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Pericarp structure and phylogeny of the *Lamiaceae-Verbenaceae*-complex

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Abstract: Pericarp structure was investigated in 158 species of the families *Lamiaceae* and *Verbenaceae*. Data from 221 out of 262 genera of *Lamiaceae* s.l. and a few of *Verbenaceae* s.str. were collected in a table. A cladistic analysis was performed on the basis of pericarp characters only. The abandonment of subfam. *Pogostemonoideae* as a taxonomic unit is considered. Examples of groups given additional support by similarities in pericarp characters are: (1) the gynobasic-styled labiates (subfamilies *Pogostemonoideae, Lamioideae, Nepetoideae*); (2) a *Lamioideae-Pogostemonoideae*-group; (3) *Nepetoideae;* (4) a *Westringia-Hemigenia-Hemiandra-Microcorys* group (in subfam. *Chloranthoideae*); (5) a *Lepechinia-Chaunostoma*-group (in *Nepetoideae*); (6) a *Prunella-Cleonia*-group (in *Nepetoideae*).

In *Verbenaceae* and *Lamiaceae*, the ovary consists of two, sometimes one or three to five, carpels. Each carpel is usually divided into two chambers by the intrusion of partitions from the carpellary midrib. As each chamber has one ovule, the entire ovary usually has 4, or sometimes 2, 6, 8, or 10 ovules which develop into as many or often fewer seeds, the latter due to abortion. The ovary (and the fruit) is entire with a terminal style or shallowly to deeply lobed with a subterminal to gynobasic style. The fruit is indehiscent or splits up into free mericarps (nutlets).

It is widely accepted that the *Lamiaceae* evolved from the *Verbenaceae*. Traditionally (Bentham 1932–1936, 1948; Briquet 1895–1897; Wunderlich 1967), the *Lamiaceae* are distinguished from the *Verbenaceae* on the basis of gynoecium and fruit structure. Whereas most genera with a more or less four-lobed fruit that splits up into four mericarps have been placed in *Lamiaceae*, those with entire, often indehiscent, fruits have been placed in *Verbenaceae*. However, examination of the variation within both families reveals a continuum rather than a clear distinction, and the traditional distinction offered neither a well-marked boundary between the two families nor a synapomorphy for *Lamiaceae*. Cantino (1992 a) carried out a cladistic analysis of the *Lamiaceae* and those *Verbenaceae* that appeared to be most closely related to the *Lamiaceae*. In this consensus tree, groups of genera assigned to *Lamiaceae* are linked to at least four verbenaceous sister groups. Whereas the family as a whole appears to be polyphyletic, most of the genera fall within a single large clade characterized by a gynobasic style, a prominent nectary disc, and a smooth to irregularly roughened (versus reticulately ridged) pericarp surface. The four closest relatives of the major clade are *Ajuga, Acrymia, Cymaria*, and *Holocheila* (all in *Ajugoideae*). *Garrettia* forms a connecting link between this more inclusive clade and the *Verbenaceae* s.l. *Scutellaria, Tinnea* and *Renschia* fall within a clade with the verbenaceous *Holmskioldia* as a sister group. The two other "labiate"-clades contain *Teucrium* with allies and *Prostanthera* with allies. The cladograms based on chloroplast DNA characters by OLMSTEAD & al. (1992, 1993) and CHASE & al. (1993) also suggest that the *Lamiaceae* s.str. is polyphyletic. However, some of their trees conflict with CANTINO's (1992 a) cladogram by also suggesting different origins for subfam. *Nepetoideae* and the other gynobasic-styled labiates. The cladistic analysis based on chemistry and morphology by RIMPLER & al. (1992) focused on the *Caryopterioideae* and some other subfamilies of *Verbenaceae* (now abandoned by CANTINO & al. 1992) and only included few representatives of the gynobasic-styles labiates. In their cladogram, *Tinnea, Prostanthera* and some of its allies are nested within the clade of gynobasic-styled labiates.

In an attempt to delimit monophyletic families, CANTINO (1992 b) and CANTINO & al. (1992) adopted JUNELL's (1934) greatly expanded circumscription of *Lamiaceae* which includes many verbenaceous groups. *Lamiaceae* sensu JUNELL (1934) and CANTINO & al. (1992) differs from the *Verbenaceae* s.str. by having the ovules attached a short distance from the carpel margin. CANTINO & al.'s (1992) subfamilial classification is heavily influenced by CANTINO's (1992 a) cladistic analysis and divides the famliy into the following eight subfamilies: the more or less 'apical-styled' *Chloanthoideae, Teucrioideae, Viticoideae*, and *Ajugoideae*, the apical- to gynobasic-styled *Scutellarioideae*, plus the gynobasic-styled *Pogostemonoideae, Lamioideae* and *Nepetoideae*.

CANTINO (1992 a) used differences in fruit type, surface structure and fleshiness of the nutlets as characters in his cladistic analysis, but he did not include characters of the pericarp ultrastructure. However, the usefulness of such characters in the classification of the labiates has been demonstrated by many authors, i.e., WAGNER (1914), BILIMOVITSCH (1935), MURTHI (1940, 1946, 1947), WOJCIECHOWSKA (1958, 1961 a, b, 1966, 1972), JAITLY (1966), MAKAROVA (1967), HEDGE (1970), WITZTUM (1978), KRESTOVSKAJA (1988), ZHAPAKOVA & MYLNIKOVA (1990), and RYDING (1992 a, 1993 a, b, 1994 a–c). On the basis of pericarp characters, BILIMOVITSCH (1935) and WOJCIECHOWSKA (1966) presented informal subfamilial classifications of the European labiates, and the latter classification has been found to be rather well-correlated to CANTINO & al.'s (1992) subfamilial classification. RYDING's (1992 a, 1993a) subtribal classification of the *Nepetoideae* tribe *Ocimeae* is influenced by the differences in pericarp characters.

The objectives of this study are: (1) to investigate the pericarp structure in as many as possible of the hitherto unstudied genera of *Lamiaceae* s.l. and in some *Verbenaceae* s. str.; (2) to present a summary of pericarp characters, which includes old reports as well as new data about pericarp structure; (3) to carry out a cladistic analysis based on these pericarp characters; (4) to compare the new cladogram with the ones presented by other authors, and to discuss the phylogeny and classification of the labiates in the light of the new data.

The circumscription and subfamilial classification of *Lamiaceae* in this study largely follows CANTINO & al. (1992).

Material and methods

This study is based on material from the following herbaria: C, E, GH, K, S, and UPS (abbreviations according to HOLMGREN & al. 1990). New vouchers are enumerated in Appendix 1. In some cases, RYDING's (1992 a, 1993 a, b, 1994 a–c) slides have been re-examined in a search for new data.

Microscope slides with sections of the pericarp have been prepared by the method described by RYDING (1993 b) and are deposited at UPS. Presence or absence of myxocarpy and starch grains have been studied by the methods described by RYDING (1992 b). The free sclereids in Fig. 5 B–I were isolated from the sclerenchyma region after the nutlets had been cut up and macerated in sodium hypochlorite.

The regions of the pericarp and their homology

In order to facilitate the anatomical description, the pericarp is often divided into three regions called exocarp (epicarp), mesocarp and endocarp. The terms are commonly used for the purpose of description without relation to ontogenetic or evolutionary origin, but in this study attempts have been made to apply the same name for presumably homologous parts of the pericarp. In the labiates, the outer pericarp epidermis is often referred to as the exocarp, the inner epidermis as the endocarp, and all the intervening layers are placed in the mesocarp. As also the case with the outermost epidermis, the inner epidermis may be assumed to correspond in all labiate mericarps, but these layers may well have duplicated in some taxa (see below). Thus, layers placed in the mesocarp might have originated from the exocarp or endocarp. In the innermost part of the mesocarp (in its traditional sense), there is usually a very characteristic and distinct portion of sclerenchyma. If traced, the vascular bundles (which are presumed to constitute homologous structures) are restricted to the usually parenchymatous mesocarp layers outside this sclerenchyma. Thus, it seems probable that this distinct sclerenchymatous layer of the pericarp is homologous in all labiate nutlets. In his treatment of *Ocimeae*, RYDING (1992 a) included it in the endocarp, but today it seems more suitable to treat it as a separate region, and in the following context it will be referred to as 'the sclerenchyma region'.

Delimitation of the sclerenchyma region. Delimitation of the sclerenchyma region is rarely problematic. However, *Stenogyne, Haplostachys, Dicrastylis* (Fig. 4 E), and *Premna* (Fig. 4 D) contain two distinct regions of sclerenchyma, an outer which contains stone-shaped and comparatively thin-walled sclereids, and an inner typical sclerenchyma region. When considering its position in the pericarp, where it surrounds the vascular bundles, it seems plausible that the outer tissue of sclerenchyma is homologous to parenchymatous mesocarp tissues of most other labiates. Hence, the outer sclerenchyma of these taxa is considered as part of the mesocarp s. str.

Delimitation of the endocarp. A few taxa have two, not one, layers of similar thin cells below the sclerenchyma region. The additional cell layer may be presumed to have evolved by duplication of the inner epidermis. Consequently, both these layers are here considered as a part of the endocarp. However, in nutlets that lack a distinct sclerenchyma region, it may be difficult to distinguish between non-epidermal cells which have originated from the endocarp and true mesocarp cells (see below).

Problems with distinction between exocarp and mesocarp. In the subtribe *Plectranthinae*, non-mucilaginous exocarp cells seem to have divided to form several cell layers next to the vertically longer mucilaginous cells. RYDING (1992 a) placed such non-mucilaginous cells in the exocarp. In many *Nepetoideae* (Fig. 3 A), *Paraphlomis, Suzukia* (Fig. 2 C), *Tinnea* (Fig. 2 H) and some other labiates, the outer epidermis and the layers immediately below are similar. Thus, it is possible that layers here referred to as mesocarp might have originated from the exocarp.

Problems of the homology when the sclerenchyma region seems to be lacking. The absence of a sclerenchyma region provides considerable difficulties with the identification of cell layers. Fibres and elongate cells with a large pits or scalariform wall thickening mainly occur in taxa that apparently lack a sclerenchyma region. For the sake of convenience, such cells are (in the following chapter and Table 1) described under the mesocarp, but it is uncertain to which region they really belong. Four different hypotheses about their origin are here discussed (1) **Xylem elements**. The large cells with a scalariform wall thickening in *Ajuga* (see WAGNER 1914: fig. 63) have been found to be elongate and (as the veins in many other apical-styled labiates) at the edges of the large reticulum of the sclerenchyma region. Hence, these cells apparently belong to the vascular bundles. The same may also apply to cells with large pits in some *Mosla* species (illustrated by WAGNER 1914: fig. 17). In *Comanthosphace*, which lacks a sclerenchyma region, cells with scalariform wall thickening form a more or less coherent tissue, and RYDING (1994 a) suggested that they may be tracheids. However, the similar but solitary cells in the presumably related *Leucosceptrum* may hardly have this function. Fibres in *Chelonopsis*, which form several layers below the tracheary elements, and sometimes are absent from areas between these elements were suggested to represent remnants of the xylem (RYDING 1994 b). (2) **Elements of the sclerenchyma region**. Fibres in *Chelonopsis, Tinnea* and *Renschia* occur in the inner part of the pericarp at or near the position which, in other taxa, is occupied by the sclerenchyma region. This is also the case with the sclereids of *Gomphostemma*, which vary from being almost bone-shaped to almost fibre-shaped. (3) **Endocarp elements**. Endocarp cells often have a large-pitted or scalariform to reticulate wall thickening. According to WAGNER (1914: fig. 53), several of the innermost cell layers may be identical in *Scutellaria*. The same may perhaps also apply to *Rostrinucula*. However, the fact that the presumably related *Leucosceptrum, Comanthosphace, Achyrospermum, Tinnea* and *Renschia*, which have an ornamented 'mesocarp' cell, lack such wall structures in the cells of the inner epidermis, contradicts the suggestion that the ornamented cells may originate from the endocarp. (4) **Ordinary mesocarp elements**. In *Newcastelia*, which has a typical sclerenchyma region, all mesocarp cells have a scalariform-reticulate wall thickening. Ordinary mesocarp cells differ from the xylem elements by being less elongate and more thin-walled. Stone cells in *Haplostachys* and *Stenogyne* have rather large pits. Thus, scalariform, reticulate or large-pitted cells in *Leucosceptrum, Achyrospermum* and related species may have originated from ordinary mesocarp cells.

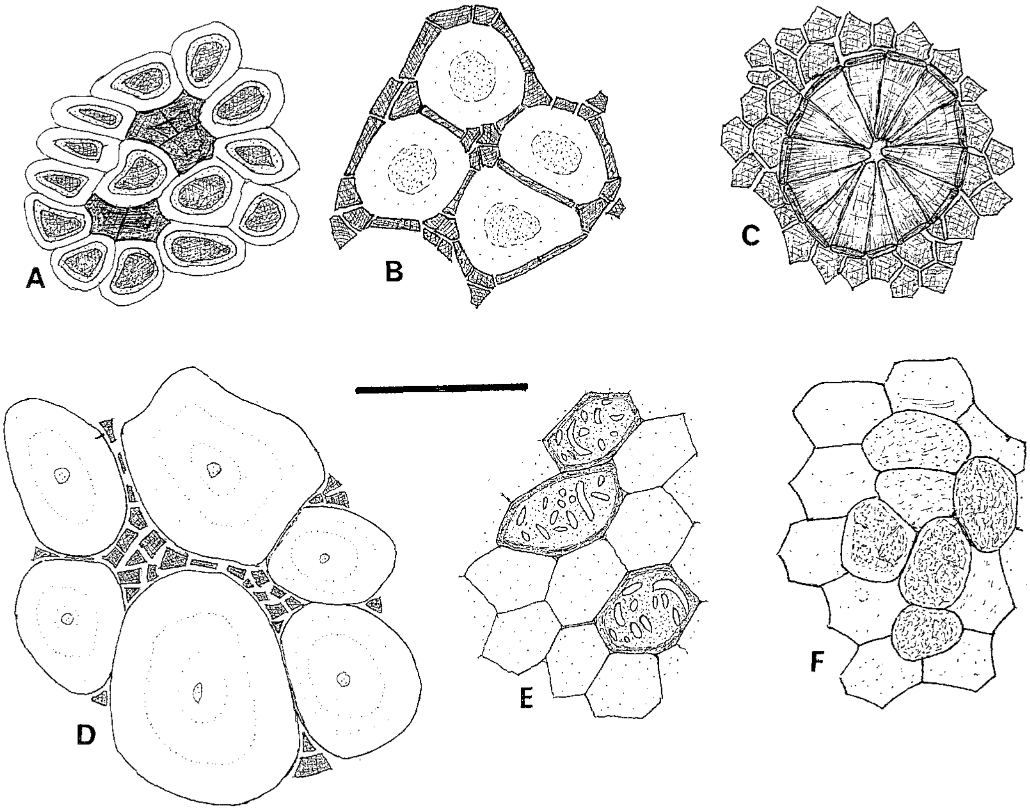


Fig. 1. The exocarp of the *Lamiaceae* in tangential section. *A Neohyptis paniculata*, mucilaginous cells which contain a reduced plate, and darker non-mucilaginous cells. *B Pitardia nepetoides*, mucilaginous cells surrounded by smaller non-mucilaginous cells. *C Drepanocaryum sewerzowii* with a 'mucilage bud'. *D Hedeoma molle*, large mucilaginous cells and much smaller, brownish non-mucilaginous cells. *E Ballota africana*, showing two cell types, ordinary thin-walled cells and brownish, thick-walled cells with large pits. *F Callicarpa japonica*, showing two types of cells. The vouchers are cited in Appendix 1. Bar: 50 μm

Description of the pericarp structure

The thickness of the pericarp varies from 20 μm (in *Tetradenia*) up to at least 8 mm (recorded in *Teijsmanniodendron*), and it consists of (3-)4 to numerous layers of cells. Immediately below the pericarp, there are layers that belong to the seed.

The variation in the most prominent and/or distinctive characters of the pericarp ultrastructure is described below, and their distribution in the genera is given in Table 1. Data about the following types of characters, which are presumed to be of little systematic value mainly due to great variations within genera, are often omitted in this study.: (1) the size of the cells and the thickness of their layers; (2) the colour of the cells; (3) the nutlet indumentum, which is often given in many Floras and revision works of genera. The hairs and glands often got very damaged during the preparation of the slides, and would better be studied by a stereo microscope or SEM.

Pericarp surface characters. Witztum (1978), Ryding (1982, 1986, 1992 a, 1993 b, 1994 b), Rejdali (1990), Sebsebe Demissew & Harley (1992), Bouman & Meeuse (1992), Paton (1992), Campion-Bourget & al. (1993), Budantsev (1993 a, b), and Marin & al. (1994) have demonstrated the presence of interesting nutlet surface structures. Such characters may be useful in a study of phylogeny, particularly within genera. However, similarities in surface structure do not always reflect homology in anatomical structure. Such structures are here described under several different subheadings on the basis of their ultrastructural background (see below).

A plicate pericarp. *Macbridea* has a plicate pericarp which forms ribs at the proximal side of the nutlets (Ryding 1994 b: fig. 1 E).

Shape of exocarp cells. When seen from the nutlet surface, the exocarp cells are usually isodiametric or slightly elongate along the nutlet axis (Fig. 1), but in some species, e.g., of *Leucas, Leonurus* and *Stachys*, they have been found to be very elongate (Ryding 1993 b, Wojciechowska 1966, Sebsebe Demissew & Harley 1992). The cells may be convex or concave and then form minutely colliculate or reticulate nutlet surfaces (see Ryding 1986: fig. 11 D, P).

A sclerenchymatous exocarp. Exocarp cells are usually parenchymatous, but *Amasonia, Bostrychanthera, Chaunostoma, Lepechinia, Gmelina, Spartothamnella,* and *Tectona* have sclerenchymatous exocarp cells. In *Lepechinia* and *Chaunostoma* these cells have long parallel pit canals in their apical part (Fig. 3 E).

A fleshy exocarp. Exocarp cells are usually dry, but *Prasium* (Wagner 1914: fig. 58) and *Clerodendrum cephalantha* have vertically very elongate exocarp cells that form a fleshy layer. In other taxa, the fleshy portion of the mericarp is formed by the mesocarp (see below).

A thick outer wall in the exocarp cells and/or a thick cuticle. A highly lustrous nutlet surface usually reflects the presence of a thick outer cell wall and/or a thick cuticle (Ryding 1993 b: fig. 1 G). That probably applies to the taxa in Cantino's (1992 a) cladistic analysis. However, the character is vague, and a glossy surface may also reflect the presence of plates in mucilaginous exocarp cells (see below).

Indumentum and conic exocarp cells. Nutlet hairs are modified exocarp cells. They are represented in all the subfamilies of *Lamiaceae*, but are more frequent in the *Verbenaceae* and the apical-styled labiates than in the gynobasic-styled members of the family. As in the stems and leaves of the same plants, they may be unicellular and/or multicellular, simple and/or branched, eglandular and/or glandular.

Dicrastylis has a peculiar type of hairy surface in which all exocarp cells form hairs, mostly unicellular ones and some multicellular and branched ones (Fig. 4 E). Unlike the multicellular hairs, the unicellular hairs are covered by a thick cuticle. The following Australian and E Asiatic *Chloanthoideae* and *Teucrioideae*, which have conic to papillose exocarp cells, may be regarded as intermediate between *Dicrastylis* and other labiates which have a comparatively smooth surface: *Caryopteris incana, Teucridium parvifolium, Hemigenia purpurea, Hemiandra incana, Microcorys barbata, Westringia rosmarinifolia,* and *W. rigida.*

In *Callicarpa, Lamioideae* and *Nepetoideae*, glandular and/or eglandular hairs often occur together with the two other types of differentiated exocarp cells (mentioned below) on the same nutlets. This condition suggests that the latter cell types do not correspond to hairs.

Mucilaginous cells and myxocarpy. In some labiates, the exocarp cells produce mucilaginous material upon wetting. The mucilage is formed by the cell walls which consist of hygroscopic spiral fibrillae that slit up (Ryding 1992 a). In most cases, the swelling mucilaginous cells protrude on the pericarp surface, but in *Pycnostachys* the mucilaginous material emerges from the inside of flakes (Ryding 1992 a). Functional mucilaginous cells always have colourless walls, but vestigial cells often have brownish walls. Mucilaginous cells usually have a plug-shape, sometimes brownish, content in the centre, but in the tribe *Ocimeae* subtribe *Plectranthinae*, the cell content forms a peltate, usually brownish plate (Fig. 3 G). When the plate covers the apical surface of the cells, the nutlet surface usually appears lustrous (Ryding 1992 a: fig. 1 X). Data on the size of this plate in the different species (covering viz. more or less reduced) have been provided by Ryding (1992 a).

According to Ryding (1992 b), who studied the presence or absence of myxocarpy in most genera of *Lamiaceae*, the phenomenon has only been recorded in subfam. *Nepetoideae*. Some additions to Ryding's (1992 b) list are given here: *Zhumeria majdae* was found to show a strong mucilaginous reaction (obtaining c. 0.7 mm long cells). *Drepanocaryum sewerzowii* was found to show a moderately strong mucilaginous reaction (obtaining 0.2 mm long cells). The following taxa were found to show a weak mucilaginous reaction (obtaining less than 0.1 mm long cells): *Cyclotrichium stamineum, Elsholtzia flava, Minthostachys mollis,* and *Xenopoma bolivianum.* The following taxa did not show any mucilaginous reaction: *Caryopteris incana, C. paniculata, Chaunostoma mecistandrum, Dicrastylis verticillata, Duranta erecta, Heterolamium debile, Hymenopyramis brachiata, Kurzamra pulchella, Lantana camara, Oxera oblongifolia, Peronema canescens.*

Non-mucilaginous cells (in an otherwise mucilaginous exocarp). In addition to functional or vestigial mucilaginous cells, the exocarp usually contains ordinary non-mucilaginous cells (Table 1). When studied on the nutlet surface, the non-mucilaginous exocarp cells are usually smaller than the mucilaginous cells, usually asteroid due to concave anticlinal walls and are usually brownish (Fig. 1 A–D). At the base and centre, these cells are usually much thinner than the mucilaginous cells, but are more or less widened towards the apex. Unlike other *Nepetoideae*, the subtribe *Plectranthinae* and perhaps also some other members of the *Ocimeae* have the non-mucilaginous cells vertically short and forming more than one cell layer beside vertically longer mucilaginous ones (Fig. 3 G; Ryding 1992 a).

Arrangement of mucilaginous and non-mucilaginous cells on the nutlet surface. On the nutlet surface, mucilaginous and non-mucilaginous cells form different types of patterns. Three main types of patterns are distinguished here, but the data on their distribution is very incomplete and intermediates between the two first types are apparently common. (1) In the following taxa, solitary or small groups of mucilaginous cells have been found to be separated from each other by smaller non-mucilaginous cells (Fig. 1 B, D): *Conradina, Dicerandra, Hedeoma, Hymenocrater, Lallemantia, Lavandula* (Wagner 1914: fig. 11), *Mentha* p.p., *Pitardia, Pycnanthemum, Rhabdocaulon, Xenopoma.* (2) In subtribe *Plectranthinae,* the non-mucilaginous cells are arranged in groups surrounded by mucliagi-

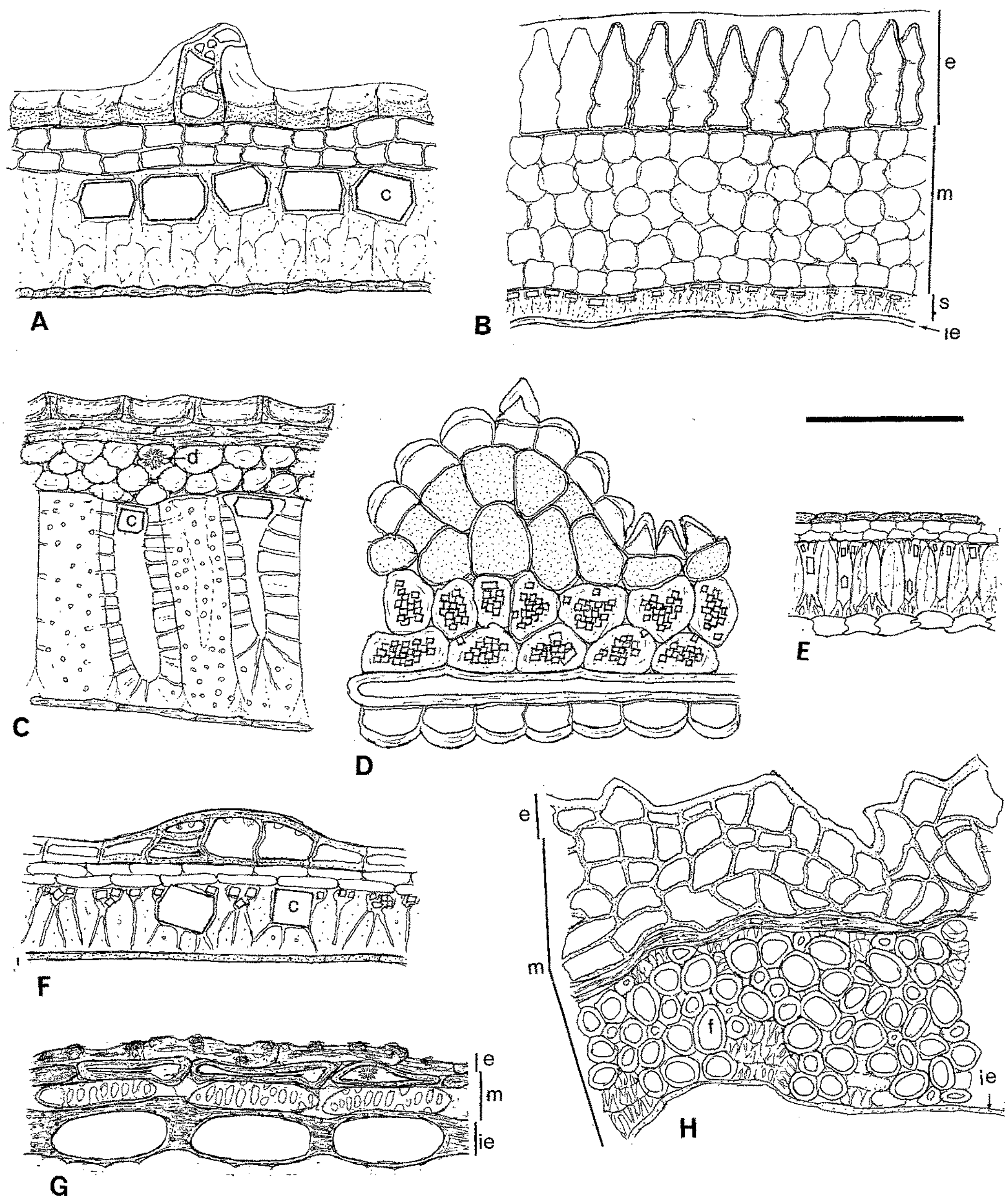


Fig. 2. The pericarp of *Lamiaceae* subfamilies *Lamioideae* and *Scutellarioideae*. *A Ballota frutescens* in transverse section (t.s.) with two types of exocarp cells, ordinary pale cells and brownish, thick-walled cells with reticulate secondary thickenings in the walls. *B Microtoena delavayi* in t.s. with two types of exocarp cells. *C Suzukia luchensis* in t.s. *D Renschia heterotypica*, longitudinal section of a papilla, upper cells of the mesocarp bluish to violet, central cells containing small prismatic crystals, lower cells fibre-shaped. *E Craniotome furcata* in t.s. with small crystals in the bone cells. *F Wiedemannia orientalis* in t.s.; the exocarp contains two cell types. *G Achyrospermum radicans* in longitudinal section with elongate, large-pitted cells in the mesocarp. *H Tinnea gracilis* in t.s. without sclerenchyma region, with fibres and cells with scalariform thickening in the mesocarp, with a layer of crystals above these cells. Abbreviations for the regions and structures: *c* prismatic crystal; *d* druse; *e* exocarp; *f* fibre; *ie.* endocarp; *m* mesocarp; *s* sclerenchyma region. The vouchers are cited in Appendix 1. Bar: 50 µm

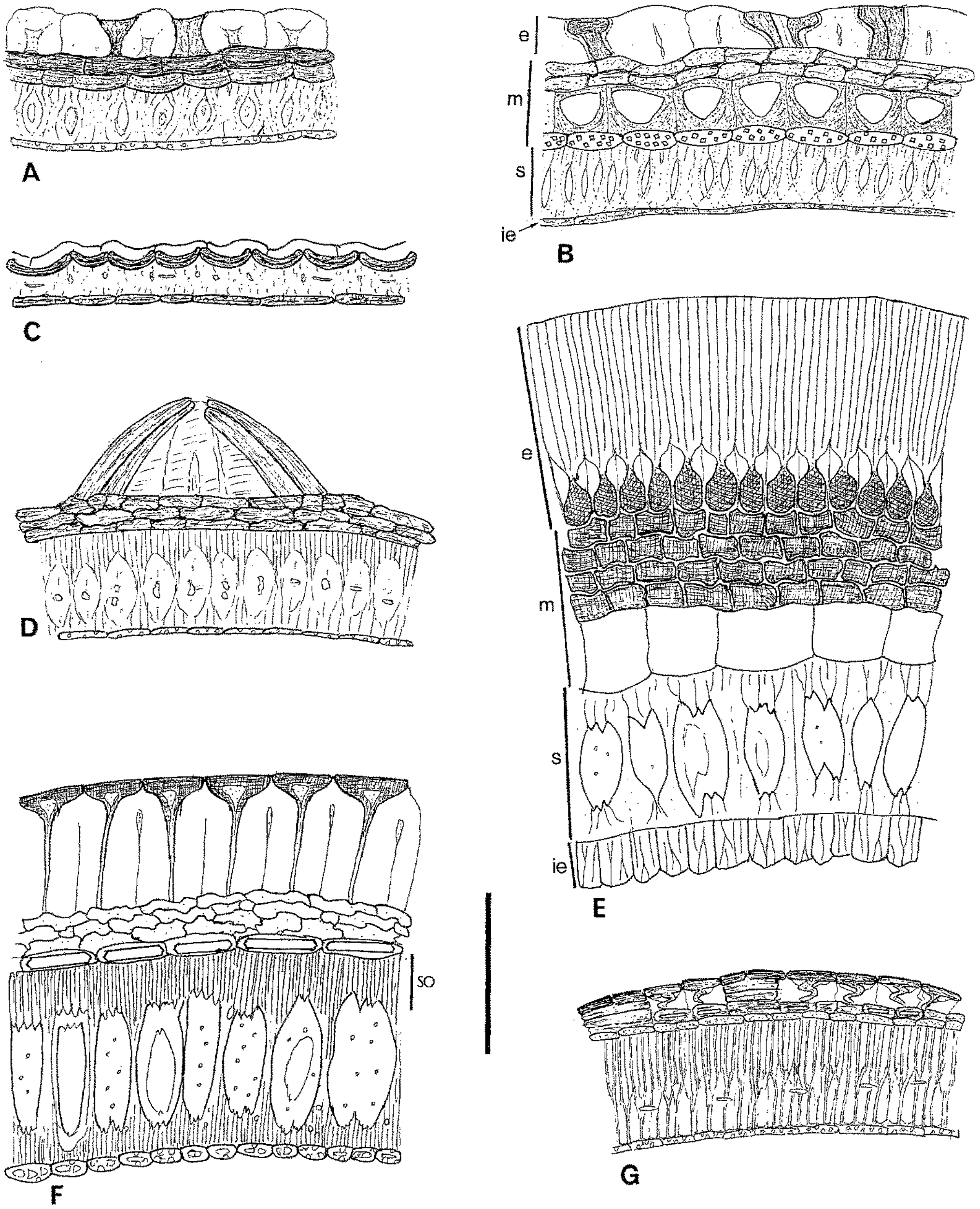


Fig. 3. The pericarp of *Lamiaceae* subfamily *Nepetoideae* in transverse sections. *A Schizonepeta tenuifolia* with mucilaginous and non-mucilaginous cells in the exocarp. *B Cleonia clusitanica* with a sclerenchymatous second innermost cell layer of the mesocarp, with small crystals in the innermost cell layer of the mesocarp. *C Micromeira juliana* with a minutely sculptured sclerenchyma region. *D Drepanocaryum sewerzowii* with a 'mucilage bud'. *E Lepechinia chamaedryoides* with sclereids in the exocarp which have parallel pit channels at the apex. *F Zhumeria majdae* with the non-mucilaginous exocarp cells covering the mucilaginous ones, with crystals in the innermost layer of the mesocarp. *G Capitanya otostegioides* with two cell types in the exocarp; mucilaginous cells containing a plate-like structure; the nonmucilaginous cells form several layers; the second innermost layer of the mesocarp contains prismatic crystals. Abbreviations for the regions and structures: *c* prismatic crystal; *d* druse; *e* exocarp; *ie* endocarp; *m* mesocarp; *s* sclerenchyma region. *so* "striate" outer part of the bone cells. The vouchers are cited in Appendix 1. Bar: 50 µm

nous cells (Fig. 1 A). Due to differences in their surface, the contrast between mucilaginous and non-mucilaginous cells often appears on the nutlet surface (Witztum 1978; Ryding 1982, 1986). *Callicarpa* and *Petitia* lack myxocarpy, but have differentiation of the exocarp cells similar to the one in *Nepetoideae* (Figs. 1 F, 4 B). However, in *C. japonica,* it is the cells with a convex anticlinal walls that are darker and occur together in large groups on the nutlet surface. (3) In *Zhumeria* from arid Iran, the non-mucilaginous cells are longer, strongly widened at the apex and cover the shorter mucilaginous cells completely (Fig. 3 F). When mucilage is formed, a skin consisting of non-mucilaginous cells flakes off from the nutlet surface.

Surface structures formed by groups of enlarged non-mucilaginous exocarp cells. Vertically longer non-mucilaginous cells sometimes form outgrowths on the nutlet surface. Examples are the tubercles on *Aeollanthus abyssinicus* Hochst. ex Benth. and *A. pinnatifidus* Hochst. ex Benth. (Ryding 1982: fig. 1 I). In some *Hemizygia* and *Syncolostemon*, enlarged non-mucilaginous cells form irregularly arranged ribs that are covered by a thick cuticle and appear as wrinkles (Ryding 1992 a: fig. 1 K). *Drepanocaryum, Hymenocrater,* some *Nepeta* (e.g., *N. azurea*) and perhaps also *Cedronella canariense* have a type of structure that forms bud-shaped outgrowths (Wojciechowska 1966: plate 43, 46; Budantsev 1993 b: plate 2.13, 3.6). They consist of functional or vestigial mucilaginous cells surrounded and more or less covered by long scale-shaped non-mucilaginous cells (Figs. 1 C, 3 D). When swelling in water, the mucilaginous cells may force the scale-shaped cells to bend out or break off.

Thick- and thin-walled exocarp cells and surface structures formed by such cells. Many *Lamioideae* show a different type of differentiation of the cells in the exocarp (Table 1). Ordinary exocarp cells are intermixed with solitary or small groups of divergent cells (Fig. 1 E). The latter cells are comparatively thick-walled, usually large-pitted to scalariform or reticulate, usually slightly wider and often have a brownish cell wall (Fig. 1 E). In some species, e.g., *Ballota frutescens* (Fig. 2 A) and some *Leucas* (Ryding 1993 b: fig. 4 N) the thick-walled cells are vertically longer and form tubercles on the nutlet surface. The 'spinulose structures' and 'blunt protrusions' on nutlets of *Stachys hildebrandtii* and *Lamium maculatum L.*, studied by Sebsebe Demissew & Harley (1992) and Bouman & Meeuse (1992), respectively, are probably also formed by this type of cells. In *Microtoena delawayi* slightly thick-walled cells form large groups or cover a large part of the nutlet surface.

Reticule and scales formed by exocarp cells. In *Melittis* (Wojciechowska 1966: plate 63), *Eurysolen* and *Perilla,* enlarged exocarp cells form a reticulum, but in *Perilla* thick vascular bundles also contribute to this sculpturing. The characteristic scales on the nutlets of *Achyrospermum* seem to be two cell layers thick, and both these layers apparently belong to the exocarp.

Starch grains in the exocarp. All investigated species of the following genera have been found to have starch grains in the exocarp cells: *Alvesia, Becium, Fuerstia, Melittis* (Wojciechowska 1966: plate 73), *Moluccella, Notochaete,* and *Orthosiphon* subg. *Nautochilus.* Such grains have also been found in some but not all the species of the following genera: *Aeollanthus, Dracocephalum, Hyptis, Lallemantia, Ocimum,* and *Orthosiphon* subg. *Orthosiphon.* In *Nepetoideae,* the grains are with few exceptions restricted to mucilaginous cells (Ryding 1992 a). Large starch grains in the exocarp cells may form minute tubercles on the nutlet surface (Ryding 1986: fig. 11 X).

The mesocarp. The mesocarp usually consists of two to many layers of soft cells, or sometimes of only one layer. They are colourless, yellowish to brown, sometimes violet or rarely reddish, and their colour is usually provided by the cytoplasm content. The cells ar parenchymatous or sometimes sclerenchymatous or collenchymatous. The mesocarp cells are variously shaped but tend to be less strongly branched than the cells of the sclerenchyma region and usually form a distinct layer. Variation in the number of cell layers, given in Table 1, usually refers to differences between species, but may also reflect uncertainty in the observations or known variation in the number of cell layers within the same nutlet (e.g., in *Monardella* and *Renschia*).

A fleshy mesocarp. In drupaceous labiates, the fleshy portion is usually formed by the mesocarp, the entire region or by the outer part of this region (but some exceptions are mentioned above under the exocarp).

Differentiation of the cell layers in the mesocarp. Within the same layers, the cells are usually similar, but there are often differences between the layers. Differentiations of the cell layers in the mesocarp may be classified as follows: (1) In many *Nepetoideae* (Table 1), the innermost cell layer of the mesocarp contrasts with the yellowish to brownish outer layers by being hyaline (or sometimes violet) and/or by being thicker than the ones above (Fig. 4 A). *Monardella* has a divergent violet cell layer in the innermost part of the mesocarp which is restricted to parts of pericarp and forms irregular patterns. (2) *Amasonia, Paraphlomis* and *Suzukia* have a similar type of differentiation of the mesocarp, but have more than one layer of colourless cells in the inner part of the region (Table 1). (3) Most *Lamioideae* have colourless or homogeneously coloured mesocarp cells. Many members of this subfamily have the upper cell layers of the mesocarp broader than the innermost one (e.g., *Acrotome,* Ryding 1993 b: fig. 3 E). (4) In *Eremostachys,* the mesocarp is weakly differentiated into three parenchymatous main layers. (5) *Phyllostegia, Stenogyne, Dicrastylis, Karomia,* and *Haplostachys* have a coherent tissue of stone cells in the mesocarp. Such cells are prominently pitted (Fig. 4 E). In *Phyllostegia* and *Stenogyne*, the outer part of the mesocarp consists of vertically elongate, parenchymatous and more or less fleshy cells. In *Haplostachys* and *Karomia*, the mesocarp is entirely sclerenchymatous (Ryding 1994 c: fig. 1 D). In *Dicrastylis*, the inner and central cell layers are rather thick-walled, while the outer ones are gradually incrasingly thin-walled (Fig. 4 E). (6) In *Newcastelia*, the entire mesocarp consists of cells with a scalarifom wall thickening. (7) In *Prunella* and *Cleonia*, the outer and the innermost cell layers are parenchymatous but between these layers, there are stone cells. In *Cleonia*, the sclerenchyma forms a single layer, and the sclereids are more thick-walled at the base than at the apex (Fig. 3 B).

Other types of differentiation of mesocarp cells. The following taxa have stone cells, fibres or collenchymatous cells in the mesocarp, and these cells are often not strictly confined to certain layers, but show different types of arrangements: (1) *Hymenopyramis* and some other labiates (see Table 1) have solitary stone-cells or small groups of such cells intermixed with ordinary soft mesocarp

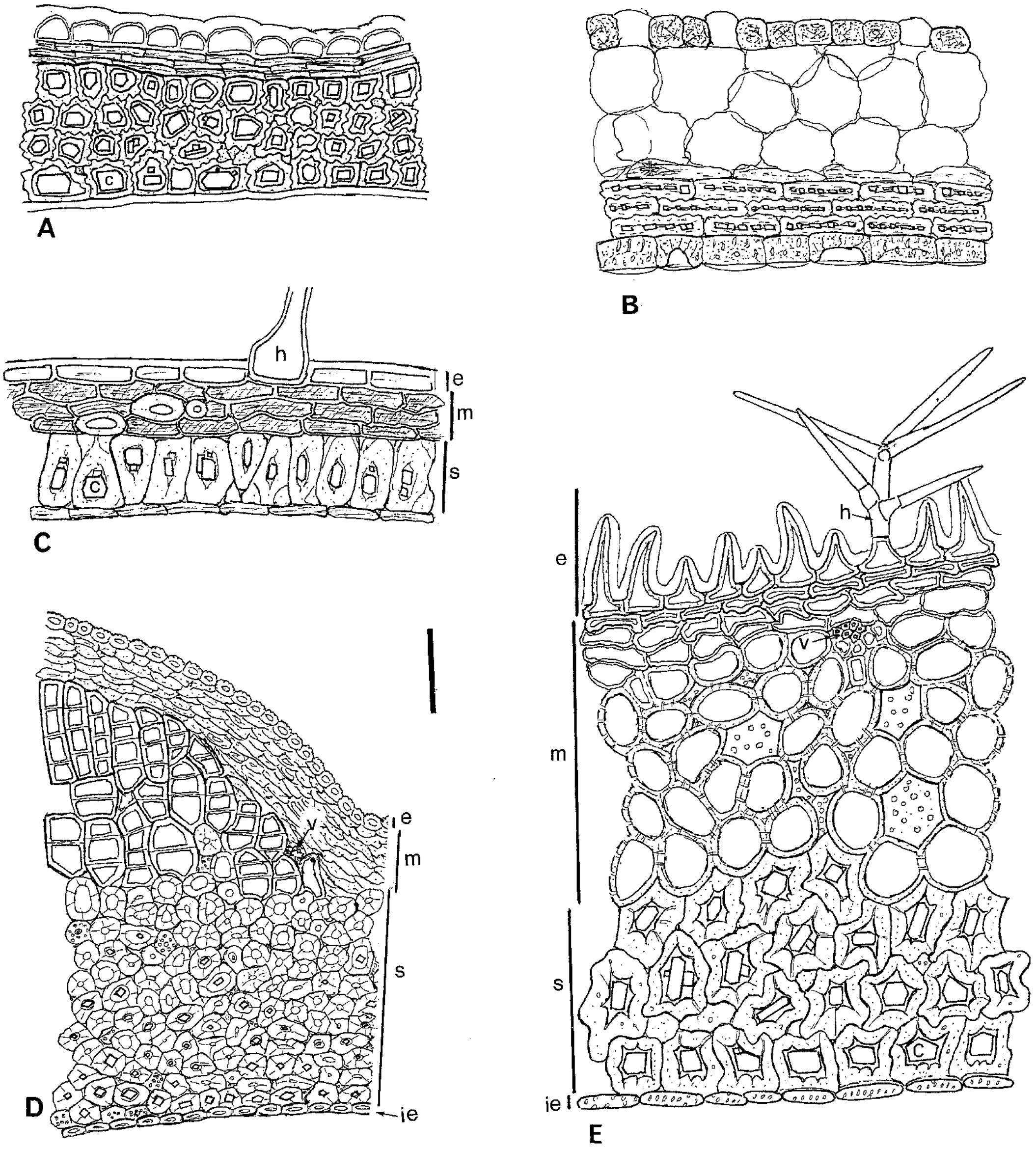


Fig. 4. The pericarp of the *Lamiaceae* subfamilies *Chloanthoideae* and *Viticoideae* in transverse sections. *A Pityrodia loxocarpha*. *B Callicarpa japonica*, mesocarp containing druses, innermost layer of the mesocarp may have become compressed during the preparation of the slides. *C Hymenopyramis brachiata* with sclereids scattered among the ordinary mesocarp cells. *D Premna resinosa* with a peculiar type of stone cells in the inner part of the mesocarp. *E Dicrastylis verticillata* with all the exocarp cells hair-like, with stone cells in the mesocarp. Abbreviations for the regions and structures: *c* prismatic crystal; *e* exocarp; *h* base of hair; *ie* endocarp; *m* mesocarp; *s* sclerenchyma region; *v* vascular bundle. The vouchers are cited in Appendix 1. Bar: 100: 50 µm

cells (Fig. 4 C). (2) In *Premna resinosa*, the sclerenchymatous cells are restricted to groups placed in the inner part of the mesocarp (Fig. 4 D). Such groups appear as papillae which form a colliculose nutlet surface. The stone cells are vertically elongate or are divided into two to four cells by the formation of horizontal walls

(Fig. 4 D). (3) *Chelonopsis* has fibres in the inner part of the mesocarp (Ryding 1994 b: fig. 2 B). Below the vascular bundles, there are several layers of fibres, and between the vascular bundles, the layer is thin or broken up by the presence of intervening mesocarp cells. In addition to typical fibres, *Chelonopsis moschata* Miq. has an atypical broad type of fibres which are placed between the vascular bundles where the fibre layer is interrupted by parenchyma (Ryding 1994 b: fig. 1 H). (4) *Tinnea* and *Renschia* have fibres in the inner part of the mesocarp which are intermixed with parenchymatous cells and cells with a scalariform wall thickening (Figs. 2 H, 5 H). (5) *Caryopteris incana* has horizontal, fibre-shaped parenchymatous cells at some places near the endocarp. (6) *Leucosceptrum, Comanthosphace, Rostrinucula* (Ryding 1994 a: fig. 2) and *Achyrospermum* (Fig. 2 G) have a type of elongate collenchymatous cells with large-pitted to scalariform or reticulate wall thickening.

Crystals in the mesocarp. Several labiates have prismatic crystals or druses (spherical conglomerate crystals) in the mesocarp. When present, the druses are usually few and seem to be more or less scattered all over the mesocarp (Figs. 2 C, G, 4 B). However, in *Callicarpa* they are perhaps restricted to the innermost layer of the mesocarp. Prismatic crystals are common in the subfamilies *Nepetoideae* and *Scutellarioideae* where, with few exceptions, they occur in genera that lack crystals in the sclerenchyma region (Table 1). When present (in *Nepetoideae*), they are usually restricted to certain layers of the mesocarp, and their position apparently constitutes an important character. They are restricted to the innermost layer (Fig. 3 F), to the second innermost layer (Fig. 3 G), or are sometimes present farther out in the mesocarp.

Papillae formed by parenchymatous mesocarp cells, and some peculiar structures connected to such outgrowths. In *Renschia* (Fig. 2 D), *Holmskioldia,* some *Scutellaria* (Paton 1990, 1992: figs. 3–7) and doubtfully also in *Tinnea*, the nutlets have 'papillae' formed by additional cell layers in the mesocarp. Wojciechowska (1972: plates 1–4) and Paton (1990: fig. 1) reported the presence of air spaces in the papillae of *Scutellaria* species. *Tinnea* have a long ray placed at the apex of minute or obsolete 'papillae'. Together, these rays form a wing on the nutlets. The rays contain a long, hair-like sclereid which is covered by thin layers of mesocarp and exocarp cells (Fig. 5 A). Some of the exocarp cells form hairs which constitute the secondary rays of the feathers. At the apex of the long sclereid, there is a gland and no other cells. According to an illustration by Wagner (1914: fig. 55), *Scutellaria tournefortii* Benth. seems to have similar hair-like sclereids which, except for its apex, are sunken into the mesocarp.

Other structures formed by the mesocarp. In *Chloanthes coccinea* and *Pityrodia bartlingii* enlarged mesocarp cells form a reticulum. 'Air sacks' in *Hyptis fasciculata* Benth. are formed by additional layers of large slightly collenchymatous mesocarp cells (Ryding 1992 a: fig. 7 J). In *Lycopus*, which grows in damp habitats, the pericarp is considerably thickened at the nutlet edges where it contains an additional tissue of loose mesocarp cells (Wojciechowska 1961 b: figs. 7–13).

A reticulum formed by the veins. Thick veins that are over-layered by thin cell layers often appear as a loose reticulum on the nutlet surface (Ryding 1992 a: fig. 1 R).

The sclerenchyma region. The sclerenchyma region consists of one to many layers of sclereids, or is absent. At the ridges of a sclerenchyma reticulum, the number of layers is usually higher. The cells are colourless or sometimes brownish, the latter probably due to lignification of the cell walls. RIMPLER & al. (1992) used the presence of several versus one or no layer of sclerenchymatous cells as a character in their cladistic analysis, but more detailed data about their number is provided in Table 1. Differences in surface structure, cell types and presence of crystals in the sclerenchyma region provide other important characters.

The surface of the sclerenchyma region. Sculpturing of the sclerenchyma region (pyrene) appears on the nutlet surface or may be completely obscured by the overlaying meso- and exocarp. Sculptured sclerenchyma surfaces may be divided into three main types: (1) The first type consists of a large reticulum (WOJCIECHOWSKA 1966: plates 2–9) or, along the sides of the nutlets, of ribs. Veins are often seen above the edges of this reticulum. In the edges, there are often additional layers of comparatively small cells which lack crystals. The data on the presence or absence of a reticulum in Table 1 refers to this type of sculpturing. The data on the presence of a reticulum in CANTINO's (1992 a) cladistic analysis also appear to refer to these sculptures, but in a few cases the sculpturing is formed by the mesocarp (see above). (2) *Cyanostegia angustifolia* has a corrugated or warted sclerenchyma region. (3) The third type of sculpturing is minutely reticulate, minutely pitted or striated. In such a surface, the cavities are filled up by a single mesocarp cell or by some cells arranged in a row along the nutlet axis (Fig. 3 C). This type of minutely sculptured pericarp surface is particularly common in the *Nepetoideae*, where its presence or absence may be of systematic value, RYDING (1992 a).

Cell types in the sclerenchyma region. On the basis of the shape of the cells, different types of sclerenchyma tissues can be distinguished, of which the first three types are the most frequent ones: (1) The first type consists of irregularly star-shaped to almost stone-shaped sclereids (Fig. 5 B). (2) The second type is palisade-shaped and consists of a layer of vertically arranged bone-cells. These cells have the luminar cavity enlarged at or near the centre and are branched and/or have pit canals at the apex as well as at the base (Fig. 5 F). In most *Nepetoideae*, the branches are often thin, and due to this the cells appear striated (Fig. 3 F–G). (3) The third type is also palisade-shaped, but contains a different type of bone cells. The luminar cavity of these calls is short and restricted to the apical part of the cells (Fig. 5 E) or is longer and extends well below the centre of the cell (Fig. 2 C). At the apex of the cell the wall is thin, and branches or pit canals only occur at the base of the cells (Fig. 5 E). In *Lamioideae*, the bone cells, which usually are of this type, often have large pits or pit canals in the anticlinal walls (Fig. 2 C), but the character is often very variable within the genera. (4) The sclereids of *Gomphostemma* sect. *Gomphostemma* may belong to the sclerenchyma region or may be of another origin. They may resemble those of the second category but are very deeply branched with few and thick branches and form a very rough surface. They may also be almost unbranched and are then more similar to fibres. (5) The sclereids of *Peronema, Caryopteris paniculata, Congea, Hymenopyramis, Perilla, Collinsonia, Keiskea* and some members of *Ocimeae* essentially form one cell layer and are intermediate between bone cells and stone cells. In

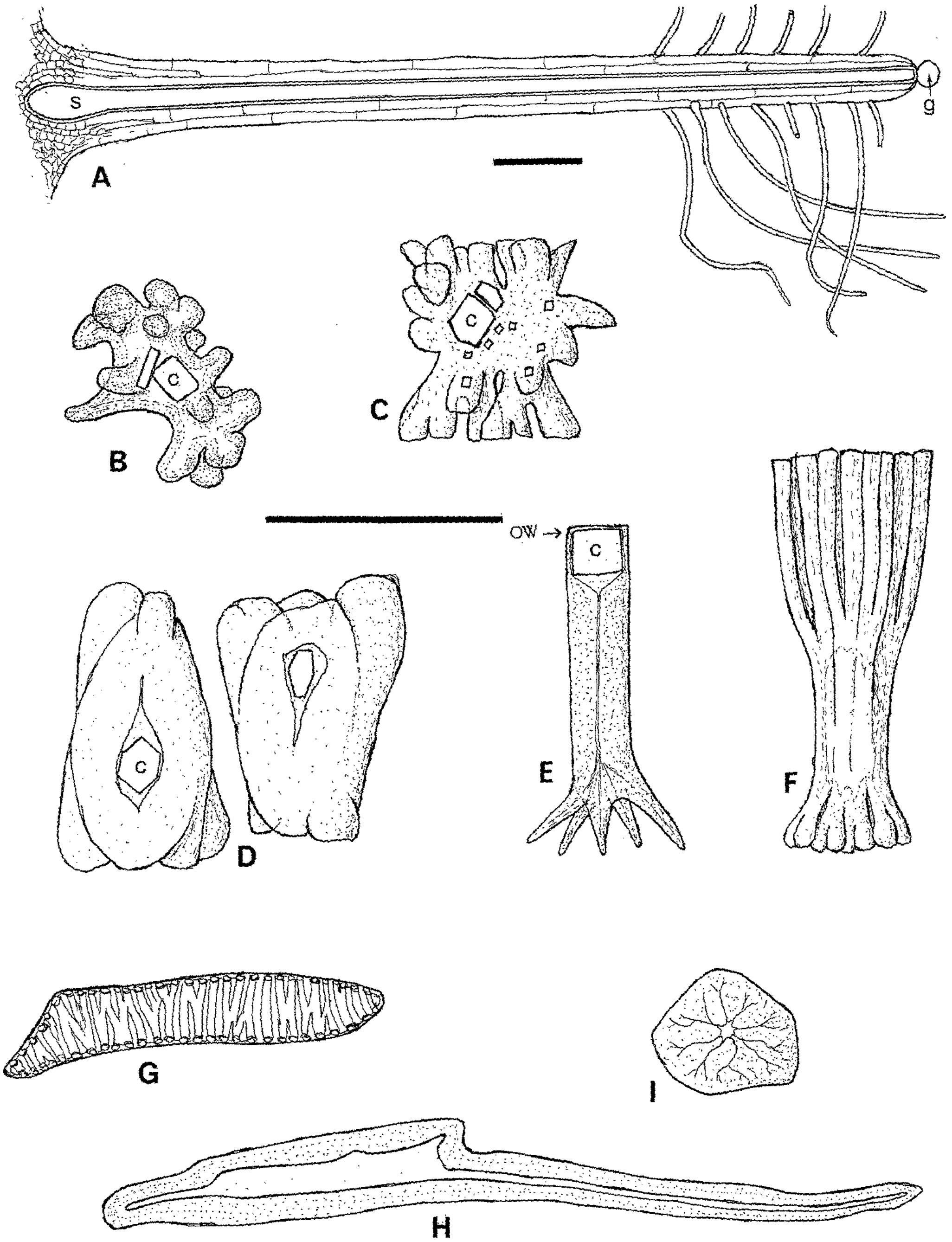


Fig. 5. *A* A comparatively short ray of the wing in a nutlet of *Tinnea gracilis* containing a long sclereid. *B–F* Sclereids from the sclerenchyma region of different labiates. *B* Irregularly star-shaped cell from *Newcastelia cephalantha*. *C* Cell from *Caryopteris paniculata*. *D* Two cells from *Hymenopyramis brachiata*. *E* Bone cells from *Anisomeles malabarica* (the basal branches have apparently become bent downwards during the preparation of the slide). *F* Bone cells from *Cedronella canariensis* (apical branches have perhaps become more spreading during the preparation of the slide). G–I Sclereids from the mesocarp of different labiates. *G* Scalariform cell from *Tinnea gracilis*. *H* Fibre (comparatively short) from *Tinnea gracilis*. *I* Stone cell from *Aegiphila pendula*. Abbreviations: *c* prismatic crystal; *g* gland; *ow* thin outer cell wall; *s* a long sclereid. The vouchers are cited in Appendix 1. Bar for *A*: 0.2 mm; bar for *B–I*: 50 μm

Table 1. Pericarp characters in *Verbenaceae* and *Lamiaceae*. After the names of the subfamilies and tribes, their number of genera is given within brackets. **Characters**: Many of the characters states are coded by letters followed by '+' (present), '±' (present or absent) or '–' (absent). The features under columns 1–10 are as follows: **1.** Cell types in the exocarp: *a* presence or absence of the *Lamioideae*-type of cell differentiation; *m* presence or absence of a reticulum formed by divergent cells; *n* presence or absence of the *Nepetoideae*-type of cell differentiation; *o–* cell differentiations of the above-mentioned types lacking. **2.** Number of cell layers in the mesocarp. If the mesocarp is differentiated into two or three distinct main layers, the numbers of cell layers in each main layer is given as separate figures, the outermost mentioned first and the innermost last. The following letter codes given before the numbers indicate the type of cells (if no letter code is given the cells are parenchymatous): *E* layers of elongate often thick-walled cells (fibres and/or ornamented cells, see text); *P* cells parenchymatous, colourless (or violet), differentiated from outer more or less yellowish to brownish cell layers (coding only applied for inner mesocarp layers); *S* layers of sclerenchymatous but not conspicuously elongate cells; *SS* layers very slightly sclerenchymatous; *Z* layers mainly parenchymatous but containing solitary sclereids or groups of such cells. Codes given within brackets after the figures: *p+* innermost cell layer paler than the outer ones (when *no p+* is given the layers have the same colour or the innermost is darker). **3.** *t* the condition of having the innermost cell layer of the mesocarp much thicker than the other layers; *t2* the condition of having the 2 or 3 innermost cell layers much thicker than the outer cell layers. **4.** *c–* crystals (incl. druses) absent in the mesocarp; *c1* presence or absence of prismatic crystals in the innermost layer of the mesocarp; *c2* presence or absence of prismatic crystals in the second innermost layer of the mesocarp; *c3* presence or absence of prismatic crystals in the third innermost layer of the mesocarp; *d* presence or absence of druses in the mesocarp. **5.** Number of cell layers in the sclerenchyma region. **6.** The sculpturing of the sclerenchyma (the minute type is not indicated): *i* very rough; *r* reticulate (or reticulate at the nutlet apex and otherwise ribbed); *s* smooth; *t* tuberculate or rugose. **7.** Shape of sclerenchyma cells (two or three letters in combination indicate intermediates): *a* bone cells with the lumen reaching the apex, and wall thin at the apex; *b* bone cells with the lumen enlarged below the centre; *c* bone cells with the lumen enlarged at the centre; *f* fibre-shaped sclereids (perhaps not belonging to the sclerenchyma region); *l* low cells which are not bone-shaped, but are presumed to be reduced sclerenchyma cells; *s* star- or stone-shaped cells, not forming palisade-shaped layer; *u* bone cells with the lumen enlarged above the centre but not reaching the apex. **8.** *c* presence or absence of crystals in the sclerenchyma region; *d* presence or absence of druses in the sclerenchyma region. **9.** *o* presence or absence of prominent pits or scalariform to reticulate wall thickening in the walls of the endocarp cells. **10.** Number of species in the genus which have been studied and references. Abbreviations of authors who have reported these data: *A* new data by the author in this study; *B* Bilimowitsch (1935); *C* Chatin (1874); *H* Hedge (1970); *K* Krestovskaja (1988); *Ma* Makarova (1967); *M1* Murthi (1946); *M2* Murthi (1947); *P* Paton (1990); *R1* Ryding (1982, 1986); *R2* Ryding (1992 a); *R2** Ryding (1992 a), but some modifications of this report made in this study; *R3* Ryding (1993 a); *R4* Ryding (1993 b); *R5* Ryding (1994 a); *R6* Ryding (1994 b); *R7* Ryding (1994 c); *Wa* Wagner (1914); *Wz* Witztum (1978); *W1* Wojciechowska (1958); *W2* Wojciechowska (1961 a); *W3* Wojciechowska (1961 b); *W4* Wojciechowska (1966); *W5* Wojciechowska (1972); *Z* Zhapakova & Mylnikova (1990)

Genera	1.	2.	3.	4.	5.	6.	7.	8.	9.	10
Phrymataceae (1)										
Phryma	o –	(0)	–	–	(0)	–	–	–	o –	1 A

Cyclocheilaceae (1)											
Cyclocheilon	o –	2	t –	c –	1	s	s	c –	o –	1	A
Symphoremataceae (c. 4)											
Congea	o –	2–4	t –	c –	0–2	?	sc	c +	o –	1	A
Verbenaceae (c. 30)											
Duranta	o –	2–3	t –	c –	4–7	s	s	c +	o +	1	A
Lantana	o –	1–4 (p?)	t –	c –	> 4	?	s	c +	o ±	1	A
Phyla	o –	SS 2–4	t –	c –	c · 3	?	s	c +	o +	1	A
Stachytarpheta	o –	3–4	t –	c –	4–5	r	s	c +	o ±	1	A
Verbena	o –	3–4	t –	c –	3–6	r	s	c +	o +	1	A
Chloanthoideae (17):											
Chloanthes	o –	2	t –	c –	3–4	r?	s	c +	o –	1	A
Cyanostegia	o –	2–3	t –	c –	3–5	t?	s	c +	o +	1	A
Dicrastylis	o –	2–3, S 5–6	t –	c –	3–4	s	s	c +	o +	1	A
Hemiandra	o –	1–2	t –	c –	2–6	r	s	c +	?	1	A
Hemigenia	o –	2–3	t –	c –	2–3	r	s	c +	o –	1	A
Microcorys	o –	1	t –	c –	2–3	r	s	c +	o +	1	A
Newcastelia	o –	3	t –	c –	3–4	r?	s	c +	o +	1	A
Pityrodia	o –	2–3	t –	c –	4–6	s	s	c +	o –	2	A
Prostanthera	o –	4	t –	c –	3–5	s	s	c +	?	1	Wa
Tectona	o –	SS9	t –	c –	> 9	?	s	c +	o +	1	A
Westringia	o –	3–6	t –	c –	4–5	r	s	c +	o –	1	Wa A
Wrixonia	o –	1	t –	c –	3–4	r	s	c +	o –	1	A
Teucrioideae (23):											
Aegiphila	o –	Z > 9	t –	c –	> 6	r	s	c +	o –	1	A
Amasonia	o –	4–6, P 0–2	t 2+	c –	4–5	r	s	c +	o ±	1	A
Amethystea	o –	3–4	?	c –	> 1	r?	s	c +	?	1	WA
Caryopteris incana	o –	3–4, E 0–4	t –	d +	0	–	–	–	o –	1	A
C. paniculata	o –	3–4	t –	c –	1 (– 2)	s	sc	c +	o –	1	A
Clerodendrum	o –	6–8	t –	c –	7–9	s	s	c +	o ±	2	A
Glossocarya	o –	2–3	t –	c –	2 (– 3)	s	s	c +	?	1	A

Table 1 (continued)

Genera	1.	2.	3.	4.	5.	6.	7.	8.	9.	10
Kalaharia	o –	> 9	t –	c –	2–4	?	s	c –	o –	1 A
Karomia	o –	S 2–6	t –	c –	2–3	r	s	c +	o –	1 A
Oncinocalyx	o –	3	t –	c –	3–6	r	s	c +	?	1 A
Oxera	o –	> 9	t –	c –	c · 4	r	s	c –	o ±	1 A
Peronema	o –	2–4	t +	c –	1–2	s	sc	c –	o –	1 A
Spartothamnella	o –	2, 1	t +	c –	4–5	r	s	c +	o –	1 A
Tetraclea	o –	3, S 0–3	t +	c –	5–8	r	s	c +	o –	1 A
Teucridium	o –	5–6	t –	c –	4–5	r	s	c +	o –	1 A
Teucrium	o –	2–6	t –	c –	> 3	r/s	s	c +	o ±	10 Wa W4
Trichostema	o –	1–3	t –	c –	5–9	r	s	c –	o –	2 A
Viticoideae (15):										
Callicarpa	n +	2–4	t ±	d +	2–6	s	s	c +	o +	2 A
Cornutia	o –	7–9	t –	c –	4–5	r	s	c +	o +	1 A
Gmelina	o –	> 9	t –	c –	> 9	s	s	c –	?	1 A
Hymenopyramis	o –	Z4	t –	c –	1 (– 2)	s	sc	c +	o –	1 A
Paravitex	o –	2–7	t –	c –	?	?	s	c –	o –	1 A
Petitia	n +	5–6	t –	c –	> 9	?	s	c +	o +	1 A
Premna	o –	1–5, S 0–6	t –	c –	3–6	s	s	c +	o +	1 A
Teijsmanniodendron	o –	Z > 9	t –	c –	3–7	?	s	c –	o –	1 A
Tsoongia	o –	4–7, P 0–2	t 2 +	d +	5–7	r	s	c –	o +	1 A
Vitex	o –	2–3, P 6	t –	c –	3–4	s	s	c +	o +	1 A
Viticipremna	o –	4–7	t –	c –	> 9	r	s	c –	?	1 A
Scutellarioideae (4):										
Holmskioldia	o –	2 P 3–8	t –	c –	1 (-2)	s	s	c +	o –	1 A
Renschia	o –	3–4, E 1	t –	c 2 +	0	–	–	–	o ±	1 A
Scutellaria	o –	> 1, E? 0–1	t –	c 3 + d ±	0	–	–	–	o ±	13 Wa W4 C P A
Tinnea	o –	2–4, E 3–5	t –	c 3 + d ±	0	–	–	–	o –	2 A

Ajugoideae (6):										
Acrymia	o –	1–3	t –	c –	1	r	sc	c –	o ±	1 A
Ajuga	o –	1–5	t –	c –	2–5	r	s	c +	o +	6 Wa W4 A
Cymaria	o –	1–2	–	c –	c · 4	r	s	c +	?	1 A
Garrettia	o –	2–4	t –	c –	2–3	r	s	c +	o –	1 A
Pogostemonoideae (7):										
Anisomeles	o –	2	t –	c –	1	s	a	c +	o –	2 J M1 R5
Colebrookea	o –	1–2	t –	c –	1	s	cu	c +	o –	1 R5
Comanthosphace	o –	2, E 1–3	t –	d +	0	–	–	–	?	2 R5
Eurysolen	o –	2	t –	c –	c · 3	s	s	c +	o –	1 A
Leucosceptrum	o –	2, E 1–2	t –	d +	0	–	–	–	o –	1 R5
Pogostemon	o –	2	t –	c –	1	s	c	c +	o –	4 R5
Rostrinucula	o –	E 2–3	t –	d +	0	–	–	–	?	1 R5
Lamioideae (54):										
Achyrospermum	o –	1–3, E 1	–	d +	0	–	–	–	o –	2 A
Acrotome	1 ±	2	t –	c –	0 ?–1	–	1	c –	o –	5 R4
Alajja	o –	2	t –	c –	1	s	a	c +	o –	1 A
Ballota	o ±	2–3	t –	c –	1	s	a	c +	o –	7 Wa W4 A
Bostrychanthera	o –	5–6	t –	c –	0	–	–	–	?	1 R7
Brazoria	o –	2	t –	c –	1	s	a	c +	o –	2 R6
Chaiturus	o –	2	t –	c –	1	s	a	c +	–	1 W5
Chamaesphacos	o –	1–2	–	c –	1	s	a	c +	o –	1 A
Chelonopsis	o –	1, E 0–6	–	c –	0	–	–	–	o –	3 R6
Colquhounia	o –	1 (-2)	t –	c –	1	s	a	c +	o –	1 A
Craniotome	o –	2	t –	c –	1	s	cu	c +	o –	1 A
Eremostachys	o –	> 9	t –	d +	0	–	–	–	o –	1 Wa
Eriophyton	o –	2	t –	c –	1	s	a	c +	o –	1 A
Galeopsis	1 +	2–3	t –	c –	1	s	a	c +	o –	8 Wa W4 A
Gomphostemma										
sect. *Gomphostemma*	o –	2–3 ?	t –	c –	(1)	(i)	(cf)	(c +)	o –	2 R7
sect. *Pogosiphon*	o –	1–7 ?	t –	d +	(?)	(i)	(f?)	(c –)	o –	2 R7
Haplostachys	o –	S 4–8	t –	c –	1	s	a	c +	o –	1 R7
Hypogomphia	1 +	2–4	t –	c –	1	s	a	c +	o –	1 A

Table 1 (continued)

Genera	1.	2.	3.	4.	5.	6.	7.	8.	9.	10
Isoleucas	1 +	2	t –	c –	1	s	a	c +	o –	1 R4
Lagochilus	o –	3–7	t –	c –	1	s	a	c +	o –	2 A
Lagopsis	1 ±	2–3	t –	c –	1	s	a	c +	o –	1 A
Lamium	1 ±	2–3	t –	c –	1	s	a	c +	o –	5 C Wa W4 W5 R6 A
Lamiophlomis	o –	2	t –	c –	1	–	1	c –	o –	1 A
Leonurus	1 ±	3–4	t –	c –	1	s	a	c +	o –	6 Wa W3 K W4 W5
Leonotis	1 ±	2–3	t –	c –	1	–	1	c ±	o –	8 R4 Wa
Leucas	1 ±	0–3	t –	c –	1	s	a/1	c ±	o –	61 R4
Loxocalyx	o –	1–2	–	c –	1	s	a	c +	o –	1 A
Macbridea	o –	3–4	t –	c –	1	s	1	c +	o –	1 R6
Marrubium	1 ±	2–3	t –	c –	1	s	a	c +	o –	4 Wa W4
Melittis	r +	3–4	t–	c –	1	s	a	c +	o –	1 Wa W4 R6 A
Microtoena	1 +	5	t –	c –	1	s	a	c +	o –	1 A
Moluccella	1 +	2	t –	c –	1	s	a	c +	o –	2 A
Notochaete	o –	3	t –	c –	1	–	1	(d +)	o –	1 A
Otostegia	1 +	0–4	t –	c –	1	s	a	c +	o –	5 R5
Paraphlomis	s	2, P 2	t 2 +	c –	1	s	a	c +	o –	1 A
Phlomiodeschma	o –	2–4	t –	c –	1	s	a	c +	o –	1 A
Phlomis	1 ±	> 3	t –	c –	1–? 2	?	a/1	c ±	o –	4 Wa W4 A
Phyllostegia	o –	> 2, S 1–3	t –	d ±	1	s	a	c +	o –	5 R7
Physostegia	o –	2	t –	c –	1	s	a	c +	o –	5 R6
Prasium	o –	c · 4	t –	c –	1	s	a	c +	o –	1 Wa
Roylea	o –	4	t –	c –	1	–	1	c +	o –	1 A
Sideritis	1 ±	3–4	t –	d ±	1	s	a	c +	o –	8 Wa W5 A
Stachyopsis	o –	2	t –	c –	1	s	a	c +	o –	1 A
Stachys	1 ±	3–8	t ±	d ±	1	s	a	c +	o –	9 C Wa W3 W4

Stenogyne	o –	3–9, S > 7	t –	c –	1	s	a	c +	o –	3 R7
Suzukia	o –	2, P 2–3	t –	d +	1	s	a	c +	o –	1 A
Synandra	o –	2	t –	c –	1	s	a	c +	o –	1 R6
Thuspeinantha	o –	2–4	t –	c –	1	s	a	c +	o –	1 A
Wiedemannia	1 +	2	t –	c –	1	s	a	c +	o –	1 A
Nepetoideae (134):										
Heterolamium	o –	2 (p +)	t +	c –	1	s	b	c –	o +	1 A
Elsholtzieae (6):										
Collinsonia	o –	2–4	t –	c –	1	s	sbc	c –	o +	1 A
Elsholtzia	n ±	0–2 (p +)	t ±	c –	1	s	cb/?	c –	o +	2 W4 A
Keiskea	o –	2–4	t –	c –	1	s	sbc	c –	o +	1 A
Mosla	o –	1–3 (p ?)	t –	c –	1	r/s ?	sbc/c	c –	o +	3 Wa A
Perilla	r +	3–4	t –	c –	1	s	sbc	c –	o +	1 W3 A
Perillula	o –	1–2	t –	c –	1	s	c	c –	o +	1 A
Mentheae (72):										
Acanthomintha	?	2	t –	c –	1	s	b	c –	?	1 A
Acinos	n +	2–3 (p ±)	t ±	c –	1	s	cb	c –	o +	2 W4 A
Agastache	o –	2 (p ?)	t –	c –	1	s	cb	c –	o +	1 A
Blephilia	?	1–2 (p ?)	t –	c –	1	s	b	c +	?	1 A
Bystropogon	n +	2	t –	c –	1	s	b	c +	?	1 A
Calamintha	n +	1	–	c –	1	s	cb	c –	?	1 W4
Cedronella	n +	2	t –	c –	1	s	b	c –	o +	1 Wa A
Chaunostoma	o –	5 (p +)	t +	c –	1	s	cb	c–	o +	1 A
Cleonia	n +	2, S1, P1	t –	c 1 +	1	s	cb	c–	o +	1 A
Clinopodium	o –	2 (p ?)	t –	c –	1	s	b	c –	?	1 W4
Conradina	n +	2	t –	c –	1	s	b	c –	?	1 A
Coridothymus	n +	1	–	c –	1	s	1	c –	?	1 Wa
Cuminia	n +	3–5 (p ?)	?	c –	?	s	?	c +	?	1 A
Cunila	n +	2 (p +)	t –	c –	1	s	b	c ±	o +	2 A
Cyclotrichium	n +	1–2 (p ?)	–	c –	1	s	cb	c –	?	1 A
Dicerandra	n +	2	t +	c –	1	s	b	c +	o +	1 A
Diodeilis	n +	4	t –	c –	1	s	b	c –	?	1 A

Table 1 (continued)

Genera	1.	2.	3.	4.	5.	6.	7.	8.	9.	10
Dorystaechas	?	3 (p +)	t ±	c 1 +	1	s	b	c –	o +	1 A
Dracocephalum	n ±	2–5 (p?)	t –	c –	1	s	cb	c –	o +	5 Wa W4
Drepanocaryum	n +	2	t –	c –	1	s	cb	c –	o +	1 A
Gardoquia	?	2	t –	c –	1	s	cb	c –	?	1 A
Glechoma	o –	2–4 (p ?)	t +	c –	1	s	cb	c –	o +	1 Wa W4
Glechon	? +	2	t –	c –	1	s	b	c +	?	1 A
Hedeoma	n +	2	t –	c –	1	s	cb	c –	?	1 A
Hesperozygis	n +	2	t –	c –	1	s	b	c –	?	1 A
Hoehnea	n +	2–3	t –	c –	1	s	b	c –	o +	1 A
Horminum	n +	3 (p ?)	t –	c –	1	s	cb	c –	?	1 Wa
Hymenocrater	n +	2	t –	c –	1	s	b	c –	o +	1 A
Hyssopus	n +	3 (p ?)	t –	c –	1	s	cb	c –	?	1 Wa W3
Kurzamra	n +	1	–	c –	1	s	cb	c –	o ±	1 A
Lallemantia	n +	4–6 (p ?)	t –	c –	1	s	cb	c –	o +	2 Wa W4 Ju
Lepechinia	o –	3–10 (p +)	t +	c –	1	s	c/cb	c –	o +	5 A
Lophanthus	o –	3 (p ?)	t –	c 1 +	1	s	cb	c –	?	1 Wa
Lycopus	o –	> 2 (p ?)	t –	c –	1	s	c	c +	?	2 W3 Wa
Marmoritis	o –	2	t –	c –	1	s	cb	c –	o +	1 A
Melissa	n +	2–3 (p ?)	t +	c –	1	s	c	c +	o +	1 C Wa W3
Mentha	n ±	2–7 (p ?)	t –	c 3 ±	1	s	cb	c +	o +	7 Wa W4
Meriandra	n +	3–4 (p +)	t –	c 1 +	1	s	b	c –	o +	1 A
Micromeria	?	1	–	c –	1	s	cb	c –	o +	1 A
Minthostachys	n +	2–3 (p ?)	t –	c –	1	s	cb/1	c –	?	3 A
Monarda	n +	7–8 (p ?)	t –	c 1 ±	1	s	c	c ±	o +	2 Wa
Monardella	?	1–2 (p ±)	–	c –	1	s	b	c ±	o +	2 A
Nepeta	n ±	2–4	t –	c –	1	s	c/b	c ±	o +	10 Wa W4 A
Origanum	n ±	1–2 (p ?)	t –	c –	1	s	cb	c –	?	3 Wa W4
Perovskia	?	1–2 (p +)	–	c –	1	s	cb	c –	o +	1 A
Piloblephis	n +	2	t –	c –	1	s	u	c +	?	1 A
Pitardia	n +	1–2 (p ?)	–	c –	1	s	b	c –	o +	1 A
Pogogyne	n +	1	–	c –	1	s	cb	c –	?	1 A

Poliomintha	?	1	–	c –	1	s	b	c –	?	1 A
Prunella	n ±	2, S 2–3, P 1	t ±	c +	1	s	cb	c –	o +	4 Wa W2
Pycnanthemum	n +	1–2	–	c –	1	s	b	c +	?	2 A
Rhabdocaulon	n +	1	–	c –	1	s	b	c –	o +	2 A
Rhododon	o –	1–2 (p ?)	–	c –	1	s	cb	c –	?	1 A
Rosmarinus	n +	3–4 (p +)	t –	c 1 ±	1	s	cb	c –	o +	1 Wa W4 A
Saccocalyx	?	1	–	c –	1	s	cb	c –	o +	1 A
Salvia	n ±	> 2 (p ±)	t –	c 1 ±	1	s	cb/c	c –	o +	35 H Wa W2
Satureja	?	2–3 (p ?)	?	c –	1	s	cb	c –	o +	2 Wa W4
Schizonepeta	n +	2 (p ±)	t –	c –	1	s	cb	c –	?	1 A
Stachydeoma	? +	1	–	c –	1	s	b	c +	o –	1 A
Thymbra	o –	2 (p ?)	t –	c –	1	s	cu	c +	o +	1 Wa
Thymus	n +	0–1	–	c –	1	s	cb/1	c –	?	4 Wa W4
Xenopoma	n +	1	–	c –	1	s	1	c –	?	1 A
Zhumeria	n +	c · 5	t –	c 1 +	1	s	b	c –	o +	1 A
Ziziphora	o –	1–5 (p ?)	?	c –	1	s	cb	c –	o +	2 W4 Z
Lavanduleae (1):										
Lavandula	n ±	1–3 (p ±)	t –	c 1 ±	1	s	cb	c –	o +	6 Wa W4 R2
Ocimeae (52):										
Hanceola	n +	2 (p +)	t –	c –	1	s	cb	c –	o +	2 R2 R3
Isodon	n +	2–3 (p +)	t ±	c –	1	s	b/c/1	c –	o +	12 R2
Skapanthus	n +	2 (p +)	t +	c 1 +	1	s	b	c +	o +	1 R3
Tetradenia	n +	2 (p +)	t +	c –	1	s	1	c –	?	2 R3
Thorncroftia	n +	2–3 (p +)	t +	c –	1	s	c	c –	o +	2 R2 R3
Ocimeae-Hyptidinae:										
Asterohyptis	n +	2–3 (p +)	t –	c –	1	s	c	c ±	o +	1 R2
Eriope	n +	3 (p +)	t ±	c –	1	s	c	c +	o +	4 R2
Eriopidion	n +	3 (p +)	t –	c –	1	s	c	c +	o +	1 R2
Hypenia	n +	3 (p +)	t +	c –	1	s	c	c +	o +	1 R2
Hyptidendron	n +	2–4	t –	c –	1	s	b	c +	o +	1 R2
Hyptis	n ±	2–4 (p +)	t ±	c –	1	s	b/c/u	c ±	o +	22 R2
Marsypianthes	n +	1	–	c –	1	s	c	c +	o +	1 R2

Table 1 (continued)

Genera	1.	2.	3.	4.	5.	6.	7.	8.	9.	10
Peltodon	n +	3	t –	c –	1	s	cb	c ±	o +	2 R2
Raphiodon	o –	3	t –	c –	1	s	c	c +	o +	1 R2
Ocimeae-Ociminae:										
Acrocephalus	?	1–2	t –	c –	1	s	u	c +	?	6 R2
Basilicum	n +	2 (p +)	t –	c –	1	s	cu	c +	o +	1 R2
Becium	n +	1–3	t –	c –	1	s	a	c +	o +	7 R2
Benguellia	n +	2	t –	c –	1	s	u	c +	o +	1 R2
Ceratanthus	?	1 (-2)	–	c –	1	s	u	c +	o +	2 R2
Catoferia	n +	2–3 (p +)	t +	c –	1	s	a	c +	o +	1 R2
Endostemon	n +	2–3 (p +)	t ±	c –	1	s	cu	c +	o +	6 R2
Erythrochlamys										
E. fruticosa	o –	2–3 (p ?)	t +	c –	1	s	ua	c +	o +	1 R2
E. leucospharea	n +	2 (p +)	t –	c –	1	s	u	c +	o +	1 R2
E. spectabilis	o –	2–3 (p ?)	t ±	c –	1	s	ua	c +	o +	1 R2
Fuerstia	n +	3 (p +)	t +	c –	1	s	cu	c +	o +	2 R2
Geniosporum	? +	1–3	t –	c –	1	s	c/u	c +	o +	6 R2 R3
Haumaniastrum	? +	1–2	t –	c –	1	s	u	c +	o +	1 R2
Hemizygia	n ±	2–3	t –	c –	1	s	a	c +	o +	9 R2
Hoslundia	? +	1 (p +)	t +	c –	1	s	cu	c +	o +	1 R2
Limniboza	?	(0–) 1	–	c –	1	s	u	c +	o +	1 R3
Mesona	? +	2	t –	c –	1	s	u	c +	?	1 R2
Nosema	? +	2	t –	c –	1	s	u	c +	o +	1 R2
Ocimum sect. *Ocimum*	n ±	1–4	t –	c –	1–? 4	s	?/ua	c +	o +	14 WA W R2
O. sect. *Hierocynum*	n ±	c · 3 (p ?)	t ±	c –	1	s	a	c +	o +	1 R2
O. circinatum	?	2 (p +)	t +	c –	1	s	a	c +	o +	1 A
Octomeron	? +	2	t –	c –	1	s	cu	c +	?	1 R2
Orthosiphon										
subg. *Nautochilus*	n +	2–3 (p +)	t +	c –	1	s	ua	c +	o +	2 R2 *
subg. *Orthosiphon*	n +	2–3 (p +)	t +	c –	1	s	cu	c +	o +	6 R2

Platostoma	? +	2	t –	c –	1	s	cu	c +	o +	1 R2
Syncolostemon	n ±	2–3	t –	c –	1	s	a	c +	o +	4 R2
Ocimeae-Plectranthinae:										
Aeollanthus	n +	1–3 (p +)	t –	c –	1	s	a	c +	o +	40 R2
Alvesia	n +	2–5 (p +)	t –	c 2 ±	1	s	b	c –	o +	2 R2
Anisochilus	n ±	2–3	t –	c 2 ±	1	s	b/1	c –	o +	4 R2
Capitanya	n +	2	t –	c 2 +	1	s	b	c –	o +	1 R2 *
Englerastrum	n +	2–3 (p +)	t ±	c 2 ±	1	s	b	c –	o +	2 R2
Holostylon	n +	2–3	t –	c –	1	s	b	c –	o +	2 R2
Isodictyophorus	n +	2	t –	c –	1	s	b	c –	o +	1 R2
Leocus	n +	3	t –	c 2 ±	1	s	b	c –	o +	2 R2 A
Neohyptis	n +	2 (p +)	t –	c –	1	s	b	c –	o +	1 R2
Plectranthus	n +	2–5 (p +)	t –	c 2 ±	1	s	b/c	c –	o +	34 Wa R2
Pycnostachys	n +	2–4 (p +)	t –	c 2 +	1	s	b/c	c –	o +	11 R2
Solenostemon	n +	2–4 (p +)	t –	c 2 +	1	s	b/c	c –	o +	6 R2

Caryopteris paniculata, these cells have rather spreading branches (Fig. 5 C), and as in *Hymenopyramis* (Fig. 5 D), they are rather irregularly arranged and sometimes form more than one cell layer. (6) In *Ocimum gratissimum* L. (Ryding 1992 a: fig. 7 B) and *Cuminia* the sclerenchyma forms a confused tissue. Superficially, it seems to be multi-layered, but it might equally well be formed by one layer of cells.

Large cells in the sclerenchyma region. According to Wagner (1914: fig. 62), some of the cells in the sclerenchyma region of *Teucrium cubense* Jacq. are strongly enlarged.

Crystals in the sclerenchyma region. According to Ryding (1992 a), prismatic crystals in the pericarp contain calcium oxalate. The shape and size of the crystals usually seem to reflect the shape of the space in which they have been formed. Presence or absence of prismatic crystals in the sclerenchyma region apparently constitutes an important systematic character (Table 1). Most *Lamioideae* have a large crystal in the bone cells. The same also applies to some genera of the *Nepetoideae* subtribe *Ocimeae* (Ryding 1992 a). Most other members of *Nepetoideae* have small or no crystals, but *Piloblephis* constitutes an exception and has large crystals in these cells. Druses are rare in the sclerenchyma region.

The endocarp. With few exceptions, the endocarp consists of a single thin cell layer. In *Gmelina, Paraphlomis* and some *Ocimum,* it forms two cell layers. *Scutellaria* may perhaps have several layers of such cells (see above under Homology). In most *Lamiaceae* s. l. the cells are parenchymatous or only slightly sclerenchymatous (Table 1). In *Achyrospermum* (Fig. 2 G), *Acrymia, Callicarpa* (Fig. 4 B), *Duranta, Lantana, Stachytarpheta,* and *Verbena*, the endocarp cells are strongly sclerenchymatous. The presence or absence of wall thickening (as large pits or scalariform to reticulate patterns, Fig. 3 A, E) apparently constitutes an important systematic character (Table 1). In *Stachytarpheta* and *Duranta*, the endocarp cells contain prismatic crystals. *Amasonia, Tinnea, Renschia* and several species of *Scutellaria* (Wagner 1914, Wojciechowska 1972) have short glandular hairs on the endocarp.

The pericarp of scars. Apart from the lack of exocarp, the scars seem to be structurally rather similar to the ordinary pericarp at the distal side of the same nutlets. As seen in *Oncinocalyx*, the outermost cell layer, which is analogous but not homologous to the exocarp, consists of brownish, more thick-walled cells. In contrast to typical exocarp cells, present at the distal side of the same nutlet, these cells lack indumentum and a distinct cuticle. Above this layer, there are occasionally fragments of thin-walled cells which apparently belonged to a zone of dehiscence.

The internal walls between the chambers. Internal walls between chambers of indehiscent fruits are usually rather simple in their anatomical structure. (1) In some taxa, e.g., *Dicrastylis* and *Caryopteris paniculata*, the internal walls, which constitute a part of the pyrene, apparently consist of a coherent sclerenchymatous tissue. In accordance with Junell's (1934) observations in ovaries of many apical-styled labiates, *Dicrastylis* was found to have four vascular bundles in the centre of the fruit. (2) The pyrene of *Hymenopyramis* has parenchyma in the centre of the wall between the two carpels. (3) The fruit of *Peronema* has two pyrenes which are separated by parenchyma. Along the centre of this wall, there is a structure which resembles a zone of dehiscence.

Cladistic analysis

A data matrix showing the pericarp characters in selected genera of *Lamiaceae* was compiled. The few pericarp characters used in Cantino's (1992 a) cladistic analysis have here been excluded. Autapomorphies are included in order to demonstrate monophyly of sinlge taxa (which often are composed of more than one genus). The characters are listed in Appendix 2 and the matrix is reproduced in Table 2.

The original set of taxa were selected to represent most of the variation in the family. Genera which are consistent in pericarp characters were more often selected than polymorphic ones. Due to difficulties with interpretation of homology and/or lack of information about the presumably most informative pericarp characters, the taxa that lack a characteristic sclerenchyma region have not been included in the analysis. Genera that are identical in all the pericarp characters (used in the Appendix 2) have been treated as a single taxon in the analysis.

The cladograms were rooted with the presumed closest relative, the family *Verbenaceae* s. str. as outgroup.

The data matrix was analysed using Swofford's (1993) PAUP 3.1.1. program. Cladograms were generated with the heuristics and 100 repetitions were made using the random addition sequence option. The multistate character 12 was treated as ordered, but all the other characters were treated as unordered.

The first run with the entire data matrix yielded too many equally parsimonious solutions, causing overflow in computer memory. Because of variation, character conflicts and unknown character states, *Acrymia, Aeollanthus, Caryopteris paniculata, Collinsonia, Eremostachys, Eriope, Holmskioldia, Hymenopyramis, Peronema, Pycnanthemum, Skapanthus, Teijsmanniodendron* and *Trichostema* assumed different positions on the cladograms, causing excessive numbers of solutions. Hence, these genera were excluded from the subsequent analyses.

The reduced data matrix yielded 108 equally parsimonious cladograms. The consistency and retention indexes (Farris 1989), calculated without the exclusion of autapomorphies, are 0.683 and 0.877, respectively. One of the cladograms is shown in Fig. 6 and a semistrict consensus tree in Fig. 7 B.

The set of 108 cladograms involves two different arrangements of the genera *Vitex* and *Newcastelia*, three different positions for the genus *Callicarpa* at the base of the cladogram, two different arrangements within the *Chloanthoideae*-clade (at node A) and eight different arrangements within the *Nepetoideae*-clade (at node G), the latter partly due to a different position for the *Glechoma-Lepechinia*-clade.

Phylogenetic discussion

Congruence between the pericarp cladogram and other phylogenetic trees. As shown in the consensus tree (Fig. 7 A), the new cladogram based on pericarp characters (Fig. 7 B) and Cantino's (1992 a) cladogram, which are based on analyses of entirely different characters, show a rather high degree of congruence. However, there are some conflicts between these two trees. The pericarp cladogram is less congruent with the rbcL tree by Olmstead & al. (1993) and the morphological and chemical tree by Rimpler & al. (1992).

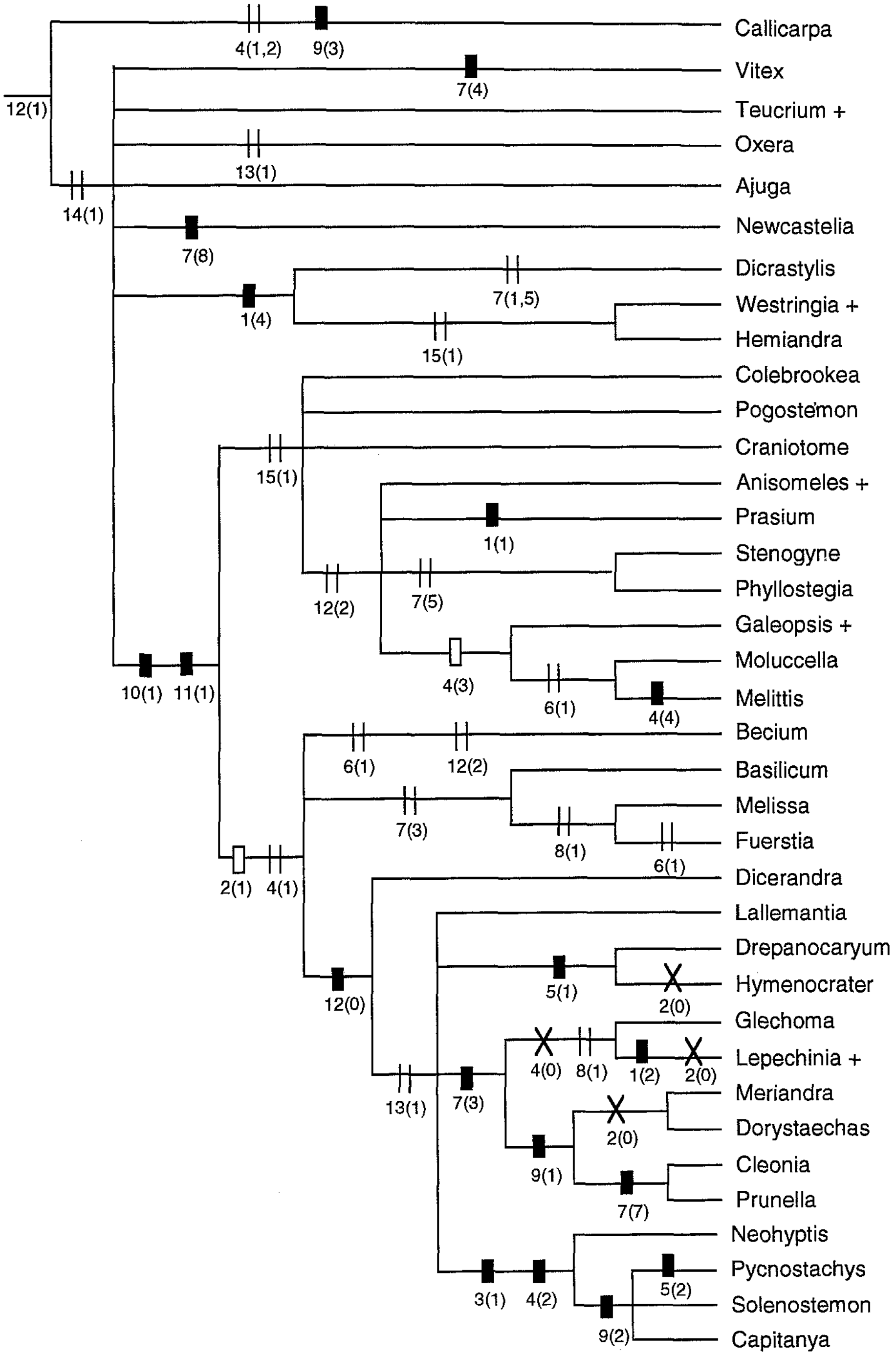


Fig. 6. One of the 108 equally parsimonious cladograms obtained from analysis of taxa in the data matrix in Table 2. *Filled bar* apomorphy; *empty bar* apomorphy with reversal or additional steps higher up in the clade; *crosses* reversal; *double lines* parallelism (without or with reversals or additional steps). '+' after the genus name indicates that the taxon in the analysis comprises more than one genus. The names of the other genera in the taxon are included in the Fig. 7 B

The positions of the subfamilies *Chloanthoideae, Teucrioideae, Viticoideae,* and *Ajugoideae*. Most members of *Chloanthoideae, Teucrioideae, Viticoideae,* and *Ajugoideae* have a multi-layered sclerenchyma region consisting of star- to stone-shaped cells, and in this respect these 'apical-styled' labiates agree with the outgroup in the cladistic analysis, the *Verbenaceae* s. str. Other members of these families (*Caryopteris paniculata, Peronema, Hymenopyramis, Acrymia*) which are more or less intermediate between the above-mentioned taxa and the gynobasic-styled labiates, had to be excluded from the cladistic analysis. Consequently, these subfamilies emerge at the base of the cladogram (in Fig. 7 B), and the result may be taken as support for the prevailing opinion that these apical-styled labiates are comparatively ancestral.

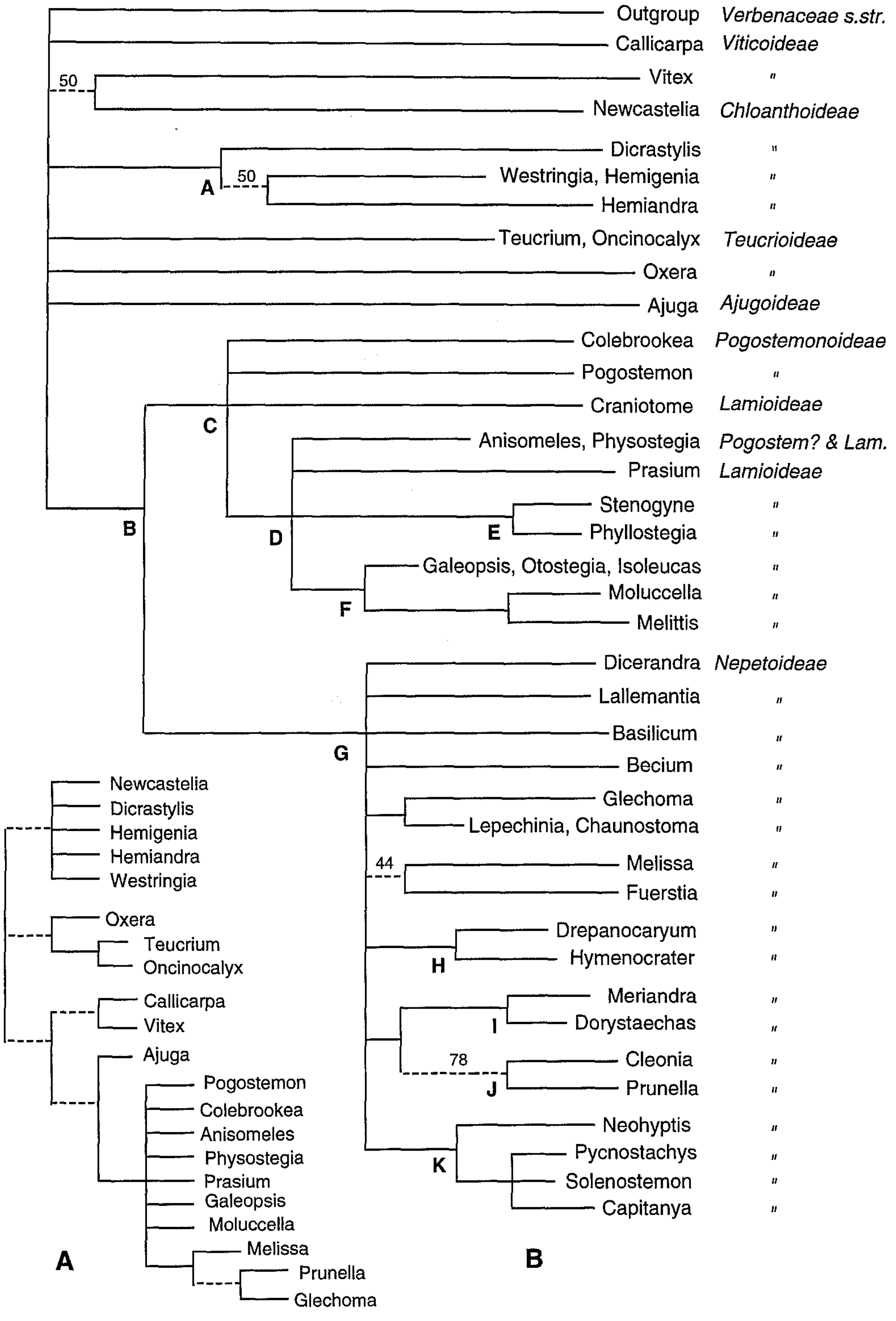
Monophyly of the gynobasic-styled labiates. The large clade at node B (in Fig. 7 B) is supported by the conditions of having the sclerenchyma region reduced to one layer of bone-shaped sclereids. It contains the representatives of the gynobasic-styled subfamilies *Pogostemonoideae, Lamioideae* and *Nepetoideae*, and corresponds to CANTINO's (1992 a) clade of gynobasic-styled labiates. The result contradicts the cladogram by RIMPLER & al. (1992) in which taxa of *Chloanthoideae* are nested within the clade of the gynobasic-styled labiates. It also contradicts the rbcL trees by OLMSTEAD & al. (1993) in which the *Nepetoideae* emerge as a sister group to *Callicarpa*. Actually, however, the *Nepetoideae* agrees with the apical-styled *Callicarpa* by having a differentiated exocarp, and in the cladograms (Fig. 7 B) the similarity constitutes a parallelism. Trees in which the *Nepetoideae* emerge as a sister group to *Callicarpa* are only one step less parsimonious than the ones in Fig. 7 B. Thus, the new data provide additional support for the gynobasic-styled labiates as a monophyletic group, but not very strongly so, and when consisdering the conflict with the chloroplast-DNA trees by OLMSTEAD & al. (1993), the question about monophyly of the gynobasic-styled labiates remains open.

Monophyly of the *Nepetoideae*, and the relationships within this subfamily. The clade at node G (in Fig. 7 B) corresponds to CANTINO's (1992 a) *Nepetoideae* clade and contains the representatives of this subfamily. In addition to pericarp characters, this subfamily is supported by differences in pollen, endosperm, rbcL, and chloroplast DNA restriction site data (ERDTMAN 1945, CANTINO & SANDERS 1986, CANTINO 1992 a, CHASE & al. 1993, WAGSTAFF, unpubl. data). Thus, subfam. *Nepetoideae* apparently constitutes an extremely well corroborated monophyletic group. Due to character conflicts, there is rather little resolution within the *Nepetoideae*-clade (in Fig. 7 B). Most of the small subclades essentially correspond to tribes and subtribes defined by BENTHAM (1848), BRIQUET (1895–1897) and EPLING (1948):

1) The group of *Lepechinia* and *Chaunostoma* which has a very distinctive type of pericarp structure, corresponds to the tribe *Lepechinieae* sensu EPLING (1948).

2) *Hymenocrater* and *Drepanocaryum* in BENTHAM's (1848, 1976) and BRIQUET's (1895–1897) tribe *Nepeteae* fall in the subclade (at node H), which is supported by having 'mucilage buds', *Nepeta*, which is polymorphic for 'mucilage buds' also belongs to this tribe.

3) The subclade at node I contains *Dorystaechas* and *Meriandra* in the tribe *Meriandreae* sensu BRIQUET (1895–1897), and it is characterized by having crys-


Outgroup Verbenaceae s.str.
Callicarpa Viticoideae
50
Vitex "
Newcastelia Chloanthoideae
Dicrastylis "
A
50
Westringia, Hemigenia "
Hemiandra "
Teucrium, Oncinocalyx Teucrioideae
Oxera "
Ajuga Ajugoideae
Colebrookea Pogostemonoideae
Pogostemon "
Craniotome Lamioideae
C
Anisomeles, Physostegia Pogostem? & Lam.
Prasium Lamioideae
Stenogyne "
B
D
E
Phyllostegia "
Galeopsis, Otostegia, Isoleucas "
Moluccella "
F
Melittis "
Dicerandra Nepetoideae
Lallemantia "
Basilicum "
G
Becium "
Glechoma "
Lepechinia, Chaunostoma "
44
Melissa "
Fuerstia "
Drepanocaryum "
H
Hymenocrater "
Meriandra "
I
Dorystaechas "
78
Cleonia "
J
Prunella "
Neohyptis "
K
Pycnostachys "
Solenostemon "
Capitanya "
Newcastelia
Dicrastylis
Hemigenia
Hemiandra
Westringia
Oxera
Teucrium
Oncinocalyx
Callicarpa
Vitex
Ajuga
Pogostemon
Colebrookea
Anisomeles
Physostegia
Prasium
Galeopsis
Moluccella
Melissa
Prunella
Glechoma
A
B

tals in the innermost layer of the mesocarp. *Dorystaechas* and *Meriandra* have the posterior stamens reduced to staminodes. It may be worth mentioning that the above-mentioned type of crystals has also been found in some of the material of three other 2-staminate genera: *Monarda, Rosmarinus* and *Salvia.*

4) The two genera at subclade J (*Prunella* and *Cleonia*) were placed in the subtribe *Prunellinae* by BRIQUET (1895–1897). The third genus in BRIQUET's subtribe, *Brazoria,* is apparently extraneous and is now placed in the *Lamioideae* (by CANTINO & al. 1992). The present classification of *Brazoria* is also supported by pericarp characters (RYDING 1994 b).

5) The subclade at node K contains genera of *Ocimeae* subtribe *Plectranthinae.* Most of the members of this subtribe (including the ones which are not included in the analysis) share the character states of the clade, i.e., the presence of a plate in the mucilaginous cells (see Table 1). However, *Alvesia* and the most divergent member of the subtribe, the genus *Aeollanthus,* diverge in various respects.

The *Lamioideae* and *Pogostemonoideae*, monophyly and relationships within this group of subfamilies. In CANTINO's (1992 a) cladogram, *Pogostemonoideae* and *Lamioideae* fall in separate clades, in a *Pogostemonoideae*- and a *Lamioideae*-clade. Together the two clades form a paraphyletic group in which the *Nepetoideae* is nested. In CANTINO's (1992 a) analysis which mainly focuses on the more ancestral part of the family, the *Lamioideae* are represented by comparatively few genera, and if a larger sample is made, some of the character states supporting the *Lamioideae* as a monophyletic group will break down. For example many of the *Lamioideae* agree with the *Pogostemonoideae* by having an almost flat upper lip of the corolla. According to RUDALL & CLARK (1992), the contention that the embryo sac shape with the micropylar lobe much longer and broader than the chalazal lobe represents a synapomorphy for BENTHAM's *Lamieae* and *Prasieae* (excluding *Anisomeles* and *Scutellaria*) is an over-simplification. In the pericarp cladogram (Fig. 7 B) as well as in the rbcL trees by CHASE & al. (1993) and OLMSTEAD & al. (1992, 1993), the two subfamilies form one clade. In the pericarp cladogram, the representatives of *Lamioideae* and *Pogostemonoideae* are both nested into each other. Whereas *Pogostemon, Colebrookea* (in *Pogostemonoideae*) and *Craniotome* (in *Lamioideae*) emerge at the unresolved base of the *Lamioideae-Pogostemonoideae*-clade, *Anisomeles* in the *Pogostemonoideae* and several *Lamioideae* form a subclade (at node D). Most genera of the *Lamioideae* (of which many were not included in the analysis) possess the character state of this subclade, the condition of having the lumen enlarged at the apex of the bone cells

Fig. 7. *A* A semistrict consensus tree between CANTINO's (1992 a) strict consensus tree and the strict consensus tree based on pericarp characters (see *B*). Branches which only are represented in one of the trees are drawn with dashed lines. Other branches are drawn with ordinary lines. *B* Semistrict consensus tree of 108 equally parsimonious cladograms obtained from analysis of taxa in the data matrix in Table 2. Branches which only occur in some of the trees are drawn by dashed lines, and the percentage of the total number of trees in which they occur is indicated by figures. Other branches (which also are present in a strict consensus tree) are drawn with ordinary lines. The letters in bold indicte clades discussed in the text. The subfamily according to the subfamilial classification by CANTINO & al. (1992) is given after the names of the taxa

(Table 1). The similarity in pericarp structure between the *Leucosceptrum*-group in *Pogostemonoideae* and *Achyrospermum* in *Lamioideae* (genera which were not included in the analysis, see below) also conflicts with the present delimitation of the two subfamilies. Thus, together, the *Lamioideae* and *Pogostemonoideae* may well form a monophyletic group, but the abandonment or recircumscription of the *Pogostemonoideae* as a taxonomic unit should be seriously considered.

The subclade at node E contains the Hawaiian *Phyllostegia* and *Stenogyne*. The third indigenous labiate genus on these islands, *Haplostachys,* resembles the first two genera in pericarp characters, and as mentioned by RYDING (1994 c), the similarities support the prevailing opinion that these three genera have originated from a single colonist.

The subclade at node F is supported by the presence of thick-walled usually large-pitted cells in the exocarp. This type of differentiated exocarp is frequent in the European, African and West Asiatic members of the subfamily, and is rare in East Asiatic, Pacific, and American members.

Relationship between some genera with conic exocarp cells. The genera in the clade at node A belong to the *Chloanthoideae*, but several other members of this subfamily lack the character state of this clade, the condition of having conic to hair-shaped exocarp cells. The character was not used in CANTINO's (1992 a) and CONN's (1992) cladistic analyses, but it supports their clade of *Hemiandra, Hemigenia, Microcorys,* and *Westringia.*

Relationships between some taxa with a reticulum formed by mesocarp cells. The nutlets of *Chloanthes* and *Pityrodia bartlingii* have a reticulum which is formed by the mesocarp. This character state may provide additional support to CANTINO's (1992 a) clade of *Chloanthes, Hemiphora* and *Pityrodia* (p.p.), but the true nature of the pericarp reticulum in *Hemiphora* and some other *Pityrodia* species remains to be investigated.

The relationship between the *Ajugoideae* and the gynobasic-styled labiates. According to Cantino's (1992 a) cladogram, the *Ajugoideae* may constitute the closest relatives of the gynobasic-style labiates. The finding of almost bone-shaped sclereids, suggests that *Acrymia* may be particularly close to the gynobasic-style labiates. The finding of almost bone-shaped sclereids suggests that *Acrymia* may be particularly close to the gynobasic-styled labiates.

The position of the genus *Holmskioldia*. BRIQUET (1895–1897) placed *Holmskioldia* in subfam. *Viticoideae*, but CANTINO & al. (1992) moved the genus to the *Scutellarioideae*. The additional pericarp characters provided in this study suggest that *Holmskioldia* either belongs to *Viticoideae* or forms a connecting link between the *Viticoideae* and the *Scutellarioideae*, the latter in agreement with *Cantino*'s (1992 a) cladogram.

The position of the genus *Eurysolen*. The systematic position of *Eurysolen* is an open question. WU (1959) and some other authors placed the genus in *Ajugoideae*, but CHERMSIRIVATHANA (1963) discovered that the genus deviates from *Ajugoideae* by having a small instead of a large scar on the nutlets, and CANTINO & al. (1992) suggested *Lamioideae* or *Pogostemonoideae*. However, the apparent presence of stone- to star-shaped cells in the sclerenchyma (see Table 1) disagrees with that of the gynobasic-styled labiates and agrees with *Ajugoideae* (and other apical-styled labiates).

Polyphyly of the genus *Caryopteris*. The two species of *Caryopteris* investigated, *C. incana* and *C. paniculata*, are strongly divergent in pericarp characters (see Table 1). These differences provide additional support to the suggestions of CANTINO (1992 a), RIMPLER & al. (1992) and ABU-ASAB & al. (1993) that the genus is paraphyletic or polyphyletic.

The positions of genera which lack a sclerenchyma region in the pericarp. As shown in the cladogram (Fig. 7 B), the characters of the sclerenchyma region are particularly consistent and useful in the study of phylogeny of the labiates. Due to the lack of such characters and uncertainties about the homology of other layers (see above under this heading), taxa which lack a typical sclerenchyma region could not be included in the analysis. Nevertheless, the information provided by the pericarp characters may still be very useful in the study of the phylogeny. In addition to the apparent absence of a sclerenchyma region, several of the taxa agree by having fibre-shaped and/or elongate cells with a large-pitted or scalariform wall thickening in the mesocarp. However, the fact that the same taxa often show great differences in gross morphological characters suggests that the similarities in pericarp structure often may be the result of a convergent evolution. When considering the overall resemblance, the taxa without a sclerenchyma region may form about six groups:

1) The first group belongs to subfam. *Scutellarioideae. Tinnea, Renschia,* and *Scutellaria* agree by having the following pericarp characteristics represented in at least some of their species: tubercles formed by additional mesocarp cells; glands on the endocarp; crystals in the mesocarp; and cells with a scalariform wall thickening in the mesocarp; fibres in the mesocarp (in *Tinnea* and *Renschia*). The unique type of hair-like sclereids, recorded in *Scutellaria tournefortii*, may correspond to the long sclereids which form the spectacular wings in the nutlets of *Tinnea*.

2) Although *Achyrospermum, Leucosceptrum, Comanthosphace,* and *Rostrinucula* have been placed in two different subfamilies (*Lamioideae* and *Pogostemonoideae*), these four East Asiatic (and African) genera may be closely related. They agree by having large-pitted to scalariform cells and druses in the mesocarp, very broad bracts and a very short upper lip of the corolla. In contrast to the claims by BRUCE (1936), the East Asiatic *Colquhounia* does not resemble *Achyrospermum*, either in pericarp structure or in other characters.

3) *Chelonopsis,* which has fibres in the mesocarp belongs to the *Lamioideae* and may be related to *Achyrospermum* and the *Leucosceptrum*-group. The same may also apply to *Bostrychanthera*, which lacks such cells. *Gomphostemma*, which has bone- to fibre-shape sclereids and often has a short upper lip of the corolla, may be transitional between *Chelonopsis* and some of the members of the *Pogostemonoideae-Lamoideae*-group such as *Pogostemon, Colebrookea* or *Craniotome.*

4) The genus *Leucas* (subfam. *Lamioideae*) apparently shows an evolutionary trend towards reduction of the bone cells (RYDING 1993 b). Whereas some *Leucas* have typical bone cells of the *Lamioideae*-type, other species of this genus have thin or obsolete cells in the sclerenchyma region. The *Leonotis* and *Acrotome*, which have thin or obsolete sclereids, may well have evolved from *Leucas* with similar cells (RYDING 1993 b).

5) The situation in the group of *Phlomis* and allied genera (subfam. *Lamioideae*) resembles the one of the *Leucas*-group. Whereas *Phlomis* has or lacks typical bone cells, *Eremostachys* and *Lamiophlomis* have obsolete sclereids or lack such cells completely.

6) *Caryopteris incana* in subfam. *Teucrioideae* also lacks a sclerenchyma region.

Future research

The systematic value of pericarp characters is apparently greatest above genus level, but in some cases the variation in these characters has been found useful within genera, e.g., *Plectranthus* and *Leucas* studied by Ryding (1992 a, 1993 b). Great differences between the few species studied suggest that pericarp characters may also be very useful in the study of the following genera: *Caryopteris, Clerodendrum, Gomphostemma, Monarda,* and *Phlomis.*

According to Cantino (1992 a), his cladogram should be considered as a preliminary study of the phylogeny of the labiates. Rimpler & al. (1992), Olmstead & al. (1993) and the present study of the pericarp have provided additional sets of useful characters. Investigations of the chloroplast DNA genes rbcL and ndhF (Wagstaff & al. 1993) are ongoing. According to Barrett & al. (1991), an analysis which combines all data would provide a better hypothesis about the phylogeny than a consensus tree (such as the one in Fig. 7 A). When more data have become available, the aims will be to perform such an analysis which hopefully will provide a greatly improved understandithe phylogeny of the labiates.

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Appendix 1. Abbreviated collection data for voucher specimens. Herbarium abbreviations follow Holmgren & al. (1990). *Acanthomintha ilicifolia* A. Gray: USA, California, Lewis & Rose 32227 (UPS). *Achyrospermum radicans* Gürke: Tanzania, Kis & al. 91168 (UPS). *A. schimperi* (Hochst. ex Briq.) Perkins: Kenya, Perdue & Kibua 8409 (UPS). *Acinus alpinus* (L.) Moench: Austria, Ryding 961 (UPS). *Acrymia ajugiflora* Prain: Malaysia, Melville 4747 (K). *Aegiphila pendula* Moldenke: Ecuador, Asplund 18677 (UPS). *Agastache urticifolia* (Benth.) Kuntze: USA, Washington, Tureson s.n. (UPS). *Ajuga integrifolia* Buch.-Ham. var. *canescens* (Benth.) Cufod.: Eritrea, Ryding 1367 (UPS). *Alajja rhomboidea* (Benth.) Ikonn.-Gal.: India, Stewart 2698 (E). *Amasonia hirta* Benth.: Brazil, Amapa State, Pires & Cavalcante 51993 (S). B*allota africana* (L.) Benth.: South Africa, Drege s.n. (UPS). *B. frutescens* (L.) Woods: unknown (UPS). *Blephilia ciliata* (L.) Raf.: USA, Ohio, Herb. Tuckerm (UPS). *Bystropogen canariensis* (L.) L'Hér.: Canary Islands, Teneriffa, Tullgren s.n. (UPS). *Callicarpa americana* L.: USA, Louisiana, Moldenke 726 (UPS). *C. japonica* Thunb.: Japan, Tokyo, Yatabe s.n. (UPS). *Caryopteris incana* (Thunb.) Miq.: China, illegible 3847 (UPS). *C. paniculata* C. B. Clarke: Bhutan, Ludlow & al. 18635 (UPS). *Cedronella canariensis* (L.) Webb & Bertol: Madeira, O. Dahlgren s.n. (UPS). *Chamaesphacos ilicifolius* Schrenk: Kazakhstan, unknown (UPS). *Chaunostoma mecistandrum* Don.-Sm.: Mexico, Matuda 3915 (GH). *Chloanthes coccinea* Bartl.: Australia, Western Australia, Rechinger 9113 (S). *Cleonia lusitanica* (L.) L.: Algeria, Faure 8 (UPS). *Clerodendrum cephalanthum* Oliv.: Tanzania, Borhidi & al. 82153 (UPS). *C. myricoides* (Hochst.) Vatke: Kenya, Harmsen 6528 (UPS). *Collinsonia canadensis* L.: USA, Washington D.C., Seaman s.n. (UPS). *Colquhounia coccinea* Wall.: Nepal, Polunin & al. 5079 (UPS). *Congea tomentosa* Roxb.: Burma, Kingdon Ward 20514 (UPS). *Conradina canescens* A. Gray: USA, Moldenke 1133 (K). *Cornutia pyramidata* L.: Trinidad, Hart 1949 (UPS). *Craniotome forcata* (Link) Kuntze: Nepal, Stainton 1773 (UPS). *Cuminia eriantha* (Benth.) Benth. var. *fernandezia* (Colla) Harley: Chile, Juan Fernandez Islands, Bertero 1490, (S). *Cunila incisa Benth.*: Brazil, Dusén 17818 (S). *C. origanoides* (L.) Benth.: USA, New Jersey, A. Gray s.n. (UPS). *Cyanostegia angustifolia* Turcz.: Australia, Western Australia, Pritzel 880 (S). *Cyclotrichium stamineum* (Boiss. & Hohen.) Manden, & Scheng. (syn. *Micromeria staminea* Boiss. & Hohen): Iraq, Kurdistan, Kotschy 311 (S). *Cymaria acuminata* Decne.: Philippines, Cumingham 446 (UPS). *Dicerandra frutescens* Shinners: USA, Florida, Tehler & al. 110 (S). *Dicrastylis verticillata* Black.: Australia, Queensland, Anderberg & Anderberg 7130 (S). *Diodeilis coccinea* (Nutt. ex Sm.) Raf.: Brazil, Rio de Janeiro State, Glaziou 6663 (C). *Dorystaechas hastata* Boiss. & Heldr.: Turkey, Davis 13948 (K). *Drepanocaryum sewerzowii* (Regesl) Pojark (syn. *Nepe-*

ta sewersowii Regel): Uzbekistan, Knorring 99 (S). *Duranta erecta* L. (syn. *D. repens* L.): Thailand, Bangkok, Zimmermann 11 (S). *Elsholtzia ciliata* (Thunb.) Hyl.: Poland, Jasiewicz & Piekos 167 (UPS). *E. flava* (Benth.) Benth.: China, Szechuan, H. Smith 13518 (UPS). *Eremostachys molucelloides* Bunge vel. sp. aff.: China, Sinkiang, Herb. Acad. Petrop. (UPS). *Eriophyton wallichianum* Benth.: India, Lepecha s.n. (K). *Eurysolen gracillis* Prain: Indonesia, Robinson & Kloss s.n. (K). *Galeopsis segetum* Necker: Germany, Reinland-Pfalz, Kalheber 82-2513 (UPS). *Gardoquia glabrata* Kunth.: Ecuador, Asplund 17961 (UPS). *Garrettia siamensis* Fletcher: Indonesia, Java, Jacobs 4726 (K). *Glechon ciliata* Benth.: Brazil, Regnell s.n. (S). *Glossocarya siamensis* Craib.: SE Asia, Pierre s.n. (S). *Gmelina arborea* Roxb.: cult. in Malawi, Brummitt 12133 (UPS). *Hedeoma molle* Torr.: USA, Texas, Havard s.n. (UPS). *Hemiandra incana* Bartl.: Australia, Western Australia, Pritzel 1001 (S). *Hemigenia purpurea* R. Br.: Australia, New South Wales, Mauritzon & Blakely s.n. (S). *Hesperozygis myrtoides* (Benth.) Epling: Brazil, Rio de Janeiro State, Dusén s.n. (S). *Heterolamium debile* Hemsl.: East Asia, Wilson 4348 (K). *Hoehnea epilobioides* Epling: Paraguay, Hassler 6847 (S). *Holmskioldia sanguinea* Retz.: Mexico, Veracruz, Marino Rosas 71 (UPS). *Hymenocrater bituminosus* Fisch. & E. Mey.: Iran, Rechinger 312 (S). *Hymenopyramis brachiata* Wall.: Asia, unknown (UPS). *Hypogomphia turkestana* Bunge: Kazakhstan, Krascheninnikov 5127 (S). *Kalaharia uncinata* (Schinz) Mold.: Zaire, Thiebaut 609 (C). K*aromia tettensis* (Klotzsch) R. Fern.: Malawi, Southern Region, Brummitt 8882 (UPS). *Keiskea japonica* Miq.: Japan, Musashi Province, Furese s.n. (S). *Kurzamra pulchella* (D. Clos.) Kunze: Chile, Atacama Province, Werdermann 957 (S). *Lagochilus ilicifolius* Bunge ex Benth.: China, Mongolia, Andersson 738 (S). *L. pungens* Schrenk: Asia, Kurokinger s.n. (UPS). *Lagopsis supina* (Steph.) Ikonn.-Gal. (syn. *Marrubium incisum* Benth.): China, Hupeh Region, Beach 17 (UPS). *Lamiophlomis rotata* (Benth. ex Hook. f.) Kudo: China, Tibet, King 115/4 (UPS). *Lamium eriocephalum* Benth.: Turkey, Kotschy 210 (UPS). *Lantana camara* L.: Madagascar, Afzelius s.n. (UPS). *Leocus lyratus* A. Chev: Sierra Leone, Morton 2595 (K). *Lepechinia betonicaefolia* (Kunth.) Epling: Ecuador, Asplund 6646 (UPS). *L. calycina* (Benth.) Epling: USA, California, Clokey 5044 (UPS). *L. chamaedryoides* (Balbis) Epling: Chile, Hohenacker 707 (UPS). *L. graveolens* (Reg.) Epling: Argentina, Tucumán Prov., Meyer 13988 (UPS). *L. mutica* Epling: Ecuador, Sparre 16111 (UPS). *Loxocalyx urticifolius* Hemsl.: East Asia (K). *Marmoritis pharica* (Prain) Clement: Nepal, Stainton & al. 7255 (E). *Marrubium alysson* L.: Spain, Lopez & al. s.n. (UPS). *M. parviflorum* Fisch & C. A. Mey.: Armenia, Grossheim 10 (UPS). *Melittis melissophyllum* L.: Mediterranean, Sangerhausen s.n. (UPS). *Meriandra bengalensis* (König ex Roxb.) Benth.: Eritrea, Pappi 1538 (S). *Microcorys barbata* R. Br.: Australia, Western Australia, Strid 22432 (S). *Micromeria juliana* (L.) Benth. ex Reichenb.: Greece, Corfu Island, Ryding 2297 (UPS). *Microtoena delavayi* Prain: China, Forrest 15144 (K). *Minthostachys mollis* (Kunth.) Griseb.: Argentina, Cordoba Prov., Hieronymus 5189 (UPS). *M. tomentosa* (Benth.) Epling: Ecuador, Asplund 7200 (UPS). *M. verticillata* (Griseb.) Epling: Argentina, Tucumán Prov., Risso 581 (UPS). *Moluccella laevis* L.: Turkey, Kotschy s.n. (UPS). *M. spinosa* L.: Italy, Gurrino s.n. (UPS). *Monardella odoratissima* Benth.: USA, Oregon, T. Howell s.n. (UPS). *Mosla punctulata* (J. F. Gmel.) Nakai: Japan, Ohwi 113 (UPS). *Nepeta azurea* R. Br.: Eritrea, Ryding 2054 (UPS). *Newcastelia cephalantha* F. Muell. var. *cephalantha*: Australia, South Australia, Donner 5363 (UPS). *Notochaete hamosa* Benth.: India, Drummond 1904 (k). *Ocimum circinnatus* Paton: Somalia, Thulin & Abdi Dahir 6524 (UPS). *Oncinocalyx betchei* F. Muell.: Australia, New South Wales, Bourman s.n. (UPS). *Oxera oblongifolia* Vieill.: New Calendonia, Skottsberg 219 (S). *Paraphlomis javanica* (Blume) Prain (syn. *P. rugosa* Benth.): Sabah, Haviland 1228 (K). *Paravitex siamica* Fletcher: Thailand, Kerr 19329 (C). *Perilla frutescens* (L.) Britt.: China, H. Smith 696 (UPS). *Perillula reptans* Maxim.: Japan, Kyushu Prov., T. Makino 37181 (S). *Peronema canescens*

JACK.: Indonesia, Java, unknown (UPS). *Perovskia abrotanoides* KIR.: India, Herb. India Orient. HOOK. F. & THOMSON s.n. (S). *Petitia domingensis* JACQ.: Bahamas, KURTISS 136 (K). *Phlomiodeschma parviflorum* (BENTH.) VVED. (syn. *Stachys parviflora* BENTH.): Afghanistan, Herb. GRIFFITH 4032 (S). *Phlomis crinita* CAV.: Spain, Valencia, VICIOSO (UPS). *P. setifera* BUR. & FRANCH. (syn. *P. megalantha* DIELS): China, Shansi Prov., H. SMITH 7321 (UPS). *Phyla nodiflora* (L.) GREENE: Tanzania, MHORO & BACKÉUS 1973 (UPS). *Piloblephis rigida* RAFIN.: USA, Florida, DIVERS 4 (K). *Pitardia nepetoides* BATT. EX PITARD: Morocco, JAHANDIEZ 45 (C). *Pityrodia bartlingii* (LEHM.) BENTH.: Australia, Western Australia, WHIBLEY 4908 (UPS). *P. loxocarpha* (F. MUELL.) DRUCE: Australia, Western Australia, CHINNOCK 3833 (UPS). *Pogogyne douglasi* BENTH.: USA, California, SKOTTSBERG s.n. (UPS). *Poliomintha incana* (TORR.) GRAY: USA, Utah, HOLMGREN & al. 2043 (S). *Pycnanthemum incanum* (L.) MICHX.: USA, Washington D.C., illegible (UPS). *P. virginicum* (L.) DURAND & JACKSON: Canada, Ontario, BREITUNG & DORE 9296 (UPS). P*remma resinosa* (HOCHST.) SCHAU: Kenya, LARSSON 32 (UPS). *Renschia heterotypica* (S. MOORE) VATKE: Somalia, North, THULIN 4264 (UPS). *Rhabdocaulon denudatus* EPLING: Brazil, Minas Gerais State, WIDGREN s.n. (UPS). *R. lavanduloides* (BENTH.) EPLING: Brazil, Minas Gerais State, REGNELL I/325 (UPS). *Rhododon ciliatus* (BENTH.) EPLING: USA, HALL 443 (K). *Rosmarinus officinalis* L.: Portugal, RYDING 428 (UPS). *Roylea cinerea* (D. DON) BAILL.: Nepal, POLUNIN & al. 837 (UPS). *Saccocalyx satureioides* COSS. & DUR: Algeria, illegible (UPS). *Schizonepeta tenuifolia* (BENTH.) BRIQ.: Japan, TOGASI 1519 (UPS). *Scutellaria mexicana* (TORREY) PATON (syn. *Salazaria mexicana* TORREY): USA, Nevada, CLOKEY 4687 (UPS). *Sideritis incana* L. subsp. *glauca* (CAV.) MALAG.: Spain, Alicante, DÖRFER 609 (UPS). *Spartothamnella juncea* (A. CUNN EX WALP.) BRIQ.: Australia, New South Wales, BOORMAN s.n. (S). *Stachydeoma graveolens* SMALL: USA, Florida, GODFREY 62494 (UPS). *Stachyopsis oblongata* (SCHRENK) POPOV & VVED.: Turkemenistan, REGEL s.n. (UPS). *Stachys aculeolata* HOOK. f.: Kenya, VERDCOURT 2060 (UPS). *S. hildebrandtii* VATKE: Somalia, North, BALLY & MELVILLE 15931 (UPS). *S. micheliana* BRIQ.: Ecuador, ASPLUND 18493 (UPS). *Stachytarpheta cayennensis* (RICH.) M. VAHL: Argentina, Formosa, MOREL 22× (UPS). *Suzukia luchensis* KUDO: Japan, Ryukyu Islands, FURESE 4552 (K). *Tectona grandis* L. f.: cult. in Tanzania, HUGHES 96 (UPS). *Teijsmanniodendron pteropodum* (MIQ.) BAKER.: Indonesia, Sumatra, SOEPADMO 43 (UPS). *Tetraclea coulteri* A. GRAY: USA, Texas, HAVARD s.n. (UPS). *Teucridium parvifolium* HOOK. f.: New Zealand, BERGGREN s.n. (S). *Thuspeinantha brahuica* (BOISS.) BRIQ.: Iran, Khorasan Prov., RECHINGER 4350 (S). *Tinnea aethiopica* KOTSCHY ex HOOK. f. subsp. *aethiopica*: Kenya, FRIES & FRIES 279 (UPS). *T. gracilis* GÜRKE: Tanzania, BIGOOD & al. 1084 (UPS). *Trichostema brachiatum* L. (syn. *Isanthus coeruleus* MICHX.): USA, Ohio, SULLIVANT s.n. (USA). *T. dichotomum* L.: USA, Missouri, STEYERMARK 65053 (UPS). *Tsoongia axillariflora* MERR.: Vietnam, TSANG 30314 (UPS). *Verbena stricta* VENT.: USA, Illinois, ABUTIS s.n. (UPS). *Vitex agnus-castus* L.: France, Corsica, DEBEAUX 242 (UPS). *Viticipremna philippinensis* (TURCZ.) H. J. LAM: Philippines, WENZEL 3430 (C). *Westringia ridiga* R. BR.: Australia, New South Wales, FRASER s.n. (UPS). *Wiedemannia orientalis* FISCH. & C. A. MEY.: E Turkey or N Iraq, BALNSA 1175 (UPS). *Wrixonia prostantheroides* F. MUELL.: Australlia, Western Australia, CONN & SCOTT 3253 (E). *Xenopoma bolivianum* (BENTH.) GRISEB. [Syn. *Satureja boliviana* (BENTH.) BRIQ.]: Bolivia, STEINBACH 8458 (S). *Zhumeria majdae* RECH. f. & WENDELBO: Iran, WENDELBO & FOROUGHI 15731 (E).

Appendix 2. Characters used in the cladistic analysis of Lamiaceae. The numbers of the characters correspond to the data matrix in Table 2.

The exocarp. 1. Excocarp cells neither sclerenchymatous nor vertically elongate or conic (0); exocarp cells very elongate vertically, forming a flesh layer (1); exocarp cells all thick-walled and with parallel pit canals at the apex (2); exocarp cells sclerenchymatous but without pit canals (3); exocarp cells all high conic or forming short hairs (4). 2. Nutlets not mucilaginous (0); nutlets mucilaginous (1). Data on presence or absence of

Table 2. Data matrix for selected genera of *Lamiaceae*. The characters are listed in Appendix 2. *A* the states 0 or 1; *B* the states 0 or 2; *C* the states 0 or 3; *D* the states 1 or 2; *E* the states 1 or 3; *F* the states 2 or 3; *G* the states 1 or 5; '–' inapplicable character

Outgroup	0 0 0 0 0 0 0 0 0 0	0 1 0 A 0
Acrymia	0 0 0 0 0 0 B 0 0 1	A 1 1 0 A
Aeollanthus	0 1 1 2 0 A B 0 0 1	1 2 0 1 0
Ajuga	0 0 0 0 0 0 0 0 0 0	0 1 0 1 0
Anisomeles, Physostegia	0 0 0 0 0 0 0 0 0 1	1 2 0 1 1
Basilicum	0 1 0 D 0 0 3 0 0 1	1 1 0 1 0
Becium	0 1 0 D 0 1 B 0 0 1	1 2 0 1 0
Callicarpa	0 0 0 D 0 0 0 A 3 0	0 1 0 0 0
Capitanya	0 1 1 2 0 0 0 0 2 1	1 0 1 1 0
Caryopteris paniculata	0 0 0 0 0 0 0 0 0 A	A 1 0 1 1
Cleonia	0 1 0 D 0 0 7 0 1 1	1 A 1 1 0
Colebrookea	0 0 0 0 0 0 B – 0 1	1 1 0 1 1
Craniotome	0 0 0 0 0 0 0 0 0 1	1 1 0 1 1
Dicerandra	0 1 0 1 0 0 0 – 0 1	1 0 0 1 0
Dicrastylis	4 0 0 0 0 0 G 0 0 0	0 1 0 1 0
Drepanocaryum	0 1 0 1 1 0 0 0 0 1	1 A 1 1 0
Eiope	0 1 0 D 0 0 C A 0 1	1 1 0 1 0
Fuerstia	0 1 0 D 0 1 3 1 0 1	1 1 0 1 0
Glechoma	0 1 0 0 0 0 C 1 0 1	1 A 1 1 0
Hemiandra	4 0 0 0 0 0 B – 0 0	0 1 0 1 ?
Holmskioldia	0 0 0 0 0 0 4 0 0 1	0 1 0 1 1
Hymenocrater	0 0 0 1 1 0 0 0 0 1	1 0 1 1 0
Hymenopyramis	0 0 0 0 0 0 6 0 0 1	A 1 0 1 1
Lallemantia	0 1 0 1 0 A C 0 0 1	1 A 1 1 0
Lepechinia, Cahunostoma	2 0 0 0 0 0 3 1 0 1	1 A 1 1 0
Melissa	0 1 0 D 0 0 C 1 0 1	1 1 0 1 0
Melittis	0 0 0 4 0 1 0 0 0 1	1 2 0 1 1
Meriandra	0 0 0 D 0 0 3 0 1 1	1 0 1 1 0
Moluccella	0 0 0 3 0 1 0 0 0 1	1 2 0 1 1
Neohyptis	0 1 1 2 0 0 C 0 0 1	1 0 1 1 0
Newcastelia	0 0 0 0 0 0 8 0 0 0	0 1 0 1 0
Galeopsis, Otostegia, Isoleucas	0 0 0 3 0 0 0 0 0 1	1 2 0 1 1
Oxera	0 0 0 0 0 0 0 0 0 0	0 1 1 1 A
Perilla	0 0 0 4 0 0 0 0 0 1	A 0 1 1 0
Peronema	0 0 0 0 0 0 0 1 0 A	A 1 1 1 1
Phyllostegia	0 0 0 0 0 0 5 0 C 1	1 2 0 1 1
Pogostemon	0 0 0 0 0 0 0 0 0 1	1 1 0 1 1
Prasium	1 0 0 0 0 0 0 0 0 1	1 2 0 1 1
Prunella	0 1 0 D 0 0 7 A 1 1	1 A 1 1 0
Pycnanthemum	0 0 0 1 0 0 B – 0 1	1 0 0 1 0
Pycnostachys	0 1 1 2 2 0 C 0 2 1	1 A 1 1 0
Skapanthus	0 0 0 D 0 0 3 A 1 1	1 0 0 1 0
Solenostemon	0 1 1 2 0 0 C 0 2 1	1 A 1 1 0
Stenogyne	0 0 0 0 0 0 5 0 0 1	1 2 0 1 1
Teijsmanniodendron	0 0 0 0 0 0 6 0 0 0	0 1 1 1 1
Teucrium, Oncinocalyx	0 0 0 0 0 0 0 0 0 0	0 1 0 1 A
Trichostema	0 0 0 0 0 0 B 0 0 0	0 1 1 1 1
Vitex	0 0 0 0 0 0 4 0 0 0	0 1 0 1 0
Westringia, Hemigenia	4 0 0 0 0 0 0 0 0 0	0 1 0 1 ?

myxocarpy are mainly taken from Ryding (1992 b, 1993 a, b). Assuming that a character of this type is more easily lost than gained, polymorphic genera are coded for the presence of myxocarpy. 3. Exocarp cells without a peltate plate (0); mucilaginous exocarp cells with a peltate plate (1). The data on this character are taken from Ryding (1992 a). 4. Exocarp cells all similar except for presence of hairs or glands (0); exocarp with two cell types, a pale type, and a darker, angular to asteroid, much smaller type which surrounds the pale cells (1); exocarp with two cell types, a pale type, and a darker, angular to asteroid, slightly smaller type which forms small groups surrounded by the pale cells (2); exocarp with two cell types, a thin-walled type and thick-walled, usually distinctly pitted, scalariform or reticulate type (3); exocarp with two cell types, a vertically short type, and a vertically longer type which forms ridges on a reticulate nutlet surface (4). 5. Exocarp without 'mucilage buds' (0). Exocarp with 'mucilage buds' (1); exocarp with 'upside-down' mucilage (2). 6. Exocarp cells without starch grains (0); exocarp cells with starch grans (1).

The mesocarp. 7. Mesocarp of two to several similar parenchymatous cell layers (0); mesocarp of stone cells only (1); mesocarp of one cell layer of similar parenchymatous cells (2); mesocarp of two to several parenchymatous cell layers, the innermost layer differing by being colourless or violet (3); mesocarp of three to several parenchymatous cell layers, the two or three innermost layers differing by being colourless or violet (4); inner layers of the mesocarp sclerenchymatous, outer parenchymatous (5); mesocarp parenchymatous with solitary sclereids and groups of sclereids scattered throughout (6); mesocarp with sclerenchymatous layer(s) above a parenchymatous inner most layer (7); all mesocarp cells with a scalariform wall thickening (8). 8. Innermost cell layer of the mesocarp about as thick or thinner than the outer cell layers (0); innermost cell layer of the mesocarp much thicker than the outer layers (1). In taxa which only have one layer of mesocarp cells, this character is scored missing. Taxa with the two innermost cell layers thicker are also coded with '-'. 9. Mesocarp without crystals and druses (0); mesocarp with prismatic crystals in the innermost layer, without druses (1); mesocarp with prismatic crystals in the second innermost layer and/or in the layers above, without druses (2); mesocarp with druses (3).

The sclerenchyma region. 10. Sclerenchyma region of two or more cell layers (0); sclerenchyma region of a single layer (1). 11. Sclereids of the sclerenchyma region star to stone-shaped (0); sclereids bone-shaped (1). 12. Sclereids with the luminar cavity placed distinctly below the centre of the cell, with distinct pit canals at the cell apex (0); sclereids with the luminar cavity placed at the centre or above the centre of the cells but separated from the cell apex by a thick cell wall, with distinct or obsolete pit canals at the apex (1); sclereid with the luminar cavity reaching the cell apex, with a thin apical cell wall (2). 13. The cells of the sclerenchyma region containing crystals (0); the cells of the sclerenchyma region lacking crystals (1).

The endocarp. 14. Endocarp cells sclerenchymatous (0); endocarp cells parenchymatous or almost so (1). 15. Endocarp cells distinctly pitted or with scalariform or reticulate wall thickening (0); endocarp cells with a smooth cell wall or almost so (1).