

MAGDALENA SZCZEPANIK-JANYSZEK, MAŁGORZATA KLIMKO

**APPLICATION OF ANATOMICAL METHODS
IN THE TAXONOMY OF SEDGES (*CAREX* L.)
FROM THE SECTION *MUEHLENBERGIANAE*
(L.H. BAILEY) KÜK. OCCURRING IN POLAND**

*From Department of Botany
Augusta Cieszkowski Agricultural University of Poznań*

ABSTRACT. This paper presents the results of the research on the anatomical structure of the stems and leaves and on the sculpture of the nuts of the sedges from section *Muehlenbergianae* (L.H. Bailey) Kük. The results show, that the anatomical structure of the vegetative organs cannot be an effective criterion of a taxonomical division. The most important interspecific differences occur among shapes and size of the exocarp cells, and among the presence or absence of the silica bodies on the surfaces of the cells. The greatest variation in the features listed above is observed in *Carex divulsa* Stokes subsp. *leersii* (Kneucker) W. Koch.

Key words: sedges, *Carex*, anatomy, utricle, nut, exocarp

Introduction

In terms of taxonomy the section *Muehlenbergianae* (L.H. Bailey) Kük. is one of the most controversial groups within the genus *Carex* L. It has stirred up emotions since the mid 18th century, i.e. since the description of *C. muricata* L. by Linnaeus, followed by the separation of *C. spicata* Huds. by Hudson. For more than two centuries no universal, unchanging key or taxonomic classification has been created. In addition, different authors (see e.g. **Hallier** 1881, **Ascherson** and **Graebner** 1902, **Krechetovich** 1935, **Garcke** 1972) give mutually exclusive or even contradictory morphological descriptions of some taxa of this section, or have different opinions on relationships between the taxa. For example, *C. pairaei* F.W. Schultz is treated as a separate species (**Szafer et al.** 1986) or as a form of *C. divulsa* Stokes (**Hallier** 1881), or as a subspecies of *C. muricata* L. (**Ascherson** and **Graebner** 1902), although it is common knowledge that *C. muricata* L. differs

significantly in many aspects from *C. divulsa* Stokes. Equally ambiguous is the systematic position of the other taxa of this section. In this study the taxonomic classification found in "Flora Europaea" (Chater 1980) was adopted. Consequently, the section *Muehlenbergiana* (L.H. Bailey) Kük. is assumed to include the following species and subspecies:

- *Carex spicata* Huds. (= *C. contigua* Hoppe),
- *Carex muricata* L. with two subspecies: *C. muricata* L. subsp. *muricata* (= *C. pairaei* subsp. *borealis* Hyl.), and *C. muricata* subsp. *lamprocarpa* Čelak. (= *C. pairaei* F.W. Schultz = *C. cuprina* auct. non Nendtvich ex A. Kerner),
- *Carex divulsa* Stokes with subspecies: *C. divulsa* Stokes subsp. *divulsa* and *C. divulsa* subsp. *leersii* (Kneucker) W. Koch. (= *C. pairaei* var. *leersii* (Kneucker) Kük.).

The adopted classification is one of many divisions applied by botanists. The situation is even more complicated when synonyms of those names are used and their diagnoses are analysed. In most classifications *C. muricata* L. subsp. *lamprocarpa* Čelak. is regarded as an equivalent of *C. pairaei* F.W. Schultz, whereas *C. divulsa* Stokes subsp. *leersii* (Kneucker) W. Koch as an equivalent of *C. pairaei* var. *leersii* (Kneucker) Kük. This means that one of those taxa is a species described by Schultz, and the other is its subspecies described by Kneucker. Another taxon, namely *C. pairaei* F.W. Schultz subsp. *borealis* Hyl. distinguished by Hylander, is equivalent to *C. muricata* L. subsp. *muricata* (Chater 1980). This means that similarities and differences between these doubtful taxa were noticed already when they were being described as *C. pairaei* F.W. Schultz and its subspecies. In such a situation, it is questionable to distinguish *C. divulsa* Stokes subsp. *leersii* (Kneucker) W. Koch as a subspecies within *C. divulsa* Stokes. Revision of herbarium materials from a number of institutions showed that specimens identified as *C. pairaei* F.W. Schultz or as *C. muricata* L. had features listed in Chater (1980) as characteristic for three taxa: *C. muricata* L. subsp. *muricata*, *C. muricata* L. subsp. *lamprocarpa* Čelak. and *C. divulsa* Stokes subsp. *leersii* (Kneucker) W. Koch. It is also controversial to distinguish *C. leersii* F.W. Schultz as a separate species, very similar to *C. muricata* L. (analysis of diagnoses), and not to *C. divulsa* Stokes (see Ascherson and Graebner 1902).

All species of the section *Muehlenbergiana* (L.H. Bailey) Kük. are very similar to each other, have many morphological features in common, grow in similar habitats, frequently in the same plant communities, and have similar ecological requirements.

Systematics and geography of those species of the *Muehlenbergiana* (L.H. Bailey) Kük. which are native to Poland were studied by Szczepanik-Janyszek (1999). Although a large number (over 30) of morphological features were analysed on the basis of a large amount of material collected all over Poland, the relationships between those taxa were not clarified. Modern statistical methods did not permit to identify any crucial feature that could form a basis of classification. All these species can be distinguished only basing on a complex of features.

Thus, morphological features are not a clear criterion delimiting the individual taxa within the section. In agreement with the suggestions of many researchers, anatomical features have been taken into account, as they are relatively constant and are not as strongly modified as morphological characters. Nevertheless, even they can be variable to some extent within a genus. In this study an attempt was made to see if these features are variable within a much narrower taxonomic category, namely a section. Therefore, the major aim of this work was to compare and analyse similarities and differences in the anatomical structure of selected elements of vegetative and generative organs of individual taxa. It must

be noted that no studies of the anatomical structure of species belonging to the section *Muehlenbergianae* (L.H. Bailey) Kük. had been conducted before.

Material and methods

Herbarium specimens from north and south Poland were used in this study (Fig. 1). The morphological-anatomical analysis involved vegetative and generative organs of mature plants: leaves, stems and fruits. Cross-sections of central parts of all these elements were made.

Semipermanent preparations of leaf and stem sections were observed and documented using the light microscope. Generative organs (30-50 nuts of each taxon) were removed from utricles and observed under the scanning electron microscope.

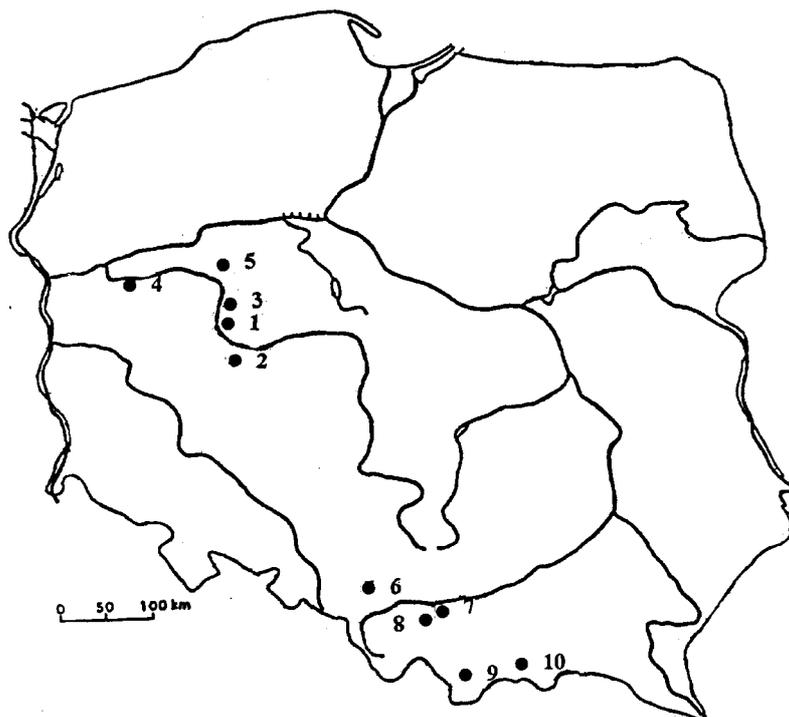


Fig. 1. Localities of samples

Ryc. 1. Stanowiska prób pobranych do badań

1 – Poznań, 2 – Kościan, 3 – Murowana Goślina, 4 – Międzychód, 5 – Chodzież, 6 – Katowice,
7 – Kraków, 8 – Skawina, 9 – Nowy Targ, 10 – Nowy Sącz

The following characters of leaves were recorded:

- number and shape of hinge cells,
- presence and number of silica bodies on the upper epidermis,
- size proportions between cells of the lower and the upper epidermis,
- keel shape.

In stems the following features were analysed:

- shape of stem cross-section,
- number of layers of chlorenchyma,
- number of layers in the sclerenchyma ring under vascular bundles.

In the case of fruits, the investigations focused on their sculpture, as this feature is constant within a taxon in the case of many members of the *Cyperaceae*. Values of the analysed features of individual taxa are presented in tables using the binary system.

Results

Leaves

No significant differences in the morphological structure of leaves were observed among species of the studied section. Most conspicuous were the differences in the width of the middle part of the leaf blade. *C. spicata* Huds. had the widest leaves, particularly in habitats typical for this species, like sunny meadows, lawns, etc. The narrowest leaves were recorded in *C. divulsa* Stokes subsp. *divulsa*. In some cases, however, individuals growing in habitats which are not typical for this species (e.g. in sunny spots or sometimes in mountains of south Europe), had leaves up to twice as wide as those usually observed in *C. spicata* Huds. For the other taxa of this group, i.e. *C. muricata* L. subsp. *muricata*, *C. muricata* L. subsp. *lamprocarpa* Čelak. and *C. divulsa* Stokes subsp. *leersii* (Kneucker) W. Koch, no significant differences could be noticed and their numerical values overlapped. It must be noted that all these three taxa occur in the same types of habitat and are the most similar morphologically among the *Muehlenbergianae* (L.H. Bailey) Kük.

Other morphological characteristics of the leaf, namely leaf length and the ratio of leaf length to the height of fully developed flowering stems, as well as the colour of vegetative organs, seem to be related more to the type of habitat than to a given taxon. In fact, the morphological similarity is so great that it is impossible to identify these species faultlessly in the vegetative phase. Although ligule shape is regarded as a diagnostic feature by some authors (Rothmaler 1984, Dostal 1989, Rutkowski 1998), this seems to be unjustified as this feature is not useful in practice in our opinion. Listing of this feature in many publications is probably due to duplication of an idea of some earlier researchers (e.g. Ascherson and Graebner 1902) rather than a thoughtful action.

Leaves of sedges, like leaves of most members of the family *Cyperaceae*, are characterized by a specific structure (Fig. 2). They are bilateral and V-shaped in cross-section. They have one row of vascular bundles surrounded by sheaths composed of two layers: the inner sclerenchyma layer and the outer parenchyma layer. In the keel of the leaf, on the upper side hinge cells are located. Air spaces may be present between vascular bundles. Epidermal cells on the upper side of the leaf are larger than cells on bottom. Stomata are

located on the adaxial surface; guard cells and subsidiary cells lie even with the surface of the epidermis. Epidermal cells do not form any trichomes; they are rectangular, slightly elongated, and on the edge of the leaf they have one or several silica bodies. Parenchyma is not differentiated: palisade mesophyll and hypodermis are missing (Metcalf 1969, Standley 1990).

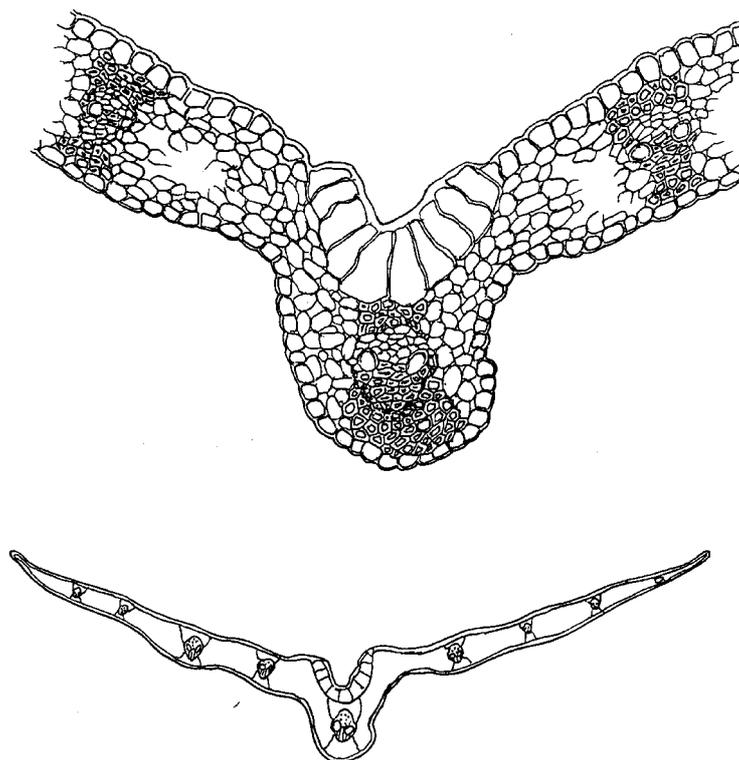


Fig. 2. Anatomical structure of the leaves of *Carex* L. from section *Muehlenbergianae* (L.H. Bailey) Kük.

Ryc. 2. Budowa anatomiczna liści turzyc z sekcji *Muehlenbergianae* (L.H. Bailey) Kük.

On the basis of the analysed material four anatomical features of leaves were distinguished and evaluated in all the studied taxa (Tab. 1). Results of the analysis of leaf sections showed that there are some differences in the anatomical structure between the taxa. However, this does not apply to all the analysed features. Their relationships within the analysed section were as follows.

Number and shape of hinge cells. In members of all the taxa a similar number of hinge cells was recorded: 9 in *C. spicata* Huds., 6 or 8 in *C. muricata* L. subsp. *muricata*, 7, 9 or 10 in *C. muricata* L. subsp. *lamprocarpa* Čelak., 6 or 9 in *C. divulsa* Stokes subsp. *divulsa*, and 5, 6 or 7 in *C. divulsa* Stokes subsp. *leersii* (Kneucker) W. Koch. Thus, this is not an invariable feature, linked with any of the taxa. Also shapes of those cells in all the taxa were generally the same.

Table 1
Comparison of the selected anatomical features of stems of sedges from the section *Muehlenbergianae* (L.H. Bailey) Kük.

Porównanie analizowanych cech anatomicznych liści turzyc z sekcji *Muehlenbergianae* (L.H. Bailey) Kük.

Feature Cecha	<i>C. spicata</i> Huds.	<i>C. muricata</i> L. subsp. <i>muricata</i>	<i>C. muricata</i> L. subsp. <i>lampro-</i> <i>carpa</i> Čelak.	<i>C. divulsa</i> Stokes subsp. <i>divulsa</i>	<i>C. divulsa</i> Stokes subsp. <i>leersii</i> (Kneucker) W. Koch
Number of hinge cells Liczba komórek zawiasowych	9	6, 8	7, 9, 10	6, 9	5, 6, 7
Silica bodies on upper epidermis Ciałka krzemionkowe na górnej epi- dermie	1	1	1	1	1
Cells of upper epidermis 2.5 times larger than cells of lower epidermis Komórki górnej epidermy 2,5 raza większe od komórek dolnej epidermy	0	0	0	1	0
Cells of upper epidermis 3 times larger than cells of lower epidermis Komórki górnej epidermy 3 razy większe od komórek dolnej epidermy	1	1	1	0	0
Cells of upper epidermis 4 times lar- ger than cells of lower epidermis Komórki górnej epidermy 4 razy większe od komórek dolnej epidermy	0	0	0	0	1
Keel triangular Kil trójkątny	1	0	0	0	1
Keel triangular, narrowed at apex Kil trójkątny zwężony na szczycie	0	1	0	0	0
Keel rounded Kil zaokrąglony	1	0	1	1	0

Presence and number of silica bodies on the upper epidermis. Within the analysed group no significant differences in the number and shape of silica bodies were observed, although this feature is very characteristic for many species of the family *Cyperaceae*.

Size proportions between cells of the lower and the upper epidermis. In all the studied species cells of the upper epidermis are larger than cells of the lower epidermis. Differences concern only the proportions between them: in *C. divulsa* Stokes subsp. *divulsa* the former are 2.5 times larger than the latter, in *C. spicata* Huds. and both subspecies of *C. muricata* L. the former are 3 times larger than the latter, whereas in *C. divulsa* Stokes subsp. *leersii* (Kneucker) W. Koch. the former were 4 times larger than the latter.

Keel shape. Among the studied taxa three types of keel shape may be distinguished: decidedly triangular in *C. divulsa* Stokes subsp. *leersii* (Kneucker) W. Koch, triangular but narrowed at apex in *C. muricata* L. subsp. *muricata*, and clearly rounded in *C. muricata* L. subsp. *lamprocarpa* Čelak. and *C. divulsa* Stokes subsp. *divulsa*. In *C. spicata* Huds. two types of shapes occurred: decidedly triangular and rounded.

Stems

The morphological structure of stems of all sedge species is generally the same: they are always triangular in cross-section. Differences are concerned only with stem angles, which may be rounded, with convex faces (e.g. *C. lasiocarpa* Ehrh.); or sharp, with concave faces (sometimes even winged at angles: e.g. *C. vulpina* L. or *C. nemorosa* Reben.); or may form the classic acute angle, with plane faces (e.g. members of the section *Muehlenbergianae* (L.H. Bailey) Kük.). Another feature is roughness of the whole stem or only below the inflorescence, or the stem may be smooth all over. This feature, however, is not constant within a given taxon. The other morphological features, e.g. stem height, are closely related to the site where the plant grows.

The anatomical structure of sedge stems is also generally similar (Fig. 3). Stem surface is covered in epidermis composed of one layer of cells whose walls are slightly thickened and incrustated with silica. The underlying chlorenchyma is interspersed with sclerenchyma cells forming bridges. Sclerenchyma surrounds closed collateral bundles. The centre of the stem is filled with ground parenchyma containing vascular bundles. The number of vascular bundles is usually constant within each taxon, although considerable variation is observed in many species, and sometimes even within one individual. In some species there is one larger or several smaller air channels inside the stem.

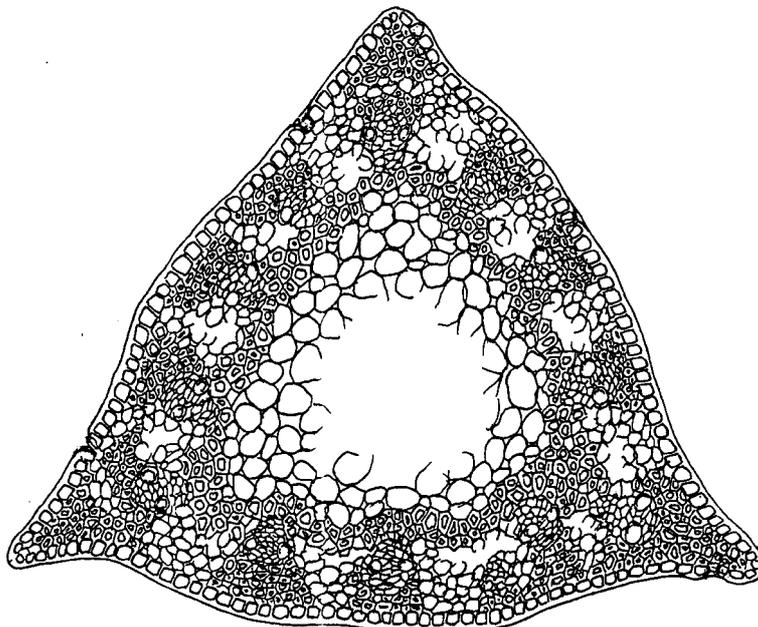


Fig. 3. Anatomical structure of the stems of *Carex* L. from section *Muehlenbergianae* (L.H. Bailey) Kük.

Ryc. 3. Budowa anatomiczna łodyg turzyc z sekcji *Muehlenbergianae* (L.H. Bailey) Kük.

In this study it was determined if there are any significant differences in the anatomical structure of this organ (Tab. 2) reflecting the taxonomic classification of the studied group. Relationships of the analysed anatomical features were as follows.

Table 2

Comparison of the selected anatomical features of stems of sedges from the section *Muehlenbergianae* (L.H. Bailey) Kük.

Porównanie analizowanych cech anatomicznych łodyg turzyc z sekcji *Muehlenbergianae* (L.H. Bailey) Kük.

Feature Cecha	<i>C. spicata</i> Huds.	<i>C. muricata</i> L. subsp. <i>muricata</i>	<i>C. muricata</i> L. subsp. <i>lampro-</i> <i>carpa</i> Čelak.	<i>C. divulsa</i> Stokes subsp. <i>divulsa</i>	<i>C. divulsa</i> Stokes subsp. <i>leersii</i> (Kneucker) W. Koch
Stem angles sharp Krawędzie łodyg ostre	0	0	1	0	0
Stem angles blunt Krawędzie łodyg łagodnie trój- kątne	1	0	0	0	1
Stem angles broadly rounded Krawędzie łodyg zaokrąglone	0	1	0	1	1
Chlorenchyma composed of 1-3 layers Miękkisz 1-3-warstwowy	1	1	1	1	0
Chlorenchyma composed of 2 layers Miękkisz 2-warstwowy	0	1	0	1	1
Sclerenchyma ring under bund- les composed of 3 layers Pierścień sklerenchyny pod wią- zkami 3-warstwowy	0	0	1	0	0
Sclerenchyma ring under bund- les composed of 1 layer Pierścień sklerenchyny pod wią- zkami 1-warstwowy	1	1	0	1	1

Shape of stem cross-section. It is triquetrous (with sharp angles) in *C. muricata* L. subsp. *lamprocarpa* Čelak., trigonal (with blunt angles) in *C. spicata* Huds. and *C. divulsa* Stokes subsp. *leersii* (Kneucker) W. Koch, and nearly terete (with broadly rounded angles) in *C. muricata* L. subsp. *muricata* and *C. divulsa* Stokes subsp. *divulsa*.

Chlorenchyma. In *C. spicata* Huds. and *C. muricata* L. subsp. *lamprocarpa* Čelak. it is composed of one-three layers, whereas in the other three taxa it consists of two layers.

Sclerenchyma ring under vascular bundles. This feature permits to divide the analysed group into two subgroups: the ring is composed of three layers in *C. muricata* L. subsp. *lamprocarpa* Čelak., whereas in the others it consists of one layer.

Fruits

Utricle shape is a characteristic morphological feature, relatively constant within the section. It is markedly different and distinct in two taxa: *C. spicata* Huds. and *C. divulsa*

Stokes subsp. *divulsa*. The other three taxa are sometimes very similar as regards this feature. Thus, those taxa are virtually impossible to distinguish on the basis of morphology. This is additionally complicated by the fact that they frequently grow in the same type of habitat, sometimes literally next to one another. It seems that one of those taxa is described from one extreme of variation, the second from the other extreme, while the third one represents the middle values of one and the same species. These observations complement the discussion of the morphological similarity of leaves and stems within the studied section, suggesting the actual taxonomic classification, and – in our opinion – they form a logical whole with the above analysis of synonyms.

No significant differences in the shape of epidermal cells between the adaxial and abaxial surfaces of utricles were recorded within this section. Results of this study confirm those reported by **Berggren** (1983), who in addition analysed nut sculpture.

The morphological structure of fruits of sedges is quite uniform. They are nuts enclosed in utricles. In some species the nuts are partly (*C. spicata* Huds.) or completely (*C. paradoxa* Willd.) surrounded by an additional tissue of unexplained significance. In nut cross-section one can see the exocarp and the underlying tiers of parenchyma cells surrounding the nutritive tissue enclosing the embryo.

It seems that nut sculpture is a feature allowing to distinguish between the individual taxa. Five types of nut sculpture were recorded among the analysed species. In *C. spicata* Huds. the cells of nut surface are rectangular or polygonal, convex, each with a central cone-shaped silica body on its rounded apex. *C. muricata* L. subsp. *muricata* has pentagonal (or rarely tetragonal) cells, convex, pointed at apex, each with one silica body. *C. muricata* L. subsp. *lamprocarpa* Čelak. also has pentagonal cells on nut surface but they are somewhat concave and lack silica bodies. In *C. divulsa* Stokes subsp. *divulsa* they are convex but not rounded, and only slightly sharp on sides, whereas in *C. muricata* L. subsp. *leersii* (Kneucker) W. Koch two distinct kinds of cell shapes were noticed. More numerous, particularly along the edges of the nut, are concave cells, each with a silica cone located near the radial wall. Cells of the second kind are found on the central part of the nut. They are tetragonal, pentagonal or hexagonal, isodiametric and elongated, convex, lacking silica bodies (Fig. 4). Thus, the greatest variation in cell shape and silica bodies is observed in *C. divulsa* Stokes subsp. *leersii* (Kneucker) W. Koch.

Summary and conclusions

On the basis of the presented study it was found that the analysed anatomical features of stems and leaves are not good diagnostic criteria in the studied group. Only the analysis of nut sculpture allowed for identification of differences between the described taxa. This applies mostly to the shape and size of cells of the exocarp as well as to the presence and location of silica bodies. Five types of exocarp structure were distinguished, each representing one taxon.

This work was an attempt to verify the usefulness of particular anatomical features for creation of taxonomic classifications and as supplements to morphological features. Combination of these two types of features seems to be the best solution explaining the actual relationships between the studied taxa.

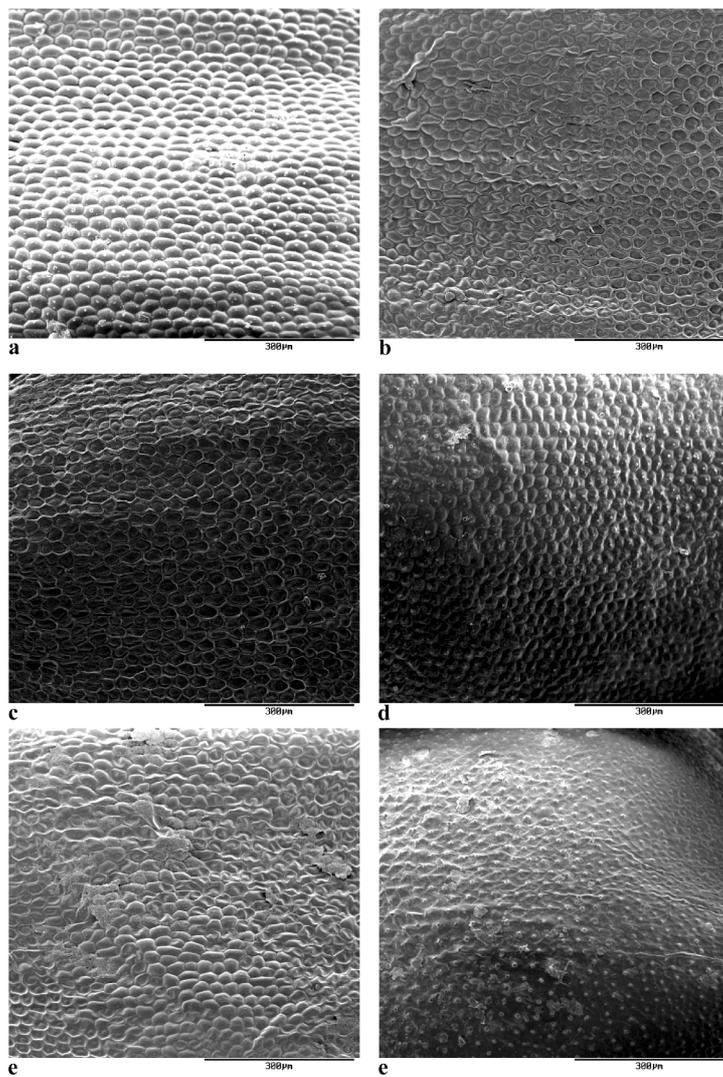


Fig. 4. Sculpture of the nuts of *Carex* L. from section *Muehlenbergianae* (L.H. Bailey) Kük.

Ryc. 4. Powierzchnia egzokarpu orzeszków poszczególnych taksonów turzyc z sekcji *Muehlenbergianae* (L.H. Bailey) Kük.

a – *C. spicata* Huds., b – *C. muricata* L. subsp. *muricata*, c – *C. muricata* L. subsp. *lamprocarpa* Čelak., d – *C. divulsa* Stokes subsp. *divulsa*, e – *C. divulsa* Stokes subsp. *leersii* (Kneucker) W. Koch

This study aimed to determine what anatomical differences between the taxa exist, and to find out if they may form a basis for taxonomic classification within the section *Muehlenbergianae* (L.H. Bailey) Kük. Moreover, this analysis brought the frequently neglected anatomical features to attention as additional, important criteria of identification.

A detailed and unambiguous identification of criteria and features that could be determinants of such a classification requires further research based on materials coming not only from the area of Poland but also from other parts of the geographical range of the studied taxa.

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ZASTOSOWANIE ANATOMICZNYCH METOD W TAKSONOMII TURZYC (*CAREX* L.) Z SEKCJI *MUEHLENBERGIANAE* (L.H. BAILEY) KÜK. WYSTĘPUJĄCYCH W POLSCE

Streszczenie

Praca dotyczy próby zastosowania metod anatomicznych w taksonomii roślin i sprawdzenia przydatności poszczególnych cech budowy wewnętrznej w tworzeniu podziałów systematycznych, a także w uzupełnianiu nimi opisów morfologicznych.

Dotychczasowe badania prowadzone w obrębie sekcji *Muehlenbergianae* (L.H. Bailey) Kük., oparte na znacznej liczbie cech morfologicznych, nie dały jednoznacznych rozstrzygnięć w kwestii relacji zachodzących pomiędzy taksonami tej grupy. Badania były prowadzone na materiale zielnikowym pochodzącym z Polski północnej i południowej. Szczegółowej analizie zostały poddane cztery cechy dotyczące liści, trzy dotyczące łodygi oraz jedna związana z budową owocu. Na podstawie przeprowadzonych badań okazało się, że w przypadku łodygi i liści cechy anatomiczne nie stanowią zdecydowanego kryterium taksonomicznego. Dopiero analiza skulptury orzeszka pozwoliła na wychwycenie różnic pomiędzy taksonami. Wyróżniono pięć typów egzokarpu, z których każdy reprezentował określony takson. Jednakże dokładne i jednoznaczne określenie kryteriów, na których miałyby się opierać podział taksonomiczny, wymaga dalszych badań na materiale pochodzącym z całego obszaru zasięgu opracowywanych taksonów.