Phylogenetische und taxonomische Untersuchungen an der Subtribus Menthinae (Lamiaceae, Nepetoideae, Mentheae) unter besonderer Berücksichtigung des *Satureja*-Komplexes

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Abkürzungsverzeichnis:

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2n	diploider Chromosomensatz
5,8s	**5,8 S**vedberg-Einheiten (=Sedimentationskoeffizient bei Ultrazentrifugation)
Abb.	**Abb**ildung
AFLP	**A**mplified **F**ragment **L**ength **P**olymorphism
al.	**al**ii (lateinisch für: der, die, das andere/die anderen; Abkürzung bei Autorenzitat)
äther.	**äther**isch
bp	**b**ase**p**air (englisch für: Basenpaar; bei gepaarten DNA-Strängen)
bzw.	**bez**iehungs**w**eise
BGM	**B**otanischer **G**arten **M**ünchen
ca.	**c**irc**a** (lateinisch für: ungefähr, in etwa)
CB	**C**hristian **B**räuchler
Co.	**Co**mpany
cp	**c**hloro**p**last (englisch für: Chloroplasten-; Vorsilbe zur Spezifizierung der DNA-Herkunft)
d.h.	**d**as **h**eißt
DNA	**D**eoxy Ribo**N**ucleic **A**cid (englisch für: Desoxyribonukleinsäure)
ed./eds.	**ed**itor/**ed**itor**s** (englisch für: der/die Herausgeber)
engl.	**engl**isch
EST	**E**xpressed **S**equence **T**ag
etc.	**et c**etera (lateinisch für: und übriges)
***fps*2**	nukleäres low copy Gen
***gap*C**	nukleäres low copy Gen
gen.	**gen**us (lateinisch für: Gattung)
inkl.	**inkl**usive
ISSR	**I**nter **S**ingle **S**equence **R**epeats
ITS	**I**nternal **T**ranscribed **S**pacer
k.A.	**k**eine **A**ngabe
LMU	**L**udwig-**M**aximilians-**U**niversität (München)
***mat*K**	codierender Bereich des Chloroplastengenoms
max.	**max**imal
Mt.	**M**oun**t** (englisch für: Berg)
N.	**N**umero (lateinisch für: Nummer)
***ndh*F**	codierender Bereich des Chloroplastengenoms
nov.	**nov**us/a/um (lateinisch für: neuer/e/es)
pers. Mitt.	**pers**önliche **Mitt**eilung
P.	**p**age
p.p.	**p**ro **p**arte (lateinisch für: zum Teil)
Pp.	**p**ages
***rbc*L**	codierender Bereich des Chloroplastengenoms
rDNA	**r**ibosomale **DNA**
REM	**R**aster-**E**lektronen-**M**ikroskop
RJB	**R**eal **J**ardín **B**otanico (Madrid)

RNA	**R**ibo**N**ucleic **A**cid (englisch für: Ribonukleinsäure)
s.	**s**iehe
sect.	**sect**io (lateinisch für: Sektion; Standardabkürzung für die taxonomische Rangstufe „sectio“)
s.l.	**s**ensu **l**ato (lateinisch für: im weit(er)en Sinn)
sp./spp.	**sp**ecies (Singular/Plural; lateinisch für: Art)
ssp./subsp.	subspecies (alternative verwendete Abkürzungen, lateinisch für: Unterart)
s.str.	**s**ensu **str**icto (lateinisch für: im eng(er)en Sinn)
t.	**t**abula (lateinisch für: (Abbildungs-)Tafel)
Tab.	**Tab**elle
TM	**T**rade**m**ark
***trn*K**	Intergenerischer Spacer des Chloroplastengenoms
***trn*L-F**	Intergenerischer Spacer des Chloroplastengenoms
***trn*T-L**	Intergenerischer Spacer des Chloroplastengenoms
u.a.	**u**nter **a**nderem
v.a.	**v**or **a**llem
vgl.	**v**er**gl**eiche
vol.	**vol**ume (englisch für: Band)
z.B.	**z**um **B**eispiel
z.T.	**z**um **T**eil

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1. Einleitung

Die Lamiaceae oder Labiatae (Lippenblüter) stellen mit derzeit mehr als 7000 bekannten Species in über 230 Gattungen (Harley & al., 2004) eine abgeleitete und sehr artenreiche Familie innerhalb der Angiospermae (Bedecktsamer) dar. Es handelt sich dabei überwiegend um Kräuter oder (Halb-)Sträucher, selten auch Bäume, mit häufig vierkantigem Stängel und gegenständigen, meist dekussiert angeordneten Blättern. Die typische Infloreszenz ist ein Thyrsus mit cymösen Teilblütenständen und zygomorphen, zweilippigen Blüten. Der Fruchtknoten ist meist vierteilig gespalten mit laminar oder submarginal plazentierten Samenanlagen. Allgemein bekannt sind die Lamiaceae wegen der Verwendung vieler Arten als Gewürz- und Arzneipflanzen. Salbei, Minze, Thymian, Bohnenkraut und Basilikum sind nur einige Vertreter, die hier angeführt werden sollen. Ihre große Bedeutung verdanken sie vor allem dem Vorkommen von ätherischen Ölen, die fast ausschließlich in den subkutikulären Räumen der Drüsenschuppen sowie den Köpfchen der Drüsenhaare abgelagert werden und hauptsächlich Monoterpene (z.B. Menthol, Thymol, Pulegol) oder seltener Sesquiterpene beinhalten (Hegnauer, 1989). Desweiteren kommen z.T. bittere und biologisch vielseitig aktive Diterpene, Triterpene, Iridoide, Kaffeesäurederivate (teilweise mit Bitterstoffeigenschaften) und Flavonoide vor.

Trotz der Wichtigkeit vieler Arten und ihrer Inhaltsstoffe war die Familie seit Linné (1753) weit von einer natürlichen Einteilung entfernt. Vor allem in der zweiten Hälfte des 18. Jahrhunderts wurden neu endeckte Arten von einzelnen Bearbeitern so unterschiedlich auf diverse Gattungen verteilt, dass Lindley (1829) den taxonomischen Zustand der Labiatae sogar als „disgrace of botany“ bezeichnete. Die erste umfassende Bearbeitung von Bentham (1832-36) leistete einen wesentlichen Beitrag zur Klärung der chaotischen Verhältnisse. Vor allem in seiner später modifizierten Form (Bentham, 1848; 1876) hat dieses Konzept bis heute viel von seiner Bedeutung behalten.

1.1 Abgrenzung und infrafamiliäre Gliederung der Lamiaceae

Nicht nur die Unterteilung der Familie sondern auch die Abgrenzung zu den nahestehenden Verbenaceae war lange Zeit unklar. Bis vor ca. 25 Jahren wurden die Lamiaceae als Gruppe verstanden, die durch einen gynobasisch inserierten Griffel charakterisiert ist. Bereits Junell (1934) hatte jedoch darauf hingewiesen, dass die Familie so umgrenzt keine natürliche Einheit darstelle und eher alle Vertreter mit laminarer Plazentation der Samenanlagen und cymösen Infloreszenzen in den Lamiaceae zusammengefasst werden sollten; in die Verbenaceae stellte er alle Taxa mit marginaler Plazentation und racemösen Infloreszenzen. Sein Konzept wurde allerdings wenig beachtet und erhielt erst durch die morphologisch-kladistischen Untersuchungen von Cantino (1992a, b) und verschiedene molekulare Untersuchungen (Wagstaff & al., 1995; Wagstaff & Olmstead, 1997; Wagstaff & al., 1998, s. Abb. 1; Lindqvist & Albert, 2002) neue Unterstützung. Mit der Veröffentlichung von Harley & al. (2004) kann es als gesichert und gemeinhin akzeptiert angesehen werden.

Die infrafamiliäre Unterteilung war wesentlich häufiger Gegenstand von Diskussionen und unterlag zahlreichen Änderungen. Bentham (1832-1836) gliederte die Familie in elf Tribus (Ocimoideae, Menthoideae, Monardeae, Satureineae, Melissineae, Scutellarineae, Prostanthereae, Nepeteae, Stachydeae, Prasieae, Ajugoideae), wobei - wie in vielen späteren Werken auch - noch nicht auf eine durchgehende Verwendung der nomenklatorisch korrekten Endungen geachtet wurde. In seinen späteren Bearbeitungen reduzierte Bentham (1848, 1876) die Anzahl der Untergruppen auf acht Tribus (Ocimoideae, Satureineae, Monardeae, Nepeteae, Stachydeae, Prasieae, Prostanthereae, Ajugoideae). Briquet (1895-97) publizierte ein daran angelehntes, allerdings in Teilen stark abweichendes Konzept, in dem er acht

Unterfamilien anerkannte (Ajugoideae, Prostantheroideae, Prasioideae, Scutellarioideae, Lavanduloideae, Stachydoideae, Ocimoideae, Catopherioideae). Das Verständnis der Gruppen änderte sich grundlegend mit der Arbeit von Erdtman (1945). Anhand von Pollenuntersuchungen schlug er eine Einteilung der Lamiaceae in zwei Unterfamilien vor, die Lamioideae mit tri- oder tetracolpatem, zweikernigem Pollen und die Nepetoideae mit hexacolpatem, dreikernigem Pollen. Dabei war er sich der Probleme bei der Unterteilung der Lamioideae und deren Abgrenzung gegenüber den Verbenaceae durchaus bewusst. Wunderlich (1967) griff die Ideen von Erdtman (1945) auf, bezog neben palynologischen Merkmalen aber zusätzlich die Samenanatomie mit ein. Basierend auf diesen neuen Untersuchungen erweiterte sie die Unterteilung auf sechs Unterfamilien (Prostantheroideae, Ajugoideae, Scutellarioideae, Lamioideae, Catopherioideae, Saturejoideae), wobei die Nepetoideae auf Saturejoideae und Catopherioideae aufgeteilt wurden. Basierend auf ersten kladistischen Analysen morphologisch-anatomischer Daten (Cantino, 1992a, b) präsentierten Cantino & al. (1992) ein deutlich verbessertes Einteilungskonzept, dass von allen bisherigen Vorschlägen deutlich abwich. Es orientierte sich am ehesten an Junell (1934) und Wunderlich (1967) und beinhaltete die Unterfamilien Chloanthoideae, Viticoideae, Teucrioideae, Ajugoideae, Scutellarioideae, Pogostemonoideae, Lamioideae und Nepetoideae. In der Folge war die Gruppe Gegenstand verschiedener molekular-kladistischer Untersuchungen (Kaufmann & Wink, 1994; Wagstaff & al., 1995; Wink & Kaufmann, 1996; Wagstaff & Olmstead, 1997; Olmstead & al., 1998; Wagstaff & al., 1998, s. Abb. 1; Lindqvist & Albert, 2002), in denen die bisherigen taxonomischen Konzepte überprüft wurden.

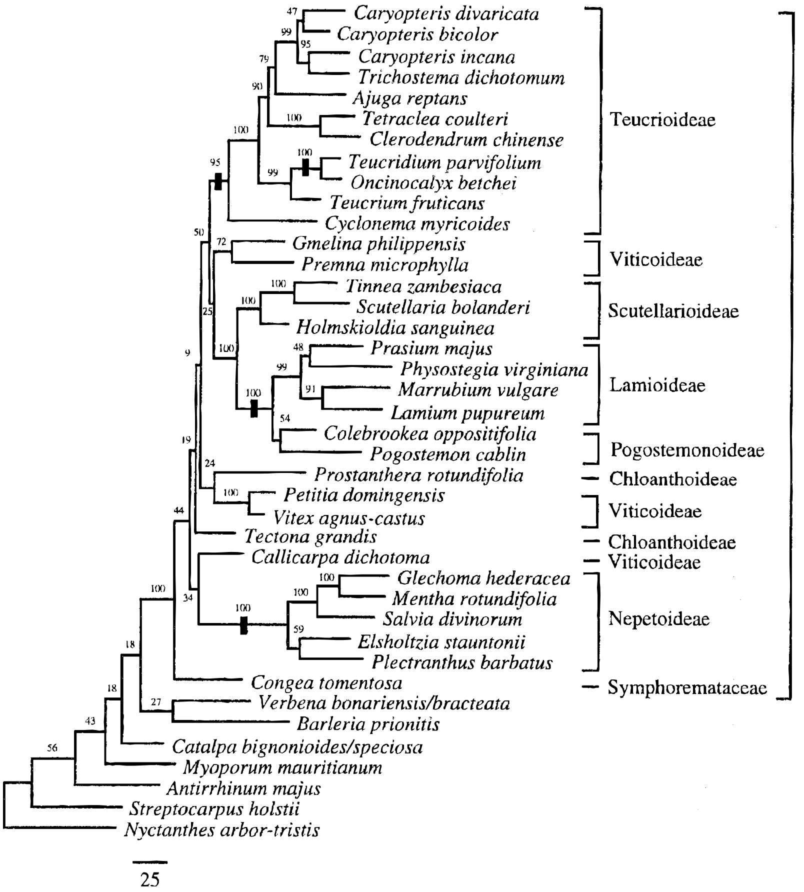

Abb. 1: Molekulare Phylogenie der Labiatae s.l. basierend auf der Analyse von *rbc*L und *ndh*F Sequenzdaten (aus Wagstaff & al., 1998)

In der bisher umfangreichsten Arbeit (Wagstaff & al., 1998, s. Abb. 1) wurden Teucrioideae, Scutellarioideae, Lamioideae, Pogostemonoideae und Nepetoideae als natürliche Gruppen angezeigt, Chloanthoideae und Viticoideae allerdings nicht. Die Symphorematoideae wurden hier noch als eigene Familie (Symphoremataceae) angeführt. Die aktuellste Gliederung von Harley & al. (2004) in Kubitzki´s „Families and Genera of Vascular Plants“ baut im wesentlichen auf die neueren Befunde auf. Es werden sieben Unterfamilien anerkannt: Symphorematoideae, Viticoideae, Ajugoideae (inkl. Teucrioideae), Prostantheroideae (=Chloanthoideae), Scutellarioideae, Lamioideae (inkl. Pogostemonoideae) und Nepetoideae. Wesentliche Unterschiede gegenüber Cantino & al. (1992) sind die Zusammenfassung von Ajugoideae und Teucrioideae sowie Lamioideae und Pogostemonoideae, die Einführung des älteren Namens Prostantheroideae für die bis dahin Chloanthoideae genannte Gruppe, die Einbeziehung der Symphoremataceae in die Lamiaceae und schließlich die Listung der Gattungen *Callicarpa* und *Tectona* als „taxa incertae sedis“ (Sippen unklarer Zugehörigkeit). Durch diesen „Kunstgriff“ löst sich das Problem der Nicht-Monophylie für die Prostantheroideae (*Tectona*) ganz und die Viticoideae (*Callicarpa*) teilweise. Die Autoren betonen jedoch ausdrücklich den vorläufigen Charakter ihrer Einteilung. Da die Viticoideae selbst in ihrer aktualisierten Umschreibung keine natürliche Gruppe darzustellen scheinen und einige Gattungen noch nicht oder nur unbefriedigend zugeordnet werden konnten, ist auch in näherer Zukunft mit Änderungen zu rechnen; die Großgruppen dürften davon allerdings unberührt bleiben. In Tabelle 1 sind die unterschiedlichen Konzepte der oben angeführten Autoren nochmals im Überblick dargestellt.

Bentham 1832-36	Bentham (1848, 1876)	Briquet (1895-1897)
Ajugoideae Melissineae Menthoideae Monardeae Nepeteae Ocimoideae Prasieae Prostanthereae Satureineae Scutellarineae Stachydeae	Ajugoideae Monardeae Nepeteae Ocimoideae Prasieae Prostanthereae Satureineae Stachydeae	Ajugoideae Catopherioideae Lavanduloideae Ocimoideae Prasioideae Prostantheroideae Scutellarioideae Stachyoideae

Erdtman (1945)	Wunderlich (1967)	Cantino & al. (1992)	Harley & al. (2004)
Lamioideae Nepetoideae	Ajugoideae Catopherioideae (=Nepetoideae p.p.) Lamioideae Prostantheroideae Saturejoideae (=Nepetoideae p.p.) Scutellarioideae	Ajugoideae Chloanthoideae Lamioideae Nepetoideae Pogostemonoideae Scutellarioideae Teucrioideae Viticoideae	Ajugoideae (=Teucrioideae) Lamioideae (inkl. Pogostemonoideae) Nepetoideae Prostantheroideae (=Chloanthoideae) Scutellarioideae Symphorematoideae Viticoideae

Tab. 1: Überblick über die wichtigsten Einteilungskonzepte für die Familie der Lamiaceae

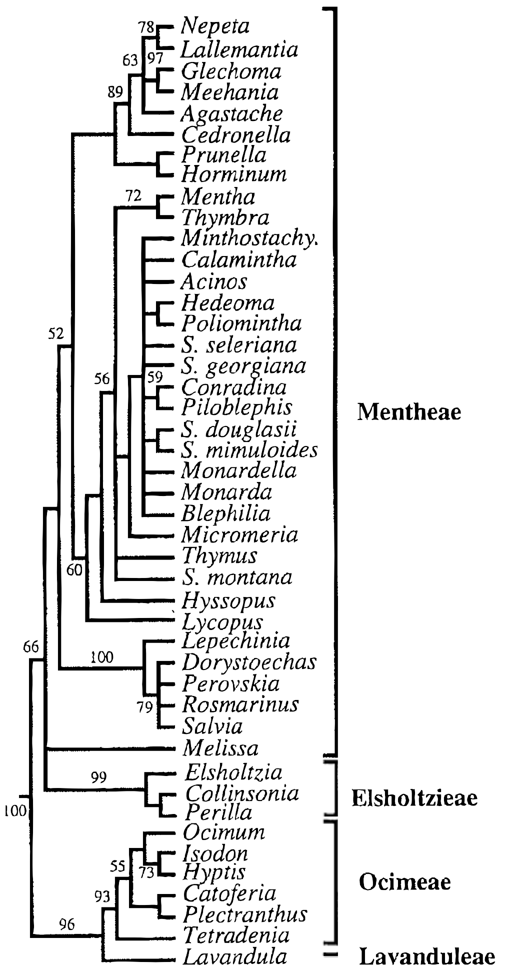

Abb. 2: Phylogenie der Nepetoideae basierend auf cpDNA Restirktionsanalysen, verändert nach Wagstaff & al. (1995).

Nach Harley & al. (2004) sind die Nepetoideae die am klarsten abgegrenzte Gruppe innerhalb der Lamiaceae, sowohl morphologisch als auch molekular. Zum einen bestätigten alle bisher durchgeführten molekularen Untersuchungen die Monophylie der Unterfamilie, zum anderen ist sie auch durch ein Reihe weiterer Merkmale klar abgesetzt. Charakerisiert sind die Nepetoideae v.a. durch hexacolpaten, dreikernigen Pollen, das Vorkommen von Rosmarinsäure und einen „investing embryo" (Martin, 1946), bei dem die Basis der Kotyledonen verlängert und dadurch Hypokotyl und Radicula größtenteils überdeckt sind. Innerhalb der Unterfamilie erhielt die Einteilung von Cantino & al. (1992) in vier Tribus (Mentheae, Elsholtzieae, Ocimeae und Lavanduleae) zusätzliche Unterstützung durch eine cpDNA Restriktionsanalyse von Wagstaff & al., (1995; s. Abb. 2). Harley & al. (2004) erkennen allerdings nur drei Tribus an, die Lavanduleae werden in die Ocimeae eingeschlossen, was nicht im Widerspruch zu den molekularen Befunden steht. Die Gattung *Melissa* wird als unsicher bezüglich ihrer Stellung innerhalb der Mentheae eingestuft. Die morphologische Abgrenzung der Tribus ist eher schwammig und beruht, wie so oft bei höheren taxonomischen Einheiten, eher auf einer Kombination von Charakteren als auf einem gemeinsamen abgeleiteten Merkmal. Die Ocimeae sind durch abwärts gebogene Stamina relativ gut abgesetzt, während die Unterschiede zwischen Elsholtzieae und Mentheae weniger konstant scheinen: Krone eher schwach zweilippig versus Krone deutlich zweilippig und Diskus asymmetrisch versus Diskus symmetrisch (wenn asymmetrisch, dann Krone deutlich zweilippig). Unter den Mentheae sind wiederum drei Subtribus aufgeführt deren morphologische Charakterisierung noch unzureichender ausfällt: Salviinae (*Salvia* u.a.), Nepetinae (*Nepeta* u.a.) sowie Menthinae (*Mentha* u.a.).

1.2 Die Subtribus Menthinae und ihre Charakterisierung

Die Subtribus Menthinae sensu Harley & al. (2004) enthält fast zwei Drittel der Gattungen der Mentheae (43 von 66), allerdings weniger als die Hälfte der Arten (ca. 760 von 2075). Ausserhalb der Menthinae finden sich die Arten allerdings im wesentlichen in zwei Gattungen wieder, *Salvia* und *Nepeta* (>900 bzw. >200 spp. von ca. 1310). Bei den Menthinae handelt es sich um eine beinahe kosmopolitisch verbreitete Gruppe, in den Tropen weichen die Sippen allerdings meist in höhere Lagen mit eher gemäßigtem Klima aus. Morphologisch wird die Gruppe wie folgt beschrieben:

Ausdauernde oder einjährige Kräuter oder Sträucher mit einfachen, selten verzweigten Haaren; Blätter vielgestaltig, selten spießförmig, Blattstiel ungeflügelt, Spreite selten fein rugos. Blüten mit 5—15-nerviger Kelchröhre; Staubblätter 4, das obere Paar länger als das untere, oder Staubblätter auseinander gekrümmt, annähernd gleichlang, oder Staubblätter 2, das untere Paar zu Staminodien reduziert oder fehlend; Staubblätter normalerweise mit 2 Theken, diese normalerweise elliptisch, getrennt oder miteinander verschmolzen, parallel bis auseinanderweisend, Konnektiv oft ausgeprägt; Nektar-Diskus ungeteilt oder oft 4-lappig, mit normalerweise mehr oder weniger gleichen Lappen. Nüsschen oft areoliert.

Zur besseren Übersicht sind die Gattungen der Menthinae in Tabelle 2 aufgelistet. Dabei war der Einschluss einiger Gattungen in die Menthinae ein Kompromiss, mit dem nicht alle Autoren zufrieden waren (R. Harley, pers. Mitt.), zumal er den molekularen Befunden von Wagstaff & al. (1995, s. Abb. 2) nur teilweise entsprach. Die betreffenden Taxa sind in Tab. 2 durch * hervorgehoben und werden in dieser Arbeit aus den Menthinae im engeren Sinn ausgeschlossen. Auf die oben angeführte Umschreibung hat dieser Ausschluss keine weiteren Auswirkungen

Acanthomintha (A.Gray) Benth. & Hook.f. (4)
Blephilia Raf. (3)
Bystropogon L´Hér. (7)
Cleonia L.* (1)
***Clinopodium* L. (100)**
(inkl. *Acinos* Mill., *Calamintha* Mill.)
***Conradina* A.Gray (6)**
Cuminia Colla (1)
***Cunila* D.Royen ex L. (15)**
***Cyclotrichium* (Boiss.) Manden. & Scheng. (8)**
***Dicerandra* Benth. (8-9)**
Eriothymus (Benth.) Schmidt (1)
Glechon Spreng. (6-7)
***Gontscharovia* Boriss. (1)**
***Hedeoma* Pers. (42)**
Hesperozygis Epling (8)
Hoehnea Epling (4)
Hyssopus L.* (2)
Horminum L.* (1)
Kurzamra Kuntze (1)
Lycopus L.* (14)
***Mentha* L. (20)**
(inkl. *Preslia* Opiz)
***Micromeria* Benth. (70)**
Minthostachys (Benth.) Spach (17)
Monarda L. (20)
Monardella Benth. (30)
Neoeplingia Ramamoorthy, Hiriart & Medrano (1)
***Obtegomeria* P.D.Cantino & Doroszenko (1)**
Origanum L. (40)
(inkl. *Majoranum* Mill.)
Pentapleura Hand.-Mazz. (1)
***Piloblephis* Raf. (1)**
Pogogyne Benth. (7)
Poliomintha A.Gray (7)
Prunella L.* (7)
***Pycnanthemum* Michx. (17-21)**
Rhabdocaulon (Benth.) Epling (7)
Rhododon Epling (1)
***Saccocalyx* Coss. & Durieu (1)**
***Satureja* L. (38)**
(inkl. *Euhesperida* Brullo & Furnari;
***Argantoniella* López & Morales)**
Stachydeoma Small (1)
Thymbra L. (4)
***Thymus* L. (220)**
Zataria Boiss. (1)
Ziziphora L. (20)

Tab. 2: Die Gattungen der Menthinae und Artenzahlen aus Harley & al. (2004); mit Fettdruck sind alle Taxa hervorgehoben, die Arten enthalten, die im Laufe der unterschiedlichen Abhandlungen in *Satureja* s.l. eingeschlossen waren. Mit * gekennzeichnete Gattungen sind nach neueren Erkenntnissen nicht Bestandteil der Menthinae s.str. Häufig anerkannte Taxa, die jedoch von Harley & al. (2004) nur als Teil anderer Gattungen akzeptiert werden, sind in Klammern an der entsprechenden Stelle angeführt.

Bei vielen der in Tab. 2 aufgelisteten Gattungen handelt es sich um seltene oder auf ein kleines Areal begrenzte Taxa, von denen bisher nur teilweise Bilder publiziert wurden. Um einen möglichst umfassenden Eindruck von der Gruppe zu geben, wurden die folgenden Abbildungstafeln zusammengestellt und dabei nicht nur ein Vertreter jeder Gattung ausgewählt, sondern möglichst die gesamte Variabilität der jeweiligen Sippen abgedeckt. Zu erwähnen ist, dass auf Bilder der südafrikanischen Vertreter der im Rahmen dieser Arbeit neu beschriebenen Gattung *Killickia* an dieser Stelle verzichtet wurde, da sie sich im Anhang in Manuskript 4 finden. Das Copyright liegt für eigene Bilder beim Verfasser dieser Arbeit, bei allen anderen sind Urheber und Quelle (Homepage) im Folgenden angegeben. CB steht dabei für Christian Bräuchler, BGM für Botanischer Garten München, RJB für Real Jardín Botanico (Madrid), k.A. für keine Angaben. Neben dem Artnamen sind das Ursprungsland und in einzelnen Fällen auch häufig verwendete Synonyme angegeben.

Die Quellen für die einzelnen Abbildungen lauten wie folgt:
Abb. 3 - A: K. L. Bowles; http://www.kenbowles.net/SDwildflowers/ReadMe.htm; **B**: k.A., http://reddeparquesnacionales.mma.es/parques/garajonay/flora/flora050.htma, **C**: D. Tenaglia, http://www.missouriplants.com/Blueopp/Blephilia_ciliata_page.html; **D**: D. Tenaglia, http://www.alabamaplants.com/Pinkopp/Conradina_canescens_page.html; **E**: D. Tenaglia, http://www.missouriplants.com/Blueopp/Cunila_origanoides_page.html; **F**: P. Novoa, http://www.conaf.cl/cd_sitio_web_flora_regional/comprimidos/Plantillas/Archipielago/Cumi nia_eriantha_mata.htm; **G**: CB. **Abb. 4 - A**: CB; **B**: T. Jurkiewicz & M. Szajowski, http://www.szajowski.pl/rosl39.html; **C**: CB; **D**: k.A., http://www.cardoncosasnuestras.com.ar /web724/cosas_nuestras/mag/FOTREVISTA/FOTONUMERO,1/anio_2/numero9/tepampa9.h tml; **E**: J. Duft/MNHP, http://nhp.nris.state.mt.us/plants/SearchPhoto.asp; **F**: D. Alarcón, http://www.chilebosque.cl/shrb/smult.html; **G**: CB. **Abb. 5 - A**: CB; **B**: T. Dirmenci, Türkei, Balikesir; **C**: S. Shirah, http://www.centerforplantconservation.org/ASP/CPC_ProfileImage. asp?FN=1402a; **D**: G. Konings, http://museum.utep.edu/chih/gardens/plants/GtoM/hedeoma costatum.htm; **E**: CB; **F**: J. Maschinski, http://www.centerforplantconservation.org/ASP/CPC _ProfileImage.asp?FN=2159a; **G**: aus Gunckel, H. 2006. Significado de nombres genéricos de alguna splantas de la flora chilena. Chloris chilensis 9(2)d; http://www.chlorischile.cl/ (zu zitieren als Gunckel, H. 1982. Significado de nombres genéricos de algunas plantas de la flora chilena. Academia N° 4. Academia Superior de Ciencias Pedagógicas. 157-180.); **Abb. 6 - A-D**: CB; **E**: M. Kleikamp, http://planto.de/foto-themen.php?Reihe=Gr; **F-G**: CB. **Abb. 7 - A**: CB; **B**: J. Hlasek 6541, www.hlasek.com; **C**: k.A., Davesgarden.com; **D**: K. L. Bowles, http://www.kenbowles.net/SDwildflowers/ReadMe.htm; **E**: A. Schneider, http://www.Swcol oradowildflowers.com; **F**: k.A., http://www.syringa-samen.de/katalog/deutsch/pflanzenkata log/p/poliomintha_longiflora_-_mexikanischer_oregano.html; **G**: E. Saulys, http://www.ct-botanical-society.org/galleries/pycnanthemumvirg.html; **H**: J. R. Manhart, http://www.csdl. tamu.edu/FLORA/imaxxlam.htm; **I**: CB. **Abb. 8 - A**: CB; **B**: G. Lopez, http://www.rjb.csic.es/pdfs/Anales_61(1)_023_026.pdf; **C**: A. Danin, http://www.botanic.co. il/a/catalog.asp?qcat=SATTHM; **D-H**: CB.

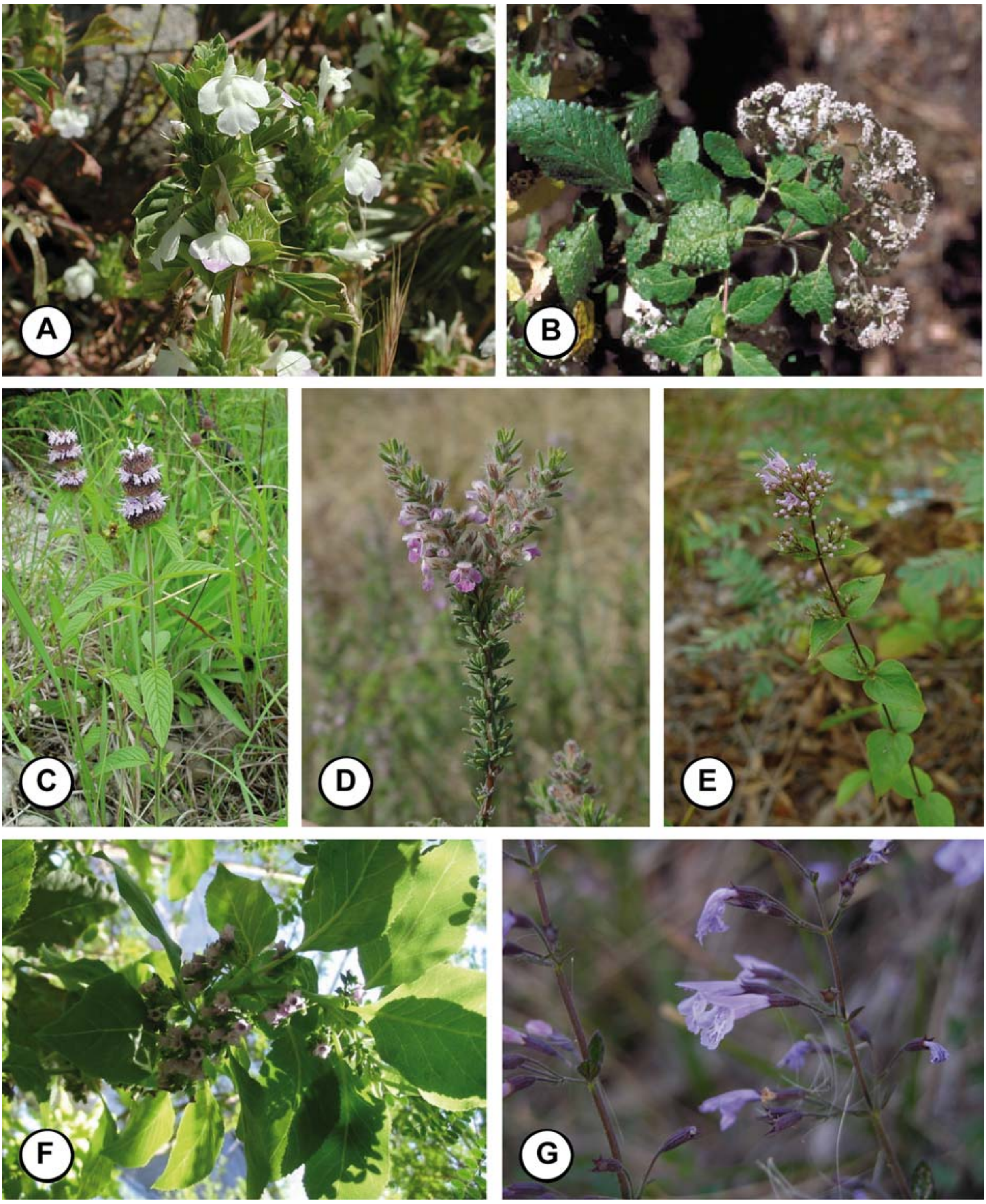

Abb. 3 - A: ***Acanthomintha ilicifolia***, USA, Kalifornien; B: ***Bystropogon canariensis***, Spanien, Kanarische Inseln, La Gomera; C: ***Blephilia ciliata***, USA, Missouri; D: ***Conradina canescens***, USA, Alabama; E: ***Cunila origanoides***, USA, Missouri; F: ***Cuminia eriantha***, Chile, Juan Fernandez Inseln; G: ***Clinopodium menthifolium*** (=***Calamintha sylvatica***), Italien, Ligurien, Seealpen.

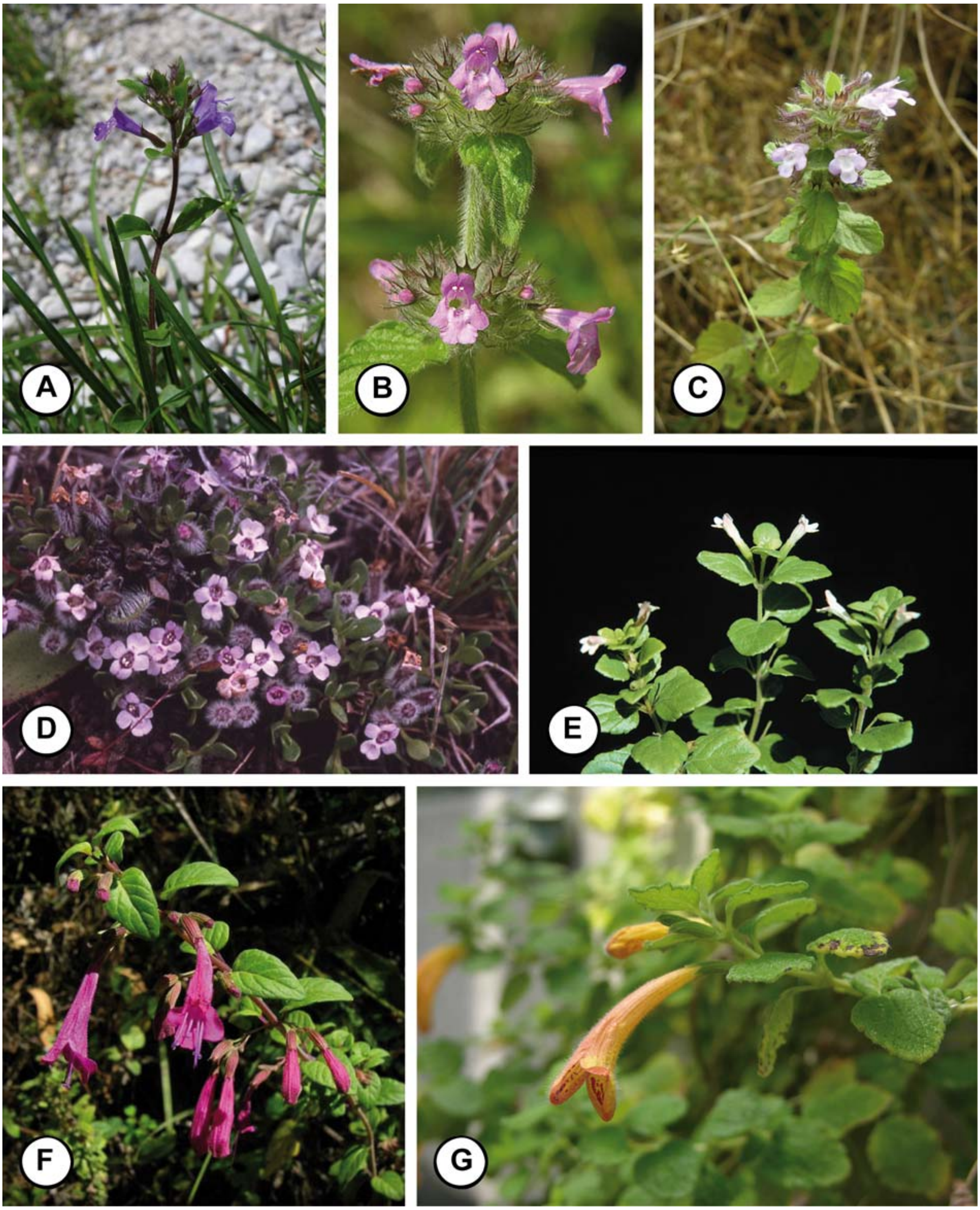

Abb. 4 - A: ***Clinopodium alpinum*** (=***Acinos alpinus***), Deutschland, Bayern; B: ***Clinopodium vulgare***, Tschechien; C: ***Clinopodium uhligii*** var. ***obtusiflorum*** (=***Calamintha pseudosimensis***), Kamerun, Mt. Oku; D: ***Clinopodium darwinii***, Chile; E: ***Clinopodium douglasii***, USA, Montana; F: ***Clinopodium multiflorum***, Chile; G: ***Clinopodium tomentosum***, Ecuador, kultiviert im BGM.

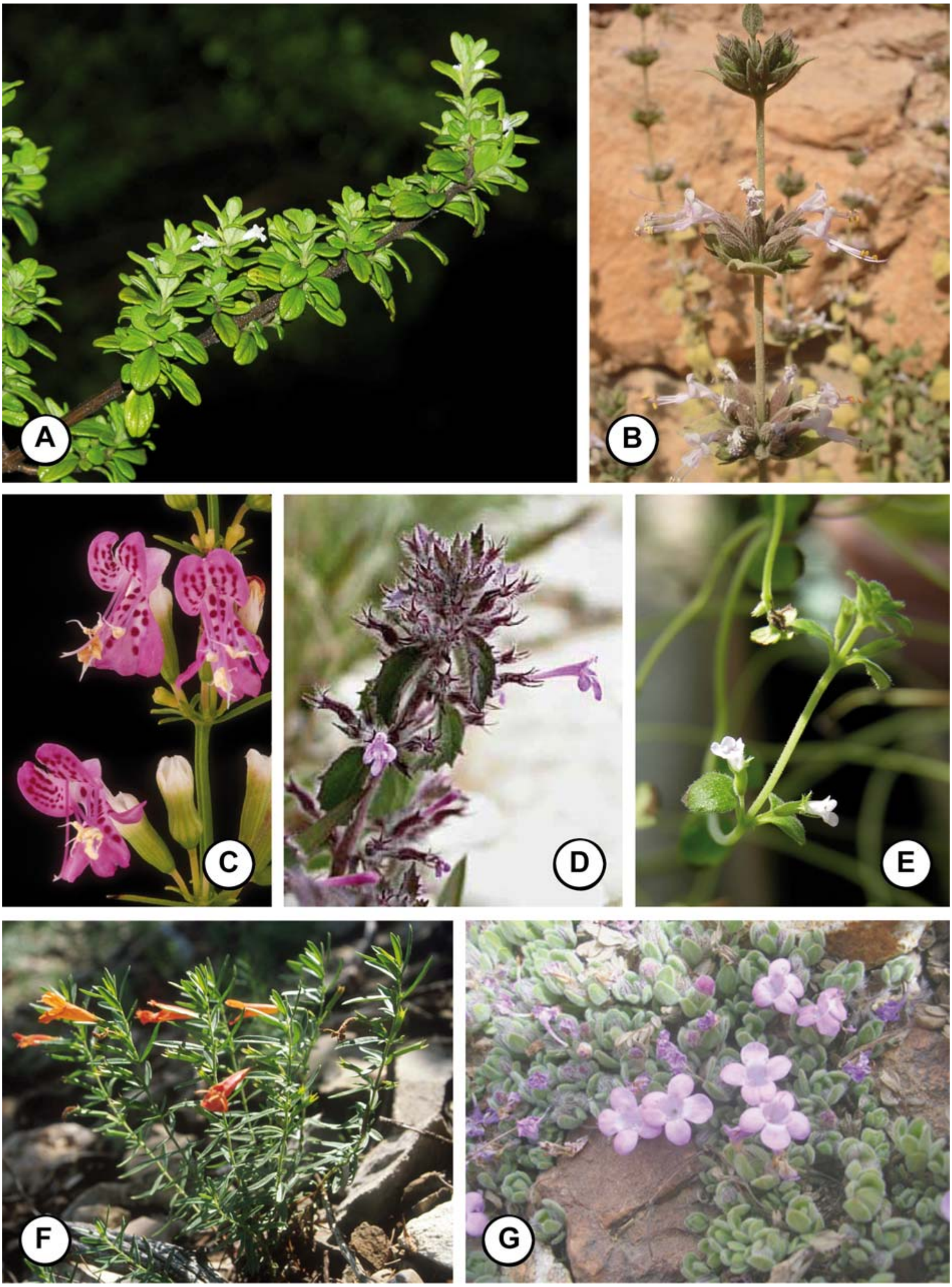

Abb. 5 - A: ***Clinopodium vimineum***, Costa Rica?, kultiviert im Botanischen Garten Bogota, Kolumbien; B: ***Cyclotrichium leucotrichum***, Türkei; C: ***Dicerandra cornutissima***, USA; D: ***Hedeoma costatum***, USA, New Mexico; E: ***Hedeoma mandoniana***, Bolivien, kultiviert im BGM; F: ***Hedeoma todsenii***, USA, New Mexico; G: ***Kurzamra pulchella***, Chile, Atacama-Wüste.

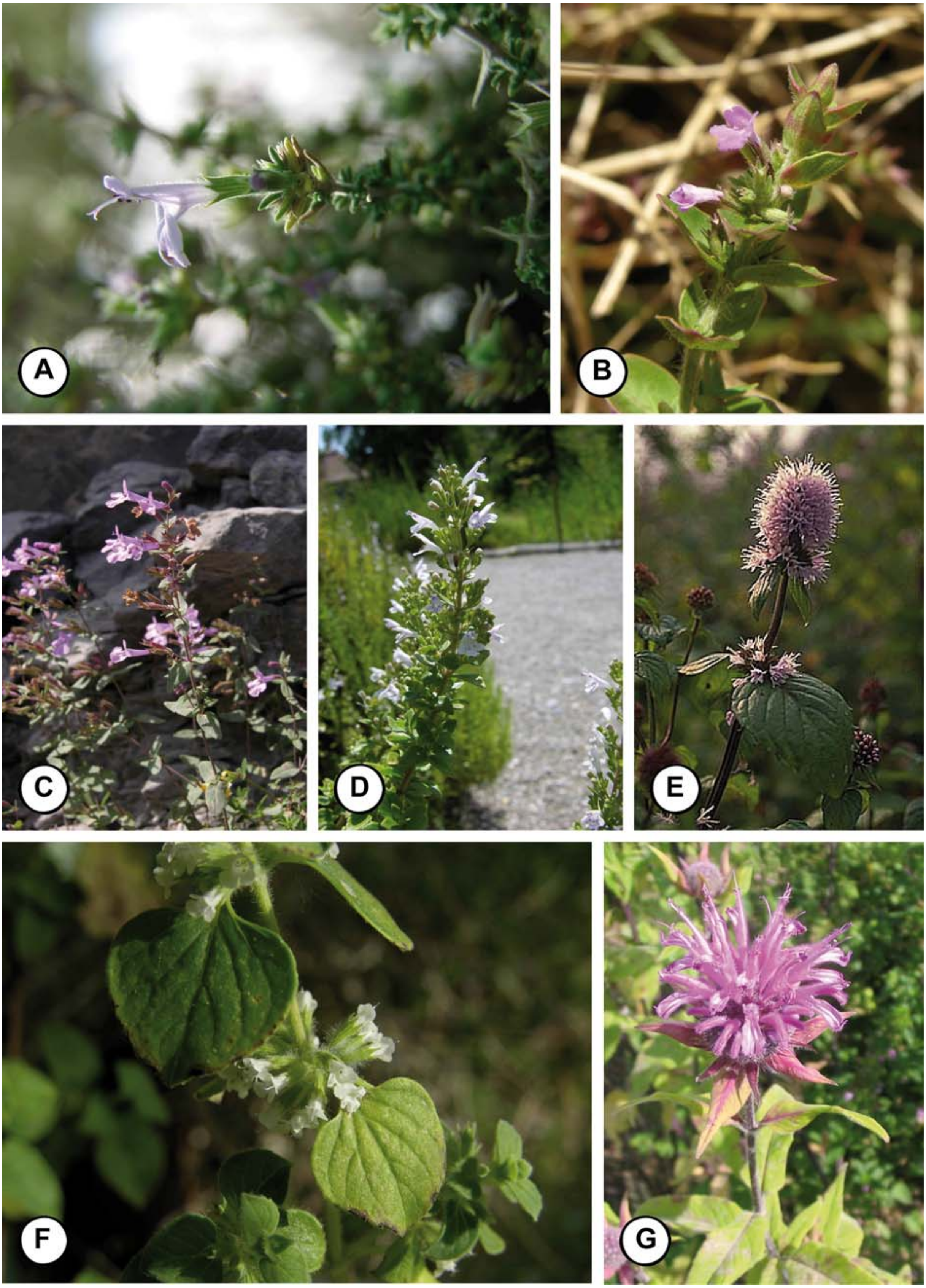

Abb. 6 - A: ***Micromeria inodora***, Spanien, Balearische Inseln, Formentera, kultiviert im BGM; B: ***Micromeria imbricata***, Kamerun, Mt. Oku; C: ***Micromeria marginata***, Italien, Ligurien, Seealpen; D: ***Micromeria dalmatica***, Serbien und Montenegro, kultiviert im BGM; E: ***Mentha aquatica***, Deutschland; F: ***Minthostachys spicata***, Ecuador, kultiviert im BGM; G: ***Monarda bradburiana***, USA, kultiviert im BGM.

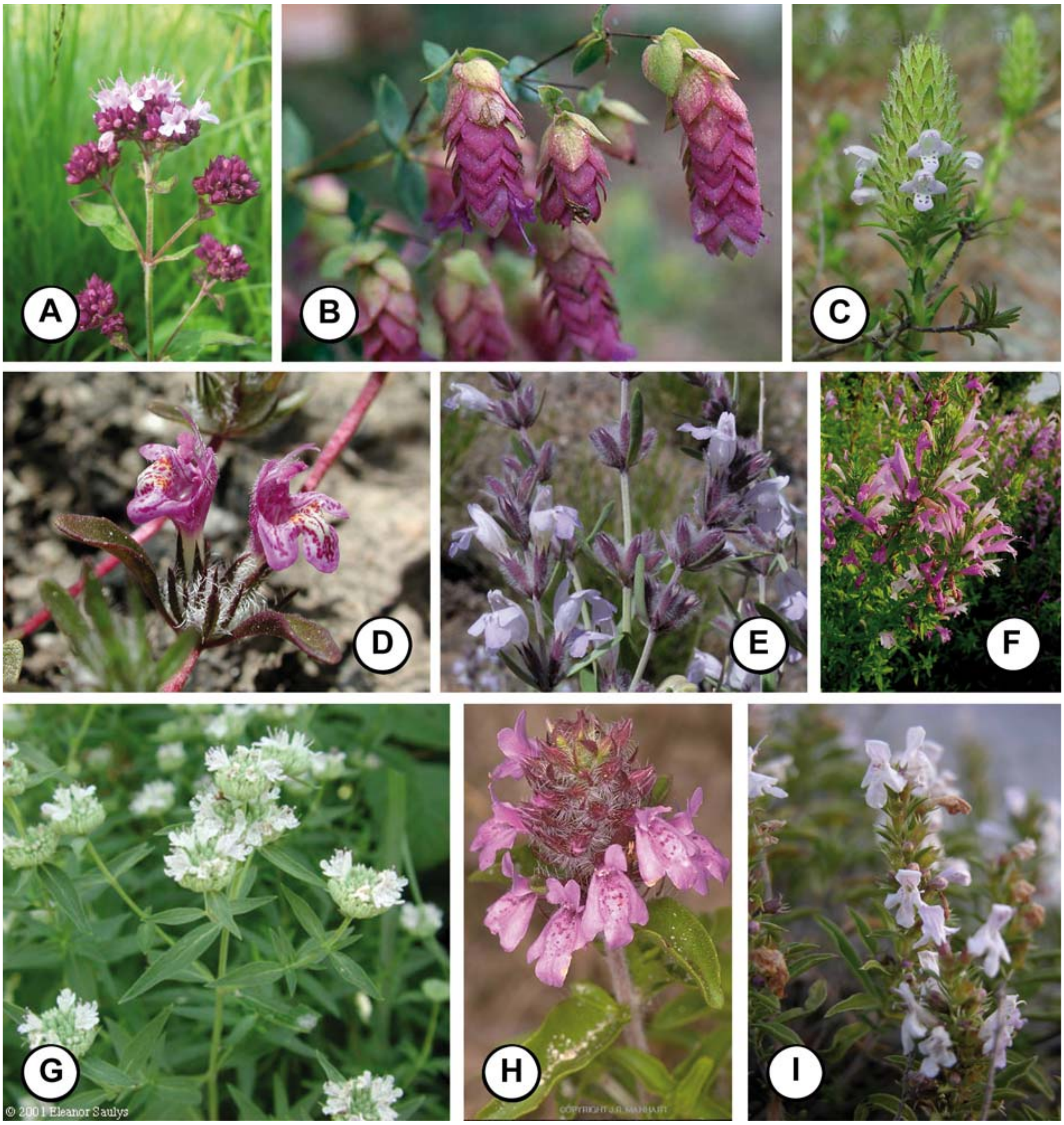

Abb. 7 - A: ***Origanum vulgare***, Deutschland, Bayern; B: ***Origanum scabrum***, Greece; C: ***Piloblephis rigida***, USA; D: ***Pogogyne abramsii***, USA, Kalifornien; E: ***Poliomintha incana***, USA, Utah; F: ***Poliomintha longiflora***, Mexiko, kultiviert von der Gärtnerei Syringa, Deutschland; G: ***Pycnanthemum virginianum***, USA; H: ***Rhododon ciliatum***, USA, Texas; I: ***Satureja montana***, Italien, Ligurien, Seealpen.

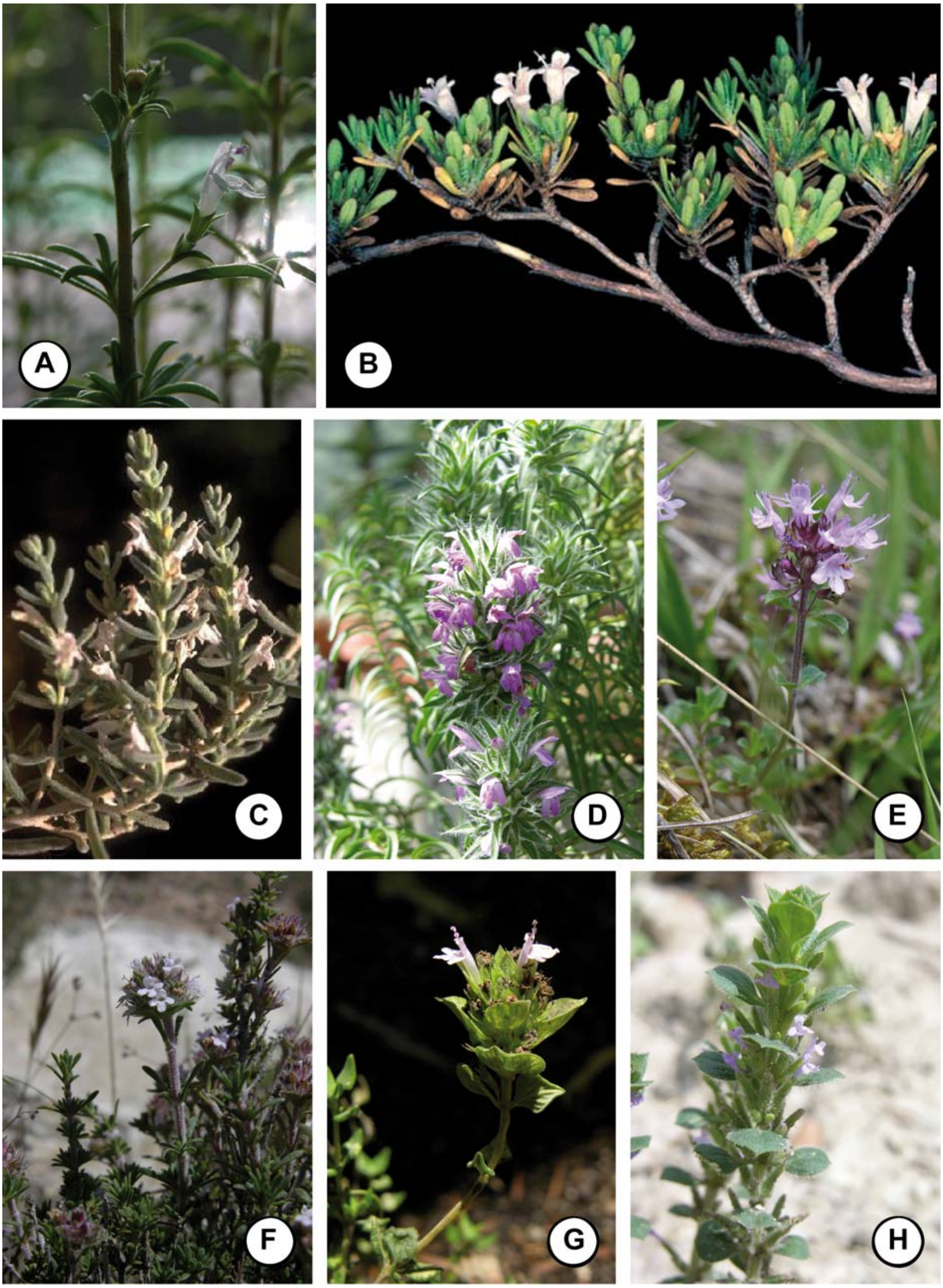

Abb. 8 - A: ***Satureja cuneifolia***, Italien, Toskana, kultiviert im BGM; B: ***Satureja salzmannii*** (***Argantoniella salzmannii***), Spanien, Cadiz; C: ***Satureja thymbrifolia***, Israel; D: ***Thymbra spicata***, Türkei, kultiviert im BGM; E: ***Thymus pulegioides***, Deutschland, Bayern; F: ***Thymus lacaitae***, Spanien, Madrid; G: ***Thymus camphoratus***, Spanien, kultiviert im RJB Madrid; H: ***Ziziphora hispanica***, Spanien, Madrid.

1.3 Historischer Überblick zur Taxonomie des *Satureja*-Komplexes

Eine der größten Gruppen innerhalb der Subtribus Menthinae bildet ein traditionell eher vage definierter Komplex, der weithin unter dem Namen *Satureja*-Komplex oder *Satureja* s.l. (Bohnenkraut und Verwandte, engl. savory) bekannt ist. Arten dieser Gruppe finden sich auf der ganzen Welt (mit Ausnahme Australiens). Die Taxonomie ist seit Linné (1753) so komplex geworden, dass ein vollständiger Überblick hier nicht gegeben werden kann. Im folgenden soll daher nur auf Werke des 18. und 19. Jahrhunderts eingegangen werden, die für die sich heute bietende Situation von weitreichender Bedeutung sind. In Tabelle 2 sind ausserdem zur Verdeutlichung alle Gattungen hervorgehoben, aus denen Arten zumindest zeitweise in *Satureja* eingeschlossen wurden.

Linné (1753) verteilte die Arten des Komplexes auf die vier Gattungen *Satureja*, *Clinopodium*, *Melissa* und *Thymus*. *Satureja* (9 spp.) beinhaltete u.a. noch Arten von *Cunila*, *Pycnanthemum* und *Thymus*. *Clinopodium* bestand aus der Typusart *C. vulgare* sowie einer *Pycnanthemum*- und einer *Hyptis*-Art. *Micromeria* in der heutigen Umschreibung, war verteilt auf *Satureja* und *Melissa*, in *Thymus* und *Melissa* fanden sich auch *Clinopodium* Arten. Nur ein Jahr später schlug Miller (1754) in der 4. Ausgabe seines „Gardener´s Dictionary“ *Acinos* und *Calamintha* neu vor und listete daneben noch *Satureja* und *Clinopodium* (noch inkl. je einer Art von *Nepeta*, *Pycnanthemum* und *Acinos*). Moench (1794) war der erste, der eine Trennung der heutigen Gattungen *Satureja* und *Micromeria* vorschlug, nannte letztere jedoch *Sabbatia*. Auf Grund der früheren Beschreibung einer Gattung (nahezu) gleichen Namens (*Sabatia*) innerhalb der Gentianaceae (Adanson, 1763), schuf Moench (1794) damit allerdings einen illegitimen Namen. Um die neuweltlichen *Satureja* Arten besser unterzubringen, beschrieben Ruiz & Pavon (1794) *Gardoquia*, was von Persoon (1807) aufgegriffen wurde. Allerdings findet sich bei diesem *Micromeria* nicht als eigenes Taxon, sondern verteilt auf *Thymus* und *Satureja*. In beiden Gruppen waren auch neuweltliche *Clinopodium* Arten eingeschlossen, die restlichen Arten dieser Gattung waren auf *Acinos* und *Melissa* verteilt. Um die aberrante, neuweltliche *Satureja viminea* L. (heute ebenfalls *Clinopodium*) besser zu platzieren, beschrieb Willdenow (1811) die monotypische Gattung *Xenopoma*.

Dieser Neuerungen ungeachtet, erschienen spätere Auflagen von Linné´s „Species Plantarum“ bis 1825 mit praktisch unverändertem Gattungsarrangement, was die bestehende taxonomische Unklarheit sicherlich noch verstärkte. Einen ersten Schritt in Richtung eines verlässlicheren Systems machte Bentham 1829 mit der Ersetzung von Moench´s (1794) illegitimem Namen *Sabbatia* durch *Micromeria*, gefolgt von seinem fundamentalen Werk „Labiatarum Genera et Species“ (1832-1836). Darin wurden *Satureja*, *Micromeria* und *Gardoquia* getrennt, sowie *Melissa* sehr weit gefasst, d.h. inkl. *Clinopodium*, *Calamintha*, *Acinos* und einer Art von *Gardoquia*. *Satureja* beinhaltete noch eine Art der heutigen *Micromeria* sect. *Pseudomelissa* (*Satureja rupestris* = *Micromeria thymifolia*), die als überleitend zu *Melissa* angesehen wurde, sowie die nordamerikanische *Satureja rigida*, später von Rafinesque (1838) in die monotypische Gattung *Piloblephis* ausgegliedert. Innerhalb von *Micromeria* wurden drei Sektionen anerkannt, *Hesperothymus* (inkl. Arten von *Conradina* und *Clinopodium*), *Piperella* (*Micromeria* s.str., *Xenopoma* und die australischen Vertreter von *Mentha*) und *Pseudomelissa*. In der Bearbeitung der Labiatae für DeCandolle´s „Prodromus“ (Bentham, 1848) wurde das Konzept dann weiter verfeinert: *Melissa* und *Calamintha* wurden getrennt, letztere enthielt *Clinopodium*, *Acinos* sowie je eine Art von *Conradina* und *Gardoquia*. *Satureja rupestris* fand ihren Platz in *Micromeria* sect. *Pseudomelissa*, *Piloblephis* blieb – unter Zweifel – in *Satureja* eingeschlossen. *Xenopoma* wurde als Sektion von *Micromeria* anerkannt, dabei stellte er *M. bonariensis* in die Nähe von *Hedeoma*, die Gattung, zu der sie heute (als Synonym) gerechnet wird. Die australischen Arten wurden in *Mentha* eingruppiert, die Sektion *Piperella* beinhaltete u.a. zwei heutige

Cyclotrichium Arten sowie *M. capitellata* (später in der Sektion *Pseudomelissa*). In seiner letzten umfassenden Arbeit (Bentham, 1876) blieb dieses System weitgehend unverändert, allerdings schloss er *Saccocalyx*, von Cosson & Durand (1853) als monotypische Gattung aus dem Hochland Algeriens beschrieben, in *Satureja* ein und ergänzte die bis dahin rein neuweltliche *Micromeria* sect. *Hesperothymus* um eine Art aus Südafrika (*M. pilosa*). Die Gattung *Cuspidocarpus*, beschrieben von Spennen (1843) für *Satureja rupestris* (heute ein Synonym von *Micromeria thymifolia*), wurde in die Sektion *Pseudomelissa* eingeschlossen (*M. rupestris*). Boissier (1879) stellte in seiner „Flora Orientalis“ für die neu beschriebene *Micromeria cymuligera* die Sektion *Cymularia* innerhalb *Micromeria* auf und schuf innerhalb von *Calamintha* die Sektion *Cyclotrichium*, in der die zwei oben erwähnten Arten aus Bentham´s (1848) *Micromeria* sect. *Piperella* platziert wurden. Mandenova & Schengelia (1953) erhoben diese Gruppe später auf Gattungsniveau, was heute noch akzeptiert ist.

Die sich zum Teil widersprechenden Ansichten über die Gattungsunterteilung veranlassten Kuntze (1891) als ersten dazu *Satureja*, *Micromeria*, *Calamintha* und *Clinopodium* zu vereinigen und zwar unter letzterem Namen. Seine Auffassung wurde von den meisten Labiaten-Forschern jedoch schlicht übergangen oder wenig beachtet, möglicherweise aufgrund des zwar sehr umfassenden, dabei aber etwas unübersichtlichen Charakters seines Werkes „Revisio Generum Plantarum“.

Von wesentlich größerer Bedeutung war Briquet´s (1896) Bearbeitung für Engler & Prantl´s „Die Natürlichen Pflanzenfamilien“. Darin wurden ebenfalls alle Gattungen vereinigt, diesmal allerdings unter *Satureja*, worin auch der Name *Satureja*-Komplex oder *Satureja* s.l. begründet liegt. Die 14 Sektionen, die Briquet (1896) unter *Satureja* listet (*Tragoriganum*, *Pycnothymus* (=*Piloblephis*), *Sabbatia*, *Cymularia*, *Piperella*, *Cyclotrichium*, *Xenopoma*, *Hesperothymus*, *Gardoquia*, *Pseudomelissa*, *Calamintha*, *Calomelissa*, *Clinopodium*, *Acinos*) spiegeln nur zum Teil die Gruppen vorheriger Abhandlungen wider. So sind in Sektion *Sabbatia* z.B. *Satureja* und *Micromeria* Arten vereinigt. Damit wurde der Grund für die Einführung von *Sabbatia* durch Moench (1794) nicht berücksichtigt, der seine Gattung gerade zur Abgrenzung der beiden Taxa errichtet hatte. Briquet´s (1896) *Piperella* enthält entgegen Bentham (1848) nur zwei Arten statt 39, *Saccocalyx* wird wieder von *Satureja* abgetrennt.

1.4 Einfluß unterschiedlicher taxonomischer Konzepte des *Satureja* Komplexes auf Florenwerke des 20. Jahrhunderts

Aus dem oben skizzierten historischen Abriss kann man zweifelsohne die Bearbeitungen von Bentham (1848) und Briquet (1896) als die beiden einflussreichsten und bedeutendsten herausheben. Im 20. Jahrhundert wurden diese beiden konträren Ansätze von Autoren unterschiedlicher Floren parallel verfolgt. Vor allem in Europa und Asien folgten Florenbearbeiter überwiegend Bentham (1848). Die bekanntesten Beispiele hierfür sind wohl die Flora der UdSSR (Schischkin, 1954), „Flora Europaea“ (Ball & Getliffe, 1972;), „Flora of Turkey“ (Davis, 1982) und „Flora Iranica“ (Rechinger, 1982). Bereits Kudo (1929) folgte für die Bearbeitung der ostasiatischen Labiatae dagegen Briquet (1896) und gruppierte die relevanten Taxa in dessen *Satureja*-Sektionen *Sabbatia* und *Clinopodium*, schuf allerdings für zwei Arten (*Micormeria barosma* und *M. euosma*) aus Yünnan die neue Sektion *Barosma*. Viel später griffen auch Greuter & al. (1986) für die „MedChecklist“ das Konzept von *Satureja* s.l. (Briquet, 1896) auf, was allerdings auf Grund der langen Tradition einer engeren Sippenauffassung im Bearbeitungsgebiet für heftige Debatten sorgte. In Afrika wurde nur zu Beginn für die „Flora of Tropical Africa“ (Baker, 1900) Bentham (1848) gefolgt. Spätere Bearbeitungen hatten einen regional meist beschränkteren Fokus und bevorzugten angesichts der geringen Artenzahl in den jeweiligen Gebieten und der Schwierigkeiten, diese in eine der kleineren Gattungen einzuordnen, das bequemere Konzept von *Satureja* s.l. (z.B. Brenan, 1954; Killick, 1961; Quezel & Santa, 1963; Seybold, 1988). In der Neuen Welt wurden zunächst noch enge Gattungsgrenzen bevorzugt (z.B. Small, 1903); mit Carl Epling´s Arbeiten über die nord- und südamerikanischen Arten von *Satureja* s.l. (Epling, 1927; Epling & Jativa, 1964, 1966) setzte sich allerdings weithin Briquet´s Ansatz durch.

1.5 Neuere Arbeiten an den Menthinae und dem *Satureja* Komplex

Wie dargelegt konnte sich keines der beiden konkurrierenden Systeme durchsetzen, was zu einer hohen Zahl von Synonymen und nomenklatorischen Inkonsistenzen führte. Doroszenko (1986) unternahm in seiner Doktorarbeit einen eindrucksvollen Versuch, die Gruppe zum ersten Mal seit Briquet (1896) weltweit zu revidieren. Er bevorzugte dabei einen engen Gattungsbegriff, veränderte die Umschreibung vieler Taxa, setzte in Vergessenheit geratene Namen wieder ein und schlug auch einige neue Gattungsnamen vor. Insgesamt verteilte er alle „seine“ Gattungen auf vier informelle Gruppen:

Satureioid genera (*Satureja*, *Gontscharovia*, *Euhesperida*),
Micromerioid genera (*Micromeria*, „Brenaniella“, „Killickia“),
Calaminthoid genera (*Calamintha*, *Clinopodium*, *Acinos*, *Cyclotrichium*) sowie
American genera (*Diodeilis*, „Hesperothymus“, *Gardoquia*, „Montereya“, „Obtegomeria“, *Piloblephis*, *Xenopoma*).

Leider wurde diese wichtige Arbeit, mit Ausnahmen einer Art- und einer Gattungsbeschreibung (Davis & Doroszenko, 1988, Cantino & Doroszenko, 1998) nie im gesamten Umfang publiziert. Daher hatte sie auch keine weitreichenderen Auswirkungen auf das gängige taxonomische Konzept.
Wagstaff & al. veröffentlichten 1995 die Ergebnisse einer ersten molekular-phylogenetischen Untersuchung der Nepetoideae basierend auf Restriktionsanalysen der Chloroplasten-DNA. Darin wurde klar gezeigt, dass *Satureja* im weitesten Sinn als paraphyletisch bezüglich einiger alt- und neuweltlicher Gattungen anzusehen ist, u.a. *Thymbra*, *Mentha*, *Monardella*, *Monarda*, *Hedeoma*. In der Folge transferierten Cantino & Wagstaff (1998) die nordamerikanischen *Satureja*-Arten in *Clinopodium*. Obwohl die Autoren einräumten, dass es sich dabei um eine vorläufige Eingruppierung handle, trafen sie damit, nach morphologischen und phylogenetischen Aspekten die natürlichen Verhältnisse besser, als alle bisherigen Konzepte. Die Gattung *Obtegomeria*, ursprünglich auch in *Satureja* s.l., wurde aus dieser Gruppe wenig später ausgeklammert (Cantino & Doroszenko, 1998). Analog zu den nordamerikanischen Taxa (Cantino & Wagstaff, 1998) wurden die übrigen neuweltlichen *Satureja* s.l. Arten von Govaerts (1999) und Harley & Granda (2000) ebenfalls in *Clinopodium* überführt, um eine einheitliche Linie in der Nomenklatur der Gruppe beizubehalten. Innerhalb von *Satureja* im engeren Sinn ist ausserdem die Arbeit von Lopez (1981) zu nennen, der basierend auf rein morphologisch-anatomischen Untersuchungen die aberrante Sektion *Salzmannii* abtrennte und sie später zusammen mit Morales (Lopez & Morales, 2004) in die monotypische Gattung *Argantoniella* auslagerte. Alle diese neueren Arbeiten flossen schließlich in die Bearbeitung der Lamiaceae für Kubitzki´s „Families and Genera of Vascular Plants“ durch Harley & al. (2004) mit ein. Ihre Gattungsumgrenzungen unterscheiden sich dabei allerdings in einigen Punkten von bisherigen Konzepten (vgl. Tab. 2). Besonders ist die Auffassung der Gattung *Clinopodium*, in welche die neuweltlichen *Satureja* s.l. Arten und, entsprechend Stace (1991), *Acinos* und *Calamintha* gestellt sind. Die monotypischen Gattungen *Euhesperida*, beschrieben von Brullo & Furnari (1979), und *Argantoniella* wurden in *Satureja* im engeren Sinne gruppiert.

1.6 Fragestellung und Zielsetzung

In den letzten zehn Jahren hat sich gezeigt, welche wichtige Rolle molekulare Analysen bei der Aufklärung der Verwandschaftsverhältnisse innerhalb Lamiaceae (s. 1.1) und *Satureja* s.l. (s. 1.3 und 1.4) spielen können. Bisherige Untersuchungen basierten in Anbetracht der Gattungs-/Artenzahl innerhalb der Nepetoideae auf einer eingeschränkten Stichprobenzahl. Bei den berücksichtigten Gattungen wurde zudem auf den Einbezug isolierter Gruppen verzichtet. Aufgrund der schlechten Auflösung der Phylogenien waren die gezogenen Schlussfolgerungen noch eher provisorisch. In der vorliegenden Arbeit sollte daher ein möglichst breites Spektrum der Diversität von *Satureja* s.l. molekular untersucht werden. Basierend auf Proben von Vertretern möglichst vieler der im Lauf der taxonomischen Historie anerkannten Gruppen (Gattungen, Sektionen etc.), sollte eine möglichst umfassende und aussagekräftige Phylogenie basierend auf plastidären (*trn*K, *trn*L-F) und nukleären Sequenzen (ITS) erstellt werden. Ein weiterer Aspekt war die Methodenoptimierung, d.h. Verbesserung der DNA-Isolationsprotokolle, Primeranpassung/Design neuer Primer und schließlich Anpassung der PCR Strategie an die teilweise schlechte Qualität des zur Verfügung stehenden Materials. Aufbauend auf den rekonstruierten Phylogenien sollten folgende Aspekte besonders berücksichtigt werden:

- Decken sich die Gruppen in den Phylogenien mit einem der bisherigen taxonomischen Konzepte?

- Wie natürlich sind die aktuellsten Einteilungen nach Doroszenko (1986) und Harley & al. (2004)?

- Sind *Micromeria* und *Clinopodium* in ihrer derzeitigen Umschreibung monophyletisch und kann man Hypothesen zur raum-zeitlichen Entfaltung der Gattungen aufstellen?

- Lassen sich auf Basis der molekularen Analysen Charaktere neu bewerten um einzelne Gattungen innerhalb *Satureja* s.l. besser voneinander abzugrenzen und schließlich auch die Nomenklatur zu präzisieren?

2. Ergebnisse und Diskussion

2.1 Materialbeschaffung

Im Rahmen der vorliegenden Dissertation wurden phylogenetische Untersuchungen an der Subtribus Menthinae unter besonderer Berücksichtigung des *Satureja* s.l.-Komplexes durchgeführt und deren Ergebnisse mit bestehenden taxonomischen Konzepten verglichen. Distinkte Linien der Phylogenie wurden systematisch charakterisiert und teilweise taxonomisch bearbeitet. Besonderes Augenmerk galt ausserdem der Merkmalsevolution, sowie der Biogeographie und Ausbreitungsgeschichte der einzelnen Gattungen. In ausgewählten Gruppen wurde versucht einen Einblick in rezente Artbildungsprozesse zu erhalten. Die Taxa der Menthinae sind, wie eingangs erwähnt, weltweit verbreitet und einige Arten kommen nur in sehr entlegenen oder schlecht zugänglichen Gegenden vor. Damit war auch zu erwarten, dass es bei der Materialbeschaffung Schwierigkeiten geben würde. Manche Proben wurden von in Kultur befindlichen Pflanzen aus verschiedenen Botanischen Gärten (Berlin, Frankfurt, Freiburg, München, Wien) andere auf zahlreichen Sammelreisen (Kreta, Teneriffa, Türkei, Kamerun, Südafrika) beschafft. Zusätzliches Material wurde von verschiedenen Botanikern anderer Institute gesammelt und zur Verfügung gestellt. Der Großteil der Proben wurde allerdings von Herbarbelegen abgenommen, wobei überwiegend auf Material der Botanischen Staatssammlung München (M) und des Herbariums des Instituts für Systematische Botanik der LMU München (MSB) zurückgegriffen werden konnte. Durch Besuch verschiedener anderer Herbarien (B, BM, C, E, FR, HAL, JE, K, LZ, NU, P, STU, TUB, W, WU; Herbariumakronyme hier und im Folgenden gemäß Holmgren & Holmgren, 1998) und nicht zuletzt durch das Einverständnis der zuständigen Sammlungsdirektoren bzw. Kuratoren zur Probennahme war es möglich, Lücken in der Artauswahl für die phylogenetische Untersuchung zu schließen.

Aus den angeführten Gründen konnte erst im fortgeschrittenen Stadium der Arbeit ein relativ vollständiges Probensampling erreicht werden. Zudem ergaben sich während der Bearbeitung zahlreiche neue Fragestellungen.

2.2 Methodenoptimierung

Bei der DNA-Isolierung ergaben sich Probleme, bedingt durch die für Lamiaceae typische hohe Konzentrationen an Sekundärstoffen (äther. Öle, Gerbstoffe), so dass ein modifiziertes Protokoll (Bräuchler & al., 2004) entwickelt werden mußte, um PCR fähige DNA zu erhalten. Als geeignete Marker für phylogenetische Untersuchungen auf infra- und supragenerischer Ebene haben sich vor allem die hier verwendeten Regionen des Plastoms *trn*K und *trn*L-F erwiesen. Um Vergleichsdaten eines Markers aus dem Kern-Genom zu erhalten, wurde auch die häufig verwendete Internal Transcribed Spacer Region (ITS 1, 5,8s rDNA, ITS 2) als Bestandteil des ribosomalen Operons miteinbezogen. Im Gegensatz zu *trn*L-F ergab jedoch die Amplifikation mit den in der Literatur zitierten Standardprimern bei *trn*K (Johnson & Soltis, 1994) und ITS (White & al., 1990) häufig kein Produkt. Dies wurde je nach Ursache auf verschiedene Weise gelöst. Die zu amplifizierende *trn*K Region hat eine Länge von über 2500 bp, bei Extraktion aus Herbarmaterial war allerdings die DNA oft zu stark degradiert um Fragmente einer solchen Länge zu erhalten. Ausserdem reichte die Leseweite bei Sequenzierungen nicht aus, den gesamten Bereich abzudecken. Daher wurde ein Set aus 10 internen Primern konstruiert, um den Bereich in mehreren kleineren Teilstücken zu amplifizieren und zu sequenzieren. Alle verwendeten Primer sind in einer Tabelle in Manuskript 1 zusammengefasst. Die ITS Region konnte auch bei Verwendung eines optimierten Primerpaares (leu 1, aITS 4) häufig nicht amplifiziert werden und zwar teilweise unabhängig von der Qualitlät des Ursprungsmaterials. Dies konnte in manchen Fällen durch die Verwendung einer neuartigen Polymerase mit sehr hoher DNA-Bindeaffinität (Phusion$^{\text{TM}}$, s. Manuskript 6) behoben werden, weitere Lücken in der Probenabdeckung wurden durch Einbeziehung bereits in GenBank publizierter Sequenzen geschlossen. Dabei waren von einigen dieser Akzessionen keine plastidären Daten verfügbar. Für die vorliegende Arbeit war es zudem leider nicht möglich entsprechendes Pflanzenmaterial zu erhalten um diese Sequenzen selbst zu generieren. Insgesamt war die Abdeckung auf Artebene im ITS Datensatz trotz der Ergänzungen geringer als bei den Plastidenmarkern.

2.3 Manuskripte

Die grundlegenden Ergebnisse der hier vorliegenden Arbeit sind in den einzelnen Veröffentlichungen (Manuskripte 1-6) dargelegt und ausführlich diskutiert. Einige wesentliche Punkte zu Material und Methoden wurden zusätzlich vorangehend aufgeführt. Zur besseren Übersicht folgt zu jeder Veröffentlichung eine kurze deutschsprachige Zusammenfassung sowie ein abschließender Ausblick auf weitere Forschungsansätze.

2.3.1 Zusammenfassung Manuskript 1: Bräuchler, C., Meimberg, H., Abele, T. & Heubl, G. 2005: Polyphyly of the genus *Micromeria* (Lamiaceae) – evidence from cpDNA sequence data. Taxon 54(3): 639-650.

Die Arbeiten zum ersten Manuskript wurde begleitend zum DFG geförderten Projekt „Radiation der Gattung *Micromeria* auf den Kanarischen Inseln“ (SPP-1127 „Radiationen – Genese biologischer Diversität) durchgeführt. Als Grundlage für diese und weitere Arbeiten wurden zunächst Merkmale der anerkannten Sektionen zusammengestellt und mit Zeichnungen typischer Vertreter illustriert. Unter Verwendung der plastidären Marker *trn*L-F und *trn*K wurde eine molekulare Phylogenie der Gattung *Micromeria* erstellt. Dabei wurden auch ausgewählte Vertreter verschiedener Gattungen miteinbezogen, die traditionell als nah verwandt mit *Micromeria* angesehen wurden. Die phylogenetische Position von *Micromeria* Sektion *Pseudomelissa* innerhalb von *Clinopodium* stellt *Micromeria* als polyphyletische Gruppe dar. Vertreter der Sektionen *Micromeria* s.str. und *Pineolens* bilden eine Monophylie, wobei letztere in ersterer interkalieren. Die kanarischen *Micromeria* Arten sind als eine zusammengehörige natürliche Gruppe angezeigt. Eine Besiedelung von der Westmediterraneis aus ist wahrscheinlich, da *M. inodora* (Balearen) und *M. fontanesii* (Marokko) die Schwestergruppe zur Kanarischen Linie bilden. Die Kapverdischen Inseln wurden der phylogenetischen Rekonstruktion zufolge von einer anderen evolutionären Linie besiedelt. Morphologische Affinitäten zwischen *M. forbesii* (Kapverden) und *M. teneriffae* (Teneriffa) basieren entweder auf konvergenter Entwicklung oder auf der Überbewertung plesiomorpher Merkmale beider Arten.

Hinsichtlich der Taxonomie ergaben sich als neue Aspekte, dass Sektion *Pseudomelissa* aus *Micromeria* ausgeschlossen werden sollte, da die Typus-Art *M. juliana* topologisch in einer dissozierten evolutionären Linie platziert ist. Eine Einbeziehung der Sektion *Pineolentia* in Sektion *Micromeria* erscheint angebracht. Damit würde *Micromeria* zu einer homogeneren, morphologisch besser umschreibbaren Gruppe, gekennzeichnet durch das gemeinsame Merkmal eines sklerenchymatisch verdickten Blattrandnerves. Die Position der Sektion *Cymularia* sowie der madegassischen Arten, aber auch jene der südafrikanischen Vertreter der Sektion *Hesperothymus* bleibt weiter unklar. Die Problematik der Umschreibung von *Clinopodium* angesichts der topologischen Stellung der neuweltlichen Gattung *Monarda* wird diskutiert.

2.3.2 Zusammenfassung Manuskript 2: Bräuchler, C., Meimberg, H. & Heubl, G. 2006: New names in Old World *Clinopodium* – the transfer of the species of *Micromeria* sect. *Pseudomelissa* to *Clinopodium*. Taxon 55(4): 977-981.

Die Befunde aus der molekularen Studie in Manuskript 1 sollten sich auch in einer verbesserten, den natürlichen Verwandschaftsbeziehungen angemesseneren Taxonomie widerspiegeln. In Manuskript 2 wurden daher die Arten der Sektion *Pseudomelissa* von *Micromeria* in *Clinopodium* umkombiniert. Um die molekularen Ergebnisse auch morphologisch zu stützen wurden umfangreiche Herbarstudien durchgeführt. Dabei bestätigten sich die anfängliche Annahme, dass Merkmale wie Form von Kelch und Kelchzähnen, die traditionell für die Zuordnung zu *Micromeria* angeführt wurden, falsch interpretiert worden waren. Im Kontext der Sequenzdaten erwiesen sich Blattmerkmale als wesentlich verlässlicherer Hinweis auf natürliche Verwandtschaft. Da bereits in früheren Studien alle neuweltlichen Vertreter aus *Micromeria* aus- und in *Clinopodium* eingeschlossen worden waren, stellte die Sektion *Pseudomelissa* die einzigen in *Micromeria* verbliebenen Vertreter mit Blättern ohne verdicktem Randnerv und mit meist crenatem Blattrand; alle übrigen *Micromeria* Arten sind hingegen gekennzeichnet durch ganzrandige Blätter mit einem von aussen klar sichtbarem sklerenchymatischem Randnerv. Die wenigen existierenden Chromosomenzählungen (2n=20, 22) entsprechen auch eher denen für *Clinopodium,* als jenen der verbleibenden *Micromeria* Arten (2n=30). Weitere Untersuchungen ergaben, dass nach einem Transfer der entsprechenden Arten in *Clinopodium* nicht sicher ist, ob sich *Pseudomelissa* als Einheit auch innerhalb dieser Gattung halten lässt; daher wurde nicht die Sektion als Gesamtes in *Clinopodium* eingeschlossen, sondern nur deren untergeordnete Taxa. Auf Ebene der Nomenklatur waren dafür 15 Neukombinationen nötig. Um weitere taxonomische Arbeiten an der Gruppe zu erleichtern wurde Typusmaterial aller Arten (mit Ausnahme von *Micromeria nepalense*) gesichtet, was allerdings erst durch Besuch der Herbarien BM, E und K (alle Großbritannien), sowie die Übersendung digitaler Bilder durch die Kuratoren des Herbariums G in vollem Umfang möglich wurde. Für drei Namen war ein Typus bisher nicht designiert, weshalb nach umfangreicher Einarbeitung in die Regeln der Nomenklatur drei Typifizierungen vorgenommen wurden,

2.3.3 Zusammenfassung Manuskript 3: Meimberg, H., Abele, T., Bräuchler, C., McKay, J., K., Pérez de Paz, P. & Heubl, G. 2006: Molecular evidence for adaptive radiation of *Micromeria* Benth. (Lamiaceae) on the Canary Islands as inferred from chloroplast and nuclear DNA sequences and ISSR fingerprint data. Molec. Phylogen. Evol. 41: 566-578.

Als Modell für eine mögliche adaptive Radiation wurden in Manuskript 3 die kanarischen Arten der Gattung *Micromeria* mit verschiedenen molekularen Methoden näher untersucht. So wurden neben umfangereichen Sequenzanalysen zweier plastidärer (*trn*T-L und *trn*K) und eines neu abgeleiteten nukleären Markers (FPS2; ein Teil eines nukleären low copy Genes, von Harald Meimberg abgeleitet nach *Mentha*-EST-Daten aus GenBank) durch den Verfasser dieser Arbeit auch ISSR fingerprint Analysen (Inter Single Sequence Repeats) durch Tilmann Abele durchgeführt. Die Besiedelungsgeschichte und Monophylie der kanarischen *Micromeria* Arten wurde bereits in Manuskript 1 gezeigt. In dieser weiterführenden Arbeit wurden Proben von *M. varia* subsp. *thymoides* von Madeira miteinbezogen und gezeigt, dass diese in den kanarischen Clade eingebettet sind. In allen Analysen zeigt sich ein Split in eine östliche Linie (Proben verschiedener Arten von Gran Canaria, Lanzarote und Fuerteventura) und eine westliche Linie (Proben verschiedener Arten von Teneriffa, La Palma, El Hierro und Madeira). Proben von La Gomera finden sich in beiden Clades. In den ISSR fingerprint

Analysen werden Proben der jeweiligen Inseln als Cluster angezeigt und zwar unabhängig von der Artzugehörigkeit. Auch hier zeigt sich der Split in eine westliche und östliche Gruppe und die Präsenz beider Linien auf La Gomera. Somit scheinen alle ausser dieser Insel nur von einer evolutionären Linie besiedelt worden zu sein. Der Zeitpunkt der Besiedelung ist mit hoher Wahrscheinlichkeit nach der Entstehung der Hauptinseln Gran Canaria und Teneriffa vor ca. 9-12 Millionen Jahren anzusetzen. Da die Proben von den ältesten Inseln Lanzarote und Fuerteventura (16-20 Millionen Jahre) zumindest in der cpDNA Phylogenie eine Untergruppe der Sequenzen von Gran Canaria Proben bilden, und in keiner Analyse als basale Gruppe angezeigt werden, ist eine schrittweise Besiedelung von Ost nach West auszuschließen. Da Proben von La Gomera, La Palma, El Hierro und Madeira paraphyletisch bezüglich Proben von Teneriffa sind und einige Proben jeder Insel identische Sequenzen zu letzteren aufweisen, begann die Besiedelung der anderen Inseln, auch die Madeiras (Alter max. 5 Millionen Jahre), von Teneriffa aus. Insgesamt scheinen „Inter-Island-Colonisation“ und „Ecological shifts“ die Artbildung vorangetrieben zu haben. Radiationen auf den einzelnen Inseln scheinen im wesentlichen zur morphologischen Diversifizierung von *Micromeria* beigetragen zu haben. Da *M. varia* eine polyphyletische Gruppe darstellt, könnte es sich dabei um Pflanzen oder Populationen handeln, die den Vorläufern der Radiationen auf den einzelnen Inseln ähneln und ihre ursprüngliche Anpassung an den küstennahen semiariden Sukkulentenbusch behalten haben. Zu beachten ist dabei, das die Ergebnisse von ISSR-Analysen stark von Introgressions- und Hybridisierungsereignissen beeinflußt sein können, da es sich um kodominante Marker handelt. Damit verbundene Homogenisierung der Genotypen einer Insel könnte spätere Einwanderung zusätzlicher Allele durch erneute Kolonisierung molekular verschleiern. Indizien dafür wären das Vorkommen natürlicher Hybriden. Die Präsenz gleicher Haplotypen auf mehreren Inseln und in unterschiedlichen Arten könnte auf Introgressionen zwischen den Inseln hinweisen. Allerdings scheinen zwischen den beiden auf La Gomera vorkommenden Entwicklungslinien reproduktive Barrieren zu bestehen. Weitere Untersuchungen die sowohl vergleichende Sequenzierung eines größeren Abschnitt des FPS2 Genes, Klonierungsexperimente und Mikrosatellitenanalysen beinhalten werden derzeit in der Arbeitsgruppe durchgeführt und liegen ausserhalb des Fokus der vorliegenden Arbeit.

2.3.4 Zusammenfassung Manuskript 4: Bräuchler, C., Doroszenko, A., Esser, H.-J. & Heubl, G. 2008: *Killickia* (Lamiaceae) – a new genus from KwaZulu-Natal, South Africa. Bot. J. Linn. Soc. 157: 575-586.

Obwohl Phylogenien basierend auf unterschiedlichen Markern (nukleär und plastidär) die altweltlichen Arten von *Micromeria* section *Hesperothymus* (*M. pilosa*, *M. grandiflora*, *M. compacta*) an leicht abweichenden Positionen in der Baumtopologie zeigen (siehe Manuskript 6), sind sie durchweg mit maximaler Unterstützung als monophyletische Gruppe angezeigt, die topologisch und auch morphologisch klar von *Clinopodium* in engeren Sinne abgesetzt ist. Ein Einschluß dieser Arten in *Clinopodium*, würde einen äußerst weit gefassten Gattungsbegriff erfordern, falls Gattungen als monophyletische Gruppen charakterisiert sein sollten. Trotz der unterschiedlichen Topologien der Phylogenien ist offensichtlich, dass auch alle z.T. sehr gut abgrenzbaren neuweltlichen Taxa sowie *Bystropogon* und evtl. sogar *Mentha* und *Cyclotrichium* einbezogen werden müßten. Da dies morphologisch nicht nachvollziehbar wäre und auch weitreichende Konsequenzen auf Grund der allgemeinen Bedeutung vieler dieser Taxa (z.B. *Monarda* als Zierpflanze, *Mentha* als Gewürz- und Heilpflanze) hätte, erscheint diese Alternative nicht wünschenswert. Dies ist umso mehr von Bedeutung, als von der Taxonomie vor allem das Erreichen einer nomenklatorischen Stabilität erwartet wird.

Einem engeren Gattungskonzept folgend, wurde daher in Manuskript 4 die Gattung *Killickia* beschrieben. Der Name war von Doroszenko (1986) in seiner Doktorarbeit vorgeschlagen, allerdings nie veröffentlicht worden. Die Abgrenzung zu nächstverwandten Gruppen war sehr unzureichend, da manche Gattungen in Doroszenko´s Revision des *Satureja* Komplexes nicht miteinbezogen wurden. Ausserdem war die Bearbeitung auf Herbarmaterial beschränkt. Für molekulare (Manuskript 6) und umfangreichere morphologische Untersuchungen wurde auf einer Expedition in das Drakensberg-Massiv (östliches Südafrika) Material von *M. grandiflora* und *M. compacta* an den Typusstandorten gesammelt. Von *M. pilosa* konnten zwei verschiedene Populationen aufgefunden werden, eine davon im Gebiet, aus dem der Typus stammt (die Angabe auf dem Original-Beleg und in der Literatur sind relativ ungenau). In einem Tal im Garden Castle Nature Reserve im südlichen Drakensberg wurde zudem eine neue Art der Gruppe entdeckt, die sich von allen anderen auf den ersten Blick durch zitronengelbe Blüten, Form der Kelchzipfel und Habitat unterschied. Spätere Herbarstudien zeigten, dass die Art bisher mehrmals gesammelt, allerdings fälschlicherweise als *M. compacta* bestimmt worden war. Die Art wurde als *Killickia lutea* neu beschrieben um der für die gesamte Tribus sehr ungewöhnlichen Blütenfarbe Rechnung zu tragen. Nach Studie des selbst gesammelten Materials sowie zahlreicher zusätzlicher Herbarbelege (inkl. Typusmaterial aller Arten) konnte neben detaillierten Beschreibungen und der Gattungsabgrenzung auch ein Bestimmungsschlüssel für *Killickia* angefertigt werden. Neben REM Aufnahmen der Früchte wurden auch noch Blattquerschnitte (von L. Dimitrov angefertigt) und Zeichnungen (von G. Heubl) erstellt, und jede Art zum ersten Mal durch detaillierte Farbfotos illustriert. Mit der Abgrenzung dieser neuen Gattung ist ein erster Schritt getan, die komplexen Verhältnisse innerhalb der *Clinopodium* Gruppe aufzulösen.

2.3.5 Zusammenfassung Manuskript 5: Bräuchler, C., Heubl, G. & Ryding, O. (2008) The genus *Micromeria* Benth. (Lamiaceae) – a synoptical update. Willdenowia 38: 363-410.

Während innerhalb des *Clinopodium*-Verwandtschaftskreises vieles noch unklar erscheint, konnten die Abgrenzungsprobleme im Fall von *Micromeria* angesichts der in Manuskript 6 präsentierten molekularen Daten und umfangreicher Herbar- und Literaturstudien weitgehend geklärt werden. Wie bereits in den Manuskripten 1 und 2 erwähnt, ist *Micromeria* auf jene Arten zu beschränken, die vor allem durch Blätter mit einem verdickten Randnerv und durch einen nicht sigmoiden, nicht gibbosen Kelch charakterisiert sind. Die nötige detaillierte Neuumschreibung wurde in Manuskript 5 geliefert, die Sektionen *Pineolentia* und *Micromeria* wurden vereinigt. Eine neu erstellte Arealkarte soll eine aktualisierte Übersicht über die Verbreitung der Gattung geben. Als Beitrag zur derzeit an den Royal Botanical Gardens Kew unter Leitung von Alan Paton und Rafael Govaerts erstellten „World Checklist of Seed Plants“, sind schließlich alle bisher unter *Micromeria* publizierten Namen auf Artniveau und darunter, sowie deren Basionyme aufgelistet. Dabei konnte eine große Zahl bisher übersehener Namen ergänzt, einige in ihrer Synonymy unklare Namen geklärt, sowie in vielen Fällen die Autoren- und Literaturangaben korrigiert werden. Soweit dies im Rahmen eigener Herbarstudien und Literaturrecherche möglich war, wurden Typusbelege zitiert. 24 Namen konnten typifiziert werden, eine neue Kombination (*Micromeria cristata* subsp. *kosaninii*) und ein neuer Name (*M. longipedunculata* als Ersatz für die illegitime *M. parviflora* Rchb.) wurden validiert. In vielen Fällen wurden Probleme bei der Typifizierung, Zuordnung von Namen und Abgrenzung der Sippen festgehalten. Die Arbeit soll die Auffindung des aktuell gültigen Namens eines Taxons sowie weiterführende Untersuchungen erleichtern und als nützliches und umfassendes Nachschlagewerk für die Gattung dienen, beansprucht jedoch keineswegs die Vollständigkeit einer biosystematischen Revision.

2.3.6 Zusammenfassung Manuskript 6: Bräuchler, C., Meimberg, H. & Heubl, G.: Molecular phylogeny of Menthinae (Lamiaceae, Nepetoideae, Mentheae) – taxonomy, biogeography and conflicts. Molec. Phylogen. Evol., accepted for publication

Die Gattung *Micromeria* hatte sich im Laufe der Arbeit bereits als polyphyletisch in Hinsicht auf Sektion *Pseudomelissa* gezeigt (Manuskript 1), was allerdings durch den Transfer der betroffenen Arten in *Clinopodium* gelöst wurde (Manuskript 2). In der Folge wurde Material der fehlenden Gruppen innerhalb von *Micromeria* und *Clinopodium* im Speziellen sowie der Subtribus Menthinae im Allgemeinen zusammengetragen. Damit sollte geprüft werden, ob sich noch weitere Taxa als unnatürlich in ihrer derzeitigen Umschreibung erweisen würden. Die Ergebnisse der vergleichenden DNA-Sequenzierung und phylogenetischen Rekonstruktion wurde in Manuskript 6 zusammengefasst. Basierend auf den Chloroplasten-Loci *trn*K und *trn*L-F wurde eine Phylogenie erstellt und mit einer ITS-basierten nukleären Phylogenie verglichen. Dabei wurden die meisten Plastidensequenzen selbst generiert, während in die ITS Analyse auch Sequenzen vorangegangener Studien miteinbezogen wurden, zum einen um die Homologie mit den selbstgewonnenen Sequenzen zu überprüfen und zum anderen um die Analyse auf eine breitere Basis zu stellen. Insgesamt wurden 278 Proben aus 38 der 40 in diesem Manuskript zu den Menthinae gerechneten Gattungen berücksichtigt. Es wurden zudem morphologisch abweichende Gruppen innerhalb vieler Gattungen abgedeckt und bei kritischen Formenkreisen mehrere Akzessionen pro Spezies eingeschlossen. Dadurch war es zum ersten mal möglich, eine umfassende phylogenetische Hypothese für die Subtribus aufzustellen. Die aus beiden Markern ermittelten Stammbäume zeigten teilweise inkongruente Topologien. Da sich die terminalen Gruppen der Bäume beider Datensätze allerdings weitestgehend entsprachen, nur deren Position zueinander nicht, und die Probenabdeckung nahezu lückenlos war, konnte in vielen Fällen die Gattungsabgrenzung sowie die phylogenetische Beziehung strittiger Taxa geklärt werden.

Trotz einer vergleichsweise engeren Umschreibung in Harley & al. (2004) erwies sich *Satureja* als nach wie vor polyphyletisch. Eine Gruppe von Arten um *S. linearifolia* ist wohl zur Gattung *Thymbra* zu stellen um beide Taxa zu monophyletischen Gruppen zu machen. Die Abspaltung von *Argantoniella*, von Harley & al. (2004) ebenfalls in *Satureja* einbezogen, wird durch die molekularen Daten gut gestützt. Nähere Verwandschaft dieser Gattung zu *Saccocalyx* und *Thymus* sind neue Erkentnisse dieser Studie und weisen auf die Notwendigkeit weiterführender Untersuchungen hin. Die auf Basis der hier präsentierten Daten und zusätzlicher Herbar- und Literaturrecherche vorweggenommene Neuumschreibung der Gattung *Micromeria* ist sehr gut gestützt. Der Ausschluss der bisher noch nicht überarbeiteten „*M.*“ *madagascariensis* Gruppe und „*M.*“ *cymuligera* von *Micromeria* im engeren Sinn wurde in Manuskript 5 zwar vollzogen (daher die Anführungszeichen beim Gattungsnamen), jedoch sind weiterführende Arbeiten nötig um die betroffenen Arten taxonomisch angemessen zu platzieren. Entsprechend dem Verfahren für die südafrikanischen „*Micromeria*“ Arten, die in Manuskript 4 in die neue Gattung *Killickia* gestellt wurden, ist für die „*Micromeria*“ *madagascariensis* Gruppe die Beschreibung einer neuen Gattung vorgesehen, allerdings sind dazu zusätzliche Herbarstudien nötig. Die molekularen Daten erwiesen sich als besonders nützlich bei der Überprüfung der Umschreibung von *Clinopodium*. Nach der Bearbeitung von Harley & al. (2004), sowie den in Manuskript 3 präsentierten taxonomischen Änderungen enthält diese Gattung mittlerweile ca. 100 Arten und stellt damit, ähnlich der früheren Situation in *Satureja* s.l., eine sehr heterogene, morphologisch diverse Gruppe dar. Die 22 neuweltlichen Gattungen der Menthinae (darunter so bekannte Vertreter wie die Indianernessel *Monarda*) sind, durchmischt mit neuweltlichen *Clinopodium*-Arten, als monophyletische Gruppe gestützt, wodurch die derzeitige Umschreibung von *Clinopodium* eindeutig unnatürlich erscheint. Um ein natürliches

Klassifikationssystem zu erreichen, werden für die entsprechenden neuweltlichen Taxa wohl bereits existierende Gattungsnamen, die derzeit in Synonymie zu *Clinopodium* stehen, wiedereingeführt werden müssen. Mit Ausnahme eingeschleppter Arten sind die typischen Vertreter von *Clinopodium* demnach ebenso auf die Alte Welt beschränkt wie dies, entgegen traditoneller Auffassung, auch für *Satureja* und *Micromeria* gilt. Innerhalb der altweltlichen *Clinopodium*-Gruppe erscheinen die Abgrenzungen zu *Ziziphora* und anderen Gattungen nicht klar.

Für die einzelnen terminalen Gruppen der Phylogenien wurden eine detailliertere Beschreibung von diagnostischen Merkmalen, taxonomischen Problemen und möglicher verwandtschaftlicher Beziehungen aus Übersichtsgründen in den Appendix des Manuskripts gestellt auf den bezüglich weiterführender Informationen hier verwiesen werden soll.

Die festgestellten Inkongruenzen zwischen Baumtopologien basierend auf plastidären *trn*K/*trn*L-F und nukleären ITS Sequenzdaten entspricht den Befunden von ähnlichen Untersuchungen sowohl in anderen Pflanzenfamilien als auch einer Reihe von Gattungen der Lamiaceae. Bei neuweltlichen Menthinae wurden unvollständige Angleichung der Allele in Populationen sowie Hybridisierungsereignisse in der älteren und jüngeren evolutionären Vergangenheit der Gruppen als mögliche Ursachen für derartige Inkongruenzen angeführt (Edwards & al., 2006; 2008 a, b; Schmidt-Lebuhn, 2007). Trusty & al. (2004) vermuteten allerdings Homoplasie-Effekte in den ihren Berechnungen zugrunde liegenden ITS Daten als Ursache für die widersprüchliche Position der makaronesischen Gattung *Bystropogon* zu den neuweltlichen Gattungen. Während dies ebenfalls eine mögliche Erklärung für die abweichende Position der *Clinopodium simense* Gruppe in den in diesem Manuskript präsentierten Phylogenien wäre, ließen sich in unserem ITS Alignment beispielsweise keine Positionen ausmachen, die nähere Beziehungen der *Clinopodium nepalense* Gruppe zu „*Acinos*“ (als Teil von *Clinopodium*, daher „...“) stützen würden, wie sie in der plastidären Phylogenie angezeigt werden. Damit läßt sich zumindest die Trennung beider Gruppen im ITS Baum wohl nicht auf Homoplasie-Effekte zurückführen. Die Introgression eines Plastiden aus einer entfernt verwandten Linie, wie kürzlich für den *Verbena* Komplex nachgewiesen (Yuan & Olmstead, 2008), könnte eine plausiblere Erklärung darstellen. Desweiteren konnte nach Untersuchung unserer Sequenzalignments, ausgeschlossen werden, dass darin nicht homologe ITS Kopien enthalten waren, was als weitere potentielle Ursache für inkongruente Anordnung einzelner Gruppen angenommen werden könnte. Innerhalb der neuweltlichen Entwicklungslinie stehen die vergleichsweise geringeren Sequenzunterschiede im deutlichen Gegensatz zu einer bemerkenswerten morphologischen und ökologischen Diversität. Eine schnelle Besiedlung begleitet von Artbildung/Radiation könnte damit die Erklärung für die fehlende topologische Struktur an der Basis der Linie sein. Insgesamt ist davon auszugehen, dass alle angeführten Prozesse zur Ausbildung des dargestellten komplexen phylogenetischen Musters beigetragen haben.

Trotz der angeführten Inkongruenzen lassen sich durch Vergleich der Gesamtverbreitung von Gattungen und Taxa monophyletischer Linien mit den Baumtopologien einige interessante biogeographische Schlüsse ziehen. Da im weiteren Umfeld der Mediterraneis sowohl die höchste Artenzahl als auch zahlreiche basale, morphologisch isolierte Gruppen im Osten des Gebietes zu finden sind (sowohl für die *Satureja* als auch die *Micromeria*-Gruppe), ist eine Besiedelung in Ost-West Richtung wahrscheinlich, wie schon für andere Gattungen nachgewiesen (z.B. *Limonium*; Lledo & al., 2005). Innerhalb von *Micromeria* zeigte sich, dass die Kapverdischen Inseln wohl unabhängig von den Kanaren über eine sub-saharische Migrationsroute besiedelt wurden. Die Aufspaltung von *Origanum* und *Thymus* könnte einem Ost/West-Split entsprechen, mit jeweiligen sekundären Wanderungen in westlicher bzw. östlicher Richtung. Dabei scheint die Region um den Isthmus von Gibraltar eine große Bedeutung als Rückzugsgebiet für *Thymus* gehabt zu haben. Innerhalb der *Clinopodium* Gruppe sind die Verhältnisse entsprechend den Baumtopologien schwieriger zu interpretieren.

Sehr früh scheint sich eine Entwicklungslinie abgespalten zu haben und vermutlich entlang der ostafrikanischen Gebirgszüge nach Südafrika und von dort nach Madagaskar gewandert zu sein. Die südafrikanische Gattung *Killickia* und die „*Micromeria*“ *madagascariensis* Gruppe stellen damit ein interessantes Beispiel für eine Schwestergruppenbeziehung zwischen nur schwach diversifizierten Gruppen ökologisch sehr ähnlicher Habitate montaner bis alpiner Lagen des südafrikanischen Drakensberg-Massivs und der zentralmadagassischen Gebirge dar. Es wurden nur wenige Proben von *Mentha* Arten in unsere Analysen eingeschlossen, allerdings weisen die Verbreitung der in beiden Phylogenien nah verwandten Gattung *Cyclotrichium* sowie die der in der plastidären Baumtopologie nahe stehenden „*M.*“ *cymuligera* auf einen möglichen irano-turanischen Ursprung.

Für die neuweltliche Entwicklungslinie ist in der cpDNA basierten Phylogenie durch die Anordnung von *Bystropogon* und der *Clinopodium simense* Gruppe deutlich ein afrikanischer Ursprung angezeigt. Die widersprüchliche Topologie des ITS Baumes ist wie dargelegt vermutlich auf Homoplasie-Effekte zurückzuführen. Über Vektor und Route der Besiedlung für die Neue Welt kann nur vermutet werden, dass es sich um eine einmalige von Afrika ausgehende Fernverbreitung nach Zentral- oder Südamerika handelt, da in der Phylogenie keine basalen Linien durch nordamerikanische Taxa angezeigt sind. Dies wäre bei einer angenommenen Besiedelung über die Bering-Landbrücke oder die Nordatlantik-Landbrücke zu erwarten. Die Diversifikation der Entwicklungslinie in Nord- und Südamerika scheint stark durch Ereignisse wie Auffaltung der Anden und damit verbundene Entstehung neuer ökologischer Nischen, Habitatsausdehnung und anschließende –fragmentierung durch Vereisungen im Pleistozän, sowie die Anpassung an neue Bestäuber (z.B. Kolibris).

Um das Problem der Inkongruenz zwischen den hier präsentierten Datensätzen genauer zu untersuchen, wird derzeit an einer Ausdehnung der Probenabdeckung vor allem für die neuweltlichen Arten gearbeitet. Zusätzlich sind weitere Studien zum Ploidiegrad vieler diesbezüglich unbearbeiteter Gruppen, sowie die Sequenzierung zusätzlicher nukleärer Marker nötig um sowohl die phylogenetische Auflösung zu verbessern als auch die komplexe raum-zeitliche Differenzierung der Menthinae weiter aufzuklären.

3. Ausblick

In den einzelnen Schritten dieser Arbeit wurde erstmalig ein kompletter Überblick über die Phylogenie dieser wirtschaftlich und medizinisch so bedeutenden Familie der Lamiaceae gegeben. Viele taxonomische Unklarheiten, die Generationen von Botanikern die Arbeit sehr erschwerten und Anlaß zu zahlreichen Diskussionen gaben, konnten geklärt werden. Allerdings sind auch sehr viele neue Probleme und Fragestellungen aufgeworfen worden, an erster Stelle die Umschreibung der Gattung *Clinopodium*, die Abgrenzung der Gattung *Thymus* und die widersprüchlichen phylogenetischen Szenarien rekonstruiert aus Kern- und Chloroplasten-Sequenzen.

Die hier präsentierten Ergebnisse werden Ausgangspunkt diverser Folgeprojekte sein. Derzeit wird die taxonomische Probenabdeckung auf alle Gattungen der Mentheae erweitert um die Untergliederung der Tribus zu testen. Auf der Basis eines erweiterten Datensatzes soll eine Zeitabschätzung für die Abspaltung der einzelnen Entwicklungslinien vorgenommen werden, was auf Grund des Fehlens geeigneter Fossilien zur Kalibrierung der molekularen Uhr problematisch ist. Die Sequenzierung zusätzlicher Marker aus allen drei Genomen (Kern, Mitochondrium, Chloroplast) soll die Auflösung innerhalb der Menthinae erhöhen und zur weiteren Klärung der Ursache für die topologischen Inkongruenzen zwischen einzelnen Datensätzen beitragen. Neben der Aufklärung der Verhältnisse innerhalb der *Clinopodium*-Gruppe steht vor allem die Erstellung einer Phylogenie der Gattung *Thymus* und deren Abgrenzung zu verwandten Sippen im Fokus. Phylogeographisch sollen weitverbreitete Sammelarten wie *Clinopodium alpinum* oder *C. serpyllifolium* im Mediterranraum vor einem klimatisch-geologischem Hintergrund untersucht werden. Für die *Killickia*-Arten und die madegassischen „Micromerien“, sind Studien zur vergleichenden Radiation vorgesehen. Letztere Gruppe wird derzeit revidiert, die notwendig und gerechtfertigt erscheinende Abtrennung in einer neuen Gattung ist in Vorbereitung.

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5. Abbildungs- und Tabellenverzeichnis

Abbildungen

Tabellen

6. Appendix

6.1 Manuskript 1:

Bräuchler, C., Meimberg, H., Abele, T. &Heubl, G. 2005: Polyphyly of the genus *Micromeria* (Lamiaceae) – evidence from cpDNA sequence data. Taxon 54(3): 639-650.

Polyphyly of the genus *Micromeria* (Lamiaceae) — evidence from cpDNA sequence data

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Micromeria Benth. (Lamiaceae, Nepetoideae) is a very common genus in the Mediterranean region. To test the monophyly of the genus and to elucidate its phylogenetic placement within subtribe Menthinae (Dumort) Endl. of tribe Mentheae Dumort we performed parsimony analysis of *trnK* intron sequence data of 51 accessions representing 15 genera of Nepetoideae and two genera of subfamily Ajugoideae. Tree topology reveals a well-supported "core group" indicating four distinct lineages. The first one comprises three species of *Satureja* L. s.str., the second one includes taxa of the genus *Clinopodium* L. from both the Old and the New World, paraphyletic with respect to *Monarda* L. and two species of *Micromeria* section *Pseudomelissa* Benth. A third group contains all samples of the remaining *Micromeria* species. Within this monophyly, a western lineage including taxa from NW Africa, the Balearic, and the Canary Islands, is sister to an eastern lineage with species distributed from SE Asia to the western Mediterranean. In a further clade the genera *Thymbra* L., *Thymus* L., and *Origanum* L. are grouped together. Combined analysis using a reduced dataset of *trnK/trnL-F* sequences increased support for the infrageneric resolution within *Micromeria*. Based on the phylogenetic reconstructions there is evidence that the genus as currently circumscribed is polyphyletic. Results are discussed in the context of morphology, karyology, and biogeography, outlining the necessity of removing section *Pseudomelissa* from *Micromeria*.

KEYWORDS: *Clinopodium*, Lamiaceae, *Micromeria*, molecular phylogeny, polyphyly, *trnK*, *trnL-F*.

INTRODUCTION

The genus *Micromeria* Benth. (Lamiaceae, Nepetoideae) is part of a complex group of genera in tribe Mentheae subtribe Menthinae. It contains about 70 species with a distribution range extending from the Himalayan region to the Macaronesian Archipelago and from the Mediterranean to South Africa and Madagascar. According to the latest generic circumscription by Harley & al. (2004), all species are perennial or annual herbs, subshrubs or shrubs, often with an aromatic scent. The flat to revolute leaves are linear to ovate in shape with an entire or toothed margin. Inflorescences are thyrsoid to sometimes racemoid with (1) 2–20 flowers arranged in opposite axillary cymes, forming verticillasters with bracts (more or less similar to leaves) and frequently bracteoles. When present, pedicels are sometimes very long. The calyx is 13–15-nerved, campanulate or cylindrical, 5-lobed, and actinomorphic to weakly 2-lipped. Calyx lobes are equal to slightly unequal (3 forming upper lip, 2 forming lower lip), sometimes curved or spreading, with anterior ones often longer than posterior ones. The calyx throat is sometimes bearded. The small corolla ranges from white to yellowish, mauve pink, or purple in colour and is 2-lipped (1 lobe forming upper lip, 2 lobes forming lower lip) with the posterior lip straight and emarginated and the anterior spreading. The corolla tube is cylindrical and sometimes hairy at the throat. The four stamens are included or exserted, with straight or connivent filaments and divaricate, ellipsoidal, distinct thecae. The style branches are subequal (with the lower branch often slightly longer), the nutlets are ovoid, sometimes apiculate, and sometimes hairy. Chromosome numbers reported are $2n = 20, 22, 30, 50$ and 60.

Concerning infrageneric subdivision, Harley & al. (2004) accept four sections: *Micromeria*, *Pineolentia* P. Pérez, *Cymularia* Boiss. and *Pseudomelissa*. The morphological characters for each of these sections were described in detail by Doroszenko (1986) and are summarised in Table 1. Illustrations of characteristic representatives of the sections are provided in Fig. 1 (A–D). Section *Micromeria* includes perennial suffruticose herbs and shrubs, with approximately 50 species in the Mediterranean, Macaronesia and northern Africa. According to a revision of the Macaronesian taxa by Pérez (1978), 14 species of this section are endemic to the Canary Islands. The two species of section *Pineolentia* (*Micromeria pineolens* and *M. leucantha* Svent.), both robust perennial shrubs, are restricted to the

Table 1. Characterisation of the four currently recognised sections of genus *Micromeria* (Harley & al., 2004) as described in detail by Doroszenko (1986) with chromosome numbers according to Morales (1993).

Section	*Micromeria*	*Pineolentia*	*Cymuligera*	*Pseudomelissa*
Growth form	perennial, suffruticose herbs and shrubs	perennial, robust shrubs	annual herbs	perennial, suffruticose herbs
Leaves	2–16 mm × 0.3–8 mm; ovate, elliptic, lanceolate, linear or oblong; flat or tightly revolute; entire with thick marginal vein	14–30 mm × 3.3–7 mm; narrowly ovate-lanceolate; revolute or tightly revolute; entire with narrow but distinct marginal vein	7–11 mm × 2–6 mm; ovate; flat or slightly revolute at margin; entire, marginal vein absent	5–35 mm × 2–22 mm; broadly ovate, lanceolate or almost orbicular; flat or scarcely revolute at margin; crenate to ± entire, marginal vein absent
Petioles	0–1.5(2) mm	1.5–2 mm	1–3.5 mm	0.5–7(11) mm
Flowers	1–10(20) per cyme (in floral leaf axils)	1–10 per cyme (in floral leaf axils)	4–10 per cyme in leaf axils (no distinct floral leaves)	1–30(40) per cyme (in floral leaf axils)
Bracteoles	narrowly linear-filiform, lanceolate or elliptic; 0.6–3(6) mm; not distinctly ciliate	linear or narrowly lanceolate; 3.5–8 mm; not ciliate	ovate; 3–4 mm; long acuminate; ciliate on margin	linear to narrowly elliptic or lanceolate; 0.4–3(5.5) mm; not conspicuously ciliate
Calyx	mostly hairy in throat; teeth ciliate or not	throat glabrous or sparsely hairy; teeth not ciliate	throat sparsely hairy; teeth long-ciliate	mostly hairy in throat; teeth almost never ciliate
Corolla	not resupinate	not resupinate	resupinate	not resupinate
Stamens	included or anterior pair (rarely both) exserted from tube; never beyond upper corolla lip	posterior stamens included, anterior ± exserted; never beyond upper corolla lip	all barely exserted; never beyond upper corolla lip	mostly exserted, or rarely included; anterior pair longer than upper lip
Anthers	all similar in size	all similar in size	posterior stamens anthers only half the size of anterior stamen anthers; posterior stamens sometimes entirely absent	all similar in size
Style	branches equal to very rarely slightly unequal, narrowly subulate or broadly lanceolate, rarely very short with blunt apices	branches equal, broadly lanceolate	branches equal, narrowly subulate	branches mostly unequal, sometimes ± equal, nearly always narrowly subulate or very short with blunt apices
Nutlets	nearly always glabrous, rarely minutely eglandular hairy at apex	glabrous	glabrous	minutely glandular or eglandular hairy or with minute sessile glands at apex, rarely glabrous
Chromosome number	$2n = 30, 50, 60$	unknown	unknown	$2n = 20, 22$
Distribution	W Mediterranean to Indian subcontinent, N Mediterranean to South Africa	Gran Canaria	South Eastern Anatolia	W Mediterranean to E Himalayan region, N Mediterranean to Southeast Africa

northern parts of Gran Canaria, whereas the only representative of section *Cymularia*, *Micromeria cymuligera* Boiss. & Hausskn., is endemic to the mountains of southeastern Anatolia. Due to its annual habit, resupinate flowers, special anther structure and different other characters (see Table 1), this taxon is regarded as being very isolated within the genus. Finally, the 14 species (according to Morales, 1993) of section *Pseudomelissa* are distributed from the Indian Subcontinent to the Iberian Peninsula and Southeast Africa. This section of herbs or suffruticose herbs is more distinct from the others by its crenate leaves and anterior anthers longer than the upper lip of the corolla (see Table 1 for a detailed characterisation of sections).

While the generic limits and infrageneric subdivision of *Micromeria* are now widely accepted, for more than one hundred years they have been subject of intensive taxonomic discussion and confusion. Bentham's (1848) narrow concept placed this taxon as a genus of its own including New World as well as Old World species. However, Briquet (1895–1897) lumped *Micromeria* into *Satureja* s.l. scattering the species over different sections (*Cyclotrichium*, *Cymularia*, *Hesperothymus*, *Piperella*, *Pseudomelissa, Sabbatia*, *Xenopoma*). In the last century many Old World floras (e.g., Ball & Getliffe, 1972; Chater & Guinea, 1972; Davis, 1982a) followed the narrow generic concept of Bentham (1848), while authors of New World and African floras (e.g., Killick, 1961; Epling & Jativa, 1964, 1966), as well as Greuter & al. (1986) for the MedChecklist, adopted Briquet's (1895–1897) opinion. Pérez (1978) and Morales (1993), however, accepted the generic status of *Micromeria* recognising the six sections *Cymularia*, *Hesperothymus* Benth., *Micromeria*, *Pineolentia*, *Pseudomelissa*, and *Xenopoma* (Willd.) Benth. In his taxonomic investigations of the *Satureja* complex on a worldwide scale, Doroszenko (1986) only included the Old World sections (*Cymularia*, *Micromeria*, *Pineolentia*, *Pseudomelissa*) in the genus *Micromeria*, within which he created a new section (*Madagascarenses* Doroszenko) to accomodate

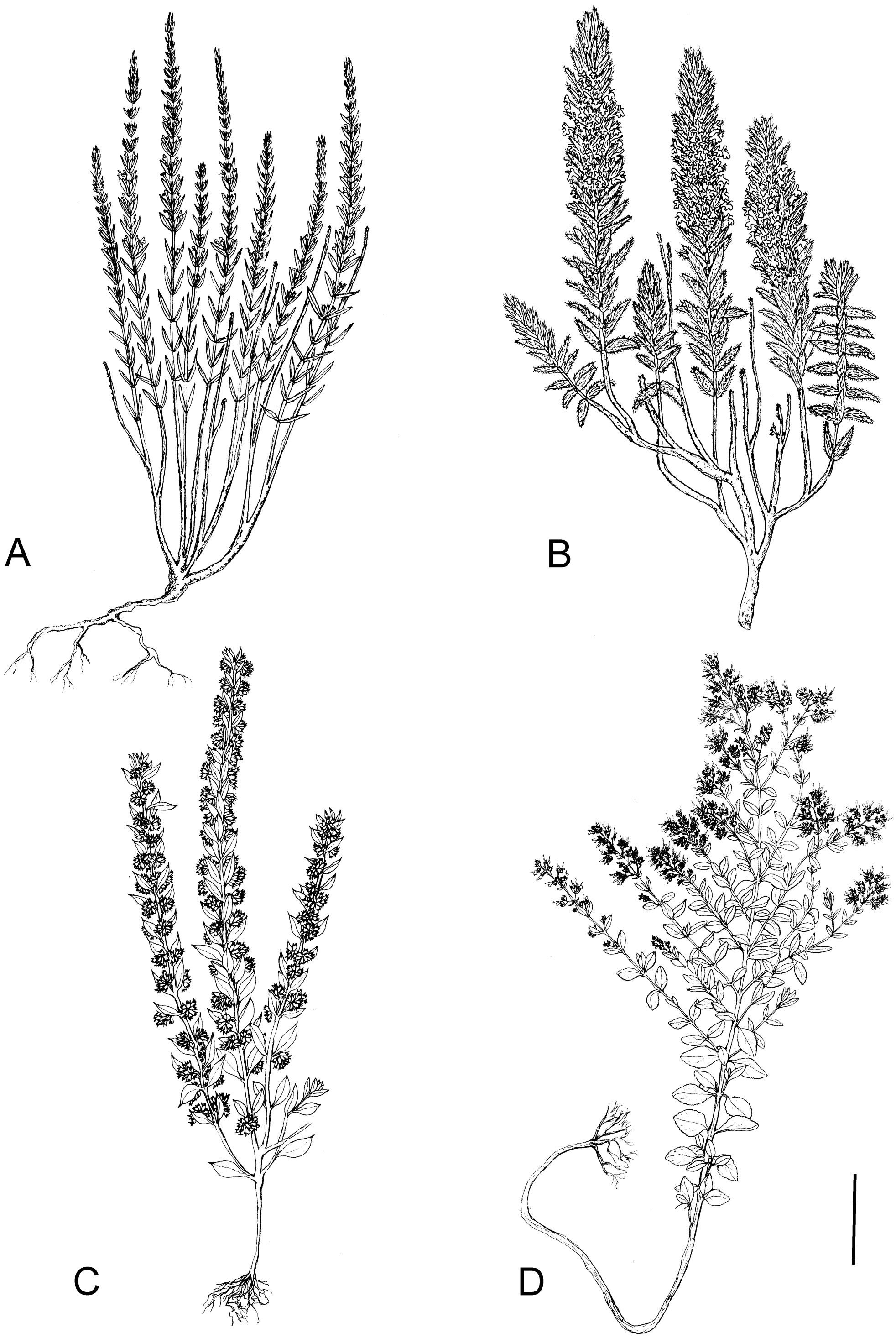

Fig. 1. Representatives of the four recognised sections within *Micromeria*. A, *M. juliana* (section *Micromeria*); B, *M. pineolens* (section *Pineolentia*); C, *M. cymuligera* (section *Cymularia*); D, *M. fruticosa* (section *Pseudomelissa*). Scale bar = 3.8 cm (A), 3.0 cm (B), 3.4 cm (C) and 4.5 cm (D).

the three Malagasy species (*M. madagascarensis* Baker, *M. flagellaris* Baker and *M. sphaerophylla* Baker). Based on recent molecular data (Wagstaff & al., 1995) compared to morphology, sections *Hesperothymus* and *Xenopoma* (still of *Micromeria*) have been transferred to an expanded genus *Clinopodium* (Cantino & Wagstaff, 1998; Harley & Granda, 2000). As delimited by Harley & al. (2004), *Micromeria* has become a morphologically more homogeneous taxonomic unit. Like infrageneric relationships within *Micromeria*, the boundaries with closely related taxa as *Satureja*, *Thymus*, *Origanum* (Ietswaart, 1980) and *Clinopodium* (Doroszenko, 1986) still remain speculative.

The aim of this paper is to examine the phylogenetic relationships within *Micromeria* (sensu Harley & al., 2004) using plastid *trnK* and *trnL-F* sequence data and to compare the findings with existing morphology-based taxonomic concepts.

MATERIALS AND METHODS

Plant material and DNA extraction. — 24 samples of 18 *Micromeria* species, representing three of the four recognised sections, were included in the analysis. Unfortunately material of the monotypic section *Cymularia* (*M. cymuligera*) endemic to Turkey was not available due to its rareness and consequent weak representation in herbaria. Also none of the Malagasy species could be investigated here.

Ajuga L. and *Clerodendrum* L. were sampled as outgroups since there is evidence from morphology (Cantino & Sanders, 1986; Cantino 1992) and in case of *Ajuga* also from molecular analysis (Wagstaff & al., 1995), that these genera are not part of the well defined monophyletic subfamily Nepetoideae. Additionally 27 species representing the genera *Agastache* Gronov., *Clinopodium*, *Collinsonia* L., *Glechoma* L., *Horminum* L., *Lycopus* L., *Monarda*, *Nepeta* L., *Origanum*, *Plectranthus* L'Hér., *Salvia* L., *Satureja*, *Thymbra*, and *Thymus* were included to investigate the placement of *Micromeria* within Nepetoideae in more detail than in Wagstaff & al. (1995), where it was represented only by one species (*M. juliana*). Appendix 1 lists all taxa included in this study and summarises sources, voucher specimen data, and GenBank accession numbers of the sequences. Total DNA was extracted from fresh material or herbarium specimen as described previously (Bräuchler & al., 2004).

Amplification and sequencing. — To clarify the phylogenetic position of *Micromeria* within subtribe Menthinae the *trnK* intron was analysed for all species included in this study and amplified from total DNA as described elsewhere (Meimberg & al., 2001). From fresh material of *Satureja montana* and *Micromeria juliana*, the whole *trnK* intron was amplified using the forward primer 2-*trnK*-3914F and the reverse primer 16-*trnK*-2R (Johnson & Soltis, 1994). For comparative sequencing the *trnK* intron was amplified in two parts using the primer pair 2-*trnK*-3914F/Sat16-1200R and Sat2-1200F/16-*trnK*-2R, using the following cycle profile: (1) 94°C for 2 min, (2) 35 cycles at 94°C for 1 min, 54°C for 1 min, 72°C for 1 min 30 sec and (3) a terminal extension phase at 72°C for 10 min. For achieving the *trnK* intron from highly degraded DNA from herbarium specimens, smaller fragments using internal primers were amplified (Table 2). Primer pairs used were 2-*trnK*-3914F/Sat16-880R, Sat2-500F/Sat16-1000R, Sat2-880F/Sat16-1200R, Sat2-1000F/Sat16-1780R, Sat2-1200F/Sat16-2150R and Sat2-1780F/16-*trnK*-2R. For these fragments from 500 up to 900 bp (division of the entire *trnK* intron in four or six parts) the cycles were modified to 94° C for 45 sec, T_m (°C) for 45 sec and 72°C for 1 min using the specific melting temperature (T_m) for each primer pair as provided in Table 2.

For examination of infrageneric relationships within *Micromeria* for all samples of this genus and of some selected additional taxa (*Satureja montana*, *Origanum vulgare*, *Thymbra spicata*, *Clinopodium vulgare*, *C. alpinum*) the *trnL-F* region was amplified as described previously (Bräuchler & al., 2004) using the primers of Taberlet & al. (1991). PCR products were purified and sequenced directly using the same primers as for amplification. Sequencing was performed as described elsewhere (Bräuchler & al., 2004) using an ABI 377 automated sequencer.

Table 2. Primers designed for this study including names, sequences, positions according to the reference sequence of *Micromeria inodora* (for Acc. No. see Appendix 1), and the melting temperatures (T_m) used for annealing in PCR cycles.

Primer	Sequence	Position	T_m [°C]
Sat2-500F	CGA AAT CAA AAG AGC GAT TGG	430–450	55.9
Sat16-880R	AAT CGT TTC ACA ATC CGT AAA C	822–843	54.7
Sat2-880F	GTT TAC GGA TTG TGA AAC GAT T	822–843	54.7
Sat16-1000R	CAG AGG GGT TTG CTT TTA TTG	948–968	55.9
Sat2-1000F	CAA TAA AAG CAA ACC CCT CTG	948–968	55.9
Sat16-1200R	CTC ATG TAT GTG AAT ACG AAT C	1308–1329	54.7
Sat2-1200F	GAT TCG TAT TCA CAT ACA TGA G	1308–1329	54.7
Sat16-1780R	TGG TAC GGA GTC AAA TTC TAG	1695–1715	55.9
Sat2-1780F	TCT AGA ATT TGA CTC CGT ACC	1695–1715	55.9
Sat16-2150R	TCA TAT CCA AAT ACC AAA TCC G	2132–2153	54.7

Table 3. Characteristics of the alignment (number of sequences included) and statistics of MP analysis.

		combined analysis (29)		
Characteristic	***trnK*** (51)	***trnK***	***trnL-F***	***trnK/trnL-F***
aligned length (excl. 80 positions)	2456	2373	841	3214
number of indels	48	8	12	20
number of indels coded	46	8	9	17
number of potentially informative indels coded	17	3	4	7
number of autapomorphic indels	29	5	5	10
number of constant sites	1918	2271	801	3072
number of potentially informative sites	236	46	21	67
number of autapomorphic sites	302	56	19	75
CI	0.842	0.917	0.962	0.910
RI	0.883	0.952	0.982	0.950
CI excl. uninformative positions	0.712	0.831	0.929	0.824
RC	0.743	0.873	0.945	0.864
number of equally most parsimonious trees	4	4	1	2
length of strict consensus tree	795	121	-	178
length of shortest most parsimonious tree	793	120	53	175

Alignment and phylogenetic analysis. — Sequences were aligned manually with each indel coded as an additional binary character in a separate matrix which was attached at the end of the sequence alignment before creating the nexus file. Indels resulting from poly A or T repeats were not coded. Eighty bases were excluded from the analysis, corresponding to positions 692 and 1270–1348 of the sequence of *Micromeria inodora*. The resulting data matrix was subsequently analysed using PAUP version 4.0b10 (Swofford, 2002). All heuristic searches were carried out using 10 random addition sequence replicates, TBR swapping, MULTREES option and one tree held at each step. Bootstrap values (bs) from 1000 replicates were calculated (Felsenstein, 1981). Strict consensus trees were constructed from all most parsimonious trees. The sequences reported in this study are available from GenBank; their accession numbers are provided in Appendix 1. The alignment is available from the authors upon request. To assess character congruence between the *trnK* and the *trnL-F* dataset (excluding indels) a partition homogeneity test as implemented in PAUP 4.0b10 (Swofford, 2002) was performed with the same heuristic search settings as used in the phylogenetic analysis. The test included 1000 replicates with a maxtrees setting of 100 per replicate.

RESULTS

In Figs. 2 and 3 tree topologies of the *trnK* phylogeny alone and the reduced combined *trnK*/*trnL-F* analysis are shown. For the latter both datasets have been combined as the homogeneity partition test revealed significant congruence (p-value = 0.75). Alignment and maximum parsimony specifications are summarised in Table 3. Positions and length of indels along with names of taxa with sequences containing these indels are shown in Appendices 2 and 3.

For the *trnK* intron dataset the matrix included sequences from 51 samples of 45 taxa from the genera *Micromeria* (24), *Satureja* (3), *Clinopodium* (10), *Monarda* (1), *Origanum* (1), *Thymbra* (1), *Thymus* (1) along with one each of several members of subfamily Nepetoideae (*Glechoma*, *Agastache*, *Nepeta*, *Horminum*, *Lycopus* and *Salvia* of tribe Mentheae; *Plectranthus* of tribe Ocimeae and *Collinsonia* of tribe Elsholtzieae) and two outgroup taxa from subfamily Ajugoideae, *Ajuga reptans* and *Clerodendrum thomsoniae*.

In the topology of the strict consensus tree (Fig. 2) a core group (bs = 100) containing species of *Micromeria*, *Satureja*, *Thymbra*, *Origanum*, *Thymus*, *Clinopodium* and *Monarda* is indicated. The remaining taxa of subfamily Nepetoideae, *Collinsonia canadensis*, *Plectranthus fruticosus*, *Salvia coccinea*, *Lycopus europaeus*, *Horminum pyrenaicum* and a lineage containing *Nepeta supina* along with *Agastache foeniculum* and *Glechoma hederacea* are subsequent sisters to this core group, mostly separated with high bootstrap support (Fig. 2). The core group including all species of *Micromeria* is divided into four clades (A–D, Fig. 2) all supported by high bootstrap values from 86 to 100. In the strict consensus tree these four lineages are shown as a polytomy.

The first lineage (clade A, bs = 86) of the core group is formed by taxa of the genera *Thymbra*, *Thymus* and *Origanum*, indicating the first as sister to the latter two, which are grouped together with maximum support (bs = 100). *Satureja* s.s. is indicated as a second monophyletic group (clade B, bs = 86), with *S. thymbra* from Crete as sister to *S. montana* (Mediterranean) and *S. mutica* (Persia) (bs = 86).

A third lineage (clade C, bs = 98) consists of *Clinopodium* species along with two species of *Micromeria* section *Pseudomelissa* (*M. fruticosa*, *M. thymifolia*) and *Monarda bradburiana*. Within this clade,

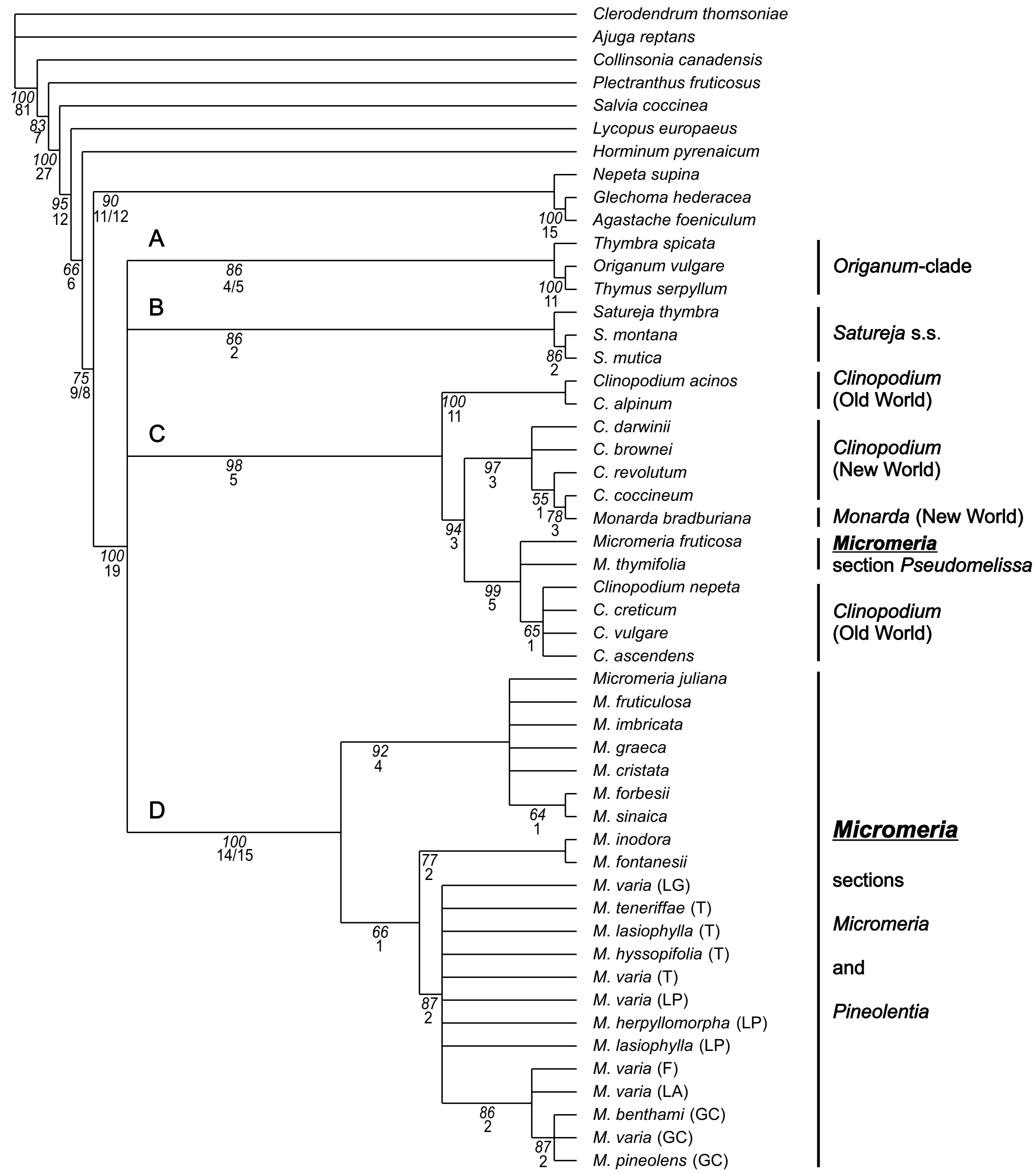

Fig. 2. Strict consensus cladogram of the four most parsimonious trees based on *trnK* intron sequence data. Bootstrap values (italic, upper numbers) and branch lengths (lower numbers) are indicated below each branch (in case two branch lengths are indicated, both appear in 50% of the single most parsimonious trees). Bootstrap values are expressed as percentages of 1000 bootstrap replications. Branches with support less than 50% are shown as polytomies. Current taxonomic identities of clades are given on the right, partly with geographic origin. Clades A–D indicate the core group polytomy. F = Fuerteventura, GC = Gran Canaria, LA = Lanzarote, LG = La Gomera, LP = La Palma, T = Tenerife.

Clinopodium acinos and *C. alpinum*, both members of former genus *Acinos* Mill., are grouped together with maximum bootstrap support (bs = 100) and are clearly separated from the remainders (bs = 94). These are split

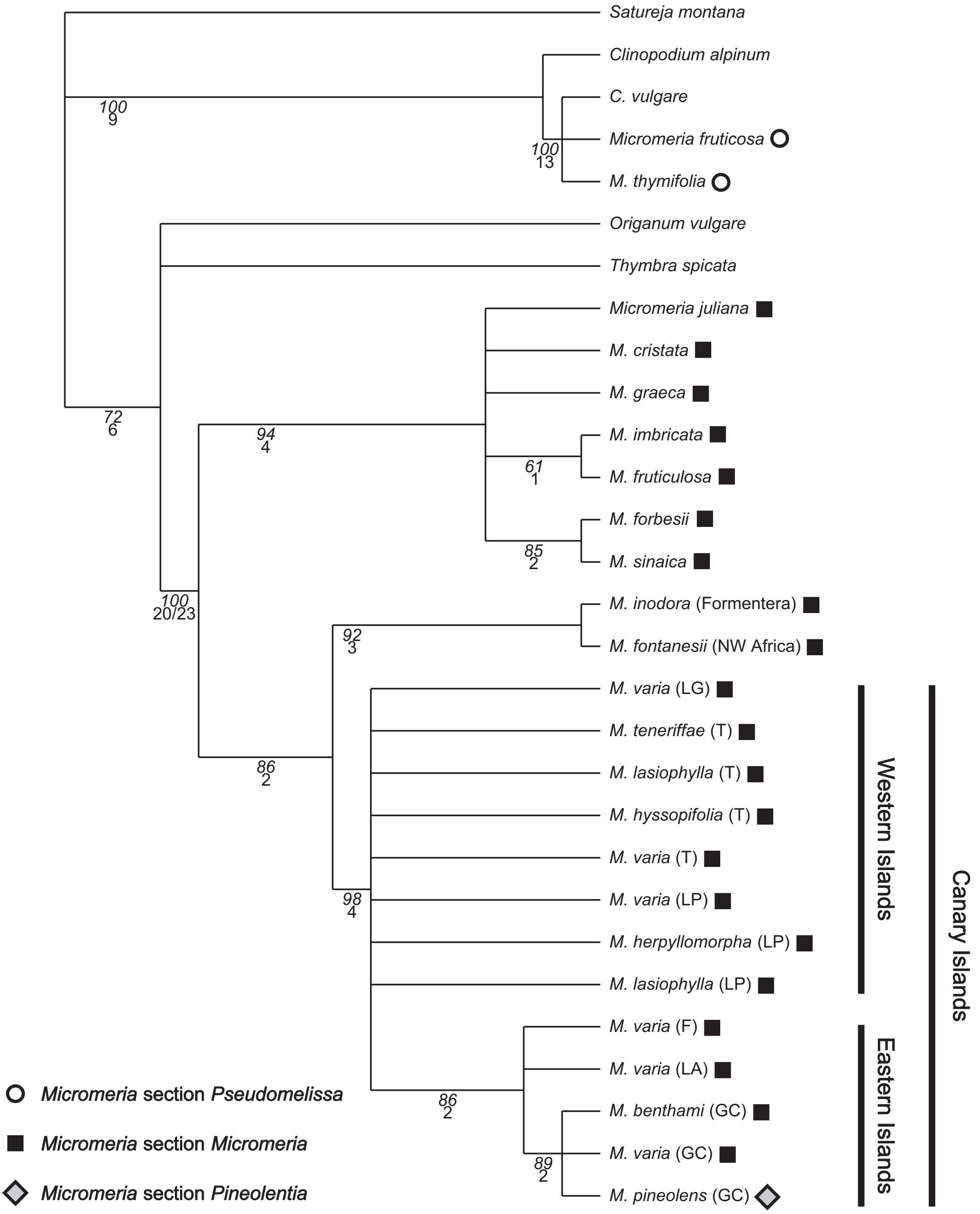

Fig. 3. Strict consensus cladogram of the two most parsimonious trees, based on the combined sequence dataset of *trnK* and *trnL-F*. Bootstrap values (italic, upper numbers) and branch lengths of single most parsimonious trees (lower numbers) are indicated below each branch (as in Fig. 2). Bootstrap values are expressed as percentages of 1000 bootstrap replications. Branches with support less than 50% are shown as polytomies. Symbols following taxon name indicate sectional affiliation. Geographic origins of Canarian taxa are given to underline their monophyly and separation in eastern and western lineages. F = Fuerteventura, GC = Gran Canaria, LA = Lanzarote, LG = La Gomera, LP = La Palma, T = Tenerife.

into two subclades exclusively containing New World taxa (bs = 97) on the one hand and Old World taxa on the other hand (bs = 99). The New World group contains *Clinopodium darwinii*, *C. brownei*, *C. revolutum* and *C.*

coccineum, all transferred to *Clinopodium* recently (Cantino & Wagstaff, 1998; Harley & Granda, 2000) plus *Monarda bradburiana*. The North American *Clinopodium coccineum* and *Monarda bradburiana* together (bs = 78) are indicated as sister to the South American *Clinopodium revolutum* though with low support (bs = 55). Affinities of *C. darwinii* (SW South America) and *C. brownei* (Bahama Islands) are not clear, as these two species are shown in a polytomy to the latter group. Within the Old World lineage *Micromeria fruticosa* and *M. thymifolia* are indicated in a polytomy with a moderately supported (bs = 65) European/ Mediterranean assembly of *Clinopodium* species (namely *C. vulgare*, *C. creticum*, *C. nepeta*, *C. ascendens*). The position of *Monarda* and *Micromeria* section *Pseudomelissa* renders *Clinopodium* paraphyletic in the *trnK* analysis.

While members of *Micromeria* section *Pseudomelissa* (*Micromeria fruticosa* and *M. thymifolia*) are embedded within *Clinopodium*, samples of all other *Micromeria* species included in this study are grouped in a well defined monophyly (clade D, bs = 100). To increase resolution this clade was investigated using the *trnL-F* region, additionally resulting in a reduced combined *trnK*/*trnL-F* sequence data matrix (see materials and methods). In the strict consensus tree of the combined analysis (Fig. 3) clade B (represented by *Satureja montana*) and clade C of Fig. 2 (represented by *Clinopodium alpinum*, *C. vulgare*, *Micromeria fruticosa* and *M. thymifolia*) are also shown as distinct lineages, whereas *Origanum* and *Thymbra* (representing clade A of Fig. 2) are moderately supported (bs = 72) shown as neighbours to the clade containing exclusively *Micromeria* species. However this position could also be influenced by reduced sampling of investigated taxa.

The monophyletic main group of *Micromeria* (clade D, Fig. 2) shows maximum bootstrap support in the combined *trnK*/*trnL-F* as well as in the *trnK* analysis alone (bs = 100/100) and is split in two subclades. In both analyses (bs = 94/92) the first subclade contains samples of *Micromeria* imbricata, *M. fruticulosa*, *M. juliana*, *M. graeca*, *M. cristata*, *M. forbesii* and *M. sinaica*, with an overall distribution range from the Himalayan region to the western Mediterranean and as far as the Cape Verde Islands. The second subclade (bs = 86/66) includes taxa from the West Mediterranean region, NW Africa and the Canary Islands. Within this "western lineage" *M. inodora* (Formentera, Balearic Islands) and *M. fontanesii* (NW Africa) are linked (bs = 92/77) and sister to a clade comprising all taxa from the Canary Islands (bs = 98/87). Canarian *Micromeria* species therefore are strongly indicated as monophyletic. Taxa from the eastern islands (Gran Canaria, Fuerteventura and Lanzarote) are shown as a distinct evolutionary lineage (bs = 86/86). Samples from Gran Canaria (representing *M. benthami*, *M. varia*, *M. pineolens*) appear monophyletic (bs = 89/87) and are grouped together with *M. varia* from Fuerteventura and Lanzarote. All samples from the western islands (Tenerife, La Palma, La Gomera) without further resolution are placed at the base of the eastern lineage.

Though in the combined analysis with the *trnL-F* region ca. 900 bp more have been included, no better infrageneric fine-scale resolution within *Micromeria* could be achieved as with the *trnK* analysis alone. However, as seen above, bootstrap support for internal nodes of *Micromeria* was overall increased by combining the two datasets. With *Micromeria fruticosa* and *M. thymifolia* embedded within members of the genus *Clinopodium* and all other *Micromeria* species assigned to a different clade of the core group in both the single *trnK* and the combined *trnK*/*trnL-F* analysis, *Micromeria* as currently circumscribed (Harley & al., 2004) is presumed to be polyphyletic.

DISCUSSION

Since Bentham (1848), close relationships between *Micromeria*, *Clinopodium*, *Satureja*, *Thymus*, *Thymbra* and *Origanum* have not been questioned substantially, though minor changes in the placement of single genera within the higher level system have been done from treatment to treatment (Doroszenko, 1986). Despite a consensus about common origin, the generic boundaries have been severely disputed, as species can be found that show intermediate characters linking one genus to the other (Ietswaart, 1980). Our data show the core group as an assembly of closely related genera so far confirming former assumptions. The position of *Monarda* within this group traditionally has not been discussed; both Bentham (1848) and Briquet (1895–1897) even placed it in a different tribe (Monardeae Benth.). First hints on a closer relationship have been given by the findings of Wagstaff & al. (1995) and Cantino & Wagstaff (1998) from cpDNA restriction site data. Their work probably influenced the concept of Harley & al. (2004), who placed all taxa included in our core group in subtribe Menthinae of tribe Mentheae. Along with support for monophyly of this subtribe, our data reveal new aspects especially concerning generic boundaries within the core group.

A closer relationship between *Thymbra*, *Thymus* and *Origanum* as shown in our tree topology was also assumed by Ietswaart (1980) due to similarities in calyx structure and inflorescence. Strong affinities between members of the genera *Origanum* and *Micromeria* based on phenetic similarities and chromosome numbers (Ietswaart, 1980) seem to be indicated in the combined analysis with *Origanum* and *Thymbra* as neighbour group to *Micromeria*. However, as stated above, this position could be a result of reduced sampling and needs further investigation.

In our analysis, species of *Satureja* s.s. are shown in a strongly supported monophyly. The generic distinctiveness of *Satureja* s.s. (Bentham, 1848) has been rejected by Briquet (1895–1897) and more recently by Greuter & al. (1986) but has also been at least equivocally accepted (López, 1982; Davis, 1982b; Harley & al., 2004). Our molecular data are also strongly supported by morphological traits, as *Satureja* s.s. is the only genus showing conduplicate leaves with glands all over the surface.

The most interesting findings of our study concern the genera *Clinopodium* (sensu Harley & al., 2004) and *Micromeria*. The status of former *Micromeria* sections *Xenopoma* and *Hesperothymus* (Morales, 1993) as members of *Clinopodium* (Cantino & Wagstaff, 1998; Harley & Granda, 2000) once more is strongly supported by our data where the sections are represented by *Clinopodium darwinii* and *C. brownei*, respectively. However the position of *Monarda* in our tree topologies renders *Clinopodium* paraphyletic. While Cantino & Wagstaff (1998) still maintained the generic rank of *Monarda* due to phenetic distinctness in combination with an uncertain affinity in the molecular data (Wagstaff & al., 1995), our analysis reveals that, if one wants to avoid paraphyly, *Monarda* probably should be included in *Clinopodium* sensu Harley & al. (2004).

The placement of section *Pseudomelissa* within the *Clinopodium* clade has important implications on generic concepts within the study group. The position of *Micromeria fruticosa* and *M. thymifolia* (section *Pseudomelissa*) reveals *Clinopodium* as paraphyletic and in reverse the genus *Micromeria* as polyphyletic. Although only two species of section *Pseudomelissa* have been investigated using molecular methods, the transfer of the section as a whole to the genus *Clinopodium* is suggested, as *Micromeria fruticosa* and *M. thymifolia* are indicated as closely related to the type species *Clinopodium vulgare* with high support from both markers. Striking similarities to *Calamintha* Mill., which along with *Acinos* is regarded to be part of *Clinopodium* (Stace, 1991; Harley & al., 2004), and apparent differences to other sections of *Micromeria* in leaf anatomy confirmed the assumption of Doroszenko (1986) on a close relationship of section *Pseudomelissa* to the genus *Calamintha* (now *Clinopodium*). However, he continued to keep *Pseudomelissa* under *Micromeria*. Briquet (1895–1897) regarded the species of section *Pseudomelissa* as intermediate between section *Piperelloides* (*Micromeria* sections *Micromeria* and *Xenopoma*, sensu Morales, 1993) and section *Calamintha* of his *Satureja* s.l. A survey of herbarium specimens of *Clinopodium* and all recognised sections of *Micromeria* showed that the similarity between *Clinopodium* and *Micromeria* section *Pseudomelissa* especially concerning leaf margin and shape is obvious. Finally the reported chromosome numbers for section *Pseudomelissa* ($2n$ = 20, 22; Morales, 1993) fit much better with those of *Clinopodium* species ($2n$ = 22, 24, 48 in Morales & Luque, 1997; $2n$ = 20 for *C. vulgare* in Van Loon & Van Setten, 1982) than to those reported for *Micromeria* section *Micromeria* ($2n$ = 30, 50, 60; Morales, 1993). Thus, for reasons of molecular, morphological, and karyological affinities the removal of section *Pseudomelissa* from *Micromeria* and its transfer to *Clinopodium* seems justified. The rank of this taxon at subgeneric level remains to be clarified. A list of new combinations, synonyms and valid names is in preparation.

The placement of *Monarda* and *Micromeria* section *Pseudomelissa* together with the position of *Clinopodium acinos* and *C. alpinum* as sister to the remainders of *Clinopodium* in our phylogenetic analysis emphasises the necessity of a thorough morphological and molecular revision of the genus *Clinopodium*.

The remaining species of *Micromeria* (including the type species *M. juliana*) are shown as a strongly supported monophyly and therefore are indicated as a natural group. Only these representatives of the traditional genus *Micromeria* remain in line with *M. juliana*, all characterised by at least one morphological synapomorphy, which is a thickened leaf margin (Doroszenko, 1986; Ryding, pers. comm.).

Reevaluation of the sectional concepts of *Micromeria* is incomplete, as material of the poorly collected *M. cymuligera* (endemic to SE Turkey and only member of section *Cymularia*) could not be obtained for our molecular analysis. The isolated position of this species due to special structure of the anther connective, annual growth form, and a resupinate flower has been mentioned frequently (Davis, 1982c; Doroszenko, 1986; Harley & al., 2004). There is evidence from *Echium* (Böhle & al., 1996) that annual species can evolve from perennial progenitors in a quite short period. Thus, the annual habit of *M. cymuligera* could be a recent adaption to the alpine habitat where it occurs (Davis, 1982c). Examination of type material (iso JE!, W!) reveals an overall similarity of this species to taxa of section *Micromeria*, as already suggested by Davis (1982c) and Doroszenko (1986), but further investigations are necessary.

Pérez's (1978) concept of placing *M. pineolens* together with *M. leucantha* in a section of its own (section *Pineolentia*) seems not appropriate, as our data suggest that section *Pineolentia* originated from an existing species (probably *M. varia*). The remarkable morphological divergence of these taxa (Pérez, 1978), therefore, is most likely not due to long separation between sections *Micromeria* and *Pineolentia* or an independent rapid development of each taxon on the Canary Islands. One might hypothesize that the robust shrubby habit and large leaves of section *Pineolentia* could have evolved under similar selection pressures as woody growth forms in *Echium* (Böhle & al., 1996) or *Sonchus* (Kim & al., 1996).

Within *Micromeria* one group showing a wide distribution, mainly in the Mediterranean and North Africa, but also reaching as far as the Himalayan region and South Africa, is sister to representatives native to the western Mediterranean and Macaronesia (excluding Cape Verde Islands). Our data favour the hypothesis of a single colonisation event on the Canary Islands starting from the western Mediterranean/NW Africa, with monophyly of the eastern islands species indicating a colonisation from east to west. Detailed investigations concerning mechanisms of radiation and speciation of *Micromeria* on the Canary Islands are in progress. Especially the generic recircumscription of *Micromeria*, its infrageneric subdivision and affinities to *Origanum* and *Thymbra*, as well as relationships within the expanding genus *Clinopodium*, are subject of ongoing research.

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Appendix 1. List of taxa investigated, including synonyms (names on labels differing from valid taxon name are underlined), voucher specimen data (country/source, collector, number, date, herbarium acronym; image numbers for specimens scanned at B are listed additionally) and GenBank accession number. BGM = Bot. Garten München.

Taxon, Synonyms, Source, Accession (*trnK/trnL-F*)

Agastache foeniculum (Pursh) Kuntze, -, cult. BGM, *Bräuchler 2513*, 26 Jun 2003, M, AY840146; ***Ajuga reptans*** L., -, cult. BGM, *Bräuchler 2508*, 26 Jun 2003, M, AY840130; ***Clerodendrum thomsoniae*** Balf., -, cult. BGM, *Bräuchler 2511*, 26 Jun 2003, M, AY840129; ***Clinopodium acinos*** (L.) Kuntze, *Calamintha arvensis* Lam., *Acinos arvensis* (Lam.) Dandy, *Thymus acinos* L., *Satureja acinos* (L.) Scheele, France, *Podlech 50287*, 21 Jun 1992, M, AY840144; ***C. alpinum*** (L.) Kuntze, *Thymus alpinus* L., *Satureja alpina* (L.) Scheele, *Acinos alpinus* (L.) Moench, cult. BGM, *Bräuchler 2502*, 26 Jun 2003, M, AY840145/AY840180; ***C. ascendens*** (Jordan) Samp., *Calamintha ascendens* Jordan, *Calamintha sylvatica* Bromf. subsp. *ascendens* (Jordan) P.W. Ball, France, *Bellotte 89/1994*, 04 Oct 1994, M, AY840152; ***C. brownei*** (Sw.) Kuntze, *Thymus brownei* Sw., *Micromeria brownei* (Sw.) Benth., *Micromeria domingensis* Shinners, *Satureja brownei* (Sw.) Briq., Bahamas, Inagua, *Gillis & Proctor 11737*, 18 Feb 1973, B, AY840176; ***C. coccineum*** (Hook.) Kuntze, *Cunila coccinea* Hook., *Calamintha coccinea* (Hook.) Benth., *Satureja coccinea* (Hook.) Bert., *Diodeilis coccinea* (Nutt.) Rafin., U.S.A., Florida, *Bridges 12136*, 14 Sep 1989, M, AY840150; ***C. creticum*** (L.) Kuntze, *Melissa cretica* L., *Calamintha cretica* (L.) Lam., *Satureja cretica* (L.) Briq., Greece, Crete, *Merxmüller & Podlech 30851*, 26 Sep 1975, M, AY840175; ***C. darwinii*** (Benth.) Kuntze, *Micromeria darwinii* Benth., *Satureja darwinii* (Benth.) Briq., Chile, *Landero 655*, 09 Jul 1986, M, AY840171; ***C. nepeta*** (L.) Kuntze, *Melissa nepeta* L., *Calamintha nepeta* (L.) Savi, *Satureja nepeta* (L.) Scheele, cult. BGM, *Bräuchler 2392*, 26 Jun 2003, M, AY840151; ***C. revolutum*** (Ruiz & Pav.) Govaerts, *Gardoquia revoluta* Ruiz & Pav., *Satureja revoluta* (Ruiz & Pav.) Briq., Peru, *Dostert 98/195*, 16 May 1998, M, AY840170; ***C. vulgare*** L., *Micromeria clinopodium* Benth., *Satureja clinopodium* Car., Spain, *Morales & Vitek 97-269*, 16 Jul 1997, M, AY840153/AY840185; ***Collinsonia canadensis*** L., -, cult. BGM, *Bräuchler 2412*, 26 Jun 2003, M, AY840148; ***Glechoma hederacea*** L., -, cult. BGM, *Bräuchler 2504*, 26 Jun 2003, M, AY840143; ***Horminum pyrenaicum*** L., -, cult. BGM, *Bräuchler 2507*, 26 Jun 2003, M, AY840177; ***Lycopus europaeus*** L., -, cult. BGM, *Bräuchler 2505*, 26 Jun 2003, M, AY840154; ***Micromeria benthami*** Webb & Berth., *Satureja benthamii* (Webb & Berth.) Briq., *Clinopodium benthamii* (Webb & Berth.) Kuntze, Spain, Canary Islands, Gran Canaria, *Meimberg cc40b*, 18 Apr 2003, M, AY840131/AY840183; ***M. cristata*** (Hampe) Griseb., *Thymus cristatus* Hampe, *Satureja cristata* (Hampe) Nym., *Clinopodium cristatum* (Hampe) Kuntze, Yugoslavia, Serbia, *Stevanovic s.n.*, 20 Apr 2003, M, AY840156/AY840194; ***M. fontanesii*** Pomel, *Satureja battandieri* Briq., Morocco, *Podlech s.n.*, 05 Jul 1989, M, AY840158/AY840195; ***M. forbesii*** Benth., *Satureja forbesii* (Benth.) Briq., *Clinopodium forbesii* (Benth.) Kuntze, Cap Verde, *Kilian 1123*, 13 Jan1986, B (Image-nr. B 10 0086724), AY840128/AY840192; ***M. fruticosa*** (L.) Druce, *Melissa fruticosa* L., *Satureja fruticosa* (L.) Briq., *Clinopodium fruticosum* (L.) Kuntze, Spain, *Lippert 25633*, 05 Sep 1989, M, AY840161/AY840197; ***M. fruticulosa*** (Bertol.) Silic, *Thymus fruticulosus* Bertol., *Satureja fruticulosa* (Bertol.) Grande, Italy, Sicily, *Erben s.n.*, 19 Apr 1994, M, AY840174/AY840196; ***M. graeca*** (L.) Rchb., *Satureja graeca* L., *Clinopodium graecum* (L.) Kuntze, Spain, *Podlech 51192*, 12 Apr 1996, M, AY840157/AY840198; ***M. herpyllomorpha*** Webb & Berth., *Satureja herpyllomorpha* (Webb & Berth.) Briq., Spain, Canary Islands, La Palma, *Franke lp27*, 04 Dec 2002, M, AY840137/AY840190; ***M. hyssopifolia*** Webb & Berth., *Satureja hyssopifolia* (Webb & Berth.) Briq., Spain, Canary Islands, Tenerife, *Heubl ten44*, M, AY840140/AY840204; ***M. imbricata*** (Forssk.) C. Chr., *Thymus imbricatus* Forssk., *Thymus biflorus* D. Don, *Micromeria biflora* (D. Don.) Benth., *Satureja biflora* (D. Don) Briq., Afghanistan, *Anders 11049*, 30 Aug 1973, M, AY840155/AY840193; ***M. inodora*** (Desf.) Benth., *Thymus inodorus* Desf., *Satureja barceloi* (Willk.) Pau, cult. BGM (wild coll. Spain, Formentera), *Bräuchler 2423*, 20 Jul 2003, M, AY840149/AY840181; ***M. juliana*** (L.) Rchb., *Satureja juliana* L., *Clinopodium julianum* (L.) Kuntze, cult. BGM, *Bräuchler 2411*, 26 Jun 2003, M, AY840159/AY840199; ***M. lasiophylla*** Webb & Berth., *Satureja lasiophylla* (Webb & Berth.) Briq., Spain, Canary Islands, Tenerife, *Heubl ten46*, 04 Oct 2003, M, AY840141/AY840205; ***M. lasiophylla*** Webb & Berth., -, Spain, Canary Islands, La Palma, *Franke lp19*, 04 Dec 2002, M, AY840136/AY840189; ***M. pineolens*** Svent., -, Spain, Canary Islands, Gran Canaria, *Meimberg cc36b*, 18 Apr 2003, M, AY840178/AY840182; ***M. sinaica*** Benth., *Satureja sinaica* (Benth.) Briq., *Clinopodium sinaicum* (Benth.) Kuntze, Israel, *Danin s.n.*, 20 Apr 1992, B (Image-nr. B 10 0086716), AY840160/AY840200; ***M. teneriffae*** (Poir.) Benth., *Thymus teneriffae* Poir., *Satureja tener-*

Appendix 1 (continued.)

iffae (Poir.) Briq., Spain, Canary Islands, Tenerife, *Heubl ten71*, 06 May 2002, M, AY840142/AY840206; ***M. thymifolia*** (Scop.) Fritsch, *Satureja thymifolia* Scop., *Clinopodium thymifolium* (Scop.) Kuntze, Croatia, *Künne s.n.*, Aug 1994, M, AY840162/AY840201; ***M. varia*** Benth., *Satureja varia* (Benth.) Briq., Spain, Canary Islands, La Gomera, *Franke gof20*, 12 Mar 2003, M, AY840134/AY840187; ***M. varia*** Benth., -, Spain, Canary Islands, Tenerife, *Heubl ten26*, M, AY840139/AY840203; ***M. varia*** Benth., -, Spain, Canary Islands, La Palma, *Franke lp31*, 04 Dec 2002, M, AY840138/AY840191; ***M. varia*** Benth., -, Spain, Canary Islands, Fuerteventura, *Heubl FU16*, 28 Feb2003, M, AY840133/AY840186; ***M. varia*** Benth., -, Spain, Canary Islands, Lanzarote, *Heubl LA19*, 02 Mar 2003, M, AY840135/AY840188; ***M. varia*** Benth., -, Spain, Canary Islands, Gran Canaria, *Meimberg cc9a*, 12 Apr 2003, M, AY840132/AY840184; ***Monarda bradburiana*** Beck, -, cult. BGM, *Bräuchler 2506*, 26 Jun 2003, M, AY840163; ***Nepeta supina*** Stev., -, Georgia, *Gröger & Schewardnadse 1466*, 15 Aug 2003, M, AY840164; ***Origanum vulgare*** L., -, cult. BGM, *Bräuchler 2512*, 26 Jun 2003, M, AY840165/AY840202; ***Plectranthus fruticosus*** L´Hér., -, cult. BGM, *Bräuchler 2510*, 26 Jun 2003, M, AY840166; ***Salvia coccinea*** Murr., -, cult. BGM, *Bräuchler 2390*, 26 Jun 2003, M, AY840147; ***Satureja montana*** L., *Micromeria montana* (L.) Rchb., *Clinopodium montanum* (L.) Kuntze, cult. BGM, *Bräuchler 2509*, 26 Jun 2003, M, AY840167/AY840179; ***S. mutica*** Fisch. & C. A. Mey., -, Iran, *Akhani 12362*, 18 Nov 1996, M, AY840169; ***S. thymbra*** L., *Micromeria thymbra* (L.) Kostel., *Clinopodium thymbra* (L.) Kuntze, Greece, Crete, *Bräuchler 2896*, 02 Apr 2004, M, AY840168; ***Thymbra spicata*** L., -, Israel, *Keller & Shammash 14432*, 07 Jun 1989, M, AY840172/AY840207; ***Thymus serpyllum*** L., -, cult. BGM, *Bräuchler 2514*, 26 Jun 2003, M, AY840173.

Appendix 2. Coded indels of the *trnK* matrix with alignment positions, length, number and names of taxa with sequences containing indels indicated.

Position	Length	Number and taxa with indel present
25	1	1 (*Nepeta*)
165	1	1 (*Ajuga*)
210–212	3	2 (*Agastache*, *Glechoma*)
231–234	4	1 (*Plectranthus*)
239–243	5	1 (*Plectranthus*)
313–315	1-3	not coded
334–338	5	1 (*Collinsonia*)
341–350	10	2 (*Ajuga*, *Clerodendrum*)
368–370	1 and 3	not coded
392	1	2 (*Lycopus*, *Nepeta*)
422–423	2	22 (*Micromeria* sections *Micromeria* and *Pineolentia*)
425	1	1 (*Salvia*)
459	1	4 (*Ajuga*, *Clerodendrum*, *Collinsonia*, *Plectranthus*)
460	1	1 (*Agastache*)
484	1	1 (*Glechoma*)
523–530	8	1 (*Micromeria inodora*)
531–535	5	2 (*Ajuga*, *Clerodendrum*)
544–548	5	3 (*Ajuga*, *Clerodendrum*, *Agastache*)
568–569	2	2 (*Ajuga*, *Clerodendrum*)
574–575	2	1 (*Ajuga*)
621–627	7	2 (*Clinopodium coccineum*, *Monarda bradburiana*)
938–943	6	1 (*Micromeria fruticulosa*)
1276–1290	15	1 (*Plectranthus*)
1279–1290	12	2 (*Horminum*, *Thymus*)
1285–1290	6	1 (*Clinopodium revolutum*)
1401–1406	6	1 (*Collinsonia*)
1437–1443	7	2 (*Ajuga*, *Clerodendrum*)
1690–1692	3	1 (*Collinsonia*)
2096–2098	3	2 (*Agastache*, *Glechoma*)
2182–2188	7	24 (all but *Micromeria* sections *Micromeria* and *Pineolentia*, *Satureja*, *Agastache*, *Nepeta*)
2185–2190	6	1 (*Salvia*)
2195–2200	6	1 (*Collinsonia*)
2208–2213	6	1 (*Nepeta*)
2226–2232	7	2 (*Ajuga*, *Clerodendrum*)
2233–2280	48	3 (*Origanum*, *Thymbra*, *Thymus*)
2238–2257	20	1 (*Salvia*)
2241–2252	10	1 (*Nepeta*)
2242–2245	4	1 (*Micromeria thymifolia*)
2246–2253	8	1 (*Ajuga*)
2262–2274	13	1 (*Collinsonia*)
2263–2274	12	1 (*Ajuga*)
2263–2282	20	1 (*Clerodendrum*)
2290–2302	13	1 (*Nepeta*)
2295–2300	6	3 (*Ajuga*, *Clerodendrum*, *Horminum*)
2329	1	1 (*Collinsonia*)
2363–2367	5	1 (*Lycopus*)
2377–2380	4	41 (*Menthinae*)
2407–2411	5	1 (*Origanum*)

Appendix 3. Indels of the reduced combined *trnK/trnL-F* matrix with alignment positions, length, number and names of taxa with sequences containing indels indicated.

trnK

Position	Length	Number and names of taxa with indel present
300	1	1 (*Satureja*)
394–395	2	22 (*Micromeria* sections *Micromeria* and *Pineolentia*)
493–500	8	1 (*Micromeria inodora*)
899–904	6	1 (*Micromeria fruticulosa*)
2118–2124	7	6 (*Clinopodium alpinum*, *C. vulgare*, *Micromeria fruticosa*, *M. thymifolia*, *Origanum*, *Thymbra*)
2156–2203	44	2 (*Origanum*, *Thymbra*)
2165–2168	4	1 (*Micromeria thymifolia*)
2324–2328	5	1 (*Origanum*)

trnL-F

Position	Length	Number and names of taxa with indel present
2439–2442	4	22 (*Micromeria* sections *Micromeria* and *Pineolentia*)
2450–2455	6	1 (*Clinopodium vulgare*)
2465–2484	20	1 (*Origanum*)
2477	1	not coded
2485–2489	1–6	not coded
2573–2578	6	23 (*Micromeria* sections *Micromeria* and *Pineolentia*)
2653	1	1 (*Thymbra*)
2911	1	22 (*Micromeria* sections *Micromeria* and *Pineolentia*)
2925–2930	1–6	not coded
3044–3048	5	1 (*Satureja*)
3071–3074	4	1 (*Satureja*)
3101–3110	10	3 (*Clinopodium vulgare*, *Micromeria thymifolia* and *M. fruticosa*)

6.2 Manuskript 2:
Bräuchler, C., Meimberg, H. & Heubl, G. 2006: New names in Old World *Clinopodium* – the transfer of the species of *Micromeria* sect. *Pseudomelissa* to *Clinopodium*. Taxon 55(4): 977-981.

New names in Old World *Clinopodium*—the transfer of the species of *Micromeria* sect. *Pseudomelissa* to *Clinopodium*

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Micromeria has recently been revealed polyphyletic by molecular analyses, with members of sect. *Pseudomelissa* placed in close relationship to *Clinopodium vulgare*. Morphological data suport transferring the section to *Clinopodium*. A list of names under *Clinopodium* (including 15 new combinations) is provided for the taxa hitherto included in *Micromeria* sect. *Pseudomelissa*. Three species names are typified.

KEYWORDS: *Clinopodium*, Lamiaceae, *Micromeria*, sect. *Pseudomelissa*, taxonomy, typification.

INTRODUCTION

In the last 100 years many treatments have dealt with the taxonomy of *Satureja* s.l., either splitting the complex into different genera (*Satureja* L., *Clinopodium* L., *Calamintha* Mill., *Micromeria* Benth., *Acinos* Mill. to mention but a few; Bentham, 1848; Boissier, 1879; Ball & Getliffe, 1972; Davis, 1982; Doroszenko, 1986) or lumping all together in *Satureja* (Briquet, 1895–97; Greuter & al., 1986) or *Clinopodium* (Kuntze, 1891). Recent molecular studies (Wagstaff & al., 1995; Prather & al., 2002; Trusty & al., 2004; Bräuchler & al., 2005), however, have favoured abandonment of the concept of *Satureja* s.l. and maintenance of smaller genera. The latter approach has also been adopted by Harley & al. (2004). Thus, *Satureja* was restricted to Old World species with conduplicate, obovate to spathulate leaves (*Satureja* s.s.) and the New World taxa were transferred to the genus *Clinopodium* (Cantino & Wagstaff, 1998; Harley & Granda, 2000).

Thus far, no molecular investigations have been conducted on the generic boundaries among members of the former *Satureja* s.l. complex in the Old World. To close this gap, the authors performed a molecular phylogenetic study to explore relationships in *Micromeria* sensu Harley & al. (2004), including several other genera of subfamily Nepetoideae (Lamiaceae), using two chloroplast markers (*trnK* and *trnL-F*) (Bräuchler & al., 2005). This analysis revealed *Micromeria* to be polyphyletic with *M.* sect. *Pseudomelissa* Benth. nested within *Clinopodium* and most closely related to a clade containing *C. vulgare* L. This section has been regarded as a link between *Micromeria* and *Calamintha* (now included in *Clinopodium*; see Harley & al., 2004) by Doroszenko (1986). Calyx shape has been the most important character for the separation of *Clinopodium* (13-nerved, bilabiate calyx) from *Micromeria* (13-nerved, subequally 5-dentate calyx) (e.g., Bentham, 1848; Boissier, 1879). Despite this delimitation, Bentham (1848) considered the *Pseudomelissa* group to be intermediate between his *Calamintha* (= *Clinopodium*) and *Micromeria*, favouring inclusion in the latter due to subequal calyx teeth and a non gibbous calyx base. However, after the transfer of Bentham's (1848) *Micromeria* sect. *Hesperothymus* and sect. *Xenopoma* to *Clinopodium* (Cantino & Wagstaff, 1998; Harley & Granda, 2000), *M.* sect. *Pseudomelissa* is the only group within *Micromeria* characterised by leaves with a crenate margin and no marginal vein. While unique in *Micromeria*, these characters are very common in *Clinopodium*, clearly suggesting the morphological affinities of the *Pseudomelissa* group to the latter genus. In addition, chromosome numbers are more similar to those found in *Clinopodium* than in other sections of *Micromeria* (Morales, 1993; Morales & Luque, 1997). These facts together with phylogenetic reconstruction based on molecular data (Bräuchler & al., 2005) indicate that the taxonomic importance of calyx characters has been overestimated. Transfer of the species currently included in *Micromeria* sect. *Pseudomelissa* to *Clinopodium* will lead to a clearer distinction between the two genera, with more emphasis on characters derived from, a.o., leaf morphology and anatomy. The transfer would hardly affect the current circumscription of *Clinopodium* (Ryding, pers. comm.), while *Micromeria* would become a more homogeneous taxonomic unit. As *trnL-F* and *trnK* sequences of representatives of *Micromeria* sect. *Pseudomelissa* are almost equal to those of *C. vulgare* the type of *Clinopodium*, transferring the species of

M. sect. *Pseudomelissa* to *Clinopodium* seems well justified.

The still unsatisfactory placement of the aberrant species *Micromeria cymuligera* Boiss. & Hausskn. (*M.* sect. *Cymularia* Boiss.) will be addressed elsewhere.

One problem arising by the transfer of *Micromeria* sect. *Pseudomelissa* to *Clinopodium* is the phylogenetic position of *Monarda* L., which is grouped among New World species of *Clinopodium* (Bräuchler & al., 2005). To avoid paraphyly, transfer of members of the genus *Monarda* to *Clinopodium* might also be considered. At the moment, however, this seems premature given the morphological distinctiveness of *Monarda* as a genus (e.g., only two stamens, hummingbird-pollinated flowers in some species). In addition, some other New World genera such as *Blephilia* Raf., *Minthostachys* (Benth.) Spach and *Hedeoma* Pers. are probably more closely associated with New World *Clinopodium* (Wagstaff & Cantino, 1995; Prather & al., 2002; Trusty & al., 2004; Bräuchler, unpubl.) than traditionally suggested. These problems require more investigation and are beyond the scope of this paper.

Some Asian species included in *Micromeria* sect. *Pseudomelissa* by Doroszenko (1986) have not been mentioned in Morales (1993) (*Micromeria barosma, M. euosma*) or have been included in *Micromeria* sect. *Micromeria* (*M. nepalensis, M. wardii*). Smith (1916) considered the first two species very similar, with *M. euosma* probably deserving only varietal status. Our study of the types and additional collections in E and WU, however indicates that species rank is justified and that the two species are better placed in *Clinopodium* than in *Satureja* or *Micromeria* based on leaf morphology. The same applies to *M. nepalensis* and *M. wardii*: Examination of numerous specimens at BM, E and FR revealed none of the characters typical and unique for *M.* sect. *Micromeria* (e.g., prominent marginal leaf vein). Indeed, preliminary molecular results indicate an affiliation with *Clinopodium* rather than with *Micromeria*. To aid future systematic work on these taxa and to reflect our taxonomic conclusions, a list of names under *Clinopodium* (including 15 new combinations) is provided for the taxa hitherto included in *Micromeria* sect. *Pseudomelissa*. Three species names are typified.

TAXONOMIC SURVEY

Clinopodium abyssinicum (Hochst. ex Benth.) Kuntze, Revis. Gen. Pl. 2: 515 (1891) ≡ *Micromeria abyssinica* Hochst. ex Benth. in DC., Prodr. 12: 224 (1848) ["*Melissa abyssinica* Hochst." in Flora 24(1), Intell. 2: 23 (1841), nom. nud.] ≡ *Calamintha abyssinica* (Hochst. ex Benth.) A. Rich., Tent. Fl. Abyss. 2: 191 (1850) ≡ *Satureja abyssinica* (Hochst. ex Benth.) Briq. in Engler & Prantl, Nat. Pflanzenfam. 4, 3a: 301 (Nov 1896) – Type: [Ethiopia] Abyssinia, plantae Adoense, in regione septentrionali superioris partis et inferioris montis Scholoda, 3.10.1837, *Schimper I, 326* (holotype: K!; isotype: B!, HOH!, JE!, M!, P!, S, STU!, TUB!, UPS).

Clinopodium barosmum (W.W. Sm.) Bräuchler & Heubl, **comb. nov.** ≡ *Calamintha barosma* W. W. Sm. in Notes Roy. Bot. Gard. Edinburgh 9: 88 (1916) ≡ *Micromeria barosma* (W.W. Sm.) Hand.-Mazz., Symb. Sin. 7: 932 (1936) ≡ *Satureja barosma* (W.W. Sm.) Kudo in Mem. Fac. Sci. Taihoku Imp. Univ. 2: 99 (1929). – Type: [China,] Yunnan, mountains in the NE of the Yangtze bend, lat 27° 45′ N, 12000 ft., 7.1913, *G. Forrest 10371* (holotype: E!; isotype: K!).

Clinopodium capitellatum (Benth.) Kuntze, Revis. Gen. Pl. 2: 515 (1891) ≡ *Micromeria capitellata* Benth. in DC., Prodr. 12: 218 (1848) ≡ *Marrubium malcolmianum* Dalz. in Hooker's J. Bot. Kew Gard. Misc. 4: 109 (1852). – Type: [India] Pl. Ind. or. (Mont. Nilagiri); Ed. *R. F. Hohenacker*. [on label:] 1402. *Micromeria malcolmiana Bth. m.s.*, (*Marrubium M.* Dalz.) — Bth.; Incolis: Kodangu. Prope Kaderu. Apr. m. [coll. Fr. Metz] (holotype: K!; isotype: B!, FR! HOH!, JE!, M!, P!, STU!, TUB!).

Clinopodium caricum (P.H. Davis) Bräuchler & Heubl, **comb. nov.** ≡ *Micromeria carica* P.H. Davis in Kew Bull. [4] 1949: 109 (1949) ≡ *Satureja carica* (P. H. Davis) Greuter & Burdet in Willdenowia 14: 302 (1985). – Type: Turkey, Vil. Denizli (Caria), Boz dag (near Ajipoyam) above Geyram yaila. In limestone rocks, 5000–5200 ft., 16.7.1947, *P. H. Davis 13422* (holotype: K!; isotype: E!).

Clinopodium cilicicum (Hausskn. ex P.H. Davis) Bräuchler & Heubl, **comb. nov.** ≡ *Micromeria cilicica* Hausskn. ex P.H. Davis in Kew Bull. [4] 1949: 109 (1949) ≡ *Satureja sieheana* Greuter & Burdet in Willdenowia 14: 305 (1985). – Type: [Turkey, Icel,] Cilicien, 1895, *W. Siehe 315* (holotype: K!; isotype: JE!).

Clinopodium congestum (Boiss. & Hausskn. ex Boiss.) Kuntze, Revis. Gen. Pl. 2: 515 (1891) ≡ *Micromeria congesta* Boiss. & Hausskn. ex Boiss., Fl. Orient. 4: 575 (1879) ≡ *Satureja congesta* (Boiss. & Hausskn. ex Boiss.) Briq. in Engler & Prantl, Nat. Pflanzenfam. 4, 3a: 301 (Nov 1896). – Type: [Turkey, Adiyaman,] Akdagh inter Adiaman et Malatia 6000′, 12.9.1865 *Haussknecht s.n.* (holotype: G-BOISS photo!; isotype: BM!, G-BOISS photo!; JE!, K!).

Clinopodium dalmaticum (Benth.) Bräuchler & Heubl, **comb. nov.** ≡ *Micromeria dalmatica* Benth. in DC., Prodr. 12: 225 (1848) ≡ *Satureja dalmatica* (Benth.) Nyman, Syll. Fl. Eur.:102 (1855). – Type: In saxosis prope Cataro in Dalm., ann. 1837, *Visiani s.n.* (syntype: K!); Montenegro ad Nepeg, *Visiani s.n.* (syntype: K!).

Clinopodium dolichodontum (P.H. Davis) Bräuchler & Heubl, **comb. nov.** ≡ *Micromeria dolichodonta* P. H. Davis in Kew Bull. [6] 1951: 75 (1951) ≡ *Satureja dolichodonta* (P.H. Davis) Greuter & Burdet in Willdenowia 14: 305 (1985). – Type: Turkey, C4 Icel, distr. Gulnar, Kizilyokus De. near Bozagas (near Gulnar), flat and sloping limestone rocks, 500 m, 20.8.1949, *P. H. Davis 16356* (holotype: K!; isotype: E!).

Clinopodium euosmum (W.W. Sm.) Bräuchler & Heubl, **comb. nov.** ≡ *Calamintha euosma* W.W. Sm. in Notes Roy. Bot. Gard. Edinburgh. 9: 89 (1916) ≡ *Satureja euosma* (W. W. Sm.) Kudo in Mem. Fac. Sci. Taihoku Imp. Univ. 2: 100 (1929) ≡ *Micromeria euosma* (W. W. Sm.) C.Y. Wu in Acta Phytotax. Sin. 10: 229 (1965). – Type: [China,] Yunnan, Mountains NE of the Yangtze bend, 11000 ft., open limy pastures. Lat. 27° 45′ N, 7.1913, *G. Forrest 10574* (holotype: E!; isotype: K!).

Clinopodium frivaldszkyanum (Degen) Bräuchler & Heubl, **comb. nov.** ≡ *Zygis frivaldszkyana* Degen in Bull. Herb. Boissier 4: 523, pl. 8 (Jul 1896) ≡ *Satureja frivaldszkyana* (Degen) Briq. in Engler & Prantl, Nat. Pflanzenfam. 4, 3a: 301 (Nov 1896) ≡ *Micromeria frivaldszkyana* (Degen) Velen. in Österr. Bot. Zeitschr. 49: 291 (1899). – Type: [Bulgaria] Rum. 1837 *Frivaldszky s.n.* (probable isosyntype: K!).

Note: Degen (1896) cites numerous syntypes (probably kept at BP, not seen).

Clinopodium hydaspidis (Falc. ex Benth.) Kuntze, Revis. Gen. Pl. 2: 515 (1891) ≡ *Micromeria hydaspidis* Falc. ex Benth. in DC., Prodr. 12: 224 (1848) ≡ *Satureja hydaspidis* (Falc. ex Benth.) Briq. in Engler & Prantl, Nat. Pflanzenfam. 4, 3a: 301 (Nov 1896). – Type: [Kashmir,] from Patlee to Magha valley of the Gheleena, Sept. 1837, *Falconer 1250* (holotype: K!).

Clinopodium libanoticum (Boiss.) Kuntze, Revis. Gen. Pl. 2: 515 (1891) ≡ *Micromeria libanotica* Boiss., Diagn., Ser. 1, 12: 50 (1853) ≡ *Satureja libanotica* (Boiss.) Briq. in Engler & Prantl, Nat. Pflanzenfam. 4, 3a: 301 (1896). – Lectotype (designated here by Bräuchler): Libanos supra Eden, Syria, Mai-Jul. [vi] 1846, *E. Boissier s.n.* (lectotype: G-BOISS photo!; isolectotype: JE!).

Note: At G-BOISS another syntype is present (Liban, Orient, *Labillardier*, photo!). The Boissier collection, however, has both richer material and a collection date on it. Therefore the latter is chosen as lectotype.

Clinopodium molle (Benth.) Kuntze, Revis. Gen. Pl. 2: 515 (1891) ≡ *Micromeria mollis* Benth. in DC., Prodr. 12: 225 (1848) – Type: [Iraq] Pl. Mesopot., Kurdistan et Mossul, ann. 1841, *Kotschy 552a* (holotype: K!).

Clinopodium nepalense (Kitam. & Murata) Bräuchler & Heubl, **comb. nov.** ≡ *Micromeria nepalensis* Kitam. & Murata in Acta Phytotax. et Geobot., Kyoto 16: 3 (1955). – Type: Nepal, Bangu Khola, 3400 m, 11.06.1953, *S. Nakao s.n*. (holotype: KYO).

Clinopodium nummulariifolium (Boiss.) Kuntze, Revis. Gen. Pl. 2: 515 (1891) ≡ *Micromeria nummulariifolia* Boiss., Diagn. Ser. 1, 12: 50 (1853) ≡ *Satureja nummulariifolia* (Boiss.) Briq., Engler & Prantl, Nat. Pflanzenfam. 4, 3a: 301 (Nov 1896). – Type: Montanus supra Eden, Syria, Mai-Jul. [vi] 1846, *E. Boissier* (holotype: G photo!; isotype: BM!, E!, JE!, K!).

Clinopodium pulegium (Rochel) Bräuchler, **comb. nov.** ≡ *Melissa pulegium* Rochel, Pl. Banat. Rar.: 62, tab. XXII, fig. 48 a—e (1828) ≡ *Micromeria pulegium* (Rochel) Benth., Labiat. Gen. Spec.: 382 (1834) ≡ *Satureja pulegium* (Rochel) Briq. in Engler & Prantl, Nat. Pflanzenfam. 4, 3a: 301 (Nov 1896). – Lectotype (designated here by Bräuchler): [Romania] In rupibus ad thermas Herculis, Topletz, et aquaeducti in valle Mehadia Banatus. 28. Jl. 1815, *Rochel s.n.* (lectotype: M!, isolectotype: JE!).

Note: The original set of Rochel's collections was sold to the King of Saxony (Ullepitsch 1884), transferred to DR and destroyed in WW II (Stafleu & Cowan, 1983). The specimen in JE and one of the two at M, however, are the only ones that are labelled with a date fitting the time of the type collection cited in the protologue. The M collection is therefore chosen as lectotype, the collection in JE represents an isolectotype.

Clinopodium serpyllifolium (M. Bieb.) Kuntze, Revis. Gen. Pl. 2: 515 (1891) ≡ *Nepeta serpyllifolia* M. Bieb, Fl. Taur.-Cauc. 2: 40 (1808). – Type: [Russia, Crimea] "Habitat in Tauriae rupestribus, circa ruinas castelli Inkiermen" (holotype: LE).

subsp. *serpyllifolium* ≡ *Micromeria fruticosa* subsp. *serpyllifolia* (M. Bieb.) P. H. Davis in Kew Bull. [6] 1951: 77 (1951).

subsp. *barbatum* (P.H. Davis) Bräuchler, **comb. nov.** ≡ *Micromeria fruticosa* subsp. *barbata* P.H. Davis in Kew Bull. [6] 1951: 77 (1951) ≡ *Micromeria barbata* Boiss. & Kotschy in Boiss., Diagn. Ser. 2, 4: 14 (1859), nom. illeg., non C.A. Mey. in Fisch. & Mey., Ind. Sem. Hort. Petrop. 8: 67 (1842). – Type: [Lebanon] Iter Syriacum in Libano ad Dschene et circa Cedretum. In jugis inferioribus regionibus Danie, 5500 ped., 28. Jul. 1855. *Th. Kotschy 342* (holotype: G photo!; isotype: BM!, K!, P!).

subsp. *brachycalyx* (P.H. Davis) Bräuchler, **comb. nov.** ≡ *Micromeria fruticosa* subsp. *brachycalyx* P.H. Davis in Kew Bull. [6] 1951: 77 (1951). – Type: [Turkey, Icel,] Rochers du château en ruine dominant des Portes Ciliciennes Julliet.-Août. 1855, *Balansa 538* (holotype: K!; isotype: E!, W!).

subsp. *fruticosum* (L.) Bräuchler, **comb. nov.** ≡ *Melissa fruticosa* L., Sp. Pl.: 593 (1753) ≡ *Clinopodium fruticosum* (L.) Kuntze in Revis. Gen. Pl. 2: 516 (1891), nom. illeg., non Forssk. in Fl. Aegypt. Arab.: 107 (1775) ≡ *Satureja fruticosa* (L.) Briq. in Engler & Prantl, Nat. Pflanzenfam. 4, 3a: 301 (Nov 1896) ≡ *Micromeria fruticosa* (L.) Druce in Bot. Exch. Club Soc. Brit. Isles 3: 421 (1914). – Lectotype (designated by Morales in Anales Jard. Bot. Madrid: 138 (1991)): "Habitat in Hispania". Herb. Linn. No. 745.9 (lectotype: LINN; microfiche: M!).

subsp. *giresunicum* (P.H. Davis) Bräuchler, **comb. nov.** ≡ *Micromeria fruticosa* subsp. *giresunica* P.H. Davis in Notes Roy. Bot. Gard. Edinburgh 38: 39 (1980). – Type: Turkey A7 Giresun: Tamdere to Yavuzkemal, nr. Karinca, 1500 m, crevices of granite rocks, near road tunnel, 13.8.1952, *P. H. Davis 20750, Dodds & Cetik* (holotype: E!; isotype: K!).

Clinopodium taygeteum (P.H. Davis) Bräuchler & Heubl, **comb. nov.** ≡ *Micromeria taygetea* P.H. Davis in Kew Bull. [4] 1949: 110 (1949) ≡ *Satureja taygetea* (P.H. Davis) Greuter & Burdet in Willdenowia 14: 306 (1985). – Type: Greece, Peloponnesi, in rupium calcar. fissuris montis Taygeti supra pagum Trypi, c. 1530 m, 2.10.1938, *P. H. Davis* [E seminibus in monte Taygeto Laconiae lectis educate, Barneby & Ripley] (holotype: E!).

Clinopodium thymifolium (Scop.) Kuntze, Revis. Gen. Pl. 2: 516 (1891) ≡ *Satureja thymifolia* Scop. in Fl. Carn. ed. 2, 1: 428, t.29 (1771) ≡ *Calamintha thymifolia* (Scop.) Rchb., Fl. Germ. Excurs.: 328 (1831); Host, Fl. Austr. 2.: 132 (1831) ≡ *Micromeria thymifolia* (Scop.) Fritsch in A. Kerner, Sched. Fl. Exs. Austro-Hung. 8: 119 (1899). – Lectotype (designated here by Bräuchler): "Habitat in muris, Idriae.", t. 29 in Scop., Fl. Carn. ed. 2, 1 (1771). Epitype (designated here by Bräuchler): F. Schultz, herbarium normale. Cent. 6. 541*bis*, *Calamintha thymifolia.* 10. aout 1852. Fentes de rochers et débris calcaires dans les forets des montagnes à Strug, près d´Idria (Carniole, Autriche). Rec. *Dolliner s.n.* (epitype: M!, P!).

Type material has been searched for in various herbaria (B, BM, E, JE, K, M, P, W, WU) but without success. In the absence of a specimen, the illustration t. 29 in Scop., Fl. Carn. ed. 2, 1 (1771) is chosen as lectotype. As the illustration is not unambiguous, material collected in proximity of the locus classicus is designated as epitype supporting this illustration (F. Schultz, herbarium normale. Cent. 6. 541*bis*; see above).

Note: When publishing *Clinopodium thymifolium,* Kuntze only referred to Host (1831), who had, however, based his *Calamintha thymifolia* on Scopoli's (1771) *Satureja thymifolia*, as Reichenbach (1831) had done in the same year. There is no evidence as to whether Host's or Reichenbach's treatment was published first. It is obvious that all four combinations are nomenclatural synonyms, and the correct author combination of *Clinopodium thymifolium*, therefore, is (Scop.) Kuntze (Greuter pers. comm.).

Clinopodium wardii (C. Marquand & Shaw) Bräuchler, **comb. nov.** ≡ *Micromeria wardii* C. Marquand & Shaw, J. Linn. Soc. 48: 216 (1929). – Type: [China Tibet:] Tsangpo Gorge, 7000ft., 28.xi.1924, *F. Kingdon Ward 6324* (holotype: BM!; isotype: E!, K!).

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Molecular evidence for adaptive radiation of *Micromeria* Benth. (Lamiaceae) on the Canary Islands as inferred from chloroplast and nuclear DNA sequences and ISSR fingerprint data

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Abstract

The Canary Islands have been a focus for phylogeographic studies on the colonization and diversification of endemic angiosperm taxa. Based on phylogeographic patterns, both inter island colonization and adaptive radiation seem to be the driving forces for speciation in most taxa. Here, we investigated the diversification of *Micromeria* on the Canary Islands and Madeira at the inter- and infraspecific level using inter simple sequence repeat PCR (ISSR), the *trn*K-Intron and the *trn*T-*trn*L-spacer of the cpDNA and a low copy nuclear gene. The genus *Micromeria* (Lamiaceae, Mentheae) includes 16 species and 13 subspecies in Macaronesia. Most taxa are restricted endemics, or grow in similar ecological conditions on two islands. An exception is *M. varia*, a widespread species inhabits the lowland scrub on each island of the archipelago and could represent an ancestral taxon from which radiation started on the different islands. Our analyses support a split between the "eastern" islands Fuerteventura, Lanzarote and Gran Canaria and the "western" islands Tenerife, La Palma and El Hierro. The colonization of Madeira started from the western Islands, probably from Tenerife as indicated by the sequence data. We identified two lineages of *Micromeria* on Gomera but all other islands appear to be colonized by a single lineage, supporting adaptive radiation as the major evolutionary force for the diversification of *Micromeria*. We also discuss the possible role of gene flow between lineages of different *Micromeria* species on one island after multiple colonizations.

Keywords: *Micromeria*; Lamiaceae; Canary Islands; *trn*K; *trn*T-F; FPS2; ISSR markers; Adaptive radiation

1. Introduction

The Canary Islands, part of the Macaronesian phytogeographic region, consist of an archipelago of seven major volcanic islands located in the northeastern Atlantic Ocean in close proximity to the western Sahara coast. The geological history of the archipelago is characterized by a temporal sequence of volcanic eruptions over the past 20 million years with the ages of the islands decreasing from east to west (i.e. 20.7 Ma for Fuerteventura to 0.7–0.8 Ma for El Hierro) (Carracedo, 1994; Guillou et al., 2004). The older, eastern islands contain mountain ridges of low altitude (i.e. Lanzarote 671 m, Fuerteventura 807 m), whereas the highest volcanoes in the central and western islands exceed 1400 m with the Teide-peak on Tenerife rising to 3718 m. The Canary Islands are characterized by a subtropical climate that is strongly influenced by the humid trade winds from the northeast and the cold Canaries Current that causes persistent, dense fog at around 1000 m in elevation. South sides of the islands as well as high altitudes

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frequently experience desert and semi-desert conditions with very low levels of precipitation. In contrast, the slopes of the mountains are characterized by high to medium humidity and rainfall augmented by condensation and fog. These sharp elevational gradients in climate have resulted in the formation of distinct ecological zones: coastal deserts and arid low land scrub, humid and semi-arid subtropical scrub and woods, humid laurel forest (“laurisilva”) in the cloud belt, a heath belt (Fayal-Brezal) as transition vegetation between laurel forest and, at high altitudes, humid to dry temperate pine forests as well as dry subalpine scrub. Local adaptation to these habitats within islands, as well as physical isolation among the islands, are main factors responsible for the rich flora of Macaronesia with at least 831 species and 40 genera endemic in this region (Humphries, 1979; Hansen and Sunding, 1993).

In the last decade, the Canary Islands have been in the focus for phylogeographic studies on the colonization and diversification of endemic angiosperm taxa (e.g. Böhle et al., 1996; Kim et al., 1996; Barber et al., 2000; Francisco-Ortega et al., 2001; Mort et al., 2002; Allan et al., 2004; Fairfield et al., 2004; Trusty et al., 2005). Based on phylogeographic patterns, inter island colonization has been proposed as a driving force for species differentiation within highly diverse genera on the Canary Islands (i.e. Francisco-Ortega et al., 1996, 2001). This mechanism was supported by phylogenies indicating niche conservatism, where taxa with similar ecological preferences comprise a single clade, and suggests that adaptation to specific ecological zones occurred only once within the archipelago (Francisco-Ortega et al., 2001). An alternative explanation is adaptive radiation, where adaptation to the distinct habitats occurs independently on each island. Examples supporting an adaptive radiation on each island are found in several taxa (e.g. Kim et al., 1996; Percy and Cronk, 2002). Both colonization and adaptive radiation seem to be important in most taxa (Panero et al., 1999; Barber et al., 2000; Francisco-Ortega et al., 2002; Mort et al., 2002; Allan et al., 2004; Trusty et al., 2005). Studies of the evolution of plant diversity on the Canary Islands indicate that most of the plant groups of the Canary Islands evolved by adaptation to different ecological zones as well as by inter-island colonization.

The genus *Micromeria* Benth. (Lamiaceae, Nepetoideae) as currently understood (Harley et al., 2004) contains about 70 species with a distribution range extending from the Himalayan region to the Macaronesian Archipelago (with Madeira, the Cape Verde and Canary Islands) and from the Mediterranean to South Africa and Madagascar (Doroszenko, 1986; Morales, 1993; Bräuchler et al., 2005). Molecular data suggest the transfer of sect. *Pseudomelissa* to *Clinopodium* (Bräuchler et al., 2005) and the exclusion of sect. *Cymularia* (with *M. cymuligera* Boiss. and Hausskn. an endemit of southeastern Anatolia as the only representative) from *Micromeria* (Bräuchler, unpublished anatomical and preliminary molecular data). From the remaining sections of *Micromeria* s.str., sect. *Micromeria* includes approximately 50 species of perennial suffruticose herbs and shrubs. Centers of diversity are found in the Mediterranean region and the Canary Islands.

Comparative analysis of cpDNA data revealed Macaronesian *Micromeria* (excluding *M. forbesii* from Cape Verde Islands) as monophyletic with a group of taxa from the Western Mediterranean (e.g. *M. inodora* and *M. fontanesii*) as neighbor group (Bräuchler et al., 2005). According to the revision by Pérez de Paz (1978), the genus *Micromeria* includes 16 species and 13 subspecies in Macaronesia, with the highest diversity on Tenerife and Gran Canaria (seven species each). Lower numbers of species are found on La Palma (3), Gomera (2), El Hierro (2), Lanzarote (1) and Fuerteventura (1); (see Fig. 1, Table 1). Only one species, *M. varia* L. colonized the whole archipelago. It occurs mainly in dry to medium dry lowland habitats and is taxonomically split into seven subspecies. *M. hyssopifolia* Webb et Berth. is found in the pine forests of Tenerife and El Hierro while *M. lasiophylla* Webb et Berth. inhabits the high altitude desert of Tenerife and La Palma. The remaining species are narrow endemics. Two of them, *M. leucantha* Svent ex P. Perez and *M. pineolens* Svent., both occurring on Gran Canaria, are forming sect. *Pineolentia* (Pérez de Paz, 1978) because of their morphological distinctness. The most striking features of *M. pineolens* are its shrubby habit (up to 80 cm), leaves exceeding 1 cm in length and large flowers with a corolla size ranging from 10 to

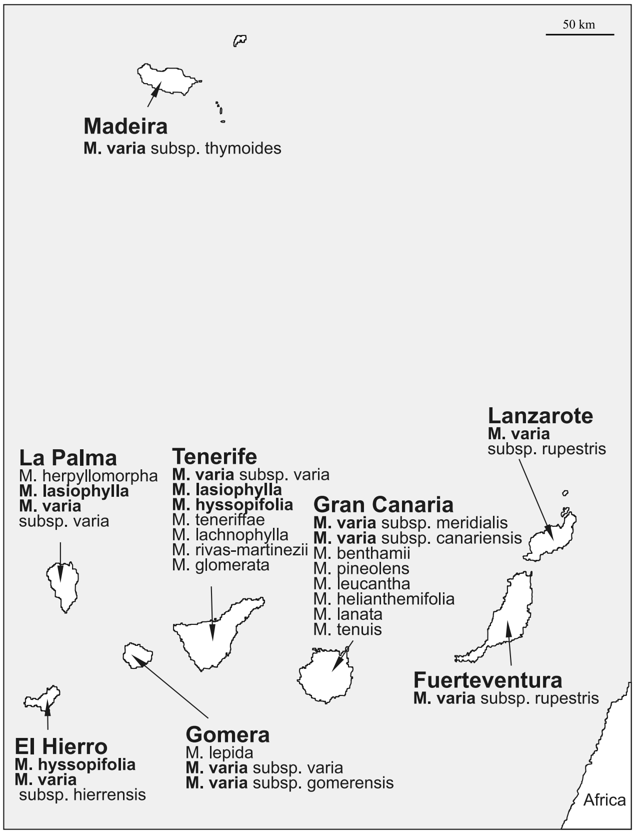

Fig. 1. The Canary Islands and Madeira and the distribution of the species of the genus *Micromeria* on the islands. Species distributed on more than one island are marked bold.

Table 1
Taxonomy of the genus *Micromeria* in Macaronesia according to Pérez de Paz (1978)

Species	Distribution	Ecology	Subspecies	Section
M. benthamii	Gran Canaria	Open areas medium altitude and open pine forest	—	Micromeria
M. forbesii	Cape Verde Islands	Open mountain slopes	—	Micromeria
M. glomerata	Tenerife	Humid lowland	—	Micromeria
M. helianthemifolia	Gran Canaria	Semi arid scrub land	—	Micromeria
M. herpyllomorpha	La Palma	Open pine forest	—	Micromeria
M. hyssopifolia	Tenerife/El Hierro	Open pine forest	—	Micromeria
M. lachnophylla	Tenerife	High altitude desert	—	Micromeria
M. lanata	Gran Canaria	Open rocks in pine forest belt	—	Micromeria
M. lasiophylla	Tenerife/La Palma	High altitude desert	2	Micromeria
M. lepida	Gomera	Open pine forest	2	Micromeria
M. leucantha	Gran Canaria	Cliffs in semi desert	—	Pineolentia
M. pineolens	Gran Canaria	Dense pine forest	—	Pineolentia
M. rivas-martinezii	Tenerife	Humid lowland	—	Micromeria
M. teneriffae	Tenerife	Semi arid scrub land	—	Micromeria
M. tenuis	Gran Canaria	Open areas medium altitude and open pine forest	2	Micromeria
M. varia	All islands	Dry lowland areas	7	Micromeria

15 mm. *M. pineolens* can be found only in north eastern Gran Canaria in the Tamadaba pine forest (800–1200 m). *M. leucantha*, is characterized by xeromorphic, needle shaped leaves that are presumably an adaptation to their habitat of sun exposed cliffs. This species occurs only in the dry southwestern region of Gran Canaria.

The patterns of species distribution in *Micromeria* make this genus a good system in which to test the relative importance of inter-island colonization versus ecological shift within monophyletic groups. Several taxa are restricted endemics, others grow in similar ecological conditions on different islands, and one species inhabits the lowland scrub on each island of the archipelago and could represent an ancestral taxon from which radiation started on the different islands.

Here, we present a population based study of genetic similarities of *Micromeria* from the Canary Islands at the inter- and intraspecific level using inter simple sequence repeat PCR (ISSR). These data were compared to phylogenetic reconstruction of multiple samples from different populations using the *trn*K-intron and the *trn*T-*trn*L-spacer of the cpDNA as well as a low copy nuclear gene. The purpose of the present study was to determine (i) if inter-island colonization as implicated by the species concept can be supported by molecular data, (ii) if the speciation of taxa confined to similar ecological zones is attributed to parallel adaptive speciation, (iii) if *Micromeria varia*, the most widespread species, is an ancestral taxon or a taxon that was distributed recently to the single islands, and (iv) if the sectional status of the morphological most aberrant forms within the genus can be supported or if these morphological peculiarities are rather a result of adaptation to extreme habitats in relatively young taxa.

2. Material and methods

2.1. Plant material

During several excursions to all major islands of the Canary archipelago and Madeira, about 400 specimens were collected in total, representing 14 species. Sampling was performed covering the whole island, with up to four individuals from one sampling site. For *M. pineolens* a higher number of individuals were sampled, because of the restricted distribution. One sample of *M. helianthemifolia* Webb. et Berth. from Gran Canaria was taken from a plant cultivated at the Botanical Garden Tafira, Gran Canaria. The narrow endemics of northwestern Tenerife, *M. glomerata* P. Perez and *M. rivas-martinezii* Wildpr. were not available for the analyses (Table 2). Sampling consisted of 2–3 leaves from one individual that were fixed in DNA isolation buffer in the field. One voucher specimen per sampling site was made for some typical representatives of the species, vouchers were not taken from small and protected populations. Most species could be determined unambiguously, but for several samples the species assignment was doubtful. These samples are shown in the analyses with both potentially applicable species names. This applied in particular to the samples from Gomera (*M. varia* or *M. lepida* Webb et Berth.) where only a small number of samples with typical *M. varia* characters were found. Due to these uncertainties we did not assign species names to the samples from Gomera. Sequences of three herbarium specimen were included in the FPS2 dataset.

DNA isolation of buffer-fixed material, amplification and sequencing was performed as described previously (Meimberg et al., 2000, 2001; Bräuchler et al., 2004, 2005). The resulting DNA solution was used for ISSR-PCR and for amplification of the *trn*K intron the *trn*T-*trn*F spacer region of the cpDNA and the farnesyl-pyrophosphate-synthethase 2 (FPS2).

2.2. Amplification and sequencing

The *trn*K intron was analysed for 64 samples and amplified from total DNA as described previously (Meimberg et al., 2000, 2001; Bräuchler et al., 2005). For comparative sequencing the *trn*K intron was amplified in two parts using

Table 2
Number of samples used for ISSR and sequence analysis

	Lanzarote	Fuerteventura	Gran Canaria	Tenerife	Gomera	La Palma	El Hierro	Madeira
No. samples collected	20	4	90	90	83	30	27	25
ISSR analysis (sum)	4	4	80	79	83	30	27	13
M. varia	4	4	20	18–31	0–83	0–1	3	13
M. helianthemifolia	—	—	1	—	—	—	—	—
M. leucantha	—	—	2	—	—	—	—	—
M. pineolens	—	—	10	—	—	—	—	—
M. lanata	—	—	11	—	—	—	—	—
M. tenuis	—	—	13–22	—	—	—	—	—
M. benthamii	—	—	14–23	—	—	—	—	—
M. lachnophylla	—	—	—	3	—	—	—	—
M. lasiophylla	—	—	—	5	—	3–12	—	—
M. teneriffae	—	—	—	6	—	—	—	—
M. hyssopifolia	—	—	—	34–47	—	—	24	—
M. lepida	—	—	—	—	0—83	—	—	—
M. herpyllomorpha	—	—	—	—	—	17–27	—	—
cpDNA analysis (sum)	3	4	11	14	7	11	7	4
M. varia	3	4	0	3	0–7	0–1	1	4
M. helianthemifolia	—	—	1	—	—	—	—	—
M. leucantha	—	—	2	—	—	—	—	—
M. pineolens	—	—	2	—	—	—	—	—
M. lanata	—	—	1	—	—	—	—	—
M. tenuis	—	—	3–4	—	—	—	—	—
M. benthamii	—	—	1–2	—	—	—	—	—
M. lachnophylla	—	—	—	2	—	—	—	—
M. lasiophylla	—	—	—	2	—	3	—	—
M. teneriffae	—	—	—	1	—	—	—	—
M. hyssopifolia	—	—	—	6	—	—	6	—
M. lepida	—	—	—	—	0–7	—	—	—
M. herpyllomorpha	—	—	—	—	—	7	—	—
FPS2 analysis (sum)	3	4	11	20	2	9	2	4
M. varia	3	4	0	4	0–2	0	0	4
M. helianthemifolia	—	—	0	—	—	—	—	—
M. leucantha	—	—	1	—	—	—	—	—
M. pineolens	—	—	2	—	—	—	—	—
M. lanata	—	—	2	—	—	—	—	—
M. tenuis	—	—	4–5	—	—	—	—	—
M. benthamii	—	—	1–2	—	—	—	—	—
M. lachnophylla	—	—	—	5	—	—	—	—
M. lasiophylla	—	—	—	3	—	1	—	—
M. teneriffae	—	—	—	4	—	—	—	—
M. hyssopifolia	—	—	—	4	—	—	2	—
M. lepida	—	—	—	—	0–2	—	—	—
M. herpyllomorpha	—	—	—	—	—	8	—	—

In cases in which species determination could not be performed unambiguously, values are given as the range of possible numbers for the corresponding samples.

the primer pair 2-*trn*K-3914F/Sat16-1200R and Sat2-1200F/16-*trn*K-2R (Bräuchler et al., 2005; primers 2-*trn*K-3914Fand 16-*trn*K-2R are according to Johnson and Soltis, 1994), respectively using the following cycle profile: (1) 94 °C for 2 min, (2) 35 cycles at 94 °C for 1 min, 54 °C for 1 min, 72 °C for 1 min 30 sec and (3) a terminal extension phase at 72 °C for 10 min. The *trn*T-*trn*F region was amplified using the primers suggested by Taberlet et al. (1991) in two parts using either the primer pair A/B or C/F using the following cycle profile: (1) 94 °C for 2 min, (2) 35 cycles at 94 °C for 1 min, 54 °C for 1 min, 72 °C for 1 min 15 s and (3) a terminal extension phase at 72 °C.

PCR products were purified and sequenced directly using the same primers as for amplification. Sequencing was performed using an ABI 377 (Applied Biosystems) automated sequencer according to the manufacturer's protocol.

2.3. Amplification of FPS2

The ITS region of *Micromeria* species could not be used due to frequent co-amplification of paralog sequences and probably pseudogenes (data not shown), so identification of homologous sequences would have been difficult (Álvarez and Wendel, 2003; Bailey et al., 2003). As an alternative, markers for a low copy gene were developed. For this purpose, ESTs published for *Mentha*, a close relative of *Micromeria* (Wagstaff et al., 1995) were

BLASTed (Altschul et al., 1997) on the *Arabidopsis* genome. Primers were designed for regions that covered about 1000 bp on the *Arabidopsis* genome and were flanked by regions homologous to strings of one EST. In total we tested five regions for which the FPS2 (*Mentha* mRNA: gi14488052; Lange et al., 2000) turned out to be the most applicable because of the lower length variability and the relative high amount of point mutations found in the pairwise comparison in the first experiments. We identified ca. 2000 bp of this sequence in *Micromeria*, of which we used a ca. 600 bp section for comparative sequencing (Fig. 2). Amplification was performed using the primers 900F (CAT GAG CAA TGC RCA AGC AAC) and 1565R (CCM AAG GTT GGT ATG ATT GCC) according to the following temperature profile: 1 × 94 °C 1,5 min; 35 × 94 °C 1 min; 54 °C, 1 min; 72 °C, 1 min; 1 × 72 °C 1 min. The resulting PCR products were sequenced directly using the same primers as for PCR.

2.4. ISSR fingerprints

Inter simple sequence repeat PCR (ISSR) was performed in accordance with available published protocols (e.g. Gupta et al., 1994; Martin and Sánchez-Yélamo, 2000) using 10 different 3′-anchored primers. In each case, two primers were used together in one reaction to increase

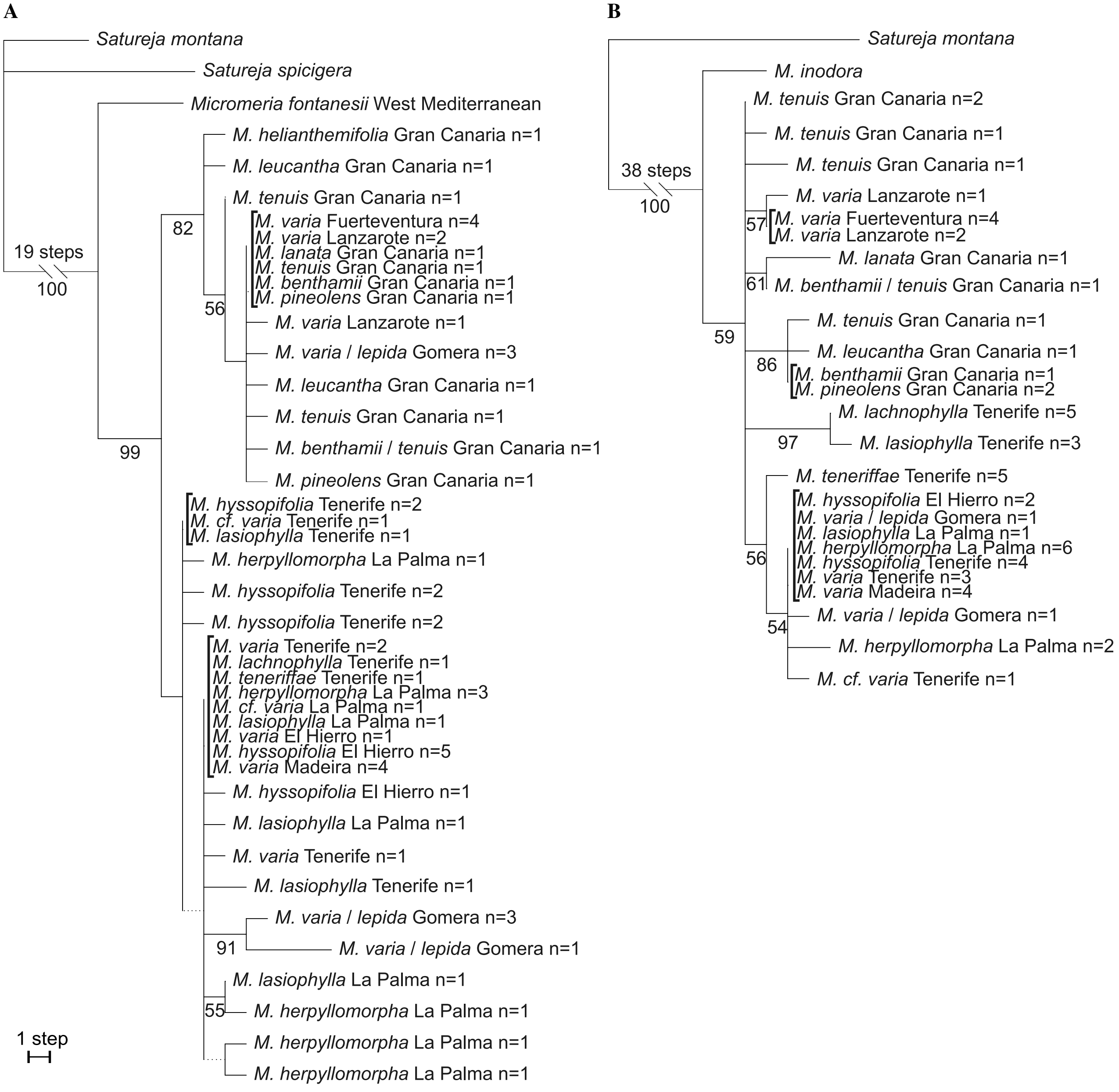

Fig. 2. MP analysis of the cpDNA dataset (A) and FPS2 (B). Shown is one of 192 shortest trees (A) and the shortest tree (B). Branches that collapse in the strict consensus tree are marked dashed. Bootstrap values >50 are indicated below branches. Only one example for equal sequences was included in the analysis. In this case either the number of samples for which a sequence was found is given after the respective species name, or names are summarized by brackets, in case of sequences that had been found in different species or different islands.

Table 3
ISSR primers used in this study

	Primer	Sequence 5′–3′	T_m (°C)	No. fragments
1	I-CT9G	CTCTCTCTCTCTCTCTCTG	57	82
	I-GAC5C	GACGACGACGACGACC		
2	I-GA8C	GAGAGAGAGAGAGAGAC	53	50
	I-CA9G	CACACACACACACACACAG		
3	I-AC9G	ACACACACACACACACACG	55	73
	I-AC9C	ACACACACACACACACACC		
4	I-ACG5G	ACGACGACGACGACGG	57	60
	I-ACG5C	ACGACGACGACGACGC		
5	I-TCG5G	TCGTCGTCGTCGTCGG	57	56
	I-TCG5C	TCGTCGTCGTCGTCGC		

Two primers were included in one PCR to increase the number of fragments. The annealing temperature (Tm) is shown for this reaction, as well as the number of scored fragments.

the number of fragments (Table 3). The PCR was optimized for each reaction with respect to the annealing temperature, the amount of DNA, and the amount of primers used. For all primers, a concentration of 0.8 µM proved to be optimal while using 1 µl DNA solution in a 50 µl total reaction volume. Annealing temperatures were set according to Table 3. Amplification was carried out with the following protocol: (1) 94 °C for 2 min, (2) 35 cycles with 94 °C for 1 min, specific annealing temperature for 1 min, 72 °C for 1 min, and (3) a terminal extension phase at 72 °C for 5 min. For fragment separation 6% Poly(NAT) Wide Mini S-2x25 Gels (Fa. Elchrom) were used. Fifteen microliters of the PCR solution were loaded and the fragments were separated within 240 min at 100 V in an electrophoresis chamber with 30 cm gel length. As a size standard, a mixture between 100 bp ladder and 20 bp ladder (Fa. Promega) was used. The DNA was stained 1 h in ethidiumbromide solution (100 µg/l), and subsequently destained with water several times. Fragments of length between 150 and 1000 bp were scored. Fragment lengths were determined with the program ONE-Dscan 1.0 (Scanalytics) under manual control and data were converted into a 0/1-matrix, scoring the fragments as diallelic. This matrix was used for distance analysis.

2.5. Phylogenetic and distance analysis

Sequences were aligned manually. A gap in a sequence was inserted when it was more parsimonious under the assumption of equal weight for a gap and a point mutation. Indels were coded as an additional binary character (Simmons and Ochoterena, 2000) in a separate matrix which was attached at the end of the sequence alignment before creating the nexus file. Poly-A or poly-T length polymorphisms were coded as a single state for each observed number of repeated bases. The resulting data matrix was subsequently analysed using PAUP version 4.0b10 (Swofford, 2002) as described previously (Meimberg et al., 2000, 2001). All heuristic searches were carried out using random addition (10 replicates), tree-bisection-reconnection (TBR) branch swapping, with the *Collapse* option in effect and saving multiple trees (MulTrees). Ensemble consistency (CI; Kluge and Farris, 1969) and retention indices (RI; Farris, 1989) were determined after exclusion of uninformative positions. Bootstrap values from 1000 replicates were calculated using the same settings as for heuristic searches (Felsenstein, 1985). Strict consensus trees were constructed from all most parsimonious trees. The sequences reported in this study are available from GenBank (Accession Nos. DQ640403–DQ640475; previously generated *trn*K sequences that had been used as outgroup are published under gi58045273 and gi58045291; Bräuchler et al., 2005). Sequence matrices used in this study and corresponding trees and are available in TreeBase. To assess character congruence between the cpDNA and the FPS2 data set a partition homogeneity test (Farris et al., 1995) as implemented in PAUP 4.0b10 (Swofford, 2002) was performed with the same heuristic search settings as used in the phylogenetic analysis. The test included 1000 replicates with a maxtrees setting of 100 per replicate.

Distance analysis of the ISSR 0/1-matrix was performed with the software package NTSYSpc (Applied Biostatistics, 2002), using the Dice coefficient and the Jaccard coefficient, as implemented in NTSYSpc, or the Nei–Li distance model (Nei and Li, 1979), as implemented in PAUP. The Nei–Li distance model corresponds to the Dice coefficient (NTSYSpc manual) and comparison between both methods revealed only minor differences in the subsequent analysis. No differences were observed using the Dice or Jaccard coefficient, so only the results of the Dice coefficient distance matrix are shown. The distance matrix was used for UPGMA and neighbor joining or principle component analyses (PCoA). PCoA was performed using the double center, eigenvalue procedure as implemented in NTSYSpc.

3. Results

3.1. Analysis of cpDNA sequences

CpDNA sequences were determined for 61 samples, including multiple samples from 13 species. The data matrix included the entire *trn*K intron and the spacer between *trn*T and *trn*L; in total about 3000 bp. The *trn*L intron and the spacer between *trn*L and *trn*F were less variable (data not shown), and not used in this study. The alignment consisted of 28 different cpDNA haplotypes including three outgroup taxa *M. fontanesii* Pomel, *Satureja montana* L. and *Satureja spicigera* (Koch) Boiss. Of these, 18 haplotypes were unique for a single sample, four haplotypes were found in several samples from the same species from one island, and three haplotypes were found in more than one species, including two of them in different species from different islands. Samples of *M. varia* subsp. *rupestris* from Lanzarote and Fuerteventura had equal sequences with samples assigned to *M. lanata*, *M. tenuis*, *M. benthamii* and *M. pineolens* from Gran Canaria as well as 19 samples from six species from Tenerife, La Palma, El Hierro and Madeira.

The alignment consisted of 2983 positions, 10 of those referring to the coded indels. Sequence variation was very low, only 67 positions were variable and of these only 33 were informative. For the ingroup only 11 characters were informative and, of these, four were length polymorphisms. MP analysis resulted in 128 shortest trees of 72 steps with CI = 0.958 and RI = 0.961 (Fig. 2A).

In the cpDNA phylogeny two major clades were indicated, one containing all samples from the eastern islands Lanzarote, Fuerteventura and Gran Canaria (bootstrap support, bts = 82). Further resolution in this clade was low and only weakly supported. The other clade contained the samples from the western islands Tenerife, La Palma and El Hierro together with those from Madeira, although this grouping was only weakly supported by one length polymorphism and was not supported by bootstrap analysis. Samples from Gomera were assigned to both clades.

3.2. Analysis of FPS2 sequences

FPS2 sequences had been determined for 120 samples by direct sequencing of the PCR product. As expected for a nuclear low copy gene, several samples of FPS2 were heterozygous. These samples were excluded from the analysis, so only 61 samples with homozygous sequences were considered. The alignment consisted of 19 different sequences including *S. montana* L. and *M. inodora* (Desf.) Benth. from Morocco as outgroup taxa. From the 17 ingroup sequences, eight sequences only existed in a single sample and six sequences were found in multiple individuals from one species on the same island. Equal sequences were found in *M. pineolens* and *M. benthamii* from Gran Canaria and *M. varia* from Lanzarote and Fuerteventura. One sequence was found in 21 samples representing five different species from the western islands Tenerife, La Palma, El Hierro and Gomera as well as Madeira. The alignment consisted of 549 positions. Of these, 453 were constant, 96 variable but uninformative and 20 parsimony informative. Within the ingroup, 10 positions were parsimony informative. No length polymorphisms were observed in the ingroup, so no indels were coded. The region investigated was formed by 3 exons of 46–90 bp length and 2 introns of 77–225 bp length. From a third intron, 35 bp were determined. Exon regions (210 bp in total) with 12 positions (5.7%) showed a lower variability than intron regions (359 bp in total) with 62 positions (17.3%). Considering only the ingroup, this difference was smaller with five positions (2.4%, one informative position) in the exons and 20 (5.6%, nine informative positions) in the introns. MP analysis of this dataset resulted in one shortest tree of 80 steps with a CI = 0.988 and a RI = 0.947 (Fig. 2B).

As in the cpDNA phylogenetic reconstruction, the samples appear to form a monophyletic group, albeit with low support by bootstrap analysis (bts = 59). The internal resolution of the FPS2 dataset is lower. The only major clade contained all samples from Gomera, La Palma, El Hierro and Madeira, and the majority of samples from Tenerife, except the high altitude desert taxa (bts = 56). *M. teneriffae*, was indicated as neighbor group to the rest of the members of this clade (bts = 54).

A combination of the cpDNA and FPS2 datasets was possible with 21 samples represented in both matrices. These 21 samples exhibited 14 different combined cytonuclear haplotypes. The partition-homogeneity test (Farris et al., 1995) as implemented in PAUP was not significant ($P = 0.33$) so both matrices did not show a significant incongruence, though it has to be considered that the low number of informative positions in the sequencing datasets could diminish the power of detecting incongruencies. The combined analysis using a combined sequence from *M. fontanesii* and *M. inodora* as outgroup resulted in six most parsimonious trees with the length of 50 steps and a CI = 0.818 and an RI = 0.907. The consensus tree provided no additional support for the respective clades. All internal nodes were supported by synapomorphies of only one of the single matrices, so bootstrap support was not increased. Samples from the western islands formed a monophyletic group, supported by two synapomorphic indels from the cpDNA dataset and were further subdivided, with *M. lasiophylla* and *M. lachnophylla* from Tenerife and *M. teneriffae* as subsequent sisters to the rest of the samples from the western islands by apomorphies from the FPS2 dataset. For the samples from the eastern islands, only one clade was indicated in the consensus tree, which was supported exclusively by synapomorphies from the cpDNA dataset. Combining the cpDNA and FPS2 sequences did not result in further resolution of this clade, probably due to the reduced number of samples. As this analysis did not provide additional support or new information, the phylogenetic reconstruction is not shown. Nevertheless, among samples that were included in both matrices, equal sequences in all loci were shown by a sample from El Hierro, La Palma and Madeira and by samples from Fuerteventura and Lanzarote.

3.3. ISSR fingerprint analysis

In total ISSR fingerprints of about 400 samples were investigated. Samples yielding poor amplification products were excluded from the analysis. The 0/1 matrix from fingerprint pattern was constructed from 324 samples. ISSR amplifications using 10 primers in five reactions generated 321 different fragments (Table 3). Of these fragments, 304 were observed in more than one sample. Using the Dice or Jaccard Coefficient and UPGMA or Neighbor joining led to similar results, so only UPGMA from a Dice coefficient distance matrix is shown (Fig. 3).

In the UPGMA, nearly all samples of one island clustered together and all species found on more than one island (*M. varia*, *M. hyssopifolia* and *M. lasiophylla*) were grouped within the cluster of samples of the respective island. Accordingly, no fragments could be found that were shared by these species in samples from different islands. However, fragments supporting clusters for samples from

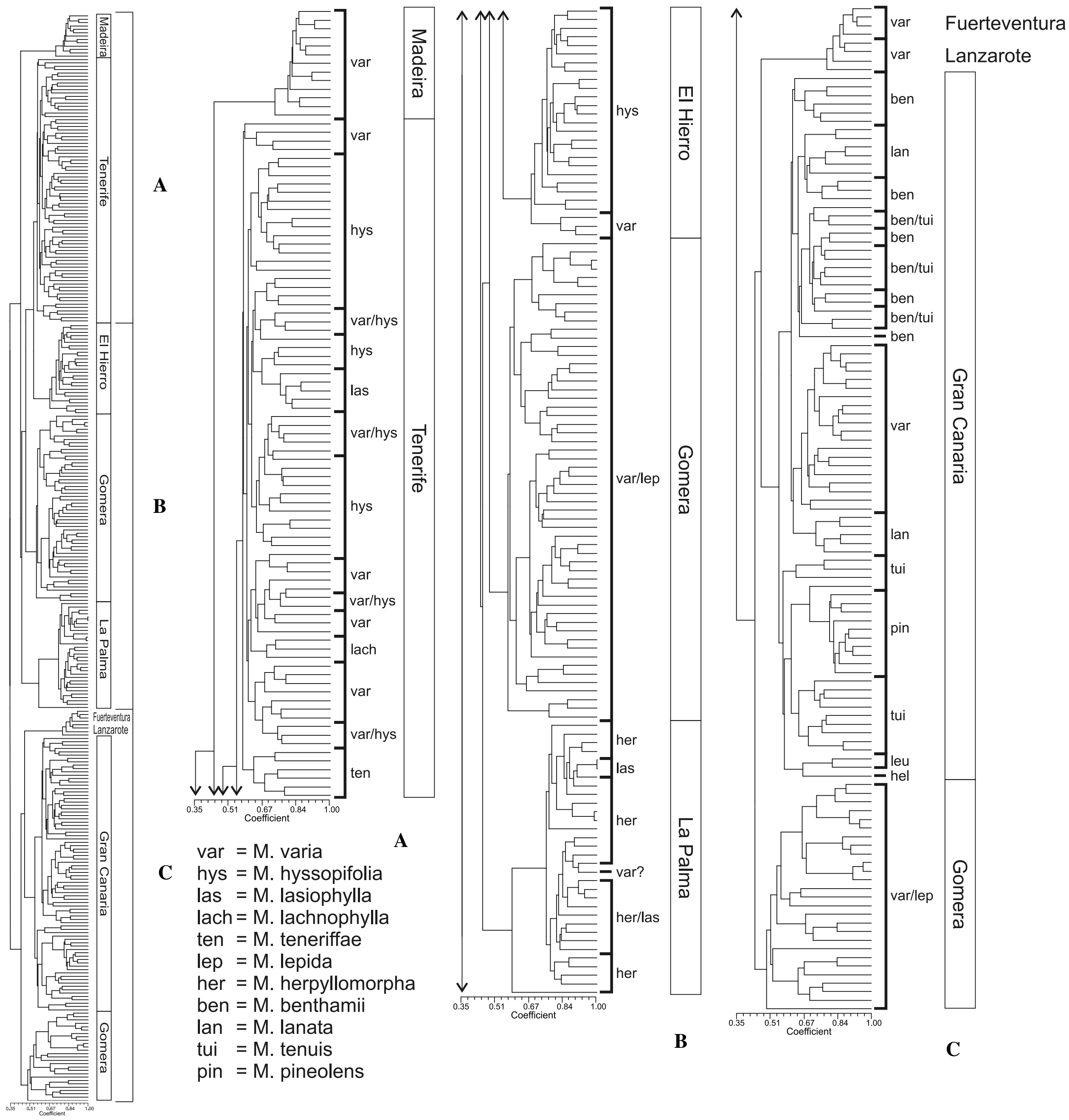

Fig. 3. UPGMA of dice similarities of ISSR fingerprinting patterns of *Micromeria* of the Canary Islands and Madeira in comparison to species assignment of the samples and origin. For samples which could not have been identified unambiguously the names of the species they could be assignable to are given.

the single islands were identified. Closer similarities between the clusters of one island were obvious among the samples from Tenerife, El Hierro and La Palma on the one hand and Gran Canaria, Fuerteventura and Lanzarote on the other. The latter two showed very high similarities to each other. Samples from Madeira were positioned closer to the first group of clusters than to the group containing the samples from Gran Canaria. Only *Micromeria* from Gomera formed two distinct clusters: one (55 samples) positioned between the samples from La Palma and the samples from Tenerife and the other (26 samples) positioned next to the samples from Lanzarote and Fuerteventura and from Gran Canaria.

Single species from the islands were only weakly separated from each other in the single clusters (Fig. 3). The best division was achieved between the samples from Gran Canaria. Here, the single species formed subclusters, even if some were not distant from each other (Fig. 4). The most clearly delimited cluster was formed by the samples of *M. pineolens*. From Tenerife only samples of *M. teneriffae*, *M. lasiophylla* and *M. lachnophylla* clustered together. *M. varia* and *M. hyssopifolia* are grouped in a single cluster

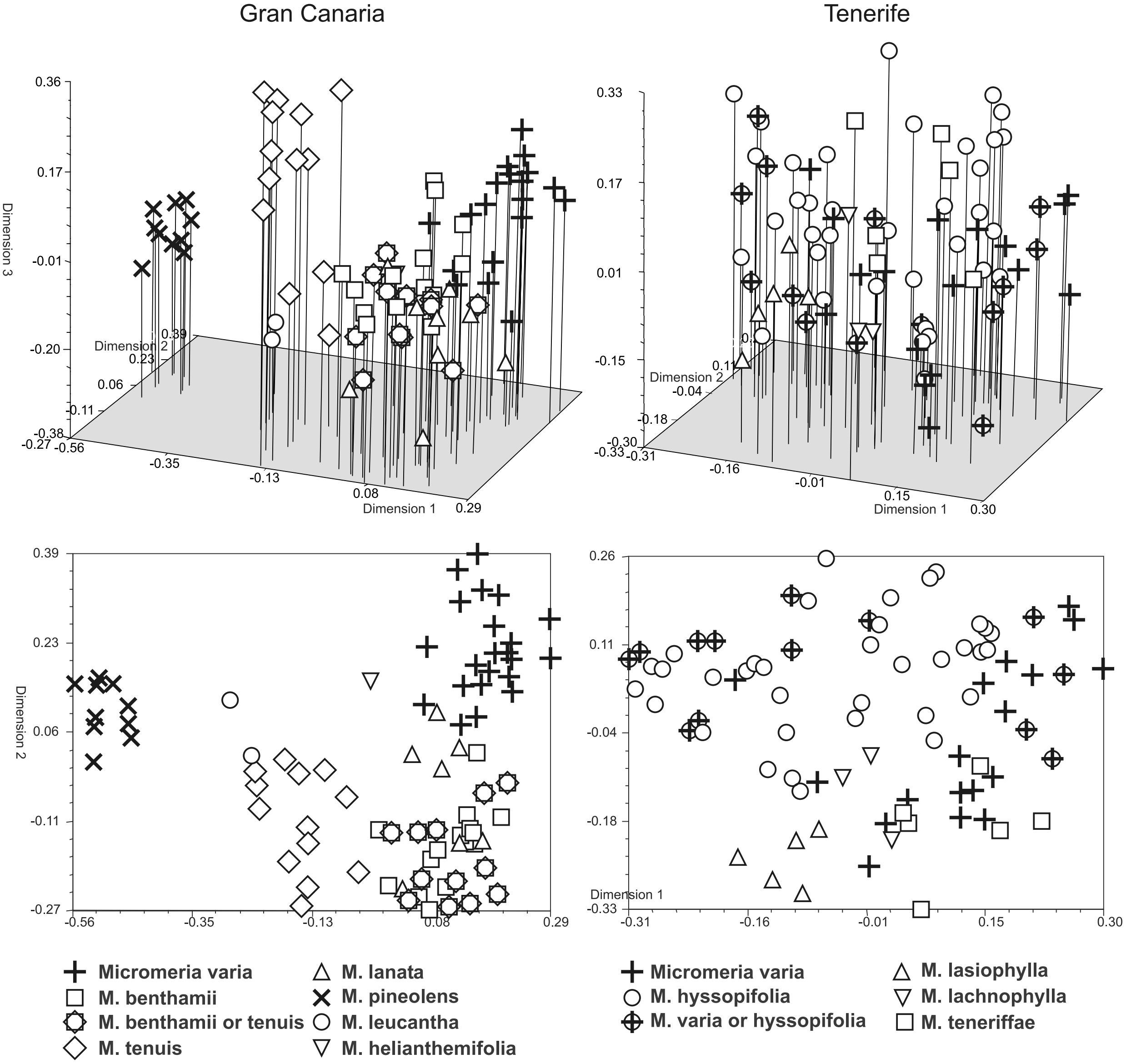

Fig. 4. Comparison of the distance analysis of ISSR fingerprints of samples from Gran Canaria (left) and samples from Tenerife (right), shown as PCoA—plot. Top two panels show three dimensionals, the bottom panels show two.

that showed no obvious separation according to the different species. Samples of *M. teneriffae* represented a cluster which was divided from all other samples from Tenerife.

In El Hierro, a division between the three samples of *M. varia* and the samples from *M. hyssopifolia* could be recognized, while in La Palma samples from different species did not form recognizable major cluster.

4. Discussion

In this study, we performed a survey of genetic similarities using ISSR fingerprints and comparative sequencing of chloroplast and nuclear loci. In all datasets we observed a split between the "eastern" islands Fuerteventura, Lanzarote and Gran Canaria and the "western" islands Tenerife, La Palma and El Hierro. We identified two lineages of *Micromeria* in Gomera but all other islands appear to be colonized by a single lineage.

4.1. Colonization pattern in macaronesia

As indicated by the cpDNA phylogeny, there is strong support for the hypothesis that *Micromeria* from the Canary Islands and Madeira are monophyletic. With the exception of *M. forbesii* Benth. from the Cape Verde Islands, the Macaronesian *Micromeria* form a closely related group that exhibits sequences with low divergence. As revealed by a recent comparative sequence analysis, the closest relatives of this Macaronesian clade are *M. fontanesii* and *M. inodora* from NW Africa and the Balearic Islands, so colonization started probably from the western Mediterranean or NW Africa (Bräuchler et al., 2005).

Results from this study support a division of individuals of Gran Canaria and Lanzarote/Fuerteventura from the rest of the islands. Representatives of both lineages can only be found in Gomera. The assignment of samples from the "eastern" islands to one monophyly and the ones from the "western" to another can be interpreted as a colonization of the archipelago after the appearance of the major islands (at least Gran Canaria and Tenerife). The islands of Lanzarote and Fuerteventura are assumed to be the oldest islands of the archipelago, followed by Gran Canaria. Chloroplast DNA haplotypes from Lanzarote and Fuerteventura were equal to haplotypes found on Gran Canaria so they represent a subset of haplotypes from Gran Canaria, rather than a unique evolutionary lineage. Furthermore, the samples from Lanzarote and Fuerteventura were very similar to each other in respect to their ISSR fingerprinting pattern and sequences. A stepwise colonization from east to west is therefore not supported by the ISSR dataset.

In the FPS 2 as well as in the cpDNA dataset, samples from Gomera, La Palma, El Hierro and Madeira are paraphyletic to samples from Tenerife, with some samples of all these islands and Tenerife exhibiting the same sequence. This pattern indicates that a colonization of these islands was starting from Tenerife and Madeira, about 5 Ma old, had been colonized from one of the younger Canary Islands. As summarized in Trusty et al. (2005), this dispersal route had been identified so far for six taxa: *Aeonium* (Mort et al., 2002; Fairfield et al., 2004) *Convolvulus* (Carine et al., 2004), *Crambe* (Francisco-Ortega et al., 2002), *Pericallis* (Panero et al., 1999), *Sonchus* (Kim et al., 1996) and *Bystropogon* (Trusty et al., 2005). On the contrary, the Cape Verde Islands have been colonized by representatives of another lineage, so *Micromeria forbesii* is part of a neighboring group to all *Micromeria* from the Canary Islands including Madeira (Bräuchler et al., 2005).

4.2. Adaptive radiation, inter island colonization and hybridization

When islands exist in close proximity as they do in the Canary Archipelago, inter-island colonization is very likely. To date, inter-island colonization and ecological shift within one monophyletic group appear to be of similar importance in explaining the evolution of endemic species on the Canary Islands (summarized in Trusty et al., 2005). In our study, inter-island colonization within either the western islands or the eastern islands is consistent with the sequence datasets. However, the ISSR analysis supports the hypothesis that all islands except Gomera have been colonized by a single lineage.

ISSR fingerprint patterns as co-dominant markers are strongly influenced by hybridization events (Wolfe et al., 1998). It is feasible that the genetic similarities derived from the ISSR analysis reflect patterns of introgressions that led to a homogenization of the genotypes of different *Micromeria* species on one island. Introgressions had been proposed by Herben et al. (2005) as an explanation for the finding that most investigated taxa on the Canary Islands appear to have evolved after a single dispersal event to the islands, despite the great age of the islands and their relatively close proximity to the African coast. Herben et al. (2005) suggested that multiple colonizations of the Canary Islands could remain undetected in phylogenetic analyses, because of hybridization between arriving individuals with earlier established populations. Such a mechanism is also feasible for inter island colonization and could lead to the high genetic similarity of species of *Micromeria* on a single island.

Natural interspecific hybrids are recognized for *Micromeria* on several Canary Islands (Pérez de Paz, 1978) and we observed intermediate forms for some of the species where they grow together (e.g. *M. lanata* and *M. benthamii* on Gran Canaria and *M. varia* and *M. teneriffae* on Tenerife). Also the occurrence of equal cpDNA haplotypes in different species from the same as well as different islands indicates some degree of introgression between islands. On the other hand, the samples from Gomera fall within two distinct groups in the analyses, so there appears to be reproductive isolation between these populations, although we failed to differentiate between species in most of these samples. In addition, *M. pineolens* and *M. leucantha* are very similar in their ISSR fingerprint patterns to *M. benthamii* or *M. tenuis* and grow together in near proximity. However, *M. pineolens* and *M. leucantha* are very different from *M. benthamii* or *M. tenuis* morphologically and intermediate forms were not observed. The same applies to *M. varia* in Gran Canaria and the high altitude species *M. lasiophylla* and *M. lachnophylla* on Tenerife. In addition, in Gran Canaria the single species can be differentiated to some extent by the similarity analysis, so at least in some cases species specific bands are present in the matrix.

Our data support a high amount of insular radiation after a single colonization event as primary evolutionary force that led to the high diversity of *Micromeria* on the Canary Islands. However, our FPS 2 results are still preliminary because they do not include subcloned sequences, and thus, an identification of all alleles of this locus within the single species. In addition, the amount of gene flow between species that may influence the pattern we have observed could not be conclusively estimated. In this context, we are currently working on an intensive comparative study on the FPS 2 locus, including about 1200 bp of subcloned PCR product, as well as ongoing analysis of a microsatellite dataset. With identification of the alleles occurring in the different species, we hope to determine if alleles that could be remnants of early diversifications exist in the samples, and introgressions led to a homogenization of genetic similarities. This would be of particular interest for *M. varia*, which could be considered an ancient taxon indicated by its wide distribution. With this approach we also want to verify the phylogenetic position of *M. teneriffae*, which is indicated in the FPS2 dataset with low support as neighbor group to samples from Tenerife, Gomera, La Palma, El Hierro and Madeira and is forming a cluster slightly separated from the remaining Tenerife samples in the ISSR analysis.

4.3. Taxonomic implications

Distance analysis of ISSR fingerprints showed a higher amount of interspecific differentiation within samples from Gran Canaria than from samples from Tenerife, these being the two islands with the highest diversity of *Micromeria* species. Considering the morphological distinctness, the most clearly defined taxa according to the revision of Pérez de Paz (1978) are *M. pineolens* and *M. leucantha* from Gran Canaria which have been placed in their own section Pineolentia. *M. pineolens* is characterized by a shrubby habit (up to 80 cm), ovate, densely pubescent leaves exceeding 10 mm and large pink flowers (10–15 mm). *M. leucantha* is an ascending shrublet up to 20 cm, with leaves grouped towards the tip of the branchlets and large typically white flowers (15–20 mm). Both species are local endemics in the northwestern part of Gran Canaria and show different ecological preferences, *M. pineolens* occurring exclusively in the humid pine forest and *M. leucantha* being part of the coastal low land scrub where it is found predominately on sun exposed cliffs. Our molecular data indicate close relationships to other taxa from Gran Canaria, so the sectional status seems not justified.

In Gran Canaria several taxa are morphologically distinct from *M. varia*. *M. benthamii*, a twiggy shrublet with erect or ascending branchlets, pubescent leaves and flowers of medium size (7–10 mm) is found in the central parts of Gran Canaria (600–1900 m). Similar to *M. benthamii* is *M. tenuis* with slightly smaller flowers (5–6 mm), pubescent leaves and pedunculate cymes that are longer than the leaves. This taxon occurs on dry slopes in the lower zone of Gran Canaria. *M. lanata* a species of the higher parts in central Gran Canaria is distinguished from all other taxa by its narrow elliptical, white-woolly leaves and very small flowers (2–4 mm). The ISSR fingerprint analysis showed these species as slightly delimited from each other, so the results are not contradictory to their status as species.

On Tenerife species are less well characterised. The most widespread taxon on this island is *M. hyssopifolia*, which occurs in the coastal region as well as in the humid laurel forest, Fayal-Brezal and pine forest from sea level up to 2000 m, as well as in El Hierro. It is difficult to separate this species from *M. varia* subsp. *varia* which is found on the coastal zone of northern Tenerife. Both taxa have linear to lanceolate, needle-like leaves with slightly revolute border, very small flowers (3–4 mm) and short pedunculate or sessile cymes. Considering the weak morphological differences between *M. varia* and *M. hyssopifolia* the species status is doubtful. Our molecular data also fail to support a species status for the high altitude species *M. lachnophylla* from Tenerife and *M. lasiophylla* from Tenerife and La Palma. The ISSR fingerprint analysis showed high genetic similarity to samples from other species on the respective island and no closer relationships between samples from *M. lasiophylla* on Tenerife and La Palma. Both species are perhaps ecotypes of *M. hyssopifolia* or *M. herpyllomorpha* (La Palma) respectively.

A morphologically distinct species is *M. teneriffae*, which is a procumbent shrublet with opposite, suborbicular to cordate, glabrous leaves and small flowers (3–5 mm). *M. teneriffae* is restricted to the southern slopes of the Anaga mountains one of the two older parts of Tenerife (4 Ma; Ancochea et al., 1990; Guillou et al., 2004), recently referred to as paleoislands (Trusty et al., 2005). It has been stated that *M. teneriffae* as well as the restricted endemics *M. glomerata*, and *M. rivas-martinezii* might be ancient relicts from these older parts from Tenerife. In the ISSR analysis *M. teneriffae* is forming an own cluster which could support the status as species

Samples from Gomera were the only ones that fell in two clearly separated clusters in all of our analyses, so the occurrence of at least two different species on this island can be supported. *M. lepida* is characterized by lax inflorescenses and peduncles and pedicels longer than the leaves. Additionally *M. varia* with typical small flowers and inflorescences with short peduncled verticillasters occurs between 200–800 m in various parts on Gomera.

Micromeria varia, the possible progenitor of this radiation is distributed in the drier parts of each island of the archipelago, including Madeira. Within *M. varia* various subspecies have been described for different islands which are characterized by similar leaf shape, indumentum, and small flowers (Pérez de Paz, 1978), but slightly different concerning habit, calyx and corolla length. According to our analysis, samples of this species are polyphyletic and more closely related to the other species from the respective island than to conspecific taxa on other islands. Some of the characters may represent pre-adaptations to this xeric habitat. In this case they would resemble the ancient state of the progenitors that originally settled the archipelago. As a consequence, colonization of new islands would have been initiated repeatedly from dry lowland habitats. In this case the status as species would be justified and *M. varia* would be the progenitor of the radiation on the single islands. However, with the exception of El Hierro, samples assigned to *M. varia* are embedded within the clusters of the respective island in the ISSR analysis, so this scenario is not supported by our results. However, the resolution of our datasets is too low to decide between these scenarios, so further research is needed.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.ympev.2006.05.037.

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Killickia (Lamiaceae): a new genus from KwaZulu-Natal, South Africa

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The genus *Killickia* is described to accommodate the South African endemic species formerly placed in *Micromeria* sect. *Hesperothymus*. Morphological data, as well as results from unpublished phylogenetic studies support its separation from the genera *Micromeria* and *Clinopodium*. A new species *Killickia lutea* Bräuchler is described and three new combinations are made. *Killickia* is characterised as comprising solitary- or few-flowered cymes, a campanulate to subcampanulate (obconical) calyx with similar teeth, a corolla tube with two pubescent ridges and nutlets with scattered minute hairs. A thickened marginal vein in the leaves as typical for *Micromeria* is absent. As currently understood all species are restricted to the Drakensberg mountains and KwaZulu-Natal Midlands in eastern South Africa. A key to the species, brief notes on anatomy and ecology are provided.

ADDITIONAL KEYWORDS: anatomy – Mentheae – Menthinae – *Micromeria* – Nepetoideae – new species – revision – *Satureja* – SEM – taxonomy.

INTRODUCTION

The genus *Micromeria* Benth. (Lamiaceae, Nepetoideae) has been subject to long-term taxonomic uncertainty and substantial changes in its generic circumscription in the last decade. Since the synopsis of the genus published by Morales (1993), many species have been transferred to *Clinopodium* L. This concerns all species of the New World section *Xenopoma* and all New World species of section *Hesperothymus* Benth. (Cantino & Wagstaff, 1998; Harley & Granda, 2000) as well as all species of the Old World section *Pseudomelissa* Benth. (Bräuchler, Meimberg & Heubl, 2006; Ryding, 2006). The most recent treatments restrict *Micromeria* s.str. to the two sections *Micromeria* and *Pineolentia* P. Pérez (Bräuchler *et al.*, 2005, 2006) which include species having a more or less entire, clearly visible thickened leaf margin (Bräuchler *et al.*, 2006; Ryding, 2007). Regarding recent molecular and morphological studies it became evident that the Malagasy species formerly included in *Micromeria* (Hedge, 1998) were erroneously placed within that genus and cannot be accommodated in *Clinopodium*. Consequently a new genus will be introduced in due course (C. Bräuchler, unpubl. data). However, this leaves unplaced: Section *Cymularia* from south-eastern Anatolia, which will be discussed elsewhere and the Old World species of section *Hesperothymus*. Recent phylogenetic analysis based on molecular data focussing on the whole subtribe Menthinae (C. Bräuchler, unpubl. data) revealed the latter to be topologically completely dissociated from *Micromeria* s.str., and sister to the new genus from Madagascar mentioned above. Additionally leaf sections show that none of the species has the conspicuous sclerenchymatic vascular bundle at the margin, which is diagnostic for *Micromeria* s.str.

Old World members of sect. *Hesperothymus* form a small group of taxa endemic to the Drakensberg

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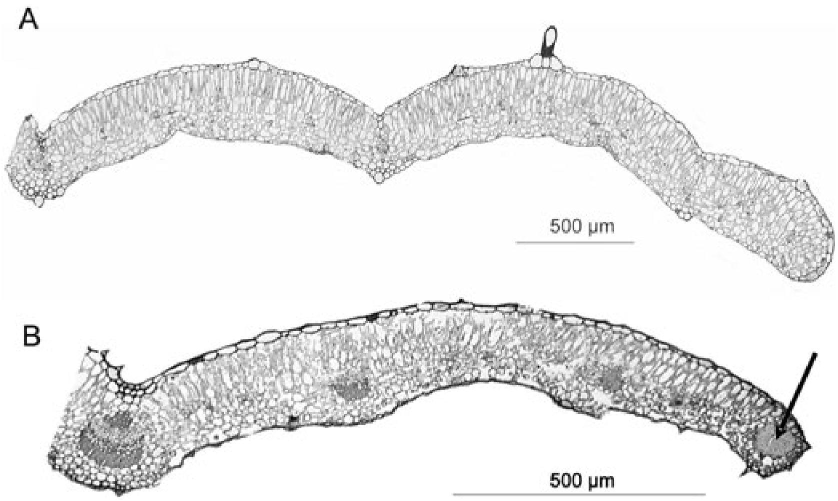

Figure 1. Leave cross-sections of *Killickia lutea* (A) and *Micromeria lepida* (B), revealing the presence of a marginal vein in *Micromeria* s.str. (indicated by the black arrow) and its absence in *Killickia*.

Mountains in South Africa and the adjacent KwaZulu-Natal Midlands. Within this alliance the first species has been described by Bentham (1876) under *Micromeria*, a second was, added by Killick (1954). When establishing a third species, Killick (1961) transferred the group to *Satureja* s.l. to maintain uniformity of treatment with Thonner (1915); Brenan (1954) and Hedberg (1957). Doroszenko (1986) in his PhD thesis accomodated the species in a new genus '*Killickia*', which was, however, neither effectively nor validly published. Finally Morales (1993) formally reincluded the group in *Micromeria* sect. *Hesperothymus*. All treatments so far were based on limited herbarium material and (except for Killick, 1954, 1961) observations in the natural habitat were rare. Since that time many new collections have been made, in first place by O.M. Hilliard and B.L.Burtt (both now at Royal Botanic Garden Edinburgh). Herbarium studies and intensive field observations by the first author suggested that species limits should be re-examined.

This paper presents a morphological description of *Killickia* including a taxonomic treatment with three new combinations and one newly described species. The delimitation towards related genera is pointed out and cross-sections of leaves are shown in Figure 1 to underline it's distinctness from *Micromeria*. For each species illustrations (drawings and photographs) as well as SEM-images of nutlets are provided.

DESCRIPTION OF THE GENUS *KILLICKIA*

KILLICKIA BRÄUCHLER, HEUBL & DOROSZENKO, **GEN. NOV.**

(Lamiaceae, Nepetoideae, Mentheae, Menthinae)

Based on *Micromeria* sect. *Hesperothymus* Benth. pro parte, quoad species austro-africanes.

Typus: Killickia pilosa (Benth.) Bräuchler, Heubl & Doroszenko (designated here).
≡ *Micromeria pilosa* Benth. in Bentham & Hooker, Gen. Plant. 2: 1188 (1876). – Type: [South Africa, KwaZulu-Natal] Faku's Territory, *Sutherland s.n.* (holotype K!).

Genus novum affine generibus *Micromeria* et *Clinopodio*. A *Micromeria* differt imprimis foliis sine nervis marginalibus, a *Clinopodio* differt calycibus campanulatis et nucellis laxe breviter pilosis.

Prostrate to decumbent, perennial, strongly aromatic herbs, glandular-punctate, heavy sweetish mint scented; stoloniferous or not. Root either one hardly branched taproot or tuberous underground organs (forming on nodes of underground runners) from which annually new shoots arise. Leaves clearly petiolate, broadly ovate to orbicular, flat, with simple, multicellular hairs scattered on upper surface and concentrated on the nerves at the lower surface; margin not revolute, serrate or crenate, marginal vein absent, lateral veins distinct, camptodromous, palisade mesophyll dorsiventral often with two layers of palisade parenchyma. Bracts similar to ordinary leaves. Inflorescence composed of solitary to few flowered cymes, often with long pedicels. Bracteoles always present, foliose or minute-linear. Calyx mostly obconical (subcampanulate) to campanulate, not tubular, straight, 15-nerved, actinomorphic or subbilabiate, lobes half as long or as long as tube, throat glabrous inside, enlarging in fruit; teeth triangular to triangular-lanceolate, all similar in shape, not ciliate, spreading or appressed to corolla tube. Corolla cobalt-

Key to the species of *Killickia*

1a Bracteoles ovate-cordate, resembling the leaves, 5–11 mm long, calyx teeth 3.0–5.0 mm; corolla 20–24 mm long, light cobalt-violet, lower lip straight with tip and edges curved downwards .... **2. *K. grandiflora***
1b Bracteoles linear, 1–2.5 mm long; calyx teeth 0.9–2.0 mm; corolla 5–19 mm long, violet or not, lower lip mostly curved downwards 2
2a Corolla tube 5.0–12.0 mm, upper lip less than half as long as lower lip; root forming tubers with underground runners; calyx tube 1.5–4 mm long .... **1. *K. pilosa***
2b Corolla tube 3.0–5.0 mm, upper lip as long as or slightly longer than lower lip; deep, hardly branched not conspicuously tuberous root; calyx tube 1.3–2.0 mm long 3
3a Corolla deep cobalt-violet to violet; cymes on short peduncles (< 3 mm) with mostly solitary to very rarely 3 flowers; calyx always shorter than corolla tube, teeth triangular, curved outwards from the beginning of anthesis; habit quite compact, short internodes (5–15(20) mm) .... **3. *K. compacta***
3b Corolla intense to pale yellow (rarely almost white); cymes on long peduncles (4–19 mm) with solitary or often 2–4 flowers; calyx as long as corolla tube, teeth narrowly triangular ending in a filiform part in the distal half, straight, not spreading at anthesis; habit not compact, long internodes (5–40 mm) .... **4. *K. lutea***

violet, light violet, yellow or white, not resupinate; tube wide at throat, not annulate inside, with two more or less prominent, densely to sparsely pubescent ridges extending from base of lower lip inside tube; upper lip emarginate or retuse, lower lip 3-lobed, longer than upper. Stamens 4, arcuate, convergent on upper side of corolla tube; filaments short, anterior pair longer, posterior included in tube, anterior sometimes exserted but not beyond upper lip; anthers 2-celled, cells parallel or divergent. Style included, often in a furrow on the upper inside of the tube; stigma bifid, lobes unequal, with anterior lobe up to 3–4 × longer than shorter and (in some species) broader posterior lobe. Nutlets oblong *c.* 1.8 × 1.2 mm to 3.5 × 2.5 mm, covered with scattered minute hairs all over, often only 1–2 maturing, the others abortive.

Note: Killickia is clearly distinct from *Micromeria* due to the lack of a thickened marginal vein in the leaves (Fig. 1) and crenate to dentate instead of entire leaf margins. In addition molecular data strongly support an isolated position outside of *Micromeria* or *Clinopodium* (Bräuchler *et al.*, submitted). The new genus is more similar to *Clinopodium* concerning habit and leaf shape. However, it is distinguished by the combination of solitary- or few-flowered cymes (sometimes on very long peduncles up to 24 mm) with obconical (subcampanulate) to campanulate, not tubular, actinomorphic to sub-bilabiate calyces, not sigmoid or gibbous at base, with similar upper and lower teeth, straight or bent outwards. While some *Clinopodium* species (e.g. *C. simense* and *C. kilimandscharii*) sometimes do have solitary flowered cymes, unlike *Killickia* they have sigmoid calyces, whereas a number of species having campanulate to tubular, but not obconical to campanulate calyces, usually show a higher number of flowers per cyme. Nutlets are comparatively large with scattered minute hairs all over. Those of *Micromeria* and *Clinopodium* species are either glabrous or have longer hairs only at the apex (cf. Hussein *et al.*, 1990) and as a rule are of smaller dimensions. The Malagasy species are sufficiently distinct in having generally smaller leaves with fewer teeth at the margin, other calyx shape and nutlet structure. They are currently being revised by the first author and will be treated in a forthcoming publication.

Etymology: The new genus is named in honour of Donald J.B. Killick who carried out botanical inventories throughout the Drakensberg Mountains and enormously increased our knowledge of the group, its species, ecology and distribution.

Note: To avoid confusion peduncle is here defined as the proximal part of the primary cyme axis below its bracteoles. Pedicels are understood as all secondary axes of the cyme (including both parts below and above bracteoles) and the distal part of the primary axis above its bracteoles. Measurements of floral organs due to restricted material available have only been taken from a few flowers with little variation revealed. In case types have only be seen as digital images the barcode number of the specimen is provided. Images marked with * have been consulted at the African Plants section of the ALUKA online library (http://www.aluka.org).

SPECIES TREATMENTS

1. ***Killickia pilosa*** (Benth.) Bräuchler, Heubl & Doroszenko, **comb. nov.**

≡ *Micromeria pilosa* Benth. in Bentham & Hooker, Gen. Plant. 2: 1188 (1876). ≡ *Satureja reptans* Killick in Bothalia 7:436 (1961), nom. nov., non *Satureja pilosa* Velen. in Sitzungsber. Königl. Böhm. Ges. Wiss. Prag., Math.-Naturwiss. Cl. 40: 6 (1899). – Type:

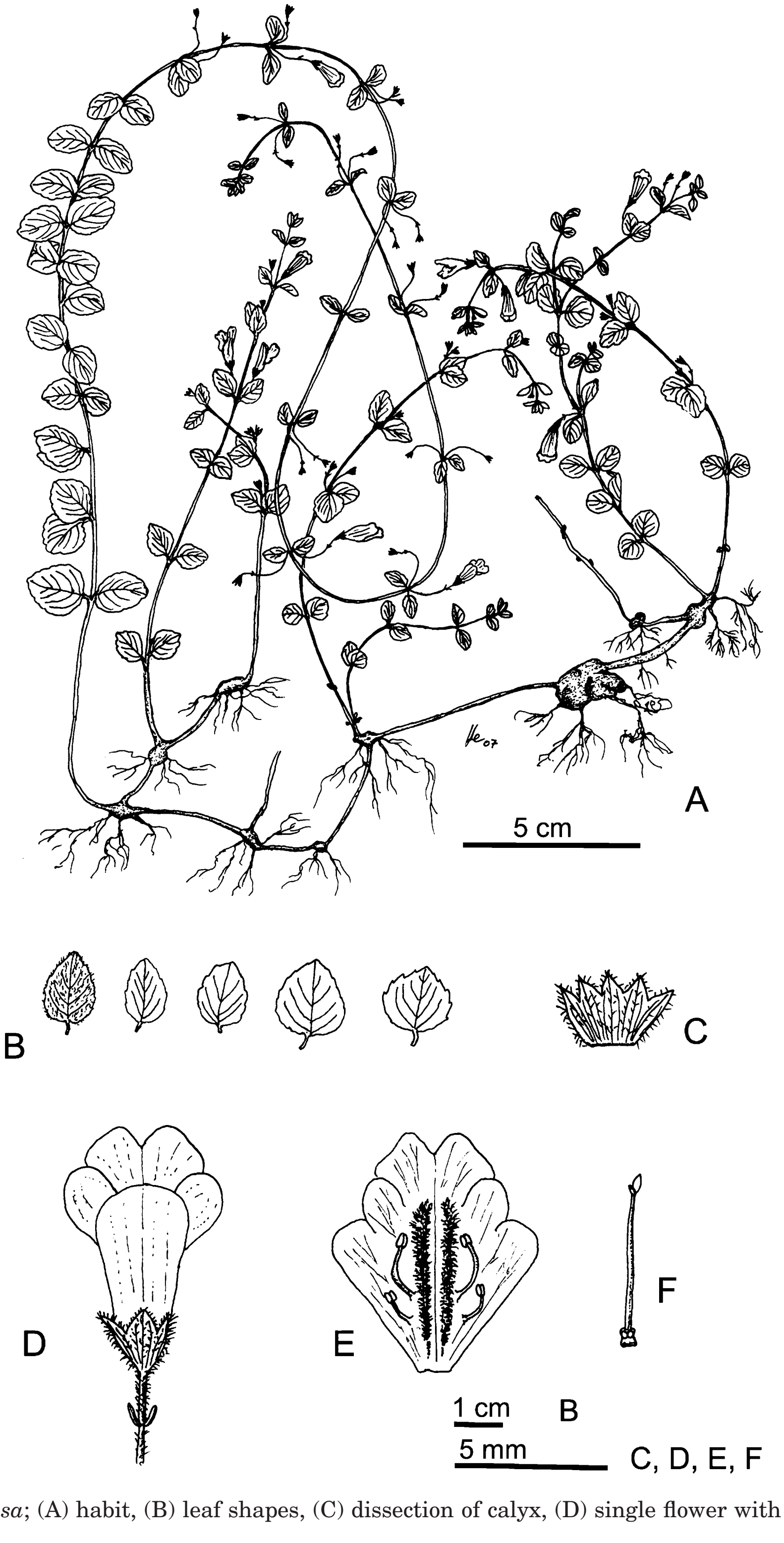

Figure 2. *Killickia pilosa*; (A) habit, (B) leaf shapes, (C) dissection of calyx, (D) single flower with pedicel, (E) dissection of corolla, (F) pistil.

[South Africa, KwaZulu-Natal] Faku's Territory, *Sutherland s.n.* (holotype K!).

Icon.: Benth. in Hook. Icon. Pl. 15: t.1522 (1886), ic. nostra (Figs 2, 6A, B, 7)

Note: Killick (1961) cites two syntypes for this species: 'Faku's Territory, *Sutherland* s.n.' (K) and 'Natal, *J. M. Wood* 3712' (K). He referred to the publication of *M. pilosa* by Bentham (1886: t.1522). Bentham (1876:

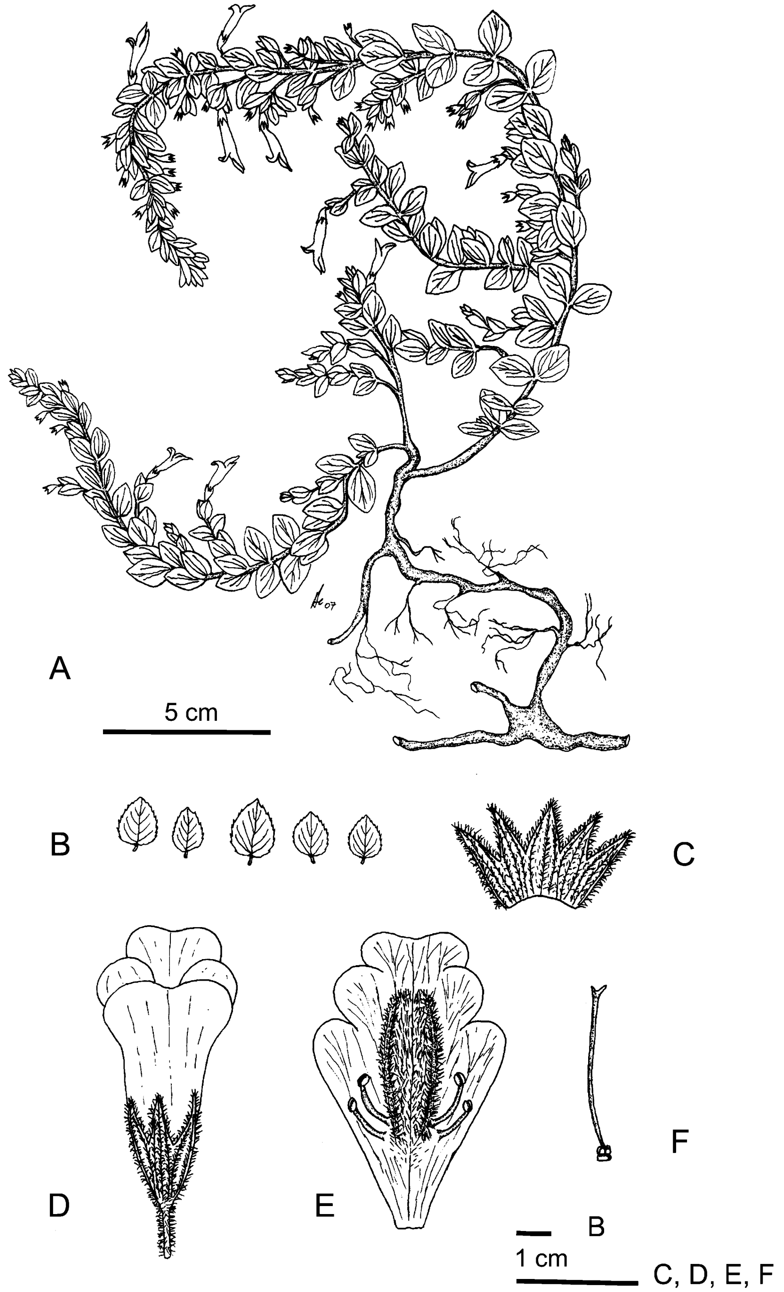

Figure 3. *Killickia grandiflora*; (A) habit, (B) leaf shapes, (C) dissection of calyx, (D) single flower with pedicel, (E) dissection of corolla, (F) pistil.

1188), however, first published the name accompanied by a short diagnosis and only the Sutherland collection cited, thus representing the holotype; consequently the J.M. Wood collection has no type status at all.

Prostrate aromatic herb with slender branches up to 75 cm; internodes 1–5 cm long. Leaves ovate (basal ones sometimes suborbicular), 7–28 × 6–27 mm (4–6 × 4–5 mm on protruding stems), apex acute to rounded, base shallowly cordate to broadly cuneate, margins crenate with few teeth (2–8); petioles 1–5 mm long. Flowers 1–2 per bract (up to very rarely almost 6 in lax cymes). Peduncles threadlike, 5–24 mm long, bibracteolate in the distal half, sometimes bracteoles just 1–2 mm from flower, pedicels 1–10 mm, bracteoles linear, 1–2.5 mm long. Calyx campanulate, 15-nerved; tube 1.5–4 mm long, teeth subequal, triangular, 1–2 mm long, straight to slightly bent outwards, enlarging in fruit. Corolla

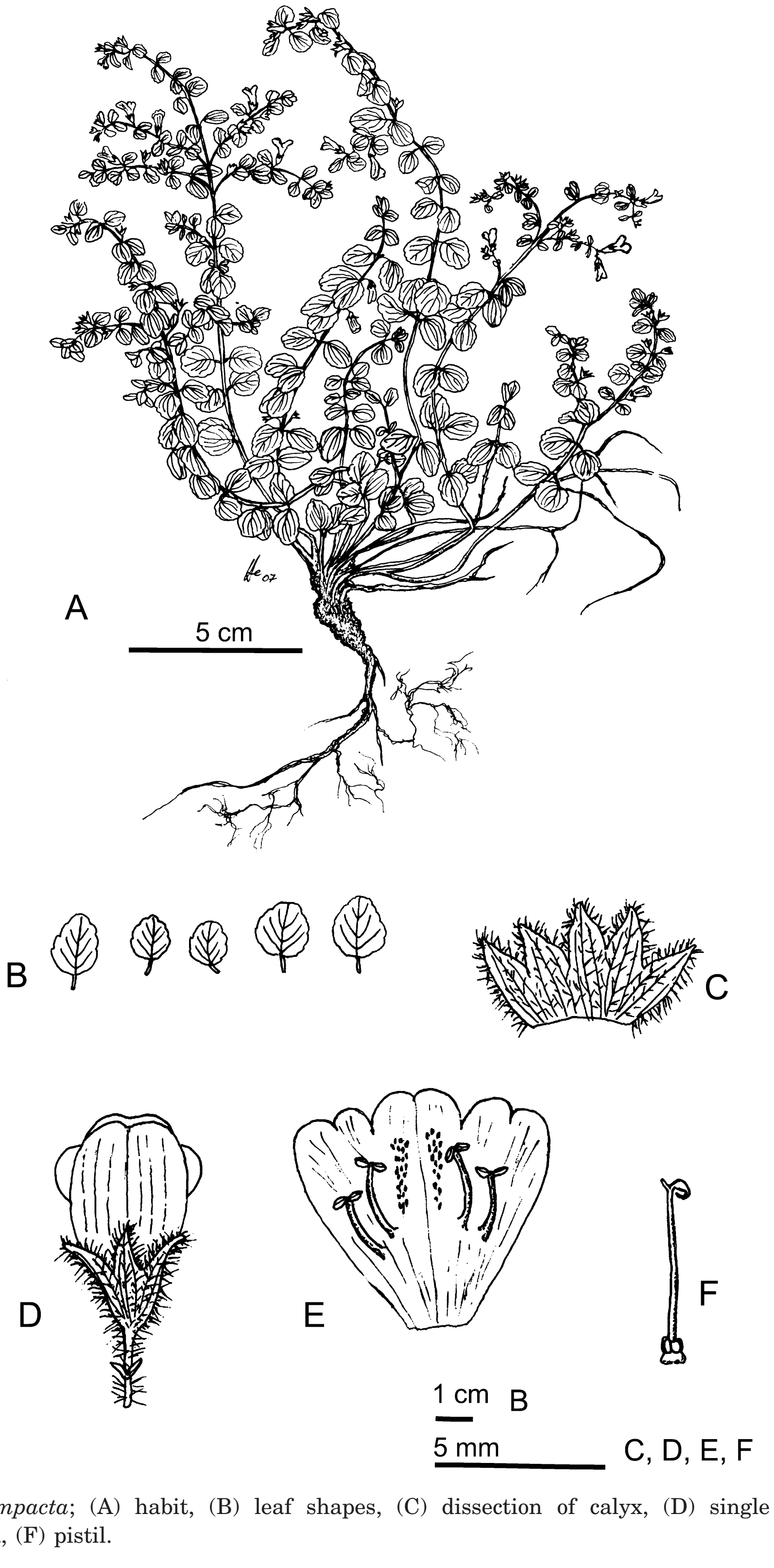

Figure 4. *Killickia compacta*; (A) habit, (B) leaf shapes, (C) dissection of calyx, (D) single flower with pedicel, (E) dissection of corolla, (F) pistil.

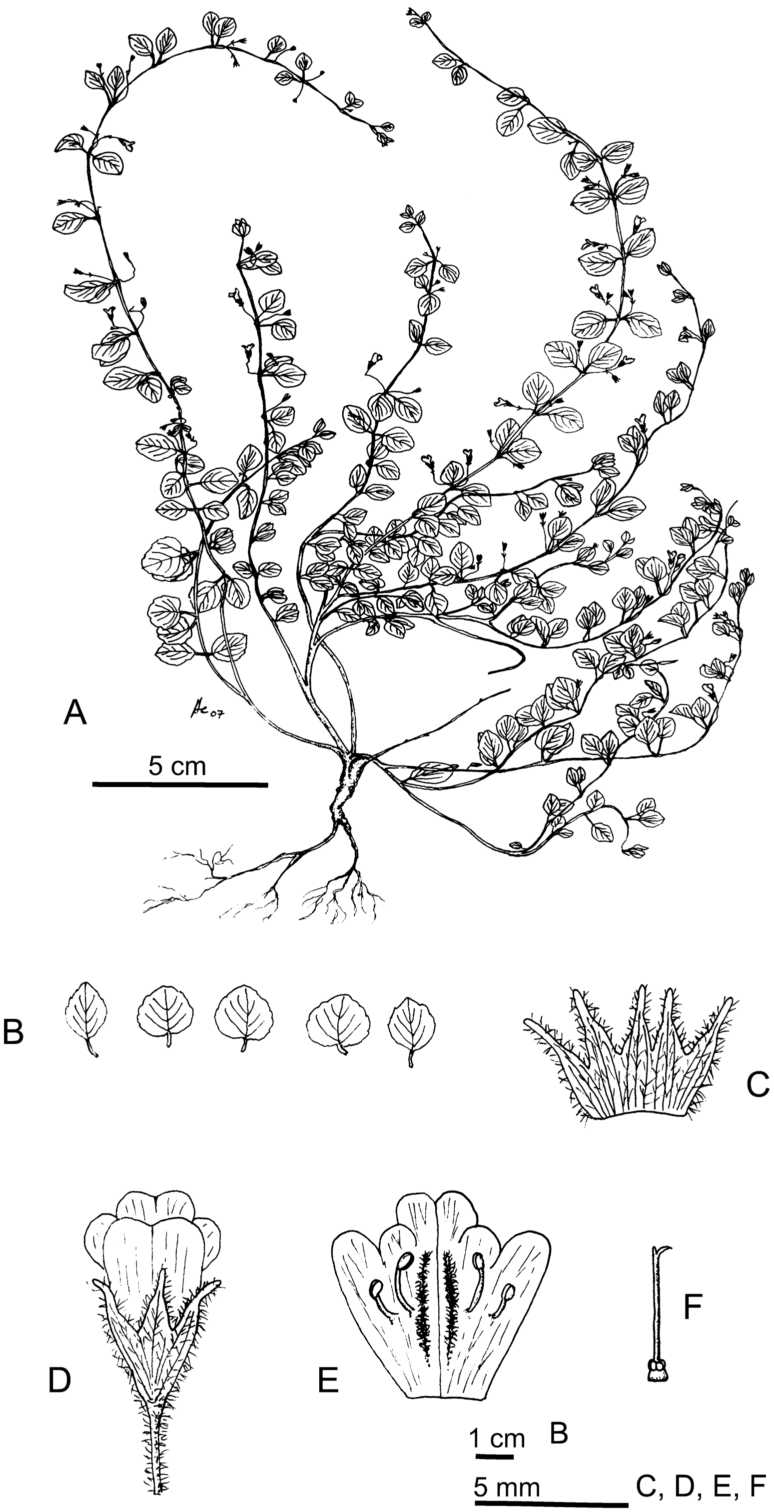

Figure 5. *Killickia lutea*; (A) habit, (B) leaf shapes, (C) dissection of calyx, (D) single flower with pedicel, (E) dissection of corolla, (F) pistil.

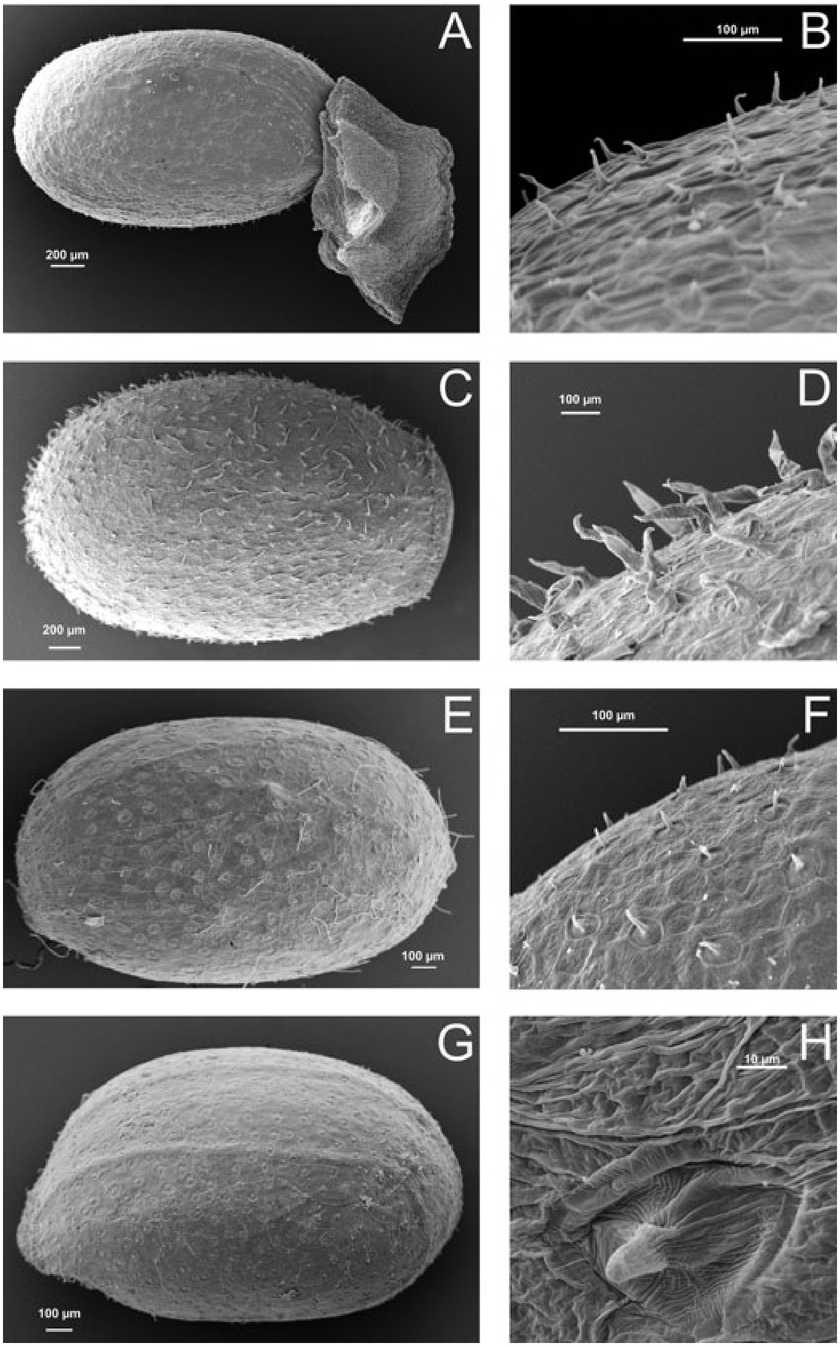

Figure 6. SEM-images of nutlets of *Killickia* species; left column overview, right column details; (A, B) *Killickia pilosa*, (C, D) *Killickia grandiflora*, (E, F) *Killickia compacta*, (G, H) *Killickia lutea*.

almost white to violet suffused, often creamy yellow on lower side between the two hairy ridges (sometimes with a deeper violet touch), 9–19 mm long; tube 5–12 mm long, 3–7 mm wide at mouth; upper lip emarginate, 1–2 × 3–6 mm; lower lip curved downwards, 3-lobed, middle lobe emarginate, 4–7 × 3–7 mm, lateral lobes round, 2–3 mm in diameter. Filaments: upper ones up to 1.5 mm long, lower ones up to 4.5 mm long. Anthers < 1 mm long. Disc slightly lobed. Style straight, 1cm long, hidden in a furrow on upper inside of corolla tube. Stigma lobes very unequal, the anticous being about 0.8 mm and rhomboid, the posticous being very short, filiform. Nutlets *c.* 2 × 1 mm (Fig. 6A, B).

Figure 7. *Killickia pilosa*, habit and flower close up.

Distribution: Ukhalamba Drakensberg National Park and adjacent KwaZulu-Natal Midlands in mountain grassland at altitudes of 1500–2500 m. It is the most widespread one of these species.

Note: Cymes in some individuals from Loteni Nature Reserve or the Lions River dist. (e.g. A.J. Phelan 481, Wright 1383) have more than 4 flowers. In most collections however the usual number of flowers is 1, 2 or (more rarely) 3. Populations observed in the Cathedral Peak area tend to have violet suffused corollas with the upper lip only slightly retuse and the stigma hidden under the upper lip, while those observed in the Underberg Midlands (close to the type locality) have corollas almost white with strongly retuse upper lip and stigmas bent downwards and clearly visible. These characters need further field observations, may be they are of taxonomic importance, may be they only represent different developmental stages (though from plants in one population there was no evidence for this).

Specimens examined in addition to the type:

K. Balkwill & M-J. Balkwill 5238 (E); C. Bräuchler *et al.* 3810 (FR, M, NU, to be distributed), 3832 (FR, M, NU, to be distributed); F. Brown s.n. in herb. F.A.Rogers 27780 (Z); J. Compton s.n. (E); T. Cooper 2903 (Z); T. Edwards 743 (NU); E.E. Galpin 11745 (BOL, M, PRE); P. Goldblatt & J. Manning 8451 (E); C. Gordon-Gray 70 (NU); M. Grice s.n. (NU), s.n. (NU); Hilliard & Burtt s.n. (NU), 3430 (E), 5663 (E, SA, Z), 8033 (E), 8094 (E, NU, P), 15085 (E), 15837 (E), 18096 (E); K.D. Huntley 153 (NU); D.J.B. Killick 1272 (P, PRE, BM, BR), 1429 (PRE), 3848 (BR); A.J. Phelan 481 (NU), 465 (NU); Potgieter & I. Johnson 620 (NU); C. Potgieter & P. Thompson 739 (NU); M.A. Rennie 574 (NU), 1072 (NU); F.A. Rogers 27860 (Z), 27872(Z); R. Schlechter 6808 (BOL, C, P, Z); D.L. Smith 201 (NU); J. Stewart 1717 (E, NU); J.M. Wood s.n. (BOL), s.n. (SAM), 1019 (E, BM), 3142 (BOL, BM), 3712 (K, wrongly cited as syntype), 5909 (E), 9743 (NBG), 11161 (E, BM, Z); F.B. Wright 1383 (E, NU).

Figure 8. *Killickia grandiflora*, habit.

2. ***KILLICKIA GRANDIFLORA*** (KILLICK) BRÄUCHLER, HEUBL & DOROSZENKO, **COMB. NOV.**

≡ *Micromeria grandiflora* Killick in Bothalia 6: 439 (1954) ≡ *Satureja grandibracteata* Killick in Bothalia 7: 435 (1961), nom. nov., non *Satureja grandiflora* Scheele in Flora 26: 577 (1843). – Type: Natal, Bergville district, Cathedral Peak Forest Influences Research Station, locally frequent in *Thedema triandra* grassveld, 6400ft., 19.2.1952, *Killick 1684* (holotype PRE 0123422!*, isotype CPF, K!, L 0003725!, MO 694862!*, NH 0042501!*, P!).

Icon: Killick, Bothalia 6: 439 (1954), ic. nostr. (Figs 3, 6C, D, 8).

Perennial, aromatic herb, decumbent shoots 10–43 cm arising from the base, sparingly branched with underground runners, sometimes thickened to a tuberous organ from which several branches arise. Stems decumbent, often with small branchlets in the axils of the lower leaves. Leaves subsessile, occasionally with petioles up to 3 mm long, ovate–cordate, 10–25 × 7–22 mm, serrate, 4–8 teeth. Flowers usually solitary. Very rarely further branches arise from the axils of the bracteoles forming small foliose cymes with up to 4 flowers. Peduncles 5–14 mm long, bibracteolate in the distal half, pedicels 3–9 mm long. Bracteoles resembling the leaves, 5–11 × 3–10 mm. Calyx in flower 7–8 mm long; tube subcampanulate, 4–5 mm long, 15-nerved; calyx teeth 5, subequal, triangular-lanceolate, 3–5 mm long, usually about as long as tube or longer; calyx in fruit 9–10 mm long. Corolla pale to deep cobalt-violet, 20–24 mm long; tube 11–17 mm long, subcylindric at base (up to 4 mm), flattened-campanulate above, 7–9 mm wide at throat, *c.* 2 mm wide at base, two ridges inside tube on lower side, pubescent and gland-dotted outside, with long thick hairs inside chiefly on the two ridges; upper lip emarginate, slightly reflexed, 2.5 × 7–10 mm, pilose and gland-dotted outside, glabrous inside; lower lip straight with tips curved downwards, 3-lobed, lateral lobes emarginate or entire, 4 × 5–6 mm, sparingly pilose and golden gland-dotted outside, glabrous inside, median lobe emarginate, 4.5 × 6 mm, glabrous outside and inside, several scattered marks in darker violett on upper surface. Upper stamens *c.* 7 mm long, shortly decurrent, lower pair *c.* 3 mm long; filaments glabrous; anther cells parallel, *c.* 1 mm long with 6–14 headlike yellow glands inserted situated ventrally on the connective between the cells. Style 10–13 mm long; stigma lobes acute, unequal, the posticous shorter. Nutlets *c.* 3.5 × 2.5 mm (Fig. 6C, D).

Distribution: Found at about 2000 m altitude on the Little Berg in the Cathedral Peak Area of the Ukhalamba Drakensberg National Park. According to Killick (1954) the species is restricted to only two small catchment areas of the old Cathedral Peak Forest Research Station.

Note: The species has affinities to *K. pilosa* but differs in decumbent stems (instead of prostrate to decumbent), shorter internodes, shorter and stouter pedicels, larger flowers, bracteoles and nutlets and the absence of particularly long overground runners. The leaves have a sharp mentha-like scent. According to Killick (1954) this taxon occupies drier environments than *Killickia pilosa*.

Specimens examined in addition to the type:

C. Bräuchler *et al.* 3811 (FR, M, NU, to be distributed); L.E. Codd 6241 (M, NU 0015702!*; paratype); O.M. Hilliard, B.L. Burtt No. 18579 (E, NU); D.J.B. Killick 1102 (BM, NU; paratype).

Figure 9. *Killickia compacta*, habit and flower close up.

3. ***KILLICKIA COMPACTA*** (KILLICK) BRÄUCHLER, HEUBL & DOROSZENKO, **COMB. NOV.**

≡ *Satureja compacta* Killick in Bothalia 7: 437 (1961). ≡ *Micromeria compacta* (Killick) Morales in Bot. Complutensis 18: 164 (1993). – Type: Natal, Bergville, below Amphletts, Cathkin Peak Area, 12.12.1952, Killick 1866 (holotype PRE 0588127!*, isotype B!, BM!, BOL!, CPF, E!, GRA!, K!, M!, MO 391156!*, NH 0042501!*).

Icon.: Ic. nostr. (Figs 4, 6E, F, 9).

Perennial herbs with a strong hardly branched woody rootstock; overground shoots prostrate mat forming, much branched, up to 40 cm long, sometimes rooting at the nodes and via fragmentation forming clones (at least in type collection), internodes 5–15(20) mm; leaves broadly ovate to orbicular, 3–11 × 2–10 mm, round at base and apex, margins shallowly crenate; petioles 2–4 mm long. Flowers solitary (very rarely up to 3 as in one side branch of K. Balkwill, J. Manning & S. Meyer 1065). Peduncles always shorter than 3 mm (usually 0.1–1.5 mm), primary cyme axis bibracteolate mostly in proximal half (only in very rare cases in distal half through elongation of proximal half to situate the flower correctly), pedicels 1–2.5 mm; bracteoles linear–lanceolate, *c.* 1.5 mm long, keeled. Calyx campanulate, 15-nerved; tube just under 2 mm long; teeth equal, triangular-lanceolate, *c.* 2 mm long, moderately to strongly bent outwards, not apressed thus upper part of the corolla tube appearing free. Corolla cobalt-violet, pubescent outside, glabrous inside except for two, very little prominent, sparingly pubescent ridges at the bottom of the tube; tube narrowly campanulate, 3–5 mm long; upper lip emarginate, 2 × 3 mm wide, lower lip curved downwards, 3-lobed, lateral lobes round, *c.* 2 mm in diameter, middle lobe emarginate 2 × 2–5 mm. Upper stamens *c.* 2 mm long, lower ones *c.* 3 mm long; anther cells divaricate. Style *c.* 6 mm long; stigma lobes very unequal, the posticous shorter. Nutlets *c.* 1.8 × 1.2 mm (Fig. 6E, F).

Distribution: Below the Amphletts in the Cathkin Peak area and Ships Prow Path area of the Ukhalamba Drakensberg National Park.

Note: Concerning the root system the available material is ambiguous to some extent: The type collection contains only branches with roots at the basal nodes in one duplicate even with a woody shoot base but no real rootstock. Taking into account, however, the most recent collections from the type locality by the first author, these seem to be only side branches which develop roots when the plant gets covered by soil via earth slips which are common in the typical habitat (terracelets on steep slopes). The usual growth form is most likely to be that of several annual stems arising from a woody rootstock and eventually enabling clonal growth by fragmentation of branches. The root penetrating deep into the soil probably is an adaptation to the earth slips and frequent grass fires caused by lightnings. The fact that Killick cited them to 'form mats 45 cm in diameter' favours the conclusion that the parts he collected were branches spreading from one point (i.e. the woody rootstock). Concerning the solitary flowers, there seem to be some exceptions (K. Balkwill, J. Manning & S. Meyer 1065; C. Bräuchler *et al.* 3816) which are basically the result of extreme reduction of side branches.

Specimens examined in addition to the type:

K. Balkwill, J. Manning & S. Meyer 1065 (NU); C. Bräuchler *et al.* 3816 (FR, M, NU, to be distributed).

4. ***KILLICKIA LUTEA*** BRÄUCHLER, **SP. NOV.**

Similis *Killickia compacta* (Killick) Bräuchler, Heubl & Doroszenko sed differt internodiis longioribus, foliis generaliter majoribus, pedicelis saepe multe longioribus, floribus saepe in cymis 2–4, corollis luteis, calycis corollarum tubis aequilongis nec brevioribus et dentibus calycis oblongis anguste-triangulatis, ab medio ad apicem linearis, florendi tempore adpressis corollam ad fructum leviter reflexis.

Type: South Africa, KwaZulu-Natal, Ukhalamba Drakensberg National Park, Underberg district, Garden Castle Nature Reserve, common along path in small river valley from Forresters House to Sleeping Beauty Cave, starting upwards from the place where the slopes leave little space on both sides, creeping in Grassveld and over rocks on valley bottom. C. Bräuchler 3828, collected with C. Carbutt, S. Dressler & H.-J. Esser, 27.1.2006 (holotype M, isotype B, BM, BOL, C, CPF, E, FR, GRA, herb. Bräuchler, K, MA, MSB, NBG, NH, NU, P, PRE).

Figure 10. *Killickia lutea*, habit and flower close up.

Icon: Ic. nostr. (Figs 5, 6G, H, 10)

Perennial herbs with a strong hardly branched woody rootstock; overground shoots prostrate and mat forming, moderately branched, up to 92 cm long, occasionally rooting at the nodes; internodes 5–40 mm; leaves broadly ovate to orbicular, 3–21 × 2–21 mm, obtuse to rounded at base, rounded to obtuse at apex, margins crenate; petioles 2–8 mm long. Flowers solitary to often 3–4 per cyme. Peduncles 4–19 mm long, primary cyme axis bibracteolate mostly in distal half, but secondary cyme axes usually in proximal half, pedicels 2–7 mm long; bracteoles linear-lanceolate, up to 2 mm long, keeled. Calyx subcampanulate, 15-nerved, 3–4.5 mm; tube 1.5–2 mm long; teeth equal, triangular with the distal half linear (appearing filiform in dried specimens), 1.5–2.5 mm long, equally long as free part of corolla tube, straight, rarely slightly bent outwards at the ends, apressed, thus upper part of corolla tube appearing embraced by calyx lobes. Corolla (rarely) almost white to yellow, pubescent outside, glabrous inside except for two, little prominent, pubescent ridges at the bottom of the tube; tube narrowly campanulate, *c.* 5 mm long; upper lip emarginate, *c.* 2 × 3 mm, lower lip 3-lobed, lateral lobes round, c, 2 mm in diameter, middle lobe emarginate 2 × 2–5 mm. Upper stamens *c.* 2 mm long, lower ones *c.* 3 mm long; anther cells parallel. Style *c.* 6 mm long; stigma lobes very unequal, the posticous shorter. Nutlets *c.* 1.8 × 1.2 mm (Fig. 6G, H).

Distribution: Quite common in the Southern Drakensberg, in narrow river valleys creeping in grass pastures, along paths and in the lowest parts of the adjacent banks.

Note: Recent collections and field studies of *Killickia* have revealed this new species which is similar and obviously most closely related to *K. compacta*. It differs, however, in its ecological preferences, habit, colour of flower (completely yellow corollas – a very uncommon, if not unique feature throughout Old World Menthinae) and calyx characters (calyx teeth ending in a filiform distal part and not spreading at anthesis) to such extent that there is no doubt about its distinctness.

Paratypes: O.M. Hilliard & B.L. Burtt, 9344 (E!, S), 9726 (M!), 9287 (M!, E!, S), 9876 (E!, M!, NU!, PRE, S), 9385 (E!), 9573 (E!, M!, NU!, S).

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6.5 Manuskript 5:

Bräuchler, C., Heubl, G. & Ryding, O. 2008:
The genus *Micromeria* Benth. (Lamiaceae) –
a synoptical update. Willdenowia 38: 363-410.

CHRISTIAN BRÄUCHLER, OLOF RYDING & GÜNTHER HEUBL

The genus *Micromeria (Lamiaceae),* a synoptical update

Abstract

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No comprehensive revision of *Micromeria* is available and uncertainties about the taxonomy of the genus have lasted for a long time. Since the last synopsis many new data from both morphological and molecular genetic studies have been accumulated and, consequently, the number of accepted taxa and the delimitation of the genus have changed considerably. The authors provide a review of recent and unpublished research on the genus, a new circumscription and description of the genus and an updated distribution map. All published *Micromeria* names are listed with a reference to their current taxonomic position. Names of taxa currently placed in *Micromeria* are provided with type citations. A new combination, *M. cristata* subsp. *kosaninii,* is validated, along with the new name *M. longipedunculata* for the illegitimate *M. parviflora* of Reichenbach. The author standard abbreviation E. F. Chapm. is proposed for one of the authors of *M. graeca* subsp. *cypria* and 24 names are typified. Taxonomic problems needing special attention in future research are identified.

Additional key words: generic circumscription, taxonomy, nomenclature, typification, checklist

Introduction

The genus *Micromeria,* distributed from the Macaronesian-Mediterranean region to southern Africa, India and China, was described by Bentham (1829). It belongs to *Lamiaceae* subfam. *Nepetoideae* tribe *Mentheae* subtribe *Menthinae* and is considered as part of the vaguely defined "*Satureja* complex". To accommodate the apparent morphological diversity many taxonomists have split this complex into several genera, mainly *Satureja* L., *Clinopodium* L., *Calamintha* Mill., *Acinos* Mill. and *Micromeria* Benth. (Bentham 1848; Boissier 1879; Ball & Getliffe 1972; Davis 1982; Doroszenko, unpubl. Ph.D. thesis Edinburgh Univ. 1986). Others lumped the group to a single genus *Satureja* s.l. (Briquet 1896; Brenan 1954; Greuter & al. 1986; Seybold 1988) or *Clinopodium* (Kuntze 1891: 513-516). These different views on the generic limits of the "*Satureja* complex" resulted in considerable taxonomic confusion.

Recent studies of the phylogeny and generic status of *Satureja* s.l. using cladistic analyses of molecular data have contributed a lot to a better understanding of the group. Of particular relevance are papers by Wagstaff & al. (1995), Prather & al. (2002), Trusty & al. (2004) and Bräuchler

& al. (2005). The new data clearly show that *Satureja* s.l. is not monophyletic. Division of the complex into smaller genera (such as *Micromeria*) is obviously a more feasible solution than the alternative approach, to achieve monophyly by even further expanding the group to include a number of distinct genera such as *Thymus* L., *Origanum* L., *Mentha* L. and *Monarda* L.

Since the last comprehensive synopsis of *Micromeria* by Morales (1993), the genus has undergone considerable changes in circumscription and number of accepted taxa. Cantino & Wagstaff (1998), Govaerts (1999) and Harley & Granda (2000) transferred the American species of *Micromeria* (sect. *Xenopoma* and sect. *Hesperothymus* p.p.) to *Clinopodium,* and their treatments resulted in an updated generic circumscription in Harley & al. (2004). However, recent phylogenetic analyses based on both molecular and morphological/anatomical data (Bräuchler & al. 2005; Bräuchler, unpubl. data) give evidence that *Micromeria* remains polyphyletic also after the exclusion of the American taxa. Consequently the species of *M.* sect. *Pseudomelissa* had to be transferred to *Clinopodium* (Bräuchler & al. 2006; Ryding 2006). The results of the analyses also favour the exclusion of the Old World species of the *M.* sect. *Hesperothymus* (from South Africa) and the Malagasy *Micromeria* species that were omitted by Morales (1993) and placed provisionally in a section "Madagascarenses" by Doroszenko (unpubl. Ph.D. thesis, Univ. Edinburgh 1986). The latter two groups represent two new genera, one recently described (Bräuchler & al. 2008), the other in preparation (Bräuchler & al. unpubl.). Another still unpublished study by Bräuchler & al., which considers all genera of *Menthinae,* also shows that *M.* sect. *Cymularia* is extraneous in *Micromeria* (see species enumeration for further details).

Exclusion of the above-mentioned groups not only renders *Micromeria* monophyletic, it also makes the genus more homogeneous, better defined and distinct. Characteristic are leaves with a thickened, almost entire margin. The thickening is caused by a continuous sclerenchymatous "ring"-vein, and not by a revolute leaf margin as in the Madagascan species hitherto included in *Micromeria* or in some *Clinopodium* taxa. This feature is otherwise only shared by very few species of *Clinopodium* s.l. (e.g., *C. nanum, C. corsicum*), which, however, differ in calyx characteristics to such an extent that confusion is not likely. The leaves are never conduplicate as in *Satureja* s.str. or *Thymbra*. Perfoliate inflorescences, found in, e.g., *Mentha, Clinopodium* and *"Micromeria" cymuligera,* are not found in *Micromeria* as circumscribed here. Bracteoles are always present. The calyx tube is neither sigmoid nor gibbous at the base (as common in *Clinopdium* s.l.) and not strongly widening at throat (as in *Satureja* s.str.). The calyx lobes are usually straight or spreading and not curved. The posterior lip of the corolla is emarginate, curved upwards, not straight; the stamens are not exceeding the corolla lips.

As outlined above, four of the six sections recognized by Morales (1993) should be excluded from *Micromeria*. The remaining two, *M.* sect. *Micromeria* and sect. *Pineolentia,* should be fused. Phylogenetic reconstructions based on molecular data have shown that *M.* sect. *Pineolentia* is embedded in a clade of Canarian species of *M.* sect. *Micromeria* (Bräuchler & al. 2005; Meimberg & al. 2006). The abandonment of *M.* sect. *Pineolentia* is also supported by the fact that the most important diagnostic features (large leaves and large flowers) are shared by some species of *M.* sect. *Micromeria,* particularly by the Ethiopian *M. unguentaria*. These peculiarities could readily be explained by adaptation to the special growth conditions on Gran Canaria. Regarding all available information summarized in the synopsis presented here, it seems not possible to delimit subgroups within *Micromeria* that are sufficiently divergent to merit recognition at infrageneric level.

Due to the great changes in the circumscription of *Micromeria,* there is a need for a survey on the progress that has been made towards clarifying the species-level taxonomy. A further aim of the synopsis is to provide an updated description of the genus, to give information on typification, accepted names, taxonomically difficult species groups and distribution of the genus. Problems that need to be clarified by more thorough revisional work are additionally emphasized. For taxa that are not part of *Micromeria* as circumscribed here, but cannot be appropriately accommodated elsewhere, provisional names are indicated. One new name is established, one new combination is made, 24 names are typified.

Material and methods

The studies conducted by the authors were based on extensive herbarium work, including material of the herbaria B, BM, BOL, BOLO, BP, BR, C, DBN, E, EA, FR, FT, G, GOET, HAL, HBG, HEID, HOH, JE, K, LISC, LZ, M, MA, MO, MPU, MSB, NBG, NU, P, S, SAM, SRGH, STU, TCD, TO, TUB, UPS, W, WAG, WU, Z and ZT (herbarium abbreviations according to Holmgren & Holmgren 1998+) and literature research accompanied by observations of plants both in the wild and in cultivation.

Digital images of type specimens cited are found in ALUKA (2008), the Zürcher Herbarien Database (2008), the Virtual Herbaria (2008) and the Virtual Herbarium Berlin (Röpert 2008). Standard abbreviations of authors, periodicals and exsiccatae conform to IPNI (2008), BPH online (2008) and IndExs (Triebel & Scholz 2008), respectively. Of great help were also the following digital resources: for literature Bibliotheca Digital CSIC (2008), Botanicus Digital Library (2008), BHL (2008) and Gallica (2008); for collector and author details TL-2 Online (2008); for completion of the names list IPNI (2008) and the World Checklist of *Lamiaceae* (Govaerts & al. 2008). The work presented here will in turn serve as a revision of *Micromeria* names in the latter two databases.

Micromeria Benth. in Bot. Reg. 15: sub t. 1282. 1829, nom. cons.
Type: *Micromeria juliana* (L.) Benth. ex Rchb., Fl. Germ. Excurs.: 311. 1831 ≡ *Satureja juliana* L., Sp. Pl. 2: 567. 1753.

Perennial herbs, subshrubs or shrubs, rarely annual herbs (only a few specimens of *M. imbricata* from NE tropical Africa), ± aromatic, 2-130 cm tall, with simple hairs and glands. *Leaves* opposite, petioles usually distinct but short or minute; blade ± leathery, up to 2-30 × 1-11 mm, often revolute, margin thickened, entire or with a few obscure teeth. *Inflorescence* thyrsoid or sometimes raceme-like, lax or dense and spike-like; bracts usually similar to the ordinary leaves (sometimes much narrower) but mostly gradually smaller upwards in the inflorescence; cymes 1-many-flowered, often 2 or rarely 3 in the axils of the same node; peduncles minute to 12 mm long, sometimes flat; bracteoles present (also in 1-flowered cymes), small, rather narrow. *Calyx* 5-lobed, scarcely accrescent, almost actinomorphic to distinctly 2-lipped, 2-11 mm long; tube (12-)13-15-veined with prominent veins, hairy or sometimes glabrous inside near the throat; posterior lip 3-lobed; anterior lip 2-lobed, divided to the base, with the lobes mostly longer and narrower than those of the posterior lip. *Corolla* strongly 2-lipped, purple, pink violet or white, 3-20 mm long, sometimes shorter and cleistogamous, rarely female; posterior lip emarginate; anterior lip almost flat, 3-lobed with the mid-lobe broader. *Stamens* 4, ascending under the posterior corolla lip, thecae divaricate, apparently separated on a short connective. *Style* lobes equal, subequal or sometimes with lower branch slightly longer. *Disc* rather small, hardly lobed. *Nutlets* brown or brownish, matt, glabrous or rarely with a single eglandular hair at apex (in *M. imbricata*), 0.6-1.5 × 0.3-0.8 mm, 1.15-4 times longer than broad, apex acuminate, acute, subacute or rounded to obtuse, with a ± distinct areole at the scar, producing mucilage when wet. $2n$ = 20(?), 26, 30, 48, 60.

No sections accepted within the genus. As circumscribed here, *Micromeria* includes about 54 accepted species with 32 subspecies and 13 varieties. The number will probably change in the near future since on the one hand some new species are to be described while on the other hand at least 15 of the species are doubtful concerning their distinctness from closely related taxa and might prove conspecific. The infraspecific classification in many parts is in need of a thorough revision.

The name *Micromeria* has been conserved against *Xenopoma* Willd. in Mag. Neuesten Entdeck. Gesammten Naturk. Ges. Naturf. Freunde Berlin 5: 399. 1811 and *Zygis* Desv. in W. Hamilton, Prodr. Pl. Ind. Occid.: 46. 1825 (Babu 1969), both then monotypic New World genera. The corresponding types represent one and the same species, today included in *Clinopodium* (*C.*

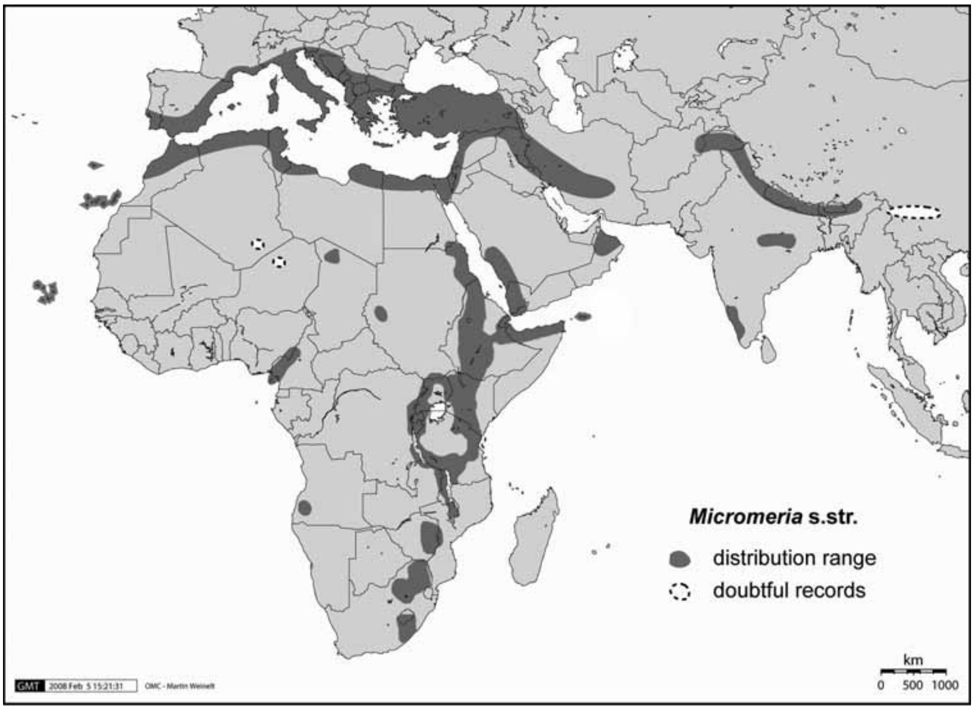

Fig. 1. Distribution map of *Micromeria* s.str.

vimineum (L.) Kuntze) and thus are no longer regarded as congeneric with the species here included in *Micromeria*.

Distribution

Mediterranean area, Portugal, Madeira, Canary Islands, Cape Verde Islands, E Nigeria, Equatorial Guinea (Bioco), Cameroon, Tschad (Tibesti), Sudan, Ethiopia, Eritrea, Djibouti, Somalia, D. R. Congo, Rwanda, Burundi, Uganda, Kenya, Tanzania, Angola (Huila Plateau), E Zambia, Malawi, Mozambique (Manica Prov.), South Africa, Lesotho, SW Saudi Arabia, Yemen, Oman, Iraq (Kurdistan), Iran, Afghanistan, N Pakistan, Nepal, Bhutan, India, Myanmar, China (Yunnan and Guizhou) (Fig.1). Reports from S Algeria and N Niger are doubtful and need confirmation by recollecting. There are uncertainties about the distribution area in Myanmar and China.

Rearching from sea level to more than 2000 m in the Mediterranean and Macaronesia; 400-4500(?-4800 m) in tropical to subtropical Africa and Asia; mostly occurring in moderately dry areas with a rather long dry season.

List of published names

All names published in *Micromeria* at the rank of species or below are recorded in alphabetical order. Currently accepted names are marked in bold, invalidly published names are put in square brackets. The records of synonyms contain a cross reference to the currently accepted name. The basionyms are given. Infraspecific taxa are listed alphabetically under the species entry irrespective of rank; combinations of the same basionym at different ranks are united under one entry. Autonyms are only included where infraspecific taxa are accepted. Types belonging to *Micromeria* names are listed, but types of names that are referred to other genera have been omitted.

The type citation is given under the basionyms, or if the basionym was not described in *Micromeria,* under the currently accepted *Micromeria* name. Type citations are made to the best of our knowledge, and where information was lacking this is explicitly stated. Herbarium barcode numbers (where present) are cited for type specimens that we have only seen as digital images, those from ALUKA (2008) are additionally marked with an asterisk (*). In some cases digital images have been provided directly by the curators of the corresponding herbaria (BOLO, G, STU, TO). A regularly updated version of this list will be made available at the homepage of the first author's institution.

Micromeria abyssinica Hochst. [in Flora 24, Intell. 2: 23. 1841, nom. nud.] ex Benth. in Candolle, Prodr. 12: 224. 1848 ≡ ***Clinopodium abyssinicum*** (Hochst. ex Benth.) Kuntze, Revis. Gen. Pl. 2: 515. 1891.

M. acropolitana Halácsy ex Maire & Petitmengin in Bull. Soc. Sci. Nancy, ser. 3, 9: 421. May 1908 & Halácsy, Consp. Fl. Graec., Suppl. 1: 87. Jun 1908. – Lectotype (designated here by Bräuchler): [Greece] "In Acropoli Athenarum", 30.8.1906, *Maire & Petitmengin, Mission Botanique en Orient no. 1073* (WU [herb. Halácsy]!). = *?* ***M. microphylla*** (d'Urv.) Benth.

Note. – The NCY syntype could not be traced so far (C. Drechsler, pers. comm.), the WU syntype after several fruitless efforts, however, was found by H. Rainer and W. Till stored under the unpublished name *Micromeria athenae*. This specimen contains a handwritten diagnosis by Halácsy and is here designated as lectotype. Nowhere in the treatment containing the protologue or one of its prior parts published in earlier volumes of the same journal it is stated that Halácsy contributed to the descriptions in any way. The authorship therefore has to be attributed to Maire & Petitmengin, and this publications predates Halácsy's own publication of the species by one month. The status of this taxon is not settled, it seems very similar to the type of *M. sphaciotica* Boiss. & Heldr. ex Benth. and thus might not be specifically distinct from *M. microphylla* (d'Urv.) Benth. (see under the respective name entries below).

[*M. aetnensis* Lacaita in Lojacono-Pojero, Fl. Sicul. 2(2): 211. 1907, pro syn.] – ***M. graeca*** (L.) Benth. ex Rchb.

[*M. aetnensis* var. *elata* Lacaita in Lojacono-Pojero, Fl. Sicul. 2(2): 211. 1907, pro syn.] – ***M. graeca*** (L.) Benth. ex Rchb.

[*M. aetnensis* var. *humilis* Lacaita in Lojacono-Pojero, Fl. Sicul. 2(2): 211. 1907, pro syn.] – ***M. graeca*** (L.) Benth. ex Rchb.

M. affinis Hook. f. in J. Bot. 6: 274. 1847 = ***Mentha diemenica*** Spreng., Syst. Veg. 2: 724. 1825.

M. afghanica Freitag in Notes Roy. Bot. Gard. Edinburgh 31: 353. 1972 = ***Gontscharovia popovii*** (B. Fedtsch. & Gontsch.) Boriss. in Bot. Mater. Gerb. Bot. Inst. Komarova Akad. Nauk SSSR 15: 321. 1953.

M. albanica (Griseb. ex K. Malý) Šilić, Monogr. Satureja Fl. Jugosl.: 202. 1979 ≡ *Satureja albanica* Griseb. ex K. Mal1 in Bull. Inst. Jard. Bot. Univ. Belgrade 1-3: 229-230. 1930 = ***Clinopodium serpyllifolium*** (M. Bieb.) Kuntze, Revis. Gen. Pl. 2: 515. 1891.

M. alpestris Urb. in Repert. Spec. Nov. Regni Veg. 16: 143. 1919 ≡ ***Clinopodium alpestre*** (Urb.) Harley in Kew Bull. 55: 919. 2000.

M. alternipilosa K. Koch in Linnaea 19: 25. 1846 = ***Satureja spicigera*** (K. Koch) Boiss., Fl. Orient. 4: 566. 1879.

M. amana Rech. f. in Svensk. Bot. Tidsskr. 43: 42. Mar 1949. – Holotype: [Turkey] "Syria borealis: Mons Amanus, mont. de Düldül, 1500-2000 m", 8.1911, *Haradjan 3887* (G; isotypes: E!, W!). ≡ ***M. cremnophila*** subsp. ***amana*** (Rech. f.) P. H. Davis.

Note. – The W isotype has no original label and the collection date apparently was retyped erroneously as "avril" instead of "août" as is mentioned in the protologue and written on the label of the E isotype.

M. approximata (Biv.) Rchb., Fl. Germ. Excurs.: 859. 1832, nom. illeg. ≡ *Satureja approximata* Biv., Stirp. Rar. Sicilia 4: 13. 1818, nom. illeg. ≡ *Satureja fasciculata* Raf., Précis Découv. Somiol.: 39. 1814 = ***M. graeca*** subsp. ***fruticulosa*** (Bertol.) Guinea

Note. – Both Bivona-Bernardi and Reichenbach included the older valid name *Satureja fasciculata* Raf. in the synonymy rendering their names illegitimate.

M. approximata subsp. *barceloi* (Willk.) Nyman, Consp. Fl. Eur.: 590. 1881, nom. illeg. ≡ *M. approximata* [unranked] *barceloi* (Willk.) Gand., Nov. Consp. Fl. Eur.: 397. 1910, nom. illeg. ≡ *M. barceloi* Willk. = ***M. inodora*** (Desf.) Benth.

Note. – Gandoger (1910) listed several names as infraspecific taxa without indication of rank ("sous-espèces, races ou formes"). His names therefore are validly published but inoperative in questions of priority except for homonymy (see McNeill & al. 2006: Art. 35.3 & 53.4). This combination, however, is illegitimate, because it includes the legitimate name "*barceloi*" under the illegitimate "*approximata*".

[*M. approximata* var. *cymulosa* Lojac., Fl. Sicul. 2(2): t. XVIII. 1907, nom. inval.] – ***M. graeca*** (L.) Benth. ex Rchb.

Note. – This name applies to an illustration not accompanied by an analysis (McNeill & al. 2006: Art. 42.4) and therefore is not validly published.

M. arganietorum (Emb.) R. Morales in Anales Jard. Bot. Madrid 48: 153. 1991 ≡ *Satureja arganietorum* Emb. in Bull. Soc. Sci. Nat. Maroc 15: 182. 1936. – Holotype: [Morocco] "Anti Atlas occidental: Falaises siliceuses dominant le gué de Taderrast sur l'oued Massa, 200 m", 30.4. 1934, *Emberger s.n.* (MPU-006094*!).

M. arkansana (Nutt.) Benth., Labiat. Gen. Spec.: 730. 1835 ≡ *Hedeoma arkansana* Nutt. in Trans. Amer. Philos. Soc., ser. 2, 5: 186. 1834 = ***Clinopodium glabrum*** (Nutt.) Kuntze, Revis. Gen. Pl. 2: 515. 1891.

M. australis (R. Br.) Benth., Labiat. Gen. Spec.: 380. 1834 ≡ ***Mentha australis*** R. Br., Prodr. Fl. Nov. Holland.: 505. 1810.

M. bahamensis Shinners in Sida 1: 96. 1962 = ***Clinopodium brownei*** (Sw.) Kuntze, Revis. Gen. Pl. 2: 514. 1891.

M. balcanica Velen., Fl. Bulg. Suppl. I: 235. 1898 = ***Clinopodium frivaldszkyanum*** (Degen) Bräuchler & Heubl in Taxon 55: 979. 2006.

Note. – Doroszenko (unpubl. Ph.D. thesis, Univ. Edinburgh 1986) includes this name in the synonymy of *M. frivaldszkyana,* which is followed here. A final decision on the synonymy of *Clinopodium dalmaticum* (Benth.) Bräuchler & Heubl, *C. frivaldszkyanum* (Degen) Bräuchler & Heubl and *C. pulegium* (Rochel) Bräuchler cannot be made without a thorough revision of the group, which is in progress but beyond the scope of this manuscript.

M. balcanica var. *moesica* Urumoff in Oesterr. Bot. Z. 49: 203. Jun 1899 = ***Clinopodium frivaldszkyanum*** (Deg.) Bräuchler & Heubl in Taxon 55: 979. 2006.

Note. – See note under *M. balcanica.*

M. barbata C. A. Mey. in Fischer & Meyer, Index Seminum (St. Petersburg) 8: 67. 1842 = ***Clinopodium douglasii*** (Benth.) Kuntze, Revis. Gen. Pl. 2: 515. 1891.

M. barbata Boiss. & Kotschy in Boissier, Diagn. Pl. Orient., ser. 2, 4: 14. 1859, non C. A. Mey. 1842 ≡ ***Clinopodium serpyllifolium*** subsp. ***barbatum*** (P. H. Davis) Bräuchler in Taxon 55: 980. 2006.

M. barceloi Willk. in Oesterr. Bot. Z. 25: 111. 1875. – Lectotype (designated here by Bräuchler): [Spain] "Baleares, Mallorca colina calcarea al O. de Palma", 14.11.1873, *Willkomm s.n.* (MA!). = ***M. inodora*** (Desf.) Benth.

[*M. barceloi* var. *africana* Batt. in Bull. Soc. Bot. France 44: 323. 1897, nom. inval.] – ***M. inodora*** (Desf.) Benth.

Note. – This variety was described from Algeria as being simply more robust than the typical variety. Given this apparent lack of a diagnosis, we consider this name not validly published.

M. barosma (W. W. Sm.) Hand.-Mazz., Symb. Sin. 7: 932. 1936 ≡ *Calamintha barosma* W. W. Sm. in Notes Roy. Bot. Gard. Edinburgh 9: 88. 1916 ≡ ***Clinopodium barosmum*** (W.W. Sm.) Bräuchler & Heubl in Taxon 55: 978. 2006.

M. benthamii Webb & Berthel., Hist. Nat. Iles Canaries 3: 77. 1845 [as *"benthami"*]. – Lectotype (designated by Pérez 1978: 122): [Spain, Canary Islands] "In rupestribus altioribus Magna Canariae prosertum in jugo Montium Saucillo", *Barker-Webb* (FI [lower individual]).

M. biflora (Buch.-Ham. ex D. Don) Benth., Labiat. Gen. Spec.: 378. 1834 ≡ *Thymus biflorus* Buch.-Ham. ex D. Don, Prodr. Fl. Nepal.: 112. 1825. – Type: [Nepal] "Ad Suembu Nepaliae superioris", *Hamilton s.n.* (not traced, probably lost).

Note. – Perhaps better included in *M. imbricata* or considered as a variety of this species. The type could not be traced at BM, E or K.

[*M. biflora* subsp. *arabica* K. H. Walther in Collenette, Wildfl. Saudi Arab.: 452. 1999 & in Al-Rehaily in Pakistan J. Biol. Sci. 9: 2726-2728. 2006, nom. nud.] – ***M. imbricata*** (Forssk.) C. Chr. var. ***imbricata***

M. biflora var. *cinereotomentosa* (A. Rich.) Chiov. in Nuov. Giorn. Bot. Ital., ser. 2, 26: 163. 1919 ≡ *M. ovata* var. *cinereotomentosa* A. Rich. = ***M. imbricata*** (Forssk.) C. Chr. var. ***imbricata***

M. biflora f. *filiformis* (Aiton) Knoche, Fl. Baléar. 2: 348. 1922, nom. illeg. ≡ ***M. filiformis*** (Aiton) Benth.

Note. – Knoche included the indirect reference "*M. filiformis* Benth." to the older name *Thymus filiformis* Aiton, when establishing *"filiformis"* as infraspecific taxon under *M. biflora* (Buch.-Ham. ex D. Don) Benth., making his new combination illegitimate.

M. biflora var. *hirsuta* Fiori in Nuov. Giorn. Bot. Ital., ser. 2, 20: 371. 1913. – Holotype: [Eritrea] "Acchelè-Guzai, tra Mai-Harazat ed Halai", *Fiori 1570* (not traced). = ***M. imbricata*** (Forssk.) C. Chr. var. ***imbricat****a*

M. biflora var. *indica* Elly Walther & K. H. Walther in Mitt. Thüring. Bot. Ges. 1(4): 6. 1957. – Holotype: [India, Prov. Medes] "Cornon", *Coonoor* (HBG!). = ***M. biflora*** (Buch.-Ham. ex D. Don) Benth.

M. biflora var. *punctata* (Benth.) Fiori in Nuov. Giorn. Bot. Ital., ser. 2, 20: 371. 1913 ≡ *M. punctata* Benth. = ***M. imbricata*** (Forssk.) C. Chr. var. ***imbricata***

M. biflora var. *rhodesiaca* Elly Walther & K. H. Walther in Mitt. Thüring. Bot. Ges. 1(4): 7. 1957. – Holotype: [Malawi] "Mt Mlanje", *Adamson 368* (K!). ≡ ***M. imbricata*** var. ***rhodesiaca*** (Elly Walther & K. H. Walther) Ryding

M. biflora var. *rodriguezii* (Freyn & Janka) Knoche, Fl. Baléar. 2: 346. 1922 ≡ *M. rodriguezii* Freyn & Janka ≡ ***M. filiformis*** subsp. ***rodriguezii*** (Freyn & Janka) Bonafè

M. biflora var. *typica* Elly Walther & K. H. Walther in Mitt. Thüring. Bot. Ges. 1(4): 6. 1957 [nom. inval.?]. – Holotype: [India] Kamoun, *Wallich* (K!). = ***M. biflora*** (Buch.-Ham. ex D. Don) Benth.

Note. – Despite not explicitly including the type of *Micromeria biflora*, this variety name could be regarded as not validly published (McNeill 2006: Art. 24.3). The protologue, however, includes a type citation (not the type of the species), a diagnosis and a status designation as var. nov.

M. biflora var. *villosa* Elly Walther & K. H. Walther in Mitt. Thüring. Bot. Ges. 1(4): 7. 1957. – Holotype: [Kenya] "Klinangop", *Dale 2965* (K!). ≡ ***M. imbricata*** var. ***villosa*** (Elly Walther & K. H. Walther) Ryding

M. boliviana Benth., Labiat. Gen. Spec.: 731. 1835 ≡ ***Clinopodium bolivianum*** (Benth.) Kuntze, Revis. Gen. Pl. 2: 515. 1891.

M. boliviana var. *angustifolia* Wedd., Chlor. Andina 2: 150. 1860 = ***Clinopodium bolivianum*** (Benth.) Kuntze, Revis. Gen. Pl. 2: 515. 1891.

M. bonariensis (Ten.) C. A. Mey. in Fischer & Meyer, Index Seminum (St. Petersburg) 10: 56. 1845 ≡ *Thymus bonariensis* Ten. in Index Seminum (Napoli) 1839: 12. 1839 = ***Hedeoma multiflora*** Benth., Labiat. Gen. Spec.: 367. 1834.

M. bourgaeana Webb ex Bolle in Bonplandia (Hannover) 8: 283. 1860. – Holotype: [Spain, Canary Islands] "Hab. in Canaria Magna in rupestribus loci dicti Arecife, rara", *Bourgeau* [*Bourgeau, Pl. Canar. 1845-46, 508*] (B†; isotypes: K!, P!, TCD!, W!, WU!, Z!). = ***M. tenuis*** subsp. ***linkii*** (Webb & Berthel.) P. Pérez

M. bracteolata (Nutt.) Benth., Labiat. Gen. Spec.: 371. 1834 ≡ *Hedeoma bracteolata* Nutt., Gen. N. Am. Addend.: 4. 1818 = ***Conradina*** sp.

Note. – Synonymy follows Epling & Stewart (1939: 46).

M. brevicalyx (Epling) R. Morales in Bot. Complut. 18: 164. 1993 ≡ *Satureja brevicalyx* Epling in Ann. Missouri Bot. Gard. 14: 82. 1927 ≡ ***Clinopodium brevicalyx*** (Epling) Harley & A. Granda in Kew Bull. 55: 919. 2000.

M. brivesii Batt. in Bull. Soc. Hist. Nat. Afrique N. 13: 69. 1922. – Type: [Algeria] "Près de l'Oued Amismiz", 4.11.1909, *Brives s.n.* (not traced, MPU?).

Note. – Some other Brives types are present at MPU, but this one is not included in ALUKA (2008). According to Stafleu & Cowan (1976) part of Battandier's types are present at AL, but more recent information (P. Schäfer, pers. comm.) indicate these collections either as transferred to MPU or lost.

M. browiczii Ziel. & Kit Tan in Polish Bot. J. 46: 31. 2001. – Holotype: "Greece, Ionian Islands. Nomos and eparchia of Zakinthou: Zakinthos, between Agalas and the promontory of Ketinaria, calcareous rocky slope, c. 100 m", 25.5.1988, *Boratysńki, Browicz, Tomlik & Zielisoki 765* (KOR; isotypes: ATH, herb. Kit Tan!).

M. brownei (Sw.) Benth., Labiat. Gen. Spec.: 372. 1834 ≡ *Thymus brownei* Sw., Prodr. Descr. Veg.: 89. 1788 ≡ ***Clinopodium brownei*** (Sw.) Kuntze, Revis. Gen. Pl. 2: 514. 1891.

Note. – Sometimes erroneously listed as *"M. brownii"*.

M. brownei var. *ludens* Shinners in Sida 1: 96. 1962 = ***Clinopodium brownei*** (Sw.) Kuntze, Revis. Gen. Pl. 2: 514. 1891.

M. brownei var. *pilosiuscula* A. Gray, Syn. Fl. N. Amer. 2(1): 359. 1878 = ***Clinopodium brownei*** (Sw.) Kuntze, Revis. Gen. Pl. 2: 514. 1891.

M. bucheri P. Wilson in J. New York Bot. Gard. 23: 93. 1922 ≡ ***Clinopodium bucheri*** (P. Wilson) Harley in Kew Bull. 55: 920. 2000.

M. buchii Webb & Berthel., Hist. Nat. Iles Canaries 3: t. 161. Jun 1849 - Mar 1850, nom. illeg. – Type: forecited illustration (apparently based on a specimen at FI labelled "*Micromeria buchii* Webb"). ≡ ***M. tenuis*** subsp. ***linkii*** (Webb & Berthel.) P. Pérez

Note. – Table 161 represents an illustration with an analysis (McNeill & al. 2006: Art. 42.4) and *M. buchii* would thus have been validly published. The corresponding illustration legend and species description in the text volume of the same work were, however, published at least four years in advance (l.c.: 73. Apr 1845). Since both refer to *M. linkii, M. buchii* is to be regarded as illegitimate. In addition, Peréz (1978: 138) designated a specimen at FI labelled *"Micromeria buchii"* as lectotype for *M. linkii*. Dates for the Webb names are taken from Stearn (1937).

M. bulgarica (Velen.) Vandas in Magyar Bot. Lapok 4 (8-11): 267. 1905 ≡ *M. origanifolia* subsp. *bulgarica* Velen. = ***Clinopodium dalmaticum*** (Benth.) Bräuchler & Heubl in Taxon 55: 979. 2006.

Note. – See comments under *M. balcanica* Velen. The citation "*M. bulgarica* (Velen.) Hayek in Repert. Spec. Nov. Regni Veg. Beih. 30(2): 323. 1929", is incorrect, because the latter author refers in a footnote to Vandas' name.

M. byzantina (K. Koch) Walp., Ann. Bot. Syst. 3: 251. 1852 ≡ *Calamintha byzantina* K. Koch in Linnaea 21: 672. 1849 = ***Clinopodium nepeta*** subsp. ***glandulosum*** (Req.) Govaerts, World Checklist Seed Pl. 3(1): 18. 1999.

M. calaminthoides Lojac., Fl. Sicul. 2(2): 212. 1907. – Syntypes: [Italy, Sicily] "Rupi di M. Pellegrino (?)" 3.1825, *Tineo*, "in Herb. Pan. & Herb. Tod. sub *M. graeca longiflora*" (not traced). = ***M. graeca*** (L.) Benth. ex Rchb.

Note. – Many of the *Micromeria* names published by Lojacono-Pojero (1907) without doubt are to be placed in synonymy to *M. graeca*. Judging from the diagnoses and the accompanying illustrations it is, however, often not possible to assign the taxa to one of the currently accepted subspecies without revising the whole group. Types of Lojacono's names have not been traced for this paper. His herbarium according to Stafleu & Cowan (1981) is integrated in PAL.

M. calaminthoides var. *contracta* Lojac., Fl. Sicul. 2(2): 213. 1907. – Syntypes: [Italy, Sicily] "Palermo alla Scala di Maseddo", *Tineo*, "Monti di Castellammare", "Gibilrossa", "Busambra" (not traced). = ***M. graeca*** (L.) Benth. ex Rchb.

M. calaminthoides var. *elongata* Lojac., Fl. Sicul. 2(2): 213. 1907. – Type: [Italy, Sicily] "Pizzuta" ("herb. Pan.", not traced). = ***M. graeca*** (L.) Benth. ex Rchb.

M. calostachya Rech. f. in Denkschr. Akad. Wiss. Wien, Math.-Naturwiss. Kl. 105: 122. 1943 ≡ ***Thymbra calostachya*** (Rech. f.) Rech. f. in Kulturpflanze, Beih. 3: 64. 1962.

[*M. calvertii* Boiss. in Fl. Orient. 4: 571. 1879, pro syn.] – ***M. elliptica*** K. Koch

M. canescens (Guss.) Benth., Labiat. Gen. Spec.: 376. 1834 ≡ *Satureja canescens* Guss., Pl. Rar.: 228, t. 42. 1826. – Syntypes: [Italy] "In collibus maritimis Japygiae: Taranto, Punta di Cutaro, Gallipoli, Torricella, Otranto", *Gussone* (NAP?). = ***M. graeca*** (L.) Benth. ex Rchb.

Note. – This name is accepted at species rank by Pignatti (1982) and with doubt placed in synonymy to *Satureja graeca* subsp. *garganica* by Briquet (1895: 421). Doroszenko (unpubl. Ph.D. thesis, Univ. Edinburgh 1986) places it in synonymy to *M. graeca* subsp. *longiflora*. Regarding Gussone's description and illustration, the latter might be more appropriate.

M. canescens (K. Koch) Walp., Ann. Bot. Syst. 3: 251. 1852, non Benth. 1834 ≡ *Calamintha canescens* K. Koch in Linnaea 21: 672. 1849 = ***Clinopodium nepeta*** (L.) Kuntze, Revis. Gen. Pl. 2: 515. 1891.

M. capitellata Benth. in Candolle, Prodr. 12: 218. 1848 ≡ ***Clinopodium capitellatum*** (Benth.) Kuntze, Revis. Gen. Pl. 2: 515. 1891.

M. carica P. H. Davis in Kew Bull. 1949: 109. 1949 ≡ ***Clinopodium caricum*** (P. H. Davis) Bräuchler & Heubl in Taxon 55: 978. 2006.

M. carminea P. H. Davis in Kew Bull. 1949: 400. 1949. – Holotype: "Turkey, Denizli: d. Acipayam, Boz Da. above Geyran yayla, 1800-1900 m, cervices of limestone rock with *Globularia dumulosa*, flowers almost pure carmine", 16.7.1947, *Davis 13403* (K!; isotypes: E!, W!). ≡ ***M. cristata*** subsp. ***carminea*** (P. H. Davis) P. H. Davis

M. carpatha Rech. f. in Phyton 1: 208. 1949. – Lectotype (designated here by Bräuchler): [Greece] "Karpathos", 5.6.1886, *Forsyth Major 165a* [protologue: "*Vrondi, FM. 165a* in hb. Barbey"] (G-00087102!). = ***M. microphylla*** (d'Urv.) Benth.

Note. – This name is sometimes placed in synonymy to *M. sphaciotica* Boiss. & Heldr. ex Benth., which in turn mostly has been included in synonymy to *M. microphylla* (d'Urv.) Benth. (e.g., Boissier 1879; Šilić 1979; Doroszenko, unpubl. Ph.D. thesis, Univ. Edinburgh 1986). This opinion is accepted here. The second syntype cited is "Karpathos, *Rechinger 8249* (W)".

M. chamissonis (Benth.) Greene, Man. Bot. San Francisco: 289. 1894 ≡ *Thymus chamissonis* Benth. in Linnaea 6: 80. 1831 = ***Clinopodium douglasii*** (Benth.) Kuntze, Revis. Gen. Pl. 2: 515. 1891.

[*M. chanonis* Muschl. in Just's Bot. Jahresber. 36(3): 607. 1912, erroneous for *M. chamissonis* (Benth.) Greene]. – ***Clinopodium douglasii*** (Benth.) Kuntze, Revis. Gen. Pl. 2: 515. 1891.

Note. – When citing an article of Power & Salway (1908), Muschler mistranslated the original title "Chemical examination of *Micromeria chamissonis*" to "Chemische Untersuchung von *Micromeria chanonis* (Verba buena)", the name thus merely represents a type error.

M. chionistrae Meikle in Ann. Mus. Goulandris 6: 92. 1983. – Holotype: "Cyprus, Phini, 1000 m, in cracks of bare rock", 6.6.1939, *Kennedy 1495* (K!).

M. cilicica Hausskn. ex P. H. Davis in Kew Bull. 1949: 109. 1949 ≡ ***Clinopodium cilicicum*** (Hausskn. ex P. H. Davis) Bräuchler & Heubl in Taxon 55: 978. 2006.

[*M. cinerea* Doroszenko in Ryding in Bot. J. Linn. Soc. 155: 438. 2007, pro syn.] – ***M. imbricata*** (Forssk.) C. Chr. var. ***imbricata***

Note. – This name was given to a new species by Doroszenko's (unpubl. Ph.D. thesis, Univ. Edinburgh 1986), but is neither effectively nor validly published. Ryding (2007), however, mentions this name under *M. imbricata* var. *imbricata*. It therefore is included here to complete the list of names found in literature available to us.

M. compacta (Killick) R. Morales in Bot. Complut. 18: 164. 1993 ≡ *Satureja compacta* Killick in Bothalia 7: 437. 1961 ≡ ***Killickia compacta*** (Killick) Bräuchler, Doroszenko & Heubl in Bot. J. Linn. Soc. 157: 584. 2008.

Note. – One of three species endemic to the South Afrikan Drakensberg. All three have previously been included in *Satureja* or *Micromeria* sect. *Hesperothymus*. While New World members of the latter section have been transferred to *Clinopodium,* these three species remained in *Micromeria* and recently have been placed in a genus of their own named *Killickia* (Bräuchler & al. 2008).

M. conferta (Coss. & Daveau) Stefani in Boll. Reale Orto Bot. Palermo 11: 148. 1912 ≡ *M. juliana* var. *conferta* Coss. & Daveau

Note. – Obviously this was intended to be a new combination for *M. juliana* var. *conferta* Coss. & Daveau and according to Art. 33.2 and 33.3 of the Vienna Code (McNeill & al. 2006) needs to be treated as such. The reference to the basionym, however, is very cryptic ("*Micromeria conferta* Cass." apparently a miss-citation of Coss. & Daveau).The fact that only one specimen is cited and a description (in Italian) is given obscures the new combination even more. This species is included under *M. juliana* by Siddiqi (1985).

M. congesta Boiss. & Hausskn. in Boissier, Fl. Orient. 4: 575. 1879 ≡ ***Clinopodium congestum*** (Boiss. & Hausskn.) Kuntze, Revis. Gen. Pl. 2: 515. 1891.

M. consentina (Ten.) N. Terracc. in Nuov. Giorn. Bot. 5: 227. 1873 [as "*M. cosentina*"] ≡ *Satureja consentina* Ten. ≡ ***M. graeca*** subsp. ***consentina*** (Ten.) Guinea

M. consentina var. *aeolica* Lojac., Fl. Sicul. 2(2): 210. 1907. – Syntypes: [Italy] "Isole Eolie: colli vulcanici: Panaria", *Lojacono-Pojero,* "Salina a S Marina", *Lojacono-Pojero,* "Alicuari" *Tineo*, "Lipari", *Lojacono-Pojero* (not traced). = ***M. graeca*** subsp. ***consentina*** (Ten.) Guinea

Note. – See note under *M. calaminthoides.*

M. consentina var. *chamaepitys* Lojac., Fl. Sicul. 2(2): 210. 1907. – Syntypes: [Italy, Sicily] "Ad rupes graniticas v. schistosas in Sicilia sept. Capo d'Orlando", *Milazzo*, "Antennamare", *Gussone*, "Prov. Messina", *Gussone* (not traced). = ***M. graeca*** subsp. ***consentina*** (Ten.) Guinea

M. consentina var. *glabrata* (Guss.) Strobl in Flora 68: 369. 1885 ≡ *Satureja consentina* var. *glabrata* Guss., Fl. Sicul. Syn. 2: 88. 1844. – Syntypes: "Palermo a S. Maria a Gesu, ed alla Pizzuta, Catania, Aci, Giarre, Scaletta, Capo S. Alessio, Taormina, Messina, Capo di Calava, Capo Tindaro" (NAP?). = ***M. graeca*** subsp. ***consentina*** (Ten.) Guinea

[*M. consentina* var. *glabrescens* Lojac., Fl. Sicul. 2(2): 210. 1907, pro syn.] – ***M. graeca*** subsp. ***consentina*** (Ten.) Guinea

M. consentina var. *minutissima* Lojac., Fl. Sicul. 2(2): 210. 1907. – Type: [Italy, Sicily] "Ad rupes vulcanicas apricas calidissimas in coespites late pulvinatos pulchre floriferos, Ins. Alicuri", 1.8.1905 (NAP?). = ***M. graeca*** subsp. ***consentina*** (Ten.) Guinea

M. consentina var. *pseudotodari* Lacaita ex Lojac., Fl. Sicul. 2(2): 210. 1907. – Syntypes: [Italy, Sicily] "rupi primitive: Castanea", *Todaro,* "Capo d'Orlando, Fiumara di Zappulla, Sic. Nord.-Orient", *Todaro,* "Capo Tindaro", *Gussone,* "Capo Calava", *Gussone,* "Vetta dell'Antennamare", *Gussone* (not traced). = ***M. graeca*** subsp. ***consentina*** (Ten.) Guinea

M. consentina var. *rossii* Lojac., Fl. Sicul. 2(2): 210. 1907 [as "*rossi*"]. – Syntypes: [Italy, Sicily] "Aetna", *Rossi*, "Nicolosi", *Tineo, Torn*., "Catania Chiuse" *Torn*., *Tineo*, *Luglio* (not traced). = ***M. graeca*** subsp. ***consentina*** (Ten.) Guinea

M. cordata (Moris ex Bertol.) Moris, Diag. Stirp. Sard. Nov.: 2. Mar 1857 ≡ *Satureja cordata* Moris ex Bertol., Fl. Ital. 10: 519. Jan-Feb 1857. – Lectotype (designated here by Bräuchler): [Italy, Sardinia,] *Moris* (BOLO [photo!]).

Note. – This species is included as subspecies in *M. filiformis* (Pignatti 1977) or in *M. microphylla* (Doroszenko unpubl. Ph.D. thesis, Univ. Edinburgh 1986). Further studies are needed to examine the delimitation between the two taxa, even more so since obvious morphological and ecological affinities with *M. marginata* exist. For the time being we think it is best to follow Valsecchi (1978) and treat it as a distinct species. The latter author has designated a lectotype for "*M. cordata* Moris" from TO ("*M. cordata* Moris, nelle fissuri delle rupi, Monti di Oliena, Giugno 1852", photo!). Bertoloni's name, however, has priority and there is no evidence that the Moris collection received by him was a duplicate of the "lectotype", consequently the typification by Valsecchi is rejected here. The only specimen preserved at BOLO and annotated as "*Satureja cordata* Moris" by Bertoloni has no locality on the label but a note indicating it as sent by Moris in 1856, which means prior to publication of the species description. This is the only collection unambiguously representing original material and therefore is chosen as lectotype here.

M. cordata [unranked] *allionii* (Zumagl.) Gand., Nov. Consp. Fl. Eur.: 397. 1910 ≡ *Thymus allionii* Zumagl., Fl. Pedem. 1: 226. 1859 ≡ *Thymus piperella* All., Fl. Pedem. 1: 21, t. 37, fig. 3. 1785, non L. 1753 ≡ ***M. marginata*** (Sm.) Chater

Note. – See note under *M. approximata* subsp. *barceloi.*

M. corsica (Pers.) H. Lév., Dict. Invent. Fl. Franc.: 22. 1916 ≡ *Thymus corsicus* Pers., Syn. Pl. 2: 131. 1806 ≡ ***Acinos corsicus*** (Pers.) Getliffe in Bot. J. Linn. Soc. 65: 263. 1972.

M. cremnophila Boiss. & Heldr. in Boissier, Fl. Orient. 4: 570. 1879. – Holotype: [Greece] "Ad rupes verticales regionis abietinae Parnassi ad Gourna 4000'-4500'", *Heldreich* (G-BOIS).

M. cremnophila subsp. ***amana*** (Rech. f.) P. H. Davis in Notes Roy. Bot. Gard. Edinburgh 38: 40. 1980 ≡ *M. amana* Rech. f.

M. cremnophila subsp. ***anatolica*** P. H. Davis in Notes Roy. Bot. Gard. Edinburgh 38: 40. 1980. – Holotype: "Turkey B9 Van: 5 km N of Certak, in cervices of boulders", 25.7.1954, *Davis 23258 & Polunin* (E!; isotype: K!).

M. cremnophila Boiss. & Heldr. subsp. ***cremnophila***

M. cremnophila var. *glandulosa* Micevski in Prilozi Oddel. Biol. Med. Nauki, Makedonska Akad. Nauk. Umet. 23: 17. 2002. – Holotype: [Macedonia] "In fauce ad flumen Radika inter pagos Trnica et Volkovija, in rupibus calcareis 800 m", 23.8.1986, *Micevski* (SKO). = ***M. cremnophila*** Boiss. & Heldr. subsp. ***cremnophila***

M. cremnophila var. *thessala* Formánek in Verh. Naturf. Vereins Brünn 35: 142 & 183. 1896. – Type: [Greece] "Thessalia, Pindus: Oxya 'Despoti', untere Lage 210-400 m, Kastri et in sylvaticis Metochi Vavlavi, pr. Vlachava", 1896, *Formánek* (not traced). = ***M. cremnophila*** Boiss. & Heldr. subsp. ***cremnophila***

M. cristata (Hampe) Griseb., Spicil. Fl. Rumel. 2: 122. 1844 ≡ *Thymus cristatus* Hampe in Flora 20: 233. 1837. – Lectotype (designated here by Bräuchler): [Bulgaria] "Rumelia", [1835] *Frivaldszky* (BP-334973!).

Note. – This plant has been distributed by Frivaldszky (1836) as part of his "Centuria plantarum exsiccatarum anno 1835 in Turcia-europaea collectarum" under the name *Thymus inodorus* Desf. It was collected in Rumelia (probably in the Rhodopian mountains) by Füle, Hinke or Manolesko (all then collectors sent out by Frivaldszky; Degen 1896). Hampe (1837) subsequently indentified the plant as representing a new species, which he described as *T. cristatus*. Since the whereabouts of his herbarium of phanerogams are uncertain, a specimen of Frivaldsky's "Centuria" traced at BP is designated as lectotype here. The plants on this sheet represents part of the original material, probably an isotype (though neither annotated by Hampe nor labelled with his name, but Frivaldszky's original determination instead). No duplicates have been traced so far, but might be present in numerous herbaria (e.g., G, K, P, W).

M. cristata f. *albiflora* Sili6 in Glasn. Zemaljsk. Muz. Bosne Hercegovine Sarajevu. Prir. Nauke 13: 116. 1975. – Holotype: [Serbia] "Jelašnićka klisura prope Niš, in valle fluminis", 22.8.1953, *Lindtner* (BEO). = ***M. cristata*** (Hampe) Griseb. subsp. ***cristata***

M. cristata f. *canescens* Vandas in Rel. Form.: 483. 1909 ≡ *M. cristata* subf. *canescens* (Vandas) Hayek, Prodr. Fl. Penins. Balcan. 2: 319. 1929 ≡ *M. cristata* var. *canescens* (Vandas) Sili6 in Glasn. Zemaljsk. Muz. Bosne Hercegovine Sarajevu. Prir. Nauke 13: 116. 1975. – Syntypes: [Macedonia] "Plantae e Flora et Hadžibarica pl.", *Formánek* (not traced). = ***M. cristata*** (Hampe) Griseb. subsp. ***cristata***

M. cristata subsp. ***carminea*** (P. H. Davis) P. H. Davis in Notes Roy. Bot. Gard. Edinburgh 21: 65. 1952 ≡ *M. carminea* P. H. Davis

M. cristata (Hampe) Griseb. subsp. ***cristata***

M. cristata var. *glandulosa* Micevski in Prilozi Oddel. Biol. Med. Nauki, Makedonska Akad. Nauk. Umet. 23: 12. 2002. – Holotype: [Macedonia] "Fauces Demir Kapija", 9.6.1972, *Micevski* (SKO). = ***M. cristata*** (Hampe) Griseb. subsp. ***cristata***

Micromeria cristata subsp. ***kosaninii*** (Sili6) Bräuchler & Govaerts, **comb. nov.** ≡ *Micromeria kosaninii* Šili6*,* Monogr. Satureja Fl. Jugosl.: 234. 1979. – Holotype: [Macedonia] "Galičica, Poljce, c. 1600 m, solo calcareo", 11.10.1970, *Sili6* (SARA; isotype: LJU).

Note. – This taxon was described as a species by Šilić (1979) and included as a subspecies under *Satureja cristata* by Greuter & al. (1986). This concept is followed here, making a new combination under *Micromeria* necessary.

M. cristata subsp. ***orientalis*** P. H. Davis in Notes Roy. Bot. Gard. Edinburgh 38: 41. 1980. – Holotype: "Turkey B6 Malatya: Gurun to Malatya, 40 km from Malatya, c. 1400 m, cliff ledges and cracks, fls. pale lilac", 7.8.1956, *McNeill 461* (E!).

M. cristata subsp. ***phrygia*** P. H. Davis in Notes Roy. Bot. Gard. Edinburgh 38: 40. 1980. – Holotype: "Turkey B2 Kutahya: d. Gediz, Saphane Da., 1900-2000 m, sunny rocks, flowers white with mouve spotting on lip", 27.8.1950, *Davis 18457* (E!; isotype: K!).

M. cristata f. *subuniflora* Bornm. in Bot. Jahrb. Syst. 61, Beibl. 140: 73. 1927. – Holotype: [Macedonia] "Macedonia centralis: In distr. Montium Duditza- et Suharupa-planina, in m. Dwe Uschi (= Zwei-Ohrenberg), c. 1700 m", 24.7.1917, *Schultze 326* (B!; isotype: JE!). = ***M. cristata*** subsp. ***cristata***

M. cristata f. *umbrosa* Bornm. in Bot. Jahrb. Syst. 61, Beibl. 140: 73. 1927. – Holotype: [Macedonia] "In rupe Markov-Kamen vallis fluvii Lepenac (infra pag. Kačanik), 500 m" 5.7.1918, *Bornmüller, Plantae Macedonicae 4851* (HBG; isotypes: B!, BP!, JE!). = ***M. cristata*** subsp. ***cristata***

Note. – Bornmüller's 1918 trip to Macedonia was financed by the Institut für Allgemeine Botanik in Hamburg, the top set of the corresponding collections, unlike other Bornmüller material, therefore is kept at HBG (H. Manitz, pers. comm.).

M. cristata subsp. ***xylorrhiza*** (Boiss. & Heldr. ex Benth.) P. H. Davis in Notes Roy. Bot. Gard. Edinburgh 21: 64. 1952 ≡ *M. xylorrhiza* Boiss. & Heldr. ex Benth.

M. croatica (Pers.) Schott in Oesterr. Bot. Wochenbl. 7: 93. 1857 ≡ *Thymus croaticus* Pers. in Syn. Pl. 2: 130. 1806. – Type: [Croatia] "Hab. in alpibus Croatiae, rupes calcareas opplens" (P?).

M. croatica f. *glabrata* (K. Malý) Sili6 in Glasn. Zemaljsk. Muz. Bosne Hercegovine Sarajevu. Prir. Nauke 13: 117. 1975 ≡ *Satureja croatica* f. *glabrata* K. Malý in Glasn. Zemaljsk. Muz. Bosne Herzegovine 40: 154. 1928. – Holotype: [Bosnia and Hercegovina] "Lisičići prope Konjic, solo calcareo, c. 260 m", *Malý* (SARA). = ***M. croatica*** (Pers.) Schott

M. croatica f. *linearilanceolata* Sili6 in Glasn. Zemaljsk. Muz. Bosne Hercegovine Sarajevu. Prir. Nauke 13: 117. 1975. – Holotype: [Bosnia and Hercegovina] "Kanjon Rakitnice, solo calcereo, c. 400 m", 15.10.1967, *Sili6* (SARA). = ***M. croatica*** (Pers.) Schott

M. croatica var. *longidens* Rohlena in Sitzungsber. Königl. Böhm. Ges. Wiss. Prag, Math.-Naturwiss. Cl. 1912: 103. 1913 ≡ *M. croatica* f. *longidens* (Rohlena) Hayek, Prodr. Fl. Penins. Balcan. 2: 321. 1929. – Holotype: [Montenegro] "Auf felsigen Ufern des Flusses Piva bei Goransko (ca. 660 m)", *Rohlena* (PRC). = ***M. croatica*** (Pers.) Schott

Note. – Sili6 (1979) cites this as "f. *longidens* Rohl.", whereas originally it has been described as a variety and was reduced to the rank of a forma later (see above).

M. croatica f. *multicaulis* Sili6 in Glasn. Zemaljsk. Muz. Bosne Hercegovine Sarajevu. Prir. Nauke 13: 117. 1975. – Holotype: [Bosnia and Hercegovina] "in valle Drežanka pr. Drežnica, c. 150 m, solo calcareo", 4.8.1900, *Malý* (SARA). = ***M. croatica*** (Pers.) Schott

M. croatica f. *ovalifolia* Sili6 in Glasn. Zemaljsk. Muz. Bosne Hercegovine Sarajevu. Prir. Nauke 13: 117. 1975. – Holotype: [Bosnia and Hercegovina] "Idbar pr. Božić, c. 500 m", 7.9. 1970, *Sili6* (SARA). = ***M. croatica*** (Pers.) Schott

M. croatica var. *panciciana* (Briq.) Hayek, Prodr. Fl. Penins. Balcan. 2: 321. 1929 ≡ *Satureja croatica* var. *panciciana* Briq., Lab. Alp. Marit. 3: 427. Sep 1895. – Lectotype (see Note): [Serbia] "Mokra Gora", 1875, *Pančić 8580* (BEOU). = ***M. croatica*** (Pers.) Schott

Note. – On a web page containing information on the Serbian botanist Pančić (http://pancic.bio.bg.ac.yu/Engl/index.html) a lectotypification for *Satureja croatica* var. *panciciana* Briq. is indicated without citation of the source. We were not able to trace the corresponding publication. No type material of this taxon seems to be present at G.

M. cunninghamii Benth., Labiat. Gen. Spec.: 730. 1835 ≡ ***Mentha cunninghamii*** (Benth.) Benth. in Candolle, Prodr. 12: 174. 1848.

M. cymuligera Boiss. & Hausskn. in Boissier, Fl. Orient. 4: 569. 1879 =? ***Mentha* sp.**

Note. – *Micromeris cymuligera* has always been regarded as isolated within the genus with respect to its annual habit and special anther structure (Boissier 1879; Bräuchler & al. 2005; Bräuchler & al. 2006; Briquet 1896; Davis 1982). Weak affinities towards sect. *Micromeria* (Doroszenko unpubl. Ph.D. thesis, Univ. Edinburgh 1986) have been suggested based on overall similarity rather than on shared characters. Preliminary molecular data indicate this species as dis-associated from *Micromeria* s. str. and more closely related to the genus *Mentha* (Bräuchler, unpubl.). However, results were not clear enough to make a final decision. The lack of a marginal vein as revealed by anatomical studies (Bräuchler, unpubl.) favours exclusion of *M. cymuligera* from the genus. The perfoliate inflorescence is another feature shared with *Mentha* rather than with *Micromeria* s.str., where the bracts tend to get reduced towards the tip of the inflorescence. The ecological range from what is known (humid alpine pastures, torrent beds) is similar to that of *Mentha*. None of the species of *Micromeria* s.str. occur in such a habitat. Whether this species should be included in *Mentha* or placed in a monotypic genus ("*Cymularia*") remains to be clarified.

M. cypria Kotschy in Unger & Kotschy, Ins. Cypern: 270. 1865. – Lectotype (designated here by Bräuchler): [Cyprus] "In scopulorum fissures montis Pentadactylos et Buffavento 1500'", 4.1862, *Kotschy*, *Pl. Ins. Cypro 338* (W-0014293!; isolectotypes: BP!, G, JE!, K!, P!). = ***M. microphylla*** (d'Urv.) Benth.

Note. – The second syntype cited is *Kotschy 390* (K!, traced neither at W nor at WU) "Um Castello della Regina, 15.4.1862". It seems that less duplicates of this collection number have been distributed, therefore *Kotschy 338* is chosen as lectotype.

M. cypria var. *villosissima* H. Lindb., Iter Cypr.: 29. 1946. – Holotype: [Cyprus] "Ayios Hilarion, in fissuris rupis siccissimis", 1939, *Lindberg* (H?). = ***M. microphylla*** (d'Urv.) Benth.

M. dalmatica Benth. in Candolle, Prodr. 12: 225. 1848 ≡ ***Clinopodium dalmaticum*** (Benth.) Bräuchler & Heubl in Taxon 55: 979. 2006.

Note. – See note under *M. balcanica.*

M. dalmatica f. *angustifrons* Rohlena in Věstn. Král. České Spolecn. Nauk, Tr. Mat.-Prir. 2: 11. 1933 = ***Clinopodium dalmaticum*** (Benth.) Bräuchler & Heubl in Taxon 55: 979. 2006.

M. dalmatica subsp. *bulgarica* (Velen.) Guinea in Bot. J. Linn. Soc. 64: 381. 1971 ≡ *M. dalmatica* f. *bulgarica* (Velen.) Stoj., Stefanov & Kit., Fl. Bulg. 2: 924. 1967 ≡ *M. origanifolia* subsp. *bulgarica* Velen. = ***Clinopodium dalmaticum*** (Benth.) Bräuchler & Heubl in Taxon 55: 979. 2006.

M. dalmatica f. *multiflora* Sili6 in Glasn. Zemaljsk. Muz. Bosne Hercegovine Sarajevu. Prir. Nauke 13: 115. 1975 = ***Clinopodium dalmaticum*** (Benth.) Bräuchler & Heubl in Taxon 55: 979. 2006.

M. dalmatica Fenzl in Index Seminum (Vienna) 1851: 1851, non Benth. 1848 = ***Mentha pulegium*** L., Sp. Pl. 2: 577. 1753.

Note. – This name is probably a mere misinterpretation and should read *M. dalmatica* sensu Fenzl, non Benth. instead. It has been published later as *Calamintha fenzlii* Vis. in Atti Reale Ist. Veneto Sci. Lett. Arti, ser. 2, 6: 300. Mar 1855, and/or *M. fenzlei* Regel (see name entry below). The synonymy (= *Mentha pulegium* L.) as provided in Govaerts & al. (2008), seems faulty regarding material traced at W and WU, which represents *Clinopodium thymifolium* (Scop.) Kuntze or a closely related species. We were, however, unable to consult the reference and relevant material at PAD or LE.

M. danaensis Danin in Willdenowia 27: 161. 1997. – Holotype: "Jordan, Edom, Dana Reserve, Wadi Barra area, 2 km SE of the visitor center, in crevices of smooth-faced white sandstone outcrops", 14.5.1996, *Danin 963013* (HUJ; isotype: B!).

M. darwinii Benth. in Candolle, Prodr. 12: 222. 1848 ≡ ***Clinopodium darwinii*** (Benth.) Kuntze, Revis. Gen. Pl. 2: 515. 1891.

M. darwinii var. *imbricatifolia* Speg. in Anales Soc. Ci. Argent. 53: 251. 1902 = ***Clinopodium darwinii*** (Benth.) Kuntze, Revis. Gen. Pl. 2: 515. 1891.

M. darwinii var. *pallida* Speg. in Anales Soc. Ci. Argent. 53: 251. 1902 = ***Clinopodium darwinii*** (Benth.) Kuntze, Revis. Gen. Pl. 2: 515. 1891.

M. darwinii var. *pusilla* (Phil.) Speg. in Anales Soc. Ci. Argent. 53: 250. 1902 ≡ *M. pusilla* Phil. = ***Clinopodium darwinii*** (Benth.) Kuntze, Revis. Gen. Pl. 2: 515. 1891.

[*M. darwinii* var. *typica* Speg. in Anales Soc. Ci. Argent. 53: 250. 1902, nom. inval.] – ***Clinopodium darwinii*** (Benth.) Kuntze, Revis. Gen. Pl. 2: 515. 1891.

M. darwinii var. *virescens* Speg. in Anales Soc. Ci. Argent. 53: 250. 1902 = ***Clinopodium darwinii*** (Benth.) Kuntze, Revis. Gen. Pl. 2: 515. 1891.

M. debilis Pomel in Nouv. Mat. Fl. Atl.: 122. 1874. – Lectotype (designated here by Bräuchler): [Algeria] "Rochers de Zouia. 1400 m, Gar Roub., jn. 1855-56", *Pomel* (MPU-004936*!).

Note. – Two sheets of *M. debilis* Pomel exist at MPU, one of which has been labelled "holotype" when the types were databased (MPU-004395*!). This is the richest "type collection". Since there is no original label bearing Pomel's handwriting on that sheet, it is not considered to be suitable to serve as a lectotype. The second sheet bears two individuals each labelled with a different barcode (left hand: MPU-005512*!; right hand: MPU-004936*!) and labels written by Pomel and Maire respectively. The right hand individual is a bit richer and has more leaves on it. It therefore is chosen as lectotype here.

M. debilis var. *mauritii* Sennen, Diagn. Nouv.: 240. 1936. – Holotype: "Maroc: Beni-Snassen, Taforait, rochers calcaires, vers 900 m", *Mauricio*, *Sennen, Pl. Espagne 9532* (BC!; isotypes: MPU-009542*!, MPU-009543*!). = ***M. debilis*** Pomel

M. debilis var. *villosissima* Batt. & Trab. in Fl. Algérie 1: 677. Dec 1890. – Holotype: [Algeria] "Grands rochers des Cascades à Tlemcen" (AL?). = ***M. debilis*** Pomel

M. densiflora Benth., Labiat. Gen. Spec.: 375. 1834. – Lectotype: (designated by Pérez 1978: 157): [Spain, Canary Islands] "Hab. in ins. Canariensibus", *Broussonet* (K!).

Note. – A label written by Pérez de Paz in 1976 and attached to the holotype at K indicates this as most probably not collected on the Canary Islands but similar to some forms of *M. varia* Benth. For the purpose of this paper, we decided to list this name as accepted until a more detailed study on its affinities is undertaken.

M. densiflora var. *pitardii* (Bornm.) Knoche, Vagandi Mos. [page?]. 1923 ≡ *M. pitardii* Bornm. = ***M. lepida*** Webb & Berthel.

Note. – This citation is taken from Pérez (1978), who does not list a page number. We were not able to consult the reference.

M. despreauxii (Briq.) Bornm. in Repert. Spec. Nov. Regni Veg. 19: 198. 1924 ≡ *Satureja despreauxii* Briq. in Annuaire Conserv. Jard. Bot. Genève 2: 186. 1898. – Holotype: [Spain, Canary Islands] "Iles Canaries", *Desperaux 321* (G). = ***M. helianthemifolia*** Webb & Berthel.

Note. – This name was omitted by Pérez (1978) and all other treatments so far. This might be due to its listing in a footnote of the protologue of *M. kuegleri*. Doroszenko (unpubl. Ph.D. thesis Univ. Edinburgh 1986) placed the basionym in synonymy to *M. helianthemifolia,* which is followed here.

M. diffusa Lojac., Fl. Sicul. 2(2): 216. 1907. – Type: [Italy, Sicily] “Monti di Palermo, Maggio”, *Todaro* (not traced). = ***M. graeca*** (L.) Benth. ex Rchb.

Note. – See note under *M. calaminthoides.*

M. dolichodonta P. H. Davis in Kew Bull. 1951: 75. 1951 ≡ ***Clinopodium dolichodontum*** (P. H. Davis) Bräuchler & Heubl in Taxon 55: 979. 2006.

M. domingensis Shinners in Sida 1: 96. 1962 = ***Clinopodium brownei*** (Sw.) Kuntze, Revis. Gen. Pl. 2: 514. 1891.

M. douglasii (Benth.) Benth., Labiat. Gen. Spec.: 372. 1834 ≡ *Thymus douglasii* Benth. in Linnaea 6: 80. 1837 ≡ ***Clinopodium douglasii*** (Benth.) Kuntze, Revis. Gen. Pl. 2: 515. 1891.

M. echioides Lacaita ex Lojac., Fl. Sicul. 2(2): 215. 1907 = ***M. graeca*** (L.) Benth. ex Rchb.

Note. – *“Strigosa”* would be the variety to choose the specific lectotype from (Lojacono-Pojero, Fl. Sicul. 2(2): 215. 1907: “La forma piu comune e prototipa”). Furthermore see note under *M. calaminthoides*.

M. echioides var. *angustifolia* Lojac., Fl. Sicul. 2(2): 216. 1907. – Type: [Italy, Sicily] “Palermo, Porto Empedocle?” (not traced). = ***M. graeca*** (L.) Benth. ex Rchb.

[*M. echioides* var. *gasparinii* Lacaita in Lojacono-Pojero, Fl. Sicul. 2(2): 216. 1907, nom. nud.] – Based on a specimen from: [Italy, Sicily] “M. Gebbia non procul a Palazzo-Adriana” *Gasparrini 1* (not traced). – ***M. graeca*** (L.) Benth. ex Rchb.

M. echioides var. *gossypina* Lojac., Fl. Sicul. 2(2): 216. 1907. – Type: [Italy, Sicily] “Trapani, Marsala”, *Lehm.* (not traced). = ***M. graeca*** (L.) Benth. ex Rchb.

M. echioides var. *griseocanescens* Lojac., Fl. Sicul. 2(2): 215. 1907. – Syntypes: [Italy, Sicily] “Ad rupes elatiores, Madonie, Busambra” *Pan.*, “Meretimo” *Tineo* (not traced). = ***M. graeca*** (L.) Benth. ex Rchb.

M. echioides var. *humillima* Lojac., Fl. Sicul. 2(2): 215. 1907. – Syntypes: [Italy, Sicily] “Ad rupes muscosas, Palermo M. Grifone”, *Tineo* (not traced); “Palermo”, 1872, *Ajuti* (K). = ***M. graeca*** (L.) Benth. ex Rchb.

M. echioides var. *strigosa* Lojac., Fl. Sicul. 2(2): 215. 1907. – Syntypes: [Italy, Sicily] “Ad rupes montanas, Palermo, S. Martino, Cometa, Pizzuta ed altrove” (not traced). = ***M. graeca*** (L.) Benth. ex Rchb.

Note. – See note under *M. echioides.*

M. ekmaniana (Epling & Alain) Borhidi in Acta Bot. Hung. 37: 79. 1992 ≡ *Satureja ekmaniana* Epling & Alain in Brittonia 20: 156. 1968 ≡ ***Clinopodium ekmanianum*** (Epling & Alain) Harley in Kew Bull 55: 921. 2000.

M. elegans Boriss. in Bot. Mater. Gerb. Bot. Inst. Komarova Akad. Nauk SSSR 15: 330. 1953. – Holotype: [Turkey, distr. Artvin] “Prope opp. Gurshany”, 30.5.1910, *Nesterov 68* (LE). = ***M. elliptica*** K. Koch

M. ellenbeckii (Gürke) Chiov. in Savoia-Aosta, Explor. Uabi-Uebi Scebeli: 443. 1932 ≡ *Satureja ellenbeckii* Gürke in Bot. Jahrb. Syst. 36: 129. 1905. – Holotype: [Ethiopia. Harege region] “Gara Mulata” *Ellenbeck 533* (B†); neotype (designated here by Ryding): “Ethiopia, Harege region, Gara Mulata”, *Gillett 5319* (K!; isoneotype: FT!). = ***M. imbricata*** var. ***villosa*** (Elly Walther & K. H. Walther) Ryding

Note. – The neotype was indicated by Ryding (2007: 442) for the first time, but not accompanied by the statement “designated here” or an equivalent. It is therefore formally chosen here by Ryding.

M. elliptica K. Koch in Linnaea 21: 669. 1849. – Holotype: [Turkey, A8 Çoruh] “Im Hochgebirge des Gaues Pertakrek auf Urgestein, c. 5000-6000' hoch”, *Koch* (B†).

Note. – Davis (1982) cited the holotype at B unseen and an isotype at G seen. Although the holotype was listed as extant in Edmondson & Lack (1977), it could not be traced at B and probably has been destroyed. The holotype of *M. elliptica* var. *nana* (or more probably a fragment there of), however, was traced at B, whereas it was not listed in Edmondson & Lack (1977). Obviously the two taxa have been confused during compilation of the list of Koch types present at B for that publication. The identity of the (fragmentary) “isotype” at G is questionable since the label indicates this as *M. elliptica* var. *nana* as well and provides only cryptic evidence for the specimen being a type (“H.C.K.” =? Herbarium Carolus Kochii). No original material of the typical variety could be traced at B, G, GOET, P or W.

M. elliptica var. *nana* K. Koch in Linnaea 21: 670. 1849. – Holotype: [Turkey, A8 Çoruh] “Im Hochgebirge des Gaues Pertakrek auf Urgestein, c. 5000-6000' hoch”, *Koch* (B!; putative isotype: G-00087141!). = ***M. elliptica*** K. Koch

Note. – See preceding entry.

M. elliptica var. *pubescens* Boiss. & Kotschy ex Boiss., Fl. Orient. 4: 571. 1879. – Holotype: [Turkey] “Hab. in rupibus verticalibus vallis Teng prov. Musch Armeniae 6500'”, 9.9.1859, *Kotschy, Iter Cilic.-Kurd. 453* (G-BOIS; isotypes: B!, BP!, JE!, K!, P!, W!). = ***M. cristata*** subsp. ***orientalis*** P. H. Davis

Note. – The text on the labels of the isotypes slightly differs from that mentioned in the protologue: “Plantae ex schistosis in alpibus prope Musch lectae; In rupestribus praeruptis ad parietes excelsas vallis Teng 6500'.”

M. ericifolia (Roth ex Willd.) Bornm. in Repert. Spec. Nov. Regni Veg. 19: 198. 1924, nom. rejic. prop. ≡ *Thymus ericifolius* Roth [Bot. Cat. 2: 50. 1802, nom. nud.] ex Willd., Enum. Pl. Horti Berol.: 624. 1809 [as *“ericaefolius”*]. – Holotype: [Spain, Canary Islands] (B-W 11017!). = ***M. varia*** Benth.

Note. – This name has been proposed by Pérez (1978) for rejection in favour of *M. varia* Benth., the formal proposal, however, so far has not been published. At GOET a Roth specimen is present, almost identical to the type found in the Willdenow herbarium of B.

M. eugenioides (Griseb.) Hieron. in Bol. Acad. Nac. Ci. 4: 413. 1881 ≡ *Xenopoma eugenioides* Griseb. in Abh. Königl. Ges. Wiss. Göttingen 19: 237. 1874 = ***Clinopodium gilliesii*** (Benth.) Kuntze, Revis. Gen. Pl. 2: 515. 1891.

M. euosma (W. W. Sm.) C. Y. Wu in Acta Phytotax. Sin. 10: 229. 1965 ≡ *Calamintha euosma* W. W. Sm. in Notes Roy. Bot. Gard. Edinburgh 9: 89. 1916 ≡ ***Clinopodium euosmum*** (W. W. Sm.) Bräuchler & Heubl in Taxon 55: 979. 2006.

[*M. fasciculata* Benth., Labiat. Gen. Spec.: 375. 1834, nom. nud. in notas ad *M. inodora*] – ***M. graeca*** subsp. ***fruticulosa*** (Bertol.) Guinea

Note. – Bentham cites this name in his description of *M. inodora* without indication of author. It is most likely to be interpreted as representing a new combination, both unintended and invalid, for *Satureja fasciculata* Raf., which in turn he listed in synonymy to *M. approximata*.

M. fasciculata (Raf.) Strobl in Flora 68: 370. 1885, nom. illeg. ≡ *Satureja fasciculata* Raf., Précis Découv. Somiol.: 39. 1814 = ***M. graeca*** subsp. ***fruticulosa*** (Bertol.) Guinea

Note. – Strobl listed *Thymus fruticulosus* Bertol., Amoen. Ital.: 101. 1819, in synonymy to his combination of *S. fasciculata* under *Micromeria* and missed on the priority of the original description Bertol. in J. Bot. Agric. 2: 76. Aug 1813, as referred to in Bertoloni (1819: 101). Strobl’s name is therefore illegitimate.

M. fasciculata var. *gracilis* (Guss.) Strobl in Flora 68: 370. 1885, nom. illeg. ≡ *Satureja fasciculata* var. *gracilis* Guss., Fl. Sicul. Syn. 2: 92. 1844. – Type: not indicated (NAP?). = ***M. graeca*** subsp. ***fruticulosa*** (Bertol.) Guinea

M. fasciculata var. *hirsuta* (Guss.) Strobl in Flora 68: 370. 1885, nom. illeg. ≡ *Satureja fasciculata* var. *hirsuta* Guss., Fl. Sicul. Syn. 2: 92. 1844. – Type: not indicated. = ***M. graeca*** subsp. ***fruticulosa*** (Bertol.) Guinea

M. fenzlii Regel in Fischer & Meyer, Index Seminum (St. Petersburg) 1866: 93. 1866 [as "*M. fenzlei* Vis."] =? ***Mentha pulegium*** L., Sp. Pl. 2: 577. 1753.

Note. – See note under *M. dalmatica* Fenzl. Regarding synonymy as provided here, the diagnosis indicates differences to specimens traced at W and WU. Thus the plant cultivated at LE based on seeds recieved from Vienna might not be identical to the species cultivated at W and PAD by that time. A final decision is not possible without consulting further literature and material at LE and PAD. The species according to the diagnosis, however, is not part of *Micromeria* as circumscribed here.

[*M. filicaulis* Schott & Kotschy in Tchihatcheff, Asie Min. Bot. 2: 131. 1860, nom. nud.] – ***M. cremnophila*** subsp. ***anatolica*** P. H. Davis.

Note. – This name is listed as an undescribed species by Tchihatcheff. At W a specimen labelled with this name ("441. M. filicaulis Kotschy & Schott, in monte Tauro, aestate 1836, No. 702.I, *Th. Kotschy*") has been identified as *M. cremnophila* subsp. *anatolica* by P. H. Davis.

M. filiformis (Aiton) Benth., Labiat. Gen. Spec.: 378. 1834 ≡ *Thymus filiformis* Aiton, Hort. Kew. 2: 313. 1789. – Lectotype (designated here by Bräuchler): [Spain] "Insulae Baleares", *Jacquin* (BM [Banks herbarium]).

Note. – According to the protologue ("nat. of the Balearic islands, introduced 1770 by Mr. William Malcolm. Fl. June and July, G.H. h.") a preserved specimen from a plant of that name cultivated in the greenhouses at K prior to the description would be the first choice for a lectotype. No such specimen, however, is present at K or BM, where many specimens from plants cultivated at Kew Gardens prior to 1800 are kept. The diagnoses in Hort. Kew. vols. 1 & 2 were largely written by Dryander, who used a manuscript left by Solander (Britten 1912; Krok 1925). In this manuscript (present at the Botany Library at BM), *Thymus filiformis* is stated as described from a Jacquin collection or a specimen from his herbarium (Roy Vickery, pers. comm). At BM there is a sheet in the Banks herbarium that contains three gatherings: the first labelled "Herb. Helvet.", i.e., a collection of (supposedly) Swiss plants, made by Dick, and purchased by Banks from Pitcairn in 1775; a second labelled "Hort. Pitcairne", cultivated at Pitcairn's garden and finally the third collection "Insulae Baleares. Jacquin". The original description by Solander most probably was based on this latter collection and the species later has been introduced to Kew Gardens by Malcolm. The Jacquin collection to our knowledge represents the only preserved part of the original material and therefore is designated as lectotype here. Nevertheless, the authorship for the species is to be attributed to Aiton (McNeill & al. 2006: Art. 46.7, Ex. 35). Morales (1993) includes this species under *M. microphylla*. Until a full revision of the species group is done, we prefer to keep both taxa separate, in case of merging, the choice would have to be for *M. filiformis* for reasons of priority. The status of the infraspecific taxa of *M. filiformis* and its delimitations towards *M. microphylla* remains to be settled.

[*M. filiformis* var. *condensata* (L. Chodat) Bonafè, Fl. Mallorca 4: 56. 1980, nom. inval.] = *Satureja rodriguezii* var. *condensata* L. Chodat in Bull. Soc. Bot. Geneve, ser. 2, 15: 234. 1924. – Lectotype (designated here by Bräuchler): [Spain, Balearic Islands, Mallorca,] "Torre d'en Pau" (G-00087103 [individual on the lower right hand side]!). = ***M. filiformis*** subsp. ***rodriguezii***

Note. – Bonafè does neither include the basionym nor the reference to the protologue, rendering his new combination invalid. He cites the plant as "*M. filiformis* var. *condensata* L. Chod.". At G no specimen labelled with this name could be traced (L. Gautier, pers. comm.). There is, however, a collection labelled as *Micromeria rodriguezii* collected by R. Chodat, father of L. Chodat, at Torre d'en Pau on 3.4.1921. This sheet consists of several individuals (fragments of one individual?) the three right hand sided of which fit the diagnosis. Since L. Chodat explicitly states that her treatment was partially based on her father's material, this sheet most probably represents part of the original material. The right hand lower individual therefore is designated as lectotype here.

M. filiformis subsp. *cordata* (Moris ex Bertol.) Pignatti in Giorn. Bot. Ital. 111: 52. 1977 ≡ ***M. cordata*** (Moris ex Bertol.) Moris

M. filiformis (Aiton) Benth. subsp. ***filiformis***

M. filiformis var. *glandulosa* Sennen & Pau in Treb. Inst. Catalana Hist. Nat. 3: 193. 1917 [– *M. filiformis* subsp. *glandulosa* (Sennen & Pau) Bonafè, Fl. Mallorca 4: 56. 1980, nom. inval.]. – Holotype: [Spain, Balearic Islands] "Soller, fentes des rochers, jusqu'a 900 m", *Sennen, Pl. Espagne 2038* (BC!; isotype: MA!). = ***M. filiformis*** subsp. ***filiformis***

Note. – Sennen, Pl. Espagne 2039, a number included immediately after listing of the type locality, could erroneously be regarded as syntype; it is, however, the "type" number of *M.* ×*knochei* (MA!), whose description follows in the next clearly separated paragraph in Sennen's paper. Bonafè does include the basionym, but not the reference to the protologue, rendering his new combination invalid.

M. filiformis subsp. ***minutifolia*** (L. Chodat) Kerguélen in Lejeunia 120: 128. 1987 ≡ *Satureja filiformis* var. *minutifolia* L. Chodat in Bull. Soc. Bot. Genève, ser. 2, 15: 246. 1924. – Type: Described from Corse without indication of collector, date or precise place.

Note. – No original material labelled with this name could be traced at G (L. Gautier, pers. comm.).

M. filiformis subsp. ***rodriguezii*** (Freyn & Janka) Bonafè, Fl. Mallorca 4: 56. 1980 ≡ *M. rodriguezii* Freyn & Janka

M. filiformis var. *rubrifolia* Sennen & Pau in Treb. Inst. Catalana Hist. Nat. 3: 193. 1917. – Holotype: [Spain, Balearic Islands] "Soller, murs et collines (Bianor in sched.)", *Sennen, Pl. Espagne 2041* (BC!; isotype: MA!). = ***M. filiformis*** subsp. ***filiformis.***

M. flacca (Náбělek) Hedge in Notes Roy. Bot. Gard. Edinburgh 25: 51. 1965 ≡ *Satureja flacca* Nábělek in Publ. Fac. Sci Univ. Masaryk (Brno) 70: 44. 1926 = ***Clinopodium molle*** (Benth.) Kuntze, Revis. Gen. Pl. 2: 515. 1891.

M. flagellaris Baker in J. Linn. Soc., Bot. 20: 232. 1883.

Note. – One of currently three accepted species endemic to Madagascar. Traditionally included in *Micromeria* section *Micromeria*, they were omitted in the last synopsis of *Micromeria* by Morales (1993). Morphological affinities with E African members of *M.* sect. *Pseudomelissa* were assumed previously (e.g., I. Hedge, pers. comm.) but more recent studies favour the placement in a new genus (Bräuchler, unpubl. data). The lack of a marginal leaf vein along with several other features (e.g. ecology, growth form, inflorescence) supports exclusion from *Micromeria* as circumscribed here.

M. fontanesii K. Koch in Linnaea 6: 670. 1849 & Pomel, Nouv. Mat. Fl. Atl.: 123. 1874 ≡ *Satureja filiformis* Desf., Fl. Atl. 2: 8, t. 121. 1798 [non *Thymus filiformis* Aiton, Hort. Kew. 2: 313. 1789, non *M. filiformis* (Aiton) Benth. 1834]. – Type: [Morocco?] "in fissuris rupium Atlantis", *Desfontaines* (P, illustrated in Desf., Fl. Atlant. 2: t. 121. 1798).

M. fontanesii var. *depauperata* Pomel, Nouv. Mat. Fl. Atl.: 123. 1874. – Holotype: [Algeria] "environs d'Oran, Union du Sig (?), rochers", 1852, *Durando* (MPU-004938*!). = ***M. fontanesii*** K. Koch.

M. fontanesii var. *major* Batt. & Trab., Fl. Algérie 1: 677. Dec 1890. – Syntypes: [Algeria] "R.R. Les 2 Cèdres (Blida), Le Chenoua" (not traced, AL/MPU?). = ***M. fontanesii*** K. Koch

Note. – See note under *M. brivesii.*

M. fontanesii var. *typica* Batt. & Trab. Fl. Algérie 1: 677. 1890 [nom. inval.?]. – Syntypes: [Morocco] “Tell oranais, Dahra, Tiaret, Maroc” (not traced, P?). = ***M. fontanesii*** K. Koch.

Note. – Despite not explicitly including the type of *Micromeria fontanesii,* this variety name could be regarded as not validly published. The protologue, however, includes a type citation (herb. Coss.; not the type of the species) and a diagnosis.

M. forbesii Benth., Labiat. Gen. Spec.: 376. 1834. – Holotype: [Cape Verde Islands] “Ins. Sancti Nicolai”, 1822, *Forbes* (K!).

Note. – A considerably variable species with many forms on each island of the Cape Verde archipelago. Since no clear delimitations can be drawn among the variation over the whole distribution range, the varieties published are placed in synonymy to *M. forbesii* here. A specimen with less detailed label data collected by Forbes is present at G (G-00018940*!) and probably represents a duplicate of the holotype at K.

M. forbesii var. *altitudinum* Bolle in Bonplandia (Hannover) 8: 282. 1860. – Holotype: [Cape Verde Islands] “Hab. in ins. S. Antonii jugi excelsi Cumbre rupibus siccissimis”, November, *Bolle* (B†). = ***M. forbesii*** Benth.

Note. – The holotype together with Bolle’s herbarium was integrated in the general herbarium at B and destroyed in WW II. To our knowledge no isotypes exist at B or at Z/ZT where some Bolle duplicates are kept. A specimen of *M. forbesii* collected by Bolle in 1853 (TCD!) according to the original description might represent this variety, but indication of locality is more general, the name is not on the label or elsewhere on the specimen and flowers are absent.

M. forbesii var. *inodora* J. A. Schmidt, Beitr. Fl. Cap. Verd. Ins.: 222. 1852. – Holotype: [Cape Verde Islands] “Hab. in rupibus S. Antonii, pr. Riberiram grandem”, 3.1851, *Schmidt* (not traced). = ***M. forbesii*** Benth.

Note. – Unlike other Schmidt material, the type is not to kept at HBG. At B, HAL, HEID and W specimens of the typical variety cited by Schmidt were traced, but not the type of var. *inodora*.

M. formosana C. Marquand in Hooker’s Icon. Pl. 33: t. 3230. 1934 = ***Origanum vulgare*** L., Sp. Pl. 2: 590. 1753.

M. forsskahlii Benth., Labiat. Gen. Spec.: 379. 1834, nom. superfl. [as *“forskahlei”*] ≡ *Thymus imbricatus* Forssk. ≡ ***M. imbricata*** (Forssk.) C. Chr. var. ***imbricata***

M. frivaldszkyana (Degen) Velen. in Oesterr. Bot. Z. 49: 291. 1899 ≡ *Zygis frivaldszkyana* Degen in Bull. Herb. Boissier 4: 523, t. 8. Jul 1896 ≡ ***Clinopodium frivaldszkyanum*** (Degen) Bräuchler & Heubl in Taxon 55: 979. 2006.

M. fruticosa (L.) Druce in Bot. Exch. Club Soc. Brit. Isles 3: 421. 1914 ≡ *Melissa fruticosa* L., Sp. Pl. 2: 593. 1753 ≡ *Clinopodium fruticosum* (L.) Kuntze, Revis. Gen. Pl. 2: 516. 1891, non Forssk., Fl. Aegypt. Arab.: 107. 1775 ≡ ***Clinopodium serpyllifolium*** subsp. ***fruticosum*** (L.) Bräuchler in Taxon 55: 980. 2006.

M. fruticosa subsp. *barbata* P. H. Davis in Kew Bull. 1951: 77. 1951 ≡ ***Clinopodium serpyllifolium*** subsp. ***barbatum*** (P. H. Davis) Bräuchler in Taxon 55: 980. 2006.

M. fruticosa subsp. *brachycalyx* P. H. Davis in Kew Bull. 1951: 77. 1951 ≡ ***Clinopodium serpyllifolium*** subsp. ***brachycalyx*** (P. H. Davis) Bräuchler in Taxon 55: 980. 2006.

M. fruticosa subsp. *giresunica* P. H. Davis in Notes Roy. Bot. Gard. Edinburgh 38: 39. 1980 ≡ ***Clinopodium serpyllifolium*** subsp. ***giresunicum*** (P. H. Davis) Bräuchler in Taxon 55: 980. 2006.

M. fruticosa var. *italica* (Huter) Fen. in Webbia 28: 375. 1973 ≡ *M. marifolia* var. *italica* Huter = ***Clinopodium serpyllifolium*** (M. Bieb.) Kuntze

M. fruticosa subsp. *serpyllifolia* (M. Bieb.) P. H. Davis in Kew Bull. 1951: 77. 1951 ≡ *Nepeta serpyllifolia* M. Bieb., Fl. Taur.-Cauc. 2: 40. 1808 ≡ ***Clinopodium serpyllifolium*** (M. Bieb.) Kuntze, Revis. Gen. Pl. 2: 515. 1891.

M. fruticulosa (Bertol.) Šili6, Monogr. Satureja Fl. Jugosl.: 256. 1979 ≡ *Thymus fruticulosus* Bertol. ≡ ***M. graeca*** subsp. ***fruticulosa*** (Bertol.) Guinea

Note. – The first to propose this name at the rank of a species under *Micromeria* was Sili6 (1979), who erroneously treated it as *M. fruticulosa* (Bertol.) Grande, which was actually published as *Satureja fruticulosa* (Bertol.) Grande in Nuov. Giorn. Bot. Ital., ser. 2, 32: 91. 1925.

M. gilliesii Benth., Labiat. Gen. Spec.: 381. 1834 ≡ ***Clinopodium gilliesii*** (Benth.) Kuntze, Revis. Gen. Pl. 2: 515. 1891.

M. glabella (Michx.) Benth., Labiat. Gen. Spec.: 371. 1834 ≡ *Cunila glabella* Michx., Fl. Bor.-Amer. 1: 13. 1803 ≡ ***Clinopodlium glabellum*** (Michx.) Kuntze, Revis. Gen. Pl. 2: 515. 1891.

M. glabella var. *angustifolia* Torr., Fl. New York 2: 67. 1847 = ***Clinopodium glabrum*** (Nutt.) Kuntze, Revis. Gen. Pl. 2: 515. 1891.

M. glomerata P. Pérez in Vieraea 3: 78. 1974. – Holotype: [Spain, Canary Islands] "In fissuris rupis regione septentrionale Anaga (400 m), circa Taganaga. Stirps nivariensis rarissima", 27. 5.1972, *Pérez de Paz* (TFC 1710; isotype: K!, MA!).

M. gontscharovii Vved. in Bot. Mater. Gerb. Inst. Bot. Acad. Nauk. Uzbeksk. SSR 16: 17. 1961, nom. superfl. ≡ ***Gontscharovia popovii*** (B. Fedtsch. & Gontsch.) Boriss. in Bot. Mater. Gerb. Bot. Inst. Komarova Akad. Nauk SSSR. 15: 321. 1953.

M. gracilis (R. Br.) Benth., Labiat. Gen. Spec.: 380. 1834 ≡ *Mentha gracilis* R. Br., Prodr. Fl. Nov. Holland.: 505. 1810 = ***Mentha diemenica*** Spreng., Syst. Veg. 2: 724. 1825.

M. graeca (L.) Benth. ex Rchb., Fl. Germ. Excurs.: 311. 1831 ≡ *Satureja graeca* L., Sp. Pl. 2: 568. 1753. – Lectotype (designated by Morales 1991: 143): Herb. Linnaeus no. 723.4 (LINN).

Note. – The whole *M. graeca* alliance is very variable, resulting in numerous synonyms especially for taxa described from the Italian islands and coasts. The infraspecific classification is far from being satisfactory. In accordance to the treatment in Flora Europaea (Ball & Getliffe 1972) many taxa described are accepted here for the time being at the rank of subspecies, by may not represent natural units. A thorough revision is badly needed. Most *Micromeria* taxa described by Lojacono-Pojero (1907) are to be included under *M. graeca* but assignment to a certain subspecies in most cases is not possible without consulting the original collections.

M. graeca var. *angustifolia* (C. Presl) Benth. in Candolle, Prodr. 12: 214. 1848 ≡ *Satureja angustifolia* C. Presl, Fl. Sicul.: 36. 1826. – Holotype: [Italy, Sicily] (not traced, PR?). =? ***M. graeca*** subsp. ***tenuifolia*** (Ten.) Nyman.

M. graeca [unranked] *canescens* (Guss.) Gand., Nov. Consp. Fl. Eur.: 367. 1910 ≡ *M. canescens* (Guss.) Benth., Labiat. Gen. Spec.: 376. 1834 ≡ *Satureja canescens* Guss., Pl. Rar.: 228, t. 42. 1826 = ***M. graeca*** (L.) Benth. ex Rchb.

Note. – See notes under *M. canescens* and *M. approximata* subsp. *barceloi.*

M. graeca subsp. ***consentina*** (Ten.) Guinea in Bot. J. Linn. Soc. 64: 381. 1971 ≡ *M. graeca* var. *consentina* (Ten.) Nyman, Consp. Fl. Eur.: 590. 1881 ≡ *Satureja consentina* Ten., Fl. Neapol. Prodr. App. 5: 17. 1826. – Holotype: [Italy, Naples] *Tenore* (NAP).

Note. – This taxon has been included in synonymy to *M. graeca* var. *longiflora* by Bentham (1834), which is here listed as subspecies. The latter name would have priority at subspecies level if the two subspecies prove to be one taxon.

M. graeca subsp. *cypria* (Kotschy) E. F. Chapm., Cyprus Trees Shrubs: 73. 1949 Rech.f. in Arkiv Bot., ser. 2, 1(9): 430. 7 Dec 1949 ≡ *M. cypria* Kotschy = ***M. microphylla*** (d'Urv.) Benth.

Note. – Chapman cites this as *"M. graeca* subsp. *cypria* Holm." providing an indirect reference to Kotschy's basionym *M. cypria* via *Satureja graeca* subsp. *cypria* (Kotschy) Holmb., Stud. Veg. Cyprus: 159. 1914. We found no evidence for the precise publication date of Chapman's work in

1949. Since Rechinger made the same combination in December of that year, it is very likely but not sure that Chapman should be cited as the author of this combination. No standard form has been proposed for this author (see IPNI 2008), so we introduce "E. F. Chapm." here in concordance with other abbreviations for authors of the same surname as listed there.

M. graeca var. *densiflora* Benth., Labiat. Gen. Spec.: 373. 1834. – Type: not designated. = ***M. graeca*** subsp. ***tenuifolia*** (Ten.) Nyman

Note. – A number of collections is cited under *M. graeca*. In case a specimen is preserved at K (herb. Bentham) labelled with the name *M. graeca* var. *densiflora* this could serve as lectotype.

M. graeca var. *densiflora* Post, Fl. Syria: 621. 1896, non Benth. 1834. – Holotype: [Lebanon] "Subalpine and alpine Lebanon; Zahleh", *Post* (BEI) = ***M. graeca*** Benth. ex Rchb.

M. graeca subsp. ***fruticulosa*** (Bertol.) Guinea in Bot. J. Linn. Soc. 64: 381. 1971 ≡ *Thymus fruticulosus* Bertol. in J. Bot. Agric. 2: 76. Aug 1813. – Lectotype (designated here by Bräuchler): [Italy, Sicily, Palermo] "*Satureja fruticosa* Cyrilli; Ex Panormo dedit Pisis(?)", 1806, *Bivona-Bernardi* (BOLO [photo]!).

Note. – This seems to be one of the more distinct forms of the *M. graeca* alliance. There is no indication of the type in the protologue, which seems to be an abridged pre-print extract of the Amoenitates Italicae (Bertoloni 1819), since both numbering of the account and species diagnosis are exactly the same. In the latter treatment, the name *Satureja fasciculata* is cited in synonymy to *T. fruticulosus* along with two old Boccone names from specimens seen by Bertoloni in herb. DD Josephi & Cajetan Monti. Another specimen cited (Bertoloni 1819: 101) is one collected under the name *Satureja fruticosa* Cyrilli in Sicily by Bivona-Bernardi in 1806; it represents the only collection for which there is proof that it was in Bertoloni's posession when writing the original diagnosis. This specimen is preserved at BOLO, forming part of Bertoloni's "Hortus siccus Florae Italicae" (A. Managlia, pers. comm.) and in our opinion is the best choice for a lectotype.

M. graeca subsp. ***garganica*** (Briq.) Guinea in Bot. J. Linn. Soc. 64: 381. 1971 ≡ *Satureja graeca* subsp. *garganica* Briq., Lab. Alp. Mar. 3: 421. 1895. – Type: [Italy] "Mte. Gargano" (not traced).

Note. – Pignatti (1982) includes *Satureja graeca* subsp. *garganica* in synonymy to *M. canescens,* which he recognizes as distinct species and in turn is listed in synonymy to *M. graeca* subsp. *micrantha* by Govaerts (1999). This seems to be among the more distinct forms of *M. graeca* s.l. At G there is only one specimen of this taxon that could represent original material, though it is neither labelled with the name nor with Briquet's handwriting (G-00087140!). We therefore decided to wait until better material is available for typification.

M. graeca (L.) Benth. ex Rchb. subsp. ***graeca***

M. graeca var. *hirsuta* (C. Presl) K. Koch ≡ *Satureja hirsuta* C. Presl in Presl & Presl, Del. Prag.: 79. 1822 = ***M. juliana*** (L.) Benth.

M. graeca subsp. *imperica* Chater in Bot. J. Linn. Soc. 64: 381. 1971 ≡ *M. thymoides* De Not., Repert. Fl. Ligust.: 353. 1844, non (Sol. ex Lowe) Webb & Berthel., Hist. Nat. Iles Canaries 3: 71. Dec. 1844 = ***M. graeca*** (L.) Benth. ex Rchb. subsp. ***graeca.***

Note. – Pignatti (1982) includes this in synonymy to *M. graeca* subsp. *graeca* which is followed here after examination of material from the area of the type collection. When establishing a new subspecific name for this taxon Chater missed on the probable priority of *M. thymoides* De Not. (1844) over *M. thymoides* (Sol. ex Lowe) Webb. & Berthel. (Dec 1844). Chater's *"imperica"*, however, to our knowledge, is the oldest available name for this taxon at subspecies level. The date for the Webb & Berthel. name is taken from Stearn (1937).

M. graeca var. *latifolia* Boiss., Voy. Bot. Espange 1(16): 496. 1841. – Syntypes: "Hispania, Graecia, Italia meridionali", *Boissier* (G-BOIS?, putative isosyntypes: GOET!, W!). = ***M. graeca*** (L.) Benth. ex Rchb. subsp. ***graeca***

Note. – The specimens traced at GOET and W are duplicates from G-BOIS ("In colibus reg. calidae Regn. Granat.", Mai 1837, *Boissier*).

M. graeca subsp. ***laxiflora*** (Post) Mouterde, Nouv. Fl. Liban Syrie 3(2): 3. 1979 ≡ *M. graeca* var. *laxiflora* Post, Fl. Syria: 621. 1896. – Holotype: [Lebanon] "Subalpine and alpine Lebanon; Zahleh", *Post* (G).

Note. – Citation of the type is taken from Musselmann & Saoud (2004).

M. graeca subsp. ***longiflora*** (C. Presl) Nyman, Consp. Fl. Eur.: 590. 1881 ≡ *M. graeca* var. *longiflora* (C. Presl) Benth., Labiat. Gen. Spec.: 373. 1834 ≡ *Satureja longiflora* C. Presl, Fl. Sicul: 36. 1826. – Type: [Italy, Sicily] (not traced, PR?).

M. graeca subsp. *micrantha* (Brot.) Rivas Mart., T. E. Díaz & Fern. Gonz. in Itin. Geobot. 3: 138. 1990 ≡ *M. graeca* f. *micrantha* (Brot.) Hayek, Prodr. Fl. Penins. Balcan. 2: 320. 1929 ≡ *Thymus micranthus* Brot., Fl. Lusit. 1: 176. 1804. – Type: [Portugal] "In collibus calcareis, praesertim in Alcantara prope Olisiponem", *Brotero* (not traced, LISU?). = ***M. graeca*** (L.) Benth. ex Rchb. subsp. ***graeca***

Note. – Synonymy is following Morales (1991).

M. graeca [unranked] *notarisii* (Zumagl.) Gand., Nov. Consp. Fl. Eur.: 367. 1910 ≡ *Thymus notarisii* Zumagl. 1849, nom. superfl. ≡ *Micromeria thymoides* De Not. 1844 [& 1846], non (Sol. ex Lowe) Webb & Berthel., Dec 1844 ≡ *M. graeca* subsp. *imperica* Chater = ***M. graeca*** subsp. ***graeca***

Note. – See notes under *M. notarisii* and *M. thymoides.*

M. graeca var. *pauciflora* Vis., Fl. Dalm. 2: 196. 1847. – Type: [Croatia] "Ad rupes maritimas scopuli S. Andrea prope Lesina", *Stalio* (not traced, PAD?.) = ***M. graeca*** (L.) Benth. ex Rchb. subsp. ***graeca***

M. graeca var. *rariflora* K. Koch in Linnea 21: 670. 1848. – Holotype: "Im Gundelsh. Herbar als *Calamintha cretica,* angusto oblongo folio J. H. R. *Clinopodium creticum* P. Alp." (B, extant?). = ***M. graeca*** (L.) Benth. ex Rchb. subsp. ***graeca***

Note. – The herbarium of Andreas von Gundelsheimer after his death in 1715 was divided and transferred to B and M. The material studied by Koch most likely was incorporated in Willdenow's herbarium by that time. This herbarium is still extant at B, but was not searched for the type. At M a specimen labelled with "*Calamintha cretica,* P. Alp." is present, most likely one of Gundelsheimer's duplicates from his journey to Crete with Tournefort.

M. graeca var. *rupestris* (Guss.) Strobl in Oesterr. Bot. Z. 33: 331. 1883 ≡ *Satureja graeca* var. *rupestris* Guss. in Fl. Sic. Syn. 2(1): 90. 1844 = ***M. graeca*** (L.) Benth. ex Rchb. subsp. ***graeca***

M. graeca var. *sicula* (Guss.) Nym. in Consp. Fl. Eur.: 590. 1881 ≡ *Satureja sicula* Guss., Fl. Sic. Syn. 2(1): 90. 1844 = ***M. graeca*** (L.) Benth. ex Rchb. subsp. ***graeca***

M. graeca [unranked] *sicula* (Guss.) Gand., Nov. Consp. Fl. Eur.: 367. 1910 ≡ *Satureja sicula* Guss., Fl. Sic. Syn. 2(1): 90. 1844 = ***M. graeca*** (L.) Benth. ex Rchb. subsp. ***graeca***

Note. – See note under *M. approximata* subsp. *barceloi.*

M. graeca subsp. ***tenuifolia*** (Ten.) Nyman, Consp. Fl. Eur.: 590. 1881 ≡ *M. graeca* var. *tenuifolia* (Ten.) Vis., Fl. Dalm. 2: 196. 1847 ≡ *Satureja tenuifolia* Ten., Fl. Napol.: 33. 1811. – Holotype: [Italy], *Tenore* (NAP).

Note. – Authentic material was traced at BP! and W! ("*Satureja tenuifolia* nobis", *Tenore*). Šili6 (1979) cites this under synonymy to *M. graeca* var. *densiflora* Benth. which has priority at varietal level. At rank of a subspecies, however, *M. graeca* subsp. *tenuifolia* (Ten.) Nyman is the oldest valid name.

M. graeca var. *villicaulis* Borb. ex Formánek in Verh. Naturf. Vereins Brünn 33: 141. 1894. – Type: [Greece] "Korfu, Analypsis et Kanali", 1894, *Formánek* (not traced). = ***M. graeca*** (L.) Benth. ex Rchb. subsp. ***graeca***

M. grandiflora Killick in Bothalia 6: 439. 1954 ≡ ***Killickia grandiflora*** (Killick) Bräuchler, Doroszenko & Heubl in Bot. J. Linn. Soc. 157: 583. 2008.

Note. – See note under *M. compacta.*

M. grandis Lojac., Fl. Sicul. 2(2): 213. 1907. – Syntypes: [Italy, Sicily] "Ad rupes calcareas Palermo", *Pan.*, "Pupi nell'interno dell'Isola, forse gessose. Campofranco", *Rossi* (not traced). = ***M. graeca*** (L.) Benth. ex Rchb.

Note. – See note under *M. calaminthoides*. Syntypes not designated to a variety.

M. grandis var. *humilior* Lojac., Fl. Sicul. 2(2): 214. 1907 = ***M. graeca*** (L.) Benth. ex Rchb.

Note. – See note under species entry.

M. grisea (Epling) R. Morales in Bot. Complut. 18: 164. 1993 ≡ *Satureja grisea* Epling in Brittonia 7: 139. 1951 ≡ ***Clinopodium griseum*** (Epling) Harley in Kew. Bull. 55: 921. 2000.

M. guichardii (Quézel & Zaffran) Brullo & Furnari in Webbia 34: 168. 1979 ≡ *Satureja guichardii* Quézel & Zaffran in Bull. Soc. Hist. Nat. Afrique N. 52: 219. 1962. – Lectotype (designated here by Bräuchler): [Libya] "Cyrenaica, escarpment north of Barce, plain amongst limestone rocks", 26.4.1954, *Guichard KG/CYR/155* (BM-000778845!).

Note. – In the protologue, types are stated to be deposited at AL and BM without indication of a holotype. Since the whereabouts of the AL specimen are unclear (see note under *M. brivesii*), the specimen preserved at BM is here designated as lectotype. In the protologue the collector erroneously is cited as L. G. Guichard, while in the introduction of the corresponding article and on the label of the lectotype he is cited as K. M. Guichard.

M. hedgei Rech. f., Fl. Iran. 150: 507, t. 400. 1982. – Lectotype (designated here by Bräuchler): "Iran, Kerman, Bashaguerd, Ghorichi. 1000 m" 20.2.1973, *Iranshahr & Moussavi 15436-E* (W-1973-0020347!, illustrated in t. 400).

Note. – A second syntype cited is *Iranshahr & Moussavi 35809* (E!), which is according to the protologue a duplicate of the other one, but was distributed under a different number in a different year. Since the top set of Rechinger's collections is kept at W and the W specimen is illustrated in the protologue, it is here chosen as lectotype.

M. helianthemifolia Webb & Berthel., Hist. Nat. Iles Canaries 3: 79. 1845. – Lectotype (designated by Pérez 1978: 82): [Spain, Canary Islands] "In fissuris rupium ad pylas vallis Tiraxanae, Degollada de Manzanilla dicta, in regione alta Canaria", *Barker-Webb 27* (FI [individual in the centre]).

M. helianthemifolia f. *albiflora* G. Kunkel in Cuad. Bot. Canaria 16: 43. 1972. – Holotype: [Spain, Canary Islands] "Bco. de Arguineguín, 700 m", *Kunkel 15194* (G-00018865*!). = ***M. helianthemifolia*** Webb & Berthel.

M. helianthemifolia f. *glomerata* G. Kunkel in Vieraea 8: 359. 1980. – Holotype: [Spain, Canary Islands] "Gran Canaria, Barranco de Siberio, 900 m", 25.6.1974, *Kunkel 17368* (G-00018866*!). = ***M. helianthemifolia*** Webb & Berthel.

M. helianthemifolia var. *mary-annae* P. Pérez & G. Kunkel in Cuad. Bot. Canaria 26-27: 27. 1976. – Holotype: [Spain, Canary Islands] "In magno cavo vulgo dicto 'Barranco de Siberio'. Ca. Tejede, Canaria Magna (Gran Canaria dicta)", 25.7.1974, *Pérez* (TFC 5518; isotypes: MA!, FI, TFC, TFMC, herb. Kunkel) = ***M. helianthemifolia*** Webb & Berthel.

M. herpyllomorpha Webb & Berthel., Hist. Nat. Iles Canaries 3: 72. 1844. – Lectotype (designated by Pérez 1978: 238-239): [Spain, Canary Islands] "In ins. Palma", *Barker-Webb* (FI [labelled "*Thymus herpylloides* Nob."]; possible isolectotype: K!).

M. hirsuta (C. Presl) Gand., Fl. Cret.: 80. 1916 ≡ *Satureja hirsuta* C. Presl in Presl & Presl, Del. Prag.: 79. 1822 = ***M. juliana*** (L.) Benth.

Note. – Gandoger refers to this as "*M. hirsuta* Benth." which can be interpreted as indirect reference to the basionym *Satureja hirsuta* C. Presl via the illegitimate name *M. juliana* var. *hirsuta* (C. Presl) Benth., Labiat. Gen. Spec.: 373. 1834.

[*M. hirsuta* Mazziari in Nyman, Consp. Fl. Eur.: 590. 1881, pro syn.] – ***M. nervosa*** (Desf.) Benth.

M. hispida Boiss. & Heldr. ex Benth. in Candolle, Prodr. 12: 215. 1848. – Holotype: [Greece] "In rupestribus Cretae", 4.1846, *Heldreich* (G-BOIS; isotypes: BP!, GOET!, P!, TCD!, WU [herb. Halácsy]!).

Note. – Doroszenko (unpubl. Ph.D. thesis, Univ. Edinburgh 1986) puts this species in vincity of *M. microphylla.* Judging from the types we confirm the close affinity. Although there is considerable difference in length of calyx teeth and indumentum the two taxa might be conspecific.

M. hochreutineri (Briq.) Maire in Bull. Soc. Hist. Nat. Afrique N. 7: 273. 1916 ≡ *Satureja hochreutineri* Briq. in Ann. Conserv. Jard. Bot. Genéve 7-8: 201. 1904. – Lectotype (designated here by Bräuchler): [Algeria] "Province d'Oran, Oasis de Tiout, près Aïsi Sefra, chaine rocheuse au S. de l'oasis, c. 1050 m", 31.5.1901, *Hochreutiner*, *Voyage botanique en Algérie 549* (G-000 18055*!; isolectotypes: G-00018054*!, Z-000021056!).

Note. – At G two sheets of *Hochreutiner 549* and one of *Hochreutiner 644* (both syntype numbers) are preserved. Collections of both numbers are equally rich. Since *Hochreutiner 549* has one known duplicate at Z, the specimen labelled "*Satureja hochreutineri* sp. nov., J. Briquet 1903" in Briquet's handwriting (G-00018055) is here chosen as lectotype.

M. hydaspidis Falc. ex Benth. in Candolle, Prodr. 12: 224. 1848 ≡ ***Clinopodium hydaspidis*** (Falc. ex Benth.) Kuntze, Revis. Gen. Pl. 2: 515. 1891.

M. hyssopifolia Webb & Berthel., Hist. Nat. Iles Canaries 3: 72. 1844. – Lectotype (designated by Pérez 1978: 209): [Spain, Canary Islands] "In rupestribus siccis Ins. Canar. vulgatissima", *Barker-Webb* (FI [labelled "*Thymus polimorpha* sp.n.?", left hand individual in upper part of sheet with 5 individuals mounted on it]).

M. hyssopifolia var. ***glabrescens*** (Webb & Berthel.) P. Pérez, Rev. Gen. Micromeria Reg. Macarones.: 212. 1978 ≡ *M. hyssopifolia* f. *glabrescens* Webb & Berthel., Hist. Nat. Iles Canaries 3: 72. 1844. – Lectotype (designated by Pérez 1978: 213): [Spain, Canary Islands] "Prope Orotavam, Nivaria", *Barker-Webb* (FI).

Note. – In a footnote Webb & Berthelot indicate both varieties as formae, but they are explicitly stated as var. in the main body of the text; Pérez (1978) treats them as formae.

M. hyssopifolia f. *hirta* Webb. & Berthel., Hist. Nat. Iles Canaries 3: 72. 1844 = ***M. hyssopifolia*** var. ***hyssopifolia*/*M. hyssopifolia*** var. ***glabrescens*** (Webb & Berthel.) P. Pérez

Note. – Pérez (1978) put this name in synonymy "per partem" (p.p.) to both varieties.

M. hyssopifolia Webb & Berthel. var. ***hyssopifolia***

M. hyssopifolia var. ***kuegleri*** (Bornm.) P. Pérez, Rev. Gen. Micromeria Reg. Macarones.: 214. 1978 ≡ *M. kuegleri* Bornm. in Repert. Spec. Nov. Regni Veg. 19: 197. 1924.

M. illyrica (Host) Tomm. in Flora 18, Beibl. 1: 44. 1835 ≡ *Satureja illyrica* Host, Fl. Austriac. 2: 133. 1831 = ***Satureja subspicata*** Bartl. ex Vis., Stirp. Dalmat. Spec. 2: t. 4. 1826.

Note. – This name is listed as "*Micromeria illyrica* (Host)" in an itinerary by Tommasini, at the cited place obviously unintentionally making a new combination.

M. imbricata (Forssk.) C. Chr. in Dansk Bot. Ark. 4, 3: 21. 1922 ≡ *Thymus imbricatus* Forssk., Fl. Aegypt.-Arab.: 108. 1775. – Holotype: [Yemen] "Kurmae", *Forsskål* (C!; photos of holotype in Seybold 1988: 21-22).

Note. – Some authors (e.g., Walther & Walther 1957; Seybold 1988) preferred to divide this tropical African to Arabic taxon into two to five more narrowly delimited species, but Ryding (2007) recognizes only one species with three varieties. The large and widespread var. *imbricata* is extremely polymorphic, and much more variable than the Mediterranean species of the genus. However, Ryding (2007) was not able to detect any discontinuities in the variation. Different forms may grow together and appear to be distinct at some localities, while intermediates are common at other localities. Ryding (2007) suggested that this variation pattern may be explained by partial autogamy. It does also seem uncertain whether *M. imbricata* is distinct from the Mediterranean *M. graeca.*

M. imbricata (Forssk.) C. Chr. var. ***imbricata***

M. imbricata var. ***rhodesiaca*** (Elly Walther & K. H. Walther) Ryding in Bot. J. Linn. Soc. 155: 439. 2007 ≡ *M. biflora* var. *rhodesiaca* Elly Walther & K. H. Walther in Mitt. Thüring. Bot. Ges. 1(4): 7. 1957.

M. imbricata var. ***villosa*** (Elly Walther & K. H. Walther) Ryding in Bot. J. Linn. Soc. 155: 442. 2007 ≡ *M. biflora* var. *villosa* Elly Walther & K. H. Walther in Mitt. Thüring. Bot. Ges. 1(4): 7. 1957.

M. inodora (Desf.) Benth., Labiat. Gen. Spec.: 375. 1834 ≡ *Thymus inodorus* Desf., Fl. Atlant. 2: 30. 1798. – Lectotype (designated by Morales 1991: 141): [Algeria] "In collibus aridis et incultis", *Desfontaines s.n.* (P [herb. Desfontaines, central individual]).

[*M. inodora* f. *decumbens* Sennen, Diagn. Nouv.: 273. 1936, nom. nud.] – ***M. inodora*** (Desf.) Benth.

[*M. inodora* var. *elata* (Maire) Sennen, Diagn. Nouv.: 273. 1936, nom. inval.] – *Satureja fontanesii* var. *elata* Maire in Jahandiez & Maire, Cat. Pl. Maroc 3: 645. 1934 = ***M. inodora*** (Desf.) Benth.

Note. – Maire as a rule did not accept *Micromeria* and described all of his respective new taxa under *Satureja*. Sennen transferred this taxon to *Micromeria,* but listed f. *erecta* Sennen as optional name, rendering his combination of var. *elata* invalid.

[*M. inodora* f. *erecta* Sennen in Diagn. Nouv.: 273. 1936, nom. inval.] – Based on the specimen: "Maroc: Beni-Sicar, coteaux sablonneux de Hidum" *Sennen & Mauricio*, *Sennen, Pl. Espagne 9940*. – ***M. inodora*** (Desf.) Benth.

Note. – Sennen listed f. *erecta* as optional name for *M. inodora* var. *elata,* rendering both names invalid (see also note above).

M. insularis Candargy in Bull. Soc. Bot. France 44: 149. 1897 ≡ ***Clinopodium insulare*** (Candargy) Govaerts, World Checklist Seed Pl. 3(1): 17. 1999.

M. japonica Miq. in Ann. Mus. Bot. Lugduno-Batavi 2: 106. 1865 ≡ ***Mentha japonica*** (Miq.) Makino in Bot. Mag. (Tokyo) 20: 1. 1906.

M. juliana (L.) Benth. ex Rchb., Fl. Germ. Excurs.: 311. 1831 & Benth., Labiat. Gen. Spec.: 373. 1834 ≡ *Satureja juliana* L., Sp. Pl. 2: 567. 1753. – Lectotype (designated by Siddiqi 1985: 108): Herb. Linnaeus No. 723.1 (LINN).

M. juliana f. *angustifolia* (Vis.) Šili6 in Glasn. Zemaljsk. Muz. Bosne Hercegovine Sarajevu. Prir. Nauke 13: 115. 1975 ≡ *M. juliana* subf. *angustifolia* (Vis.) Hayek, Prodr. Fl. Penins. Balcan. 2: 318. 1929 ≡ *M. juliana* var. *angustifolia* Vis. [Stirp. Dalm.: 46. 1826, nom. nud.] Fl. Dalm. 2: 196. 1847. – Syntypes: [Croatia] "In asperis siccis apricis in insulis Ossero et Lesina", *Visiani* (not traced, PAD?). = ***M. juliana*** (L.) Benth.

M. juliana f. *barbulata* (K. Malý) Šili6 in Glasn. Zemaljsk. Muz. Bosne Hercegovine Sarajevu. Prir. Nauke 13: 116. 1975 ≡ *Satureja juliana* var. *canescens* f. *barbulata* K. Malý in Bull. Inst.

Jard. Bot. Univ. Belgrade 1-3: 229. 1930. – Syntypes: [Serbia] "Šarplanina (Scardus): Globocicka Kamen", 8.1890, *Petrović* (BEOU), "Globočicka klisura", 6.1921, *Soška* (BEOU). = ***M. juliana*** (L.) Benth. ex Rchb.

M. juliana var. *canescens* (Guss.) Vandas, Rel. Form.: 484. 1909 ≡ *Satureja canescens* Guss., Pl. Rar.: 228, t. 42. 1826 =? ***M. graeca*** subsp. ***longiflora*** (C. Presl) Nyman.

Note. – Sili6 (1979) when citing this variety, included *M. obtusiflora* in synonymy. The latter today is regarded as synonym of *M. myrtifolia*, while *Satureja canescens* is included in the synonymy of *M. graeca* subsp. *longiflora* by Doroszenko (unpubl. Ph.D. thesis Univ. Edinburgh 1986); see note under *M. canescens*.

M. juliana var. *conferta* Coss. & Daveau in Bull. Soc. Bot. France 36: 105. 1889. – Type: [Libya] "In rupestribus prope Dernah ad 200 metr. florifera et fructifera", 7.1875, *Daveau* (not traced, MPU?) ≡ ***M. conferta*** (Coss. & Daveau) Stefani

Note. – The type of this variety apparently is not kept at P.

[*M. juliana* [unranked] *hellenica* Gand., Nov. Consp. Fl. Eur.: 367. 1910, nom. nud.] – ***M. juliana*** (L.) Benth. ex Rchb.

Note. – See note under *M. approximata* subsp. *barceloi.*

M. juliana var. *hirsuta* (C. Presl) Benth., Labiat. Gen. Spec.: 373. 1834, nom. illeg. ≡ *Satureja hirsuta* C. Presl in Presl & Presl, Del. Prag.: 79. 1822. – Type: [Italy, Sicily] (not traced, PR?). = *S. graeca* var. *canescens* Guss. in Fl. Sic. Prodr. 2: 114. 1828 = ***M. juliana*** (L.) Benth. ex Rchb.

Note. – Bentham's combination as a variety is illegitimate. *Satureja hirsuta* C. Presl has priority at species level but since *Satureja graeca* var. *canescens* Guss. is cited in synonymy this would have had priority at variety level.

M. juliana [unranked] *kerneri* (Murb.) Gand., Nov. Consp. Fl. Eur.: 367. 1910 = ***M. kerneri*** Murb.

Note. – See note under *M. approximata* subsp. *barceloi.*

M. juliana f. *latifolia* (Vis.) Šili6 in Glasn. Zemaljsk. Muz. Bosne Hercegovine Sarajevu. Prir. Nauke 13: 115. 1975 ≡ *M. juliana* subf. *latifolia* (Vis.) Hayek, Prodr. Penins. Balcan. 2: 318. 1929 ≡ *M. juliana* var. *latifolia* Vis., Fl. Dalm. 2: 196. 1847. – Syntypes: [Croatia] "In asperis siccis apricis totius Dalmatiae litoralis et insulari", *Visiani* (not traced, PAD?). = ***M. juliana*** (L.) Benth. ex Rchb.

M. juliana var. *minoa* (Coustur. & Gand.) Rech. f. in Oesterr. Bot. Z. 84: 177. 1935 ≡ *M. minoa* Coustur. & Gand. = ***M. myrtifolia*** Boiss. & Hohen.

M. juliana var. *myrtifolia* (Boiss. & Hohen.) Boiss., Fl. Orient. 4: 570. 1879 ≡ ***M. myrtifolia*** Boiss. & Hohen.

M. juliana var. *tenuifolia* (Ten.) Bornm. in Bot. Jahrb. Syst. 61, Beibl. 140: 73. 1927 ≡ *Satureja tenuifolia* Ten. ≡ ***M. graeca*** subsp. ***tenuifolia*** (Ten.) Nyman

Note. – Sili6 (1979) cites this variety in synonymy to *M. juliana* f. *angustifolia* stating that Bornmüller's use of the name is a misinterpretation of the cited basionym. However, Bornmüller's concept is of no relevance for the synonymy of this name.

M. juliana var. *velutina* Tocl & Rohlena in Sitzungsber. Königl. Böhm. Ges. Wiss. Prag, Math.-Naturwiss. Cl. 49: 5. 1902 ≡ *M. juliana* f. *velutina* (Tocl & Rohlena) Šilić, Monogr. Satureja Fl. Jugosl.: 234. 1979. – Holotype: [Greece] "Peninsula Athoa, circa monster. Chilandar", *Breuer* (not traced, PR?). = ***M. juliana*** (L.) Benth. ex Rchb.

M. julianoides Webb & Berthel., Hist. Nat. Iles Canaries 3: 78. 1845. – Syntypes: [Spain, Canary Islands] "In altis jugis Teneriffae Filo de las Canadas", *Barker-Webb* (FI), "In viam ad Tagananam", *Smith* (B†). = ***M. lachnophylla*** Webb & Berthel.

M. julianoides var. *palmensis* Bolle in Bonplandia (Hannover) 8: 283. 1860. – Holotype: [Spain, Canary Islands] "In summi jugi la Cumbre de la Palma rupibus crateri ingenti primaevo la Caldera supereminentibus" (B†); neotype (designated by Pérez 1978: 266): [Spain, Canary Islands] "Cumbre, Insel Palma, über der Caldera", 8,1852, *Bolle* (Z!). ≡ ***M. lasiophylla*** subsp. ***palmensis*** (Bolle) P. Pérez

M. kerneri Murb. in Acta Univ. Lund. 27(5): 53. 1892. – Holotype: [Bosnia and Hercegovina] "Auf Felsenterrassen im Flussbett der Narenta an der Franz Josephs Brücke in Mostar, c. 70 m" (not traced, LD?, putative isotype: B!, JE!, K!).

Note. – Some authors included this in synonymy to *M. juliana.* Judging from authentic material from the locus classicus, the two taxa in fact might be conspecific.

M. kosaninii Šilić, Monogr. Satureja Fl. Jugosl.: 234. 1979. – Holotype: [Macedonia] "Galičica, Pljce, cca 1600 ms.m, solo calcareo", 11.10.1970, *Šili6* (SARA; isotype: LJU). ≡ ***Micromeria cristata*** subsp. ***kosaninii*** (Čili6) Bräuchler & Govaerts

M. kosaninii subsp. *prilepensis* Micevski in Prilozi Oddel. Biol. Med. Nauki Makedonska Akad. Nauk. Umet. 23: 14. 2002. – Holotype: [Macedonia] "Prilep – ms. Kozjak, 1000-1500 m", 17.7.1984, *Micevski* (SKO). = ***Micromeria cristata*** subsp. ***kosaninii*** (Sili6) Bräuchler & Govaerts

M. kuegleri Bornm. in Repert. Spec. Nov. Regni Veg. 19: 197. 1924. – Holotype: [Spain, Canary Islands] "Teneriffa: In insulae meridionalis faucibus Barranco de Infierno prope Adeje", 13.5. 1895, *Kuegler* (B†); lectotype (designated here by Bräuchler): "Bco. Infierno", *Kuegler* (B). ≡ ***M. hyssopifolia*** var. ***kuegleri*** (Bornm.) P. Pérez

Note. – Pérez (1978: 215) believed all original material of this name destroyed in B during WW II and designated a neotype: Los Revueltos, Abona, Tenerife. Sobre cenizas pumiticas; frecuente, *P. Pérez 12* (TFC; isoneotypes: FI, K!, TFC, Z!). At JE duplicates of many *Micromeria* collections of Kuegler's 1895 Canary Island travel bearing original labels are present, but not for *M. kuegleri*. Duplicates of the Kuegler collections were purchased by Haussknecht, while the top set was probably kept at B, since Kuegler lived there. Also the type specimens of *M. kuegleri* were kept at B (according to the protologue) and sent to Bornmüller for determination (as was the case with all Canary Island collections by Kuegler; H. Manitz, pers. comm.). While the original specimen probably was destroyed with the general herbarium at B, a fragment of the holotype was preserved in Bornmüller's private collection, which was later acquired by B. The fragment is labelled as n.sp. in Bornmüller's handwriting, but only with an abridged citation of locality and collector without date. Given the presence of this original material the neotypification cannot persist. The Kuegler material at B is designated as lectotype. Given the fragmentary nature of the lectotype, Pérez's neotype could be designated as epitype, but this needs a more thorough revision.

M. lacaitae Lojac., Fl. Sicul. 2(2): 214. 1907. – Type: [Italy, Sicily] "Rupi basse colline sul calcareo, rarissima a Palermo a Chiaranda", June, *Lojacono-Pojero* (not traced). =? ***M. graeca*** subsp. ***graeca***

Note. – See note under *M. calaminthoides.*

M. lachnophylla Webb & Berthel., Hist. Nat. Iles Canaries 3: 73. 1845. – Lectotype (designated by Pérez 1978: 254): [Spain, Canary Islands] "In rupestribus elatis aridissimis ultra pagum Chasnam, non longe a monte Pico del Almendro dicto", *Barker-Webb* (FI).

M. lanata (C. Sm. ex Link) Benth., Labiat. Gen. Spec.: 374. 1834. – Holotype: [Spain, Canary Islands] *Chr. Smith* (B†); neotype (designated by P. Pérez 1978: 113): [Spain, Canary Islands] "In Covalle Tejeda jugisque montium vecinis Magna Canaria rupibus aridis", *Barker-Webb* (FI [lower right hand individual]).

Note. – On the page cited for this name, Bentham made new combinations under *Micromeria* for *Satureja lanata* Link and *S. tenuis* Link and cited Chr. Smith specimens seen at Lambert's herbarium as source for his taxonomic statement. On p. 731 however, he replaced the names *M. lanata*/*S. lanata* by *M. tenuis*/*S. tenuis* and vice versa. Apparently there has been a confusion of specimens which he discovered just after printing of the concerned chapter. His corrections on p. 731 simply are to be understood as advices for correct application of the names he generated on p. 374. However, the *Micromeria* names on p. 374, sometimes have been regarded erroneously as illegitimate (Pérez 1978; Govaerts & al. 2008). From a nomenclatural point Bentham's correction is irrelevant, since the fascicule containing p. 731 has been published in April 1835 while the one containing p. 374 was printed in May 1834 (Stafleu & Cowan 1976). The correct names read *M. lanata* (Chr. Sm. ex Link) Benth. and *M. tenuis* (Chr. Sm. ex Link) Benth. respectively. The typifications by Pérez (1978) remain unaffected because they are linked to the basionym not the combination. The situation is further blurred by the fact that Webb & Berthelot when newly describing *M. benthamii* included the names "*M. lanata* Benth., Lab., p. 374 non Chr. Smith" and "*M. tenuis* Benth., Lab. p. 731, non Link" in synonymy. At C the original set of Chr. Smith's collections is present including several specimens labelled with the name "*Satureja lanata*". Choice of a lectotype from this material could make the neotype designation superfluous. This requires, however, a thorough study of comprehensive herbarium material including the neotype which is beyond the focus of this study.

M. lanata (Chr. Sm. ex Link) Benth., Labiat. Gen. Spec.: 731. 1835, non Benth. 1834, nom. superfl.

Note. – See preceding entry.

M. lasiophylla Webb & Berthel., Hist. Nat. Iles Canaries 3: 74. 1845. – Lectotype (designated by P. Pérez 1978: 264): [Spain, Canary Islands] "In fissuris rupium deustorum jugi cyclici Teneriffae Filo de Las Canadas dicti ad pylas alpinas al Paso de Guadalajara", *Barker-Webb* (FI).

M. lasiophylla Webb & Berthel. subsp. ***lasiophylla***

M. lasiophylla subsp. ***palmensis*** (Bolle) P. Pérez, Rev. Gen. Micromeria Reg. Macarones.: 265. 1978 ≡ *M. julianoides* var. *palmensis* Bolle

M. lepida Webb & Berthel., Hist. Nat. Iles Canaries 3: 74. 1845. – Lectotype (designated by P. Pérez 1978: 152): [Spain, Canary Islands] "In rupibus praeruptis montium Gomerae", *Despréaux 316* (FI [left hand individual]).

M. lepida var. ***argagae*** P. Pérez, Rev. Gen. Micromeria Reg. Macarones.: 153. 1978. – Holotype: [Spain, Canary Islands] "Ex insula Junonia Minor (Insula Gomera dicta) in anfractu vulgo dicto "Barranco de Argaga" ad 200 m altitudinis", 4.5.1976, *Pérez 4* (TFC [herb. P. Pérez]; isotypes: FI, MA!, TFC 5551, Z!).

M. lepida subsp. ***bolleana*** P. Pérez, Rev. Gen. Micromeria Reg. Macarones.: 154. 1978. – Holotype: [Spain, Canary Islands] "In rupibus Barranco de la Laja, Gomerae", 9.1856, *Bolle* (B†); neotype (designated by Pérez 1978: 152): [Spain, Canary Islands] "Ex insula Junonia Minor (Insula Gomera dicta) in covallis dicto "Barranco de la Laja" versus 500 m", 6.1972, *Pérez 5* (TFC [herb. P. Pérez]). – *M. densiflora* sensu Bolle in Bonplandia 8: 283. 1860, non Benth. 1834

Note. – According to Pérez (1978), Bolle's (1860) description does not match the type of *M. densiflora* Benth. at K.

M. lepida var. ***fernandezii*** P. Pérez, Rev. Gen. Micromeria Reg. Macarones.: 158. 1978. – Holotype: [Spain, Canary Islands] "Ex insula Junonia Minor (Insula Gomera dicta) in rupium trachythicarum supra loco dicto 'Puntallana'", 20.7.1975, *Fernández* (ORT 6574; isotype: TFC).

M. lepida Webb & Berthel. subsp. ***lepida***

M. leucantha Svent. ex P. Pérez in Vieraea 5: 82. 1975. – Holotype: [Spain, Canary Islands] "In fissuris rupis regione SW Canaria Magna 200-800 m, c. San Nicolás de Tolentino", 28.7.1974, *Pérez* (TFC 1730; isotype: FI, MA!, O).

Note. – Pérez cites his own collection as lectotype, since he regarded a collection made and annotated by Sventenius ("*Micromeria leucantha* sp. nov") as syntype. However, he validly describing the species and citing a single type ("lectotype"), he automatically designated a holotype. The other collection cited is a paratype.

M. libanotica Boiss., Diagn. Pl. Orient., ser. 1, 12: 50. 1853 ≡ ***Clinopodium libanoticum*** (Boiss.) Kuntze, Revis. Gen. Pl. 2: 515. 1891.

M. linkii Webb & Berthel., Hist. Nat. Iles Canaries 3: 79. Apr 1845. – Lectotype (Pérez 1978: 138): [Spain, Canary Islands] "In rupibus iisdem prope oppidulum Guia insula Canaria, *M. buchii*", *P. Barker-Webb* (FI). ≡ ***M. tenuis*** subsp. ***linkii*** (Webb & Berthel.) P. Pérez

Note. – See note under *M. buchii*

M. longiflora Hochst. ex Baker in Dyer, Fl. Trop. Afr. 5: 453. 1900, nom. illeg. – Holotype: [Ethiopia] "In montibus pr. Dschadscha, 5700", 30.9.1854, *Hohenacker, Schimper, Pl. Abyss. Agow. 2192* (K!; isotypes: B!, BM-000797469!, GOET!, HEID!, Z!) = ***M. unguentaria*** Schweinf.

Note. – This name is illegitimate since the protologue includes *M. unguentaria* Schweinf. in synonymy. Triebel & Scholz (2008) do not list a standard abbreviation for the exsiccate-series the type is part of, thus it is proposed here ("Hohenacker, Schimper, Pl. Abyss. Agow.").

[*M. longiflora* (C. Presl) Nyman in Lojacono-Pojero, Fl. Sicul. 2(2): 211. 1907, pro syn.] – ***M. graeca*** subsp. ***tenuifolia*** (Ten.) Nyman.

M. longifolia Scheele in Linnaea 22: 593. 1849. – Type: [Croatia] "In ins. Lessina Dalmatiae", *Botteri* (not traced, it is not at B). = ***M. graeca*** subsp. ***tenuifolia*** (Ten.) Nyman.

Note. – This synonymy is given by Doroszenko (unpubl. Ph.D. thesis, Univ. Edinburgh 1986).

[*M. longifolia* Hochst. in Flora 39: 463. 1856, nom. nud., erroneous for *M. longiflora* Hochst.] – ***M. unguentaria*** Schweinf.

Note. – This name is listed in an enumeration of Schimper's collection distributed by Hohenacker ("Pl. abyssinicae e territoriae Agow") instead of *"M. longiflora"* as indicated on the labels of the corresponding specimens.

Micromeria longipedunculata Bräuchler, **nom. nov.** ≡ *M. parviflora* Rchb., Fl. Germ. Excurs.: 859. 1832, nom. illeg. ≡ *Satureja parviflora* Vis. in Flora 12, Ergänzungsbl. 1: 13. 1829, non C. Presl, Fl. Sicula: 36. 1826. – Holotype: [Montenegro] "In montibus Pastrovich in extremo Dalmatiae confinio prope Albaniam", August, *Visiani* (not traced, PAD?). = *Satureja inodora* Host, Fl. Austr. 2: 135. 1831 [non *M. inodora* (Desf.) Benth. 1834]. – Holotype: [Montenegro] "In Dalmatia in monte Pastrovich, aestate", *Tommasini* (W!).

Note. – *M. parviflora* is illegitimate even when considering Art. 58.1 of the ICBN (McNeill & al. 2006), since Reichenbach, when transferring Visiani's illegitimate *Satureja parviflora* to *Micromeria*, cited *Satureja inodora* Host 1831, a legitimate name, in synonymy (see also McNeill & al. 2006: Art. 53.1, Note 1 & Ex. 4). Both names, however, might be based on duplicates of the same Tommasini collection from Mt. Pastrovich, Montenegro. Though Visiani does not directly indicate Tommasini as collector, in the introduction of his treatment he referres to Tommasini as having contributed part of the material for the study. All later workers accepting this species under *Micromeria* referred to Reichenbach and Visiani repeating their errors. The name *M. inodora* since Bentham (1834) is occupied by a combination for *Thymus inodorus* Desf. As no published epithet is available, the new name *M. longipedunculata* Bräuchler is proposed here with respect to the species unique characteristic among its congeners, the very long-peduncled cymes.

M. lycia Stapf in Denkschr. Kaiserl. Akad. Wiss., Wien. Math.-Naturwiss. Kl. 50: 94. 1885. – Lectotype (designated here by Bräuchler): [Turkey, Antalya: Gölbaşi] "Piankaifa [?]", *Luschan* (WU!). = ***M. myrtifolia*** Boiss. & Hohen.

Note. – The specimen at WU is stored in a type folder, labelled "Lectotype, *Micromeria lycia* Stapf; = *M. graeca* (L.) Benth. ex Reichb. subsp. *lycia* (Stapf) Davis." and a determination slip with the same name by P. H. Davis written in 1979. The specimen is listed as examined syntype in Flora of Turkey (Davis 1982) under the synonymy to *M. myrtifolia*. The locality (except ?"Piankaifa") is not written on the specimen but taken from Davis (1982). The name *M. graeca* subsp. *lycia* was never published and the typification apparently never was made. Therefore the lectotype is formally designated here. The other syntype at WU ("Gölbaschi", 29.5.1882, *Luschan*") was labelled paratype and identified as *M. myrtifolia* Boiss. & Hohen. by Davis and has a duplicate.

M. macrosiphon Coss. in Bull. Soc. Bot. France 27: 72. 1880. – Lectotype (designated here by Bräuchler): [Morocco] "Maroc méridional, Gorge d'Amsemsey, vers b. cap Guir, N d'Agadir", 16.5.1877, *Cosson* (P-00446725*!; isolectotype: K!).

M. madagascariensis Baker in Journ. Bot. 20: 244. 1882.
Note. – See note under *M. flagellaris* Baker.

[*M. malcolmiana* Benth. in Hooker f., Fl. Brit. India 4: 650. 1885, pro syn.] – ***Clinopodium capitellatum*** (Benth.) Kuntze, Revis. Gen. Pl. 2: 515. 1891.

M. marginata (Sm.) Chater in Bot. J. Linn. Soc. 64: 381. 1971 ≡ *Thymus marginatus* Sm. in Dickson, Coll. Dried Pl. fasc. 3: t. 71. 1791. – Lectotype (designated here by R. Harley): Unlocalized and distributed in cited volume (K; isolectotype: BM).

Note. – When citing the type from a volume at the K library, Harley & Hall (2001) did not conform to Art. 7.11 (McNeill & al. 2006). Starting from 1.1.2001 the code requires an explicit statement "designated here/hic designatus" or equivalent in the typification. Therefore the lectotype is formally designated here by R. Harley.

M. marifolia (Cav.) Benth., Labiat. Gen. Spec.: 382. 1834 ≡ *Nepeta marifolia* Cav. in Anales Hist. Nat. 2(2): 192. 1800 = ***Clinopodium serpyllifolium*** subsp. ***fruticosum*** (L.) Bräuchler in Taxon 55: 980. 2006.

M. marifolia var. *italica* Huter, Herb.-Stud. 22: 402. 1907 = ***Clinopodium serpyllifolium*** subsp. ***fruticosum*** (L.) Bräuchler in Taxon 55: 980. 2006.

M. maritima Yıldırımlı, Sadıkoğlu & Keskin in Ot Sist. Bot. Dergisi 13(1): 29. 2006. – Holotype: "Turkey. C2 Muğla: Marmaris, Turunç köyü, maquis vegetation, near coast, c. 5 m", 23.7.1983, *Yildirimli 5647* (herb. Yildirimli; isotype: GAZI) =? ***Mentha*** sp.

Note. – The type of this species seems to lack not only leaves and corollas but also bracteoles, a characteristic feature for *Micromeria* as circumscribed here. The species is to be excluded from *Micromeria* and in our opinion should not have been described given the poor material it is based on. The characters come closest to those of *Mentha* species.

[*M. melitensis* Tin. in L. Chodat in Bull. Soc. Bot. Geneve, ser. 2, 15: 245. 1924, pro syn.] – ***M. microphylla*** (d'Urv.) Benth.

M. microcalyx Peyr. in Sitzungsber. Kaiserl. Akad. Wiss., Math.-Naturwiss. Cl., Abt. 1, 66: 155 & t. 2, fig. 1-4. 1872 = ***Clinopodium serpyllifolium*** (M. Bieb.) Kuntze s.l.

Note. – Peyritsch unintentionally described this species in an article dealing with floral abnormities ("Über Pelorienbildung") based on a plant raised at the Botanical Garden Vienna from seeds sent by Kotschy. Along with a drawing of a flowering shoot he provided flower details, thus establishing an illustration with analysis (McNeill & al. 2006: Art. 42.4). Additionally a cryptic diagnosis is provided: "Die zygomorphen Blüthen von *Micromeria microcalyx* waren mit kleinen atrophischen Staubgefässen versehen". The synonymy provided here is provisionally until the revision of the *Clinopodium serpyllifolium* group is completed.

M. microphylla (d'Urv.) Benth., Labiat. Gen. Spec.: 377. 1834 ≡ *Thymus microphyllus* d'Urv. in Mem. Soc. Linn. Paris 1: 327. 1822. – Lectotype (designated here by Bräuchler): [Malta] "Malte", *d'Urville* (P [labelled *"Thymus melitensis"* by d'Urville]!).

Note. – Meikle (1985) cites the type from P as unseen: "In collibus aridis insulae Melitae copiosissime" which is merely a citation from the protologue. Dumont D'Urville however cites two collections (which are regarded to be syntypes) from the herbaria of Tournefort and Vaillant

(“Calamintha minima, annua, thymi-folia Herb. Tourn., Herb. Vaill.”). Additionally the title of the whole article indicates a collection made by the author as further syntype (“Enumeratio Plantarum quas in insulis Archipelagi aut littoribus Ponti-Euxini, annis 1819 et 1820, collegit atque detexit J. Dumont d’Urville”). At P a D’Urville specimen of *M. microphylla* from Malta could be traced, which has been collected on a stop en route to the main collection area (Black Sea region). This specimen is labelled by D’Urville as *Thymus melitensis,* a name never published but listed in synonymy to *Satureja microphylla* by Gussone (1844). However this specimen contains a printed label “Herbier de l’Archipel et des côtes de la Mer-noire donné par M. Dumont d’Urville“ bearing the name “*M. microphylla* Benth.“ in Bentham’s handwriting, thus representing one of the specimens cited by Bentham (1834). This one specimen without doubt is part of the original material of *Thymus microphyllus* d’Urv. and is therefore chosen as lectotype.

M. microphylla var. *glabriuscula* Benth., Labiat. Gen. Spec.: 377. 1834. – Type: not designated. = ***M. microphylla*** (d’Urv.) Benth.

[*M. microphylla* var. *gussonei* Lojac. in L. Chodat in Bull. Soc. Bot. Geneve, ser. 2, 15: 245. 1924, pro syn.] – ***M. microphylla*** (d’Urv.) Benth.

M. microphylla var. *imbricata* Balf. f. in Transact. Roy. Soc. Edinburgh 31 [Botany of Socotra]: 241. 1888. – Lectotype (designated by Ryding 2007: 435): [Yemen] “Socotra, Ostseite von Wadi Digal”, *Schweinfurth 600* (K!); isolectotypes: P!, WU!). = ***M. imbricata*** (Forssk.) C. Chr. var. ***imbricata***

Note. – The P specimen is mounted on one sheet together with *Schweinfurth 529* (isolectotype of var. *remota,* see following entry); both isolectotypes are labelled “Granitfelsen oberstes Wadi Dilal”, 30.4.1881.

M. microphylla var. *remota* Balf. f. in Transact. Roy. Soc. Edinburgh 31 [Botany of Socotra]: Bot. Socotra: 241. 1888 ≡ *Satureja remota* (Balf. f.) Vierhapper in Denkschr. Kaiserl. Akad. Wiss. Wien, Math.-Naturwiss. Kl. 71: 437 [Beitr. Fl. Südarab. Sokotra: 117]. 1907. – Lectotype (designated by Ryding 2007: 435): [Yemen] Socotra, *Schweinfurth 529* (K!; isolectotypes: P!, W!, WU!). = ***M. imbricata*** var. ***imbricata***

M. microphylla subsp. *rodriguezii* (Freyn & Janka) A. M. Romo, Fl. Sylvestres Baleares: 261. 1994 ≡ *M. rodriguezii* Freyn & Janka ≡ ***M. filiformis*** subsp. ***rodriguezii*** (Freyn & Janka) Bonafè

M. microphylla [unranked] *sphaciotica* (Boiss. & Heldr. ex Benth.) Gand., Nov. Consp. Fl. Eur.: 367. 1910 ≡ *M. sphaciotica* Boiss. & Heldr. ex Benth. = ***M. microphylla*** (d’Urv.) Benth.

Note. – See notes under *M. approximata* subsp. *barceloi, M. carpatha* and *M. hispida.*

[*M. microphylla* var. *villosa* Benth., Labiat. Gen. Spec.: 377. 1834, nom. inval.] ≡ ***M. microphylla*** (d’Urv.) Benth.

Note. – When describing “var. *villosa*”, Bentham included *Thymus microphyllus* in synonymy to this variety of his *M. microphylla*. Since the former is basionym to the latter, “*villosa*” represents the typical variety and must not be named other than var. *microphylla*.

M. minoa Coustur. & Gand. ex Gand., Fl. Cret.: 80. Dec 1916 & Coustur. & Gand. in Bull. Soc. Bot. France 63: 14. 1917. – Syntypes: [various syntypes cited from Greece] *Gandoger 3503, 3739, 4606, 5760, 7436, 7648, 7950, 8468, 8554, 11099, 11768* (LY). = ***M. myrtifolia*** Boiss. & Hohen.

Note. – This name was intended to be published prior to Fl. Cret. in Bull. Soc. Bot. France 63. Publication of that volume, however, was delayed to 1917, so the names in Gandoger’s Flora Cretica, according to Stafleu & Cowan (1976) published in late 1916, have priority.

[*M. minoa* f. *strigoso-villosa* Gand., Fl. Cret.: 80, Dec. 1916, nom. nud. based on *Gandoger* no. *2166, 2325, 2427, 2712, 5213, 5453, 5879, 6604, 12046, 12207, 12386, 12957*] – ***M. myrtifolia*** Boiss. & Hohen.

M. mollis Benth. in Candolle, Prodr. 12: 225. 1848 ≡ ***Clinopodium molle*** (Benth.) Kuntze, Revis. Gen. Pl. 2: 515. 1891.

M. monantha (Font Quer) R. Morales in Anales Jard. Bot. Madrid 48: 154. 1991 ≡ *Satureja monantha* Font Quer in Mem. Real Acad. Ci. Barcelona 25: 351. 1936. – Type: "In rupibus arenaceis vallis fl. Uad Sidi Ifni, c. 10-30 m", 4.1835 [*Font Quer*] (fragment of holotype BC!).

Note. – At BC, two fragments are mounted on one sheet with two labels indicating them as different collections: "In rupibus arenaceis vallis fl. Nad Sidi Ifni, 10-30 m", 9.4.1935, *Font y Quer* [indicated as "Typus" but the whole label crossed out]; "Maroc: rochers arides de la vallée de l'Oued Noun", 7.1936, *Ollivier.* There is, however, no clear indication which label applies to which fragment. Given the citation of a rich and flowering type in the protologue, the material traced could only represent a fragment of the original type, which was not found at BC. Judging from the fragments, the plant seems correctly placed in *Micromeria* but is unusual compared to its congeners in the Mediterranean.

M. montana (L.) Rchb., Fl. Germ. Excurs.: 311. 1831 ≡ ***Satureja montana*** L., Sp. Pl. 2: 568. 1753.

M. mutabilis (Epling) R. Morales in Bot. Complut. 18: 164. 1993 ≡ *Satureja mutabilis* Epling in Repert. Spec. Nov. Regni Veg. Beih. 85: 157. 1936 ≡ ***Clinopodium mutabile*** (Epling) Harley in Jorgensen & León Yánez, Cat. Vasc. Pl. Ecuad.: 954. 1999.

M. myrtifolia Boiss. & Hohen. in sched. Hohenacker, Kotschy Pl. Alepp. Kurd. Moss.: 305. 1843 & in Boissier, Diagn. Pl. Orient., ser. 1, 5: 19. 1844. – Holotype: [Iraq] "In rupestribus umbrosis ad aquaeductus pr. pagum Gara Kurdist.", 24.7.1841, *Hohenacker, Kotschy Pl. Alepp. Kurd. Moss. 305* (G?; isotypes: GOET!, K-000193718/19!, TCD!, W!).

Note. – This species was part of an exsiccate edited and distributed by Hohenacker in 1843. The labels of this series are printed and, as is the case here, partially include Latin diagnoses for the accompanying plants, constituting effective and valid publication (McNeill & al. 2006: Art. 30.4, Ex. 4).

[*M. myrtifolia* f. *albiflora* H. Lindb., Iter Cypr.: 29. 1946, nom. nud.] – ***M. myrtifolia*** Boiss. & Hohen.

M. nepalensis Kitam. & Murata in Acta Phytotax. Geobot. 16: 3. 1955 ≡ ***Clinopodium nepalense*** (Kitam. & Murata) Bräuchler & Heubl in Taxon 55: 979. 2006.

M. nervosa (Desf.) Benth., Labiat. Gen. Spec.: 376. 1834 ≡ *Satureja nervosa* Desf., Fl. Atl. 2: 9. 1798. – Lectotype (designated by Morales 1991: 147): [Algeria?] "In fissuris rupium Atlantis", *Desfontaines s.n.* (P).

[*M. nervosa* [unranked] *cretensis* Gand., Nov. Consp. Fl. Eur.: 367. 1910, nom. nud.] – ***M. nervosa*** (Desf.) Benth.

Note. – See note under *M. approximata* subsp. *barceloi.*

M. nervosa var. *plumosa* (Hampe) Nyman, Consp. Fl. Eur.: 590. 1881 ≡ *Satureja plumosa* Hampe in Flora 25, Beibl. 1: 127. 1842. – Type: [Greece] "Attica", *Spruner* (not traced, ATH?). = ***M. nervosa*** (Desf.) Benth.

Note. – This species has been described based on material distributed by Spruner in 1840 under the name *Thymus mastichina*.

M. nervosa subsp. *rodriguezii* (Freyn & Janka) Nyman, Consp. Fl. Eur.: 590. 1881 ≡ *M. rodriguezii* Freyn & Janka ≡ ***M. filiformis*** subsp. ***rodriguezii*** (Freyn & Janka) Bonafè

[*M. nervosa* [unranked] *rodriguezii* (Freyn & Janka) Gand., Nov. Consp. Fl. Eur.: 367. 1910 ≡ ***M. filiformis*** subsp. ***rodriguezii*** (Freyn & Janka) Bonafè

Note. – See note under *M. approximata* subsp. *barceloi.*

[*M. neumannii* Gürke vel O. Hoffm. in Engler in Sitzungsber. Preuss. Akad. Wiss. 40: 744. 1906, nom. nud.] – ***M. imbricata*** (Forssk.) C. Chr.

M. notarisii Gand., Nov. Consp. Fl. Eur.: 367. 1910, nom. superfl. ≡ *Thymus notarisii* Zumagl., Fl. Pedem. 1: 226. 1849, nom. superfl. ≡ *Micromeria thymoides* De Not. 1844 [& 1846], non (Sol. ex Lowe) Webb & Berthel. Dec 1844 ≡ *M. graeca* subsp. *imperica* Chater = ***M. graeca*** (L.) Benth. ex Rchb. subsp. ***graeca***

Note. – See *M. thymoides* De Not. for further details. Gandoger lists this at the rank of species as nom. nov. for *M. thymoides* De Not., non Webb. & Berthel., without any reference to Zumaglini. *Thymus notarisii* Zumagl., however, he lists as basionym to an unranked infraspecific combination under *M. graeca*. Both alternative names, since published prior to 1.1.1953, are to be regarded as validly published (McNeill & al. 2006: Art. 34.2), but superfluous.

M. nubigena (Kunth) Benth., Labiat. Gen. Spec.: 381. 1834 ≡ *Thymus nubigenus* Kunth in Humboldt & al., Nov. Gen. Sp. Pl. 2: 313. 1818 ≡ ***Clinopodium nubigenum*** (Kunth) Kuntze, Revis. Gen. Pl. 2: 515. 1891.

M. nubigena var. *angustifolia* Wedd., Chlor. Andina 2: 150. 1860 = ***Clinopodium nubigenum*** (Kunth) Kuntze, Revis. Gen. Pl. 2: 515. 1891.

M. nubigena var. *cordifolia* Wedd., Chlor. Andina 2: 150. 1860 = ***Clinopodium nubigenum*** (Kunth) Kuntze, Revis. Gen. Pl. 2: 515. 1891.

M. nubigena var. *glabrescens* Benth. in Candolle, Prodr. 12: 222. 1848 ≡ *M. nubigena* subvar. *glabrescens* (Benth.) Wedd., Chlor. Andina 2: 150. 1860 = ***Clinopodium nubigenum*** (Kunth) Kuntze, Revis. Gen. Pl. 2: 515. 1891.

M. nummulariifolia Boiss., Diagn. Pl. Orient., ser. 1, 12: 50. 1853 ≡ ***Clinopodium nummulariifolium*** (Boiss.) Kuntze, Revis. Gen. Pl. 2: 515. 1891.

[*M. nuttallii* Torr. & A. Gray in Candolle, Prodr. 12: 230. 1848, pro syn.] – ***Clinopodium glabrum*** (Nutt.) Kuntze, Revis. Gen. Pl. 2: 515. 1891.

M. obovata (Willd.) Benth., Labiat. Gen. Spec.: 381. 1834 ≡ *Xenopoma obovatum* Willd. in Mag. Neuesten Entdeck. Gesammten Naturk. Ges. Naturf. Freunde Berlin 5: 399. 1811 = ***Clinopodium vimineum*** (L.) Kuntze, Revis. Gen. Pl. 2: 516. 1891.

M. obtusiflora Gand., Fl. Cret.: 80. 1916. – Holotype: [Greece, Crete] "Creta austro-orient., Prov. Hierapetra in saxosis ad H. Joannis", *Gandoger 5764* (LY). = ***M. myrtifolia*** Boiss. & Hohen.

M. odora (Griseb.) Hieronym. in Bot. Acad. Nac. Cordoba 4: 413. 1881 ≡ *Xenopoma odora* Griseb. in Abh. Königl. Ges. Wiss. Göttingen 19: 236. 1874 ≡ ***Clinopodium odorum*** (Griseb.) Harley in Kew Bull. 55: 923. 2000.

M. origanifolia (Labill.) Benth. in Candolle, Prodr. 12: 214. 1848 ≡ *Clinopodium origanifolium* Labill., Icon. Pl. Syr. 1: 14. 1791 ≡ ***Cyclotrichium origanifolium*** (Labill.) Manden. & Scheng. in Bot. Mater. Gerb. Bot. Inst. Komarova Akad. Nauk SSSR 15: 337. 1953.

M. origanifolia (Vis.) Boiss., Fl. Orient. 4: 575. 1879, non (Labill.) Benth. 1848 ≡ *Thymus origanifolius* Vis. in Flora 13: 51. 1830 = ***Clinopodium dalmaticum*** (Benth.) Bräuchler & Heubl in Taxon 55: 979. 2006.

Note. – See note under *M. balcanica.*

M. origanifolia subsp. *bulgarica* Velen. in Oesterr. Bot. Z. 49: 292. 1899 ≡ ***Clinopodium dalmaticum*** (Benth.) Bräuchler & Heubl in Taxon 55: 979. 2006.

Note. – See note under *M. balcanica.*

M. ovata Benth., Labiat. Gen. Spec.: 377. 1834. – Holotype: [Eritrea or N Ethiopia], *Salt s.n.* (BM!). = ***M. imbricata*** (Forssk.) C. Chr. var. ***imbricata.***

[*M. ovata* Beck. in Hooker, Fl. Brit. India 4: 650. 1885, pro syn.] – ***M. biflora*** (Buch.-Ham. ex D. Don) Benth.

M. ovata var. *cinereotomentosa* A. Rich., Tent. Fl. Abyss. 2: 189. 1850. – Type: [Ethiopia] "Tchélikote" [collector not cited; *A. Petit* or *Quartin Dillon?*] (P; isotype: W!) = ***M. imbricata*** (Forssk.) C. Chr. var. ***imbricata***

Note. – This variety is described in a footnote of the cited page indicating it as collected in Tchélikote province. The cited Quartin Dillon and the Schimper collection are referred to as *M. ovata* var. *ovata*. Citation of the latter two as types resulted from the cryptic indication of the type of var. *cinereotomentosa*. At least one known collection from Tchélikote province was made by A. Petit (type of *Solanum grossidentatum* A. Rich., Tent. Fl. Abyss. 2: 101. 1850).

M. palmensis (Bolle) Lid in Skr. Norske Vidensk.-Akad. Oslo, Mat.-Naturvidensk. Kl., ser. 2, 23: 152. 1968 ≡ *M. julianoides* var. *palmensis* Bolle ≡ ***M. lasiophylla*** subsp. ***palmensis*** (Bolle) P. Pérez

M. parviflora Rchb., Fl. Germ. Excurs.: 859. 1832, nom. illeg. ≡ *Satureja parviflora* Vis. 1829, non C. Presl 1826 ≡ ***M. longipedunculata*** Bräuchler = *Satureja inodora* Host 1831, non *M. inodora* (Desf.) Benth. 1834.

Note. – See note under *M. longipedunculata*.

M. parviflora f. *effusa* Rohlena ex Sili6, Monogr. Satureja Fl. Jugosl.: 262. 1979, nom. illeg. – Holotype: [Serbia] "Podgorica", 6.1900, *Rohlena* (PRC). = ***M. longipedunculata*** Bräuchler

M. parviflora f. *monantha* Latzel ex Sili6, Monogr. Satureja Fl. Jugosl.: 262. 1979, nom. illeg. – Holotype: [Bosnia and Hercegovina] "Bijela Gora, in rupibus calcareis, 370 m", 25.6.1911, *Latzel* (SARA). = ***M. longipedunculata*** Bräuchler

M. parviflora f. *multiantha* Sili6 in Glasn. Zemaljsk. Muz. Bosne Hercegovine Sarajevu. Prir. Nauke 13: 118. 1975, nom. illeg. – Holotype: [Montenegro] "In rupestribus ad Bukovica pr. Cetinje", 8.1931, *Pejovi6* (PR). = ***M. longipedunculata*** Bräuchler

M. parviflora f. *rubrotincta* Sili6 in Glasn. Zemaljsk. Muz. Bosne Hercegovine Sarajevu. Prir. Nauke 13: 118. 1975, nom. illeg. – Holotype: [Montenegro], "Lov6en, Ivanova Korita s. Bjeloši, in rupibus calcareis", 25.8.1968, *Sili6* (SARA). = ***M. longipedunculata*** Bräuchler

M. parvula Chiov., Racc. Bot.: 103. 1935 = ***Clinopodium abyssinicum*** (Hochst. ex Benth.) Kuntze, Revis. Gen. Pl. 2: 515. 1891.

M. peltieri (Maire) R. Morales in Anales Jard. Bot. Madrid 48: 154. 1991 ≡ *Satureja peltieri* Maire in Bull. Soc. Hist. Nat. Afrique N. 20: 34. 1929. – Holotype: [Morocco] "Boujad, rocailles calcaires", 17.4.1927, *Peltier* (MPU-004297*!).

M. perezii Bolle in Bonplandia (Hannover) 8: 282. 1860. – Holotype: [Spain, Canary Islands] "In Caldera ins. Palmae", September, *Bolle* (B†). = ***M. herpyllomorpha*** Webb & Berthel.

M. perforata Miq. in Ann. Mus. Bot. Lugd. Bat. 2: 106. 1865 = ***Mosla japonica*** (Benth.) Maxim. in Bull. Acad. Imp. Sci. Saint-Pétersbourg 20: 461. 1875.

M. perrottetii Gand. in Bull. Soc. Bot. France 65: 67. 1918. – Holotype: "India orient., in montibus Nilagiri", *Perrottet 938* (not traced, LY?). = ***M. biflora*** (Buch.-Ham. ex D. Don) Benth.

M. persica Boiss., Diagn. Pl. Orient., ser. 1, 7: 48. 1846. – Lectotype (designated here by Bräuchler): [Iran] "Th. Kotschy, Pl. pers. austr., Ed. R.F. Hohenacker 1845, Prope ruinas u. Persepolis, pr. monumentum Nakschi Rustam", 4.1842, *Kotschy, Pl. Pers. Austr. 882* (G-BOIS: G-00150059!; isolectotypes: K!, W!).

Note. – The second syntype cited is *Aucher-Eloy 5190* (G, P!). The labels indicate the lectotype and its duplicates as forming part of Kotschy's "Plantae Persiae australis". The standard abbreviation for this series would be "Hohenacker, Kotschy Pl. Pers. Austr.". According to Triebel & Scholz (2008) only c. 600 numbers were issued by Hohenacker. Judging from the high number and the handwritten labels on all types seen (instead of printed ones for the Hohenacker series) this collection has not been edited as part of the latter exsiccate.

M. pilosa Benth. in Bentham & Hooker, Gen. Pl. 2: 1188. 1876 = ***Killickia pilosa*** (Benth.) Bräuchler, Doroszenko & Heubl in Bot. J. Linn. Soc. 157: 577. 2008.
Note. – See note under *M. compacta.*

M. pilosiuscula (A. Gray) Small, Fl. S.E. U.S.: 1042. 1903 ≡ *M. brownei* var. *pilosiuscula* A. Gray = ***Clinopodium brownei*** (Sw.) Kuntze, Revis. Gen. Pl. 2: 514. 1891.

M. pineolens Svent., Addit. Fl. Canar. 1: 55. 1960. – Lectotype (designated by Pérez 1978: 274): [Spain, Canary Islands] "Tamadaba", 21.4.1958, *Sventenius* (ORT 6504).
Note. – Sventenius. cites three collections, none of them collected in 1958: Gran Canaria, In montibus Goyedrae, 25.9.1948 (ORT 6500); Gran Canaria, Tamadaba, In pineto, 19.7.1949; Gran Canaria, Tamadaba, In pineto 19.9.1951. Pérez (1978) states his lectotype to be labelled "*Micromeria pineolens* Svent., Original: Tamadaba 21.4.1958". However, this specimen includes in a small celophane capsule the dissected flower and calyx that served the author for the illustration accompanying the species description (drawn in 1958 by Sventenius himself) and therefore unambiguously represents original material.

M. piperella Benth., Labiat. Gen. Spec.: 379. 1834, nom. illeg. ≡ *Thymus piperella* All., Fl. Pedem. 1: 21, t. 37, fig. 3. 1785, non L., Sp. Pl. 2:. 1753. – Syntypes: [Italy, Piemonte] "In alpibus maritimis ad rupes ubique, uti illis, quae pertinent ad Monregalensem Provinciam, atque ad oppida di Garressio, Carlin, la Briga etc." (TO?). = ***M. marginata*** (Sm.) Chater
Note. – *M. piperella* is illegitimate even when considering Art. 58.1 (McNeill & al. 2006), since Bentham (1834), when transferring Allioni's *Thymus piperella* to *Micromeria*, cited *Thymus marginatus* Sm., a legitimate name, in synonymy (see also McNeill & al. 2006: Art. 53.1, Note 1 & Ex. 4). The illustration (t. 37, fig. 3) in Allioni clearly identifies his *Thymus piperella* as conspecific with *M. marginata*.

[*M. piperella* Panči6 in Nyman in Consp. Fl. Eur.: 591. 1881, pro syn.] – ***M. croatica*** (Pers.) Schott

M. piperella var. *croatica* (Pers.) Benth. in Candolle, Prodr. 12: 221. 1848, nom. illeg. ≡ *Thymus croaticus* Pers., Syn. Pl. 2: 130. 1806 ≡ ***M. croatica*** (Pers.) Schott
Note. – See *M. piperella.*

M. pitardii Bornm. in Repert. Spec. Nov. Regni Veg. 6: 1. 1908. – Holotype: [Spain, Canary Islands] "Gomera: Roque de Valle Hermoso, ad rupes, 600 m", 6.1905, *Pitard 1473* (B†?; isotypes: JE!, P-00446723*!; Z!). = ***M. lepida*** Webb & Berthel.

M. plumosa (Hampe) Gand., Nov. Consp. Fl. Eur.: 367. 1910 ≡ *Satureja plumosa* Hampe = ***M. nervosa*** (Desf.) Benth.
Note. – See also *M. nervosa* var. *plumosa*

M. polioides Webb & Berthel., Hist. Nat. Iles Canaries 3: 76. 1845. – Type: [Spain, Canary Islands] "Insula Canaria", *Despréaux* (not traced, FI?). = ***M. tenuis*** (Link) Benth. subsp. ***tenuis***

M. popovii (B. Fedtsch. & Gontsch.) Vved., Fl. Uzbekist. 5: 404. 1961 ≡ *Satureja popovii* B. Fedtsch. & Gontsch. in Acta Hort. Petrop. 41: 117. 1929 ≡ ***Gontscharovia popovii*** (B. Fedtsch. & Gontsch.) Boriss. in Bot. Mater. Gerb. Bot. Inst. Komarova Akad. Nauk SSSR. 15: 321. 1953.

M. preauxii Webb & Berthel., Hist. Nat. Iles Canaries 3: 75. 1845. – Lectotype (designated by Pérez 1978: 128): [Spain, Canary Islands] "Rochers de Goyavrae", 5.1930, *Despréaux 30* (FI [lower left hand individual]). ≡ ***M. ×preauxii*** Webb & Berthel.

Note. – Described as species, as hybrid established by Pérez (1978: 127).

M. pseudocroatica Sili6, Monogr. Satureja Fl. Jugosl.: 248. 1979. – Holotype: [Croatia] "Dalmatia, Peninsula Pelješac, supra pagum Pijavičino, s. calc., expos. merid., c. 200 m", 10.10.1975, *Sili6* (SARA; isotype: LJU). = ***M. croatica*** (Pers.) Schott.

Note. – At BP a specimen collected by Sili6 on the same day and at the same locality is present but indicated to grow on "solo dolomit., S-exp."

[*M. pubescens* Boiss. & Kotschy in Boissier, Fl. Orient. 4: 571. 1879, pro syn.] – *M. elliptica* var. *pubescens* Boiss. = ***M. cristata*** subsp. ***orientalis*** P. H. Davis

M. pulchella (Clos) Wedd., Chlor. Andina 2: 151. 1860 ≡ *Soliera pulchella* Clos in C. Gay, Fl. Chil. 4: 489, t. 53. 1849 ≡ ***Kurzamra pulchella*** (Clos) Kuntze, Revis. Gen. Pl. 2: 521. 1891.

M. pulegium (Rochel) Benth., Labiat. Gen. Spec.: 382. 1834, nom. illeg. ≡ *Melissa pulegium* Rochel in Pl. Banat. Rar. 62. 1828 ≡ ***Clinopodium pulegium*** (Rochel) Bräuchler in Taxon 55: 979. 2006.

Note. – When making his combination under *Micromeria* for *Melissa pulegium* Rochel, Bentham included the older valid name *Melissa subnuda* Waldst. & Kit. at variety level, rendering his combination illegitimate. To our knowledge, no legitimate combination under *Micromeria* has been made so far, all later works cite Bentham and thus repeat his error. The two taxa with respect to the types (*Melissa pulegium* Rochel, lectotype M! and *Melissa subnuda* Waldst. & Kit., holotype BP!) represent different species.

M. pulegium var. *subnuda* (Waldst. & Kit.) Benth. in Candolle, Prodr. 12: 224. 1848, nom. illeg. = *Melissa subnuda* Waldst. & Kit., Descr. Icon. Pl. Hung. 3: 291 & t. 262. 1812 = ***Clinopodium nepeta*** nothosubsp. ***subisidoratum*** (Borbás) Govaerts, World Checklist Seed Pl. 3(1): 18. 1999.

M. punctata Benth., Labiat. Gen. Spec.: 378. 1834. – Holotype: [Eritrea or N Ethiopia], *Salt s.n.* (BM!; photo of holotype in Seybold 1988: 27) = ***M. imbricata*** (Forssk.) C. Chr. var. ***imbricata***

[*M. punctata* var. *angustifolia* Vatke in Linnaea 43: 93. 1881, nom. nud.] – ***M. imbricata*** (Forssk.) C. Chr. var. ***imbricata***

M. purpurea (Kellogg) A. Gray, Bot. California 1: 595. 1876 ≡ *Hedeoma purpurea* Kellogg in Proc. Calif. Acad. Sci. 5: 52. 1873 = ***Mentha canadensis*** L., Sp. Pl. 2: 577. 1753.

Note. – Kellogg was in doubt about the proper generic placement of this species. Affinities to *Pogogyne* were mentioned. Gray when transferring it to *Micromeria* states it to be "in no respect a *Hedeoma*". Greene (1893) identified it as *Mentha pulegium* L., launching an attack on both forementioned workers. This in turn was corrected by Brandagee (1893) later that year, who defended Gray and placed the taxon in synonymy to *Mentha canadensis* L. This finding obviously has been overlooked by later workers (e.g., Epling & Stewart 1939) until today.

M. purtschelleri Gürke in Engler, Hochgebirgsfl. Afrika: 365. 1892. – Holotype: [Tanzania, Moshi District] "Kilimandscharo, am Muëbach", *Meyer 244* (B†). = ***M. imbricata*** (Forssk.) C. Chr. var. ***imbricata***

M. pusilla Phil. in Anales Univ. Chile 90: 556. 1890 [as *"pasilla"*] = ***Clinopodium darwinii*** (Benth.) Kuntze

M. pygmaea Rchb., Fl. Germ. Excurs.: 311. 1831 = ***Satureja subspicata*** Bartl. ex Vis., Stirp. Dalmat. Spec. 2: t. 4. 1826.

M. quartiniana A. Rich., Tent. Fl. Abyss. 2: 190. 1850. – Holotype: [Ethiopia, Tigray region] "Crescit in montosis lapidosis prope Dobra-Sina" [Durasina], 9.8.1839, *Quartin-Dillon* (P!). = ***M. imbricata*** (Forssk.) C. Chr. var. ***imbricata***

"*M. reinholdii* Heldr. in Boissier, Fl. Orient. 4: 570. 1879, pro syn.] – ***M. myrtifolia*** Boiss. & Hohen.

[“*M. remota* (Balf. f.) Vierh.” [actually as *Satureja remota*] in Denkschr. Kaiserl. Akad. Wiss. Wien, Math.-Naturwiss. Kl. 71: 437 [Beitr. Fl. Südarab. Sokotra: 117]. 1907] = ***M. imbricata*** (Forssk.) C. Chr. var. ***imbricata***

Note. – This erroneous citation of *Satureja remota* as *Micromeria remota* goes to back to Walther & Walther (1957: 7). The unintentional combination by these authors in *Micromeria* is, however, not valid, because no direct reference to the protologue of the basionym as required by Art. 33.4 since 1953 (McNeill & al. 2006) was given. Another erroneous variant (“*Micromeria remota* Balf. f.”, nomenclaturally likewise irrelevant) was published by Miller & Morris (2004: 582).

M. repens Hook. f. in London J. Bot. 6: 274. 1847 = ***Mentha diemenica*** Spreng., Syst. Veg. 2: 724. 1825.

M. rivas-martinezii Wildpret in Vieraea 3: 72. 1974. – Holotype: [Spain, Canary Islands] “In fissuris rupium loco vulgo dicto – Roque de Juan Bay – insula Nivaria, Tenerife dicta”, 7.4.1973, *Wildpret* (TFC 1708; isotype: MAF 85542, herb. Rivas-Martínez).

Note. – Although a holotype was indicated (TFC 1708), Wildpret gives two collection dates (9.4.1971 and 7.4.1973). Pérez (1978) does not mention that fact and cites the holotype (TFC 1708) as having been collected on 7.4.1973. In Paris a duplicate of TFC 1708 is preserved, that was collected by W. Wildpret on 9.4.1971 (“Locus classicus, Roque de Juan Bay. Peninsula de Anaga. Tenerife. Canarias”).

M. rivas-martinezii f. *angustifolia* Wildpret in Vieraea 3: 73. 1974. – Holotype: [Spain, Canary Islands] “Roque Juan Bay”, *Wildpret* (TFC 1709). = ***M. rivas-martinezii*** Wildpret.

Note. – A holotype is indicated by Wildpret (TFC 1709) but two collection dates are given (9.4.1971 and 7.4.1973).

M. rodriguezii Freyn & Janka in Oesterr. Bot. Z. 24: 16. 1874. – Lectotype (designated here by Bräuchler): [Spain, Balearic Islands, Ins. Minorca] “Menorca, in valle Varranco del Favaret prope Mahon ad rupes calcareas”, 29.3.1873, *Hegelmaier*, *Iter gallico-hispanicum 1873* (STU!; isolectotype: JE!). ≡ ***M. filiformis*** subsp. ***rodriguezii*** (Freyn & Janka) Bonafè.

Note. – The protologue cites various syntypes collected by Friedrich Hegelmaier on the Balearic Islands, during his “Iter gallico-hispanicum 1873” and subsequently sent to the authors: “Ins. Minorca, in valle Varranco del Favaret prope Mahon ad rupes calcareas 29.3.” (isosyntype JE!, STU!); “Ins. Minorca, in declivibus apricis vallis Son Blanc (cum M. filiformi Benth.)” (isosyntype STU!); “Ins. Minorca, Varranco de Algendar ad rupes calcareas, 1.4.” (isosyntype STU!); “Ins. Majorca: ad munimenta urbis Palma, 11.4.” (isosyntypes STU!). According to Stafleu & Cowan (1976), the whereabouts of Freyn’s herbarium are uncertain (possibly BRNM), Janka’s herbarium is at CL with many duplicates at BP (Stafleu & Cowan 1979). Only BP could be consulted for this study, but none of the syntypes was traced there. Hegelmaier’s herbarium, however, is kept at STU and duplicates of all syntypes are preserved there. Given the uncertainty of the “true” syntypes’ whereabouts, the STU specimens are candidates to serve as lectotype, though neither annotated by Freyn nor Janka. The collection made on 29.3.1873 bears the richest individual, fits the description and is known from a duplicate at JE as well and therefore is chosen as lectotype here.

M. rupestris (Wulfen) Benth. in Candolle, Prodr. 12: 225. 1848 ≡ *Satureja rupestris* Wulfen in Jacquin, Collectanea 2: 130. 1789 = ***Clinopodium thymifolium*** (Scop.) Kuntze, Revis. Gen. Pl. 2: 516. 1891.

M. rutenbergiana Vatke in Abh. Naturwiss. Vereine Bremen 9: 135. 1885 = ? *M. flagellaris* Baker

Note. – See note under *M. flagellaris.*

M. satureioides (R. Br.) Benth., Labiat. Gen. Spec.: 380. 1834 ≡ ***Mentha satureioides*** R. Br., Prodr. Fl. Nov. Holland.: 505. 1802.

M. schimperi Vatke in Linnaea 37: 326. 1872. – Holotype: [Ethiopia, Tigray region] “Anadehr”, *Schimper 576* (B†; isotypes: K!, E!, Z!). = ***M. imbricata*** (Forssk.) C. Chr. var. ***imbricata***

M. serbaliana Danin & Hedge in Notes Roy. Bot. Gard. Edinburgh 32: 261. 1973. – Holotype: “Egypt, S Sinai: Gebel Serbal, cliffs of smooth red granite, NW exposure, 1850 m”, 6.8.1968, *Danin* (HUJ; isotype: E!).

[*M. serbica* Adamovi6 in Sili6, Monogr. Satureja Fl. Jugosl.: 247. 1979, pro syn.] – ***M. croatica*** (Pers.) Schott

M. serpyllifolia Scheele in Linnaea 22: 593. 1849. – Type: [Croatia?] “Dalmatia” (not traced). = ***M. croatica*** (Pers.) Schott

M. serpyllifolia (M. Bieb.) Boiss., Diagn. Pl. Orient., ser. 2, 4: 13. 1859, non Scheele 1849 ≡ *Nepeta serpyllifolia* M. Bieb., Fl. Taur.-Cauc. 2: 40. 1808 ≡ ***Clinopodium serpyllifolium*** (M. Bieb.) Kuntze, Revis. Gen. Pl. 2: 515. 1891.

M. serpyllifolia var. *barbata* Boiss., Fl. Orient. 4: 574. 1879 ≡ *M. fruticosa* subsp. *barbata* P. H. Davis ≡ ***Clinopodium serpyllifolium*** subsp. ***barbatum*** (P. H. Davis) Bräuchler in Taxon 55: 980. 2006.

[*M. serpyllimorpha* Benth. in Candolle, Prodr. 12: 217. 1848, erroneous for *M. herpyllomorpha*] – ***M. herpyllomorpha*** Webb & Berthel.

[*M. sessiliflora* (C. Presl) Gand., Nov. Consp. Fl. Eur.: 367. 1910, pro syn.] – ***M. graeca*** subsp. ***tenuifolia*** (Ten.) Nyman

M. sessilis Benth. in J. Bot. 6: 274. 1847 = ***Mentha diemenica*** Spreng., Syst. Veg. 2: 724. 1825.

M. shepardii (Post) Post in Bull. Herb. Boissier 1: 405. 1893 ≡ *Nepeta shepardi* Post in J. Linn. Soc. Bot. 24: 439. 1888 = ***Clinopodium congestum*** (Boiss. & Hausskn.) Kuntze, Revis. Gen. Pl. 2: 515. 1891.

M. sinaica Benth., Labiat. Gen. Spec.: 380. 1834. – Holotype: [Egypt] “Rochers du Sinaï”, 6.1832, *Bové 61* (K!; isotype: P!, W!).

M. sphaciotica Boiss. & Heldr. ex Benth. in Candolle, Prodr. 12: 220. 1848 & Boiss. & Heldr. in Boissier, Diagn. Pl. Orient. ser. 1, 12: 48. 1853. – Holotype: [Greece] “In rupestribus regionis sempervirentis Cretae in fauce Aratana provinciae Sphakia”, 7.1846, *Heldreich* (K!; isotypes: BP!, G-BOIS, GOET!). = ***M. microphylla*** (d’Urv.) Benth.
Note. – See notes under *M. carpatha* and *M. hispida.*

[*M. sphaciotica* f. *villosa* Gand., Fl. Cret.: 80. Dec. 1816, nom. nud.] – ***M. microphylla*** (d’Urv.) Benth.

M. sphaerophylla Baker in J. Linn. Soc. Bot. 20: 232. 1883.
Note. – See note under *M. flagellaris.*

M. spicata Vis. ex Rchb., Fl. Germ. Excurs.: 311. 1831 = ***Satureja cuneifolia*** Ten., Fl. Napol.: 33. 1811.

M. spicigera K. Koch in Linnaea 17: 295. 1844 ≡ ***Satureja spicigera*** (K. Koch) Boiss., Fl. Orient. 4: 566. 1879.

M. spicigera (K. Koch) Walp., Ann. Bot. Syst. 3: 251. 1852, non K. Koch 1844 ≡ *Calamintha spicigera* K. Koch in Linnaea 21: 671. 1848 = ***Clinopodium serpyllifolium*** (M. Bieb.) Kuntze

M. staminea Boiss. & Hohen. in Boissier, Diagn. Pl. Orient., ser. 1, 5: 19. 1844 ≡ ***Cyclotrichium stamineum*** (Boiss. & Hohen.) Manden. & Scheng. in Bot. Mater. Gerb. Bot. Inst. Komarova Akad. Nauk SSSR 15: 337. 1953.

M. stolonifera Benth., Labiat. Gen. Spec.: 371. 1834 = ***Clinopodium brownei*** (Sw.) Kuntze, Revis. Gen. Pl. 2: 514. 1891.

M. subcordata Vis. ex Benth., Labiat. Gen. Spec.: 379. 1834. – Holotype: [Croatia?] "In Dalmatia", *Visiani* (K). = ***M. croatica*** (Pers.) Schott

M. subnuda (Waldst. & Kit.) Degen, Fl. Velebit 2: 632. 1937 ≡ *Melissa subnuda* Waldst. & Kit., Descr. Icon. Pl. Hung. 3: 291, t. 262. 1812 = ***Clinopodium nepeta*** nothosubsp. ***subisidoratum*** (Borbás) Govaerts, World Checklist Seed Pl. 3(1): 18. 1999.

M. suborbicularis (Alain) Borhidi in Acta Bot. Acad. Sci. Hung. 26: 264. 1981 ≡ *Satureja suborbicularis* Alain in Contr. Ocas. Mus. Hist. Nat. Colegio "De La Salle" 15: 13. 1956 = ***Clinopodium bucheri*** (P. Wilson) Harley in Kew Bull. 55: 920. 2000.
Note. – Synonymy follows Cantino & Wagstaff (1998).

M. subulifolia Rech. f. in Biol. Skr. 8(1): 74. 1955 ≡ ***Hyssopus subulifolius*** (Rech. f.) Rech. f., Fl. Iran. 150: 525. 1982.

M. taygetea P. H. Davis in Kew Bull. 1949: 110. 1949 ≡ ***Clinopodium taygeteum*** (P. H. Davis) Bräuchler & Heubl in Taxon 55: 980. 2006.

M. tenella (Epling) R. Morales in Bot. Complut. 18: 164. 1993 ≡ *Satureja tenella* Epling in Repert. Spec. Nov. Regni Veg. Beih. 85: 161. 1936 ≡ ***Clinopodium tenellum*** (Epling) Harley in Jorgensen & León Yánez, Cat. Vasc. Pl. Ecuad.: 954. 1999.

M. teneriffae (Poir.) Benth. ex G. Don in Loudon, Hort. Brit.: 483. 1830 ≡ *Thymus teneriffae* Poir. in Lamarck, Encycl. 7: 650. 1806. – Lectotype (designated by Pérez 1978: 52): [Spain, Canary Islands] "*Thymus canariensis* Vent. […] Teneriffa" (P [herb. Lamarck]).

M. teneriffae var. *brevidens* Bornm. in Repert. Spec. Nov. Regni Veg. 6: 2. 1909. – Holotype: [Spain, Canary Islands] 1901, *Bornmüller, Pl. exsicc. Canar. 2719* (B†?). = ***M. varia*** subsp. ***gomerensis*** P. Pérez

M. teneriffae var. ***cordifolia*** P. Pérez, Rev. Gen. Micromeria Reg. Macarones.: 55. 1978. – Holotype: [Spain, Canary Islands] "In fisuris rupium soleatarum in Bco. de las Vigas, Fasnia, Nivaria – Tenerife dicta", 18.2.1973, *Pérez 6* (herb. Pérez; isotype: TFC 1738).

M. teneriffae var. *ramosa* Webb & Berthel. ex Christ in Bot. Jahrb. Syst. 9: 134. 1888 ≡ *M. teneriffae* f. *ramosa* (Webb & Berthel. ex Christ) P. Pérez, Rev. Gen. Micromeria Reg. Macarones.: 53. 1978. – Lectotype (designated by Pérez 1978: 54): [Spain, Canary Islands] "*M. terebinthinacea* spec. nov. var. ß, Habit. in fissuris rupium regionis inferioris Teneriffae! et Canariae?", *Barker-Webb* (FI). = ***M. teneriffae*** (Poir.) Benth. ex G. Don

M. teneriffae f. *subramosa* P. Pérez, Rev. Gen. Micromeria Reg. Macarones.: 56. 1978. – Holotype: [Spain, Canary Islands] "Plante que je n'ai trouvée qu'une seule fois, Tenerife", *Despéraux 312* (FI). = ***M. teneriffae*** (Poir.) Benth. ex G. Don).

M. teneriffae (Poir.) Benth. ex G. Don var. ***teneriffae***

M. tenuifolia (Ten.) Rchb., Fl. Germ. Excurs.: 311. 1831 & Benth. in Candolle, Prodr. 12: 215. 1848 ≡ *Satureja tenuifolia* Ten. ≡ ***M. graeca*** subsp. ***tenuifolia*** (Ten.) Nyman

M. tenuis (Link) Benth., Labiat. Gen. Spec.: 374. 1834, non Benth., Labiat. Gen. Spec.: 731. 1835, nom. superfl. ≡ *Satureja tenuis* Link in Buch, Phys. Beschr. Canar. Ins.: 143. 1828. – Holotype: [Spain, Canary Islands] "Canarische Inseln", *Smith* (B†); neotype: (designated by Pérez 1978: 135): [Spain, Canary Islands] "Gde. Canaria, statione exacta non notata", *Despréaux 296* (FI).
Note. – In the literature there is an erroneous attribution of the authorship of *M. tenuis* to Webb & Berthel., Hist. Nat. Iles Canaries 3: 75. 1845, resulting from Bentham's wrong application of the

name *M. tenuis* to *M. benthamii*. Later workers without justification considered Bentham's nomenclaturally correct combination as irrelevant and regarded Webb & Berthelot's treatment of *M. tenuis* as place of the legitimate new combination for *Satureja tenuis* Link. See also note under *M. lanata* (Chr. Sm. ex Link) Benth.

M. tenuis subsp. ***linkii*** (Webb & Berthel.) P. Pérez, Rev. Gen. Micromeria Reg. Macarones.: 137. 1978 ≡ *M. linkii* Webb & Berthel., Hist. Nat. Iles Canaries 3: 79. 1845.

M. tenuis var. ***soriae*** P. Pérez, Rev. Gen. Micromeria Reg. Macarones.: 136. 1978. – Holotype: [Spain, Canary Islands] "Ex insula Canaria Magna (Gran Canaria dicta) in magno cavo „Bco. de Arguineguin" dicto, prope pagum Soria dicto", 21.4.1973, *Pérez 13* (herb. Pérez; isotypes: FI, K!, LPA, MA!, ORT, TFC, TFMC, Z!).

M. tenuis (Link) Benth. subsp. ***tenuis***

M. tenuis (Link) Benth. var. ***tenuis***

M. therebinthinacea (Brouss. ex Willd.) Webb & Berthel., Hist. Nat. Iles Canaries 3: 80. 1845 [as *"M. terebinthinacea"*] ≡ *Thymus therebinthinaceus* Brouss. [Elench. horti bot. monspel. 59. 1805, nom. nud.] ex Willd., Enum. Pl.: 624. 1809. – Holotype: *Broussonet* (B-W 11016). = ***M. teneriffae*** (Poir.) Benth. ex G. Don

M. teydensis Bolle in Bonplandia (Hannover) 8: 282. 1860. – Syntypes: [Spain, Canary Islands] "Hab. gregarie in regione excelsa montis Pico de Teyde et in la Cumbre proxima, unde in pineta supra Igueste descendit (…) colitur in horto botanico Berolinensi" (B†). = ***M. lachnophylla*** Webb & Berthel.

M. thymbra (L.) Kostel., Allg. Med.-Pharm. Fl. 3: 763. 1834 ≡ ***Satureja thymbra*** L., Sp. Pl. 2: 567. 1753.

M. thymifolia (Scop.) Fritsch in Kerner, Sched. Fl. Exs. Austro-Hung. 8: 119. 1899 ≡ *Satureja thymifolia* Scop., Fl. Carn., ed. 2, 1: 428, t. 29. 1771 ≡ ***Clinopodium thymifolium*** (Scop.) Kuntze, Revis. Gen. Pl. 2: 516. 1891.

M. thymifolia f. *albida* K. Malý in Wiss. Mitt. Bosnien & Herzegovina 7: 538. 1900 = ***Clinopodium thymifolium*** (Scop.) Kuntze, Revis. Gen. Pl. 2: 516. 1891.

M. thymifolia f. *albiflora* K. Malý in Wiss. Mitt. Bosnien & Herzegovina 7: 538. 1900 = ***Clinopodium thymifolium*** (Scop.) Kuntze, Revis. Gen. Pl. 2: 516. 1891.

M. thymifolia f. *condensata* Sili6 in Glasn. Zemaljsk. Muz. Bosne Hercegovine Sarajevu. Prir. Nauke 13: 114. 1975 = ***Clinopodium thymifolium*** (Scop.) Kuntze, Revis. Gen. Pl. 2: 516. 1891.

M. thymifolia f. *hirsutior* Sili6 in Glasn. Zemaljsk. Muz. Bosne Hercegovine Sarajevu. Prir. Nauke 13: 114. 1975 = ***Clinopodium thymifolium*** (Scop.) Kuntze, Revis. Gen. Pl. 2: 516. 1891.

M. thymifolia f. *macrodonta* Sili6 in Glasn. Zemaljsk. Muz. Bosne Hercegovine Sarajevu. Prir. Nauke 13: 114. 1975 = ***Clinopodium thymifolium*** (Scop.) Kuntze, Revis. Gen. Pl. 2: 516. 1891.

M. thymifolia f. *obscura* K. Malý in Wiss. Mitt. Bosnien & Herzegovina 7: 538. 1900 = ***Clinopodium thymifolium*** (Scop.) Kuntze, Revis. Gen. Pl. 2: 516. 1891.

M. thymifolia f. *parvifolia* Sili6 in Glasn. Zemaljsk. Muz. Bosne Hercegovine Sarajevu. Prir. Nauke 13: 114. 1975 = ***Clinopodium thymifolium*** (Scop.) Kuntze, Revis. Gen. Pl. 2: 516. 1891.

M. thymifolia f. *picta* (L. F. Čelak. & Rohlena) Sili6, Monogr. Satureja Fl. Jugosl.: 189. 1979 ≡ *Satureja thymifolia* f. *picta* L. F. Čelak. & Rohlena in Acta Bot. Boh. 1: 3. 1922. = ***Clinopodium thymifolium*** (Scop.) Kuntze, Revis. Gen. Pl. 2: 516. 1891.

M. thymoides De Not., Repert. Fl. Ligust.: 319-320. 1844 & Prosp. Fl. Lusit.: 53. 1846, non (Sol. ex Lowe) Webb. & Berthel., Hist. Nat. Iles Canaries 3: 71. Dec 1844. – Type: [Italy] "In glareis secus amnem Uneliae", *Berti* (not traced, GE?). ≡ *M. graeca* subsp. *imperica* Chater = ***M. graeca*** (L.) Benth. ex Rchb. subsp. ***graeca***

Note. – According to Stearn (1937) Webb & Berthelot's name dates from December 1844; there is no evidence about the month of publication of De Notaris' work in 1844. For futher details see notes under *M. graeca* subsp. *imperica*.

M. thymoides (Sol. ex Lowe) Webb & Berthel., Hist. Nat. Iles Canaries 3: 71. Dec 1844, non De Not. 1844 ≡ *Satureja thymoides* Sol. ex Lowe ≡ ***M. varia*** subsp. ***thymoides*** (Sol. ex Lowe) P. Pérez

Note. – See previous entry.

M. thymoides (Sol. ex Lowe) Webb & Berthel. subsp. *cacuminicolae* (P. Pérez) Rivas Mart. in Itinera Geobot. 15: 704. 2002, nom. illeg.? ≡ *M. varia* var. *cacuminicolae* P. Pérez = ***M. varia*** subsp. ***thymoides*** (Sol. ex Lowe) P. Pérez

M. thymoides (Sol. ex Lowe) Webb & Berthel. var. *citrodora* Webb & Berthel., Hist. Nat. Iles Canaries 3: 71. 1844, nom. illeg.? – Holotype: [Spain, Canary Islands] "In sylvis Teneriffae", *Barker-Webb* (not traced, FI?). = ***M. varia*** Benth.

M. thymoides (Sol. ex Lowe) Webb & Berthel. var. *rupestris* Webb & Berthel., Hist. Nat. Iles Canaries 3: 71. 1844, nom. illeg.? – Lectotype (designated by Pérez 1978: 183): [Spain, Canary Islands] "*M. thymoides* Webb et Berth. a. rupestris. Pedunculi multiflori, in rupibus Lancerotta septentrionum, 28" (FI). ≡ ***M. varia*** subsp. ***rupestris*** (Webb & Berthel.) P. Pérez

M. todari Lacaita ex Lojac., Fl. Sicul. 2(2): 211. 1907 ≡ *Satureja longiflora* C. Presl [non *M. longiflora* Hochst. ex Baker] = ***M. graeca*** subsp. ***longiflora*** (C. Presl) Nyman

M. tragothymus Webb & Berthel., Hist. Nat. Iles Canaries 3: 73. 1845. – Type: [Spain, Canary Islands] "In montosis Teneriffae", *Barker-Webb* (not traced, FI?). = ***M. varia*** Benth.

M. unguentaria Schweinf., Beitr. Fl. Aethiop.: 124. 1867. – Type: [Ethiopia, Gondar region] "Auf 5700' hohen Bergen bei Dschadscha", 30.9.1854, *Schimper* [s.n.?] (holotype: B†); lectotype (designated by Ryding 2007: 442): [Ethiopia, Gondar region] "Dschadscha", 30.9. 1854, *Schimper 112* (Z-000039175!; isolectotypes: E!, FI, HEID!).

M. vana (Epling) R. Morales in Bot. Complut. 18: 164. 1993 ≡ *Satureja vana* Epling in Ann. Missouri Bot. Gard. 14: 79. 1927 ≡ ***Clinopodium vanum*** (Epling) Harley & A. Granda in Kew Bull. 55: 926. 2000.

M. varia Benth., Labiat. Gen. Spec.: 374. 1834., nom. cons. prop. – Lectotype (designated by Pérez 1978: 174): [Spain, Canary Islands] "Ins. Teneriffa" (K [right hand individual]).

Note. – See note under *M. ericifolia.*

M. varia var. *angustissima* Bolle ex Christ in Bot. Jahrb. Syst. 9: 131. 1888. – Type: [Spain, Canary Islands] "In Canaria magna supra Tafira", 3.1884, *Christ* (not traced, BAS?). = ***M. varia*** subsp. ***canariensis*** P. Pérez

M. varia var. *cacuminicolae* P. Pérez, Rev. Gen. M. Reg. Macarones.: 186. 1978. – Holotype: [Spain, Canary Islands] "Ex insula Maderae, regione cacuminalis juxta „Pico do Arrieiro“ ad 1750 m. supra Mare", 6.1976, *Pérez* (TFC 5577; isotypes: B!, FI, K!, MA!, O, TFMC, Z!). = ***M. varia*** subsp. ***thymoides*** (Sol. ex Lowe) P. Pérez

M. varia subsp. ***canariensis*** P. Pérez, Rev. Gen. Micromeria Reg. Macarones.: 180. 1978. – Holotype: [Spain, Canary Islands] "Ex insula Canaria Magna (G. Canaria dicta) in magno anfractu "Bco. Oscuro“ dictum, prope Tamadaba, versus 900 m. supra Mare", 10.7.1974, *Pérez* (herb. Pérez).

M. varia f. *citrodora* (Webb & Berthel.) Christ in Bot. Jahrb. Syst. 9: 133. 1888 ≡ *M. varia* var. *citriodora* (Webb & Berthel.) Burch., Biblioth. Bot. (Stuttgart) 98: 182. 1929 ≡ *M. thymoides* var. *citrodora* Webb & Berthel. = *M. herpyllomorpha* Webb & Berthel., p.p. = ***M. varia*** Benth.

M. varia subsp. ***gomerensis*** P. Pérez, Rev. Gen. Micromeria Reg. Macarones.: 179. 1978. – Holotype: [Spain, Canary Islands] "Ex insula Junonia Minor (Insula Gomera dicta) in loco vulgo dicto 'Ladera de Pilas' in anfractu 'Bco. de la Villa', juxta S. Sebastián", 5.1976, *P. Pérez 8* (herb. Pérez; isotypes: TFC, MA!).

M. varia f. *herpyllomorpha* (Webb & Berthel.) Christ in Bot. Jahrb. Syst. 9: 133. 1888 ≡ ***M. herpyllomorpha*** Webb & Berthel.

M. varia subsp. ***hierrensis*** P. Pérez, Rev. Gen. Micromeria Reg. Macarones.: 184. 1978. – Holotype: [Spain, Canary Islands] "Ex insula Hierro dicta, in rupibus abruptis super pagum Sabinosa dictum proclivibus ad nebulas diurnas expositis", 7.1973, *Pérez 11* (herb. Pérez; isotypes: MA!, TFC, TFCM).

M. varia f. *hyssopifolia* (Webb & Berthel.) Christ in Bot. Jahrb. Syst. 9: 133. 1888 ≡ ***M. hyssopifolia*** Webb & Berthel.

M. varia f. *lachnophylla* (Webb & Berthel.) Christ in Bot. Jahrb. Syst. 9: 133. 1888 ≡ ***M. lachnophylla*** Webb & Berthel.

M. varia subsp. ***meridialis*** P. Pérez, Rev. Gen. Micromeria Reg. Macarones.: 181. 1978. – Holotype: [Spain, Canary Islands] "In regione australe insulae Canariae Magnae (Gran Canaria dicta) in rupibus circumstantibus loco Fataga dicto, ubi est frequens", 20.7.1974, *P. Pérez 10* (herb. Pérez).

M. varia f. *microphylla* Christ in Bot. Jahrb. Syst. 9: 134. 1888. – Type: [Spain, Canary Islands] "In convallibus reg. marit. insular. fere omnium", *Barker-Webb* (not traced, FI?). = ***M. varia*** Benth.

M. varia subsp. ***rupestris*** (Webb & Berthel.) P. Pérez, Rev. Gen. Micromeria Reg. Macarones.: 182. 1978 ≡ *M. varia* f. *rupestris* (Webb & Berthel.) Christ in Bot. Jahrb. Syst. 9: 133. 1888 ≡ *M. thymoides* (Sol. ex Lowe) Webb & Berthel. var. *rupestris* Webb. & Berthel.

M. varia subsp. ***thymoides*** (Sol. ex Lowe) P. Pérez, Rev. Gen. Micromeria Reg. Macarones.: 185. 1978 ≡ *Satureja thymoides* Sol. ex Lowe in Trans. Cambridge Philos. Soc. 4: 19. 1831. – Holotype: Madeira, *Solander* (not traced, K?).

M. varia Benth. subsp. ***varia***

M. variegata (Host) Rchb., Fl. Germ. Excurs.: 859. 1832 ≡ *Satureja variegata* Host, Fl. Austr. 2: 134. 1832 ≡ ***Satureja montana*** subsp. ***variegata*** (Host) P. W. Ball in Bot. J. Linn. Soc. 65: 352. 1972.

M. viminea (L.) Druce in Rep. Bot. Exch. Club Brit. Isles 3: 421. 1914 & Urb. in Repert. Spec. Nov. Regni Veg. 16: 142. 1919 ≡ *Satureja viminea* L., Syst. Nat., ed. 10, 2: 1096. 1759 ≡ ***Clinopodium vimineum*** (L.) Kuntze, Revis. Gen. Pl. 2: 516. 1891.

M. wardii C. Marquand & Airy Shaw in J. Linn. Soc., Bot. 48: 216. 1929 ≡ ***Clinopodium wardii*** (C. Marquand & Airy Shaw) Bräuchler in Taxon 55: 980. 2006.

M. weilleri (Maire) R. Morales in Anales Jard. Bot. Madrid 48: 154. 1991 ≡ *Satureja weilleri* Maire in Bull. Soc. Hist. Nat. Afrique N. 19: 62. 1928. – Lectotype (designated here by Bräuchler): [Morocco] "Rochers volcaniques, bords de l'Oued Ksiksou, Oulmès (Zaïan), 800 m", 29.4.1927, *Jahandiez* [*& Weiller*] *74* (MPU-001919*!; isolectotype: P-00083230*!).

Note. – Two collections of *S. weilleri* Maire collected by Jahandiez and determined by R. Maire on 7.2.1928 exist, one at P one at MPU. In a database the P specimen was indicated as holotype and the MPU specimen as isotype, but such a designation has neither been made by the author himself nor by a subsequent publication on *Micromeria* or *Satureja* so far (P. Schäfer, pers. comm. Since MPU houses the complete herbarium of R. Maire and the sheet at MPU represents the richer collection and has – in contrast to the P sheet – the original Jahandiez Herbarium label, it is here chosen as lectotype.

M. xalapensis (Kunth) Benth., Labiat. Gen. Spec.: 372. 1834 ≡ *Thymus xalapensis* Kunth in Humboldt & al., Nov. Gen. Sp. Pl. 2: 316. 1818 = ***Clinopodium brownei*** (Sw.) Kuntze, Revis. Gen. Pl. 2: 514. 1891.

M. xylorrhiza Boiss. & Heldr. ex Benth. in Candolle, Prodr. 12: 217. 1848. – Lectotype (designated by Davis 1982: 345): [Turkey] "In fissuris rupium Tauri Lycaonici, 1520 m, in monte Anemas", *Heldreich* (G). ≡ ***M. cristata*** subsp. ***xylorrhiza*** (Boiss. & Heldr. ex Benth.) P. H. Davis

Note. – At W a putative isosyntype ("Mt. Bondracun[?] Pisidiae", *Heldreich 1148*) is present.

M. yezoensis Miyabe & Tatew. in Trans. Sapporo Nat. Hist. Soc. 14: 8. 1935 = ***Mentha japonica*** (Miq.) Makino in Bot. Mag. (Tokyo) 20: 1. 1906.

Hybrids

Hybridisation seems a quite common phenomenon in *Micromeria* with the majority of hybrids described from the Canary Islands (Pérez 1978) but also from other areas between taxa as morphological distinct as *M. inodora* and *M. graeca* (Lièvre 1921). To our knowledge, no crossing experiments have been conducted so far. Taking into account the great variability of many taxa, it is questionable whether some of the taxa described as hybrids actually are of such origin or simply represent extreme forms of a natural range of variation. The names for hybrids are here listed without further evaluation of their status.

M. ×*angosturae* P. Pérez, Rev. Gen. Micromeria Reg. Macarones.: 146. 1978 ≡ *M. tenuis* subsp. *linkii* × *M. varia* subsp. *canariensis*

M. ×*benthamineolens* Svent. in Index Seminum (Agron. Investig. Nat. Hispan. Inst.) 1968: 48. 1969 ≡ *M. benthamii* × *M. pineolens*

M. ×*bourlieri* Maire & Gauth.-Lièvre in Bull. Soc. Hist. Nat. Afrique N. 12: 173. 1921 ≡ *M. graeca* × *M. inodora*

Note. – The second author sometimes has wrongly been cited as "Le Lièvre", which is, however, the standard form (IPNI 2008) for J. F. Le Lièvre, from the USA. Obviously the second author, Lucienne Lièvre, later married and carried the name Gauthier-Lièvre, the standard form according to IPNI (2008) is Gauth.-Lièvre.

M. ×*confusa* G. Kunkel & P. Pérez in Cuad. Bot. Canaria 26-27: 21. 1976 ≡ *M. benthamii* × *M. lanata*

M. ×*glandulosa* Sennen in Bol. Soc. Ibér. Ci. Nat. 32: 62. 1934

M. ×*hybrida* Zagan. in Actes Inst. Bot. Univ. Athènes 1: 250. 1940 ≡ *M. graeca* × *M. nervosa*

M. ×*intermedia* G. Kunkel & P. Pérez in Cuad. Bot. Canaria 26-27: 23. 1976 ≡ *M. benthamii* × *M. helianthemifolia*

M. ×*knochei* Sennen & Bianor in Sennen, Treb. Inst. Catalana Hist. Nat. 3: 193. 1917 ≡? *M. nervosa* × *M. rodriguezii*

Note. – Knoche (1922: 346), includes this in synonmy to his *M. biflora* var. *rodriguezii* (Freyn & Janka) Knoche

M. ×*meteorica* Hausskn. in Mitt. Thüring. Bot. Vereins, ser. 2, 11: 48. 1897 ≡ *M. cremnophila* × *M. juliana*

M. ×*nogalesii* G. Kunkel & P. Pérez in Cuad. Bot. Canaria 26-27: 25. 1976 ≡ *M. lanata* × *M. varia* subsp. *canariensis*

M. ×*perez-pazii* G. Kunkel in Vieraea 8: 360. 1980 ≡ *M. benthamii* × *M. tenuis*

M. ×*preauxii* Webb & Berthel., Hist. Nat. Iles Canaries 3: 75. 1845 ≡ *M. benthamii* × *M. varia* subsp. *canariensis*

Note. – Described as species, as hybrid established by P. Pérez, Rev. Gen. Micromeria Reg. Macarones.: 127. 1978

M. ×*tagananensis* P. Pérez, Rev. Gen. Micromeria Reg. Macarones.: 108. 1978 ≡ *M. glomerata* × *M. varia*

M. ×*tapeinantha* Rech. f. in Denkschr. Akad. Wiss. Wien, Math.-Naturwiss. Kl. 105: 123. 1943 ≡ *M. graeca* × *M. nervosa*

M. ×*wildpretii* P. Pérez, Rev. Gen. Micromeria Reg. Macarones.: 99. 1978 ≡ *M. rivas-martinezii* × *M. varia*

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6.6 Manuskript 6:

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Molecular phylogeny of Menthinae (Lamiaceae, Nepetoideae, Mentheae) – taxonomy, biogeography and conflicts

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Abstract

Although the subfamily Nepetoideae (Lamiaceae) is considered to be monophyletic, relationships between tribes, subtribes and genera within the subfamily are poorly understood as complex and possibly homoplasious morphological characters make taxa difficult to delimit. DNA sequence data from three regions (chloroplast: *trn*K intron; *trn*L-F; nuclear: ITS) in total including 278 accessions, representing 38 out of 40 genera of subtribe Menthinae and 11 outgroup genera, were used to reconstruct the evolutionary history, test previous hypotheses of classification, explain biogeographic patterns and elucidate character evolution. Using maximum parsimony (MP) and Bayesian analysis phylogenetic reconstructions based on nuclear and chloroplast sequence data were incongruent, consequently the data were analyzed separately.

Both nuclear and chloroplast datasets provide strong support for three major lineages: the "*Satureja*", "*Micromeria*" and "*Clinopodium*" group. The first contains members of *Satureja* and *Gontscharovia*. In the second lineage *Micromeria* s.str. and *Origanum* were resolved as monophyletic, *Pentapleura* and *Zataria* indicated as sister groups. *Thymbra* includes two species of *Satureja* turning the latter genus polyphyletic. *Thymus* is revealed as paraphyletic with respect to *Argantoniella* and *Saccocalyx* in both and *Origanum* in the plastid dataset only. In the third lineage, the *Clinopodium* group, branching pattern is highly incongruent among datasets and possibly influenced by recent and ancient hybridization, chloroplast capture and incomplete lineage sorting. However identical terminal groups are inferred in both analyses. A Madagascan lineage of "*Micromeria*", sister to the recently described South African *Killickia*, is suggested to represent a new genus. The Himalayan *Clinopodium nepalense* group and the tropical African *C. abyssinicum* alliance are monophyletic but indicated in different positions. Both groups appear in the ITS phylogeny in a clade with *Cyclotrichium* and *Mentha*, relationships not suggested previously. The enigmatic *Micromeria cymuligera* is close to *Mentha* and possibly is a representative of this genus. Species of *Acinos*, now regarded as part of *Clinopodium*, are mixed up with species of *Ziziphora*, questioning either the inclusion of *Acinos* in *Clinopodium* or generic distinctness of *Ziziphora*. All data sets suggest a monophyly of the New World taxa and argue for long-distance dispersal from the Old World, rather than a vicariance explanation. *Bystropogon* marks the split up between the two lineages. Inclusion of 22 genera intermixed with *Clinopodium* spp. in the New World clade provides evidence that the current circumscription of the genus is highly unnatural. Low sequence divergence resulting in low phylogenetic resolution especially at the base of the clade indicate a rapid radiation accompanied by considerable ecological diversification and speciation.

Key words

generic delimitations, Lamiaceae, Menthinae, molecular phylogeny, *Satureja*

Running title: Phylogeny of Menthinae

Introduction

The plant family Lamiaceae Martinov (= Labiatae Adans., the mint family) has a world-wide distribution and comprises more than 7200 species across approximately 240 genera which are classified in seven subfamilies: Ajugoideae Kostel., Lamioideae Harley, Nepetoideae (Dumort.) Luerss., Prostantheroideae Luerss., Scutellarioideae (Dumort.) Caruel, Symphorematoideae Briq. and Viticoideae Briq. (Harley et al., 2004). Among these subfamlies Nepetoideae is one of the most clearly defined, characterized by: hexacolpate, three nucleate pollen (Erdtman, 1945; Cantino and Sanders, 1986); an investing embryo (Martin, 1946); and presence of rosmarinic acid (Harley et al., 2004). It is indicated as monophyletic in various molecular analyses (e.g. Wagstaff et al., 1995; Wagstaff and Olmstead, 1997).

The tribal subdivision of Nepetoideae differed fundamentally from treatment to treatment (Bentham, 1876; Briquet, 1895--97; Wunderlich, 1967, a detailed overview is provided in Cantino, 1992a). Based on morphology, but influenced by molecular phylogenetic analyses (Cantino, 1992a; Cantino, 1992b; Wagstaff, 1992), Cantino et al. (1992) proposed a new classification for Nepetoideae. The authors recognized four tribes Elsholtzieae, Ocimeae, Lavanduleae and Mentheae, with the last undergoing the most substantial changes compared to earlier taxonomic treatments. The most recent work of Harley et al. (2004) basically adopted this concept, though slightly modified by incorporating Lavanduleae in Ocimeae. The vast number of genera and species are placed in tribe Mentheae which in itself is subdivided in three subtribes, Salviinae, Nepetinae and Menthinae. The latter includes 43 out of 66 genera in Mentheae (Tab. 1) among them many spices and medicinal herbs (such as mint, savory, thyme, oregano or bergamot) along with several ornamental plants (e.g. *Monarda*, the Indian nettle). Despite the economic importance of the group there has been much discussion about generic boundaries in Menthinae especially concerning the taxa associated with the former *Satureja* s.l. complex (e.g. *Satureja*, *Micromeria*, *Calamintha*, *Clinopodium*, *Acinos*). Looking at floristic treatments worldwide many favoured Briquet´s (1895-97) broad concept of *Satureja* (e.g. Epling and Jativa, 1964, 1966; Greuter et al., 1986, Killick, 1961; Thonner, 1915; Brenan, 1954; Hedberg, 1957) while others (Morales, 1993; Davis, 1982; Chater and Guinea, 1972; Ball and Getliffe, 1972) preferred the narrow delimitation of Bentham (1848; 1876).

Recently there has been an increasing number of molecular studies in Nepetoideae with focus on the tribes Ocimeae (Paton et al., 2004) and especially Mentheae. All of the latter were restricted to selected genera, e.g, *Bystropogon* (Trusty et al., 2004; Trusty et al., 2005), *Conradina* (Edwards et al., 2006; 2008a, b), *Mentha* (Bunsawat et al., 2004), *Micromeria* (Bräuchler et al., 2005), *Minthostachys* (Schmidt-Lebuhn, 2007; 2008), *Monarda* (Prather et al., 2002) and *Salvia* (Walker et al., 2004; Walker and Sytsma, 2007) with some preliminary investigations at the tribal level only. Some critical genera were revealed as not monophyletic in their current circumscription. *Salvia* seems to be paraphyletic with regard to at least *Dorystoechas* and *Perovskia* (Walker et al., 2004; Walker and Sytsma, 2007). The polyphyly of *Satureja* with regard to the New World species as detected in Wagstaff et al. (1995) resulted in transfer of these taxa to *Clinopodium* (Cantino and Wagstaff, 1998; Govaerts, 1999; Harley and Granda, 2000). *Clinopodium* in turn was shown to be non monophyletic concerning the placement of e.g. the Macaronesian endemic *Bystropogon* (Trusty et al., 2004) and species of *Micromeria* section *Pseudomelissa* or the New World *Monarda* (Bräuchler et al., 2005). While members of section *Pseudomelissa* recently have been placed in *Clinopodium* (Bräuchler et al., 2006) the current generic delimitation has not addressed the paraphyly of *Clinopodium* with respect to *Bystropogon*, *Monarda* and a couple of other New World taxa.

The newer concepts for *Satureja* or *Clinopodium* are only partially accepted. Authors working in the New World keep describing new taxa under *Satureja*, (e.g. Fernández-Alonso, 2002; Méndez et al., 2005) while in the Old World a new genus, *Argantoniella*, has been split from *Satureja* (Lopez and Morales, 2004) and the inclusion of *Calamintha* in *Clinopodium* is rejected by some authors (e.g. Bacchetta and Brullo, 2005).

What is urgently needed is a more comprehensive study dealing with both subtribal classification and generic boundaries to resolve long-standing controversies and improve our understanding of the evolutionary processes that have shaped this alliance.

Here we present a study of the phylogeny of subtribe Menthinae based on sequence data of two plastid regions (*trn*L-F and *trn*K) and one nuclear ribosomal DNA region (ITS). We sampled globally and often included multiple accessions especially in respect of taxonomically critical genera.With our analyses we aim to (1) investigate if Menthinae are monophyletic, (2) determine the major evolutionary lineages within this group, (3) test support for current generic circumscription and (4) figure out potential evolutionary relationships of taxa with uncertain placement in traditional classifications. In addition we used our data to develop biogeographical hypotheses and to determine morphological characters that are suitable to support a comprehensive, phylogeny-based classification.

Materials and methods

Sampling strategy and Plant material

Sampling was designed to cover a representative number of species/taxonomic groups for each genus of Menthinae. According to recent studies (Bräuchler, unpubl. data; Trusty et al., 2004; Walker and Sytsma, 2007) several genera previously included in Menthinae (Harley et al., 2004) are clearly dissociated from other members of the subtribe: *Cleonia* L., *Horminum* L., *Hyssopus* L., *Lycopus* L., and *Prunella* L. Consequently, Menthinae are treated in our study with these genera excluded (=Menthinae s.str.). Table 1 presents an updated list of genera of Menthinae including the recently segregated *Argantoniella* and *Killickia*. Nearly all genera were sampled by the inclusion of at least one species. Only for two monotypic genera, *Eriothymus* and *Neoeplingia*, no suitable material was available. In addition, potential morphological subdivisions of large genera were determined by examining the literature and during the extensive herbarium studies by the first author. For most of these potential groups (e.g. sections or morphologically isolated species) specimens had been included in the molecular analysis.

Outgroups were chosen in accordance to previous phylogenetic studies (e.g. Trusty et al., 2004; Bräuchler et al., 2005; Walker and Sytsma, 2007) with one representative of the following genera: *Ajuga*, *Clerodendrum* (Ajugoideae); *Collinsonia* (Nepetoideae, Elsholtzieae); *Lavandula*, *Plectranthus* (Nepetoideae, Ocimeae); *Salvia* (Nepetoideae, Mentheae, Salviinae); *Agastache*, *Glechoma*, *Nepeta* (Nepetoideae, Mentheae, Nepetinae); *Horminum*, *Lycopus* (formerly Nepetoideae, Mentheae, Menthinae, now excluded). For some taxa fresh or silica gel dried material was available either from Botanical Gardens or field collections by the authors, but the majority of samples consisted of herbarium specimen material. For several New World taxa for which no material was available sequences deposited in GenBank were included in the ITS analysis. Table 2 lists all taxa included in this study and summarizes sources, voucher, GenBank accession numbers and references for previously published sequences.

The name *Acinos*, included in the synonymy of *Clinopodium* by Harley et al. (2004) is used here provisionally to refer to the species previously placed in that genus (see Tab. 1). Accordingly, species excluded from *Micromeria* by Bräuchler et al. (2008a), but not placed elsewhere yet are referred to as "*Micromeria*" *cymuligera*, "*M.*" *flagellaris*, "*M.*". *madagascariensis* and "*M.*" *sphaerophylla*).

DNA extraction, amplification, sequencing and alignment

Total DNA was extracted from fresh or silica-gel dried tissue or herbarium specimens as described previously (Bräuchler et al., 2004) using the Macherey-Nagel NucleoSpin Plant Kit. Due to degradation of DNA in the herbarium material the *trn*K intron was amplified in several parts from total DNA as described in Bräuchler et al. (2005). For most samples, the parts were not overlapping in the matK gene coding region at the site of the complementary primers Sat16-1200R (GAT TCG TAT TCA CAT ACA TGA G) and Sat2-1200F (CTC ATG TAT GTG AAT ACG AAT C). The respective region was excluded from the analysis. Amplification was performed using the following alternative flanking primers: 2-*trn*K-3914F (Johnson and Soltis, 1994) or Sat2-500F (CGA AAT CAA AAG AGC GAT TGG) as forward and Sat16-880R (AAT CTG TTC ACA ATC CGT AAA C), Sat16-1000R (CAA TAA AAG CAA ACC CCC TCT G) or Sat16-1200R as reverse primers on the one hand, and Sat2-1200F or Sat2-1780F (CAG AGG GGT TTG CTT TTA TCC G) as forward and Sat16-1780R (TCT AGA ATT TGA CTC CGT ACC) or 16-*trn*K-2R(Johnson and Soltis, 1994) as reverse primers on the other hand. The *trn*L-F region was amplified as described previously (Bräuchler et al., 2004) using the primer pairs C/F, C/D and E/F according to Taberlet et al. (1991). Amplification of the ITS region was conducted using the primers leu1 (Vargas et al., 1998) and its4 (White et al., 1990) as described in Bräuchler et al. (2004). For the ITS region and the cpDNA markers from very old herbarium specimens Phusion® polymerase (New England Biolabs) was used for amplification following the manufacturer´s protocol with an initial denaturation step of 1 min at 98°C, followed by 35 cycles of 30 sec at 98°C, 30 sec at 53,5°C and 1 min at 72°C, and a final extension step of 10 min at 72°C. PCR products were purified using Microcon YM 100 filter devices (Millipore, USA) and sequenced bidirectionally using the Amersham Kit (Amersham, Freiburg) and an ABI 377 automated sequencer. Sequences were aligned and edited manually using GeneDoc (Nicholas and Nicholas, 1997). Unambiguous indels were coded using the program SeqState (Müller, 2005) applying the "simple indel coding" approach (Simmons and Ochoterena, 2000). Indels in ambiguously aligned parts or resulting from poly-nucleotide regions were not coded and the respective regions excluded for analysis.

Phylogenetic analyses

The individual datasets for each marker as well as the combined plastid dataset were analysed using maximum parsimony and Bayesian inference.

Parsimony analyses were conducted using PAUP 4b10 (Swofford, 2002) and PRAP (Müller, 2004). The latter generates command files for PAUP that allow parsimony ratchet searches as designed by Nixon (1999) for analysis of large data sets. In the present study, 10 random addition cycles of 500 ratchet iterations each were used. Each iteration comprised two rounds of TBR branch swapping, one on a randomly re-weighted data set (25% of the positions), and the other on the original matrix saving one shortest tree. Since each random addition cycle rapidly converged to equal tree scores, cycles were not extended to more than 500 iterations, nor were further cycles added. Shortest trees collected from the different tree islands were used to compute a strict consensus tree.

Bayesian analyses were conducted using the Markov-chain-Monte-Carlo algorithm of MrBayes 3.1.4 (Ronquist and Huelsenbeck, 2003) for 10 million generations under the GTR model (Rodríguez-Sánchez et al., 1990), assuming invariable positions and a gamma-distributed substitution rate heterogeneity (GTR+G+I). This model had been determined as best-fit model by the likelihood ratio test implemented in Modeltest 3.7 (Posada and Crandall, 1998). Four chains were run simultaneously for each dataset, according to MrBayes' default setting, with every 1000th tree sampled. In all analyses average standard deviation of split frequencies had dropped below 0.01 after completion of the generations. After discarding trees yielded before likelihood stationary (burnin=2000), the remaining 8000 trees were summarized in a 50% majority rule consensus tree, using posterior probabilities (PP) as a measure of clade support. All branchings below 0.75 posterior probability were collapsed and only PP's of 95 and higher were considered significant. Since branching patterns of both approaches were highly congruent and no bootstrapping algorithm was available for PRAP, only the Bayesian trees are illustrated here. To assess degree of phylogenetic congruence between the two different datasets, an Incongruence Length Test (ILD), as implemented in PAUP 4b10 (Hompart) was performed using 1000 simple addition sequence replicates and a maximum of 1000 trees held at each step.

Results

The *trn*K sequences of the 208 accessions ranged from 2375-2477 bp. The alignment was 2655 bp long and contained 81 indels. For Analysis 148 positions were excluded, a block of 141 bp due to the "primer-gap" and another 7 bp where the alignment was ambiguous. Of the remaining 2507 positions, 414 were parsimony informative. Eighty Indels had been coded of which 33 were informative.

The 208 accessions of the *trn*L-F matrix ranged from 772-838 bp, resulting in an alignment length of 1000 bp with 14 positions excluded. 138 bp and 27 of the 59 indels coded were parsimony informative.

ITS sequences generated for this study ranged from 593-621 bp. The aligned matrix, including outgroups, consisted of 180 was 704 bp long and contained 95 indels. 28 positions were excluded due to ambiguity of alignment. For ITS 265 positions were parsimony informative, and 31 indels.

Tree topologies resulting from Bayesian inferences of the combined *trn*K/*trn*L-F and the nuclear ITS dataset with indels coded as additional binary characters are shown in Fig. 1.A-E, with the partially conflicting topologies plotted against each other. Maximum parsimony analysis using a parsimony ratchet as implemented in SeqState (Müller 2005) resulted in highly similar tree topologies (data not shown). Coding of indels did not affect tree topology while it increased support for internal nodes in part considerably.

Corresponding to the number of informative characters, resolution of branches increased from *trn*L-F to *trn*K and ITS. Among the single plastid phylogenies no incongruences were observed. Since both share the same evolutionary history as part of the halpoid chloroplast genome, they were analyzed in a combined matrix (Yuan and Olmstead, 2008). In chloroplast and ITS tree topologies the same monophyletic crown groups are indicated. Relationship between these groups can differ remarkably. Accordingly, the homogeneity partition test was significant (P=0.001) and a combined analyses of plastid and the nuclear dataset was not supported.

Chloroplast *trn*K/*trn*L-F

In the *trn*K/*trn*L-F analysis, the ingroup (= Menthinae s.str.) consists of a polytomy with three maximum supported clades. According to taxonomic affiliation of the majority of taxa included therein, they are labeled as *Satureja*-, *Micromeria*- and *Clinopodium*-group here (Fig. 1.A).

The *Satureja*-group (Fig. 1 B), is composed of all but two species of *Satureja* and of *Gontscharovia*. Samples of the latter genus and a lineage containing *Satureja thymbra* and *S. pallaryi* are placed as basal polytomy to the core group of *Satureja*. The latter is split in two subclades, one containing *S. montana* and the other *S. hortensis*.

The *Micromeria*-group (Fig. 1.C) is formed by representatives of *Micromeria*, *Origanum*, *Pentapleura*, *Saccocalyx*, two *Satureja* species, *Thymbra*, *Thymus*, and *Zataria*. *Micromeria* is monophyletic as circumscribed in Bräuchler et al. (2008a; pp=1.00), internal branching pattern is consistent with previous analysis (Bräuchler et al., 2005). The sister group to

Micromeria though weakly supported (pp=0.79), shares a remarkable 60 bp deletion in the 3′-terminal part of the *trn*K intron (indicated by the black bar in Fig. 1.C). Its two subgroups yield maximum support. *Pentapleura* and *Zataria* are indicated as monophyletic (pp=1.00) as sister to the rest of the species. *Thymbra* and a group of species currently included in *Satureja* are strongly supported as sister (pp=0.95) to a clade containing *Thymus* and *Origanum* species along with the monotypic genera *Argantoniella* and *Saccocalyx* with *Thymus* indicated as paraphyletic with respect to other taxa.

In the *Clinopodium*-group (Fig. 1.D) three major lineages are placed as basal polytomy. The first is strongly supported and contains as sister groups the recently described genus *Killickia* (Bräuchler et al., 2008b, Fig. 1.D-2) and the "*Micromeria*" *madagascariensis* group (Fig. 1.D-1) respectively. The second lineage contains a monophyletic group comprising all representatives of *Cyclotrichium* (Fig. 1.D-3) as sister to species of *Mentha* (Fig. 1.D-4) and "*Micromeria*" *cymuligera*. Most taxa placed in the third lineage, are currently included in *Clinopodium* (see introduction for details). Sister to all other accessions is a clade containing *C. nepalense* (*Clinopodium nepalense*-group, Fig. 1.D-5) and the "*Acinos*"/*Ziziphora* lineage (Fig. 1.D-6) with the position of *Clinopodium debile* not resolved among these two groups. In the "*Acinos*"/*Ziziphora* lineage species of both entities are intercalating and do not form discrete clusters with their congeners. The next group also consists of three strongly supported clusters. The first consists of *Clinopodium* s.str. (Fig. 1.D-7) with the type species (*C. vulgare*) included in one subcluster, *C. chinense* and associated species in another one. The second cluster consists of species related to *C. abyssinicum* (Fig. 1.D-8). In the third cluster *C. simense* and allies (Fig. 1.D-9) are strongly supported sister to the remaining accessions. Two lineages of *Bystropogon* (Fig. 1.D-10) are placed at the base of a highly supported monophyletic group including all New World genera of Menthinae along with the New World species of *Clinopodium* (New World group, Fig. 1. E).

Resolution within the New World group is rather poor. Affinities of *Clinopodium douglasii*, *C. brownei*, *C. vimineum*, *Cunila origanoides*, *C. leucantha*, *Hesperozygis rhodon* and *Obtegomeria caerulescens* are unclear, given their placement in a large polytomy. The first among the more species rich lineages therein comprises *Minthostachys* and *Clinopodium* species (Fig. 1.E-1; pp=1.00; *Minthostachys* group). Further groupings indicated are: *Cuminia*, *Kurzamra*, *Clinopodium darwinii* and *C. multiflorum* (Fig. 1.E-2; pp=0.94; *Kurzamra* group); *Acanthomintha*, *Pogogyne* and *Monardella* (Fig. 1.E-3; pp=1.00; *Acanthomintha* group); *Hoehnea*, *Rhabdocaulon* and *Hesperozygis nitida* (Fig. 1.E-4; pp=1.00; *Hoehnea* group). The largest clade (pp=0.94) is split in two with the first branch (Fig. 1.E-5; pp=1.00; *Hedeoma* group) containing all sampled species of *Hedeoma* along with *Poliomintha*, *Rhododon* and *Clinopodium glabrum*. The second branch includes *Blephilia*, *Pycnanthemum/Monarda* (Fig. 1.E-6; called the *Monarda* group though not forming a clade here) and a cluster of *Clinopodium georgianum*, *C. coccineum*, *C. dentatum*, *Conradina canescens* and *Piloblephis rigida* (Fig. 1.E-7; pp=1.00; *Conradina*-group).

Nuclear ITS

In the nuclear ITS phylogeny *Horminum* is sister to *Agastache* supporting its dissociation from subtribe Menthinae. The ingroup is split in the same three major groups found in the plastid marker analysis (Fig. 1.A). Terminal groups are generally in accordance with the *trn*K/*trn*L phylogeny, their relationships, however, are not congruent in several cases.

In the *Micromeria*-group (Fig. 1.C). *Thymus* is indicated as paraphyletic with respect to *Saccocalyx* and *Argantoniella* but not *Origanum* which is placed as sister to this lineage. Topology in the *Clinopodium*-group (Fig. 1.D) differs to a great extent from the chloroplast phylogeny. For better overview the corresponding crown groups thus are labelled with an asterisk in Fig. 1. The group is split weakly supported into two lineages (pp=0.91/0.93). In the first the *Killickia* and "*Micromeria*" *madagascariensis* group (Fig. 1, D-1*+2*; pp=1.00/1.00) are sister to a group containing *Cyclotrichium* (Fig. 1.D-3*; pp=1.00) and *Mentha* (Fig. 1.D-4*; pp=1.00) which are also indicated as closely related in the plastid data set. In the ITS phylogeny, the *Clinopodium nepalense* (Fig. 1.D-5*; pp=1.00) and the weakly supported *C. abyssinicum* group (Fig. 1.D-8*; pp=0.93) form a monophyletic lineage with the former genera, but are assigned to different clades in the plastid phylogeny (Fig. 1.D8/9). The weakly supported New World group (pp=0.93; Fig. 1.D) is placed as sister to an Old World lineage that includes as subsequent sister taxa: *Bystropogon* (Fig. 1.D-10*; pp=1.00), the "*Acinos*"/*Ziziphora* group (Fig. 1.D-6*; pp=1.00), the *Clinopodium simense* group (Fig. 1.D-9*; pp=1.00) and *Clinopodium* s.str. (Fig. 1.D-7*). In the plastid phylogeny these taxa are paraphyletic with respect to the New World group. It is important to emphasize that accessions of this group are comparatively poorly represented in the ITS matrix, but the mixture of "*Acinos*" and *Ziziphora* species is confirmed. Within the New World group (Fig. 1.D/E) there is not much increase in resolution in comparison to the plastid dataset, and some groups indicated in the plastid phylogeny are not resolved. The *Minthostachys* group is not indicated as monophyletic (Fig. 1.E-1*). *Minthostachys* forms a weakly supported monophyletic lineage (pp=0.90) with *C. sericeum* as sister (pp=0.96). *C. gilliesii*, *C. vanum*, *C. axillare* and *C. bolivianum* show closer relationships (pp=0.94), while in the plastid phylogeny the latter groups with *Minthostachys*. The *Kurzamra* and *Acanthomintha* group are also not resolved using ITS (Fig. 1.E-2*/3*).

Monardella, in the ITS phylogeny, is represented by three accessions and strongly supported as monophyletic (pp=1.00). The *Hedeoma* group is split into subsequent sisters to the remaining species which form the only large and well supported monophyletic group in the New Word group in the ITS phylogeny. *Poliomintha incana* and *Rhododon ciliatus* form one cluster (pp=0.98) at the base, and a monophyletic *Hedeoma* cluster (pp=1.00) is sister to the other taxa (pp=0.97). The species of *Glechon* (pp=0.85) group with *Hesperozygis spathulata* (pp=0.97) while the affinities of *Hoehnea epilobioides* (only representative of the plastid *Hoehnea* group included), *Hesperozygis rhodon* and *Cunila galioides* are unclear. A predominantly North American group (pp=0.96) comprises *Cunila incana* placed in a polytomy with two distinct clades (pp=0.85/1.00) corresponding to the *Monarda* and the *Conradina* group respectively. The weakly supported *Monarda* group (Fig. 1.E-6*) includes in the ITS phylogeny the three monophyletic genera *Monarda* (pp=0.97), *Blephilia* (pp=1.00) and *Pycnanthemum* (pp=0.99). In the *Conradina* group (Fig. 1.E-7*), the two genera *Dicerandra* and *Conradina* are indicated as monophyletic (pp=1.00). Three species of *Clinopodium* cluster together strongly (pp=1.00), while affinities of *Stachydeoma graveolens*, *C. georgianum* and *Piloblephis rigida* are unclear.

Discussion

This study represents the first comprehensive phylogeny of subtribe Menthinae. For numerous taxa this is the first phylogenetic assessment overall, other taxa were subject to previous studies but have not been investigated in a broader context. In the cpDNA dataset, where we included a higher number of outgroups, the sister group of the Menthinae was formed by representatives of subtribe Nepetinae (*Agastache*, *Glechoma*, *Nepeta*), strongly supporting the monophyly of Menthinae as defined here (Tab. 1). Accordingly *Lycopus* and *Horminum*, included in Menthinae by Harley et al. (2004) based on evidence available then, are considered as part of the outgroup here.

The ingroup in both datasets, is divided in three major evolutionary lineages with terminal groups largely congruent between markers. Despite topological conflicts in relationships between terminal groups, both the congruence of crown groups and the broad sampling of this study allow a number of taxonomic conclusions, especially changes in generic delimitations and species assignments to certain genera.

For example, a high percentage of taxa in Menthinae had been regarded as part of the genus *Satureja* at one moment of their taxonomic history causing much of today´s confusion (see Tab. 1). Harley et al. (2004) incorporated much of the most recent molecular and morphological findings and restricted *Satureja* to a comparatively small number of species. Despite this narrow description, our study revealed a persistent polyphyly of *Satureja* sensu Harley et al. (2004), indicating the necessity of further changes in the generic circumscription. In our analysis a group containing *S. linearifolia* and *S. thymbrifolia* is associated with *Thymbra* and clearly divided from the remaining *Satureja* s.str. in both datasets. Further, the split of *Argantoniella* from *Satureja* is confirmed. *Micromeria* as redefined based on morphological and molecular data by Bräuchler et al. (2008a), is highly supported as monophyletic. Some of the phylogenetically clearly separated taxa, now excluded from the genus ("*Micromeria*" *madagascariensis* group and "*M.*" *cymuligera*), are still awaiting alternative placement (see Tab. 2).

We regard our data as especially useful in evaluating the circumscription of *Clinopodium*. Recently a high number of species have been included in *Clinopodium* resulting in a large genus of high morphological variability, similar to the earlier treatments of *Satureja*. The New World Menthinae, here represented by species of 22 genera (*Acanthomintha*, *Blephilia*, *Conradina*, *Cuminia*, *Cunila*, *Dicerandra*, *Glechon*, *Hedeoma*, *Hesperozygis*, *Hoehnea*, *Kurzamra*, *Minthostachys*, *Monarda*, *Monardella*, *Obtegomeria*, *Piloblephis*, *Pogogyne*, *Poliomintha*, *Pycnanthemum*, *Rhabdocaulon*, *Rhododon* and *Stachydeoma*) shown to be monophyletic. Both phylogenies illustrate that New World species currently included in *Clinopodium* (see asterisks in Fig. 1.E) do not form a monophyletic group but are scattered throughout this large New World clade, demonstrating that the current circumscription of the *Clinopodium* is highly unnatural. Some existing alternative generic names for these taxa now in the synonymy of *Clinopodium*, for example, *Diodeilis* Raf., *Gardoquia* Ruiz and Pavon, *Oreosphacus* Phil. or *Xenopoma* Willd., will need to be re-employed to achieve a classification system representing monophyletic, well characterized groups. It seems however clear that typical *Clinopodium* is absent from the Americas as are *Micromeria* and *Satureja* (except for introduced species as *C. menthifolium*, *C. nepeta* and *C. vulgare*). The monotypic genera *Eriothymus* (probably extinct according to Harley et al., 2004) and *Neoeplingia* were not sampled for this study since in both cases only type collections were at hand. At least in the case of *Eriothymus rubiaceus* there is evidence from morphology that the genus is embedded in the New World Menthinae clade. Similar to some *Hesperozygis* species it has a 13-nerved calyx, 2 stamens and ovate, coriaceous, shortly petiolate leaves. *Neoeplingia* seems to be more difficult to place for the obovate spathulate leaves with a serrate margin are unusual in other New World Menthinae. In addition the deeply lobed calyx as well as the broad and obtuse calyx lobes with only one prominent median vein per lobe would be unique in context of the group. In our opinion it may even be placed in another subtribe of Mentheae, molecular analysis of material available just now will help clarify this soon. In the Old World, delimitation of *Clinopodium* to *Ziziphora* and other genera remains unclear and need further research.

Comparing our molecular results with current concepts demonstrates that it will be difficult to diagnose the genera by a single synapomorphy each, but that it might be possible by a combination of characters. Part of todays taxonomic confusion undoubtfully can be attributed to the fact that many scientists making floristic treatments or describing new species preferred following one of the already existing concepts rather than taking on the daunting task of a global revision. Another major point, however, is that many of the traditional concepts obviously have been based on homoplasious morphological characters. One example are the number of calyx veins. *S. linearifolia and S. thymbrifolia* have been considered as part of *Satureja* sect. *Zatarioideae* Boiss. due to it´s five-nerved calyx (Hedge & Feinbrun, 1968). According to our analysis equal number of veins is rather a matter of convergence, while shape of the calyx at throat seems to be a more diagnostic character. It is useful for distinguishing *Satureja* from *Thymbra*, in which the two mentioned species of *Satureja* are embedded (Fig. 1.C; see Appendix for full discussion). The number of stamens (4 or 2) has been used to characterize certain genera or larger entities in traditional concepts (e.g. Briquet 1895-1897) in both the New and the Old World. While tendencies towards reduction to 2 stamens can be observed e.g. in *Clinopodium* ("*Acinos*" and some New World taxa) there are only two instances where this character seems to support natural groups in our tree topologies (Fig. 1.E: *Hedeoma* and *Hoehnea* group). Transitions are also observed between straight and sigmoid calyces, characters used to distinguish between "*Acinos*" and *Ziziphora*. While most of *Clinopodium* taxa in the Old World have sigmoid calyces there are at least two groups that have a tendency to straight ones (Fig. 1.D: *C. abyssinicum*, *C. nepalense*), further emphasizing homoplasy in this feature. In the New World *Clinopodium* the species with large orange red corollas frequently have been regarded as forming a natural unit ("*Gardoquia*") as well as those with small white flowers ("*Xenopoma*"). However, these groups are unlikely to be monophyletic. *Minthostachys* for example, characterized by small white fly pollinated flowers, is indicated as closely related to *Clinopodium sericeum*, characterized by large red hummingbird pollinated flowers, rather than to other small white flowered *Clinopodium* taxa. Pollinator switches are suggested as a driving force for diversification resulting in a high level of homoplasy in corolla characters. Taxonomic implications of our findings for all groups are discussed in the Appendix in detail and in order of the groups appearance in the trees (cf. Fig. 1.A-E). Problems and potential morphological synapomorphies or other shared features are addressed, using own investigations of the herbarium material used for this study or extracted from literature.

Incongruence between tree topologies for phylogenies inferred from datasets of different cellular compartments are reported from an increasing number of groups throughout the Angiosperms (e.g. Rieseberg and Soltis, 1991; Soltis and Kuzoff, 1995; Hardig et al., 2000; Albach and Chase, 2004; Guo et al., 2004; Jakob and Blattner, 2006; Fehrer et al., 2007). In Lamiaceae examples are the genera *Phlomis* (Albaladejo et al., 2005), *Sideritis* (Barber et al., 2007), and, within subtribe Menthinae, *Bystropogon* (Trusty et al., 2004), *Conradina* (Edwards et al., 2006, 2008a), *Dicerandra* (Oliveira et al., 2007) and *Mentha* (Gobert et al., 2006). In New World Menthinae incomplete lineage sorting of ancestral polymorphisms as well as ancient or recent hybridizations (Edwards et al., 2006, 2008a, 2008b; Schmidt-Lebuhn, 2007) have been suggested as potential sources for the incongruences. Trusty et al. (2004) argued for homoplasy in the ITS dataset to account for differing affinities of *Bystropogon*. While this could also be considered for other topologically close groups (e.g. the *Clinopodium simense* group), visual inspection of the underlying ITS sequence alignment revealed no position linking the *C. nepalense* group to "*Acinos*". Chloroplast capture, as recently detected for the *Verbena* group (Yuan and Olmstead, 2008), could be a more appropriate explanation for this as well as other conflicts at deeper nodes, for incomplete lineage sorting at this level could be rejected due to a four times faster coalescence in organelles (Moore, 1995). PCR capture of non paralogous ITS sequences, another potential source of incongruences, was neither detected in our analysis nor in one of the previous studies based on the ITS sequences obtained from GenBank. In the New World group low overall sequence divergence in both datasets is in strong contrast to the considerable morphological and ecological diversity (as indicated by placement of the corresponding taxa in more than 20 genera). Thus a fast colonization accompanied by speciation/radiation could be assumed to account for the lack of topological structuring at the base of the clade. Considering both previous findings and results from our study, it seems likely that all of the mentioned processes contributed to the complex phylogenetic pattern observed.

Biogeographical implications

Considering the overall distribution of genera and distinct lineages in light of our tree topology, several interesting patterns are revealed that can be used to draw general biogeographic conclusions for Menthinae s.str.

Many of the major lineages in the Mediterranean, both basal, morphologically isolated taxa and the most species rich are found in the east of the region. This indicates that these groups differentiated earlier then their relatives in the west as postulated by Quezel (1978) and suggested for other groups, e.g. *Limonium* by Lledo et al. (2005).

In the *Satureja* lineage (Fig. 1.B), *S. montana* and allies extend more westwards (with a centre of morphological diversity on the Balkan Peninsula), while the *S. cuneifolia* group includes several accesions stemming from the east, with *S. mutica* at the base. The position of *S. pallyari* from Syria as sister to the widespread *S. thymbra* and that of *Gontscharovia*, distributed from Iran to Pakistan, in a basal polytomy to all other taxa, further support an eastern origin for the lineage. Increased sampling will probably not change this picture, for most unsampled taxa are found in the Irano-Turanian region.

In *Micromeria* s.str. (Bräuchler et al., 2008a), two centres of diversity can be found, one in the W Mediterranean (especially Canary Islands and adjacent Morocco) and the E Mediterranean (Turkey and adjacent areas), apparently correlating to the clades found in the plastid phylogeny (Fig. 1.C). Species coverage needs to be extended to allow general conclusions on the origin of the group. However, distribution of *Pentapleura*, *Zataria* (both restricted to the Irano-Turanian region) and *Thymbra* (probably originating from the East, since all but one taxa are found there) along with the position of the widespread *M. biflora*/*imbricata* complex, spanning the distance from the mountains of N India and S China to the South African Transvaal, indicate an origin of the whole lineage in the east. The placement of *M. forbesii* favours colonization of the Cape Verde Islands independent to that of the Canary Islands (Bräuchler et al., 2005), possibly using a sub-Saharan migration route (Quezel, 1978). Our data do not support close relationship among taxa of the two Island groups (Pérez, 1978) as consequence of long distance dispersal between them, as suggested for e.g. *Echium* L. (Böhle et al., 1996), *Sonchus* L. (Lee et al., 2005) and *Tolpis* Adans. (Moore et al., 2002) is not supported by our data. Sampling of relictual populations in the inner Saharan mountains (Tibesti) and more widespread ones from western Central Africa may help clarify the actual origin of *Micromeria forbesii*.

Irrespective of the incongruent topologies and limited taxon sampling, *Origanum* and *Thymus* could mark another Mediterranean E/W split with secondary migrations west- and eastwards respectively. In *Origanum*, *O. dayi* found in the east is sister to the remaining species. While this could be an artefact of low sampling density, an eastern origin has been postulated by Ietswaart (1980) and is supported by distribution ranges of species as well. Apart from the most widespread *O. vulgare* (Spain to Taiwan), only very few species reach the W Mediterranean. About 75% of the total number are restricted to the east (Ietswaart, 1980). Thus the largest part of the morphological diversity in the genus is represented in the eastern Mediterranean. In *Thymus* in contrast, the greatest morphological diversity is found in the western Mediterranean, though the genus extends as far east as Japan. The taxa of *Thymus* sect. *Micantes*, sister to all other taxa irrespective of the position of *Origanum*, are found in the W further underlining an origin in that area. Such E/W splits in Mediterranean lineages are not uncommon and have been reported for other taxa before (e.g. *Digitalis*, Bräuchler et al., 2004). The monotypic genera *Saccocalyx* and *Argantoniella*, restricted to few localities in northern Algeria and the surroundings of the isthmus of Gibraltar respectively, might represent relicts of this split, probably isolated as consequence of the Messinian salinity crisis, which accounts for the high level of endemism in that area (Ojeda et al., 1996; Rodríguez-Sánchez et al., 2008).

The *Clinopodium* lineage (Fig. 1.D) appears quite complex not only from a taxonomic but also from a biogeographical perspective. An early diverging lineage (the ancestor of *Killickia* and the "*Micromeria*" *madagascariensis* group) probably migrated to South Africa along the East African mountain chains followed by a single dispersal event to Madagascar. This fits the general trend for the Madagascan floristic elements being of African origin (for review see Yoder and Nowak, 2006). The sister group relationship of the two groups is of particular interest. Both occur in similar montane to alpine habitats in the Drakensberg and the Central Madagascan mountains and show comparatively low scale radiation, with the South African taxa being more diverse in floral traits. While previous studies primarily have focused on endemic, species rich groups of tropical habitats (e.g. Janssen et al., 2008), to our knowledge there is no report on taxa restricted to those montane habitats, so far. Studies to help understanding speciation in both groups are in progress.

Tropical African and S African *Mentha* are clearly derived from N Temperate/Mediterranean populations, representing a third dispersal/migration event to that region in Menthinae. *Mentha canadensis* L. the only species native to the New World, according to Tucker and Chambers (2002) has a disjunct distribution range across the Beringian Sea. In accordance the molecular results of Bunsawat et al. (2004) place it close to taxa of Europe and Japan.

Though affinities of *Clinopodium abyssinicum* and allies basically occurring in Tropical African mountain chains and highlands (Ryding, 2006a) are unclear, the close position of *Cyclotrichium* in the ITS dataset might indicate a colonization from the Irano-Turanian region. Despite the doubtful placement of one accession of *C. myrianthum* (see Fig. 1.D) in the plastid phylogeny, two distinct subgroups are indicated in both nuclear and plastid phylogeny. The *C. abyssinicum*/*paradoxum* group occurs from the southern tip of the Arabian penisula through the Ethiopian and Kenyan highlands to Tanzania. *C. paradoxum* with its long runners much resembles some species of *Mentha* or *Clinopodium* s.str. in general habit, while *C. abyssinicim* in its transitional series from herbs to shrubs, the lack of runners and (in var. *condensatum*) similar inflorescence structure seems to link to the *C. myrianthum*/*robustum* group. This group has a more southern distribution range from S Tanzania to Cameroon and Angola and comprises basically tall woody herbs or shrubs reaching up to 2.5 m, with spike-like inflorescences. Overlap of distribution of the two groups according to Ryding (2006a) is restricted to a very small zone in the S of Tanzania indicating a geographical separation as driving force for divergence of the two groups.

The precise position of the monophyletic New World lineage within the *Clinopodium* group remains unclear. The plastid dataset contains a strong signal for a distribution from Africa to the New World indicated by the basal position of two *Bystropogon* lineages and the *Clinopodium simense* group. The grouping of the latter with the type species *C. vulgare* and that of *Bystropogon* with "*Acinos*"/*Ziziphora* and *Clinopodium* s.str. in the ITS tree topology (Fig. 1.D), could result from homoplasy. Much has been discussed about the means and routes of dispersal/migration between Old and New World resulting in two major theories, each supported by numerous molecular studies: migration via ancient land bridges (primarily the Beringian landbridge (BLB and the North Atlantic landbridge, NALB; Milne, 2006) or long distance dispersal (for review see Renner, 2004). Recently, the landbridge theory was favoured for Lamoideae tribe Synandreae of Lamioideae (Scheen et al., 2008), though without clear support for one or the other possibility. For genera of Nepetinae (*Agastache* and *Meehania*) and the aforementioned *Mentha canadensis*, however, the BLB can be assumed as a possible corridor for colonization based on current patterns of distribution, while it seems unlikely for the rest of Menthinae. None of the taxa indicated closer to the root of the New World clade are distributed through eastern Asia. The position of the Canarian endemic *Bystropogon* either at the base of the New World group or of Old World *Clinopodium* might indicate a migration via the NALB. Under this assumption presence of clearly basal lineages would be expected to be restricted to North America. The candidate clades in our study, the *Conradina* and members of the *Monarda* group, however, are indicated as crown groups in both datasets. Despite the basal polytomy in the New World lineages, the placement of generally rather South/Central American groups, supports a long distance dispersal scenario. Area of origin was probably NW Africa or the West Mediterranean as inferred at genus level for *Eryngium* (Calviño et al., 2008) and even at species level for *Senecio* (Coleman et al., 2003) and *Oligomeris* (Martín-Bravo et al., 2009).

The vector for long distance dispersal, in our case, however, remains enigmatic. Myxocarpy, observed in most members of Nepetoideae (Ryding, 2001) is assumed to facilitate attachment of nutlets to animals, presumably birds; according to Renner (2004) there are, however, no known bird migratory routes across the Atlantic. Wind dispersal may be an alternative explanation, though equally speculative.

In this study numerous accessions of New World groups stemming in part from several smaller scale studies are analyzed together to get a first insight on evolution of the New World group in a global context. Lack of resolution at the base of the monophyletic group including no less than 22 genera (Fig. 1.E) is mainly caused by comparatively low content of phylogenetic informative positions in the sequence data. Considering the overall distribution of the included taxa, this indicates a fast colonization/dispersal across large parts of South and Central America with possibly several dispersals/migrations to North America; followed by considerable radiation in each of the diverging lineages. Driving forces for this might be both availability of new pollinators (e.g. hummingbirds) and newly emerging niches by rise of the Andes as indicated for e.g. *Lupinus* (Hughes and Eastwood, 2006) or *Castilleja* (Tank and Olmstead, 2008). In addition Pleistocene glaciations apparently affected distribution of the spreading lineages especially in Northern America. Today´s distributions of the monophyletic lineages found there to a great extent overlap, probably due to several subsequent range fragmentations and expansions. In the *Monarda* group, a concentration of diversity more towards the west (especially Texas) can be observed (McClintock and Epling, 1942; Grant and Epling, 1942), with one species (*Pycnanthemum californicum*) extending as far as California. The *Conradina* group in contrast has its centre of diversity in the east on the Florida Peninsula and the adjacent Panhandle (Edwards et al., 2006; Oliveira et al., 2007). This deep split probably results from habitat fragmentation into different glacial refugia and fits the results from other studies dealing with taxa from SE North America (for review see Soltis et al., 2006). The plastid topology indicates a single colonization of the Californian area by the *Acanthomintha* group. Lack of monophyly of the group in the ITS dataset is probably a consequence of the mechanisms cited above and probably does not reflect reality. Radiation of the group in the changing environment was probably triggered by uplift of the surrounding mountain chains and resulting isolation and aridification of the Californian Basin as found in numerous other groups of organisms (for review see Calsbeek et al., 2006). It remains to be tested whether the three New World *Clinopodium* species endemic to that area, *C. chandleri* (Brandegee) P.D.Cantino & Wagstaff, *C. ganderi* (Epling) Govaerts and *C. mimuloides* (Benth.) Kuntze are descendants from one common ancestor or, as would be concluded from morphology, represent at least two further distinct lineages. Doroszenko (1986) placed the latter species in the monotypic genus "*Montereya*" (a name never published), while for the former two he created an also unpublished section of *Xenopoma*. For South America the plastid dataset indicates at least three distinct lineages, which could result from a deep split of the range of a widespread ancestor. The *Hoehnea* group, is centred in the Parana region and comprises some ecological and morphologically similar genera, adapted to at least seasonally very humid habitats. Another lineage, the *Kurzamra* group, is restricted to the Southern Andes of Chile and adjacent Argentina and the Juan Fernandez Archipelago. Though the placement of the island endemic genus *Cuminia* fits the distribution of other members of the clade, the relationships are neither corroborated by any morphological trait nor the ITS data. Finally a group, not supported by ITS, but with support in the chloroplast tree topology, consists of *Minthostachys* and species of *Clinopodium*, primarily distributed to the Northern and Central Andes. The lack of affinities of *Obtegomeria* to any of the subclades in addition to its isolated distribution in the paramos of the Sierra Nevada de la Santa Martha, Colombia, suggests it might constitute a relict of an early diverging lineage. To address the problem of incongruent topologies and to test the robustness of the groups indicated in our study, taxon sampling is currently being expanded to cover more taxa of New World *Clinopodium*, *Cunila*, *Hedeoma* and other poorly represented genera such as *Glechon*. Future approaches will include ploidy level assessment for many more additional taxa and employment of alternative nuclear markers to increase resolution and discriminate between effects of incomplete lineage sorting, homoplasy or true hybridization/introgression events. This will hopefully help to further elucidate the complex evolutionary and biogeographic history of the group.

Appendix I: Taxonomic implications

Satureja: The genus as circumscribed in Harley et al. (2004) is unambiguously revealed as polyphyletic. The group of *S. linearifolia* and *S. thymbrifolia* is excluded here but associated with *Thymbra* instead (see under that genus for details). *Argantoniella salzmannii*, recently considered as generically distinct (López and Morales, 2004), but included in *Satureja* in Harley et al. (2004) is highly supported as forming not part of *Satureja* s.str. but embedded in *Thymus*. The polyphyly of *Satureja* as currently circumscribed could be settled by excluding these groups from the genus, requiring only slight modifications in its circumscription. The calyx lobes (teeth) are usually narrow linear towards the apex and comparatively longer in relation to the calyx tube than in *S. linearifolia* and allies. The best character however separating the two groups is the calyx not dorsiventraly compressed and wide at throat in *Satureja* s.str. and slightly compressed and narrow at throat in the aforementioned taxa. The close position of *Gontscharovia* to *Satureja* s.str. is corroborated by similarities in ptyxis, leaf anatomy (Bräuchler, unpubl. data) and phytochemistry (Sefidkon and Jamzad, 2006). The importance of the 15-nerved calyx in distinguishing the two genera seems doubtful given the difficulties in counting calyx “nerves”, especially those regarded as secondary or tertiary ones (Ryding, 2007). The acute nutlet apex as opposed to an obtuse apex seems a more reliable character to distinguish *Gontscharovia*. The generic status has been questioned by Vvedensky (1961) due to erroneously described characters in the diagnosis (Borissova, 1953). The former author, however, placed the taxon in *Micromeria* which is neither supported by morphology nor our molecular data.

Micromeria: Monophyly of the genus as recircumscribed in Bräuchler et al. (2008a) is strongly supported. Exclusion of the South African (Bräuchler et al., 2008b) and Madagascan *Micromeria* species along with section *Cymularia* Boiss. & Hausskn. turned the genus into a homogeneous unit, morphologically more easily defined by the combination of a thickened marginal leaf vein with the calyx tubular to campanulate, not sigmoid and gibbous at base. More detailed studies on the monophyletic group of Canary Island species have been presented by Meimberg et al. (2006).

***Pentapleura*/*Zataria*:** Distant relationships between these two genera and towards *Origanum* have been assumed by Handel-Mazzetti (1913) based on inflorescence and calyx structure, but doubted by Davis (1982). Resembling some *Origanum* species in vegetative features, the two genera appear taxonomically isolated. *Zataria* is more widespread from Iran to Pakistan and characterized by very small actinomorphic calyces with equal lobes and five nerves visible. *Pentapleura* in contrast is a genus restricted to SE Turkey and N Iraq and has cylindrical 10-nerved calyces, with the five primary veins forming weak wings. Both distant affinities to *Origanum* and the isolated position of these genera within the "*Micromeria*-group" are underlined by the basal position in the *Thymbra-Origanum* lineage. The closer relationships between the two taxa as indicated by placement in a clade of their own and low sequence divergence, however are surprising judging from overall habit. However, similarities in leaf shape, indumentum and venation are apparent.

Thymbra: The latest treatments (Morales, 1987; Harley et al., 2004) accept four species, all of which were sampled for our study. The genus is indicated paraphyletic with respect to two species currently included in *Satureja* (*S. linearifolia* and *S. thymbrifolia*) occurring from Jordan to Lybia. *S. linearifolia* was originally placed in a genus of its own, *Euhesperida* (Brullo and Furnari, 1979). *S. thymbrifolia* was described earlier (Hedge and Feinbrun, 1968), but Doroszenko (1986) included it in *Euhesperida*, without effectively publishing the new combination. The authors responsible for the description of *S. nabateorum* (Danin and Hedge, 1998), a third taxon from that alliance not sampled here, recognized the close relationships of their respective new species towards *S. linearifolia* and *S. thymbrifolia*. They did not accept the generic distinctness of *Euhesperida* but preferred all three species being placed in *Satureja*. At a first glance there are morphological affinities towards species of *Satureja*, particularly shape of inflorescence, leaf arrangement and similarity in calyx structure (e.g. *S. bachtiarica*). The conduplicate leaf arrangement, however, is also found in all *Thymbra* species and the same lax inflorescence is characteristic for *T. calostachya*. The dense indumentum and shape of the leaves (rather linear but never spatulate or broadest distally from the middle) are features further linking them to the latter species. Leaf architecture is more similar to that found in *Thymbra* than to that in *Satureja* (Bräuchler, unpubl. data). A dorsiventrally compression of the calyx is diagnostic for *Thymbra* and caused by condensation of flowers in headlike inflorescences tightly embraced by bracts. This feature is very weakly developed in *S. linearifolia* and allies as is the case in *Thymbra calostachya*, for all these species have long, lax inflorescences instead. Another diagnostic character is the calyx being narrow at the throat, as also found in the *S. linerarifolia* group, compared to wide at the throat in *Satureja* s.str. species. As outlined, both molecular data and morphological characters favour transfer of the *S. linearifolia* group to *Thymbra*.

Thymus: In our analysis *Thymus* is represented by accessions of 5 sections of the 8 currently recognised (Jalas, 1971; reviewed in Morales, 2002): sect. *Thymus* (*T. vulgaris*), sect. *Mastichina* (*T. mastichina*), sect. *Serpyllum* (*T. magnus*, *T. pulegioides*, *T. quinquecostatus*, *T. serpyllum*), sect. *Hypodromi* (*T. broussonetii* subsp. *hannonis*, *T. haussknechtii*), sect. *Micantes* (*T. caespititius*, *T. saturejoides*). The genus is indicated as paraphyletic with respect to a number of taxa. Since the inclusion of *Origanum* was only inferred in the plastid dataset analysis, it might be a result of plastid introgression rather than one of common ancestry. Thus we feel it is premature to reflect this possible relationship in the classification and nomenclature. The position of the monotypic genera ***Argantoniella*** and ***Saccocalyx*** is a different story, for they are nested within *Thymus* in both analyses. Both differ from *Thymus* in having oblong nutlets as opposed to ovoid to globose ones (pers. obs.) and an unusual calyx structure. In *Argantoniella* the calyx is tubular, very weakly bilabiate with the semi-obtuse lobes equal. In *Saccocalyx*, the calyx greatly enlarges in fruit, resulting in a blown up "capsule" for the seeds which is dispersed by wind and giving the plant an unmistakeable aspect. Despite these considerably aberrant features both taxa fit well within the range of *Thymus* section *Micantes* – accessions of which cluster with the latter in both analyses – regarding leaf shape, anatomy (Bräuchler, unpubl. data) and in the case of *Argantoniella* also growth form (especially *T. saturejoides* or *T. caespititius* from which they are hard to distinguish at the vegetative stage). The ciliate margins towards the leaf base and prostrate rooting stems are characters shared with several *Thymus* species from Spain and the North African Mediterranean and in addition to the calyx clearly separating *Argantoniella* from *Satureja*. Given the striking dissimilarities towards other *Thymus* species, we feel however it is premature to make nomenclatural changes until completion of an ongoing comprehensive phylogenetic study at species level. We hope this will provide a better understanding of calyx and nutlet character evolution in the group. The phylogeny is not well enough resolved to make statements about sectional classification except for the clear separation of sect. *Micantes* from the rest.

Origanum: This genus is supported as monophyletic group in both analyses. Morphologically very diverse it is yet well characterized by cymes often condensed in spikes with comparatively large bracts which are often imbricate and brightly coloured, and by lacking bracteoles. Six of the ten sections recognized by Ietswaart (1980) covering most part of the genus morphological variation were sampled: *Amaracus* (Gleditsch) Benth. (*O. dictamnus*), *Brevifilamentum* Ietswaart (*O. rotundifolium*), *Campanulaticalyx* Ietswaart (*O. dayi*), *Chilocalyx* (Briq.) Ietswaart (*O. microphyllum*), *Elongatispica* Ietswaart (*O. elongatum*), *Origanum* (*O. vulgare*). *O. dayi* is placed at the base in both analyses, fitting the relict character of its distribution area (Sinai).

Killickia: This isolated lineage is placed within the "*Clinopodium*-group" and not part of *Micromeria* s.str.. These species are similar to other taxa of *Clinopodium* and allied genera but clearly differ in the combination of a campanulate to sub-campanulate actinomorphic calyces and nutlets being covered all over in scattered minute hairs. Consequently they were placed in the newly created genus *Killickia* by Bräuchler et al. (2008b).

"*Micromeria*" *madagascariensis* group: The Madagascan species group *M. flagellaris*, *M. sphaerophylla* and *M. madagascariensis* are sister to *Killickia* and neither part of *Micromeria* nor *Clinopodium*. Though Doroszenko (1986) placed them in a section of their own within *Micromeria,* the corresponding name ("sect. *Madagascarenses*") was never validly or effectively published. The dissociation from *Micromeria* has never been discussed before. The noted overall similarity to East African *Clinopodium* (Hedge et al., 1998; Doroszenko, 1986) is not supported as significant by our molecular analysis. Examination of types and other herbarium material, lead us to the conclusion that generic status will be the best solution to unambiguously place these species. The corresponding publication is in preparation.

Cyclotrichium: While accepted as generically distinct in the most recent treatments (Davis, 1982; Harley et al., 2004), the species of this genus have been placed under *Calamintha*, *Micromeria* or *Satureja* by former workers (e.g. Bentham, 1848; Boissier, 1879; Briquet, 1895--97). Our analyses indicate that they are a strongly supported distinct entity in all markers, which is also supported by two key features, a dense annulus of hairs within the corolla tube and long exserted stamens and styles. According to Harley et al. (2004), a revolute corolla further distinguishes the genus. Though topologically close to *Mentha* in the ITS phylogeny, the sister group relationship as indicated in the cpDNA analysis is not supported. So far there are no reports of morphological or anatomical characters closer linking both genera. Some species of *Mentha* (e.g. *M. aquatica* and *M. arvensis*), however, show a ring of hairs in the corolla throat. Branching pattern within *Cyclotrichium* apparently fits that of a forthcoming study on the genus (T. Dirmenci, pers. comm.) and will be addressed there in more detail.

Mentha: *Mentha* is supported as monophyletic by both nuclear and cp DNA analyses (though based on very restricted sampling) including *M. cervina*, which sometimes has been placed in a genus of its own (*Preslia* Opiz). None of the Australian *Mentha* species have been sampled for this study but corresponding *trn*L-F sequences (Bunsawat et al., 2004) clustered with the other accessions from the genus when included in our dataset (data not shown). It is unlikely these data have been affected by chloroplast introgression due to the geographic isolation of the Australian taxa. A surprise is the affiliation of the enigmatic **"*Micromeria*" *cymuligera***, formerly placed in section *Cymularia*, with this clade. Sequences gained from an isotype sample (JE) partially were of poor quality and obtaining an ITS sequence was not possible. There are several other facts favouring placement close to *Mentha* and outside of *Micromeria*. Although the species would still be morphologically isolated within *Mentha*, the overall habit resembles some *Mentha* species. Foliose bracts and bracteoles and a calyx with ciliate lobes occur also in e.g. *M. pulegium*. The reduced corollas and the clearly pedunculate cymes are another feature not uncommon in *Mentha*. The ecological preferences of "*Micromeria*" *cymuligera* (damp alpine grassland and torrent beds) also are similar to those of *Mentha* species, whereas true *Micromeria* species as a rule are absent from these humid places but prefer a more xeric habitat (pers. obs.). Moreover "*M.*" *cymuligera* lacks the most characteristic generic feature, leaves with a thickened marginal ring vein, and thus is clearly not part of *Micromeria* s.str.. Consequently the species has been excluded from that genus by Bräuchler et al. (2008a). Since there is doubt about the inclusion in *Mentha* as well, we decided, however, not to make any nomenclatural change until better material for analysis is available.

Bystropogon: The results of our study fit those of Trusty et al. (2004; 2005), based on comprehensive sampling of the genus. In the nuclear phylogeny the genus is strongly supported as monophyletic and placed as sister to the *Clinopodium*/"*Acinos*"/*Ziziphora* clade. The chloroplast phylogeny does not support this and places the two different lineages of the genus at the base of the New World group. Two divergent lineages corresponding to the two recognised sections are revealed by both analyses. The poor support for the sister group relationship of the two lineages in the cpDNA analysis could be explained by an ancient rapid split followed by geographically independent radiation (Trusty et al., 2005). Previously assumed close relationships to *Minthostachys* (Epling, 1936) or *Cuminia* (Harley, 1986) are not corroborated in our analysis.

Clinopodium s.l.

As stated above, in its current circumscription, this is taxonomically the most difficult and morphologically most diverse genus in Menthinae. Most of the groups recently transferred to *Clinopodium* without doubt fit much better here than in any of the other genera currently accepted. Due to the conflicts in the different tree topologies it iscurrently not feasible to draw a conclusion regarding the precise delimitation of the genus. Each of the monophyletic subgroups, corroborated by both nuclear and plastid data, are discussed below.

***Clinopodium abyssinicum* group**: Members of this predominantly tropical African group were until recently kept separately under *Satureja* (*C. robustum*, *C. myrianthum*) and *Micromeria* (*C. abyssinicum*) or united under *Satureja* (Seybold, 2006). Doroszenko (1986) placed some of the species in a genus of their own ("*Brenaniella*", a name never published), while *C. abyssinica* was included in *Micromeria* (sect. *Pseudomelissa*) and *C. paradoxum* in *Calamintha*. Ryding (2006a), preferred to accommodate all the species in *Clinopodium*. Placed in a polytomy with core *Clinopodium* and the expanded New World clade (including *Bystropogon* and the *C. simense* group) in the cp DNA analysis, the group is placed close to *Mentha* in the ITS phylogeny. The species all share a narrowly funnel-shaped to tubular calyx and parallel anthers (Ryding, 2006a), but the delimitation with regard to *Clinopodium* s.str. remains unclear. Generic rank might be appropriate.

Clinopodium debile: This species has been regarded as generically distinct, under the name *Antonina* Vved., by Vvedensky (1961). To date there have been no suggestions of relationships to either "*Acinos*", *Ziziphora* or the *Clinopodium nepalense* group. Doroszenko (1986) mentions the similarity in leaf shape between *C. debilis* and *C. piperitum* but reinvestigation of type material (at W and K) revealed this as insignificant. Shape of the calyx seems somehow intermediate between "*Acinos*" and the *C. nepalense* group. Since no ITS sequence could be obtained for this species, its relationship need further investigations.

***Clinopodium nepalense* group**: These Himalayan species formerly of *Micromeria* sect. *Pseudomelissa*, have recently been transferred to *Clinopodium* (Bräuchler et al., 2006) and are highly supported as a natural group in both nuclear and chloroplast data. The close affinities of *Clinopodium piperitum* to date have not been recognized, probably due to a lack of a comprehensive treatment. Doroszenko (1986), who includes that species in *Calamintha*, only states that it is isolated within the genus due to a narrowly tubular calyx. Topologically the group is not close to other members of sect. *Pseudomelissa* (e.g. *C. serpyllifolium*) underlining its anomalous character even within *Clinopodium*. Clearly dissociated from *Micromeria* s.str., the *C. nepalense* group could also be regarded as deserving recognition at genus level if *Clinopodium* is to be understood in a narrow sense. Shared characters of all species of the group are narrowly tubular, comparatively long calyces, long corolla tubes and leaves with slightly lobed or very rarely few-toothed margins. Closer affinities to the "*Acinos*"/*Ziziphora* group, as found in the cpDNA tree (Fig. 1.D), are neither supported by ITS data nor by morphology (see also discussion about conflict of topologies).

"Acinos"/Ziziphora: *Clinopodium* sensu Harley at al. (2004) is revealed as unnatural with respect to the placement of this lineage. While "*Acinos*" either has been kept separate or included in *Clinopodium*, the generic status of *Ziziphora* was never questioned. A closer relationship between "*Acinos*"and *Ziziphora* was indicated by both morphological (López and Bayer, 1988) and molecular (Trusty et al., 2004) data. Though the first study showed a transitional series of calyx and anther structures, only a common ancestry of the two genera was suggested, but not a unification under one generic name. Trusty et al. (2004) only included one species per genus, thus the relationships of the two taxa remained unclear. The close relationship is indicated in both cp and nuclear DNA. The ITS data currently suggests two options: to keep the lineage separate under one generic name or include it in *Clinopodium*. In the former case *Ziziphora* would be recognized for reasons of priority. The plastid data also favour this option due to the position of *Bystropogon* and the New World group, which would also have to be included in *Clinopodium*, if the inclusive *Clinopodium* option was chosen.

***Clinopodium* s.str.** : A well defined group of the cp DNA phylogeny consists of Old World members of the genus *Clinopodium* (including *Calamintha* and some species formerly placed in *Micromeria* sect. *Pseudomelissa*). In the ITS dataset this group is represented by *C. vulgare* alone due to problems with PCR amplification from herbarium material. More detailed study of this group is underway.

***Clinopodium simense* group**: All taxa of this group appear closely related and have been assigned to *Satureja* (Briquet, 1895--97; Hedberg, 1957; Seybold, 1988), *Calamintha* (Bentham, 1848; Vatke, 1872) or even *Acinos* (Doroszenko, 1986). Recently they were placed in *Clinopodium* (Ryding, 2006b) since they share a two lipped calyx, often with a gibbous base and unequal style branches. While placed as sister to *Bystropogon* and the New World group and dissociated from typical *Clinopodium* in the cpDNA analysis, the group is sister to the latter in the ITS phylogeny, though placed on a long branch.

***Clinopodium* and the New World group**: The species of subtribe Menthinae native to the New World (except for *Mentha canadensis*) are indicated as a single evolutionary lineage in both nuclear and chloroplast phylogeny. Weaker support for this clade in the ITS dataset probably results from homoplasy (Trusty et al., 2004). While the content of phylogenetically informative characters is low in the plastid dataset, branching pattern as shown in the ITS dataset might further be affected by hybridization and incomplete lineage sorting. However, introgression of chloroplasts, might account for the biogeographic signal found in the plastid dataset. The clade includes 22 genera as well as New World species of *Clinopodium* whose taxonomic placement appears artificial given the topological dissociation from typical (Old World) *Clinopodium*. Some workers accomodated the taxa in several smaller genera such as *Gardoquia* (e.g. Bentham 1848, 1876) or *Xenopoma* (Willdenow, 1811; Grisebach, 1874, 1879). According to the most commonly accepted system, all of these taxa have been placed in *Satureja* s.l. (Briquet, 1896; Epling and Játiva, 1964) with several of the former segregates upheld as subunits of one large genus. Recently this concept was more or less simply renamed as *Clinopodium* s.l. Due to the scattered distribution of *Clinopodium* species thoughout the New World clade, some of the aforementioned older generic names probably will need to be reestablished though most likely none of the resultant genera will match previous delimitations. The type species of *Xenopoma* for example, *X. obovata* Willd. (a synonym of the older *Satureja viminea* L., now *Clinopodium vimineum*) is unresolved at the base, while taxa associated with that generic name by Grisebach (1874, 1879), e.g. *Minthostachys verticilata* or *C. bolivianum*, are embedded in separate groups. The same is true for *Gardoquia* where the type species (*Gardoquia multiflora* Ruiz & Pav., now *C. multiflorum*) is separated from other taxa previously included under this name (e.g. C. *sericeum*, *C. revolutum*).

The ITS dataset for the New World clade is much more comprehensive than the plastid dataset since a large number of sequences were available from GenBank due to previous studies on e.g. *Bystropogon* (Trusty et al., 2004), *Conradina* (Edwards et al., 2006), *Dicerandra* (Oliveira et al., 2007), *Minthostachys* (Schmidt-Lebuhn, 2008), *Monarda* (Prather et al., 2002), and *Salvia* (Walker and Sytsma, 2007). Though there are considerable differences in the fine scale resolution of the lineages between the chloroplast and the DNA datasets, again some of the crown groups are supported in both analyses. The low level of informative characters favours the theory of a very fast radiation of the group. Since many of the branches of our analysis are weakly supported even in the Bayesian inference tree, only some well characterized groups are listed below.

***Minthostachys* group:** The monophyly of *Minthostachys* as inferred by Schmidt-Lebuhn (2008) is weakly corroborated by inclusion of the ITS sequence data in our comprehensive generic dataset, but not in the plastid dataset, due to the lower number of informative characters. It is interesting that in our analysis *C. sericeum*, not included in Schmidt-Lebuhn (2008) but mentioned to be habitually similar to *Minthostachys* by the occasional presence of drooping branches, is indicated as sister to that genus. However, floral characters do not support the assumption of a close relationship between C. *sericeum*, having large orange-red flowers, and *Minthostachys* having rather inconspicuous white flowers. *C. bolivianum*, also clustering with *Minthostachys* in the cpDNA tree, is placed separately in the ITS dataset, forming part of a group including *C. axillare*, *C. gilliesii* and *C. vanum*, all sharing a similar calyx shape. Since *Minthostachys* is neither close to *Bystropogon* nor *Cuminia* nor

Pycnanthemum in any of the tree topologies, these previously suggested relationships (Epling, 1936; Ruiz et al., 2000) could be ruled out here.

Kurzamra* group:** This group is supported in the plastid but not in the ITS dataset, for which sequences were available only for *Clinopodium multiflorum* and *Cuminia eriantha*. The high Andean Atacama endemic *Kurzamra* in the plastid phylogeny is forming a clade with two ***Clinopodium species (*C. darwinii* and *C. multiflorum*) and ***Cuminia***. *Clinopodium darwinii* has a low mat to cushion forming habit remarkably similar to that of *Kurzamra*, while it greatly differs in calyx structure. The Chilean *C. multiflorum*, type of the formerly separate genus *Gardoquia* (see above), is highly divergent from the other members of the clade in having large, dark pink, possibly hummingbird pollinated corollas. In the ITS phylogeny it groups with another Chilean species characterized by similar corollas, but different leaf shape. While placed in basal polytomy of the New World clade in the ITS dataset, there is weak support for inclusion of *Cuminia* in this clade in the plastid dataset. The genus is not indicated closely related to *Bystropogon*, as previously suggested based on similarities in corolla structure, general habit and inflorescence (Harley 1986). Assumptions of close relationships to *Minthostachys* suggested by similarities in calyx structure (Ruiz et al., 2000) are also not corroborated by our analysis. Further distinction of two species within *Cuminia* as argued for by Ruiz et al. (2000) based on morphology and ITS sequence data remains doubtful given the pseudogene identity of the ITS 1 sequences of that study as revealed by incorporation in our dataset. Minor differences between the ITS sequence of *Cuminia* generated for the study of Trusty et al. (2004) and our own corresponding sequence, apparently are rather to be attributed to uncorrected base detection errors in the raw sequence files, than to the existence of true sequence divergence among individuals. From a conservation biology point of view it would be most interesting to investigate the genetic structure of *Cuminia* populations assigned to different taxa previously. Whether forming of the group in the plastid phylogeny is artificial and result of chloroplast introgression, as suggested by the biogeographical proximity of all taxa, or the lack of support for the group in the ITS phylogeny is an artifact of reduced sampling or orther factors affecting ITS needs further research.

Acanthomintha* group: *Monardella is supported as monophyletic in the ITS phylogeny though affinities are not clear. In the chloroplast dataset, the single accession for this genus comes out close to ***Pogogyne*** and *Acanthomintha,* while this is not supported by the nuclear data. *Acanthomintha* is shown strongly supported monophyletic in the cp DNA phylogeny, but weakly in the ITS phylogeny (0.55 pp, branch collapsed). The sequences obtained for this study cluster well, the one obtained from GenBank in contrast is dissociated. The plastid phylogeny again is in concordance with biogeography since all three genera are distributed in SW USA and NW Mexico. In addition at least *Acanthomintha* and *Pogogyne* are ecologically very similar, and some species are sympatric vernal pool plants.

Hoehnea* group:** This group includes two species of ***Rhabdocaulon (as sisters), *Hoehnea epilobioides* and ***Hesperozygis nitida***. These genera together with other species have been united in Bentham´s (1848) *Keithia* previously and at least the former two are similar in habit primarily by having almost sessile leaves and distinctly quadrangular stems. Inclusion of a second *Hesperozygis* species is only weakly supported (0.75 pp) in the cp DNA analysis. This group is not indicated in the ITS dataset where two of the species without resolution are placed together with some North American clades (Fig. 1.E). ITS sequences for *Rhabdocaulon* could not be obtained for this study. The two species of *Hesperozygis* included in the ITS phylogeny are dispersed and might not form a natural group.

Hedeoma* group:** The species of *Hedeoma* are shown in a strongly supported clade in both analyses. Since neither any of the species from South America nor the type species have been included here, it is premature to conclude the genus as currently circumscribed is monophyletic. The distinctness of ***Obtegomeria , included in *Hedeoma* by Bentham (1848), is underlined by its topological dissociation from *Hedeoma*. ***Rhododon*** and ***Poliomintha***

indicated as sisters dissociated from *Hedeoma* in the ITS phylogeny, without further resolution are placed in the same clade in the plastid phylogeny. The placement of *Clinopodium glabrum* in this group in the latter tree topology is interesting considering its original description as a species of *Hedeoma* (Nuttall, 1818), but needs further confirmation by ITS data.

Monarda **group**: *Monarda* is supported as monophyletic in the ITS phylogeny supporting the findings of Prather et al. (2002). In the cp DNA phylogeny the two samples represented are sisters. ***Pycnanthemum*** and ***Blephilia*** are supported as monophyletic in the ITS phylogeny. In the former included taxa cover both the morphological variation and geographical distribution, in the latter two out of three accepted species are included. Their placement close to *Monarda* is supported by cp DNA analyses also, though with slightly different branching patterns. All taxa are similar in both vegetative and inflorescence features.

Conradina **group**: Within this group the monophyly of the genera *Conradina* and ***Dicerandra***, as revealed in Edwards et al. (2006) and Oliveira et al. (2007) on reduced datasets, is confirmed in the ITS phylogeny. The latter genus with maximum support was the first to diverge, which is supported by its unique spurred anthers (Huck et al., 1989). Whereas closer affinity of the monotypic ***Stachydeoma*** remains unclear, several ***Clinopodium*** species (*C. coccineum*, *C. dentatum* and *C. ashei*) strongly group together. These taxa are very similar in inflorescence and flower structure and leaf shape, and have been placed in *Diodeilis* by Doroszenko (1986), a genus proposed by Rafinesque (1836) but never used since then. The monotypic *Piloblephis* and *C. carolinianum* (better known under the younger name *C. georgianum*) are indicated as more closely related to *Conradina*.

Non-monophyletic groups: Several genera of the New World lineage are indicated as not monophyletic in our analysis: *Cunila*, *Hesperozygis* and possibly *Acanthomintha* and *Hedeoma* (Bräuchler, unpubl. data).

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Legends for tables and figure:

Table 1: Genera of Menthinae as defined here (Menthinae s.str.) with total species numbers (italics indicate uncertainity of exact number) and taxa sampled in each dataset (plastid/ITS). Genera containing species at one point or another in time included in *Satureja* s.l. are marked in bold. Important generic names currently not recognized as distinct (following Harley al., 2004) are indicated in brackets.

Table 2: List of taxa included in this analysis including voucher information and repository (herbarium abbreviations according to Holmgren and Holmgren, 1998). Genbank accession numbers for sequences are provided for each marker along with reference to place of original publication in those cases where sequences of previous studies were included. References are indicated by running numbers following the corresponding accession number and are as follows: (1) Bräuchler et al., 2005; (2) Prather et al., 2002; (3) Trusty et al., 2005; (4) Walker and Sytsma, 2007; (5) Schmidt-Lebuhn, 2007; (6) Edwards et al., 2006; (7) Trusty et al., 2004; (8) Freeman, published in GenBank; (9) Sitthithaworn et al., published in GenBank; (10) Kim et al., published in GenBank; generic names are given in bold on their first occurrence and abridged to the initial letter for the following entries. Taxa with more than one accession sampled are indicated by running numbers following the name. Generic concept according to Table 1, accepted species names are those of Bräuchler et al. (2008a, b) and Govaerts (1999); and partially differ from those under which the original sequences have been submitted. Author abbreviations are in accordance with IPNI (2009). For each sample a running number is provided in the last column, which corresponds to the sequence number in the alignment (see supplementary material). Data entry for each sample follows the following scheme: taxon/voucher information/accession-nr. *trn*K/accesion-nr. *trn*L-F/accession-nr. ITS/alignment number for sequences.

Figure 1: 50% majority rule consensus tree of the 8000 single trees inferred from Bayesian analysis of the combined *trn*K/*trn*L-F (left) and the ITS (right) dataset. Topologies are plotted against each other to illustrate topological conflicts. Posterior probablilities are provided as measure of clade credibility and indicated above branches. All branches below 0.75 pp have been collapsed. Indels supporting clades are indicated by dots (*trn*K) or circles (*trn*LF) under the corresponding branches. Due to the large number of taxa, the tree is divided in five parts. -- **A:** Overview, with outgroup (taxa present in both datasets printed in bold) and the three major lineages; the New World group embedded within the *Clinopodium* group. **B:** *Satureja* group. **C:** *Micromeria* group. **D:** *Clinopodium* group, with subgroups numbered subsequently. Those inferred from the ITS analysis (right) are followed by an asterisk. Dashed lines are linking corresponding groups of the two datasets. **E**: New World group; asterisks here indicate position of taxa currently included in *Clinopodium*. To faciliate discussion, same groups are marked in both datasets though sometimes either not monophyletic in both datasets or including additional accessions.

Table 1:

Genus with synonyms	number of species	sampled in cp/ITS dataset
Acanthomintha (A.Gray) Benth. & Hook.f.	4	3/3
***Argantoniella* López & Morales**	1	1/1
Blephilia Raf.	3	1/2
Bystropogon L´Hér.	7	2/5
***Clinopodium* L. (*Acinos* Mill., *Calamintha* Mill.)**	ca. 100	48/36
***Conradina* A.Gray**	6	1/5
Cuminia Colla	1	1/1
***Cunila* D.Royen ex L.**	15	2/3
***Cyclotrichium* (Boiss.) Manden. & Scheng.**	8	6/6
***Dicerandra* Benth.**	8-9	-/4
Eriothymus (Benth.) Rchb.	1	-/-
Glechon Spreng.	6-7	-/2
***Gontscharovia* Boriss.**	1	1/1
***Hedeoma* Pers.**	42	4/5
Hesperozygis Epling	8	2/2
Hoehnea Epling	4	1/1
***Killickia* Bräuchler, Doroszenko & Heubl**	4	4/4
Kurzamra Kuntze	1	1/-
***Mentha* L.**	20	5/2
***Micromeria* Benth.**	54	18/3
Minthostachys (Benth.) Spach	17	2/8
Monarda L.	20	2/16
Monardella Benth.	30	1/3
Neoeplingia Ramamoorthy, Hiriart & Medrano	1	-/-
***Obtegomeria* P.D.Cantino & Doroszenko**	1	1/1
Origanum L. (*Majoranum* Mill.)	40	6/6
Pentapleura Hand.-Mazz.	1	1/1
***Piloblephis* Raf.**	1	1/1
Pogogyne Benth.	7	1/1
Poliomintha A.Gray	7	2/1
***Pycnanthemum* Michx.**	17-21	1/5
Rhabdocaulon (Benth.) Epling	7	2/-
Rhododon Epling	1	1/1
***Saccocalyx* Coss. & Durieu**	1	1/1
***Satureja* L. (*Euhesperida* Brullo & Furnari)**	38	14/9
Stachydeoma Small	1	1/1
Thymbra L.	4	4/4
***Thymus* L.**	ca. 220	5/6
Zataria Boiss.	1	1/1
Ziziphora L.	20	5/4

Table 2:

Taxon	**Voucher**	***trn*K**	***trn*L-F**	**ITS**	**Number in alignment**
Acanthomintha *ilicifolia* (A.Gray) A.Gray	Mexico, Baja California, R. Moran 23495, 5.6.1976, W	GU381738	GU381575	GU381414	>1
A. lanceolata Curran	USA, California, R. Alava 891, 20.5.1957, W	GU381737	GU381574	DQ667333 (4)	>2
A. obovata Jepson	USA, California, H.A.Walker 5094, 18.5.1919, M	GU381736	GU381573	GU381413	>3
Agastache *foeniculum* (Pursh) Kuntze	cult. BGM (origin USA), C. Bräuchler 2513, 26.06.2003, M	AY840146 (1)	GU381480	AY506660 (7)	>4
Ajuga *reptans* L.	cult. BGM (origin Germany), C. Bräuchler 2508, 26.06.2003, M	AY840130 (1)	GU381470	-	>5
Argantoniella *salzmannii* (Kuntze) G. López & R.Morales	Spain, Prov. Cadiz, A.Barra, G.Lopez & R.Morales 2673 GL, 25.6.1981, M	GU381795	GU381640	GU381461	>6
Blephilia *ciliata* (L.) Benth.	USA, Tennessee, R. Kral 46722, 24.5.1972, BM000927115	GU381743	GU381580	GU381416	>7
B. hirsuta (Pursh) Benth.		-	-	AF369168 (2)	>8
Bystropogon *canariensis* (L.) L'Hér.	Spain, Canary Islands, Tenerife, C. Bräuchler 2092, 12.06.2004, M	GU381726	GU381563	-	>9
B. canariensis var. *smithianus* Christ 1	Spain, Canary Islands, El Hierro, G. Heubl, 28.3.2003, M	GU381725	GU381562	GU381408	>10
B. canariensis var. *smithianus* Christ 2		-	-	AY706475 (3)	>11
B. origanifolius L’Hér. 1	Spain, Canary Islands, Tenerife, C. Bräuchler 2296, 15.06.2004, M	GU381727	GU381564	GU381409	>12
B. origanifolius L’Hér. 2	Spain, Canary Islands, Tenerife, C. Bräuchler 2323, 16.06.2004, M	GU381728	GU381565	-	>13
B. origanifolius L’Hér. 3	-	-	-	AY704591 (3)	>14
B. origanifolius var. *canariae* La Serna	-	-	-	AY704587 (3)	>15
B. origanifolius var. *ferrensis* (Ceballos & Ortuño) La Serna	-	-	-	AY704585 (3)	>16
B. origanifolius var. *palmensis* Bornm.	-	-	-	AY704588 (3)	>17
B. plumosus (L.f.) L’Hér.	-	-	-	AY704586 (3)	>18
B. punctatus L’Hér.-	-	-	-	AY704582 (3)	>19
B. wildpretii La	-	-	-	AY704584 (3)	>20

Serna					
Clerodendrum *thomsoniae* Balf.f.	cult. BGM (origin unknown), C. Bräuchler 2511, 26.06.2003, M	AY840129 (1)	GU381471	-	>21
Clinopodium *abyssinicum* (Benth.) Kuntze 1	Ethiopia, Shewa Region, J. J. DeWilde, 8730, 09.11.1965, B	GU381708	GU381545	-	>22
C. abyssinicum (Benth.) Kuntze 2	Ethiopia, Shewa Region, I. Friis, A. Tesfay & G. Gibre-Hiwot 8212, 17.11.1997, C	GU381709	GU381546	-	>23
C. abyssinicum (Benth.) Kuntze 3	Kenya, Marsabit Distr., Hepper & Jaeger 6839, 16.11.1978, P	GU381711	GU381548	-	>24
C. abyssinicum (Benth.) Kuntze 4	Kenya, Cherangani Mts. A.G. & L.C. Miller 1163, 25.8.1979, E, E00207250	GU381707	GU381544	GU381403	>25
C. abyssinicum var. *condensatum* (Hedberg) Ryding	Ethiopia, Kaffa Prov., I. Friis, A. Hounde, & K. Jacobsen 490, 27.11.1970, C	GU381710	GU381547	-	>26
C. acinos (L.) Kuntze 1	France, Podlech 50287, 21.06.1992, M	AY840144 (1)	GU381497	GU381384	>27
C. acinos (L.) Kuntze 2	Germany, Bavaria, C. Bräuchler 3132, 08.07.2004, M	GU381664	GU381498	-	>28
C. alpinum (L.) Kuntze	cult. BGM, C. Bräuchler 2502, 26.06.2003, M	AY840145 (1)	AY840180 (1)	AY227141 (7)	>29
C. ashei (Weath.) Small	-	-	-	DQ667237 (4)	>30
C. atlanticum (Ball) N. Galland	Morocco, Prov. Marrakech, D. Podlech 47788a, 8.7.1989, MSB	GU381697	GU381531	-	>31
C. axillare (Rusby) Harley	-	-	-	DQ017565 (5)	>32
C. barosmum (W.W.Sm.) Bräuchler & Heubl	China, Prov. Yünnan, McLaren "N" Collection 193, July 1933, BM	GU381683	GU381517	GU381393	>33
C. betulifolium (Boiss. & Balansa) Kuntze	Turkey, M. Nydegger 42298, 09.10.2003, B	GU381698	GU381532	-	>34
C. bolivianum (Benth.) Kuntze	Peru, Depto Moaquegua, Weigend, M., Rodriguez R., Lawrence, C., Ludwig, D., Peter, H. & Caceres H. 2000-575, 29.04.2000, M	GU381766	GU381607	GU381434	>35
C. brownei (Sw.) Kuntze	Bahamas, Inagua, W.T.Gillis & G.R.Proctor 11737, 18.2.1973, B	AY840176 (1)	GU381593	GU381426	>36
C. carolinianum Mill.	USA, South Carolina, Leonard 1926, 09.09.1968, M	GU381748	GU381587	GU381422	>37
C. chilense (Benth.) Govaerts	Chile, Prov. Coquimbo. C.Jiles 2855, 20.11.1955, M	-	-	GU381431	>38

C. chinense var. *parviflorum* (Kudô) H.Hara	Japan, Hokkaido, S. Kariyama 53250, 28.08.2003, M	GU381704	GU381541	-	>39
C. coccineum (Nutt. Ex Hook.) Kuntze	USA, Florida, S.L. Orzell & E.L.Bridges, 14.9.1989, M	AY840150 (1)	GU381585	GU381421	>40
C. creticum (L.) Kuntze	Greece, Crete, Merxmüller & Podlech 30851, 26.09.1975, M	AY840175 (1)	GU381533	-	>41
C. cylindristachys (Epling & Játiva) Govaerts	Peru, Prov. Bongara, Dept. Amazonas, Hutchison & Wright 3869, 29.1.1964, M (Isotype)	GU381764	GU381605	GU381433	>42
C. darwinii (Benth.) Kuntze	Chile, Prov. Ultima Esperanza, A. Landero 655, 9.12.1986, M	AY840171 (1)	GU381601	-	>43
C. debile (Bunge) Kuntze	Uzbekistan, M.Popov 6799, 25.7.1926, M	GU381696	GU381530	-	>44
C. dentatum (Chapm.) Kuntze	USA, Florida, R.Kral 52169, 24.9.1973, M	GU381747	GU381586	AY943486 (6)	>45
C. discolor (Diels) C.Y.Wu & S.J. Hsuan ex H.W.Li	China, Yunnan, Sino-Amer. Bot. Exped. 289. 19.06.1984, E, E00207257	GU381702	GU381539	-	>46
C. douglasii (Benth.) Kuntze	Cult. BGFB (bought at local market as Indian mint, origin USA), C. Bräuchler 3682, 9.2.2009, M	GU381753	GU381592	GU381425	>47
C. fasciculatum (Benth.) Govaerts	-	-	-	DQ017558 (5)	>48
C. flabellifolium (Epling & Játiva) Govaerts	Peru, Depto Piura, M. Weigend & N.Dostert 98-193, 16.5.1998, M	GU381767	GU381608	GU381435	>49
C. gilliesii (Benth.) Kuntze	-	-	-	DQ017566 (5)	>50
C. glabrum (Nutt.) Kuntze	USA, Tennessee, D.L. Holland 13, 5.6.1996, MO	GU381742	GU381579	-	>51
C. graveolens subsp. *rotundifolium* (Pers.) Govaerts	Morocco, D. Podlech 47181, 27.06.1989, M	GU381667	GU381501	-	>52
C. hydaspidis (Falc. ex Benth.) Kuntze	Pakistan, J. Mohd 133, 8.9.1956. BM000927119	GU381681	GU381515	GU381391	>53
C. jacquelinae Schmidt-Leb.	-	-	-	DQ017557 (5)	>54
C. kilimandschari (Gürke) Ryding	Kenya, Kilimandscharo (Plot Re2), Rehder s.n., 15.03.1983, M	GU381721	GU381558	-	>55
C. megalanthum (Diels) C.Y.Wu & S.J.Hsuan ex H.W.Li	China, Yunnan: Gaoligong Shan Expedition (GSE97) 8978, 13.09.1997, E00114673	GU381703	GU381540	-	>56
C. menthaefolium subsp. *ascendens* (Jordan) Govaerts	France, Bellotte 89-1994, 04.10.1994, M	AY840152 (1)	GU381535	-	>57
C. micranthum	Japan, Hokkaido, S.	GU381705	GU381542	-	>58

(Regel) H.Hara	Kariyama 53251, 28.08.2003, M				
C. multiflorum (Ruiz & Pav.) Kuntze	Chile, Prov. Concepción, J. Grau s.n., 30.3.1968, M	GU381761	GU381602	GU381432	>59
C. myrianthum (Baker) Ryding 1	Tanzania, Songea District, E. Milne-Redhead & P. Taylor 10517, 25.05.1956, B	GU381714	GU381551	GU381405	>60
C. myrianthum (Baker) Ryding 2	Malawi, Distr. Nitchisi, Blackmoore, S.; Brummitt, R.K.; Badna, E.A.K. 1419, 04.05.1980, C	GU381717	GU381554	-	>61
C. nanum (P.H.Davis & Doroszenko) Govaerts	Greece, Crete, C. Bräuchler 2796, 31.03.2004, M	GU381666	GU381500	GU381385	>62
C. nepalense (Kitam. & Murata) Bräuchler & Heubl 1	Nepal, J.D.A.Stainton 6024, 5.10.1967, FR	GU381680	GU381514	GU381390	>63
C. nepalense (Kitam. & Murata) Bräuchler & Heubl 2	Nepal, M.Mikage, N.Anjiki, N.Kondo, R.Lacoul & K. Yonekura 9550294, 1995, BM000927128	GU381679	GU381513	GU381389	>64
C. nepeta (L.) Kuntze	cult. BGM, Bräuchler 2392, 26.06.2003, M	AY840151 (1)	GU381534	-	>65
C. nubigenum (Kunth) Kuntze	Venezuela, B. & F. Oberwinkler 12933, 3.10.1968, M	GU381765	GU381606	DQ017563 (5)	>66
C. paradoxum (Vatke) Ryding	Ethiopia, Mooney 8633, s.d., M	GU381706	GU381543	GU381402	>67
C. piperitum (D.Don) Murata 1	Nepal, A.R.Vickery 454, 24.3.1974, BM000927118	GU381677	GU381511	GU381388	>68
C. piperitum (D.Don) Murata 2	Nepal, J.D.A. Stainton 7320, 20.3.1975, E00207255	GU381678	GU381512	-	>69
C. polycephalum (Vaniot) C.Y.Wu & S.J.Hsuan ex P.S.Hsuan	China, Yunnan, Gaoligong Shan Expedition (GSE96) 7463, 13.10.1996, E00161610	GU381701	GU381538	-	>70
C. revolutum (Ruiz & Pav.) Govaerts	Peru, Weigend & Dostert 98-195, 16.05.1998, M	AY840170 (1)	GU381609	GU381436	>71
C. robustum (Hook.f.) Ryding 1	Cameroon, Bamenda div., Hepper 2122, 21.2.1958, P	GU381715	GU381552	-	>72
C. robustum (Hook.f.) Ryding 2	Ecuatorial Guniea, Bioco, Fernández Casas 11176, 05.02.1999, BR	GU381716	GU381553	-	>73
C. robustum (Hook.f.) Ryding 3	Cameroon, Mt. Cameroon, S. Dressler s.n., 27.2.2007, M	GU381713	GU381550	GU381404	>74
C. robustum (Hook.f.) Ryding 4	Cameroon, Mt. Oku, C. Bräuchler 4005, 05.03.2007, M	GU381712	GU381549	-	>75
C. sericeum (C.	Peru, Depto Cajamarca,	GU381768	GU381610	GU381437	>76

Presl ex Benth.) Govaerts	Weigend, M., Dostert, N., Drießle, K. 97-378, 5.2.-2.4.1997 MSB				
C. serpyllifolium (M.Bieb.) Kuntze	Turkey , A8, Erzurum, K.P.Buttler & T.Saglamtimur 16045, 13.9.1971, FR	GU381699	GU381536	-	>77
C. serpyllifolium (M.Bieb.) Kuntze subsp. *fruticosum* (L.) Bräuchler	Spain, Lippert 25633, 05.09.1989, M	AY840161 (1)	AY840197 (1)	-	>78
C. simense (Benth.) Kuntze	Ethiopia, Gamo Gofa, O. Ryding, C. Puff, N. Sileshi, & A. Tibebu 1642, 10.12.1988, UPS	GU381722	GU381559	GU381407	>79
C. speciosum (Hook.) Govaerts		-	-	DQ017560 (5)	>80
C. suaveolens (Sm.) Kuntze	Sizilien, Erben, 04.06.1988, M	GU381665	GU381499	-	>81
C. thymifolium (Scop.) Kuntze	Croatia, Künne s.n., 08.1994, M	AY840162 (1)	AY840201 (1)	-	>82
C. tomentosum (Kunth) Govaerts	-	-	-	DQ017559 (5)	>83
C. troodi (Post) Govaerts	Cyprus, P.H.Davis 1856, 14.7.1940, W	GU381671	GU381505	-	>84
C. uhligii (Gürke) Ryding	Kenya, Rehder s.n., 15.03.1983, M	GU381720	GU381557	-	>85
C. uhligii var. *obtusifolium* (Avetta) Ryding 1	Cameroon, Mt. Cameroon, Franke, T. & Beenken, L., 26.10.2002, M	GU381718	GU381555	GU381406	>86
C. uhligii var. *obtusifolium* (Avetta) Ryding 2	Cameroon, Mt. Oku, C. Bräuchler 4006, 05.03.2007, M	GU381719	GU381556	-	>87
C. uhligii var. *obtusifolium* (Avetta) Ryding 3	Tanzania, J. Raynal 19455, 6.10.1977, P	GU381723	GU381560	-	>88
C. uhligii var. *obtusifolium* (Avetta) Ryding 4	Burundi, M. Reekers 8193, 8.6.1979, P	GU381724	GU381561	-	>89
C. umbrosum (M.Bieb.) Kuntze	Azerbaidschan, G.M.Schneeweiß & A.Tribsch 6758, 26.5.2001, WU	GU381700	GU381537	-	>90
C. vanum (Epling) Harley & A.Granda	-	-	-	DQ017568 (5)	>91
C. vimineum (L.) Kuntze	Costa Rica, cult. BG San José, C. Morales, M	GU381760	GU381600	-	>92
C. vulgare L.	Spain, Morales & Vitek 97-269, 16.07.1997, M	AY840153 (1)	AY840185 (1)	DQ667324 (4)	>93
C. wardii (C. Marquand & Airy Shaw) Bräuchler	China, SE Tibet, F.Ludlow, G.Sherriff & H.H. Elliot 14234, 7.8.1947, BM000927132	GU381682	GU381516	GU381392	>94
***Collinsonia** canadensis* L.	cult. BGM, Bräuchler 2412, 26.06.2003, M	AY840148 (1)	GU381474	-	>95
***Conradina** brevifolia* Shinners	-	-	-	AY943461 (6)	>96
C. canescens A.Gray	USA, Florida, R.K. Godfrey 84060,	GU381749	GU381588	DQ667238 (4)	>97

	16.3.1991, BM000927131				
C. etonia Kral & McCartney	-	-	-	AF369165 (2)	>98
C. glabra Shinners	-	-	-	AY943471 (6)	>99
C. grandiflora Small	-	-	-	AY943474 (6)	>100
***Cuminia** eriantha* (Benth.) Benth.	Chile, Juan Fernandez Islands, C. Marticorena, R.Rodriguez, E. Ugarte & J.Arriagada 9159, 8.2.1980, M	GU381729	GU381566	-	>101
C. eriantha (Benth.) Benth.	Chile, Masatierra, T.Stuessy & D.Crawford, 23.1.1991, MA	-	-	GU381410	>102
***Cunila** galioides* Benth.	-	-	-	DQ667305 (4)	>103
C. incana Benth.	-	-	-	DQ667316 (4)	>104
C. leucantha Kunth ex Cham. & Schltdl.	Mexico, Chiapas, P.J. Stafford, R.J.Hampshire, A.Reyes Garcia, M. Heath & A. Long 397, 9.2.1990, BM000927127	GU381751	GU381590	GU381424	>105
C. origanoides (L.) Britton	USA, Missouri, M.Merella, J.S.Miller, H.H.Schmidt & B.Sirót 1550, 23.9.1996, MO	GU381752	GU381591	-	>106
***Cyclotrichium** leucotrichum* (Stapf ex Rech.f.)Leblebici	Iran, Iranshahr & Termé 12325E, 25.7.1967, W	GU381690	GU381524	GU381396	>107
C. longiflorum Leblebici	Iraq, Distr. Mosul, K.H. Rechinger 10891, 04-09.07.1957, M	GU381692	GU381526	GU381398	>108
C. niveum (Boiss.) Manden. & Scheng.	Turkey, Prov. Malatya, McNeill 450, 7.8.1956, B	GU381691	GU381525	GU381397	>109
C. origanifolium (Labill.) Manden. & Scheng.	Turkey, Anatolia, M. Nydegger 46865, 26.07.1992, M	GU381693	GU381527	GU381399	>110
C. stamineum (Boiss. & Hohen.) Manden. & Scheng.	Iraq, Distr. Mosul, K. H. Rechinger 11618, 10.-12.07.1957, M	GU381694	GU381528	GU381400	>111
C. straussii (Bornm.) Rech.f.	Iran, Chakrmakal-e Bakhtiari, V.Mozaffarian (54939), 28.6.1986, B	GU381695	GU381529	GU381401	>112
***Dicerandra** densiflora* Benth.	-	-	-	AY943488 (6)	>113
D. frutescens Shinners	-	-	-	AY506642 (7)	>114
D. odoratissima R.M.Harper	-	-	-	DQ667234 (4)	>115
D. thinicola H.A.Mill.	-	-	-	AY943489 (6)	>116
***Glechoma** hederacea* L.	cult. BGM (origin Germany), Bräuchler 2504, 26.06.2003, M	AY840143 (1)	GU381476	-	>117

***Glechon** marifolia* Benth.	-	-	-	DQ667303 (4)	>118
G. thymoides Spreng.	-	-	-	DQ667310 (4)	>119
***Gontscharovia** popovii* (B.Fedtsch. & Gontsch.) Boriss. 1	Tadzhikistan, Vvedensky, 25.10.1928, M	GU381769	GU381611	GU381438	>120
G. popovii (B.Fedtsch. & Gontsch.) Boriss. 2	Pakistan, Prov. de Chitral, F.Schmid 2419, 16.10.1954, BM000927129.	GU381770	GU381612	GU381439	>121
***Hedeoma** acinoides* Scheele	USA, Texas, M.H.Mayfield & G.Nesom 1964, 28.4.1994, M	GU381754	GU381594	-	>122
H. apiculata W.S.Stewart	-	-	-	AY771706 (8)	>123
H. costata Hemsl.	Mexico, C.Troll 419, 3.4.1954, M	GU381755	GU381595	GU381427	>124
H. hyssopifolia A.Gray	USA, Gila Co., J. L. Gentry Jr. & E. Jensen 2263, 6.8.1968; C	-	-	GU391426	>125
H. martirense Moran	Mexico, Baja California,.S.Boyd 2315, w. T. Ross, K. McCulloh, 3.6.1988, BM000927121	GU381756	GU381596	GU381428	>126
H. palmeri Hemsl.	Mexico, Estado Queretaro, R.Fernández N. 2493, 31.07.1984, BM000927122	GU381757	GU381597	GU381429	>127
***Hesperozygis** nitida* (Benth.) Epling	Brazil, Paraná, J.Coudeiro & O.S.Ribes 1368, 30.11.1996, M	GU381730	GU381567	-	>128
H. rhodon Epling	Brazil, Parana, J.M. Silva & J.M. Cruz 2405, 20.06.1998, C	GU381734	GU381571	GU381412	>129
H. spathulata Epling	-	-	-	AF369166 (2)	>130
***Hoehnea** epilobioides* (Epling) Epling	Brazil, Paraná, V. Nicolack & J. Cordeiro 86, 23.11.1989, M	GU381731	GU381568	GU381411	>131
***Horminum** pyrenaicum* L.	cult. BGM, Bräuchler 2507, 26.06.2003, M	AY840177 (1)	GU381477	DQ667257 (4)	>132
***Killickia** compacta* (Killick) Bräuchler, Doroszenko & Heubl	South Africa, KwaZulu-Natal, C.Bräuchler 3816, 26.01.2006, M	GU381655	GU381488	GU381377	>133
K. grandiflora (Killick) Bräuchler, Heubl & Doroszenko 1	South Africa, KwaZulu-Natal, O.M. Hilliard, B.L.Burtt 18579, 5.11.1985, NU	GU381659	GU381492	-	>134
K. grandiflora (Killick) Bräuchler, Heubl & Doroszenko 2	South Africa, KwaZulu-Natal, C.Bräuchler 3811, 25.01.2006, M	GU381660	GU381493	GU381380	>135
K. lutea Bräuchler 1	South Africa, KwaZulu-Natal, O.M. Hilliard B.L.Burtt 4876 or 9876 eher nicht!!, 31.1.1975,	GU381656	GU381489	-	>136

	NU				
K. lutea Bräuchler 2	South Africa, KwaZulu-Natal, O.M. Hilliard B.L.Burtt 9287, 20.11.1976, M	GU381657	GU381490	GU381378	>137
K. lutea Bräuchler 3	South Africa, KwaZulu-Natal, C. Bräuchler 3828, 28.01.2006, M	GU381658	GU381491	GU381379	>138
K. pilosa (Benth.) Bräuchler, Heubl & Doroszenko 1	South Africa, KwaZulu-Natal, C. Potgieter & P. Thompson 739; 14.3.2002. NU	GU381661	GU381494	GU381381	>139
K. pilosa (Benth.) Bräuchler, Heubl & Doroszenko 2	South Africa, KwaZulu-Natal, C. Bräuchler 3810, 25.01.2006, M	GU381662	GU381495	GU381382	>140
K. pilosa (Benth.) Bräuchler, Heubl & Doroszenko 3	South Africa, KwaZulu-Natal, C. Bräuchler 3832, 28.01.2006, M	GU381663	GU381496	GU381383	>141
***Kurzamra** pulchella* (Clos) Kuntze	Chile, Prov. Atacama, E.Werdermann 957, 1.1926, M	GU381758	GU381598	-	>142
***Lavandula** angustifolia* Mill.	Cult. BGM (origin France), C. Bräuchler 3681, 9.02.2009, M	GU391427	GU381472	-	>143
***Lycopus** europaeus* L.	cult. BGM (origin Germany), C. Bräuchler 2505, 26.06.2003, M	AY840154 (1)	GU381478	-	>144
***Mentha** cervina* L.	cult. BGM (origin Spain), C. Bräuchler 2394, 26.06.2003, M	GU381688	GU381522	-	>145
M. pulegium L.	Spain, Canary Islands, Tenerife, C. Bräuchler 2300, 15.06.2003, M	GU381687	GU381521	-	>146
M. x *rotundifolia* (L.) Huds.	cult. BGM (origin unknown), C. Bräuchler 2381, 26.06.2003, M	GU381686	GU381520		>147
M. spicata L. "crispa"	cult. BGM (origin unknown), C. Bräuchler 2377, 26.06.2003, M	GU381684	GU381518	GU381394	>148
M. spicata L.	-	-	-	DQ667244 (4)	>149
M. suaveolens Ehrh. 1	cult. BGM (origin unknown), C. Bräuchler 2380, 26.06.2003, M	GU381685	GU381519	GU381395	>150
M. suaveolens Ehrh. 2	-	-	-	AY506645 (7)	>151
M. x villosa Huds.	-	-	-	AB291546 (9)	>152
***Micromeria** benthami* Webb & Berthel.	Spain, Canary Islands, Gran Canaria, Meimberg cc40b, 18.04.2003, M	AY840131 (1)	AY840183 (1)	GU381446	>153
M. biflora (Buch.-Ham. Ex D.Don) Benth.	Afghanistan, Anders 11049, 30.08.1973, M	AY840155 (1)	AY840193 (1)	-	>154
M. cristata (Hampe) Griseb.	Serbia, Stevanovic s.n., 20.04.2003, BEOU (dupl. M).	AY840156 (1)	AY840194 (1)	-	>155
M. croatica (Pers.) Schott	cult. BGV (origin Croatia), C. Bräuchler 3139, 16.7.2004, M	GU381780	GU381624	-	>156
„*M.*" *cymuligera* Boiss. & Hausskn.	Turkey, Haussknecht 1265, 16.8.1865, JE	GU381689	GU381523	-	>157

	(Isotype)				
„*M.*” *flagellaris* Baker 1	Madagascar, Fianarantsoa, R.A. Clement, P.B. Phillipson & G. Rafamantanantsoa 2140, 2.4.1992., E	GU381650	GU381483	-	>158
„*M.*” *flagellaris* Baker 2	Madagascar, Fianarantsoa, P.B. Phillipson, S. Bürki, C. Rakotovao & J. Razanatsoa PP5776, 16.03.2005, MO	GU381653	GU381486	GU381375	>159
„*M.*” *flagellaris* Baker 3	Madagascar, Fianarantsoa, Malcomber 1388, 15.03.1992, P	GU381649	GU381482	-	>160
„*M.*” *flagellaris* Baker 4	Madagascar, Antananarivo, H. van der Werff & G. McPherson 13570, 27.10.1994, E	GU381651	GU381484	-	>161
M. fontanesii K.Koch	Morocco, Podlech s.n., 05.07.1989, M	AY840158 (1)	AY840195 (1)	-	>162
M. forbesii Benth.	Cap Verde, Kilian 1123, 13.01.1986, B (Image-nr. B 10 0086724)	AY840128 (1)	AY840192 (1)	-	>163
M. graeca (L.) Benth. ex Rchb.	Spain, Podlech 51192, 12.04.1996, M	AY840157 (1)	AY840198 (1)	-	>164
M. graeca subsp. *fruticulosa* (Bertol.) Guinea	Italy, Sicily, Erben s.n., 19.04.1994, M	AY840174 (1)	AY840196 (1)	-	>165
M. herpyllomorpha Webb & Berthel.	Spain, Canary Islands, La Palma, Franke lp27, 04.12.2002, M	AY840137 (1)	AY840190 (1)	-	>166
M. hyssopifolia Webb & Berthel. 1	-	-	-	AY227142 (7)	>167
M. hyssopifolia Webb & Berthel. 2	Spain, Canary Islands, Tenerife, Heubl ten44, M	AY840140 (1)	AY840204 (1)	GU381448	>168
M. imbricata (Forssk.) C. Chr.	Cameroon, Mt. Oku, Bräuchler 4004, 05.03.2007, M	GU391424	GU391425	-	>169
M. inodora (Desf.) Benth.	cult. BGM (origin Spain, Formentera), C. Bräuchler 2423, 20.07.2003, M	AY840149 (1)	AY840181 (1)	-	>170
M. juliana (L.) Benth. ex Rchb.	cult. BGM (origin Greece), C. Bräuchler 2411, 26.06.2003, M	AY840159 (1)	AY840199 (1)	-	>171
M. lasiophylla Webb & Berthel. 1	Spain, Canary Islands,La Palma, Franke lp19, 04.12.2002, M	AY840136 (1)	AY840189 (1)	-	>172
M. lasiophylla Webb & Berthel. 2	Spain, Canary Islands, Tenerife, Heubl ten46, 04.10.2003, M	AY840141 (1)	AY840205 (1)	-	>173
„*M.* ” cf. *madagascariensis* Baker	Madagascar, Antananarivo, J.J.Morawetz 205, 08.12.2005, P	GU381648	GU381481	GU381374	>174

M. pineolens Svent.	Spain, Canary Islands, Gran Canaria, Meimberg cc36b, 18.04.2003, M	AY840178 (1)	AY840182 (1)	-	>175
M. sinaica Benth.	Israel, Danin s.n., 20.04.1992, B (Image-nr. B 10 0086716)	AY840160 (1)	AY840200 (1)	-	>176
„*M.* ” *sphaerophylla* Baker 1	Madagascar, Fianarantsoa, B. Lewis, J. Raharilala, P.J. Rakotomalala, M. Andrianarisata & J. McDonagh 1064, 9.-16.12.1993, E	GU381652	GU381485	-	>177
„*M.* ” *sphaerophylla* Baker 2	Madagascar, Fianarantsoa, P.B. Phillipson, H.H. Schmidt & S. Rakotonandrasana 5667, 05.11.2003, MO	GU381654	GU381487	GU381376	>178
M. teneriffae (Poir.) Benth. ex G.Don	Spain, Canary Islands, Tenerife, Heubl ten71, 06.05.2002, M	AY840142 (1)	AY840206 (1)	-	>179
M. varia Benth. 1	Spain, Canary Islands, Gran Canaria, Meimberg cc9a, 12.04.2003, M	AY840132 (1)	AY840184 (1)	-	>180
M. varia Benth. 2	Spain, Canary Islands, Fuerteventura, Heubl FU16, 28.02.2003, M	AY840133 (1)	AY840186 (1)	-	>181
M. varia Benth. 3	Spain, Canary Islands, Lanzarote, Heubl LA19, 02.03.2003, M	AY840135 (1)	AY840188 (1)	-	>182
M. varia Benth. 4	Spain, Canary Islands, La Gomera, Franke gof20, 12.03.2003, M	AY840134 (1)	AY840187 (1)	GU381447	>183
M. varia Benth. 5	Spain, Canary Islands, La Palma, Franke lp31, 04.12.2002, M	AY840138 (1)	AY840191 (1)	-	>184
M. varia Benth. 6	Spain, Canary Islands, Tenerife, Heubl ten26, M	AY840139 (1)	AY840203 (1)	-	>185
Minthostachys *acris* Schmidt-Leb.	-	-	-	DQ017579 (5)	>186
M. acutifolia Epling	-	-	-	DQ017575 (5)	>187
M. andina (Britton ex Rusby) Epling	-	-	-	DQ017573 (5)	>188
M. elongata Schmidt-Leb.	-	-	-	DQ017570 (5)	>189
M. mollis (Kunth) Griseb.	Peru, Depto Cajamarca, M.Weigend, T.Henning & O.Mohr 7610 [147], 10.5.2003, M	GU381763	GU381604	DQ017574 (5)	>190
M. setosa (Briq.) Epling	-	-	-	DQ017576 (5)	>191
M. spicata (Benth.) Epling	Cult. BGM (origin Ecuador), C. Bräuchler 4538, 27.06.2006, M	GU381762	GU381603	DQ017578 (5)	>192
M. verticillata (Griseb.) Epling	-	-	-	DQ017572 (5)	>193

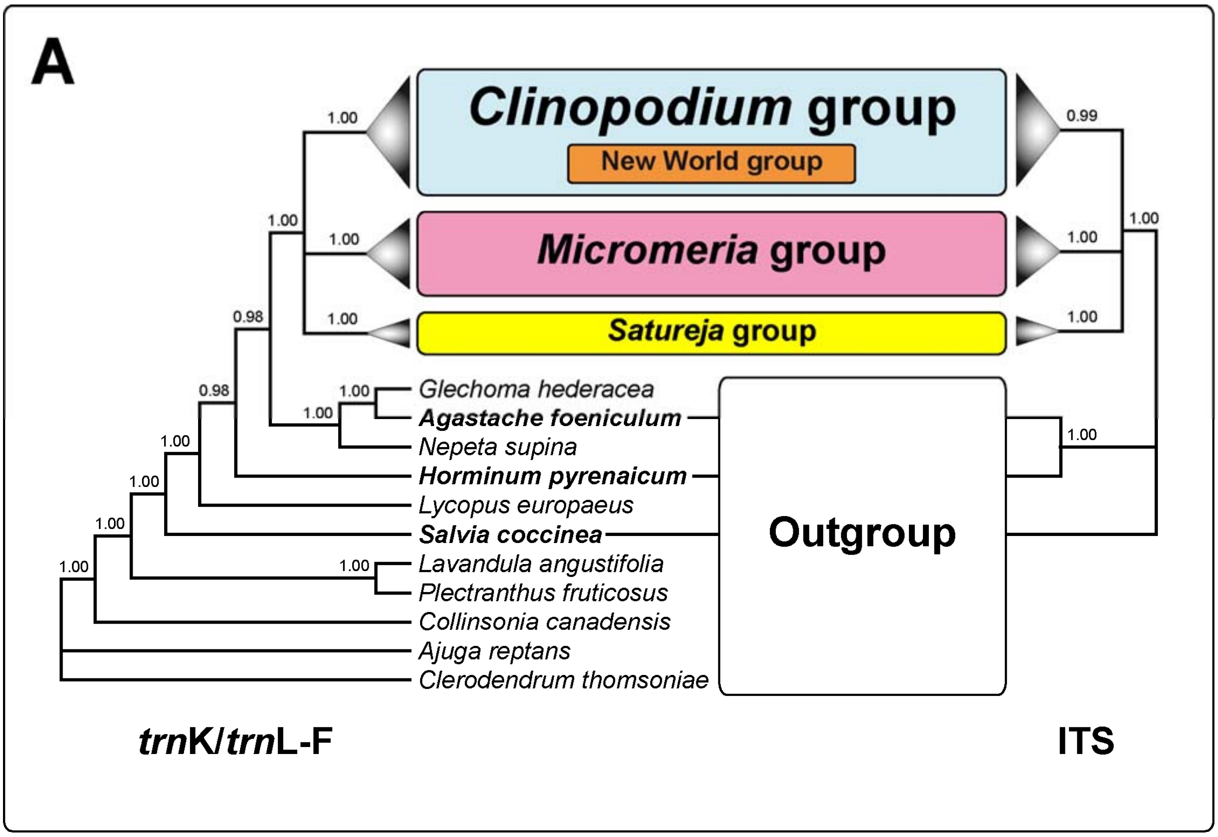
Monarda *bartlettii* Standl.	-	-	-	AF369191 (2)	>194
M. bradburiana Beck	cult. BGM (origin USA), C. Bräuchler 2506, 26.06.2003, M	AY840163 (1)	GU381582	GU381418	>195
M. citriodora var. *austromontana* (Epling) B.L.Turner	-	-	-	AY771705 (8)	>196
M. citriodora Cerv. ex Lag.	-	-	-	AF369177 (2)	>197
M. clinopodia L.	-	-	-	AF369190 (2)	>198
M. clinopodioides A.Gray	-	-	-	AF369171 (2)	>199
M. didyma L.	-	-	-	AF369194 (2)	>200
M. eplingiana Standl.	-	-	-	AF369196 (2)	>201
M. fistulosa L.	cult BGB (origin USA), C. Bräuchler 4456, 22.08.2008, M	GU381745	GU381583	GU381419	>202
M. fruticulosa Epling	-	-	-	AF369185 (2)	>203
M. lindheimeri Engelm. & A.Gray	-	-	-	AF369206 (2)	>204
M. pectinata Nutt.	-	-	-	AF369173 (2)	>205
M. pringlei Fernald	-	-	-	AF369208 (2)	>206
M. punctata L.	-	-	-	AF369181 (2)	>207
M. russeliana Nutt.	-	-	-	AF369187 (2)	>208
M. stipitatoglandulosa Waterf.	-	-	-	AF369209 (2)	>209
M. viridissima Correll	-	-	-	AF369180 (2)	>210
Monardella *hypoleuca* A.Gray	-	-	-	AY506637 (7)	>211
M. linoides A.Gray	-	-	-	AF369163 (2)	>212
M. odoratissima Benth.	USA, New Mexico, H.H.Schmidt, M.Merello & J.Stone 2736, 6.7.1998, MO	GU381744	GU381581	GU381417	>213
Nepeta *supina* Steven.	Georgia, Gröger & Schewardnadse 1466, 15.08.2003, M	AY840164 (1)	GU381479	-	>214
Obtegomeria *caerulescens* (Benth.) Doroszenko & P.D.Cantino	Colombia, J.R.I. Wood 4974, K (Genebank no. 22742)	GU381759	GU381599	GU381430	>215
Origanum *dayi* Post	Israel, Negev, Liston 7-85-3931, 26.7.1985, MSB	GU381800	GU381645	GU381466	>216
O. dictamnus L.	cult. BGF (origin Greece, Crete), C. Bräuchler 2519, 25.09.2003, M	GU381798	GU381643	GU381464	>217
O. elongatum (Bonnet) Emb. & Maire	Morocco, Prov. de Taza, D.Podlech 46949, 25.6.1989, MSB	GU381799	GU381644	GU381465	>218
O. microphyllum (Benth.) Vogel	cult. BGM (origin Greece, Crete), C.	GU381801	GU381646	GU381467	>219

	Bräuchler 3402, 03.06.2005, M				
O. rotundifolium Boiss.	cult. BGF (origin Armenia), C. Bräuchler 2517, 25.09.2003, M	GU381797	GU381642	GU381463	>220
O. vulgare L. 1	cult. BGM, Bräuchler 2512, 26.06.2003, M	AY840165 (1)	AY840202 (1)	GU381468	>221
O. vulgare L. 2	Germany, Bavaria, C. Bräuchler 3131, 08.07.2004, M	GU381802	GU381647	GU381469	>222
***Pentapleura** subulifera* Hand.-Mazz.	Iraq, Distr. Mosul, K.H. Rechinger 12085, 4.-9.7.1957, W	GU381781	GU381625	GU381449	>223
***Piloblephis** rigida* (Bartram ex Benth.) Raf.	USA, Forida, 31.1.1960, R.K. Godfrey 58331, M	GU381746	GU381584	GU381420	>224
***Plectranthus** fruticosus* L´Hér.	cult. BGM (origin Africa), Bräuchler2510, 26.06.2003, M	AY840166 (1)	GU381473	-	>225
***Pogogyne** floribunda* Jokerst	-	-	-	DQ667331 (4)	>226
P. zizyphoroides Benth.	USA, California, A.A. Heller 13915, 29.03.1926, B	GU381735	GU381572	-	>227
***Poliomintha** incana* (Torr.) A.Gray	USA, Utah, J.T.Howell & G.H.True 44698, 3.9.1968, B	GU381741	GU381578	GU381415	>228
P. longiflora A.Gray	Mexico, C.G.Pringle 2536, 5.6.1889, M (Isotype of *Poliomintha bicolor* S.Watson)	GU381739	GU381576	-	>229
***Pycnanthemum** californicum* Torr. ex Durand	-	-	-	AF369169 (2)	>230
P. incanum (L.) Michx.	-	-	-	AY506640 (7)	>231
P. muticum (Michx.) Pers.	-	-	-	AY943494 (6)	>232
P. tenuifolium Schrad.	USA, Missouri, P.H.Raven 27284, 30.7.1986, BM	GU381750	GU381589	GU381423	>233
P. virginianum (L.) T.Durand & B.D.Jacks. ex B.L.Rob. & Fernald	-	-	-	DQ667319 (4)	>234
***Rhabdocaulon** lavanduloides* (Benth.) Epling	Brazil, Parana, G. Hatschbach 35548, 01.12.1974, C	GU381732	GU381569	-	>235
R. stenodontum (Briq.) Epling	Brazil, Sta. Catarina, s.n. 15937, 01.02.1994, C	GU381733	GU381570	-	>236
***Rhododon** ciliatus* (Benth.) Epling	USA, Texas, D.S.Correll 37399, 6.6.1969, BM000927130	GU381740	GU381577	DQ667312 (4)	>237
***Saccocalyx** satureioides* Coss. & Dur.	Algeria, Dep. de Saida, L.Faurel 5650, 26.5.1965, MSB	GU381796	GU381641	GU381462	>238
***Salvia** coccinea* Buc´hoz ex Etl.	cult. BGM, Bräuchler 2390, 26.06.2003, M	AY840147 (1)	GU381475	AY506651 (7)	>239

Satureja *cuneifolia* Ten.	Irak, Rechinger 11142, 01.08.1957 M	GU381777	GU381621	-	>240
S. hortensis L.	cult. BGM, 26.06.2003, Bräuchler 2422, M	GU381776	GU381620	AY227143 (7)	>241
S. innota (Pau) G.López	Spain, prov. Tarragona, A. Barra, G. López & R. Morales 2484 GL, 26.09.1980, M	GU381772	GU381615	-	>242
S. intermedia C.A. Mey.	Iran, Prov. Azerbaijan, K:H.Rechinger 43441, 16.07.1971, M	GU381778	GU381622	-	>243
S. linearifolia (Brullo & Furnari) Greuter	Libya, Brullo & Furnari s.n., 21.5.1981, M	GU381787	GU381631	GU381455	>244
S. montana L.	Cult. BGM (origin Mediterranean), Bräuchler 2509, 26.6.2003, M	AY840167 (1)	AY840179 (1)	GU381442	>245
S. mutica Fisch. & C.A.Mey.	Iran, Akhani 12362, 18.11.1996, M	AY840169 (1)	GU381619	-	>246
S. pallaryi J.Thiébaut	Syrien, W.Frey & H.Kürschner 83-747, 13.8.1983, TUB	GU381771	GU381613	GU381440	>247
S. parnassica Heldr. & Sart. ex Boiss.	Cult. BGB (origin Greece), C. Bräuchler 4453, 22.08.2008, M	GU381773	GU381616	GU381443	>248
S. pilosa Velen.	Cult. BGB (origin Greece), C. Bräuchler 4448, 22.08.2008, M	GU381774	GU381617	GU381444	>249
S. spicigera (K.Koch) Boiss.	Georgia, Kartli, R. Gagnidze, M. Ivanishvili & G. Nakhutsrishvili 2726, 30.8.1997, M	GU381779	GU381623	-	>250
S. spinosa L.	Cult. BGB (origin Greece, Crete), C. Bräuchler 4449, 22.08.2008, M	GU381775	GU381618	GU381445	>251
S. thymbra L.	Greece, Crete, Bräuchler 2896, 02.04.2004, M	AY840168 (1)	GU381614	GU381441	>252
S. thymbrifolia Hedge & Feinbrun	Israel, Danin s.n., 29.4.1994. M	GU381786	GU381630	GU381454	>253
Stachydeoma *graveolens* (Chapm. ex A.Gray) Small	-	-	-	AY943492 (6)	>254
Thymbra *calostachya* (Rech.f.) Rech.f.	Greece, Crete, R. Ulrich s.n., 15.6.1990, M	GU381784	GU381628	GU381452	>255
T. capitata L.	Cult. BGF (origin Spain), C. Bräuchler 2518, 25.09.2003, M	GU381785	GU381629	GU381453	>256
T. sintenisii subsp. *isaurica* P.H.Davis	Turkey, Göner 12628, E	GU381783	GU381627	GU381451	>257
T. spicata L. 1	Israel, Keller & Shammash 14432, 07.06.1989, M	AY840172 (1)	AY840207 (1)	GU381456	>258
T. spicata L. 2	Cult. BGM (origin Turkey), Bräuchler 4548, 23.06.2008, M	GU381788	GU381632	-	>259

Thymus *broussonetii* subsp. *hannonis* (Maire) R.Morales	Morocco, Podlech 142, MSB	GU381791	GU381635	GU381458	>260
T. caespititius Brot.	Madeira, Heubl s.n., 27.8.2004, M	GU381789	GU381633	GU381457	>261
T. haussknechtii Velen.	Turkey, Anatolia, M. Nydegger 43838, 19.7.1988, M	GU381793	GU381638	-	>262
T. magnus (Nakai) Nakai	-	-	-	AY443448 (10)	>263
T. mastichina (L.) L.	-	-	-	AY029168 (2)	>264
T. pulegioides L.	Germany, Bavaria, C. Bräuchler 3129, 8.7.2004, M	GU381790	GU381634	-	>265
T. quinquecostatus Čelak.	-	-	-	AY443444 (10)	>266
T. satureioides subsp. *commutatus* Batt.	Morocco, Prov. d´Agadir 12.7.1989, D. Podlech 47906, 12.7.1989, M	GU381794	GU381639	GU381460	>267
T. serpyllum L.	cult. BGM (origin unknown), C. Bräuchler 2514, 26.06.2003, M	AY840173 (1)	GU381637	GU381459	>268
T. vulgaris L.	cult. BGM (origin France), C. Bräuchler 3683, 9.2.2009, M	GU381792	GU381636	AY329369 (7)	>269
Zataria *multiflora* Boiss.	Afghanistan, K.H. Rechinger 34481, 13.05.1967, C	GU381782	GU381626	GU381450	>270
Ziziphora *capitata* L.	Turkey, C. Bräuchler 3142, 17.07.2004, M	GU381675	GU381509	-	>271
Z. clinopodioides Lam.	Turkey, C. Bräuchler 3209, 18.07.2004, M	GU381674	GU381508	GU381386	>272
Z. hispanica L.	Morocco: Prov. d´Er-Rachidia, W.Lippert 24827, 1.7.1989, M	GU381669	GU381503	AF369162 (2)	>273
Z. hispanica subsp. *aragonensis* (Pau) O.Bolòs 1	Spain, Prov. Toledo, D.Podlech & W.Lippert 2492, 14.6.1973, M	GU381668	GU381502	-	>274
Z. hispanica subsp. *aragonensis* (Pau) O.Bolòs 2	Spain, Aragona, Vicioso s.n., 22.06.1910, M	GU381670	GU381504	-	>275
Z. pamiroalaica Juz.	Leninsky district, D. Murray, Thomas et al. 10090, 02.08.1985, C	GU381676	GU381510	GU381387	>276
Z. taurica M.Bieb.	-	-	-	DQ667314 (4)	>277
Z. tenuior L. 1	Turkey, Anatolia, M. Nydegger 43557, 2.7.1988, MSB	GU381672	GU381506	-	>278
Z. tenuior L. 2	Armenia, Syunik province, G. Fayvush, K. Tamanyan, H.Ter-Voskanian, E. Vitek, 03-1503, 9.7.2003, MSB	GU381673	GU381507	-	>279

Fig. 1:


A
Clinopodium group
New World group
Micromeria group
Satureja group
Glechoma hederacea
Agastache foeniculum
Nepeta supina
Horminum pyrenaicum
Lycopus europaeus
Salvia coccinea
Lavandula angustifolia
Plectranthus fruticosus
Collinsonia canadensis
Ajuga reptans
Clerodendrum thomsoniae
Outgroup
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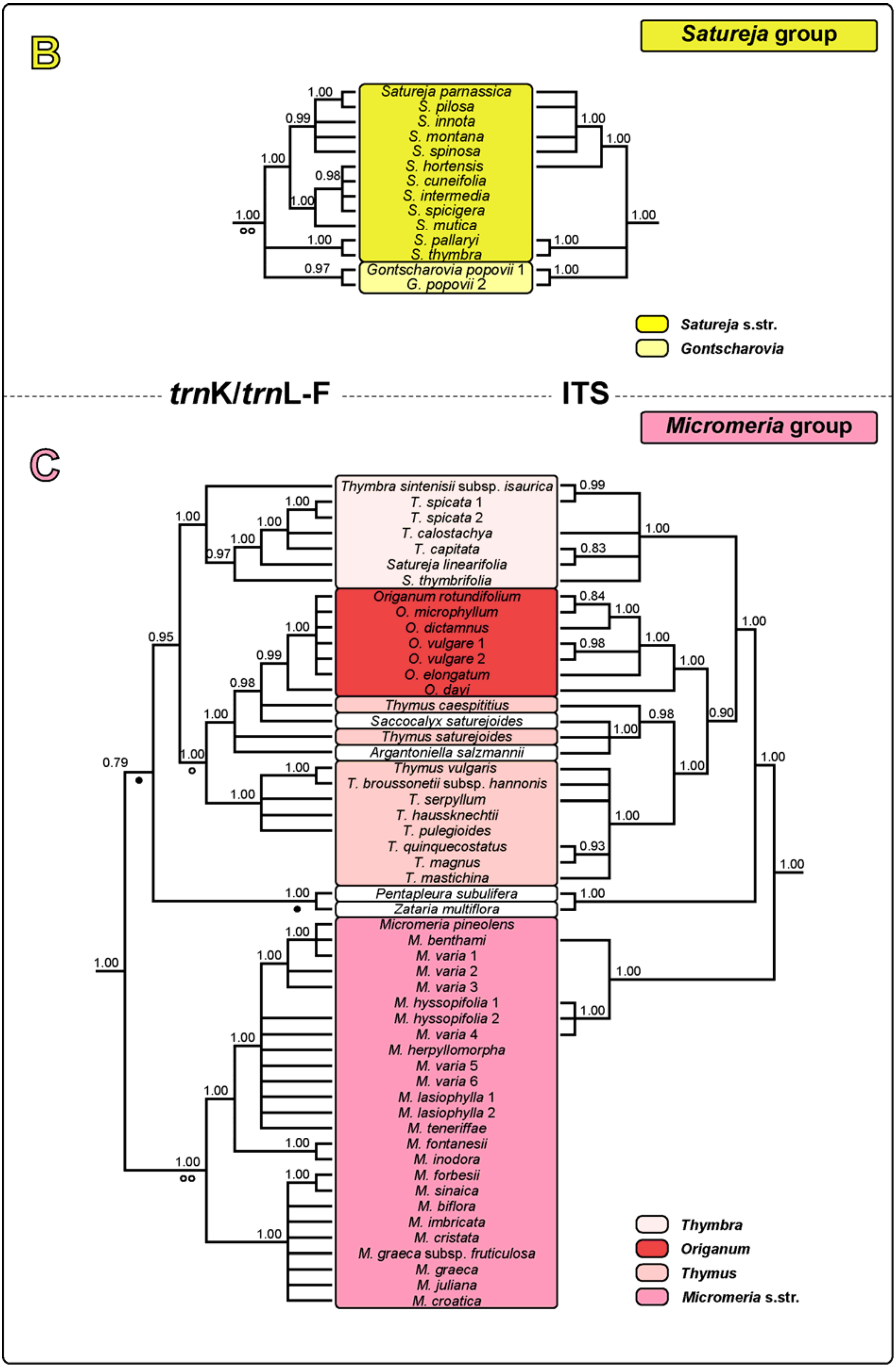
0.99
0.98
trnK/trnL-F
ITS


B
Satureja group
Satureja parnassica
S. pilosa
S. innota
S. montana
S. spinosa
S. hortensis
S. cuneifolia
S. intermedia
S. spicigera
S. mutica
S. pallaryi
S. thymbra
Gontscharovia popovii 1
G. popovii 2
1.00
0.99
1.00
0.98
1.00
1.00
1.00
0.97
1.00
1.00
1.00
1.00
1.00
Satureja s.str.
Gontscharovia
trnK/trnL-F
ITS
C
Micromeria group
Thymbra sintenisii subsp. isaurica
T. spicata 1
T. spicata 2
T. calostachya
T. capitata
Satureja linearifolia
S. thymbrifolia
Origanum rotundifolium
O. microphyllum
O. dictamnus
O. vulgare 1
O. vulgare 2
O. elongatum
O. dayi
Thymus caespititius
Saccocalyx saturejoides
Thymus saturejoides
Argantoniella salzmannii
Thymus vulgaris
T. broussonetii subsp. hannonis
T. serpyllum
T. hausknechtii
T. pulegioides
T. quinquecostatus
T. magnus
T. mastichina
Pentapleura subulifera
Zataria multiflora
Micromeria pineolens
M. benthami
M. varia 1
M. varia 2
M. varia 3
M. hyssopifolia 1
M. hyssopifolia 2
M. varia 4
M. herpyllomorpha
M. varia 5
M. varia 6
M. lasiophylla 1
M. lasiophylla 2
M. teneriffae
M. fontanesii
M. inodora
M. forbesii
M. sinaica
M. biflora
M. imbricata
M. cristata
M. graeca subsp. fruticulosa
M. graeca
M. juliana
M. croatica
1.00
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1.00
0.95
0.99
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0.84
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0.90
1.00
1.00
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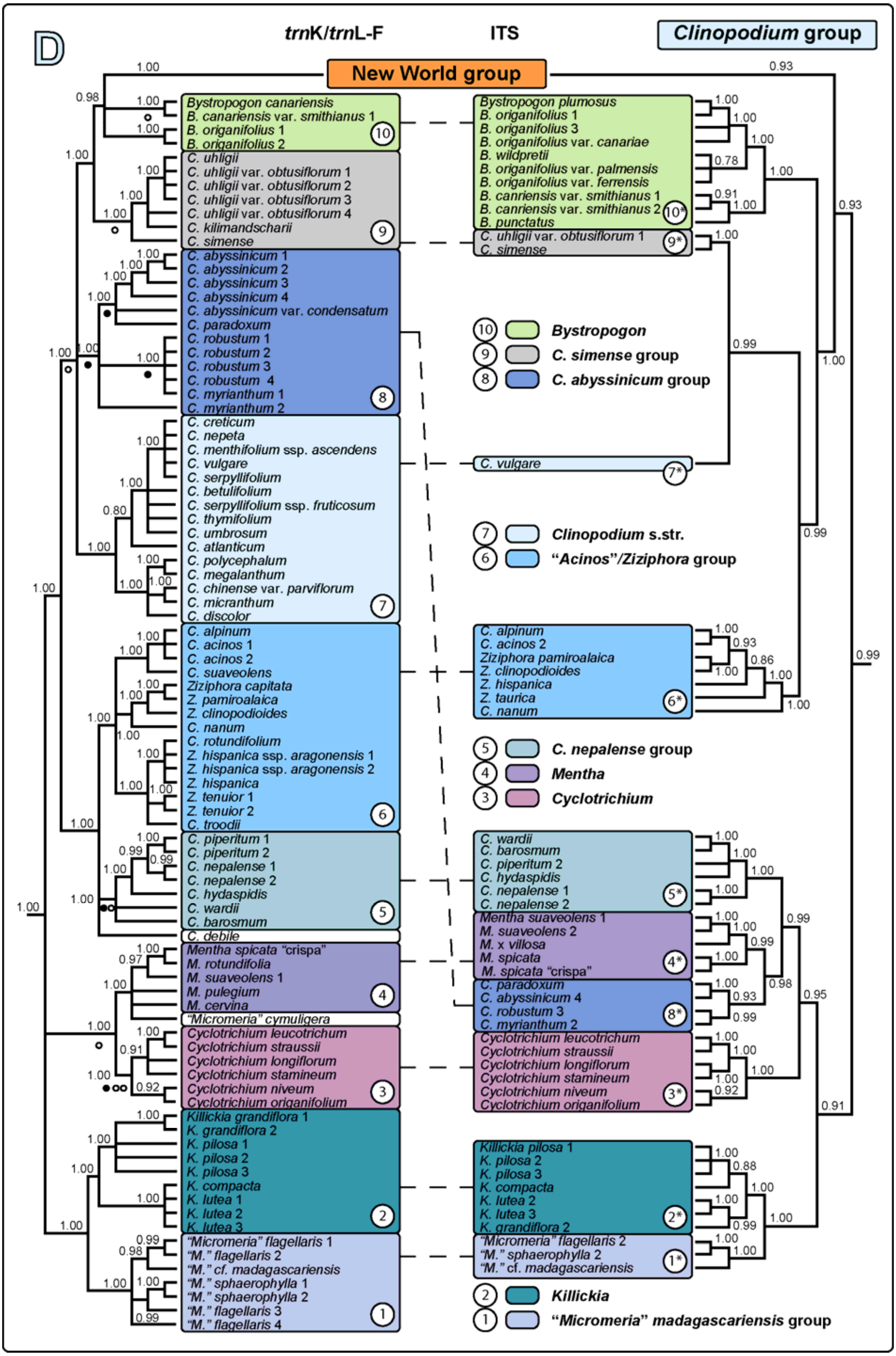
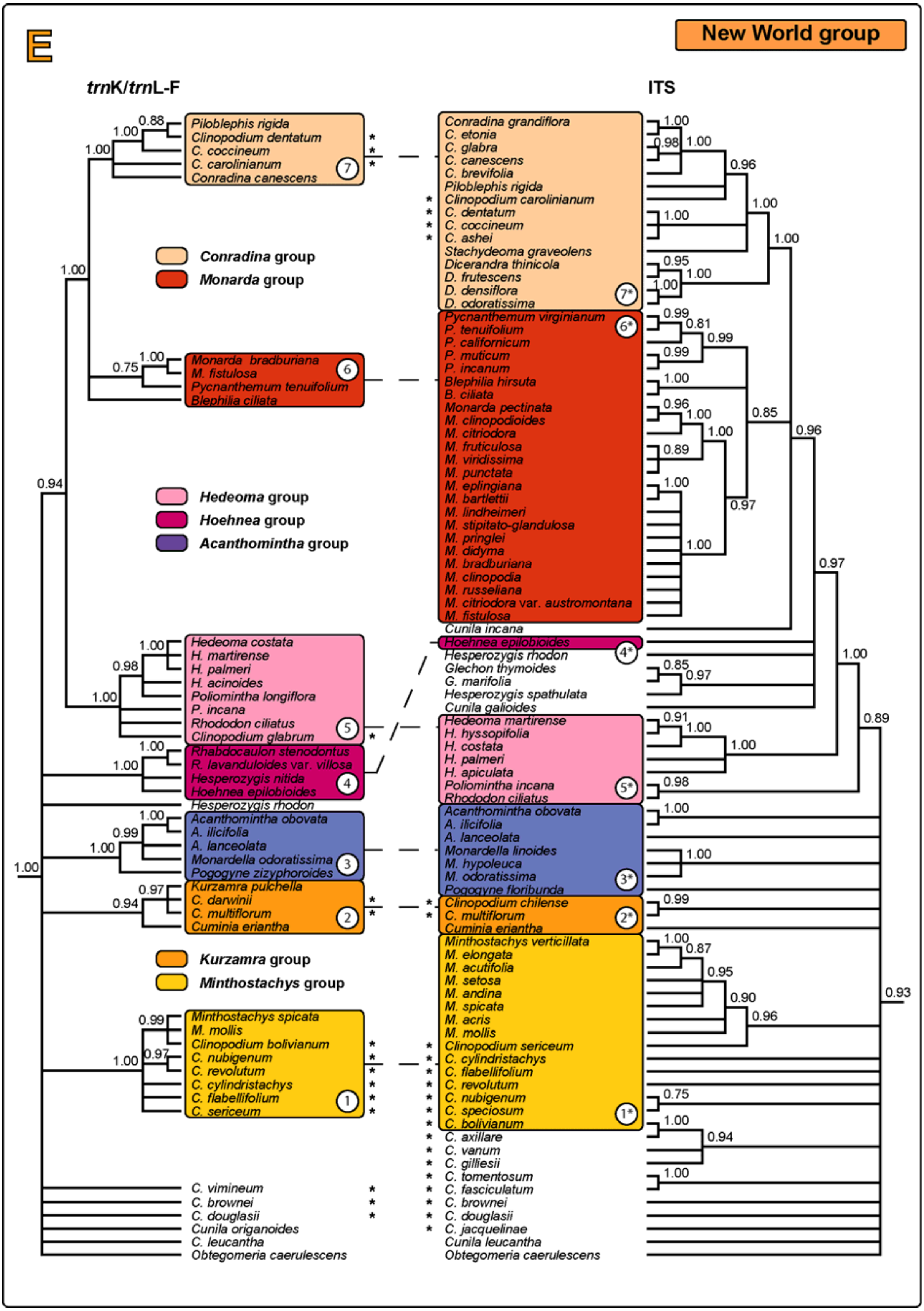
Thymbra
Origanum
Thymus
Micromeria s.str.


D
trnK/trnL-F
ITS
Clinopodium group
New World group
Bystropogon canariensis
B. canariensis var. smithianus 1
B. origanifolius 1
B. origanifolius 2
C. uhligii
C. uhligii var. obtusiflorum 1
C. uhligii var. obtusiflorum 2
C. uhligii var. obtusiflorum 3
C. uhligii var. obtusiflorum 4
C. kilimandscharii
C. simense
C. abyssinicum 1
C. abyssinicum 2
C. abyssinicum 3
C. abyssinicum 4
C. abyssinicum var. condensatum
C. paradoxum
C. robustum 1
C. robustum 2
C. robustum 3
C. robustum 4
C. myrianthum 1
C. myrianthum 2
C. creticum
C. nepeta
C. menthifolium ssp. ascendens
C. vulgare
C. serpyllifolium
C. betulifolium
C. serpyllifolium ssp. fruticosum
C. thymifolium
C. umbrosum
C. atlanticum
C. polycephalum
C. megalanthum
C. chinense var. parviflorum
C. micranthum
C. discolor
C. alpinum
C. acinos 1
C. acinos 2
C. suaveolens
Ziziphora capitata
Z. pamiroalaica
Z. clinopodioides
C. nanum
C. rotundifolium
Z. hispanica ssp. aragonensis 1
Z. hispanica ssp. aragonensis 2
Z. hispanica
Z. tenuior 1
Z. tenuior 2
C. troodii
C. piperitum 1
C. piperitum 2
C. nepalense 1
C. nepalense 2
C. hydaspidis
C. wardii
C. barosmum
C. debile
Mentha spicata "crispa"
M. rotundifolia
M. suaveolens 1
M. pulegium
M. cervina
"Micromeria" cymuligera
Cyclotrichium leucotrichum
Cyclotrichium straussii
Cyclotrichium longiflorum
Cyclotrichium stamineum
Cyclotrichium niveum
Cyclotrichium origanifolium
Killickia grandiflora 1
K. grandiflora 2
K. pilosa 1
K. pilosa 2
K. pilosa 3
K. compacta
K. lutea 1
K. lutea 2
K. lutea 3
"Micromeria" flagellaris 1
"M." flagellaris 2
"M." cf. madagascariensis
"M." sphaerophylla 1
"M." sphaerophylla 2
"M." flagellaris 3
"M." flagellaris 4
Bystropogon plumosus
B. origanifolius 1
B. origanifolius 3
B. origanifolius var. canariae
B. wildpretii
B. origanifolius var. palmensis
B. origanifolius var. ferrensis
B. canriensis var. smithianus 1
B. canriensis var. smithianus 2
B. punctatus
C. uhligii var. obtusiflorum 1
C. simense
C. vulgare
C. alpinum
C. acinos 2
Ziziphora pamiroalaica
Z. clinopodioides
Z. hispanica
Z. taurica
C. nanum
C. wardii
C. barosmum
C. piperitum 2
C. hydaspidis
C. nepalense 1
C. nepalense 2
Mentha suaveolens 1
M. suaveolens 2
M. x villosa
M. spicata
M. spicata "crispa"
C. paradoxum
C. abyssinicum 4
C. robustum 3
C. myrianthum 2
Cyclotrichium leucotrichum
Cyclotrichium straussii
Cyclotrichium longiflorum
Cyclotrichium stamineum
Cyclotrichium niveum
Cyclotrichium origanifolium
Killickia pilosa 1
K. pilosa 2
K. pilosa 3
K. compacta
K. lutea 2
K. lutea 3
K. grandiflora 2
"Micromeria" flagellaris 2
"M." sphaerophylla 2
"M." cf. madagascariensis
⑩ Bystropogon
⑨ C. simense group
⑧ C. abyssinicum group
⑦ Clinopodium s.str.
⑥ "Acinos"/Ziziphora group
⑤ C. nepalense group
④ Mentha
③ Cyclotrichium
② Killickia
① "Micromeria" madagascariensis group


E
New World group
trnK/trnL-F
ITS
Conradina group
Monarda group
Hedeoma group
Hoehnea group
Acanthomintha group
Kurzamra group
Minthostachys group
Piloblephis rigida
Clinopodium dentatum
C. coccineum
C. carolinianum
Conradina canescens
7
Monarda bradburiana
M. fistulosa
Pycnanthemum tenuifolium
Blephilia ciliata
6
Hedeoma costata
H. martirense
H. palmeri
H. acinoides
Poliomintha longiflora
P. incana
Rhododon ciliatus
Clinopodium glabrum
5
Rhabdocaulon stenodontus
R. lavanduloides var. villosa
Hesperozygis nitida
Hoehnea epilobioides
4
Hesperozygis rhodon
Acanthomintha obovata
A. ilicifolia
A. lanceolata
Monardella odoratissima
Pogogyne zizyphoroides
3
Kurzamra pulchella
C. darwinii
C. multiflorum
Cuminia eriantha
2
Minthostachys spicata
M. mollis
Clinopodium bolivianum
C. nubigenum
C. revolutum
C. cylindristachys
C. flabellifolium
C. sericeum
1
C. vimineum
C. brownei
C. douglasii
Cunila origanoides
C. leucantha
Obtegomeria caerulescens
Conradina grandiflora
C. etonia
C. glabra
C. canescens
C. brevifolia
Piloblephis rigida
Clinopodium carolinianum
C. dentatum
C. coccineum
C. ashei
Stachydeoma graveolens
Dicerandra thinicola
D. frutescens
D. densiflora
D. odoratissima
7*
Pycnanthemum virginianum
P. tenuifolium
P. californicum
P. muticum
P. incanum
Blephilia hirsuta
B. ciliata
Monarda pectinata
M. clinopodioides
M. citriodora
M. fruticulosa
M. viridissima
M. punctata
M. eplingiana
M. bartlettii
M. lindheimeri
M. stipitato-glandulosa
M. pringlei
M. didyma
M. bradburiana
M. clinopodia
M. russeliana
M. citriodora var. austromontana
M. fistulosa
6*
Cunila incana
Hoehnea epilobioides
Hesperozygis rhodon
Glechon thymoides
G. marifolia
Hesperozygis spathulata
Cunila galioides
4*
Hedeoma martirense
H. hyssopifolia
H. costata
H. palmeri
H. apiculata
Poliomintha incana
Rhododon ciliatus
5*
Acanthomintha obovata
A. ilicifolia
A. lanceolata
Monardella linoides
M. hypoleuca
M. odoratissima
Pogogyne floribunda
3*
Clinopodium chilense
C. multiflorum
Cuminia eriantha
2*
Minthostachys verticillata
M. elongata
M. acutifolia
M. setosa
M. andina
M. spicata
M. acris
M. mollis
Clinopodium sericeum
C. cylindrachys
C. flabellifolium
C. revolutum
C. nubigenum
C. speciosum
C. bolivianum
1*
C. axillare
C. vanum
C. gilliesii
C. tomentosum
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C. brownei
C. douglasii
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Obtegomeria caerulescens
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Staatssammlung heraussheben ohne deren sehr artenreiche Sammlung als Basis keine derartige Probenabdeckung hätte erreicht werden können.

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Ehrenwörtliche Versicherung

Ich versichere hiermit ehrenwörtlich, dass die vorgelegte Dissertation von mir selbständig und ohne unerlaubte Hilfe angefertigt wurde.

München, den 05.05.2009

Erklärung

Hiermit erkläre ich, Christian Bräuchler

1) dass die Dissertation nicht ganz oder in wesentlichen Teilen einer anderen Prüfungskommission vorgelegt worden ist.

2) dass ich mich anderweitig einer Doktorprüfung ohne Erfolg nicht unterzogen habe.

München, den 05.05.2009