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# *Proustia* and *Lophopappus* (Asteraceae, Mutisieae): generic and subtribal relationships based on pollen morphology

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## Abstract

Pollen of *Proustia* (10 specimens examined) and *Lophopappus* (12 specimens examined) (Asteraceae, Mutisieae) are described as part of an analysis of the classification of these genera. Their exine structure is determined and compared with structures found in other genera of Mutisieae (25 specimens examined and data of other authors), in order to clarify the subtribal position of *Proustia* and *Lophopappus*. Pollen of *Proustia* and *Lophopappus* have the following characters in common: Grains radially symmetrical and isopolar; tricolporate, long colpi with a microgranulate membrane, endoaperture lalongate with acute or bifurcate equatorial ends; subprolate or prolate-spheroidal; elliptic or spheroidal; polar caps conspicuous or not so distinctive, and exine microechinate. Two types of sexine structure are observed: (1) Trixis type, with two columellate ramified sublayers, the inner sublayer thicker than the outer one (found in *Lophopappus berberidifolius*, *L. tarapacanus*, *Proustia cuneifolia* var. *cuneifolia*, *P. cuneifolia* var. *mendocina*, *P. cuneifolia* var. *mollis*, *P. ilicifolia* var. *baccharoides*, and *P. pyrifolia*); and (2) *Proustia* type, with two equally thick sublayers of ramified columella (found in *Lophopappus blakei*, *L. cuneatus*, and *L. foliosus*). *Proustia ilicifolia* var. *ilicifolia* and *Lophopappus peruvianus* have both types of sexine structure. Pollen analysis of other genera of Mutisieae subtribes Nassauviinae, Mutisiinae and Gochnatiinae demonstrate two new exine types: (1) Ainsliaea type, with two sublayers poorly distinguishable, the exine appearing compact, the outer surface microechinate; and (2) Wunderlichia type, with two well-differentiated sublayers, the outer surface echinate, the spines with apical channels. The results show that: (1) *Proustia* and *Lophopappus* cannot be differentiated from each other by pollen characters; (2) the genera of subtribe Nassauviinae can be differentiated from the other two subtribes by having sexine sublayers with similar structure; (3) *Proustia* and *Lophopappus* have the pollen exine structural types that are typical of pollen of subtribe Nassauviinae; (4) subtribes Gochnatiinae and Mutisiinae are characterized by having sexine sublayers with different structures; but (5) those two subtribes cannot be differentiated based on pollen characters.

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## 1. Introduction

*Proustia* Lagasca and *Lophopappus* Rusby (Asteraceae, Mutisieae) are distributed from Peru to Northern Argentina and Chile. *Proustia* comprises three species and seven infraspecific taxa

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of shrubs and vines, and *Lophopappus* six species of shrubs. Within the subtribal classification of Mutisieae sensu Cabrera (1977), various authors have placed these two genera alternatively into subtribe Gochnatiinae (Cabrera, 1953, 1961), subtribe Mutisiinae (Fabris, 1968; Cabrera, 1961), and subtribe Nassauviinae (Crisci, 1974a), primarily using features of the corollas and styles. Both genera have style branches with rounded tips (characteristic of Mutisiinae and Gochnatiinae) and bilabiate corollas (characteristic of Nassauviinae), and *Lophopappus* has occasionally 5-partite corollas (characteristic of Gochnatiinae). Most recently, in a morphological study of Mutisieae, Hansen (1991a) suggested that these two genera may be misplaced in tribe Mutisieae.

Following the taxonomic treatments of *Lophopappus* by Cabrera (1953), and *Proustia* by Fabris (1968), most recent authors agree that they are distinct but closely related. Their close resemblance led Ferreyra (1995) to consider *Proustia* and *Lophopappus* as congeneric, treating them all as species of *Proustia*.

In the first palynological studies in *Proustia*, Wodehouse (1929) examined pollen of *Proustia cuneifolia* var. *cuneifolia* (sub *P. pungens*) and *P. pyrifolia* with light microscopy. Later, Parra and Marticorena (1972) established several pollen groups in their study of the Chilean Mutisieae. They analyzed the pollen grains of *Proustia cuneifolia* var. *cuneifolia*, *P. ilicifolia*, *P. pyrifolia* and *Lophopappus tarapacanus*, and established for them the ‘*Proustia* pollen group’, characterized by a bi-layered columellate sexine, with the two sublayers of similar thickness. They suggested a close relationship between the ‘*Proustia* pollen group’ and the ‘*Trixis* pollen group’ of the Nassauviinae. The ‘*Trixis* pollen group’, characteristic of *Leunisia*, *Macrachaenium*, *Pleocarphus*, and *Trixis*, also has bi-layered columellate sexine, but the inner sublayer is thicker than the outer sublayer. The ‘*Proustia* pollen group’ was related to a lesser degree with the ‘*Perezia* pollen subgroup’, found in *Nassauvia*, *Triptilion*, and *Perezia*, which is characterized by two sublayers of the same thickness and separated by a thin non-parallel (‘zigzag’) nexine layer.

Crisci (1974a) summarized the palynological

data for subtribe Nassauviinae, recognizing six types of exine patterns, one being the *Proustia* type found in *Proustia* and *Lophopappus*, which resembles the *Trixis* type, as noted by Parra and Marticorena (1972). Crisci (1974a) emphasized the importance of the pollen exine structure in *Proustia* and *Lophopappus* for their inclusion in Nassauviinae.

Hansen (1991b) examined general pollen characteristics (size, sculpture and structure) of some species of Mutisieae, including *Proustia cuneifolia* and *Lophopappus foliosus*. Hansen observed that Gochnatiinae and Mutisiinae have a poorly differentiated ectosexine (as tectum), with the endosexine (as infratectum) differentiated into stout, spaced columellae, whereas the Nassauviinae have both sublayers differentiated into stout, spaced columellae.

The aims of this study are: (1) To describe and to illustrate the pollen morphology of all species of *Proustia* and *Lophopappus*; (2) to determine the pollen types for all of these taxa; (3) to determine whether *Proustia* and *Lophopappus* can be distinguished based on pollen data; and (4) to determine whether the exine structure of *Proustia* and *Lophopappus* can provide support for the placement of these genera within the subtribal classification of tribe Mutisieae sensu Cabrera.

## 2. Materials and methods

Pollen samples were collected from herbarium specimens from AAU, BKF, C, CM, LP, MO, UC, and W (Holmgren et al., 1990; see Appendix A). For light microscopy (LM), pollen was acetylyzed (Erdtman, 1960), mounted in glycerol jelly and sealed with paraffin. Measurements of the polar axis (P), equatorial diameter (E) and exine thickness (measured in equatorial view), are based on 25 grains. The P/E ratio was calculated for each specimen. Table 1 lists species examined and pollen data. For scanning electron microscopy (SEM), unacetylyzed grains were suspended in 90% ethanol, mounted on stubs, sputter-coated with gold palladium, and examined with a Jeol JSM T-100 microscope. Terminology in general follows Punt et al. (1994). Table 2 lists the exine structural type

Table 1  
List of species and varieties of *Lophopappus* and *Proustia* examined<sup>a</sup>

Taxa	a. P ( $\mu\text{m}$ )	b. E ( $\mu\text{m}$ )	c. P/E	d. Exine ( $\mu\text{m}$ )	e. Polar caps	f. Exine structure
1. <i>Lophopappus berberidifolius</i>	45–50	37	Subprolate	ca. 7	+	Trixis
2. <i>L. blakei</i>	42.5–45	31–36	Subprolate	6–7	+(-)	Proustia
3. <i>L. cuneatus</i>	40–45	36–38	Subprolate	4–5	+(-)	Proustia
4. <i>L. foliosus</i>	45–50	37–45	Prolatespheroidal	5–6	+(-)	Proustia
5. <i>L. peruvianus</i>	42–54	35–40	Subprolate	ca.6	+	Proustia+Trixis
6. <i>L. tarapacanus</i>	44–46	40–44	Prolatespheroidal	4–6	+(-)	Trixis
7a. <i>Proustia cuneifolia</i> var. <i>cuneifolia</i>	32–39.5	28–34	Subprolate	4.0–5.5	+(-)	Trixis
7b. <i>P. cuneifolia</i> var. <i>mendocina</i>	31–40	28–37	Subprolate	4.0–6.0	+(-)	Trixis
7c. <i>P. cuneifolia</i> var. <i>mollis</i>	29–37	25–35	Subprolate	4.5–6.0	+(-)	Trixis
8a. <i>P. ilicifolia</i> var. <i>baccharoides</i>	28–33	23–29	Subprolate	2.0–4.5	+(-)	Trixis
8b. <i>P. ilicifolia</i> var. <i>ilicifolia</i>	23–30	19–21	Subprolate	2.5–3.5	+(-)	Proustia+Trixis
9. <i>P. pyriformis</i> var. <i>pyriformis</i>	30–33	23–27	Subprolate	3.5	+	Trixis

<sup>a</sup> The measurements of polar diameter (P,  $\mu\text{m}$ ), equatorial diameter (E,  $\mu\text{m}$ ); shape (P/E), exine thickness ( $\mu\text{m}$ ), polar caps, and structure types are indicated; + = presence; - = absence.

Table 2  
Exine types in genera of subtribes Nassauviinae, Gochnatiinae and Mutisiinae (tribe Mutisieae sensu Cabrera, 1977)<sup>a</sup>

a. Exine types	b. Nassauviinae	c. Gochnatiinae	d. Mutisiinae
1. Calopappus	<i>Calopappus</i> <sup>2</sup>		
2. Cephalopappus	<i>Cephalopappus</i> *		
3. Oxyphyllum	<i>Leucheria</i> <sup>4</sup> , <i>Moscharia</i> <sup>6</sup> , <i>Nassauvia</i> <sup>6</sup> , <i>Oxyphyllum</i> *, <i>Perezia</i> <sup>6</sup> , <i>Polyachyrus</i> <sup>6</sup> , <i>Triptilion</i> <sup>6</sup>		
4. Proustia	<i>Lophopappus</i> *, <i>Proustia</i> *		
5. Trixis	<i>Acourtia</i> <sup>2</sup> , <i>Ameghinoa</i> <sup>2</sup> , <i>Burkartia</i> *, <i>Criscia</i> <sup>2</sup> , <i>Dolichlasium</i> <sup>2</sup> , <i>Holocheilus</i> <sup>2</sup> , <i>Jungia</i> <sup>2</sup> , <i>Leumisia</i> <sup>6</sup> , <i>Lophopappus</i> *, <i>Macrachaenium</i> *, <i>Marticoenia</i> <sup>3</sup> , <i>Pleocarphus</i> <sup>6</sup> , <i>Proustia</i> *, <i>Trixis</i> <sup>2</sup>		
6. Ainsliaea		<i>Ainsliaea</i> *	
7. Erythrocephalum		<i>Erythrocephalum</i> *	
8. Dicoma		<i>Dicoma</i> <sup>8</sup>	
9. Mutisia		<i>Aphyllocladus</i> <sup>6</sup> , <i>Chimantaea</i> *, <i>Cnicothamnus</i> *, <i>Gochnatia</i> <sup>5</sup> , <i>Gypothamnium</i> <sup>6</sup> , <i>Hecastocleis</i> *, <i>Hyaloseris</i> *, <i>Mutisia</i> <sup>1*</sup> , <i>Lulia</i> *, <i>Hyalis</i> *, <i>Lycoseris</i> *, <i>Onoseris</i> <sup>7</sup> , <i>Plazia</i> <sup>6</sup> , <i>Stenopadus</i> * <i>Stiffitia</i> *, <i>Urmenetea</i> <sup>6</sup>	<i>Brachyclados</i> <sup>6</sup> , <i>Chaetanthera</i> <sup>6</sup> , <i>Chaptalia</i> <sup>6</sup> , <i>Glossarion</i> <sup>7</sup> , <i>Hyaloseris</i> *, <i>Mutisia</i> <sup>1*</sup> , <i>Lulia</i> *, <i>Pachylaena</i> <sup>6</sup> , <i>Trichocline</i> <sup>9</sup>
10. Wunderlichia		<i>Wunderlichia</i> *	<i>Gongylolepis</i> *

<sup>a</sup> Taxa analyzed in this study indicated by asterisk. Species of *Proustia* and *Lophopappus* are cited in Table 1, the other taxa are cited in Appendix A. Numbers refer to the literature where the data were extracted: (1) Cabrera, 1965; (2) Crisci, 1974a; (3) Crisci, 1974b; (4) Crisci, 1976; (5) Morbelli, unpubl.; (6) Parra and Marticoena, 1972; (7) Skvarla et al., 1977; (8) Stix, 1960; (9) Zardini, 1975.

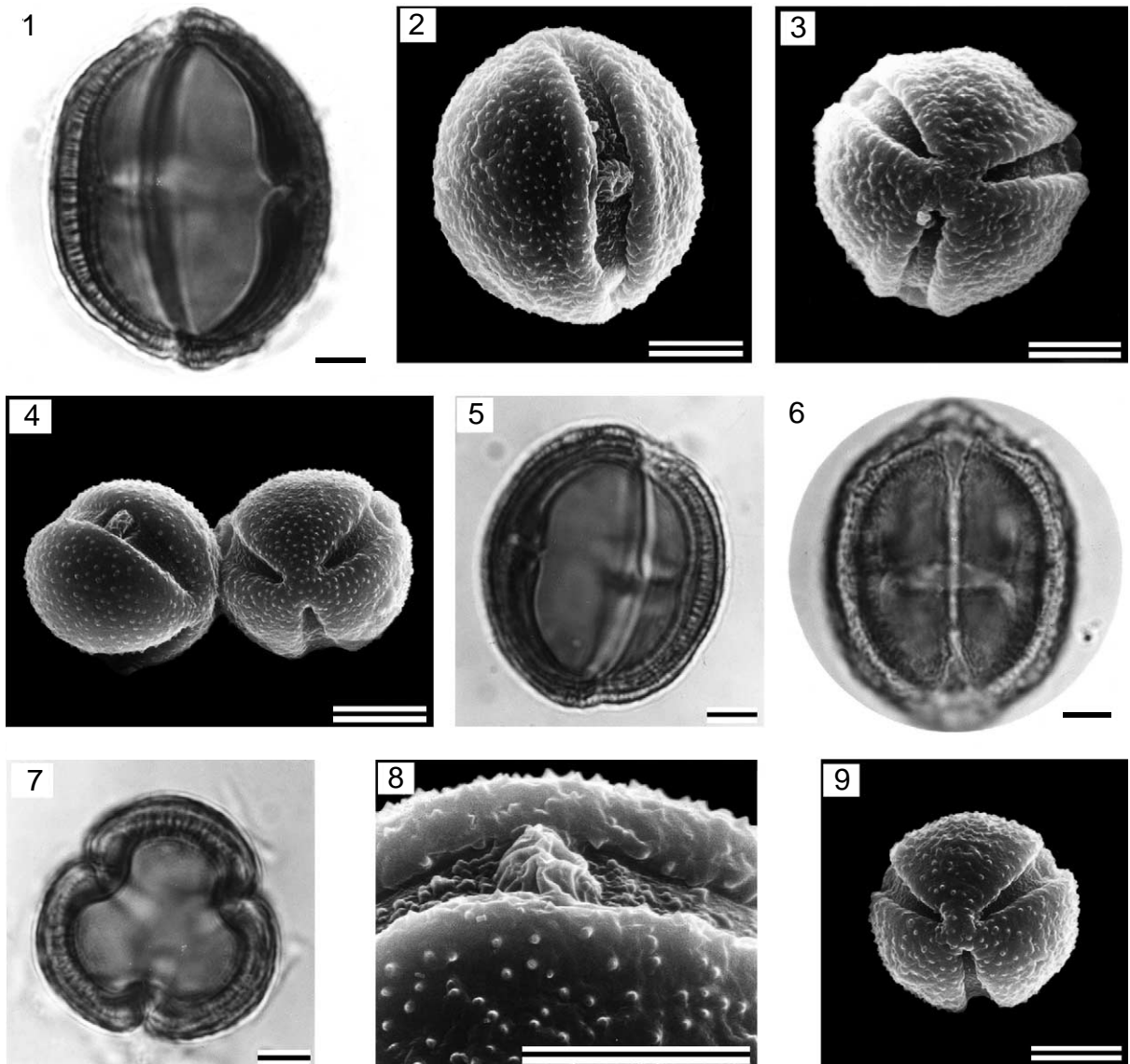
for genera of subtribes Nassauviinae, Mutisiinae and Gochnatiinae, based on our own observations or from the literature (see [Appendix A](#)).

### 3. Results

#### 3.1. *Proustia* ([Plate I](#)) and *Lophopappus* ([Plate II](#)) pollen description

*General description* ([Table 1](#)). Pollen radially

symmetrical and isopolar; subprolate or prolate-spheroidal, spheroidal or elliptic in equatorial view, circular in polar view. Tricolporate, long colpi with a microgranulate membrane. Endoaperture lalongate, with bifurcate ([Plate I](#), fig. 6) or acute equatorial ends ([Plate II](#), fig. 15). Exine tectate, microechinate. Sexine about 2 or 3 times as thick as nexine; thickened at polar areas ([Plate I](#), fig. 6), equatorial areas ([Plate I](#), fig. 1), at both equatorial and polar areas ([Plate II](#), fig. 10), or not; consisting of two ramified columellate sub-



layers; the sublayers equal in thickness (Proustia type) (Plate II, fig. 12; Fig. 1) or the endosexine thicker than the ectosexine (Trixis type) (Plate I, figs. 1 and 5; Fig. 1). Internal tectum parallel to the nexine. Nexine thickened towards apertures, forming costae.

*Size* (Table 1, a,b). Pollen grains of *Lophopappus* are larger (40–50 × 31–45 µm) than those of *Proustia* (23–40 × 19–37 µm), with overlap. Thus, it is not possible to distinguish species within *Proustia* and *Lophopappus* based on pollen size.

*Shape in equatorial view*. Most species have a mixture of elliptic and spheroidal pollen grains, except for *Lophopappus berberidifolius*, *L. peruvianus*, *Proustia cuneifolia* var. *mollis*, *P. ilicifolia* var. *baccharoides*, and *P. pyrifolia* var. *pyrifolia*, which have exclusively elliptic grains.

*Shape (ratio P/E)* (Table 1, c). Pollen grains of all species of *Proustia* and most species of *Lophopappus* are subprolate, except for *Lophopappus foliosus* and *L. tarapacanus*, which have prolate–spheroidal pollen. Pollen of these genera were described as prolate by Parra and Marticorena (1972) and Hansen (1991b) or prolate–spheroidal to prolate by Crisci (1974a).

*Exine thickness* (Table 1, d). The exine of *Lophopappus* pollen (4–7 µm) is generally thicker than that of *Proustia* (2–6 µm), with considerable overlap in size.

*Polar caps* (Table 1, e). These structures are conspicuous in *Lophopappus berberidifolius* (Plate II, fig. 10), *L. peruvianus*, and *Proustia pyrifolia* var. *pyrifolia* (Plate I, fig. 6), but are indistinct in the other taxa. Hansen (1991b) noted that the caps

may be related to the shape of the pollen grains, i.e. polar caps are well-developed on elliptic grains, and poorly developed on spheroidal grains.

*Exine structure* (Table 1, f; Fig. 1). All of the taxa of *Proustia* and *Lophopappus* are characterized by either the Trixis or Proustia exine structural type. *Lophopappus berberidifolius*, *L. tarapacanus*, *Proustia cuneifolia* var. *cuneifolia*, *P. cuneifolia* var. *mendocina*, *P. cuneifolia* var. *mollis*, *P. ilicifolia* var. *baccharoides* and *P. pyrifolia* var. *pyrifolia* have the Trixis type (ectosexine thinner than endosexine, both sublayers columellate; microechinate). *Lophopappus blakei*, *L. cuneatus* and *L. foliosus* have the Proustia type (ectosexine of same thickness as endosexine, both sublayers columellate; microechinate). *Lophopappus peruvianus* and *Proustia ilicifolia* var. *ilicifolia* have both types of exine structure.

### 3.2. Exine types found in other genera of Mutisieae

We recognize eight types of exine of Mutisieae in addition to the Proustia and Trixis types described above. Six of these types coincide with the exine types previously reported, and two new types are reported here. These are based on the number of sexine sublayers, the relative thickness of the two sublayers, the distinction of columellae (clearly differentiated or not), and the orientation of the internal tectum (parallel to the nexine or zigzag; Crisci, 1974a). We added an additional character: type of surface (echinate or microechi-

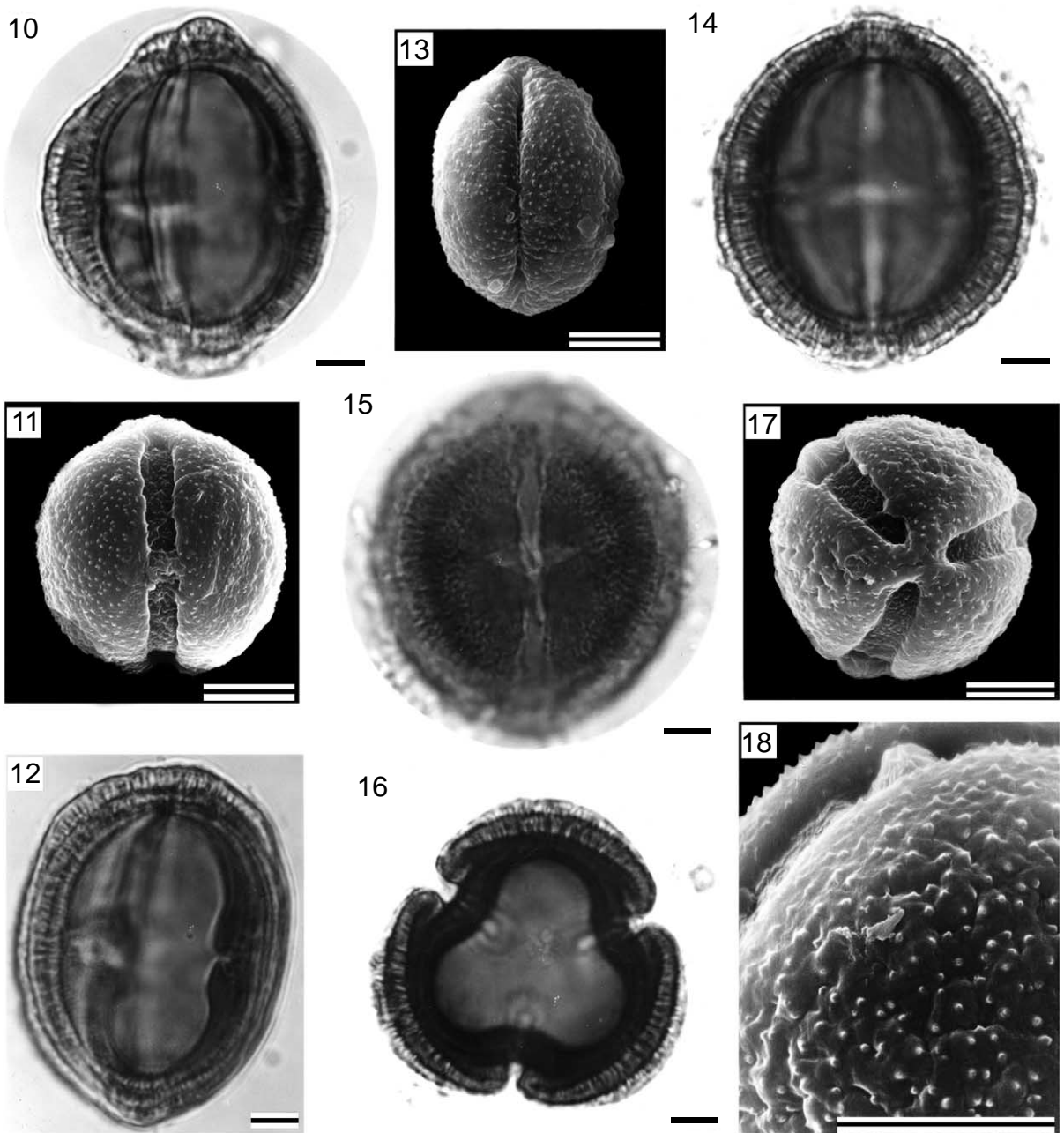
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#### Plate I. *Proustia*

- 1–3. *P. cuneifolia* var. *cuneifolia* (Okada 3036 LP).
  1. LM, equatorial view in optical section.
  2. SEM, equatorial view.
  3. SEM, polar view.
- 4–5. *P. ilicifolia* var. *ilicifolia* (Ricardi 5553 LP).
  4. SEM, equatorial and polar views.
  5. LM, equatorial view in optical section.
- 6–9. *P. pyrifolia* var. *pyrifolia* (Friedrich LP 071038).
  6. LM, equatorial view, showing the endoaperture with bifurcate ends.
  7. LM, polar view in optical section.
  8. SEM, details of aperture showing granular membrane.
  9. SEM, polar view.

nate). These eight exine types are as follows (Fig. 1):  
 Ainsliaea type (established here; Table 2, a.6):  
 Ectosexine and the endosexine poorly differentiated; both compact. Microechinate.

Calopappus type (Crisci, 1974a; Table 2, a.1):  
 Ectosexine thinner than the endosexine; both layers columellate and separated by a zigzag (non-parallel to nexine) internal tectum. Microechinate.



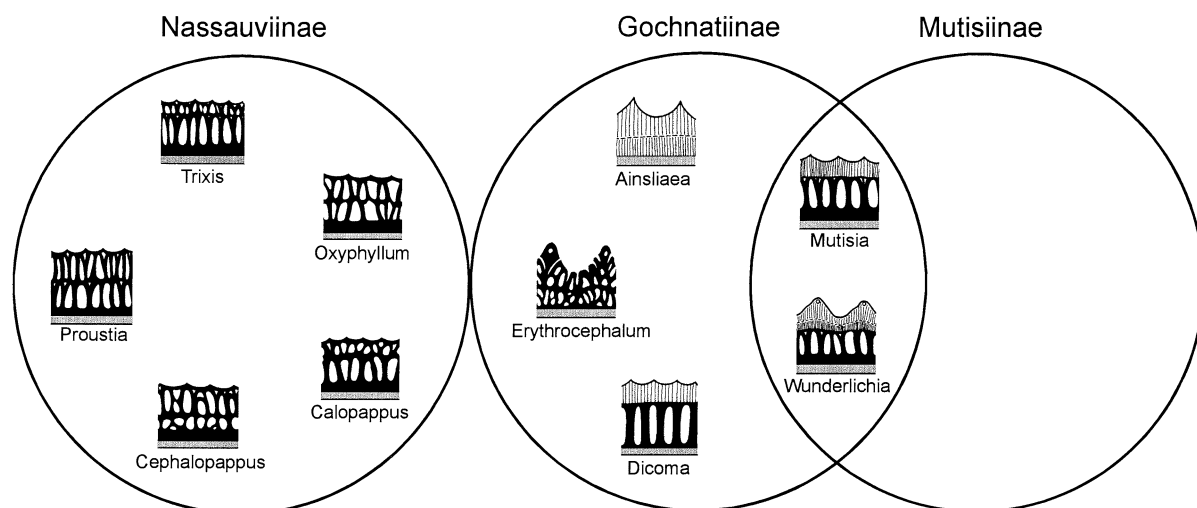


Fig. 1. Exine types of the three subtribes (Nassauviinae, Gochnatiinae and Mutisiinae) of Mutisieae sensu Cabrera (1977), showing the degree of overlapping. The Ainsliaea and Wunderlichia exine types are described here.

Cephalopappus type (Crisci, 1974a; Table 2, a.2): Ectosexine thicker than endosexine; both layers columellate and separated by an internal tectum more or less parallel to nexine. Microechinate.

Dicoma type (Stix, 1960; Table 2, a.8): Ectosexine slightly thinner than endosexine; ectosexine compact or scarcely columellate, endosexine with stout, unramified columellae. Microechinate.

Erythrocephalum type (Stix, 1960; Table 2, a.7): Ectosexine (bi-layered) thicker than endosexine; both layers columellate. Echininate, spines with apical channels.

Mutisia type (Stix, 1960; Table 2, a.9): Ectosexine slightly thinner than endosexine; ectosexine compact or scarcely columellate, endosexine with stout, ramified columellae. Microechinate.

Oxyphyllum type (Crisci, 1974a; Table 2, a.3):

Ectosexine and endosexine equally thick, separated from each other by zigzag internal tectum. Microechinate.

Wunderlichia type (established here; Table 2, a.10): Ectosexine slightly thinner than endosexine; ectosexine with compact inner layer and thinner scarcely columellate outer layer, endosexine with stout ramified columellae. Echininate or microechinate, spines with apical channels.

#### 4. Discussion

##### 4.1. Generic status and relationships between Proustia and Lophopappus

The exine structure of the pollen of *Lophopap-*

#### Plate II. *Lophopappus*.

10. *L. berberidifolius* (Tovar 961 LP), LM, equatorial view in optical section.
11. *L. cuneatus* (Meyer et Bianchi 33175 LP), SEM, equatorial view.
12. *L. blakei* (Cabrera et Fabris 13462 LP), LM, equatorial view in optical section.
13. *L. foliosus* (Cabrera 25270 LP), SEM, equatorial view.
- 14–18. *L. tarapacanus* (Ricardi et Marticorena 25604 LP)
14. LM, equatorial view in optical section.
15. LM, equatorial view, high focus showing aperture.
16. LM, polar view in optical section.
17. SEM, polar view.
18. SEM, detail of apertural membrane and sculpture.

pus and *Proustia* clearly belongs to the Anthemoid pattern established by Skvarla et al. (1977). This pattern is characterized by the absence of a cavus and the presence of thick columellae that support a level of shorter columellae with an internal tectum.

Based on pollen data, *Proustia* and *Lophopappus* differ in several ways: (1) *Lophopappus* pollen grains (polar diameter 40–54 µm) are larger than those of *Proustia* (polar diameter 23–40 µm); (2) in general, the exine is thicker in *Lophopappus* (4–7 µm) than in *Proustia* (2–6 µm), although they overlap considerably; and (3) most taxa of *Lophopappus* have *Proustia* type (except *L. berberidifolius* and *L. tarapacanus* with *Trixis* type, and *L. peruvianus* with both *Proustia* and *Trixis* types), whereas most taxa of *Proustia* have the *Trixis* type (except *Proustia ilicifolia* var. *ilicifolia* with both *Proustia* and *Trixis* types). The *Proustia* type is found exclusively in *Proustia* and *Lophopappus*, whereas the *Trixis* type occurs in some species of *Proustia* and *Lophopappus* as well as other several genera of Nassauviinae (Table 2). Prior to this study, the *Proustia* type was the only one known for *Proustia* and *Lophopappus* (Parra and Marticorena, 1972; Crisci, 1974a), but we also found the *Trixis* type to be present in both genera.

This analysis reinforces the general taxonomic consensus (Parra and Marticorena, 1972; Crisci, 1974a; Ferreyra, 1995) that these two genera are very closely related. Moreover, we should emphasize that they are the only genera of Mutisieae with the *Proustia* type. It may be significant to note that the three species of *Lophopappus* with *Proustia* type (*L. blakei*, *L. cuneatus* and *L. foliosus*) are also the only species with exclusively bilabiate florets, the other three species of *Lophopappus* having mainly or uniquely tubular florets.

#### 4.2. Subtribal relationships and position of *Proustia* and *Lophopappus*

We found, like Hansen (1991b), that pollen of Nassauviinae differ from those of Gochnatiinae and Mutisiinae. The exine of Nassauviinae pollen is distinctly bilayered, with both ectosexine and

endosexine clearly columellate (i.e. *Calopappus*, *Cephalopappus*, *Oxyphyllum*, *Proustia*, and *Trixis* types). This pattern is consistent throughout the subtribe, the sublayers differing only in relative thickness and in the orientation of the internal tectum (parallel to the nexine or zigzag). *Proustia* and *Lophopappus* appear strongly and clearly related to the pollen of the genera of Nassauviinae, supporting Crisci's (1974a) statement that both genera belong to this subtribe.

The types of exine structure found in Gochnatiinae and Mutisiinae are heterogeneous, with most having a compact ectosexine constituted by columellae very thickly disposed, and an endosexine with the columellae clearly distinguishable, stout and ramified. Exine types do not differentiate these two subtribes from one another, since the *Mutisia* and *Wunderlichia* types are found in both subtribes (Table 2; Fig. 1).

Because the pollen data demonstrate a broad overlap in exine features among the genera of Mutisiinae and Gochnatiinae, these data support the hypothesis of other authors (Robinson, 1991; Hansen, 1991a; Bremer, 1994) that the subtribes Gochnatiinae and Mutisiinae are artificially delimited, and that the tribe Mutisieae is comprised of only two subtribes, that is, Nassauviinae and Mutisiinae sensu lato.

We should note that several distinctive exine structural types are to be found, especially in tribe Gochnatiinae. The species of *Ainsliaea* (Gochnatiinae) have a unique exine type, characterized by a compact structure with poorly differentiated sublayers.

Likewise, the echinate pollen sculpturing of *Erythrocephalum*, *Gongylolepis*, and *Wunderlichia* is unique in Mutisieae, but is quite very similar to exine features found in some members of the Cardueae (Tormo Molina and Uberta Jiménez, 1995), a cichorioid tribe closely related to Mutisieae. We hope to expand our analysis of pollen features, including size, shape, exine thickness, and apertural characteristics, to a more complete sampling of genera and species groups of Mutisieae and its relatives, in order to contribute to our understanding of the diversity of pollen types and of the relationships within Mutisieae and among Mutisieae and other tribes of Cichorioideae.



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## Appendix A

Specimens examined and voucher data.

Subtribe Nassauviinae

*Burkartia lanigera* (Hooker et Arnott) Crisci. Argentina. Prov. Chubut. Kreibohm 290 (LP). Prov. Santa Cruz. Ruiz Leal 25930 (LP).

*Cephalopappus sonchifolius* Nees et Martius. Brasil. Edo. Río de Janeiro. Cabrera 12243 (LP).

*Lophopappus berberidifolius* Cabrera. Perú. Dpto. Huancavelica. Tovar 961 (LP). *L. blakei* Cabrera. Perú. Dpto. Cusco. Cabrera et Fabris 13462 (LP). *L. cuneatus* R.E. Fries. Argentina. Prov. Jujuy. Cabrera 9496, 15330, 19023 (LP), Cabrera et al., 15425, 21480, 21494 (LP). Meyer et Bianchi 33175 (LP). *L. foliosus* Rusby. Argentina. Prov. San Juan. Cabrera 25270 (LP). *L. peruvianus* Cabrera. Perú. Dpto. Ancash. Cerrate 1552 (LP). *L. tarapacanus* (Phil.) Cabrera. Chile. Prov. Tarapacá. Ricardi et Marticorena 25604 (LP).

*Macrachaenium gracile* Hooker f. var. *gracile*. Argentina. Prov. Tierra del Fuego. Correa et Pérez Moreau 1978 (LP).

*Oxyphyllum ulicinum* Philippi. Chile. Prov. Antofagasta. Zöllner 3892 (LP).

*Proustia cuneifolia* D. Don var. *cuneifolia*. Argentina. Prov. Jujuy. Cabrera 12009 (LP), Cabrera et al., 13322 (LP), Okada 3036 (LP). *P. cuneifolia* D. Don var. *mendocina* (Philippi) Ariza. Argentina. Prov. Mendoza. Dawson 1085 (LP).

*P. cuneifolia* D. Don var. *mollis* (Kuntze) Cabrera. Argentina. Prov. Jujuy. Cabrera et Fabris 21042 (LP). Bolivia. Dpto. Cochabamba. Herzog 2021 (LP). *P. ilicifolia* Hooker et Arnott. var. *baccharoides* (D. Don) Fabris. Chile. Prov. Aconcagua. Garaventa 332 (LP). *P. ilicifolia* Hooker et Arnott var. *ilicifolia*. Chile. Prov. Coquimbo. Ricardi 5553 (LP). Argentina. Prov. La Rioja. Hunziker 1821 (LP). *P. pyrifolia* de Candolle var. *pyrifolia*. Chile. Prov. Cautín. Friedrich s.n. (LP 071038).

Subtribe Gochnatiinae sensu Cabrera (1977)

*Ainsliaea acerifolia* Schultz var. *subapoda* Nakai. Japan. Honshu, Pref. Miyagi. Boufford 19871 (CM). *A. latifolia* (D. Don) Schultz var. *latifolia*. China. Prov. Yunnan. Handel et Mazzetti 8501 (W). *A. pertyoides* Franchet var. *pertyoides*. China. Prov. Yunnan. Delavay s.n. (UC). *A. okinawensis* Hayata. Japan. Ryukyu. Pref. Okinawa. Murata 17066 (AAU). *A. spanocephala* Y.C. Tseng. Thailand. Loei. Nuijomdha et Vidal 438 (C); Smithland 077323 (BKF).

*Chimantaea cinerea* (Gleason et S.F. Blake) Maguire, Steyermark et Wurdack subsp. *cinerea*. Venezuela. Edo. Bolívar. Steyermark et al., 116028 (MO).

*Cnicothammus lorentzii* Grisebach. Argentina. Prov. Salta. Maldonado 408 (LP).

*Erythrocephalum zambesianum* Oliver et Hiern. Tanzania. Lovett et Congdon 1097 (MO).

*Hecastocleis shockleyi* A. Gray. U.S.A. Nevada State. Train 3973 (LP).

*Hyalis argentea* Hooker et Arnott. Argentina. Prov. Buenos Aires. Pertusi 259 (LP).

*Lycoseris trinervis* (D. Don) S.F. Blake. Perú. Dpto. Chanchamayo. Diers 1249 (LP).

*Stenopadus talaumifolius* S.F. Blake. Venezuela. Territorio Federal Amazonas. Liesner 18346 (MO).

*Stiffitia uniflora* Ducke. Brasil. Edo. Amazonas. Ducke s.n. (LP).

*Wunderlichia mirabilis* Riedel ex Baker. Brasil. Edo. Minas Gerais. Hatschbach 26992 (LP).

Subtribe Mutisiinae sensu Cabrera (1977)

*Gongylolepis huachamacari* Maguire. Venezuela.

Dpto. Río Negro. Liesner et Delascio 21960 (MO).

*Hyaloseris cinerea* (Grisebach) Grisebach var. *tomentella* Grisebach. Argentina. Prov. Córdoba. Nicora 1589 (LP).

*Lulia nervosa* (Lessing) Zardini. Brasil. Edo. Santa Catarina. Smith et Klein 1–576 (LP).

*Mutisia kurtzii* R.E. Fries var. *kurtzii*. Argentina. Prov. Jujuy. Budin s.n. (LP).

*Mutisia sinuata* Cavanilles. Argentina. Prov. Mendoza. Pérez Moreau 12751 (LP).

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