Palynological contribution to the systematics of Rindera and the allied genera Paracaryum and Solenanthus (Boraginaceae-Cynoglosseae)

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Palynological contribution to the systematics of *Rindera* and the allied genera *Paracaryum* and *Solenanthus (Boraginaceae-Cynoglosseae)*

Abstract

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The pollen of thirteen species of *Rindera,* ten of *Solenanthus* and eight of *Paracaryum* was examined by light and scanning electron microscopy. Two main pollen types are recognised, one typical of most *Rindera* species (*Rindera tetraspis* type) and one occurring in all but one species examined of *Paracaryum* and *Solenanthus* (*Cynoglossum officinale* type). Deviations from the *Rindera tetraspis* type in *Rindera* were observed in *R. tianschanica,* which is characterised by the *Cynoglossum officinale* pollen type, and *R. gymnandra,* which shows the *Pardoglossum atlanticum* type as already published. Within *Paracaryum* and *Solenanthus* the only remarkable deviation from the *Cynoglossum officinale* type was found in *Solenanthus hupehensis* from China. In the constricted shape and the lack of an ectocingulus, the pollen of this species approaches the *Myosotis arvensis* type, which is rarely found in the tribe *Cynoglosseae.* Combined with other morphological peculiarities, pollen characters support the placement of *S. hupehensis* in a subgenus of its own, *S.* subg. *Silvestria,* named after the discoverer of this species.

Key words: angiosperms, micromorphology, pollen, scanning electron microscopy, *Solenanthus* subg. *Silvestria,* taxonomy.

Introduction

The genus *Rindera* Pall. (incl. *Mattia* Schult., *Cyphomattia* Boiss. and *Bilegnum* Brand) belongs to *Boraginaceae* tribe *Cynoglosseae* DC. and includes about 25 species mostly distributed in central and western Asia. *R. graeca* (A. DC.) Boiss. & Heldr. and *R. gymnandra* (Coss.) Gürke are the only taxa ranging into the Mediterranean region, being endemic to restricted mountain areas of Greece and Algeria, respectively. Morphologically the genus is characterized by tubular corollas, long anthers with staminal filaments usually inserted at the throat, a style often exserted from the corolla, and large, mostly eglochidiate mericarpids with a broad, membranous wing. All species are perennial and linked to the dry and continental climate of the steppe and semidesertic belts.

Rindera, however, is not unanimously accepted as a separate genus mainly because some taxa show a transition to *Paracaryum* subg. *Mattiastrum* (Boiss.) R. R. Mill. in fruit characters, and to *Solenanthus* Ledeb. in floral features. Both *Paracaryum* and *Solenanthus* are, in turn, closely related to *Cynoglossum* L., a broad genus, the limits of which have long been a source of controversy (Mill 1979). The lack of a satisfactory correlation between floral and fruit characters in this group of *Cynoglosseae,* which is possibly due to parallel evolution, led Greuter (1981) to merge *Rindera, Solenanthus* and *Paracaryum* with *Cynoglossum,* in the wait for additional evidence to elucidate the phylogenetic relationships in the group. This treatment, however, is in contrast with that of most students of *Boraginaceae* (e.g., Kusnetsov 1910, Brand 1921, Johnston 1924, Popov 1950, 1953, Mill 1979), who kept the above genera separate (except Johnston who placed *Solenanthus* under *Cynoglossum*).

Although previous studies showed that *Cynoglosseae* pollen is morphologically variable and therefore taxonomically and phylogenetically useful (e.g. Barbier & Mathez 1973, Clarke & al. 1979, Díez & Valdés 1991, Liu & al. 2001), most taxa of the tribe still wait for even basic palynological analyses. In the present paper we provide a brief survey of pollen types in *Rindera, Paracaryum* (incl. *Mattiastrum* (Boiss.) Brand) and *Solenanthus,* and discuss some aspects that may contribute to a better insight in the difficult taxonomy in this group.

Material and methods

Pollen samples of 13 species of *Rindera,* 10 of *Solenanthus* and 8 of *Paracaryum* were obtained from herbarium specimens in B, FI and W (herbarium abbreviation according to Holmgren & Holmgren 1998-) and from plants collected by the authors. A list of the taxa investigated with geographical origin and herbarium vouchers is given in the Appendix.

Pollen grains from herbarium specimens were rehydrated in a solution of Aerosol-OT 20 % for 10 min and then conventionally acetolyzed. Pollen samples for scanning electron microscopy (SEM) examination were prepared with or without acetolysis, mounted on aluminium stubs and coated with gold in an Emitech EMK 550 sputter. Observations and measurements were made with a Zeiss Axiophot light microscope and a Philips XL 20 SEM at 20kV.

Descriptive terminology follows Erdtman (1966) and Clarke (1977) but unusual terms follow Clarke & al. (1979).

Results

The basic pollen characters of *Rindera, Solenanthus* and *Paracaryum* are summarized in Table 1. In general the pollen of these taxa is 6-heterocolpate, with three colporate apertures alternating with three simple colpi (or pseudoapertures) lacking endo-apertures, and provided with a transverse groove ("ectocingulus") linking the simple and composed apertures along the equator (Liu & al. 2001). In the light of our observations, the pollen of *Rindera* can be distinguished from that of *Paracaryum* and *Solenanthus* by a combination of features concerning size, type of aperture and tectum ornamentation.

Rindera. – The dominant pollen morphology in this genus is here termed "*Rindera tetraspis* type" (after the name of the generitype) and is shown in Fig. 1A-F. The grains are small (sensu Erdtman 1966; P = 10.7-14.4 µm, E = 10.2-13.4 µm), elliptic in equatorial view and ± hexagonal in polar view, from prolate-spheroidal to subprolate in shape (P/E = 1.06-1.25), (3-)6-heterocolpate and ectocingulate. The composed apertures are spindle-shaped, more rarely rhombic, with margins not or slightly thickened; the endoapertures are lalongate, about 1.5 × 3 µm situated at the equator and provided with a granular membrane; the simple colpi are very narrow and generally shorter than the colporate apertures.

Under the light microscope the exine is 0.5-0.8 µm thick, with sexine and nexine of about the same thickness and columellae regularly spaced. Four main patterns of tectum ornamentation can be distinguished. The tectum is entirely covered with microgranules of about 13-18 nm in diameter

Table 1. Main pollen characters of the taxa sampled in this study.

Taxa	P (µm)	E (µm)	P/E	No. apert. (no. pseudoap.)	Colpus length (µm)	Pseudocolpus length (µm)	Ectocing. (*)	Apert. margins (**)	Tectum	Pollen type	Subgenus or section
Rindera											
R. albida	14.4	12.6	1.1	3 (3)	12.8	10.4	+	nt	reticulate	*Rindera tetraspis*	subg. *Bilegnum*
R. bungei	10.7	9.2	1.2	3 (3)	7.9	7.0	+	nt	punctate-microreticulate	*Rindera tetraspis*	subg. *Bilegnum*
R. caespitosa	13.1	10.6	1.2	3 (3)	10.5	7.7	+	nt	scabrate	*Rindera tetraspis*	sect. *Mattia*
R. cyclodonta	11.3	10.5	1.1	3 (3)	10.0	8.4	+	nt	microgranulate	*Rindera tetraspis*	sect. *Rindera*
R. echinata	11.8	11.1	1.1	3	9.8	-	+	nt	microgranulate	*Rindera tetraspis*	sect. *Echinorindera*
R. graeca	12.4	10.2	1.2	3 (3)	9.3	6.7	+	nt	scabrate	*Rindera tetraspis*	sect. *Mattia*
R. gymnandra	14.3	13.4	1.1	3 (3)	6.4	12.4	-	t	irregularly granular	*Pardoglossum atlanticum*	sect. *Mattia*
R. lanata	12.8	11.5	1.1	3 (3)	10.1	7.2	+	nt	scabrate	*Rindera tetraspis*	sect. *Cyphomattia*
R. neubaueri	12.5	10.3	1.2	3 (3)	10.2	9.7	+	nt	microreticulate	*Rindera tetraspis*	sect. *Mertensiopsis*
R. ochroleuca	12.1	11.0	1.1	3 (3)	9.8	9.7	+	nt	microgranulate	*Rindera tetraspis*	sect. *Oxirindera*
R. tetraspis	12.3	11.1	1.1	3 (3)	10.5	8.8	+	nt	microgranulate	*Rindera tetraspis*	sect. *Rindera*
R. tianschanica	9.4	7.0	1.3	3 (3)	6.3	6.1	+	t	psilate-punctate	*Cynoglossum officinale*	sect. *Pseudomattia*
R. umbellata	13.3	10.6	1.3	3 (3)	8.6	8.2	+	nt	scabrate	*Rindera tetraspis*	sect. *Mattia*
mean	12.3	10.7	1.2		9.4	8.5					
st. dev.	1.5	1.9	0.1		1.8	2.0					
Solenanthus											
S. albiflorus	7.5	6.3	1.2	3 (3)	5.2	5.2	+	t	psilate-punctate gran.	*Cynoglossum officinale*	
S. apenninus	10.1	8.2	1.2	3 (3)	5.8	7.0	+	t	psilate-punctate	*Cynoglossum officinale*	
S. biebersteinii	8.9	7.6	1.2	3 (3)	6.2	6.0	+	t	psilate-punctate	*Cynoglossum officinale*	
S. circinnatus	9.1	7.9	1.2	3 (3)	5.4	6.0	+	t	psilate-punctate	*Cynoglossum officinale*	
S. hirsutus	9.1	8.2	1.1	3 (3)	6.6	5.9	+	t	psilate-punctate rug.	*Cynoglossum officinale*	
S. hupehensis	10.7	5.9	1.8	3 (3)	5.8	7.7	-	t	psilate-punctate	close to *Myosotis arvensis*	
S. reverchonii	9.6	7.7	1.2	3 (3)	7.0	5.7	+	t	psilate-punctate	*Cynoglossum officinale*	
S. scardicus	8.4	7.5	1.1	3 (3)	6.0	5.5	+	t	psilate-punctate	*Cynoglossum officinale*	
S. stamineus	11.0	9.9	1.1	3 (3)	7.9	9.4	+	t	psilate-punctate rug.	*Cynoglossum officinale*	
S. turkestanicus	7.4	6.4	1.2	3 (3)	4.3	4.0	+	t	psilate-punctate rug.	*Cynoglossum officinale*	
mean	9.2	7.6	1.2		6.0	6.2					
st. dev.	1.2	1.2	0.2		1.0	1.5					
Paracaryum											
P. ancyritanum	11.7	9.4	1.3	3 (3)	7.9	8.2	+	t	psilate-punctate rug.	*Cynoglossum officinale*	subg. *Mattiastrum*
P. artvinense	8.3	4.4	1.9	3 (3)	4.3	5.8	+	t	psilate-punctate	*Cynoglossum officinale*	subg. *Modestomattiastrum*
P. cappadocicum	9.9	5.7	1.7	3 (3)	5.4	7.3	+	t	psilate-punctate	*Cynoglossum officinale*	subg. *Modestomattiastrum*
P. laxiflorum	10.5	8.6	1.2	3 (3)	4.9	7.2	+	t	psilate-punctate	*Cynoglossum officinale*	subg. *Mattiastrum*
P. leptophyllum	11.3	9.9	1.1	3 (3)	7.3	7.5	+	t	psilate-punctate rug.	*Cynoglossum officinale*	subg. *Mattiastrum*
P. polycarpum	8.2	5.1	1.6	3 (3)	4.4	5.1	+	t	psilate-punctate	*Cynoglossum officinale*	subg. *Modestomattiastrum*
P. racemosum	14.0	12.2	1.2	3 (3)	7.3	8.6	+	t	punctate-scabrate	*Cynoglossum officinale*	subg. *Mattiastrum*
P. rugulosum	9.0	5.2	1.7	3 (3)	4.4	6.2	+	t	psilate-punctate	*Cynoglossum officinale*	subg. *Paracaryum*
mean	10.4	7.6	1.5		5.7	7.0					
st. dev.	2.0	2.8	0.3		1.5	1.2					

(*) + present - absent; (**) nt = not thickened. t = thickened

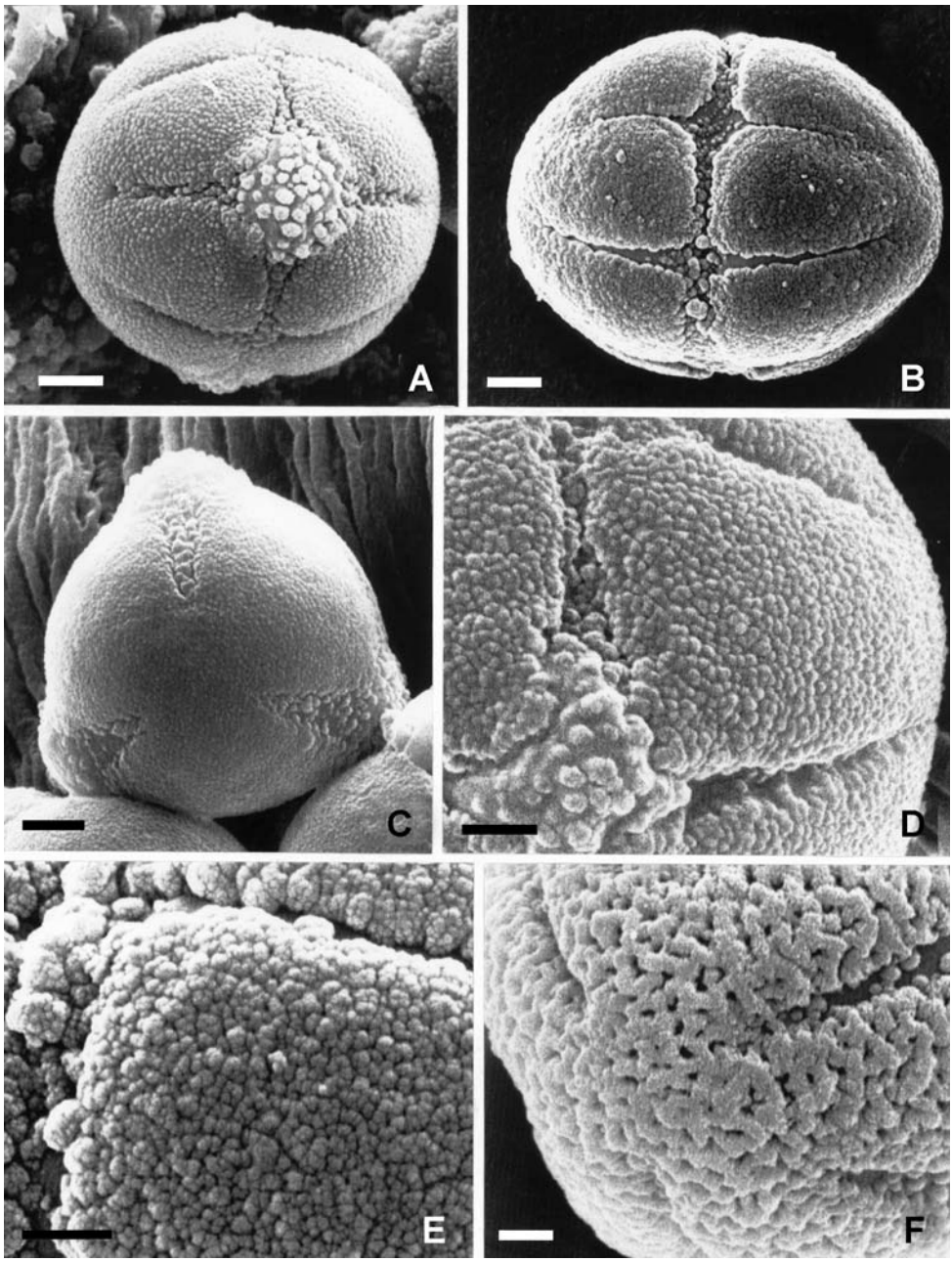

Fig. 1. Pollen of *Rindera, Rindera tetraspis* type – A: *R. ochroleuca:* pollen grain in equatorial view; B: *R. lanata:* acetolysed grain in equatorial view; C: *R. echinata:* grain in polar view showing the three apertures; D: *R. cyclodonta:* close up of microgranulate tectum and not-thickened margins of the apertures; E: *R. caespitosa:* close up of scabrate tectum; F: *R. albida:* close up of polar region showing reticulate tectum. – Scale bars A-C = 2 μm; D-F = 1 μm.

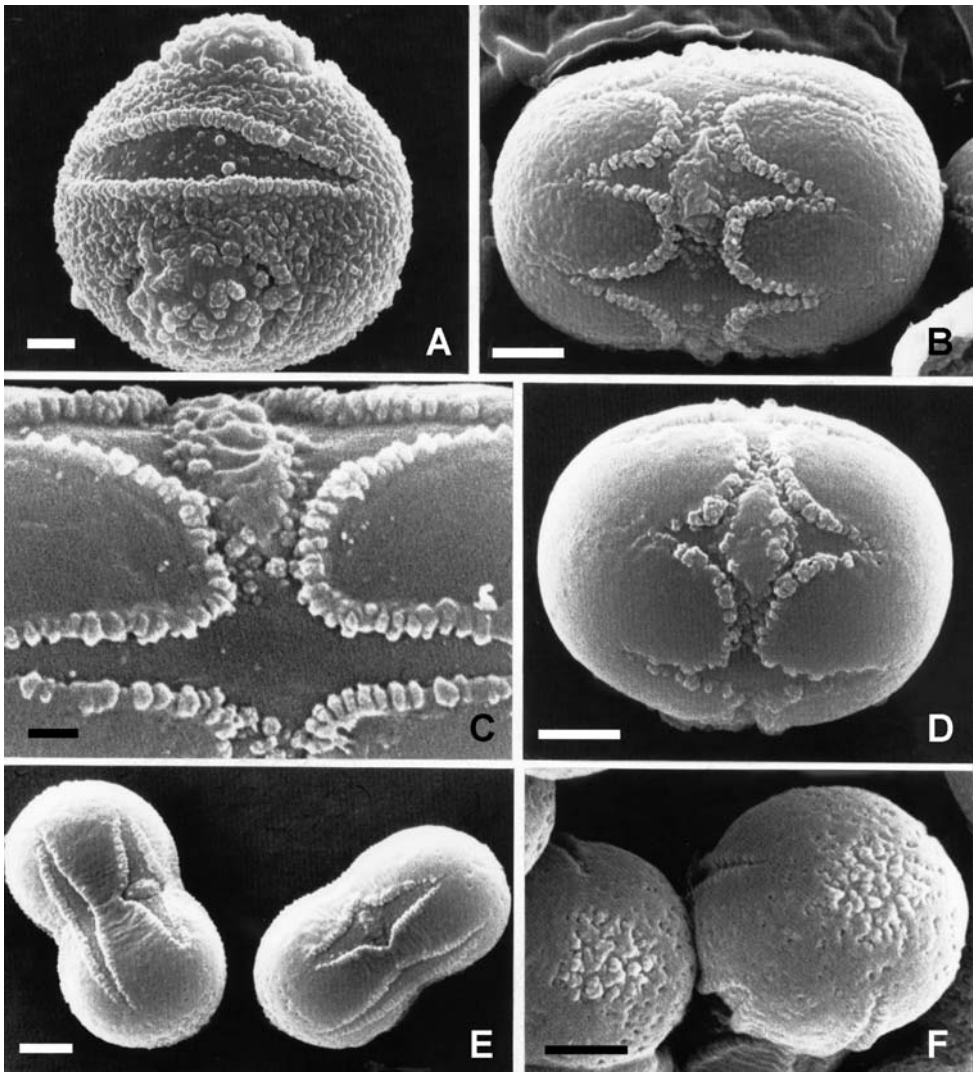

Fig. 2. Pollen of *Rindera, Paracaryum* and *Solenanthus* – A: *Rindera gymnandra:* grain in equatorial view; B: *R. tianschanica: Cynoglossum officinale* type, grain in equatorial view; C: *Paracaryum cappadocicum:* close up of equatorial ectocingulus and apertures with thickened margins; D: *Solenanthus biebersteinii:* grain in equatorial view; E-F: *S. hupehensis:* two grains showing constricted shape and lack of ectocingulus (E); tectum with verrucate and baculate processes at the polar ends (F). – Scale bars A-B, D-F = 2 µm, C = 0.5 µm.

in *R. cyclodonta* (Fig. 1D), *R. echinata, R. ochroleuca* and *R. tetraspis,* while it appears scabrate by the presence of closely packed, irregular granules in *R. caespitosa* (Fig. 1E)*, R. graeca, R. lanata* and *R. umbellata*. *R. bungei* and *R. neubaueri* show a punctate-microreticulate ornamentation, while *R. albida* (Fig. 1F) has a reticulate pattern.

Three significant deviations were found: (1) *Rindera echinata* is the only species with 3-isocolporate grains lacking pseudoapertures (Fig. 1C). This feature, unusual in *Cynoglosseae,* may justify the recognition of a distinct "subtype".

(2) In *Rindera gymnandra* the pollen grains are non-ectocingulate and colporate (Fig. 2A). The pori are (sub)circular and have endoapertures with a densely granular membrane; the three colpi are longer, narrowly fusiform and devoid of endoapertures. As already highlighted by Barbier & Mathez (1973) and Clarke & al. (1979), *R. gymnandra* shares with the species of *Pardoglossum* Barbier & Mathez the peculiar *Pardoglossum atlanticum* type pollen.

(3) In *Rindera tianschanica* (Fig. 2B) the pollen largely matches the *Cynoglossum officinale* type (Clarke 1977, or *Cynoglossum creticum* type of Díez 1984), which is found in most species of *Paracaryum* and *Solenanthus,* as described below.

Paracaryum and Solenanthus. – All investigated taxa of these two genera plus *Rindera tianschanica* share the same basic pollen morphology, which is close to the *Cynoglossum officinale* type of Clarke (1977), with the only remarkable exception of *Solenanthus hupehensis* (see below). The pollen grains are very small to small (P = 6.3-14 µm, E = 4.4-12.2 µm), elliptic in equatorial view and ± hexagonal in polar view, prolate-spheroidal to prolate (P/E = 1.11-1.89), 6-heterocolpate and ectocingulate (Fig. 2C, D). The ectoapertures are rhombic in outline with lalongate endoapertures (1.2 × 3.2 µm), situated at about the equator; the colporate apertures are equal to or shorter than the fusiform, simple colpi; the aperture margins are strongly thickened by the presence of baculate and verrucate processes; the tectum is psilate or psilate-punctate, smooth to slightly rugulose, but punctate-scabrate in *Paracaryum racemosum;* the exine thickness under the light microscope is 0.5-1 µm.

Two subgroups can be recognized in *Paracaryum* based on size and shape of the grains (Table 1). The first includes *P. artvinense, P. cappadocicum, P. polycarpum* (all subg. *Modestomattiastrum*) and *P.* (subg. *Paracaryum*) *rugulosum,* which have very small (polar length <10 µm) prolate grains (P/E = 1.62-1.89); the second comprises *P. ancyritanum, P. laxiflorum, P. leptophyllum* and *P. racemosum* (all subg. *Mattiastrum*), which have slightly larger grains (polar length > 10 µm) with a prolate-spheroidal shape (P/E = 1.13-1.25).

Solenanthus is essentially uniform. All species have the *Cynoglossum officinale* type, except *S. hupehensis*. The pollen grains of this species differ in such unusual features as (1) the lack of an ectocingulus, (2) the prolate shape (P/E = 1.81), (3) the presence of a marked equatorial constriction, (4) the tectum which is psilate at the mesocolpia and punctate at the apocolpia, and (5) the verrucate and baculate deposits at both polar ends (Fig. 2E-F). With the exception of the latter character, they are similar to the *Myosotis arvensis* type of Clarke (1977).

Discussion

The results underscore the broad variation in quantitative and qualitative characters of the pollen in *Boraginaceae* and their relevance for the taxonomy and phylogeny of the family.

Rindera. – Barbier & Mathez (1973) in their palynological investigation of *Cynoglosseae* based on light microscopy, recognised four main morphotypes. Their "type B" pollen, heterocolpate and characterized by the small size and the prolate-spheroidal to prolate shape, was reported for *Lindelofia* Lehm., *Paracaryum* (incl. *Mattiastrum*), *Rindera, Solenanthus, Suchtelenia* Kar. and *Cynoglossum* subg. *Cynoglossum*. Our SEM analyses allowed more detailed stereostructural observations and to distinguish the pollen of *Rindera* from that of *Solenanthus* and *Paracaryum,* except *R. tianschanica* and *R. gymnandra.* The *Rindera tetraspis* type substantially differs from the *Cynoglossum officinale* type (Clarke 1977, *C. creticum* type of Díez 1984) in: (1) the larger size, (2) the smooth, not thickened, margins of the colpia, (3) the colporate apertures being longer than the pseudoapertures, and (4) the tectum ornamentation never being psilate-punctate.

Three notable deviations from the *Rindera tetraspis* type were observed within our sample of taxa. The first is the 3-aperturate pollen of *R. echinata*. The other palynological characters of this species fit into the basic type, suggesting that the lack of the three simple colpi, which are present in most *Cynoglosseae,* represents a "derived" palynological autapomorphy of *R. echinata*.

In one species, *Rindera tianschanica,* we observed the *Cynoglossum officinale* pollen type, the usual type of the genera *Solenanthus* and *Paracaryum*. This species, which belongs to *R.* sect.

Pseudomattia Popov like other endemics of the Tian Shan region, shares with most *Solenanthus* members also a floral character peculiar to this section, i.e. the narrowly spathulate scales inserted at about the middle of the corolla tube (Popov 1953). Pollen and flower morphology would suggest to assign this species to *Solenanthus,* but the broadly winged, eglochidiate mericarpids leave no doubt that its correct placement is in *Rindera*.

The strongest deviation from the *Rindera tetraspis* type is found in the N African endemic *R. gymnandra,* which represents a remarkable extension of the genus into the W Mediterranean basin. Its *Pardoglossum atlanticum* pollen type provides a connection of possible phylogenetic relevance with the five members of *Solenanthus*/*Pardoglossum,* as already discussed by Barbier & Mathez (1973) and Clarke & al. (1979). This is also supported by floral characters, e.g., the distinctly exserted stamens occurring in this group of N African taxa. On the basis of this affinity, *Pardoglossum* and *R. gymnandra* were included by Greuter (1981) in *Cynoglossum* subg. *Mattiaria* (Coss.) Greuter. However, the predominance of the *Rindera tetraspis* pollen type combined with the "rinderoid" (winged) mericarpids peculiar to *Rindera* are strong indications against such a unification, in line with Kusnetsov (1910), Brand (1921), Johnston (1924), Popov (1950, 1953), Barbier & Mathez (1973), Mill (1979) and Aytaç & Mill (2005).

Tectum ornamentation is the most diverse palynological character in *Rindera* and appears to be correlated with floral traits of systematic relevance at the infrageneric level. A microgranulate ornamentation occurs in *R.* sect. *Rindera* and the related sections *Echinorindera* Popov, *Oxyrindera* Popov and *Mattiorindera* Popov, in which the faucal scales are reduced to small sacciform folds at the throat (Popov 1953). The taxa with well developed scales show different ornamentation patterns, e.g. scabrate in sect. *Mattia* Boiss. and sect. *Cyphomattia* Boiss., and punctate-microreticulate and reticulate in *R. bungei* and *R. albida* of *R.* subg. *Bilegnum* (Brand) R. R. Mill, respectively. *R.* subg. *Bilegnum* has recently been established in view of its peculiar nutlets with a double margin to the wing (Aytaç & Mill 2005) and tectum ornamentation supports this decision. One species in our sample, *R.* (sect. *Mertensiopsis* H. Riedl) *neubaueri* has a microreticulate tectum but strongly reduced scales.

Paracaryum. – This genus, with pollen basically of the *Cynoglossum officinale* type, shows a similar relationship between palynological and floral characters. Size and shape of the grains are useful to distinguish between its three subgenera (Mill 1977). *P.* subg. *Mattiastrum* (Boiss.) R. R. Mill, characterised by tubular corollas with exserted style, scales longer than broad and an anther base situated above the scale base, has small pollen grains (P > 10 µm) with a prolate-spheroidal shape. The subgenera *Paracaryum* and *Modestomattiastrum* (Brand) R. R. Mill, with prolate and very small (P < 10 µm) pollen, are associated with a small, rotate corolla including style, scales broader than long and an anther base situated below the scale base. Though not matched by fruit morphology, this relationship may suggest the existence of two lineages, one represented by *P.* subg. *Mattiastrum,* which seems closer to *Solenanthus,* and one by *P.* subg. *Paracaryum* and *P.* subg. *Modestomattiastrum,* which seem closer to *Cynoglossum* subg. *Cynoglossum.*

Solenanthus. – The pollen of *Solenanthus* is more uniform than that of *Rindera* and *Paracaryum* and almost invariably of the *Cynoglossum officinale* type. This supports its inclusion in *Cynoglossum,* as proposed by Johnston (1924) and Greuter (1981). Apart from the N African species referred to *Pardoglossum,* the only remarkable deviation we could find is in *S. hupehensis*. This rare species is known only from the type collection brought by the Italian missionary Rev. Cipriano Silvestri from the Hubei region in China. Lacking fruiting material it was provisionally referred to *Solenanthus* by Pampanini (1911) and then described as a new species by Mill (1987) in view of remarkable characters such as the very low-growing habit, the condensed, pseudocapitate inflorescence and the deeply lobed corolla. This author observed that *S. hupehensis* "may even be worthy of generic status" and still today its placement is uncertain in the lack of additional collections with mericarpids (Mill 1987, Ge-lin & al. 1995). Pollen morphology, here described for the first time (see Liu & al. 2001), confirms the systematic isolation of this easternmost species, which differs from all other investigated taxa of *Rindera, Solenanthus,*

Paracaryum and *Cynoglossum* by the presence of a marked equatorial constriction, the lack of an ectocingulus and the occurrence of supratectal processes at the polar ends. A constricted shape without ectocingulus is typical of the *Myosotis arvensis* pollen type occurring in *Myosotis* L. *(Myosotideae)* and some genera of *Eritrichieae* (e.g. *Cryptantha* Lehm. ex Fisch. & C. A. Mey., *Lappula* Moench, *Asperugo* L. and others), but within *Cynoglosseae* known only from *Omphalodes* Mill. (Clarke 1977, Díez & Valdés 1991, Popova & Zemskova 1995, Hargrove & Simpson 2003, own obs.).

Accordingly, macro- and micromorphological characters suggest that *Solenanthus hupehensis* is distinct enough to be placed in a subgenus separate from *Solenanthus* subg. *Solenanthus* (type: *S. circinnatus* Ledeb.), which is named here after its discoverer Rev. Silvestri.

Taxonomy

Solenanthus subg. ***Silvestria*** Bigazzi, Nardi & Selvi, **subg. nov.**
Type: *Solenanthus hupehensis* R. R. Mill in Notes Roy. Bot. Gard. Edinburgh 44: 271. 1987 [Holotype: China, "Hu-peh, Ou-pan-chan, 600 m, trovati lungo ruscello, umido e ombra", 14.-23.3.1910, *C. Silvestri 3368* (K; isotype: FI!)].

Herba humilis; foliis ovatis subcordatis, singulis in caulibus floriferis; inflorescentia arcte condensata, pseudocapitata; corollae limbo ad basim diviso, segmentis obovatis; pollinis granulis in zona aequatoriali constrictis ectocinguli expertibus, in areis polaribus processibus supratectalibus praeditis.

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Appendix

List of the investigated taxa with geographical origin and herbarium vouchers

Rindera

R. albida (Wettst.) Kusn. – Turkey, Van, 2002, *Bigazzi & Selvi 02.60* (FI); ***R. bungei*** (Boiss.) Gürke – Turkmenistan, Sopay Dag, 1958, *Nikitin 2886* (W); ***R. caespitosa*** (DC.) Bunge – Turkey, 1847, *Aucher Eloy 2282* (FI); ***R. cyclodonta*** Bunge – Afghanistan, Badghis, 1885, *Aitchinson* (FI); ***R. echinata*** Regel – Russia, Kara-tau, 1931, *Nablov 148* (B); ***R. graeca*** (A. DC.) Boiss. & Heldr. – Greece, 1899, *Zahn 1566* (FI); ***R. gymnandra*** (Coss.) Gürke – Algeria, Djurdura Mts, 1854, *Copon* (FI); ***R. lanata*** (Lam.) Bunge – Turkey, Bingöl, 2002, *Bigazzi & Selvi 02.51* (FI); ***R. neubaueri*** (Rech. f.) Rech. f. & H. Riedl – Afghanistan, Bamian, 1967, *Rechinger 36310* (W); ***R. ochroleuca*** Kar. & Kir. – Kazakhstan, Tas, 1860, *Roldugin* (B); ***R. tetraspis*** Pall. – Russia, Yergeni, 1993, *Sagalaev & Rusanovich* (FI); ***R. tianschanica*** Popov – Russia, Kara-tau, 1931, *Nablov 383* (B); ***R. umbellata*** (Waldst. & Kit.) Bunge – Serbia, Kiadov, 1903, *Bierbach* (FI).

Paracaryum

P. ancyritanum Boiss. – Turkey, Nevşehir, 2002, *Bigazzi & Selvi 02.39* (FI); ***P. artvinense*** R. R. Mill – Turkey, Tortum, 2002, *Bigazzi & Selvi 02.65* (FI); ***P. cappadocicum*** Boiss. & Balansa – Turkey, Malatya, 2002, *Bigazzi & Selvi 02.41* (FI); ***P. cristatum*** (Schreb.) Boiss. – Turkey, Bingöl, 2002, *Bigazzi & Selvi 02.52* (FI); ***P. leptophyllum*** (DC.) Boiss. – Turkey, Kars, 2000, *Bigazzi & Selvi 00.16* (FI); ***P. polycarpum*** (Rech. fil.) R. R. Mill – Turkey, Eğridir, 2002, *Bigazzi & Selvi 02.24* (FI); ***P. racemosum*** Schreb. – Turkey, Niğde, 2002, *Bigazzi & Selvi 02.33* (FI); ***P. rugulosum*** (DC.) Boiss. – Turkey, Sivas, 2002, *Bigazzi & Selvi 02.42* (FI).

Solenanthus

S. albiflorus Czukav. & Meling – Russia, 1981, *Kozkareva* (B); ***S. apenninus*** (L.) Fisch. & C. A. Mey. – Italy, L'Aquila, 2003, *Bigazzi & Selvi 03.07* (FI); ***S. biebersteinii*** DC. – Russia, 1987 (B); ***S. circinnatus*** Ledeb. – Turkey, Van, 2002, *Bigazzi & Selvi 02.58* (FI); ***S. hirsutus*** Regel – Tadzjikistan, Mt Kugitek, 1982, *Koczkareva* (B); ***S. hupehensis*** R. R. Mill – China, Hubei, 1910, *Silvestri 3368* (FI, isotypus); ***S. reverchonii*** Degen – Spain, Granada, *Reverchon 1190* (B); ***S. scardicus*** Bornm. – Greece, Ioannina, *Willing 2942* (B); ***S. stamineus*** (Desf.) Wettst. – Turkey, Erzurum, 2000, *Bigazzi & Selvi 00.26* (FI); ***S. turkestanicus*** (Regel & Smirn.) Kusn. – Afghanistan, Badghis, 1885, *Aitchinson* (FI).