

PHYLOGENY OF THE GENUS EREMURUS (ASPHODELACEAE) BASED ON MORPHOLOGICAL CHARACTERS IN THE FLORA IRANICA AREA

K. Naderi Safar, S. Kazempour Osaloo & M. Zarrei

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A phylogenetic analysis of *Eremurus* (*Asphodelaceae*) based on morphological data is presented. A total of twenty-five characters including 20 gross morphological, 4 palynological and 1 chromosomal characters were analyzed to reconstruct phylogenetic relationships for 24 taxa of *Eremurus* and *Trachyandra malosana* plus *Asphodelus tenuifolius* and two *Asphodeline* species as outgroups. Maximum parsimony approach as implemented in PAUP* using heuristic search and branch swapping option of tree bisection-reconnection were used for phylogenetic analyses. The analysis of characters with successive weighting using rescaled consistency index generated more resolved and supported trees than the analysis with equally weighting characters. The analyses showed that *T. malosana* is well allied with a clade of *Eremurus* species. Among *Eremurus* species analyzed, *E. persicus* and a subclade of *E. kopetdaghensis* and *E. luteus* comprise the basal most branches as sisters to the remainder. *Eremurus* subgenus *Henningia* with 15 taxa was paraphyletic; whereas, nine members of *Eremurus* subgenus *Eremurus* formed a well supported monophyletic group for which *E. furseorum* of the former subgenus was sister taxon. Sections *Henningia* (of subgenus *Henningia*) and *Eremurus* (of subgenus *Eremurus*) are also appeared to be non-monophyletic while the section *Ammolirion* (of subgenus *Eremurus*) is monophyletic. Medium size pollen grain, (25-50 μm) and chromosome number of $2n=14$ are shared by *Eremurus* and *Trachyandra*. Three characters including non-branched inflorescence, basifixed stamens and ellipsoidal pollen grains are synapomorphies for the genus *Eremurus* solely. Tubular/campanulate flowers, incurved tepals and tepals with 3-5 nerves are synapomorphies for the subgenus *Eremurus*. Similarly exerted stamen is a synapomorphy for the subgenus *Eremurus* and *E. forseorum* (from subgenus *Henningia*). The tubular flowers (rather than campanulate) and the thinnest pollen exine are putative synapomorphies for the section *Ammolirion*. The remaining characters were evolved homoplasiously or ambiguously among these taxa.

Kosar Naderi Safar & Shahrokh Kazempour Osaloo (correspondence skosaloo@modares.ac.ir; skosaloo@yahoo.com), Department of Plant Biology, Faculty of Basic Sciences, Tarbiat Modares University, P.O. Box 14115-175, Tehran, Iran. -Mehdi Zarrei, Department of Biology, Faculty of Sciences, Shahed University of Tehran, Po Box 18151-159, Tehran, Iran.

Key words. Asphodelaceae, Phylogeny, Morphology, *Eremurus*, Iran.

فیلوژنی جنس سریش (*Asphodelaceae*) بر اساس صفات ریخت‌شناسی در منطقه فلورا ایرانیکا

کوثر نادری صفار، دانشجوی کارشناسی ارشد گروه زیست‌شناسی گیاهی دانشگاه تربیت مدرس.

شاهرخ کاظم پور اوصالو، استادیار گروه زیست‌شناسی گیاهی دانشگاه تربیت مدرس.

مهدی زارعی، استادیار گروه زیست‌شناسی دانشگاه شاهد تهران.

آنالیز فیلوژنی جنس سریش (*Eremurus*) بر اساس داده‌های حاصل از صفات ریخت‌شناسی منطقه فلورا ایرانیکا ارائه می‌شود. در مجموع 25 صفت ریخت‌شناسی برای بازسازی روابط فیلوژنی 24 تاکسون از جنس سریش (*Eremurus*) در ناحیه فلورا ایرانیکا و گونه *Trachyandra malosana* به اضافه *Asphodelus tenuifolius* و دو گونه از جنس *Asphodeline* به عنوان برون‌گروه، مورد آنالیز قرار گرفت. آنالیز فیلوژنی به روش Maximum parsimony تعبیه شده در نرم افزار PAUP* با استفاده از جستجوی ابتکاری (heuristic) و

گزینه تبادل شاخه دونیمه شدن و اتصال مجدد درخت صورت گرفت. از آنالیز صفات با وزن‌دهی متوالی با استفاده از شاخص سازگاری تصحیح شده درختانی با روابط فیلوژنی بهتر و حدود اطمینان کلادهای بیشتر نسبت به وزن‌دهی یکسان صفات بدست آمد. آنالیز نشان داد که *E. persicus*, *Eremurus* به خوبی با کلاد متشکل از گونه‌های *Eremurus* متحد شده است. در میان گونه‌های آنالیز شده از *Eremurus* به اضافه زیر کلادی شامل *E. luteus* و *E. kopetdaghensis* اولین شاخه‌ها و گروه خواهری برای سایر گونه‌های *Eremurus* هستند. در جنس *Eremurus* زیرجنس *Henningia* با 15 تاکسون پیراتبار است، در حالی که زیرجنس *Eremurus* با 9 تاکسون تک تبار می‌باشد. به نظر می‌رسد بخش‌های *Henningia* (از زیرجنس *Henningia*) و *Eremurus* (از زیرجنس *Eremurus*) نیز تک‌تبار نیستند. در حالی که بخش *Ammolirion* (از زیرجنس *Eremurus*) تک تبار است. از میان 25 صفت آنالیز شده، شیارهای گرده با اندازه متوسط (25–50 μm) و عدد کروموزومی $2n=14$ برای جنس‌های *Eremurus* و *Trachyandra* مشترک‌اند. سه صفت شامل گل آذین غیر منشعب، پرچم‌های پایه چسب و شیارهای گرده ای بیضوی سیناپومورفی‌های ویژه جنس سریش هستند. گل‌های لوله‌ای/استکانی، گلپوش‌های خمیده به سمت داخل و 3 تا 5 رگه بودن گلپوش‌ها سیناپومورفی‌های زیر جنس *Eremurus* هستند. همچنین پرچم‌های بیرون زده مختص زیر جنس *Eremurus* و *E. forseorum* (از زیرجنس *Henningia*) است. گل‌های لوله‌ای (نه استکانی) و نازکترین آگزین گرده‌ای صفات مشترک برای اعضای بخش *Ammolirion* می‌باشند. بقیه صفات به صورت هم‌نما یا مبهم در میان این تاکسون‌ها تکامل یافته‌اند.

INTRODUCTION

Eremurus M. Bieb. (*Asphodelaceae*) with 45 species worldwide (Mabberley 1990) is distributed over large area in Central Asia, Caucasia, Afghanistan, Iran, Pakistan, Iraq, Turkey, Lebanon, India and China (Wendelbo & Furse 1969). Its centre of diversity is in Central Asia (Hedge & Wendelbo 1963). In the Flora Iranica area, *Asphodeloideae* as a subfamily of *Liliaceae* has three genera including *Eremurus*, *Asphodelus* L. and *Asphodeline* Reichenb (Wendelbo 1982). Seven species of *Eremurus* have been recorded in Iran, and 24 species described for the Flora Iranica area. Among them only *Eremurus kopetdaghensis* M. Pop. ex B. Fedtsch. is sub-endemic to Iran. It is also distributed in Turkmenistan (Wendelbo 1982). Angiosperm Phylogeny Group (APG 1998) determined *Asphodelaceae* as a family of *Asparagles*. *Xanthorrhoeaceae* sensu lato as a large unit circumscribed by APG II (APG 2003) includes *Asphodelaceae*, *Hemerocallidaceae* and *Xanthorrhoeaceae* s. str.

Eremurus is well known for its large colourful racemes. It is distinguished from *Asphodelus* with not branched inflorescence and from *Asphodeline* by lacking membranous leaf sheaths at the base of inflorescence. *Eremurus* has been divided into two subgenera and three sections (Wendelbo 1982). The subgenus *Eremurus* is characterized by light brown-green or cream tubular/campanulate flowers, incurved tepals and tepals with 3–5 nerves abaxially and exerted filaments. Whereas, the subgenus *Henningia* has white,

pink or yellow rotate flowers, mostly non-exerted filaments and tepals one nerved abaxially.

Apart from several studies conducted by Wendelbo (1962, 1964, 1968, 1982, 1985) and Wendelbo & Furse (1969) which are mainly concentrated on Central Asia, there is no intensive contribution to this genus in Iran. In addition to this fact that most species are of great horticultural potential, this genus has several other commercial usages such as, extracting natural glue from rhizomes, edible young leaves as vegetable and very beautiful ornamental flowers (Kamenetsky & Rabinowitch 1999).

The goals of the present study are: (1) to evaluate phylogenetic status of the *Eremurus* and its infrageneric subdivisions including subgenera and sections and (2) to examine evolutionary trend of morphological characters in the context of the hypothesized phylogeny.

MATERIALS AND METHODS

Twenty-four taxa representing three currently recognized sections belonging to the two subgenera of *Eremurus* and one species of *Trachyandra* (*T. malosana* (Baker) Oberm.), as the closest genus to *Eremurus* (Chase & al. 2000), were included in the analysis. *Asphodelus tenuifolius* and the two *Asphodeline* species were selected as outgroups. Characters used in the phylogenetic analysis were obtained through examination of fresh materials in the field and herbarium specimens deposited at four major herbaria of Iran (TARI, IRAN, TUH & FUMH, see Holmgren & Holmgren 1998 for herbarium acronyms)

Table 1. List of morphological characters of *Eremurus* species used in phylogenetic analyses.

I. Height of plant: ≤ 70 cm (0) > 70 cm (1)

Scape:

2. Indumentum: Pubescent (0) Glabrous (1)

Bract:

3. Shape: Subulate (0) Lanceolate (1) Ovoid (2)

4. Margin: Glabrous (0) Ciliate (1)

5. Surface: Glabrous (0) Hairy (1)

Leaves indumentum:

6. Margin: Glabrous (0) Ciliate (1)

7. Surface: Glabrous (0) Hairy (1)

Inflorescence:

8. Branched (0) Non branched (1)

9. Length: ≤ 30 cm (0) > 30 cm (1)

10. No. of flowers: ≤ 70 (0) > 70 (1)

Flower:

11. Flower shape: Subrotate (0) Tubular (1) Campanulate (2)

12. Tepal color: White-cream (0) Pink (1) Yellow (2) Brown (3)

13. Tepal length: ≤ 15 mm (0) > 15 mm (1)

14. Tepal width: Equal (0) Unequal (1)

15. Tepal tip: Erect or recurved (0) Incurved (1)

16. Tepal nerve: 1 (0) 3-5 (1)

Stamen:

17. Anther type: Dorsifixed (0) Basifixed (1)

18. Stamen position: Non exerted (0) Exerted (1)

Fruit:

19. Shape: Globose (0) Ellipsoidal (1) Pyriform (2)

20. Surface sculpturing: Present (0) Absent (1)

Pollen grain:

21. Shape: Oblate-spheroidal (0) Ellipsoidal (1)

22. Size: Large (50-100 μ m) (0) Medium (25-50 μ m) (1)

Exine:

23. Thickness: Thick, > 1.5 μ m (0) Thin, ≤ 1.5 μ m (1)

24. Surface sculpturing: Rugulate-perforate (0) Microreticulate (1) Distinct reticulate (2)

Chromosome number:

25. $2n=28$ (0) $2n=14$ (1)

or adopted from appropriate references (Wendelbo 1982; Matthews 1986; Fedchenko 1968; Kosenko & Sventorzhetkaya 1999; Kativu 2001).

Twenty-five informative characters with relevant character states used in the present analysis were given in Table 1. The polarity of characters was determined using the outgroup method (Maddison & al. 1984).

Phylogenetic analyses were performed on the data matrix (Table 2) using maximum parsimony method (MP) as implemented in PAUP* version 4.0b10 (Swofford 2002) installed in a Macintosh computer. All characters were considered as equally weighted. The heuristic search option was selected using 100 replications of random addition sequence with ACCTRAN optimization and TBR (tree bisection reconnection) branch-swapping with MulTrees on and steepest descent off. Analyses were then conducted

using a successive re-weighting strategy (Farris 1969) in order to improving the trees indices and decreasing the effect of characters showing high homoplasy on tree topologies. Weights were assigned to characters using the re-weight characters option based on the rescaled consistency index (RC) (Farris 1989) with a base weight of one. When the tree length and consistency index (CI), retention index (RI) and RC remained unchanged in successive rounds, these trees were accepted as the successive re-weighting trees. In both analyses, supports for clades were evaluated by bootstrapping (Felsenstein 1985) using 20000 replications with the heuristic search option, simple addition sequence, TBR branch swapping and MulTrees off.

Character evolution was surveyed on the strict consensus tree resulting from successive weighting of

Table 2. Data matrix used in the phylogenetic analyses of *Eremurus* and its related genera. Missing data are coded as “?” a= {01}.

Taxon	characters
<i>Asphodelus tenuifolius</i>	001001000010000000000010
<i>Asphodeline szovitsii</i>	0000010000001100000?00000
<i>A. dendroides</i>	0100010000000?00000100000
<i>Eremurus inderiensis</i>	0001111101100011110111111
<i>E. cappadocicus</i>	00010001??130011110111111
<i>E. comosus</i>	10110111?0110011110111111
<i>E. dolichomischus</i>	10110111?1130011110111111
<i>E. spectabilis</i> subsp. <i>spectabilis</i>	1101000111200111110011021
<i>E. spectabilis</i> subsp. <i>subalbiflorus</i>	1101011111200011111011021
<i>E. korshinskii</i>	1101000100231011110111021
<i>E. soogdianus</i>	100101a1?0200111110011021
<i>E. fuscus</i>	11010001?1220011110111021
<i>E. kopetdaghensis</i>	0111010100011100101111021
<i>E. persicus</i>	0021111100011100100111021
<i>E. stenophyllus</i> subsp. <i>stenophyllus</i>	1100010111020100100111021
<i>E. stenophyllus</i> subsp. <i>aurantiacus</i>	1001011111020100100111021
<i>E. olgae</i>	1100000110011100100111021
<i>E. luteus</i>	0101010100021100101011021
<i>E. kaufmanii</i>	10210111?1001000100111021
<i>E. himaliacus</i>	11010101?1001000100111021
<i>E. aitchisonii</i>	11010101?0011000100111021
<i>E. bucharicus</i>	1001010110000100100011021
<i>E. bacterianus</i>	10011111??001100100111021
<i>E. afghanicus</i>	10011111?1000000100111021
<i>E. suworowii</i>	0010101?0020000100111021
<i>E. roseolus</i>	10010111?1011100102111021
<i>E. furseorum</i>	10001101?1010000110111021
<i>Trachyantra malosana</i>	0020011001000000000001011

characters with ACCTRAN optimization and interpreting polytomies as multiple speciation events (hard polytomies) using MacClade version 4.3 (Maddison & Maddison 2004).

RESULTS

The first phylogenetic analysis using equally weighted characters generated 423 most parsimonious trees of 86 steps with CI= 0.360 and RI= 0.656. The strict consensus tree of the analysis was not shown. The relationships among *Eremurus* species remain unresolved in this tree. The second analysis based on re-weighted characters by rescaled consistency index yielded 60 well resolved and supported trees with length= 20.2 steps, CI= 0.694, RI= 0.901. The strict

consensus tree of the analysis is shown in Fig. 1. In both analyses, *Trachyantra malosana* is closest taxa to *Eremurus*. Among *Eremurus* species analyzed, *Eremurus persicus* (Jaub. & Spach) Boiss. and a subclade of *E. kopetdaghensis* and *E. luteus* Baker, as unresolved branches, comprised the basal most taxa. The remaining species formed a large polytomy of several individual branches and two weakly subclades (Fig. 1.).

DISCUSSION

Monophyly and infrageneric relationships of *Eremurus*

The present analysis based on morphological characters indicates that *Eremurus* is a monophyletic taxon

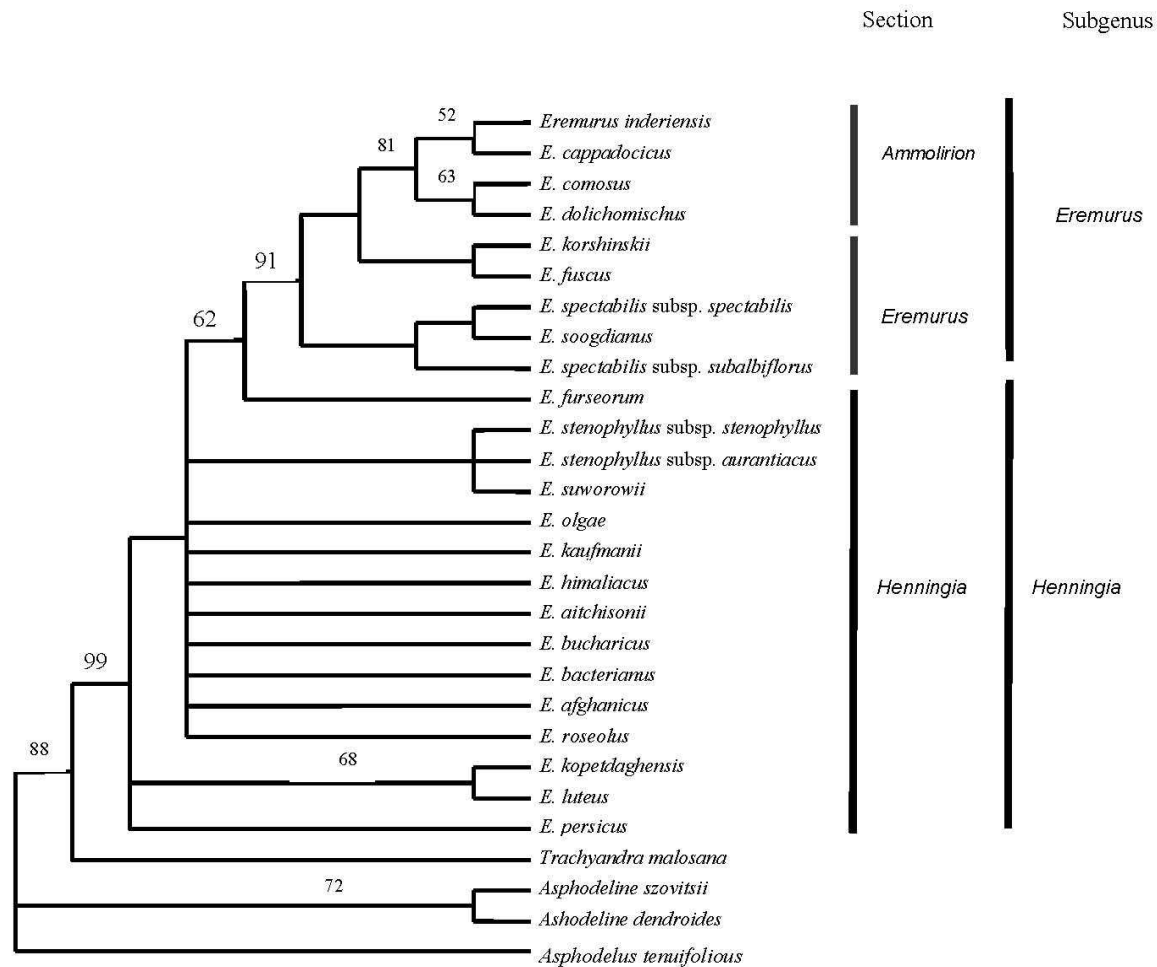


Fig. 1. Strict consensus of the 60 most parsimonious trees obtained from morphological characters after successive weighting by rescaled consistency index. Numbers above branches are bootstrap values. Numbers <50% were not indicated.

(bootstrap=99%). Our molecular analyses based upon both nrDNA ITS and chloroplast *trnL-F* sequences is also consistent with this finding (Naderi & Kazempour Osaloo 2008, and Naderi & al. unpubl. data). According to latest treatment of Wendelbo (1982), *Eremurus* has been divided into two subgenera, *Eremurus* and *Henningia*. The former subgenus is composed of sections *Eremurus* and *Ammolirion*, and the latter one includes only section *Henningia*. Phylogenetic analyses of the morphological data suggested that the subgenus *Eremurus* is well supported monophyletic group (bootstrap=91%). The subgenus is characterized by three synapomorphies including tubular/campanulate flowers, incurved tepals and tepals with 3–5 abaxial nerves. The section *Eremurus* is not monophyletic while the section *Ammolirion* is monophyletic (bootstrap=81%). This

section is distinguished from the section *Eremurus* by having tubular flowers rather than campanulate flowers and by the thinnest pollen exine (Wendelbo 1982; Kosenko & Sventorzhetzkaya 1999). The subgenus *Henningia* has white, pink or yellow subrotate flowers, non-exserted filaments and erect or recurved tepals with one abaxial nerve. The present phylogeny shows that these characters are primitive (symplesiomorphies), since they are shared by *Trachyandra*, the closest relative of *Eremurus* (Chase & al. 2000; Devay & al. 2006) and outgroup taxa (see Figs. 2B & 3A). Therefore, the subgenus *Henningia* (and section *Henningia*) is paraphyletic. *Eremurus furseorum* Wendelbo is the only species of *Henningia* that allied with *Eremurus* subgenus *Eremurus*. They do share exerted stamens.

Evolutionary trend of characters

MacClade reconstruction of character evolution indicated that all 25 characters but characters no. 14 and 20 were evolved unambiguously. Characters 22 (medium-sized pollen grain, 25-50 μm) and 25 (Chromosome number of $2n=14$) are shared by *Eremurus* and *Trachyandra*. The three characters including non-branched inflorescence (character 8), basifixed anthers (character 17) and ellipsoidal pollen grains (character 21) are synapomorphies for the genus *Eremurus* solely (Fig. 2A). As noted at the previous part, tubular/campanulate flowers (character 11) incurved tepals (character 15) and tepals with 3-5 abaxial nerves (character 16) are synapomorphy for the subgenus *Eremurus* (Figs. 2B & 3A). Similarly, character 18 (exserted stamens) is a synapomorphy for the subgenus *Eremurus* and *E. forseorum* (from subgenus *Hennigia*). The tubular flowers (character 11) and the thinnest pollen exine (character 23) are putative synapomorphies for the section *Ammolirion* (Fig. 3B).

Characters 1, 4, 9, 10, 13 and 24 were undergone reversal evolution among *Eremurus* species. For example, the plesiomorphic state for characters 10 and 24 are number of flowers < 70 and pollen exine with microreticulate sculpturing, respectively. The number of flowers > 70 and pollen exine with distinct reticulate sculpturing are derived (Figs. 4A & 4B). Likewise, characters 2, 3, 5, 6, 7, 12 and 19 were evolved in parallel evolution among *Eremurus* species and *Trachyandra malosana*. For instance, evolutionary trend for characters 3, having three character states, was occurred from subulate bract as a plesiomorphic condition to both lanceolate (in *Eremurus comosus* O. Fedtsch., *E. dolichomischus* Vved. & Wendelbo and *E. kopetdaghensis*) and ovate (in *E. kaufmanii* Regel, *E. persicus* and *T. malosana*). Similar results were found for the evolution of character no. 19 (fruit shape). The analysis indicated that globose fruit is plesiomorphic and fruits with ellipsoidal and pyriform shape are derived. According to this study, ellipsoidal fruits that are found in both *E. kopetdaghensis* and *E. luteus* as well as in the far related *E. spectabilis* subsp. *subalbiflorus* evolved in parallel, and pyriform fruit is unique to *E. roseolus* Vved. (Figs. 5A & 5B).

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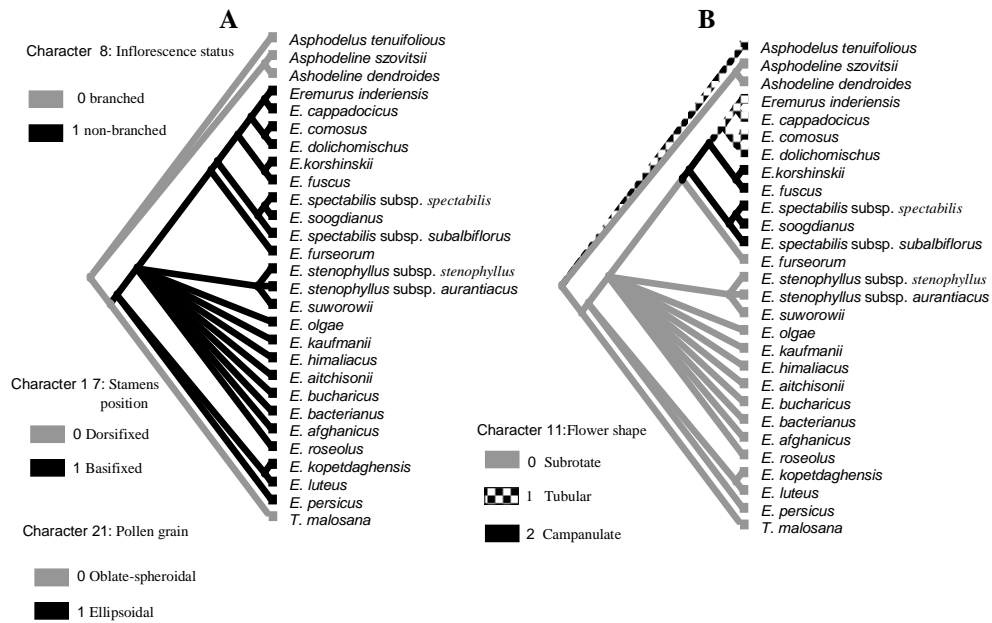


Fig. 2. MacClade reconstruction of character evolution of: A (characters 8, 17, 21); B (character 11) on the tree.

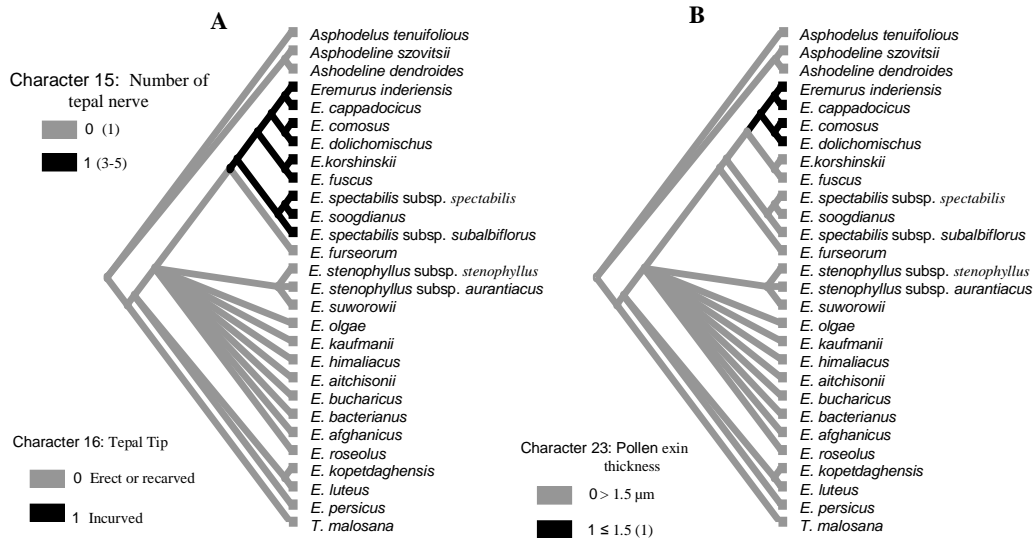


Fig. 3. MacClade reconstruction of character evolution of: A (characters 15, 16); B (character 23) on the tree.

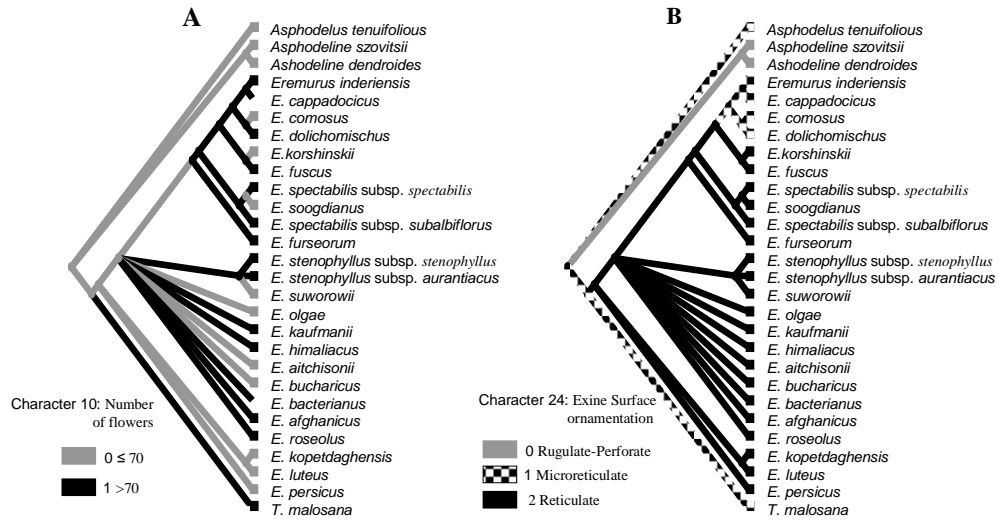


Fig. 4. MacClade reconstruction of character evolution of: A (character 10); B (character 24) on the tree.

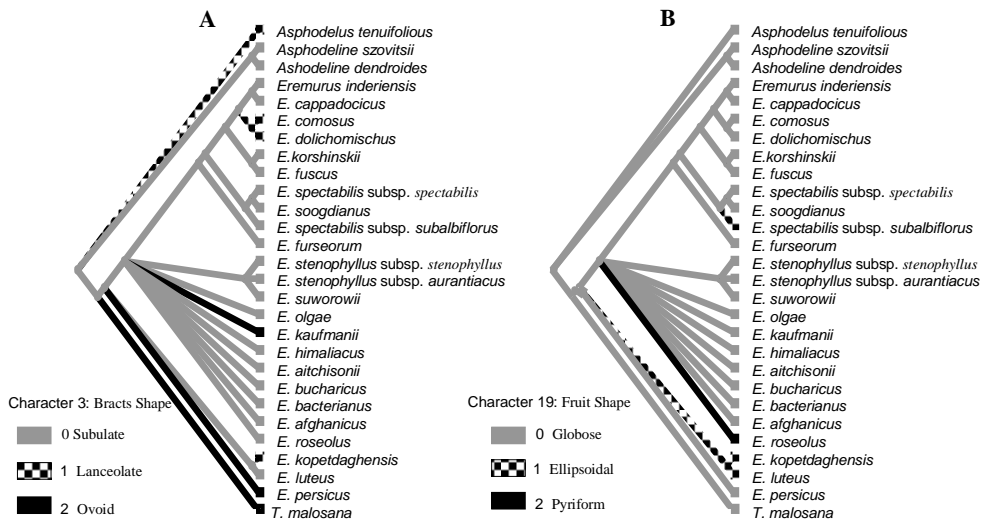


Fig. 5 MacClade reconstruction of character evolution of: A (character 3); B (character 19) on the tree.

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