VARIABILITY IN THE ORDOVICIAN ACRITARCH *DICRODIACRODIUM*

by THOMAS SERVAIS, RAINER BROCKE *and* OLDA FATKA

ABSTRACT. Species of the Ordovician acritarch genus *Dicrodiacrodium*, with a single apical process, are evaluated critically, based on a review of published literature and new studies on material from Belgium, Bohemia, China, Germany, and Morocco. Investigations of large populations of such species show a wide variability between specimens. Biometric studies, including measurements on type area material, show that the subdivision into varieties and even into species is not justified. There is a complete gradation between all of the predescribed taxa, which are impossible to distinguish. Therefore, all specimens with a single apical process are classified as a single taxon: *Dicrodiacrodium ancoriforme* emend. nov. *D. ancoriforme* is very easy to recognize and of great biostratigraphical and palaeogeographical importance. Its First Appearance Datum (FAD) is in the Arenig *Undulograptus sinodentatus/Didymograptus nexus* graptolite Zone in South China (approximately equivalent to the British Arenig *Isograptus gibberulus* Biozone). Palaeobiogeographically, it is typical of the cold to temperate Gondwanan and peri-Gondwanan ('Mediterranean') Palaeoprovince.

A MAJOR problem of acritarch research is the abundant literature and the enormous number of published taxa; both very difficult to survey. In the Ordovician, taxonomic confusion is common: a great number of genera and species have been described without sufficient comparison with similar taxa, and the diagnoses commonly overlap from one taxon to another.

Acritarch taxa generally show a very wide variability. The study of larger populations indicates that the original descriptions are sometimes based on poorly preserved material and/or a small number of specimens. To establish the limits between taxa and to eliminate overlap, thorough reviews of existing species and genera are needed, rather than the publication of further 'new' taxa, which may only increase the existing taxonomic confusion.

The problem of variability is not unique to acritarchs. Hughes (1994), for example, published a review of the Late Cambrian trilobite *Dikelocephalus*, in which no fewer than 25 species were suppressed as junior synonyms of *D. minnesotensis*, following bivariate and multivariate analyses of variation. While such biometric investigations are today common in the study of most fossil groups, they are still neglected in acritarch research.

Burmann (1968) erected the genus *Dicrodiacrodium* for acritarchs with a heteropolar vesicle, one pole bearing a network of fine filaments, the other provided with one or several appendices which branch distally into simple pinnae. Burmann (1968) described the new genus, its five species, and nine varieties from (1) the 'upper Llanvirn' of the boreholes Rügen 3h and Arkona 101, both drilled on the Island of Rügen, Baltic Sea (north-east Germany), and (2) from exposures of the Griffelschiefer-section 'Bahnhang nördlich Unterhermsgrün', Vogtland (south-east Germany), which is assigned to the Arenig. The exact positions and the precise ages of the samples were not indicated and remain uncertain. The type material has not been accessible until now.

The present paper is an attempt to rationalize the taxonomy of *Dicrodiacrodium*. It is based on a review of published literature and on new investigations on material from different localities, including the type area. A biometric approach is used to study intraspecific variation in specimens with a single apical process. It is based on bivariate analyses of variation using parameters such as the process length and the central body length and width.

MATERIAL AND METHODS

The new material studied comes from Germany, Belgium, Morocco, Bohemia, and China. The German material is from the boreholes Binz 1 and Rügen 5 on the Island of Rügen (type area of

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the genus). The material from Binz 1 is of late Llanvirn *Didymograptus murchisoni* graptolite Zone age (Servais and Katzung 1993). Six samples from the following depths have been analysed: 5041·8 m (sample no. 4); 5102·4 m (22); 5117·1 m (27); 5139·1 m (28); 5163·0 m (34); 5217·6 m (37). The sample from Rügen 5 (sample no. 61, depth 3287·3 m) is of early Llanvirn *D. artus* graptolite Zone age (Jaeger, pers. comm.). The type material of all taxa with a single apical process (Burmann 1968) comes from levels attributed to the 'upper Llanvirn' (*D. murchisoni* graptolite Zone age) from the same area, but from other boreholes (Rügen 3 and Arkona 101). It has not been accessible for the present study.

The Belgian material was collected from exposures of the Huy Formation in the Bande de Sambre-et-Meuse, of early Llanvirn *D. artus* graptolite Zone age (Servais and Maletz 1992), and from levels in the Ordovician Rigenée Formation in the Brabant Massif, the precise age of which is unknown (Servais 1991).

The Moroccan material comes from the borehole Boujad-109, Tadla Basin. Two samples from depths 360 m and 511 m have been investigated. Previous acritarch studies on this material were published by Cramer *et al.* (1974*a*, 1974*b*) and Cramer and Díez (1976, 1977), indicating a late Arenig or a late Arenig to early Llanvirn age based on palynological evidence. Recent studies on Chitinozoa (Soufiane and Achab 1993) provide evidence for a late Arenig age for depths between 481 m and 512 m in borehole Boujad-109.

The Bohemian samples, of late Arenig age, were collected from the upper part of the Klabava Formation in the Mýto section, and in the lowermost layers of the Šárka Formation in the Drahouš section (cf. Kraft and Kraft 1993). The sample from the Mýto section is dated as belonging to the *D. bulla* chitinozoan Zone (Paris and Mergl 1984, sample 16). The samples from the Drahouš section (S-1 to S-15) were collected from the *Corymbograptus retroflexus* graptolite Zone (Fatka and Brocke in press, figs 1, 3).

The Chinese material occurs in the *Azygograptus suecicus* and *Undulograptus sinodentatus/Didymograptus nexus* graptolite zones in the Dawan Formation in the Wangjiazei and Datianba sections, Yangtze Platform, Hubei Province, south-east China (Fatka and Brocke in press; Brocke, unpublished data).

All samples were subjected to standard palynological preparation techniques and were sieved at 10 or 12 μm. The Belgian, German and Moroccan samples were oxidized using Schulze's solution.

SYSTEMATIC PALAEONTOLOGY

INCERTAE SEDIS

Group ACRITARCHA Evitt, 1963

Genus DICRODIACRODIUM Burmann, 1968

Type species. Dicrodiacrodium ancoriforme Burmann, 1968.

Original diagnosis. 'Heteropolar gebaute Formen mit starker morphologischer Betonung des länglich–ovalen oder zylindrischen Zentralkörpers. Der apikale Pol trägt ein, zwei oder mehrere Fortsätze, die sich terminal schwingenförmig oder ankerartig in einfache Fortsatzanhänge aufspalten. Das Längenverhältnis von apikalen Fortsätzen zum Zentralkörper schwankt (*c.* 0·2–1). Der Zentralkörper ist glatt oder von paralleler Längsrippung bedeckt, selten skulptiert. Der antapikale Pol trägt ein Netzwerk, das meist erst an der Polkappe ansetzt, aber auch auf den Zentralkörper übergreifen kann. Das Netzwerk besteht entweder nur aus dünnen Bögen und Streben, oder es wird von stärkeren Stützfortsätzen (zwei peripheren Hauptfortsätzen oder/und mehreren feineren Fortsätzen) getragen' (Burmann 1968).

Translation of original diagnosis (new translation). Heteropolar forms with a strong morphological accentuation of the cylindrical or oblong–oval central body. The apical pole bears one, two or several processes which split distally into simple anchor- or flail-shaped pinnae. The ratio of the length of the apical processes to that of the central body varies (approximately 0·2 to 1). The central

body is smooth or covered by a system of longitudinally arranged parallel ribs; it is rarely sculptured. The antapical pole bears a network which generally originates at the polar cap but which may extend to the central body. The network consists of either thin arches and props only, or is borne by strongly developed supporting processes (two peripheral major processes and/or several thinner processes).

List of species and varieties of Dicrodiacrodium *described in the literature*

Dicrodiacrodium ancoriforme Burmann, 1968.
  var. *ancoriforme* (1968) Autonym.
  var. *minutum* Burmann, 1968.
Dicrodiacrodium bicrure Burmann, 1968.
Dicrodiacrodium fulcratum Burmann, 1968.
  var. *fulcratum* (1968) Autonym.
  var. *procerum* Burmann, 1968.
Dicrodiacrodium normale Burmann, 1968.
  var. *breviuscula* nomen nudum (cited in Burmann 1976)
  var. *cylindricum* Burmann, 1968.
  var. *doliiforme* Burmann, 1968.
  var. *longiusculum* Burmann, 1968.
  var. *normale* (1968) Autonym.
Dicrodiacrodium retiforme Burmann, 1968.

Remarks. All species and varieties attributed to the genus *Dicrodiacrodium* were described by Burmann (1968), based on material from eastern Germany. No further species, subspecies, or varieties have been described.

Only the two species with a single apical process, *D. ancoriforme* and *D. normale*, have been widely cited in later references. Their identification is very easy. The other species with two or more apical processes (*D. bicrure*: two processes; *D. retiforme*: more than two processes; *D. fulcratum*: *c.* four processes) have not been cited since Burmann's (1968) original description, except for one record of *D.* aff. *fulcratum* Burmann by Vavrdová (1990*b*, p. 241, specimen not figured).

Burmann (1968) described all species and varieties with a single apical process from the 'upper Llanvirn' of Rügen, while all species and varieties with two or more apical processes were recorded from the 'Arenig' Griffelschiefer of the Vogtland. Only *Dicrodiacrodium normale* var. *breviuscula* nomen nudum with a single apical process was indicated by Burmann (1976) to occur in the Griffelschiefer. This form, however, has never been described formally.

The specimens with more than one apical process, described from the 'Arenig' Griffelschiefer, appear to be very rare. In the present study, very few specimens were recorded (five specimens in the *A. suecicus* graptolite Zone in China and one in the Moroccan material). Future studies will possibly show that they should be related to another genus of the large 'diacrodian' group of acritarchs. This group includes a great number of genera with heteropolar vesicles, such as *Arbusculidium* Deunff, 1968, *Barakella* Cramer and Díez, 1977, *Buchinia* Volkova, 1990, *Calyxiella* Golub and Volkova *in* Volkova and Golub, 1985, *Dasydiacrodium* Timofeev, 1959, *ex* Deflandre and Deflandre-Rigaud, 1962, *Ladogella* Golub and Volkova *in* Volkova and Golub, 1985, *Nellia* Golub and Volkova *in* Volkova and Golub, 1985, *Schizodiacrodium* Burmann, 1968, and *Stephanodiacrodium* Vavrdová, 1986. The taxonomy of this group needs to be revised.

In the present paper, the genus *Dicrodiacrodium* is neither emended nor split, because information on the complete plexus of forms is still too poor. At present, no species are removed from the genus. The biometric investigations in the present study are limited to specimens with a single apical process. Further studies are needed to clarify the taxonomy of the complete genus and the relation to other genera of the 'diacrodian' plexus.

All specimens with a single apical process are here classified as *Dicrodiacrodium ancoriforme* emend., because the biometric studies clearly indicate that there are no arguments for splitting them into several species and varieties. The overloaded original diagnosis of *D. ancoriforme* in Burmann

(1968) is here emended and simplified to include all species and varieties of *Dicrodiacrodium* with a single apical process.

No excystment structure of *Dicrodiacrodium* has yet been observed.

Dicrodiacrodium ancoriforme Burmann, 1968 emend. nov.

Plate 1

ǂ = specimen(s) not illustrated
? = attribution to the species questionable
?? = attribution to the species very questionable
non = attribution to the species incorrect

Bold numbers after each synonym refer to Text-figures 4–5.

	1968	*Dicrodiacrodium ancoriforme* Burmann, p. 643, pl. 3, fig. 1; pl. 7, fig. 2a–c. (**1**)
	1968	*Dicrodiacrodium ancoriforme* var. *minutum* Burmann, p. 644, pl. 5, fig. 5. (**1**)
	1968	*Dicrodiacrodium normale* Burmann, p. 644, pl. 3, fig. 2. (**1**)
	1968	*Dicrodiacrodium normale* var. *doliiforme* Burmann, p. 645, pl. 3, figs 5–6. (**1**)
	1968	*Dicrodiacrodium normale* var. *longiusculum* Burmann, p. 645, pl. 7, fig. 1a–c. (**1**)
	1968	*Dicrodiacrodium normale* var. *cylindricum* Burmann, p. 645, pl. 3, figs 3–4; pl. 7, fig. 3. (**1**)
ǂ	1970	*Dicrodiacrodium normale* Burmann, 1968 (*cf.*) [*sic*]; Martin *et al.*, p. 344. (**2**)
ǂ	1970	*Dicrodiacrodium normale* Burmann; Martin *et al.*, p. 347. (**2**)
	1973*a*	*Dicrodiacrodium normale* Brm.; Burmann, p. 760, pl. 1, fig. 1a–b. (**3**)
??	1973*a*	*Dicrodiacrodium normale* Brm.; Burmann, pl. 2, fig. 2a–d. (**3**)
	1973*b*	*Dicrodiacrodium normale* Brm.; Burmann, p. 13, pl. 2, figs 1–2; pl. 3, fig. 2. (**4**)
non	1974*a*	*Dicrodiacrodium ancoriforme* Burmann; Cramer *et al.*, p. 190, pl. 28, figs 13–14, 20. (**5**)
??	1974*a*	*Arbusculidium filamentosum* (Vavrdová 1965) [*sic*]; Cramer *et al.*, p. 190, pl. 28, figs 15–16, 18–19, 23. (**5**)
	1974*b*	*Dicrodiacrodium ancoriforme* Burmann; Cramer *et al.*, p. 64, pl. 26, fig. 18. (**6**)
ǂ	1974	*Dicrodiacrodium normale* Burmann; Jardiné *et al.*, p. 108, fig. 3:53. (**7**)
	1974	*Dicrodiacrodium ancoriforme* Burm.; Lefort and Deunff, p. 77, pl. 1, figs 10, 14, 17. (**8**)
	1974	*Dicrodiacrodium normale* Burm.; Rauscher, p. 106, pl. 7, fig. 1. (**9**)
??	1975	*Dicrodiacrodium normale* Burm.; Deunff and Massa, p. 22, pl. 1, fig. 20. (**10**)
	1976	*Dicrodiacrodium ancoriforme* n. sp. [*sic*]; Burmann, table 1:26. (**11**)
	1976	*Dicrodiacrodium ancoriforme* var. *minuta* n. var. [*sic*]; Burmann, table 1:27. (**11**)
	1976	*Dicrodiacrodium normale* n. sp. [*sic*]; Burmann, p. 51, table 1:22. (**11**)
	1976	*Dicrodiacrodium normale* var. *breviuscula* Burmann, p. 51, table 1:21 (nomen nudum). (**11**)
	1976	*Dicrodiacrodium normale* var. *longiuscula* n. var. [*sic*]; Burmann, table 1:23. (**11**)

EXPLANATION OF PLATE 1

Figs 1–9. *Dicrodiacrodium ancoriforme* Burmann, emend. nov. 1, Institut für Geologie und Paläontologie, Technische Universität Berlin, sample WJZDW-14, slide C2, England Finder graticule co-ordinates N 42/1; Dawan Formation, Wangjiazei section, south-east China; *Undulograptus sinodentatus/Didymograptus nexus* graptolite Zone; × 850. 2, Palaeontological Institute, Charles University, Prague, slide S-2. S-2/A, England Finder graticule co-ordinates S 55/4; Šárka Formation, Drahouš section, Bohemia; *Corymbograptus retroflexus* graptolite Zone; damaged specimens; × 850. 3–9, Services Associés de Paléontologie de l'Université de Liège. 3, 6, 9, Boujad-9 borehole, Tadla Basin, Morocco; *Desmochitina bulla* chitinozoa Zone; × 750. 3, slide 20542, England Finder graticule co-ordinates L42/3; depth 511 m. 6, slide 20539, England Finder graticule co-ordinates F 38/1; depth 360 m. 9, slide 20540, England Finder graticule co-ordinates S 38/3–4; depth 360 m. 4, 7, Rügen 5 borehole, north-east Germany, depth 3287·1 m; ?*Didymograptus artus* graptolite Zone; × 750. 4, slide 22821, England Finder graticule co-ordinates L 43. 7, slide 22804, England Finder graticule co-ordinates Y 47/4–Y 48/3. 5, slide 22835, England Finder graticule co-ordinates P 43/3; Binz 1 borehole, north-east Germany, depth 5117·1 m; *Didymograptus murchisoni* graptolite Zone; × 750. 8, slide 22250b, 22666, England Finder graticule co-ordinates G34/2; Sart-Bernard section, Belgium; Huy Formation, *Didymograptus artus* graptolite Zone; × 1000.


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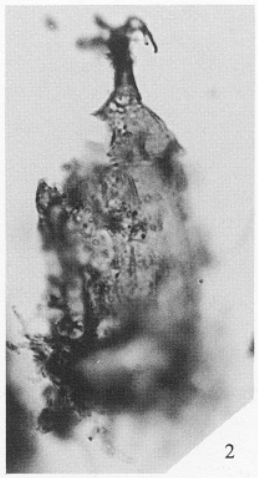
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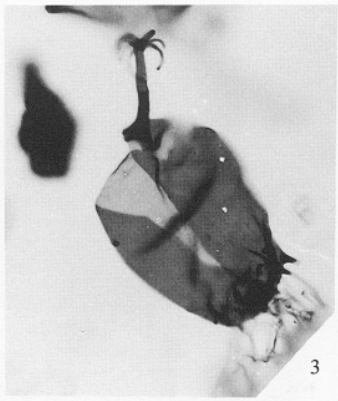
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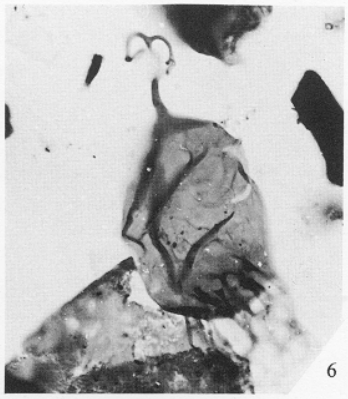
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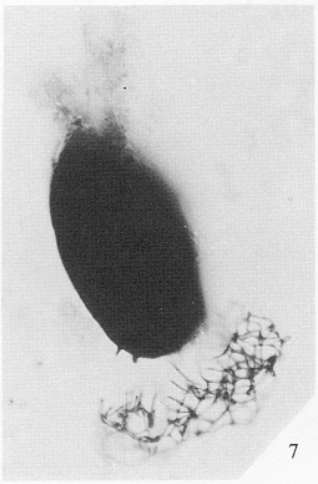
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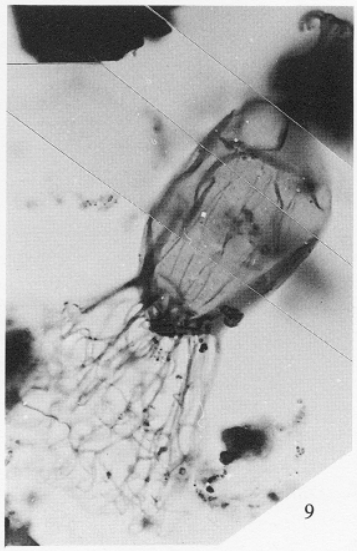
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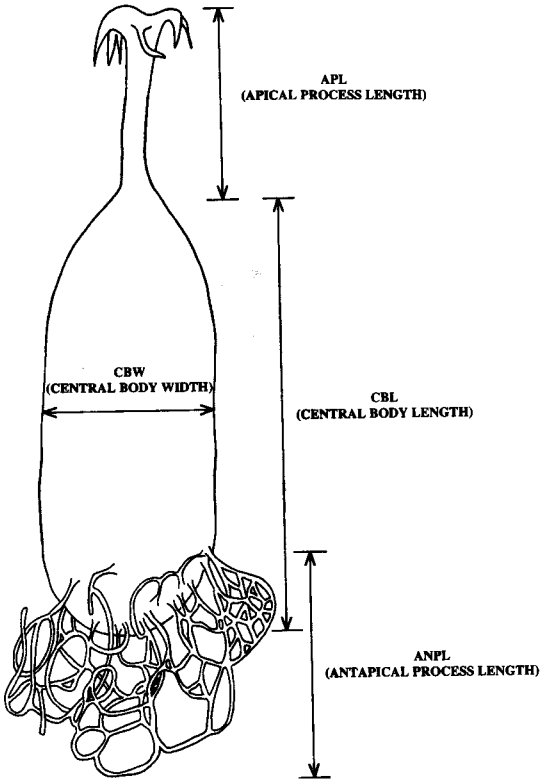
SERVAIS *et al.*, *Dicrodiacrodium*

1976 *Dicrodiacrodium normale* var. *cylindrica* n. var [*sic*]; Burmann, table 1:24. (**11**)
1976 *Dicrodiacrodium normale* var. *doliiformis* n. var. [*sic*]; Burmann, table 1:24. (**11**)
1976 *Dicrodiacrodium ancoriforme* Burmann 1968; Eisenack *et al.*, p. 205. (**12**)
1976 *Dicrodiacrodium ancoriforme minutum* Burmann; Eisenack *et al.*, p. 207. (**12**)
1976 *Dicrodiacrodium normale* Burmann; Eisenack *et al.*, p. 215. (**12**)
1976 *Dicrodiacrodium normale cylindricum* Burmann; Eisenack *et al.*, p. 217. (**12**)
1976 *Dicrodiacrodium normale doliiforme* Burmann; Eisenack *et al.*, p. 219. (**12**)
1976 *Dicrodiacrodium normale longiusculum* Burmann; Eisenack *et al.*, p. 221. (**12**)
± 1976 *Dicrodiacrodium normale* Burmann, Vavrdová, p. 62. (**13**)
± 1977 *Dicrodiacrodium ancoriforme* Burmann; Díez and Cramer, p. 3. (**14**)
± 1977 *Dicrodiacrodium ancoriforme minutum* Burmann; Díez and Cramer, p. 3. (**14**)
± 1977 *Dicrodiacrodium normale* Burmann; Díez and Cramer, p. 17. (**14**)
± 1977 *Dicrodiacrodium normale cylindricum* Burmann; Díez and Cramer, p. 17. (**14**)
± 1977 *Dicrodiacrodium normale doliiforme* Burmann; Díez and Cramer, p. 17. (**14**)
± 1977 *Dicrodiacrodium normale longiusculum* Burmann; Díez and Cramer, p. 17. (**14**)
1977 *Dicrodiacrodium normale* Burmann; Vavrdová, p. 110, pl. 2, fig. 3; text-fig. 3. (**15**)
1978 *Dicrodiacrodium normale* Burmann; Kalvacheva, p. 306, pl. 1, fig. 1. (**16**)
± 1978 *Dicrodiacrodium normale* Burmann; Vavrdová, p. 72. (**17**)
1979 *Dicrodiacrodium ancoriforme* Burmann; Cramer and Díez, p. 42, fig. 58. (**18**)
± 1979 *Dicrodiacrodium normale*; Cramer and Díez, p. 127. (**18**)
± 1979 *Dicrodiacrodium ancoriforme* Burmann; Martin and Rickards, p. 191. (**19**)
?? 1979 *Dicrodiacrodium* cf. *ancoriforme* Burmann; Martin and Rickards, p. 193, pl. 1, fig. 20. (**19**)
± 1979 *Dicrodiacrodium normale* Burmann; Vanguestaine, p. 251. (**20**)
?? 1979 *Dicrodiacrodium* cf. *normale* Burmann; Vanguestaine, p. 249, pl. 5, fig. 11. (**20**)
1982 *Dicrodiacrodium normale* Burmann; Martin, p. 30, pl. 1, fig. 4. (**21**)
1982 *Dicrodiacrodium normale* Burmann; Turner, p. 122, pl. 17, fig. 5. (**22**)
± 1982*a* *Dicrodiacrodium normale* Burmann; Vavrdová, p. 149. (**23**)
± 1982*b* *Dicrodiacrodium normale*; Vavrdová, p. 338. (**24**)
1984 *Dicrodiacrodium ancoriferum* Burmann [*sic*]; Downie, p. 14, text-fig. 5: 59. (**25**)
1984 *Dicrodiacrodium normale* Burmann; Downie, p. 14, fig. 5:60. (**25**)
?? 1985 *Dicrodiacrodium normale* Burmann; Fournier-Vinas, p. 809, pl. 1, fig. 4. (**26**)
± 1986 *Dicrodiacrodium normale* Burmann; Kalvacheva, p. 40. (**27**)
± 1986 *Dicrodiacrodium normale* Burmann; Vavrdová, p. 355. (**28**)
± 1988 *Dicrodiacrodium normale* Burmann; Vavrdová, p. 8. (**29**)
± 1989 *Diacrodium* cf. *normale* Burmann [*sic*]; Steemans, p. 305. (**30**)
± 1989 *Diacrodium normale* Burmann [*sic*]; Steemans, p. 331. (**30**)
? 1989 *Dicrodiacrodium normale* Burmann; Vavrdová, p. 404, text-fig. 1:L5. (**31**)
± 1990 *Dicrodiacrodium normale* Burmann; Fensome *et al.*, p. 191. (**32**)
± 1990 *Dicrodiacrodium ancoriforme* Burmann; Fensome *et al.*, p. 191. (**32**)
± 1990 *Dicrodiacrodium ancoriforme* var. *ancoriforme* Burmann; Fensome *et al.*, p. 191. (**32**)
± 1990 *Dicrodiacrodium ancoriforme* var. *minutum* Burmann; Fensome *et al.*, p. 191. (**32**)
± 1990 *Dicrodiacrodium normale* var. *cylindricum* Burmann; Fensome *et al.*, p. 191. (**32**)
± 1990 *Dicrodiacrodium normale* var. *doliiforme* Burmann; Fensome *et al.*, p. 191. (**32**)
± 1990 *Dicrodiacrodium normale* var. *longiusculum* Burmann; Fensome *et al.*, p. 191. (**32**)
± 1990 *Dicrodiacrodium normale* var. *normale* Burmann; Fensome *et al.*, p. 191. (**32**)
± 1990 *Dicrodiacrodium normale* Burmann [*sic*]; Ghavidel-Syooki, p. 217. (**33**)
± 1990 *Dicrodiacrodium* spp.; Molyneux, p. 616. (**34**)
± 1990*a* *Dicrodiacrodium normale* Burmann; Vavrdová, p. 238. (**35**)
± 1991 *Dicrodiacrodium ancoriforme* Burmann; Fensome *et al.*, p. 4. (**36**)
± 1991 *Dicrodiacrodium normale* Burmann; Fensome *et al.*, p. 66. (**36**)
1991 *Dicrodiacrodium* sp.; Servais, p. 240, pl. 1, fig. 10. (**37**)
1992 *Dicrodiacrodium ancoriforme minutum* Burmann; Millward and Molyneux, p. 81, fig. 3j. (**38**)
± 1992 *Dicrodiacrodium normale* Burmann 1970 [*sic*]; Servais and Maletz, p. 272. (**39**)
± 1993 *Dicrodiacrodium normale* Burmann; Vavrdová, p. 128. (**40**)
± 1994 *Dicrodiacrodium* spp.; Servais, p. 574. (**41**)
± 1994 *Dicrodiacrodium ancoriforme-normale* Burmann group; Servais *et al.*, p. 37. (**42**)
± 1994 *Dicrodiacrodium* spp.; Fatka *et al.*, p. 35. (**43**)



TEXT-FIG. 1. Measurement parameters of *Dicrodiacrodium ancoriforme*.

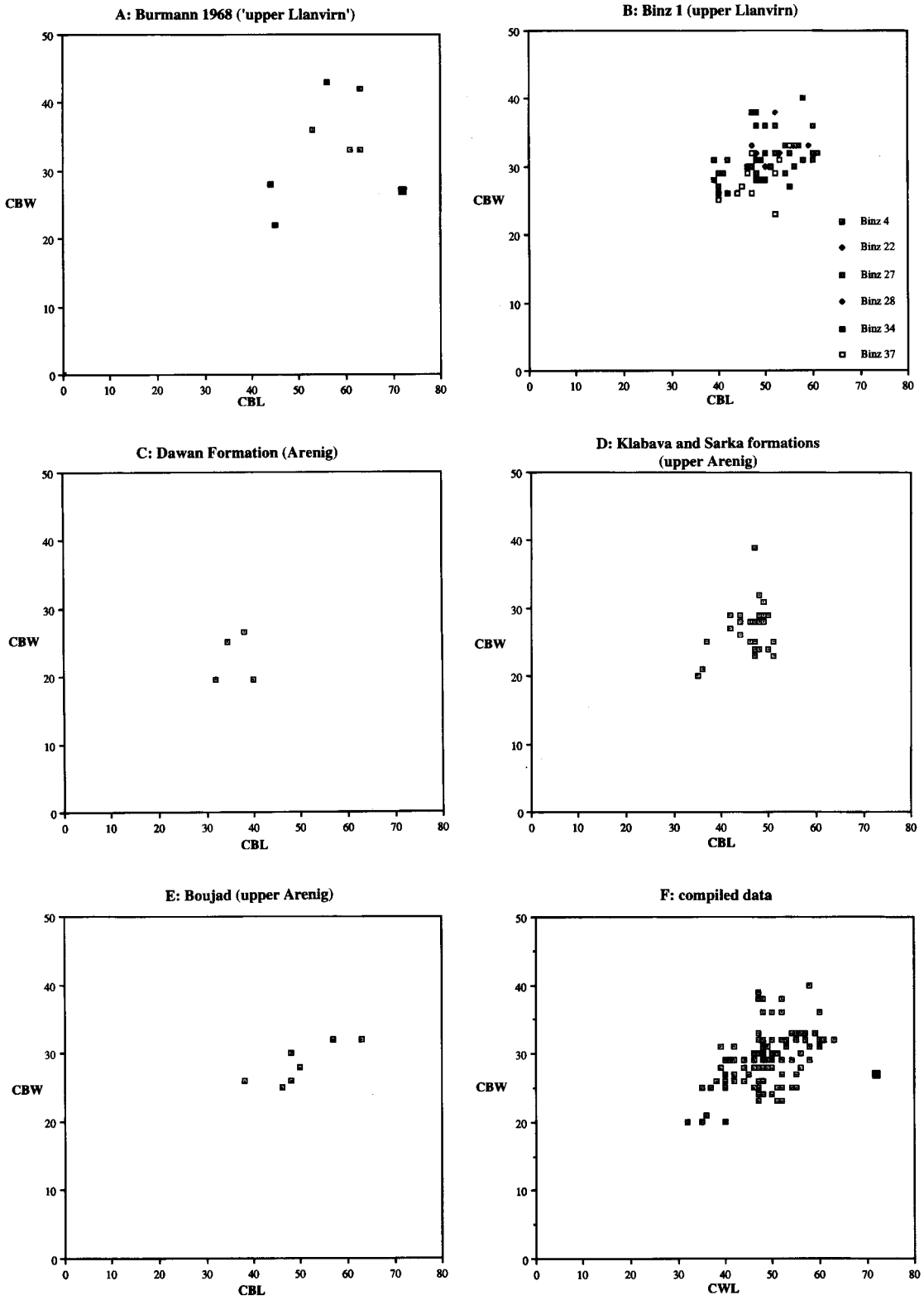
Holotype. Burmann (1968, pl. 3, fig. 1; pl. 7, fig. 2a–c). S 1880/65 (3,5/106,7).

Type locality. Borehole Rügen 3h, north-east Germany. Sample 117 ('upper Llanvirn'), exact depth and position of the sample unknown.

Original diagnosis. 'Heteropolar differenzierter Zentralkörper länglich-oval, am apikalen Pol in einen starken, sich nicht verjüngenden, jedoch relativ kurzen Einzelforsatz übergehend, der sich terminal ankerartig in mehrere (*c*. 6) stachelförmige Fortsatzanhänge aufspaltet. Das Längenverhältnis Fs (und Mh): Zk ist sehr gering. Eine Basisfassung des apikalen Fortsatzes ist nicht erkennbar, wohl aber stärkere Pigmentierung an der Ansatzstelle. Der gewölbte antapikale Pol trägt ein blasenartiges Maschenwerk unterschiedlicher Maschengrösse. Das Netzwerk besteht aus feinen (d < 1 μm), relativ kurzen Bögen und gleichartigen Stützstreben. Dadurch ist das Netz recht straff und gut erhalten. Stützfortsätze fehlen' (Burmann 1968).

Emended diagnosis. Heteropolar central body of variable oblong–oval to cylindrical shape, smooth or with longitudinal parallel ribs. The apical pole bears a single process of variable length, not tapering, with or without a basal plug, distally splitting from a single point into tapering, unbranched, barb-shaped pinnae, *c*. four to eight in number. The antapical pole bears a dense anastomosing network of fine threads with or without supporting rods.

Measurements (Text-fig. 1).
Central body length (CBL) 25–61 μm.
Central body width (CBW) 19–44 μm.
Apical process length (APL) 6–28 μm.


A: Burmann 1968 ('upper Llanvirn')
B: Binz 1 (upper Llanvirn)
C: Dawan Formation (Arenig)
D: Klabava and Sarka formations (upper Arenig)
E: Boujad (upper Arenig)
F: compiled data
CBW
CBL
CWL
Binz 4
Binz 22
Binz 27
Binz 28
Binz 34
Binz 37

Apical process width 2–4 μm.
Terminal pinnae up to 8 μm long.
Antapical process length (ANPL) up to 40 μm long.

Remarks. D. ancoriforme is very easy to recognize. Its characteristic shape, with one single apical process, is so typical that a scanning electron microscope is not needed for its determination.

Burmann (1968) erected two species (*D. ancoriforme* and *D. normale*) and four varieties, without autonyms, to describe her specimens. According to Burmann (1968), *D. ancoriforme* has a rather short apical process, whereas that of *D. normale* is longer. She subdivided *D. ancoriforme*, erecting var. *minutum* for specimens of smaller size. *D. normale* was divided into var. *cylindricum* for specimens with a cylindrical central body, var. *doliiforme* for those with a barrel-shaped central body, and var. *longiusculum*, for specimens with a very long apical process (Burmann 1968). This splitting into six different taxa appears exaggerated and may lead to the supposition that Burmann (1968) investigated very few specimens. Subsequent workers generally followed Burmann's (1968) classification scheme and determined their specimens at the species and even at the varietal level.

It is evident that the ratio between the central body length and the apical process length is the main diagnostic feature at the species level. However, Burmann's (1973*a*, 1973*b*) determinations of *D. normale* do not accord with the original diagnosis: the apical process length of the figured specimens is either too small or was not correctly measured (see below). Burmann (1973*a*, pl. 2, fig. 2a–d) even determined a specimen as *D. normale* with an apical process which is broken. Cramer *et al.* (1974*a*), Deunff and Massa (1975), Vanguestaine (1979), Martin *in* Martin and Rickards (1979) and Fournier-Vinas (1985) also determined specimens with broken processes at the species level.

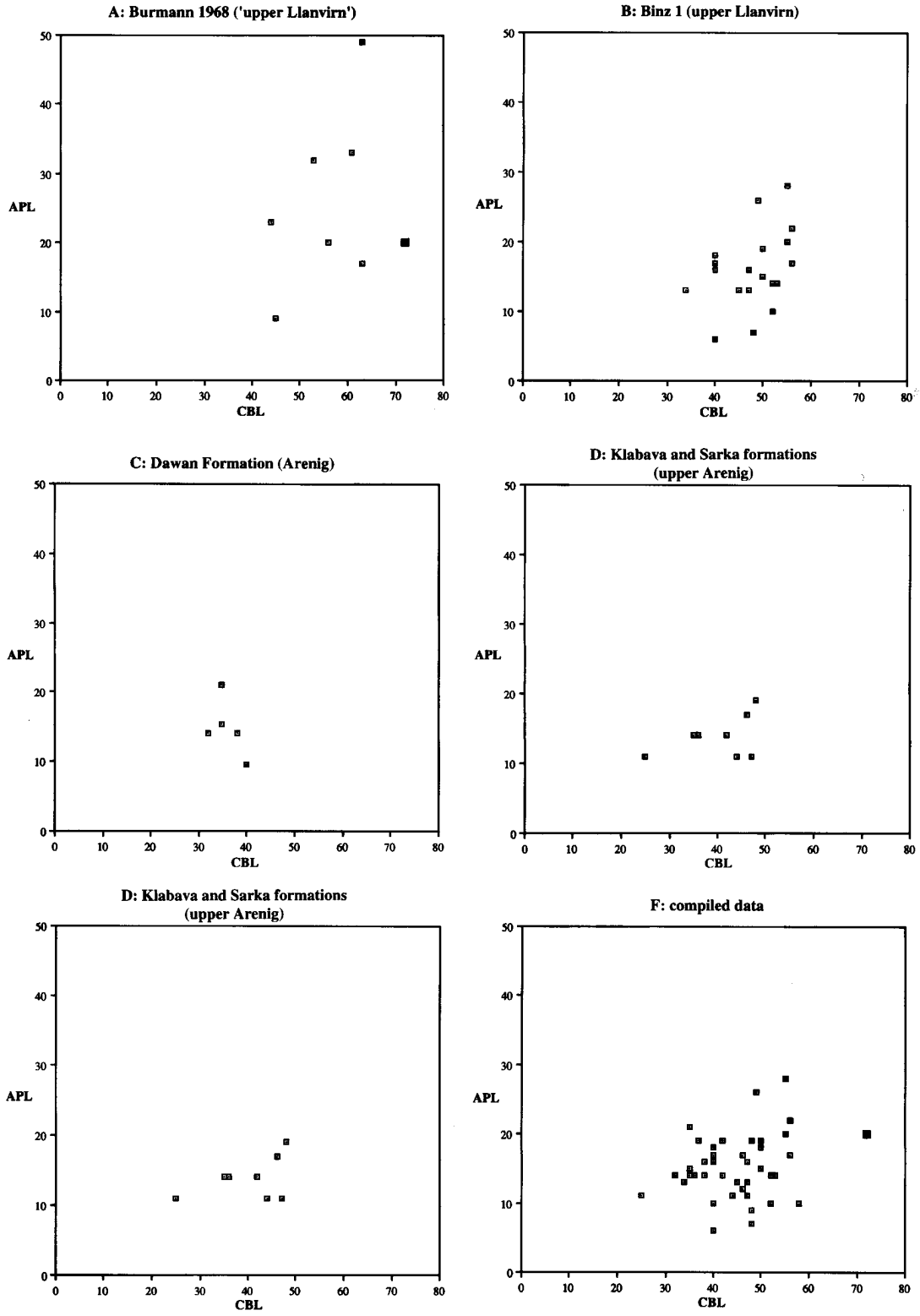
Biometric investigations. Cramer *et al.* (1974*a*, p. 188) noted that they found 'all kinds of transitional forms' in the Moroccan material and that a distinction between Burmann's taxa was difficult.

In the present work, large populations of *Dicrodiacrodium* specimens with a single apical process were measured to understand the relations between Burmann's taxa: 66 German, 33 Bohemian, 14 Belgian, 11 Chinese, and 9 Moroccan specimens were investigated. The following parameters were measured (Text-fig. 1): the central body length (CBL), the central body width (CBW), the apical process length (APL) and the antapical process length (ANPL). In addition, the width of the apical process, and the length of the terminal pinnae were also measured.

Text-figure 2A–F shows the scatter diagrams of CBL against CBW, Text-figure 3A–F the scatter diagrams of CBL against APL. The data plotted include Burmann's (1968) measurements, taken from the original descriptions (including that for the holotype), and new measurements of specimens from the upper Llanvirn of borehole Binz 1 (Germany), the Arenig Dawan Formation (South China), the upper Arenig of the Klabava and Šárka formations (Czech Republic) and the upper Arenig of borehole Boujad-9 (Morocco).

All scatter diagrams show that the data of each individual area (Text-figs 2B–E, 3B–E) are reasonably concentrated in clusters. Only minor differences between the data from different areas have been observed. The scatter diagrams of the compiled data (Text-figs 2F, 3F) indicate that all specimens are clearly concentrated in a single cluster. There are no arguments for splitting the specimens into several units, using either the ratio of CBL to CBW, or the ratio of CBL to APL. On the contrary, Text-figure 2F clearly shows that all intermediates between specimens with small and large central bodies exist. Text-figure 3F illustrates the presence of a continuous transition between specimens with short and long processes. Therefore, it appears evident that only one name should be used for all specimens: *C. ancoriforme.*

TEXT-FIG. 2. Scatter diagram of central body length (CBL) against central body width (CBW) for specimens of *Dicrodiacrodium ancoriforme* in Burmann (1968) (A); and samples from borehole Binz 1, Germany (B); the Dawan formation, China (C); the Klabava and Šárka Formations, Czech Republic (D); borehole Boujad-9, Morocco (E); and compiled data of all specimens investigated in the present study (F). The holotype of Burmann (1968) is represented by a larger black square in figures A and F.


A: Burmann 1968 ('upper Llanvirn')
B: Binz 1 (upper Llanvirn)
C: Dawan Formation (Arenig)
D: Klabava and Sarka formations (upper Arenig)
D: Klabava and Sarka formations (upper Arenig)
F: compiled data
APL
CBL
0
10
20
30
40
50
60
70
80

The only data which are not in accord with the clusters of Text-figures 2F and 3F are those from the original description of Burmann (Text-figs 2A, 3A). Neither do Burmann's (1968) measurements correspond with the data from Binz in the type area (Text-figs 2B, 3B).

There is, however, a very simple explanation for Burmann's exaggeration of some of her CBL, CBW, and APL values: Burmann (1968, 1973*a*, 1973*b*) worked with thin sections, not palynological slides. On specimens which were partly fragmented, she measured the total length (of CBL, CBW, and APL) by also including the interstices in her values. The APL of the holotype of *D. normale* var. *longiusculum*, for example, was measured as 49 μm, which is a value which has never been recorded in other populations; the longest apical process found in the present investigation is only 28 μm long (borehole Binz, sample 28). However, it is possible that long, slender apical processes were not observed after Burmann's (1968) description from thin sections, because poorly preserved material commonly breaks during palynological preparation treatment.

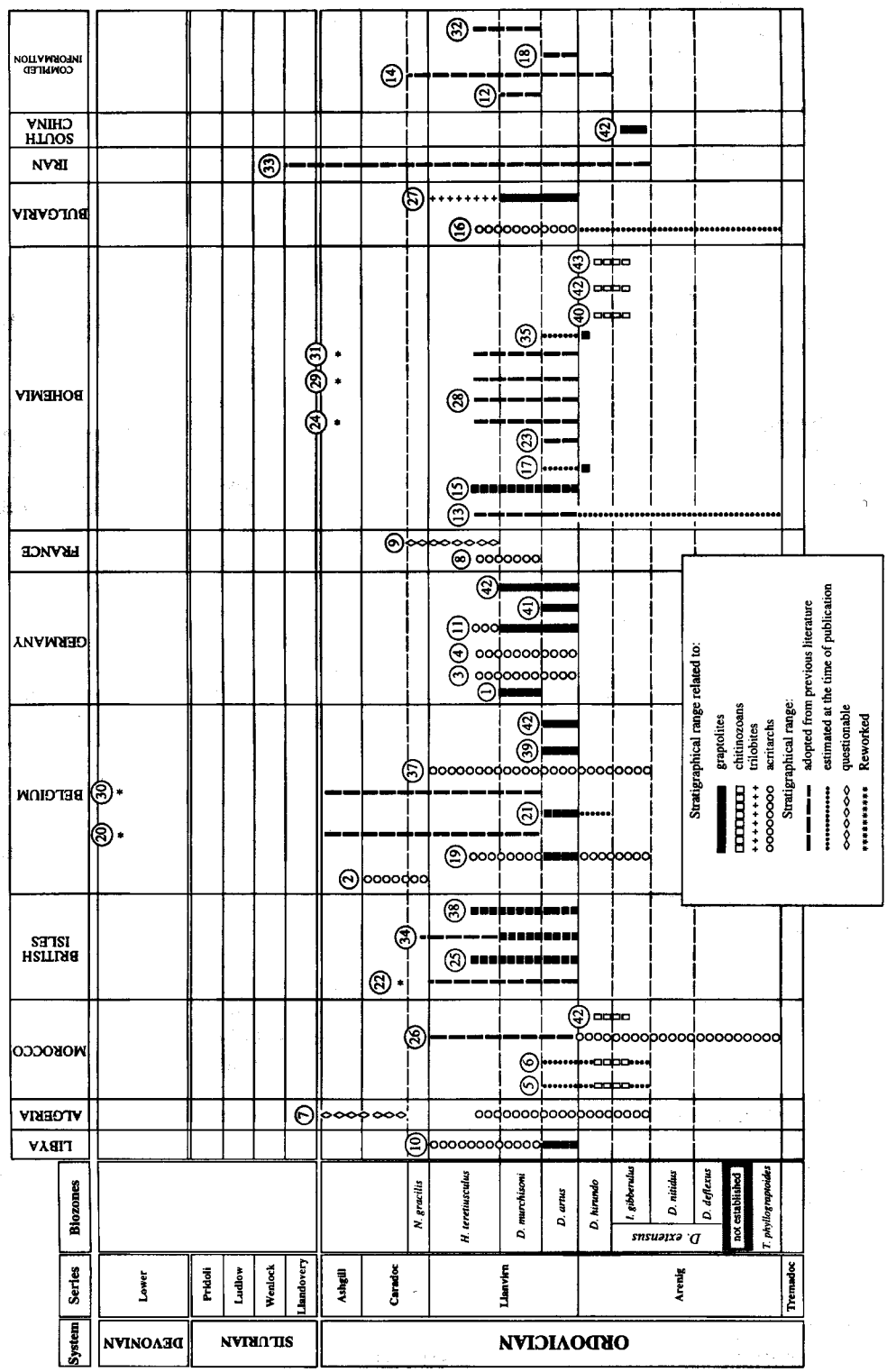
The holotype of *D. ancoriforme* emend. nov. is unfortunately also outside the clusters obtained in the present study (Burmann indicated a CBL of 72 μm, a CBW of 27 μm and a APL of 20 μm). The specimen of Burmann (1968) which corresponds more or less to the mean of the values (CBL about 45 μm; CBW about 30 μm, and APL about 15 μm) is the paratype of *D. normale* var. *cylindricum*. The problem of the holotype being outside of the measured range found in this study is not in contradiction with the attribution of all specimens to the taxon *D. ancoriforme*, because, according to Article 7.3 of the International Code of Botanical Nomenclature (Greuter *et al.* 1994), 'the nomenclatural type is not necessarily the most typical or representative element of a taxon'.

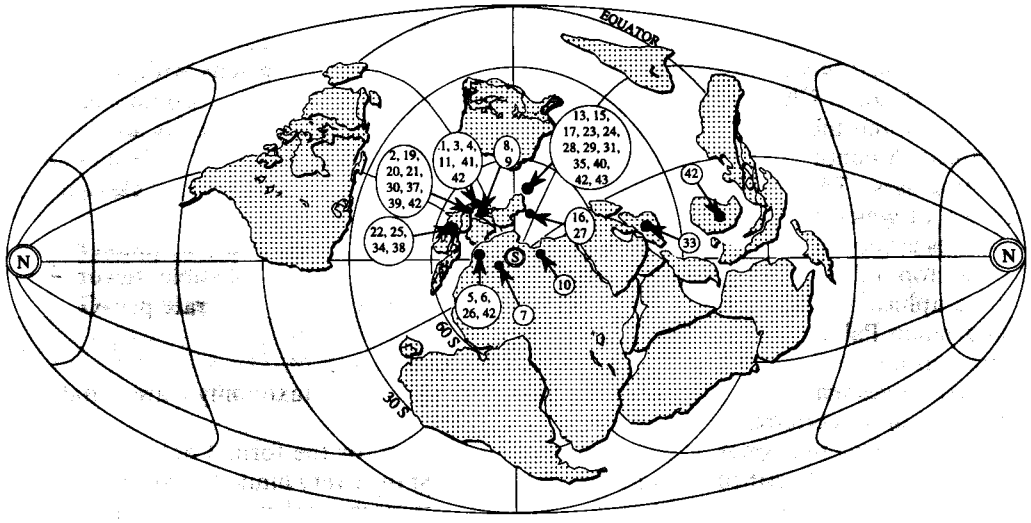
Stratigraphical range. Text-figure 4 shows the stratigraphical distribution of *D. ancoriforme*, based on a review of the literature. The stratigraphical ranges are those indicated by the original authors. They must be regarded critically, because some of them were not correct; others are no longer justified or still questionable. The ranges indicated by the authors were either based on other fossil groups, such as graptolites (e.g. Burmann 1968), chitinozoans (e.g. Fatka *et al.* 1994), and trilobites (e.g. Kalvacheva 1986), or were the result of acritarch evidence only (e.g. Lefort and Deunff 1974). In several works, the indicated stratigraphical range was adopted from previous publications (e.g. Downie 1984), or estimated by the author at the time of the publication, but not precisely documented (e.g. Vavrdová 1976). Some ranges indicated in the literature should be considered as questionable, because the levels bearing the species were insecurely dated (e.g. Rauscher 1974). In other papers, the occurrence of the species is the result of reworking into younger sediments (e.g. Steemans 1989). Finally, only few occurrences of the species are adequately dated and, therefore, only few of the indicated ranges can be justified.

Initially, *D. ancoriforme* was considered to be an indicator for rocks of late Llanvirn age (e.g. Burmann 1973*a*, 1973*b*; Lefort and Deunff 1974). Subsequently, the species was for a long time considered to be typical of Llanvirn or younger rocks, because the species had never been recorded in pre-Llanvirn rocks in the British Isles (Molyneux 1990), and because undisputed occurrences in the Arenig had not been published. However, such occurrences in the Arenig are now known. In Morocco, the samples of Cramer *et al.* (1974*a*, 1974*b*) from 'upper Arenigian to lower Llanvirnian' rocks have recently been redated by chitinozoans as being of late Arenig age (Soufiane and Achab 1993).

In Bohemia, precise biostratigraphical information on the Arenig–Llanvirn interval is missing from the numerous publications of Vavrdová (1976–1993). Recent studies on the Arenig–Llanvirn boundary indicate that the lowermost part of the Šárka Formation is of late Arenig age (Kraft and Kraft 1993, fig. 2). In the Bohemian sequence, *D. ancoriforme* first appears in the late Arenig

TEXT-FIG. 3. Scatter diagram of central body length (CBL) against apical process length (APL) for specimens of *Dicrodiacrodium ancoriforme* in Burmann (1968) (A); and samples from borehole Binz 1, Germany (B); the Dawan formation, China (C); the Klabava and Šárka Formations, Czech Republic (D); borehole Boujad-9, Morocco (E); and compiled data of all specimens investigated in the present study (F). The holotype of Burmann (1968) is represented by a larger black square in figures A and F.


System
Series
Biozones
LIBYA
ALGERIA
MOROCCO
BRITISH ISLES
BELGIUM
GERMANY
FRANCE
BOHEMIA
BULGARIA
IRAN
SOUTH CHINA
COMPILED INFORMATION
ORDOVICIAN
SILURIAN
DEVONIAN
Tremadoc
Arenig
Llanvirn
Caradoc
Ashgill
Llandovery
Wenlock
Ludlow
Pridoli
Lower
T. phyllograptoides
not established
D. extensus
D. deflexus
D. nitidus
I. gibberulus
D. hirundo
D. artus
D. murchisoni
H. teretiusculus
N. gracilis
Stratigraphical range related to:
graptolites
chitinozoans
trilobites
acritarchs
Stratigraphical range:
adopted from previous literature
estimated at the time of publication
questionable
Reworked



TEXT-FIG. 5. Palaeogeographical map for the Early Ordovician (Arenig), modified after Scotese and Denham (1988) and Torsvik and Trench (1991), showing the geographical distribution of *Dicrodiacrodium ancoriforme*. Numbers correspond with those listed in the synonymy.

D. bulla chitinozoan Zone in the Mýto section (Vavrdová 1993; Fatka *et al.* 1994) and is also present in the lowermost layers of the Šárka Formation in the Drahouš section.

The first appearance of *D. ancoriforme* in the Chinese Dawan Formation is in the *Undulograptus sinodentatus/Didymograptus nexus* graptolite Zone (Brocke, unpublished data), which can be correlated approximately with the British Arenig *Isograptus gibberulus* Biozone (Wang *et al.* 1992).

All other previously cited occurrences in the Arenig are not proven and are mainly dated on acritarch evidence only. Therefore, the First Appearance Datum of *D. ancoriforme* is in the *U. sinodentatus/D. nexus* graptolite Zone in South China.

The species is frequently recorded in rocks of Llanvirn age. Younger occurrences have not been clearly documented. The species is considered to be reworked in the Upper Ordovician (e.g. Turner 1982; Vavrdová 1982*b*) and Lower Devonian (Vanguestaine 1979; Steemans 1989), but the upper range of the species is as yet unknown.

Palaeogeographical distribution. Published information about the distribution of *D. ancoriforme* is plotted on a palaeogeographical map of the Early Ordovician (Text-fig. 5). The species has only been recorded in areas of cold to temperate water-masses in the southern hemisphere. It is widely distributed in sediments from Gondwana (Morocco, Algeria, Libya) and peri-Gondwana (British Isles, Belgium, Germany, France, Bohemia and Bulgaria). So far, the species has only been recorded from two areas which are supposed to be at a slightly lower latitude (Iran and South China), but it has never been cited from warmer water mass provinces, such as Baltica and Laurentia. *D. ancoriforme* can therefore be considered as typical of the cold to temperate Gondwanan and peri-Gondwanan ('Mediterranean') Palaeoprovince.

TEXT-FIG. 4. Stratigraphical distribution of *Dicrodiacrodium ancoriforme*, based on a literature review. Numbers correspond with those in the synonymy list. The stratigraphical ranges are those indicated by the authors. Some are questionable. For explanation, see text. Stratigraphical units and zones are modified from Rushton (1990), Fortey and Owens (1991), Wang *et al.* (1992), Cooper *et al.* (1995) and Fortey *et al.* (1995).

CONCLUSIONS

Biometric investigations (bivariate analyses) on *Dicrodiacrodium* specimens with a single apical process from Belgian, Chinese, Czech, German (type area), and Moroccan assemblages, show a wide variability and indicate clearly that splitting the specimens into two species and six varieties is not justified. A continuous transition exists between both small to long central bodies and short to long processes. Therefore, all specimens with a single apical process are classified as *D. ancoriforme*, of which the diagnosis is emended.

The species is very easy to recognize. It appears in the middle Arenig and is common in Llanvirn rocks. The top of its stratigraphical range is not certain, due to possible reworking. The palaeogeographical distribution of the species is limited to the cold to temperate peri-Gondwanan and Gondwanan Palaeoprovince.

The biometric investigation leads to the following conclusions.

1. Biometric investigations, generally neglected in acritarch taxonomy, are vital to the understanding of an acritarch taxon.
2. It appears evident that small populations cannot be used for the formal description of a new taxon. However, most described acritarch species are based on a very limited number of specimens. There should be a debate amongst a wider group of acritarch workers to consider a minimum number of specimens required for the description of a new taxon.
3. The description of (new) acritarch taxa necessitates absolutely a study of variability.
4. The study of assemblages from different areas and different stratigraphical horizons gives a more complete view of an acritarch taxon.
5. *Dicrodiacrodium ancoriforme*, with its easily measurable parameters, may serve as a typical example for future studies on acritarch biometrics with the aim of understanding acritarch variability and relationships between predefined taxa. The bivariate plots used for *Dicrodiacrodium* seem adequate for demonstrating the extent of intraspecific variation. In future studies the application of multivariate analyses should be tested also.

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