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Status of the genera *Aetanthus* and *Psathyranthus* (Loranthaceae)

JOB KUIJT

RÉSUMÉ

KUIJT, J. (1983). Statut des genres *Aetanthus* et *Psathyranthus* (Loranthaceae). *Candollea* 38: 661-672. En anglais, résumé français.

Une revue des caractéristiques de l'androecium, de l'inflorescence et de la géographie d'*Aetanthus*, de *Psittacanthus* et de *Psathyranthus* (Loranthaceae) amène à conclure que les deux premiers sont nettement distincts et devraient être maintenus au niveau générique, tandis que le dernier devrait être mis en synonymie sous *Psittacanthus*. De cette clarification résultent une nouvelle espèce, *Psittacanthus krameri* Kuijt, et deux combinaisons nouvelles, *Psittacanthus zonatus* (Diels) Kuijt et *P. amazonicus* (Ule) Kuijt.

ABSTRACT

KUIJT, J. (1983). Status of the genera *Aetanthus* and *Psathyranthus* (Loranthaceae). *Candollea* 38: 661-672. In English, French abstract.

A review of androecial, inflorescence, and geographical features of *Aetanthus*, *Psittacanthus* and *Psathyranthus* (Loranthaceae) leads to the conclusion that the first two are sharply distinct and should be maintained at the generic level, while the last should be placed in synonymy under *Psittacanthus*. One new species, *Psittacanthus krameri* Kuijt, and two new combinations, *Psittacanthus zonatus* (Diels) Kuijt and *P. amazonicus* (Ule) Kuijt, result from this clarification.

Among American Loranthaceae s.s., there is a large and clearly natural group of species which is characterized by exalbuminous fruits. This feature, which was questioned by BENTHAM & HOOKER (1880) but about which there is little doubt at present (see, for example, ENGLER, 1894; KUIJT, 1967, 1970, 1973), has received taxonomic recognition from most writers in the group. VAN TIEGHEM (1895) recognized the group as the tribe Psittacanthae, while

ENGLER & KRAUSE (1935) regarded it as a subtribe, Psittacanthinae, of tribe Lorantheae, in turn of subfamily Lorantheae.

A peripheral controversy has surrounded the species which at times has been known as *Psittacanthus cuneifolius* (R. & P.) G. Don. VAN TIEGHEM (1895) maintained that its fruit lacked endosperm (as BENTHAM & HOOKER, 1880, had also stated), and thus placed it within the context of Psittacanthaeae. In recent years BHATNAGAR & CHANDRA (1968) have convincingly demonstrated the presence of endosperm, and have cast doubt on the taxonomic value of this feature in the genus. There is ample justification, however, to segregate the species as the monotypic genus *Ligaria*, since its chromosome number ($x = 10$) seems to be unique in the family (BARLOW & WIENS, 1973), its palynology contrasts strongly with that of other species of *Psittacanthus* (FEUER & KUIJT, 1979, 1980), and its inflorescence morphology is unique at least within the New World (KUIJT, 1981). *Ligaria* thus having been removed, the remaining species all share the exalbuminous character. There remains the problem of what genera are to be maintained within this group, a problem to which the present paper addresses itself.

Twenty-four generic names have been applied to the group of species in question, 19 of which were proposed by Van Tieghem. It is not my purpose here to deal with all of these; rather I take as my point of origin the second edition of "Die Natürlichen Pflanzenfamilien" (ENGLER & KRAUSE, 1935), itself different from ENGLER (1897) only in *Psathyranthus* having been added. I add one proviso, however, viz. that *Ligaria* be removed and given separate generic status as indicated above (cf. BARLOW & WIENS, 1973). There is no doubt in my mind that the subordination of Van Tieghem's generic names in "Die Natürlichen Pflanzenfamilien" is a reasonable answer to that author's proliferation of names. Indeed, whether any of Van Tieghem's genera (except *Ligaria*) will at any level survive generic treatments in the group cannot at this time be predicted. Thus my present concern is limited to *Aetanthus*, *Psathyranthus*, and *Psittacanthus*. The application of the latter generic name to the vast majority of species belonging to the alliance has not been questioned at least since EICHLER'S (1868) masterful treatment, except for a nomenclatural controversy laid to rest with the conservation of the name *Loranthus* N. J. Jacquin (Nom. Gen. Cons. No. 2074; cf. BALLE & al., 1960). There would seem to be no further threats to the nomenclatural stability of this name.

The neotropical genera *Aetanthus* and *Psathyranthus* have received an uncertain reception over the years. Even though EICHLER'S (1868) original diagnosis of *Aetanthus* (as a subgenus of *Psittacanthus*) is remarkably precise, it is incomplete and has been much misinterpreted. He did not, unfortunately, illustrate the crucial androecial features of *Aetanthus*; in fact, to my knowledge, these features have never been illustrated. In the case of *Psathyranthus*, we are concerned with a monotypic genus so far based on a single collection.

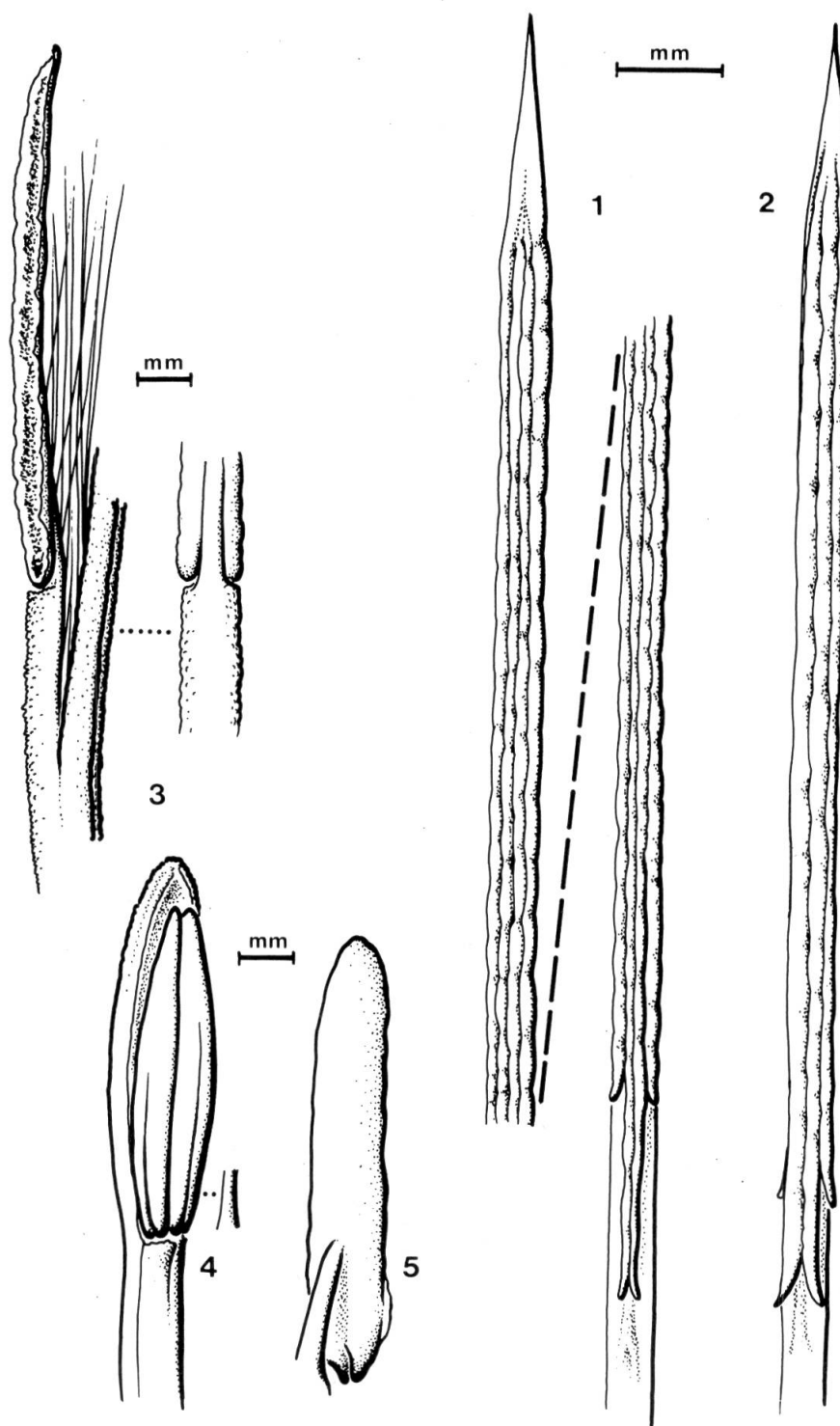
1. *Aetanthus*

Aetanthus first appears in the literature as *Psittacanthus* subgenus *Aetanthus* (EICHLER, 1868). The first species was based on a specimen, *James 244*, collected in the Andes near Quito. This is the same specimen upon which HOOKER (1848) had based his *Loranthus macranthus* Hook. and it is illuminating to see, in his text, that this author had a very clear perception of the unusual nature of the anther. It is thus quite conceivable that Hooker's text and illustration led to Eichler's subgenus, and it may be questioned whether Eichler ever saw the specimen involved. Hooker, in turn, may have been kept from discovering that there are other species in the Northern Andes with similarly basifixed, acicular anthers by the erroneous illustration of versatile anthers for *Loranthus dichotomus* Ruiz & Pavón, 1802 (*Aetanthus nodosus* (Desr.) Engler) a species to which he refers as a close relative but different in the crucial androecial characters.

Aetanthus was accorded generic status by ENGLER (1894). Engler retained substantially the same diagnosis as Eichler, which is here translated: "Flowers bisexual, 6-merous, long and thin. Perianth segments united into a long tube, free parts linear, recurved. Anthers immobile, narrow, linear, the innermost thecae extending downward much further than the outer ones. Flowers in 2-rayed umbels in the axils of leaves." VAN TIEGHEM (1895) raised the genus to subtribal level, *Aetantheae*, adding three new genera. The fact that *Aetanthus* has not been thoroughly accepted, however, is reflected in BARLOW & WIENS (1973) where, in the key to American genera (p. 34), *Aetanthus* as well as *Psathyranthus* are included in *Psittacanthus*.

Study of numerous species in South and Central America over a period of years has convinced me that, whatever taxonomic significance is attached to it, the difference between the two anther types is absolute, showing no true intergradations. The common "*Psittacanthus*" type of anther is rarely if ever more than 5 mm long. In virtually all cases it is clearly versatile and dorsifixed by means of an attenuated filament. In very few species is the filament short and attached near the base of the anther (but still clearly dorsifixed). The extreme may be *P. pusillus* Kuijt, the anther of which is virtually immobile and very nearly basifixed (KUIJT, 1978). It will be seen, however, that the anther of this species is still very different from the acicular type.

In contrast, the *Aetanthus* type of anther is exceedingly long and slender, in the species seen being at least 10 mm long. Not only is it basifixed, but the filament is also in no way constricted or attenuated as it passes into the anther (Fig. 1, 2). Thus each of the four pollen sacs is a thread-like structure on the surface of the connective, merging with an extremely acute and slender connective tip above, and ending in a small spur below. The four spurs at the base of the anther are at two different heights, the inner two extending far below the outer two. It is of more than passing interest that a similar, basifixed anther



Figs. 1-5. — Anther morphology of selected Psittacanthineae.

1, *Aetanthus holtoni* (Eichl.) Engl., Holton 649 (GH). 2, *Aetanthus* sp., Cuatrecasas & al. 12 393 (GH). 3, *Psittacanthus zonatus* (Diels) Kuijt, Harling 3687 (GB; the back of the anther, with hairs removed, is shown on the right). 4, *Psittacanthus* sp., Wurdack and Adderley 43 442 (GH; filament shown on the right). 5, *Psittacanthus cinctus* Martius, back of anther, Gentry & al. 15 694 (MO).

is characteristic of the great majority of paleotropical Loranthaceae (DANSER, 1933; BALLE, 1956). Within the New World, all other Loranthaceae with flowers of medium to large size have versatile anthers; the minute basifixed anthers of small-flowered genera such as *Oryctanthus* (KUIJT, 1976), *Phthirusa* (KUIJT & WEBERLING, 1973) and *Cladocolea* (KUIJT, 1975) are clearly of a different derivation. The close relationship of *Aetanthus* with *Psittacanthus*, s.s., itself a highly advanced taxon without close affinities outside the Americas, indicates that the *Aetanthus* anther has evolved independently.

Associated with these androecial characters are three others. Plants with *Aetanthus*-type anthers always have inflorescences which are umbels of 2-4 dyads (cf. KUIJT, 1981). These inflorescences are always borne in the axils of foliage leaves, never terminating the shoot. Flowers are always extremely long, slender, tubular, and pendulous. Finally, these plants are limited exclusively to high elevations in the Northern Andes. In contrast, the versatile-dorsifixed anther is found on species the great majority of which have terminal inflorescences composed of one or more umbels or racemes of triads or dyads; a very few species (e.g., *P. dichrous*, *P. ramiflorus*, and *P. krameri*) have axillary umbels of dyads, but in these cases the flowers are not excessively long or slender, and are not pendulous. In fact, the only pendulous flowers with the versatile-dorsifixed type of anther are found in *Psathyranthus* and two other, as yet undescribed species referred to below. In this case the inflorescence is triadic, and species have low-elevation preferences.

My conclusion, therefore, is that taxonomic purposes are best served by the recognition of *Aetanthus* as a genus separate from *Psittacanthus*. This is not a distinction based on a solitary androecial character. First of all, the androecial distinction of *Aetanthus* has several separate components: the linear shape of the pollen sacs; the excessive length of the anther, and its extreme, acicular form, making it difficult to separate from the filament; and its basifixed attachment without any constriction. Additionally, there are general (but not universal) inflorescence differences as described above, and an apparently consistent altitudinal separation.

That this distinction clarifies individual cases is demonstrated by what has been called *Psittacanthus nodosus* (Desr.) G. Don in Central America (KUIJT, 1978) and by *Aetanthus zonatus* Diels in Ecuador. In the former case we have a mistletoe which in terms of leaf shape and flower shape closely resembles the type material of *A. nodosus*. It is very surprising (but, of course, not impossible) to find an *Aetanthus* species so far from the nearest species in Andean Columbia. In fact, when we scrutinize the plant more carefully we find that its flower is a rather typical *Psittacanthus* flower in being relatively short and stout and in standing in a spreading position. More importantly, the anther is dorsifixed and at least three times as wide as the filament (KUIJT, 1978, Fig. 8). We are thus concerned with a rather typical *Psittacanthus* except that the inflorescence

is apparently only axillary and made up of dyads (features also seen, for example, in *P. ramiflorus* (DC.) G. Don) and that the filament is unusually short.¹

***Psittacanthus krameri* Kuijt, spec. nova**

Caules teretes, nodis aliquantum incrassatis, internodiis ad 12 cm longis. Folia regulariter verticillatim quaterna (interdum bina), ad 8×4 cm, raro multo majora, ovata vel obovata ad late lanceolata, coriacea, statu sicco textura aspera. Inflorescentiae axillares, quaque ut videtur umbellam ex dyadibus nonnullis efformans. Flores inferne laete rubri vel aurantiaci, superne lutei, prae anthesi 4-6 mm longi, alabastra apicaliter rotundata, recta; calyx ad basim vix dilatatus; antherae monomorphae, insertae 5 mm sub apicibus tepalorum, basifixae, filamentum brevissimo (1-1.5 mm), ad dorsum pilis longis rufis lunariter aggregatus concomitatae; ovarium 4 mm longum, stylo recto, stigmate parvo, clavato, papilloso, antheras paulo superante. Fructus atropurpureus, circa 9×5 mm, calyculo inconspicuo.

Stems terete, the nodes somewhat swollen, internodes up to 12 cm long. Leaves in regular whorls of 4 (sometimes paired), to 8×4 cm, rarely much larger, ovate or obovate to broadly lanceolate, leathery, with a rough texture when dry. Inflorescences axillary, each apparently an umbel of several dyads. Flowers bright red or orange below, yellow above, 4-6 cm long in bud, buds rounded at apex, straight; calyx scarcely dilated at base; anthers monomorphic, inserted 5 mm below petal tips, basifixed on very short (1-1.5 mm) filament and backed by a crescent of long, reddish hairs; ovary 4 mm long, style straight, with small, clavate, papillate stigma just beyond anthers. Fruit dark purple, ca. 9×5 mm, with inconspicuous calyculus.

Type. Panamá: near La Eneida, 100 m, *Luteyn & Foster 1122* (Duke, MO). Holotype at MO.

See illustrations, descriptions, and specimen citations in KUIJT (1964) under *Psittacanthus* No. 29, and (1978) under *Psittacanthus nodosus*.

In the case of *Aetanthus zonatus* even the original description (DIELS, 1941) provides characters to place it in *Psittacanthus* instead: the inflorescence is terminal and is made up of triads. No adequate anther details are provided, however; Diels claims that the species is related to *A. nodosus*. In fact, careful study of the anther shows Diels' species to be a typical *Psittacanthus* in this respect, also (Fig. 3). The filament is short but clearly dorsifixed, and the anther

¹The species in question thus requires a name. It is appropriate that I honor my good friend and colleague Prof. Dr. Karel U. Kramer from Zürich by naming this attractive species after him. Prof. Kramer has provided numerous Latin diagnoses for mistletoes in the past — including this one — and has thus contributed to the quality of my published work.

does not have any *Aetanthus* features.¹ Thus there are several species of *Psittacanthus* in which the anther at first sight seems basifixed but in reality is not. Figures 4 and 5 show the anther of an unidentified species and *P. cinctus* Martius, respectively, illustrating the same characteristic. This is not to be interpreted as a transition to *Aetanthus*: in fact, no transitions have been observed in any material.

2. *Psathyranthus*

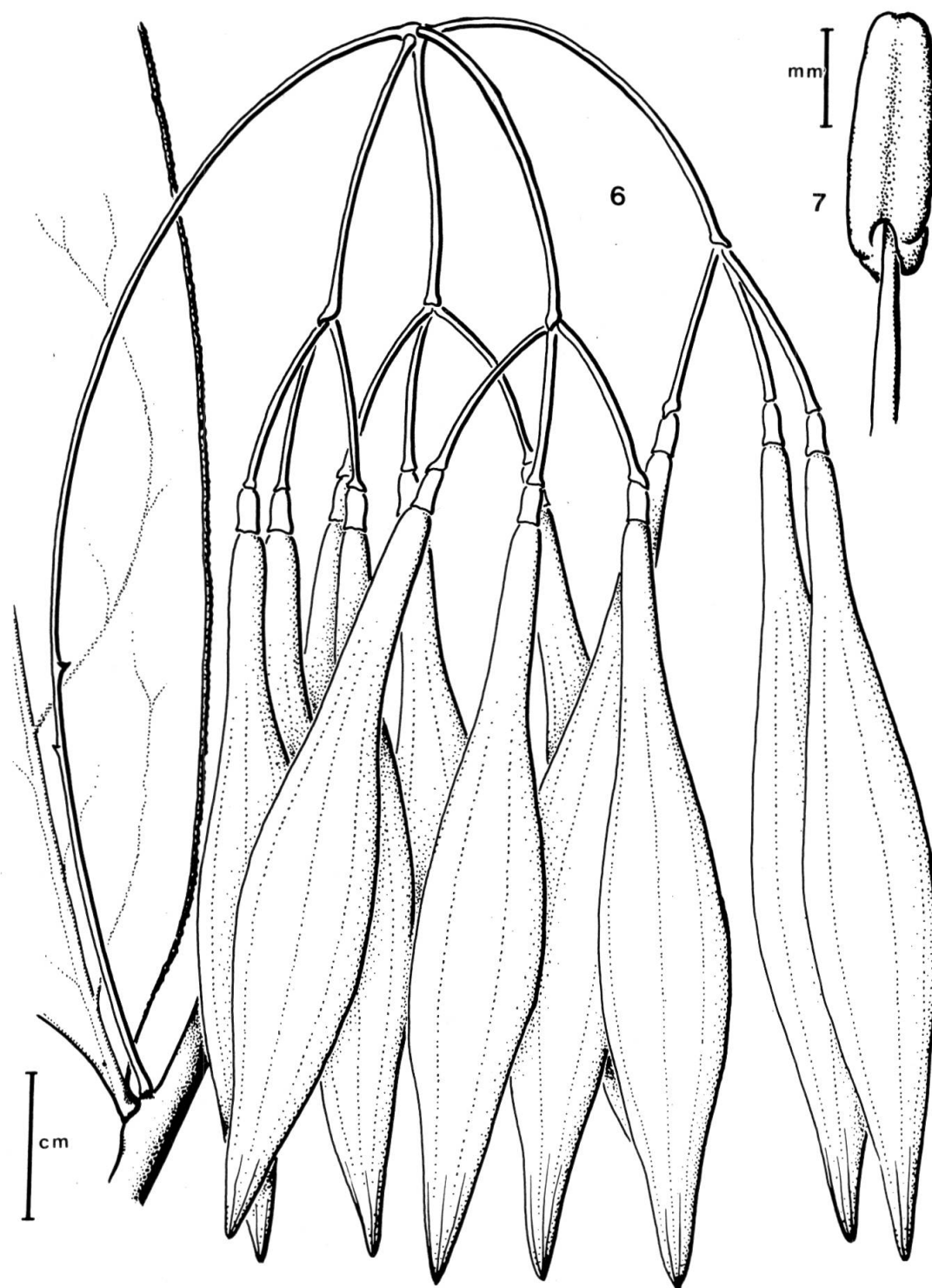
The genus *Psathyranthus* has remained an enigmatic entity since its description and illustration appeared just after the turn of the century (ULE, 1907). The full illustration was reproduced by ENGLER & KRAUSE (1935). Ule based his publication on a single collection from Boja de Tejo, Jurua, Brazil, the only collection ever reported in the literature. His illustration shows an extraordinary plant somewhat reminiscent of *Psittacanthus*. However, anthers are said to be basifixed, the filaments not narrowing below the anther. It is obvious from the illustrations, however, that the anthers are distinct from and much broader than the filaments. In view of the above discussion on *Aetanthus* it can be understood that Ule found it difficult to place his new species in either *Aetanthus* or *Psittacanthus*, and thus was moved to propose a new genus. Ule's statement to the effect that endosperm is absent amounts to no more than a speculation (although almost certainly an accurate one; see below), as he also writes that no fruits were present. The inflorescences illustrated are variable in structure, some not corresponding to any known in other Loranthaceae.

I have recently located both the holotype (*Ule 5461*, HBG) and one isotype (G). In addition, a second collection has emerged from Peru (Prov. Huánuco, Villa Ysabel, Río Cuchara, vicinity of Tingo María, *J. Schunke V. 6152*, K). This combined material allows for a re-assessment of the validity of *Psathyranthus*.

Ule's general description and illustration of the flower and the leaves were accurate and need no emendation. The same cannot be said, however, about the anther and inflorescence, both requiring some comments.

The anther is not truly basifixed (Fig. 7). The upper end of the filament is inserted into a very short, tubular portion of the anther which is invisible from the adaxial side, the two inner pollen sacs extending slightly further down than the outer ones. Thus at least 0.5 mm of the filament extends above the lowest portion of the anther. It is clear that Ule's interpretation is not accurate, and that the anther has a modified form of dorsifixed attachment.

¹*Psittacanthus zonatus* (Diels) Kuijt, **comb. nov.** Basionym: *Aetanthus zonatus*, Notizbl. Bot. Gart. Berlin 15: 368. 1941.

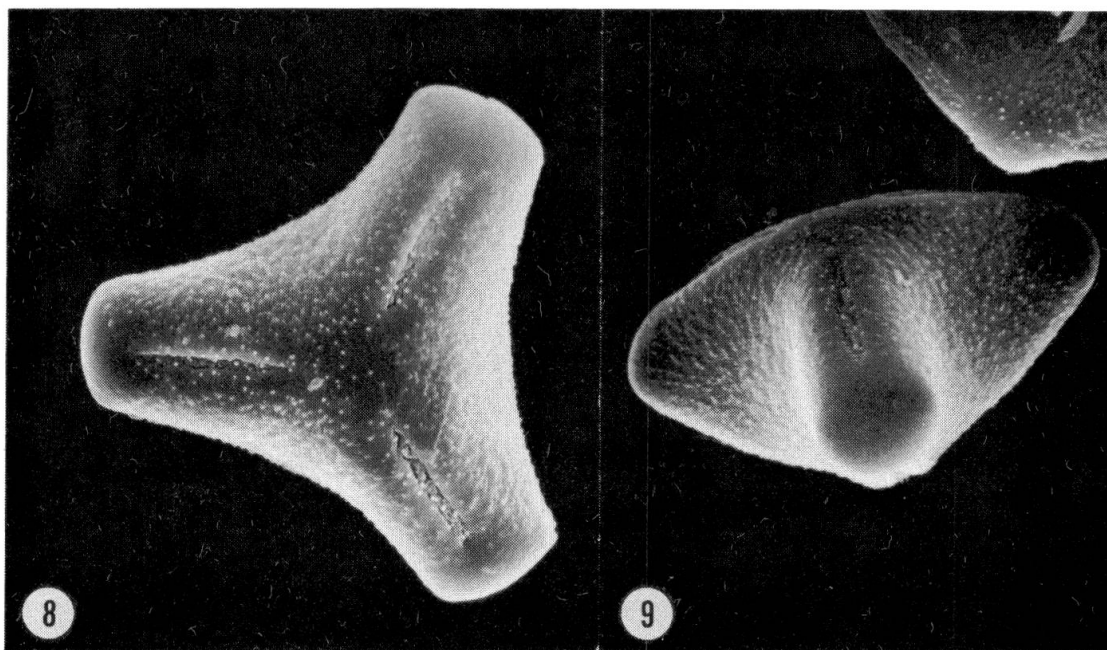


Figs. 6-7. — *Psittacanthus amazonicus* (Ule) Kuijt, Schunke V. 6152 (K). 6, inflorescence, reconstructed. 7, anther as seen obliquely from the dorsal side.

Even though the remarkably delicate inflorescences are broken in nearly all cases, a reconstruction is possible. It turns out to be an umbel of four triads, each triad having three pedicellate flowers (Fig. 6). These floral pedicels are 10-15 mm long; the two lateral ones each terminate in a small, oblique bracteole. Flowers appear to be pendent as in Ule's illustration. In the case of Schunke's collection the corolla is said to be dark reddish orange, the "calyx" (the ovary and calyculus are probably meant) strong greenish yellow. The perianth is paper-thin, showing clearly all internal organs when held against the light. In other words, the basic inflorescence structure, an umbel of triads, is quite compatible with *Psittacanthus* at large (KUIJT, 1982).

The pollen of *Psathyranthus* is typical of that of *Psittacanthus* (Figs. 8 and 9), being close to *P. clusiaefolius* Willd. ex Eichl. with respect to shape and sculpturing, and to *P. hamulifer* Kuijt and *P. peronopetalus* Eichl. with respect to aperture shape (cf. FEUER & KUIJT, 1979).

It is useful to add here that, in the forthcoming treatment of the Loranthaceae of Ecuador, two new species of *Psittacanthus* will be described which are closely related to *P. amazonicus* in having a similar aspect and anther structure. Mature fruit has been studied for one of these, confirming Ule's speculation that the seed lacks endosperm. It may well be that, when the genus can be surveyed as a whole, these three species together will warrant formal recognition at some infrageneric level. My contention at this point, however, is that when



Figs. 8-9. — *Psittacanthus amazonicus*, SEM photographs of pollen, Schunke V. 6152 (K). $\times 1100$. Courtesy Dr. S. Feuer.

all facts are gathered together there remain no significant differences from the remainder of *Psittacanthus* which warrant recognition at the generic level. I am thus proposing the recombination ***Psittacanthus amazonicus* (Ule) Kuijt, comb. nov.**, the basionym being *Psathyranthus amazonicus* Ule, Verhandl. Bot. Ver. Brandenburg 48: 156. 1906 (1907).

Conclusions

Psittacanthinae sensu Engler & Krause is thus considered to consist of two very unequal genera, *Aetanthus* with probably fewer than half a dozen species found exclusively at high elevations in Andean Peru, Ecuador and Columbia, and *Psittacanthus* with perhaps 50 or 60 species distributed at lower and middle elevations from northwestern Mexico (KUIJT, 1973) to northern Argentina (ABBIATTI, 1946), Bolivia, and Peru. Both genera, but especially the latter, are urgently in need of careful attention, including detailed floral analyses, as many new species have been added in a rather uncritical fashion in the present century.

A key facilitating distinction between the two accepted genera of *Psittacanthinae* follows. I do not, however, wish to imply here that a future revision of generic relationships must necessarily maintain this taxon; for example, recent work on seedling morphology (KUIJT, 1982) has pointed out some possible connection to the genus *Tristerix*. there can be little doubt, however, that *Aetanthus* and *Psittacanthus* are more closely related to each other than to any other genus.

Key to genera of Psittacanthinae

1. Anthers dorsifixed and mostly versatile, much wider than the filament, the latter usually narrowing conspicuously near the point of attachment; inflorescence basically a raceme or umbel of triads, frequently terminal, in some reduced to dyads; flowers not pendulous except in 3 triadic Amazonian species; low to middle elevations from N.W. Mexico into Argentina, Bolivia and Peru ***Psittacanthus***
2. Anthers basifixed, exceedingly narrow and sharply pointed, acicular, continuous with and of the same width as the filament, the latter not narrowing near the point of attachment; inflorescence in axils of foliage leaves, being an umbel of 2-4 dyads; flowers long and slender, pendulous; high elevation in the northern Andes ***Aetanthus***

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