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Contribution to floral structure and palynological features of Turkish Periplocoideae and Asclepiadoideae taxa

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Abstract

Background The Apocynaceae are characterized by highly specialized flowers, including three derived structures, corona, gynostegium and pollinarium, which play an important role in explaining the evolutionary relationships among the major groups of the family. The floral morphology and microstructure of pollinaria in pollinia-bearing subfamilies, Periplocoideae and Asclepiadoideae, are not well understood. In the present study, we examined the detailed floral and pollen characters of six species from Türkiye—Asclepiadoideae: *Araujia sericifera* Brot., *Cionura erecta* (L.) Griseb., *Cynachum acutum* L. and *Gomphocarpus fruticosus* (L.) W.T.Aiton; Periplocoideae: *Periploca gracilis* Boiss. and *P. graeca* L.—using light and scanning electron microscopy for taxonomic insights.

Results Macro- and micromorphological observations were performed on both herbarium samples and fresh field specimens preserved in 70% ethanol. Floral and pollen descriptions were amended, and a dichotomous identification key was prepared for the studied taxa. Morphological and palynological traits were also analyzed numerically. Principal components analysis revealed that length of pedicel, sepal, petal and corona segment, pubescence of anther (hairy/glabrous), shape of stigma (unlobed/bifid), length of pistil, type of pollen aggregation (tetrad/pollinium), number of tetrad mass or pollinium per pollen translator (single/in pairs), pollen translator structure (receptacle + stalk + adhesive disc or corpusculum + caudicles), and pollen grain dimensions were diagnostically informative traits for distinguishing taxa at both subfamily and genus levels.

Conclusions The dendrogram inferred from macro- and micromorphological floral and pollen traits generally agrees with the traditional subfamilial classification of the Periplocoideae and Asclepiadoideae. These findings offer insights into the evolution and diversification of pollinia-bearing Apocynaceae, and may reflect the role of key traits in reproductive strategies and ecological interactions.

Keywords Apocynaceae, Flower, Pollen grains, Pollinium, Türkiye

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Introduction

In the most recent classification, Apocynaceae sensu lato is recognized as a combination of two previous families: Apocynaceae sensu stricto and Asclepiadaceae. At the recent circumscription, the family is divided into five major groups: two non-monophyletic informally recognized as rauvolfioids and apocynoids grades (lacking pollinia), and three monophyletic, Periplocoideae, Secamonoideae, and Asclepiadoideae subfamilies, known as the pollinia-bearing subfamilies [1]. The enlarged Apocynaceae is one of the largest 10 angiosperm families containing approximately 5,350 species belonging to 378 genera in various habitats and growth forms. Members of the family include large trees, shrubs, lianas, and epiphytes in tropical rainforests, succulents in dry, open landscapes, and perennial herbs in temperate grasslands [1–3].

The Apocynaceae have attracted much interest from plant taxonomists due to their highly specialized floral construction. Flowers of the family are characterized by 3 derived structures: (I) corona, a sterile floral structure belonging to the corolla or androecium, (II) gynostegium, a reproductive structure formed by union of the gynoecium and androecium, and (III) pollinarium, a functional pollen dispersal unit consisting of tetrad masses or pollinia joined to a specialized translator produced by a hardened stylar exudate [1, 2, 4, 5]. In the current classification of Apocynaceae, the reproductive features of flower play a key role in delimiting the major groups (grades and subfamilies). Of the two grades, rauvolfioids, considered to be the most early divergent group of Apocynaceae, are almost always characterized by sinistrorse corolla lobe (rarely dextrorse) and anthers free from style-head (lacking a gynostegium). In contrast, the remaining taxa of the APSA clade (Apocynoids, Periplocoideae, Secamonoideae and Asclepiadoideae) typically have dextrorse corolla lobe (rarely sinistrorse or valvate) and anthers adnate to style head in the form of a gynostegium [1]. Furthermore, pollen characteristics have long been recognized as important evolutionary traits for major groups in Apocynaceae. Both rauvolfioids and apocynoids, which are, palynologically, the most early divergent groups in Apocynaceae, commonly have monad pollen grains without translator or rarely with tetrads shed on undifferentiated translators [2]. These two groups have traditionally been differentiated from the remaining pollinia-bearing subfamilies (Periplocoideae, Secamonoideae, and Asclepiadoideae), which are characterized by the aggregation of pollen grains into tetrad masses or pollinia joined to quite specialized translators (acellular bodies derived from style-head exudates) [2, 5].

In the Apocynaceae, highly characteristic floral structures, gynostegium and corona, have an important role in pollinator attraction, reward, and/or positioning [6]. The complexity of floral structures varies depending on the pollinator interactions within the Apocynaceae. Periplocoideae and Asclepiadoideae, the two subfamilies evaluated in this study, have contrasting flowers, which have led them to develop distinct pollination mechanisms. In Periplocoideae, the pollination mechanism is defined as open, because the pollinator can easily reach the sticky translator carrying tetrads, which hangs directly above the nectar trough (anthers lack lignified guide rails) on the style-head. On the other hand, the pollination mechanism of the Asclepiadoideae is enclosed since the pollinia are attached to a clamp-shaped translator hidden behind the guide rails of adjacent anthers. In this system, the pollinator's proboscis or leg is caught and guided into the pollination unit [1, 2]. Among the advantages of transportation of pollen grains in the form of tetrad masses or pollina are the strengthening adaptation of Apocynaceae representatives to drier climatic conditions by delaying pollen desiccation. Additionally, this mechanism increases pollination rates for small populations [7].

Revealing the floral structure and pollen morphology in detail not only contributes to the differentiation of Apocynaceae taxa but also provides valuable information about the pollinators of these plants, their habitats and ecological conditions. This is especially true for members of Periplocoideae and Asclepiadoideae. Flower morphology and palynological features, regarding Periplocoideae and Asclepiadoideae were generally outlined in several studies [2, 4–6, 8]. These investigations showed that morphological features on the shape, size and origin of corona; shape and pubescence of anther and stigma; palynological traits of the shape and size of pollen masses (tetrad and pollinium) and translator structures (spoon shaped translator, corpusculum and caudicle); surface ornamentation of tetrad and pollinia were the most valuable traits in delimiting the genera of Periplocoideae and Asclepiadoideae [1–5, 8–19].

Floral and palynological traits of Apocynaceae are crucial for understanding evolutionary relationships. These traits are similarly expressed in the Turkish taxa of Periplocoideae and Asclepiadoideae, providing a valuable opportunity to examine their floral and palynological variation within the local flora. The first taxonomic revision of Turkish Periplocoideae and Asclepiadoideae was made by Browicz [20], who treated both of them under the family Asclepiadaceae. Browicz [20] assumed that more comprehensive studies, especially on reproductive structures such as corona, gynostegium, and pollinium, were needed to separate the members of Periplocoideae and Asclepiadoideae in Türkiye. Güner [21] listed 11 genera, including *Amsonia* Walter, *Araujia* Brot., *Cionura* Griseb., *Cyprinia* Browicz, *Gomphocarpus* R.Br., and *Nerium* L., each represented by a single species, as well as *Apocynum* L. (2 subspecies), *Cynanchum* L. (2

subspecies), *Periploca* L. (2 varieties), *Vinca* L. (3 species and 2 subspecies) and *Vincetoxicum* Wolf (7 species and 4 subspecies) under the expanded Apocynaceae (Apocynaceae sensu stricto and Asclepiadaceae) in the vascular plant checklist of Türkiye, without any taxonomic treatment. Subsequent comprehensive taxonomic studies on the Turkish Periplocoideae and Asclepiadoideae taxa resulted in the description of *V. coskuncelebiana* S. Makbul & S. Güven (syn. *V. anatolicum* S. Güven, S. Makbul & Coşkunç.) as a new species [22]. Among the Periplocoideae taxa, *Cyprinia* was merged with *Periploca*, and *P. graeca* var. *vestita* was reduced to synonymy under *P. graeca* [23, 24]. Of the Asclepiadoideae taxa, *V. raddeanum* Alboff was reduced to synonymy under *V. tmoleum* Boiss., and *V. hirundinaria* Medik. was reclassified as *V. hirundinaria* subsp. *hirundinaria* [22, 25]. In the present study, this updated taxonomic treatment is followed for the investigated taxa. According to the recent taxonomic studies [22–25], the subfamilies Periplocoideae and Asclepiadoideae are represented by 6 genera and 18 taxa, including infraspecific taxa in Türkiye. Periplocoideae is represented by two species, *Periploca gracilis* Boiss. and *P. graeca* L., while Asclepiadoideae comprises the remaining taxa, including *Araujia sericifera* Brot., *Cionura erecta* (L.) Griseb., *C. acutum* L. subsp. *acutum*, *C. acutum* subsp. *sibiricum* (Willd.) Rech.f., *Gomphocarpus fruticosus* (L.) W.T.Aiton, and *Vincetoxicum* Wolf, with 6 species and 5 subspecies. In the previous studies based on the cytological and molecular data, *Vincetoxicum* was recovered as monophyletic within the subfamily [22, 25]. In addition, morphological [22, 26], anatomical [27, 28] and palynological data [29] also provided valuable information for delimitation of the Turkish *Vincetoxicum* at the species level. However, to date, limited studies have been conducted in Türkiye on the genera with pollinia-bearing subfamilies (Periplocoideae and Asclepiadoideae), which have taxonomic deficiencies and complexities in terms of morphology of reproductive organs in the Flora of Türkiye [20]. Recently, morphological and corological features of Periplocoideae [24], fruit and seed micromorphology of Periplocoideae and Asclepiadoideae (excluding *Vincetoxicum*) [23], micromorphological and anatomical features of stem and leaf parts of taxa of *C. erecta*. [30] and *A. sericifera* [31] from Türkiye was examined from a taxonomic point of view. Despite all these cited studies, there are still gaps in the biosystematics properties of both subfamily members. The present study aims to investigate the detailed floral and pollen characteristics of the four Asclepiadoideae species (*A. sericifera*., *C. erecta*, *C. acutum* and *G. fruticosus* and pollen features of the two Periplocoideae species (*P. gracilis* and *P. graeca*), for the first time, will provide important taxonomical contributions to systematics of the both subfamilies.

Taking into consideration the points raised so far, the objective of the present study is (I) to document and illustrate detailed descriptions of floral and pollen morphology of 3 species and 2 subspecies of Asclepiadoideae and pollen morphology of 2 species of Periplocoideae from Türkiye using light and Scanning Electron Microscopy (SEM), (II) to evaluate the taxonomic or diagnostic importance of floral morphological and palynological characteristics within the examined Periplocoideae and Asclepiadoideae taxa.

Material and methods

Specimens

The examined plant material was collected from 13 different populations (p) in Türkiye belonging to seven taxa of the two subfamilies: Periplocoideae, including *P. gracilis* (1p) and *P. graeca* (2p), and Asclepiadoideae, comprising *A. sericifera* (1p), *C. erecta* (4p), *C. acutum* subsp. *acutum* (3p), *C. acutum* subsp. *sibiricum* (1p) and *G. fruticosus* (1p). Detailed locality information of the examined specimens is given in Table 1. Plant material comprising non-protected species was collected in compliance with the national legislation of the Republic of Türkiye within the framework of a project supported by the Scientific and Technological Research Council of Türkiye (TÜBİTAK, Project No: 122Z547).

Floral and palynological data belonging to the four Asclepiadoideae species and palynological data of the two Periplocoideae species were observed and measured for the first time in the present study. Data of floral features related to the examined Turkish Periplocoideae species (Appendix) were obtained from a previous study performed by Güven and Sarıkaya [24]. Morphological and palynological examinations were carried out on fresh field plant specimens fixed in FAA (5 parts stock formalin, 5 parts glacial acetic acid, 90 parts 70% ethanol) for 24 h and stored in 70% ethanol [32]. The dried herbarium specimens were rehydrated in tap water at 75 °C for 2 h and then stored in 70% ethanol [33]. All measurements and observations related to pollen morphology of the examined Periplocoideae taxa and both flower and pollen morphology of the studied Asclepiadoideae taxa were made on mature flowers belonging to 10 different individuals per population for seven taxa (a total of 130 individuals were examined: *P. gracilis* (10 individuals), *P. graeca* (20 individuals), *A. sericifera* (10 individuals), *C. erecta* (40 individuals), *C. acutum* subsp. *acutum* (30 individuals), *C. acutum* subsp. *sibiricum* (10 individuals) and *G. fruticosus* (10 individuals). Measurements obtained from replicate observations of flowers and pollinia were averaged per population, and these mean values were used in subsequent multivariate analyses. All photographic measurements were performed using scale-calibrated images,

Table 1 Locality information of the examined taxa

Taxon	Taxon Locality	Coordinates	Collector's no
Periplocoideae			
Periploca gracilis Boiss.	C5 İçel: Silifke, Ovacık Village, from Deveini to Keşlitürkmenli, 831 m, 25.05.2021.	N 36.51, E 33.97	S. Güven 177 & S. Makbul, RUB!
Periploca graeca L.	A6 Ordu: From Ordu to Fatsa, 14 m, 27.05.2014.	N 41.02, E 37.55	S. Güven 100 & S. Makbul, RUB!
	A8 Trabzon: Sürmene, Çamburnu, 2 m, 25.06.2021.	N 40.92, E 40.21	S. Güven 178 & & S. Makbul, RUB!
Asclepiadoideae			
Araujia sericifera Brot.	A6 Ordu: Perşembe, Medreseönü, near Bolaman, 20 m, 01.10.2021.	N 41.12, E 37.69	S. Güven 185 & S. Makbul, RUB!
Cionura erecta (L.) Griseb.	A1(E) Çanakkale: Eceabat, Şahindere - Behramlı road, 100 m, 06.08.2021.	N 40.12, E 26.27	S. Güven 181 & S. Makbul, RUB!
	A3 Düzce: Gölormanı Village, Elmacık Mountain, roadside, forest clearing, 162 m, 16.06.2013.	N 40.83, E 30.97	S. Güven 40 & S. Makbul, RUB!
	C2 Denizli: Honaz Mount road, around Cankurtaran, 1166 m, 21.06.2013.	N 37.74, E 29.21	S. Güven 54 & S. Makbul, RUB!
	C5 Niğde: Ulukışla, Çiftehan, Pozantı-Ulukışla road, 1007 m, 24.05.2014	N 37.50, E 34.72	S. Güven 92 & S. Makbul, RUB!
Cynanchum acutum L. subsp. *acutum*	A1(E) Çanakkale: Eceabat, Seddulbahir-Alçıtepe road, 06.08.2021.	N 40.06, E 26.20	S. Güven 183 & S. Makbul, RUB!
	B3 Afyon: Afyon–Eskişehir road, 930 m, 21.07.2021,	N 39.25, E 31.10	S. Güven 188 & S. Makbul, RUB!
	C2 Antalya: Aksu, 11 m, 31.07.2021.	N 36.93, E 30.87	S. Güven 190 & Makbul, RUB!
Cynanchum acutum subsp. *sibiricum* (Willd.) Rech.f.	B7 Erzincan: Erzincan-Sivas road, 1300 m, 16.08.2021.	N 39.44, E 39.76	S. Güven 06 & S. Makbul, RUB!
Gomphocarpus fruticosus (L.) W.T.Aiton	A2(A) İstanbul: Maltepe, 06.05.1972.	N 40.90, E 29.50	A. Baytop 23571, ISTE! (Cultivated plant)

and multiple replicates were taken for each trait to ensure accuracy and minimize potential errors.

The formal identification was carried out by Dr. Seher Güven according to Flora of Türkiye [20], Flora of Russia [34] and Flora of Europe [35], and then the identified plant samples were stored as voucher specimens in the Herbarium of Recep Tayyip Erdogan University, Department of Biology (RUB)—a publicly accessible herbarium. Specimens belonging to *G. fruticosus* were examined at the Herbarium of Istanbul University, Faculty of Pharmacy (ISTE). The collector numbers provided in Table 1 correspond to the voucher specimen numbers. Taxonomic names were assigned according to Venter [36] and Endress et al. [1], and cross-checked with the Plants of the World Online Database (POWO) [37].

Morphological studies

Mature flowers of Asclepiadoideae were examined and photographed using a Leica S6D digital camera attached to the stereomicroscope. All measurements and observations were performed on the saved photographs. The floral parts such as corolla, corona, stamen and pistil were illustrated by hand. The terminology of floral characteristics follows that of Endress and Bruyns [4], Endress [5], and Fishbein et al. [2].

Palynological studies

Polleniferous materials of both the examined Periplocoideae and Asclepiadoideae taxa were obtained from mature flowers, following Güven et al. [29]. For light microscopy studies, pollinaria were directly dissected from the fixed flowers and preserved in 100% ethanol, then mounted with glycerine–gelatine in order to obtain permanent slides. The obtained pollen grain slides were photographed using a research light microscope BAB Bs200 Pro Comet Image Process and Analysis Software. For SEM studies, pollinaria, which were preserved in 100% ethanol, were dried outdoors and transferred to aluminum stubs, coated with gold for 4 min in a sputter-coater, and then examined and photographed using a JEOL-JSM 6610 SEM microscope at the Central Research Laboratories of Recep Tayyip Erdogan University [29]. Palynological measurements and observations were performed on the saved photographs. The terminology of pollen characteristics follows that of Endress and Bruyns [4], Verhoeven and Venter [8], Fishbein et al. [2], and Endress [5].

Multivariate data analysis

In multivariate data analysis, data obtained from 22 morphological and 26 palynological traits (Table 2) belonging to six species (seven taxa) (Table 1) were evaluated numerically. Some of the most distinguishing characteristics were illustrated with drawings (Fig. 1). In multivariate data analysis, mean values of each morphological and palynological character were evaluated separately per population, for the seven taxa. Firstly, a raw data matrix generated by the average measurements of 48

Table 2 List of characters examined comparatively for studied taxa (Characters used in numerical analyses are coded with X)

No	Code	Character
1		Peduncle length (mm)
2		Peduncle pubescence: glabrous: 0, hairy:1
3		Number of flowers in inflorescence (number)
4	X_1	Pedicel length (mm)
5	X_2	Pedicel pubescence: glabrous: 0, hairy:1
6	X_3	Sepal width (mm)
7	X_4	Sepal length (mm)
8	X_5	Sepal abaxial surface pubescence: glabrous: 0, hairy:1
9	X_6	Corolla type: rotate: 0, campanulate: 1
10	X_7	Petal width (mm)
11	X_8	Petal length (mm)
12	X_9	Petal adaxial surface pubescence: glabrous: 0, hairy along the margins:1
13	X_{10}	Corona origin: corolline corona: 0, gynostegial corona: 1
14		Corona segments: free: 0, partly fused:1
15	X_{11}	Corona inner segment: absent: 0, present: 1
16	X_{12}	Corona segment shape: filiform: 0, laminaris: 1, fleshy: 2
17	X_{13}	Corona segment length: more than twice as long as the gynostegium: 0, shorter than twice the length of the gynostegium: 1
18	X_{14}	Stamen width (mm)
19	X_{15}	Stamen length (mm)
20	X_{16}	Pubescence of the abaxial surface of the anther: hairy: 0, glabrous:1
21	X_{17}	Stigma shape: unlobed: 0, bifid: 1
22	X_{18}	Pistil length (mm)
23	X_{19}	Pollen aggregation: tetrad: 0, pollinium:1
24	X_{20}	Number of pollen aggregation (tetrad mass or pollinium) on a pollen translator: single: 0, in pairs: 1
25	X_{21}	Pollen translator structure: receptacle+stalk+adhesive disc: 0; corpusculum+caudicles: 1
26	X_{22}	Pollen grain width (µm)
27	X_{23}	Pollen grain length (µm)
28	X_{24}	Pollen ornamentation: psilate or rough: 0, with crystals:1
29		Tetrad width (µm)
30		Tetrad length (µm)
31		Receptacle shape: spoon shaped:0; elliptical: 1
32		Receptacle width (µm)
33		Receptacle length (µm)
34		Stalk width (µm)
35		Stalk length (µm)
36		Adhesive disc width (µm)
37		Adhesive disc length (µm)
38		Pollinium position: erect: 0, pendulous: 1
39		Pollinium shape: ovate: 0, obovate:1
40		Pollinium width (µm)
41		Pollinium length (µm)
42		Corpusculum shape: ovate:0, oblong:1
43		Corpusculum width (µm)
44		Corpusculum length (µm)
45		Corpusculum wing: absent: 0, present: 1
46		Caudicle shape: flattened: 0, cylindrical: 1, conical:2
47		Caudicle width (µm)
48		Caudicle length (µm)

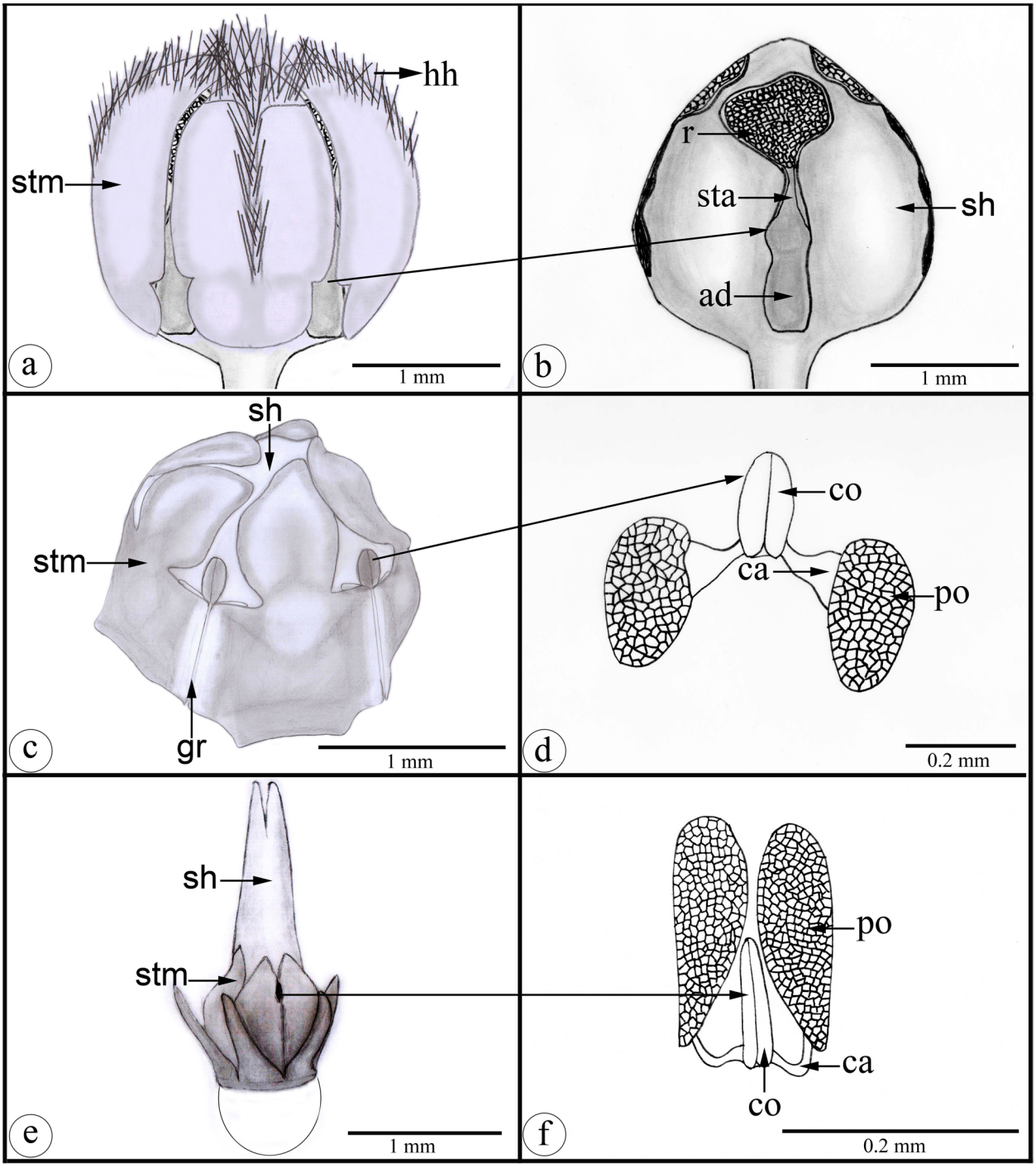


Fig. 1 The distinguishing floral and palynological characteristics of (**a**-**b**) *Periploca graeca* (S. Güven 178 & S. Makbul), (**c**-**d**) *Cynanchum acutum* subsp. *sibiricum* (S. Güven 06 & S. Makbul), (**e**–**f**) *Cionura erecta* (S. Güven 92 & S. Makbul), (**a**) Hairy anther, (**b**) Unlobed stigma with tetrads on receptacle + stalk + adhesive disc, (**c**) Unlobed stigma and glabrous anther, (**d**) Pendulous pollinia attached to corpusculum + caudicles, (**e**) Bifid stigma and glabrous anther, (**f**) Erect pollinia attached to corpusculum + caudicles (ad: adhesive disc, ca: caudicle, co: corpusculum, gr: guide rail, hh: hispid hair, po: pollinium, r: receptacle, sh: style-head, sta: stalk, stm: stamen)

traits was used for preliminary multivariate data analysis in order to determine the most effective characters in distinguishing the examined taxa. Based on these analyses, 24 traits (Table 2 and Appendix) showing the highest variance and taxonomic informativeness were selected for subsequent Cluster Analysis (CA) and Principal Components Analysis (PCA). Of the selected 24 characters, 14 characters were nominally scored (0, 1 or 2) and the

remaining 10 characters were quantitative, including linear measurements and digit numbers. Missing data were minimal and were accounted for by substituting population mean values for the respective traits. For CA, a pairwise matrix of resemblance values was calculated from the raw standardized data matrix, using Gower's coefficient of resemblance designed for mixed data sets. A dendrogram was generated by the Unweighted Pair-Group Method (UPGMA) by using arithmetic averages. For PCA, the raw mixed data (binary and continuous) were used to create a correlation matrix. All analyses were performed using Multivariate Statistical Package (MVSP) ver. 3.22 computer programs for multivariate data analysis in ecology and systematics [38].

Results

Floral properties

Asclepiadoideae

In the examined sub-family Asclepiadoideae of Apocyanaceae, the floral characteristics are inflorescences terminal, lateral, axillar or extra-axillar, composed of branched or umbellate cymes (rarely flowers solitary axillary) (Fig. 2). Flowers are bisexual, pentamerous and hypogynous. Corolla is rotate or campanulate, white, yellowish or pinkish. Corona has five separate segments inserted at inner base of the corolla tube, alternating with the petals (corolline corona), or with five separate or partially fused segments attached to the back of the stamens (gynostegial corona); corona segments are laminaris or succulent, basally unsegmented or with an inner lobe. Stamens are fused with the gynoecium to form gynostegium. Filaments are very short, thick; anthers are glabrous, 2-locular, with an apical appendage postgenitally fused to the base of style-head or above its thickest portion, margins are either narrowly lignified margins along the both sides forming five guide rails between the anthers, or membranous margins without guide rails. Gynoecium, forming a central column, is apocarpous, semi-inferior; two ovaries and styli are joined to the unlobed or apically bifid style-head, which includes

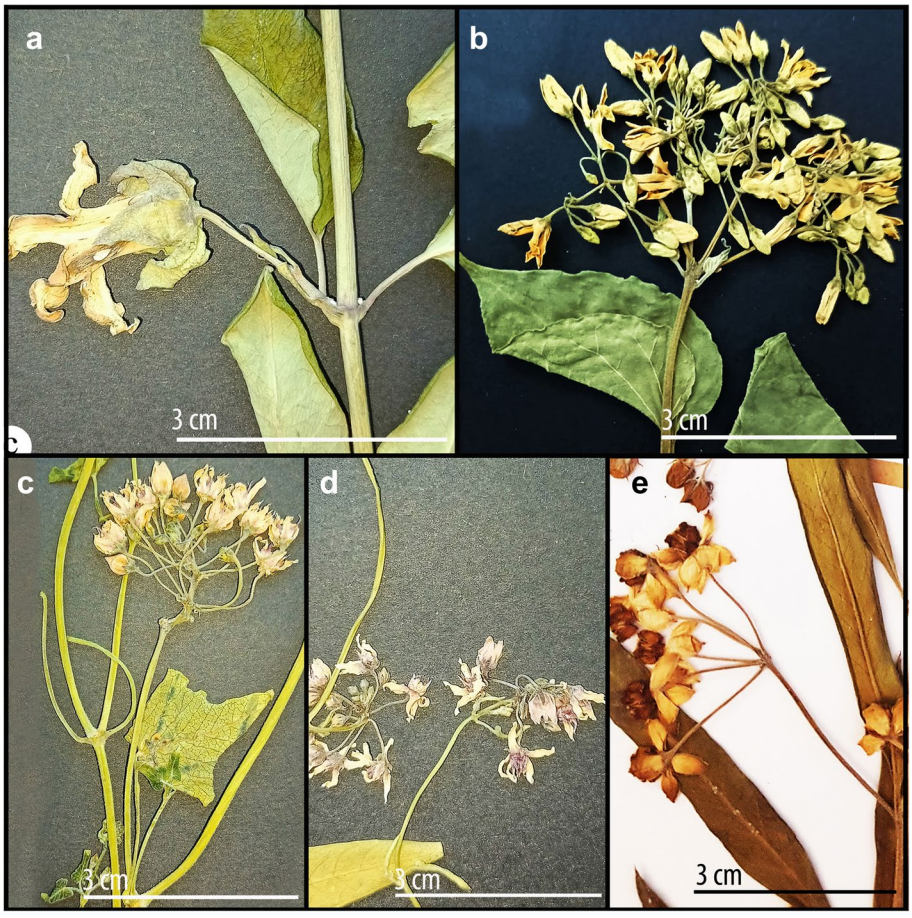


Fig. 2 Inflorescences types of (**a**) *Araujia sericifera* (S. Güven 185 & S. Makbul)–solitary axillary, (**b**) *Cionura erecta* (S. Güven 92 & S. Makbul)–terminal or lateral erect branched cymes, (**c**) *Cynanchum acutum* subsp. *acutum* (S. Güven 188 & S. Makbul)–terminal or lateral, umbellate cymes, (**d**) *Cynanchum acutum* subsp. *sibiricum* (S. Güven 06 & S. Makbul)–terminal or lateral, umbellate cymes, (**e**) *Gomphocarpus fruticosus* (A. Baytop 23571)–extra-axillary erect nodding umbel

five stigmatic zones located alternately with the anthers. Translator parts, including corpusculum and caudicles, are secreted in these zones (Figs. 3, 4, 5, 6, 7 and 8).

Araujia sericifera Brot. in Trans. Linn. Soc. London 12: 62 (1818) [39]: Flowers are solitary axillary (rarely in inflorescences axillary of 2–5 flowers); pedicel is 17.6 ± 3.4 mm long (Fig. 2a), with crisped indument. Calyx segments are divided almost to the base; sepals are 7.48 ± 1.03 × 15.02 ± 1.68 mm, ovate or ovate-lanceolate, acute at apex, abaxially with dense crisped indumenta. Corolla is campanulate, swollen at the base, five-lobed near the apex; petal lobes are 7.74 ± 1.27 × 23.24 ± 2.11 mm, white or yellowish, patent, ovate, obtuse at apex, adaxially glabrous and abaxially with white minute hairs (Fig. 3a–b). The corolline corona is white or yellowish; corona segments are 2.67 ± 0.21 mm long, succulent, ligulate, slightly curved outwards at margins, obtuse at apex (Fig. 3c–f). Stamens are 3.46 ± 0.13 × 4.10 ± 0.23 mm; anthers have an apical appendage postgenitally fused to the base of style-head, margins are narrowly lignified along the both sides forming five guide rails between the anthers (Fig. 3g–h). The style-head is rostrate and apically bifid; pistil is 10.85 ± 0.52 mm long (Fig. 3i–j).

Cionura erecta (L.) Griseb. in Spic. Fl. Rumel. 2: 69 (1844) [40]: Inflorescences are terminal or lateral, erect, with branched cymes bearing 22–58 flowers. Peduncle is 26.6 ± 9.8 mm and pedicel is 9.6 ± 2.5 mm long (Fig. 2b); peduncle and pedicel with crisped indumenta. Calyx segments are divided almost to the base; sepals are 0.76 ± 0.21 × 1.62 ± 0.31 mm, ovate-lanceolate with membranous margins, acute at apex, abaxially with sparse crisped indumenta. Corolla is rotate, white or cream-yellow; petals are 2.03 ± 0.34 × 7.76 ± 1.06 mm, oblong-lanceolate, obtuse at apex, glabrous (Fig. 4a–b). The gynostegial corona is white or cream-yellow; corona segments are 1.08 ± 0.19 mm long, laminaris, ovate-lanceolate, erect, acute at apex (Fig. 4c–d). Stamens are 0.51 ± 0.18 × 0.94 ± 0.1 mm; anthers have an apical appendage postgenitally fused to the base of style-head, margins are narrowly lignified along the both sides forming five guide rails between the anthers (Fig. 4e–f). The style-head is rostrate and apically bifid; pistil is 3.18 ± 0.68 mm long (Fig. 4g–h).

Cynanchum acutum L. in Sp. Pl.: 212 (1753) [41]: Inflorescences are terminal or lateral, with umbellate cymes bearing 8–35 flowers. Peduncle is 37.8 ± 17.5 mm and pedicel is 9.1 ± 2.3 mm long (Fig. 2c–d); peduncle and pedicel with crisped indumenta. Calyx segments are divided almost to the base; sepals are 0.84 ± 0.18 × 2.07 ± 0.31 mm, ovate, acute at apex, with sparse crisped indumenta. Corolla is rotate, white or pinkish; petals are 1.85 ± 0.32 × 5.55 ± 1.01 mm, oblong, obtuse at apex, glabrous (Figs. 5a–b, 6a–b, 7a–b). The gynostegial corona is pinkish, with five segments divided to the base (Fig. 5c–d), or fused up to 2/3 of their length (Fig. 6c–d), indicating intrasubspecific variation in corona structure within *C. acutum* subsp. *acutum*. In *C. acutum* subsp. *sibiricum*, the corona is also determined as pinkish, with five segments fused up to 2/3 of their length (Fig. 7c–d). Corona segments are laminaris, composed of an inner and an outer lobe united at the base; inner lobe is ovate, rarely long linear, 1.94 ± 0.30 mm long, outer lobe is tridentate, triangular, 3.13 ± 0.63 mm long (Figs. 5e–f, 6e–f, 7e–f). Stamens are 0.88 ± 0.17 × 1.78 ± 0.47 mm; anthers have an apical appendage postgenitally fused to style-head, margins are narrowly lignified along the both sides forming five guide rails between the anthers (Figs. 5g–h, 6g–h, 7g–h). The style-head is unlobed, broad and slightly convex; pistil is 2.74 ± 0.46 mm long (Figs. 5i–j, 6i–j, 7i–j).

Gomphocarpus fruticosus (L.) W.T.Aiton in Hortus Kew., ed. 2. 2: 80 (1811) [42]: Inflorescences are extra-axillary with 6–8 flowers in an erect nodding umbel. Peduncle is 30 ± 2 mm and pedicel is 19 ± 1.6 mm long (Fig. 2e); peduncle and pedicel with dense crisped indumenta. Calyx segments are divided almost to the base; sepals are 0.55 ± 0.07 × 1.90 ± 0.14 mm, lanceolate, acuminate at apex, with dense crisped indumenta. Corolla is rotate, white; petals are reflexed, 3.01 ± 0.20 × 6.50 ± 0.30 mm, abaxially glabrous, adaxially with lanate indument along right margins, ovate, acute at apex (Fig. 8a–b). The gynostegial corona is greenish-yellow or purple toned, with five separate segments inserted at 1–1.5 mm above base of ginostegial column, the same length as the gynostegium; corona segments are 4.43 ± 0.22 mm long, succulent, urceolately scaphoid, apically truncate with two falcate recurved teeth on the inner side (Fig. 8c–d). Stamens are 0.33 ± 0.06 × 2.90 ± 0.10 mm; anthers have an apical appendage postgenitally fused to style-head, membranous margins are not lignified along the both sides (Fig. 8e–f). The style-head is unlobed, broad and slightly convex; pistil is 4.67 ± 0.15 mm long (Fig. 8g–h).

Palynological properties

Periplocoideae

Pollen grains are arranged in tetrads which are derived from two adjacent anther thecae, form a loosely connected pollen mass at anthesis and shed onto the spoon-shaped translators composed of a basal adhesive disc, a stalk, and an apical receptacle (Figs. 9a–b, 10a–f).

Periploca gracilis Boiss. in Fl. Orient. 4: 50 (1875) [43]*:* Pollen grains are 13.8 ± 1.90 × 16.8 ± 2.07 µm, 6–8 porate, arranged in rhomboidal or decussate tetrads; tetrads are 28.1 ± 2.31 × 33.3 ± 2.69 µm (rhomboidal), exine ornamentation is rough. Receptacle is spoon shaped, 289.5 ± 20.5 × 333.6 ± 36.5 µm; stalk is 75.8 ± 6.91 × 145.8 ± 8.92 µm; adhesive disc is 135.4 ± 20.1 × 158.1 ± 118.1 µm (Figs. 9a, 10a–c).

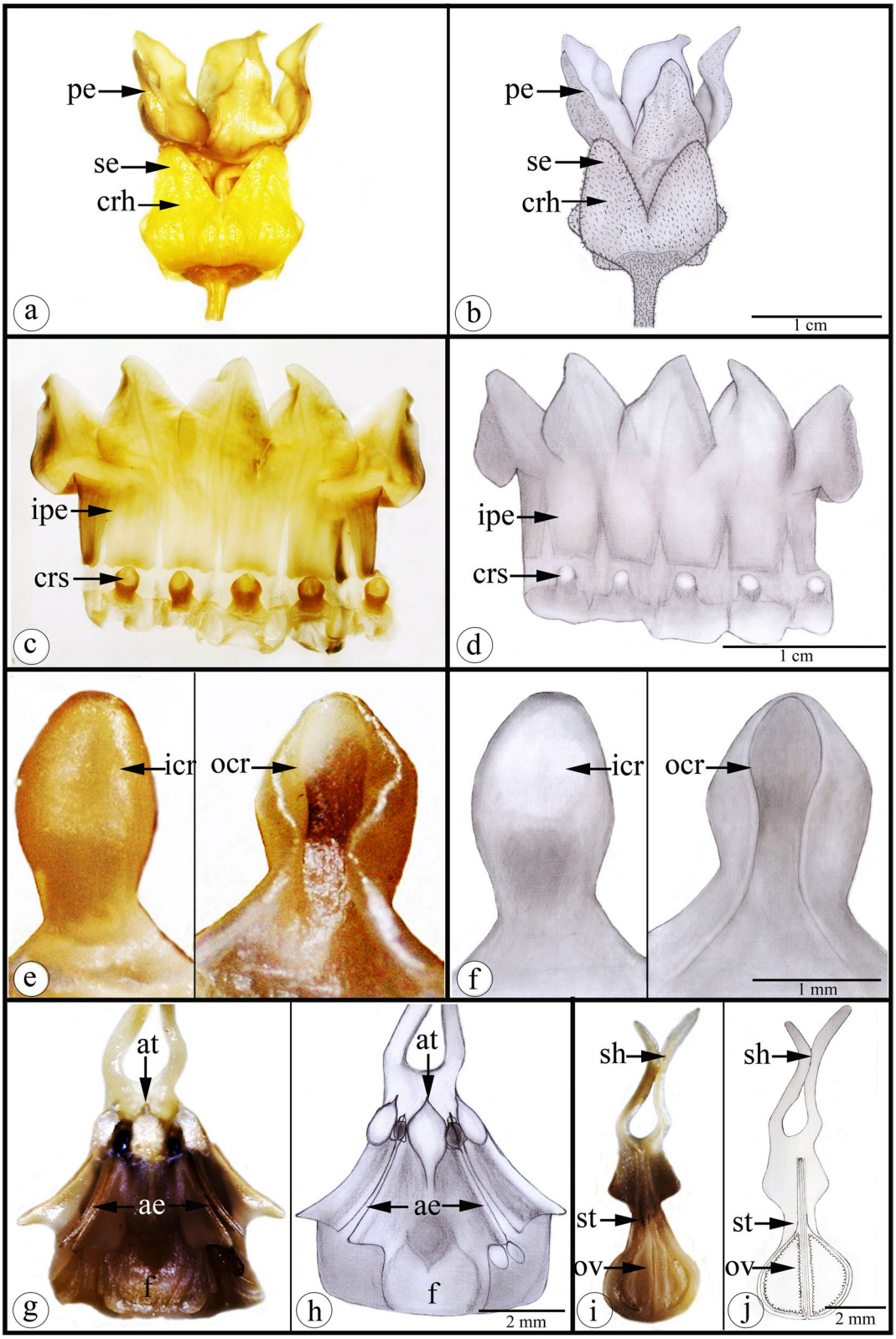


Fig. 3 Floral structures of *Araujia sericifera* (S. Güven 185 & S. Makbul), (**a**-**d**) Corolla, (**e**–**f**) Corona, (**g**-**h**) Stamens, (**i**-**j**) Pistil, (**a**, **c**, **e**, **g**, **i**) Stereomicroscope image, (**b**, **d**, **f**, **h**, **j**) Graphical representation (ae: anther edge, at: anther tip, crh: crisped hair, crs: corona segment, f: filament, icr: inner side of corona, ipe: inner side of petal, ocr: outer side of corona, ov: ovary, pe: petal, se: sepal, sh: style-head, st: style)

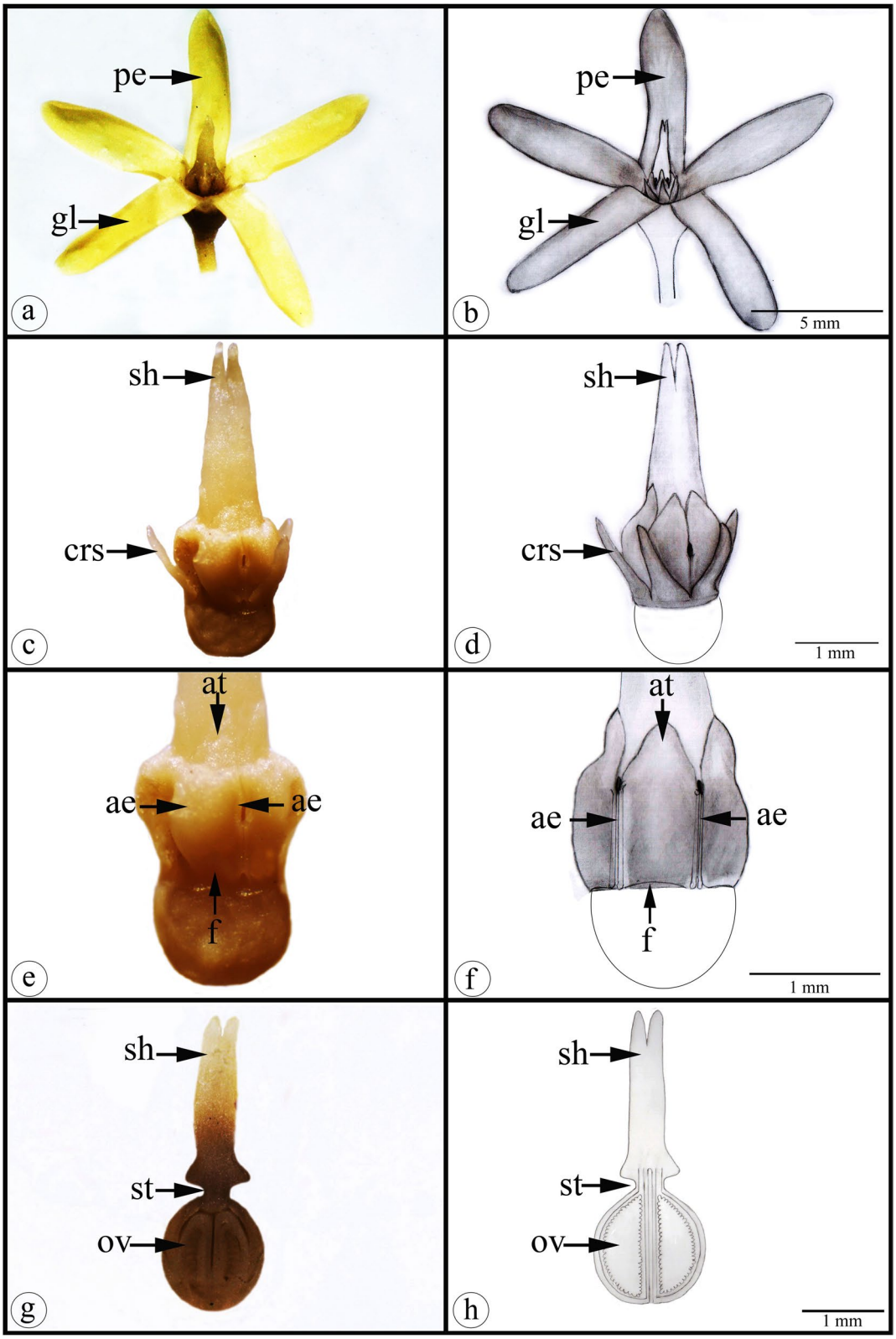


Fig. 4 Floral structures of *Cionura erecta* (S. Güven 92 & S. Makbul), (**a**-**b**) Corolla, (**c**-**d**) Corona, (**e**–**f**) Stamens, (**g**-**h**) Pistil, (**a**, **c**, **e**, **g**) Stereomicroscope image, (**b**, **d**, **f**, **h**) Graphical representation (ae: anther edge, at: anther tip, crs: corona segment, f: filament, gl: glabrous, ov: ovary, pe: petal, se: sepal, sh: style-head, st: style)

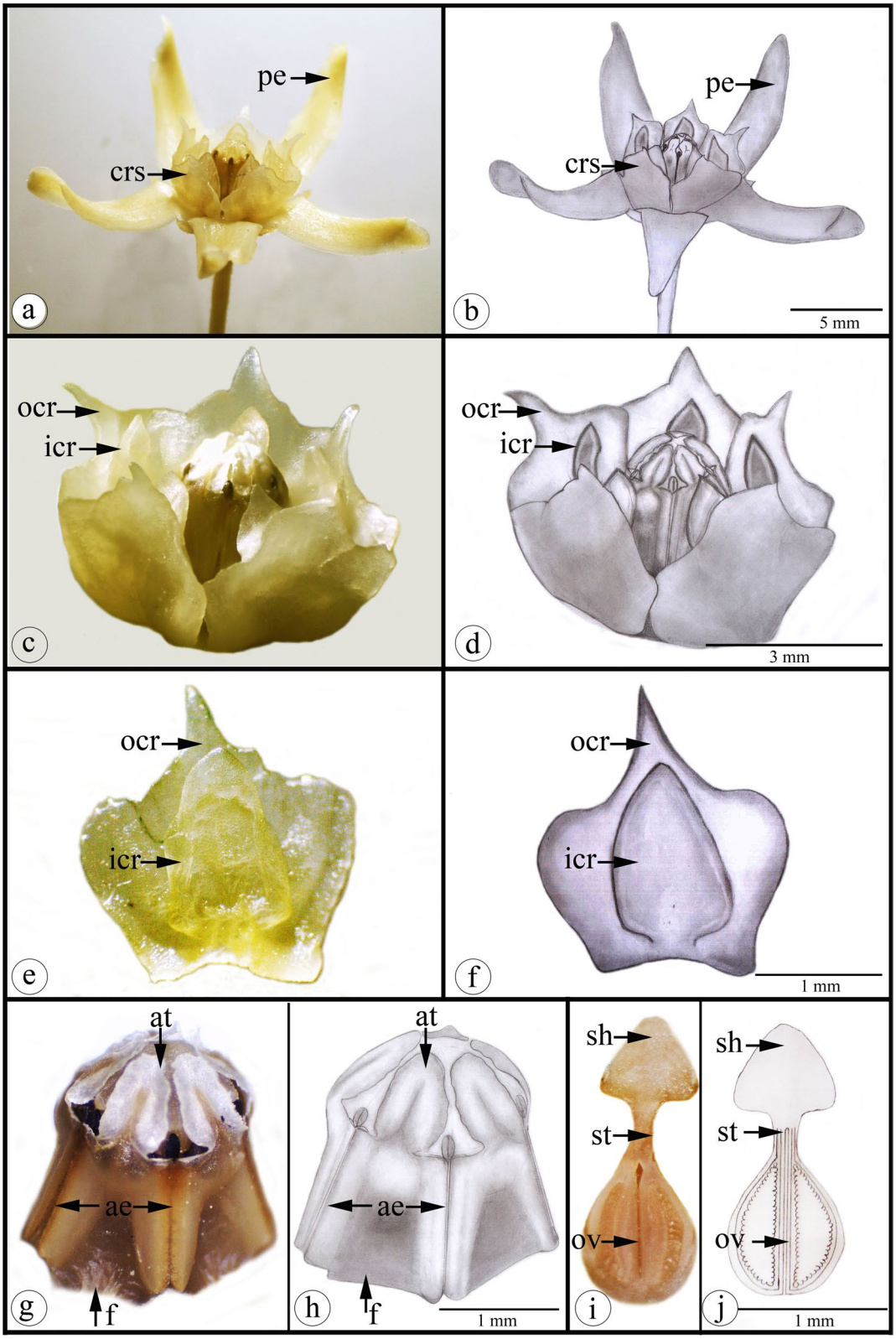


Fig. 5 Floral structures of *Cynanchum acutum* subsp. *acutum* (S. Güven 188 & S. Makbul), (**a**-**b**) Corolla, (**c**-**d**) Corona with free segments, (**e**–**f**) Corona segment structure, (**g**-**h**) Stamens, (**i**-**j**) Pistil, (**a**, **c**, **e**, **g**, **i**) Stereomicroscope image, (**b**, **d**, **f**, **h**, **j**) Graphical representation (ae: anther edge, at: anther tip, crs: corona segment, f: filament, icr: inner corona lobe, ocr: outer corona lobe, ov: ovary, pe: petal, sh: style-head, st: style)

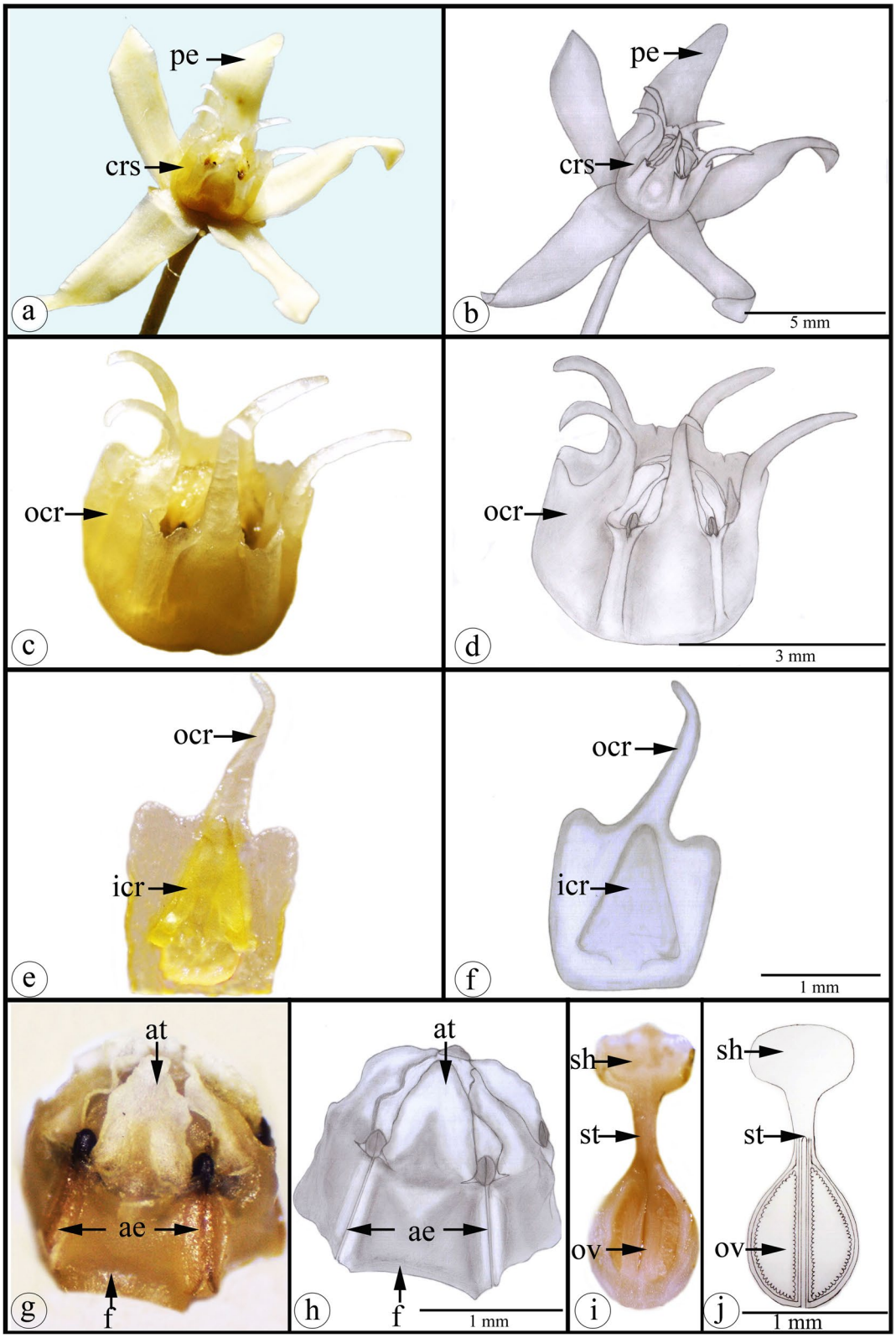


Fig. 6 Floral structures of *Cynanchum acutum* subsp. *acutum* (S. Güven 183 & S. Makbul), (**a**-**b**) Corolla, (**c**-**d**) Corona with united segments, (e–f) Corona segment structure, (**g**-**h**) Stamens, (**i**-**j**) Pistil, (**a**, **c**, **e**, **g**, **i**) Stereomicroscope image; (**b**, **d**, **f**, **h**, **j**) Graphical representation (ae: anther edge, at: anther tip, crs: corona segment, f: filament, icr: inner corona lobe, ocr: outer corona lobe, ov: ovary, pe: petal, sh: style-head, st: style)

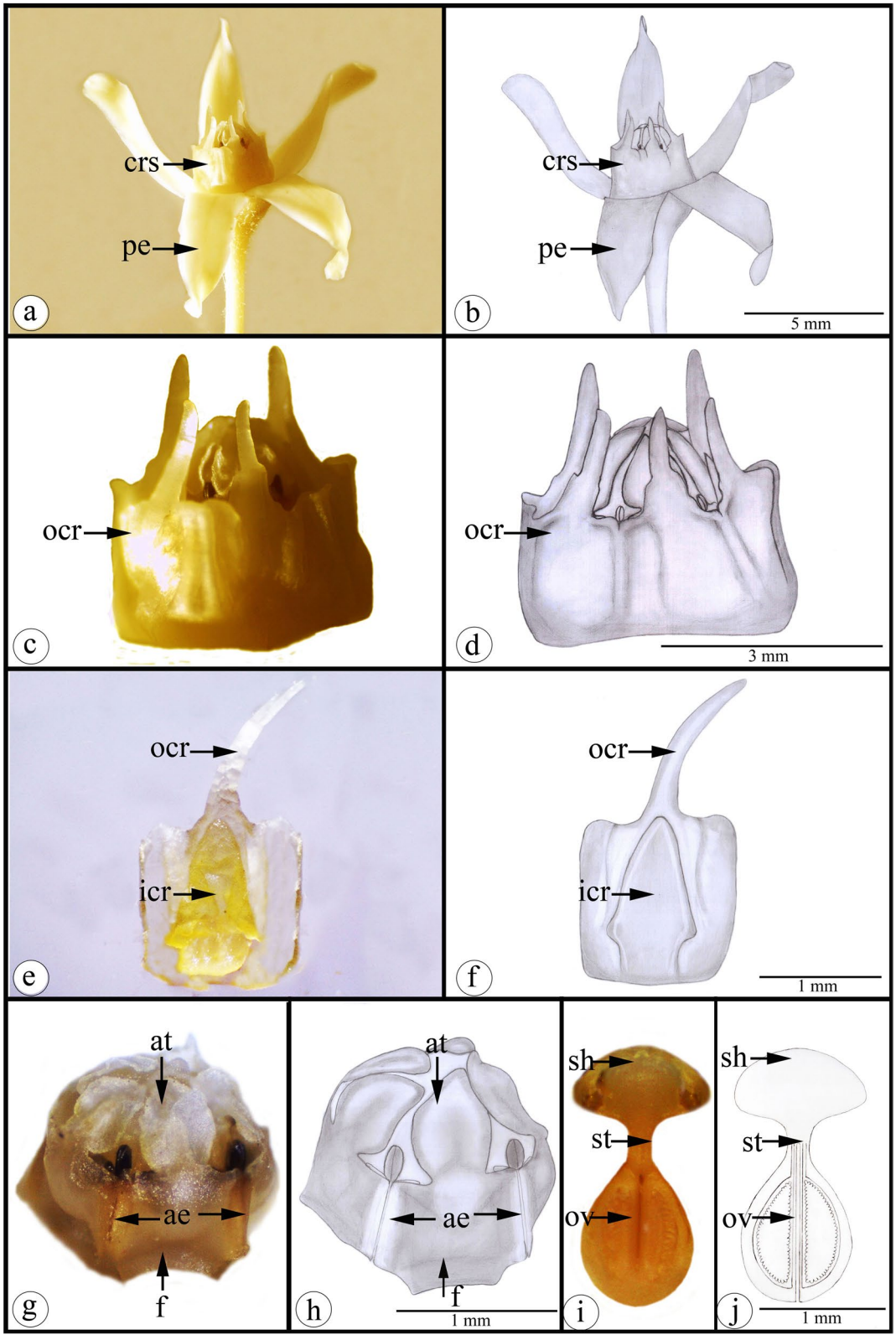


Fig. 7 Floral structures of *Cynanchum acutum* subsp. *sibiricum* (S. Güven 06 & S. Makbul), (**a**-**b**) Corolla, (**c**-**d**) Corona with united segments, (**e**–**f**) Corona segment structure, (**g**-**h**) Stamens, (**i**-**j**) Pistil, (**a**, **c**, **e**, **g**, **i**) Stereomicroscope image, (**b**, **d**, **f**, **h**, **j**) Graphical representation (ae: anther edge, at: anther tip, crs: corona segment, f: filament, icr: inner corona lobe, ocr: outer corona lobe, ov: ovary, pe: petal, sh: style-head, st: style)

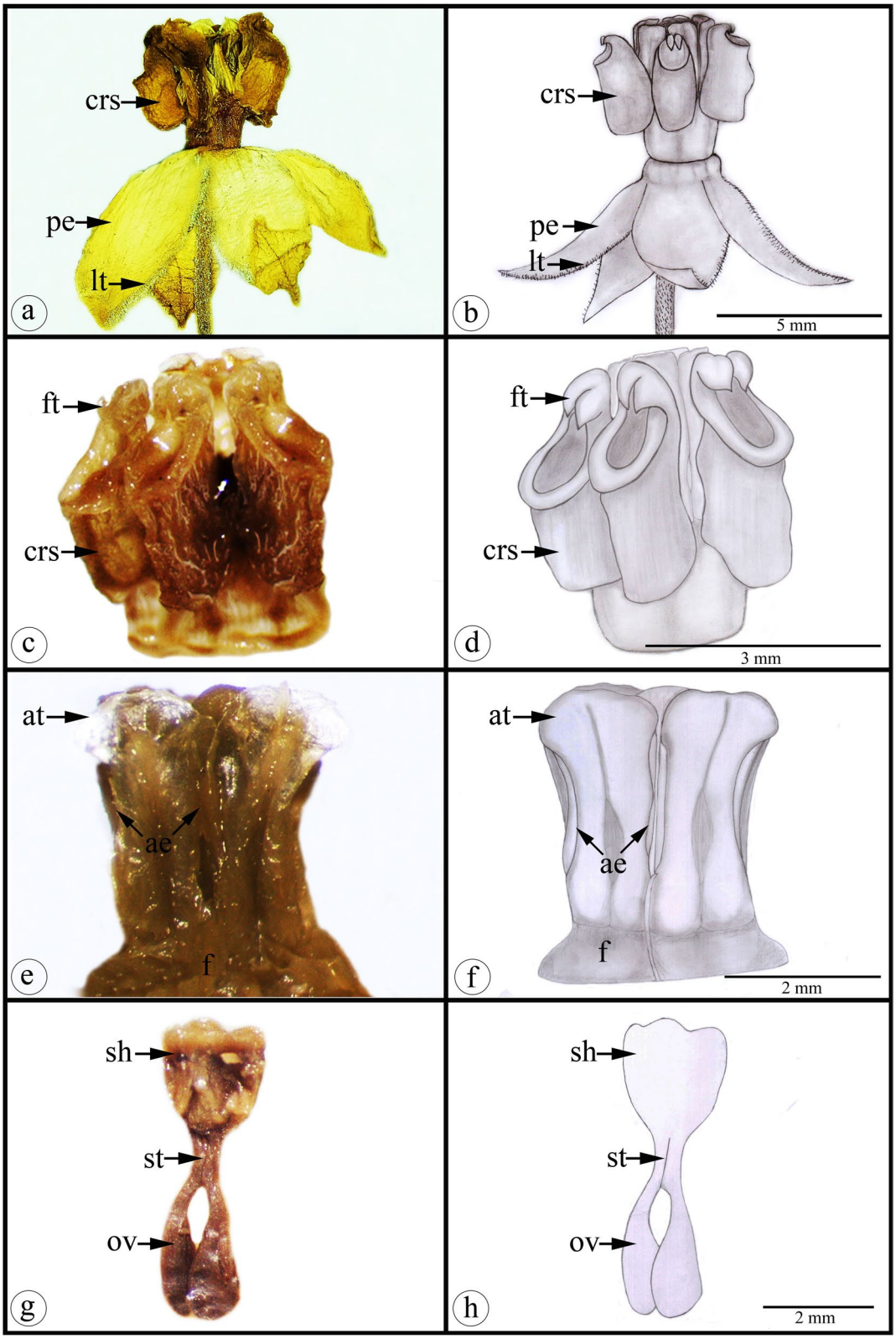


Fig. 8 Floral structures of *Gomphocarpus fruticosus* (A. Baytop 23571), (**a**-**b**) Corolla, (**c**-**d**) Corona, (**e**–**f**) Stamens, (**g**-**h**) Pistil, (**a**, **c**, **e**, **g**) Stereomicroscope image, (**b**, **d**, **f**, **h**) Graphical representation (ae: anther edge, at: anther tip, crs: corona segment, f: filament, ft: falcate teeth, lt: lanate hair, ov: ovary, pe: petal, sh: style-head, st: style)

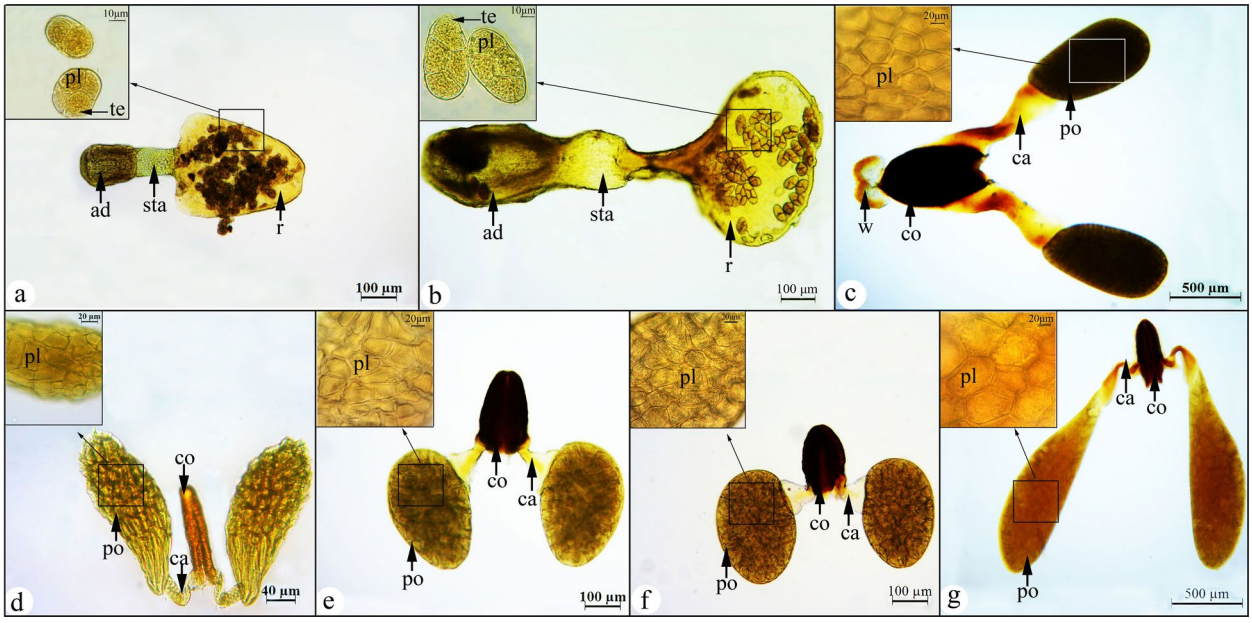


Fig. 9 Pollen structures in light microscopy of (**a**) *Periploca gracilis* (S. Güven 177 & S. Makbul), (**b**) *Periploca graeca* (S. Güven 178 & S. Makbul), (**c**) *Araujia sericifera* (S. Güven 185 & S. Makbul), (**d**) *Cionura erecta* (S. Güven 92 & S. Makbul), (**e**) *Cynanchum acutum* subsp. *acutum* (S. Güven 188 & S. Makbul), (**f**) *Cynanchum acutum* subsp. *sibiricum* (S. Güven 06 & S. Makbul), (**g**) *Gomphocarpus fruticosus* (A. Baytop 23571) (ad: adhesive disc, ca: caudicle, co: corpusculum, pl: pollen grain, po: pollinium, r: receptacle, sta: stalk, t: tetrad, w: wing)

Periploca graeca L. in Sp. Pl.: 211 (1753) [44]*:* Pollen grains are 18.9 ± 2.55 × 23.15 ± 2.69 µm, 6–8-porate, arranged in rhomboidal or decussate tetrads; tetrads are 34.3 ± 2,31 × 60.4 ± 6.05 µm (rhomboidal), exine ornamentation is rough. Receptacle is elliptical, 580.1 ± 35.2 × 648.5 ± 36.9 µm; stalk is 167.5 ± 8.76 × 219.6 ± 18.35 µm; adhesive disc is 232.5 ± 32.8 × 442.1 ± 30.3 µm (Figs. 9b, 10d–f).

Asclepiadoideae

Pollen grains in each anther lobe are united as a single sac called pollinium and transported in the form of pollinarium, which consists of a pair of pollinia (devired from two adjacent anther lobes) attached to a central corpusculum by two flexible arms (Figs. 9c–g, 10g–l, 11a–i).

Araujia sericifera: Pollinium is pendulous, ovate, 482.86 ± 21.46 × 888.09 ± 31.09 µm; pollen grains are 35.45 ± 4.84 × 55.72 ± 7.63 µm, inaperturate, ornamentation is psilate. Corpusculum is ovate, 444.21 ± 18.86 × 746.30 ± 32.06 µm, winged at base, wings are 410.10 ± 11.74 × 491.25 ± 32.05 µm; caudicle is flattened, attached to the corpusculum laterally and to the pollinium basally, 298.32 ± 18.34 × 784.41 ± 15.18 µm (Figs. 9c, 10g–i).

Cionura erecta: Pollinium is erect, obovate, 98.96 ± 9.65 × 255.01 ± 15.84 µm; pollen grains are 22.25 ± 5.35 × 29.81 ± 6.05 µm, inaperturate, ornamentation is psilate. Corpusculum is oblong, 30.39 ± 4.36 × 141.7 ± 14.4 µm; caudicle is cylindrical, attached to the corpusculum sub-apically and to the pollinium sub-basally 16.1 ± 2.1 × 98.5 ± 9.6 (Figs. 9d, 10j–l).

Cynanchum acutum: Pollinium is pendulous, ovate, 205.61 ± 11.21 × 314.80 ± 14.56 µm; pollen grains are 33.35 ± 4.56 × 43.09 ± 5.02 µm, inaperturate, ornamentation is psilate or sparsely rough. Corpusculum is ovate, 146.72 ± 13.83 × 228.68 ± 11.88 µm; caudicle is conical, attached to the corpusculum sub-apically and to the pollinium sub-basally 74.33 ± 6.99 × 111.85 ± 7.57 µm (Figs. 9e–f, 11a–f).

Gomphocarpus fruticosus: Pollinium is pendulous, obovate, 380.5 ± 11.4 × 1414.3 ± 31.7 µm; pollen grains are 60.1 ± 7.63 × 84.7 ± 9.75 µm, inaperturate, with crystals on the surface. Corpusculum is ovate, 117.5 ± 7.59 × 463.8 ± 24.3; caudicle is cylindrical, attached to the corpusculum sub-apically and to the pollinium basally 173.1 ± 12.8 × 384.7 ± 5.47 µm (Figs. 9g, 11g–i).

Numerical outputs

The dendrogram resulting from UPGMA is given in Fig. 12. This dendrogram showed that *A. sericifera* (labeled a) was clearly separated from the remaining six taxa at a 48% similarity level. The remaining four Asclepiadoideae taxa (labeled b) and two Periplocoideae taxa (labeled c) were grouped under the same main cluster at approximately 55% similarity level. In cluster "b", *G. fruticosus* was positioned as a distinct lineage within this cluster at a 72% similarity level, separating it from the *C. acutum* and *C. erecta* groups. Individuals of *C. acutum* clustered at the 94% similarity level, and individuals of *C. erecta*

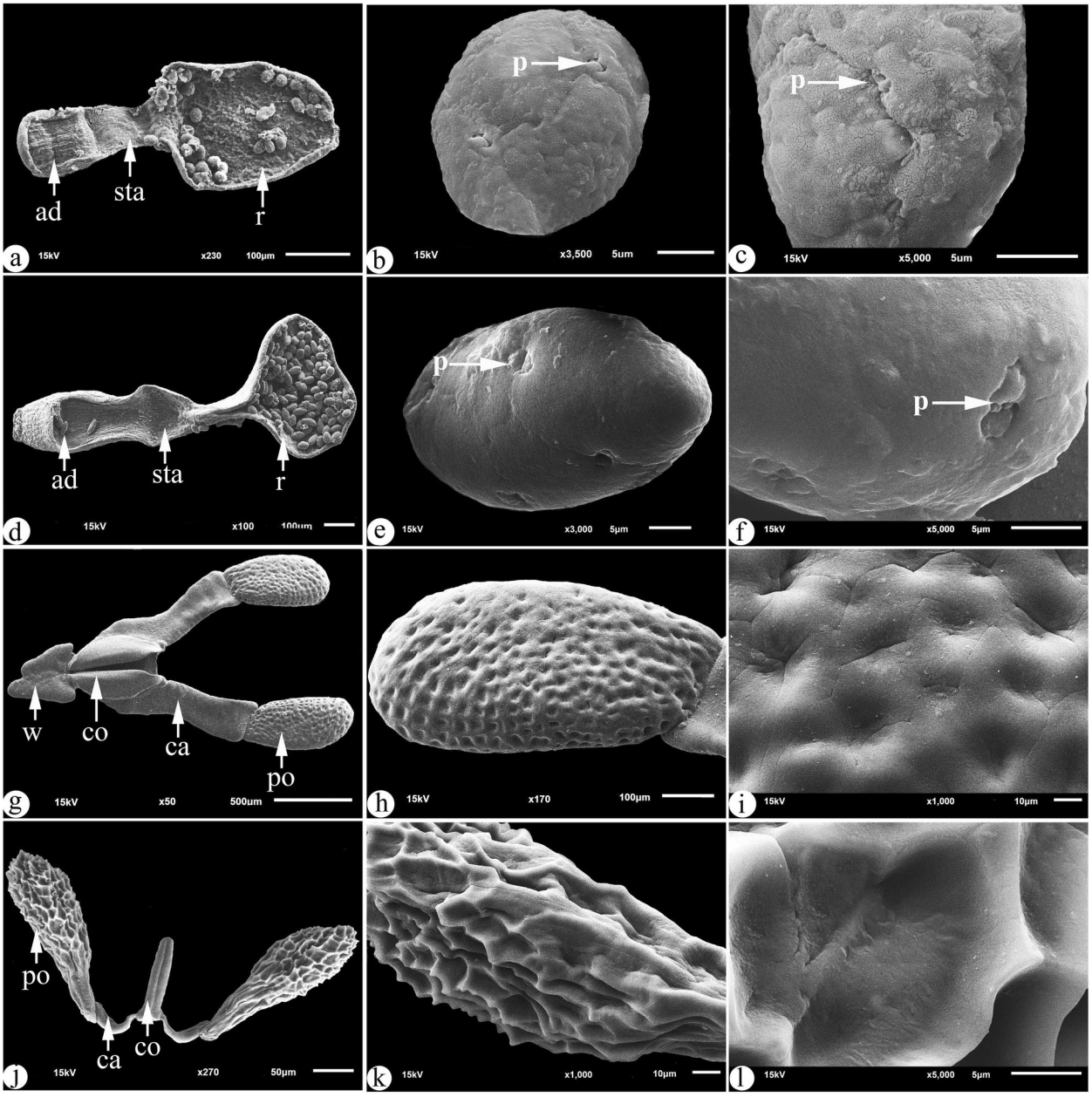


Fig. 10 Pollen structures in SEM of (**a**-**c**) *Periploca gracilis* (S. Güven 177 & S. Makbul), (**d**-**f**) *Periploca graeca* (S. Güven 178 & S. Makbul), (**g**-**i**) *Araujia sericifera* (S. Güven 185 & S. Makbul), (**j**-**l**) *Cionura erecta* (S. Güven 92 & S. Makbul), (**a**, **d**, **g**, **j**) Pollen translator, (**b**, **e**) Rhomboidal tetrad, (**h**, **k**) Pollinium, (**c**, **f**, **i**, **l**) Pollen ornamentation (ad: adhesive disc, ca: caudicle, co: corpusculum, po: pollinium, r: receptacle, sta: stalk, w: wing, p: pore)

clustered at the 96% similarity level, both showing very high within-group similarity. In cluster "c", the two investigated *Periploca* species (Periplocoideae) were grouped at an 81% similarity level, whereas the both *P. graeca* individuals, forming a highly cohesive group and separating from *P. gracilis* at high similarity level (98%).

Principal components analysis of 13 taxa and 24 morphological and palynological traits projected on the first two components (PC-1 and PC-2) are given in Fig. 13a and b, respectively. The eigenvalues of the first, second, and third component in percentages are 97.74%, 1.86%, 0.24%, respectively (Table 3). The first three components explain 99.84% of the total variation among the investigated taxa. These three components emphasize that pedicel length (X_1), pollen grain width (X_{22}), pollen grain length (X_{23}), sepal length (X_4), petal length (X_8), and pistil length (X_{18}) are the most valuable traits contributing to separation of the examined taxa (Table 3). The PCA score and loading plots show a clear separation of *A. sericifera* along the PC-2 axis, mainly driven by petal length (X_8), while sepal length (X_4) and pistil length (X_{18}) contribute less. Along PC-1, pollen grain length (X_{23}) and

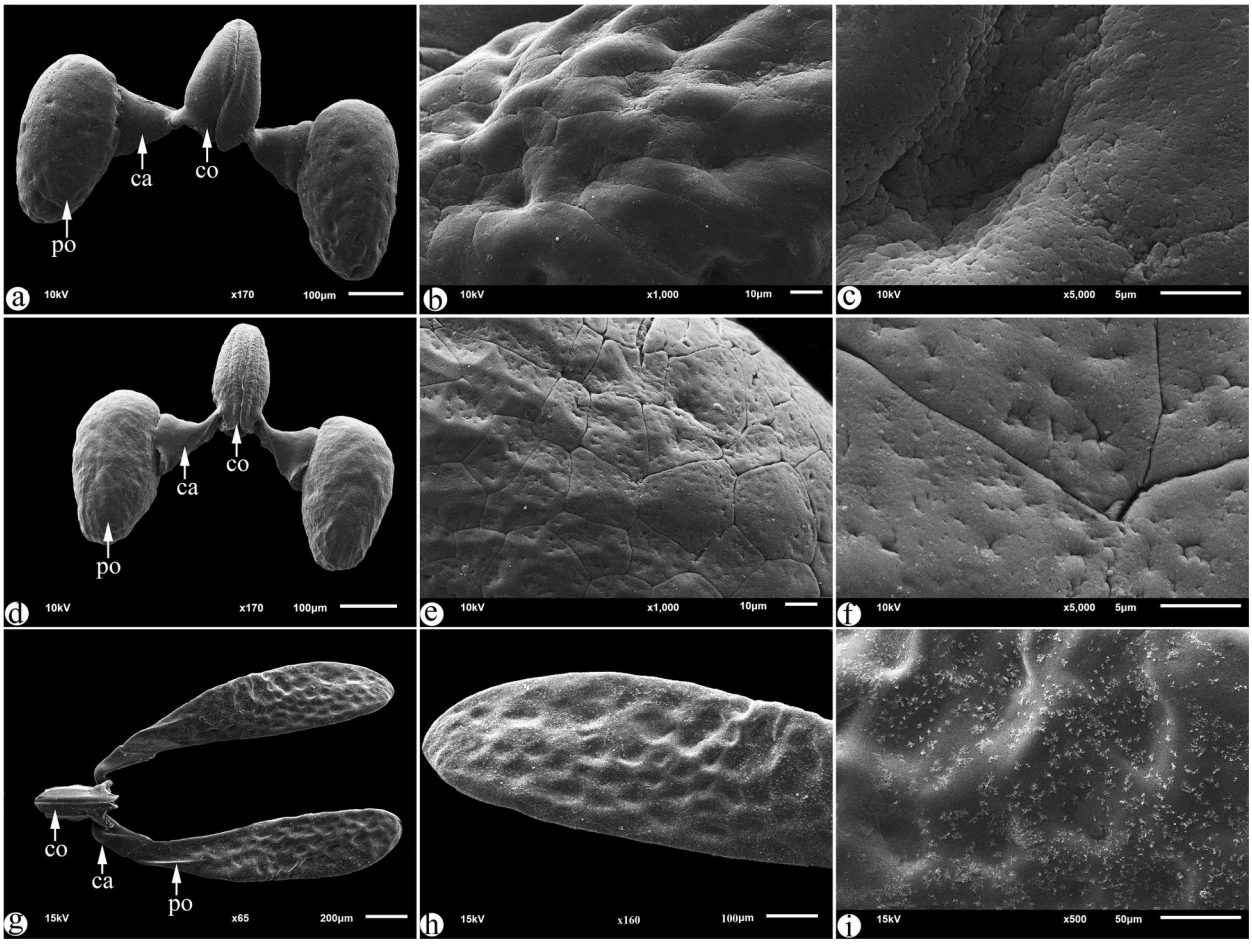


Fig. 11 Pollen structures in SEM of (**a**-**c**) *Cynanchum acutum* subsp. *acutum* (S. Güven 188 & S. Makbul), (**d**-**f**) *Cynanchum acutum* subsp. *sibiricum* (S. Güven 06 & S. Makbul), (**g**-**i**) *Gomphocarpus fruticosus* (A. Baytop 23571), (**a**, **d**, **g**) Pollen translator, (**b**, **e**, **h**) Pollinium, (**c**, **f**, **i**) Pollen ornamentation. (ca: caudicle, co: corpusculum, po: pollinium)

width (X_{22}) show strong contributions, particularly in the separation of taxa such as *G. fruticosus*, whereas pedicel length (X_1) has a weaker effect.

Overall, both UPGMA and PCA analyses are in agreement and support the separation of the investigated taxa, particularly *A. sericifera* and *G. fruticosus*, based on the studied floral and pollen characters.

Floral and palynological key to the investigated Periplocoideae and Asclepiadoideae taxa of Türkiye

This dichotomous key based on floral and palynological data regarding the investigated Periplocoideae and Asclepiadoideae taxa was developed mainly according to the Flora of Türkiye [20], Flora of Russia [34], and Flora of Europe [35]. The key reflects the main groupings observed in the dendrogram and the patterns of variation highlighted by the PCA analysis, thus providing a practical tool for identifying the studied taxa in accordance with their morphological and palynological differentiation.

1. Corona corolline, segments filiform, basally trisegmented without an inner lobe (Fig. 12); anthers abaxially with hispid indumenta (Fig. 1a), 4-locular; pollen grains in tetrads, translators spoon-shaped, composed of a basal adhesive disc, a stalk, and an apical receptacle (Fig. 1b)… ….[Subfamily Periplocoideae] 2.

—Corona corolline with succulent segments, or gynostegial with laminaris or succulent segments, basally unsegmented, or with an inner lobe (Fig. 12); anthers glabrous (Fig. 1c, e), 2-locular; pollen grains in pollinia, translators clip-like, composed of a central corpusculum joined to two flexible arms called caudicles (Fig. 1d, f) … … … … … …….Subfamily Asclepiadoideae] 3.

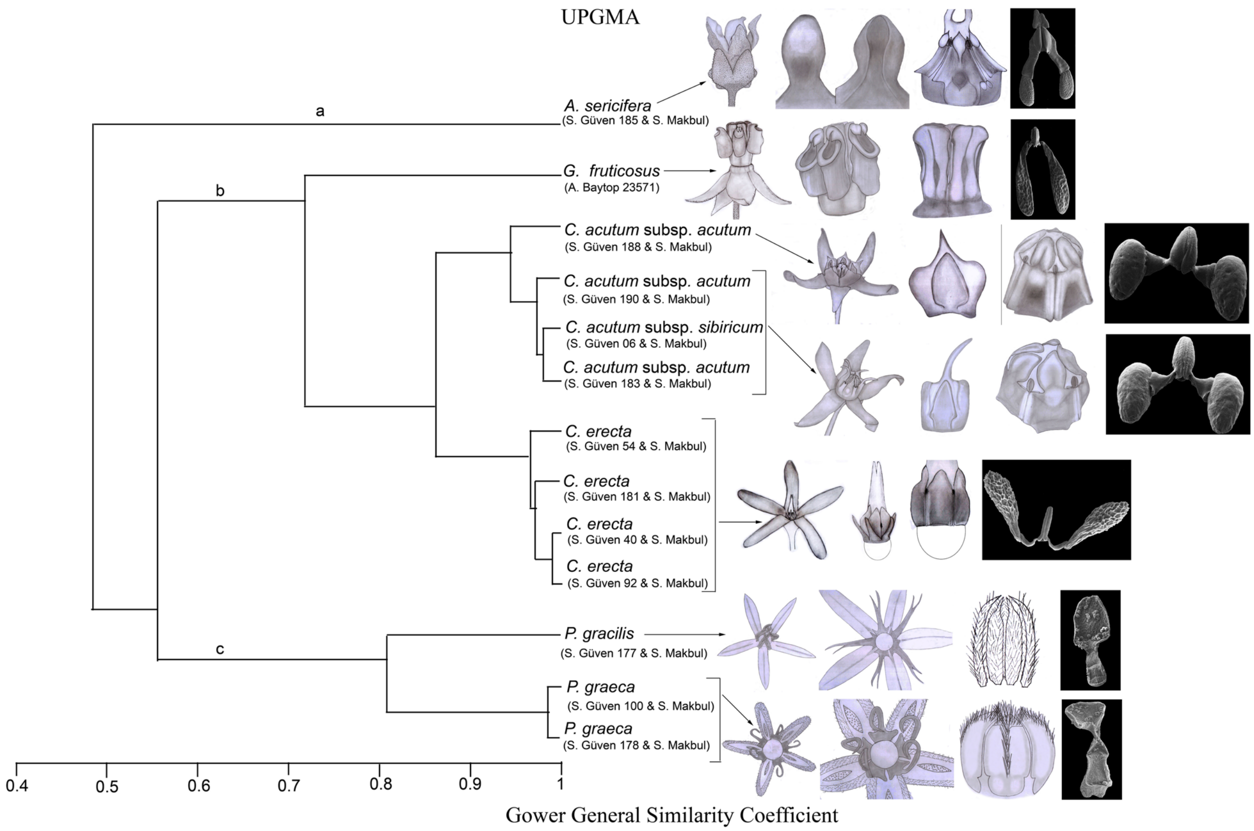


Fig. 12 Dendrogram resulting from cluster analysis-UPGMA of the investigated Periplocoideae and Asclepiadoideae taxa based on 24 floral and pollen characters (Figures on the dendrogram represent the corolla, corona, stamen and pollinarium of the taxa, respectively)

2. Petals white or greenish yellow, glabrous; corona segments apically bifid (Fig. 12); receptacle spoon shaped (Fig. 9a), 260–320 µm wide … … … … … … … … … … … … … … … … … …..1. *Periploca gracilis.*

   —Petals purple-violet, hairy along margins; corona segments unsegmented (Fig. 12); receptacle elliptical (Fig. 9b), 570–680 µm wide … ….. … … … ……. … … … … … …. …….2. *Periploca graeca.*

3. Corolla campanulate, petals 22–25 mm long; corona corolline (Fig. 12); corpusculum winged (Fig. 9c) … …….. … … … … … … … … … … … …….. … … … … … ….…. … …..3. *Araujia sericifera*

   —Corolla rotate, petals 2–10 mm long; corona gynostegial (Fig. 12); corpusculum wingless (Figs. 9j, 10a, d, g) … … … … … …. …. … … … ……..4

4. Petal hairy; corona succulent (Fig. 8d); pollinium lenght higher than 1 mm …….0.6. *Gomphocarpus fruticosus*

   —Petal glabrous; corona laminaris (Figs. 4d, 5d, 6d, 7d); pollinium lenght less than 1 mm … …..5

5. Corona segment without inner lobe (Fig. 4d); stigma bifid (Fig. 4h); pollinia erect (Fig. 9d) …..4. *Cionura erecta*

   —Corona segment with a basal inner lobe (Figs. 5f, 6f, 7f); stigma unsegmented (Figs. 5j, 6j, 7j); pollinia pendulous (Fig. 9e-f) … … … … … … … … … … … … … … ……5. *Cynanchum acutum.*

Discussion

Floral features

The inflorescence type of the studied Asclepiadoideae taxa is basically a cyme developed mainly on axillary

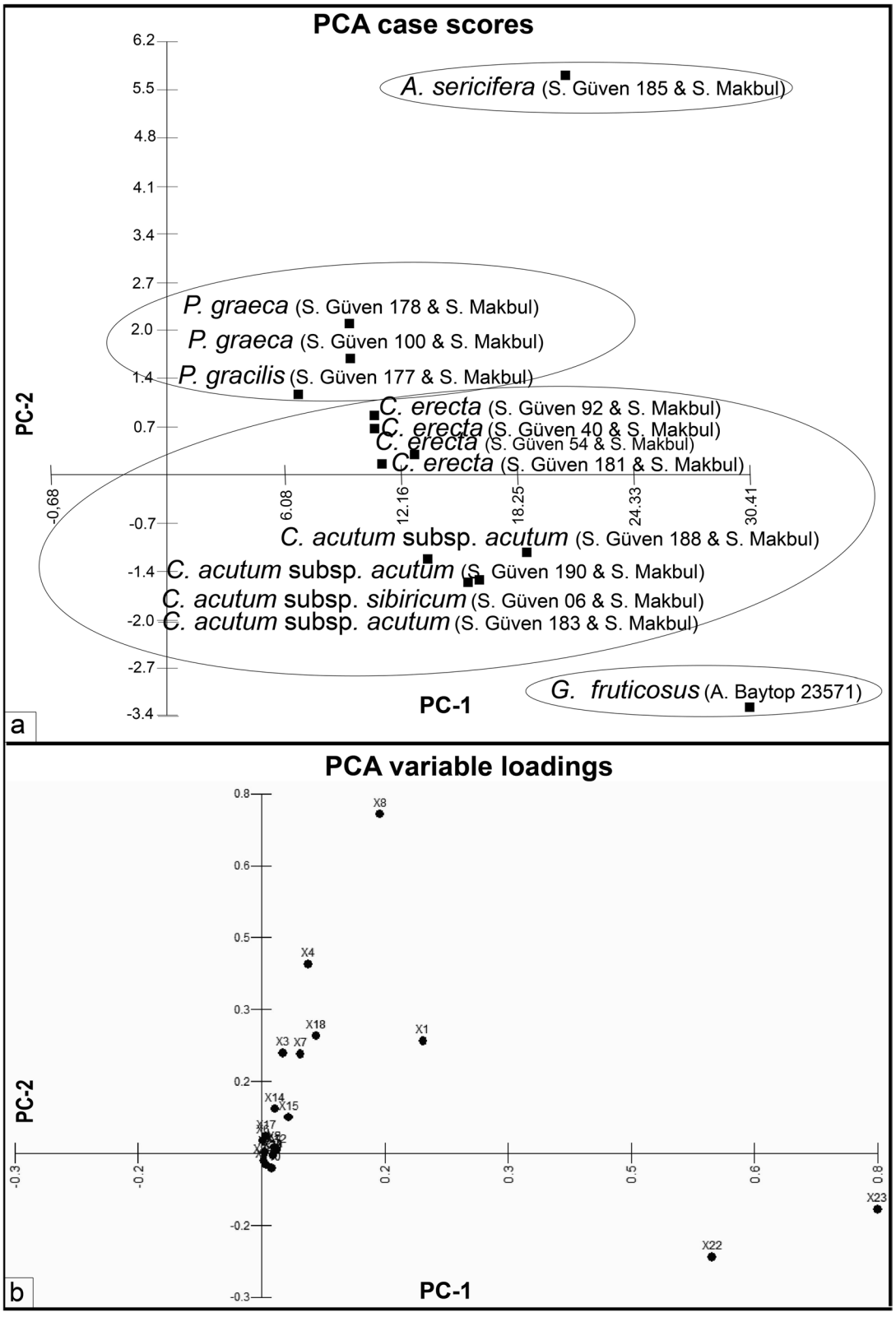


Fig. 13 Ordination resulting from principal components analysis (PCA) of the investigated Periplocoideae and Asclepiadoideae taxa based on 24 floral and pollen characters, (**a**) PCA case scores, (**b**) PCA variable loadings

Table 3 Eigenvalues of the characters on the first five principal components (PC1, PC2, PC3, PC4, PC5)

Sym.	Axis 1	Axis 2	Axis 3	Axis 4	Axis 5
X_1	**0.203**	0.243	0.423	**-0.596**	-0.150
X_2	0.016	0.014	0.084	0.079	-0.108
X_3	0.027	0.216	-0.222	0.138	-0.041
X_4	0.059	**0.407**	**-0.473**	0.269	-0.119
X_5	0.016	0.014	0.084	0.079	-0.108
X_6	0.002	0.027	-0.056	0.000	-0.021
X_7	0.049	0.214	-0.015	0.035	0.194
X_8	0.149	**0.731**	0.315	0.103	0.155
X_9	0.005	0.003	0.052	-0.043	0.271
X_{10}	0.013	-0.032	0.064	0.031	-0.275
X_{11}	0.006	-0.025	-0.007	0.254	-0.077
X_{12}	0.019	0.007	-0.072	-0.061	-0.233
X_{13}	0.015	-0.005	0.008	0.031	**-0.295**
X_{14}	0.017	0.096	-0.059	0.176	-0.033
X_{15}	0.034	0.077	-0.019	0.124	0.203
X_{16}	0.015	-0.005	0.008	0.031	**-0.296**
X_{17}	0.006	0.036	0.039	-0.131	**-0.302**
X_{18}	0.069	**0.254**	-0.142	-0.036	-0.281
X_{19}	0.015	-0.005	0.008	0.031	**-0.296**
X_{20}	0.015	-0.005	0.008	0.031	**-0.296**
X_{21}	0.015	-0.005	0.008	0.031	**-0.296**
X_{22}	**0.567**	-0.224	**0.445**	**0.540**	-0.035
X_{23}	**0.775**	-0.121	**-0.442**	**-0.298**	0.095
X_{24}	0.003	-0.016	-0.024	-0.091	0.083
Eigenvalues	3151.93	60.02	7.64	2.29	1.54
Percentage	97.74	1.86	0.24	0.07	0.05
Cum. Percentage	97.74	99.59	99.84	99.91	99.95

and/or terminal parts, except for *A. sericifera* with solitary flower per node (Fig. 2). Floral features, commonly used as key characters in many floras and revision studies, had always played an important role in explaining the evolutionary relationships among the major groups of Apocynaceae [4, 6]. Previous morphological studies showed that Periplocoideae were characterized with the type of inflorescence varying from terminal and/or axillary branching thyrses to extra-axillary branching ones with racemose, corymbose or sciadioidal inflorescences [1, 24]. However, the Asclepiadoideae were reported to exhibit mostly extra axillary, and less commonly axillary inflorescences, which were rarely solitary (one inflorescence per node) or paired (two inflorescences per node) [1], consistent with the observations of the present study.

Significant differences are determined within the examined Asclepiadoideae taxa by means of corolla morphology at genus level. In the examined Asclepiadoideae taxa, white, yellowish or pinkish petals are glabrous (*C. erecta* and *C. acutum*), or exhibite lanate indumenta along right margins (*G. fruticosus*), and white minute hairs on the abaxial side (*A. sericifera*). Two corolla types are observed in Asclepiadoideae such as rotate and campanulate. *A. sericifera* clearly differentiates from the remaining Asclepiadoideae taxa by its campanulate flowers, but the given character (X_6) is insignificant for meaningful taxonomic discrimination from the studied taxa (Table 3). Consistent with our findings, Fishbein et al. [2] stated that corolla shape within the APSA clade is highly labile due to the frequency of occurrence of campanulate, rotate, and tubular corollas and rarity of funnelform and salverform forms, than among the rauvolfioid lineages with predominant salverform corollas. Similarly, it was stated that type (campanulate/rotate), color (white, yellow, yellowish-green, blackish-purple, and brown), and pubescence (glabrous or with hirsute, lanate, pilose, and crisped indument) of corolla exhibited significant variation among the Turkish *Vincetoxicum* [22, 25] taxa at species and even sub-species levels. In addition, of the two examined Turkish *Periploca* taxa, *P. gracilis* with uniform white or greenish-yellow, and glabrous petals, could easily be distinguished from *P. graeca* in terms of petal

color (purple-violet) and pubescence (with villous indument along margins). However, principal components analysis showed that corolla type (X_6) and pubescence of petal inner surface (X_9) were not among the most important traits to distinguish the examined taxa in the present study (Table 3).

In the present study, the observed variation in corona structure supports its diagnostic value in distinguishing closely related taxa. Among the examined Asclepiadoideae taxa, only *A. sericifera* has corolline corona, while the remaining four Asclepiadoideae taxa exhibit gynostegial corona (Fig. 12). It has been observed that the two Turkish Periplocoideae species, which are characterized with filiform, basally tri-segmented corolline corona segments, are also quite different by means of corona shape. *P. gracilis* has apically bifid corona segments, while those of *P. graeca* are unsegmented. The significance of corona is also demonstrated in previous studies on Turkish *Vincetoxicum* taxa [22, 25]. Corona is a special floral structure and plays a key role in pollination of the Apocynaceae taxa by producing and storing nectar to attract pollinators [45], and guiding body parts of insects for pollinia removal and insertion [5, 6]. Two main types of corona were defined for Apocynaceae taxa depending on their location: (I) corolline corona arising from corolla, and (II) gynostegial corona derived from androecium. There is a great variety of corona forms as rings, scales, pads, or cups, often with highly specialized components within the Apocynaceae. Corolline coronas could be seen in the form of free lobes, or fused to varying degrees into petaloid structures, whereas gynostegial corona displayed two basic forms composed of free staminal segments or united staminal segments joined to eachother by smaller interstaminal parts [2, 6, 46, 47]. Fishbein et al. [2] confirmed that the corolline corona was an ancestral character, indicating an evolutionary transition within the family associated with increasing floral specialization and pollination efficiency. However, no homogeneity was determined in the corona morphology within the large groups of the Apocynaceae family. In rauvolfioids, apocynoids and Periplocoideae coronas were mostly corolline, whereas the majority of the Asclepiadoideae were chacterized by gynostegial coronas [1, 2], reflecting a general evolutionary trend toward derived corona forms in Asclepiadoideae. The examined Periplocoideae taxa, representing a more basal group, are characterized by the ancestral corolline corona. In contrast, the majority of the examined Asclepiadoideae taxa, considered a more derived lineage, predominantly exhibit the gynostegial corona. This pattern indicates an evolutionary shift from corolline to gynostegial corona within the family, supporting the generally accepted view.

Significant differences in gynostegium morphology were observed between the two studied subfamilies. In the Asclepiadoideae taxa examined, the gynostegium is characterized by glabrous anthers with lignified guide rails along both margins (except in *G. fruticosus*, where guide rails are absent). The style-head is unlobed in *C. acutum* and *G. fruticosus*, but bifid in *A. sericifera* and *C. erecta*. Also, the gynostegia of the two Turkish Periplocoideae species are characterized by anthers with non-lignified, membranous margins, abaxially hispid indumentum, and an unlobed style-head. Principal components analyses also revealed that pubescence of the anther (X_{16}), shape of style-head (X_{17}), and length of pistil (X_{18}) are among the partially effective characters in delimiting the investigated taxa at both subfamily and genus levels (Table 3). The gynostegium is a key evolutionary feature in Apocynaceae, formed by the fusion of anthers and the style-head. It is absent in basal groups but becomes progressively more complex in Periplocoideae, Secamonoideae, and Asclepiadoideae. This increasing structural complexity is associated with enhanced pollination efficiency and specialization, reflecting both phylogenetic relationships and functional adaptation. The patterns observed in the present study are in agreement with this evolutionary trend and further support the role of gynostegium morphology in distinguishing major lineages within the family [1, 2, 5].

Palynological features

Style-head differentiation and pollen morphology constitute the main pathways for the evolution of the major groups in Apocynaceae [1]. The enlarged upper part of the postgenitally fused region, the style-head, not only performs as a stigma, but also produces adhesive components forming the transporter parts of the pollen grains in Periplocoideae and Asclepiadoideae [1, 2, 5]. The main distinguishing characters of the investigated taxa, including style-head differentiation and pollen morphology, are illustrated in Fig. 1. Pollen grains are transported in two quite specialized forms within the investigated taxa: in the form of a large tetrad mass shed onto a translator composed of a receptacle, stalk, and adhesive disc in Periplocoideae (Fig. 1b), and in the form of two pollinia linked to a central corpusculum via two caudicles (pollinarium) in Asclepiadoideae (Fig. 1d, f). The present principal components analyses revealed that pollen aggregation (X_{19}), number of tetrad mass or pollinium on a pollen translator (X_{20}), and pollen translator structure (X_{21}) were found to be partially effective characters in delimiting the investigated taxa at the subfamily level (Table 3).

Although the two examined *Periploca* species (*P. gracilis* and *P. graeca*) reflect the general palynological characteristics of the subfamily, shape of receptacle and size of translator parts differ from each other. In the investigated *P. gracilis*, receptacle is spoon shaped and receptacle,

stalk and adhesive disc is smaller in size compared to the examined *P. graeca* species with elliptical receptacle. At anthesis, pollen grains, which are arranged in rhomboidal or decussate tetrads, shed onto the receptacle from each two adjacent anther theca, form a loosely connected pollen mass. The present findings related to tetrad morphology of *P. gracilis* and *P. graeca* are compatible with those of Verhoeven and Venter [48].

In the present study, two types of pollinium shape are identified: ovate in *A. sericifera* and *C. acutum*; and obovate in *C. erecta* and *G. fruticosus*. Among the examined taxa, *A. sericifera* and *G. fruticosus* species had the largest pollinia, while *C. erecta* had the smallest pollinium. Within the Asclepiadoideae members, the pollinium shows great diversity in shape such as reniform, clavate, circular, elliptical, square, lanceolate, ovate, obovate and oblong, and this character contributes significantly to the distinction of taxa at both generic and specific levels [8, 17, 29]. Feng et al. [14] reported pollinium shape as perprolate (width/length < 0.5) for *C. acutum* subsp. *sibiricum*, unlike our data (ovate and with the rate of width/length 0.66). The data on pollinium width and length has provided useful results in distinguishing Asclepiadoideae members at both the genus and species levels as agreed by Chang et al. [13], Feng et al. [14], and Güven et al. [29].

In the current study, pollen grain surface is smooth in *A. sericifera* and *C. erecta*, psilate and sparsely rough in both subspecies of *Cynanchum*, and crystalized in *G. fruticosus*. Pollen grain surface ornamentation is among the widely used palynological characters to elucidate the taxonomic problems in developed plant groups [49]. This character varies at both the genus and species levels within the members of Asclepiadoideae [9, 11]. Mo et al. [11] reported that pollen grain surface ornamentation of some Asclepiadoideae taxa was rugose, papillose-smooth, sinuous-striate, sinuous-smooth and sulcate-granulate. Similar to our findings, pollen grain surface was reported as psilate for *C. acutum* [14, 16, 17]. Güven et al. [22, 29] reported that pollen grain surface of *Vincetoxicum* taxa varied from rugulate to gemmate. In the present paper, pollen grain width and length are important diagnostic characters, whereas pollen grain ornamentation are negligible to distinguish the examined taxa.

Among the examined taxa, majority of the taxa has pendulous pollinia with an exception to *C. erecta* with erect pollinia (Fig. 12). Pollinia orientation within Asclepiadoideae varies from erect to horizontal, or pendulous [6, 15]. This character was determined as stable at the genus and species levels in the subfamily Asclepiadoideae, but showed significant changes at the suprageneric level [15, 16].

In the taxa examined (except for *A. sericifera*), caudicles are connected to the corpusculum near the tip and to the pollinia near the base. However, in *A. sericifera*, it is observed that the caudicles are attached to the pollinia at the base and to the corpusculum along the two sides, and it is clearly distinguished from other examined taxa by a winged corpusculum (Fig. 12). Many studies on the Asclepiadoideae demonstrated that, in a pollinarium, caudicles may be attached to the pollinia from the base, near the base or in the middle, and to the corpusculum from the tip, near the tip, from the base, near the base or the middle [29, 43]. Shape of the caudicles, contributing significantly to the distinction of the examined taxa, is determined as flattened in *A. sericifera*, cylindrical in *C. erecta* and *G. fruticosus*, and triangular in *C. acutum* (Fig. 12). Among the studied taxa, the largest caudicle is measured for *A. sericifera* and the smallest one for *C. erecta*. Palynological studies on members of Asclepiadoideae revealed that caudicles may be cylindrical, triangular, flattened, straight or curved, and their sizes vary significantly among taxa. These variations in caudicle attachment shape and size provide useful diagnostic characters for distinguishing both genera and species within the taxa studied and reflect structural diversification associated with pollination mechanisms [10, 15, 29].

C. erecta with an oblong corpusculum was clearly distinguished from the other examined taxa characterized with ovate corpusculum (Fig. 12). Among the taxa examined, *A. sericifera* has the largest corpusculum and *C. erecta* has the smallest one. It is known that the shape of corpusculum in the Asclepiadoideae greatly varied among the species such as ovate, oblong, circular, elliptical, rhombic and square. Similarly, differences in corpusculum shape and size contribute to the clear delimitation of taxa at both genus and species levels and further support their taxonomic significance within Asclepiadoideae [18, 29].

Pollen grains are traditionally considered conservative structures with strong genetic control; however, accumulating evidence demonstrates substantial intraspecific variability in palynological traits driven by ecological conditions [50]. To evaluate environmental effects, samples from different populations of some taxa were included. Although habitat conditions may cause minor variation in pollen traits, numerical analyses consistently grouped individuals of the same species together, indicating that palynological characters are stable and reliable at the species level.

A floral and palynological perspective on Periplocoideae ve Asclepiadoideae

In some earlier classifications, Asclepiadaceae and Periplocoideae were treated as distinct families due to their diverse flower and pollen grain characteristics [51–55]. In Periplocoideae, the style-head has five vertically oriented grooves between anthers, where pollen translators are secreted. Each translator consists of a basal adhesive

disc, a stalk, and an apical receptacle, onto which tetrads are shed, forming a loosely connected pollen mass at anthesis [4, 5]. On the other hand, Asclepiadoideae are characterized with five pollinaria located alternately with the anthers on each stigmatic zone near the lower edges of the style-head, in which translator parts (corpusculum and caudicles) are secreted. Each pollinarium consists of a pair of pollinia attached to a central corpusculum by two flexible arms [4, 5]. However, both Periplocoideae and Asclepiadoideae are related at a lower level because their flowers expose a similar synorganization between androecium and gynoecium, forming a gynostegium. The style-head produces specialized translators that are connected to aggregated pollen grains or pollinia. These features represent key synapomorphic characters shared by both subfamilies. Such an anther–style synorganization is required for formation and transport of aggregated pollen grains in both Periplocoideae and Asclepiadoideae. The two subfamilies only develop distinct floral structures and pollination mechanisms in order to reach their goals [1, 2, 5]. In contrast, differences in translator structure and pollinarium organization represent lineage-specific derived traits that distinguish the two subfamilies.

The examined taxa of Periplocoideae and Asclepiadoideae were evaluated using cluster analysis and principal components analysis based on the selected 24 morphological and palynological traits. Both analyses showed a general grouping tendency rather than a complete separation at subfamily and genus levels. In both the dendrogram derived from UPGMA (Fig. 12) and the ordination resulting from PCA (Fig. 13), the members of Periplocoideae grouped closely, taxa of *Cynanchum* and *Cionura* positioned closer to this group, while taxa of *A. sericifera* and *G. fruticosus* were distinctly aggregated in separated locations away from the remaining Asclepiadoideae taxa. However, the overall pattern indicated partial overlap between Periplocoideae and Asclepiadoideae, suggesting that the separation is not completely distinct in multivariate space. The investigated Periplocoideae and Asclepiadoideae taxa exhibited quite different flower and pollen morphology at the subfamily level. All the Periplocoideae taxa used in numerical analyses are characterised by corolline coronas with filiform segments, 4-locular anthers with abaxially a hispid indument, and pollen grains in tetrads carried by spoon-shaped structures, while those of Asclepiadoideae have corolline or gynostegial coronas with laminaris or succulent segments, glabrous, 2-locular anthers, and pollen grains in pollinia carried by clip-like transporters (Fig. 12). Within the taxa examined, several characters show different evolutionary significance. In Periplocoideae, tetrad-based pollen structure and spoon-shaped pollen transport system and in Asclepiadoideae, the presence of pollinia and a specialized pollinarium system consisting of corpusculum, caudicles, and pollinia is also regarded as synapomorphic features. In contrast, pedicel, sepal, petal and corona segment lengths, stigma shape, pistil length, shape and size of pollen translator, and pollen grain size, represent more variable and potentially derived (autapomorphic) features (Table 3). Similar to our results, Sarıkaya and Güven [23] have recently identified important fruit and seed morphological characteristics that contribute to the distinction of the species constituting the subject of the present study at both subfamily and genus levels. They reported that the two Turkish *Periploca* taxa, which were characterized by a pair of follicles, flattened, narrowly oblong, and winged seeds with rugulate ornemantation, were clearly distinct within Periplocoideae based on these fruit and seed traits. In contrast, taxa of *Araujia*, *Cionura*, *Cynanchum* and *Gomphocarpus* (Asclepiadoideae) were characterized by single follicles, and ovoid to narrowly ovoid, winged or wingless seeds, with a distinct convex raphae side and a concave hilar side, and smooth to tuberculate or colliculate ornemantation [23].

Araujia sericifera and *Gomphocarpus fruticosus* were positioned far from the other examined taxa in the present numerical analysis (Fig. 12). Both *A. sericifera*, a recently naturalized species for Türkiye, and *G. fruticosus*, an ornamental plant, are quite remarkable due to their floral and pollen characteristics. We observed that both species have specific succulent coronas and the largest pollinia within the investigated Asclepiadoideae taxa. Additionally, *A. sericifera* is the only Asclepiadoideae taxon with individual flowers, campanulate corolla, corolline corona, and winged corpusculum. Similarly, these two species draw attention with their characteristic large fruits, and wingless and warty seeds with tuberculate ornamentation. While follicles of *A. sericifera* are oblong-ovoid and densely covered with short crisped hairs, those of *G. fruticosus* are inflated-ovoid with a short beak at apex, and echinate surface composed of soft bristles up to 1 cm [23].

According to Browicz [20], *Cynanchum acutum* is represented by two subspecies in Türkiye, separated from each other by leaf and fruit morphology. The first one, *C. acutum* subsp. *acutum*, has leaves one to two times as long as broad, broadly ovate-cordate or narrow linear with basal lobes scarcely divergent, and 6–15 cm long follicles. The second, *C. acutum* subsp. *sibiricum*, is characterized by leaves one to three times as long as broad, broadly cordate to hastate-cordate, or oblong-hastate, basal lobes distinctly divergent, and follicles 12.5–16 cm in length. However, Sarıkaya and Güven [23] determined that the follicle length gave similar results within individuals collected from different populations of *C. acutum* subsp. *sibiricum* (110–150 mm) and *C. acutum* subsp. *acutum* (90–175 mm). Therefore, the follicle length was found to be insufficient to distinguish the subspecies, as

being the seed morphology [23]. The present morphological and palynological examinations showed that these two subspecies exhibited very similar morphological and palynological characteristics. However, the level of inter connection of corona segments partly differs at the subspecies level. While corona segments were fused up to 2/3 of their length in all the *C. acutum* subsp. *sibiricum* (Fig. 7c–d) and the majority of *C. acutum* subsp. *acutum* (Fig. 6c–d), some taxa of *C. acutum* subsp. *acutum* had distinct coronas with segments divided to the base (Fig. 5c–d). Detailed examinations on samples collected from different populations of *C. acutum* subsp. *acutum*, demonstrated that corona segments were partially united in some populations and were free in others. The current results revealed two corona types (free and united) for *C. acutum* subsp. *acutum* for the first time, and this difference has been accepted as a variation within the subspecies. In addition, as seen in Fig. 12, all the examined individuals belonging to two subspecies of *C. acutum* from a total of four populations clustered under the same branch at the 94% similarity level. However, specimens of *C. acutum* subsp. *acutum* from two populations (S. Güven 190 & S. Makbul and S. Güven 183 & S. Makbul) clustered with *C. acutum* subsp. *sibiricum*, while the third one, *C. acutum* subsp. *acutum* (S. Güven 188 & S. Makbul), formed a separate branch. It can easily be seen in Appendix that *C. acutum* subsp. *acutum* individuals with S. Güven 188 & S. Makbul collector no, have pedicel (X_1), sepal (X_3, X_4), petal (X_7, X_8), stamen (X_{14}, X_{15}), pistil (X_{18}) and pollen grains (X_{22}, X_{23}) in larger size compared the remaining *C. acutum* individuals.

Conclusion

Consequently, in the present study four Asclepiadoideae species (*A. sericifera*, *C. erecta*, *C. acutum* and *G. fruticosus*), which have important deficiencies in their descriptions in the flora of Türkiye (Browicz 1978), were investigated by means of both flower and pollen morphology, and two Periplocoideae species (*P. gracilis* and *P. graeca*) by means of pollen morphology, for the first time. The results highlight that several reproductive characters such as length of pedicel, sepal, petal and corona segment, pubescence of outer surface of anther, shape of stigma, length of pistil, type of pollen aggregation, number of tetrad mass and pollinium per pollen translator, pollen translator structure, and width and length of pollen grains were effective in distinguishing the examined taxa at subfamily and genus levels. These findings emphasize the taxonomic value of combined floral and palynological traits in distinguishing closely related taxa and contribute to a better understanding of character evolution within Apocynaceae. Additionally, despite the relatively limited taxon sampling, this study is an important breakthrough for the Turkish taxa of Periplocoideae and Asclepiadoideae by explaining the deficiencies in flower and pollen morphology of the examined species in the flora of Türkiye. Notably, the identification of two corona types (free and united) within *C. acutum* subsp. *acutum* provides additional evidence supporting infraspecific distinction of the species *C. acutum*.

Supplementary Information

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Supplementary Material 1.

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Authors' contributions

All listed authors meet the authorship criteria according to the editorial policies of BMC, and contributed to the study conception and design. SG and SM conceived and designed research, contributed to the field support and sample collection processes, and supervised the overall work and critically analyzed all the results. SG wrote the initial draft of the manuscript. SG, SM, ES and DA conducted experiments and prepared figures. SG, SM and KC prepared tables, analyzed the data and contributed to the interpretation of the data. All authors read and approved the manuscript.

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Data availability

Data that support the findings of this study are openly available the supplementary material of this article.

Declarations

Ethics approval and consent to participate

Not applicable. The collection of plant material was carried out in accordance with the national legislation of the Republic of Türkiye and within the scope of a project supported by the Scientific and Technological Research Council of Türkiye (TÜBİTAK, Grant ID: 122Z547). The investigated taxa are not endangered or legally protected species. Voucher specimens were deposited in publicly accessible herbaria as indicated in the Material and Methods section.

Consent for publication

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Competing interests

The authors declare no competing interests.

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