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THE PHYTOGEOGRAPHY OF SCUTELLARIA L.

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ABSTRACT. The phytogeography of the subcosmopolitan *Scutellaria* (Labiatae) is considered using a new global classification. An isoflor map and maps of the distribution of the infrageneric taxa are presented. The genus has its centre of maximum diversity in the Irano-Turanian region of Asia, particularly in the mountains of Central Asia and Afghanistan. There are secondary centres in the eastern Mediterranean and the Andes. Diversity is greater in the Old World than in the New. The origin and migration of the genus is discussed. It is hypothesized that *Scutellaria* spread to North America from Asia via Beringia in the early to mid-Tertiary, reaching South America as late as 3 million years ago.

INTRODUCTION

Scutellaria is a large, subcosmopolitan genus of the Labiatae with about 425 currently recognized species, although the actual species number is probably nearer 350 as a large number doubtfully meriting specific status have been recognized, especially in the USSR and China. This paper aims to describe the present day distribution of *Scutellaria* and to indicate centres of diversity. Hypotheses are made concerning the origin, migration and adaptive radiation of the genus.

To facilitate comparison within the genus on a world scale, a new, globally consistent classification is proposed. Full details of this classification will be published later, but the major infrageneric taxa are proposed below. It should be noted that *Salazaria* Torrey, *Perilomia* Kunth and *Harlanlewisia* Epling have all been placed within *Scutellaria*.

TAXONOMY

Scutellaria L., Sp. Pl. 598 (1753); Gen. Pl. ed. 5, 260 (1754).
Syn.: *Anaspis* Rech. f. in Notizbl. Bot. Gart. Berlin-Dahlem 15: 630 (1941).
Salazaria Torrey in Emory, Rep. U.S. Mex. Bound. 2(1), Botany of the boundary: 133 (1858).
Perilomia Kunth in Humboldt, Bonpland & Kunth, Nova Gen. Sp. (ed. qu.) 2: 326 (1818).
Lectotype species: *S. galericulata* L. (Hitchcock & Green, 1929).

1. Subgenus **Scutellaria**
(i). Sect. **Scutellaria**
Syn.: Subgenus *Euscutellaria* Briq. in Die Natürlichen Pflanzenfamilien ed. 1,4.3a: 225 (1896).
Subgenus *Scutellariopsis* Briq. op. cit.: 227.
Section *Stachymacris* A. Hamilton, Esq. monogr. Scutellaria 17 (1832).
Section *Galericularia* A. Hamilton op. cit. 31.
Section *Heteranthesia* Benth., Labiat. Gen. Spec. 425 (1834).
Section *Vulgares* Benth. in Benth. & J. D. Hook., Gen. Pl. 2: 1201 (1876).
Lectotype species: *S. galericulata* L.

All sections listed by Epling (1942) except sects *Theresa, Perilomia* and *Perilomioideae* are synonyms of this section.

(ii). Sect. **Salviifoliae** (Boiss.) Edmondson in Davis, Flora of Turkey 7: 87 (1982).
Syn.: Subsection *Salviifoliae* Boiss. in Fl. Orient. 4: 686 (1879).
Lectotype species: *L. salviifolia* Benth.

(iii). Sect. **Perilomia** (Kunth) Epling **emend.** Paton.
Syn.: *Perilomia* Kunth in Humboldt, Bonpland & Kunth, Nova Gen. Sp. (ed. qu.) 2: 326 (1818).
Harlanlewisia Epling in Am. J. Bot. 42: 436 (1955).
Perilomia sect. *Euperilomia* Briq. in Die Natürlichen Pflanzenfamilien ed. 1, 4, 3a: 233 (1896).
Perilomia sect. *Holocraspeda* Briq. loc. cit.
Perilomia sect. *Aprosphylla* Briq. loc. cit.
Scutellaria sect. *Perilomia* (Kunth) Epling in Repert. Spec. Nov. Regni. Veg. Beih. 85: 178 (1936).
Scutellaria sect. *Perilomioideae* (Benth.) Epling loc. cit.
Scutellaria sect. *Theresa* (Clos) Epling loc. cit.
Lectotype species: *S. scutellarioides* (Kunth) R. Harley (Epling, 1936) as *Scutellaria perilomia*.

(iv). Sect. **Anaspis** (Rech. f.) Paton, **stat. nov.**
Syn.: *Anaspis* Rech. f. in Notizbl. Bot. Gart. Berlin-Dahlem 15: 630 (1941).
Subgenus *Anaspis* (Rech. f.) Juz. in Komarov, Flora URSS 20: 207 (1954).
Type species: *S. fedtschenkoi* Bornm. The only species listed as a member of the genus *Anaspis* by Rechinger (Rechinger, 1941). Type: Turkestan: *Bornmüller* 1150 (JE–n.v.).

(v). Sect. **Salazaria** (Torrey) Paton, **comb. et stat. nov.**
Syn.: *Salazaria* Torrey in Emory, Rep. U.S. Mex. Bound. 2(1), Botany of the boundary: 133 (1858).
Type species: *Scutellaria mexicana* (Torrey) Paton, **comb. nov.**
Syn.: *Salazaria mexicana* Torrey in Emory, Rep. U.S. Mex. Bound. 2(1), Botany of the boundary: 133 (1858). Type: [Mexico] Chihuahua: Valley of Rio Grande: *Parry, Bigelow, Wright & Shott,* s.n. (K).

2. Subgenus **Apeltanthus** (Nevski ex Juz.) Juz. **emend.** Paton.
(i). Sect. **Apeltanthus**
Syn.: Sect. *Apeltanthus* Nevski ex Juz. in Bot. Mater. Gerb. Bot. Inst. Komarov Akad. Nauk SSSR 14: 427 (1951).
Subgenus *Apeltanthus* (Nevski ex Juz.) Juz. in Komarov, Flora URSS 20: 217–225 (1954).
Lectotype species: *S. orbicularis* Bunge.

(ii). Sect. **Lupulinaria** A. Hamilton in Esquisse d'une monographie du genre Scutellaria ou toque 11 (1832).

(a). Subsect. **Lupulinaria**
Syn.: Sect. *Nevskinthe* Juz. in Komarov, Flora URSS 20: 115 (1954).
Lectotype species: *S. orientalis* L.

(b). Subsect. **Cystaspis** (Juz.) Paton, **stat. nov.**
Syn.: Sect. *Cystaspis* Juz. in Bot. Mater. Gerb. Bot. Inst. Komarov Akad. Nauk. SSSR 14: 413 (1951)
Subgenus *Cystaspis* (Juz.) Juz. in Komarov, Flora URSS 20: 199 (1954).
Lectotype species: *S. physocalyx* Rgl. & Schmalh. chosen here because its characteristics concur best with sect. *Cystaspis* described by Juzepczuk (1951).
Type: [Pamir-Alay]: In Kokaniae jugis montium Alai, 8000' alt., *O. Fedtschenko* s.n. (TASH–n.v.).

PHYTOGEOGRAPHY

THE PRESENT-DAY DISTRIBUTION OF SCUTELLARIA

An isoflor map (Fig. 1), based on the number of species inhabiting particular areas, was compiled using numerous Floras, Epling's monograph of the New-World species (Epling, 1942), and data from herbarium specimens.

This map is, in part, misleading as an indicator of diversity in different areas. The number of species recorded from the areas of *Flora Reipublicae Popularis Sinicae* (Wu & Li, 1977) and *Flora URSS* (Juzepczuk, 1954) are apparently both much inflated because of the very narrow species concepts of the authors. For example, Juzepczuk (1954) lists 53 species which are equivalent to '*Scutellaria orientalis* L. of earlier authors *sensu latissimo*', whereas Edmondson, in dealing with the *S. orientalis* complex in Turkey, recognizes one species with 16 subspecies (Edmondson, 1982). Another source of difficulty concerning species number is that the same taxon may be given different specific epithets or treated differently in different areas. For example, *S. orientalis* is recognized in the *Flora of Turkey* (Edmondson, 1982) and *S. pinnatifida* A. Hamilton in *Flora Iranica* (Rechinger, 1982) yet these taxa are probably conspecific. Thus mere species number may not necessarily reflect true diversity within the genus. However the map reveals the following facts: *Scutellaria* is absent or poorly represented in the arctic, in lowland tropical areas such as the Amazon basin, desert regions, southern Africa* and on the Pacific Islands. In the tropics and Southern Hemisphere it is present mainly on the temperate mountains. Species number is greatest in the mountains of Central Asia and China: 50 species are found in the Pamir-Alay region, (as delimited by Komarov *et al.*, 1934–64); 41 in Yunnan; 35 in Tien Shan (as recognized by Komarov *et al.* 1934–64, but extended to include the range in Xinjiang); 22 in Sichuan and 18 in the mountains of Afghanistan and Pakistan.

Figures 2–4 show the distributions of the infrageneric taxa of *Scutellaria*.

Table 1 combines the information of these maps giving the number of species and endemics in each section and subsection and also the total number of species and endemics in each of Takhtajan's floristic regions of the world (Takhtajan, 1986).

***S. racemosa*, native to South America is widely naturalized in South Africa.

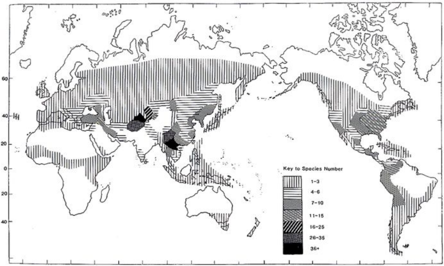

FIG. 1. An isoflor map of *Scutellaria*. Species number is highest in the mountains of Central Asia and in Yunnan and Sichuan. The genus is absent from the Arctic, southern Africa, desert regions and from the Amazon basin.

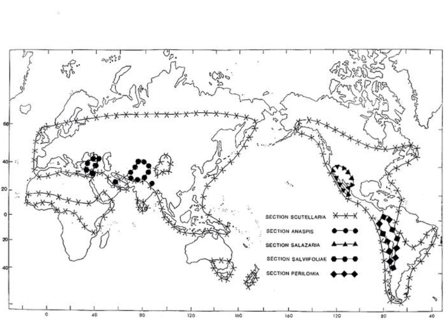

FIG. 2. Map showing the distributions of the sections of subgenus *Scutellaria*. Only sect. *Scutellaria* is present in both the Old and New Worlds. The other sections have localised distributions.

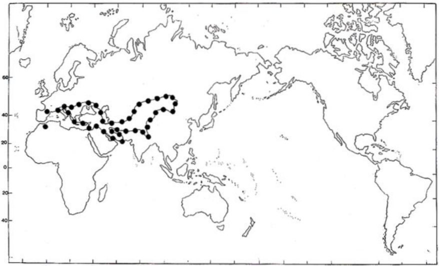

FIG. 3. Map showing the distribution of sect. *Lupulinaria* subsect. *Lupulinaria*. This taxon is confined to the mountainous areas of Eurasia. Note its absence from the New World.

FIG. 4. Map showing the distribution of sects *Anaspis* (●), *Apeltanthus* (▼) and subsect. *Cystapsis* (■). These taxa are largely confined to the mountains of Central Asia, but sect. *Anaspis* is present, disjunctly, in south Iran and Xizang (Tibet).

The number of sections and subsections in a particular area gives a more accurate measure of diversity than does species number. The large number of species in Yunnan and Sichuan all belong to sect. *Scutellaria* while in Tien Shan most of the 35 species belong to sect. *Lupulinaria.*

It can be seen that the major centre of diversity is in the Irano-Turanian Region. Both subgenera are present here: sects *Scutellaria, Anaspis,* and *Salviifolia* of subgenus *Scutellaria*; and both subsections of sect. *Lupulinaria* and sect. *Apeltanthus* of subgenus *Apeltanthus*. Smaller centres are in the Mediterranean Region, particularly the East Mediterranean province with sects *Lupulinaria, Scutellaria* and *Salviifolia* all being present, and in the Andean Region where sect. *Scutellaria* is more variable and sect. *Perilomia* is present. Generally, there appears to be less diversity in the New World than in the Old.

The diversity of the Irano-Turanian Region is examined in more detail in Table 2. The greatest diversity, based on the number of sections and species, is in the Pamir-Alay range. The Hindu-Kush and mountains of western Pakistan show similar diversity but fewer species. Both these areas have very high degrees of endemism, 92% and 67% respectively.

The distribution of *Scutellaria* with species number high in the mountains of Central Asia, Afghanistan and Iran, but low in the low-lying Turanian (Aralo-Caspian) area, supports Rechinger's (1986) suggestion that the highland part of the Irano-Turanian region be renamed the Irano-Turkestanian region, with the removal of the lowland Turanian area.

THE ORIGIN AND MIGRATION OF SCUTELLARIA

The subcosmopolitan distribution of *Scutellaria* is similar to that of *Gentiana* (Gentianaceae) except that this taxon is absent in Africa, and to *Rumex* (Polygonaceae) and *Viola* (Violaceae) which differ in being present in southern Africa and in Hawaii. Unlike *Rumex,* the distribution of *Scutellaria,* is not the result of numerous, readily dispersed, weedy species; these are rare in the genus. Thus *Scutellaria* is probably an ancient taxon as it is isolated in the family and it is present in both the New and Old Worlds.

How then did the widespread distribution of *Scutellaria* arise? One possibility is that *Scutellaria* crossed between Europe and North America before the North Atlantic opened in the Eocene, 55–40 million years ago (55–40my) (Briggs, 1987). However, it is unlikely that *Scutellaria* spread in this manner. If the genus was present in Europe in the Eocene it would be expected today to show a considerable amount of diversity in SE Europe, an area mostly unglaciated in the Pleistocene. In fact, only three species are present here and only one, *S. balearica,* is endemic to the area. It could be argued that this lack of development is due to competition and lack of available habitats, but it is hard to belive that *Scutellaria* would now be so species-poor if it had been present here for 50 million years. Also if *Scutellaria* was in Europe and North America in the Eocene it would still have to reach Central Asia, its area of maximum diversity today. Europe was isolated from Asia by the Turgai Sea from the Jurassic to Oligocene (c.155–30my) (Briggs, 1987) and then any migration to Asia would be hampered by the Paratethys Sea which covered a substantial part of western Asia from the mid-Miocene to the Pliocene

TABLE 1

Showing sections and species number present in Takhtajan's (1986) floristic regions of the world with the number of endemic species in parentheses. The high number of species in Yunnan and Sichuan all belong to Sect. *Scutellaria*.

	Subgenus *Scutellaria*					Subgenus *Apeltanthus*			
Region	Section Salazaria	Section Perilomia	Section Salviifoliae	Section Anaspis	Section Scutellaria	Section Apeltanthus	Subsection Lupulinaria	Subsection Cystaspis	TOTAL
Circumboreal			3(2)		14(5)		31(30)		48(37)
East Asian					87(74)				87(74)
North American Atlantic					32(26)				32(26)
Rocky Mountain					8(2)				8(2)
Macaronesian					1(0)				1(0)
Mediterranean			3(2)		13(6)		3(0)		19(8)
E Med Province			3(2)		11(6)		2(0)		16(8)
Irano-Turanian			1	15(15)	11(2)	12(12)	70(65)	11(11)	120(105)
Madrian	1(1)				43(30)				44(41)
Sudano-Zambesian					4(4)				4(4)
Indian					6(2)				6(2)
Indochina					13(8)				13(8)
Malesian					3(1)				3(1)
Caribbean					25(15)				25(15)
West Indian Province					5(3)				5(3)
Central American Province					20(12)				20(12)
Andean		9(8)			22(19)				31(25)
Brazilian					5(3)				5(3)
Chile-Patagonian		3(2)			3(1)				6(3)
North-East Australian					2(2)				2(2)
Neozeylandic					1(1)				1(1)
TOTAL	1	11	5	15	242	12	119	11	

(c.15–3my) (Adams, 1981). As there is greater diversity in Asia, it is more likely that *Scutellaria* migrated to Europe from Asia.

The other possibility is that *Scutellaria* crossed between the New and Old Worlds via Beringia. Beringia could have served as a migration route throughout most of the Tertiary (65–3my) (Briggs, 1987). This may have been interrupted by high sea levels between 10–12 million years ago, and intermittently during the Pleistocene (Hopkins, 1967). *Scutellaria* probably did not cross Beringia in the glacial periods of the Pleistocene. Such a recent migration would make it difficult to explain the areas of maximum diversity at lower latitudes in both the Old and New Worlds.

Possibly it was the ancestral species of sect. *Scutellaria* which crossed

Beringia as this is the only section present in the Old and New Worlds. The species of this section are typically associated with mixed deciduous temperate forest. Such a forest linked Asia and North America via Beringia in the mid-Miocene. These forests retreated southwards as the climate of Beringia became colder and drier in the late-Miocene (Axelrod, 1983). Examination of the migration of *Acer* by Wolfe (1981) shows that these forests were probably in existence in the Eocene when this genus first crossed Beringia. Thus it is possible that *Scutellaria* first crossed Beringia as a component of the herbaceous layer of these forests in the early to mid-Tertiary (c.65–40my).

Assuming that a genus will be more diverse in an area that it has occupied for a longer period of time, having had opportunity to colonize a wide range of habitats, it should be possible to determine in which direction *Scutellaria* crossed Beringia by examining the diversity of the genus in the early to mid-Tertiary.

Sect. *Scutellaria* today is largely absent from Central Asia apart from the widespread *S. galericulata*. However, trees such as *Quercus, Tilia* and *Ulmus* which are often associated with species of sect. *Scutellaria* are also absent there today, but fossil evidence shows these to have been present in the Eocene-Oligocene (50–30my) (Kamelin, 1967). Sect. *Scutellaria* may also have been present then, especially as sect. *Anaspis*, which inhabits this area today, may have evolved from this section. Kamelin (1965, 1967) postulated the concept of Prashibljak vegetation, a complex of *Quercus, Cedrus, Pinus, Pistacia* and herbs such as *Eremurus* (Liliaceae), *Cousinia* (Compositae), *Ziziphora* (Labiatae) and *Eremostachys* (Labiatae), which developed on the foothills of Central Asia in the Oligocene. This vegetation is thought to have degraded with the onset of orogeny and the continuing xerophilization and cryophilization in the late-Miocene to Pliocene. The oak forests of the South Zagros Mountains and the oak and cedar forests of Nuristan, in east Afghanistan, are thought to be impoverished relicts of this vegetation (Kamelin, 1965). From present-day distributions (Figs 2–4) it can be argued that the ancestors of sect. *Anaspis* (Central Asia, South Zagros, Hindu-Kush, Nuristan, and possibly eastern Xizang (Tibet)), sect. *Apeltanthus* (Central Asia, Hindu-Kush and Nuristan), and sect. *Lupulinaria* (mountains of Eurasia with the main development in Central Asia) were present in the Prashibljak along with the ancestors of sect. *Scutellaria*. In North America, in the early to mid-Tertiary, only the ancestors of sect. *Scutellaria* and possibly sect. *Salazaria* were present. Thus as the genus was more diverse in the Old World than in the New, it is possible that *Scutellaria* migrated from Asia to North America via Beringia in the early to mid-Tertiary. Later migrations across Beringia are also possible. Old and New World populations of *S. galericulata* are indistinguishable. Recent migrations of this species are likely as there must be sufficient geneflow to maintain this uniformity. Migration may even be occurring today by long-distance dispersal. The nutlets of this waterside species float and could easily be transported by water birds. The morphological similarity between *S. scordifolia* from east Asia and *S. angustifolia* from western USA may also be attributed to a more recent migration.

It may be that sect. *Scutellaria* being the most widespread infra-generic taxon and having the simplest form of inflorescence structure, is the most primitive section of the genus. But it may not have been the most widespread section in the mid-Tertiary, perhaps it was the only taxon which could survive the ecological conditions of Beringia. However, by looking at the assumed diversity and distribution of the genus in the early to mid-Tertiary it is reasonable to suggest that the centre of origin of *Scutellaria* lies within the range of sect. *Scutellaria* and in the Old World, probably in Asia.

THE PHYTOGEOGRAPHY AND RADIATION OF SCUTELLARIA IN THE OLD WORLD

1. SUBGENUS SCUTELLARIA

Sect. *Scutellaria* in the northern Old World seems adapted to more mesic, lowland habitats than are sect. *Anaspis* and subgenus *Apeltanthus*. The species number is greatest in east Asia. This area was not glaciated in the Pleistocene, unlike northern Asia and much of Europe where, today at least, the section has few species. The low number of species in Europe may also be explained by the late arrival of this taxon. From the mid-Miocene to the Pliocene (c.15–3my) the Paratethys Sea and earlier the Turgai Sea, would have provided considerable barriers to migration (Adams, 1981; Briggs, 1987).

Of the four species present in the islands of Indonesia and New Guinea, two, *S. indica* and *S. discolor*, are widespread in continental south east Asia. This suggests a recent arrival in these areas as isolation has not produced many endemic species. The two species in south-east Australia may have also arrived recently. *S. mollis* and *S. humilis* may be isolated relicts evolved from a previously widespread *S. javanica*-like ancestor, now surviving only on the extra-tropical mountains of SE Australia. Such a widespread distribution could have occurred during the Pleistocene glaciation when the islands of south-east Asia would have been attached to the mainland and New Guinea would be linked to Australia as the sea level dropped (Briggs, 1987). *S. novae-zealandiae* probably reached New Zealand from Australia. Many species and 75% of genera of New Zealand seed plants are shared with Australia (Briggs, 1987). Such migrations may have occurred during a glacial period when the sea level was lower.

The disjunction of sect. *Scutellaria* between north-east India on one hand and the Western Ghats and Sri Lanka on the other probably also dates from the Pleistocene. Three of the four species present in the north-east are also present in the Western Ghats. Kurup (1974) suggests that such disjunctions are due to taxa widespread across the Deccan peninsula in glacial periods contracting into refugia. Sect. *Scutellaria* has died out on the rest of the Deccan peninsula due to the dry conditions, but has survived in the Western Ghats and Sri Lanka which have a moist climate similar to that of north-east India.

The fact that sect. *Scutellaria* is represented on the temperate mountains of the Sudan and east Africa by only four or five similar species, suggests that representatives of this taxon have also arrived here recently.

Sect. *Scutellaria* is now largely absent from Iran, Afghanistan and Central Asia (Table 2). Evidence from nutlet anatomy suggests that the ancestors of sect. *Anaspis* were very similar to *S. albida* of sect. *Scutellaria*. Sect. *Anaspis* probably diverged from sect. *Scutellaria* before the latter was driven from the area by the continuing xerophilization which began in the mid-Tertiary. The testudinate* calyx of sect. *Anaspis* is displayed by sect. *Apeltanthus* which is also chasmophytic. This character may be an adaption to the rock-crevice habitat. The south Iran-Afghanistan disjunction shown by sect. *Anaspis* is also

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*A domed or vaulted calyx upper lip resembling a tortoise shell.

TABLE 2

Showing sections and species number present in the Irano-Turanian Region with the number of endemic species in parentheses. Takhtajan's (1986) provinces are used for the west of the region, and areas delimited in Flora URSS (Komavov 1934–64) are used in the east for better resolution

	Subgenus *Scutellaria*					Subgenus *Apeltanthus*			
							Section *Lupulinaria*		
	Section Salazaria	Section Perilomia	Section Salviifoliae	Section Anaspis	Section Scutellaria	Section Apeltanthus	Subsection Lupulinaria	Subsection Cystaspis	Total
1. Irano-Turanian Region			1	15(15)	11(2)	12(12)	70(65)	11(11)	120(105)
2. Mosopotamian Province									0
3. Central Anatolian Province			1(0)		4(0)		1(0)		5(0)
4. Armeno-Iranian Province				1(1)	5(1)		10(8)		16(10)
5. Hyrcanian Province					3(0)		4(2)		7(2)
6. Turanian Province					1(0)		1(1)		2(1)
7. Hindu Kush mountains of Pakistan				4(4)	0	2(1)	10(6)	2(1)	18(12)
8. Pamir-Alay				9(9)	1(0)	10(9)	22(20)	8(8)	50(46)
9. Syr Darya					1(0)				1(0)
10. Tien Shan (including range in Xinjiang)					1(0)	2(1)	32(30)		
11. Dungaria-Tarbagatai					1(0)		8(6)		9(6)
12. Mongolia					7(1)		4(1)		12(2)
13. Himalaya (Kashmir and east)				1(1)	7(4)		1(0)	1(0)	8(3)

1–6 as Takhtajan, (1986); 8–12 as delimited in Komarov *et al.*, (1934–64).

TABLE 3

Showing the distribution of sect *Salviifoliae*. Provinces as Takhtajan (1986).

	No. of Species	No. of Endemic Species
Euxine Province	3	2
Central Anatolian Province	1	1
East Mediterranean Province	3	2

demonstrated by *S. multicaulis* and several other taxa in different families, such as *Dionysia* (Primulaceae), *Chalcanthus* (Cruciferae) and *Fritillaria imperialis* (Liliaceae) (Hedge & Wendelbo, 1978). This disjunction is probably the result of the fragmentation of a wider distribution. *S. tibetica,* possibly a synonym of *S. kingiana* Prain, may also belong to sect. *Anaspis*. Found in the eastern Himalaya (Fig. 4) the species may represent a relict of an eastern expansion of this taxon through Tibet.

Sect. *Salviifoliae* contains five species, only one of which (*S. salviifolia*) is found throughout the range of the section (see Fig. 2 and Table 3). This distribution is consistent both with sect. *Salviifoliae* being a newly evolved taxon, diverged from sect. *Lupulinaria,* or being related to a *S. albida*/*S. rubicunda*-like ancestor belonging to sect. *Scutellaria*. Both these taxa are morphologically similar to sect. *Salviifoliae* and both are represented in the area.

2. SUBGENUS APELTANTHUS

Subgenus *Apeltanthus* has its area of maximum diversity in the Pamir-Alay and Hindu-Kush mountains. Radiating out from this area the number of species and the level of diversity decreases, only sect. *Lupulinaria* subsect. *Lupulinaria* being present at the edge of the distribution of subgenus *Apeltanthus*. This pattern of distribution and variation is shown by several other taxa, e.g. *Eremostachys* Bunge (Labiatae), *Acantholimon* Boiss. (Plumbaginaceae), *Eremurus* M. Bieb. (Liliaceae) (Hedge & Wendelbo, 1970). These Central Asiatic mountains have also been considered the centre of diversity of the Labiate genera *Salvia* and *Perovskia* (Hedge & Wendelbo, 1970). Both sect. *Lupulinaria* subsect. *Cystaspis* and sect. *Apeltanthus* are restricted to this area of maximum diversity of the subgenus as a whole, showing a high degree of endemism, with species being found either in Pamir-Alay, Tien Shan, or the Hindu-Kush and mountains of western Pakistan (Table 2).

Sect. *Lupulinaria* is the most widespread taxon of this subgenus ranging from the Altai Mountains in the east to the mountains of Morocco in the west (Fig. 3). Again sect. *Lupulinaria* has its greatest number of species in the Pamir-Alay and Hindu-Kush mountains but unlike the genera listed above it shows development in the Caucuses with 24 species, 22 of which are endemic. *S. orientalis* is disjunct between Spain and Morocco in the west and the Balkans in the east. The vicariads *Lonicera nummulariifolia* and *L. arborea* (Caprifoliaceae) have a similar distribution. Davis & Hedge (1971) suggest that such taxa may have migrated westwards through south and central Europe in the interglacial periods; glaciation having caused extinction in these areas. If this is so then sect. *Lupulinaria* may have been much more widespread than it is now.

THE PHYTOGEOGRAPHY AND RADIATION OF SCUTELLARIA IN THE NEW WORLD

After invading the New World, via Beringia, the ancestors of *Scutellaria* sect. *Scutellaria* would have spread south finding new habitats and speciating. Today in North America the section has most species in eastern USA. The Pleistocene glaciations would have largely removed the genus from Canada and the deterioration of the climate over the last 3000 years (Kozhevnikov, 1979), would have driven the section south to its present northern boundary. Sect. *Scutellaria* is poorly represented in the Rocky Mountains and western USA. This may be accounted for by the uplift of the western mountains and the associated xeric climate which developed and continued from the late-Miocene (c.15–6my), to the present day (Briggs, 1987). This change would have resulted in the extinction of many species. Eastern USA would not have been affected by such changes and so maintains its species diversity.

In the New World sect. *Scutellaria* shows most diversity in the mountains of Mexico and the northern Andes, where forms with red flowers, spirally arranged flowers, or a combination of both, occur with the usual forms with secund, opposite, blue, white or pink flowers. Migration between North and South America was possible before and during the early-Tertiary: Cretaceous marsupials are found on both continents and caviomorph rodents reached South America from the North in the Eocene (Briggs, 1987). Nevertheless, it is unlikely that *Scutellaria* crossed to South America before the end of the Tertiary (c.3my) because the high Andean habitats which *Scutellaria* now occupies did not exist until then (Simpson, 1975). A permanent land connection was formed 5–3 million years ago which would have enabled *Scutellaria* to enter South America. Such a recent arrival implies that the genus has undergone a vast amount of speciation and diversification and produced remarkable floral variation in the Andes in a very short time. How can this burst of evolution be explained? Simpson (1975) demonstrates that *Scutellaria* and other upper montane forest elements in Colombia, Venezuela, Ecuador and on the eastern slopes of the Peruvian Andes may have extended their ranges during Pleistocene glaciations when vegetation zones were lowered. In the now arid Andes of western Peru the glacial climate produced humid conditions which would also allow expansion of the genus. Populations would be isolated when the vegetation zones were raised in the north and east Andes and when arid conditions returned to western Peru during interglacial periods. Repeated cycles of climatic change, presence of bird pollinators which would provide the selection pressure for long tubed, red corollas, and migrations back and forth across Central America in the Pleistocene are probably responsible for the present diversity of sect. *Scutellaria* in the Andes and Sierra Madre. A similar diversity of corolla form is seen in the South and Central American members of *Salvia* L. and *Satureja* L. *sensu lato*.

From the northern Andes sect. *Scutellaria* appears to have migrated along the southern border of the Amazon basin to the coast of Brazil and also down the Andes to as far south as Tierra Del Fuego. *S. nummulariifolia* probably reached the Falkland Islands by long distance dispersal. This is presumably also how the section reached the West Indies although it may have been transported there by man. The very attractive *S. ventenatii*, native to Colombia and Venezuela, is widely naturalized in the West Indies.

Sect. *Perilomia* probably arose in Peru where the highest number of species and endemic species are found, as shown in Table 4. The taxon seems to have spread out from Peru/Ecuador, having fewer species at the edge of its distribution. Sect *Perilomia* probably diversified from sect *Scutellaria* during the climatic changes in the Pleistocene, and is thus of comparatively recent origin.

Sect. *Salazaria* may be a relict taxon like several mono- and di-typic genera

TABLE 4

Showing the distribution of sect *Perilomia*.

Area	No. of Species	No. of Endemic Species
Colombia	2	0
Peru	7	3
Ecuador	5	1
Argentina	2	1
Chile	1	1

of the Compositae (e.g. *Phalacoseris* A. Gray, and *Chaetodelpha* A. Gray) found in California. These are thought to have migrated across Beringia by hopping from one pocket of xeric environment to another during the early Tertiary (Stebbins & Major, 1965). However sect. *Salazaria*, which is absent from the Old World, occupies a wide geographical area from California and S Utah to Chihuahua. This widespread colonization of semi-desert environment does not seem typical of a genetically impoverished, early-Tertiary invader. Neither has section *Salazaria* undergone speciation to form large, complex groups like *Erigeron* L. (Compositae), and *Astragalus* L. (Leguminosae) which are also thought to be early-Tertiary invaders (Stebbins & Major, 1965). It is more likely that *Scutellaria mexicana* is the product of a later adaptive radiation, into xeric habitats, from the very similar sect. *Scutellaria*. *S. mexicana* has 50 chromosomes which is large for *Scutellaria* and may indicate a high level of ploidy. This species may have evolved from some suffruticose diploid member of sect. *Scutellaria* adapted to xeric environments but which is now extinct. This suffruticose ancestor may have resembled *S. resinosa* or *S. suffrutescens,* whose ploidy levels are unknown. Generally there are very few polyploid species of *Scutellaria*. The only ones identified as such are North American members of sect. *Scutellaria*: *S. lateriflora* (88 chromosomes) and *S. churchilliana* (60) (Gill & Morton, 1978).

CONCLUSIONS

Obviously the mountains of Central Asia and Afghanistan are important centres of speciation and diversity in *Scutellaria*. The area has a wide range of habitats: steppes, forests, rock crevices and screes. It was probably not glaciated in the Pleistocene (Kamelin, 1967), so the stock of genetic diversity built up in the Tertiary would not have been depleted. The large number of endemic species in this area may be due to changes which have occurred more recently in geological time, notably the uplift of the Hindu-Kush. This would have provided new habitats and also deprived the Pamirs of monsoons leading to increased aridity in the area in the late-Pleistocene. These changes would have isolated populations and lead to speciation.

Viewing the genus as a whole, over its entire distribution, there are striking phytogeographical similarities to *Salvia,* another large, sub cosmopolitan genus in the Labiatae. Both have a centre of maximum diversity in Central Asia, both seem impoverished in North America but well developed in South America (*Salvia* has c.50 species in North America and c.250 in South and Central America), and both are poorly represented in Australia, Indonesia and in East Africa. However unlike *Scutellaria, Salvia* is present in the Cape of Africa and in Madagascar (Hedge, 1986).

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