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Definitions of dichasium, cyme, and thyrse present in the literature

The inflorescence terminology used by many workers is based on Weberling (1989) which, in turn, is an extension of the unfinished work of his mentor, Wilhelm Troll (1964). The purpose of this paper is not to review the utility of Troll's inflorescence concepts in Santalales or angiosperms in general. Our goal is to provide clear definitions of existing inflorescence terminology applicable to Santalales and tie these terms to the primary literature where they were more fully discussed. While doing this, we point out where we disagree with the terminology used by SGP and indicate with italics non-standard terms. Because the literature describing inflorescences in Santalales is already replete with terms, we advocate using existing terms whenever possible, instead of generating additional ones. Our list is partitioned into general inflorescence terms and ones that apply specifically to Phoradendreae of Viscaceae. The unusual inflorescence type seen in the latter clade has required the use of specialized terms that are, in some cases, unique among angiosperms. To assist interpretation, labeled, diagrammatic representations of the inflorescence types seen in Phoradendreae are presented in Fig. 2.

<u>General</u>

Bracteole. A general term for a small bract of any sort, foliaceous or not, including prophylls (see below).

Coenosome. An inflorescence, formed from congenital fusion (syndesmy), where the inflorescence axis is "only apparently homogeneous" (Weberling, 1989; from Troll (1964). This definition is obscure for it is unclear whether or not the axis is actually homogeneous or, if one had the proper anatomical or developmental evidence, that it only outwardly appears homogeneous. Coenosomes typically involve cymose partial inflorescences (Endress, pers. comm.).

Compound inflorescence. An inflorescence where there is primary, secondary and possibly higher orders of branches. The pattern of the different orders may or may not be of the same type.

Conflorescence. A compound inflorescence where the overall structure differs substantially from that of the individual branches of the inflorescence (see thyrse). Not equivalent to coflorescence (Troll, 1964) where the lateral branches repeat the structure of the main axis.

Cyme. A general term for a determinate inflorescence or a specific term that is equivalent to dichasium (a simple cyme). The many different uses of the term limit its usefulness. According to Endress (pers. comm.) a cyme is a partial inflorescence in which each axis order has not more than two lateral branches, but the number of axis orders is not restricted. Therefore, the term "compound cyme" is redundant. See also under "Dichasium".

Determinate inflorescence. An axis where the apical meristem aborts or is converted into a flower resulting in cessation of growth of that axis; corresponds to a monotelic inflorescence Weberling (1989).

Dichasium. A simple dichasium is a determinate partial inflorescence with two paired, opposite or subopposite lateral axis orders. The flowers may be pedicellate or sessile. The terminal flower may be missing or abortive. The lateral branches bearing flowers may be of equal developmental age or not exactly. In a compound dichasium the axis orders can be repeated many times. Such an arrangement has been called a "many flowered cyme composed of repeatedly branching simple dichasium units" (Simpson, 2006). This is also sometimes called a compound cyme. See also under "Triad".

Dyad. A solely descriptive term (morphologically noncommittal) for an inflorescence or partial inflorescence that bears two flowers, either pedicellate or sessile. Those with ebracteate peduncles may derive from two monads and have affinity with racemes or umbels (Kuijt,

1981). Those with a recaulescent floral bract on the peduncle may derive from a triad without a terminal flower (Kuijt, 1981). Examples include *Aetanthus* and some *Psittacanthus* (Loranthaceae).

Fascicle (adjective fasciculate). As defined in Judd et al. (2016) "a reduced, axillary inflorescence (either determinate or indeterminate) with flowers in a bundle or cluster and no obvious inflorescence axis". Kiger and Porter (2001) specify that the flowers are pedicellate and the whole inflorescence sessile or subsessile. Simpson (2006) suggests this inflorescence is raceme-like or panicle-like, but that the internodes are very short. This term is related to the superficial appearance of an inflorescence and only refers to the case where the pedicels are long but other axes are short and the branching pattern was not analyzed.

Glomerule. A dense cluster of flowers; a dense headlike cyme (Harris and Harris, 2001). A small, compact, head-like cyme; any dense, small cluster (Gleason and Cronquist, 1991). An inflorescence of sessile or subsessile flowers in which the internodes between flowers are very short, with flowers appearing congested (Simpson, 2006). A glomerule is not a precise morphological term, likely representing a condensed version of other inflorescence types (cymes, capitula, etc.). It is used here only for descriptive purposes.

Indeterminate inflorescence. An inflorescence with potentially unlimited terminal growth, producing flowers that usually mature from the axis base to the apex; corresponds to a polytelic inflorescence Weberling (1989).

Monad. A solely descriptive term (morphologically noncommittal) for an inflorescence or partial inflorescence unit with a single flower, either pedicellate or sessile, accompanied or not by a pair of prophylls (Kuijt, 1981; Kuijt, 2015). Lateral units of racemes or spikes may be called monads. Examples include *Cladocolea* spp., *Oryctanthus*, and *Dendropemon.*

Monochasium. A determinate, partial inflorescence in which each axis order has only one lateral branch, and these orders can be repeated many times. The terminal and lateral flowers may be pedicellate or not.

Partial inflorescence. The basic subunits of the branching system of an inflorescence (Troll, 1964) which may be single flowers, monochasia, dichasia, etc. This usage is somewhat problematic because it apparently includes even single axillary flowers, with or without bracteoles, thus limiting its usefulness to perhaps more complex inflorescences.

Prophyll. One of the two (or one in monocots) often minute foliar organs that may flank axillary axes in angiosperms, whether flowers, inflorescences, or vegetative ramifications (Kuijt, 2013). A type of bracteole but the two terms are not equivalent. Both prophyllar and non-prophyllar bracteoles occur in Santalales.

Syndesmy. A phenomenon found in thyrsoid inflorescences where the partial inflorescences and all their branches seem developmentally incorporated into the main axis and appear, so to speak, “fastened to it” (Troll, 1964). Troll recognized concaulescent, recaulescent and retrocaulescent syndesmoid cymes. Syndesmy was reported by SGP to be involved in the evolutionary development of fertile internodes in Phoradendreae.

Thyrse. A compound conflorescence where the main axis of this inflorescence is racemose whereas the lateral axes are cymes. See discussion of this type in Endress (2010 p. 228)).

Triad. In Santalales there are three morphologically distinct inflorescence units that bear three flowers each (Kuijt 1981).

a) The median flower lacks a bracteole and is flanked by two lateral flowers. The bracts of these lateral flowers are not modified prophylls but represent leafy organs of the inflorescence axis, the latter being axillary to a foliar organ. This unit represents a full

inflorescence rather than a partial one. Examples include *Cladocolea dimorpha*, *C. oligantha*, and *Viscum album*.

b) All three flowers are morphologically equivalent; the peduncle may or may not have a recaulescent bract. This type also represents a full inflorescence, and is comparable to a small umbel. Examples include several species of *Amyema*.

c) Two lateral flowers are are subtended by a prophyll each and are subordinate to the median flower; the latter's bracteole is usually recaulescent with the peduncle. This type of arrangement is a partial inflorescence and is comparable to the dichasium or triad as used here and in SGP. Examples may be seen in *Amylotheca*, *Gaiadendron*, *Nuytsia*, *Passovia*, *Psittacanthus*, and *Struthanthus*.

Phoradendreae (see Fig. 2)

Alveolus. A shallow cup or collar-like outgrowth on the fertile internode that bears a single flower. Referred to in SGP as *pits* or *fovea*, terms not previously used for *Phoradendreae*.

Apical flower. The distalmost flower above a fertile bract that occupies a median position; the primary axillary flower (Kuijt, 2003 p. 14).

Article or *Joint*. Defined by SGP as successive *metamers* along an individual inflorescence in Phoradendreae. This usage is apparently equivalent to a fertile internode.

Biseriate. An arrangement of flowers in one flower area of a fertile internode where two columns (series) are produced above the fertile bract, one on each side of a single apical flower. The apical flower has a 2/1 flower orientation (Eichler, 1868; Kuijt, 1961) vs. 1/2 for all subsequent flowers. Equivalent to the 1a seriation type (Kuijt, 1961, 1963).

Fertile bract. A scale leaf of an inflorescence subtending a fertile internode. Sometimes called a fertile scale leaf (Kuijt, 2003, p. 14).

Fertile internode. A flower-bearing inflorescence internode that, during development, elongates from its base that is situated above a pair of fertile bracts, thus seeming to "telescope out".

Floral column. Defined by SGP as "the longitudinal series that results when two or more floral rows are formed and aligned with each other." Apparently equivalent to floral series; however, this definition excludes the many uniseriate inflorescences especially in *Dendrophthora*.

Floral group. Defined by SGP as an "aggregation of one or more floral rows axillary to the subtending bract, which corresponds to a partial inflorescence." Apparently equivalent to flower area sensu Kuijt (2003, p. 14).

Floral row. Defined by SGP as "a transverse series of flowers in each floral group formed by an odd number of flowers (3, 5, 7, or 9)." As discussed herein, the concept of a floral row depends upon an interpretation that does not hold up to scrutiny.

Flower area. The region along one of the two sides of a fertile internode that is occupied by flowers (Kuijt, 1959). The number of flowers in this area can vary between one and dozens but are always topped by an apical flower. See Fig. 1.

Flower series or seriation. Referring to the arrangement of vertical columns of flowers on the fertile internode (Kuijt, 1959, p. 528). See also inflorescence types.

Inflorescence types. Referring to the flower seriation categories in Phoradendreae, Kuijt (1961) first gave numbers such as 1a, 1b, 2a, etc. and later (Kuijt, 2003) these were called uniseriate, biseriate, triseriate, and multiseriate (Fig. 1).

Intercalary flowers or inflorescences. Flowers arising on axes not completely specialized as inflorescences, i.e. where the axis continues into further vegetative growth (e.g. *Dendrophthora cupressoides*).

Intercalary meristem. Meristems localized in the nodal region between fertile or other internodes. Flower production is basipetal, usually in longitudinal series with the oldest at the distal end of the internode and youngest at the proximal end. In some *Phoradendron* species, regular seriation breaks down such that the entire annular surface produces a densely massed, irregular cylinder of flowers at the lower end of the flower area. See Fig. 1.

Lateral flowers. Flowers formed at positions parallel to the median plane of the fertile bract.

Median flower(s). A flower or vertical series of flowers produced in the median plane of the fertile bract.

Metamer. See also *article*. Apparently used by SGP as equivalent to a fertile internode. Rarely used in botany (an exception being found in (Bradford, 1998)). Not to be confused with metamere, a zoological term for one unit of a linear series of similar segments or to metamer (metamerism), colors with different spectral properties that are perceived to match.

Multiseriate. An arrangement of flowers in one flower area of a fertile internode where five or more, often irregular, series of flowers are produced above the fertile bract. Possibly derived from the triseriate type (Kuijt, 2003, p. 17), this has not received a separate seriation type number.

Peduncle. The sterile axis that bears the fertile internode(s) of the inflorescence. It may be simple (one internode) or compound (two or more internodes).

Serial accessory dichasia. Defined by SGP as “when two or more dichasia are formed, such ontogenetic unit repeats itself basipetally as serial accessory dichasia.” This requires the assumption that *floral rows*, representing dichasia in Phoradendreae, are distinct morphological units.

Triseriate. An arrangement of flowers in one flower area of a fertile internode where three vertical columns (series) of flowers are produced above the fertile bract. Equivalent to the 1b seriation type (Kuijt, 1961, 1963).

Uniseriate. An arrangement of flowers in one flower area of a fertile internode where a single column (series) of flowers is produced in a median position above the fertile bract. Equivalent to the 2a seriation type (Kuijt, 1961, 1963).

Definitions of Dichasium, Cyme and Thyrse by Other Workers

Dichasium

Bailey and Bailey (1976). Not defined per se. A dichasial cyme is a falsely dichotomous cyme, in which the axis bears a terminal flower between two more or less equal branches, the branches repeating the process one or more times (in a compound dichasial cyme) or bearing each only a terminal flower (in a simple dichasial cyme). The lowermost flower, terminating the primary axis, opens first.

Bell (1991). Not defined per se. See cyme (below).

Fernald (1950). A cyme with two lateral axes.

Gleason (1958). Dichasial. Indicating a cyme with two main branches.

Gleason and Cronquist (1991). A 3-flowered cymule in which the development of the terminal flower is followed by that of the two opposite or subopposite lateral flowers.

Harris and Harris (2001). A cymose inflorescence in which each axis produces two opposite or subopposite lateral axes.

Kiger and Porter (2001). Determinate and falsely dichotomous with each axial segment bearing a sessile terminal flower and either a pair of opposite pedicellate lateral flowers or a pair of opposite lateral branches.

Lawrence (1951, page 60). In its simplest form the primitive dichasium consisted of three flowers disposed in a cluster formed on a single peduncle by a dichotomous branching immediately beneath a terminal flower (Fig. 3a). From this simple dichasium there may be developed a more complex dichasium that is formed by “a repetition of the same apparent dichotomy in each lateral branch.” In nature, the dichasium may be simple or compound, ample or restricted, and it would be hazardous to speculate as to which form preceded the other in ancestral types. On page 749: a determinate inflorescence

represented by a false dichotomy with the first flower to open situated between 2 lateral flowers (Figs. 312e, 313b).

Rickett (1955). Typically three-flowered cluster composed of a peduncle which bears a terminal flower and, below it, two bracteoles which subtend lateral flowers. (The bracteoles may be abortive; and one or two flowers also may fail to develop.) A compound dichasium arises from repetitive branching of a simple dichasium.

Simpson (2006). A determinate inflorescence that develops along two axes, forming one or more pairs of opposite, lateral axes.

Stauffer (1963). Partial florescence, beginning with a flower with two prophylls which blooms first; from the axils of the two prophylls two flowers provided with prophylls of the second order follow, which bloom secondarily, and from whose prophyll axes four flowers of the third order emerge, etc.

Weberling (1989). A branching pattern such that only the two uppermost (often opposite) branches develop below the apex. If these (decussate or alternate) lateral axes only develop the two prophylls and their axillary shoots below their terminal flower, the dichasium appears to be similar to cymose branching.

Webster (1956). A cyme having two branches.

Cyme

Bailey and Bailey (1976). A determinate inflorescence, usually broad and more or less flat-topped, the central or terminal flower opening first. Cymes have many forms, however.

Bell (1991). A cyme is constructed sympodially. In its simplest form it consists of a series of flowers each borne in the axil of the bracteole of a preceding flower. Such a cyme is termed monochasial. If each unit of the sympodium bears two flowers, the cyme is dichasial, more than two pleiochasial. If such sympodial sequences are arranged along a

single monopodial axis the inflorescence is termed a thyrse or verticillaster if lateral branches occur in whorls.

Fernald (1950). A usually broad and flattish determinate inflorescence, i.e. with its central or terminal flowers blooming earliest.

Gleason (1958). A type of inflorescence in which each flower is strictly terminal either to the main axis or to a branch. (See raceme and racemose). Cymes assume many forms depending on the number and position of the branches. They are sometimes distinguished with difficulty from a racemose inflorescence, but may often be known by the position of the bracts opposite the base of the pedicel instead of below it.

Gleason and Cronquist (1991). A broad class of inflorescences characterized by having the terminal flower bloom first, commonly also with the terminal flower of each branch blooming before the others on that branch.

Harris and Harris (2001). A flat-topped or round-topped determinate inflorescence, paniculate, in which the terminal flower blooms first.

Judd et al. (2016, page 622). Determinate, compound inflorescence composed of repeating units of a pedicel bearing a terminal flower and below it, one or two bracteoles; each bracteole is associated with an axillary flower, and further bracteoles, and so on. Page 86: cyme (or determinate thyrse), the lateral branches of which are composed of usually numerous three-flowered units, usually showing opposite branching. Cymes can be of many different shapes because of differences in their branching patterns.

Kiger and Porter (2001). Determinate and constituting a compound dichasium or monochasium, the flowers maturing from the center outward (i.e., the distal or inner flowers maturing first); often more or less flat-topped.

Lawrence (1951). A broad, more or less flat-topped, determinate flower cluster, with central flowers opening first.

Radford et al. (1974). A cymule is a simple, small dichasium. Neither cyme nor dichasium are listed or defined.

Rickett (1955). A compound, more or less flat-topped sympodial inflorescence, sometimes simulating a compound umbel but the branches less regularly disposed.

Simpson (2006). General term for a determinate inflorescence.

Weberling (1989). A cymose partial inflorescence, which develops no further leaves apart from the prophylls and thus has only one or two possibilities for lateral branches. Cymose branching is where "branching only takes place from the axils of prophylls, i.e. branching is confined to 1 or 2 lateral branches".

Weberling (1989). A cluster of flowers in which each main and secondary stem bears a single flower, the bud on the main stem blooming first, as in phlox and sweet William.

Thyrse

Bailey and Bailey (1976). A dense, paniclelike inflorescence in which the main axis is indeterminate and the lateral axes are determinate, i.e., cymose, as usually in *Buddleia*, *Syringa*.

Bell (1991). See cyme above.

Fernald (1950). A contracted cylindrical or ovoid and usually compact panicle as a cluster of grapes.

Gleason (1958). A compound inflorescence composed of cymes racemosely arranged; also commonly but loosely used to designate a compact panicle.

Gleason and Cronquist (1991). An elongate, narrow, mixed panicle, consisting of a series of racemosely arranged small cymes.

Harris and Harris (2001). A compact, cylindrical, or ovate panicle with an indeterminate main axis and cymose subaxes.

Kiger and Porter (2001). An elongate, indeterminate main axis bearing numerous lateral branches, each the principal axis of a cymose subdivision.

Lawrence (1951). Compact and more or less compound panicle; more correctly a paniclelike cluster with main axis indeterminate and lateral axes determinate, as in most lilacs.

Radford et al. (1974). A many-flowered inflorescence with an indeterminate central axis and with many opposite lateral dichasia.

Rickett (1955). A compact panicle of more or less cylinidrical form.

Simpson (2006). A secondary inflorescence with an indeterminate central axis bearing opposite, lateral, pedicellate cymes, e.g. in *Echium* (Boraginaceae), *Penstemon* (Plantaginaceae).

Stauffer (1963) = cymo-botrys (Eichler), pleiochasium (Parkin pro parte, Bolle pro parte, Takhtajan, non Eichler) Inflorescence of the main axis ending with or without a terminal flower, monopodial in any number (minimum 1). Bearing dichasia or monochasia, which can be reduced to triads or individual flowers apically. From the terminal flowers of the lateral axes of the first order, the basal open first, then ascending the others.

Weberling (1989). An indefinite complex inflorescence with cymose branches on a dominating main axis.

Webster (1956). A flower cluster in which the main stem is racemose and the secondary stems are cymose, as in the lilac.

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