Late Cambrian acritarch *Lusatia*: Taxonomy, palaeogeography, and biostratigraphic implications

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Intraspecific variability of the herein emended diacrodian acritarch *Lusatia dendroidea* is described based on late Cambrian (Furongian) well preserved material from Spain, the High Arctic of Russia, and the East-European Platform. *L. dendroidea*, displays bipolar asymmetric morphology and, as originally defined, consists of three long major processes originating from the "corners" of its vesicle. Specimens with one, two and four major processes are considered to represent morphological variations of the most common three process form. Based on its narrow stratigraphic range, wide-spread palaeogeographic distribution, and distinctive morphology, *L. dendroidea* is an excellent guide fossil for the Furongian.

Key words: Acritarcha, taxonomy, biostratigraphy, Cambrian, Furongian.

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Introduction

The marine phytoplankton experienced a remarkable increase in taxonomic diversity and abundance during the late Cambrian (Furongian). At that time marine organic-walled microorganisms underwent a relatively rapid development of morphological innovations within a wide range of cell morphostructural patterns. These novelties were further elaborated during the diversification in phytoplankton that occurred during the Ordovician, producing new directions of evolutionary trends (e.g., an "archaeopyle" excystment opening in galeate taxa, first appearing in the middle Furongian, and a bipolar arrangement of diacrodian acritarchs that started to develop at approximately the same time). A large number of new morphotypes at the species and genus level occurred soon afterwards in the latest Cambrian (e.g., Vecoli and Le Hérissé 2004).

Because of their rapid changes in taxonomic content, as well as their wide geographic distribution during the Furongian, acritarchs have a high biostratigraphic potential. However, high morphological intraspecific variability, intermediate features among morphologically close taxa, and different states of preservation generate taxonomic problems that can limit the usefulness of acritarchs in biostratigraphic and palaeogeographic studies. Large numbers of acritarch species are described from the upper Cambrian, but only some of them are taxonomically and biostratigraphically well constrained (Servais and Eiserhardt 1995; Paalits and Heuse 2000; Stricanne and Servais 2002; Vanguestaine 2002; Raevskaya and Servais 2004; Blanchon et al. 2004; Stricanne et al. 2005). Therefore, accurate taxonomical investigation including revision of large published data together with biometrical study and analysis of variability on rich material is both important and topical.

This paper investigates *Lusatia* Burmann, 1970, a form showing bipolar symmetry and the morphology of a diacrodian acritarch. Diacrodian acritarchs (formerly the subgroup "Diacromorphitae" e.g., Downie et al. 1963) are one of the most diverse, variable, and abundant morphotypes with processes at the two opposite poles of the vesicle; they are typical of the late Cambrian–Early Ordovician phytoplankton assemblages.

Lusatia dendroidea, the type species of the genus, was originally described by Burmann (1970) from the ?Ordovician of Germany. Nevertheless, except for the first record, and a report of a single incomplete specimen of *L*. aff. *L. dendroidea* in the Tremadocian of eastern Newfoundland (Dean and Martin 1978), this species has never been reported from unequivocal Ordovician strata. It has been documented from several upper Cambrian successions from various areas where it is a biostratigraphic marker of regional importance (Volkova 1990; Volkova and Kirjanov 1995; Bogolepova et al. 2001). However, identification of this species in palynological assemblages has not always been correct.

The type specimens of *L. dendroidea* are from metamorphosed (and possibly reworked) rocks from the Lausitz area



B



Fig. 1. **A**. Map of the Asturian coast showing position of El Fabar fossil locality (star). **B**. A summary lithological column with stratigraphic position of the acritarch yielding sample (Tun-Filocar, asterisk).

in Saxo-Thuringia, Germany. Because metamorphism resulted in breaking and fragmenting the specimens, normal palynologic techniques could not be employed. Thus, specimens were studied in thin sections and both the holotype and paratypes were illustrated by line drawings (Burmann 1970: 296, pl. 6: 1–4). *Lusatia dendroidea* has a pronounced bipolar morphology with notable difference between the apical and antapical poles. Intricate ramification of the very long processes had resulted in specimens that are often not satisfactorily preserved. Commonly, only the vesicles with the basal portions of processes are found in acritarch assemblages, thus hampering their recognition.

An abundant and exceptionally well preserved assemblage of *L. dendroidea* has been recovered from northwestern Spain. This region was in the Furongian a part of the Iberia plate situated close to Saxo-Thuringia in a chain of discrete terrains along the northern margin of Perigondwana (Linnemann 2003). A new collection of coeval acritarchs from Severnaya Zemlya, Arctic Russia, and independently dated by its macrofauna, consists of numerous well-preserved *Lusatia*. In addition, a palynological collection from the Moscow syneclise from which several species of *Lusatia* were described by Volkova (1990), were made available for examination, thus providing an opportunity to analyse in detail and describe intraspecific variability of *L. dendroidea* from three widely separated geographic areas.

Institutional abbreviations.—GIN RAN, Geological Institute, Russian Academy of Science, Moscow, Russia; IGGD RAN, Institute of Precambrian Geology and Geochronology RAN, Saint-Petersburg, Russia; MGM, Museo Geominero of Madrid (accession number MGM-1080K–MGM-1097K).

Material

Recent construction of a highway along the Asturian coast, in northwestern Spain, has resulted in fresh exposures of the usually scattered and discontinuous Cambrian-Ordovician sequence in that region. The lithologically monotonous and more than 800 m thick Barrios Formation was exposed during excavation of the El Fabar tunnel (Fig. 1). The lower part of this formation (the La Matosa Member), consisting of quartz sandstone with about 50 m of shale in the middle, is considered middle-upper Cambrian (Gutiérrez-Marco et al. 2003). Only one sample (Tun Filocar) from the dark shale interval (El Fabar beds) produced an abundant and well preserved acritarch assemblage. The taxonomic composition and biostratigraphic position of the palynological assemblage have been discussed in detail elsewhere (Albani et al. 2006). Only the large population of Lusatia from this assemblage is analyzed in the present study.

Samples were also taken in the upper Cambrian Kurchavinskaya Formation exposed in the central part of the October Revolution Island (the central island of the Severnaya Zemlya Archipelago) in the high Arctic of Russia (Fig. 2). The Kurchavinskaya Formation consists of 800 m of rhythmically alternating siltstones, sandstones, and claystones with limestone concretions. Detailed description of the lithology, stratigraphy, and recovered acritarch assemblages from this area is given in Bogolepova et al. (2001) and Raevskaya and Golubkova (2006). Sample 99-37 from the top of the Kurchavinskaya Formation (just below a Lower Ordovician unconformity) produced an assemblage whose



Fig. 2. A. Map of the October Revolution Island, Severnaya Zemlya Archipelago showing position of the fossil locality (star). B. A summary lithological column (B) with stratigraphic position of the horizon yielding the studied acritarchs (asterisk).

taxonomic content is remarkably similar to the assemblage from the Spanish El Fabar tunnel, including less numerous, but also well-preserved representatives of *Lusatia*.

In addition, we have reexamined the Volkova's palynological collections from the Moscow syneclise of the East-European Platform, from whence *Lusatia dendroidea* and other forms of *Lusatia* have been recorded (Volkova 1990). Two samples from two boreholes (Danilovskaya-11, interval 2125.7–2132.0 m, and Rybinskaya-1, interval 1848.0–1856.0 m, Yaroslavl region) provided abundant material that is moderately preserved (Fig. 3). The acritarch taxonomy and biostratigraphy of the above intervals are discussed by Volkova (1990) and Volkova and Kirjanov (1995).

The examined material for this study thus includes specimens of *Lusatia* from three different regions: Spain, the High Arctic of Russia, and the East-European Platform.

Methods

All samples were processed according to standard palynological procedures using hydrochloric and hydrofluoric acids to remove carbonates and silicates respectively. Neither oxidation nor alkali treatment were applied. Organic residues from the Moscow syneclise samples were mounted in glycerin-jelly; other samples were mounted permanently in polyester resin. All slides were examined by light-transmitted microscopy and only the specimens from Spain were also studied by scanning electron microscopy.

More than 1000 specimens of *Lusatia* were examined for this study. In addition all complete specimens were studied biometrically.

Systematic paleontology

Incertae sedis

Group Acritarcha Evitt, 1963

Genus Lusatia Burmann, 1970

Type species: Lusatia dendroidea Burmann, 1970, Lausitz area of eastern Germany, ?Tremadocian.

Lusatia dendroidea Burmann, 1970 emend.

Figs. 4, 5.

1970 Lusatia dendroidea sp. nov.; Burmann 1970: 296, pl. 6: 1-4.

- 1976 Multiplicisphaeridium dendroideum (Burmann, 1970); Eisenack et al. 1976: 455–456.
- ?1978 Lusatia aff. L. dendroidea Burmann; Dean and Martin 1978: 8, pl. 3: 21.
- 1990 Lusatia dendroidea Burmann; Volkova 1990: 71, pl. 21: 1, 2.
- 1990 Lusatia triangularis (N. Umnova, 1975) comb. nov.; Volkova 1990: 71–72, pl. 21: 5–7.
- 1990 Lusatia sp. 1; Volkova 1990: 72-73, pl. 21: 3, 4.
- 1993 Lusatia? sp. 1; Ribecai and Vanguestaine 1993: pl. 1: 11.
- 2000 Orthosphaeridium? extensum sp. nov.; Parsons and Anderson 2000: 61–62 (partim), pl. 9: 1, 3, 4, 10, 13 (non 2, 11, 12).
- 2000 Orthosphaeridium? triangulare Umnova, 1975, comb. nov.; Parsons and Anderson 2000: 62, pl. 9: 5.
- 2001 *Lusatia dramatica* Ribecai and Tongiorgi; Bogolepova et al. 2001: 83: 6: E, F.
- 2005 Lusatia dendroidea Burmann; Ribecai et al. 2005: pl. 1: 5.

2006 *Lusatia dendroidea* Burmann; Albani et al. 2006: 49–50, pl. 2: 1–4, 7.

- 2006 *Lusatia dendroidea* Burmann; Raevskaya and Golubkova 2006: pl. 4: 12, pl. 5: figs. 1, 4–6.
- 2006 Lusatia triangularis (N. Umnova, 1975); Raevskaya and Golubkova 2006: pl. 4: 7.
- 2006 Lusatia sp.; Raevskaya and Golubkova 2006: pl. 4: 8, 9.

Emended diagnosis.—Vesicle sub-circular to triangular in outline, bearing one to four long processes. Processes simple to branched, freely communicating with the vesicle interiors, thin-walled, psilate. In specimens with more than one process, one process is always simple. Additional thinner and shorter processes or filaments can be present. The process branching originates at a variable distance from vesicle and







Fig. 3. A. Map of the Baltic region with studied localities (stars) in the Jaroslaw region, Russia. **B**. Lithological column and stratigraphic position of the horizons yielding the studied acritarchs in Rybinskaya-1 and Danilovskaya-11 boreholes (asterisks).

can attain up to the fourth order. Vesicle thin-walled to thick-walled, smooth to scabrate. Excystment by median split.

Description.—Vesicle outline subcircular, ellipsoidal, or triangular with straight to convex sides. Vesicle wall varies from thin to thick. One to four major processes. Processes hollow, long, thin-walled, well differentiated from the central body, with a subangular to angular basal contact, communicating with vesicle interior.

Processes are simple to branched. One process is always simple in specimens with more than one process. Simple processes conical, tapering gradually to acuminate distal tip which is very flexible, resulting in a distal looping in some specimens (Figs. 4F, 5D₁). Branched processes nearly cylindrical to point of branching, i.e., maintaining near constant width to point of branching. Furcation originates at a variable distance from proximal end of process. Subdivisions in pinnae is highly variable, and up to fourth order. Distal branches of pinnae or pinnulae can be straight or curly (e.g., Figs. 4A, 5D), and in some specimens the high number of subdivisions produces a distal crown. One or two minor, thinner, shorter and simple processes may also be present (e.g., Figs. 4E, 5A, E). Small filaments can be present along the process-stem (e.g., Fig. 5H).

Specimens with three processes have processes originating at the corner of the triangular to subcircular vesicle (Fig. $4A_1$, D), with the apical process simple. Specimens with two processes have a mostly ellipsoidal vesicle with the processes, one of which is simple, at the opposite poles. Some specimens have only one branched process and an ovoid vesicle. Rare specimens have four processes, with the apical process simple and the other three branched.

Most specimens have three processes; specimens with two processes are common, whereas only a few have one process; specimens with four processes are very rare.

The free communication of processes with the vesicle interior is evident in translucent and thin-walled specimens. Specimens with a dark, thick-walled vesicle and thin-walled processes may simulate a separation between vesicle and processes and give the impression of a bi-layered vesicle.

Fig. 4. Diacrodian acritarch Lusatia dendroidea Burmann, 1970 emended -> herein. Upper Cambrian, El Fabar tunnel, Cantabrian Zone, Spain. All specimens from sample Tun-Filocar. For each illustrated specimen slide number, repository number, and England Finder Graticule are given. All specimens with three processes. A. Stub LU2, MGM-1080K, R42; specimen with subtriangular vesicle (A1), detail of branching of antapical process, with curly terminations (A2). B. Slide >10/1, MGM-1081K, N36/3, specimen with thick-walled vesicle and excystement by median split. C. Slide II/1, MGM-1082K, P29, specimen showing base of processes slightly constricted simulating a sort of plug. D. Slide >10/1, MGM-1083K, U44/4, specimen with darker central area extending as a spine into the base of the processes. E. Stub 6, MGM-1084K, O45, specimen with an auxiliary filament. F. Slide >10/1, MGM-1085K, M28, specimen with a thick-walled vesicle and distal loop of apical process. G. Slide >10/1, MGM-1086K, E44. H. Slide >10/3, MGM-1087K, P30/4, specimen with a thick-walled vesicle and excystement by median split.



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The darker central area may extend shortly into the base of the processes as a spine, or a rod, or simulating a sort of plug with a slight constriction at the base (e.g., Fig. 4C, D). The vesicle wall and the processes are psilate to scabrate. Excystment by median split (e.g., Fig. 4B).

Measurements (118 specimens).—Russian material (Moscow syneclise): vesicle length 28 (36.5) 44 μ m, vesicle width 24 (27.8) 40 μ m, apical process length 48 (44) 80 μ m, antapical processes length 48 (60) 76 μ m, length of branches 8 (26) 40 μ m.

Russian material (Severnaya Zemlya): vesicle length 20 (27.5) 36 μ m, vesicle width 16 (21.7) 26 μ m, apical process length 48 (56) 76 μ m, antapical processes length 36 (54.5) 76 μ m, length of branches 16 (27.3) 44 μ m.

Spanish material (El Fabar tunnel): vesicle length 23.5 (33.2) 40.2 μ m; vesicle width 18.4 (26) 34.5 μ m, apical process length 43.7 (69.9) 90.8 μ m; antapical process length 42.5 (62.7) 88.5 μ m; length of branches 12.6 (31.1) 49.5 μ m.

Discussion.—Burmann (1970), in erecting *Lusatia* and the type species *Lusatia dendroidea*, included only specimens with three processes. Specimens with one to four processes were mentioned in the original diagnosis of the genus, but were not illustrated, nor included in the variability of the type species. The abundant and well-preserved material from the three different geographical areas allows for more precise evaluation of intraspecific variability of *L. dendroidea*. Analysis based on more than 1000 specimens indicates intraspecific variation of one to four processes for this species.

Volkova (1990) recorded Lusatia from the Moscow syneclise of the East European Platform and described three species: L. dendroidea Burmann, 1970, L. triangularis (Umnova, 1975) Volkova, 1990, and Lusatia sp. 1. According to Volkova (1990), L. triangularis differs from L. dendroidea by having processes not communicating with the vesicle interior. She also indicated that L. triangularis could have a double wall, with the processes formed by the outer layer. Incomplete specimens with two processes and a vesicle interpreted as bi-layered were assigned by Volkova (1990) to Lusatia sp. 1. Based on examination of the specimens from Spain and from the High Arctic of Russia, and reexamination of the Volkova's collection, the vesicle of Lusatia is considered unilayered, even though with variable thickness (see description). In the material examined in this study, specimens with a thin wall co-occur with specimens with a thicker wall, independent of the number of processes. They are therefore

viewed as falling within the range of variation of a single species, *L. dendroidea*. The different wall thickness could be an artefact of differing preservation or due to different stages in the life cycle of the species.

In her description of *L. dendroidea*, Volkova (1990) indicated that the termination of the apical process formed a loop. In our material, with hundreds of complete specimens, the terminal loop of the apical process is not a constant feature and therefore is not considered diagnostic.

Parsons and Anderson (2000) transferred *Lusatia* sp. 1 of Volkova (1990) and *L. triangularis* of Volkova (1990) to *Orthosphaeridium*? due to the presence of an inner body and a median splitting. Our material and a reexamination of Volkova (1990) original collections indicate that these features fall within the variability of *L. dendroidea*.

We included in our synonymy specimens figured by Parsons and Anderson (2000) that conform well with *L. dendroidea*, as emended here. We excluded specimens they figured with broader-based processes that merge more gradually with the vesicle (Parsons and Anderson 2000: pl. 9: 2, 11, 12).

Lusatia dramatica Ribecai and Tongiorgi, 1997 from the upper Cambrian of Sweden differs from *L. dendroidea* because it has always three processes, all of them ramified, although the apical process displays fewer and less regular branches. This taxon could represent an extreme differentiation, derived from forms of *L. dendroidea* with three processes.

The younger species *Lusatia heteromorpha* Vavrdová, 1986 from the lower Llanvirnian (Darriwilian) of Bohemia differs from *L. dendroidea* in the ornamentation of the vesicle (microgranulate to granulate), in the pattern of branching (processes have shorter, less numerous and more irregular branches) and in the capitate terminations of pinnae.

Biostratigraphic distribution

Lusatia dendroidea was originally described by Burmann (1970) from the Lausitz area of eastern Germany and tentatively assigned to the Tremadocian, although neither geological nor stratigraphical data were provided. The geological context of this region, however, accords with reworking of the considered interval. Current knowledge on the geology and geodynamic evolution of Saxo-Thuringia is summarized in Linnemann (2003). Because of the Early Paleozoic rifting,

Fig. 5. Diacrodian acritarch *Lusatia dendroidea* Burmann, 1970 emended herein. Upper Cambrian, El Fabar tunnel, Cantabrian Zone, Spain. All specimens from sample Tun-Filocar. For each illustrated specimen slide number, repository number, and England Finder Graticule are given. **A**. Slide II/2, MGM-1088K, E30/1, specimen with two processes and an auxiliary filament. **B**. Stub 6, MGM-1089K, N42/3, specimen showing one simple process and one branched process with distal crown. **C**. Slide >10/1, MGM-1090K, T38/3, specimen with two processes. **D**. Stub 5, MGM-1091K, P31/3; specimen with two processes showing a distal looping of the simple process (D_1); detail of branching of the antapical process, with straight terminations (D_2). **E**. Slide SN, MGM-1092K, M30, specimen with two processes and thin-walled vesicle showing communication between process and vesicle interior. An auxiliary thin process is present. **F**. Slide SN, MGM-1094K, L47/1, specimen with one process and ovoid outline of the thick-walled vesicle. **G**. Stub 4, MGM-1093K, K43/1, specimen with one process. **I**. Stub 5, MGM-1094K, Stude vesicle ornamentation. **H**. Slide >50/2, MGM-1095, U33/3, specimen with four processes and small filaments along the stem of the apical process. **I**. Stub 5, MGM-1096, M33/2, specimen with four processes and psilate vesicle. **J**. Slide >50/2, MGM-1097, P49/1, specimen with thick-walled vesicle, one simple apical process, and three branched antapical processes.

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Fig. 6. Late Cambrian palaeogeographic map (based on Scotese 2002). Numbers on the map refer to the known locations where *Lusatia dendroidea* has been recorded. 1, Jaroslav region, Russia (Volkova 1990); 2, Eastern Newfoundland, Canada (Parsons and Anderson 2000); 3, October Revolution Island, Severnaya Zemlya Archipelago (Raevskaya and Golubkova 2006); 4, Cantabrian zone, Spain (Albani et al. 2006); 5, Rocroi Massif, France (Ribecai and Vanguestaine 1993); 6, Sardinia, Italy (Ribecai et al. 2005); 7, Saxo-Thuringia, Germany (Burmann 1970); 8, Oman (Molyneux et al. 2004).

erosion, chemical processes and denudation, the Cambrian is usually not preserved in much of Saxo-Thuringia. In the Lausitz anticlinorium, the Ordovician quartzite overlies the volcanic Cadomien Neoproterozoic basement. The Tremadocian Dubrau Formation starts with a thick succession of conglomerates (Linnemann 2003). It is reasonable to assume that *Lusatia dendroidea* occurs in the Tremadocian sequence in clasts reworked from older beds.

Lusatia aff. *L. dendroidea*, which we include questionably in our synonymy of *L. dendroidea*, is based on a single incomplete specimen from the lower part of the Bell Island Group, northern Newfoundland (Dean and Martin 1978). A Tremadocian age for this interval is based on acritarchs (Dean and Martin 1978: 10–11, 17), although, the associated assemblage seems to be transitional from the late Cambrian, with none of the listed taxa having its earliest occurrence within the Ordovician. Reference of that acritarch assemblage to the Tremadocian was based on the presence of *Arbusculidium destom*- *besii* Deunff, 1968 (Martin in Dean and Martin 1978) which was considered to be restricted to beds with *Dictyonema* (= *Rhabdinopora*) at Shineton. It was emphasized, nevertheless, that the lowest part of the Bell Island Group "could be of early Tremadocian age if the restriction of *A. destombesii* to the *Dictyonema flabelliforme* Zone was confirmed" (Dean and Martin 1978: 11). However, *A. destombesii* was subsequently reported from the late Cambrian (upper *Peltura–Acerocare* trilobite zones) of the East-European Platform (Volkova 1990) and from the *Acerocare* Zone of eastern Newfoundland (Parsons and Anderson 2000). Thus, the Tremadocian range for *L. dendroidea* is doubtful at best.

Precise biostratigraphic assignment of *L. dendroidea* is provided by recent discoveries of trilobites in the upper part of the Kurchavinskaya Formation in the Russian High Arctic where *Lusatia dendroidea* (incorrectly identified as *L. dramatica*) occurs in the Furongian *Protopeltura praecursor* trilobite Zone (Bogolepova et al. 2001; Rushton et al. 2002).

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L. dendroidea occurs in an interval of the Barrios Formation in the El Fabar tunnel, northern Spain, where trilobite remains are present but, unfortunately, without tightly biostratigraphically restricted taxa. Biostratigraphic correlation, based on a rich acritarch assemblage (Albani et al. 2006) indicates the lower part of microflora RA5 of Parsons and Anderson (2000). According to them, the lower part of microflora RA5 corresponds to the *Protopeltura praecursor* trilobite Zone. The age-assignment proposed by Albani et al. (2006) thus agrees well with palaeontological data from the upper part of the Kurchavinskaya Formation of the High Arctic of Russia.

Acritarch assemblages including specimens here assigned to *L. dendroidea* from the Moscow syneclise were referred by Volkova (1990) to the upper part of assemblage VK3 and assemblage VK4, corresponding to the *Leptoplastus* and *Peltura* trilobite zones of the Furongian (Volkova 1990; Volkova and Kirjanov 1995). According to the cited authors, no species of *Lusatia* range into the younger interval of the *Acerocare* trilobite Zone (Volkova 1990), and none of them have been found in the Tremadocian (Volkova 1995).

Thus, the biostratigraphic range of *L. dendroidea*, as now emended, is restricted to the *Leptoplastus* and *Peltura* trilobite zones based on their co-occurrence with trilobites from these zones.

Paleogeographic distribution

Until recently there were few records of L. dendroidea. New material and taxonomical reevaluation of published data has allowed reconsideration of its paleobiogeographic distribution during the Furongian. It is now known to have been widely distributed in the Southern Hemisphere in cold to temperate phytoplankton assemblages (Fig. 6). It is known from the Severnaya Zemlya Archipelago on the Kara Plate, situated in the Early Paleozoic between Siberia and Baltica (Bogolepova et al. 2001), and it also occurs in Baltica (Volkova 1990) and northern Gondwana. It has been reported from several localities on the northern margin of Gondwana, namely Saxo-Thuringia, Germany (Burmann 1970), eastern Newfoundland, Canada (Parsons and Anderson 2000), and the Cantabrian Zone, Spain (Albani et al. 2006). Specimens of L. dendroidea with two processes occur in an acritarch assemblage corresponding to the lower part of the Peltura trilobite Zone (Ribecai and Vanguestaine 1993) from the Rocroi Massif, France. Poorly preserved specimens of L. dendroidea with two processes occur also in Sardinia, Italy, in a section dated as late Cambrian by Ribecai et al. (2005).

Lusatia dendroidea also occurs in the late Cambrian of Oman (Molyneux et al. 2004; Stewart G. Molyneux, personal communication 2005), thus extending its known paleogeographic distribution into warmer latitudes. This widespread distribution across temperature gradients confirms the cosmopolitan character of the Furongian acritarch assemblages (Volkova 1997; Moczydłowska 1998).

Conclusions

Samples from three widespread geographic areas has provided sufficient data for an in-depth study of the morphology and intraspecific variability of *Lusatia dendroidea*, leading to the emended diagnosis herein. Species described in the literature as *L. triangularis*, *Orthosphaeridium? extensum*, and *Lusatia* sp. 1 are considered to fall within the variability of *L. dendroidea* and thus are considered junior synonyms. The bipolar asymmetrical morphology of *Lusatia* allows assignment to the diacrodian acritarchs.

The biostratigraphic distribution of *L. dendroidea* is now more precisely defined as restricted to the *Leptoplastus* and the *Peltura* trilobite zones of the Furongian. The previous questionable upper range of this taxon into the Lower Ordovician is doubtful because the original material from which it was recovered in the ?Tremadocian of Germany is now assumed to be reworked from eroded upper Cambrian strata.

The paleogeographic distribution of *L. dendroidea* includes the northern margin of Gondwana in the Southern Hemisphere, Baltica, and the Kara Plate, all of which fall within cold to temperate latitudes, reaching warmer latitudes in Oman.

Based on its restricted stratigraphic range, distinctive morphology and wide geographic distribution, *L. dendroidea* is an excellent guide fossil for the Furongian.

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