigraptus kinnegraptoides **(Erdtmann, Maletz & Gutiérrez-Marco, 1987)**

Figure 19A, B

1987 *Paradelograptus kinnegraptoides* n. sp. Erdtmann, Maletz & Gutiérrez-Marco, 1987, p. 120, figs 7A, B, 10A.
2000 *Paradelograptus kinnegraptoides* Erdtmann, Maletz & Gutiérrez-Marco, 1987; Jackson & Lenz, p. 1187, fig. 10A–I.
2019 *Lignigraptus kinnegraptoides* (Erdtmann, Maletz & Gutiérrez-Marco, 1987); VandenBerg, fig. 1B (no description).

Type material. – Holotype MBg Di 709/59B-1 (Fig. 19A), designated and figured by Erdtmann *et al.* (1987, figs 7A, 10A). The specimen is from the *Baltograptus vacillans* Biozone of Diabasbrottet, Hunneberg.

Material. – Several specimens from Diabasbrottet at 3.7–3.8 m above the base of the Floian, including the type series and a few additional specimens from the same locality. The species is associated with *Baltograptus vacillans*, *Expansograptus holmi*, *Cymatograptus minutus* and *Paratetragraptus acclinans*.

Description. – The species is multiramous with a biradiate proximal end and variably placed and delayed distal dichotomies. Four orders of stipes are known from the largest specimen. The sicula is about 1.5 mm long and slender with an aperture showing only a slight indication of a rutellum. The proximal development is strongly asymmetrical with two slender crossing canals. The exact development is uncertain as all specimens are flattened. The thecal apertures possess conspicuous rutella. The stipe width across the thecal apertures is about 0.8 mm and 0.15 mm across the prothecal parts. Prothecal parts are strongly differentiated from the triangular metathecal parts and the wide apertures with prominent rutella. There are about 7–8 thecae in 10 mm.

Remarks. – The species is characterized by its size and the typically extended rutella. Most species of *Paradelograptus* are less robust.

Occurrence. – The species appears to be restricted to an interval in the late Tremadocian and early Floian. In Scandinavia it is known so far only from the Floian *Baltograptus vacillans* Biozone.

Suborder Dichograptina Lapworth, 1873

Diagnosis. – Multiramous to two-stiped graptoloids with biradiate isograptid proximal development and maeandrograptid symmetry; colony shape scandent to reclined, horizontal and pendent; prosicula small, with widening and much larger metasicula; thecae simple, widening tubes with or without rutellum; a sicular bitheca may be present in early taxa; branching dichotomous or cladial (Maletz *et al.* 2018b, p. 1).

Remarks. – Maletz *et al.* (2018b) discussed the Dichograptina and provided the most recent compilation of the suborder. The suborder Dichograptina includes most of the large multiramous graptoloid taxa of the Lower to Middle Ordovician, but also the derived Didymograptidae and Pterograptidae. The precise origin and diversification from the Tremadocian Anisograptidae is still uncertain and the Dichograptina may have originated through more than one independent lineage from their Tremadocian ancestors, implying a polyphyletic taxon. Fortey & Cooper (1986, fig. 3) discussed the possible polyphyletic origin of the 'Graptoloidea without bithecae', and suggested to include the planktic Anisograptidae in the Graptoloidea to create a monophyletic clade. This interpretation does not, however, eliminate the problems of the origin and early evolution of the Dichograptina and Sinograptina from different stocks of the Anisograptidae and the paraphyly of the Anisograptidae. The main problem of the interpretation of late Tremadocian graptoloids is the lack of reliable data from the interval, considered to represent a Tremadocian crisis in graptolite evolution by Sadler *et al.* (2011, fig. 13). Very few graptolite faunas have been described from this time interval, which needs more research until we can understand the early evolution of the non-bithecate Dichograptina and Sinograptina around the Tremadocian‑Floian boundary interval.

Family Dichograptidae Lapworth, 1873

Diagnosis. – Biramous to multiramous graptoloids with biradiate isograptid proximal development, symmetrically placed crossing canals and maeandrograptid proximal symmetry; prosicula small, with widening and much larger conical metasicula; sicular bitheca may be present in early taxa; thecae simple, widening tubes with or without rutellum; branching dichotomous to lateral (Maletz *et al.* 2018b, p. 6).

Remarks. – The emendation of Rickards & Chapman (1991, p. 34) is not used here, as the authors retained the old concept of the Treatise (Bulman 1955, 1970) with the informal sections Anomalograpti, Dichograpti, Temnograpti, Schizograpti, Pendeograpti, Tetragrapti, Mimograpti and Didymograpti (Rickards & Chapman 1991, pp. 36, 37). Maletz (2014) provided an emendation of the family Dichograptidae and provided a list of included genera and Maletz *et al.* (2018b) more recently revised the Dichograptidae for the revised Graptolite Treatise volume. There are still numerous problems in the taxonomic identification and interpretation, especially for the multiramous taxa, as these rarely show details of their proximal development and even their thecal style is often impossible to determine in the dorso-ventral preservation of the specimens.

Genus *Hunnegraptus* Lindholm, 1991a

Type species. – *Hunnegraptus copiosus* Lindholm, 1991a from the late Tremadocian (Lower Ordovician) *Hunnegraptus copiosus* Biozone of Galgeberg, central Oslo, Norway; original designation.

Diagnosis. – Multiramous dichograptids with long first-order stipes of unequal length; thecae slender, dichograptid with moderate overlap; proximal end isograptid, dextral or sinistral with sicular bitheca; sicula parallel-sided, obliquely placed between the stipes; thecae along stipes with dorsal origins, lacking bithecae (Maletz *et al.* 2018b, p. 7).

Species. – *Hunnegraptus copiosus* Lindholm, 1991a; *Hunnegraptus tjernviki* Lindholm, 1991a, *Hunnegraptus robustus* Lindholm, 1991a; *Didymograptus novus* Berry, 1960; ?*Bryograptus divergens subsimus* Benson & Keble, 1935.

Remarks. – The genera *Hunnegraptus* Lindholm, 1991a and *Herrmannograptus* Monsen, 1937 (type species: *Graptolithus Milesi* Hall, 1861) are the only genera known to retain a sicular bitheca in the Dichograptidae. Their origin from a bithecate anisograptid is likely, but it is impossible to relate these taxa to any of the known anisograptids. As the genera have a biradiate proximal end, an *Adelograptus*-like ancestor must be postulated, but taxa from the late Tremadocian with bithecae that might relate to *Hunnegraptus* are unknown and the transition has not been traced yet. Most derived dichograptids (Dichograptidae) possess a tetragraptid proximal end with th3^1 and th3^2 as the first distal dichotomies, while *Hunnegraptus* has long first-order stipes with dicalycal thecae considerably delayed. In *Herrmannograptus* a slight delay of the dicalycal thecae can be seen, but the first-order stipes possess only two thecae before the next distal dichotomies take place (Lindholm & Maletz 1989; Maletz *et al.* 2018b). Other differences from *Hunnegraptus* can be seen in the higher inclination of the thecae and the more closely spaced distal dichotomies.

Rushton *et al.* (2021) illustrated several proximal ends as *Hunnegraptus*? sp. from the Alborz Mountains of Iran, clearly showing the sicular bitheca. The specimens are small and it is impossible to refer them to any of the recognized species without doubt. They are quite similar to *Hunnegraptus novus* (Berry, 1960) from the Marathon region of Texas, USA. Maletz (2006) used the distance of the first dichotomies to argue for a separation of *Hunnegraptus novus* and *Hunnegraptus copiosus*. *Hunnegraptus novus* also appears to have slightly wider stipes. However, all material described under the genus name *Hunnegraptus* so far could easily be incorporated in a single, somewhat variable species that would be called *Hunnegraptus novus*. Little is known on the infraspecific variation of *Hunnegraptus* as most specimens are juveniles and mature specimens with long stipes and a higher number of distal dichotomies are rare.

The specimens of *Bryograptus divergens subsimus* Benson & Keble, 1935 from from New Zealand appear to be very similar to *Hunnegraptus novus* and may be referred to the genus *Hunnegraptus*, showing the wider distribution and the difficulty of the identification of the genus.

Hunnegraptus copiosus Lindholm 1991a

Figures 21F–H, 22G–I, 23D

1991a *Hunnegraptus copiosus* n. sp. Lindholm, p. 299, figs 8A–H, 18F, ?H, J.
1991a *Hunnegraptus tjernviki* n. sp. Lindholm, p. 302, fig. 8I–K.
1991a *Hunnegraptus robustus* n. sp. Lindholm, p. 299, text-fig. 9.
1996 *Hunnegraptus copiosus* Lindholm, 1991; Maletz, Löfgren & Bergström, fig. 13: 2–4.
1999 *Hunnegraptus copiosus* Lindholm, 1991; Maletz, Egenhoff & Erdtmann, fig. 1D.
2001 *Hunnegraptus copiosus* Lindholm, 1991; Maletz & Egenhoff, fig. 5A, B, E.
2003 *Hunnegraptus copiosus* Lindholm, 1991; Maletz & Egenhoff, fig. 5F.
2003 *Hunnegraptus copiosus* Lindholm, 1991; Jackson & Lenz, p. 153, fig. 11j.
2006 *Hunnegraptus copiosus* Lindholm, 1991; Maletz, p. 427, fig. 3: 11–13.
2006 *Hunnegraptus copiosus* Lindholm, 1991; Sachanski, Özgül & Arpat, p. 49, figs 2, 3.
2010 *Hunnegraptus copiosus* Lindholm, 1991; Toro, de la Puente & Rubinstein, p. 27, fig. 3A–E.
2011 *Hunnegraptus copiosus* Lindholm, 1991; Maletz & Ahlberg, fig. 3G.
?2016 *Hunnegraptus copiosus* Lindholm, 1991; Martin *et al.*, fig. 5N, O (no description).

Type material. – Holotype PMO 58.969 from the *Hunnegraptus copiosus* Biozone of Galgeberg, central Oslo, Norway (Lindholm 1991a, fig. 8E–F). The specimen shows the first and three second-order stipes and the presence of the sicular bitheca in a low relief specimen in black shale.

Material. – Numerous specimens from a single graptolitic layer at Storeklev (2.15–2.32 m: Tjernvik 1956). Additional specimens from a correlatable level at Holsbrotten and a smaller locality closer to Nygård in which the species occurs in black shales (Fig. 21H).

Remarks. – Lindholm (1991a) described the species in all available detail. Relief specimens from Storeklev show the proximal end in relief in reverse and obverse views (Lindholm 1991a: fig. 8A, B; Maletz 2006, fig. 3: 11 and 12). The species commonly occurs as small specimens, easily misidentified as horizontal to subhorizontal expansograptids (Fig. 21F, G), with branching specimens or fragments rare. However, the small and somewhat oblique sicula serves to differentiate the proximal ends of *Hunnegraptus copiosus* from any expansograptid. Larger specimens have rarely been collected and illustrated. They appear to show relatively evenly spaced branching divisions with the specimens attaining a considerable size (Fig. 22I, 23D).

Lindholm (1991a) referred three species to the genus *Hunnegraptus*. These can easily be interpreted as astogenetic stages of a single, variable species. While *Hunnegraptus copiosus* is based on juvenile and small specimens, *Hunnegraptus tjernviki* tubaria are larger, medium sized with four long second-order stipes, appearing more robust than the juveniles. *Hunnegraptus robustus* is based on mature specimens with considerable development of cortical overgrowth. The development of secondary stipes in the holotype is difficult to verify as the material is strongly prepared and the secondary stipes may be fragments accidentally crossing the stipes of the specimen. Secondary lateral branches have otherwise not been recognized in *Hunnegraptus*. Sachanski *et al.* (2006) described the species from large specimens from the Kaledibi area of the Central Taurus of Turkey. The material shows that the tubaria may have reached a diameter of at least 20 cm, even though complete specimens were not found and this estimation is based on the reconstruction of fragmented tubaria.

Occurrence. – *Hunnegraptus copiosus* is restricted to the *Hunnegraptus copiosus* Biozone. It was first found in Scandinavia and regarded characteristic for the local *Hunnegraptus copiosus* Biozone. Subsequently, the successions of southern Bolivia provided information on the wider paleobiogeographical distribution of the taxon (Maletz *et al.* 1999; Maletz & Egenhoff 2001). More recently, specimens from the Canadian Arctic (Jackson & Lenz 2003) and Turkey (Sachanski *et al.* 2006) were described. Phylogenetically related forms are known from Texas, USA (Berry 1960; Maletz 1999) and China Zhang *et al.* (2003). Therefore, the species appears to be a good index for this interval in the intermediate to cold-water regions. It may be widely distributed in peri-Gondwana once it can be identified with certainty.

Genus *Clonograptus* Nicholson, 1873

Type species. – *Graptolithus rigidus* J. Hall, 1858, p. 121, from the basal *Paratetragraptus approximatus* Biozone of Levis, Québec, Canada (Lindholm & Maletz 1989, p. 719); subsequently designated by Miller (1889, p. 179).

Diagnosis. – Multiramous, horizontal to subhorizontal dichograptid with increasing distances of numerous distal, more irregularly placed dichotomies; thecae simple widening tubes with moderate overlap and without extended rutella; proximal development isograptid, dextral or sinistral (Maletz *et al.* 2018, p. 7).

Remarks. – The genus *Clonograptus* was redefined by Lindholm & Maletz (1989) as 'dichograptaceans' with a tetragraptid proximal end, e. g. th3^1 and th3^2 are the first distal dicalycal thecae, and a multiramous rhabdosome [tubarium] without bithecae. This definition excludes any species with a delay of the first distal dicalycal thecae. The diagnosis is based on the development of *Clonograptus flexilis* (Hall, 1858), not on *Clonograptus rigidus* (Hall, 1858), a species that shows such a delay (see Lindholm & Maletz 1989, fig. 3), sharing this character with *Herrmannograptus milesi* (Hall, 1861). *Clonograptus flexilis* and *Clonograptus rigidus* were considered synonymous or forming astogenetic morphs of a single species for a considerable time (see Ruedemann 1947; Braithwaite 1976). However, Lindholm & Maletz (1989) opined that they are separate species and differ in age. *Clonograptus rigidus* appears in the late Tremadocian, while *Clonograptus flexilis* is a Floian species, appearing in the *Paratetragraptus approximatus* Biozone. Maletz *et al.* (2018b) did not comment on the statement of Lindholm & Maletz (1989, p. 722) that *Clonograptus rigidus* may bear a sicular bitheca and elongated first-order stipes. Lindholm & Maletz (1989) regarded the genus *Herrmannograptus* as a synonym of *Clonograptus*. The proximal development of

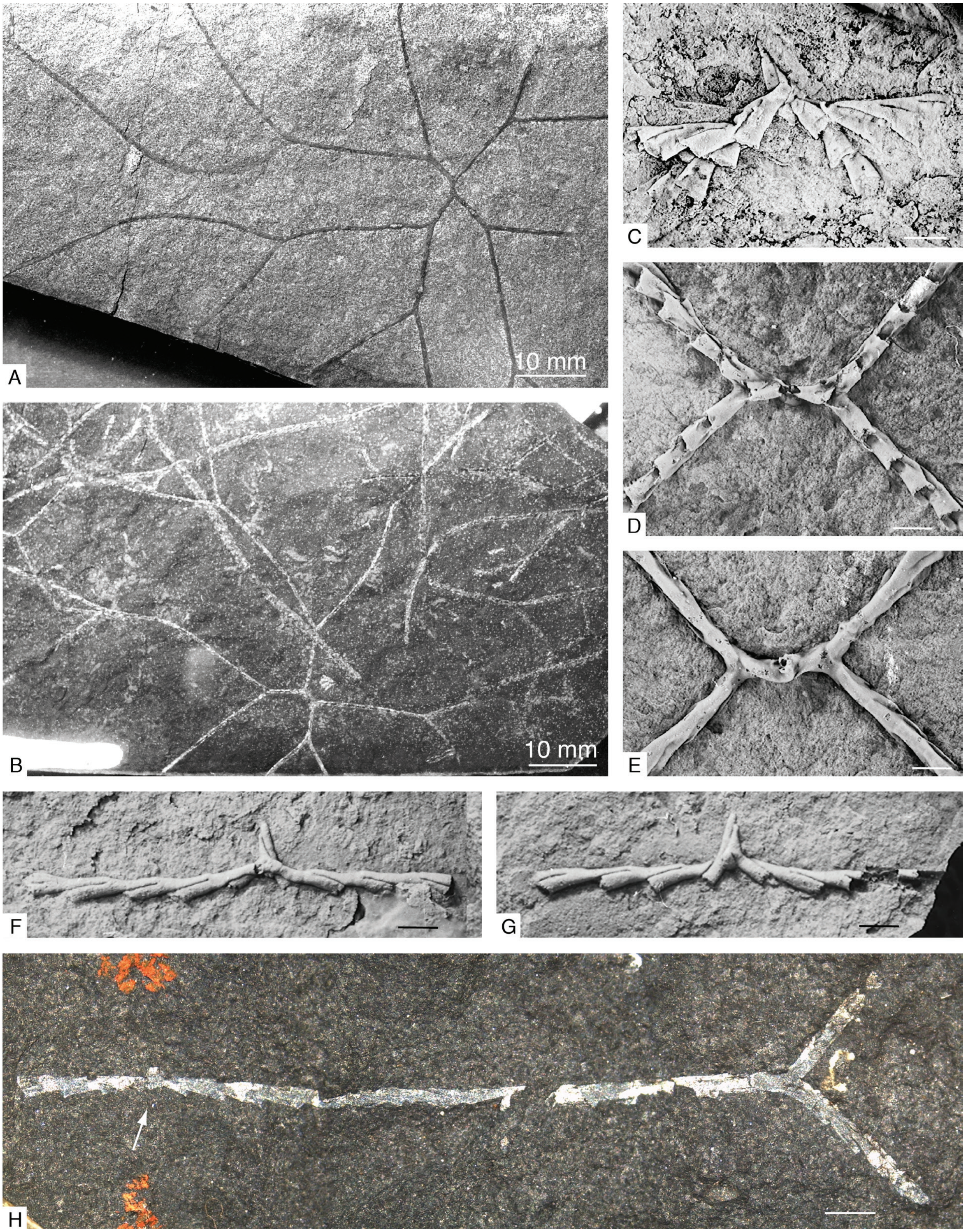

Fig. 21. Tubarium development of *Hunnegraptus* & *Clonograptus*. **A–E**. *Clonograptus multiplex* (Nicholson, 1868), Diabasbrottet. **A**, LO (LR-material) Di 381/1. **B**, LO (LR-material) Di 390/1. **C**, LO 6025t, proximal end in reverse view. **D**, LO 6027t, latex cast, ventral view, showing tetragraptid proximal foundation and thecal apertures. **E**, LO 6027t+, latex cast, dorsal view, showing apex of sicula and dorsal side of four second order stipes. **F–H**. *Hunnegraptus copiosus* Lindholm, 1991a. **F**, **G**, reverse (**F**) and obverse (**G**) views of the latex cast of a single specimen, MBg St material, Storeklev. **H**, PMU 38405, proximal end in black shale, Nygård, arrow indicates position of sicula. Scale bars are 1 mm unless otherwise stated.

Clonograptus multiplex, with its tetragraptid proximal foundation of dicalycal thecae at th3^1 and th3^2, is here regarded as typical of the genus *Clonograptus*.

***Clonograptus multiplex* (Nicholson, 1868)**

Figures 21A–E, 22C, D, 23B, 27A

1868 *Dichograpsus multiplex* n. sp. Nicholson, p. 129, pl. 6, figs 1–3.
1876 *Temnograptus multiplex* (Nicholson, 1868); Nicholson, p. 248, pl. 9, fig. 1.
1882 *Dichograptus* (?) *Milesi* (J. Hall, 1861); Herrmann, p. 351, pl. 2, figs 17, 18.
1885 *Clonograptus* sp.; Herrmann, p. 88, fig. 11.
1886 *Clonograptus multiplex* (Nicholson, 1868); Herrmann, p. 25, fig. 9.
1898 *Temnograptus multiplex* (Nicholson, 1868); Elles, p. 477, fig. 6.
1902 *Temnograptus multiplex* (Nicholson, 1868); Elles & Wood, p. 86, pl. 12, fig. 1; text-fig. 48.
1904 *Temnograptus multiplex* (Nicholson, 1868); Törnquist, p. 21, pl. 3, figs 1–4.
1904 *Dichograptus regularis* n. sp. Törnquist, p. 20, pl. 2, fig. 19.
1904 *Anthograptus nidus* n. sp. Törnquist, p. 22, pl. 4, figs 4, 5.
pars 1904 undetermined irregular Dichograptidae. Törnquist, p. 22, pl. 2, figs 22, 23 (*non* pl. 2, fig. 24 = *Clonograptus* sp. aff. *C. flexilis*).
1937 *Herrmannograptus milesi* (J. Hall, 1861); Monsen, p. 190, pl. 5, fig. 31; pl. 14, fig. 10; pl. 15, fig. 9.
1937 *Herrmannograptus regularis* (Törnquist, 1904); Monsen, p. 192, pl. 14, figs ?3, ?8, 9.
1989 *Clonograptus* (*Clonograptus*) *multiplex* (Nicholson, 1868); Lindholm & Maletz, p. 728, pl. 83, figs 1–6; text-figs 7–11.
1997a *Clonograptus multiplex* (Nicholson, 1868); Toro, pl. 1, fig. 1.
2009 *Temnograptus multiplex* (Nicholson, 1868); Zalasiewicz, Taylor, Rushton, Loydell, Rickards & Williams, fig. 20.
2016 *Clonograptus multiplex* (Nicholson); Gutiérrez-Marco & Martin, fig. 4Q.

Type material. – Lectotype BMNH Q31 (Lindholm & Maletz 1989), from the Skiddaw Group of the English Lake District. Cooper *et al.* (2004) cited the species only from the *Tetragraptus phyllograptoides* Biozone. The fauna of this zone does not include *Tetragraptus phyllograptoides* in the English Lake District and likely should be correlated with the *Cymatograptus protobalticus* Biozone of Scandinavia, the interval in which the species is common at Hunneberg.

Material. – Many specimens from the Diabasbrottet and Mossebo sections. All specimens are from the *Cymatograptus protobalticus* to *Baltograptus vacillans* biozones.

Remarks. – Lindholm & Maletz (1989) redescribed the species and also discussed its thecal style and proximal development. They illustrated a number of mature specimens to show the intraspecific variation of the species. New information is not available. The species is similar to *Clonograptus flexilis* (Hall, 1858), but has much more widely spaced dichotomies (cf. Fig. 22C, D). The type material of *Clonograptus flexilis* is from in the *Paratetragraptus approximatus* Biozone of Québec, Canada and appears to be slightly older than *Clonograptus multiplex* from the *Cymatograptus protobalticus* to *Baltograptus vacillans* biozones of Scandinavia and Britain.

Occurrence. – The species can be found in the *Cymatograptus protobalticus* and *Baltograptus vacillans* biozones of the Floian. It is common in the Diabasbrottet section at Hunneberg. A few fragmentary specimens are found in the Lerhamn drill core of Scania (Maletz & Ahlberg 2011). The species is also common in the Oslo Region of Norway, from where Monsen (1937) illustrated good specimens under a variety of names. It is a large and easily recognizable species, but has not been found to be more widely distributed. Zalasiewicz *et al.* (2009) identified the species as *Temnograptus multiplex* in their *Corymbograptus varicosus* and *Didymograptus simulans* biozones of Britain. A single record from Argentina (Toro 1997a) found *Clonograptus multiplex* in the *Tetragraptus akzharensis* Biozone of the Eastern Cordillera.

***Clonograptus flexilis* (J. Hall, 1858)**

Figures 22B, 23A

1858 *Graptolithus flexilis* n. sp. Hall, p. 119.
1865 *Graptolithus flexilis* Hall, 1858; Hall, p. 103, pl. 10, figs 3–9.
1989 *Clonograptus* (*Clonograptus*) *flexilis* (Hall, 1858); Lindholm & Maletz, p. 723, text-figs 2A, 6A–E.
1989 *Clonograptus* (*Clonograptus*) sp. (spp.?) aff. *C.* (*C.*) *flexilis* (J. Hall, 1858); Lindholm & Maletz, p. 722, text-fig. 5b.
cf. 2018b *Clonograptus flexilis* (Hall, 1858); Maletz *et al.*, fig. 4.1 (no description).

Type material. – GSC 965a–d includes the type material, from the G-locality at Lévis, Québec, Canada (see Maletz 1997a). Lindholm & Maletz (1989, p. 724, fig. 2a) selected GSC 965c as the lectotype of the species (Lindholm & Maletz, 1989, fig. 2a), originally illustrated by Hall (1865, pl. 10, fig. 5). The designation of a holotype for *Clonograptus flexilis* by Braithwaite (1976, p. 19) from his Utah material was in error, as a holotype for *Clonograptus flexilis* can only originate from the type series of Hall (1865).

Material. – Three specimens were described by Lindholm & Maletz (1989), of which two are from

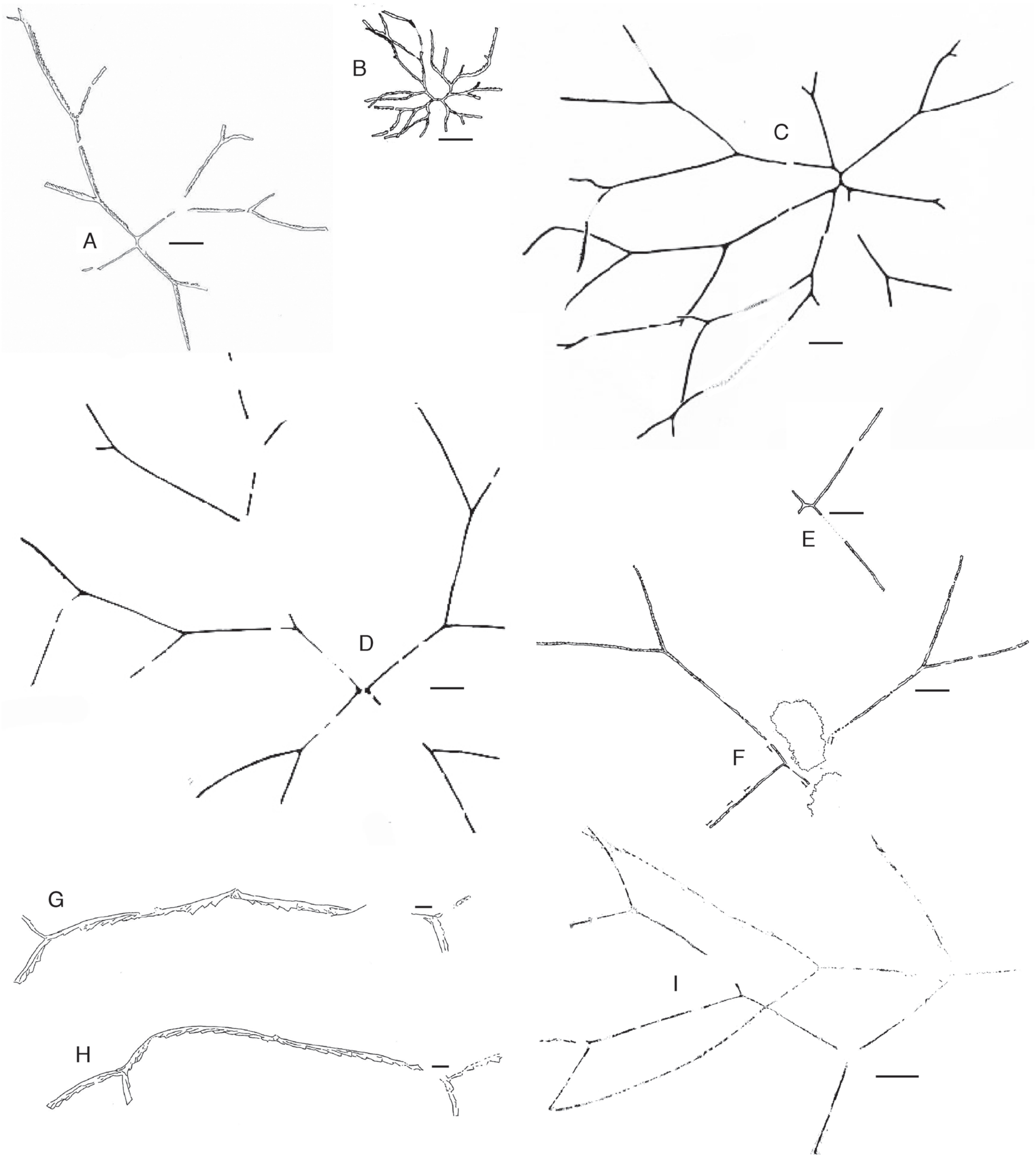

Fig. 22. Multiramous Dichograptina.**A**, *Paratemnograptus magnificus* (Hall), SGU 5468, 'Mossebo', coll. von Schmalensee. **B**, *Clonograptus flexilis* (Hall, 1858), RM Cn1467, 'Mossebo', coll. Holm. **C**, **D**. *Clonograptus multiplex* (Nicholson, 1868). **C**, LO 6051t. **D**, LO 6035t. **E**, **F**, *Clonograptus galgebergi* (Monsen, 1937). **E**, LO 6057t, Diabasbrottet, coll. Lindholm. **F**, PMO K932, holotype, Galgeberg, Oslo, Norway. **G**–**I**. *Hunnegraptus copiosus* Lindholm, 1991. **G**, **H**, MBg Sto 01a, b, Storeklev, two four-stiped specimens. **I**, PMO 236.680, large fragment showing typical distal branching, Slemmestad, precise locality and level unknown. Scale bars are 10 mm.

the Hunneberg sections (LO 5868t, LO 6024t; RM Cn 1467–1468).

Remarks. – Lindholm & Maletz (1989) described the species in great detail. The Hunneberg specimens differ from *Clonograptus multiplex* largely in the closer spacing of the dichotomous branchings and having slightly more slender stipes. Lindholm & Maletz (1989) expressed uncertainty about the identity of their material based on their biostratigraphic occurrence and slight differences in the tubarium shape. The material is here referred to *Clonograptus flexilis* (J. Hall, 1858), as it does not differ in any detail from the Canadian type material. *Clonograptus flexilis* reaches a considerable size with numerous distal stipes as was shown by Hall (1865, fig. 3) (see also Maletz *et al.* 2018, fig. 4/1). The distances between the dichotomies increase considerably distally. A large example from the G-locality, Lévis, Québec, collected by John F. Riva (Québec, Canada) is illustrated here (Fig. 23A) to show the difference from *Clonograptus multiplex* with its much wider spacing of the dichotomies (Fig. 23B).

Occurrence. – The associated faunas (see Lindholm & Maletz 1989, p. 726) indicate that the Hunneberg material most probably originated in the interval between the upper *Expansograptus protobalticus* Biozone to the *Baltograptus vacillans* Biozone. LO 5868t is associated with *Trichograptus dilaceratus*, indicating the *Baltograptus vacillans* Biozone. RM Cn 1467 and 1468 are associated with the conodont *Oelandodus elongatus* and extensiform didymograptids of the *constrictus*–*similis* group (Lindholm & Maletz 1989, p. 726), probably indicating a level at 3.2–3.7 m above the top of the Upper Planilimbata Limestone. The species occurs in a similar interval in its type locality at Lévis, Québec, Canada, starting at a level below the first occurrence of extensiform didymograptids, but ranging much higher (Maletz 1992a, fig. 4). *Clonograptus flexilis* was identified in the *Aorograptus victoriae* Biozone in the Lancefield Quarry (PL 1144) in Victoria, Australia (cf. Morris 1988; VandenBerg & Cooper 1992). Maletz *et al.* (2018, fig. 4.1) illustrated an Australian specimen as *Clonograptus flexilis*, showing the distally thinning stipes in which no thecal details were recognizable. The identity of this material is uncertain as the specimens are distinctly older than the better preserved type material from the Floian of Québec, Canada.

Clonograptus galgebergi (Monsen, 1937)

Figure 22E-F

1937 *Herrmannograptus galgebergi* n. sp. Monsen, p. 191, pl. 6, fig. 5; pl. 15, fig. 10 (*non* pl. 15, fig. 3 = indeterminable fragment).
1937 *Clonograptus* cf. *flexilis* (J. Hall, 1858); Monsen, p. 195, pl. 6, fig. 1.8 (*non* pl. 6, fig. 3).
1989 *Clonograptus* (*Clonograptus*) *galgebergi* (Monsen, 1937); Lindholm & Maletz, p. 735, fig. 13.

Type material. – Holotype PMO K 932 (Fig. 22F) (Monsen, 1937, pl. 6, fig. 5, refigured by Lindholm & Maletz, 1989, fig. 13a). The specimen is from the Galgeberg locality in the city of Oslo, most probably from the *Baltograptus vacillans* or *Cymatograptus protobalticus* Biozone.

Remarks. – The species was differentiated by more slender stipes and straighter thecae from *Clonograptus multiplex* by Lindholm & Maletz (1989), who illustrated two specimens from Diabasbrottet. The specimens originated from a level ca 1.5 m below the 'base of the main *C. multiplex* horizon', which was also stated to be 3.2 m above the Lower Planilimbata Limestone (Lindholm & Maletz, 1989, p. 735). This level is the 3.2 m level, at the top of the *Cymatograptus protobalticus* Biozone (Fig. 6). The biostratigraphic range of this species is not known and it has not been found outside Scandinavia.

Occurrence. – The distribution of this species is uncertain, as very few specimens are available and Egenhoff & Maletz (2007) did not report it from the Diabasbrottet section. Lindholm & Maletz (1989) recorded the species from the '*Paratetragraptus approximatus* Zone sensu Monsen (1937)'. The precise age of the Norwegian material (Monsen, 1937) is uncertain, as the specimens are not associated with other taxa.

Genus *Schizograptus* Nicholson, 1876

Type species. – *Dichograpsus reticulatus* Nicholson 1868, p. 143 from the *Didymograptus simulans* Biozone (Zalasiewicz *et al.* 2009) of the Skiddaw Slates of the British Lake District; original designation.

Diagnosis. – Multiramous tubarium with two dichotomous bifurcations producing a tetragraptid proximal end, followed by three or more orders of lateral branching, which follows the growth direction of second-order stipes; thecal style poorly known (Maletz *et al.* 2018b, p. 9).

Remarks. – *Trochograptus* is here considered to be a synonym of *Schizograptus* (cf. Maletz *et al.* 2018, p. 9). The main difference is the more widely spaced branching. This character is regarded as a merely specific character and cannot be used for the differentiation of genus level taxa. The type species of *Trochograptus* is *Trochograptus expansus* from the Tøyen Shale of Slemmestad, Oslo, Norway (Holm 1881). The exact biostratigraphic level at which it was found is unclear.

Most species of *Schizograptus* are known from one or two specimens only and their taxonomic status and

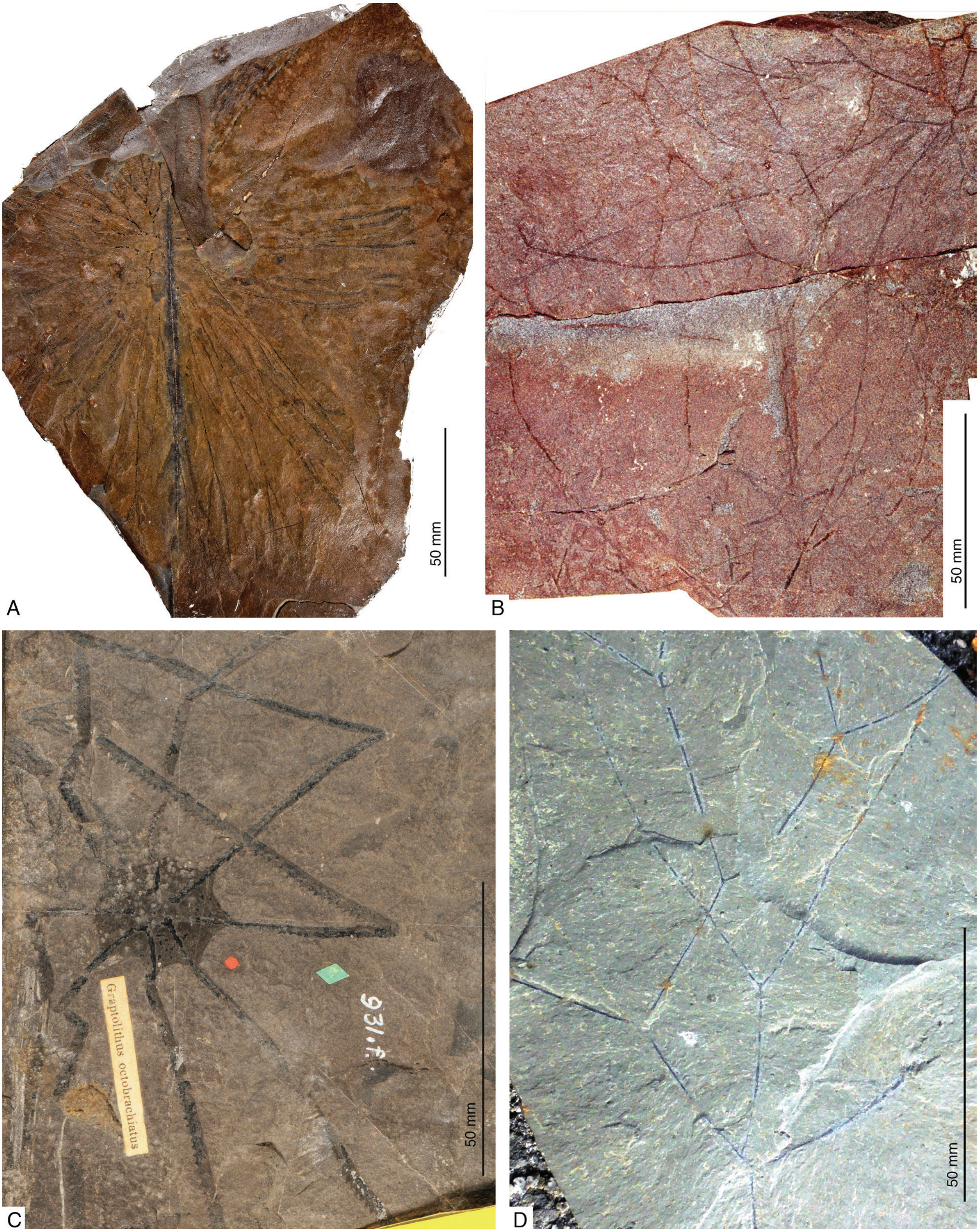

Fig. 23. **A**, *Clonograptus flexilis* (Hall, 1858), JM 140, large specimen, Lévis, Québec, G-locality, coll. Riva. **B**, *Clonograptus multiplex* (Nicholson, 1868), LO (LR-material), large specimens from Diabasbrottet, Hunneberg, found in highly contact-metamorphous shales. **C**, *Dichograptus octobrachiatus* (Hall, 1858), GSC 931f. Lévis, Québec, Canada (see Hall 1865, pl. 8, fig. 1). **D**, *Hunnegraptus copiosus* Lindholm, 1991a, PMO 236.680, Slemmestad, Norway.

biostratigraphic ranges are uncertain. The main differences are the distances between third-order stipes and the size of the colonies. A revision of the genus and the intraspecific variation of its species is urgently needed.

Occurrence. – *Schizograptus* species have been described from the Floian to Dapingian time interval and appear to be distributed worldwide.

Schizograptus ambiguus **Törnquist, 1904**

Figure 24B, F–H

1904 *Schizograptus ambiguus* n. sp. Törnquist, 1904, p. 25, pl. 3, fig. 8 [misspelled *ambignus* on p. 25; but *S. ambiguus* in other places, indicating this to be the intended correct spelling of the species name].

Type material. – Holotype LO 1745T and its counterpart LO 1745T+ (by monotypy) (Fig. 24B). The specimen was collected by von Schmalensee at 'Mossebo', thus most probably from the modern Diabasbrottet locality.

Diagnosis. – Medium sized *Schizograptus* with lateral stipes of two orders; thecal details and proximal development unknown.

Description. – The tubarium has a diameter of about 10 cm with the individual second-order stipes reaching about 5 cm in length. Each of these bears lateral stipes of at least third-order. The distances between the third-order stipes are between 3 and 1.2 mm. The distal half or third of the second-order stipes do not bear lateral third-order stipes. The short funicle (indicated by white arrows in Fig. 24B) indicates a possible tetragraptid configuration of the proximal end with th3^1 and th3^2 as the likely first distal dicalycal thecae (cf. Maletz 1992a). The four second-order stipes show a slightly convex curvature. The dorsal width of the stipes is less than 1 mm, but stipe width increases to 1.5 mm in lateral view. A single fourth-order stipe is found (red arrow in Fig. 24B), originating about 4 mm from the origin of the third-order stipe at a high angle, but quickly bending outwards to become parallel to the parent? stipe. This fourth-order stipe may be an anomaly in the development of the colony. The thecae are simple, distinctly widening tubes without a rutellum at the aperture, showing moderate overlap. Their lateral profiles are only visible in the most distal parts of the stipes, where the stipes are flattened, so that details of the thecal development are not visible.

Remarks. – The type specimen is associated with a number of other graptolites including *Baltograptus geometricus* (Fig. 24C), *Expansograptus holmi* (Fig. 24D) and *Expansograptus urbanus* (Fig. 24E). A single incomplete specimen of *Baltograptus* sp. (Fig. 24A) appears to show a more declined tubarium and might be referrable to *Baltograptus vacillans*. The fauna indicates an origin of the slabs from the upper part of the *Cymatograptus protobalticus* Biozone or basal *Baltograptus vacillans* Biozone. A tetragraptid proximal end on the type slab (Fig. 24B; green arrows) may be a juvenile of *Schizograptus*. Several small or juvenile specimens were found in the Lindholm collection and are here shown (Fig. 24F–H) to indicate the close similarity to early growth stages of *Clonograptus multiplex*. The only difference appears to be the clear lateral growth of the stipes of the third order (Fig. 24H), while in *Clonograptus multiplex*, each branching is dichotomous and none of the stipes continues the original direction of growth (Figs 21A, B; 22C).

Occurrence. – The species is known from a single large specimen and several early growth stages. The intraspecific variation of such multiramous dichograptids may be much larger than currently thought and a number of described taxa may belong to a single variable species.

Schizograptus rotans **Törnquist, 1904**

Figures 25B, 26C

1904 *Schizograptus rotans* n. sp. Törnquist, 1904, p. 24, pl. 4, figs 1–3.

Type material. – Lectotype LO 1746T from 'Mossebo', Västergötland (designated herein) and paratype LO 1747t from Flagabro, Scania. Törnquist (1904) referred the material to his *Didymograptus balticus* Biozone.

Diagnosis. – Robust, medium sized *Schizograptus* with widely spaced lateral stipes of three (rarely four) orders.

Description. – The size of the colony reaches at least 20–25 cm in diameter based on the longest stipes preserved, but all available specimens are fragmentary. The proximal end is tetragraptid with the funicle ca 3.5 mm long. The four main stipes are very slightly curved and the next order stipes are positioned on their convex side. The third-order stipes are spaced at distances of 8–25 mm and the very few

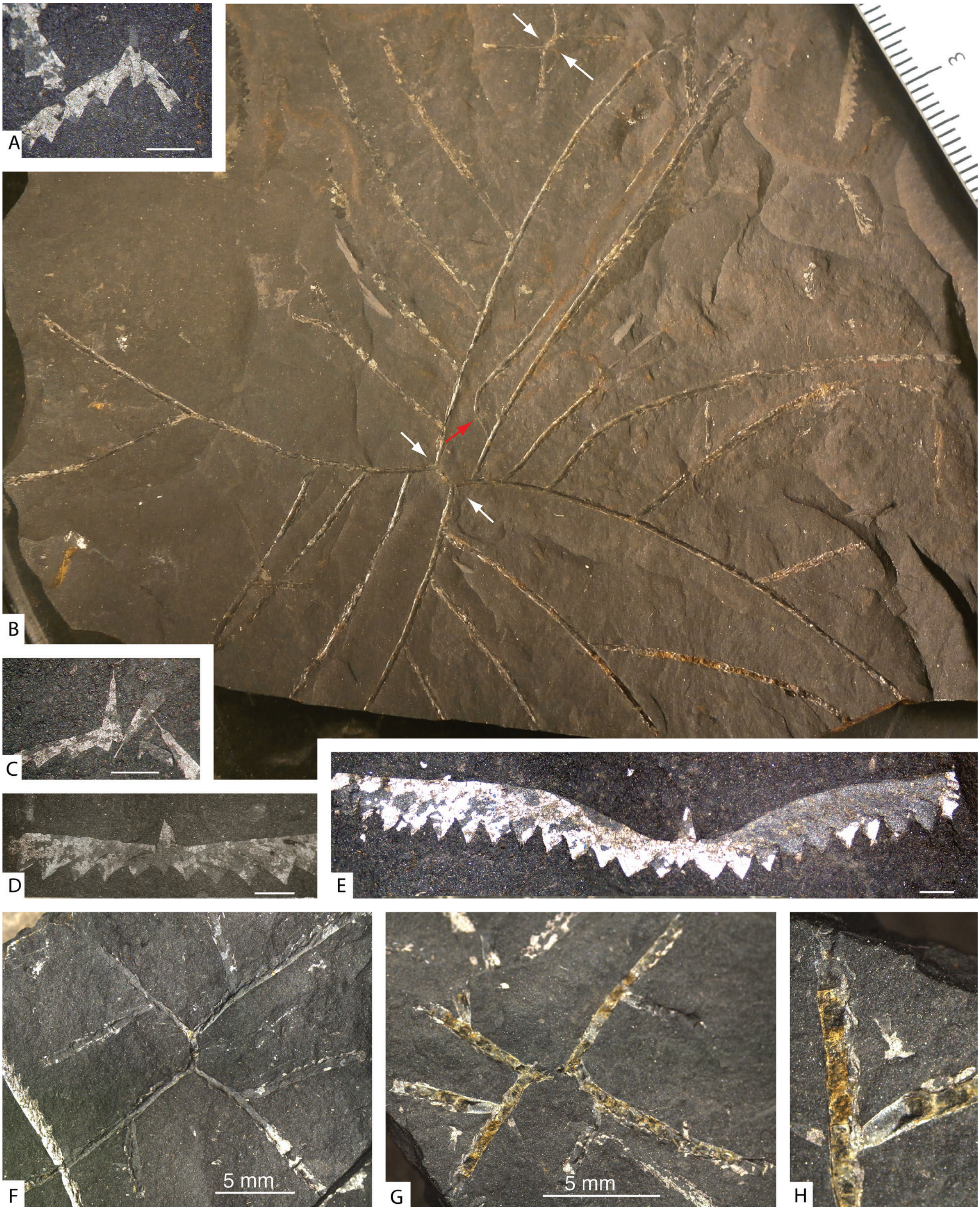

Fig. 24. Schizograptus ambiguus Törnquist, 1904 and associated specimens. **A–E** are preserved on a single slab. **B, F–H**. *Schizograptus ambiguus* Törnquist, 1904 (LO 1745T and counterpart LO 1745T+), 'Mossebo', Hunneberg, coll. von Schmalensee. **B**, counterpart of holotype, white arrows indicate tetragraptid proximal end, unusual stipe development (red arrow), scale in mm. **F**, PMU 38406, Lindholm 189, small specimen, Diabasbrottet. **G**, **H**, PMU 38407, Lindholm 187, Diabasbrottet, small specimen, (**G**) and enlargement to show lateral origin of third order stipe (**H**). **A**, *Baltograptus* sp., obverse view, flattened. **C**, *Baltograptus geometricus* (Törnquist, 1901), small specimen. **D**, *Expansograptus holmi* (Törnquist, 1901), flattened specimen with incomplete tip of sicula. **E**, *Expansograptus urbanus* (Monsen, 1937), flattened specimen. Scale bars indicate 1 mm unless otherwise stated.

fourth-order stipes appear to be even more widely spaced. The stipes reach a dorsoventral width of 1 mm near the proximal end, possibly due to the addition of cortical material, as distally, they are only ca 0.5 mm wide in dorsal view. The few places in which a lateral view of the stipes shows the thecal outlines, the stipes are 1.8–2.0 mm wide. The thecal inclination is about 35° and the thecae may show a very slight rutellum, that could, however, have been produced by flattening of the stipes. Details of the proximal end and the thecal development are not known.

Remarks. – The exact age of the type specimen is uncertain. Associated graptolites include *Expansograptus urbanus* and *Cymatograptus* sp. cf. *Cymatograptus demissus* (Fig. 25A) indicating the upper *Cymatograptus protobalticus* Biozone to *Baltograptus vacillans* Biozone. The specimens differ from *Schizograptus ambiguus* by the wider spacing of the stipes and the more robust thecae. As only few specimens of both taxa are available, the intraspecific variation of these characters cannot be evaluated. It may be possible that both species are end-members of a single, highly variable taxon.

Occurrence. – The species has been found at Mossebo and Diabasbrottet in a small number of specimens. Additional material is from Scania (Törnquist 1904). Based on the associated fauna, all specimens appear to be from the upper *Cymatograptus protobalticus* to lower *Baltograptus vacillans* Biozone.

Genus *Holograptus* Holm, 1881

Type species. – *Holograptus expansus* Holm, 1881 from the *Tetragraptus phyllograptoides* Biozone of Hunneberg; original designation.

Fig. 25. Schizograptus rotans Törnquist, 1904. LO 1746T and associated specimen. **A**, ?*Cymatograptus* sp. cf. *Cymatograptus demissus* (Törnquist, 1901), juvenile showing long and slender sicula. **B**, *Schizograptus rotans*, holotype (1), note second specimen on slab (2).

Remarks. – Multiramous colony based on tetragraptid proximal end; lateral stipes of third and later orders spaced at irregular intervals on either side of parent stipes, which follow the growth direction of second-order stipes; lateral stipes can themselves produce lateral stipes; central web may be present; often long second-order stipes before insertion of initial third-order stipes (Maletz *et al*. 2018b, p. 9).

Species. – *Holograptus expansus* Holm, 1881; *Rouvilligraptus richardsoni* Barrois, 1893; *Holograptus deani* Elles & Wood, 1902; ?*Schizograptus tardibrachiatus* Bouček, 1973.

Remarks. – The genus *Holograptus* is based on a single specimen from the *Tetragraptus phyllograptoides* Biozone of Diabasbrottet, Hunneberg. Spjeldnaes (1986, p. 100) considered the genus *Trochograptus* Holm, 1881 to be a synonym of *Holograptus*, which is not accepted here, as *Trochograptus* is considered a synonym of *Schizograptus*. The differentiation of species in this genus is difficult due to the scarcity specimens and the resulting lack of understanding of the intraspecific variation. Different branch spacing is the main character used to separate the species.

Kraft (1987, p. 63) regarded *Schizograptus tardibrachiatus* Bouček, 1973 as a member of *Holograptus* based on the branching patterns, showing lateral branches on both sides of the second-order stipes seen in a number of larger specimens.

Occurrence. – Species of *Holograptus* occur from the Lower Floian *Tetragraptus phyllograptoides* Biozone to at least the Lower Dapingian, but specimens are rare and most are not dated precisely. Spjeldnaes (1986, p. 97) described the distribution of '*Trochograptus*' *diffusus* in the Oslo Region and discussed its occurrence as abnormal as it occurs together with exotic elements like *Sigmagraptus* aff. *S. crinitus* (T. S. Hall) (probably a gerontic form of *S. praecursor*; VandenBerg, pers. comn. 2023) at a level probably within the Lower Dapingian *Isograptus victoriae* Biozone. The layer is at the base of the green shales of the upper part of the Tøyen Shale Formation (Spjeldnaes 1986, fig. 10).

Large specimens are known from the Middle Skiddaw Slates of Britain (Elles & Wood 1902). Cooper *et al.* (2004) reported *Holograptus deani* from the *Didymograptus simulans* Biozone and *Trochograptus diffusus* from the *Baltograptus varicosus* Biozone of the Skiddaw Group. Zalasiewicz *et al.* (2009) made a questioned reference to the presence of *Holograptus deani* in the *Didymograptus simulans* to *Isograptus victoriae* biozones of Britain.

***Holograptus expansus* Holm, 1881**

Figure 26A

1881 *Holograptus expansus* n. sp. Holm, p. 46, pl. 12, figs 1, 2.
?1933 *Holograptus expansus* Holm; Bouček, p. 4, fig. 4.
?1973 *Holograptus deani* Lapworth, MS in Elles & Wood, 1902; Bouček, p. 32, pl. 4, fig. 1; text-fig. 8a, b.

Type material. – Holotype RM Cn 1499 and RM Cn 1500 (counterparts), from the Tøyen Shale Formation at Diabasbrottet, collected by G. Holm in 1877 from 'Mossebo', Hunneberg. The slabs contain specimens of *Tetragraptus phyllograptoides*, *Tshallograptus* sp., *Cymatograptus demissus* (Fig. 26B) and *Tetragraptus amii* (4-stiped). The association indicates the *Tetragraptus phyllograptoides* Biozone.

Remarks. – The species is based on a single large specimen and further definite material is not available to understand the intraspecific variation of this taxon. The thecae appear to be simple dichograptid with no evidence of plaited overlap. Maletz (1987) referred a number of long-stiped tetragraptid proximal ends from the *Cymatograptus protobalticus* Biozone to this genus, but did not have larger and more complete specimens at hand. The identity of this material remains uncertain and the species is not re-described herein.

Occurrence. – The only reliable record of *Holograptus expansus* from Scandinavia is from the *Tetragraptus phyllograptoides* Biozone at Diabasbrottet (former Mossebo in Holm 1881) as the fauna associated on the type slab indicates.

Bouček (1933) referred a single large specimen from the early Ordovician of Bohemia to this species and described a number of specimens of *Schizograptus tardibrachiatus* Elles, 1898 from the same layers. Bouček (1973), however, referred to this material to *Holograptus deani* Lapworth, 1902 and *Schizograptus tardibrachiatus* Bouček, 1973. Interestingly, Kraft (1987) transferred *Schizograptus tardibrachiatus* to the genus *Holograptus*.

Genus *Dichograptus* Salter, 1863

Type species. – *Dichograpsus sedgwickii* Salter, 1863, p. 137 from the Skiddaw Slates of the English Lake District; subsequent designation by Gurley (1896, p. 64).

Diagnosis. – Large multiramous horizontal to subhorizontal tubarium with two to three consecutive bifurcations starting from a tetragraptid proximal end

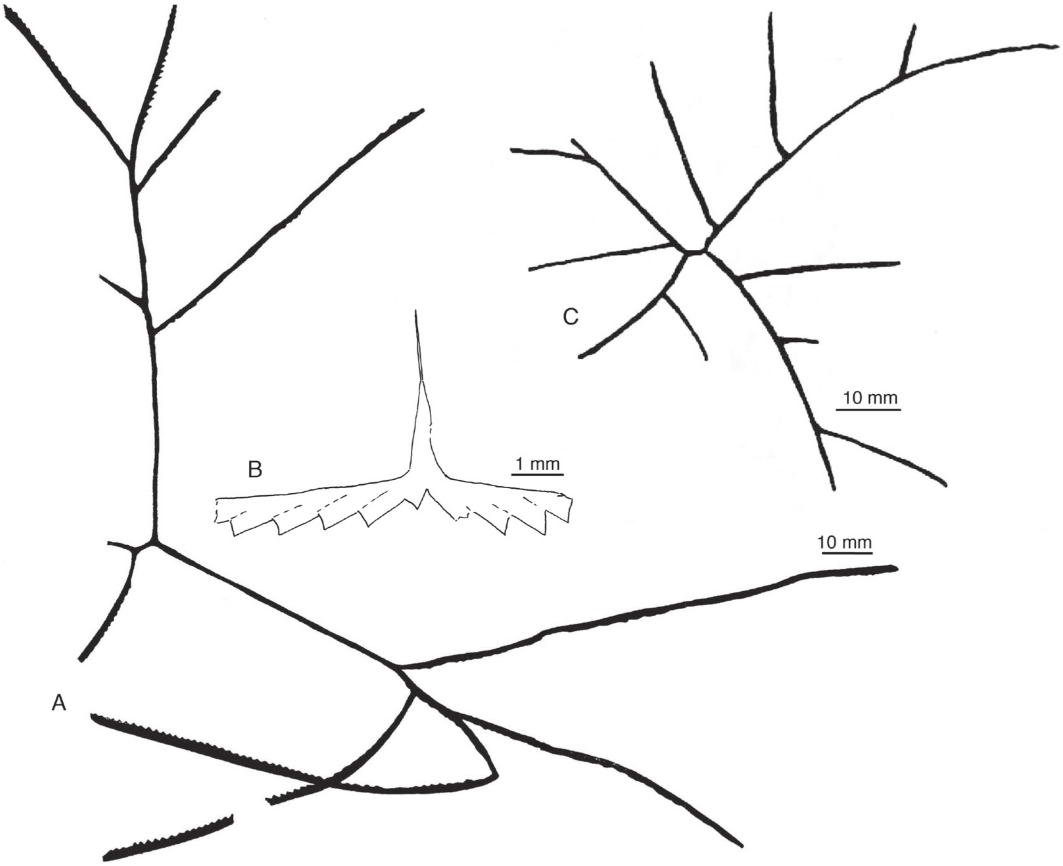

Fig. 26. *Holograptus* and *Schizograptus*. **A**, *Holograptus expansus* Holm, 1881, holotype, RM Cn 1499 (from Holm 1881, pl. 12, fig. 1). **B**, *Cymatograptus demissus* (Törnquist, 1901), specimen on RM Cn 1500, counterpart slab of holotype of *Holograptus expansus*. **C**, *Schizograptus rotans* (Törnquist, 1904), PMU 38408a, poor specimen, Mossebo.

and without distal dichotomies; central disc in some species; thecae simple with moderate overlap (Maletz *et al*. 2018b, p. 7).

Remarks. – Elles & Wood (1902, pl. 10, fig. 3a) illustrated the lectotype of *Dichograptus sedgwickii*. Cooper *et al*. (2004) reports the species from the *varicosus* and *simulans* biozones of the English Lake District.

The proximal development of *Dichograptus* is not known in detail and a comparison with the similar genus *Loganograptus* is not possible. They do not, however, appear to show any significant differences and can only be distinguished by the wider stipes and higher thecal inclination in *Dichograptus*. The two genera are here regarded as synonymous. The genus *Anomalograptus* Clark (1924) from the Lower Darriwilian differs in having thecae with lower inclination and elaborated thecal apertures, and lack a central membrane. Specimens of *Anomalograptus* tend to be more variable in the insertion of dicalycal thecae and have longer first-order stipes. According to Maletz *et al*. (2018a) *Anomalograptus* has a sinograptid proximal end and can be included with the Sinograptidae. A number of specimens referred by Hall (1865) to *Loganograptus logani* can be identified as *Anomalograptus reliquus* (Clark, 1924) due to the lack of a central membrane, the thecal style and the associated fauna of the material. The genus *Anomalograptus* is confined to the lower Darriwilian (Da1–2).

Dichograptus logani **(Hall, 1858)**

Figure 27B–F

1858 *Graptolithus logani* n. sp. Hall, p. 115.
1865 *Graptolithus logani* Hall; Hall, p. 100, pl. 9, figs 2–9, ?pl. 11, fig. 7 (*non* pl. 9, fig. 1 = *Anomalograptus reliquus* Clark, 1924).
1882 *Loganograptus kjerulfi* n. sp. Herrmann, p. 343, figs 1–16.
1904 *Dichograptus octobrachiatus* Hall; Törnquist, p. 17, pl. 2, fig. 14.

1904 *Dichograptus octobrachiatus* var. *kjerulfi* Herrmann; Törnquist, p. 18, pl. 2, figs 15–18.
1937 *Loganograptus kjerulfi* Herrmann; Monsen, p. 183, pl. 15, fig. 11, pl. 17.
1992 *Loganograptus logani* (Hall); Williams, fig. 6G, H.
2021 *Dichograptus logani* (Hall); Maletz, p. 516, fig. 3.

Type material. – Lectotype GSC 932a (Hall, 1865, pl. 9, fig. 2), from Point Lévis, Québec, Canada (Bolton 1960) (designated herein). It is from material labelled GSC 932a-i, from two different localities and levels in the Lévis Formation as is clear from differences in lithology and associated faunas. Specimens without a central disc (Hall, 1865, text-fig. 5, pl. 9, fig. 1) are in silty grey shale, associated with poor specimens of *Arienigraptus* sp. and *Levisograptus* sp., indicating a Darriwilian age. Specimens with a central disc (Hall, 1865, text-fig. 6, pl. 9, figs 2–9) are in black shale, usually not associated with other graptolites, but rare *Pseudotrigonograptus* and stipes fragments of dichograptids are present. The specimens without a central disc are here identified as *Anomalograptus reliquus* Clark, 1924 and excluded from *Dichograptus logani* (Hall). GSC 932a (Hall 1865, pl. 9, fig. 2) is here selected as the lectotype of *Graptolithus logani* Hall, 1858, following the original concept of Hall (1865, p. 100), who stated that 'All these, in their perfect condition, have their bases embraced within a broad disc'.

Only some of the syntypes of Herrmann's (1882) *Loganograptus kjerulfi* have been located in the collections at the Geological Museum, Oslo (PMO). Of these, PMO K 915 (see Monsen, 1937, pl. 15, fig. 11) is selected as lectotype. The specimens are comparable with *Dichograptus logani* (Hall, 1865) from Québec in their dimensions and construction and both taxa are here considered synonyms.

Material. – Four specimens from Mossebo and Diabasbrottet and additional specimens illustrated and described by Törnquist (1904). One proximal end is preserved in relief as a mould (LO 1732t) and shows part of the branching pattern in dorsal view (Fig. 27B, D).

Description. – The species has slender, long distal stipes, reaching a final lateral width of 1.8 mm. The branching of the proximal end appears to be largely consecutive, but often somewhat irregular, with the investigated specimens bearing 7–13 terminal stipes. The stipes of the first to third order generally have a length of 1.0–1.2 mm, indicating, that they consist of only one theca each. The central web structure (Fig. 27C) is always well developed in larger specimens and is only missing in juveniles. Two specimens, associated with *Acrograptus filiformis*, from the Törnquist collection (Fig. 27E, F) show incompletely developed web structures, apparently leaving the first-order stipes free of any webbing. The webs are clearly formed between the second- and later order stipes, but not in the most proximal part of the colonies. However, this may be based on the preservation and parts of the webs may be covered by sediment. It is unclear at what stage in the astogeny of the colony the webbing starts to grow and how the pattern develops. Strong webbing can be seen in other specimens (Fig. 27C), in which all stipes of the first to fourth orders are connected by the webbing. Monsen (1937, pl. 17) provided a photo of a slab with several mature specimens in which the extensive web structure is visible, forming a circular, umbrella-like shape around the proximal end. In other specimens, the web extends to different distances from the proximal end and appears quite irregular.

The proximal development is not seen in most of the Hunneberg material, but has been reconstructed from a single proximal end preserved as a mould (Fig. 27B, D). A latex cast of the specimen shows much detail of the development of the stipes in dorsal view, in which the thecal origins and the isograptid branching are visible. The proximal end is dextral isograptid with th1^2 as the first dicalycal theca. The first order stipes are formed by th1^1 and th1^2. The first distal dicalycal thecae are th3^1 and th3^2, formed after the insertion of a monocalycal theca (th2^1 and th2^2) on each side of the tubarium. These monocalycal thecae form a ca 90–110° angle with the associated distal dicalycal thecae, producing the second-order stipes. There are about 12 to 13 dicalycal thecae in the colony forming the 14 stipes. Each dicalycal theca is separated from the next dicalycal theca by a single monocalycal theca in the proximal end. However, some of the distal development is not visible. Maletz (2021) used the specimen to understand dextral and sinistral development in the distal branching of multiramous graptoloids, showing that dextral and sinistral growth occurs alternately along the stipes. The development confirms the suggestion of Maletz (1992b) concerning proximal and distal dicalycal thecae in anisograptids and multiramous dichograptids.

Remarks. – J. Hall's (1865) type material of *Loganograptus logani* includes two different species, the most important difference being the absence of the central membrane in one of them. The specimens without webs are associated with a fauna containing biserials of early Darriwilian age and are assigned to *Anomalograptus reliquus*, described from the Lévis Shale of Québec (Clark, 1924).

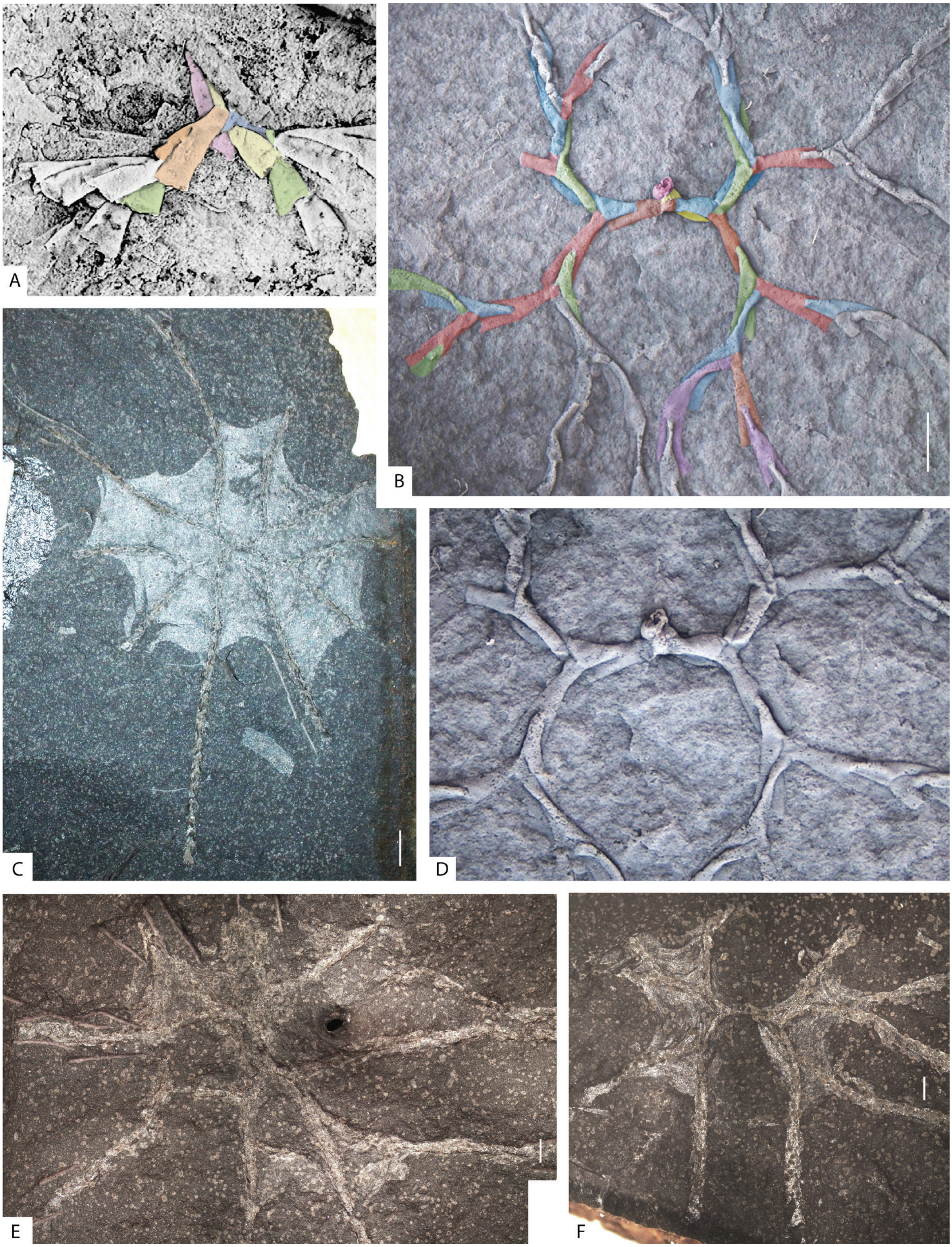

Fig. 27. Dichograptidae. **A**, *Clonograptus multiplex* (Nicholson, 1868), LO 6025t, latex cast, proximal end in reverse view, somewhat distorted (modified from Lindholm & Maletz, 1989, pl. 83, fig. 1). **B–F**. *Dichograptus logani* (Hall). **B**, **D**, LO 1732t, latex cast of specimen showing proximal end in dorsal view, 'Mossebo', *Didymograptus balticus* Biozone (Törnquist, 1904, pl. 2, fig. 18), thecae color coded in (B), red indicates dicalycal thecae, blue and green monocalycal thecae. **D**, Magnification of proximal end without color-coding for comparison. **C**, MBg Di 1340/08, specimen showing proximal web. **E**, **F**, PMU 38409/1, PMU 38409/2, 'Mossebo', coll. Törnquist, specimens showing incomplete proximal webs. Scale bars are 1 mm.

Dichograptus octobrachiatus (Hall, 1858) from Lévis, Québec, Canada is more robust and easily differentiated. Williams & Stevens (1988) discussed the species in detail and designated the largest specimen of Hall (1865) as the lectotype. They indicated that it occurs in the interval from the *Tshallograptus fruticosus* Biozone to the *Didymograptellus bifidus* Biozone. One of the specimens illustrated by Hall (1865) is shown here for comparison (Fig. 23C). It has a large central web and fairly robust stipes. Maletz (1997a) found *Dichograptus octobrachiatus* in the *Tshallograptus fruticosus* to *Didymograptellus bifidus* Biozones at Lévis.

Occurrence. – *Loganograptus logani* is reasonably common in the *Baltograptus jacksoni* Biozone of the Diabasbrottet and Mossebo sections, but a precise range is impossible to determine. The specimens are strongly modified by contact metamorphism. Little is known about the distribution of this species in Scandinavia and its wider palaeogeographical distribution as many of the described multiramous taxa are in need of revision.

Family Phyllograptidae Lapworth, 1873

Diagnosis. – Four- to two-stiped, pendent to horizontal, reclined, reflexed, and scandent, biradiate graptoloids produced by one proximal dichotomy and with th3^1 and th3^2 as the only distal dicalycal thecae; sicula conical, widening distinctly towards the aperture, with rutellum and small prosicula; thecae simple, widening tubes often with distinct rutellum; proximal end development isograptid, dextral (Maletz *et al.* 2018b, p. 13).

Remarks. – All Phyllograptidae bear fairly robust stipes with aperturally highly inclined thecae widening conspicuously towards their apertures. Bithecate taxa and forms with plaited overlap of the thecae are unknown. The main defining synapomorphy of the group is the position of the first and only distal dicalycal thecae at th3^1 and th3^2, thus, the loss of all distal dichotomies after the first one. The Phyllograptidae show a strong tendency to reclined and scandent habits. The group appears abruptly at the base of the Floian with a number of species apparently unrelated to any four-stiped taxa from the upper Tremadocian. Thus, the origin of the group remains elusive.

Maletz (2014) identified the family as the Tetragraptidae Frech, 1897, but as Lapworth (1873) had already established the Phyllograptidae, his term has priority and was also used by Maletz *et al.* (2018b). Fortey & Cooper (1986) introduced the Tetragraptinae as a sister group to the Dichograptinae and included both in the Dichograptidae, but referred the genus *Phyllograptus* to the Virgellina. Williams & Stevens (1988) used the family Phyllograptidae as a separate family for virgellate phyllograptid taxa and included the genera *Tetragraptus* and *Pseudophyllograptus* in the Dichograptidae. Maletz (2010) regarded the dorsal virgellar spine in *Phyllograptus typus* as separately derived from the dorsal virgella in the Pterograptidae and the ventral virgella of the axonophorans and followed Maletz *et al.* (2009) to relate the genus *Phyllograptus* to *Pseudophyllograptus* and the tetragraptids.

Genus *Tetragraptus* Salter, 1863

Type species. – *Tetragrapsus bryonoides* Hall [= *Fucoides serra* Brongniart, 1828 (see Cooper & Fortey, 1982, p. 191)] from the Floian–Dapingian, Middle Ordovician of Lévis, Québec, Canada; original designation by Salter (1863, p. 137).

Diagnosis. – Phyllograptid with three or four horizontal to reclined, reflexed or scandent stipes; proximal end isograptid, dextral, with wide crossing canals and tetragraptid proximal end; thecae with considerable overlap and moderate development of rutella (modified from Maletz *et al.* (2018b, p. 15)

Species. – *Fucoides serra* Brongniart, 1828; *Graptolithus bryonoides* Hall, 1858; *Graptolithus bigsbyi* J. Hall, 1865; *Tetragraptus phyllograptoides* Strandmark, 1902; *Tetragraptus reclinatus* Elles & Wood, 1902; *Tetragraptus phyllograptoides triumphans* Cooper & Fortey, 1982; *Tetragraptus amii* Elles & Wood, 1902; *Phyllograptus cor* Strandmark, 1902. Many more taxa have been included in the (form) genus *Tetragraptus*, but a thorough revision is not possible here.

Remarks. – The genus *Tetragraptus* is used generally for four-stiped horizontal to reclined dichograptids. A true phylogenetic concept for the genus does not exist, even though desired by Cooper & Fortey (1982) and Cooper & Lindholm (1985). A number of subgenera and presumably related genera have been described to subdivide the genus into more usefull and phylogenetically sound taxonomic units. These include *Tetragraptus* (*Etagraptus*) Ruedemann, 1904; *Tetragraptus* (*Eotetragraptus*) Bouček & Přibyl, 1952; *Paratetragraptus* Obut, 1957; *Pendeograptus* Bouček & Přibyl, 1952 and *Tshallograptus* VandenBerg, 2017. Cooper & Fortey (1982) discussed the various genera and subgenera in some detail and revised them. These taxa are here regarded as independent genera (see Maletz *et al.* 2018b).

Williams & Stevens (1988) rejected the genus *Paratetragraptus* for the *Paratetragraptus approximatus* group, based on isolated material showing identical proximal structure to the species of the genus *Tetragraptus sensu stricto*. Maletz *et al.* (2018b), however, accepted the genus and defined it through the horizontal tubarium with two pairs of parallel-oriented stipes. VandenBerg (2017) used specimens preserved in lateral view to redefine its habit as a declined funicle with declined or deflexed stipes, pointing out that most described material is from large tubaria that are inevitably preserved in dorsoventral view which does not display their true shape.

The genus *Eotetragraptus* Bouček & Přibyl, 1952 is based on the type species *Tetragraptus quadribrachiatus* Hall, 1865, of which the type material came from the Lévis Shale of Québec, Canada. Williams & Stevens (1988) recognized the inclusion of two populations in the type material, one from the upper Tremadocian and one from the Darriwilian. A recent investigation of the material indicates that a separate group of four-stiped graptoloids, most closely related to the sinograptids can be recognized in the material from the early Darriwilian. Therefore, Maletz *et al.* (2018a) included the genus *Eotetragraptus* in the Sigmagraptidae based on its sicular development, typically with a distinct rutellum and two lateral apertural lobes.

Isolated material of tetragraptids is rare and restricted to a few levels in the Lower and Middle Ordovician. The earliest descriptions and illustrations were by Holm (1895) and Bulman (1936). Williams & Stevens (1988) described and illustrated specimens of *Paratetragraptus approximatus*, *Paratetragraptus akzharensis*, *Tetragraptus serra*, *Tetragraptus bigsbyi*, *Tetragraptus reclinatus*, *Tshallograptus fruticosus* and *Tshallograptus* cf. *pendens* from the Cow Head Group of western Newfoundland. Many of the specimens are preserved in full relief and show the proximal development and thecal style in some detail. The material originates from the *Paratetragraptus akzharensis* to *Didymograptellus bifidus* biozones, but some of the identifications may be questioned.

Skevington (1965) described a number of *Tetragraptus* specimens from the Lower Darriwilian of Öland as *Tetragraptus* cf. *Tetragraptus serra* (Brongniart), *Tetragraptus bigsbyi* (Hall) and *Tetragraptus* cf. *T. reclinatus* Elles & Wood. As the material is fragmentary, it does not provide much information about the proximal structural development. The isolated juveniles include specimens with prosicular and metasicular origin of th1^1, referred to two different species by Skevington (1965). A metasicular origin of th1^1 has not been mentioned in other material of tetragraptids.

Early tetragraptids. – The origin of *Tetragraptus* is unknown as the earliest species, described from the basal Floian, already have all features characteristic of the genus. The base of the Floian is defined by the first appearance of *Paratetragraptus approximatus* and coincides with the FAD of *Tetragraptus phyllograptoides*. However, Lindholm (1991a, b) discussed, but did not describe, tetragraptids from levels directly below the base of the Floian. A number of tetragraptid species appear in the *Tetragraptus phyllograptoides* Biozone of southern Scandinavia and may shed light onto the origin and early evolution of the genus in the future.

Tshallograptus simplex (Törnquist, 1901) is common in the *Tetragraptus phyllograptoides* Biozone at Hunneberg (Törnquist 1901, Egenhoff & Maletz 2007) and may indicate an evolutionary link between the horizontal to reclined species of the genus *Tetragraptus* and the declined to pendent *Tshallograptus*. The similarites and possible common root of *Tshallograptus* VandenBerg, 2017 (formerly *Pendeograptus*) and *Tetragraptus* is also expressed in the cladistic analysis of Maletz *et al.* (2009), producing a clade that includes *Pendeograptus*, *Tetragraptus* and the phyllograptids.

Distribution. – The genus *Tetragraptus* is widely distributed from the early Floian to the mid-Darriwilian. Due to the poor knowledge of the structure and development of most of the species and their biostratigraphic ranges, the genus is not used for biostratigraphic purposes. A number of easily recognizable species, however, have been used as index species for biostratigraphical intervals in the past, such as *Tetragraptus phyllograptoides* in Scandinavia and *Paratetragraptus approximatus* on a world-wide scale.

***Tetragraptus amii* Elles & Wood, 1902**

Figures 28A–C, 29I, J

	1902	*Tetragraptus amii* n. sp. Elles & Wood, p. 60, pl. 5, fig. 4a–c.
pars	1904	*Tetragraptus serra* (Brongniart); Törnquist, p. 8, pl. 1, figs 17–19, 21 (*non* pl. 1, fig. 20 = *Tetragraptus gerhardi* n. sp.).
	1982	*Tetragraptus* (*Tetragraptus*) *amii* Elles & Wood; Cooper & Fortey, p. 198, fig. 19a–f; pl. 5, figs 6, 9.

Type material. – Lectotype SMA 17838 (Elles & Wood, 1902, pl. 5, fig. 4b), from the Skiddaw Slates of White Horse, NW of Skiddaw (designated Cooper & Fortey 1982, p. 198). Cooper *et al.* (2004) indicated that the species occurs in the *Didymograptus simulans*, *Isograptus gibberulus* and *Aulograptus cucullus* biozones, with questionable occurrences in the *Tetragraptus phyllograptoides* and *Baltograptus varicosus* biozones in the United Kingdom.

Material. – Numerous specimens from the *Tetragraptus phyllograptoides* to *Cymatograptus protobalticus* biozones of Diabasbrottet and Mossebo. Törnquist (1904) illustrated five specimens from the *Tetragraptus phyllograptoides* Biozone of Diabasbrottet as *Tetragraptus serra* Brongniart. The specimens are identified as LO 1709t–1712t in the Lund type collection. LO 1709t (Törnquist 1904, pl. 1, fig. 17) also shows a specimen of *Tetragraptus phyllograptoides*, supporting the age of the specimen. The remaining specimens most probably also originated from this interval, but LO 1712t (Törnquist 1904, pl. 1, fig. 20) is a three-stiped form and originates from a different horizon (see Fig. 6 for biostratigraphic data of the Diabasbrottet section).

Diagnosis. – *Tetragraptus* species with relatively slender, horizontal to subhorizontal stipes; stipes proximally slightly declined to deflexed; sicula long and slender; proximal development isograptid, dextral.

Description. – The tubarium has a normal tetragraptid shape with four horizontal stipes, measuring more than 4 cm in length in larger specimens. The stipes are 1.2–1.3 mm wide at th3[1] and th3[1], quickly widening to 1.5–1.7 mm distally. The 2TRD is 1.6–1.7 mm proximally and fairly consistently 1.7–1.8 mm distally. The proximal development is known from a number of specimens preserved in full relief.

The sicula is 2.2–2.5 mm long with a short rutellum visible in most specimens. The prosicula is visible in one specimen due to a constriction at its aperture. It measures about 0.2 mm in length and is nearly parallel-sided. The sicula is initially slender and starts to widen gradually after ca 0.5 mm of its length. The metasicula attains a width of 0.4–0.5 mm across the aperture, but this may be affected by flattening of the apertural area in most specimens. Th1[1] originates from the lowermost part of the prosicula and grows down along the sicula as a parallel-sided tube. After 0.3–0.4 mm it begins to expand considerably and reaches a width of 0.4 mm at the point of origin of the right-handed th1[2]. Th1[2] originates at a 0.3 mm wide foramen on the right side of th1[1], quickly expands and grows obliquely across the sicula. Very early in its development it forms the foramen for th2[1] on its left side. Th2[1] grows back on to the dorsal side of th1[1] to form the first stipe. The next dicalycal theca begins to form on th2[1] when it is about 0.8–1.0 mm long. The differentiation of the two second-order stipes occurs on the th1[1] side at nearly the same level.

The proximal development is isograptid, dextral in all observed specimens. In reverse view the two crossing canals form a symmetrical isograptid arch. Crossing canal 1 is about 0.4–0.5 mm wide, while crossing canal 2 is much more slender, measuring not more than 0.3 mm. A very short isograptid suture is visible below the isograptid arch, separating the visible apertural parts of the sicula and th1[1].

The thecae are about 2 mm long and show an overlap of ca 50%, but this is difficult to measure in the usual dorso-ventral preservation. The preservation also often makes it impossible to measure the thecal inclination, which is 30–35° in laterally preserved stipes. There is a very short rutellum at each thecal aperture, exaggerated by flattening in most specimens.

Remarks. – The identification of *Tetragraptus amii* is still difficult, even though the species was redescribed by Cooper & Fortey (1982). Cooper *et al.* (2004) indicated an extremely long biostratigraphic range for the species in Britain, ranging possibly from the *Tetragraptus phyllograptoides* Biozone (basal Floian) to the *Aulograptus climacograptoides* Biozone (early Darriwilian). It is possible that more than one species has been identified as *T. amii* from this interval. Elles & Wood (1902) referred the species to their group 1 (horizontal series) and discussed a transition to group 4 (reclined series). Cooper & Fortey (1982) concluded that the species has gently reclined stipes, but most specimens are preserved in a horizontal (dorsoventral) form in the shale.

The Scandinavian specimens from the *Tetragraptus phyllograptoides* and *Cymatograptus protobalticus* Biozones differ from typical, slightly younger *Tetragraptus amii* of Elles & Wood (1902) in the posssession of strictly horizontal stipes. A proximally slight reclination of the stipes is not visible in any of the specimens studied. Relief specimens preserved in lateral view may even show a slight declination of the stipes in the proximal end, before they attain their horizontal orientation.

Occurrence. – The specimens from Hunneberg are from the higher part of the *Tetragraptus phyllograptoides* Biozone and the lower part of the *Baltograptus vacillans* Biozone. Material referred to the species from other regions has an extremely long biostratigraphic range and wide distribution (e.g. Cooper *et al.* 2004). Williams & Stevens (1988) did not report the species from the Cow Head Group of western Newfoundland, where *Tetragraptus serra* appears in the higher part of the *Tetragraptus akzharensis* Biozone and all earlier

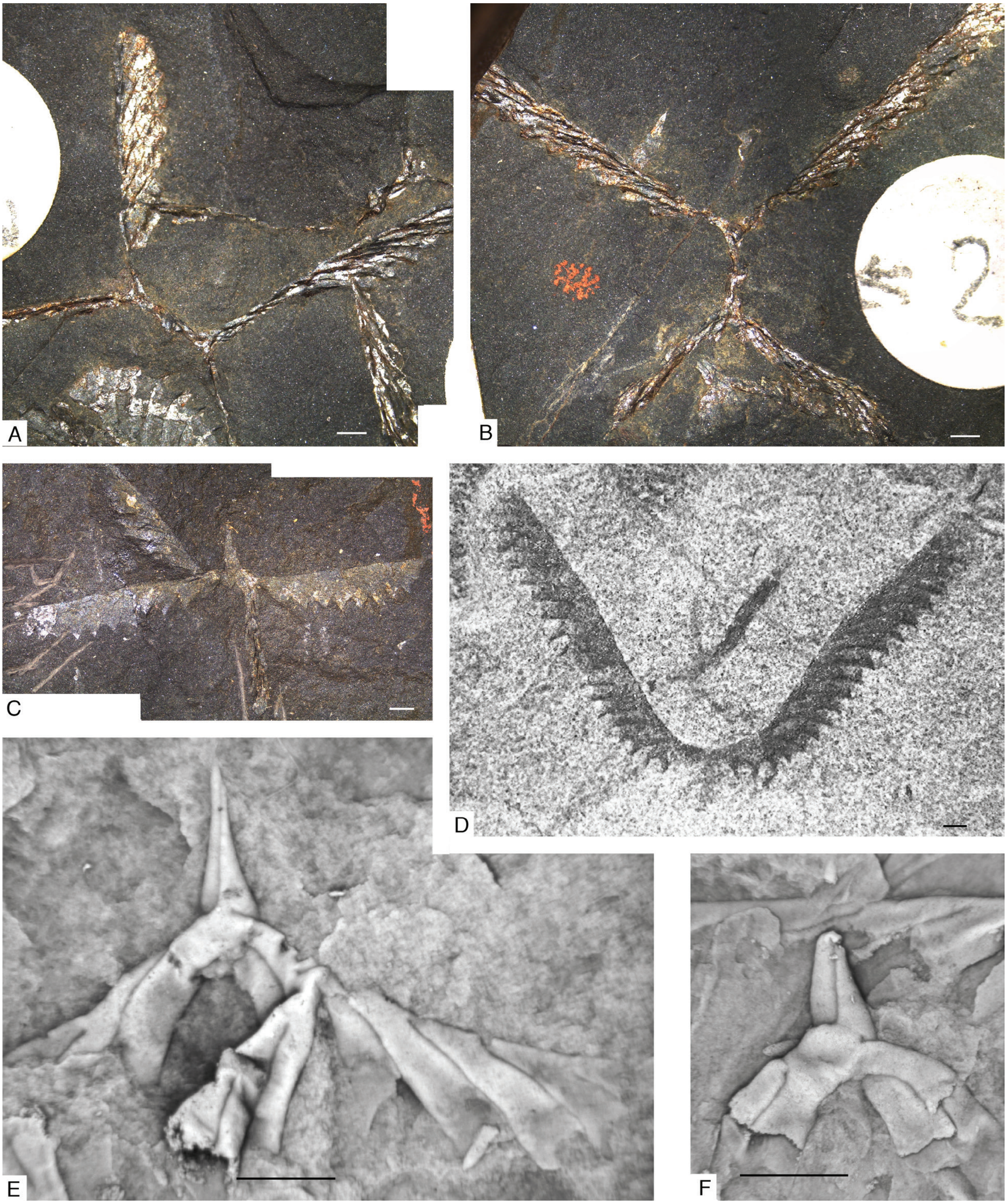

Fig. 28. Tetragraptids. **A–C**. *Tetragraptus amii* Elles & Wood, 1902. **A**, **B**, PMU 38402/2, PMU 38402/3, Diabasbrottet, 1.7–1.8 m. **C**, LO 1711t, small specimen in lateral view (Törnquist, 1904, pl. 1, fig. 19). **D**, *Tetragraptus serra* (Brongniart, 1828). PMU 38410, Diabasbrottet at 8.1–9.1 m, showing more reclined tubarium and wider stipes, poor specimen in contact-metamorphosed shale. **E**, **F**, *Tetragraptus gerhardi* n. sp., PMU 23156/1, 23156/2, Diabasbrottet, latex casts of two proximal ends on one slab in reverse view, showing isograptid proximal development and distal dichotomy on stipe 1. Scale indicated by 1 mm long bar close to each specimen.

tetragraptids have the H-shaped tubarium of the *Paratetragraptus approximatus* group.

Tetragraptus serra (Brongniart, 1828)

Figure 28D

1828 *Fucoides serra* n. sp. Brongniart, p. 71, pl. 6, figs 7, 8.
1858 *Graptolithus bryonoides* n. sp. Hall, p. 126.
1865 *Graptolithus bryonoides* Hall; Hall, p. 84, pl. 3, figs 11, 12 (?); pl. 4, figs 1–11; pl. 6, fig. 4 (?).
non 1904 *Tetragraptus serra* (Brongniart); Törnquist, p. 8, pl. 1, figs 17–21.
?1988 *Tetragraptus serra serra* (Brongniart); Williams & Stevens, p. 27, pl. 2, figs 3, 4, ?5; pl. 3, figs 3–9; pl. 9, figs 1, 2; text-figs 16A–H?, 16I–R; 17.

Type material. – BM (NH) 26995 and BM (NH) Q5060-2 (Cooper & Fortey, 1982, p. 191) from Point Lévis, Québec, Canada. The age of the material is unknown, as no other graptolites are preserved on the slabs of grey shale and the Lévis Formation in Québec ranges from the Upper Tremadocian to the Lower Darriwilian (Maletz 1997a).

Material. – Several poorly preserved specimens from strongly contact metamorphosed shale at Diabasbrottet, probably from the *Baltograptus jacksoni* Biozone (Fig. 6).

Remarks. – The species has been described in detail by Cooper & Fortey (1982). The identity of many specimens from the Floian to early Darriwilian interval is uncertain and may include a number of different species. The specimens from Hunneberg have been identified based on the reclined stipes and the stipe width is clearly different from the closely related *Tetragraptus amii* occurring in the same succession. The proximal development cannot be seen in the Diabasbrottet material.

Occurrence. – A few poorly preserved reclined tetragraptids in the Diabasbrottet section may belong to this species. The species is widely distributed in North America, Scandinavia, Britain and Australasia (see references in Williams & Stevens 1988, VandenBerg & Cooper 1992), where it ranges through the Floian to Dapingian, and possibly early Darriwilian.

Tetragraptus gerhardi n. sp.

Figures 28E, F; 29E–H; 30A–J

pars 1904 *Tetragraptus serra* (Brongniart); Törnquist, p. 8, pl. 1, fig. 20 (*non* pl. 1, figs 17–19, 21 = *Tetragraptus amii*).
?1969 *Tetragraptus decipiens* Hall, 1899 (three-stiped form); Bulman & Cooper, p. 216, fig. 3a–c.
?1979a *Tetragraptus decipiens* Hall; Cooper, p. 62, figs 31e–g; pl. 7A, B, E.
1991a *Tetragraptus* sp. 1 Lindholm, fig. 13B, J.

Type material. – Holotype PMU 38439a, b (Fig. 30H), small specimen in lateral preservation from Mossebo. The specimen is associated with *Cymatograptus validus*, *Cymatograptus undulatus* and fragments of a *Paradelograptus* species in contact metamorphosed shale. It shows the tubarium in lateral view in low relief.

Diagnosis. – Three-stiped tetragraptid with proximally often slightly deflexed, distally horizontal to slightly reclined stipes; stipes slender, gradually widening over the first 3–5 thecae, distally parallel-sided; proximal development isograptid dextral with th3^1 as the only distal dicalycal theca.

Description. – The tubarium has three largely straight, slightly reclined stipes with an angle of ca 120° between them. In dorso-ventral view the sicula can often be seen (Fig. 30D, arrow) at about 1.2–1.5 mm from the branching point of the two distal stipes, indicating that the first-order stipe has only one theca before the first and only distal dichotomy. The stipes show a slight curvature in the proximal end when preserved laterally (Figs 29E–H, 30A, C), showing that the first-order stipes are slightly declined or deflexed. Distally, the stipes appear to be oriented horizontally, as can be interpreted from dorso-ventral preservation of most specimens (Fig. 30D). The apparent reclination of the stipes, thus, is an effect of distortion (see Fig. 30B) and in extreme cases, specimens appear to be more strongly reclined.

The sicula is about 2.2–2.5 mm long and widens gradually from the apex. A short nema is visible in many specimens, but it is impossible to recognize a conus and cauda development. At the aperture, the sicula is about 0.4–0.5 mm wide and bears a very small rutellum. The prosicula is mitre-shaped and is about 0.2 mm long. The origin of th1^1 is in the lower part of the prosicula (Fig. 28E). The sicula is initially slender and starts to widen gradually after ca 0.5 mm from its apex. The metasicula attains a width of 0.4–0.5 mm across the aperture, but widths may be affected from flattening. Th1^1 originates from the lowermost part of the prosicula and grows down along the sicula as a parallel-sided tube. After ca 0.3–0.4 mm it starts to expand considerably and reaches a width of 0.4 mm at the point of origin of the right-handed th1^2. Th1^2 originates through a 0.3 mm wide foramen on the right side of th1^1, quickly expands and grows obliquely across the sicula (Fig. 28F). Very early

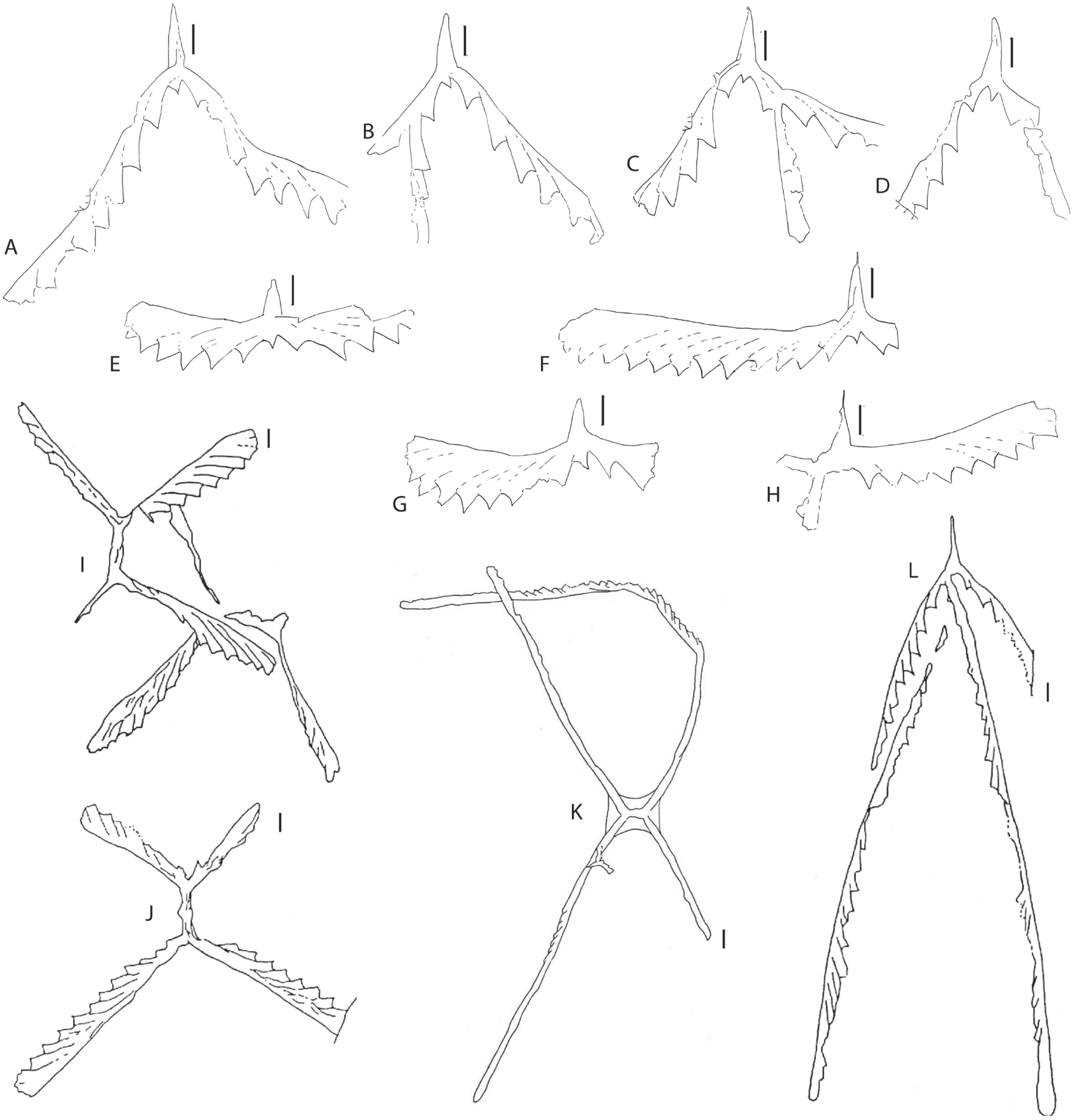

Fig. 29. Drawings of tetragraptid specimens. **A–D**. *Tshallograptus simplex* (Törnquist, 1904), Mossebo, coll. G. Holm, 1877. **A**, RM Cn 1140, declined to deflexed proximal end in which only two stipes are preserved. **B**, RM Cn 1143, proximal end with three preserved stipes. **C**, RM Cn 1142, proximal end with indications of four stipes. **D**, RM Cn 1144, poor proximal end with two preserved stipes. **E–H**. *Tetragraptus gerhardi* n. sp., proximal ends in lateral preservation, Mossebo, coll. Gerhard Holm, 1877, all specimens on one slab. **E**, RM Cn 1432.2. **F**, RM Cn 1432.4. **G**, RM Cn 1432.1. **H**, RM Cn 1432.3, specimen showing indications of three stipes. **I**, **J**. *Tetragraptus amii* (Elles & Wood, 1902), Diabasbrottet, coll. J. Maletz, PMU 38402/2, PMU 38402/3. **K**, *Paratetragraptus vestrogothus* (Törnquist, 1904), Mossebo, MBg Mo 440/10B. **L**, *Tshallograptus fruticosus* (Hall, 1858), PMU 38411a. All scale bars indicate 1 mm. The locality Mossebo of Holm is most likely modern Diabasbrottet.

in its development it forms the foramen for th2^1 on its left side. Th2^1 grows back on to the dorsal side of th1^1 to form the first stipe. The theca starts to form the next dicalycal theca after it is about 0.8–1.0 mm long. The two second-order stipes begin on the th1^1 side at nearly the same level (Fig. 28E), but there is no evidence of the development of a dichotomy at stipe 2. All specimens of this taxon have three stipes.

The proximal development is isograptid, dextral in all observed specimens. In reverse view the two crossing canals form a symmetrical isograptid arch (Fig. 28E). Crossing canal 1 is about 0.4–0.5 mm wide, while crossing canal 2 is much more slender, measuring not more than 0.3 mm. A very short isograptid suture is visible below the isograptid arch, separating the visible apertural parts of the sicula and th1^1.

The thecae are about 2 mm long and show an overlap of ca 50%, but overlap is difficult to measure in the usual dorso-ventral preservation. The preservation also often distorts the thecal inclination, measured at ca 30–35° in laterally preserved stipes. The very short rutella at thecal apertures are exaggerated by flattening in most specimens. The thecae are simple dichograptid, gradually widening towards the aperture. The stipes widen slightly from 1.2–1.3 mm proximally to 1.7–1.9 mm distally. Most of the stipe widening is achieved over the first five to six thecae, after which the stipes are parallel-sided.

Remarks. – Törnquist (1904) recognized this form, but included it in his *Tetragraptus serra* as a three-stiped morph. Lindholm (1991a) described a few specimens of *Tetragraptus krapperupensis* from the *Sagenograptus murrayi* Biozone (*Araneograptus murrayi* Biozone) of the Krapperup drill core. The material may have plaited thecal overlap or triad budding, but the preservation is not good enough to be sure of this detail. Its morphometric characters are very close to those of *Tetragraptus gerhardi* n. sp. and both species could be synonymous. Lindholm (1991a) described *Tetragraptus* sp. 1 from one large specimen collected at Mossebo by Holm in 1877 (Fig. 30B: proximal end only) and a second, smaller specimen from the collections at Sveriges Geologiska Undersökning (SGU).

The material of the three-stiped *Tetragraptus decipiens* described by Bulman & Cooper (1969) and Cooper (1979) is quite similar and is from the same general biostratigraphic unit, the *Paratetragraptus approximatus* Biozone. The material, however, appears to be more slender and the sicula is smaller. Thus, the identity is difficult to establish at the moment.

The very slender *Trichograptus triograptoides* (Harris & Thomas, 1938a) from the Lower Ordovician of Victoria, Australia was initially described as a species of *Tetragraptus* with three stipes. Lindholm (1991a) regarded the species as a sigmagraptine and it was referred to *Trichograptus* by Rickards & Chapman (1991) and VandenBerg (2008b).

Occurrence. – The species is common in the lower part of the *Tetragraptus phyllograptoides* Biozone, where it has been discovered only at Hunneberg so far. Poor specimens or fragments may be mistaken for *Tetragraptus amii*. However, stipe fragments of *Tetragraptus amii* are slightly wider, with a higher thecal inclination and more curved thecae. Monsen (1937) did not find the taxon in the *Tetragraptus phyllograptoides* Biozone of the Oslo Region of Norway.

***Tetragraptus phyllograptoides* Strandmark, 1902**

Figures 31A–G, K

1902 *Tetragraptus phyllograptoides* Linrs.; Strandmark, p. 552, pl. 17, figs 2–4.
1904 *Tetragraptus phyllograptoides* Linnarsson MS; Törnquist, p. 10, pl. 1, figs 22–25; pl. 2, figs 1–8.
1937 *Tetragraptus phyllograptoides* Linnarsson; Monsen, p. 175, pl. 4, figs 29–31; pl. 19, fig. 7.
1937 *Tetragraptus mobergi* n. sp. Monsen, p. 173, pl. 13, fig. 12.
1976 *Tetragraptus* cf. *Tetragraptus phyllograptoides* Linnarsson; Acenolaza, Gorustovich & Solis, s. 282, taf. 3, fig. 10.
1984 *Tetragraptus* (*Tetragraptus*) *phyllograptoides* Strandmark; Gutiérrez-Marco, Rabano & Robardet, p. 17, pl. 1, fig. 3.
1985 *Tetragraptus* (*Tetragraptus*) *phyllograptoides phyllograptoides* Strandmark; Cooper & Lindholm, p. 280, fig. 1A–K, M–Q.
non 1988 *Tetragraptus phyllograptoides* cf. *phyllograptoides* Strandmark; Williams & Stevens, p. 37, text-fig. 25a–h; pl. 6, fig. 5; pl. 9, figs 4, 5.
?1991 *Tetragraptus phyllograptoides* Strandmark; Lindholm, p. 322, fig. 14D, E, G, H.
1992 *Isograptus caduceus* cf. *I. caduceus* (Salter, 1853); Cuerda, Alfaro, Cortes, Franchi & Mendenez, p. 23, pl. 1, fig. 9; pl. 2, fig. 8.
1992 *Tetragraptus* sp. Cuerda, Alfaro, Cortes, Franchi & Mendenez, p. 24, pl. 1, fig. 5; pl. 2, fig. 6.
1992 *Tetragraptus* cf. *T. bigsbyi* Hall; Cuerda, Alfaro, Cortes, Franchi & Mendenez, p. 25, pl. 1, figs 1–3; pl. 2, figs 2, 3.
1992 *Tetragraptus phyllograptoides* cf. *T. phyllograptoides* Strandmark; Cuerda, Alfaro, Cortes, Franchi & Mendenez, p. 25, pl. 1, figs 6, 7; pl. 2, figs 4, 5.
1992 *Skiagraptus* sp. Cuerda, Alfaro, Cortes, Franchi & Mendenez, p. 26, pl. 1, fig. 8; pl. 2, fig. 7.
1994 *Isograptus* sp. Moya, Malanca, Monteros & Cuerda, pl. 4, figs 9, 10.
1994 *Tetragraptus* sp. Moya, Malanca, Monteros & Cuerda, pl. 4, fig. 12.
1997a *Tetragraptus phyllograptoides* cf. *phyllograptoides* Strandmark; Toro, pl. 1, fig. 2.
1997b *Tetragraptus phyllograptoides* Strandmark; Toro, pl. 1, figs 6, 8, 9.
2001 *Tetragraptus phyllograptoides* Strandmark; Maletz & Egenhoff, fig. 8: 1.
2001 *Tetragraptus* (*Tetragraptus*) *phyllograptoides phyllograptoides* Strandmark; Tolmacheva, Koren’, Holmeer, Popov & Raevskaya, p. 558, text-fig. 6, figs 13–24; text-fig. 7, figs 1–3, 5, 6.
2015 *Tetragraptus phyllograptoides* Strandmark; Maletz & Steiner, fig. 10C.
2021 *Tetragraptus phyllograptoides* Strandmark; Maletz & Ahlberg, fig. 1E, F (no description).

Type material. – Lectotype LO 5369T (Fig. 31A), designated by Cooper & Lindholm (1985, p. 280, fig. 1P), from Mossebo, Hunneberg (now Diabasbrottet; see

Fig. 30. *Tetragraptus gerhardi* n. sp. **A**, LO 1712t (Törnquist 1904, pl. 1, fig. 20), note specimen of *Cymatograptus demissus* (arrow) on slab. **B**, RM CN 1838.1, proximal end of large specimen, Mossebo, coll. G. Holm, 1877 (see Lindholm 1991a, fig. 13J). **C**, RM Cn 1335, laterally preserved proximal end associated with two dorso-ventrally preserved specimens (arrows). **D**, RM Cn 1507, dorso-ventral view. **E**, RM Cn 1525. **F**, PMU 38468a, ?Mossebo, showing A–B stipe pair. **G**, RM Cn 1824, small specimen in lateral aspect showing sicula. **H**, PMU 38469a, b, holotype, Mossebo. **I**, PMU 38470, Mossebo. **J**, PMU 38471a/1. Scale bar is 1 mm in each photo.

Maletz *et al.* 1996). Paratypes LO 5369T–LO 5380t; LO 5620, from the same locality.

Material. – Numerous specimens from the *Tetragraptus phyllograptoides* Biozone of Hunneberg (Mossebo, Diabasbrottet, Storeklev, Floklev). Material from the Oslo Region of Norway was examined for comparison.

Remarks. – Cooper & Lindholm (1985) decribed the species in detail and re-illustrated the type material. They also discussed its phylogenetic relationships in some detail. The species is one of the earliest reclined to scandent tetragraptids, but little is known about earlier forms in the Upper Tremadocian. While in a 1-2 preservational aspect, the sicula is visible between the first order stipes (Fig. 31F), the a-b aspect shows a line of connection between the second order stipes (cf. Cooper & Fortey, 1982) and the sicula is covered and invisible (Fig. 31G). Juvenile specimens in a-b aspect could easily be misidentified with a phyllograptid when poorly preserved and not associated with mature specimens (see Cooper & Lindholm 1985, fig. 1B),

Tetragraptus (*Tetragraptus*) *phyllograptoides triumphans* (Cooper & Fortey, 1982) may be closely related, but shows some important differences in the tubarium development with more horizontal growth of the first thecal pair and a less rounded proximal end. The species is found in the much younger *Didymograptellus bifidus* and *Isograptus victoriae lunatus* zones of Spitsbergen and, thus, is distinctly younger than *Tetragraptus phyllograptoides*. The taxon is here elevated to species rank.

Lindholm (1991a) illustrated several very slender specimens as *Tetragraptus phyllograptoides* from the basal *Tetragraptus phyllograptoides* Biozone at Slemmestad, Norway (Fig. 31B). The specimens also show fewer dorsally fused thecae in the proximal end. The proposal of Lindholm (1991a) that the Slemmestad material is of early members of the species is followed here, especially as the form is known from only a single locality. Comparable material is unknown from the Hunneberg sections.

Tetragraptus phyllograptoides cf. *phyllograptoides* from western Newfoundland (Williams & Stevens, 1988) may belong to *Tetragraptus triumphans*. The material is poorly preserved and comes from the *Tetragraptus akzharensis* zone, thus is slightly younger than the typical *Tetragraptus phyllograptoides*, but older than *Tetragraptus triumphans*. The proximal development is unknown, but the general shape of the proximal end (Williams & Stevens 1988, text-fig. 25G, H) indicates a subhorizontal growth of the first thecal pair and probably an isolated metasicula, thus, differing from *Tetragraptus phyllograptoides*.

Similarities can also be seen with *Pseudophyllograptus archaios* (Braithwaite, 1976) from the *Didymograptellus bifidus* Biozone of Nevada and Idaho (Maletz *et al*. 2005). The stipes of *Pseudophyllograptus archaios* merge distally but leave a free space around the supradorsal part of the sicula. In a-b aspect, however, the species closely resembles *Tetragraptus phyllograptoides*. The point where stipes merge appears to be quite variable in *Pseudophyllograptus archaios* and specimens with mostly separate stipes occur (Maletz *et al.* 2005). This suggests *P. archaios* man be conspecific with *Tetragraptus triumphans* from the equivalent biostratigraphic interval in Spitsbergen. However, *Tetragragraptus triumphans* is mainly described from isolated proximal fragments and the tubarium shape is not well known.

Occurrence. – *Tetragraptus phyllograptoides* is a typical species of the *Tetragraptus phyllograptoides* Biozone and is restricted to this interval. It is common in Scandinavia (Strandmark 1902, Törnquist 1904, Monsen 1937), Argentina (Cuerda *et al*. 1992, Moya *et al.* 1998) and Bolivia (Maletz & Egenhoff 2000).

Cuerda *et al.* (1992) described this important species under different names from the Sierra de Cajas in the Cordillera Oriental of Argentina, based on misidentified and unrecognized preservational aspects. A fragment in a-b aspect was called *Skiagraptus* sp. Specimens in 1-2 aspect were identified as *Tetragraptus* cf. *T. bigsbyi* and *Isograptus caduceus*. The material is associated with fragments of *Paradelograptus* (recorded as *Kinnegraptus* sp.), *Didymograptus* sp. (= dichograptid fragment indet.) and *Tetragraptus quadribrachiatus* (= dichograptid indet.). *Tetragraptus phyllograptoides* was also misidentified as *Isograptus* sp. and *Tetragraptus* sp. by Moya *et al.* (1994) from the Cordillera Oriental. The faunas of their faunal associations X & XI are therefore early Arenig (Floian), not late Arenig.

The species was cited from the Russian Platform by Kaljo (1974) without illustrations. Tolmacheva *et al.* (2001) described and figured material of *Tetragraptus phyllograptoides* from the St. Petersburg area of Russia. Here the species occurs together with *Cymatograptus rigoletto* (Maletz, Rushton & Lindholm, 1991) in the *Paroistodus proteus* Conodont Zone in the upper part of the Lakity beds of the Leetse Formation and with *Cymatograptus kristinae* n. sp. (*Didymograptus* cf. *protobalticus in* Tolmacheva *et al*. 2001) in the *Prioniodus elegans* Conodont Zone.

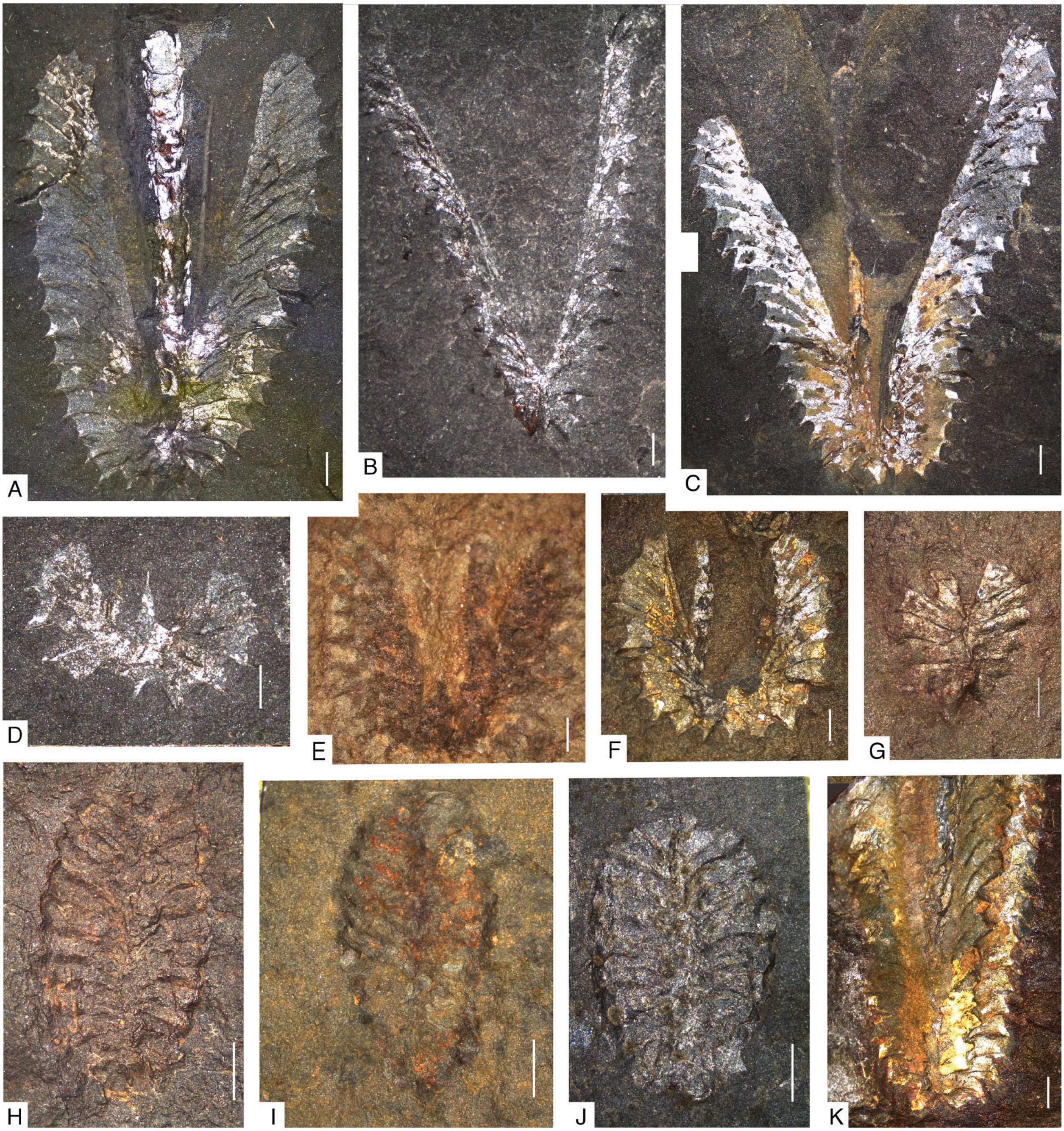

Fig. 31. **A–G, K**. *Tetragraptus phyllograptoides* Strandmark, 1901. **A**, LO 5369t, lectotype, Diabasbrottet (Cooper & Lindholm, 1985, fig. 1P). **B**, LO 5997t, Slemmestad, Norway, a-b preservation of very slender specimen from basal part of its range, Slemmestad, Norway (Lindholm, 1991a, fig. 14G). **C**, RM Cn 1141, Diabasbrottet, large specimen. **D**, PMU 38471a/2, Mossebo, small specimen showing sicula. **E**, PMU 38472, Storeklev, specimen in highly contact metamorphic shale. **F**, PMU 38492, small specimen in 1-2 aspect showing sicula in the center. **G**, PMU 38493, juvenile in a-b aspect with covered sicula. **K**, PMU 38494, large specimen with apparent scandent biserial shape in a-b aspect. **H–J**. *Pseudophyllograptus* sp., all Diabasbrottet (or old Mossebo section). **H**, RM Cn 1482e. **I**, PMU 38473, Diabasbrottet at 6.9–7.0 m. **J**, LO 1727t (Törnquist, 1904, pl. 2, fig. 13). Scale indicated by 1 mm long bar in each photo.

A single record of *Tetragraptus phyllograptoides* is known from the Sinclinal de Valle of Spain (Gutiérrez Marco *et al.* 1984), but the species has not been discovered from elsewhere in western Gondwana. Gutiérrez-Marco & Martin (2016: zone 7) identified an interval in the Fezouata Formation as the *Tetragraptus phyllograptoides* Biozone, even though the interval was barren.

Genus *Paratetragraptus* Obut, 1957

Type species. – *Tetragrapsus approximatus* Nicholson, 1873, p. 136 from the lower Floian *Paratetragraptus approximatus* Biozone of Lévis, Québec, Canada; original designation.

Diagnosis. – Phyllograptids with nearly horizontal tubarium; proximal end with slightly declined to deflexed funicle; paired, parallel-oriented second-order stipes; proximal development isograptid, dextral, with robust and wide crossing canals (slightly emended from Maletz *et al*. 2018b, p. 15).

Species. – *Paratetragraptus approximatus* Nicholson, 1873; *Tetragraptus vestrogothus* Törnquist, 1904; *Tetragraptus acclinans* Keble, 1920; *Tetragraptus* (*Etagraptus*) *laverdieri* Ruedemann & Laverdière, 1935; *Tetragraptus* (*Etagraptus*) *lavalensis* Ruedemann & Laverdière, 1935; *Tetragraptus* (*Etagraptus*) *quebecensis* Ruedemann & Laverdière, 1935; *Tetragraptus volitans* Harris & Thomas, 1938a; *Tetragraptus* (*Etagraptus*) *pacificus* Ruedemann, 1947; *Tetragraptus* (*Etagraptus*) *putillus* Ruedemann, 1947; *Tetragraptus* (*Etagraptus*) *scandens* Ruedemann, 1947; *Tetragraptus* (*Etagraptus*) *scandens curvatus* Ruedemann, 1947; *Tetragraptus* (*Etagraptus*) *prionodus* Xu & Huang, 1979; *Paratetragraptus approximatus robustus* Williams & Stevens, 1988; *Paratetragraptus thomassmithi* VandenBerg, 2017; ?*Paratetragraptus henrywilliamsi* VandenBerg, 2017.

Quite a number of species have been described from the lower Floian, but most of them might be considered as synonyms of a variable *Paratetragraptus approximatus*. The material of Ruedemann & Laverdière (1935) and Ruedemann (1947) are in need of revision. The list of included taxa may not be complete.

Remarks. – VandenBerg (2017) redefined the genus *Paratetragraptus* based on material from Victoria, Australia and described two new species from the lower Floian. Maletz *et al*. (2018b) regarded the genus as separate from *Tetragraptus*, but the differences are minor. *Paratetragraptus* can be separated from *Tetragraptus* mainly through the largely parallel-sided stipes. The proximal development appears to be identical in *Paratetragraptus* and *Tetragraptus* (cf. Williams & Stevens 1988).

Occurrence. – The genus appears to be restricted to the lower Floian *Paratetragraptus approximatus* to *Tshallograptus fruticosus* biozones. It is distributed worldwide and is an important index taxon for this interval. *Paratetragraptus approximatus* is the index species of the GSSP for the Floian Stage of the Ordovician System, defined in the Diabasbrottet section at Hunneberg (Bergström *et al.* 2001, 2006).

Paratetragraptus approximatus (Nicholson, 1873)

Figure 32D, E, G, H, K

1873 *Tetragraptus approximatus* n. sp. Nicholson, p. 136, fig. 2.
1904 *Tetragraptus approximatus* Nicholson; Törnquist, p. 6, pl. 1, fig. 11.
1935 *Tetragraptus* (*Etagraptus*) *quebecensis* n. sp. Ruedemann & Laverdière, p. 12, pl. 1, fig. 5.
1935 *Tetragraptus* (*Etagraptus*) *lavalensis* n. sp. Ruedemann & Laverdière, p. 12, pl. 1, fig. 6.
1937 *Tetragraptus approximatus* Nicholson; Monsen, p. 156, pl. 4, figs 8, 20, 21, 25, 26; pl. 11, fig. 4; pl. 12, figs 4, 5.
1987 *Tetragraptus approximatus* Nicholson; Martin, Malanca & Sureda, p. 609, pl. 1, fig. 6; pl. 2, fig. 12.
1988 *Tetragraptus approximatus approximatus* Nicholson; Williams & Stevens, p. 33, pl. 1, figs 5, 6; pl. 5, figs 1–11; pl. 7, figs 1–9; pl. 8, fig. 1, ?9; text-figs 20A–GG, 21.
?1988 *Tetragraptus approximatus robustus* n. sp. Williams & Stevens, p. 34, pl. 6, fig. 9; text-fig. 22A–G.
1996 *Tetragraptus approximatus* Nicholson; Maletz, Löfgren & Bergström, fig. 13.1.
1997 *Tetragraptus approximatus* Nicholson; Maletz, p. 748, fig. 6n.
1997a *Tetragraptus approximatus* Nicholson; Toro, pl. 1, fig. 3.

Type material. – Lectotype BM(NH) P 1196 from Point Lévis, Québec, Canada, designated by Williams & Stevens (1988, p. 34, pl. 1, fig. 5), figured by Nicholson (1873, fig. 2). It most probably originated from the G-locality at Lévis (see Maletz 1997a).

Diagnosis. – H-shaped horizontal *Paratetragraptus* species with tetragraptid proximal end and isograptid, dextral development; stipe orientation variabe, from strictly parallel to curved and parallel only distally, proximal end slightly declined.

Remarks. – VandenBerg (2017) described the species in detail and provided illustrations of laterally preserved proximal ends showing the proximally declined form of the tubarium. He provided an extensive synonymy list. Thus, a detailed list is not provided here and only references not listed by VandenBerg (2017) are included. His interpretation supported that of Williams & Stevens (1988) based on isolated material. The sicula is similar to the siculae in the genus *Tetragraptus*, measuring ca 2.0–2.2 mm in length with a 0.3–0.35 mm long prosicula. It is similar to the mitre-shaped sicula in *Tshallograptus fruticosus*, but the latter is longer and therefore appears more slender. The shape of the prosicula seems to be identical in both, but details are not available.

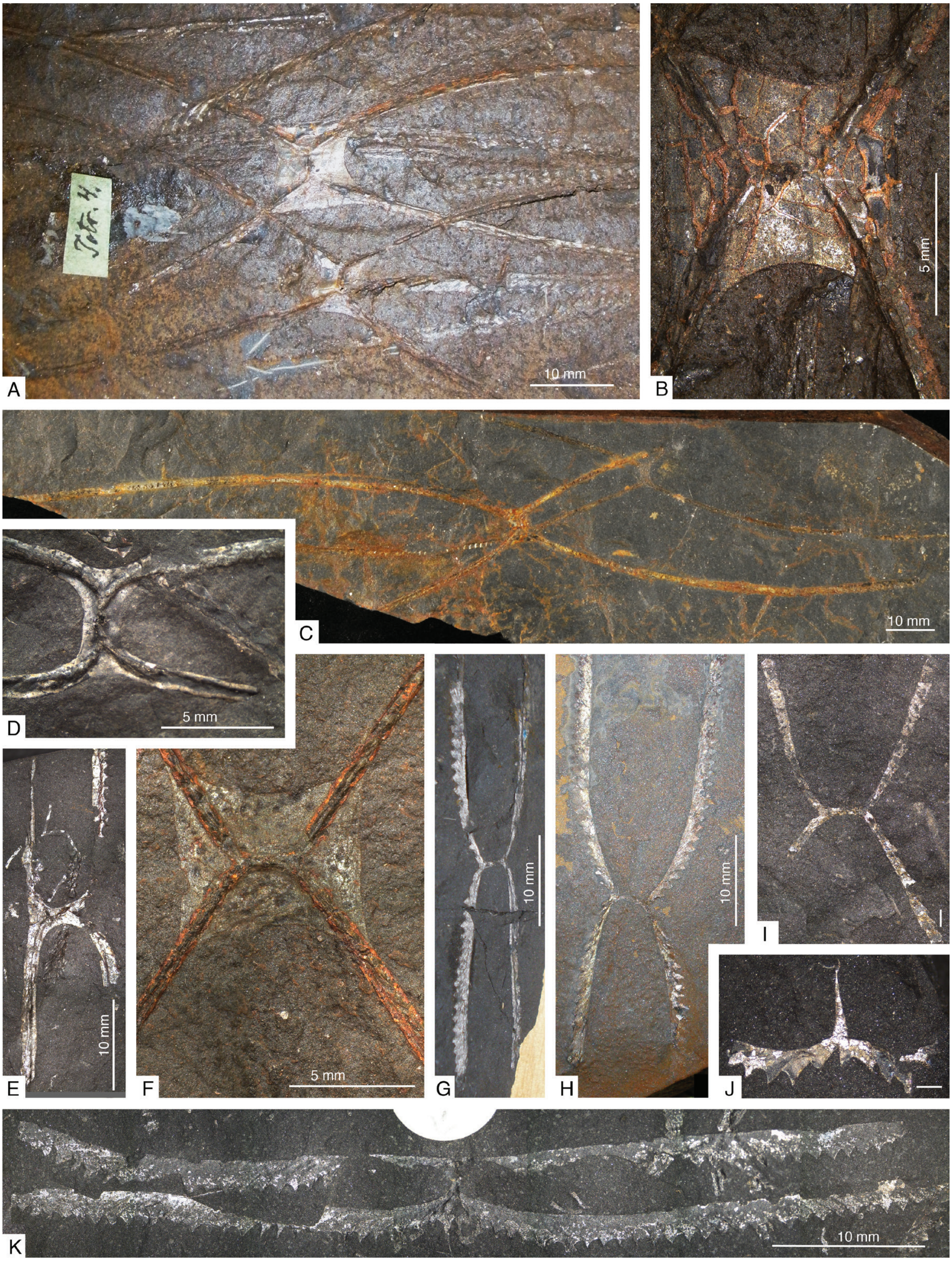

Fig. 32. **A–C**, **F, I, J**. *Paratetragraptus vestrogothus* Törnquist, 1904. **A**, **B**, LO 1707T, syntypes and proximal end of lower specimen (**B**) in higher magnification. **C**, PMU 38474a, Diabasbrottet, 2.5–2.6 m, two associated large specimens, somewhat weathered. **F**, PMU 38475a, Mossebo, proximal end showing web, dotted shale surface indicates strong contact metamorphism. **I**, PMU 38488, Diabasbrottet, 2.5–2.6 m, slender specimen without web. **J**, PMU 38489, Diabasbrottet, 2.5–2.6 m, proximal end in lateral view. **D**, **E**, **G, H, K**. *Paratetragraptus approximatus* (Nicholson, 1873). **D**, RM Cn 1546, proximal end showing small web. **E**, PMU 38476b, poor specimen, Mossebo. **G**, RM Cn 1549. **H**, RM Cn 1700, coll. G. Holm, det. *Tetragraptus parabolicus* by Holm on label (nomen nudum). **K**, PMU 38394/4, Diabasbrottet, 5.6–5.7 m.

A proximal web has not been described for *Paratetragraptus approximatus*, but a few specimens from Diabasbrottet show an indication of a proximal web structure (Fig. 32D, E). This proximal web is, however, small and extends as a fine rim around the first order stipes and also around the outer side of the initial part of the second order stipes. The development is not comparable with the extensive webs in the proximal ends of *Paratetragraptus vestrogothus*. VandenBerg (2017, fig. 8) illustrated a specimen as *Paratetragraptus acclinans* with an extensive, but poorly preserved web structure.

Paratetragraptus approximatus is an important index species for the base of the second stage of the Ordovician System, the Floian Stage (Berry 1998, Bergström *et al.* 2004). It has been described by Williams & Stevens (1988) based partly on isolated material and provided an extensive discussion. A number of specimens are illustrated to document the presence at Hunneberg. This is especially important as the FAD of this species at Diabasbrottet defines the base of the Floian Stage of the Ordovician System (Maletz *et al.* 1996; Bergström *et al.* 2004).

Paratetragraptus approximatus is one of the most characteristic faunal elements of the pandemic faunal association in the Floian at Hunneberg. Due to its long biostratigraphic range, its usefulness is restricted, but the FAD of the species is one of the few main 'golden spikes' in Ordovician stratigraphy. The species is usually rare in shelf faunas and occurs only sporadically. In the deeper shelf regions, however, it appears to be more persistently present. In Scandinavia it can be one of the dominant species in individual horizons, but is absent from long intervals, particularly so at Hunneberg (Egenhoff & Maletz 2000, 2001, 2007).

Paratetragraptus quebecensis (Ruedemann & Laverdière, 1935) and *Paratetragraptus lavalensis* (Ruedemann & Laverdière, 1935) are regarded as synonyms of *Paratetragraptus approximatus* and are astogenetic stages. The type material of these taxa is from the same general area where the type of *Paratetragraptus approximatus* was collected.

Williams & Stevens (1988) introduced *Paratetragraptus approximatus robustus* from western Newfoundland based having wider stipes. The subspecies has not been described subsequently and it is uncertain whether it can be separated at all or is an intraspecific variant.

Occurrence. – *Paratetragraptus approximatus* appears first at the base of the *Tetragraptus phyllograptoides* Biozone at Hunneberg and ranges into the *Baltograptus vacillans* Biozone at least. The species has a worldwide distribution and is commonly found in the lower Floian (Williams & Stevens 1988, VandenBerg 2017).

***Paratetragraptus vestrogothus* (Törnquist, 1904)**

Figures 29K, 32A–C, F, I, J

1904 *Tetragraptus vestrogothus* n. sp. Törnquist, p. 7, pl. 1, figs 13, 14.
?1937 *Tetragraptus* (*Etagraptus*) *laverdieri* nov. Ruedemann & Laverdière, p. 11, pl. 1, fig. 4.
?1937 *Tetragraptus* cf. *vestrogothus* Törnquist; Monsen, p. 158, pl. 11, fig. 3.
1968 *Tetragraptus* (*Paratetragraptus*) *akzharensis* n. sp. Tzaj, p. 496, pl. 5, fig. 5.
1987 *Eotetragraptus vestrogothus* (Törnquist); Maletz, p. 72, figs 20: 5, 7.
1988 *Tetragraptus akzharensis* Tzaj; Williams & Stevens, p. 36, pl. 2, fig. 1; pl. 8, fig. 2?; text-fig. 24A–K.
1997a *Tetragraptus akzharensis* Tzaj; Toro, pl. 2, figs 1, 3.
?1997b *Tetragraptus akzharensis* Tzaj; Toro, pl. 1, figs 4, 5.

Type material. – LO 1707T, a single slab with two specimens preserved in low relief, asssociated with numerous fragments (Fig. 32A), from Mossebo (Törnquist 1904), the modern Diabasbrottet locality. The specimens are here regarded as syntypes, but it is not necessary to designate a lectotype as both are clearly conspecific. The parallel orientation of the specimens with their long stipes indicates they are current-aligned. Additional graptolite species are not found on the slab to verify the age of the material.

Material. – Several specimens from the *Expansograptus protobalticus* to *Baltograptus vacillans* biozones of Diabasbrottet and Mossebo, Hunneberg.

Description. – The details of the proximal development are unknown, but juveniles (Fig. 32J) indicate a long, slender sicula, ca 2.5–2.8 mm, reaching an apertural width of 0.5 mm. A small rutellum may be present. The precise origin of th1^1 is not visible, but a 0.8 mm long free ventral side of the sicula indicates where th1^1 separates from the sicula. The stipes appear to reach their final width quickly after the growth of 2–3 thecae.

Most specimens are preserved in dorso-ventral view and the proximal end is covered by a characteristic, large proximal web in mature specimens (Fig. 32A, B). The A-B stipe pairs include an angle of about 110–130°, whereas 1-2 stipe pairs include an angle of 60–70°. The funicle length is 2.5–3.0 mm. In many specimens the sicula is visible as a small elevation or depression (Fig. 32B). The dorsal stipe width is about 0.8–1.0 mm. The lateral stipe width is 1.5–1.6 mm when thecae are shown in their true lateral aspect. The thecae are simple tubes, widening and curving distinctly towards their apertures, as is typical for dichograptid thecae. Their apertural inclination reaches 35–40°. Apertural rutella appear to be absent. A number of relatively slender specimens with stipes up to 20 mm long do not show any proximal web structure (Fig. 32I) and may indicate that the proximal webbing is developed only in gerontic specimens in this species. These specimens may easily be referred to another species unless the astogeny is not considered.

Remarks. – The new specimens collected at Hunneberg do not differ from Törnquist's (1904) types, except that they do not show the gentle stipe curvature of the type specimens. This character is based on a preservational aspect of the distally flexible stipes and should not be used as a diagnostic character of the species. The consistency of the angles between the second order stipes and the difference of this character with *Paratetragraptus approximatus* indicates that this is a distinct species. Proximal webs as found in *Tetragraptus vestrogothus* have never been discovered in mature specimens of *Paratetragraptus approximatus*, nor in *Paratetragraptus acclinans*. It is unclear at what stage in the astogeny of the species they are developed.

Paratetragraptus laverdieri (Ruedemann & Laverdière, 1937) differs by its more robust tubarium, but could be interpreted as a gerontic morph of this species. It was described from a single specimen.

Monsen (1937) described proximal ends of a similar tetragraptid as *Tetragraptus astericus* from an interval that was interpreted as the *Pseudophyllograptus densus* Biozone based on the associated fauna. However, this specimen may be considerably younger and a relationship with *Paratetragraptus vestrogothus* is uncertain.

There appears to be considerable confusion about the identification of *Paratetragraptus* specimens with stipes that are parallel (as in *Paratetragraptus approximatus*) and forms with more X-shaped stipe configurations as in *Paratetragraptus vestrogothus*. Recently forms with more open shapes have been included in *Tetragraptus akzharensis* Tzaj, 1968, following Williams & Stevens (1988). *Paratetragraptus akzharensis* is here regarded as a synonym of *Paratetragraptus vestrogothus*. Web structures typical of large specimens from Scandinavia are rare and are unknown from Newfoundland material. However, specimens with and without webs, showing a considerable variation of final stipe width, seem to be restricted to a short time interval and show an intergradation that would allow them to be regarded as intraspecific variants of a variable species. Some specimens here referred to *Paratetragraptus approximatus* (cf. Fig. 32H) may show transitional forms to *Paratetragraptus vestrogothus*, but do not show any evidence of proximal web structures.

The distinction of *Paratetragraptus acclinans* Keble, 1920, originally described from Victoria, Australia, is based on the robustness of the stipes (see Williams & Stevens 1988, p. 35), but is similar to *Paratetragraptus akzharensis* in other respects. Both taxa are present in the *Paratetragraptus akzharensis* biozone in western Newfoundland, but *Paratetragraptus acclinans* first appears in the local *Paratetragraptus approximatus* Biozone. The specimen in Figure 32H could alternately be identified as *Paratetragraptus acclinans*, but it is here referred to *Paratetragraptus approximatus*.

Occurrence. – The species appears to be common in the lower part of the *Cymatograptus protobalticus* Biozone at Hunneberg, where it may be associated with *Cymatograptus rigoletto*, but has rarely been found elsewhere. A wider distribution of *Tetragraptus vestrogothus* may be indicated if *Tetragraptus laverdieri* from Lévis, Québec (Canada) is a synonym.

Genus *Tshallograptus* VandenBerg, 2017

Type species. – *Graptolithus fruticosus* Hall, 1858 from the lower Floian of Lévis, Québec, Canada; original designation.

Diagnosis. – Pendent to deflexed phyllograptids; proximal development isograptid, dextral; low prosicular origin of th1^1 in most taxa; crossing canals low on sicula; sicula long and slender, with mitre-shaped prosicula (slightly emended from Maletz *et al.* 2018b, p. 15).

Species. – *Graptolithus fruticosus* Hall, 1858; *Didymograptus Pantoni*? Etheridge, 1874; *Didymograptus flagellifer* Törnquist, 1901; *Bryograptus simplex* Törnquist, 1904; *Tetragraptus pendens* var. *praesagus* Törnquist, 1904; *Tetragraptus fruticosus* var. *campanulatus* Ruedemann, 1904; *Tetragraptus fruticosus* var. *tubiformis* Ruedemann, 1904; *Tetragraptus fruticosus* var. *distans* Monsen, 1937; *Tshallograptus tridens* VandenBerg, 2017; *Tshallograptus cymulus* VandenBerg, 2017; *Tshallograptus furcillatus* VandenBerg, 2017.

Remarks. – VandenBerg (2017) erected the genus *Tshallograptus* for the *fruticosus* group of tetragraptids from the Floian, Lower Ordovician. Earlier workers had placed the *fruticosus* group in *Pendeograptus* Bouček & Příbyl (1952) with *Tetragraptus pendens*

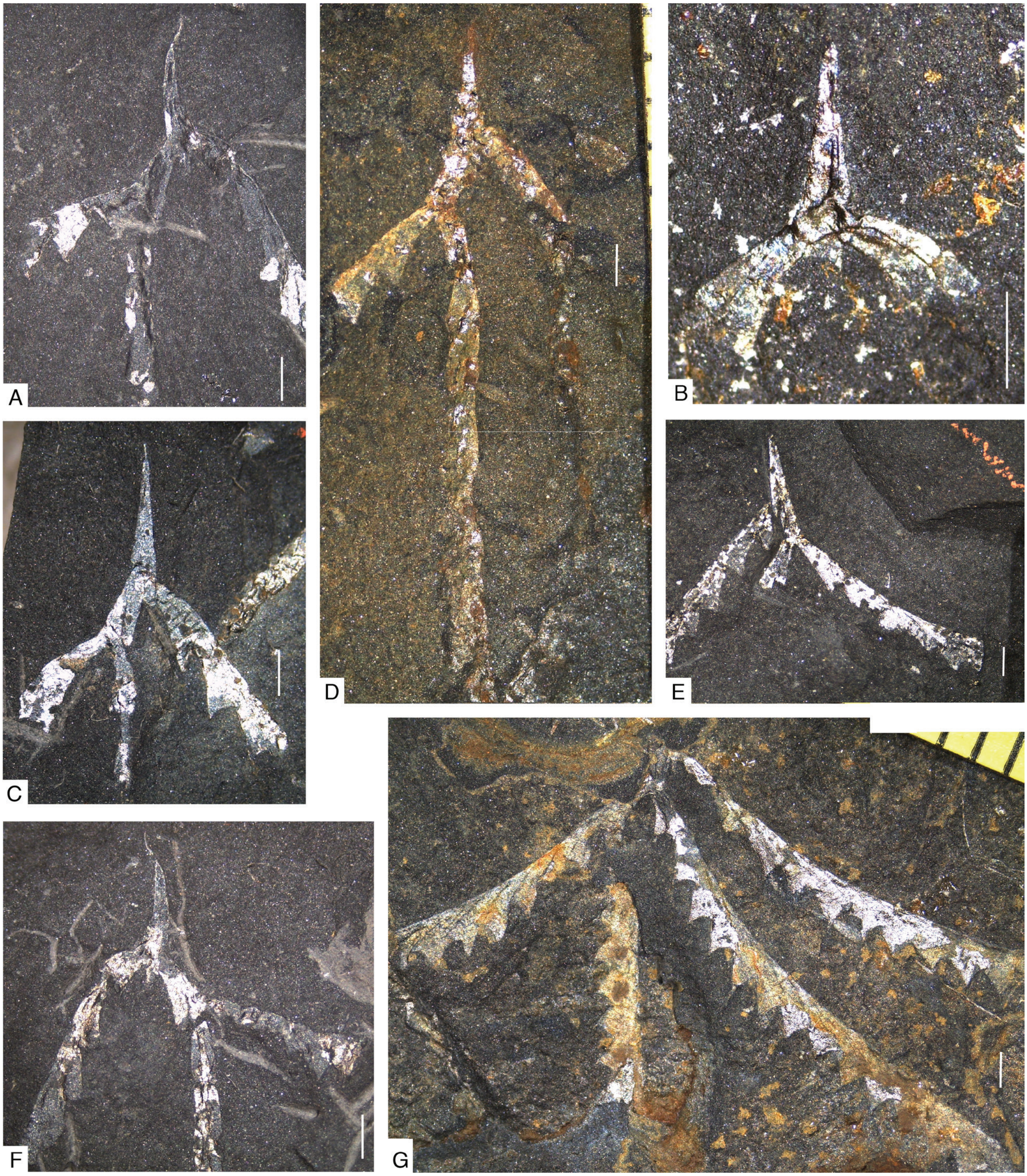

Fig. 33. *Tshallograptus simplex* (Törnquist, 1904). **A**, LO 1700t, lectotype, Mossebo (Diabasbrottet). **B**, PMU 38477, low relief proximal end showing isograptid development, Diabasbrottet, 1.0–1.1 m. **C**, RM Cn 1801, small specimen showing three stipes, Mossebo (Diabasbrottet), coll. G. Holm, 1877. **D**, RM Cn 1146, incomplete specimen with one long stipe preserved, Mossebo (Diabasbrottet), coll. G. Holm, 1879. **E**, RM Cn 1137, specimen showing slender, declined stipes, Mossebo (Diabasbrottet), coll. G. Holm, 1877. **F**, LO 1698t, counterpart of LO 1700t, lectotype. **G**, RM Cn 1800, specimen with long, deflexed stipes, Mossebo (Diabasbrottet), coll. G. Holm, 1877. Scale bars indicate 1 mm.

Elles, 1898 as the type species, which was problematic as *T. pendens* is poorly known. Cooper & Fortey (1982, p. 210) considered that the type specimen of *Tetragraptus pendens* Elles was too poorly preserved to derive a definition of the genus *Pendeograptus*. Williams & Stevens (1988) discussed the species and suggested that *Pendeograptus pendens* might have a different proximal development from the *fruticosus* group. They designated BM (NH) Q37 (Elles 1998, fig. 13, left-hand specimen) as the lectotype of *Pendeograptus pendens* and re-illustrated the specimen. They discussed its possible age and the synonymy with *Pseudobryograptus cumbrensis* (Elles, 1898). The lectotype is from Barf, northern England, which is also the type locality of *Pseudobryograptus cumbrensis*.

With the possibility that *Pendeograptus pendens* and *Pseudobryograptus cumbrensis* are conspecific, the assigment of *Graptolithus fruticosus* Hall, 1858 to the genus *Pendeograptus* remained tentative. VandenBerg (2017) therefore introduced the new genus *Tshallograptus* with *Graptolithus fruticosus* Hall, 1858 as its type species. Williams & Stevens (1988) described the proximal development of *Tshallograptus fruticosus* from chemically isolated material. It is of the isograpid type, dextral, with a low prosicular origin of th1^1 and a long, mitre-shaped prosicula. Maletz (2004) discussed Chewtonian material referred to the species and noted a metasicular origin of th1^1 in some of his specimens.

VandenBerg (2017) erected a number of new species from Victoria, Australia and separated the three-stiped specimens as *Tshallograptus tridens* VandenBerg, 2017. Their biostratigraphic distribution and usefulness must be investigated in more detail, as ranges are only known from the Victorian successions.

***Tshallograptus fruticosus* (Hall, 1858)**

Figures 29L, 34A, ?B, C

1858 *Graptolithus fruticosus* n. sp. Hall, p. 128.
1865 *Graptolithus fruticosus* n. sp. Hall, p. 90, pl. 5, figs 6–8, pl. 6, figs 1–3.
?1904 *Tetragraptus pendens* var. *praesagus* n. var. Törnquist, p. 5, pl. 1, figs 8–10.
1937 *Tetragraptus fruticosus* var. *distans* n. var. Monsen, p. 165, pl. 3 figs 22, 26, 32, 33; pl. 5, fig. 27; pl. 13, fig. 9.
1937 *Tetragraptus fruticosus* var. *campanulatus* Ruedemann; Monsen, p. 166, pl. 3, figs 20, 25, 36; pl. 4, fig. 4.
1937 *Tetragraptus fruticosus* var. *tubiformis* Ruedemann; Monsen, p. 167, pl. 3, figs 14, 15, 17, 19, 21; pl. 12, fig. 6.
1947 *Tetragraptus fruticosus* (Hall); Ruedemann, pp. 304, 305, pl. 51, figs 25–32.
1982 *Tetragraptus* (*Pendeograptus*) *fruticosus* (Hall); Cooper & Fortey, pp. 210–213, pl. 3, fig. 4; pl. 4, fig. 2; text-fig. 3a–f.
1988 *Pendeograptus fruticosus* (Hall); Williams & Stevens, p. 39 (cum syn), pl. 9, figs 3, 8–12; pl. 10, figs 5, 9–14; pl. 11, figs 1, 2, 6–7, 12; pl. 30, fig. 12; text-fig. 27A–U.
1992 *Pendeograptus fruticosus* (Hall); Williams, fig. 6A–C, V–X.
1994 *Pendeograptus fruticosus* (Hall); Maletz, p. 33, fig. 4H.
1997a *Pendeograptus fruticosus* (Hall); Toro, pl. 3, fig. 1.
1997b *Pendeograptus fruticosus* (Hall); Toro & Brussa, fig. 3a.
2017 *Tshallograptus fruticosus* (Hall); VandenBerg, p. 55 (with extensive synonymy list), figs 18I, 20–22, 25I–N.

Type material. – Lectotype GSC 926 (Hall, 1865, pl. 5, fig. 6), from 'Orleans Island, three miles above River St. Anne, Quebec', designated Williams & Stevens (1988, p. 39). There are actually two distinct localities that fit the label–Orleans Island is in the St. Lawrence River N of Québec City, while the 'three miles above the river St. Anne' locality is exactly three miles SW of St. Anne des Monts, Québec on the southern shore of the St. Lawrence River, a locality exposing strongly contorted Floian shales in a tidal platform exposure. It is unclear from which locality the specimen originated, as the species can be found in both localities.

Remarks. – A few poorly preserved specimens from Hunneberg can be referred to this species. They do not show much detail of the colony development and are not described here. Williams & Stevens (1988) provided a detailed description including chemically isolated proximal ends. Maletz (2004) illustrated and described additional chemically isolated material from the Chewtonian, probably from the uppermost biostratigraphic range of the species. This material shows the origin of th1^1 at various levels in the lower part of the prosicula and in the upper to middle part of the metasicula (Maletz 2004, figs 1A–C, 2A–I, K).

Törnquist (1904) described a very slender form as *Tetragraptus pendens* var. *praesagus* n. var. from the *Phyllograptus densus* Zone of Flagabro, Scania, southern Sweden (Fig. 34B, C). The type (LO 1703T) shows a very slender pendent colony with four stipes and a proximal end with a long sicula in obverse view. The specimen is largely flattened however, and details of the proximal development and branching of the stipes are not recognizable. As no associated faunal elements are known, its precise age is uncertain. The taxon is here regarded as a possible extreme variant of *Tshallograptus fruticosus*. It is only known from its type material.

Occurrence. – *Tshallograptus fruticosus* is rare in the Hunneberg sections and it is impossible to provide more information on the precise biostratigraphic range in the region. It can be found in the Bendigonian Be2 and Be3 of Australasia (VandenBerg 2017) and in the *Tshallograptus fruticosus* to *Didymograptellus bifidus* biozones of North America (Williams & Stevens

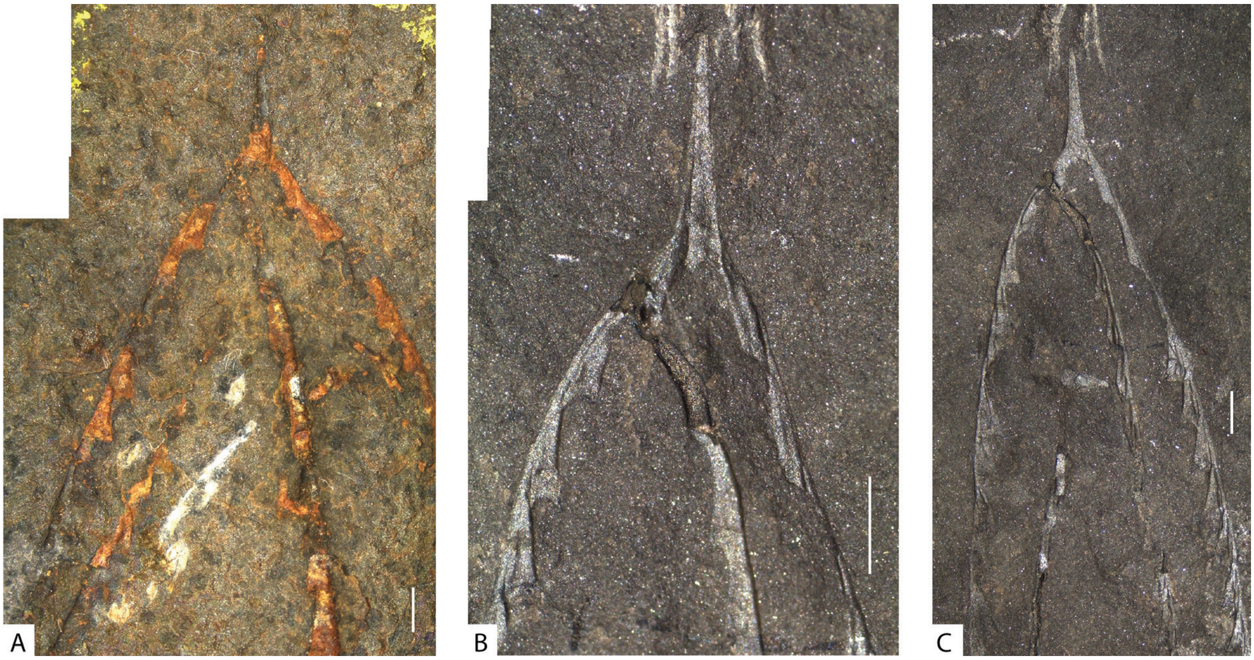

Fig. 34. *Tshallograptus fruticosus* (Hall). **A**. PMU 38411a, Diabasbrottet, specimen in contact metamorphous shale. **B**, **C**. *Tetragraptus pendens* var. *praesagus* Törnquist, 1904, LO 1703T, lectotype, Flagabro, Scania, Sweden. Scale bars indicate 1 mm.

1988). Monsen (1937) described several variants of *Tshallograptus fruticous* from her *Didymograptus validus* to *Phyllograptus angustifolius elongat*us biozones of the Oslo Region of Norway, including two new ones.

Tshallograptus simplex (Törnquist, 1904)

Figures 29A–D, 33A–G

1904 *Bryograptus simplex* n. sp. Törnquist, p. 3, pl. 1, figs 1–4.
?1935 ?*Bryograptus simplex* Törnquist; Benson & Keble, p. 270, pl. 30, figs 12–15.
2017 *Paratetragraptus cooperi* sp. nov. VandenBerg, p. 49, figs 11–12.

Type material. – Lectotype LO 1700t (Fig. 33A) and its counterpart LO 1698t (Fig. 33F), and paratype LO 1697T from the *Tetragraptus phyllograptoides* Zone of Mossebo (= Diabasbrottet), designated herein. All specimens are flattened early growth stages and show little detail. LO 1698t is the most complete and shows all relevant features for an identification.

Material. – Numerous specimens from the *Tetragraptus phyllograptoides* Biozone at Diabasbrottet and Mossebo, mostly proximal ends and fragmentary specimens, some preserved in partial relief.

Diagnosis. – Moderately declined four-stiped *Tshallograptus* with straight to somewhat deflexed stipes.

Description. – The tubarium is three- or four-stiped, with the second-order stipes reaching a length of at least 20 mm, but all available specimens may be fragmentary and the colonies may have been larger. The stipes are declined and widen gradually from 0.9–1.0 mm at the first thecae to distal widths of 1.5–1.7 mm, reached at the fifth or sixt theca. Distal stipes are parallel-sided. The proximal end shows a tetragraptid development with th3^1 and th3^2 as the first distal dicalycal thecae.

The sicula is about 2.2–2.8 mm long in laterally preserved proximal ends. It widens gradually from the apex to the aperture from 0.2 mm at the prosicula to ca 0.5 mm at the aperture. The supradorsal part of the sicula and th1^1 form a slender cone, 1.8 mm long and 0.5 mm wide at the base. The aperture of the sicula is nearly straight and a ventral rutellum is barely visible. A short nema is visible in many specimens, but appears not to be extended or thickened. The proximal development is isograptid, dextral in all specimens in which the development was visible (Fig. 33B). Th1^1 has a possibly prosicular origin at 0.2–0.3 mm below the tip of the sicula. Th1^1 runs down along the sicula as a slender, gradually widening tube and bends outwards at about 0.3 mm above the sicular aperture. The crossing canal of th1^2 is about 0.3 mm wide, while the crossing canal of th2^1 is only 0.1–0.15 mm wide. The ventral sides of the crossing canals form a wide arch below which the apertures of the sicula and th1^1 are visible (Fig. 33B), the ventral sides of which form a very short suture between them (cf. isograptid suture of Maletz 1994).

Remarks. – The species has originally been referred to the genus *Bryograptus* based on its pendent or declined habit. The proximal end development and the lack of bithecae clearly indicate the relationship with *Tshallograptus* and its proximal end is difficult to separate from those of *Tshallograptus fruticosus*.

Occurrence. – *Tshallograptus simplex* occurs in the *Tetragraptus phyllograptoides* Biozone of Diabasbrottet. Little is known of its wider distribution. However, *Tshallograptus cooperi* (Vandenberg, 2017) is here regarded as a synonym of *Tshallograptus simplex* as it is very similar. The proximal end is identical to that of other *Tshallograptus* species, which warrants its inclusion in *Tshallograptus*. *Tshallograptus cooperi* is restricted to the Australian La3 *Paratetragraptus approximatus* Biozone, correlatable to the *Tetragraptus phyllograptoides* Biozone of Scandinavia. The record of this species in Australia indicates that the taxon might be quite widely distributed, even though it has rarely been described. Material described by Benson & Keble (1935) consists of proximal ends with more slender stipes and may not belong to *Tshallograptus simplex*.

Genus *Corymbograptus* Obut & Sobolevskaja, 1964

Type species. – *Didymograptus v-fractus* Salter, 1863 from the middle Skiddaw Slates of Keswick, Lake District, England; original designation, Out & Sobolevskaya (1964, p. 27). As the original of Salter's (1863) specimen is missing, BU 1005a from the Skiddaw Slates of Buttermere (Elles & Wood, 1901, pl. 2, fig. 10a) was regarded as the holotype of the species (Strachan 1996, p. 26) and was designated as the neotype by Rushton (2011).

Diagnosis. – Deflexed two-stiped phyllograptids with distally variably widening stipes; proximal development isograptid, dextral; low prosicular origin of th 1^1; crossing canals low on sicula; sicula long and slender as in *Tshallograptus* with mitre-shaped prosicula (slightly emended from Maletz *et al.* 2018b, p. 15).

Species. – *Didymograptus retroflexus* Perner, 1895; *Corymbograptus retroflexus maximus* Bouček, 1973; *Didymograptus v-fractus* Salter, 1863; *Didymograptus v-fractus tullbergi* Monsen, 1937; *Didymograptus v-fractus scandinavus* Monsen, 1937; *Didymograptus v-fractus volucer* Nicholson, 1890; *Didymograptus v-fractus wieli* Legrand, 1964c; ?*Didymograptus v-fractus gigas* Robillard, 1935.

Remarks. – Maletz (1994) redefined the genus to include only deflexed didymograptids with a long, slender sicula and an isograptid proximal development with a prosicular origin of th1^1. Other deflexed species were included with the genera *Baltograptus* and *Xiphograptus*, based on differences in the sicular development, the proximal development and the presence of a dorsal virgellar spine in the latter.

The original specimen of *Corymbograptus v-fractus* (Salter, 1863, fig. 13e) has not been found and Rushton (2011) designated and illustrated a neotype from the Skiddaw Slates of Buttermere, Cumbria. It is preserved in partial relief, but is tectonically distorted. The proximal development can be interpreted to be of isograptid, dextral type with a high, possibly prosicular origin of th1^1, thus is comparable with relief specimens of *Corymbograptus* from Scandinavia. The specimen may be from the *Baltograptus jacksoni* Biozone (Rushton 2011, p. 321). *Corymbograptus v-fractus* or a closely related taxon has been recognized in eastern North America (Berry 1962; Maletz 1997a).

Corymbograptus has a fairly long range from the Floian *Baltograptus vacillans* Biozone to the Lower Darriwilian *Corymbograptus retroflexus* Biozone. The proximal development is known from relief specimens of *Corymbograptus v-fractus* (Elles & Wood 1901, text-fig. 21a, b) and *Corymbograptus v-fractus tullbergi* (Maletz 1994).

The proximal development of *Corymbograptus retroflexus* (Perner, 1895) has never been illustrated and decribed, but Bouček (1973) claimed it to be isograptid (*bifidus* stage). Specimens from the Sarka Formation preserved in full relief show an isograptid development with a high, most probably prosicular, origin of th1^1 (Fig. 35A). The sicula is about 2.2–2.3 mm long and at least 0.4 mm wide at the aperture. The origin of th1^1 is 0.3 mm below its apex and the ventral side of the crossing canals is at 0.6 mm above the sicula aperture, a considerably higher position than the crossing canals in *Tshallograptus* and *Corymbograptus* (ca 0.3 mm), casting some doubt on the inclusion of *C. retroflexus* in *Corymbograptus*. The proximal development of other taxa from the Upper Dapingian to Lower Darriwilian is unknown.

Occurrence. – The genus is widely distributed in the Floian to early Darriwilian from Bohemia, France, Britain, Scandinavia to Morocco and even eastern North America. The Scandinavian material is largely Floian (Törnquist 1901; Monsen 1937), but Zalasiewicz

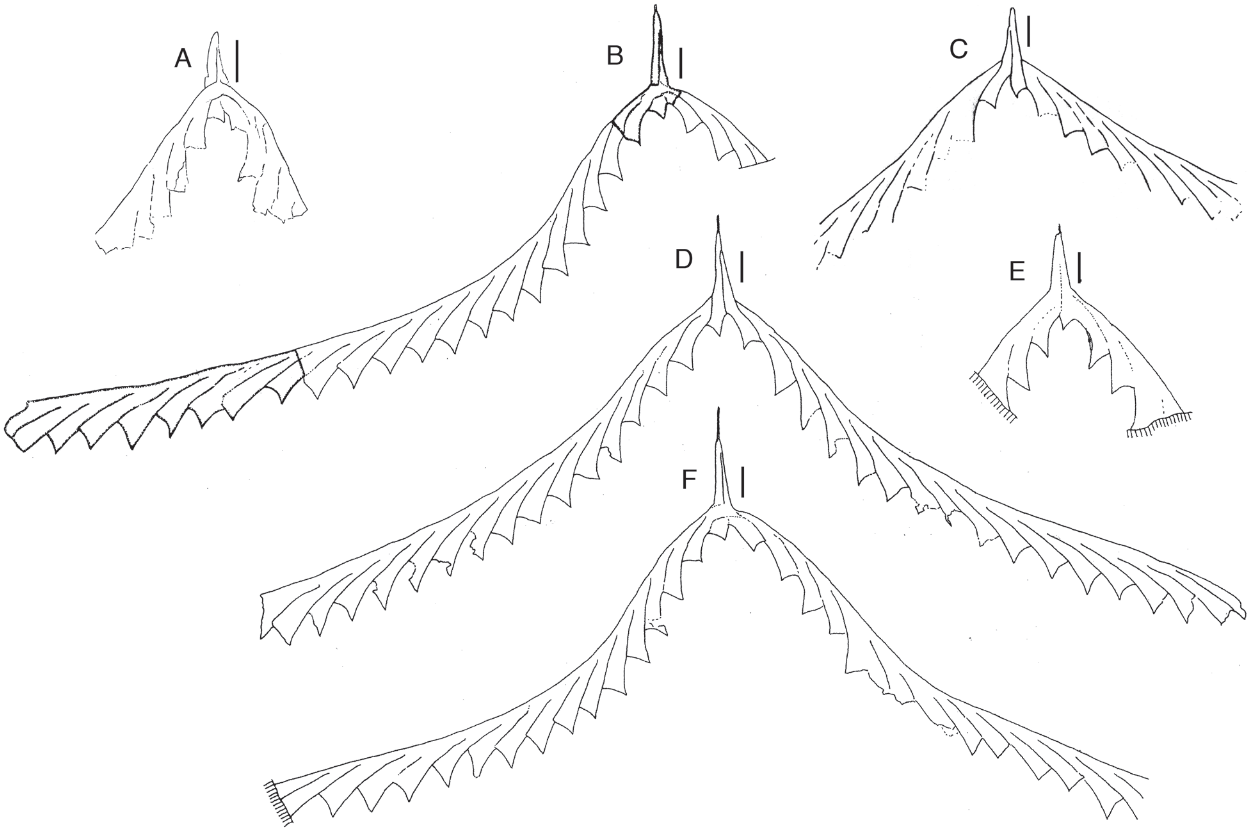

Fig. 35. Corymbograptus retroflexus (Perner, 1895). **A**, Kraft 5419, Drahous, Czech Republic, coll. P. Kraft, proximal end in reverse view. **B–F**. *Corymbograptus v-fractus tullbergi* (Monsen, 1937). **B**, PMO K 498, holotype, relief in reverse view. **C**, PMU 38.412, proximal end in partial relief, obverse view, Diabasbrottet at 6.8–6.9 m. **D**, PMO 59.957, relief, obverse view. **E**, PMO K 498-2, flattened proximal end. **F**, PMO K 484, holotype, counterpart, drawing of latex cast in reverse view. Scale bar is 1 mm close to each specimen.

et al. (2009) indicated that the British *Corymbograptus v-fractus volucer* was found in the Dapingian *Isograptus gibberulus* Biozone and *Corymbograptus v-fractus* is questionably from the '*Didymograptus*' *simulans* Biozone, Dapingian. Maletz (1997) illustrated a single specimen of *Corymbograptus v-fractus* from the *Didymograptellus bifidus* Biozone of Québec, Canada. The Czech material of the *Corymbograptus retroflexus* species-group appears in the early Darriwilian (Bouček 1973), while *Corymbograptus v-fractus wieli* from Morocco (Legrand 1964) appears to be from the Dapingian ('Uper Arenig').

Corymbograptus v-fractus tullbergi (Monsen, 1937)

Figures 35B–F, 36B, C, F, G, 37C, D, I

1937 *Didymograptus v-fractus* Salter var. *tullbergi* n. var. Monsen, p. 144, pl. 3, figs 12, 16, 23; pl. 9, fig. 3; pl. 10, figs 9, 10.
1994 *Corymbograptus v-fractus tullbergi* (Monsen); Maletz, p. 35, text-fig. 4e–g.
1996b *Corymbograptus v-fractus tullbergi* (Monsen); Maletz, figs 1I, 3E.
1996b *Corymbograptus* (?) *vicinatus* (Törnquist); Maletz, fig. 3B.

Type material. – Holotype PMO K 0484 and PMO K 0498 (counterparts) (Monsen, 1937, pl. 3, fig. 16; pl. 10, figs 9, 10), probably from the *Pseudophyllograptus densus* Biozone of the Galgeberg locality in the city of Oslo, Norway, collected by Otto Herrmann.

Material. – Several specimens from Diabasbrottet and Mossebo.

Remarks. – Monsen (1937) described the species in some detail. Maletz (1996b, fig. 1i) illustrated the holotype from the drawing of a latex cast, showing the proximal development in detail and also illustrated a second specimen in obverse view (Maletz, 1996b, fig. 3e) from Ensjö, Oslo Region.

Corymbograptus v-fractus tullbergi has a slender deflexed colony with little distal widening of the stipes. The sicula is 3.1–3.6 mm long and slender with

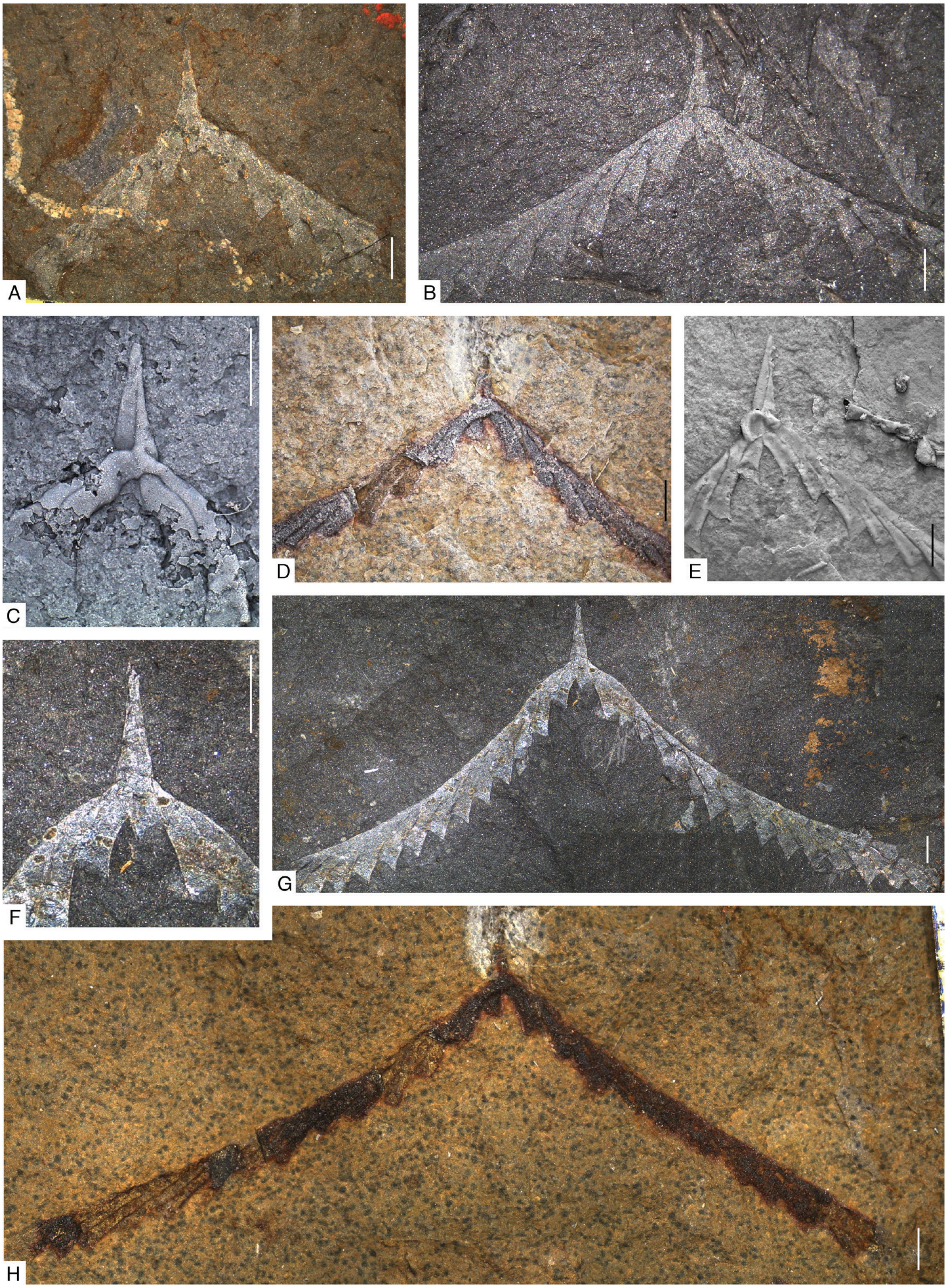

Fig. 36. **A**, **D, E**, **H**. *Corymbograptus vicinatus* (Monsen, 1937). **A**, PMU 38413, poor proximal end. **D**, **H**, PMU 38414, 'skeletal' specimen in metamorphic shale, partially preserved proximal end in reverse view, showing isograptid, dextral development (**D**) and low inclined thecae with high overlap. **E**, LO 1626t, latex cast of reverse view, showing distortion of proximal development, Mossebo (*Didymograptus balticus* in Törnquist, 1901, pl. 2, fig. 24). **B**, **C**, **F**, **G**. *Corymbograptus v-fractus tullbergi* (Monsen, 1937). **B**, LO 1625t, flattened specimen, Mossebo (*Didymograptus balticus* of Törnquist, 1901, pl. 2, fig. 23). **C**, PMU 23168, latex cast in reverse view, Diabasbrottet at 4.1–4.2 m (identified as *Expansograptus* sp. by Maletz *et al.* 2018b, fig. 15.1). **F**, **G**, RM Cn 1364, flattened specimen in obverse view showing contact metamorphous growth of minerals, Mossebo, coll. G. Holm, 1879. Scale indicated by 1 mm long bar in each photo.

a low position of the crossing canals. A short nema is present. The proximal development is isograptid, dextral and does not differ from that of *Tshallograptus fruticosus*. The origin of th1^1 is about 0.3–0.4 mm below the apex of the sicula and may be in the lowermost part of the prosicula.

Occurrence. – *Corymbograptus v-fractus tullbergi* occurs in the *Baltograptus vacillans* Biozone of Diabasbrottet (Egenhoff & Maletz 2007) and in the *Baltograptus vacillans* and *Baltograptus* sp. cf. *Baltograptus deflexus* biozones of the Lerhamn drill core. It seems to be rare at Hunneberg where it occurs in the upper, strongly contact-metamorphosed shales. Monsen (1937) reported the species from *Corymbograptus balticus* and *Pseudophyllograptus densus* biozones of the Tøyen Shale Formation in the Oslo Region, where specimens show excellent preservation in full relief. *Corymbograptus v-fractus tullbergi* is widely distributed in the Floian of Scandinavia and can be common at many levels. Proximal ends are easily mistaken for juveniles of *Tshallograptus fruticosus* or may be misidentified as *Corymbograptus vicinatus*. There appears to be a gradual change from the more declined *Corymbograptus vicinatus* to the deflexed *Corymbograptus v-fractus tullbergi* in the *Baltograptus vacillans* Biozone, making the differentiation of these species difficult as intermediates are not uncommon.

Corymbograptus vicinatus (Monsen, 1937)

Figures 36A, D, E, H, 37A, B, E–H, J

1901 *Didymograptus balticus* Tullberg; Törnquist, p. 12, pl. 2, figs 21–25 (LO 1623t–1627t).
1937 *Didymograptus balticus* var. *vicinatus* n. var. Monsen, p. 141, pl. 3, figs 28, 37; pl. 10, figs 1, 3, 4.
non 1996b *Corymbograptus* (?) *vicinatus* (Törnquist); Maletz, fig. 3B (= *Corymbograptus v- fractus tullbergi*).

Type material. – Lectotype PMO K 0467, from the *Didymograptus balticus* Biozone (= *Baltograptus vacillans* Biozone herein) of Galgeberg, Oslo, Norway, designated by Monsen (1937, p. 141, pl. 3, fig. 28; pl. 11, fig. 1).

Material. – LO 1623t (Törnquist 1901, pl. 2, fig. 21: Diabasbrottet), LO 1625t (Törnquist 1901, pl. 2, fig. 23: Flagabro), LO 1626t (Törnquist 1901, pl. 2, fig. 24: Diabasbrottet), LO 1627t (Törnquist 1901, pl. 2, fig. 22: Diabasbrottet) and additional new material from the Diabasbrottet and Mossebo localities.

Description. – The tubarium has two moderately declined, sometimes slightly proximally deflexed stipes with a stipe width of 1.1–1.3 mm across the first thecal pairs and 1.5–1.7 mm distally. The 2TRD is 1.8–2.1 mm proximally and reaches 1.9–2.1 mm distally (measured at th10–12). The final length of the stipes is unknown. The sicula is 2.9–3.2 mm long and slender with the origin of th1^1 about 0.3 mm below its apex. The supradorsal part of the sicula and th1^1 is up to 1.8 m long and forms a slender cone. The crossing canals are robust and directed obliquely downward. The isograptid suture below the isograptid arch is 0.2–0.3 mm long. The free ventral side of the sicula is 0.5–0.7 mm long. The thecae are slender tubes, gradually widening towards the aperture, showing ca 2/3 overlap and an inclination of about 25°. The apertures appear straight or may be provided with a short, broad rutellum that is exaggerated by flattening.

Remarks. – The species differs from the very similar *Corymbograptus v-fractus tullbergi* by its less deflexed stipes and the longer free ventral side of the sicula. Poorly preserved specimens may be difficult to differentiate and intermediate forms are common. The available material does not show all details of the proximal development neccessary for confident identification. A single relief specimen from Diabasbrottet (Fig. 36E) is preserved as a mould in partial relief, but shows distortion in the proximal end. The curved structure visible in the specimen may represent a parasitic feature or an epibiont (cf. Cooper *et al.* 2017). The specimen clearly exhibits the long free ventral part of the sicula and the isograptid proximal development. The development is similar to the proximal development of the genus *Cymatograptus* and the species might have to be transferred to the latter genus when better known.

Törnquist (1901) described the species from a number of specimens from Diabasbrottet, but identified it as *Didymograptus balticus*. *Cymatograptus balticus* (Tullberg, 1880) has a distinctly longer sicula and can therefore be easily separated. Both species overlap considerably in their biostratigraphic ranges.

Occurrence. – Egenhoff & Maletz (2007) reported *Corymbograptus*(?) *vicinatus* from the upper part of the *Cymatograptus protobalticus* and the *Baltograptus vacillans* biozones of Diabasbrottet. The species is widely distributed in southern Scandinavia, but has not been discovered outside this region.

Genus *Pseudophyllograptus* Cooper & Fortey, 1982

Type species. – *Phyllograptus angustifolius angustifolius* J. Hall, 1858 from the early Darriwilian

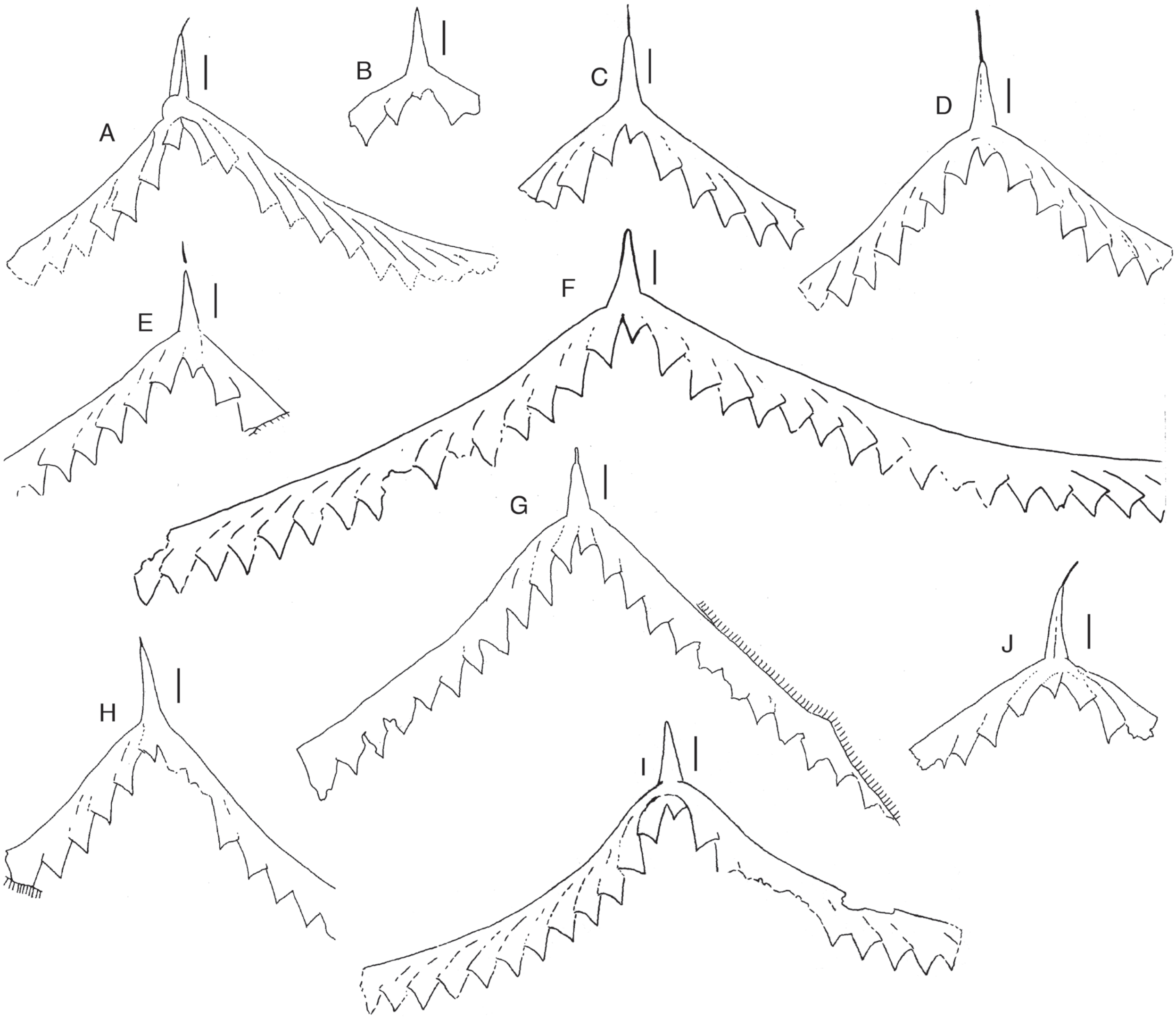

Fig. 37. **A**, **B**, **E–H**, **J**. *Corymbograptus vicinatus* (Monsen, 1937). **A**, LO 1626t, drawing from latex cast. **B**, PMO K 467-2, paratype (unfigured, on slab with holotype). **E**, MBg Di 47/01. **F**, MBg Di 30/08. **G**, PMO 60.363, paratype. **H**, PMO K 467-4, paratype (unfigured, on slab with holotype). **J**, PMO K 467-3, paratype (unfigured, on slab with holotype). **C**, **D**, **I**. *Corymbograptus v-fractus tullbergi* (Monsen, 1937). **C**, MBg Di 23/04. **D**, MBg Di 31/15. **I**, MBg Di 30/01. Scale bar close to each specimen indicates 1 mm.

(?*Levisograptus austrodentatus* to *Holmograptus lentus* Biozone: Maletz, 1997a) of Lévis, Québec, Canada; original designation.

Diagnosis. – Phyllograptids with four stipes united along dorsal margins, producing a cruciform cross section; median septa cruciform, imperforate; proximal development isograptid, dextral (Maletz *et al.* 2018b, p. 15).

Remarks. – Cooper & Fortey (1982) erected the genus *Pseudophyllograptus* for phyllograptids with an imperforate median septum, initial thecae distally inclined or horizontal and a sicula lacking a rutellum ('lack of the virgella'). They referred a number of species from Scandinavia to this genus, including the species *Phyllograptus angustifolius elongatus* Bulman, 1931 and *Phyllograptus densus* Törnquist, 1879. They referred an additional six taxa to their new genus, including the new *Pseudophyllograptus angustifolius chors*, of which some specimens were chemically isolated. Mu *et al.* (2002) listed 26 species and subspecies of *Phyllograptus* and only three species of *Pseudophyllograptus* from China. More species may have been described from other regions and are in need of revision.

Numerous phyllograptid species may belong to this genus, but have in the past been referred to the genus *Phyllograptus* Hall, 1858. A list is not provided here as most are poorly known and need to be revised. Ruedemann (1947) listed thirteen species and subspecies in his compilation of North American graptolites.

The species of *Pseudophyllograptus* range from the Lower Floian (*Baltograptus vacillans* Biozone) to the Middle Ordovician (*Pterograptus elegans* Biozone) and are distributed worldwide. The oldest phyllograptids may be from the basal Bendigonian of Australasia (cf. VandenBerg & Cooper 1992). Cooper & Fortey (1982, fig. 3) suggested two maxima in the distribution of this genus, one in the Bendigonian and a second in the higher Castlemainian to Darriwilian. They postulated two independent origins of the pseudophyllograptid organizational type as they found a *Tetragraptus phyllograptoides*-type species (*Tetragraptus phyllograptoides triumphans* Cooper & Fortey, 1982) below the highest occurrence of *Pseudophyllograptus* in the lower Castlemainian. This occurrence cannot be correlated with the presence of *Tetragraptus phyllograptoides* at the base of the Floian and before the first appearance of the genus *Pseudophyllograptus*. As further species of the *Tetragraptus phyllograptoides* type are found in the *Didymograptellus bifidus* Biozone of Utah and Idaho, U.S.A. (*Pseudophyllograptus archaios*: Braithwaite, 1976) and *Pseudophyllograptus cor* (Strandmark, 1902) in the Lower Darriwilian (Strandmark 1902; Cooper & Lindholm 1985), the evolutionary relationships of the genera *Tetragraptus*, *Phyllograptus* and *Pseudophyllograptus* need to be investigated in more detail. Maletz *et al.* (2005) suggested that *Pseudophyllograptus archaios* (Braithwaite, 1976) is identical to *Tetragraptus phyllograptoides triumphans* Cooper & Fortey, 1982, as both appear in a generallly identical biostratigraphical interval and do not differ in the general outline of their tubaria. Maletz *et al.* (2018b) included all three mentioned genera in the family Phyllograptidae and considered the dorsal virgellar spine of *Phyllograptus typus* (see also Maletz 2004) as an independently evolved character, following the interpretation of Maletz (2010). A phylogenetic relationship to the Axonophorans (biserial graptoloids with a ventral virgella) and the Pterograptidae with a dorsal virgella was not considered to be likely.

The precise distribution of the presence of separate stipes or the central columella in the scandent phyllograptids (see Cooper & Fortey 1982: *Phyllograptus*, *Pseudophyllograptus*) is uncertain, as three-dimensionally preserved and preferably chemically isolated material would be needed to recognize these features.

***Pseudophyllograptus* sp.**

Figure 31H–J

cf. 1865 *Phyllograptus anna* n. sp. Hall, p. 124, pl. 16, figs 11–16.
1904 *Phyllograptus* cf. *anna* Hall; Törnquist, p. 14, pl. 2, fig. 13.
?1937 *Phyllograptus anna* (Hall); Monsen, p. 216, pl. 18, fig. 2.
cf. 1982 *Phyllograptus anna* Hall, 1865; Cooper & Fortey, p. 285, fig. 79a–d.

Material. – A few specimens from the *Baltograptus vacillans* Biozone at Diabasbrottet. One slab (Fig. 31J: LO 1727t) with specimens illustrated by Törnquist (1904) also shows a specimen of *Expansograptus holmi*.

Diagnosis. – Small pseudophyllograptid with oval outline; thecae slowly widening, with apertures perpendicular to the dorsal side of the stipes; rutella apparently short; proximal development unknown due to poor preservation.

Description. – All specimens are largely flattened, with outlines affected by weathering. The tubaria are small, about 6–8 mm long and 3.5 mm wide at the widest. The 2TRD is 3–3.5, but it is unclear whether this is representative in view of the dearth of specimens present. The sicula is not visible in any of the specimens and thus, the orientation of the specimens is arbitrary.

Remarks. – The Hunneberg material has previously been compared with *Phyllograptus anna* Hall, 1865, but may not be closely related. Cooper & Fortey (1982) re-illustrated the type material of *Phyllograptus anna* and selected GSC 938a (Hall, 1865, pl. 16, fig. 15) as the lectotype. They did not give the type locality, but assumed that it is Lévis, Québec, Canada, as they discuss the lack of biostratigraphic control of the Lévis section and referred to Raymond (1914) and an unpublished manuscript of Bulman. Hall (1865, p. 124), however, clearly stated that the specimens originated from a locality 'three miles above the River Ste. Anne', a tidal platform exposure near St. Anne des Monts, Québec. The locality has graptolites ranging from the *Tshallograptus fruticosus* Biozone to the *Didymograptellus bifidus* Biozone (Maletz 1992a). Hall (1865) also described *Expansograptus similis*, *Didymograptellus bifidus*, *Tshallograptus fruticosus* and a few other species from this often overlooked locality. Cooper & Fortey (1982, p. 286) considered the possibility that *Phyllograptus anna* represents juveniles of *Phyllograptus typus* or *Phyllograptus ilicifolius*, leaving the identity of this taxon in doubt.

Unfortunately, the faunal association of the types of *Phyllograptus anna* is unknown and a precise age cannot therefore be determined. However, *Phyllograptus typus* is present at the St. Anne des Monts locality supporting the idea that *Phyllograptus anna* is an early growth stage of *Phyllograptus typus*. This identification is supported by the recognition of an incipient virgellar spine in a specimen associated with the lectotype of *Phyllograptus anna* by Cooper & Fortey (1982, fig. 79b). Williams & Stevens (1988, fig. 3) indicated a possible range of *Phyllograptus typus* from the upper part of the *Paratetragraptus approximatus* Biozone to the *Isograptus victoriae victoriae* Biozone, but identifiable specimens apparently were only found in the *Pendeograptus fruticosus* Biozone to the *Isograptus victoriae lunatus* Biozone interval. As they did not illustrate or describe the older material, the cited range cannot be verified.

The Hunneberg material of *Pseudophyllograptus* sp. resembles the types of Hall's (1865) *Phyllograptus anna* in dimensions, but appears to be considerably older. It is here included in the genus *Pseudophyllograptus*, as there is no evidence of a virgellar spine or other characters typical of the genus *Phyllograptus*. The Scandinavian specimens may therefore not be related to *Phyllograptus anna*. *Pseudophyllograptus* sp. from Hunneberg may be one of the oldest phyllograptids. It is uncertain, if the size of the available material represents the total size range of the species or if all specimens may have to be regarded as immature.

Occurrence. – *Pseudophyllograptus* sp. occurs at a number of levels in the *Baltograptus vacillans* Biozone at Diabasbrottet, and is locally abundant. It has not been described from elsewhere in Scandinavia, except for a possible specimen from the *Pseudophyllograptus densus* Biozone at Slemmestad, Oslo Region, Norway (Monsen 1937).

Family Didymograptidae Mu, 1950

Diagnosis. – Two-stiped, pendent to horizontal, reclined, reflexed, and deflexed graptoloids; sicula conical, widening distinctly towards aperture, with small prosicula; thecae simple widening tubes; rutella present in derived taxa; thecae rarely complex or with prothecal folding; proximal development isograptid, dextral or derived artus-type (Maletz *et al.* 2018b, p. 17).

Remarks. – The family Didymograptidae Mu, 1950 has rarely been used in graptolite taxonomy, but Maletz (2014) revised the family and excluded the pterograptids, which have a dorsal virgellar spine. He regarded the Didymograptidae as a possibly monophyletic taxon and useful for including a number of two-stiped dichograptids united by their proximal development and simple thecal style. Nothing is known of the evolutionary origin of the Didymograptidae, but a number of two-stiped species occur in the late Tremadocian. *Kiaerograptus*, with two or more stipes (cf. Maletz *et al.* 2010), show a free, probably elongated apertural part of the sicula, and bithecae along the stipes. Maletz *et al.* (2018b) included *Kiaerograptus supremus* Lindholm, 1991a in the genus only with reservation, as the proximal end does not show a free pendent apertural portion and therefore is more similar to the younger expansograptid development. The species still has the plaited thecal overlap of the anisograptids with bithecae alternating on both sides of the stipes. Numerous species have been incorporated in the genera *Didymograptus* and *Expansograptus* and it is difficult to gain an overview on the validity of these, but a number of subgenera have been established subsequently (see Maletz *et al.* 2018b) in order to understand the taxonomy and evolution of this group. Mu *et al.* (2002) still listed all taxa under the genus name *Didymograptus*, but separated them into pendent (28 species), deflexed (17), declined (40), horizontal (53) and reflexed (6 species) habits, with a total of 144 species recorded from China.

Genus *Expansograptus* Bouček & Přibyl, 1952

Type species. – *Graptolithus extensus* Hall, 1858, probably from the Begin's Hill section at Lévis, Québec, Canada (see Maletz 1997a): original designation. Cooper & Fortey (1982) selected and illustrated a lectotype from Hall's original specimens (Hall 1865, pl. 2, fig. 12) (Cooper & Fortey 1982, fig. 40a).

Diagnosis. – More or less horizontal didymograptids with isograptid, dextral proximal development; proximal portion of sicula perpendicular to stipes; sicular and thecal apertures straight, without elaborations; origin of $th1^1$ low on prosicula; stipe width variable; crossing canals more or less symmetrically placed on sicula; crossing canal one is initially much wider than crossing canal two; length of isograptid suture variable (Maletz *et al.* 2018b, p. 21).

Included species. – *Graptolithus extensus* Hall, 1858; *Graptolithus constrictus* J. Hall, 1865; *Graptolithus similis* J. Hall, 1858; *Didymograptus suecicus* Tullberg, 1880; *Didymograptus holmi* Törnquist, 1901; *Didymograptus urbanus* Monsen, 1937. Numerous further species have been included in the genus *Expansograptus*, often based on poorly preserved material. They are not listed as their inclusion is largely uncertain and the species are in need of revision.

Remarks. – Cooper & Fortey (1982) redescribed the type material of *Graptolithus extensus* Hall, 1858 and provided an illustration of the lectotype. The specimen shows very little structural detail and its exact level of origin is unknown, making it difficult to compare with other specimens assigned to the species. The specimen is a slender expansograptid with a small, straight sicula and distinctly widening stipes and is here recognized to belong to a species illustrated as *Didymograptellus* sp. by Maletz (1994). The better preserved and well known extensiform taxa *Expansograptus suecicus* (Tullberg, 1880) and *Expandograptus urbanus* (Monsen, 1937) were used to demonstrate the tubarium development of the genus *Expansograptus* by Maletz *et al.* (2018b).

The species of the genus *Expansograptus* show many proximal end characteristics that can only be recognized in well-preserved relief specimens, making the taxonomy extremely difficult (Fig. 38). The geometry of the proximal end, the sicular inclination, the position of the isograptid arch, the orientation and development of the crossing canals all are important characters to differentiate the species (Maletz 1992a, 1996b). Many early expansograptids (Fig. 38B, F: *Expansograptus holmi*) have a nearly vertical sicula, but in younger species like *Expansograptus grandis* (Fig. 38D) the sicula is inclined. This is often difficult to measure due to the proximal reflection or deflection of the stipes, but the horizontal plane can generally be determined from the symmetrical stipe arrangement. The easiest way of determining the sicular inclination is to draw a line through its apex and the ventral tip of the sicular aperture as these points are most easily determined, and measure the inclination of this line to the horizontal plane (Figs 38B, D). The inclination of the sicula is impossible to determine in most tectonically distorted specimens.

The positions of the crossing canals can be measured as the distance of the highest point from the isograptid arch (see Cooper & Fortey 1982) to the tip of the sicula on the reverse side in relief specimens.

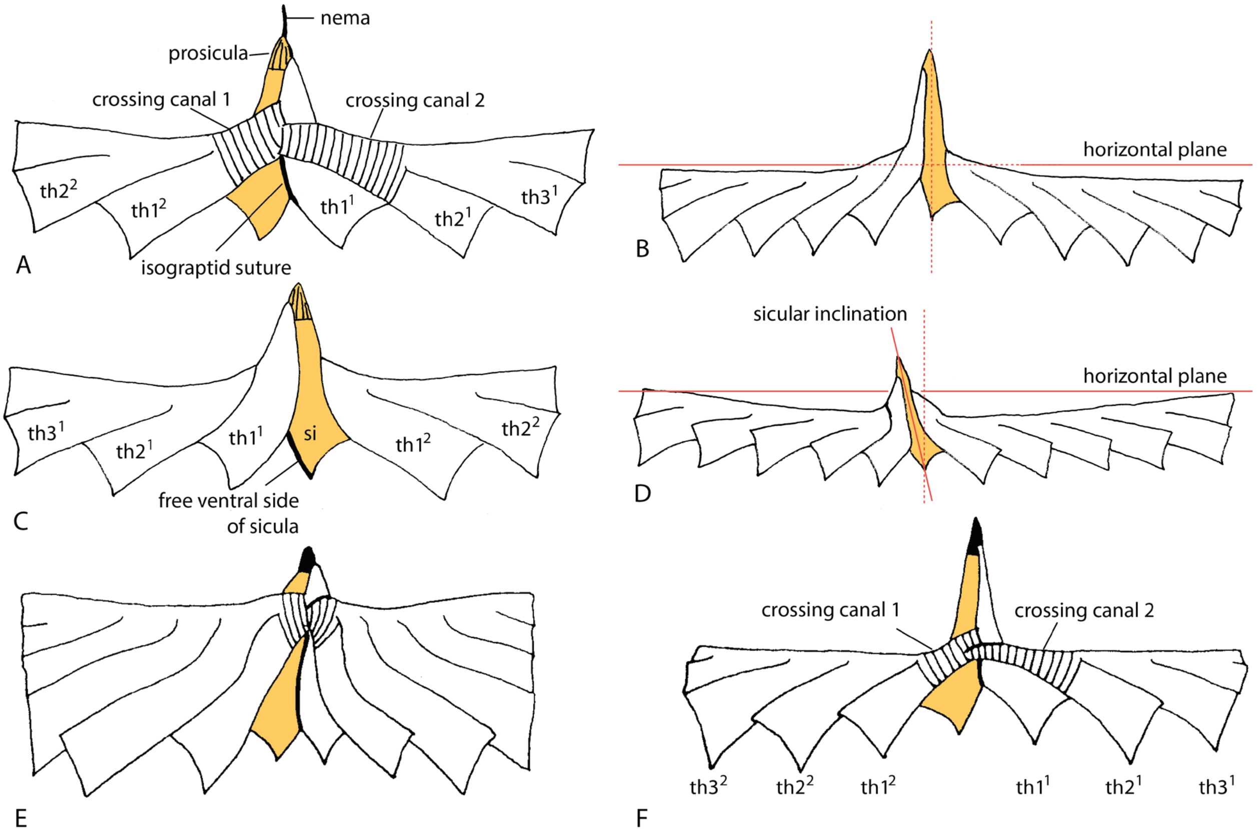

Fig. 38. Proximal end development of expansograptids showing thecal notation, position of crossing canals and measurement of sicular inclination. **A**, **C**. *Expansograptus suecicus* (Tullberg, 1880) in reverse (**A**) and obverse (**C**) views. **B**, **F**. *Expansograptus holmi* (Törnquist, 1904) in reverse (**F**) and obverse (**B**) views. **D**. *Expansograptus grandis* (Monsen, 1937), obverse view. **E**. *Expansograptus validus* (Törnquist, 1904), reverse view. Reconstructions not to scale. Sicula highlighted in color.

The length of the supradorsal part of the sicula and th1^1 can be characteristic for some species and easily measured. For example, in many *Expansograptus holmi* specimens this is long and slender whereas it is short and wide in *Xiphograptus lofuensis* (Maletz 2010).

Below the isograptid arch, the isograptid suture (Fig. 38A) can be seen on the reverse side. It also produces a useful character to define the position of the isograptid arch and its length is highly variable. An extremely long isograptid suture is present in *Expansograptus validus* (Fig. 38E), but in most taxa it is much shorter (Fig. 38A, F). The isograptid suture is absent or extremely short in *Baltograptus* (see Maletz 1994) and in many *Xiphograptus* species (see Maletz 2010).

Occurrence. – *Expansograptus* species are common in the Floian worldwide and may range into the Darriwilian. They first appear in the higher part of the *Cymatograptus protobalticus* Biozone at Hunneberg, but the precise FAD of the genus is uncertain. VandenBerg & Cooper (1992) indicated the presence of *Expansograptus similis* and *Expansograptus extensus* as the earliest expansograptids in the Lancefieldian (La3 *Paratetragraptus approximatus* Biozone) in Australasia, but did not illustrate specimens. A single specimen of ?*Expansograptus* sp. from the *Tetragraptus phyllograptoides* Biozone was found in the Törnquist collection.

Expansograptus extensus (Hall, 1858)

Figure 39A–I

	1858	*Graptolithus extensus* sp. nov. Hall, p. 132 (no illustration).
	1865	*Graptolithus extensus* Hall, 1858; Hall, p. 80, pl. 2, figs 11–16.
non	1901	*Didymograptus extensus* Hall; Törnquist, p. 14, pl. 1, figs 25–30 (= *Xiphograptus lofuensis*).
	1982	*Didymograptus extensus* (Hall, 1858); Cooper & Fortey, p. 231, fig. 40a–e, pl. 6.
	?1982	*Didymograptus* (*Expansograptus*) *praenuntius* Törnquist; Cooper & Fortey, p. 235, fig. 43a, b; pl. 4, fig. 12.
	?1988	*Didymograptus* (*Expansograptus*) *extensus* (Hall); Williams & Stevens, p. 44, text-figs 31I–K, 32, 33; pl. 14, fig. 18?
	1992	*Didymograptellus horizontalis* n. sp. Maletz, p. 155, figs 80/1–3, 81, 82 (in unpublished thesis).
	1994	*Didymograptellus* sp. Maletz, p. 40, fig. 7B, C, H (no description).
	1997a	*Didymograptellus* sp. Maletz, fig. 6i (no description).

Type material. – Lectotype GSC 976 and paratype GSC 979 from Point Lévis, Québec, Canada, designated Cooper & Fortey (1982, fig. 40d, e). These authors re-illustrated the specimens and discussed the species in some detail. They concluded that the species has strictly straight, horizontal stipes and that specimens from Britain and Scandinavia are most likely misidentified. The species has a wide distribution in low latitude regions during the *Tshallograptus fruticosus* to *Didymograptellus bifidus* time interval.

The lectotype (Fig. 39A–D) is a long tubarium in which the proximal end (the 'radicle' of Hall 1865) is preserved, but details of the development are not recognizable in the poor, flattened material. A rich fauna is associated on the slab, including *Dichograptus* sp., *Tshallograptus fruticosus, Phyllograptus illicifolius, Tetragraptus serra* and *Didymograptellus pennatulus*. Also, the specimen of Hall (1865, pl. 2, figs 15, 16), a small fragment, may be present on this slab, preserved in low relief, but the identity of this specimen remains uncertain. The paratype slab with GSC 979 (Fig. 39E, F) also bears *Phyllograptus illicifolius, Tshallograptus fruticosus* and *Tetragraptus serra*. Both slabs consist of grey to yellowish silty, probably dolomitic shale, indicating the origin from the *Tshallograptus fruticosus* Biozone or the *Phyllograptus typus* layers of the G-locality or from the Bégin's Hill section at Lévis, Québec (cf. Maletz 1997a, fig. 2).

The proximal end of the lectotype is poorly preserved. It shows a relatively small, slightly inclined sicula (Fig. 39a), but a sicula is not distinguishable in the paratype specimen (Fig. 39F). Hall's (1865) illustrations suggest that both specimens have a complete proximal portion but did not show the apertural part of the sicula, probably due to the incomplete understanding of the proximal development. This interpretation, however, was wrong.

Identity. – The species is difficult to identify, as additional specimens from Hall's collection from the type locality at Lévis were not available. Hall (1865) identified the type locality as 'Point Lévis', which probably means the locality known as the Bégin's Hill section. Maletz (1992a) illustrated a number of horizontal expansograptids with thecae having relatively low inclination as *Didymograptellus horizontalis* (Fig. 39G–I herein) from this locality and also illustrated the isograptid proximal development from this material preserved in partial relief. Maletz (1994, 1997a) identified this material as *Didymograptellus* sp.

Didymograptellus nitidus (Hall, 1858) appears in approximately the same biostratigraphic interval (Maletz 1997a, fig. 5), but shows a distinctly deflexed tubarium with more strongly widening stipes and a shorter and wider sicula (Fig. 39J).

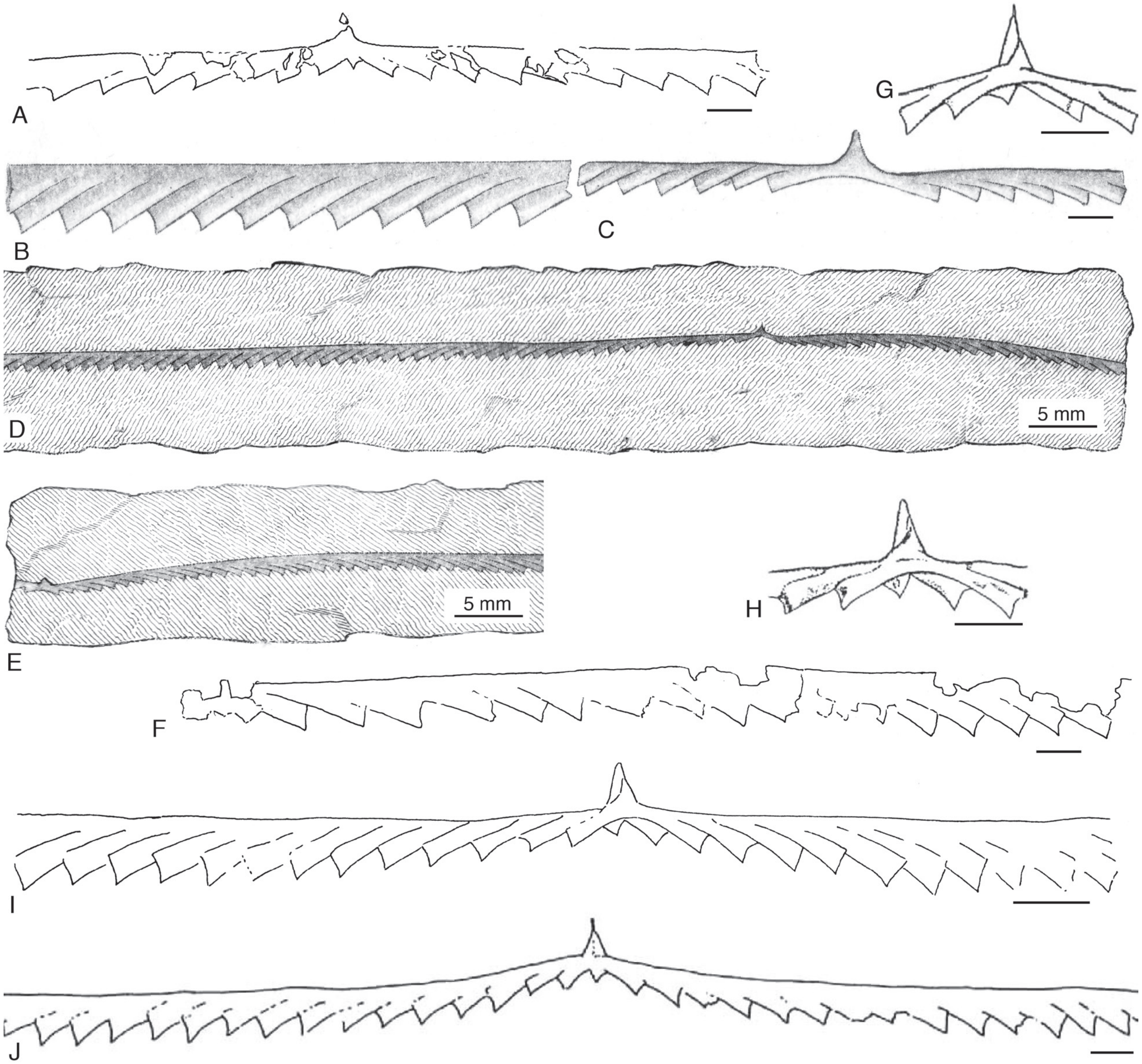

Fig. 39. Expansograptus extensus (Hall, 1858). **A–D**, GSC 976, lectotype. **A**, new drawing of proximal end. **B**, **C**, portions of Hall's drawings; **B**, distal end (Hall 1865, pl. 2, fig. 14). **C**, proximal end (Hall 1865, pl. 2, fig. 13). **D**, nearly complete specimen (Hall 1865, pl. 2, fig. 12). **E**, **F**, GSC 979, paratype, original illustration of proximal part (**E**) and new drawing (**F**). **G–I**, specimens from Québec. **G**, GSC 102569, reverse view in partial relief (Maletz 1992a, fig. 80-1). **H**, **I**, GSC 102568, specimen in partial relief, reverse view (Maletz 1992a, fig. 80-2). **J**, *Didymograptellus nitidus* (Hall, 1858), GSC 102574, flattened specimen with slightly deflexed stipes (Maletz 1994, fig. 7A). Scale bars 1 mm, unless otherwise indicated.

Remarks. – The species is discussed here only because it is important for the understanding of the concept of the genus *Expansograptus*. Törnquist (1901, p. 14, pl. 1, figs 25–30) illustrated a specimen of *Xiphograptus lofuensis* under the name *Didymograptus extensus* Hall. The species is similar in its general outline to species of the genus *Xiphograptus*, but differs by the absence of a virgellar spine.

Törnquist (1901) illustrated a number of specimens from the *Isograptus mobergi* Biozone (Maletz 2011: Törnquist's *Isograptus gibberulus* Biozone) at Killeröd, Scania as *Didymograptus extensus* Hall. The material (LO 1597t–1602t) includes unidentifiable stipe fragments, but not all specimens are identified in the type collection at Lunds University. LO 1598t (Törnquist 1901, pl. 1, fig. 26) is a specimen of *Xiphograptus lofuensis* (Lee, 1961), showing a dorsal virgellar spine (Figs 41L, 42K). There is no evidence that *Expansograptus extensus* occurs in Scandinavia.

?*Expansograptus* sp.

Figure 40B–D

Material. – PMU 38415/1, a single specimen from Mossebo (modern Diabasbrottet section), *Tetragraptus phyllograptoides* Biozone, coll. Törnquist.

Description. – The specimen is about 11 mm long, with each stipe having seven completed thecae before the growing end. The stipe width is about 0.9 mm, but the apertures of the proximal thecae appear to be slightly incompletely preserved. The sicula is ca 1.5–1.6 mm long and has a short nema ca 0. 5 mm long. However, this structure may alternately be interpreted as the cauda. The sicula is nearly vertical, curving only very slightly towards stipe 1 at the aperture. The thecal inclination is ca 30°. The thecal overlap is difficult to see due to the flattening of the specimen, but appears to be at about 50%. The supradorsal part of the sicula (without the nema) is 0.8 mm. The origin of th1^1 (orange in Fig. 40C) is approximately 0.3 mm below the apex of the sicula. The origin of the sicular bitheca (red in Fig. 40C) is 0.45 mm below the apex of the sicula. It grows downwards and slightly bends towards stipe 1, reaching a width of 0.2 mm. The position of the aperture is uncertain, as the apertural part of the fusellum of the proximal end of the specimen is broken off, leaving a faint imprint on the shale surface (Fig. 40D).

Remarks. – The specimen is from the lower part of the *Tetragraptus phyllograptoides* Biozone. It is associated with *Tetragraptus phyllograptoides* and *Cymatograptus undulatus* (Fig. 40E) on the slab, verifying the age. The slender specimen is flattened, but shows slight relief in the proximal end and is preserved in obverse view. It appears to have a prominent sicular bitheca between the sicula and th1^1 (Fig. 40C, D). If correctly identified, the specimen represents the earliest appearance of the genus *Expansograptus* in the Hunneberg region and probably worldwide. *Expansograptus* specimens appear in the higher part of the *Cymatograptus protobalticus* Biozone at Diabasbrottet and have not previously been found in the *Tetragraptus phyllograptoides* Biozone. Thus, a considerable biostratigraphical gap can be seen between these two occurrences of *Expansograptus*. The specimen is very similar in its outline to *Expansograptus suecicus* with its relatively short sicula (Fig. 40A). Altogether, *Expansograptus suecicus* is, however, somewhat more robust. Due to the flattening of the specimen, the details of the proximal development are unknown, even though an isograptid, dextral development can be interpreted. This is seen from the orientation of the sicula and th1^1 with the sicular bitheca in the center (Fig. 40C, D) on the obverse side of the colony and th1^1 on the left side of the sicula (cf. Maletz 2021, fig. 2). The specimen shows some similarities with *Cymatograptus demissus*, but the latter has a much longer supradorsal part of the sicula.

Occurrence. – The specimen is the earliest *Expansograptus*-type taxon. Slabs with graptolites from the *Tetragraptus phyllograptoides* Biozone are numerous and have been given close scrutiny, but this is the only specimen, showing that it is extremely rare.

***Expansograptus suecicus* (Tullberg, 1880)**

Figures 40A, 41A–K, M, N, 42L

1880 *Didymograptus suecicus* sp. nov. Tullberg, p. 43, pl. 2, figs 15, 16.
non 1901 *Didymograptus suecicus* Tullberg; Törnquist, p. 13, pl. 1, figs 19, 20, 22, 23. (=*Expansograptus grandis* (Monsen, 1937)).
?1901 *Didymograptus suecicus* Tullberg; Törnquist, p. 13, pl. 1, fig. 21 (specimen not identified in the LO type collection).
1937 *Didymograptus suecicus* Tullberg; Monsen, p. 104, pl. 1, figs 35, 36, 49; pl. 7, figs 6–8; pl. 9, fig. 13.
1937 *Didymograptus suecicus robustus*; Monsen, p. 105, pl. 1, fig. 44, pl. 8, fig. 1.
?1938 *Didymograptus asperus* n. sp. Harris & Thomas, p. 76, pl. 2, fig. 25a–c; pl. 4, fig. 23.
?1976 *Didymograptus suecicus* Tullberg; Tzaj, p. 227, pl. 2, fig. 1.
?1991 *Didymograptus asperus* Harris & Thomas; Rickards & Chapman, p. 76, pl. 22, fig. a; pl. 23, fig. f; text-figs 117, 118.
1996a *Expansograptus suecicus* (Tullberg); Maletz, p. 204, figs 1A, C, J–K; 3C, D.
2018 *Expansograptus suecicus* (Tullberg); Maletz & Ahlberg, fig. 8H (no description).

Type material. – Lectotype LO 353T, paratype LO 5643t (Tullberg 1880, figs 15, 16) from the Tøyen Shale of Kiviks-Esperöd, Scania, designated Maletz (1996a; explanation of Fig. 1) (Fig. 41A). The lectotype is flattened in a laminated grey to dark grey shale and does not show much proximal detail. A poor specimen of *Baltograptus vacillans* occurs on the counterpart slab.

LO 5643t (Fig. 41M) is preserved as a pyritic cast in relief in obverse view on a slab of laminated grey and dark grey shale and is associated with another poorly preserved flattened specimen of this species. Additional graptolites include poorly preserved flattened *Acrograptus filiformis* and *Baltograptus vacillans*. A pyrite-filled burrow and further indications of bioturbation are also present.

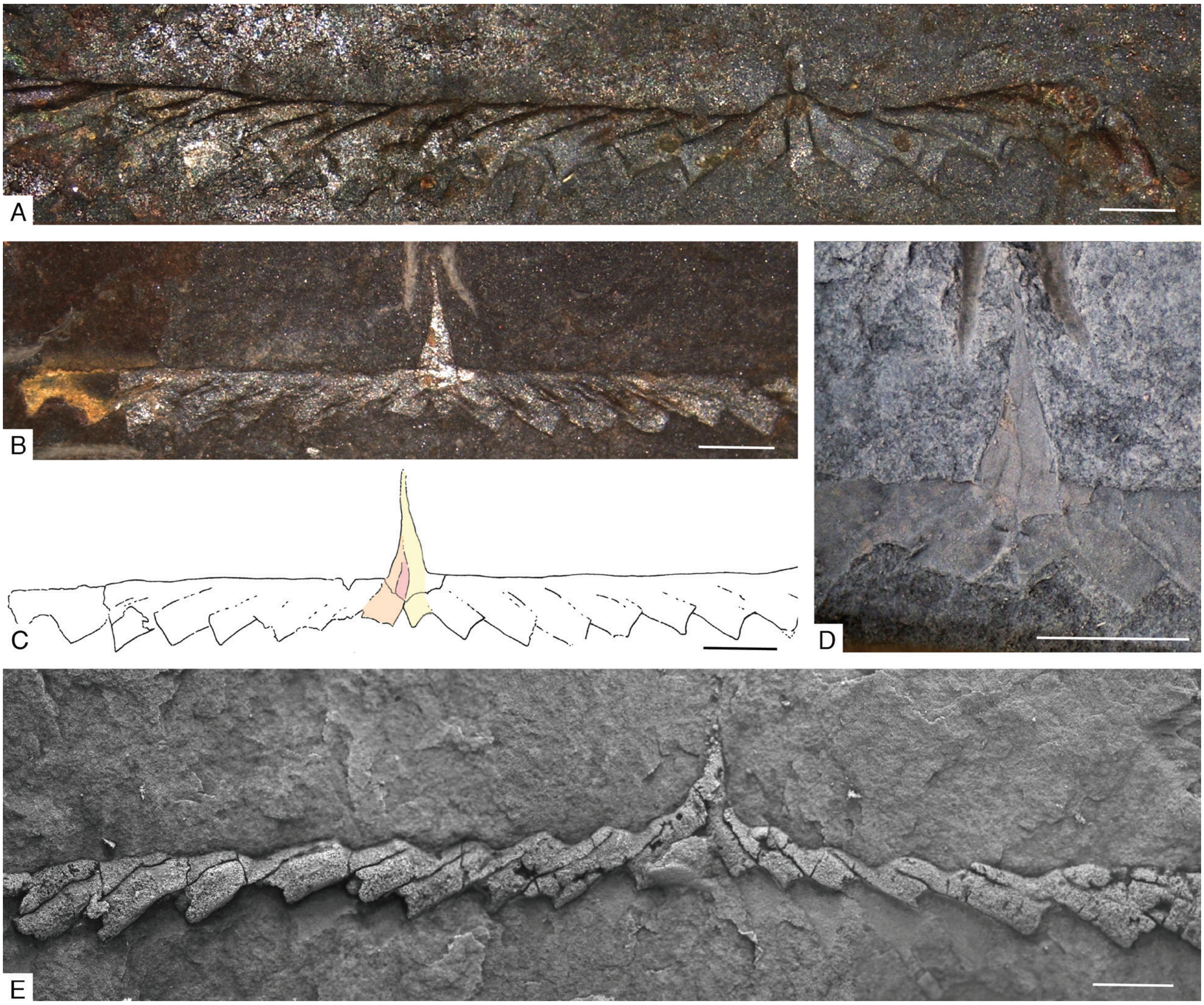

Fig. 40. Comparing early expansograptids. **A**, *Expansograptus suecicus*, PMU 038396/2, mould of specimen for comparison with ?*Expansograptus* sp. **B–E**. Graptolites on PMU 38415, Diabasbrottet, *Tetragraptus phyllograptoides* Biozone, Törnquist collection. **B–D**, ?*Expansograptus* sp., PMU 38415/1, low-relief specimen. **B**, photo. **C**, interpretation showing sicular bitheca in red. **D**, proximal end coated with ammonium chloride to show sicular bitheca. **E**, *Cymatograptus undulatus* (Törnquist, 1901), PMU 38415/2, latex cast of reverse view, somewhat incomplete, coated. Scale bars indicate 1 mm.

Diagnosis. – Horizontal didymograptid with parallel-sided stipes and a robust sicula, ca 2 mm long and slightly inclined to dorsal sides of stipes; proximal development isograptid, dextral; stipes horizontal to slightly reflexed (emended from Maletz 1996a, p. 205).

Remarks. – Maletz (1996a) described the species in detail and was the first to record it from the Hunneberg area. It is similar to *Expansograptus holmi* with which is occurs in the Diabasbrottet and Mossebo sections, but differs by having a shorter and wider sicula and a low sicular inclination. It appears to be intermediate between *Expansograptus holmi* and the robust *Expansograptus urbanus* (Monsen, 1937), but does not possess the distinct proximal reflection of the stipes.

Törnquist (1901) described and illustrated a few specimens as *Expansograptus suecicus* from Flagabro, Scania and Diabasbrottet, Hunneberg. Only some of these (LO 1592T–LO 1597t) are identified and can be commented on. The illustrations of LO 1592T and LO 1593t are apparently based on the same specimen, which bears an oblique sicula and proximally reflexed stipes, widening distally more than typical *Expansograptus suecicus* (Fig. 42I). The specimen came from the *Pseudophyllograptus densus* Biozone, i.e. younger than the type material of the species. It is here assigned to *Expansograptus grandis* (Monsen, 1937). LO 1594t is a specimen in full relief in obverse

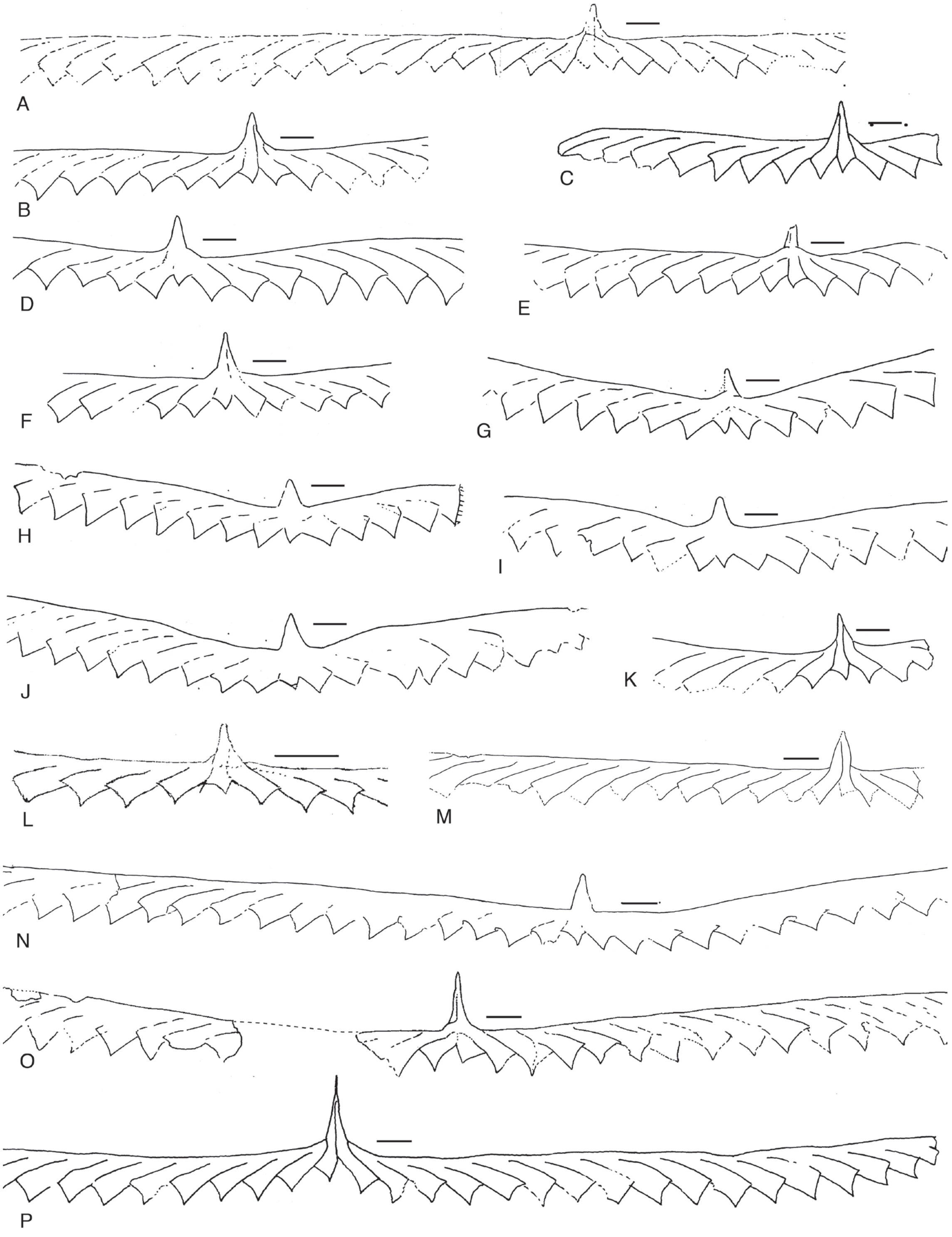

Fig. 41. **A–K**, **M**, **N**, *Expansograptus suecicus* (Tullberg, 1880). **A**, LO 353T, lectotype, Diabasbrottet, drawing by Kristina Lindholm. **B**, MBg DI 39/03, Diabasbrottet at 5.1–5.2 m, mould. **C**, T226, Tøyen section, Oslo, Norway. **D**, MBg Di 39/04/02, Diabasbrottet at 5.1–5.2 m. **E**, PMU 38396/2, Diabasbrottet at 5.3–5.4 m, mould. **F**, PMU 38395/2, Diabasbrottet at 5.3–5.4 m. **G**, MBg Di 43/03, Diabasbrottet at 5.7–5.8 m. **H**, PMU 38416, Diabasbrottet at 6.6–6.7 m. **I**, PMU 38417, Diabasbrottet at 6.6–6.7 m. **J**, MBg Di 21/03, Diabasbrottet at 3.2–3.3 m. **K**, MBg Di 39/02, Diabasbrottet at 5.1–5.2 m, mould. **M**, LO 5643t (Tullberg 1880, pl. 2, fig. 16). **N**, PMU 38418, Diabasbrottet, 4.7–4.8 m. **L**, *Xiphograptus lofuensis* (Lee, 1961), LO 1598t, Killeröd, Scania, drawing by Kristina Lindholm (Kävlinge, Sweden), first illustrated by Törnquist (1901, pl. 1, fig. 26) as *Didymograptus extensus*). **O**, **P**. *Expansograptus holmi* (Törnquist, 1901). **O**, PMU 38419, Diabasbrottet, 6.4–6.5 m, mould in reverse view. **P**, LO 1590t, lectotype, mould in obverse view, after pencil drawing by K. Lindholm. Scale bars indicate 1 mm.

view (Fig. 42J), but parts of the sicula are missing. It may belong to *Expansograptus grandis* judging by the inclination of the sicula and the distinctly widening stipes, but alternately may be referred to *Xiphograptus lofuensis*.

Expansograptus holmi (Törnquist, 1901)

Figures 17N, 41O, P, 42A–H

1901 *Didymograptus holmi* n. sp. Törnquist, p. 12, pl. 1, figs 15–18.
1937 *Didymograptus holmi* Törnquist; Monsen, pp. 94, pl. 1, figs 1, 9, 11, 14.
1937 *Didymograptus holmi* Törnquist var. *solidus* n. var. Monsen, p. 95, pl. 1, figs 6, 10, pl. 7, fig. 1.
1987 *Didymograptus* (*Expansograptus*) *similis* (Hall); Williams & Stevens, fig. 3A (no description).
pars 1988 *Didymograptus* (*Expansograptus*) *similis* (Hall); Williams & Stevens, p. 46, pl. 12, fig. 16.
1996a *Didymograptus* (*Expansograptus*) *holmi* (Törnquist); Maletz, p. 206, figs 1B, D–I; 3A, B.
1996 *Expansograptus holmi* (Törnquist); Maletz, Löfgren & Bergström, p. 156, fig. 13: 9.
1997a *Expansograptus holmi* (Törnquist); Maletz, p. 748, fig. 6j.
1997b *Expansograptus holmi* (Törnquist); Maletz, fig. 3d (no description).
1997a *Didymograptus* (s.l.) *holmi* Törnquist; Toro, pl. 2, figs 6, 7.

Type material. – Lectotype LO 1590t (Törnquist 1901, pl. 1, fig. 17), from the *Cymatograptus protobalticus* Biozone of Diabasbrottet, Hunneberg, designated Maletz (1996a) (Fig. 42A, B); paratypes LO 1588T–1591t, of which only LO 1589t and LO 1590t are in the type collection. The lectotype is preserved as a mould in obverse view and shows the development of the species in some detail.

Material. – Many specimens from the upper part of the *Cymatograptus protobalticus* Biozone and the *Baltograptus vacillans* Biozone of Diabasbrottet and Mossebo.

Description. – The tubarium is horizontal, often slightly deflexed or reflexed in the proximal end, with slender stipes and a prominent sicula. The sicula has a length of 1.8–2.4 mm and an apertural width of 0.3 mm and is positioned nearly vertically between the two stipes. The supradorsal part of the sicula is prominent, 0.9–1.3 mm long and forms a slender conical feature. A short and slender nema is often present, but its final length is uncertain as it may be broken in most specimens. The sicular aperture is bent slightly towards stipe 1 and possesses a short rutellum.

The proximal development is isograptid, dextral with slender crossing canals forming a wide and rounded isograptid arch as is seen from in a few specimens (Fig. 42C, F, G), in which the sicula is flattened, while the crossing canals and other parts of the proximal end are preserved in partial relief. The sicula and $th1^1$ form a short isograptid suture below the isograptid arch. The thecae are simple tubes, widening distinctly towards the apertures, which bear small rutella. The thecal inclination increases from 25°–30° initially to ca 40° at the apertures. The stipes are 1.0 mm wide at $th1^1$ and $th1^2$ and increase to 1.5–1.7 mm distally, rarely more. The 2TRD is 1.75–1.9 mm at th1–3 and th5–7 distally.

Remarks. – Maletz (1996a) discussed this species in detail and compared it with the contemporaneous and similar species *Expanograptus suecicus* and *Expansograptus similis*. Flattened specimens may be difficult to separate from *Expansograptus suecicus* (Tullberg, 1880), especially specimens with a relatively short sicula.

Occurrence. – The species is common at many levels from the upper part of *Cymatograptus protobalticus* Biozone to the *Baltograptus jacksoni* Biozone at Hunneberg. Williams & Stevens (1987, 1988) illustrated one flattened specimen of this species as *Didymograpus* (*Expansograptus*) *similis*, but the additional illustrated specimens in Williams & Stevens (1988) may not belong to *Expansograptus holmi*. The species is present in the Eastern Cordillera of Argentina (Toro 1997a), but little is known on its further distribution.

Expansograptus urbanus (Monsen, 1937)

Figures 24E, 43A–L, 44A–O

1901 *Didymograptus constrictus* Hall; Törnquist, pp. 17, 18, pl. 2, figs 13–17 (LO 1615–1619; specimens not located in Lund type collection).
?1937 *Didymograptus validus* Törnquist; Monsen, pp. 96, 97, pl. 1, figs 3, 12, 13, 16.
1937 *Didymograptus urbanus* n. sp.; Monsen, p. 99, pl. 1, figs 18, 19, 28, pl. 8, fig. 10.
1937 *Didymograptus constrictus* Hall; Monsen. p. 101, pl. 1, fig. 23, pl. 7, fig. 2, pl. 8, fig. 2
1937 *Didymograptus constrictus* Hall var. *repandus* n. var. Monsen, p. 102, pl. 1, fig. 20, pl. 7, fig. 5, pl. 8, fig. 4.
1996 *Expansograptus urbanus* (Monsen); Maletz, Löfgren & Bergström, fig. 13: 10.
2003 *Expansograptus urbanus* (Monsen); Maletz & Egenhoff, fig. 6M (not desecibed).
2004 *Expansograptus urbanus* (Monsen); Egenhoff *et al*., fig. 5G (not described).
2012 *Expansograptus latus* (Hall); Vento, Toro & Maletz, p. 353, figs 5C, 6B–C.
2014 *Expansograptus latus* (Hall); Maletz, fig. 13A, C.
2015 *Expansograptus urbanus* (Monsen); Maletz & Steiner, fig. 5C.

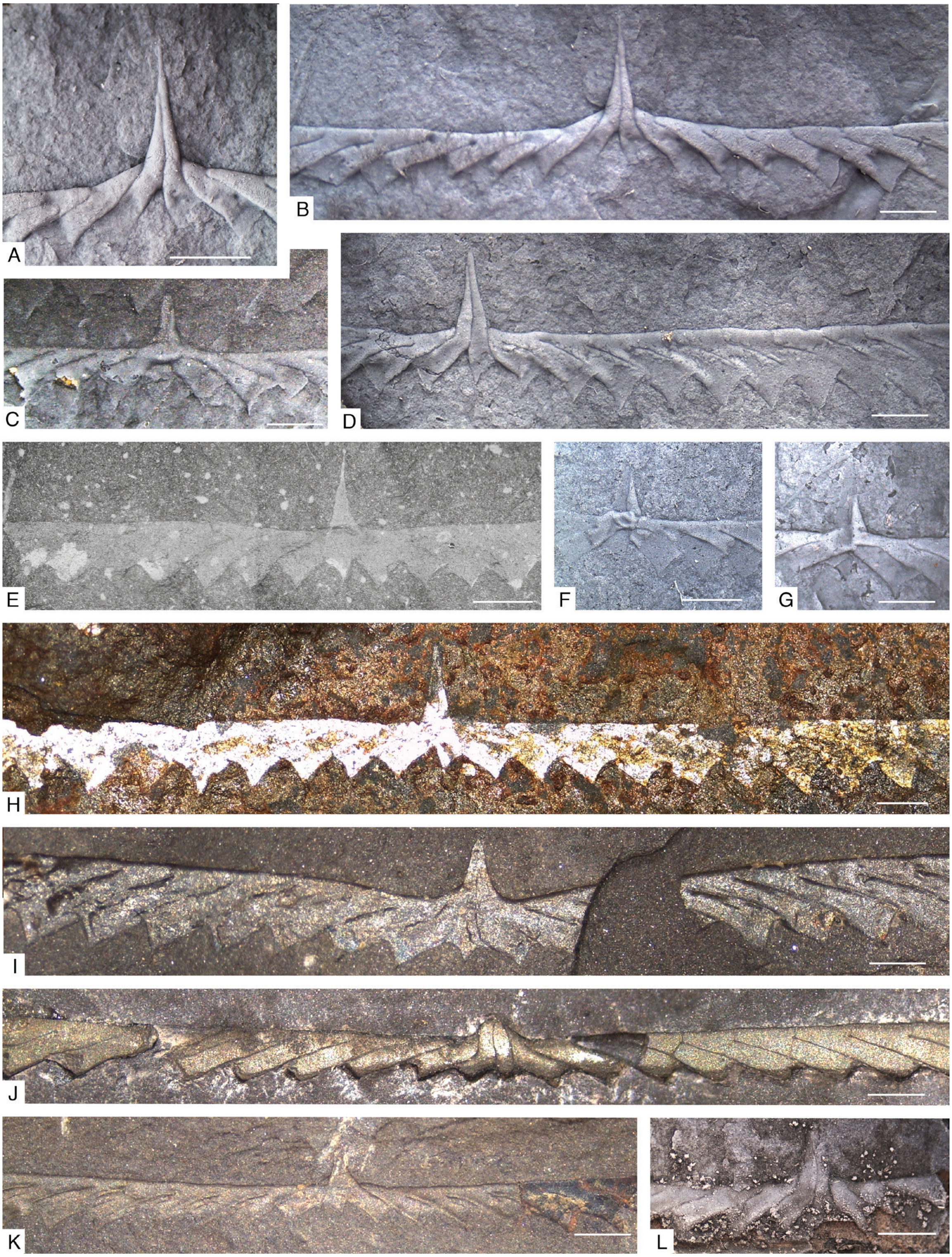

Fig. 42. Expansograptus and *Xiphograptus*. **A–H**. *Expansograptus holmi* (Törnquist, 1901). **A**, **B**, LO 1590t, lectotype, latex cast in obverse view. **C**, PMU 38420a, latex cast, proximal end of large specimen, Diabasbrottet, 4.5–4.6 m. **D**, PMU 23166/1, latex cast, Diabasbrottet at 4.2–4.3 m. **E**, LO 1589T, paratype, flattened specimen. **F**, PMU 38421, latex cast, reverse view, Diabasbrottet at 4.8–4.9 m. **G**, PMU 38422a/1, latex cast, reverse view, Diabasbrottet at 4.2–4.3 m. **H**, PMU 38423/2, Diabasbrottet, 4.0–4.1 m, flattened specimen. **I**, *Expansograptus grandis* (Monsen, 1937), LO 1592t, Flagabro (Törnquist, 1901, pl. 1, fig. 19 as *Expansograptus suecicus*). **J**, ?*Expansograptus grandis* (Monsen, 1937), LO 1594t, internal pyritic cast in full relief, obverse view, Flagabro (Törnquist, 1901, pl. 1, fig. 22 as *Expansograptus suecicus*). **K**, *Xiphograptus lofuensis* (Lee, 1961), LO 1598t, illustrated as *Didymograptus extensus* by Törnquist (1901, pl. 1, fig. 26). **L**, *Expansograptus suecicus* (Tullberg, 1880), LO 5643t, proximal end, obverse view, coated. Scale bar is 1 mm in each photo.

Type material. – Holotype PMO K 0442 (Monsen, 1937, pl. 1, fig. 19), from Galgeberg, Oslo (coll. Otto Herrmann), designated Monsen (1937); paratypes PMO 60.628, PMO K 0434 from the same locality, and two additional specimens from Stensbergstrasse, Oslo (Monsen, 1937, pl. 1, fig. 28; pl. 8, fig. 10).

Material. – Numerous specimens from the Diabasbrottet and Mossebo sections.

Description. – The stipes are variably reflexed proximally, then curve to become less so distally. Stipes widen rapidly from 1.2–1.3 mm proximally to 1.9–2.0 mm distally. The reflexed portion of the tubarium generally includes the proximal 4–8 thecae of each stipe, but this number is quite variable and smaller specimens may appear variably reclined. Stipes may reach a length of more than 10 cm.

The sicula is 1.9–2.1 mm long and mostly cylindrical, widening quickly from the apex to its full width. The sicula is about 0.2 mm wide near the apex, probably at the prosicular aperture, and then widens rapidly to 0.5 mm distally. The origin of th1^1 is at about 0.2–0.25 mm below the apex of the sicula, possibly in the lower part of the prosicula. The supradorsal part of the sicula and th1^1 forms a prominent triangle about 1.1 mm long and 0.8–0.9 mm wide. The sicula is inclined ca 4–5° from the midline of the tubarium. A short nema is present in most specimens. The sicular aperture is distinctly bent towards stipe 2, but does not bear a rutellum. A small lip is formed by the partial lateral flattening of the wide aperture.

The proximal development is isograptid, dextral (Fig. 43F, G) with a low, possibly prosicular origin of th1^1. A single specimen from Diabasbrottet has a sinistral development (Fig. 43D, H). It does not differ otherwise in its development, but the preservation is moderate and appears to show some irregularities, best seen on the obverse side (Fig. 43D). Here the downward growing initial part of th1^1 forms an undulating path that may indicate an early trauma.

The two crossing canals are compact, directed obliquely downwards and forming an angular isograptid window, encompassing an angle of ca 120° with their ventral sides (Fig. 43G). The isograptid suture below the isograptid arch in reverse view is short, barely reaching 0.2 mm in most specimens. The free ventral side of the sicula is about 0.5–0.6 mm long.

The thecae are simple tubes, widening considerably towards their apertures and in partially flattened specimens show considerable lateral overlap. The widening also produces a slight ventral curvature of the thecae. The thecae rapidly lengthen from initially ca 2 mm to more than 4 mm after a few thecae and distally possess a constant length and width. The apertures are straight and lack rutella. The thecal inclination measures 35–40° in distal thecae, but may be slightly less proximally. The 2TRD is about 1.9–2.0 mm along the entire stipes.

Remarks. – *Expansograptus urbanus* is easily recognizable, restricted to the lower part of the Floian. It has been described under a number of names before and may be easily misidentified as *Expansograptus constrictus*. It shows a nearly perpendicular sicula, inclined at 5° maximum, whereas *Expansograptus constrictus* has a shorter, more highly inclined sicula and somewhat more slender stipes.

Törnquist (1901) described the species under the name *Didymograptus constrictus* Hall from the *Cymatograptus balticus* Biozone of Flagabro, Scania and Mossebo, Hunneberg. The three specimens originated from Mossebo (Törnquist, 1901, pl. 2, figs 13, 16, 17). All specimens clearly show the reflexed proximal end of *Expansograptus urbanus* with its prominent and robust sicula.

Vento *et al.* (2012) and Maletz (2014) illustrated the species under the name *Expansograptus latus* (Hall, 1907), but this species is clearly different. The holotype is NMV P14283 (counterpart NMV P14289) from Smith Street East, 60 m from Arnold Street, Bendigo, re-illustrated by Rickards & Chapman (1991, pl. 24a). The specimen originates from the Bendigonian Be1 (*Tshallograptus fruticosus* + *Paratetragraptus approximatus* Biozone), approximately equivalent to the upper part of the *Cymatograptus protobalticus* Biozone and the *Baltograptus vacillans* Biozone. It shows a shorter and wider supradorsal part of the sicula and th1^1, and consequently relatively wider stipes that do not widen along the first few thecae as in *Expansograptus urbanus*.

Occurrence. – The species is the most common and most easily recognizable expansograptid in the upper *Cymatograptus protobalticus* and *Baltograptus vacillans* biozones at Diabasbrottet (Egenhoff & Maletz 2007) and is commonly preserved in relief. The species is also common in the Norwegian successions, but little is known about it wider distribution, except for its presence in Argentina (Vento *et al.* 2012).

Expansograptus validus (Törnquist, 1901)

Figures 38E, 45A–G, 46A–F

1901 *Didymograptus validus* n. sp. Törnquist, p. 18, pl. 2, figs 18–20.

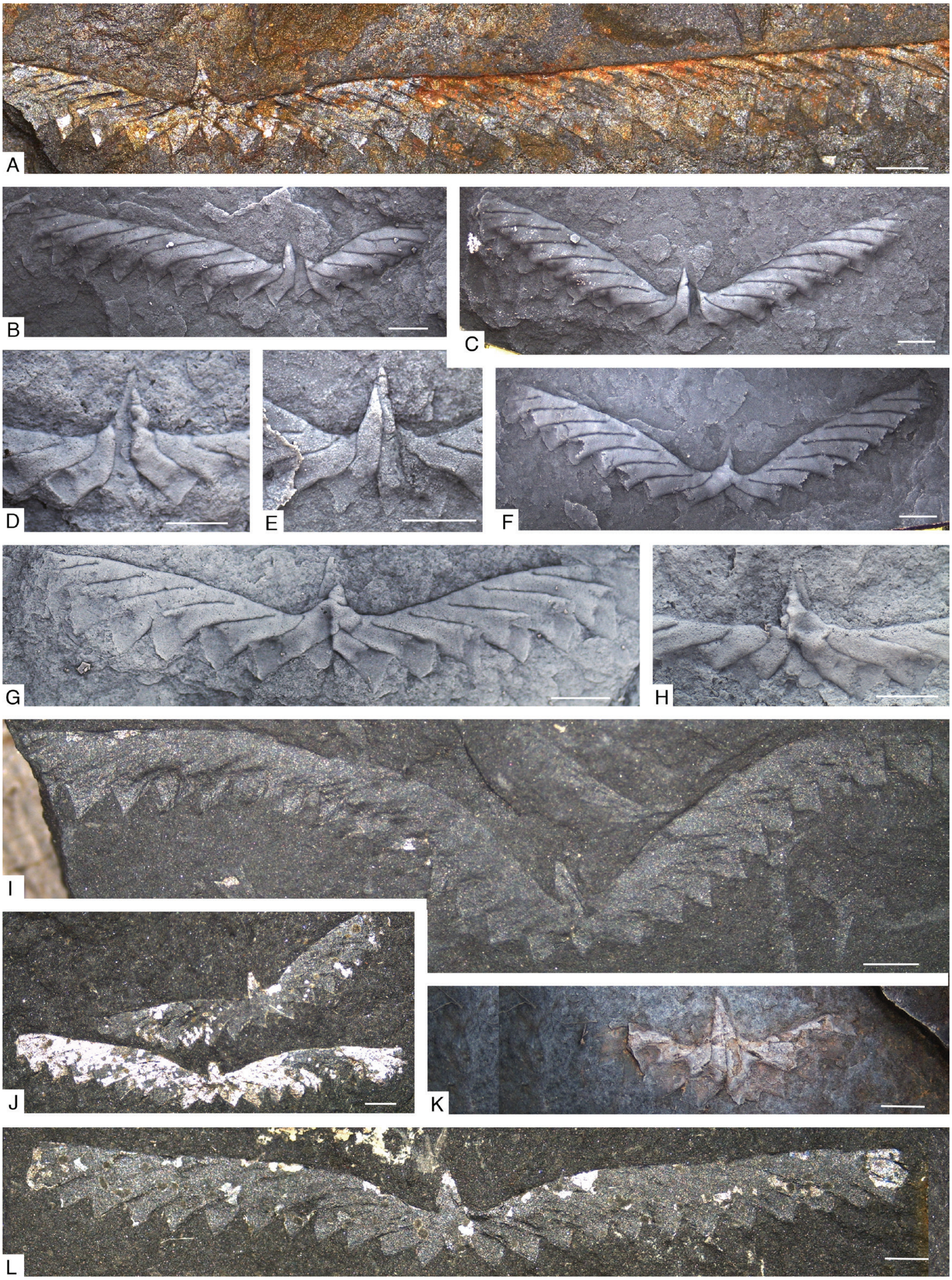

Fig. 43. Expansograptus urbanus (Monsen, 1937), photos. **A**, PMU 38423, Diabasbrottet at 4.0–.1 m, mould of specimen with long stipes in reverse view, only parts of stipes shown. **B**, **C**, PMU 23152/1, PMU 23152/2, Diabasbrottet at 4.0–4.1 m, two associated specimens in obverse view. **D**, **H**, PMU 38356A, B, Diabasbrottet at 6.7–6.8 m, left-handed specimen in obverse (**D**) and reverse (**H**) views. **E**, PMU 23166/2, Diabasbrottet at 4.2–4.3 m, obverse view of right-handed specimen. **F**, PMU 23152/2B, Diabasbrottet at 4.0–4.1 m, reverse view, counterpart of specimen in Fig. 43C. **G**, PMU 38422a/2, Diabasbrottet at 4.2–4.3 m, reverse view. **I**, RM Cn 1279, flattened specimen, strongly reflexed, Mossebo. **J**, RM Cn 1434, two associated flattened specimens, coll. G. Holm, 1886. **K**, PMU 38424, Diabasbrottet at 4.0–4.1 m, partial relief in obverse view, coated. **L**. PMU 38425, Diabasbrottet, 4.2–4.3 m. B-H are from latex casts of the original moulds. Scale bar is 1 mm each photo.

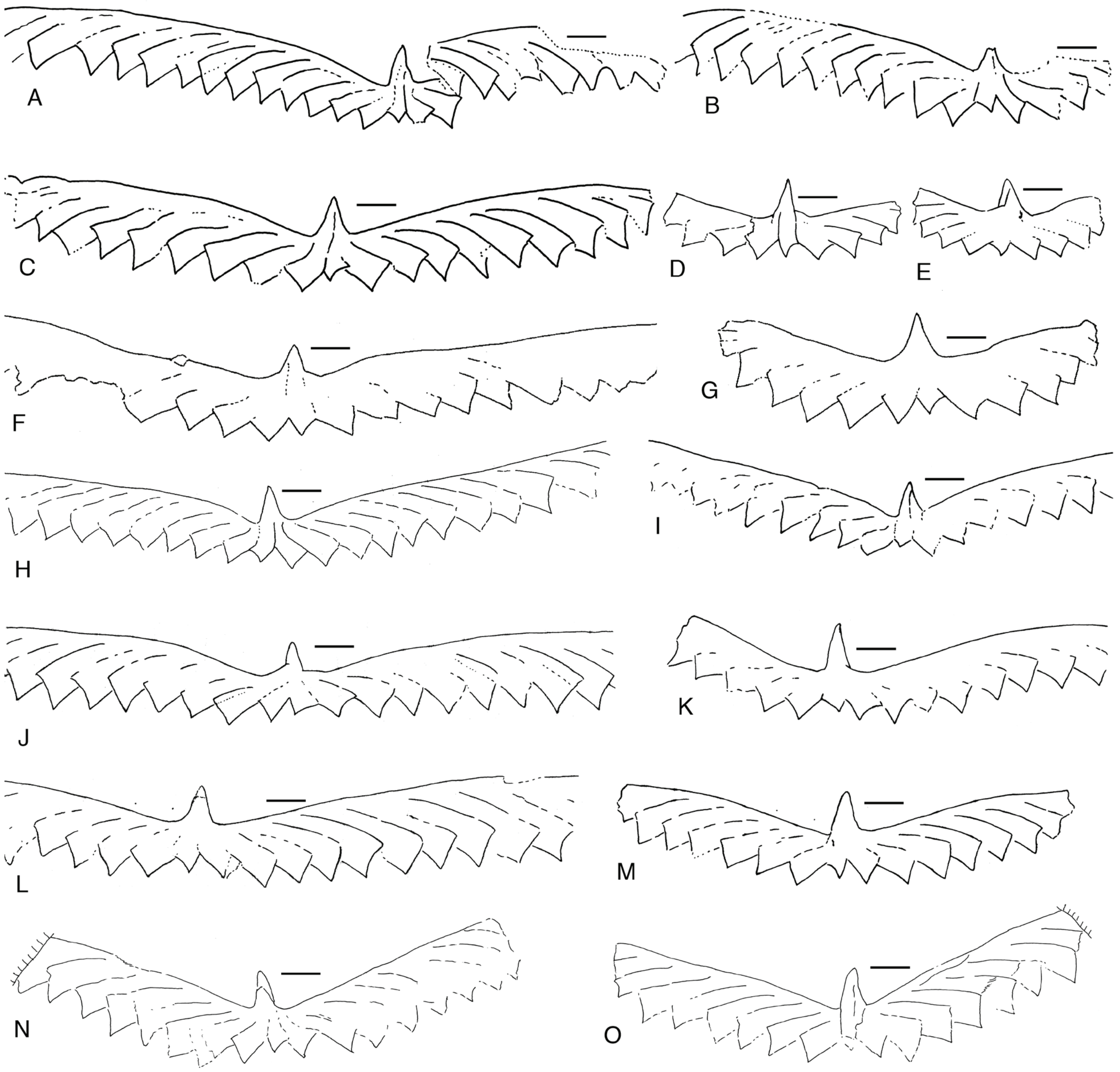

Fig. 44. Expansograptus urbanus (Monsen, 1937), drawings. **A**, PMO K 0442, holotype, Galgeberg, Oslo, Norway, coll. Otto Herrmann (Monsen, 1937, pl. 1, fig. 19). **B**, PMO K 0449, paratype, Stensbergstrasse, Oslo, Norway (Monsen, 1937, pl. 1, fig. 18). **C**, PMO 60.628. **D**, MBg Di 20/2, Diabasbrottet at 3.1–3.2 m. **E**, MBg Di 30/7, Diabasbrottet at 4.1–4.2 m. **F**, PMU 38426a/1, Diabasbrottet, 4.5–4.6 m. **G**, PMU 38426a/2, Diabasbrottet, 4.5–4.6 m. **H**, MBg Di 779/186b, Diabasbrottet at 4.4–4.5 m. **I**, PMU 38357a, Diabasbrottet at 6.2–6.3 m. **J**, PMU 38427, Diabasbrottet at 2.8–2.9 m. **K**, MBg Di 25/4, Diabasbrottet at 3.6–3.7 m. **L**, MBg Di 26/1, Diabasbrottet at 3.7–3.8 m. **M**, MBg Di 29/9, Diabasbrottet, 4.0–4.1 m. **N**, **O**, PMU 38358a, b, moulds of a specimen in reverse (**N**) and obverse (**O**) views, Diabasbrottet, 4.0–4.1 m. Scale bar is 1 mm for each specimen.

?1935 *Didymograptus latus* Hall; Benson & Keble, p. 284, pl. 30, fig. 31.
1937 *Didymograptus validus* Törnquist; Monsen, p. 96, pl. 1, figs 3, 12, 13, 16.
?1938 *Didymograptus latus* Hall; Harris & Thomas, p. 74–5, pl. 2, figs 18a–d; pl. 4, fig. 17.
1938 *Didymograptus latus* var. *aequalis* var. nov. Harris & Thomas, p. 75, pl. 2, fig. 19a, b; pl. 4, figs 18a, b.
?1935 *Didymograptus latus* Hall; Benson & Keble, p. 284, pl. 30, fig. 31.
non 1937 *Didymograptus validus* Törnquist; Monsen, p. 96, 97, pl. 1, figs 3, 12, 13, 16 (= *Expansograptus latus*).
1937 *Didymograptus constrictus* var. *repandus* n. var. Monsen, p. 102, pl. 1, fig. 20; pl. 7, fig. 5; pl. 8, fig. 4.
1986 *Didymograptus latus* Hall; Lenz & Jackson, fig. 7J, R.
non 1988 *Didymograptus* (*Expansograptus*) *latus* Hall; Williams & Stevens, pp. 48, 49, pl. 12, fig. 14; text-fig. 34A–H.
1990 *Expansograptus* cf. *constrictus* (Hall); Bahlburg, Breitkreuz, Maletz, Moya & Salfity, pl. 2a.
1997a *Expansograptus validus* (Törnquist); Maletz, p. 748, fig. 6M.

Type material. – Lectotype LO 1621t (Figs 45C, 46A) and paratype LO 1620T (Törnquist, 1901, pl. 2, figs 19, 18) from the *Cymatograptus protobalticus* Biozone at Diabasbrottet indicated by the presence of *Baltograptus geometricus* on LO 1620T, designated herein. Törnquist's illustrations are somewhat inaccurate as neither specimen shows the extremely rapid stipe widening and both also have more reflexed stipes.

Material. – Specimens of various growth stages from the Törnquist collection from Diabasbrottet. The slabs show considerable contact metamorphism, indicating an origin from the higher part of the *Cymatograptus protobalticus* or the *Baltograptus vacillans* Biozone. In addition, several specimens from Tøyen (Erdtmann collection) and from Bégin's Hill, Lévis, Québec, Canada (Maletz, 1997a) have been investigated.

Description. – The tubarium is robust, characteristically slightly reflexed proximally. The stipes are 2.0–2.1 mm wide at the first thecal pair and attain distal widths of 2.2–2.4 mm at th5. The thecae show an inclination of 35–42° and high overlap. A cross-section through the stipes usually cuts through three thecae. The 2TRD is 1.8–2.0 mm in the proximal end (th1–3) and 1.7 at th5–7, but as all specimens are small, this is close to the growing end of the stipes and the low value may indicate immaturity.

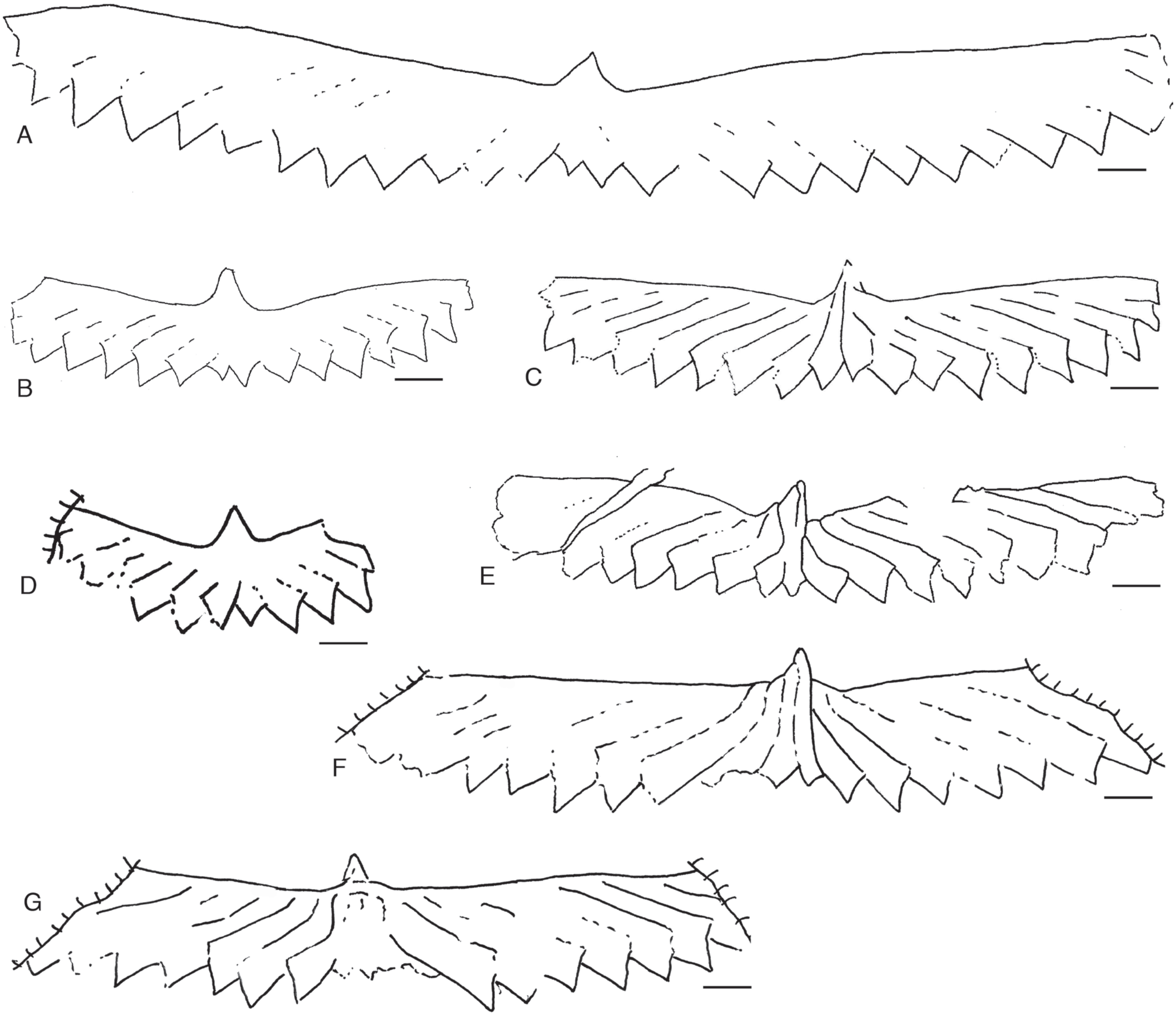

Fig. 45. *Expansograptus validus* (Törnquist, 1901), drawings. **A**, LO 1620T, Diabasbrottet (Törnquist, 1901, pl. 2, fig. 18). **B**, T1375, Tøyen section, Oslo, Norway (see Erdtmann 1965b). **C**, LO 1621t, lectotype, drawing after Kristina Lindholm (specimen in Törnquist 1901, pl. 2, fig. 19). **D**, T1375-2, Tøyen section, Oslo, Norway. **E**, GSC 102561, latex cast, relief specimen in obverse view, Bégin's Hill section at 44.5-45.5 m, Lévis, Québec, Canada (see Maletz 1997a). **F**, GSC 102563, obverse view, specimen before preparation, Côte Fréchette anticline, coll. John F. Riva (Québec, Canada). **G**, GSC 102563, reverse view, from latex cast after preparation. Scale bar is 1 mm for each specimen.

The sicula is about 2.4–2.7 mm long and widens rapidly from the apex, being parallel-sided for most of its length. It reaches a width of 0.5–0.6 mm across the aperture. A very short rutellum may be present, but this may be enhanced due to flattening. The supradorsal parts of the sicula and th1[1] form a broad triangular structure, 0.6–0.7 mm high, including the dorsal parts of the crossing canals. The feature is up to 1.4 mm wide at the base.

The proximal development is known from relief specimens from the Bégin's Hill section, Lévis, Québec, Canada, in reverse and obverse views (Figs 45E–G; 46B). The development is isograptid, dextral with a high position of the crossing canals on the sicula, but the size and shape of the prosicula is unknown. Th1[1] widens rapidly as it grows down along the sicula and bends outwards distally. Th2[1] and th2[2] initially grow horizontal, but almost immediately bend downwards to grow down on the dorsal sides of the sicula and th1[1], forming a high isograptid arch. The window below the isograptid arch shows a very long isograptid suture between the sicula and th1[1] as one of the characteristics of *Expansograptus validus* (Fig. 38E). The origins of th1[2] and sometimes of th2[1] are hidden on the reverse side of the tubarium, showing the close origin of the initial thecae of the stipes.

Remarks. – *Expansograptus validus* at first sight shares a number of characteristics with *Expansograptus constrictus* (Hall, 1865) and *Expansograptus urbanus* (Monsen, 1937). However, it differs in possessing much longer thecae with higher overlap. The tubarium shows a wide but relatively low supradorsal part of sicula and th1[1] and appears more massive in the proximal end due to the increased downward growth of the proxial thecae and the high position of the crossing canals. It shares its reflexed proximal stipes with many other Floian expansograptids.

Occurrence. – *Expansograptus validus* is poorly known even in Scandinavia and does not appear to be common. Egenhoff & Maletz (2007) did not report it from its type locality at Diabasbrottet, even though their biostratigraphy was based on very detailed collecting. This leaves the numerous specimens collected by Törnquist as the sole material available for investigation. The association with *Cymatograptus protobalticus* and *Baltograptus geometricus* indicates it is from the higher part of the *Cymatograptus protobalticus* and the *Baltograptus vacillans* Biozone.

Monsen (1937) used the species to define the *Didymograptus validus* Zone in the Tøyen Shale of the Oslo Region, an interval that probably correlates with the *Cymatograptus protobalticus* Biozone of Västergötland. The species is not present in the detailed logged collections of the Tøyen section in Slemmestad, Oslo Region, Norway (Erdtmann 1965b), but a few specimens are in the Erdtmann collection (Fig. 45B, D), probably found on loose slabs, so that the precise level from where the material originated is not known.

Maletz (1992a) illustrated a few specimens from the Lévis Formation at Bégin's Hill, Québec. Maletz (1997a, figs 68–5, 68–6; pl. 3, figs 3, 4) figured a single specimen from the *Tshallograptus fruticosus* Biozone of the Lévis Formation of Québec, providing the first record of *Expansograptus validus* from North America and indicating its presence in the upper *Paratetragraptus approximatus* and the *Tshallograptus fruticosus* biozones. Another North American record occurs as *Didymograptus latus* in the *Tshallograptus fruticosus* Biozone of British Columbia, Canada (Lenz & Jackson 1986; fig. 7J, R).

Genus *Baltograptus* Maletz, 1994

Type species. – *Didymograptus vacillans* Tullberg, 1880 from the *Baltograptus vacillans* Biozone at Kiviks-Esperöd, Scania, Sweden; original designation.

Diagnosis. – Horizontal to deflexed, declined and pendent didymograptid; sicula is a slender, gradually widening cone with long supradorsal part; proximal development of isograptid or artus-type with moderately low metasicular origin of th1[1] and comparably long ventral free apertural portion of sicula; isograptid suture very short or absent (artus-type development); stipe width and thecal overlap variable, increasing thecal length leads to higher overlap; thecae straight to undulating; apertures simple, without rutella (Maletz & Slovacek 2013, p. 1113).

Remarks. – The species included in *Baltograptus* are highly variable in tubarium shape, ranging from horizontal to declined and deflexed to pendent (Fig. 47). The proximal development is either artus-type or isograptid, known from numerous specimens preserved in full relief, and from isolated material (see Maletz 1994; Toro & Maletz 2007; Toro *et al.* 2011; Maletz & Slovacek 2013), but the development appears to be consistent in a given species. All species share the moderately low origin of th1[1] that has been observed to be in the metasicula in chemically isolated material. Maletz & Slovacek (2013) demonstrated the presence of a metasicular origin of th1[1] in *Baltograptus kurcki* (Fig. 48D) from chemically isolated material as the first clear evidence of the metasicular origin of th1[1] in the genus *Baltograptus*. However, no isolated material

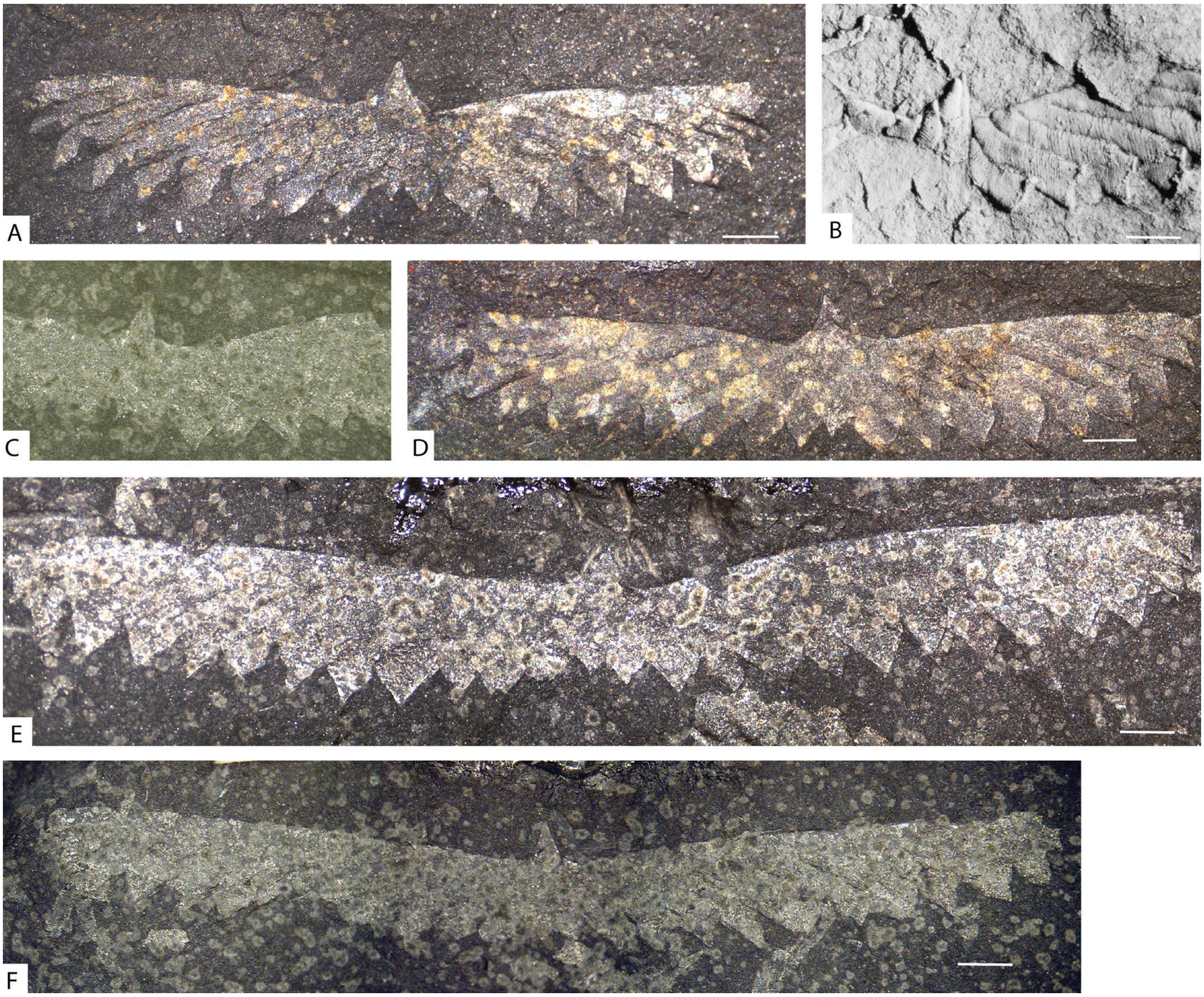

Fig. 46. Expansograptus validus (Törnquist, 1901), photos. **A**, LO 1621t, lectotype (Törnquist, 1901, pl. 2, fig. 19). **B**, GSC 102561, latex cast, relief specimen in obverse view, Bégin's Hill section at 44.5–45.5 m, Lévis, Québec, Canada. **C**, Törnquist collection, Diabasbrottet. **D**, LO 1621t+, lectotype, counterpart (Törnquist, 1901, pl. 2, fig. 19). **E**, LO 1620T, paratype, Diabasbrottet (Törnquist, 1901, pl. 2, fig. 18). **F**, Törnquist collection, 5-2, Diabasbrottet. Scale bar is 1 mm in each photo.

of other species exists that shows the metasicular origin of th1[1]. In these cases the evidence for a metasicular origin of th1[1] in *Baltograptus* is the common occurrence of oblique constrictions in the upper part of the sicula (Fig. 48A–C). These can be interpreted as an expression of the helical line of the prosicula and are typical of *Baltograptus* specimens, but have not been observed in other Tøyen Shale graptolites.

The main differences between species can be seen in the development of the interthecal septa, defining the stipe width, thecal overlap and thecal length. Early species like *Baltograptus geometricus* and *Baltograptus vacillans* show moderate thecal overlap of ca 50% with the origin of new thecae approximately at the position of the previous thecal aperture. In some slender species of *Baltograptus* the thecal overlap is considerably less and *Baltograptus* sp. cf. *Baltograptus kurcki* (Törnquist, 1901) shows very little thecal overlap. Increased thecal overlap occurs in species of the *Baltograptus calidus* group (cf. Toro & Maletz 2007; Toro *et al*. 2011; Zhang & Zhang 2014). A cross-section through the stipe can cross three thecae in extremely wide-stiped forms. A further change in development of the interthecal septa occurs in *Baltograptus bolivianus* (Finney & Branisa, 1984). This species shows considerable thecal undulations, thus giving a considerably different outline, which led Finney & Branisa (1984) to refer this species to *Maeandrograptus* and include it in the Sinograptidae following Jaanusson (1965).

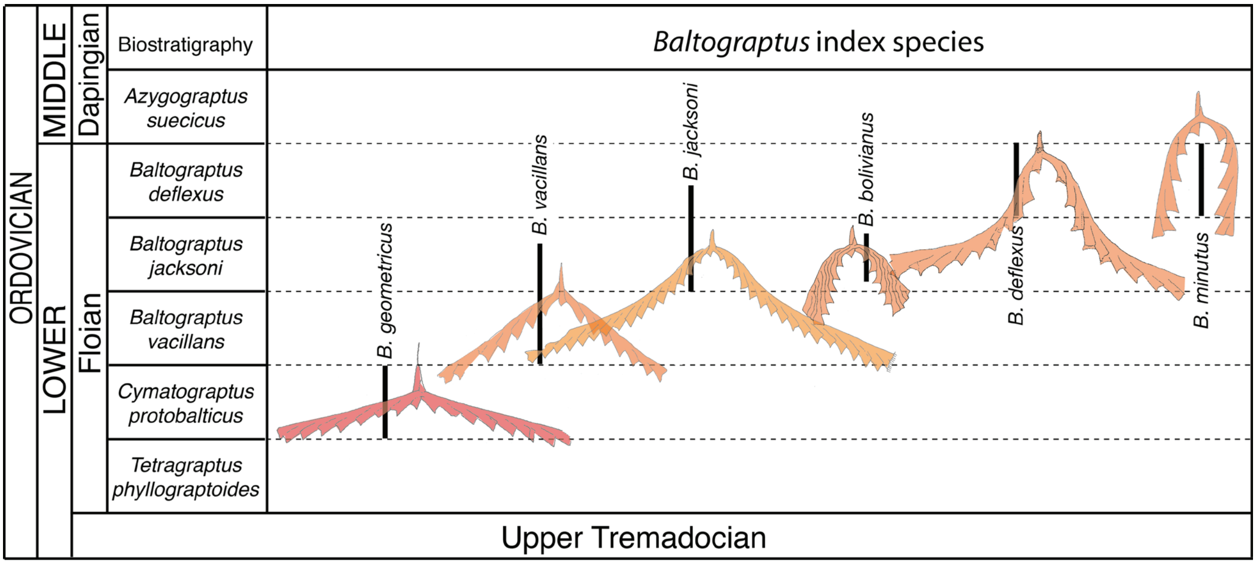

Fig. 47. Biostratigraphy of *Baltograptus* showing some of the most important taxa (based on Maletz 2017a, fig. 1.4). Drawings not to scale.

Distribution. – *Baltograptus* species are restricted to the Atlantic Faunal realm (cf. Egenhoff & Maletz 2007) or the higher palaeolatitude regions of Goldman *et al.* (2013). It can be used with great precision for biostratigraphic purposes in the Floian (Toro & Maletz 2007, 2008; Maletz & Ahlberg 2011, 2018). Maletz (2017a, fig. 1.4) illustrated the biostratigraphic range of a number of *Baltograptus* species demonstrating their use for precise zonation in the high palaeolatitude realm. A modification of the diagram (Fig. 47) shows the age of *Baltograptus bolivianus* as an example of the wide-stiped *Baltograptus* species of the *Baltograptus turgidus* group (see Mu *et al.* 1979).

Numerous species have been described and the differentiation of these is often uncertain, as is their intraspecific variation. Specimens of *Baltograptus vacillans* (Tullberg, 1880) from Diabasbrottet, preserved on a single shale surface, show the variation due to the flexibility of the tubaria and the impact of transport to the preservational aspects (Fig. 49). The shapes range from declined to deflexed to pendent. In flattened specimens, little detail is available, but relief specimens show the proximal development in obverse and reverse views. The wide-stiped species of the *Baltograptus turgidus* group are particular easily recognized. Many of the included species may be extreme variants of fewer species and are in need of further research. Zhang & Zhang (2014) revised some of the species described from South China (e.g. Mu *et al.* 1979) and demonstrated the intraspecific variation of these.

***Baltograptus vacillans* (Tullberg, 1880)**

Figures 17M, 49A–F; 51A–K; 52D

1880 *Didymograptus vacillans* n. sp. Tullberg, p. 42, pl. 2, figs 4–7.
1901 *Didymograptus vacillans* Tullberg; Törnquist, p. 20, pl. 2, figs 26–29.
1937 *Didymograptus vacillans* Tullberg; Monsen, pp. 142, 143, pl. 3, figs 8, 35, 43; pl. 9, fig. 9.
1987 *Expansograptus vacillans* (Tullberg); Maletz, pp. 93–95, fig. 28/1–11; pl. 2, figs 3–5.
cf. 1991 *"Corymbograptus"* cf. *vacillans* (Tullberg); Bahlburg, Breitkreuz, Maletz, Moya & Salfity, pl. 1, fig. i.
1994 *Baltograptus vacillans* (Tullberg); Maletz, p. 36, fig. 6a, b; pl. 1, figs b–d, g.
1994 *Corymbograptus* aff. *C. vacillans* (Tullberg, 1880); Ortega & Rao, p. 23, figs 3, 4; pl. 1.
1996 *Baltograptus vacillans* (Tullberg); Maletz, Löfgren & Bergström, p. 156, fig. 13: 12, 13.
1997b *Baltograptus vacillans* (Tullberg); Maletz, fig. 3h (G-14 well).
1997a *Baltograptus vacillans* (Tullberg); Toro, pl. 2, figs 2, 5.
?1997b *Baltograptus vacillans* (Tullberg); Toro & Brussa, fig. 3k, m, n.
2011 *Baltograptus vacillans* (Tullberg); Maletz & Ahlberg, fig. 5K.

Type material. – Lectotype LO 345t (Tullberg (1880, fig. 7) (Maletz & Ahlberg 2011, fig. 5K); paratypes LO 344T, 346t–347t, from the 'Undre Graptolitskiffer (=Tøyen Shale) of Kiviks-Esperöd, Scania, designated herein. All are flattened, preserved as films of coalified organic material, preserved on two slabs of black shale. Both slabs have numerous flattened specimens and it is difficult to recognize which of Tullberg's illustrations matched which specimens (Kristina

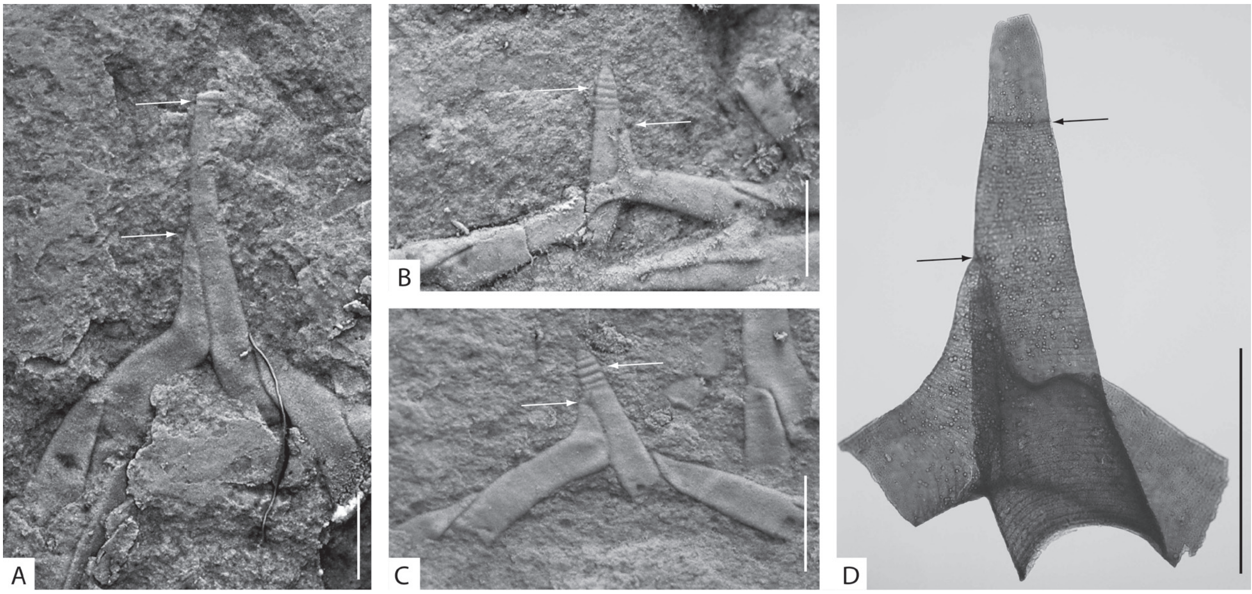

Fig. 48. Proximal development in *Baltograptus* species. **A**, *Baltograptus extremus* Maletz & Slovacek, 2013, specimen on LO 10581T+, Lerhamn drillcore, 43.0–43.02 m, latex cast, specimen showing part of prosicula (arrow) with constrictions. **B**, **C**, *Baltograptus* sp. 4 (of Maletz & Ahlberg, 2011), specimens on LO 10587t, Lerhamn drillcore at 44,4–44.5 m, latex cast, two specimens in reverse (**B**) and obverse (**C**) views showing constrictions of the prosicula. **D**, *Baltograptus kurcki* (Törnquist, 1901), SGU 9615, obverse view with crossing canal of th1^2 shining through the transparent sicula, Talubäcken section, Dalarna (see Maletz & Slovacek 2013). Scale bar is 0.5 mm in each photo.

Lindholm pers. com. 1988) and mis-identifications may have happened. The best specimen from the type slabs is here selected as the lectotype. The specimen was fully illustrated in Maletz & Ahlberg (2011, fig. 5K). The specimen selected here is labeled LO 345t, but actually is more similar to the specimen in Tullberg (1880, fig. 7), supposed to be LO 347t. The specimen is selected because it is well preserved and shows important features not visible on the remaining syntypes, including the low origin of th1^1 and the isograptid proximal development.

Material. – Numerous specimens from Diabasbrottet and Mossebo, some in full relief, preserved as moulds in obverse and reverse views.

Diagnosis. – Declined to slightly deflexed *Baltograptus* with slender stipes and moderate thecal overlap, proximal development isograptid, dextral.

Description. – The stipes are slender, usually declined to slightly deflexed with a distal stipe width of 0.8–0.9 mm and a stipe length of rarely more than 10 mm. The sicula is a slender cone, 1.7–1.9 mm long and about 0.4 mm wide at the aperture. The aperture is provided with a very short rutellum, less than 0.1 mm long. The sicula is slightly inclined towards stipe 2.

Most specimens have a short nema, not longer than 2–3 mm. The origin of th1^1 is about 0.6–0.7 mm below the apex of the sicula, supposedly in the metasicula (Maletz 1994; Ortega & Rao 1994). The proximal development is isograptid, dextral in all specimens. The stipes widen from 0.6–0.7 mm at the aperture of th1^1 to 0.8–0.9 mm distally, slightly less in relief specimens. The 2TRD is 1.5 mm at th1^1–3^1 and 1.6 mm at th5^1–7^1. The tubarium shape varies considerably due to the flexibility of the slender stipes. Most are declined (Fig. 49C–F) to slightly deflexed, but pendent specimens are not uncommon (Fig. 49A, B). The stipe habit may have been modified considerably by preservational aspects, as the stipes appear to be quite flexible.

Remarks. – *Baltograptus vacillans* is easily misidentified in juvenile specimens as differences between species become evident only in the distal parts of the colonies and in the general shape of the stipes. Tullberg (1880) claimed that the stipe width is up to 1.5 mm, but in specimens on the type slabs, stipes barely reach a width of 1.0 mm distally.

Occurrence. – *Baltograptus vacillans* is widely distributed in Scandinavia (Tullberg 1880; Törnquist 1901; Monsen 1937; Lindholm 1981; Tjernvik 1960; Maletz & Ahlberg 2011, 2018) and South America (e.g. Ortega & Rao 1994; Toro 1997a; Toro & Brussa 1997b). It is common in the *Baltograptus vacillans* Biozone, but then grades into *Baltograptus jacksoni* Rushton, 2011 which is deflexed and has more robust stipes, and with which it overlaps stratigraphically.

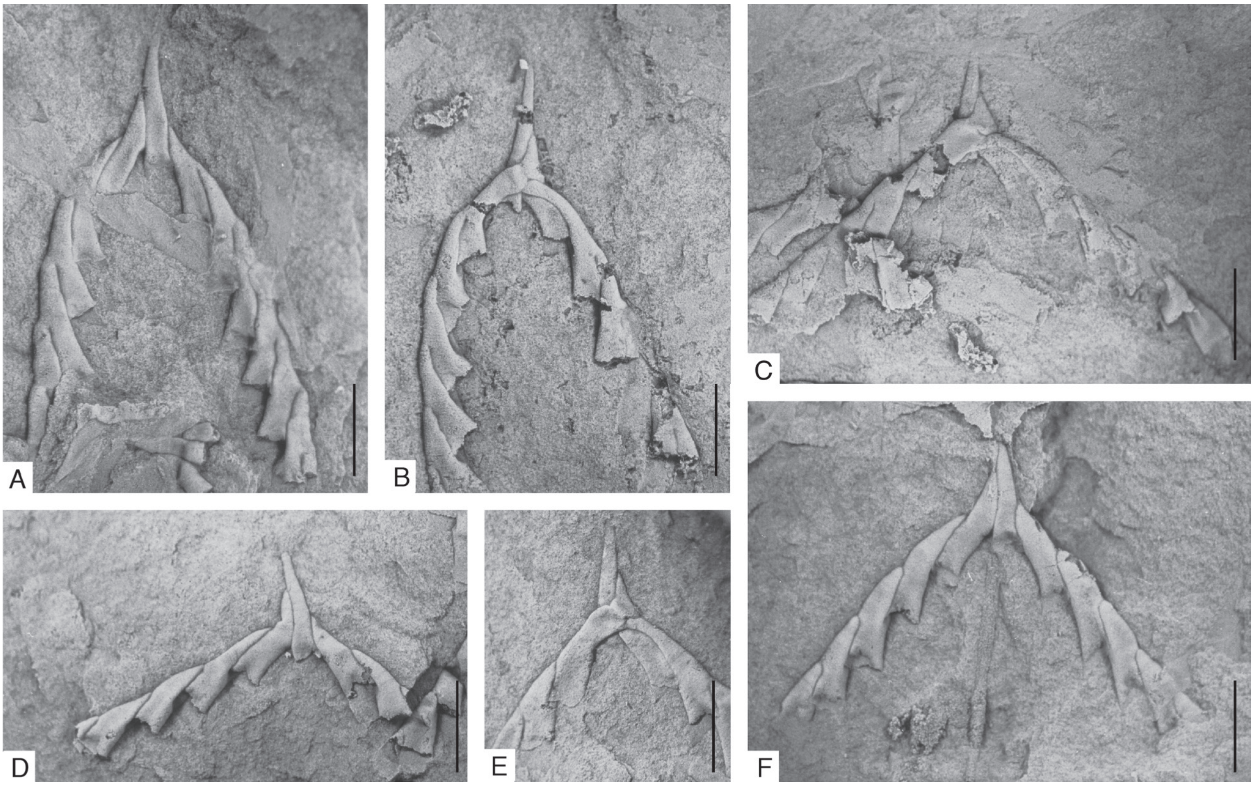

Fig. 49. *Baltograptus vacillans* (Tullberg, 1880), PMU 23157, Diabasbrottet at 5.0–5.1 m. All specimens from one single slab, photos of latex casts of the specimens preserved as moulds. **A**, pendent specimen, obverse view. **B**, pendent specimen, reverse view. **C**, declined specimen, reverse view. **D**, declined specimen, obverse view. **E**, declined specimen, reverse view. **F**, declined specimen, obverse view, tip of sicula missing. Scale bar is 1 mm in all photos.

Baltograptus jacksoni **Rushton, 2011**

Figures 50A–G, 51L–N

1987 *Corymbograptus* sp. 2 Maletz, p. 107, fig. 33: 3, 4.
1994 *Baltograptus* cf. *deflexus* (Elles & Wood, 1902); Maletz, fig. 6F (stated wrongly as fig. 6G in figure caption).
2007 *Baltograptus* sp. nov. Toro & Maletz, p. 494, figs 4A, 5A–D.
2011 *Baltograptus jacksoni* sp. nov. Rushton, p. 323, figs 4–7, 8D, E?
2015 *Baltograptus* sp. Maletz & Steiner, fig. 5E, F.
2015 *Baltograptus jacksoni* Rushton; Maletz & Steiner, fig. 10.
?2016 *Baltograptus* cf. *jacksoni* Rushton; Gutiérrez-Marco & Martin, fig. 4O (no description).

Type material. – Holotype BGS Ht 1260 and 1260a (Fig. 50C, D) from Jonah's Gill, Howgill Wood, Loweswater Formation, *Baltograptus jacksoni* Biozone (see Rushton, 2011 for details).

Material. – Several specimens from the Diabasbrottet section, preserved as partial remains with the pyrite-filled proximal portion in relief and the apertural portions of thecae missing (see Maletz & Steiner 2015) have been identified as *Baltograptus jacksoni*. Additional material from the Tøyen section, Oslo, Norway (Erdtmann 1965) provides further information on its dimensions and development.

Diagnosis. – *Baltograptus* species with deflexed stipes up to 1.3 mm wide, proximal development of isograptid, dextral type.

Description. – The species has a slender, deflexed tubarium with a relatively short and wide deflexed initial part, ranging from three to four thecae in the declined part and subhorizontal to declined stipes distally. The proximal end is isograptid, dextral, with a fairly symmetrical divergence of the stipes. The sicula is 1.6–1.8 mm long, slender and widens very gradually towards the aperture, which is 0.35 mm wide. The free ventral side of the sicula is about 0.5–0.6 mm long. The origin of th1^1 is about 0.7 mm below the apex of the sicula. The thecae are simple with a slight widening at the aperture. The stipes are about 0.7–0.8 mm wide at the first thecae and widen quickly to a maximum of 1.1–1.3 mm. The 2TRD is 1.7 mm at the first proximal thecae (th 1-3) and appears to be nearly constant. Distal 2TRD are between 1.6 and 1.7 mm.

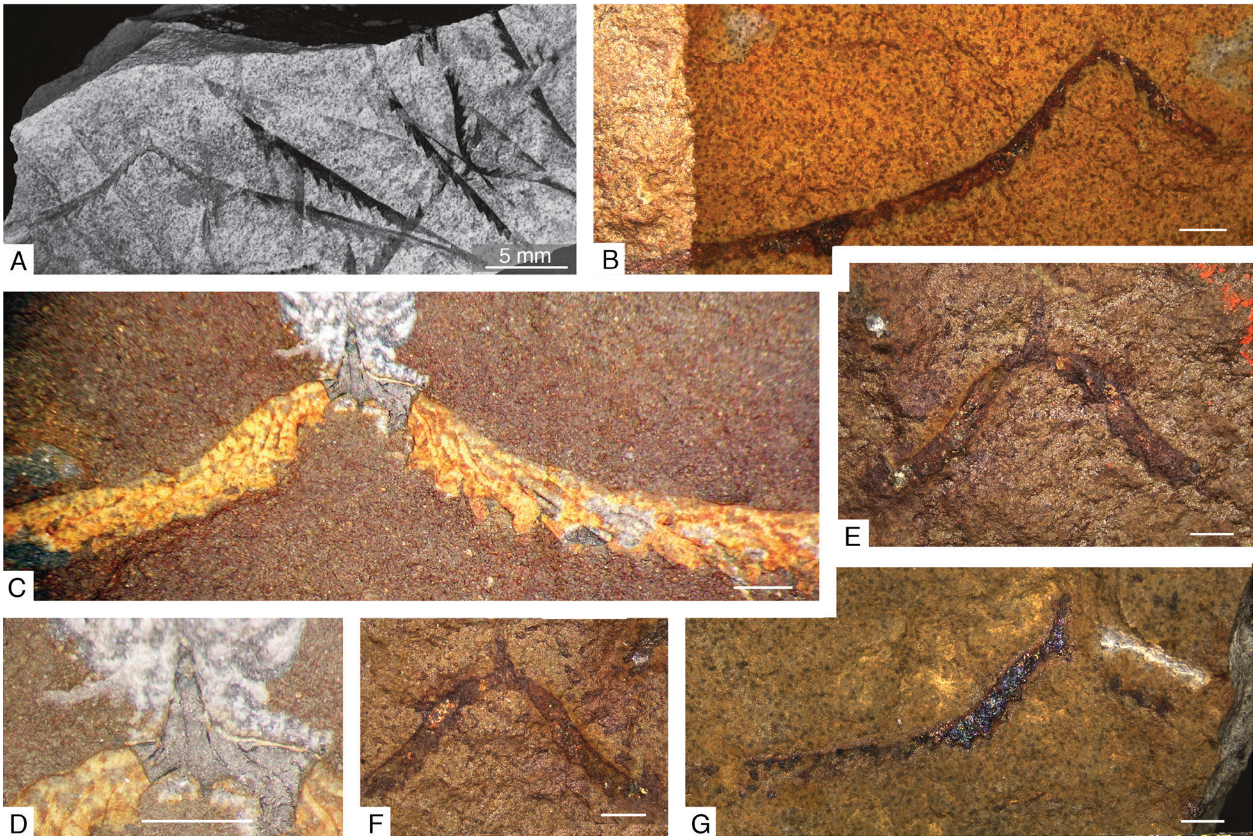

Fig. 50. Baltograptus jacksoni Rushton, 2011. Hunneberg specimens in strongly metamorphous shales, showing incomplete outlines. **A**, MBg Di 12-50, several poor specimens, Diabasbrottet, 9.2–9.5 m. **B**, PMU 23164a. **E**, **F**, PMU 38428a, b, counterparts. **G**, PMU 38429. **C**, **D**, holotype, BGS Ht 1260, Jonah's Gill, see Rushton (2011) for details. Scale bars are 1 mm unless otherwise indicated.

Remarks. – Rushton (2011) described this species and differentiated it from *Baltograptus vacillans* and *Baltograptus varicosus* Wang, 1974, species for which it has been mistaken in the past. Specimens from Hunneberg appear to be more slender, but this is due to the poor preservation and the intraspecific variation in stipe width. Most of the specimens are preserved as contact metamorphic modified specimens in which the original thecal apertures are not visible. Largely the only preserved parts of the specimens are those that were filled with pyrite. The British material is more strongly deformed, which may affect the dimensions measured, but has the fusellum preserved in flattened specimens surrounded by presure shadow minerals (Maletz & Steiner 2015).

Occurrence. – *Baltograptus jacksoni* occurs in the *Baltograptus jacksoni* Biozone and is widely distributed in Scandinavia and Britain. It also occurs in South China and South America, but has been described under different names, which are in need of revision. Zhang & Zhang (2014) suggested a possible synonymy with *Baltograptus varicosus* (Wang, 1974), but their described material of *Baltograptus varicosus* seems to be considerably wider in distal stipes (ca 1.5–1.9 mm), a final stipe width that is also seen in the holotype of *Baltograptus varicosus* (Zhang 2008).

***Baltograptus geometricus* (Törnquist, 1901)**

Figures 52A–C, E-I; 53A–K; 54C

1901 *Didymograptus geometricus* n. sp. Törnquist, p. 11, 12, pl. 1, figs 12–14.
?1937 *Didymograptus* aff. *geometricus* Törnquist; Monsen, p. 132, pl. 2, figs 1, 23, 33, 45, 51, 52.
1962 *Didymograptus sinensis* sp. nov. Lee & Chen, p. 24, pl. 3, figs 12–16; text-fig. 5.
1979 *Didymograptus saukros* sp. nov. Ni *in* Mu *et al.*, p. 81, pl. 28, figs 7–12.
1979 *Didymograptus stamineus* sp. nov. Chen *in* Mu *et al.*, p. 100, pl. 35, figs 17–21.
1991 *Didymograptus* (s.l.) *geometricus* Törnquist; Maletz, Rushton & Lindholm, figs 7f–h.
?1994 *Didymograptus* (*Expansograptus*) *simulans* Elles & Wood; Moya, Malanca, Monteros & Cuerda, pl. 4, figs 1–7.
1995 *Baltograptus geometricus* (Törnquist); Maletz, Kley & Reinhardt, p. 171, fig. 3: 1–4, 6.
1996 *Baltograptus geometricus* (Törnquist); Maletz, Löfgren & Bergström, p. 156, figs 13–7.

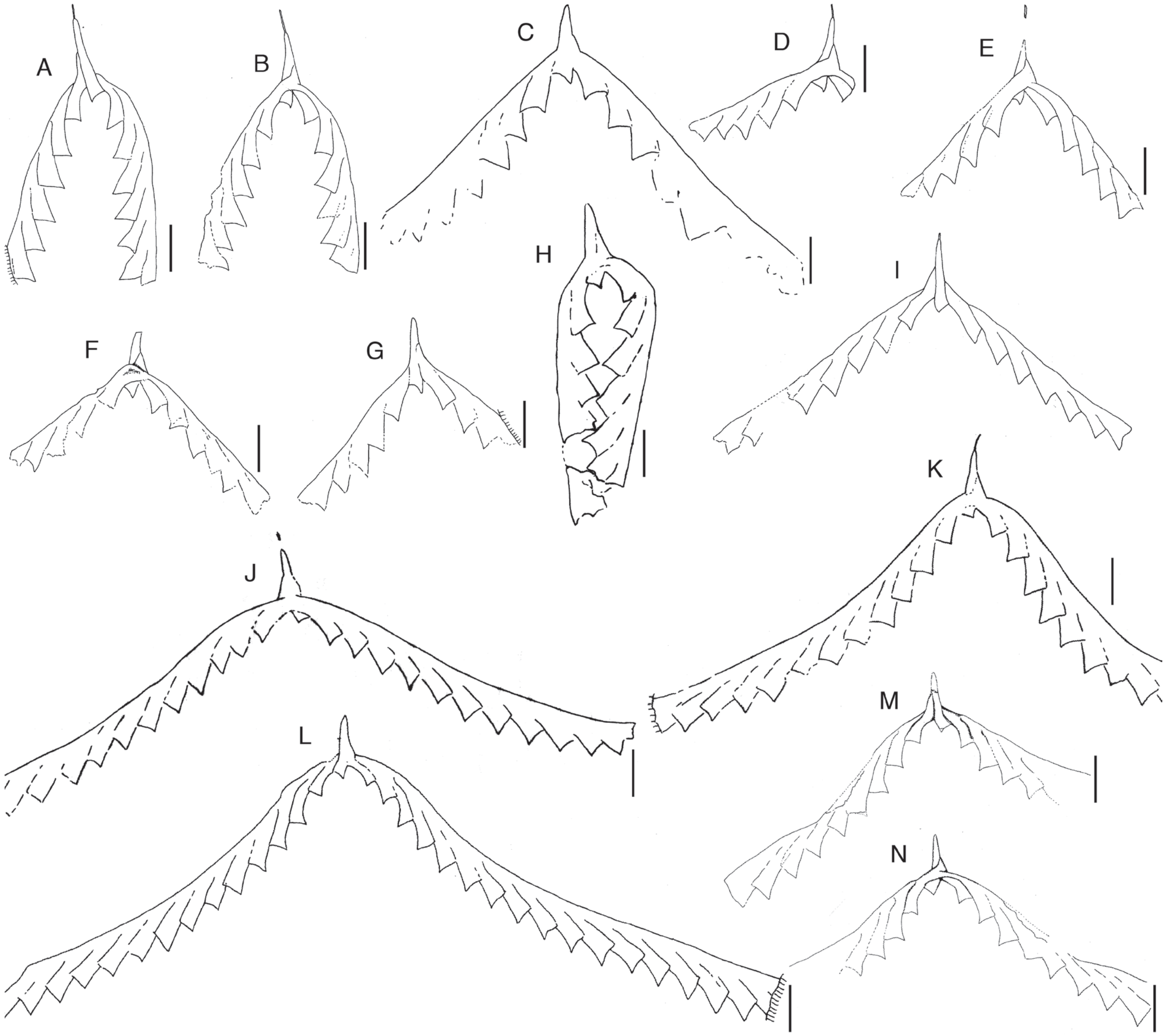

Fig. 51. *Baltograptus* species. **A–I**, **?K**. *Baltograptus vacillans* (Tullberg). **A–G**, Diabasbrottet at 5.0–5.1 m. **A**, **B**, PMU 23157, latex cast of a pendent specimen obverse (**A**) and reverse (**B**) views. **C**, PMU 38430, flattened specimen. **D–F**, PMU 23157, latex casts of three declined specimens in reverse view. **G**, MBg Di 832/205B, flattened specimen. **H**, MBg Di 37/04, Diabasbrottat at 4.8–4.9 m, pendent specimen, flattened. **I**, PMU 23157, latex cast of declined specimen in obverse view. **J**, MBg Di 25/01, Diabasbrottet at 3.6–3.7 m, slightly deflexed specimen, flattened. **K**, MBg Di 27/01, Diabasbrottet at 3.8–3.9 m, deflexed specimen. **L–N**. *Baltograptus jacksoni* Rushton, 2011, Tøyen section at 10.35–10.50 m, Oslo, Norway, coll. Erdtmann. **L**, T249/01. **M**, **N**, T243/01, latex casts of relief specimen in obverse and reverse views. Scale bar is 1 mm for each specimen.

1997a *Baltograptus geometricus* (Törnquist); Toro, pl. 1, figs 7, 8.
?1997a *Didymograptus* (s. l.) cf. *D. demissus* Törnquist; Toro, pl. 1, fig. 9.
2011 *Baltograptus geometricus* (Törnquist); Maletz & Ahlberg, fig. 5J.
2018 *Baltograptus geometricus* (Törnquist); Maletz & Ahlberg, fig. 8G.
2021 *Baltograptus geometricus* (Törnquist); Rushton, Ghobadi Pour, Popov, Jahangir & Amini, p. 7, fig. 6a–l; ?m–o.

Type material. – LO 1585T (Törnquist 1901, pl. 1, figs 13, 14) (Fig. 52A), from the *Cymatograptus protobalticus* Biozone of Mossebo (most probably modern Diabasbrottet) is identified as the holotype as it is the only specimen illustrated by Törnquist (1901). A number of poorly preserved, flattened specimens of *Baltograptus geometricus*, two specimens of *Corymbograptus*(?) *vicinatus* and a fragmented specimen of *Clonograptus multiplex* are on the slab that shows considerable metamorphic mineral growth due to the overlying dolerite sill (Fig. 52A, B). The additional originals of Törnquist (1901, pl. 1, figs 13, 14; LO 1586t, LO 1587t) are

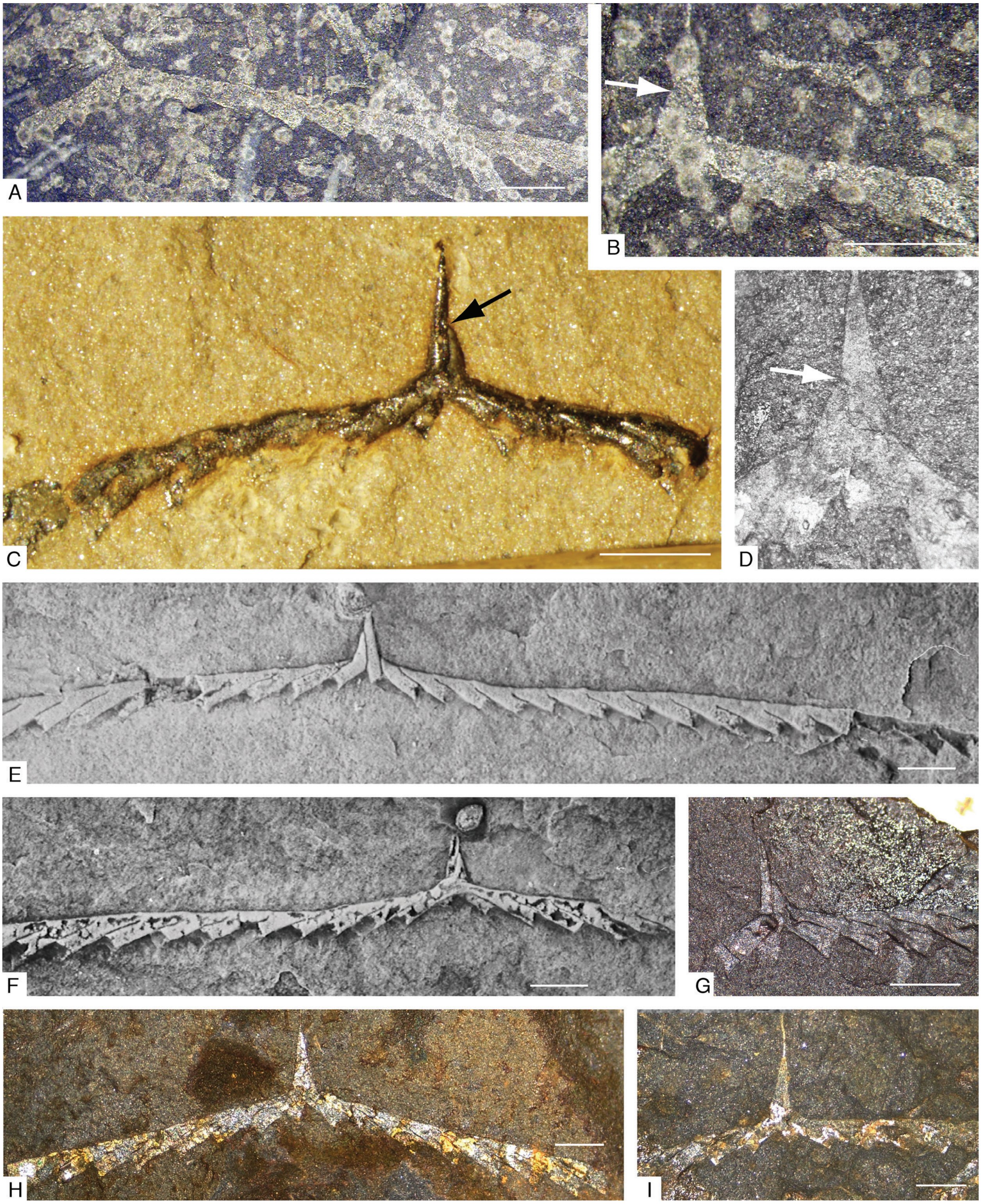

Fig. 52. Baltograptus geometricus (Törnquist, 1901). **A**, LO 1585T, holotype, Diabasbrottet. **B**, LO 1585Ta, obverse view, specimen on slab with holotype, showing proximal end with the origin of th1^1 (arrow). **C**, NIGP 32160, reverse view in relief, syntype of *Didymograptus stamineus* Chen *in* Mu *et al.* (1979, pl. 35, fig. 19). **E**, **F**, LO 6287t and counterpart, latex cast in obverse (**E**) and reverse (**F**) views (Maletz *et al.* 1991, fig. 7f, g). **G**, T 130, Tøyen section, Oslo, Norway, 8.17–8.20 m, latex cast in reverse view. **H**, PMU 38431, typical flattened specimen not showing origin of th1^1, Diabasbrottet, 2.1–2.2 m. **I**, PMU 38432, flattened specimen, Diabasbrottet, 2.1–2.2 m. **D**, *Baltograptus vacillans* (Tullberg, 1880), LO 345t, Kiviks-Esperöd, Scania, Sweden, coll. Tullberg, 1878, enlargement of proximal end of syntype, showing low origin of th1^1 in metasicula. Scale bar is 1 mm in each photo.

absent from the Lund collection and may be impossible to trace or represent magnified pieces from the holotype specimen.

Material. – Numerous specimens from Diabasbrottet and Mossebo. The species is restricted to the *Cymatograptus protobalticus* Biozone and the basal part of the *Baltograptus vacillans* Biozone.

Description. – The sicula is slender, nearly parallel-sided, 1.6–1.8 mm long and an apertural width of 0.4–0.5 mm. It bends slightly towards stipe 2 aperturally. The nema is conspicuous and can reach a length of several mm. The sicula is inclined about 4–5° to the midline of the tubarium. The origin of th1^{1} is about 0.5–0.6 mm below the apex and is interpreted to be in the metasicula. The proximal development is isograptid, dextral. A wide isograptid arch is present on the reverse side and an isograptid suture is not developed (Fig. 54C). The thecae are slender, with an inclination of about 25–28° in relief specimens, but slightly more in some flattened material and lack rutella. The 2TRD is about 1.5–1.6 mm at th2 and 1.6–1.7 mm at th10. The stipe width ranges from 0.4–0.5 mm at the first thecal pair to about 0.7–0.8 mm distally.

Remarks. – Even though the type material of *Baltograptus geometricus* is poorly preserved (Figs 52A, B; 53J, K), the most important characteristics are clear. The holotype only shows the general outline of the tubarium, but an additional proximal end on the slab (Fig. 52B) clearly confirms the low origin of th1^{1}. Relief specimens are not uncommon at the type locality and provide additional data for the identification. Maletz *et al.* (1991) illustrated relief specimens of *Baltograptus geometricus* from the Diabasbrottet section to show the proximal development in obverse and reverse views (Fig. 52E, F).

Monsen's (1937) specimens of *Didymograptus* aff. *D. geometricus* are intermediate to *Baltograptus vacillans*, showing more strongly declined, wider stipes. Specimens of *Baltograptus geometricus* are, however,

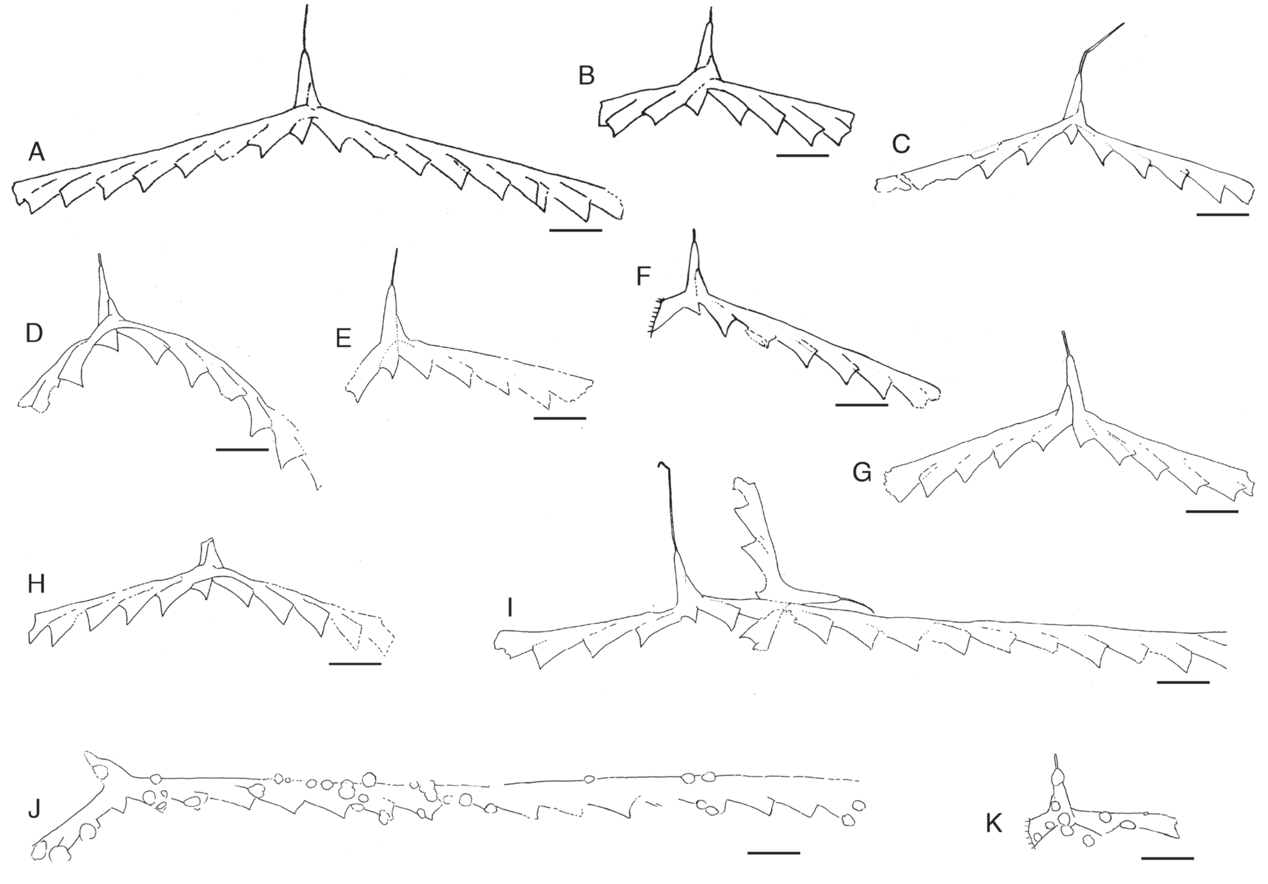

Fig. 53. Baltograptus geometricus (Törnquist, 1901). **A**, DI 543/252, Diabasbrottet at 2.1–2.2 m. **B**, PMU 38433, Diabasbrottet at 2.1–2.2 m. **C**, Di 89/02/02, Diabasbrottet. **D**, MBg Di 89/01/01, Diabasbrottet. **E**, LO 6288t, Diabasbrottet at 2.1–2.2 m. **F**, MBg Di 89/02/03, Diabasbrottet. **G**, LO 6288t, Diabasbrottet at 2.1–2.2 m. **H**, LO 6288t, Diabasbrottet at 2.1–2.2 m. **I**, MBg Di 89/02-01, Diabasbrottet. **J**, LO 1585T, holotype. **K**, previously unfigured specimen on LO 1585T, paratype. Scale bar is 1mm at each specimen.

present in the Tøyen section in the city of Oslo (Fig. 52G).

Hede (1951) and Tjernvik (1960) indicated the presence of this species in the Flagabro drill core in Scania (see Maletz & Ahlberg 2018, fig. 8G), but Lindholm (1981) did not mention it in the Krapperup drill core, suggesting that further work is needed to determine the distribution of *Baltograptus geometricus* in Scandinavia.

Occurrence. – *Baltograptus geometricus* is common in the *Cymatograptus protobalticus* Biozone, and often co-occurs with the index species. It has recently been found in many sections in South America (Moya *et al.* 1994; Toro 1997a; Toro & Maletz, 2007).

Baltograptus geometricus has not been described from China, but specimens identified as *Didymograptus sinensis* Lee & Chen, 1962, *Didymograptus saukros* Ni *in* Mu *et al.*, 1979 and *Didymograptus stamineus* Chen *in* Mu *et al.*, 1979 belong to *Baltograptus geometricus* as recent research indicated. The type material of *Didymograptus stamineus* Chen *in* Mu *et al.,* 1979 includes well preserved relief specimens showing the proximal development in detail in reverse view (Fig. 52C), clearly demonstrating it represents *Baltograptus geometricus*.

***Baltograptus novus* n. sp.**

Figure 54A, B, D, E, G

1987 *Expansograptus pusillus* (Tullberg); Maletz, p. 104, fig. 35–4.

Diagnosis. – Slightly declined *Baltograptus* with short ventral apertural side of sicula, separating it from the similar *Baltograptus geometricus*.

Holotype. – PMU 38434a, b, (Fig. 54B); from the 6.9–7.0 m level at Diabasbrottet; designated herein.

Paratype. – PMU 38435, from the 6.9–7.0 m level at Diabasbrottet, designated herein.

Etymology. – From *novus* (latin) for new, as the species is recognized as a new one, surprisingly as quite a number of species have already been included in the genus.

Description. – The tubarium is slender, with and interstipe angle of ca 130–150°, but this may be more variable due to the flexibility of the of the stipes and induced bending of the stipes on the sediment surface. The stipes are at least 10 mm long, but may be much longer. They are parallel-sided with a width of 0.5–0.7 mm, reached at the second theca of each stipe. The thecal inclination is about 22–25°, but slightly higher when measured at the apertures, which may be due to the flattening of the apertural parts of the thecae.

The sicula is about 1.5–1.6 mm long and mostly straight. It is 0.15 mm wide initially, widens to 0.2 m and then parallel-sided. The apertural part is slightly bent towards stipe 2. The aperture is straight and without a rutellum. The prosicula cannot be differentiated in any of the available specimens. The blunt apex with a short nema suggests a parallel-sided prosicula of sigmagraptine type. The free ventral side of the sicula is 0.2 mm long. The supradorsal part of the sicula is about 1.0 mm long and slender. The origin of th1^1 is at 0.7 mm below the apex of the sicula and is probably in the metasicula. Th1^1 forms a triangular feature 0.3 mm long and 0.2 mm wide above the crossing canals on the reverse side of the colony. Crossing canal one is a 0.2 mm wide tube, from which crossing canal two originates. It is 0.15 mm wide and grows back to the stipe 1 side and on top of th1^1 to form the next theca in a typical isograptid proximal development. This development is also visible on the obverse side by the long prothecal portion of th2^1 above the dorsal side of th1^1.

Remarks. – Maletz (1987) described and illustrated a single specimen of this species as *Expansograptus pusillus*, but the proximal development with the low origin of th1^1 indicates it belongs to *Baltograptus*. *Baltograptus novus* n. sp. is very similar to *Baltograptus geometricus* and the two species are easily confused. The free ventral side of the sicula in *Baltograptus novus* is shorter, measuring only 0.2 to 0.3 mm, while in *Baltograptus geometricus* it is 0.4–0.5 mm long.

Occurrence. – A number of specimens were found at 6.4–7.0 m in the *Baltograptus jacksoni* Biozone, associated with *Expansograptus urbanus* and *Pseudophyllograptus* sp. on the slabs. Nothing is known of its further distribution.

***Baltograptus floianus* n. sp.**

Figure 55A–I

Holotype. – PMU 38438/1a, b (Figs 55A–D), from the 2.8 to 2.9 m level at Diabasbrottet.

Paratypes. – All additional, largely juvenile specimens from the sample (Figs 55E–I) are regarded as paratypes. The slabs also contain *Paratetragraptus approximatus*, *Paratetragraptus vestrogothus*(?) and phosphatic brachiopods.

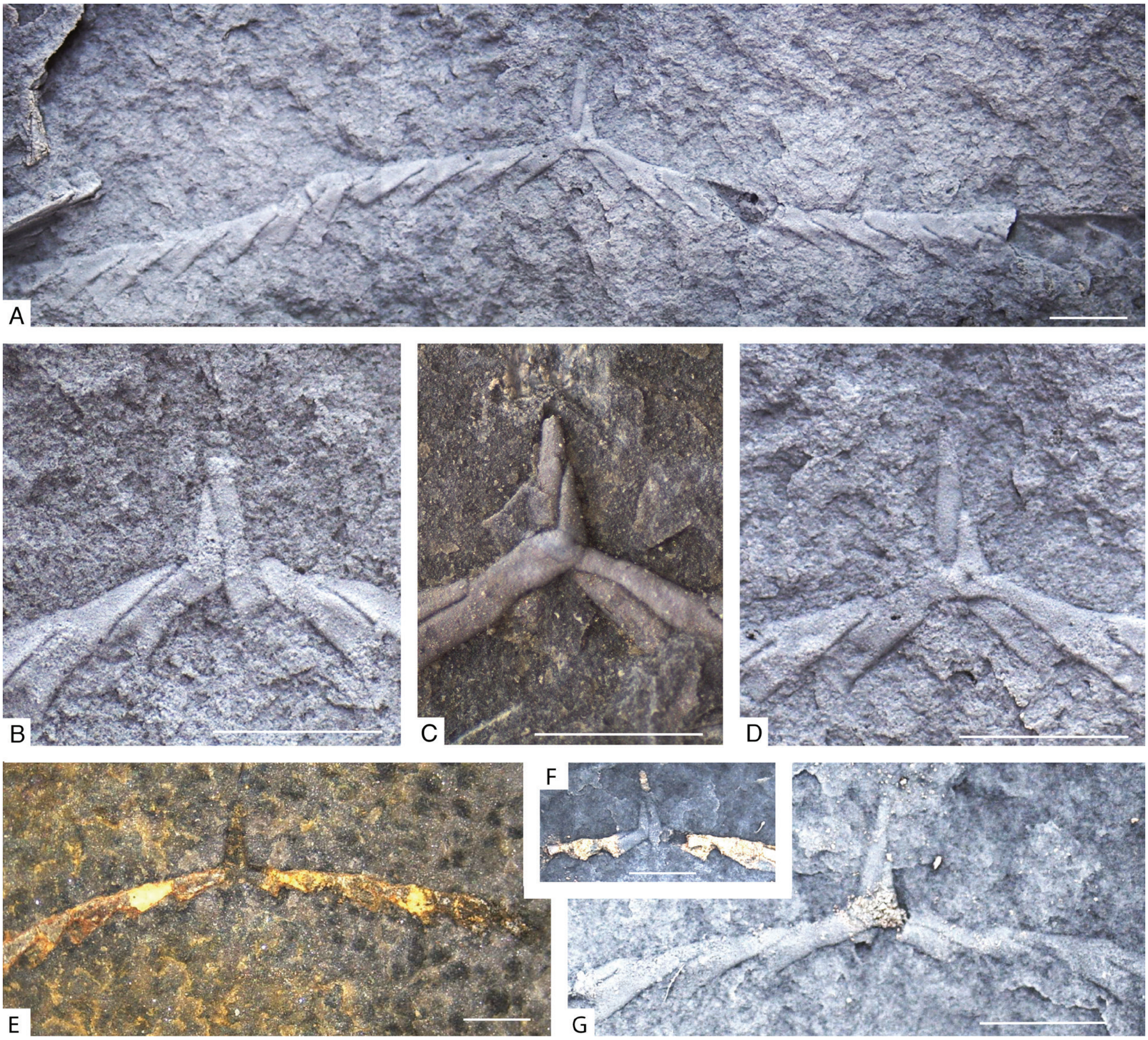

Fig. 54. Comparison of *Baltograptus novus* n. sp. and *Baltograptus geometricus* (Törnquist, 1901). **A**, **B**, **D**, **E**, **G**. *Baltograptus novus* n. sp. **A**, **D**, PMU 38435, Diabasbrottet at 6.9–7.0 m, paratype, proximal end in reverse view. **B**, PMU 38434a, Diabasbrottet at 6.9–7.0 m, holotype, proximal end in obverse view. **E–G**, PMU 38436a, b, low relief specimen, preserved as a mould in obverse (**E**) and reverse views (**G**), **F**, **G** are latex casts of the specimen, Diabasbrottet, 6.4–6.5 m. **C**, *Baltograptus geometricus*. PMU 38437, Diabasbrottet at 2.1–2.2 m, proximal end in reverse view for comparison. Scale bar is 1 mm in each photo.

Etymology. – The name is based on the village of Flo, name-giver of the Floian Stage of the Ordovician System (Bergström *et al*. 2004, 2006). The type material is from the GSSP section of the Floian Stage.

Diagnosis. – Declined *Baltograptus* with an unusually long and slender sicula, measuring more than 2.2 mm long.

Description. – *Baltograptus floianus* n. sp. has a slender, declined to slightly deflexed tubarium with a relatively long sicula and thecae with low inclination. The sicula is 2.2–2.4 mm long and gradually widens from the apex to the mid-length, after which it is parallel-sided. The apex often bears a short nema. The supradorsal part of the sicula is about 1.4–1.6 mm long and slender with the origin of th1^1 at 0.8–0.9 mm below its apex. It is impossible to differentiate the prosicula from the metasicula in the available material. The stipe width increases from 0.6 mm proximally to 0.1–1.0 mm distally in the first ten thecae. The 2TRD appears to be constant and is between 1.7 and 1.8 mm. The thecal inclination is 20–25° and increases slightly

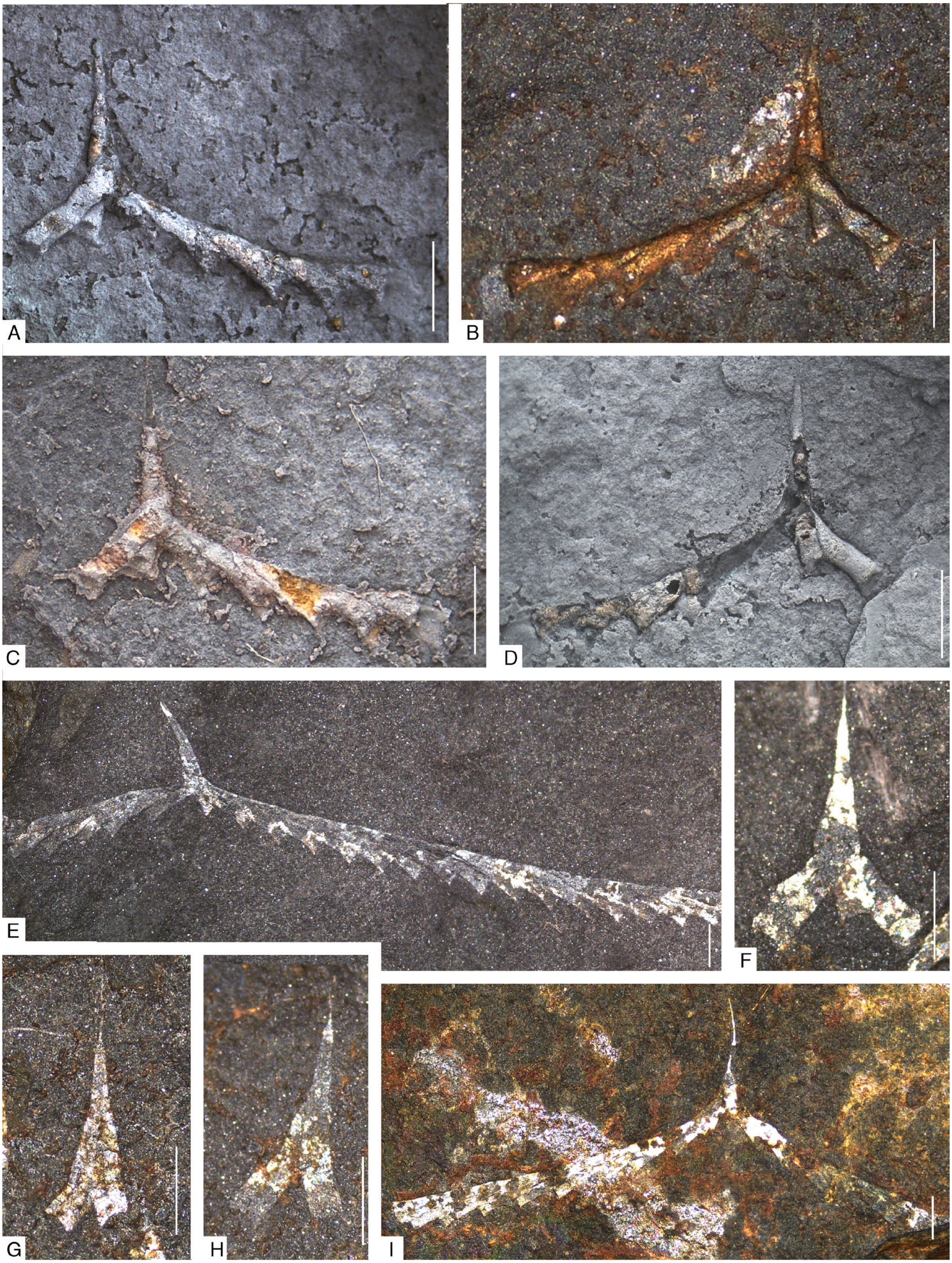

Fig. 55. Baltograptus floianus n. sp., Diabasbrottet at 2.8–2.9 m. **A–D**, PMU 38438a, b, (counterparts), holotype. **A**, latex cast coated with ammonium chlorite. **B**, mould in reverse view. **C**, specimen in reverse view. **D**, latex cast showing length of sicula. **E**, PMU 38439a, largest specimen, flattened. **F**, PMU 38438a/2, small specimen. **G**, PMU 38438a/3, juvenile. **H**, PMU 38438a/4, juvenile. **I**, PMU 38440, flattened specimen. Scale bar is 1 mm in each photo.

across the apertures due to a slight flare. The species lacks rutella.

Remarks. – The species is known from only a few specimens, but these are quite characteristic and can easily be differentiated from the similar *Baltograptus geometricus* by the long sicula and the more deflexed tubarium habit. It is the oldest known *Baltograptus* species with an elongated sicula. A strongly elongated sicula is also found in the strongly deflexed *Baltograptus extremus* Maletz & Slovacek, 2013 from the Dapingian of Dalarna with an artus-type proximal development. *Baltograptus extremus* is also present in the Lerhamn drillcore in Scania (Maletz & Ahlberg 2011).

Occurrence. – *Baltograptus floianus* has been found only at the 2.8–2.9 m level in the Diabasbrottet section in the middle part of the *Cymatograptus protobalticus* Biozone.

Genus *Cymatograptus* Jaanusson, 1965

Type species. – *Didymograptus undulatus* Törnquist, 1901 from the basal Floian *Tetragraptus phyllograptoides* Biozone of the Tøyen Shale of Mossebo (Diabasbrottet), Hunneberg, Sweden; original designation.

Diagnosis. – Horizontal to deflexed or declined didymograptids; sicula slender, with long supradorsal portion; proximal development of isograptid or artus type, dextral, with moderately low origin of th1^1 from the prosicula and comparably long free ventral apertural length of sicula; isograptid suture very short or absent; second stipe may be absent (slightly revised from Maletz *et al.* 2018b, p. 20).

Included species. – *Didymograptus balticus* Tullberg, 1880; *Didymograptus undulatus* Törnquist, 1901; *Didymograptus demissus* Törnquist, 1901; *Azygograptus validus* Törnquist, 1901; *Didymograptus protobalticus* Monsen, 1937; *Didymograptus* sp. cf. *Didymograptus rigoletto* Maletz, Rushton & Lindholm, 1991; *Azygograptus minutus* Beckly & Maletz, 1991; *Didymograptus rigoletto* Maletz, Rushton & Lindholm, 1991; *Cymatograptus bidextro* Toro & Maletz, 2008. Additional species may belong to this genus, but need to be investigated in more detail.

Remarks. – Jaanusson (1965) defined the genus to accommodate biramous didymograptids with prothecal folds and simple, dichograptid thecal apertures, but did not consider the proximal development. The type species *Didymograptus undulatus* Törnquist, 1901 shows quite variably developed prothecal folds and is in all characters of the proximal end structure comparable with a number of mostly subhorizontal to declined didymograptids from the early Floian.

The prothecal folds in *Cymatograptus undulatus* are here interpreted as a character of that species, but not of the genus and does not indicate a phylogenetic relationship with the sinograptids. The structure of these prothecal folds differs from the prothecal folds in the Sinograptdae. In the genus *Sinograptus* and related taxa, the folds are formed from the initial prothecal tubes growing upwards from their origin and then back on themselves (Fig. 56A). The prothecal folds protrude above the dorsal margins of the thecae. In *Cymatograptus undulatus*, by contrast, the prothecae are slender and parallel-sided (Fig. 56B). After growing along the dorsal side of the previous theca for a few tenths of a millimetre, the theca abruptly widens (at point m in Fig. 56B) to more than double the width of the protheca whilst continuing growing along the parent theca. At the point where the theca reaches its maximum width, the next protheca originates (point o in Fig. 56B). The dorsal undulation of the thecae is, thus, formed through the widening of the metathecae and cannot be interpreted to represent a prothecal fold in the sense of the prothecal fold development in the Sinograptidae. The dorsal undulation in *Cymatograptus undulatus* is quite variable (e.g. see Fig. 57J) and populations without it do occur. In

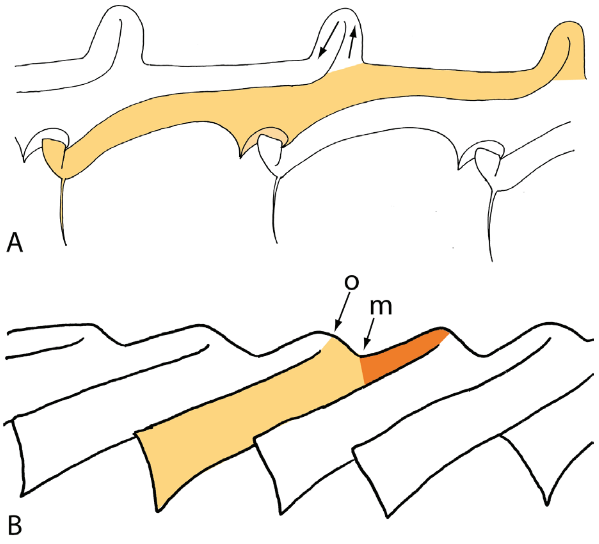

Fig. 56. 'Prothecal folding'. **A**, prothecal fold in *Sinograptus* (based on Maletz *et al.* 2018a). **B**, *Cymatograptus undulatus* (Törnquist, 1901), showing slender prothecae (darker color) and quickly widening metathecae (lighter color) at (m) forming a dorsal undulation of the stipe, but not a prothecal fold in the strict sense. Illustrations not to scale.

some specimens, the undulation decreases drastically distally (Fig. 40E). Dorsal undulation also occurs in a specimen of *Cymatograptus demissus* (Törnquist) from the Lerhamn drillcore (Maletz & Ahlberg 2011, fig. 3F).

The early single-stiped species *Azygograptus validus* and *Azygograptus minutus* (see Beckly & Maletz 1991) possess a long and distinctly widening sicula and a high, possibly prosicular origin of th1^1. Their sicular structure and th1^1 development closely resemble those of the coeval *Cymatograptus*. These two are here therefore re-interpreted as single-stiped *Cymatograptus* species. A revision of the single-stiped dichograptids from the Tøyen Shale Formation of Scandinavia is beyond the scope of this paper, but their proximal development and sicular structure are quite variable. Maletz (2014) included the genera *Azygograptus* and *Jishougraptus* in the Sigmagraptidae and discussed the single-stiped specimens from the Chewtonian of western Newfoundland (Maletz 2004) as an indication for the sigmagraptine relationships of the azygograptids.

Cymatograptus bidextro Toro & Maletz, 2008 from the Floian *Baltograptus deflexus* Biozone is the only species of the genus with either dextral or sinistral development of the proximal end. The species is the only one of the genus with an artus-type proximal end. It shows a variably developed dorsal undulation, similar to *Cymatograptus undulatus*.

Cymatograptus undulatus (Törnquist, 1901)

Figures 40E; 56B; 57A–J; 58A–L

1901 *Didymograptus undulatus* n. sp. Törnquist, p. 10, pl. 1, figs 1–7.
1965 *Cymatograptus undulatus* (Törnquist); Jaanusson, p. 419, fig. 5.
1987 *Cymatograptus undulatus* (Törnquist); Maletz, p. 133, fig. 43: 1, 2.
1996 *Cymatograptus undulatus* (Törnquist); Maletz, Löfgren & Bergström, fig. 13: 6.
2011 *Cymatograptus undulatus* (Törnquist); Maletz & Ahlberg, fig. 3E.
?2015 *Cymatograptus* cf. *undulatus* (Törnquist); Percival, Kraft, Zhang & Sherwin, fig. 1: 3.

Type material. – LO 1574T (Fig. 57E, F) is here selected as the lectotype of *Cymatograptus undulatus*. LO 1575t (Törnquist 1901, pl. 1, fig. 3), LO 1576t (Törnquist 1901, pl. 1, figs 2, 7), the latter listed as LO 1580t in type catalogue, but clearly representing the same specimen, LO 1577t (Törnquist 1901, pl. 1, fig. 4; not identified) and LO 1578t & counterpart (Törnquist 1901, pl. 1, figs 5, 6; fig. 6 listed as LO 1579t in type catalogue) are the paratypes.

Material. – Numerous specimens from the *Tetragraptus phyllograptoides* Biozone of Mossebo and Diabasbrottet found in several museum collections and collected by the author at Diabasbrottet and Mossebo. Additional material from the Oslo Region of Norway has been investigated.

Diagnosis. – Robust *Cymatograptus* with horizontal to proximally deflexed stipes and variably developed dorsal undulation.

Description. – This description is based on the majority of the material, but excludes the slender or wide forms included in the species. The tubarium is generally horizontal, but stipes range from slightly deflexed to declined proximally. The supradorsal part of the sicula and th1^1 is slender but prominent. The sicula is 2.4–2.6 mm long and nearly straight, bending slightly towards stipe 2 aperturally. It gradually widens from the apex to an apertural width of ca 0.4 mm. The nema is preserved in many specimens and can reach a length of up to 10 mm. A short rutellum of 0.1–0.2 mm occurs in well-preserved specimens. The origin of th1^1 is about 0.2–0.25 mm below the apex of the sicula, thus presumably is in the lower part of the prosicula. Th1^1 gradually widens and bends outwards at about 1.5 mm below the apex of the sicula. The proximal development is dextral, isograptid type. The dorsal undulation appears to begin with the development of th1^2, which is from a lateral bulge on the right side of th1^1 (Fig. 57I), but the details are unclear. Relief specimens show the parallel-sided prothecae and the abrupt widening of the metathecae with the distally often diminishing height of the dorsal undulation. Further widening towards the aperture is minimal. The rutella are barely visible, but this may be increased by the flattening of the colonies. The thecal inclination is about 35° and is constant throughout the colony. A slight curvature of the thecae is enhanced by the usual compression of the material and is not visible in the few relief specimens. The stipes widen rapidly to a final width of 1.2–1.3 m, rarely wider. They reach lengths of more than 10 mm.

Remarks. – The species is well known from flattened and relief material. Jaanusson (1965) showed the development of the prothecal folds from relief specimens. Stipe width is highly variable, with end members ranging from extremely slender to extremely wide and could easily be mistaken for different species. Specimens from the 1.4–1.6 m level at Diabasbrottet are robust, showing a higher thecal inclination reaching 45–50° and a stipe width of 1.5–1.7 mm (Figs 57B; 58A, B). However, they do not

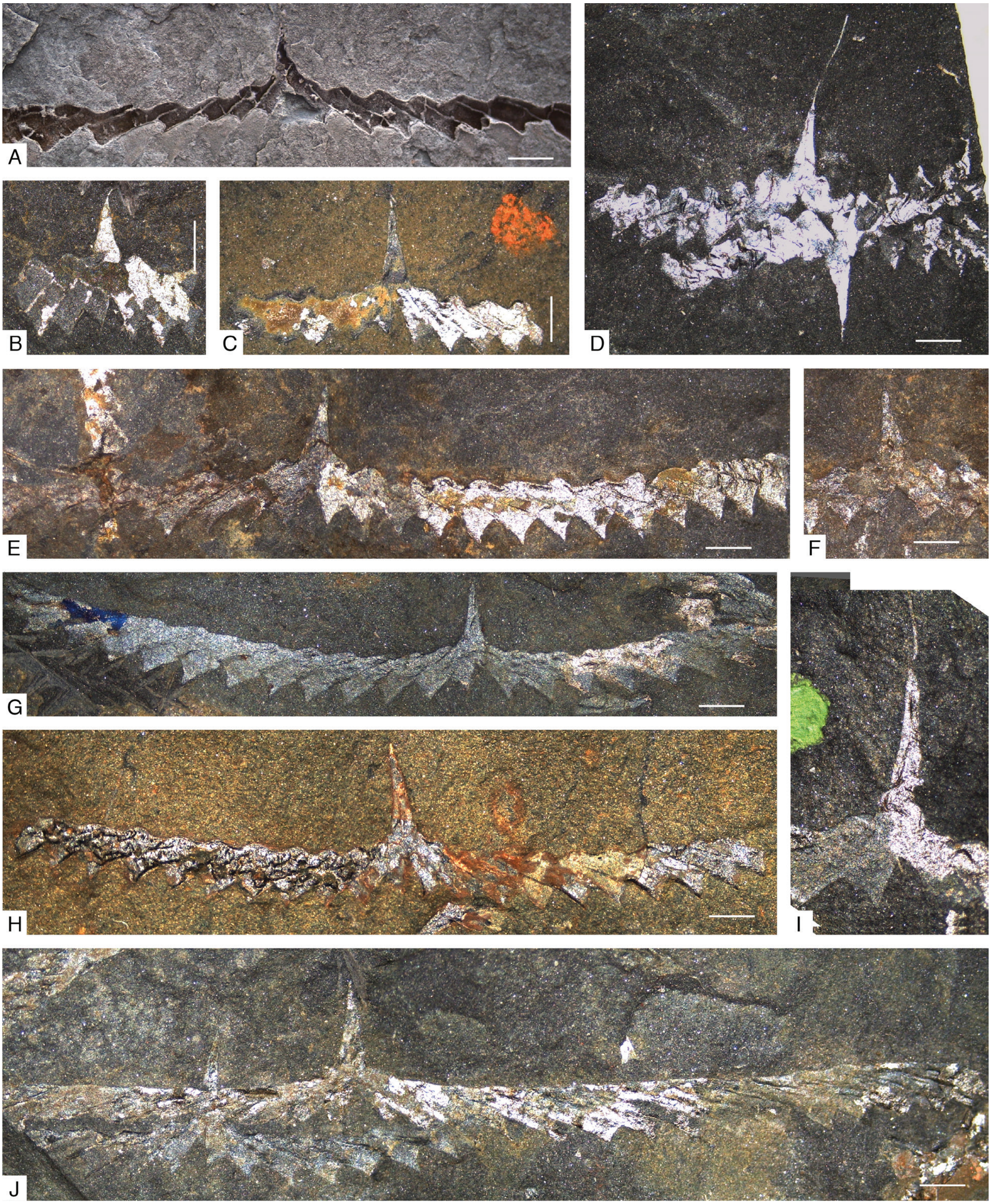

Fig. 57. *Cymatograptus undulatus* (Törnquist, 1901). **A**, PMU 38415/2, mould in reverse view, coll. Törnquist. **B**, PMU 38441, specimen with highly inclined thecae, Diabasbrottet at 1.4–1.5 m. **C**, RM Cn 1838, Mossebo, coll. G. Holm, 1877. **D**, RM Cn 1614, specimen with high undulation, coll. G. Holm, Mossebo. **E**, **F**, LO 1574T, lectotype (**E**) and proximal end of counterpart (**F**), Mossebo. **G**, RM Cn 1209, flattened specimen in reverse view, showing isograptid arch, Mossebo, coll. G. Holm, 1879. **H**, RM CN 1973, partial relief, reverse view, Mossebo, coll. G. Holm, 1877. **I**, RM Cn 1212, Mossebo, coll. G. Holm, 1879. **J**, RM Cn 1431, coll. G. Holm, 1879, specimen with barely any dorsal undulation, low undulation visible in second specimen on slab (left side). Scale indicated by 1 mm long bar in each photo.

differ in other respects and are regarded as intraspecific variants of *Cymatograptus undulatus*. There is no information on any biostratigraphic relevance of this form as it was only found in one locality.

Slender forms without the prominent dorsal undulation are more widely distributed and occur together with the undulose forms. The specimen with very low undulations shown in Fig. 57J occurs together with a more 'normal' specimen (lower left side of photo) showing higher dorsal undulation. The two specimens occur together with *Tetragraptus phyllograptoides* and *Tetragraptus gerhardi* n. sp.

Occurrence. – The species has been found only in the *Tetragraptus phyllograptoides* Biozone of Sweden and Norway, where it is extremely abundant at some levels. Percival *et al.* (2015) illustrated a proximal end of an expansograptid as *Cymatograptus* cf. *undulatus* from the Floian of New South Wales, Australia, but the specimen shows only a vague undulation of the dorsal side of the stipes. The specimen is a proximal end with two complete thecae preserved on stipe 1 and only one theca on stipe 2. The development of folds cannot therefore be seen. The proximal end with the long ventral free side of the sicula may indicate a *Cymatograptus* species.

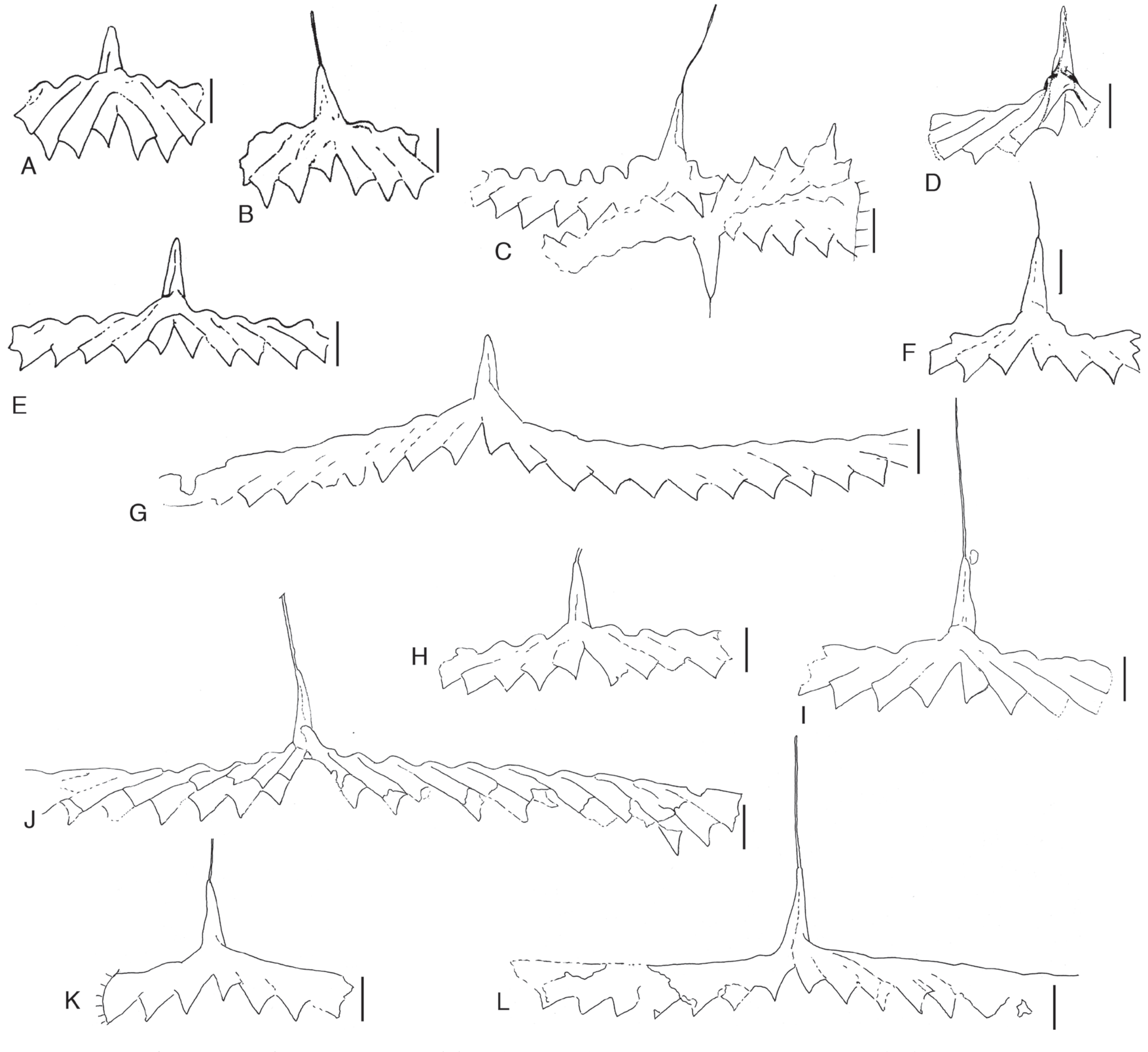

Fig. 58. Intraspecific variation of *Cymatograptus undulatus* (Törnquist). **A**, PMU 38441, reverse view, Diabasbrottet at 1.4–1.5 m. **B**, PMU 38442a, reverse view, Diabasbrottet at 1.5–1.6 m. **C**, RM Cn 1614, specimen showing very strong dorsal undulation, Mossebo, coll. G. Holm, 1879. **D**, T 54, latex cast in reverse view, Tøyen section at 7.32–7.85 m, Oslo, Norway. **E**, PMU 38443, low relief specimen in reverse view, Diabasbrottet at 1.0-1.1 m. **F**, RM Cn 1242, Mossebo, coll. G. Holm, 1879. **G**, RM Cn 1211, Mossebo, specimen with low undulation, coll. G. Holm, 1878. **H**, PMU 38444b, Mossebo. **I**, LO 1578t (Törnquist, 1901, pl. 1, fig. 5). **J**, PMU 38415/2, mould of specimen showing loss of undulation distally, aperture of sicula not preserved. **K**, **L**, PMU 38445/1, PMU 38445/2, Mossebo, coll. Erdtmann, specimens with barely any dorsal undulation. Scale bar is 1 mm for each specimen.

Cymatograptus balticus (Tullberg, 1880)

Figures 59B, D, E, H; 60F–I

pars 1880 *Didymograptus balticus* n. sp. Tullberg, p. 41, pl. 2, figs 2, 3 (*non* pl. 2, fig. 1 = *Corymbograptus v-fractus tullbergi*).
non 1901 *Didymograptus balticus* Tullberg; Törnquist, p. 19, pl. 2, figs 21, 22, 24 (=*Cymatograptus* sp. cf. *C. balticus* Tullberg); *non* pl. 2, figs 23, 25 (= Didymograptid indet).
1937 *Didymograptus balticus* Tullberg; Monsen, p. 140, pl. 3, fig. 24; pl. 10, figs 2, 5.
?1939 *Didymograptus* aff. *balticus* Tullberg; Schmidt, p. 183, pl. 4, fig. 8.
1987 *Expansograptus balticus* (Tullberg); Maletz, p. 95, figs 29/1; 30/2,3 (*non* fig. 30/1 = *Corymbograptus v-fractus tullbergi*).
1993 *Didymograptus balticus* Tullberg; Toro, p. 71, fig. 3: 1; fig. 4: 1, 2.
1996b *Didymograptus* (s.l.) *balticus* Tullberg; Maletz, p. 108, figs 1a–h, 3a, d.
1996 *Didymograptus balticus* Tullberg; Maletz *et al.*, p. 156, fig. 13: 11.
non 1997 *Didymograptus* (s.l.) *balticus* Tullberg; Toro, pl. 2, figs 9, 10 (= *Cymatograptus protobalticus*).
?2008 *Corymbograptus balticus* (Tullberg); Luo & Zhang, fig. 7H, I (NIGP 140867, 140868).
2009 *Didymograptus* s. l. *balticus*; Zalasiewicz, Taylor, Rushton, Loydell, Rickards & Williams, fig. 3: 27.

Type material. – Lectotype LO 342t, from the Lower Didymograptus Shale (now Tøyen Shale) of Kiviks-Esperöd, Scania, Sweden, designated Maletz (1996b). The specimen occurs together with a specimen of *Expansograptus suecicus*. Of the three syntypes, LO 341T was referred to *Corymbograptus v-fractus tullbergi* (Monsen, 1937) by Maletz (1996b). The third specimen is considered lost.

Material. – Several specimens from the *Cymatograptus protobalticus* and *Baltograptus jacksoni* biozones at Diabasbrottet and Mossebo. The species is uncommon.

Diagnosis. – Robust, declined *Cymatograptus* with long and slender sicula and deep indentation between ventral sides of sicula and th1^1. Crossing canals positioned at mid-length of the sicula.

Description. – The species is characterized by a robust, declined tubarium with an extremely long sicula. The angle between the stipes is about 80–90° initially, but the stipes have gentle dorsal curvature, decreasing the divergence to to 140–150°. They are more than 40 mm long and have a uniform width of 1.7–1.9 mm. The thecae are simple without rutella, and with an inclination of about 16–20°, rarely more, with a maximum of 25°. Higher angles at the thecal apertures are likely to be caused by flattening of the stipes. They show considerable overlap and a cross section close to the thecal apertures intersects three to four thecae.

The proximal development is known from relief specimens (Maletz 1996b). It is isograptid, dextral with a relatively high position of the isograptid arch at around the mid-length of the sicula (Fig. 59B). The crossing canals grow obliquely downwards. They differ considerably in width with crossing canal 1 being much wider than crossing canal 2. The sicula is 4.2–4.8 mm long, forming a long and slender cone that widens little towards the aperture. The length of the prosicula is unknown as no isolated material is available. A long nema occurs in a number of specimens, but is often broken off distally. The ventral walls of the sicula and th1^1 form a deep indentation. The ventral wall of the sicula is often more than 1 mm long, an important character of the species that is also visible in poorly preserved, flattened material.

Remarks. – In poor preservation, *Cymatograptus balticus* (Tullberg, 1880) has been confused with *Corymbograptus v-fractus tullbergi* (Monsen, 1937), a deflexed species with a shorter sicula and slightly curved, aperturally widening thecae (see Maletz,1996b). Törnquist (1901) described a number of specimens from the Hunneberg as *Didymograptus balticus*. His specimens, however, are smaller as was already remarked by Monsen (1937) and they are here referred to *Corymograptus*(?) *vicinatus*, as do the specimens from Flagabro (Törnquist 1901, pl. 2, figs 23, 25).

Harris & Thomas (1938a, fig. 35) figured a specimen as *Didymograptus* cf. *balticus* from the Chewtonian Ch3 of Victoria, Australia. The specimen is more horizontal and bears relatively slender stipes. Thomas (1960) identified the same specimen as *Didymograptus* cf. *balticus*.

Occurrence. – The species has been described from Norway and Sweden, but a wider distribution is uncertain. The species is restricted to the *Cymatograptus protobalticus* and *Baltograptus jacksoni* biozones in Scandinavia. As it is not common, Maletz (1996b) suggested not to use it as a zonal index and provided an overview of all material of this species identified up to then. *Cymatograptus balticus* probably occurs in the Baltic countries, where it has been used as a zonal index, but has never been figured (see Kaljo 1974; Ulst 1976; Paškevičius 2011). Zalasiewicz *et al.* (2009) mentioned *Cymatograptus balticus* from the *Baltograptus varicosus* Biozone in Britain and provided a poor illustration of unknown origin. The occurrence of *Cymatograptus balticus* in Australia is uncertain, even though VandenBerg & Cooper (1992) indicated its presence in the upper Bendigonian and Chewtonian, but stated that the occurrence of the species is 'not well documented in Australasia'.

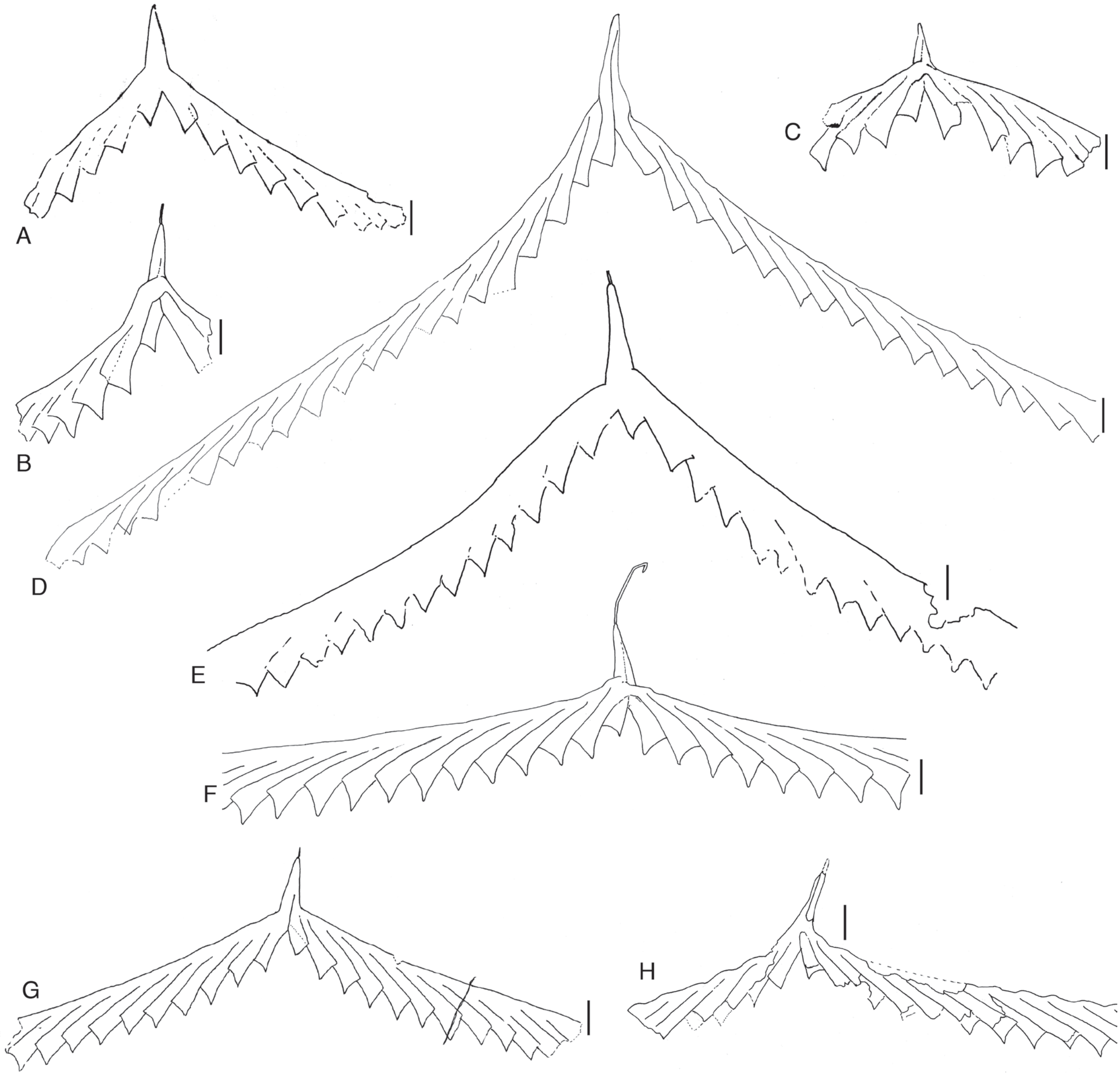

Fig. 59. *Cymatograptus* species. ?**A**, **C**, **F**, **G**. *Cymatograptus protobalticus* (Monsen, 1937). **A**, PMU 38446, declined specimen, Diabasbrottet at 6.0–6.1 m. **C**, LO 7132t, low relief specimen in reverse view, Diabasbrottet at 2.1–2.2 m. **F**, PMU 23154, slightly deflexed specimen, Diabasbrottet, 2.0–2.1 m. **G**, PMO K 953, paratype, Galgeberg, Oslo, Norway, after drawing by K. Lindholm. **B**, **D**, **E**, **H**. *Cymatograptus balticus* (Tullberg, 1880). **B**, LO 7131t, reverse view, Diabasbrottet at 2.9–3.0 m. **D**, PMU 38447, mould of large specimen, Diabasbrottet at 5.9–6.0 m. **E**, PMU 38393/1, old collection 'Mossebo'. **H**, RM Cn 1280, drawing of latex cast of relief specimen, Mossebo. All scale bars indicate 1 mm.

Cymatograptus protobalticus (Monsen, 1937)

Figures 59A?, C, F–G; 60A–E, J–L; 62L

1933 *Didymograptus patulus* (J. Hall); Elles, p. 100, fig. 9.
1937 *Didymograptus protobalticus* n. sp. Monsen, p. 138, pl. 3, figs 2, 3, 40; pl. 9, fig. 5.
1979 *Didymograptus protobalticus* Monsen; Jackson, p. 28, fig. 4a–c (no description).
1987 *Expansograptus protobalticus* (Monsen); Maletz, p. 98, figs 29: 2, 3; 31: 1–5.
1987 *Corymbograptus* sp. 1; Maletz, p. 106, fig. 33: 1, 2.
cf. 1988 *Didymograptus* (*Expansograptus*) *latus* Hall; Williams & Stevens, p. 48, pl. 12, fig. 14; text-fig. 34a–h.
1991 *Expansograptus protobalticus* (Monsen); Palmer & Rickards, pl. 96.
1992a *Cymatograptus protobalticus* (Monsen); Maletz, p. 142, figs 54: 1; 72: 3: 74: 1–12.
1995 *Didymograptus* (*Expansograptus*) sp.; Ortega & Rao, p. 306, pl. 1, figs 11, 15, 16; pl. 2, fig. 9.
1995 *Didymograptus* (s.l.) cf. *protobalticus* Monsen; Ortega & Rao, p. 309, pl. 1, fig. 9.

1996b *Didymograptus* (s.l.) *protobalticus* Monsen; Maletz, p. 111, figs 2A–E, 3C, F–H.
1996 *Didymograptus protobalticus* Monsen; Maletz, Löfgren & Bergström, p. 156, fig. 13: 8.
?1997 *Didymograptus* (s.l.) *balticus* Tullberg; Toro, pl. 2, figs 9, 10.
?1997 *Didymograptus* (s.l.) *protobalticus* Monsen; Toro, pl. 2, fig. 11.
2004 *Didymograptus protobalticus* Monsen; Cooper *et al.*, fig. 9q (no description).
?2016 *Cymatograptus* cf. *protobalticus* (Monsen); Gutiérrez-Marco & Martin, fig. 4J (no description).
2018 *Cymatograptus protobalticus* (Monsen); Maletz & Ahlberg, fig. 8F (no description).
2021 *Cymatograptus protobalticus* (Monsen, 1937); Maletz & Ahlberg, fig. 1G (no description).

Type material. – Holotype PMO K0955 (Monsen 1937, pl. 9, fig. 5), from the *Paratetragraptus approximatus* Biozone at Galgeberg, Oslo, Norway; paratypes PMO K0953 (Fig. 59G) and PMO K0639, see Maletz (1996b).

Material. – Many specimens from the *Cymatograptus protobalticus* Biozone and the lower part of the *Baltograptus vacillans* Biozone at Diabasbrottet and Mossebo sections, Hunneberg, Västergötland.

Diagnosis. – Robust, subhorizontal to slightly declined *Cymatograptus* with moderately long and slender sicula and deep indentation between ventral sides of sicula and th1^1. Crossing canals positioned at mid-length of the sicula.

Description. – The species is characterized by a slightly declined to deflexed tubarium with a relatively long sicula perpendicular to the stipes. The sicula is 3.0–3.3 mm long and 0.4–0.5 mm wide at the aperture. The nema is conspicuous and can be several mm long. The sicula is slightly bent towards stipe 2 distally. The sicular aperture appears straight, with no rutellum, as are the apertures of the thecae. The supradorsal length of the sicula is about 1.4–1.6 mm. The origin of th 1^1 is high on the sicula, most probably in the prosicula, but isolated material is not available to determine this. The free ventral part of the sicula varies strongly in *Cymatograptus protobalticus* and increases from 0.2–0.3 mm in juveniles to up to 0.9 mm in mature specimens. Due to this growth, they develop a deep indentation between the ventral sides of the sicula and th1^1, similar to *Cymatograptus balticus*. The proximal development is also similar to that of *Cymatograptus balticus*, with an isograptid, dextral development (Fig. 59C). The isograptid suture is fairly short.

The stipes have a width of 1.6–1.8 mm at the apertures of th1^1 and th1^2 and increase distally to 1.9–2.2 mm. The 2TRD is a constant 1.8–2.1 mm in most specimens. The thecal inclination is 20–22° initially and increases to 40–45° at apertures. Fragments with stipe length of more than 80 mm occur. The usual length of the stipes in mature specimens is about 30 mm.

Remarks. – The proximal development and thecal style is very similar to that of *Cymatograptus balticus* and the main differences are the longer sicula and the more declined stipes in *Cymatograptus balticus* (Maletz 1996b).

Occurrence. – *Cymatograptus protobalticus* is common in Scandinavia, where it has been described or listed from Hunneberg (Maletz 1996b; Maletz *et al.* 1996), from a number of drill cores in southern Sweden (Lindholm 1981, 1992; Maletz & Ahlberg 2011) and from the Oslo Region of Norway (Monsen 1937). Jackson (1979) described it from the Skiddaw Slates of Britain.

Cymatograptus kristinae n. sp.

Figures 61A-I; 62A–E, J–K; 63A–C

1987 *Expansograptus demissus* (Törnquist) Maletz, p. 86, fig. 26: 7–10.
?1991 *Cymatograptus* sp. cf. *C. rigoletto*; Maletz, Rushton & Lindholm, p. 341, fig. 7a–c.
1992 *Cymatograptus* sp. cf. *Cymatograptus rigoletto*; Maletz, p. 142, figs 73.7–73.14.
?1995 *Didymograptus* (s. l.) *rigoletto* Maletz, Rushton & Lindholm; Ortega & Rao, p. 308, pl. 1, figs 8, 10, 12, 13.
?1997a *Didymograptus* (s.l.) cf. *D. rigoletto* Maletz, Rushton & Lindholm; Toro, pl. 1, figs 4–6.
2001 *Didymograptus* aff. *protobalticus* Monsen; Tolmacheva, Koren', Holmer, Popov & Raevskaja, p. 559, text-fig. 6, figs 9–12; text-fig. 7, figs 4, 7–10; text-fig. 8, figs 1–3.

Holotype. – PMU 38459, (Fig. 62A) from the upper part of the *Tetragraptus phyllograptoides* Biozone at Diabasbrottet at the 1.6–1.7 m level.

Paratypes. – All additional illustrated specimens (Figs 62B–E, J–K, 63A–C) are regarded as paratypes.

Material. – Several flattened specimens from the Diabasbrottet section at 1.6–1.7 m in the *Tetragraptus phyllograptoides* Biozone.

Etymology. – The species is named after Kristina Lindholm, graptolite specialist from Lund, Sweden, who established the *Hunnegraptus copiosus* Biozone and its fauna from material collected at Storeklev, Hunneberg.

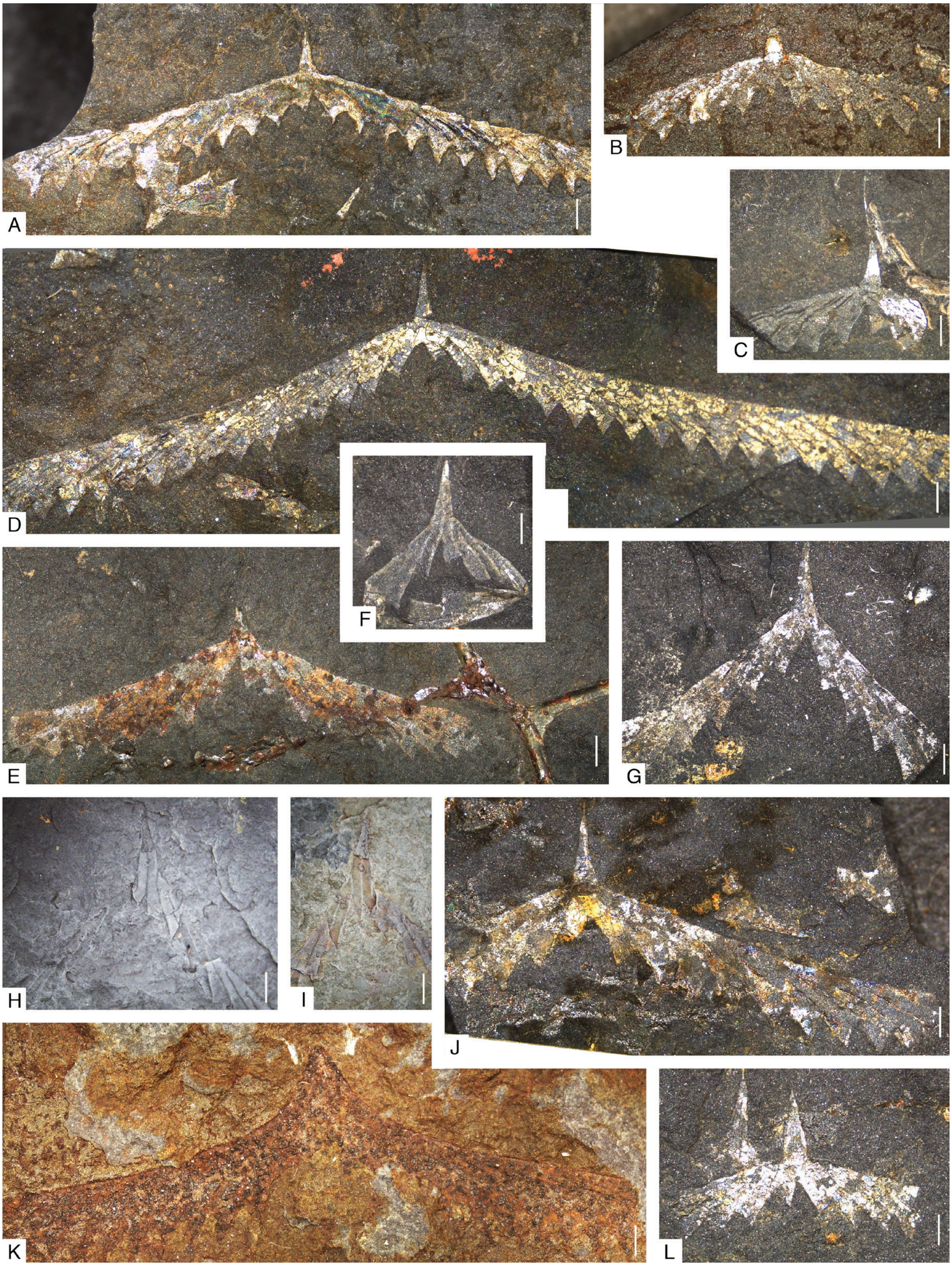

Fig. 60. *Cymatograptus* species. **A–E**, **J–L**. *Cymatograptus protobalticus* (Monsen, 1937). **A**, PMU 38448, Diabasbrottet at 2.1–2.2 m, two flattened specimens. **B**, PMU 38449, Diabasbrottet at 2.1–2.2 m. **C**, PMU 38450, proximal end, Diabasbrottet at 2.0–2.1 m. **D**, RM Cn 1340, specimen with long stipes, Mossebo, coll. G. Holm, 1879. **E**, PMU 38451/1, specimen associated with *Clonograptus multiplex*, PMU 38451/2, Diabasbrottet at 4.5–4.6 m. **J**, PMU 38452, flattened specimen, Diabasbrottet, 2.9–3.0 m. **K**, PMU 38453b, proximal end of large specimen with poor, more declined to deflexed proximal end. **L**, PMU 38454, small specimen, Diabasbrottte, 2.9-3.0 m. **F–I**. *Cymatograptus balticus* (Tullberg, 1880). **F**, PMU 38455, proximal end of larger specimen, Diabasbrottet at 2.9–3.0 m. **G**, PMU 38456, Diabasbrottet at 2.9–3.0 m. **H–I**. PMU 38447, latex cast (**H**) and mould (**I**) of proximal end. Scale bar is 1 mm in each photo.

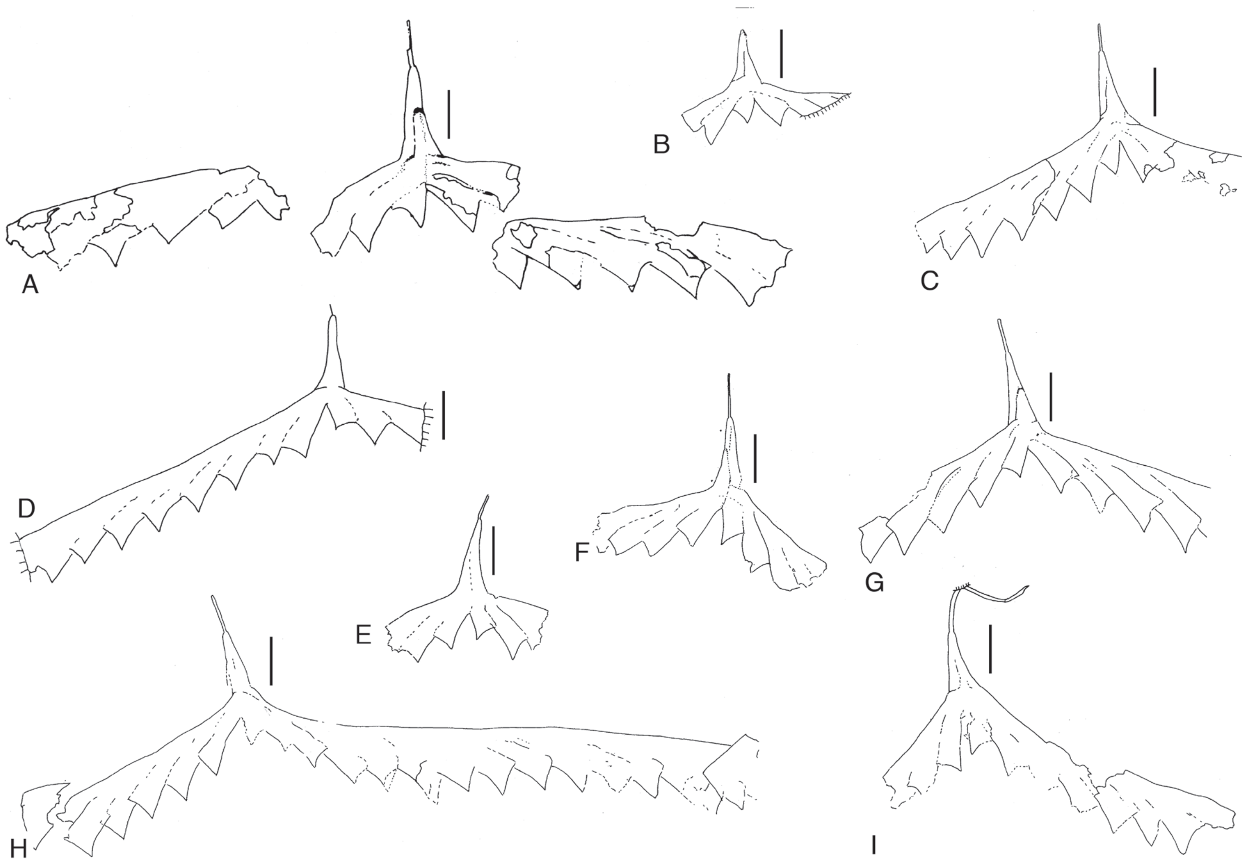

Fig. 61. *Cymatograptus kristinae* n. sp. All specimens from Diabasbrottet at 1.6–1.7 m. **A**, MBg Di 491/82/2. **B**, PMU 38457/1, DI 494/89A-10. **C**, PMU 38457/2. **D**, PMU 38478. **E**, PMU 38457/3. **F**, PMU 38458/1. **G**, MBg DI 494/87. **H**, PMU 38458/2, longest specimen. **I**, PMU 38458/3. Scale bars are 1 mm long at each specimen.

Diagnosis. – Medium-sized *Cymatograptus* with a slightly declined to proximally deflexed, fairly robust tubarium and a slender supradorsal part of sicula and th1^1 and a possibly delayed origin of th1^1.

Description. – The tubarium is subhorizontal to somewhat deflexed with a stipe width of ca 1.6–1.7 mm distally. The sicula is perpendicular to the stipes and bends slightly towards stipe 2 aperturally. It has a length of 2.2–2.3 mm and lacks a rutellum. The sicular aperture is 0.4–0.5 mm wide. The origin of th1^1 is 0.6 mm below the sicular apex and may be in the upper part of the metasicula. The free ventral side of the sicula is 0.7 mm long. Many specimens have a short nema that appears to be broken distally. The proximal development is isograptid, dextral but is difficult to see in the largely flattened material. The reverse side shows a wide and rounded isograptid arch with a very short isograptid suture. The stipe width is 0.9–1.0 mm proximally and increases to 1.6–1.7 mm distally. The increase in width is achieved in the first four to five thecae and the stipe width appears to be constant afterwards. The thecal inclination is 28–30°. The 2TRD is 1.6 mm proximally and increases to 1.8–2.0 mm distally. Specimens are relatively small, with the longest stipe having 10 thecae.

Remarks. – The species differs from related forms by the position of the origin of th1^1, which appears to be fairly low and may be in the metasicula, unless the tubaria have elongated prosiculae. The high supradorsal part of the sicula is similar to that of *Cymatograptus rigoletto*, but the latter has more slender stipes with a lower thecal inclination.

Occurrence. – The species was known only from the Hunneberg sections (Maletz 1987, 1992), but has recently been described also from the St. Petersburg area of Russia (Tolmacheva *et al.* 2001), where it occurs together with *Tetragraptus phyllograptoides* in the *Prioniodus elegans* conodont zone. The material of *Didymograptus* aff. *rigoletto* from the Krapperup

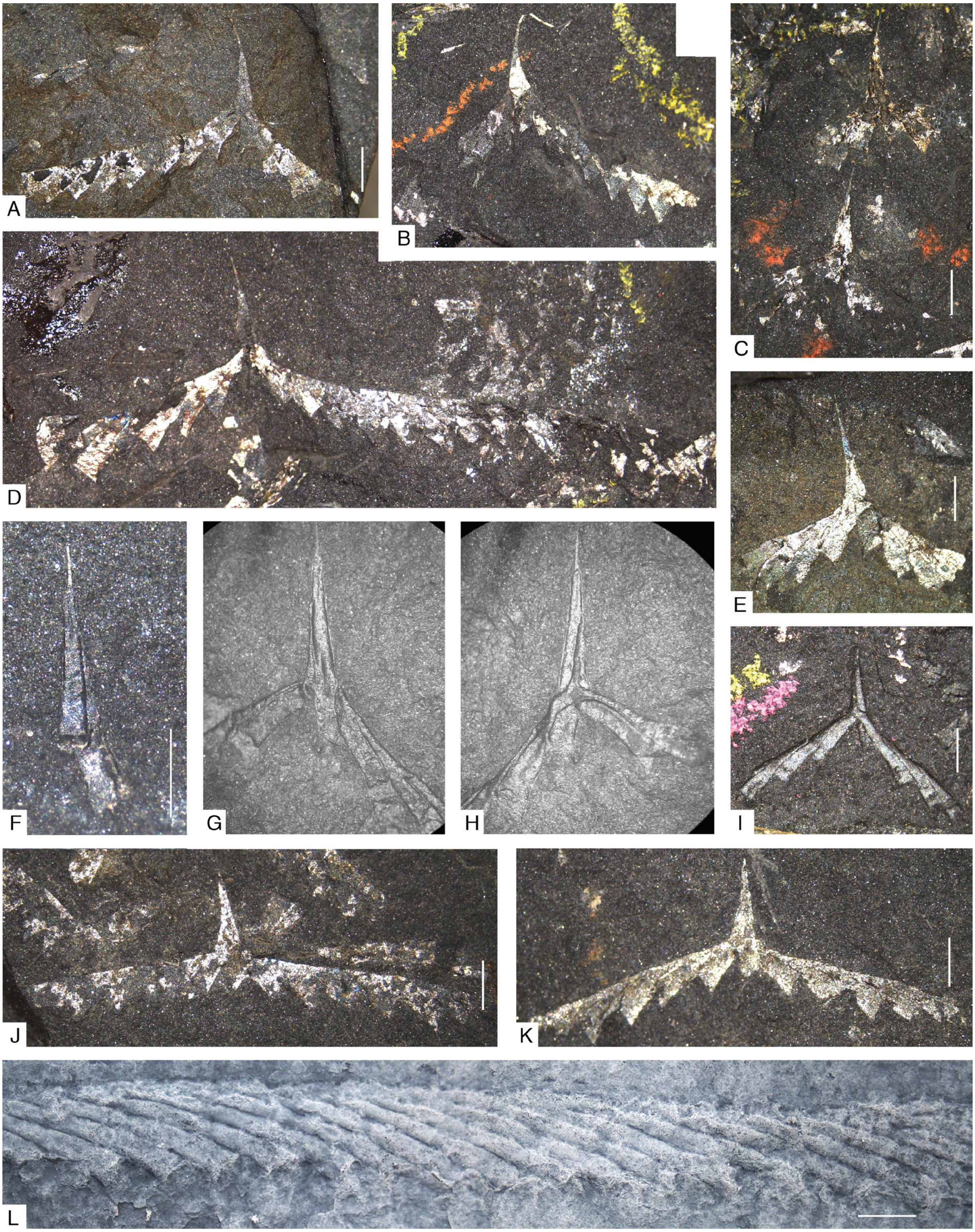

Fig. 62. **A–E, J**, **K**. *Cymatograptus kristinae* n. sp. All specimens from Diabasbrottet at 1.6–1.7 m. **A**, PMU 38459, holotype. **B**, PMU 38458/3. **C**, PMU 38457/3 (upper), PMU 38457/4 (lower), two small specimens. **D**, PMU 38458/2. **E**, PMU 38458/1, flattened proximal end in obverse view. **J**, PMU 38460, Diabasbrottet, 1.7–1.8 m. **K**, PMU 38461, Diabasbrottet, 1.7–1.8 m. **F**. *Cymatograptus validus* (Törnquist, 1904), juvenile on slab with LO 1755T, 1756t (*C. validus* types), Mossebo, coll. Moberg, 1892. **G–I**. *Cymatograptus rigoletto* (Maletz *et al*., 1991). **G**, **H**, LO 6270T, holotype, latex casts of counterparts in obverse (**G**) and reverse (**H**) views. **I**, LO 6276t, Krapperup drillcore at 95.64–96.71 m. **L**. *Cymatograptus protobalticus* (Monsen, 1937), PMU 38465, latex cast of distal part showing thecal overlap. Scale bar is 1 mm in each photo.

drill core illustrated by Maletz *et al.* (1991, fig. 7a–c) is similar, but has a longer sicula. Until more is known of the intraspecific variation of *Cymatograptus* species, it cannot be assigned to *Cymatograptus kristinae* with certainty.

Material of *Didymograptus* (s. l.) *uniformis* Elles & Wood from the *Paratetragraptus akzharensis* Biozone of the Argentinian Cordillera Oriental (Toro 1997a) may also belong to this species. The illustrations show that the sicula is at least 2.2–2.5 mm long and that the origin of th1^1 is relatively low. The material is slightly younger than the Hunneberg specimens. Ortega & Rao (1995) described a fairly robust form that might belong to *Cymatograptus kristinae* as *Didymograptus* (*s. l.*) *rigoletto* from the Sierra de Cajas, eastern Cordillera of Argentina.

Cymatograptus demissus (Törnquist, 1901)

Figures 26B; 63D–M; 64K, L

1901 *Didymograptus demissus* n. sp. Törnquist, p. 11, pl. 1, figs 8–11.
non 1937 *Didymograptus* cf. *demissus* Törnquist; Monsen, p. 132, pl. 2, fig. 2 (?= *Cymatograptus rigoletto*).
1991 *Didymograptus* (s.l.) *demissus* Törnquist; Maletz, Rushton & Lindholm, fig. 7d.
1995 *Expansograptus demissus* (Törnquist); Maletz, Kley, & Reinhardt, p. 171, text-fig. 3: 5.
?1995 *Didymograptus* (s.l.) aff. *demissus* Törnquist; Ortega & Rao, p. 307, pl. 1, fig. 18.
1996 *Didymograptus demissus* (Törnquist); Maletz, Löfgren & Bergström, p. 156, fig. 13: 5.
1997b *Expansograptus demissus* (Törnquist); Maletz, fig. 3g.
2001 *Expansograptus demissus* (Törnquist); Maletz & Egenhoff, fig. 8: 6.
?2016 *Cymatograptus demissus* (Törnquist); Gutiérrez-Marco & Martin, fig. 4H.

Type material. – The type material is a single flattened specimen and counterpart from the *Tetragraptus phyllograptoides* Biozone of Mossebo, Hunneberg. LO 1581T (Törnquist 1901, pl. 1, figs 8, 10) was refigured by Maletz *et al.* (1991). The counterpart LO 1581T+ is probably the figure in Törnquist (1901, pl. 1, fig. 9).

Material. – Several specimens from the upper part of the *Tetragraptus phyllograptoides* Biozone at Diabasbrottet. The species appears to be uncommon in the section.

Diagnosis. – Slender subhorizontal *Cymatograptus* with long supradorsal part of sicula and th1^1.

Description. – The tubarium is slender with slightly declined to subhorizontal stipes with a prominent sicula 2.6–2.9 mm long and an apertural width of 0.35–0.4 mm. The sicula bends slightly towards stipe 2 near its aperture. The supradorsal length of the sicula is 1.9–2.0 mm. The proximal development is isograptid, dextral in all specimens in which the development is visible. The free ventral length of the sicula is 0.5–0.7 mm. The interstipe angle is 155–170°. The stipe width is 0.7–0.8 mm proximally and increases

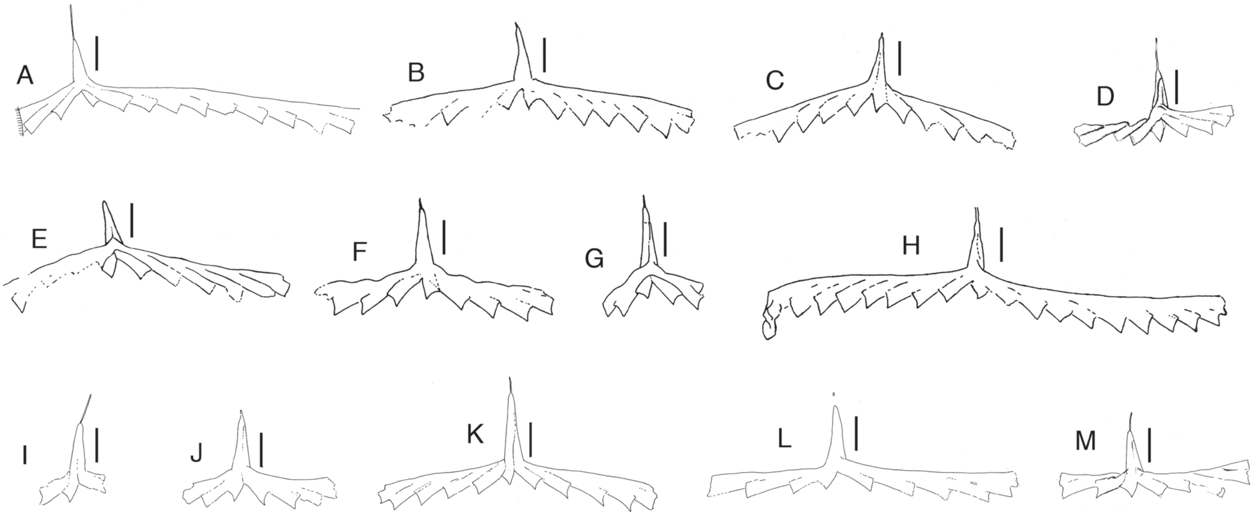

Fig. 63. Cymatograptus kristinae n. sp. **A**, MBg Di 543/131-1, Diabasbrottet at 2.1–2.2 m. **B**, PMU 38460, Diabasbrottet at 1.7–1.8 m. **C**, PMU 38461, Diabasbrottet at 1.7–1.8 m. *Cymatograptus demissus* (Törnquist, 1901). **D**, T63-1, Tøyen section, Oslo at 7.32–7.85 m. **E**, PMU 38462, Diabasbrottet at 1.0–1.1 m. **F**, PMU 38463, Diabasbrottet at 1.0–1.1 m. **G**, PMU 38464/1, Diabasbrottet at 1.0–1.1 m. **H**, PMU 38464/2, Diabasbrottet at 1.0–1.1 m. **I**, T103/2, Tøyen section, Oslo at 7.91 m. **J**, MBg Di 434/37a-8, Diabasbrottet at 1.0–1.1 m. **K**, PMU 38466, Diabasbrottet at 1.0–1.1 m. **L**, MBg Di 434/37a-6, Diabasbrottet at 1.0–1.1 m. **M**, T63/4, Tøyen section, Oslo at 7.32–7.85 m. Scale bar is 1 mm at each specimen.

to 0.95 mm distally. The thecal inclination is low, not more than 20–22°.

Remarks. – The species can easily be recognized by its high supradorsal part of the sicula and the low thecal inclination. In these characters it is similar to slender specimens of *Cymatograptus undulatus*, but does not show the prothecal folds of *C. undulatus*.

Occurrence. – *Cymatograptus demissus* is restricted to the *Tetragraptus phyllograptoides* Biozone. It has been found in Scania (Tjernvik 1960; Lindholm 1981) and Västergötland (Törnquist 1901). Material recorded as *Didymograptus* cf. *demissus* from the Oslo Region of Norway (Monsen 1937) does not belong to this species. Its slender, more declined habit indicates that it may belong to *Cymatograptus rigoletto*. However, material of *Cymatograptus demissus* is now known from the 7.32–7.85 m interval in the *Tetragraptus phyllograptoides* Biozone of the Tøyen section, Oslo (Figs 63D, I, M) confirming its wider distribution. The specimens from the Tøyen section are consistently smaller and have a shorter supradorsal part of the sicula. In their dimensions, they are in the lower range of the variation of the species. It is not clear whether this indicates that the intraspecific variation is greater, or whether the material might have to be referred to a separate species.

The specimens of Ortega & Rao (1995) might belong to this species, but the identification remains uncertain as they are poorly preserved. Maletz & Egenhoff (2001) found the species in the *Tetragraptus phyllograptoides* Biozone at Cienneguillas, southern Bolivia.

Cymatograptus rigoletto (Maletz, Rushton & Lindholm, 1991)

Fig. 62G–I

1937 *Didymograptus* cf. *demissus* Törnquist; Monsen, p. 132, pl. 2, fig. 2.
1979 *Didymograptus* aff. *nicholsoni* Lapworth; Jackson, p. 28, fig. 4e, f.
1987 *Expansograptus asymmetricus* n. sp. Maletz, p. 87, fig. 26: 1–6; pl. 2, figs 1, 2.
1991 *Didymograptus* (s.l.) *rigoletto* n. sp. Maletz, Rushton & Lindholm, pp. 337–341, figs 3–6.
?1997a *Didymograptus* (s.l.) *rigoletto* Maletz, Rushton & Lindholm; Toro, pl. 1, fig. 4.
?1997a *Didymograptus* (s.l.) cf. *D. rigoletto* Maletz, Rushton & Lindholm; Toro, pl. 1, figs 5, 6.
2001 *Didymograptus rigoletto* (Maletz, Rushton & Lindholm); Maletz & Egenhoff, fig. 8.8.
2001 *Didymograptus rigoletto* Maletz, Rushton & Lindholm; Tolmacheva, Koren', Holmer, Popov & Raevskaya, p. 559, text-fig. 6: 1–8; text-fig. 8: 4–11.
2021 *Cymatograptus rigoletto* (Maletz *et al.* 1991); Maletz & Ahlberg, fig. 1D (no description).

Type material. – Holotype LO 6270T (Figs 62G, H) from the upper part of the *Tetragraptus phyllograptoides* Biozone in the Diabasbrottet section at 1.6–1.7 m.

Diagnosis. – Slender, declined *Cymatograptus* with long supradorsal portion of sicula and th1^1.

Remarks. – The species is well known from Scandinavia and Britain and is not redescribed here. Maletz *et al.* (1991) gave detailed illustration of the species from relief specimens in obverse and reverse views.

Occurrence. – *Cymatograptus rigoletto* was originally described from the Hunneberg and from the Oslo Region, but specimens have been illustrated under other names prior to this (cf. Monsen 1937; Jackson 1979). It ranges from the upper part of the *Tetragraptus phyllograptoides* Biozone into the lower *Cymatograptus protobalticus* Biozone. In Britain it occurs on loose blocks in the Skiddaw Group in an equivalent of the *Tetragraptus phyllograptoides* Biozone (Maletz *et al.* 1991, fig. 2). Zalasiewicz *et al.* (2009) listed the species as *Acrograptus*? *rigoletto* which, together with *Acrograptus*? *protobalticus* and *Temnograptus multiplex*, was regarded as indicative of the *Tetragraptus phyllograptoides* Biozone of Britain.

More recently the species has been found as rare occurrences in southern Bolivia (Maletz & Egenhoff 2001). A single specimen in partial relief was found associated with *Tetragraptus phyllograptoides, Tetragraptus amii* and *Clonograptus multiplex* in the *Tetragraptus phyllograptides* Biozone of the Cieneguillas section.

Cymatograptus rigoletto is common in the St. Petersburg area of Russia (Tolmacheva *et al.* 2001). The figured specimens are similar in all respects to the Scandinavian material, even though the authors indicate less closely spaced thecae, which can be explained by intraspecific variation.

Cymatograptus validus (Törnquist, 1904)

Figures 16G; 62F; 64E–G, I, J

1904 *Azygograptus validus* Moberg MS; Törnquist, p. 27, pl. 4, figs 12–14.
1991 *Azygograptus validus* Törnquist; Beckly & Maletz, p. 910, pl. 1, fig. 13; text-fig. 19a–d, ?e, f: l.

Type material. – Lectotype LO 1755T (mistakenly identified as holotype by Beckly & Maletz 1991) and paratype LO 1756t from Mossebo, Hunneberg, designated herein. They were collected by Moberg in 1892 but the precise level is unknown. The slab includes a juvenile of *Tetragraptus phyllograptoides*. The type material was refigured by Beckly & Maletz (1991, text-fig. 19I, K). The species is the oldest single-stiped graptolite found worldwide.

Material. – Numerous specimens from the *Tetragraptus phyllograptoides* Biozone at Diabasbrottet and Mossebo (Egenhoff & Maletz 2007). Monsen (1937) did not mention this species from the Oslo Region, but a few specimens have been discovered in the *Tetragraptus phyllograptoides* Biozone at Slemmestad and were part of this investigation.

Remarks. – Beckly & Maletz (1991) described the species in detail. A single specimen preserved in full relief provides the structural details (Fig. 16G). The long sicula (2.1–2.3 mm) is very similar in shape to the siculae of two-stiped species of *Cymatograptus*, as is the high origin of th1^1, most probably in the lower part of the prosicula. Slight constrictions in the upper part of the sicula may indicate the spiral line of the prosicula, suggesting a prosicular origin of th1^1.

Occurrence. – The species is well known from the *Tetragraptus phyllograptoides* Biozone at Diabasbrottet and Mossebo. Beckly & Maletz (1991) figured specimens from Tøyen (Norway) and Robinson Mountain (Lake District, England). The single specimen from the British Lake District is very poorly preserved and its identification may be questioned. The specimen is associated with *Acrograptus filiformis* (Beckly & Maletz 1991, p. 911), indicating the origin from a slightly higher horizon than the Swedish material, possibly the *Baltograptus vacillans* Biozone.

Cymatograptus minutus (Beckly & Maletz, 1991)

Figure 64A–D, H

1991 *Azygograptus minutus* sp. nov. Beckly & Maletz, p. 914, pl. 1, fig. 12; text-fig. 19m–u.
1997b *Azygograptus minutus* Beckly & Maletz; Maletz, fig. 3j.
2011 *Cymatograptus minutus*; Maletz & Ahlberg, fig. 2 (range chart, no illustration).

Type material. – Holotype SGU 7560, from the lower part of the *Baltograptus vacillans* Biozone (3.7–3.8 m level) in the Diabasbrottet section, designated Beckly & Maletz (1991). It is currently housed in the Museum für Naturkunde (Berlin, Germany).

Material. – A number of generally small and immature specimens from the Diabasbrottet section. Some specimens from the Lerhamn drill core of Scania (49.50–49.45 m) have also been investigated (Fig. 64A–D).

Description. – The tubarium is slender and consists of a single, stipe with slight to strong curvature. The stipe width is about 0.6 mm and appears to be constant. The sicula is slender and quite short, reaching a length of 1.6–1.9 mm, with small dorsal and ventral apertural lips. The origin of th1 is ca 0.3–0.4 mm below the apex of the sicula but does not show whether it is in the prosicula or metasicula. As all specimens are flattened, details of the development are unknown.

Remarks. – The description is from flattened material in the Diabasbrottet section. Additional material collected recently at Diabasbrottet and Mossebo is similar in all respects with the described specimens.

Occurrence. – A single specimen of *Cymatograptus minutus* was figured by Maletz (1997b) from the Tøyen Shale of the G-14 well in the Baltic Sea north of the island of Rügen. It is the first specimen from outside its type locality. The species is restricted to the *Baltograptus vacillans* Biozone.

Other fossils

Graptolites make up the largest fraction of the fossils present in the Tøyen Shale Formation at Hunneberg, but a number of other fossil groups have been noted or described (Fig. 65). These are listed here, even though no comprehensive investigation has been undertaken. It is unfortunate, that, in general, other fossil groups are commonly neglected and not described from graptolite shales, even though they may provide important information on the ecology of the sedimentary succession. Therefore, an overview is provided here, showing that most additional fossil groups are in dire need of re-evaluation and description.

Phyllocarids. – Phyllocarids (Fig. 65K) have been recognized in the Hunneberg sections, but have not been described or illustrated. They are relatively uncommon and fragmentary. Tjernvik (1956) listed *Ceratiocaris*? sp. from the *Megistaspis* (*Paramegistaspis*) *planilimbata* Trilobite Zone at Mossebo. Størmer (1937) discussed phyllocarid occurrences in the Tøyen Shale Formation of Norway and identified the material as *Caryocaris* cf. *C. monodon* (Gurley, 1896).

Organophosphatic brachiopods. – Phosphatic brachiopod shells are not uncommon in the shales of the Hunneberg sections (Fig. 65G–J, L–N), but have not been described so far. Tjernvik (1956, p. 119) found *Broeggeria* cf. *B. salteri* Holl, 1865 in the *Ceratopyge*

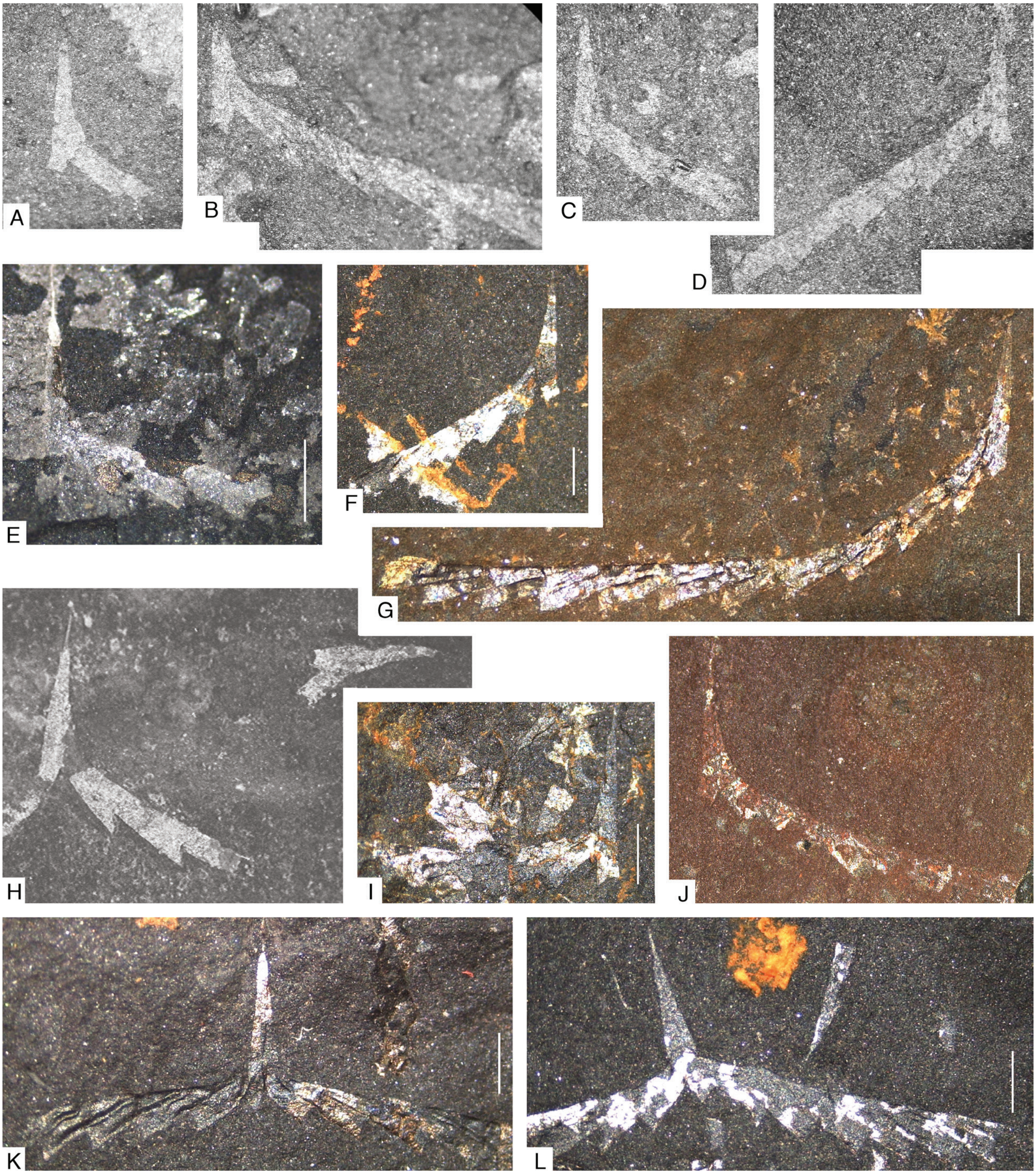

Fig. 64. One- and two-stiped *Cymatograptus* species for comparison. **A–D, H**. *Cymatograptus minutus* (Beckly & Maletz, 1991). **A**, Lerhamn, 49.45–49.5 m. B, Lerhamn, 49.45–49.5 m. **C**, Lerhamn, 49.45–49.5 m. **D**, Lerhamn, 49.45–49.5 m. **H**, holotype, MBg DI 709, Diabasbrottet, 3.7-3.8 m. **E–G, I, J**. *Cymatograptus validus* (Törnquist, 1904). **E**, LO 1755T, lectotype. **F**, PMU 38467, Diabasbrottet, 1.6–1.7 m. **G**, RM Cn 1442, ‘Mossebo; coll. G. Holm, 1879. **I**, PMU 38442a/2. **J,** PMU 38491A, Diabasbrottet, 1.5–1.6 m. **K,** *Cymatograptus demissus* (Törnquist, 1901), PMU 38466, Diabasbrottet, 1.0–1.1 m. **L**, RM Cn 1596, Diabasbrottet. Scale bar is 1 mm in each photo.

beds at Mossebo and *Broeggeria* sp. in the *Megistaspis* (*Ekeraspis*) *armata* trilobite zone at Mossebo and mentioned *Broeggeria* and *Acrotreta* from his *Didymograptus balticus* Zone.

Popov & Holmer (1994, pp. 8, 9) discussed a single sample of limestone from the Bjørkåsholmen Formation and listed *Lingulella antiquissima* (Jeremejew, 1856), *Lamanskya splendens*Moberg &

Fig. 65. Non-graptolite fauna. **A–C**. *Protorthis* (?) *nunnebergensis* Walcott, 1905, Diabasbrottet, 2.5–2.6 m. **A**, PMU 38479. **B**, PMU 38480. **C**, PMU 38474b/2. **D–F**. Orthids indet. **D**, PMU 23153/2. **E**, PMU 38481a, pyritic remains. **F**, PMU 38482b, lightly coated. **G–J**, **L–N**. phosphatic brachiopods. **G**, PMU 38483a/1. **H**, PMU 38474b/3, note the simple cone conodont in the upper left corner of the photo. **I**, PMU 38484a/1. **J**, PMU 38484a/2. **L**, PMU 38483a/2. **M**, PMU 38490a. **N**, PMU 38485. **K**, phyllocarid indet, PMU 38445/3. **O**, *Megistaspis (Paramegistaspis) planilimbata*?, PMU 38486a, flattened specimens in shale. **P**, Trace fossils indet, very slender, PMU 38487/2, Mossebo, *Tetragraptus phyllograptoides* Biozone, coll. Erdtmann. Scales bars are 1 mm unless stated otherwise.

Segerberg, 1906, *Siphonotretella jani* Popov & Holmer, 1994, *Pomeraniotreta biernatae* Bednarczyk, 1986, *Eurytreta minor* Biernat, 1973, Acrotretidae gen. et sp. nov. a, and in addition indicated the presence of *Broeggeria salteri* Holl, 1865 and *Ottenbyella carinata* (Moberg & Segerberg, 1906) in their figure. The sample was collected by Torsten Tjernvik at Mossebo.

Calcareous brachiopods. – Lindström (1880; pl. 15, fig. 33a, b) described and illustrated a single brachiopod from Mossebo as *Orthis pectiniformis* (re-illustrated in Moberg & Segerberg 1906). Walcott (1905, p. 284) described *Protorthis* (?) *nunnebergensis*, new species from Mossebo, Nunneberg, Vestergotland, Sweden (Fig. 65A–C). He stated that the material was collected by von Schmalensee in a 'dark, argillaceous shale above the *Ceratopyge* Limestone and below the lower graptolite shale'. Moberg & Segerberg (1906, p. 70, pl. 2, fig. 5a–c) identified the species from the upper part of the *Ceratopyge* interval, the '*Apatocephalus* Zone' and corrected the name to *Protorthis* (?) *hunnebergensis*. The species name '*nunnebergensis*' is certainly based on a misreading of the area at Hunneberg. Walcott (1912, explanation to pl. XCV) stated that the illustrations in Moberg & Segerberg (1906, pl. 2) are copies of his own photos. Tjernvik & Johansson (1980, p. 186) also mentioned the species, but a modern description does not exist.

Tjernvik (1956) indicated the presence of *Lycophoria laevis* Stolley and *Apheoorthis*? *suecica* Tjernvik, 1956 from the *Megistaspis* (*Ekeraspis*) *armata* Trilobite Zone at Storeklev, but did not illustrate the material. He did, however, illustrate *Apheoorthis*? *suecica* and *Nanorthis*? *billingensis* as new species from the *Megistaspis* (*Ekeraspis*) *armata* trilobite zone in other sections in Västergötland, species that might be found at Hunneberg also. Tjernvik & Johansson (1980, p. 181) referred the material of '*Lycophoria laevis*' to *Leiocardia difformis* (Moberg & Segerberg, 1906; actually referred to *Meristella*). It is interesting that the name *Lycophoria laevis* is commonly found in older literature referring to the *Ceratopyge* layers of Hunneberg or Västergötland. A description and illustration as *Lycophoria lævis* Stolley can be found in Wiman (1906), based on material from glacial boulders collected at Grisslehamn.

Tjernvik (1956) stated that brachiopods are common in the shales of his *Didymograptus balticus* Zone at Mossebo, mentioning especially '*Protorthis*' *hunnebergensis*. A small number of orthid specimens have been collected from the Hunneberg sections (Figs 65D–F), probably belonging to several different species. The material is very poorly preserved as casts in the shale and may not be identifiable to species level.

Trilobites. – Westergård (1922) described the upper Cambrian trilobites of Sweden and illustrated a few specimens from Hunneberg, including *Olenus rotundatus* from Mossebo and *Ctenopyge erecta* (now *Ctenopyge* (*Mesoctenopyge*) *erecta*: see Rasmussen *et al.* 2016) from Nygård, but detailed descriptions of the Cambrian trilobites from the region are not available. The biostratigraphic succession at Nygård was first documented by Westergård (1909, 1922) but is now better known from the work of Rasmussen *et al.* (2016). The upper Cambrian succession of other sections in the region have never been investigated in any detail.

The first detailed descriptions of Ordovician trilobites from Hunneberg appeared in Tjernvik (1956), but Angelin (1854) already listed a number of species from Hunneberg. Moberg & Segerberg (1906) indicated the presence various trilobites at Hunneberg, but did not illustrate material from this region. All trilobites described from the region were collected from limestones, but the Tøyen Shale occasionally also includes poorly preserved trilobite remains (Fig. 65O).

Conodonts. – Lindström (1957) made the first investigation of the Early Ordovician conodont faunas from Mossebo. The detailed work of Löfgren (1993) provide the now accepted conodont biostratigraphy from the late Tremadocian to the early Floian time interval of southern Scandinavia and the basis for the conodont zonation in the GSSP section (Maletz *et al.* 1996; Bergström *et al.* 2004). Conodonts are common in many of the limestone layers, but specimens may be found in shale layers also, in this case often associated with a hash of brachiopod shells (Fig. 65H).

Trace fossils. – Trace fossils have never been described from the Tøyen Shale of Hunneberg, but are not uncommon even in many black shale layers (Fig. 65P). Egenhoff & Maletz (2012) discussed the abundance of burrows in the Hunneberg succession as a reflection of hospitable living conditions even during the deposition of the Floian black shales. Egenhoff *et al.* (2019, p. 57) suggested that sedimentary structures of the Tøyen Shale of southern Sweden may often have been destroyed by abundant trace fossils making an interpretation of the conditions of sedimentation difficult.

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