

ORDOVICIAN GRAPTOLITES FROM THE EARLY HUNNEBERG OF SOUTHERN SCANDINAVIA

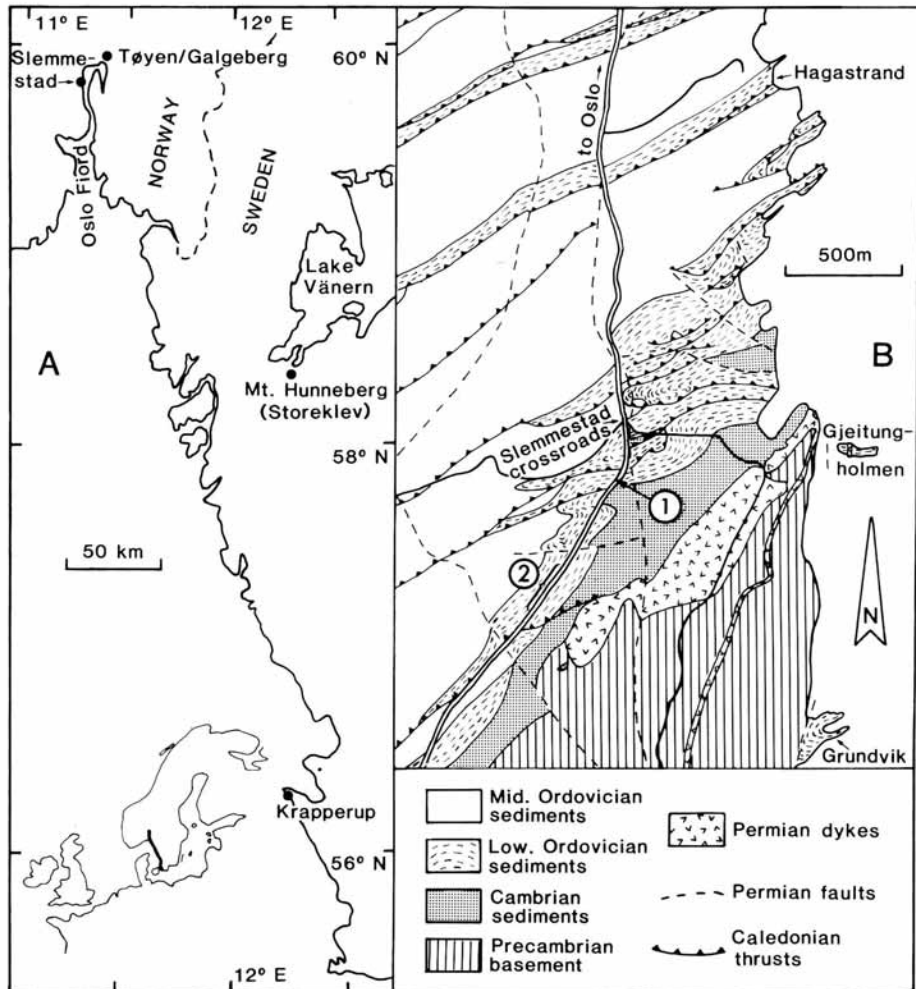
by KRISTINA LINDHOLM

ABSTRACT. A graptolite fauna of Early Hunneberg age is described from southern Scandinavia (Scania, Västergötland, Oslo region). Correlation and boundaries within the interval are discussed and it is suggested that the Hunneberg Stage be elevated to series rank, interposed between the Tremadoc and the Arenig. One new dichograptid genus, *Hunnegraptus*, and three Scandinavian representatives of it, *H. copiosus*, *H. tjernviki*, and *H. robustus*, are erected. The genus is multiramous, with long first-order stipes, and shows presumed rejuvenation of gerontic specimens. It is likely to be most closely related to *Clonograptus*. Six additional species are formally named: *Kiaerograptus supremus* (Anisograptidae), *Clonograptus (C.) magnus*, *Tetragraptus longus*, *T. krapperupensis* (Dichograptidae), *Paradelograptus elongatus*, and *P. tenuis* (Sinograptidae). The sequence containing these taxa is divided into three zones: the *K. supremus* Zone which probably starts in the Late Tremadoc, the *A. murrayi* Zone, and above that the *H. copiosus* Zone, which underlies the Late Hunneberg *Tetragraptus phyllograptoides* Zone. The fauna covers part of the interval when anisograptids gave way to graptolites of the dichograptid development stage, and the observed steps in this evolution (loss of bithecae) are described.

GRAPTOLITES from the Upper Tremadoc and Lower Arenig of southern Scandinavia have been known for over a hundred years, e.g. Tullberg (1880), Holm (1881), Brøgger (1882), Herrmann (1883, 1885), Törnquist (1901, 1904), Strandmark (1902), Monsen (1925, 1937), Spjeldnaes (1963), and Erdtmann (1965a). Yet, the fauna described in this paper, which comes from a 'post-Tremadoc, pre-Arenig' level, remained unrecognized until Tjernvik (1956) made his overview of the Lower Ordovician of Sweden. From a darker band in a grey shale unit at Storeklev, at Mt Hunneberg (Text-fig. 1A), he mentioned a few peculiar graptolites, which he referred to as 'undescribed dichograptids' in his correlation table. No description of this fauna has been given to this day. The fauna, together with several accompanying species, was later found in lithologically similar beds in the Oslo region, mainly by N. Spjeldnaes in the Slemmestad area and by B.-D. Erdtmann in central Oslo. More recently, I re-collected both the Storeklev and the Slemmestad localities. Finally, I identified the fauna, and also older post-Tremadoc graptolites, in a grey to nearly black shale sequence in the Krapperup drillcore in NW Scania. The rarity of identifiable graptolites in the basal beds of the core and absence of the otherwise ubiquitous *Ceratopyge* Limestone make lithostratigraphic and chronostratigraphic correlation of these basal beds difficult. Judging by circumstantial evidence, however, all of the basal beds probably belong to the Hunneberg.

From my own observations in the Lower Ordovician of southern Scandinavia (Lindholt 1991), a closely similar sequence of facies and faunas is developed in the Oslo region, Mt Hunneberg in Västergötland, and SE Scania. All areas can be regarded as lying within a single confacies belt, equivalent to Jaanusson's (1976, 1982) Scanian and Oslo confacies belts, at least until the end of Arenig time. They undoubtedly represent a single, original depositional basin which included, as a thicker and further offshore facies, the NW Scanian sequence of the Krapperup bore core.

All three areas, Oslo, Mt Hunneberg, and Krapperup, have been cut by various forms of late Carboniferous to early Permian intrusives. In other respects, the geological settings of the three areas, as seen today, differ due to their later geological history. The Oslo region is a large, more or less continuous area of well exposed Cambrian to Silurian sediments close to the Scandinavian fold



TEXT-FIG. 1. Location of the study area. A, Outline map showing location of investigated localities. B, Detail map of the Slemmestad area, showing the structural complexity; redrawn from Bockelie (1982). The main sampling localities of Lower Hunneberg rocks were the coastal sections at Grundvik and Hagastrand, a road-cut just south of Slemmestad crossroads (eastern side of the road), the new standard section (1; western side of the road), and a long continuous roadside exposure (western side) marked '2'. This is the 'Rortunet' section (Bødalen or Buss-stop Nybygget of previous collectors), which is most complete stratigraphically at its southern end. It is cut by a couple of minor thrust faults and Permian dykes. South of area '2' is another roadside exposure (western side), partly hidden behind trees. This section is the *Klaerograptus* locality of Spjeldnaes (1963) which, however, also contains Hunneberg age beds. In addition, a few samples are labelled with street names, and one sample derives from the islet Gjeitungholmen.

belt. The beds are gently, to somewhat more complexly, folded, with minor associated thrust faults particularly in the Slemmestad area where structure can be easily observed (Text-fig. 1B). Mt Hunneberg, on the other hand, constitutes a very small, isolated but well exposed area of Cambrian and Lower Ordovician sediments on a Precambrian basement, protected by a thick dolerite cap. The beds are flat-lying. Finally, the Krapperup area (NW Scania) is a small (1 × 7 km) fault-bounded block, surrounded by Mesozoic rocks, and lying within a zone of intense block faulting, the individual blocks of which are sometimes less than 1 km in width. The NW Scania area forms part of a broad tract of discontinuous outcrops, extending from NW to SE Scania, of Lower Palaeozoic rocks. The beds, and graptolite faunas described here, however, are known only from the western part of Scania.

STRATIGRAPHY

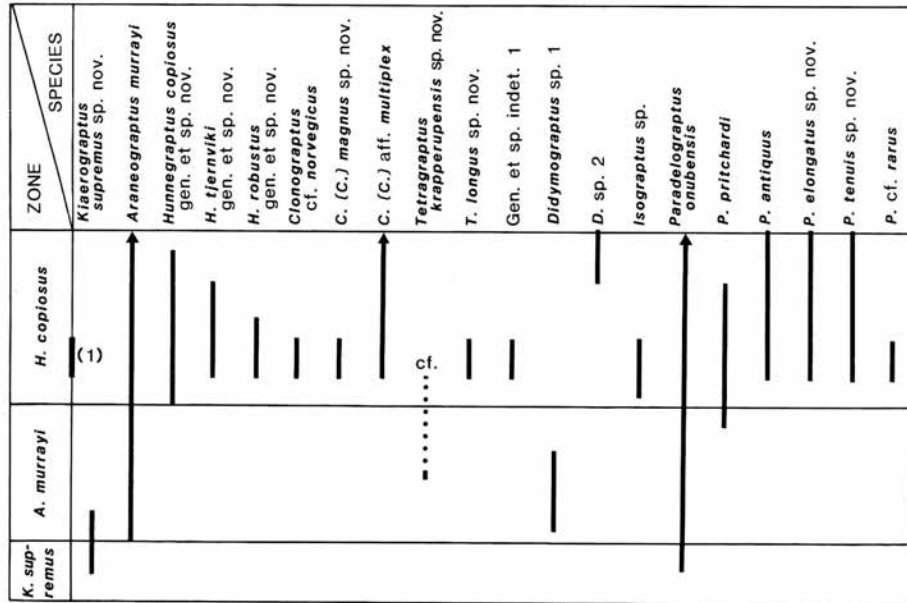
Zonation of the sequence. In Scandinavia, the interval from the base of the Ceratopyge Limestone to the base of the *T. phyllograptoides* Zone (roughly corresponding to the faunas described herein) has not formally been divided into graptolite zones; a '*Didymograptus? stoermeri* Zone' was indicated by Erdtmann (1965b, text-fig. 5; not defined in text) for the time interval spanning the Ceratopyge Limestone, but based on finds from the very top of the unit only (Erdtmann 1965a, p. 108). The same graptolite fauna is also present in W. Scania, in the Fågelsång core (Hede 1951; '*D. balticus*' Zone, followed by a major hiatus). Here, *D.? stoermeri* is found well above the Ceratopyge Limestone. The species was not found in the Krapperup core, despite examination of every cm of the lowermost metres of the core, nor was anything else as primitive-looking.

I propose a subdivision, based on the Krapperup core sequence, into (Text-fig. 2): a *Kiaerograptus supremus* Zone (Krapperup core, 155.06 m (base)–148.22 m); an *Araneograptus murrayi* Zone (148.22 m–132.73 m); and a *Hunnegraptus copiosus* Zone (132.73 m–112.80 m). The base of the *K. supremus* Zone corresponds to an undefined level within the Ceratopyge Limestone. The bases of the *A. murrayi* and *H. copiosus* Zones are defined by the incoming of their zone fossils. The base

NW SCANIA	HUNNEBERG	OSLO	WALES
<i>D. balticus</i>	<i>D. balticus</i>	<i>D. balticus</i>	Arenig
<i>T. phyllograptoides</i>	<i>T. phyllograptoides</i>	<i>T. phyllograptoides</i>	— ? —
<i>H. copiosus</i>	<i>H. copiosus</i>	<i>H. copiosus</i>	Hiatus
<i>A. murrayi</i>	<i>M. (E.) armata</i>	Hiatus?	* (in an oval)
<i>K. supremus</i>	<i>A. serratus</i>	<i>A. serratus</i>	— ? —
?	Hiatus	<i>S. pusilla</i>	<i>A. sedgwicki</i>
			<i>S. pusilla</i>

TEXT-FIG. 2. Attempted correlation of part of the Lower Ordovician between Scandinavia and Wales. The lithologies are clastic, except where indicated; * shows stratigraphic position of beds described by Molyneux and Dorning (1989).

of the overlying *T. phyllograptoides* Zone is defined by the incoming of *T. phyllograptoides* or a considerable increase in horizontal and reclined tetragraptids, whichever comes first, and roughly corresponds to the base of the *T. approximatus* Zone elsewhere. The approximate distribution of species is shown in Text-figure 3.



TEXT-FIG. 3. Summary of observed ranges of taxa present in topmost Tremadoc to Lower Hunneberg beds in southern Scandinavia. (1) indicates estimated relative position of the graptolite-rich horizon at Mt Hunneberg and in the Oslo region.

The case for a Hunneberg Series. It has long been known (e.g. Skevington 1966) that there is a sizeable hiatus between the Tremadoc and the Arenig in their respective type areas in Wales. The fauna described herein, of Hunneberg age, fits into this hiatus. Also, there is no general agreement yet as to where to put the boundary between the Tremadoc and the Arenig. This uncertainty concerns mainly beds of an age corresponding to La 2–La 3 in the Australasian stratigraphic scheme, and sometimes also beds of Be 1–Be 2 age (e.g. Rushton 1985). As things stand, the Hunneberg interval can thus be regarded in four different ways:

1. as a series filling the gap between the Tremadoc and the Arenig;
2. as the basal stage of the Arenig;
3. as the topmost stage of the Tremadoc;
4. as part Tremadoc, part Arenig.

The trend is nowadays towards a reduction of the number of series, e.g. the suggested amalgamation of the Llanvirn and the Llandeilo. Still, I am in favour of the introduction of a new Hunneberg Series, interposed between the Tremadoc and the Arenig, as previously suggested by Erdtmann (1988). In my opinion, this is the easiest way round a difficult problem. Even from the British point of view, it would be an advantage: what is now Tremadoc and Arenig in their respective type areas would remain so, whereas the beds of 'uncertain' age in the Lake District and

South Wales described by Rushton (1985), Molyneux and Rushton (1988), and Molyneux and Dorning (1989) would belong to the Hunneberg. The beds described in the above papers are all of La 2 age. My examination of the graptolites described by Molyneux and Rushton (1988) and comparison with Scandinavian and Spanish material proves them to be considerably older than the *T. approximatus* Zone (La 3).

I would recommend a Hunneberg Series of the extent originally suggested by Tjernvik (1956), not the revised concept of Tjernvik and Johansson (1980) who referred the topmost zone, that of *D. balticus*/*M. (V.)* aff. *estonica* ('Transition beds'), to the overlying Billingen Stage. It seems that the most practical definition of the Hunneberg Series would be in terms of conodonts, as comprising the conodont zones of *P. proteus* and *P. elegans*. This would closely fill the Tremadoc/Arenig hiatus in the type areas. The base of the Hunneberg would correspond to the Scandinavian top of the Tremadoc, however, which is equivalent to a level higher than the top of the Tremadoc in its type area in Wales (Skevington 1966; Henningsmoen 1973). From elsewhere in Wales and adjacent areas, Rushton (*in* Whittington *et al.* 1984) mentions younger beds which he refers to the Tremadoc. He includes a trilobite fauna correlated with the *Shumardia pusilla* Zone of Scandinavia which (Regnéll 1960) lies within the Ceratopyge Shale, and a younger *Angelina sedgwicki* Zone fauna which cannot be correlated with Scandinavia. Therefore, beds equivalent to the Scandinavian topmost Tremadoc *Apatokephalus serratus* Zone (Ceratopyge Limestone) are not definitely known in Wales. An approximate correlation between the Scandinavian and Welsh faunas is given in Text-figure 2.

The top of the graptolite sequence here described is considerably older than the oldest graptolite fauna in the type area of the Arenig. That fauna was described by Zalasiewicz (1986) and corresponds to a level no lower than the upper part of the *D. balticus* Zone or more probably the *P. densus* Zone of Scandinavia (Lindholm 1991). According to Fortey and Owens (1987, p. 99) no strata of *Tetragraptus approximatus* Zone age have been proven to exist in Wales, although they suspect rocks equivalent in age to the upper part of the zone to be present. All of the graptolite fauna described herein appears to be older than the *T. approximatus* Zone.

Cooper and Lindholm (1991) have made an attempt at estimating the relative duration of the different intervals in the Early Ordovician. That study indicates that the duration of the Hunneberg Series, as proposed here, is longer than the Tremadoc, taken as the *Rhabdinopora flabelliformis desmograptoides* Zone – *Apatokephalus serratus* Zone (the Scandinavian concept). It is only slightly shorter than the 'remaining' Arenig and of approximately equal length to the combined Llanvirn–Llandeilo. A further argument for a Hunneberg Series is the disagreement between workers on different fossil groups if the beds in question are 'Tremadoc' or 'Arenig' in age. Graptolite workers have generally considered the 'La 2' beds as 'Tremadoc', whereas conodont workers, working in different facies, call coeval beds 'Arenig'. It should be noted here that the base of the conodont zone of *P. proteus* lies considerably lower than the base of the *T. approximatus* Zone, contrary to the views of Barnes *et al.* (1988) (Löfgren *in prep.*). Different graptolitic facies have been treated equally ambiguously (Lindholm 1984): typical La 2 beds have been referred to the Tremadoc, whereas the coeval *A. murrayi* beds have been considered to be of Arenig age (e.g. Thorall 1935; Destombes *et al.* 1969). The works of Williams and Stevens (1991), Stouge and Bagnoli (1988) and Löfgren (*in prep.*) have added to the precision in correlation between the graptolite and conodont zonation. According to conodont evidence, the lower part of the La 2 graptolite fauna is of Tremadoc age (that described by Williams and Stevens (1991) from Newfoundland) whereas higher parts (this work) belong to the *P. proteus* conodont zone, generally regarded as of Arenig age.

LOCALITIES

In Scandinavia, the Lower Hunneberg beds outcrop only in the Oslo region (east-central Oslo and Slemmestad) and at Mt Hunneberg. In Scania they are known only from the Krapperup core, the basal beds also from the Fågelsång core (*D. balticus* Zone of Hede (1951)). Based on lithological similarity, they appear to be present

both further to the south (SE Scania) and to the north (Hamar at Lake Mjøsa). These beds are, however, unfossiliferous.

The only graptolite-bearing outcrop of Lower Hunneberg beds at Mt Hunneberg is at Storeklev, in the south-west wall of the mountain. Here, the Lower Hunneberg is represented by shale, and is thicker than elsewhere. The sequence gradually thins and shale gives way to limestone towards the eastern wall of the mountain. At Storeklev, graptolites are found scattered through the lower part of the shale, within which there is one rich band, 2.15–2.32 m above the hiatus separating the Cambrian from Ordovician beds (Tjernvik 1956). The collections investigated from Storeklev consist of T. Tjernvik's original material (PU Vg 124–127), B.-D. Erdtmann's collections from the early 1960s (TUB HUN-S/2. 18–2.3/001-058) and my own collections from 1979–1986, belonging to Lund University.

The Oslo region, *c.* 200 km north-west of Mt Hunneberg, contains several outcrops of Lower Ordovician graptolite shale, but the Lower Hunneberg beds are found only in the central part, at Galgeberg and Tøyen (both in east-central Oslo) and in the Slemmestad area (*c.* 20 km south-west of the Oslo localities). The Galgeberg and Tøyen localities were temporary construction sites, and are now inaccessible, whereas the Slemmestad area contains several well-exposed localities (road sections and beach sections; Text-fig. 1B). My own collecting at Slemmestad has shown the graptolites to be less rare than at Storeklev, but at both localities there are unusually rich horizons. The collections investigated from the Oslo region consist of material from Galgeberg collected in the 1930s by T. Strand and A. Heintz (PMO 58.965–58.970); B.-D. Erdtmann's collection from the Tøyen underground station (GPI T1–T30; PMO 73.652); collections from various localities in the Slemmestad area, mainly by N. Spjeldnaes, to a minor extent by G. Henningsmoen and D. Bruton (PMO 137, 73.187–73.192, 73.200, 73.204, 97.702, 97.705–97.706, 97.708, 108.557–108.574, 108.598–108.599, 112.966–112.970, 113.031–113.033, 120.751); and finally, my own collections from various localities in the Slemmestad area – the most productive one being Grundvik between Slemmestad and Naersnes to the south. My collections are all measured in sections, and belong to Lund University.

The investigated part of the Krapperup core (situated *c.* 230 km S of Mt Hunneberg) consists of the lowermost *c.* 42 m (155.06–112.80 m), comprising the Lower Hunneberg beds. 193 samples, not all of which contained identifiable graptolites, have been taken out of this part of the core. The core was drilled in the 1940s and belongs to Lund University. Its diameter is 62 mm.

All the material examined consists of medium grey to almost black, non-calcareous, shale/mudstone. The preservation of the graptolites varies from flattened to full relief, infilled with pyrite or, commonly in the lowermost part of the Krapperup core, with calcite. In the latter case, the periderm is usually very brittle and partly flakes off during splitting of the slab or preparation. Also, some of these graptolites were partly compressed and deformed before infilling with calcite. They are, consequently, often hard to identify.

GRAPTOLITE TERMINOLOGY

The terminology in general follows that of Bulman (1970) and Cooper and Fortey (1982, 1983; isograptid development type, dextral and sinistral mode, consecutive and delayed dichotomies etc.). Didymograptid and tetragraptid proximal part refers to the length of first-order stipes (several *vs.* one theca each). Profile stipe width refers to measurements made from the dorsal edge of the specimen to the ventral wall of a theca, at its aperture – the aspect of the stipe is referred to as 'profile view'. Lateral stipe width refers to specimens in dorsal or ventral view ('dorsoventral view'; horizontal preservation of multiramous specimens), that is, measurements are made from side to side of the stipe. The number of thecae in 10 mm has usually been measured over the available number of thecae, and then recalculated. Stipe divergence angles are measured as the angle resulting from the tangents of the dorsal side of the stipes across a specified thecal aperture. Secondary cortex cover in general refers to what appears to be an 'envelope' around the stipe, compressed to a film in the bedding plane in an arbitrary preservational aspect of the specimen; only exceptionally does the cortex cover appear to have thickened the stipe into a robust 'rod'. The terms sicular bitheca and plaited thecal structure are explained in the section on evolution. Dichograptid stipe indicates a stipe without triad budding or plaited thecal structure, i.e. 'fully graptoloid'. Graptoloid thecal notation is used throughout.

In the systematic section, the suprageneric classification of Fortey and Cooper (1986) has, in general, been followed (see discussion on the Sigmagraptinae, however). In the synonymy lists the signs recommended by Matthews (1973) have been used. Under the heading of 'Associated species' are listed only the species found on the same bedding plane as the species under discussion.

EVOLUTION AND PHYLOGENY

The fauna discussed in this paper represents a stage in graptolite evolution when (along various lineages) biradiality had generally been attained and bithecae were in the process of being lost. The coexistence of sinistral and dextral forms of a species is a common feature in early Hunneberg time. The fauna does not verify any general trend towards reduction in the number of stipes present in a rhabdosome.

Loss of bithecae. Bithecae were lost along different lineages in a rather restricted time period, Late Tremadoc and Early Hunneberg. Late Tremadoc graptolites showing various degrees of bithecal reduction were described by Williams and Stevens (1991).

I have not been able to verify if the various steps in this transformation follow in the same order (homotaxially) in different groups, nor if bithecae were lost progressively along a stipe or instantaneously. I have seen a limited number of combinations of primitive and advanced traits (Text-fig. 4A) that can be listed as five steps in a morphological series:

1. The typical anisograptid: a fully bithecate rhabdosome, with normal triad budding, i.e. successive groups of one autotheca, one bitheca, and a stolotheca, produced at stolonal nodes. These groups alternate regularly (Bulman 1970, fig. 8), so that, from one side of the rhabdosome, only every second bitheca can be seen (Text-fig. 4A:1, B). In profile view, the thecae are seen to bud laterally (Text-figs 4C, D, 5A, B). The alternation is seen as a zig-zag or sinuous pattern in dorsal view.

2. A fully bithecate rhabdosome with irregularities in the triad budding, that is, two or more successive bithecae may be present on one side of the rhabdosome (Text-fig. 4A:2, C, D), e.g. *Kiaerograptus supremus*.

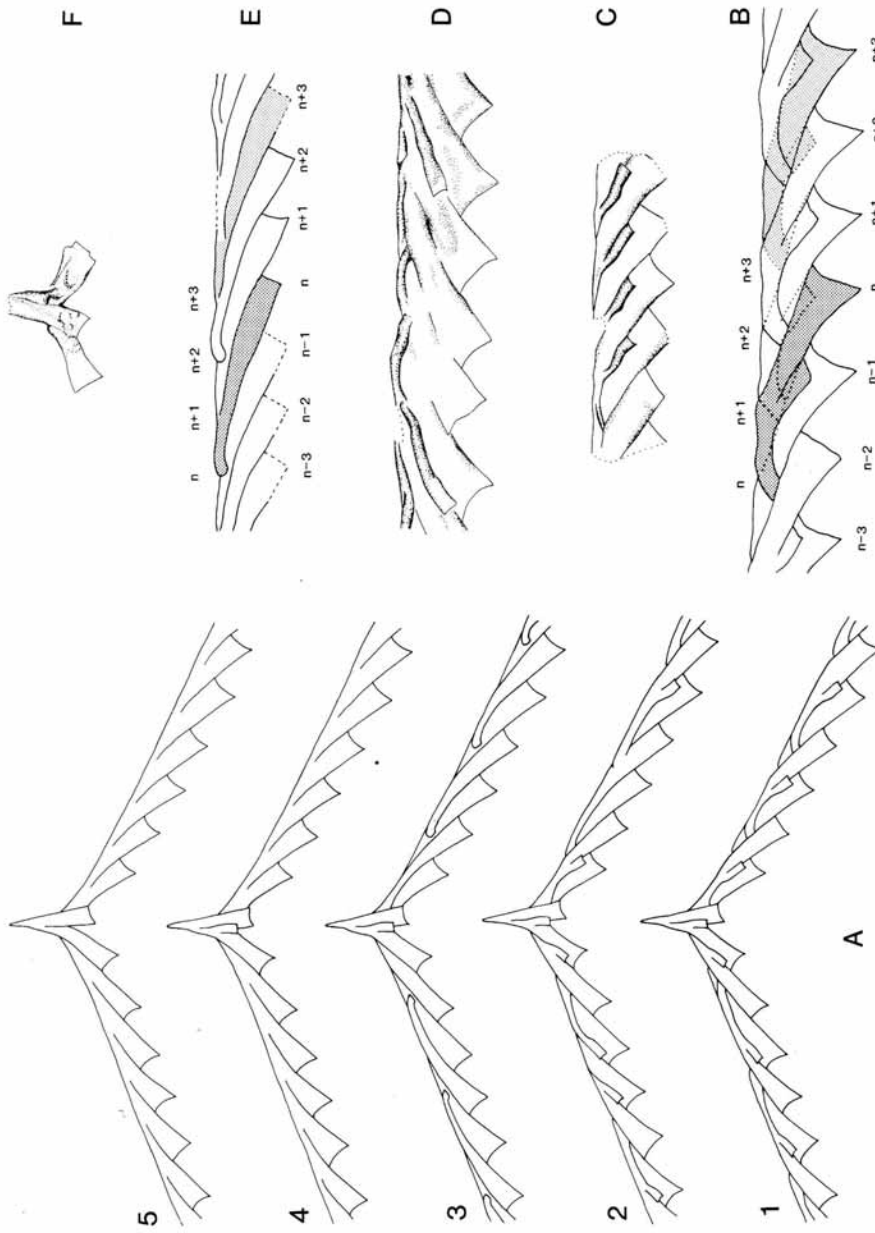
3. Only a sicular bitheca is present, i.e. the bitheca associated with $th\ 1^1$ and present between the sicula and $th\ 1^1$ on the obverse side. The stipes have traces of triad budding, here termed *plaited thecal structure*. The name has been chosen to illustrate the zig-zag or sinuous path of the common canal, as seen in dorsal view, caused by the fact that the thecae still alternate, even though the bithecae have been lost (Text-fig. 4A:3, E), and their proximal parts produce a 'herringbone' or plaited structure (in dorsal view). The budding is closer to the dorsal side of the rhabdosome than in the bithecate species examined, suggesting the possibility that the transition from lateral to dorsal budding was a gradual one.

4. The sicular bitheca remains, but the stipes are of normal dichograptid appearance (Text-fig. 4A:4), as in *Hunnegraptus copiosus*. This change in the stipes is apparently coupled with a reduction in total thecal length. A growth stage preserved in relief (Text-fig. 4F), might give a clue as to the disappearance of the sicular bitheca. It appears to have the proximal part of the bitheca, which has stopped growing. The 'aperture' is covered by periderm. Since only one specimen has been found, this interpretation is uncertain. The specimen could be pathological or deformed by compression.

5. The last primitive character, the sicular bitheca, is lost, and the 'dichograptid' development stage is reached (Text-fig. 4A:5).

In addition to what I have observed, Williams and Stevens (1991), using isolated specimens, found that residual bithecae may be found associated with dichotomies after disappearance of bithecae from the rest of the stipes.

Phylogeny. The phylogeny of the fauna is difficult to trace, mainly because of the rarity of well-preserved graptolites of Late Tremadoc age. What is evident is that the *Paradelograptus* group flourished in Early Hunneberg time, with at least six species present in Scandinavia. The genus belongs in the family Sinograptidae (see further discussion with systematic descriptions) which, judging from proximal and thecal characters, derives its origin from *Adelograptus tenellus*, and thus not *via* an unspecified dichograptid, as suggested by Fortey and Cooper (1986, text-fig. 11). The Sinograptidae constitutes one of the independent lineages with bithecal reduction. Another is the *Clonograptus s.s.* lineage. The earliest representatives of the lineage known from relief material



TEXT-FIG. 4. The observed steps in the evolution from a regularly bithecate anisograptid to a dichograptid. A, 1-5 shows a hypothetical development plan, involving the observed combinations of primitive and advanced characters. B, diagrammatic sketch of the budding principle of *Kiaerograptus*; dotted lines show thecal outlines on the unexposed side. C, PMO 72.834, Upper Tremadoc Ceratopyge Shale, Slemmestad, an unidentified stipe fragment showing irregular triad budding with four consecutive bithecae on the same side of the stipe; $\times 15$, drawn from latex cast under vertical light. D, the same slab, a distal part of a large *Kiaerograptus kiaeri* specimen with three consecutive bithecae on the unexposed side of the stipe; $\times 15$, drawn from latex cast under vertical light. E, diagrammatic sketch of a stipe with selected thecal structures based on a specimen of *Kiaerograptus kiaeri* (see text).

(Lindholm and Maletz 1989) have a sicular bitheca and plaited thecal structure (*C. aff. multiplex*) or a sicular bitheca and normal dichograptid stipes (*C. rigidus*). Lindholm and Maletz (1989) restricted *Clonograptus s.s.* to species without bithecae along the stipes. *Hunnegraptus* is a probable descendant of an early *Clonograptus* species or of one of its ancestors. A certain variation in first-order stipe length is known in *Clonograptus*, and the length was accentuated in *Hunnegraptus*. It is possible that one group of didymograptids (*D. undulatus*, *D. protobalticus-balticus*, *D. geometricus* etc.) derives its origin from *Hunnegraptus*, through suppression of higher-order dichotomies. Likewise, a number of horizontal and reclined tetragraptids (and *Dichograptus* species?) may derive their origin from a species of *Clonograptus s.s.* related to *C. magnificus-multiplex*. Broad stipe fragments with thecae of reclined tetragraptid type (long, somewhat curved thecae, with high inclination and high thecal overlap) are sometimes met with in the Lower Hunneberg fauna.

Other taxa are more problematic. For instance, did *Kiaerograptus* give rise to another group of didymograptids (another separate lineage with bithecal reduction) and/or the earliest isograptids (see p. 320)? What is the origin of the early 'corymbograptids' found in Scandinavia, Britain and Spain – probably the very earliest didymograptids – and the 3- and 5-stiped forms?

SYSTEMATIC PALAEOLOGY

Repositories of specimens. Abbreviations used are as follows: GPI, Institute of Geology and Palaeontology, Göttingen, Germany; GSC, Geological Survey of Canada, Ottawa, Canada; LO and LR, Department of Historical Geology and Palaeontology, Lund, Sweden; PMO, Palaeontological Museum, Oslo, Norway; PU, Palaeontological Institute, Uppsala, Sweden; RM, National Museum of Natural History, Stockholm, Sweden; SGU, Geological Survey of Sweden, Uppsala, Sweden; TUB, Technical University, Berlin, Germany.

Order GRAPTOLOIDEA Lapworth, 1875

Diagnosis (from Fortey and Cooper 1986). Graptolites in which the nema is retained in the adult stage.

Incerti subordinis

Family ANISOGRAPTIDAE Bulman, 1950

Diagnosis (from Fortey and Cooper 1986). Paraphyletic group, sicula retains nema in adult stage, bithecae present, rhabdosome more or less bilaterally symmetrical, and quadriradiate, triradiate or biradiate.

Remarks. The Anisograptidae is a very heterogenous group, with many of its biradiate taxa closely similar to various taxa within the Dichograptina, the only difference being the presence of bithecae along the stipes in anisograptids. In my opinion, to obtain a phylogenetically based classification, the inclusion of taxa with bithecae along the stipes will eventually have to be accepted in the Dichograptina, thus necessitating a redefinition of that group. What would be left in the Anisograptidae, in that case, would be its tri- and quadriradiate taxa, which are probably rather closely genetically related, since they appear in a relatively short interval of time just after the origin of planktonic forms. Additionally included would be those biradiate taxa that cannot be linked with a dichograptinid form. For practical purposes, this change would make classification (above the genus level) easier, since most forms are not well enough preserved to reveal bithecae.

Genus KIAEROGAPTUS Spjeldnaes, 1963

Type species. *Kiaerograptus kiaeri* (Monsen, 1925).

Diagnosis (based on Spjeldnaes 1963; Rushton 1981; and author's observations). Rhabdosome biradiate, composed of two reclined to declined stipes, one of which may be aborted after the first

theca; one stipe may branch near, or at some distance from, the sicula. In some rare cases, an extra proximal theca may represent an aborted third stipe. Autothecae are of dichograptid type but may have isolated distal parts. Bithecae present at sicula and along stipes. Triad budding not always regular.

Kiaerograptus supremus sp. nov.

Text-fig. 5

v 1965a *Kiaerograptus kiaeri* (Monsen); Erdtmann, pp. 106–107, pl. 2, figs 1 and 2; pl. 3, fig. 4.

Name. Latin *supremus*, uppermost, indicating its position as the last of the fully bithecate species in the Krapperup core.

Material. 46 specimens, of which 44 come from the 151.96–144.57 m level of the Krapperup core and 2 from the Tøyen section, Oslo (both found on PMO 73.652; illustrated by Erdtmann 1965a). Holotype LO 5970T (Text-fig. 5A), paratype LO 5971t.

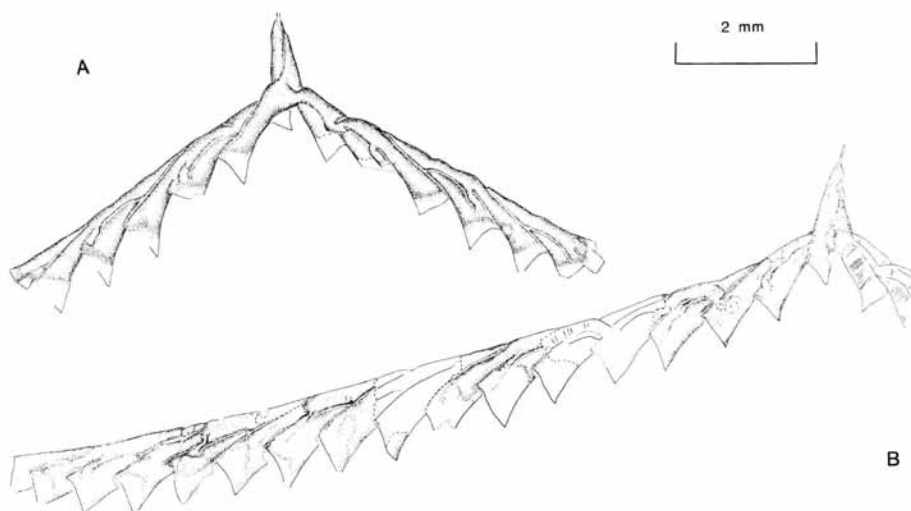
Associated species. ?*Trograptus* sp., *P. onubensis*, *A. murrayi*.

Stratigraphic range. *K. supremus* and *A. murrayi* Zones.

Diagnosis. Rhabdosome composed of two undivided declined stipes. Proximal development comparable to isograptid type. Bithecae present throughout stipes but sometimes not regularly alternating. Length of sicula 1.7–2.0 mm, stipe width 0.8–1.1 mm, 12–13 thecae in 10 mm, divergence of stipes 115–140°.

Description. The species is a typical anisograptid, with bithecae developed at most or all available nodes (with possible reductions in the stratigraphically youngest specimens – no pyritized specimens are available above 147.66 m). The proximal development type resembles the isograptid development, i.e. th 1² is dicalycal. As seen in Text-figure 5A, though, theca 2² emerges from the sicula-facing side of th 1², indicating that the triad (alternate) budding mechanism operates already in this position. Both sinistral and dextral forms are found (compare Text-fig. 5A with 5B). A sclerotized stolon system has not been observed: a relief specimen (now unfortunately lost) from the Krapperup core, filled with clear calcite, appeared 'empty' inside. The sicula is tube-like, 1.7–2.0 mm long and 0.3–0.45 mm wide at the aperture, depending on the degree of compression. The first bud emerges approximately 0.25 mm from the apex of the sicula. The stipes show typical triad budding, i.e. the autothecae are seen to emerge alternately from opposite sides of the stipe. The first bitheca of each stipe (as well as the sicular bitheca) seems to occur on the obverse side. Thecal length, including stolothecae, can be estimated at 2 mm. Thecal width at the aperture is 0.5 mm, sometimes slightly more in flattened specimens. The free ventral part of the thecae is somewhat curved, especially if the proximal part of the theca is more completely pyritized than the distal part (see Text-fig. 5A). The inclination of the distal parts of thecae varies from 30° to 45° depending on the degree of compression. There are 12–13 thecae in 10 mm. The thecal overlap is difficult to estimate due to the triad budding: the thecae do not bud dorsally, but laterally. In regular triad budding, the budding point of every second theca is on the unexposed side of the specimen. Such a theca will be seen only as a wedge between the preceding and the following theca (see Text-figs 4 and 5). The bithecae are about 0.4 mm long and 0.1–0.15 mm wide. They do not reach the aperture of the previous autotheca. Text-figure 5B shows a stipe with irregular triad budding: the bithecae associated with th 2² and 4² are on the obverse side, whereas that associated with th 6² is on the reverse side. The profile stipe width is 0.8–0.9 mm in relief specimens, and 0.9–1.1 mm in flattened ones. The stipe divergence angle is 115–140°.

Remarks. Within the studied area, the species was found only in the Krapperup core and the Tøyen section in Oslo (Erdtmann 1965a). From the latter area only two specimens from a shale band at the very top of the Ceratopyge Limestone unit were found. This limestone is considered as the top of the Tremadoc in Scandinavia. Most or all of it is younger than the youngest Tremadoc beds present in the type area. Because the Krapperup core lacks the limestone, it is a little difficult to correlate the two occurrences of the species. On circumstantial evidence (Fågelsång core), the Krapperup specimens are somewhat younger.



TEXT-FIG. 5. *Kiaerograptus supremus* sp. nov. from the Krapperup core. A, holotype, LO 5970T, a dextral specimen in full relief, 151.46–151.50 m. B, LO 5971t, a sinistral specimen in low relief, with irregular triad budding, 150.13–150.17 m. Both specimens drawn under vertical light.

The specimens found in the Krapperup core are mostly rather small, the longest stipe seen consisting of 16 thecae (Text-fig. 5B), whereas an average stipe consists of only 3–6 thecae. On the whole, the beds with *K. supremus* are fairly poor in graptolites, at least those well enough preserved for identification. *A. murrayi* appears in the higher part of the range of *K. supremus*.

K. supremus seems most closely related to *K. klotschichini* (Obut, 1961). This species was referred to *Didymograptus*, but the original illustration (Obut 1961, pl. 1, fig. 7, 7a) shows indications of triad budding along the stipes. The measurements of that species are close to those of *K. supremus*, except for a shorter sicula (but the illustration gives the impression of a longer sicula than mentioned in the description) and a slightly narrower final stipe width. *K. klotschichini* was found in clay shales in the southern part of the Ural Mountains. Apparently it was not associated with any other species and its precise age is unknown. *?Didymograptus* sp. Bulman, 1954, is probably the oldest *Kiaerograptus* species so far known, found at a rather low level of the Dictyonema Shale in the Oslo region; it has an outline fairly close to that of *K. supremus*. It differs mainly in having a longer sicula, a slightly narrower final width, and stipes that distally become nearly horizontal. Bulman (1954, p. 36) noted that there was no trace of bithecae or stolothecae, but the material is totally flattened, thus making it impossible to see such details. Both *K. klotschichini* and *?Didymograptus* sp. are known only from a few specimens, so it can be supposed that only a part of the full range of variation has been revealed. Two other species, *K. kiaeri* (Monsen, 1925) and *K. quasimodo* Rushton, 1981, show a great inherent variation. I have studied the material of *K. kiaeri*, 470 specimens, that formed the basis of the publication by Monsen (1925), and among these specimens the variation in, for example, stipe attitude, number of thecae in 10 mm, and the number of thecae with isolated distal parts is such that the end members of the variation would hardly have been recognized as belonging to the same species, were it not for all the intermediate specimens. The excellently preserved material of *K. kiaeri* described by Spjeldnaes (1963) shows, in addition to this variation, at least three successive bithecae on the same side of the stipe (see Text-fig. 4D) – a type of irregularity found also in *K. supremus*. *K. quasimodo* resembles *K. kiaeri* in the variation of, for example, stipe attitude and

distal isolation of thecae, but also has a variable number of stipes (which is comparatively rare in *K. kiaeri* – less than 2%); sometimes stipes are ‘aborted’ after their first theca (see Rushton 1981, figs 2 and 3). *K. quasimodo* also has occasional second-order branching close to the sicula, giving three-stiped specimens. Compared with these two species, *K. supremus* has differently shaped bithecae, a more constant and lower stipe divergence angle, more rigid stipes, and apparently no thecae with isolated distal parts. The stipes also diverge from the sicula closer to its aperture. I interpret the latter three characters as more advanced, probably indicating that *K. supremus* comes from a higher stratigraphical level.

Genus ARANEOGRAPTUS Erdtmann and VandenBerg, 1985

Type species. *Dictyonema macgillivrayi* nom. nov. T. S. Hall, 1897 (= *Dictyonema grande* T. S. Hall, 1891; non *D. grandis* Nicholson, 1873).

Diagnosis (taken from Erdtmann and VandenBerg 1985). ‘Rhabdosome sciculate, biradial, produced by dichotomous division (similar to *Clonograptus*), generally at steadily increasing intervals, to eighth or ninth order [or possibly more] (usually fourth to sixth); adjacent branches connected by more or less regularly spaced dissepiments; autothecae in proximal portions denticulate with concave ventral margins and of moderate inclination; bithecae not observed. Juvenile specimens, up to the third-order dichotomy, cannot be assigned to a particular species, because of their identical morphology and structural development.’

Remarks. The absence of bithecae in the type species cannot be considered proven on the basis of the Australian material used by Erdtmann and VandenBerg, since this material is completely flattened and cannot possibly reveal such characters. For this reason I leave *Araneograptus* with the Anisograptidae. Also the biradiality of the rhabdosome is not proven beyond doubt. All the illustrated details of proximal ends (Erdtmann and VandenBerg 1985, fig. 6A–C) show an asymmetry which could be interpreted, instead, as three primary stipes. If this is the case, the genus is a junior synonym of *Rhabdinopora* Eichwald.

Araneograptus murrayi (J. Hall, 1865)

Text-figs 6, 7, ?18c

- 1865 *Dictyonema Murrayi* J. Hall, pp. 138–139, pl. 20, figs 6 and 7 [photographs seen].
- 1865 *Dictyonema quadrangularis* J. Hall, p. 138, pl. 20, fig. 5.
- 1873 *Dictyonema grandis* Nicholson, pp. 134–136, fig. 1.
- v 1937 *Dictyonema* cf. *murrayi* J. Hall; Monsen, pp. 89–92, pl. 11, fig. 2.
- 1982 *Dictyonema murrayi* J. Hall; Mu *et al.*, p. 295, pl. 73, fig. 1.
- 1982 *Dictyonema quadrangulare* J. Hall; Mu *et al.*, p. 295, pl. 73, figs 2–4.
- 1982 *Dictyonema maximum* Xu sp. nov.; Mu *et al.*, pp. 295–296, text-fig. 101, pl. 73, figs 5–7.
- 1982 *Dictyonema ziyangense* Xu sp. nov.; Mu *et al.*, p. 296, pl. 74, fig. 3.
- 1985 *Dictyonema pulchellum* T. S. Hall; Rushton, p. 332, figs 1 and 2.
- 1985 *Dictyonema* sp. Rushton, p. 332, figs 3 and 4.
- 1987 *Araneograptus murrayi* (J. Hall); Gutiérrez Marco and Aceñolaza, pp. 325–330, pl. 1.
- v 1988 ‘*Dictyonema*’ cf. *yaconense* Turner; Molyneux and Rushton, pp. 65–66, fig. 8.

Lectotype. GSC 962a, J. Hall’s (1865) pl. 20, fig. 7; Text-fig. 6 herein; designated lectotype by Gutiérrez Marco and Aceñolaza (1987).

Material. From the Krapperrup core (148.22–109.86 m), c. 30 surfaces (each 30 cm²) with 1–> 5 specimens of different sizes, ranging from juveniles to fragments of giants. The species is most common in the lower part of

its range, up to 136.69 mm. At 141 m the species is very common, forming layers each a couple of millimetres thick.

The species is absent at Mt Hunneberg, and only a few specimens have been found in the Oslo region, all except one slab from the Slemmestad area: PMO 58.967 from the *T. phyllograptoides* Zone (more probably lower) at Galgeberg (east-central Oslo), a large specimen figured by Monsen (1937), associated with a juvenile; PMO 137 from Gjeitungholmen, Slemmestad, allegedly from the upper Tremadoc Ceratopyge Shale; PMO 108.568, 108.569, 108.572 – together containing 6 specimens (of which 3 are juveniles) from 0.5–1.0 m above the Ceratopyge Limestone at Slemmestad crossroads; PMO 112.967+112.969, PMO 112.969+112.966, two relatively large specimens from Prestengveien, Slemmestad; and PMO 120.751, three specimens from 21.70 m at the new standard section (= 4.1 m above the Ceratopyge Limestone), central Slemmestad.

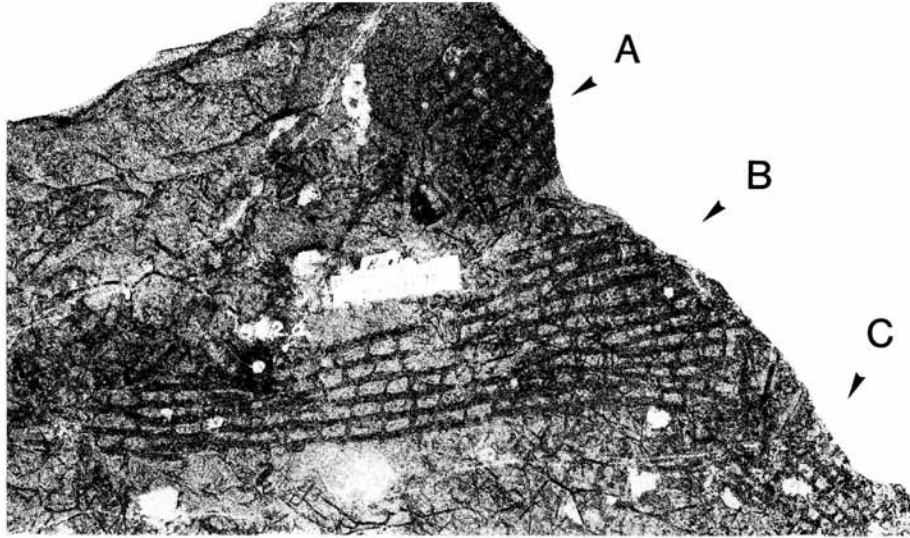
Associated species. *K. supremus*, *H. copiosus*, *T. krapperupensis*, horizontal tetragraptids ('quadribrachiatus'-type), three-stiped extensiform tetragraptids, *Didymograptus* sp. 1, *P. antiquus*, *P. elongatus*, *P. tenuis*.

Stratigraphic range. *A. murrayi* to *T. phyllograptoides* Zones, possibly also lower and higher. Maximum abundance in the *A. murrayi* Zone.

Diagnosis (based on the Scandinavian material and Gutiérrez Marco and Aceñolaza (1987)). Rhabdosome conical, mostly subtending an angle of 60–75° when flattened, angle decreasing distally in big specimens. Meshwork normally has 3–4 stipes in 10 mm, and 2–3 dissepiments in 10 mm, but the total variation ranges well outside these limits. The shape of the meshes is variable, from rectangular to oval. The lateral stipe width is over 1 mm, the thickness of the dissepiments is variable. The maximum length of the rhabdosome is unknown, but at least 30 cm.

Description. Not much is known about the details of proximal growth pattern of the species. A few immature specimens have been found at different levels in the Krapperup core. A couple of these could possibly support a biradial origin of the rhabdosome, while others seem asymmetrical enough to indicate a triradial origin. The sicula is 1.8–1.9 mm long where seen in full but presumably somewhat longer, perhaps up to 2.5 mm, in some more mature specimens. A very short nema of normal thickness is seen in a couple of the immature specimens. No specimen is well enough preserved to show beyond doubt a biradial origin or any details of proximal development. At two levels (those of Text-figs 17 and 18), pyritized immature specimens of various species occur. Some of these are pendent and may belong to *A. murrayi* but, due to the lack of dissepiments, this cannot be proved unequivocally. All pendent forms seen in obverse view have a sicular bitheca. One of the specimens seen in reverse view (Text-fig. 18c), shows a dicalyca theca 1² and a two-stiped origin. It apparently lacks plaited thecal structure. In some of the slightly larger specimens (Text-fig. 7F, H) the sicula, and sometimes also more of the proximal region, is covered with cortical tissue, extending on to the nema, which is then up to more than 1 mm thick. A couple of thecae are seen in partial profile view in one of the immature specimens, giving an estimate of 11.5 thecae in 10 mm. The thecae seem to be straight tubes of normal dichograptid appearance. On the other hand, a Moroccan specimen (Text-fig. 7B) shows a few thecae in relief which are very denticulate, the distal part of the ventral side being almost at right angles to the dorsal margin of the stipe. This high angle could, however, be due to distortion. The thecae number about 12.5 in 10 mm in this specimen. The difference in thecal shape between the two specimens can be explained in different ways: either the thecal shape changes along the rhabdosome, or the slightly oblique position of the thecae in the Scandinavian specimens obscures their true shape. Another possibility is, of course, that there is more than one species which cannot be distinguished on the basis of cone shape and mesh pattern alone. Ruedemann (1947, p. 171) commented on the thecae thus: 'Thecae numbering 9–10 in 10 mm; apparently with acute extensions of apertural margins.' Rushton (1985, fig. 2c) showed elongate thecae with high overlap and high distal inclination.

Normally, only the dorsal side of the stipes is seen, since this is the outward-facing side of the cone and also represents the surface most easily exposed by splitting. The lateral stipe width is mostly 1.2–1.5 mm in flattened specimens. Specimens with some relief often have thinner stipes, down to 1.0 mm. The stipe width of immature specimens is sometimes as low as 0.6–0.7 mm. The dissepiments are rather regularly spaced within a specimen (closer in the proximal part, though), but the number of dissepiments per length unit varies markedly from one specimen to another, from about 4 in 10 mm down to 1.5. The average density is about 2–3 dissepiments in 10 mm. Also the stipe density varies between specimens. This variation is due to the frequency of dichotomies

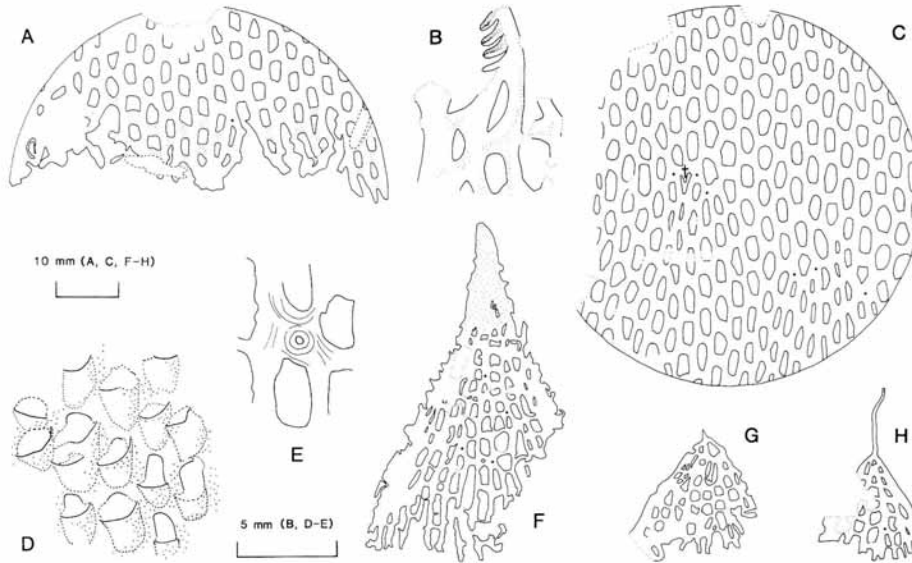


TEXT-FIG. 6. GSC 962a, lectotype slab of *A. murrayi* (J. Hall) containing three specimens, x 1. A, specimen of *quadrangularis* type with short meshes and relatively broad dissepiments. B, lectotype. C, specimen with short meshes and relatively thin dissepiments. The specimens are associated with numerous rhabdosomes of *Clonograptus rigidus*.

(see Text-fig. 7C) and the angle of the cone. There are normally about 3.5–4 stipes in 10 mm, but the total variation ranges from 3 to 5. The variation in stipe and dissepiment density gives a marked variation in size and shape of the meshes. Another factor influencing this is the thickness and shape of the dissepiments. The meshes can thus be square, rectangular, nearly circular, or oval. The thickness of the dissepiments varies from considerably thicker to noticeably thinner than the stipes, but in most specimens they are of about the same thickness as the stipes. The dissepiments are sometimes uniformly thick, in others thinner in their middle part. Secondary cortical additions to the stipes and dissepiments can, under special circumstances, almost fill out the meshes (Text-fig. 7E). The formation of dissepiments seems to have been very regular, these being inserted in every second or third position at the same time (or rather, the same distance from the sicula), so that the meshes form diagonal rows across the specimen (see Text-fig. 7A, C). This pattern is disturbed where dichotomies occur. These are relatively frequent in proximal parts (see Text-fig. 7F) but rare in the distal part of large specimens. Text-figure 7C shows two zones of stipe division, both apparently induced by irregularities in the mesh pattern. The left zone compensates for the loss of a stipe († in the figure), the right-hand one seems to compensate for a deflection to the right of one stipe, as seen by the very small mesh to the right of this stipe slightly more proximally than the point of dichotomy (this interpretation seems more probable than that a stipe division was planned for). In both cases the dichotomies compensating a disturbance are paired, followed by an additional dichotomy slightly later. Paired dichotomies were illustrated also by Rushton (1985, fig. 4).

A couple of relief specimens (see Text-fig. 7D) have what appears to be later additions attached on the outside of the rhabdosome, pouch-like 'balconies' that join the stipes on their dorsal side. They do not seem to form part of the normal dissepiments. Their function is likely to have been to direct water currents through the rhabdosome meshwork. A distal end fragment (Text-fig. 7A) shows that dissepiments are present at normal frequency to the very distal end of the stipes, i.e. they are produced as the stipe grows. Further, the distalmost dissepiments have full width, but the 2–3 last produced of them seem to be less dense. This may explain the apparent lack of strength, leading to the disruption shown in Text-figure 7A.

The angle of the cone is normally 60–75°, but in a couple of cases angles as low as 40–50° have been observed. As seen from some very large Spanish specimens, the angle of the cone decreases distally. The angles of the larger Scanian specimens were impossible to measure, since the drillcore surfaces contain only small fragments



TEXT-FIG. 7. *Araneograptus murrayi* (J. Hall). Black dots in rhabdosomes indicate the positions of stipe divisions. A, LO 5972t, Krapperup core, 137-70 m, the distal end of a large specimen; stippling indicates not fully corticized dissepiments, dashed outlines represent superposed phyllocarids. B, PMO 120.752, detail of a Moroccan specimen showing thecae in some relief. C, LO 5973t, Krapperup core, 137-60 m, part of a large specimen with relatively elongate meshes and two zones of branching; † represents the termination of a stipe. D, PMO 112.966, Slemmestad, detail of a specimen with pouch-like 'balconies'. E, PMO 58.967 (= Monsen 1937, pl. 11, fig. 2), Galgeberg, Oslo, detail showing cortical overgrowth of a mesh. F, PMO 137, upper Tremadoc (?), Gjeitungholmen, Slemmestad, a specimen with the proximal part covered by cortical tissue (stippling). G, LO 5974t, Krapperup core 147-66-147-72 m, a specimen without cortical overgrowth of the proximal part, and possibly indicating a triradial origin. H, LO 5975t, Krapperup core 140-30 m, a specimen with cortical overgrowth of sicula and nema.

of rhabdosomes. The maximum number of stipe dichotomies is unknown but, judging from the very low number of branchings on the drillcore surfaces, the rhabdosomes must have been very big, with a cone length of perhaps more than 20 cm.

Remarks. The large Scanian specimens are closely similar to the specimen figured by J. Hall (1865, pl. 20, fig. 7), except that their dissepiments are on the average somewhat thicker. Hall, according to the figured material of *Dictyonema murrayi*, allowed a certain variation in the number of dissepiments per length unit, the specimen in plate 20, figure 6 having a dissepiment spacing equal to that of *D. quadrangularis* figured on the same plate. Hall seems to have found the thickness of the dissepiments more important than their spacing. But, on the type slab GSC 962a, containing plate 20, figure 7 and two additional specimens (Text-fig. 6), all three shapes co-occur on one surface, indicating their probable conspecificity.

Gutiérrez Marco and Aceñolaza (1987) also synonymized *D. yaconense* from South America and *Nyssenia zemmourensis* from northern Africa, as well as some variously named European finds, with *A. murrayi*. Interestingly, they noted that the descriptions of different species fitted different parts of one rhabdosome. They hesitated to synonymize *A. pulchellus*, although they noted that in some

characters the two species were partly overlapping. Their main argument was that no specimen of *A. pulchellus* of the size of the larger *A. murrayi* specimens has ever been found. Although they did not regard *D. grandis* Nicholson as a junior synonym, I suggest that it is. According to Nicholson (1873), *D. grandis* differs from *D. murrayi* by having conical form, more frequent bifurcation, and meshes wider than long. The first two differences are easily explained by Nicholson's specimen being the proximal part of a rhabdosome and Hall's specimens more distal fragments. The third difference, the shape of the meshes, can be explained by tectonic distortion, coupled with more closely-spaced dissepiments in the proximal part of the rhabdosome. Both J. Hall's and Nicholson's types derive from Lévis, Quebec.

A. murrayi has a world-wide distribution, including Europe (Scandinavia, Great Britain, Germany, France, Spain), northern Africa, eastern North America, South America (as *D. yaconense*; Argentina, Bolivia), and NW China. The species was listed, but not illustrated, from the Taimyr area of the Soviet Union by Obut and Sobolevskaya (1962). A more detailed account of the distribution is given by Gutiérrez Marco and Aceñolaza (1987). In addition, the possibly conspecific *A. pulchellus* is found in Australasia and western Canada. Both species seem to be restricted to a relatively narrow stratigraphical interval, corresponding to the Australasian stage La 2, and in some cases the basal part of La 3.

Suborder DICHOGRAPTINA Lapworth, 1873

Diagnosis (from Fortey and Cooper 1986; emended by Lindholm and Maletz 1989). Graptoloids lacking bithecae along the stipes, and without virgella.

Remarks. The diagnosis by Fortey and Cooper has been emended to incorporate in the Dichograptina the anisograptid/dichograptid intermediary forms with a sicular bitheca, but without bithecae along the stipes. Since the loss of bithecae apparently occurred in different lineages during a relatively short period of time, the Dichograptina, like the Anisograptidae, will be a paraphyletic group, no matter where the boundary between the two groups is drawn (however, see remarks on the Anisograptidae, p. 291).

Superfamily DICHOGRAPTACEA Lapworth, 1873

Diagnosis (from Fortey and Cooper 1986; slightly emended by Lindholm and Maletz 1989). Dichograptinids lacking isograptid symmetry, number of orders of dichotomy in rhabdosome not limited.

Remarks. The diagnosis by Fortey and Cooper has been emended to include forms which apparently have unlimited capacity for dichotomy, e.g. the genus *Clonograptus*.

Family DICHOGRAPTIDAE Lapworth, 1873

Diagnosis (from Fortey and Cooper 1986). Dichograptaceans lacking prothecal folds and sigmagraptine proximal end.

Genus HUNNEGRAPTUS gen. nov.

Name. From Mt Hunneberg.

Type species. *Hunnegraptus copiosus* gen. et sp. nov.

Diagnosis. Dichograptids with a didymograptid proximal part and two or more orders of stipes produced by dichotomous division; first-order stipes extensiform or declined, normally consisting of approximately 5–25 thecae. Sicula tube-like; a sicular bitheca present at least in the type species. Proximal development isograptid, sinistral and dextral forms co-occurring. Thecae straight tubes of dichograptid type, no bithecae observed along stipes. Secondary cortical thickening may be present; possible stipe regeneration in gerontic specimens.

Species included. *H. copiosus* sp. nov., *H. tjernviki* sp. nov., *H. robustus* sp. nov., and provisionally *H. novus* (Berry, 1960), *H. gulinensis* (Wang, 1981), *H. minor* (Wang, 1981), *H. sichuanensis* (Wang, 1981), *H. sp.* (Wang, 1981). Wang's taxa are probably synonyms.

Remarks. The Scandinavian specimens of the genus are here divided into three contemporaneously occurring species. However, it is possible that they all belong to one species, representing different growth stages. Unfortunately, though, the 'mature' and 'gerontic' specimens are very rare compared to the 'adolescents' and a continuous spectrum of variation cannot be proven based on the available material. Therefore the three species *H. copiosus* (abundant, and the only one of the three found as immature specimens; 'young stage'), *H. tjernviki* (less common; 'mature stage'), and *H. robustus* (rare; 'gerontic stage') are here described as separate entities. If their synonymy can be proved, the name *H. copiosus* takes precedence. Synonymy would imply that all thecae kept growing through the entire life of the colony (cf. Williams and Stevens 1988), or until the apertures were covered by cortex. The 'gerontic' rhabdosomes are too flattened to prove that such 'choking' with cortex took place, but nearly all specimens of *H. robustus* have irregularly placed thin lateral stipes, as thin as those of the other two species. These stipes are connected to the main body of the rhabdosome by the cortex, and thus cannot be superimposed stipes belonging to other specimens. They do not influence the direction or thickness of the main stipes. They appear to represent a rejuvenation of the colony, extra stipes being inserted later than the surrounding branches. This could be to compensate for zooids no longer active in that part of the rhabdosome. These stipes are probably not metacladia, and I have seen no report of comparable stipe formation in any other graptoloid.

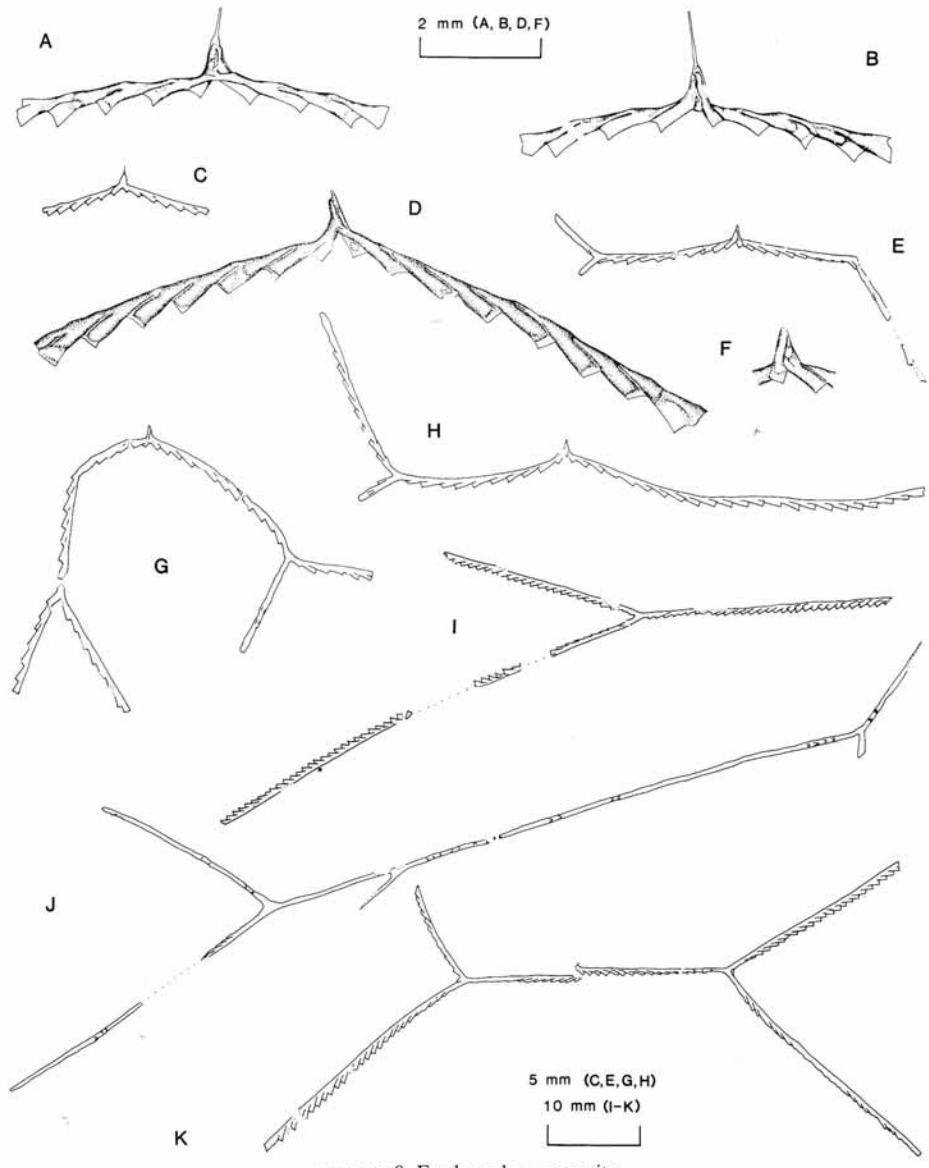
The Scandinavian occurrences are restricted to the *H. copiosus* Zone, the zone directly underlying the *Tetragraptus phyllograptoides* Zone. Provisionally included in *Hunnegraptus* is *H. novus* (Berry, 1960), which has a sicular bitheca but normally no bithecae along the stipes. This taxon is probably older than the Scandinavian occurrences, however, since it is reported to co-occur with *Anisograptus* (Berry 1960). Provisionally included are also *Kiaerograptus? gulinensis*, *K.? sp.*, *Adelograptus minor*, and *A. sichuanensis*, all described by Wang (1981) from probable Late Xinchangian beds of Sichuan, central China. All of these are most likely conspecific, the amount of variation among them being smaller than that within the type species of *Hunnegraptus*. Multiramous species with dichograptid thecae and prolonged first-order stipes have also been described from Spain (Gutiérrez Marco 1982, 1986, pp. 290–304) and Czechoslovakia (Kraft and Mergl 1979). The material from Spain is of Early Hunneberg age, and the associated fauna contains i.a. *A. murrayi*. The age of the Czech material is uncertain. The relationship of these species to *Hunnegraptus* is not clear.

The genus is presumably most closely related to *Clonograptus*, in which first-order stipes may be prolonged, e.g. in the type species, *C. rigidus*. The sicular bitheca seen in *H. copiosus* is also found in *Clonograptus milesi*, and probably also in the type species (Lindholm and Maletz 1989). Regenerated stipes of *Hunnegraptus* type are unknown in *Clonograptus*. The latter fact has convinced me that the distinction between the two taxa should be on a generic, rather than subgeneric, level.

Hunnegraptus copiosus gen. et sp. nov.

Text-figs 8A–F and 18F, ?H, J

- 1987 Dichograptid sp. 1 Maletz, p. 136, text-fig. 44:9; 10, pl. 5, figs 1 and 2.
 p 1987 Dichograptid sp. 2 Maletz, pp. 136–137, text-fig. 44:3?, 5–8.



TEST-FIG. 8. For legend see opposite.

Name. Latin *copiosus*, abundant, refers to the abundance of the species in all sections.

Material. 736 specimens, of which 111 come from east-central Oslo (Tøyen, 3.55–3.68 m above the Ceratopyge Limestone, and Galgeberg), 213 from various localities in the Slemmestad area, 165 from Storeklev, Mt Hunneberg, and 247 from the Krapperup core (132.73–117.00 m). Except for Krapperup, the stratigraphic range is rather limited, with specimens collected from a single horizon in a section or, as in Storeklev and the new standard section in central Slemmestad, from a relatively thin band (1.4–1.8 m and 4.6–5.6 m above the Ceratopyge Limestone, respectively). The holotype is found on PMO 58.969 from Galgeberg, central Oslo (Text-fig. 8E, F); the paratypes are LO 5976t–5979t, LO 6090t, LO 6094t, and PMO 108.599 (localities given in figure captions). The species is very common and is found on most slabs within its range, mostly as two-stiped, didymograptid-like, specimens.

Associated species. *H. tjernviki*, *H. robustus*, *A. murrayi*, *Clonograptus* s.s. sp. indet., *T. longus*, *T. cf. krapperupensis*, narrow- and broad-stiped horizontal tetragraptids ('quadribrachiatus'-type), three-stiped extensiform tetragraptids, gen. et sp. indet. 1, *Didymograptus* sp. 2, *Isograptus* sp., *P. antiquus*, *P. pritchardi*, *P. elongatus*, *P. tenuis*, *P. cf. rarus*.

Stratigraphic range. *H. copiosus* Zone.

Diagnosis. Didymograptid proximal part and one, two, or possibly more orders of stipes. First-order stipes normally declined, consisting of approx. 7–22 thecae each. Sicula mostly 1.1–1.2 mm long, sicular bitheca present. Thecae straight tubes with a thecal inclination of 15–20°. Stipe width 0.5–0.6 mm, approx. 12 thecae in 10 mm. No bithecae along stipes.

Description. The sicula is tube-shaped, 1.0–1.3 mm long, 0.25 mm wide at the aperture; and its distal part is inclined towards the stipe² side. The proximal part of the nema is somewhat thickened, like the cauda (Hutt 1974). A slightly curved bitheca is present on the obverse side of the sicula, budding from th 1¹ at mid-length of the sicula (Text-figs 8B, F and 18F). The aperture of the bitheca is positioned where th 1¹ bends away from the sicula. Theca 1¹ buds from the sicula approximately 0.1–0.2 mm from its apex. In early growth stages consisting of the sicula and th 1¹, the sicula and theca make a more or less symmetrical pair, with the bitheca in a central position. The proximal development type is isograptid, theca 2¹ budding from th 1² in its most proximal part. There are both sinistral and dextral specimens (compare Text-fig. 8A with 8D) but too few well-preserved specimens have been found for any statistical evaluation of predominance. The proximal part of the protheca is relatively narrow, resulting in a rather low thecal inclination (15–20°). A slight prothecal folding can be seen in pyritized relief specimens (Text-fig. 8A, B, D). The metathecae are simple tubes, straight or nearly so; the total thecal length is about 1.2 mm, the dorsoventral thecal width at the aperture about 0.25–0.3 mm. The thecal overlap is about 40–50%, and there are normally 11.5–13 thecae in 10 mm (total range 10.5–14). The profile stipe width is 0.5–0.6 mm, bithecae are absent along stipes, both in their proximal and distal parts. The first-order stipes consist of 7–22 thecae (observed range) and make an angle of about 120–180° (normally 130–160°) if seen in profile view. A pyritized specimen possibly belonging to the species (Text-fig. 18H) shows a first-order stipe consisting of only 3 thecae. Stipe division is dichotomous; the longest second-order stipes

TEXT-FIG. 8. A–H *Hunnegraptus copiosus* sp. nov. A, B, LO 5976t and LO 5976+, Storeklev 2.15–2.32 m, counterparts of a dextral relief specimen. C, LO 5977t, Storeklev 2.32 m, an almost flattened specimen, showing the most typical appearance of the species. D, PMO 108.599, Slemmestad, a full relief sinistral specimen; note the difference in thecal spacing between the stipes; associated specimens show no tectonic distortion. E, F, holotype, PMO 58.969, Galgeberg, east-central Oslo, a sinistral specimen (proximal part is a mould) with the fourth second-order stipe presumably primarily missing; part of one stipe is pyritized, showing absence of bithecae; F is drawn from a latex cast and shows the sicular bitheca in low relief. G, LO 5978t, 22.2 m in the standard section, Slemmestad, a dextral specimen (the sicular part is a mould), one of the bigger specimens, in a preservation showing the low degree of rigidity of the stipes. H, LO 5979t, associated with specimen shown as A and B; the specimen has highly unequal length of first-order stipes. A, B, D, F are drawn from latex casts under vertical light. I–K, *H. tjernviki* sp. nov. I, PU Vg 125, Storeklev 227–230 cm, a stipe fragment in profile view. J, LO 5980t, Grundvik, Slemmestad, the longest stipe fragment, showing four orders of stipes; the drawing is a combination of counterparts. K, holotype, PU Vg 124, Storeklev 227 cm.

seen are more than 40 mm long. A branching stipe fragment probably belonging to the species (Text-fig. 18J) shows isograptid type branching. No complete specimen shows more than two orders of stipes, but it cannot be excluded that the branching continues. In one specimen (LR 6, from Storeklev) an 'aborted' stipe division can be seen: part of a theca projects from the dorsal side of a stipe, but the stipe continues in its previous direction. Also the holotype may have lost a stipe in the same way (Text-fig. 8E): no trace of a fourth second-order stipe is seen, but in this case the stipe is bent as if branching had occurred. The majority of the specimens found are too small for branching to have occurred. These specimens look like declined didymograptids, but relief specimens in obverse view show the characteristic sicular bitheca. No marked secondary cortical thickening has been observed in this species. Specimens are often somewhat flexuous. No gerontic specimens were found, however, and the possibility of cortical thickening at a later growth stage cannot be ruled out.

Remarks. The low thecal inclination and the faint prothecal folding observed in relief specimens of *H. copiosus* might suggest a relationship with the Sigmagraptidae. However, the proximal part differs markedly from that of the type species of *Sigmagraptus* (cf. Cooper and Fortey 1982, fig. 61): the length/width ratio of the sicula is smaller, the prothecal part of theca 1¹ is shorter, th 2¹ buds off th 1² slightly later, so that it crosses th 1¹ instead of following its dorsal side, and also neither th 1¹ nor th 1² has the characteristic sharp bend seen in sigmagraptids. Except for the sicular bitheca, the proximal structure in *Hunnegraptus* is normal dichograptid. The presence of both sinistral and dextral forms must be assumed to be a primitive character (common among the Anisograptidae).

The Chinese species described by Wang (1981) are all very similar to *H. copiosus*. The illustrations show a proximal part virtually identical to that of *H. copiosus*, and sicular length and figures given for thecal characters differ insignificantly from those of that species. The only visible difference lies in the position of second-order dichotomy, which is closer to the sicula in the Chinese species. All the specimens illustrated by Wang (1981) have one or two stipe orders, like *H. copiosus*. *H. novus* (Berry, 1960) is known only as a two-stiped form. Also this taxon has a thecal shape reminiscent of *H. copiosus*.

Hunnegraptus tjernviki gen. et sp. nov.

Text-fig. 8I-K

p 1987 Dichograptid sp. 2 Maletz, pp. 136-137, fig. 44:1, 2, 4; pl. 5, fig. 3.

Name. In honour of Torsten Tjernvik, the discoverer of the Early Hunneberg graptolite fauna.

Material. 32 more or less fragmentary specimens, of which 11 are from Oslo, 10 from the Slemmestad area, 9 from Storeklev, and 2 from Krapperup. The range coincides with that of *H. copiosus*. Holotype PU Vg 124 (Text-fig. 8K) and paratype PU Vg 125 from Storeklev; paratype LO 5980t from Grundvik, Slemmestad.

Associated species. *H. copiosus*, *T. longus*, *P. antiquus*.

Stratigraphic range. *H. copiosus* Zone.

Diagnosis. Didymograptid proximal part and up to four or possibly more orders of stipes. First-order stipes horizontal or slightly declined, consisting of several thecae. Sicula approximately 1.5 mm long, sicular bitheca suspected. Thecae straight tubes with an inclination of about 30°. Stipe width 0.8-1.2 mm, about 11.5 thecae in 10 mm. No bithecae along stipes.

Description. The species is known from fewer specimens, and also in less detail, than *H. copiosus*. Most specimens consist of stipe fragments only. The sicula is about 1.5 mm long; no specimen is well enough preserved to reveal a possible sicular bitheca or the proximal development. The thecae are simple straight tubes, approximately 1.4-1.7 mm long and 0.4-0.5 mm wide at the aperture. The thecal inclination is about 30° in full profile view, less in obliquely preserved specimens. Profile stipe width is 0.8-1.0 mm in proximal parts, 0.9-1.2 mm in more distal parts; lateral stipe width (dorsoventral view) is about 0.5-0.6 mm. There are 10.5-12 thecae in 10 mm, and the thecal overlap is about 50%. Bithecae are not present along the stipes. The observed

length of first-order stipes falls within the range of variation seen in *H. copiosus*; the branching is dichotomous. The first-order stipes diverge at ≈ 150 – 180° . A stipe fragment from Grundvik, Slemmestad (Text-fig. 8j) shows four orders of stipes, the most proximal stipe seen being of second or higher order, judging from the angles of dichotomy. Cortical thickening of stipes is variable, but mostly not readily observed.

Remarks. The species differs from *H. copiosus*, and the species described by Wang (1981), primarily in having broader and somewhat more rigid stipes. The more rigid appearance might be explained in part by longer thecae and higher thecal overlap and in part by slight cortical thickening. In contrast to *H. copiosus*, no immature specimens of *H. tjernviki* have been observed.

Hunnegraptus robustus gen. et sp. nov.

Text-fig. 9

? 1987 Dichograptid sp. 3 Maletz, p. 138, pl. 5, fig. 4.

Name. Denoting the robust character of the species, as compared to *H. copiosus* and *H. tjernviki*.

Material. Six specimens, all illustrated in Text-figure 9. Holotype LO 5981T, from 2.60 m at Storeklev, Mt Hunneberg. Paratypes PU Vg 126, LO 5982t, LO 5983t, from the graptolite-rich band 2.15–2.32 m at Storeklev; LO 5985t, Storeklev, 2.60 m; LO 5984t from Grundvik.

Associated species. *H. copiosus*.

Stratigraphic range. *H. copiosus* Zone.

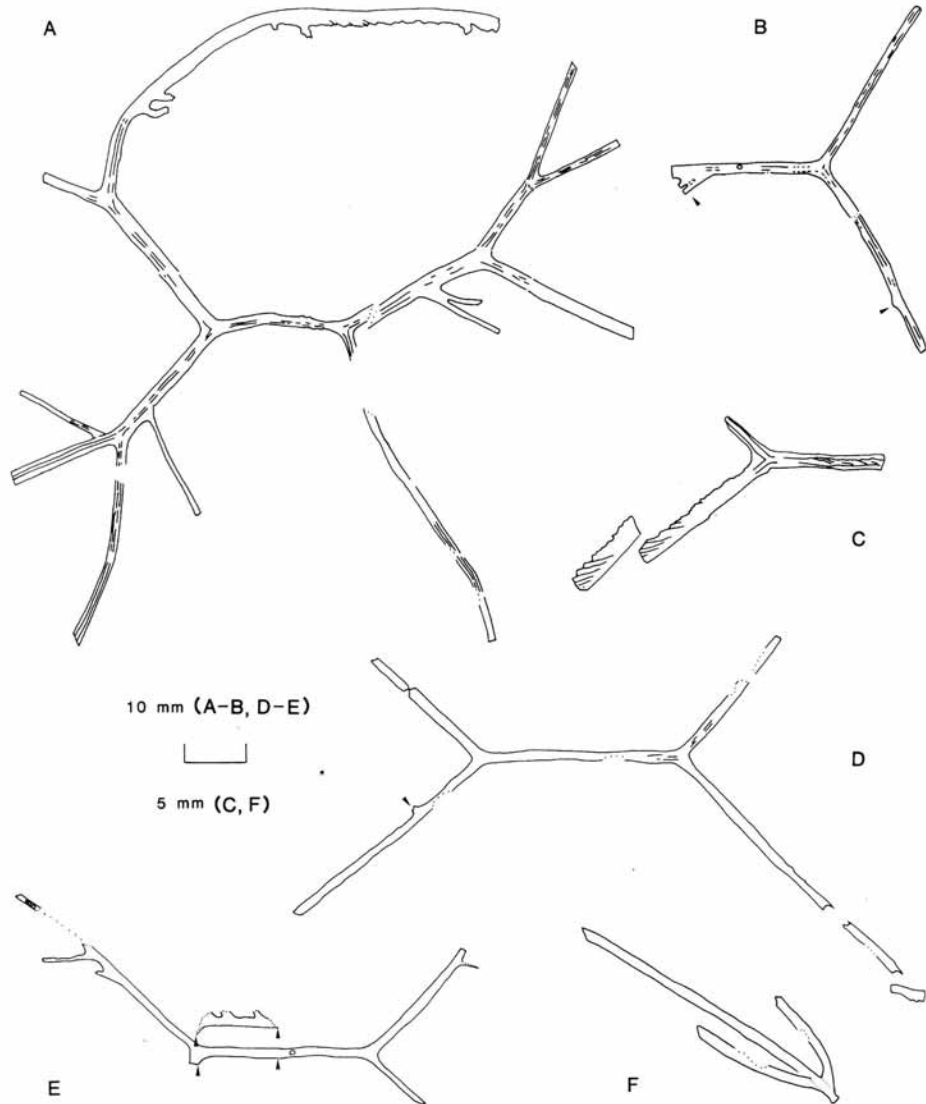
Diagnosis. Didymograptid proximal part and up to four or more orders of stipes. First-order stipes consist of several thecae. Profile stipe width 1.8–2.5 mm; lateral stipe width 1.0–2.5 mm, depending on cortical cover. Dichotomous and irregular lateral branching. Lateral stipes usually narrower than the rest of the rhabdosome.

Description. The sicula and proximal development are unknown, since only distal parts are seen in profile view. The observed combined length of first-order stipes is 24–33 mm; the observed range of second-order stipes is from 24 to more than 50 mm. The thecae are long straight tubes, their length *c.* 3 mm, width 0.4 mm, and overlap about 75%. There are about 12 thecae in 10 mm. The profile stipe width is 1.8–2.5 mm (Text-fig. 9C). The lateral stipe width varies considerably, depending on the amount of secondary cortex cover: normally 1.5–2.5 mm, but in some cases as thin as 1.0 mm. Secondary cortical cover is less marked in a distal direction, but this is in no way regular (see Text-fig. 9A). Thin (0.7–1.0 mm wide) lateral stipes occur irregularly in five of the six specimens (see Text-fig. 9A–B, D–F). These stipes are connected to the rest of the rhabdosome by the cortical thickening, and thus cannot represent superimposed fragments of other specimens. As discussed for the genus, I consider these stipes to have been formed secondarily and thus ignore them when counting the stipe order: the maximum found is four stipe orders, in the holotype. Text-figure 9E shows a specimen and its counterpart, with three broken lateral stipes seen on the counterpart only (after some preparation), indicating that they did not grow in the plane represented by the four main stipes. The lateral stipes shown in Text-figure 9F seem to have been originally directed slightly upwards, and later bent down to the bedding plane by compaction.

Remarks. The species differs from the other two described *Hunnegraptus* species, and the species of Wang (1981), in its longer thecae, more robust stipes and thick cortex cover, as well as the occasional lateral stipes. No immature specimens have been identified. The lateral stipes appear to have been formed later than the surrounding parts of the rhabdosome (see the remarks on the genus).

Genus CLONOGRAPTUS Nicholson, 1873

Type species. *Graptolithus rigidus* J. Hall, 1858.



TEXT-FIG. 9. *Hunnegraptus robustus* sp. nov. A, holotype, LO 5981T, Storeklev 2.60 m, showing numerous thin lateral stipes, possibly a sign of regeneration; the drawing is a combination of counterparts. B, LO 5982t, Storeklev 2.32 m, arrows point to lateral stipes; note the two closely arranged stipes on the first-order stipe, connected proximally by cortical tissue. C, LO 5983t, Storeklev 2.15–2.32 m, a stipe fragment showing thecae in profile view. D, PU Vg 126, Storeklev 227–230 cm, the specimen commented on by Tjernvik (1956,

Diagnosis (from Lindholm and Maletz 1989). Dichograptid with bilateral rhabdosome produced by dichotomous division occurring at irregular intervals; second dichotomy in most species consecutive, forming a tetragraptid proximal part, but can be delayed for a couple of thecae; branches diverging proximally, while distally diverging, subparallel, or flexuous; thecal shape variable, unknown in many species assigned to the genus; central disc unknown, secondary development of cortical overgrowth in many species, particularly in proximal parts.

Remarks. The genus *Clonograptus* was treated by Lindholm and Maletz (1989). It was reinterpreted as a form genus (*Clonograptus sensu lato*) consisting of the phylogenetically based subgenus *Clonograptus* (*Clonograptus*) (= *Clonograptus sensu stricto*) and additionally a number of species not known in enough detail for inclusion in any phylogenetically based group. In the same paper *Clonograptus* was transferred to the Dichograptidae, since there are no bithecae along the stipes in the type species.

Clonograptus cf. norvegicus Mosen, 1937

Text-fig. 10F

- cf. 1937 *Clonograptus norvegicus* Mosen, pp. 198–200, pl. 20; non pl. 5, fig. 22.
cf. 1987 *Clonograptus norvegicus* Mosen; Maletz, p. 58, fig. 41:1, 2.

Material. One incomplete, nearly flattened, specimen with proximal part, associated with scattered stipe fragments of the species, found on PMO 73.200 and 73.204 (counterparts), in grey shale from 0.5 m above the Ceratopyge Limestone at Bødalen, Slemmestad.

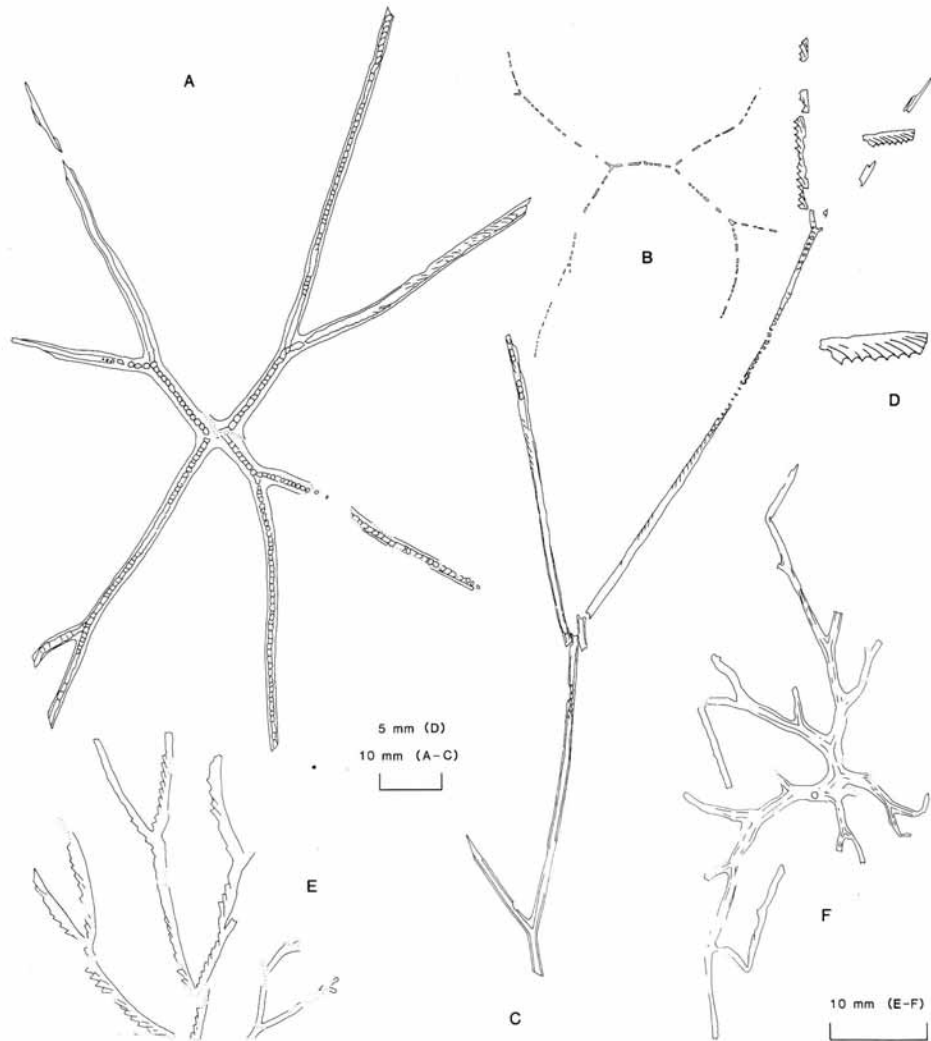
Associated species. None.

Stratigraphic range. *H. copiosus* Zone, possibly also *T. phyllograptoides* Zone.

Diagnosis (of *C. norvegicus*, based on Mosen 1937). A clonograptid, irregularly branching to at least 13 orders of stipes. Second- to fourth-order stipes progressively longer, but within 3–8 mm in length; higher orders on average 10 mm long or more. A marked cortex cover (peridermal film?) gives a lateral width of 3 mm proximally and down to less than 2 mm distally. The cortex obscures all thecal details. Possibly 8–9 thecae in 10 mm.

Description. In my specimen, no details of proximal development or thecae are visible due to the cortex cover and the horizontal orientation of the rhabdosome. The position of the sicula can be seen, and the outline of the stipes and branching points within the cortex film can be partly discerned, indicating that the primary stipes are of unequal length. There is probably one theca in one first-order stipe and 2–3 in the other. The thecal spacing is unknown, however, and if it is much less than 10 in 10 mm it could indicate that the specimen is triradiate rather than biradiate. The lateral width of the stipes excluding the cortex cover is 0.3–0.6 mm, the total lateral width varies from 1.5 to 2.0 mm in the proximal part down to less than 1 mm in distal parts. The branching pattern seems to be somewhat irregular, but in general the distances between branchings increase in a distal direction. Seven orders of stipes are seen, and the length of second- to fifth-order stipes are (assuming two primary stipes) 2–6 mm, 3–7 mm, 4–9 mm, and 6–10 mm. The specimen may not have been fully planar; it appears that at least one stipe crosses the others at a lower level in the slab. The branching angles are variable, c. 60–120° in proximal branchings and 45–70° in the more distal parts. Higher-order stipes sometimes curve to adopt a more parallel orientation.

pp. 117–118); a broken lateral stipe (arrow) is seen on the lower left stipe. E, LO 5984t, Grundvik, Slemmestad, piece and mirror image of counterpart shown to illustrate lateral stipes at an angle to the plane formed by the main stipes; the lateral stipes on the upper left are connected to the main stipe by thick cortex proximally. F, LO 5985t, Storeklev 2.60 m, a stipe fragment with paired lateral stipes. Stippling indicates flexure – the lateral stipes were originally directed upwards.



TEXT-FIG. 10. A, C, D, *Clonograptus magnus* sp. nov.; A, holotype PMO 108.564–108.565, Slemmestad; the drawing is a combination of counterparts; C, D, PMO 108.561–108.562, same locality as A; D is an enlargement of the obliquely positioned fragment in C, showing the thecae in profile view; C is combined from piece and counterpart. B, *Clonograptus* sp. 1, PMO 97.708, Slemmestad; drawing from latex cast. E, *Clonograptus* sp. 2, LO 5986t, Krapperup core 142.46–142.56 m. F, *Clonograptus* cf. *norvegicus*, PMO 73.200, 73.204; the drawing is a combination of counterparts.

Remarks. The fragmentary nature and lack of information on proximal development and thecal shape of the specimen makes identification very difficult. *C. norvegicus* is a rare species and the original description by Mønsen (1937) was based on only one specimen with most details obscured by the cortex cover. That specimen has at least 13 orders of stipes and is more robust than the present specimen, which is unlikely to have been of that size. The robustness may be caused entirely by a thicker cortex cover, associated with its greater size. Mønsen's specimen was said to be associated with '*Didymograptus minutus* var. *pygmaeus*', hence Mønsen assigned it to the middle part of the Arenig. However, small pendent specimens very much resembling *D. minutus* occur also at a level slightly below the base of the *T. phyllograptoides* Zone (see Text-fig. 14c, f). Mønsen's specimen comes from Grundvik, Slemmestad, one of the localities where the beds below the *T. phyllograptoides* Zone are easily accessible. Erdtmann (1965b, p. 496) reported having found fragments of the species at a very low level in the Tøyen section. However, his specimens have since been lost and the statement cannot be verified.

Maletz (1987) reported the species from Mt Hunneberg, from the localities Tunhem and Storeklev. At the latter locality it was found at the same level as the richest finds of the *H. copiosus* fauna. Large-sized stipe fragments with thick cortex cover are present also in the *T. phyllograptoides* Zone at Mt Hunneberg (one specimen from Mossebo, SGU collections) as well as at Galgeberg, Oslo (Bergen Museum, Mønsen collection 231).

The only other *Clonograptus* s.l. species of a similar outline is *C. trochograptoides* Harris and Thomas, 1939. The pattern of branching and cortex cover is identical, but stipes of a given order are somewhat shorter, giving a more compact rhabdosome. *C. trochograptoides* was said to have thecae of *Clonograptus* s.s. type, 8–9 in 10 mm.

Subgenus CLONOGRAPTUS (CLONOGRAPTUS) Nicholson, 1873

Diagnosis. As for genus, but with thecae straight or slightly curved simple tubes, overlapping one-third to two-thirds of their length; proximal development isograptid, dextral.

Remarks. A number of genera were synonymized with *Clonograptus* (*Clonograptus*) by Lindholm and Maletz (1989), most importantly *Temnograptus* Nicholson, 1876.

Clonograptus (*Clonograptus*) *magnus* sp. nov. Text-fig. 10A, C, D

Name. Latin *magnus*, big.

Material. One specimen with proximal part preserved (holotype PMO 108.564–108.565; Text-fig. 10A) and one distal stipe fragment (paratype PMO 108.561–108.562) from 0.5–1.2 m above the Ceratopyge Limestone at Slemmestad crossroads. Additionally there are four stipe fragments from 3.42–3.60 m (+ a gap of unknown extent, probably 0.5–2 m) above the Ceratopyge Limestone at Grundvik, Slemmestad.

Associated species. *H. copiosus*, reclined *Tetragraptus* indet. (juvenile).

Stratigraphic range. *H. copiosus* Zone, possibly also *T. phyllograptoides* Zone.

Diagnosis. A very robust *Clonograptus* s.s. with a considerable cortical thickening in mature specimens. Tetragraptid proximal part, second-order stipe length approximately 10–40 mm, third and higher order generally over 40 mm. There are at least five stipe orders. 9–10 thecae in 10 mm, thecal overlap two-thirds or more, profile stipe width 1.5–2.0 mm.

Description. Details of the proximal development are unknown. In the only specimen with proximal part (Text-fig. 10A), first-order stipes consist of one theca each and second-order stipes are from 10 to 38 mm long. The specimen does not show complete third-order stipes, but the five longest fragments are 38–54 mm long.

The angle between the second-order stipes is rather high, *c.* 105°, whereas the angle between the third-order stipes is low, *c.* 45–70°. There are 9–10 thecae in 10 mm. A third-order stipe is preserved in partial profile view, giving an estimate of profile stipe width of 1.5 to 2.0 mm. As far as can be seen the thecae are rather long and narrow. All of this specimen is covered by cortex, giving a lateral stipe width of approximately 4 mm for the first-order stipes, 2.5–2.8 mm for second-order stipes, and 1.5–2.3 mm for third-order stipes.

The largest stipe fragment (Text-fig. 10c, d) has less cortical cover than the previous specimen. The fragment has four orders of stipes, the most proximal one probably of third or higher order. The length of the two middle orders of stipes is 47 and 77 mm. There are 9.5 thecae in 10 mm. The thecae are slightly curved, with about two-thirds to three-quarters of overlap. The thecal apertures are concave. The profile stipe width is 1.8 mm and the lateral stipe width is 1.3–1.5 mm. There are no bithecae.

The remaining stipe fragments contain only one dichotomy each. They all have 9–10 thecae in 10 mm, and a profile stipe width of 1.5–2.0 mm.

Remarks. The only *Clonograptus* species of a comparable size are *C. multiplex* (Nicholson, 1868) and *C. magnificus* (Pritchard, 1892). Neither of these have the massive cortical thickening characteristic of this species. Also, its branching angles differ from those of these two species.

A stipe fragment from Taimyr, identified by Obut and Sobolevskaya (1962) as *Temnograptus* aff. *noveboracensis* Ruedemann, may be conspecific with *C. magnus*.

Form genus TETRAGRAPTUS Salter, 1863 (= TETRAGRAPTUS *s.l.*)

Tetragraptus longus sp. nov.

Text-figs 11A–D and 12

Name. Latin *longus*, long, referring to the length of the stipes.

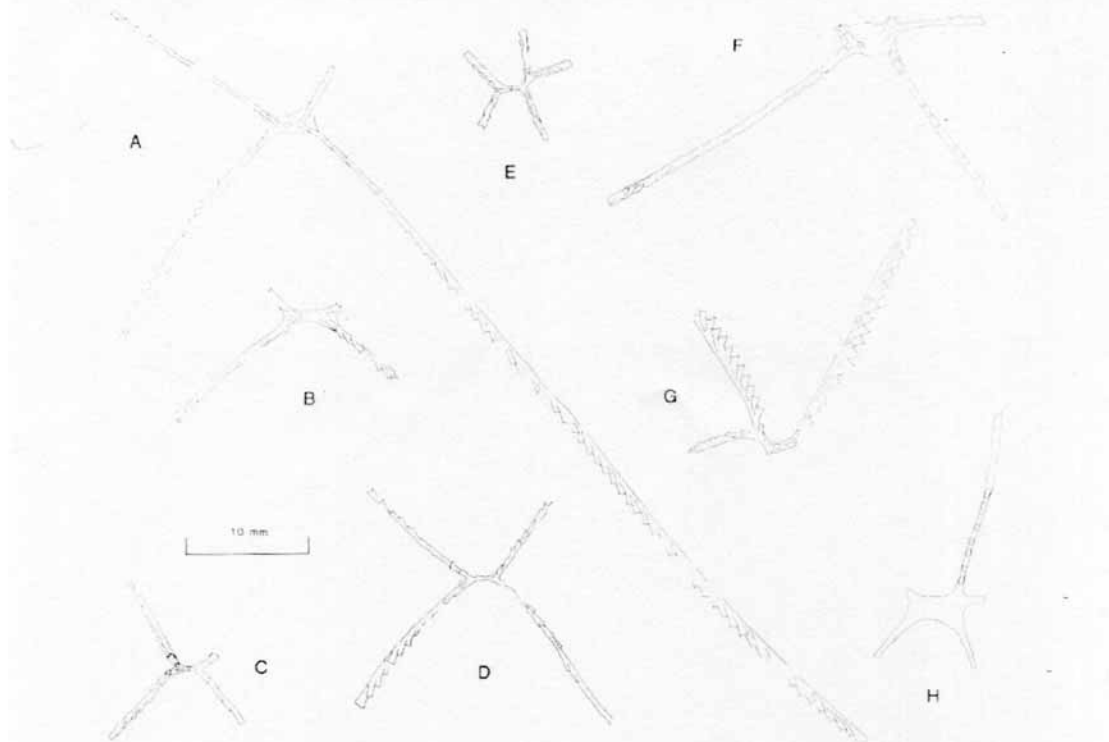
Material. 121 specimens in all, most of them more or less broken. Nearly all of them are from Galgeberg, east-central Oslo (found on PMO 58.969, 58.970); 14 specimens come from Slemmestad (PMO 97.702, 97.708 and one specimen, LR 1, in the Lund collections), and one from the Krapperup core (129.46–129.54 m). The holotype is found on PMO 58.970 (text-fig. 11A), the paratypes on PMO 58.969 and 97.708.

Associated species. *H. copiosus*, *H. tjernviki*, *T. cf. krapperupensis*.

Stratigraphic range. *H. copiosus* Zone.

Diagnosis. A thin-stiped (0.7–1.1 mm) horizontal tetragraptid, with small central disc in mature specimens. The divergence angle between second-order stipes is 90° or less. There are 9.5–11 thecae in 10 mm. The stipes may become extremely long.

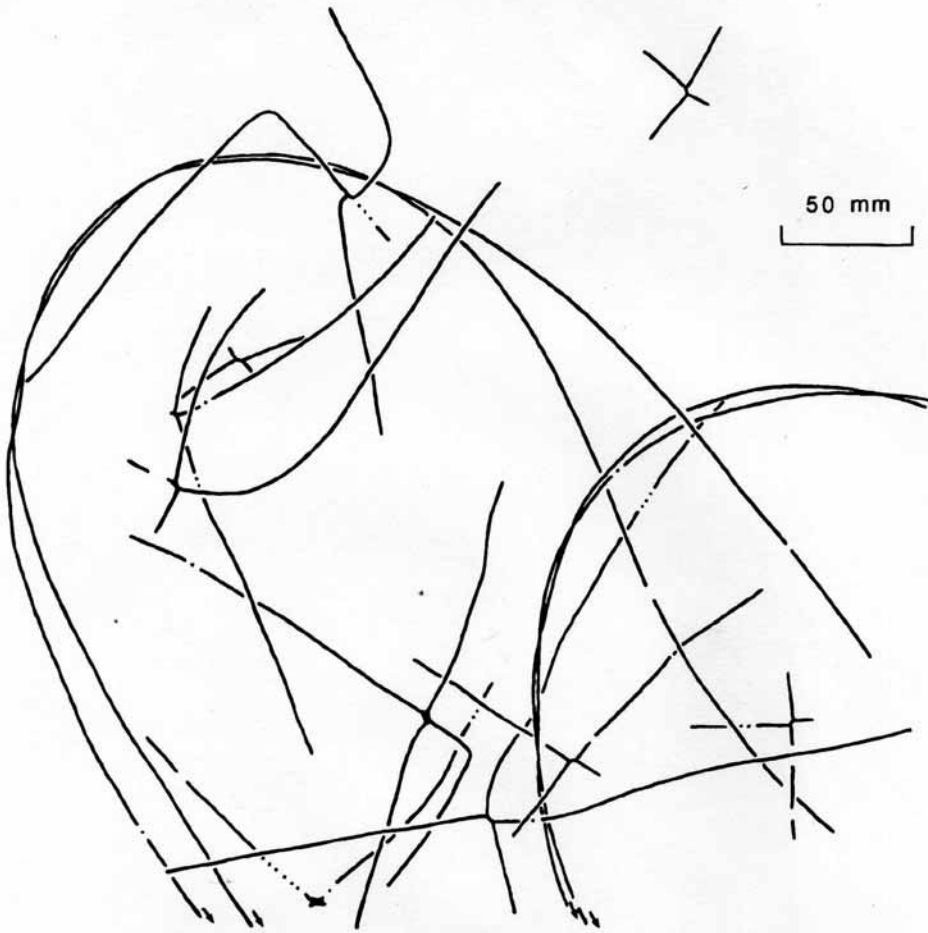
Description. The species has a normal tetragraptid proximal part (Text-fig. 11c), i.e. the first-order stipes are composed of one theca each. All specimens are preserved horizontally, and thus do not reveal any details of proximal development or the possible presence of a sicular bitheca. Many stipes are preserved in relief and show total absence of bithecae. The stipes are 0.7–0.9 mm wide in profile view, up to 1.1 mm in very large specimens. The lateral width is about 0.4–0.5 mm, but the stipes very often show the profile view. The longest stipe fragments encountered were 710 and 680 mm respectively (Text-fig. 12; all specimens on the slab are fragmented – cf. Text-fig. 10b – but there appears to be no tectonic distortion). They probably both belong to one specimen. The thecae are straight tubes, about three times as long as wide and with straight apertures. There are 9.5–11 thecae in 10 mm and they overlap for one half of their length or slightly less. The thecal inclination is about 20°. Mature specimens develop a small central disc (Text-fig. 11a, b). The largest one seen is approximately 2 by 4 mm. No more than 2–3 thecae per second-order stipe are encroached upon by the disc. Cortical thickening has not been noticed along the second-order stipes, but is likely to be present to some degree, considering the relative straightness of most stipes seen in Text-figure 12. The second-order stipes normally make an angle of 80–90°, slightly more in a few specimens. The long stipe fragments in Text-figure 12 seem to have been curved by rotational movement during post-mortem descent to the sediment surface.



TEXT-FIG. 11. A–D, *Tetragraptus longus* sp. nov., Gålgeberg, east-central Oslo. A, holotype, PMO 58.970, with a well-developed central disc; judging from the size of the disc, the stipes must have been very long. B–D, PMO 58.969: B, a specimen with the beginnings of a disc; C, specimen partly preserved in relief in the proximal part, showing a normal tetragraptid branching pattern; D, typical specimen, without central disc. E–H, Gen. et sp. indet. 1, all from Slemmestad. E, PMO 108.599, a complete immature specimen. F, PMO 108.566, a specimen showing the proximal branching pattern inside the central disc. G, PMO 108.567, a specimen with thecae in profile view and an immature central disc. H, PMO 108.599, proximal fragment of a presumably large specimen with a well-developed central disc.

Remarks. Thin horizontal tetragraptids are most commonly lumped together under the name *T. quadribrachiatus*. As was shown by Williams and Stevens (1988), even the type collection of J. Hall contains specimens of two unrelated taxa of different age. Their recommendation was that the name should not be used until the taxon was redefined. *T. longus* differs from the original description of *T. quadribrachiatus* in having a central disc in mature specimens. J. Hall (1865) noted that he had never seen one in *T. quadribrachiatus*. Also, the stipe divergence angles of *T. longus* are somewhat unusual, being more often below than above 90°. The great length of the stipes is also unique.

The number of specimens found might suggest that the species is a common one. This is not the case – it appears to be an invasion species, found covering surfaces in almost monotypic assemblages, and being very rare in intervening beds.



TEXT-FIG. 12. *Tetraraptus longus* sp. nov., PMO 97.708, Slemmestad. Illustration of part of a very big slab, showing ten (of a total of twelve) specimens with proximal part, and two pairs of very long stipes of the species, possibly both belonging to one specimen. The arrows point in the distal direction, and are placed along the ventral side of the stipe. Associated fauna is not shown.

Tetraraptus krapperupensis sp. nov.

Text-fig. 13 A, C, E; cf. Text-fig. 13 F

Name. From the Krapperup core.

Material. 6 specimens, all from the Krapperup core, three of them at 140-87 m, the other three at 140-30 m. Holotype LO 5988T (140-87 m; Text-fig. 13c), paratypes LO 5987t and LO 5989t (both from 140-30 m). One specimen of *T. cf. krapperupensis* (LO 5990t) is present at 129-46-129-54 m.

Associated species. *A. murrayi*, *Didymograptus* sp. 1.

Stratigraphic range. *A. murrayi* Zone, possibly also *H. copiosus* Zone.

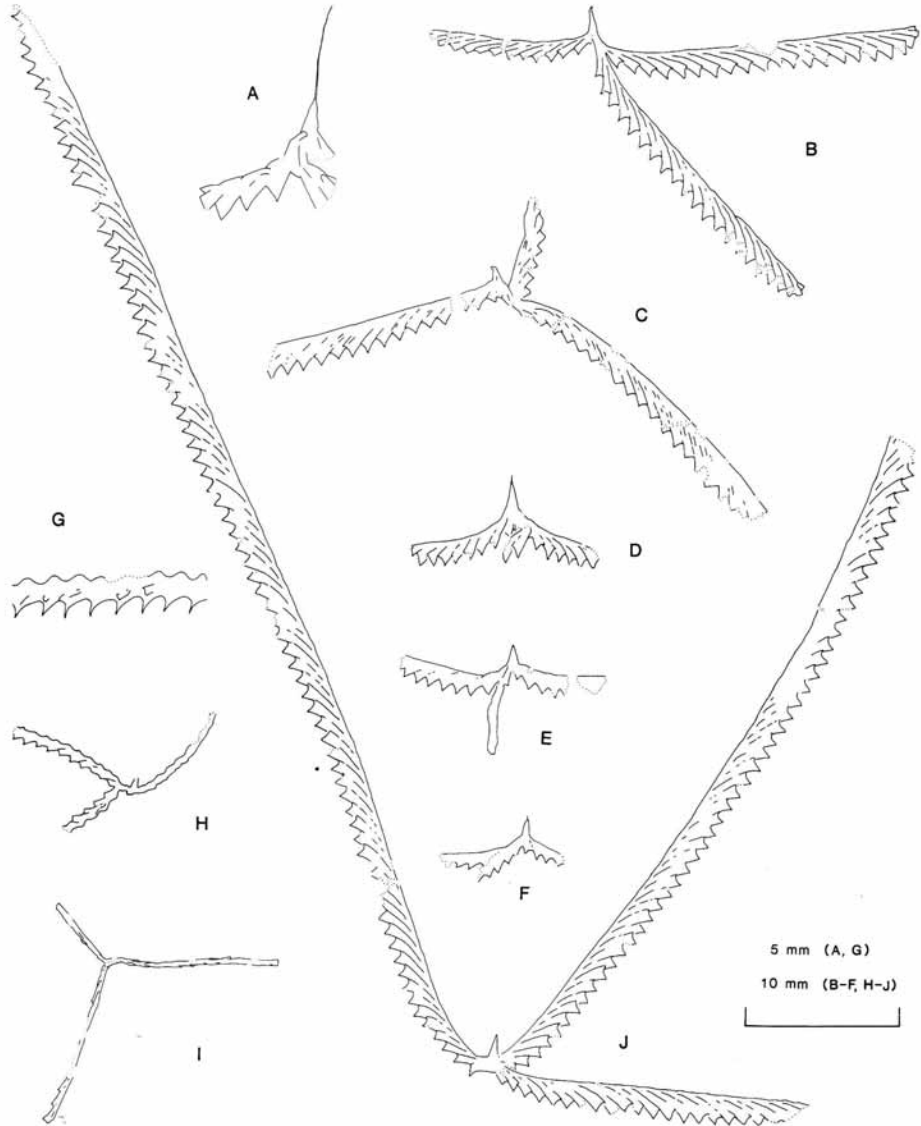
Diagnosis. A three-stiped species of slightly declined habit. Sicular length 2.2–2.5 mm, stipe width 1.3 mm proximally and up to 2.1 mm distally, 9.5–11 thecae in 10 mm, thecal overlap about one half, distal thecal inclination 35–45°.

Description. The sicula is 2.2–2.5 mm long and about 0.4–0.7 mm wide at the aperture. No specimen shows any details of proximal development. Only stipe¹ has a second dichotomy, after the first theca, resulting in 3 final stipes. The thecae are straight or slightly curved, about 2–3 times as long as wide. They are inclined at about 35–45° to the dorsal margin of the stipes. Well-preserved thecae are somewhat denticulate and have a concave aperture. The aperture is generally inclined at 60–70° to the dorsal margin of the stipes. The thecal overlap is mostly difficult to see, but appears to be approximately one half. There are 9.5–11 thecae in 10 mm, the lower value being found in the largest specimen. The proximal stipe width is about 1.3–1.4 mm, the maximum stipe width varies with the length of the stipes, from 1.5 mm in small specimens to 2.1 mm in the largest one. Across a specified theca the stipes are somewhat wider in larger specimens, possibly suggesting a certain amount of continued thecal growth. Two specimens (see Text-fig. 13A) indicate a plaited thecal structure – or triad budding: due to the relatively low relief, the presence or absence of bithecae along the stipes cannot be verified. The species could belong to the transitional forms with only traces remaining of an anisograptid structure (Lindholm and Maletz 1989). The stipes are declined in their proximal part. They are straight throughout or have a slight dorsally concave curvature. In life, the stipes were probably slightly declined.

One specimen, found a few metres higher in the core, has somewhat narrower stipes and more closely set thecae (Text-fig. 13F). Until more material of the species is known, I refer to it as *T. cf. krapperupensis*.

Remarks. No four-stiped rhabdosomes have been observed in the beds containing *T. krapperupensis* and the assignment of the species to the dichograptid form genus *Tetragraptus* is based on the fact that no bithecae have been identified, and that there are only two orders of dichotomy; there appears to be no other existing dichograptid genus for three-stiped forms. However, since preservation precludes observation of bithecae, these could in fact be present, in which case the species would have to be referred to an anisograptid genus. *Triograptus* is the only three-stiped anisograptid genus. It has three 'primary' stipes, i.e. the second-order dichotomy follows the first without intervening unicalycal theca (Cooper and Fortey 1983), although one specimen (Text-fig. 13H) in the collection forming the basis of Monsen's (1925) original description of the type species, *Triograptus osloensis*, appears to have two primary stipes, one of them branching after theca 1, just like the species here described. However, the thecal morphology of *Triograptus osloensis* (Text-fig. 13G) makes it very unlikely that the two species are closely related. Near the base of the Krapperup core there is one specimen probably belonging to another *Triograptus* species (Text-fig. 13I). Also this species has a thecal shape quite unlike that of *T. krapperupensis*.

Three-stiped rhabdosomes of roughly the same shape are found also in younger beds in southern Scandinavia. Five specimens were found with the *H. copiosus* fauna in Slemmestad (PMO 108.566, 108.569–108.570, 108.598; Text-fig. 13D). The thecal morphology agrees reasonably well with that of *T. krapperupensis*, but the sicula is much stouter and longer. This form is found together with four-stiped specimens. Three-stiped forms are especially common in the overlying *T. phyllograptoides* Zone (more than 150 specimens from Mt Hunneberg in RM, SGU, and Lund collections have been investigated), where three typical shapes can be seen among the declined to slightly reclined forms. Some additional specimens are preserved horizontally, so that thecal characteristics are obscured. This fauna has not yet been studied in enough detail to see if there is a continuous range of variation among its members or not, but it seems possible that there are distinct forms, some or all of which may be related to four-stiped forms, i.e. merit the name *Tetragraptus*. One form (Text-fig. 13B, J) is very similar in outline to *T. krapperupensis*. I hesitate to synonymize them since there are indications of a plaited thecal structure in *T. krapperupensis*, whereas specimens of the younger fauna have normal dichograptid stipes. Perhaps they formed part of a three-stiped lineage with separate bithecal reduction. Where three- and four-stiped specimens occur in the same beds it



TEXT-FIG. 13. *Tetraraptus krapperupensis* sp. nov. and comparative material. A, C, E, *T. krapperupensis* sp. nov., all from the Krapperup core; A, LO 5987t, 140.30 m, the left-hand stipe shows plaited thecal structure; C, holotype, LO 5988T, 140.87 m, the largest specimen; the drawing is a combination of counterparts; E, LO 5989t, 140.30 m, a smaller specimen with narrower maximal width. B, J, *Tetraraptus* sp. 1, Mossebo, Mt

is often difficult to see if they are conspecific since the proximal parts of the four-stiped specimens tend to be preserved horizontally (dorsoventral view), so that the sicula and proximal width of stipes etc. cannot be seen.

Three-stiped rhabdosomes of various species appear to be present through most of the Arenig of southern Scandinavia. In the *T. phyllograptoides* Zone, in addition to the forms discussed above, there is a pendent three-stiped form which has no associated four-stiped pendent specimens. According to S. H. Williams (pers. comm.) it is identical to *P. cf. pendens* from Newfoundland (Williams and Stevens 1988). The Newfoundland fauna, however, contains both three- and four-stiped specimens. In beds above the *T. phyllograptoides* Zone in Scandinavia, practically all three-stiped forms have reclined rhabdosomes.

Some three-stiped forms from the *T. phyllograptoides* Zone at Mt Hunneberg were described by Maletz (1987) under the name of *T. triograptoides* (nomen nudum; junior homonym of *T. triograptoides* Harris and Thomas, 1938), but had been observed already by Törnquist (1904, pl. 1, fig. 20), who grouped them with four-stiped forms as *T. serra* (= *T. amii* according to current usage).

Non-triograptid, more or less horizontal, three-stiped forms of Tremadoc–Arenig age are known also from other areas. *Tetragraptus otagoensis* and *T. decipiens* (three-stiped form) from New Zealand were shown by Bulman and Cooper (1969) to have the same branching pattern as the Scandinavian forms. *T. otagoensis* is of La 2 zone age, and is therefore roughly coeval with *T. krapperupensis*, but has considerably narrower stipes than the latter. The three-stiped form of *T. decipiens* is somewhat younger, La 3 zone, approximately coeval with the *T. phyllograptoides* Zone fauna of Mt Hunneberg. It appears to have stipes narrower than the mature Scandinavian specimens, but it is worth noting that immature Scandinavian specimens, with stipes of comparable length to that of the New Zealand specimens, also have a comparable stipe width. As in the Scandinavian specimens, the second-order dichotomy in the New Zealand specimens is based on stipe¹ (the stipe developed on the th¹ side), quoted erroneously (R. A. Cooper pers. comm.) by Bulman and Cooper (1969) and Cooper (1979) as the stipe² side. The three-stiped form of *T. decipiens* has not yet been reported from Australia (R. A. Cooper pers. comm.).

Harris and Thomas (1938) described *Tetragraptus triograptoides* from the lowermost part of the Bendigonian of Victoria. This is a very slender form, belonging to the sigmagraptines, judging by its thecal characters. Chen *et al.* (1983) reported a specimen of a three-stiped extensiform species, *Adelograptus robustus*, from Jiangxi, South China, associated with *T. approximatus*. Its dimensions, apart from the comparatively broad proximal part of the stipes, are not far from those of certain specimens found at Mt Hunneberg, but it has bithecae along the stipes. A probably middle Arenig form was described from Czechoslovakia (*T. postlethwaitii*; Kraft 1987). It resembles the form illustrated in Text-figure 13B except in having slightly narrower stipes. The species contains both three- and four-stiped forms.

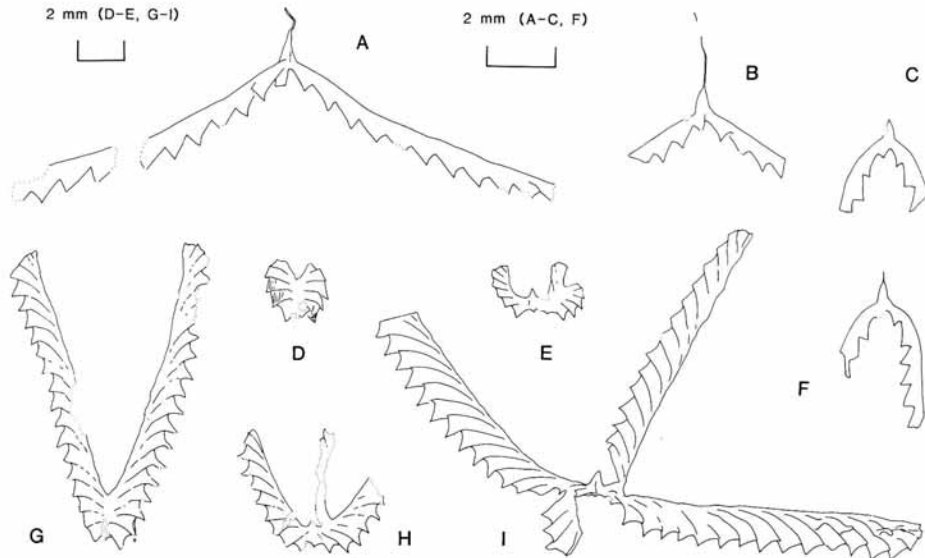
Form genus DIDYMOGRAPTUS M'Coy, 1851 (= DIDYMOGRAPTUS *s.l.*)

Didymograptus sp. 1

Text-fig. 14A, B

- v cf. 1986 *Corymbograptus* sp. 1 Gutiérrez Marco, pp. 445–447, text-fig. 39D–M; pl. 14, figs 2, 4, 5.
v cf. 1988 *Didymograptus* cf. *sinensis* Lee and Chen; Molyneux and Rushton, p. 66, fig. 9a, b.

Hunneberg; b, SGU Type 8020; j, RM Cn 1838, the biggest specimen found. d, *Tetragraptus* sp. 2, PMO 108.569–108.570, Slemmestad; the drawing is a combination of counterparts. f, *T. cf. krapperupensis*, LO 5990t, Krapperup core 129.46–129.54 m. g–h, *Triograptus osloensis* Monsen, both on PMO 59.215, Stensberggaten, central Oslo, Ceratopyge Shale, 155–180 cm below the Ceratopyge Limestone; g, part of a stipe fragment showing shape of thecae; h, an aberrant specimen with two primary stipes and a second-order dichotomy. i, *Triograptus?* sp. 1, LO 6015t, Krapperup core, 151.45–151.46 m.



TEXT-FIG. 14. A, B, *Didymograptus* sp. 1, Krapperup core 137.72–137.76 m, two associated specimens; A, LO 5991t, the largest specimen found, slightly deflexed; B, LO 5992t, a seemingly declined specimen. C, F, *Didymograptus* sp. 2, Krapperup core, 118.50–118.54 m, two associated specimens; C, LO 5993t; F, LO 5994t. D, E, G, H, *Tetragraptus phyllograptoides* from near the base of the species; all have considerably narrower stipes than the typical form; from two localities in the Slemmestad area; D, LO 5995t, immature *Phyllograptus*-like specimen, a–b pair; dotted circle indicates the broken connection towards the sicula; E, LO 5996t, a probably three-stiped specimen; the drawing is a combination of counterparts; G, LO 5997t, the largest specimen found, a–b pair; as in D, the connection towards the sicula is broken; H, LO 5998t, a probably three-stiped specimen showing few thecae in the conjoined part of the stipes. I, *Tetragraptus* sp. 3, PMO 112.967, 112.969, Slemmestad, associated with a *Hunnegraptus* fauna; a specimen in medium relief with the proximal part preserved as a mould; sicular outline drawn from counterpart.

Material. 10 specimens from the interval 147.33–137.70 m of the Krapperup core. Most specimens are small, showing no more than 4 thecae per stipe.

Associated species. *A. murrayi*, *T. krapperupensis*.

Stratigraphic range. *A. murrayi* Zone, and possibly higher beds.

Diagnosis. A thin (c. 0.7–0.8 mm) deflexed to declined didymograptid with sicular length about 1.4 mm and around 12 thecae in 10 mm. Thecae straight, inclined at c. 30°.

Description. All specimens are too flattened to show any details of proximal development or the possible presence of bithecae. The sicula is straight, 1.2–1.6 mm long and about 0.3 mm wide at the aperture. It protrudes about 0.7–0.9 mm above the dorsal margin of the rhabdosome. The thecae are almost straight tubes, inclined at about 30°. Their apertures are straight or slightly concave, inclined at 70–80° to the dorsal margin of the rhabdosome. There are normally 12 thecae in 10 mm, but the total variation seen is 11–14. The stipes are 0.6–0.7 mm wide proximally, widening to about 0.8 mm or, rarely, 1.0 mm distally. The shape of the rhabdosome is slightly deflexed or declined, with a stipe divergence angle of 120–145°.

Remarks. The assignment of this species to *Didymograptus s.l.* is based on the fact that no bithecae have been seen along the stipes. Considering the age of the fauna, however, it is possible that bithecae are present, but not detectable due to the flattened state of the rhabdosomes. If so, the species will have to be referred to *Kiaerograptus*.

The general shape of the rhabdosome of this species is common to several species throughout higher parts of the Arenig and even the lower part of the Llanvirn, but the only similar species of roughly the same age are *Corymbograptus* sp. 1 Gutiérrez Marco, 1986, and *Didymograptus* cf. *sinensis* described by Molyneux and Rushton (1988). *Corymbograptus* sp. 1 differs only in having a somewhat shorter sicula and narrower proximal width, as well as a more accentuated deflexed shape in some of the specimens. *D. cf. sinensis* is, in my opinion, a synonym of that species, differing only in having slightly more thecae in 10 mm, well within the normal limits of variation of a species of that age. There are only a couple of reasonably large Swedish specimens, not necessarily representative of the mean of the population, hence further finds may prove the Swedish species to be conspecific with the Spanish/English one.

Gen. et sp. indet. 1

Text-fig. 11E-H

Material. 4 specimens from Slemmestad crossroads, c. 0.5–1.0 m above the Ceratopyge Limestone, found on PMO 108.566, 108.567 and 108.599.

Associated species. *H. copiosus*, *Clonograptus* s.s. sp. indet., 3-stiped extensiform tetragraptids, *P. tenuis*, *P. cf. rarus*.

Stratigraphic range. *H. copiosus* Zone.

Diagnosis. A five-stiped rhabdosome, with a tetragraptid proximal part. Stipe width c. 1.6 mm, 9.5–11 thecae in 10 mm. A central disc is found in mature specimens.

Description. All four specimens are preserved horizontally, obscuring details of proximal morphology. The proximal part is tetragraptid, however, with one theca per first-order stipe. A well-developed central disc is found in the most mature specimens. The two largest discs measure 2 by 4 and 2 by 5 mm respectively (Text-fig. 11F, H). The only specimen showing thecae in profile view (Text-fig. 11G), has faint beginnings of a disc. The specimen is preserved in low relief and shows possible plaited thecal structure along one stipe (alternatively, it represents a compression structure). A characteristic of the species is that one of the second-order stipes divides consecutively. There are no indications in the available material of any further dichotomies, and it may be presumed that the final number of stipes is five, especially since there seems to be a certain amount of readjusting of the stipe angles, to even out the distances between the stipes. However, this is unfortunately difficult to prove due to the fragmentary state of the rhabdosomes. The thecae are slightly curved and somewhat expanded tubes, and slightly denticulate. The thecal overlap is about 60% and there are 9.5–11 thecae in 10 mm. The profile stipe width is 1.6 mm, the lateral width 0.5–0.7 mm.

Remarks. The three orders of stipes present in these specimens would suggest the use of the genus name *Dichograptus*. A reduction of the final stipe number is known to occur within *Dichograptus*. However, for the following reasons I prefer not to assign these specimens to that genus. Firstly, the Slemmestad form is older than any reported species of the genus and, secondly, I have not come across any definite *Dichograptus* specimens from the lower Arenig of Scandinavia. Additionally *Dichograptus* (as well as *Tetragraptus*) is likely to be a form genus and its type species, *D. sedgwicki*, has never been properly described (see Salter 1863; Elles and Wood 1902) and apparently has no associated fauna confirming its age. It was referred to as a subspecies of *D. octobrachiatus* by Elles and Wood (1902). Compared with *D. octobrachiatus*, the present form is much less robust and, due to the lack of details known from the proximal part of either taxon, their phylogenetic relationship is unclear. The beds containing my five-stiped form are of an age when great changes took place in

the graptolite fauna, including not only the loss of bithecae along several lineages but, as far as I have seen, also an instability in the number of stipes present in a specimen. It thus seems more probable to me that the present form has a derivation separate from that of the later *Dichograptus* species.

Family SINOGRAPTIDAE Mu, 1957

Subfamily SIGMAGRAPTINAE Cooper and Fortey, 1982

Diagnosis (from Fortey and Cooper 1986): Dichograptinids with sigmagraptine proximal region.

Remarks. The Sigmagraptinae was originally described as a subfamily of the Dichograptidae with included species united by the characteristic proximal part and generally slender thecae. The taxon was raised to family rank by Fortey and Cooper (1986), consisting of the nominate subfamily only. Williams and Stevens (1988) lowered the rank back to subfamily level, and included it in the family Sinograptidae. I follow the classification of Williams and Stevens (1988), and also their concept of the content of the family (sinograptines, sigmagraptines, and the previously 'obscure' *Kinnegraptus*). The use of the name Sinograptidae follows priority rules, even though a sigmagraptid is the ancestor of the sinograptines.

The kinnegraptids were raised to family rank by Mu (1974) and were used at this level for *Paradelograptus* by Erdtmann *et al.* (1987). Also Williams and Stevens (1988), though temporarily including them in the Sigmagraptinae, considered the possibility that further study might show that the kinnegraptids merit family rank. However, my own investigations have shown them to be very close to the main stock of sigmagraptines. *Acrograptus gracilis* has an equally prolonged prosicula, and the exaggerated apertural lip (rutellum; Williams and Stevens 1988) of thecae and sicula is found among some of the *Paradelograptus* species, as well as in some specimens of *A. tenellus* (Hutt 1974, fig. 8A), the species which must be considered the best candidate for an ancestor of the Sigmagraptidae.

Genus PARADELOGRAPTUS Erdtmann, Maletz and Gutiérrez Marco, 1987

Diagnosis. See Erdtmann *et al.* (1987). The most important features mentioned are biradiality, irregular dichotomies, isograptid development, asymmetrical proximal part, and a characteristic thecal shape with long thin ptothecae and expanding metathecae, sometimes provided with 'lappets' [here meaning *ventral* prolongation]. Bithecae were not observed.

Remarks. When defined by Erdtmann *et al.* (1987), the genus *Paradelograptus* was referred to the family Kinnegraptidae Mu, 1974. However, the authors base this family only on the shape of the thecae, disregarding features of the proximal end (1987, p. 113): 'This character [shape of the proximal part], however, is not a discriminating factor for *Paradelograptus* alone nor for the Kinnegraptidae and Sigmagraptinae [of the Dichograptidae], as was suggested by Cooper and Fortey (1982, p. 259), but it is observed quite frequently in many other dichograptids, dating back to the ancestral *Adelograptus tenellus* (Hutt, 1974, fig. 5B, Maletz and Erdtmann 1987) and to other adelograptinid forms (i.e. to *Choristograptus* Legrand, 1964). Therefore, no taxonomic significance may be attached to this feature alone [my italics]'. With this statement I disagree. In my opinion, they have defined a group of genetically related taxa. Further, figure 2 of Erdtmann *et al.* (1987), showing the 'phyletic relations' of taxa, disagrees with the text. The text states that the concepts of Cooper and Fortey (1982) have been used, that is, that Sigmagraptinae is a subunit of Dichograptidae. The figure, on the other hand, shows a possibly diphyletic Sigmagraptinae branching off the Kinnegraptidae, and possibly also the Clonograptinae.

Paradelograptus differs from *Adelograptus* solely in the absence of bithecae along the stipes. It includes both two-stiped and multi-stiped taxa. Among the *Paradelograptus* species described by Erdtmann *et al.* (1987) the proximal development is known only for the type species, *P. onubensis*.

It is quite possible that the genus *Paradelograptus*, with the constituent species as given by Erdtmann *et al.* (1987, p. 115; 15 species in all, those mentioned below and *P. sedecimus*, *P. rarus*, *P. smithi*, *P. ramulosus*, *P. chapmani*, *P. ? tenuiramis*, *P. ? clarkefieldi*, *P. ? bulmani*, *C. tenellus* var. *problematica* Harris and Thomas, and *C. tenellus s.l.* Cooper and Steward), is a polyphyletic assemblage of similar-looking forms, which have responded in a similar way to peculiarities of the environment. However, the external shape of the proximal parts, with an adelograptid type of sicula, in *P. onubensis*, *P. antiquus*, *P. pritchardi* and *P. mosseboensis*, and *P. elongatus* and *P. tenuis* described here, is so similar as to make it likely that at least this group is monophyletic. *P. kinnegraptoides* appears from illustrations not to have an adelograptid sicula. The proximal development of *P. smithi* was not seen in the specimens from Mt Hunneberg, and the inclusion of that species by Erdtmann *et al.* (1987) seems to be based on thecal morphology alone.

Two new species are described here. A number of other species present in the Scandinavian Lower Hunneberg beds are mentioned under 'Other species' (p. 320).

Paradelograptus elongatus sp. nov.

Text-fig. 15C, G-I

Name. Latin *elongatus*, elongated, referring to the long first-order stipes.

Material. 16 specimens, 15 of which come from Slemmestad (14 of them on PMO 108.568-108.570, Slemmestad crossroads; 1 specimen, LR 2, from the base of the *T. phyllograptoides* Zone at Hagastrand, Lund collections). One specimen was found in the Krapperup core (124.87-124.89 m). A questionable specimen was found at Storeklev (2.32 m, Lund collections). Both the holotype (Text-fig. 15I; the only mature specimen) and the paratypes are found on PMO 108.570.

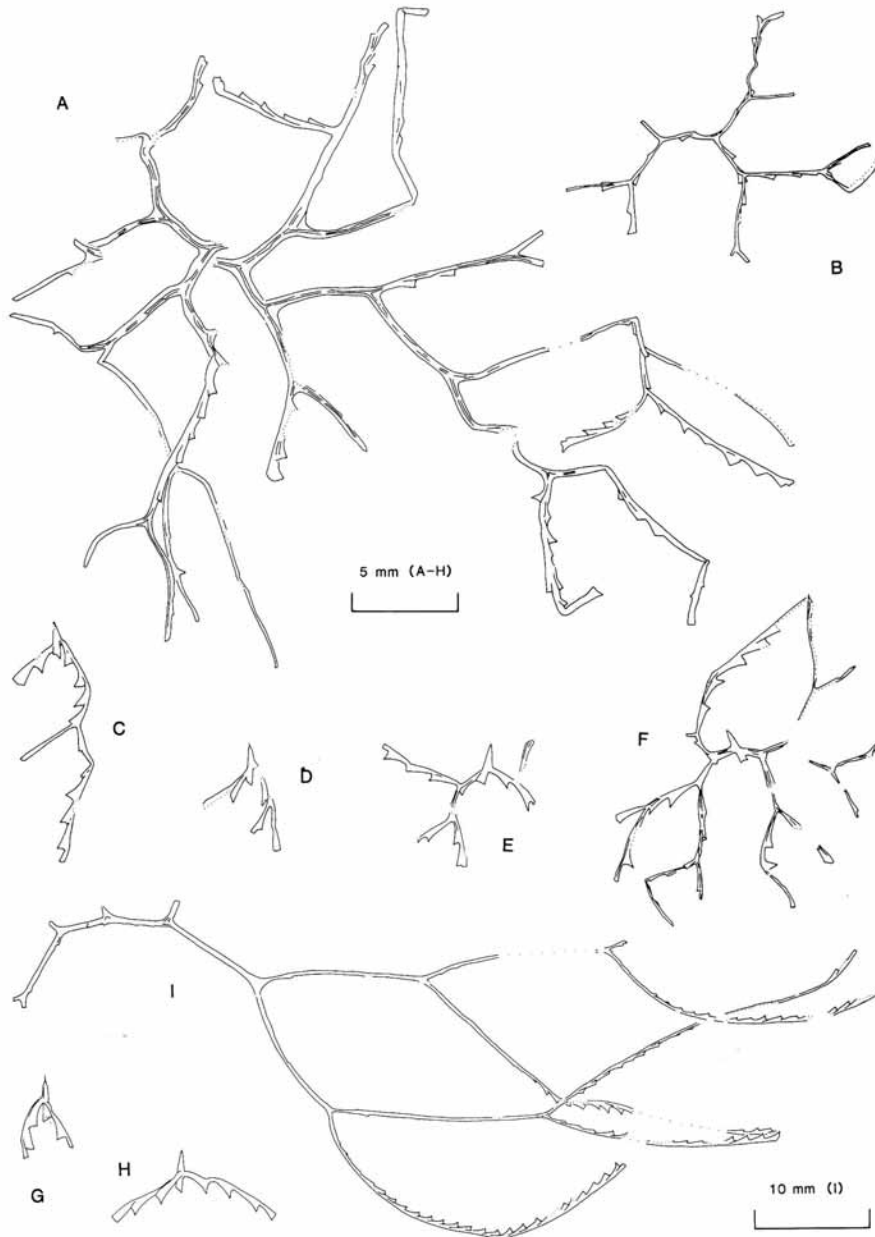
Associated species. *A. murrayi*, *H. copiosus*, *P. antiquus*.

Stratigraphic range. *H. copiosus* Zone, and at least the basal beds of the *T. phyllograptoides* Zone.

Diagnosis. Biradiate, declined to pendent in profile view, branching dichotomously at irregular intervals; first-order stipes consist of more than one theca. Proximal development probably isograptid; both sinistral and dextral forms occur. A sicular bitheca has been observed. Metathecae somewhat flared, but less so than in *P. mosseboensis*. Dimensions close to the latter.

Description. The sicula is straight and tube-like, 1.9-2.0 mm long and 0.3-0.4 mm wide at the aperture. Theca 1¹ originates close to the apex of the sicula. The development is probably isograptid, the prothecal part of th 2¹ is seen in the specimen in Text-figure 15G, and can be traced back almost to the point of origin of theca 1². A sicular bitheca is present on the obverse side of the sicula (Text-fig. 15C). There are both dextral and sinistral forms. The thecae are 2 mm long or longer, have relatively thin prothecal parts and somewhat flaring metathecae, which are sometimes seen to have a short denticle. Thecal width at the apertures reaches 0.4-0.5 mm. There are 8-9 thecae in 10 mm and the thecal overlap is about 40-50% (the point of origin of thecae is commonly obscure). The profile stipe width is 0.6-0.7 mm in proximal parts, up to 0.9 mm in distal parts. The first-order stipes vary in attitude from almost horizontal to pendent, if seen in profile view. The first dichotomy occurs at th 3 or later, sometimes considerably later: in one unbranched specimen, first-order stipes have 8 and 14 thecae. The holotype is a mature specimen showing five orders of stipes, the greatest number known. There is a considerable amount of cortical strengthening of proximal stipes in the holotype, giving it a much more rigid appearance than the associated smaller specimens. No bithecae have been observed along the stipes, but the material is mostly of low to no relief.

Remarks. *P. elongatus* most closely resembles *P. mosseboensis*, which occurs at a considerably higher level, around the lower boundary of the *D. balticus* Zone at Diabasbrottet, Hunneberg (Erdtmann *et al.* 1987, fig. 1). The dimensions of the two species are virtually the same, but the ventral thecal processes are less pronounced in *P. elongatus*. The latter is widely variable in the position of the second-order branching, whereas the corresponding range for *P. mosseboensis* was



TEXT-FIG. 15. For legend see opposite.

indicated as theca 2-3 (Erdtmann *et al.* 1987, p. 120). This range might be considerably wider, since the species was only represented by three incomplete specimens. The holotype of *P. elongatus* very much resembles that of *P. kinnegraptoides* in general shape, but not in size and thecal details.

Paradelograptus tenuis sp. nov.

Text-fig. 15A-B, D-F

? 1979 *Clonograptus tenellus* Linnarsson *s.l.*; Cooper and Stewart, pp. 785-786, text-fig. 8m.

Name. Latin *tenuis*, thin, small-sized.

Material. 15 specimens, 13 of which come from various localities in the Slemmestad area (12 of them, some with counterpart, are found on PMO 73.188-73.189, 73.191-73.192, 108.557-108.560, 108.566, 112.966-112.969, 113.031; one specimen, LR 3, from the base of the *T. phyllograptoides* Zone at Hagastrand, Lund collections). The other two specimens are from Storeklev (TUB HUN-S/2.18-2.3/006+030 and 036). Two additional questionable specimens from Storeklev were found on PU Vg 127 and one slab in the Lund collections (from 2-32 m). The holotype is a mature specimen on PMO 108.566 (Text-fig 15A), the four paratypes, all illustrated in Text-figure 15, are found on PMO 108.557-108.559.

Associated species. *A. murrayi*, *H. copiosus*, *C. aff. multiplex*, *Isograptus* sp., horizontal tetragraptids ('quadribrachiatus'-type).

Stratigraphic range. *H. copiosus* Zone and at least the basal beds of the *T. phyllograptoides* Zone.

Diagnosis. A small, thin paradelograptid with tetragraptid proximal part and frequent branchings. Sicula 1.6-1.9 mm long, 7.5-8 thecae in 10 mm, profile stipe width 0.5-0.65 mm, lateral width 0.2 mm or more.

Description. The sicula is of general paradelograptid shape, 1.6-1.9 mm long and 0.3-0.4 mm wide at the aperture. The two stipes diverge from the sicula at different levels, stipe¹ at sicular mid-length or slightly closer to the aperture, stipe² leaving 0.2 mm or less protruding on the ventral side of the stipe. The first-order stipes consist of one theca each (resulting in a tetragraptid proximal plan), the second-order ones of 1-3 thecae. The following orders each get a little longer, but in general aspect, the rhabdosome is very thin-stiped and rather densely branching. Six orders of stipes were found in the largest specimen.

The thecae have very low inclination, their ventral margins are concave, and they are denticulate. The apertural margins are straight to markedly concave, making an angle of 90° or more with the dorsal margin of the stipes. The profile stipe width is 0.5-0.65 mm and there are 7.5-8 thecae in 10 mm. The amount of thecal overlap could not be determined. The lateral stipe width is variable, 0.2-0.6 mm, depending above all on the amount of cortex overgrowth. A noticeable amount of cortex cover is only found in the most mature specimen where, due to slight pyritization, the outline of the stipes can be traced inside the cortex. No specimen was well enough preserved to verify presence or absence of bithecae. Badly preserved stipe fragments appear as thin branching 'threads' with no thecae visible.

Remarks. The size and shape of sicula and thecae are very close to those of *P. elongatus* (see Text-fig. 15). However, the two species differ in branching density and the position of the second dichotomy (tetragraptid proximal part only in *P. tenuis*).

TEXT-FIG. 15. A-B, D-F, *Paradelograptus tenuis* sp. nov., Slemmestad; A, holotype, PMO 108.566, the largest specimen, with considerable cortical thickening; B, PMO 108.557-108.558, horizontally preserved specimen; the drawing is a combination of counterparts; D, PMO 108.559, immature specimen with (secondarily?) pendent proximal part; E, PMO 108.557; F, PMO 108.559, combination of counterparts. C, G-I, *Paradelograptus elongatus* sp. nov., Slemmestad, all on PMO 108.570; C, specimen showing presumed sicular bitheca; G, H, specimens showing variation in proximal stipe attitude; I, holotype, the only mature specimen found; the sicula points downwards into the sediment, the two shortest second-order stipes point slightly upwards.

The general aspect of the species is very close to that of *C. tenellus s.l. sensu* Cooper and Stewart, 1979, from the La 2 zone of Victoria, Australia. The distal stipe width of *P. tenuis* is somewhat broader and, also, no cortical thickening was mentioned for *C. tenellus s.l.* There is a certain resemblance in shape also to *Adelograptus altus* Williams and Stevens (1991) but, due to the indifferent preservation of the mature specimens of that species and the generalized shape of the proximal part (similar to *P. elongatus*, *P. tenuis* and probably other species), no closer comparison can be made.

Other species

In the Early Hunneberg fauna there are several species in addition to the ones described above. Here, they are only briefly discussed as some of them are quite well known from other areas, others are hard to identify due to a fragmentary preservation, and still others are very rare and are not diagnostic of the fauna, e.g. horizontal tetragraptids.

Clonograptids s.l. Several specimens of a thin-stiped *Clonograptus* species with slightly prolonged first-order stipes (Text-fig. 10B) are present on PMO 97.708, from the Slemmestad area, together with *Tetragraptus longus* sp. nov. The species is very similar in outline to *Clonograptus rigidus*, but it appears to be thinner and the thecae are not well enough preserved for a definite identification.

Clonograptus (Clonograptus) aff. multiplex (PMO 108.557–108.559) occurs at Slemmestad and in the *T. phyllograptoides* Zone of Mt Hunneberg. It was described by Lindholm and Maletz (1989).

Robust stipe fragments probably belonging to *Clonograptus s.s.* (Text-fig. 10E) occur at a couple of levels low in the Krapperup core. A cortex-covered specimen was found in the Slemmestad area (PMO 113.032). It may belong to *Clonograptus norvegicus*.

Horizontal tetragraptids. These are extremely rare below the *T. phyllograptoides* Zone in the Krapperup succession: two very badly preserved specimens of tetragraptid outline ('quadribrachiatus'-type) were found at 152.89–93 m (LR 4–5), a level which probably equals a very early Hunneberg age. The longest stipe of the larger specimen is 15 mm. No thecal details are visible in this specimen, but a stipe of the other specimen, preserved in relief, seems to show a plaited thecal structure. Apart from this, only a possible immature specimen was found at 131.70–131.73 m.

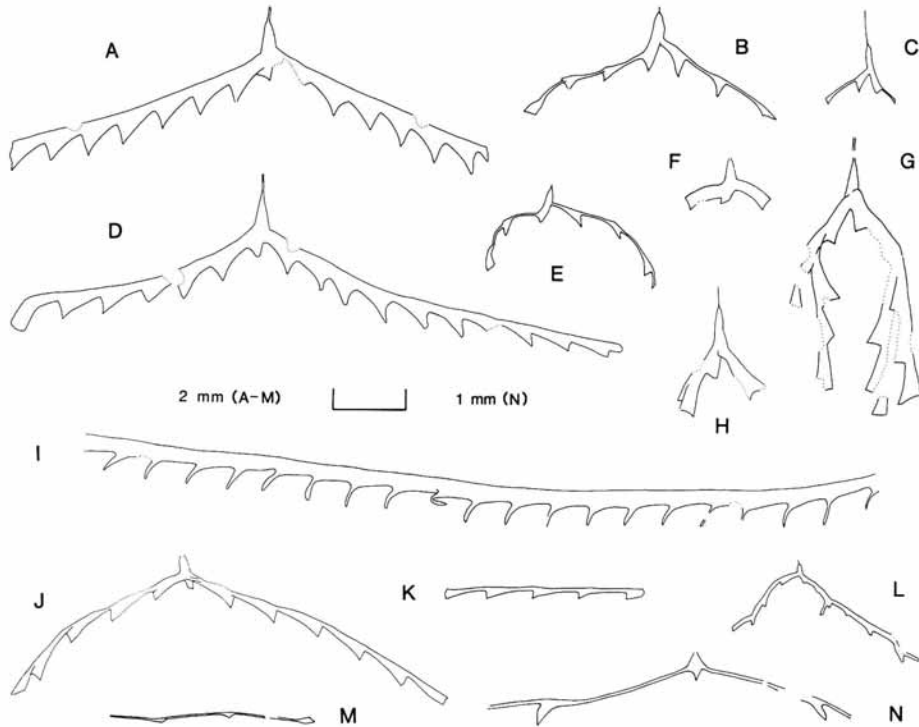
In the Storeklev section at Mt Hunneberg I have not found any tetragraptids. However, two specimens of '*Eotetragraptus* sp. 1' were reported by Maletz (1987; the stratigraphic level most likely corresponds to low *T. phyllograptoides* Zone). Thecal characters were not observable.

Tetragraptids are somewhat more frequent along with the *Hunnegraptus* fauna of Norway. Six specimens of varying stipe width have been found in the Slemmestad area (PMO 108.560, 108.569+108.570, 112.968, 112.969, 120.751, and one specimen in the Lund collections). Text-figure 14i illustrates the broadest specimen found. It is in moderate relief, but the irregularities seen in the lower right of the figure are hard to interpret: do they represent a plaited thecal structure or merely the effects of compression? A 3 mm wide stipe fragment of tetragraptid appearance was found on PMO 108.599.

Pendent didymograptids. A small pendent (or immature deflexed?) didymograptid species (Text-fig. 14c, f) has been found in the highest beds of the early Hunneberg fauna, just below the base of the *T. phyllograptoides* Zone. It is the most diagnostic species of this interval. It occurs at 118.54–112.75 m in the Krapperup core (47 specimens; the majority of them associated on a couple of surfaces and too badly preserved to form the basis of a description), and a few specimens were also found both at Mt Hunneberg and in the Slemmestad area.

Isograptids. Primitive isograptids have been found in the *H. copiosus* Zone in the Slemmestad area. These are apparently the oldest isograptids found anywhere. They will be described in a separate paper (Lindholm in prep.). The oldest specimens have isograptid symmetry, but much less reclined stipes than the majority of isograptids. They also possess a sicular bitheca. An additional specimen was found at 125.67–69 m of the Krapperup core.

Paradelograptids (Erdtmann *et al.* 1987). *Paradelograptus* is represented by several species, especially in the Krapperup core, see Text-figure 16.



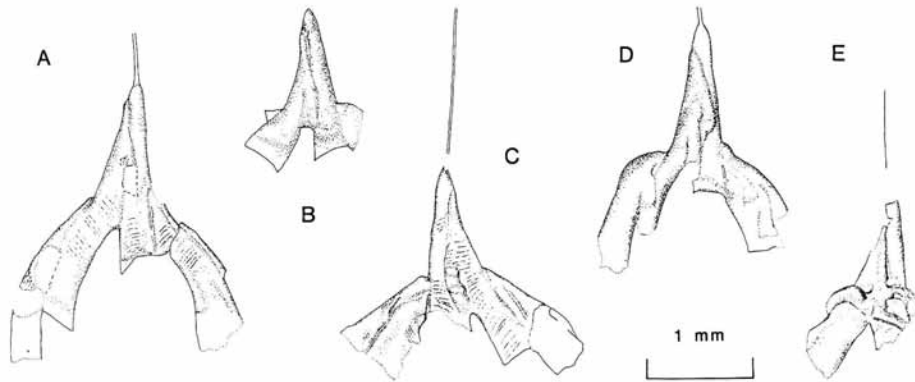
TEXT-FIG. 16. *Paradelograptus* species present in the topmost Tremadoc and lower Hunneberg of Scandinavia, but not described in this paper. A, D, *P. pritchardi* (T. S. Hall), two associated specimens, Krapperup core 134.20–134.26 m; A, LO 5999t; D, LO 6000t, the stipes are slightly twisted. B, *P. antiquus* (T. S. Hall), LO 6301t, Storeklev. C, *P. sp. 1*, PMO 112.967, Slemmestad. E, *P. onubensis* Erdtmann, Maletz and Gutiérrez Marco, LO 6001t, Krapperup core 151.46–151.50 m. F, *P. sp. 2*, LO 6002t, Krapperup core, 153.20–153.29 m. G, H, *P. sp. 3*, LO 6003t and 6004t, Krapperup core 151.96–151.99 m; the specimens are associated. I, *P. cf. rarus* (Harris and Thomas), LO 6302t, Storeklev. J, K, *P. sp. 4*; J, LO 6005t, Krapperup core 141.75 m; K, LO 6006t, Krapperup core 150.71–150.75 m. L, *P. sp. 5*, LO 6007t, Krapperup core 153.20–153.29 m. M, N, *P. sp. 6*; M, LO 6008t, Krapperup core 148.79 m; N, LO 6009t, Krapperup core 150.71–150.75 m.

One specimen of *P. onubensis* was found at 151.46–151.50 m. It is rather immature, with only two stipes, but the shape of the proximal part is unmistakable (Text-fig. 16E). A second specimen was found at 111.40–111.45 m.

P. pritchardi (Text-fig. 16A, D) occurs in the 135.09–118.50 m interval. *P. antiquus* (Text-fig. 16B) was found between 117.88 and 114.17 m of the Krapperup core. The species is also represented at Storeklev (LO 6301t, TUB HUN-S/2.18–2.3/023, PU Vg 124, and one specimen in the Lund collections), at Tøyen (GPI T4, T6), and at Slemmestad (PMO 108.568, 108.572, one specimen in the Lund collections).

Stipe fragments indistinguishable from *P. rarus* (Text-fig. 16I) were found at Storeklev (LO 6302t and counterpart; one specimen in the Lund collections) and Slemmestad (PMO 108.567, 109.148). Stipes probably belonging to the same species are not uncommon, but the thecal outline needed for identification is seldom seen.

In addition to these species, unidentifiable proximal parts and stipe fragments occur in the Krapperup core



TEXT-FIG. 17. Graptoloidea indet. spp. Relief specimens, all (and more) associated on one surface, near the base of the *A. murrayi* Zone, Krapperup core 147.66–147.72 m, LO 6010t–6014t. A–D show the sicular bitheca; D shows a bitheca in stipe 1. E could be interpreted as triradiate. C was drawn from a latex cast; E was combined from both counterparts. All illustrations were made under vertical light.

in the interval 153.29–134.20 m. Some of them are illustrated in Text-figure 16F–H, J–N. One of the species is minute – its sicula is only 0.3 mm long (Text-fig. 16M, N).

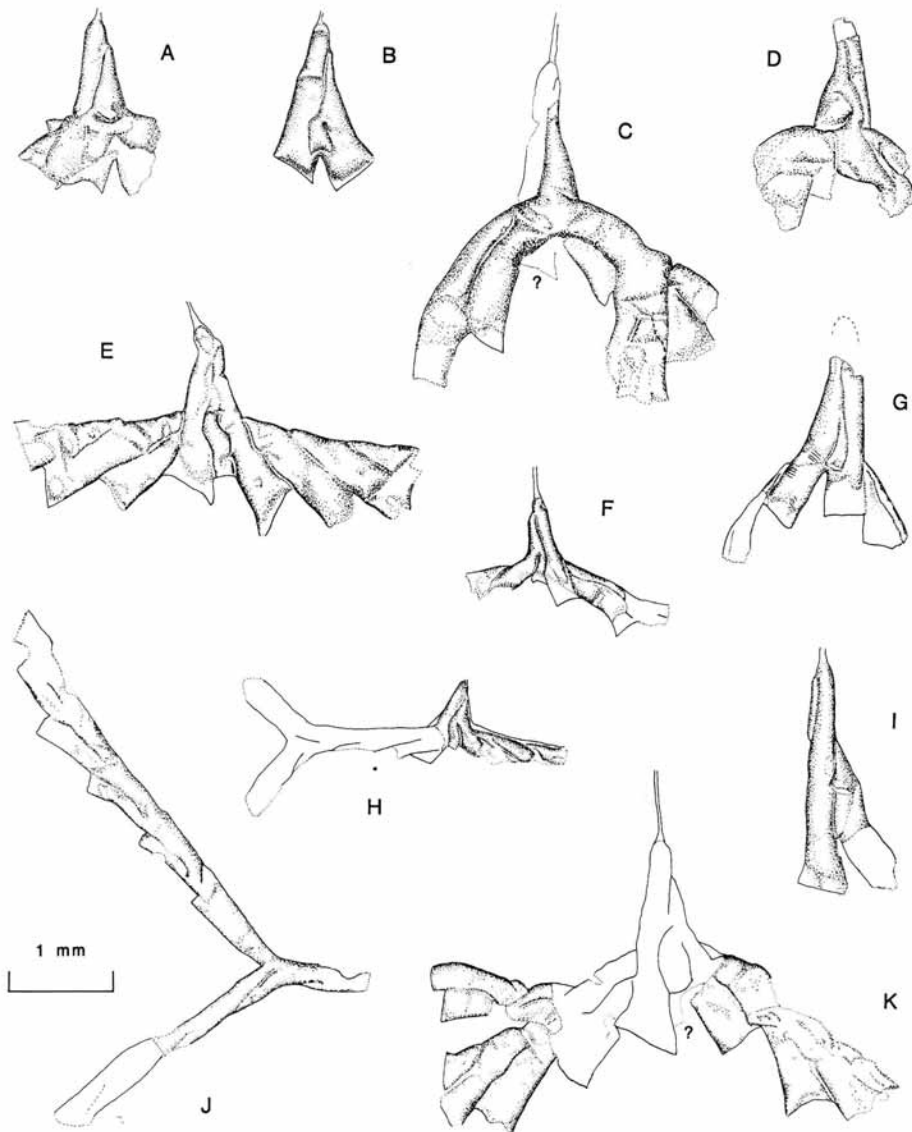
Relief specimens of unknown affinity. Text-figures 17 and 18 show some of the immature relief specimens of various kinds that have been found at two levels in the Krapperup core, 147.66–147.72 m and 132.63–132.66 m, i.e. close to the bases of the *A. murrayi* and *H. copiosus* Zones. At both levels all specimens in obverse view show a sicular bitheca. The stipes are mostly too incomplete to show presence or absence of bithecae. Specimens with bithecate stipes are present at the lower level (Text-fig. 17D), as well as possibly triradiate forms (Text-fig. 17E). The specimens are of extensiform, declined, and pendent types. Because stipes are incomplete, it is also difficult to say how many branchings the mature specimens would have had, but some of the pendent forms may belong to *A. murrayi* (Text-fig. 18C).

Kiaerograptids or didymograptids? The lower part of the Krapperup core, mainly below the level of the *Hunnegraptus* fauna, contains several badly preserved specimens that are declined to deflexed. They are seldom very big, mostly containing 5 thecae per stipe or less, but it seems unlikely that they would have branched further, had they lived longer. Because of their flatness (bithecae undetectable) and the short stipes (immaturity), their identity is uncertain.

The earliest T. phyllograptoides. This species does not belong in the fauna under discussion, but is present in the succeeding *T. phyllograptoides* Zone. It appears right at the base of its zone in Slemmestad, but some of the earliest specimens found there, in the lowermost metre, deviate from the typical form described by Cooper and Lindholm (1985). As seen in Text-figure 14E, H, some of the specimens could be three-stiped. Preparation gave no evidence of a fourth stipe. The atypical specimens also differ in having considerably narrower stipes (1.3–1.6 mm) and fewer thecae (2–4) in the conjoined part of the stipes. Only one specimen with normal width of stipes was found in the lowermost horizon at Grundvik, Slemmestad. Some specimens also have slightly less strongly reclined stipes.

So far, only 13 specimens (all belonging to the Lund collections) have been found this low, at three different localities, in the Slemmestad area: 3 specimens from 6.25 m above the Ceratopyge Limestone at Hagastrand; 8 specimens from 2.50 m above the missing part at Grundvik (c. 10 cm higher than Hagastrand) and one specimen 12 cm higher; finally one specimen from about 80 cm higher than the lowest Grundvik level at the Rortunet section.

In the Krapperup core, some weakly reclined tetragraptids are found a couple of metres below the first find of *T. phyllograptoides*. They are mostly very short-stiped, and no species identification has been attempted.



TEXT-FIG. 18. Relief specimens, all (and more) associated on one surface, near the base of the *H. copiosus* Zone, Krapperup core, 132.63–132.66 m, LO 6085t–6095t. A, B, D, E, G, I, K, Graptoloidea indet. spp; B shows a typical symmetrical pair formed by the sicula and th 1¹, with the bitheca in the centre; E has no bithecae along the stipes; I shows th 1¹ growing around the sicula; in K, the proximal part is a mould; all specimens in obverse view show a sicular bitheca. C, *?Araneograptus murrayi* (J. Hall), the stipes are of dichograptid type. F, J, *H. copiosus* sp. nov. H, cf. *H. copiosus*; the apex of the sicula points somewhat downwards. J and K were made from latex casts, C and E from combinations of counterparts. All illustrations were made under vertical light.

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