THE ORDOVICIAN GRAPTOLITES *AZYGOGRAPTUS* AND *JISHOUGRAPTUS* IN SCANDINAVIA AND BRITAIN

by A. J. BECKLY *and* JÖRG MALETZ

ABSTRACT. Two groups within *Azygograptus* are identified on the presence or absence of adpressed growth of th 1^1 along the sicula. The second group has an unusual facies association and this is interpreted to reflect adaptation to a shoreward, and possibly *r*-selective environment. Adaptation to such an environment is argued to have the potential to affect proximal development and consequently the evolutionary origins of this group are obscure. The subgenera previously erected are not used because of difficulties with the type species. Features of the proximal development are the main characters used to distinguish the species, and all the previously named Scandinavian and British species are redescribed except for *A. coelebs* for which no reliable specimens can be found. Three new species are described, *Azygograptus minutus*, *Jishougraptus novus* and *J. lindholmae*. *Jishougraptus* is recognized for the first time outside China, and the first specimens of *Azygograptus* from South America are illustrated.

THE genus *Azygograptus* was established by Nicholson (1875) with *A. lapworthi*, from the Skiddaw Slates of the English Lake District, as the type species. The single-stiped morphology and simple thecal form make the genus easily recognizable, but the differences between species are relatively subtle and identification has been further complicated by the lack of modern descriptions for many of the species from Scandinavia and Britain. This paper redescribes the type material for the species from these areas, and three new species are described from Scandinavia, two of which are placed in *Jishougraptus*. A summary of the other species that have been placed in *Azygograptus*, but which are not described in this paper, is given, with a brief comment on their probable validity as species and placement in *Azygograptus*.

Azygograptus has been recognized as one of the most characteristic genera of the Atlantic Province during the Arenig (Skevington 1973), and Fortey (1984) suggested that the genus belonged to the epiplanktonic fauna which allowed it to penetrate more shoreward than other graptolite genera (Fortey and Owens 1987, p. 278; Chen and Yang 1987, fig. 2*a*). We examine the distribution of the genus not only with regard to palaeogeography, but also with respect to facies association. This provides a guide to the ecology of the genus from which its evolution and biostratigraphic usefulness are reviewed.

DISTRIBUTION

Facies association

Biofacies association. In Wales *Azygograptus* is generally the first graptolite to occur in the transgressive succession above the basal Arenig unconformity, where it commonly forms abundant, monospecific assemblages (Fortey and Owens 1987; Beckly 1987). Locally *Azygograptus* is replaced in this position by extensiform graptolites comparable to *D. simulans* (Beckly 1985; Zalasiewicz 1986) which share a number of characteristics with *Azygograptus*: low thecal inclination, metasicular origin of th 1^1 (Beckly 1985) and the production of synrhabdosomes (Zalasiewicz 1984).

The relationship of the Welsh occurrences to the trilobite communities identified by Fortey and Owens (1978) also indicates a position low in a transgressive succession (Text-fig. 1). *Azygograptus* typically occurs shortly above sandstone beds that either yield a fauna indicative of the *Neseuretus*

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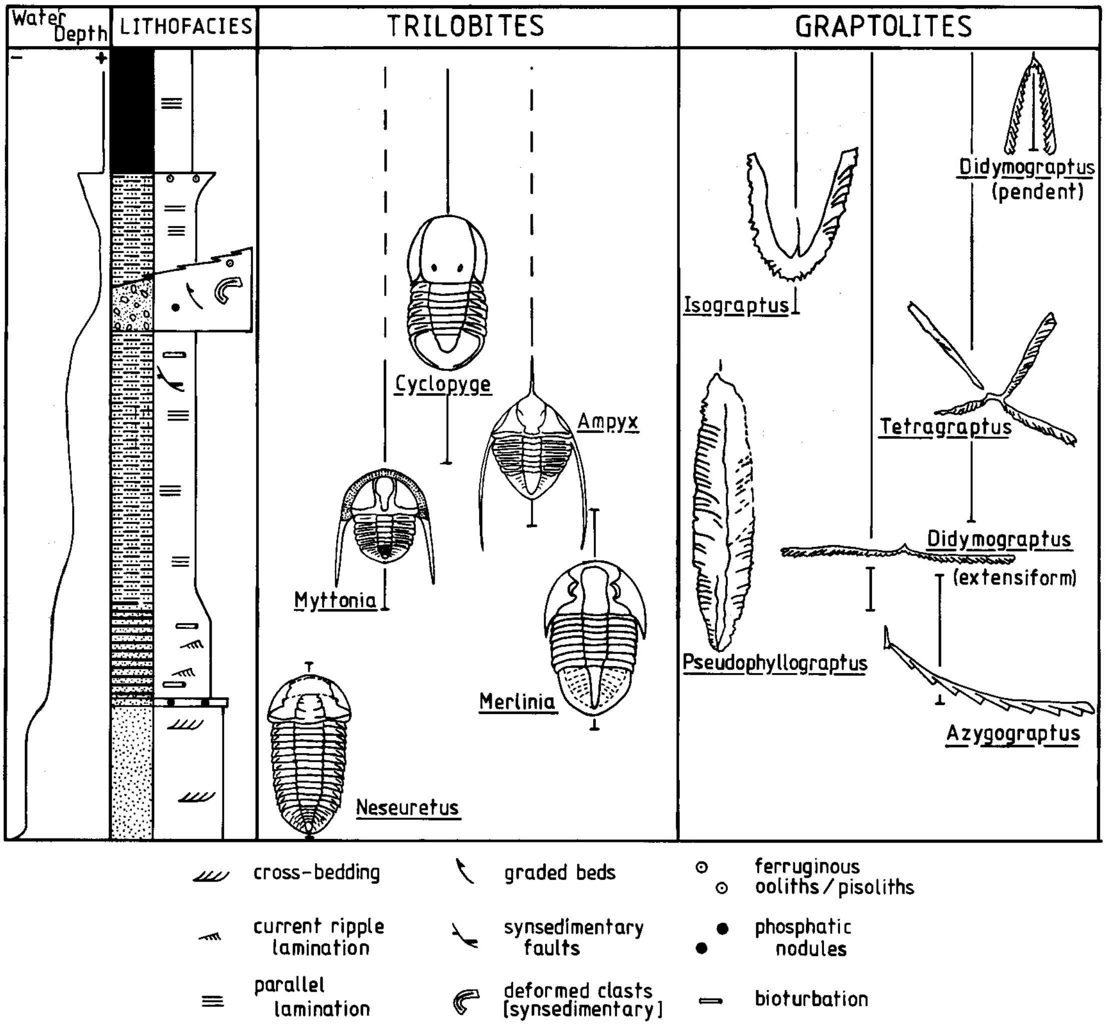


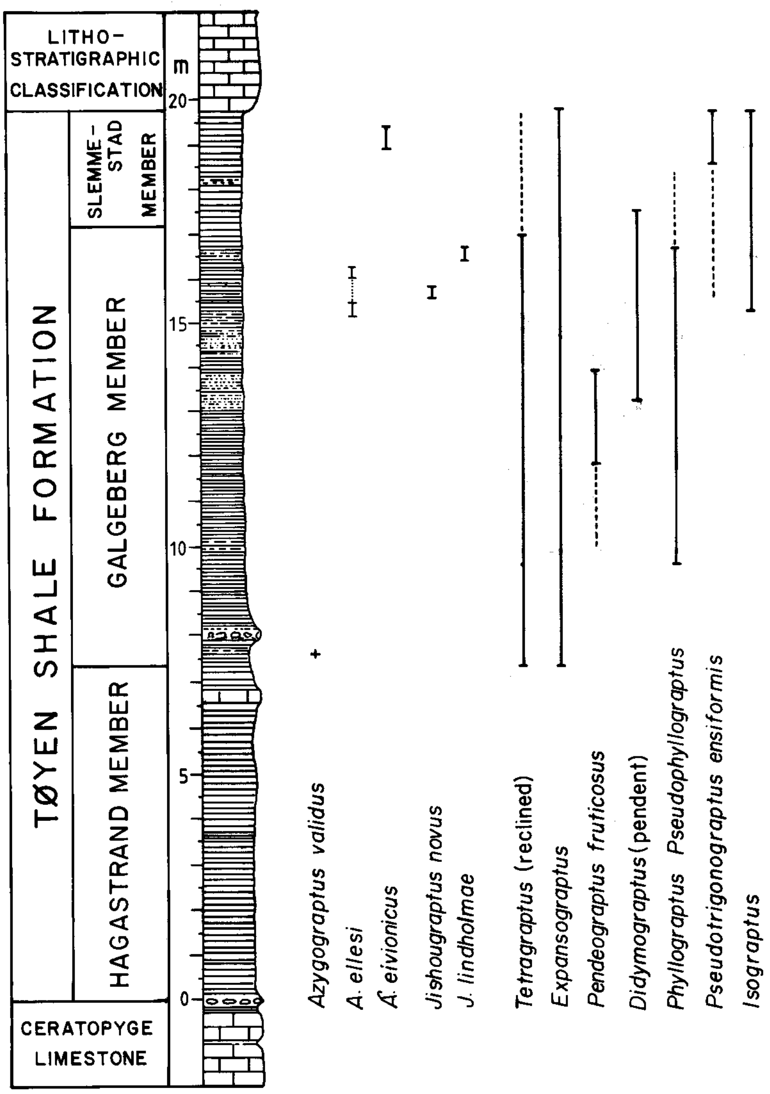
TEXT-FIG. 1. Graptolite and trilobite distribution within the Arenig transgressive succession of North Wales.

Community (e.g. Bangor Area) or for which it is implied by the presence of *Cruziana* (cf. Fortey and Morris 1982): in the Arenig area rare specimens of *Azygograptus* are associated with a *Neseuretus* fauna. The raphiophorid community generally overlies the occurrences of *Azygograptus* in North Wales and the associates of *A. eivionicus* in the Aberdaron Area (see *A. eivionicus*, p. 904) suggest a position at the shoreward limit of this community.

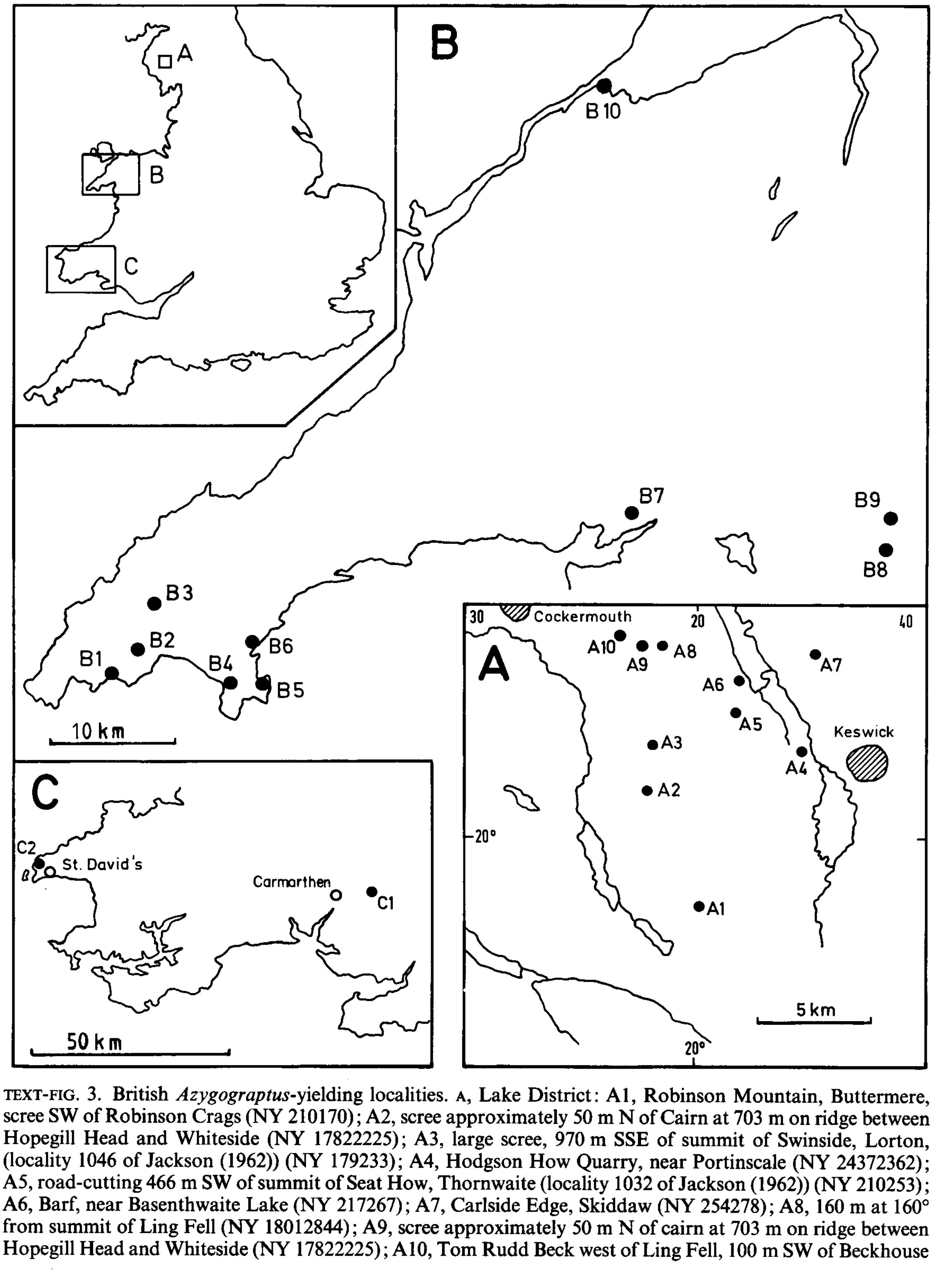
These occurrences contrast with those of *Azygograptus* in Scandinavia where the genus is generally associated with diverse graptolite faunas, which occasionally indicate the deep water isograptid biofacies (cf. Fortey and Cocks 1986). However, *A. eivionicus* is the only species common to both areas and in the Tøyen Shale this species occurs just below the Orthoceras Limestone, which has been taken as indicative of a regressive eustatic event (Fortey 1984). *A. suecicus* appears to have a more restricted distribution and to have a positive association with *I. gibberulus sensu* Moberg, which may reflect some degree of biofacies association.

In the English Lake District *Azygograptus* occurs in both low diversity to monospecific assemblages and as a member of more diverse faunas. However, even among the more diverse faunas *Azygograptus* tends to occur as fairly abundant populations on certain bedding-planes from which other species are absent or rare. In addition, adjacent graptolite assemblages are often slightly unusual and difficult to correlate (e.g. Barf and Hodgson How Quarry), and may reflect a slightly different biofacies. Interestingly, *D. simulans*, which appears to favour a similar facies to *Azygograptus* in North Wales, also occurs at Barf. The only suggestion of association with a more oceanic biofacies is the presence of a juvenile isograptid from Hodgson How Quarry, but this cannot be taken as diagnostic and *Azygograptus* and isograptids are generally not associated in the Lake District.

Lithofacies association. Azygograptus occurs mainly in three different lithofacies: (1) flaggy sandstone facies (cf. Beckly 1987); (2) turbidite sandstone beds interbedded with siltstone; (3) massive siltstone or mudstone.



TEXT-FIG. 2. Graptolite distribution within the Tøyen Shale Formation of Oslo. Lithological column after Erdtmann (1965).



TEXT-FIG. 3. British *Azygograptus*-yielding localities. A, Lake District: A1, Robinson Mountain, Buttermere, scree SW of Robinson Crags (NY 210170); A2, scree approximately 50 m N of Cairn at 703 m on ridge between Hopegill Head and Whiteside (NY 17822225); A3, large scree, 970 m SSE of summit of Swinside, Lorton, (locality 1046 of Jackson (1962)) (NY 179233); A4, Hodgson How Quarry, near Portinscale (NY 24372362); A5, road-cutting 466 m SW of summit of Seat How, Thornwaite (locality 1032 of Jackson (1962)) (NY 210253); A6, Barf, near Basenthwaite Lake (NY 217267); A7, Carlside Edge, Skiddaw (NY 254278); A8, 160 m at 160° from summit of Ling Fell (NY 18012844); A9, scree approximately 50 m N of cairn at 703 m on ridge between Hopegill Head and Whiteside (NY 17822225); A10, Tom Rudd Beck west of Ling Fell, 100 m SW of Beckhouse

The flaggy sandstone facies comprises thinly interbedded and interlaminated fine sandstone and siltstone. The sandstone laminae are often lenticular and show ripple cross-lamination, whilst bioturbation is moderately abundant but is predominantly parallel to bedding. This is the typical facies in which *Azygograptus* is found in North Wales and generally occurs between an underlying cross-bedded sandstone unit and overlying parallel laminated siltstone (see Text-fig. 1). This, and the nature of the facies suggest deposition in a shelf setting, probably below normal wave base (Beckly 1987).

The other two lithofacies generally suggest a deeper water depositional environment, with the exception of the silty mudstone in which *Azygograptus* occurs in the Aberdaron Area. This is comparable to the flaggy sandstone facies in both its stratigraphic position and associated biofacies, and is thought to have been deposited in a similar environment which was starved of coarser clastic material (Beckly 1987).

The shales in which *Azygograptus* occurs in Scandinavia, are predominantly dark in colour, and sandstone is generally absent. In the Tøyen Shale Formation (Text-fig. 2), *A. eivionicus* occurs in the slightly paler, greenish, Slemmestad Member, and the occurrences of *A. suecicus* in Scania are in yellowish-green shale.

Though much of the material from the Lake District is derived from screes, an indication of the lithofacies is provided by the slabs on which the specimens occur, and *Azygograptus* is predominantly associated with sandier lithologies, and not massive mudstone. Since graptolites are preserved on siltstone slabs the association is not a function of the less penetrative deformation in sandy lithologies. In-situ occurrences further support this with the appearance of *Azygograptus* locally associated with the incoming of sandy beds and laminae (A. W. A. Rushton pers. comm.). The two populations collected from Hodgson How Quarry both occur in parallel laminated, micaceous, fine sandstone, whilst the interbedded mudstone is virtually barren of graptolites.

The significance of the association with turbidite beds is less clear because the amount of fragmentation appears inadequate for the material to have been transported by a turbulent flow. Alternative explanations are:

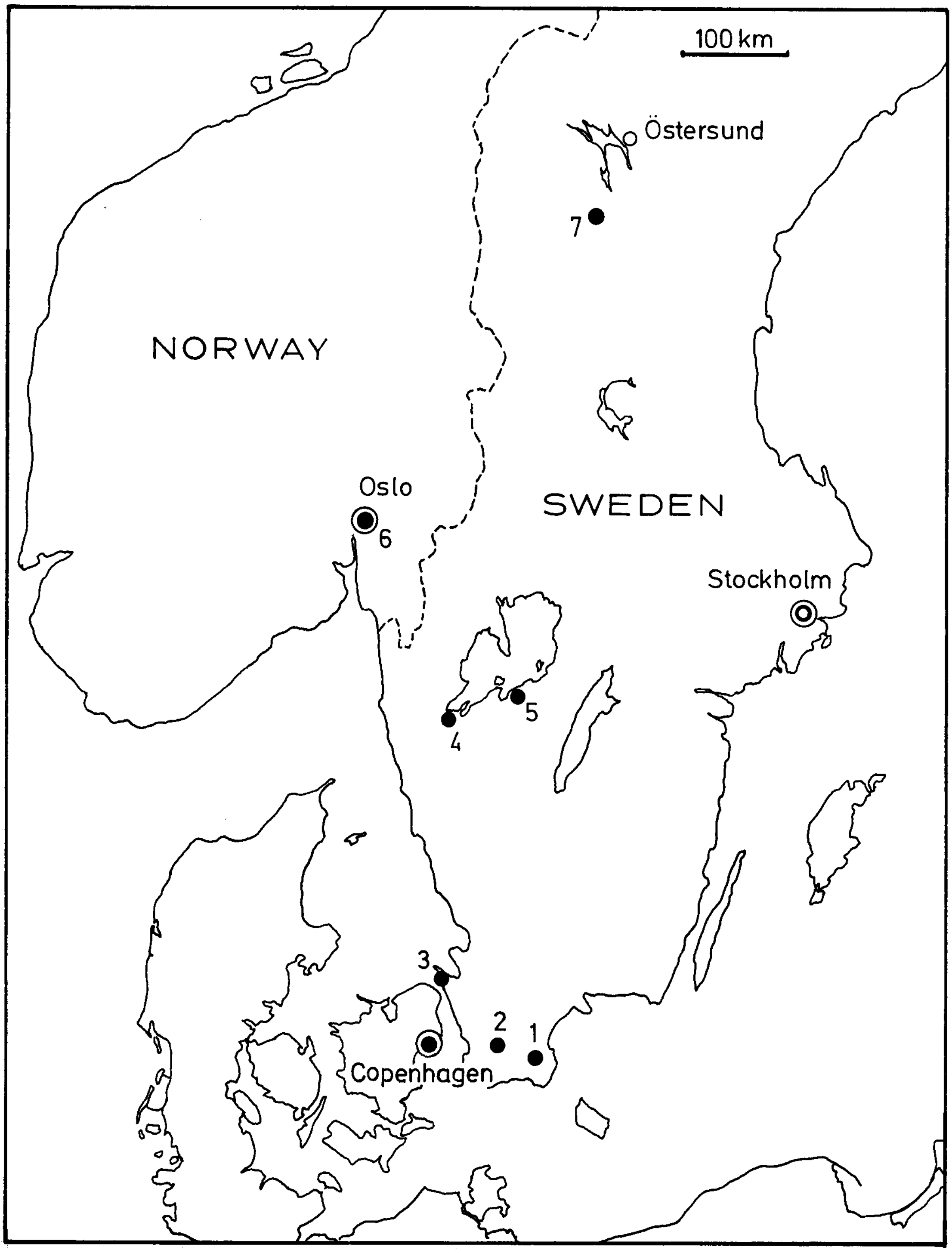
1. *Azygograptus* was carried into the area of deposition by processes affecting the higher part of the water column which have a functional relationship to the turbidite flows, but this still fails to explain the absence of other graptolites.
2. Rapid burial by the sandstone beds allowed preservation on an oxic sea-floor, in an environment not favoured by other graptolites.
3. The turbidite beds reflect a change to an environment which *Azygograptus* favoured, e.g. increased turbidity of the water.

The common factor in all these explanations is a change in habitat to one which was favoured by *Azygograptus*, and the low diversity of many associated faunas suggests the change was disadvantagous to most other graptolite species.

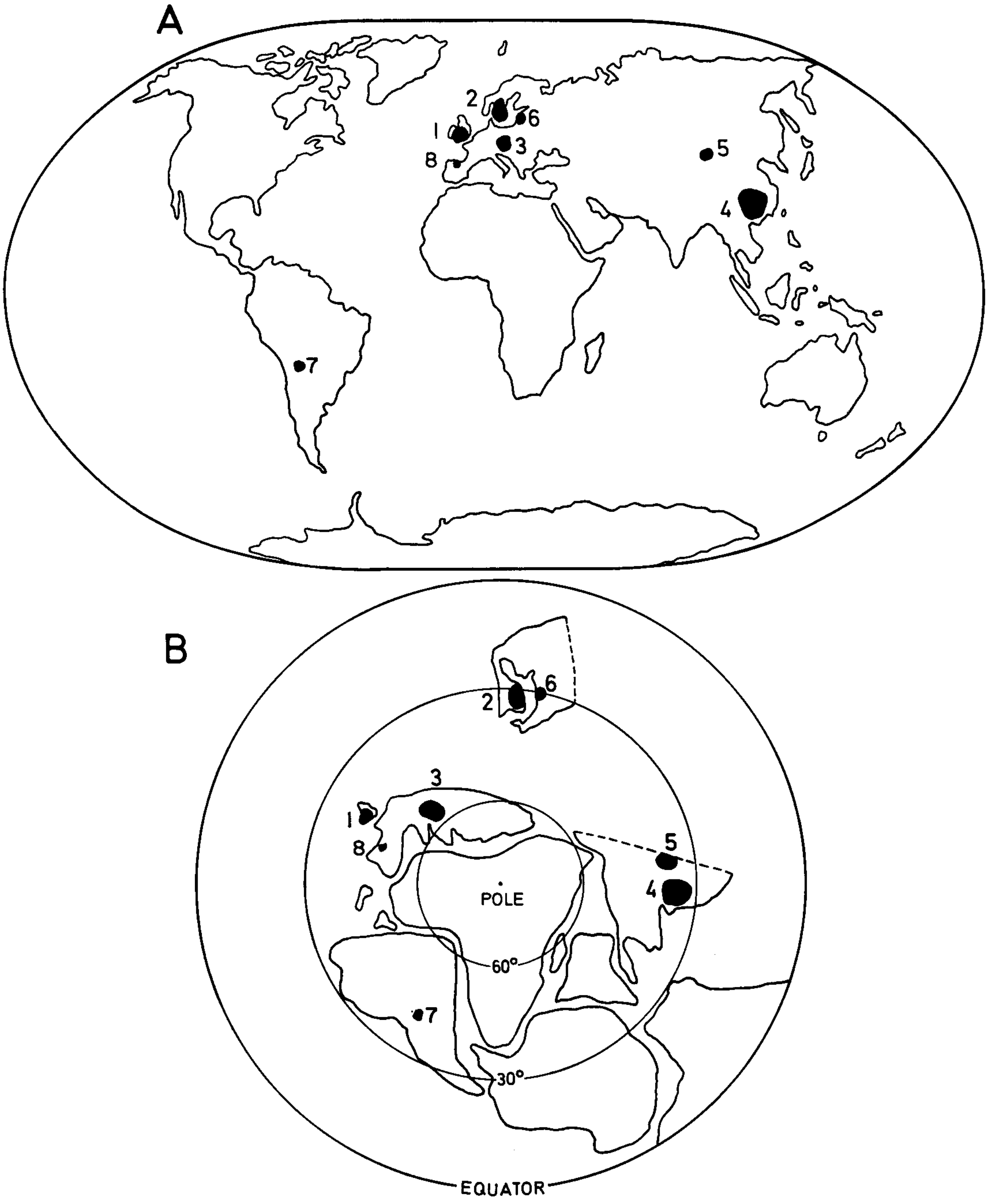
Geographical distribution

The *Azygograptus* yielding localities of Britain and Scandinavia are shown in Text-figures 3 and 4 respectively, whilst the global distribution is shown in Text-figure 5. When plotted on the same palaeogeographic reconstruction, *Azygograptus* shows a very similar distribution to the trilobite genus *Neseuretus* (cf. Fortey and Morris 1982, fig. 2). The major difference is that *Azygograptus* is not restricted to Gondwana but extends into Baltica. However, all occurrences lie above 30° latitude, and a high latitude position is now thought to characterize the Atlantic graptolite province.

Cottage (NY 16382898). B, North Wales: B1, Maen Gwenonwy (SH 20052596); B2, Rhiw (SH 22322847); B3, Bryncroes (SH 23173150); B4, Nant (SH 297293); B5, Penrhyn Dû (SH 31742653); B6, Castlemarch Farm (SH 31452980); B7, Penrhyndeudraeth (SH 616401); B8, scree on northern slopes of Moel Llyfnant, Arenig (SH 80793616); B9, above Hafotty Ffilltirgerig, Arenig (SH 81613960); B10, Bangor (SH585731 and SH 591726). C, South Wales: C1, Afon Ffinnant (SN 510198); C2, Whitesand Bay (SM 732274).



TEXT-FIG. 4. Scandinavian *Azygograptus* yielding localities. 1, Flagabro-Killeröd, Scania; 2, Fagelsang Boring, Scania; 3, Krapperup Boring, Scania; 4, Hunneberg Mountain, Västergötland (2 localities, Diabasbrottet (Mossebo of Törnquist 1901) and Mossebo (Maletz 1987)); 5, Kinnekulle, Västergötland (see Skoglund 1961); 6, Oslo Region (includes Slemmestad, Tøyen Underground Station); 7, Nipan, Jemtland.



TEXT-FIG. 5. Global distribution of *Azygograptus*. A, Present day geography. B, Lower Ordovician reconstruction (after Fortey and Morris 1982). 1, British occurrences (see Text-fig. 3) and SE Ireland (Brenchley and Harper 1967); 2, Scandinavia (see Text-fig. 4); 3, Bohemia (Bouček 1973); 4, SW China (Mu *et al.* 1979); 5, Gorny Altai (Obut and Sennikov 1984); 6, Middle East Baltic Area (Ulst 1976, pp. 214–221; Paškevičius 1976, p. 135); 7, near Tarija, southern Bolivia (new material); 8, Cantabria, northern Spain (Gutierrez Marco and Rodrigues 1987).

Ecology of Azygograptus

In both bio- and lithofacies associations, differences exist between the Scandinavian and British representatives of the genus. However, this may be largely explained by the predominance of *A. lapworthi* and *A. eivionicus* in Britain, compared to their virtual absence from Scandinavia. The facies association and position within the succession of *Azygograptus* in North Wales support the shoreward distribution advocated by Fortey and Owens (1987) but an epiplanktonic mode of life should result in the presence of *Azygograptus* in all graptolite faunas of the Atlantic province. This is not observed and therefore appears to be fairly good evidence that at least some species of *Azygograptus* favoured a shoreward environment.

The distribution of extensiforms similar to *D. simulans* is comparable to that of *Azygograptus* and both groups develop synrhabdosomes (Zalasiewicz 1984), suggesting these are also a feature with functional significance to the particular environment. Though the function of synrhabdosomes is uncertain, Zalasiewicz (1984) suggested they maximized breeding in temporary, highly favourable, conditions, implying an *r*-selective environment. Adaptation to an unstable environment may also, at least in part, explain the association of *Azygograptus* with sandstone beds in the Lake District.

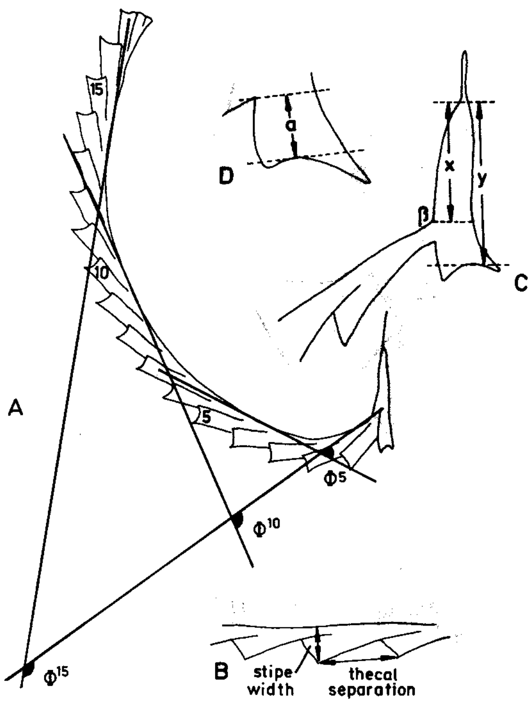
At Barf (Locality A6 of Text-fig. 3), *D. simulans* is associated with *A. ellesi*, a species more common in Scandinavia. However the Scandinavian occurrences, with the possible exception of *A. suecicus*, do not display significant differences in distribution to the majority of other graptolites. This may be a consequence of the different palaeogeographic position of Baltica (see Text-fig. 5B).

SYSTEMATIC PALAEONTOLOGY

Parameters used in descriptions. The measurements used in descriptions are summarized in Text-figure 6:

1. Basal free length of sicula (A on Text-fig. 6D). The distance along a line parallel to the dorsal sicula margin, between the aperture and the final point of contact of the first theca.

2. Stipe Divergence Angle (β on Text-fig. 6C). Angle between dorsal wall of sicula and dorsal wall of proximal part of stipe.



TEXT-FIG. 6. Parameters used in descriptions. A, entire rhabdosome; Φ^5, Φ^{10}, Φ^{15}, stipe rotation by each of these thecae. B, stipe detail showing stipe width and thecal separation. C, sicula: x, distance to origin of th. 1^1; y, sicular length; β, stipe divergence angle. D, detail of sicular aperture: a, basal free length.

3. Origin of th 1^1 is given as a fraction of the length of the sicula measured away from the apex (x/y on Text-fig. 6C).

4. Thecal Separation/Density. Thecal density is given as a recalculated value in thecae/10 mm, based on measurements of thecal separation: the distance between successive thecal apertures (see Text-fig. 6B).

5. Stipe curvature: Quantified as the degrees of rotation between lines tangential to the proximal and distal dorsal stipe margin, measured at th 5, th 10, th 15 etc. (see Text-fig. 6A).

Repositories of material mentioned. The following abbreviations are used to indicate where material mentioned is lodged: BU, University Museum, Birmingham; BGS, British Geological Survey, Keyworth; BM, British Museum (Natural History), London; IC, Imperial College, London (teaching collection); LO, Palaeontological Institute, University of Lund; NMW, National Museum of Wales, Cardiff; PMO, Paleontologisk Museum, Oslo; SGU, Sveriges Geologiska Undersökning, Uppsala; SM, Sedgwick Museum, Cambridge; TUB, Technische Universität Berlin.

Order GRAPTOLOIDEA Lapworth, 1875
Family DICHOGRAPTIDAE Lapworth, 1873
Subfamily AZYGOGRAPTINAE Mu, 1950

Diagnosis. Dichograptids with single stipe originating from th 1^1. The sicula bears two processes on aperture.

Discussion. Mu (1950) erected a monotypic family Azygograptidae containing *Azygograptus*, but since then a number of other genera have been established for single-stiped species: *Nicholsonograptus* Bouček and Pribyl, 1953, *Parazygograptus* Kozlowski, 1954, *Pseudazygograptus* Mu, Lee and Geh, 1960, *Hemiholmograptus* Hsu and Chao, 1976, and *Jishougraptus* Geh, 1988.

In all these genera the stipe is formed by th 1^1, except for *Parazygograptus* in which the stipe is based on th 1^2 and is pendent. This genus is founded on a single isolated specimen of the type species *P. erraticus* Kozlowski. In other respects this specimen is very similar to the co-occurring pendent *Didymograptus rozkowskae* Kozlowski and could therefore represent a broken rhabdosome. For this reason, *Parazygograptus* is tentatively regarded as a junior synonym of *Didymograptus*.

Nicholsonograptus was included within the Sinograptidae by Skevington (1966), Bulman (1970) and Bouček (1973). Wang (1975) placed *Nicholsonograptus* in his new family Paradidymograptidae though the necessity for this family is questionable. *Hemiholmograptus* is now regarded as a junior synonym of *Nicholsonograptus* (Geh 1988). *Pseudazygograptus* Mu *et al.*, 1960, with *A. incurvus* as the type species, was referred to the Virgellina by Fortey and Cooper (1986) on account of the prominent virgellar structure illustrated by Finney (1980). However, this structure seems to be an extended growth of the rutellum rather than a virgellar spine and inclusion of *Pseudazygograptus* within the Dichograpidae is therefore preferred.

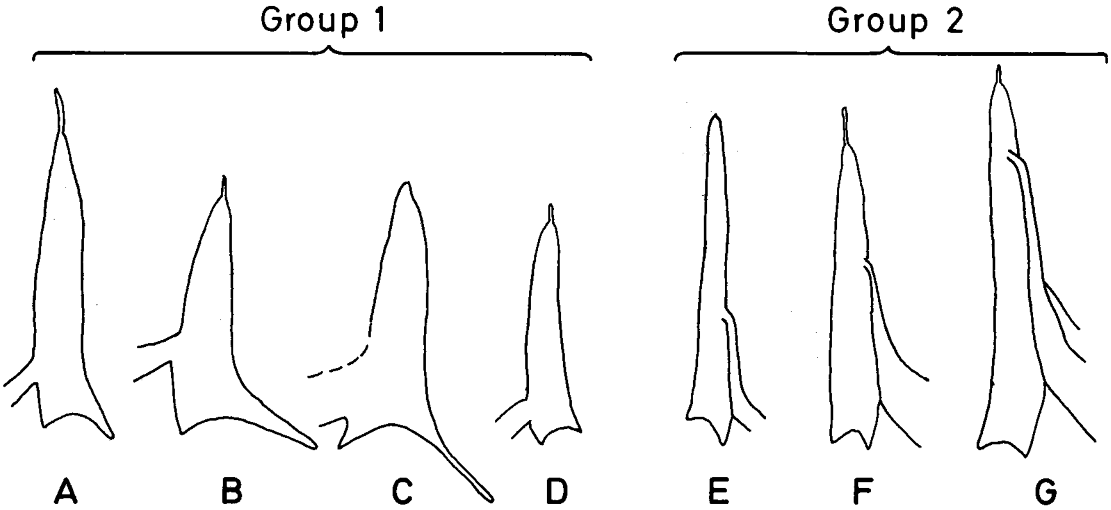
Genus AZYGOGRAPTUS Nicholson and Lapworth, *in* Nicholson, 1875

Type species. Azygograptus lapworthi Nicholson, 1875.

Diagnosis. Rhabdosome of single, uniserial, declined stipe originating from th 1^1. Stipe either straight or curved (causing stipe to be reclined in distal part). Thecae simple, elongate, conical and inclined at low angle to the dorsal margin.

Discussion. Elles and Wood (1902, p. 93) recognized three informal groupings of *Azygograptus* which Obut and Sennikov (1984) elevated to subgenera: *A.* (*Azygograptus*), *A.* (*Eoazygograptus*), and *A.* (*Metazygograptus*). One of the main characters on which these groups were based was the origin of th 1^1 and its growth relative to the sicula. Only two groups are recognized reliably by the present study on the presence or absence of adpressed growth of th 1^1 and the sicula (see Text-fig. 7). However, the named subgenera have not been used because of difficulties with the type species.

The type species of the subgenus *Metazygograptus* is *A. suecicus* but the characters of the Elles



TEXT-FIG. 7. Groupings of *Azygograptus* on proximal development (all ×20). Group 1 – lacking adpressed growth of th 1^1. Group 2 – with adpressed growth of th 1^1. Species illustrated are: A, *A. eivionicus*; B, *A. lapworthi*; C, *A. hicksii*; D, *A. suecicus*; E, *A. ellesi*; F, *A. minutus*; G, *A. validus*.

and Wood grouping (1902) were based on material from Barf, now thought to be *A. ellesi*. As a result *A.* (*Metazygograptus*) is a subjective junior synonym of *A.* (*Azygograptus*) which is characterized by the absence of adpressed growth on th 1^1 and the sicula.

The type species of *A.* (*Eoazygograptus*) is *A. coelebs* but no specimens adequate to confirm the character of this species have been found. The published descriptions (Elles and Wood 1902) would indicate placement in Group 2 (see Text-fig. 7), but until this can be confirmed the use of the subgenus is unsupported.

Azygograptus lapworthi Nicholson, 1875.

Pl. 1, fig. 2; Text-figs 10A–O, 11 A–E, 12

1875 *Azygograptus lapworthi* Nicholson, p. 270, pl. 7, fig. 2–2*c*.
1898 *Azygograptus lapworthi* Nicholson; Elles, p. 513.

EXPLANATION OF PLATE 1

Figs 1 and 11. *Azygograptus ellesi* Monsen. 1, SGU 7554; Nipan, Jemtland, ×10. 11, PMO 118.576; 16·25–16·42 m interval of Tøyen Section, Oslo, ×20.

Fig. 2. *Azygograptus lapworthi* Nicholson. SM A55166*a*; Castlemarch Farm, North Wales, ×20.

Figs 3, 4, 7, 8. *Azygograptus eivionicus* Elles. 3, NMW 85.16G.94; Garth Point, Bangor, North Wales, ×15. 4, 7, 8, Rhiw, North Wales; 4, BM Q5884, ×15; 7, BM Q5896, ×20; 8, SM A22601, ×10.

Fig. 5. *Azygograptus suecicus* Moberg. SGU 7895; Killeröd, Scania, ×8.

Figs 6, 9, 10. *Jishougraptus novus* sp. nov. Paratypes; from 16·15–16·25 m interval of Tøyen Section, Oslo, ×20. 6, PMO 118.582–3. 9, PMO 118.593. 10, PMO 118.588.

Figs 7 and 8. *Azygograptus eivionicus* Elles. Rhiw, North Wales. 7, BM Q5896, ×20. 8, SM A22601, ×20.

Figs. 11. *Azygograptus ellesi* Monsen. PMO 118.576; 16·25–16·42 m interval of Tøyen Section, Oslo, ×20.

Fig. 12. *Azygograptus minutus* sp. nov. SGU 7556 [paratype]; Diabasbrottet Section at 7·09 m level, Hunneberg Mountain, Västergötland, Sweden, ×20.

Fig. 13. *Azygograptus validus* Törnquist. SGU 7557; Diabasbrottet Section at 4·74 m level. Hunneberg Mountain, Västergötland, Sweden, ×15.

PLATE 1

BECKLY and MALETZ, *Azygograptus*, *Jishougraptus*

1902 *Azygograptus lapworthi* Nicholson; Elles and Wood, p. 93, text-fig. 54; pl. 13, fig. 1*a*–*b*.
1915 *Azygograptus lapworthi* Nicholson; Nicholas, pp. 112, 121.
1938 *Azygograptus eivionicus* Elles; Matley, p. 559.
1943 *Azygograptus lapworthi* Nicholson; Fearnsides and Davies, p. 253.
?1979 *Azygograptus lapworthi* Nicholson; Mu *et al*., pp. 109–110, pl. 38, figs 3–7.
1984 *Azygograptus lapworthi* Nicholson; Zalasiewicz, p. 427, fig. 2*e*–*f*.
1988 *Azygograptus lapworthi* Nicholson; Beckly, p. 325.

Diagnosis. *Azygograptus* with no adpressed growth of th 1^1 and sicula and basal free length of the sicula commonly exceeding 0·2 mm. Prominent rutellum on sicular aperture in some populations.

Type material. The original slab figured by Nicholson from Dover's collection has not been traced. Differing populations of *Azygograptus* are certainly present at the type locality, and there is no clear evidence on the level from which the original material came. A considerable amount of material from Hodgson How is present in many museum collections and the original slab may be amongst this.

Type locality. Hodgson How Quarry, Keswick, English Lake District (National Grid Reference NY 243236). The succession comprises turbidite sandstone beds, some over 30 cm thick, interbedded with siltstone. Two *Azygograptus* populations have been recovered during this study; one close to the base of the exposed section and the other about 20 m above, both from parallel laminated, micaceous sandstone. These populations show quite marked differences (see Text-figs 9 and 10) and further variations shown by some museum material suggest at least a third population. The lower of the *in situ* populations is sufficiently different to the original description to suggest it is unlikely to be topotype (see discussion).

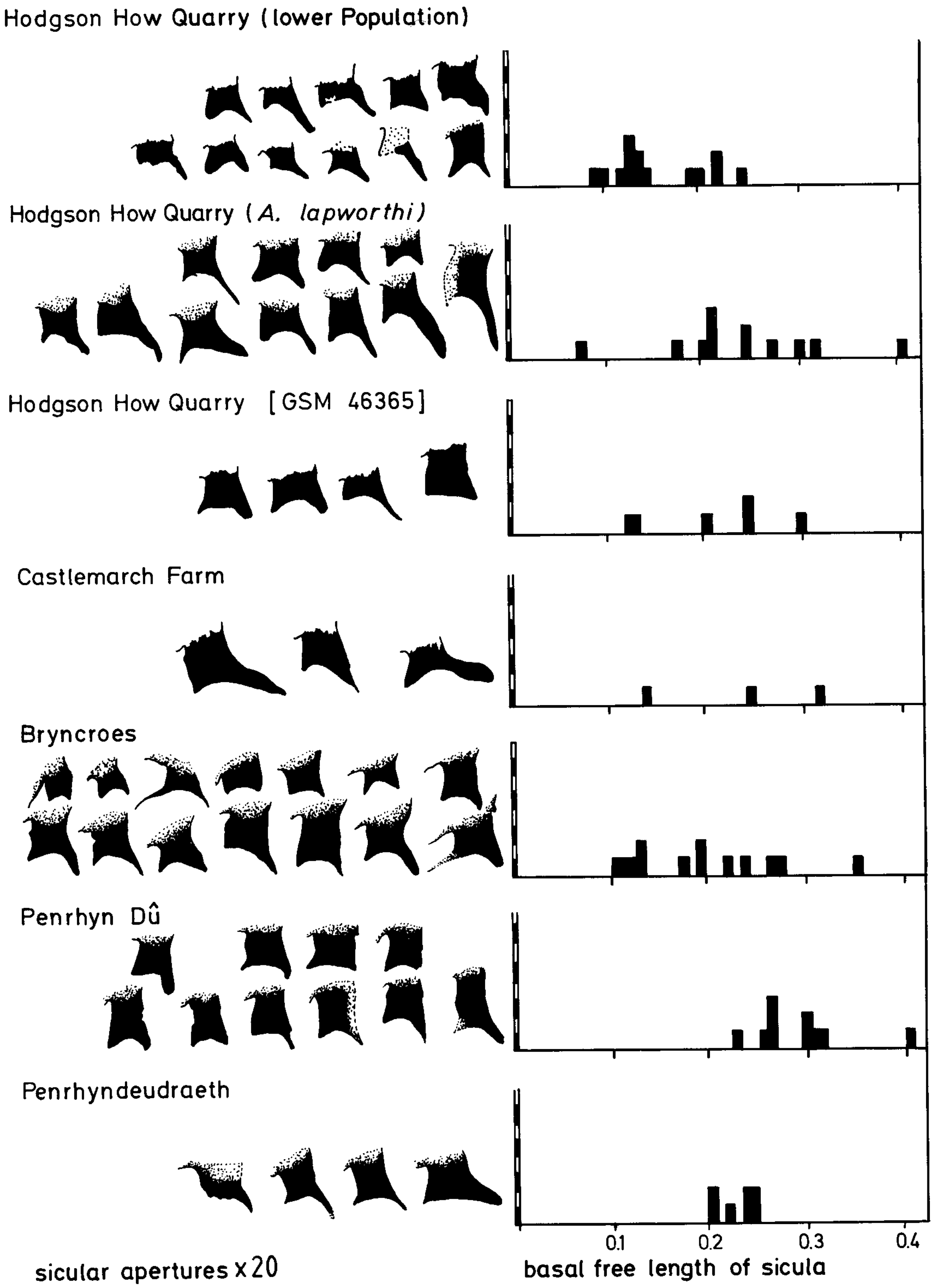
Jackson (1962) claimed the fauna from Hodgson How Quarry indicated the *nitidus* biozone, whilst Eastwood *et al*. (1968) claimed the assemblage was indicative of the *Dichograptus* biozone, a subdivision rejected by Jackson (1962). Material collected during this study, which includes *D. hirundo* and a juvenile '*Isograptus*', indicates a higher horizon and probably the *gibberulus* biozone. Lower *in situ* population: BM Q5630–Q5631. Higher *in situ* population: BM Q5108–Q5117.

Other occurrences.

1. Carlside Edge (locality A7 of Text-fig. 3). A poorly preserved fauna in micaceous grey siltstone. BM P7211–P7212, P7218.
2. Castlemarch Farm, North Wales (SH 31452980) (locality B6 of Text-fig. 3). Sparse fauna, occasionally preserved in partial relief. Only faunal element known. SM A55166; NMW 85.16G. 73–74.
3. Penrhyn Dû (locality B5 of Text-fig. 3); 1·5 km south-southeast of Abersoch (NGR SH 31742653) (Localities η_3 and η_4 of Nicholas 1915, pl. 13). Material comes from the 'Transition Beds' between the St Tudwal's Sandstone and Llanengan Mudstone (cf. Nicholas 1915). The lithofacies is typical of the 'flaggy sandstone facies' and the population forms a monospecific assemblage. NMW 85. 16G. 122–124.
4. Small Valley 400 m west of Bryncroes (SH 23173150) (locality B3 of Text-fig. 3) Abundant population forming monospecific assemblage in 'flaggy' sandstone facies of Sarn Formation (Beckly 1988). BM Q5876–Q5879.
5. Abandoned mine workings just north of Penrhyndeudraeth (SH 616401) (locality B7 of Text-fig. 3). Termed Pant-y-wrach Beds by Fearnsides and Davies (1943), who mention a fauna comprising *A. lapworthi* and *Phyllograptus angustifolius*. Only specimens of *A. lapworthi* have been examined and these occur in parallel laminated coarse siltstone. All specimens have been collected from the spoil of the mine workings. NMW 8516G.121; BGS Z1672; IC 1514.
6. Near Tarija, southern Bolivia. Few specimens as monospecific assemblage, preserved as silvery periderm in grey silty mudstone. The succession comprises 4,500 m of shale with few sedimentary structures, and all other graptolites found indicate a lower to middle Arenig age, TUB BOL 387P 01–05.

Description. Sicula 1·0–1·5 mm long and 0·2–0·35 mm wide at aperture excluding ventral lip (see Text-fig. 8). Stipe originates at about 0·7 of sicular length and diverges immediately at an angle of about 135–140°. Prominent basal free length to sicula up to 0·45 mm long and often greater than 0·2 mm.

Stipe moderately flexed with rotation by th 5 between 15° and 30° but ranging up to 55° by th 10 or th 15. Rhabdosomes up to 30 mm long observed but 50 mm has been claimed (Elles 1898). Initial stipe width at first theca about 0·5 mm or less but rapidly increases to fairly constant width 0·8–1·05 mm. Maximum widths in



TEXT-FIG. 8. Sicular apertures and basal free length histograms for different populations of *Azygograptus lapworthi*.

excess of 1 mm are more characteristic of longer stipes and may indicate a slow distal stipe expansion. Thecal spacing 1·2–1·6 mm; thecal density 6–9 th/10 mm; thecal inclination 10–12°; thecal overlap a little over one-third. Thecal density and overlap generally increase over the first few thecae. One specimen from Penrhyndeudraeth (Text-fig. 10G) has some thecae with apertures isolated by a notch about 0·2 mm deep.

Zalasiewicz (1984) described a synrhabdosome of *A. lapworthi* from Hodgson How. Another possible synrhabdosome has been recognized during this study in the population from Bryncroes (Text-fig. 12). It appears to comprise predominantly juvenile rhabdosomes and is more unidirectional than the example from Hodgson How.

Discussion. The narrower stipe and higher thecal density serve to distinguish *A. lapworthi* from *A. hicksii* (Text-fig. 15), but stipe characters are inadequate to distinguish it from *A. eivionicus*, with only slightly greater stipe width in *A. lapworthi*. Distinction of *A. lapworthi* from *A. eivionicus* is therefore dependent on features of proximal development and in particular the basal free length of the sicula, which in *A. eivionicus* only rarely exceeds 0·2 mm (Text-fig. 9). A more prominent rutellum (see Text-fig. 8) and shorter sicula also distinguish some populations of *A, lapworthi* but these characters are not always developed. *A suecicus* is distinguished by the absence of a rutellum.

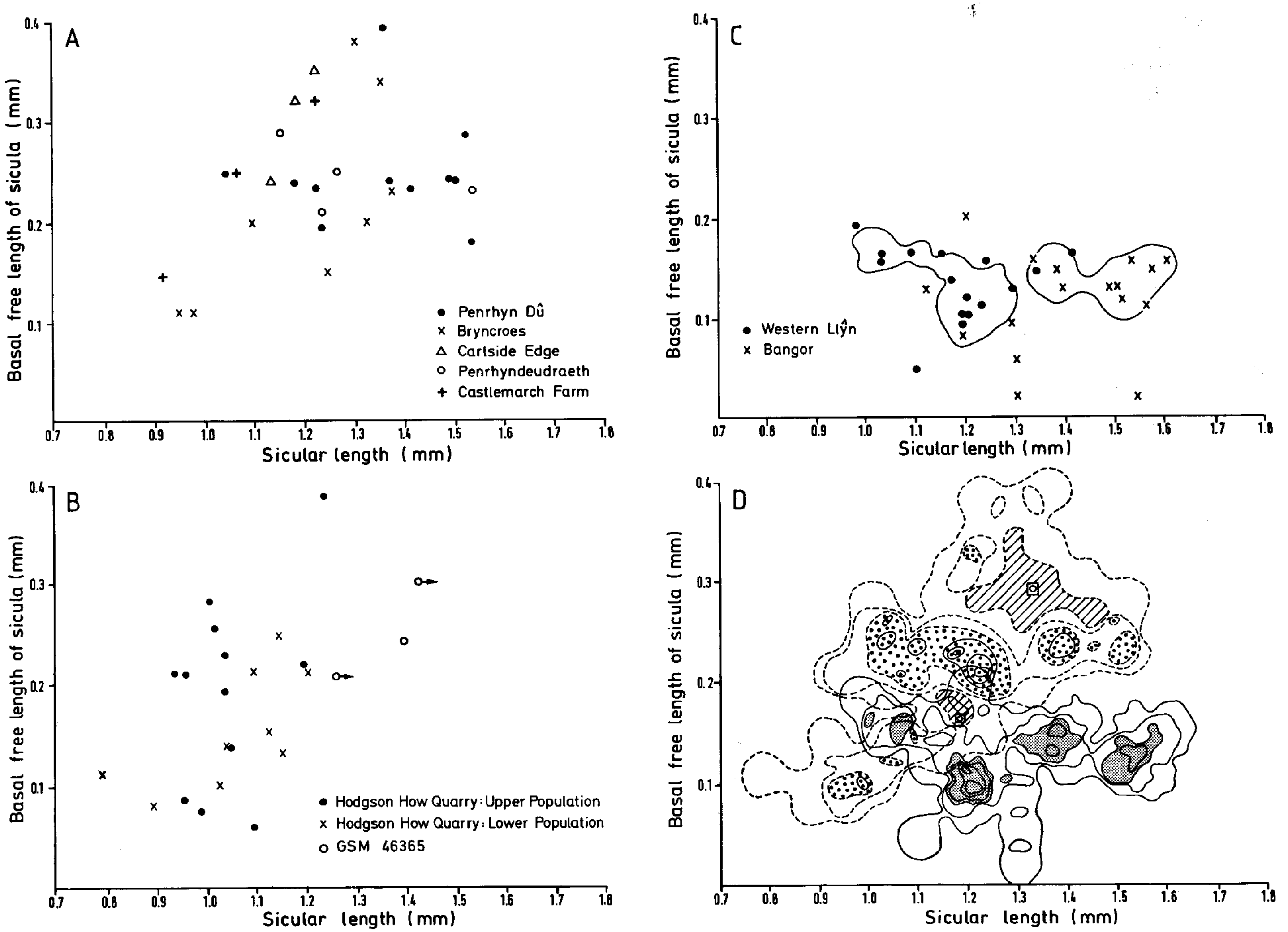
The majority of published descriptions of *A. lapworthi* (Nicholson 1875; Elles 1898; Elles and Wood 1902) have been based on material from the type locality, and therefore synonymy is assumed. Despite this direct comparison, there are quite significant differences in the values quoted, particularly sicular length. The value given by Nicholson (1875) in the original description was 1·05 mm, but Elles (1898) and Elles and Wood (1902) quoted values of 1·26 mm and 1·5 mm respectively.

These differences may be largely explained by the presence of more than one population at the type locality, and that more than one form of the species may exist. The population from the base of the exposed succession in Hodgson How Quarry has lower thecal separation (1·1–1·3 mm) and narrower stipes (0·4–0·5 mm, max. 0·75 mm) than is typical of either *A. eivionicus* or *A. lapworthi*, though the longest only reaches th 7. The sicular characters are a mixture of those seen in *A. eivionicus* and *A. lapworthi* (see Text-fig. 9) with the basal free length ranging above 0·2 mm, though predominantly less, and a sicular length of about 1 mm. The population is more similar to *A. eivionicus* but with some aspects of a transitional form.

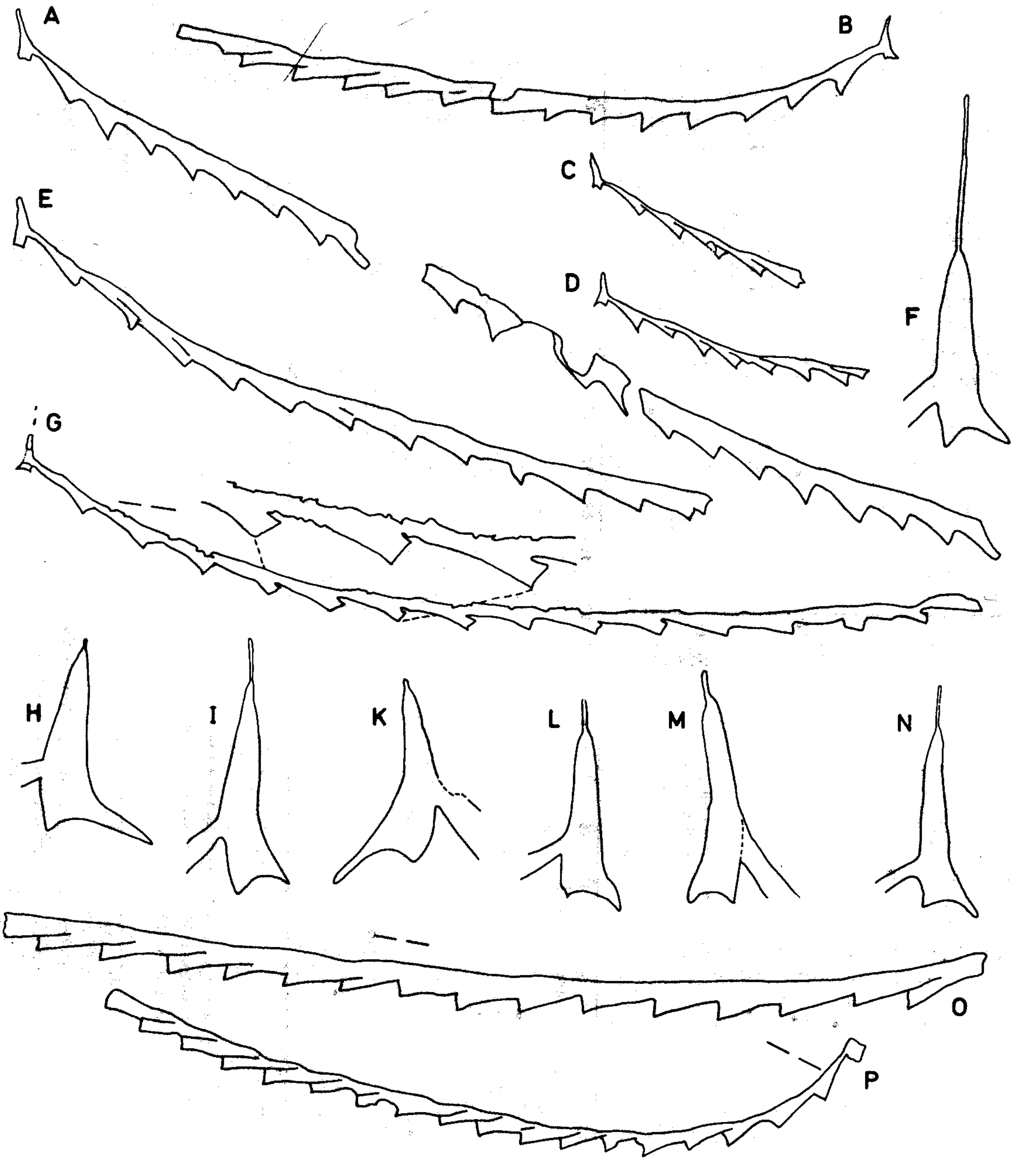
The population from 20 m above is characterized by a short sicula, about 1·0 mm long, significant basal free length to the sicula and a very prominent rutellum (see Text-figs 8 and 9). However, indications of at least a third population are provided by a slab in the BGS collections (GSM 46365) in which the sicular length ranges up to 1·5 mm and there is only slight development of a rutellum, but with a significant basal free length. The specimen is labelled *A. lapworthi* in Nicholson's handwriting.

These differences appear subtle but similar variation is shown by the occurrences in North Wales. Though few specimens are available, the population from Castlemarch Farm shows the prominent rutellum associated with a sicular length of about 1 mm. However the other three North Wales populations lack the prominent rutellum, and have a sicular length ranging up to 1·5 mm. Since both these forms appear to occur at the type locality, either could be the true type-population. The original description is also inadequate to distinguish them, since it combines short sicular length with a poorly developed rutellum. For these reasons the species is broadly defined on the basal free length of the sicula only.

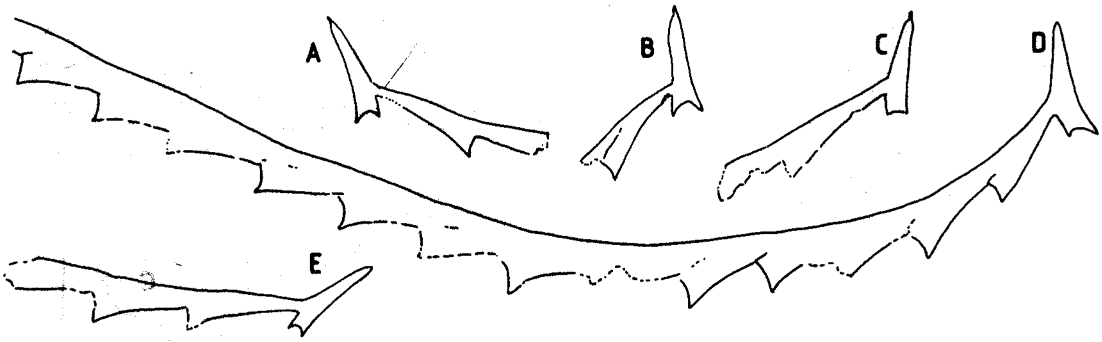
The only confirmed occurrence of *A. lapworthi* from outside Britain is the new material from Bolivia (Text-fig. 11). The basal free length of the sicula clearly places this population in *A. lapworthi* but the stipe width appears to be greater than in the British populations. The material described by Mu *et al.* (1979) from China as *A. lapworthi* may also belong to the species. From translations provided by Chen Xu, they quote a sicular length of 1·6 mm and for which a basal free length of 0·4 mm may be inferred. However, it is unclear from the description whether there is adpressed growth of th 1^1 and the sicula; th 1^1 is described as growing 'downward and outward'.



TEXT-FIG. 9. Cross-plots of sicular basal free length and sicular length for *Azygograptus lapworthi* and *A. eivionicus*. A, *A. lapworthi* populations other than from the type locality. B, *Azygograptus* populations from Hodgson How Quarry (type locality for *A. lapworthi*). C, *A. eivionicus* populations from Western Llŷn and Bangor (areas of densest distribution for each population outlined). D, comparison of density contouring for all the populations of each of the species: *A. eivionicus* contours are shown in solid lines with the areas of densest distribution highlighted in fine stipple; *A. lapworthi* contours are shown in dashed lines with areas of densest distribution highlighted with heavy stipple (internal areas of zero density for *A. lapworthi* are cross-hatched).



TEXT-FIG. 10. *Azygograptus lapworthi* Nicholson. A, B, BM H3365, Hodgson How Quarry, ×5. C, BM Q6331, Hodgson How Quarry, lower population, ×5. D, BM Q6330, Hodgson How Quarry, lower population, ×5. E, BM Q5876, Bryncroes ×20. F, BM Q5877, Bryncroes, ×5. G, BGS Z1672, Penrhyndeudraeth, ×5 (detail ×20). H, BM Q5879, Castlemarch Farm, ×20. I, BM Q5877, Bryncroes, ×20. K, BM Q5110, Hodgson How Quarry, higher population, ×20. L, BM Q6331, Hodgson How Quarry, lower population, ×20. M, NMW 85.16G.124, Penrhyn Dû, ×20. N, IC 1514, Penrhyndeudraeth, ×20. O, NMW 85.16G.123. P, NMW 85.16G.122, different distal stipe morphologies, Penrhyn Dû, ×5.



TEXT-FIG. 11. *Azygograptus lapworthi* Nicholson; from near Tarija, southern Bolivia, × 10. A, TUB BOL387P 01. B, TUB BOL387P 02. C, TUB BOL387P 03. D, TUB BOL387P 04 (× 10). E, TUB BOL387P 05.

Azygograptus hicksii (Hopkinson *in* Hopkinson and Lapworth, 1875)

Text-fig. 13A–C

1875 *Tetragraptus hicksii* Hopkinson *in* Hopkinson and Lapworth, p. 651, pl. 33, fig. 12*a–d*.
1902 *Azygograptus hicksii* (Hopkinson); Elles and Wood, p. 94, text-fig. 55*a–b*; pl. 13, fig. 2*a–e*.
1987 *Azygograptus hicksii* (Hopkinson); Fortey and Owens, p. 275, text-fig. 128*b–c*.

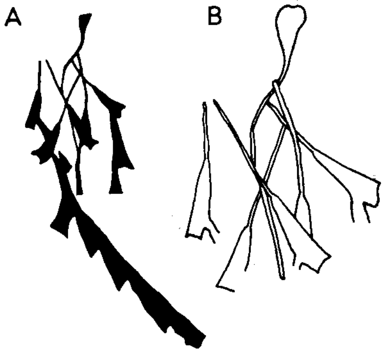
Diagnosis. *Azygograptus* with larger stipe than other species: maximum stipe width 1·0–1·5 mm, thecal density 4–6 th/10 mm. Sicular aperture with elongate rutellum. No adpressed growth of th 1^1 and sicula.

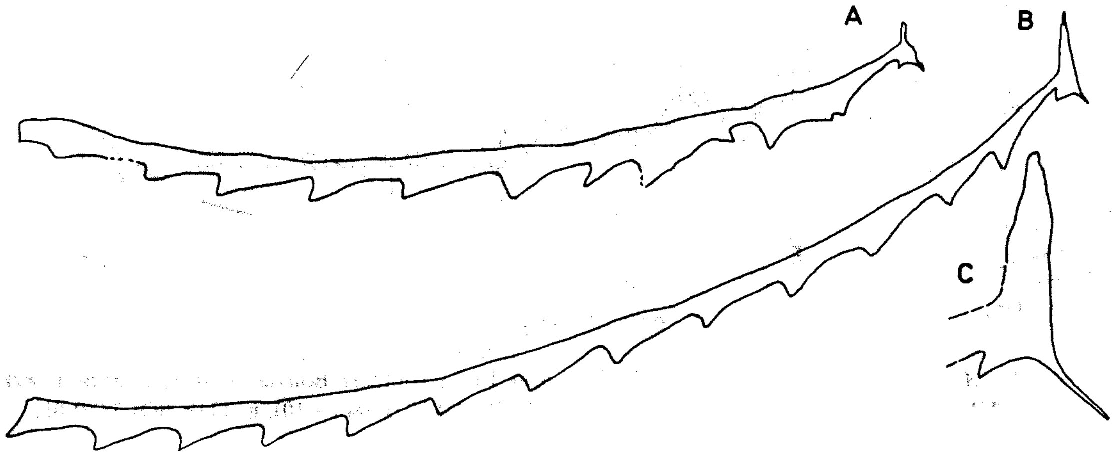
Type material. Lectotype (SM A17381); selected as 'type' by Elles and Wood (1902). All other available specimens (SM A17379–94) are paratypes.

Type locality. Pwlluog, Whitesand Bay, near St David's, Dyfed (SM 732274) (locality C2 of Text-fig. 3). Specimens occur as carbonaceous films in fissile siltstone of Whitlandian age, *Gymnostomix gibbsii* Biozone (Fortey and Owens 1987).

Other occurrences. Afon Ffinnant, east of Carmarthen, South Wales (SN 51061973 to SN 51032003) (locality C1 of Text-fig. 3). Specimens collected from isolated outcrops of shale. Described by Fortey and Owens (1987) and considered transient between *A. eivionicus* and *A. hicksii*. BM Q5172–Q5173.

TEXT-FIG. 12. *Azygograptus lapworthi* Nicholson, BM Q5878, possible synrhabdosome of juvenile rhabdosomes, Bryncroes; A, × 5; B, × 10.





TEXT-FIG. 13. *Azygograptus hicksii* (Hopkinson); Whitesand Bay, South Wales. A, SM A17392, ×5. B, SM A17933, ×5. C, SM A17933, ×20.

Description. Sicula 1·3–1·5 mm long; 0·4 mm wide at aperture. Prominent rutellum up to 0·5 mm long, on opposite side to stipe. Stipe originates at 0·7–0·8 of sicular length and diverges immediately at an angle of 130–140° leaving a basal free length to the sicula of up to 0·3 mm. Stipe slightly to moderately flexed with 20–30° rotation by th 5 and 40° rotation by th 10. Stipe width at th 1 is about 1 mm (0·8–1·1 mm) and slight expansion gives a distal stipe width of up to 1·5 mm. Thecal separation 1·7–2·7 mm (4–6 th/10 mm) with little variation along the stipe. Thecal inclination about 18°; thecal overlap not visible.

Discussion. The massive form of the stipe and elongate rutellum on sicular aperture make the species readily distinguishable. Forty and Owens (1987) concluded that the size is unlikely to be the product of deformation. The values given in the above description closely match those given by Fortey and Owens (1987) except for sicular length which they give as reaching 2·1 mm, but no specimens of this length have been observed in the type population during this study.

Apart from the transient population from Afon Ffinnant described by Fortey and Owens (1987), the species has not been recognized other than at the type locality, and therefore on present evidence is restricted to South Wales.

Azygograptus eivionicus Elles, 1922

Plate 1, figs 3, 4, 7, 8; Text-figs 16, 17A–P, 18F–O

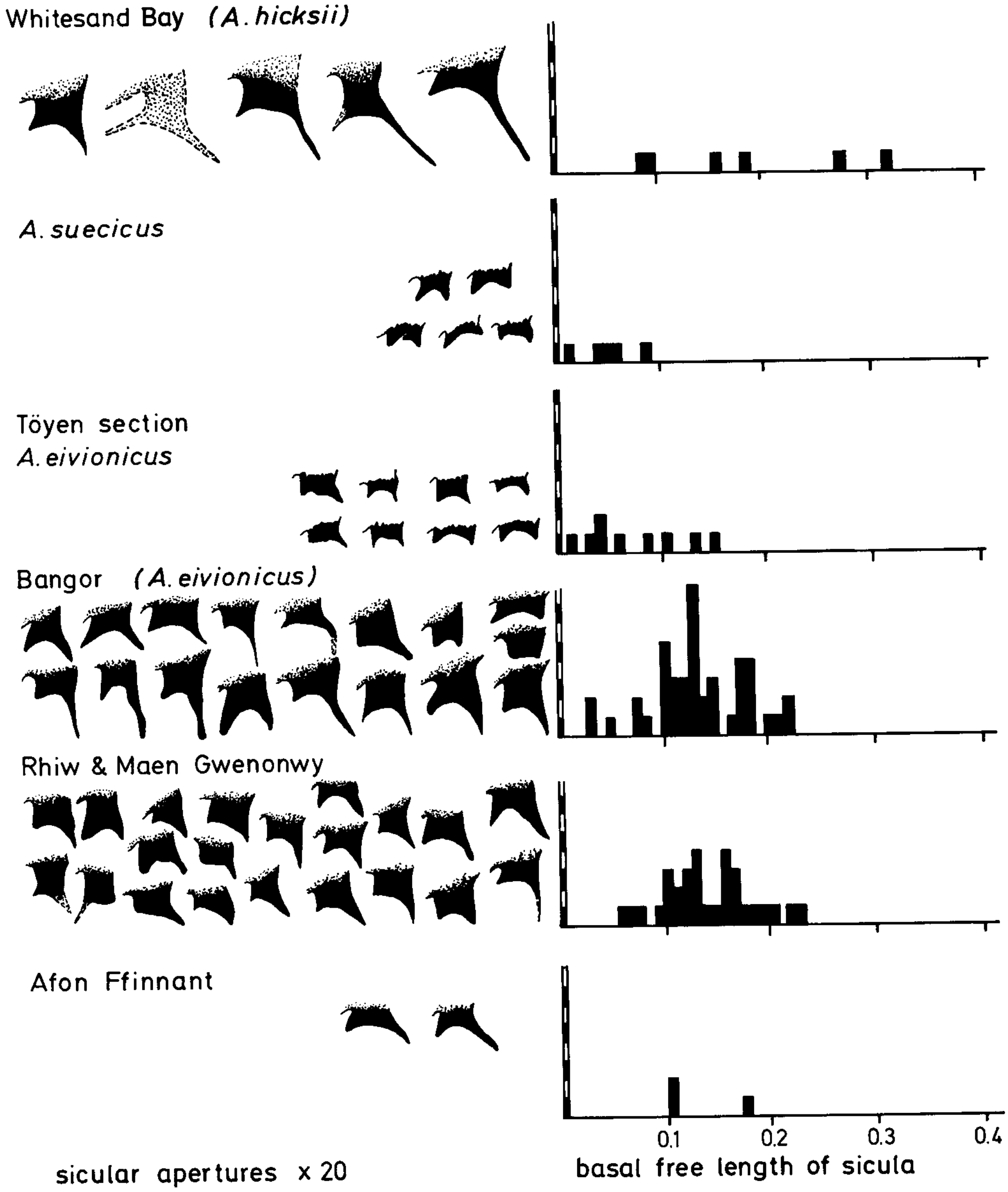
1915	*Azygograptus lapworthi* Nicholson; Nicholas, 1915, p. 113.
1922	*Azygograptus eivionicus* Elles, p. 299, figs 1–3.
1932	*Azygograptus suecicus* Moberg; Matley, p. 261.
1987	*Azygograptus eivionicus* Elles; Fortey and Owens, p. 276, figs 128*a* and 129*a–c*.

Diagnosis. Basal free length of sicula consistently less than 0·2 mm. Slight to moderate development of rutellum. No adpressed growth of th 1^1 and sicula.

Type material. Holotype, SM A17372; Paratypes, SM A17373–A17374. Strachan (1971, p. 19) listed all these specimens as syntypes, though in the original description a type specimen is clearly designated.

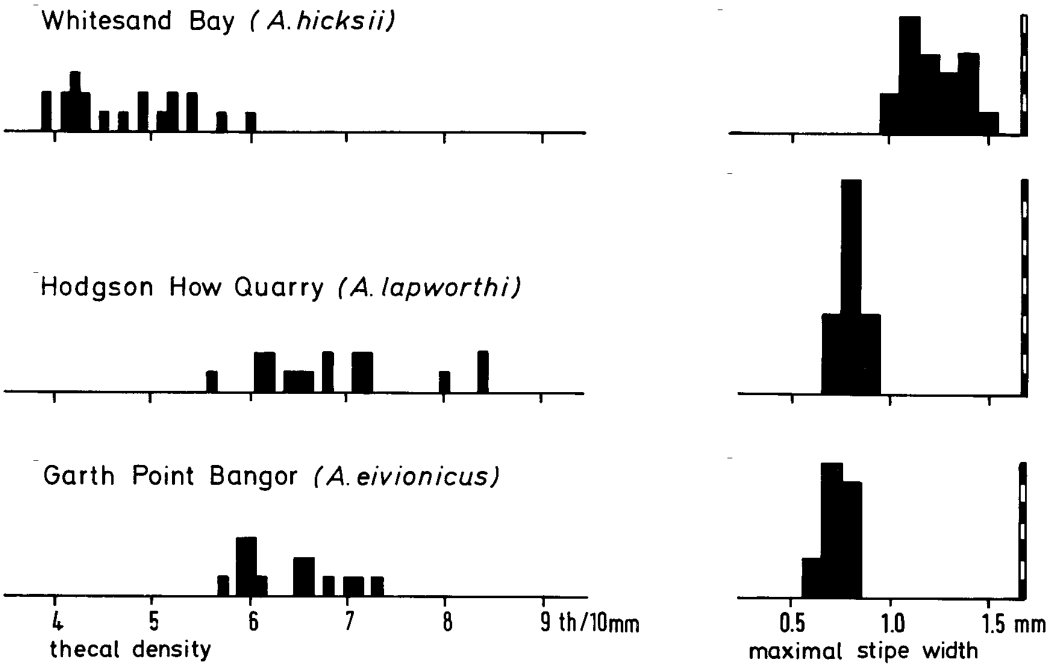
The type material is flattened, matted, fragmentary and strongly deformed. The three specimens figured by Elles (1922) are shown in Text-figure 16 against her original drawings. The differences are most significant in the case of the holotype, for which there is no evidence of the sicula indicated and it is possible that the proximal end is not even reached.

There are very few proximal ends among the material and only one complete sicula (A 17373): 1·1 mm long



TEXT-FIG. 14. Sicular aperture and basal free length in populations of *Azgograptus hicksii* (Hopkinson) and *A. eivionicus* Elles.

with a basal free length of 0·08 mm. The basal free lengths in two other measurable siculae are 0·05 and 0·1 mm. None of these are associated with more than a couple of thecae and therefore all may be immature. In figuring A17373, Elles (1922) showed th 1^1 as originating in the mid-part of the sicula and growing adpressed to it for a short distance. There is no evidence for the shoulder this produces and the stipe diverges abruptly at 0·8 of the length. There is a slight inflation of the sicula approximately at its mid-point, but this is also developed on the ventral side and may represent the expansion at the base of the metasicula. The stipe divergence angles measurable on two specimens are 138° and 144° (no correction made for deformation).



TEXT-FIG. 15. Comparison of stipe characters between *Azygograptus lapworthi* Nicholson, *A. eivionicus* Elles and *A. hicksii* (Hopkinson).

Stipe characters are difficult to quantify because of the deformation but are probably most reliable on the holotype which lies almost parallel to the lineation. This has a stipe width of 0·6 mm and a thecal density of 7·4 th/10 mm. Stipes are gently flexed.

Type locality. Valley southeast of Nant, St Tudwal's Peninsula, North Wales (SH 297253), Loc. β of Nicholas (1915, pl. 13), in the Llanengan Mudstone.

Other occurrences.

1. Bangor, North Wales. Two localities on the Bangor foreshore were given in the original description of *A. eivionicus* (Elles 1922): Garth Point (SH 585731) and University College Cliff (SH 59117260). Populations have been collected from two levels at Garth Point (SH 58467320 and SH 58547315), and that from University College Cliff comes from the same part of the succession repeated by faulting. All the populations are very similar and are treated as one. The fauna is monospecific, and occurs in 'flaggy sandstone' of the Maes y Geirchen Sandstone Member of the Nant Ffrancon Formation. The only independent faunal control is an endemic trilobite fauna from the sandstone beds towards the base of the succession (Beckly 1989), and the presence of the Arenig-Llanvirn boundary a few hundred metres above. Material from Bangor Pier: NMW 85·16G·89–99; BM Q5880–Q5883, Q5895. Material from University College Cliff: BM Q5886.
2. Aberdaron Area, Western Llŷn. Populations from Maen Gwenonwy (SH 20052596) (locality B1 of Text-fig. 3) and Rhiw (SH 22322847) (locality B2 of Text-fig. 3) identified as *A. eivionicus* and *A. suecicus* respectively by Elles (*in* Matley, 1932), but now considered to occur in the same stratigraphic unit, the Wîg Member of the Aberdaron Formation, and both to be *A. eivionicus* (Beckly 1988). The lithofacies is a massive silty mudstone, and *Azygograptus* along with the trilobite *Merlinia* is very abundant whilst the rest of the fauna is only known from rare specimens and comprises *Hanchungolithus primitivus* (Born), ?*Furcolithus*, and *Expansograptus praenuntius* (Törnquist). The fauna is interpreted to come from the lower part of the Arenig succession and to

be overlain by proven Whitlandian and Fennian Faunas. The *Merlinia* is a transient form between *M. selwynii* (Salter) and *M. rhyacos* Fortey and Owens (R. A. Fortey pers. comm.), and this would suggest a late Moridunian to early Whitlandian age (cf. Fortey and Owens 1987). Material from Maen Gwenonwy: NMW 85·16G·100–103; BM Q5885. Material from Rhiw: NMW 85·16G·103–108; BM Q5844, Q5871, Q5875, Q5896–Q5897; SM A22601.

3. Afon Ffinant, South Wales (SN 51032003) (locality C1 of Text-fig. 3). Material described by Fortey and Owens (1987), and occurring as monospecific assemblages in a succession of interbedded turbidite sandstone beds and siltstone. *A. eivionicus* is the lowest graptolite to occur in the succession of the area, and is identified as coming from the *F. radix* biozone at the base of the Whitlandian. BM Q5174–Q5179; NMW 84·17G·105–107.

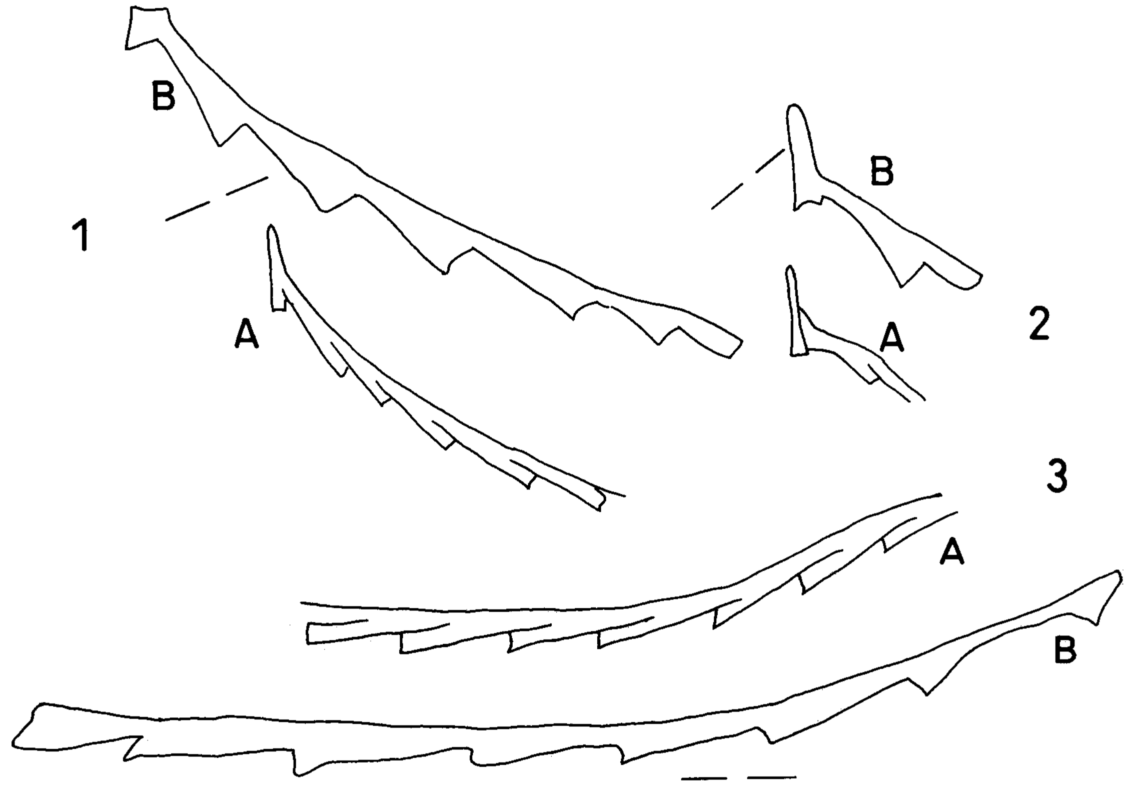
4. Hodgson How Quarry, English Lake District (NY 243236) (locality A4 of Text-fig. 3). Lower *in situ* population discussed under *A. lapworthi*.

5. Tom Rudd Beck, west of Ling Fell, English Lake District (NY 16382898) (locally A10 of Text-fig. 3). Specimens preserved as rusty films in fairly homogeneous dark grey micaceous, fissile siltstone. BGS Rx2207, Rx2210–Rx2211.

6. Ling Fell, English Lake District (NY 18012844) (locality A8 of Text-fig. 3). Specimens preserved as chlorite lined moulds in crenulated mudstone. BGS Rx1691–Rx1692.

7. Tøyen Shale, Oslo. Abundant specimens from an interval just below the Orthoceras Limestone between 19·19 and 19·75 m (Text-fig. 2). Graptolite abundance is reduced, compared to the darker lithology of the Galgeberg Member, but the fauna is still diverse and includes *Pseudotrigonograptus ensiformis*, *Holograptus diffusus*, *Xiphograptus cypselo*, *X. svalbardensis*, *Expansograptus abditus*, *E. distinctus*, *Tetagraptus taraxacum*, and *Dichograptus* sp. PMO 118·601–610.

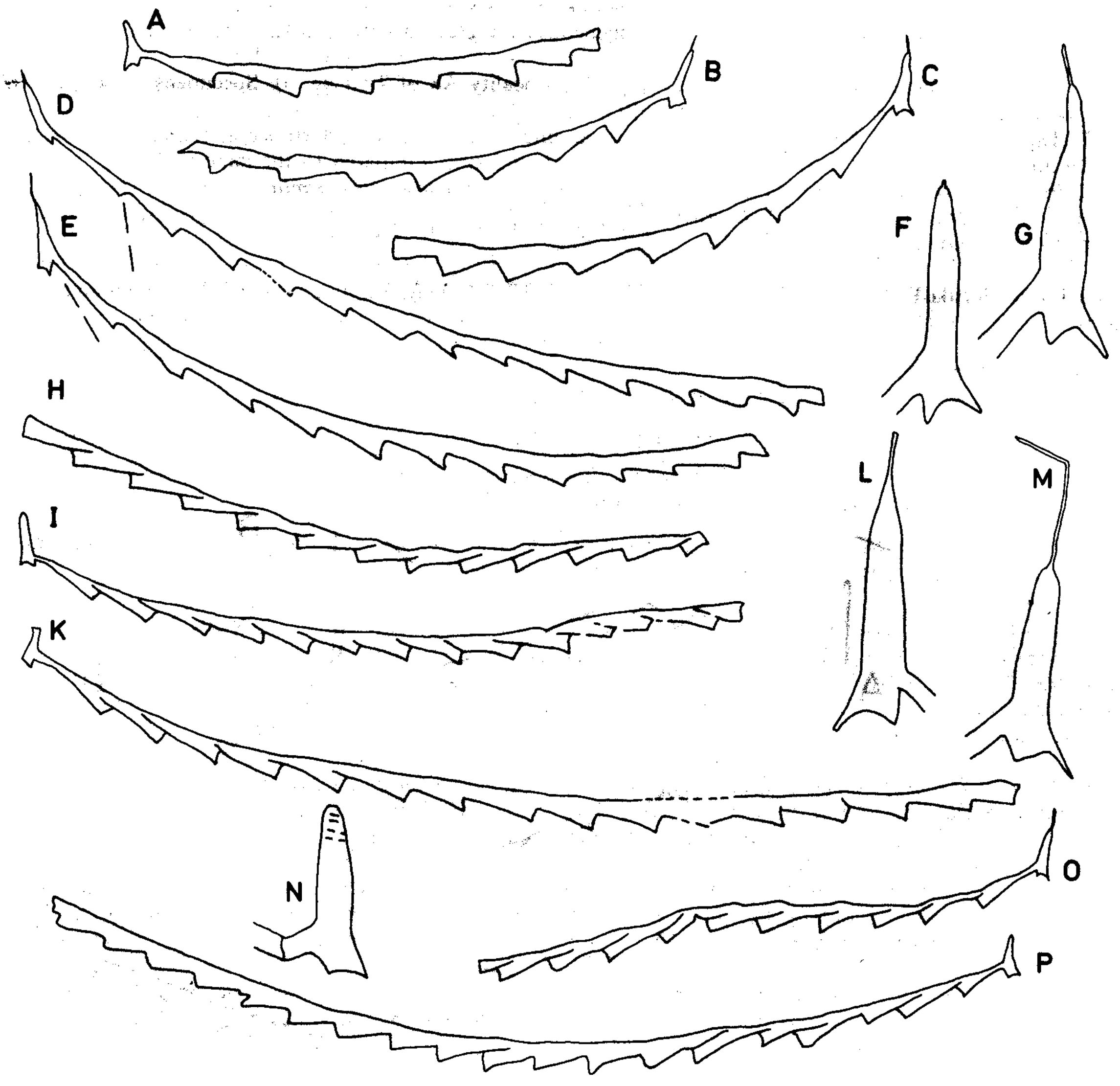
Description. Sicula 1·13–1·62 mm long. Stipe originates at 0·7–0·9 along sicular length and diverges at an angle



TEXT-FIG. 16. Type specimens of *Azygograptus eivionicus* Elles. A, Elles's original drawings (1922) quoted as × 5. B, same specimens redrawn at × 10. 1, SM A17372 (holotype); 2, SM A17377; 3, SM A17374.

between 120° and 160°. Basal free length of sicula 0·1–0·2 mm. Development of rutellum variable but is readily apparent in the majority of specimens. Stipe moderately flexed with up to 50° rotation by th 10 or th 15. Stipe width and thecal separation both vary over the first five thecae. Thecal separation falls from as much as 2·5 mm (4 th/10 mm) to the more typical value of 1·5–1·7 (6–7 th/10 mm); stipe width increases from 0·4–0·6 mm at the aperture of th 1^1 to 0·7–0·8 mm more distally. These changes result mainly from increasing overlap. Thecal inclination 8–13°. Thecae fairly straight, conical with slight ventral concave curvature. Thecal overlap about two-fifths.

Discussion. Because of the poor preservation of the type material, the population from Garth Point,



TEXT-FIG. 17. *Azygograptus eivionicus* Elles from North Wales (A–G, Bangor; H–P, Rhiw, Western Llŷn). A, BM Q5881, ×5. B, BM Q5880, ×5. C, BM Q5880, ×5. D, BM Q5883, ×5. E, BM Q5882, ×5. F, BM Q5880, ×20. G, BM Q5880, ×20. H, BM Q5871, ×5. I, BM Q5872, ×5. K, BM Q5874, ×5. L, NMW 85.16G.103, ×20. M, BGS A22601, ×20. N, BM Q5873, ×20. O, BM Q5884, ×5. P, BM Q5875, ×5.

Bangor was selected as the basis for the description because that, and University College Cliff, Bangor, were the only other occurrences accurately located in the original description of the species.

The population from the Aberdaron area is similar to that from Bangor in all characters except sicular length, which is more restricted (1·1–1·4 mm), and in a slightly less pronounced rutellum.

The population from South Wales described by Fortey and Owens (1987) is closely comparable to the populations from North Wales, the only significant difference being the form of the rutellum which is slightly longer and turns away from the aperture more sharply (see Text-fig. 14). The populations from the Lake District are sparse and only the population from Hodgson How Quarry shows significant differences from the North Wales material with more slender stipes and shorter sicula.

The specimens from the Tøyen Shale formation are also closely comparable, but with a slightly more slender sicula, and a less prominent basal free length and rutellum (see Text-fig. 14). These features make them similar to *A. suecicus* from which it is distinguished by the presence of a rutellum. The population may be considered transient. Fortey and Owens (1987) suggested specimens described as *A. suecicus* by Mu *et al.* (1979) are *A. eivionicus*, but the description indicates adpressed growth of th 1^1 and sicula and therefore they may be excluded from either of these species.

A. eivionicus is distinguished from *A. hicksii* by its narrower stipe width and smaller thecal separation, and from *A. suecicus* by the presence by a rutellum. Distinction from *A. lapworthi* is more subtle, and is mainly dependent on the basal free length of the sicula which only rarely exceeds 0·2 mm in *A. eivionicus*, and then only slightly (compare Text-figs 9 and 14). Sicular length ranges above that seen in *A. lapworthi*, particularly in the Bangor populations (see Text-fig 9).

Azygograptus suecicus Moberg, 1892

Pl. 1 fig. 5; Text-fig. 18A–E, P

1892 *Azygograptus suecicus* Moberg, p. 342, pl. 8 figs 1 and 2.
1904 *Azygograptus suecicus* Moberg; Törnquist, p. 27, pl. 4 figs 6–11.

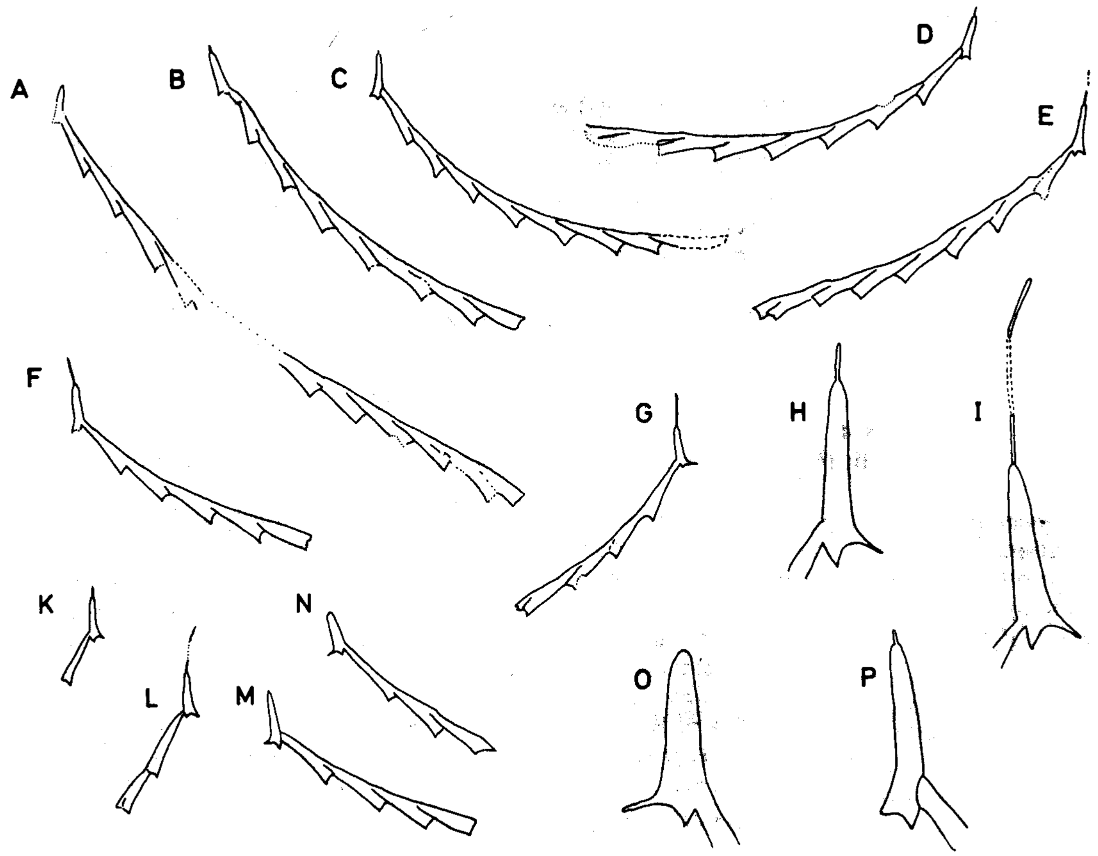
Diagnosis. *Azygograptus* with very short basal free length to sicula ($<$ 0·2 mm); no rutellum, and no adpressed growth of th 1^1 and sicula.

Type material. The specimen figured by Moberg (1892, pl. 8, fig. 1) was selected as the lectotype by Bouček (1973). However Bouček (1973, p. 107) stated that the type specimens were in the collection of the Geological Institute of Lund, whilst they are in fact held in the type collection of the Sveriges Geologiska Undersokning. There is therefore some doubt that Bouček examined the type specimens, and unfortunately the lectotype he selected is poorly preserved.

Type locality. Flagabro-Killeröd, Scania from just below Komstad Limestone. A translation of the original description of the locality was given by Lindholm (1985, pp. 39–41). The species occurs in the uppermost part of the Tøyen Shale together with *Isograptus gibberulus* (sensu Moberg, 1892), *Maeandrograptus schmalenseei*, *Didymograptus mobergi*, *Expansograptus hirundo*, *E.* cf. *abditus*, *Pseudotrigonograptus ensiformis*, *Kinnegraptus kinnekullensis* (*sensu* Williams and Stevens 1988, *non* Skoglund 1961). The overlying Komstad limestone belongs to the *Megistaspis* (*Megistaspis*) *simon* trilobite zone (Nielsen 1985). The graptolites indicate the *I. v. lunatus* or *I. v. victoriae* biozone of the Australian zonation and the Scandinavian *D. hirundo* biozone.

Other occurrences. Though the species has been listed from a number of localities in Scandinavia the majority are probably *A. ellesi*. Only one occurrence outside the type locality has been reliably identified. This is at Graptolittdalen, Slemmestad, Oslo Region (PMO 118·570), and is a single slab with specimens in the silvery carbonaceous preservation typical of the area. Indirect evidence which supports the occurrence is that *Isograptus gibberulus* sensu Moberg is also present at Slemmestad (Spjeldnaes 1953, pl. 1, fig. 5) and is also only known from the Moberg locality in Scania.

Description. Sicula 1·1–1·3 mm long and curves away from the stipe at the aperture which is 0·25–0·3 mm wide.



TEXT-FIG. 18 A–E, P. *Azygograptus suecicus* Moberg, from Killeröd, Scania; A, SGU 5247, lectotype, ×5; B, SGU 5248, paratype, ×5; C, SGU 7895, drawing in latex, ×5; D, SGU 7896, proximal part in relief, distal part preserved as mould, ×5; E, SGU 5247, same slab as holotype, preserved as mould, ×5; P, SGU 7895, detail of sicula, ×20. F–M, *A. eivionicus* Elles, from Tøyen Section, Oslo, 19·43–19·55 m interval; F, PMO 118.608, ×5; G, PMO 118.603–2, ×5; H, PMO 118.604, ×5; I, PMO 118.603–1, detail of sicula, ×20; K, PMO 118.604, detail of sicula ×20; L, PMO 118.603–1, ×5; M, PMO 118.605, ×5. N–O, *A. eivionicus* Elles, from Tøyen Section, Oslo, 19·19–29 m interval; N, PMO 118.602, ×5; O, PMO 118.602, ×20.

Sicular aperture is symmetrical without rutellum. Stipe originates low on the sicula and diverges abruptly at an angle of 140–150°, leaving a basal free length to the sicula of 0·1–0·2 mm. Stipe moderately flexed with up to 35° rotation by th 5. Thecae are slender, with stipe width at aperture of first theca 0·45–0·5 mm; distal stipe width 0·7–0·8 mm. Thecal separation 1·4–1·7 mm (6–7 th/10 mm), but the first theca appears somewhat longer. Thecal inclination 14–18°.

Discussion. *A. suecicus* is easily distinguished from other members of the genus by the simple form of the sicular aperture (see Text-fig. 14) associated with the lack of adpressed growth of th 1^1 and the sicula.

Azygograptus validus Törnquist, 1904

Plate 1, fig. 13; Text-fig. 19A–L

1904 *Azygograptus validus* Moberg MS.; Törnquist, p. 27, pl. 4, figs 12–14.

Diagnosis. Azygograptus with higher thecal inclination (approximately 25°) than other species. Obvious adpressed growth of sicula and th 1^1 with origin of th 1^1 very high on the sicula.

Type material. LO 1755T, LO 1756*t*; additional topotype SGU 7555–7557, 7889–7892.

Type locality. Diabasbrottet, Hunneberg Mountain (previously called Mossebo) (see Lindholm and Maletz 1989). Moderately abundant specimens, predominantly occurring as silvery organic films on black shale. Topotype specimens came from the interval 4·74–4·89 m of the section in Erdtmann *et al.* (1987, p. 112). Associated with *T. phyllograptoides*.

Other occurrences.

1. Krapperup boring in Scania (Lindholm 1981); 6 specimens at the 96·45 m level, together with *D. undulatus* in the *T. phyllograptoides* biozone.
2. Robinson Mountain, Lake District (locality A1 of Text-fig. 3); solitary, very poorly preserved specimen in medium grey mudstone (BGS Rx 1273–Rx 1274); associated with *Acrograptus filiformis*.
3. Tøyen Shale, Tøyen Underground Station, City of Oslo, Norway; single, poorly preserved specimen (PMO 118·571) from the interval 7·65–7·85 m (Text-fig. 2), associated with *T. phyllograptoides*.

Description. Sicula long and slender; 2·0–2·3 mm long; 0·3–0·4 mm wide at aperture. A short nema is sometimes present. Th 1^1 originates very high on the sicula, possibly from the prosicula, though this is irresolvable from available material. The stipe turns away at about 120–150° leaving 0·3–0·4 mm basal free length to sicula. Thecae slender, slowly expanding; overlap about one-half. Thecal inclination 24–26°. Stipe characters uniform with largest specimen reaching th 14.: thecal density 11–12 th/10 mm; stipe width 0·5–0·8 mm. Significant stipe curvature, stipe becoming reclined in some larger specimens.

Discussion. Törnquist (1904), in describing a few small specimens from Mossebo, remarked on the strong resemblance to *Azygograptus coelebs*. *A. validus* differs from the published descriptions of *A. coelebs* (see below) in possessing a much longer sicula and shorter thecae. Thecal inclination serves to distinguish it from other species.

Azygograptus ellesi Monsen, 1937

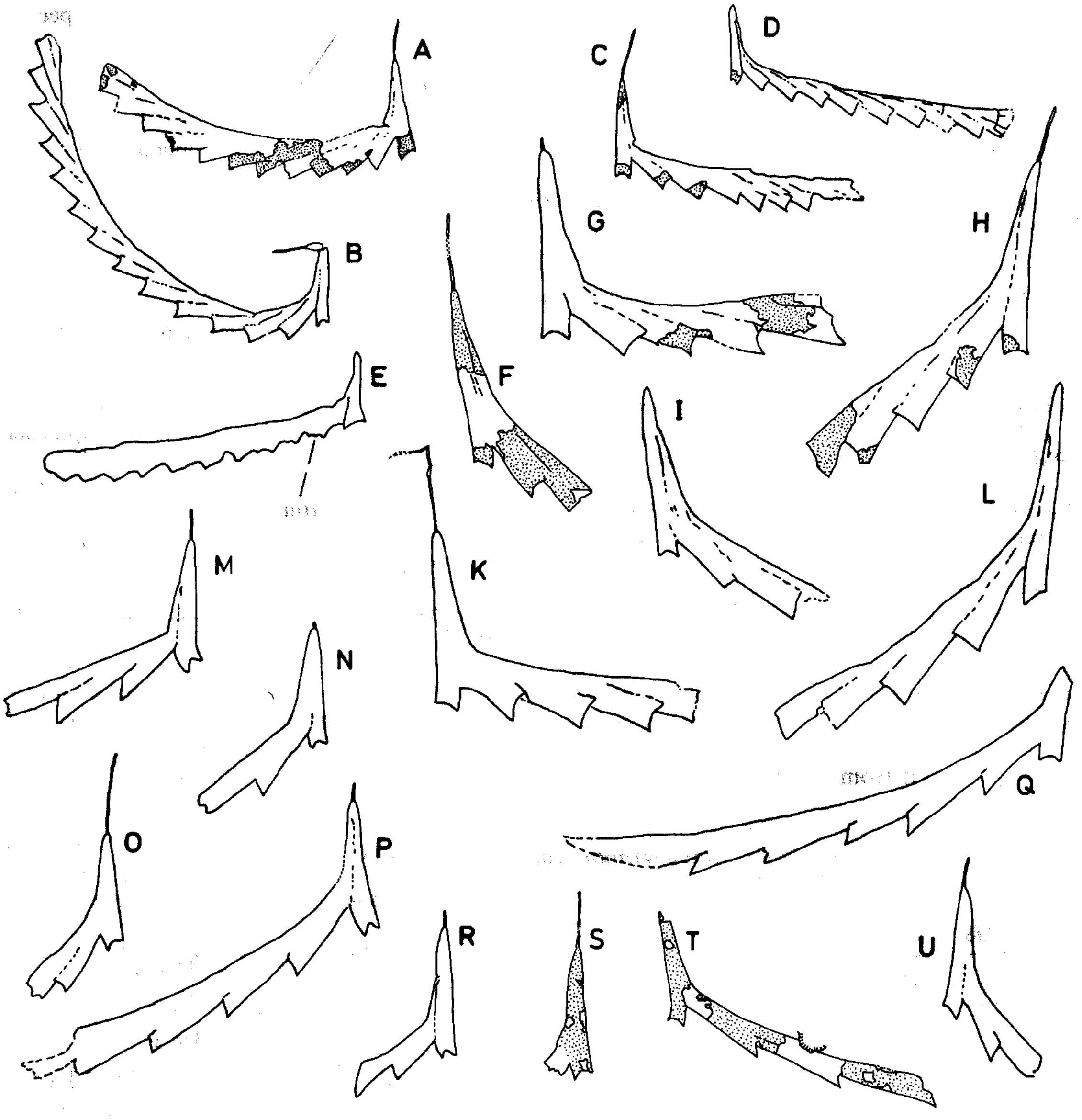
Plate 1, figs 1 and 11; Text-fig. 20A–S

1898	*Azygograptus suecicus* Moberg; Elles p. 514, fig. 29.
1902	*Azygograptus suecicus* Moberg; Elles and Wood p. 95, text-fig. 56; pl. 3, fig, 3*a–b*.
1937	*Azygograptus ellesi* Monsen, p. 205, pl. 5, figs 21, 28, ?30.
1937	*Azygograptus* cf. *suecicus* Moberg; Monsen, p. 204, pl. 5, figs 2 and 20.
1973	*Azygograptus suecicus* Moberg; Bouček, p. 107, pl. 19, figs 1–4; text-fig. 33*a–g*.

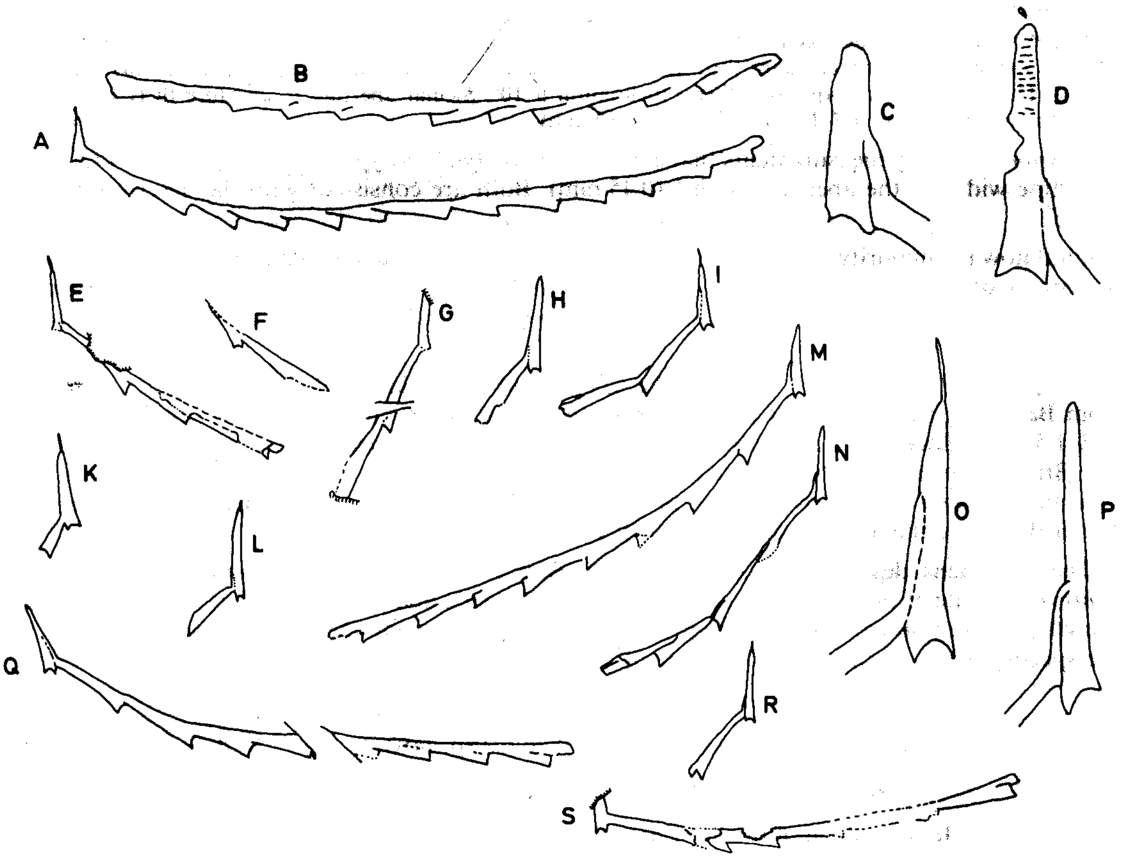
Emended diagnosis. Azygograptus with long sicula (1·8–2·4 mm); origin of th 1^1 in distal half of sicula and adpressed growth of th 1^1 and sicula till close to sicular aperture. Little overlap in proximal thecae.

Type material. PMO K 0288. Slab contains two specimens figured by Monsen (1937, pl. 5, figs 21 and 28) both of which were described as a 'holotype' in the plate explanation. The specimen represented in plate 5 figure 21 is indicated as the holotype on the label for the slab and is here adopted as the holotype; the other specimen is certainly conspecific and is regarded as a paratype. The specimen figured on plate 5, figure 30 is a distal fragment on a slab from the *P. angustifolius elongatus* biozone at Ensjo, Oslo region. Though there are several specimens of *A. ellesi* on the slab, the figured specimen is only a distal fragment and thecal spacing and inclination suggest it may not belong to *A. ellesi*.

Type locality. Tøyen shale at Slemmestad, Oslo Region. The specimens come from the *P. angustifolius elongatus* biozone and are associated with *Phyllograptus s.s*, *Didymograptus ?protoindentus*, *Expansogratus* sp. and *Tetragraptus* cf. *serra*.



TEXT-FIG. 19. A–D, F–H, *Azygograptus validus* Törnquist from Diabasbrottet, Hunneberg Mountain, Västergötland, Sweden; A, SGU 7890B, 4·83 m level, × 5; B, SGU 7556, 4·89 m level, × 5; C, SGU 7557–2, 4·74 m level, × 5; D, SGU 7557–1, drawing of mould, 4·74 m level, × 5; F, SGU 7892, 4·79 m level, × 10; G, SGU 7889B-2, 4·79 m level, × 10; H, SGU 7889B-1, 4·79 m level, × 10. E, ?*A. validus*, BGS 1273, Robinson Mountain, Lake District, England, × 5. I, K, *A. validus* from Mossebo (now Diabasbrottet), Hunneberg Mountain, Västergötland, Sweden; I, paratype, LO 1756*t*, × 10; K, holotype, LO 1755T, × 10. L, *A. validus*, PMO 118.571, 7·65–7·85 m level, Tøyen Section, Oslo, Norway, × 10. M–U, *A. minutus* sp. nov. from Diabasbrottet, Hunneberg Mountain, Västergötland, Sweden, × 10. M, SGU 7564, paratype, 7·09 m level; N, SGU 7593, paratype, 7·09 m level; O, SGU 7565, paratype, 7·09 m level; P, SGU 7560, holotype, 7·09 m level; Q, SGU 7562, paratype, 7·09 m level; R, SGU 7559, paratype, 7·09 m level; S, SGU 7893, paratype, 7·09 m level; T, SGU 7894, 8·29 m level; U, SGU 7561, paratype, 7·09 m level; Remarks: Diabasbrottet section as figured in Erdtmann *et al.* (1987).



TEXT-FIG. 20. *Azygograptus ellesi* Monsen. A–D, Barf, Lake District, England; A, BM H948, × 5; B, BM P7216, × 5; C–D, BM P2010, two specimens on same slab, × 20. E–G, Slemmestad, Norway; E, PMO K 0187, paratype, × 5; F, PMO K 0288, paratype × 5; G, PMO K 0288 holotype, × 5. H, M–N, P–R, from 16·25–16·42 m level in Tøyen Section, Oslo, Norway; H, PMO 118.578, × 5; M, PMO 118.575, × 5; N, PMO 118.576, × 5; P, PMO 118.576, × 20; Q, PMO 118.579, × 5; R, PMO 118.959, × 5. I, O, SGU 7554, drawing of mould, Nipan, Jemtland; I, × 5; O, × 20. K, PMO K 0658, figured as *A.* cf. *suecicus* by Monsen (1937, pl. 5, fig. 20), Stensbergstrafe, Oslo, Norway, × 5. L, S, Ensjo, Norway, from slab with stipe fragment of *A. ellesi* figured by Monsen (1937, pl. 5, fig. 30), PMO K 0657, × 5.

Other occurrences.

1. Tøyen Underground Station, City of Oslo, Norway; several specimens from the section described by Erdtmann (1965). The specimens from the intervals 15·35–15·95 m and 16·25–16·42 m, within the upper part of the *P. a. elongatus* biozone, and are associated with *Pseudophyllograptus augustifolius*, *Tetragraptus bigsbyi askerensis*, *Expansograptus grandis* and *Acrograptus* sp.
2. Nipan, Jemtland; single relief specimen (SGU 7554) on a loose slab with no associated fauna; a nearby outcrop has yield a fauna indicating the *P. densus* biozone, or higher parts of the Tøyen Shale.
3. Barf, English Lake District (NY 217267) (locality A6 of Text-fig. 3); fairly numerous specimens preserved in partial relief as limonitic internal moulds in monospecific assemblages or associated with *Pseudophyllograptus*, but the locality has yielded a very diverse fauna indicative of the *D. nitidus* biozone. BM P7216, P2010, G948.

Description. Sicula straight and slender, 1·8–2·4 mm long; 0·25 mm wide in relief specimens, a little wider (0·3 mm) in flattened specimens and with both dorsal and ventral processes on the aperture. Th 1^1 originates at 0·6–0·75 of the sicular length and grows down along sicula until 0·1–0·2 mm above the sicular aperture. Declined stipe very slender, generally straight but may be slightly curved in some specimens. Stipe width 0·45–0·7 mm and is nearly constant throughout rhabdosome, with the only increase over the first couple of thecae. Thecal overlap one-quarter; thecal inclination 6–10°. Sicular aperture to aperture th 1: 1·9–2·2 mm, distal thecal separation: 1·7–1·5 mm (6·5–8·5 th/10 mm).

Discussion. The only measurements that can be made on the holotype are the length of th 1 (2·2 mm) and stipe width at the aperture of th 1 (0·45 mm). Both are consistent with the description given above.

Until now the majority of azygograptids from Scandinavia have been identified as *A. suecicus*, but the origin of th 1 apparent from the relief material shows this to be incorrect. The specimens described as *A.* cf. *suecicus* by Monsen (1937) also clearly belong to *A. ellesi* and one specimen is refigured here (Text-fig. 20K).

The proximal development (see Text-fig. 20C,D) and stipe width (0·45–0·8 mm) of the specimens from Barf, English Lake District, are comparable to *A. ellesi*, but the sicula is somewhat shorter (1·2–1·5 mm). Thecal density is also slightly higher in the distal part of the stipe (7–9 th/10 mm) of the British specimens, which appears to result from the slightly greater thecal overlap. The specimens figured as *A. suecicus* by Elles and Wood (1902. pl. 13, fig. 3*a–b*) are also from Barf, for which they note the adpressed growth of th 1^1 and the sicula.

The specimens described as *A. suecicus* by Bouček (1973) from the *Tetragraptus reclinatus abbreviatus* zone of Bohemia, possess a relatively long sicula and are described as having downward growth of the initial part of th 1. The proximal development cannot be discerned on the photos, but the specimens are tentatively included in *A. ellesi*.

Azygograptus minutus sp. nov.

Plate 1, fig. 12; Text-fig. 19M–U

Origin of name. In recognition of the small size of the species.

Diagnosis. *Azygograptus* with origin of th 1^1 high on sicula and adpressed growth until close to sicular aperture associated with low thecal inclination and high thecal density (9–10 th/mm).

Type material. Holotype: SGU 7560. Paratypes: SGU 7558–7559; 7561–7565.

Type locality. Västergötland, north-eastern edge of Hunneberg Mountain, Diabasbrottet. A few specimens in association with *Paradelograptus kinnegraptoides*, *Expansograptus vacillans* and *E. holmi* on a single bedding plane in the *Didymograptus balticus* biozone, at 7·09 m in the section of Erdtmann *et al.* (1987, p. 112).

Other occurrences. None known.

Description. Slender and small species with longest specimen only 6 mm long which reaches th 7. All specimens may therefore be immature. Sicula 1·6–1·9 mm long with apertural width 0·25–0·3 mm. Th 1 originates high on the sicula and grows down adpressed for the majority of the sicular length before flexing away at an angle of 120–150°. The basal free length to the sicula is 0·2–0·4 mm and the sicular aperture has symmetrical, small, dorsal and ventral lips. Thecae slender and long, thecal inclination 10–15° and thecal overlap about a half. Thecal density 9–10 th/10 mm. Stipe is slightly flexed and reaches a maximum width of 0·6 mm; no variation along stipe has been recognized.

Discussion. *A. minutus* is characterized by its high thecal density. The only species with which it is likely to be confused is *A. validus* which also has a high origin of th 1^1. The main differences are the lower inclination of thecae in *A. minutus* and shorter sicula.

Other species which have been placed in *Azygograptus* are as follows:

1. *A. canadensis* Ruedeman, 1947, p. 357, pl. 58, figs 9–11. Glenogle Shale, Glenogle, Canada. Belongs to *Pseudazygograptus*.

2. *A. coelebs* Lapworth, 1880, p. 159, pl. 5 fig. 16*a–c*. This species has only been described from the Skiddaw Slate Group of the Cross Fell Inlier, Northern England, though it has been identified from Algeria (Whitman 1971). The original description was based on material from Ellergil, and the species has been recorded from Milburn Beck (Shotton 1935). The associated fauna, which includes biserial and pendent graptolites, indicates a Llanvirn age. The validity of the species is in doubt because only the two specimens (SM A18016 and BM 1027) figured by Elles and Wood (1902, pl. 13 fig. 4*a–b*) appear to exist and neither is adequate to characterize the species or confirm the generic placement.

3. *A. flexilis* Chen and Xia, *in* Mu *et al.* 1979, pp. 110–111, pl. 38, figs 13 and 14. Described from the *A. suecicus* biozone of Southwest China. The description states that th 1 grows down beside the sicula and on this feature it may be grouped with *A. ellesi*. It differs from *A. ellesi* in having a shorter sicula (1·3 vs 1·8–2·4 mm). No description is given here because the original material has not been examined. The only reason this may not be a valid species is synonymy with another Chinese species.

4. *A. fluitans* Geh, *in* Mu *et al.* 1979, p. 112, pl. 39, figs 1–5. Described from the *A. suecicus* biozone of Southwest China. No material of this species has been examined but it may be synonymous with *A. undulatus* (Chen Xu, pers. comm.).

5. *A. groenwalli* Monsen, 1937, p. 206, pl. 5, fig. 29. From the *Pseudophyllograptus densus* biozone, Ensjo, Oslo Region, Norway. Only known from the type specimen which is almost certainly a broken specimen of the co-occurring *Didymograptus* cf. *minutus*. The species is therefore considered a junior synonym of *D.* cf. *minutus*.

6. *A. hexianensis* Jiao, 1984, p. 623, text-fig. 2; pl. 2, figs 31 and 32. *A. suecicus* biozone of Hexian, Anhui. This species is difficult to interpret from illustrations but appears to belong to group 1. Occurs with *A. undulatus*, *A. suecicus* and *A. lapworthi*.

7. *A. novozealandicus* Skwarko, 1962, p. 224, text-fig. 4; fig. 6. South side of Peel Range, northwest Nelson, New Zealand, Lower Gisbornian. From the drawing alone this may be a fragment of a dichograptid, though the description states every specimen has a long nema implying a proximal end is present. However, positive identification with *Azygograptus* is not possible.

8. *A.* (?) *oelandicus* Bulman, 1936, pp. 46–48, pl. 2, figs 16–29; text-fig. 17. An indeterminable fragment; sicula unknown. The species was transferred to the Dendroidea as *Parvitubus oelandicus* by Skevington (1963, pp. 47–51, figs 62–72).

9. *A. prolixus* Keble and Benson, 1929, fig. 14. Northwest Nelson, New Zealand, Lower Aorere Series, Douglas zone, Cobb subzone, ?upper Arenig–Llanvirn.

10. *A. saltaensis* Loss, 1949. From the drawing this may be a fragment of an expansograptid, but the original material would need to be examined to confirm this.

11. *A.* (?) *simplex* Ruedemann, 1908, pp. 258–260, text-figs 163–171; pl. 14, fig. 10. A very curious form with a huge sicula and only one associated theca. Certainly not closely related to *Azygograptus*.

12. *A. undulatus* Chen and Xia, *in* Wang 1974, p. 157, pl. 68. fig. 4. This species has only been recognized from the *A. suecicus* biozone in Southwest China. It displays adpressed growth of th 1 and has a high origin on sicula suggesting comparison with *A. validus* or *A. minutus*. Probably a valid species. The sicular length is less than in *A. validus* or *A. minutus*, but the taxonomic importance of pro-thecal folds is uncertain. *A. fluitans* and *A. undulatus spinosus* may be junior synonyms of *A. undulatus* (Chen Xu, pers. comm.). This species has also been described from northern Spain (Gutierrez Marco and Rodriguez 1987).

13. *A. undulatus spinosus* Chen, *in* Mu *et al.* 1979, p. 112, pl. 38, figs 24 and 25. Described from the *A. suecicus* biozone of Southwest China. Probably synonymous with *A. undulatus* (Chen Xu, pers. comm.).

14. *A.* (?) *walcotti* Gurley, 1896, pp. 69, 92. Lower *Dicellograptus* biozone, Stockport, New York, USA. The species has never been redescribed but was figured by Ruedeman (1947, pl. 58, fig. 8). Its relationships remain unclear, but it might belong to *Pseudazygograptus*.

Genus JISHOUGRAPTUS Geh, 1988

Type species. Jishougraptus mui Geh, 1988.

Emended diagnosis. Single deflexed, uniserial stipe, dorsal margin undulate but without folds, thecae long and thin, tending to leptograptid type but not forming bundles. Thecae simple to elaborate.

Discussion. The only change made from the original diagnosis is the inclusion of simple thecae as well as elaborate. Neither of the species described below show the ventral geniculation or elaborate thecal aperture of the type species. The only difference from *Azygograptus* is the elongate, thin form of the thecae with greater overlap.

Jishougraptus novus sp. nov.

Plate 1, figs 6, 9, 10; Text-fig. 21A–N

Origin of name. Novus = new, in reference to the fact that this is the first species to show sigmoidally curved thecae.

Diagnosis. Jishougraptus with simple cylindrical thecae, and elongate sicula (1·8–2·4 mm).

Type material. Holotype: PMO 118·585, preserved as a mould in dark shale. Paratypes: PMO 118·580–584, 118·586–594.

Type locality. Tøyen Underground station, City of Oslo, Norway. Abundant specimens in the interval 16·15–16·25 m in the Tøyen section (see Text-fig. 2). The specimens are associated with *Tetragraptus bigsbyi divergens*, *Pseudophyllograptus augustifolius*, *Expansograptus extensus linearis*, *E. decens*, *F. grandis* and *Acrograptus* sp. Most specimens are preserved in relief, with only a few preserved as flattened films.

Other occurrences. Slemmestad, section 2*b* of Spjeldnaes (1985). PMO 117·553, 555. A few poor specimens collected by B.-D. Erdtmann on an excursion in 1988. The species occurs with *Oslograptus peculiaris* and *T. bigsbyi divergens*.

Description. Sicula 1·8–2·4 mm long and very slender. Short nema, up to 0·4 mm long, sometimes detectable but apex of sicula often poorly defined. Th 1^1 originates at half of sicular length and is adpressed until 0·1–0·15 mm above sicular aperture, where it diverges at 140–160°. Thecae are simple, slender and cylindrical with slight sigmoidal curvature. Prothecal folds not developed but distinct 'ridges' present at origins of thecae in relief specimens. Thecal separation 1·5–2·3 mm (4·5–6·5 th/10 mm) and relatively constant along rhabdosome. Stipe width at th 1 0·35–0·5 mm; distally 0·7–0·8 mm.

Discussion. J. novus is very similar to *J. lindholmae* and distal stipe fragments of the two species are virtually indistinguishable. However proximal development does show significant differences: *J. novus* has a sicula almost twice as long on average and much shorter th 1^1.

Jishougraptus lindholmae sp. nov.

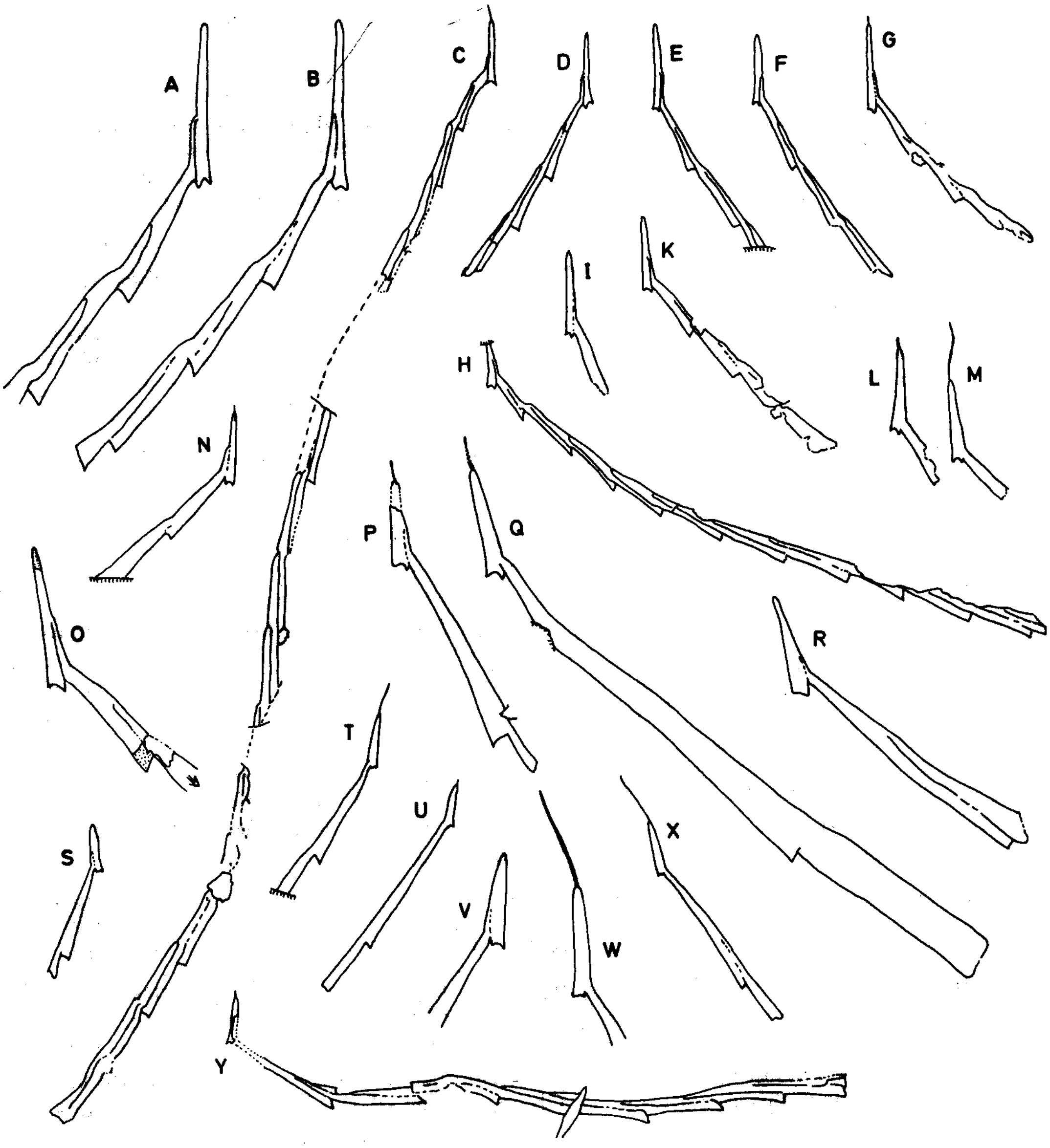
Text-fig. 21P–Y

1981 *Azygograptus* n. sp., Lindholm, p. 15, fig. 6*a–b*.

Origin of name. Named after Miss Kristina Lindholm (Lund University) who first recognized and described the species, though she did not name it.

Diagnosis. Jishougraptus with small sicula (1·0–1·5 mm) and simple, cylindrical thecae.

Type material. Holotype: PMO 118·595; flattened specimen in dark shale. Slab is crowded with other



TEXT-FIG. 21. *Jishougraptus novus* sp. nov. and *J. lindholmae* sp. nov. from the Tøyen Section, Oslo, Norway. A–O, *J. novus*, C is the holotype, the rest are paratypes, from 16·15–16·25 m interval, Tøyen Section; A, PMO 118.582-2, × 10; B, PMO 118.588, × 10; C, PMO 118.585, × 5; D, PMO 118.592-1, × 5; E, PMO 118.590, × 5; F, PMO 118.589, × 5; G, PMO 118.593-2, × 5; H, PMO 118.582-1, × 5; I, PMO 118.581, × 5; K, PMO 118.592-2, × 5; L, PMO 118.583, × 5; M, PMO 118.583, × 5; N, PMO 118.580, × 5; O, PMO 118.592-2, × 10. P–Y, *J. lindholmae*, Q is the holotype, the rest are paratypes, from 16·81–17·10 m interval, Tøyen Section; P, PMO 118.599-3, × 10; Q, PMO 118.595, × 10; R, PMO 118.600, × 10; S, PMO 118.597, × 5; T, PMO 118.599, × 5; U, PMO 118.596, × 5; V, PMO 118.597, × 10; W, PMO 118.600, × 10; X, PMO 118.600, × 5; Y, PMO 118.596, × 5.

fragments of the same species. Paratypes: PMO 118·596–600; mainly flattened specimens in dark shale. A few incomplete specimens are in very low relief.

Type locality. Tøyen Underground Station, City of Oslo, Norway, from the Tøyen Shale (16·81–17·10 m) within the *P. augustifolius elongatus* biozone (see Text-fig. 2). Abundant fragmentary specimens on slabs of black mudstone. Usually preserved as flattened films of silvery periderm, but a few specimens are preserved in low relief. The associated fauna comprises *P. angustifolius elongatus*, *Expansograptus* sp., *Tetragraptus isograptoides*, *T.* cf. *serra*, *T. reclinatus*, *Pendeograptus* cf. *pendens*, *Janograptus* sp., *Acrograptus gracilis* and ?*Trichograptus*.

Other occurrence. Krapperup Core in Scania (Lindholm 1981), from the zone of *P. augustifolius elongatus*.

Description. Small, slender sicula: 1·0–1·5 mm long; 0·25 mm wide at aperture. Short nema occasionally present to 0·8 mm long, but sicula apex narrow and poorly differentiated from nema. Near apex of sicula distinct corrugations apparent, probably indicating prosicula. Th 1^1 originates mid-way along the sicula and grows down adpressed to it. Thecae are very long, slender and slightly sigmoidally curved. Thecal overlap about one-half proximally and increases slowly distally. Thecal spacing: more than 3 mm proximally, 1·4–1·6 mm (6–7 th/mm) distally; thecal inclination: 5–8°. The stipe width increases slowly from 0·3–0·4 mm proximally to 0·6–0·8 mm at about th 7.

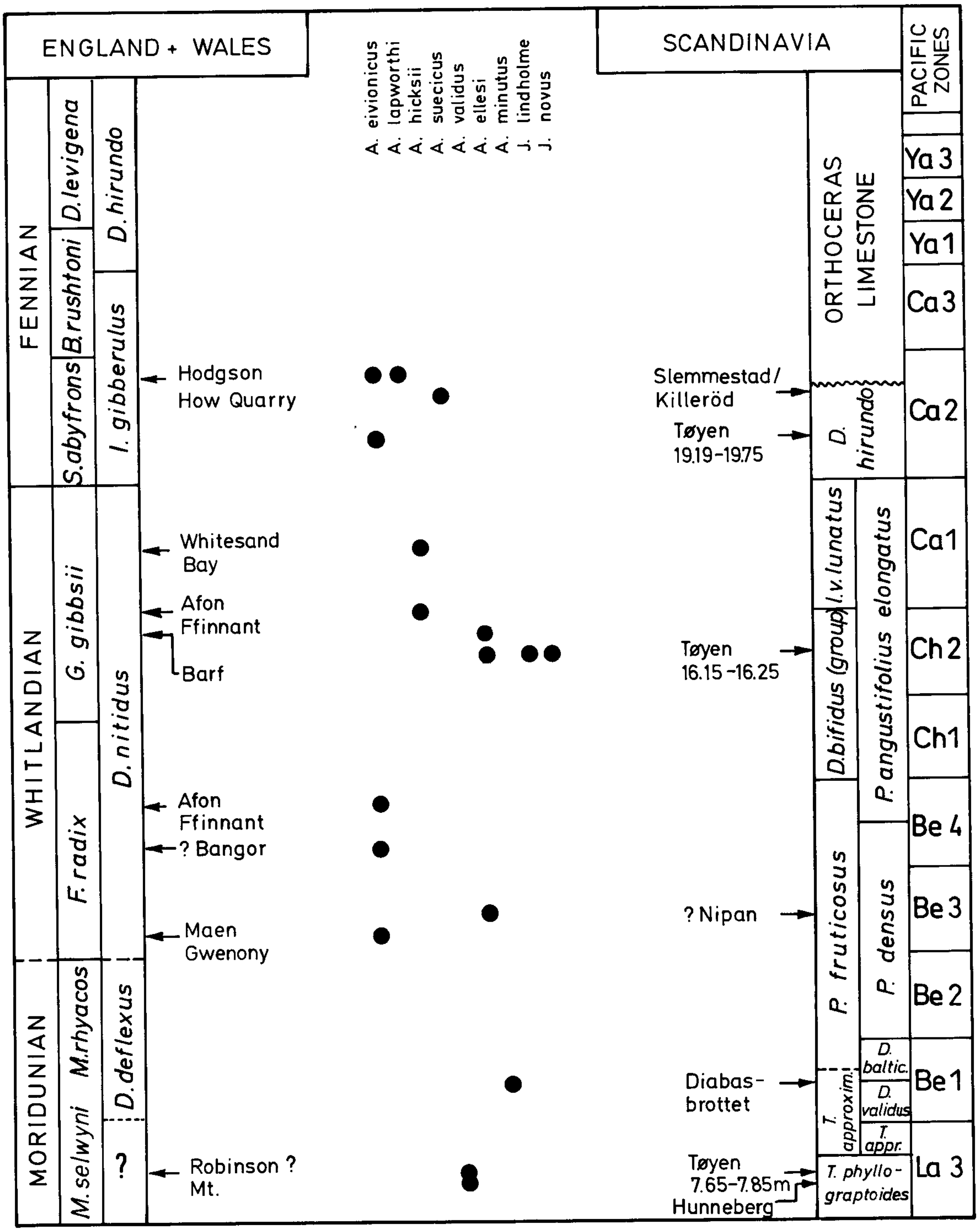
Discussion. Stipe characters distinguish *J. lindholmae* and *J. novus* from other species but do not allow distinction between them. This is only possible on features of proximal development; *J. lindholmae* has a sicula only half as long on average, and longer th 1 than *J. novus*.

The material from the Krapperup core in Scania (Lindholm 1981) is closely comparable to that described above but the description of the former would suggest some slight differences. Constrictions at the level of the aperture of the preceeding theca and the development of true prothecal folds are not seen in the Tøyen specimens but such features could be the product of preservation. The prothecal folds in figure 6*b* of Lindholm (1981) are weakly developed and are thought to be induced by the origin of the next theca: at the point of origin of a theca a small ridge is usually visible and might be over-interpreted as a prothecal fold. In flattened material there is no evidence of prothecal folds (Lindholm 1981, fig. 6*b*). Constrictions of the thecal apertures could be the product of differential compaction of the apertures in otherwise relief material.

BIOSTRATIGRAPHIC USE

Azygograptus may be considered a good biostratigraphic indicator of the Arenig Series since species described from the Llanvirn (e.g. *A. coelebs*) cannot be confirmed as belonging to the genus, if valid species. However, its use in the biostratigraphic subdivision of the Series has proved more limited. Elles (1922) proposed a lineage from *A. lapworthi* through *A. eivionicus* to *A. suecicus*, but provided little evidence to support this conclusion. In China, a zone of the Ningkuoan has locally been referred to as the *A. suecicus* biozone. However, this appears to reflect an abundance of the genus at the given level rather than a limited range for the named species. Due to the difficulty in reliably identifying species from descriptions and illustrations alone, the following discussion concentrates on the evidence from Britain and Scandinavia. Unless otherwise stated, the biozone refers to the local stratigraphy from which the specimens under discussion have come (cf. difference in British and Scandinavian *hirundo* biozone (Text-fig. 22)).

The major problem in using *Azygograptus* for biostratigraphy is that it displays a number of characters which are undesirable for this purpose. The absence of *Azygograptus* from the Pacific 'province' precludes its direct use for international correlation, and the nature of its distribution suggests at least the possibility of geographically isolated populations even within the Atlantic 'province'. However, it is its facies controlled distribution, which often causes the genus to be isolated from other biostratigraphic control, that makes the possibility of using the genus for correlation desirable.



TEXT-FIG. 22. Stratigraphic distribution of *Azygograptus* and *Jishougraptus* in Britain and Scandinavia with a correlation between the two areas.

Objective evidence for the succession of species in *Azygograptus* is very limited. The Diabasrottet section on the Hunneberg Mountain has *A. minutes* overlying *A. validus*, and the Tøyen section has yielded three species of *Azygograptus* and two of *Jishougraptus* but these come from a very small proportion of the overall succession. The biostratigraphic use of the genus is therefore largely dependent on ranges inferred by independent correlation of isolated occurrences (see Text-fig. 22).

The oldest species identified in the Tøyen section is *A. validus* and here, as elsewhere in Scandinavia, it is only known from the *T. phyllograptoides* biozone. The overlying Scandinavian biozone, *D. balticus*, has also yielded a single species only, *A. minutus*, which is unknown outside its type locality.

Since the international correlation of the base of the Moridunian Stage (cf. Fortey and Owens 1987) is uncertain, the single specimen of *A. validus* from Robinson Mountain may be the only representative of *Azygograptus* in Britain from strata equivalent to the lowest two biozones of the Arenig in Scandinavia. The biostratigraphic use of the genus is therefore difficult to evaluate over this interval and must await evidence from a wider area.

A. ellesi appears to range through the *densus* (Nipan) and *augustifolius elongatus* (Slemmestad) biozones, and the British occurrence at Barf may reasonably be considered to come from the same time interval, though the difference in sicular length does reduce the confidence in the identification of the two populations as conspecific. The species of *Jishougraptus* that occur with *A. ellesi* at Tøyen are both known only from the *P. angustifolius elongatus* biozone. The genus, based on the evidence of the type species, ranges somewhat higher.

Given the uncertainty in the correlation of the British Stages (Moridunian and Whitlandian) with the Scandinavian succession, the precise ranges of contemporary British species are unclear. *A. eivionicus* is associated with a Moridunian trilobite fauna at Arennig (Zalasiewicz 1986) and may range as high as the *gibberulus* biozone (Hodgson How Quarry). There is little to constrain independently the age of the occurrence at Bangor, but it may well be approximately contemporary with other occurrences in Wales and close to the Moridunian/Whitlandian boundary. *A. eivionicus* therefore appears to be a long ranging species of little biostratigraphic potential.

This contrasts with the species to which *A. eivionicus* may be related on the evidence of transient populations. *A. hicksii* is unknown outside South Wales and appears to be restricted to the *Gymnostomix gibbsii* biozone (late Whitlandian). *A. lapworthi* has not been found associated with any independent age control outside the type locality, where it may be placed in the *gibberulus* biozone on the basis of an isograptid associated with *D. hirundo*. Circumstantial evidence for the North Wales occurrences is compatible with a Fennian age and at present the species may be considered restricted to this interval in Britain. However, the material from Bolivia may extend the range downward. *A suecicus* in Scandinavia is a similarly rare form and appears to be restricted to the Scandinavian *D. hirundo* biozone, and may occur contemporary with *A. lapworthi.*

In summary, neither *Azygograptus*, nor the related genus *Jishougraptus*, have species that provide useful or reliable correlative indicators between Scandinavia and Britain. Interestingly the species that do provide some hints of use are *A. ellesi* and *A. validus* which have a less restricted biofacies association. The restriction of all species of Group 1, apart from *A. eivionicus*, to either Scandinavia or Britain may indicate that the Tornquist Sea was a partial barrier to migration. For this reason the British species may prove to have more potential for correlation with other peri-Gonwannan localities.

EVOLUTION OF *AZYGOGRAPTUS*

Azygograptus forms part of the adaptive radiation of the Dichograptidae that took place in the early Ordovician, and a possible origin of the genus is during the upper Tremadoc regression (cf. Erdtmann 1986; Fortey 1984). However, the evolutionary position of *Azygograptus* in this radiation is less clear, particularly with regard to whether the genus represents a mono- or polyphyletic grouping.

As illustrated in Text-figure 7, two morphological groups can be recognized in *Azygograptus* on the presence (Group 2) or absence (Group 1) of adpressed growth of th 1^1 and the sicula.

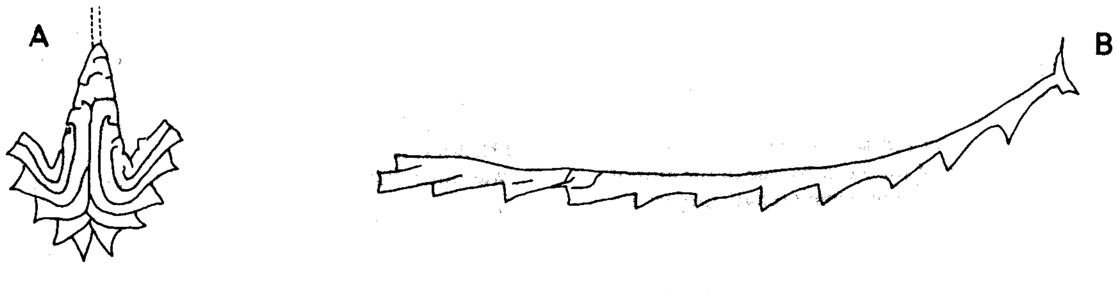
Fortey and Cooper (1986) proposed a phylogenetic classification for graptoloids on the principle that the earlier a growth decision in the development of the rhabdosome the greater its evolutionary and taxonomic significance. Within this classification *Azygograptus* was taken as separating from *Expansograptus* by suppression of dichotomy d1. However the growth decision series proposed (Fortey and Cooper 1986, table 1) has nine decisions which preceed that affecting dichotomy d1, and the majority of these concern the form of the sicula and its relationship to th 1^1. The concept of growth decisions therefore implies a polyphyletic origin for *Azygograptus*, with suppression of dichotomy d1 having occurred in at least two separate lineages.

An alternative way of examining the origin of *Azygograptus* is to consider the mechanisms by which the genus may have originated and the ancestors indicated. Skevington (1966) suggested that a dimorphic population with both biramous and uniramous forms would provide a suitable ancestor for *Azygograptus*. Support for this model is provided by a population of *Kiaerograptus* (Rushton 1981) which does show variation in the number of stipes. However in this population, as in the single, questionable specimen of *Parazygograptus*, the first theca of a second stipe is present, probable th 1^1.

The presence of a vestigal stipe can be explained by failure of th 1^2 to be dicalycal in an ancestor with isograptid development. The origin of the second stipe in isograptid development is therefore not strictly the result of a dicalycal theca, but of the opposite direction of growth of th 1^2 and th 1^1. Similarly, from a dicalycal theca the new thecae grow in opposite directions. The azygograptid morphology can therefore be derived from an ancestor with either isograptid or artus development by the loss of the ability for a new theca to develop in the opposite direction to that from which it buds, and this automatically causes failure of dichotomy d1.

From the arguments presented earlier on the ecology of *Azygograptus* the more restricted ecology of the species in group 1 may indicate that they are better adapted to an *r*-selective environment. The selective pressures of such an environment are ideally suited to the formation of isolated marginal populations that may be founded on only a few individuals. Since all the species of group 1 grade into *A. eivionicus* to a greater or lesser extent, they may almost be regarded as end members in an extremely variable species, and in this respect the differences between the species are much less marked than in group 2. Therefore, despite the apparently greater number of species in group 1 the evolutionary pool represented by group 2 is probably much greater.

A possibly more important aspect of the peculiar ecology of the species in group 1 is that adaptation to an *r*-selective environment could have affected proximal development. Such an environment favours rapid development and the morphology of azygograptids can be explained as a response to this pressure in that is maximizes stipe length for a given number of budding events (see Text-fig. 23):

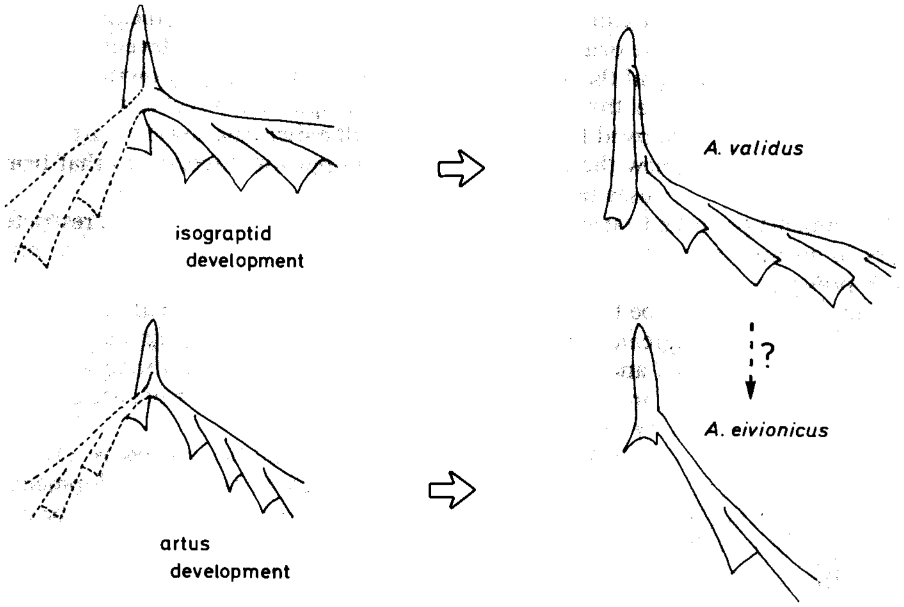


TEXT-FIG. 23. Comparison of rhabdosome form for the same number of budding events between *Pseudisograptus* (A) and *Azygograptus* (B). 11 thecae present in each.

1. abrupt metasicular origin of th 1^1 maximizes the stipe length provided by the first theca;
2. suppression of dichotomy d1 removes 'doubling-back' and overlap;
3. low thecal inclination with limited overlap maximizes stipe length for a given number of thecae.

An effect of the above is to maximize the separation of thecal apertures and therefore a selective pressure favouring this could be an explanation for the morphology, but the implications for proximal development remain the same.

No firm conclusion can therefore be reached on the evolutionary origins of *Azygograptus*. The oldest known species is *A. validus* and an origin from a extensiform didymograptid with isograptid development is attractive for this species (see Text-fig. 24). Once the single stipe morphology had originated the other members of the genus could have evolved from it by progressive adaptation to an *r*-selective environment. Alternatively, the species of group 1, and possibly *A. ellesi*, could have evolved separately from an extensiform with artus development such as *D. simulans*, with which they appear to be geographically and ecologically associated. Therefore, the same selective pressures that may have caused convergence in rhabdosome morphology for a polyphyletic group, could also have produced differences in proximal development in a monophyletic group.



TEXT-FIG. 24. Alternative extensiform ancestors for *Azygograptus* species.

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