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THE UPPER TREMADOCIAN (ORDOVICIAN) GRAPTOLITE *BRYOGRAPTUS*: TAXONOMY, BIOSTRATIGRAPHY AND BIOGEOGRAPHY

by JÖRG MALETZ*, SVEN EGENHOFF† *and* RICARDO ALONSO‡

*Department of Earth Sciences, St Francis Xavier University, Antigonish, Nova Scotia, Canada; e-mail jmaletz@stfx.ca
†Department of Geosciences, Colorado State University, 322 Natural Resources Building, Fort Collins, CO 80523-1482, USA; e-mail sven@warnercnr.colostate.edu
‡Universidad Nacional de Salta, Facultad de Ciencias Naturales, Buenos Aires 177, 4400 Salta, Argentina; e-mail rnalonso@uolsinectis.com.ar

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Abstract: The taxonomy, biostratigraphical and palaeogeographical distribution of the Lower Ordovician graptolite genus *Bryograptus* is evaluated. *Bryograptus* is recognized as a distinct triradiate anisograptid with a multiramous, pendent rhabdosome. The species of the genus *Bryograptus* can be interpreted as shallow water faunal elements with a strongly limited biogeographical distribution to the Atlantic Faunal Realm. *Bryograptus* is restricted to a narrow interval in the Upper Tremadocian, the *Bryograptus* Biozone of Scandinavia and South America (Argentina), making it a taxon with a high potential for precise biostratigraphical correlations. The proximal end development can be used to differentiate the genus *Bryograptus* from other pendent multiramous graptoloid genera with a homoplastic rhabdosome development. Characteristics of the proximal end development and structure easily differentiate these genera in relief specimens, but not in flattened material.

Key words: Ordovician, graptolites, taxonomy, biostratigraphy, Baltica, South America, Argentina, *Bryograptus*.

THE genus *Bryograptus* Lapworth, 1880 (Text-fig. 1) is easily one of the most commonly misidentified and misunderstood graptolite genera of the Lower Ordovician. Since its introduction by Lapworth (1880), numerous taxa have been assigned to the genus, and it became a 'waste basket' for pendent to declined multiramous Ordovician graptolites. Species referred to this genus range in age from the Upper Tremadocian (Lower Ordovician) to the Upper Darriwilian (Upper Middle Ordovician) and are found on all continents, except for Antarctica. This wide biostratigraphical and biogeographical distribution renders the genus useless for any further biostratigraphical and palaeogeographical interpretations.

One of the main problems in identifying *Bryograptus* is the poor original definition of the genus, combined with lack of detailed information of the rhabdosome development of its type species. A further contributing factor is the presence of numerous instances of homoplasy in early and mid Ordovician multiramous graptolites. The general outline of flattened graptolite specimens preserved on shale surfaces does not provide sufficient information for the differentiation of these homoplastic faunal elements as structural details of the proximal end development and thecal style are only revealed in relief specimens.

The enormous biostratigraphical and palaeogeographical potential of *Bryograptus* shows only after considerable revision of the taxon with a restriction of the genus to phylogenetically closely related taxa found in the Upper Tremadocian of the Atlantic Faunal Realm. The revision provides biostratigraphical data for an inter-continental chronostratigraphical correlation and for biogeographical interpretation. It also provides new information on the structural development of graptolite rhabdosomes in the Lower Ordovician, useful for a better understanding of the evolutionary patterns of early planktic graptolites. The restriction of the genus *Bryograptus* to the Upper Tremadocian *Bryograptus* Biozone pinpoints to the exact time of the structural change from triradiate to biradiate rhabdosome developments in early Ordovician graptoloids and helps to understand tempo and mode of evolutionary change in graptolite evolution.

BRYOGRAPTUS IN ARGENTINA

Frequent specimens of the genus *Bryograptus* were discovered at Cuesta de la Pedrera in the Sierra de Mojotoro of northern Argentina and led to the question of identification and hence biogeographical distribution of this

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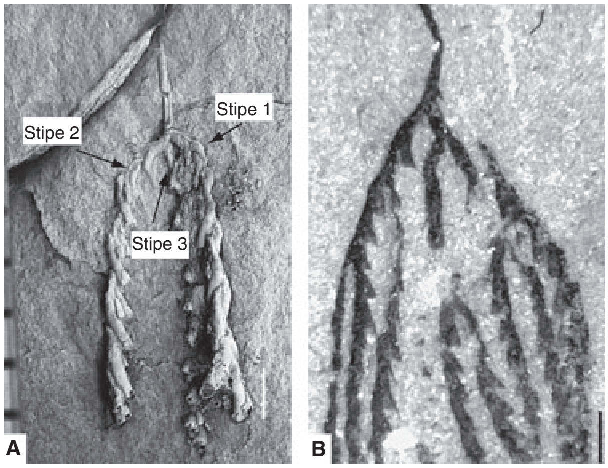
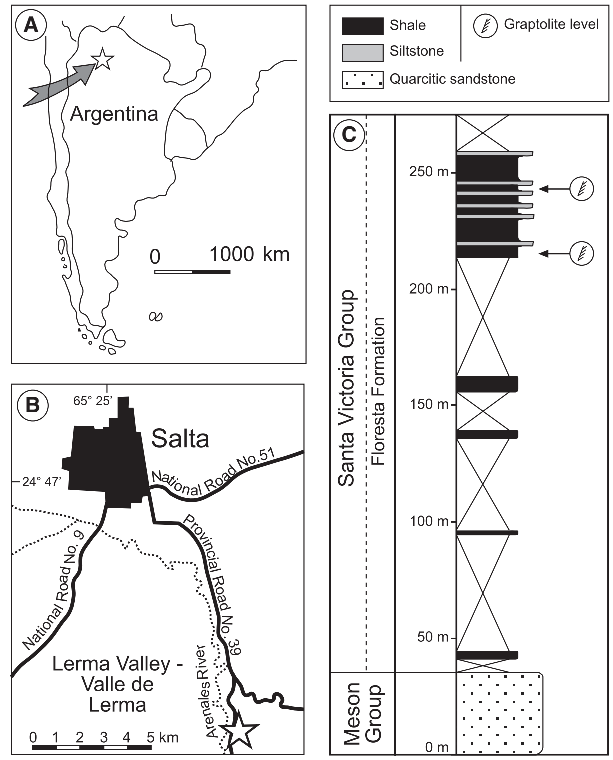


TEXT-FIG. 1. *Bryograptus ramosus* Brøgger, 1882. A, PMO 72.831, Slemmestad, Norway. Latex casts of specimen illustrated by Spjeldnæs (1963), showing triradiate proximal end in reverse view and bithecate stipes, stipe three largely hidden. B, *Bryograptus kjerulfi* Lapworth, 1880, Cuesta de la Pedrera, Argentina, flattened specimen with nemal vane, IANIGLA-PI 2263 (see also Text-fig. 7C).



TEXT-FIG. 2. Location of the Argentinian record of *Bryograptus* and section (based on Gonzalez Barry and Alonso 1984).

generally rare Lower Ordovician graptolite genus. Even though Lower Ordovician graptolite faunas occur frequently in Argentina (e.g. Toro and Brussa, 2003) and Bolivia (Maletz and Egenhoff 2003; Egenhoff *et al.* 2004) and are well documented, the genus *Bryograptus* was not found in unequivocal specimens in South America, except for the material illustrated by Gonzalez Barry and Alonso (1984), Moya *et al.* (1994) and more recently by Albanesi *et al.* (2008).

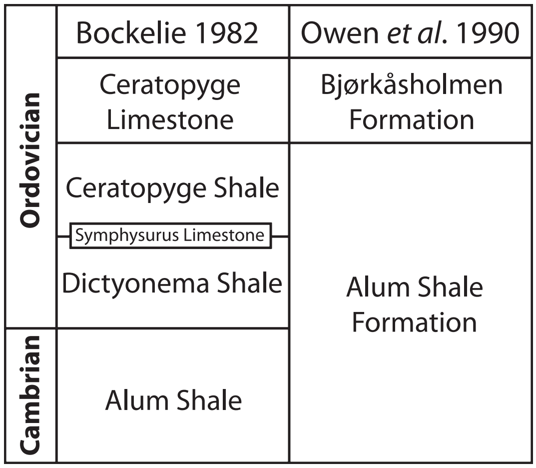
The Lower Palaeozoic succession of northwestern Argentina was deposited in a north–south running trough that was initiated in the Late Cambrian as an extensional back-arc basin (Bahlburg 1990) and transformed into a compressional foreland basin in the Floian (*Expansograptus holmi* Biozone) (Coira *et al.* 1999; Egenhoff 2007). The initial fill into the nascent basin consisted of shallow-marine siliciclastic sediments represented by the Upper Cambrian Meson Group (Kumpa and Sanchez 1988). Overlying Tremadocian, Floian and Dapingian sandstones, siltstones and shales are combined into the Santa Victoria Group (Turner 1960; Moya 1988).

The *Bryograptus* locality is situated about 10 km south of the city of Salta, northwestern Argentina (Text-fig. 2), in the Cuesta de la Pedrera (Gonzalez Barry and Alonso 1984). The sediments yielding the graptolites are only exposed in an interval about 50 m thick, whereas the rest of the section is covered by scree. The succession forms part of the Floresta Formation (Moya 1988) of the Santa Victoria Group, erroneously referred to as the Mojotoro Formation by Gonzalez Barry and Alonso (1984). The base of the Floresta Formation is not exposed in this locality, nor is the contact to the underlying quartzitic sandstones of the Meson Group. According to Moya (1988), three more formations, each of them several hundred metres thick, should be present between the Meson Group and the Floresta Formation. It is therefore likely that the base of the Floresta Formation is cut out by a fault in the Cuesta de la Pedrera section.

The Floresta Formation in the studied locality consists of laminated greenish-grey, silty siliciclastic mudstones with some centimetre- to decimetre-thick rippled siltstone beds. The sedimentary environment is thought to be deep shelf below storm wave base on the eastern flank of the Ordovician basin (Moya 1988). The *Bryograptus* samples come from two levels within mudstones in the upper portion of the exposed succession, and scree accumulated directly below the two levels where the graptolites occur.

BRYOGRAPTUS IN NORWAY

The Tremadocian succession of Norway provides one of the best-known graptolite successions of this time interval worldwide and adds important biostratigraphical and palaeontological data to the understanding of the distribution



TEXT-FIG. 3. Upper Cambrian to Lower Ordovician lithostratigraphy in the Oslo Region, Norway. Bockelie (1982) is used as an example of previous usage of lithstratigraphical units. The author did not indicate the presence of the Symphysurus Limestone in his compilation.

of *Bryograptus*. The genus *Bryograptus* was recorded from the Alum Shale (Lapworth 1880, p. 165; Alum Slates), the Etage 2 (Kjerulf 1865), the Dictyonema Shale (Brøgger 1882) and the Ceratopyge Shale (Monsen 1925) of Norway, reflecting a variable understanding and assignment of the strata containing *Bryograptus*, but also the changing lithostratigraphic interpretation of the Lower Palaeozoic succession of the Oslo Region (Text-fig. 3). In the newest lithostratigraphic concept, the Alum Shale Formation of Scandinavia (Andersson *et al.* 1985; Owen *et al.* 1990) includes the Middle Cambrian to Lower Ordovician interval and reaches to the base of the Upper Tremadocian Bjørkåsholmen Formation, thus, including the former Ceratopyge Shale. The Ordovician part of the Alum Shale Formation, in which graptolites can be found, has previously been included in the Dictyonema Shale and Ceratopyge Shale formations. The part of the Alum Shale Formation corresponding to the former Ceratopyge Shale is about 6 m thick in the Slemmestad Region (NRC section measured by David L. Bruton, pers. comm. 1985) from the top of the Symphysurus Limestone (a layer of large limestone concretions; 'orsten limestones') to the base of the Bjørkåsholmen Formation. The thickness reaches 6–7 m in the city of Oslo (Brøgger 1882; Monsen 1925).

Bulman (1954) described the Tremadocian graptolite succession of the Oslo Region, part of which was revised by Bruton *et al.* (1982, 1988) in an aim to define the base of the Ordovician System at Nærsnes. The succession contains quadriradiate *Rhabdinopora flabelliformis* ('*Dictyonema flabelliforme*', see Cooper *et al.* 1998) and triradiate *Anisograptus* in the Lower Tremadocian interval (the former *Dictyonema* Shale: Owen *et al.* 1990), but Bulman (1954) also mentioned the presence of *Bryograptus* specimens, which has not been confirmed as this material has never been illustrated. Faunas with definitive *Bryograptus* follow in the interval above the *Symphysurus* Limestone (see Bulman 1954, text-fig. 1). The general picture shows an evolutionary succession from quadriradiate to triradiate and finally to biradiate genera and species in the upper Alum Shale Formation, but details are uncertain.

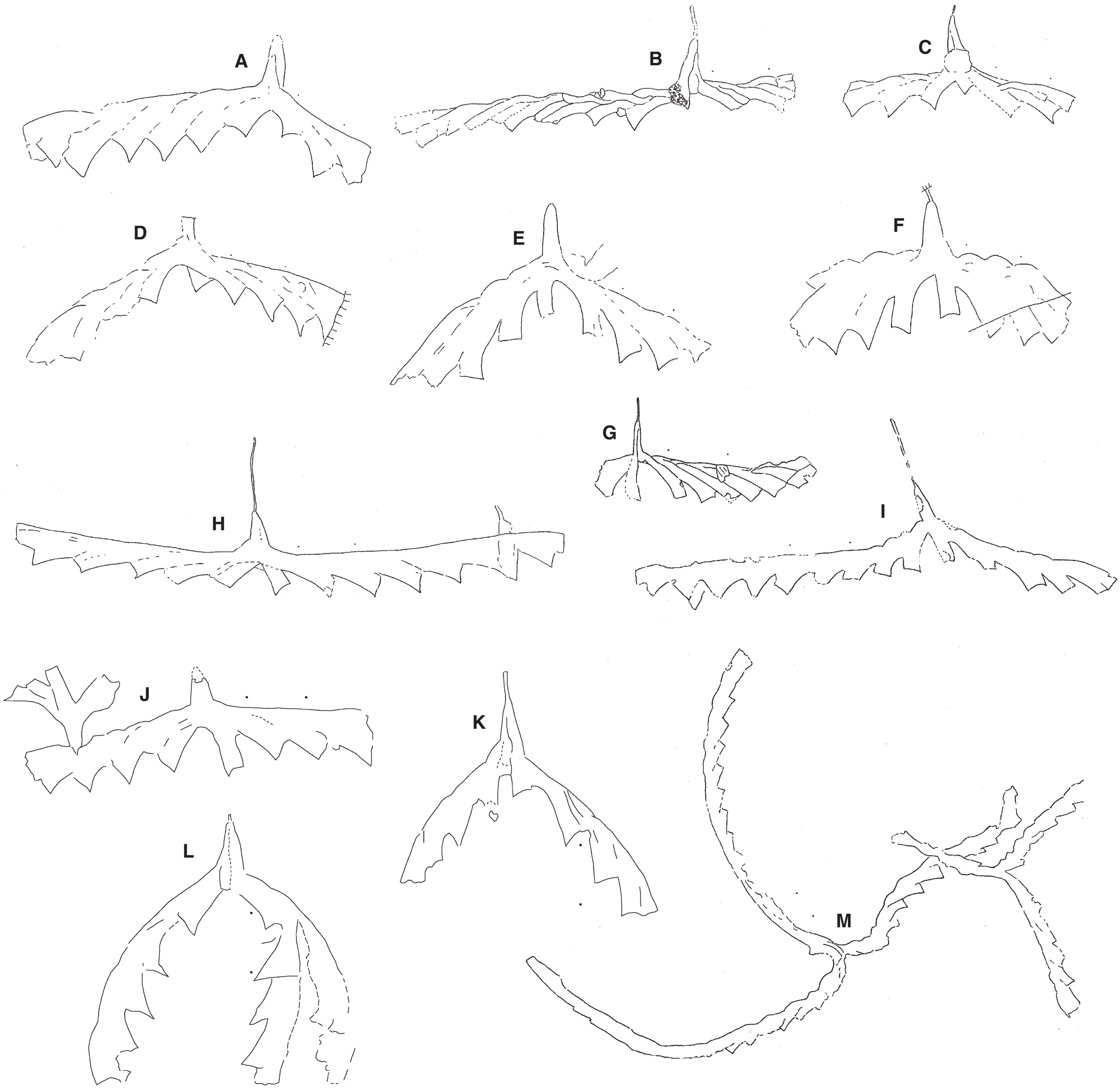
Monsen (1925) first described the graptolite fauna of this interval in some detail and gave exact levels for the occurrence of her material in the uppermost 2 m of the Alum Shale Formation, even providing a schematic section (Monsen 1925, fig. 1). She differentiated two graptolite subzones, a lower subzone with *Bryograptus ramosus*, *Bryograptus broeggeri* and *Triograptus osloensis* and an upper subzone with *Kiaerograptus kiaeri* and *Adelograptus tenellus*.

Spjeldnæs (1963), for the first time, described relief material of *Bryograptus ramosus* and *K. kiaeri* from an interval about 0.4–1.8 m below the base of the *Ceratopyge* Limestone in two sections at Slemmestad, south of the city of Oslo. He also introduced the new species *Adelograptus*? *bulmani* (now *Ancoragraptus bulmani*, Jackson and Lenz 1999) from the upper part of the *Ceratopyge* Shale of Bødalen, *c.* 1.5 km WSW of Slemmestad. The exact level of occurrence of the graptolites in the section was not given in the descriptions, however.

Henningsmoen found the youngest graptolite fauna of 'Tremadocian' aspect in a thin shale layer directly above the main limestone of the Bjørkåsholmen Formation, but below the last occurrence of limestone lenses with a typical *Ceratopyge* trilobite fauna, at the Tøyen underground train station, but did not publish his finds. Erdtmann (1965) subsequently described this fauna and provided taxonomic and biostratigraphical information. Erdtmann (pers. comm. 1986) found a similar, but more poorly preserved, fauna in a thin shale layer within the Bjørkåsholmen Formation at Slemmestad, now preserved in the Erdtmann collection at Plsen (Czech Republic).

Monsen's (1925) and Erdtmann's (1965) faunas have been re-evaluated, and important faunal elements are illustrated in Text-figure 4. The specimens identified by Erdtmann (1965) as *K. kiaeri* belong to *Kiaerograptus?* sp. cf. *Kiaerograptus? supremus* Lindholm (Text-fig. 4A, D) and do not bear the long isolated apertural part of the sicula so typical of *K. kiaeri* (Text-fig. 4G–J). The labels in Erdtmann's handwriting indicate that the material comes from 0.06–0.10 m below the base of 3b (base of the Tøyen Shale Formation). The specimens are distinctly larger than material illustrated as *Kiaerograptus supremus* by Maletz (1992*a*, fig. 5a) and referred to as *Kiaerograptus?* sp. cf. *K.? supremus* herein (Text-fig. 4B, C).

Kiaerograptus stoermeri Erdtmann, 1965 (Text-fig. 4E, F), according to the original labels, is from a level 0.05–



TEXT-FIG. 4. Drawings of important Upper Tremadocian graptolite species of the uppermost part of the Alum Shale Formation of Norway. A, *Kiaerograptus? supremus* Lindholm, 1991. PMO 73.652.1. B, *Kiaerograptus?* sp. cf. *K.? supremus* Lindholm, 1991. PMO 139.919.1, latex cast, showing irregular placing of bithecae. C, *Kiaerograptus?* sp. cf. *K.? supremus* Lindholm. PMO 139.919.3. D, *Kiaerograptus? supremus* Lindholm, 1991. PMO 73.652.2. E, *Kiaerograptus stoermeri* Erdtmann, 1965. PMO 73.651, holotype. F, *Kiaerograptus stoermeri* Erdtmann, 1965. PMO 73.650, paratype. G, *Kiaerograptus kiaeri* (Monsen, 1937). PMO 72.833, latex cast. H, *Kiaerograptus kiaeri* (Monsen, 1937). PMO 60.217.2. I, *Kiaerograptus kiaeri* (Monsen, 1937). PMO 60.212. J, *Kiaerograptus kiaeri* (Monsen, 1937). PMO 214.021, ROR 10.2. K, *Aorograptus victoriae* (Hall, 1899). PMO 214.022, ROR 12.01b. L, *Aorograptus victoriae* (Hall, 1899). PMO 214.023, ROR 12.10a. M, *Triograptus osloensis* Monsen, 1937. PMO 60.232. The magnification is given by two dots at a distance of 1 mm close to each specimen.

0.25 m below the base of 3b, thus, from a level slightly below the occurrence of *Kiaerograptus?* sp. cf. *K.? supremus*. The material is similar in its rhabdosome characters to *K. kiaeri*, but the specimens have distinctly wider stipes and longer isolated apertural parts of their thecae. All specimens are juveniles with a typical two-stiped rhabdosome, subhorizontal stipes and a maximum of four thecae on each stipe. The specimens do not show any indication of distal branching. Maletz and Egenhoff (2001) illustrated similar specimens with slightly longer stipes from the Lower Ordovician of Quebec as *K. stoermeri*, indicating a wider distribution of this species.

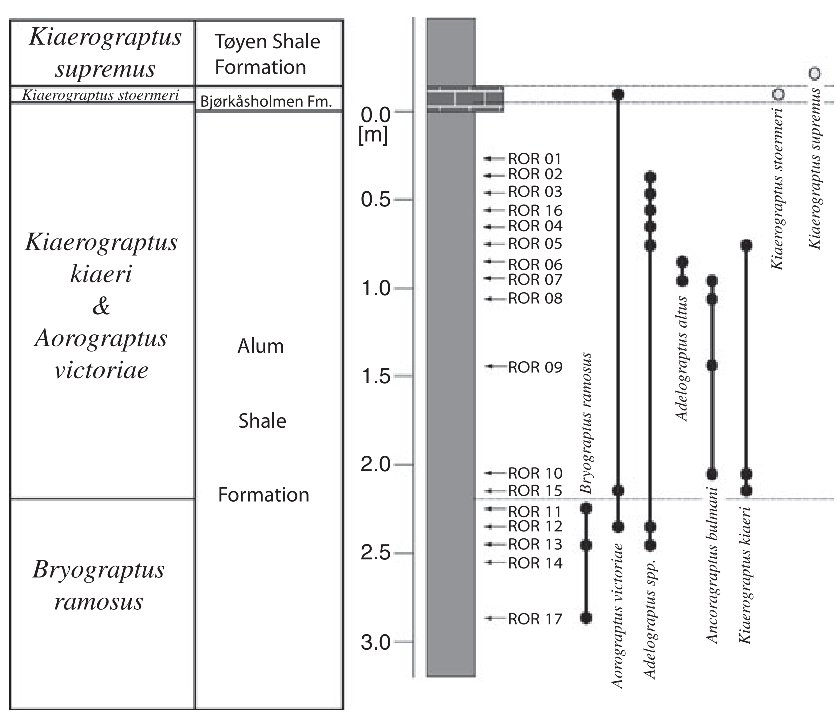
The specimen of *B. ramosus* (illustrated as a free-hand reconstruction by Erdtmann 1965) is a graptolite fragment without a sicula and may not be assigned to *Bryograptus*, while Erdtmanns' specimens of *Bryograptus* sp. (Erdtmann, 1965, pl. 1, figs 3, 4; pl. 2, figs 2, 3) show a biradiate rhabdosome and can be referred to *Aorograptus victoriae*.

A detailed investigation of the uppermost part of the Alum Shale Formation in the Slemmestad NRC section (Text-fig. 5) shows that the interval is rich in graptolites at a few levels, while in a number of layers only fine 'graptolite hash' can be found. A specific identification of any graptolite from this strongly fragmented material is impossible. Even though most graptolites are broken into small pieces, proximal ends and juveniles are frequent in most layers, associated with a few larger specimens and branching fragments. *B. ramosus* is present in an interval *c.* 2–3 m below the base of the Bjørkåsholmen Formation, but not higher up in the succession. In this interval, complete rhabdosomes of this graptolite species are common, and some reach a considerable size. *Kiaerograptus?* sp. cf. *K.? supremus* (see Maletz 1992*a*, *b*, fig. 5a; Maletz 1999, fig. 1C) was only found in scree material at Slemmestad. Thus, its exact position in the section is uncertain, and its occurrence is inferred from other records.

The exact biostratigraphical ranges of most of the species in the Upper Alum Shale Formation of the Oslo Region remain tentative and await improvement. The main problem is the strongly fragmented nature of the graptolites in this interval and a tectonic distortion of the succession. Parts of the soft shale of the upper Alum Shale Formation may be cut out by thrusting, and thicknesses are not comparable between sections.

The Upper Tremadocian graptolite ranges of the Slemmestad region (Text-fig. 5) clearly show the presence of two distinct faunas, the lower *Bryograptus* fauna and the upper *Kiaerograptus* fauna, as first documented by Monsen (1925). Even though both faunas are still poorly known, some important observations can be made. The *Bryograptus* fauna shows a very low diversity. *Bryograptus* often occurs in monospecific assemblages, but biradiate, multiramous anisograptids are also present. They are referred here to the genera *Adelograptus* and *Aorograptus*. *Aorograptus victoriae* originates in the upper part of the *Bryograptus* interval and ranges through most of the Upper Alum Shale Formation. The rare genus *Triograptus* (Text-fig. 4M), a clearly triradiate genus, may originate from this interval (Monsen 1925). It is known only from the type material, and additional specimens are not available.

The *Kiaerograptus* interval (*Aorograptus victoriae* Biozone in Maletz and Egenhoff 2001) starts with the FAD of *K. kiaeri*. The interval also bears common *Adelograptus* and *Ancoragraptus* specimens. A change in the fauna is seen in the uppermost shale layers, where *K. stoermeri* appears, indicating the local *K. stoermeri* Biozone (Erdtmann 1965; Maletz and Egenhoff 2001). A clearly different fauna appears with *Kiaerograptus? supremus* directly above the Bjørkåsholmen Formation, leading to the *Hun-*



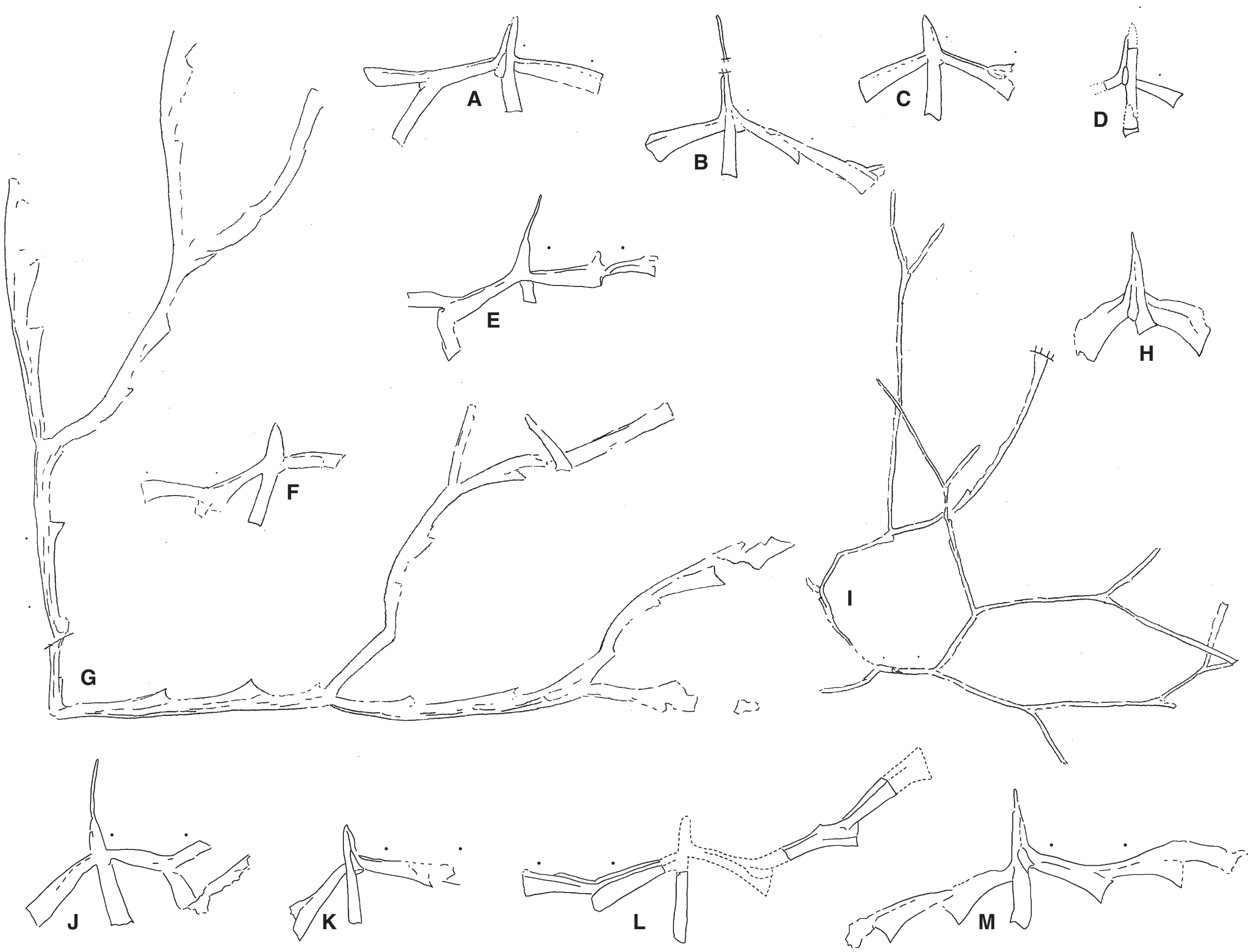
TEXT-FIG. 5. Slemmestad NRC section showing graptolite ranges. Ranges indicated with gray circles indicate interpolation from data provided by Monsen (1925), Spjeldnæs (1963) and Erdtmann (1965) from sections in the city of Oslo, not found in the Slemmestad NRC section.

negraptus copiosus Biozone (Lindholm 1991; Maletz and Egenhoff 2001). Unfortunately, *Kiaerograptus? supremus* is a rare species in Scandinavia, and the specimens of Erdtmann (1965) are the only ones found in the Oslo Region of Norway. Lindholm (1991) described the species originally from the Krapperup drillcore of Scania, southern Sweden, where it occurs in the upper part of the Alum Shale Formation. As the Bjørkåsholmen Formation is not present in the drillcore, a precise correlation is impossible.

Maletz and Egenhoff (2001) correlated the *Aorograptus victoriae* Biozone of western Newfoundland with the *Kiaerograptus* interval in Norway, based on a number of *Kiaerograptus* species, and documented the presence of multiramous *Kiaerograptus* species. In Scandinavia, so far, multiramous *Kiaerograptus* species have not been discovered. *K. kiaeri*, however, is the only species found in mature specimens, where branching could have been observed. Similarly, Jackson and Lenz (1999) described the genus *Ancoragraptus* as a small two-stiped anisograptid with a special development of the sicula. Even though many specimens of this genus appear to be two-stiped, there is enough evidence to show a multiramous rhabdosome shape for the genus (Text-fig. 6). Specimens of *Ancoragraptus* are widely distributed in this interval, as is seen from the record in Scandinavia, the Canadian Arctic (Jackson and Lenz 2003; Jackson and Norford 2004), Argentina (Zeballo *et al.* 2008), Australasia (Cooper and Stewart 1979, fig. 6A, D), South Korea (Cho *et al.* 2009) and possibly China (see Yu *et al.* 1984).

THE IDENTITY OF *BRYOGRAPTUS*

The definition of the genus *Bryograptus* is based on relief specimens of *Bryograptus ramosus* from Slemmestad, Nor-



TEXT-FIG. 6. *Ancoragraptus bulmani* (Spjeldnæs, 1963) specimens from the Upper Alum Shale of Slemmestad. NRC section, Norway (see Text-fig. 4 for levels). A, PMO 214.024.1, ROR 9.08.2. B, PMO 214.024.2, ROR 9.08.2. C, PMO 214.024.3, ROR 9.08.4. D, PMO 214.024.4, ROR 9.08.3. E, PMO 214.025, ROR 6.1. F–G, PMO 214.026, ROR 9.14. H, PMO 214.027, ROR 6.28. I, PMO 214.028, ROR 9.7. J, PMO 214.029, ROR 01.1. K, PMO 214.030, ROR 08.1.2. L, PMO 214.031, ROR 08.3. M, PMO 214.032, ROR 09.06. The magnification is given by two dots at a distance of 1 mm close to each specimen.

way (Spjeldnæs 1963), showing proximal end structure and thecal development in detail. A number of different and not closely related forms can easily be mis-identified as *Bryograptus* based on their pendent, multiramous rhabdosome development. The rhabdosome shape in these forms is highly variable and strongly affected by preservational aspects, such as floating and fragmentation after death or bending and breakage of stipes. The rhabdosome appears quite different in lateral and in dorso-ventral preservation, as do most multiramous species (see Maletz and Erdtmann 1987). Thus, it is difficult to rely on the general rhabdosome shape in the identification of genera and species in many Lower Ordovician multiramous graptoloids. Misinterpretation of preservational aspects and poor preservation of material often led to the subsequent inclusion of unrelated forms in the genus *Bryograptus*. Differences, however, can be found in all cases in their proximal end development.

Rhabdinopora. Specimens of *Rhabdinopora* may be misidentified easily as *Bryograptus*, especially when poorly preserved without visible dissepiments or in juveniles. A good example is *Bryograptus tintinniformis* from the Yangtze Craton, used as a zonal index by Mu *et al.* (1979). Wang and Wang (2001, p. 157) considered this species to represent juveniles of *R. flabelliformis anglica*. *Rhabdinopora* species are invariably quadriradiate (see Legrand 1974; Cooper *et al.* 1998) and not quadri- to biradiate as claimed by Erdtmann (1986, 1988) and Wang and Wang (2001). Similarities exist to *Bryograptus* in the bithecate stipes and the pendent habit, but *Rhabdinopora* species invariably possess a shorter sicula and dissepiments connecting the stipes.

Pseudobryograptus. Mu (1957) described the genus *Pseudobryograptus* from the Ningkuo Shale of Changshan, China as a biradiate dichograptid and, thus, easily differentiated the genus from *Bryograptus*, based on its proximal end development. Mu's material of *Pseudobryograptus* originates from the Lower Darriwilian (DA 1–2), as is shown by associated sinograptid and biserial graptolites (Mu 1957). Details of the proximal development were not described. Material referred to *Pseudobryograptus* has a short sicula (*c.* 1 mm long) and a variable number of slender, pendent stipes, originating from a biradiate proximal end. Bithecae are not present in the material. The proximal development of *Pseudobryograptus* has not yet been illustrated from relief specimens, but the presence of two-first-order stipes is clearly shown in Mu's (1957) illustrations.

Bulman (1971) referred the material of *B. cumbrensis* Elles and Wood, 1902 from the Skiddaw Slates of the British Lake District to the genus *Pseudobryograptus* and discussed the proximal development of *Bryograptus* and *Pseudobryograptus*. Maletz (1992*b*) referred specimens from the Dapingian of the Tøyen Shale of Norway to this genus.

Aorograptus. Williams and Stevens (1991) erected the genus *Aorograptus* with the type species *Bryograptus victoriae* Hall, 1899 based on isolated three-dimensionally preserved material from the Cow Head Group of western Newfoundland. The diagnosis stated a biradiate, pendent to declined rhabdosome with simple dichograptid thecae and regularly positioned, alternate bithecae along the stipes. The few isolated specimens illustrated by Williams and Stevens (1991) show both, dextral and sinistral proximal end development with a prominent sicular bitheca and two-first-order stipes. The origin of later thecae was not illustrated and, thus, the position of the first distal dicalycal thecae is uncertain. The origin of th 1^1 is in the prosicula (Williams *et al.* 1999, fig. 4C) in *Aorograptus victoriae* and also in a second species of the genus (Williams *et al.* 1999, fig. 4i–k), as is seen in partially translucent specimens. The sicula appears to be variable in length, but does not reach the size of the *Bryograptus* sicula. *Aorograptus* appears to be restricted to the Upper Tremadocian and overlaps biostratigraphically with *Bryograptus* (Text-fig. 5).

Pendeograptus. The genus *Pendeograptus* is based on the type species *Tetragraptus pendens* Elles, 1898 from the mid-Arenig (Lower Dapingian) of Barf, northern England. The material is from the same beds as *Pseudobryograptus cumbrensis* (Elles 1898), and both species may be synonymous. Williams and Stevens (1988) discussed *Pendeograptus pendens* and the problem associated with its taxonomy.

The discussion herein follows Cooper and Fortey (1982) in using *Pendeograptus fruticosus* as a substitute for the genus *Pendeograptus*, even though there are doubts about its inclusion in the genus (Williams and Stevens 1988). *Pendeograptus fruticosus* is a dichograptid species without any remains of bithecae in the proximal end or distal thecae. The prosicula is typically mitra-shaped, elongate. The metasicula is slender, slowly widening towards the aperture, with an indistinct and short rutellum. The complete sicula reaches a length of up to 3 mm in some specimens. Biostratigraphically younger specimens of *Pendeograptus fruticosus* may develop a metasicular origin of th 1^1 (Maletz 2004).

The genus *Pendeograptus* appears in the Floian (Lower Ordovician) and may range into the early Middle Ordovician. In Australasia, it is restricted to the Bendigonian to Chewtonian stages (VandenBerg and Cooper 1992). *Pendeograptus pendens liber* from the Darriwilian of the Ledbetter Slates of Washington (Carter 1989) may represent a species of *Pseudobryograptus* instead.

Pterograptus. The genus *Pterograptus* is frequent in the *Pterograptus elegans* Biozone in the Upper Darriwilian (Da 3). The structure of the sicula of *Pterograptus* with its typical dorsal virgella shows that it can be interpreted as a pendent xiphograptid with a short and slender sicula and secondary, cladial branching, but is not related to older multiramous dichograptids (Maletz 1994, 1998). Ruedemann (1947, pl. 49, figs 5, 6) included specimens of *Pterograptus elegans* from the Glenogle Shale with *Bryograptus pusillus*.

Adelograptus. A number of species were described originally under *Bryograptus* before the genus *Adelograptus* was established (e.g. Hall 1899; Westergård 1909; Benson and Keble 1935). Bulman (1941, p. 103) established the genus *Adelograptus* and noted that the species previously included in *Bryograptus* made this genus 'a dumping-ground for little understood species'. He listed a number of species that are now referred to other genera, including *Bryograptus*. Species of the genus *Adelograptus* possess a horizontal to sub-horizontal rhabdosome, a biradiate proximal development and bithecate stipes (Bulman 1941; Hutt 1974; Maletz and Erdtmann 1987).

BIOSTRATIGRAPHY AND BIOGEOGRAPHY OF *BRYOGRAPTUS*

The biostratigraphical understanding of the distribution of *Bryograptus* (Text-fig. 7) is hampered by the poor state of knowledge on Tremadocian biostratigraphy. Even though the basal Tremadocian graptolite faunas are well known (e.g. Cooper *et al.* 1998), and the uppermost Tremadocian faunas have been described in some detail (Lindholm 1991; Williams and Stevens 1991; Maletz 1999; Maletz and Egenhoff 2001), a considerable gap in our knowledge on Tremadocian graptolite biostratigraphy is still in existence. The lower part of the upper Tremadocian is often referred to a fairly unspecified *Adelograptus* or *Adelograptus tenellus* Biozone (e.g. Jackson and Lenz 2003; Egenhoff *et al.* 2004; Moya 2008), and a correlation is difficult.

Baltica. The genus *Bryograptus* is common in the Oslo Region of Norway (Kjerulf 1865; Lapworth 1880; Brøgger 1882; Monsen 1925; Spjeldnæs 1963; Erdtmann 1965), where it occurs in the Upper Tremadocian above the Symphysurus Limestone, while faunas with abundant *Anisograptus* occur below the Symphysurus Limestone

		Scandinavia Egenhoff et al. 2004	Bolivia Egenhoff et al. 2004	Argentina Gonzalez Barry & Alonso 1984	Argentina Moya et al. 1994	Arctic Canada Jackson & Lenz 2003
Tremadocian	Upper	*Hunnegraptus copiosus*	*Hunnegr. copiosus*	no fauna	no fauna	*Hunnegr. copiosus*
		Araneograptus murrayi	*Araneogr. murrayi*			*Kiaerogr. pritchardi*
		Kiaerograptus kiaeri	*Aorograptus victoriae*		*Adelograptus*	*Kiaerogr. antiquus Adelogr. tenellus*
		Bryograptus ramosus		*Bryograptus* aff. *kjerulfi*	*Bryograptus kjerulfi*	
		Adelograptus tenellus	*Adelograptus*	*Triarthrus tetragonalis Shumardia minutula*	*R. socialis R. flabelliformis*	*Anisogr. matanensis*
	Lower	*Rhabdinopora f. anglica*	*Rhabdinopora flabelliformis*			
		Anisograptus matanensis		*Jujuyaspis keideli*		
		Rhabdinopora f. parabola				*Rhabd. f. parabola*
		Rhabdinopora praeparabola			*Rhabdinopora rustica*	*Rhabd. praeparabola*

		E. North America Maletz & Egenhoff 2001	South China Feng et al. 2009	Jiangnan Region Zhang et al. 2007	U. Yangtze Region Zhang et al. 2007	Australasia V. & C. 1992
Tremadocian	Upper	*Hunnegraptus copiosus*	*Hunnegraptus copiosus*	'*Adelograptus-Clonograptus*'	*Hunnegraptus copiosus*	La 2
		Araneograptus murrayi	*Araneograpus murrayi*		*Acanthograptus sinensis*	
		Kiaerograptus supremus	*Aorograptus victoriae*		*Bryograptus tintinniformis*	La 1.5
		Aorograptus victoriae		*Aorograptus victoriae*		
		faunas not investigated	*Adelograptus tenellus*	?	?	
	Lower	*Rhabdinopora f. anglica*	*Rhabdinopora f. anglica*	*Rhabdinopora f. anglica*		La 1
		Anisograptus matanensis	*Anisograptus matanensis*	*Anisograptus matanensis*	*Rhabdinopora flabelliformis*	
		Rhabdinopora f. parabola	*Rhabdinopora f. parabola*	*Rhabdinopora f. parabola*		
		Rhabdinopora praeparabola	*R. ? taojiangensis*	*R. ? taojiangensis*		

TEXT-FIG. 7. Biostratigraphy of the Lower Ordovician and confirmed range of the genus *Bryograptus* (in grey).

(Bulman 1950). Moberg and Segerberg (1906) recognized a *Bryograptus kjerulfi* and *Clonograptus tenellus* Biozone in the upper part of the Dictyograptus Shale (= Dictyonema Shale of many older Scandinavian authors; now the upper part of the Alum Shale Formation: Owen *et al.* 1990) of Scania, southern Sweden. Westergård (1909) differentiated the *Clonograptus tenellus* Biozone in the Upper Tremadocian and above it the *B. kjerulfi* Biozone. Hede (1951) and Tjernvik (1958) confirmed the presence of *B. kjerulfi* in the range charts for the Fågelsång and Flagabro drillcores of southern Sweden, but did not illustrate the graptolite material. Szymanski (1966) recorded *B. ramosus* from the Upper Tremadocian of Bialowieza, NE Poland, part of Baltica during the Ordovician.

The correlation between Norway and Sweden is problematic, as the Norwegian succession shows a distinct interval with *Anisograptus* below the *Bryograptus* interval (Bulman 1954), whereas in southern Sweden the interval below the *Bryograptus* Zone is called the *Adelograptus tenellus* Zone. As the Swedish material has never been illustrated properly, it might be possible that the material was misidentified and actually belongs to *Anisograptus*. Therefore, the Tremadocian succession of Scandinavia needs to be re-investigated, and the biostratigraphical succession discussed by Egenhoff *et al.* (2004) and shown in Text-figure 6 may be partly incorrect.

Great Britain. According to Strachan (1996), *Bryograptus* is not present in Great Britain. Elles (1898) and Elles and Wood (1902) described and illustrated *B. kjerulfi* and *B. kjerulfi* var. *cumbrensis* from Barf in the Lake District, but Bulman (1971) referred the material to *Pseudobryograptus* instead. The material of ?*Bryograptus callavei* Lapworth 1880 belongs to *Adelograptus tenellus* as was discussed by Maletz and Erdtmann (1987).

North America. Bryograptus has frequently been mentioned from North America, one of the last examples probably being the identifications of graptolites of the Cow Head Group sections in James and Stevens (1986). This material was later included in *Aorograptus* (Williams and Stevens 1991) or may be referred to poorly preserved *Rhabdinopora* and other anisograptids of early Tremadocian age. Ruedemann (1947, p. 151) gave a list of synonyms of species that have wrongly been identified as *Bryograptus* and described five species of *Bryograptus* from the Lower to Middle Ordovician of North America. *Bryograptus kirki* from the Arenig of the Trail Creek region appears to be a subhorizontal adelograptid with a biradiate proximal development and delayed dichotomies, but is not related to *Bryograptus*. Its age may be mid-Arenig or upper Floian to Dapingian, as the existence of strata of Tremadocian age has not been confirmed from the Trail Creek region (Maletz *et al.* 2005).

Bryograptus lapworthi is a slender, subhorizontal dichograptid from the Deep Kill Shales of New York, probably related to the Chewtonian to Castlemainian genus *Zygograptus*. Ruedemann (1947) also assembled a number of possible specimens of *Pseudobryograptus* and *Pterograptus* (see Mu 1957, p. 423) under the name *Bryograptus pusillus*. Thus, most probably none of the North American species described by Ruedemann (1947) actually belongs to *Bryograptus*.

The best Lower Ordovician graptolite succession in North America can be found in the Cow Head Group of western Newfoundland, but faunas with *Bryograptus* have not been discovered. The graptolite succession of this interval was described as a result of the focus on two proposed GSSPs for the base of the Ordovician System (Fortey *et al.* 1982; Barnes 1988; Cooper *et al.* 2001) and the base of the second Series of the Ordovician System (Williams & Stevens 1991; Williams *et al.* 1994, 1999). A considerable interval between the *R. flabelliformis anglica* Biozone and the *Aorograptus victoriae* Biozone is virtually unknown ('faunas not investigated': see Text-fig. 7) and faunal comparisons are therefore difficult. Another excellent succession was recently described from Arctic Canada (Jackson & Lenz 2003), but again did not produce any specimens of *Bryograptus* (Text-fig. 7).

Gondwana. Albanesi *et al.* (2008) recently updated the Lower to Middle Ordovician graptolite biostratigraphy of Argentina and provided good evidence for the completeness of the succession. The authors (Albanesi *et al.* 2008, fig. 4.11) demonstrated unequivocally the presence of the genus *Kiaerograptus* in the Eastern Cordillera of Argentina. The genus *Bryograptus* has frequently been mentioned from South America (see Harrington and Leanza 1957; Suarez-Soruco 1975; Gonzalez Barry and Alonso 1984; Moya *et al.* 1994), but most specimens belong to the genus *Aorograptus* (Egenhoff *et al.* 2004). Ortega and Albanesi (2003, 2005) described and illustrated specimens of *Bryograptus* from the Parcha area and discussed the biostratigraphy of the succession, in which *Bryograptus* sp. was stated to occur in a monospecific assemblage. Monteros and Moya (2003) illustrated a single specimen of *Bryograptus*? sp. nov. from the San Bernardo Formation of the Mojotoro Range. The specimen is too poorly preserved for a specific identification and apparently lacks part of the proximal end.

A *Bryograptus* Zone is used frequently in South America (Albanesi *et al.* 2008; Zeballo *et al.* 2008). Botello-Loza and Suárez-Sorucco (1973) discussed the presence of *Bryograptus* in their *Clonograptus* Zone for the Culpina region of southern Bolivia. Subsequent research showed that the material belongs to *Aorograptus* instead (see Maletz and Egenhoff 2003, fig. 4). Egenhoff *et al.* (2004) did not recognize *Bryograptus* in the successions of southern

Bolivia, but recognized an *Aorograptus victoriae* Biozone in the Upper Tremadocian (Text-fig. 6).

Gonzalez Barry and Alonso (1984) established a zone of *Bryograptus* aff. *B. kjerulfi* for the interval in the Sierra de Mojotoro, northern Argentina (Text-fig. 7), changed to the *B. kjerulfi* faunal association by Moya *et al.* (1994), while Ortega and Albanesi (2003) used the term *Bryograptus* Zone for the same interval. Biostratigraphical ranges are not available, and faunal assemblages are based on isolated occurrences, unfortunately. Ortega and Albanesi (2003) described the interval from the *Bryograptus* Biozone to the *Hunnegraptus copiosus* Biozone, while Monteros and Moya (2002, 2003) provided biostratigraphical data for their *Aorograptus victoriae* Biozone, correlatable with the *Kiaerograptus* to *Araneograptus murrayi* biozones of Ortega and Albanesi (2003, 2005).

Very little is known of Tremadocian graptolite faunas of other parts of Gondwana. Blain (1963) mentioned *Bryograptus* sp. from the Algerian Sahara, which may be the only record from North Africa, but the material has not been illustrated.

China. A number of *Bryograptus* species have been described from China. The latest overview in Mu *et al.* (2002) refers 15 taxa to this genus. Most of these are poorly preserved and inadequately illustrated. Thus, it is impossible at the moment to derive a coherent picture. There is the possibility that specimen identified as *B. ramosus* (Mu *et al.* 2002, pl. 40, fig. 10) actually belongs to this species, confirming the presence of the genus *Bryograptus* in China. The species *B. tintinniformis* was used to define the Lower Ordovician *Bryograptus tintinniformis* Biozone, correlatable with the *Aletograptus-Triograptus* Biozone (Mu *et al.* 2002, p. 9). Wang and Wang (2001, p. 157) considered this species to represent juveniles of *Rhabdinopora f. anglica*.

Zhang and Erdtmann (2004*a*, *b*), Zhang *et al.* (2003, 2005, 2007) and Feng *et al.* (2009) recently discussed the biostratigraphy of the Lower Ordovician of China. The Tremadocian graptolite succession of North and South China is divided into six graptolite biozones and two barren intervals (Text-fig. 7). In South China, the late Tremadocian is partly covered by the *Aorograptus victoriae* Biozone with a gap below and above, followed by the *Acanthograptus sinensis* and *Hunnegraptus copiosus* biozones in the latest Tremadocian. Interestingly Zhang *et al.* (2003) indicated the presence of *B. kjerulfi orientalis* in their early Tremadocian time interval, above the first occurrence of *Staurograptus* specimens and associated with these. They also showed the presence of *Bryograptus chekiangensis* and *B. tintinniformis* (= *Rhabdinopora f. anglica*; see above) in their *Aorograptus victoriae* Biozone. Feng *et al.* (2009) discussed in detail the correlation of the South China plate and recognized four biozones, but did not mention the genus *Bryograptus*.

For the North China region, the gap below the *Aorograptus victoriae* Biozone is filled in by the *Psigraptus jacksoni* Biozone (Zhang and Erdtmann 2004*a*, fig. 3). Illustrated specimens of the *Bryograptus* material does not show unequivocal characters for their identification as *Bryograptus*, and the material may belong to *Aorograptus* instead.

Australasia. The genus *Bryograptus* is not present in Australasia, as Williams and Stevens (1991) referred material formerly included in *B. victoriae* Hall to *Aorograptus*. However, in older literature, the name *Bryograptus* appears commonly associated with *Aorograptus victoriae* and other multiramous Lancefieldian forms. VandenBerg and Cooper (1992) reviewed the Ordovician graptolite biostratigraphy of Australasia and provided data for the biostratigraphical interpretation and identification of key taxa in the Australasian region, listing all identified species. They also listed under *Bryograptus* a number of species now referred to *Aorograptus* and *Paradelograptus*.

The biostratigraphical correlation of the Lower Ordovician faunas of Australia is difficult because of the poor record (Text-fig. 7). The La 1.5 (*Psigraptus* Zone) can be correlated with a level in the lower part of the Upper Tremadocian through the presence of *Ancoragraptus* (Cho *et al.* 2009), but there is no hint to the exact correlation of the Australasian succession with the *Bryograptus* Zone of the Atlantic Faunal Realm.

SYSTEMATIC PALAEONTOLOGY

Order GRAPTOLOIDEA Lapworth, *in* Hopkinson and Lapworth, 1875

Family ANISOGRAPTIDAE Bulman, 1950

Genus BRYOGRAPTUS Lapworth, 1880

Type species. Bryograptus kjerulfi Lapworth, 1880 (subsequently designated by Gurley 1896, p. 64).

Included species. Bryograptus kjerulfi Lapworth, 1880; *B. ramosus* Brøgger 1882 and *B. broeggeri* Monsen, 1925.

Diagnosis (emended). Pendent, anisograptid with triradiate proximal end and conical, multiramous rhabdosome; sicula slender, elongated and sometimes provided with long and slender vane; stipes frequently branching dichotomously with irregular branching intervals, including autothecae and bithecae; bithecae alternately arranged on the stipes; dissepiments lacking.

Proximal development. The proximal end development is isograptid, dextral in the few available specimens with th 1^2 constituting the first dicalycal theca (Text-fig. 1). Th 1[1] originates high on the sicula, most probably in the lower part of the prosicula. It turns distinctly outwards after growing along about 3/4 of the sicula length and slightly below the origin of th 1[2]. Th 1[2] is right-handed. It grows down the sicula until the dorsal side of the sicular aperture and starts stipe 2. Further development is not clear, but the third stipe diverges from the sicula at about the same level as stipe 2, supporting the model of Maletz (1992*a*, *b*) for the proximal development of anisograptids, which predicts the presence of two successive dicalycal thecae. The stipes show bithecae on alternating sides, but the sicular bitheca on the obverse side of the rhabdosome has not been seen as all relief specimens preserve the reverse side. The bithecae are long and slender and originate laterally on the stipes and grow upwards initially, as do the autothecae, forming a distinct plaited structure (Lindholm 1991).

Remarks. Kjerulf (1865) illustrated and described for the first-time specimens of *Bryograptus* under the name of *Graptolithus tenuis* Portlock from the Lower Ordovician of the Oslo Region of Norway. Lapworth (1880) erected the genus *Bryograptus* for this material and described the taxon as a pendent dichograptid with a loosely branching habit and numerous stipes. He referred two species, *B. kjerulfi* from Vækkerø, Norway, and *B. callavei* (= *Adelograptus tenellus*: see Maletz and Erdtmann 1987) from the Shineton Shales of Shropshire, Britain, to this genus, but did not select a type species. Gurley (1896, p. 64) designated *B. kjerulfi* Lapworth, 1880 as the type species of the genus *Bryograptus*. Bulman (1941, 1970, 1971) emended the genus *Bryograptus* to include only triradiate forms with dichotomous branching.

Lapworths' (1880) original description of *B. kjerulfi* is short, incomplete and partly misleading. Thus, the description of Bulman (1971) is the only one dealing with the more detailed development of the rhabdosome of *B. kjerulfi*, providing the necessary information for unanimously identifying this species. Bulman (1971) noted a tri-radiate rhabdosome with a compact dendroid form and a relatively large sicula of 1.5 mm in length, but details of the proximal development in the type material of *B. kjerulfi* were not available because of the flattening of the specimen.

Spjeldnæs (1963) for the first time illustrated and described relief material of the closely related species *B. ramosus* (Brøgger, 1882) from the Upper Tremadocian of Norway. This material confirmed the tri-radiate proximal end development and the typical bithecate stipes of *Bryograptus*. It also demonstrated the presence of an unusually long sicula (up to 2 mm) in *B. ramosus*. Even though this species is not the type species of the genus, its' development has to be regarded as typical of the genus *Bryograptus* and is analysed in more detail later. Relief specimens of *B. kjerulfi* and *B. broeggeri* do not exist, and the proximal development of these species remains uncertain.

Bulman (1971) differentiated three species in the genus *Bryograptus*. Differences, however, appear to be vague and characters may overlap, making a species identification difficult, especially in poorly preserved material. All three species were originally described from the Upper Tremadocian of the Oslo Region of Norway and must be regarded as closely related or even synonymous.

Evolutionary relationships. The genus *Bryograptus* has never been used in any evolutionary investigation because of the poor knowledge of its rhabdosome structure. A number of distinct features, like the typical bithecate stipes, the presence of a sicular bitheca, the triradiate proximal development, all support an inclusion of the genus in the Anisograptidae. The elongated sicula, however, is distinct and differs from the siculae of all other known genera of the Anisograptidae. Unfortunately, details of the development are not available, and the structure of the prosicula (conus and cauda: see Hutt 1974) is unknown. The triradiate development of the proximal end conforms to the development in the genus *Anisograptus* from the upper part of the Lower Tremadocian (see Maletz 1992*a*, *b*; Cooper *et al.* 1998). The genus *Bryograptus*, thus, represents the youngest anisograptid with a triradiate proximal development. All younger graptoloids known from the Tremadocian (see Text-fig. 5) are biradiate. *Bryograptus* therefore is close to the origin of the biradiate anisograptids and helps to precisely pinpoint the evolutionary origin of this group.

Bryograptus kjerulfi Lapworth, 1880
Text-figures 1B, 8A–M

1865 *Graptolithus tenuis* Portlock; Kjerulf, p. 3, figs 6a, b, A, B, non fig. 6c.
1880 *Bryograptus kjerulfi* sp. nov. Lapworth, p. 164, pl. 5, figs 22a, b.
1882 *Bryograptus kjerulfi* Lapworth; Brøgger, p. 37, pl. 12, fig. 20, 20a.
1906 *Bryograptus kjerulfi* Lapworth; Moberg and Segerberg, p. 61, pl. 1, fig. 14.
1909 *Bryograptus kjerulfi* Lapworth; Westergård, p. 66, pl. 5, figs 8, ?7.
1984 *Bryograptus* aff. *B. kjerulfi* Gurley; González-Barry and Alonso, p. 65, figs. 1–3.
1984 *Staurograptus* sp. González-Barry and Alonso, p. 65, figs 4, 5.
1994 *Bryograptus kjerulfi* Lapworth; Moya *et al.*, p. 96, pl. 2, figs 8, 9.
2003 *Bryograptus* sp. Ortega and Albanesi, p. 83, fig. 3A, K.
2008 *Bryograptus* cf. *kjerulfi* Lapworth. Albanesi, Ortega and Zeballo, fig. 4.13 (no description).

Diagnosis. Bryograptus with moderately long sicula and wide, cone shaped rhabdosome.

Type material. PMO 71.284 is the lectotype specimen of *B. kjerulfi*, selected by Bulman (1971). The type specimen comes from the upper part of the Upper Alum Shale Formation of Vækkerø, Oslo Region, Norway. The exact biostratigraphical level is unknown.

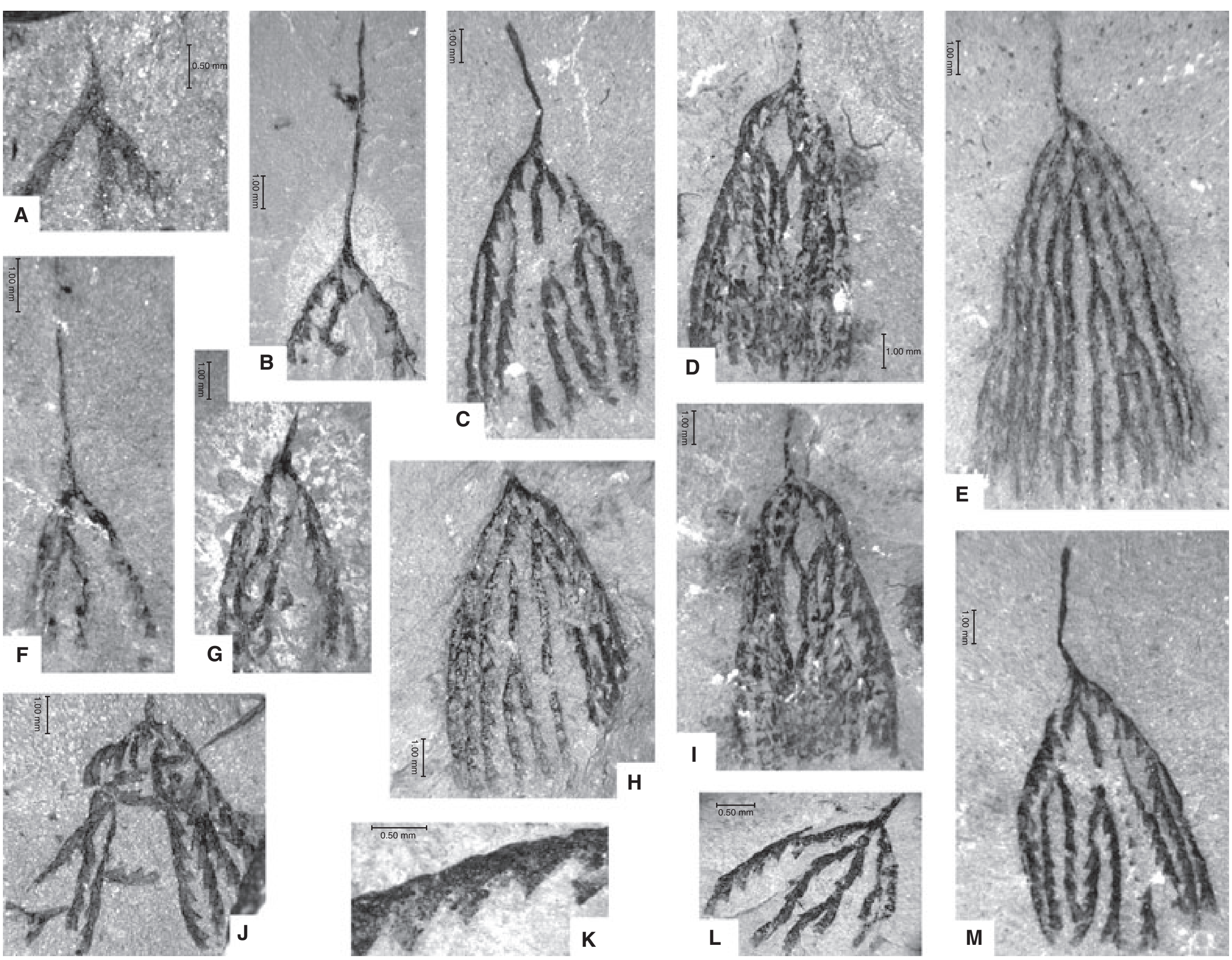
Investigated material. Approximately 20 specimens in various growth stages from the Cuesta de la Pedrera locality, Salta Province, Argentina.

Description of Argentinian specimens. The rhabdosome forms a cone with a maximum measured length of about 15 mm and a width attaining 8–10 mm. Many specimens bear a long and slender float at the tip of the nema, starting most probably as a thickened nema. The detailed structure of this 'nemal vane' is unknown as all specimens are flattened. The vane reaches a length of at least 6 mm, but a width of less than 0.4 mm.

The sicula is about 1.5–1.8 mm long and slender. The prosicula cannot be differentiated in any of the specimens. The thecae are visible in several laterally preserved stipes in many specimens. The 2TRD (Howe 1983) varies from 1.5 to 1.9 mm and is variable within individual specimens. In lateral view, indications of bithecae are visible in some specimens as the periderm is thin and partly transparent, but otherwise well preserved. Details of the proximal development are not visible in the material.

Remarks. The Argentinian material appears to differ from typical *B. kjerulfi* only in more densely spaced thecae, but otherwise differences are minor. The material is also very close to *B. ramosus* in its dimensions. Juveniles can easily be mis-identified as *Staurograptus* (Gonzalez Barry and Alonso 1984; Moya *et al.* 1994), as they tend to be preserved as radiating forms with the sicula in the centre. The material, however, includes specimens preserved in lateral view, typically indicating the triradiate development of *Bryograptus*.

The species was also mentioned and illustrated by Moya *et al.* (1994) from a number of localities in the Eastern Cordillera of Argentina. The authors referred the

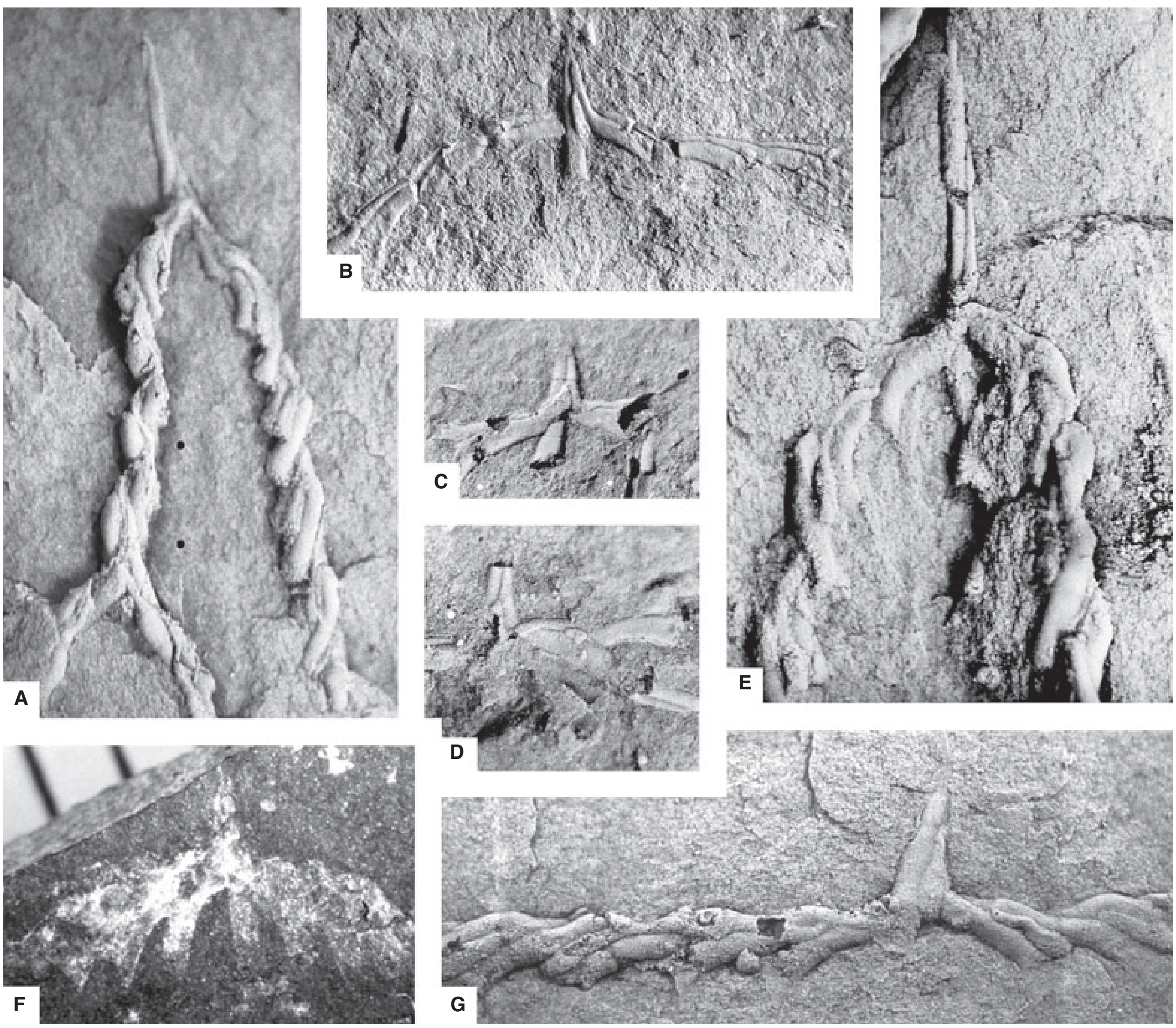


TEXT-FIG. 8. *Bryograptus kjerulfi* Lapworth, 1880, Cuesta de la Pedrera locality, Salta Province, Argentina. A, IANIGLA-PI 2261, juvenile. B, IANIGLA-PI 2262, juvenile with long float. C, IANIGLA-PI 2263, mature specimen. D, IANIGLA-PI 2264, largest specimen. E, IANIGLA-PI 2265. F, IANIGLA-PI 2266. G, IANIGLA-PI 2267. H, IANIGLA-PI 2268. I, IANIGLA-PI 2269. J, IANIGLA-PI 2270. K, IANIGLA-PI 2271, thecal detail, showing evidence of bithecae and slightly undulating dorsal side of stipe. L, IANIGLA-PI 2271. M, IANIGLA-PI 2272, specimen with float. The magnification is given by a 1-mm long bar on each photograph.

interval to their Asociacion V, characterized by *B. kjerulfi* and identified a number of juvenile specimens of this species as *Anisograptus* sp. cf. *A. compactus* Cooper and Stewart, *Staurograptus* sp. cf. *S. dichotomous* Emmons, *Anisograptus compactus* Cooper and Stewart and *Staurograptus* sp.

Bryograptus ramosus Brøgger, 1882
Text-figures 1A, 9A, E

1882 *Bryograptus ramosus* n. sp. Brøgger, p. 37, pl. 12, fig. 21.
non 1894 *Bryograptus ramosus* Brøgger; Marr, p. 125, figs 1–5.
1925 *Bryograptus ramosus* Brøgger; Monsen, p. 160, pl. 1, fig. 9; text-fig. 3.
1954 *Bryograptus* cf. *ramosus* Brøgger; Bulman, p. 34, pl. 4, fig. 9.
1963 *Bryograptus ramosus* Brøgger; Spjeldnæs, p. 122, pl. 17, figs 7–9.
non 1965 *Bryograptus ramosus* Brøgger; Erdtmann, p. 105, pl. 2, fig. 5.
1966 *Bryograptus ramosus* Brøgger; Szymanski, p. 50, pl. 6, fig. 9.
1971 *Bryograptus ramosus* Brøgger; Bulman, p. 365, figs 1e, f, 2c.



TEXT-FIG. 9. A, *Bryograptus ramosus* Brøgger, 1882. PMO 72.832, latex cast, reverse view. B, *Ancoragraptus bulmani* (Spjeldnæs, 1963), PMO 169.181, Slemmestad NRC section, 16.2–16.3 m, latex cast, obverse view with sicular bitheca (*Kiaerograptus* sp. A in Maletz and Egenhoff, 2001, fig. 4I). C–D, *Ancoragraptus* sp., juveniles in reverse view, ror 9.01, PMO 214.026.1, 214.026.2. E, *B. ramosus* Brøgger, 1882, PMO 72.831, latex cast, reverse view. F, *Kiaerograptus stoermeri* Erdtmann, 1965. flattened specimen with development of pressure shadow minerals, PMO 73.650. G, *Kiaerograptus?* sp. cf. *K.? supremus* Lindholm, 1991, PMO 139.919.1, latex cast in obverse view, showing several successive bithecae on one side of stipe 2.

Diagnosis. Slender *Bryograptus* species with few, widely spaced stipes and long sicula.

Type material. PMO 72.829 is the lectotype of the species (Spjeldnæs 1963). The material comes from Vækkero, Oslo Region, Norway.

Description. The species has a sicula of more than 2 mm in length. It widens quickly from the apex and is parallel-sided for most of its length. The origin of th 1^1 is about 0.4 mm below the apex of the sicula. The length of the prosicula cannot be determined in the material. Thus, it is unclear whether the origin is in the prosicula or metasicula. The protheca of th 1^1 is about 1 mm long and slender, before it widens considerably to produce th 1^2. Th 1^2 is the first dicalycal theca. It produces initially th 2^1 and distally th 2^2. The proximal development is clearly isograptid dextral, with a distinctly asymmetrical position of the crossing canals. The first stipe, following the direction of th 1^1, originates from a higher position on the sicula than the later stipes. The later stipe development matches the prediction of Maletz (1992*a*, *b*). There appear to be two successive dicalycal thecae, th 2^1 and th 3^1, forming the tri-radiate proximal end.

Remarks. Bryograptus ramosus is the only species of the genus known from relief specimens showing the proximal development. The general dimensions and rhabdosome development was described by Bulman (1941). The few relief specimens of *B. ramosus* all show a dextral proximal development. The origin of th 1^2 from th 1^1 is right-handed. Other anisograptids show a more variable development with dextral and sinistral development being equally common in *Adelograptus tenellus* (Stubblefield 1929; Hutt 1974; Maletz and Erdtmann 1987). Cooper and Fortey (1982, 1983) discussed the proximal development and concluded that in dichograptids in general show a dextral development of the proximal end.

Distribution. The species is known only from Norway, where it occurs in the uppermost part of the Alum Shale Formation. The species differs from *B. kjerulfi* and *B. broeggeri* through a much longer sicula.

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