

**Cymoid evolution resulting in (closed) thyrses: *Talinum* Adans.
(Portulacaceae) versus Wilhelm Troll**

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Summary: GOEBEL (1931) and TROLL (1964) have maintained that a cymoid is a derivation of a closed thyrses caused by pre-displacement of its terminal flower. Neither morphology of *Talinum*'s inflorescences nor their development confirm an inflorescence evolution as outlined above. Moreover, evolution thus maintained does not cover all variant forms of the inflorescence revealed in *Talinum* species so far. An alternative hypothesis is presented here: the closed thyrses has derived from the cymoid *via* incorporating distal paracladium(ia) into the main florescence and reshaping it (them) into partial florescence(s) viz. cyme(s). Every variant form of *Talinum*'s inflorescences revealed fits well the hypothesised evolution as a presumed stage of cymoid to closed thyrses transformation. As evolutionary stages, the inflorescences show vestiges of such an evolution. The incorporative evolution of *Talinum*'s inflorescences has mostly resulted in extending thyrses. It has transformed a bi-nodal thyrses into a (advanced) cymoid *via* uniting both nodes into one at least in *T. triangulare*, however. Incorporative change from primitive cymoid through closed thyrses to advanced cymoid is a display of 'pseudocyclic evolution' which has no connection with the well-known 'pseudocyclic evolution' of inflorescences *via* truncation. Incorporative origin of an extended main florescence is alternative to ordinal distal homogenisation of a panicle. Paracladium incorporation as an universal evolutionary trend of *Talinum*'s inflorescences is a contestation of an actual practice to segregate *Talinum* s. l. species into a set of genera.

Keywords: inflorescence, cymoid, thyrses, incorporative evolution, pseudocyclic evolution, homogenisation, *Talinum*, Portulacaceae

Evolution from closed (~monotelic) inflorescences to open (~polytelic) ones has been shadowing evolutionary transformations of the closed inflorescences *per se* (comp. STAUFFER 1963; TROLL 1964; WEBERLING 1965; GÜNTHER 1975; SELL 1976; GUÉDÈS 1981; KUSNETZOVA 1985, 1988, 1991; SCHROEDER 1987; KUNZE 1989, etc.). The latter are nevertheless rather diverse to make a botanist reflect seriously on evolutionary lineages of the closed inflorescences. The problem seems to be even more intriguing as there is a set of Angiosperm families in which two types of closed inflorescences co-occur, viz. the cymoid (reiterative dichasium or monochasium, respectively) and the closed thyrses.

There are some purists considering the thyrses as the only inflorescence type with an indeterminate main axis bearing lateral cymes (= partial florescences) (THEODOROV & ARTJUSCHENKO 1979; ENCYCLOPEDIA BRITANNICA 2000, etc.). If the main axis is terminated by a flower, the inflorescence has to be regarded as 'thyrsoïd'. TROLL provided a consistent definition of the thyrses at first. He was inclined to attach paramount importance for presence/absence of a terminal flower (in the sense of SCHROEDER (1987), KUNZE (1989), KUSNETZOVA (1991) and others, he overrated this importance), but he classified without any hesitation every multi-nodal inflorescence of lateral cymes as thyrses, irrespective of a flower-termination (TROLL 1957, 1964). TROLL discerned open respectively closed thyrses in accord with absence/presence of the terminal flower on its main axis. Because it is possible to characterise every inflorescence of cymes unequivocally with the adjective open/closed, the term 'thyrsoïd' is superfluous.

Co-occurrence of cymoid and closed thyse in close relatives, raises the question about their evolutionary interrelations. The cymoid is especially similar to the thyse top which consists of the terminal flower and one(two) uppermost node(s) bearing cyme(s). Then, GOEBEL (1931) interpreted, as expected, the cymoid as a reduced thyse whose nodes are diminished to one(two). GOEBEL's theory has generally been shared by TROLL (1964) and SCHROEDER (1987). TROLL assumed correctly that rather progressing precocity of the terminal flower (according to DE BEER (1930), a pre-displacement mode of timing evolution) than thyse reduction causes retrogressive transformation of a multi-nodal thyse into a cymoid. Has only the terminal flower started developing, it unavoidably obstructs the development of thyse subsequent nodes with their axillar cymes. The earlier the flower starts, the less numerous are nodes of the thyse. TROLL (l. c.) believed the cymoid to be a result of an ultimate precocious origin of the terminal flower just after the first node of the former thyse has arisen. He has also hypothesised that branching of remaining cyme(s) is proceeding with thyse to cymoid evolution to compensate the diminishing number of thyse nodes.

The evolutionary course, as outlined, can easily be illustrated with a set of members of families: Caryophyllaceae, Rosaceae, and, perhaps, Boraginaceae (GOEBEL 1931; TROLL 1964) are fitting well in a nearly unbroken series of multi-nodal closed thyse to cymoid of reiterative cyme(s). Nobody has succeeded in demonstrating convincingly such a series to conform to the real evolution of inflorescence timing, however. Though retrogression seems to be one of the most usual ways of inflorescence evolution (TROLL 1964; SELL 1976; KUSNETZOVA 1991, 1998), neither the definite structure of the cymoid nor its developmental pathway shows vestiges of its presumably deteriorative origin. Thus the thyse to cymoid transformation, as speculated by GOEBEL (l. c.) and TROLL (l. c.), must thus fall in a class of special evolutionary events which leave no vestigial structures. Such events are clearly displayed by an available diversity of living beings, but direction(s) of the evolution are hardly detectable, if any (MEYEN 1973; TIMONIN 1993). Indeed, that kind of evolution is still customary regarded as retrogression, though there was GOEBEL in 1933 who was a bit bewildered by this practice. It was shown later, that biologist's strong inclination for retrogressive interpreting evolution was sometimes due to some cognitive aberration innate in human being (TIMONIN 1993). Therefore I think that evolutionary interrelation(s) between closed thyse and cymoid is(are) not settled until yet. It is worth being retried.

Materials & methods

The genus *Talinum* has been chosen for investigation because there are closed thysses in some of its species and cymoids in others (PAX 1889; TIMONIN, in press). Voucher specimens of the following taxa were used: *Talinum calycinum* Engelm. (= *Phemeranthus calycinum* (Engelm.) Kiger), *T. crassifolium* Willd., *T. cuneifolium* Willd., *T. grandiflorum* hort. ex G. Don, *T. greenmanii* Harshk., *T. mengesii* W. Wolf (= *Phemeranthus mengesii* (W. Wolf) Kiger), *T. nanum* Nees (= *Parakeeleya nana* (Nees) Hershk.), *T. napiforme* DC. (= *Phemeranthus napiformis* (DC.) Okanpo), and *T. parviflorum* Nutt.; all deposited in the Herbarium of the Komarov Botanical Institute of the Russian Academy of Science, St. Petersburg [LE]. Quite a lot of living plants of *T. paniculatum* (Jacq.) Gaertn. and *T. triangulare* (Jacq.) Willd. were examined. They are growing as weeds in greenhouses of the Komarov Botanical Institute, the Botanical Garden of the Moscow State University and the Main Botanical Garden of the Russian Academy of Science

in Moscow. Mass material of the two species allows me to account intraspecific variability of synflorescence structure. Inflorescence structure was scrutinised by recording all branches of a specimen up to pedicels according to a protocol described in KUSNETZOVA et al. (1992).

Results

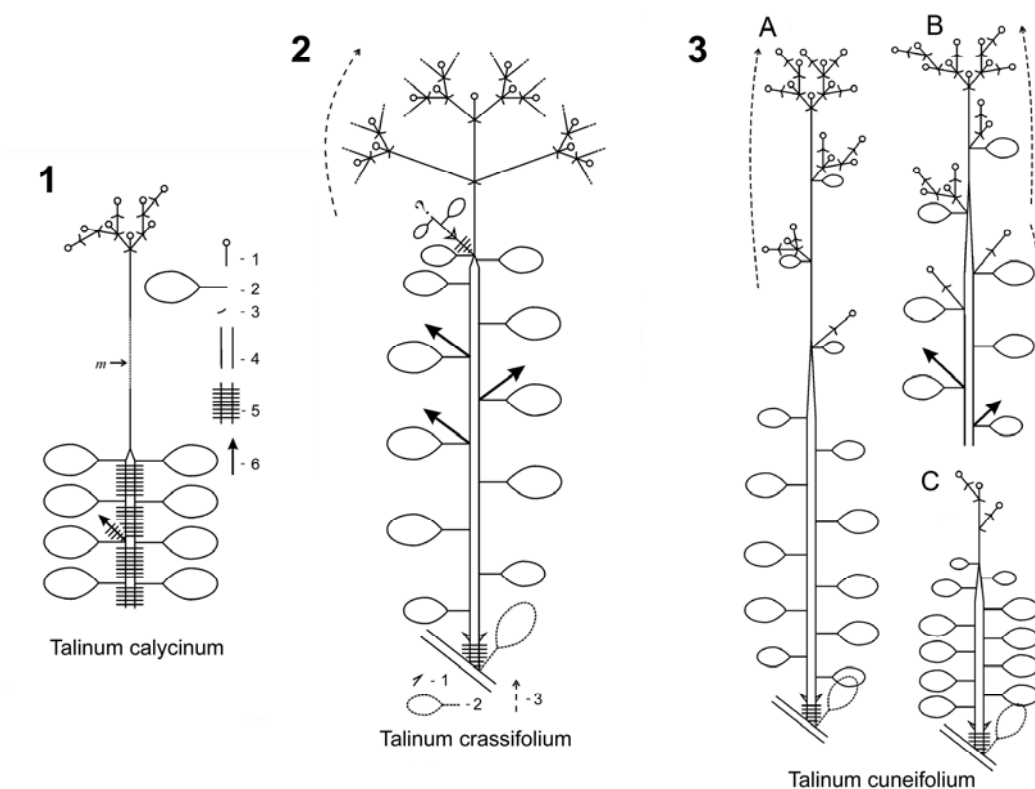
Talinum calycinum. Voucher shoot fragments which I had at my disposal show, that the plants must be sympodial, mesotonous subshrubs. Annual innovation shoots consist of a basal vegetative zone, a terminal bracteate cymoid, and a long main internodium (Hauptinternodium) in between (fig. 1). The vegetative zone has short internodia and few nodes bearing decussate leafy trophophylls. The cymoid is a dichasium or trichasium. Its cymes are reiterative few-flowered monochasia or anisoclamous dichasia, the latter changing into monochasia with III order branches. The hypopodia of the cymes are rather long while those of the innovation shoots are nearly absent.

Talinum crassifolium is a sympodial, mesotonous subshrub. Annual innovation shoots consist of basal vegetative zones and bracteate, closed terminal thyrses (fig. 2). A nearly absent hypopodium, opposite scaled decaying prophylls, and alternate leafy trophophylls are constituents of the vegetative zone. Most internodia of this zone are elongated but few distal ones acropetally shorten up. The two distalmost trophophylls are subopposite. The main internodium between the vegetative zone and the thyse highly exceeds adjacent internodia of the vegetative zone at length, though it is about as long as internodia in the middle vegetative zone. There are only two to three nodes bearing opposite scaled bracts and their axillary cymes in the thyrses of investigated specimens. The cymes are long-hypopodial, reiterative, a bit anisoclamous dichasia which change into monochasia with higher branching order. The thyse is pyramidal because its basal cymes surpass their distal counterparts in ramifying and hypopodium length. The terminal flower typically (STAUFFER 1963; TROLL 1964; KUSNETZOVA 1991, etc.) anticipates others in blooming. The cymes start blossoming acropetally.

The innovation shoots can be cataleptic to even proleptic *sensu* MÜLLER-DOBLIES & WEBERLING (1984). One of the investigated branches shows a proleptic developing shoot in the axil of the uppermost trophophyll. The shoot consists of a nearly absent hypopodium, paired scaled prophylls, quite visible epipodium, and a set of crowned leaves in progress. This shoot is equivocally regarded as leafy paracladium, occasionally as well as distal innovation shoot.

Talinum cuneifolium is a sympodial, mesotonous subshrub or, perhaps, a shrub. Annual innovation shoots (fig. 3) can be cataleptic to proleptic. Each has a basal vegetative zone of 10 to more alternate leafy trophophylls and elongated internodia. The trophophylls decrease to the terminal closed thyse. In all investigated shoots, except for one, the thyse is blurry distinctive from the vegetative zone because there is no longer main internodium, and series of trophophylls extend to the subultimate node of the thyse (fig. 3 A, B). Typically the ultimate node bears two(three) opposite (whorled) scaled bracts. Thyse trophophylls are usually alternate, though subalternate in some thyrses. The cymes are bracteate throughout. Each is a long-hypopodial, highly anisoclamous dichasium converting to monochasia with higher branching order.

There are usually one to a few basal nodes of the thyse that bear cymes impoverished to a single flower. All dichasial cymes start blooming upwards (fig. 3 A, B). As upward blooming



Figures 1–3: 1) Innovation shoot of *Talinum calycinum*. *m* – main internodium; 1 – flower; 2 – leafy trophophyll; 3 – scaled bract; 4 – elongate internodium; 5 – short internodium; 6 – growing innovation shoot. 2) Innovation shoot of *Talinum crassifolium*. 1 – prophyll; 2 – decayed trophophyll of a biennial shoot; 3 – blooming direction; ? – proleptic paracladium or innovation shoot; 3) Innovation shoots of *Talinum cuneifolium*.

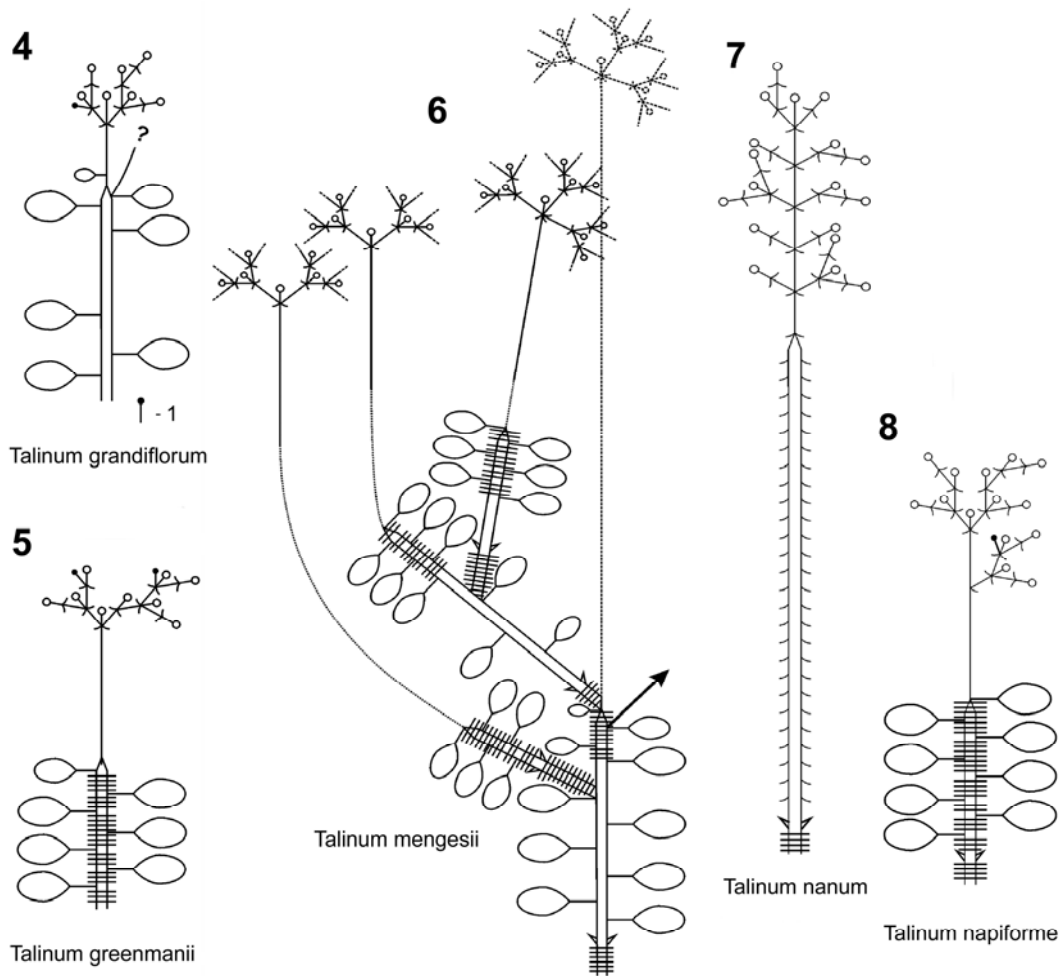
characterises partial florescences of the main florescence (STAUFFER 1963; MARESQUELLE & SELL 1965; KUNZE 1989; KUSNETZOVA 1991, etc.), I believe all of them to be partial florescences of the closed thyse irrespective of their subtending phyllome (scaled bract or leafy trophophyll, respectively). The one-flowered cymes contrast with them in downward blooming (fig. 3 B) which is typical for paracladia (STAUFFER 1963; MARESQUELLE & SELL 1965; KUNZE 1989; KUSNETZOVA 1991, etc.). Therefore the single-flowered thysses can be interpreted as paracladia.

One to a few rudiments of lateral shoots under the zone of one-flowered paracladia (fig. 3 B) are often visible. I have failed to recognise whether these are leafy (long) paracladia or acrotonous innovation shoots.

The exceptional shoot, disposed on a fragment of a perennial branch, has a highly impoverished terminal closed bi-nodal thyse which is bracteate throughout (fig. 3 C). There is one single bract on its lower node and two opposite ones on the upper node. The lower bract and one of the upper bracts subtend one reduced one-flowered cyme *per* bract.

Talinum grandiflorum is represented in this study only by a fragment of an annual innovation shoot without base (fig. 4). It has irregularly alternate leafy trophophylls and a bracteate terminal cymoid consisting of highly anisocladous reiterative dichasia, which change into

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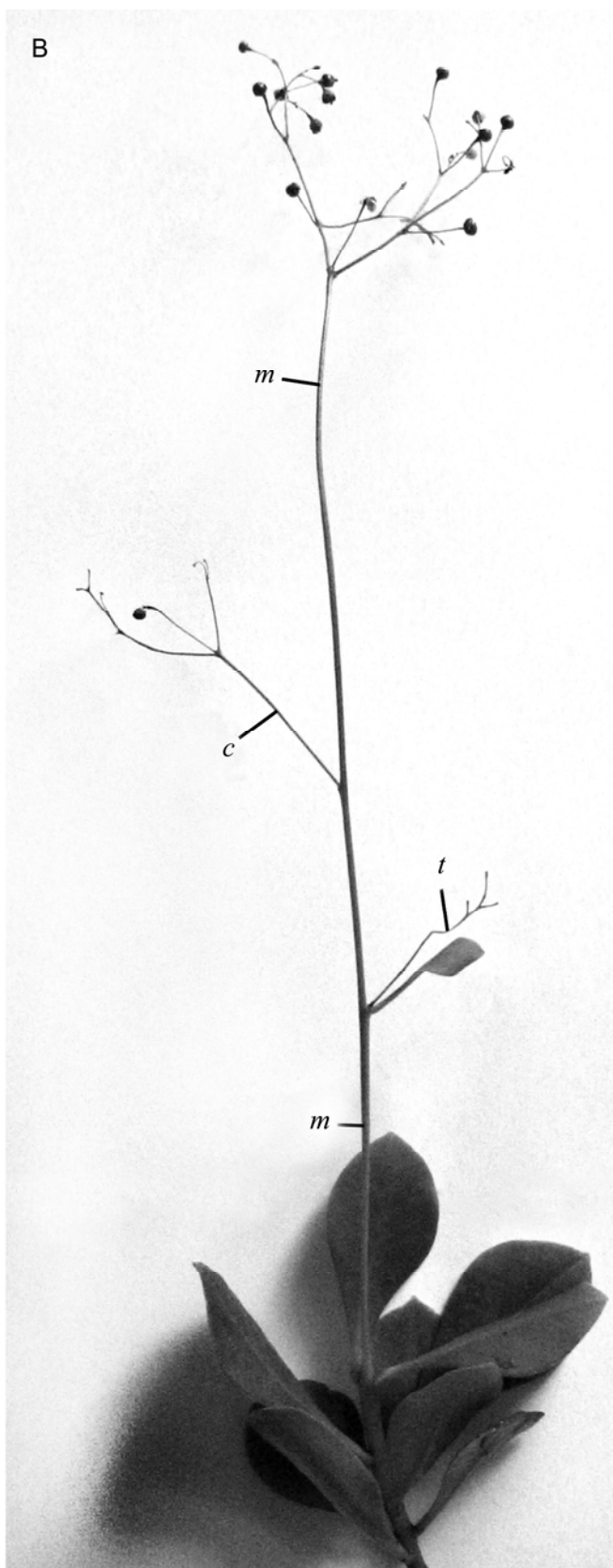
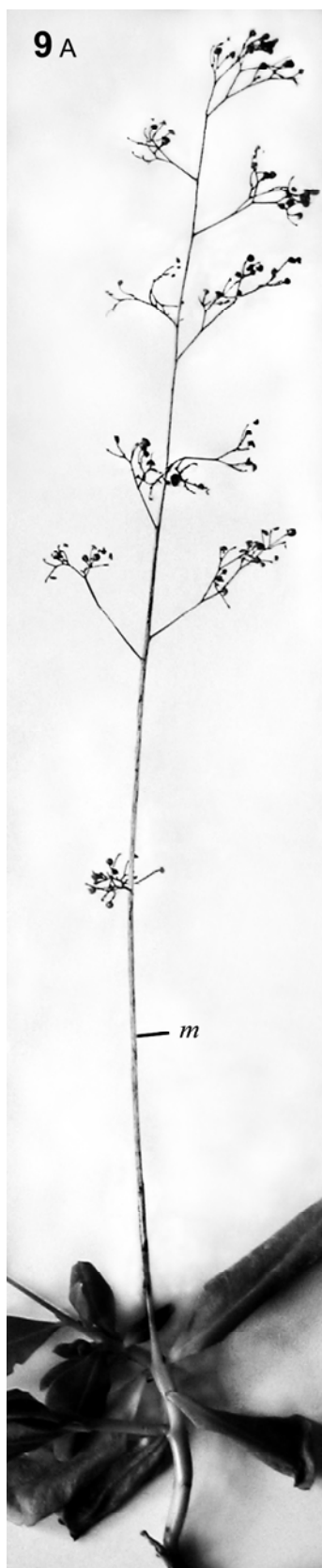
Figures 4–8: 4) Fragment of the innovation shoot of *Talinum grandiflorum*. 1 – inhibited flower; 5) Fragment of the innovation shoot of *Talinum greenmanii*. 6) System of innovation shoots of *Talinum mengesii*. 7) Innovation shoot of *Talinum nanum*. 8) Innovation shoot of *Talinum napiforme*. For further explanations, see legends of figs. 1–4.

monochasia with higher branching order. The main internodium is longer than its forerunners though not very long. In the axil of the subultimate trophophyll occurs a shoot rudiment. It might be a proleptic innovation shoot.

Talinum greenmanii The voucher specimen is too fragmentary to recognise its habit with certainty. The plant is a sympodial, meso- or basitonous rosette perennial or subshrub. Its alternate-leaved rosette is terminated with a bracteate cymoid which is an anisoclamous reiterative dichasium converting into monochasia with higher branching order (fig. 5).

Talinum mengesii A short, taprooted stump is crowned by few wooden branches. These branches have a nearly absent hypopodium, paired scars of decayed prophylls, vegetative zone, and a withered terminal cymoid elevated by a very long main internodium. Internodia between alternate leafy trophophylls decrease upward causing a condensed crown of leaves at the top of the vegetative zone. In the axils of some distal trophophylls, proleptic flowering shoots develop. These shoots are miniaturised images of their mother branch with the exception of

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the vegetative zone: in some shoots it is a rosette (fig. 6). One shoot is evidently sylleptic branched. All these shoots can be leafy paracladia. Among the paracladia an axillar, presumably proleptic, still vegetative rosette shoot can be found. It is either a delayed paracladium or a precocious innovation shoot. The cymoid is a bracteate di- or trichasium with long-hypopodial, reiterative dichasial cymes changing into monochasia with higher branching order.

Talinum nanum is a sympodial, basitonous perennial. Annual innovation shoots consist of a nearly absent hypopodium, opposite decaying scaled prophylls, long multi-nodal vegetative zone, and a terminal multi-nodal closed thyrs (fig. 7). Uniform scaled, decussate leaves are on the stem of the vegetative zone and on the axis of the thyrs. The main internodium is as long as the others. Cymes are long-hypopodial, bracteate dichasia; a lot of them are reduced to a single flower.

Talinum napiforme is possibly perennial with a sympodial rosette. The terminal closed bracteate thyrs is elevated on a distinctive main internodium which is much longer than the internodia of the vegetative zone (fig. 8). Only one specimen could be examined. It has a bi-nodal thyrs: the lower node with one bract, the upper one bears two opposite bracts. Each bract subtends a long-hypopodial, few-flowered, highly anisoclamous dichasium.

Talinum paniculatum is an acrotonous, sympodial subshrub. Its innovation shoots arise just under the enrichment zone of the synflorescence. The primary shoot and the innovation shoots are nearly uniform with the exception that the latter have nearly absent hypopodia and opposite, scaled decaying prophylls instead of a hypocotyl and cotyledons. The basal, leafy part of the shoot is multi-nodal and long-internodial. It is completely vegetative (fig. 9 B) or its distalmost one to three nodes constitute the enrichment zone of the synflorescence (fig. 9 A). The trophophylls are decussate; in some plants few upper trophophylls are subalternate.

The synflorescence is highly variable (TIMONIN, in press). The main florescence is a bi- to multi-nodal, bracteate, closed thyrs (fig. 9 A). Among all investigated plants, occurred only one exception with a bracteate, dichasial cymoid (fig. 9 B). The cymes of the thyrs/cymoid are long-hypopodial, reiterative, and a bit anisoclamous dichasia. Their subultimate branches are usually transformed into monochasia. Bracts of the thyrs are predominantly subalternate, only the two uppermost are opposite. Thyrses with completely decussate or completely alternate (fig. 11 B) to subalternate bracts are rare. The cymes are blooming acropetally, the terminal flower anticipates its neighbouring cymes. Opposite cymes very often start blooming successively (TIMONIN, l.c.).

The part between the main florescence and the trophophyll zone is of special interest (figs. 9 A; 11 B). In many plants the thyrs is plainly elevated by a long main internodium (figs. 9 A; 10 B), but two long internodia with a pair of nodes in between are in rather many plants (fig. 9 B). The lower node bears a small trophophyll to transitional phyllome, the upper node bears a transitional phyllome to scaled bract. In few plants both nodes bear bracts. Only one of the investigated specimens has one node bearing a small trophophyll between two long internodia (fig. 11 A). In this case, a bracteate reiterative dichasium, quite similar to those in the thyrs, is in the axil of the leafy phyllome (fig. 11 B). If two nodes are developed, the upper node bears a



Figure 9: Innovation shoots of *Talinum paniculatum*. *c* – cyme (dichasium); *m* – main internodium; *t* – lateral thyrs.

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dichasium, rarely the lower node, too (fig. 9 B). In the last case, a bracteate, few- to multi-nodal closed thyrs is developed on the lower node (fig. 9 B). This thyrs generally has a nearly absent hypopodium and opposite scaled decaying prophylls. In few plants a discernible hypopodium and alternate prophylls occur. Prophyll axils are mostly empty; only in one plant one of the two prophylls subtends an inhibited button. The lateral thyrs bracts subtend anisophyllous reiterative dichasia which are transformed into monochasia with higher branching order. A lot of dichasia are underdeveloped and represented by solitary flowers or even inhibited buds. Lateral inflorescences of the intermediates start blooming downwards and after the lowermost dichasia of the main thyrs have blossomed. The cymes of the lateral thyrs start blooming acropetally.

Sylleptic paracladia are in the axils of one to three upper pairs of trophophylls, but not in weaker annual plants. Four sorts of paracladia are recognisable in investigated specimens:

Most paracladia have a nearly absent hypopodium (fig. 10 C), opposite scaled decaying prophylls, one to three alternate leaves which change acropetally from scales to intermediate phyllomes to small trophophylls, one to few pairs of decussate trophophylls, the intermediate (if any), and the coflorescence (figs. 10 A, B, right; 12 A). The latter is a bracteate, closed, multi-nodal thyrs which usually exceeds its counterpart of the main florescence. Transition from the trophophyll zone to the coflorescence is often less distinctive than in innovation shoots, as the main internodium of the paracladium is approximately as long as its adjacent internodia. The condition is typical for paracladia (KUSNETZOVA 1991). There is/are sylleptic short- or long-hypopodial bracteate, few-flowered thyrs(s) to only bracteolate flower(s) in the transitional zone of the paracladium (fig. 12 A). Robust paracladia give rise to rather proleptic next-ordered paracladium(ia) in the axil(s) of their paired trophophylls. These either reiterate their mother paracladium in a small scale or are bracteate throughout. All paracladia of the next order (or only the uppermost) are often long-term inhibited before blooming (fig. 12 A).

Weak leafy paracladia have a nearly absent hypopodium, opposite scaled decaying prophylls, numerous decussate to subalternate transitional phyllomes or small trophophylls, short but discernible internodia, and a terminal long-stalked flower. Axillary flowers of the paracladium are withering in an early bud-stage (fig. 12 C). In some plants this happens also to the terminal flower.

Leafy alternate-leaved paracladia (fig. 12 B) are characterised by a nearly absent hypopodium, paired scaled decaying prophylls, one scaled phyllome, a few leafy trophophylls, and a terminal bracteate closed thyrs. The scaled phyllome and every trophophyll subtend a paracladium of the next order which is a closed, completely bracteate thyrs with a long hypopodium, distinctively alternate prophylls, each subtending a reiterative dichasium (fig. 11 C).

Completely bracteate paracladia have a nearly absent hypopodium, opposite scaled decaying prophylls with empty axils, a rather long epipodium, a long to very long main internodium, and a terminal multi-nodal closed thyrs (fig. 10 B, left, C). The bracts of the thyrs are alternate to subalternate; the two uppermost are opposite. All bracts subtend cymes with a range



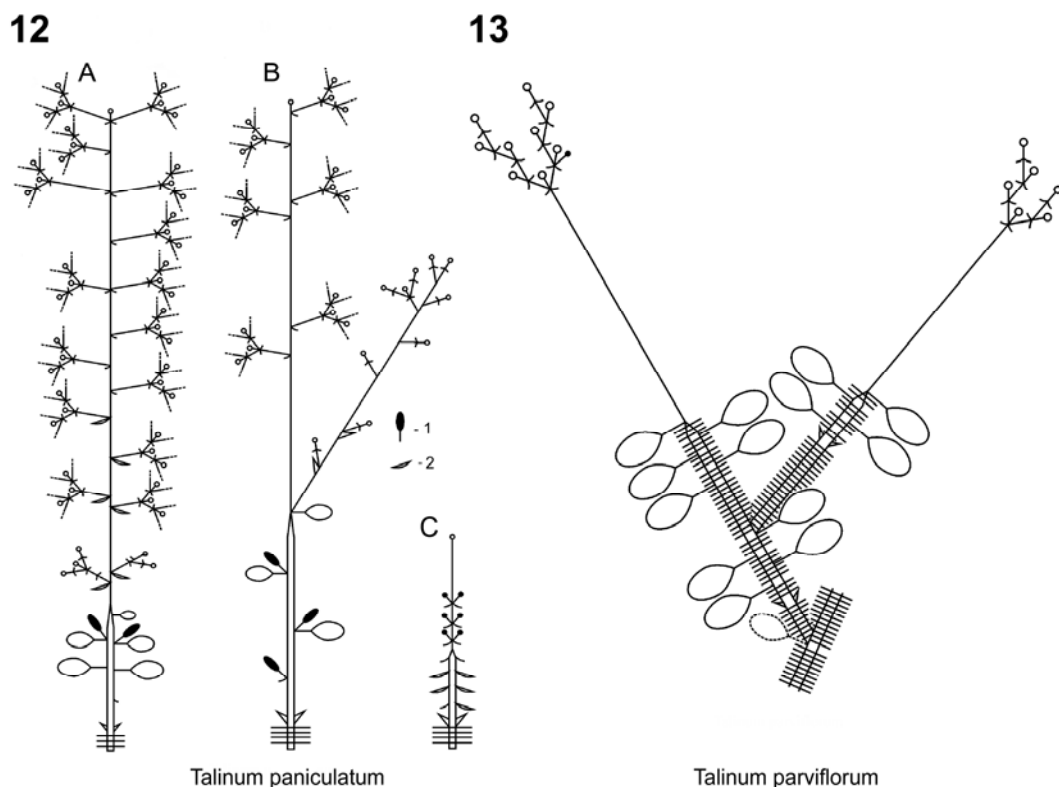
Figure 10: Frondose bracteate (A) paracladium, synflorescence (B, C, detail) of *Talinum paniculatum*. *b.p* – bracteate paracladium; *l.p* – frondose bracteate paracladium; *p* – prophyll.

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Fig. 11: Synflorescence (A, B, detail) and bracteate long-hypopodial paracladium (C) of *Talinum paniculatum*. *h* – hypopodium; *m* – main internodium; *p* – prophyll.

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Figures 12–13: 12) Paracladia of *Talinum paniculatum*. 1 – developing or inhibited next-ordered paracladium; 2 – intermediate phyllome. 13) System of the innovation shoots of *Talinum parviflorum*. For further explanations, see legends of figs. 1–4.

of variation from a reiterative dichasium to a bracteolate flower. Bracteolate flowers on lower nodes sometimes die off at the stage of buds.

Paracladia of the synflorescence usually start blooming downwards, rarely upwards.

Talinum parvifolium is a sympodial, mesotonous to basitonous, rosette subshrub. Some shoots likely are sylleptic. Nevertheless, every shoot seems to be an innovation shoot. Paracladia are completely absent. The innovation shoot has a nearly absent hypopodium, opposite scaled decaying prophylls, a more or less dense rosette of alternate trophophylls, and a terminal, very long-peduncled, bracteate cymoid (fig. 13). The cymoid is dichasial and its cymes are dichasia or reiterative monochasia.

Talinum triangulare is a sympodial, mostly mesotonous subshrub, with cataleptic to proleptic innovation shoots. The innovation shoot has a nearly absent hypopodium, opposite scaled decaying prophylls, and a long vegetative zone. Alternated trophophylls are regularly dispersed nearly throughout the whole vegetative zone and progressively condensed upwards on its top. The two uppermost trophophylls are subopposite to genuine opposite. Distal trophophylls are small leaves to intermediate phyllomes. The shoot is terminated by a long-peduncled, bracteate cymoid or closed thyrses. In the case of a cymoid, a trichasium of anisoclamous reiterative dichasia is developed. Dichasia change into monochasia with higher branching order (fig. 14 B). The thyrses is bi-nodal with an internodium up to 1.5 cm long in between (fig. 14 A). The lower

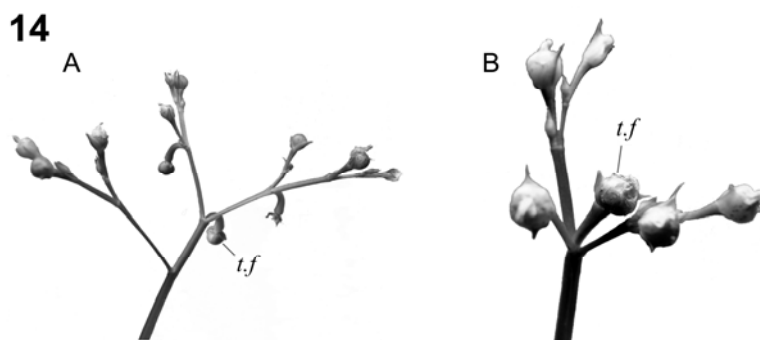


Figure 14: Terminal florescences of *Talinum triangulare*. *t.f* – terminal flower.

node bears one bract and its axillar cyme. The upper node bears two opposite bracts, each subtending a cyme. Thyrses cymes are the same as those of the trichasium. They start blooming upwards.

Proleptic shoots, growing from the axils of (one)two uppermost trophophylls, closely resemble innovation shoots with less trophophylls. Perhaps environmental impacts cause these shoots to die off completely after blooming or give rise to new innovation shoot(s) on upper trophophyll node(s) after their terminal florescence has been inhibited (TIMONIN, in press). Thus, the shoots are either seasonal paracladia or perennial innovation shoots as influenced by the environment.

Discussion

If some inflorescences of *Talinum* remain unknown, and some inflorescences revealed in this paper are missing, the cymoids of *T. calycinum*, *T. grandiflorum*, *T. greenmanii*, *T. mengesii*, *T. parviflorum*, and *T. triangulare* as well as the closed bi-nodal thyrses of *T. napiforme* and *T. triangulare* will be interpreted in accordance with the concept of Goebel and Troll (GOEBEL 1931; TROLL 1964) as reduced derivatives of (multi-nodal) closed thyrses because of the abbreviation of their development.

The thyrses of *T. cuneifolium* and to a less extent that of *T. paniculatum* is proximally frondose. If such a thyrses is abbreviated as Troll speculated, the distal bracteate part of the thyrses would have been lost and its leafy proximal part would have remained (fig. 15 A). As a result, we would expect that *Talinum* species with frondose cymoids evolve. As far as I know, all cymoids are invariably bracteate in *Talinum*.

Two explanations for the absence of frondose cymoids in the genus *Talinum* can be discussed:

(i) Frondose cymoids as starting point might have been precluded by some evolutionary constraint(s). However, frondose reiterative cymoids are typical of a lot of Centrosperms (GOEBEL 1931; TROLL 1964; TROLL & WEBERLING 1981; HOFFMAN 1973, etc.) and especially some Portulacaceae (TIMONIN & FEODOROVA 2004). Therefore, it is improbable that evolutionary constraints preclude frondose cymoids in Portulacaceae.

(ii) Thyrses to cymoid evolution fortuitously affected only bracteate thyrses. I believe that fortuitous events took place in biological evolution but such events are neither profoundly interpretable nor correctly recordable.

Cymoid to thyrses evolution

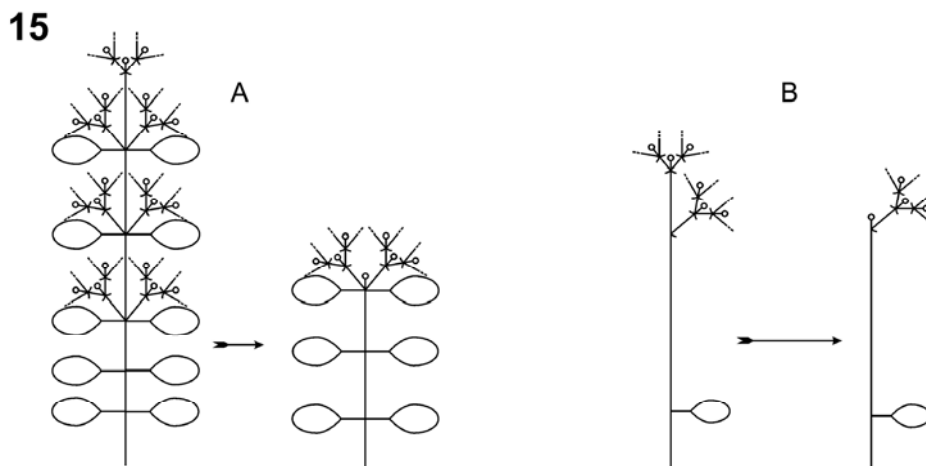


Fig. 15: Hypothetical cymoids that would have derived from closed thyrses according to Troll's concept. *Explanations in the text.*

Talinum triangulare must convincingly demonstrate the interrelation between cymoid and closed thyrses because the species has both inflorescence types. If its thyrses had evolved into a cymoid in accordance with the concept of Goebel and Troll, the upper node of the thyrses bearing two opposite cymes and subtending bracts would have been lost while the lower node of the thyrses bearing only one cyme would have been retained (fig. 15 B). The terminal flower with only one cyme would have constituted the cymoid, i.e. the monochasium. But cymoids of *T. triangulare* invariably are trichasia of three whorled cymes in axils of three bracts.

Thyrses reduction on weak paracladia in *T. paniculatum* shows comprehensive, suppressing (lateral) cymes to highly underdeveloped buds while the number of thyrses nodes *per se* remains unaffected (fig. 12 C). So a simplification of the thyrses *via* abbreviation, as TROLL (1964) has ascertained, is certainly not typical of *Talinum*.

Finally, a pair of long main internodia and small lateral thyrses in between, inherent in very many terminal inflorescences of *T. paniculatum*, do not fit the thyrses to cymoid evolution outlined by TROLL (l. c.). Therefore, an enigmatic evolutionary pathway has to be accepted to explain such an unusual character of the species.

The above mentioned discrepancies between the inflorescence diversity in *Talinum* and the concept of thyrses to cymoid evolution of Goebel and Troll are easily cleared up if *abbreviation* is replaced by *incorporation* as a keystone of inflorescence evolution in the genus. Incorporation as a sort of structure evolution has been revealed by BEKLEMISHEV (1942: as 'integration'). Studying articulate animals, he showed that more integral body parts had an evolutionary tendency to incorporate partly or totally their less integral neighbour(s). It is not reasonable to restrict this tendency only to animals. Moreover, centrospermous Cactaceae significantly show an incorporation of the less integral distal shoot (including inflorescence) into the much more integral terminal flower (VOLGIN 1981, 1988).

Structures are increasing the number of constituents during their incorporative evolution. Therefore, the more advanced a structure is, the more constituents it consists of. Hence, the multi-nodal closed thyrses should be rather considered as a more advanced inflorescence in

Talinum. On the contrary, the bracteate cymoid of the dichasial/trichasial type must be regarded as original inflorescence of *Talinum* because it is the minimal inflorescence known in the genus.

I hypothesise that original *Talinum* was a sympodial subshrub with uniform shoots (fig. 16 A). Each shoot resembled its counterpart of actual *T. calycinum*, *T. grandiflorum*, *T. greenmanii*, *T. mengesii*, and *T. parviflorum*, i.e. it had a nearly absent hypopodium, opposite paired scaled prophylls with empty axils, a multi-nodal zone of trophophylls, and a terminal long-peduncled bracteate dichasial to trichasial cymoid; except for the primary shoot which had a long hypocotyle and paired cotyledons instead of a hypopodium and prophylls. Probably the shoots were mostly mesotonous, cataleptic to proleptic, like those of *T. parviflorum*. Proleptic shoots were most unlikely predetermined to develop into innovation shoots or into paracladia like distal shoots of modern *T. triangulare* (the origin of the cymoid of *T. triangulare* is discussed below). Generally, the more distally such a shoot arose, the more probable it developed into a leafy paracladium.

If only lateral shoots differentiated into mesotonous innovation shoots and proleptic leafy paracladia, occupying axils of the distalmost trophophylls, the original modular (*sensu* SCHROEDER 1987) inflorescence became a paracladial synflorescence and the distal part of the trophophyll zone became its enrichment zone (fig. 16 B). A similar synflorescence is inherent in actual *T. paniculatum* which main florescence is a bracteate, closed thyrs, but not a cymoid, however. Paracladial synflorescences certainly displayed more integrity, in spite of the fact that the long main internodium between the cymoid (= main florescence) and the enrichment zone still remained. The greater integrity probably caused the paracladia to become strictly sylleptic. In addition, it was the prerequisite for subsequent incorporative evolution of *Talinum*'s inflorescence.

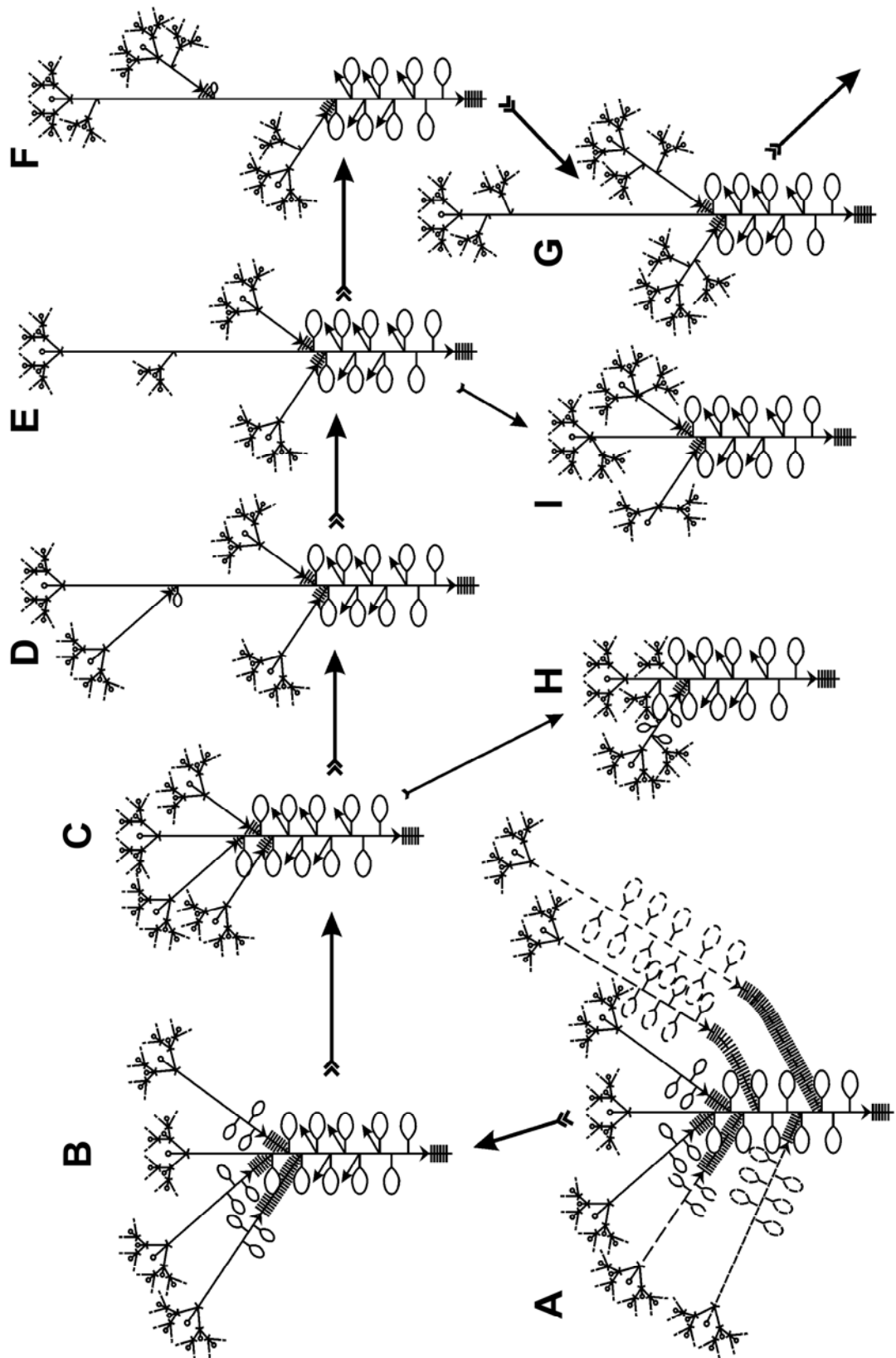
As hypothesised here, the incorporative evolution of the synflorescence started by transforming (uppermost) leafy paracladium(ia) into bracteate one(s) by suppressing its (their) vegetative trophophyll zone and reducing trophophylls to scaled phyllomes (fig. 16 C). Bracteate paracladia with only one scaled sterile leaf between the prophylls and the terminal inflorescence can be seen in *T. paniculatum*: but they are terminated by a thyrs. A paracladium, transformed that way, became incorporable into the (terminal) main florescence.

Incorporated into the main florescence, the former paracladium had to resemble the lateral constituents of the cymoid; i.e. it had to change into a dichasial cyme. Nearly complete transitional series from bracteate paracladia to lateral dichasia of the terminal thyrs (= main florescence) can be found in *T. paniculatum* (figs. 9–12). This series leads into temptation to assume a gradual evolution from paracladia to partial florescences in *Talinum*. Nevertheless, MEYEN (1978) and LODKINA (1983) show quite a number of presumed 'evolutionary transitions' which are results of a secondary resemblance caused by coincidence of different developmental programmes. Therefore, I do not really believe the series mentioned above to be a reflection of the evolutionary pathway. Intermediate flower aggregates could develop due to a coincidental working of two developmental programmes; viz. the programme of paracladium formation and the programme of partial florescence formation under a remaining competence of the inflorescence rudiment to both. I think that paracladium to partial dichasial florescence evolution in *Talinum* is a saltation basing on a sort of homeiotic mutation(s) (fig. 16 D → E).



Fig. 16: Inflorescence evolution *via* paracladium incorporation. *Explanations in the text.*

Cymoid to thyrs evolution



The synflorescence of *T. paniculatum* as shown in fig. 11 A and the inflorescence of *T. cuneifolium* support this assumption.

A supernumerary long internodium evolved between incorporated former paracladium(ia) and the remaining enrichment zone. This internodium temporarily co-existed with the original long main internodium (fig. 16 D, E) and resulted in a thyrses with two main internodia like those inherent in actual *T. paniculatum*. Such a thyrses subsequently get normalized by shortening the original (upper) main internodium (fig. 16 E → F). In *T. cuneifolium* the original main internodium evidently shortened but no new long internodium arose during the evolution of its thyrses (fig. 16 C → H). Trophophylls, which subtended incorporated former paracladium(ia), are typically reduced to bract(s), but they are retained in *T. cuneifolium* (fig. 16 H). The results are completely bracteate thyrses (fig. 16 F) and proximally frondose thyrses (fig. 16 H).

One to very few paracladia were incorporated into the terminal inflorescence simultaneously. In case of one or two opposite incorporated paracladia, the bi-nodal thyrses (fig. 16 F), similar to those revealed in *T. crassifolium*, *T. napiforme*, and *T. triangulare*, evolved. Incorporation of more than two (but few) paracladia lead to the development of a few-nodal thyrses.

After the closed (terminal) thyrses was developed, it certainly caused the corymbes of the remaining paracladia to change from cymoid to thyrses (fig. 16 E → F). The change was probably a saltation like a homeiotic mutation.

Incorporation continues in two forms after the thyrses has evolved. First, the thyrses becomes augmented by incorporating more and more paracladia as described above (fig. 16 F → G → ...). Such an 'incorporation in progress' must be observable in modern *T. paniculatum*. Second, the lower node of a bi-nodal thyrses approximates the upper one and becomes absorbed into the latter (fig. 16 E → I). Thus, the bi-nodal thyrses is transformed into a secondary cymoid with additional reiterative cyme(s). Such an incorporation is demonstrable actual in *T. triangulare*.

Conclusion

Inflorescence evolution in *Talinum* as modelled here, completely covers its inflorescence diversity revealed so far. Every variant form of the inflorescence may be placed as a stage of the mainstream of its evolution *via* incorporating paracladia into the main florescence and reshaping them into partial florescences of the latter. The main florescence thus changes from cymoid to few-nodal thyrses to multi-nodal thyrses. So unusual structures like double main internodium, or reduced lateral thyrses on the place of the basalmost cyme of terminal thyrses, can consistently be regarded as traces of incorporative evolution of *Talinum*'s inflorescence. Thus, the hypothesised evolutionary model can directly be corroborated by structural characters of inflorescences of actual species. On the contrary, the concept of Goebel and Troll is based on assumed changes of timing of inflorescence ontogeny which left vestiges neither in structure of modern *Talinum*'s inflorescences nor in their development. Therefore, the concept should be considered speculative and less substantial so far. My hypothesis surely does not refute Goebel's and Troll's concept in general. I believe, however, that it allows a more realistic version of inflorescence evolution in *Talinum*.

The concept of Goebel and Troll needs transformations to be assumed to be analogous to MEYEN's (1984) 'tempodesinentio'. The latter is really unverifiable because it leaves no vestiges

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of a former structure in the resulted one (MEYEN 1984, *see also* TIMONIN 1993). That is why the concept under reconsideration unluckily can hardly be proved, but it is lucky to be unrefutable. As not falsifiable, it does not fit POPPER's (1979) standard of science.

It is hypothesised here that the original inflorescence of *Talinum* has been a reiterative (dichasial?) cymoid which is characteristic of a lot of Centrosperms (GOEBEL 1931; TROLL 1964; TROLL & WEBERLING 1981; HOFFMAN 1973, etc.). This cymoid is considered to have evolved into a closed thyrses *via* incorporating distal paracladia. When continuing, the incorporation causes either downward increasing of the thyrses or changing a bi-nodal thyrses to a cymoid. The latter process is consistently different from that proposed by GOEBEL (l. c.) and TROLL (l. c.), because none of the distal nodes of the thyrses has been lost due to pre-displacement of the terminal flower. Quite contrary, the former upper node of the thyrses remains enriched as it has completely absorbed the lower one with its partial florescence(s). Therefore, the resulting cymoid is by no means identical to the original cymoid but an advanced simulation to the latter. It can be an illustrative example of GAUSSEN's (1952) 'pseudocyclic evolution'. It has no connection with the readily accepted truncation of the synflorescence (SELL 1969, 1976; KUSNETZOVA 1985, 1988, 1991; KUNZE 1989, etc.).

Repeating incorporation of distal paracladia into the main florescence results in an extended distal synflorescence zone which bears uniform lateral assemblages of flowers. This process is an alternative to the well-known homogenisation of distal panicles (SELL 1969, 1976; KUSNETZOVA 1985, 1988, 1991; KUNZE 1989, etc.).

Incorporating paracladia into the main florescence should be considered as common evolutionary trend of *Talinum*'s inflorescences because it covers all its variant forms so far revealed in the genus. A common evolutionary trend must be regarded as important indication that a taxon is quite natural as a set of common diagnostic traits (TATARINOV 1976). Then, the actual practice to segregate *Talinum* species into few genera (*Talinum* s. str., *Phemeranthus*, *Parakeeleya* etc.) can be contested. Inflorescence morphology shows that *Talinum* s. l. is worth being retained.

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