

Echinate fossil pollen of Asteraceae from the Late Oligocene of Patagonia: an assessment of its botanical affinity

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Received: 31 October 2009 / Accepted: 28 December 2009 / Published online: 21 February 2010
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Abstract The Late Oligocene *Mutisiapollis telleriae*, which is the oldest echinate fossil pollen of Asteraceae from Patagonia, was tentatively related to the subfamily Mutisioideae. A detailed comparison of *M. telleriae* with extant asteraceous pollen indicates strong similarities with both Mutisioideae (in particular the Gongylolepis type) and Carduoideae (some genera of Carduinae) subfamilies. This morphotype, as an example of the exceptional diversity of fossil pollen of Asteraceae found in Patagonia, contributes to the knowledge of the early history of the family.

Keywords Mutisioideae · Carduoideae · Spiny fossil pollen · LM · SEM · Late Oligocene · Patagonia

Introduction

Within the family Asteraceae, the subfamily Mutisioideae is particularly interesting because of its basal placement in the phylogenetic tree of the family along with the subfamily Barnadesioideae (Funk et al. 2009). Members of Mutisioideae are mainly South American and, because of the basal

phylogenetic position of the subfamily, southern South America was postulated as the most likely area of origin of Asteraceae (Stuessy et al. 1996; Funk et al. 2009). Therefore, fossil findings in this area are fundamental for tracing the history of the family (Graham 1996). Asteracean fossil pollen grains related to Mutisioideae have been documented through late Paleogene–early Neogene deposits from Africa (Partridge 1978; Zavada and De Villiers 2000; Scott et al. 2006) and Tasmania (Macphail and Hill 1994). In recent years, seven different microechinate pollen morphotypes assigned to subfamilies Mutisioideae and Barnadesioideae have been recognized in Oligocene–Miocene sediments of Patagonia (Katinas et al. 2007; Barreda et al. 2008; Palazzesi et al. 2009). Recently, an echinate new morphotype with likely Mutisioideae affinity was defined: *Mutisiapollis telleriae* Barreda and Palazzesi in a characterization of palynomorph assemblages recovered from the Río Leona Formation (Barreda et al. 2009). This morphotype constitutes the oldest record of Asteracean echinate pollen in Patagonia. However, there are still some uncertainties concerning the accurate relationship of this morphotype with Mutisioideae because pollen with conspicuous spines associated with a bilayered exine and a very perforate tectum also occur in other groups of Asteraceae. In this work we explore the botanical affinity of *Mutisiapollis telleriae* through a comparison with pollen of living relatives with palynological similarities and analyze its taxonomic relationships with other closely related morphotypes from elsewhere (Australia and Africa).

Materials and methods

Fossil pollen grains of *Mutisiapollis telleriae* (Asteraceae) recovered from Late Oligocene deposits from Patagonia

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were examined using light and scanning electron microscopy (LM and SEM, respectively). Slides containing fossil specimens are housed in the palynological collection of the Museo Regional Provincial “Padre Manuel Jesús Molina,” Río Gallegos, Santa Cruz Province, Argentina, with prefix MPM-MP, under the catalogue number 1929. To compare with pollen grains of extant Asteraceae, we used (1) a collection of pollen slides obtained from ca. 310 herbarium specimens from BAF, FM, LP, SI, US, and WIS cited in Tellería and Katinas (2004) and Tellería (2008), and (2) bibliographic data from Stix (1960), Petit et al. (1996), Tellería (1995), Tormo Molina and Ubera Jiménez (1995), Zao et al. (2006), Punt and Hoen (2009), and Ubiergo et al. (2009). The terminology in general follows Punt et al. (2007) and Tellería (2008).

Currently, there are two concepts of Mutisioideae in use: the broad concept, Mutisioideae sensu lato (Katinas et al. 2008), employed here and a more restricted concept, the Mutisioideae sensu stricto (Panero and Funk 2002). According to the sensu stricto concept, the Mutisioideae is split in many branches with tribal and subfamilial taxonomic ranks.

Closest living relatives of *Mutisiapollis telleriae*

As the most generalized pollen type of Asteraceae, *Mutisiapollis telleriae* is tricolporate, with long colpi and lalongate endoaperture; the main informative features are related to the structure and the sculpture of pollen exine. The exine structure of *M. telleriae* is typically anthemoid, i.e., characterized by the lack of cavus (Skvarla et al. 1977). The sexine consists of ectosexine and endosexine, both layers are separated by an internal tectum. The endosexine is four times than the ectosexine. Under light and scanning electron microscopy the ectosexine appears slightly columellate with a perforate tectum surface whereas the endosexine has stout and ramified columellae. The exine sculpture is echinate, this means that the spines are larger than 1 μm (Punt et al. 2007) (Figs. 1 and 2).

Throughout the family Asteraceae, the anthemoid exine pattern in combination with the echinate surface, as occurs in *M. telleriae*, is found in some members of the Guayana Highland-centered genera of the subfamily Mutisioideae (Katinas et al. 2008), in Carduoideae (sub Cynareae, Skvarla et al. 1977), and in Asteroideae (tribe Anthemiidae, Skvarla et al. 1977; Vezey et al. 1994). However, the spines in Asteroideae, when present, are generally long in proportion to the overall size of the pollen grain (Wodehouse 1935), whereas those of the echinate pollen in Mutisioideae and Carduoideae are short. Therefore, only

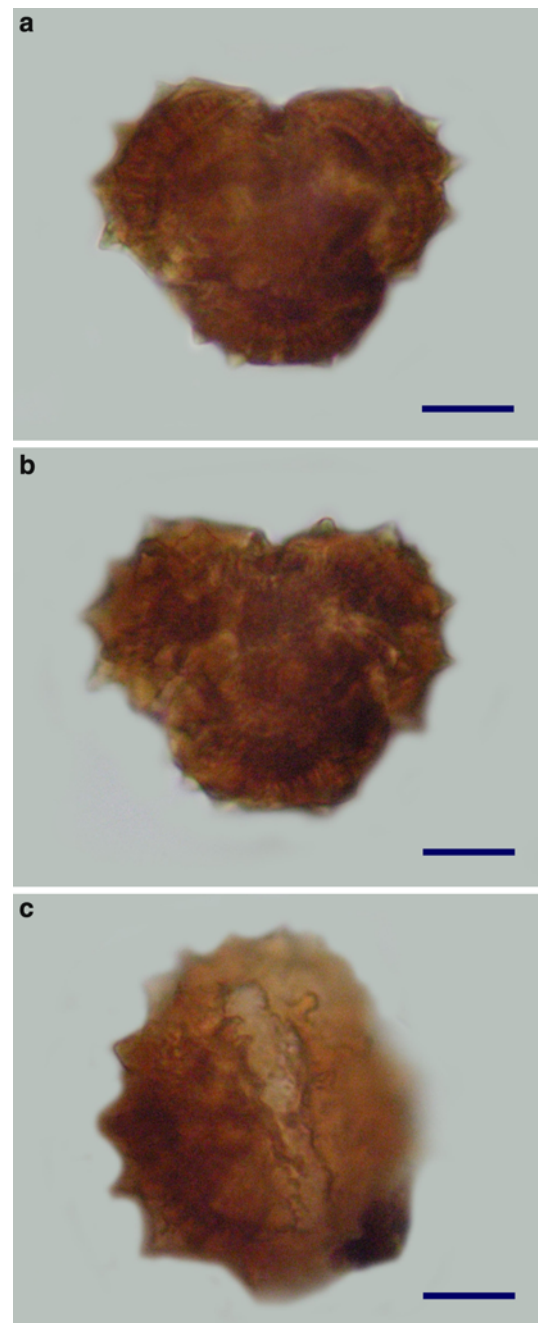


Fig. 1 Light micrographs of inclined polar view of *Mutisiapollis telleriae* showing exine features. **a** Optical section showing the different exine layers and the spines. **b** Intermediate focus showing the colpi. **c** Upper focus of equatorial view. Scale bars 10 μm

the pollen types from these two last subfamilies were found to be comparable with *M. telleriae*.

It is difficult to make a clear distinction between the echinate pollen of Carduoideae and Mutisioideae based on the exine structure because they also share the anthemoid pattern described above. However, some sculptural features such as the shape of the spines as well as

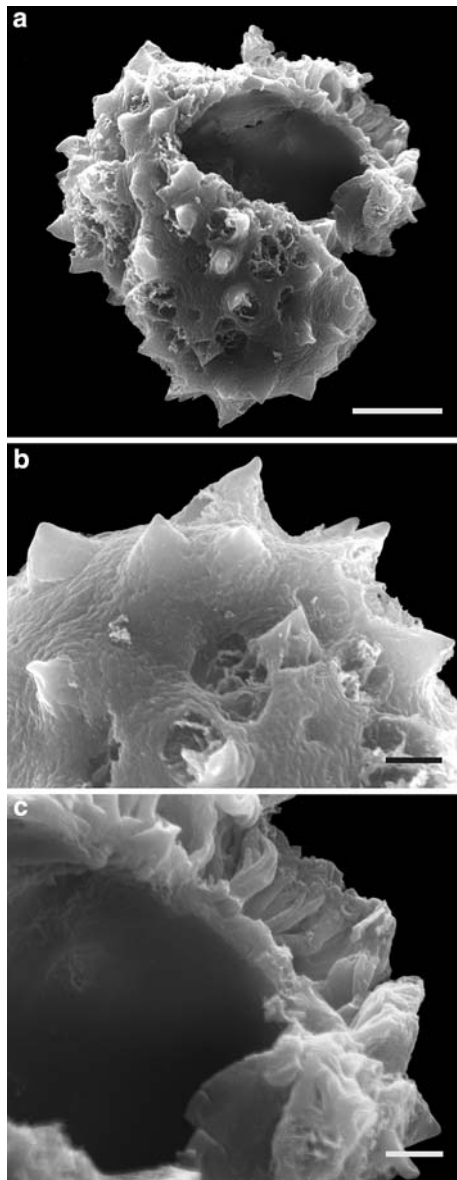


Fig. 2 Scanning electron micrographs of *Mutisiapollis telleriae*. **a** Inclined polar view of broken grain showing the spines of the surface partially corroded. **b** Detail of exine surface. Note the uneven arrangement of spines. **c** Detail of exine showing the thick columellae of the endosexine. Scale bars **a** = 10 µm, **b**, **c** = 2 µm

their arrangement patterns on the pollen surface provide significant taxonomic value. We have extensively studied the pollen of extant taxa in Mutisioideae (Tellería et al. 2003; Jiménez et al. 2004; Tellería and Katinas 2004, 2005, 2009; Katinas et al. 2008; Tellería 2008) and found both microechinate and echinate pollen grains (Appendix 1). In the echinate grains, the spines are quite irregular in shape and size. Pollen surface commonly exhibits conspicuous spines—with broad basis and more or less rounded tips—alternating with small and conical spines arranged in an uneven pattern as a whole. In the same

grain, it is possible to observe areas with few and sparse spines and other areas where spines are grouped (Fig. 3) (and see Figs. 90, 117 in Katinas et al. 2008; Tellería 2008; Ubiergo et al. 2009). Within the echinate exine types, the *Gongylolepis* exine type, which characterizes some genera of the Guayana Highland-centered genera, in particular *Gongylolepis* (Tellería 2008), is the best candidate to compare with *M. telleriae* because of their resemblance. In the *Gongylolepis* type the ratio between the ecto- and the endosexine is intergraded in a range similar to that of the morphotype (i.e., 1:4; 1:5). They also share additional pollen features that are of value in establishing affinity of dispersed pollen; these include the spheroidal to subprolate shape and the long ectoaperture.

With regard to Carduoideae, although the pollen of this subfamily is very diverse (Blackmore et al. 2009), the *Serratula* pollen type (Wagenitz 1955), i.e., ecaeate pollen, can be compared to *M. telleriae*. This type also has spines with broad basis and rounded tip, but commonly displays a geometric (e.g., *Cirsium vulgare*, Fig. 3, and see Fig. 4 H in Tormo Molina and Uebera Jiménez 1995; and plate 21- Fig. 1 in Punt and Hoen 2009) or almost geometric arrangement pattern (e.g., Fig. 1f in Garnatje and Martín 2007). Of the 339 species belonging to 28 genera from the Iberian peninsula (Tormo Molina and Uebera Jiménez 1995), only a few showed an uneven arrangement pattern of spines (e.g., *Arctium minus*, Fig. 3) (Appendix 2). The taxonomic significance of spines in Carduoideae was stressed early on by Wodehouse (1935), who observed that the number, arrangement, and size of spines differ considerably in different species, but they are nearly always geometrically arranged, making this the most conspicuous character of the pollen grain. Uneven spine arrangements in the pollen of Carduoideae do not seem to be representative of echinate types of the subfamily as a whole. Interestingly, spines with an uneven arrangement pattern appear to be common in pollen of most Carduoideae regarded as primitive by Petit et al. (1996) (Appendix 2). In a recent molecular phylogenetic study of Carduoideae (Susanna and García Jacas 2009), these genera were placed in the subtribe Carduinae, a relatively basal branch of the subfamily that follows the basal-most Carlininae. In short, *Mutisiapollis telleriae* is linked to both Mutisioideae (through some of the Guayana Highland-centered genera) and Carduoideae (through some genera of Carduinae).

It is worth mentioning that the group of Guayana Highland genera were suggested to be one of the most basal within Asteraceae (Pruski 1991; Bremer 1994). On the other hand, some members of the Guayana Highland genera (e.g., *Gongylolepis* and *Wunderlichia*) were regarded as close to those of some members of the “Gochnatia

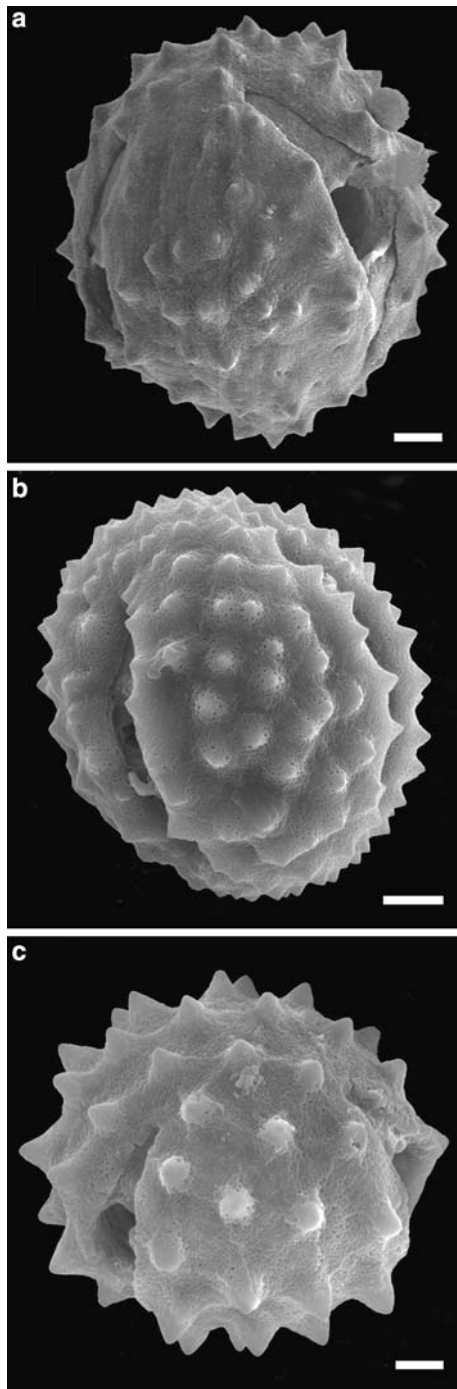


Fig. 3 Scanning electron micrographs of the pollen of species of Mutisioideae and Carduoideae with uneven or geometric spine arrangement pattern. **a, b** Equatorial view showing uneven arrangement pattern of spines. **a** *Gongylolepis paniculata* (Mutisioideae) (Maguire 35392 FM). **b** *Arctium minus* (Carduoideae) (Roig 18787 LP). **c** Inclined polar view showing the geometric arrangement pattern of spines. *Cirsium vulgare* (Carduoideae) (Cabrera 3021 LP). Scale bars 10 μ m

complex” (sensu Freire et al. 2002) (e.g., *Gochnatia* and *Actinoseris*) and Carduoideae by the exine features (Tellería 2008).

Mutisiapollis telleriae in the context of other Asteraceous morphotypes

Other morphotypes of asteraceous fossil pollen records in the southern Hemisphere also demonstrate a mosaic of characters of living Mutisioideae or Carduoideae (Fig. 5). It should be emphasized, however, that most of these morphotypes are microechinate. The microechinate *Mutisiapollis* (sub *Tubulifloridites viteauensis*) is known from the African Paleocene-Eocene (Zavada and de Villiers 2000). This morphotype was previously found in Oligocene deposits of Patagonia, Argentina, and considered essentially similar to modern Mutisioideae pollen (Barreda 1993). Recent studies have established that *M. viteauensis* possesses a recognizable similarity with two genera of the “*Gochnatia* complex” (Mutisioideae): *Cnicothamus* and *Actinoseris* (Katinas et al. 2007). Scott et al. (2006) reassessed the Mutisioideae specimens from the same core samples studied by Zavada and de Villiers (2000) and referred the fossils to the *Mutisia* type and *Dicoma*, this latter previously a member of Mutisioideae and at present referred to Carduoideae (Ortíz et al. 2009). The microechinate *Mutisiapollis patersonii*, defined from the early Oligocene of Tasmania (MacPhail and Hill 1994) and recorded since the Miocene in Patagonia (Palazzesi and Barreda 2004; Palazzesi 2008), was considered close to *Mutisia* and *Chaetanthera* (Mutisioideae) and *Echinops* (Carduoideae). The echinate *Mutisiapollis* sp. (sub *Tubulifloridites* sp.) from the Late Tertiary of Africa (Partridge 1978) was also considered very similar to those genera. From LM images, this morphotype (page 959, Figs. 12 and 13) seems to be similar to *M. telleriae* according to its exine features and pollen shape; however, more data on African fossil pollen are necessary to elucidate whether it belongs to this morphotype.

Conclusions

Mutisiapollis telleriae morphotype exhibits some problems of preservation, however, the structure and the sculpture of exine as well as the aperture type and the pollen shape could be analyzed and compared with pollen of living and fossil related taxa. The spine features, i.e., regularity in size and shape and arrangement pattern of spines, seem to provide evidence to relate *M. telleriae* with some members of the Guayana Highland-centered genera of the subfamily Mutisioideae on one hand and Carduoideae on the other. The botanical affinity of *M. telleriae* in the context of fossil records of pollen of Asteraceae provides evidence that Mutisioideae and Carduoideae share a long evolutionary history. This is in

Fig. 4 Light micrographs of pollen of extant Mutisioideae and Carduoideae similar to *Mutisiapollis telleriae*. All pollen grains in optical section show the spines and the ratio between ecto- and endosexine. **a, b** *Gongylolepis paniculata* (Mutisioideae). **a** Equatorial view, **b** inclined polar view. **c** *Gongylolepis huachamacari* (Maguire et al. 30080 US), inclined polar view. **d** *Arctium minus* (Carduoideae), equatorial view. Scale bars **a, b, c** = 15 μm , **d** = 8 μm

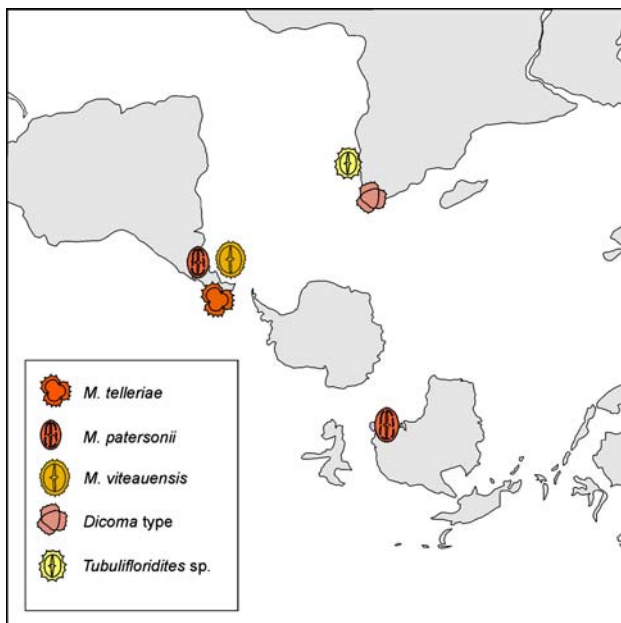
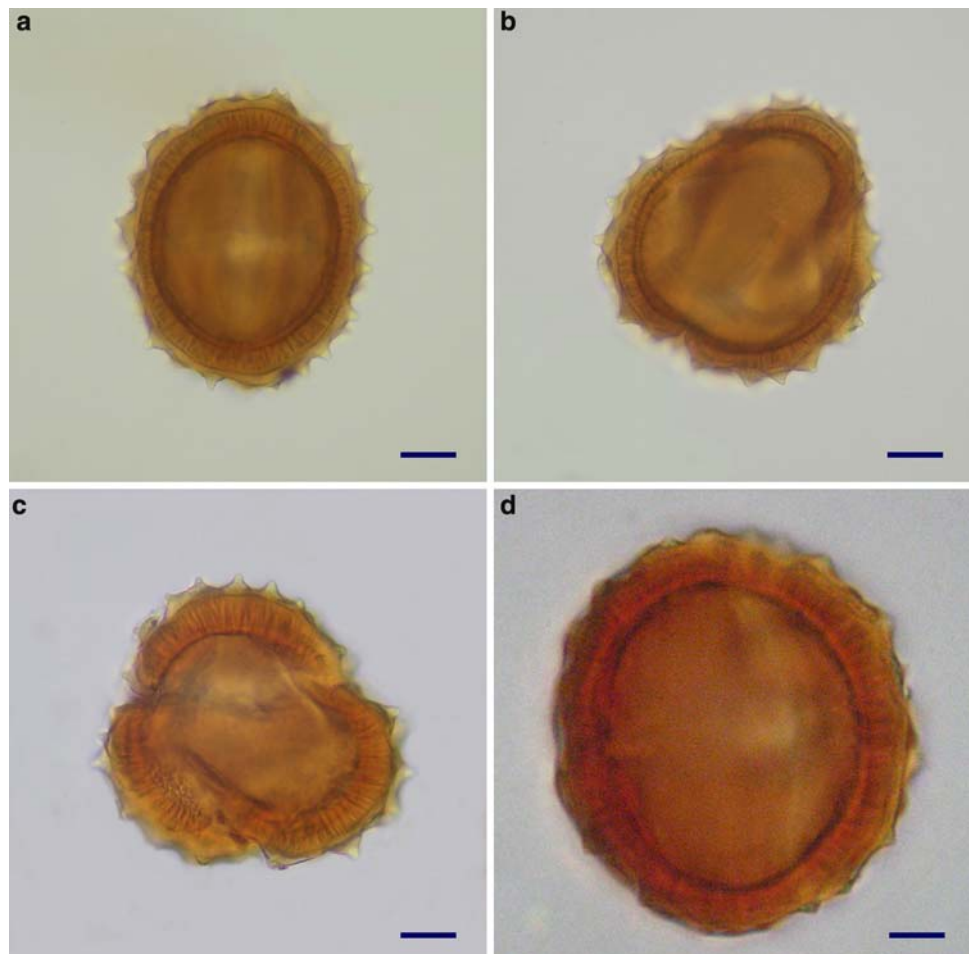


Fig. 5 Paleogeographic distributions of fossil morphotypes with Mutisioideae-Carduoideae affinity in the Oligocene and Miocene. Paleogeographic map modified from Smith and Briden (1977)

agreement with recent molecular phylogenetic studies that consider these groups within the basal branches of the Asteraceae (e.g., Funk et al. 2005, 2009). Southern South America is considered the place of early evolution and diversification of the sunflower family (Stuessy et al. 1996; Bremer and Gustafsson 1997). This observation, coupled with the fact that numerous fossils of Asteraceae have been recovered from Patagonia, supports the notion that the family may have radiated from the austral region elsewhere (Africa, Australia, South America). At present, the Guayana Highlands genera are also present in northern and eastern Brazil, Colombia, Dominican Republic, as well as the Andes of Colombia, Ecuador, and Peru (Katinas et al. 2008), whereas the Carduoideae are mainly found in the Old World (Bremer 1994). It is very likely that the current distribution of above mentioned taxa may have been induced by the cooling trend of the Neogene.

Acknowledgments We would like thank G. Sancho for her constructive comments on the manuscript. This study was supported by projects PIP 02340 and PICT 26298, 01877, 32344.

Appendix 1

Distribution of echinate and microechinate sculpture within the subfamily Mutisioideae from Tellería (2008) and Katinas et al. (2008). In bold: genera belonging to Guayana Highland-centered genera.

ECHINATE: **Achnopogon**, *Actinoseris*, *Cnicothamnus*, **Duida**, **Eurydochus**, **Glossarion**, **Gongylolepis**, *Macroclinidium*, **Quelchia**, **Salcedoa**, **Wunderlichia**.

MICROECHINATE: *Adenocaulon*, *Ainsliaea*, *Aphyll cladus*, *Brachyclados*, *Chaetanthera*, *Chaptalia*, *Chucoa*, *Cyclolepis*, *Dinoseris*, *Eriachaenium*, *Gerbera*, *Gypothamnium*, *Hecastocleis*, *Hyalis*, *Hyaloseris*, *Ianthopappus*, *Leibnitzia*, *Lycoseris*, *Mutisia*, *Myriopsis*, *Neblinaea*, *Onoseris*, *Pachylaena*, *Perdicium*, *Pertya*, *Plazia*, *Trichocline*, *Urmenetea*. **Chimantaea**, **Stenopadus**, **Stomatochaeta**, **Stiffia**. All the members of the tribe Nassauvieae.

ECHINATE AND MICROECHINATE: *Gochnatia*.

Appendix 2

Spine pattern arrangement in subfamily Carduoideae based on SEM images from Tormo Molina & Ubera Jiménez (1995)⁽¹⁾, Petit et al. (1996)⁽²⁾, and Punt & Hoen (2009)⁽³⁾.

Even pattern: *Atractylis cancellata* type⁽¹⁾: *Atractylis cancellata*. *Carduncellus* type⁽¹⁾: *C. cuatrecasasii*, *Carthamus arborescens*. *Carduus* type⁽¹⁾: *Cirsium nigrescens*, *C. oleraceum*. *Centaurea* type⁽¹⁾: *Centaurea linaresii*, *C. alpina*. *Cyanopsis* type⁽¹⁾: *Serratula muricata*. *Galactites* type⁽¹⁾: *Galactites tomentosa*, *G. duriaei*. *Mantiscalca* type⁽¹⁾: *Mantiscalca salmantica*. *Notobasis* type⁽¹⁾: *Silybum eburneum*. *Onopordum* type⁽¹⁾: *Onopordon acanthium*. *Ptilostemon* type⁽¹⁾: *Ptilostemon hispanicum*. *Xeranthemum* type⁽¹⁾: *Xeranthemum cylindraceum*. *Carduus crispus* type⁽³⁾, *Cirsium eriophorum* type^(2, 3), *Cirsium palustre* type⁽³⁾

Uneven pattern: *Arctium* type⁽¹⁾: *Leucea rhaponticoides*, *Jurinea humilis*, *J. pinnata*. *Cynara* type⁽¹⁾: *Cynara tournefortii*, *C. humilis*. *Serratula* type⁽¹⁾: *Serratula baetica*. *Centaurea nigra* type⁽³⁾, *Centaurea nemoralis* type⁽³⁾: *Acantholepis orientalis*⁽²⁾, *Arctium lappa*⁽²⁾, *Chardinia orientalis*⁽²⁾, *Cousinia pseudomollis*⁽²⁾, *Cardiopatium corymbosum*⁽²⁾, *Echinops ritro*⁽²⁾, *Jurinea humilis*⁽²⁾, *Leuzea conifera*⁽²⁾, *Saussurea alpina*⁽²⁾, *Serratula tinctoria*⁽²⁾, *Siebera pungens*⁽²⁾, *Staelhelia dubia*⁽²⁾, *Xeranthemum modestum*⁽²⁾

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