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RESEARCH

Macro- and micromorphology of *Carex pauciflora*-type fossils (Cyperaceae) from Europe and Siberia reveals unexpected affinity to *Carex* sect. *Cyperoideae*

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Abstract
Elongated biconvex *Carex* fossil fruits are relatively common in fossil assemblages, but they are of much uncertain taxonomic affinity. Three fossil-species have been erected to accommodate the materials from the respective type localities (*C. klarae*, *C. paucifloriformis* and *C. paucifloroides*) and a number of superficially similar-looking fossils were reported from other sites. The formerly proposed affinities mostly pointed to the extant *C. pauciflora* (subgen. *Euthyceras*) or *Carex* sect. *Cyperoideae* (subgen. *Vignea*), depending on the authors. But despite the similar superficial resemblance of the fossil remains to these not very closely related sedge taxa, other groups are also possible matches. We used a comparative approach employing stereomicroscope and SEM to analyze the affinities of several Old World "mummified" fossils (ca. 23 to 0.1 Ma) of elongated biconvex fruits. Several samples showed a fair preservation of previously unattested microscopic characters. In particular, one of them allowed us to detect an indirect record of fine silica body morphologies (impressions) on the periclinal walls, which permitted the sound taxonomic placement of the remains from the Miocene of Siberia as a *Carex* sect. *Cyperoideae*. In all the other fossils analyzed, the epidermal cell outline and the central position of the main silica body were sufficient to discard assignment to subgen. *Euthyceras*, despite a purported affinity to *C. pauciflora* reported in previous literature. In the absence of detailed information on silica bodies, epidermal cell (exocarp) details in fossil specimens do not seem to be determinant for the systematic placement. However, the addition of diagnostic style characters pointed to sect. *Cyperoideae* as the best match with the available information. Our data support a continued presence of *Carex* sect. *Cyperoideae* in the Old World since the Miocene, which candidates Eurasia as a possible place of origin for it, despite DNA-based reconstructions alone proposed North America. This study underlines the importance of detailed taxonomic studies to properly address the identity of fossils and unravel the biogeographic history of plants.

Keywords Achene · *Carex* sect. *Ovales* · *Carex* subgen. *Euthyceras* · *Carex* subgen. *Psyllophorae* · *Carex* subgen. *Vignea* · Carpology · Cenozoic · Exocarp · Sedges

Introduction

Carex L. is one of the largest plant genera of the world with about 2000 accepted species (POWO 2024). The knowledge on the general systematics of *Carex* has been consistently updated in recent times by contributions from the Global *Carex* Group consortium (Jiménez-Mejías et al. 2016a; Martín-Bravo et al. 2019; Villaverde et al. 2020; Roalson et al. 2021). The genus is now organized in six subgenera that match the six deepest known lineages: *Siderosticta* Waterway, *Psyllophorae* (Degl.) Peterm., *Euthyceras* Peterm., *Uncinia* (Pers.) Peterm., *Vignea* (P.Beauv. ex T.Lestib.) Heer, and *Carex* (Villaverde et al. 2020). The global biogeographic history of the genus has been recently addressed by using several fossil records of quite certain taxonomic ascription to calibrate a molecular phylogeny based on DNA analysis of extant plants (Martín-Bravo et al. 2019). The main results pointed out that differentiation of the six main subgeneric lineages seems to have occurred simultaneously during the Oligocene, while it was during the Miocene when most extant sectional lineages were established. Before Martín-Bravo et al. (2019), fossils of *Carex* did not receive due attention in phylogenetic studies, even if several fossil-species have been described from intervals which

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are deemed to be crucial for the diversification of the genus (e.g. Oligocene; Jiménez-Mejías et al. 2016a). Indeed, the affinities of certain fossil remains have been proposed just on the basis of superficial analogies to extant species, so that systematic botanists preferred to ignore such past records for further purposes such as molecular dating. This is just the consequence of a comprehensible but inconvenient cultural gap. It has been demonstrated that, with accurate analyses, including microstructural details, systematic affinities of fossils can be unveiled for fruits of sedge genera (Tucker and Miller 1990). Those analyses, which combine macroscopic and microscopic characters, represent today the best available way of suggesting taxonomic affinities of fossil remains and addressing uncertainties.

As shown by Jiménez-Mejías et al. (2016b), *Carex* has a rich fossil record, mainly conformed by achenes and, in a lesser amount, also by utricles (a bract-derived false fruit; see Jiménez-Mejías et al. 2016c). However, the lack of a comprehensive study on *Carex* carpological characters useful for taxonomic studies hampered the understanding of the fossil remains. Some comparative analyses carried out on several species showed that, when studied in combination, carpological characters in sedge achenes may allow fine identification to relatively shallow phylogenetic levels (Martinetto et al. 2014), and even distinction at species level in taxonomically complex groups (Jiménez-Mejías and Martinetto 2013) of recent divergence (Benítez-Benítez et al. 2021).

Micromorphological taxonomic characters in *Carex* achene epidermis

Carex achenes are regarded as having limited taxonomic value. All of the most obvious ones (e.g., shape, dimensions, section outline, style pattern, wall thickness, attachment to the utricle, etc.) were evaluated as potentially useful to approach the taxonomic identity of fossils (e.g., Mai 2000; Nikitin 2005; Velichkevich and Zastawniak 2006; Jiménez-Mejías and Martinetto 2013). On a small scale, epidermal cells bear a set of micromorphological features (Fig. 1) that show variation among supraspecific taxa (e.g., Fig. 1a vs. b). The extracellular side of the external periclinal wall has been mostly reported as void of characters. However, its intracellular side can show a record of more diagnostic silicified parts (see below).

The anticlinal wall thickness and curvature often varies within a single cell. It can be undulated internally, straight in the middle, and show again undulation externally (Guerriero et al. 2020). In addition, what may appear as the protrusion of the anticlinal wall on the outer surface of the achenes is actually a more complex structure (here defined as the anticlinal-periclinal walls junction, from herein "a-p junction"; Fig. 1), result of the transition of the anticlinal walls of two adjacent cells to the respective external periclinal walls. The "a-p junction" is often straight, but it may well subtend an undulated anticlinal wall. All these intricate situations heavily limit the taxonomic use of anticlinal wall and "a-p junction" in taxonomy and defer further evaluations to future observations.

The internal periclinal walls contain silicified parts (Fig. 1a, b), phytoliths, that most authors pointed out as taxonomically relevant (e.g. Toivonen and Timonen 1976; Tallent and Wujek 1983; Dan and Hoshino 1994; Starr and Ford 2001; Zhan 2004). The intracellular (from here onwards, intra- and extracellular referred to the epidermal cells) surface of the internal periclinal wall is largely or totally covered by a silica platform, which in some cases may display a central protrusion, called the central silica body, and additional peripheral smaller protuberances known as the satellite bodies (Fig. 1a, b). Platforms may vary in thickness, and bodies may vary in size, number, scattering and shape. Most authors agree on the utility of the characters visible on the internal periclinal wall when working at medium/deep phylogenetic scales (i.e. genus, subgenus or section levels; e.g., Dan and Hoshino 1994; Zhan 2004; Lu et al. 2021). However, the particular variation of its states might be addressed within each study case, since its variability and consistency can be fairly different depending on the taxonomic group. Some groups of closely related *Carex* species exhibit fairly constant combinations of characters/states, which can constitute a valuable set of diagnostic features at a deep evolutionary scale.

At the same time, the uniformity of characters hampers the distinction of taxa at the shallowest microevolutionary level (e.g., Waterway 1990; Jiménez-Mejías et al. 2017; Więcław, et al. 2017; Míguez et al. 2018; Lu et al. 2021). In some groups, such as *Carex* sect. *Confertiflorae,* these features may even display intraspecific variation (e.g. Lu et al. 2021), so that the internal periclinal wall characters have been regarded as useless, non-diagnostic features. The opposite is true in subgen. *Vignea*, in which species belonging to different sections (e.g., *Ammoglochin* Dumort., *Cyperoideae* G.Don, *Elongatae* Kunth) showed diagnostic micromorphological characters (Toivonen and Timonen 1976).

Analysis of intracellular epidermal cell features in sedge achenes has been limitedly applied to fossil specimens because the prevailing preservation state is "mummification" (Mustoe 2018; or waterlogged preservation, e.g., Xia et al. 2018, if the criticism by Luczaj et al. 2018 is accepted). Several SEM studies on "mummified" fossil achenes (Jiménez-Mejías and Martinetto 2013) showed empty spaces where a platform was expected (Fig. 1a') or a partial preservation of what is probably the organic framework of the original silica platforms (Fig. 1b'). This implies that the most diagnostic silicified structures are prone to dissolution and usually lacking in fossils.

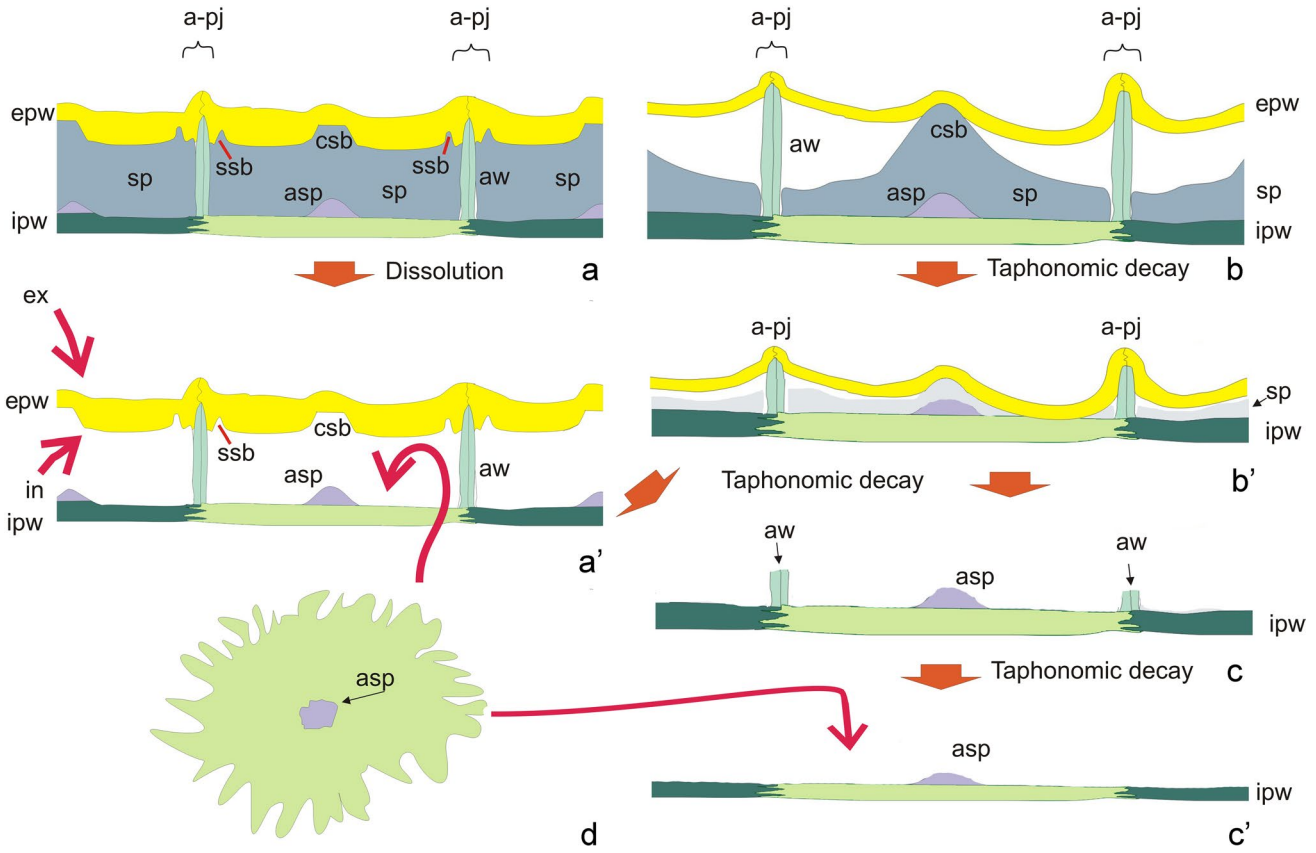


Fig. 1 Schematic drawings of the achene epidermis (exocarp) in cross-section for the interpretation of two settings (**a**, **b**) observed in *Carex*; see Gonzalez and López (2010) for a good rendering of the tridimensional context of the exocarp in Cyperaceae. A tentative representation of the main alterations seen in fossils (**a'**, **b'**, **c**, **c'**) is also provided. **a** Epidermal cell structure observed in dry modern achenes of *Carex* sect. *Cyperoideae* (e.g., *C. bohemica*), in which the whole silica platform of a cell contacts the intracellular side of the external periclinal wall; this epidermal architecture is rarely retained unchanged in weakly altered fossils, while usually they show dissolution of the silicified parts, which does not preclude the preservation of an indirect record of the platform's morphology (**a'**); **b** Epidermal cell structure observed in dry modern achenes of many taxa (e.g., *C. anthoxanthea*, *C. pulicaris*, and taxa treated by Jiménez-Mejías et al. 2016b), in which only the central silica body contacts the intracellular side of the external periclinal wall; **b'** Modifications seen in some fossil achenes, in which the platforms may retain only the organic part, after dissolution of silica; **c** Example of a fossil that may derive either from (**a**) or (**b**), where taphonomic decay determined a complete removal of the platforms and external periclinal walls, **c'** Extreme modification with vanishing of the anticlinal walls and thinning of the internal periclinal walls; **d** jigsaw-puzzle-like pattern (Guerriero et al. 2020) of the internal periclinal wall in a view orthogonal to the cross-section; *a-pj* anticlinal-periclinal junction; *asp* attachment structure of the silica platform; *aw* anticlinal walls; *csb* central silica body; *epw* external periclinal walls; *ex* extracellular side of the external periclinal walls; *in* intracellular side of the external periclinal walls; *ipw* internal periclinal walls; *sp* silica platform; *ssb* satellite silica body

Only rougher traits, such as cell outlines and attachment structures (Fig. 1c) of platforms, are commonly present. Regardless of these limitations, the residual epidermal structure of fossils is not useless for taxonomical studies, but its evaluation can be challenging (Fig. 1c'). In particular, it is very difficult to analyze the possible presence of such useful characters as the impressions of silica bodies on the intracellular side of the periclinal walls (Fig. 1a'), and any specific methods of preparation are suggested by the literature on fossil achene micromorphology. We will show below that a lucky chance helped us in this sense.

The problem with *Carex pauciflora*-type fossil remains

An especially challenging set of fossil remains (Fig. 2) is represented by the records grouped under four different names: the extant *C. pauciflora* Lightf. (Fig. 2m), and the fossil (Table 1) *C. klarae* Mai (2000: pl. 15, Fig. 1–4), *C. pauciflo-riformis* V.P.Nikitin (Fig. 2d), and *C. paucifloroides* Wieliczk. (Fig. 2a–c) (from herein broadly defined as *C. pauciflora*-type remains). Remains placed under those names were presented as of uncertain systematic affinities in the revision of *Carex*

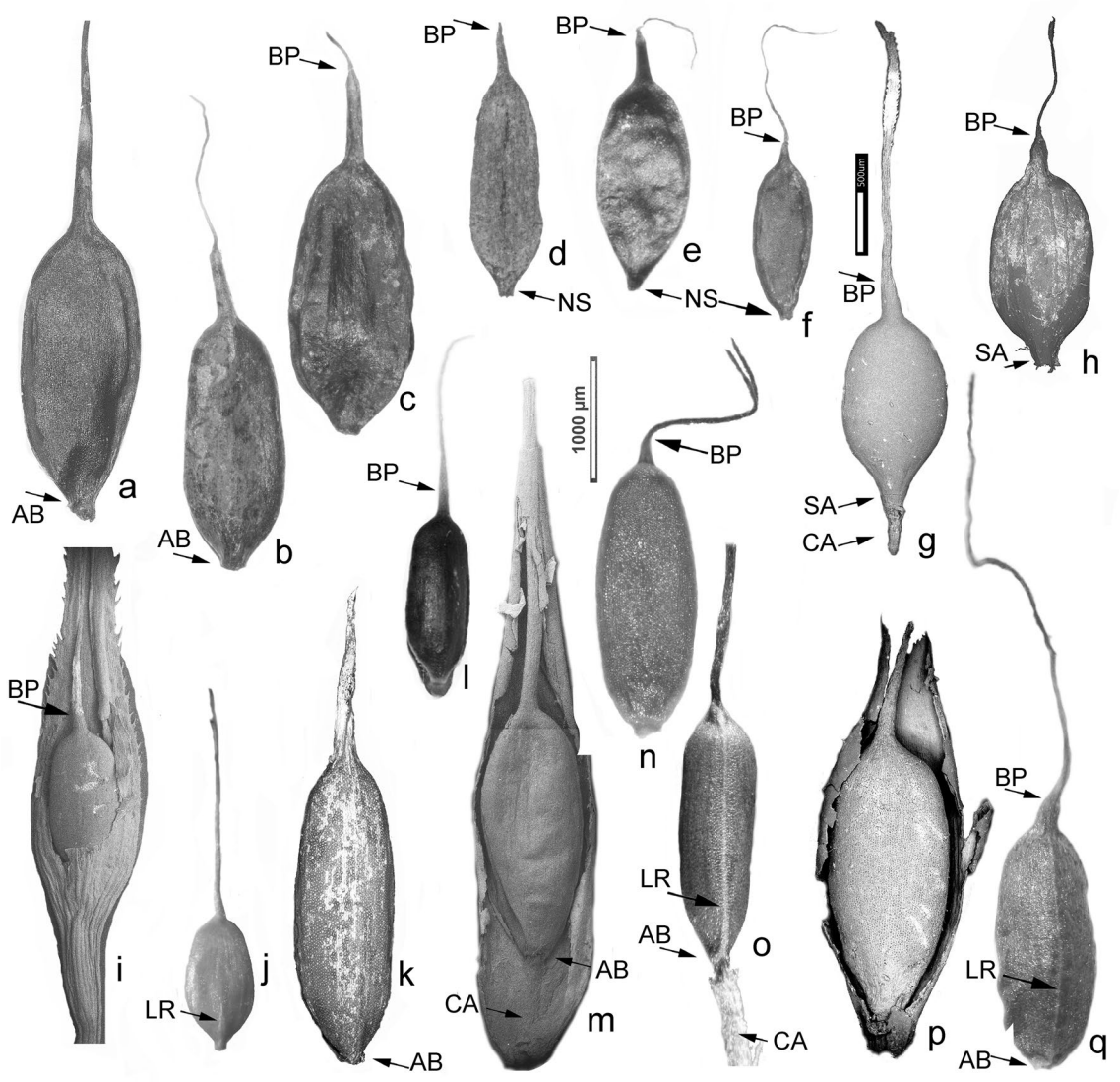


Fig. 2 Comparison of selected elongated, plano-convex to very obtusely trigonous fossil achenes (**a**–**f**) with the most similar ones produced by extant species of *Carex* (**g**–**q**). A few relevant, shared or divergent × 40 characters are pointed out: *AB* attenuate base; *CA* carpophore; *BP* boundary point of the style (see Jiménez-Mejías and Martinetto 2013); *LR* longitudinal ridge; *NS* narrowly stipitate achene; *SA* stipitate achene. See references to this figure in Table 2 and Table 3 for more detailed data concerning each specimen. **a**–**c** Pleistocene fossils from Siberia assigned by us to *C. pauciflоroides* sp. inc.; **a** achene with exceptionally well-preserved style, "soft" style pattern; **b** style with apparent "proboscis" style pattern; **c** more altered style, showing a constriction (BP arrow) suggesting a "proboscis" style pattern; **d** *C. pauciflоroides* sp. inc., Oligocene–Miocene transition, achene with altered style, keeping only the proximal, more lignified part with a distal constriction (BP arrow), compatible with a "proboscis" style pattern; **e** *C. pauciflоroides* sp. inc., Pliocene of Italy, achene with apparent "proboscis" style pattern; **f** *C. bohemica*, Pleistocene of West Siberia, achene with apparent "proboscis" style pattern; **g** *C. leporina*, achene, notice the non-constricted style which, however, shows a robust and smooth proximal portion passing (BP arrow) to a wrinkled and weaker distal portion, were we verified a marked decrease in lignification ("soft" style pattern); SEM photo; **h** *C. leporina*, achene washed out from a soil sample, covered by utricle remains with veins and bearing a style with an apparent constriction (BP arrow), marking a "proboscis" style pattern; SEM photo; **i** *C. bohemica*, partly opened utricle showing the achene inside, notice the non-constricted style with a change of brightness in the point indicated by the arrow, above which we verified a marked decrease in lignification ("soft" style pattern); **j** *C. synchnocephala*, achene with a partial longitudinal ridge (LR arrow), which determines an obtusely trigonous shape in cross-section; **k** *C. muskingumensis*, achene, SEM photo; **l** *C. projecta*, achene with non-constricted style showing a change of brightness in the point indicated by the BP arrow, separating two parts with different lignification ("soft" style pattern); **m** *C. pauciflora*, opened utricle showing the achene inside with a firm style pattern (lignification and style width do not decrease from bottom to top); SEM photo; **n** *C. macrostyla*, achene with a constriction (BP arrow) of the style, also corresponding to a decrease in lignification; **o** *C. hakkodensis*, achene with poorly lignified style and a longitudinal ridge with a distinct vascular bundle; **p** *C. pulicaris*, opened utricle showing the achene inside, with a firm style pattern (lignification does not decrease from bottom to top, but the style is progressively narrower); SEM photo; **q** *C. circinata*, achene with constriction of the style (BP arrow), whose longest, distal portion is poorly lignified; longitudinal ridge with a distinct vascular bundle

Table 1 Details on the type materials of the fossil-species indicated as similar to the achenes of *Carex pauciflora*

Name	Type locality	Collection code	Analysis	Dimensions (mm)	Age	Number of type specimens	Protologue publication and illustrations
Carex klarae	Germany, Klara II near Kausche	MfN Berlin 1993/4720	×40, SEM	1.6–1.9×0.4–0.6	Late Miocene	Holotype + 1 figured paratype	Mai 2000, pl. 15, Figs. 1–4
Carex pauciflo-riformis	Russia, West Siberia, Kartashovo	BIN-Pb-H3296	×40	1.3–2.0×0.6–0.9	Middle Miocene	Holotype + 3 figured paratypes	Nikitin 1976, pl. 65, Figs. 28–31
Carex pauciflo-roides	Belarus, Dvorets	AN BSSR-D-73–2-1 (current storage place unknown)	×40	1.6–2.6×0.6–1.1	Pleistocene (as "Pliocene")	Holotype + 1 figured paratype	Velichkevich 1975, pl. 1, figs. 24–25

fossils by Jiménez-Mejías et al. (2016b). Somehow morphologically similar are also the fossil achenes assigned to the extant *C. bohemica* Schreb. (Fig. 2f), which have been indicated (Velichkevich and Zastawniak 2006) as smaller, but not easily distinguishable from *C. paucifloroides*. Based on such indications, assignment of unidentified fossil specimens of intermediate dimensions to either species can be challenging (Fig. 2e). Fossil specimens assigned to each of the fossil-species named above span from the Oligocene to the Pleistocene (Raniecka-Bobrowska 1959; Velichkevich 1975; Dorofeev 1985; Mai and Walther 1988; Mamakowa and Velichkevich 1993; Nikitin 2006; Velichkevich and Zastawniak 2003, 2006, 2007; Stachowicz-Rybka 2015; Zyuganova et al. 2015; Jiménez-Mejías et al. 2016b; Teodoridis et al. 2017 and references herein). These fossils (e.g., Fig. 2a–d) were obviously associated by a superficial resemblance to *C. pauciflora* achenes (Fig. 2m; see Materials and Methods for a detailed account of the involved characters). However, there are other extant *Carex* groups that display similar combinations of characters, rendering *Carex pauciflora*-type remains as a putative good match for additional related species (see below in Materials and Methods, Sampling). Relying on available photographs and descriptions, the revision led by two of the authors of the present paper (Jiménez-Mejías et al. 2016b) allowed to narrow down the possible affinities of these fossils to two distantly related clades of *Carex* species: *Carex* sect. *Cyperoideae* (Fig. 2g-l), in subgen. *Vignea* (then named sect. *Ovales* Kunth; see Roalson et al. 2021), and the so-called Caricoid Clade (Fig. 2m–q: with their members now placed in two different subgenera: *Euthyceras* and *Psyllophorae*). The evolutionary history of both groups as interpreted to date is also different. Section *Cyperoideae* has been reported to be of relatively recent divergence (mean age 3–5 Ma, Pliocene) and it seems to have undergone radiation at the shallowest evolutionary level. Conversely, the main clades within either subgenera *Euthyceras* and *Psyllophorae* go deeper in the phylogeny (mean ages reaching the Middle and Early Miocene at 12–20 Ma: Martín-Bravo et al. 2019).

The purpose of the present study is to shed light on the taxonomic affinities of *C. pauciflora*-type remains by the direct study of presently available fossil specimens and the comparison with modern materials of extant species. The possibility to study several rich picked collections (sets of specimens of a definite type gathered from sediment samples processed by previous authors) stored in Russian repositories was particularly relevant. We followed Jiménez-Mejías and Martinetto's (2013) approach on the examination of *Carex* sect. *Phacocystis* Dumort. achenes to analyze the morphology and figure out the affinities of these fossil remains. In addition, we studied micromorphological features of the epidermis with the aid of SEM.

We also aimed to show an improved method of analysis of fossil achenes of *Carex*, in order to assess whether they may or may not provide characters for their assignment to subgeneric taxa. However, we are aware that a standard procedure cannot be fully outlined yet, and further studies are necessary to achieve this target. Anyway, we wanted to verify if the validly described names of *C. pauciflora*-type fossil-species will convincingly refer to distinct taxa. After the assessment of nomenclature, we also planned to assign uniform names to the fossils stored in different collections, even by using open nomenclature. For open nomenclature we follow, for the first time in this paper, the suggestions by Sigovini et al. (2016) to use the expression "sp. inc." [species incerta = uncertain species], for fossils showing several characters of a precise species, even if we could not state that the identification was certain and definitive.

Material and methods

Delimitation of study group

Carex pauciflora-type fossil remains display a set of macromorphological characters in common (Fig. 2a-d): (1) achene outline narrowly oblong, constricted at the apex towards the style and thus forming a definite inflexion; (2) achene cross-section from plano-convex to obtusely trigonous; and (3) style more or less elongated, persistent in the form of a cylindrical remnant (apiculus: Rothrock and Reznicek 1996) at the top of the achene. Our sampling strategy intended to approach as much as possible the affinities of the morphologically similar *C. pauciflora*-type fossil remains through the comparative analysis of their achene features with those of selected extant species.

In addition, we analyzed samples of two outgroup species (*C. brizoides*, sect. *Ammoglochin*; *C. elongata*, sect. *Elongatae*) to broaden the field of our observations on the effects of bleaching on modern achenes (see below). These last ones have been of paramount relevance for the comprehension of the micromorphological details of fossils.

Sampling

Modern material

Given the huge size of *Carex* and the open affinities of the *C. pauciflora*-type fossil remains, we tried narrowing down as much as we could which groups of species may display achenes that could be a putative match to the fossil ones (from now on *C. pauciflora*-like achenes). A first literature search was performed on confident sources of data that we located (Egorova 1999; Ball and Reznicek 2002; Dai et al. 2010; Ercole et al. 2012), according to the current phylogenetic views on the genus (Roalson et al. 2021). As a result, we were able to identify five extant morphological groups, whose achenes bear the above-cited combination of features of the *C. pauciflora*-type remains: (1) *Carex* sect. *Circinatae* Meinsh. (subgen. *Euthyceras*: Fig. 2o, q); (2) *C. pauciflora* (subgen. *Euthyceras*, sect. *Leucoglochin* Dumort.: Fig. 2m); (3) unispicate species from *Carex* subgen. *Psyllophorae* (*C. macrostyla* Lapeir., Fig. 2n, and C. *pulicaris* L., Fig. 2p); (4) species within *C.* sect. *Cyperoideae* (=sect. *Ovales*; subgen. *Vignea*: Fig. 2g–l). From all the studied taxonomic groups, sect. *Cyperoideae* is by far the largest with ca. 100 species, while all the others are phylogenetically isolated species or fairly small lineages (up to six species in sect. *Circinatae*) (Roalson et al. 2021).

Initially we also considered as possible candidates with *C. pauciflora*-like achenes the sections *Dornera* Heuff. and *Rarae* C.B.Clarke, but after the examination of a few specimens (results not shown) we excluded them from any subsequent step because: (1) achene length/width ratio was too low; (2) cross-section was clearly sharp-trigonous; and (3) style was poorly lignified, thus leaving a short (not elongated) remain on the top of the achene. We also excluded three species with oblong achenes, but readily separated from the *C. pauciflora*-type, either because of the attenuated apex of the achenes (and thus without a clear inflexion; i.e. *C. microglochin* Wahlenb.) or because of the broad and short style remain (i.e. *C. bostrychostigma* Maxim. and *C. mucronata* All.).

Utricles containing achenes were taken from herbarium collections (LE, MTDO, UPOS; acronyms according to Thiers 2023 +) or from carpological collections (Table 2). Whenever possible, material from different locations was analyzed to evaluate variability within a same species. Recovery of fruits from the soil, which is known to produce alterations in Cyperaceae achenes which are readily comparable to those seen in fossils (Jiménez-Mejías and Martinetto 2013; Martinetto et al. 2014), was only possible for a sample of *C. leporina* (Fig. 2h).

Fossil materials assignable to extant species

Fossils from Quaternary deposits that may potentially represent some of the above-cited extant species were analyzed to understand the taphonomic alteration of characters (Jiménez-Mejías and Martinetto 2013; Martinetto et al. 2014). We obtained material from four rich collections (BIN-Pb-H, Nikitin collections at the Komarov Botanical Institute, St. Petersburg, Russia; CCN, CENOFITA palaeocarpological collection of the Turin University, Italy; IGMN, Institute of Geology and Mineralogy SB RAS, Novosibirsk State University, Russia; MfN, Mai collection at the Museum für Naturkunde of Berlin, Germany; Table 2). Two Pleistocene picked collections from West Siberia (BIN-Pb-H273 and H535) provided a few achenes and an utricle (Fig. 3e, f) assigned to *C. pauciflora* (Nikitin 2006). Among the other species, we could study two picked collections of Pleistocene achenes (Figs. 2f; 4l–n; 12) and a few utricles assigned to *C. bohemica* (Krivonogov 1988; Nikitin 2006). We have been also able to analyze two fossil achenes from the Pleistocene of Germany, which were previously assigned to *C. pulicaris* (Mai 2010: p. 120). Finally, two Pleistocene achenes assigned to *C. leporina* (Martinetto et al. 2014) were available in the Italian CCN collection (Table 3).

Characters visible with a stereomicroscope to up to×40 (here considered as macromorphological) were checked to confirm the putative identity of all these specimens. We proceeded with SEM analyses (see below) to study

Table 2 Details of the extant plant specimens

Subgen Section	Species	Voucher/source reference	Analysis	Collection code	Figures
Subg. *Vignea*					
Sect. *Ammoglochin*					
	Carex brizoides	Italy, province of Torino, Front, ab. 300 m a. s. l.	×40, SEM	MCC2554	9f, g
Sect. *Cyperoideae*					
	Carex bohemica	Germany, Botanical Garden of Berlin-Dahlem, cultivated	×40, SEM	MCC0219	2i, j; 7l, m; 9e
	Carex leporina	Italy, province of Torino, above Case Rui, Piano Audi near Corio, 1200 m a. s. l.	×40, SEM	MCC2069	9a; 11a-c
	Carex leporina	Italy, province of Aosta, Lake of Cignana, ab. 2000–2300 m a. s. l.	×40, SEM	MCC2550	2g
	Carex leporina	Italy, province of Torino, San Carlo Canavese, 350 m a. s. l.	×40, SEM	MCC—Soil sample	2h, 11f
	Carex leporina	Italy, province of Torino, San Carlo Canavese, 350 m a. s. l.	×40	MCC0266	
	Carex muskingumensis	Germany, Botanical Garden of Berlin-Dahlem, cultivated	×40, SEM	MCC0275	2k, 9b
	Carex scoparia	Sample from Index Seminum of Montreal Botanical Garden	×40, SEM	MCC0307	9c
	Carex synchnocephala	USA, Oregon State University, photo provided by Barbara Wilson	×40	OSC	2j
	Carex projecta	USA, MICH Herbarium	×40, SEM	MICH-V-1327055	2l
Sect. *Elongatae*					
	Carex elongata	Italy, province of Torino, Terre Ballerine wet woodland, near Sirio Lake of Ivrea, ab. 300 m a. s. l.	×40, SEM	MCC2551	9d
Subg. *Euthyceras*					
Sect. *Leucoglochin*					
	Carex pauciflora	Russia, Yekaterinburg Botanical Garden	×40, SEM	LE without number, here coded LE-a	
	Carex pauciflora	Russia, Tobol'sk governorate, Tura uyezd, Pelym river, Portakh-Ryam yurts, leg. *B.N. Gorodkov*, 24 Jul 1916	×40, SEM	LE without number, here coded LE-b	
	Carex pauciflora	Russia, Tobol'sk governorate, Surgut uyezd, Vakh river basin, between Sabun and Kur'yogan rivers, leg. *B.N. Gorodkov*, 19 Jul 1913	×40, SEM	LE without number here coded LE-c	
	Carex pauciflora	Switzerland, Ticino Valley, Peat bog Bolla di Cadagno, 2100 m a. s. l.	×40, SEM	MCC2549	2m, 10f-h
Sect. *Circinatae*					
	Carex anthoxantea	Russia, Kamchatka, Aleutskiy rayon, Bering island, slope of the valley of river Poludennaya 2 km from estuary 54° 59′ 27"N / 166° 12′ 20"E; leg. *P. Volkova, N. Tikhomirov* and *Yu. Kopylov-Guskov*, 17 Jul 2015	×40, SEM	UPOS	10a-e
	Carex circinata	USA, Mt Colonel Bob, Olympic National Forest. leg. *M. Sheehan*, 19 Jul 1979	×40, SEM	WS 294208	2q
	Carex hakkodensis	Japan, Akita pref. Tazawako-machi, Mt. Komagatake, 1530 m a. s. l.	×40	MTDO21634	2o

Table 2 (continued)

Subgen Section	Species	Voucher/source reference	Analysis	Collection code	Figures
Subg. *Psyllophorae*					
Sect. *Psyllophorae*					
	Carex macrostyla	Spain, Burgos Espinosa de los Monteros, 30TVN4577 1420, leg. *J.A. Alejandre* and *M.J. Escalante*, 18 Jul 2003	×40, SEM	UPOS	2n; 10i-l
	Carex pulicaris	France, Savoye, Saint Maurice, Marais des Rives, about 600–800 m a. s. l.	×40, SEM	MCC2552	2p; 10m, n

micromorphological structures in those cases in which identity was assessed with confidence.

Carex pauciflora*-type fossil material* – We revised picked collections of *C. pauciflora*-type remains (Table 3, Figs. 3, 4), with particular attention to type material of the three above-mentioned fossil-species (*C. klarae, C. pauciflori-formis* and *C. paucifloroides*) and additional material from the type localities (topotypes) (Table 3). This approach allowed us to achieve a better understanding of the morphological variability directly linked to the names of each fossil-species, and to look for additional features that may vary from or be missing in the type specimens. We did not exclude material that was not assigned to any fossil-species or left in open nomenclature.

Ages of the fossils ranged from the Oligocene/Miocene transition (Fig. 4) to the Pleistocene (Fig. 3), covering the entire chronological span known for the *C. pauciflora*-type remains (about 25 My). All the materials consisted of "mummified" achenes with poor remains of a few utricles. This kind of fossils does not show straightforward preservation of silicified parts.

From *Carex paucifloriformis*, we studied the holotype (Fig. 4b; Table 1; Nikitin 1976) as well as topotype material (Kartashovo locality; Figs. 4a; 5, 6; Table 3). In addition, we also studied other materials assigned to this taxon by Nikitin himself, originating from Miocene sites of western Siberia (BIN-Pb-H2681, H3016, H3390; Table 3, Fig. 4h-n; Nikitin 2006).

From *C. paucifloroides* (Fig. 7a-g), we were unable to locate the type collection itself (according to T. Yakubovskaya, pers. comm.), but we did study material from its type locality (Table 3). We also considered several published reports of *C. paucifloroides* (Czech, German, Polish and Russian specimens: Raniecka-Bobrowska 1959; Dorofeev 1985; Mai and Walther 1988; Mamakowa and Velichkevich 1993; Velichkevich and Zastawniak 2003, 2006, 2007; Stachowicz-Rybka 2015; Zyuganova et al. 2015; Teodoridis et al. 2017).

Regarding *C. klarae*, our observations were limited to the published SEM pictures of a specimen assigned to this taxon from the Late Miocene type locality in Germany (Klara II near Kausche, Late Miocene; Mai 2000: pl. 15, Fig. 4).

Study of morphological characters

Samples preparation

Utricles from modern material were dissected with forceps, razors and needles to allow the observation of the enclosed achene. Achenes from fossil material were readily available in the collections. Some modern utricles of several species (as specified in Table 2) were treated with 5% chlorine-based bleaching agent for 2 days. This treatment was intended to produce a taphonomic-like effect on the enclosed achenes, thus approaching the overall appearance of characters displayed by the modern achenes to that of the fossils (Jiménez-Mejías and Martinetto 2013). Differences and similarities between treated achenes and fossils were dragged by comparative observation of the two types of material (see Results and Discussion).

Macromorphological characters

Observations on small-scale macromorphological characters were primarily performed under stereomicroscope. We focused on three main sets of small-scale macromorphological characters already regarded as useful for discriminating taxonomic groups: (1) utricle-achene attachment; (2) style morphology and fracture; and (3) cross-section and outline, although this latter is almost invariably similar among the *C. pauciflora*-type achenes as defined here (see above).

Micromorphological characters

We also studied the micromorphology of the epidermal cell structure as an additional useful character in *Carex* taxonomy (Jiménez-Mejías and Martinetto 2013). Features were observed using both stereomicroscopes at ×40 magnification (from now on: ×40 characters) and scanning electron microscopes ("SEM") available at different laboratories (at Minsk: JSM-5610 LV; at Saint Petersburg: Jeol JSM-6390LA SEM; at Seville: GeminiSEM 300, Zeiss, Oberkochen, Germany; at Turin: Leica M205 C and JSM-IT300 SEM). Given the

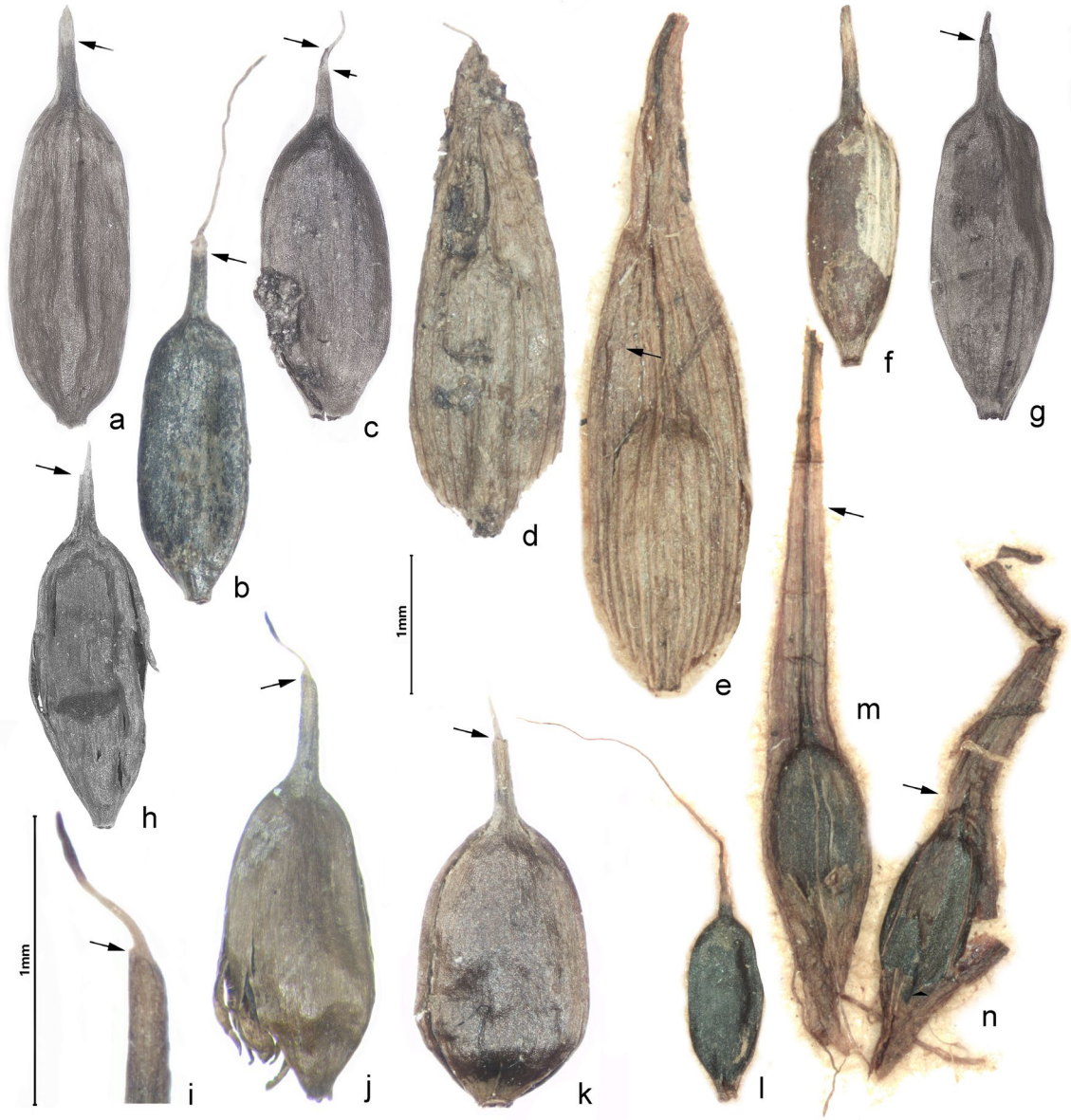


Fig. 3 Macrophotographs of specimens from the Pleistocene of West Siberia (mostly achenes, apart **d**, **e**, **m**, **n** = utricles with the achene inside); see references to this figure in Table 3 for more detailed data concerning each specimen; **a**–**d** Kazantsevo integlacial, the achenes can confidently be assigned to *C. paucifloroides* sp. inc., whereas we cannot rule out that the utricle found in the same picked collection may belong to a different species (= *Carex* sp.); **e, f** Kas River, due to the firm style pattern and elongated cells in the middle of the achene, it cannot, in this case, be confidently assigned to *C. paucifloroides* sp. inc., but rather to *C. pauciflora* sp. inc.; the utricle, which covers an achene with unknown characters, has to be treated as *Carex* sp.; **g** *C. paucifloroides* sp. inc., Tobol flora; notice the style constriction (arrow); **h**–**k** *C. paucifloroides* sp. inc., Tobol flora; again the same type of style constriction (arrow); **l-n** *C. bohemica*, fossils from Yeutskiye, Early or Middle Pleistocene; the absence of teeth at the margin of the utricle's beak (compare with Fig. 2i) may be the consequence of a selective preservation of only the most resistant parts during fossilization

fervent care that palaeobotanical curators deposit on their collections, the observation of the different fossil materials could not be uniform: some were studied only under stereomicroscope, others under SEM, and just a few under both. This depended on a multitude of conditionings for each particular specimen: preservation state, owner institution protocols, and even the opportunity window for studying it. In Table 2 it is specified how was studied each particular specimen.

SEM analyses were carried out on dry materials mounted on stubs with nail polish or conductive tape, partly without any metal/graphite cover, and partly with gold cover, as indicated in Tables 2–3. Only one achene per each extant species or fossil collection was studied. In most specimens we did

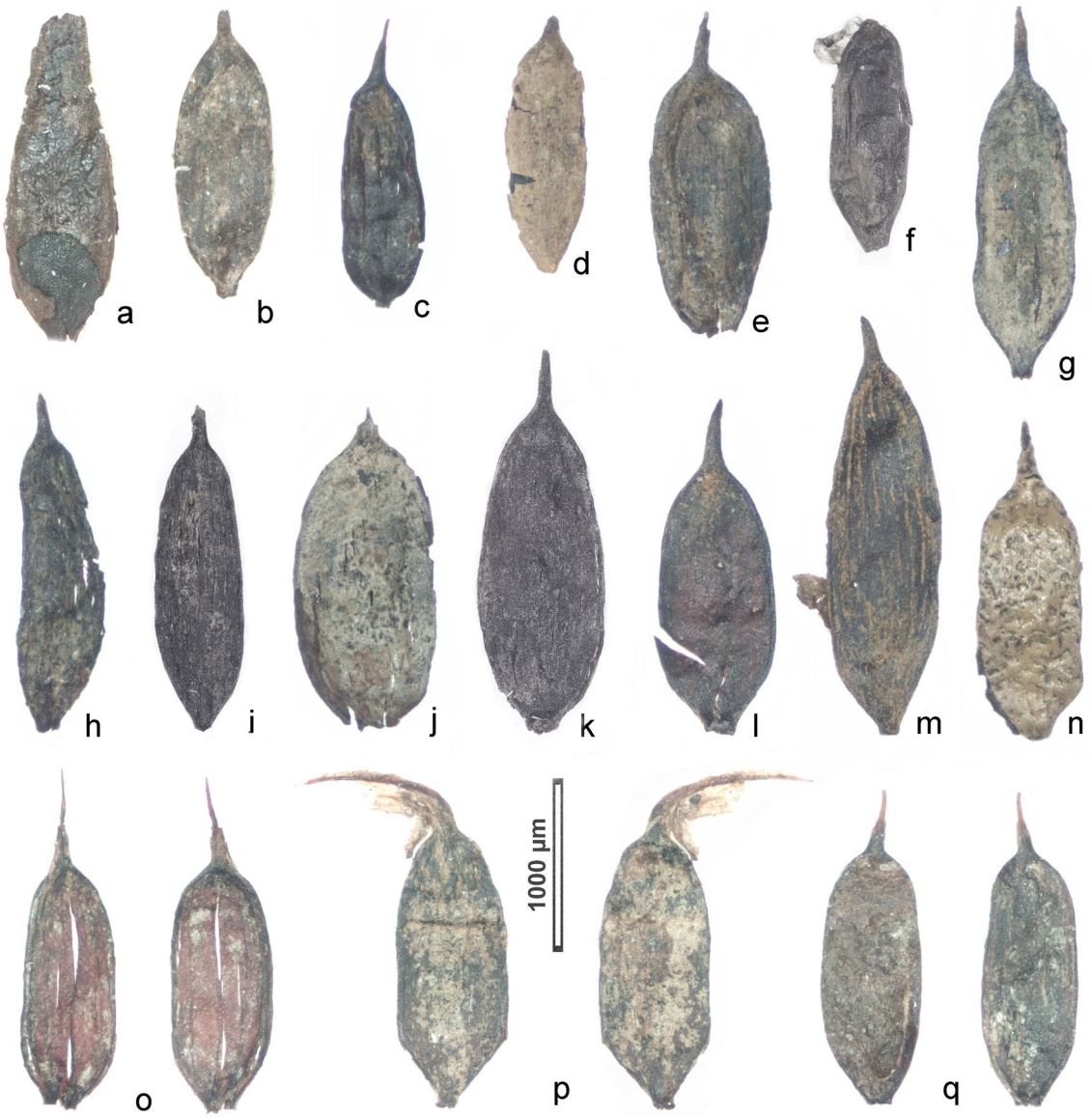


Fig. 4 Macrophotographs of fossil achenes from the Oligocene–Miocene of West Siberia, assigned here to *Carex paucifloroides* sp. inc., see references to this figure in Table 3 for more detailed data concerning each specimen; **a** achene partly covered by utricle remains, paratype of *C. paucifloriformis* (Nikitin 1976, Fig. 30); **b** naked achene designated by Nikitin (1976, Fig. 31) as the holotype of *C. paucifloriformis*; **c–e** specimens listed in BIN-Pb-database as *Carex* sp., most probably of Miocene age, notice the style constriction in **c**; **f–j** specimens of Early Miocene age; **k–n** specimens of Late Oligocene or Early Miocene age; **o–q** specimens of Early Miocene age with better preserved styles

not use "sonication", a standard procedure in the study of sedges epidermic micromorphology (Toivonen and Timonen 1976). Sonication leads to the removal of the external periclinal wall, exhibiting the epidermal cell lumen and thus allowing the observation of the phytoliths on the internal periclinal walls. Since such phytoliths are strongly altered or missing in most mummified fossil material, such approach was deemed as not useful. We did perform sonication on one modern achene of *C. antoxanthea* (sect. *Circinatae*) and one of *C. macrostyla* (sect. *Psyllophorae* Degl.) with the intention to understand their epidermal cell structure and to compare the structural alterations induced by sonication with those of modern bleached achenes and fossils.

Our preliminary observations revealed that cells may vary in outline depending on the part of the achene (e.g. side, top, edge, etc.; see Results and Fig. 8a–d), thus we limited descriptive comparisons to the cells on the central parts of achene sides. We paid special attention to damaged areas in

Table 3 List of fossil specimens examined (spm. = specimen), ordered alphabetically according to species names and, secondarily, to the collection codes: CCN, CENOFITA palaeocarpological collection of the Turin University; IGMN, Institute of Geology and Mineralogy SB RAS, Novosibirsk State University; H = BIN-Pb-H, Nikitin collections at the Laboratory of Palaeobotany of the Komarov Botanical Institute, St. Petersburg, Russia; MfN, Palaeobotanical collection of the Museum für Naturkunde of Berlin, Germany; MGPT, Museum of Geology and Palaeontology of the Turin University; MIGG, Scientific-Exploration Centre for Geology, Minsk, Belarus

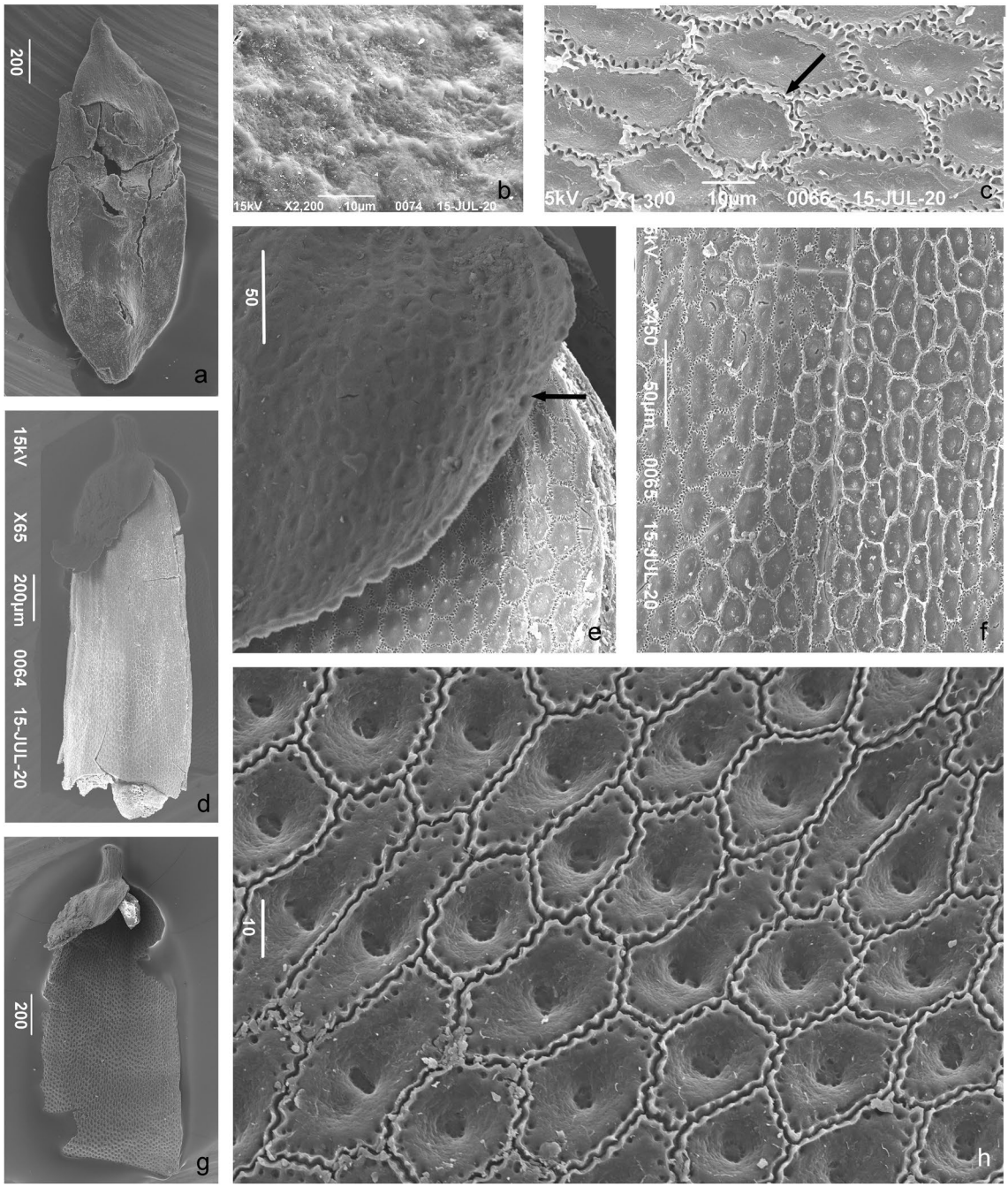
Revised identification	Original identification	Voucher/source reference	Collection code	Analysis	Age and references	Figures
Carex bohemica	*Carex* cf. *pauciflora*	Russia, West Siberia, Tyumen' oblast', Khanty-Mansi autonomous okrug — Yugra, Surgut rayon, Yeutskiye, approximate coordinates 60.706790, 73.798775. Probably glued on paper in the mid-twentieth century by P.A. Nikitin	BIN-Pb-H406	×40	Early or Middle Pleistocene (unpublished data of the former Novosibirsk palaeocarpological laboratory, age considered to be earliest Pleistocene by V.P. Nikitin)	2f (spm. 15); 3l (spm. 7), 3m (spm. 1), 3n (spm. 2)
Carex bohemica	*Carex bohemica*	Russia, West Siberia, Khanty-Mansi autonomous okrug, Irtysh River, Alymka Village	IGMN 81-K-40–3, 7/17	×40, SEM	Late Pleistocene, late glacial stage, ^{14}C dated to 16,770 ± 160 years BP (Krivonogov 1988)	12a-f
Carex leporina	*Carex leporina*	Italy, Cava Butteri, sample BUT1 B6X	CCN05942	×40, SEM	Late Pleistocene (Martinetto et al. 2014)	11d, e
Carex pauciflora sp. inc	*Carex* cf. *pauciflora*	Russia, West Siberia, Krasnoyarsk kray, Yeniseysk rayon, Kas River (no coordinates)	BIN-Pb-H273	×40	Early or Middle Pleistocene (unpublished data of the former Novosibirsk palaeocarpological laboratory)	3f (spm. 3)
Carex pauciflora sp. inc.	*Carex* cf. *pauciflora*	Russia, West Siberia, Tomsk oblast', Aleksandrovskoye rayon, Chagin Yar, approximate coordinates 59.486175, 79.432667	BIN-Pb-H535	×40	Pleistocene ("early-middle Neopleistocene): Tobol flora, unpublished data by V. P. Nikitin)	
Carex paucifloroides	*Carex paucifloroides*	Belarus, Dvorets, type locality of the species, see Velichkevich (1975)	MIGG 315-Dvorets and MIGG 317-Dvorets	×40, SEM	Early Pleistocene (Matveyev et al. 2019) MIGG 315-Dvorets and MIGG 317-Dvorets	7a-d (spm. MIGG 315-Dvorets-5–3-1, 1979); 7e-g (spm. MIGG 317-Dvorets-1–3-1, 1979)
Carex paucifloroides sp. inc.	*Carex pauciflora*	Russia, West Siberia, Tyumen' oblast', Khanty-Mansi autonomous okrug — Yugra, Khanty-Mansiysk rayon, Semeykin Yar, approximate coordinates 60.259154, 69.918237	BIN-Pb-H1499	×40, SEM	Pleistocene ("early–middle Neopleistocene"): Tobol flora (unpublished data by V. P. Nikitin)	2a (spm. t4); 3 g (spm. 2); 8e (spm. of Fig. 2a)
Carex paucifloroides sp. inc	*Carex pauciflora*	Russia, West Siberia, Semeykin Yar, same site as BIN-Pb-H1499	BIN-Pb-H1500	×40, SEM	Pleistocene: Tobol flora, see above	2c (spm. 106); 3i, j (spm. 105); 3k (spm. 104); 3h + 8a-d, f (spm. t5)

Table 3 (continued)

Revised identification	Original identification	Voucher/source reference	Collection code	Analysis	Age and references	Figures
Carex paucifloroides sp. inc.	*Carex* sp.	Russia, West Siberia, Omsk oblast', Muromtsevo rayon, Kartashovo, approximate coordinates 56.11314, 74.738843	BIN-Pb-H1525	×40	Middle Miocene: Bescheul flora, Isakovka floristic level (Nikitin 2006); collection number corresponding to the label K-4 mentioned by Nikitin (1976)	4c (spm. 176), 4d (spm. 175), 4e (spm. 174)
Carex paucifloroides sp. inc.	*Carex paucifloriformis*	Russia, West Siberia, Omsk oblast', Sargatskoye rayon, Novopokrovka II, approximate coordinates 55.579598, 73.186481	BIN-Pb-H2120	×40,	Early Miocene (Aquitanian): Tara-Vasyugan flora (Nikitin 2006), Abrosimovka Suite (Nikitin 2009)	4o (spm. 98), 4p (spm. 107)
Carex paucifloroides sp. inc.	*Carex* sp.	Russia, West Siberia, Novosibirsk oblast', Potyukanovo, approximate coordinates 56.049903, 78.453485	BIN-Pb-H2681	×40, SEM	Late Oligocene – Early Miocene (Chattian-Aquitanian): Tara–Vasyugan flora, Lyamin floristic level (Nikitin 2006), Abrosimovka Suite (Nikitin 2009)	4k (spm. t3), 4l (spm. 117), 4m (spm. 23), 4n (spm. 118); 8i, j (spm. of Fig. 4k)
Carex paucifloroides sp. inc.	*Carex paucifloriformis*	Russia, West Siberia, Tomsk oblast', Kozhevnikovo rayon, Voronovskiy Yar I, approximate coordinates 56.03777, 83.831752	BIN-Pb-H3016	×40, SEM	Early Miocene (Burdigalian): Tara–Vasyugan flora, Kireyevsk floristic level (Nikitin 2006), Kireyevsk Suite (Nikitin 2009)	4f (spm. t1)
Carex paucifloroides sp. inc.	*Carex paucifloriformis*	Russia, West Siberia, Omsk oblast', Muromtsevo rayon, Kartashovo, approximate coordinates 56.114492, 74.748083, collected by Nikitin in 1959	BIN-Pb-H3296	×40, SEM	Middle Miocene (Serravallian): Bescheul flora, Isakovka floristic level (Nikitin 2006), Bescheul Suite (Nikitin 2009)	4a (spm. 129; Nikitin 1976, Fig. 30), 4b (spm. 130; designated as holotype by Nikitin 1976, Fig. 31); 5c-h (spm. 128)
Carex paucifloroides sp. inc.	*Carex* sp.	Russia, West Siberia, Omsk oblast', Gor'kovskoye rayon, Gorskiy Log, approximate coordinates 55.501267, 73.462461	BIN-Pb-H3390	×40, SEM	Early Miocene: (Aquitanian–Burdigalian): Tara-Vasyugan flora, Vasyuganskiy Yar floristic level (Nikitin 2006), Abrosimovka Suite (Nikitin 2009)	2d, 4g (spm. 128), 4h (spm. 129), 4i (spm. t2), 4j (spm. 127); 8g (spm. t2)

Table 3 (continued)

Revised identification	Original identification	Voucher/source reference	Collection code	Analysis	Age and references	Figures
Carex paucifloroides sp. inc.	*Carex paucifloriformis*	Russia, West Siberia, Omsk oblast', Muromtsevo rayon, Kartashovo village, right bank of Irtysh river 2.5 m upstream from the end of the outcrop, 0.5 m above the water level, sand with plant detritus collected by Vadim Petrovich Nikitin in 1959. Approximate coordinates 56.114921, 74.756418	BIN-Pb-H3397	×40, SEM	Middle Miocene (Serravallian), Isakovka floristic level (the age is only indicated in Nikitin's unpublished materials), Bescheul Suite (Nikitin 2009)	5a, b (spm. 131), 6a-d (spm. 132)
Carex paucifloroides sp. inc	*Carex pauciflora*	Russia, West Siberia, Tyumen' oblast', Uvat rayon, Gornaya Subbota, approximate coordinates 59.810707, 69.786542	BIN-Pb-H3450	×40	Pleistocene ("late Neopleistocene"): Kazantsevo interglacial (Nikitin and Hvalj 2011)	2b (spm. 112); 3a (spm. t6), 3b (spm. 112), 3c (spm. t7), 3d (spm. 111); 8h (spm. t7)
Carex paucifloroides sp. inc.	*Carex paucifloroides*	Italy, Momello-Lanzo, layer MO3	CCN0715	×40, SEM	Pliocene (Martinetto et al. 2007)	2e (MGPT-PU105680); 7h-j
Carex paucifloroides sp. inc	*Carex klarae*	Germany, Klara II near Kausche (Mai 2000, pl. 15, Fig. 1–4)	MfN 1993/4720	×40, SEM	Late Miocene (Mai 2000)	
Carex paucifloroides sp. inc.	*Carex pulicaris*	Germany, Neumark-North	MfN 2007/262	×40	late Middle Pleistocene (Mai 2010, p. 120)	
Carex sp. (utricle)	*Carex* cf. *pauciflora*	Russia, West Siberia, Kas River, see above	BIN-Pb-H273	×40	Early or Middle Pleistocene, see above	3e (spm. 1)
cf. *Dulichium*	*Carex* cf. *paucifloriformis*	Russia, West Siberia, Novosibirsk oblast', Barabinsk rayon, Dunayevka, approximate coordinates 55.216108, 78.220106	BIN-Pb-H1707	×40 SEM	Early Oligocene: Novomikhaylovka flora, late variant (Nikitin 2006)	



both modern and fossil achenes to understand the organization of cell layers (e.g., Figs. 5, 6, 7l). In order to be able to approach the variation of the altered/missing silicified parts in the epidermis of most of the mummified fossils with that observed on the extant species, we considered only coarse (at cell scale) characters with two states for each: the silica platform (massive/thin), the satellite bodies (absent/present), and the central body (conical/flattish) (Table 4). Additionally, the number of satellite bodies was considered, when detectable.

Literature sources

Additional information complementing our observations, including comparison with taxa outside the study group, was carried out based on competent specialized literature sources (Velichkevich 1975; Tallent and Wujek 1983; Egorova 1999; Mai 2000; Reznicek and Ball 2002; Velichkevich and Zastawniak 2003; Dai et al. 2010; Ercole et al. 2012; Jiménez-Mejías and Martinetto 2013; Jiménez-Mejías et al. 2016b; Guerriero et al. 2020).

◂**Fig. 5** *Carex paucifloroides* sp. inc. Epidermal cell structures seen on two fossil achenes from the type site of *C. paucifloriformis*, Nikitin's collection, SEM photos. **a**, **b** BIN-Pb-H3397-131; **c**–**h** BIN-Pb-H3296-128. **a** achene with preservation of the external periclinal walls; **b** detail of the left side of (**a**), outer surface of the exocarp with undulated cell outlines evidenced by the network of "a-p junctions" (see Fig. 1a, b), without any morphological evidence of the silica platforms; **c** detail of the right side of (**d**) showing the internal periclinal walls of the epidermal cells, which probably lost the silica platform (see (**e**)) and mostly show the basal attachment structures with a small tubercle corresponding to the central body; the two rows of tiny holes bordering each cell correspond to the undulations of adjacent cell walls (as in Fig. 10d); the basal part of the anticlinal walls is sparsely preserved, particularly in the central cell (arrow); **d** achene with a robust sheet of external periclinal walls peeling off (apex); **e** detail of the detachment belt of the sheet of external periclinal walls in (**d**), seen from the outside at the top, where cell outlines are evidenced by the network of "a-p junctions", and from the inside in the middle, where the impression of a massive central silica body (arrow) is preserved in each cell, suggesting the former presence of a silica platform; the bottom of the image shows what is better seen in (**f**); **f** detail of the central part of (**d**) showing the pavement formed by the internal periclinal walls of the epidermal cells; where the borders between cells are clearer, the basal part of the anticlinal walls is preserved and the attachment structures of the silica platforms (see (**c**)) are more apparent; **g** remains of the external cuticle-like sheet of the periclinal walls of the same achene shown in (d), after the detachment of the other parts from the stub, repeated gold coating and SEM analysis; **h** central portion of (g) showing intact external periclinal walls seen from the intracellular side and cell outlines evidenced by evenly wide furrows; the morphology of the lost platforms is faithfully replicated as a detailed impression on the external periclinal walls, with apparent, flat-tipped central silica bodies and satellite bodies

Results

Modern material

As a general comment, bleached achenes approached their superficial appearance to those of fossils, regarding style and utricle-achene attachment decay (see parallel results in Jiménez-Mejías and Martinetto 2013). However, bleaching produced an effect on the micromorphological features of epidermal cells that was different from what we observed in fossilized material (see below), that however allowed complementary observations. A summary of the morphological features observed in each of the taxonomic groups is provided in Table 5.

Utricle-achene attachment

All the studied specimens display a loose attachment of the achene to the utricle, lacking a conspicuously thickened basal callus (see Jiménez-Mejías and Martinetto 2013). Hence, we consider that character useless for taxonomic discrimination. The base of some achenes can be described as substipitate because it is much narrower than the achene's middle part. Real stipes (flower axis-derived structures) show a discontinuity in tissues and mostly a different appearance and color from the achene. These have never been observed in any *Carex pauciflora*-type fossil.

Style morphology and fracture

The study of all the modern materials revealed three different patterns of style configuration in *C. pauciflora*-like achenes.

The first two patterns shared styles with two clearly defined parts of different robustness: (1) a proximal part forming a lignified elongated cylindrical appendage attached to the tip of the achene; and (2) a distal part, formed by a poorly-lignified portion. In sect. *Cyperoideae* materials the boundary point between the two parts (BP in Fig. 2) does not show any joint and corresponds to a very small change (poorly apparent) in style outline. It can altogether be recognized on the basis of an overall slightly minor thickness and wrinkled appearance of the distal part, or it can be verified through a different resistance to the manipulation with a needle. This state is here defined as a "soft" style pattern (Fig. 2g). On the contrary, in sect. *Circinatae* and *C. macrostyla* the style is gradually and bilaterally symmetrically constricted along the distal part (Fig. 2q). The appearance of these styles was surprisingly similar to that of some altered achenes of sect. *Cyperoideae* extracted from a soil sample. Accordingly, we suggest that this characteristic constriction can be either formed during the ontogenetic development of an achene (and thus of primary origin; Fig. 2q) or induced by taphonomic alteration of a "soft" style pattern achene buried in terrigenous materials (and then of secondary origin; Fig. 2h). In both cases the distal part of the style displays a curved and flexible appearance, markedly different from the proximal one. We define herein this state as "proboscis" style pattern.

A third type of style configuration was found in *C. pauciflora* (Fig. 2m) and *C. pulicaris* (Fig. 2p), where the style was continuously lignified until the apex. This style pattern is from herein called "firm" style pattern. We hypothesize that such pattern could be retained by the fossils of these species, because it was preserved almost unaltered in bleaching experiments and even after needle manipulation (Fig. 2m), whereas the "soft" style of sect. *Cyperoideae* was not.

Achene cross-section

In *C. pauciflora* and the studied material of sect. *Circinatae* (subgen. *Euthyceras*) we always detected three faces on the achenes, with a vascular bundle at each of the 3 edges. Biconvex achenes with only two faces occur in *C. macrostyla, C. pulicaris* and several studied modern materials of sect. *Cyperoideae* (*C. bohemica, C. leporina, C. muskingumensis, C. scoparia, C. projecta*). However, in certain species of this last section, such as *C. muskingumensis* and

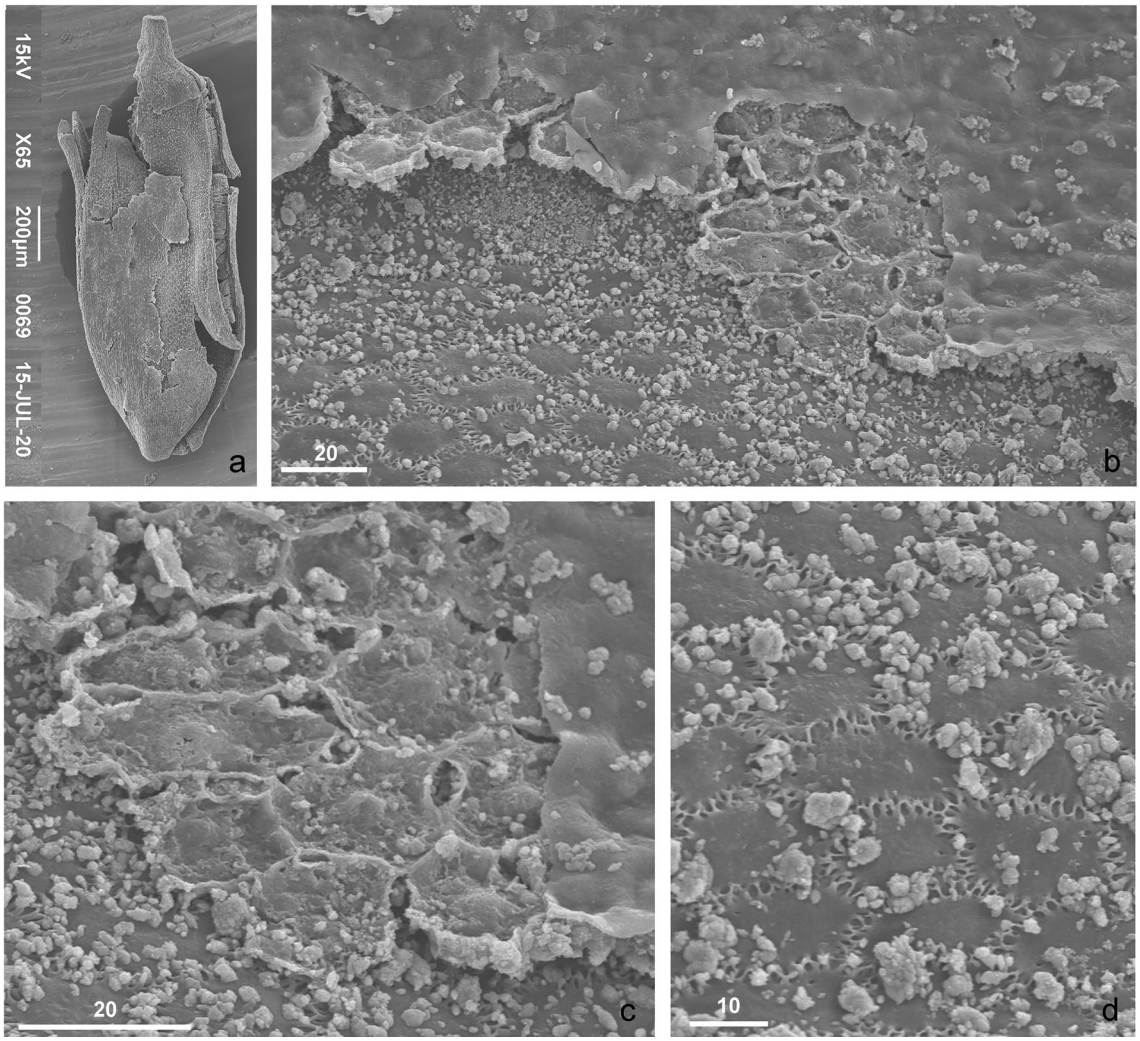


Fig. 6 *Carex paucifloroides* sp. inc. Epidermal cell structures seen on a fossil achene from the type locality of *C. pauciflorifformis*, Nikitin's collection (BIN-Pb-H3397-132), SEM photos. **a** achene with exceptional preservation of important details for the comprehension of the epidermal architecture; **b** central portion of (a) showing three states of the exocarp: 1- minimal modification at the top, with intact external periclinal walls and cell outlines evidenced by the network of "a-p junctions"; 2- medium modification in the middle, with absence of the external periclinal walls, but exceptional preservation of what is probably the organic part of the original silica platforms, after the dissolution of the mineral part; 3- extreme modification at the bottom, where only the internal part of the periclinal walls, under the lost platforms, is preserved, but limitedly to the deepest portion. This is suggested by the absence of the attachment structures of the silica platforms; **c** detail of (b) showing the remains of the silica platforms which appear as "deflated", what is interpreted as a consequence of the loss of the mineral component during fossilization; the residual morphology indicates the former presence of a central silica body, without any evidence of satellite ones; **d** detail of the area with extreme modification, in which the lower portion of the internal periclinal walls forms a jigsaw-puzzle pattern; the abundant granules are probably a residue of the sediment from which the fruit was extracted

partly (basal part of the achene) in *C. bohemica* and *C. projecta*, one of the two faces shows a distinct, rounded longitudinal ridge, that generates a bluntly 3-sided section. Relevantly, there is no evidence of any vascular bundle running under the edge of the ridge.

Epidermal cell structure

Epidermal cell outline and size are variable in different parts of a single achene. The broad variation of epidermal cell outlines seen in the marginal parts of all the achenes suggested to us that comparisons should be based on the central part of the achene surface (Fig. 8c). Roughly, a general hexagonal-pentagonal pattern is shared among most studied species (Figs. 9a–d; 10; Table 4). Only in *C. pauciflora* (Fig. 10f–h) the central part of the achene surface from several samples showed more definitely elongated, mainly 4-sided cells.

The consistency of the external periclinal walls often differed among modern materials, but seemed to be easily

modified by chemical treatments (Fig. 11a–c) and by natural decay in soils (Fig. 11f), so that this feature can be hardly exploited for taxonomical purposes in fossil specimens (see below). In fact, consistency was carefully evaluated for possible deviations from the morphology resulting from the development of the fruit.

In general, untreated modern materials displayed epidermal cell features different from that attested in the fossils, when studied under SEM. As a general observation, bleaching does not remove the silicified parts (Fig. 9d–g), which are mostly missing after the taphonomic transformations in fossils. However, bleaching induced a partial and variable damage to some cell walls (Fig. 9a), helping us to understand the ultrastructure of the epidermis, which, in turn, contributes to the better understanding of the taphonomic process (see below and Discussion). In particular, some specimens developed wrinkles (Fig. 9b) or cracks (Fig. 9c) on the outer parts of the epidermis that exposed the subjacent ultrastructure. In other specimens a whole sheet of external periclinal walls peeled away (Fig. 9e), thus exposing the platforms with silica bodies, resting on the intracellular surface of the internal periclinal wall. In this condition the anticlinal walls can be either concealed by the silica platforms (Fig. 9e–g) or perfectly visible (Fig. 9d). The non-silicified portion of the periclinal wall under the platforms was at times visible and showed a jigsaw-puzzle-like pattern (Guerriero et al. 2020) with many tiny teeth (Fig. 11c).

Fossil materials assignable to extant species

Fossils assignable to extant species (Table 2) are represented by "mummified" (or waterlogged) fruits, that only in one case showed preservation of silicified parts (sample IGMN 81-K-40–3, 7/17; Fig. 12c). The comparison of these fossil materials with somehow similar extant achenes (*C. bohemica* and *C. leporina*) provided interesting information about the alterations undergone by the epidermal cells during taphonomic decay. As a general comment, the clear distinction between "soft" and "proboscis" style patterns observed in fresh achenes does not seem to be so straightforward, nor it is always retained after fossilization. Rather, as already observed for decayed soil materials (compare Fig. 2g with Fig. 2h), the weak resistance to alteration (not implying abscission) of the distal softer part of the style in sect. *Cyperoideae* may determine a "proboscis" pattern in fossil achenes.

Carex bohemica

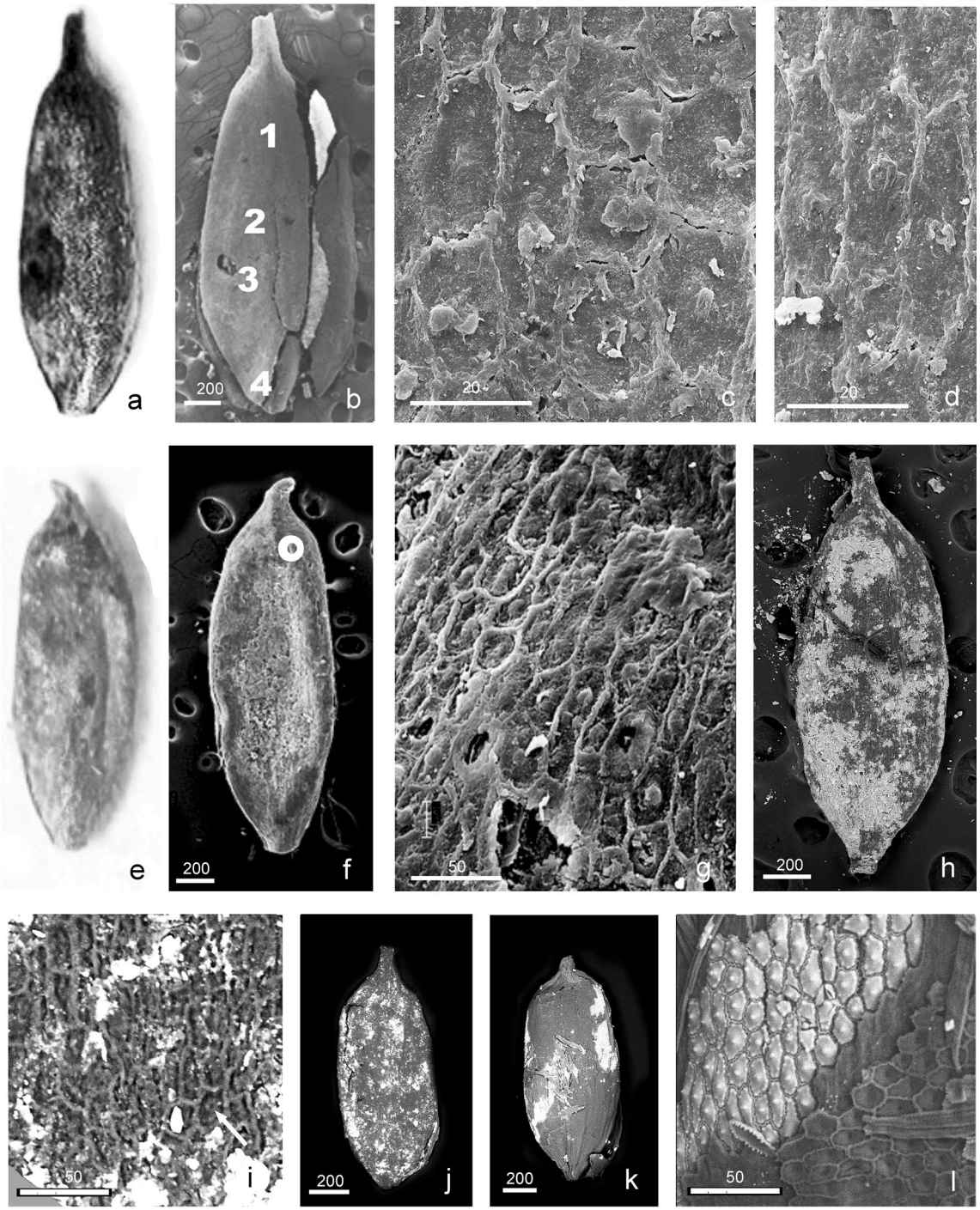
Assignment of BIN-Pb-H406 achenes to *C. bohemica* is corroborated by the occurrence of two exceptionally preserved utricles that clearly show the achene contained inside (Fig. 3m, n). The morphology of those specimens totally agrees with that of modern *C. bohemica*, a species characterized by an utricle with an extreme length/width ratio associated to an achene with an elongated cylindrical apiculus; such a combination of characters is not known in other *Carex* species from Western Eurasia. These fossils also show a complete agreement in × 40 and SEM characters (Table 4) with the modern material of *C. bohemica* (Figs. 2i, 7j-l), and the "proboscis" style pattern observed in some fossils (Fig. 4m) can be regarded as a taphonomic transformation of the "soft" style pattern of modern achenes of *C. bohemica* (Fig. 2i).

SEM analysis (Fig. 12) showed a generalized preservation of the external periclinal walls in undamaged areas, implying that the details of the silicified parts are mostly hidden on the outer surface, and only the presence of a central silica body is hinted at by a prominence of the extracellular periclinal wall in the center of each cell (Fig. 12e). The achene shown in Fig. 12 has indeed been preserved in a silica-rich environment, as demonstrated by the frequent occurrence of diatom frustules on its surface (Fig. 12f). Consequently, the silicified parts, rarely reported in other fossil specimens (Jiménez-Mejías et al. 2016b), do occur in this specimen, even if a single platform was appropriately exposed to show most of its satellite bodies (11 visible, but probably 13–14 in total: Fig. 12d). The "a-p junctions" are not apparent in this fossil (Fig. 12f), which is in agreement with the situation observed in modern achenes of *C. bohemica* (Fig. 7l).

Carex leporina

An achene from the Pleistocene of Italy assigned to *C. leporina* shows a complete agreement with the × 40 and SEM characters (Table 4) of modern material of this extant species (Fig. 2g, h and 11a–c, f). However, this conclusion was reached only through careful consideration of the different alterations observed in modern achenes, either simply dried (Fig. 2g), bleached (Fig. 11 a–c) or collected from a soil (Fig. 11f). As already noticed for *C. bohemica*, the "soft" style pattern observed in the modern simply dried achene of *C. leporina* indicates that the "proboscis" style pattern observed in the achene from the soil (Fig. 2h) and in the fossil one (Fig. 11d) is derived from a taphonomically induced transformation of a "soft" style.

SEM analysis of the fossil (Fig. 12) pointed out that the external periclinal walls are always preserved and show thin and straight "a-p junctions", as in the extant simply dried achene. The periclinal walls of the fossil achene appear as simply compressed against the underlying parts, and only in a few cells the resistance of the central silica body seems having produced a perforation (arrow in Fig. 11e). The darkness of such perforation (compare to the whitish areas in Fig. 11f, where the silica parts are certainly retained) suggests that the silica parts may have been dissolved during



fossilization. In the specimen from the soil sample the "a-p junctions" have been strongly altered, so that the undulated pattern of the underlying anticlinal walls caused the formation of two series of tiny holes at each junction of two cells (Fig. 11f). In addition, the periclinal walls appear so thinned and stretched that the central silica bodies tend to become visible. Only in the bleached specimen the external periclinal walls tend to break up in "tiles", each corresponding to a single cell, and they partly are thinned and stretched (Fig. 11b) and partly seem to have retained the original thickness (Fig. 11 c). A few "tiles" were rotated upside down, and showed the impression of the central and satellite silica bodies on the intracellular side of the periclinal wall. Unfortunately, the preparation of the fossil did not allow us to observe the internal side of the periclinal walls (Fig. 11e), so that we lack any information on its satellite bodies.

◂**Fig. 7** Morphology and epidermal cell structure of late Cenozoic achenes and a modern analogue. **a–g** *Carex paucifloroides* Wieliczk. from the type locality of this fossil-species, Dvorets (Belarus); **a**, **b** specimen MIGG 315-Dvorets-5–3-1; **c–g** specimen MIGG 317-Dvorets-1–3-1 (Table 3). **a** macrophotograph of an achene; **b–d** SEM photos of the same specimen, showing the epidermal cell structure in the point indicated by number 2 in (**c**), the point indicated by number 1 in (**d**); the external periclinal walls were compressed during fossilization, but still show the morphology of the central silica body; silica platforms are never visible; **e** macrophotograph of another specimen; **f–g** SEM photos of the same showing the epidermal cell structure in the point indicated by the circle in (**g**); external periclinal walls are mostly preserved and show the morphology of the central silica body; where they have been removed, the cell lumen appears as empty and silica platforms are never visible (possibly dissolved); **h–j** SEM photos of achenes from the Italian Pliocene (Momello-Lanzo locality, MGPT-PU105680) which were assigned by Martinetto (1995) and Jiménez-Mejías et al. (2016b) to *C. paucifloroides* (an achene with "proboscis" style pattern, considered to belong to the same species, is shown in Fig. 2e); **i** epidermal cell structure of (**j**) indicating the preservation of the external periclinal walls, whose central part sometimes shows signs of the central silica body (arrow); **k, l** SEM photos of a modern, bleached achene of *C. bohemica* with a detail showing the epidermal cell structure in its central part. The light objects are the exposed silica platforms with their central and satellite silica bodies; the sheet of external periclinal walls is displaced, upside down, in the bottom right corner, where the impressions of silica bodies on the internal side of the periclinal walls is visible. Scale bars in micrometers

Carex pauciflora

Two Quaternary samples (BIN-Pb-H273 and H535), seem to be compatible as for × 40 characters with those of extant *C. pauciflora* (Table 4). These were glued on paper and, unfortunately, could not be analyzed at the SEM. We suggest to regard them as *Carex pauciflora* sp. inc., pending further studies.

Characters of *Carex pauciflora*-type fossil materials

We distinguished five groups of fossils based on morphology, geographical origin and age. All relevant information is summarized in Table 4. We also shortly present comments on a misidentified remain not assignable to *Carex*.

As a general remark, epidermal cell features have provided useful information, especially in the case of a particular preparation that revealed the details of the silica bodies through their impressions on the external periclinal walls. To our knowledge, this is the first report of such a kind of observation, providing indirect evidence of this micromorphological feature, which is not detectable through SEM analysis of the external surface.

Siberian Miocene specimens

Achenes medium-sized (1.5–2.3 mm), with one of the two faces showing a small, rounded longitudinal ridge (without any vascular bundle: Fig. 4j). Substipitate base mostly present, and then short and narrow.

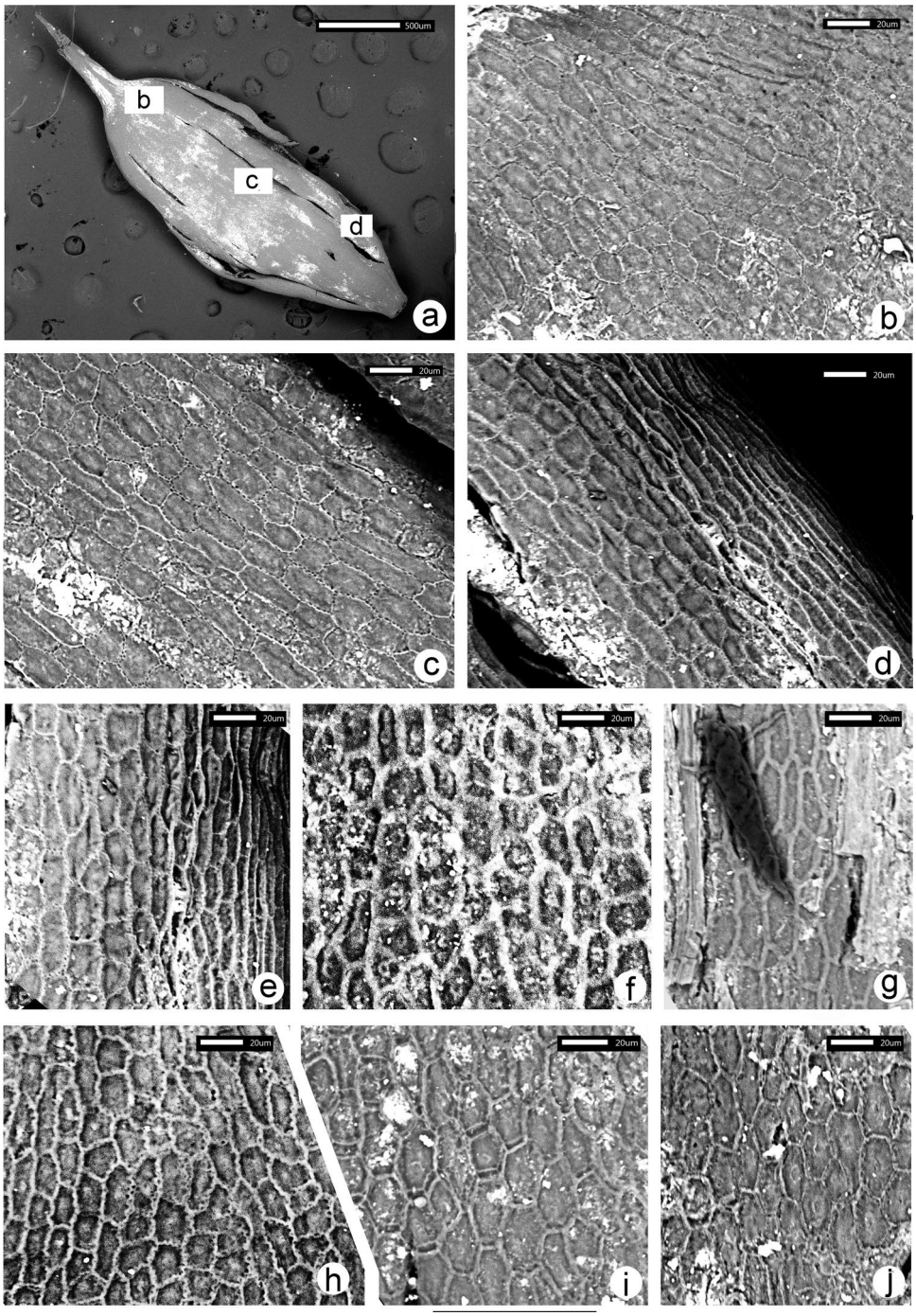
Style with a proximal lignified cylindrical apiculus 1/4 to 1/5 as long as the achene length. The poorly lignified distal part is decay-prone and, in the majority of specimens, either missing or just preserved as a filament ("proboscis" pattern: Fig. 4o, q). Several specimens have just a short portion of filament above the constriction (sharply restricted and often with asymmetrical limit: Fig. 4c, e, g). An almost complete style with "soft" pattern is exhibited by an achene of the sample BIN-Pb-H2120 (Fig. 4p), which appears as non-jointed (see Jiménez-Mejías and Martinetto 2013) and poorly lignified in the distal part, whereas the proximal portion (ca. 3/10 as long as the achene length) is strongly lignified and preserved as a thin, but robust, cylindrical apiculus (Fig. 4c, g, o, q).

Despite a certain degree of variation in outline and dimensions of epidermal cells (Fig. 4), there is an overall agreement between the characters of the original material of *Carex paucifloriformis* (Fig. 4a, b) and those of the many specimens from the Siberian Miocene. Epidermal cells show a regular cell pattern of slightly longitudinally elongated polygons with 5–6 angles and, in prevalence, evenly long sides (Fig. 5c, f, h). External periclinal walls are preserved as a thick sheet, easily peeling off (Fig. 5d, e); they show, on the extracellular surface, protrusions of originally massive silica platforms, apparently with a single central silica body (Fig. 5c, 6c). However, the absence of satellite bodies is just due to the poor record of the platform's morphology on the extracellular side of the periclinal walls. In fact, an exceptionally preserved and prepared specimen (Fig. 5g, h) shows perfect impressions of the silica platforms on the intracellular side of the external periclinal walls, with blunt central silica bodies and 20–30 satellite bodies along the platform's outline. The non-silicified portion of the periclinal cell wall under the platforms, often exposed in part or on the whole surface of some achenes (Fig. 5d, e and 6b, d), shows a jigsaw-puzzle-like pattern (Guerriero et al. 2020) with many tiny teeth (Fig. 6d).

German Miocene specimens and a compatible Siberian Miocene one

The achenes picked from a German Miocene assemblage, including the types of *C. klarae,* share with those of the Siberian Miocene most of the characters. Unfortunately, the analyses carried out so far (Mai 2000; Velichkevich and Zastawniak 2003; this study too: Fig. 8g) did not provide further details on the morphology of the phytoliths.

In an Early Miocene collection from West Siberia (BIN-Pb-H3390) there are typical examples of Nikitin's species *C. paucifloriformis* (e.g., Fig. 4j, i) together with a narrower achene, which we found to be indistinguishable



from the types of *C. klarae* in both macro- (Fig. 4g) and micromorphological (Fig. 8g) characters. This achene is 1.8 mm long and 0.55 mm wide, with a short and narrow substipitate base and a fractured style (so that style pattern cannot be assessed). The set of external periclinal walls does not appear as a thick sheet, even if it peels off at some areas (Fig. 8g). The portion of the periclinal cell wall lying beneath the platforms is never exposed. Other characters are listed in Table 4 and point out the lack of disagreement between this particular Siberian achene and the type specimens of *C. klarae* (the holotype is ca. 1.8 × 0.5 mm).

Pleistocene specimens from Belarus and neighboring areas

The three studied Belarusian achenes originating from the type locality of *C. paucifloroides* are 1.9–2.0 mm long, with short substipitate base. The style is always fractured, so that the style pattern cannot be assessed. External periclinal walls

◂**Fig. 8** SEM photos of epidermal cell structures seen on the fossil *Carex pauciflora*-type achenes of the Nikitin collections (BIN-Pb). **a**–**e** fossil achene from the Pleistocene Tobol'sk flora (BIN-Pb-H1500), showing the epidermal cell structure in three different areas; specimen assigned by us to *C. paucifloroides* sp. inc.; SEM photos; **b** apex of the achene: Epidermal (exocarp) cells tend to be longer towards the style; **c** central part of the achene with prevailing isodiametric, irregularly polygonal cells, intermingled with sparse elongated cells; **d** margin of the achene, exclusively showing elongated cells with a gradual transition to isodiametric cells towards the central part of the achene. **e** marginal part of the achene shown in (a); external periclinal walls preserved, but more modified than in (**f**), so that the network of "a-p junctions" appears as thinner; silica bodies, which were probably dissolved during fossilization, did not produce a hole, their former presence being only suggested by a low central relief in each cell**; f** central part of the scarcely altered achene shown in Fig. 2a (BIN-Pb-H1499, assigned to *Carex paucifloroides* sp. inc.); external periclinal walls well preserved with cell outlines evidenced by the network of "a-p junctions" (see Fig. 1a, b); the central silica bodies were probably dissolved during fossilization, but left an apparent central hole in the external periclinal wall of each cell; **g** central part of the achene shown in Fig. 4i (BIN-Pb-H3390), assigned to *C. paucifloroides* sp. inc., which is totally corresponding in morphology to the holotype of *C. klarae* (Mai 2000); external periclinal walls removed in the central part, with cell outlines evidenced by the network of anticlinal walls; silica bodies probably dissolved during fossilization, without leaving any record; the cells are elongated as in the marginal part of (**f**), but show a more regular shape; **h** central part of the achene shown in Fig. 3c (BIN-Pb-H3450), assigned to *Carex paucifloroides* sp. inc.; external periclinal walls preserved, but more modified than in (f), as suggested by the two rows of tiny holes in each "a-p junction"; these correspond to the undulations of adjacent cell walls (as in Fig. 10d), which are not visible when the periclinal walls are intact; the former presence of silica bodies, probably dissolved during fossilization, is suggested by a low central relief in each cell**; i** central part of the achene shown in Fig. 4k (BIN-Pb-H2681), assigned to *C. paucifloroides* sp. inc.; the cell outlines seem to be duplicated, what is interpreted as a result of the compression of the network of the "a-p junctions" above the basal outline of the cells; silica bodies probably dissolved during fossilization, as suggested by a low, poorly visible central relief in each cell**; j** another portion of the epidermis of the achene shown in Fig. 4k, less affected by compression and showing an apparent central relief in each cell

never appear as a thick sheet, and never peel off (Fig. 7g). Sometimes they bear, from the outside, what seems to be the bulge caused by the impression of a single blunt central silica body (Fig. 7c, d, g). The portion of periclinal cell wall lying beneath the platforms is never exposed. The specimen of Fig. 7e, f is very similar in outline and dimensions to the holotype (Velichkevich 1975, pl. 1, Fig. 24), and that of Fig. 7a, b matches the paratype (Velichkevich 1975, pl. 1, Fig. 24). The longer apiculus in the type specimens does not represent a meaningful difference, because the same part is broken in the fossils of Fig. 7.

Siberian Early Pleistocene specimens

Achenes (Fig. 2a-c, 4a-d,g–k; 7a–g; 8a–f, h) relatively large (2.5–3.0 mm), mostly larger than the Miocene ones from the same area (assigned to *C. pauciflorifformis* by Nikitin 1976). Cross section with a blunt longitudinal ridge without evidence of a vascular bundle. The complete style, exceptionally preserved in one specimen (Fig. 2a), appears poorly lignified in the distal part ("soft" style pattern), whereas the proximal portion (ca. 1/3 of the achene length) is strongly lignified (Fig. 3a). The poorly lignified distal part is decay-prone and, in the majority of specimens, either missing or just preserved as a filament ("proboscis" style pattern: Fig. 3b), several specimens retaining just a short portion of it (Fig. 3c, g-k). The two parts are usually separated by a constriction (e.g., Fig. 3j) that should be interpreted as taphonomically induced (Fig. 3i), because in the above-mentioned, less altered achene (Fig. 2a) such constriction is not present. The isodiametric epidermal cells in the central part of the achene (Fig. 8c, e, h), often have unequally long sides and display external periclinal walls persisting in all fossils (robust in origin, as shown in Fig. 8e). This irregular polygonal pattern of epidermal cells in Pleistocene achenes from Siberia represents the only possible, but inconstant difference from the rather regular cell pattern of slightly longitudinally elongated hexagons (Fig. 5f) observed in the Miocene achenes from the region and the earliest Pleistocene *C. paucifloroides* from Belarus (Fig. 7c, d, g). Otherwise, the agreement of characters is strong and the most apparent differences among the three groups of achenes can be attributed to the state of preservation. Cells bear, from the outside, a bulge caused by the impression of a single, blunt central silica body. The apparent lack of satellite bodies cannot be pinpointed as a differential character, because we only observed the extracellular surface of the external periclinal walls, and in Siberian Miocene specimens only the intracellular side displayed evidence of satellite bodies.

Italian Pliocene specimens

Achenes 1.2–1.8 mm, as a mean slightly smaller than those of the Siberian Miocene and Belarusian Pleistocene (Table 3), mostly with narrower substipitate base (Fig. 2e), and with a poorly apparent, rounded longitudinal ridge only in the basal part, without any vascular bundle. A clear "proboscis" style pattern is shown by a better preserved achene (Fig. 2e, see also Jiménez-Mejías et al. 2016b, Fig. 7l), whereas several others only show a robust proximal apiculus that is about 1/4–1/5 of the achene length (Fig. 7h, j). The external periclinal walls are always preserved, and the "a-p junctions" are robust and well-preserved. Unfortunately, we cannot infer any information about the silica bodies from these remains.

These Italian Pliocene specimens were tentatively assigned to *C. paucifloroides* by Martinetto (1995) and Jiménez-Mejías et al. (2016b) and here we can confirm their similarity to the Belarusian types. However, the Italian specimens are intermediate in their dimensions between the

Table 4 Scoring of the most diagnostic achene characters of both modern and fossil-species

Sect	Species	Achene section, center	Achene section, base	Bundle on longitudinal ridge	Style pattern (P = presumed)	Style pattern in fossils (P = presumed)	Usual beak ratio	Obs. method
Cyper	*C. bohemica*	Biconvex	Bluntly 3-faced (base)	No	Soft	Proboscis	1/7–1/10	40x, SEM
Cyper	*C. leporina*	Biconvex	Biconvex	No	Soft	Proboscis	1/7	40x, SEM
Cyper	*C. muskingumensis*	Biconvex	Bluntly 3-faced	No	Soft	Proboscis (P)	1/3–1/4	40x, SEM
Cyper	*C. projecta* (from literature)	Biconvex	Bluntly 3-faced	No	Soft	Proboscis (P)	1/7	40x
Psyllo	*C. macrostyla*	Simply 2-faced	Simply 2-faced	Not applicable	Proboscis	Proboscis (P)	1/9–1/10	40x, SEM
Psyllo	*C. pulicaris*	Simply 2-faced	simply 2-faced	Not applicable	Solid	Solid (P)	-	40x, SEM
Circin	*C. antoxanthea*	3-faced	3-faced	Yes	Proboscis	Proboscis (P)	?	40x, SEM
Circin	*C. circinata*	3-faced	3-faced	Yes	Proboscis	Proboscis (P)	1/6	40x, SEM
Circin	*C. hakkodensis*	3-faced	3-faced	Yes	Proboscis	Proboscis (P)	1/20	40x
Leuco	*C. pauciflora*	3-faced	3-faced	Yes	Solid	Solid (P)	-	40x, SEM
Fossils								
Cyper	*C. pauciflo-roides* sp. inc.—Pleistocene of Siberia	Biconvex	Bluntly 3-faced	No	Soft	Soft (rare) and proboscis	1/3	40x, SEM
Cyper	*C. pauciflo-roides*—Pleistocene of Belarus	Biconvex	Bluntly 3-faced	No	?	?	Not applicable	40x, SEM
Cyper	*C. pauciflo-roides* sp. inc. (“*C. pauciflo-riformis”*)—Miocene of Siberia	Biconvex	Bluntly 3-faced	No	Soft	Soft (rare) and proboscis	1/3–1/5	40x, SEM
Cyper	*C. pauciflo-roides* sp. inc. (“*C. klarae”*)—Miocene of Germany	Biconvex	Bluntly 3-faced	No	Soft (P)	Proboscis (P)	1/7	40x, SEM
Cyper	*C. pauciflo-roides* sp. inc.—Pliocene of Italy	Biconvex	Bluntly 3-faced	No	Soft (P)	Proboscis	1/5	40x, SEM

Sect	Species	Main cell pattern at the SEM, achene center	Cell sides (mostly)	Diameter range of isodiametric cells (microns)	External evidence of central body	Central body evidence, altered walls	Apex of central body	Satellite bodies
Cyper	*C. bohemica*	Isodiametric and elongate, 5–6-sided	Heterogen	10–18 (11 cells)	Invisible	Hole or mound	Flat-tipped	Present- 7–12, max. 14
Cyper	*C. leporina*	Isodiametric, 5–6-sided	Heterogen	10–22 (40 cells)	Invisible	Hole or mound	Flat-tipped	Present-6–12
Cyper	*C. muskingumensis*	Isodiametric, 5–6-sided	Homogeneous	10–18 (18 cells)	Hole	Hole	Flat-tipped	Present
Cyper	*C. projecta* (from literature)	Isodiametric, 5–6-sided	Homogeneous	15–25 (12 cells)	Mound	Mound	Flat-tipped	Present-6–12

Table 4 (continued)

Sect	Species	Main cell pattern at the SEM, achene center	Cell sides (mostly)	Diameter range of isodiametric cells (microns)	External evidence of central body	Central body evidence, altered walls	Apex of central body	Satellite bodies
Psyllo	*C. macrostyla*	Isodiametric, 5–6-sided	Homogeneous	Ca. 20	Mound	?	Conical-tipped	No
Psyllo	*C. pulicaris*	Isodiametric, 5–6-sided	Homogeneous	15–22 (46 cells)	Mound	Mound	Granulose	Present
Circin	*C. antoxanthea*	Isodiametric, 5–6-sided	Homogeneous	Ca. 15–22 (6 cells)	Mound	?	Conical-tipped	?
Circin	*C. circinata*	Isodiametric, 5–6-sided	Homogeneous	Ca. 20	Mound	?	Conical-tipped	Max. 2, rare
Circin	*C. hakkodensis*	?	?	?	?	?	?	?
Leuco	*C. pauciflora*	Elongated, mostly 4-sided	Heterogen	10–14 (31 cells)	Eccentric granules	Eccentric granules	Granulose	Present-4–6 max. 7
Fossils								
Cyper	*C. pauciflo-roides* sp. inc.—Pleistocene of Siberia	Isodiametric, 5–6-sided	Heterogen	15–20 (28 cells)	Mound	Hole or mound	Flat-tipped	?
Cyper	*C. pauciflo-roides*—Pleistocene of Belarus	Isodiametric, 5–6-sided	Homogeneous	Ca. 20 (2 cells)	Mound	Mound	Flat-tipped	?
Cyper	*C. pauciflo-roides* sp. inc. (“*C. pauciflo-riformis*”)—Miocene of Siberia	Isodiametric, 5–6-sided	Homogeneous	15–20 (13 cells)	Mound	Mound	Flat-tipped?	Present-20–30
Cyper	*C. pauciflo-roides* sp. inc. (“*C. klarae*”)—Miocene of Germany	Elongated, mostly 6-sided	Homogeneous	?	Mound	Mound	?	?
Cyper	*C. pauciflo-roides* sp. inc.—Pliocene of Italy	Isodiametric and elongated, 5–6-sided	Homogeneous	Ca. 15–20 (6 cells)	?	Hole or mound	?	?

cited fossil-species and the extant *Carex bohemica* (Fig. 7l, Fig. 2f), which may rise some doubts on the correctness of the former assignment. In this respect, the missing information about the number of satellite bodies (see the difference between a specimen reported as *Carex paucifloroides* sp. inc. and *C. bohemica* in Table 3) constitutes a strong limit for interpretation.

Specimen not assignable to Carex

The single Early Oligocene achene we studied (BIN-Pb-H1707, formerly classified as *C. pauciflorifformis*), although badly preserved, showed a thickened outline (Nikitin 2006, pl. 19, Figs. 58–62), which suggests assignment to *Dulichium* (Table 3). This restricts the temporal range of *C. pauciflora*-type remains from the Early Miocene to the Late Pleistocene.

Discussion

Relevant carpological characters in *Carex* and their utility in palaeotaxonomy

The homologies that we found in the structure of fossil and similar modern achenes of *Carex* (especially bleached

Table 5 Summary of micromorphological features that showed differences in extant species with *Carex pauciflora*-type achenes, belonging to different taxonomic groups

Supraspecific taxon	Species studied	Characters
Carex sect. *Circinatae*	Only *C. anthoxanthea* studied at SEM: Fig. 10a-e	Epidermal cells sub-isodiametric, square, rectangular and polygonal. Silica platforms large, filling entirely the bottom of the cell lumen, with a single large and conical central silica body that protrudes into the shallow cell lumen (ca. 3–5 µm high), still noticeable also under the ca. 2 µm thick, peel-like external periclinal wall (probably covered by a thick cuticle); rarely, one or two small satellite bodies are present in the longest cells
Carex subgen. *Eutyceras*	*C. pauciflora*: Fig. 10f-h	Epidermal cells longitudinally elongated, mostly 4-sided, oblong to more or less narrowly rectangular. Extracellular and intracellular sections of the anticlinal walls similar, thin (ca. 1 µm), finely sinuous. Silica platform, when present, covering entirely the intracellular side of the inner periclinal wall; silica bodies small and irregular in shape (ca. 2–3 µm), eccentric, usually located near the anticlinal walls orthogonal to the long achene's axis
Carex subgen. *Psyllophorae*	*C. macrostyla* and *C. pulicaris*: Fig. 10i-n	Epidermal cells isodiametric, irregularly polygonal (5- or 6-sided). Extracellular and intracellular sections of the anticlinal walls similar, thin (ca. 0.5 µm), straight, not sinuous nor undulate. Silica platform poorly developed, filling the bottom of the cell lumen (*C. macrostyla*) or not (*C. pulicaris*), with a single central silica body (ca. 5 µm) noticeable under the inflexed external periclinal wall
Carex sect. *Cyperoideae*	*C. bohemica, C. leporina, C. muskingumensis, C. projecta, C. scoparia*: Fig. 7k-l; Fig. 9a-d; Fig. 11a-f	Epidermal cells isodiametric to slightly elongated longitudinally, 5- or 6-sided. Silica platform large and thick, filling entirely the bottom of the cell lumen and conspicuously protruding outwards, with a central silica body (ca. 5 µm) and several (even more than 20 in some species: Rothrock et al. 1997), smaller satellite bodies at its margin (Fig. 11c)

The characters were observed in a few species and cannot be assumed as characteristic of supraspecific taxa

specimens) helped us to establish affinities that can eventually help us to trace back —and even rewrite— the history of sedge groups (see below). We underline here the variation that we have observed in carpological characters and its taxonomic implications, with the intention of stimulating further similar studies in other sedge groups and plants in general. A relevant piece of advice that we wish to provide in this sense is to use bleaching, rather than "sonication", to prepare modern sedge achenes for the micromorphological comparison with fossils. Bleaching produces different states of alteration in a single achene (Fig. 9, 11), that are useful to reveal the three-dimensional architecture of the epidermal cell walls, largely preserved in fossils. Conversely, "sonication" often removes completely the external periclinal walls, that may bear the most diagnostic characters in fossils (Fig. 5h).

Our study shows that carpological characters of the tiny *Carex* fossil fruits have a considerable potential for understanding the evolution of this group of plants. A similar potential has been demonstrated for many groups of seed plants, whose most common fossil remains are also fruits and seeds (e.g., Cornaceae, Menispermaceae, Vitaceae: Atkinson 2018; Jacques et al. 2011; Manchester et al. 2013).

Approximately biconvex achenes with an elongated shape and a strong but slender lignified style base (apiculus), here named *Carex pauciflora*-type, have been observed in three of the six extant subgenera (Fig. 13): *Euthyceras* (e.g., *C. anthoxanthea, C. circinata*, *C. pauciflora*), *Psyllophorae* (e.g., *C. macrostyla*, *C. pulicaris*) and *Vignea* (members of sect. *Cyperoideae*), indicating the convergent origin of such carpological plan. The combined study of macro- and micromorphological characters has allowed us to discriminate among the different groups of samples, illustrating the potential of detailed carpological studies. Our main taxonomic result is the unequivocal characterization of sect. *Cyperoideae* achenes by the combination of outline, isodiametric or shortly elongated epidermal cell shape (achene's center), phytoliths with numerous satellite bodies (see also Rothrock et al. 1997), and the above described "soft" style pattern. Initially, preliminary observations of Jiménez-Mejías and Martinetto (2013) led them to conclude that species of subgen. *Vignea* seemed to lack persistent

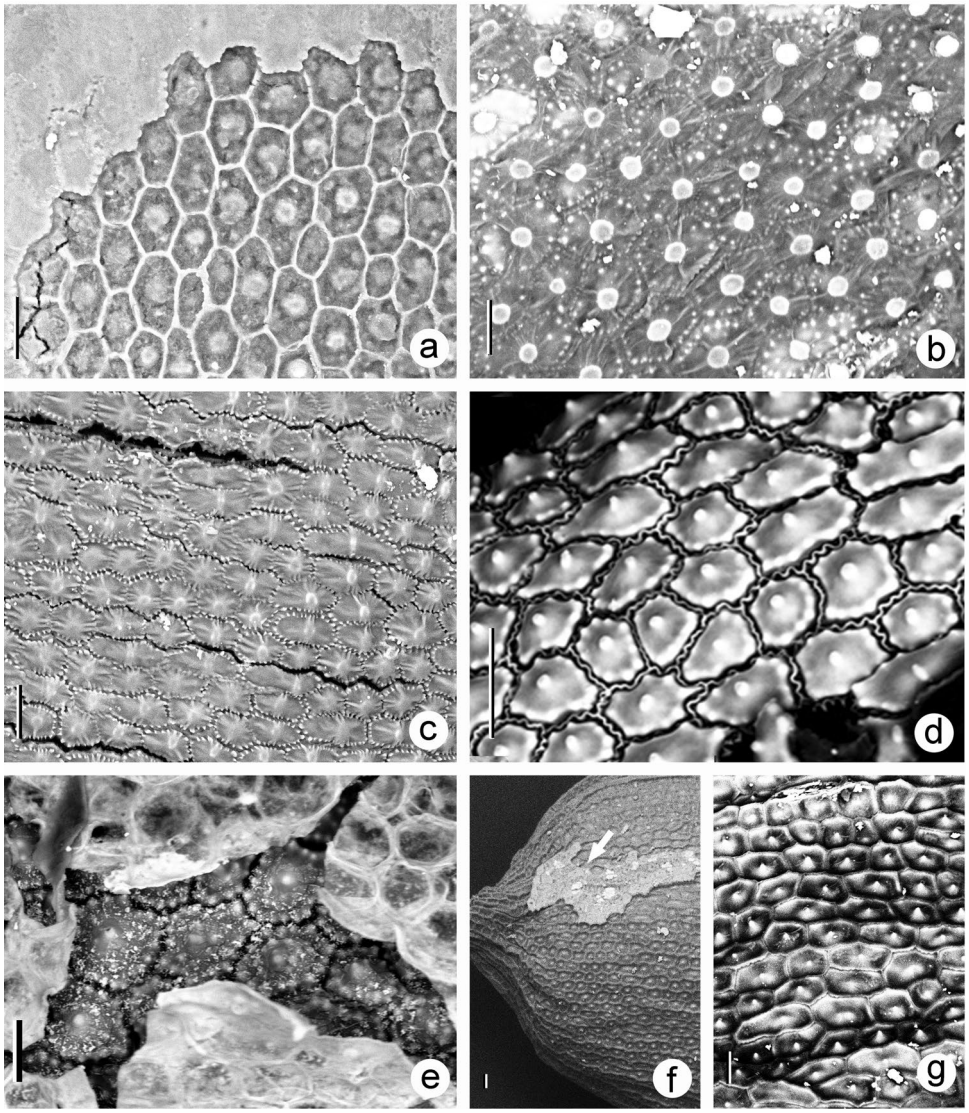


Fig. 9 Epidermal (exocarp) cell structure of subgen. *Vignea* achenes (outer surface, central part) in different states of modification, detected after treatment with bleach for 48 h ("digestion"); see references to this figure in Table 2 for more detailed data concerning each specimen; **a** *Carex leporina*, showing two states of the exocarp due to differential response to laboratory preparations: 1- minimal modification at the top left corner, with external periclinal walls partly intact and partly cracked along the undulated cell borders; morphology of the central silica bodies hardly visible, and only in a few cells; 2- consistent modification elsewhere, with removal of an external layer of the periclinal walls, exposure of the network of anticlinal walls (not undulated) and of the internal layer of the periclinal walls, showing a central relief representing the attachment structure of the silica platform (see Fig. 11a-c for further information on this same achene); **b** *C. muskingumensis*, with wrinkled, but still continuous external periclinal walls covering the silica platforms (one, appearing as whitish, is exposed in the top left corner), characterized by a central silica body and several satellite ones, all of which are morphologically detectable from the outside (it is unclear whether this is a primary condition or a secondary effect of the digestion); **c** *C. scoparia*, wrinkled external periclinal walls covering the silica platforms, with frequent cracking along undulated lines in correspondence of the anticlinal walls; central silica body morphologically detectable from the outside, satellite ones not visible; **d** *C. bohemica*, periclinal walls totally removed with exposure of the network of undulated anticlinal walls, separated from the massive silica platforms, which completely fill the cell lumina; **e** *C. elongata*, a continuous sheet of external periclinal walls (probably with a thick cuticle) is peeling off and permits to observe the underlying silica platforms, each of which is surrounded by a gap, without apparent anticlinal walls; central silica body and satellite ones similar, small and not detectable on the extracellular surface of the periclinal walls; **f**, **g** *C. brizoides*, external periclinal walls almost completely removed (apart in the area indicated by the arrow) and silica platforms connected to a thin network of straight anticlinal walls, thus forming a continuous pavement

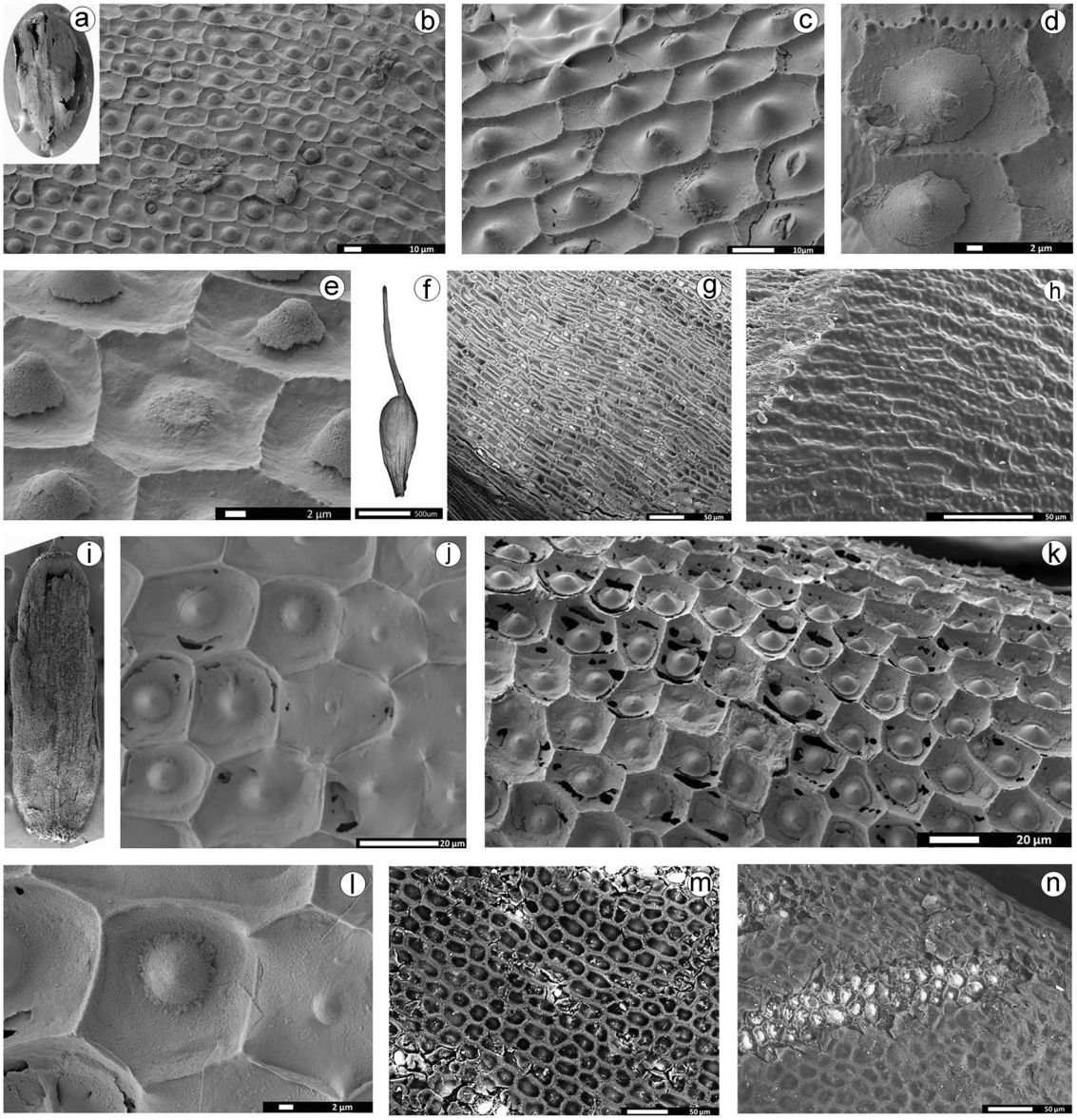


Fig. 10 SEM photos of modern achenes of subgen. *Euthyceras* and *Psyllophorae*. **a**–**e** *Carex anthoxanthea* (sect. *Circinatae*), see references to this figure in Table 2 for more detailed data concerning each specimen; **a** aspect of a sonicated achene whose epidermal cell structures, with various modifications, are shown in the following images, showing a total removal of the external periclinal walls; **b** exocarp with sub-isodiametric, polygonal cells with sharp angles, often subrectangular; **c** detail of a portion where the continuous pavement of silica platforms is well preserved; each platform bears a central body and a few ones have one or two satellite bodies; **d** exocarp cells with a corroded portion of the platforms around the central silica body, clearly separated from a deeper, altered portion of the internal periclinal walls, showing undulated cell margins (arrow); **e** consistently modified (altered???) exocarp cells, one of which (centre) lost the silica platforms and mostly shows a basal attachment structure (see Fig. 1c'); **f**–**h** *C. pauciflora* (sect. *Leucoglochin*), bleached achene; **f** aspect of the achene whose epidermal cell structures are shown in (**g**); **g**, **h** epidermal cell structures of two achenes with narrow, elongated cells showing finely undulated walls; silica bodies (whitish) are isolated (no platform), mostly two per each cell and eccentric; **i**–**l** *C. macrostyla* (sect. *Psyllophorae*); **i** aspect of the sonicated achene whose epidermal cell structures are shown in the following images; **j** portion of the achene with preserved, cuticle-like external periclinal walls on the right side, while these are lacking on the left side where the internal, silicified periclinal walls (platform with a central bodies) are exposed; **k** oblique view of the achene surface with mostly pentagonal and hexagonal cells; **l** detail of two adjacent cells, the right one with external periclinal wall, the left one without, and showing the internal, silicified periclinal wall with a central silica body; **m**, **n** epidermal cell structures of two achenes of *C. pulicaris* (sect. *Psyllophorae*), respectively a bleached specimen with a network of "a-p junctions" and an untreated one with a damaged portion (clear band), where the cells show sharp angles at the junction of the relatively thin anticlinal walls (thinner than the respective "a-p junctions", see Fig. 1a, b); the platform with a central silica body fills a minor part of the rather deep lumen of each cell; the cells outside the damaged portion show rounded angles and apparently thicker walls, simply because what is perceived is the network of "a-p junctions" (see Fig. 1a, b) and not of anticlinal walls

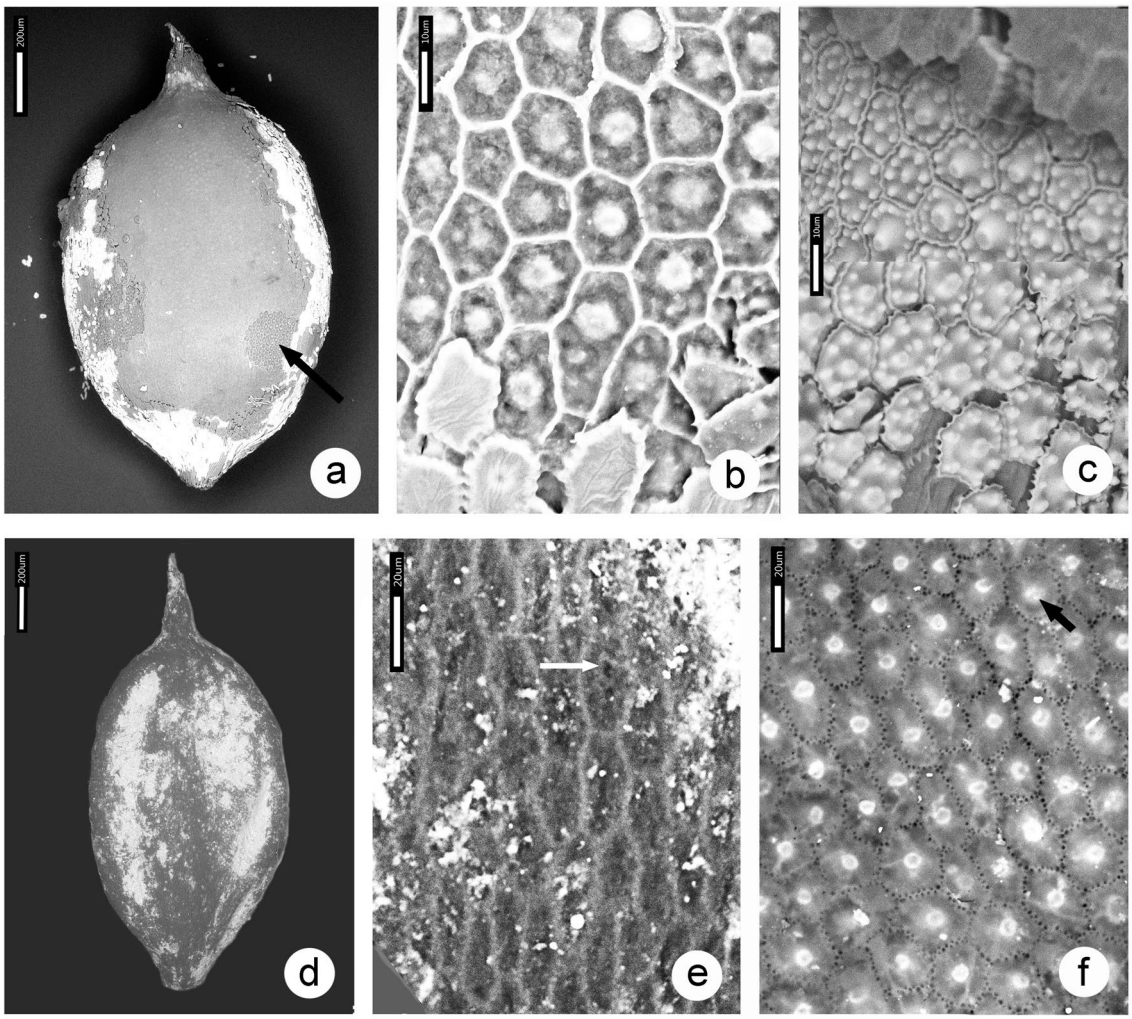


Fig. 11 Achenes of *Carex leporina* (sect. *Cyperoideae*) and their epidermal cell structure, SEM photos; see references to this figure in Table 2 for more detailed data; **a** bleached achene (48 h) whose white margin corresponds to a strongly digested part, where silica platforms have been exposed; the arrow indicates an area, enlarged in **b** (see also Fig. 9a)**,** where an external layer of the periclinal walls (cuticle?) peeled off in tiles; **b** detail of the "tile-like" break-down (image bottom) of the external periclinal walls, uncovering the internal layer with evidence of the silica platforms; **c** marginal part of the same achene with a continuous sheet of exposed silica platforms, each surrounded by undulated anticlinal walls; the break-down of silica platforms shows a jigsaw-puzzle pattern; the epidermis shows progressive decortication from top to bottom; individual tiles of the periclinal walls are displaced, upside down, at the top right corner, and show the inner side with the impression of the central silica bodies; **d**, **e** aspect of a Pleistocene fossil achene from central Italy which was assigned to *Carex leporina* (Martinetto et al. 2014), with detail of the surface, whose appearance does not correspond to either the bleached achene (**b**, **c**) or that extracted from a soil sample (**f**); the external periclinal walls seem to be well preserved, compressed towards inner side of the achene (concave) and only in a few cases showing a hole produced by the central silica body (arrow); **f** surface of an achene extracted from a soil sample, whose appearance differs from the bleached sample; the outlines of cells are evidenced by two rows of tiny holes, which correspond to the undulations of adjacent cell walls (as in Fig. 10d); silicified elements are partly preserved, at least the central silica bodies (arrow)

style remains (apiculi), the achenes just bearing a flattened remain at the apex without any rest of the style itself, which is entirely deciduous ("jointed" style). However, with the study of samples from sect. *Cyperoideae*, it seems now that the four extant members that we investigated (Table 2) consistently retain elongated style remains. The style in sect. *Cyperoideae* appears to have two clear parts. First, a particularly elongated and lignified proximal part. This has been already pointed out before in previous treatments ("short apiculus formed by persistent base of style"; Mastrogiuseppe et al. 2002). And, second, a poorly lignified distal part, persistent even when fully ripe or in taphonomically altered soil and fossil samples. These characteristics of the style seem to be exclusive of sect. *Cyperoideae* and its sister group, the Australasian sect. *Inversae* Kük., among all subgen. *Vignea*

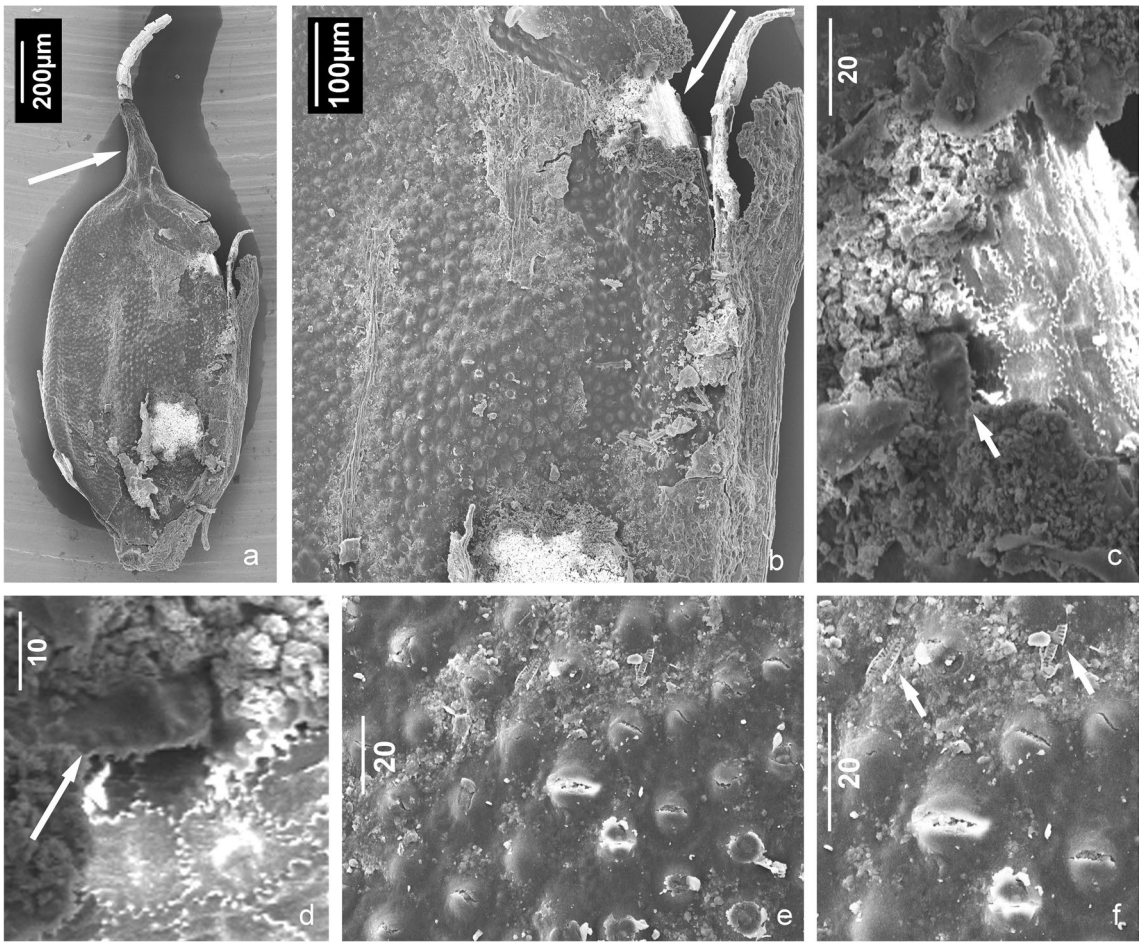


Fig. 12 Late Pleistocene achene assigned to *Carex bohemica* from Alymka, Western Siberia (IGMN 81-K-40–3, 7/17 in Table 3); **a** Overview of the fossil achene with the arrow showing the constriction of the "soft" style**; b** detail of the external periclinal walls, with papillae suggesting the persistence of the central silica bodies on platforms; the arrow points to a small damaged area exposing a silica platform; **c** marginal part of the same achene with detail of the damaged area showing an exposed silica platform (arrow) and the underlying internal periclinal walls with jigsaw-puzzle pattern (see Fig. 1d); **d** detail of the platform with a flat-tipped central silica body and less than 15 satellite bodies (arrow); **e** detail of a portion of undamaged epidermis with papillae, some of which are cracked for the pressure of the central silica bodies; **f** Detail of an area with two frustules of diatoms (arrow). Numbers indicate the length of scale bars in microns

groups (see descriptions in Egorova 1999; Reznicek and Ball 2002; Dai et al. 2010; Ercole et al. 2012).

Some of the characters observed in other studied groups seem to potentially be limited to a few taxa, e.g.: entirely lignified ("firm") styles in *C. pauciflora* and *C. pulicaris*, elongated epidermal cells in *C. pauciflora*, and 3-sided achenes with vascular bundles in the edges in *C. pauciflora* and sect. *Circinatae*. But our sparse sampling, together with the lack of informative references in external sources, prevents us from making additional considerations. However, we believe that such variation may point to potentially differential characters and deserves further study.

Our work also dismisses the potential of characters usually considered in works focusing on *Carex* achene micromorphology. This is the case of the anticlinal cell walls, which are often described with detail because of showy states, such as undulate or highly waving (e.g. Toivonen and Timonen 1976). We have demonstrated that the morphology of the anticlinal wall can vary within a single cell: one same portion of anticlinal wall can change from wavy to straight as it extends from the external "a-p junctions" to the internal side of the cell. This makes the description of anticlinal walls of a particular section rather useless, since the morphology observed in SEM pictures highly depends on

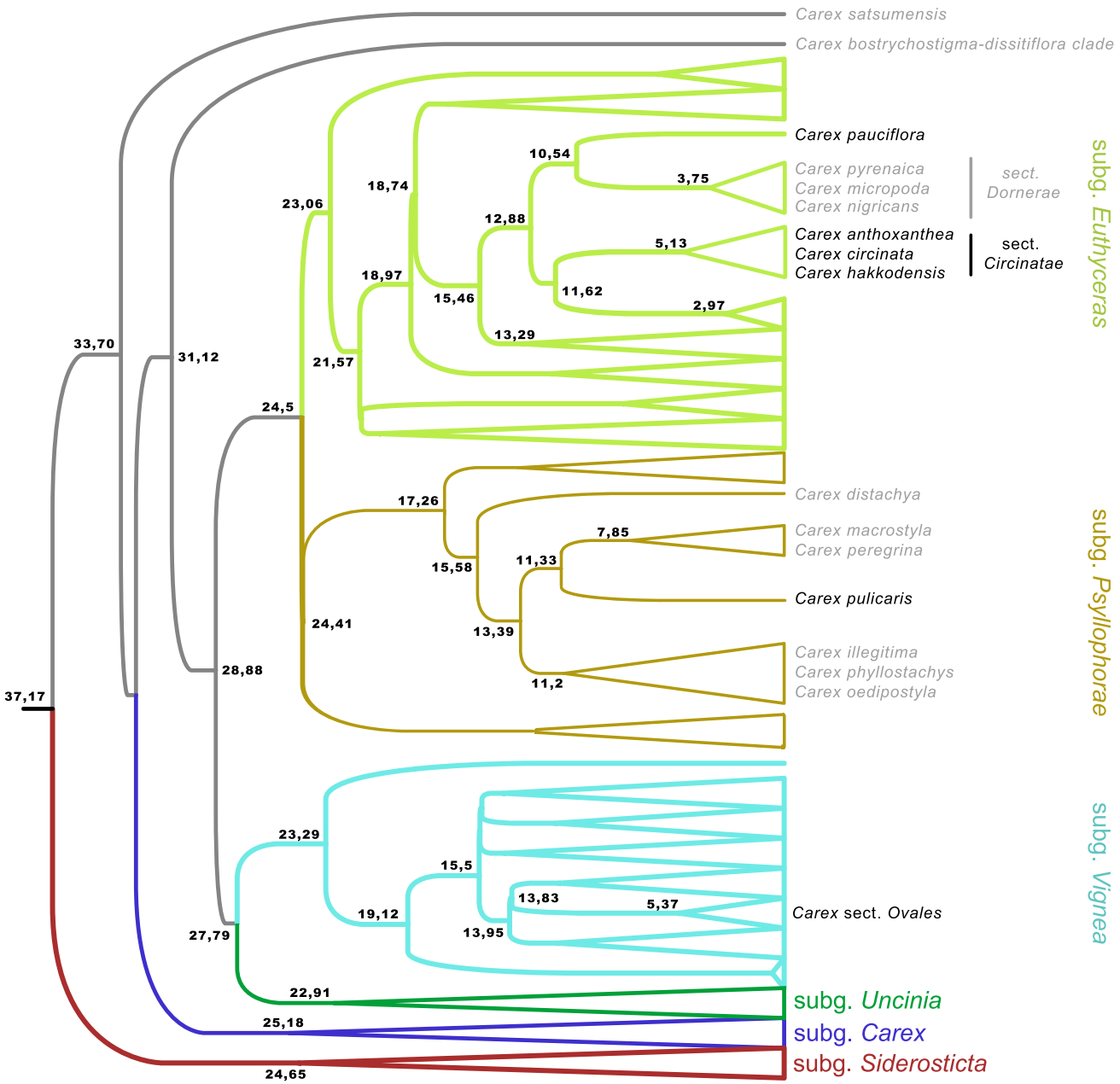


Fig. 13 Summary phylogenetic tree showing the relationships of *Carex* groups that display *C. pauciflora*-like achenes (in bold type). Modified from Martín-Bravo et al. 2019

the degree of erosion of the anticlinal walls after the decay of the external periclinal walls.

The potential of the phytoliths, despite them having not received much attention in the study of fossils, deserves further consideration. Silica platforms of the epidermal cells are known to be quite variable in *Carex* and be taxonomically relevant (e.g. Toivonen and Timonen 1976; Tallent and Wujek 1983; Waterway 1990; Dan and Hoshino 1994; Rothrock et al. 1997; among many others). Our observations support that the phytoliths in fossil remains are neither eroded nor dismantled, but dissolved (Fig. 1a'). This consideration is supported by the absence of silica platforms, even when the external periclinal wall is persisting (Figs. 5e, 7g), as well as by the rare preservation of platforms in fossils of silica-rich environments (not prone to dissolve the silica phytoliths; Fig. 12d). Therefore, there is a chance of finding phytolith characters in the form of impressions on the external periclinal wall, as we remarkably found in specimen 128 of our sample BIN-Pb-H3296 (Fig. 5h). It would be desirable

to develop guidelines for the observation or characterization of the intracellular side of the periclinal walls, when carrying out accurate studies of fossil remains in sedges and other groups of plants that frequently experience the loss of phytoliths.

Revised delimitation of species and nomenclature of *Carex pauciflora*-type fossil remains

Morphological variation in fruits of extant *Carex* species is quite broad (e.g., Martinetto et al. 2014, plate 1) and proliferation of fossil-species based on small morphological differences is certainly not useful for the advancement of our knowledge. In this context, *C. pauciforiformis* and *C. klarae* do not seem to be separated by clear and relevant differential characters from *C. paucifloroides*, the earliest validly described species (Table 1). Likewise, the Siberian earliest Pleistocene findings only differ from *C. paucifloroides* for the slightly larger dimensions (and not in all the specimens), and the Italian Pliocene ones for the slightly smaller dimensions (Table 4). Overall, the morphological variation of *Carex pauciflora*-type fossils through time and space is not sufficiently known, and any formal subdivision into different species would be hazardous at the present state of the art. Many *Carex pauciflora*-type fossil achenes from the Miocene of Poland (Raniecka-Bobrowska 1959), Pliocene of Russia (Dorofeev 1985) and Czechia (Teodoridis et al. 2017), and Pleistocene of Central and Eastern Europe (Mai and Walther 1988; Mamakowa and Velichkevich 1993; Velichkevich and Zastawniak 2003, 2006, 2007; Stachowicz-Rybka 2015; Zyuganova et al. 2015; Jiménez-Mejías et al. 2016b), have been indicated as strongly agreeing to the type material of *Carex paucifloroides*. Overall, these specimens display an agreement in the characters also with many Siberian Miocene specimens of *Carex pauciforiformis* and the few differences could be simply due to the state of preservation.

In conclusion, we suggest to treat as *Carex paucifloroides* only the specimens from the Early Pleistocene of Belarus and we underline the urgent need to highlight the yet unknown characters (distal part of the style, satellite bodies) of the fruits from the type locality Dvorets. We suggest, temporarily, to apply the open nomenclature *Carex paucifloroides* sp. inc. (Sigovini et al. 2016) to all the other *Carex pauciflora*-type fossil remains from Europe and Siberia (Table 3).

By using the single name *Carex paucifloroides* sp. inc. for many remains, from the Early Miocene to the Middle Pleistocene and from Siberia to Italy, we do not exclude that different species could be pointed out in the future within this large set of fossils. For example, it is certainly odd to group under the same name 57 achenes from the Pleistocene of Kholmech (Belarus), all shorter than 1.8 mm and narrower than 0.6 mm (Velichkevich and Zastawniak 2003, assigned by them to *C. klarae*), and 10 achenes from the Pleistocene Tobol flora (Siberia), which are all longer and broader. However, the complexity of the situation is demonstrated by the occurrence of longer and broader achenes also at the above-cited locality Kholmech (assigned to *C. paucifloroides* by Velichkevich and Zastawniak 2003). Therefore, in the light of the broad size variation detected in a single extant species and without carrying out further studies on the size variation of achenes in each fossil site, we deem it impossible to point out different species within the complex treated here as *Carex paucifloroides* sp. inc.

The single group of fossils referable to another species, i.e. *C. bohemica*, is represented by achenes that are only 1.0–1.5 mm long (instead of more than 1.6 mm) and have less than 14 (instead of 20–30) satellite bodies. Indeed, fossil achenes referred to *C. bohemica* were indicated as similar, but distinguishable from those of the *Carex pauciflora*-type (Velichkevich and Zastawniak 2006).

Taxonomic affinities of *Carex pauciflora*-type fossil remains

We approached the affinities of the five groups of *Carex* fossil fruits according to the three sets of characters that we deemed useful for the taxonomic discrimination of extant groups with *C. pauciflora*-like achenes: style, cross-section and epidermal cell structure including silica bodies (Table 5). We did not consider the utricle-achene attachment since we regarded it as invariable among *C. pauciflora*-like achenes.

Fossils with a full set of characters

Achenes from the Siberian Miocene were the only set that allowed us the detailed observation and interpretation of the three groups of characters considered (Table 3; Figs. 2, 5): styles matching the "proboscis" pattern (Fig. 4o, q), presence of a rounded longitudinal ridge without any vascular bundle, and epidermal cell pattern of slightly longitudinally elongated hexagons with impressions of phytoliths, each bearing 20–30 satellite bodies on the intracellular side of the external periclinal wall (Fig. 5h). Moreover, a few exceptionally preserved specimens with scarcely altered style (Fig. 4p) matched the "soft" style pattern, allowing us to conclude that the dominant "proboscis" style pattern is actually of taphonomic origin.

Remarkably, the combination of these three features excludes the main candidate for the nearest living species proposed to date: *C. pauciflora* (see Table 4, Fig. 10h), as well as close relationship with sect. *Circinatae* and sect. *Psyllophorae*. In the light of the available data, we consider

that all the characters displayed by the Siberian Miocene set point to sect. *Cyperoideae* as the best possible match.

When Nikitin (1976) reasoned about the affinities of *C. paucifloriformis* with *C. pauciflora*, he based his observations on the study of macroscopic features of the fossil achenes. Our work shows that a better understanding of the epidermal cell features provides new evidence on the systematic affinity of these problematic fossils.

Fossils without detailed information on silica bodies

Three groups of studied fossil achenes yield fine morphological evidence and just lack information about the silica bodies: Siberian Early Pleistocene specimens, German Miocene specimens and similar Siberian ones, and Italian Pliocene specimens. In all the three cases the very good preservation of primary features is suitable for a detailed comparison with modern achenes and for considerations on the most probable systematic affinities of these remains. Summarizing, the three groups of achenes have in common the following characters (Table 4): (1) a "proboscis" style pattern, (2) cross section with a blunt longitudinal ridge without traces of vascular bundle; and (3) epidermal cells slightly longitudinally elongated, 5- and 6-sided. All these available features allow us to discard as putative matches *C. pauciflora*, sect. *Circinatae* and sect. *Psyllophorae* (see Table 5). With the available evidence, sect. *Cyperoideae* is again the best possible match for these remains, pending a further confirmation from the possible future detection of some record of satellite silica bodies.

Fossils without information on silica bodies and style pattern

All the Pleistocene Belarusian achenes here grouped as *C. paucifloroides* displayed a strong alteration of the style (Fig. 7b, f), which did not allow us to assess the style pattern with certainty. A tentative assignment to sect. *Cyperoideae* would only be supported by the combination of mostly isodiametric epidermal cells and blunt ridge without vascular bundle. All this renders the Pleistocene Belarusian achenes as the set of *C. pauciflora*-type fossils with the most unclear systematic affinities. It is unfortunate that the type material of the name *C. paucifloroides*, that for priority we apply (in open nomenclature) to most of the *Carex pauciflora*-type fossil remains from Europe and Siberia, falls right within this systematically ambiguous group.

Implications for the biogeographic history of *Carex* sect. *Cyperoideae*

The study of the *C. pauciflora*-type fossils sheds light on the biogeography of sect. *Cyperoideae*. For this section an ambiguous origin in North America and Asia during the Late Miocene, followed by Pliocene diversification (5.4 Ma) centered in North America, was inferred (Martín-Bravo et al. 2019). Since our oldest reliable fossils belonging to sect. *Cyperoideae* date back, at least, to 20 Ma (Early Miocene) in Siberia, this supports an Asian origin for the ancestors of the group. From the Americas, the section seems to have passed back to the Old World in four different events during Pleistocene, according to the independent origins of the four native Eurasian species of the section (*C. iljinii*, *C. leporina, C. bohemica* and *C. macloviana*). The Western Palearctic fossils from the Pleistocene assigned by us to *C. bohemica* and *C. leporina* are also in agreement with these dispersal events. This is not in conflict with the presence of Pliocene and Early Pleistocene remains (*C. paucifloroides* sp. inc.), which may indicate the existence in Europe of now extinct members of the section at that time.

Conclusion

Some of the elongated biconvex fossil fruits of *Carex* from the Old World analyzed by us showed definite clues to assess their phylogenetic relationships, whereas others provided weaker, but not contrasting evidence.

The most exhaustive morphological information was gathered for Miocene (23 to 20 My old) specimens from Siberia, including the detailed morphology of silica bodies. These Miocene fossils showed the association of all relevant characters to those in extant members of *Carex* sect. *Cyperoideae*. For other four groups of fossils, we could not assess whether satellite bodies were present or not, but a detailed comparison allowed us to propose their close morphological affinity to the above-mentioned Siberian achenes. The distinction from *C. paucifloroides* of the fossil-species *C. klarae* was not supported in this work, and its material was treated as *C. paucifloroides* sp. inc. Other Pleistocene fossil achenes, with definite affinity to the extant *C. bohemica*, are distinguished from those of *C. paucifloroides* by the smaller size and the very short to absent longitudinal ridge. Achenes with intermediate size between *C. paucifloroides* and *C. bohemica* occur in the Pliocene of northern Italy and are again treated as *C. paucifloroides* sp. inc. All the above-cited *C. pauciflora*-type fossils could represent past occurrences of *Carex* sect. *Cyperoideae*. Conversely, our analysis did not point out any definite fossil occurrence of *C. pauciflora* or of subgen. *Euthyceras*, but it is possible that further studies on the two above-cited Pleistocene samples of *C. pauciflora* sp. inc. (BIN-Pb-H273 and H535) could fill this gap. We did not detect reliable records for subgen. *Psyllophorae* either, since the purported record of fossil achenes of *C. pulicaris* from the Pleistocene of Germany (Mai 2010) seems to correspond

to the Siberian Pleistocene group that we treat as *C. pauciflo-roides* sp. inc.

For phylogenetic considerations it is remarkable that the oldest elongated biconvex fossil fruits from the Old World, dating at least from the Early Miocene (the youngest age of the Oligocene–Miocene "Vasyuganskiy Yar" floristic complex), show a combination of morphological traits characteristic of extant members of *Carex* sect. *Cyperoideae.* We are aware that the hypothetic assignment of the Miocene fossils to sect. *Cyperoideae* is in contrast with the relatively recent origin of the group indicated by Martín-Bravo et al. (2019), but the evidence provided by the morphology of fossil achenes is strong and should be used to improve the phylogenetic analysis.

Further analyses and experiments (e.g. silica removal and detailed analysis of the persistent morphologies) on fossil and modern achenes, also including additional species, would be desirable. In particular, the single fortunate case of the detachment of an achene, previously fixed on a stub with nail polish, provided such a detailed record of the intracellular side of the external periclinal walls (Fig. 5h) that it would be convenient to develop a standard method to obtain the same result for further fossil and modern specimens. The SEM analysis of such preparations would be certainly useful to gather more abundant information on the original morphology of the silicified parts, even when they vanished during fossilization, with obvious advantages for phylogenetic analyses.

Given the complicate situation, where there is a mix of validly described names, whose types cannot be discerned as distinct, and different levels of taxonomic certainty, we strongly suggest to refer to the achenes studied here as *C. paucifloroides* sp. inc. (based on nomenclatural priority), to avoid confusion. We are aware that from the Miocene to the Pleistocene we are probably talking about different species. In the hopeful event that more data will be available in the future, perhaps the proper use of the names *C. pauciflori-formis* or *C. klarae* could be recovered.

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Author contributions Author Contributions Statement - E.M. and P.J.M. designed the study and wrote the paper with input from all authors. E.H. analyzed most of the materials and elaborated the results in collaboration with E.M.; P.J.M. compared the systematic relationships of extant taxa and with fossil ones; A.V.H. managed all the data and results on the material stored in Russia, obtained information from Russian literature and provided critical input about that in the text; S.K. analyzed the data and revised the results concerning his area of competence.

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Data availability All data generated or analyzed during this study are included in this published article.

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval The authors declare the compliance of ethical standards. All authors consent with the paper and are aware of its content and organization. The corresponding author is prepared to provide further documents of compliance with ethical standards upon request along the editorial process.

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