

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

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3 **1 A new diverse charophyte flora and biozonation of the Eocene bauxite**  
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6 **2 cover-sequence at Gánt (Vértes Hills, Hungary)**  
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3 22 A diverse Eocene charophyte flora from a section at Gánt (Vértes Hills), Transdanubian Central  
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5 23 Range, north-western Hungary, provides significant new information to previous studies only  
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8 24 based on subsurface data published from the mid-20<sup>th</sup> century. This newly acquired material  
9  
10 25 facilitates the taxonomic revision and emendation of the species *Raskyella peckii* and thereby  
11  
12 26 defines a new anagenetic lineage based on three successive varieties which were formerly  
13  
14 27 considered as separate species or subspecies: *Raskyella peckii* var. *peckii* (early Lutetian–early  
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16 28 Bartonian), *Raskyella peckii* var. *caliciformis* (early Bartonian), and *Raskyella peckii* var.  
17  
18 29 *vadaszii* (late Bartonian). Based on this lineage, we propose a new local charophyte biozonation  
19  
20 30 that consists of a ‘*Raskyella peckii* Superzone’ (Lutetian–Bartonian), subdivided into three  
21  
22 31 successive charophyte partial range zones: The ‘*Raskyella peckii peckii* Zone’ (Lutetian–  
23  
24 32 lowermost Bartonian) characterized by an assemblage of *R. peckii peckii*, *Gyrogona caelata*  
25  
26 33 *forma caelata*, *G. caelata* forma *monolifera* and *Nitellopsis (Tectochara)* aff. *palaeohungarica*,  
27  
28 34 the ‘*Raskyella peckii caliciformis* Zone’ (lower Bartonian) characterized by the assemblage of  
29  
30 35 *R. peckii* var. *caliciformis*, *G. caelata* forma *caelata*, *G. caelata* forma *monolifera*, *G. caelata*  
31  
32 36 forma *baccata*, *Nitellopsis (Tectochara)* aff. *palaeohungarica* and *Chara media*, and the  
33  
34 37 ‘*Raskyella peckii vadaszii* Zone’ (upper Bartonian) characterized by *R. peckii* var. *vadaszii*, *G.*  
35  
36 38 *caelata* forma *bicincta*, *G. caelata* forma *baccata*, *G. caelata* forma *fasciata*, *G. tuberosa*,  
37  
38 39 *Psilochara polita*, *Psilochara* sp., *Chara media* and *Chara subcylindrica*. Future research may  
39  
40 40 show the new local biozonation as applicable to the whole of Europe and complementary to the  
41  
42 41 current European charophyte biozonation. Our results show that the sequences from Gánt,  
43  
44 42 which were previously regarded as upper mid-Eocene (upper Lutetian–lower Bartonian) in age,  
45  
46 43 appear to represent a longer chronostratigraphic interval: lower Lutetian to upper Bartonian.  
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48 44 Our chronostratigraphic results imply a longer and more stepwise Eocene major transgression  
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50 45 in the Transdanubian Central Range than previously thought.  
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3 47 **Keywords:** Characeae, Raskyellaceae, phylozone, gradualistic evolution, Paleogene, Central  
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13 50 **Introduction**  
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21 52 Charophytes represent one of the most useful tools in the biostratigraphic analysis of Cenozoic  
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23 53 non-marine deposits worldwide. During the Eocene, charophytes have been the object of  
24  
25 54 significant taxonomic, biostratigraphic, palaeoecological and palaeobiogeographic interest,  
26  
27 55 particularly in South European basins from France and Spain (Grambast 1958, 1962a, 1972;  
28  
29 56 Feist-Castel 1970, 1972, 1975, 1977a; Feist & Ringeade 1977; Anadón & Feist 1981; Riveline  
30  
31 57 1986; Anadón *et al.* 1992; Sanjuan & Martín-Closas 2012). As a result, a European Charophyte  
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33 58 Biozonation based largely on these basins was proposed by Riveline *et al.* (1996). For the  
34  
35 59 Eocene, up to 11 charophyte biozones were defined based mainly on data from Western Europe.  
36  
37 60 This biozonation has been updated since then, e.g., by Sanjuan *et al.* (2014) for the upper  
38  
39 61 Eocene. In contrast, the Eocene charophyte flora from Central and Eastern Europe is relatively  
40  
41 62 poorly known; and in the case of Hungary, the pioneer study by Rásky (1945) based on  
42  
43 63 subsurface data is practically the only one available. This author described for the first time a  
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45 64 species-rich charophyte flora from Hungary, at a time when charophyte taxonomy was still at  
46  
47 65 an early stage. She had already assigned the flora studied in this area to the middle Eocene, and  
48  
49 66 her work was the basis for future studies in charophyte taxonomy, including the definition of  
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51 67 the new family Raskyellaceae by Grambast & Grambast (1954). Later, Bignot *et al.* (1985),  
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53 68 based on an exhaustive palaeontological study of the Gánt section including molluscs,  
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3 69 foraminifers, ostracods, palynomorphs and charophytes, assigned the bauxite cover-sequence  
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5 70 to the Upper Lutetian or Bartonian, respectively.  
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9 71 This study aims to update the compendium of knowledge on Eocene Hungarian and Central  
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11 72 European charophytes, providing a taxonomic revision of the respective flora that is based on  
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13 73 surface samples of sections at the Gánt locality, as well as a discussion regarding its  
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15 74 biostratigraphic significance and utility.  
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## 23 76 **Geological setting**

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28 78 Within the Transdanubian Central Range (TCR), several bauxite deposits that developed across  
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30 79 the Cretaceous–Early Tertiary boundary interval are well known for their industrial use as  
31  
32 80 sources of aluminium ore; and among these, the famous karst bauxite of the Vértes Hills from  
33  
34 81 the Gánt locality (north-western Hungary) is a prominent example. Strata overlying the bauxite  
35  
36 82 represent the sedimentary record of progressive subcrustal erosion along the East Alpine–West  
37  
38 83 Carpathian forearc basin (Kázmér *et al.* 2003). The bauxite represents the base of the Eocene  
39  
40 84 charophyte-bearing strata investigated in this study (Fig. 1). The Eocene succession sampled  
41  
42 85 shows a remarkable lateral and vertical change of facies (Pálfalvi *et al.* 2006; Pálfalvi 2007)  
43  
44 86 that has been attributed to tectonic forces acting on the sedimentary body (Fodor 2007). The  
45  
46 87 development of the post-bauxite deposits was laid down during oscillation of the groundwater  
47  
48 88 table and eustatic sea level variations (Carannante *et al.* 1994; Mindszenty 2010), occurring  
49  
50 89 before the region was flooded by a marine incursion during the late Bartonian (Bignot *et al.*  
51  
52 90 1985).  
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3 91 At the Gánt section, the bauxite cover-sequence shows five stratigraphic units in a vertical  
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5 92 orientation dating from the middle Eocene (Fig. 2), called ‘Packets’ in the sense of Bignot *et*  
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7 93 *al.* (1985). ‘Packet 1’, about 1.5 m thick, corresponds to the bauxite itself, which unconformably  
8  
9 94 overlies Triassic dolomites. ‘Packet 2’, 1.5–2 m in thickness, forms the ‘blue-hole’ freshwater  
10  
11 95 limestone facies (Carannante *et al.* 1994; Pálfalvi 2007) alternating with clays, rich in  
12  
13 96 charophytes, ostracods and gastropods. ‘Packet 3’, *ca.* 6.5 m thick, includes alternating sandy  
14  
15 97 clay, coal and fresh- to brackish water limestone, rich in charophytes, ostracods, molluscs and  
16  
17 98 large benthic foraminifera (Bignot *et al.* 1985). ‘Packet 4’ is *ca.* 12 m thick and is mainly  
18  
19 99 dominated by shallow marine limestone, rich in nummulites, miliolids, molluscs and ostracods.  
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22  
23 100 Finally, ‘Packet 5’ is *ca.* 6m thick and displays an alternation of shallow marine marl and  
24  
25 101 limestone, rich in *Nummulites* and *Orbitolites*. ‘Packets’ 2 and 3 were sampled for charophytes  
26  
27 102 and are studied here.  
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33 104 -----Figures 1, 2 near here-----  
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## 38 106 **Material and methods**

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43 108 Intensive sampling for charophytes during two consecutive field work sessions in 2018 and  
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45 109 2019 was carried out on the cover sequence of the bauxite at Gánt (Vértes Hills, Hungary).  
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47 110 Moderately- to well-preserved gyrogonites were recovered from marly limestone to hard  
48  
49 111 limestone using acetolysis. This method, first applied by Nötzold (1965) to the study of  
50  
51 112 charophytes, has been recently improved by Trabelsi *et al.* (2010, 2016) and shown to be very  
52  
53 113 effective in recovering charophyte fructifications and thalli from consolidated carbonate rocks.  
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55 114 It consists of soaking the sample of hard calcareous rock, perfectly dried and mechanically  
56  
57 115 comminuted into fragments of about 1–3 mm across, in equal amounts of anhydrous acetic acid  
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3 116 and anhydrous copper sulphate (acid reacts exothermically). After neutralization by ammonia,  
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5 117 the residue is treated with ultra-sound, then washed and rinsed. Gyrogonites were measured  
6  
7 118 using the software Motic Images Plus 2.0 ML with a Motic BA310 stereomicroscope in the  
8  
9 119 *Departament de Dinàmica de la Terra i de l'Oceà* (University of Barcelona, Catalonia, Spain).  
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11  
12 120 Scanning electron microscopy on gold-sputtered selected specimens was conducted with a  
13  
14 121 JEOL JSM-6400 at the Faculty of Earth Sciences, Geography and Astronomy, University of  
15  
16 122 Vienna (Austria) and with a Quanta 200 device at the *Centres Científics i Tecnològics* of the  
17  
18 123 University of Barcelona (CCiTUB). The studied materials are housed in the Hungarian Natural  
19  
20 124 History Museum (Budapest, Hungary), Botanical Department, Palaeobotanical Collection. The  
21  
22 125 figured specimens are deposited under the inventory numbers: HNHM-PBO 1501–1591.  
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## 30 127 **Systematic palaeontology**

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33 128 The charophyte flora from the bauxite cover sequence at Gánt (Vértes Hills, Hungary) studied  
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35 129 here yields gyrogonites from two families: Raskyellaceae and Characeae. The different  
36  
37 130 charophyte species described below are stratigraphically distributed in the section as shown in  
38  
39 131 the Fig. 2.  
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47 133 Division **Charophyta** Migula, 1897

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50 134 Class **Charophyceae** G. M. Smith, 1938 emend. Schudack, 1993

51  
52  
53 135 Order **Charales** Lindley, 1836

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56 136 Family **Raskyellaceae** Grambast, 1957

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59 137 Sub-Family **Raskyelloideae**, Grambast et Grambast, 1955  
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3 138 Genus *Raskyella* (Grambast et Grambast, 1954) emend. Grambast, 1962b  
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9 140 **Type species.** *Raskyella peckii* Grambast et Grambast, 1954  
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15 142 **Remarks.** This species is understood as including several traditional taxa belonging to the  
16 143 genus *Raskyella*, which form a gradualistic lineage during the Eocene. These traditional taxa  
17 144 have been newly combined here to anagenetic varieties within a single evolutionary lineage or  
18 145 an evolutionary species, following the recommendations of Wiley (1981) and Ax (1978).  
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29 147 *Raskyella peckii* var. *peckii* Grambast et Grambast, 1954  
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32 148 (Fig. 3A–H)  
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38 150 1954 *Raskyella pecki* sp. nov. L. & N. Grambast: p. 670, text-figs 1a–c.  
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41 151 1957 *Raskyella pecki* Grambast: p. 358, pl. 5, figs 7–9.  
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44 152 1958 *Raskyella pecki* Grambast: p. 190, figs 87, a–c; p. 191, text-fig. 88.  
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47 153 1959 *Raskyella pecki* Horn af Rantzien: pl. 19, figs 7–13.  
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50 154 1971 *Raskyella peckii* subsp. *ganesensis* Soulié-Märsche: pl. 2, 1–5.  
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53 155 1981 *Raskyella pecki* Anadón & Feist: pl. 1, figs 1–2; pl. 2, figs 3–4.  
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56 156 1986 *Raskyella pecki* Riveline: pl. 37, figs 7–9.  
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59 157 1999a *Raskyella pecki* Martín-Closas *et al.*: p. 11, figs 6, 1–3.  
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158

159 **Material.** Up to 65 gyrogonites in sample G-2.4, and dozens in samples G-2.2 and G-2.3.

160 Collection numbers of figured specimens: HNHM-PBO 1501–1508.

161 **Description.** Gyrogonites are ovoidal to ellipsoidal in shape, spherical to subprolate (ISI 100–  
162 120) and of large size, 800–1050  $\mu\text{m}$  in height and 750–1050  $\mu\text{m}$  in width, showing laterally  
163 7–10 (usually 9) convolutions (Fig. 4). Spiral cells often flat (Fig. 3A) to slightly convex (Fig.  
164 3C), or concave (Fig. 3B), but regularly without any kind of ornamentation. Apex broadly  
165 rounded, truncated and flattened, with the spiral cells abruptly discontinuous and ending acutely  
166 in the apical periphery to be replaced by the development of five opercular cells, each obliquely  
167 disposed at the end of a spiral cell (Fig. 3F). Germinated specimens (Fig. 3G) show a rose-  
168 shaped apical opening. Internal casts of these gyrogonites were also found (Fig. 3E).

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

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

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

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3 182 Riveline 1984, 1986) and Spain (Anadón & Feist 1981; Anadón *et al.* 1992; Martín-Closas *et*  
4  
5 183 *al.* 1999a; Martín-Closas & Ramos 2005). The total range of this variety (early Lutetian–late  
6  
7 184 Bartonian) has been characterized in the Eastern Ebro basin (Catalonia) by Martín-Closas *et al.*  
8  
9 185 (1999) based on correlation with larger foraminifera (mainly *Nummulites*). Furthermore, *R.*  
10  
11 186 *peckii* var. *peckii* has been also reported from North Africa, i.e. in the lower Eocene of Algeria  
12  
13 187 (Gevin *et al.* 1974; Mebrouk *et al.* 1997; Vianey-Liaud 1994), in the late lower Eocene–early  
14  
15 188 middle Eocene of Tunisia (Abdeljaoued *et al.* 1984) and in the Lutetian of Libya (Megerisi &  
16  
17 189 Mamgain 1980).

190

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

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

194

Closas

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(Fig. 3I–P)

196

197 **Basionym.** *Raskyella caliciformis* Soulié-Märsche, 1974, Compte Rendu 96<sup>ème</sup> Congrès

198 National des Sociétés Savantes, Toulouse, 1971, Section Science, 2, p. 114, text-figure 2 (pl.

199 I), 1–5.

200

201 1974 *Raskyella caliciformis* sp. nov., Soulié-Märsche: p. 112, pl. 1, figs 1–5.

202 1981 *Raskyella caliciformis*, Anadón & Feist: pl. 1, figs 6–7; pl. 2, figs 7–8.

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**Material.** 63 gyrogonites in sample G-2.5. Collection numbers of figured specimens: HNHM-

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8 205 PBO 1509–1516.

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11 206 **Description.** Large sized gyrogonites (650–1000  $\mu\text{m}$  high and 750–1050  $\mu\text{m}$  wide) of globular

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13  
14 207 to oblate shape (ISI 80–105), showing laterally 6–9 (usually 8) convolutions (Fig. 5). Spiral

15  
16 208 cells flat to slightly concave ornamented with stout, vertical to slightly inclined, well

17  
18 209 individualized tubercles (Fig. 3I–K), which are the main diagnostic character of this variety.

19  
20 210 Apex broadly rounded to truncated showing five opercular cells placed at the end of the spiral

21  
22 211 cells. The opercular cells are sometimes convex and somewhat polygonal in shape (Fig. 3N),

23  
24 212 rather than rounded, which is the reason why the dehiscence opening appears sometimes

25  
26 213 irregularly star-shaped (Fig. 3O), rather than rose-shaped (Fig. 3L), as already noted by Soulié-

27  
28 214 Märsche (1974) in the type material. The internal cast of the gyrogonite (Fig. 3M) shows

29  
30 215 straight ridges perpendicular to the well-marked, undulated spiral cells. This wavy surface is

31  
32 216 uncommon in the inside of other raskyellacean gyrogonites and is thought to correspond

33  
34 217 internally to the external tubercle ornamentation.

35  
36 218 **Distribution.** This is the first record of *R. peckii* var. *caliciformis* in Hungary. It was previously

37  
38 219 described from the Bartonian of South France (Soulié-Märsche 1974; Riveline 1986), and from

39  
40 220 the lower Bartonian (Auversian local stage) of the Ebro Basin, Catalonia, Spain (Anadón &

41  
42 221 Feist 1981; Anadón *et al.* 1992).

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46 223 ----- Figure 5 near here -----

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3 225 *Raskyella peckii* var. *vasdaszii* (Grambast et Grambast 1954) comb. nov. Trabelsi et Martín-

4  
5 226 Closas

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8 227 (Fig. 6A–S)

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15 229 **Basionym.** *Raskyella vadaszi* (Rásky) L. & N. Grambast (1954), Revue Générale de

16  
17 230 Botanique (61), p. 670.

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23 232 1945 *Aclistochara vadaszi*, sp. nov. Rásky: p. 45, pl. II, figs 22–24.

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26 233 1954 *Raskyella vadaszi*, comb. nov. L. and N. Grambast: p. 670.

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29 234 1957 *Raskyella vadaszi*, Grambast: p. 358, pl. 5, figs 1–6.

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32 235 1959 *Raskyella vadaszi*, Horn af Rantzien: pl. 20, figs 1–3.

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35 236 1981 *Raskyella vadaszi*, Anadón & Feist: pl. 1, fig. 5; pl. 2, fig. 5.

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38 237 1981 *Raskyella* aff. *vasdaszi*, Anadón & Feist: pl. 1, figs 3–4; pl. 2, figs 1–2, 6.

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41 238 1985 *Raskyella vadaszi*, Bignot *et al.*: p. 36, pl. 3, figs 8–11.

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44 239 1986 *Raskyella vadaszi*, Riveline: pl. 37, figs 1–6.

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51 241 **Material.** Hundreds of gyrogonites in samples G-6a and G-6b. Collection numbers of figured

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53 242 specimens: HNHM-PBO 1517–1534.

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56 243 **Description.** Large sized gyrogonites (800–1150  $\mu\text{m}$  high and 800–1150  $\mu\text{m}$  wide) of oblate to

57  
58 244 ovoidal shape (ISI 80–120), showing laterally 7–10 (usually 9) convolutions (Fig. 7). Spiral

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2  
3 245 cells often convex and ornamented with stout tubercles of different shapes and sizes, in most  
4  
5 246 cases oriented parallel to the intercellular sutures (Fig. 6A–C), or more rarely tilted 20–30° but  
6  
7 247 keeping parallelism between adjacent nodules (Fig. 6E–G), this being a diagnostic character of  
8  
9 248 this morphotype. Three tubercle morphologies have been observed: (1) rounded tubercles, well  
10  
11 249 individualized in the upper half of the gyrogonite, but fused to neighbouring tubercles in the  
12  
13 250 lower half (Fig. 6I–K), (2) elongated tubercles more or less connected to each other and  
14  
15 251 producing slightly wavy (undulated) sutures (Fig. 6H), (3) irregularly alternating round and  
16  
17 252 elongated tubercles (Fig. 6D). Base of gyrogonite rounded (Fig. 6C, J) to slightly tapered (Fig.  
18  
19 253 6A, G) and showing a small, superficial and pentagonal basal pore, sometimes within a less-  
20  
21 254 marked funnel (Fig. 6Q). Apex of gyrogonite truncated or broadly rounded and covered by five  
22  
23 255 independent opercular cells at the end of the spiral cells. Opercular cells roughly prismatic, with  
24  
25 256 its outer surface concave, flat or slightly convex (Fig. 6L–M). Germinated specimens show a  
26  
27 257 rounded or rose-like opening (Fig. 6N–P). The inside of the gyrogonite allows observation of a  
28  
29 258 characteristic crenulation of the intercellular sutures near their internal side (Fig. 6R–S), while,  
30  
31 259 to the outside, sutures are flat. Besides, this crenulation occurs also between the opercule cells  
32  
33 260 themselves and between spiral and opercule cells as already described by Feist *in* Anadón and  
34  
35 261 Feist (1981).  
36  
37  
38  
39  
40  
41  
42

43 262 **Distribution.** *R. vadaszii* has been first described by Rásky (1945) from middle Eocene  
44  
45 263 borehole samples (60 m depth) at Gánt, in beds roughly equivalent laterally to the outcrop  
46  
47 264 succession studied here. Therefore, the samples studied may be considered topotypes.  
48  
49 265 Subsequently, the age of this variety was suggested to be upper Bartonian by Bignot *et al.*  
50  
51 266 (1985) based on the associated microfossils (foraminifers, ostracods, and pollen) from the same  
52  
53 267 beds of the bauxite cover-sequence at the Gánt section (Vértes Hills). *R. peckii* var. *vadaszii*  
54  
55 268 has also been well documented in France, in the upper Bartonian of the Paris Basin (Grambast  
56  
57 269 1957, 1958, 1962a; Riveline 1986) and from several basins in southern France (Feist-Castel  
58  
59  
60

1  
2  
3 270 1976). Anadón & Feist (1981) and Anadón *et al.* (1992) documented this variety also in the  
4  
5 271 upper Bartonian of the Eastern Ebro Basin (Catalonia, Spain).  
6  
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9 272

10  
11 273 ----- Figures 6, 7 near here-----  
12  
13

14  
15 274

16  
17  
18 275 Family **Characeae** (Richard ex C.A. Agardh, 1824) emend. Martín-Closas et Schudack, 1991  
19

20  
21 276 Subfamily **Charoideae** Braun *in* Migula, 1897  
22

23  
24 277 Genus **Gyrogona** (Lamarck, 1804 *ex* Lamarck, 1822) emend. Grambast, 1956  
25  
26

27  
28 278

29  
30 279 ***Gyrogona caelata*** (Reid et Groves, 1921) Grambast, 1956  
31

32  
33  
34 280 (Fig. 8A–V)  
35

36  
37 281

38  
39  
40 282 1921 *Chara caelata* sp. nov., Reid & Groves: p. 184, pl. 4, figs 4–6.  
41

42  
43 283 1927 *Kosmogyrca caelata*, Pia: p. 90.  
44

45  
46 284 1954 *Brachychara caelata*, L. & N. Grambast: p. 667.  
47

48  
49 285 1956 *Gyrogona caelata*, Grambast: p. 280.  
50

51  
52 286 1977b *Gyrogona caelata*, Feist-Castel: p. 117.  
53

54  
55 287 1981 *Gyrogona caelata*, Grambast & Grambast-Fessard: p. 22, text-fig. 11, a–f; pl. 4, figs 1–9.  
56

57  
58 288 1981 *Gyrogona cf. Caelata*, Anadón & Feist: p. 163.  
59  
60

1  
2  
3 289 1986 *Gyrogona caelata*, Riveline: pl. 38, figs 1–5, 7–8.  
4  
5

6 290 1989 *Gyrogona caelata*, Choi: pl. 2, figs 1–11.  
7  
8

9 291 1991 *Gyrogona caelata*, Weidmann *et al.*: p. 900, fig. 3, C.  
10  
11

12 292 2014 *Gyrogona caelata*, Sanjuan & Martín-Closas: p. 403, fig. 7, A–C.  
13  
14

15  
16 293  
17  
18

19 294 **Material.** 56 gyrogonites in sample G-2.2, 38 in sample G-2.3, 29 in sample G-2.4, 18 in sample  
20  
21 295 G-2.5, and 23 in sample G-6a. Collection numbers of figured specimens: HNHM-PBO 1535–  
22  
23 296 1553.  
24  
25

26 297 **Description.** Medium to large gyrogonites, 600–800  $\mu\text{m}$  high and 700–1000  $\mu\text{m}$  wide with  
27  
28 298 generally oblate to suboblate spheroidal shape (ISI 80–100) and showing laterally 5–7 (usually  
29  
30 299 6) convolutions (Fig. 9). Apex and base broadly rounded to subtruncate. Apex showing a less-  
31  
32 300 marked spiral cell periapical thinning (e.g., Fig. 8G) and, in some specimens, apical nodules of  
33  
34 301 different shape, generally flat or slightly convex (e.g. Fig. 8S). Base showing a small pentagonal  
35  
36 302 basal pore (Fig. 8F), sometimes flared by a shallow funnel (Fig. 8P). Basal plate unicellular and  
37  
38 303 only visible from the gyrogonite interior (Fig. 8U–V). Spiral cells flat to slightly concave and  
39  
40 304 ornamented with different patterns of tubercles, which allowed Grambast (1958) and Grambast  
41  
42 305 & Grambast-Fessard (1981) to distinguish a number of morphotypes, ranking them as *formae*  
43  
44 306 of the same species. The following five forms were recognized in the material studied: (1) *G.*  
45  
46 307 *caelata* forma *caelata* characterized by small nodules well-spaced and irregularly ranged along  
47  
48 308 the spiral cell median line (e.g. Fig. 8A, D), (2) *G. caelata* forma *bicincta* characterized by  
49  
50 309 nodules irregularly ranged along two lines parallel to spiral cell sutures (Fig. 8H, I), (3) *G.*  
51  
52 310 *caelata* forma *monolifera* showing medium-sized nodules close to each other, sometimes fused  
53  
54 311 and forming a thin, irregular mid-cellular crest (e.g., Fig. 8L), (4) *G. caelata* forma *baccata*  
55  
56  
57  
58  
59  
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1  
2  
3 312 characterized by large nodules very closely ranged along the spiral-cell median line (e.g., Fig.  
4  
5 313 8N–Q), (5) *G. caelata* forma *fasciata* characterized by a broad median band of variable width  
6  
7 314 (e.g., Fig. 8R–T).

8  
9  
10 315 **Distribution.** The species *Gyrogona caelata* is reported here from Hungary for the first time.  
11  
12 316 According to Riveline (1986), this species was widely distributed in the upper Lutetian–  
13  
14 317 Priabonian non-marine deposits of Western Europe. It was first recorded from the Isle of Wight,  
15  
16 318 England by Reid & Groves (1921). Thereafter, it was reported from the upper Lutetian to upper  
17  
18 319 Priabonian of France (Grambast 1958; Grambast & Grambast-Fessard 1981; Feist-Castel 1971;  
19  
20 320 Feist & Ringeade 1977; Feist-Castel 1977a, b; Ollivier-Pierre *et al.* 1988), Spain (Anadón &  
21  
22 321 Feist 1981; Choi 1989; Anadón *et al.* 1992; Sanjuan & Martín-Closas 2014), Switzerland  
23  
24 322 (Weidmann *et al.* 1991), as well as from the middle Eocene of Romania (Iva 1987). In North  
25  
26 323 Africa, the species has also been documented from the central part of the Sahara, Algeria, by  
27  
28 324 Mebrouk *et al.* (1997).  
29  
30  
31  
32  
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38 326 ----- Figures 8, 9, near here -----  
39  
40  
41 327

42  
43  
44 328 ***Gyrogona tuberosa*** (Reid et Groves, 1921) Grambast *in* Grambast et Grambast-Fessard, 1981  
45  
46

47 329 (Fig. 10A–J)  
48  
49

50 330  
51  
52

53 331 1921 *Chara wrighti* var. *rhytidocarpa*, Reid & Groves: p. 183, pl. 4, fig. 3.  
54  
55

56 332 1958 *Gyrogona tuberosa*, Grambast: p. 139, fig. 54.  
57  
58

59 333 1976 *Gyrogona tuberosa*, Feist-Castel: p. 26.  
60



1  
2  
3 334 1981 *Gyrogona tuberosa*, Grambast & Grambast-Fessard: p. 25, text-fig. 12, a–d; pl. 5, figs 1–  
4  
5 335 6.

6  
7  
8 336 1986 *Gyrogona tuberosa*, Riveline: pl. 14, figs 8–11.

9  
10  
11 337

12  
13  
14 338 **Material.** 35 gyrogonites in sample G-6b. Collection numbers of figured specimens: HNHM-  
15  
16 339 PBO 1554–1563.

17  
18  
19  
20 340

21  
22  
23 341 **Description.** Large gyrogonites, 820–1000  $\mu\text{m}$  high and 835–1050  $\mu\text{m}$  wide with generally  
24  
25 342 oblate to suboblate spheroidal shape (ISI 80–100) and showing laterally 6–7 convolutions  
26  
27 343 (usually 6). Apex subtruncate (Fig. 10A, C) to somewhat pointed (Fig. 10D, G) with spiral cells  
28  
29 344 protruding (Fig. 10H). Base broadly rounded (Fig. 10B, F) to slightly tapered (Fig. 10A, C, E)  
30  
31 345 and showing a small, superficial and pentagonal basal pore, sometimes within a less-marked  
32  
33 346 funnel (Fig. 10I–J). Spiral cells flat or concave, smooth or somewhat ornamented and separated  
34  
35 347 by protruding narrow to weakly undulated intercellular ridges.

36  
37  
38  
39  
40 348 **Distribution.** *Gyrogona tuberosa* is reported here from Hungary and central Europe for the  
41  
42 349 first time. According to Riveline (1986) and Riveline & Cavelier (1987), this species was  
43  
44 350 widely distributed in upper Bartonian non-marine deposits of Western Europe. It was first  
45  
46 351 recorded from the Isle of Wight and Hampshire (England) by Reid & Groves (1921).  
47  
48 352 Subsequently, it was reported from the upper Bartonian of the Paris Basin (Grambast 1958;  
49  
50 353 Grambast & Grambast-Fessard 1981; Riveline 1986; Riveline & Cavelier 1987), as well as  
51  
52 354 from several basins of southern France (Feist-Castel 1976).

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3 356 ----- Figure 10 near here-----  
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9 358 Genus *Psilochara* Grambast, 1959  
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11

12 359  
13  
14

15 360 *Psilochara polita* (Reid et Groves, 1921) Grambast, 1959  
16  
17

18 (Fig. 11A–F)  
19 361  
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22 362  
23  
24

25 363 1921 *Chara polita*, sp. nov. Reid & Groves: p. 187, pl. 5, figs 9, 12.  
26  
27

28 364 1927 *Gyrogona politus*, Pia: p. 90.  
29  
30

31 365 1958 *Ovochara polita*, comb. nov. Grambast: p. 167.  
32  
33

34 366 1959 *Peckichara polita*, Horn af Rantzien: p. 116, pl. 13, figs 1–3.  
35  
36

37 367 1959 *Psilochara polita*, Grambast: p. 11.  
38  
39

40 368 1977b *Psilochara polita*, Feist-Castel: p. 153.  
41  
42

43 369 1986 *Psilochara polita*, Riveline: p. 59, pl. 22, figs 8–12.  
44  
45

46 370  
47  
48

49 371 **Material.** 58 gyrogonites in sample G-6a. Collection numbers of figured specimens: HNHM-  
50  
51

52 372 PBO 1564–1569.  
53  
54

55 373 **Description.** Medium-sized gyrogonites (550–700  $\mu\text{m}$  in height 500–650 and  $\mu\text{m}$  in width)  
56  
57

58 374 with ovoidal shape (ISI 100–120) and laterally showing 7–10 convolutions (Fig. 11A–C; Fig.  
59  
60

375 12). Apex round to pointed (Fig. 11A–C). Base tapering to prolonged into a stout basal column

1  
2  
3 376 (Fig 11A–C) and showing a small pentagonal basal pore (Fig. 11F). Spiral cells smooth,  
4  
5 377 concave or flat and separated by protruding narrow to weakly undulated intercellular ridges.  
6  
7

8  
9 378 **Distribution.** *Psilochara polita* is described here from the middle Eocene of Hungary for the  
10  
11 379 first time. It has previously been described from the upper Bartonian of the Isle of Wight,  
12  
13 380 England, (Reid & Groves 1921; Feist-Castel 1977b; Riveline 1986) and of the Paris Basin  
14  
15 381 (Grambast 1958; Riveline 1986).  
16  
17

18  
19 382

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22 383 ----- Figures 11, 12 near here -----  
23  
24

25 384

26  
27  
28 385 ***Psilochara* sp.**

29  
30  
31 386 (Fig. 11G–I)  
32  
33

34 387

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36  
37 388 **Material.** 17 gyrogonites in sample G-6a. Collection numbers of figured specimens: HNHM-  
38  
39 389 PBO 1570–1571.  
40  
41

42  
43 390 **Description.** Medium to large-sized gyrogonites (780–905  $\mu\text{m}$  wide and 670–775  $\mu\text{m}$  high)  
44  
45 391 with elongated ovoidal (subprolate) shape (ISI 110–125) and laterally showing 8–10  
46  
47 392 convolutions (Fig. 11G). Apex truncated. Apical end of spiral cells enlarged and pointing  
48  
49 393 upwards (Fig. 11H). Base truncated to somewhat tapering, bearing a small pentagonal basal  
50  
51 394 pore. Basal plate unipartite and visible from the gyrogonite interior (Fig. 11I). Spiral cells  
52  
53 395 concave or flat and smooth, except at the periapical area, where they are irregularly ornamented  
54  
55 396 with a broad mid-cellular crest.  
56  
57  
58  
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1  
2  
3 397 **Remark.** The low number of gyrogonites hinders a more precise taxonomic attribution of this  
4  
5 398 population. However, it is reported here since it differs in size and shape from the other species  
6  
7  
8 399 of *Psilochara* found at Gánt.

400

401

Genus *Nitellopsis* Hy, 1889

402

403

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

404

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

406

1972

407

(Fig. 11J–N)

408

409 1945 *Chara palaeohungarica*, sp. nov. Rásky: p. 38, pl. 1, figs 16–18.

410

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

411

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

412

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

413

4.

414

415 **Material.** 28 gyrogonites in sample G-2.3 and 33 in sample G-2.5. Collection numbers of

416

figured specimens: HNHM-PBO 1572–1576.

1  
2  
3 417 **Description.** Gyrogonites very large (900–1200  $\mu\text{m}$  high and 800–1050  $\mu\text{m}$  wide), oval, prolate  
4  
5 418 spheroidal (ISI 100–120) in shape, showing 8–11 (often 9) convolutions in lateral view (Fig.  
6  
7 419 11J–L; Fig. 13). Spiral cells concave to flat. Apex prominent with spiral cells protruding to  
8  
9 420 form a central rosette. Spiral cells show both narrowing and thinning in the periapical area (Fig.  
10  
11 421 11M). Base rounded to almost conical, occasionally lengthened in a short broad column. A  
12  
13 422 large (155–230  $\mu\text{m}$  across) pentagonal basal pore occurs within a wide basal funnel (Fig. 11N).  
14  
15  
16

17  
18 423 **Distribution.** The species '*Chara palaeohungarica*' was first described from subsurface beds  
19  
20 424 attributed to the Paleocene in Dorog, Hungary, by Rásky (1945). Here this species is described  
21  
22 425 from beds cropping out at Gánt, which are probably time-equivalent to those of the type locality.  
23  
24 426 The present study supports reassignment of this species to the middle Eocene rather than to the  
25  
26 427 Paleocene.  
27  
28  
29

30 428 **Remarks.** The gyrogonites studied here are diagenetically deformed, which hinders a more  
31  
32 429 definitive taxonomic attribution. A re-study of the type material (HNHM 55.1458–55.1460) by  
33  
34 430 one of the authors of this study (CMC) showed that, besides the holotype, which is a  
35  
36 431 subspherical gyrogonite as illustrated by Rásky (1945, pl. I, Fig. 16), there were more oval to  
37  
38 432 elongated gyrogonites present in the collection similar to those described here, which Rásky  
39  
40 433 (1945, p. 38) termed 'cylindrical'.  
41  
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48 435 ----- Figure13 near here-----  
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54 437 Genus *Chara* Vaillant, 1719

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2  
3 439 *Chara media* Grambast, 1958  
4  
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6 440 (Fig. 14A–I)  
7  
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9 441  
10  
11

12 442 1958 *Chara media*, Grambast: p. 178, fig. 81b.  
13  
14

15 443 1986. *Chara media*, Riveline: p. 68, pl. 29, figs 6–12.  
16  
17  
18

19 444  
20  
21

22 445 **Material.** Up to 80 gyrogonites in both samples G-2.5 and G-6a. Collection numbers of figured  
23  
24 446 specimens: HNHM-PBO 1577–1585.  
25  
26

27 447 **Description.** Gyrogonites of medium size (400–650 µm high and 300–500 µm wide) ellipsoidal  
28  
29 448 subprolate (ISI 110–145), laterally showing 8–11 (usually 9–10) convolutions (Fig. 14A–G,  
30  
31 449 Fig. 15). Maximum width nearly at the half to 2/3 of height. Apex rounded to slightly conical,  
32  
33 450 with distinctly widening of the spiral cell endings (Fig. 14H). Spiral cells concave, smooth and  
34  
35 451 without any periapical modification. Base tapering showing a superficial pentagonal basal pore  
36  
37 452 (Fig. 14I).  
38  
39  
40  
41

42 453 **Distribution.** *Chara media* is described here from the upper Eocene (upper Bartonian) of  
43  
44 454 Hungary for the first time. Grambast (1958) and Riveline (1986) documented this species from  
45  
46 455 the upper Bartonian–lower Oligocene of several basins in France, Belgium, and Germany.  
47  
48  
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50 456  
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53 457 ----- Figures 14, 15 near here-----  
54  
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56 458  
57  
58

59 459 *Chara subcylindrica* Reid et Groves, 1921  
60

1  
2  
3 460 (Fig. 14J–O)  
4  
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6 461  
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9 462 1921 *Chara subcylindrica*, sp. nov. Reid & Groves: p. 187, pl. 5, fig. 4–5.  
10  
11

12 463 1959 *Grambastichara subcylindrica*, Horn af Rantzien: p. 76, pl. 3, figs 5–7.  
13  
14

15 464 1986 *Chara cf. subcylindrica*, Riveline: p. 67, pl. 30, figs 5–8.  
16  
17  
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19 465  
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21

22 466 **Material.** Up to 250 gyrogonites in sample G-6b. Collection numbers of figured specimens:  
23

24 467 HNHM-PBO 1586–1591.  
25  
26

27 468 **Description.** Medium-sized gyrogonites (500–750 µm high and 200–400 µm wide) ellipsoidal  
28  
29 469 prolate to perprolate (ISI 130–200) in shape, laterally showing 8–11 (usually 9–10)  
30  
31 470 convolutions (Fig. 14J–M; Fig. 16). Maximum width at the equator. Apex rounded with  
32  
33 471 widening of the spiral cell endings (Fig. 14N). Spiral cells often slightly concave to flat,  
34  
35 472 separated by narrow intercellular ridges, cells non-ornamented and without any periapical  
36  
37 473 modification. Base regularly tapering to round, showing a superficial pentagonal basal pore  
38  
39 474 (Fig. 14O).  
40  
41  
42  
43

44 475 **Distribution.** This is the first report of *Chara subcylindrica* in Hungary. According to Reid &  
45  
46 476 Groves (1921) and Riveline (1986), this species occurs in the upper Bartonian–lower Oligocene  
47  
48 477 of England, France, Belgium and Germany.  
49  
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52 478  
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55 479 ----- Figure 16 near here -----  
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## 481 Discussion

482

### 483 Definition of the *Raskyella peckii* anagenetic lineage

484 Evolutionary lineages formed by a succession of charophyte fructifications changing gradually  
485 in time were first described in the family Clavatoraceae by Grambast (1974). Later, similar  
486 lineages were found as well in the family Characeae (e.g. lineage *Harrisichara vasiformis-*  
487 *tuberculata* described by Feist-Castel 1977b; or lineage *Peckichara pectinata* by Vicente *et al.*  
488 2018). Here we describe the first of such lineages in the family Raskyellaceae. In the Lutetian  
489 and Bartonian of Gánt (Hungary), three former species of the genus *Raskyella* – *R. peckii*, *R.*  
490 *caliciformis*, and *R. vadaszii* – have been found to form a continuous succession of gyrogonite  
491 morphologies, connected by intermediate morphotypes. This gradualistic lineage is interpreted  
492 as an evolutionary species in the sense of Wiley (1981) and Ax (1987), and the original taxa  
493 have been newly combined as anagenetic varieties of the species with nomenclatural priority,  
494 which is *R. peckii*.

495 The first evolutionary stage of the *R. peckii* lineage (Fig. 17) is represented by *R. peckii* var.  
496 *peckii*, and includes, as well, the smallest gyrogonite morphotype initially described as  
497 *Raskyella peckii ganesensis* Soulié-Märsche, 1971. *R. peckii* var. *peckii* is characterized by  
498 gyrogonites which are very variable in size, but consistently unornamented. This stage has a  
499 long duration, since it was documented from the lower Lutetian to the upper Bartonian of the  
500 Ebro Basin, Catalonia, by Martín-Closas *et al.* (1999a) and can thus be superimposed onto some  
501 of the ulterior morphotypes of the lineage, this being quite a common situation in charophyte  
502 lineages (e.g., Grambast, 1974). The coeval *Raskyella peckii* subsp. *meridionale* Grambast,  
503 1960, was not found in the section studied and corresponds to a southern geographic subspecies



1  
2  
3 504 of this lineage, thriving in North Africa and the Prebetic Domain in the Balearic Islands in Spain  
4  
5 505 (Grambast 1960; Martín-Closas & Ramos 2005).  
6  
7

8 506 The second evolutionary stage in the lineage of *R. peckii* is represented by *R. peckii* var.  
9  
10 507 *caliciformis*. Intermediate morphotypes between *R. peckii* var. *peckii* and *R. peckii* var.  
11  
12 508 *caliciformis* display a progressive increase in the gyrogonite size (up to 1000 µm in height),  
13  
14 509 and a change in shape from elongated to rounded, between samples G-2.2 and G-2.4 of the Gánt  
15  
16 510 section. Furthermore, there is a progressive development of the ornamentation corresponding  
17  
18 511 to *R. peckii* var. *caliciformis* in the same sequence, with for instance 100% of gyrogonites  
19  
20 512 corresponding to *R. peckii* var. *peckii* in sample G-2.4, while in sample G-2.5, there is only 10%  
21  
22 513 of *R. peckii* var. *peckii*, resulting in 90% of *R. peckii* var. *caliciformis* (Fig. 17).  
23  
24  
25  
26  
27

28 514 The third stage of the lineage is represented by *R. vadaszii* from the upper Bartonian, which  
29  
30 515 shows an additional increase of the gyrogonite size of about 150–250 µm in height and 100–  
31  
32 516 125 µm in width, and especially the development of progressively more complex ornamentation  
33  
34 517 patterns in comparison to the previous evolutionary step (Fig. 17). This gradual change can be  
35  
36 518 observed between samples G-2.5 and G-6b of the Gánt section. Thus, sample G-5 displays a  
37  
38 519 homogeneous population with 100% of gyrogonites corresponding to *R. peckii* var.  
39  
40 520 *caliciformis*, while in the overlying sample G-6a, the gyrogonite population of *R. peckii*  
41  
42 521 contains only 15% of specimens of *R. peckii* var. *caliciformis* and 85% of *R. peckii* var. *vadaszii*.  
43  
44 522 Finally, in sample G-6b there is a homogeneous population of gyrogonites corresponding to *R.*  
45  
46 523 *peckii* var. *vadaszii*.  
47  
48  
49  
50

51 524 Overall, the *R. peckii* lineage follows the general evolutionary trend in the evolutionary lineages  
52  
53 525 of other charophyte families, characterized by an increase in size and sphericity (Clavatoraceae  
54  
55 526 and Raskyellaceae), and a progressive development of ornamentation (Characeae), as shown  
56  
57  
58  
59  
60

1  
2  
3 527 by Feist-Castel (1977b), Martín-Closas *et al.* (1999b), Sille *et al.* (2004) and Vicente & Martín-  
4  
5 528 Closas (2018).  
6  
7  
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11  
12 530 ----- Figure 17 near here -----  
13  
14  
15 531

16  
17  
18 532 **New local charophyte biozonation**  
19

20  
21 533 Among the charophyte species described from the bauxite cover-sequence at the Gánt section  
22  
23 534 (Vértes Hills, Hungary), *Raskyella peckii* represents the most significant species for use in  
24  
25 535 biostratigraphy within the non-marine Lutetian and Bartonian, as previously suggested by  
26  
27 536 Riveline *et al.* (1996) and Martín-Closas *et al.* (1999a). The *Raskyella peckii* biozone was  
28  
29 537 defined by Riveline *et al.* (1996) as a ‘partial range zone comprising the interval from the first  
30  
31 538 appearance of *Raskyella peckii* L. and N. Grambast, 1954, to the first appearance of *Chara*  
32  
33 539 *friteli* Grambast, 1958, lower Lutetian to lower Bartonian in age. This study proposes to extend  
34  
35 540 this biozone to cover also the upper Bartonian, and to redesignate it as a superzone subdivided  
36  
37 541 into the following three successive biozones (Fig. 18):  
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42 542 - **Raskyella peckii peckii Zone**: partial range zone defined from the first occurrence of the  
43  
44 543 morphotype *peckii* to the first occurrence of the morphotype *caliciformis*, Lutetian–lower  
45  
46 544 Bartonian in age. The local charophyte assemblage characterizing this zone in Gánt occurs in  
47  
48 545 the basal part of the studied section (‘Packet 2’, ‘blue-hole’ freshwater limestone facies,  
49  
50 546 samples G-2.2, G-2.3 and G-2.4), and is composed of *R. peckii* var. *peckii*, *G. caelata* forma  
51  
52 547 *caelata*, *G. caelata* forma *monolifera*, and *Nitellopsis (Tectochara)* aff. *palaeohungarica*, some  
53  
54 548 of which are well known to occur in several European basins (Rásky 1945; Grambast 1958;  
55  
56 549 Riveline 1986; Martín-Closas *et al.* 1999a) during the same time interval.  
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3 550 - **Raskyella peckii caliciformis Zone**: partial range zone defined from the first occurrence of  
4  
5 551 the morphotype *caliciformis* to the first occurrence of the morphotype *vadaszii*, lower Bartonian  
6  
7 552 in age. This zone includes in Gánt the assemblage found in the lower part of ‘Packet 3’ (samples  
8  
9 553 G-2.5) and composed of *R. peckii* var. *caliciformis*, *G. caelata* forma *caelata*, *G. caelata* forma  
10  
11 554 *monolifera*, *G. caelata* forma *baccata*, *Nitellopsis (Tectochara)* aff. *palaeohungarica*, and  
12  
13  
14 555 *Chara media*.

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17  
18 556 - **Raskyella pecki vadaszii Zone**: partial range zone defined from the first occurrence of the  
19  
20 557 morphotype *vadaszii* to the first occurrence of the next zone defined in the Paris Basin, which  
21  
22 558 is *Psilochara repanda*. This zone would be upper Bartonian in age. The assemblage occurring  
23  
24 559 in the middle part of the Gánt section (‘Packet 3’, samples G-6a and G-6b), composed of *R.*  
25  
26 560 *peckii* var. *vadaszii*, *G. caelata* forma *bicincta*, *G. caelata* forma *baccata*, *G. caelata* forma  
27  
28 561 *fasciata*, *Psilochara polita*, *Psilochara* sp., *Chara media*, and *Chara subcylindrica*  
29  
30 562 characterizes locally this biozone.  
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#### 36 37 38 564 **Implications on the age of the bauxite cover-sequence**

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40  
41 565 The biostratigraphic analysis carried out suggests a relative age of Lutetian– Bartonian (Fig.  
42  
43 566 18) of the bauxite cover-sequence at the Gánt section (Vértes Hills, Hungary), rather than  
44  
45 567 constraining it to the Bartonian as previously suggested by Bignot (1985). A Lutetian age,  
46  
47 568 deduced from the charophytes and attributed to the lower part of the studied series, has been  
48  
49 569 already suggested in several works preceding that of Bignot (1985), notably those of Szóts  
50  
51 570 (1938), Kopek (1980), and Dudich & Kopek (1982), on the basis of mollusc and palynomorph  
52  
53 571 biostratigraphy. The data presented herein support the idea that the Eocene succession in the  
54  
55 572 studied area reflects a stepwise marine transgression upon the bauxite deposits, beginning in  
56  
57 573 the Lutetian. Our new chronostratigraphic framework sheds new light on the timing of the long-

1  
2  
3 574 lasting subaerial exposure and alteration process generating the bauxite strata. Consequently,  
4  
5 575 coeval strata from surrounding localities within the Transdanubian Central Range should be re-  
6  
7 576 studied and analysed from the viewpoint of charophyte biostratigraphy, in order to correlate the  
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9 577 post-bauxite depositional event(s) on a regional scale and to improve the understanding of its  
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11 578 tectono-eustatic control.  
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19 580 ----- Figure 18, near here-----  
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## 23 24 582 **Conclusions**

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30 584 Eocene (Lutetian–Bartonian) charophyte assemblages are taxonomically described for the first  
31  
32 585 time from an outcrop of the bauxite cover-sequence at Gánt (Vértes Hills), Hungary's  
33  
34 586 Transdanubian Central Range. The sections show for the first time that the raskyellacean  
35  
36 587 charophytes also evolved in gradualistic lineages, similarly to what is already known for other  
37  
38 588 charophyte families. The *Raskyella peckii* lineage is formed by three successive stages and is  
39  
40 589 interpreted here in terms of the anagenesis of the evolutionary species *Raskyella peckii*,  
41  
42 590 including its gradual change to the morphotype previously known as *R. vadaszi*.  
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47 591 From a biostratigraphic viewpoint, the assemblages studied belong to the *Raskyella peckii*  
48  
49 592 biozone of Martín-Closas *et al.* (1999a), which is here reinterpreted as a superzone extending  
50  
51 593 to cover the *Raskyella vadaszii* Zone of Riveline *et al.* (1996) and attributed to the Lutetian–  
52  
53 594 Bartonian interval. In this study, this superzone is subdivided into three successive local partial  
54  
55 595 range biozones, defined by each of the successive varieties of the evolutionary species *R. peckii*:  
56  
57 596 (1) the *Raskyella peckii peckii* partial range zone is characterized by *R. peckii peckii*, *G. caelata*  
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3 597 forma *caelata*, *G. caelata* forma *monolifera* and *Nitellopsis (Tectochara)* aff. *palaeohungarica*,  
4  
5 598 Lutetian–lowermost Bartonian in age; (2) the *Raskyella peckii caliciformis* partial range zone  
6  
7 599 is characterized by *R. peckii caliciformis*, *G. caelata* forma *caelata*, *G. caelata* forma  
8  
9 600 *monolifera*, *G. caelata* forma *baccata*, *Nitellopsis (Tectochara)* aff. *palaeohungarica* and  
10  
11 601 *Chara media*, lower Bartonian in age; and (3) the *Raskyella peckii vadaszii* partial range zone  
12  
13 602 is characterized by *R. peckii vadaszii*, *G. caelata* forma *bicincta*, *G. caelata* forma *baccata*, *G.*  
14  
15 603 *caelata* forma *fasciata*, *G. tuberosa*, *Psilochara polita*, *Psilohara* sp., *Chara media* and *Chara*  
16  
17 604 *subcylindrica*, upper Bartonian in age.

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23 605 In light of the new results presented here, the charophyte-bearing sequences studied in this work  
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25 606 represent a longer time span than previously thought, running from the Lutetian to the  
26  
27 607 Bartonian. This has direct implications on the understanding of the Eocene regional  
28  
29 608 stratigraphic scheme of the Transdanubian Central Range, particularly in terms of  
30  
31 609 synchronism/diachronism in the regional stratigraphic correlation, as well as the timing of the  
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33 610 tectono-sedimentary control and palaeogeographic evolution.  
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## 835 **Figure Captions**

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3 837 **Figure 1.** **A**, geographical and geological setting of the study area (after Fodor 2007). **B**,  
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5 838 panoramic view of the studied Gánt section at the Vértes Hills (north-western Hungary).  
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11 840 **Figure 2.** Distribution of the charophytes species in the bauxite cover-sequence of the studied  
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13 Gánt section (Vértes Hills, Hungary), according to Bignot *et al.* (1985), updated for  
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15 charophyte content.  
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22 844 **Figure 3.** *Raskyella peckii* gyrogonites from the Gánt bauxite cover-sequence. **A–H**,  
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24 *Raskyella pecki* var. *peckii* (samples G-2.2, G-2.3, G-2.4, and G-2.5), HNHM-PBO 1501–  
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26 1508. **A–E**, lateral view; **F–G**, apical view; **H**, basal view. **I–P**, *Raskyella peckii* var.  
27  
28 *caliciformis* (samples G-2.5 and G-6a), HNHM-PBO 1509–1516. **I–K**, lateral view; **L**, lateral  
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30 847 view of gyrogonite partially broken showing internal cast. **M**, internal cast with well-  
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32 848 view of gyrogonite partially broken showing internal cast. **M**, internal cast with well-  
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34 849 developed undulations. **N–O**, apical view; **P**, basal view.  
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40 851 **Figure 4.** Frequency distribution of the height (A), width (B), number of convolutions (C),  
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42 852 and height/width ratio (ISI) (D) of the *Raskyella peckii* var. *peckii* population (50 gyrogonites  
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44 853 measured), from samples G-2.2, G-2.3, and G-2.4 in the bauxite cover-sequence of the Gánt  
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46 854 section.  
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53 856 **Figure 5.** Frequency distribution of the height (A), width (B), number of convolutions (C),  
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55 857 and height/width ratio (ISI) (D) of the *Raskyella peckii* var. *caliciformis* population (50  
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57 858 gyrogonites measured), from sample G-2.5 in the bauxite cover-sequence of the Gánt section.  
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6 860 **Figure 6.** *Raskyella peckii vadaszii* gyrogonites from the Gánt bauxite cover-sequence (A–S,  
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8 861 samples G-6a and G-6b, HNHM-PBO 1517–1534). A–K, lateral view. L–P, apical view; Q,  
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10 862 basal view; R–S, inside wall of a gyrogonite showing the crenate undulation of the cellular  
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12 863 sutures in contact with the spiral cells and the apical cells.  
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19 865 **Figure 7.** Frequency distribution of the height (A), width (B), number of convolutions (C),  
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21 866 and height/width ratio (ISI) (D) of the *Raskyella peckii* var. *vadaszii* population (50  
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23 867 gyrogonites measured), from samples G-6a and G-6b in the bauxite cover-sequence of the  
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25 868 Gánt section.  
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32 870 **Figure 8.** *Gyrogona caelata* gyrogonites from the Gánt bauxite cover-sequence. A–G,  
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34 871 *Gyrogona caelata* forma *caelata* (samples G-2.2, G-2.3, G-2.4, and G-2.5), HNHM-PBO  
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36 872 1535–1553. A–B, D–E, basal view C, detail of the ornamentation pattern; F, basal view; G,  
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38 873 apical view. H–K, *Gyrogona caelata* forma *bicincta* (samples G-6a and G-6b). H, lateral  
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40 874 view; I, detail of the ornamentation pattern; J–K, apical view. L–M, *Gyrogona caelata* forma  
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42 875 *monolifera* (samples G-2.2, G-2.3, G-2.4, and G-2.5). L, lateral view; M, basal view. N–Q,  
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44 876 *Gyrogona caelata* forma *baccata* (samples G-2.5, G-6a, and G-6b). N–O, lateral view; P,  
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46 877 basal view; Q, apical view. R–V, *Gyrogona caelata* forma *fasciata* (samples G-6a and G-6b).  
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48 878 R, lateral view; S–T, apical view; U–V, detail of the simple (unipartite) basal plate.  
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57 880 **Figure 9.** Frequency distribution of the height (A), width (B), number of convolutions (C),  
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59 881 and height/width ratio (ISI) (D) of the *Gyrogona caelata* population (50 gyrogonites  
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3 882 measured), from samples G-2.2, G-2.3, G-2.4, G-2.5, and G-6a in the bauxite cover-sequence  
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5 883 of the Gánt section.  
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11 885 **Figure 10.** *Gyrogona tuberosa* gyrogonites from the Gánt bauxite cover-sequence (sample G-  
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13 6b), HNHM-PBO 1554–1563. **A–G**, lateral view; **H**, apical view; **I–J**, basal view.  
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20 888 **Figure 11.** Gyrogonites of genera *Psilochara* and *Nitellopsis* from the Gánt bauxite cover-  
21  
22 889 sequence. **A–F**, *Psilochara polita* (sample G-6a), HNHM-PBO 1564–1569. **A–C**, lateral  
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24 890 view; **D–E**, apical view; **F**, basal view. **G–I**, *Psilochara* sp. (sample G-6a), HNHM-PBO  
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26 891 1570–1571. **G**, lateral view; **H**, apical view; **I**, internal view showing simple (unipartite) basal  
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28 892 plate (arrowed). **J–N**, *Nitellopsis (Tectochara)* aff. *palaeohungarica* (samples G-2.3 and G-  
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30 893 2.5), HNHM-PBO 1572–1576. **J–L**, lateral view; **M**, apical view; **N**, basal view.  
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38 895 **Figure 12.** Frequency distribution of the height (A), width (B), number of convolutions (C),  
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40 896 and height /width ratio (ISI) (D) of the *Psilochara polita* population (50 gyrogonites  
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42 897 measured), from sample G-6a in the bauxite cover-sequence of the Gánt section.  
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49 899 **Figure 13.** Frequency distribution of the height (A), width (B), number of convolutions (C),  
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51 900 and height /width ratio (ISI) (D) of the *Nitellopsis (Tectochara)* aff. *palaeohungarica*  
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53 901 population (50 gyrogonites measured), from samples G-2.3 and G-2.5 in the bauxite cover-  
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55 902 sequence of the Gánt section.  
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3 904 **Figure 14.** *Chara* gyrogonites from the Gánt bauxite cover-sequence. **A–I**, *Chara media*  
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5 905 (samples G-2.5 and G-6a), HNHM-PBO 1577–1585. **A–G**, lateral view; **H**, apical view; **I**,  
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7 906 basal view. **J–O**, *Chara subcylindrica* (sample G-6b), HNHM-PBO 1586–1591. **J–M**, lateral  
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9 907 view; **N**, apical view; **O**, basal view.  
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16 909 **Figure 15.** Frequency distribution of the height (A), width (B), number of convolutions (C),  
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18 910 and height /width ratio (ISI) (D) of the *Chara media* population (50 gyrogonites measured),  
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20 911 from samples G-2.5 and G-6a in the bauxite cover-sequence of the Gánt section.  
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27 913 **Figure 16.** Frequency distribution of the height (A), width (B), number of convolutions (C),  
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29 914 and height/width ratio (ISI) (D) of the *Chara subcylindrica* population (50 gyrogonites  
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31 915 measured), from sample G-6b in the bauxite cover-sequence of the Gánt section.  
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38 917 **Figure 17.** Stratigraphic distribution of variants of the anagenetic lineage of the species  
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40 918 *Raskyella peckii*.  
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46 920 **Figure 18.** Charophyte Biostratigraphy, age and correlation of the bauxite cover-sequence of  
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48 921 the Gánt section.  
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4 1 **A new diverse charophyte flora and biozonation of the Eocene bauxite**  
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6 2 **cover-sequence at Gánt (Vértés Hills, Hungary)**  
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13 4 Khaled ~~Trabelsi~~<sup>1,2,3</sup>Trabelsi<sup>a,b,c\*</sup>, Benjamin ~~Sames~~<sup>3,4</sup>Sames<sup>c,d</sup>, Michael ~~Wagreich~~<sup>3</sup>Wagreich<sup>c</sup>,  
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24 ~~A largely new and~~ diverse Eocene charophyte flora from a section at Gánt (Vértes Hills),  
 25 Transdanubian Central Range, north-western Hungary, provides significant new information to  
 26 previous studies only based on subsurface data published from the mid-20<sup>th</sup> ~~Century. The~~  
 27 ~~century. This newly acquired material facilitates the~~ taxonomic ~~study of this flora allows~~  
 28 revision and emendation of the species *Raskyella peckii* ~~facilitates the definition of and thereby~~  
 29 ~~defines~~ a new ~~evolutionary~~-anagenetic lineage based on three successive ~~anagenetic~~-varieties  
 30 ~~of this species~~ which were formerly considered as separate species or subspecies: *Raskyella*  
 31 *peckii* var. *peckii* (early Lutetian–early Bartonian), *Raskyella peckii* var. *caliciformis* (early  
 32 Bartonian), and *Raskyella peckii* var. *vadaszii* (late Bartonian). Based on ~~thesethis lineage~~, we  
 33 propose a new local charophyte biozonation ~~with the new that consists of a~~ ‘*Raskyella peckii*  
 34 ~~SuperzoneSuperzone~~’ (Lutetian–Bartonian), subdivided into three successive charophyte  
 35 partial range zones: The ‘*Raskyella peckii peckii* Zone’ (Lutetian–lowermost Bartonian) ~~is~~  
 36 ~~locally~~ characterized by an assemblage of *R. peckii peckii*, *Gyrogona caelata* forma *caelata*, *G.*  
 37 *caelata* forma *monolifera* and *Nitellopsis (Tectochara)* ~~aff. palaeohungarica. The, the~~  
 38 ‘*Raskyella peckii caliciformis* Zone’ (lower Bartonian) ~~includescharacterized by the local~~  
 39 assemblage of *R. peckii* var. *caliciformis*, *G. caelata* forma *caelata*, *G. caelata* forma  
 40 *monolifera*, *G. caelata* forma *baccata*, *Nitellopsis (Tectochara)* ~~aff. palaeohungarica~~ and  
 41 *Chara media*. ~~The, and the~~ ‘*Raskyella peckii vadaszii* Zone’ (upper Bartonian) ~~is composed of~~  
 42 ~~the local assemblage of~~ ~~characterized by~~ *R. peckii* var. *vadaszii*, *G. caelata* forma *bicincta*, *G.*  
 43 *caelata* forma *baccata*, *G. caelata* forma *fasciata*, *G. tuberosa*, *Psilochara polita*, *Psilochara*  
 44 sp., *Chara media* and *Chara subcylindrica*. Future research may show the new local  
 45 biozonation as applicable to ~~the whole of Europe and complementingcomplementary to~~ the  
 46 current European charophyte biozonation. Our results show that the sequences from Gánt,  
 47 ~~which were~~ previously regarded as upper mid-Eocene (upper Lutetian–lower Bartonian) ~~in age,~~

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4 48 appear to ~~comprise~~represent a longer ~~time~~chronostratigraphic interval, ~~i.e.:~~ lower Lutetian ~~tilt~~to  
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6 49 upper Bartonian, ~~with also has implications on the understanding of the regional stratigraphy~~  
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8 50 ~~of.~~ Our chronostratigraphic results imply a longer and more stepwise Eocene major  
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10 51 transgression in the Transdanubian Central Range ~~during the Eocene~~than previously thought.  
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18 53 **Keywords:** Characeae, Raskyellaceae, ~~biozonation,~~ evolutionary lineagephylozone,  
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20 54 gradualistic evolution, Paleogene, Central Europe.  
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## 26 27 56 **Introduction**

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36 58 Charophytes represent one of the most useful tools in the biostratigraphic analysis of Cenozoic  
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38 59 non-marine deposits worldwide. During the Eocene, charophytes have been the object of  
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40 60 significant taxonomic, biostratigraphic, palaeoecological and palaeobiogeographic interest,  
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42 61 particularly in South European basins from France and Spain (Grambast 1958, 1962a,  
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44 62 ~~1972a~~1972; Feist-Castel 1970, 1972, 1975, 1977a; Feist & Ringade 1977; Anadón & Feist  
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46 63 1981; Riveline 1986; Anadón *et al.* 1992; Sanjuan & Martín-Closas 2012;). As a result, a  
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48 64 European Charophyte Biozonation based largely on these basins was proposed by Riveline et  
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50 65 al. (1996). For the Eocene, up to 11 charophyte biozones were defined based mainly on data  
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52 66 from Western Europe. This biozonation has been updated since then, e.g., by Sanjuan et al.  
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54 67 (2014;) for the upper Eocene. In contrast, the Eocene charophyte flora from Central and  
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56 68 Eastern Europe is relatively ~~less well-~~poorly known; and in the case of Hungary, the pioneer  
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3 69 study by Rásky (1945) based on subsurface data is practically the only ~~known~~. ~~With the aim~~  
4 ~~one~~  
5 70 ~~available. This author described for the first time a species-rich charophyte flora from Hungary,~~  
6 ~~at a time when charophyte taxonomy was still at an early stage. She had already assigned the~~  
7 ~~flora studied in this area to the middle Eocene, and her work was the basis for future studies in~~  
8 ~~charophyte taxonomy, including the definition of~~ ~~updating the~~ ~~new family Raskyellaceae by~~  
9 ~~Grambast & Grambast (1954). Later, Bignot *et al.* (1985), based on an exhaustive~~  
10 ~~palaeontological study of the Gánt section including molluscs, foraminifers, ostracods,~~  
11 ~~palynomorphs and charophytes, assigned the bauxite cover-sequence to the Upper Lutetian or~~  
12 ~~Bartonian, respectively.~~

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25 78 ~~This study aims to update the compendium of~~ knowledge on Eocene Hungarian and Central  
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27  
28 79 European charophytes, ~~the present study provides~~ ~~providing~~ a taxonomic revision of ~~this flora~~  
29  
30 80 ~~from the respective flora that is based on surface samples of sections at the Gánt locality~~ ~~based~~  
31  
32 81 ~~on an outcropping section,~~ as well as a discussion ~~on~~ ~~regarding~~ its ~~significance~~ ~~for~~  
33  
34 82 biostratigraphic ~~purposes~~ ~~significance and utility.~~

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## 84 **Geological setting**

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86 Within the Transdanubian Central Range (TCR), several bauxite deposits that developed  
87 ~~during~~ ~~across~~ the Cretaceous–Early Tertiary boundary ~~interval~~ are well known ~~for their~~  
88 ~~industrial use~~ as ~~economically exploited~~ ~~ore~~ ~~resources~~ of aluminium, ~~from which~~ ~~ore~~; and among  
89 ~~these~~, the famous karst bauxite of the Vértes Hills from the Gánt locality, ~~(north-western~~  
90 ~~Hungary~~ ~~stands out. Above~~) is a prominent example. ~~Strata overlying the bauxite, the~~  
91 ~~succession represents~~ ~~represent~~ the sedimentary record of progressive subcrustal erosion along

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2  
3 92 the East Alpine-West Carpathian forearc basin (Kázmér *et al.* 2003). The bauxite represents the  
4  
5 93 base of the Eocene charophyte-bearing strata ~~studied herein~~investigated in this study (Fig. 1).  
6  
7  
8 94 The Eocene succession sampled shows a remarkable lateral and vertical change of sedimentary  
9  
10 95 facies (Pálfalvi *et al.* 2006; Pálfalvi 2007) that has been attributed to tectonic control forces  
11  
12 96 acting on the sedimentation sedimentary body (Fodor 2007). The development of the post-  
13  
14 97 bauxite deposits ~~occurred under dual~~was laid down during oscillation of the groundwater table  
15  
16 98 and ~~the marine relative eustatic~~ sea level variations (Carannante *et al.* 1994; Mindszenty 2010),  
17  
18 99 occurring before the region was invaded flooded by ~~an open~~ marine incursion during the late  
20  
21 100 Bartonian (Bignot *et al.* 1985).  
22  
23 101 At the Gánt section, the bauxite cover-sequence ~~vertically~~ shows five stratigraphic units ~~of in a~~  
24  
25 102 vertical orientation dating from the middle Eocene age (Fig. 2), called ‘Packets’ in the sense of  
26  
27 103 Bignot *et al.* (1985), ~~from~~. ‘Packet 1’, about 1.5 m thick, corresponds to the bauxite itself,  
28  
29 104 which ~~only units 2 and 3 are studied herein~~unconformably overlies Triassic dolomites. ‘Packet  
30  
31 105 2’, 1.5–2 m in thickness, forms the ‘blue-hole’ freshwater limestone facies (Carannante *et al.*  
32  
33 106 1994; Pálfalvi 2007), ~~while~~ alternating with clays, rich in charophytes, ostracods and  
34  
35 107 gastropods. ‘Packet 3’, ca. 6.5 m thick, includes alternating sandy clay, coal and fresh- to  
36  
37 108 brackish water limestone, rich in charophytes, ostracods, molluscs and large benthic  
38  
39 109 foraminifera (Bignot *et al.* 1985). ~~In the latter facies charophytes~~ 1985). ‘Packet 4’ is ca. 12 m  
40  
41 110 thick and is mainly dominated by shallow marine limestone, rich in nummulites, miliolids,  
42  
43 111 molluscs and ostracods. Finally, ‘Packet 5’ is ca. 6m thick and displays an alternation of shallow  
44  
45 112 marine marl and limestone, rich in *Nummulites* and *Orbitolites*. ‘Packets’ 2 and 3 were sampled-  
46  
47 113 for charophytes and are studied here.  
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56 115 -----Figures 1, 2 near here-----  
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## 117 **Material and methods**

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

139

## 140 **Systematic palaeontology**



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3 141 The charophyte flora from the bauxite cover sequence at Gánt (Vértes Hills, Hungary) studied  
4  
5 142 here yields gyrogonites from two families: Raskyellaceae and Characeae. The different  
6  
7 143 charophyte species described below are stratigraphically distributed in the section as shown in  
8  
9 144 the Fig. 2.  
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16 146 Division **Charophyta** Migula, 1897  
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19 147 Class **Charophyceae** G. M. Smith, 1938 emend. Schudack, 1993  
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22 148 Order **Charales** Lindley, 1836  
23  
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25 149 Family **Raskyellaceae** Grambast, 1957  
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28 150 Sub-Family **Raskyelloideae**, Grambast et Grambast, 1955  
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31 151 Genus **Raskyella** (L. & N. Grambast et Grambast, 1954) emend. Grambast, 1962b  
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35 153 **Type species.** *Raskyella peckii* L. & N. Grambast et Grambast, 1954  
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41 155 **Remarks.** This species is understood as including several traditional taxa belonging to the  
42  
43  
44 156 genus *Raskyella* ~~L. & N. Grambast (1954)~~, which form a gradualistic lineage during the  
45  
46  
47 157 Eocene. These traditional taxa have been newly combined here to anagenetic varieties within a  
48  
49  
50 158 single evolutionary lineage or an evolutionary species, following the recommendations of  
51  
52  
53 159 Wiley (1981) and Ax (1978).  
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60 161 ***Raskyella peckii* var. *peckii*** L. & N. Grambast et Grambast, 1954

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3 162 (Fig. 3A–H)  
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6 163  
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9 164 1954 *Raskyella pecki* sp. nov. L. & N. Grambast: p. 670, text-figs 1a–c.  
10  
11  
12 165 1957 *Raskyella pecki* Grambast: p. 358, pl. 5, figs 7–9.  
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14  
15 166 1958 *Raskyella pecki* Grambast: p. 190, figs 87, a–c; p. 191, text-fig. 88.  
16  
17  
18 167 1959 *Raskyella pecki* Horn af Rantzien: pl. 19, figs 7–13.  
19  
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22 168 1971 *Raskyella peckii* subsp. *ganesensis* Soulié-Märsche: pl. 2, 1–5.  
23  
24  
25 169 1981 *Raskyella pecki* Anadón & Feist: pl. 1, figs 1–2; pl. 2, figs 3–4.  
26  
27  
28 170 1986 *Raskyella pecki* Riveline: pl. 37, figs 7–9.  
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31 171 ~~1999b~~1999a *Raskyella pecki* Martín-Closas *et al.*: p. 11, figs 6, 1–3.  
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37 173 **Material.** Up to 65 gyrogonites in sample G-2.4, and dozens in samples G-2.2 and G-2.3.  
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39 174 Collection numbers of ~~figures~~figured specimens: HNHM-PBO ~~xxxxx-yyy~~1501–1508.  
40  
41  
42 175 **Description.** Gyrogonites ~~of~~are ovoidal to ellipsoidal ~~in~~ shape, spherical to subprolate (ISI 100–  
43  
44 176 120) and of large size, 800–1050 µm in height and 750–1050 µm in width, showing laterally  
45  
46 177 7–10 (usually 9) convolutions (Fig. 4). Spiral cells often flat (Fig. ~~3, A3A~~) to slightly convex  
47  
48 178 (Fig. ~~3, C3C~~), or concave (Fig. ~~3, B3B~~), but regularly without any kind of ornamentation. Apex  
49  
50 179 broadly rounded, truncated and flattened, with the spiral cells abruptly discontinue and ending  
51  
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53 180 acutely in the apical periphery to be replaced by the development of five ~~deciduous~~-opercular  
54  
55 181 cells, each obliquely disposed at the end of a spiral cell (Fig. ~~3, F~~). ~~In case of germinated~~  
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182 ~~specimen 3F). Germinated specimens~~ (Fig. 3, ~~G~~, 3G) show a rose-shaped apical ~~pore~~  
 183 ~~appears opening~~. Internal casts of these gyrogonites were also found (Figs 3, ~~E~~ Fig. 3E).

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

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

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

205 *al.* 1997; Vianey-Liaud 1994), in the late lower Eocene–early middle Eocene of Tunisia  
 206 (Abdeljaoued *et al.* 1984) and in the Lutetian of Libya (Megerisi & Mamgain 1980).

207

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

209

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

211 Closas

212 (Fig. 3I–P)

213

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

217

218 1974 *Raskyella caliciformis* sp. nov. Soulié-Märsche: p. 112, pl. 1, figs 1–5.

219 1981 *Raskyella caliciformis*, Anadón & Feist: pl. 1, figs 6–7; pl. 2, figs 7–8.

220

221 **Material.** 63 gyrogonites in sample G-2.5. Collection numbers of ~~figures~~figured specimens:

222 HNHM-PBO ~~xxxxx-yyy~~1509–1516.

223 **Description.** Large sized gyrogonites (650–1000 µm high and 750–1050 µm wide) of globular  
 224 to oblate shape (ISI 80–105), showing laterally 6–9 (usually 8) convolutions (Fig. 5). Spiral  
 225 cells flat to slightly concave ornamented with stout, vertical to slightly inclined, well

226 individualized ~~tuberculestuber~~cles (Fig. 3, ~~I3I~~–K), which are the main diagnostic character of  
 227 this variety. Apex broadly rounded to truncated showing five ~~deciduous~~-opercular cells placed  
 228 at the end of the spiral cells. The opercular cells are sometimes convex and somewhat polygonal  
 229 in shape (Fig. 3, ~~N)3N~~), rather than rounded, which is the reason why the dehiscence  
 230 ~~poreopening~~ appears sometimes irregularly star-shaped (Fig. 3, ~~O)3O~~), rather than rose-shaped  
 231 (Fig. 3, ~~M3L~~), as already noted by Soulié-Märsche (1974) in the type material. The internal cast  
 232 of the gyrogonite (Fig. 3, ~~M3M~~) shows ~~low and~~-straight ridges ~~delimitingperpendicular to the~~  
 233 well-marked, undulated spiral cells. This wavy surface is uncommon in the inside of other  
 234 raskyellacean gyrogonites and is thought to correspond internally to the external tubercle  
 235 ornamentation.

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

240

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

242

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

244 Martín-Closas

245 (Fig. 6A–S)

246

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

249

250 1945 *Aclistochara vadaszi*, sp. nov. Rásky: p. 45, pl. II, figs 22–24.

251 1954 *Raskyella vadaszi*, comb. nov. L. and N. Grambast: p. 670.

252 1957 *Raskyella vadaszi*, Grambast: p. 358, pl. 5, figs 1–6.

253 1959 *Raskyella vadaszi*, Horn af Rantzien: pl. 20, figs 1–3.

254 1981 *Raskyella vadaszi*, Anadón & Feist: pl. 1, fig. 5; pl. 2, fig. 5.

255 1981 *Raskyella* aff. *vadaszi*, Anadón & Feist: pl. 1, figs 3–4; pl. 2, figs 1–2, 6.

256 1985 *Raskyella vadaszi*, Bignot *et al.*: p. 36, pl. 3, figs 8–11.

257 1986 *Raskyella vadaszi*, Riveline: pl. 37, figs 1–6.

258

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

261 **Description.** Large sized gyrogonites (800–1150  $\mu\text{m}$  ~~in width~~high and 800–1150  $\mu\text{m}$  ~~in~~  
 262 highwide) of oblate to ovoidal shape (ISI 80–120), showing laterally 7–10 (usually 9)  
 263 convolutions (Fig. 7). Spiral cells often convex and ornamented with stout tubercles of different  
 264 shapes and sizes, in most cases oriented parallel to the intercellular sutures (Fig. ~~6~~, A6A–C), or  
 265 more rarely tilted 20–30° but keeping parallelism between adjacent nodules (Fig. ~~6~~, E6E–G),  
 266 this being a diagnostic character of this morphotype. Three tubercle morphologies have been  
 267 observed: (1) rounded ~~tubercles~~tubercles, well individualized in the upper half of the

268 gyrogonite, but fused to neighbouring ~~tubercles~~ tubercles in the lower half (Fig. ~~6, I6I–K~~), (2)  
 269 elongated ~~tubercles~~ tubercles more or less connected to each other and producing slightly wavy  
 270 (undulated) sutures (Fig. ~~6, H6H~~), (3) irregularly alternating round and elongated tubercles (Fig.  
 271 ~~6, A–D6D~~). Base of gyrogonite rounded (Fig. ~~6, C6C~~, J) to slightly tapered (Fig. ~~6, A6A~~, G)  
 272 and showing a small, superficial and pentagonal basal pore, sometimes within a less-marked  
 273 funnel (Fig. ~~6, Q6Q~~). Apex of gyrogonite truncated or broadly rounded ~~showing and covered by~~  
 274 five ~~deciduous independent~~ opercular cells at the end of the spiral cells. Opercular cells roughly  
 275 prismatic, with its outer surface concave, flat or slightly convex (Fig. ~~6, L6L–M~~), ~~leaving a~~  
 276 ~~rose-shaped dehiscence pore in germinated~~. ~~Germinated~~ specimens ~~show a rounded or rose-~~  
 277 ~~like opening~~ (Fig. ~~6, N6N–P~~). The inside of the gyrogonite allows observation of a  
 278 characteristic crenulation of the intercellular sutures near their internal side (Fig. ~~6, R6R–S~~),  
 279 while, to the outside, sutures are flat. Besides, this crenulation occurs also between the opercule  
 280 cells themselves and between spiral and opercule cells as already described by Feist *in* Anadón  
 281 ~~& Feist~~ (1981).

282 **Distribution.** *R. vadaszii* has been first described by Rásky (1945) from middle Eocene  
 283 borehole samples (~~60m~~ 60 m depth) at Gánt, in beds roughly equivalent laterally to the outcrop  
 284 succession studied here. Therefore, the samples studied may be considered ~~as~~ topotypes.  
 285 Subsequently, the age of this variety was suggested to be upper Bartonian by Bignot *et al.*  
 286 (1985) based on the ~~basis of the~~ associated microfossils (foraminifers, ostracods, and pollen)  
 287 from the same beds of the bauxite cover-sequence at the Gánt section (Vértes Hills). *R. peckii*  
 288 var. *vadaszii* has also ~~also~~ been well documented in France, in the upper Bartonian of the Paris  
 289 Basin (Grambast 1957, 1958, 1962a; Riveline 1986) and ~~in~~ from several basins ~~from~~ southern  
 290 France (Feist-Castel 1976). Anadón & Feist (1981) and Anadón *et al.* (1992) documented ~~also~~  
 291 this variety also in the upper Bartonian of the Eastern Ebro Basin (Catalonia, Spain).

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3 293 ----- Figures 6, 7 near here-----  
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6 294  
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9 295 Family **Characeae** (Richard ex C.A. Agardh, 1824) emend. Martín-Closas ~~and~~ Schudack,  
10  
11 296 1991  
12  
13  
14 297 Subfamily **Charoideae** Braun *in* Migula, 1897  
15  
16  
17 298 Genus **Gyrogona** (Lamarck, 1804 *ex* Lamarck, 1822) emend. Grambast, 1956  
18  
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21 299  
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24 300 ***Gyrogona caelata*** (Reid ~~&~~ Groves, 1921) Grambast, 1956  
25  
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27 301 (Fig. 8A–V)  
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30 302  
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32  
33 303 1921 *Chara caelata* sp. nov. Reid & Groves: p. 184, pl. 4, figs 4–6.  
34  
35  
36 304 1927 *Kosmogyra caelata*, Pia: p. 90.  
37  
38  
39 305 1954 *Brachychara caelata*, L. & N. Grambast: p. 667.  
40  
41  
42 306 1956 *Gyrogona caelata*, Grambast: p. 280.  
43  
44  
45 307 1977b *Gyrogona caelata*, Feist-Castel: p. 117.  
46  
47  
48 308 1981 *Gyrogona caelata*, Grambast & Grambast-Fessard: p. 22, text-fig. 11, a–f; pl. 4, figs 1–9.  
49  
50  
51 309 1981 *Gyrogona* cf. ~~*caelata*~~ *Caelata*, Anadón & Feist: p. 163.  
52  
53  
54 310 1986 *Gyrogona caelata*, Riveline: pl. 38, figs 1–5, 7–8.  
55  
56  
57 311 1989 *Gyrogona caelata*, Choi: pl. 2, figs 1–11.  
58  
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1991 *Gyrogona caelata*, Weidmann *et al.*: p. 900, fig. 3, C.

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

314

**Material.** ~~Up to 10056~~ 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 ~~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, S8S~~). Base showing a small pentagonal basal pore (Fig. ~~8, G8F~~), sometimes flared by a shallow funnel (Fig. ~~8, P8P~~). Basal plate unicellular and only visible from the gyrogonite interior (Fig. ~~8, U8U–V~~). Spiral cells flat to slightly concave and ornamented with different patterns of ~~tubercle~~ ~~stuber~~ ~~cles~~, 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. caelata* forma *bicincta* characterized by nodules irregularly ranged along two lines parallel to spiral cell sutures (Fig. ~~8, H, I~~), (4) *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)~~

336 *G. caelata* forma *baccata* characterized by large nodules very closely ranged along the spiral-  
 337 cell median line (e.g., Fig. 8, ~~N8N~~–Q), (5) *G. caelata* forma *fasciata* characterized by a broad  
 338 median band of variable width (e.g., Fig. 8, ~~R8R~~–T).

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

349

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

351

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

353 1981

354 (Fig. 10A–J)

355

356 1921 *Chara wrighti* var. *rhytidocarpa*, Reid & Groves: p. 183, pl. 4, fig. 3.

357 1958 *Gyrogona tuberosa*, Grambast: p. 139, fig. 54.

1  
2  
3 358 1976 *Gyrogona tuberosa*, Feist-Castel: p. 26.  
4

5  
6 359 1981 *Gyrogona tuberosa*, Grambast & Grambast-Fessard: p. 25, text-fig. 12, a–d; pl. 5, figs 1–  
7  
8 360 6.  
9

10  
11 361 1986 *Gyrogona tuberosa*, Riveline: pl. 14, figs 8–11.  
12  
13  
14  
15 362

16  
17  
18 363 **Material.** 35 gyrogonites in ~~samples G-6b~~ sample G-6b. Collection numbers of figured  
19  
20 364 specimens: HNHM-PBO 1554–1563.  
21  
22  
23 365

24  
25  
26 366 **Description.** Large gyrogonites, 820–1000 µm high and 835–1050 µm wide with generally  
27  
28 367 oblate to suboblate spheroidal shape (ISI 80–100) and showing laterally 6–7 convolutions  
29  
30 368 (usually 6). Apex subtruncate (Fig. ~~10, A10A~~, C) to somewhat ~~prominent and~~ pointed (Fig. ~~10,~~  
31  
32 ~~D10D~~, G) with spiral cells protruding (Fig. ~~10, H10H~~). Base broadly rounded (Fig. ~~10, B10B~~,  
33  
34 369 F) to slightly tapered (Fig. ~~10, A10A~~, C, E) and showing a small, superficial and pentagonal  
35  
36 370 basal pore, sometimes within a less-marked funnel (Fig. ~~10, I10I–J~~). Spiral cells flat or concave,  
37  
38 371 smooth or somewhat ornamented and separated by protruding narrow to weakly undulated  
39  
40 372 intercellular ridges.  
41  
42 373  
43  
44

45  
46 374 **Distribution.** *Gyrogona tuberosa* is ~~first~~ reported here from Hungary, and ~~from~~ central Europe  
47  
48 375 for the first time. According to Riveline (1986) and Riveline & Cavalier (1987), this species  
49  
50 376 was widely distributed in upper Bartonian non-marine deposits of Western Europe. It was first  
51  
52 377 recorded from the Isle of Wight and Hampshire (England) by Reid & Groves (1921).  
53  
54 378 ~~Thereafter~~ Subsequently, it was reported from the upper Bartonian of the Paris Basin  
55  
56 379 (Grambast 1958; Grambast & Grambast-Fessard 1981; Riveline 1986; Riveline & Cavalier  
57  
58 380 1987), as well as ~~in~~ from several basins ~~from~~ of southern France (Feist-Castel 1976).  
59  
60

381

382

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

383

384

Genus *Psilochara* Grambast, 1959

385

386

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

387

(Fig. 11A–F)

388

389

1921 *Chara polita*<sub>2</sub> sp. nov. Reid & Groves: p. 187, pl. 5, figs 9, 12.

390

1927 *Gyrogona politus*<sub>2</sub> Pia: p. 90.

391

1958 *Ovochara polita*<sub>2</sub> comb. nov. Grambast: p. 167.

392

1959 *Peckichara polita*<sub>2</sub> Horn af Rantzien: p. 116, pl. 13, figs 1–3.

393

1959 *Psilochara polita*<sub>2</sub> Grambast: p. 11.

394

1977b *Psilochara polita*<sub>2</sub> Feist-Castel: p. 153.

395

1986 *Psilochara polita*<sub>2</sub> Riveline: p. 59, pl. 22, figs 8–12.

396

397

**Material.** 58 gyrogonites in sample G-6a. Collection numbers of ~~figures~~figured specimens:

398

HNHM-PBO ~~xxxxx-yyyyy~~1564–1569.

399 **Description.** Medium-sized gyrogonites (~~520–830 µm in width and 580–710~~550–700 µm in  
 400 height 500–650 and µm in width) with ovoidal shape (ISI ~~105~~100–120) and laterally showing  
 401 7–810 convolutions (Fig. ~~11, A11A–C~~; Fig. 12). Apex round to pointed (Fig. ~~11, A11A–C~~).  
 402 Base tapering to prolonged into a stout basal column (Fig ~~11, A11A–C~~) and showing a small  
 403 pentagonal basal pore (Fig. ~~11, F11F~~). Spiral cells smooth, concave or flat and separated by  
 404 protruding narrow to weakly undulated intercellular ridges.

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

409  
 410 ----- Figures 11, 12 near here -----

411  
 412 *Psilochara* sp.

413 (Fig. 11G–I)

414  
 415 **Material.** 17 gyrogonites in sample G-6a. Collection numbers of ~~figures~~figured specimens:  
 416 HNHM-PBO ~~xxxxxx-yyyyy~~1570–1571.

417 **Description.** Medium to large-sized gyrogonites (780–905 µm wide and 670–775 µm high)  
 418 with elongated ovoidal (subprolate) shape (ISI 110–125) and laterally showing 8–10  
 419 convolutions (Fig. ~~11, G11G~~). Apex truncated. Apical end of spiral cells enlarged and pointing  
 420 upwards (Fig. ~~11, H11H~~). Base truncated to somewhat tapering, bearing a small pentagonal

421 basal pore. Basal plate unipartite and visible from the gyrogonite interior (Fig. ~~11, 111~~). Spiral  
 422 cells concave or flat and smooth, except at the periapical area, where they are irregularly  
 423 ornamented with a broad mid-cellular crest.

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

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

429

430 Genus *Nitellopsis* Hy, 1889

431

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

433

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

435 1972

436 (Fig. 11J–N)

437

438 1945 *Chara palaeohungarica*, sp. nov. Rásky: p. 38, pl. 1, figs 16–18.

439 1955 *Tectochara palaeohungarica*, comb. nov. Mädlar: p. 298.

440 1959 *Tectochara palaeohungarica*, Horn af Rantzien: p. 90, pl. 8, figs 4–7.

1  
2  
3 441 1972 *Nitellopsis (Tectochara) palaeohungarica*, nov. comb. Grambast & Soulié-Märsche: p.

4  
5 442 4.

6  
7  
8  
9 443

10  
11  
12 444 **Material.** ~~6128~~ gyrogonites in ~~both samples~~ sample G-2.3 and ~~33 in sample~~ G-2.5. Collection  
13  
14 445 numbers of ~~figures figured~~ specimens: HNHM-PBO ~~xxxxx-yyyyy~~ 1572–1576.

15  
16  
17 446 **Description.** ~~Very Gyrogonites very~~ large ~~gyrogonites~~ (900–1200 µm high and 800–1050 µm  
18  
19 447 wide), oval, prolate spheroidal (ISI 100–120) ~~pear-shaped and in shape~~, showing 8–11 (often 9)  
20  
21 448 convolutions in lateral view (Fig. ~~11, J11J–L~~; Fig. 13). Spiral cells concave to flat. Apex  
22  
23 449 prominent with spiral cells protruding to form a central rosette. Spiral cells show both  
24  
25 450 ~~shortening narrowing~~ and thinning in the periapical area (Fig. ~~11, M11M~~). Base rounded to  
26  
27 451 almost conical, occasionally lengthened in a short broad column. A large (155–230 µm across)  
28  
29 452 pentagonal basal pore occurs within a wide basal funnel (Fig. ~~11, N11N~~).

30  
31  
32  
33  
34 453 **Distribution.** The species ~~*Tectochara*~~ '*Chara*' *palaeohungarica* was first described from  
35  
36 454 subsurface beds attributed to the Paleocene in Dorog, Hungary, by Rásky (1945). Here this  
37  
38 455 species is described from beds cropping out ~~in at~~ Gánt, which are probably time-equivalent to  
39  
40 456 those of the type locality. The present study ~~allows reassigning~~ supports reassignment of this  
41  
42 457 species to the middle Eocene rather than to the Paleocene.

43  
44  
45  
46 458 **Remarks.** The gyrogonites studied here are diagenetically deformed, which hinders a more  
47  
48 459 definitive taxonomic attribution. A re-study of the type material (HNHM 55.1458–55.1460) by  
49  
50 460 one of the authors of this study (CMC) showed that, besides the holotype, which is a  
51  
52 461 subspherical gyrogonite as illustrated by Rásky (1945, pl. I, Fig. 16), there were more oval to  
53  
54 462 elongated gyrogonites present in the collection similar to those described here, which Rásky  
55  
56 463 (1945, p. 38) termed 'cylindrical'.

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3 464  
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6 465

----- Figure 13 near here -----

8  
9 466  
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12 467

Genus *Chara* Vaillant, 171914  
15 468  
16  
1718  
19 469*Chara media* Grambast, 195820  
21  
22 470

(Fig. 14A–I)

23  
24  
25 471  
26  
27

28 472

1958 *Chara media*, Grambast: p. 178, fig. 81b.29  
30  
31 4731986. *Chara media*, Riveline: p. 68, pl. 29, figs 6–12.32  
33  
34 474  
35  
36

37 475

**Material.** Up to 80 gyrogonites in both samples G-2.5 and G-6a. Collection numbers of38  
39  
40 476~~figures figured~~ specimens: HNHM-PBO ~~xxxxxx-yyyyy~~1577–1585.41  
42  
43 477**Description.** Gyrogonites of medium size (400–650 µm high and 300–500 µm wide) ellipsoidal44  
45 478subprolate (ISI 110–145), laterally showing ~~laterally~~ 8–11 (usually 9–10) convolutions (Fig. 14,46  
47 479A14A–G, Fig. 15). Maximum width nearly at the half to 2/3 of height. Apex rounded to slightly48  
49 480conical, with distinctly widening of the spiral cell endings (Fig. 14, H14H). Spiral cells concave,50  
51  
52 481

smooth and without any periapical modification. Base tapering showing a superficial

53  
54 482pentagonal basal pore (Fig. 14, I14I).55  
56  
57  
58  
59  
60



1  
2  
3 483 **Distribution.** *Chara media* is ~~first time~~-described here from the upper Eocene (upper Bartonian)  
4  
5 484 of Hungary for the first time. Grambast (1958) and Riveline (1986) documented this species  
6  
7 485 from the upper Bartonian–lower Oligocene of several basins in France, Belgium, and Germany.  
8  
9

10  
11 486

12  
13  
14 487 ----- ~~Figures 14~~ Figures 14, 15 near here-----  
15  
16

17 488

18  
19  
20 489 *Chara subcylindrica* Reid ~~&et~~ Groves, 1921  
21

22  
23 490 (Fig. 14J–O)  
24

25  
26 491

27  
28  
29 492 1921 *Chara subcylindrica*, sp. nov. Reid & Groves: p. 187, pl. 5, fig. 4–5.  
30

31  
32 493 1959 *Grambastichara subcylindrica*, Horn af Rantzien: p. 76, pl. 3, figs 5–7.  
33

34  
35 494 1986 *Chara* cf. *subcylindrica*, Riveline: p. 67, pl. 30, figs 5–8.  
36  
37

38  
39 495

40  
41  
42 496 **Material.** Up to 250 gyrogonites in sample G-6b. Collection numbers of ~~figures~~figured  
43

44 497 specimens: HNHM-PBO ~~xxxxx-yyyy~~1586–1591.  
45  
46

47 498 **Description.** Medium-sized gyrogonites (500–750 µm high and 200–400 µm wide) ellipsoidal  
48

49 499 prolate to perprolate (ISI 130–200), in shape, laterally showing 8–11 (usually 9–10)  
50

51 500 convolutions (Fig. ~~14, J~~14J–M; Fig. 16). Maximum width at the equator. Apex rounded with  
52

53 501 widening of the spiral cell endings (Fig. ~~14, N~~14N). Spiral cells often slightly concave to flat,  
54

55 502 separated by narrow intercellular ridges, cells non-ornamented and without any periapical  
56  
57  
58  
59  
60

503 modification. Base regularly tapering to round, showing a superficial pentagonal basal pore  
 504 (Fig. ~~14, O140~~).

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

509

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

511

## 512 Discussion

513

### 514 Definition of the *Raskyella peckii* anagenetic lineage

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

1  
2  
3 525 original taxa have been newly combined as anagenetic varieties of the species with  
4  
5 526 nomenclatural priority, which is *R. peckii*.

7  
8  
9 527 The first evolutionary stage of the *R. peckii* lineage (Fig. 17) is represented by *R. peckii* var.  
10  
11 528 *peckii*, and includes, as well, the smallest gyrogonite morphotype initially described as  
12  
13 529 *Raskyella peckii ganesesisganesensis* Soulié-Märsche, 1971. *R. peckii* var. *peckii* is  
14  
15 530 characterized by gyrogonites which are very variable in size, but ~~consistenly~~consistently  
16  
17 531 unornamented. This stage has a long duration, since it ~~has been~~was documented from the lower  
18  
19 532 Lutetian to the ~~lower~~upper Bartonian of the Ebro ~~basin~~Basin, Catalonia, by Martín-Closas *et*  
20  
21 533 *al.* (~~1999b~~1999a) and can thus be superimposed ~~to~~onto some of the ulterior morphotypes of the  
22  
23 534 lineage, this being quite a common situation in charophyte lineages (e.g., Grambast, 1974).

24  
25  
26  
27 535 The coeval *Raskyella peckii* subsp. *meridionale* Grambast, 1960, was not found in the section  
28  
29 536 studied and corresponds to a southern geographic subspecies of this lineage, thriving in North  
30  
31 537 Africa and the Prebetic Domain in the Balearic Islands in Spain (Grambast 1960; Martín-Closas  
32  
33 538 ~~*et al.*~~2004 & Ramos 2005).

34  
35  
36  
37 539 The second ~~step~~evolutionary stage in the lineage of *R. peckii* is represented by *R. peckii* var.  
38  
39 540 *caliciformis*. Intermediate morphotypes between *R. peckii* var. *peckii* and *R. peckii* var.  
40  
41 541 *caliciformis* display a progressive increase in the gyrogonite size (up to 1000 µm in high~~height~~),  
42  
43 542 and a change in shape from elongated to rounded, between samples G-2.2 and G-2.4 of the Gánt  
44  
45 543 section. Furthermore, there is a progressive development of the ornamentation corresponding  
46  
47 544 to *R. peckii* var. *caliciformis* in the same sequence, with for instance 100% of gyrogonites  
48  
49 545 corresponding to *R. peckii* var. *peckii* in sample G-2.4, while in sample G-2.5, there is only 10%  
50  
51 546 of *R. peckii* var. *peckii* ~~for~~, resulting in 90% of *R. peckii* var. *caliciformis* (Fig. 17).

52  
53  
54  
55  
56 547 The third stage of the lineage is represented by *R. vadaszii*, from the upper Bartonian, which  
57  
58 548 shows an additional increase of the gyrogonite size of about 150–250 µm in height and 100–  
59  
60

1  
2  
3 549 125 µm in width, and especially the development of progressively more complex ornamentation  
4  
5 550 patterns in comparison to the previous evolutionary step (Fig. 17). This gradual change can be  
6  
7 551 observed between samples G-2.5 and G-6b of the Gánt section. Thus, sample G-5 displays a  
8  
9 552 homogeneous population with 100% of gyrogonites corresponding to *R. peckii* var.  
10  
11 553 *caliciformis*, while in the overlying sample G-6a, the gyrogonite population of *R. peckii*  
12  
13 554 contains only 15% of specimens of *R. peckii* var. *caliciformis* and 85% of *R. peckii* var. *vadaszii*.  
14  
15  
16  
17 555 Finally, in sample G-6b there is a homogeneous population of gyrogonites corresponding to *R.*  
18  
19 556 *peckii* var. *vadaszii*.

20  
21  
22 557 Overall, the *R. peckii* lineage follows the general evolutionary trend in the evolutionary lineages  
23  
24 558 ~~from~~ other charophyte families, characterized by an increase in size and sphericity  
25  
26 559 (Clavatoraceae and Raskyellaceae), and a progressive development of ornamentation  
27  
28 560 (Characeae), as shown by Feist-Castel (1977, 1977b), Martín-Closas *et al.* (1999b), Sille *et al.*  
29  
30 561 (2004) and Vicente & Martín-Closas (2018).  
31  
32  
33  
34  
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36  
37

38 562 ----- Figure 17 near here -----  
39  
40  
41  
42  
43

#### 44 565 **New local charophyte biozonation**

45  
46  
47 566 Among the ~~charophytes~~ charophyte species described from the bauxite cover-sequence at the  
48  
49 567 Gánt section (Vértes Hills, Hungary), *Raskyella peckii* represents the most significant species  
50  
51 568 ~~in terms of biostratigraphy~~ for use in biostratigraphy within the non-marine Lutetian and  
52  
53 569 Bartonian, as previously suggested by Riveline *et al.* (1996) and Martín-Closas *et al.* (1999a).  
54  
55 570 The *Raskyella peckii* biozone was defined by ~~the latter authors (p. X~~ Riveline *et al.* (1996) as a  
56  
57 571 'partial range zone comprising the interval from the first appearance of *Raskyella peckii* L. and  
58  
59  
60

1  
2  
3 572 N. Grambast, 1954, to the first appearance of *Chara friteli* Grambast, 1958'1958, lower  
4  
5 573 Lutetian to lower Bartonian in age. This study proposes to extend this biozone to cover also the  
6  
7  
8 574 upper Bartonian, and to ~~renamer~~redesignate it as a superzone subdivided into the following three  
9  
10 575 successive biozones (Fig. 18):

11  
12  
13 576 - **Raskyella peckii peckii zoneZone**: partial range zone defined from the first occurrence of  
14  
15 577 the morphotype *peckii* to the first occurrence of the morphotype *caliciformis*, Lutetian–lower  
16  
17 578 Bartonian in age. The local charophyte assemblage characterizing this zone in Gánt occurs in  
18  
19 579 the basal part of the studied section ('Packet 2', 'blue-hole' freshwater limestone facies,  
20  
21 580 samples G-2.2, G-2.3 and G-2.4), and is composed of *R. peckii* var. *peckii*, *G. caelata* forma  
22  
23 581 *caelata*, *G. caelata* forma *monolifera*, and *Nitellopsis (Tectochara) aff. palaeohungarica*, ~~some~~  
24  
25 582 ~~of~~ which are well known to occur in several European basins (Rásky 1945; Grambast 1958;  
26  
27 583 Riveline 1986; Martín-Closas *et al.* 1999a) during the same time interval.

28  
29  
30  
31  
32 584 - **Raskyella peckii caliciformis zoneZone**: partial range zone defined from the first occurrence  
33  
34 585 of the morphotype *caliciformis* to the first occurrence of the morphotype *vadaszii*, lower  
35  
36 586 Bartonian in age. This zone includes in Gánt the assemblage found in the lower part of 'Packet  
37  
38 587 3' (samples G-2.5) and composed of *R. peckii* var. *caliciformis*, *G. caelata* forma *caelata*, *G.*  
39  
40 588 *caelata* forma *monolifera*, *G. caelata* forma *baccata*, *Nitellopsis (Tectochara) aff.*  
41  
42 589 *palaeohungarica*, and *Chara media*.

43  
44  
45  
46  
47 590 - **Raskyella pecki vadaszii zoneZone**: partial range zone defined from the first occurrence of  
48  
49 591 the morphotype *vadaszii* to the first occurrence of the next zone defined in the Paris Basin,  
50  
51 592 which is *Psilochara repanda*. This zone would be upper Bartonian in age. The assemblage  
52  
53 593 occurring in the middle part of the Gánt section ('Packet 3', samples G-6a and G-6b), composed  
54  
55 594 of *R. peckii* var. *vadaszii*, *G. caelata* forma *bicincta*, *G. caelata* forma *baccata*, *G. caelata* forma

595 *fasciata*, *Psilochara polita*, *Psilochara* sp., *Chara media*, and *Chara subcylindrica*  
596 characterizes locally this biozone.

597

### 598 **Implications on the age of the bauxite cover-sequence**

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

619

620

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

621

## 622 Conclusions

623

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

632 From ~~the biostratigraphic~~biostratigraphic viewpoint, the assemblages studied belong to the  
 633 *Raskyella peckii* biozone of Martín-Closas *et al.* (~~1999b~~1999a), which is here reinterpreted ~~here~~  
 634 as a superzone extending to cover the *Raskyella vadaszii* ~~zone~~Zone of Riveline *et al.* (1996)  
 635 and ~~therefore~~ attributed to the Lutetian–Bartonian interval ~~age~~. ~~This~~. In this study, this  
 636 superzone is subdivided ~~herein~~ into three successive local partial range biozones, defined by  
 637 each of the successive varieties of the evolutionary species *R. peckii*: (1) the *Raskyella peckii*  
 638 peckii partial range zone is ~~formed~~characterized by *R. peckii peckii*, *G. caelata* forma *caelata*,  
 639 *G. caelata* forma *monolifera* and *Nitellopsis (Tectochara)* aff. palaeohungarica, Lutetian–  
 640 lowermost Bartonian in age; (2) the *Raskyella peckii caliciformis* partial range zone is  
 641 ~~formed~~characterized by *R. peckii caliciformis*, *G. caelata* forma *caelata*, *G. caelata* forma

642 *monolifera*, *G. caelata* forma *baccata*, *Nitellopsis* (*Tectochara*) aff. palaeohungarica and  
643 *Chara media*, lower Bartonian in age; and (3) the *Raskyella peckii* vadaszivadazii partial range  
644 zone is ~~formed~~characterized by *R. peckii vadaszii*, *G. caelata* forma *bicincta*, *G. caelata* forma  
645 *baccata*, *G. caelata* forma *fasciata*, *G. tuberosa*, *Psilochara polita*, *Psilohara* sp., *Chara media*  
646 and *Chara subcylindrica*, upper Bartonian in age.

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

654

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## 894 **Figure Captions**

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

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

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

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3 908 showing ~~the oospore internal cast~~. **M**, ~~the oospore internal cast~~ with well-developed  
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5 909 undulations. **N–O**, apical view; **P**, basal view. ~~Specimen numbers HNHM-PBO-xxxxx-yyyyy~~  
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7 910 ~~will be added for each respective specimen.~~  
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14 912 **Figure 4.** Frequency distribution of the lengthheight (A), width (B), number of convolutions  
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16 913 (C), lengthand height/width ratio (ISI) (D) of the *Raskyella peckii* var. *peckii* population (50  
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18 914 gyrogonites measured), from samples G-2.2, G-2.3, and G-2.4 in the bauxite cover-sequence  
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20 915 of the Gánt section.  
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27 917 **Figure 5.** Frequency distribution of the lengthheight (A), width (B), number of convolutions  
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29 918 (C), lengthand height/width ratio (ISI) (D) of the *Raskyella peckii* var. *caliciformis* population  
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31 919 (50 gyrogonites measured), from sample G-2.5 in the bauxite cover-sequence of the Gánt  
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33 920 section.  
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40 922 **Figure 6.** ~~Gyrogonites of species~~ *Raskyella peckii* *vadaszii* gyrogonites from the Gánt bauxite  
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42 923 cover-sequence. ~~(A–S, *Raskyella peckii* var. *vadaszii* (samples G-6a and G-6b, HNHM-PBO~~  
43  
44 924 1517–1534). **A–K**, lateral view. **L–P**, apical view; **Q**, basal view; **R–S**, inside wall of a  
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46 925 gyrogonite showing the crenate undulation of the cellular sutures in contact with the spiral  
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48 926 cells and the apical cells. ~~Specimen numbers HNHM-PBO-xxxxx-yyyyy will be added for~~  
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50 927 ~~each respective specimen.~~  
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3 929 **Figure 7.** Frequency distribution of the lengthheight (A), width (B), number of convolutions  
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5 930 (C), lengthand height/width ratio (ISI) (D) of the *Raskyella peckii* var. *vadaszii* population (50  
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7 931 gyrogonites measured), from samples G-6a and G-6b in the bauxite cover-sequence of the  
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9 932 Gánt section.  
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16 934 **Figure 8.** ~~Gyrogonites of species~~ *Gyrogona caelata* gyrogonites from the Gánt bauxite cover-  
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18 935 sequence. **A–G**, *Gyrogona caelata* forma *caelata* (samples G-2.2, G-2.3, G-2.4, and G-2.5). ~~);~~  
19 936 HNHM-PBO 1535–1553. **A–B**, **D–E**, basal view **C**, detail of the ornamentation pattern; **F**,  
20  
21 937 basal view; **G**, apical view. **H–K**, *Gyrogona caelata* forma *bicincta* (samples G-6a, and G-6b).  
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23 938 **H**, lateral view; **I**, detail of the ornamentation pattern; **J–K**, apical view. **L–M**, *Gyrogona*  
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25 939 *caelata* forma *monolifera* (samples G-2.2, G-2.3, G-2.4, and G-2.5). **L**, lateral view; **M**, basal  
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27 940 view. **N–Q**, *Gyrogona caelata* forma *baccata* (samples G-2.5, G-6a, and G-6b). **N–O**, lateral  
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29 941 view; **P**, basal view; **Q**, apical view. **R–V**, *Gyrogona caelata* forma *fasciata* (samples G-6a,  
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31 942 and G-6b). **R**, lateral view; **S–T**, apical view; **U–V**, detail of the simple (unipartite) basal  
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33 943 plate. ~~Specimen numbers HNHM-PBO xxxxx-yyyyy will be added for each respective~~  
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35 944 specimen.  
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46 946 **Figure 9.** Frequency distribution of the lengthheight (A), width (B), number of convolutions  
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48 947 (C), lengthand height/width ratio (ISI) (D) of the *Gyrogona caelata* population (50  
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50 948 gyrogonites measured), from samples G-2.2, G-2.3, G-2.4, G-2.5, and G-6a in the bauxite  
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52 949 cover-sequence of the Gánt section.  
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3 951 **Figure 10.** ~~Gyrogonites of species~~ *Gyrogona tuberosa* gyrogonites from the Gánt bauxite  
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5 952 cover-sequence (~~sample~~ G-6b), HNHM-PBO 1554–1563. **A–G**, lateral view; **H**,  
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7 953 apical view; **I–J**, basal view. ~~Specimen numbers HNHM-PBO xxxxx-yyyyy will be added for~~  
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9 954 ~~each respective specimen.~~

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16 956 **Figure 11.** Gyrogonites of genus *Psilochara* and *Nitellopsis* from the Gánt bauxite  
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18 957 cover-sequence. **A–F**, *Psilochara polita* (~~sample~~ G-6a), HNHM-PBO 1564–1569.  
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20 958 **A–C**, lateral view; **D–E**, apical view; **F**, basal view. **G–I**, *Psilochara* sp. (~~sample~~ G-  
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22 959 6a), HNHM-PBO 1570–1571. **G**, lateral view; **H**, apical view; **I**, internal view showing  
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24 960 simple (unipartite) basal plate (arrowed). **J–N**, *Nitellopsis (Tectochara)* aff. palaeohungarica  
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26 961 (samples G-2.3 and G-2.5), HNHM-PBO 1572–1576. **J–L**, lateral view; **M**, apical view; **N**,  
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28 962 basal view. ~~Specimen numbers HNHM-PBO xxxxx-yyyyy will be added for each respective~~  
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30 963 ~~specimen.~~

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38 965 **Figure 12.** Frequency distribution of the length height (A), width (B), number of convolutions  
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40 966 (C), length and height /width ratio (ISI) (D) of the *Psilochara polita* population (50  
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42 967 gyrogonites measured), from sample G-6a in the bauxite cover-sequence of the Gánt section.

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49 969 **Figure 13.** Frequency distribution of the length height (A), width (B), number of convolutions  
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51 970 (C), length and height /width ratio (ISI) (D) of the *Nitellopsis (Tectochara)* aff.  
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53 971 palaeohungarica population (50 gyrogonites measured), from samples G-2.3 and G-2.5 in the  
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55 972 bauxite cover-sequence of the Gánt section.

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3 974 **Figure 14.** ~~Gyrogonites of genus~~ *Chara* gyrogonites from the Gánt bauxite cover-sequence.  
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5 975 **A–I,** *Chara media* (samples G-2.5 and G-6a-), HNHM-PBO 1577–1585. **A–G,** lateral view;  
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7 976 **H,** apical view; **I,** basal view. **J–O,** *Chara subcylindrica* (~~sample~~ sample G-6b-), HNHM-  
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9 PBO 1586–1591. **J–M,** lateral view; **N,** apical view; **O,** basal view. ~~Specimen numbers~~  
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11 HNHM-PBO xxxxxx-yyyyy will be added for each respective specimen.  
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18 980 **Figure 15.** Frequency distribution of the lengthheight (A), width (B), number of convolutions  
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20 981 (C), lengthand height/width ratio (ISI) (D) of the *Chara media* population (50 gyrogonites  
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22 982 measured), from samples G-2.5 and G-6a in the bauxite cover-sequence of the Gánt section.  
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29 984 **Figure 16.** Frequency distribution of the lengthheight (A), width (B), number of convolutions  
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31 985 (C), lengthand height/width ratio (ISI) (D) of the *Chara subcylindrica* population (50  
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33 986 gyrogonites measured), from ~~sample~~ sample G-6b in the bauxite cover-sequence of the Gánt  
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35 987 section.  
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42 989 **Figure 17.** Stratigraphic distribution of variants of the anagenetic ~~evolutionary~~ lineage of the  
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44 990 species *Raskyella peckii*.  
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50 992 **Figure 18.** Charophyte Biostratigraphy, age and correlation of the bauxite cover-sequence  
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52 993 ~~from~~ of the Gánt section.  
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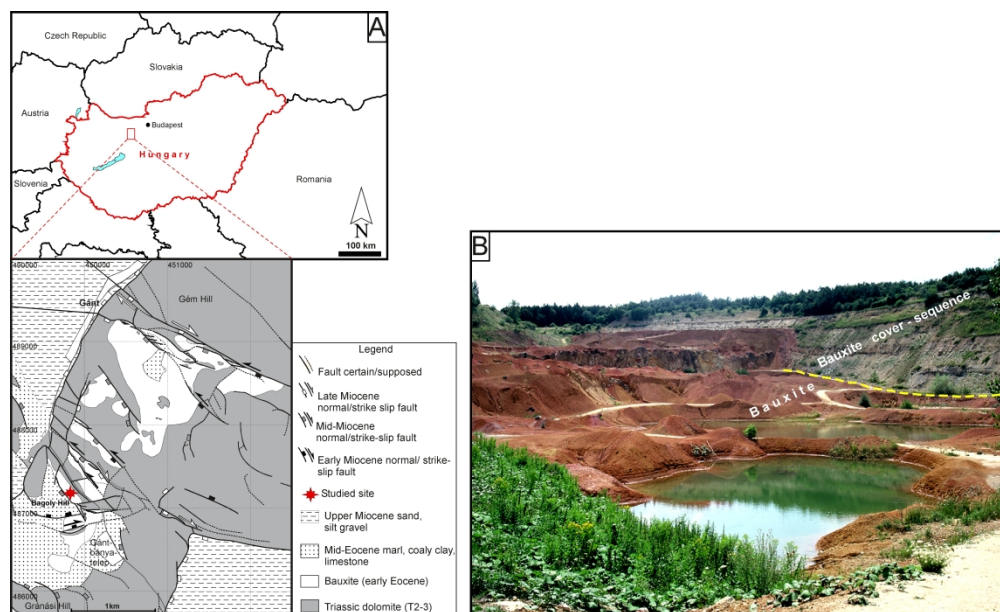


Figure 1. A, geographical and geological setting of the study area (after Fodor 2007). B, panoramic view of the studied Gánt section at the Vértes Hills (north-western Hungary).

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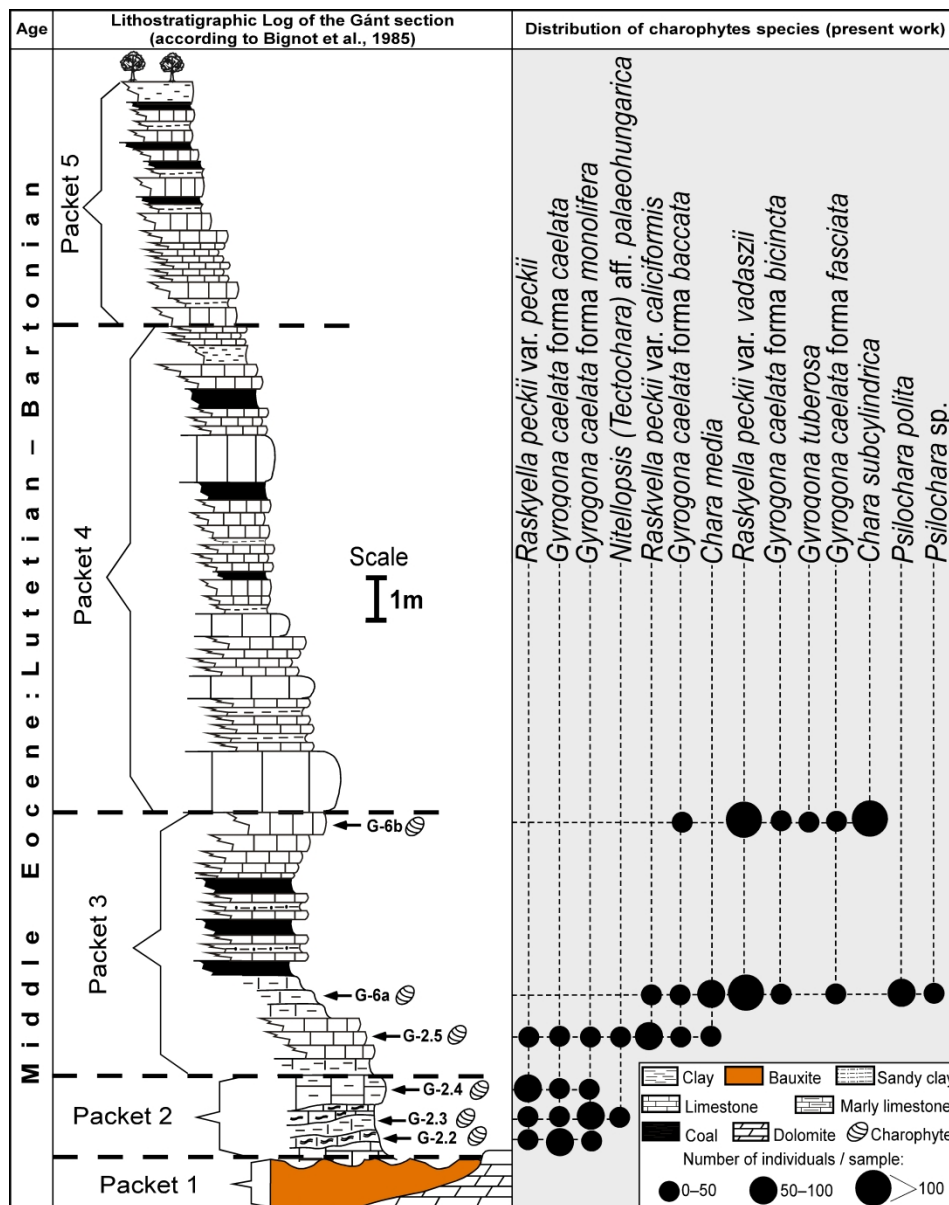


Figure 2. Distribution of the charophytes species in the bauxite cover-sequence from the studied Gánt section (Vértés Hills, Hungary), according to Bignot et al. (1985), updated for charophyte content.

467x589mm (300 x 300 DPI)



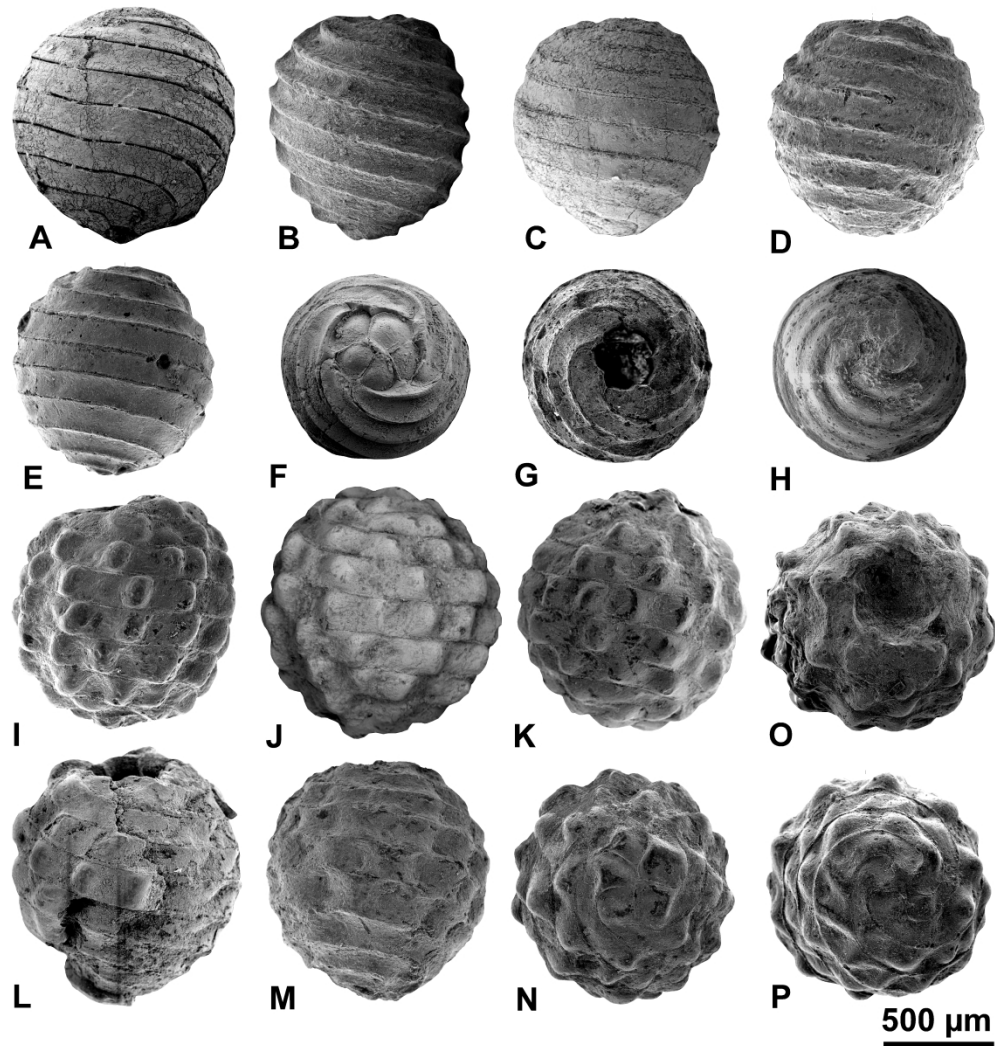


Figure 3. *Raskyella peckii* gyrogonites from the Gánt bauxite cover-sequence. A–H, *Raskyella peckii* var. *peckii* (samples G-2.2, G-2.3, G-2.4, and G-2.5), HNHM-PBO 1501–1508. A–E, lateral view; F–G, apical view; H, basal view. I–P, *Raskyella peckii* var. *caliciformis* (samples G-2.5 and G-6a), 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.

522x548mm (300 x 300 DPI)

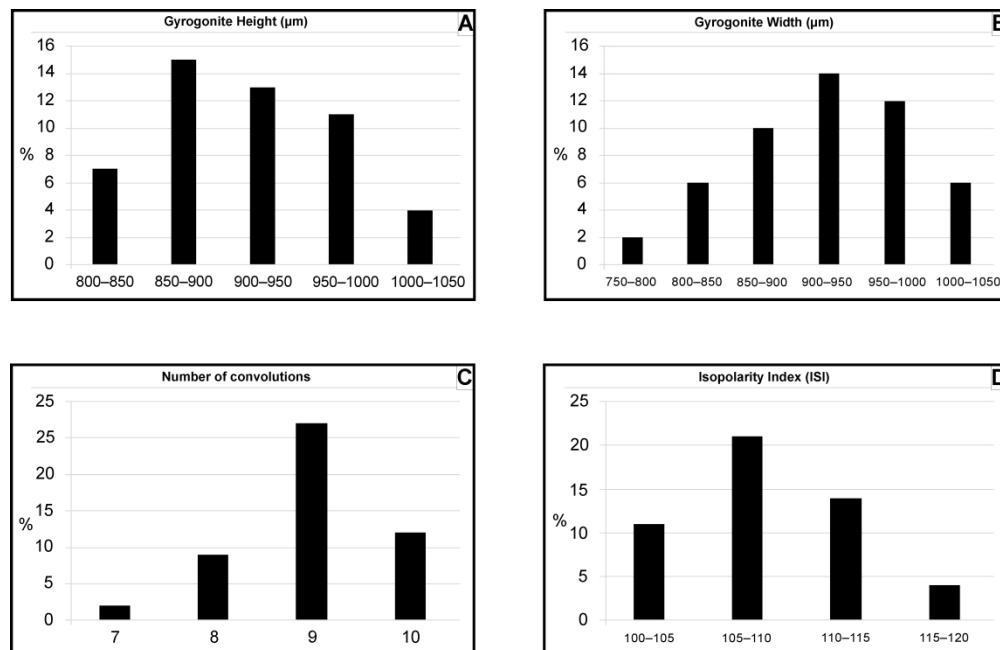


Figure 4. Frequency distribution of the height (A), width (B), number of convolutions (C), and height/width ratio (ISI) (D) of the *Raskyella peckii* var. *peckii* population (50 gyrogonites measured), from samples G-2.2, G-2.3, and G-2.4 in the bauxite cover-sequence of the Gánt section.

380x246mm (300 x 300 DPI)

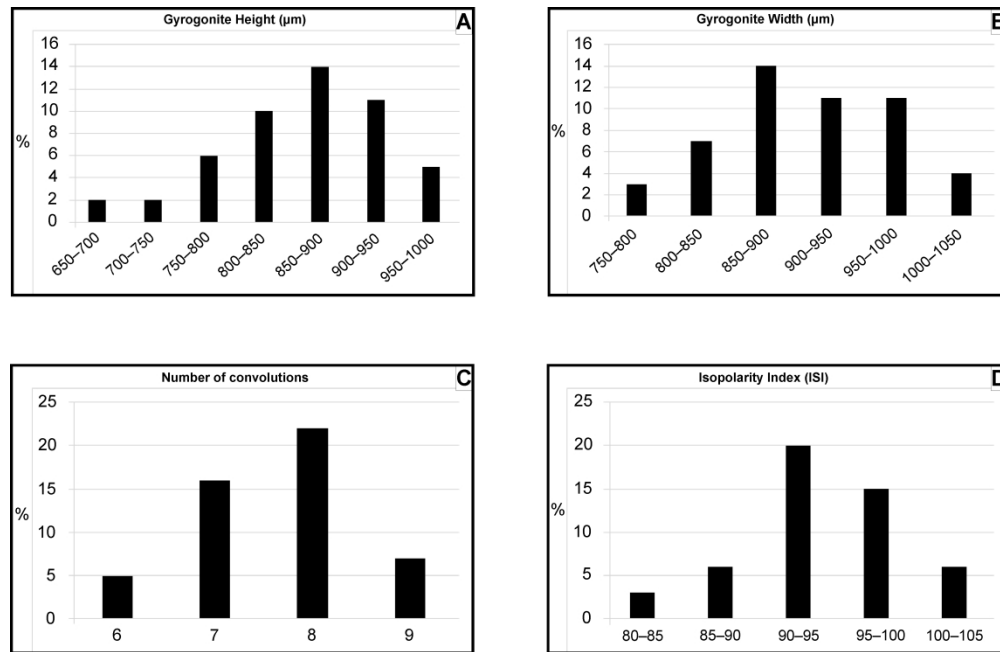


Figure 5. Frequency distribution of the height (A), width (B), number of convolutions (C), and height/width ratio (ISI) (D) of the *Raskyella peckii* var. *caliciformis* population (50 gyrogonites measured), from sample G-2.5 in the bauxite cover-sequence of the Gánt section.

384x248mm (300 x 300 DPI)

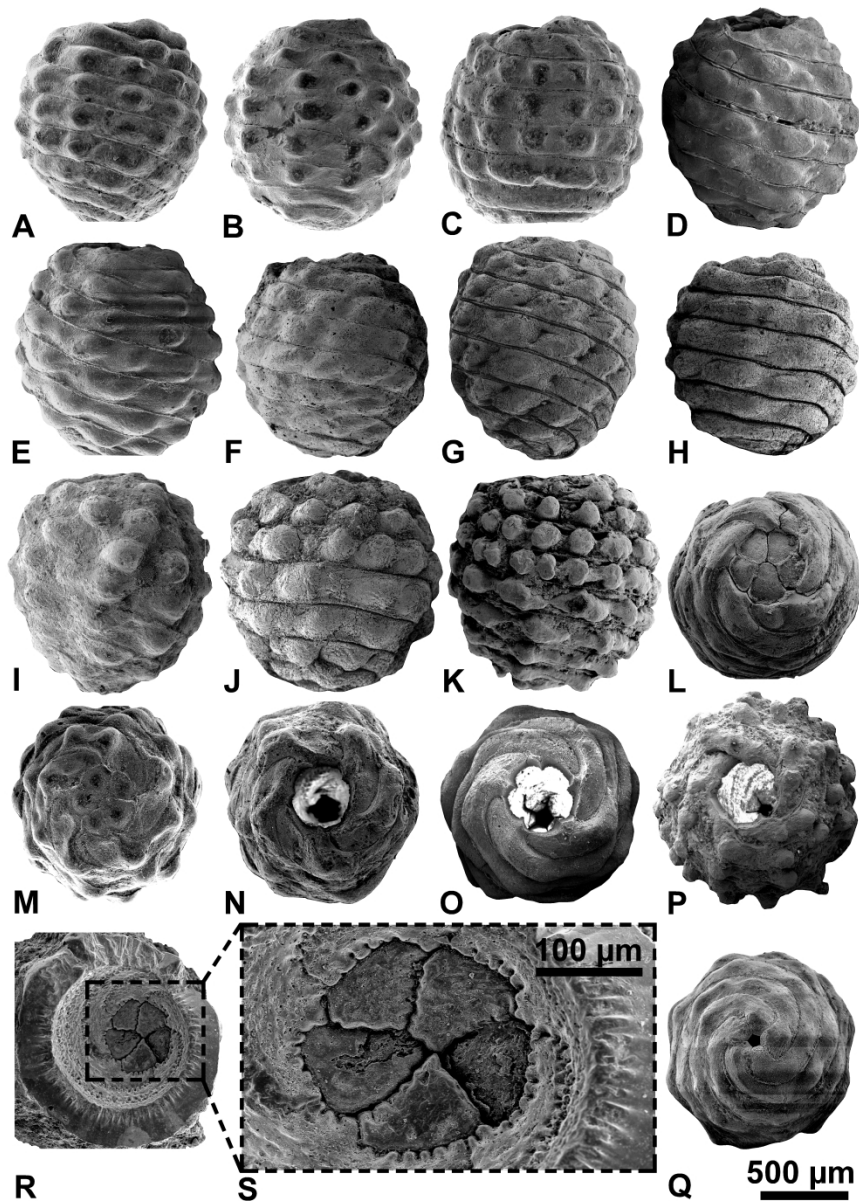


Figure 6. *Raskyella peckii vadaszii* gyrogonites from the Gánt bauxite cover-sequence (A–S, samples G-6a and G-6b, HHNM-PBO 1517–1534). A–K, lateral view. L–P, apical view; Q, basal view; R–S, inside wall of a gyrogonite showing the crenate undulation of the cellular sutures in contact with the spiral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

461x634mm (300 x 300 DPI)

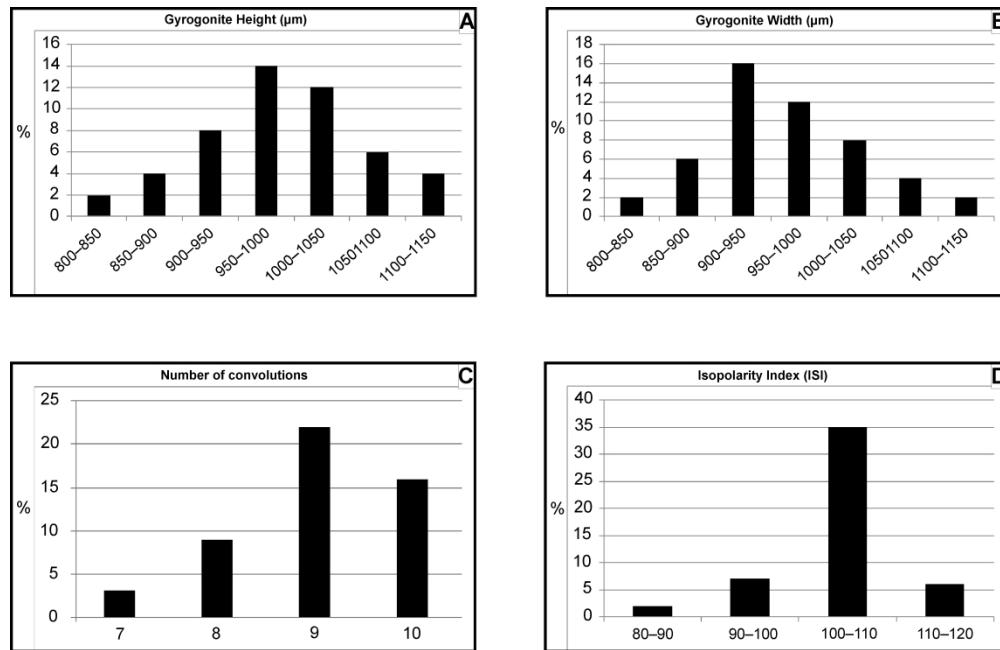


Figure 7. Frequency distribution of the height (A), width (B), number of convolutions (C), and height/width ratio (ISI) (D) of the *Raskyella peckii* var. *vadaszii* population (50 gyrogonites measured), from samples G-6a and G-6b in the bauxite cover-sequence of the Gánt section.

384x247mm (300 x 300 DPI)

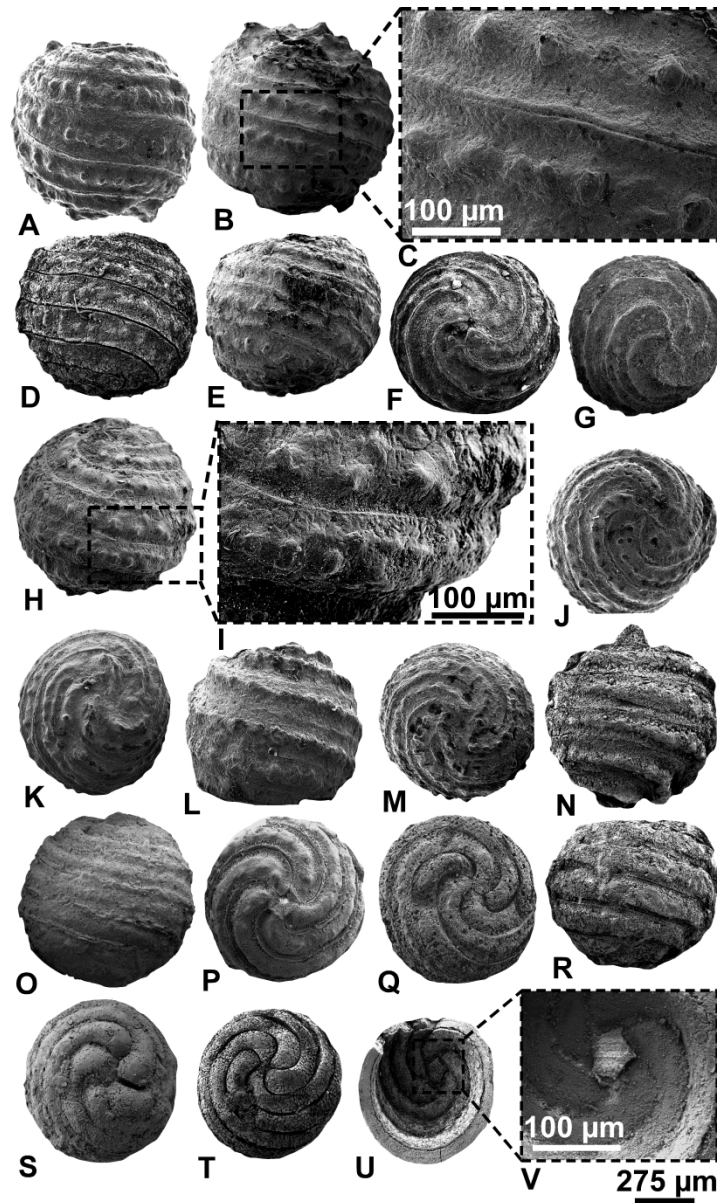


Figure 8. *Gyrogona caelata* gyrogonites from the Gánt bauxite cover-sequence. A–G, *Gyrogona caelata* forma *caelata* (samples G-2.2, G-2.3, G-2.4, and G-2.5), HHNM-PBO 1535–1553. A–B, D–E, basal view C, detail of the ornamentation pattern; F, basal view; G, apical view. H–K, *Gyrogona caelata* forma *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.

412x681mm (300 x 300 DPI)

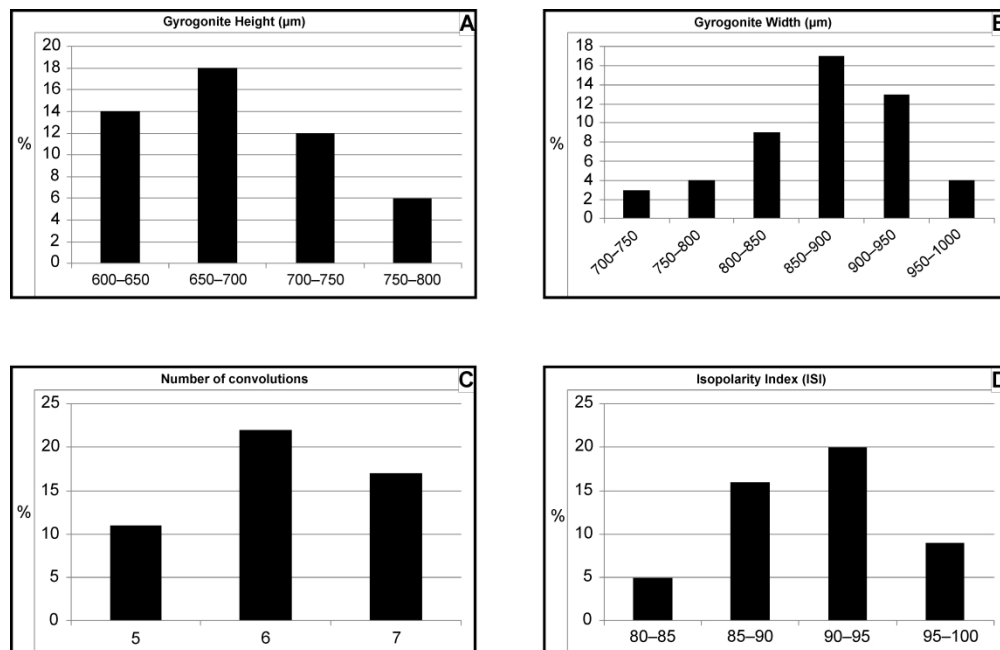


Figure 9. Frequency distribution of the height (A), width (B), number of convolutions (C), and height/width ratio (ISI) (D) of the *Gyrogonia caelata* population (50 gyrogonites measured), from samples G-2.2, G-2.3, G-2.4, G-2.5, and G-6a in the bauxite cover-sequence of the Gánt section.

384x248mm (300 x 300 DPI)

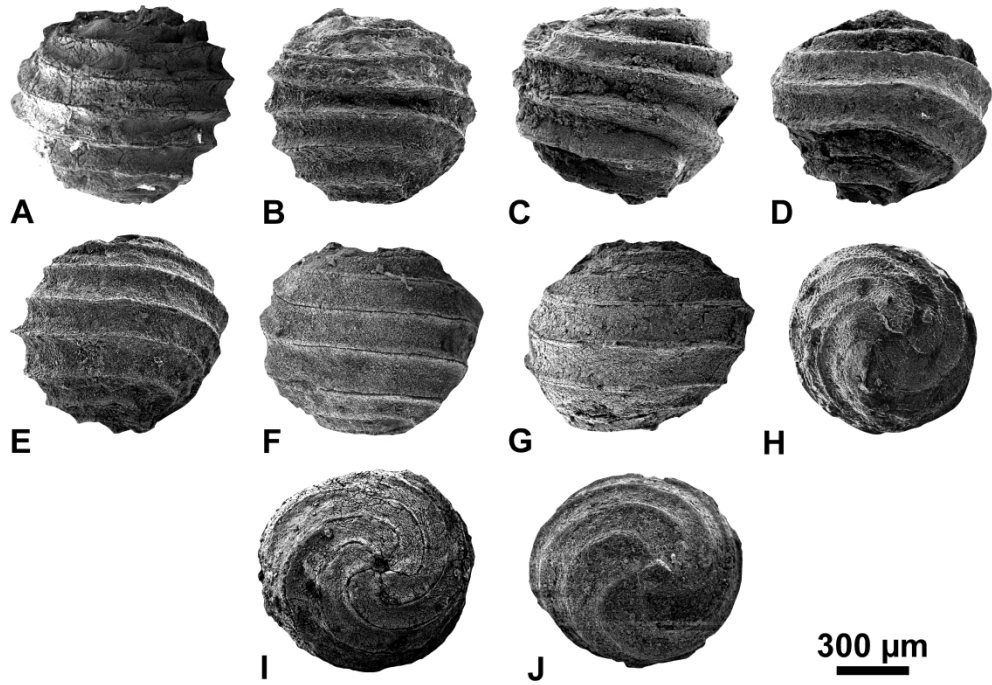


Figure 10. *Gyrogona tuberosa* gyrogonites from the Gánt bauxite cover-sequence (sample G-6b), HNHM-PBO 1554–1563. A–G, lateral view; H, apical view; I–J, basal view.

643x441mm (300 x 300 DPI)



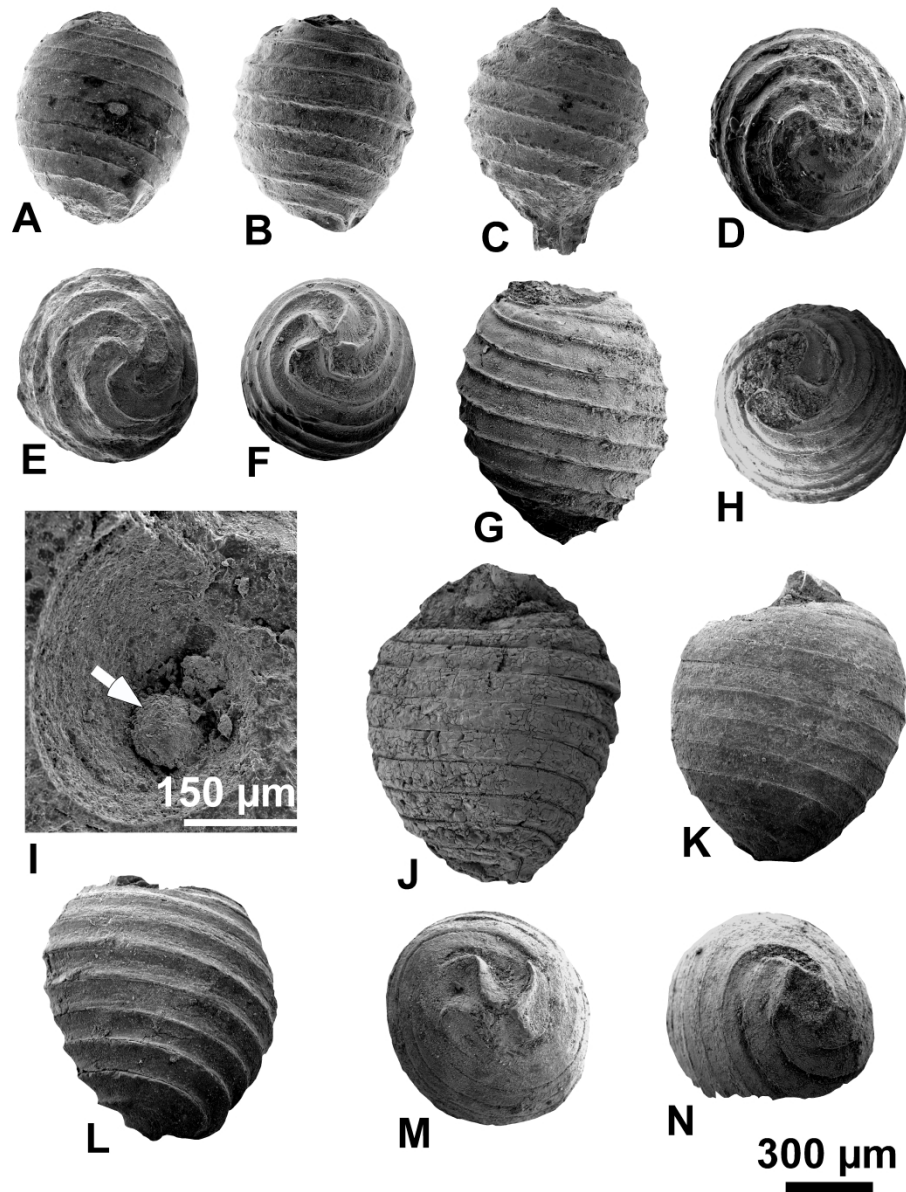


Figure 11. Gyrogonites of genera *Psilochara* and *Nitellopsis* from the Gánt bauxite cover-sequence. A–F, *Psilochara polita* (sample G-6a), HNHM-PBO 1564–1569. A–C, lateral view; D–E, apical view; F, basal view. G–I, *Psilochara* sp. (sample G-6a), HNHM-PBO 1570–1571. G, lateral view; H, apical view; 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)

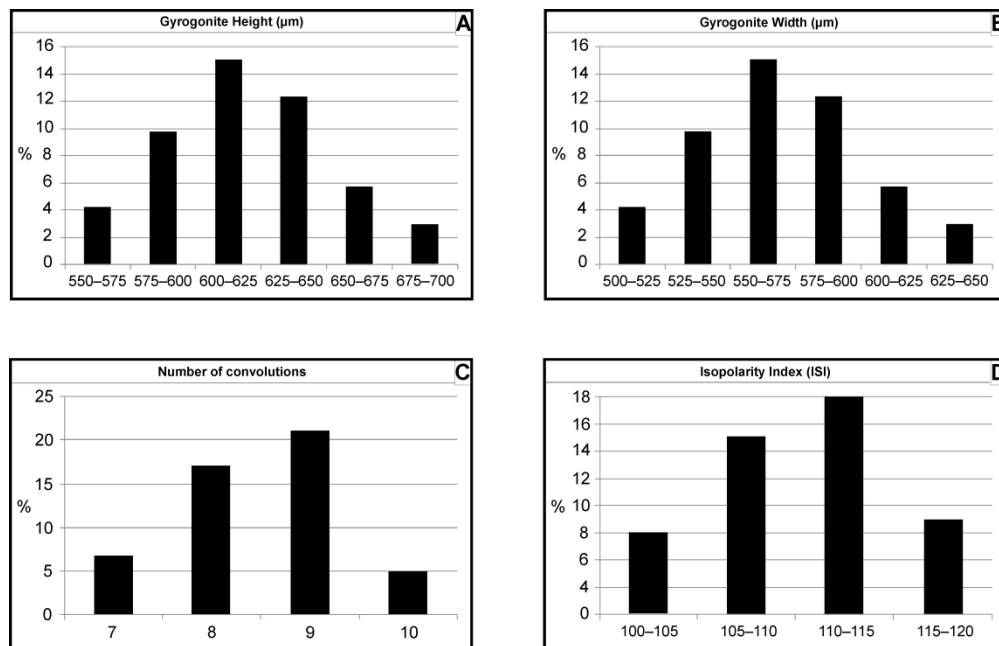


Figure 12. Frequency distribution of the height (A), width (B), number of convolutions (C), and height /width ratio (ISI) (D) of the *Psilochara polita* population (50 gyrogonites measured), from sample G-6a in the bauxite cover-sequence of the Gánt section.

381x244mm (300 x 300 DPI)

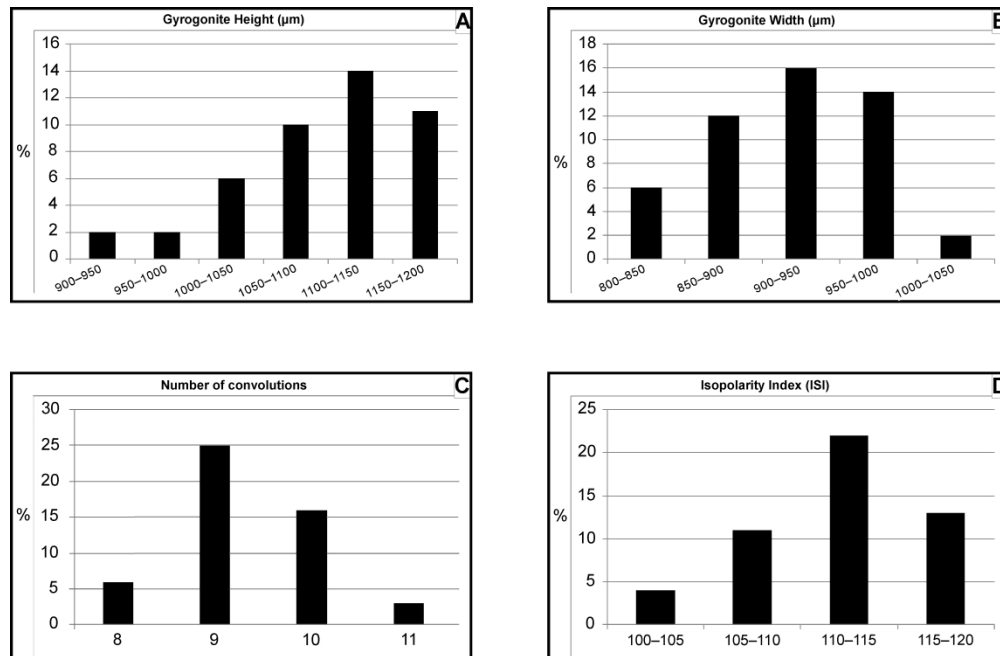


Figure 13. Frequency distribution of the height (A), width (B), number of convolutions (C), and height /width ratio (ISI) (D) of the *Nitellopsis (Tectochara) aff. palaeohungarica* population (50 gyrogonites measured), from samples G-2.3 and G-2.5 in the bauxite cover-sequence of the Gánt section.

387x252mm (300 x 300 DPI)

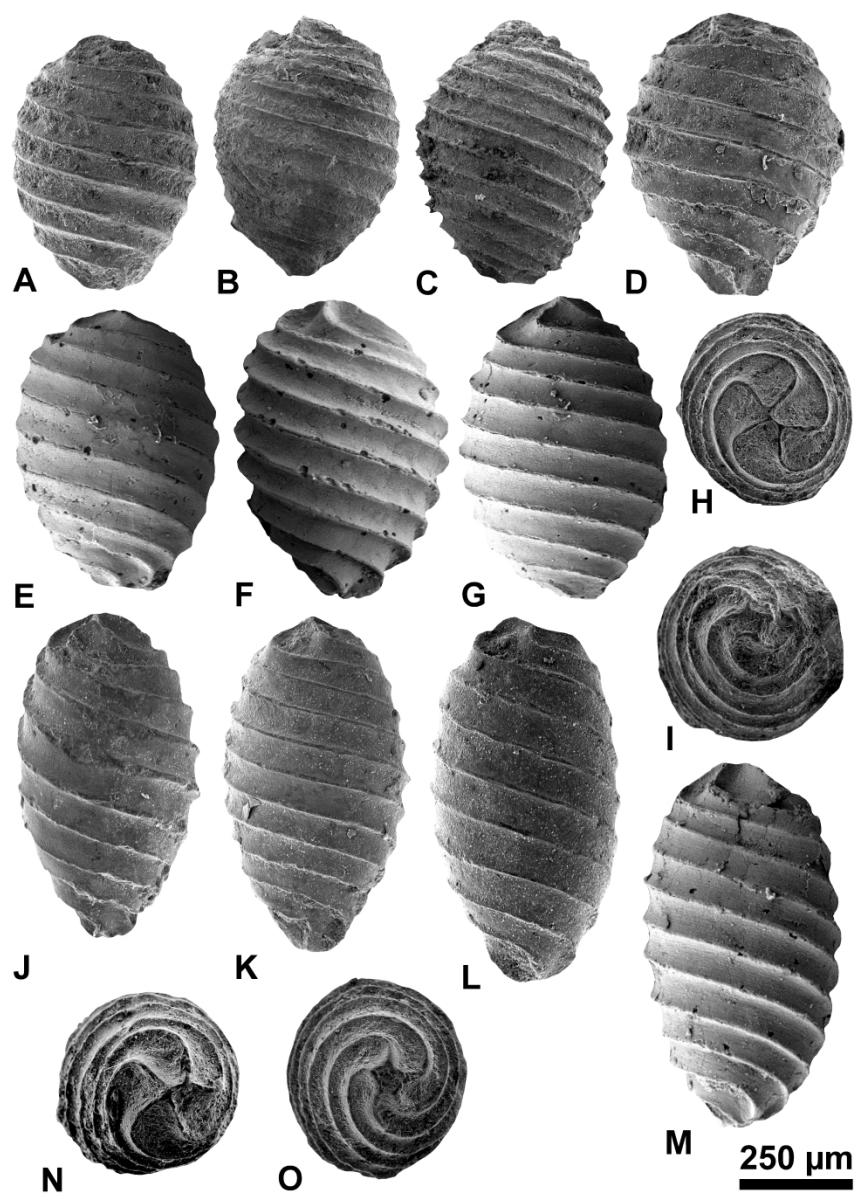


Figure 14. *Chara* gyrogonites from the Gánt bauxite cover-sequence. A–I, *Chara media* (samples G-2.5 and G-6a), HNHM-PBO 1577–1585. A–G, lateral view; H, apical view; I, basal view. J–O, *Chara subcylindrica* (sample G-6b), HNHM-PBO 1586–1591. J–M, lateral view; N, apical view; O, basal view.

456x633mm (300 x 300 DPI)

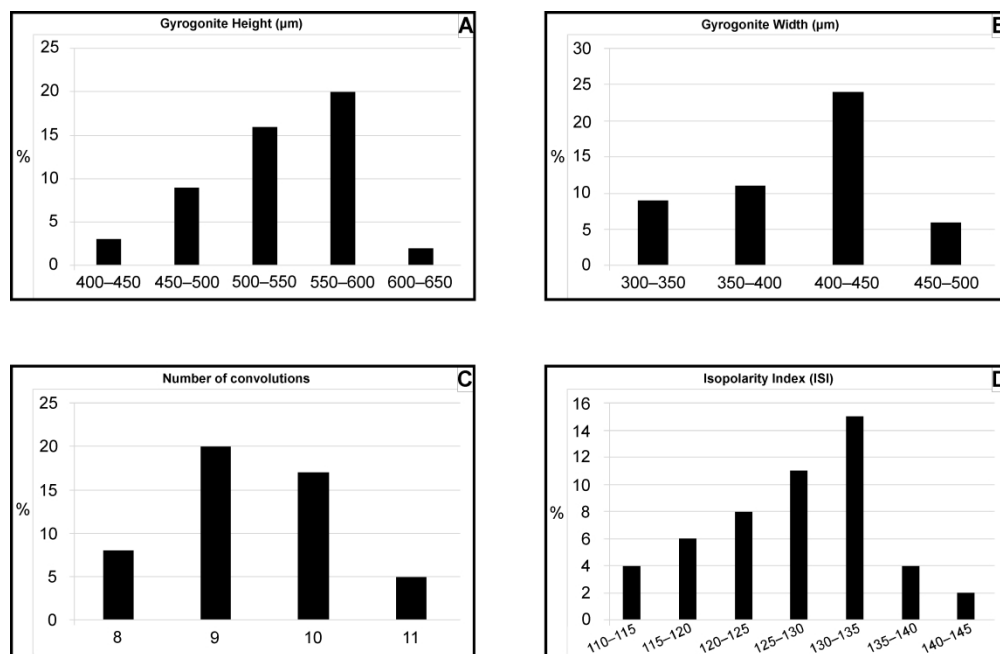


Figure 15. Frequency distribution of the height (A), width (B), number of convolutions (C), and height /width ratio (ISI) (D) of the *Chara media* population (50 gyrogonites measured), from samples G-2.5 and G-6a in the bauxite cover-sequence of the Gánt section.

384x248mm (300 x 300 DPI)

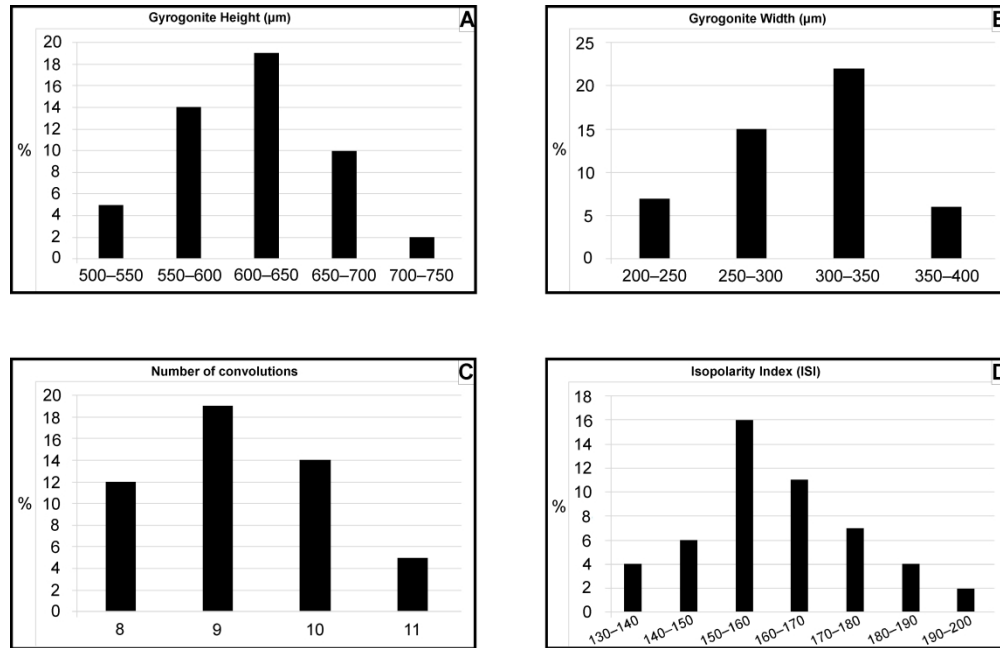


Figure 16. Frequency distribution of the height (A), width (B), number of convolutions (C), and height/width ratio (ISI) (D) of the *Chara subcylindrica* population (50 gyrogonites measured), from sample G-6b in the bauxite cover-sequence of the Gánt section.

385x248mm (300 x 300 DPI)

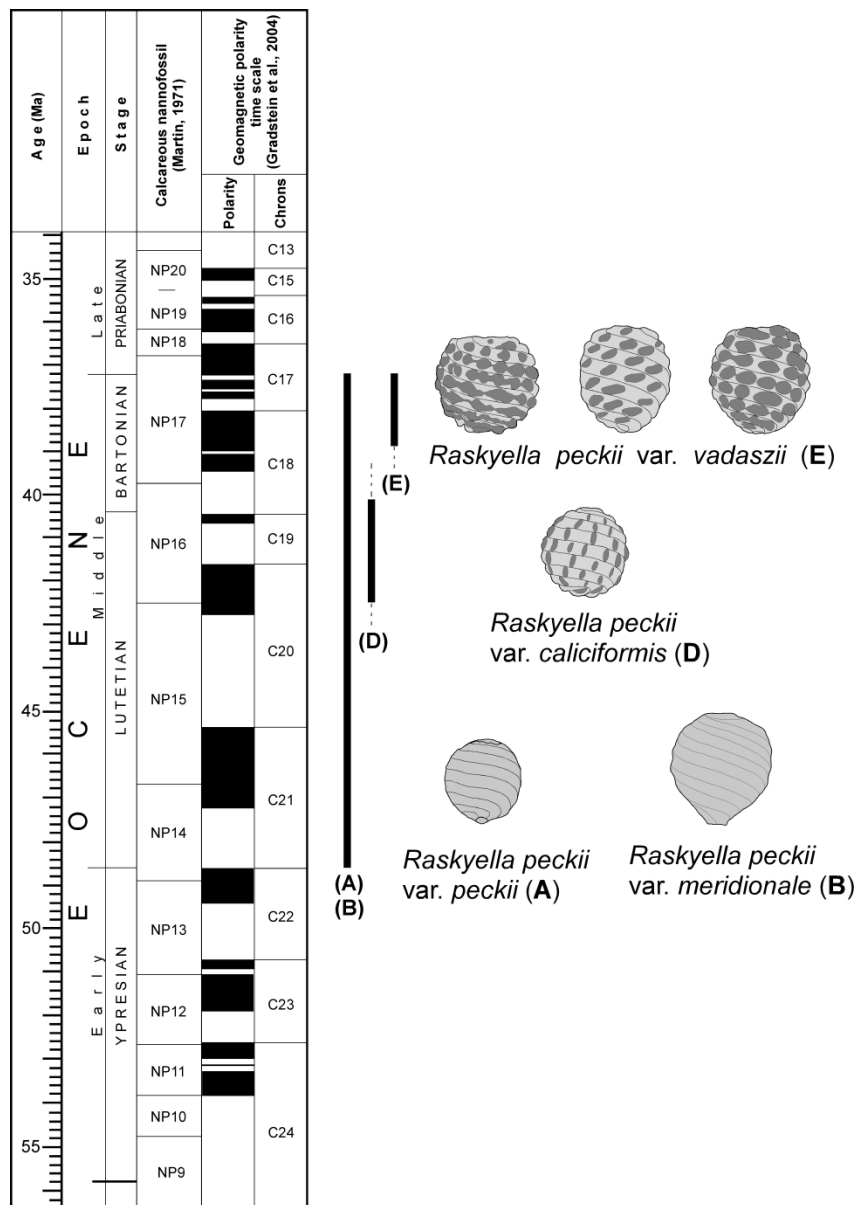


Figure 17. Stratigraphic distribution of variants of the anagenetic evolutionary lineage of species *Raskyella peckii*.

413x587mm (300 x 300 DPI)

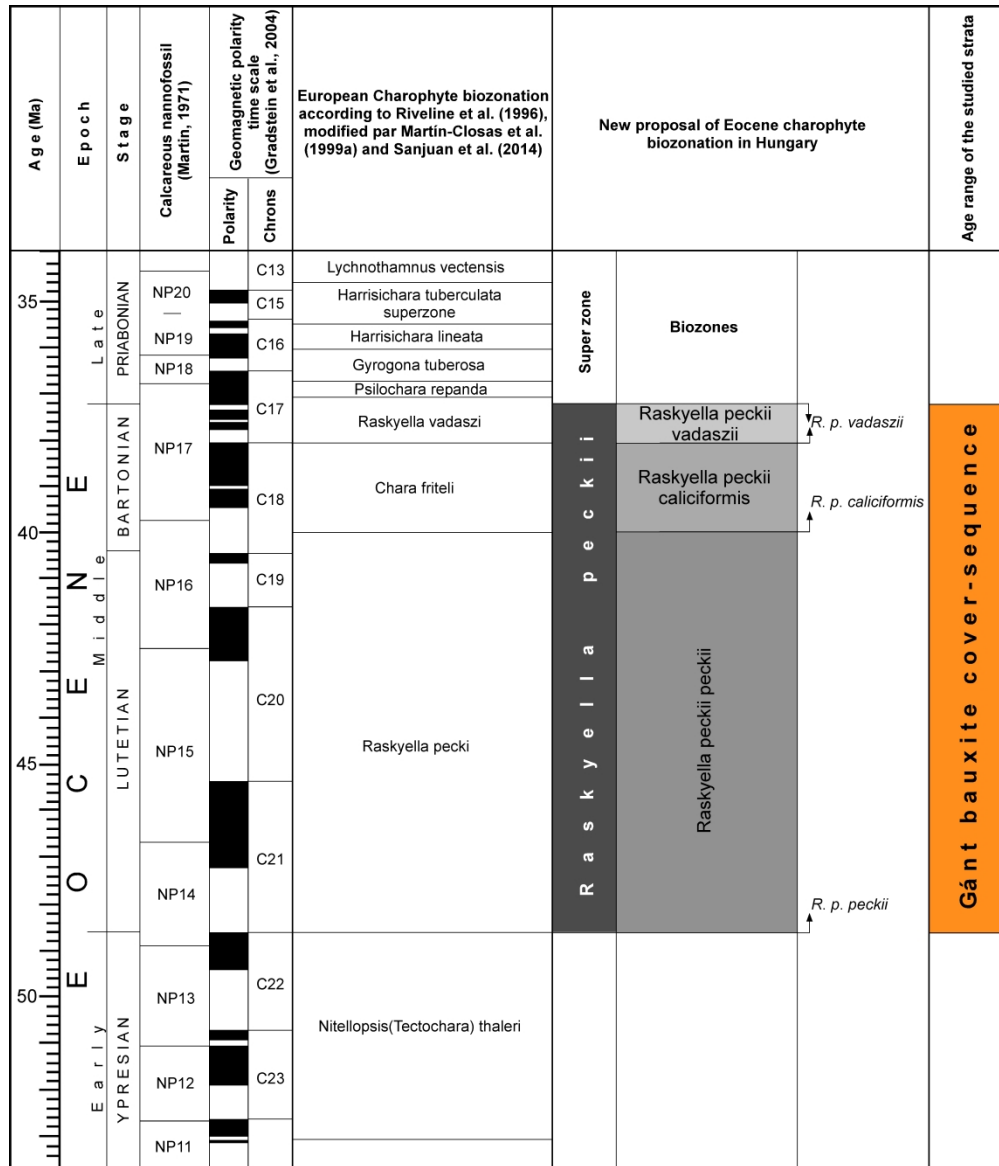


Figure 18. Charophyte Biostratigraphy, age and correlation of the bauxite cover-sequence from the Gánt section.

457x532mm (300 x 300 DPI)