



Generic Delimitation between *Alstroemeria* and *Bomarea* (Alstroemeriaceae)

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The taxonomic relationships between *Alstroemeria* and *Bomarea*, two closely related genera in Alstroemeriaceae, are controversial. With the aim of clarifying their systematic position and generic circumscription, morphological and anatomical studies were carried out on 18 species of *Alstroemeria* and 11 species of *Bomarea*. Light microscopy (LM) and scanning (SEM) and transmission (TEM) electron microscopy were used to study the morphology of mature seeds and pollen. Observations on the most distinctive characters are discussed and compared with other data available for Alstroemeriaceae. Morphology of subterranean organs, pollen exine, adaptive dehiscence of capsules, seed dispersal, seed coat and karyotype characteristics (such as basic chromosome number and symmetry) support the view that these genera are related but should have independent generic status. Results indicate that Alstroemeriaceae comprises three genera: *Alstroemeria* (including *Schickendantzia* and *Taltalia*), *Bomarea* and *Leontochir*.

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Key words: *Alstroemeria*, *Bomarea*, Alstroemeriaceae, morphology, anatomy, subterranean organs, pollen, fruit, seed, chromosomes.

INTRODUCTION

The taxonomic relationship between the New World genera *Alstroemeria* L. and *Bomarea* Mirb., two closely related genera in Alstroemeriaceae, is controversial. The characters proposed by Mirbel (1804) to establish the new genus *Bomarea* are not the most effective: 'les divisions extérieures du périanthe ne sont pas renversées en arrière, les étamines sont droites et la capsule est arrondie et aplatie de haut en bas' (the outer perianth parts are not reflexed, the stamens are straight and the capsule is rounded and flattened from top to bottom). *Alstroemeria* was described by Linnaeus (1762). Later, *Alstroemeria* and *Bomarea* were recognized by Bentham and Hooker (1883). *Alstroemeria* was characterized by erect stems and slightly dissimilar inner segments of the perianth, while *Bomarea* was characterized by its frequently tuberous root fibres, frequently sarmentose stems, and a regular perianth with uniform inner segments. Apart from the subterranean organs, these characters do not appear to be taxonomically significant at the generic level. The two genera are closely related, and different authors do not agree on the characters that define them. Some authors recognize only *Alstroemeria* (Hunziker, 1973). Previously, the two genera were included in Amaryllidaceae (Bentham and Hooker, 1883; Baker, 1888; Rendle, 1930; Pax and Hoffmann, 1930) or Liliaceae (Buxbaum, 1954). There is currently little discussion about the placement of the two genera in Alstroemeriaceae. Alstroemeriaceae also contain the monotypic genus *Leontochir* Phil. from Chile. It is

sufficiently distinct to merit generic status; its characteristics include: uni-locular ovary with triparietal placentae, strongly concave inner tepals, and a *Fritillaria*-like nectary (Wilkin, 1997).

The circumscription of both *Alstroemeria* and *Bomarea* has also been questioned, as some species have been published under both generic names with different epithets, as reported by Xifreda and Sanso (1992) and Sanso and Xifreda (1995 p. 316). The absence of a study of useful characters has resulted in generic recognition being given to segregates of *Alstroemeria* in recent publications (Bayer, 1998a, b).

The systematic circumscription of *Alstroemeria* and *Bomarea* is investigated here. *Alstroemeria*, with about 50 species, is endemic to South America and occupies a diverse range of habitats. Its northern limits are southern Venezuela and north-west Brazil (3–4°N), while it extends as far south as Tierra del Fuego in Argentina (52–53°S). *Bomarea*, with about 100 species, is a poorly known genus, found from Cuba and central Mexico (23–24°N) to 28–29°S in Argentina and 40°S in Chile. *Bomarea* has a subgeneric classification while *Alstroemeria* does not. Species of both genera are long lived, perennial herbs, with the exception of *A. graminea* Phil., which was reported by Bayer (1998b) to be annual. Resupinate leaves, terminal umbelliform inflorescences, rarely unifloral (*A. pygmaea* Herb., *A. patagonica* Phil.), and showy flowers are characteristics of both genera. *Alstroemeria* comprises erect herbaceous plants of variable size while *Bomarea* includes species of climbing habit as well as sub-erect and erect species, and is best represented in the Andean regions of South America. Members of both genera

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have been grown as ornamentals and *Alstroemeria* species and hybrids have become much valued cut flowers.

With the aim of clarifying their systematic relationships, morphological and anatomical studies were undertaken on 18 taxa of *Alstroemeria* and 11 of *Bomarea*. Data at the species level (Xifreda and Sanso, 1993; Sanso, 1998) relating to vegetative organs, pollen, fruit and seed morphology were insufficient or lacking, but are here supplemented with new observations. The characters that distinguish the two genera are discussed and compared with data already available for Alstroemeriaceae.

MATERIALS AND METHODS

All specimens examined are listed in the Appendix. Provenance and authorities for species are included. Herbarium abbreviations follow Holmgren *et al.* (1990). More detailed information about the specimens is recorded on the labels of the herbarium specimens. Only a general indication of their provenance is given in the Appendix. Several species were studied under natural conditions while a few were cultivated (see Appendix).

Pollen for scanning (SEM) and transmission (TEM) electron microscopy was obtained from herbarium specimens, fresh material or fresh material fixed in carnoy (alcohol absolute-acetic acid, 3:1 v/v) for 96 h and stored in 70% alcohol. Exine sections were cut on a Cryocut-E Reichert-Jung rapid freezing microtome at -20°C . SEM of pollen and seeds was carried out by the SEM Service of La Plata Museum, Argentina. Samples were mounted on SEM stubs using double-sided adhesive tape. Pollen grains or seeds were then coated with gold using a Jeol JFC-1100 ion sputter coater and subsequently examined with a Jeol JSM-T100 SEM. Pollen studies were carried out on mature non-acetolysed pollen, with the intention of preserving the integrity of the intine.

Pollen for light microscopy (LM) and TEM was fixed in 3% glutaraldehyde in 0.01 or 0.25 M phosphate buffer (pH 6.8) for 24 h and that for TEM was postfixed in 1% osmium tetroxide for 2 h. Pollen grains for both SEM and TEM were dehydrated in a graded ethanol-acetone series (2 h at each step) and embedded in Spurr's resin (Spurr, 1969). Semi-thin sections were cut from embedded materials and inspected under the LM before ultra-thin sections were cut using an ultramicrotome equipped with a glass knife. Sections for LM were stained with toluidine blue (O'Brien and McCully, 1981) as the metachromatic stain, and ruthenium red (Luft, 1971). Sections for TEM were mounted on grids, stained with uranyl acetate followed by lead citrate. Fuji Velvia film was used for colour photography.

Characterization of embryo types followed Johri *et al.* (1992 pp. 95–96; based on Martin, 1946). In general, pollen terminology followed Punt *et al.* (1994).

RESULTS

For both species, observations are presented under the following sub-headings: subterranean organs; pollen; fruit morphology and dehiscence; and seeds. Table 1 summarizes the principal differential characters between *Alstroemeria* and *Bomarea*.

Subterranean organs

The family comprises geophytes with sympodial rhizomes. In *Alstroemeria*, the species have either a short, nodose rhizome as in *A. pygmaea* for example (Fig. 1D), or more frequently, a long rhizome (Fig. 1F and G). In some species the rhizomes run horizontally, producing aerial vegetative leafy shoots in each growing season and, usually, one flowering stem. These stolons or runners allow rapid shoot growth by means of vegetative multiplication e.g. in

TABLE 1. *Principal differential characters between Alstroemeria and Bomarea*

	<i>Alstroemeria</i>	<i>Bomarea</i>
Subterranean organs		
Rhizome	Long, generally with stolons	Generally short
Storage roots	± Narrow, fusiform, white or cream-coloured	Thick, tuberous, brown
Pollen		
Pollen sculpturing	Striato-reticulate	Reticulate
Fruit morphology and dehiscence		
Capsule morphology	Umbonate towards the apex	Turbinate
Mature capsule consistency	Papyraceous-coriaceous	Ligneous
Fruit dehiscence	Explosive	Descending, no explosive
Seeds		
Seed morphology	Globose	Subglobose or elongate
Sarcotesta	No	Yes
Seed coat	Dry-hard	Fleshy
Mature seed colour	Yellowish-brown, tan or brown	Red-orange
Seed dispersal	Ballistic	Ornithochorous
Karyotype characteristics		
Basic chromosome number	$x = 8$	$x = 9$
Karyotype asymmetry	High	Low

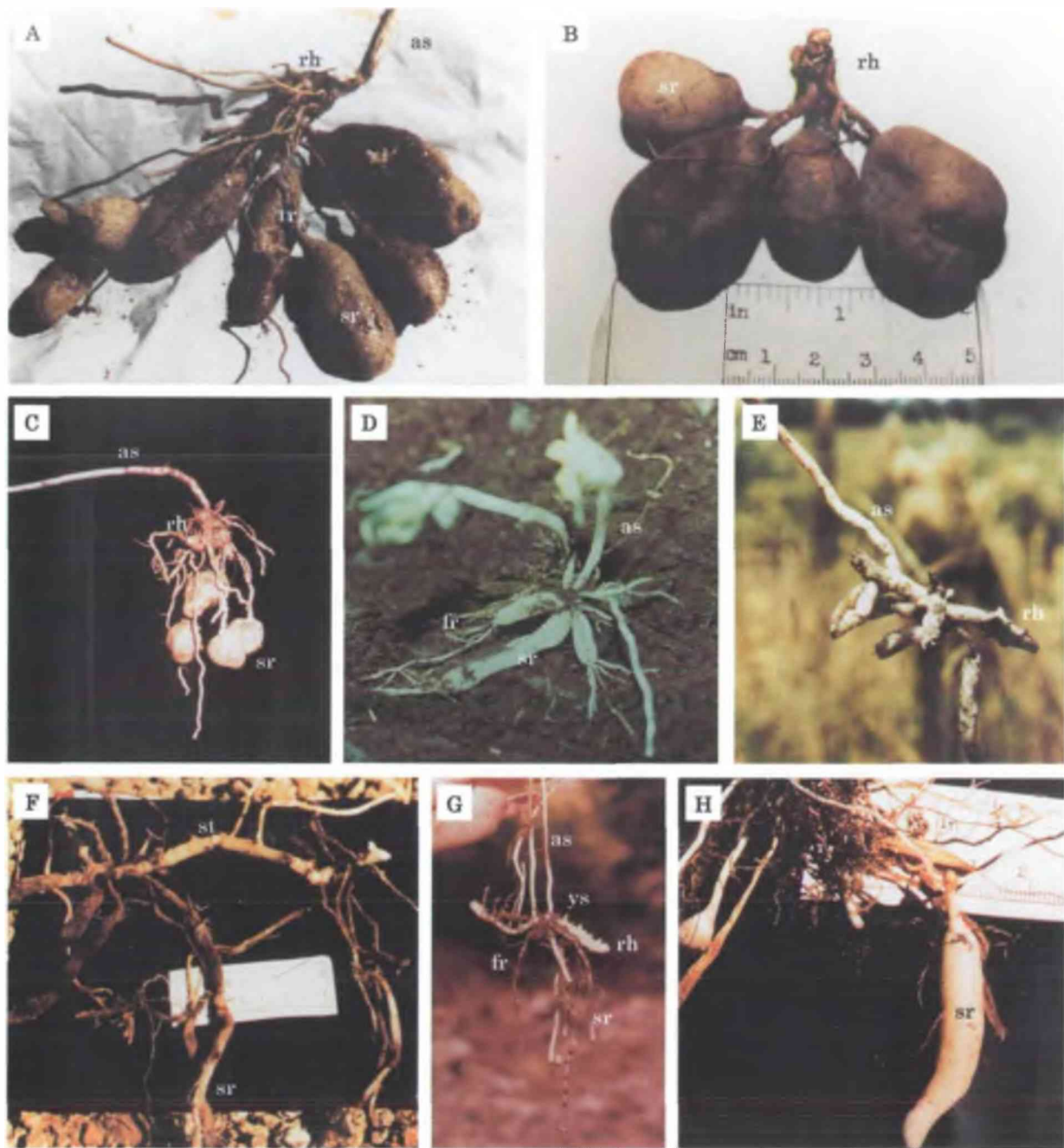


FIG. 1. Subterranean organs of *Bomarea* (A–C) and *Alstroemeria* (D–H). A, *B. macrocephala* (Xifreda & Sanso 1425, SI). B, *B. boliviensis* (J. Hunziker *et al.* 12872, SI). C, *B. edulis* (Xifreda & Sanso 871, SI). D, *A. pygmaea* (Xifreda & Sanso 1066, SI). E, *A. isabellana* (Sanso *et al.* 5, SI). F, *A. aurea* (Xifreda & Sanso 1470, SI). G, *A. presliana* (Xifreda & Sanso 1480, SI). H, *A. patagonica* (Xifreda & Sanso 1466, SI). as, Aerial stem; fr, fibrous root; rh, rhizome; sr, storage root; tr, thinner radicular zone; st, stolon; ys, young shoot.

A. aurea (Fig. 1F) and *A. presliana* (Fig. 1G). Traditionally, horticultural propagation of *Alstroemeria* is by division of the rhizomes. The rhizome can be simple or ramified as in *A. isabellana* (Fig. 1E). In *A. andina* subsp. *venustula* the rhizome is compact and covered by densely imbricate cataphylls (Sanso, 1996b: Fig. 4B). Young roots are thin and fibrous but some of these thicken apically to become cylindrical or fusiform (Fig. 2A), white or cream-coloured, starch-containing storage organs. The fleshy roots can be

enlarged as in *A. psittacina* (Sanso, 1996b: Fig. 12A), more or less enlarged as in *A. aurea* (Fig. 1F) and *A. patagonica* (Fig. 1H) or slender as in *A. presliana* (Fig. 1G). They may be grouped directly next to the rhizome as in *A. apertiflora* (Fig. 2A) and *A. pygmaea* (Fig. 1D) or separate from the rhizome as in *A. patagonica* (Fig. 1H).

The subterranean system of *Bomarea* species is generally composed of a nodose rhizome with tuberous roots that store nutrients (Fig. 2B). The storage roots are frequently

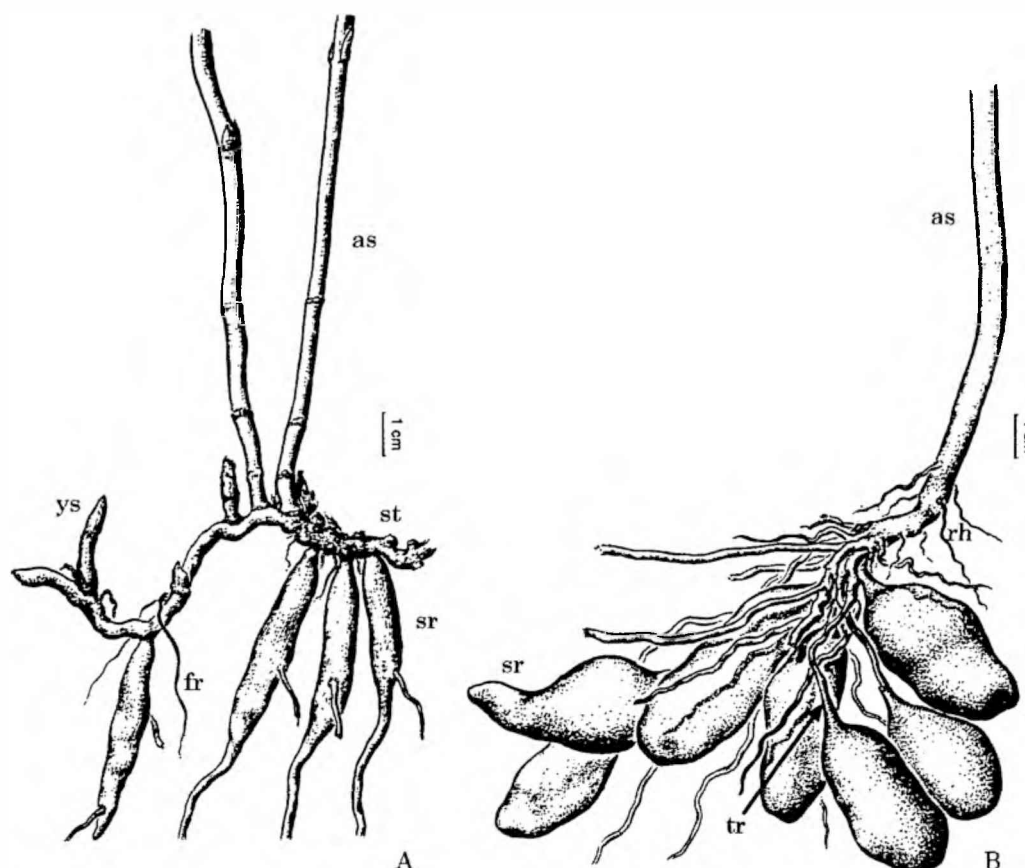


FIG. 2. Subterranean organs of *Alstroemeria apertiflora* (Hässler 9613, G) (A) and *Bomarea macrocephala* (Xifreda & Sanso 1425, SI) (B). as, Aerial stem; fr, fibrous root; rh, rhizome; sr, storage root; st, stolon; tr, thinner radicular zone; ys, young shoot.

brown outside and white or yellowish inside (Fig. 1A–C). As the plant ages, the swollen ovoid or roundish roots are found deeper in the soil, connected to the rhizome by a thinner and fragile radicular zone (Figs 1A, C and 2B).

Pollen

The pollen morphology of 18 species, indicated by an asterisk in the Appendix, has been studied for the first time. The pollen of all species investigated is ellipsoid (boat-shaped), heteropolar and monosulcate. Symmetry is bilateral. Size ranges from 50–120 μm (long axis) \times 25–62 μm (short axis). Since pollen size generally ranges from approx. 20–150 μm , these pollen grains are considered large. The tectum is tectate or semi-tectate, and brevi-striato-reticulate (*Alstroemeria*) or reticulate with tectate-perforate extremities (*Bomarea*). In SEM freeze-fractures and LM and TEM thin-sections, the infratectum corresponding with brevi-striato-reticulate comprises densely packed columellae (Fig. 5A and B), while in pollen with a reticulate exine the columellae are more widely spaced (Fig. 5G).

Pollen grains of *Alstroemeria* spp. have a brevi-striato-reticulate exine. The striate muri are arranged in a parallel to sub-parallel pattern. In some species small, interconnecting muri are apparent between striae. This structure results in the roundish to elongate perforations, and gives a semitectate

exine structure (Figs 3A–C, G, H and 5A, B). Completely striate surface patterning is not observed. The perforations are fine, for example in *A. graminea*, *A. angustifolia* subsp. *angustifolia* and *A. werdemanii* (Fig. 3D, E and J), or much coarser, for example in *A. isabellana*, *A. pseudospathulata* and *A. versicolor* (Fig. 3F, K and L).

The pollen of *Bomarea* species is characterized by a semitectate reticulate exine structure, with rounded or slightly elongated lumina, which are 1 μm in length or diameter in most species (Fig. 4). In microreticulate ornamentation, for example in *B. edulis*, the lumina are less than 1 μm in width, but are wider than or equal in width to the diameter of the muri that separate them. The lumina are notably smaller at the equatorial short axes of the grain, or these extremities may be perforate (Fig. 4A, C, E and G). Sometimes granulae are visible at the bases of the lumina; these correspond to reduced or modified columellae (Fig. 4B, D and F).

The ultrastructure of the sporoderm shows a semi-tectate tectum (Fig. 5A–G) and a columellate infratectum above a well defined foot layer. In both genera the tectum and foot layer are similar in width. However, the infratectum tends to be somewhat wider than the tectum or foot layer in *Alstroemeria*, while in *Bomarea* it is similar in width to the other layers. The columellae tend to be spaced more widely in the pollen of *Bomarea* than in the pollen of *Alstroemeria*.

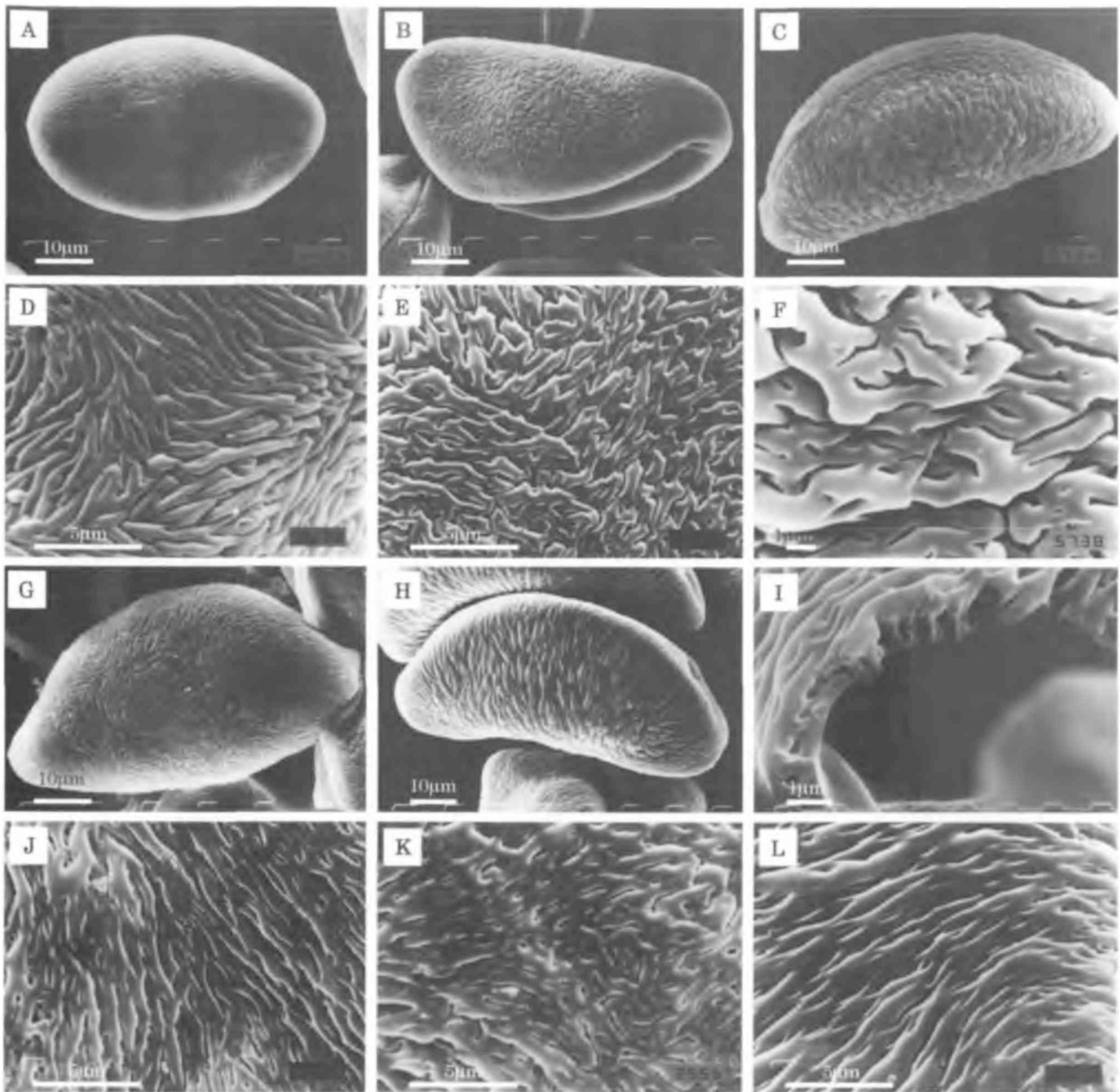


FIG. 3. SEM micrographs of *Alstroemeria* pollen. A–C, G, H, General view; D–F, J–L, detail of the striate-reticulate sexine; I, cross-section of exine. A, *A. andina* subsp. *venustula* (Luti *et al.*, Hb. Geobot. 5500, SI). B and E, *A. angustifolia* subsp. *angustifolia* (P1995/5003, SI). C and F, *A. isabellana* (Sanso *et al.* 5, SI). D and G, *A. graminea* (Werderman 802, G). H, *A. exserens* (P1995/5009, SI). I, *A. psittacina* (cult. FCEyN, UBA). J, *A. werdermannii* (Werderman 134, SI). K, *A. pseudospathulata* (Burkart *et al.* 13867, SI). L, *A. versicolor* (P1995/5052, SI).

This is associated with the difference in tectum morphology between the two genera; brevi-striato-reticulate, for example in *A. isabellana* (Fig. 5C and D), or reticulate, for example in *B. boliviensis* (Fig. 5E and F). The foot layer is often irregular and interrupted in *Alstroemeria*, while in *Bomarea* it is more regular but may be finely invaginated (Fig. 5E and F). Endexine is absent but two narrow intine layers are apparent; they are similar in width but intine 1 is denser and stains more darkly than intine 2. The exine wall, proportional to pollen grain size, is not particularly thick, being approx. 1.5–2.8 µm.

Fruit morphology and dehiscence

The fruit of *Alstroemeria* is a 3-valved loculicidal capsule or diplotegium. In superior view it is rounded, while in lateral view it is ovoid, 6-ribbed, slightly or notably umbonate towards the apex (Fig. 6 A, B), coriaceous and bright light brown when mature (Fig. 7A).

When unripe, the fruits are greenish, with six longitudinal ribs joined by a transverse rib below the high, widely conical apex, which is notably marked and more angular than in the mature fruit (Fig. 6A). Sometimes the ribs are purple

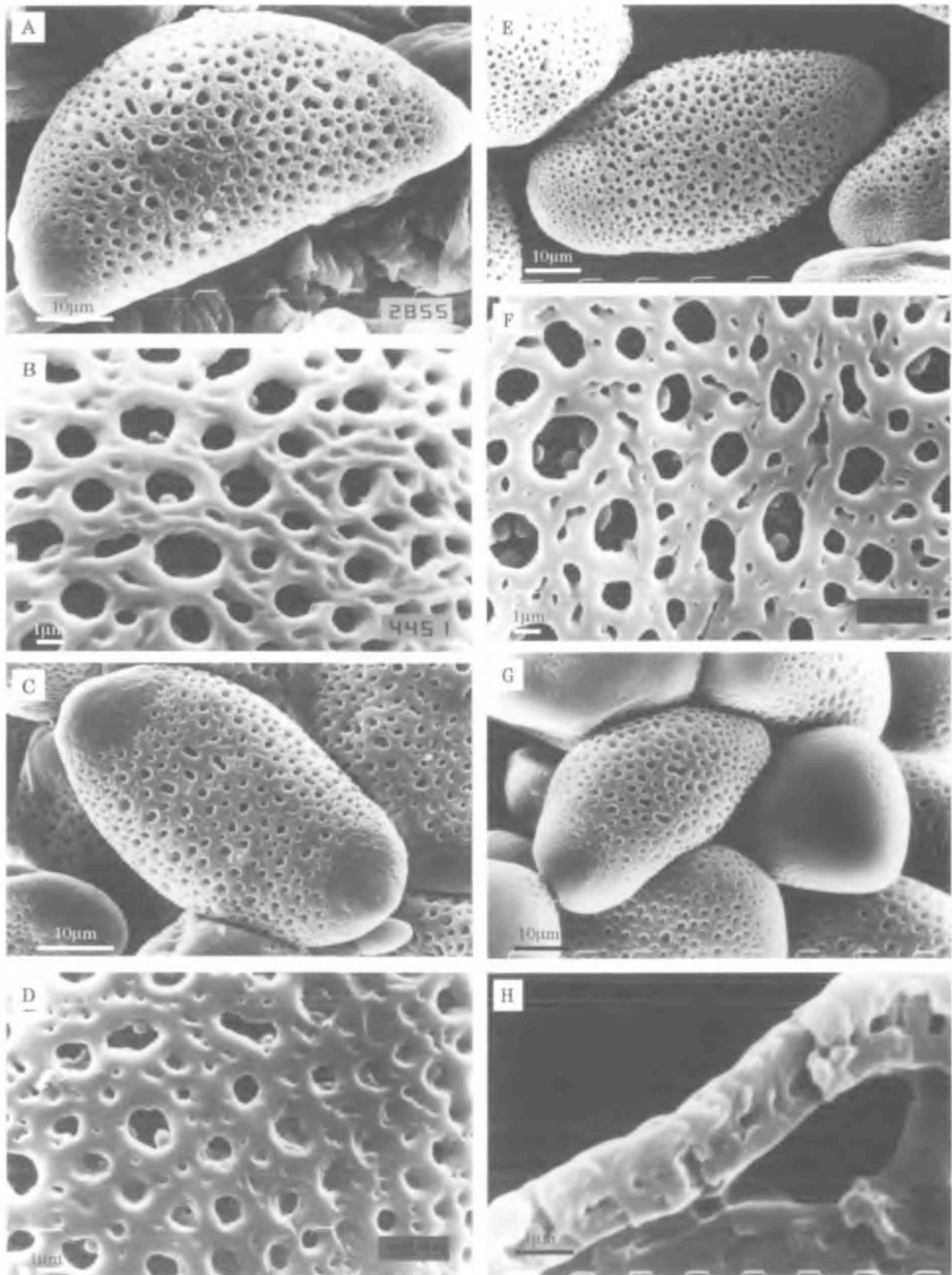


FIG. 4. SEM micrographs of *Bomarea* pollen. A, C, E, G. General view; B, D, F, detail of the reticulate sexine; H, cross-section of exine. A and B, *B. macrocephala* (Xifreda & Sanso 1180, SI). C and D, *B. tomentosa* (Sanso & Pereyra 22, SI). E and F, *B. crocea* (Sanso & Pereyra 26, SI). G, *B. boliviensis* (Castellanos 46674, BA). H, *B. edulis* (Xifreda & Maldonado 458, SI).

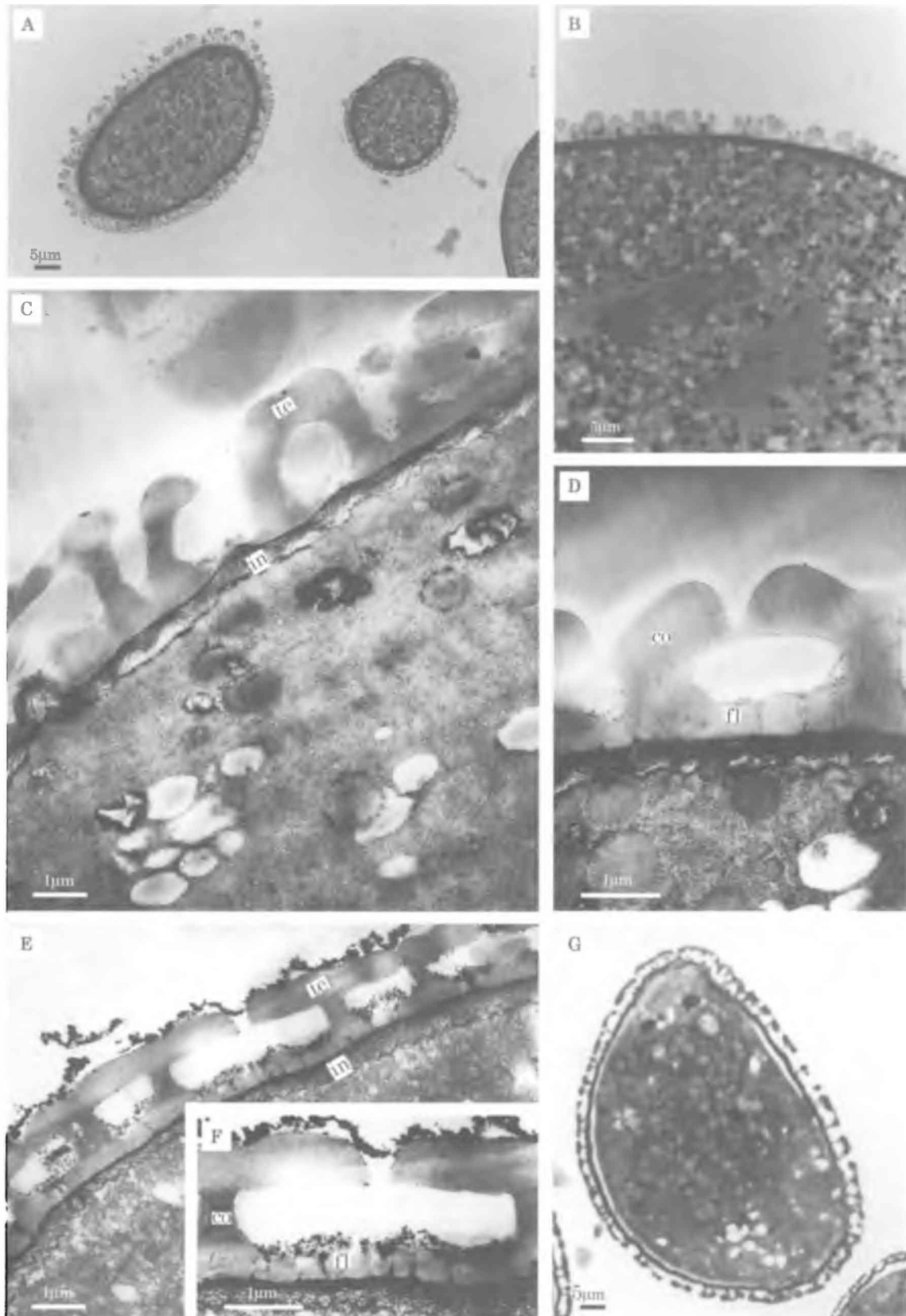


FIG. 5. LM (A, B, G) and TEM (C–F) micrographs of pollen grain sections: exine morphology. A–D, Semitectate striate-reticulate; E–G, semitectate reticulate. A and G, General view of pollen grains; B, detail of sexine; C and F, sporoderm ultrastructure; D and F, detail. A–D, *A. isabellana* (Cult. FCEyN, UBA). E–G, *B. boliviensis* (Cult. FCEyN, UBA). co, Collumella; fl, foot layer; in, intine; te, tectum.

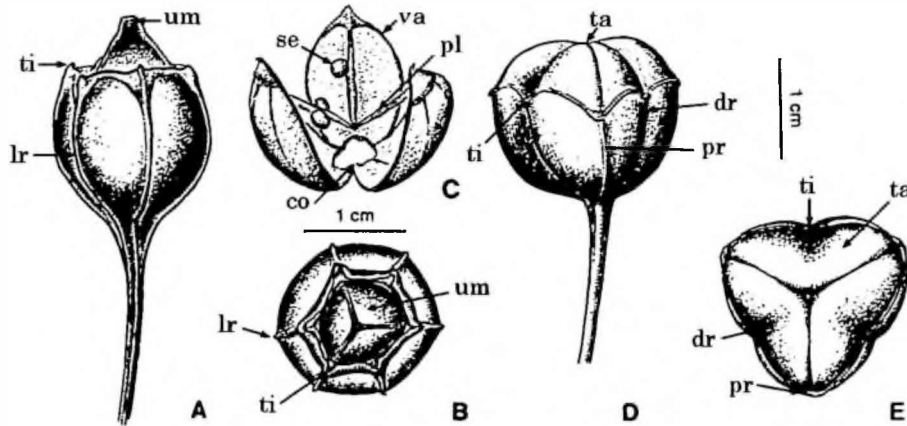


FIG. 6. Fruit. A, B, D, E, Young fruit (before dehiscence); C, post-dehiscent fruit. A and B, *A. psittacina*. A, Lateral view, umbonate. B, Superior view, outline fruit circular. C, *A. isabellana*, view of the three valves not completely separate. D and E, *B. boliviensis*. D, Lateral view, turbinate. E, Superior view, fruit markedly trigonous. A and B cult. no. 1 J. Hunziker, J. Hunziker 11743 (SI). C, Cult. FCEyN, Sanso *et al.* 5. D and E, cult. no. 22 J. Hunziker, J. Hunziker *et al.* 12872 (SI). co, Central orifice; dr, longitudinal deep-set rib; lr, longitudinal rib; pl, placenta; pr, longitudinal project rib; se, seed; ta, truncated apex; ti, point of tepal insertion; um, umbo; va, valve.



FIG. 7. Photographs of mature fruit and dehiscence. A, *A. patagonica* (Xifreda & Sanso 1466). Stem on the right with six projections in the shape of a claw following explosive dehiscence. B and C, *B. boliviensis* (cult. J. Hunziker). B, Immature capsules in three successive phases of dehiscence open in the upper region; C, completely mature capsule with ligneous consistency showing the three locules, each of which contains two adjacent rows of seeds along the placentary lines.

(*A. presliana*). At maturity, the fruits are rounded, their colour changes to golden or clear brown and the texture is papyraceous-coriaceous (Fig. 7A). In *A. pygmaea* and *A. patagonica*, two small herbs with reduced inflorescences, the immature fruits are covered by leaves. In some species the *umbo* (apex) is short, 0.5–3 mm in length (*A. aurea*, *A. isabellana*, *A. andina*), while in other species it is more pronounced and may be up to 20 mm in length (*A. pseudospathulata*, *A. pelegrina*, *A. presliana*, *A. pulchra* Sims). Sometimes tepals, filaments and style are persistent on the mature fruit, as in *A. andina* subsp. *venustula* and *A. patagonica*.

In superior view, the outline is circular, and the umbo has three faces that are slightly curved forming a pyramid (corresponding to the style base), which extends itself over the rupture scars of the tepals (Fig. 6B). From the point of insertion of these tepals downwards, it has six longitudinal ribs.

Dehiscence is explosive, the capsule splitting from the base into three parts. The three valves, together with the

seeds, are thrown a considerable distance, ensuring dispersal of the seeds. The lines of dehiscence coincide with the sides of the pyramid. Dehiscence takes place when the fruit is dry. The stem is left with three (to six) of the longitudinal ribs more or less remaining in the shape of a claw, and often with the remains of the epidermis still attached (Fig. 7A). On rare occasions, if the tension is not too great, the capsule is not destroyed completely and the three valves do not separate completely from the stem (Fig. 6C). When the capsule separates from the stem the central orifice of the capsule (the site of union of the three carpels) is evident (Fig. 6C).

The fruits of *Bomarea* are loculicidal, sub-spherical, with six longitudinal ribs, and the capsule is turbinate in lateral view (Fig. 6D and E). When young, the fruits are green and are more or less truncated at the apex. Three of the longitudinal ribs are projecting and three are deep-set. The shape of the apical zone corresponds with the base of the style, but is more developed than in *Alstroemeria* (Fig. 6D). In superior view the fruits are markedly trigonous with three obtuse angles; each of the three faces is slightly depressed in

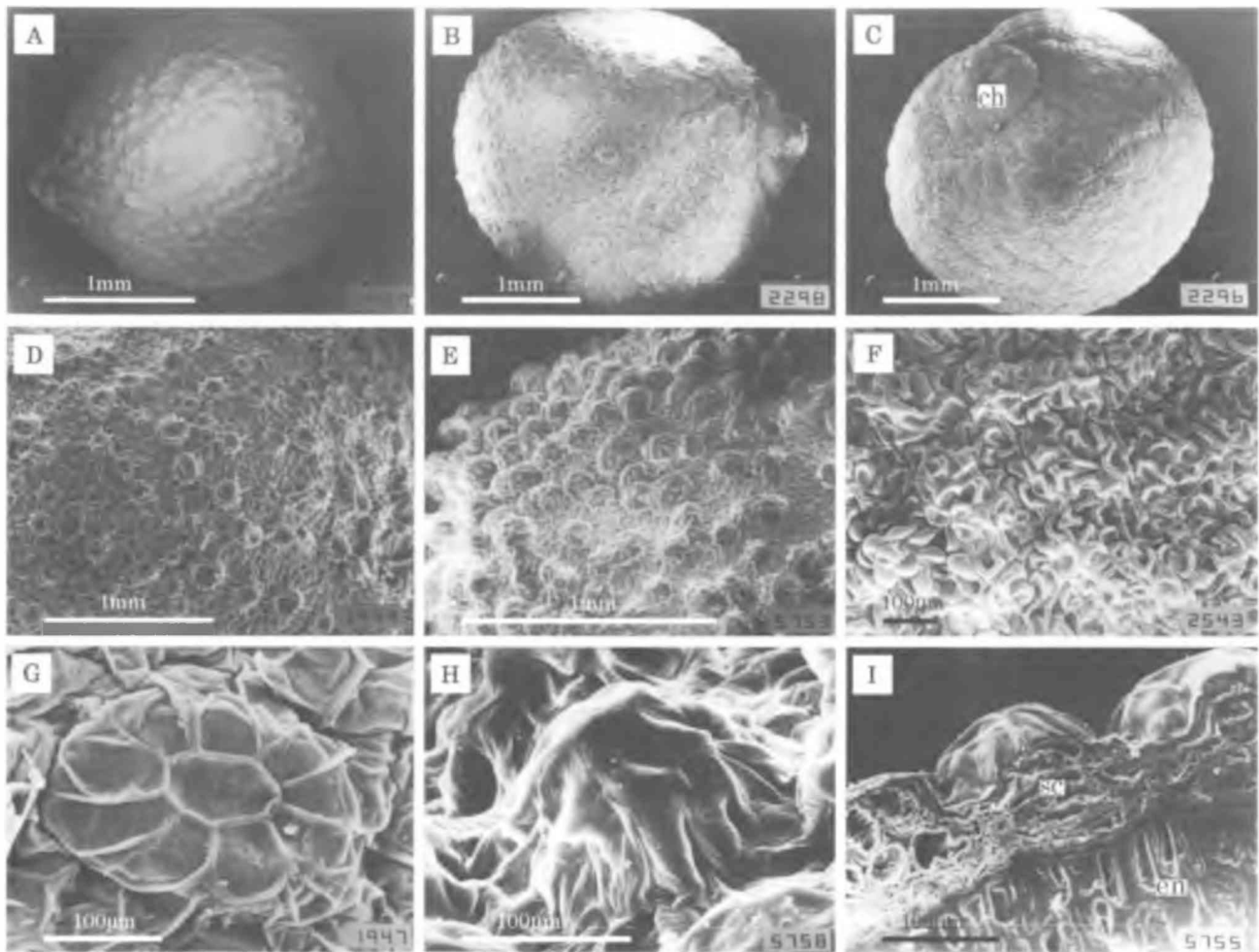


FIG. 8. SEM micrographs of seed. A–C, General view; D–F, surface ornamentation, outer integument of the seed coat; G and H, detail of ornamental units; I, longitudinal section, outer integuments of seed coat and endosperm. A, D and G, *Alstroemeria psittacina* (Xifreda & Sanso 1039, SI). B, *A. aurea* (Fabris 1140, LP). C and F, *A. patagonica* (Xifreda & Sanso 1466, SI). E, H and I, *A. andina* subsp. *venustula* (Kiesling *et al.* 8097, SI). ch, Chalazal region; en, endosperm; sc, seed coat.

the centre. When the fruit ripens it has a ligneous consistency and its dehiscence is completely different from that of *Alstroemeria*. Instead of exploding, the capsule opens in the upper region (Fig. 7B) to form a three-armed suture. Two adjacent rows of seeds are located along the length of the placenta in each of the three locules (Fig. 7C).

The numerous seeds with a bright red-orange sarcotesta remain exposed (Fig. 7C), and the infructescence contrasts vividly with the surrounding foliage and is an attractive signal for birds. In *B. macrocephala*, endemic to northern Argentina, the nodding infructescence has many large bracts at the top of the stem with marcescent leaves. In species with a climbing habit the fruit sometimes hangs more than 2 m above the arboreal vegetation.

Seeds

In *Alstroemeria* there are numerous seeds per capsule ranging in diameter from 2–4 mm. They are yellowish-brown, tan or brown, globose or subglobose (Figs 8A–C

and 9A). The seed coat is dry and hard. The primary sculpturing consists of conspicuous protuberances which give the seeds a peltate, papillose or verrucose appearance (Figs 8D–F and 9B). In several species the testa is colliculate, for example in *A. aurea* and *A. presliana*, two trans-Andean species from Argentina and Chile. High magnification with the SEM shows that the individual units of the seed surface sculpturing, although basically convex, are morphologically variable between species: some are conical with a wide base, for example in *A. andina* subsp. *venustula* (Fig. 8H), while specialized structures occur in other species. In *A. psittacina* (Fig. 8G) a central cell is surrounded by nine-ten peripheral cells. The cells that comprise these ornamental units and that are responsible for the roughness of the surface of the seed coat are thick-walled and pitted (Fig. 8I). The surface of the outer periclinal cell wall may also exhibit micro-ornamentation and secondary sculpturing, e.g. be irregularly hollowed or wrinkled (*A. andina* subsp. *venustula*, Fig. 8E and H), micro-papillate (verrucate) (*A. graminea*, Fig. 9B and C) or smooth

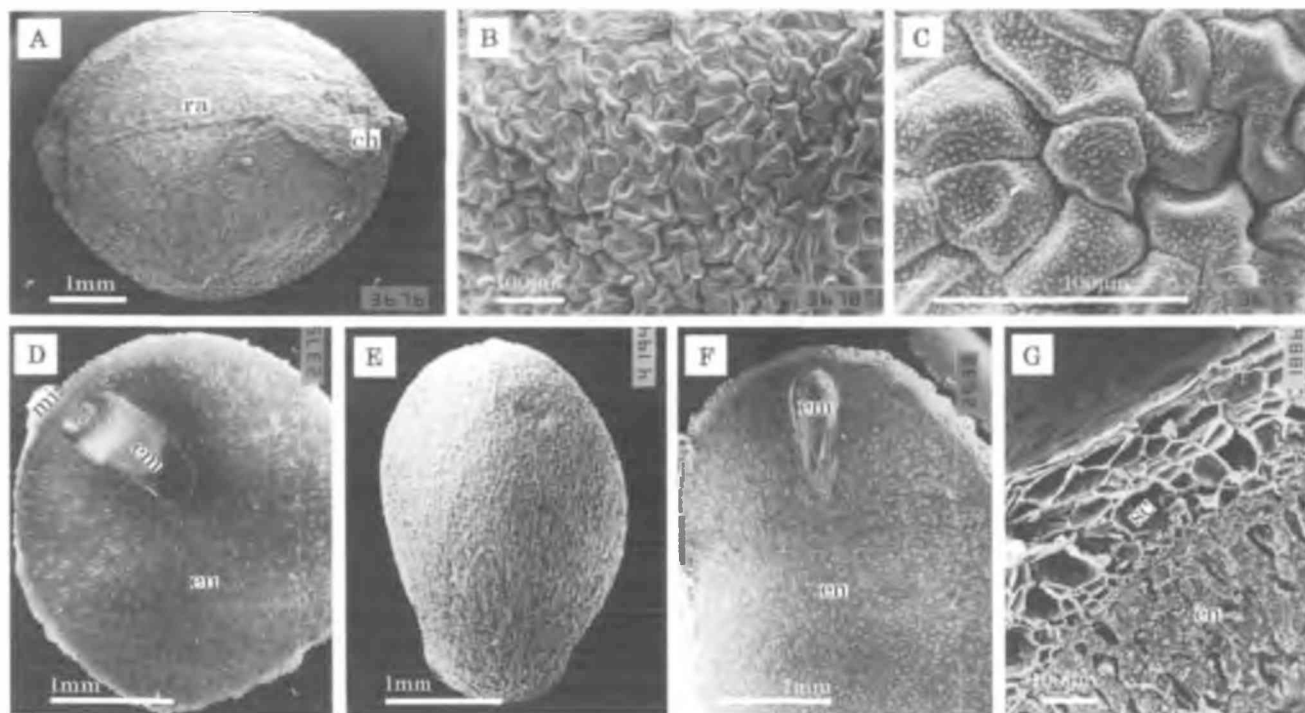


FIG. 9. SEM micrographs of seed. A, E, General view; B, C, surface ornamentation, outer integument of the seed coat; D, F, longitudinal section showing lateral position of the embryo and endosperm; G, longitudinal section, outer integuments of seed coat and endosperm. A–C, *A. graminea* (Worth & Morrison 15808 (G)). D, *A. presliana* (Xifreda & Sanso 1480, SI). E, and F, *Bomarea boliviensis* (J. Hunziker *et al.* 12872, SI). G, *B. edulis* (Xifreda & Sanso 1147, SI). ch, Chalazal region; em, embryo; en, endosperm; mi, micropyle; ra, raphe; sc, seed coat.

(*A. aurea*, *A. presliana*). A dark brownish-black discoid appendage, arising from the chalazal region, occurs in the seeds of *Alstroemeria* (Fig. 8B and C) and the raphe is a shallow longitudinal rib (Fig. 9A). The thick seed coat consists of just a few cell layers. In *A. andina* subsp. *venustula*, for example, it is basically 60 μm wide, but has a thickness of 120 μm where the protuberances occur (Fig. 8I).

The seeds are dispersed by a ballistic mechanism. The almost perfect spherical shape guarantees efficient dispersal by the centrifugal force exerted on the seed as it is expelled from the capsule. In some cases the seed coat protuberances with large surface cells may have an adhesive property. This would enable the seed to attach, for a while, to a passing animal, and thus be carried further away. In this case, the seeds would be termed diplochorous (dispersed by two, different, successive agents), with secondary zoochory ensuring a wider dispersal.

A linear embryo is enclosed in the endosperm near the micropyle. It is short, one-third to two-thirds the length of the endosperm (Fig. 9D). The endosperm is also tough and has abundant thick-walled, pitted cells (Fig. 8I). It contains lipids, proteins and hemicellulose.

The seeds of *Bomarea* are also numerous, measuring on average 4–5 mm in length and 3.5–4 mm in width, although some seeds in *B. boliviensis* may be smaller. At maturity they are bright orange-red (Fig. 7C). They are subglobose or elongate, rarely globose, and taper at the distal extreme (Fig. 9E). The raphe is generally inconspicuous. Immediately after ripening the chalaza is scarcely visible on the outer surface. Stomata that would allow gas

exchange to the embryo are observed on the seed coat (Sanso, 1996a: Fig. 1.6D). When older, a discoid appendage becomes more evident in the chalazal region. The seed is characterized by a thick, fleshy sarcotesta (Fig. 9E), which consists of several layers. In *B. edulis* it is 200–250 μm in width (Fig. 9G). The combination of the sarcotesta and the bright reddish colouration of the seeds is indicative of adaptation to ornithochory.

The embryo is short, cylindrical and linear, and is about one-third the length of the endosperm (Fig. 9F). The abundant tough endosperm has considerably thickened cell walls with pits (Fig. 9G).

DISCUSSION

This study highlights the taxonomic utility, at the generic level, of a selected range of characters for *Alstroemeria* and *Bomarea*. One of the most important characters that distinguishes the two genera is the morphology of the subterranean organs. In nearly all species of *Alstroemeria* that were investigated, stolons are present and the storage roots are cylindrical or fusiform. However, according to Bayer (1998b), *A. graminea*, an annual plant, does not develop storage roots. Recently, Meerow *et al.* (1999) described a new species, *A. hygrophila*, from Goiás and Distrito Federal, Brazil, which apparently also lacks thickened roots. The isolated starch of the swollen roots of *A. aurea* and *A. ligtu* L. subsp. *ligtu* (sub *A. chilensis* Lemaire) was characterized by Cox and MacMaster (1947). In *Bomarea* spp., notably thick, short tuberous roots occur.

In some species these storage roots have been cited as edible e.g. *B. ovata* (Killip, 1936a p. 659) and *B. edulis* (Tussac, 1808 p. 109; Killip, 1936b p. 115).

Exine sculpture differences show a generic consistency already recognized by Schulze (1978) in his LM pollen studies, with *Alstroemeria* having a striato-reticulate sexine and *Bomarea* a reticulate exine. In a detailed SEM study of pollen in Alstroemeriaceae, Kosenko (1994) pointed out that most species of *Alstroemeria* have 'perforate-cristiformis' (crest-like) ornamentation. Although there is a difference in pollen terms used, the results are similar to those obtained here, including the observation that a true striate exine is only rarely encountered.

Auriculate pollen has been reported for a few *Bomarea* spp.: *B. lyncina* Herb. (Elsik and Thanikaimoni, 1970) from Peru, *B. ceratophora* Neuend. (Neuendorf, 1977) from Ecuador, and *B. pardina* Herb. (Schulze, 1978), which ranges from southern Colombia to Peru. However the majority of species have non-auriculate pollen.

Previously published pollen data show that aperture type (a sulcus), aperture position with regard to polarity (distal polar), and the number of apertures (one) are widespread pollen characters throughout the monocots (Harley and Zavada, 2000). Nevertheless, differences in pollen grain wall structure and exine ornamentation (sculpture) are valuable characteristics for distinguishing between *Alstroemeria* and *Bomarea*. Recently studied species consistently show the same type of exine surface patterning and wall ultrastructure. Thus, accurate generic diagnosis is straightforward. Details such as arrangement of muri are sometimes found to be useful characters at the subgeneric level.

Morphology and dehiscence of fruits have not previously been investigated in any detail, and this character has often been overlooked. The earliest—and possibly the only—published morphological and anatomical study of the fruit is that of *A. aurea* (Buxbaum, 1954, sub *A. aurantiaca* D. Don). Many *Bomarea* spp. were originally described with 'fruits unknown' (Neuendorf, 1977). Fruits of selected *Bomarea* spp. were studied here; our observations differ from those published by Smith and Gereau (1991). Species such as *B. boliviensis* and *B. stans*, subgenus *Sphaerine*, also have dehiscent fruits. Consequently, we argue that species of *Bomarea* subgenus *Sphaerine* also have dehiscent fruits throughout the subgenus.

There are also differences in seed characters between *Alstroemeria* and *Bomarea* and in the mode of dehiscence and dispersal. The dissimilarity of the seeds between the genera was pointed out by Huber (1969). It is interesting to note that van der Pijl (1982) commented that the ballistic mechanism of seed dispersal in *Alstroemeria* is exceptional among monocotyledonous plants. In a comparative study of Amaryllidaceae, Oganezova (1990) described the ovary, ovule and seed of *Alstroemeria*, and indicated the isolated position of this genus. The morphology of the seed is of primary importance for recognition of the genera, especially the presence of an orange-red sarcotesta in *Bomarea*. One of the common names of *B. edulis* (subgenus *Bomarea*), a species of forest environments, is 'monte pomegranate', which highlights the resemblance of the fruit to that of *Punica granatum* L.

The number of species studied cytologically is small. *Alstroemeria* spp. were analysed by Taylor (1926), Whyte (1929), Sato (1938), Buitendijk and Ramanna (1996), Tsuchiya and Hang (1989), Hunziker and Xifreda (1991) and Sanso and Hunziker (1998a, b). About 20 *Alstroemeria* spp. have been studied cytologically and were found to be diploid, $2n = 2x = 16$, with the exception of one unidentified tetraploid collection (Goodspeed, 1940). The seven species of *Bomarea* that have been studied are also diploid, $2n = 2x = 18$. Only one tetraploid has been reported (Cave, 1967). The karyotypes of *Alstroemeria* taxa are asymmetric with large chromosomes, the majority of them having a long metacentric (no. 1) and at least three telocentric chromosome pairs. *Bomarea* spp. have more symmetrical karyotypes (Sanso and Hunziker, 1998a). Although *Bomarea* spp. have an additional chromosome pair, *Alstroemeria* spp. have a greater total chromosome length (Sanso and Hunziker, 1998a).

Karyological characters have been useful in supplementing data from morphological studies in defining these closely related genera. *Alstroemeria* and *Bomarea* differ in chromosome number and karyotype symmetry, adding support to the criteria for considering them as separate genera (Sanso and Hunziker, 1998a). According to Sanso and Hunziker (1998a), *Bomarea* does not have bimodal karyotypes as stated by Rudall *et al.* (2000 p. 352). New research on chromosomes of both genera is currently underway.

Other characteristics that have been described in the literature, such as tepal morphology, are less reliable at the generic level. However, they can be of value in the differentiation of species. Although it is true that nearly all *Alstroemeria* spp. have reflex tepals, and most *Bomarea* spp. have straight filaments, these are not consistent characters and it is not possible to use them effectively at the generic level. Raphides with calcium oxalate in both vegetative and reproductive organs are common throughout the family, despite the comment of Dahlgren *et al.* (1985) that they are known only in *Alstroemeria*.

Alstroemeriaceae was established by Dumortier in 1829. However, there is no unanimity so far regarding the number of genera in the family. Some authors (Dahlgren *et al.*, 1985; Stevenson and Loconte, 1995) have recognized four genera (*Alstroemeria*, *Bomarea*, *Schickendantzia* and *Leontochir*) while Bayer (1998a, b) recognized five (the four above plus *Taltalia* Ehr. Bayer). In contrast, Hunziker (1973) suggested sinking all the genera into *Alstroemeria*.

The reduction of the monotypic genus *Schickendantzia* to *Alstroemeria* and, in consequence, the resurrection of *A. pygmaea*, has recently been proposed (Sanso and Xifreda, 1999). This species is a small herb growing in the Andes, 3500–4400 m above sea level. It shares all the generic characteristics described here for *Alstroemeria*, in which genus it was previously included. Other characters that are particularly valuable in determining the generic affinity of this species are the axile placentation, the trilobular ovary and the two, usually spotted, inner upper tepals.

Taltalia was proposed as a monotypic genus for *A. graminea*. Nevertheless, Bayer (1998a p. 81) recognized that the differences separating these genera were slight; it is an annual and has no storage roots. We do not consider

these characters sufficient to justify recognition of this new genus even given the other characters used by Bayer (a different type of germination and solitary flowers). We propose that *A. graminea*, native to Taltal, Chile, should be retained in *Alstroemeria*. Furthermore, in a phylogenetic analysis of Alstroemeriaceae based on both morphological and on DNA sequence data from the chloroplast gene *rps16*, Aagesen and Sanso (1998) pointed out that the two *Alstroemeria* spp. that have been proposed as monotypic genera were both firmly nested within *Alstroemeria*.

In summary, the main characters discussed here with proven generic consistency are subterranean organs, especially storage root morphology, pollen morphology, morphology and adaptive dehiscence of capsules, seed coat and dispersal, and karyotype characteristics. *Bomarea* spp. are characterized by short rhizomes and short thick tuberous storage roots; reticulate pollen sculpturing; a turbinate capsule opening slowly from the top; a thick, fleshy seed coat (sarcotesta); ornithochorous dispersal; basic chromosome number $x = 9$; and fairly symmetric karyotypes. *Alstroemeria* spp. have stolons; long, narrow fusiform storage roots; striato-reticulate pollen sculpturing; an umbonate capsule with explosive dehiscence, splitting from the base into three parts; a hard dry seed coat; dispersal by a ballistic mechanism; basic chromosome number $x = 8$; and asymmetric karyotypes.

It seems reasonable to accept that the characters defined are important in the delimitation of *Alstroemeria* and *Bomarea*. We support neither the lumping of both genera nor the splitting of *Alstroemeria*. Therefore, we propose that Alstroemeriaceae be considered to comprise three genera: *Alstroemeria* (including *Schickendantzia* and *Taltalia*), *Bomarea* and the monotypic *Leontochir*.

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LITERATURE CITED

Aagesen L, Sanso AM. 1998. Phylogeny of the Alstroemeriaceae. Monocots II. *Second International Conference on the Comparative Biology of the Monocotyledons and Third International Symposium on Grass Systematics and Evolution*. Sydney. Abstracts, 61.

- Baker JG. 1888. *Handbook of Amaryllideae including the Alstroemeriaceae and Agaveae*. London: George Bells & Sons.
- Bayer E. 1998a. Alstroemeriaceae. In: Kubitzki K, ed. *Families and genera of vascular plants 3. Flowering plants. Monocotyledons: Liliaceae (except Orchidaceae)*. Berlin: Springer-Verlag, 79–82.
- Bayer E. 1998b. *Taltalia*—eine neue Gattung in der Familie der Alstroemeriaceae. *Sendtnera* 5: 5–14.
- Bentham G, Hooker JD. 1883. Amaryllideae. *Genera Plantarum* 3 (174). London: Weinheim-Verlag Von J. Cramer, 715–737.
- Buitendijk JH, Ramanna MS. 1996. Giemsa C-banded karyotypes of eight species of *Alstroemeria* L. and some of their hybrids. *Annals of Botany* 78: 449–457.
- Buxbaum F. 1954. Morphologie der Blüte und Frucht von *Alstroemeria* und der Anschluß der Alstroemeriaceae bei den echten Liliaceae. *Oesterreichische Botanische Zeitschrift* 101: 337–352.
- Cave MS. 1967. Documented chromosome numbers of plants. *Madroño* 19: 134–136.
- Cox MJ, MacMasters MM. 1947. Starch from *Alstroemeria*. *Herbertia* 14: 71–80.
- Dahlgren RMT, Clifford HT, Yeo PF. 1985. Alstroemeriaceae. *The families of the Monocotyledons*. Berlin: Springer-Verlag, 220–226.
- Elsik WC, Thanikaimoni G. 1970. *Bomarea lyncina* Herb. (Amaryllidaceae) and *Auriculioidites* Elsik. *Pollen Spores* 12: 177–180.
- Goodspeed TH. 1940. Amaryllidaceae from the University of California botanical expedition to the Andes. *Herbertia* 7: 17–31.
- Harley MM, Zavada MS. 2000. Pollen of monocotyledons: selecting characters for cladistic analysis. In: Wilson KL, Morrison DA, eds. *Monocots: Systematics and evolution*. Melbourne: CSIRO, 194–213.
- Holmgren PK, Holmgren NH, Barnett LC. 1990. *Index Herbariorum. Part I: The Herbaria of the World, 8th edn*. New York: New York Botanical Garden.
- Huber H. 1969. Die Samenmerkmale und Verwandtschaftsverhältnisse der Liliifloren. *Mitteilungen der Botanischen Staatssammlung München* 8: 219–538.
- Hunziker AT. 1973. Notas sobre Alstroemeriaceae. *Kurtziana* 7: 134.
- Hunziker JH, Xifreda CC. 1991. Chromosome studies in *Bomarea* and *Alstroemeria* (Alstroemeriaceae). *Darwiniana* 30: 179–183.
- Johri BM, Ambegaokar KB, Srivastava PS. 1992. *Comparative embryology of angiosperms 1*. Berlin: Springer-Verlag.
- Killip EP. 1936a. *Bomarea*, a genus of showy Andean Plants. *The National Horticultural Magazine* 15: 115–129.
- Killip EP. 1936b. *Bomarea*. In: Macbride JF, ed. *Flora of Peru. Field Museum of National History. Botanical Series*, 13: 659–660.
- Kosenko VN. 1994. Pollen morphology of the family Alstroemeriaceae. *Botanicheskyy Zhurnal* 79: 1–8 (in Russian).
- Linnaeus C. 1762. *Planta Alstromeria* (J. F. Falck). *Amoenitates Academicae* 6: 247–262. *Dissertationes* 114.
- Luft JH. 1971. Ruthenium red and violet. II. Fine structural localization in animal tissues. *Anatomical Record* 171: 369–392.
- Martin AC. 1946. The comparative internal morphology of the seeds. *American Midland Naturalist* 36: 513–660.
- Meerow AW, Tombolato AFC, Meyer F. 1999. Two new species of *Alstroemeria* L. (Alstroemeriaceae) from Brazil. *Brittonia* 51: 429–444.
- Mirbel CFB. 1804. *Bomarea*. *Histoire Naturelle des Plantes* 9: 71.
- Neuendorf M. 1977. *Pardinae*, a new section of *Bomarea* (Alstroemeriaceae). *Botanisk Notiser* 130: 55–60.
- O'Brien TP, McCully ME. 1981. *The study of plant structure, principles and selected methods*. Melbourne: Termarcaphi Pty.
- Oganezova GG. 1990. Seed and fruit anatomy of some Amaryllidaceae in connection with their systematics and phylogeny. *Botanicheskyy Zhurnal* 75: 615–629 (in Russian).
- Pax F, Hoffman K. 1930. Amaryllidaceae. In: Engler A, Prantl K, eds. *Die Natürlichen Pflanzenfamilien 2*. Leipzig: Verlag von Wilhelm Engelmann. Auflage, Bd 15a, 391–430.
- Punt W, Blackmore S, Nilsson S, Le Thomas A. 1994. *Glossary of pollen and spore terminology*. Utrecht: LPP Foundation.
- Rendle AB. 1930. *The classification of flowering plants, 2nd edn*. Cambridge: Cambridge University Press.
- Rudall PJ, Stobart KL, Hong W-P, Conran JG, Furness CA, Kite GC, Chase MW. 2000. Consider the Lilies: systematics of Liliales. In:

- Wilson KL, Morrison DA. eds. *Monocots: Systematics and evolution*. Melbourne: CSIRO, 347–359.
- Sanso AM. 1996a. *Estudios cariológicos y de sistemática de las especies argentinas de Alstroemeriaceae*. PhD Thesis, Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires, Argentina.
- Sanso AM. 1996b. El género *Alstroemeria* (*Alstroemeriaceae*) en Argentina. *Darwiniana* 34: 349–382.
- Sanso AM. 1998. Relaciones fenéticas entre las especies argentinas de *Alstroemeriaceae*. *Darwiniana* 35: 131–145.
- Sanso AM, Hunziker JH. 1998a. Karyological studies in *Alstroemeria* and *Bomarea* (*Alstroemeriaceae*). *Hereditas* 129: 67–74.
- Sanso AM, Hunziker JH. 1998b. Estudios cromosómicos en especies nativas de *Alstroemeria* (*Alstroemeriaceae*). *XXVI Jornadas Argentinas de Botánica*. Córdoba. Rio IV, 22–27, nov. Resúmenes: 364.
- Sanso AM, Xifreda CC. 1995. El género *Bomarea* (*Alstroemeriaceae*) en Argentina. *Darwiniana* 33: 315–336.
- Sanso AM, Xifreda CC. 1999. The synonymy of *Schickendantzia* with *Alstroemeria* (*Alstroemeriaceae*). *Systematics and Geography of Plants* 68: 315–323.
- Sato D. 1938. Karyotype alteration and phylogeny. IV. Karyotypes in *Amaryllidaceae* with special reference to the sat-chromosomes. *Cytologia* 9: 226–240.
- Schulze W. 1978. Beiträge zur Taxonomie der Liliifloren III. *Alstroemeriaceae*. *Wissenschaftliche Zeitschrift der Friedrich-Schiller-Universität Jena/Thüringen. Mathematisch-naturwissenschaftliche Reihe* 27: 79–85.
- Smith DN, Gerau RE. 1991. *Bomarea albimontana* (*Alstroemeriaceae*), a new species from high Andean Peru. *Candollea* 46: 503–508.
- Spurr AR. 1969. A low-viscosity epoxy resin embedding medium for electron microscopy. *Journal of Ultrastructure Research* 26: 31–43.
- Stevenson DW, Loconte H. 1995. Cladistic analysis of monocot families. In: Rudall PJ, Cribb PJ, Cutler DF, Humphries CJ, eds. *Monocotyledons: Systematics and evolution* (2). Kew: Royal Botanic Gardens, 543–578.
- Taylor WR. 1926. Chromosome morphology in *Fritillaria*, *Alstroemeria*, *Silphium*, and other genera. *American Journal of Botany* 13: 179–183.
- Tsuchiya T, Hang A. 1989. Cytogenetics in the genus *Alstroemeria*. *Herbertia* 45: 163–170.
- Tussac de FR. 1808. *Flora Antillarum* 1. Paris.
- van der Pijl L. 1982. *Principles of dispersal in higher plants*. Berlin, Heidelberg, New York: Springer-Verlag.
- Whyte RO. 1929. Chromosome studies. I. Relationships of the genera *Alstroemeria* and *Bomarea*. *New Phytologist* 28: 319–344.
- Wilkin P. 1997. *Leontochir ovallei*. *Kew Magazine* 14: 7–12, plate 308.
- Xifreda CC, Sanso AM. 1992. *Bomarea stricta* es sinónimo de *Alstroemeria isabellana* (*Alstroemeriaceae*). *Darwiniana* 31: 355–356.
- Xifreda CC, Sanso AM. 1993. Anatomical and morphological studies in *Alstroemeria* and *Bomarea* (*Alstroemeriaceae*). *Kew Monocotyledons Symposium*. Paper & posters abstract, supplement.

APPENDIX

Specimens examined and provenance

- Alstroemeria andina* Phil. subsp. *andina*- Castillo w/n (SGO 100086)- Chile*
- Alstroemeria andina* Phil. subsp. *venustula* (Phil.) Ehr. Bayer- Fortunato & Kiesling 5630 (BAB), Kiesling & al. 8097, 9062, Luti & al., Hb. Geobot. 5500 (SI) - Argentina*
- Alstroemeria angustifolia* Herb. subsp. *angustifolia*- Cult. Forskningscenter Årslev P1995/ 5003 (SI)- Chile*
- Alstroemeria apertiflora* Baker- Jørgensen 30801 (BAB), Hassler 5811, 10099 (G)- Argentina, Paraguay
- Alstroemeria aurea* Graham- Fabris 1140 (LP), Xifreda & Sanso 1470, 2015, 2030 (SI)- Argentina
- Alstroemeria bakeri* Pax- Spegazzini 33064 (SI)- Argentina*
- Alstroemeria exserens* Meyen.- Cult. Forskningscenter Årslev P1995/5009 (SI)- Chile*
- Alstroemeria graminea* Phil.- Von Bohlen 1275 (SGO 131118), Werderman 802 (G), Worth & Morrison 15808 (G) - Chile*
- Alstroemeria isabellana* Herb.- Krapovickas & Schinini 38243 (IBONE), Sanso et al. 5 (SI)- Brazil, Argentina
- Alstroemeria patagonica* Phil.- Cabrera et al. 33192 (SI), Spegazzini 19452 (LP), Xifreda & Sanso 1466, 2035 (SI) - Argentina*
- Alstroemeria pelegrina* L.- Garaventa 3262, 4196 (SI)- Chile
- Alstroemeria presliana* Herb.- Boelcke et al. 13562 (BAB), Xifreda & Sanso 1480, 2012 (SI)- Argentina.
- Alstroemeria pseudospathulata* Ehr. Bayer- Burkart et al. 13867, Xifreda & Sanso 2004 (SI)- Argentina*
- Alstroemeria psittacina* Lehm.- Xifreda 832 (SI), Xifreda & Sanso 1039 (SI), Cult. FCEyN- Argentina
- Alstroemeria pygmaea* Herb.- Sanso & Pereyra 8, Xifreda & Sanso 1066 (SI)- Argentina
- Alstroemeria spathulata* C. Presl- Burkart 27464 (SI)- Chile*
- Alstroemeria versicolor* Ruiz & Pav.- Cult. Forskningscenter Årslev P1995/5052 (SI)- Chile*
- Alstroemeria werdermannii* Ehr. Bayer- Werderman 134 (SI)- Chile*
- Bomarea boliviensis* Baker (*Bomarea* subg. *Sphaerine* (Herb) Baker.)- Castellanos 46674 (BA), Novara 8336 (MCNS), J. Hunziker et al. 11743, 12872, Cult. J. Hunziker 22 (SI)- Argentina*
- Bomarea crocea* (Ruiz & Pav.) Herb. (*Bomarea* subg. *Wichuraea* (Roemer) Baker)- Sanso & Pereyra 26 (SI)- Peru*
- Bomarea dulcis* (Hooker) Beaufort (*Bomarea* subg. *Wichuraea* (Roemer) Baker)- Stafford 809 (K)- Peru*
- Bomarea edulis* (Tuss.) Herb. (*Bomarea* subg. *Bomarea*)- Novara 4414 (MCNS), Sanso & Pereyra 9, Xifreda & Maldonado 458, Xifreda & Sanso 867, 871, 883, 1147 (SI)- Argentina
- Bomarea macrocephala* Pax (*Bomarea* subg. *Wichuraea* (Roemer) Baker)- Sanso & Pereyra 11, Xifreda & Sanso 1180, 1418, 1425 (SI)- Argentina*
- Bomarea ovata* (Cav.) Mirb. (*Bomarea* subg. *Bomarea*)- C. & E. Franquemont 268B (F), Xifreda 1451(SI)- Peru, Cuba
- Bomarea salsilla* (L.) Herb. (*Bomarea* subg. *Bomarea*) - Silva w/n (SGO 104724)- Chile
- Bomarea setacea* (Ruiz & Pav.) Herb. (*Bomarea* subg. *Bomarea*) - Hunziker 11407 (SI)- Colombia*
- Bomarea stans* Kraenz. (*Bomarea* subg. *Sphaerine* (Herb) Baker)- Kiesling et al. 3767 (SI), Krapovickas et al. 18984 (IBONE)- Argentina, Bolivia*
- Bomarea tomentosa* Herb. (*Bomarea* subg. *Bomarea*)- Sanso & Pereyra 22 (SI)- Peru
- Bomarea velascoana* Vargas. (*Bomarea* subg. *Bomarea* ?)- Saunders 820 (K)- Peru*

* New palynological data

