FRUIT MORPHOLOGY, ANATOMY AND TAXONOMY OF TRIBE *NEPETEAE* (LABIATAE)

A. L. BUDANTSEV* & T. A. LOBOVA*

The results of a detailed SEM study of nutlet morphology in 156 species of tribe *Nepeteae* (Labiatae) are presented. Two main types, smooth and sculptured, are described; within them such subgroups as reticulate, cellular, verrucose and tuberculate are defined. The taxonomic significance of these characters is discussed. Pericarp structure was investigated in 34 species. Mucilaginous tubercles were found on the surface of the nutlets in *Nepeta*, *Drepanocaryum* and *Lophanthus*, and their structure is described. In the 10 genera of this widespread tribe, three informal generic groups are recognized, based on a combination of nutlet morphology, pericarp structure and vegetative and floral features.

Keywords. *Drepanocaryum*, *Lophanthus*, *Nepeta*, nutlet morphology, pericarp structure.

INTRODUCTION

Nutlet morphology in the Labiatae has proved useful to varying degrees at different levels of the taxonomic hierarchy. Bentham (1848), who laid the foundations of the classification of the family, used some nutlet characters in the diagnoses of some tribes. They were taken into consideration in subsequent treatments of the Labiatae (Briquet, 1895–1897; Wunderlich, 1967) and of genera and species (Bilimovitsch, 1935; Wojciechowska, 1958, 1961a,b, 1966; Hedge, 1970; Rejdali, 1990; Ryding, 1992a,b). The tribe *Nepeteae* differs from the rest of the Labiatae in that the posterior (upper) pair of stamens are longer than the anterior (lower). It includes c.11 genera and 360 species (Budantsev, 1992b) found in most parts of Eurasia and North America. The importance of the morphology of nutlet surfaces has already been demonstrated for *Nepeta* (Hedge, 1962, 1992; Hedge & Lamond, 1968; Rechinger, 1982a; Ubera, 1982). Hedge (1962), using some nutlet characters in the taxonomy of species allied to *N. fissa* C.A. Mey., recognized three basic types of nutlet texture: smooth without tubercles, 'flatly' tuberculate and clearly tuberculate, which were all constant features in mature nutlets. A study of nutlets in Afghanistan *Nepeta* species showed little variation in their morphology within a species but frequently significant differences between species (Hedge & Lamond, 1968). Makarova (1967) showed differences in anatomical structure of the nutlets between some genera of tribe *Nepeteae*.

In recent times the importance of the SEM in the study of nutlet surfaces has been demonstrated for various genera of Labiatae (Hussain et al., 1990; Paton, 1990; Rejdali, 1990; Ryding, 1992a,b; Budantsev, 1993c,d). Ubera (1982) studied the nutlet surface of 12 *Nepeta* species in the Iberian Peninsula.

* Komarov Botanical Institute, 2 Popova Street, St Petersburg 197376, Russia.

The study of myxocarpy (the formation of mucilage when nutlets become wet) has been established as a separate area of research in the carpology of the Labiatae. The phenomenon of myxocarpy in this family was first described by Wagner (1914). Hedge (1970) investigated mucilaginous cells in several species of the genus *Salvia* and described features of their structure and formation patterns of the mucilage; he also found that characters of myxocarpy could be used in the systematics of this genus. The presence of myxocarpy has also been reported in many representatives of the family from various subfamilies and tribes (Ryding, 1992a,b; 1993a,b; 1995).

MATERIALS AND METHODS

This study is based on nutlets taken from herbarium specimens, mostly from LE and BM, E, G, K and W, and from original collections made during expeditions to Middle Asia, Russia, Caucasus and Mongolia. For SEM studies the nutlets were coated with sputtered gold. For pericarp anatomy studies dry nutlets were placed for 10 days in a mixture of distilled water, 96% ethanol and glycerol taken in equal proportions. In the middle part of nutlets cross-sections 10μm thick were made using a freezing microtome. These sections were stained with a 10% aqueous solution of gentian violet and embedded in glycerol. The presence of mucilage on the nutlet surface was determined by the method of Ryding (1992b) based on the extent of swelling of mucilaginous cells when the nutlet became wet. There were four types of reaction: a strong mucilaginous reaction (with mucilaginous cells 0.8–1.5mm long), a moderate reaction (with cells 0.1–0.5mm long), a weak reaction (with mucilaginous cells less than 0.1mm long) and a very weak reaction when no appreciable elongation of mucilaginous cells occurred after swelling in water.

RESULTS

Nepeta *L.*

This is the largest genus of tribe *Nepeteae*, with 210 species (Budantsev, 1993a). It occurs in most parts of Eurasia, except the Arctic. It is a difficult genus taxonomically due to the paucity of reliable characters, hybridization and introgression. According to the traditional classification of *Nepeta* (Bentham, 1832–1836, 1848; Boissier, 1879; Briquet, 1895–1897; Pojarkova, 1954), this genus is divided into sections based on habit, leaf, inflorescence, calyx and corolla structure and nutlet characters. The boundaries between most sections are indistinct although there are some clear-cut ones (*Oxynepeta* Benth., *Micronepeta* Benth., *Orthonepeta* Benth. etc.).

Nutlets of 92 species were examined. Their size is 1–3 × 0.5–1.5mm; they are elliptic, ovate or obovate, trigonous or rounded-trigonous in transverse section, and apically rounded or truncate, with a whitish lateral straight or bilobed areole (Fig. 1A, C; Fig. 2A, C). The nutlets in *N. brachyantha* Rech.f. & Edelb. have a prominent U- or V-shaped areole extending c.⅔ of the nutlet length. *N. leucolaena* Benth. ex Hook.f., *N. pilinux* P.H. Davis and some other species have nutlets with

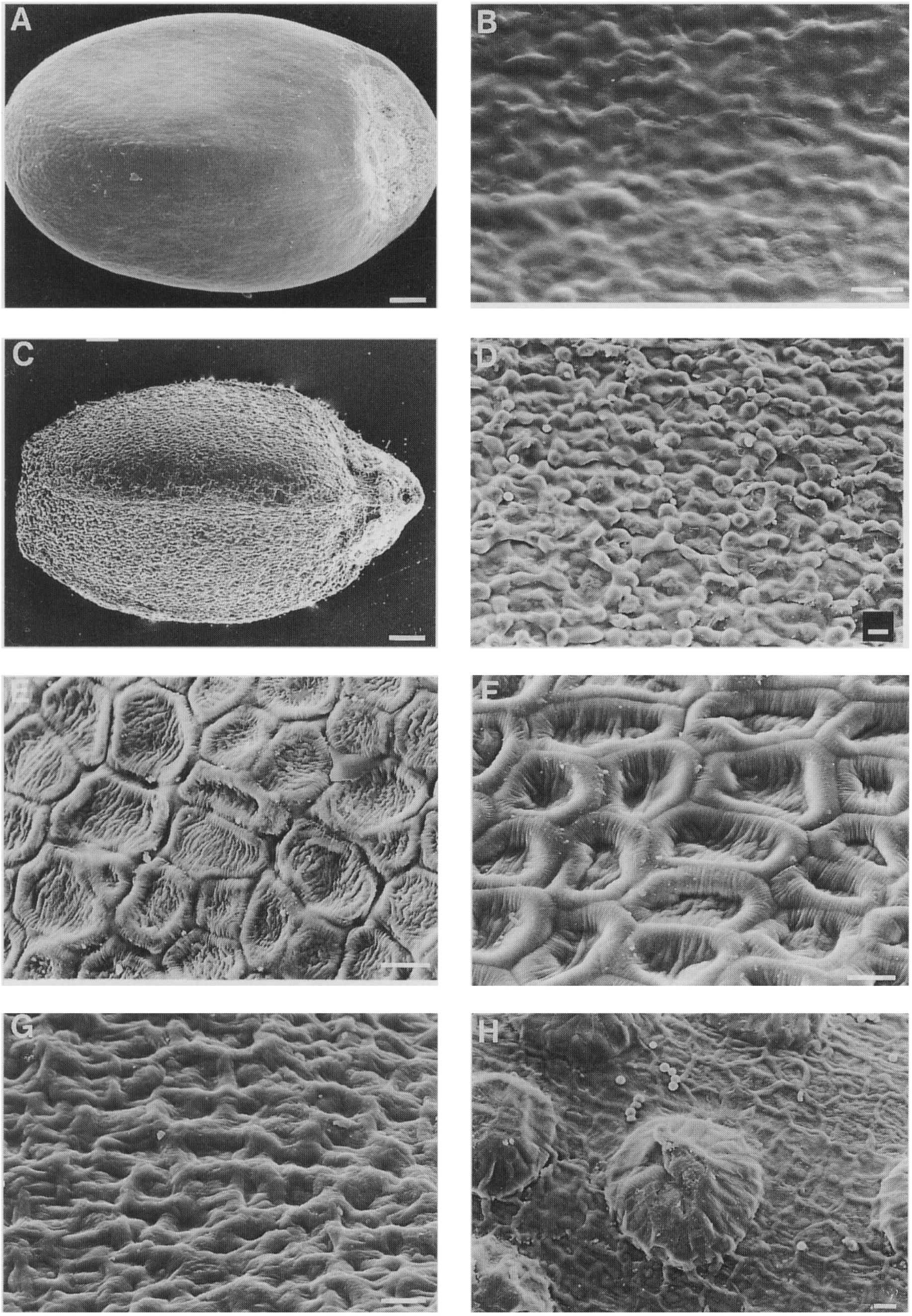

FIG. 1. Nutlets of *Nepeta*. A, *Nepeta linearis*; B, *N. daenensis*; C, D, *N. fordii*; E, *N. formosa*; F, *N. sibirica*; G, *N. lasiocephala*; H, *N. wettsteinii*. Scale bars = 10μm (except A, C = 100μm).

an apical tuft of multicellular simple hairs, and in *N. latifolia* DC. and *N. nuda* L. they are apically papillate. Similar thin hairs occur in *N. cataria* L. in very young nutlets but later they are absent.

In *Nepeta* two main types can be recognized based on surface ornamentation: smooth and sculptured. Within these types, variants can be recognized. The smooth nutlets have three variants:

1. Undulate (Fig. 1A, B): characterized by a thick cuticle masking the cell structure in the central area of the nutlets; under high magnification cellular reticulations can be seen at the apex. These cells are oblong with straight, not or slightly raised anticlinal walls (AW). The external periclinal walls (EPW) are flat or slightly depressed, smooth or fine-granular.

2. Reticulate (Fig. 1E–G): consists of oblong, rounded or polygonal cells. The AW are straight and of variable thickness. The EPW are flat or depressed, striate-furrowed or ridged. Reticulate-cellular (Fig. 1E, F) and ridged-cellular (Fig. 1G) surfaces appear as varieties of the reticulate pattern. The former has more prominent AW and depressed EPW; the latter is distinguished by irregular cells with undulate and prominent AW.

3. Bead-like pattern (Fig. 1D): has indistinctly shaped cells with small protuberances on the AW. The EPW are depressed, fine striate-furrowed.

Sculptured nutlets are characterized by having rounded or cone-shaped tubercles which occur on all surfaces, especially towards the apex. The epidermal cells of the pericarp appear rounded and polygonal, generally with prominent AW. The EPW are flat, depressed or convex, furrowed or striate-furrowed. Four variants can be recognized based on the shape of the tubercles:

1. Verrucose (Fig. 2A, B): shows tubercles formed by the ring of convex radial cells. The centre of these tubercles is mostly depressed. The papillate-verrucose texture (Fig. 2F) with papillae on the edges of the nutlets can be considered as a variant of the verrucose pattern.

2. Tuberculate (Fig. 1H): differs in that the tubercles have a convex or truncate apex forming one or more layers of radial cells.

3. Tuberculate-cellular (Fig. 2E): the tubercles have a flat apex and oblong or rounded cells with a raised AW and depressed EPW.

4. Thorn-like pattern (Fig. 2C, D): characterized by oblong or cone-shaped tubercles with a rounded or truncate apex.

Pericarp structure has been investigated in 15 species (marked by asterisks in Table 1). Pericarp thickness varies from 30μm in *N. podostachys* to 170μm in *N. amethystina*. Myxocarpy is found in four species. A moderate mucilaginous reaction occurs in *N. micrantha* and *N. trautvetteri*. *N. glomerulosa* and *N. amethystina* show a very weak reaction.

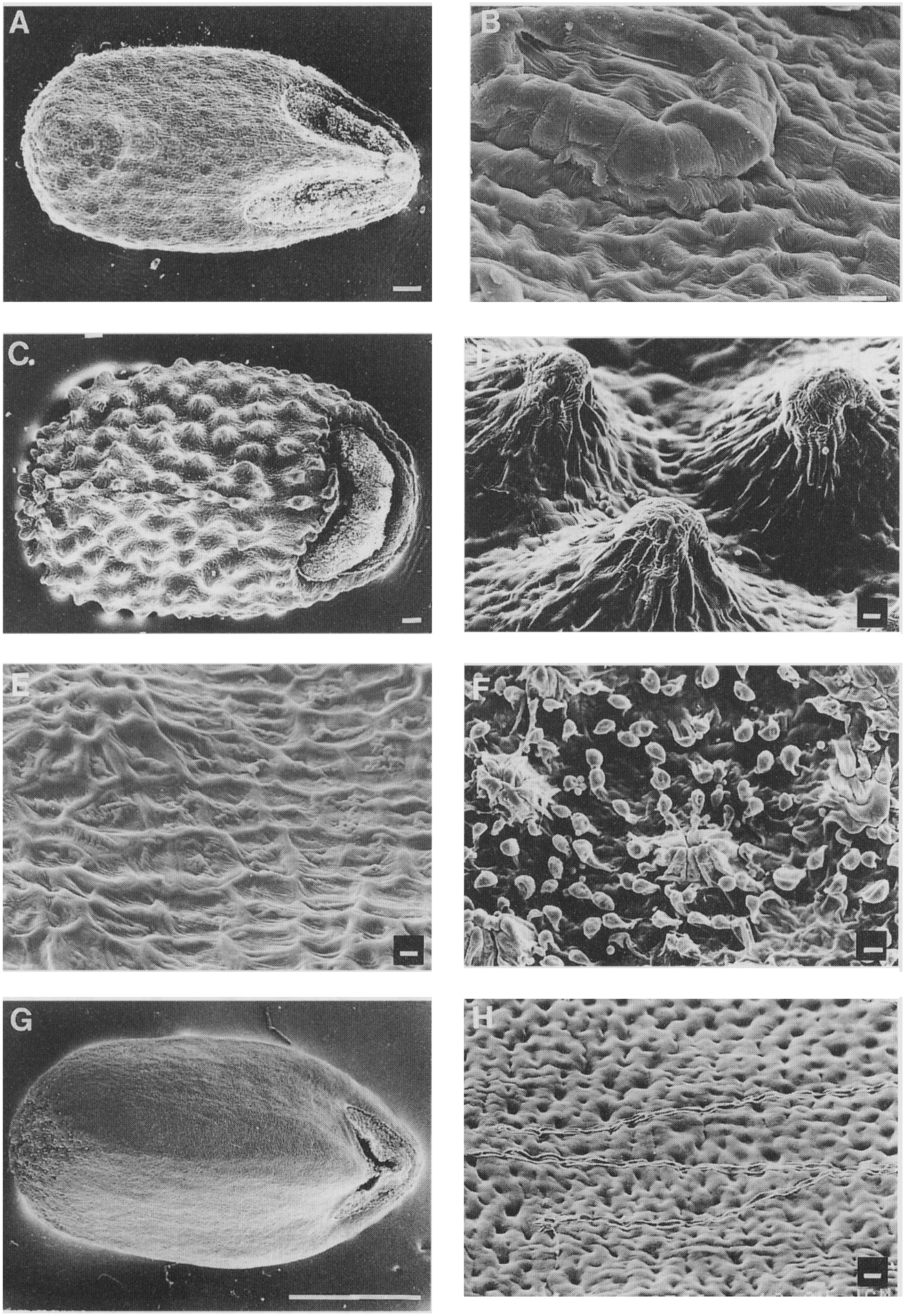

FIG. 2. Nutlets of *Nepeta* and *Dracocephalum*. A, *Nepeta glomerulosa*; B, *N. amicorum*; C, D, *N. stenantha*; E, *N. involucrata*; F, *N. suavis*; G, H, *Dracocephalum multicolor*. Scale bars = 10μm (except A, C = 100μm; G = 1000μm).

TABLE 1. Nutlet surface in *Nepeta* L.

Sect., species	Distribution	Pattern	Source of material
Sect. *Macronepeta* Benth.			
N. sibirica L.*	S Siberia, E Kazakhstan, Mongolia, China	reticulate-cellular	Altai, near Ongudaj Valley, 1986, *Budantsev* s.n. (LE)
N. manchuriensis S. Moore	Far East, E China	reticulate-cellular	Far East, Shkotov distr., *Transhel* 1050, 1053 (LE)
N. souliei H. Lév.	China (Tibet, Sichuan)	reticulate-cellular	Tibet, Ta-Tsien-Lou, *Soulie* 484, 816, 573 (E)
N. leucolaena Benth.	Himalaya, China (Tibet)	reticulate-cellular	Kashmir, Shagazthang, *Duthie* 12130 (LE)
N. formosa Kudr.	Tian-Shan	reticulate-cellular	Fergana, in Mailisu Valley, *Budantsev* 109 (LE)
Sect. *Appendiculatae* C.Y. Wu & Hsuan			
N. fordii Hemsl.	SW, SE China	bead-like	Ichang, ix 1886, *Henry* s.n. (LE)
Sect. *Glechomanthe* Pojark.			
N. longibracteata Benth.*	Pamir, Afghanistan, W Himalaya	ridged-cellular	Pamir, in Pshart Valley, *Budantsev* 270 (LE)
Sect. *Brachystegiae* (Pojark.) A.L. Budantz.			
N. glutinosa Benth.	Pamir, Afghanistan, W Himalaya, China (Tibet)	reticulate	Pamir, in Shah-Dara Valley, *Budantsev* 219 (LE)
Sect. *Catanthertae* (Pojark.) A.L. Budantz.			
N. subhastata Regel	Pamiro-Alaj	verrucose	Kara-Bulak, *Bochantsev* 120 (LE)
Sect. *Spicatae* (Benth.) Pojark.			
N. connata Royle ex Benth.	W Himalaya	undulate	Kashmir, Gilgit, 1887, *Duthie* s.n. (LE)
N. linearis Royle ex Benth.	Afghanistan, Himalaya	undulate	Kashmir, Srinagar, *Clarke* 29081 (LE)

N. nervosa Royle ex Benth.	W Himalaya, China (Tibet)	undulate	Kashmir, Nafraw, *Stewart* 12742 (LE)
N. elliptica Royle ex Benth.	Himalaya	undulate	Dalhousie, ix 1874, *Clarke* s.n. (LE)
N. discolor Royle ex Benth.	Afghanistan, Himalaya, China (Tibet)	undulate	Kashmir, Dras, *Duthie* 13744 (LE)
N. podostachys Benth.*	Pamiro-Alaj, Afghanistan, Kashmir	undulate	Pamiro-Alaj, Darwaz, *Budantsev* 470; Pamiro-Alaj, Anzob, *Budantsev* 824 (LE)
N. subincisa Benth.	Pamiro-Alaj, Afghanistan, Kashmir	undulate	Afghanistan, Kapisa, Panjir-Tal, *Podlech* 12854 (LE)
N. pubescens Benth.	Afghanistan	ridged-cellular	Kapisa, *Podlech* 12490 (LE)
N. tyttantha Pojark.	Pamiro-Alaj	ridged-cellular	Anzob, *Budantsev* 826 (LE)
N. alatavica Lipsky	Pamiro-Alaj	ridged-cellular	Uzbekistan, Tashkent, Ugam, *Z. von Minkviz* 778 (LE)
N. clarkei Hook.f.	Afghanistan, W Himalaya	ridged-cellular	Afghanistan, Kapisa, *Podlech* 12288 (LE)
N. bucharica Lipsky*	Tian-Shan, Pamiro-Alaj	ridged-cellular	Tian-Shan, in Itagar Valley, *Budantsev* 85; Pamiro-Alaj, Dzhelandy, *Budantsev* 599 (LE)
N. pamirensis Franch.	Pamir, Afghanistan, W Himalaya, China (Tibet)	undulate	Pamir, Shugnan, *Budantsev* 302; Pamir, Vahan, *Budantsev* 403 (LE)
N. crispa Willd.	Iran	ridged-cellular	Ex horto Petropol. Herb. Meyer (LE)
N. chionophila Boiss. & Hausskn.	Iraq (east), Iran (west)	reticulate-cellular	Kellal et Ssebsekuh, 1868, *Haussknecht* s.n. (G)
Sect. *Micronepeta* Benth.			
N. bracteata Benth.*	Iran, Pamiro-Alaj, Afghanistan	undulate	Pamir, Shah-Dara, *Budantsev* 367; Iran, Yezd, Mehriz, v 1849, *Buhse* s.n. (LE)
N. daenensis Benth.	Pamir, Afghanistan, W Pakistan	undulate	Pamir, Shah-Dara, *Budantsev* 368 (LE)
N. jacubii Lipsky	Pamiro-Alaj, Afghanistan	undulate	Pamiro-Alaj, Zeravshan, Zibansai, *Drobov* 367 (LE)

TABLE 1. (*continued*).

Sect., species	Distribution	Pattern	Source of material
N. petraea Benth.	Iraq (east), NW Iran	undulate	Iran, Ecbatanens, *Pichler* 1882 (LE)
Sect. *Capituliferae* (Benth.) Pojark.			
N. olgae Regel*	Tian-Shan, Pamiro-Alaj, Afghanistan	reticulate	Pamiro-Alaj, near Leninabad, ix 1989, *Budantsev* s.n. (LE)
N. floccosa Benth.	Pamir, Afghanistan, Himalaya, China	reticulate-cellular	Afghanistan, Bamian, *Podlech* 12077; Badakhshan, *Podlech* 12431 (LE)
Sect. *Denudatae* (Briq.) A.L. Budantz.			
N. denudata Benth.	Iran (Elburs)	ridged-cellular	Persia, Ghilan, *Th. Alexeenko* 471 (LE)
N. cephalotes Boiss.	Iran (Elburs)	reticulate	Iran: Tehran: Vardavard, *Wendelbo & Sanii* 12588 (LE)
N. prostrata Benth.	Iran (Kuhrud)	reticulate	1837, *Aucher-Eloy* s.n. (G)
N. eremokosmos Rech.f.	Iran (Elburs)	ridged-cellular	Iran: Damghan-Semnan, Behboudi, *Aellen* 780 (LE)
N. gloeocephala Rech.f.	Iran (Elburs)	reticulate	Teheran, *Foroughi & Assadi* 18030 (LE)
N. lasiocephala Benth.	Iran (centre)	ridged-cellular	Persia austr., Kuh-Dacna, *Kotschy* 757 (LE)
N. supina Stev.	Caucasus	ridged-cellular	Daghestan, Kurush, vii 1986, *Menitsky et al.* s.n. (LE)
Sect. *Sparthonepeta* (Briq.) Rech.f.			
N. distans Royle ex Benth.	E Afghanistan, W Himalaya	verrucose	NW India, *Royle* s.n. (LE)
N. schmidii Rech.f.	Pakistan (Chitral)	verrucose	Chitral, *R.R. Stewart* 2405 (LE)
N. amicorum Rech.f.	E Afghanistan	verrucose	Nangarhar, Torkham, *Hedge et al.* W-7437 (GB)

N. rugosa Benth.	E Afghanistan, W Pakistan	verrucose	Afghanistan, *Griffith* 4007 (LE)
N. brachyantha Rech.f. & Edelb.	E Afghanistan, Pakistan (Chitral)	tuberculate	Afghanistan, Konar, *Hewer* 1370 (LE)
N. suavis Stapf	E Afghanistan, W Pakistan	papillate-verrucose	Kurram, *Harsukh* 15441 (LE)
N. glomerulosa Boiss.*	Iran, Afghanistan, W Pakistan	verrucose	Persia, Kerman, *Bornmüller* 5124 (LE)
Sect. *Kudrjascheviae* (Pojark.) A.L. Budantz.			
N. korshinskyi Lipsky	Pamiro-Alaj, NW Afghanistan	verrucose	Badahshan, Anderab, *Ikonnikov* 3936 (LE)
N. grubovii (Kochk.) A.L. Budantz.	Pamiro-Alaj	verrucose	Darwaz, Obi-Harak, *Popov et al.* 1204 (LE)
Sect. *Macrostegiae* (Boiss.) Rech.f.			
N. italica L.	SW Europe, SW Asia	thorn-like	Turkey, Hakkari, *Davis* 45326 (LE)
N. phyllochlamys P.H. Davis	Turkey	tuberculate	Antalya, Kemer, *Davis* 15219 (LE)
Sect. *Orthonepeta* Benth.			
N. nuda L.*	From W Europe to C Siberia	tuberculate	Tian-Shan, in Itagar Valley, *Budantsev* 22; ad Budapest, Hungary, *Bernoitzky* 405 (LE)
N. latifolia DC.*	France, Spain	tuberculate	Pyrenees orientalis, 1952, *Pavillon* s.n. (LE)
Sect. *Nepeta*			
N. cataria L.*	From W Europe to Japan	reticulate	Pamiro-Alaj, Ganshino, *Budantsev* 758; Herzegovinae, Nevesine, *Velez* 227 (LE)
N. persica Boiss.	Iran, Afghanistan	thorn-like	Iran, Fars, Darreh, *Wendelbo & Foroughi* 17537 (LE)
N. betonicifolia C.A. Mey*	Turkey, Iran, Caucasus	thorn-like	Tiflis, *Wittmann* 11 (LE)
N. cyanea Stev.	Caucasus	thorn-like	Daghestan, Kurush, 1988, *Medvedeva* s.n. (LE)

TABLE 1. (*continued*).

Sect., species	Distribution	Pattern	Source of material
N. racemosa Lam.	E Iraq, Turkey, Iran, Caucasus	thorn-like	Iran, Mazandaran, *Wendelbo & Assadi* 13328; Azerbajdzhan, Lerik, *Menitsky & Popova* 11 (LE)
N. stenantha Kotschy & Boiss.	Turkey (east)	thorn-like	Cilicia, *Kotschy* 510a (LE)
N. curviflora Boiss.	W Mediterranean	thorn-like	Near Jerusalem, *Zohary & Amdursky* 174 (LE)
N. azurea R. Br. ex Benth.	NE Africa	thorn-like	Ex Horto Petropol., vi 1873, *Maximowicz* s.n. (LE)
N. biloba Hochst. ex Benth.	Africa (Ethiopia)	thorn-like	Abyssinia, inter Gernamora et Sabra, *Schimper* 720 (LE)
N. atlantica Ball	Africa (Morocco)	tuberculate	Beni-Mellal, *Davis* 55194 (E); prope Bemanot, 1879, *Rat* s.n. (LE)
N. nepetella L.	W Europe	tuberculate	France, Lux-la-Croix, *Barbezat* 6135
N. amethystina Poiret*	W Europe, NW Africa	thorn-like	Spain, Alicante, *Willkomm* 443 (LE)
Sect. *Micranthae* (Boiss.) Pojark.			
N. micrantha Bunge*	E Europe, Kazakhstan, Middle Asia, W China, W Mongolia	tuberculate	Tian-Shan, Turajgyr, vi 1953, *Goloskokov* s.n.; Kazakhstan, Betpakdala, vi 1949, *Goloskokov* s.n. (LE)
N. meyeri Benth.	Turkey (east), Iran, Transcaucasus	tuberculate	Iran, Khoi, *Furse* 2273 (LE)
N. saccharata Bunge	Iran, Turkmenia	tuberculate	Iran Esfahan: Taleghan, *Wendelbo & Foroughi* 11543 (LE)
N. humilis Benth.	E Iraq, Iran	tuberculate	Iraq, Avroman, 1867, *Haussknecht* s.n. (LE)
N. ispahanica Boiss.	Iran, Turkmenia, Afghanistan	tuberculate	Persia, Dervarin, *Bunge* s.n. (LE)
N. bornmuelleri Hausskn.	Iran (Kerman)	tuberculate	In monte Kuh-i-Hasar, *Bornmüller* 5125 (LE)
N. rechingeri Hedge	Afghanistan (centre)	tuberculate	Bamian, Ajar, *Rechinger* 16636 (G)
N. wettsteinii H. Braun	E Iraq, NW Iran	tuberculate	Zendjanab (Bignal), *Knapp* s.n. (B)

N. shiraziana Boiss.	Iran	thorn-like	Schiras, *Kotschy* 451 (G)
Sect. *Schizocalyx* (Boiss.) Pojark.			
N. teucriifolia Willd.	Iraq (east), Turkey, Iran, Caucasus	tuberculate	Teheran, Mahmudieh, *Aellen* 774 (LE)
N. trautvetteri Boiss. & Buhse*	Turkey (east), NW Iran, Transcaucasus	tuberculate	Azerbajdzhan, Shahbuz, vii 1957, *Tamamshan* s.n. (LE)
N. macrosiphon Boiss.	E Iraq, Turkey (east), Iran	tuberculate	Kurdistan, Rowanduz, vi–vii 1867, *Haussknecht* s.n. (LE)
N. lamiifolia Willd.	Turkey (east), Caucasus	tuberculate	Erzincan, *Davis & Hedge* 31632 (LE)
N. cilicia Boiss. & Benth.	E Mediterranean, Turkey	tuberculate	Liban, Ehden, *Bornmüller* 12310 (LE)
N. melissifolia Lam.	Greece, Crete	thorn-like	Crete, 1846, *Heldreich* s.n. (LE)
Sect. *Setanepeta* A.L. Budantz.			
N. ceasarea Boiss.	Turkey	thorn-like	Karaman, *Davis* 16235 (LE)
N. trichocalyx Greuter & Burdet	Turkey	tuberculate	Cilicia, *Kotschy* 458 (LE)
N. trachonitica Post	SW Asia	thorn-like	Kurdistan, Mardin, *Sintenis* 1210 (LE)
Sect. *Subinterruptae* (Benth.) Ubera & Valdes			
N. tuberosa L.	W Europe, N Africa	tuberculate	Spain, Monsanto, *Welwitsch* 60 (LE)
N. granatensis Boiss.	W Europe, Africa (Morocco)	thorn-like	Spain, Sierra Nevada, *Bourgeau* 1410 (LE)
N. stachyoides Coss. ex Maire	Africa (Morocco)	thorn-like	Djebel Ouensa, viii 1873, *Cosson* s.n. (LE)
N. viscida Boiss.	W Turkey	tuberculate	Bulgar-Dagh, *Balansa* 1178 (LE)
Sect. *Oxynepetae* Benth.			
N. ucranica L.*	From C Europe to W Siberia	tuberculate-cellular	Azerbajdzhan, Buzgow, *Tzvelev & Czerepanov* 482 (LE)
N. involucrata (Bunge) Bornm.	SW Asia, Transcaucasus	tuberculate-cellular	Persia, *Bunge* 122 (LE)

* Pericarp structure was examined.

In species with mucilage nutlets the exocarp cells form mucilaginous tubercles (Fig. 3C). Similar structures have been described in *Drepanocaryum* by Ryding (1995), and called 'mucilage buds'. These tubercles consist of two groups of cells: guard epidermal cells, which are radially elongated, sickle-shaped and contain pigment, and large mucilaginous cells with very thickened walls.

When nutlets are placed in water, the epidermal cells start to diverge, mucilaginous cells become elongated, taking the shape of 'mucilaginous hairs' and, as a result, the fruit is covered with a mucilaginous envelope. Upon drying, the tubercles become crater-shaped.

In species which lack myxocarpy the exocarp is formed by cells with thickened outer tangential walls that can be large or flattened (Fig. 3A, B) and may contain pigment.

Epidermal cells in nutlets with a sculptured surface are radially elongated and form tubercles (Fig. 3B). It is impossible to discern the exocarp in the pericarp of *N. bucharica* and *N. podostachys* because the cells are strongly compressed and their boundaries indistinct.

The mesocarp consists of 2–3 rows of cells. The lower row is mostly represented by narrow, tangentially elongated cells with or without thickenings on the walls. The upper rows of cells may be strongly compressed. The mesocarp in *N. cataria*, *N. bucharica*, *N. bracteata* and *N. micrantha* is strongly compressed and individual cells are not recognizable. All rows of the mesocarp may contain brown, dark-brown or black pigments.

The sclerenchymatous layer of the endocarp is 15–80μm thick. The sclereid cavity

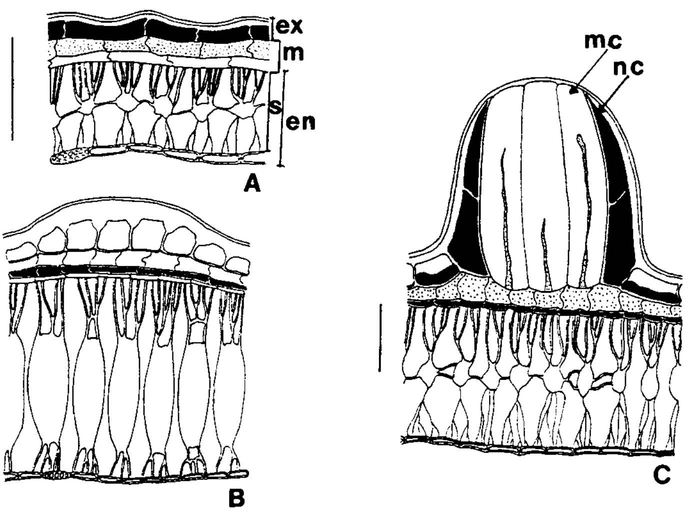

FIG. 3. The pericarp of *Nepeta* in transverse section. A, *Nepeta longibracteata*; B, *N. ucranica*; C, *N. amethystina*. Abbreviations for the regions and structures: ex, exocarp; m, mesocarp; en, endocarp; s, sclerenchyma cells; mc, mucilaginous cells; nc, non-mucilaginous cells. Scale bars = 30μm.

of smooth nutlets is small, rounded and often contains pigment, with the poral canals going towards the apical and partly to the basal parts of the cells (Fig. 3A). In sculptured nutlets the sclereids have a more or less large, oval cavity without pigment and branching poral canals (Fig. 3B). Nutlets with myxocarpy are characterized by star-like cavities in the sclerenchymatous layer (except *N. amethystina*; Fig. 3C), with or without pigment. The inner exocarp layer consists of a row of flattened cells with reticulate thickenings on the walls (Fig. 3). The tangential wall is mainly thickened. In *N. podostachys* and *N. trautvetteri* this layer is severely flattened.

The distribution of types and patterns of nutlet ornamentation in *Nepeta* species is presented in Table 1. The table shows that the sculpturing of the nutlets has a wide range of variation at infra-sectional and infra-specific levels. For example, the related pairs of species (*N. bucharica* and *N. clarkei*, *N. connata* and *N. linearis*) have a similar texture of the nutlets. The undulate pattern occurs among the *N. podostachys* species-complex (*N. subincisa*, *N. nervosa*, *N. elliptica* and *N. discolor*). Similar variants of nutlet surface appear in species of sects. *Macronepeta*, *Micronepeta*, *Denudatae*, *Sparthonepeta*, *Oxynepeta* and others. On the other hand, there is variability in the nutlets of sects. *Nepeta* and *Spicatae*. In most of the species of sect. *Nepeta* investigated the nutlets are sculptured (tuberculate and thorn-like), except in *N. cataria* which has a smooth (reticulate) surface. Pojarkova (1954), using this character, created a monotypic subsect. *Nepeta*. In sect. *Spicatae*, the smooth nutlets have an undulate and reticulate pattern. However, there are no apparent fundamental differences between them because the former differs in the thick cuticle in the middle part of the edges, whereas the reticulate texture appears only at the apex where the cuticle is thinner. Undulate nutlets characterize the species of sect. *Micronepeta* which in other morphological features (inflorescence, calyx and corolla shape) are very similar to those of sect. *Spicatae*.

The distribution of species with smooth and sculptured nutlets has a link with their geographical distribution. Species with smooth nutlets occur mainly in the eastern parts of the *Nepeta* area (from Hindu Kush and Central Asia to China and Japan). Among these are the species of sects. *Macronepeta*, *Spicatae*, *Micronepetae* and *Capituliferae*. From the 37 studied species only 11 are found west of Afghanistan – in Iran, Transcaucasia and Turkey. Among these are the species of sect. *Denudatae* allied to sect. *Capituliferae*: *N. chionophila* and *N. crispa* (sect. *Spicatae*) and some other widespread species.

Species with sculptured nutlets (sects. *Nepeta*, *Macrostegiae*, *Setanepeta*, *Orthonepeta*, *Subinterruptae*) occur in the west part of the *Nepeta* area – in western Europe, the Mediterranean, Turkey and Iran. Only 18 species out of 55 with a verrucose, tuberculate and thorn-like texture grow east of Iran. Except for the widespread *N. nuda* and *N. ucranica*, these species belong to sect. *Sparthonepeta* (restricted to Iran, Afghanistan and west Himalayas), sect. *Kudrjascheviae* (mainly Middle Asia), some species of sect. *Micranthae* (*N. rechingeri* and *N. micrantha*) and the mainly Chinese sect. *Appendiculatae* (*N. sungpanensis* and *N. hajnanensis*).

The morphological development in *Nepeta* species from smooth to sculptured nutlets possibly runs parallel to the radiation of the genus from the east (SW China, the Himalaya), where the greatest diversity of the genus and the tribe occurs, to the west, as far as the W Mediterranean. In addition to these main trends of divergence of nutlets in *Nepeta* there are bead-like (*N. fordii*) and papillate-verrucose (*N. suavis*) nutlets which have not as yet been found in other *Nepeta* species.

Dracocephalum *L.*

This is the second largest genus in the *Nepeteae*, with c.73 species (Budantsev, 1993b). The species occur in the temperate parts of Eurasia with a concentration of diversity in SW and E China, south Siberia, Middle Asia and the Irano-Turanian territories. One species, *D. parviflorum* Nutt., grows in North America.

The nutlets of 32 species were examined. They are c.2–6 × 1–2.5mm, oblong, elliptic or obovate, and trigonous with well-developed edges in transverse section (Fig. 2G, Fig. 4A); the basal end is narrowed with a lateral bilobed or straight areole, apically keeled or rounded. The nutlet surface is smooth with four patterns:

1. Cellular (Fig. 2H; Fig. 4A–C): made up of rounded or polygonal cells with a straight or slightly sinuous raised AW. The EPW are depressed, striate-furrowed. Within this pattern may be recognized pitted-granular (Fig. 4C) and pitted (Fig. 2H) textures.

2. Reticulate: similar to some *Nepeta* species.

3. Ridged-granular (Fig. 4D): differs in that the epidermal cells are of irregular shape and the AW are sinuous depressed; the EPW are sharply asymmetrical with a rough granular-furrowed surface.

4. Indistinct-reticulate (Fig. 4E, F): formed by cells with an irregular shape and indistinct borders. The AW are sinuous; the EPW are of two kinds: prominent and flattened or partly depressed, with a complex ornamentation on the nutlet edges. The texture of the EPW is smooth or striate-furrowed.

Pericarp structure was examined in seven species (marked by asterisks in Table 2). Pericarp thickness varies from 90μm in *D. stamineum* to 220μm in *D. bipinnatum*. Myxocarpy was found in *D. integrifolium*, *D. stamineum*, *D. scrobiculatum* and *D. bipinnatum*. Nutlets of *D. bipinnatum* showed a strong mucilaginous reaction; *D. scrobiculatum* had a very weak reaction. Nutlets of other species have a moderate reaction.

The exocarp of mucilaginous nutlets has two different types of cells (Fig. 5B–D). The first type is represented by large oval or round mucilaginous cells with much thickened walls and a small irregularly shaped cavity which is filled with a pigment. These cells in wet conditions take the shape of ‘papillae’. The second type is distinguished by narrow, radially elongated cells with a strongly thickened outer tangential wall. The exception is *D. bipinnatum* where all of the exocarp cell walls are thickened (Fig. 5C, D). Non-mucilaginous cells lack pigment and are arranged in

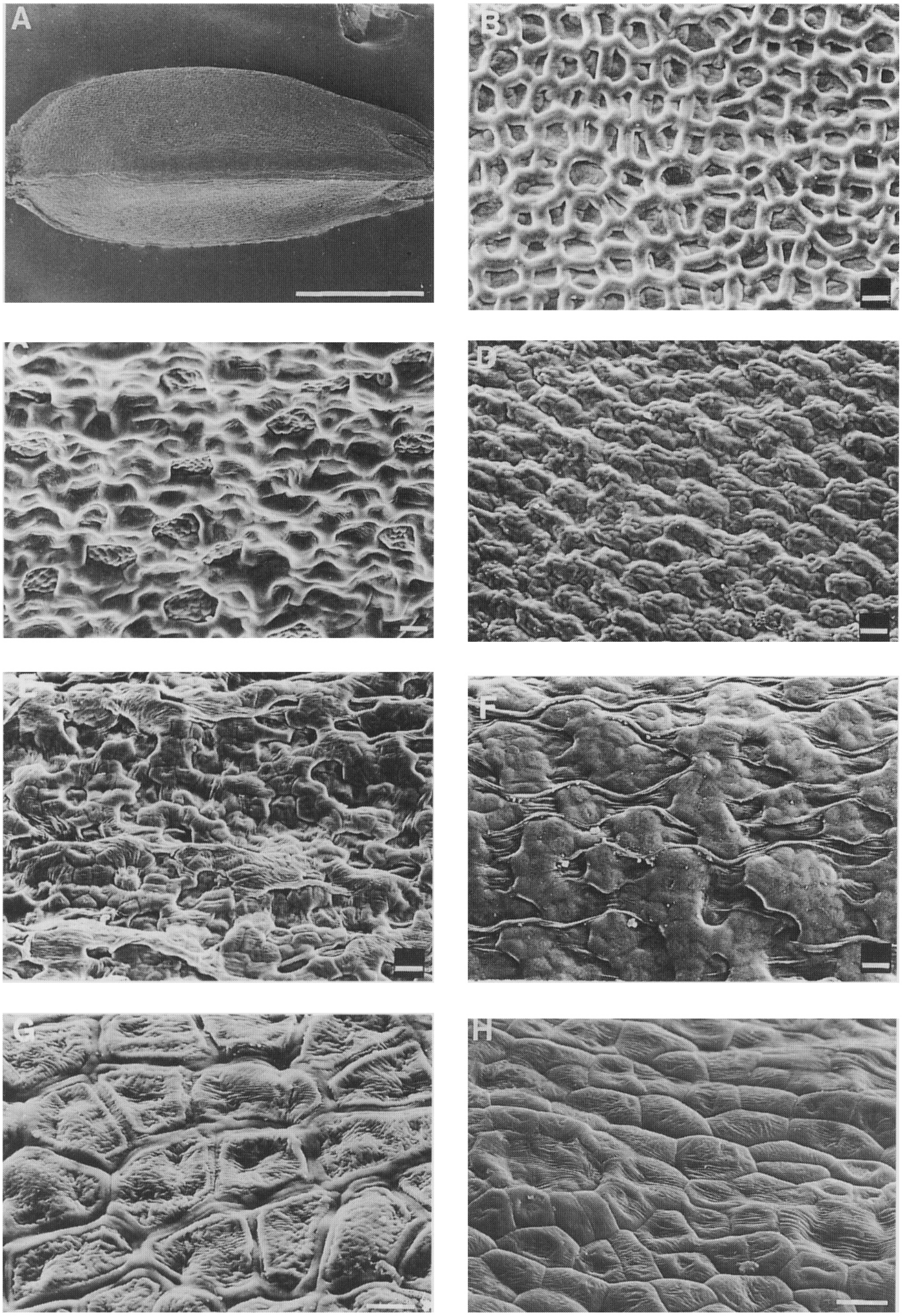

FIG. 4. Nutlets of *Dracocephalum* and *Lophanthus*. A, B, *Dracocephalum origanoides*; C, *D. fragile*; D, *D. integrifolium*; E, *D. komarovii*; F, *D. subcapitatum*; G, *Lophanthus schrenkii*; H, *L. pinetorum*. Scale bars = 10μm (except A = 1000μm).

TABLE 2. Nutlet surface in *Dracocephalum* L.

Subgen., sect., species	Distribution	Pattern	Source of material
Subgen. *Dracocephalum*			
Sect. *Sinodracon* C.Y. Wu & W.T. Wang			
D. tanguticum Maxim.	China	pitted-granular	Tibet, Mekong, Chok-Chu Valley, 1900, *Lagygin* s.n.; Hsining to Tankar, *Rock* 13260 (K)
Sect. *Calodracon* Benth.			
D. bullatum Forrest ex Diels	China (Yunnan)	indistinct-reticulate	Yunnan, at Sabaloko, *Rock* 24915 (E)
D. rupestre Hance	China (central)	indistinct-reticulate	China, Ourato, *David* 2798 (LE)
D. grandiflorum L.*	S Siberia, E Kazakhstan, Tian-Shan, Mongolia, China	reticulate	Dshungaria, *Potanin* 186-77; Altaj, *Pobedimova* 466 (LE)
D. imberbe Bunge	S Siberia, E Kazakhstan, Middle Asia, Mongolia, China	reticulate	Kazakhstan, Saur, Terekty, *Vasilevich et al.* 2799 (LE)
Sect. *Palmata* A. Budantz.			
D. multicolor Kom.	Far East	pitted	Far East, Lazovsky distr., ix 1985, *Taran et al.* s.n. (LE)
D. stellerianum Hiltebr.	Siberia, Far East	pitted	W. Verchojanje, 1959, *Yurtzev* s.n. (LE)
D. palmatum Steph.	E Siberia, Far East	cellular	Yakutia, near Verhojansk, 1913, *Mihailov* s.n. (LE)
D. fragile Turcz. ex Benth.	S Siberia, N Mongolia	pitted-granulate	Sayan, Tunkinsky Mts, 1902, *Konarov* s.n. (LE)
Sect. *Confertodracon* A. Budantz.			
D. oblongifolium Regel	Tian-Shan, Pamiro-Alaj	reticulate	Shaturgordan, *Pojarkova* 1580/619 (LE)
D. scrobiculatum Regel*	Pamiro-Alaj	indistinct-reticulate	Langar, *Nikitin* 927 (LE)
Sect. *Keimodracon* Benth.			
D. pinnatum L.	S Siberia	pitted	Baikal, 1957, *Tulin* s.n. (LE)

D. origanoides Steph.*	S Siberia, E Kazakhstan, Middle Asia, Mongolia, China	cellular	Kazakhstan, Tarbagatai, *Pozheviz* 904 (LE)
D. paulsenii Briq.	E Kazakhstan, Middle Asia, Afghanistan, Pakistan, Mongolia, W China	cellular	Pamiro-Alaj, Mt. Peter I, Kara-Shura, *Lipsky* 811 (LE)
D. botryoides Stev.	Caucasus	cellular	Transcaucasus, Azerbajdzhan, Velvelichai, vi 1970, *Prima* s.n. (LE)
Sect. *Idiodracon* (Briq.) C.Y. Wu & W.T. Wang			
D. nutans L.	From Europe to Far East	ridged-granular	Kazakhstan, Sarkan, *Matveeva* 781 (LE)
D. fruticulosum Steph.	S Siberia, Mongolia, China	ridged-granular	Tuva, Tannu-Ola, *Krylov* 606 (LE)
D. nodulosum Rupr.	Middle Asia, W China	indistinct-reticulate	Tian-Shan, Kungei Mt., in Kalmakasu Valley, *Sovetkina & Chausova* 2004 (LE)
D. integrifolium Bunge*	Altai, Middle Asia, Mongolia, China	ridged-granulate	Tarbagatai, Okpekty, *Karamysheva et al.* 5310 (LE)
Sect. *Dracocephalum*			
D. foetidum Bunge	S Siberia, Mongolia	indistinct-reticulate	Transbaikalia, between Selenga and Chikaj, *Smirnov* 1491 (LE)
D. bipinnatum Rupr.*	Middle Asia, W China	indistinct-reticulate	Tian-Shan, Ketmen, 1963, *Arystangaliew* s.n. (LE)
D. diversifolium Rupr.	Middle Asia	indistinct-reticulate	Tian-Shan, Besh Tash, 1970, *Kamelin* 806 (LE)
D. heterophyllum Benth.	Middle Asia, Afghanistan, Himalaya, China, S Siberia	indistinct-reticulate	Pamiro-Alaj, Ak-Bosoga, *Pajkova* 138 (LE)
D. spinulosum M. Pop.	Tian-Shan	reticulate	Bostandyk, Korum-Jol, *Pavlov* 356 (LE)
D. subcapitatum (O. Kuntze) Lipsky	Turkmenia, Iran	indistinct-reticulate	Kopet-Dagh, Gaudan, *Fedchenko et al.* 171 (LE)
D. komarovii Lipsky	Middle Asia	indistinct-reticulate	Chatkal, in Gava Valley, *Dzens-Litowskaja* 174 (LE)

TABLE 2. (*continued*)

Subgen., sect., species	Distribution	Pattern	Source of material
Subgen. *Fedtschenkiella* (Kudr.) Schischk.			
D. stamineum Kar. & Kir.*	Middle Asia, Afghanistan, Himalaya, W China	indistinct-reticulate	Tian-Shan, in Chakyr-Korut Valley, 1954, *Popova* s.n. (LE)
Subgen. *Ruyschiana* (Mill.) Briq.			
D. ruyschiana L.*	From W Europe to Far East	reticulate	Kazakhstan, Zajsan, Altaj, 1913, *Reznichenko* s.n. (LE)
D. argunense Fisch. ex Link	Far East, Korea, Japan, Mongolia, E China	cellular	Far East, Strilik, *Komarov* 1063 (LE)
Subgen. *Lallemantia* (Fisch. & Mey.) A. Budantz.			
D. ibericum M. Bieb.	SW Asia	indistinct-reticulate	Turkmenia, Aidere, *Linchevski* 411 (LE)
D. royleanum Benth.	SW Asia, Himalaya	indistinct-reticulate	Kazakhstan, Sary- Su, *Krasheninikov* 5160 (LE)
D. baldshuanicum (Gontsch) A. Budantz.	Pamiro-Alaj, Afghanistan, Iran	indistinct-reticulate	Tadzhikistan, Dangara to Dushanbe, *Botchanzev* 290 (LE)

* Pericarp structure was examined.

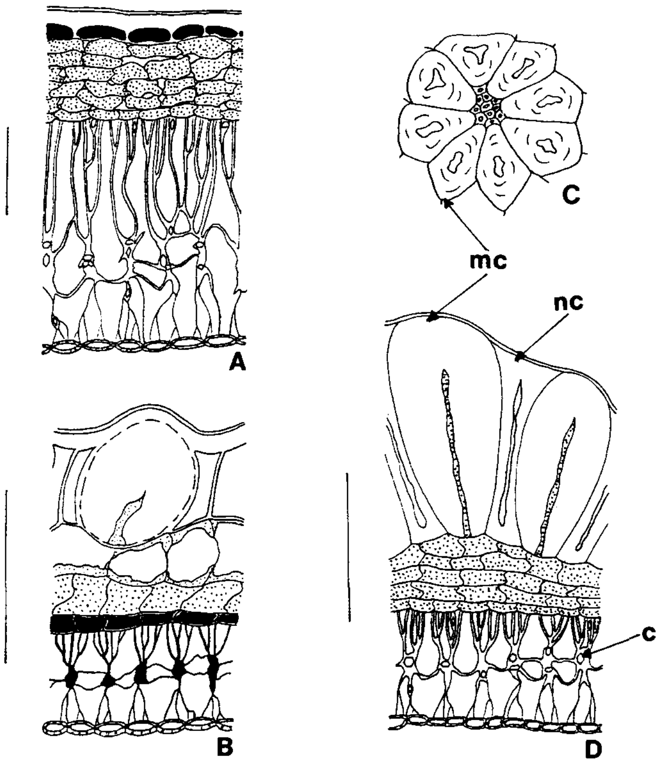

FIG. 5. The pericarp of *Dracocephalum* in transverse section. A, *D. ruyschiana;* B, *D. stamineum;* C, D, *D. bipinnatum* (C, exocarp seen from above). Abbreviations: mc, mucilaginous cells; nc, non-mucilaginous cells; c, crystal. Scale bars = 50μm.

small groups on the nutlet surface (Fig. 5C). In species without myxocarpy exocarp cells are small, filled with brown pigment and have a strongly thickened outer tangential wall (Fig. 5A). This layer in *D. origanoides* consists of large cube-shaped cells lacking pigment.

The mesocarp consists of 3–4 rows of closely spaced cells (except for *D. ruyschiana* (Fig. 5A) that differs in having intercellular spaces). In *D. stamineum* the outer row is represented by large cells with remnants of their contents (Fig. 5B). In some species the inner row is formed of flattened thick-walled cells (Fig. 5B). Cells of this layer in *D. grandiflorum* are strongly compressed. In *D. integrifolium* all rows are compressed, except the lowest one. In most cases the mesocarp cells contain brown or dark-brown pigment (Fig. 5).

The sclerenchymatous layer of the endocarp is 25–120μm thick. Sclereid cavities are rounded, large and oval or star-like. *D. ruyschiana, D. bipinnatum* (Fig. 5A, D), *D. grandiflorum* and *D. origanoides* have crystals of calcium oxalate, 2.5–7.5μm diam., in cavities and poral canals of the sclereids. The inner layer of endocarp consists primarily of a row of large cells, flattened or not and having reticulately thickened walls (Fig. 5).

Table 2 shows the diversity pattern of the nutlets in *Dracocephalum*. The four subgenera are recognized by corolla and stamen characters. The species of subgen. *Dracocephalum* are further segregated into eight sections distinguished by inflorescence, bracts, calyx and corolla shape and habit. In some cases the nutlets support morphological similarities. For instance, the species of sects. *Palmata* and *Keimodracon* have cellular and pitted patterns (except *D. fragile* of sect. *Palmata* with pitted-granular nutlets). *D. fragile* is also very distinct because of its large bracts, yellow corollas and chromosome number. Most species of subgen. *Lallemantia* have an indistinct reticulate pattern and there is a ridged-granular pattern in the species of sect. *Idiodracon* (except *D. nodulosum*).

A comparison of the variation in surface ornamentation in *Nepeta* and *Dracocephalum* shows that a ridged-granular and indistinct reticulate pattern occurs only in *Dracocephalum*. Some of the species of these genera have a reticulate pattern, in particular species of *Nepeta* sect. *Macronepeta* and *Dracocephalum* sect. *Calodracon*. They all have a similar corolla and calyx shape and are concentrated in SW China (mainly Yunnan and Sichuan). These sections are probably closest to a primitive type of *Nepeta/Dracocephalum*.

In *Dracocephalum*, in contrast to *Nepeta*, the various sculpture patterns are not correlated with geography.

Lophanthus *Adans.*

Lophanthus includes c.20 species distributed from Iran to Pakistan as well as in Middle Asia, south Siberia, Mongolia and China (Budantsev, 1992a). It is very closely allied to *Nepeta* and its definition and limits are uncertain (Levin, 1941; Hedge & Lamond, 1968; Rechinger, 1982a). The scarcely divergent thecae, pilose-annulate tube of the calyx and tendency to have resupinate flowers are more typical of *Lophanthus* than *Nepeta*. The species of *Lophanthus* are divided into two sections – *Lophanthus* and *Psilonepeta* (Benth.) A. Budantz. – which differ in calyx, corolla and stamen shape (Budantsev, 1992a).

The nutlets of 10 species were examined. They are c.2–2.3 × 1.3–1.5mm, oblong, trigonous with rounded edges and apices; the areole is lateral, bilobed with short arches; the surface of the nutlets appears smooth and sculptured. The smooth nutlets have a reticulate texture (Fig. 4G) which is formed by rounded cells. The AW are straight, thickened or not; the EPW are flat or slightly unevenly concave. The sculpturing of EPW is rugose-pitted or straight. Reticular nutlets occur in *L. chinensis* Benth., *L. schrenkii* Levin, *L. tschimganicus* Lipsky, *L. subnivalis* Lipsky, *L. schtschurowskianus* (Regel) Lipsky (sect. *Lophanthus*) and *L. elegans* (Lipsky) Levin, *L. varzobicus* Kochk. (sect. *Psilonepeta*).

Sculptured nutlets have a verrucose texture (Fig. 4H), similar to some *Nepeta* species. This sculpturing is typical for some species of sect. *Psilonepeta* (*L. ouroumit-*

anensis (Franch.) Kochk & Zuckerw., *L. dschuparensis* (Bornm.) Levin and *L. pinetorum* (Aitch. & Hemsl.) Levin).

Pericarp anatomy was examined in *L. chinensis*, *L. subnivalis* and *L. pinetorum*. The pericarp is 65–100μm thick. Myxocarpy was found in *L. pinetorum*, with a moderate mucilaginous reaction. The exocarp cells of verrucose nutlets form tubercles that consist of large mucilaginous cells with irregularly shaped cavities and of non-mucilaginous cells with much thickened outer tangential walls. The cells of these two types contain brown pigment (Fig. 6A).

The exocarp in the other species consists of large cells with strongly thickened outer walls. Nutlets of *L. chinensis* have exocarp cells with reticulate thickenings on the radial walls (Fig. 6B). The mesocarp consists of three rows of cells. The sclerenchymatous layer is 30–50μm thick with rounded or cube-shaped cavities. The inner layer of endocarp consists of flattened cells. Sometimes this row has reticulate thickenings on the walls (Fig. 6).

In the surfaces and pericarp structure of the nutlets, *Lophanthus* is very similar to *Nepeta*, especially to species of sects. *Brachystegiae* (*N. glutinosa*) and *Micronepeta*, with reticular nutlets, and *Sparthonepeta* with verrucose nutlets.

SOURCE OF MATERIAL. *L. chinensis*: Mongolia, near Ulan Bator, *Ikonnikov-Galizky* 432 (LE); *L. schrenkii*: Dshungarsky Alatau, Kul-Asu, *Rosheviz* 668 (LE); *L. subnivalis*: Samarkand distr., in Jagnob Valley, *Fedchenko* 289 (LE); *L. tschimganicus*: Chatkal, Maidantal, *Minkviz* 1373 (LE); *L. schtschurowskianus*: W Pamir, Bidshrav, *Pojarkova* 115 (LE); *L. pinetorum*: Afghanistan, Kabul, Paghman, *Podlech* 11600 (LE); *L. elegans*: Pamir, Badahshan, Padrud, *Ikonnikov* 13196 (LE); *L. varzobicus*: Tadzhikistan, Vahsh, *Chukavina* 440 (LE); *L. ouroumitanensis*: Tadzhikistan, between Surh and Darwaza, vii 1969, *Kamelin et al.* s.n. (LE); *L. dschuparensis*: Iran, Kerman, Kul-i-Dschupar, *Bornmüller* 4322 (LE).

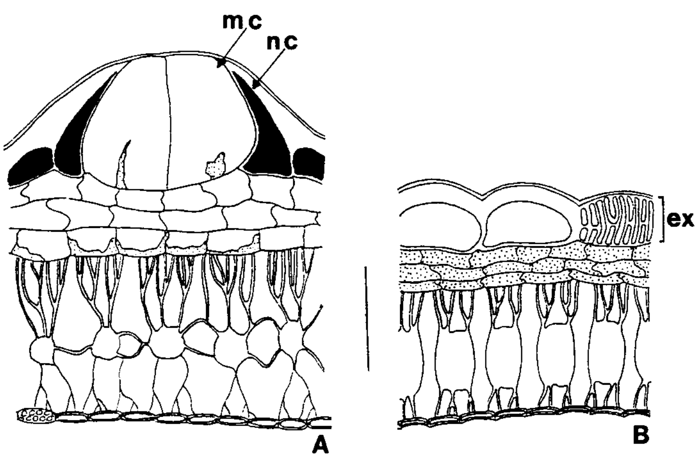

FIG. 6. The pericarp of *Lophanthus* in transverse section. A, *Lophanthus pinetorum;* B, *L. chinensis.* Abbreviations: mc, mucilaginous cells; nc, non-mucilaginous cells; ex, exocarp. Scale bar = 30μm.

Hymenocrater *Fisch. & C.A. Mey.*

This genus has c.9 species in the Irano-Turanian region of SW Asia, especially in Iran and Afghanistan (Rechinger, 1982b; Budantsev, 1992b).

The nutlet size is 3 × 1.5–2mm; they are oblong, rounded at the apex, trigonous with rounded edges (Fig. 7E); the areole is lateral, bilobed; the surface is smooth (reticular) or tuberculate (Fig. 7F). The surface of reticular nutlets (Fig. 7D) has oblong or rounded often conjugate cells with straight, not raised AW and flattened or slightly concave EPW. *H. elegans* Bunge, *H. sessilifolius* Benth. and *H. longiflorus* Benth. are characterized by smooth nutlets. *H. bituminosus* has tuberculate nutlets with flattened tubercles. The surrounding cells are rounded with the raised straight and concave plicate-furrow EPW.

The pericarp in *H. bituminosus* is c.75µm thick. Myxocarpy was not found. Cells of the exocarp have strongly thickened outer tangential walls with pores. The mesocarp is represented by three rows of similar cells that are entirely filled with pigment. The sclerenchymatous layer is c.50µm thick, with rounded cavities. Cells of the inner layer of endocarp have walls that are reticulately thickened (Fig. 8A).

On the character of surface ornamentation, *Hymenocrater* is quite similar to species of *Lophanthus* and *Nepeta*, but is distinguished from these by its lack of myxocarpy and from the other genera of the *Nepeteae* in the large, broad, membranous lobes of the calyx.

SOURCE OF MATERIAL. *H. elegans*: Persia, ex herb. *Bunge*, s.n. (LE); *H. sessilifolius*: Afghanistan, Bamian, *Podlech* 12138 (LE); *H. longiflorus*: Persia, *Aucher-Eloy* 1564 (LE); *H. bituminosus*: Transcaucasus, Darry-Dagh, 1934, *Prilipko* s.n. (LE).

Agastache *Gronov.*

Agastache (c.22 species) is distributed principally in North America (from central Canada to Mexico) and only *A. rugosa* (Fisch. & C.A. Mey.) Kuntze occurs in most parts of China, Japan and the Far East of Russia (Lint & Epling, 1945; Sanders, 1987).

Nutlet surfaces of nine species were examined. The nutlet size is 1.8–2.3 × 1–1.6mm; they are oblong or elliptic, apically rounded or truncate, trigonous (Fig. 7A); the areole is lateral, roundish or oblong, surrounded by a ridge of pericarp (Fig. 7B); there is an indumentum of eglandular trichomes at the apex of the nutlets (Fig. 8C); the length of these trichomes is gradually reduced to short papillae at the middle part of the nutlets. The nutlets in the centre are smooth with a reticulate texture (Fig. 7C). This is true for the species of sect. *Agastache* (*A. rugosa*, *A. nepetoides* (Nutt.) Britton, *A. urticifolia* (Benth.) Kuntze), as well as for those of sect. *Brittonastrum* (Briq.) Lint & Epling (*A. mexicana* (Humb., Bonpl. & Kunth) Lint & Epling, *A. pallida* (Lindl.) Cory, *A. pringlei* (Briq.) Lint & Epling, *A. pallidiflora* (Heller) Rydb., *A. micrantha* (A. Gray) Wooton & Standley, *A. wrightii* (Greenman)

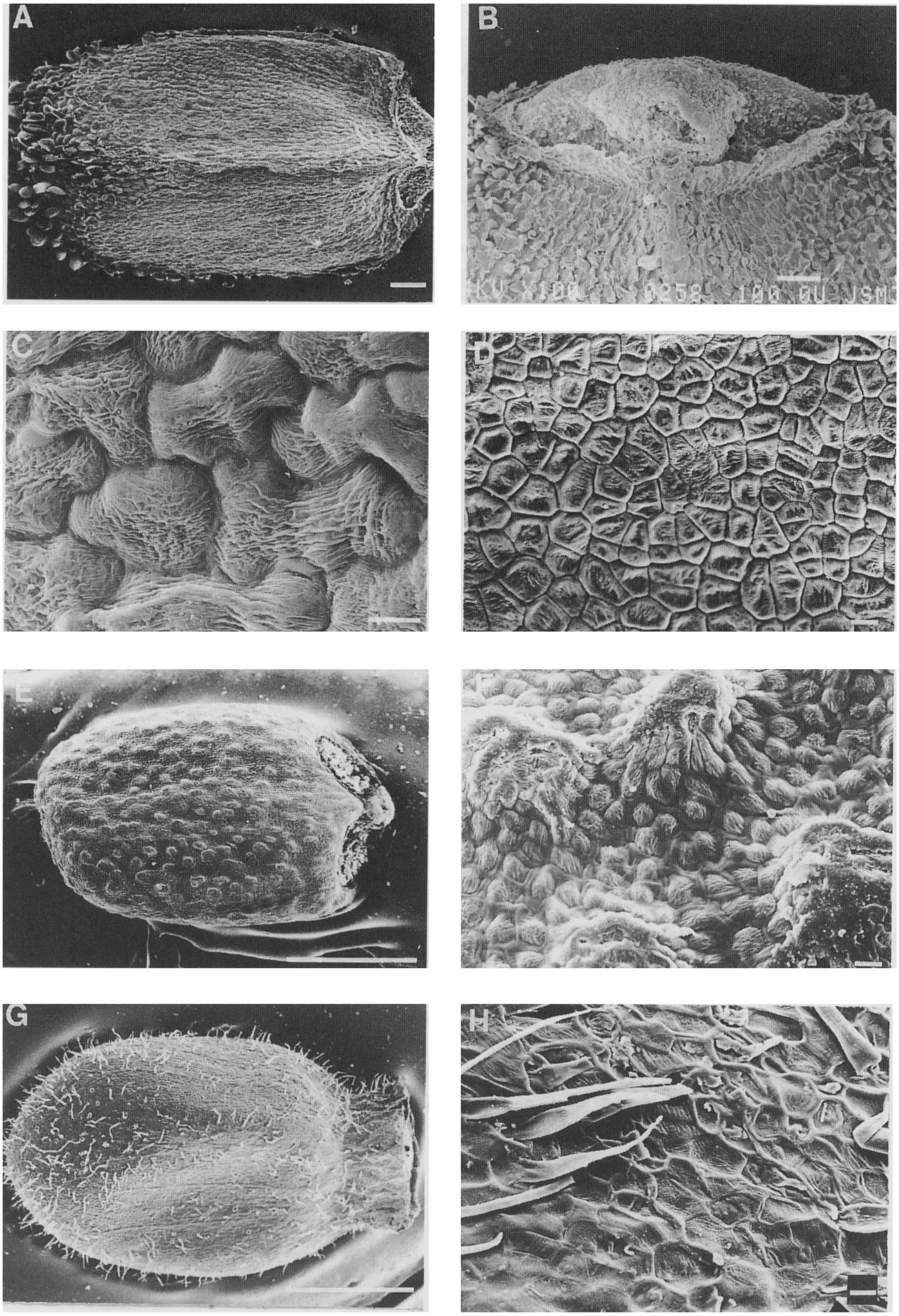

FIG. 7. Nutlets of *Agastache*, *Hymenocrater* and *Meehania*. A, *Agastache mexicana*; B, *A. aurantiaca* (basal part); C, *A. pallida*; D, *Hymenocrater haussknechtii*; E, F, *H. bituminosus*; G, *Meehania urticifolia*; H, *M. pinfaensis*. Scale bars = 10μm (except A, B = 100μm, E, G = 1000μm).

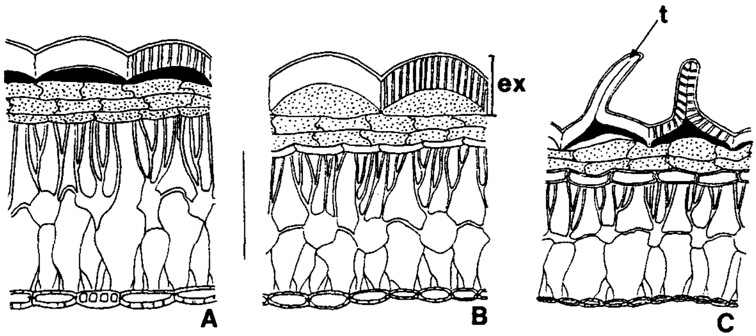

FIG. 8. The pericarp of *Hymenocrater* and *Agastache* in transverse section. A, *Hymenocrater bituminosus;* B, *Agastache mexicana;* C, *A. rugosa*. Abbreviations: ex, exocarp; t, trichome. Scale bar = 30μm.

Wooton & Standley). The exception is *A. aurantiaca* (A. Gray) Lint & Epling (sect. *Brittonastrum*) with papillose nutlets.

Pericarp structure was examined in *A. rugosa*, *A. urticifolia* and *A. mexicana*. The pericarp is 50–70μm thick. Myxocarpy was not found. The exocarp consists of large, radially elongated cells that are filled with pigment and have strongly thickened outer tangential walls with very small pores (Fig. 8B, C). The mesocarp is represented by three rows of closely spaced cells which are entirely filled with pigment. *A. rugosa* is distinguished by an inner row of cells with thickened walls (Fig. 8C). The sclerenchymatous layer is 35–40μm thick, with rounded cavities. In *A. urticifolia* and *A. rugosa* the inner layer of endocarp consists of very flattened cells.

The fine surface of the nutlets of *Agastache* favours the view of including *Brittonastrum* as a synonym of *Agastache*. In general, *Agastache* is closely related to *Nepeta* and *Lophanthus* on the base of nutlet morphology, surface ornamentation and pericarp structure, but differs in the parallel thecae and divergent pairs of stamens.

SOURCE OF MATERIAL. *A. rugosa*: Pekin, *Skachkow* s.n. (LE); *A. urticifolia*: Washington, Mount Adams, 1882, *T. Howell* s.n. (LE); *A. aurantiaca*: Mexico, Chihuahua, Norogachic, *Palmer* 402 (LE); *A. micrantha*: New Mexico, *Wooton* 436 (LE); *A. wrightii*: New Mexico, *Metcalfe* 655 (LE); *A. pringlei*: Mexico, Chihuahua: Potrero Peak, *Pringle* 789 (LE); *A. pallidiflora*: SW Chihuahua, *Palmer & Parry* 762 (LE); *A. nepetiodes*: ex horto Petropol (LE).

Meehania *Britton*

A genus of c.6 species found in E and SE China, Japan, Korea and the Far East. The type species, *M. cordata* (Nutt.) Britton ex Small, occurs in eastern North America (Budantsev, 1992b). The nutlets in *M. urticifolia* (Miq.) Makino and *M. pinfaensis* (Levl.) Sun ex C.Y. Wu are 3.2–3.6 × 2mm, from rounded to elliptic with rounded edges. The areole is basal, roundish and surrounded by a fold of pericarp

(Fig. 7G). The reticular surface of the nutlets has long 1–3-celled trichomes (Fig. 7H). The epidermal cells are rounded or irregularly shaped with slightly raised straight AW and plane or depressed EPW with a finely furrowed pattern.

The pericarp of *M. urticifolia* is 90μm thick. Myxocarpy was not found. The exocarp is represented by cells with thickened outer tangential walls. The mesocarp consists of three rows of closely spaced cells. The sclerenchymatous layer is 70μm thick. The sclereids have very undulate walls and irregular cavities. The cells of the inner layer have reticulate thickenings on their walls (Fig. 9A, B).

Meehania is related to *Nepeta* and *Dracocephalum* in calyx and corolla shape, but is clearly distinct in the nutlets.

SOURCE OF MATERIAL. *M. urticifolia*: Vladivostok, in River Elburga, *Samojlova* 270 (LE); *M. pinfaensis*: China, Ichang, 1806, *Henry* s.n. (LE); W Hupeh, *Wilson* 963 (LE).

Glechoma *L.*

Four species are recognized in this genus; they occur in steppe and broad-leaved forests of Eurasia (Budantsev, 1992b).

G. hederacea L. and *G. longituba* (Nakai) Kupr. were examined. The nutlets are c.2.1–2.3 × 1–1.3mm, oblong, slightly flattened at the base, with a rounded apex (Fig. 10A); the areole is rounded or elliptic, basal, surrounded by a fold of pericarp (Fig. 10B); the surface of the nutlets is smooth, reticulate-loop like (Fig. 10C) made up of round or polygonal cells with slightly or not raised, straight, indistinct AW and funnel-like EPW with a striate-rugose ornamentation. There are probably groups of slightly raised small rounded cells with a more raised AW making up a short chain or rosette-like pattern which most often occur at the basal part of nutlets.

The pericarp in *G. hederacea* is 160μm thick; there is myxocarpy with moderate mucilaginous reaction. The exocarp consists of large, rounded mucilaginous cells in groups of 1–4 and very narrow non-mucilaginous cells, with thin cavities, located

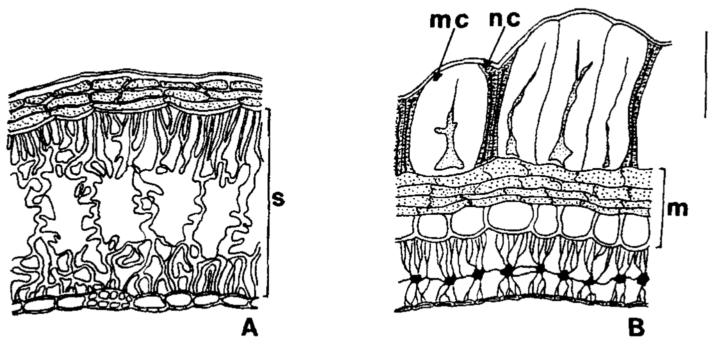

FIG. 9. The pericarp of *Meehania* and *Glechoma* in transverse section. A, *Meehania urticifolia*; B, *Glechoma hederacea*. Abbreviations: s, sclerenchyma cells; m, mesocarp; mc, mucilaginous cells; nc, non-mucilaginous cells. Scale bar = 50μm.

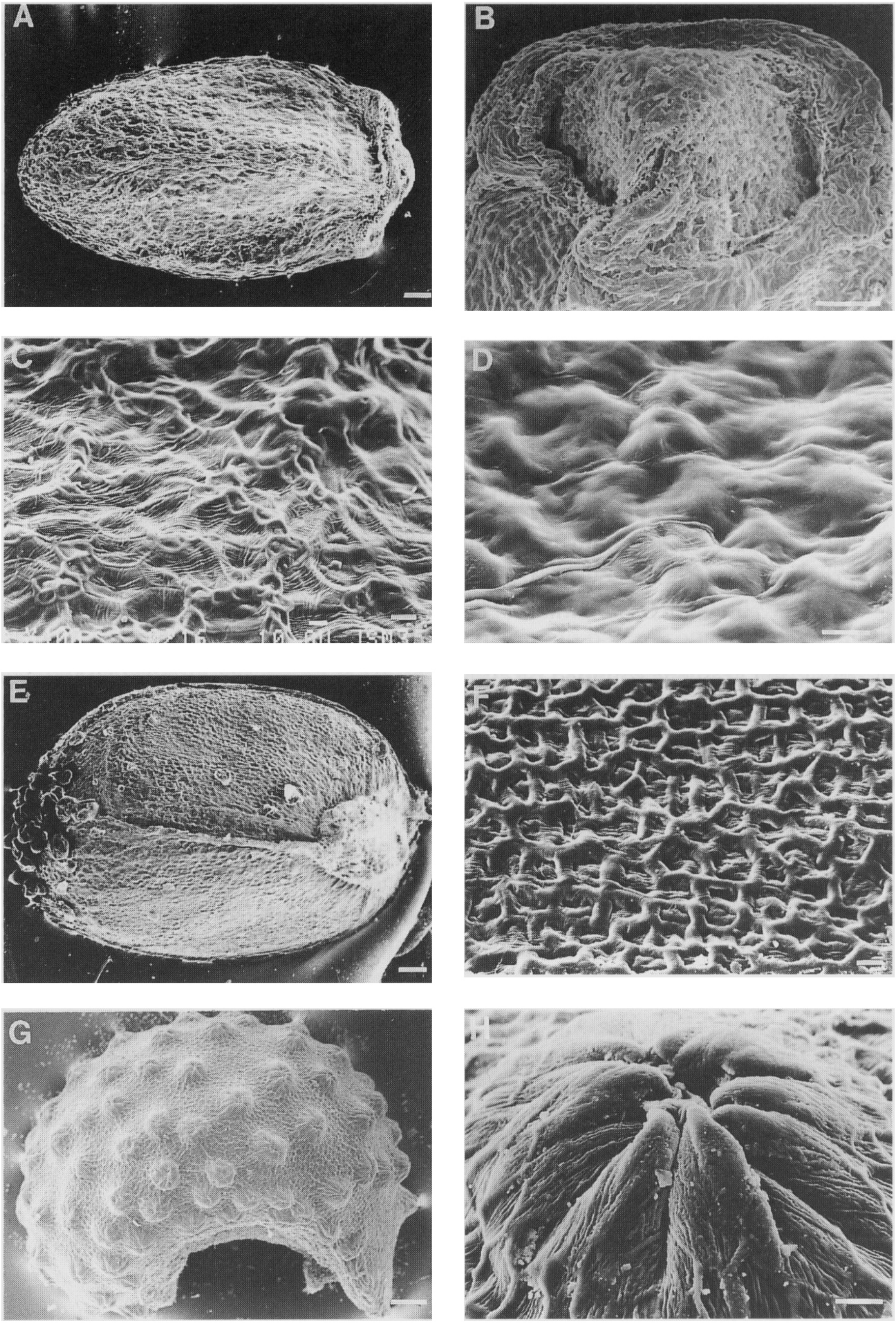

FIG. 10. Nutlets of *Glechoma*, *Schizonepeta*, *Cedronella* and *Drepanocaryum*. A, C, *Glechoma hederacea*; B, *G. longituba*; D, *Schizonepeta tenuifolia*; E, F, *Cedronella canariense*; G, H, *Drepanocaryum sewertzowii*. Scale bars: A, B, E, G = 100μm; C, D, F, H = 10μm.

between the former ones. The mesocarp is represented by five rows of cells: the upper four rows have similar, closely spaced cells; the innermost row consists of large rounded cells with thickened radial and inner tangential walls. The sclerenchymatous layer is 30μm thick and consists of small sclereids with star-like cavities. The inner layer of the endocarp has very flattened cells (Fig. 9B).

The similarities between *Glechoma* and *Meehania* in habit and inflorescence are supplemented by both the nutlet shape and the basal rounded areole. They are however clearly different in nutlet surface and pericarp structure.

SOURCE OF MATERIAL. *G. hederacea*: Japan, C Honshu, *Ohashi et al.* 1371 (LE); China, Laonin, *Chang Yui-Lieng* 96 (LE); *G. longituba*: Far East (south), in Sujphur Valley, *Shipczinsky* 212 (LE).

Schizonepeta *(Benth.) Briq.*

A small, mainly Siberian, Chinese and Mongolian genus of three species. The nutlets are c.2 × 0.8–1mm; they are oblong-ellipsoid, with a rounded apex and edge, more prominent at the basal end. Their surface is smooth with an indistinct-reticulate pattern (Fig. 10D) similar to some species of *Dracocephalum*. The epidermal cells are irregular in shape with indistinct boundaries because of the thick, striate cuticle. The EPW are depressed and sinuous; they are of two kinds: prominent, ridge-pitted, or flattened, slightly depressed, deformed.

Pericarp structure was examined in *S. multifida* (L.) Briq. and *S. annua* (Pall.) Schischk. The pericarp is 70–80μm thick; there is myxocarpy with moderate mucilaginous reaction. The mucilaginous cells are large, rounded or cuboid, and take the shape of 'papillae' after swelling in water. The non-mucilaginous cells have an X-like form, with dark-brown pigment (Fig. 11A). All exocarp cells are thin-walled. The mesocarp is represented by one (in *S. multifida*) or four (in *S. annua*) rows of closely

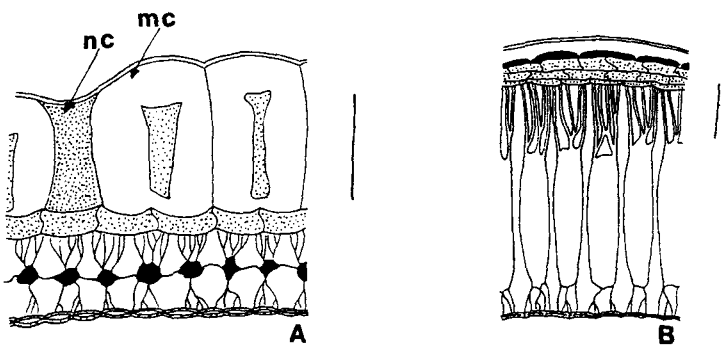

FIG. 11. The pericarp of *Schizonepeta* and *Cedronella* in transverse section. A, *Schizonepeta multifida;* B, *Cedronella canariensis.* Abbreviations: mc, mucilaginous cells; nc, non-mucilaginous cells. Scale bars = 30μm.

spaced cells. The sclerenchymatous layer is 20–30μm thick. In the round sclereid cavities are found pigment or crystals c.2.5μm diameter.

The inner layer of endocarp consists of flattened cells or of unflattened cells with reticulate thickening on their walls (Fig. 11A).

This genus is a close relative of *Dracocephalum* in calyx shape (especially *S. annua* with a clearly bilabiate calyx and swollen folds at the sinuses as in *Dracocephalum*) and nutlet pattern. It is also close to *Nepeta*, but differs in the thecae diverging at 90° (not 180°) and the divergent pairs of the stamens.

SOURCE OF MATERIAL. *S. tenuifolia*: China, She He, Sinlun, *Liou-Tchen-hgo et al.* 4948 (LE); *S. annua*: Zaisan, in Kaldshir Valley, 1908, *Keller* s.n. (LE); *S. multifida*: Mongolia, Ara-Hangai, *Junatov* 2921 (LE).

Cedronella *Moench*

A monotypic genus endemic to the Canary Islands and Madeira. The nutlets are 2–2.8 × 1.3–1.5mm, ellipsoid and trigonous (Fig. 10E); the areole is lateral and rounded; the surfaces of the ventral edges and apices are covered with sessile oil glands; they are smooth with a cellular pattern (Fig. 10F).

The pericarp is c.140μm thick. Myxocarpy was not found. The exocarp has elongated cells with thickened outer tangential walls. The mesocarp consists of three rows of closely spaced cells. The sclerenchymatous layer is c.120μm thick. The sclereids are narrow with large oval cavities. The inner layer of the endocarp is represented by very flattened cells (Fig. 11B).

This distinct genus shares some similarities with *Dracocephalum* (calyx and corolla shape, nutlet pattern and chromosome number) but its precise affinities are uncertain.

SOURCE OF MATERIAL. Teneriffe, *Bourgeau* s.n. (LE).

Drepanocaryum *Pojark*

This is a monotypic genus restricted to E Iran, Afghanistan, Middle Asia and Pakistan. It has a characteristic nutlet shape: they are c.1 × 1.2mm, basally clearly concave with a broad ventral areole extending two-thirds of the entire length of the nutlet (Fig. 10G). The nutlet surface is prominently tuberculate (Fig. 10H).

As in some *Nepeta* species, the cupola-like tubercles are formed by large oblong lobule-like cells. The cells surrounded by the tubercles are isodiametric and polygonal; the AW are straight and prominent; the EPW are irregularly depressed, with striate furrows.

The pericarp is c.110μm thick. Myxocarpy occurs with a moderate mucilaginous reaction. The mesocarp is represented by two rows of cells with pigment. The sclerenchymatous layer is c.40μm thick with star-like cavities in the sclereids. The inner layer of the endocarp consists of cells with reticulate thickenings on their walls (Fig. 13A).

SOURCE OF MATERIAL. Kazakhstan, Karatau, v 1990, *Budantsev* s.n. (LE).

Marmoritis *Benth.*

Five species in the mountains of C Asia, the Himalaya and China.

Nutlet surface and pericarp structure were examined in *M. rotundifolia* Benth. The nutlets are c.3 × 1.2mm; they are oblong-elliptic, with a rounded apex and edge (Fig. 12A). Their surface is smooth with a ridged-cellular pattern (Fig. 12B), similar to some species of *Nepeta*. The epidermal cells are irregular with undulate and prominent AW.

The pericarp is c.60μm thick. Myxocarpy was not found. The exocarp is represented by elongated cells with thickenings on the outer tangential walls. The mesocarp consists of one row of cells. The sclerenchymatous layer is c.40μm thick with rounded cavities. The inner layer of the endocarp consists of cells with reticulate thickening on the walls (Fig. 13B).

Marmoritis is a very close ally of *Nepeta* and *Glechoma*, but apparently merits independent generic status in the *Nepeteae* on inflorescence characters, habit and resupinate corollas (Hedge, 1990).

SOURCE OF MATERIAL. Tibet, Sunjar, 17,500ft, *Strachley & Winterbottom* 11 (K).

CONCLUSIONS

In the tribe *Nepeteae* the exocarp usually consists of large cells with thickened outer tangential walls. The cavity often contains brown or dark-brown pigment. In *Lophanthus chinensis* radial walls have reticulate thickenings and species of the *Agastache* and *Hymenocrater* have outer tangential walls with small pores.

In species whose nutlets produce mucilage the exocarp consists of two different

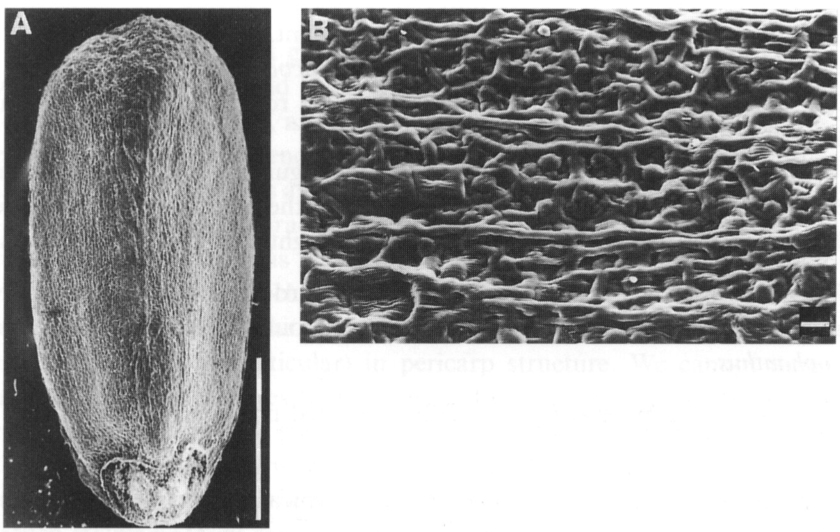

FIG. 12. Nutlets of *Marmoritis rotundifolia*. Scale bars: A, 1000μm; B, 10μm.

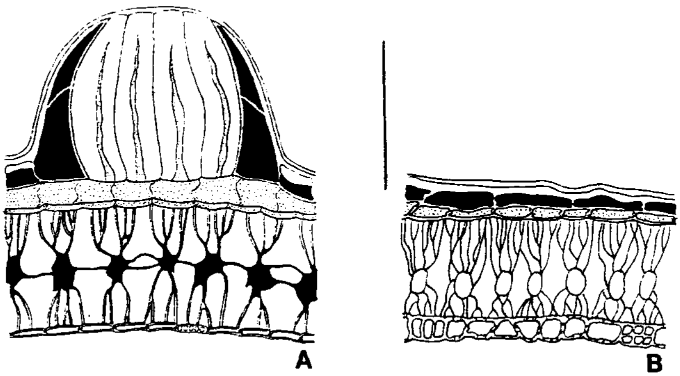

FIG. 13. The pericarp of *Drepanocaryum* and *Marmoritis* in transverse section. A, *Drepanocaryum sewertzowii*; B, *Marmoritis rotundifolia*. Scale bar = 50μm.

types of cells: mucilaginous and non-mucilaginous. Mucilaginous cells are normally much larger (after swelling of the mucilage), radially elongated, and have an oval, round or cuboid shape. Their cell walls are very thick and there is an irregularly shaped cavity often filled with pigment in the centre. The size of mucilaginous cells after swelling varies from 20μm in *Nepeta glomerulosa* to 110μm in *Dracocephalum bipinnatum*. When nutlets are placed in water, mucilaginous cells become elongated, destroy the cuticle and take the shape of 'mucilaginous hairs', i.e. long, thin strands (some species of *Nepeta*, *Drepanocaryum* and *Lophanthus*), or of 'papillae' – shorter and wider strands (some species in *Dracocephalum* as well as in *Schizonepeta* and *Glechoma*). Mucilaginous cells in *Nepeta amethystina*, *N. glomerulosa* and *Dracocephalum scrobiculatum* do not appreciably increase in size.

Non-mucilaginous cells are often narrow, radially elongated with thickened walls and have a small cavity which may contain pigment. In most cases cells of both types are distributed over the nutlet surface. In *Dracocephalum scrobiculatum*, however, the mucilaginous cells are arranged in a wide row at each distal side and in two narrow rows at the proximal side of the nutlet.

Two main types of nutlet surface can be distinguished by exocarp characters: hairless (smooth or sculptured) or slightly hairy in the apical part of the nutlet.

Tubercles of nutlets with a sculptured surface might consist of various cells:

1. Tubercles formed by mucilaginous cells and by guard non-mucilaginous cells which are radially elongated and sickle-shaped. These are found in *Nepeta*, *Drepanocaryum* and *Lophanthus*.

2. Tubercles formed by epidermal radially elongated non-mucilaginous cells. These occur in some *Nepeta* species.

Trichomes in the apical part of the nutlet are typical in the genus *Agastache* and are outgrowths of the exocarp cells. The nutlet surface in *Meehania* is covered by long, 1–3-celled trichomes.

The mesocarp in the species studied is 5–40μm thick and consists of closely spaced flattened cells. During growth and ripening of the nutlets this layer becomes strongly compressed and cell boundaries become undetectable. In some cases one can discern an outer row of cells and an inner row that consists of very flattened, thick-walled cells. The exception is *Glechoma hederacea* which has large, round, thick-walled cells in the inner row of the mesocarp, previously noted (Wojciechowska, 1966). Mesocarp cells usually contain brown, dark-brown or black pigments which may be distributed in various ways within the layer.

The outer endocarp layer varies from 15μm (*Nepeta podostachys*) to 120μm in thickness (*Dracocephalum ruyschiana*, *Cedronella canariensis*) and consists of radially elongated sclereids. In most species these cells are very large and they primarily constitute the pericarp. Sclereid walls are thickened to various degrees (they are distinguished by undulate walls in *Meehania urticifolia*) and in their centre there is a cavity which is frequently irregular, star-like or more or less round in shape. Thin and branched pore canals run to the apical and basal parts, and may link adjacent cells (with the exception of sclereids having oval cavities). Sclereids may contain pigment, and crystals of calcium oxalate. These crystals of regular quadrangular and hexagonal shape are found in cavities and poral canals in some species of *Dracocephalum* and *Schizonepeta.*

The inner endocarp layer comprises one row of smaller tangentially elongated or rounded cells with reticulate thickening on their walls. The inner tangential wall is sometimes more thickened. In many species this layer is rather flattened.

Most of the genera in *Nepeteae* have a distinctive nutlet shape, surface texture and pericarp structure. Within the tribe three informal groups can be recognized, whose constituent taxa have similar nutlets and similar vegetative and floral characteristics.

Group 1. The first and largest group includes *Nepeta*, *Drepanocaryum*, *Lophanthus*, *Hymenocrater*, *Marmoritis* and *Agastache*. Most of the species in these genera are either rhizomatous perennials, annuals or suffruticose herbs with simple leaves, paniculate or spike-like inflorescences, regular, indistinctly or clearly bilabiate calyces and nutlets with lateral areoles and smooth (mainly reticulate) or sculptured surfaces. The pericarp structure is characterized by the presence of mucilaginous tubercles with cells of the 'mucilaginous hairs' type and 1–3 rows of cells in the mesocarp. Star-like cavities in the sclerenchymatous layer are associated primarily with exocarp that produces the mucilage. The genus *Drepanocaryum* does not basically differ from *Nepeta* (*N. micrantha* in particular) in pericarp structure. We cannot agree with Makarova (1967) who believes that the main distinctive feature of *Drepanocaryum sewerzowii* is the presence of star-like cavities in sclereids. Species with a smooth nutlet surface have sclereids with rounded cavities which are connected by poral canals. The genera *Agastache*, *Marmoritis* and *Hymenocrater* are distinguished by an absence of myxocarpy (myxocarpy in *Hymenocrater bituminosum* has been described by Ryding (1995) but we were unable to confirm this). The exocarp cells are flattened and filled with a pigment, and they have heavily thickened poral outer tangential walls (except *Marmoritis*). The mesocarp consists of one or three rows; cavities of sclereids are more or less rounded.

The species of most of these genera have a chromosome base number of $x=8$ or 9 (Budantsev et al., 1992). This group of genera occurs in steppe, montane habitats, semi-deserts and more rarely in forest or alpine habitats of the Mediterranean, Irano-Turanian areas, Hindu Kush, the Himalaya, SW China and northern America (from Canada to Mexico). Weak geographical and ecological isolation of most of these taxa and frequent hybridization has resulted in polymorphic complexes, especially in *Nepeta.*

Group 2. Dracocephalum is at the core of the second group together with *Schizonepeta* and, probably, *Cedronella.* The species of these genera are also herbaceous or suffruticose herbs with spike-like or ovoid inflorescences and an indistinctly or clearly bilabiate calyx with swollen folds at the sinuses of the teeth. The nutlets are smooth with a lateral areole. The presence of large, oval or rounded mucilaginous cells of the 'papillae' type in the exocarp which alternate with radially elongated, narrow non-mucilaginous cells is typical for this group. In some species of *Dracocephalum* and *Schizonepeta* crystals of calcium oxalate are found singly or in groups in cavities or poral canals of sclereids. Non-mucilaginous nutlets are distinguished by small exocarp cells with very thickened outer tangential walls and also by very long and narrow sclereids with oval or star-like cavities. We cannot agree with Ryding (1995) who described mucilaginous cells in the exocarp of *Cedronella canariensis.*

The chromosome base number in this group is $x=5$, 6 or 7. In contrast to the first group, many species of *Dracocephalum* as well as *Schizonepeta* and *Cedronella* have pinnatisect or pinnatifid leaves (there are simple leaves in some *Dracocephalum* but they usually have lobed bracts). This group occurs less widely in the Mediterranean region but has some centres of diversity in the highlands of Siberia and Central, Middle and East Asia. The geographical and ecological isolation of the related species is very characteristic of *Dracocephalum* and hybridization between species is almost unknown.

Group 3. The essentially east Asiatic, nemoral genera *Meehania* and *Glechoma* form the third group in *Nepeteae.* They are characterized by their habit (short rhizomatous herbs with flowers in the axils of the middle and upper leaves) and nutlets without tubercles and with a basal rounded areole surrounded by edging or a fold of pericarp. The pericarp structure of *Glechoma* differs in the peculiar exocarp, which consists of groups of large mucilaginous cells among very narrow non-mucilaginous cells. The presence of large rounded cells in the lower row of the mesocarp is typical for *Glechoma.* The pericarp structure of *Meehania* is distinguished by sclereids with very undulate walls.

Perhaps these three groups of genera represent clades of development of the tribe *Nepeteae* that have diverged since the initial stages of its evolution.

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REFERENCES

BENTHAM, G. (1832–1836). *Labiatarum Genera et Species.* London.

BENTHAM, G. (1848). Labiatae. In: DE CANDOLLE, A. (ed.) *Prodromus Systematis Naturalis Regni Vegetabilis* 12: 27–603. Paris.

BILIMOVITSCH, O. (1935). On the structure of the pericarp in the *Labiatae* from a systematic viewpoint. *Trudy Voronezhsk. Gosud. Univ.* 7: 68–84 [in Russian].

BOISSIER, E. (1879). *Flora Orientalis* 4. Genevae et Basilieae.

BRIQUET, J. (1895–1897). *Labiatae.* In: ENGLER, A. & PRANTL, K. (eds) *Die naturlichen Pflanzenfamilien* 4, Abt. 3a: 183–375. Leipzig.

BUDANTSEV, A. L. (1992a). The system and synopsis of the genus *Lophanthus* (Lamiaceae). *Bot. Zhurn.* 77(9): 69–77 [in Russian].

BUDANTSEV, A. L. (1992b). A synopsis of the tribe *Nepeteae* (Lamiaceae). The genera *Meehania, Glechoma, Drepanocaryum, Marmoritis* and *Hymenocrater. Bot. Zhurn.* 77(12): 118–128 [in Russian].

BUDANTSEV, A. L. (1993a). A synopsis of the genus *Nepeta* (Lamiaceae). *Bot. Zhurn.* 78(1): 93–107 [in Russian].

BUDANTSEV, A. L. (1993b). A synopsis of the tribe *Nepeteae* (Lamiaceae). The genera *Lophanthus, Dracocephalum, Cedronella, Schizonepeta. Bot. Zhurn.* 78(2): 106–115 [in Russian].

BUDANTSEV, A. L. (1993c). Ultrastructural features of fruit surface in genus *Nepeta* (Lamiaceae). *Bot. Zhurn.* 78(4): 80–87, 3 plates [in Russian].

BUDANTSEV, A. L. (1993d). The ultrastructural features of fruit surface in some genera of the tribe *Nepeteae* (Lamiaceae). *Bot. Zhurn.* 78(5): 100–108, 3 plates [in Russian].

BUDANTSEV, A. L., ZEMSKOVA, E. A. & SEMICHEVA, T. G. (1992). Chromosome numbers in genera of the tribe *Nepeteae* (Lamiaceae) and some problems of their systematics. *Bot. Zhurn.* 77(2): 13–24 [in Russian].

HEDGE, I. C. (1962). *Nepeta fissa* and the species allied to it. *Notes Roy. Bot. Gard. Edinburgh* 24: 51–71.

HEDGE, I. C. (1970). Observations on the mucilage of *Salvia* fruits. *Notes Roy. Bot. Gard. Edinburgh* 30: 79–95.

HEDGE, I. C. (1990). Labiatae. In: ALI, S. L. & NASIR Y. J. (eds) *Flora of Pakistan* 192: 1–310.

HEDGE, I. C. (1992). A global survey of the biogeography of the Labiatae. In: HARLEY, R. M. & REYNOLDS, T. (eds) *Advances in Labiatae Science*, pp. 7–17. Kew.

HEDGE, I. C. & LAMOND, J. M. (1968). Studies in the flora of Afghanistan. VII. Labiatae: Lam.-end. *Notes Roy. Bot. Gard. Edinburgh* 28: 89–161.

HUSSAIN, S. Z. et al. (1990). A micromorphological study of some representative genera in the tribe *Saturejeae. Bot. J. Linn. Soc.* 103: 59–80.

LEVIN, E. G. (1941). The genus *Lophanthus* and its analogon *Pseudolophanthus. Trudy Bot. Inst. Akad. Nauk SSSR, Ser. 1*, 5: 256–318 [in Russian].
LINT, H. & EPLING, C. (1945). A revision of *Agastache. Amer. Midl. Naturalist* 33: 207–230.
MAKAROVA, Z. I. (1967). On the significance of the anatomical structure of the pericarp for the taxonomy of the tribe *Nepeteae. Bot. Zhurn.* 52: 33–41 [in Russian].
PATON, A. (1990). A global taxonomic investigation of *Scutellaria. Kew Bull.* 45: 399–450.
POJARKOVA, A. I. (1954). *Nepeta.* In: KOMAROV, V. L. *Flora USSR* 20: 286–437.
RECHINGER, K. H. (1982a). *Nepeta.* In: RECHINGER, K. H. (ed.) *Flora Iranica* 150: 108–216. Graz.
RECHINGER, K. H. (1982b). *Hymenocrater.* In: RECHINGER, K. H. (ed.) *Flora Iranica* 150: 239–250. Graz.
REJDALI, M. (1990). Seed morphology and taxonomy of the North African species of *Sideritis* L. (Lamiaceae). *Bot. J. Linn. Soc.* 103: 317–324.
RYDING, O. (1992a). The distribution and evolution of myxocarpy in Lamiaceae. In: HARLEY, R. M. & REYNOLDS, T. (eds) *Advances in Labiatae Science*, pp. 85–96. Kew.
RYDING, O. (1992b). Pericarp structure and phylogeny within Lamiaceae subfamily *Nepetoideae* tribe *Ocimeae. Nordic J. Bot.* 12: 273–298.
RYDING, O. (1993a). Pericarp structure and systematic positions of five genera of Lamiaceae subg. *Nepetoideae* tribe *Ocimeae. Nordic J. Bot.* 13: 631–635.
RYDING, O. (1993b). Pericarp structure of *Leucas* and related genera (Lamiaceae subfam. Lamioideae). *Nordic J. Bot.* 13: 637–646.
RYDING, O. (1995). Pericarp structure and phylogeny of the *Lamiaceae-Verbenaceae*-complex. *Plant Syst. Evol.* 198: 101–141.
SANDERS, R. W. (1987). Taxonomy of *Agastache* section *Brittonastrum* (Lamiaceae-Nepeteae). *Syst. Bot. Monogr.* 15: 1–92.
UBERA, J. (1982). Carpologia de *Nepeta* (Labiatae) en la Peninsula Iberica. *Lagascalia* 10: 217–225.
WAGNER, S. (1914). *Contribution à l'étude anatomique du fruit des labiées.* Thése Université de Paris, Paris.
WOJCIECHOWSKA, B. (1958). Taxonomy, morphology and anatomy of seeds in the genus *Salvia. Monogr. Bot.* 6: 1–56.
WOJCIECHOWSKA, B. (1961a). Fruits of the Middle European species of *Prunella. Monogr. Bot.* 12: 49–87 [in Polish].
WOJCIECHOWSKA, B. (1961b). Fruits of the Middle European species of some genera of *Stachyoideae. Monogr. Bot.* 12: 89–120 [in Polish].
WOJCIECHOWSKA, B. (1966). Morphology and anatomy of fruits and seeds in the family Labiatae with particular respect to medicinal species. *Monogr. Bot.* 21: 3–245 [in Polish].
WUNDERLICH, R. (1967). Ein Vorschlag zu einer natürlichen Gliederung der Labiaten auf Grund der Pollenkörner, der Samenentwicklung und des reifen Samens. *Österr. Bot. Z.* 114: 383–483.

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