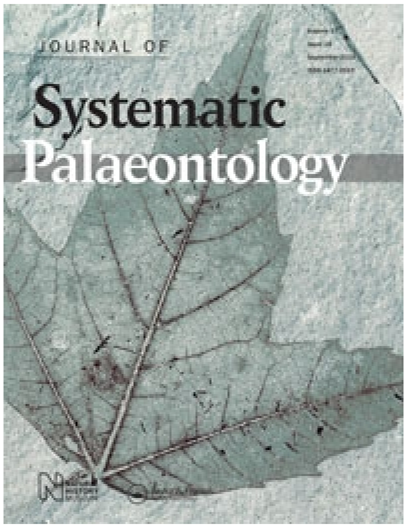

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A new diverse charophyte flora and biozonation of the Eocene bauxite cover-sequence at Gánt (Vértes Hills, Hungary)

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A diverse Eocene charophyte flora from a section at Gánt (Vértes Hills), Transdanubian Central Range, north-western Hungary, provides significant new information to previous studies only based on subsurface data published from the mid-20th century. This newly acquired material facilitates the taxonomic revision and emendation of the species *Raskyella peckii* and thereby defines a new anagenetic lineage based on three successive varieties which were formerly considered as separate species or subspecies: *Raskyella peckii* var. *peckii* (early Lutetian–early Bartonian), *Raskyella peckii* var. *caliciformis* (early Bartonian), and *Raskyella peckii* var. *vadaszii* (late Bartonian). Based on this lineage, we propose a new local charophyte biozonation that consists of a 'Raskyella peckii Superzone' (Lutetian–Bartonian), subdivided into three successive charophyte partial range zones: The 'Raskyella peckii peckii Zone' (Lutetian–lowermost Bartonian) characterized by an assemblage of *R. peckii peckii*, *Gyrogona caelata* forma *caelata*, *G. caelata* forma *monolifera* and *Nitellopsis* (*Tectochara*) aff. *palaeohungarica*, the 'Raskyella peckii caliciformis Zone' (lower Bartonian) characterized by the assemblage of *R. peckii* var. *caliciformis*, *G. caelata* forma *caelata*, *G. caelata* forma *monolifera*, *G. caelata* forma *baccata*, *Nitellopsis* (*Tectochara*) aff. *palaeohungarica* and *Chara media*, and the 'Raskyella peckii vadaszii Zone' (upper Bartonian) characterized by *R. peckii* var. *vadaszii*, *G. caelata* forma *bicincta*, *G. caelata* forma *baccata*, *G. caelata* forma *fasciata*, *G. tuberosa*, *Psilochara polita*, *Psilochara* sp., *Chara media* and *Chara subcylindrica*. Future research may show the new local biozonation as applicable to the whole of Europe and complementary to the current European charophyte biozonation. Our results show that the sequences from Gánt, which were previously regarded as upper mid-Eocene (upper Lutetian–lower Bartonian) in age, appear to represent a longer chronostratigraphic interval: lower Lutetian to upper Bartonian. Our chronostratigraphic results imply a longer and more stepwise Eocene major transgression in the Transdanubian Central Range than previously thought.

Keywords: Characeae, Raskyellaceae, phylozone, gradualistic evolution, Paleogene, Central Europe.

Introduction

Charophytes represent one of the most useful tools in the biostratigraphic analysis of Cenozoic non-marine deposits worldwide. During the Eocene, charophytes have been the object of significant taxonomic, biostratigraphic, palaeoecological and palaeobiogeographic interest, particularly in South European basins from France and Spain (Grambast 1958, 1962a, 1972; Feist-Castel 1970, 1972, 1975, 1977a; Feist & Ringeade 1977; Anadón & Feist 1981; Riveline 1986; Anadón *et al*. 1992; Sanjuan & Martín-Closas 2012). As a result, a European Charophyte Biozonation based largely on these basins was proposed by Riveline et al. (1996). For the Eocene, up to 11 charophyte biozones were defined based mainly on data from Western Europe. This biozonation has been updated since then, e.g., by Sanjuan *et al*. (2014) for the upper Eocene. In contrast, the Eocene charophyte flora from Central and Eastern Europe is relatively poorly known; and in the case of Hungary, the pioneer study by Rásky (1945) based on subsurface data is practically the only one available. This author described for the first time a species-rich charophyte flora from Hungary, at a time when charophyte taxonomy was still at an early stage. She had already assigned the flora studied in this area to the middle Eocene, and her work was the basis for future studies in charophyte taxonomy, including the definition of the new family Raskyellaceae by Grambast & Grambast (1954). Later, Bignot *et al*. (1985), based on an exhaustive palaeontological study of the Gánt section including molluscs, foraminifers, ostracods, palynomorphs and charophytes, assigned the bauxite cover-sequence to the Upper Lutetian or Bartonian, respectively.

This study aims to update the compendium of knowledge on Eocene Hungarian and Central European charophytes, providing a taxonomic revision of the respective flora that is based on surface samples of sections at the Gánt locality, as well as a discussion regarding its biostratigraphic significance and utility.

Geological setting

Within the Transdanubian Central Range (TCR), several bauxite deposits that developed across the Cretaceous–Early Tertiary boundary interval are well known for their industrial use as sources of aluminium ore; and among these, the famous karst bauxite of the Vértes Hills from the Gánt locality (north-western Hungary) is a prominent example. Strata overlying the bauxite represent the sedimentary record of progressive subcrustal erosion along the East Alpine-West Carpathian forearc basin (Kázmér *et al*. 2003). The bauxite represents the base of the Eocene charophyte-bearing strata investigated in this study (Fig. 1). The Eocene succession sampled shows a remarkable lateral and vertical change of facies (Pálfalvi *et al*. 2006; Pálfalvi 2007) that has been attributed to tectonic forces acting on the sedimentary body (Fodor 2007). The development of the post-bauxite deposits was lain down during oscillation of the groundwater table and eustatic sea level variations (Carannante *et al*. 1994; Mindszenty 2010), occurring before the region was flooded by a marine incursion during the late Bartonian (Bignot *et al*. 1985).

At the Gánt section, the bauxite cover-sequence shows five stratigraphic units in a vertical orientation dating from the middle Eocene (Fig. 2), called ‘Packets’ in the sense of Bignot *et al*. (1985). ‘Packet 1’, about 1.5 m thick, corresponds to the bauxite itself, which unconformably overlies Triassic dolomites. ‘Packet 2’, 1.5–2 m in thickness, forms the ‘blue-hole’ freshwater limestone facies (Carannante *et al*. 1994; Pálfalvi 2007) alternating with clays, rich in charophytes, ostracods and gastropods. ‘Packet 3’, *ca*. 6.5 m thick, includes alternating sandy clay, coal and fresh- to brackish water limestone, rich in charophytes, ostracods, molluscs and large benthic foraminifera (Bignot *et al*. 1985). ‘Packet 4’ is *ca*. 12 m thick and is mainly dominated by shallow marine limestone, rich in nummulites, miliolids, molluscs and ostracods. Finally, ‘Packet 5’ is *ca*. 6m thick and displays an alternation of shallow marine marl and limestone, rich in *Nummulites* and *Orbitolites*. ‘Packets’ 2 and 3 were sampled for charophytes and are studied here.

-----------------------------Figures 1, 2 near here------------------------

Material and methods

Intensive sampling for charophytes during two consecutive field work sessions in 2018 and 2019 was carried out on the cover sequence of the bauxite at Gánt (Vértes Hills, Hungary). Moderately- to well-preserved gyrogonites were recovered from marly limestone to hard limestone using acetolysis. This method, first applied by Nötzold (1965) to the study of charophytes, has been recently improved by Trabelsi *et al*. (2010, 2016) and shown to be very effective in recovering charophyte fructifications and thalli from consolidated carbonate rocks. It consists of soaking the sample of hard calcareous rock, perfectly dried and mechanically comminuted into fragments of about 1–3 mm across, in equal amounts of anhydrous acetic acid and anhydrous copper sulphate (acid reacts exothermically). After neutralization by ammonia, the residue is treated with ultra-sound, then washed and rinsed. Gyrogonites were measured using the software Motic Images Plus 2.0 ML with a Motic BA310 stereomicroscope in the *Departament de Dinàmica de la Terra i de l'Oceà* (University of Barcelona, Catalonia, Spain). Scanning electron microscopy on gold-sputtered selected specimens was conducted with a JEOL JSM-6400 at the Faculty of Earth Sciences, Geography and Astronomy, University of Vienna (Austria) and with a Quanta 200 device at the *Centres Científics i Tecnològics* of the University of Barcelona (CCiTUB). The studied materials are housed in the Hungarian Natural History Museum (Budapest, Hungary), Botanical Department, Palaeobotanical Collection. The figured specimens are deposited under the inventory numbers: HNHM-PBO 1501–1591.

Systematic palaeontology

The charophyte flora from the bauxite cover sequence at Gánt (Vértes Hills, Hungary) studied here yields gyrogonites from two families: Raskyellaceae and Characeae. The different charophyte species described below are stratigraphically distributed in the section as shown in the Fig. 2.

Division **Charophyta** Migula, 1897

Class **Charophyceae** G. M. Smith, 1938 emend. Schudack, 1993

Order **Charales** Lindley, 1836

Family **Raskyellaceae** Grambast, 1957

Sub-Family **Raskyelloideae**, Grambast et Grambast, 1955

Genus ***Raskyella*** (Grambast et Grambast, 1954) emend. Grambast, 1962b

Type species. *Raskyella peckii* Grambast et Grambast, 1954

Remarks. This species is understood as including several traditional taxa belonging to the genus *Raskyella*, which form a gradualistic lineage during the Eocene. These traditional taxa have been newly combined here to anagenetic varieties within a single evolutionary lineage or an evolutionary species, following the recommendations of Wiley (1981) and Ax (1978).

Raskyella peckii var. ***peckii*** Grambast et Grambast, 1954

(Fig. 3A–H)

1954 *Raskyella pecki* sp. nov. L. & N. Grambast: p. 670, text-figs 1a–c.

1957 *Raskyella pecki* Grambast: p. 358, pl. 5, figs 7–9.

1958 *Raskyella pecki* Grambast: p. 190, figs 87, a–c; p. 191, text-fig. 88.

1959 *Raskyella pecki* Horn af Rantzien: pl. 19, figs 7–13.

1971 *Raskyella peckii* subsp. *ganesensis* Soulié-Märsche: pl. 2, 1–5.

1981 *Raskyella pecki* Anadón & Feist: pl. 1, figs 1–2; pl. 2, figs 3–4.

1986 *Raskyella pecki* Riveline: pl. 37, figs 7–9.

1999a *Raskyella pecki* Martín-Closas *et al.*: p. 11, figs 6, 1–3.

Material. Up to 65 gyrogonites in sample G-2.4, and dozens in samples G-2.2 and G-2.3. Collection numbers of figured specimens: HNHM-PBO 1501–1508.

Description. Gyrogonites are ovoidal to ellipsoidal in shape, spherical to subprolate (ISI 100–120) and of large size, 800–1050 μm in height and 750–1050 μm in width, showing laterally 7–10 (usually 9) convolutions (Fig. 4). Spiral cells often flat (Fig. 3A) to slightly convex (Fig. 3C), or concave (Fig. 3B), but regularly without any kind of ornamentation. Apex broadly rounded, truncated and flattened, with the spiral cells abruptly discontinue and ending acutely in the apical periphery to be replaced by the development of five opercular cells, each obliquely disposed at the end of a spiral cell (Fig. 3F). Germinated specimens (Fig. 3G) show a rose-shaped apical opening. Internal casts of these gyrogonites were also found (Fig. 3E).

Remarks. The contemporaneous unornamented gyrogonites of *Raskyella peckii* subsp. *ganesensis* Soulié-Märsche, 1971 from the Aquitaine basin (France) appear to represent a gyrogonite population of relatively smaller size within *R. peckii* var. *peckii* and both are here considered synonymous. However, supplementary research on the type material is needed to verify this synonymy, since the morphotype *ganesesis* is only known from the type locality.

Additionally, the subspecies *Raskyella peckii* subsp. *meridionale* Grambast, 1960, is kept within the rank of subspecies due to its palaeogeographic restriction. The extremely large gyrogonites of this subspecies are limited to the southernmost biogeographic range of *Raskyella peckii*, i.e. Algeria (Grambast 1960; Mebrouk *et al*. 1997), and the Betic Domain of the Balearic Islands (Martín-Closas & Ramos 2005).

Distribution. This is the first record of *R. peckii* var. *peckii* in Hungary and Central Europe. This variety is widely distributed in the Lutetian and lower Bartonian of southern Europe, mainly in France (L. & N. Grambast 1954; Grambast 1958; Soulié-Märsche 1971, 1974;

Riveline 1984, 1986) and Spain (Anadón & Feist 1981; Anadón *et al*. 1992; Martín-Closas *et al*. 1999a; Martín-Closas & Ramos 2005). The total range of this variety (early Lutetian−late Bartonian) has been characterized in the Eastern Ebro basin (Catalonia) by Martín-Closas *et al*. (1999) based on correlation with larger foraminifera (mainly *Nummulites*). Furthermore, *R. peckii* var. *peckii* has been also reported from North Africa, i.e. in the lower Eocene of Algeria (Gevin *et al*. 1974; Mebrouk *et al*. 1997; Vianey-Liaud 1994), in the late lower Eocene–early middle Eocene of Tunisia (Abdeljaoued *et al*. 1984) and in the Lutetian of Libya (Megerisi & Mamgain 1980).

------------------------------- Figures 3, 4 near here-------------------------

Raskyella peckii var. ***caliciformis*** (Soulié-Märsche, 1974) comb. nov. Trabelsi et Martín-Closas

(Fig. 3I–P)

Basionym. *Raskyella caliciformis* Soulié-Märsche, 1974, Compte Rendu 96ème Congrès National des Sociétés Savantes, Toulouse, 1971, Section Science, 2, p. 114, text-figure 2 (pl. I), 1–5.

1974 *Raskyella caliciformis* sp. nov., Soulié-Märsche: p. 112, pl. 1, figs 1–5.

1981 *Raskyella caliciformis,* Anadón & Feist: pl. 1, figs 6–7; pl. 2, figs 7–8.

Material. 63 gyrogonites in sample G-2.5. Collection numbers of figured specimens: HNHM-PBO 1509–1516.

Description. Large sized gyrogonites (650–1000 µm high and 750–1050 µm wide) of globular to oblate shape (ISI 80–105), showing laterally 6–9 (usually 8) convolutions (Fig. 5). Spiral cells flat to slightly concave ornamented with stout, vertical to slightly inclined, well individualized tubercles (Fig. 3I–K), which are the main diagnostic character of this variety. Apex broadly rounded to truncated showing five opercular cells placed at the end of the spiral cells. The opercular cells are sometimes convex and somewhat polygonal in shape (Fig. 3N), rather than rounded, which is the reason why the dehiscence opening appears sometimes irregularly star-shaped (Fig. 3O), rather than rose-shaped (Fig. 3L), as already noted by Soulié-Märsche (1974) in the type material. The internal cast of the gyrogonite (Fig. 3M) shows straight ridges perpendicular to the well-marked, undulated spiral cells. This wavy surface is uncommon in the inside of other raskyellacean gyrogonites and is thought to correspond internally to the external tubercle ornamentation.

Distribution. This is the first record of *R. peckii* var. *caliciformis* in Hungary. It was previously described from the Bartonian of South France (Soulié-Märsche 1974; Riveline 1986), and from the lower Bartonian (Auversian local stage) of the Ebro Basin, Catalonia, Spain (Anadón & Feist 1981; Anadón *et al*. 1992).

---------------------------------- Figure 5 near here------------------------

Raskyella peckii var. ***vadaszii*** (Grambast et Grambast 1954) comb. nov. Trabelsi et Martín-Closas

(Fig. 6A–S)

Basionym. *Raskyella vadaszi* (Rásky) L. & N. Grambast (1954), Revue Générale de Botanique (61), p. 670.

1945 *Aclistochara vadaszi,* sp. nov. Rásky: p. 45, pl. II, figs 22–24.

1954 *Raskyella vadaszi,* comb. nov. L. and N. Grambast: p. 670.

1957 *Raskyella vadaszi*, Grambast: p. 358, pl. 5, figs 1–6.

1959 *Raskyella vadaszi,* Horn af Rantzien: pl. 20, figs 1–3.

1981 *Raskyella vadaszi,* Anadón & Feist: pl. 1, fig. 5; pl. 2, fig. 5.

1981 *Raskyella* aff. *vadaszi,* Anadón & Feist: pl. 1, figs 3–4; pl. 2, figs 1–2, 6.

1985 *Raskyella vadaszi,* Bignot *et al.*: p. 36, pl. 3, figs 8–11.

1986 *Raskyella vadaszi,* Riveline: pl. 37, figs 1–6.

Material. Hundreds of gyrogonites in samples G-6a and G-6b. Collection numbers of figured specimens: HNHM-PBO 1517–1534.

Description. Large sized gyrogonites (800–1150 µm high and 800–1150 µm wide) of oblate to ovoidal shape (ISI 80–120), showing laterally 7–10 (usually 9) convolutions (Fig. 7). Spiral cells often convex and ornamented with stout tubercles of different shapes and sizes, in most cases oriented parallel to the intercellular sutures (Fig. 6A–C), or more rarely tilted 20–30° but keeping parallelism between adjacent nodules (Fig. 6E–G), this being a diagnostic character of this morphotype. Three tubercle morphologies have been observed: (1) rounded tubercles, well individualized in the upper half of the gyrogonite, but fused to neighbouring tubercles in the lower half (Fig. 6I–K), (2) elongated tubercles more or less connected to each other and producing slightly wavy (undulated) sutures (Fig. 6H), (3) irregularly alternating round and elongated tubercles (Fig. 6D). Base of gyrogonite rounded (Fig. 6C, J) to slightly tapered (Fig. 6A, G) and showing a small, superficial and pentagonal basal pore, sometimes within a less-marked funnel (Fig. 6Q). Apex of gyrogonite truncated or broadly rounded and covered by five independent opercular cells at the end of the spiral cells. Opercular cells roughly prismatic, with its outer surface concave, flat or slightly convex (Fig. 6L–M). Germinated specimens show a rounded or rose-like opening (Fig. 6N–P). The inside of the gyrogonite allows observation of a characteristic crenulation of the intercellular sutures near their internal side (Fig. 6R–S), while, to the outside, sutures are flat. Besides, this crenulation occurs also between the opercule cells themselves and between spiral and opercule cells as already described by Feist *in* Anadón and Feist (1981).

Distribution. *R. vadaszii* has been first described by Rásky (1945) from middle Eocene borehole samples (60 m depth) at Gánt, in beds roughly equivalent laterally to the outcrop succession studied here. Therefore, the samples studied may be considered topotypes. Subsequently, the age of this variety was suggested to be upper Bartonian by Bignot *et al.* (1985) based on the associated microfossils (foraminifers, ostracods, and pollen) from the same beds of the bauxite cover-sequence at the Gánt section (Vértes Hills). *R. peckii* var. *vadaszii* has also been well documented in France, in the upper Bartonian of the Paris Basin (Grambast 1957, 1958, 1962a; Riveline 1986) and from several basins in southern France (Feist-Castel

1976). Anadón & Feist (1981) and Anadón *et al.* (1992) documented this variety also in the upper Bartonian of the Eastern Ebro Basin (Catalonia, Spain).

---------------------------------- Figures 6, 7 near here------------------------

Family **Characeae** (Richard ex C.A. Agardh, 1824) emend. Martín-Closas et Schudack, 1991

Subfamily **Charoideae** Braun *in* Migula, 1897

Genus ***Gyrogona*** (Lamarck, 1804 *ex* Lamarck, 1822) emend. Grambast, 1956

Gyrogona caelata (Reid et Groves, 1921) Grambast, 1956

(Fig. 8A–V)

1921 *Chara caelata* sp. nov., Reid & Groves: p. 184, pl. 4, figs 4–6.

1927 *Kosmogyra caelata,* Pia: p. 90.

1954 *Brachychara caelata,* L. & N. Grambast: p. 667.

1956 *Gyrogona caelata,* Grambast: p. 280.

1977b *Gyrogona caelata,* Feist-Castel: p. 117.

1981 *Gyrogona caelata,* Grambast & Grambast-Fessard: p. 22, text-fig. 11, a–f; pl. 4, figs 1–9.

1981 *Gyrogona* cf. *Caelata,* Anadón & Feist: p. 163.

1986 *Gyrogona caelata,* Riveline: pl. 38, figs 1–5, 7–8.

1989 *Gyrogona caelata,* Choi: pl. 2, figs 1–11.

1991 *Gyrogona caelata,* Weidmann *et al.*: p. 900, fig. 3, C.

2014 *Gyrogona caelata,* Sanjuan & Martín-Closas: p. 403, fig. 7, A–C.

Material. 56 gyrogonites in sample G-2.2, 38 in sample G-2.3, 29 in sample G-2.4, 18 in sample G-2.5, and 23 in sample G-6a. Collection numbers of figured specimens: HNHM-PBO 1535–1553.

Description. Medium to large gyrogonites, 600–800 µm high and 700–1000 µm wide with generally oblate to suboblate spheroidal shape (ISI 80–100) and showing laterally 5–7 (usually 6) convolutions (Fig. 9). Apex and base broadly rounded to subtruncate. Apex showing a less-marked spiral cell periapical thinning (e.g., Fig. 8G) and, in some specimens, apical nodules of different shape, generally flat or slightly convex (e.g. Fig. 8S). Base showing a small pentagonal basal pore (Fig. 8F), sometimes flared by a shallow funnel (Fig. 8P). Basal plate unicellular and only visible from the gyrogonite interior (Fig. 8U–V). Spiral cells flat to slightly concave and ornamented with different patterns of tubercles, which allowed Grambast (1958) and Grambast & Grambast-Fessard (1981) to distinguish a number of morphotypes, ranking them as *formae* of the same species. The following five forms were recognized in the material studied: (1) *G. caelata* forma *caelata* characterized by small nodules well-spaced and irregularly ranged along the spiral cell median line (e.g. Fig. 8A, D), (2) *G. caelata* forma *bicincta* characterized by nodules irregularly ranged along two lines parallel to spiral cell sutures (Fig. 8H, I), (3) *G. caelata* forma *monolifera* showing medium-sized nodules close to each other, sometimes fused and forming a thin, irregular mid-cellular crest (e.g., Fig. 8L), (4) *G. caelata* forma *baccata* characterized by large nodules very closely ranged along the spiral-cell median line (e.g., Fig. 8N–Q), (5) *G. caelata* forma *fasciata* characterized by a broad median band of variable width (e.g., Fig. 8R–T).

Distribution. The species *Gyrogona caelata* is reported here from Hungary for the first time. According to Riveline (1986), this species was widely distributed in the upper Lutetian–Priabonian non-marine deposits of Western Europe. It was first recorded from the Isle of Wight, England by Reid & Groves (1921). Thereafter, it was reported from the upper Lutetian to upper Priabonian of France (Grambast 1958; Grambast & Grambast-Fessard 1981; Feist-Castel 1971; Feist & Ringeade 1977; Feist-Castel 1977a, b; Ollivier-Pierre *et al*. 1988), Spain (Anadón & Feist 1981; Choi 1989; Anadón *et al*. 1992; Sanjuan & Martín-Closas 2014), Switzerland (Weidmann *et al*. 1991), as well as from the middle Eocene of Romania (Iva 1987). In North Africa, the species has also been documented from the central part of the Sahara, Algeria, by Mebrouk *et al*. (1997).

---------------------------------- Figures 8, 9, near here-------------------------

Gyrogona tuberosa (Reid et Groves, 1921) Grambast *in* Grambast et Grambast-Fessard, 1981

(Fig. 10A–J)

1921 *Chara wrighti* var. *rhytidocarpa,* Reid & Groves: p. 183, pl. 4, fig. 3.

1958 *Gyrogona tuberosa,* Grambast: p. 139, fig. 54.

1976 *Gyrogona tuberosa,* Feist-Castel: p. 26.

1981 *Gyrogona tuberosa,* Grambast & Grambast-Fessard: p. 25, text-fig. 12, a–d; pl. 5, figs 1–6.

1986 *Gyrogona tuberosa,* Riveline: pl. 14, figs 8–11.

Material. 35 gyrogonites in sample G-6b. Collection numbers of figured specimens: HNHM-PBO 1554–1563.

Description. Large gyrogonites, 820–1000 μm high and 835–1050 μm wide with generally oblate to suboblate spheroidal shape (ISI 80–100) and showing laterally 6–7 convolutions (usually 6). Apex subtruncate (Fig. 10A, C) to somewhat pointed (Fig. 10D, G) with spiral cells protruding (Fig. 10H). Base broadly rounded (Fig. 10B, F) to slightly tapered (Fig. 10A, C, E) and showing a small, superficial and pentagonal basal pore, sometimes within a less-marked funnel (Fig. 10I–J). Spiral cells flat or concave, smooth or somewhat ornamented and separated by protruding narrow to weakly undulated intercellular ridges.

Distribution. *Gyrogona tuberosa* is reported here from Hungary and central Europe for the first time. According to Riveline (1986) and Riveline & Cavelier (1987), this species was widely distributed in upper Bartonian non-marine deposits of Western Europe. It was first recorded from the Isle of Wight and Hampshire (England) by Reid & Groves (1921). Subesequently, it was reported from the upper Bartonian of the Paris Basin (Grambast 1958; Grambast & Grambast-Fessard 1981; Riveline 1986; Riveline & Cavelier 1987), as well as from several basins of southern France (Feist-Castel 1976).

---------------------------------- Figure 10 near here-------------------------

Genus ***Psilochara*** Grambast, 1959

Psilochara polita (Reid et Groves, 1921) Grambast, 1959

(Fig. 11A–F)

1921 *Chara polita,* sp. nov. Reid & Groves: p. 187, pl. 5, figs 9, 12.

1927 *Gyrogona politus,* Pia: p. 90.

1958 *Ovochara polita,* comb. nov. Grambast: p. 167.

1959 *Peckichara polita,* Horn af Rantzien: p. 116, pl. 13, figs 1–3.

1959 *Psilochara polita,* Grambast: p. 11.

1977b *Psilochara polita,* Feist-Castel: p. 153.

1986 *Psilochara polita,* Riveline: p. 59, pl. 22, figs 8–12.

Material. 58 gyrogonites in sample G-6a. Collection numbers of figured specimens: HNHM-PBO 1564–1569.

Description. Medium-sized gyrogonites (550–700 µm in height 500–650 and µm in width) with ovoidal shape (ISI 100–120) and laterally showing 7–10 convolutions (Fig. 11A–C; Fig. 12). Apex round to pointed (Fig. 11A−C). Base tapering to prolonged into a stout basal column

(Fig 11A−C) and showing a small pentagonal basal pore (Fig. 11F). Spiral cells smooth, concave or flat and separated by protruding narrow to weakly undulated intercellular ridges.

Distribution. *Psilochara polita* is described here from the middle Eocene of Hungary for the first time. It has previously been described from the upper Bartonian of the Isle of Wight, England, (Reid & Groves 1921; Feist-Castel 1977b; Riveline 1986) and of the Paris Basin (Grambast 1958; Riveline 1986).

---------------------------------- Figures 11, 12 near here-------------------------

Psilochara **sp.**

(Fig. 11G–I)

Material. 17 gyrogonites in sample G-6a. Collection numbers of figured specimens: HNHM-PBO 1570–1571.

Description. Medium to large-sized gyrogonites (780–905 µm wide and 670–775 µm high) with elongated ovoidal (subprolate) shape (ISI 110–125) and laterally showing 8–10 convolutions (Fig. 11G). Apex truncated. Apical end of spiral cells enlarged and pointing upwards (Fig. 11H). Base truncated to somewhat tapering, bearing a small pentagonal basal pore. Basal plate unipartite and visible from the gyrogonite interior (Fig. 11I). Spiral cells concave or flat and smooth, except at the periapical area, where they are irregularly ornamented with a broad mid-cellular crest.

Remark. The low number of gyrogonites hinders a more precise taxonomic attribution of this population. However, it is reported here since it differs in size and shape from the other species of *Psilochara* found at Gánt.

Genus ***Nitellopsis*** Hy, 1889

Sub-genus ***Tectochara*** L. et N. Grambast, 1954

Nitellopsis **(*Tectochara*) aff. *palaeohungarica*** (Rásky, 1945) Grambast et Soulié-Märsche, 1972

(Fig. 11J–N)

1945 *Chara palaeohungarica,* sp. nov. Rásky: p. 38, pl. 1, figs 16–18.

1955 *Tectochara palaeohungarica,* comb. nov. Mädler: p. 298.

1959 *Tectochara palaeohungarica,* Horn af Rantzien: p. 90, pl. 8, figs 4–7.

1972 *Nitellopsis (Tectochara) palaeohungarica*, nov. comb. Grambast & Soulié-Märsche: p. 4.

Material. 28 gyrogonites in sample G-2.3 and 33 in sample G-2.5. Collection numbers of figured specimens: HNHM-PBO 1572–1576.

Description. Gyrogonites very large (900–1200 µm high and 800–1050 µm wide), oval, prolate spheroidal (ISI 100–120) in shape, showing 8–11 (often 9) convolutions in lateral view (Fig. 11J–L; Fig. 13). Spiral cells concave to flat. Apex prominent with spiral cells protruding to form a central rosette. Spiral cells show both narrowing and thinning in the periapical area (Fig. 11M). Base rounded to almost conical, occasionally lengthened in a short broad column. A large (155–230 µm across) pentagonal basal pore occurs within a wide basal funnel (Fig. 11N).

Distribution. The species *'Chara' palaeohungarica* was first described from subsurface beds attributed to the Paleocene in Dorog, Hungary, by Rásky (1945). Here this species is described from beds cropping out at Gánt, which are probably time-equivalent to those of the type locality. The present study supports reassignment of this species to the middle Eocene rather than to the Paleocene.

Remarks. The gyrogonites studied here are diagenetically deformed, which hinders a more definitive taxonomic attribution. A re-study of the type material (HNHM 55.1458–55.1460) by one of the authors of this study (CMC) showed that, besides the holotype, which is a subspherical gyrogonite as illustrated by Rásky (1945, pl. I, Fig. 16), there were more oval to elongated gyrogonites present in the collection similar to those described here, which Rásky (1945, p. 38) termed 'cylindrical'.

---------------------------------- Figure13 near here------------------------

Genus ***Chara*** Vaillant, 1719

Chara media Grambast, 1958

(Fig. 14A–I)

1958 *Chara media,* Grambast: p. 178, fig. 81b.

1986. *Chara media,* Riveline: p. 68, pl. 29, figs 6–12.

Material. Up to 80 gyrogonites in both samples G-2.5 and G-6a. Collection numbers of figured specimens: HNHM-PBO 1577–1585.

Description. Gyrogonites of medium size (400–650 µm high and 300–500 µm wide) ellipsoidal subprolate (ISI 110–145), laterally showing 8–11 (usually 9–10) convolutions (Fig. 14A–G, Fig. 15). Maximum width nearly at the half to 2/3 of height. Apex rounded to slightly conical, with distinctly widening of the spiral cell endings (Fig. 14H). Spiral cells concave, smooth and without any periapical modification. Base tapering showing a superficial pentagonal basal pore (Fig. 14I).

Distribution. *Chara media* is described here from the upper Eocene (upper Bartonian) of Hungary for the first time. Grambast (1958) and Riveline (1986) documented this species from the upper Bartonian–lower Oligocene of several basins in France, Belgium, and Germany.

---------------------------------- Figures 14, 15 near here------------------------

Chara subcylindrica Reid et Groves, 1921

(Fig. 14J–O)

1921 *Chara subcylindrica,* sp. nov. Reid & Groves: p. 187, pl. 5, fig. 4–5.

1959 *Grambastichara subcylindrica,* Horn af Rantzien: p. 76, pl. 3, figs 5–7.

1986 *Chara* cf. *subcylindrica,* Riveline: p. 67, pl. 30, figs 5–8.

Material. Up to 250 gyrogonites in sample G-6b. Collection numbers of figured specimens: HNHM-PBO 1586–1591.

Description. Medium-sized gyrogonites (500–750 µm high and 200–400 µm wide) ellipsoidal prolate to perprolate (ISI 130–200) in shape, laterally showing 8–11 (usually 9–10) convolutions (Fig. 14J–M; Fig. 16). Maximum width at the equator. Apex rounded with widening of the spiral cell endings (Fig. 14N). Spiral cells often slightly concave to flat, separated by narrow intercellular ridges, cells non-ornamented and without any periapical modification. Base regularly tapering to round, showing a superficial pentagonal basal pore (Fig. 14O).

Distribution. This is the first report of *Chara subcylindrica* in Hungary. According to Reid & Groves (1921) and Riveline (1986), this species occurs in the upper Bartonian–lower Oligocene of England, France, Belgium and Germany.

------------------------------------- Figure 16 near here -----------------------

Discussion

Definition of the *Raskyella peckii* anagenetic lineage

Evolutionary lineages formed by a succession of charophyte fructifications changing gradually in time were first described in the family Clavatoraceae by Grambast (1974). Later, similar lineages were found as well in the family Characeae (e.g. lineage *Harrisichara vasiformis-tuberculata* described by Feist-Castel 1977b; or lineage *Peckichara pectinata* by Vicente *et al*. 2018). Here we describe the first of such lineages in the family Raskyellaceae. In the Lutetian and Bartonian of Gánt (Hungary), three former species of the genus *Raskyella* – *R. peckii, R. caliciformis*, and *R. vadaszii* – have been found to form a continuous succession of gyrogonite morphologies, connected by intermediate morphotypes. This gradualistic lineage is interpreted as an evolutionary species in the sense of Wiley (1981) and Ax (1987), and the original taxa have been newly combined as anagenetic varieties of the species with nomenclatural priority, which is *R. peckii*.

The first evolutionary stage of the *R. peckii* lineage (Fig. 17) is represented by *R. peckii* var. *peckii,* and includes, as well, the smallest gyrogonite morphotype initially described as *Raskyella peckii ganesensis* Soulié-Märsche, 1971. *R. peckii* var. *peckii* is characterized by gyrogonites which are very variable in size, but consistently unornamented. This stage has a long duration, since it was documented from the lower Lutetian to the upper Bartonian of the Ebro Basin, Catalonia, by Martín-Closas *et al*. (1999a) and can thus be superimposed onto some of the ulterior morphotypes of the lineage, this being quite a common situation in charophyte lineages (e.g., Grambast, 1974). The coeval *Raskyella peckii* subsp. *meridionale* Grambast, 1960, was not found in the section studied and corresponds to a southern geographic subspecies of this lineage, thriving in North Africa and the Prebetic Domain in the Balearic Islands in Spain (Grambast 1960; Martín-Closas & Ramos 2005).

The second evolutionary stage in the lineage of *R. peckii* is represented by *R. peckii* var. *caliciformis*. Intermediate morphotypes between *R. peckii* var. *peckii* and *R. peckii* var. *caliciformis* display a progressive increase in the gyrogonite size (up to 1000 µm in height), and a change in shape from elongated to rounded, between samples G-2.2 and G-2.4 of the Gánt section. Furthermore, there is a progressive development of the ornamentation corresponding to *R. peckii* var. *caliciformis* in the same sequence, with for instance 100% of gyrogonites corresponding to *R. peckii* var. *peckii* in sample G-2.4, while in sample G-2.5, there is only 10% of *R. peckii* var. *peckii*, resulting in 90% of *R. peckii* var. *caliciformis* (Fig. 17).

The third stage of the lineage is represented by *R. vadaszii* from the upper Bartonian, which shows an additional increase of the gyrogonite size of about 150–250 µm in height and 100–125 µm in width, and especially the development of progressively more complex ornamentation patterns in comparison to the previous evolutionary step (Fig. 17). This gradual change can be observed between samples G-2.5 and G-6b of the Gánt section. Thus, sample G-5 displays a homogeneous population with 100% of gyrogonites corresponding to *R. peckii* var. *caliciformis*, while in the overlying sample G-6a, the gyrogonite population of *R. peckii* contains only 15% of specimens of *R. peckii* var. *caliciformis* and 85% of *R. peckii* var. *vadaszii*. Finally, in sample G-6b there is a homogeneous population of gyrogonites corresponding to *R. peckii* var. *vadaszii*.

Overall, the *R. peckii* lineage follows the general evolutionary trend in the evolutionary lineages of other charophyte families, characterized by an increase in size and sphericity (Clavatoraceae and Raskyellaceae), and a progressive development of ornamentation (Characeae), as shown by Feist-Castel (1977b), Martín-Closas *et al*. (1999b), Sille *et al*. (2004) and Vicente & Martín-Closas (2018).

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New local charophyte biozonation

Among the charophyte species described from the bauxite cover-sequence at the Gánt section (Vértes Hills, Hungary), *Raskyella peckii* represents the most significant species for use in biostratigrpahy within the non-marine Lutetian and Bartonian, as previously suggested by Riveline *et al*. (1996) and Martín-Closas *et al*. (1999a). The *Raskyella peckii* biozone was defined by Riveline *et al*. (1996) as a 'partial range zone comprising the interval from the first appearance of *Raskyella peckii* L. and N. Grambast, 1954, to the first appearance of *Chara friteli* Grambast, 1958, lower Lutetian to lower Bartonian in age. This study proposes to extend this biozone to cover also the upper Bartonian, and to redesignate it as a superzone subdivided into the following three successive biozones (Fig. 18):

- **Raskyella peckii peckii Zone**: partial range zone defined from the first occurrence of the morphotype *peckii* to the first occurrence of the morphotype *caliciformis*, Lutetian–lower Bartonian in age. The local charophyte assemblage characterizing this zone in Gánt occurs in the basal part of the studied section ('Packet 2', 'blue-hole' freshwater limestone facies, samples G-2.2, G-2.3 and G-2.4), and is composed of *R. peckii* var. *peckii*, *G. caelata* forma *caelata*, *G. caelata* forma *monolifera*, and *Nitellopsis (Tectochara)* aff. *palaeohungarica*, some of which are well known to occur in several European basins (Rásky 1945; Grambast 1958; Riveline 1986; Martín-Closas *et al*. 1999a) during the same time interval.

- **Raskyella peckii caliciformis Zone**: partial range zone defined from the first occurrence of the morphotype *caliciformis* to the first occurrence of the morphotype *vadaszii*, lower Bartonian in age. This zone includes in Gánt the assemblage found in the lower part of 'Packet 3' (samples G-2.5) and composed of *R. peckii* var. *caliciformis*, *G. caelata* forma *caelata*, *G. caelata* forma *monolifera*, *G. caelata* forma *baccata*, *Nitellopsis (Tectochara)* aff. *palaeohungarica*, and *Chara media*.

- **Raskyella pecki vadaszii Zone**: partial range zone defined from the first occurrence of the morphotype *vadaszii* to the first occurrence of the next zone defined in the Paris Basin, which is *Psilochara repanda*. This zone would be upper Bartonian in age. The assemblage occurring in the middle part of the Gánt section ('Packet 3', samples G-6a and G-6b), composed of *R. peckii* var. *vadaszii*, *G. caelata* forma *bicincta*, *G. caelata* forma *baccata*, *G. caelata* forma *fasciata*, *Psilochara polita*, *Psilochara* sp., *Chara media*, and *Chara subcylindrica* characterizes locally this biozone.

Implications on the age of the bauxite cover-sequence

The biostratigraphic analysis carried out suggests a relative age of Lutetian– Bartonian (Fig. 18) of the bauxite cover-sequence at the Gánt section (Vértes Hills, Hungary), rather than constraining it to the Bartonian as previously suggested by Bignot (1985). A Lutetian age, deduced from the charophytes and attributed to the lower part of the studied series, has been already suggested in several works preceding that of Bignot (1985), notably those of Szőts (1938), Kopek (1980), and Dudich & Kopek (1982), on the basis of mollusc and palynomorph biostratigraphy. The data presented herein support the idea that the Eocene succession in the studied area reflects a stepwise marine transgression upon the bauxite deposits, beginning in the Lutetian. Our new chronostratigraphic framework sheds new light on the timing of the long-lasting subaerial exposure and alteration process generating the bauxite strata. Consequently, coeval strata from surrounding localities within the Transdanubian Central Range should be re-studied and analysed from the viewpoint of charophyte biostratigraphy, in order to correlate the post-bauxite depositional event(s) on a regional scale and to improve the understanding of its tectono-eustatic control.

---------------------------------- Figure 18, near here----------------------

Conclusions

Eocene (Lutetian–Bartonian) charophyte assemblages are taxonomically described for the first time from an outcrop of the bauxite cover-sequence at Gánt (Vértes Hills), Hungary's Transdanubian Central Range. The sections show for the first time that the raskyellacean charophytes also evolved in gradualistic lineages, similarly to what is already known for other charophyte families. The *Raskyella peckii* lineage is formed by three successive stages and is interpreted here in terms of the anagenesis of the evolutionary species *Raskyella peckii*, including its gradual change to the morphotype previously known as *R. vadaszi*.

From a biostratigraphic viewpoint, the assemblages studied belong to the *Raskyella peckii* biozone of Martín-Closas *et al*. (1999a), which is here reinterpreted as a superzone extending to cover the *Raskyella vadaszii* Zone of Riveline *et al*. (1996) and attributed to the Lutetian–Bartonian interval. In this study, this superzone is subdivided into three successive local partial range biozones, defined by each of the successive varieties of the evolutionary species *R. peckii*: (1) the *Raskyella peckii peckii* partial range zone is characterized by *R. peckii peckii*, *G. caelata* forma *caelata*, *G. caelata* forma *monolifera* and *Nitellopsis (Tectochara)* aff. *palaeohungarica*, Lutetian–lowermost Bartonian in age; (2) the *Raskyella peckii caliciformis* partial range zone is characterized by *R. peckii caliciformis*, *G. caelata* forma *caelata*, *G. caelata* forma *monolifera*, *G. caelata* forma *baccata*, *Nitellopsis (Tectochara)* aff. *palaeohungarica* and *Chara media*, lower Bartonian in age; and (3) the *Raskyella peckii vadaszii* partial range zone is characterized by *R. peckii vadaszii*, *G. caelata* forma *bicincta*, *G. caelata* forma *baccata*, *G. caelata* forma *fasciata*, *G. tuberosa*, *Psilochara polita*, *Psilohara* sp., *Chara media* and *Chara subcylindrica*, upper Bartonian in age.

In light of the new results presented here, the charophyte-bearing sequences studied in this work represent a longer time span than previously thought, running from the Lutetian to the Bartonian. This has direct implications on the understanding of the Eocene regional stratigraphic scheme of the Transdanubian Central Range, particularly in terms of synchronism/diachronism in the regional stratigraphic correlation, as well as the timing of the tectono-sedimentary control and palaeogeographic evolution.

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Figure Captions

Figure 1. **A**, geographical and geological setting of the study area (after Fodor 2007). **B**, panoramic view of the studied Gánt section at the Vértes Hills (north-western Hungary).

Figure 2. Distribution of the charophytes species in the bauxite cover-sequence of the studied Gánt section (Vértes Hills, Hungary), according to Bignot *et al*. (1985), updated for charophyte content.

Figure 3. *Raskyella peckii* gyrogonites from the Gánt bauxite cover-sequence. **A–H**, *Raskyella pecki* var. *peckii* (samples G-2.2, G-2.3, G-2.4, and G-2.5), HNHM-PBO 1501–1508. **A–E**, lateral view; **F–G**, apical view; **H**, basal view. **I–P**, *Raskyella peckii* var. *caliciformis* (samples G-2.5 and G-6a), HNHM-PBO 1509–1516. **I–K**, lateral view; **L**, lateral view of gyrogonite partially broken showing internal cast. **M**, internal cast with well-developed undulations. **N–O**, apical view; **P**, basal view.

Figure 4. Frequency distribution of the height (A), width (B), number of convolutions (C), and height/width ratio (ISI) (D) of the *Raskyella peckii* var. *peckii* population (50 gyrogonites measured), from samples G-2.2, G-2.3, and G-2.4 in the bauxite cover-sequence of the Gánt section.

Figure 5. Frequency distribution of the height (A), width (B), number of convolutions (C), and height/width ratio (ISI) (D) of the *Raskyella peckii* var. *caliciformis* population (50 gyrogonites measured), from sample G-2.5 in the bauxite cover-sequence of the Gánt section.

Figure 6. *Raskyella peckii vadaszii* gyrogonites from the Gánt bauxite cover-sequence (**A–S,** samples G-6a and G-6b, HNHM-PBO 1517–1534). **A–K**, lateral view. **L–P**, apical view; **Q**, basal view; **R–S**, inside wall of a gyrogonite showing the crenate undulation of the cellular sutures in contact with the spiral cells and the apical cells.

Figure 7. Frequency distribution of the height (A), width (B), number of convolutions (C), and height/width ratio (ISI) (D) of the *Raskyella peckii* var. *vadaszii* population (50 gyrogonites measured), from samples G-6a and G-6b in the bauxite cover-sequence of the Gánt section.

Figure 8. *Gyrogona caelata gyrogonites* from the Gánt bauxite cover-sequence. **A–G**, *Gyrogona caelata* forma *caelata* (samples G-2.2, G-2.3, G-2.4, and G-2.5), HNHM-PBO 1535–1553. **A–B**, **D–E**, basal view **C**, detail of the ornamentation pattern; **F**, basal view; G, apical view. **H–K**, *Gyrogona caelata* forma *bicincta* (samples G-6a and G-6b). **H**, lateral view; **I**, detail of the ornamentation pattern; **J–K**, apical view. **L–M**, *Gyrogona caelata* forma *monolifera* (samples G-2.2, G-2.3, G-2.4, and G-2.5). **L**, lateral view; **M**, basal view. **N–Q**, *Gyrogona caelata* forma *baccata* (samples G-2.5, G-6a, and G-6b). **N–O**, lateral view; **P**, basal view; **Q**, apical view. **R–V**, *Gyrogona caelata* forma *fasciata* (samples G-6a and G-6b). **R**, lateral view; **S–T**, apical view; **U–V**, detail of the simple (unipartite) basal plate.

Figure 9. Frequency distribution of the height (A), width (B), number of convolutions (C), and height/width ratio (ISI) (D) of the *Gyrogona caelata* population (50 gyrogonites

measured), from samples G-2.2, G-2.3, G-2.4, G-2.5, and G-6a in the bauxite cover-sequence of the Gánt section.

Figure 10. *Gyrogona tuberosa* gyrogonites from the Gánt bauxite cover-sequence (sample G-6b), HNHM-PBO 1554–1563. **A–G**, lateral view; **H**, apical view; **I–J**, basal view.

Figure 11. Gyrogonites of genera *Psilochara* and *Nitellopsis* from the Gánt bauxite cover-sequence. **A–F**, *Psilochara polita* (sample G-6a), HNHM-PBO 1564–1569. **A–C**, lateral view; **D–E**, apical view; **F**, basal view. **G–I**, *Psilochara* sp. (sample G-6a), HNHM-PBO 1570–1571. **G**, lateral view; **H**, apical view; **I**, internal view showing simple (unipartite) basal plate (arrowed). **J–N**, *Nitellopsis (Tectochara)* aff. *palaeohungarica* (samples G-2.3 and G-2.5), HNHM-PBO 1572–1576. **J–L**, lateral view; **M**, apical view; **N**, basal view.

Figure 12. Frequency distribution of the height (A), width (B), number of convolutions (C), and height /width ratio (ISI) (D) of the *Psilochara polita* population (50 gyrogonites measured), from sample G-6a in the bauxite cover-sequence of the Gánt section.

Figure 13. Frequency distribution of the height (A), width (B), number of convolutions (C), and height /width ratio (ISI) (D) of the *Nitellopsis (Tectochara)* aff. *palaeohungarica* population (50 gyrogonites measured), from samples G-2.3 and G-2.5 in the bauxite cover-sequence of the Gánt section.

Figure 14. *Chara* gyrogonites from the Gánt bauxite cover-sequence. **A–I**, *Chara media* (samples G-2.5 and G-6a), HNHM-PBO 1577–1585. **A–G**, lateral view; **H**, apical view; **I**, basal view. **J–O**, *Chara subcylindrica* (sample G-6b), HNHM-PBO 1586–1591. **J–M**, lateral view; **N**, apical view; **O**, basal view.

Figure 15. Frequency distribution of the height (A), width (B), number of convolutions (C), and height /width ratio (ISI) (D) of the *Chara media* population (50 gyrogonites measured), from samples G-2.5 and G-6a in the bauxite cover-sequence of the Gánt section.

Figure 16. Frequency distribution of the height (A), width (B), number of convolutions (C), and height/width ratio (ISI) (D) of the *Chara subcylindrica* population (50 gyrogonites measured), from sample G-6b in the bauxite cover-sequence of the Gánt section.

Figure 17. Stratigraphic distribution of variants of the anagenetic lineage of the species *Raskyella peckii*.

Figure 18. Charophyte Biostratigraphy, age and correlation of the bauxite cover-sequence of the Gánt section.

A new diverse charophyte flora and biozonation of the Eocene bauxite cover-sequence at Gánt (Vértes Hills, Hungary)

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~~A largely new and~~A diverse Eocene charophyte flora from a section at Gánt (Vértes Hills), Transdanubian Central Range, north-western Hungary, provides significant new information to previous studies only based on subsurface data published from the mid-20th ~~Century. The~~ century. This newly acquired material facilitates the taxonomic ~~study of this flora allows~~ revision and emendation of the species *Raskyella peckii* ~~facilitates the definition of~~and thereby defines a new ~~evolutionary~~ anagenetic lineage based on three successive ~~anagenetic~~ varieties ~~of this species~~ which were formerly considered as separate species or subspecies: *Raskyella peckii* var. *peckii* (early Lutetian–early Bartonian), *Raskyella peckii* var. *caliciformis* (early Bartonian), and *Raskyella peckii* var. *vadaszii* (late Bartonian). Based on ~~these~~this lineage, we propose a new local charophyte biozonation ~~with the new~~ that consists of a ‘Raskyella peckii ~~Superzone~~Superzone’ (Lutetian–Bartonian), subdivided into three successive charophyte partial range zones: The ‘Raskyella peckii peckii Zone’ (Lutetian–lowermost Bartonian) ~~is locally~~ characterized by an assemblage of *R. peckii peckii*, *Gyrogona caelata* forma *caelata*, *G. caelata* forma *monolifera* and *Nitellopsis* (*Tectochara*) aff. *palaeohungarica*~~. The~~, the ‘Raskyella peckii caliciformis Zone’ (lower Bartonian) ~~includes~~characterized by the ~~local~~ assemblage of *R. peckii* var. *caliciformis*, *G. caelata* forma *caelata*, *G. caelata* forma *monolifera*, *G. caelata* forma *baccata*, *Nitellopsis* (*Tectochara*) aff. *palaeohungarica* and *Chara media*~~. The~~, and the ‘Raskyella peckii vadaszii Zone’ (upper Bartonian) ~~is composed of the local assemblage of~~characterized by *R. peckii* var. *vadaszii*, *G. caelata* forma *bicincta*, *G. caelata* forma *baccata*, *G. caelata* forma *fasciata*, *G. tuberosa*, *Psilochara polita*, *Psilochara* sp., *Chara media* and *Chara subcylindrica*. Future research may show the new local biozonation as applicable to the whole of Europe and ~~complementing~~complementary to the current European charophyte biozonation. Our results show that the sequences from Gánt, which were previously regarded as upper mid-Eocene (upper Lutetian–lower Bartonian) in age, appear to ~~comprise~~represent a longer ~~time~~chronostratigraphic interval~~, i.e.~~: lower Lutetian ~~till~~to upper Bartonian~~, with also has implications on the understanding of the regional stratigraphy of~~. Our chronostratigraphic results imply a longer and more stepwise Eocene major transgression in the Transdanubian Central Range ~~during the Eocene~~than previously thought.

Keywords: Characeae, Raskyellaceae, ~~biozonation, evolutionary lineage~~phylozone, gradualistic evolution, Paleogene, Central Europe.

Introduction

Charophytes represent one of the most useful tools in the biostratigraphic analysis of Cenozoic non-marine deposits worldwide. During the Eocene, charophytes have been the object of significant taxonomic, biostratigraphic, palaeoecological and palaeobiogeographic interest, particularly in South European basins from France and Spain (Grambast 1958, 1962a, ~~1972a~~1972; Feist-Castel 1970, 1972, 1975, 1977a; Feist & Ringeade 1977; Anadón & Feist 1981; Riveline 1986; Anadón *et al*. 1992; Sanjuan & Martín-Closas 2012~~;~~). As a result, a European Charophyte Biozonation based largely on these basins was proposed by Riveline et al. (1996). For the Eocene, up to 11 charophyte biozones were defined based mainly on data from Western Europe. This biozonation has been updated since then, e.g., by Sanjuan *et al.* (2014~~).~~) for the upper Eocene. In contrast, the Eocene charophyte flora from Central and Eastern Europe is relatively ~~less well~~ poorly known~~,~~; and in the case of Hungary, the pioneer study by Rásky (1945) based on subsurface data is practically the only ~~known. With the aim~~one available. This author described for the first time a species-rich charophyte flora from Hungary, at a time when charophyte taxonomy was still at an early stage. She had already assigned the flora studied in this area to the middle Eocene, and her work was the basis for future studies in charophyte taxonomy, including the definition of ~~updating the~~the new family Raskyellaceae by Grambast & Grambast (1954). Later, Bignot *et al.* (1985), based on an exhaustive palaeontological study of the Gánt section including molluscs, foraminifers, ostracods, palynomorphs and charophytes, assigned the bauxite cover-sequence to the Upper Lutetian or Bartonian, respectively.

This study aims to update the compendium of knowledge on Eocene Hungarian and Central European charophytes, ~~the present study provides~~providing a taxonomic revision of ~~this flora from~~ the respective flora that is based on surface samples of sections at the Gánt locality ~~based on an outcropping section~~, as well as a discussion ~~on~~regarding its ~~significance for~~ biostratigraphic ~~purposes~~significance and utility.

Geological setting

Within the Transdanubian Central Range (TCR), several bauxite deposits that developed ~~during~~across the Cretaceous–Early Tertiary boundary interval are well known for their industrial use as ~~economically exploited ores~~sources of aluminium~~, from which~~ ore; and among these, the famous karst bauxite of the Vértes Hills from the Gánt locality~~,~~ (north-western Hungary ~~stands out. Above~~) is a prominent example. Strata overlying the bauxite~~, the succession represents~~ represent the sedimentary record of progressive subcrustal erosion along the East Alpine-West Carpathian forearc basin (Kázmér *et al*. 2003). The bauxite represents the base of the Eocene charophyte-bearing strata ~~studied herein~~investigated in this study (Fig. 1). The Eocene succession sampled shows a remarkable lateral and vertical change of ~~sedimentary~~ facies (Pálfalvi *et al*. 2006; Pálfalvi 2007) that has been attributed to tectonic ~~control~~forces acting on the ~~sedimentation~~sedimentary body (Fodor 2007). The development of the post-bauxite deposits ~~occurred under dual~~was lain down during oscillation of the groundwater table and ~~the marine relative~~eustatic sea level variations (Carannante *et al*. 1994; Mindszenty 2010), occurring before the region was ~~invaded~~flooded by ~~an open~~a marine incursion during the late Bartonian (Bignot *et al*. 1985).

At the Gánt section, the bauxite cover-sequence ~~vertically~~ shows five stratigraphic units ~~of~~ in a vertical orientation dating from the middle Eocene ~~age~~ (Fig. 2), called ‘Packets’ in the sense of Bignot *et al*. (1985~~), from~~). ‘Packet 1’, about 1.5 m thick, corresponds to the bauxite itself, which ~~only units 2 and 3 are studied herein.~~unconformably overlies Triassic dolomites. ‘Packet 2’, 1.5–2 m in thickness, forms the ‘blue-hole’ freshwater limestone facies (Carannante *et al*. 1994; Pálfalvi 2007~~), while~~) alternating with clays, rich in charophytes, ostracods and gastropods. ‘Packet 3’, *ca*. 6.5 m thick, includes alternating sandy clay, coal and fresh- to brackish water limestone, rich in charophytes, ostracods, molluscs and large benthic foraminifera (Bignot *et al*. ~~1985). In the latter facies charophytes~~ 1985). ‘Packet 4’ is *ca*. 12 m thick and is mainly dominated by shallow marine limestone, rich in nummulites, miliolids, molluscs and ostracods. Finally, ‘Packet 5’ is *ca*. 6m thick and displays an alternation of shallow marine marl and limestone, rich in *Nummulites* and *Orbitolites*. ‘Packets’ 2 and 3 were sampled~~.~~ for charophytes and are studied here.

-----------------------------Figures 1, 2 near here------------------------

Material and methods

Intensive sampling for charophytes during two consecutive field ~~works~~work sessions in 2018 and 2019 ~~has been~~was carried out on the cover sequence of the bauxite at Gánt (Vértes Hills, Hungary). Moderately-~~preserved~~ to well-preserved gyrogonites were recovered from marly limestone to hard limestone using acetolysis. This method, first applied by Nötzold (1965) to the study of charophytes, has been recently improved by Trabelsi *et al*. (2010, 2016) and shown to be very effective in recovering ~~well preserved~~ charophyte fructifications and thalli from consolidated carbonate rocks. It consists ~~in taking~~of soaking the sample of hard calcareous rock, perfectly dried and mechanically comminuted ~~in~~into fragments of about 1–3 mm across ~~and adding similar~~, in equal amounts of anhydrous acetic acid and anhydrous copper ~~sulfate~~sulphate (acid ~~attacks in an exothermic reaction~~reacts exothermically). After neutralization by ammonia, the residue is treated with ultra-sound, then washed and rinsed. Gyrogonites were measured using the software Motic Images Plus 2.0 ML with a Motic BA310 stereomicroscope in the *Departament de Dinàmica de la Terra i de l'Oceà* (University of Barcelona, Catalonia, Spain). Scanning electron microscopy on gold-sputtered selected specimens was conducted with a ~~Jeol~~ JEOL JSM-6400 ~~device~~ at the Faculty of Earth Sciences, Geography and Astronomy, University of Vienna (Austria) and with a Quanta 200 device at the *Centres Científics i Tecnològics* of the University of Barcelona (CCiTUB~~), Spain.~~). The studied materials are housed in the Hungarian Natural History Museum (Budapest, Hungary), Botanical Department, Palaeobotanical Collection. The figured specimens are deposited under the inventory numbers: HNHM-PBO ~~xxxxx–yyyyy~~1501–1591.

Systematic palaeontology

The charophyte flora from the bauxite cover sequence at Gánt (Vértes Hills, Hungary) studied here yields gyrogonites from two families: Raskyellaceae and Characeae. The different charophyte species described below are stratigraphically distributed in the section as shown in the Fig. 2.

Division **Charophyta** Migula, 1897

Class **Charophyceae** G. M. Smith, 1938 emend. Schudack, 1993

Order **Charales** Lindley, 1836

Family **Raskyellaceae** Grambast, 1957

Sub-Family **Raskyelloideae**, Grambast et Grambast, 1955

Genus ***Raskyella*** (~~L. & N.~~Grambast et Grambast, 1954) emend. Grambast, 1962b

Type species. *Raskyella peckii* ~~L. & N.~~Grambast et Grambast, 1954

Remarks. This species is understood as including several traditional taxa belonging to the genus *Raskyella*~~ L. & N. Grambast (1954),~~, which form a gradualistic lineage during the Eocene. These traditional taxa have been newly combined here to anagenetic varieties within a single evolutionary lineage or an evolutionary species, following the recommendations of Wiley (1981) and Ax (1978).

Raskyella peckii var. ***peckii*** ~~L. & N.~~Grambast et Grambast, 1954

(Fig. 3A–H)

1954 *Raskyella pecki* sp. nov. L. & N. Grambast: p. 670, text-figs 1a–c.

1957 *Raskyella pecki* Grambast: p. 358, pl. 5, figs 7–9.

1958 *Raskyella pecki* Grambast: p. 190, figs 87, a–c; p. 191, text-fig. 88.

1959 *Raskyella pecki* Horn af Rantzien: pl. 19, figs 7–13.

1971 *Raskyella peckii* subsp. *ganesensis* Soulié-Märsche: pl. 2, 1–5.

1981 *Raskyella pecki* Anadón & Feist: pl. 1, figs 1–2; pl. 2, figs 3–4.

1986 *Raskyella pecki* Riveline: pl. 37, figs 7–9.

~~1999b~~1999a *Raskyella pecki* Martín-Closas *et al*.: p. 11, figs 6, 1–3.

Material. Up to 65 gyrogonites in sample G-2.4, and dozens in samples G-2.2 and G-2.3. Collection numbers of ~~figures~~figured specimens: HNHM-PBO ~~xxxxx-yyyyy~~1501–1508.

Description. Gyrogonites ~~of~~are ovoidal to ellipsoidal in shape, spherical to subprolate (ISI 100–120) and of large size, 800–1050 µm in height and 750–1050 µm in width, showing laterally 7–10 (usually 9) convolutions (Fig. 4). Spiral cells often flat (Fig. ~~3, A~~3A) to slightly convex (Fig. ~~3, C~~3C), or concave (Fig. ~~3, B~~3B), but regularly without any kind of ornamentation. Apex broadly rounded, truncated and flattened, with the spiral cells abruptly discontinue and ending acutely in the apical periphery to be replaced by the development of five ~~deciduous~~ opercular cells, each obliquely disposed at the end of a spiral cell (Fig. ~~3, F). In case of germinated~~

~~specimen~~3F). Germinated specimens (Fig. ~~3, G),~~3G) show a rose-shaped apical ~~pore appears~~opening. Internal casts of these gyrogonites were also found (~~Figs 3, E~~Fig. 3E).

Remarks. The contemporaneous unornamented gyrogonites of *Raskyella peckii* subsp. *ganesensis* Soulié-Märsche, 1971 from the Aquitaine basin (France) appear to represent a ~~relatively smaller~~ gyrogonite population of relatively smaller size within *R. peckii* var. *peckii* and both are here considered ~~here~~ synonymous. However, supplementary research on the type material is needed to verify this synonymy, since ~~this morphotype was not found in the studied Gánt material, nor elsewhere to date~~the morphotype *ganesesis* is only known from the type locality.

Additionally, the subspecies *Raskyella peckii* subsp. *meridionale* Grambast, 1960, is kept within the rank of subspecies due to its palaeogeographic restriction. The extremely large gyrogonites of this subspecies are limited to the southernmost biogeographic range of *Raskyella peckii*, i.e. Algeria (Grambast 1960; Mebrouk *et al*. 1997), and the Betic Domain ~~in~~of the Balearic Islands (Martín-Closas ~~*et al.*~~& Ramos 2005~~)~~).

Distribution. This is the first record of *R. peckii* var. *peckii* in Hungary~~,~~ and Central Europe. This variety is widely distributed in the Lutetian and lower Bartonian of southern Europe, mainly in France (L. ~~and~~& N. Grambast 1954; Grambast 1958; Soulié-Märsche 1971, 1974; Riveline 1984, 1986) and Spain (Anadón & Feist 1981; ~~Ramos-Guerrero *et al*. 1989;~~ Anadón *et al*. 1992; Martín-Closas *et al*. ~~1999b).~~1999a; Martín-Closas & Ramos 2005). The total range of this variety (early Lutetian–~~lower~~late Bartonian) has been characterized in the Eastern Ebro basin (~~Northeast Spain~~Catalonia) by Martín-Closas *et al*. (~~1999b~~1999) based on correlation with larger foraminifera (mainly *Nummulites*). Furthermore, *R. peckii* var. *peckii* has been also reported from North Africa, i.e. in the lower Eocene of Algeria (Gevin *et al*. 1974; Mebrouk *et* *al*. 1997; Vianey-Liaud 1994), in the late lower Eocene–early middle Eocene of Tunisia (Abdeljaoued *et al*. 1984) and in the Lutetian of Libya (Megerisi & Mamgain 1980).

-------------------------------- Figures 3, 4 near here-------------------------

Raskyella peckii var. ***caliciformis*** (Soulié-Märsche, 1974) comb. nov. Trabelsi ~~&~~et Martín-Closas

(Fig. 3I–P)

Basionym. *Raskyella caliciformis* Soulié-Märsche, 1974, Compte Rendu 96ème Congrès National des Sociétés Savantes, Toulouse, 1971, Section Science, 2, p. 114, text-figure 2 (pl. I), 1–5.

1974 *Raskyella caliciformis* sp. nov~~.~~., Soulié-Märsche: p. 112, pl. 1, figs 1–5.

1981 *Raskyella caliciformis*, Anadón & Feist: pl. 1, figs 6–7; pl. 2, figs 7–8.

Material. 63 gyrogonites in sample G-2.5. Collection numbers of ~~figures~~figured specimens: HNHM-PBO ~~xxxxx–yyyyy~~1509–1516.

Description. Large sized gyrogonites (650–1000 µm high and 750–1050 µm wide) of globular to oblate shape (ISI 80–105), showing laterally 6–9 (usually 8) convolutions (Fig. 5). Spiral cells flat to slightly concave ornamented with stout, vertical to slightly inclined, well individualized ~~tubercules~~tubercles (Fig. ~~3, I~~3I–K), which are the main diagnostic character of this variety. Apex broadly rounded to truncated showing five ~~deciduous~~ opercular cells placed at the end of the spiral cells. The opercular cells are sometimes convex and somewhat polygonal in shape (Fig. ~~3, N)~~3N), rather than rounded, which is the reason why the dehiscence ~~pore~~opening appears sometimes irregularly star-shaped (Fig. ~~3, O)~~3O), rather than rose-shaped (Fig. ~~3, M~~3L), as already noted by Soulié-Märsche (1974) in the type material. The internal cast of the gyrogonite (Fig. ~~3, M~~3M) shows ~~low and~~ straight ridges ~~delimiting~~perpendicular to the well~~-~~-marked, undulated spiral cells. This wavy surface is uncommon in the inside of other raskyellacean gyrogonites and is thought to correspond internally to the external tubercle ornamentation.

Distribution. This is the first record of *R. peckii* var. *caliciformis* in Hungary. It was previously described from the Bartonian of South France (Soulié-Märsche 1974; Riveline 1986), and from the lower Bartonian (Auversian local stage) of the Ebro Basin, ~~in~~ Catalonia, Spain (Anadón & Feist~~,~~ 1981; Anadón *et al.* 1992).

---------------------------------- Figure 5 near here------------------------

Raskyella peckii var. ***vadaszii*** (~~L. & N.~~Grambast et Grambast 1954) comb. nov. Trabelsi ~~&~~et Martín-Closas

(Fig. 6A–S)

Basionym. *Raskyella vadaszi* (Rásky) L. & N. Grambast (1954), Revue Générale de Botanique (61), p. 670.

1945 *Aclistochara vadaszi*, sp. nov. Rásky: p. 45, pl. II, figs 22–24.

1954 *Raskyella vadaszi*, comb. nov. L. and N. Grambast: p. 670.

1957 *Raskyella vadaszi*, Grambast: p. 358, pl. 5, figs 1–6.

1959 *Raskyella vadaszi*, Horn af Rantzien: pl. 20, figs 1–3.

1981 *Raskyella vadaszi*, Anadón & Feist: pl. 1, fig. 5; pl. 2, fig. 5.

1981 *Raskyella* aff. *vadaszi*, Anadón & Feist: pl. 1, figs 3–4; pl. 2, figs 1–2, 6.

1985 *Raskyella vadaszi*, Bignot *et al.*: p. 36, pl. 3, figs 8–11.

1986 *Raskyella vadaszi*, Riveline: pl. 37, figs 1–6.

Material. Hundreds of gyrogonites in samples G-6a and G-6b. Collection numbers of ~~figures~~figured specimens: HNHM-PBO ~~xxxxx-yyyyy~~1517–1534.

Description. Large sized gyrogonites (800–1150 µm ~~in width~~high and 800–1150 µm ~~in high~~wide) of oblate to ovoidal shape (ISI 80–120), showing laterally 7–10 (usually 9) convolutions (Fig. 7). Spiral cells often convex and ornamented with stout tubercles of different shapes and sizes, in most cases oriented parallel to the intercellular sutures (Fig. ~~6, A~~6A–C), or more rarely tilted 20–30° but keeping parallelism between adjacent nodules (Fig. ~~6, E~~6E–G), this being a diagnostic character of this morphotype. Three tubercle morphologies have been observed: (1) rounded ~~tubercules~~tubercles, well individualized in the upper half of the gyrogonite, but fused to neighbouring ~~tubercules~~tubercles in the lower half (Fig. ~~6, I~~6I–K), (2) elongated ~~tubercules~~tubercles more or less connected to each other and producing slightly wavy (undulated) sutures (Fig. ~~6, H~~6H), (3) irregularly alternating round and elongated tubercles (Fig. ~~6, A–D~~6D). Base of gyrogonite rounded (Fig. ~~6, C~~6C, J) to slightly tapered (Fig. ~~6, A~~6A, G) and showing a small, superficial and pentagonal basal pore, sometimes within a less-marked funnel (Fig. ~~6, Q~~6Q). Apex of gyrogonite truncated or broadly rounded ~~showing~~and covered by five ~~deciduous~~independent opercular cells at the end of the spiral cells. Opercular cells roughly prismatic, with its outer surface concave, flat or slightly convex (Fig. ~~6, L~~6L–M~~), leaving a rose-shaped dehiscence pore in germinated~~). Germinated specimens show a rounded or rose-like opening (Fig. ~~6, N~~6N–P). The inside of the gyrogonite allows observation of a characteristic crenulation of the intercellular sutures near their internal side (Fig. ~~6, R~~6R–S), while, to the outside, sutures are flat. Besides, this crenulation occurs also between the opercule cells themselves and between spiral and opercule cells as already described by Feist *in* Anadón ~~&~~and Feist (1981).

Distribution. *R. vadaszii* has been first described by Rásky (1945) from middle Eocene borehole samples (~~60m~~60 m depth) at Gánt, in beds roughly equivalent laterally to the outcrop succession studied here. Therefore, the samples studied may be considered ~~as~~ topotypes. Subsequently, the age of this variety was suggested to be upper Bartonian by Bignot *et al.* (1985) based on the ~~basis of the~~ associated microfossils (foraminifers, ostracods, and pollen) from the same beds of the bauxite cover-sequence at the Gánt section (Vértes Hills). *R. peckii* var. *vadaszii* has also been ~~also~~ well documented in France, in the upper Bartonian of the Paris Basin (Grambast 1957, 1958, 1962a; Riveline 1986) and ~~in~~from several basins ~~from~~in southern France (Feist-Castel 1976). Anadón & Feist (1981) and Anadón *et al.* (1992) documented ~~also~~ this variety also in the upper Bartonian of the Eastern Ebro Basin (Catalonia, Spain).

---------------------------------- Figures 6, 7 near here-------------------------

Family **Characeae** (Richard ex C.A. Agardh, 1824) emend. Martín-Closas ~~and~~et Schudack, 1991

Subfamily **Charoideae** Braun *in* Migula, 1897

Genus ***Gyrogona*** (Lamarck, 1804 *ex* Lamarck, 1822) emend. Grambast, 1956

Gyrogona caelata (Reid ~~&~~et Groves, 1921) Grambast, 1956

(Fig. 8A–V)

1921 *Chara caelata* sp. nov~~.~~., Reid & Groves: p. 184, pl. 4, figs 4–6.

1927 *Kosmogyra caelata*, Pia: p. 90.

1954 *Brachychara caelata*, L. & N. Grambast: p. 667.

1956 *Gyrogona caelata*, Grambast: p. 280.

1977b *Gyrogona caelata*, Feist-Castel: p. 117.

1981 *Gyrogona caelata*, Grambast & Grambast-Fessard: p. 22, text-fig. 11, a–f; pl. 4, figs 1–9.

1981 *Gyrogona* cf. ~~*caelata*~~*Caelata*, Anadón & Feist: p. 163.

1986 *Gyrogona caelata*, Riveline: pl. 38, figs 1–5, 7–8.

1989 *Gyrogona caelata*, Choi: pl. 2, figs 1–11.

1991 *Gyrogona caelata*, Weidmann *et al*.: p. 900, fig. 3, C.

2014 *Gyrogona caelata*, Sanjuan & Martín-Closas: p. 403, fig. 7, A–C.

Material. ~~Up to 100~~56 gyrogonites in ~~samples~~sample G-2.2, 38 in sample G-2.3, 29 in sample G-2.4, 18 in sample G-2.5, and 23 in sample G-6a. Collection numbers of ~~figures~~figured specimens: HNHM-PBO ~~xxxxx–yyyyy~~1535–1553.

Description. Medium to large gyrogonites, 600–800 µm high and 700–1000 µm wide with generally oblate to suboblate spheroidal shape (ISI 80–100) and showing laterally 5–7 (usually 6) convolutions (Fig. 9). Apex and base broadly rounded to subtruncate. Apex showing a less-marked spiral cell periapical thinning (e.g~~.~~., Fig. ~~8, R),~~8G) and, in some specimens, apical nodules of different shape, generally flat or slightly convex (e.g. Fig. ~~8, S~~8S). Base showing a small pentagonal basal pore (Fig. ~~8, G~~8F), sometimes flared by a shallow funnel (Fig. ~~8, P~~8P). Basal plate unicellular and only visible from the gyrogonite interior (Fig. ~~8, U~~8U–V). Spiral cells flat to slightly concave and ornamented with different patterns of ~~tubercules~~tubercles, which ~~allow distinction of a number of morphotypes (~~allowed Grambast~~,~~ (1958~~; Grambast~~) and Grambast & Grambast-Fessard~~,~~ (1981~~), from which~~) to distinguish a number of morphotypes, ranking them as *formae* of the same species. The following five forms were recognized in the material studied: (1) *G. caelata* forma *caelata* characterized by small nodules well-spaced and irregularly ranged along the spiral cell median line (e.g. Fig. ~~8, A, D), (2) *G. caelata* forma *monolifera* showing medium-sized nodules close to each other, sometimes fused forming a thin, irregular mid-cellular crest (e.g. Fig. 8, L), (3) *G.*~~8A, D), (2) *G. caelata* forma *bicincta* characterized by nodules irregularly ranged along two lines parallel to spiral cell sutures (Fig. ~~8, H, I), (4) *G.*~~8H, I), (3) *G. caelata* forma *monolifera* showing medium-sized nodules close to each other, sometimes fused and forming a thin, irregular mid-cellular crest (e.g., Fig. 8L), (4) *G.* *caelata* forma *baccata* characterized by large nodules very closely ranged along the spiral-cell median line (e.g~~.~~., Fig. ~~8, N~~8N–Q), (5) *G. caelata* forma *fasciata* characterized by a broad median band of variable width (e.g~~.~~., Fig. ~~8, R~~8R–T).

Distribution. The species *Gyrogona caelata* is ~~first~~ reported here from Hungary for the first time. According to Riveline (1986), this species was widely distributed in the upper Lutetian–Priabonian non-marine deposits of Western Europe. It was first recorded from the Isle of Wight, England by Reid & Groves (1921). Thereafter, it was reported from the upper Lutetian to upper Priabonian of France (Grambast 1958; Grambast & Grambast-Fessard 1981; Feist-Castel 1971; Feist & Ringeade 1977; Feist-Castel 1977a, b; Ollivier-Pierre *et al*. 1988), Spain (Anadón & Feist 1981; Choi 1989; Anadón *et al*. 1992; Sanjuan & Martín-Closas 2014), Switzerland (Weidmann *et al*. 1991), as well as from the middle Eocene of Romania (Iva 1987). In North Africa, the species has also been documented from the central part of the Sahara, Algeria, by Mebrouk *et al*. (1997).

---------------------------------- Figures 8, 9, near here-------------------------

Gyrogona tuberosa (Reid ~~&~~et Groves, 1921) Grambast *in* Grambast ~~&~~et Grambast-Fessard, 1981

(Fig. 10A–J)

1921 *Chara wrighti* var. *rhytidocarpa*, Reid & Groves: p. 183, pl. 4, fig. 3.

1958 *Gyrogona tuberosa*, Grambast: p. 139, fig. 54.

1976 *Gyrogona tuberosa*, Feist-Castel: p. 26.

1981 *Gyrogona tuberosa*, Grambast & Grambast-Fessard: p. 25, text-fig. 12, a–d; pl. 5, figs 1–6.

1986 *Gyrogona tuberosa*, Riveline: pl. 14, figs 8–11.

Material. 35 gyrogonites in ~~samples G-6b.~~sample G-6b. Collection numbers of figured specimens: HNHM-PBO 1554–1563.

Description. Large gyrogonites, 820–1000 µm high and 835–1050 µm wide with generally oblate to suboblate spheroidal shape (ISI 80–100) and showing laterally 6–7 convolutions (usually 6). Apex subtruncate (Fig. ~~10, A~~10A, C) to somewhat ~~prominent and~~ pointed (Fig. ~~10, D~~10D, G) with spiral cells protruding (Fig. ~~10, H~~10H). Base broadly rounded (Fig. ~~10, B~~10B, F) to slightly tapered (Fig. ~~10, A~~10A, C, E) and showing a small, superficial and pentagonal basal pore, sometimes within a less-marked funnel (Fig. ~~10, I~~10I–J). Spiral cells flat or concave, smooth or somewhat ornamented and separated by protruding narrow to weakly undulated intercellular ridges.

Distribution. *Gyrogona tuberosa* is ~~first~~ reported here from Hungary~~,~~ and ~~from~~ central Europe for the first time. According to Riveline (1986) and Riveline & Cavelier (1987), this species was widely distributed in upper Bartonian non-marine deposits of Western Europe. It was first recorded from the Isle of Wight and Hampshire (England) by Reid & Groves (1921). ~~Thereafter~~Subesequently, it was reported from the upper Bartonian of the Paris Basin (Grambast 1958; Grambast & Grambast-Fessard 1981; Riveline 1986; Riveline & Cavelier 1987), as well as ~~in~~from several basins ~~from~~of southern France (Feist-Castel 1976).

---------------------------------- Figure 10 near here-------------------------

Genus ***Psilochara*** Grambast, 1959

Psilochara polita (Reid ~~&~~et Groves, 1921) Grambast, 1959

(Fig. 11A–F)

1921 *Chara polita*, sp. nov. Reid & Groves: p. 187, pl. 5, figs 9, 12.

1927 *Gyrogona politus*, Pia: p. 90.

1958 *Ovochara polita*, comb. nov. Grambast: p. 167.

1959 *Peckichara polita*, Horn af Rantzien: p. 116, pl. 13, figs 1–3.

1959 *Psilochara polita*, Grambast: p. 11.

1977b *Psilochara polita*, Feist-Castel: p. 153.

1986 *Psilochara polita*, Riveline: p. 59, pl. 22, figs 8–12.

Material. 58 gyrogonites in sample G-6a. Collection numbers of ~~figures~~figured specimens: HNHM-PBO ~~xxxxx–yyyyy~~1564–1569.

Description. Medium~~-~~-sized gyrogonites (~~520–830 µm in width and 580–710~~550–700 µm in height 500–650 and µm in width) with ovoidal shape (ISI ~~105~~100–120) and laterally showing 7–~~8~~10 convolutions (Fig. ~~11, A~~11A–C; Fig. 12). Apex round to pointed (Fig. ~~11, A~~11A–C). Base tapering to prolonged into a stout basal column (Fig ~~11, A~~11A–C) and showing a small pentagonal basal pore (Fig. ~~11, F~~11F). Spiral cells smooth, concave or flat and separated by protruding narrow to weakly undulated intercellular ridges.

Distribution. *Psilochara polita* is ~~first~~ described here from the middle Eocene of Hungary~~.~~ for the first time. It has previously been described ~~previously~~ from the upper Bartonian of the Isle of Wight, England, (Reid & Groves 1921; Feist-Castel 1977b; Riveline 1986) ~~as well as~~and of the Paris Basin (Grambast 1958; Riveline 1986).

---------------------------------- Figures 11, 12 near here------------------------

***Psilochara* sp.**

(Fig. 11G–I)

Material. 17 gyrogonites in sample G-6a. Collection numbers of ~~figures~~figured specimens: HNHM-PBO ~~xxxxx–yyyyy~~1570–1571.

Description. Medium to large-sized gyrogonites (780–905 µm wide and 670–775 µm high) with elongated ovoidal (subprolate) shape (ISI 110–125) and laterally showing 8–10 convolutions (Fig. ~~11, G~~11G). Apex truncated. Apical end of spiral cells enlarged and pointing upwards (Fig. ~~11, H~~11H). Base truncated to somewhat tapering, bearing a small pentagonal basal pore. Basal plate unipartite and visible from the gyrogonite interior (Fig. ~~11, I~~11I). Spiral cells concave or flat and smooth, except at the periapical area, where they are irregularly ornamented with a broad mid-cellular crest.

~~**Distribution.** *Psilochara* sp. is described here first time from the upper Eocene (upper Bartonian) of Hungary.~~

Remark. The low number of gyrogonites hinders a more precise taxonomic attribution of this population. However, it is reported here since it differs in size and shape from the other species of *Psilochara* found at Gánt.

Genus ***Nitellopsis*** Hy, 1889

~~Sous-genre~~Sub-genus ***Tectochara*** L. ~~and~~et N. Grambast, 1954

Nitellopsis* (*Tectochara*) aff. *palaeohungarica (Rásky, 1945) Grambast ~~&~~et Soulié-Märsche, 1972

(Fig. 11J–N)

1945 *Chara palaeohungarica*, sp. nov. Rásky: p. 38, pl. 1, figs 16–18.

1955 *Tectochara palaeohungarica*, comb. nov. Mädler: p. 298.

1959 *Tectochara palaeohungarica*, Horn af Rantzien: p. 90, pl. 8, figs 4–7.

1972 *Nitellopsis (Tectochara) palaeohungarica*, nov. comb. Grambast & Soulié-Märsche: p. 4.

Material. ~~61~~28 gyrogonites in ~~both samples~~sample G-2.3 and 33 in sample G-2.5. Collection numbers of ~~figures~~figured specimens: HNHM-PBO ~~xxxxx-yyyyy~~1572–1576.

Description. ~~Very~~Gyrogonites very large ~~gyrogonites~~ (900–1200 µm high and 800–1050 µm wide), oval, prolate spheroidal (ISI 100–120) ~~pear-shaped and~~in shape, showing 8–11 (often 9) convolutions in lateral view (Fig. ~~11, J~~11J–L; Fig. 13). Spiral cells concave to flat. Apex prominent with spiral cells protruding to form a central rosette. Spiral cells show both ~~shortening~~narrowing and thinning in the periapical area (Fig. ~~11, M~~11M). Base rounded to almost conical, occasionally lengthened in a short broad column. A large (155–230 µm across) pentagonal basal pore occurs within a wide basal funnel (Fig. ~~11, N~~11N).

Distribution. The species ~~*Tectochara*~~*'Chara' palaeohungarica* was first described from subsurface beds attributed to the Paleocene in Dorog, Hungary, by Rásky (1945). Here this species is described from beds cropping out ~~in~~at Gánt, which are probably time-equivalent to those of the type locality. The present study ~~allows reassigning~~supports reassignment of this species to the middle Eocene rather than to the Paleocene.

Remarks. The gyrogonites studied here are diagenetically deformed, which hinders a more definitive taxonomic attribution. A re-study of the type material (HNHM 55.1458–55.1460) by one of the authors of this study (CMC) showed that, besides the holotype, which is a subspherical gyrogonite as illustrated by Rásky (1945, pl. I, Fig. 16), there were more oval to elongated gyrogonites present in the collection similar to those described here, which Rásky (1945, p. 38) termed 'cylindrical'.

---------------------------------- Figure13 near here-------------------------

Genus ***Chara*** Vaillant, 1719

Chara media Grambast, 1958

(Fig. 14A–I)

1958 *Chara media*, Grambast: p. 178, fig. 81b.

1986. *Chara media*, Riveline: p. 68, pl. 29, figs 6–12.

Material. Up to 80 gyrogonites in both samples G-2.5 and G-6a. Collection numbers of ~~figures~~figured specimens: HNHM-PBO ~~xxxxx–yyyyy~~1577–1585.

Description. Gyrogonites of medium size (400–650 µm high and 300–500 µm wide) ellipsoidal subprolate (ISI 110–145), laterally showing ~~lateraly~~ 8–11 (usually 9–10) convolutions (Fig. ~~14, A~~14A–G, Fig. 15). Maximum width nearly at the half to 2/3 of height. Apex rounded to slightly conical, with distinctly widening of the spiral cell endings (Fig. ~~14, H~~14H). Spiral cells concave, smooth and without any periapical modification. Base tapering showing a superficial pentagonal basal pore (Fig. ~~14, I~~14I).

Distribution. *Chara media* is ~~first time~~ described here from the upper Eocene (upper Bartonian) of Hungary for the first time. Grambast (1958) and Riveline (1986) documented this species from the upper Bartonian–lower Oligocene of several basins in France, Belgium, and Germany.

---------------------------------- ~~Figures14~~Figures 14, 15 near here-------------------------

Chara subcylindrica Reid ~~&~~et Groves, 1921

(Fig. 14J–O)

1921 *Chara subcylindrica*, sp. nov. Reid & Groves: p. 187, pl. 5, fig. 4–5.

1959 *Grambastichara subcylindrica*, Horn af Rantzien: p. 76, pl. 3, figs 5–7.

1986 *Chara* cf. *subcylindrica*, Riveline: p. 67, pl. 30, figs 5–8.

Material. Up to 250 gyrogonites in sample G-6b. Collection numbers of ~~figures~~figured specimens: HNHM-PBO ~~xxxxx–yyyyy~~1586–1591.

Description. Medium-sized gyrogonites (500–750 µm high and 200–400 µm wide) ellipsoidal prolate to perprolate (ISI 130–200~~),~~) in shape, laterally showing 8–11 (usually 9–10) convolutions (Fig. ~~14, J~~14J–M; Fig. 16). Maximum width at the equator. Apex rounded with widening of the spiral cell endings (Fig. ~~14, N~~14N). Spiral cells often slightly concave to flat, separated by narrow intercellular ridges, cells non-ornamented and without any periapical modification. Base regularly tapering to round, showing a superficial pentagonal basal pore (Fig. ~~14, O~~14O).

Distribution. This is the first report of *Chara subcylindrica* in ~~the upper Eocene (upper Bartonian) of~~ Hungary. According to Reid ~~and~~& Groves (1921) and Riveline (1986), this species occurs in the upper Bartonian–lower Oligocene of England, France, Belgium and Germany.

------------------------------------- Figure 16 near here ------------------------

Discussion

Definition of the *Raskyella peckii* anagenetic lineage

Evolutionary lineages formed by a succession of charophyte fructifications changing gradually in time ~~have been~~were first described in the family Clavatoraceae by Grambast (1974). Later, similar lineages were found as well in the family Characeae (e.g. lineage *Harrisichara vasiformis-tuberculata* described by Feist-Castel 1977b; or lineage *Peckichara pectinata* by Vicente *et al*. 2018). ~~The~~ Here we describe the first ~~one~~of such ~~lineage is described here~~lineages in the family Raskyellaceae. ~~Three~~In the Lutetian and Bartonian of Gánt (Hungary), three former species of the genus *Raskyella*~~,~~ – *R. peckii, R. caliciformis*, and *R. vadaszii*~~,~~ – have been found ~~in the Lutetian and Bartonian of Gánt (Hungary)~~ to form a continuous succession of gyrogonite morphologies, connected by intermediate morphotypes. This gradualistic lineage is interpreted as an evolutionary species in the sense of Wiley (1981) and Ax (1987), and the original taxa have been newly combined as anagenetic varieties of the species with nomenclatural priority, which is *R. peckii*.

The first evolutionary stage of the *R. peckii* lineage (Fig. 17) is represented by *R. peckii* var. *peckii,* and includes, as well, the smallest gyrogonite morphotype initially described as *Raskyella peckii* ~~*ganesesis*~~*ganesensis* Soulié-Märsche, 1971. *R. peckii* var. *peckii* is characterized by gyrogonites which are very variable in size, but ~~consistenly~~consistently unornamented. This stage has a long duration, since it ~~has been~~was documented from the lower Lutetian to the ~~lower~~upper Bartonian of the Ebro ~~basin~~Basin, Catalonia, by Martín-Closas *et al*. (~~1999b~~1999a) and can thus be superimposed ~~to~~onto some of the ulterior morphotypes of the lineage~~.~~, this being quite a common situation in charophyte lineages (e.g., Grambast, 1974). The coeval *Raskyella peckii* subsp. *meridionale* Grambast, 1960, was not found in the section studied and corresponds to a southern geographic subspecies of this lineage, thriving in North Africa and the Prebetic Domain in the Balearic Islands in Spain (Grambast 1960; Martín-Closas ~~*et al*. 2004~~& Ramos 2005).

The second ~~step~~evolutionary stage in the lineage of *R. peckii* is represented by *R. peckii* var. *caliciformis*. Intermediate morphotypes between *R. peckii* var. *peckii* and *R. peckii* var. *caliciformis* display a progressive increase in the gyrogonite size (up to 1000 µm in ~~high~~height), and a change in shape from elongated to rounded, between samples G-2.2 and G-2.4 of the Gánt section. Furthermore, there is a progressive development of the ornamentation corresponding to *R. peckii* var. *caliciformis* in the same sequence, with for instance 100% of gyrogonites corresponding to *R. peckii* var. *peckii* in sample G-2.4, while in sample G-2.5, there is only 10% of *R. peckii* var. *peckii*~~ for~~, resulting in 90% of *R. peckii* var. *caliciformis* (Fig. 17).

The third stage of the lineage is represented by *R. vadaszii*~~,~~ from the upper Bartonian, which shows an additional increase of the gyrogonite size of about 150–250 µm in height and 100–

125 µm in width, and especially the development of progressively more complex ornamentation patterns in comparison to the previous evolutionary step (Fig. 17). This gradual change can be observed between samples G-2.5 and G-6b of the Gánt section. Thus, sample G-5 displays a homogeneous population with 100% of gyrogonites corresponding to *R. peckii* var. *caliciformis*, while in the overlying sample G-6a, the gyrogonite population of *R. peckii* contains only 15% of specimens of *R. peckii* var. *caliciformis* and 85% of *R. peckii* var. *vadaszii*. Finally, in sample G-6b there is a homogeneous population of gyrogonites corresponding to *R. peckii* var. *vadaszii*.

Overall, the *R. peckii* lineage follows the general evolutionary trend in the evolutionary lineages ~~from~~of other charophyte families, characterized by an increase in size and sphericity (Clavatoraceae and Raskyellaceae), and a progressive development of ornamentation (Characeae~~)~~), as shown by Feist-Castel (~~1977~~1977b), Martín-Closas *et al.* (1999b), Sille *et al.* (2004) and Vicente & Martín-Closas (2018).

------------------------------------- Figure 17 near here ------------------------

New local charophyte biozonation

Among the ~~charophytes~~charophyte species described from the bauxite cover-sequence at the Gánt section (Vértes Hills, Hungary), *Raskyella peckii* represents the most significant species ~~in terms of biostratigraphy~~ for use in biostratigrpahy within the non-marine Lutetian and Bartonian, as previously suggested by Riveline *et al.* (1996) and Martín-Closas *et al.* (1999a). The *Raskyella peckii* biozone was defined by ~~the latter authors (p. X~~Riveline *et al.* (1996) as a 'partial range zone comprising the interval from the first appearance of *Raskyella peckii* L. and

N. Grambast, 1954, to the first appearance of *Chara friteli* Grambast, ~~1958’~~1958, lower Lutetian to lower Bartonian in age. This study proposes to extend this biozone to cover also the upper Bartonian, and to ~~rename~~redesignate it as a superzone subdivided into the following three successive biozones (Fig. 18):

- **Raskyella peckii peckii** ~~**zone**~~**Zone**: partial range zone defined from the first occurrence of the morphotype *peckii* to the first occurrence of the morphotype *caliciformis*, Lutetian–lower Bartonian in age. The local charophyte assemblage characterizing this zone in Gánt occurs in the basal part of the studied section (‘Packet 2’, ‘blue-hole’ freshwater limestone facies, samples G-2.2, G-2.3 and G-2.4), and is composed of *R. peckii* var. *peckii*, *G. caelata* forma *caelata*, *G. caelata* forma *monolifera*, and *Nitellopsis (Tectochara)* aff. *palaeohungarica*, some of which are well known to occur in several European basins (Rásky 1945; Grambast 1958; Riveline 1986; Martín-Closas *et al.* 1999a) during the same time interval.

- **Raskyella peckii caliciformis** ~~**zone**~~**Zone**: partial range zone defined from the first occurrence of the morphotype *caliciformis* to the first occurrence of the morphotype *vadaszii*, lower Bartonian in age. This zone includes in Gánt the assemblage found in the lower part of ‘Packet 3’ (samples G-2.5) and composed of *R. peckii* var. *caliciformis*, *G. caelata* forma *caelata*, *G. caelata* forma *monolifera*, *G. caelata* forma *baccata*, *Nitellopsis (Tectochara)* aff. *palaeohungarica*, and *Chara media*.

- **Raskyella pecki vadaszii** ~~**zone**~~**Zone**: partial range zone defined from the first occurrence of the morphotype *vadaszii* to the first occurrence of the next zone defined in the Paris Basin, which is *Psilochara repanda*. This zone would be upper Bartonian in age. The assemblage occurring in the middle part of the Gánt section (‘Packet 3’, samples G-6a and G-6b), composed of *R. peckii* var. *vadaszii*, *G. caelata* forma *bicincta*, *G. caelata* forma *baccata*, *G. caelata* forma *fasciata*, *Psilochara polita*, *Psilochara* sp., *Chara media*, and *Chara subcylindrica* characterizes locally this biozone.

Implications on the age of the bauxite cover-sequence

The biostratigraphic analysis carried out ~~allows suggesting~~suggests a relative age of Lutetian–Bartonian (Fig. 18) ~~to~~of the ~~studied~~ bauxite cover-sequence at the Gánt section (Vértes Hills, Hungary~~)~~), rather than ~~uniquely uppermost middle Eocene (~~constraining it to the Bartonian~~)~~ as previously suggested by Bignot (1985). ~~Thus, the~~A Lutetian age, deduced from the charophytes and attributed to the lower part of the studied series~~ herein from the TCR~~, has been already suggested in several works preceding that of Bignot (1985), notably those of Szőts (1938), Kopek (1980~~)~~), and Dudich & Kopek (1982~~).~~), on the basis of mollusc and palynomorph biostratigraphy. The data presented herein support the idea that the Eocene succession in the studied area reflects a stepwise marine transgression ~~beginning since the Lutetian, early Eocene~~ upon the bauxite deposits~~. Such a~~, beginning in the Lutetian. Our new chronostratigraphic framework sheds new light on the timing of the long-lasting subaerial exposure and alteration process generating the bauxite strata~~, which stratigraphically seems to occur at a major regional unconformity between late Triassic and early Eocene rather than in the middle Eocene as previously assumed by Mindszenty (2010).~~. Consequently, ~~it will be significant to review the~~ coeval strata from ~~the~~ surrounding localities within the ~~TCR~~Transdanubian Central Range should be re-studied and analysed from the viewpoint of charophyte~~-based~~ biostratigraphy~~ point of view~~, in order to ~~establish a regional charophyte biozonation scheme allowing better understanding of the regional stratigraphic correlation of~~correlate the post-bauxite ~~sedimentary~~depositional event(s) on a regional scale and ~~their associated~~to improve the understanding of its tectono-eustatic control.

---------------------------------- Figure 18, near here----------------------

Conclusions

Eocene (Lutetian–Bartonian) charophyte assemblages are taxonomically described for the first time from an outcrop of the bauxite cover-sequence at ~~the~~ Gánt ~~section~~ (Vértes Hills), Hungary's Transdanubian Central Range. ~~This section shows~~The sections show for the first time that ~~Raskyellaceae did~~the raskyellacean charophytes also ~~evolve~~evolved in gradualistic lineages, similarly ~~as it was~~to what is already known for other charophyte families. The *Raskyella peckii* lineage is formed by three successive stages and is interpreted here in terms of the ~~anagenetic evolution~~anagenesis of the evolutionary species *Raskyella peckii*, including its gradual change to the morphotype previously known ~~formerly~~ as *R. vadaszi*.

From ~~the biostartigraphic~~a biostratigraphic viewpoint, the assemblages studied belong to the *Raskyella peckii* biozone of Martín-Closas *et al*. (~~1999b~~1999a), which is here reinterpreted ~~here~~ as a superzone extending to cover the *Raskyella vadaszii* ~~zone~~Zone of Riveline *et al*. (1996) and ~~therefore~~ attributed to the Lutetian–Bartonian interval ~~age. This~~. In this study, this superzone is subdivided ~~herein~~ into three successive local partial range biozones, defined by each of the successive varieties of the evolutionary species *R. peckii*: (1) the *Raskyella peckii peckii* partial range zone is ~~formed~~characterized by *R. peckii peckii*, *G. caelata* forma *caelata*, *G. caelata* forma *monolifera* and *Nitellopsis (Tectochara)* aff. *palaeohungarica*, Lutetian–lowermost Bartonian in age; (2) the *Raskyella peckii caliciformis* partial range zone is ~~formed~~characterized by *R. peckii caliciformis*, *G. caelata* forma *caelata*, *G. caelata* forma *monolifera*, *G. caelata* forma *baccata*, *Nitellopsis (Tectochara)* aff. *palaeohungarica* and *Chara media*, lower Bartonian in age; and (3) the *Raskyella peckii* ~~*vadaszi*~~*vadaszii* partial range zone is ~~formed~~characterized by *R. peckii vadaszii*, *G. caelata* forma *bicincta*, *G. caelata* forma *baccata*, *G. caelata* forma *fasciata*, *G. tuberosa*, *Psilochara polita*, *Psilohara* sp., *Chara media* and *Chara subcylindrica*, upper Bartonian in age.

In~~ the~~ light of the new results presented here, the ~~studied ~~charophyte-bearing sequences studied in this work represent a ~~larger~~longer time span than previously thought, ~~lasting during ~~running from the Lutetian ~~and~~to the Bartonian~~,~~. This has direct implications ~~in~~on the understanding of the Eocene regional stratigraphic scheme of the Transdanubian Central Range~~ during the Eocene~~, particularly in terms of synchronism/diachronism~~,~~ in the regional~~/supraregional~~ stratigraphic correlation, as well as the timing of the tectono-sedimentary control and palaeogeographic ~~reconstitution. ~~evolution.

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Figure Captions

Figure 1. A, geographical and geological setting of the study area (after Fodor 2007). **B**, panoramic view of the studied Gánt section at the Vértes Hills (north-western Hungary).

Figure 2. Distribution of the charophytes species in the bauxite cover-sequence ~~from~~of the studied Gánt section (Vértes Hills, Hungary), according to Bignot *et al*. (1985~~).~~), updated for charophyte content.

Figure 3. ~~Gyrogonites of species~~ *Raskyella peckii* gyrogonites from the Gánt bauxite cover-sequence. **A–H**, *Raskyella pecki* var. *peckii* (samples G-2.2, G-2.3, G-2.4~~,~~ and G-2.5~~).~~), HNHM-PBO 1501–1508. **A–E**, lateral view; **F–G**, apical view; **H**, basal view. **I–P**, *Raskyella peckii* var. *caliciformis* (~~sample~~samples G-2.5~~,~~ and G-6a~~).~~), HNHM-PBO 1509–1516. **I–K**, lateral view; **L**, lateral view of gyrogonite partially ~~devoided from external layer~~broken

showing ~~the oospore.~~internal cast. **M**, ~~the oospore~~internal cast with well-developed undulations. **N–O**, apical view; **P**, basal view~~. Specimen numbers HNHM-PBO xxxxx-yyyyy will be added for each respective specimen~~.

Figure 4. Frequency distribution of the ~~length~~height (A), width (B), number of convolutions (C), ~~length~~and height/width ratio (ISI) (D) of the *Raskyella peckii* var. *peckii* population (50 gyrogonites measured), from samples G-2.2, G-2.3, and G-2.4 in the bauxite cover-sequence of the Gánt section.

Figure 5. Frequency distribution of the ~~length~~height (A), width (B), number of convolutions (C), ~~length~~and height/width ratio (ISI) (D) of the *Raskyella peckii* var. *caliciformis* population (50 gyrogonites measured), from sample G-2.5 in the bauxite cover-sequence of the Gánt section.

Figure 6. ~~Gyrogonites of species~~ *Raskyella peckii* *vadaszii* gyrogonites from the Gánt bauxite cover-sequence~~.~~ (**A–S,** ~~*Raskyella peckii* var. *vadaszii* (~~samples G-6a and G-6b, HNHM-PBO 1517–1534). **A–K**, lateral view. **L–P**, apical view; **Q**, basal view; **R–S**, inside wall of a gyrogonite showing the crenate undulation of the cellular sutures in contact with the spiral cells and the apical cells.~~ Specimen numbers HNHM-PBO xxxxx-yyyyy will be added for each respective specimen.~~

Figure 7. Frequency distribution of the ~~length~~height (A), width (B), number of convolutions (C), ~~length~~and height/width ratio (ISI) (D) of the *Raskyella peckii* var. *vadaszii* population (50 gyrogonites measured), from samples G-6a and G-6b in the bauxite cover-sequence of the Gánt section.

Figure 8. ~~Gyrogonites of species~~ *Gyrogona caelata* gyrogonites from the Gánt bauxite cover-sequence. **A–G**, *Gyrogona caelata* forma *caelata* (samples G-2.2, G-2.3, G-2.4, and G-2.5~~).~~), HNHM-PBO 1535–1553. **A–B**, **D–E**, basal view **C**, detail of the ornamentation pattern; **F**, basal view; G, apical view. **H–K**, *Gyrogona caelata* forma *bicincta* (samples G-6a~~,~~ and G-6b). **H**, lateral view; **I**, detail of the ornamentation pattern; **J–K**, apical view. **L–M**, *Gyrogona caelata* forma *monolifera* (samples G-2.2, G-2.3, G-2.4, and G-2.5). **L**, lateral view; **M**, basal view. **N–Q**, *Gyrogona caelata* forma *baccata* (samples G-2.5, G-6a, and G-6b). **N–O**, lateral view; **P**, basal view; **Q**, apical view. **R–V**, *Gyrogona caelata* forma *fasciata* (samples G-6a~~,~~ and G-6b). **R**, lateral view; **S–T**, apical view; **U–V**, detail of the simple (unipartite) basal plate~~. Specimen numbers HNHM-PBO xxxxx-yyyyy will be added for each respective specimen~~.

Figure 9. Frequency distribution of the ~~length~~height (A), width (B), number of convolutions (C), ~~length~~and height/width ratio (ISI) (D) of the *Gyrogona caelata* population (50 gyrogonites measured), from samples G-2.2, G-2.3, G-2.4, G-2.5, and G-6a in the bauxite cover-sequence of the Gánt section.

Figure 10. ~~Gyrogonites of species~~ *Gyrogona tuberosa* gyrogonites from the Gánt bauxite cover-sequence (~~samples~~sample G-6b~~).~~), HNHM-PBO 1554–1563. **A–G**, lateral view; **H**, apical view; **I–J**, basal view. ~~Specimen numbers HNHM-PBO xxxxx-yyyyy will be added for each respective specimen.~~

Figure 11. Gyrogonites of ~~genus~~genera *Psilochara* and *Nitellopsis* from the Gánt bauxite cover-sequence. **A–F**, *Psilochara polita* (~~samples~~sample G-6a~~).~~), HNHM-PBO 1564–1569. **A–C**, lateral view; **D–E**, apical view; **F**, basal view. **G–I**, *Psilochara* sp. (~~samples~~sample G-6a~~).~~), HNHM-PBO 1570–1571. **G**, lateral view; **H**, apical view; **I**, internal view showing simple (unipartite) basal plate (arrowed). **J–N**, *Nitellopsis (Tectochara)* aff. *palaeohungarica* (samples G-2.3 and G-2.5~~).~~), HNHM-PBO 1572–1576. **J–L**, lateral view; **M**, apical view; **N**, basal view~~. Specimen numbers HNHM-PBO xxxxx-yyyyy will be added for each respective specimen~~.

Figure 12. Frequency distribution of the ~~length~~height (A), width (B), number of convolutions (C), ~~length~~and height /width ratio (ISI) (D) of the *Psilochara polita* population (50 gyrogonites measured), from sample G-6a in the bauxite cover-sequence of the Gánt section.

Figure 13. Frequency distribution of the ~~length~~height (A), width (B), number of convolutions (C), ~~length~~and height /width ratio (ISI) (D) of the *Nitellopsis (Tectochara)* aff. *palaeohungarica* population (50 gyrogonites measured), from samples G-2.3 and G-2.5 in the bauxite cover-sequence of the Gánt section.

Figure 14. ~~Gyrogonites of genus~~ *Chara* gyrogonites from the Gánt bauxite cover-sequence. **A–I**, *Chara media* (samples G-2.5 and G-6a~~).~~), HNHM-PBO 1577–1585. **A–G**, lateral view; **H**, apical view; **I**, basal view. **J–O**, *Chara subcylindrica* (~~samples~~sample G-6b~~).~~), HNHM-PBO 1586–1591. **J–M**, lateral view; **N**, apical view; **O**, basal view. ~~Specimen numbers HNHM-PBO xxxxx-yyyyy will be added for each respective specimen.~~

Figure 15. Frequency distribution of the ~~length~~height (A), width (B), number of convolutions (C), ~~length~~and height /width ratio (ISI) (D) of the *Chara media* population (50 gyrogonites measured), from samples G-2.5 and G-6a in the bauxite cover-sequence of the Gánt section.

Figure 16. Frequency distribution of the ~~length~~height (A), width (B), number of convolutions (C), ~~length~~and height/width ratio (ISI) (D) of the *Chara subcylindrica* population (50 gyrogonites measured), from ~~samples~~sample G-6b in the bauxite cover-sequence of the Gánt section.

Figure 17. Stratigraphic distribution of variants of the anagenetic ~~evolutionary~~ lineage of the species *Raskyella peckii*.

Figure 18. Charophyte Biostratigraphy, age and correlation of the bauxite cover-sequence ~~from~~of the Gánt section.

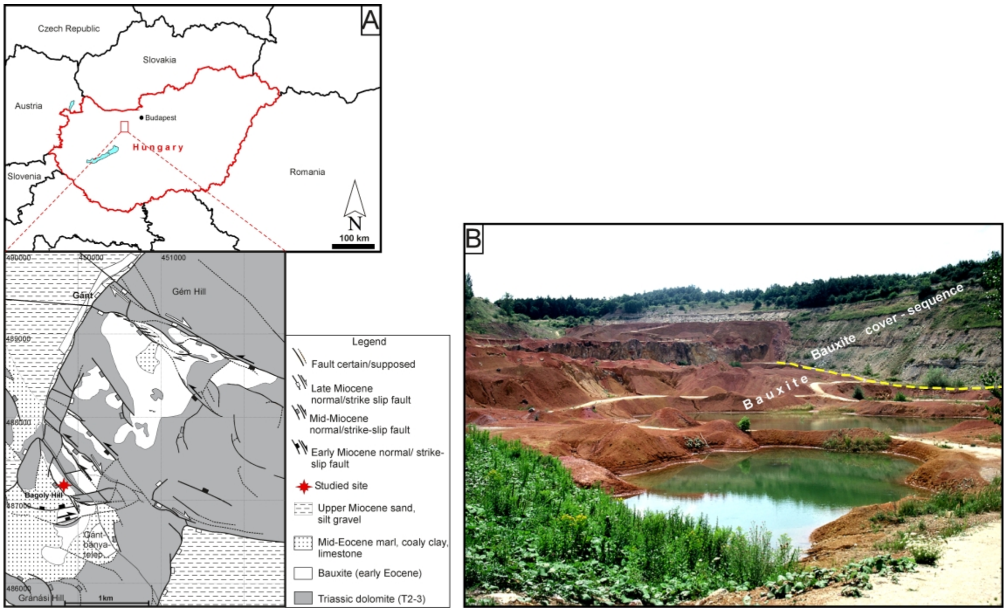

Figure 1. A, geographical and geological setting of the study area (after Fodor 2007). B, panoramic view of the studied Gánt section at the Vértes Hills (north-western Hungary).

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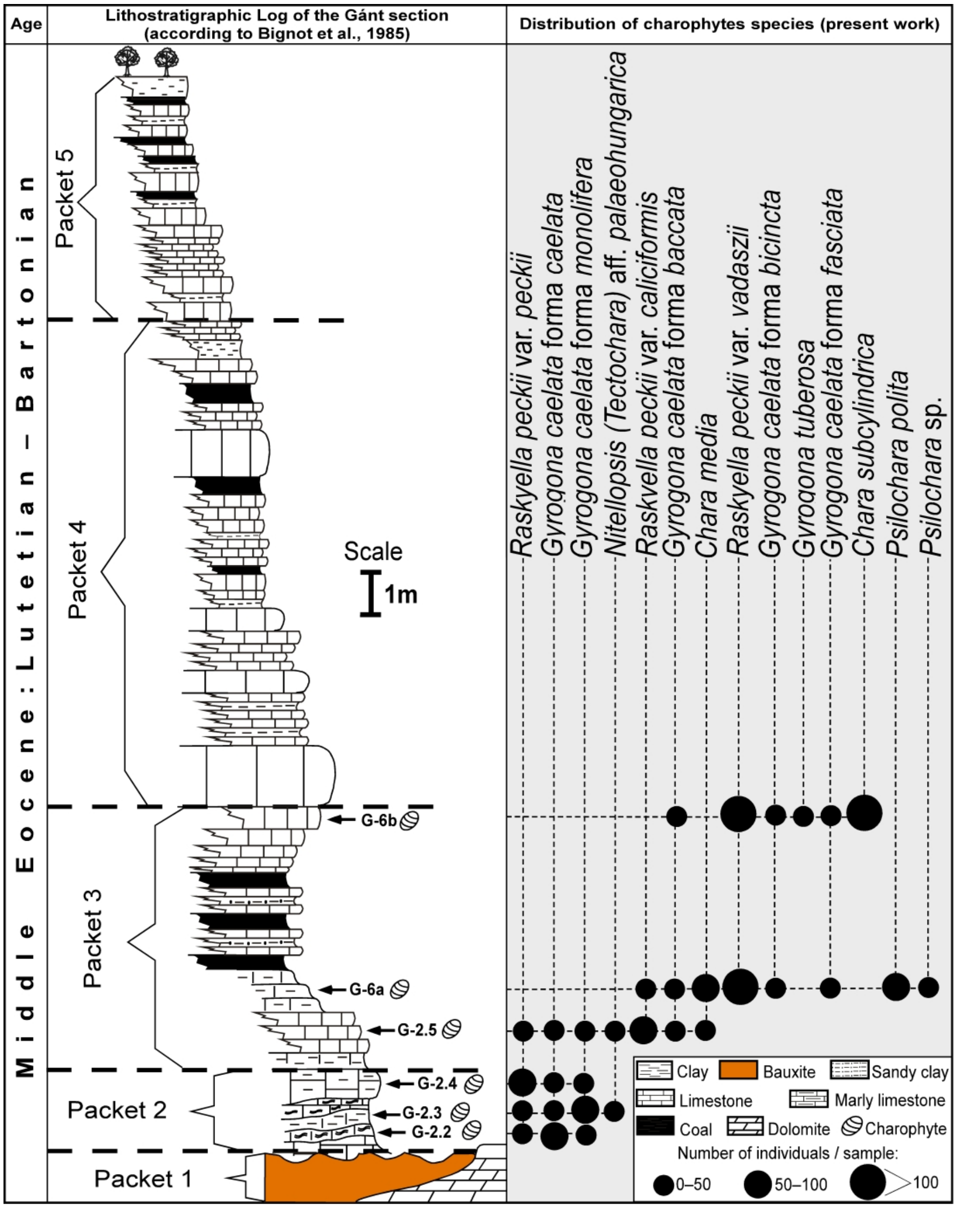

Figure 2. Distribution of the charophytes species in the bauxite cover-sequence from the studied Gánt section (Vértes Hills, Hungary), according to Bignot et al. (1985), updated for charophyte content.

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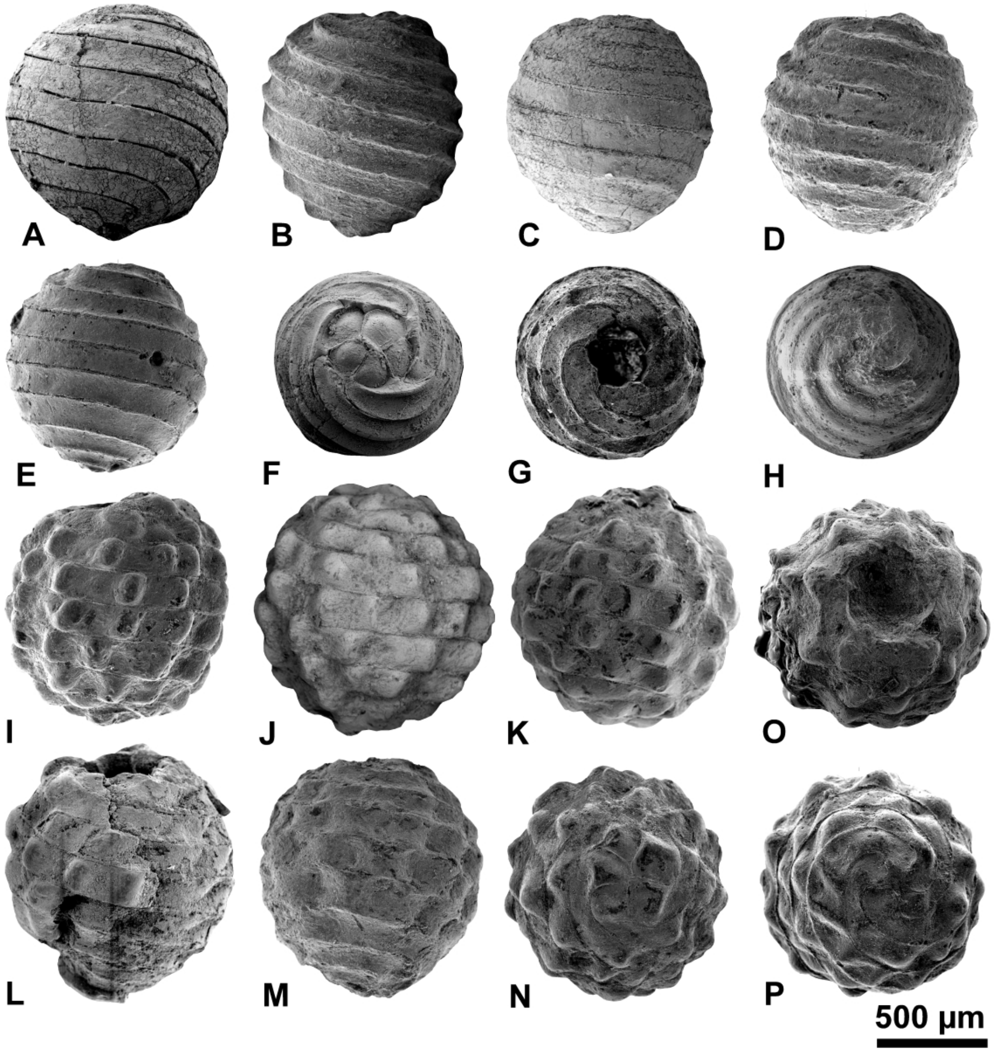

Figure 3. Raskyella peckii gyrogonites from the Gánt bauxite cover-sequence. A–H, Raskyella pecki var. peckii (samples G-2.2, G-2.3, G-2.4, and G-2.5), HNHM-PBO 1501–1508. A–E, lateral view; F–G, apical view; H, basal view. I–P, Raskyella peckii var. caliciformis (samples G-2.5 and G-6a), HNHM-PBO 1509–1516. I–K, lateral view; L, lateral view of gyrogonite partially broken showing internal cast. M, internal cast with well-developed undulations. N–O, apical view; P, basal view.

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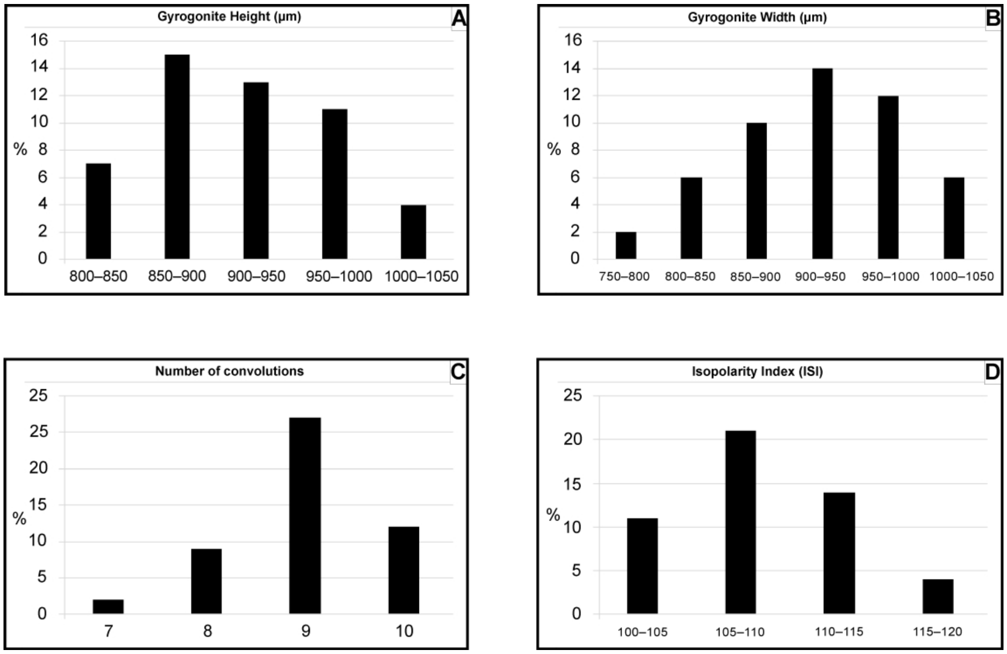

Figure 4. Frequency distribution of the height (A), width (B), number of convolutions (C), and height/width ratio (ISI) (D) of the Raskyella peckii var. peckii population (50 gyrogonites measured), from samples G-2.2, G-2.3, and G-2.4 in the bauxite cover-sequence of the Gánt section.

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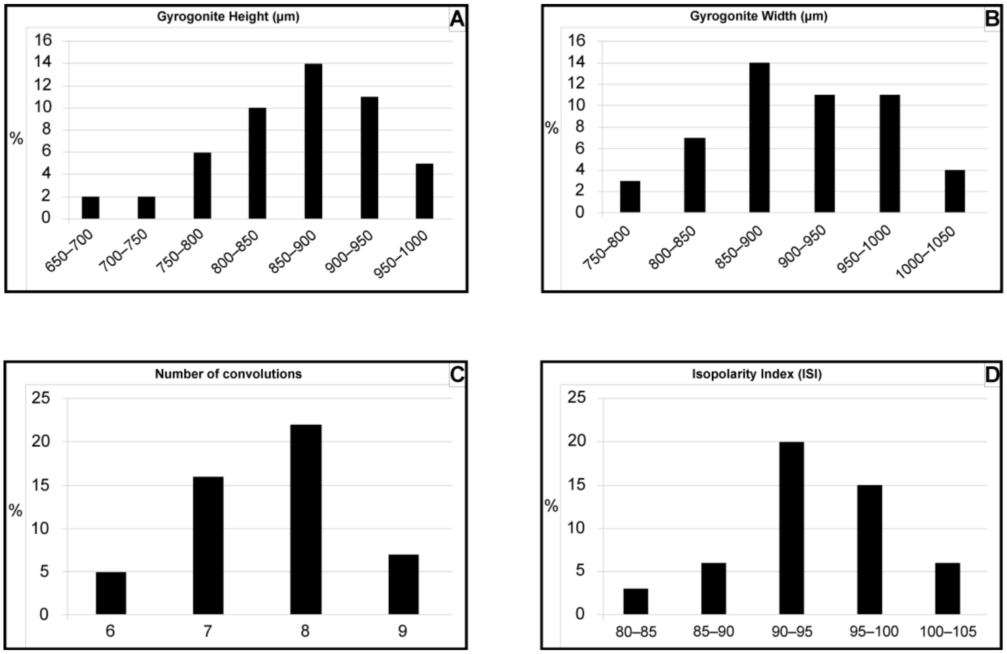

Figure 5. Frequency distribution of the height (A), width (B), number of convolutions (C), and height/width ratio (ISI) (D) of the Raskyella peckii var. caliciformis population (50 gyrogonites measured), from sample G-2.5 in the bauxite cover-sequence of the Gánt section.

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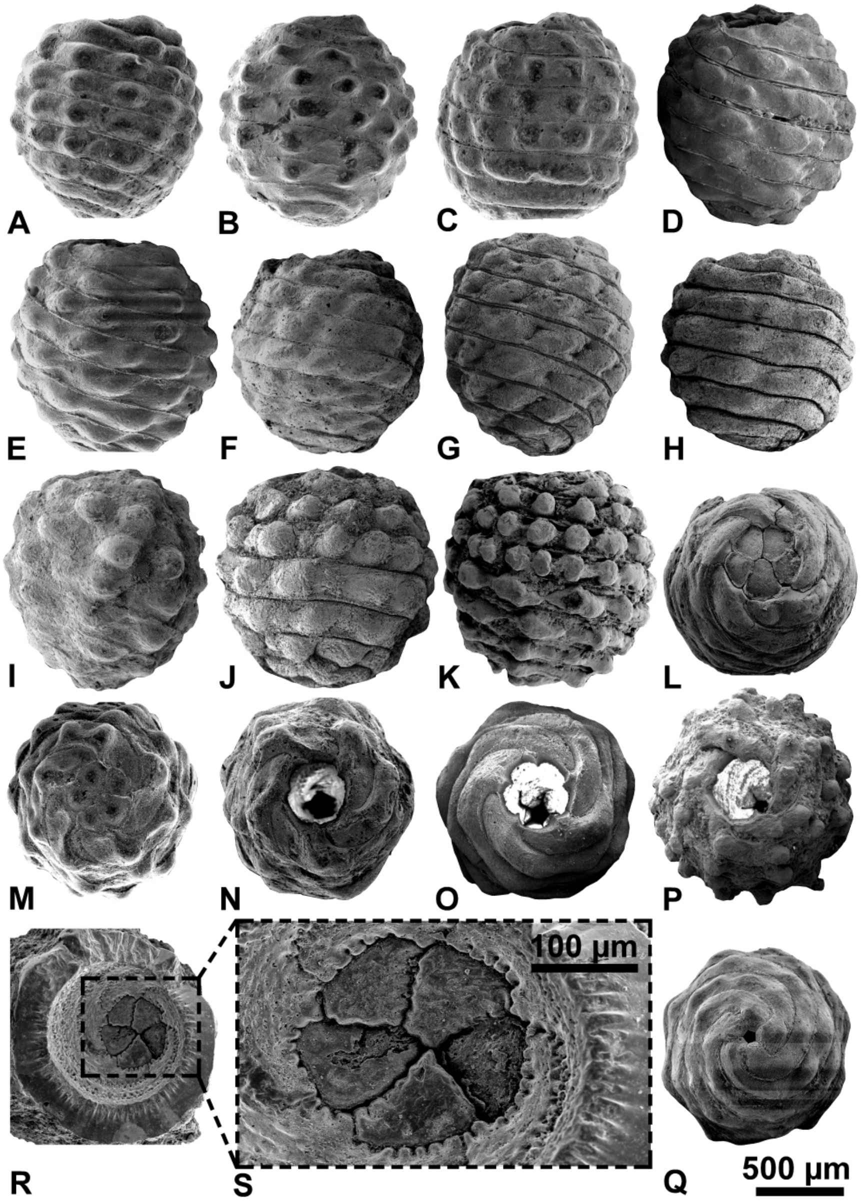

Figure 6. Raskyella peckii vadaszii gyrogonites from the Gánt bauxite cover-sequence (A–S, samples G-6a and G-6b, HNHM-PBO 1517–1534). A–K, lateral view. L–P, apical view; Q, basal view; R–S, inside wall of a gyrogonite showing the crenate undulation of the cellular sutures in contact with the spiral cells and the apical cells.

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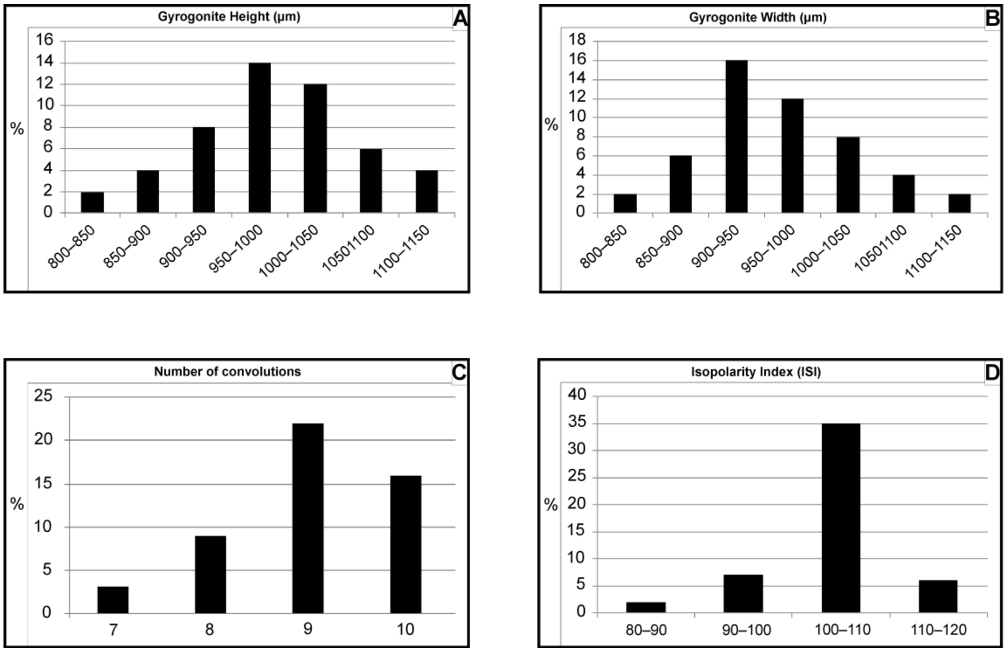

Figure 7. Frequency distribution of the height (A), width (B), number of convolutions (C), and height/width ratio (ISI) (D) of the Raskyella peckii var. vadaszii population (50 gyrogonites measured), from samples G-6a and G-6b in the bauxite cover-sequence of the Gánt section.

384x247mm (300 x 300 DPI)

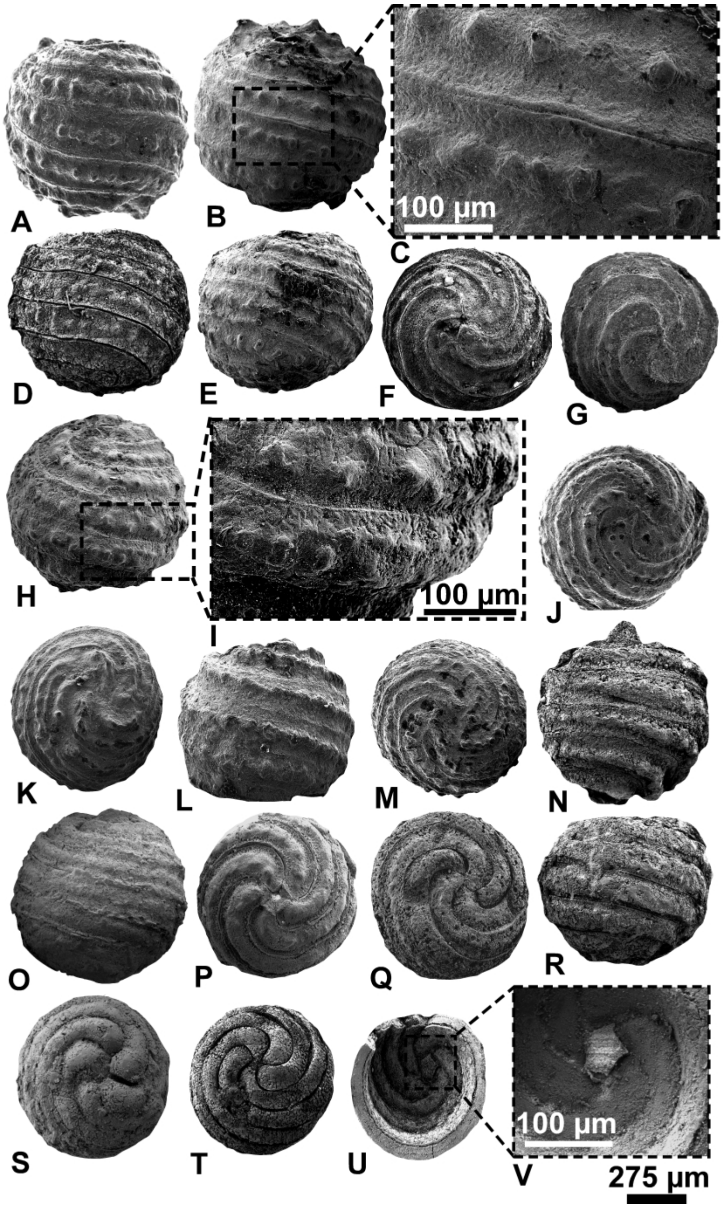

Figure 8. Gyrogona caelata gyrogonites from the Gánt bauxite cover-sequence. A–G, Gyrogona caelata forma caelata (samples G-2.2, G-2.3, G-2.4, and G-2.5), HNHM-PBO 1535–1553. A–B, D–E, basal view C, detail of the ornamentation pattern; F, basal view; G, apical view. H–K, Gyrogona caelata forma bicincta (samples G-6a and G-6b). H, lateral view; I, detail of the ornamentation pattern; J–K, apical view. L–M, Gyrogona caelata forma monolifera (samples G-2.2, G-2.3, G-2.4, and G-2.5). L, lateral view; M, basal view. N–Q, Gyrogona caelata forma baccata (samples G-2.5, G-6a, and G-6b). N–O, lateral view; P, basal view; Q, apical view. R–V, Gyrogona caelata forma fasciata (samples G-6a and G-6b). R, lateral view; S–T, apical view; U–V, detail of the simple (unipartite) basal plate.

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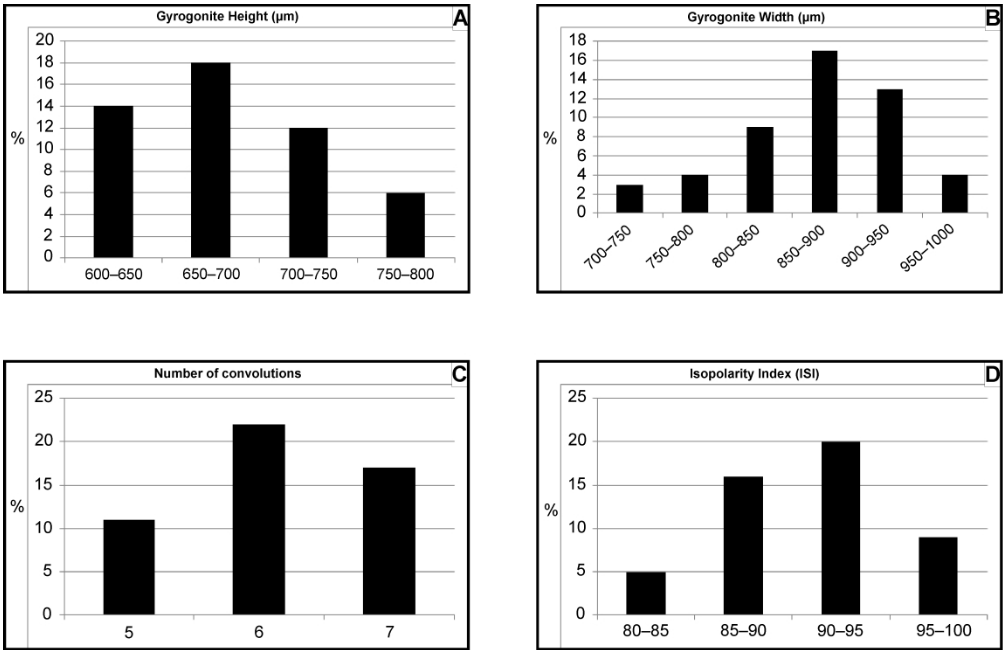

Figure 9. Frequency distribution of the height (A), width (B), number of convolutions (C), and height/width ratio (ISI) (D) of the Gyrogona caelata population (50 gyrogonites measured), from samples G-2.2, G-2.3, G-2.4, G-2.5, and G-6a in the bauxite cover-sequence of the Gánt section.

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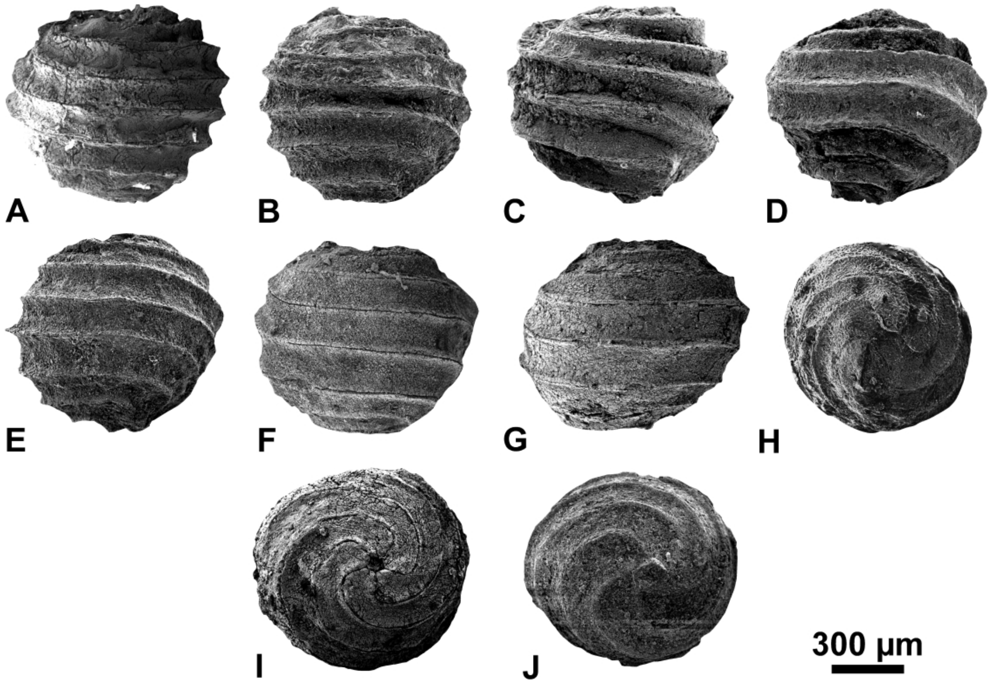

Figure 10. Gyrogona tuberosa gyrogonites from the Gánt bauxite cover-sequence (sample G-6b), HNHM-PBO 1554–1563. A–G, lateral view; H, apical view; I–J, basal view.

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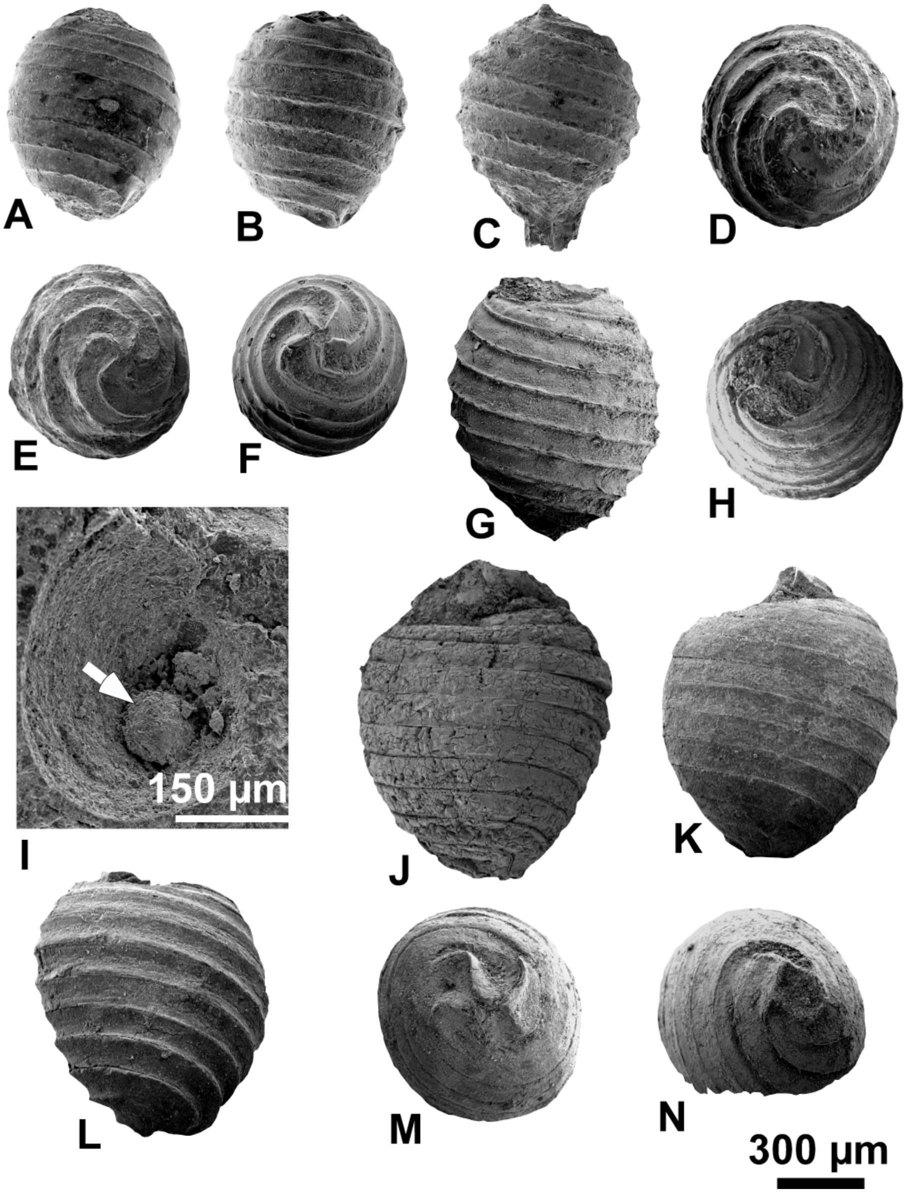

Figure 11. Gyrogonites of genera Psilochara and Nitellopsis from the Gánt bauxite cover-sequence. A–F, Psilochara polita (sample G-6a), HNHM-PBO 1564–1569. A–C, lateral view; D–E, apical view; F, basal view. G–I, Psilochara sp. (sample G-6a), HNHM-PBO 1570–1571. G, lateral view; H, apical view; I, internal view showing simple (unipartite) basal plate (arrowed). J–N, Nitellopsis (Tectochara) aff. palaeohungarica (samples G-2.3 and G-2.5), HNHM-PBO 1572–1576. J–L, lateral view; M, apical view; N, basal view.

467x610mm (300 x 300 DPI)

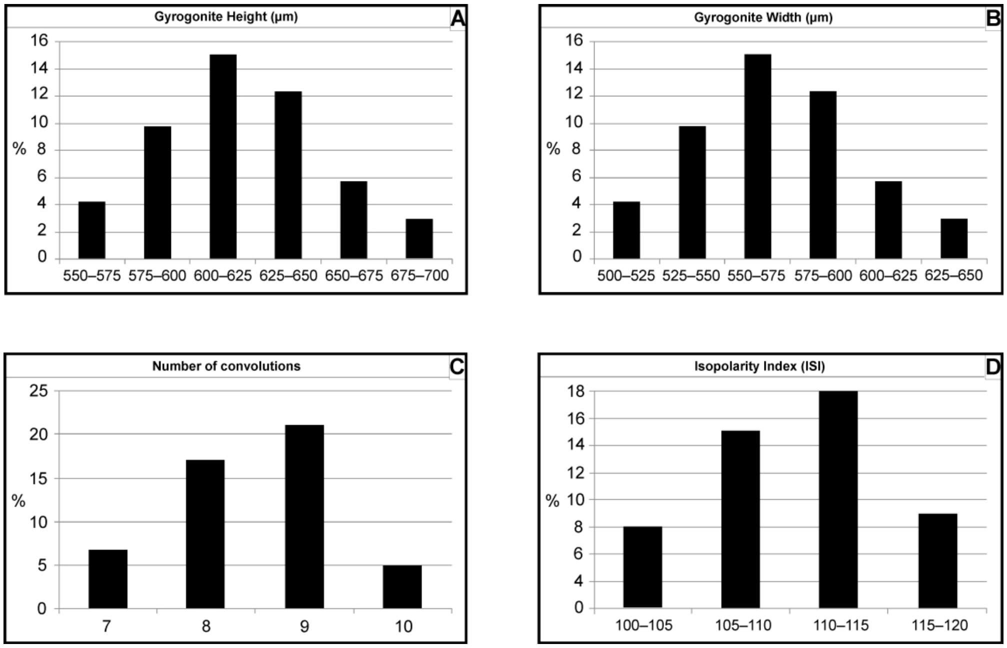

Figure 12. Frequency distribution of the height (A), width (B), number of convolutions (C), and height /width ratio (ISI) (D) of the Psilochara polita population (50 gyrogonites measured), from sample G-6a in the bauxite cover-sequence of the Gánt section.

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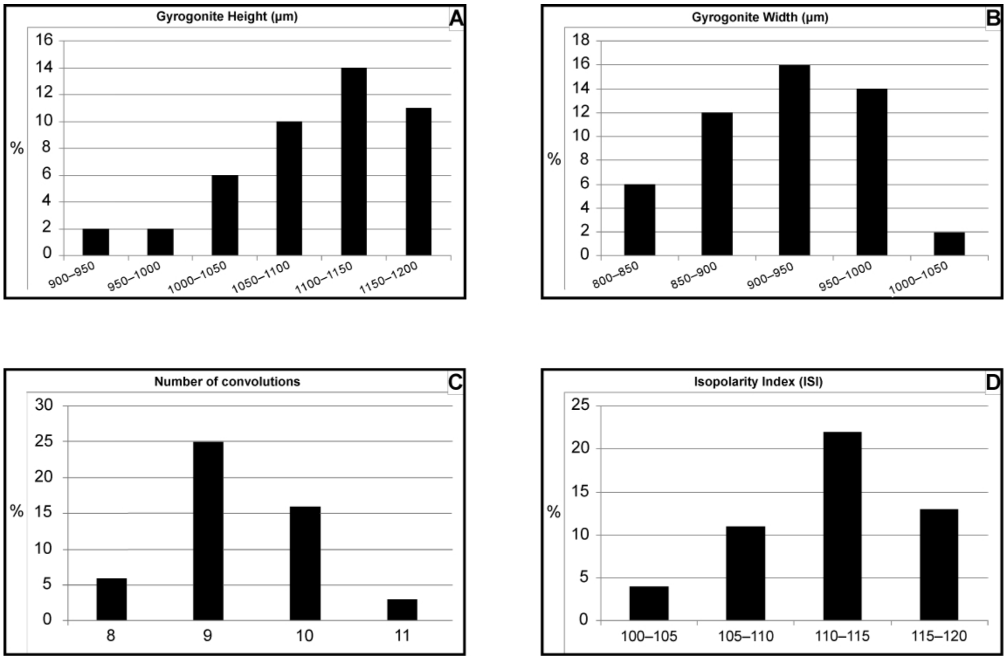

Figure 13. Frequency distribution of the height (A), width (B), number of convolutions (C), and height /width ratio (ISI) (D) of the Nitellopsis (Tectochara) aff. palaeohungarica population (50 gyrogonites measured), from samples G-2.3 and G-2.5 in the bauxite cover-sequence of the Gánt section.

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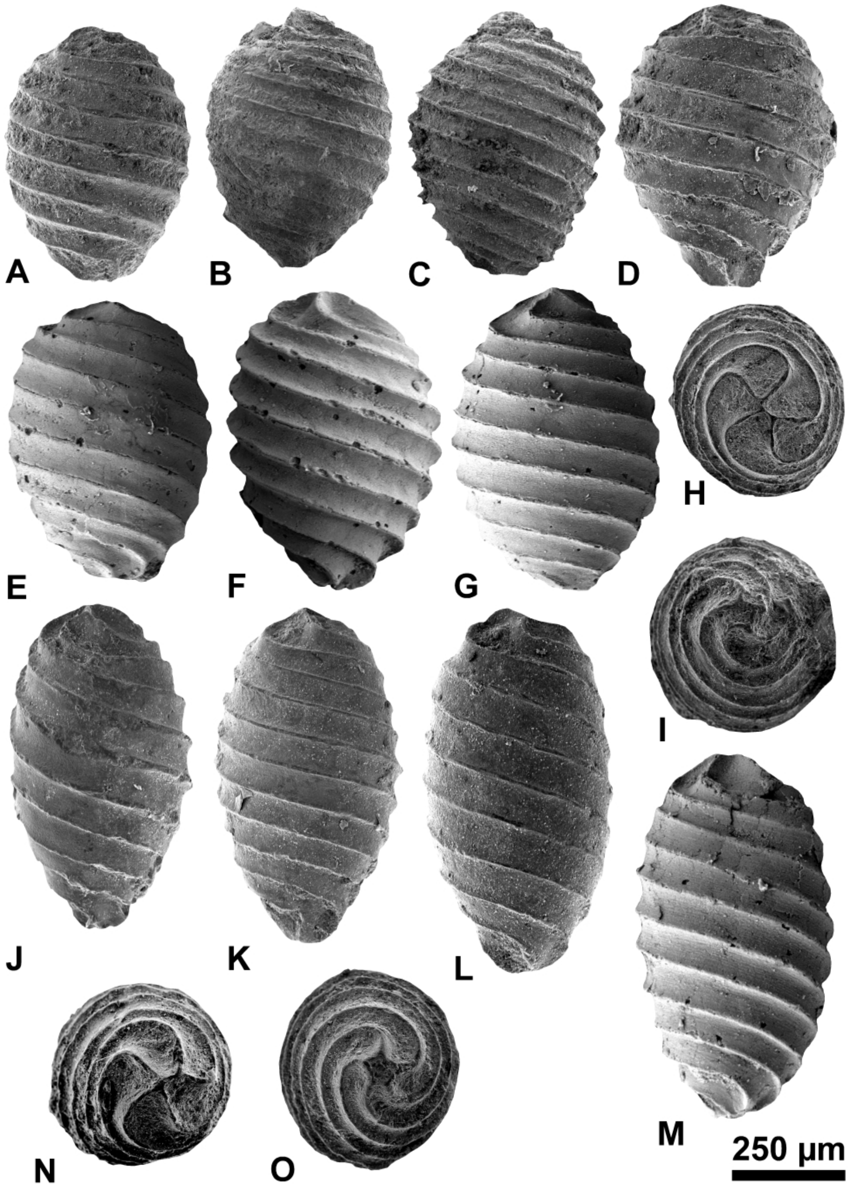

Figure 14. Chara gyrogonites from the Gánt bauxite cover-sequence. A–I, Chara media (samples G-2.5 and G-6a), HNHM-PBO 1577–1585. A–G, lateral view; H, apical view; I, basal view. J–O, Chara subcylindrica (sample G-6b), HNHM-PBO 1586–1591. J–M, lateral view; N, apical view; O, basal view.

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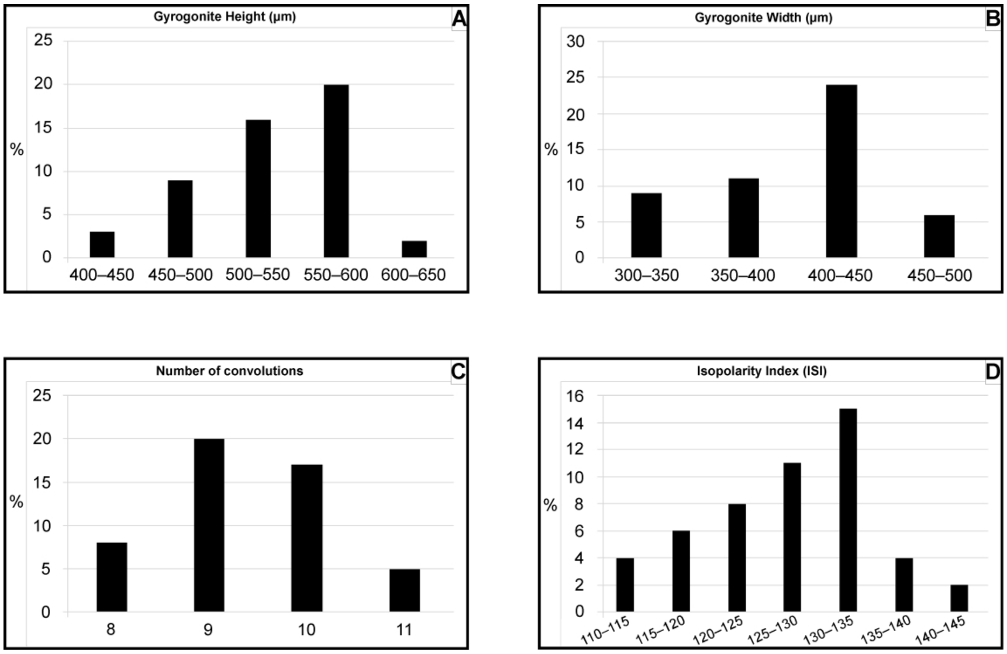

Figure 15. Frequency distribution of the height (A), width (B), number of convolutions (C), and height /width ratio (ISI) (D) of the Chara media population (50 gyrogonites measured), from samples G-2.5 and G-6a in the bauxite cover-sequence of the Gánt section.

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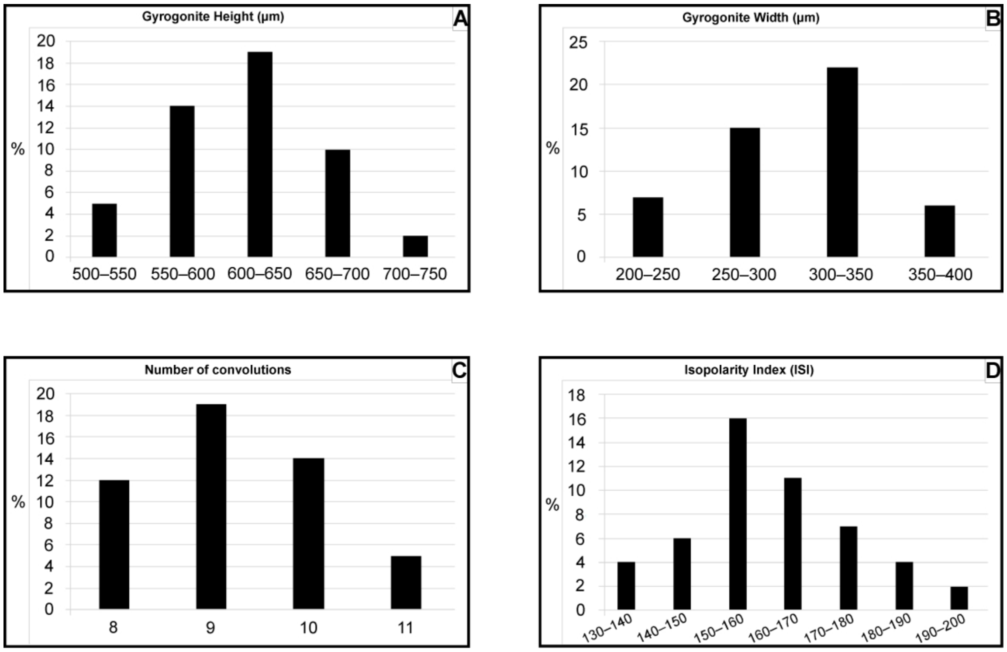

Figure 16. Frequency distribution of the height (A), width (B), number of convolutions (C), and height/width ratio (ISI) (D) of the Chara subcylindrica population (50 gyrogonites measured), from sample G-6b in the bauxite cover-sequence of the Gánt section.

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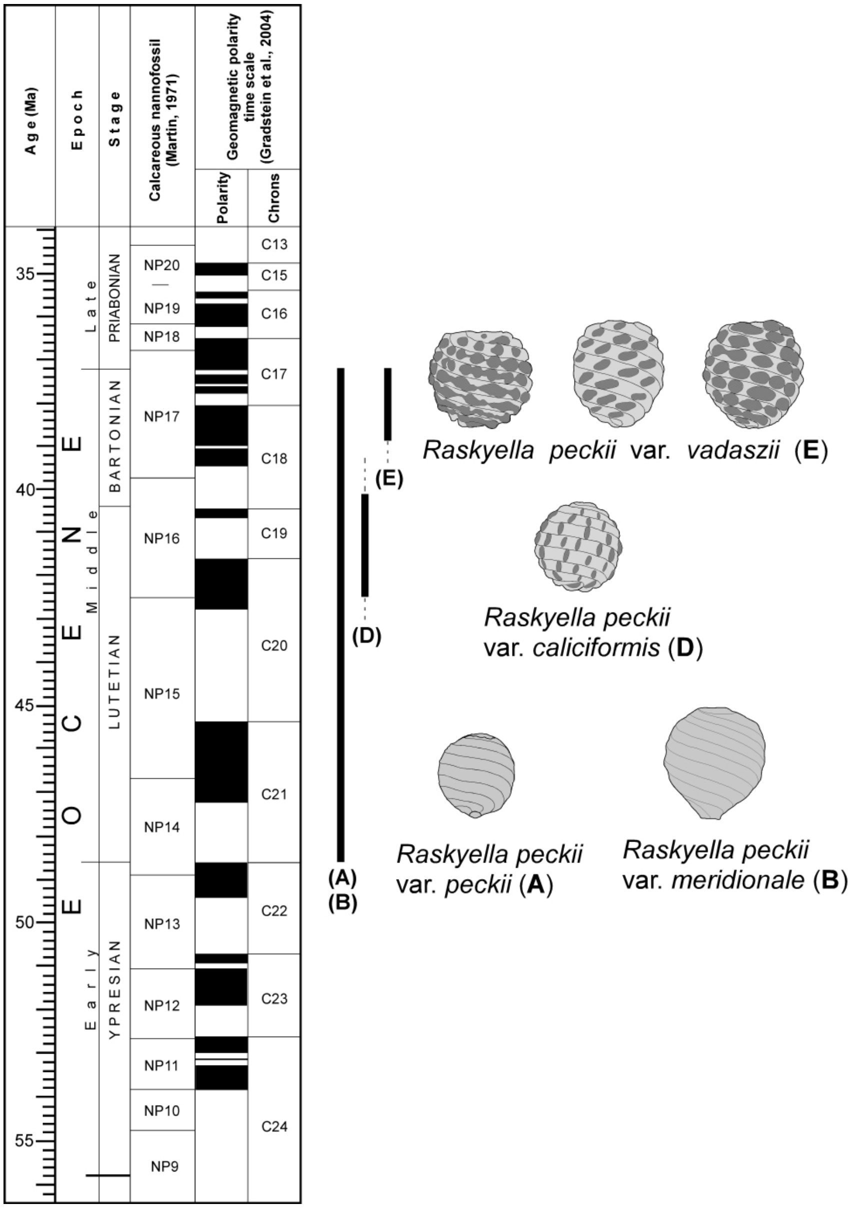

Figure 17. Stratigraphic distribution of variants of the anagenetic evolutionary lineage of species Raskyella peckii.

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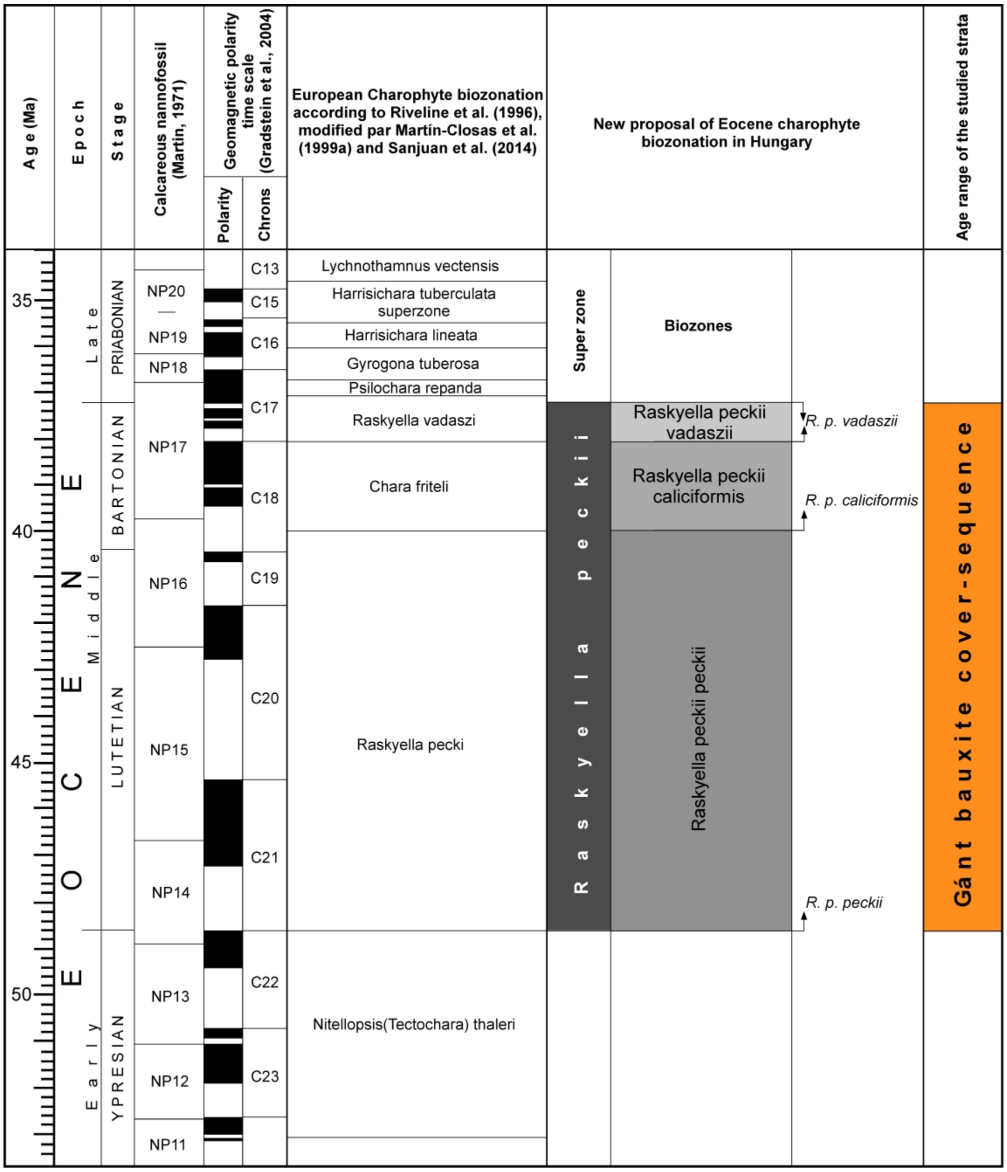

Figure 18. Charophyte Biostratigraphy, age and correlation of the bauxite cover-sequence from the Gánt section.

457x532mm (300 x 300 DPI)