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The Ordovician acritarchs *Frankea breviscula*, *F. longiuscula*, and *F. sartbernardensis*: a new study

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ABSTRACT – Detailed observations and biometric analysis, based upon numerous specimens, facilitate enhanced morphological characterization of the Ordovician acritarchs *Frankea breviscula*, *F. longiuscula*, and *F. sartbernardensis*. These species are readily distinguishable providing a sufficiency of well-preserved specimens is available for study. The nature and distribution of microsculptural elements are detailed, and the method of excystment (via epityche) in the genus *Frankea* is documented for the first time. Stratigraphic ranges of *F. breviscula*, *F. longiuscula*, and *F. sartbernardensis* are critically re-evaluated on the basis of known records and new age-constrained biostratigraphic data. *F. sartbernardensis* first occurs in uppermost Arenig-basal Llanvirn strata, and constitutes an important component of lower Llanvirn (*Didymograptus artus* graptolite Zone) acritarch assemblages. The inception of both *F. breviscula* and *F. longiuscula* is within the *D. murchisoni* graptolite Zone (Llanvirn). In the stratigraphic sections examined (from Tunisia, Spain, and Belgium), the introduction of *F. breviscula* precedes that of *F. longiuscula*, which is more common in stratigraphically higher levels.

RIASSUNTO – [Gli acritarchi ordoviciani *Frankea breviscula*, *F. longiuscula* e *F. sartbernardensis*: un nuovo studio] – Osservazioni dettagliate ed una analisi biometrica, basate su numerosi esemplari, permettono una migliore caratterizzazione morfologica delle specie di acritarchi di età ordoviciani *Frankea breviscula*, *F. longiuscula* e *F. sartbernardensis*. Queste specie risultano facilmente distinguibili tra loro a condizione di avere a disposizione un numero sufficiente di esemplari in buono stato di conservazione. La natura e la distribuzione degli elementi microstrutturali (ornamentazione) delle tre specie vengono descritti in dettaglio e il metodo di escistamento (per mezzo di epiteca) del genere *Frankea* viene documentato per la prima volta. La distribuzione stratigrafica delle specie *F. breviscula*, *F. longiuscula*, e *F. sartbernardensis* viene criticamente rivista in base alle segnalazioni riportate in letteratura e di nuovi dati biostratigrafici con controllo cronostatigrafico indipendente. *F. sartbernardensis* compare tra la parte terminale dell'Arenig superiore e il Llanvirn basale; questa specie costituisce una componente importante delle associazioni di acritarchi del Llanvirn inferiore (Zona a graptoliti *Didymograptus artus*). La prima comparsa di *F. breviscula* e *F. longiuscula* avviene all'interno della Zona a graptoliti *D. murchisoni* (Llanvirn). Nelle sezioni stratigrafiche studiate (localizzate in Tunisia, Spagna e Belgio), *F. breviscula* compare prima di *F. longiuscula*; quest'ultima è più comune nei livelli stratigrafici più alti tra quelli investigati.

INTRODUCTION

The acritarch genus *Frankea*, established by Burmann (1970), and emended successively by Colbath (1986) and Servais (1993), is of considerable stratigraphic and palaeobiogeographic significance (Colbath, 1986, 1990; Brocke *et al.*, 1995; Servais & Fatka, 1997). Its morphological attributes and taxonomy have been discussed by several authors, viz., Colbath (1986), Servais (1993), Sarjeant & Stancliffe (1994), and Fatka *et al.* (1996).

This paper aims to provide new detailed information about the morphology, including excystment mode and microsculpture, of the relatively widespread species *F. sartbernardensis* (Martin, 1969) Colbath, 1986, *F. breviscula* Burmann, 1970, and *F. longiuscula* Burmann, 1970. Some new biostratigraphic data are also presented.

NOTE ON ORDOVICIAN CHRONOSTRATIGRAPHY

A unified global nomenclature of series and stage divisions of the Ordovician has yet to be formally

agreed and promulgated. A tripartite subdivision of the system into three series named the Lower, Middle, and Upper Ordovician was endorsed in 1996 by vote of Titular Members of the Ordovician Subcommittee of the IUGS/ICS (Mitchell *et al.*, 1997; Webby, 1998). This would serve as a basis for adoption of a six-fold global stage-level subdivision whereby each series is divided into two stages. However, there is no international agreement on the scope, rank, and correlation of the various proposed series including the Llanvirn, which is most relevant for the present study. Pending formal approval by the Ordovician Subcommittee, we herein accept the revised Ordovician chronostratigraphy proposed by Fortey *et al.* (1995) in which the Llanvirn series is subdivided into Abereiddian and Llandeilian stages. The Abereiddian embraces the *Didymograptus artus* and *D. murchisoni* graptolite Zones, its base being taken at the base of the *D. artus* Zone. The Llandeilian is considered to comprise only the *Hustedograptus teretiusculus* graptolite Zone, with no formal definition of its base. This subdivision has been accepted by Mitchell *et al.* (1997), Dalziel (1997), Cocks *et al.* (1997), and

Webby (1998), although it has received some criticism by Basset and Owens (1996).

MATERIAL AND METHODS

Material for this study comprises the following: thirteen core samples from two boreholes (St1 and Tt1) in the Central Sahara of Tunisia; two samples from the Sueve section, northern Spain; and one sample from the Chemin-de-Fer section of Sart Bernard, Belgium.

Palynological processing of these samples generally followed the standard methods used in the Palynological Laboratory of the Dipartimento di Scienze della Terra, Università di Pisa (see Tongiorgi *in* Bagnoli *et al.*, 1988, pp. 168-169). Oxidative treatment was performed on the Belgian sample in order to eliminate organic amorphous material and microscopic pyrite, internally present in most of its acritarch specimens, thus improving their separation from inorganic matter.

Both palynological strew slides and SEM preparations (now permanently mounted in polyester resin) have been studied. Some of the SEM preparations resulted from the single specimen picking technique as described by Vecoli and Playford (1997, p. 18).

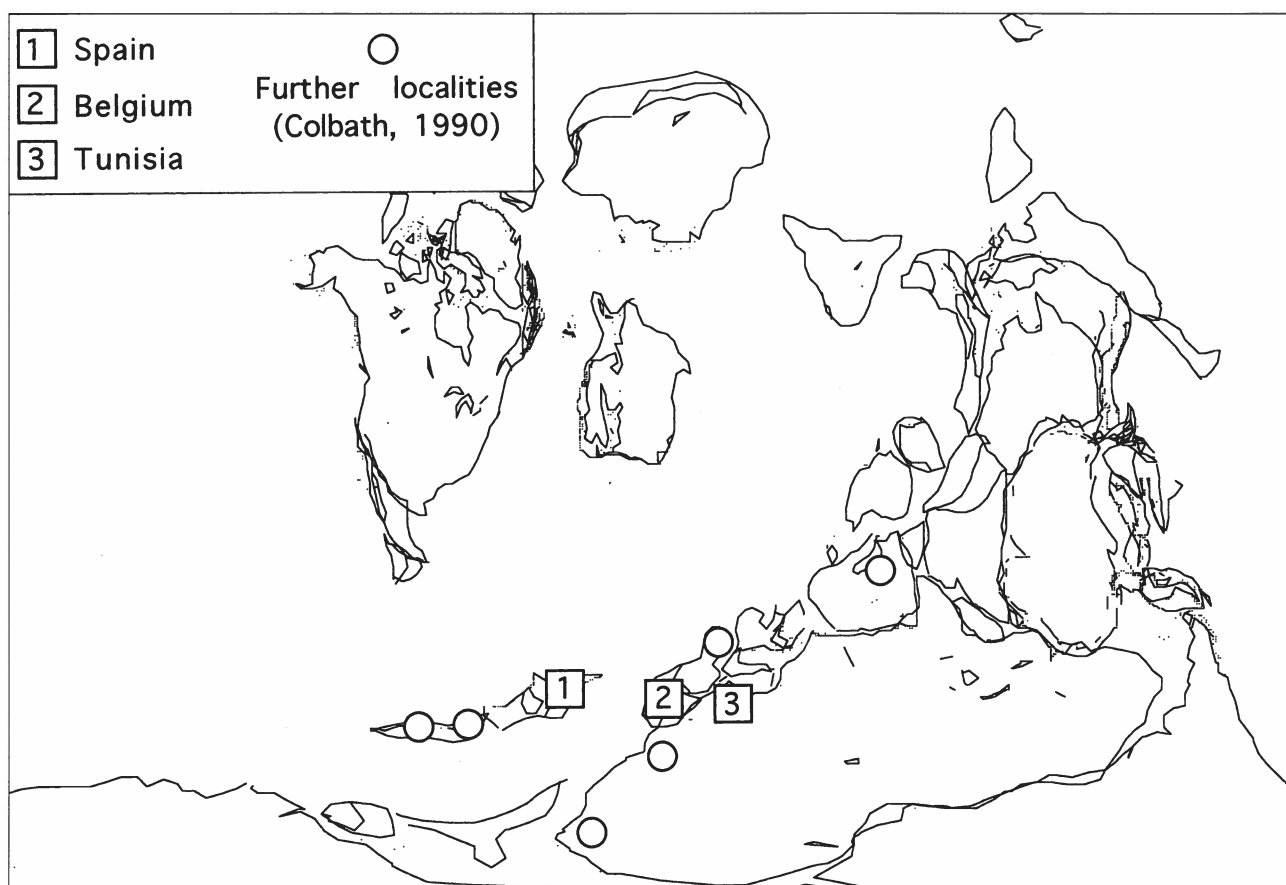
The north African samples yielded especially well preserved, yellow to dark brown acritarchs. Spanish palynomorphs are less advantageously preserved, mostly incomplete and very dark brown to black. The Belgian palynomorphs are commonly fragmented, deeply corroded and of grey to black appearance.

Palynological slides containing the study specimens are deposited in the collections of the Museum of Natural History of the Università di Pisa (Museo di Storia Naturale e del Territorio, Certosa di Calci, Pisa). Catalogue numbers (prefixed CPT) of that institution and other accessory details are incorporated in Appendix 1.

DESCRIPTION OF PALYNIFEROUS SAMPLES

TUNISIAN SAMPLES

The Tunisian samples are from two boreholes, Tt1 (lat. 32° 18' 23" N, long. 10° 59' 40" E) and St1 (lat. 32° 43' 12" N, long. 11° 07' 50" E), both drilled within the Rhadames Basin between the Djeffara and Sidi Toui uplifts. The wells are located respectively east and northeast of the town of Ramadah, close to the Libyan border (Text-fig. 1).



Text-fig. 1 - Palaeogeographic setting (Llanvirn, 440 MA; projection centered on 45° Lat S) and localities of the study samples.

From Tt1 well, six shaly samples, at 1462.3 m (core 37), 1472.0 m (core 38), 1485.0 m (core 39), 1494.3 m (core 39), 1504.0 m (core 40), and 1511.0 m (core 40), have been examined. This interval is within the Bir ben Tartar Formation, which has previously been dated as "Llanvirn-Llandeilo" (= Llanvirn; Deunff & Massa, 1975; Massa *et al.*, 1977) from the presence of graptolites indicative of *Didymograptus* (*Didymograptus*) *murchisoni* graptolite Zone. However, no clear fossil evidence exists to indicate a "Llandeilian" age (now upper Llanvirn according to the revised chronostratigraphy proposed by Fortey *et al.*, 1995); see Massa *et al.* (1977). Palynological data (Vecoli, unpubl.) suggest that the thin Kasbah Leguine Formation, supposedly Arenigian in age (Massa *et al.*, 1977), is missing (or not sampled) here. Accordingly, the Bir ben Tartar Formation is considered to directly succeed the Tremadocian Sanrhar Formation.

The seven shaly samples from St1 well, at 1476.5 m (core 29), 1487.9 m (core 30), 1509.0 m (core 31), 1520.5 m (core 32), 1529.5 m (core 32), 1543.5 m (core 34), and 1554.0 m (core 35), were also collected from the didymograptid-bearing Bir ben Tartar Formation (Massa *et al.*, 1977 and pers. comm.).

These borehole intervals are considered to be essentially coeval (Massa *et al.*, 1977; Massa, 1988 and pers. comm.; Vecoli, in press).

SPANISH SAMPLES

Two slate samples, S2-9 and AT/SU1b, were collected respectively by J.C. Gutierrez-Marco (CSIC-UCM, Madrid) and C. Aramburu (University of Oviedo), and by R. Albani and M. Tongiorgi, in stratigraphic proximity, near the top of the Cerracin Member of the Sueve Formation in the Cofiño Section, Sierra del Sueve, Cantabrian Mountains, northern Spain (Text-fig. 1). Both samples yielded *Didymograptus* (*Didymograptus*) *murchisoni* (Beck in Murchison, 1839) and *Linochitina pissotensis* Paris, 1981 and are attributed to the late Oretanian (Mediterranean terminology; Gutierrez-Marco *et al.*, 1996), which equates to the British upper Abereiddian, or upper-lower Llanvirn (Gutierrez-Marco *et al.*, 1996).

BELGIAN SAMPLE

A slate sample (SRB-72.305) was collected by M. Tongiorgi, A. Di Milia, and F. Martin at the precise type locality of *Frankea sartbernardensis* (Martin, 1966) Colbath, 1986; i.e., at the 72.305-km datum on the railway line near the station of Sart-Bernard, Condroz Ridge, Sambre-Meuse (Martin, 1969, fig. XX, p. 19; Text-fig. 1).

According to Martin (pers. comm., 1995), the sampled horizon represents the Huy Formation

(Assise de Huy). Servais and Maletz (1992) demonstrated an early Llanvirn age (*Didymograptus artus* graptolite Zone) for this unit.

BIOSTRATIGRAPHIC DISTRIBUTION

A comprehensive review of published *Frankea* occurrences has been compiled by Servais (1993, text-figs 2 and 3). Critical examination of the stratigraphic ranges documented for *Frankea breviscula* Burmann, 1970, *F. longiuscula* Burmann, 1970, and *F. sartbernardensis* reveals that most of the supposed pre-Llanvirn occurrences are based on either insecurely dated material or unreliable or equivocal stratigraphic data (e.g., Lister & Holliday, 1970; Cramer & Diez, 1977; Vanguetaine, 1978; Turner & Wadge, 1979; Downie, 1984; Fournier-Vinas, 1985). The only exception is the occurrence of *F. sartbernardensis* at a "horizon just below the Arenig-Llanvirn boundary" within the Whicham Blue Slates, a lithostratigraphic division of the Skiddaw Group in the English Lake District (Rushton & Molyneux, 1989, p. 269).

Llanvirn occurrences of *Frankea* are better documented. *F. sartbernardensis* occurs in the Llanvirn Sárka Formation, Krusna Hora, Bohemia (Vavrdová, 1977); in the Tachilla Formation (lower Llanvirn), Anti-Atlas Mountains, Morocco (Elaouad-Debbaj, 1984); and in middle Llanvirn sediments (*Didymograptus murchisoni* graptolite Zone) of Rügen and of the Ebbe Mountains (respectively northeast and west Germany: Servais, 1993, p. 91). Servais & Maletz (1992) also reported the presence of *F. sartbernardensis* in graptolitic beds (*D. artus* graptolite Zone) of the Huy Formation, Bande de Sambre-et-Meuse, Belgium. The species' holotype (Martin, 1966) also was recovered from the latter deposits.

F. breviscula is known from the Llanvirn of Bohemia (Sárka Formation, Krusna Hora: Vavrdová, 1977); from graptolite-bearing beds of the Llanvirn Eycott Volcanic Group in the English Lake District (Millward & Molyneux, 1992); and in the upper member (lower "Llandeilo") of the Cacemes Formation, Buçao Syncline, Portugal (Elaouad-Debbaj, 1981, her pl. 18, fig. 4 specimen erroneously attributed to *F. sartbernardensis*).

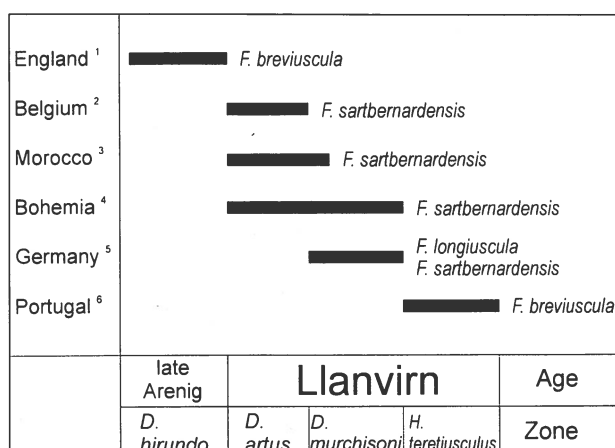
F. longiuscula has been observed by Servais (1993, p. 87) in the *D. murchisoni* graptolite Zone of Rügen. Other published records of that species (Burmann, 1970, 1973; Cramer & Diez, 1977; Molyneux in Trythall *et al.*, 1987) lack reliable locality and/or stratigraphic information.

With the possible exception of a few Caradocian reports discussed below, post-Llanvirn occurrences of *F. breviscula*, *F. longiuscula*, and *F. sartbernardensis*, evidently result from reworking (e.g., Martin *et al.*, 1970; Turner, 1982; Vavrdová, 1982), or are based on palynological age attribution only (Jardiné *et al.*, 1974; Smith, 1981, no illustrations), or lack adequate stratigraphic documentation (e.g., Martin, 1969).

Colbath (1986, 1990) suggested that the stratigraphic range of *Frankea* might be diachronous, maintaining that the genus was restricted to "Arenig-Llanvirn" in Europe, but present in the Caradoc and possibly Ashgill of North Africa. Actually, the Caradoc occurrence of *F. sartbernardensis* in North Africa, as reported by Jardiné *et al.* (1974), is unsupported by photomicrographs, locality data, or independent evidence of age attribution. Those authors did not, however, record *Frankea* in Llanvirn strata. This appears peculiar, considering that the genus is common in north African subsurface material of Llanvirn age (Vecoli, unpublished data; present study). Colbath (1986, p. 72) reported *Frankea* spp. from Libyan samples of the Djefara, Memouniat, and Melez Chograne Formations (Caradoc), but failed to provide any adequate documentation. Hill and Molyneux (1988) attributed their assemblage acritarch zone Cal to Caradoc from the co-occurrence of *F. sartbernardensis*, *Stellechinatum celestum* (Martin) Turner, 1984, and *Villosacapsula irrorata* (Loeblich and Tappan) Fensome *et al.*, 1990 (cited as *Veryhachium irroratum* in Hill & Molyneux, 1988). This species association, however, cannot be regarded as establishing a Caradoc age for the impoverished Cal acritarch assemblage of Hill & Molyneux (1988). *S. celestum* is known to range from the basal Llanvirn into the Caradoc (Molyneux *in* Molyneux *et al.*, 1996). *V. irrorata* was originally described from the Mountain Lake Member of the Bromide Formation, Oklahoma, U.S.A., by Loeblich and Tappan (1969); the latter authors indicated a Llandeilan age for those strata. Hill & Molyneux (1988, p. 29), however, reported that the member containing *V. irrorata* was possibly attributable to the basal Caradoc. At any rate, in north Africa the latter species is unequivocally present in sediments older than Caradoc (Vecoli, *in press*).

In conclusion, all the alleged post-Llanvirn occurrences of *Frankea* are from deposits lacking independent age control and there is no definitive evidence for the upper stratigraphic limit of the genus which is generally considered to be in the upper Ordovician (Colbath, 1986). Text-fig. 2 summarizes published occurrences of *F. breviscula*, *F. longiuscula*, and *F. sartbernardensis* constrained by independent fossil evidence.

In our material (Text-fig. 3), the FAD (First Appearance Datum) of *Frankea sartbernardensis* stratigraphically precedes those of *F. breviscula* and *F. longiuscula*. The last-named is more abundant in the stratigraphically higher samples, i.e., the Spanish samples (*D. purchisoni* graptolite Zone) and those from the upper levels of the north African boreholes (also attributable to *D. purchisoni* graptolite Zone). *F. breviscula* is common in all of the study samples with the exception of that from Belgium. The pattern of occurrences and relative abundances of the three species are consistent in the four stratigraphic sections investigated, thus suggesting negligible palaeoenvironmental influence on their distribution. In summary, the present study suggests that the FAD of *F. sartbernardensis* is within (or possibly just before) the *D. artus* Zone, and that of *F. longiuscula* is within the *D. purchisoni* Zone. These results are in accord with bona fide stratigraphic occurrences at other localities (e.g., Bohemia, Vavrdová, 1977; Germany, Servais, 1993). In our material, *F. breviscula* first occurs in the *D. purchisoni* Zone; this contrasts with Rushton & Molyneux's (1989) unique report of co-occurrence of *F. sartbernardensis* and *F. breviscula* in upper Arenig sediments (English Lake District). The absence of the latter species in the *D. artus* Zone of Belgium could reflect a local control on its total distribution; however, the presence of *F. breviscula* in pre-Llanvirn sediments is yet to be convincingly demonstrated. In fact, in his recent review of the stratigraphic distribution of selected Ordovician acritarchs, Molyneux (*in* Molyneux *et al.*, 1996, pp. 500-503, Text-fig. 6) indicated that *F. sartbernardensis* first occurs in upper Arenigian strata, but he provided no information on the stratigraphic range of *F. breviscula*.



Text-fig. 2 - Selected previously published stratigraphic ranges of *Frankea breviscula*, *F. longiuscula*, and *F. sartbernardensis*. The chart is based exclusively on biostratigraphic data constrained by faunal co-occurrences. 1) Rushton & Molyneux, 1989. 2) Servais & Maletz, 1992. 3) Elaouad-Debbaj, 1984. 4) Vavrdová, 1977. 5) Servais, 1993. 6) Elaouad-Debbaj, 1981.

SYSTEMATIC PALAEOONTOLOGY

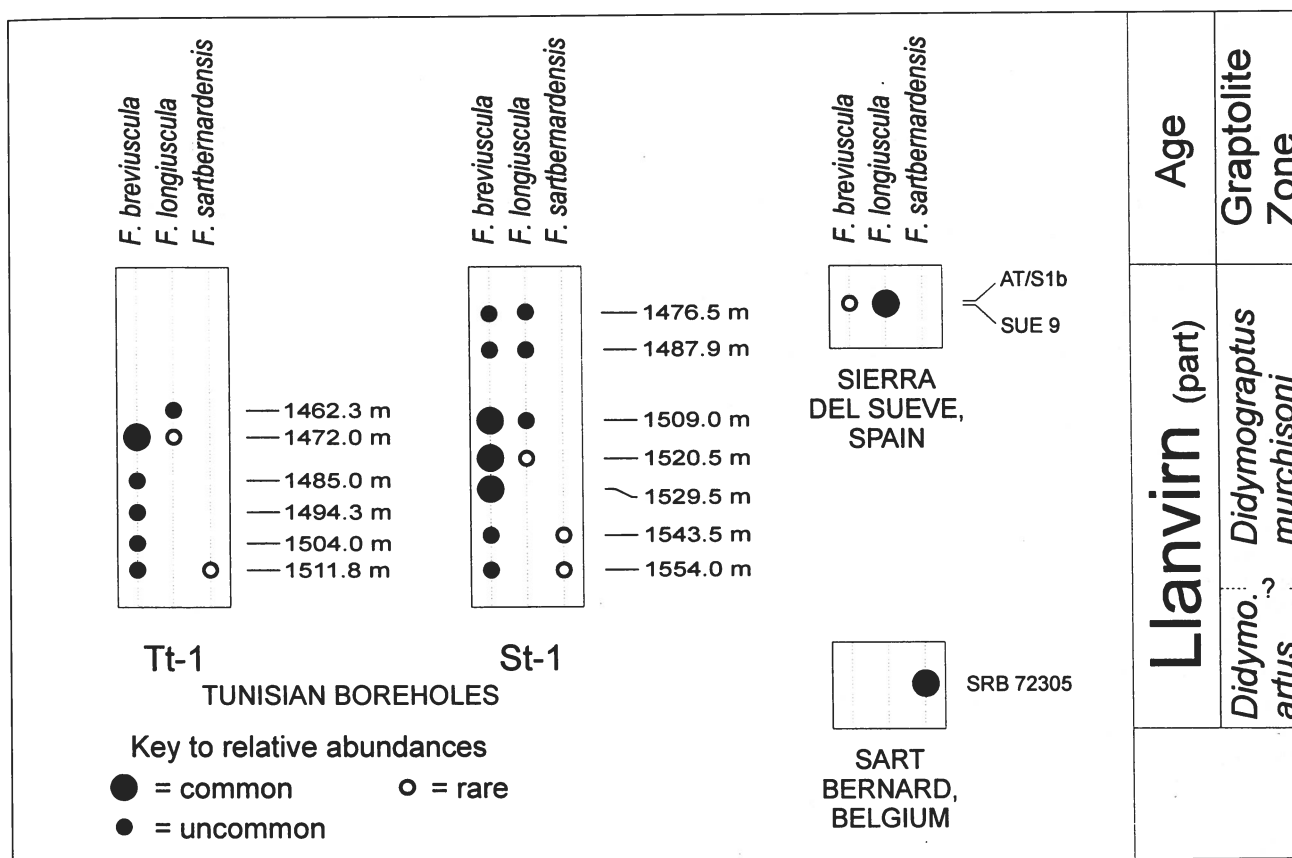
Incertae sedis "group" ACRITARCHA Evitt, 1963

Genus FRANKEA Burmann, 1970, emend. Servais, 1993

1970 *Frankea* BURMANN, p. 292.

1993 *Frankea* Burmann emend. SERVAIS, p. 80.

1995 *Fatkia* VAVRDOVÁ, p. 368.



Text-fig. 3 - Vertical distribution of *Frankea breviuscula*, *F. longiuscula*, and *F. sartbernardensis* in the study sections and chronostratigraphic correlation of the palyniferous sequences.

Type species – *Frankea hamata* Burmann, 1970, by original designation.

Discussion – *Frankea* is applied here according to the emendation by Servais (1993). We are in agreement with Fatka *et al.* (1996, pp. 322-323) in rejecting Sarjeant & Stancliffe's (1994) reassignment to *Frankea* of *Veryhachium florigerum* Deunff, 1957, *V. mucronatum* Stockmans & Willière, 1963, *V. petropolitanum* German in German & Timofeev, 1974, and *V. ramificatum* German in German & Timofeev, 1974. Allocation of *Veryhachium liujingense* Gao Lianda, 1978 to *Frankea* (see Stancliffe & Sarjeant, 1994) is also rejected. Furthermore, we consider, as do Fatka *et al.* (1996, pp. 323-324), that *Fatkia* Vavrdová, 1995 is a junior synonym of *Frankea*.

Servais (1993, p. 81) stressed the importance of the number of terminal pinnae and the ratio of process length to central body diameter for circumscription of, and differentiation within *Frankea*. He also stated that measurements of large "populations" from different palaeogeographic settings indicate that the ratio of process length to "central body diameter" is continuously variable, hence of questionable taxonomic value at species level (see also Fatka *et al.*,

1996, p. 322), particularly for distinguishing the three species *F. sartbernardensis*, *F. breviuscula*, and *F. longiuscula*. In the present study we demonstrate that, though appreciably variable, gross morphological characters can be successfully used for specific identification. This is discussed subsequently herein, under "biometric analysis".

Our observations do not support Servais' (1993, p. 81) assertion that on any given *Frankea* specimen the three processes have the same number of distal pinnae. Even on well-preserved, undamaged specimens, most possess slightly differing numbers of pinnae per process.

Hitherto, scant attention has been paid to the taxonomic value of nature and distribution of sculptural elements for the distinction of the various *Frankea* species. Optical microscopy of well-preserved specimens of *F. sartbernardensis* and *F. breviuscula* has revealed the presence of fine ridges ("striae") disposed parallel to the vesicle sides (Vavrdová, 1977; Arriaga e Cunha & Vanguetaine, 1988; Cooper & Molyneux, 1990; Servais, 1993). Our SEM studies of these species demonstrate that these sculptural elements result from alignment of more or less discrete bacula or grana paralleling the vesicle sides and, moreover,

continuing up the process trunks to the terminal pinnae. *F. longiuscula* possesses different wall sculpturing; i.e., closely spaced conical evenness dispersed on eilyma, processes and terminal pinnae. The nature and distribution of sculptural elements is here considered of high taxonomic significance, in accord with Tappan and Loeblich's (1971, p. 386) assertion that "[acritarchs'] internally formed morphologic structures (test wall microstructures, excystment mechanisms) have potentially the best taxonomic value, being virtually unaffected by environmental pressures".

Method of excystment has not been previously specified for *Frankea* (Servais, 1993, p. 80). Numerous specimens of *F. longiuscula* from Spain and a few specimens of *F. breviscula* from north Africa, all examined herein, demonstrate that an epitache (Tappan, 1980, p. 968) constitutes the excystment structure.

Wall stratification is another feature that has been used for generic discrimination (Tappan & Loeblich, 1971; Rauscher, 1974; Colbath, 1979; Le Hérisse, 1989). Our observations of a large number of *Frankea* specimens, utilizing both light and scanning-electron microscopy, testify to a unilayered wall for *Frankea*. However, future transmission electron microscopy will obviously provide definitive evidence in this regard.

FRANKEA BREVIUSCULA Burmann, 1970
Pl. 1, figs. 1-3; pl. 3, fig. 1

- ?1969 *Verhachium sartbernardense* Martin - MARTIN, p. 104; pl. 6, fig. 263; text-fig. 53.
1970 *Frankea breviscula* BURMANN, p. 292; pl. 2, fig. 2.
1993 *Frankea breviscula* Burmann - SERVAIS, pp. 81-83; pl. 1, fig. 8 (cum syn.).
1995 *Frankea sartbernardensis* auct. non Martin - JACHOWICZ, pl. 1, fig. 9.

Description – Vesicle outline equilateral-subtriangular, with straight to moderately convex sides; lenticular in lateral view. Eilyma unilayered, ca. 1 µm thick, sculptured with minute discrete bacula (ca. 0.3 µm in height, 0.2-0.3 µm in basal diameter, and ca. 0.4 µm apart) regularly aligned in rows paralleling vesicle sides and extending onto processes and associated pinnae. Bacula occasionally based on low, closely spaced ridges. Three ±homomorphic processes, each drawn out radially from a vesicle apex. Trunk hollow, cylindrical, freely communicating with vesicle interior, branching distally into 4-8 homomorphic,

solid pinnae characteristically coiled inwardly. Process walls proximally sculptured with bacula regularly aligned in close-spaced longitudinal rows; distally bacula intergrade with relatively sparse, irregularly disposed grana (of similar size to bacula). Ratio of vesicle side length : process length = ca. 2. Excystment by epitache (rarely seen).

Dimensions – Length of vesicle sides 20 (26) 35 µm; length of processes 7 (15) 23 µm; number of terminal pinnae 4-8, length of terminal pinnae 7 (10) 13 µm; length of vesicle sides: length of processes ratio 1.1 (1.9) 4.5 (based on 72 specimens).

Remarks and comparison – Sculptural elements are generally too minute to be detectable by means of light microscopy; a very faint striation of the eilyma is only sometimes observed (with difficulty), even when the quality of preservation is very good. With SEM, however, the specimens consistently display the characteristic baculate sculpture covering the vesicle and the entire processes. No unsculptured specimens have been observed. Thus the sculptural characteristics of *Frankea breviscula* are considered here as diagnostic and can assist in distinguishing that species from *F. longiuscula*.

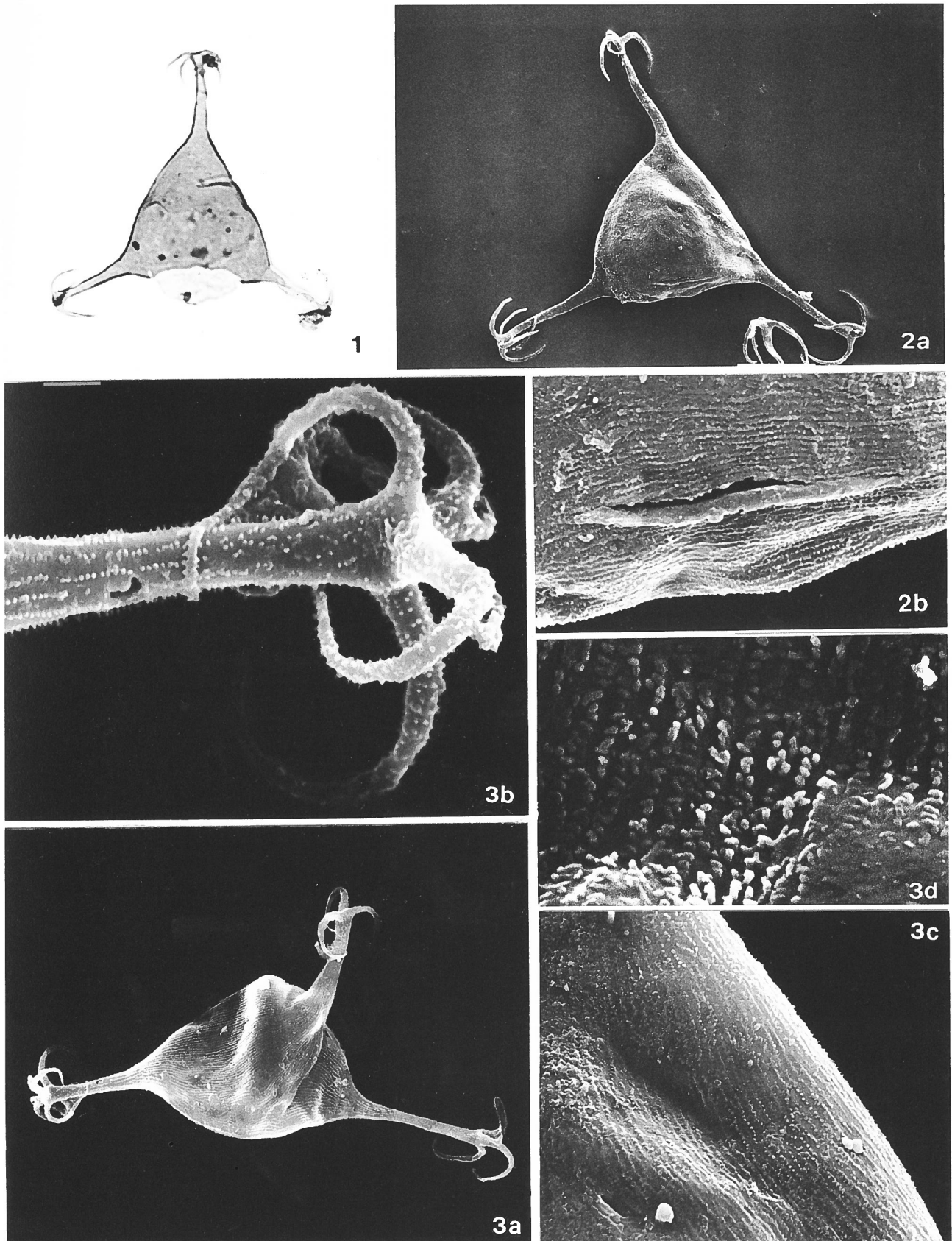
The supposedly lower Caradoc, Saudi Arabian specimen illustrated by Jachowicz (1995; pl. 1, fig. 9) and attributed by her to *F. sartbernardensis* features processes of the same length as vesicle sides and therefore is here considered to represent *F. breviscula*.

Occurrence and abundance – Samples St1-1554.0 and St1-1543.5: uncommon. Samples St1-1529.5 through St1-1509.0: common. Samples St1-1487.9 and St1-1476.5: uncommon. Samples Tt1-1511.8 through Tt1-1494.3: uncommon. Samples St1-1485.0 and St1-1472.0: common. Sample St1-1462.3: uncommon. Samples S2-9 and AT/SU1b: rare. Sample SRB-72.305: rare.

Stratigraphic range verified by independent age control – Lowest record: upper Arenig (*Didymograptus hirundo* graptolite Zone), Lake District, England (Rushton & Molyneux, 1989). Highest record: middle Llanvirn (*Didymograptus murchisoni* graptolite Zone), Cerracin Member, Sueve Formation, Sierra del Sueve, Cantabrian Mountains, northern Spain (Gutierrez-Marco *et al.*, 1996; this study). Stratigraphically higher occurrences (e.g., Caradoc of

EXPLANATION OF PLATE 1

Figs. 1-3 - *Frankea breviscula* Burmann, 1970. 1) Fully excysted specimen, × 1000. 2a) × 1200; 2b) detail of eilyma and incipient excystment structure, × 8000. 3a) × 2000; 3b) detail of process sculpture, × 10000; 3c) detail of eilyma sculpture, × 5000; 3d) detail of eilyma sculpture, × 12000.



Shropshire, England, Turner, 1984; and Silurian of Belgium, Martin, 1969) are considered to be recycled.

FRANKEA LONGIUSCULA Burmann, 1970
Pl. 2, figs. 1, 2; pl. 3, fig. 2

1970 *Frankea longiuscula* BURMANN, pp. 291-292; pl. 2, figs. 4, 12; pl. 3, figs. 1, 2.

1993 *Frankea longiuscula* Burmann - SERVAIS, pp. 86-87; pl. 1, fig. 10.

Description – Vesicle outline equilateral-subtriangular, with often strongly convex sides; lenticular in lateral view. Eilyma unilayered, *ca.* 1 μ m thick, sculptured with close-spaced coni, <0.5 μ m apart, *ca.* 0.05 μ m in basal diameter and 0.1 μ m in height, evenly distributed on eilyma and process walls up to terminal pinnae. Three $\pm$ homomorphic processes, normally longer than vesicle sides, each drawn out radially from a vesicle apex. Trunks cylindrical, hollow, freely communicating with vesicle interior, flexible, branching distally into 4-10 homomorphic, acuminate, rigid, solid pinnae. Ratio of vesicle side length : process length = *ca.* 0.7. Excystment by epityche (infrequently seen).

Dimensions – Length of vesicle sides 34 (45) 62 μ m; length of processes 47 (66) 95 μ m; number of terminal pinnae 4-10, length of terminal pinnae 7 (10) 16 μ m; length of vesicle sides: length of processes ratio 0.5 (0.7) 0.9 (based on 42 specimens).

Remarks – *Frankea longiuscula* is characterized by long, slender processes. Size range for the species scarcely overlaps with that of *F. sartbernardensis* and *F. breviuscula* in the present study material. However, a possible morphological transition between *F. breviuscula* and *F. longiuscula* was not excluded by Servais (1993, p. 91). In the following section ("Biometric analysis") we demonstrate that such transition can reasonably be discounted. Sculptural character is another distinguishing feature for the present species, consisting of diminutive coni, densely and evenly distributed on eilyma and process walls. Several Spanish specimens show the presence of an epityche.

Occurrence and abundance – Sample St1-1520.50: rare. Samples St1-1509.00: through St1-1476.50: uncommon. Sample Tt1-1472.00 rare. Sample St1-1462.30: uncommon. Samples S2-9 and AT/SU1b: common.

Stratigraphic occurrences verified by independent age control – Middle Llanvirn (*Didymograptus murchisoni* graptolite Zone), Cerracin Member, Sueve Formation, Sierra del Sueve, Cantabrian Mountains, northern Spain (Gutierrez-Marco *et al.*, 1996; this study); *D. murchisoni* Zone of the boreholes of Rügen, northeast Germany (Servais, 1993, p. 84).

FRANKEA SARTBERNARDENSIS (Martin, 1966)
Colbath, 1986
Pl. 3, figs. 3-5

1966 *Veryhachium sartbernardense* MARTIN, pp. 434, 435, 440; figs. 11-13.

1986 *Frankea sartbernardense* (Martin) COLBATH, pp. 72-73.

v1993 *Frankea sartbernardensis* (Martin) SERVAIS, pp. 87-91; pl. 1, figs. 1, 2, 7.

non 1995 *Frankea sartbernardensis* - JACHOWICZ, pl. 1, fig. 9.

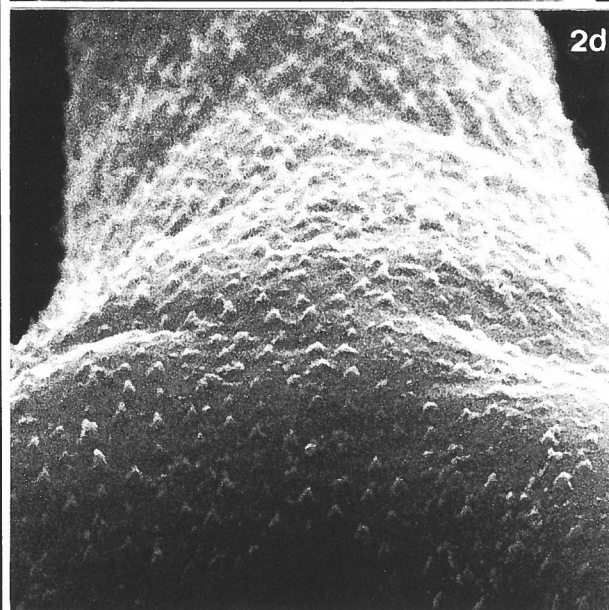
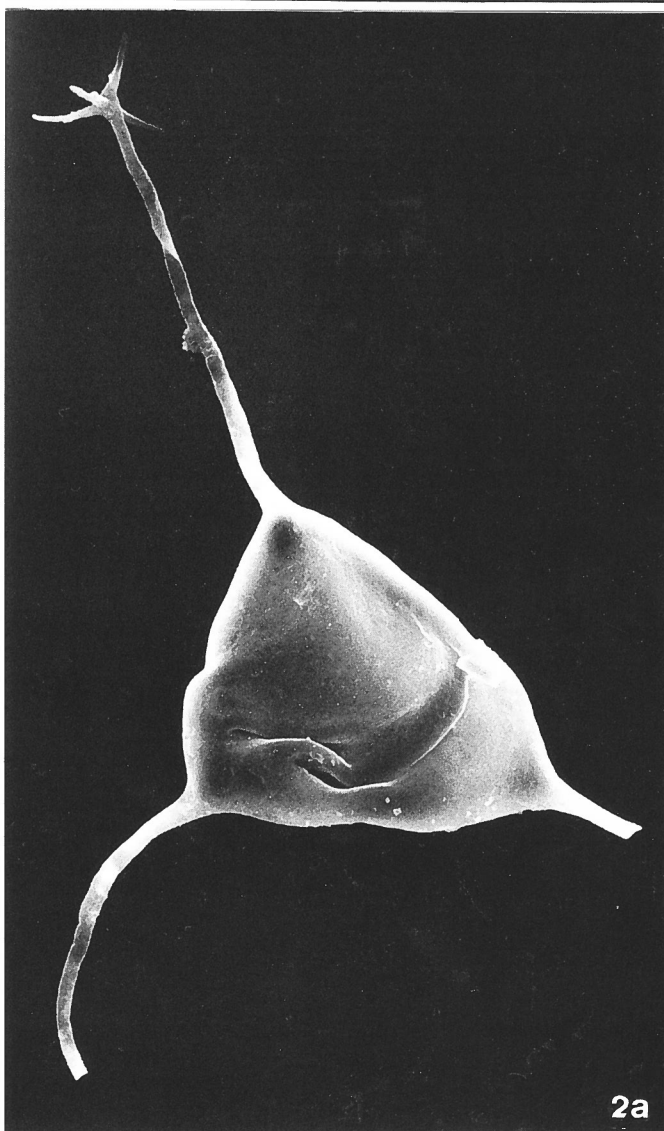
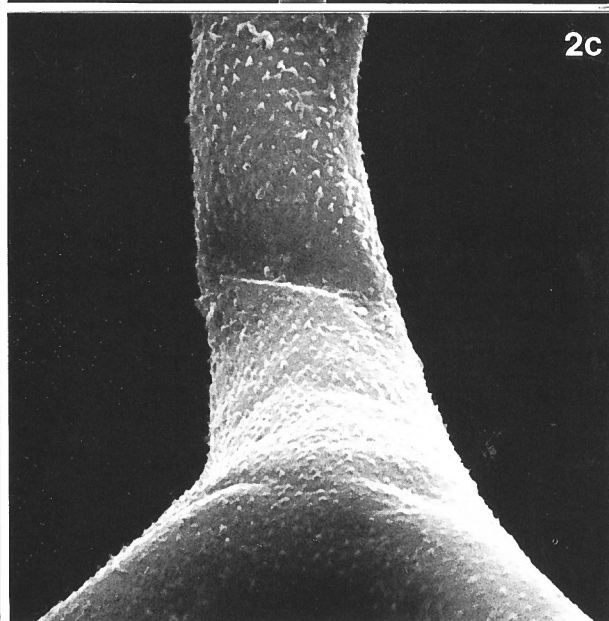
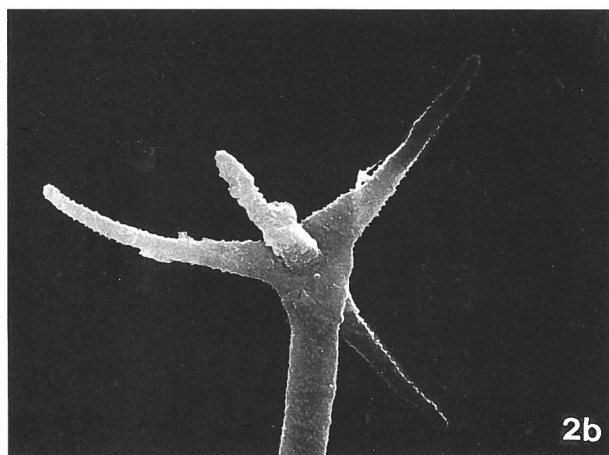
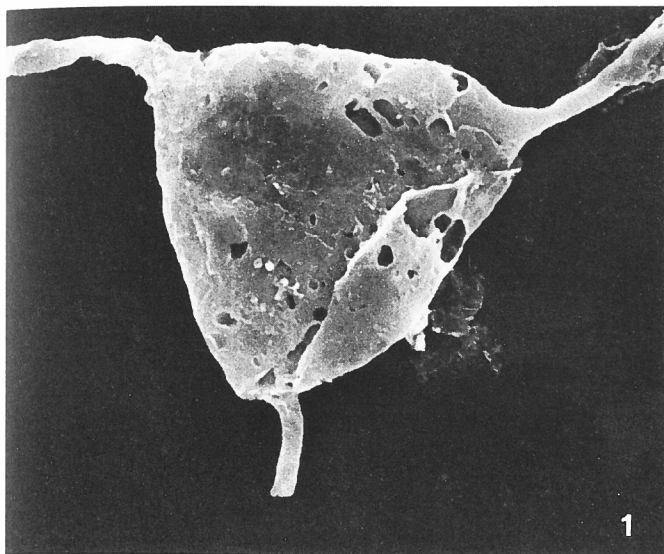
Description – Vesicle outline equilateral-subtriangular, with moderately convex sides; lenticular in lateral view. Eilyma unilayered, *ca.* 1 μ m thick, sculptured with minute discrete bacula, *ca.* 0.1 μ m in basal diameter, 0.2 μ m high, close-spaced (*ca.* 0.2 μ m apart), regularly aligned in rows paralleling vesicle sides and extending onto processes. Bacula occasionally based on low, close-spaced ridges. Three $\pm$ homomorphic processes, each drawn out radially from a vesicle apex. Trunks cylindrical, hollow, freely communicating with vesicle interior, branching distally into 3-6 homomorphic, solid pinnae characteristically coiled inwardly. Process walls proximally sculptured with bacula regularly aligned in close-spaced longitudinal rows; distally and up to pinnae, bacula intergrade with relatively sparse, irregularly disposed grana (of similar size to bacula). Ratio of vesicle side length : process length normally between 3.5 and 5.5. Excystment structure not seen.

Dimensions – Length of vesicle sides 19 (25) 33 μ m; length of processes 3 (5) 8 μ m; number of terminal pinnae 3-6, length of terminal pinnae 4 (6) 11 μ m; length of vesicle sides: length of processes ratio 3.3 (4.9) 6.2 (based on 70 specimens).

Remarks and comparison – This species is characterized by relatively short processes and a substantial ratio of vesicle side length : process length (normally about 5). Morphological variability is fairly wide but, as discussed subsequently, only in rare cases do the respective size ranges of *Frankea sartbernardensis* and *F. breviuscula* overlap. Numerous specimens observed

EXPLANATION OF PLATE 2

Figs. 1, 2 - *Frankea longiuscula* Burmann, 1970. 1) Excysted specimen, $\times 1500$. 2a) $\times 1500$; 2b) detail of terminal pinnae, $\times 4500$; 2c) detail of eilyma and process sculpture, $\times 9000$; 2d) detail of eilyma and process sculpture, $\times 18000$.



at high SEM magnifications, including specimens from Belgium and north Africa, invariably show sculpture of minute bacula arranged in rows paralleling vesicle sides. At lower magnifications, the same specimens appear "striate" or virtually psilate. Excystment mode has not been clearly observed in specimens of *F. sartbernardensis*; however, a few specimens feature a partially open curved rupture of the eilyma, closely resembling an epityche.

The specimen of supposed early Caradoc age illustrated by Jachowicz (1995; pl. 1, fig. 9) and attributed to *F. sartbernardensis*, features a much lower ratio of vesicle side length : process length than it is consonant with that species. Accordingly, the specimen cannot be attributed to *F. sartbernardensis*; it is most probably referable to *F. breviscula* (see above).

Occurrence and abundance – Samples St1-1554.00 and St1-1543.50: rare. Samples Tt1-1511.80: rare. Sample SRB-72.305: common.

Stratigraphic range verified by independent age control – Lowest record: upper Arenig (*Didymograptus hirundo* graptolite Zone), Lake District, England (Rushton & Molyneux, 1989; Molyneux, 1990). Highest record: middle Llanvirn (*D. murchisoni* graptolite Zone), Cerracin Member, Sueve Formation, Sierra del Sueve, Cantabrian Mountains, northern Spain (Gutiérrez-Marco *et al.*, 1996; this study). Stratigraphically higher occurrences [e.g., in the Caradoc of Shropshire (Turner, 1984), and the Silurian of Belgium (Martin, 1969)] are considered to result from reworking.

BIOMETRIC ANALYSIS

From the above, it will be evident that the three species of *Frankea* here described share many morphological similarities. If sculptural detail is not taken fully into account, or is not clearly observable, e.g., where the acritarchs are corroded, the only avenue for distinguishing *F. sartbernardensis*, *F. breviscula*, and *F. longiuscula* is by observation of their gross morphological characters. The ratio between length of vesicle sides and process length decreases progressively from *F. sartbernardensis* to *F. longiuscula*. A possible continuous morphological gradation was inferred by Servais (1993, p. 91) between *F. sartbernardensis* and *F. breviscula* and, further, between the latter species and *F. longiuscula*.

In order to enhance understanding of the morphology and variability of the three species, a biometric investigation was conducted on a total of 184 specimens. The measured specimens come from different rock samples, collected from different localities, and are probably of slightly differing ages (24 specimens of *F. longiuscula* and 10 specimens of *F. breviscula* from the Sierra del Sueve section, Spain; 18 specimens of *F. longiuscula*, 15 specimens of *F. sartbernardensis*, and 41 specimens of *F. breviscula* from the Tunisian sections; 55 specimens of *F. sartbernardensis* and 21 specimens of *F. breviscula* from the Sart Bernard section, Belgium). All of the specimens observed in several slides (listed in Appendix 1) were measured, taking into account the following:

VSL = vesicle side length;

PL = process length; and

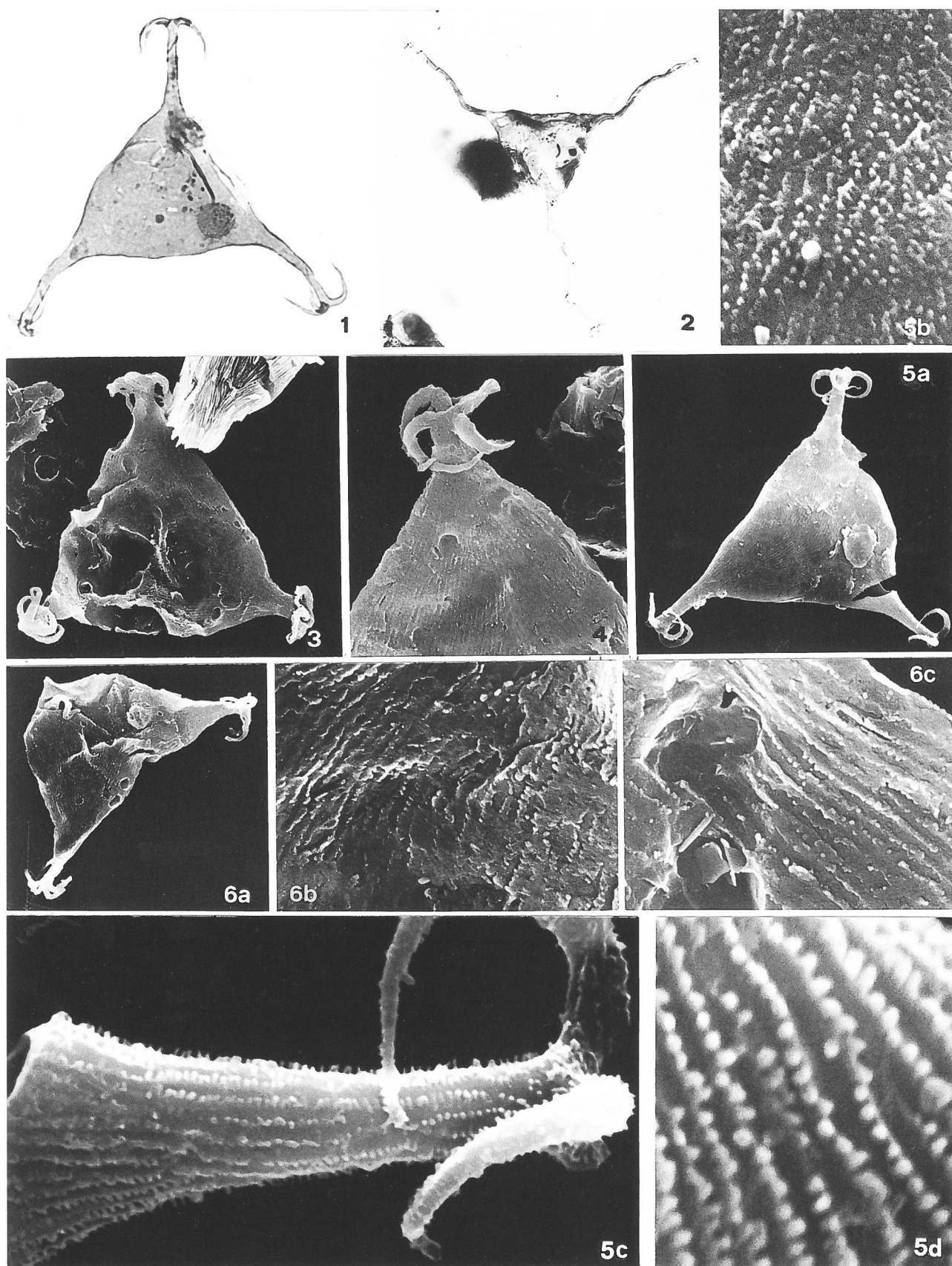
VSL:PL = vesicle side length : process length ratio.

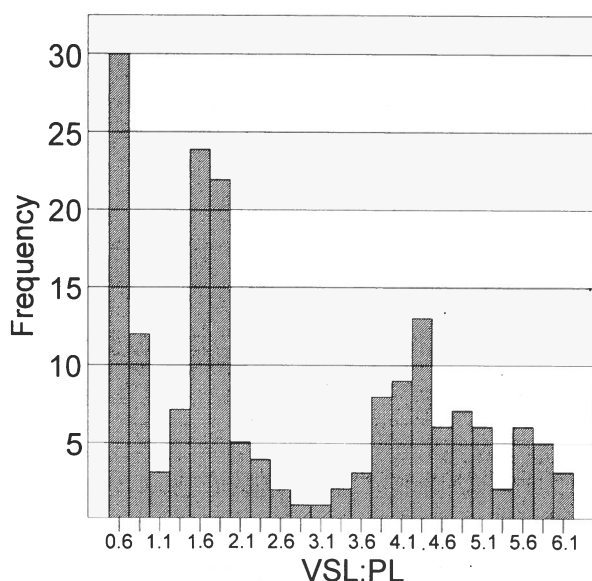
Of these parameters, the VSL:PL ratio is here regarded as the most pertinent taxonomically. In fact, the ratio between vesicle size and process length has frequently been used for the distinction of at least three of the five named species of *Frankea* (Burmann, 1970; Martin, 1969; Servais, 1993). The number and length of terminal pinnae are useful for distinguishing *F. hamata* Burmann, 1970 (only two pinnae per process) and *F. hamulata* Burmann, 1970 (several small pinnae). These morphological elements have lesser taxonomic importance for *F. sartbernardensis*, *F. breviscula*, and *F. longiuscula*. In the present study they were found to vary less regularly than was indicated by Servais (1993, text-fig. 1).

The frequency distribution of the total VSL:PL data array (Text-fig. 4) shows three major data-clustered peaks. We consider that these peaks represent the modes of three normally distributed VSL:PL sets of values, each of which singles out an acritarch species. In other words, the entire data set is divisible into three subsets, each of which is considered to represent a statistical sample of the population of a particular species. It is possible to analyze the three subsets (provisionally termed samples 1, 2, and 3) separately, and to test them for normal distribution. The statistics for each of the three samples and their frequency classes distributions are shown in Text-fig. 5. The values of VSL and PL for the specimens of sample 1 are very close to the value given by Martin (1969) for the vesicle side length and process length

EXPLANATION OF PLATE 3

- Fig. 1 - *Frankea breviscula* Burmann, 1970, $\times 1000$.
 Fig. 2 - *Frankea longiuscula* Burmann, 1970, $\times 750$.
 Figs. 3-5 - *Frankea sartbernardensis* (Martin) Colbath, 1986. 3) $\times 1500$. 4) $\times 2000$. 5a) $\times 1500$; 5b) detail of eilyma sculpture, $\times 7500$; 5c) detail of process sculpture, $\times 10000$; 5d) detail of vesicle sculpture $\times 20000$. 6a) $\times 1500$; 6b) detail of eilyma sculpture, $\times 7500$; 6c) detail of eilyma sculpture, $\times 7500$.





Text-fig. 4 - Frequency-distribution diagram of VSL:PL values.

of *F. sartbernardensis*; thus, sample 1 is considered to represent the latter species. Sample 2 is here identified with *F. breviscula*; the mean value of VSL:PL for specimens which constitute sample 2 is 1.91, which is equivalent to a ratio of process length to "central body diameter" of 0.6, approximating the value of 2/3 reported in the specific diagnosis of Burmann (1970, p. 292) and also used (with some reservation) as a species criterion by Servais (1993, text-fig. 1). Finally, sample 3 is considered identifiable with *F. longiuscula*; the mean value of VSL:PL of our material is 1.7, fairly close to the corresponding value (2) of process length to "central body diameter" reported in the original diagnosis of *F. longiuscula* (Burmann, 1970, pp. 291-292). The identification of the three subsets of the statistical sample with the *Frankea* species is based on the assumption that intraspecific morphological variation is normally distributed. From the data displayed in Text-fig. 5, it is evident that the variation ranges of VSL:PL of *F. sartbernardensis* and *F. breviscula* overlap slightly between the values 2.9 and 4.5. However, the statistics show that within each morphological group (species), at least 68% of the specimens have distinct values of VSL:PL (comprised in a distance of one standard deviation from the mean value of VSL:PL). This means that (considering also the low values of the standard deviation for the two samples), less than 15% of all the measured specimens fall within the region of overlapping values of VSL:PL of the two samples. Clearly, in these latter few cases, the specimens cannot be assigned with certainty to one or the other species, and a certain degree of ambiguity remains. The confirmation of a normally distributed morphological variation within each statistical sample as defined

above, comes from the Chi-square (χ^2) test, as shown in Table 1. Here, the observed distribution for each sample is compared to the ideal normal distribution curve (Gaussian distribution). Each data set (sample) has been divided in six intervals; the number of observations in each interval can be compared with the number of observations that we should expect in case of an ideal normal (Gaussian) distribution of the VSL:PL values in each set. The agreement between the observed values and the "expected" ones is estimated according to the following formula:

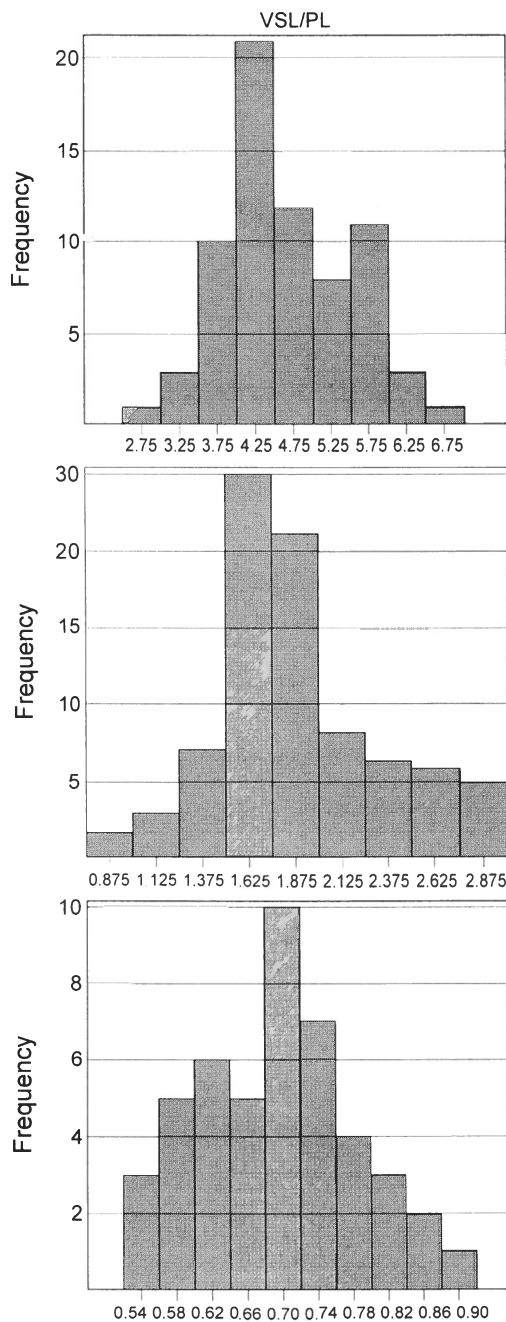
$$\chi^2 = \frac{1}{d} \sum_{k=1}^6 \frac{(O_k - E_k)^2}{E_k}$$

where O_k = Observed values; E_k = Expected values, d = degree of freedom. The degree of freedom are derived from the formula: $d = n - c$, where n is the number of intervals in which the statistical set is subdivided (6 in the present discussion), and c is the number of parameters calculated from the data set (i.e., the total number of observations, the mean, and the standard deviation). For each value of χ^2 so calculated, it is possible to estimate the probability of obtaining such a value (or a higher one) in the hypothesis that the elements in our data sets (VSL:PL measurements) are governed by a normal distribution. These probability values are commonly tabulated in many statistic manuals. The results of the Chi-square test as shown in Table 1, confirm that the morphological variation within our three samples are likely to be governed by a normal distribution. Actually, the agreement between the observed distribution and an ideal Gaussian distribution is very close for samples 1 and 3 (corresponding to the species *F. sartbernardensis* and *F. longiuscula*), there being ca. 60% probability of obtaining $\chi^2 \geq 0.5$ in case of normal distribution. Regarding sample 2 (*F. breviscula*) the agreement is less striking, but certainly there is no ground to reject the hypothesis of a normal distribution of its elements, with the probability of having a $\chi^2 \geq 1.19$ being ca. 39% in case of Gaussian distribution. We note here that the probability level at which the disagreement between the expected and the calculated distribution becomes significant is normally set at about 5% (Taylor, 1986).

Microsculptural characteristics of the study specimens confirm that the three groups identified on the basis of gross morphology constitute discrete acritarch species. The nature and distribution of sculptural elements (described in the systematic section) are in fact internally consistent in the three subsets of the statistical sample of the numerous specimens of *Frankea* examined herein.

DISCUSSION AND CONCLUSIONS

Frankea sartbernardensis, *F. breviscula*, and *F. longiuscula* are potentially important chronostrati-



Text-fig. 5 - Normal distributions of the three statistical samples (1, 2, and 3).

Sample 1 (= *F. sartbernardensis*)

	VSL	PL	VSL:PL
Max	32.5	8.7	6.8
Min	19.5	3.5	2.9
Median	25.7	5.7	4.5
Mean ($\bar{X}$)	25.7	5.6	4.7
SD	2.8	1.1	0.8

Sample 2 (= *F. breviscula*)

	VSL	PL	VSL:PL
Max	33.5	23.5	4.5
Min	20.5	5.7	1.1
Median	26.8	14.8	1.8
Mean ($\bar{X}$)	26.4	14.7	1.9
SD	2.5	3.3	0.6

Sample 3 (= *F. longiuscula*)

	VSL	PL	VSL:PL
Max	67.0	95.0	0.89
Min	34.5	47.2	0.54
Median	45.0	66.5	0.7
Mean ($\bar{X}$)	45.4	65.9	0.7
SD	5.9	9.2	0.1

graphic indices, although precise stratigraphic ranges have yet to be fully determined. This partly reflects a lack of sufficiently detailed morphological information in the literature, giving rise to problems of misidentification. Moreover, many published *Frankea* occurrences pertain to host rocks that are either yet to be dated satisfactorily (e.g., from independent faunal evidence) or are not precisely located (stratigraphically or geographically). Our morphological documen-

tation and identification of these three species focuses on microsculptural elements and biometric evaluation and is underpinned by well-constrained biostratigraphic data.

From our statistical analysis, it is clear that *F. sartbernardensis*, *F. breviscula*, and *F. longiuscula* are indeed sustainable as separate species. In fact, the frequency classes of morphometric elements measured on statistical samples, taken from each species' natur-

Frankea sartbernardensis

Interval	Observed values	Expected values
$x \leq X-1.5\sigma$	4	4.7
$X-1.5\sigma < x \leq X-\sigma$	7	6.4
$X-\sigma < x \leq \sigma X$	26	23.9
$X < x \leq X+\sigma$	20	23.9
$X+\sigma < x \leq X+1.5\sigma$	8	6.4
$x > X+1.5\sigma$	5	4.7

Chi-square value: $\chi^2 = 0.55$
Probability for normal distribution: 65%

Frankea breviscula

Interval	Observed values	Expected values
$x \leq X-1.5\sigma$	2	4.8
$X-1.5\sigma < x \leq X-\sigma$	6	6.4
$X-\sigma < x \leq \sigma X$	31	24.6
$X < x \leq X+\sigma$	22	24.6
$X+\sigma < x \leq X+1.5\sigma$	6	6.4
$x > X+1.5\sigma$	5	4.8

Chi-square value: $\chi^2 = 1.19$
Probability for normal distribution: 39%

Frankea longiuscula

Interval	Observed values	Expected values
$x \leq X-1.5\sigma$	3	2.8
$X-1.5\sigma < x \leq X-\sigma$	6	3.8
$X-\sigma < x \leq \sigma X$	15	14.3
$X < x \leq X+\sigma$	13	14.3
$X+\sigma < x \leq X+1.5\sigma$	3	3.8
$x > X+1.5\sigma$	2	2.8

Chi-square value: $\chi^2 = 0.59$
Probability for normal distribution: 60%

Tab. 1 - Chi-square test.

al populations, are normally distributed with very distinct values of the means, modes, medians, and standard deviations.

Microsculptural elements are also taxonomically efficacious, especially for distinction of *F. longiuscula* from the other two species. Some specimens observed during the present study demonstrate for the first time that *Frankea* excysted via an epitryche. All light- and electron-microscopic observations suggest the genus has a unilayered eilyma.

In the sections examined, the FAD of *F. sartbernardensis* precedes those of *F. breviscula* and *F. longiuscula*, and is no younger than early Llanvirn in relative age (*Didymograptus artus* Zone). The introduction of *F. breviscula* slightly predates that of *F. longiuscula*; this latter species attains its acme in the stratigraphically higher levels of the north African sections and in the Spanish samples attributable to the Llanvirnian *D. murchisoni* graptolite Zone.

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APPENDIX 1

REGISTER OF ILLUSTRATED SPECIMENS

Plate: figure	Sample number	England finder	Catalogue number
<i>Frankea breviscula</i>			
1:1	ST1-1520.5	H44/1	CPT205018-06
1:2	ST1-1520.5	Q39/2	CPT205018-15
1:3	ST1-1520.5	N37/3	CPT205018-13
3:1	ST1-1476.5	U20/1	CPT205028-01
<i>Frankea longiuscula</i>			
2:1	AT/SU 1b	Q39/2	CPT105110-03
2:2	ST1/1520.5	K37/3	CPT205018-17
3:2	ST1-1458.5	L47/2	CPT205029-02
<i>Frankea sartbernardensis</i>			
3:3	ST1-1543.5	K52/4	CPT205015-01
3:4	SRB72305	P39/3	CPT105110-03
3:5	ST1-1554.0	N37/4	CPT205014-09
3:6	SRB72305	M37	CPT105110-03

REFERENCES

- ARRIAGA E CUNHA, T & VANGUESTAINE, M., 1988, Acritarchs of the 'Xistos com Phyllocytes' Formation, Barrancos Region SE of Portugal: Comun. Serv. geol. Portugal, 74: 69-77.
- BAGNOLI, G., STOUGE, S. & TONGIORGI, M., 1988, Acritarchs and conodonts from the Cambro-Ordovician Furuåll (Köpingsklint) section (Öland, Sweden): Riv. ital. Paleont. Strat., 94 (2): 163-248, pls. 25-41.
- BASSETT M.G. & OWENS, R.M., 1996, Discussion on a revision of Ordovician series and stage divisions from the historical type area: Geol. Mag., 133 (6): 767-772.
- BROCKE, R., FATKA, O., MOLYNEUX, S. & SERVAIS, T., 1995, First appearance of selected early Ordovician acritarch taxa from Peri-Gondwana. In Cooper, J.D., Droser, M.L. & Finney, S.C. (eds.), Ordovician odyssey: short papers for the Seventh International Symposium on the Ordovician System. The Pacific Section for Sedimentary Geology (SEPM), California: 473-476.
- BURMANN, G., 1970, Weitere organische Mikrofossilien aus dem unteren Ordovizium: Paläont. Abh., Abt. B, Paläobot., 3 (3/4): 289-332.
- , 1973, Das Ordovizium der nördlichen Phyllitzone. Teil II: Wippraer Zone: Z. geol. Wiss., Berlin, 1 (7) (S): 9-43.

- COCKS, L.R.M., MCKERROW, W.S. & VAN STAAL, C.R., 1997, The margins of Avalonia: *Geol. Mag.*, 134 (5): 627-636.
- COLBATH, G.K., 1979, Organic-walled microphytoplankton from the Eden Shale (upper Ordovician), Indiana, U.S.A.: *Palaeontographica*, Abt. B, 171 (1-3): 1-38.
- , 1986, The lower Paleozoic organic-walled phytoplankton ('acritarch') genus *Frankea* Burmann 1970: *Micropaleontology*, 32 (1): 72-73.
- , 1990, Palaeobiogeography of Middle Palaeozoic organic-walled phytoplankton. In McKerrrow, W.S. & Scotese, C.R. (eds.), *Palaeogeography and biogeography*: Mem. geol. Soc. (London), 12: 207-213.
- COOPER, A.H. & MOLYNEUX, S.G., 1990, The age and correlation of Skiddaw Group (early Ordovician) sediments in the Cross Fell inlier (northern England): *Geol. Mag.*, 127 (2): 147-157.
- CRAMER, F.H. & DíEZ, M.D.C.R., 1977, Late Arenigian (Ordovician) acritarchs from Cis-Saharan Morocco: *Micropaleontology*, 23 (3): 339-360.
- DALZIEL, I.W.D., 1997, Neoproterozoic-Paleozoic geography and tectonics: Review, hypothesis, environmental speculation: *Geol. Soc. Amer. Bull.*, 109 (1): 16-42.
- DEUNFF, J., 1957, Micro-organismes nouveaux (Hysterosphères) du Dévonien de l'Amérique du Nord: *Bull. Soc. géol. Minéral. Bretagne*, nouv. Sér., 2: 5-14.
- & MASSA, D., 1975, Palynologie et stratigraphie du Cambro-Ordovicien (Libye nord-occidentale): *C. R. Acad. Sci. Paris*, Sér. D, 281 (1): 21-24.
- DOWNIE, C., 1984, Acritarchs in British stratigraphy: *Geol. Soc. London*, spec. Rep., 17: 1-26.
- ELAOUAD-DEBBAJ, Z., 1981, Acritarches de l'Ordovicien supérieur du Synclinal de Buçaco (Portugal), systématique-biostratigraphie-intérêt paléogéographique: *Bull. Soc. Géol. Minéral. Bretagne*, 1978, C, 10 (2): 1-101 [imprinted 1978, issued 1981].
- , 1984, Acritarches et chitinozoaires de l'Arenig-Llanvirn de l'Anti-Atlas (Maroc): *Rev. Palaeobot. Palynol.*, 43: 67-88.
- FATKA, O., MOLYNEUX, S.G. & SERVAIS, T., 1996, The Ordovician acritarch *Frankea*: some critical remarks: *Geobios*, 30 (3): 321-326.
- FENSOME, R.A., WILLIAMS, G.L., BARSS, M.S., FREEMAN, J.M. & HILL, J.M., 1990, Acritarchs and fossil prasinophytes: an index to genera, species and infraspecific taxa: *Amer. Assoc. strat. Palynolists Contrib. Ser.* 25, 771 pp.
- FORTEY, R.A., HARPER, D.A.T., INGHAM, J.K., OWEN, A.W. & RUSHTON, A.W.A., 1995, A revision of Ordovician series and stages from the historical type area: *Geol. Mag.*, 132 (1): 15-30.
- FOURNIER-VINAS, C., 1985, Acritarches ordoviciens des Zekkara (Maroc Oriental): *Geobios*, 18 (6): 807-813.
- GAO, L., 1978, Early Devonian spores and acritarchs from the Nakaoling stage of Liujing, Kwangsi. In *Symposium of the Devonian system of South China*: Inst. Geol. Miner. Res. Chin. Acad. geol. Sci: 346-358. (in Chinese).
- GERMAN, T.N. & TIMOFEEV, B.V., 1974, *Veryhachium kembriya* (Cambrian *Veryhachium*). In *Mikrofossilii Proterozoya i Rannego Paleozoya SSSR* [Plant microfossils of the Proterozoic and Early Palaeozoic of USSR]: Akad. Nauk SSSR: 13-15.
- GUTIÉRREZ-MARCO, J.C., ALBANI, R., ARAMBURU, C., ARBIZU, M., BABIN, C., GARCÍA-RAMOS, J.C., MÉNDEZ-BEDIA, I., RABANO, I., TRUYOLS, J., VANNIER, J. & VILLAS, E., 1996, Biostratigrafía de la Formación Pizarras del Sueve (Ordovicio medio) en el sector septentrional de la escama de Laviana-Sueve (Zona Cantábrica, Norte de España): *Rev. esp. Paleont.*, 11 (1): 48-74.
- HILL, P.J. & MOLYNEUX, S.G., 1988, Biostratigraphy, palynofacies and provincialism of late Ordovician-Early Silurian acritarchs from northeast Libya. In El-Arnauti, A., Owens, B. & Thusu, B. (eds.), *Subsurface palynostratigraphy of northeast Libya*: Garyounis Univ. Publ., Benghazi, Libya (SPLAJ): 27-43.
- JACHOWICZ, M., 1995, Ordovician acritarch assemblages from central and northwestern Saudi Arabia: *Rev. Palaeobot. Palynol.*, 89 (1/2): 19-25.
- JARDINÉ, S., COMBAZ, A., MAGLOIRE, L., PENIGUEL, G. & VACHEY, G., 1974, Distribution stratigraphique des acritarches dans le Paléozoïque du Sahara algérien: *Rev. Palaeobot. Palynol.*, 18 (1/2): 99-129.
- LE HÉRISSE, A., 1989, Acritarches et kystes d'algues Prasinophycees du Silurien de Gotland, Suède: *Palaeontographia Italica*, 76: 57-302.
- LISTER, T.R. & HOLLIDAY, D.W., 1970, Phytoplankton (acritarchs) from a small Ordovician inlier in Teesdale (County Durham), England: *Proc. Yorkshire geol. Soc.*, 37 (4): 449-460.
- LOEBLICH, A.R. & TAPPAN, H., 1969, Acritarch excystment and surface ultrastructure with descriptions of some Ordovician taxa: *Rev. esp. Micropaleont.*, 1 (1): 45-57.
- MARTIN, F., 1966, Les acritarches de Sart-Bernard (Ordovicien belge): *Bull. Soc. belge Géol. Paleont. Hydrol.*, 74 (3): 423-444. [imprinted 1965, issued 1966].
- , 1969, Les acritarches de l'Ordovicien et du Silurien belges. Détermination et valeur stratigraphique: *Mém. Inst. roy. Sci. nat. Belgique*, 160: 175 pp. [imprinted 1968, issued 1969].
- , MICHOT, P. & VANGUESTAINE, M., 1970, Le flysch carado-cien d'Ombret: *Ann. Soc. géol. Belgique*, 93: 337-362.
- MASSA, D., 1988, Paléozoïque de Lybie Occidentale. Stratigraphie et Paléogéographie: Thèse Sc., Univ. Nice, 1-2: 514 pp.
- , HAVLÍČEK, & BONNEFOUS, J., 1977, Stratigraphic and faunal data on the Ordovician of the Rhadames basin (Libya and Tunisia): *Bull. Centr. Rech. Explor.-Prod. Elf-Aquitaine*, 1 (1): 3-27.
- MILLWARD, D. & MOLYNEUX, S.G., 1992, Field and biostratigraphic evidence for an unconformity at the base of the Eycott Volcanic Group in the English Lake District: *Geol. Mag.*, 129 (1): 77-92.
- MITCHELL, C.E., XU, C., BERGSTRÖM, S.M., YUAN-DONG, Z., ZHI-HAO, W., WEBBY, B.D. & FINNEY, S.C., 1997, Definition of a global boundary stratotype for the Darriwilian stage of the Ordovician system: *Episodes*, 30 (3): 158-166.
- MOLYNEUX, S.G., 1990, Advances and problems in Ordovician palynology of England and Wales: *J. geol. Soc.*, 147 (4): 615-618.
- , LE HÉRISSE, A. & WICANDER, R., 1996, Chapter 16. Paleozoic phytoplankton. In Jansonius, J. & McGregor, D.C. (eds.), *Palynology: principles and applications*: Amer. Assoc. strat. Palynolists Found., 2: 493-529.
- MURCHISON, R.I., 1839, *The Silurian System*. Murray, London, 768 pp.
- PARIS, F., 1981, Les chitinozoaires dans le Paléozoïque du sud-ouest de l'Europe (Cadre géologique - étude systématique - biostratigraphie): *Mem. Soc. Géol. Minéral. Bretagne*, 26: 1-496.
- RAUSCHER, R., 1974, Recherches micropaléontologiques et stratigraphiques dans l'Ordovicien et le Silurien en France: Étude des acritarches, des chitinozoaires et des spores: *Sci. géol. (Mém.)*, Univ. Louis Pasteur, Strasbourg, Inst. Géol., 38: 1-224 [imprinted 1973, issued 1974].

- RUSHTON, A.W.A. & MOLYNEUX, S.G., 1989, The biostratigraphic age of the Ordovician Skiddaw Group in the Black Combe Inlier, English Lake District: *Proc. Yorkshire geol. Soc.*, 47 (3): 267-276.
- SARJEANT, W.A.S. & STANCLIFFE, R.P., 1994, The *Michrhystridium* and *Veryhachium* complexes (Acritarcha: Acanthomorphae and Polygonomorphae): A taxonomic reconsideration: *Micropaleontology*, 40 (1): 1-77.
- SERVAIS, T., 1993, The Ordovician acritarch *Frankea*: *Spec. Pap. Palaeont.*, 48: 79-95, 1 pl.
- & FATKA, O., 1997, Recognition of the Trans-European Suture Zone (TESZ) by the palaeobiogeographical distribution pattern of early to middle Ordovician acritarchs: *Geol. Mag.*, 134 (5): 617-625.
- & MALETZ, J., 1992, Lower Llanvirn (Ordovician) graptolites and acritarchs from the "Assise de Huy", Bande de Sambret-Meuse, Belgium: *Ann. Soc. géol. Belgique*, 115 (1): 265-285, 3 pls.
- SMITH, D.G., 1981, Progress in Irish lower Palaeozoic palynology: *Rev. Palaeobot. Palynol.*, 34: 134-148.
- STANCLIFFE, R.P.W. & SARJEANT, W.A.S., 1994, The acritarch genus *Veryhachium* Deunff 1954, emend. Sarjeant & Stancliffe 1994: a taxonomic restudy and a reassessment of its constituent species: *Micropaleontology*, 40 (3): 223-241.
- STOCKMANS, F. & WILLIÈRE, Y., 1963, Les Hystrichosphères ou mieux les acritarches du Silurien Belge. Sondage de la Brasserie Lust à Courtrai (Kortrijk): *Bull. Soc. belge Géol. Paleont. Hydrol.*, 71 (3): 450-481.
- TAPPAN, H., 1980, The paleobiology of plant protists: W.H. Freeman & Co., San Francisco: 1028 pp.
- & LOEBLICH, A.R. Jr., 1971, Surface sculpture of the wall in Lower Paleozoic acritarchs: *Micropaleontology*, 17 (4): 385-410.
- TAYLOR, J.R., 1986, Introduzione all'analisi degli errori - lo studio delle incertezze nelle misure fisiche: Zanichelli S.p.A., Bologna: 223 pp.
- TRYTHALL, R.J.B., ECCLES, C., MOLYNEUX, S.G. & TAYLOR, W.E.G., 1987, Age and controls of ironstone deposition (Ordovician), North Wales: *Geol. J.*, 22 (Spring Thematic Issue): 31-43.
- TURNER, R.E., 1982, Reworked acritarchs from the type section of the Ordovician Caradoc Series, Shropshire: *Palaeontology*, 25 (1): 119-143.
- , 1984, Acritarchs from the type area of the Ordovician Caradoc Series, Shropshire, England: *Palaeontographica*, Abt. B, 190 (4-6): 87-157.
- & WADGE, A.J., 1979, Acritarch dating of Arenig volcanism in the Lake District: *Proc. Yorkshire geol. Soc.*, 42 (3): 405-414.
- VANGUESTAINE, M., 1978, Données palynologiques nouvelles dans l'Ordovicien inférieur du Bassin de la Senne, Massif du Brabant, Belgique: *Ann. Soc. géol. Belgique*, 100: 193-198.
- VAVRDOVÁ, M., 1977, Acritarchs from the Sárka Formation (Llanvirnian): *Vestník ústřed. Ústavu geol.*, 52: 109-118.
- , 1982, Recycled acritarchs in the uppermost Ordovician of Bohemia: *Čas. Mineral. Geol.*, 27 (4): 337-345.
- , 1995, Excystment opening and the affinities of acritarchs: *Acta Universitatis Carolinae, Geol.*, 1992 (3-4): 361-383.
- VECOLI, M., in press, Cambro-Ordovician palynostratigraphy (acritarchs and prasinophytes) of the Hassi-R'Mel area and northern Rhadames Basin, north Africa: *Palaeontographia Italica*.
- & PLAYFORD, G., 1997, Stratigraphically significant acritarchs in uppermost Cambrian to basal Ordovician strata of north-western Algeria: *Grana*, 36: 17-28.
- WEBBY, B.D., 1998, Steps toward a global standard for Ordovician stratigraphy: *Newsl. Stratigr.*, 36 (1): 1-33.

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