Annales de la Société géologique de Belgique, T. 117, fascicule 2, 1994, pp. 355-369 Février 1996

THE ACRITARCH GENUS *POLYGONIUM,* VAVRDOVÁ EMEND SARJEANT AND STANCLIFFE 1994: A REASSESSMENT OF ITS CONSTITUENT SPECIES

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(2 tables & 1 appendix)

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ABSTRACT. The acritarch genus *Polygonium,* although of simple morphology, presently comprises forty-two species.The genus is re-evaluated and seven morphological groups are distinguished. Twenty-two species are retained, fourteen others being treated as junior synonyms. Two species are placed in the new genus *Quantostrobilium,* one retumed to *Buedingiisphaeridium* and three reallocated to *Dorsennidium.*

KEYWORDS: Paleozoic, Mesozoic, Tertiary, biostratigraphy, acritarch, classification.

RESUME. Le genre d'Acritarches *Polygonium* Vavrdová emend. Sarjeant et Stancliffe 1994; une remise en cause des espèces constitutives. Le genre d'acritarches *Polygonium,* bien que de morphologie simple, comprend quarante-deux espèces. Vingt-deux d'entre elles sont maintenues, quatorze autres sont traitées comme synonymes. Deux espèces sont placées dans le nouveau genre *Quantostrobilium,* une retourne à *Buedingiisphaeridium* et trois sont attribuées à *Dorsennidium.*

MOT-CLES: Paléozoique, Mésozoïque, Tertiaire, biostratigraphie, acritarche, classification.

1. INTRODUCTION

The genus Polygonium was erected by Vavrdová (1966, p. 412-413) to contain acritarchs with a polygonal vesicle and a low number of regularly arranged, broad-based spines. Eisenack, Cramer & Díez (1976, p. 629) considered the genus a junior synonym of Micrhystridium Deflandre (1937, p. 31-32) and Goniosphaeridium Eisenack (1969, p. 257-258), stating that there was no objective means to distinguish between Polygonium and Micrhystridium. This was reiterated by Díez & Cramer (1977, p. 20) and Cramer & Díez (1979, p. 98). The latter authors proposed the reattribution of the type species of Polygonium to Goniosphaeridium; however, as noted in Fensome et al. (1990, p. 405), this was not a valid transfer. Turner (1984, p. 112) stated that the only difference between Goniosphaeridium and Polygonium was the ordered arrangement of the spines; if this was not found to be a consistent condition, then the latter was the senior synonym and the former name should be abandoned. However, he retained both genera pending further studies of the type material. Jacobson & Achab (1985, p. 192) likewise noted that Polygonium had priority over Goniosphaeridium but, in a discussion of the type species, rejected the idea that the former genus was a junior synonym of the latter. The synonymy was accepted by Le Hérissé (1989, p. 181) and Albani (1989, p. 24), but Fensome et al. (1990, p. 232, 405) retained both genera.

Sarjeant & Stancliffe (1994, p. 43), during a reconsideration of many polygonomorph taxa, emended Polygonium to differentiate it from Dorsennidium and from genera whose vesicle was formed by confluent processes. The species hitherto placed into Goniosphaeridium were transferred, where appropriate, to Polygonium. Solisphaeridium Staplin, Jansonius & Pocock (1965, p. 183-184) was also treated as a taxonomic junior synonym of Micrhystridium, a number of species assigned to the

Table 1. A listing of the categories of *Polygonium* used in the text and the synonyms recognised.

Table I.- Categories	
3.1.- Stellar forms	
Polygonium "astrum"	jnr syn. of *P. gracile*
Polygonium? "connectum"	jnr syn. of *P. gracile*
Polygonium "dentatum"	jnr syn. of *P. gracile*
Polygonium gracile	
Polygonium gracile var. argentinum	
Polygonium "pungens"	jnr syn. of *P. gracile*
Polygonium "tener"	jnr syn. of *P. gracile*
Polygonium "verspertinum"	jnr syn. of *P. gracile*
3.2.- Many spined stellar forms of moderate size	
Polygonium "elongatum"	jnr syn. of *P. symbolum*
Polygonium delicatum	
Polygonium "oriens"	jnr syn. of *P. symbolum*
Polygonium "radiatusum"	jnr syn. of *P. symbolum*
Polygonium symbolum	
Polygonium "tenuispinosum"	jnr syn. of *P. symbolum*
3.3.- Long spined stellar forms of moderate size	
Polygonium conjunctum	
Polygonium "pellicidum"	jnr syn. of *P. conjunctum*
3.4.- Fewer than twenty spined stellar form of small size.	
Polygonium "heurckii"	syn. of *P. vulgare*
Polygonium? "subrobustum"	jnr syn. of *P. vulgare*
Polygonium vulgare	
3.5.- Many short spined stellar form of moderate size	
Polygonium "acuminosum"	jnr syn. of *P. kudrjawzevii*
Polygonium "breviradiatum"	jnr syn. of *P. nanum*
Polygonium kudrjawzevii	
Polygonium nanum	
3.6.- Stellar form of large size	
Polygonium christianii	
Polygonium makrosphaericum	
Polygonium polygonale	
Polygonium polygonale forma rugosum	
Polygonium polygonale forma polyacanthum	
3.7.- Vesicle with numerous rounded spines	
Polygonium clarum	
Polygonium dedalinum	
Polygonium? geminum	
Polygonium? mammulatum	
3.8.- Vesicle with very short wide spines	
Polygonium aleum	
Polygonium conobrachium	
Polygonium denticulatum	
3.9.- Other species not grouped	
Polygonium? baltoscandium	
Polygonium implicatum	
Polygonium latispinosum	
Polygonium rasulii	
Polygonium varium	
Polygonium windolphae	
3. 1 0. - Transferred	
Polygonium? aster	*to Dorsennidium*
Polygonium cuspidatum	*to Dorsennidium*
Polygonium polyaster	*to Dorsennidium*
Polygonium polyaster var. hexaster	*to Dorsennidium*

former genus being transferred to Polygonium. The genus Celtiberium Fombella (1977, p. 117) was shown to have a diagnosis indistinguishable from that of Polygonium; its constituent species were likewise transferred to the latter genus.

In the following section, the morphological features displayed by *Polygonium* are described and evaluated and their taxonomic importance is assessed. The species presently assigned to the genus are reconsidered, a number of synonyms being recognized. The resulting taxonomic placements are summarized on Table 1.

2. MORPHOLOGICAL VARIATION AND ITS TAXONOMIC SIGNIFICANCE

2.1. SHAPE OF THE VESICLE

The vesicle is generally a subpolyhedron in shape, though some variation is found. The vesicle shape has usually been altered, either by the diagenesis of the enclosing sediment during and after fossilization or by the chemical extraction process. For this reason, vesicle shape can be used in classification only when it is particularly distinctive.

2.2. VESICLE OPENING

The vesicle may exhibit an opening, though this is not the case with most fossil specimens. Sarjeant & Stancliffe, in their emended diagnosis (1994, p. 43), allowed for the possibility of cryptosuture development. However, since this feature is rarely seen, it cannot be used to differentiate forms at the specific level. This is in agreement with the remarks of Eisenack *et al.* (1979, p. XXVIII).

2.3. LATERAL PROFILE OF THE VESICLE

The vesicle may be convex, flat or concave in profile between spines. The profile is subject to change during fossilization and, in particular, during the extraction of the fossils from the host sediment. Further problems arise in quantifying the amount of variation within a species, or even in a single specimen. Consequently, use of this morphological criterion is considered inadvisable for most classificatory purposes.

2.4. VESICLE-SPINE CONTACT

Variations can range from an angular contact to an imperceptible merging of the two structures or a bulging of the spine base [e.g. *Polygonium windolphae* (Welsch, 1986) Sarjeant & Stancliffe, 1994]. On a single specimen there is frequently a range of variation in this feature; it may be influenced by the location of the spine with respect to the plane of compression. As the vesicle-spine contact is a feature that cannot be reliably quantified, it is only of minor taxonomic significance, even at the specific level.

2.5. VARIATIONS IN THE VESICLE AND SPINE EILYMA

This feature is likewise considered of limited taxonomic, being important solely when one species has a very different eilyma thickness from another. Where the difference is only between generally thick (circa 1 mm) and thin (circa 0, 5 mm) walled forms of otherwise similar morphology, then this criterion alone is considered insufficient for specific differentiation. However, a major difference between the thickness of the spine wall and vesicle eilyma can be taxonomically significant.

2.6. SPINE NUMBER AND LOCATION

The spines can number from eleven to over sixty. In forms with many spines, most published diagnoses quote a range of spine numbers as a consequence of counting difficulties. However, the approximate number, at least, is easy to record and, being generally unaffected by preservational circumstances, is of major significance in classification.

Usually the spines are, or appear to be, randomly distributed, but patterns of distribution can occasionally be discerned. When Vavrdová erected the genus *Polygonium,* she stated that the spines of the type species *P. gracilis* were regularly arranged (1966, p. 413-414). She presented a diagram showing the spine positions, in which the Kofoidean dinoflagellate tabulation notation was utilized. However, Jacobson & Achab (1985, p. 192), in an emendation of the species, stated that these spine positions were not constant. If a consistent feature, the location of the spines may prove of taxonomic significance, at least at specific level.

2.7. SPINE STYLE

The spines may be acuminate, conical or flagelliform, straight or curving. On some specimens, more than one spine type may be observed, limiting the use of spine style in classification. The description of spine style may be dependent on the size of

the specimen, since the morphological variability of large spines is more evident than that of small ones. However, chemical preparation techniques and the subjectivity of the observer may affect the reliability of this feature for species discrimination.

2.8. STRUCTURE OF THE SPINES

The diagnosis of *Polygonium* specifies that the spine interiors must conununicate freely with the vesicle interior. However, the spine interior may exhibit solid plugs near the proximal extremities, as in some specimens of *P. polygonale* (Eisenack, 1931) Le Hérissé (1989, p. 182-183). Such structures are potentially of use in characterizing species.

2.9. SPINE TIPS

The spine tips may be pointed, rounded, mammillate, truncate or capitate; in some species, one or more spines on a specimen may be briefly furcate. The spine tips may suffer degradation during fossilization and chemical processing. Nevertheless, when clearly developed, distal spine morphology is important in species differentiation.

2.10. BASAL LINKAGE OF SPINES

Two species presently assigned to *Polygonium* have structures that unite the spine bases. *Polygonium? aleum* (Martin *in* Martin & Dean, 1981) Sarjeant & Stancliffe (1994, p. 43) may exhibit thin translucent membranes extending between its spines. *Polygonium? denticulata* (Tongiorgi *in* Bagnoli *et al.,* 1988) Sarjeant & Stancliffe (1994, p. 48), may also show these, along with ridges radiating from the bases of some spines. Such structures are certainly important in taxonomic differentiation; however, both species are only questionably assigned to this genus.

2.11. VESICLE ORNAMENT

In the recent review of *Veryhachium* by Stancliffe & Sarjeant (1994, p. 227-228), 'ornement' was defined as comprising features under 2 mm in size. Variation in *Polygonium* ranges from a smooth (laevigate) to shagrinate, granulate or reticulate eilyma. Fossilisation and chemical processing can markedly degrade these features making it difficult to use them consistently in classification. Vesicle ornament is therefore not considered satisfactory as sole criterion for defining a species, though it may be a helpful accessory feature. This is in agreement with Eisenack *et al.* (1979, p. XXIII).

2.12. ULTRASTRUCTURE

The ultrastructure (i.e. morphological features only visible when using an electron microscope) of species assigned to *Polygonium* largely remains to be determined. Some electron photomicrographs have been published, for exemple, of *P. latispinosum* (Uutela & Tynni, 1991) Sarjeant & Stancliffe (1994, p. 43), but these have normally been accompanied by light photomicrographs. Such structures may ultimately prove important in taxonomy but, in our view, should not presently be utilized at the specific level, since scanning electron microscopes (S.E.M.) and transmission electron microscopes (T.E.M.) are not routinely employed in biostratigraphic work.

2.13. DIMENSIONS AND PROPORTIONAL MEASUREMENTS

The difficulty of measuring small spiny acritarchs was discussed by us earlier (Stancliffe & Sarjeant, 1994, p. 228). An imperceptible merging of spines with the vesicle is common in *Polygonium,* making measurements of spine length and vesicle diameter often subjective. However, even if a range has to be presented, a significant value can readily be resolved.

The ratio of longest spine length to maximum vesicle diameter is considered important in classification. Essentially, longer-spined forms (spines longer than the vesicle diameter) are distinguished from shorter-spined ones. A subdivision is also made when the spines are exceptionally short, i.e. less than about 30% of the vesicle diameter. Overall spine length is here utilized in assessing the similarity and possible synonymy of a number of species.

3. SYSTEMATIC PALYNOLOGY

3.1. TAXONOMY OF GENUS

Group : Acritarcha Evitt, 1963
Subgroup : POLYGONOMORPHITAE Downie, Evitt & Sarjeant, 1963
Genus *Polygonium* Vavrdová, 1966, p. 412-413, emend. Sarjeant & Stancliffe, 1994, p. 42-44.

Synonymies :
1966 *Polygonium* Vavrdová: 412-413.
1969 *Goniosphaeridium* Eisenack: 256.
1976 *Polygonium* Vavrdová; Eisenack, Cramer & Díez: 629.
1977 *Celtiberium* Fombella: 117.
1977 *Polygonium* Vavrdová; Díez & Cramer: 20.
1979 *Polygonium* Vavrdová; Cramer & Díez: 98.
1984 *Polygonium* Vavrdová; Turner: 1112.

1985 *Polygonium* Vavrdová; Jacobson & Achab: 192.
1988 *Polygonium* Vavrdová; Elaouad-Debbaj: 51.
1989 *Polygonium* Vavrdová; Albani: 24.
1989 *Polygonium* Vavrdová; Le Hérissé: 181.
1990 *Polygonium* Vavrdová; Fensome *et al.*: 405.
1994 *Polygonium* Vavrdová; emend. Sarjeant & Stancliffe: 42-44.

Original diagnosis. Organic shells of fossil microorganisms consisting of a central body of polygonal outline and a low number (about 15) of relatively long, broad-based appendages. The appendages, smooth or granulate and simple or rarely branching, are regularly arranged on the central body. (Vavrdová, 1966, p. 413).

Emended diagnosis. Vesicle hollow, polygonal to sub-polygonal, generally greater than 20 mm in diameter. Eilyma smooth to granulate, thin (about 0,5-1 mm), bearing 11 or more hollow, simple homomorphic spines distributed in more than one plane about the vesicle. Distally the spines are acuminate, closed and sometimes solid; proximally they may be relatively broad-based. When hollow, the spine interiors communicate freely with the vesicle cavity. No differentiation is apparent between the spines and vesicle wall. Opening of vesicle by cryptosuture. (Sarjeant & Stancliffe, 1994, p. 43).

Type species. *Polygonium gracile* Vavrdová 1966, p. 413, Pl. 1, Fig. 3; Pl. 3, Fig. 1, text-figs. 3b, 4b non Pl. 2, Fig. 3), emend. Jacobson & Achab (1985, p. 192). Lower Ordovician, Czechoslovakia.

Remarks. The apparent overlap of *Polygonium* with *Eomicrhystridium* Deflandre (1968, p. 2387) was discussed by Sarjeant & Stancliffe (1994, p. 28, 43) but not resolved, pending further research on the type material of the latter genus. *Goniosphaeridium* was shown to be a junior synonym of *Polygonium* by Le Hérissé (1989, p. 181) and *Celtiberium* by Sarjeant & Stancliffe (1994, p. 42).

Polygonium is differentiated from *Dorsennidium* Wicander, 1974 emend. Sarjeant & Stancliffe (1994, p. 39) by having more than eleven hollow spines. *Micrhystridium* Deflandre, 1937 emend. Sarjeant & Stancliffe (1994, p. 12) has a smaller, spherical vesicle (generally less than 20 mm in diameter) compared with the larger subpolygonal vesicle of *Polygonium* (generally greater than 20 mm in diameter). The spines of *Micrhystridium* may be hollow or solid but do not markedly flare proximally, whereas *Polygonium* has spines which always communicate with the vesicle cavity and consistently flare proximally. *Centrasphaeridium* Wicander & Playford (1985, p. 99, 101) typically has one longer axial process and may be echinate overall.

Of the larger acritarch genera which resemble *Polygonium, Estiastra* Eisenack (1959, p. 201), emend.. Sarjeant & Stancliffe (1994, p. 50) and *Barbestiastra* Sarjeant & Stancliffe (1994, p. 47), both have large acuminate spines; however, it is their proximal confluence that forms the vesicle, whereas *Polygonium* has a distinct central body. *Chalaziosphaeridium* Sarjeant & Stancliffe (1994, p. 48) and *Pulvinosphaeridium* Eisenack (1954, p. 210), emend.. Sarjeant & Stancliffe (1994, p. 52), both have large, distally rounded or blunt spines whose proximal confluence likewise forms the vesicle.

3.2. SPECIES CATEGORIES

The species assigned to the genus *Polygonium* are here organized into nine categories, based on their particular morphology. Each category is given a number and a short description, a typical species being cited.

3.2.1. Category I (typified by *Polygonium gracile)*

Species having a vesicle of moderate size, which bears spines in moderate number (12 to 20). Spine length is less than the maximum vesicle diameter but greater than half that diameter.

Polygonium gracile Vavrdová, 1966, emend. nov.

Synonymies:
1959 *Archaeohystrichosphaeridium dentatum* Timofeyev: 41, Pl. 3, Fig. 44, nomen nudum.
1959 *Archaeohystrichosphaeridium pungens* Timofeyev: 41, Pl. 3, Fig. 44, nomen nudum.
1959 *Archaeohystrichosphaeridium tener* Timofeyev: 40, Pl. 3, Fig. 39, nomen nudum.
1966 *Polygonium gracile* Vavrdová: 413, Pl. 1, Fig. 3; Pl. 3, Fig. 1; text-figs. 3b, 4b; non Pl. 2, Fig. 3.
1969 *Baltisphaeridium dentatum* Timofeyev ex Konzalovà-Mazancovà: 87.
1969 *Baltisphaeridium pungens* Timofeyev ex Martin: 60.
1971 *Goniosphaeridium connectum* Kjellström: 44-45, Pl. 3, Fig. 5.
1974 *Solisphaeridium astrum* Wicander: 31, Pl. 16, Figs. 7-9.
1980 *Polygonium verspertinum* Deunff: 512-513, Pl. 4, Fig. 13.
1988 *Goniosphaeridium tener* Timofeyev ex Elaouad-Debbaj: 103.
1989 *Polygonium dentatum* (Timofeyev ex Konzalová-Mazancová); Albani: 24-25.
1989 *Polygonium pungens* (Timofeyev ex Martin); Albani: 25-26.
1994 *Polygonium astrum* (Wicander); Sarjeant & Stancliffe: 43.

1994 *Polygonium? connectum* (Kjellström); Sarjeant & Stancliffe: 43.
1994 *Polygonium tener* (Timofeyev ex Elaouad-Debbaj); Sarjeant & Stancliffe: 44.

Original diagnosis. Shells with hexagonal or pentagonal outline, provided with long, usually simple smooth processes, communicating with the inner cavity. Processes are regularly arranged in circles after the following pattern: 1; 5'[6']; 5"[6"]; [3"']; 1"». (Vavrdová, 1966, p. 413).

Emended diagnosis. Vesicle hollow, polygonal, generally between 20-35 mm in diameter. Eilyma smooth to shagrinate bearing twelve to about twenty simple homomorphic spines distributed, occasionally in a regular manner, in several planes about the vesicle. Spine length is less than the maximum diameter of the vesicle. Distally the spines are acuminate and closed while proximally they are quite broad-based. The spine cavities communicate freely with the vesicle interior. No differentiation is apparent between spine walls and eilyma. Opening of the vesicle not observed.

Holotype. MV 3, lodged in the collection of the Geological Institute of the Academy of Science, Prague, Czech Republic. [Note: In the original description, the holotype illustration is quoted incorrectly as plate 2, not 1].

Type Horizon. Klabava Shales, Ordovician (Arenigian). U Starého hradu, SE of Klabava, Czech Republic.

Remarks. Jacobson & Achab (1985, p. 192) noted that a regular spine arrangement on the vesicle was only sometimes observable; however, they did not formally emend the diagnosis. The length of the spines is here restricted to less than the maximum vesicle diameter, in agreement with the measurements of the type material, while the number of spines is indicated. Following this emendation, a number of species fall into synonymy. The synonymizing of *Polygonium? connectum* is provisional; while the diagnosis indicates that there are about 10 spines, the illustration of the holotype suggests a larger number.

Other accepted taxon:

Polygonium gracile Vavrdová, 1966 var. *argentinum* Pöthe de Baldis, 1971, p. 286-287, Pl. 2, Fig. 4.

Remarks. This variety was erected on only two specimens; more need to be examined, to discover whether the distribution of spines is truly regular and consistently shown or whether it is observable only on some specimens.

3.2.2. Category II (typified by *Polygonium symbolum)*

Species having a vesicle of moderate size, which bears spines in higher number (around 20 to 50). Spine length is less than the maximum vesicle diameter but greater than half that diameter (as in Category I).

Polygonium symbolum Rasul, 1979, emend. nov.

Synonymies:
1979 *Polygonium symbolum* Rasul: 62, Pl. 1, Fig. 10.
1984 *Goniosphaeridium elongatum* Turner: 113, Pl. 13, Figs. 1-2.
1986 *Goniosphaeridium oriens* Welsch: 46-47, Pl. 6, Figs. 1-2, text-fig. 17.
1986 *Goniosphaeridium radiatusum* Yin: 346-347, Pl. 85, Fig. 16, text-fig. 128.
1991 *Goniosphaeridium tenuispinosum* Uutela & Tynni: 67-68, Pl. 13, Fig. 132.
1994 *Polygonium elongatum* (Turner); Sarjeant & Stancliffe: 43.
1994 *Polygonium oriens* (Welsch); Sarjeant & Stancliffe: 44.
1994 *Polygonium radiatusum* (Yin); Sarjeant & Stancliffe: 44.
1994 *Polygonium tenuispinosum* (Uutela & Tynni); Sarjeant & Stancliffe: 44.

Original diagnosis. Body polygonal, smooth, the outline of which is somewhat obscured by the broad bases of the processes which merge into the test. The processes are hollow, simple, long, smooth, tapering, sometimes end with hair-like tips. No excystment recorded. (Rasul, 1979, p. 62).

Emended diagnosis. Vesicle hollow, polygonal, generally between 20-40 mm in diameter. Eilyma smooth to shagrinate bearing about twenty to fifty simple homomorphic spines, their length less than the maximum vesicle diameter. Distally the spines are acuminate and closed, while proximally they are broad-based. The spine cavities communicate freely with the vesicle cavity. No differentiation is apparent between spine walls and eilyma. Opening of the vesicle not observed.

Holotype. Slide Reference T2/1-22.11.85. Collections of the Department of Geology, University of Sheffield, England.

Type Horizon. Transition Beds, Early Ordovician (Tremadocian), Shropshire, England.

Remarks. Uutela & Tynni (1991) did not record the total number of spines on the vesicle of *P. tenuispinosum;* since the sole illustration is a

scanning electron micrograph of the holotype, counting spines was not possible. It is assumed, pending a re-examination of the type material, that over 25 spines are developed, in which case the species can be included in the synonymy. All other species listed conform to the emended diagnosis of *P. symbolum.*

Other accepted taxon:

Polygonium delicatum Rasul, 1979, p. 60, pl. 1, fig. 11.

Remarks. This species is differentiated from *P. elongatum* by its flagelliform spines. Their number was not reported, but Rasul's illustration suggests that over 20 are present.

3.3.3. Category III (typified by *Polygonium conjunctum*)

Species having a vesicle of moderate size, which bears spines in moderate number (around 16 to 20). Spine length greater than the maximum vesicle diameter.

Polygonium conjunctum (Kjellström, 1971) Sarjeant & Stancliffe, 1994.

Synonymies:
1959 *Archaeohystrichosphaeridium pellicidum* Timofeyev: 40, Pl. 3, Fig. 37, nomen nudum.
1971 *Goniosphaeridium conjunctum* Kjellström: 43-44, Pl. 3, Fig. 4.
1975 *Goniosphaeridium pellicidum* Timofeyev ex Tynni: 20.
1994 *Polygonium conjunctum* (Kjellström) Sarjeant & Stancliffe: 43.
1994 *Polygonium pellicidum* (Timofeyev ex Tynni); Sarjeant & Stancliffe: 44.

Diagnosis. [A species with] thin, single-walled, polygonal, shagrinate, vesicle. No excystment structure recorded. Curved proximal process contact within vesicle. Free communication of the process interiors and the vesicle cavity. Processes about 15 in number, in length exceeding the vesicle diameter, shagrinate, broad bases, homomorphic with acuminate distal terminations. (Kjellström, 1971, p. 44).

Remarks. *P. pellicidum* has spines which are longer than the vesicle diameter; it is here considered a junior synonym of *P. conjunctum,* since its name was not validly published until 1975 (see Fensome *et al.,* 1990, p. 236 and Sarjeant & Stancliffe, 1994, p. 43, 44 for discussions).

Other accepted taxon:

Polygonium? windolphae (Welsch, 1986, p. 51, Pl. 8, Figs. 1-3, text-fig. 19) Sarjeant & Stancliffe, 1994, p. 44.

Remarks. This species has long, slender spines arising from distinct hemispherical to funnelshaped bases, a morphology unique in *Polygonium.*

3.3.4. Category IV (typified by *Polygonium vulgare)*

Species having a small vesicle, bearing a low number of spines (12 to 20). Spine length is less than the maximum vesicle diameter, but greater than half the diameter.

Polygonium vulgare (Stockmans & Willière, 1962) Sarjeant & Stancliffe, 1994, emend. nov.

Synonymies:
1962 *Micrhystridium vulgare* Stockmans & Willière: 63-64, Pl. 2, Figs. 12, 14-15, text-fig. 23.
1981 *Micrhystridium subrobustum* Grishina in Grishina & Klenina: 32, Pl. 1, Fig. 15.
1994 *Polygonium? subrobustum* (Grishina in Grishina & Klenina) Sarjeant & Stancliffe: 44.
1994 *Polygonium vulgare* (Stockmans & Willière); Sarjeant & Stancliffe: 44.

Original diagnosis. Body transparent, polyhedral, the angles terminated by elongate processes; bearer of 6 to 12 appendages of uniform type, perpendicular or oblique, whose bases broaden abruptly into a concave crest with two arms and dispose so as to form a sort of crown. (Stockmans & Willière, 1962, p. 63-64; new transl.).

Emended diagnosis. Vesicle hollow, polygonal, generally between 12 to 15 mm in diameter. Eilyma smooth, bearing around 16 to 20 simple homomorphic spines, their length less than the maximum vesicle diameter. Distally the spines are acuminate and closed, while proximally they are very broad-based, tapering sharply just above the base. The spine cavities communicate freely with the vesicle cavity. No differentiation is apparent between spines and eilyma. Opening of the vesicle not observed.

Holotype. Preparation no. 1103, collections of the Institut royal des Sciences naturelles de Belgique, Brussels, Belgium.

Type horizon. Upper Devonian (Frasnian). Borehole at Asile d'aliénés, Tournai, Belgium at 393 m depth.

Remarks. Though the original diagnosis states that this species has only six to twelve spines, the

drawing and photographs make evident the presence of at least sixteen! *P. subrobustum* has broad-based spines which control the vesicle outline, but it is not clear from the diagnosis or drawing whether they are open to the vesicle interior. The species is here considered a junior synonym of *P. vulgare,* pending re-examination of the type material.

Other accepted taxon:

Polygonium? heurckii (Stockmans & Willière, 1962, p. 63, Pl. 2, Fig. 8, text-fig. 22) Sarjeant & Stancliffe, 1994, p. 43.

Remarks. Differentiated from *P. vulgare* by having spines positioned at the angles, and in the middle of the sides, of a quadrangular vesicle. Although the two species are similar in number and length of spines, there is some indication in the illustrations of *P. heurckii* that two axial spines may be longer than the others. If that is so, then this species may merit transfer to the genus *Unellium* Rauscher, 1969.

3.3.5 Category V (typified by *Polygonium acuminosum)*

Species having a vesicle of moderate size, bearing many (ca. 20 to 50) spines. Spines short, less than half the maximum vesicle diameter.

Polygonium acuminosum (Cramer & Díez, 1977) Sarjeant & Stancliffe, 1994 emend. nov.

- Synonymies:

1959 *Archaeohystrichosphaeridium kudrjawzevii* Timofeyev: 48, Pl. 3, Fig. 77 nomen nudum.
1977 *Micrhystridium acuminosum* Cramer & Díez: 347, Pl. 1, Figs. 3-4, 10, text-fig. 3.3.
1986 *Goniosphaeridium kudrjawzevii* Timofeyev ex Hu: 221.
1994 *Polygonium acuminosum (*Cramer & Díez); Sarjeant & Stancliffe: 43.
1994 *Polygonium kudrjawzevii* (Timofeyev ex Hu); Sarjeant & Stancliffe: 43.

Original diagnosis. [Vesicle] with numerous conical processes which terminate in a sharp point. Some 40 processes are present. (Cramer & Díez, 1977, p. 347).

Emended diagnosis. Vesicle of moderate size, spheroidal to subpolygonal, densely set with conical processes that taper smoothly from a broad base to an acuminate tip. Processes hollow, their cavities communicating directly with the vesicle interior. Length of spines less than 50% of largest vesicle diameter; number of spines ca. 40 to 50. No differentiation is apparent between the laevigate vesicle and the spine walls. Opening of vesicle not observed.

Holotype. Specimen illustrated by Cramer & Díez, 1977, Pl. 1, Fig. 3-4. F.H. Crarner Collection (present lodgement not known).

Type horizon. Ordovician (Late Arenigian), Kasba Tadla Basin, Morocco.

Remarks. The unusually broad-based character of its spines suggests that this species may be intermediate to *Estiastra.* However, it cannot be assigned to that genus, since the vesicle wall remains distinctly visible between the spine bases. The diagnosis of *P. kudrjawzevii* by Timofeyev (1959, p. 48) is ambiguous since the spines may have been characterized as either solid or massive; the illustration of the holotype does not resolve this question, but hollow processes seem likely. *P. kudrjawzevii* was not validly published until 1986 and is here treated as a junior synonym.

Other accepted taxon:

Polygonium nanum (Deflandre, 1945, p. 19-20, Pl. 1, Figs. 5-7, emend. Lister, 1970, p. 5456) Jacobson, 1978, p. 297.

Remarks. The high number of spines gives the vesicle a subpolygonal outline, which places *P. nanum* near the extremes of *Polygonium-type* morphology. Jacobson (1978, p. 297), in a detailed discussion, states that this species was differentiated from *P. gracile* only by the latter's process formula; however, Jacobson & Achab (1985, p. 192) emended *P. gracile* and firmly placed the forms described earlier by Jacobson (1978) into *P. nanum* as now conceived. Following their work *P. nanum* can be distinguished from *P. gracile* by its shorter, more numerous spines. *Polygonium breviradiatum* (Uutela & Tynni, 1991, p. 64-65, pl. 13, fig. 9) Sarjeant & Stancliffe, 1994, p. 43 is similar in morphology to *P. nanum;* however, the total number of its spines was not recorded and cannot be determined from the S.E.M. of the holotype. We consider it provisionally to be a junior synonym of *P. nanum.*

3.3.6. Category VI (typified by *Polygonium polygonale)*

The only common feature of the species in this category is their large vesicle size; they vary considerably in spine form, number and relative length.

Polygonium polygonale (Eisenack, 1931) emend. Le Hérissé, 1989.

Synonymies:
[see Le Hérissé, 1989, p. 182 for full listing]

Emended diagnosis. Species of large size, of the group of 'giant' Acritarchs, having a subspherical to polygonal vesicle, with wall thin and smooth, from which emerge conical processes, with wide bases and pointed or rounded tips. The processes have a regular arrangement; they are hollow and communicate freely with the central cavity. The walls of both processes and vesicle have a constant thickness. The mode of opening of this species has not been observed. (Le Hérissé, 1989, p. 182).

Holotype. Illustrated by Eisenack (1931, Pl. 4, Fig. 19); lost according to Eisenack (1959, p.199).

Neotype: specimen illustrated by Paris & Deunff (1970, Pl. 1, Fig. 4); designated by Fensome*et al.* (1990, p. 235).

Remarks. Le Hérissé (1989, p. 182) noted that the transfer to *Polygonium* was first suggested by Jacobson in an unpublished doctoral thesis. He stressed that the species is separated from others assigned to this genus by its large size (overall diameter 100-200 mm; process length 40-60 mm) and lack of surface omament; the latter feature is not considered by us of taxonomic significance at the specific level. The number of processes he quotes (6-32) extends below the minimum specified in the emended generic diagnosis of *Polygonium;* it is probable that a restudy may justify transfer of the forms with few processes to another taxon.

Other accepted taxa:

Polygonium christianii (Kjellström, 1976, p. 28, fig. 21) Sarjeant & Stancliffe, 1994, p. 43.

Remarks. This species may be differentiated from *P. polygonale* by its shagrinate vesicle and bulbous spine terminations (though the first feature is considered of questionable significance). The illustration of the holotype shows one spine which branches, though this gains no mention in the diagnosis. The spine length is almost equal to the vesicle diameter.

Polygonium makrosphaericum (Eisenack, 1970, p. 318, fîg. 6B) Sarjeant & Stancliffe, 1994, p. 43.

Remarks. The spines are very short and broad; their number is not clear on the illustration of the holotype, but the figure by Eisenack, Cramer & Díez (1973, p. 489) shows ten on one surface.

Polygonium polyacanthum (Eisenack, 1965, p. 137, pl. 13, figs. 3-4) Sarjeant & Stancliffe, 1994, p. 44.

Remarks. This species accords in size and spine number with this category. Unfortunately, Eisenack's original description of his « forma *polyacantha* « was minimal— « [forms] with many appendages and well-formed central body»—and, though the name *polyacanthum* has a singularly vicissitudinous history (see Fensome *et al.,* 1990, p. 236), no satisfactory description has subsequently been published. The longest, by Górka (1969, p. 27-28), misstated the spine number as «around 18» whereas, from Eisenack's illustration, it certainly exceeds 40! Pending a proper restudy of this taxon, though we place it confidently into this category, we prefer not to comment further upon it.

3.3.7. Category VII (typified by *Polygonium clarum)*

Vesicle size small to moderate; spines short, evexate, distally rounded, spine number moderate to large.

Polygonium clarum (Fombella, 1978) Sarjeant & Stancliffe, 1994.

Synonymies:
1978 *Celtiberium clarum* Fombella: 251, Pl. 2, Fig. 3.
1994 *Polygonium clarum* (Fombella); Sarjeant & Stancliffe: 43.

Diagnosis. Species with vesicle of small dimensions. Only 20 processes are visible in optical section, distributed without topological preference over the whole vesicle. They are in direct communication with the central part of the vesicle, a hollow, cylindrical and with rounded tips. The membrane is smooth, of thickness less than 1 mm. The mode of opening is unknown. (Fombella, 1978, p. 251, new transl.).

Remarks. The species is distinguishedly its small vesicle size and relatively low number of short spines.

Other accepted taxa:

Polygonium dedalinum (Fombella, 1978, p. 251, Pl. 2, Fig. 3) Sarjeant & Stancliffe, 1994, p. 43.

Remarks. This species is distinguished from *P. clarum* by its larger dimensions and larger number of spines.

Polygonium? geminum (Fombella, 1977, p. 117-118, Pl. 1, Figs. 10-11; text-fig. 1.9) Sarjeant & Stancliffe, 1994, p. 43.

Remarks. Dimensions similar to those of *P. dedalinum,* but spines less numerous and conical, with broad bases.

3.4. SPECIES NOT ASSIGNED TO CATEGORIES

The species listed here all present taxonomic problems. Some are so broadly defined that a restudy appears necessary to clarify the extent of intraspecific variation, if it be indeed intraspecific; some exhibit features so unusual as to cast doubt concerning their placement into this genus; and, in other instances, the morphology is simply not clear.

Polygonium? aleum (Martin in Martin & Dean, 1981, p. 16, Pl. 1, Figs. 20-21; Pl. 4, Figs. 7, 9-10) Sarjeant & Stancliffe, 1994, p. 43.

Remarks. The spines are very short, sometimes with thin membranes stretching between them. Consequently, this species is only provisionally retained in *Polygonium.*

Polygonium? baltoscandium (Eklund, 1990, p. 41, Fig. 81) Sarjeant & Stancliffe, 1994, p. 43.

Remarks. Assigmnent is provisional, since the total number of processes is neither specified or nor resoluble from the illustration of the holotype; moreover, their tips are "occasionally bifurcated or branched."

Polygonium? denticulatum (Tongiorgi in Bagnoli, Stouge & Tongiorgi, 1988, p. 183-184, Pl. 25, Figs. 1-5; Pl. 26, Figs. 6-7) Sarjeant & Stancliffe, 1994, p. 43.

Remarks. The spines are very short, sometimes having a membrane stretched between them. Consequently, this species is only provisionally included in *Polygonium.*

Polygonium? implicatum (Fridriksone, 1971, p. 11-12, Pl. 3, Figs. 7-14) Sarjeant & Stancliffe, 1994, p. 43.

Remarks. Vesicle stated to be thick-walled, but «of non-uniform density» and showing grooves and wrinkles at the margins. Spines stated to be numerous (around 30 in the holotype) and variable in character—sometimes «arrow-like», sometimes «clotted (lumpy) tops», sometimes contained within a film and very often broken. Inadequate illustrations do not help to clarify the morphology of this species, which quite defies our analysis.

Polygonium? latispinosum (Uutela & Tynni, 1991, p. 85, Pl. 18, Fig. 184) Sarjeant & Stancliffe, 1994, p. 43.

Remarks. Since some spines are bifid, this species may be interpreted as intermediate to the morphology of *Multiplicisphaeridium* Staplin (1961, p. 411).

Polygonium? rasulii (Welsch, 1986, p. 47-48, nom. subst. pro *Baltisphaeridium spinosum* Rasul, 1979, p. 58-60, Pl. 1, Fig. 7) Sarjeant & Stancliffe, 1994, p. 44.

Remarks. The variation in vesicle shape, from spheroidal to ellipsoidal, and the presence of some forked processes make the generic assigmnent questionable.

Polygonium? varium (Volkova, 1969, p. 225-226, Pl. 50, Figs. 4-8; Pl. 51, Figs. 13-14) Sarjeant & Stancliffe, 1994, p. 44.

Remarks. The diagnosis presents a species with a very variable spine and vesicle shape, a morphological range which overlaps a number of other species assigned to *Polygonium.* Further study of the type material is needed prior to formulating any conclusions concerning the character of this species.

3.5. SPECIES REASSIGNED TO OTHER GENERA

Dorsennidium Wicander 1974, emend. Sarjeant & Stancliffe, 1994.

Type species. *Dorsennidium patulum* Wicander, 1974, p. 20, Pl - 9, Figs. 10- 12. Upper Devonian, Ohio, U.S.A.

Systematic reassigmnents:
Dorsennidium (Dorsennidium) aster(Sarjeant, 1967, p. 204-205, Pl. 1, Fig. 11; text-fig. la) comb.nov. Middle Jurassic, France.

Holotype: illus. by Sarjeant (1967, Pl. 1, Fig. 11). Originally *Veryhachium;* transferred to *Polygonium* by Erkmen & Sarjeant (1980, p. 73-74).

Remarks. The vesicle bears fewer than eleven spines, distributed in more than one plane; it fits well into Category IV of *Dorsennidium* (see Stancliffe & Sajeant, 1995).

Dorsennidium (Dorsennidium) cuspidatum (Timofeyev, 1959, p. 41, Pl. 3, Fig. 43, ex Pittau, 1985, p. 184-185, Pl. 6, Fig. 19) comb.nov. Middle Cambrian, Russia.

Holotype: illus. by Timofeyev, 1959, Pl. 3, Fig. 43. Originally placed in the invalid genus *Archaeohystrichosphaeridium;* validly published as *Goniosphaeridium;* subsequently placed into *Polygonium* by Sarjeant & Stancliffe (1994, p. 43).

Remarks. The species has only a few spines—the holotype is illustrated with five—distributed in more than one plane. It accords with Category VI of *Dorsennidium* (see Stancliffe & Sarjeant, 1995).

Dorsennidium (Dorsennidium) polyaster (Staplin, 1961, p. 413, Pl. 49, Fig. 20) comb. nov. Upper Devonian, Alberta, Canada.

Holotype: illus. by Staplin, Pl. 49, Fig. 20. Originally *Veryhachium;* transferred to *Polygonium* by Sarjeant & Stancliffe (1994, p. 44).

Remarks. Typical forms (var. *polyaster)* have 5 spines while others, distinguished as var. *hexaster* have 6 spines in two or several planes. Since the spines are longer than the vesicle diameter, both varities conform with Category VII of *Dorsennidium* (see Stancliffe & Sarjeant, 1995).

Dorsennidium (Dorsennidium) polyaster var. polyaster (Staplin, 1961), Autonym.

Dorsennidium (Dorsennidium) polyaster var. hexaster (Staplin, 1961, p. 413, Pl. 49, Fig. 19) comb. nov. Upper Devonian, Alberta, Canada.

Holotype: illus. by Staplin, Pl. 49, Fig. 19. Originally *Veryhachium;* subsequently, and transferred from, *Polygonium.*

Quantostrobilium Sarjeant & Stancliffe, nov.

Derivation of name. L. *quantus,* how many; *strobilus,* cone.

Diagnosis. Vesicle hollow, its shape determined by the confluent or near-confluent bases of its processes. Processes hollow, 11 or more in number, in shape conical to mammiliform and without branches. Process cavities communicating directly with vesicle cavity. Eilyma psilate, granulate or pustulose, but not echinate and without ridges. Opening, when developed, by cryptosuture.

Type species. *Quantostrobilium mammulatum* (Cramer & Diéz, 1977) emend. Sarjeant & Stancliffe, herein. Lower Ordovician, Morocco.

Remarks. This genus differs from *Palacanthus* Wicander, 1974 emend. Sarjeant & Stancliffe, 1994, in having processes in more than one plane and from *Chalaziosphaeridium* Sarjeant & Stancliffe, 1994, in having conical to mammiliform processes. It resembles the latter genus in almost consistently exhibiting cryptosutures, differing in this from *Polygonium* and also by having a vesicle whose shape is determined by confluence of process bases. The shape of the processes further differentiates this genus from *Polygonium.*

Quantostrobilium mammulatum (Cramer & Diéz, 1977), comb.nov., emend.

Synonymies:
1977 *Micrhystridium? mammulatum* Cramer & Diéz: 347, Pl. 3, Figs. 6-11; text-fig. 3.2. *1994 Polygonium? mammulatum* (Cramer & Diéz); Sarjeant & Stancliffe: 43-44.

Original diagnosis. *Micrhystridium* with numerous thick, broad-based, cylindrical processes which quickly taper distally and terminate in a distinct nipple. (Cramer & Diéz, 1977, p. 347).

Emended diagnosis. Vesicle formed from the confluence of the bases of some 40 hollow processes. Eilyma psilate. Processes almost cylindrical, though tapering slightly; distally mammillate. Process cavities open directly to vesicle interior. Length of processes ca. one-third of vesicle diameter. Opening, where observed, by cryptosuture.

Holotype. Illustrated by Cramer & Diéz (1977, Pl. 3, Fig. 6): present lodgement uncertain. Ordovician (late Arenigian), Kasba Tadla Basin, Morocco.

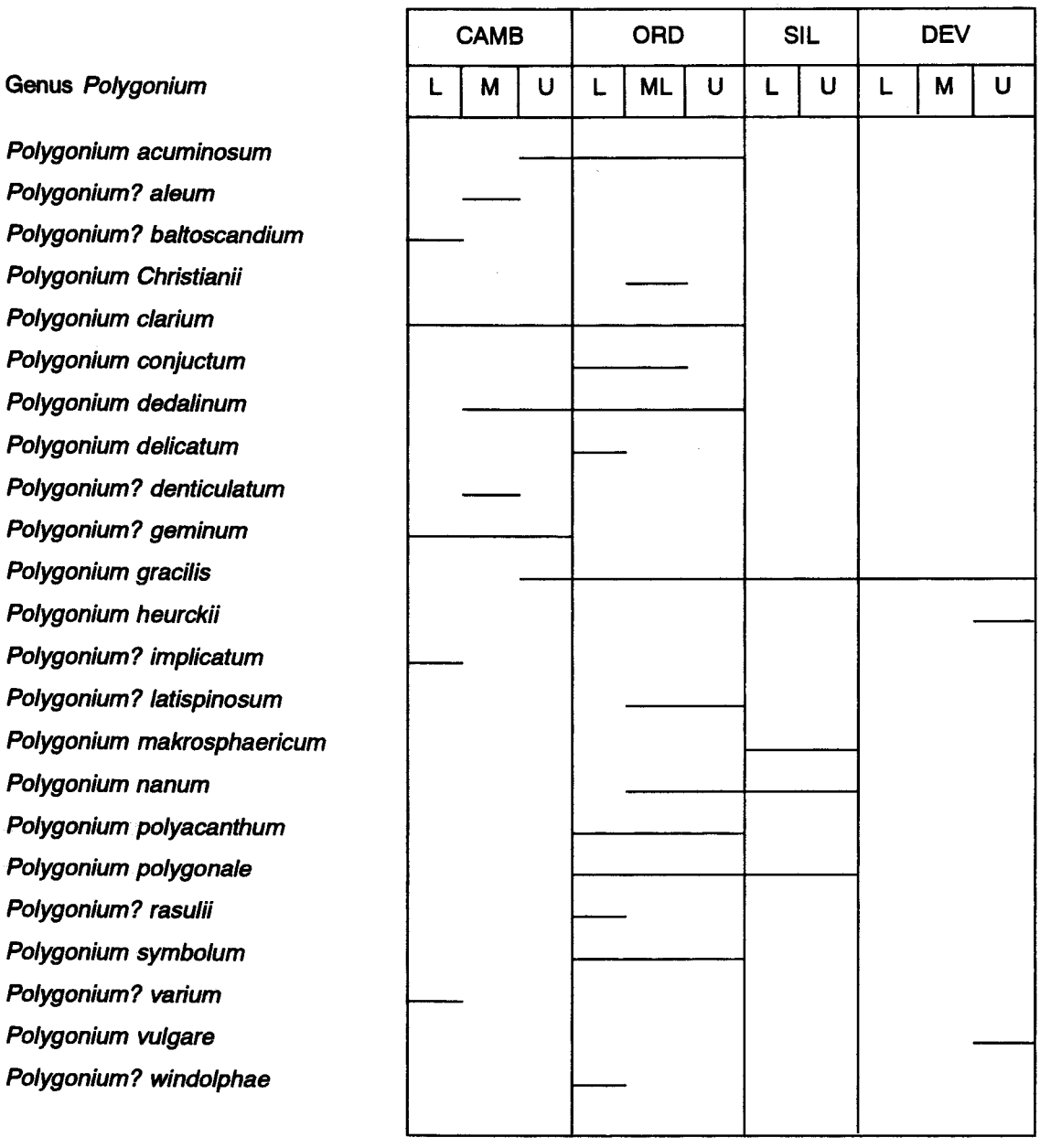
Dimensions. Range: overall diameter ca. 26-40 µm; vesicle diameter ca. 20-30 µm.

Other accepted taxon:

Quantostrobilium conobrachium (Vavrdová, 1978, p. 64, Pl. 14, Figs. 1-5) comb. nov. Ordovician (late Arenigian), Czech Republic.

Holotype: illus. by Vavrdová, 1978, Pl. 14, Fig. 3. Originally *Micrhystridium;* subsequently placed into *Polygonium* by Sarjeant & Stancliffe (1994, p. 43).

Table 2. A conservative range chart for the constituent species of *Polygonium* based on the type material.



Remarks. Differs from *Polygonium* in having processes whose bases are confluent and define the vesicle outline. Differs from *Q. mammulatum* in having fewer, broadly conical processes that are not mammillate.

Buedingiisphaeridium Schaarschmidt, 1963, emend. Sarjeant & Stancliffe, 1994.

Type species: *Buedingiisphaeridium permicum* Schaarschmidt, 1963, p. 70, Pl. 20, Figs. 4-6; text-fig. 26. Upper Permian, Germany.

Systematic correction:
Buedingiisphaeiidium matutinum (Fombella, 1977, p. 177, Pl. 1, fig. 16, text-fig. 1.6) Sarjeant & Stancliffe, 1994, p. 25, was inadvertently also listed as *Polygonium matutinum* on p. 44. The assigment to *Buedingiisphaeridium* is considered correct.

4. BIOSTRATIGRAPHY

This re-evaluation of *Polygonium* restricts its range to the Paleozoic, with its major component in the Early Paleozoic (Tab. 2). The first five taxa occur in the Lower Cambrian, ten further species appearing subsequently during that period. Twelve species have been reported from the Ordovician, when *Polygonium* atteins its highest diversity. From the Silurian, only one new taxon has been reported. A last new taxon appears in the Early Devonian; there are no records from younger sediments.

The ranges of the accepted species of *Polygonium* are shown in Tab. 2. A comparison with *Veryhachium* shows that both genera were comparably diverse in the Cambrian and Ordovician, but *Veryhachium* continued diverse during the Silurian and Devonian and persisted at least into the Late Mesozoic. The related genus *Dorsennidium* reached greatest diversity in the Devonian. This may indicate that polygonomorphic acritarchs with fewer spines were increasingly favoured as time passed. Further research is necessary before detailed paleoecological deductions can be drawn.

5. ACKNOWLEDGEMENTS

We would like to thank Boris Benko for his assistance in translating some of the original Russian diagnoses and the editors for inviting us to publish this tribute to a most distinguished palynologist and good friend. The first author's researchers were funded by Operating Grant #OGP 0008393 from the Natural Science and Engineering Research Council of Canada.

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Manuscrit reçu le 6 octobre 1994; accepté le 10 janvier 1995.

APPENDIX 1

A listing of the species considered in the text along with the Category reference number.

Category	Page
Polygonium "acuminosum"	3.5
Polygonium aleum	3.8
"Polygonium ?" aster	3.10
Polygonium "astrum"	3.1
Polygonium ? baltoscandium	3.9
Polygonium breviradiatum	3.5
Polygonium christianii	3.6
Polygonium clarum	3.7
Polygonium cojunctum	3.3
Polygonium ? "connectum"	3.1
Polygonium conobrachium	3.8
"Polygonium" cuspidatum	3.10
Polygonium dedalinum	3.7
Polygonium delicatum	3.2
Polygonium "dentatum"	3.1
Polygonium denticulatum	3.8
Polygonium "elongatum"	3.2

Polygonium ? geminum	3.7
Polygonium gracile	3.1
Polygonium gracile var. *argentinum*	3.1
Polygonium "heurckii"	3.4
Polygonium implicatum	3.9
Polygonium kudrjawzevii	3.5
Polygonium latispinosum	3.9
Polygonium makcrosphaericum	3.6
Polygonium ? mammulatum	3.7
Polygonium matutinum	3.8
Polygonium nanum	3.5
Polygonium "oriens"	3.2
Polygonium "pellicidum"	3.3
"Polygonium" polyaster	3.10
"Polygonium" polyaster var. hexaster	3.10
Polygonium polygonale	3.6
Polygonium polygonale forma polyacanthum	3.6
Polygonium polygonale forma rugosum	3.6
Polygonium «pungens»	3.1
Polygonium radiatusum	3.2
Polygonium rasulii	3.9
Polygonium? "subrobustum"	3.4
Polygonium symbolum	3.2
Polygonium "tener"	3.1
Polygonium "tenuispinosum"	3.2
Polygonium varium	3.9
Polygonium "verspertinum"	3.1
Polygonium vulgare	3.4
Polygonium windolphae	3.9