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PHYLOGENETIC ASSAY OF MATURASE *K*, RIBULOSE-BISPHOSPHATE CARBOXYLASE (*rbcL*) SEQUENCES, AND POLLEN STRUCTURE OF REPRESENTATIVES OF THE FAMILY *Amaranthaceae* Juss.

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Amino acid sequences of the *mitochondrial protein maturase K* (*matK*) and the plastid protein *ribulose-bisphosphate carboxylase* (*rbcL*) from different *Amaranthaceae* Juss. species were retrieved from the NCBI (National Center for Biotechnology Information), and used for phylogenetic analysis. A correspondence was found between phylogenetic trees derived from molecular data and those based on palynomorphological data. Clustering patterns in the trees obtained from both protein sequences support the idea of two main pollen types (*Amaranthus*-type and *Gomphrena*-type) as described in 1952 by G. Erdtman. The results also indicate that some species, which according to traditional classification, are from different subfamilies and tribes of *Amaranthaceae* Juss. may in fact be closely related. Thus molecular data support the idea that palynomorphological data can be used in systematic and phylogenetic studies of *Amaranthaceae*.

Key words: bioinformatics, *maturase K*, *ribulose-bisphosphate carboxylase*, phylogeny, *Amaranthaceae*, palynomorphology.

In recent years, biodiversity and conservation have been globally recognized as one of the critical issues facing humanity. In light of this problem, biologists are emphasizing ecological and environmental studies. However, it is not possible to study biological objects without naming and describing them, i.e. without taxonomy and nomenclature, which explores relationships within and between different groups of organisms.

By combining methods used by several different disciplines such as traditional morphology, anatomy, biochemistry, bioinformatics, and molecular biology, a new powerful identification tool has been developed. Using the unique sequences of genes from different organisms it is now possible to identify many organisms and determine their relationships with others. DNA, RNA, and protein sequences also enable us to evaluate classical methods of identification of organisms and to improve them. Existing sequences for taxa of interest obtained from international databases such as the NCBI (National Center for Biotechnology Information) can be compared and evaluated by various bioinformatics programs and tools. Bioinformatics analysis using data from these databases thus provides an inexpensive and powerful method for investigation of DNA polymorphism and its origin.

The flowering plant family Amaranthaceae sensu stricto (s.s.) which corresponds to the classical family *Amaranthaceae* Juss. (69 genera and 772 species [1]) as well as the twice-larger related family *Chenopodiaceae* Ventenat have been subject to repeated taxonomical revisions from the time they were first described (1789 and 1799 respectively [2, 3]) to the present. Recently it has been proposed to combine them into one large family: *Amaranthaceae* sensu lato (s.l.) as a result of molecular analysis [4].

The morphology of pollen grains, which are the male generative (gametophyte) stage of seed plants, is an important source of information for plant systematics. In certain cases, palynological data have been crucial for taxonomic conclusions [5–13]. The often complex structure of the pollen wall varies across taxa and is considered to be a conservative, taxo-

nomically meaningful feature. However, the rate and direction of pollen wall structure evolution is not always parallel to the macroevolution of (sporophyte) seed plants. That is why similar pollen grains might belong to plants from different taxonomical groups, and one taxon might have a variety of pollen grains among its representatives. Before the advent of molecular bioinformatics tools, scientists had to guess which morphological features: palynological or macro-morphological were most reliable. However, molecular data might now serve as arbitrators in such cases.

Both the *Amaranthaceae* and *Chenopodiaceae* have panporate pollen of the *Amaranthus* and *Gomphrena* types [14]. The existence of these two pollen types supports, with certain exceptions, the division of the *Amaranthaceae* into two subfamilies, *Amaranthoideae* and *Gomphrenoidea*e, which were described according to macromorphological data, largely anther structure. However, exceptions in pollen grain structure of some representatives of both subfamilies have lead researchers to conclude that pollen grain data are not useful as a taxonomical feature for these taxa. Within the *Amaranthus*-type pollen there is a small group of pollen grains with an unusual stellate ornamentation of their opercula [15]. Pollen grains of this type also sometimes occur in plants from *Gomphrenoideae*. However, such complex and unique pollen structure does not suggest accidental parallelism in these two subfamilies but rather it is more likely that these groups of plants share an ancestor with genes coding for both of these pollen structures. Additionally, certain genera of *Amaranthoideae* possess *Gomphrena*-type pollen.

Why are both pollen types not spread equally through both subfamilies? We have assumed that the ancestors of genera with both *Gomphrena*-type pollen and pollen with stellate opercula have their common ancestor within *Amaranthoideae*. If so, *Amaranthoideae* should be divided into two parts, and genera with Gomphrena-type pollen as well as genera from the Amaranthoideae with stellate ornamentation of the opercula should be placed into the *Gomphrenoideae*. If true, bioinformatics analysis of molecular sequences would support this conclusion. Such is the aim of our study.

Sequences from various genes and proteins have been successfully used for plant systematics studies. These include sequences of the *mitochondrial protein maturase K* (*matK*, EC-Number 2.7.10.2), the plastid protein *ribulose-bisphosphate carboxylase* (*rbcL*, EC-Number 4.1.1.39), *18S* and *16S small subunit ribosomal RNA*, and the *internal transcribed spacer rRNA* (*ITS*) gene. Since *matK* and *rbcL* sequences from *Amaranthaceae* were the most abundant in GeneBank, they were chosen for our study.

Materials and methods

Specimens and microscopy

Pollen grains of 60 species from 14 *Amaranthaceae* genera (100 samples) were examined using light microscopy (LM), and pollen grains of 120 species from 32 *Amaranthaceae* genera (140 samples) along with 5 species of the genus *Corispermum* (*Chenopodiaceae*) were examined using scanning electron microscopy (SEM). These pollen samples were taken from voucher specimens from the following institutions: M. G. Kholodny Institute of Botany of the National Academy of Sciences of Ukraine, Kiev, Ukraine (KW); V.L. Komarov Botanical Institute of the Russian Academy of Sciences, St. Petersburg, Russia (LE); and the Main Botanical Garden of the Russian Academy of Sciences, Moscow, Russia (MHW). The material for LM and portions of the material for SEM were acetolysed according to the method described by G. Erdtman [16]. For LM, pollen grains were mounted in glycerin jelly. For SEM, pollen grains were placed in a drop of 96% ethyl alcohol, and vacuum-coated with gold. In our study we used a «Biolar» microscope (for LM) and a JEOL JSM-35C microscope (for SEM). Data from literature sources on the pollen wall structure of *Amaranthaceae* were also consulted. Thirty features were used to characterize the evolutionary pattern of pollen types. Pollen wall structure from a total of 213 species from 60 genera was analyzed [17].

Sequence analysis and phylogeny

All available amino acid sequences of *maturase K* (*matK*) and *ribulose-bisphosphate carboxylase* (*rbcL*) from *Amaranthaceae* were obtained from the NCBI database (http://www.ncbi.nlm.nih.gov/Genomes/). Multiple sequence alignment and phylogenetic analysis were performed with the Molecular Evolutionary Genetics Analysis (MEGA version 3.0) program [18]. The data sets for both proteins included a wide range of taxa from Amarathaceae s.l. (both Chenopodiaceae and *Amaranthaceae* s.s.) and in both cases, three outgroup taxa from Caryophyllaceae. The individual taxa in the two data sets were somewhat different for the two proteins because of differences in the availability of sequence data.

Maximum Parsimony analysis resulted in 47 and 70 most parsimonious trees for the *rbcL* and the *matK* data respectively. The robustness of the trees and branch support was estimated by bootstrap analysis. For parsimony searches, we performed 1000 random sequence additions. For calculating bootstrap proportions, we performed 500 replicates with 10 random sequence additions per replicate. Neighbor-joining (NJ) analysis was conducted by calculating Kimura's 2-parameter distance [19].

Results and discussion

Pollen types of Amaranthaceae

Our original palynomorphological data along with additional palynomorphological data from literature sources support Erdman's conclusion [14] of the existence of two clearly recognized pollen grain types (*Amaranthus*- and *Gomphrena*-types) in *Amaranthaceae* s.l. *Amaranthus*-type pollen grains have pore membranes approximately on the same level as the pollen surface (mesoporium), whereas the pores of the Gomphrena-type sink deep into the mesaporium [20]. However, G. Erdtman [14] did not precisely define these two pollen types. For the *Gomphrena*-type we found that the walls between nearest pores never have spinules on the lateral surface and that the upper part of the wall never has the same structure as the lateral side of the wall (fig. 1). Therefore, mesoporial structure is a key feature for determination of pollen types of *Amaranthaceae* .

The majority of *Amaranthaceae* s.l. taxa have *Amaranthus*-type pollen. We examined pollen grain structure in groups of the family which are thought to retain many ancestral characteristics, in order to indicate the most conservative features. These conserved features of *Amaranthus*-type pollen appeared to be some structures of spinules, perforations, the size and number of pores, and the shape of mesoporium; these features appear to be evolutionarily significant for the family *Amaranthaceae* s.l. Pollen grains of *Amaranthus*-type with pore opercula or those of *Gomphrena*-type, belong to evolutionary advanced taxa within *Amaranthaceae* .

We developed a list of all evolutionary significant pollen features belonging to both types of pollen grains. The result was a classification of pollen into 19 groups. Pollen group 1 shows the most ancestral pollen structural features, while the last groups (19a-d, table) are the most derived. Pollen group 16–18 represents the previously-discussed *Amaranthus* type with stellate ornamentation of the operculа and groups 19b-d represent *Gomphrena*-type pollen.

The distribution these of pollen types across *Amaranthaceae* s.l. taxa was not uniform. Only group 1–6 pollen occurred in the Chenopodiaceae taxa examined in this study. Groups 1–6 were also observed in *Amaranthaceae* s.s. tribe Celosieae and tribe Amarantheae subtribe Amaranthinae; a wide range of pollen groups occurred in the Amarantheae subtribe Aervinae—including the *Gomphrena* type 19b; and many Gomphrenoideae had one of the type 19 variants (table).

Traditional classifications of *Amaranthaceae* Juss. according to Townsend [1]. The colors correspond to colors in fig. 2. Pollen groups are indicated by numerals in parentheses

Subfamily Amaranthoideae
Tribe Celosieae
Deeringia (6), *Pleuropetalum* (4,6), *Celosia* (1), *Hermbstaedtia* (2).
Tribe Amarantheae
Subtribe Amaranthinae
Bosea (*Amarathus*-type), *Chamissoa* (1), *Herbstia* (5), *Allmania* (3), *Charpentiera* (6), *Indobanalia* (*Amarathus*-type), *Lagresia* (2), *Amaranthus* (2,3), *Digera* (2).
Subtribe Aervinae
Saltia (13), *Sericostachys* (12), *Sericocomopsis* (4, 7), *Sericocoma* (3,18), *Kyphocarpa* (19b), *Centemopsis* (17), *Nelsia* (3), *Sericorema* (8), *Centema* (10), *Eriostylos* (15), *Cyathula* (3,4), *Pupalia* (16), *Marcelliopsis* (3), *Dasysphaera* (15), *Volkensinia* (6), *Arthraerua* (4), *Aerva* (10,18), *Trichuriella* (18), *Nothosaerva* (18), *Nototrichium* (3), *Omegandra* (18), *Calicorema* (3), *Chionothrix* (6), *Stilbanthus* (7), *Mechowia* (15, 17), *Nyssanthes* (3), *Ptilotus* (1, 2, 3, 4, 7, 8, 9, 11, 13, 14), *Psilotrichum* (2, 4, 13, 15, 18), *Psilotrichopsis* (19b), *Achyranthes* (3), *Centrostachys* (*Amaranthus*-type), *Achyropsis* (3, 4), *Pandiaka* (12)
Subfamily Gomphrenoideae
Tribe Pseudoplantageae
Pseudoplantago (19a).
Tribe Gomphreneae
Subtribe Froelichiinae
Guilleminea (19b), *Tidestromia* (19b,19d), *Froelichia* (19c), *Froelichiella* (19c), *Pfaffia* (13,19b,19d), *Alternanthera* (19d).
Subtribe Gomphreninae
Woechleria (2), *Gomphrena* (19b), *Pseudogomphrena* (19b), *Iresine* (6, 12, 13, 19b, 19d), *Irenella* (10), *Blutaporon* (19b), *Lithophilla* (19b).

Geographical distribution of taxa of the Amaranthaceae s.s.

Almost all the *Amaranthaceae* s.s. genera with *Gomphrena*-type pollen derive from Central and South America and the Galapagos Islands. Exceptions are few: The genus *Kyphocarpa* (Fenzl) Lopr. is found in Asia and *Psilotrichopsis* C. Townsend occurs in Africa, as does one species of *Sericocoma* Fenzl. By contrast, most genera with *Amaranthus*-type pollen grains are found either entirely or largely in Africa with the exceptions of the genus *Irenella* Suesseng from the Americas, a small number of Asian genera (*Allmania* R. Br., *Saltia* R. Br., *Stilbanthus* Hook. f., *Psilotrichopsis* C. Townsend), and the Australian genera *Nothosaerva* Wight, *Omegandra* C. Townsend, and *Ptilotus* R. Br. The American genera *Pfaffia* and *Iresine* have both *Amaranthus* and *Gomphrena* pollen types.

Genera with *Amaranthus*-type pollen grains with stellate pore ornamentation or variants approximating it (pollen groups 15–18, table), are largely from Africa or from the Old World tropics with exception of the Australian *Omegandra*. Pollen grains of the South American genus *Pseudoplantago* Suesseng. not only have a stellate operculum but also an atypical cuboidal shape.

Discussion of the palynological data

Exceptions exist between the distribution of taxa observed on the basis of different pollen groups (including the evolutionarily 'advanced' pollen groups (12–19 in table) and the arrangement of taxa according to the classical systematics of *Amaranthaceae*. Significantly, these exceptions often correspond to the exceptions in geographical distributions discussed above. This suggests that some of these groups derived from a common ancestor which had genes with the potential to code for several pollen types. That is why, despite differences in pollen structures, certain taxa with different pollen types should still be grouped together.

The unique structure of pollen grains of some genera may, we believe, represent side branches of the evolutionary tree. For example, the genus *Pseudoplantago* (*Gomphrena* pollen type, group 19a) and the genus *Herbstia* Sohmer (*Amaranthus* pollen type with unusually large mesoporial perforations, group 12) might represent a high level of specialization. On the other hand, the group 19d pollen structure of the American genus *Tidestromia* Standley has pollen walls that are triangular in cross-section (unusual for *Gomphrena*-type pollen) — a feature also found for pollen of some Chenopodiaceae [21]. This group may represent an early evolutionary branch within *Amaranthaceae* s.l. that developed separately from the main group of taxa with Gomphrenoid pollen grains.

Phylogenetic analysis

To provide a comparison with the pollen morphology of *Amaranthaceae* s.s., we used phylogenetic analysis of both *matK* and *rbcL* amino acid sequences (fig. 1). These proteins had been previously successful for determination of phylogenetic relationships among taxa of other angiosperm plants [22, 23, 24]. For both proteins, the trees we obtained by the NJ method were very similar to the trees obtained with the MP method. We display the MP consensus trees in fig. 2 (left 'A' = *matK*, right 'C' = *rbcL*).

Analyses of amino acid sequences for both the *matK* and *rbcL* proteins indicate that for *Amaranthaceae* s.l., species of *Chenopodiaceae* and *Amaranthaceae* s.s. were relatively distantly related. Among *Amaranthaceae* s.s., the Celosieae tribe and the Amaranthinae subtribe of tribe Amarantheae were related. Several taxa from the Amarantheae subtribe Aervinae including *Aerva, Centemopsis, Kyphocarpa, Mechowia, Nothosaerva, Omegandra, Psilotrichopsis, Psilotrichum, Pupalia, Sericocoma,* and *Trichuriella*, together with those of the subfamily *Gomphrenoideae* occurred as a separate, phylogenetically distinct group characterized largely by pollen types 12–19 (fig. 2).

Both of the dendrograms derived from the protein sequences of *matK* and *rbcL*, largely correspond with the palynomorphological types and subtypes of the *Amaranthaceae* s.s. (fig. 2). This indicates that palynomorphological data might be useful for determination of relationships between certain taxa of *Amaranthaceae* s.s. Dendrograms from some recent publication [22, 24] are confounded by data from the *Chenopodiaceae*, *Caryophyllaceae* and some other taxa and do not reflect clearly the situation with relationships among the highly specialized taxa of *Amaranthaceae* s.s. We do not agree with K. Muller and T. Borsh [25] about multiple origins of the stellate pore ornamentation. According to our phylogenetic reconstruction, the subfamily Gomphrenoideae along with the some members of subtribe Aervinae of the tribe *Amarantheae*, subfamily *Amaranthoideae* share a common ancestor and form a distinct

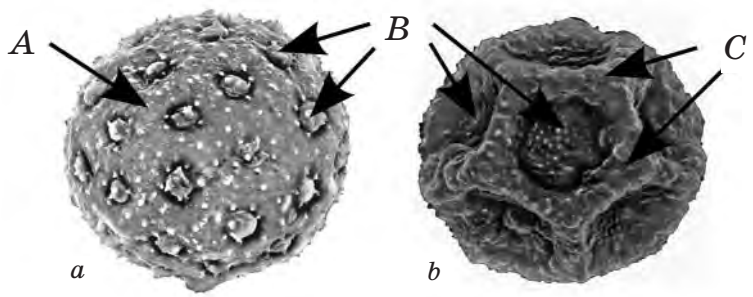

Fig. 1. **Pollen grains of (*a*) *Amaranthus cruentus* L. (*Amaranthus* pollen type) and (*b*) *Alternanthera sessilis* R.Br. (*Gomphrena* pollen type) under the scanning electron microscope:**
A — mesoporium, *B* — pores, *C* — walls of luminas

clade. These taxa have clear differences from other taxa of *Amaranthaceae* according to both palynological and molecular data. Neither palynological nor molecular data support the traditional division of the tribe Gomphreneae into the two subtribes: Froelichiinae and Gomphreinae.

The occasional appearance of different types of pollen grains in the same taxonomic group may be explained by the presence of the genetic information for several pollen types in the genome; different patterns of expression of these genes may make the pollen grains of closely related taxa different.

Bioinformatics data can thus serve as a useful tool and a source of new information to both complement and evaluate morphological methods and as an aid to identifying those 'traditional' morphological features that are taxonomically significant.

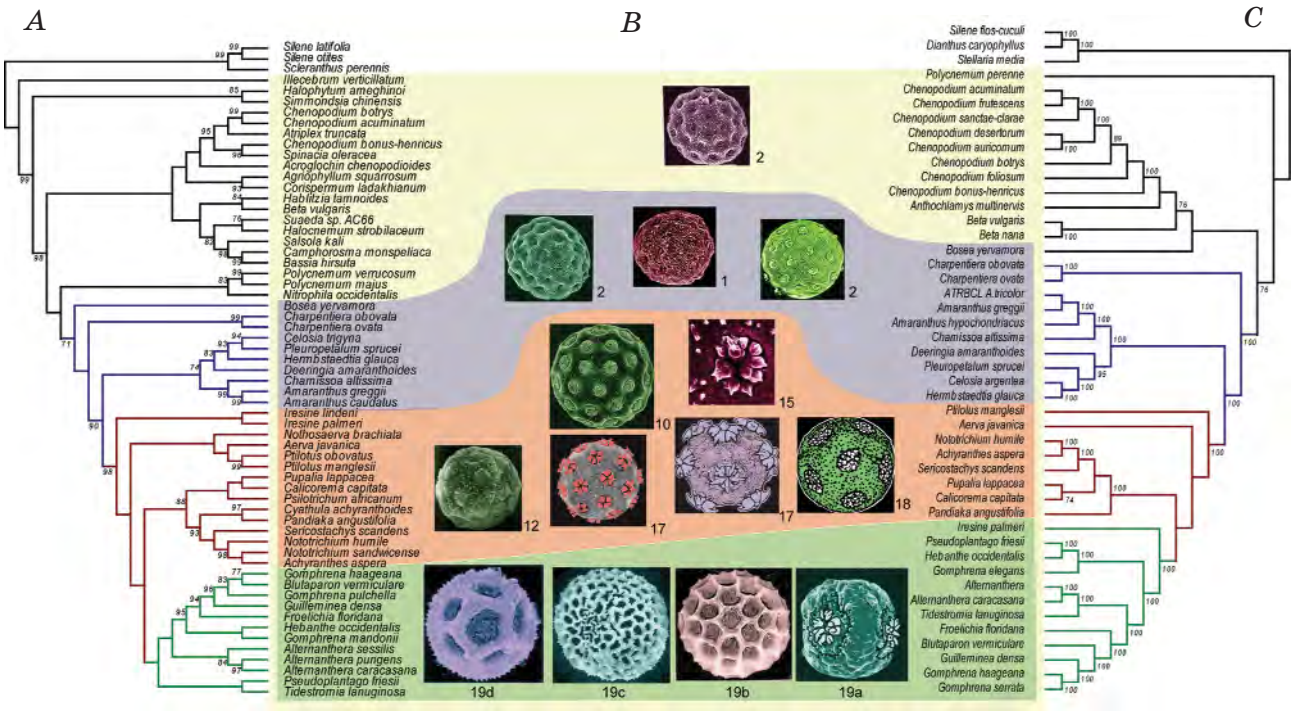

Fig. 2. **Comparison of pollen morphological data with phylogenetic trees for *matK* and *rbcL* sequences in *Amaranthaceae* s.l. and outgroups (*Caryophyllaceae*):**

(*A*) Maximum Parsimony tree of *matK* amino acid sequence, 61 species;

(*C*) Maximum Parsimony tree of *rbcL* amino acid sequence, 46 species. Bootstrap values are shown for each branch if higher than 70% based on 1000 replicates;

(*B*) Electron micrographs and pictures of representative pollen groups (full list of pollen groups given here) from different traditional taxa.

(*Chenopodiaceae* s.s. — yellow, pollen types 1–6; ancestral *Amaranthaceae* s.s. — blue, pollen groups 1–6; derived *Amaranthaceae* s.s. — 2-locular anthers — red, pollen groups 1–18, 19b; derived *Amaranthaceae* s.s., 4-locular anthers — green, pollen groups 2, 6, 10, 12, 13, and 19a-d)

Thus palynological data as well as *matK* and *rbcL* sequences show that certain taxa traditionally part of Amaranthoideae, including at least *Aerva, Centemopsis, Kyphocarpa, Mechowia, Nothosaerva, Omegandra, Psilotrichopsis, Psilotrichum, Pupalia, Sericocoma,* and *Trichuriella*, should be placed in *Gomphrenoideae*. As revised, Gomphrenoideae would then form a monophyletic clade originating from within a paraphyletic Amaranthoideae.

Using pollen grain structure for phylogenetic reconstructions of angiosperm plants is possible especially in groups like the *Amaranthaceae* where pollen type differences correspond well to geographical and molecular data.

Analysis of existing published molecular sequences may provide a powerful, economical compliment or alternative to molecular data obtained by original research.

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ФІЛОГЕНЕТИЧНИЙ АНАЛІЗ СІКВЕНСІВ МАТУРАЗИ *K*, РИБУЛОЗО-1,5-ДИФОСФАТКАРБОКСИЛАЗИ (RBCL) ТА СТРУКТУРИ ПИЛКУ ПРЕДСТАВНИКІВ РОДИНИ *AMARANTHACEAE* JUSS.

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Дані про сіквенси (послідовності) протеїну матурази *K* (*matK*) та рибулозо-1,5-дифосфаткарбоксилази (*rbcL*) із різних видів рослин, які належать до родини *Amaranthaceae* s.l., було отримано з бази даних GenBank (NCBI) та використано для побудови філогенетичних дерев (дендрограм). Результати підтвердили правильність зроблених раніше за даними паліноморфології висновків щодо близької спорідненості видів, які розташовані в класичній системі родини *Amaranthaceae* Juss. у різних підродинах та трибах. Такі висновки дозволяють більш гнучко й точно застосовувати дані паліноморфології в систематиці покритонасінних рослин.

Ключові слова: біоінформатика, матураза *K*, рибулозо-1,5-дифосфаткарбоксилаза, філогенія, *Amaranthaceae*, паліноморфологія.

ФИЛОГЕНЕТИЧЕСКИЙ АНАЛИЗ СИКВЕНСОВ МАТУРАЗЫ *K*, РИБУЛОЗО-1,5-ДИФОСФАТКАРБОКСИЛАЗЫ (RBCL) И СТРУКТУРЫ ПЫЛЬЦЫ ПРЕДСТАВИТЕЛЕЙ СЕМЕЙСТВА *AMARANTHACEAE* JUSS.

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Данные о сиквенсах (последовательностях) протеина матуразы *K* (*matK*) и рибулозо-1,5-дифосфаткарбоксилазы (*rbcL*) из разных видов растений, относящихся к семейству *Amaranthaceae* s.l., были получены из базы данных GenBank (NCBI) и использованы для построения филогенетических деревьев (дендрограмм). Результаты подтвердили правильность сделанных ранее по данным палиноморфологии выводов о близком родстве видов, расположенных в классической системе семейства *Amaranthaceae* Juss. в разных подсемействах и трибах. Такие выводы позволяют более гибко и точно применять данные палиноморфологии в систематике покрытосеменных растений.

Ключевые слова: биоинформатика, матураза *K*, рибулозо-1,5-дифосфаткарбоксилаза, филогения, *Amarantaceae*, палиноморфология.