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MORPHOLOGIC VARIABILITY IN LOWER PALAEOZOIC ACRITARCHS: IMPORTANCE FOR ACRITARCH SYSTEMATICS

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Abstract. Intraspecific variability of Lower Palaeozoic acritarchs has a basic impact on systematic classification on both species and genus levels. The description of new taxa (including taxonomic splitting) dominated the initial period of acritarch classification. A second period, indicated by the revision of morphological variability, started in the mid nineties of the last century. Major methods and results of these studies are shortly summarized.

■ Lower Palaeozoic, acritarchs, systematics.

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Introduction

Evitt (1963) established the informal group Acritarcha incorporating all organic-walled microfossils (OWM) of unknown origin. The systematic classification of Acritarcha is uncertain by its definition (Evitt 1963) and thus forms a “collection basket” of naturally not assignable organisms, belonging both to the animal and plant phyla. However, it is generally accepted that a great proportion most probably represents various cysts of phytoplankton (Downie et al. 1963; Tappan 1980; Martin 1993; Molyneux et al. 1996; Servais et al. 1997; Strother 2008).

Despite their problematic origin combined with the comparatively short history of their studies and quite extensive laboratory processing, acritarchs have been well employed for biostratigraphic purposes (Brocke et al. 1995). More recently, acritarchs are of increasing value for palaeoecological application (e.g., Le Hérissé 1989). Similarly as in other *incertae sedis* groups, the classification of acritarchs is based on morphological features like shape and symmetry of the cyst, number, length and distribution of processes, type of opening, etc.

Two major approaches are currently in use for the classification of acritarchs: an artificial system of categorisation and a naturally directed one. The artificial classification introduced by Downie et al. (1963) is purely phenetic, as they grouped the taxa by simple comparison of their morphology. Strother (1996) pointed to the most specific feature of this generally used classification: the basic taxonomic unit is the genus and not the species. The artificial classification is also represented by different subgroups as proposed by Downie et al. (1963) and Deflandre and Deflandre (1964). Downie et al. (1963) established thirteen major morphological subgroups (Acanthomorphitae, Diacromorphitae, Dinethromorphitae, Disphaeromorphitae, Herkomorphitae, Nethromorphitae, Oomorphitae, Platymorphitae, Polygonomorphitae, Prismatomorphitae, Pteromorphitae, Sphaeromorphitae, Stephanomorphitae). Deflandre and Deflandre (1964) suggested to classify Acritarcha as ”Paraordo”, and consequently they designated Downie´s et al. (1963) ”subgroups” as ”Parafamiliae” and ”genera” as ”Paragenera”, respectively. Still before the definition of acritarchs as widely used today, there were several proposals how to classify OWM obtained from Precambrian to Mesozoic sediments (e.g., Naumova 1949, 1950, Timofeev 1964).

However, within the last fifty years this artificial classification was repeatedly criticized by several acritarch workers and alternatively some of them proposed more natural classification schemes. Mädler (1963, 1964) recommended a natural system indicated as “Algae incertae sedis” and established the class Hystrichophyta for those taxa which could be excluded from the acritarchs. In this sense, he proposed the orders Tasmanales, Leiosphaeridiales and Hystrichosphaeridiales including several families. Eisenack (1969) considered acritarchs (hystrichospheres) as a heterogenetic group but many of them he regarded as unicelullar algae and thus applied the botanical nomenclature. He followed Mädler´s classification scheme in parts by using the term Hystrichophyta. However, his concept for families differs from the one Mädler had established (1964). Cramer (1970) and Cramer and Díez (1979) did not adopt Downie´s scheme as well, they introduced three, more widely defined informal units instead (Sphaeomorphitae, Acanthomorphitae, and one undefined unit for the remaining taxa) and recommended a simple alphabetical listing of taxa. Tappan (1980) did not follow the non-Linnean classification but she simply listed the earlier established subgroups, and effectively transferred some acritarchs (e.g., *Tasmanites*, *Leiosphaeridia*, *Cymatiosphaera*) to the group of Green Algae (Prasinophyta, Chlorophyta and Euglenophyta).

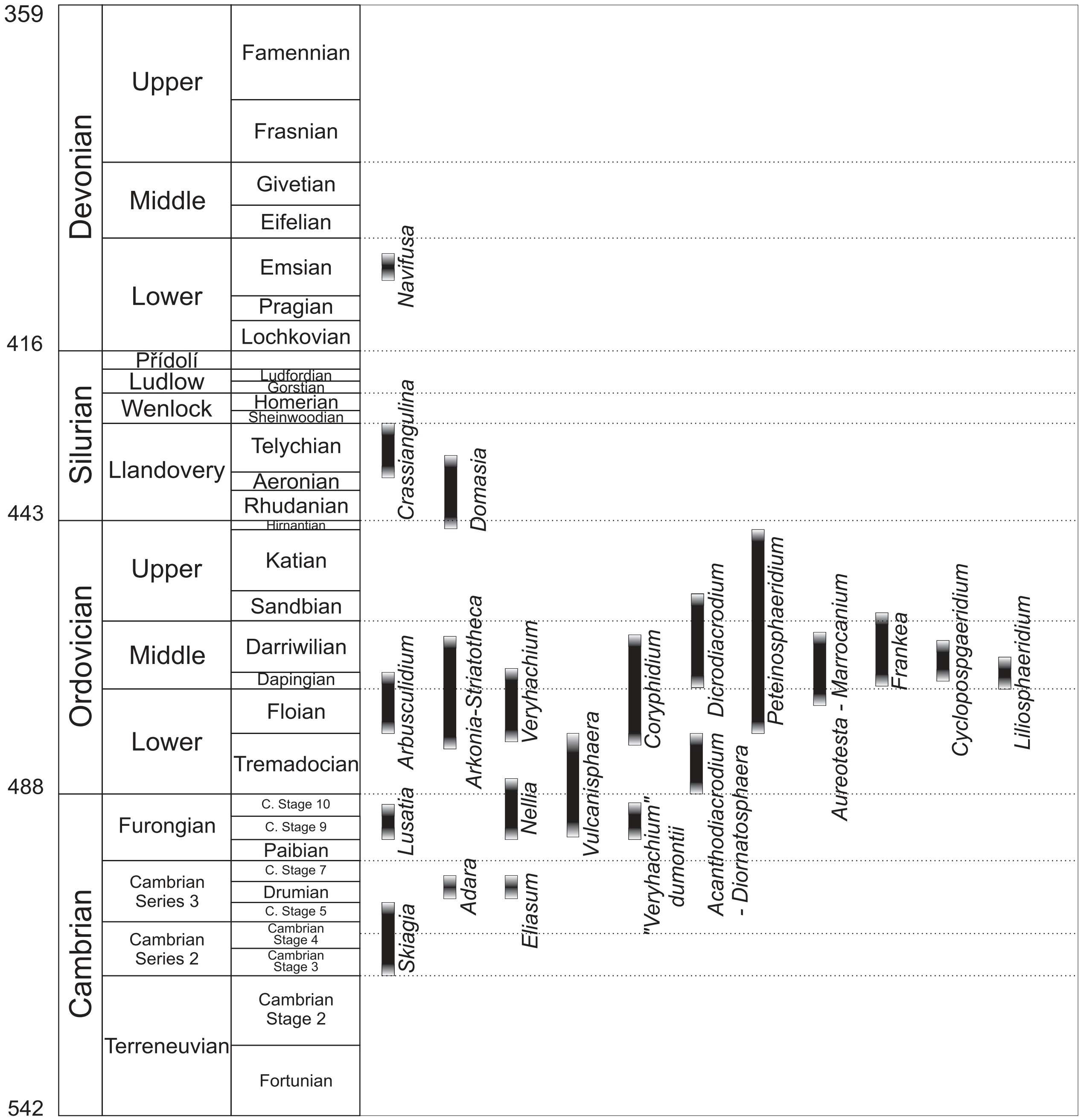
Today, the majority of acritarch workers follows Cramer´s (1970) pragmatic approach to classify acritarchs simply in alphabetical order but try to exclude those forms which show clear affinities to different groups of algae.

Methods of study

Research in OWM since the early 1930ies has given rise to two major methods of optical microscopy:

– study of isolated specimens from organic residues received after laboratory treatment (mechanical and chemical maceration)
– thin sections of preferable fine grained sediments like shale, siltstone and marl

This classical approach has been supplemented by the application of scanning electron microscopy (SEM) starting in the early 1960. More methods have followed, employed for special application, like TEM (Jux 1971, 1977), infrared microscopy (e.g., Brocke and Wilde 2001), confocal microscopy and Raman microscpopy (e.g., Kudryavtsev et al.



Text-fig. 1 Ranges of the revised taxa from Cambrian to Devonian; also indicated in table 1.

2001). The observation of objects scratched from the surface of metamorphosed rocks was introduced by Pacltová (1986), similarly as the scanning electron microscopy of fresh rock surface (Pacltová 1977). SEM of polished, slightly etched rock surface applied for sedimentological study of Silurian micritic limestones from the island of Gotland revealed three-dimensionally preserved OWM, including acritarchs and prasinophytes (Munnecke and Servais 1996).

Attempts to implement a biological approach in the classification of OWM have lead to the separation of prasinophyte phycomata from the so-called Hystrichospheres (Mädler 1963). However, not till the substantial summary of plant protists by Tappan (1980) the prasinophytes (e.g. the families Cymatiosphaeracea, Leiosphaeridacea, Pterospermatacea, Tasmanitacea, Pterosphaeridiacea and Pterospermellacea of green algae) have achieved sustained effect to exclude them from the artificial group Acritarcha.

Colbath and Grenfell (1995) recognized three, probably evolutionary clades based on wall architecture, namely

(1) the Cambrian–Permian *Baltisphaeridium* clade,
(2) the Middle-Upper Ordovician *Peteinosphaeridium* clade, and
(3) the Lower Silurian-Lower Devonian *Cymbosphaeridium* clade.

In this context, Colbath and Grenfell (1995) also emphasized the resemblance of dinocysts and members of the *Cymbosphaeridium* clade.

Until the end of 1980ies acritarch studies were mainly focused on their biostratigraphic application and thus numerous new taxa have been established. Unfortunately, the majority of these new genera and species are based on a quite restricted number of specimens studied without taking into account the obvious morphologic variability. The highest diversity of acritarchs has been reported from the Ordovician, altogether about 250 genera and more than 2.000 species are known (Servais 1998). In the recently compiled Phytopal 2007 database more than 1.000 acritarch genera were listed (Mullins et al. 2007). In 1989 Le Herissé was one of the first acritarch workers who carefully analysed a great number of well diversified assemblages. Exceptionally well-preserved material enabled detailed study and evaluation of numerous specimens of the same taxon. In this comprehensive monograph on Silurian OWM of Gotland, Le Herissé (1989) introduced the philosophy of population analyses, which verified a much higher level of morphological variability than expected previously.

Since that time more than twenty Cambrian to Devonian acritarch genera and/or species have been re-evaluated in this context (Text-fig. 1, Tab. 1). Goal of these revisions is to recognize and document morphologic variability. At least six different approaches of testing the morphologic variability have been employed:

1. simple biometric analyses; e.g., Vecoli et al. (1999), Wauthoz et al. (2003);
2. multivariante statistical analyses; e.g., Wauthoz and Gérard (1999), Stricanne et al. (2005)
3. statistical analyses of morphological parameters; e.g. Stricanne and Servais (2002);
4. analyses and comparison of populations originating from different palaeogeographical areas; e.g., Fatka and Brocke (1999);
5. general morphological trends in stratigraphical succession associated with transgression; e.g., Fatka and Brocke (2008)
6. orientation of specimens within a cluster; e.g., Vanguestaine in Streel et al. (1988).

Examples of simple biometrical analyses are shown in figures 2 and 3. Several measured morphological parameters are indicated for *Leiosphaeridia* (Text-fig. 2A), *Navifusa* (Text-fig. 2B) and *Eliasum* (Text-fig. 2C), and scatter diagrams of the central body length (CB_L) against central body width (CB_W) for specimens of *Leiosphaeridia* spp. (Text-fig. 2D) and *Navifusa bacilla* (Text-fig. 2E). Continuous variability in samples KL-45, Da-10 and DA-15 documents the presence of one single taxon, while several discrete clouds in sample KL-51 gives evidence for the presence of more taxa.

In the text-figure 3, two height histograms for a population of *Eliasum* show the number of specimens attributed to six classes which are based on the central body width (fig. 3A), and the number of thickenings on the central body (Text-fig. 3B).

The scatter diagram of measurements of central body length (CB_L) against central body width (CB_W) for specimens of *Eliasum* show a continuous morphological variability (Text-fig. 3C) and changing number of thickenings on the central body of *Eliasum* when plotted in stratigraphic order (Text-fig. 3D).

In addition to the acritarchs, a comparable morphological variability has also been documented from other OWM, e.g. from the genera *Chuaria* Walcott 1899 (see Steiner 1997), *Marpolia* Walcott 1919 and *Siphonophycus* Schopf 1968 emend. Knoll, Swett et Mark 1991 (see Steiner and Fatka 1996).

One of the most recent papers dealing with the morphologic variability of acritarch populations was published by Wauthoz et al. (2003). They effectively applied the philosophy of population analyses by using morphological features of acritarchs for a consequently variability-based systematic concept, and they established four different kinds (axes) of morphological variability (2003, p. 78-79):

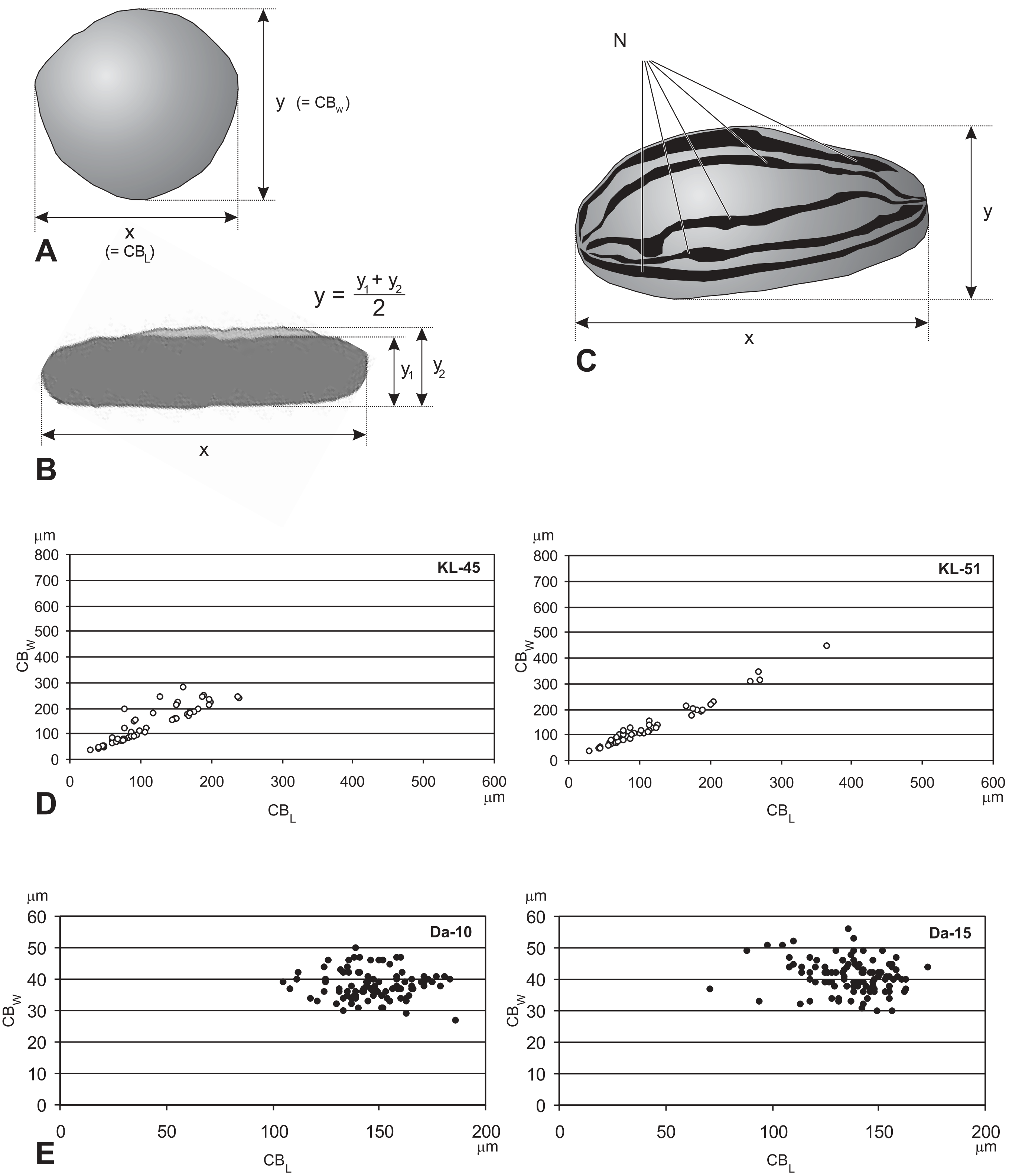
– variability allowed by genes (genotype),
– variability due to environmental stress (ecophenotype),
– variability of features through time as the taxon evolves (chronotype),
– variability due to taphonomic agents (taphotype).

Conclusion

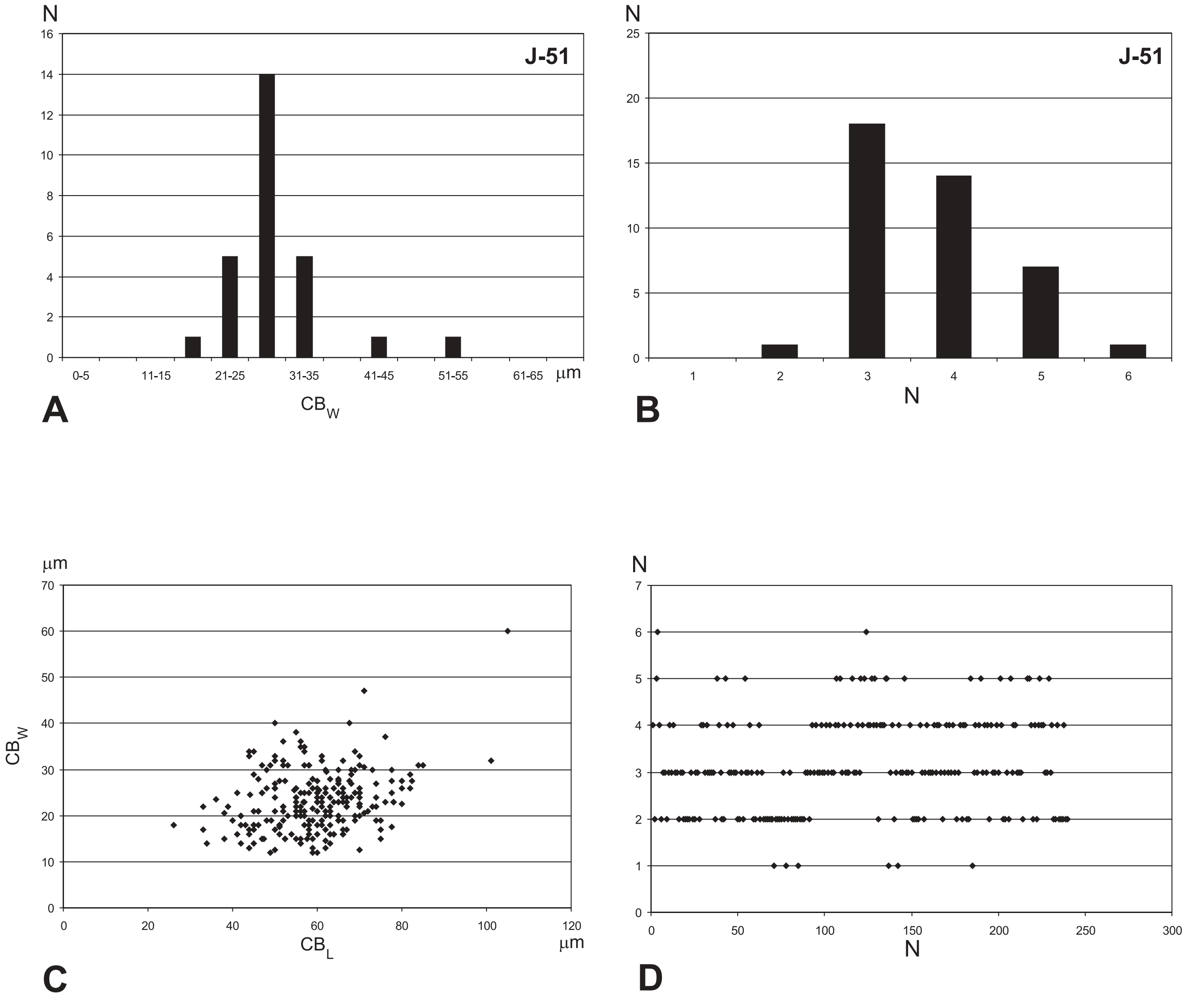
It is obvious that mere evaluation of earlier published data is not appropriate to rationalize the systematics of taxa (genera) revised. Moreover, a careful analysis of actually existing large populations is inevitable, e.g. specimens observed in a single palynological sample are a substantial part. Revisions based on extensive microscopic work combined with detailed bibliographic studies may provide us with relevant results for systematics, stratigraphy, and palaeogeography. Bibliographic revisions alone (e.g. Sarjeant and Stancliffe 1994, 1996, 2000; Servais et al. 2008a) can only comprehensively summarize earlier data, and the potential to improve and clarify systematics is considerably restricted or even highly questionable. Such an

Table 1: To date, following acritarch taxa have been re-evaluated:

	Genus/species	Stratigraphic distribution	Publication
1.	*Acanthodiacrodium* Timofeev 1958 emend. Deflandre and Deflandre-Rigaud 1962 restrict. Moczydlowska and Stockfors 2004	"Upper" Cambrian – Lower Ordovician	Paalits and Heuse (2000), Moczydlowska and Stockfors (2004)
2.	*Adara* Fombella 1977, emended Martin 1981	"Middle" Cambrian	Tonarová and Fatka (in prep.)
3.	*Arbusculidium* Deunff 1968	Lower – Middle Ordovician	Fatka and Brocke (1999)
4.	*Arkonia* Burmann 1970 plus *Striatotheca* Burmann 1970 emend. Sarjeant and Stancliffe 1994	Lower – Upper Ordovician	Servais (1997)
5.	*Aureotesta* Vavrdová 1972 plus *Marrocanium* Cramer et al. 1974	Lower – Middle Ordovician	Brocke et al. (1998)
6.	*Coryphidium* Vavrdová 1972 emend. Servais, Molyneux and Vecoli 2008	Lower – Upper Ordovician	Servais et al. (2008), Molyneux and Leader (1997)
7.	*Crassiangulina* Jardiné, Combaz, Magloire and Peniguel 1974	early Silurian	Wauthoz, Dorning and Le Hérissé (2003)
8.	*Cristallinium randomense* Martin in Martin and Dean 1981 emend. Martin in Martin and Dean 1988	"Upper" Cambrian	Vanguestaine (2002)
9.	*Cycloposphaeridium* Uutela and Tynni 1991 emend. Playford, Ribecai and Tongiorgi 1995	Lower – Middle Ordovician	Playford, Ribecai and Tongiorgi (1995)
10.	*Dicrodiacrodium* Burmann 1968	Lower – Middle Ordovician	Servais et al. (1996)
11.	*Diornatosphaera* Downie 1958	"Upper" Cambrian – Lower Ordovician	Paalits and Heuse (2000)
12.	*Domasia* Downie 1960 emend. Hill 1974	Silurian	Wauthoz and Gérard (1999)
13.	*Eliasum* Fombella 1977	"Middle" Cambrian	Tonarová and Fatka (in prep.)
14.	*Frankea* Burmann 1970 emend. Servais 1993	Middle Ordovician	Servais (1993), Fatka et al. (1997), Vecoli et al. (1999)
15.	*Liliosphaeridium* Uutela and Tynni 1991 emend. Playford, Ribecai and Tongiorgi 1995	Lower – Middle Ordovician	Playford, Ribecai and Tongiorgi 1995
16.	*Lusatia* Burmann 1970 emend. Sarjeant and Vavrdová 1997	Late Cambrian (Furongian)	Albani et al (2007)
17.	*Marrocanium* Cramer et al. 1974	Lower – Middle Ordovician	Brocke et al. (1998)
18.	*Navifusa* Combaz, Lange and Pansart 1967 *ex* Eisenack et al. 1976	Lower Devonian	Fatka and Brocke (2008)
19.	*Nellia* Golub and Volkova in Volkova and Golub 1985	Lower Ordovician	Stricanne et al. (2005)
20.	*Peteinosphaeridium* Staplin, Jansonius and Pocock 1965 emend. Eisenack 1969	Lower – Upper Ordovician	Playford, Ribecai and Tongiorgi (1995)
21.	*Skiagia* Downie 1982 emend. Moczydlowska 1991	"Lower-Middle" Cambrian	Moczydlowska and Zang (2006)
22.	*Veryhachium* Deunff 1954 emend. Downie and Sarjeant 1963 emend. Turner 1984 emend. Sarjeant and Stancliffe 1994	Lower Ordovician	Servais et al. 2008
23.	*"Veryhachium" dumontii* Vanguestaine 1973	"Upper" Cambrian	Rayevskaya and Servais (2004)
24.	*Vulcanisphaera* Deunff 1961 emend. Rasul 1976	"Middle" Cambrian – Lower Ordovician	Blanchon et al. (2004)



Text-fig. 2:
A - parameters measured in *Leiosphaeridia* spp.; B - parameters measured in *Navifusa bacilla* (Deunff 1955) Playford 1977; C - parameters measured in *Eliasum llaniscum* Fombella 1977; D - CB_L/CB_W in *Leiosphaeridia* spp. in samples KL-45 and KL-51 at the Silurian/Devonian GSSP, adapted from Brocke et al. (2006); E - CB_L/CB_W in *Navifusa bacilla* in samples Da-10 and Da-15 from the Lower Devonian Daleje Shale, adapted from Fatka and Brocke (2008).



Text-fig. 3:
A – number of specimens and their CB_W measured in *Eliasum llaniscum* from the sample J-51 (Jince Formation); B – number of thickenings in *Eliasum llaniscum* from the sample J-51 (Jince Formation); C - CB_L/CB_W in *Eliasum llaniscum* from the Jince Formation; D – number of thickenings in *Eliasum llaniscum* from the Jince Formation. All from Tonarová and Fatka (in prep.)

approach may lead to an incomplete or actually misinterpreted picture, which implies the risk of disqualifying acritarchs as an excellent tool for reconstructing biostratigraphical, palaeogeographical, and palaeoecological models.

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Explanation

PLATE 1

1. *Navifusa bacilla* (Deunff, 1955) Playford, 1977, Lower Devonian.
2. *Veryhachium lairdi* group, Middle Ordovician.
3. *Veryhachium trispinosum* group, Middle Ordovician.

4, 5. *Aureotesta clathrata clathrata* (Vavrdová, 1972) emend. Brocke, Servais et Fatka, 1997, Middle Ordovician.

6. *Deunffia* sp., Silurian.
7. *Striatotheca* sp., Lower-Middle Ordovician.
8. *Barakella* sp., Lower Ordovician.
9. *Leiosphaeridia* sp. Silurian.

10, 11. *Coryphidium-Tetraniveum* group, Middle Ordovician.

12. *Liliosphaeridium intermedium* (Eisenack, 1976) Playford, Ribecai et Tongiorgi, 1995, Upper Ordovician.
13. *Frankea sartbernardensis* (Martin, 1966) Colbath 1986, Middle Ordovician.
14. *Caldariola* sp., Lower Ordovician.
15. *Peteinosphaeridium* sp., Middle Ordovician.
16. *Eliasum llaniscum* Fombella, Cambrian, Drumian.
17. *Adara alea* Martin 1981, Cambrian, Drumian.

PLATE 1