

Santalaceae.

By

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With 17 Figures

Santalaceae R. Br. Prodr. Fl. Nov. Holl. (1810) 350.

The most important general literature.

Endlicher, Gen. Pl. (1837) 324 und (1840) 1378. - A. De Candolle, Note sur la famille des Santalacees, in Bibl. univers. de Geneve, Sept. 1857 (Flora [1857] 616); 8. in De. Prodr. XIV. (1857) 619-692. - Baillon, Memoire sur les Loranthacees, in Adansonia 11. (1861-62) 330-381, 111. (1862-63) 50-128. - Bentham, Flora austral. VI. (1873) 211-231; 8. in Bentham et Hook. f., Gen. Pl. III. (1880) 217-231. - J. Miers, On some genera of the *Olacaceae*, in Journ Linn. Soc. XVII. (1878) 126-139, T. 3-7. - Eichler, Blüthendiagramme 11. (1878) 537-542. - G. Hieronymus in E. P. 1. Aufl. III. 1. (1889) 202-227.

Characteristic features. Flowers bisexual or by abortion unisexual, polygamous, monoecious or dioecious, radial. Flower axis (receptacle) rarely in male flowers or with flat, inferior ovaries, mostly sunken, dish-shaped or jug-shaped to tubular, not extending over the ovary or to long tubular. Perianth simple; tepals 4 or 5, rarely 3, valvate in the bud, later concave, inward curved or spread, usually at the base behind the stamens, with a tuft of soft hair \pm attaching to the anthers. Stamens as many as the tepals, these basically basifixed; Filament threadlike or band-shaped, often also very short; Anthers at the base or in the proximity of the base at the back attached, dithecal, pollen sacs individual or only each thecum with a longitudinal fissure itself opening. Disk epigynous or perigynous, of very different construction. Ovary inferior or half-inferior or (in the Anthoboleae) superior, with the base the disk sunken (in it), one locular; Style cylindrical, conical or very short; ovules usually 1-3 (rarely 4 or 5), hanging from the summit of a central, often striculate and twisted placenta, without integuments, always only one develops, with the Anthoboleae only a basal ovule. Fruit not dehiscent, nut or drupe. Seed 1, without seed coat, with plentiful, fleshy endosperm, in which lies the often inclined, embedded embryo with root arranged upward; cotyledons usually narrow, approximately terete, sometimes very short. - Trees, shrubs or herbs, probably all parasites or half parasites. Leaves alternate or opposite, undivided, sometimes reduced to small, deciduous scales, without stipules, mostly glabrous. Flowers usually small to very small, axillary or in racemes, capitulae, umbels (**Scheindolden**) or panicles; bracteoles usually present, every now and then united with the bracts into a pre-assembled "Vorkelch" (calyculus?) or cupular "perianth" (becherhülle).

Vegetative organs. The germination takes place with *Thesium* (cf. Th. Irmisch in Flora XXXVI. [in 1853] 522) underground, the cotyledons are narrow; a quite long hypocotyl is developed, the primary root penetrates quite deeply into the ground and ramifies. The seeds of *Thesium* germinate only if they come to the ground immediately after maturity (compare with Heinricher in Ber. Deutsch. Bot. Ges. XVII. [1899] 247; Schulle in Flora CXXVII. [1933] 172ff.).

Haustoria are already prematurely put on the side roots in all Santalaceae (cf. with "Parasitism"). First, root hairs exist on the young root parts in more or less large numbers, before

the activity of the haustorium starts. With *Exocarpus cupressiformis* lanceolate leaves are developed as with the young plant of *Thesium* according to M. Benson (see Lit. at "parasitism"), which become gradually smaller on the side branches, until they are nearly completely suppressed in the adult stage. According to Barber (see Lit. under "Parasitism") germination takes place as follows with *Santalum album*. The cotyledons remains in the seed, the rather long hypocotyle is curved in the upper part, in the lower straight part thickened and gradually carrot-like as it takes up the nutrients from the seed. With the elongation of the hypocotyle the seed drops, at the end of the hypocotyl stands the "petiole" (Stiehl) of the cotyledons. The nutrients stored in the hypocotyle permit a pulled young plant to live for over one year in pure sand. Haustoria are numerous set on the recent roots, also without host plants in the vicinity.



Fig. 27. Seedling of *Santalum album* L. With c the stalks of the cotyledons. (After Barber.)

Herbaceous to tree-like forms belong to the Santalaceae. Also with the latter [term] (*Acanthosyris*, *Santalum*) is such height usually not meaningful; *S. album* occasionally reaches a height of up to 30 m. *Acanthosyris* develops large leaf-axillary thorns. The smallest form is *Nanodea muscosa* in southernmost South America, a small herb with creeping, branched stalks and linear leaves. Frequently in Santalaceae under xerophytic living conditions the flabellate (Rutenstrauch, literally "switch shrub") form is developed, the leaves are more or less "revertive composed" (**rückgebildet**), often of tiny scales in Santalaceae (*Anthobolus*, *Choretrum*, *Leptomeria*, also individual *Thesium* species in South Africa; the same applies to the parasitic *Phacellaria*). Otherwise the leaves are narrowly more linear (*Thesium*, *Quinchamalium* etc.) up to large, ovate to elliptic leaf forms and usually leathery, entire, and pinnately nerved (*Santalum*, *Henslowia* in part, *Acanthosyris* etc.). The leaves are alternate or opposite, also frequently the latter position is not regularly fixed. Remarkable are the thick large, rhombic, spiny at the corners leaves of *Jodina*. Very strong difference in the construction of the vegetative organs is found in individual groups of *Exocarpus* and *Thesium*. A set of species of *Exocarpus* develop large phylloclades, while their leaves diminish completely; *E. latifolius* possesses 3-8 cm long, elliptical leaves, (whereas) other Australian species carry only small scale leaves. The European *Thesium* species (see also Čelakovsky, Über Thesien, in Lotos XIII. [1863] 120-127, 133-136) are usually persistent herbs of small height. Leaf and flowering stems die in the autumn up to a shorter or longer basis and from the survivors rapidly start forming from concatenated basal sympodial rhizomes. Now in the axil of buds are formed prophylls standing close together, then the stalks of the next year become compacted, the rhizome becomes short membered (*Th. alpinum*, *Th. ramosum*). Or the stacks do not die so deeply, the prophylls stand farther away; the rhizome consists then of more stretched members (*Th. pratense*, *Th. humifusum*). Finally also the axil base in the lower part can have very stretched, thin membered, prostrate, and creeping runners (*Th. ebracteatum*, *Th. intermedium*); the upper buds become shorter shoots, the lower runner-like shoots. For *Th. intermedium*, Irmisch (Flora XXXVI. [1853] 522) pointed out the fact that already the cotyledons carry buds in their axils and that on the hypocotyl, and also at the top of the adventive root, buds seem to appear. The habits of the numerous *Thesium* species of South Africa, which are partly strongly xerophytically designed, are very diverse. Related forms, which are similar to the European, their branches occur often thorny and their leaves are reduced to small scales come to over a meter-high ["knapweed" (*Centaurea*)] subshrubs, (*Th. lineatum* L., *Th. rigidum* Sond.)

or even become hard-spiny (*Th. spinosum* L f.).



Fig. 28. *Arjona tuberosa* Cav.
Basal part of a flowering
(flourishing, thriving) plant; nat.
size. (After Skottsberg.)

On the other hand again, very broad, nearly roundish leaves occur with *Th. euphorbioides* L., which become nearly 3 cm long. The habit is strongly determined also by the form of the inflorescence (see below). Some species of *Arjona* possess underground tubers, which are eaten by the native Patagonians (see Skottsberg in Svensk Bot. Tidskr. X. [1916] 520-528). *A. tuberosa* develops threadlike runners from the underground parts of the rhizome, in the axils of small scale leaves, which thicken turnip-like into a tuber at the ends. This tuber can attain full growth then later grow out to a flowering and leafy shoot (see Fig. 28). One sees at the base of the branch beside the tuber a root bundle with haustoria and in the axil of the underground scale leaves the new young runner; at the base of the tuber is the remainder of the dead runners, which one recognizes as forming the tuber. The runner can become over 30 cm long. With *A. patagonica* not only is the point of the runner constructed as sharply as the described tuber, but the whole runner is more or less thickened.

The Santalaceae are glabrous or the pubescence is usually weak; stronger wooly to downy pubescence is with *Quinchamalium* species, with *Cervantesia*, and on the buds of *Pyrularia edulis*. Individual *Exocarpus* species are

distinguished by bundle hairs, which develop in small groups from neighboring epidermal cells and are small (narrow) and single-celled.

Anatomical Conditions.

Literature. G. A. Chatin, Anatomie comparée des végétaux (1856-62) 297-416, T. 56-73. - M. Behm, Beiträge zur anatomischen Charakteristik der Santalaceen, in Bot. Centralbl. LXII. (1895) 65-74, 97-107, 129-139, 161-170, 193-210. - G. Volkens in Notizbi. Bot. Gart. u. Mus. Berlin-Dahlem Nr.9. (1897) [Anatomie des Holzes von *Osyris*]. - H. Solereder, Syst. Anatomie der Dicotyledonen (1899) 823-831. - H. Stone, The timbers of commerce and their identification (1904) 190-192, T. XII. - H.v. Guttenberg in Engl. Bot. Jahrb. XXXVIII. (1907) 419-421 [*Osyris alba*]. - v. Brehmer in Wiesner, Die Rohstoffe des Pflanzenreiches, 4. Aufl. II. (1928) 1383-1388 [Holz von *Santalum*].

The epidermal cells of the leaves are usually not strongly thickened laterally, but are more strongly so outward. They are provided all around with thickened walls, e.g. with *Exocarpus*, *Jodina*, and *Osyris*. A usually collenchymatous two-layered hypodermis is present with *Henslowia*, *Jodina*, and *Santalum*. For the stomata, each guard cell pair is on both sides of or accompanied by several columns of parallel subsidiary cells. Frequently the stomata are oriented perpendicularly to the longitudinal direction of the leaf or the axil. Details about the construction of the stomata of *Osyris* are to be seen with v. Guttenberg l. c. The mesophyll is differentiated into multiple palisade and spongy tissues, but occurs also not rarely in isolateral leaves, e.g. with *Arjona*, *Jodina*, and *Leptomeria*. With some *Henslowia* species, a homogeneous tissue of roundish cells is present, equally the leaf tissue is homogeneous, from roundish (e.g. *Th. montanum*) or consisting of more elongated palisade-like cells with nearly all species of

Thesium; with *Th. alpinum* palisade and spongy tissues are distinctive. With *Osyris alba* the mesophyll exists nearly only of palisade in 6-8 and still more tiers from an epidermis to the other one or it lies in the middle of the leaf with 1-2 layers of roundish cells between the vascular bundles. *Cervantesia* is distinguished through particularly long three-layered palisade, as well as loose spongy tissue. Besides crystals in the form of druses and unicellular crystals, silica bodies seem to occur in the mesophyll of many genera, to siliconized thickenings of the cell wall, which can protrude far to the inside of the cell and finally fill these out nearly completely. Several to many of such cells can together form silica clumps. With most genera, tracheids with netlike or spiral wall thickening arise at the end of the nerves. The terminal tracheids usually form oblong groups of 2-5 cells. With some genera (*Thesium*, *Quinchamalium*, *Osyris*) also further cell courses of such storage tracheids are present parallel with the bundles of the nerves and independently of these in the leaf. The trunk core can consist of unligified or thickened and lignified cells (e.g. *Osyris*). In the wood flexible elements, and strongly thickened fiber tracheids with bordered pits form the substantial component. Small lumened (?) vessel elements are individually scattered (dispersed); their diameters amount to 0.02-0.07 mm with *Santalum album*, for *Osyris tenuifolia* Volkens indicates a middle diameter of 0.06 mm. The perforation is simple, circular or elliptical. Wood parenchyma is little present. The ray initials are narrow. After Wiesner l.c. with *Santalum album* probably all elements, particularly the parenchyma cells, contain the fragrant sandal oil. This appears either in small ones [cells], the wall enclosing the droplets, or in larger ones, filling in masses the lumen of the fibers and parenchyma cells here and there. The primary cortex contains plentiful assimilation tissues in the xerophytic leafless Santalaceae. On the border of the primary and secondary cortex are isolated groups of phloem cells, which are very strongly developed, e.g. with *Leptomeria*. The secondary cortex is never laminated by groups of phloem; only with *Omphacomeria* and *Santalum* are there individual phloem cells or small groups.

Parasitism and anatomy of the suction organs.

Literature. W. Mitten, On the economy of the roots of *Thesium linophyllum*, in Hook. Lond. Journ. of Bot. VI. (1847) 146-148, T. 4 (Wiederholt in Ann. Sc. Nat. 3. ser. VII. [1847] 127-128). - Th. Irmisch, Keimpflanzen von *Thesium montanum*, in Flora XXXVI. (1853) 522. - Chatin, Anatomie comparée des végétaux Livr. 8,9. (1857, 1858). - A. Pitra, Über die Anheftungsweise einiger phanerogamen Parasiten an ihre Nährpflanzen, in Bot. Zeitung XIX. (1861) 69-72. - H. Graf zu Solms-Laubach, über den Bau und die Entwicklung der Ernährungsorgane parasitischer Phanerogamen. Teil *Santalaceae*, in Pringsheim's Jahrb. wissensch. Bot. VI. (1867-68) 539-560, T.32-33. - John Scott, Untersuchungen über einige indische *Loranthus*-Arten und über den Parasitismus von *Santalum album*. Mitgeteilt von H. Grafen zu Solms-Laubach, in Bot. Zeitung XXXII. (1874) 145--150. - Leclerc du Sablon, Sur le développement des suçoirs du *Thesium humifusum*, in Bull. Soc. Bot. Fr. XXXIV. (1887) 217-220. - S. Kusano, On the parasitism of *Buckleya Quadriala* B. et H. (*Santalaceae*), in Tokyo Bot. Mag. XV. (1901) 42-46; Studies on the parasitism of *Buckleya Quadriala* B. et H., a santalaceous parasite, and on the structure of its haustorium, in Journ. Con. Sc. Imp. Univ. Tokyo XVII., Art. 10 (1902) 42 S., 1 T. - A. Fraysse, Sur la biologie et l'anatomie des suçoirs de l'*Osyris alba*, in Comptes Rend. Ac. Sc. Paris CXL. (1905) 270-271; Contribution a la biologie des plantes phanerogames parasites, Thèse Paris (1906) [not seen]. - P. Pizzoni, Contribuzione alla conoscenza degli austori dell'*Osyris alba*, in Ann. di Botanica IV. (1906) 79-98, T. 3. - C. A.

Barber, Studies in Root-Parasitism. The haustorium of *Santalum album*. Part I. Early stages, in Mem. Departm. Agric. in India. I no. 1, Part I (1906) 1-30, T: 1-7; Part II. The structure of the mature haustorium and the inter-relations between host and parasite, l.c. no.1, Part II. (1907) 1-58, T.I-16. -Margaret Benson, Root Parasitism in *Exocarpus*, in Ann. of Bot. XXIV. (1910) 667-677, T.55. - L. Planchon, Sur l'*Osyris alba* L., in Bull. Soc. Bot. France LIX. (1912) 108--112. - G. Hedgcock, Parasitism of *Comandra umbellata*, in Journ. Agric. Res. Washington V. (1915) 133-135. - G. Haberlandt, Physiol. Pflanzenanatomie 6. Auß. (1924) 233, Fig. 100 (Längsschnitt durch ein Haustorium von *Thesium pratense*). - A. Sperlich, Die Absorptionsorgane der parasitischen Samenpflanzen, in Linsbauer, Handbuch IX. 2. (1925). - Kerner, Pflanzenleben I. (1890) 164.

Only a few Santalaceae are parasites which grow like Loranthaceae on the branches of trees; here belong the genera *Phacellaria* and *Henslowia* (probably with the exception of *H. frutescens*). The foliage leaf can probably be developed with a set of *Henslowia* species, with other species as well as with *Phacellaria* they are very small or completely diminished, so that these forms live perhaps perfectly parasitic. About their food intake, no details are well-known. From a whole number of other genera of Santalaceae (*Thesium*, *Santalum*, *Osyris*, *Comandra*, *Arjona*, *Quinchamalium*, *Exocarpus*, *Buckleya*) it is well-known that their species are green, rooted in the earth hemiparasites, which sit on the roots or underground stem parts (rhizomes) of other plants and extract from them nutrients by means of haustoria. Probably this applies to all Santalaceae except the two genera specified above. From the parasitism of *Thesium*, so much I see, W. Mitten gave first in 1847 a short representation; he pointed out that the same plant of *Thesium* can associate with different host plants by its haustoria; on a plate a picture is given of the penetration of the sinkers. But probably at that time the parasitism of *Thesium* cannot have been unknown. Irmisch (1853) says, without mentioning Mitten: "*Thesium montanum* a well known parasite

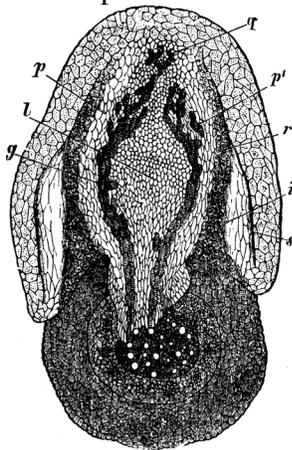


Fig. 29. *Thesium pratense* Ehrh. Cross section of a root (with g the vascular bundle of the same) with the longitudinal section of it, the halved haustorium on a dicotyledonous host root (40/1). - from E. P. 1. Aufl. III. 1. Fig. 136.

on the roots of different plants"; he also illustrates haustoria from still completely young plants. The parasitism of *Osyris alba* was discovered by Planchon (Bull. Soc. Bot. France V [1858] 289, 445). From the anatomy of the *Thesium* haustorium, Chatin (1857, 1858) first gave a demonstration, he was, however, on some points inaccurate and incorrect; the representation is substantially better with Pitra (1861). The two works, which promoted most substantially our knowledge of the development and anatomy of the haustorium, are from Count Solms-Laubach (1867-68) and Barber (1906 to 1907). Regarding host plants, Santalaceae are not discriminating; for all examined genera it could be stated that their roots associate by their haustoria with the roots or rhizomes of the most diverse neighboring plants; Barber indicates over one hundred host plants for *Santalum album*; likewise Pizzoni (gives) numerous host plants for *Osyris alba*. Earlier, the occasionally expressed view that hemiparasitic Santalaceae can also live independently in the ground without foreign roots, has not been confirmed; Barber showed for *Santalum* and Kusano for *Buckleya* that cultures of young plants prosper only if these can come into

contact with other plants. Substantial damage to the host plant generally does not arise; However,

L. Planchon (1912) reports that grape vines of certain sorts can die in the south France if they stand where a lot of *Osyris* grows; a closer examination proved that *Osyris* particularly becomes connected to these vines and takes away from them so much water that they can become momentarily desiccated. Following Kusano, the cambial activity of the host plant is increased through haustorial contact with *Buckleya*; here the cross section shows the broadest wood and the broadest cortex.

The life span of the haustorium is limited with smaller plants like *Thesium* species; conversely for *Buckleya*, Kusano proved that they can remain functional at least 15 years (he showed then a clear thickness in growth, see below). The haustorium develops laterally on the roots; they can become by that fact apparently terminal such that the small root tips going beyond the haustorium later dry and drop. They are approximately alike with the different genera. One can at first distinguish two parts, the holdfast and up to the woody part of the host plant a penetrating sinker or Saugfortsatz (“suction extension”). The holdfast has the form of a more or less conical or more flat-pressed wart, which becomes with *Santalum* to one cm high, with *Thesium* it remains smaller. It sits with its surface area on the host root and puts itself forward with two broad lobes over its rounded surface; thin roots can be enclosed mantel-like. If many mechanical thickened elements occur in the outside layers of the host plant, which can be dissolved with difficulty, then new attacking lobes are formed around and beside the core within the first haustorial lobes; a compound haustorium thus develops for the dissolution of the outside layers of the root (Fig. 30). With *Santalum* and *Buckleya* the procedure can repeat itself several times. With *Thesium* the haustorium usually remains completely simple; but, as already Pitra and Count Solms-Laubach noticed, occasionally compound haustoria can also develop here, if a

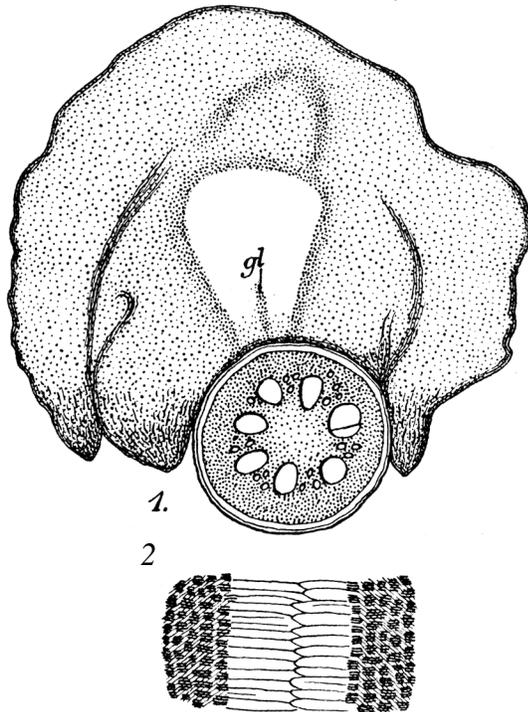


Fig. 30. 1 young haustorium of *Santalum album* L on a bamboo root; the haustorium begins to be built up; the arrangement of the gland region in the center of the core (gl). 2 extended cells from

gramineous root is attacked. Between the folds of the lobes can be jammed with cortical parts of the attacked roots. Later a more or less cylindrical or flat plug penetrates from the middle of the attempted surface as a “suction extension” (Saugfortsatz) or sinker up to the woody part of the host plant. The roots of Santalaceae are usually richly branched out and from these put on a large quantity of haustoria, of which, however, many have no opportunity to connect with host plants, and thus remain functionless.

About haustorial development, the following is to be noticed. It forms in the root by stretching and division of the cells of the pericycle, endodermis and cortex, and thus corresponds in its formation not to a side root but is to be regarded as an appendix of the root; a completely young haustorium of the genus *Santalum*, with which Barber represented in detail the history of development (the other genera did not yield substantially), is by chance pyriform in shape, turned to the narrower side of the root. The center of the broader end holds a central core of cytoplasm-rich cells, the cells of the surrounding

the gland region of the core. (after Barber.) cortex contain starch. To the core run two vessel strands from the mother root. If a host root is reached, then the core sets itself upon the cortex, puts itself forward lobed over each side of the root, as mentioned above. Between the core and the root a narrow space remains; it goes out namely from the extreme cell layers of the core (or if these die, from the next cell layer) root hair-like, which set themselves over the small gap away on the host root and eliminate dissolving enzymes. The solvent activity is then particularly promoted by the development of a gland region in the center of the core, those usually, but not always effected (also Solms suggests the development of such a region with *Thesium*). Here two rows of cytoplasm-rich cells extend transversely to the longitudinal axis of the haustorium (see Fig. 30); these also remain cytoplasm-rich further at the base, outward and inward too, where the rows are pushed together, lead it for bright secretion contents; here they are then dissolved and the secretion are in the gap in the center of the gland region. Around the core the haustorium becomes continuously larger; at each side a narrow volume of longer stretched cells, which supply the procambial strands, develops from which then the vessel strands develop, which are located in connection with the vessel strands outgoing from the host root. The haustorium can already be compound at this stage. Now advances the wedge-shaped sinker into the inside to set upon the wood of the host root and begins at the same time in the inside haustorium around a further differentiation of the tissues. The internal part of the haustorium extends around, as said, rapidly, if penetration becomes possible, which expresses part against it remains as it is; it must come thus to tearing up in the tissue. The cortex divides clearly into an outside region of continuous cells and an internal region of turgescient, content-rich cells. In addition it occurs that the core growing into the thickness exercises a strong outward pressure; the cells at the border of the internal and outside cortex are squeezed together and form a clear separation strip.

If the sinker reaches the wood of the host root, then it sets itself on this or can spread also around the wood body lobe (also with *Osyris*). Individual strands in the sinker tissue will on the one hand direct and enter the procambial strands of the core, and on the other hand connect with the wood of the host. Thus develops the finished haustorium, whose pictures have been drawn by Kusano for *Buckleya*, Margaret Benson for *Exocarpus*, count Solms for *Thesium*, and Barber for *Santalum*. Our illustration Fig. 29 represents a simple, compound haustorium from *Thesium* from count Solms Laubach, whose form essentially recurs with the other genera; the sinker lies in the woody part of the root. **First a cortex body is to be differentiated from a core. The first mainly forms around that lobe of the host root surrounding part of the haustorium.** It is on this the inner, to smaller polygonal, fewer strong prominent cells (r) and the outside situations formed differentiated from larger parenchyma cells with larger starch grains. These two zones are sharply separated from each other, a strip from crumpled, collapsed, gradually dissolving cells (s) and from air-prominent (aerenchyma?) large parenchyma cells between them, which enclose usually a larger air gap (i), is or lie close to the same (see above). Down at that parts of the cortical lobe, which lies close to the host root, ignore both zones of the cortex into one another. In the core haustorium around likewise three different tissues are to be differentiated. In the inside the nuclear parenchyma (l) lies, which is formed from small, closely closed-up, plasma-rich cells. On this parenchyma borders the vascular strands, the haustorium of *Thesium*, *Osyris* and *Santalum* possesses two strong, flat, converging strands only diverging curved in the periphery of the core in the sinker; they approach the woody part of the host root in the shortest way; with *Exocarpus* only two opposite strands are missing, but the vascular strands completely surround the parenchymatous internal part of the haustorium. The transition of the vessel system of the mother root to that of the haustorium forms around netlike thickened tracheids without

bordered pits. Also the tracheids of the haustorium around in the core and in the sinker have loosely netted thickened walls; they are short and arranged irregularly in the core, in the sinker they are longer and more regular. After M. Benson, who studied anatomy more exactly with *Exocarpus*, are the tracheids only thickened in the lignified parts, while the areoles lying between them remain unligified. The tracheids contains pellets of amyloextrin in a protoplasmic wall covering, but no cell nuclei. They serve thus also the migration of organic substances from the host and partially deposit this in pellet form; their function is thereby as phloem and xylem together. Therefore M. Benson suggests for it the name phloeotracheid. With *Thesium* the pellets are smaller and less numerous in the phloeotracheids. That becomes perhaps understandable, if one considers that *Exocarpus* lives in very dry climate and soil; with *Exocarpus* above all the water from the host is to rise more easily; the dissolved carbohydrates, which are already sufficiently present in the upper parts of the plant, are left. The phloeotracheids serve then mainly as filters. With *Thesium* the haustorium is small and probably does not remain active for a long time. With woody forms, like *Santalum* and *Buckleya*, they can become larger over a long time and function for a long time; it was already mentioned above that Kusano considers them functional from the anatomy of the root, which they sit on, with *Buckleya* at least 15 years long. Then a thickness growth due to cambial tissue appears. Already count Solms noticed for *Thesium* that on the tracheid strands border outside a cambial zone reminiscent of a tissue of thin-walled starch-fabricating cells which consists of two intergrading tiers, and indeed exhibits an internal more stretched cellular (p¹) and an outer parenchymatous cellular included (?) tier. The internal cells are real cambium, which makes possible a secondary, the core and also the cortex grow increasing thick. The first elliptical haustorium of *Buckleya* becomes roundish and then transverse-elliptical, where a growth in length does not take place. In the older haustoria rows of parenchyma cells lie such as ray initials between the tracheids. The older haustorium is surrounded in tiers by cork cells.

Floral conditions. The flowers of Santalaceae rarely stand as terminals of short branches (e.g. female flowers of *Buckleya*, female or bisexual flowers of *Osyris alba*); usually they are located in the bract-bearing axils (hochblattartigen), sometimes very small or almost rudimentary, more rarely deciduous, seldom foliage leaf-like bracts (Deckblättern) or even from real foliage leaves. Usually two lateral prophylls are available on the flower; prophyll-less are for example the flowers of *Thesium ebracteatum*. Since prophylls are often sterile, simple racemes exist (e.g. *Thesium alpinum* among other species), to spikes (species of *Arjona* and *Myoschilos*), small capitula (*Quinchamalium*), cymes (male flowers of *Buckleya*) and most frequently from such compound flower conditions (e.g. racemes of the male flowers of *Osyris*). Upon fertilization the prophylls can form dichasia, which are sometimes formed from few flowers (*Nanodea*), frequently however as partial flower conditions to racemose, capitulate, etc. Inflorescences are arranged or with very shortened internodes or form more or less rich-flowered clusters. The bracts (Deckblätter) often grow up along the pedicels of their flowers and form here with the prophylls a kind of involucre of the flower (e.g. with many species of *Thesium*, Fig. 42). With *Quinchamalium* the prophylls and the bract (Deckblatt) of a “calyx-cup” (Becherkelch) are fused into a calyculus, which appears 4-merous on the back of the flower due to the formation of a commissural tooth (see Fig. 43). Particularly remarkable is the four-leaf involucre developed on the female flowers of *Buckleya*; the leaves are probably to be interpreted as prophylls from two aborted side flowers of a dichasium (see with the genus). With 3 and 5-merous flowers usually a tepal falls before the first bract (Deckblatt), while the remaining tepals distributes

themselves accordingly; with 4-merous flowers a tepal can likewise fall before the bract (Deckblatt), the flower thus is orthogonally posed (*Thesidium*, *Leptomeria*, and *Exocarpus* species, after A. DeCandolle and Eichler), more frequently however the tepals stand diagonally to the transverse axis (*Thesium*, *Santalum*, *Osyris*, *Comandra* among other genera).

The stamen is always superposed just like with the Loranthaceae tepal isomer. The filament is \pm long and filiform or also short and thick; it is attached at the base of the tepals. The locules (pollen sacs) of the thecae dehisce either together, therefore with longitudinal fissure in the septum, so that the dehiscing locules are connected by two lateral flaps surrounding the cavity, or each loculus dehisces by itself, namely with longitudinal fissure or with a more or less terminal transverse gap. The pollen grains are tetrahedral or also ellipsoidal with blunted corners or nearly spherical, their membrane (exine?) is smooth or also finely netted thickened. H. Fischer (Beitr. zur vgl. Morphol. der Pollenkörner [1890] 55) writes about the tetrahedrons of *Thesium*: Their edges are composed “of six folds, which flow together at the corners and exhibit the greatest thinning here; the sides form four sharply bordered, rounded triangles with fine but clear netted sculpturing.” With most genera of Santalaceae one finds at the base of the tepals behind the stamen, a hair tuft of soft upright hairs which adhere to the anther at the upper end. After Ph. van Tieghem (Origine exodermique poils poststaminaux the sépales chez les Santalacées, in Journ. de Bot. XI. [1897] 41-45) takes their origin not from the epidermis, but from an underlying cell layer, which consists here at base of the tepals of high and broad cells. The cells elongate and burst from the eventually deciduous epidermis. The long hairs remains single-celled and are very cytoplasm-rich. An exception is the genus *Arjona*; here the hairs behind the stamens are of epidermal origin (*Arjona* with the genus *Quinchamalium*, in which the hairs are completely missing, forms a special family following van Tieghem). In the genus *Thesium* appears from the above mentioned hairs still a different trichome form (M. F. Ewart, On the staminal hairs of *Thesium*, in Ann. of Bot. VI. [1892] 271-290, T. XVI; see also about *Thesium* in the systematic part). Which concerns first the hair standing behind the stamen, then their subepidermal origin comes out clearly from the description of the authoress, but is not suggested by some figures. For *Thesium montanum* Schulle describes (Flora CXXVII. [1933] 148) the emergence of the single-celled trichome from surface cells. The gluing of the ends of the hair with the anther is due to the development of a resinous and oily secretion in the hair, which is withdraw through breaking the cap of the hair off easily. With a part of the species of the South African and tropical African section *Frisea*, in place of the hair tufts, the shorter or somewhat downward arranged hairs form a perfect ring (wreath) around the receptacle approximately at the height of the insertion of the stamen; they cannot because of their length and position come into connection with the anthers. In addition, with the genera of section *Frisea* at the top part of the tepals, tufts of the downward arranged hair are present. About the meaning of these trichomes, see about pollination.

The ovary is always one-locular; from the number of ovules, which usually amounts to (2-) 3 (with the Anthoboleae 1), and the number of stigma lobes, one can usually assume it is assembled from three carpels (*Thesium*, *Arjona*, *Comandra*, *Jodina* and others); but also appears the number of the stamens and tepals corresponding to the four- and five-number (*Buckleya*, *Colpoon*, species of *Santalum* among others). From the four-merous flowers of *Nanodea* is the ovary dimerous (? **dimer**). The ovary is, with the Anthoboleae, superior and only sunken a little into the disk, with *Santalum* and with several other genera at first or also still later half-inferior, with most genera more or less completely inferior. The flower axis (receptacle) thus surrounds the outside of the ovary, which is completely united with it. Usually the ovary only takes the inside of these at the top of the flower axis; the flower axis is fleshy in the lower part and

changes into the pedicel. Usually the receptacle over the ovary is extended and bears only the fleshy disk; with *Thesium*, *Quinchamalium*, *Arjona* as well as with *Santalum* however, the receptacle is transformed above the ovary into a short campanulate or an extended long tube. The ovules, from which in each case the seed continues to develop, are naked, represented thus as an integument-less nucellus; they hang down (with exception of the Anthoboleae) from the point of a free-central placenta. Goebel (*Organographie* 3. Aufl. [1933] 2043) regards a small depression at the summit of the nucellus as the remains of a micropyle, so suggesting it would be a thick integument. The placenta following van Tieghem is not of axillary construction, but is carpellary in origin, thus fused from parts of the carpel, those existing in same number as the ovules (see Ph. van Tieghem, *Anatomie de la fleur la Santalacées*, in *Ann. Sc. Nat.* 5. Sér. XII. [1869] 340-346). One can draw a comparison with the Primulaceae, with which after Warming, however, the axis takes part in the development of the central placenta. After Schulle (*Flora CXXVII.* [1933] 143, 154), who more exactly studied the history of the development of *Thesium montanum*, the indication of van Tieghem is unproven. Carpel and flower axes grow together so intimately during the whole development that a demarcation is not possible; the question about the affiliation of the placenta therefore can not be decided. In a set of genera the placenta is short and straight, conversely in others it has extended into the ovary space and turns in twists, thus with *Thesium*, *Thesidium*, *Osyridocarpus*, *Cervantesia*, *Jodina*, *Comandra*, *Acanthosyris*, *Pyrularia*, and *Nanodea*. With *Santalum* the common terete-shaped placenta remains short, but the top, which is together formed by placenta and the bases of the ovules, extends inside the pointed stylar channel (see Fig. 31). On the placenta down-hanging ovules remain either straight stretched or bend upward hook-shaped at the time of the development of the embryo sacs (see e.g. Fig. 31 F), so with *Osyris*, *Myoschilos*, *Colpoon*, *Eucarya*, *Comandra*, *Acanthosyris*, *Pyrularia*, and *Nanodea*.

Van Tieghem (see with “Relationships”) does not attribute a nucellus to Santalaceae, but according to him it is a reduced integument-less ovule on the funiculus, or it is better a whole integument (Ovularblättchen), that is not arranged into **Stiel** and **Spreite** here, while with the nucellate phanerogams only at the Ovularblaettchen of the nucellus stalk of the funiculus develops.

The other genera of Anthoboleae behave substantially differently (see van Tieghem in *Bull. Soc. Bot. France* XLIII. [1896] 562). The one-locular ovary has a conical projection at the base. At its summit only one embryo sac under the epidermis develops, which soon dissolves the epidermis and themselves then increasing stand out. Thus only an upright, basifixed (basal), naked ovule is present. During the development of the embryo and the endosperm the ovular tissue is completely used up.

The disk serving as a nectary is developed and is replaced at the lower part of the receptacular tube, so particularly with Thesieae, weakly with *Osyridocarpus*, where this is strongly thickened and certainly without a doubt dissected (? **sezerniert**). With the other groups the disk is more strongly developed and with *Santalum*, *Comandra*, *Acanthosyris*, *Pyrularia*, *Jodina* and *Cervantesia* larger, inserting itself between the stamens in lobes or drawn-out scales. With some genera (*Choretrum*, *Comandra*, *Myoschilos*) one notices that at the receptacle, where it separates from the ovary, a weak seam is present, that is sometimes drawn out into small teeth alternating with the tepals. This seam might not have a special morphological meaning, but with Eichler is was regarded as an extension of the upper rim of the ovary .

Pollination, fertilization, embryo development

Literature. W. Griffith, On the ovulum of *Santalum album*, in Trans. Linn. Soc. XVIII. (1838) 59-70, T. 1-2; On the ovulum of *Santalum*, *Osyris*, *Loranthus* and *Viscum*, l. c. XIX. (1844) 171-214, T.17-20. - W. Hofmeister, Neuere Beobachtungen über Embryobildung der Phanerogamen, in Jahrb. wissensch. Bot. I. (1858); Neue Beiträge zur Kenntnis der Embryobildung der Phanerogamen (1859). - H. Schacht, Die Blüte und die Befruchtung von *Santalum album*, in Jahrb. wissensch. Bot. IV. (1865) 1-22, T.I-5. - E. Strasburger, Zu *Santalum* und *Daphne*, in Ber. Deutsch. Bot. Ges. III. (1885) 105-113, T. IX. - L. Guignard, Observations sur les Santalacees, in Ann. sc. nato 7. Sér. II. (1885) 181-202, T.12-14. - O. Kirchner, Fl. Stuttgart (1888) 521 (Beobachtungen über die Bestäubung bei *Th. pratense* u. *montanum*). - Knuth, Handh. Blütenbiologie II.2. (1899) 361-363, III. 1. (1904) 254. - J. Modilewski, Die embryologische Entwicklung von *Thesium intermedium*, in Bull. Jard. Bot. Kieff, Livr. VII-VIII. (1928) 65-70, 1 T. H. Schulle, Zur Entwicklungsgeschichte von *Thesium montanum* Ehrh., in Flora CX XVII. (1933) 141-184, 13 Fig.

For several genera cross (outside) pollination was observed through smaller bees, flies and beetles. The insect attendance refers also to the strong development of the nectary functioning disk. Nevertheless cross pollination might not be impossible by the wind, particularly with species with dioecious flowers, in which an overproduction of male flowers takes place, so e.g. with *Osyris alba* L. also e.g. with *Thesium* species, those whose stigma and anther stand at the same height, self pollination occurs with some species. Following Schulz heterostyly appears with *Thesium intermedium*; in the homogametic long-styled form the stigma stands out over the anthers, so that self pollination is difficult, in the short-styled form the anthers sit closely over the stigma, so that self pollination is possible (see also E. Loew, Blütenbiolog. Floristik [1894] 328). After Skottsberg (in Bot. Notiser [1915] 198-202) are also species of *Arjona* heterostylous. Bachmann reported on cleistogamy in *Thesium montanum* (Mitt. Bayer. Bot. Pflanzenleben II Nr. 21. [1911] 376); the perigone remains completely closed. After Kerner (Pflanzenleben II. [1891] 124) with *Thesium* the already opened anther closes for the protection of the pollen against rain and humidity from dew; that happens with *Th. alpinum* with humidification within 30 seconds. Kerner sees the meaning of the hair tuft behind the anther in a support of this procedure (see under "flower conditions"); the easily wettable hairs lead the rain water with like a wick to the anthers and arrange a rapid fastening. After Ewart (l. c.) the meaning of the hair lies in the fact that they hold back the pollen close to the flower entrance and also prevent a false entry of insects penetrating to the nectar. With the *Thesium* species with a hair ring, the hair holds the pollen by means of their secretion. Finally, also with reference to the hair tufts, the opinion was expressed that they adjust the position of the anthers to the stigma during flowering. The anthers are to be kept away from the stigma by being glued to the hair threads, thus making self pollination more difficult. - after Porsch (in Biologia Generalis VI. 2. [1930] 202) perhaps the *Santalum* species of the Hawaiian islands should be bird flowers.

The following is to be noticed about the development of the embryo. The genus *Thesium* was examined more in detail *Th. divaricatum* by Guignard and *Th. intermedium* recently by Modilewski; with it some subepidermal cells become larger and become embryo sac mother cells in the naked nucellus, which is downward arranged outward from the summit of the placenta. Following Modilewski, with *Th. intermedium* to eleven of such "archesporial" cells are present, which transform directly into embryo sac mother cells. One of them divides with *Th. divaricatum* into three cells, one above the other, whose lowest increasing becomes the embryo sac. With *Th. montanum* and *Th. intermedium* the full development of the daughter cells does not take place. Further development takes place only in one of the three ovules, so that in the ovary only a

developed embryo sac is finally present. During the nuclear division and cell formation in the embryo sac it is remarkable that the antipodals are present as nuclei only and soon disappear. Next to these two the two secondary embryo sac nuclei soon combine into polar nuclei and the egg cell and two small synergids are present. Meanwhile the embryo sac strongly extends tube-like at its base and penetrates, turning downward, as an haustorium, far into the placenta. After fertilization the secondary embryo sac nucleus divides and between the partial nuclei immediately develops a wall. Thus the embryo sac is separated into two parts; in the front lies the endosperm develops and the fertilized egg cell; in the rear part, outgoing into the haustorium lies a nucleus that gradually becomes larger, and which never continues to divide. With the development of the embryo and the endosperm the embryo sac stretches itself completely from the nucellus. The growing seed displaces the placenta and the remains of the two other ovules; also an internal part of the carpel tissue dissolves. The seed fills the whole ovary cavity. The embryo possesses only a completely reduced suspensor (Embryoträger = “embryo carrier”), or this is not developed at all, so that everything from the fertilized egg cell develops into the emerging tissue of the embryo.

Following Guignard, with *Osyris* the embryo sac mother cells are nearly always solitary. The antipodals remain longer, until the haustorium bends and extends upward. The embryo sac protrudes soon from the nucellus. All three ovules can develop the embryo sac perfectly with the sexual apparatus, also fertilization can take place; finally, however, like always with Santalaceae, nevertheless only one seed is developed. With the genus *Santalum*, in which the first stages were particularly examined by Strasburger, takes place a very strong haustorial extension of the embryo sac. The synergids have large caps with longitudinal stripes, which are well set off against the main body. Over the caps of the synergids the wall of the embryo sac is absorbed, in which area of the exterior of the synergid the wall is cutinized.

Fruit and seed. The fruit of the Santalaceae does not open, it is either nut-like or drupe-like; only with *Jodina* does the fleshy exocarp divide into five easily removable segments (see Fig. 34). With the inferior ovary of *Thesieae* and *Osyrideae*, the exocarp forms from a part of the ovary wall and from the deformed receptacle; it is dry or fleshy, frequently juice-rich and strongly developed and then richly sugary (*Acanthosyris*). Sometimes also the lower part of the fruit wholly formed by the flower axis, so e.g. with *Leptomeria* and *Osyris* (see Fig. 36). With *Anthobolus* and *Exocarpus* the drupe formed from the superior ovary sits on a juicy strongly swollen pedicel, which is red or yellow colored when ripe. The seed is spherical or ovate and is usually more or less connected with the endocarp; from a dissection (herauspräpariert) it often appears rugose or also furrowed. Thus with *Henslowia* the endocarp intrudes with borders into the seed, which is consequently provided with more or less deep longitudinal furrows. With *Phacellaria* the seed is lobed above by the endocarp (Lecomte in Bull. Mus. Hist. Nat. Paris XX. [1914] 399). The seed does not possess an actual seed coat, which is replaced in the absence of the integument by the fruit wall; the hardened layer, to which the endosperm lies close, forms on the border of the original carpel tissue and receptacle tissue; the internal carpel tissue is absorbed (see Embryologie). The endosperm, whose fat cells contain oil and aleurone, is plentifully developed, white and fleshy, and surrounds in the center or somewhat inclined to the side an embedded embryo whose rootlet upwardly arranged. The spreading of the seeds takes place with many Santalaceae via the fact that birds and mammals are attracted to the sweet parts of the fruit; the seed included in the hard endocarp probably goes through the intestinal channel, without losing germinability. With *Thesium* myrmecochory was determined (R. Sernander in K. Sv.

Vetensk. Ak. Handl. XLI. no. 7, 1906). The elaiosome is for *Th. alpinum* 2 mm long, cylindrical and is formed by the yellow part of the flower axis, which lies directly under the inferior ovary; see E. Ulbrich, Karpobiologie (1928) 101 Abb. 18 VI (Scheinfrucht von *Thesium alpinum*).

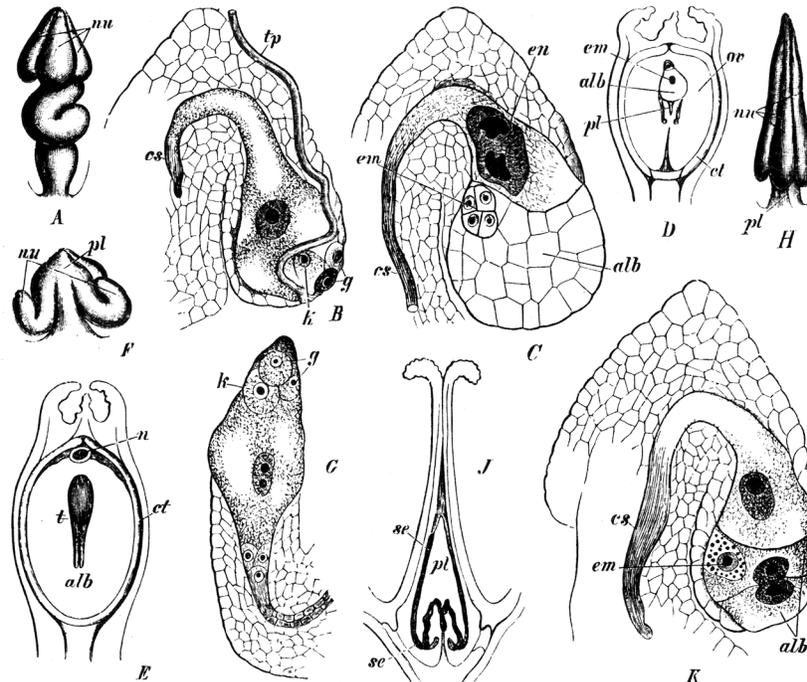


Fig. 31. A-E and K *Thesium divaricatum* Reichenb. A isolated placenta with the three ovules *nu*. B longitudinal section of an ovule at time of fertilization; *tp* pollen tube; *g* synergids; *k* egg cell; *cs* haustorium of the embryo sacs. Vergr. 380. K longitudinal section of an ovule after fertilization; *em* fertilized egg cell; with *alb* 2 cells of the developing endosperm. Vergr. 380. C longitudinal section at a later stage; *em* more cellular embryo; *alb* young endosperm; *en* the increased nucleus of the haustorium. Vergr. 210. D longitudinal section of a young fruit; *ov* carpel parenchyma; *ct* later sclerenchyma-becoming layer of the fruit wall; *em* embryo; *alb* endosperm; *pl* placenta. Vergr. 7. E longitudinal section of a nearly mature fruit; *t* hypocotyl of the embryo; *n* conserved remaining nucleus together with remainders of the rear part of the embryo sacs and with the other ovules. Vergr. 7. - F, G *Osyris alba* L. F isolated placenta with the three ovules *nu*. G ovule still unfertilized; the embryo sac already protruding from the nucellus; *g* synergids; *k* egg cell; in the center of the embryo sac combining with the polar nucleus; at the base the three antipodals. Vergr. 210. - H, J *Santalum album* L. H isolated placenta with the three ovules *nu*. Vergr. 20. J longitudinal section of the ovary of a flower; *pl* placenta with two ovules: on the left one sees the embryo sac *se* on the side from the nucellus and upward in the direction to the bent stigma, on the other side deeply penetrating into the nucellus and bending downward into the placenta; with the right ovule only the rear part of the embryo sac is visible. Vergr. about 11. - from E. P. 1. Aufl. III 1. 208, Fig. 137.

Geographical distribution. From Santalaceae about 400 species are well-known, which are widely distributed in the tropics and temperate zones. A predominant part of the genera appear only in the drier areas and relatively few also belong to damper climates. In Europe *Thesium* is represented by a larger number of species, particularly in the south and southwest, otherwise only *Osyris alba* in the whole Mediterranean region, to *O. lanceolata* in the western Mediterranean region, furthermore *Comandra* with a species in the Sandpußten of Hungary and in the northern Balkans. Africa is enriched with approximately 190 species, as many as every other part of world, but this number is completely and substantially involved only in the genus

Thesium (with approximately 175 species), which particularly arise in South Africa in largest form, abundance and with special groups. Furthermore, in the Cape area the genus *Thesidium*, which differs from *Thesium* mainly by dioecious flowers, is endemic with 7 species. The genus *Osyridocarpus*, which represents a transitional member of Thesieae to Osyrideae, is common with 6 species of eastern South Africa by East Africa to Abyssinia and Eritrea. The genus *Osyris* includes *O. abyssinica* with a wide area in East Africa and southwest Africa and *O. Wightiana* in East Africa and tropical Asia. The monotypic genera *Rhoiacarpus* and *Colpoon* are unique to South Africa. Also in Asia the genus *Thesium* species numbers exceed all remaining genera together; representatives of the same are in the Siberian mountains, but might not reach to 60 degrees north. From Osyrideae *Pyrularia edulis* in the Himalayas, *Santalum album* in India and on the Sunda islands, *Buckleya* with 3 species in China and Japan, *Osyris Wightiana* is widespread from India to S. China, furthermore *Scleropyrum* with a few species in India, on the Malay peninsula and New Guinea, *Phacellaria* with 6 species from India to China. Richer in development is the genus *Henslowia*; with approximately 30 species, it extends from east India over the Malay peninsula to S. China, then to the Sunda Islands, New Guinea, and the Philippines. From the substantially Australian and Pacific Anthoboleae, only some *Exocarpus* species come over to New Guinea, the Philippines and the Sunda Islands. With 5 species *Anthobolus* is limited to the Australian mainland, the northern, central and western parts. *Exocarpus* has about 8 species in Australia, New Zealand and Tasmania, then are distributed a few characteristic species on the Norfolk and Lord Howe islands, Hawaii, and New Caledonia. The genus *Santalum* has a particularly far and scattered distribution. The occurrence of *S. album* in India was mentioned already above, but here [whether it is] indigenous is doubtful; the species on the Lesser Sunda islands is surely domestic. Then rich from New Guinea to north and east Australia and on to the Pacific islands to Hawaii, where it is particularly richly developed; furthermore a species on Juan Fernandez now seems exterminated. With *Santalum* are the closely related genera *Eucarya* and *Mida*, the first represented by 4-6 species in south and west Australia, the latter with a species or perhaps several species endemic on New Zealand. Furthermore the Australian flora contains one species of *Thesium*, 7-8 species of *Choretrum*, 15-16 species of *Leptomeria* and the monotypic genus *Omphacomeria*. North America possesses only Osyrideae, together with tropical Asia the genus *Pyrularia* (1 species), with Europe *Comandra* (about 5 species), and with eastern Asia *Buckleya* (1 species). Endemic with one species each are the genera *Darbya* and *Geocaulon*. Richer in genera is the Andean and extra-tropical southern South America. Here the Thesieae genera *Quinchamalium* (about 20 species) and *Arjona* (10-12 species) are endemic; in *Thesium* one finds only 2 species in south Brazil, which form a special section. From Osyrideae are exclusively represented by the genera *Cervantesia* (3-4 species), *Jodina* (1), *Acanthosyris* (2), *Nanodea* (1) and *Myoschilos* (1 species). The Anthoboleae are missing. The peculiar distribution of some genera (e.g. *Comandra*, *Buckleya*, *Santalum*) refers to an earlier stronger development.

Fossil remains. Following Schimper are fossils in the Tertiary period: four species of *Santalum*, one *Osyris*, one *Exocarpus* and seven *Leptomeria*. But the opinion is given (the fossil plant remains, p. 255) that almost all proof is missing for the presence of the Santalaceae in the Tertiary period of Europe, since the remains concerned consist only of branches or leaves. Also fruits described by Unger as *Excoecaria radobojana* are not with certainty attributable to Santalaceae. On the other hand, in the Bernstein amber a flower was found, which Conwentz described as *Thesianthium inclusum*, and which is probably safely Santalaceae (see S. 91). Also

Casparry described two male flowers called *Osyris Schiefferdeckeri* and *O. ovata*, which probably belong to this genus, since it can be accepted that in the old Tertiary time the distribution of the genus *Osyris* itself extended far north.

Familial relationships. Santalaceae are next related to Olacaceae (see there), furthermore with Loranthaceae, with which, however, the ovules and the placenta are not clearly developed and which form a floral axis around the base of the flower frequently covered by a calyculus. In the first edition of *Die Natürlichen Pflanzen Familien*, of the genera placed in Santalaceae, only *Champereia* was separated, which was specified under Anthoboleae because of the superior ovary, with which it obviously had no familial relations. *Champereia* was combined with some other genera in the family Opiliaceae by Engler after the procedure by van Tieghem (see E. P. Nachtr. I. [1897] 142), which is to be placed in the proximity of Santalaceae; the superior ovary contains only one ovule, a reduced calyx is frequently present. With van Tieghem (Sur les phanérogames à ovule sans nucelle, le groupe des Innucellées ou Santalinées, in Bull. Soc. France XLIII. [1896] 543-572; see also A. Engler in E. P. Nachtr. I. [1897] 141-142) the families at the periphery of Loranthaceae were established in the group “Inovulées”, while Santalaceae, Arjoneae, Schoepfiaceae, Myzodendraceae, Opiliaceae, Anthobolaceae, Olacaceae, Aptandraceae, Harmandiaceae are united in the group “Innucellées”, since with them no nucellus is developed. *Arjona* is with van Tieghem the type of its own family; the disk is not “calicinal”, i.e. does not take its origin from the flower axis but is developed epigynously around the style [it is to be noticed that the disk always covers the ovary above and is usually expanded only up to the base of the tepals]; the ovary is only one locular above, to multi-locular below; the hairs behind the stamens are not subepidermal but epidermal in origin (see S. 59). *Arjona* is attached to *Quinchamalium*, which does not possess staminal hairs. One cannot agree as to the separation of the two genera as their own family. Rather the family Anthobolaceae could already be recognized, particularly because of the position of the ovule.

Use. The main use, which the Santalaceae offer, lies in the use of the wood of a number of genera (*Santalum*, *Eucarya*, *Acanthosyris*). In the first place stands *Santalum*, whose wood supplies also the sandal oil (see with *Santalum*). The often sweet fruit flesh of the drupe of some Santalaceae is edible (e.g. *Acanthosyris*); *Arjona* supplies edible tubers. Details are to be seen under the genera.

Organization of the family.

A. Perianth hypogynous. Ovary superior, unilocular with one basal ovule, sunken into the disk only at the base, fruit on end of a fleshy swollen pedicel. Tribe 1.

Anthoboleae.

B. Perianth more or less epigynous. Receptacle not extended beyond the ovary or short to bell-shaped (campanulate) extended over the ovary and then inside clothed more or less within the disk. Tribe 2. **Osyrideae.**

C. Perianth epigynous. Receptacle more or less extended beyond the ovary, mostly tubular, inside not clothed with the disk. Ovary inferior. Tribe 3. **Thesieae.**

Tribe 1. **Anthoboleae.**

A. Each thecum of the anther opening introrsely by a longitudinal slit which is common to both

loculae.- Australia

B. Each locule of the anther opening with an individual longitudinal slit. - from the Malay archipelago to Polynesia.

1. *Anthobolus*.

2. *Exocarpos*.

Tribe 2. **Osyrideae**.

A. Thecal locules of the anthers usually roundish or egg-shaped (ovoid), short, more or less separated from each other, terminal or obliquely terminal (then the rear locule sitting somewhat higher). Each locule with an individual slit.

a. Flowers bisexual. Leaves usually very small or deciduous.

α. Flowers individual (solitary) axillary or a few in small axillary groups. Disk hardly lobed.- Australia

3. *Choretrum*.

β. Flowers in axillary spikes or racemes. Disk more strongly lobed. - Australia

4. *Leptomeria*.

b. Flowers mostly unisexual, dioecious or monoecious, rarely polygamous.

α. Leaves small, flabellate (with scale leaves) or lacking. Parasitic shrublets on Loranthaceae. – East India to S. China

6.

Phacellaria.

β. Leaves developed.

I. Endocarp with ridges protruding into the seed. Nearly always parasitic on branches of trees; shrubs or shrublets. - Indian Malaysian area

6. *Henslowia*.

II. Endocarp without ridges. Trees or shrubs frequently with thorny, spiny twigs. - tropical Asia

7. *Scleropyrum*.

B. Thecal locule of the anther ovoid or ellipsoid, parallel to each other and attached to the connective. Each theca opening with only one longitudinal slit. [really should say, each thecal locule opening separately by a longitudinal slit]

a. Exocarp (hollow floral axis) fleshy, fused to the ovary, and after anthesis easily disintegrating into segments.

α. Leaves rhombic, spiny on the corners (margins). – S. America

8.

Jodina.

β. Leaves oval to elliptic, pubescent. – Andean South America

9. *Cervantesia*.

b. Exocarp (hollow floral axis) fused more or less with the ovary, not disintegrating into segments.

α. Flowers without a hair tufts behind the stamens. Flowers dioecious; staminate (male) in small umbels; carpellate (female) flowers solitary with 4 bracts which are fused to the ovary below the tepals and the bracts are also apically spreading.. - North America, Eastern Asia

10. *Buckleya*.

β. Flowers with hair tufts behind the stamens.

I. Leafless “switch shrubs” (unbranched stems). – Australia

11. *Omphacomeria*.

II. Leaves developed.

1. Flowers dioecious or polygamodioecious, in separate or individual inflorescences.

X. Male flowers with extended (elongated), wedge-shaped (cuneate), hollow receptacle covered by the disk. Low bush. - North America

12.

Darbya.

XX. Male flowers with short receptacle.

+. Drupe (stonefruit) large, 1.5-5 cm long. - North America

13. *Pyrularia*.

++. Drupe (stonefruit) smaller. - Mediterranean area, trop. Africa, warmer Asia

14. *Osyris*.

2. Flowers bisexual or also rarely unisexual, not in separate inflorescences.

X. Herbs of low subshrubs.

+ . Flowers monoecious, the central of the cyme usually carpellate. Rhizome thin, creeping. - North America 15. *Geocaulon*.

++ . Flowers bisexual. Receptacle over the ovary campanulate. Woody creeping rhizome and upright (erect) shoots. 16. *Comandra*.

+++ . Flowers bisexual. Receptacle over the ovary shallow bowl-shaped. Small herb with creeping axis- Southern South America 17. *Nanodea*.

XX. Shrubs or trees.

+ . Flowers in catkin-like spikes, sessile, enveloped by the broad bracteole. Disk unlobed. - South America 18. *Myoschilos*.

++ . Flowers in small cymes at the base of scale leaves of the short shoots. Disk lobed. Trees or shrubs with spines. - South America 19. *Acanthosyris*.

+++ . Inflorescence paniculate.

• . Receptacle elongated; Style rather long. - Malay area, Australia, Polynesia 20. *Santalum*.

•• . Receptacle not or only shortly elongated above the ovary, style short.

Δ . Receptacle over the ovary absent or almost absent.

~ . Fruit globose ovoid, crowned by the persistent tepals. - South Africa 21. *Rhoiacarpus*.

~~ . Fruit obovoidal or ellipsoidal, tepals not persistent. - South Africa 22. *Colpoon*.

ΔΔ . Receptacle shortly elongated above the ovary.

~ . Fruit globose. Receptacle bowl-shaped. Tepals grading into the receptacle with broad bases. Leaves opposite. - Australia

23. *Eucarya*.

~~ . Fruit top-shaped (turbinate), receptacle short cup-shaped. tepals fused to the receptacle with a contracted at the base; leaves more or less alternate. - New Zealand 24. *Mida*.

Tribe 3. **Thesieae**.

A. Fruit drupe-like. - South Africa, East Africa

25. *Osyridocarpus*.

B. Fruit nut-like.

a. Flowers dioecious. - South Africa

26. *Thesidium*.

b. Flowers bisexual.

α . Bracts and bracteoles not fused to each other.

I. Placenta long threadlike, usually bent. - South Africa, trop. Africa, Mediterranean area, moderate and warmer areas of Europe and Asia; Brazil 27. *Thesium*.

II. Placenta thick and short. South America.

28. *Arjona*.

β . Bract and bracteole fused into a cup-shaped "calyx". Hairs behind the stamens absent. - South America 29. *Quinchamalium*.

Genus of uncertain position. - Sumatra

Calyptosepalum.

Tribe. 1. **Anthoboleae.**

Anthoboleae Bartl. Ord. Nat. Plant. (1830) 113; Spach, Hist. nat. vég. Phanér. X. (1841) 461; Bentham, 1. c. (1880) 219; Hieronymus, 1. c. (1889) 212.

1. **Anthobolus** R. Br. Prodr. Fl. Nov. Holl. (1810) 357; A. DC. in DC. Prodr. XIV. (1857) 687; Benth. et Hook. f. Gen. Pl. 111. (1880) 230; Benth. Fl. Austral. VI. (1873) 226; Hieronymus in E. P. 1. Aufl. III. 1. (1889) 212; Bailey, Queensl. Flora V. (1902) 1389. - Flowers dioecious, 3-4-merous, very small. Male flowers in one usually 3-5-flowered “umbel-shaped” cymes at the end of a short axillary peduncle, prophylls 2, deciduous. Tepals separate up to the base, obtuse. Disk flat, lobed. Filament short, thickish, nearly flat, anthers 4-loculate, each theca with both loculae dehiscing introrse from a common longitudinal fissure. Female flowers solitary (rarely two) axillary at the end of a short sprig, which changes itself upward into the actual, thickening pedicel. Tepals at the base somewhat united, bent back, blunt. Disk and staminodia 0. Ovary superior, free, pyramidal; stigma sessile, thickly cushion-like. Drupe on thickened pedicel, ellipsoid, exocarp somewhat fleshy, endocarp crusty; embryo in the fleshy endosperm. Low bushes with glabrous, thin or rigid, thicker branches; leaves narrow, persisting or very soon deciduous.

Name after $\alpha\nu\nu\omicron\zeta$ flower, and $\beta\alpha\lambda\epsilon\lambda\iota\nu$ throw; the flowers are easily dehisced (dropped, abscised). - Type species *A. filifolius* R. Br.

5 species in northern, western and central Australia. - **A.** Leaves developed, persisting. *A. foveolatus* F. Muell. in west Australia; 1-2 m high, also upright which are spiky, rigid branches; Leaves fleshy, narrowly linear-coiling, 2-4 cm long; Fruit 7-9 mm long, Endocarp with fine pitting. - *A. filifolius* R. Br. in north Australia, Queensland; Leaves nearly threadlike, Endocarp not pitted; related *A. triqueter* R. Br. in Queensland. - **B.** Leaves very small, soon abscised, leafless branches thorn-like. *A. leptomerioides* F. Muell. in Queensland. - *A. exocarpoides* F. Muell. in central Australia.

2. **Exocarpus** (Exocarpos) Labill. Rel. Voy. Rech. De LaPerouse I. (1798) 155, T.14; R. Br. Prodr. Fl. Nov. Holl. I. (1810) 356; A. DC. in DC. Prodr. XIV. (1857) 687; Benth. Fl. Austral. VI. (1873) 227; Benth. et Hook. f. Gen. III. (1880) 230; Hieronymus in E.P. 1. Aufl. III.1. (1889) 212; Bailey, Queensland Flora V. (1902) 1390; Pilger in Engl. Bot. Jahrb. LIX. (1924) 118 (*Xylophyllos* Rumph. Herb. Amboin. VII. [1755] 19, T. 12; O. Kuntze, Rev. gen. 11. [1891] 589; *Xylophylla* L. Mant. II. [1771] 147 pr. p.; *Xynophylla* Montrousier, Fl. de l'ile Art, in Mem. Acad. Lyon X. [1860] 250; *Sarcocalyx* Zippel ex A. DC. 1. c.; *Canopus* Presl, Epimel. bot. [1849] 248). - Flowers polygamous or usually bisexual, monoecious or rarely dioecious, usually in the mixed racemes, little different from one another, the female with developed staminodea, the male flowers with \pm developed pistillodia, in cavities of the rachis nearly sessile or rarely clearly short-pedicellate, very small, 4-5merous. Tepals, particularly in the male flowers broadly radiate. Disk developed, flat or nearly flat, blunt-sharp-edged. Stamens inserted at the base of the tepals, shorter than these, small: Filament broad: Anther four-loculate, introrse, the locules next to each other, each one opening (dehiscing) with its own longitudinal fissure. Ovary superior or somewhat sunken, cone-shaped (conical): Stigma sessile, weakly lobed. Flowering axis in the male flowers nearly flat; in the female it gradually develops more fully underneath the fruit usually (into) thick, top-shaped, fleshy, colored, juicy, often longer than the fruit. Fruit egg-shaped or ellipsoid, with broad base of the thickened axis encompassed or rarely surrounding up to the center of the axis: Exocarp thin leathery, endocarp faintly boney (angular?), fragile. Embryo small in the endosperm. - Creeping subshrubs or upright shrubs or small trees, glabrous or on the recent parts with hair tufts: with some species developing phylloclades: Leaves rarely rather large, linear to elliptical, more frequently very small, awl-shaped or reduced to deciduous tooth-shaped scales. Flowers usually solitary or rarely two to three per axil, \pm extended,

pedicellate, multi-flowered or shortened and few-flowered, sessile spikes, rarely also flowers at the nodes clustered or solitary: rachis of the spike, if developed, rather thick, usually very briefly downy; bract (Tragblatt) very short, tooth-shaped or undeveloped, prophylls rarely developed, the bract similarly.

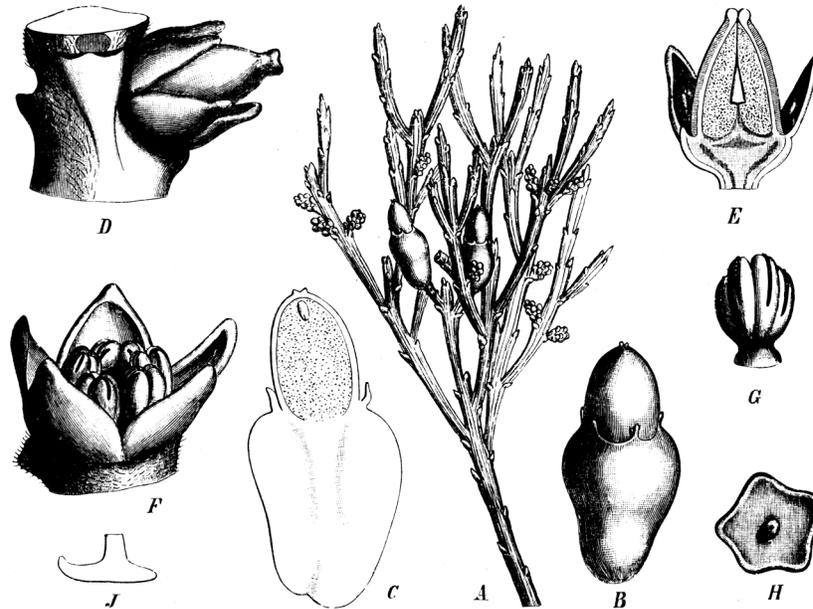


Fig. 32. A-C *Exocarpus Bidwillii* Hook. f. A habit of ramified branches with flowers and fruits. B ripe fruit (about 3/1). C median longitudinal section through a fruit and its thickened pedicel (3/1). - D-J *E. sparteus* R. Br. D part of an inflorescence with one female flower and the rudimentary scales (Deckschuppen) of 2 abscised male flowers, the female flower in the condition after pollination, in which the ovary is already strongly swollen (18/1). E median longitudinal section of one female flower, in the center the conical placenta (18/1). F highest (pseudoterminal) male bloom on an inflorescence (18/1). G a stamen with a longitudinally dehiscent locule of the anther theca seen from the inner side (30/1). H disk with the rudimentary style from the male flower seen from above (18/1). J median longitudinal section of the disc (18/1). - from E. P. 1. Aufl. III. 1, 213, Fig. 138.

Name from έξω, outside, and καρποζ, fruit, because it sits freely on a thickened pedicel. Fruit. - the name *Exocarpus* Labill. stands on the list of the nomina conservanda; Briquet, Règl. internat. nomencl. bot. ed. 2. (1912) 85. - type species *E. cupressiformis* Labill. About 20 species in Australia, Tasmania, New Zealand, New Caledonia, Hawaii, the Philippines, Bonin Islands, New Guinea, Sunda Islands.

Subgenus I. *Xylophyllos* [Rumph.] Pilger l. c. 119. - flowers solitary at the nodes or more bunched (clustered), pedicellate. Bracts 0, prophylls several, often 4 under the flower crossed. Phylloclades ± developed. 3-4 species. *E. Lauterbachianus* Pilger, in New Guinea; shrublet with narrow, flattened, hardly phyllocladous branches. - *E. Pullei* Pilger, in New Guinea, a subshrub with developed phylloclades. - doubtfully *E. epiphyllanthus* (L.) Merrill Interpret. Rumph. Herb. Amb. (1917) 208, on the Molokken (*Xylophyllos ceramica* Rumph.).

Subgenus II. *Chamexocarpus* Pilger l. c. 119. - flowers at the nodes geknäuel, sessile in a concavity formed of the bract and prophyll, prophylls 2, small, transverse; flowers 5-merous; phylloclades developed. *E. neocaledonicus* Schlecht. & Pilger, on New Caldeonia.

Subgenus III. *Autexocarpus* Pilger l. c. 119. - flowers in (often strongly reduced) spikes, prophylls 0.

Section 1. *Phyllodanthus* A. DC. in De. Prodr. XIV. (1857) 691 (*Xylophyllos* and

Euxylophyllos O. Ktze.). – flowering branches phyllocladous; spikes 1-1.5 cm long, fruit on the thickened axis. *E. phyllanthoides* Endl., on the Norfolk islands; small trees, branches downward too turning approximately, upward strongly squeezed together, narrow leaves soon abscising; flowering branch phyllocladous of changing form. Here probably *Xylophyllos artensis* Montr. of New Caldeonia.

Section 2. *Sarcocalyx* A. DC. l. c. 688 (*Canopus* Presl l. c). - no phylloclades; young parts with short bundle hairs; Leaves large, parallel-nerved, not running down. *E. latifolius* R. Br. in east and north Australia, the Philippines, Celebes, with var. *miniatus* on New Guinea, Java; Bush or small tree, leaves elliptic, 3-8 cm long. - *E. spathulatus* Schlecht. et Pilger, on New Caledonia; Leaves spatulate.

Section 3. *Euexocarpus* A. DC. l. c. 689. - no phylloclades; no bundle hairs; Leaves briefly linear or usually scale-like, rarely larger. About 10-12 species in Australia, New Zealand, Tasmania, Hawaii. - **A.** Leaves different, largely, elliptical and scale-like; Branches densely branched. *E. Gaudichaudii* A. DC and *E. sandwicensis* Baill., on Hawaii, small trees or bushes. - **B.** leaves homogeneous, usually scale-like. - **a.** leaves linear lanceolate, to 3 cm long; Flowering axis under the fruit hardly thickened. *E. odoratus* (Miq.) A. DC, in west Australia, small bush; - **b.** leaves scale-like, usually abscising, axis under the fruit fleshy, thickened. - **ba.** spikes pedicellate, ± extended. *E. cupressiformis* Labill., widespread in south and east Australia (Black, Fl. S. Austral. [1924] 167), Tasmania; small tree with branches branched out strongly (Native cherry, fruit edible). - *E. sparteus* R. Br. (Fig. 32 D-J) in west Australia, bush with thicker branches. - **bβ.** racemes sessile, few-flowered. *E. nanus* Hook. f. and *E. humifusus* R. Br. on Tasmania, prostrate subshrub, similar to *E. Bidwillii* Hook. f. (Fig. 32A-O) on New Zealand. - *E. aphyllus* R. Br., in west Australia, *E. homocladus* F. Muell., on Lord Howes Island (= Ontong Java Atoll), upright bushes branched out strongly. *E. amboinensis* Merrill of Amboina (=Kwajalein Atoll), doubtful relationship, with large leaves to 11 cm long and axillary, solitary, long-pedicellate fruits.

Tribe 2. **Osyrideae.**

Osyrideae Reichenb. Consp. (1828) 80 pr. p.; Bentham l. c. (1880) 218; Hieronymus l. c. (1889) 214.

3. **Choretrum** R. Br. Prodr. Fl. Nov. Holl. I. (1810) 357; A. DC. in DC. Prodr. XIV. (1857) 675; Bentham, Fl. Austral. VI. (1873) 217; Hieronymus in E. P. 1. Aufl. III.1. (1889) 215. - flowers small, whitish or yellow, 5-merous. Flowering axis united with the ovary, from the tepals in the texture differently and separated by a line or narrow groove, sometimes between the tepals in small little teeth going out. Tepals lobed, direct, never spread out, fleshy, with inwards turned, keeled(?), up to middle of the tepals to reaching (to being enough), after the top to free part, so covering the anthers like in a concavity. Disk hardly lobed or 5-parted. Filament of the stamen very short; Locule of the anther 4, inward turned, around the small central connective broadly individually dehiscing. Style very short, thick, stigma five-parted; ovary inferior, broadly turbinate (top-shaped). Fruit crowned by the persistent tepals, spherical or ellipsoid; Exocarp thin, leathery-fleshy, Endocarp thick-woody. - Subshrubs or “rod-shaped” bushes, mostly strongly branched; Leaves very small, scale-like, quite often long-persisting.

Meaning of the name doubtful. – type species *Ch. glomeratum* R. Br.

7-8 species in Australia. - **A.** Flowers several (2-5) in small, axillary inflorescences; that are about 3-6 mm long sprigs bearing several small sterile scales, then followed by bracts with an axillary flower with 2 prophylls, which are decussate with the bracts. *Ch. glomeratum* R. Br. (Fig. 33A-B) in south and west Australia; richly branched bush, subulate (awl-shaped) scale leaves 1-1.5 mm long; related to *Ch. chrysanthum* F. Muell., in south Australia. - **B.** Flowers solitary axillary, almost sessile, surrounded at the base by several prophylls. *Ch. Candollei* F. Muell., in east Australia; small bush, young branches densely occupied with subulate scale leaves; prophylls under the flower 7-9. – *Ch. lateriflorum* R. Br., in west Australia; Bush with

extended young branches and loosely standing scale leaves; Prophylls 4 decussate.

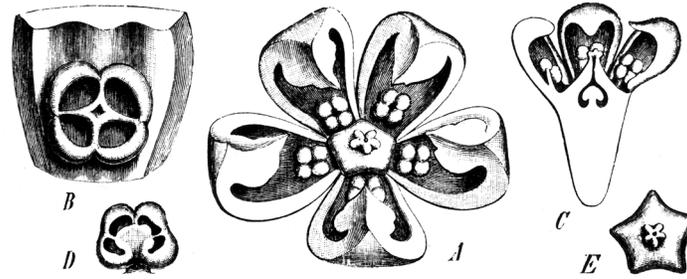


Fig. 33. A, B *Choretrum glomeratum* R. Br. A flower seen from above (20/1). B lower part of a tepal with a stamens, whose anther is already empty (37/1). - C-E *Leptomeria acida* R. Br. C median longitudinal section of a flower (20/1). D stamen, whose anther is already empty, seen from the internal side (37/1). E disk with the style seen from above (20/1). - from E. P. 1. Aufl. III. 1,215, Fig. 139.

4. **Leptomeria** R. Br. Prodr. Fl. Nov. Holl. I. (1810) 353 (excl. sect. II); Endl. Gen. Pl. (1837) 326 (excl. sect. 11); A. DC. in DC. Prodr. XIV. (1857) 677; Benth. Fl. Austral. VI. (1873) 219; Benth. et Hook. f. Gen. Pl. III. (1883) 229; Hieronymus in E. P. 1. Aufl. III. 1. (1889) 215. - Flowers very small, nearly always 5-merous, apparent always bisexual, sessile or short pedicellate. Tepals usually spreading, valvate, persisting, pudgy or thick, at the apex somewhat thickened or frequently cap-shaped (capitate). Disk epigynous, cut, repeatedly, deeply lobed, lobes free or adnate, gland-shaped. Stamens attached at the base of the tepals, very small; Filaments very short, to being nearly missing; Anthers with locules turned inward, these posed around the connective in a semi-circle or more frequently posed in pairs one above the other, broadly opening, last usually still 4, more rarely only 2-3 distinguishable, the upper shorter. Style and stigma small, the latter weakly lobed; inferior ovary wedge-shaped or turbinate; ovules of the placenta not clearly separated in the center of the ovary. Fruit ellipsoidal-spherical, small, smooth or serrated, crowned by the persistent tepals; Exocarp thin, leathery or juicy-fleshy, endocarp thin, fragile; seeds with fleshy endosperm, embryo very small. - small or low shrubs, often strongly branched from the base; Branches often striate-stripped, frequently (from time to time) thorny, leaf scars \pm apparent (standing out); Leaves usually soon dropping, very small scale-like, more rarely persisting, small, subulate- **drehrund** to obovate. Flowers rarely solitary in the axil of short branches (short shoots), usually very numerous, short, axillary spikes (or better in some species racemes); bracts more rarely persisting and themselves approximating the leaf form (with the species with persistent leaves), more frequently easily dropping.

Name from λεπτομερής, compound from fine parts. - Type species *L. acida* R. Br. 15-16 species, usually in west Australia, some in south and southeast Australia and on Tasmania.

Section 1. *Xeromeria* Endl. l. c. 326. - flowers solitary or in spikes with persistent bracts; Leaves persistent. - **A.** bracts differing rather strongly from the leaves (leaf forms). *L. squarrulosa* R. Br., in west Australia; to 1 m high, strongly branched; Leaves distant, to 5 mm long; bracts 1 mm long. - *L. Cunninghamii* Miq. and *L. empetriformis* Miq., in west Australia, small subshrub. - **B.** bracts leaf-like, thus flowers solitary, axillary. *L. obovata* Miq., in southwest Australia; leaves obovate to spatulate, 4-7 mm long. - *L. axillaris* R. Br., in southwest Australia; shrublet with subulate-twisted, 3-4 mm long leaves.

Section 2. *Oxymeria* Endl. l. c. 326 (Sect. *Oxymeria* and *Acanthomeria* A. DC; Sect. *Xeromeria* Benth.). - bracts and leaves soon dropping. - **A.** spikes branch-like, extended at the flowering time (anthesis). *L. Dielsiana* Pilger, in west Australia. - **B.** spikes of the branches different. **a.** Branches with tooth-shaped leaf scars. *L. scrobiculata* R. Br., in west Australia, small shrublets. **b.** leaf scars not or hardly protruding. **I.** Branches thick, thorny. *L. aphylla* R. Br., in south Australia. **II.** Branches not thorny. *L. acida* R. Br., in new south Wales, a 2 m high bush, and a number of related species, among these others *L. drupacea* (Labill.) Pilger (*L. Bidwillii* R. Br.) on Tasmania, *L. pauciflora* R. Br. in west Australia.

Fossil indicated from the Tertiary period in Europe: *Leptomeria gracilis, flexulosa, distans* Ettingsh., Tert. Fl. von Haring in Tirol, in Abh. k. k. geol. Reichsanst. II. Abt. 3 Nr.2. (1853) 48; Engelhardt in Abh. Hess. Geol. Landesanst. VII. 4. (1922) 62.

5. Phacellaria Benth. in Benth. et Hook. f. Gen. Pl. III. (1880) 229, in Hook. Icon. T. 1324 (1880); Hook. f. Flora Brit. India V. (1886) 235; Hieronymus in E. P. 1. Aufl. III.1. (1889) 216; Collett et Hemsley in Journ. Linn. Soc. XXVIII. (1890) 122, T.17. – Flowers small, monoecious (or also dioecious?), rarely bisexual, 4-6-merous. Male flowers nearly spherical or more depressed. Tepals triangular, few, distant. Disk nearly flat, notched at the insertion of the stamens. Stamens shorter than the tepals; Filament very short, thick; Anthers with inwardly turned four-loculate thecae, each locule with a longitudinal fissure opening separately. Pistillode very small. Disk of the female flowers hardly notched. Staminodia 0. Stigma nearly sessile, thick; central placenta of the inferior ovary columnar, 3 ovules hanging down from the apex. Fruit crowned by the persistent tepals; Exocarp fleshy, endocarp bony, striped; seed ellipsoidal, at its apex 5-lobed; Embryo small, in the endosperm. – On Loranthaceae - species (are) parasitic shrublets with glabrous or somewhat soft-hairy branches; leaves small scales or 0. Flowers to several sitting in the scale axils, bracts and prophylls hardly differentiated.

Name from φαχελος (φαχελλος), Bundle, cluster (fascicle); because of the clustered flowers.. – Type species *Ph. rigidula* Benth.

6 species from east India to south China. *Ph. rigidula* Benth., Mergui; Branches clustered, 8-12 cm long, normally or with few short sprigs; leaves only very small, about 3/4 mm long scales; flowers usually in triads sessile in the leaf axil, only continues to develop; by the inflorescence repeatedly a branch from the leaf axil grows through; bracts and 2 (to 4) prophylls hardly developed, only with completely narrow edge of skin free, not clearly separate, under the sessile flower a type of small calyculus forms; tepals up to 1 mm long. – *Ph. compressa* Benth., Tenasserim, Burma; with squeezed together branches; flowers encompassed at the base of the branch, everywhere at the branches rather numerous in small groups; bracts and prophylls under the male flower hardly recognizable, under the female flower 0. – *Ph. Wattii* Hook. f., Manipur; Branches to 16-17 cm long; flowers numerous in groups, bracts and prophylls clearly separated, only a small “edge of skin” (Hautrand) forming. – *Ph. caulescens* Collett et Hemsl. in Burma; to 30 cm high; flowers individually axillary. – *Ph. tonkinensis* Lecomte, in Tonkin. – *Ph. Fargesii* Lecomte in China, Sutchuen; flowers bisexual.

6. Henslowia Blume, Mus. Bot. Lugd. Bat. I. (1850) 242, T. 43; A. DC. in DC. Prodr. XIV. (1857) 630; Benth. et Hook. f. Gen. Pl. III. (1880) 228; Hook. f. Fl. Brit. India V. (1886) 232 [*Henslowia*]; Hieronymus in E. P. 1. Aufl. III. 1. (1889) 216 (*Dendrotrophe* Miq. Fl. Ind. Bat. I (1855) 779; *Dufrenoya* Chatin in Camp. Rand. Acad. Paris LI. (1860) 657; *Tupeia* spec. Blume, Korthals, non *Tupeia* Cham. et Schlechtendal). – Flowers dioecious or monoecious, rarely also bisexual, 5-6-merous. Male flowers with flat receptacle. Tepals at the base behind the stamens with hair tufts. Stamen with very short filament; Anther small, locules of the theca terminal or pseudoterminal (inclined), each locule with a terminal fissure that opens individually, the valves spreading later. Female flowers with small staminodia or without such. Ovary inferior, receptacle not extended beyond the ovary; disk lightly concave or convex; stigma nearly sessile, 2-5-lobed; ovules 2-3, down-hanging from the apex of a short, thick placenta. Drupe small, spherical or egg-shaped; exocarp fleshy, endocarp hard, outside rugose, inside substituted with borders of the seeds, seed thereby with more or less deep longitudinal furrows, above nearly lobed; embryo short, with very short cotyledons, in the center of the endosperm. – Shrublets or shrubs, very mostly parasitic on tree branches; leaves alternate, usually thick. Flowers few or in axillary groups, very small.

Name after J. S. Henslow, professor in Cambridge (1796-1861). – Type species *H. umbellata* Blume. Vgl. auch Lecomte, Fl. Indochine V. (1915) 215 Fig. 23. About 30 species are described,

partly are imperfectly known to them; probably limited to a smaller number. East India (Himalaya), Malay peninsula to south China, Sunda Islands, New Guinea, Philippines; usually in mountains. - **A.** Terrestrial, probably root parasitic. *H. frutescens* Benth. in south China: Shrub, leaves obovate, to 4 cm long; male flowers small axillary cymes with pedicel up to 6-7 mm long, (single, solitary) peduncle short, female flowers individually axillary. - **B.** “tree inhabiting” parasite (dendroparasite). - **a.** leaves small, under 1 cm. *H. microphylla* Lauterbach, *H. acutata* Pilger, *H. nivalia* Ridley, in New Guinea. - **b.** leaves larger. **α.** male flowers axillary, sessile or in nearly sessile groups, individually in the axils of bracts sessile with two very advanced small prophylls, quite often under the group of some sterile scales. - *H. Reinwardtiana* Blume, Sunda islands, new Guinea: leaves obovate, to 7 cm long. - *H. Ledermannii* Pilger, on New Guinea, with thin, looping (twining) branches; leaves very variable. - *H. sessilis* Craib, in Siam; leaves ovate-lanceolate, to 7 cm long. **β.** male flowers at the apex of the axis (axils?), branched out or normal, often provided with small crowded scales stems (pedicels?), in the axils of small bracts, prophylls 0. *H. umbellata* Blume, on the Sunda islands and in **Hinterindien**; leaves oval-obovate, to 4 cm long. - *H. granulata* Hook. f. et Thoms., in the Himalayas: *H. Ridleyi* Gamble, on the Malay peninsula. - see Ridley, Gamble, auf der malayischen Halbinsel. - Vgl. Ridley, Fl. Malay Penins. 111. (1924) 166.

7. Scleropyrum Arnott in Magaz. Zool. and Bot. 11. (1838) 549; Benth. et Hook. f. Gen. Pl. 111. (1880) 228; Hook. f. Fl. Brit. India V. (1886) 234; Hieronymus in E. P. 1. Aufl. III. 1. (1889) 216 (*Sclerophyron*); Pilger in Engl. Bot. Jahrb. LIX. (1924) 122 (*Heydia* Dennst. Schlüss. Hort. malab. [1818] 30: *Scleromelum* K. Schum. et Lauterbach, Fl. Deutsch. Schutzgeb. Südsee [1901] 300, T. 5 [vgl. R. Pilger 1. c.]). – Flowers dioecious or polygamous, 4-5-merous. In the male flower the axis is flat, styles only incompletely developed or 0; filaments of the stamen short; theca of the anther separated from each other, every one of the four loculae with an inclined fissure at the upper end separately dehiscing; the filaments accrued a small hair tuft on the back. Disk circular, at the edge wavy or notched. Ovary inferior; style short, thick, stigma broadly shield-like, at the edge toothed; ovules 3, hanging down from the apex of a straight placenta. Drupe large, obovate to egg-shaped or pyriform: exocarp thick fleshy, endocarp hard; seed spherical, embryos terete in the center of the fleshy endosperm. - Trees or shrubs with frequently thorny branches; leaves large, alternate, short petiolate, pinnately nerved, leathery, entire. Flowers solitary to clustered at the nodes in spikes on older persistent branches.

Name von σκληρόζ, hard, and *Pyrus*, pear: because of form and construction of the fruit. The name *Scleropyrum* stands on the list of the nomina conservanda; Briquet, Règl. internat. nomencl. bot. ed. 2. (1912) 85. Type species *S. Wallichianum* (Wight et Arn.) Arn. (*Sphaerocarya Wallichiana* Wight et Arn.; 1833). Several closely related species in tropical Asia. *S. Wallichianum* to east India and Ceylon, Hinterindien: leaves glabrous or weakly pubescent, to 15 cm long. - *S. Ridleyi* Gamble in Malakka: leaf lower surface softly pubescent, to 20 cm long. - *S. mekongensis* Gagnepain, in Laos. *S. aurantiacum* (Lauterb. et K. Schum.) Pilger and *S. leptostachyum* Pilger in New Guinea.

8. Jodina Hook. et Arn. in Hook. Bot. Miscell. III. (1833) 172; Endl. Gen. Pl. (1840) 1093; Reisseck in Fl. Bras. XI. 1. (1861) 77, T. 23; Cesati in Atti Accad. Sc. Fis. e Mat. Napoli V. Nr. 7. (1873) T. 3; Miers in Journ. Linn. Soc. Bot. XVII. (1878) 85 t. 4; Benth. et Hook. f. Gen. Pl. III. (1880) 223; Hieronymus in E. P. 1. Aufl. III. 1. (1889) 222. - Flowers bisexual, 4-5-merous. Receptacle over the ovary short campanulate. Tepals behind the stamens with a hair tuft. Stamen with a short filament, locules of the anther thecae oblong, dehiscing with a shared fissure. Disk between the stamens extending as rather thick, oblong, blunt lobes. Ovary in the recent flower

half-inferior, thereafter inferior; style rather thick, conical, stigma weakly 3-lobed; ovules 3, hanging from the point of a corkscrewed “to and fro” wound placenta, whose turns lie closely together. Fruit spherical, drupaceous; exocarp fleshy, divided into 5 easily removable segments, endocarp crusty, sometimes splitting into 2-3 valves; seed spherical; embryo short, in the top of the oily-fleshy endosperm, inclined embedded, cotyledons usually as long as the lobar thickened hypocotyl. - Shrub or tree; leaves alternate, glabrous, rhombic, at the corners spiny on the edges. Flowers pubescent, in close, short bundles in the leaf axils.

Name from ῥοδιζ, rust-like, of the plant dried because of the brownish color and the pubescence of the flowers.

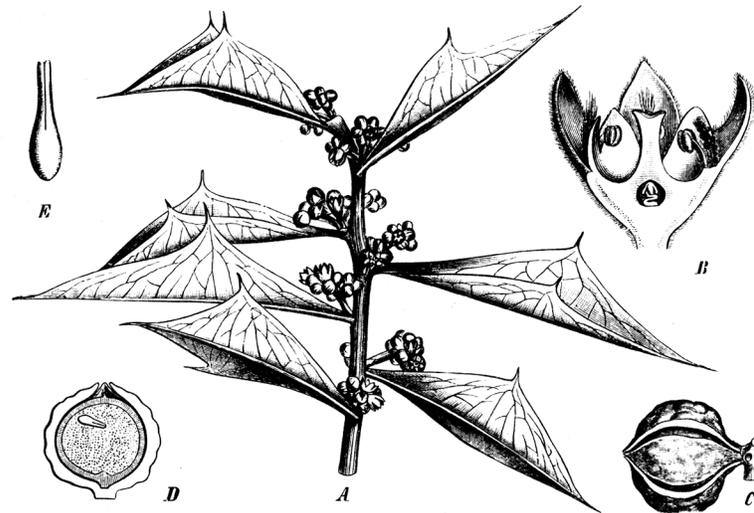


Fig. 34. *Jodina rhombifolia* Hook. et Arn. A habit of a flowering branch, nat. size. B median longitudinal section of a flower (10/1). C ripe fruit (2/1). D median longitudinal section of the same (2/1). E embryo from mature fruit (10/1). - from E. P. 1. Aufl. III. 1, 223, Fig. 143.

One species, *J. rhombifolia* Hook. et Arn. (Fig. 34), in south Brazil, Uruguay and Argentina; leaves 3-6 cm long. The leaves and the oil extracted from the seed, with the native names quebracho flojo, sombre del toro, quinchirin or quinchilin or peje, the denoted tree finds use in folk medicine; also the wood is used. See also Hauman et Irigoyen, Catal. Phanér. Argent., in Anal. Mus. Nac. Buenos Aires XXXII. (1923-25) 45. In former times falsely aligned with the species *Ilex cuneifolia* L. (*Jodina cuneifolia* [L.] Miere p. p.) vgl. O. Kuntze, Rev. gen. III. 2. (1898) 283, and Urban, Symb. Antill. VIII. (1920) 332; it is the Meliaceae *Trichelia cuneifolia* (L.) Urban.

9. **Cervantesia** Ruiz et Pav. Fl. Peruv. et Chil. Prodr. (1794) 39 T. 7, Fl. Peruv. et Chil. III. (1802) 19 T. 241; A. DC. in DC. Prodr. XIV. (1857) 692; Miers in Journ. Linn. Soc. XVH. (1878) 78 T. 3; Benth. et Hook f. Gen. Pl. III. (1880) 222; Hieronymus in E. P. 1. Aufl. III. 1. (1889) 222 (*Casimiroa* Domb. ex Baill. in Adansonia III. [1862 -63] 126). – Flowers bisexual, 5-merous. Receptacle over the ovary short campanulate. Tepals inside behind the stamens with hair tufts. Stamens with short filaments; Locules of the anther oblong, parallel, opening together lengthwise with a longitudinal fissure. Disk at the edge between the stamens protruding as fleshy, ovate or oval, lobes. Ovary first at the base of the receptacle nearly free, then half-inferior and finally nearly inferior; style short, shortish (pudgy), stigma somewhat widened, weakly 2-3-lobed; ovules 2-3, hanging from the apex of thin “to and fro” wound placenta. Fruit drupe-like; exocarp fleshy, from the base divided into 5 easily removable segments, endocarp crustaceous, usually also split into 2-3 segments; seed spherical; embryo linear cylindrical, inclined in the

fleshy endosperm. - Small trees; leaves entire, oval to elliptic, on the top side weakly, on the lower surface pubescent, usually closely; young branches and inflorescences also closely pubescent. Flowers in small balls at short, spike-like, to 1-2 axillary or at the end of the branches paniculate united inflorescences.

Name after Vicente Cervantes, Professor of botany in Mexico, born 1829. – Type species *C. tomentosa* Ruiz et Pav.

3-4 species in Peru and Ecuador. – *C. tomentosa* Ruiz et Pav., in lower mountain forests of Peru; small tree, leaves leathery, to 8-10 cm long, lower surface reddish downy. – *C. glabrata* Stapf, in Ecuador; leaves glabrous, elliptical, to 3-4 cm long.

10. **Buckleya** Torr. in Amer. Journ. Sc. XLV. (1843) 170; Benth. et Hook. f. Gen. Pl. III. (1880) 226; Hieronymus in E. P. 1. Aufl. III. 1. (1889) 219; Small, Man. Fl. Southeast. U. St. (1933) 1249 (*Quadriala* Sieb. et Zucc. in Abh. Math.-Phys. Classe Akad. Wissensch. München IV. 2. Abt. [1845] 194, T. II. B). – Flowers dioecious. Male flowers small, in small cymes, 4-merous, flat, without deepened receptacle. Tepals egg-shaped, disk disk-shaped, four-sharp-edged, hardly lobed. Stamens shorter than the tepals; filament very short, anther 4-loculate, each theca opening inwardly by a longitudinal fissure; hair tuft behind the stamen 0. Pistillodia 0. Female flowers solitary terminal or axillary, 4-merous. Receptacle does not extend over the ovary. Ovary narrowly turbinate, with 8 ribs or younger plain (flat), a little below the tepals and alternating with this, the ovary is provide with four spreading lanceolate, pinnately-nerved bracts (Hochblättern) ¹). Tepals roughly egg-shaped. Disk weakly concave, four-sharp-edged, with the edges between the tepals. Staminodia 0. Style short columnar, stigma clearly four-lobed. Ovules 3-4, very small, hardly recognizable before pollination, hanging down at the apex of the short, thick placenta. Fruit obovate or ellipsoidal, crowned by the persistent and strongly increasing tepals and bracts (Hochblättern) and tepals dropping before ripe; Fruit dry, exocarp thin, endocarp crustaceous; embryo in the center of the fleshy endosperm, only little shorter than this, with short hypocotyl and narrow cotyledons. - Shrubs with lanceolate or oval, short pedicellate, pinnately-nerved, entire, alternate or nearly alternate, usually thin leaves.

Named after S. B. Buckley, a North American botanist and zoologist (1809-1884).

Type species *B. distichophylla* (Nutt.) Torrey (*Borya distichophylla* Nutt. Gen. N. Am. Pl. II. [1818] 232).

The name *Buckleya* Torr. (1843) stood on the list of the nomina conservanda, opposite *Nestronia* Raf. (1836); see Briquet, Règl. internat. nomencl. bot. ed.2. (1912) 85. Now however *Nestronia* is counted as *Darbya* A. Gray.

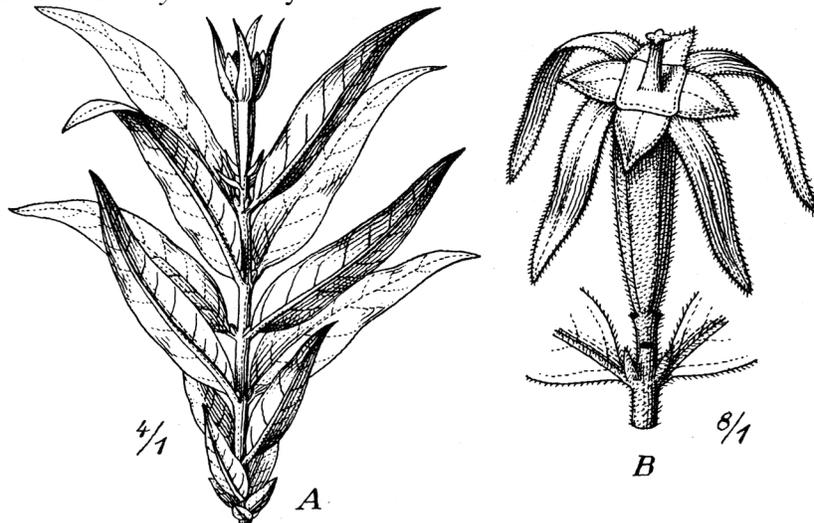


Fig. 35. Female floral spray of *Buckleya distichophylla* (Nutt.) Torr. A. young; B point of a sprig at somewhat older stage. - original.

¹⁾ With the species *B. distichophylla*, from which was presented to me material of recent female flowers from the Arnold Arboretum, the female flower is terminal at a short bracted sprig. The highest pair of leaves on a younger female sprig is about 15 mm long, beyond that follows a completely short axil, which changes into the flowering axis with the inferior ovary. At this axis end sits still 2-3 pairs of more decussate very small, lanceolate scale leaves, then follows the narrow about 3 mm long flowering axis, which carries above four tepals. With this alternating and completely with them moved close four lanceolate ca. 3 mm long leaflets, which surround and protect the upright young flower. The uppermost pair of scale leaves at the axis terminus fall into the gap between two of the leaflets. Now one could interpret the four leaves as two more pairs of leaflet pairs at the axis terminus, which have moved up to the tepals, however their position speaks against the crossed highest scale pair. They are probably better understood as prophylls from two aborted side flowers of a dichasium, which increased the floral axis of the central flower with their peduncle. With older small sprays the scale leaves at the axis terminus dropped, there is (then) only a stigma available. The four bracts (Hochblätter) are then spread just like the tepals cup-like, about 8 mm long. With *B. distichophylla* the bracts (Hochblätter) drop with the ripe fruit; with which Asiatic species they persist and importantly increased still (see above).

Section 1. *Eubuckleya* Pilger nov. sect. - tepals and bracts (Hochblätter) dropping from the ripe ovary, the latter becoming hardly longer than the ovary. *B. distichophylla* (Nutt.) Torr. in the southern United States; after Rehder parasitic on roots of *Tsuga*; leaves oval-lanceolate to broadly lanceolate, often long narrowed, to 5-6 cm long; Fruit obovate elliptical, to over 1 cm long. Gard. and Forest III. (1890) 236. Rarely in culture; Schneider, Ill. Handb. Laubholz. I. (1904) 245; Rehder, Man. Cult. Trees N. Amer. (1927) 202. Vgl. Chatin, Anat. végét. Atlas (1856) t. 91. Fig. 35.

Section 2. *Quadriala* (Sieb. et Zucc.) Pilger nov. sect. - tepals and bracts (Hochblättern) persisting and greatly increasing in fruit. *B. lanceolata* (Sieb. et Zucc.) Miq. (*Quadriala lanceolata* Sieb. et Zucc., *B. Joan* [Sieb.] Makino), in Japan and China; lower branch leaves oval, upper lanceolate, long narrowed, to 7-9 cm long; Fruit to 1.5 cm long, ellipsoid, strongly serrated, the crowning wings of the bracts (Hochblätter) to 3-4 cm long, lanceolate, rough-dry epidermis, strongly pinnately-nerved. - *B. Graebneriana* Diels and *B. Henryi* Diels in China¹⁾. - with the two latter species still more strongly than with *B. lanceolata* the peculiarity steps out the fact that particularly the lower branch leaves rough-dry epidermis, often reddish colored from which green Spreite strongly set off point shows, which corresponds to the bud segment; with the small leaves at the base of the branches that are often half as large as the leaf, for upper leaves often have only a small dry acute (acuminate apex) present. See George M. Schulze, Vergleichend morphologische Untersuchungen an Laubknospen und Blättern australischer u. neuseeländ. Pflanzen, in Feddes Repert. Beiheft LXXVI. (Beiträge zur Syst. u. Pflanzengeogr. XI.) (1934) 62 Tafel XVI (*Buckleya Henryi*).

11. **Omphacomeria** (Endl.) A. DC. in DC. Prodr. XIV. (1857) 680 (pr. p.); Bentham, Fl. Austral. VI. (1873) 225 (pr. p.), in Hook. Icon. T. 1172 (1876); Benth. et Hook. f. Gen. Pl. III. (1880) 227 (pr. p.); Hieronymus in E. P. 1. Aufl. III. 1. (1889) 217 (pr. p.) (*Leptomeria* sect. II R. Br. Prodr. Fl. Nov. Holl. [1810] 354; *Leptomeria* sect. *Omphacomeria* Endl. Gen. [1837] 326). - Flowers monoecious (or rarely bisexual or polygamous); Bracts 0. (sometimes appearing on the thick pedicel, which bears the female flowers, at the end completely short nearly 3-lobed; perhaps a vestige of a bract and two prophylls.) Male flowers small, to 4-6 at the end of a very

short, thick peduncle, sessile, 4- (rarely 5-)merous; axis under the tepals hardly developed, nearly flat. Tepals ovate, spread. Disk lobed flat, hard. Stamens very small, reaching 1/2 the tepal (length); filament very short, thick; anther with thick connective, with two 2-loculate parallel thecae, each theca with longitudinal fissure opening separately. Pistillodium very small or hardly developed. Female flowers solitary or to two at the end of a short, thick peduncle. Receptacle under the tepals little developed. Staminodia \pm developed. Style short columnar, at the end two-lobed. Fruit egg-shaped, exocarp fleshy, endocarp bony, rather thick. – Leafless “switch shrub” (Rutenstrauch) (of the available leafless specimens I have seen, they have at most small denticles at the basis of the inflorescence peduncles).

Name from $\sigma\upsilon\varphi\alpha\chi\eta$, Baurer fleshy raceme; doubtfully related to *-meria*. 1 species, *O. acerba* (R. Br.) A. DC. in east Australia; Branches striated, thin, spiky; flowers only 2 mm in diameter.

The second species indicated by A. De Candolle in the Prodrusus, *O. psilotoides* A. DC, is = *Exocarpus stricta* R. Br.

12. **Darbya** A. Gray in Amer. Journ. Science and Arts 2. Ser. I. (1846) 388 (*Nestronia* Raf. New Fl. Amer. III. (1836) 12 [genus incert.]; Small, Fl. Southeast. Un. St. [1903] 1103; Fernald in Rhodora XXX. [1928] 22; *Comandra* Sect. *Darbya* A. DC. in DC. Prodr. XIV. [1857] 637; *Buckleya* spec. aut.). – Flowers polygamo-dioecious, 4-5-merous. Male flowers with wedge-shaped, hollow receptacle lined by the disk. Stamens with short filaments, behind them at the base of the tepals clear hair tufts. Disk thin, at the edge wavy or 4-5-lobed. Pistillodium 0. Inferior ovary wedge-shaped, receptacle not extending over the ovary; style short, stigma 3-4-lobed. drupe nearly as broad as long. - Low, parasitic shrub; leaves opposite, thickish, ovate. Male flowers in cymose axillary cymes, female flowers solitary axillary. Name after J. Darby, professor in Macon, later in New York. 1 species, *D. umbellulata* A. Gray (*Nestronia umbellula* Raf.; see Rehder, Man. cult. trees N. America [1927] 202), in southeastern United States; leaves 2-7 cm long, fruit 10-13 mm long.

¹⁾ Diels in Englers Bot. Jahrb. XXIX. (1901) 306.

13. **Pyrularia** Michx. Fl. Bor. Amer. 11. (1803) 231: A. DC. in DC. Prodr. XIV. (1857) 628 pr. p.: Benth. et Hook. f. Gen. Pl. III. (1880) 223: Hook. f. Fl. Brit. India. V. (1886) 230: Hieronymus in E. P. 1. Aufl. III.1. (1889) 222: Small, Fl. Southeast. Un. St. (1903) 1103: Rehder in Bailey, Stand. Cyclop. Horticult. V. (1922) 2865 (*Hamiltonia* Mühlenb. in Willd. Spec. Pl. IV. [1805] 1114: *Sphaerocarya* Wall. in Roxb. Fl. Ind. ed. Carsy 11. [1824] 371: *Calinux* Raf. in Med. Repos. New York V. [1808] 352). – Flowers dioecious or polygamous, 5-merous. Tepals behind the stamens with one the anther-attaching hair tuft. Male flowers with a smaller spherical axis. Stamen with short filament; locule of the thecae oblong, dehiscing together by a longitudinal fissure. Disk between the stamens clearly extended into scales. Inferior ovary of the female or bisexual flowers turbinate; placenta twisted, ovules upward back-curved; style thickish, short columnar, stigma depressed-head-like (capitate). Drupe pyriform or nearly spherical, relatively large, is well crowned by the tepals; exocarp fleshy, endocarp hard, thin; seed spherical; embryo in the upper half of the fleshy-oily endosperm, short, terete, cotyledons as long as the hypocotyl. - Trees or shrubs; leaves alternate, thin-membranous. Male flowers arranged in small to terminal racemes or raceme-like cymose-panicles; fruit-bearing flowers solitary or in two.

Name a diminutive of *Pirua* (*Pyrua*). – Type species *P. pubera* Michx.

2 species. *P. pubera* Michx., in North America in southeastern United States, oil-nut, Buffalo nut; shrub 1-3 m high; leaves ovate-elliptic; buds with nearly glabrous scales; fruit 1.5-2 cm in diameter. Rarely in culture. Schneider, Illustr. Handb. Laubholzk. I. (1904) 246; Rehder, Man.

Cultiv. Trees (1927) 202 (parasitic on roots of *Tsuga*. - *P. edulis* (Wall.) A. DC, in the central and eastern trop. Himalaya; small or large, sometimes thorny tree; buds large, with silky-haired scales; leaves to 15 cm long; drupe to 5 cm long, into which pedicel diminishes, eaten by the natives.

14. **Osyris** L. Spec. pl. ed. 1. (1753) 1022, Gen. pl. ed. 5. (1754) 448: Grenier et Godron, Fl. de France 111. (1855) 68: Willkomm et Lange, Prodr. Fl. Hispan. I. (1861) 294: Boissier, Fl. Orient. IV. (1879) 1058: Benth. et Hook. f., Gen. Pl. III. 1. (1880) 227: Hieronymus in E. P. 1. Aufl. III. 1. (1889) 218: Engler U. Volken in Notizbl. Bot. Gart. u. Mus. Berlin-Dahlem I. (1897) 269: Fl. Trop. Afr. VI. 1. (1911) 433: Engler, Pflanzenwelt Afrikas 111. 1. (1915) 69 (*Osyris* L. sect. *Euosyris* A. DC. in DC. Prodr. XIV. [1857] 633). – Flowers dioecious or polygamous (male and bisexual), 3-4-merous. Male flowers compacted into axillary racemes, often cymose, small. Tepals valvate, broadly triangular, behind the stamens at the base of the filament with small hair tufts. Disk slightly concave, 3-4-lobed. Filaments of the stamen short, anther with 4 locules, the thecae dehiscent by a longitudinal fissure. Pistillodium nearly 0. Female (or bisexual) flowers usually solitary, rarely to three terminals on a short sprig or axillary peduncle. Disk 3-4-lobed. Ovary inferior; style short or somewhat extended, stigma 3-4, short, thickish; Ovules 2-4, hanging down from a rather thick and short placenta, with the apex upward back-curved. Fruit drupe-like, spherical or egg-shaped, at the end with the remainders of the tepals and disk; exocarp somewhat fleshy, endocarp thin crusty. Seed spherical; embryo in upper parts of the plentiful endosperm, straight, cotyledon longer than the hypocotyl. – Branching shrubs or small to medium sized trees, strongly branched, branches sharp-edged; leaves alternate, linear to broadly elliptic, usually leathery, glabrous, rarely somewhat soft-pubescent.

δσυριζ, Greek plant name with an unknown relationship. – Type species *O. alba* L.

6-7 species in the Mediterranean area, trop. Africa, India, Tibet, Siam, Indochina, south China, in the tropics not in the lowlands. *O. alba* L. (Fig. 36): widespread in lowland dry places and the hill country in the whole Mediterranean area; smaller, strongly branched shrub, leaves linear-lanceolate to lanceolate, 10-20 mm long; male flowers compacted in numerous axillary short racemose cymes, the broad small bracts very deciduous, upper 3-4 flowers nearly cymose; frequently the small axillary sprays more strongly developed, those foliage leaf-like or also sprigs further weakly paniculately branched; female flowers solitary terminal on short branches, which above bear several nearly whorled compacted leaves under the flower; drupe red, somewhat juicy, soon drying, pea-sized. - related *O. lanceolata* Bochst. et Steud. (*O. quadripartita* Decne.) in south Spain, Algiers, Morocco; leaves broader; male flowers in 3-flowered axillary cymes; female flowers solitary axillary, pedicellate, 2 deciduous prophylls at the basis of the flower. - *O. abyssinica* Hochst., in mountain areas at stony places, Abyssinia, 1500-3200 m, Eritrea, Yemen, East Africa up to eastern Cape country, German southwest Africa, Huilla; strongly branched shrub or smaller tree with variable, oval to egg-shaped, to 5 cm long, leathery leaves; fruit ellipsoid or obovoid; after R. Marloth, Fl. South Afr. I. (1913) 162, calling the species Bergbastoder Transvaal sumac (leaves for tanning). - related to *O. Wightiana* Wall. (*O. tenuifolia* Engl., *O. arborea* Wall.); German East Africa, Somali country, Sokotra, India (temp region), Burma, Siam to south China; high bush or tree to 10-15 m high; leaves usually thin, fruit spherical. With the natives in East Africa the cooked extract of the young shoots is given to cattle that have gotten sick with the fever from drinking; the wood is appreciated because of its pleasant smell upon burning. For *O. tenuifolia* Volken observed a grasshopper, which pretends [to be this plant by its] pairs of leaves with its bluish green coloring and the position of the legs and the dorsal shell (mimicry). - *O. divaricata* Pilger, east India, Sindh; leaves small, elliptic.

Conwentz, Flora des Bernsteins II. (1886) 133 & 134, mentions the fossil flowers of *Osyris schiefferdekeri* Caspary and *O. ovata* Caspary from the amber.



Fig. 36. *Osyris alba* L. *A* habit of a male branch, nat. size. *B* habit of female branch, nat. size. *C* male flower seen from above (10/1). *D* female flower halved (10/1). *E* ripe fruit (2/1). From E. P. 1. Aufl. III. I, 219, Fig. 140.

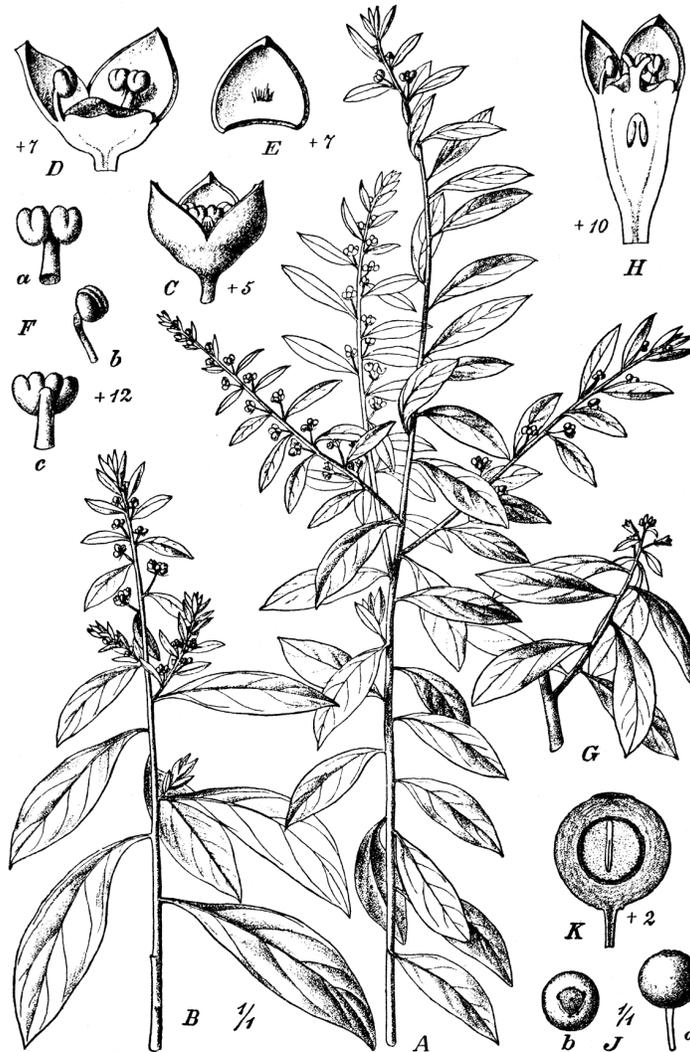


Fig. 37. *Osyris Wightiana* Wall. (*O. tenuifolia* Engl.). A. Branch of the male plant of Kilimanjaro. B. Branch of the female plant of Kwale (Kenya). C, D male flowers. E tepals. F Stamen. G branch of female plant of the Kilimanjaro. H female flower in longitudinal section. J Fruit. K fruit and seed in longitudinal section. - Aus Engler, Pflanzenwelt Afrikas III. 1. (1915) 70. Fig. 38.

15. **Geocaulon** Fernald in *Rhodora* XXX. (1928) 23 (*Comandra* aut.; *Comandra* sect. *Haplocomandra* Benth. et Hook. f. Gen. Pl. 111. [1880] 224). – Flowers bisexual, the central in the cyme usually female, the lateral male, or rarely all male. Receptacle of the male flowers turbinate, inferior ovary of the female flower bell-like; receptacle not extended over the ovary. Filament subulate, anther egg-shaped. Epigynous disk with extended lobes. Style conical, short, stigma head-like (capitate). Drupe ovoid-spherical, red, crowned by the tepals. – Subshrub with creeping, branched rhizome; flowering branches upright, with alternate leaves. Only few 3-flowered cymes with thin peduncles in the axil of the middle leaves; small bracts deciduous.

Name from γη earth, and χαυλοζ, stem (stalk); because of the long creeping, underground rhizomes.

Only species *G. lividum* (Richardson) Fernald, south from Labrador to Alaska and up to the northernmost United States; rhizome thin (1.5-3 mm), creeping in moss or damp humus, upright flowering. Branches 10-30 cm high; leaves elliptical, 2-5 cm long; Fruit 6-10 mm in diameter, fleshy, stone core thin-walled.

16. **Comandra** Nuttall, Gen. North Amer. Pl. I. (1818) 157; Hieronymus in E. P. 1. Aufl. III. 1. (1889) 221 (*Hamiltonia* Willd. ex Spreng. Syst. Veg. I. [1825] 831 pr. p.; *Thesium* a. *Thesiosyris* Reichenb. Fl. Germ. Exc. [1830-32] 157; *Comandra* Sect. 1. *Eucomandra* A. DC. in DC. Prodr. XIV. [1857] 636, excl. *C. livida*; *Comandra* sect. *Eucomandra* Benth. et Hook. f. Gen. Pl. III. [1880] 224). - Flowers bisexual, 4-5-merous. Receptacle campanulate over the ovary. Tepals behind the stamens with hair tufts. Filaments of the stamen rather thick, short; Locules of the anther thecae oblong, dehiscent together by a longitudinal crack. Disk between the stamens advanced into short lobes. Ovary inferior; style thin, rather long; stigma small-capitate; ovules 2-3, hanging down from the apex of a bent back and forth, rather long and rather thick placenta, later from the apex upwardly back-curved. Fruit nearly dry, egg-shaped or nearly spherical, above crowned by the receptacle and the persistent tepals; exocarp thin, endocarp crusty; embryo terete in the fleshy endosperm. - Herbs or shrublets with creeping rhizomes; upright, shoots with alternate leaves. Flowers small in 3-flowered terminal and axillary, often numerous, rounded cymes.

Name from $\chi\omicron\mu\eta$ tuft, und $\delta\upsilon\eta\omicron$, male; after the hair tuft behind the stamen. – Type species *O. umbellata* (L.) Nutt.

About 6 species, one in the Danube countries, the others in North America. - *C. umbellata* (L.) Nutt., widespread in the United States; rhizome woody, creeping, branched, upright shoot thin, nearly herbaceous, to 30 cm high, normally or weakly branches out; leaves elliptical obovate, to 3-3.5 cm long; 3-flowered cymes terminal and more axillary in the upper often \pm strongly reduced leaves. - *C. Richardsiana* Fernald, from Canada to Saskatchewan and in northeastern United States. - *C. elegans* (Rochel) Reichenb. f., in Hungary and the Balkans states up to northeastern and middle Greece, Macedonia and up to northern lower Asia; woody rhizome creeping far in the sand; upright leafy and flowering shoots branched out, to 40 cm high; leaves oblong-lanceolate.

17. **Nanodea** Banks ex Gaertner f., De Fruct. et Sem. III. (1805) 251, T. 225; Gay, Fl. Chil. V. (1849) 324; A. DC. in D9. Prodr. XIV. (1857) 675; Benth. et Hook. f. Gen. Pl. III. (1880) 220; Hieronymus in E. P. 1. Aufl. III. 1. (1889) 218; De Wildeman, Les Phanerog. des Terres Magellan. (1905) 78; Skottsberg, Feuerländische Blüten, in Wissensch. Erg. Schwed. Südpolar-Exped. 1901-1903, IV. Lief. 2. (1905) 50, Fig. 71-75 (*Balenerdia* Commers. ex Steud. Nom. Bot. [1821] 99; *Ballezerda* Commers. ex A. DC. l. c.). – Flowers bisexual, 4-merous; Receptacle over the ovary flat dish-shaped. Tepals at the base somewhat diminished, at the base behind the stamen with hair tufts. Filaments of the stamens very short; locule of the anther thecae ovoid, parallel inward arranged, dehiscing with a common longitudinal fissure. Disk concave, lining the receptacle, between the stamens angular or alternately very short lobed. Ovary inferior, turbinate; style short, thick, stigma nearly spherical, somewhat two-lobed; ovules 2 hanging down from the apex of the short placenta. Drupe spherical, exocarp fleshy, endocarp bone-hard thickened; Embryo in the fleshy endosperm, short, approximately terete with small cotyledons. - Small herb with creeping, branched stems; leaves alternate, narrowly linear. Flowers small, to three between the highest leaves, the lateral in the axil of flabellate bracts (Hochblättern).

Name from $\nu\alpha\upsilon\pi\delta\eta\zeta$, dwarfish.

1 species, *N. muscosa* Gaertn. f., in southern South America (Andean Patagonia, Tierra del Fuego, Staten-Islands [Argentina], Falkland-Islands). - Hauman et Irigoyen in Anal. Mus. Nac. Buenos Aires XXXII. (1923-25) 46.

18. **Myoschilos** Ruiz et Pav. Fl. Peruv. et Chil. Prodr. (1794) 41, T. 34, Fl. Peruv. et Chil. III. (1802) 20, T. 242 Fig. a; Gay, Fl. Chil. V. (1849) 326 (*Myoschilos* A. DC. in DC. Prodr. XIV. [1857] 6271); Miers in Journ. Linn. Soc. XVII. [1878] 127, T.5; Benth. et Hook. f. Gen. Pl. III. [1880] 226; Hieronymus in E. P. 1. Aufl. III. 1. [1889] 218). – Flowers bisexual, 5-merous.

Receptacle not extended beyond the ovary. Stamens shorter than the tepals; filament filiform; anthers small, nearly terminal, connective not outstanding between the thecae; locules of the thecae ovoid, parallel attached inward, opening by a common longitudinal fissure. Disk broad, even, rather thickish. Inferior ovary turbinate; style short threadlike, stigma 2-5-lobed, with lobes that are horizontally distant; ovules 3-5, hanging down from the apex of a short, thick placenta, with apex upwardly back curved. Fruit small, ovoid, exocarp thin fleshy, endocarp crustaceous; fruit crowned by the tepals, later by a circular stigma, surrounded at the base by substantial prophylls and the broad wrapper-like bracts; seed roundish, embryos small, cylindrical, within the fleshy endosperm. - Rather richly branched, glabrous shrub; leaves alternate, oblong oval, membranous, entire. Flowers in catkin-like racemes, which stand solitary or by twos at the nodes of the previous-year's branches; flowers sessile, by broad prophylls and one sometimes surrounded by the fused floral axis bracts.

1 species, *M. oblongus* Ruiz et Pav., in central and southern Chile; the leaves used as a light purgative (?); common name Codocoypu or Orocoypu., also Senna. - Hauman et Irigoyen in Anal. Mus. Nac. Buenos Aires XXXII. (1923-25) 45.

¹⁾ In Prodr. l. c. is used the more correct way of writing *Myoschilos*; the name comes from μνζ, mouse, and χνλοζ, juice. Ruiz und Pavon noted l. c.: Genus *Myoschilos* graece quasi pabulum muris Coypu a Molina descripti, qui ejus fructu vescitur, nominavimus.

19. **Acanthosyris** (Eichl.) Griseb. in Götting. Abh. XXIV. (Symb. Fl. Argent. 1871) 151; Benth. et Hook. f. Gen. Pl. III. (1880) 221; Hieronymus in E. P. 1. Aufl. III. 1. (1889) 224 (*Osyris* L. Sect. *Acanthosyris* Eichl. in Fl. Bras. XIII. I. [1864] 236, T. 53). – Flowers bisexual, 4-5-merous. Receptacle above the ovary shortly campanulate. Tepals free up to the disk, behind the stamens with a hair tuft. Stamens with short, thin filaments; Anther thecal locules oblong, parallel dehiscing with a common longitudinal fissure. Disk between the stamens waning into extended, somewhat fleshy scales. Ovary half-inferior; style rather long; stigma indistinct 5-lobed; ovules 3, hanging down from a long and back-and-forth twisted placenta, with the apex upwardly back-curved. Drupe spherical, relatively large, crowned by the receptacle remainders with style remainders and ± remainders of the tepals, with juicy, sugary exocarp and hard, woody endocarp; embryo small. - Trees or shrubs, frequently with leaf axillary thorns; leaves on short shoots clustered, on young long shoots slightly spiral. Flowers in small 3-5-flowered cymes, these numerous in the axils of the basal scales of the short shoots, with longer, fine petioles (however always shorter than the foliage leaves) or short petiolate. Bracts (Hochblätter) small, easily dropping.

Name von *αχάνυα*, thorn, and *Osyris*. – Type species *A. spinescens* (Mart. et Eichl.) Griseb. 2-3 species in South America. *A. spinescens* (Mart. et Eichl.) Griseb. (Fig. 38 A-O), tree in south Brazil, Argentina; on young long shoots the leaves stand far away spiral and carry in their axil a branch thorn, over this stands a further bud or also two to three serial; after dropping the leaves usually only the lowest bud attains full growth to a tufted, leafy, short branch, so that over the leaf scar then the thorn and a short shoot follow; the short branch carries scale leaves at the base, in whose axil the fine stems of the small cymes are located; individual short shoots can attain full growth again to long shoots; thorns about 1 cm long, Thorns about 1 cm long, leaves broadly oblanceolate to ovate, 3-8 cm long. - *A. falcata* Griseb. (Fig. 38 D), in Argentina, Paraguay and east Bolivia, with smallish, long, falcate leaves and very short inflorescences; thorns present or missing; more substantially or at unfavorable locations small tree; the ripe, red fruits, mentioned in the Guarani language as Ybá hehé, are extraordinarily sweet and cherry sized; they are eaten by the natives and also used for the production of liqueur. The wood of both related species “quebrachillo” or “sombra del toro hembra” is mentioned by cabinet makers etc.. - Hauman et Irigoyen in Anal. Mash Nac. Buenos Aires XXXII. (1923-25) 40.

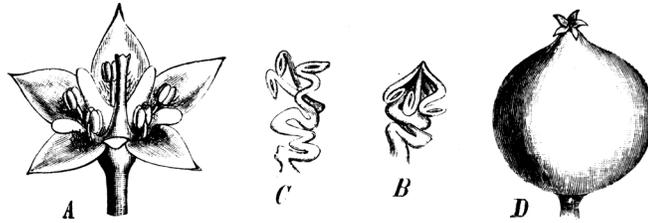


Fig. 38. A-C *Acanthosyris spinescens* (Mart. et Eichl.) Griseb. A flower (6/1). B placenta with three ovules, C the same separate from each other (10/1). - D fruit from *A. falcata* Griseb., nat. size. - from E. P. 1. Aufl. III. 1, 221, Fig. 142.

20. **Santalum** L. [Gen. pl. ed. 2. (1742) 165] Spec. pl. ed. 1. (1753) 349, Gen. pl. ed. 5. (1754) 165; Benth. et Hook. f. Gen. Pl. III. (1880) 224; Hieronymus in E. P. 1. Aufl. III. 1. (1889) 220 (*Sirium* Schreb. Gen. Pl. [1789] 82; *Santalum* sect. *Eusantalum* A. DC. in DC. Prodr. XIV. [1857] 681). - Flowers bisexual, 4-5-merous. Receptacle campanulate-cylindrical or obconic-funnel-shaped (infundibuliformis). Tepals up to the disk free, inside behind the stamens with hair tufts. Stamens shorter than the tepals; filament short; anthers with parallel locules, thecae dehiscent by a longitudinal fissure. Disk of the receptacle a thin lining between the stamens into fleshy, spatulate, triangular or nearly square or oval lobes taken off. Style extended, stigma short 2-4-lobed. Ovary half-inferior or inferior; ovules 2-4, attached below the middle of the long pointed, straight placenta. Drupe nearly spherical, with circular scar of the tepals and flat conical remainder of the upper part of the ovary (with half-inferior ovary) or within the ring flat above (with inferior ovary); exocarp rather thin, endocarp hard, often rugose; seed spherical; embryo in the center of the endosperm upright or inclined, linear-terete, hypocotyle longer than the cotyledons. - Hemiparasitic trees or shrubs; leaves usually opposite, \pm leathery or fleshy, pinnately-nerved. Small panicles axillary or terminal; bracts deciduous, small.

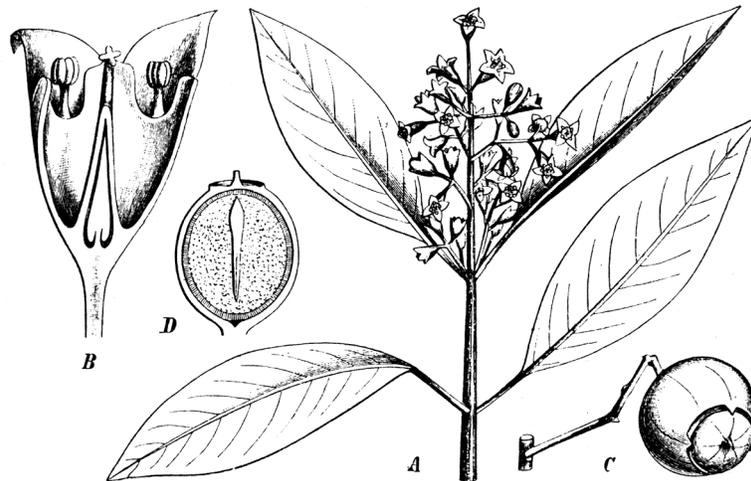


Fig. 39. *Santalum album* L. A Habit of a flowering branch, nat. size. B nearly median longitudinal section of a flower (10/1). C ripe fruit (2/1). D longitudinal section of the fruit (2/1). - from E. P. 1. Aufl. III. 1, 220, Fig. 141.

Most important special literature: F. G. Hayne, Darst. Arzneykunde Gew. X. (1827) T. 1, 2. - B. Seemann, Flora Vitiensis (1865--68) 210, T. 55. - Bentham; Flora Austral. VI. (1873) 213-215. - W. Hillebrand, Flora of the Hawaiian Islands (1888) 388-390. - G. Meurisse, Etude du genre *Santalum* L., in Bull. Soc. Linn. Paris no. 129. (1892) 1025-1027. - J. F. Rock, The indigenous trees of the Hawaiian Isl. (1913) 126-135: The sandalwoods of Hawaii, Hawaiian Board of Agric. and For., Bot. Bull. 3 (1916). - C. Skottsberg, The genus *Santalum*, in Bernice P.

Bishop Mus. Bull. XLIII. (1927) 40-64: The geographical distribution of the sandal-woods and its significance, in Proc. Fourth Pacif. Sc. Congress, Java (1929) 435-440: Further notes on Pacific sandalwoods, in Meddel. Göteborgs Bot. Trädg. V. (1930) 135-145: Additional notes, l. c. IX. (1934) 185-190. - O. Degener, Fl. Pl. Hawaii Nat. Park (1931) 142.

Name of the Arab Ssandal = sandalwood (see Rumphius, Herb. Amboin. II. (1750) 44 [Sandalum]).

Type species *S. album* L. 19 species in north and east Australia, southeast New Guinea, on the Lesser Sunda Islands and the Pacific islands to Hawaii, Juan Fernandez: doubtfully whether originally in east India.

Section I. *Eusantalum* Skotts. in Proc. Fourth Pacif. Sc. Congress, Java (1919) 436. Receptacle bell-like, cylindrical; ovary half-inferior, thus remaining conical on the fruit; style long, thin; flowers relatively large, red. - *S. album* L, Sandal tree (Fig. 39), on the small Sunda islands, to Timor, in drier areas of east India, particularly in the west, at an elevation of 700-1200 m. [the indigent of the sandal tree in east India is doubtful, an introduction already from the east in pre-Christian times is probable, see C. E. C. Fisher in Kew Bull. (1927) 200-202 und in Journ. Ind. Bot. Soc. VII. (1928) 12-13]: under favorable conditions to 30 m high tree, usually lower; Leaves oval to ovate-oval, 4-8 cm long; small floral axes axillary and terminal, 2-4 cm long. The tree supplies the probably-smelling close, with difficulty fissile Sandal wood: the young wood is white, the heartwood yellow, smelling more strongly; the first is used for smaller carpenter works, caskets etc. (see Warburg, Pflanzenwelt I. [1913] 509), the latter for perfumes and for the production of the strongly smelling sandal oil. This is present in all elements of the wood present to 3-5% and extracted as a thick, yellow liquid; it is found in medicinal and perfume uses (see G. Watt, Dict. Econ. Products India VI. IL [1893] 461-467: Rahm, Sandelhout op Timor, in Tectona XVIII.. [1925] 499-545; Gard. Chron. 3.ser. IL. [1911] 20-21: W. Holtz in Pflanze IX. Beih. I. [1913] 13-18, T.2: von Brehmer in Wiesner, Rohstoffe 4. Aufl. II. [1928] 1384). Incidentally sandal wood is also the name for woods of other different plants, first other *Santalum* species, then also e.g. of *Pterocarpus santalinus* L. in India (see from Brehmer l. c.). - *S. Freycinetianum* Gaudich., tree on Hawaii, leaves narrowly elliptical or broadly lanceolate, 5-10 cm long: Flowers 7-10 mm long. On Hawaii 8 *Santalum* species come forwards (see next section); in earlier times a rich existence was present, which was strongly decimated, however, by the robbery economy; sandalwood was the first important export article of the islands and until 1840 went particularly to China; today is the sandalwood only sparse to find (see also Ch. J. Judd, The parasite habit of the Sandalwood Tree, in Proc. Hawai. Acad. Sc., Bernice P. Bishop Spec. Publ. XX. [1932]; Trop. Woods no. XXXV. [1933] 59). - *S. yasi* Seemann on the Fiji islands, nearly exterminated. - *S. lanceolatum* R. Br. in north and east Australia; shrub or small tree; Fruit 1 1/2 cm in the diameter. Several species in addition of north and east Australia described. - *S. austrocaledonicum* Vieill., on New Caledonia and the New Hebrides. - *S. papuanum* Sumo of merhayes, on New Guinea.

Section III. *Polynésica* Skotts. l. c. 437. - receptacle shortly conical; style rather short; ovary half-inferior; flowers small, whitish or greenish. - *S. insulare* Bert. ex DC on Tahiti; Tree with elliptical or elliptic-lanceolate leaves to 10 cm long; inflorescence paniculate. - *S. multiflorum* J. W. Moore, on Raiatea (Society Islands), Tahiti Archipelago. - *S. marchionense* Skotts., on the Marquesas islands. - *S. fernandezianum* Phil., on Juan Fernandez. The sandalwood of Juan Fernandez was in former times common on both islands, is now, however, completely exterminated; Skottsberg saw the last living specimen (Oliver in Hook. Ic. T. 2430 [1896]; Johow, Fl. Juan Fernandez [1896] 127-133, T.14; Skottsberg, Nat. Hist. Juan Fernandez 11. [1922] 117).

Fossil indicated from the Tertiary period of Europe: *Santalum acheronticum*, *salicinum*, *osyrinum*, *microphyllum* Ettingshausen, Tert. Fl. Häring in Tirol. Abh. k. k. geol. Reichsanst. II. Abt. 3 Nr. 2 (1853) 49-50.

21. **Rhoiacarpus** A. DC. in DC. Prodr. XIV. (1857) 634; Hill in Fl. Capens. V. (1915) 207 (*Hamiltonia* spec. Harv. Gen. South Afr. Pl. [1838] 298; *Colpoon* spec. Benth. et Hook. f. Gen. Pl. III. [1880] 225; Hieronymus in E. P. 1. Aufl. III. 1. [1889] 217; Sim, For. and For. Flora Col. Cape of Good Hope [1907] 303). – Flowers in small axillary and terminal cymes, whose short terminal sprig is 1- to 5-flowered; bracts persistent. Flowers bisexual, 5-merous. Tepals ovate, acute (spitzlich), behind the stamens with small hair tufts. Disk somewhat concave, with very blunt short lobes. Style cylindrical-conical, stigma (lobes) 5 short. Placenta of the inferior ovary cylindrical, ovules 5 hanging down from the point of the placenta.

Drupe spherical-egg-shaped, crowned by the persistent tepals. - shrub; recent branches sharply four-edged; leaves opposite, leathery, ovate, at the base somewhat cordate.

Name from *ροια*, (*Punica granatum*) and *χαρποζ*, fruit; because of the red, edible fruits. 1 species, *Rh. capensis* (Harv.) A. DC. in eastern South Africa; leaves to 5 cm long. Cymes to 2 cm long; Fruit (whether ripe?) 1 cm long, red, edible.

22. **Colpoon** Berg. Descr. Pl. Cap. Bon. Spei (1767) 38, T. I, Fig. 1; Benth. et Hook. f. Gen. Pl. III. (1880) 225 pr. p.; Hieronymus in E. P. 1. Aufl. III. 1. (1889) 217 pr. p.; Sim, For. and For. Fl. Col. Cape of Good Hope (1907) 303 pr. p. (*Fusanus* Murray in L. Syst. Veg. ed. XIII. [1774] 765; Lam. Ill. Genr. [1791] 300, T. 73 et 842; *Thesium* spec. Thunb. Fl. Cap. [1823] 211; *Osyris* L. sect. II *Colpoon* A. DC. in DC. Prodr. XIV. [1857] 634; *Osyris* spec. in Fl. Capens. V. [1915] 209). – Flowers in small terminal panicles, whose lower sprig stems are naked and at the end small, nearly head-shaped, bearing about 10-flowered cymes; bracts small, subulate or lanceolate, soon deciduous. Flowers bisexual not extended over the ovary. Tepals obtuse, tip somewhat cap-shaped. Stamens short, behind the filaments some hair; thecae opening by one longitudinal fissure. Disk weakly 4-lobed. Stylus short, stigma very short 4-parted. Ovules 4-5 hanging down from a thick, central placenta, upwardly back-curved. Fruit usually developing only one in the capitulate cymule, upper capitulate stem thickened; fruit reddish, later brown, obovoid or ellipsoid; only above with weak remains of the tepals and disk; exocarp fleshy, endocarp crust-like; embryo embedded in the center of the endosperm inclined, terete with very short cotyledons. - Small tree or shrub; Branches strongly compacted; leaves opposite or on strong branches also \pm alternate, leathery, elliptical or obovate-elliptical.

Name after a designation by the natives? 1 species, *C. compressum* Berg., of South Africa widespread, particularly in coastal dunes, in addition, in mountain forests, to Natal; with utilizable wood of small importance; leaves 2-3 (-4) cm long, panicles 1.5-2 cm long; fruit 8-11 mm long. - after Marloth, Fl. South Africa I.(1913) 162 T. 37A, is called the plant Prumbast, Cape Sumach; the leaves contain a glycoside osyritrin and much tannin; used for the tanning.

23. **Eucarya** T. L. Mitchell, Three Exped. II. (1839) 100, nomen subnudum; Sprague et Summerhayes in Kew Bull. (1927) 195 (*Fusanus* L. see. R. Br. Prodr. Fl. Nov. Holl. [1810] 355; *Fusanus* R. Br. see. Benth. Fl. Austr. VI. [1873] pr. p.; *Fusanus* sect. *Eufusanus* Benth. et Hook. f. Gen. Pl. III. [1880] 225, Hieronymus in E. P. I. Aufl. III. 1. [1889] 217; *Santalum* sect. *Eusantalum* & 2 A. DC. in DC. Prodr. XIV. [1857] 684; *Mida* sect. *Eucarya* O. Ktze. in Post et Kuntze, Lex. Gen. Phan. [1903] 367). –

Flowers in small terminal or axillary panicles with small and deciduous bracts. Flowers bisexual, 4-merous. Receptacle over the ovary cup-shaped. Lobes of the disk short, broad, nearly truncate. Filament of the stamen short, thecae parallel with one longitudinal fissure; behind the filament small hair tufts. Ovary half-inferior; style very short or nearly 0, stigma lobes 2-3; ovules 2-3. Fruit spherical or nearly spherical, tepal remnants often remaining at the tip; exocarp \pm fleshy, endocarp hard, usually rugose; seed spherical, embryos in the center of the endosperm. - Small trees or shrubs with opposite leaves.

Type species *E. Murrayana* Mitchell.

4-6 species in Australia. *E. acuminata* (R. Br.) Sprague et Summerhayes (*Fusanus acuminatus* R. Br.), in N. S. Wales, south and west Australia; shrub or to 10 m high tree with lanceolate, to 10 cm leaves; panicle terminal; tepals persisting nearly up to fruit ripening; fruit to nearly 2 cm in diameter (Fig. 67 in Diels, Die Pflanzenwelt von West. Australien [1906]). - *E. spicata* (R. Br.) Sprague et Summerhayes (*Fusanus spicata* R. Br.), in south and west Australia; inflorescences more axillary.

E. acuminata is called native Peach or Quandong; the fleshy fruits are eaten and preserved; also the almondlike cores (Quandangnuesse) serves as a food for the natives; see e.g. Black, Fl. South Australia II. (1924) 168. Quadang-Nüsse (vgl. Wehmer, Pflanzenstoffe I. [1929] 260). - *E. Murrayana* T. L. Mitchell (*Santalum persicarium* F. Muell.), in south and west Australia, is called after Black Bitter Quandong (under *Fusanus persicarius* F. Muell.).

24. **Mida** A. Cunn. ex Endl. Gen. Pl. (1837) 327; A. Cunn. in Ann. Nat. Hist. I. (1838) 376; Cockayne and Allan in Trans. New Zeal. Inst. LVII. (1927) 57; Sprague and Summerhayes in Kew Bull. (1927) 196 (*Santalum* spec. Hook. Ic. T. 563, 575 [1843]; *Santalum* sect. *Mida* A. DC. in DC. Prodr. XIV. [1857] 686; *Fusanus* R. Br. sec. Kirk, For. Fl. New Zeal. [1889] 137, T. 75, 76; Cheeseman, Illustr. New Zeal. Fl. II. [1914] T. 177, Manual New Zeal. Fl. sec. ed. [1925] 387; *Fusanus* sect. *Mida* Benth. et Hook. f. Gen. Pl. III. [1880] 225; Hieronymus in E. P. 1. Aufl. III. 1. [1889] 218; *Mida* sect. *Eumida* O. Ktze. in Post et Kuntze, Lex. Gen. Pl. [1903] 367). – Flowers in small axillary panicles. Flowers bisexual or unisexual, 4-6-merous. Receptacle over the ovary shortly cup-shaped. Tepals cordate, at the base fused together, with that. Receptacle only in the middle part of the base connected. Disk lobes short and broad, nearly truncate. Ovary half-inferior, style 0, stigma weakly 3-4-lobed; ovules 2-3. Fruit turbinate, above truncate, only with scars of the tepals. - Small tree with alternate or more rarely ± opposite leaves.

M. salicifolia A. Cunn. (*Fusanus Cunninghamii* Benth. et Hook.), on New Zealand, north island; to approximately 8 m high tree with thin trunk; leaves variable, lanceolate to obovate, to 10 cm long; Fruits light red, to over 1 cm long. (perhaps several species are to be differentiated; Coekayne and Allan indicate a hybrid of *Mida myrtifolia* and to *Mida salicifolia*, Ann. of Bot. XLVIII. [1934] 19; Cockayne, Veget. N. Zealand [1928] 156). - about *M. fernandeziana* (Phil.) Sprague et Summerhayes, see under *Santalum*.

Tribe 3. **Thesieae.**

Thesieae Reichenb. Handb. (1837) 167 (Rect. *Osyridearum*); Bentham l. c. (1880) 218 Hieronymus l. c. (1889) 223.

25. ***Osyridocarpus*** (*Osyridicarpos*) A. DC. in DC. Prodr. XIV. (1857) 635; Benth. et Hook. f. Gen. Pl. III. (1880) 222; Hieronymus l. c. 223; Baker and Hill in Fl. Trop. Afr. VI. 1. (1911) 431; Hill in Fl. Capens. V. 2. (1915) 206. –

Flowers bisexual, 5-merous. Receptacle over the ovary cylindrical-funnel-shaped, rather thick, fleshy. Tepals inside behind the stamens with a hair tuft. Stamens attached at the base of the tepals, with short, thin filaments; locules of the anther theca attached inward & parallel, dehiscing together by a longitudinal fissure. Disk not clearly defined. Ovary inferior; style long, thin, with more head-shaped or indistinctly 2-3-lobed stigma; ovules 2-3, hanging down from the apex of a threadlike and curved placenta. Fruit drupe-like, crowned by a persistent piece of the receptacle. - Glabrous subshrubs or climbing shrubs with loose, thin branches; leaves alternate, short-petiolate, linear, lanceolate or ovate. Flowers solitary in the axils, shortly petiolate or in small axillary, pedunculate cymes; bracts (Hochblätter) small, easily dropped. [note: the word “gestielt” as used above referred to a petiole of a leaf, pedicel of a flower, and peduncle of an inflorescence!]

Name from *Osyris* and χαρπός, fruit. – Type species *O. natalensis* A. DC.

6 species, of eastern South Africa through East Africa to Abyssinia and Eritrea. - *O. schimperianus* (Hochst.) A. DC. in Eritrea, Abyssinia, Uganda; leaves small lanceolate; flowers usually solitary; receptacle tube 2-3 times as long as tepals. - *O. natalensis* A. DC. in eastern South Africa (see also Burt Davy, Fl. Pl. Transvaal II. [1932] 462); leaves ovate, acute; flowers usually to three. - *O. linearifolius* Engl., in German East Africa; leaves linear; flowers 3-7 in loose, pedunculate cymes.

26. **Thesidium** Sonder in Flora XL. (1857) 364; A. DC. in DC. Prodr. XIV. (1857) 673; Benth. et Hook. f. Gen. Pl. III. (1880) 222; Hieronymus in E. P. 2. Aufl. III. 1. (1889) 224; Hill in Fl. Cap. V.2. (1915) 201 (*Hagnothesium* A. DC. Espèc. nouv. Thesium [1857] 4, DC. Prodr. XIV. [1857] 673 sect. Thesii; Post et O. Ktze. Lexic. gen. Phan. [1804] 263, genus). - Flowers dioecious, four-, rarely five-merous. Receptacle of the male flower short, cup-shaped. Tepals at the base with a hair tuft standing behind the stamen. Stamen with short filament; anther small, locule of the theca short, ellipsoidal, dehiscing with a common longitudinal fissure. Style rudimentarily or 0. Ovary of the female flower egg-shaped, inferior, receptacle over the ovary indistinct or very briefly bell-shaped. Disk not clearly defined.

Style short, stigma indistinctly 2-3-lobed; ovules 2-3, hanging down from the apex of the central, threadlike, upright or to and fro wound placenta. Fruit small nut-like, spherically or egg-shaped, 5-ribbed and clearly netted, crowned by the persisting tepals; endocarp crust-like; seed spherical or egg-shaped; embryo terete, embedded in the center of the fleshy endosperm, often inclined. - Very branched small subshrubs or herbs with alternate, usually very small, scale-shaped leaves. Flowers small, very numerous either individually or posed to three in the axil by scale-shaped bracts (Tragblättern), or solitary in the axil of bracts in a terminal spike; bracts and prophylls small, particularly with the male flowers,

Type species Art *Th. Thunbergii* Sonder.

7 species in southwest South Africa. A. Male and female plants similar; bracts and prophylls small, scale-shaped, fleshy. - *Th. exocarpoides* Sonder (Fig. 40); to 40 cm high; rootstock woody, branches thin, wound, leaves very small, flaky. - *Th. Thunbergii* Sonder; - B. male and female plants different; male with narrow, small bracts, female with substantial, leaf-like bracts. *T. hirtum* Sonder. *Th. longifolium* Hill.

About *Th. fragile* see R. Marloth. Fl. South Afr. I. (1913) 162 T. 37B: not rare on the Cape Flats, grows on the roots of *Metalasia muricata*, *Chymococca empetroides* and probably still different bushes.

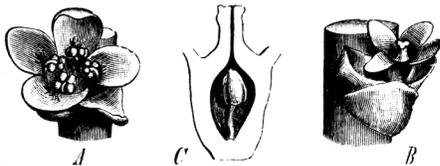


Fig. 40. *Thesidium exocarpoides* Sonder. A. male flower (15/1). B female flower (15/1). C longitudinal section through the ovary (30/1). - Aus E. P. 1. Aufl. III. 1, 224, Fig. 144.

27. **Thesium** L. [Gen. pl. (1737) 60] Spec. pl. (1753) 207. Gen. pl. cd. 5. (1754) 97; A. DC. in DC. Prodr. XIV. (1857) 637; Benth. et Hook. f. Gen. Pl. III. (1880) 221; Hieronymus in E. P. 1. Aufl. III. 1. (1889) 224; Baker and Hill in Fl. Trop. Afr. VI. 1. (1911) 411-431; Hill in Fl. Capensis V. 2. (1915) 136-200; Hegi, Illustr. Fl. Mittel-Europa III. (1912) 151 (*Rhinostegia* Turcz. in Bull. Soc. Natural. Moscou XIV. [1843] 56; *Linosyris* [Moehr. Hort. priv. [1736] 60] O. Ktze. Rev. Gen. II. [1891] 587; *Steinreitera* Opiz. Seznam [1852] 93; *Xerolophus* Dulac. Fl. Hautes Pyrén. [1867] 1160; *Linophyllum* Bubani. Fl. pyren. I. [1897] 125). - Flower 5 (4)-merous, bisexual. Tube of the receptacle usually short and broad, rarely extended. Tepals short or longer than the tube, inside glabrous or richly bearded with hair, usually behind the anther small tufts of soft, upright, arranged backwards hairs, attaching to one the anthers. Stamens at the base of the tepals or something attached below the same the tube aperture, enclosed or exerted;

filament usually short. Ovary inferior; style short to long; stigma capitate or indistinctly 3-lobed; ovules 2-3, hanging down from the apex of a thin, usually to and from wound placenta. Fruit nut-like, nerved, spherical or egg-shaped, mostly crowned by the withering receptacle and the rolled up petals; seed spherical or egg-shaped; embryo embedded in the center or in the upper half of the fleshy endosperm, sometimes inclined, straight or bent club-shaped, with somewhat thickened hypocotyl; cotyledons as long or shorter than the hypocotyl. - Perennial herbs with \pm woody, branched basic axis or subshrubs to small shrubs; leaves very small scale-like or linear, very rarely broader and large. Inflorescences simple racemose or spicate or from 3- more-flowered compound cyme; prophylls sometimes missing.



Fig. 41. *Thesium alpinum* L. A. Habit of a lanky plant, nat. size. B flower with the involucre, which is formed from the pedicel's expanded bract and from the prophyll. C flower in median longitudinal section, the anther on the right side is cut off. D ripe fruit crowned by the drying flower covering. E ripe fruit in longitudinal section. (6/1). - from E. P. 1. Aufl. III. 1, 225, Fig. 145.

Name after a Greek plant name $\tau\eta\sigma\epsilon\iota\omicron\nu$, of unknown meaning; about the name see Linne, Hort. Cliffort. (1737) 41. - type species: *Th. Linophyllon* L (stands with Linne in the first place); Hitchcock in. *Propos. British Botanists* (1929) 135 called *Th. alpinum* L. the designated species.

About 220 species, particularly in the southern Africa (see also N. E. Brown in *Burt Davy, Fl. Pl. Transvaal II.* [1932] 455). then developed in the tropical Africa and in the Mediterranean area - our German species, usually inhabitant sunny grassier hills, are called Vermeinkraut (or Verneinkraut), Bergflachs, Leinblatt; English Toad-flax. - the nearly leafless *Thesium strictum* Berg. is shown in R. Marloth. *Fl. South Africa I.* (1913) 162 T. 37C, and 160 Fig. 80 (an den Abhängen des Tafelberges).

Section I. *Frisea* Reichenb. *Consp. Regn. Veg.* (1828) 80 nomen!; A. DC. l. c. 662; Hieronymus l. c. 225 (*Thesium* Sect. *Frisea* Reichenb. sec. Endl. *Gen. Pl.* [1837] 326). - Tepals inside dressed with backwards arranged densely bearded hair. About 80 species in South Africa and 15 species in tropical Africa.

Group 1. *Annulata* Hill (as section I. c. [1915] 144). Tepals without hair tufts behind the anthers, but at the base with a small ring of short, downward arranged, gold-yellow hair; tube over the ovary short and broad. - 15 species. - A. flowers in extended spikes or racemes. *Th. funale* L. (Fig. 42 A, B), in the southwest Cape country; subshrublet with thin branches, strongly branched out; leaves few, narrow; flowers 3 mm long. - B. flowers compacted into heads or shortly racemose. - *Th. aggregatum* Hill, in the southwest Cape country; also prostrate stems and branches with small, flat leaves; bracts egg-shaped, 4 mm long, toothed (dentate), prophylls somewhat narrower; tepals 3 mm long, also in-curved tip, inside covered with close, taut, down-hanging

hairs. - *Th. Frisea* L., in the southwestern Cape country; branches thin, much branched; leaves small, narrow needle-like; prophylls lanceolate, about half so long as 3 the mm long flower; tepals with soft down-hanging hairs.

Group 2. *Penicillata* Hill (as section I. c. [1915] 144). Tepals behind the anthers with a small tuft of thicker, soft, free hair (not attaching to the anther); tube over the ovary very short, broad. Only *Th. penicillatum* Hill in the southwest Cape country; stems woody, **oberwaerts** branched out; leaves short, linear; bracts about as long as the flower, 4 mm, lanceolate, prophylls half as long.

Group 3. *Barbata* Hill (as section I. c. [1915] 140). Tepals at the base behind the anthers with one the anthers attaching to a tuft of soft, straight hair; tube of the receptacle over the ovary short and broad or extends campanulate; flowers condensed in extended racemes, spikes or heads. About 80 species. *Th. capitellatum* A. DC. (Fig. 42 E), in southwest Cape region; small, rich-branched subshrub, leaves linear, 5 mm long; flowers few in terminal small heads; Bracts 3 mm, as long as flower, lanceolate, prophylls somewhat shorter and narrower; tube short and broad, anthers in small cavities, enclosed in the tube; Style very short. - *Th. capitalatum* L. (Fig. 42 C, D), in southwestern Cape country; weakly branched subshrub; branches closely leafy, leaves linear, up to 15 mm long; bracts ovate, lanceolate, about 7 mm long, somewhat longer than the lanceolate prophyll; flower 6 mm long, tube extended campanulate; anthers somewhat exserted; style extended up to the height of the anthers. - *Th. flexuosum* A. DC, in the southwest and central Cape country; branches thin, with scattered, needle-shaped leaves; flowers in close spikes; bracts ovate, 2 mm long, prophylls somewhat narrower; flower 3 mm long, tube campanulate. - *Th. Schlechteri* Hill, in German southwest Africa; a subshrublet with thick rootstock and thickish rough-papillose leaves. - *Th. Schweinfurthii* Engl. in Central Africa (Jur) and Nyassaland; herbaceous, low. - *Th. Goetzeanum* Engl. in German East Africa; *Th. angolense* Pilger in Angola.

Section II. *Chrysothesium* Jaub. et Spach, Illustr. Pl. Orient. II. (1844-46) T. 104; A. DC. in DC. Prodr. XIV. (1857) 638. Tepals inside glabrous, but also behind the stamens, small, with the anthers connected to the hair tuft. Free part of the receptacle long tubular, membranous, golden-petaled. Flowers in spikes, with bracts and two prophylls. 2 species in eastern Mediterranean region, Armenia, Mesopotamia. - *Th. stelleroides* Jaub. et Spach (Fig. 42, F-H); perennial with strong rootstock, upright, up to a foot high, in the upper part rigidly ramifying floral branches; leaves narrowly linear; lower, part of the receptacle deformed by the short ovary; wooly pubescence, likewise the fruit; free part 6 mm long, tepals 4 mm long, narrow; Filaments increased to a large part the tube, these appearing **nerved, upward free**, anther small, dense below the tepal tip; size long thin. - related to *Th. aureum* Jaub. et Spach; lower part of the receptacle glabrous.

Section III. *Psilotesium* A. DC. in DC. Prodr. XIV. (1857) 670. - flowers 5 or also 4-parted. Tepals inside glabrous, but also behind the stamen stands small hair tufts; receptacle tube with tepals deciduous at the fruiting; leaves very small; filament much longer than anther, style long. 2 species in south Brazil. *Th. aphyllum* Mart. (Fig. 42 I, K); with strongly woody rootstock; stem to a foot high, rigid, sharp-edged, weakly branching out; leaves scattered, diminutive; flowers in spikes, with 2 prophylls, very small. - related *Th. brasiliense* A. DC.

Section IV. *Euthesium* A. DC. in DC. Prodr. XIV. (1857) 639. Tepals inside glabrous, but also behind the stamens small, with the anther connected to the hair tuft; tube of the receptacle usually short and broad, with the tepals remaining on the fruit; filament usually very short, anther ± enclosed or exserted; herbs to subshrubs.

A. African species. About 80 species. - a. strong woody, larger forms, rigid, often thorny. - α. Tepals with long, soft “shaggy eyelashes” (Zottelwimpern) at the edge (Sect. *Imberia* Subsect. *Fimbriata* Hill in Fl. Cap.). Few species in western and central South Africa. *Th. horridum* Pilger, (Fig. 42 L, M), in western Cape country; spreading bushy, with rigid, sting-pointed branches; leaves small, narrow; flowers in few-flowered, close, axillary groups, surrounded by bracts and spatulate lanceolate prophylls; tube broad, short, styles short. - β. Tepals without such eyelashes; leafy or ± leafless. *Th. xerophyticum* Hill in German southwest Africa; **sparriger** subshrub; leaves reduced to tiny scales; Blooms very small, nearly sessile. - *Th. lineatum* L. f., in

central and western South Africa, German southwest Africa, to a meter high; tube short, broad, disk distinct, forming a thickish edge between the stamens. - *Th. spinosum* L. f., in the southwest Cape country; leaves spreading, thorny-rigid, up to 7-8 mm long; flowers solitary axillary, pedicellate, very small. - **b.** slightly rigid, \pm herbaceous forms, not thorny, usually smaller; leaves \pm developed. - α . leaves large and broad (Sect. *Aetheothesium* A. DC. l. c. 660). *Th. euphorbioides* L., in the southwest Cape country; to 2 m high, upright, somewhat woody; leaves cordate, oval to roundish, lying close, 1-3 cm long, leathery; flowers in close cymes with very broad bracts and prophylls. - β . leaves smaller, narrower, to nearly 0. - **I.** Tepals long and narrow, with shaggy scattered lashes; filament extended, high at the tepals standing for anthers; style long. Few species. *Th. leucanthum* Gilg (Fig. 42 N q), in Angola; herbaceous perennial, upright, thin branches; leaves 0 or tiny scales; flowers 2 in the bracts ¹⁾; Tube of the receptacle short campanulate, at the top margin with "shaggy eyelashes", 1 mm long; tepals narrow, 5 mm long. - *Th. Stuhlmannii* Engl., in trop. East Africa. - **II.** Tepals shorter, broader; filament short. - **1.** Tube of the receptacle somewhat extended campanulate. *Th. costatum* Hill, in the eastern Cape country and Kalahari area; thin, branched stems to 20 cm high, leaves small, narrowly linear; flowers usually solitary axillary. - in addition few species in the Cape country. - **2.** Tube short and broad. - **X.** flowers in spikes or loose cymes. *Th. squarrosum* L (Fig. 42 R,S), in southwestern Cape country; about 25 cm high, stems woody, plentifully branched out downward; leaves small, narrow; flowers of lax cymes, small (tube and tepals together 1 1/4 mm). - *Th. pallidum* A. DC. in the eastern cape country, also small loosely placed cymes terminal on the branches. - *Th. galoides* A. DC, in the southwest Cape country, with very loose, 4-flowered cymes and small flowers. - **XX.** flowers compacted into close, small capitulate cymes. *Th. angulosum* A. DC, in the southern and eastern Cape country; nearly shrubby, to 1.5 m high, loosely branched out, branches winged; flowers in small, close, short pedunculate cymes loosely along the branches; tepals 2 mm. *Th. Schumannianum* Schlecht, *Th. virgatum* L., in the southwest Cape country.

B. European-Asiatic species. About 40 species, particularly developed in the Mediterranean area, from southeast to middle Europe ¹⁾ with few species widespread but one species to Denmark, South Sweden, southern England; a set of species in central Asia, to China, Japan and up to the Philippines, a species in Australia. - **a.** flowers in simple racemes, solitary in the axil of the bract, without prophylls. *Th. rostratum* Mert. et Koch, Central Europe, east alps, Bohemia; 20-30 cm high, a number of stems closely posed; leaves very narrow. - *Th. ebracteatum* Hayne, Southeast Europe, northeast German flat country, west to Denmark, Bremen; with runners, to 30 cm high; very rarely is the prophyll present or both exist, forma *subbracteata* Vahl sec. Aschers. and Graebn. l. c. 663. - **b.** flowers with prophylls, in simple racemes or weak cymes ramified from prophylls. *Th. pratense* Ehrh., south Europe and Central Europe, not in Northern Germany; to 50 cm high; leaves linear, to 1 cm long; tepals on the fruit only weakly rolled up, with the tube longer than these. - related to *Th. alpinum* L, in the mountains of south Europe, Caucasus, Central Europe to South Sweden. - *Th. Linophyllon* L. (*Th. intermedium* Schrad.), from Southeast Europe to Central Europe; with long thin runners, leaves very narrow. - *Th. humile* Vahl, widespread in the Mediterranean region, also completely in North Africa. - in central Asia *Th. longifolium* Turcz., *Th. saxatile* Turcz., *Th. multicaule* Ledeb.; in the Himalayas *Th. himalense* Royle, *Th. packyrhizum* A. DC; in China and Japan *Th. chinense* Turcz., *Th. decurrens* flower, *Th. psilotoides* Hance, the latter also in the Philippines; in southeast Australia, Tasmania *Th. australe* R. Br.

¹⁾ In the axil of a bract two flowers, the one are located younger, closely before each other, each one with 2 prophylls at the same level; the younger can have come out only from a dual bud. This behavior was not observed otherwise with *Thesium*; it occurs in otherwise cymose ramifications from one or from both prophylls.

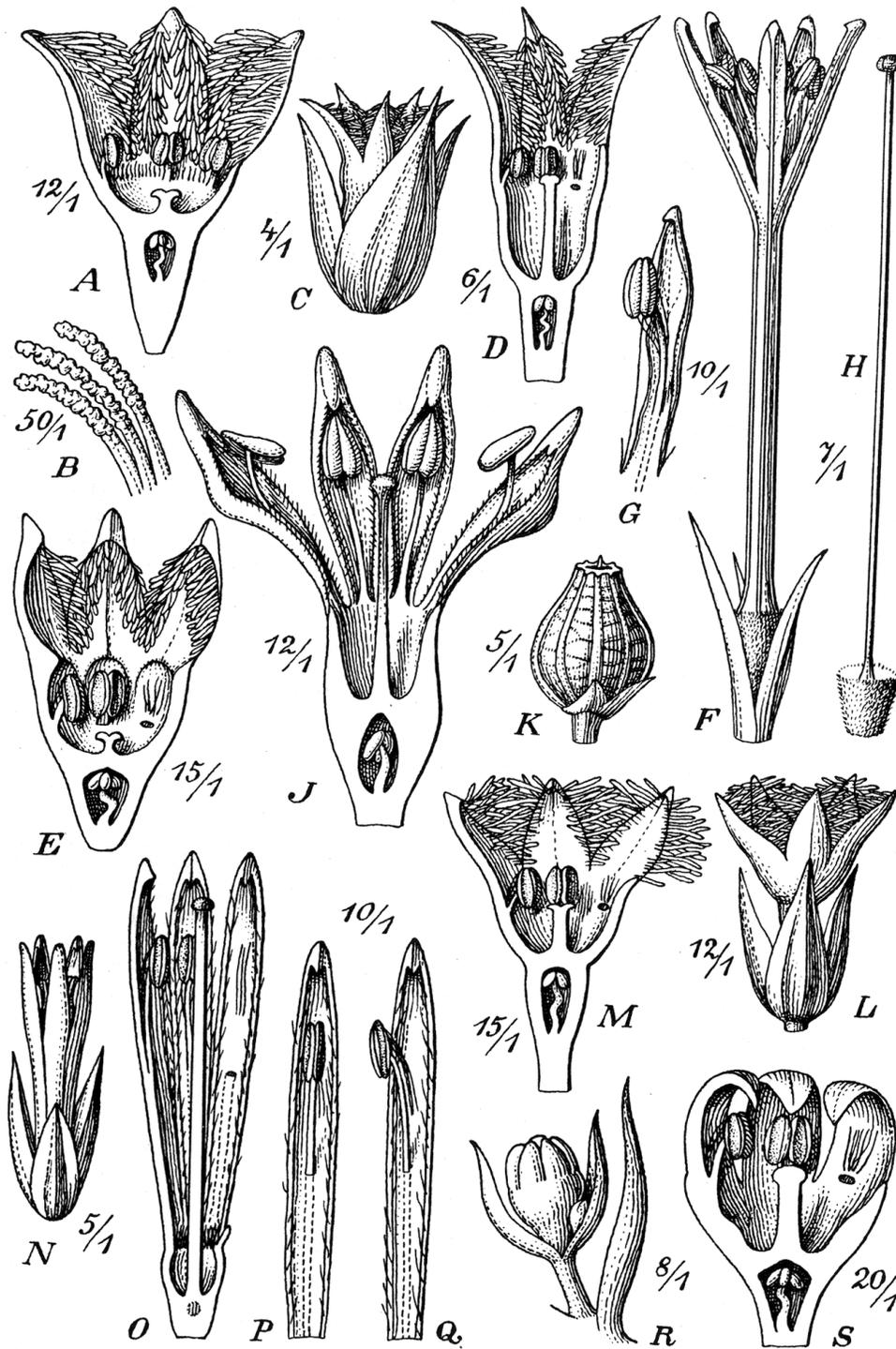


Fig. 42. Flowers of several species of *Thesium*, with bract and prophyll or in longitudinal section. A *Th. funale* L. B hair of the tepal of these species. C, D *Th. capitatum* L. E *Th. capitellatum* A. DC. F-H *Th. steleroides* Jaub. et Spach. J, K *Th. aphyllum* Mart. L, M *Th. horridum* Pilger. N-Q *Th. leucanthum* Gilg. Q shows the attaching hair behind the anther. R, S *Th. squarrosus* L (F, H after Jaubert et Spach, J, K after A. De Candolle, the others after nature).

28. **Arjona** Cav. Icon. IV. (1797) 57, T. 383; A. DC. in DC. Prodr. XIV. (1857) 626; Miers in Journ. Linn. Soc. XVII. (1880) 128-134; Benth. et Hook. f. Gen. Pl. III. (1880) 220; Hieronymus in E. P. 1. Aufl. III. 1. (1889) 226 (*Arivona* Steud. Nom. Ed. H. 1. [1840] 130; *Arjoona* Endl. Gen. [1837] 325; *Arjonaea* O. Ktze. Rev. Gen. III. 2. [1898] 282). – Flowers bisexual, 4-5merous. Receptacle over the ovary tubular, usually narrow and long, usually softly pubescent. Tepals at their base with hair tufts. Stamens attached at the mouth of the receptacle tube, not exerted; Anthers with very short filament at the back, attached at the middle; Locules of the thecae parallel, linear, longitudinally and introrsely dehiscent. Disk cushion shaped or ring shaped. Ovary inferior; Style filiform with the head shaped or short three-lobed stigma; Ovules 3 down-hanging from the point of a short, thick placenta. Fruit small, nut-like, crowned by the disk; Seeds egg shaped; Embryo small, linear-terete, in the center of the fleshy endosperm, hypocotyl (?) about as long as the cotyledons. – Herbs with branched underground rhizomes or with underground swollen knotty runners, rarely woody below (unterwärts ?) subshrub; Leaves alternate, linear or lanceolate, usually rigid and pointed. Flowers rather numerous sitting crowded in short terminal spikes or only few axillary, white, lilac or crimson.

Most important Literature: C. Skottsberg, Zur Morphologie und Systematik der Gattung *Arjona* Cav., in Svensk Bot. Tidskr. X. (1916) 520-628.

Name after Francisco Arjona, teacher of botany in Cadiz, expired in the 1800s (Colmeiro, Bot. Penins. Hisp. Lusit. [1858] 188). – Type species *A. tuberosa* Cav.

About 10-12 species in south America, from Tierra del Fuego to Peru, Argentina, southern Brazil (?). – Vgl. auch Hauman et Irigoyen in Anal. Mus. Nac. Buenos Aires XXXII. (1923-25) 41, 421.

Section I. *Euarjona* Skottsberg l. c. 526. – underground rhizome terminally branched, which are more or less completely knotty thickened at the end and then in aboveground, from which weakly branched leaf shoots and flowering shoots emerge. – *A. tuberosa* Cav., in Tierra del Fuego and Patagonia; Tubers to 2 cm long, sharply defined at the ends of the thin runner; branched aboveground shoots to 15 cm high; Leaves rigid, lanceolate, pointed, strongly nerved; Flowers in a condensed umbel. The above mentioned “Macachi” tubers is sweet and is eaten by the natives. – *A. patagonica* Hombrón et Jacquinet, in Patagonia; with more evenly thickened runners, otherwise similarly. – *A. ruscifolia* Poepp., in Chile and northwestern Argentina; Rhizome as with the previous species; Leaves broad, very rigid, strongly spine-tipped (c.f. *A. rigida* Miers). – *A. tandilensis* O. Ktze., from Uruguay to Córdoba Province in Argentina; Leaves very narrow.

Section II. *Psilarjona* Pilger in Engl. Bot. Jahrb. XXXVII. (1906) 399; Skottsberg l. c. 528. – Underground with branched rhizome, its branches for a long time remaining in connection with the mother shoot and on the outer surface with short-lived short foliar shoots and flowering shoots above. – *A. pusilla* Hook. f., in Tierra del Fuego and Patagonia; Main axis more than a decimeter long; Leaves small, thick, not rigid; Flowers few. Related to *A. minima* Hieron., in Argentina, San Juan Province. – *A. glaberrima* Pilger, in the Hochanden of Peru, creeping in wet lawns of moorlands; leafy branches only 1-2 cm long; Flowers 1-2.

Section III. *Xylarjona* Skottsberg l. c. 528. – Small subshrubs; the basal part of the upright foliar shoot woody and in the form of a xylopodium (typical of the Campos plants). *A. Schumanniana* Pilger (in Uruguay or south Brazil, collection Sellow); Branch thin, to 30 cm high; Leaves narrowly linear, to 5-6 cm long; Bracts long and narrow, flowers rather numerous crowded. – *A. longifolia* Phil., in Argentina, Mendoza and Rioja; Leaves and bracts shorter.

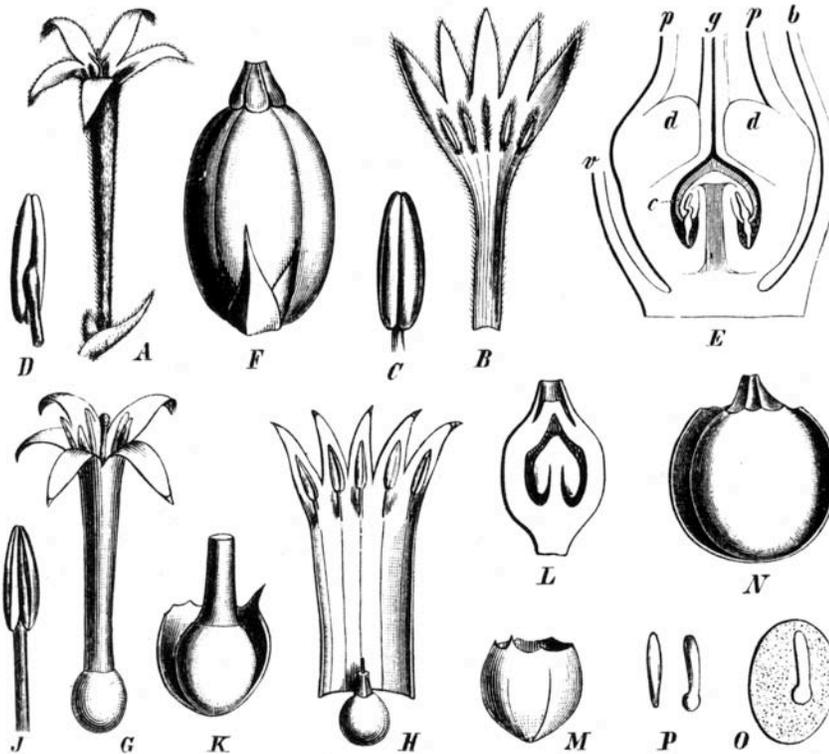


Fig. 43. A-E *Arjona longifolia* Phil. A Flower in the axil of a bract, to the left a bracteole is visible (2/1). B receptacular tube cut open and spread, the middle stamen cut off (2/1). C stamen from the front, D from the back (10/1). E nearly median profile of the ovary of a flower already pollinated, *b* first bract, *v* bracteole, *p* receptacle, *g* style, *d* disk, *c* to the placenta rises a mass of tissue, which encloses the seeds - F *A. rigida* Miers, ripe fruit (4/1). G-P *Quinchamalium chilense* Lam. G flower (2/1). H flower cut open and tube of the receptacle spread out; the style is cut off (2/1). J stamen as seen from the front. K ovary in the halved cupular (tubular) calyx. L longitudinal section of the ovary. M cupular "calyx" (J-M 4/1). N ripe fruit in the cupular "calyx". O longitudinal section of the seed, showing the embryo lying in the endosperm. P embryo as seen from a different side. (NP 3/1). - From Engler & Prantl. 1. Aufl. IIITH I, 226, Fig. 146.

29. **Quinchamalium** Jussieu¹), Gen. Pl. (1789) 75; Ruiz et Pav. Fl. Peruv. II. (1797) 1 T. 107b; Endl. Gen. Pl. (1837) 325 no. 2070; A. DC. in DC. Prodr. XIV. (1857) 624; Philippi in Bot. Zeit. XV. (1857) 745-749; Benth. et Hook. f. Gen. Pl. III. (1880) 220; Hieronymus in E. P. 1. Aufl. III. 1. (1889) 227 (*Quinchamala* Willd. Spec. Pl. I. [1797] 1217). - Flowers bisexual, 5-merous, at the base surrounded by a nearly spherical or sharp-edged, weakly toothed cupular "calyx", which is formed from the fusion (growing together) of the bract and bracteole. Tube of the receptacle extends, narrowly cylindrically. Tepals lanceolate, folded, later sticking out erect. Stamens attached at the base of the tepals, \pm shorter than these. Filament very short to moderately long; Anthers basifixed, thecae with one longitudinal fissure dehiscing introrsely; Hairs at the base of the filaments missing. Disk fleshy, ring or cup-shaped on the ovary, separate from the receptacle. Ovary inferior; Style filiform, going up to the center of the petals or still beyond this, stigma small head-shaped; Ovules 3 hanging down from the summit of a short placenta. Fruit nut-like, enclosed by the persistent spherical or sharp-edged cupular "calyx", receptacle over the cupular "calyx" dropping or drying persisting; Seeds spherical or egg-shaped;

Embryo in the center of the fleshy endosperm, small, linear, handle-roundish. - Low, half parasitic herbs or herbaceous plants, often with plumper primary roots, small stems usually branch out from the base, branches often prostrate. Leaves subulate to linear, prickle-tipped. Flowers in terminal dense racemes often numerous from the receptacle over the cupular “calyx” (Becherkelch) dropping or drying persistent; seed spherical or egg-shaped; embryo in the center of the fleshy endosperm, small, linear, compacted into small heads, often in pits easily encompassed in the spindle, yellow to brown or red-brown, after the age the color changing. Cupular “calyx” as long as the fruit, due to development of the usually 4-merous commissural teeth, the bract appropriate tooth somewhat more largely than the bracteole of appropriate teeth.

Name after the native designation Quinchamali (Feuillée, Journ. des observ. III. Hist. pl. medio. [1725] 57 T. 44; *Quinchamali Linifolio*; Beschreib. II. [1758] 80). - Typische Art *Qu. chilense* Lam.

Over 20 species, usually mountain inhabiting, from southern Chile to central Peru; Species close related and separated with difficulty. Receptacle with tepals to over 1 cm long. See Hauman et Irigoyen in Anal. Mash. Nac. Buenos Aires XXXII. (1923-25) 46. **A.** Cupular “calyx” sharp-edged. *Qu. parviflorum* Phil., in Chile; Filament of the anther very short. - *Qu. gracile* Brongn., in Chile; Filament as long as anthers. - **B.** Cupular “calyx” spherical-roundish. *Qu. chilense* Lam. (*Qu. procumbens* Ruiz et Pav.), from central Peru to the high country of Bolivia; Branches prostrate, to for instance 30 cm long; Leaves very narrowly linear, to approximately 2 cm long; Receptacle 4-5 mm long, tepals 2-2 1/2 mm long, anther 1-1 1/3 mm long, filament 1/3 - 1/2 mm long. - *Qu. majus* Brongn., in Chile; Shoot upright, to 25 cm long; filament as long as anther. - after Hauman & Irigoyen (l.c. 44) designated it as a genus in Santalaceae specified as *Bryodes Philippi* (in Anal. Univ. Chile XCI. [1895] 503; *B. minutissima* Phil.) perhaps a dwarf form of *Quinchamalium chilense* Lam. - in Index Kewensis Suppl. I. (1906) 65 is the aforementioned *Bryodes minutissima* Phil. erroneously specified under the genus *Bryodes* Benth. of the Scrophulariaceae.

¹⁾ The generic name was originally created by Molina (*Quinchamalium* Molina, Saggio sulla storia naturale de Chile [1782] 151); its description cannot refer to *Quinchamalium* Juss. One has taken up with A. De Candolle the specific name *Qu. chilense* Lamarck (Illustr. II [1797] 125T. 142), to which *Qu. procumbens* Ruiz Pav. is quoted as a synonym (see Skottsberg Bot. Ergebn. Patagonien und Feuerland, in Sv. Vetensk. Akad. Handl. LVI. Nr. 5. [1916] 208). Hauman et Irigoyen (l. c. 46) figured that *Qu. chilense* had the following varieties: var. *gracile* (Brongn.) Hook.; var. *majus* (Brongn.) Spegazzini; var. *patagonicum* (F. Phil.) Speg.; var. *procumbens* (Ruiz et Pav.) O. K.

Genera of uncertain position.

Calyptosepalum Sp. Moore in Journ. of Bot. LXIII. (1925) Suppl. p. 91, with figure. – flowers monoecious (?), only male ones well-known. Receptacle flat. Arranged in pairs, in the bud the outside larger, from each other free, but the two inside strongly covering, of the internal one with the edge other covering Tepals 4, covering; tepals in the flower a little unequal, roundish, free up to the disk. Stamens before the tepals, shorter than these; Filament very short, anther egg-shaped, introrse (about the opening no closer data). Disk thickish, weakly concave. Style vestige small, obtuse. - Tree; leaves alternate, petiolate. Flowers in few-flowered, axillary cymes.

1 species, *C. sumatranum* S. Moore, on Sumatra; Branches very finely grey white hairy, soon glabrous; leaves glabrous, 8-10 cm long, narrowly obovate, acuminate; cyme 1 cm long, tepals 3

mm long.

A specimen carries some fruits; these pyriform, 14 mm long, with weak suggestions of tepal remains at the summit; exocarp thin, somewhat fleshy, endocarp crusty, with weak suggestions of projections into the seed; Seed? - it seems to me, since only male flowers are present, and the fruit is inadequately known, it is doubtful whether the species belongs to Santalaceae. The covering of the tepals is completely unusual. No specimen seen.

Fossil Genus Close to Thesieen.

Thesianthium Conwentz, Flora des Bernsteins II. (1886) 132 Tafel XIII Fig. 1-5. Flowers bisexual, on short, thickened pedicels, which by an affiliation separated to a furrowed handle thickened hardly at the top sits. Flower covering 5-merous, glabrous. Tube of the flower covering increased down the ovary, over the same 5-lobed-campanulate extension. Tepals triangular subulate, at the apex bending together. Stamens attached below the tepals, much shorter than these, on very short filaments; anther at the back scooped out. Disk epigynous, not protruding. Ovary inferior; style very short; stigma capitate, nearly sessile.

1 species, *Th. inclusum* Conwentz, in the Baltic Sea amber.