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Floral morphology of North American Eriocaulaceae and its taxonomic implications*

With 7 Figures

Summary

Due to the small size of the flower even basic information about the floral diagram in some genera of Eriocaulaceae is lacking. In this study it is shown, that the anthers of *Lachnocaulon* are not monothebatebisporangiate by lateral reduction as assumed in the past but bithecat-bisporangiate by facial reduction. This is in contrast to the findings in *Tonina* and *Philodice* (STÜTZEL 1985), where occasional and irregular lateral reductions may occur. The dehiscence mechanism of the anthers of *Lachnocaulon* is very uncommon in opening the sporangia of both thecae with a single longitudinal slit. No rudiments of petals can be found in *Lachnocaulon* during the whole morphogenesis of male and female flowers.

Species of *Syngonanthus* without gynoeceal nectaries do not have the stigmas in carinal position but in commissural position as it is typical for the genus. There is no argument to regard species of *Syngonanthus* without gynoeceal glands as a link to *Eriocaulon*, which lacks also gynoeceal nectaries but has the stigmas in carinal position.

Zusammenfassung

Wegen der winzigen Blüten fehlt für einige Gattungen der Eriocaulaceen selbst grundlegende Information über das Blütendiagramm. Hier wird gezeigt, daß die Antheren der Gattung *Lachnocaulon* nicht wie früher angenommen monotheecat bisporangiat durch laterale Reduktion, sondern bithecat bisporangiat durch faziale Reduktion sind. Dies steht im Widerspruch zu den Ergebnissen an *Tonina* und *Philodice* (STÜTZEL 1985), bei denen gelegentliche und unregelmäßige laterale Reduktionen vorkommen. Der Dehiscenzmechanismus der Antheren von *Lachnocaulon* ist sehr ungewöhnlich, die beiden einzigen Pollensäcke beider Theken öffnen sich durch einen gemeinsamen Längsschlitz auf der Ventralseite. Weder in männlichen noch in weiblichen Blüten können zu irgendeinem Zeitpunkt der Ontogenese Rudimente der Petalen nachgewiesen werden.

Bei einigen Arten der Gattung *Syngonanthus* fehlen die Nektarien (appendices sensu RUHLAND) am Gynoeceum. An *Syngonanthus flavidulus* (MICHAX) RUHL. konnte gezeigt werden, daß auch in diesen Fällen die Narben kommissural zu den Fächern stehen und diese Arten nicht als Zwischenformen zu *Eriocaulon* mit ebenfalls fehlenden Nektarien, aber karinaler Stellung der Narben aufgefaßt werden dürfen. Auch als Beleg für die Vermutung, bei der Morphologie des Gynoeceums von *Eriocaulon* handle es sich um ein Reversal sind *S. flavidulus* und vergleichbare Arten unbrauchbar.

Introduction

One of the most basic informations used in taxonomic botany are comparative studies of the floral diagram. It is somewhat surprising, that such information about plant species which are

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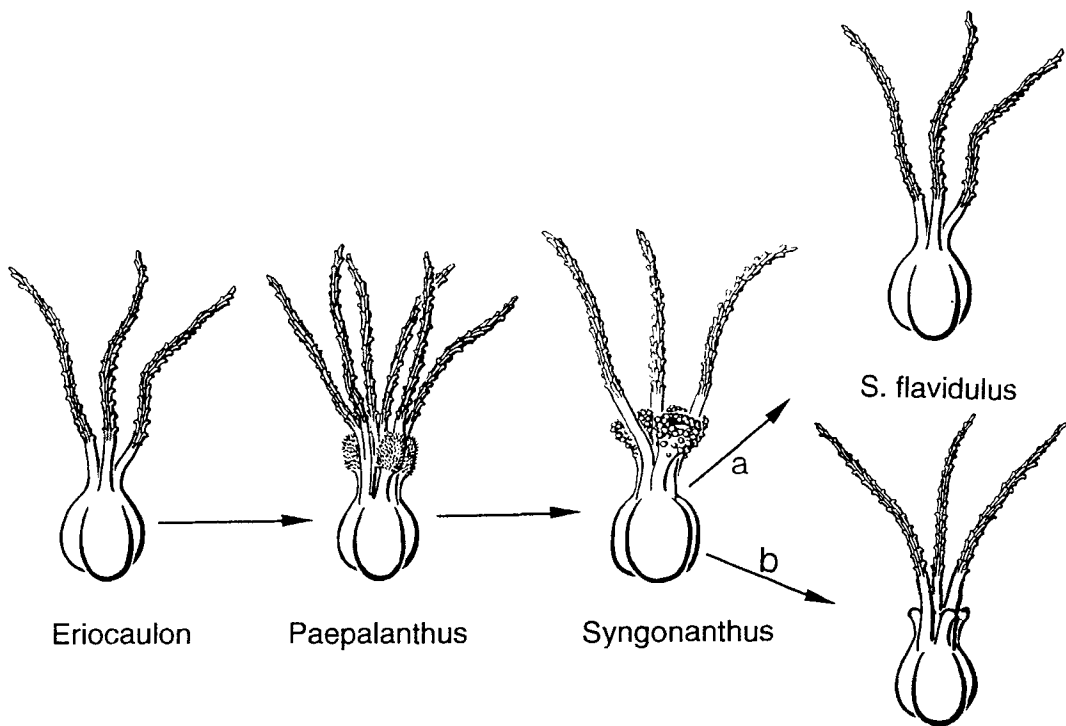


Fig. 1

Character state evolution of the gynoecium in Eriocaulaceae and two possible interpretations for the gynoecium of *Syngonanthus flavidulus*; a) would represent a reversal to the condition of *Eriocaulon* and support the view, that *Eriocaulon* itself represents such a reversal, b) would represent an additional step in the character state evolution without taxonomic implications on the generic level.

not too rare in the southern United States is still lacking, incomplete or wrong. But this is due to the very tiny flowers which can be studied even in anthesis only with the scanning electron microscope or with the best stereo lightmicroscopes that are available today.

Lachnocaulon RUHL. differs from the rest of Eriocaulaceae in having the petals reduced. In male flowers the petals are described usually as "lacking", in female flowers as "reduced to hairs" (RUHLAND 1903) assuming that the densely set hairs between sepals and gynoecium represent very little and hairy rudiments of the petals. The anthers are described as monothecate-bisporangiate, a condition which was mentioned also for *Tonia* AUBLET and *Philodice* MARTIUS and which was sometimes used to form a taxonomic group "haplantherae" for these genera. The fact that monothecate-bisporangiate anthers do not fit into the floral symmetry of Eriocaulaceae was ge-

nerally ignored. It was therefore suggested, that the stamens might be bithecate-bisporangiate (STÜTZEL 1985) as explained in Fig. 1.

In *Syngonanthus*, the gynoecium shows typical nectaries in carinal (dorsal) position to the three locules and the stigmas are in commissural position. The primitive condition is without gynoecial nectaries and the stigmas in carinal position and occurs (probably due to a reversal) in *Eriocaulon* L. In some species of *Syngonanthus* however the gynoecial nectaries are lacking. The question here is whether the stigmas are in commissural position like in other species of *Syngonanthus* or in carinal position like in *Eriocaulon* (Fig. 2). In the latter case these species might form a link to *Eriocaulon*, otherwise this interpretation is impossible. If the gynoecium of *S. flavidulus* would have the stigmas in carinal position like *Eriocaulon*, this would be an additional support for the assump-

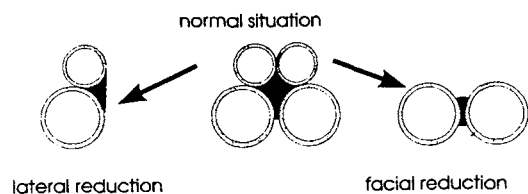


Fig. 2

Lateral and facial reduction in stamens. Despite the fact that lateral reduction hardly fits in trimerous actinomorphic flowers, this situation was assumed generally for *Lachnocaulon*.

tion that the condition with bifid stigmas might be primitive in Eriocaulaceae (STÜTZEL 1990) and the plesiomorphic character state in *Eriocaulon* the result of a reversal.

Material and methods

Lachnocaulon anceps (WALT.) RUHLAND, *Lachnocaulon minus* (CHAPM.) SMALL and *Syngonanthus flavidulus* (MICHAX) RUHLAND were collected during a field trip in Florida in 1993. *L. anceps* and *S. flavidulus* were collected near a Taxodium swamp in the region of Orlando and *L. minus* was found in the area of the Apalachicola forest in a pokosin swamp.¹ Voucher specimens are BOCH 10894 (*L. anceps*), 10895 (*L. minus*) and 10896 (*S. flavidulus*). All three species are cultivated since this time in the botanic garden of the Ruhr-Universität Bochum in a greenhouse together with species of *Sarracenia* and *Drosera* on turfose soil. All three species set seeds.

Young inflorescences were fixated in FAA. For SEM study, dissected heads were critical point dried using FDA for dehydration and CO₂ as intermedium according to GERSTENBERGER & LEINS (1978). For slides classical paraffin technique was used. Slides were stained with safranin and astrablue.

Results and discussion

Lachnocaulon

The ontogeny of male flowers starts with the formation of the sepal primordias. The next organs which become visible are the primordia of the stamens (Fig. 3b). In contrast to the investigated species of *Eriocaulon* and *Paepalanthus*, the floral axis above the sepal whorl is relatively

long when the staminal whorl is formed. The anthophor between calyx and stamens develops earlier than in other genera. But while in *Paepalanthus* or *Eriocaulon* the petals appear slightly later than the stamens or by division of a previously uniform primordium, no sign of a petal can be detected during the whole ontogeny in *Lachnocaulon*. Due to this "ablast" (reduction without any reminder of the lacking organ during the whole ontogenesis) the flower becomes regularly tricyclic. The primitive condition for Eriocaulaceae is pentacyclic with two perianth whorls, two whorls of stamens and one whorl of carpels. In the first step of reduction the outer whorl of stamens gets lost due to ablast, and a tetracyclic flower with the stamens opposed to the petals results. This situation is in contrast to the common rule, that the floral organs of successive whorls should alternate and therefore the only reminder of the original pentacyclic condition. The complete loss of the petal whorl makes the flowers of *Lachnocaulon* regularly tricyclic.

The primordia of the stamens become somewhat flattened in a very early stage of the development (Fig. 4b, c). The first steps of the formation of the sporangia can also be seen sometimes in female flowers (Fig. 6b). The actinomorphic symmetry of the male flowers is maintained during the whole morphogenesis. In later stages (Fig. 4c, d) one can see, that each theca forms only a single sporangium. This impression from the SEM study was supported by anatomical studies. Both sporangia open with a single common longitudinal slit on the ventral side (Fig. 5). Dehiscence with a single longitudinal slit is very uncommon for stamens which are bisporangiate due to facial reduction, but common for stamens which are bisporangiate due to lateral reduction. This explains, why the monothecate condition was the favoured interpretation in the past.

The initial stages of the morphogenesis of female flowers are very similar to male flowers. The first time that female flowers can be distinguished from male flowers is the formation of the three locules and the central placenta (Fig. 6a). The stamens may abort very late even after the formation of the sporangia (Fig. 6b) and this indicates that the filiform rudiments which are usually to be seen (Fig. 6c) are no petal rudiments but stamen rudiments. The first hairs are formed between the stamen rudiments and this indicates

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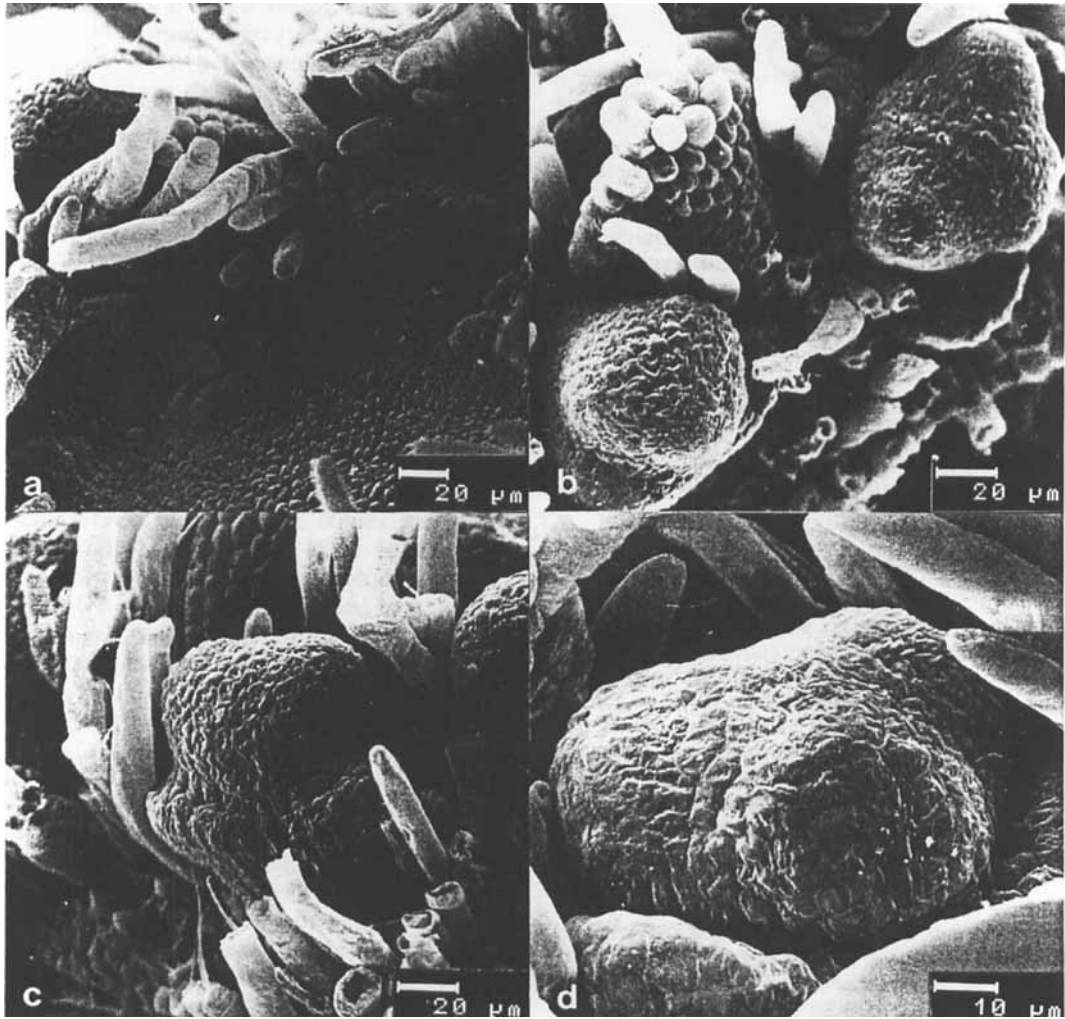


Fig. 3
Ontogeny of male flowers of *Lachnocaulon anceps*

a) formation of the floral primordia in the axil of bracts; b) early stage of sepal development in the lower left corner and older stage with the primordia of the stamens being formed in the upper right corner; c, d) the androecial primordium forms a solid triangular block above the very small sepal primordia.

that these hairs cannot be interpreted as rudiments of the petals. The female flowers of *Lachnocaulon* are therefore tricyclic like the male flowers.

It is very likely, that the reduction from pentacyclic flowers to tricyclic flowers as described here gives the correct character state evolution but does not coincide with the evolution of the taxa in Eriocaulaceae. Recent studies by HENSOLD & GIULIETTI (1991) indicate, that *Rondo-*

nanthus is probably closer to the phylogenetic base of Eriocaulaceae than *Eriocaulon*. The pentacyclic condition in *Eriocaulon* and *Mesanthemum* is therefore either a reversal or the only primitive character in a group with many derived features. Within Paepalanthoideae, *Lachnocaulon* seems to be derived from the ancestral stock of the subfamily. Growthform as well as seedcoat structure show mainly characters, which have to be regarded as plesiomorphic for the group. The

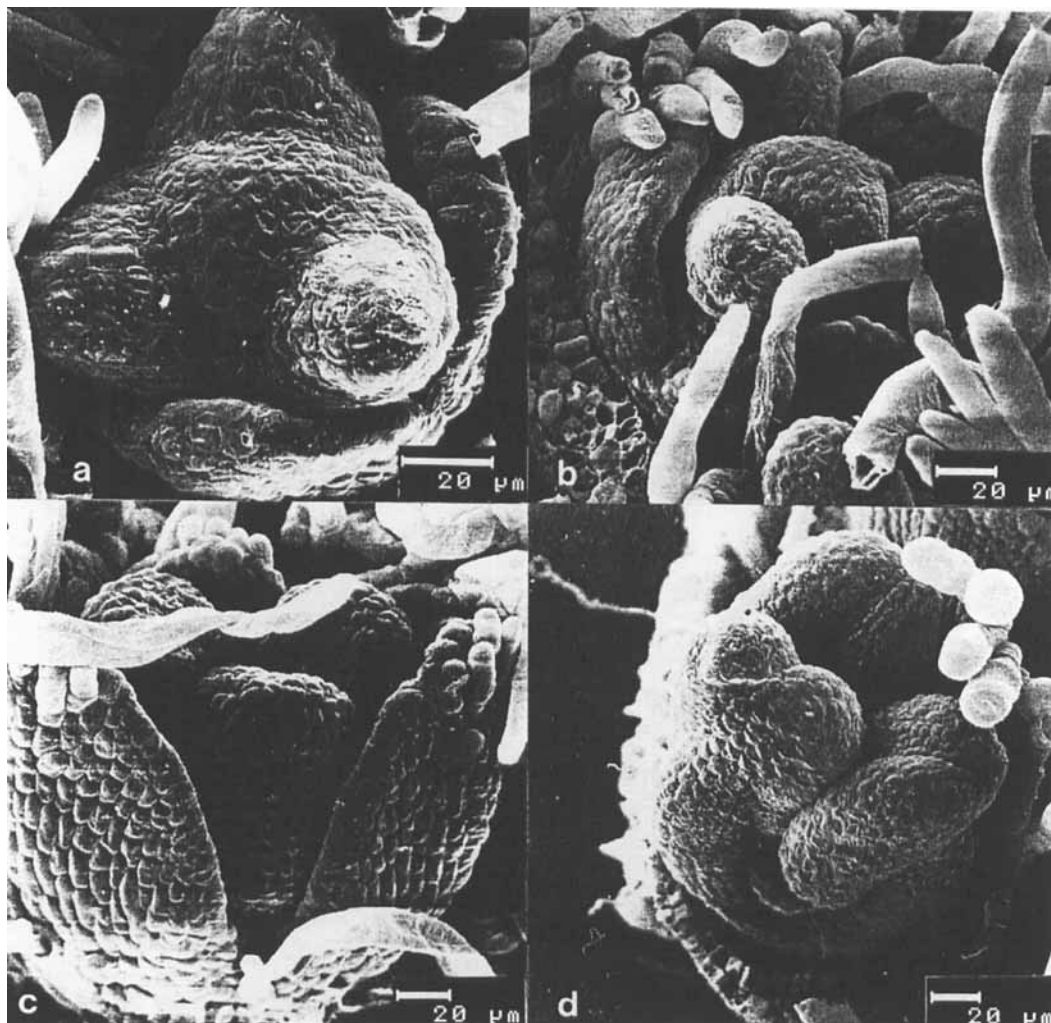


Fig. 4
Development of the reduced gynoecium in male flowers and final steps of primary morphogenesis of the staminal primordia

a, b) the rudimentary gynoecium forms a triangular block, formation of locules cannot be seen; c, d) the staminal primordia flatten early and it becomes clear, that they are bisporangiate by facial reduction.

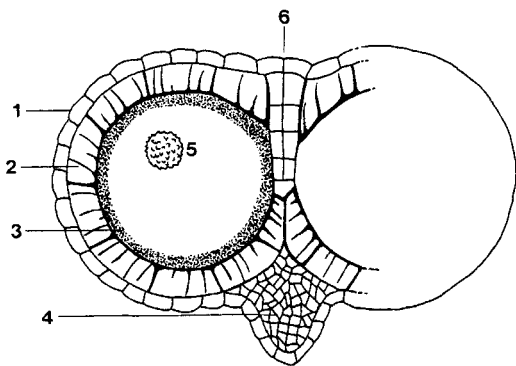


Fig. 5
Transversal section through a stamen of *Lachnocaulon anceps*. The stamen opens by one single longitudinal slit on the margin between both unilocular theca.

1 – epidermis; 2 – endothecium; 3 – remnants of inner layers and tapetum; 4 – filament; 5 – pollen grain; 6 – dehiscence zone

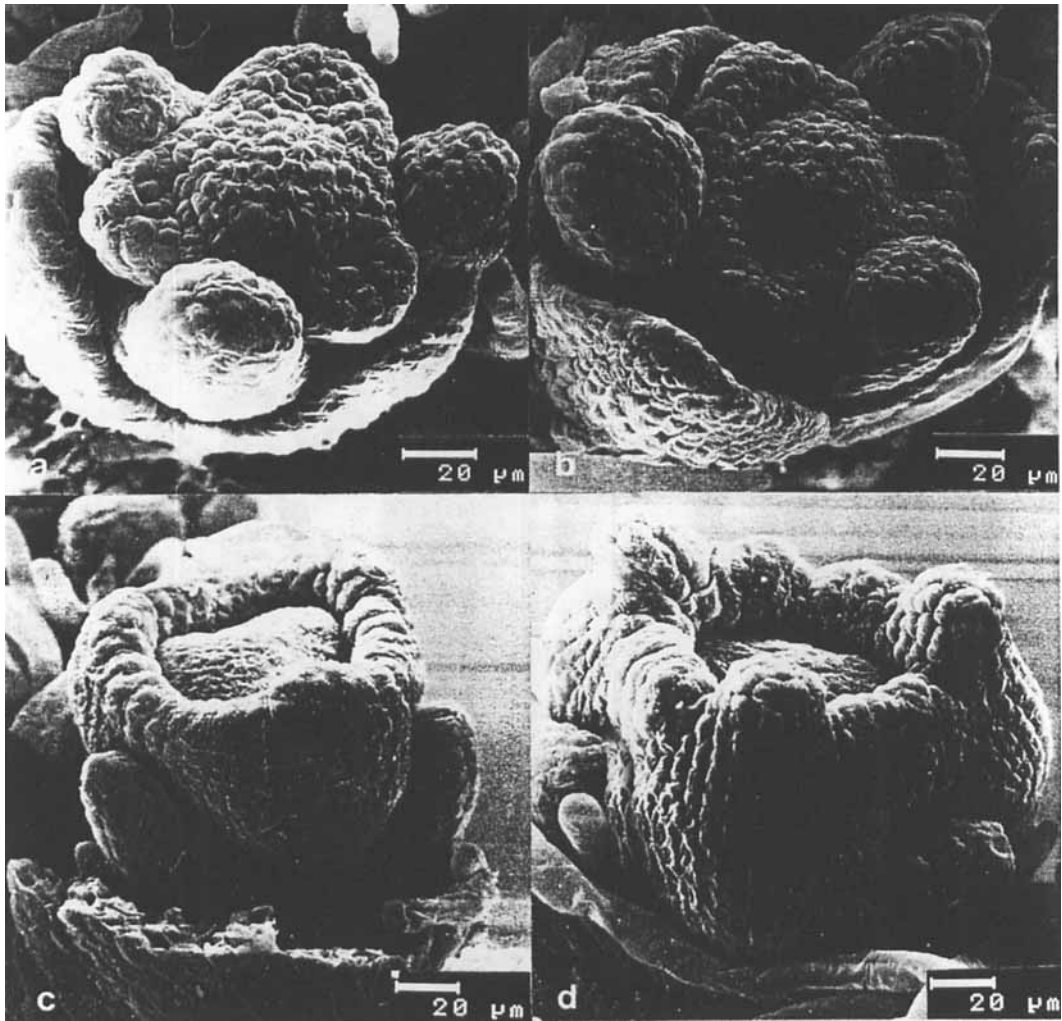


Fig. 6

Ontogeny of female flowers

a, b) the formation of the three locules indicates that the flower will become female, b) the may stamens start to flatten and to form sporangia before degenerating; c) the carpell wall has formed a ring surrounding the central placenta, the stamens are less developed than in Fig. b what indicates that the androeceum in female flowers may stop its development in different stages of the development; d) the upper margin of the carpells shows the primordia of the gynoeclial glands in carinal position and the primordia of the bifid stigmas in commissural position.

study of stamen morphology and ontogeny however clearly demonstrates, that there is no close relation between *Lachnocaulon* and *Tonina* and *Philodice*. *Philodice* and *Tonina* have often normal bithecate-tetrasporangiate stamens and sometimes and irregularly monothebate-bisporangiate stamens due to lateral reduction. The only

other genus with bisporangiate stamens, which are most likely the result of the same kind of facial reduction is *Blastocaulon* RUHLAND. All species of *Blastocaulon* show this bisporangiate condition, but several other species [e.g. *Paepalanthus bryoides* (BONG.) KUNTH.] have also bisporangiate stamens.

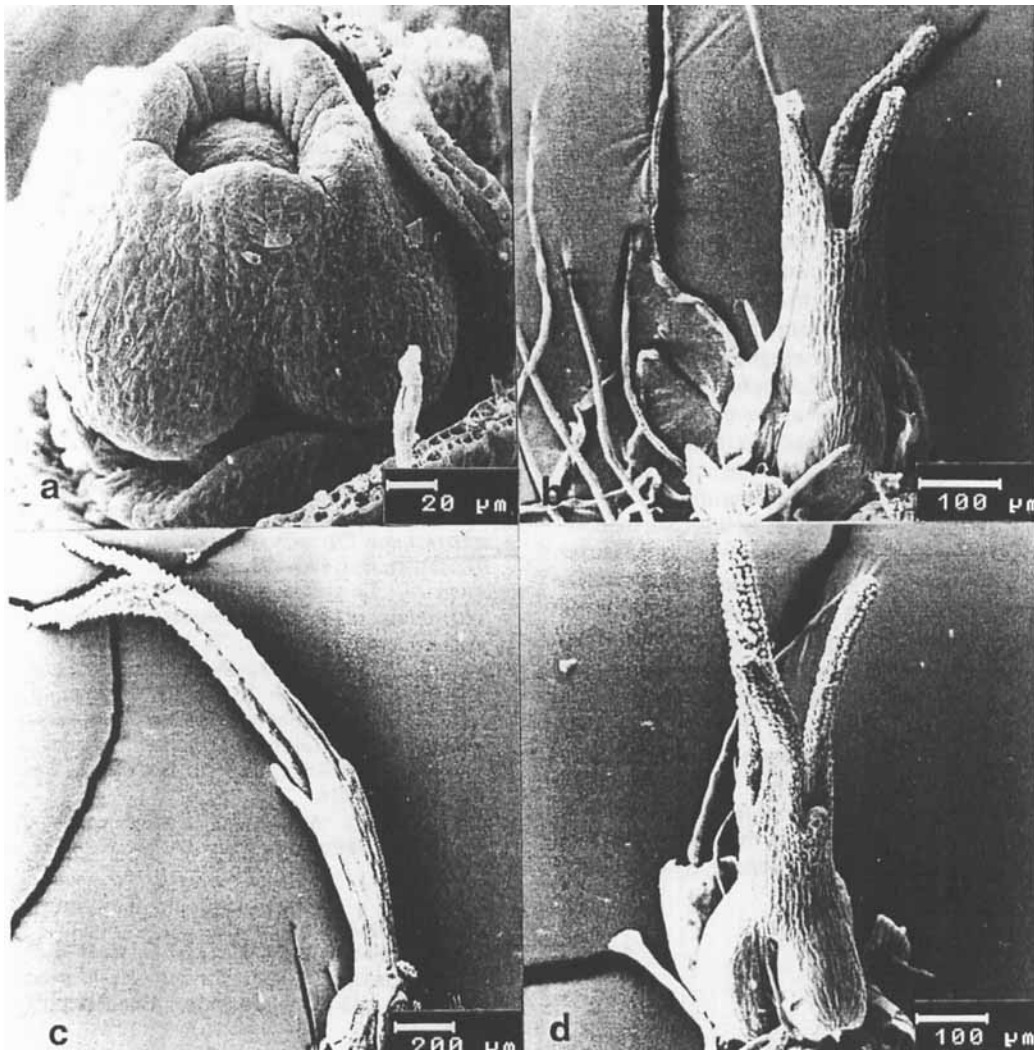


Fig. 7
Morphogeny and morphology of the gynoecium in *Syngonanthus flavidulus*

a) Late stage in primary morphogenesis, the upper margin shows the six primordia of which the carinal ones become glands and the commissural ones become stigmas, the primordium at the base of the gynoecium is one of the petals, which are still very small and do not cover the gynoecium; b) gynoecium without glands but with the stigmas clearly in commissural position; c, d) two examples with small rudiments of the gynoecial glands in carinal position.

Syngonanthus

The genus *Syngonanthus* can be defined by two characters. First by the syngonanthoid fusion of the petals, being free at the base, fused to a tube in the middle and again free at the apex, and second by gynoecial glands combined with

simple stigmas. The gynoecial glands are formed by the apex of the carpel primordium, the stigmas have to be interpreted as the result of congenital fusions of the carpel flanks. *Eriocaulon* does not have gynoecial glands and the apex of the carpel primordia develops directly to the filiform stigmas.

Some species of *Syngonanthus* lack the gynoecial glands and show only the three filiform stigmas. It must be questioned, if this condition is similar to *Eriocaulon* or if it is due to secondary lack of the glands with the stigmas being in the commissural position as typical for *Syngonanthus*.

Previous studies of fresh material of *Syngonanthus chrysanthus* (BONG.) RUHL. by one of us (T.S.²) showed small rudiments of the nectaries. But it was not possible to reproduce this result with material from the same collection in SEM studies. The study of the ontogeny of the gynoecium in *Syngonanthus flavidulus* showed, that there is some variability in the morphology and morphogeny of the gynoecium. If the ontogeny starts with a pronounced tip of the carpel primordia (Fig. 7a), one can find rudiments of the gynoecial glands (Fig. 7c, d). In this case it becomes obvious at once that the morphological situation is like in a typical *Syngonanthus* and not like in *Eriocaulon*. But it may also happen, that the upper margins of the gynoecium form a ring like structure without pronounced carpel tips. In this case, no rudiments of the nectaries can be found in the mature gynoecium (Fig. 7b). In both cases the stigmas are in commissural position as typical for *Syngonanthus*. The variability which could be found in *S. flavidulus* also explains, why it was not possible to reproduce the first correct results obtained from the study of *S. chrysanthus*.

Conclusions

The facial reduction of the stamens in *Lachnocaulon* seems to indicate, that the genus is closely related to a group of species in *Paepalanthus*. Some of these species have been separa-

ted from *Paepalanthus* as a distinct genus *Blastocaulon* due to the bisporangiate stamens. At present it is difficult to understand, why the North-American *Lachnocaulon* is geographically isolated from its closest relatives. But as other species of *Paepalanthus* may show the same bisporangiate condition, the geographic isolation may turn out less severe than it seems in the moment.

The floral morphology of *Syngonanthus* seems to be very constant and does not show variations which could be of any help in understanding the phylogeny of the family.

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