



Hidden diversity in bent-winged bats (Chiroptera: Miniopteridae) of the Western Palaearctic and adjacent regions: implications for taxonomy

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The taxonomic status of bent-winged bats (*Miniopterus*) in the Western Palaearctic and adjacent regions is unclear, particularly in some areas of the eastern Mediterranean, Middle East and Arabia. To address this, we analysed an extensive collection of museum materials from all principal parts of this distribution range, i.e. North Africa, Europe and southwest Asia, using morphological (skull) and genetic approaches (mitochondrial DNA). Linear and geometric morphometric analysis of cranial and dental characteristics, together with molecular phylogeny, suggested that *Miniopterus* populations comprise four separate species: (1) *M. schreibersii* sensu strictissimo (s.str.) – occurring in Europe, coastal Anatolia, Levant, Cyprus, western Transcaucasia, and North Africa; (2) *M. pallidus* – occurring in inland Anatolia, Jordan, eastern Transcaucasia, Turkmenistan, Iran and southern Afghanistan (Kandahar); (3) a *Miniopterus* sp. – recorded from Nangarhar province in eastern Afghanistan, which we tentatively assign to *M. cf. fuliginosus*; and (4) a *Miniopterus* sp. with Afro-tropic affinities confirmed from south-western Arabia and Ethiopia, which we tentatively name *M. cf. arenarius*. The latter two species are well differentiated by skull morphology, while *M. pallidus* possesses very similar skull morphology to *M. schreibersii*. The results also suggest the existence of a possible new taxon (subspecies) within *M. schreibersii* s.str. inhabiting the Atlas Mountains of Morocco.

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INTRODUCTION

Bent-winged bats, family Miniopteridae, are represented by a single genus, *Miniopterus* Bonaparte, 1837. The genus includes up to 19 species occurring

mostly in the tropics and subtropics of the Old World, viz. Africa (except the Sahara), southern and central Europe, southern Asia from Anatolia, across the Middle East and Transcaucasia to China and Japan, the Sunda archipelago, the Philippines, and the Australasian region (Simmons, 2005). Morphological analysis suggests that the named forms (species/subspecies) of this genus are very similar in their cranial and external characteristics (e.g. Tate, 1941; Maeda, 1982; Benda *et al.*, 2006), meaning that

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identification of many taxa is difficult and the classification of many populations of this genus remains unclear. Further, a number of recent molecular phylogenetic studies have indicated that the taxonomy of this genus is in urgent need of revision (Appleton, McKenzie & Christidis, 2004; Tian *et al.*, 2004; Miller-Butterworth *et al.*, 2005; Furman *et al.*, 2009, 2010c; Furman, Öztunç & Çoraman, 2010b). This is particularly true for *Miniopterus schreibersii* (Kuhl, 1817) *sensu lato* (s.l.), the only species considered as inhabiting the whole south-western portion of the Palaearctic region (Koopman, 1993, 1994; Simmons, 2005).

For a long time, this species was considered a polytypic and widespread bat, with up to 25 subspecies recognised within its distribution range, which is almost identical to that of the genus and comprises most of the Old World region (e.g. Tate, 1941; Hayman & Hill, 1971; Corbet, 1978; Harrison & Bates, 1991; Corbet & Hill, 1992; Koopman, 1994). Nowadays, *M. schreibersii* *sensu stricto* (s.s.) is most often accepted as a south-western Palaearctic faunal element occurring in southern and central Europe, supra-Saharan Africa, south-west Asia, and eastern Afghanistan (cf. Appleton *et al.*, 2004; Tian *et al.*, 2004; Miller-Butterworth *et al.*, 2005; Benda *et al.*, 2006; Bilgin *et al.*, 2006, 2008; Furman *et al.*, 2009, 2010b). It is interesting to note, however, that these geographical limits for *M. schreibersii* had already been proposed by Maeda (1982) in his precise morphometric analysis of the Palaearctic and Oriental populations of the genus.

The newly delimited species rank of *M. schreibersii* (as reviewed by Simmons, 2005) consists of two subspecies, *M. s. schreibersii* [type locality (t.l.): Kolumbács Cave, left bank of the River Danube, near Coronini, Romania; *sensu* Ansell & Topál, 1976] and *M. s. pallidus* Thomas, 1907 [t.l.: vicinity of Bandar-i-Gaz (Golestan Province), Iran; *sensu* Lay, 1967]. These subspecies are very similar in both external and cranial characteristics (e.g. Ognev, 1928; Albayrak & Coskun, 2000; Benda *et al.*, 2006; Furman *et al.*, 2009) and differ mainly in pelage coloration. Evidence of seasonal and geographic changes in this trait, however, has shown it to be unsuitable for taxonomic identification (Kuzâkin, 1950; Lay, 1967; Karataş & Sözen, 2004; Gazaryan, 2005). Furman *et al.* (2010c) studied differentiation between these taxa in populations inhabiting Asia Minor and found statistically significant genetic, morphological (body size and wing shape) and echolocation differences. Following these findings, they suggested that the two taxa were reproductively isolated and considered them to be two separately evolving units representing distinct cryptic species, *M. schreibersii* *sensu strictissimo* (s.str.) and *M. pallidus*. This taxonomic proposal, however, was based almost solely on the

populations from Turkey, while most of the Palaearctic range of the bent-winged bats still remains questionable from a taxonomic and phylogeographic point of view (cf. Bilgin, 2011, 2012).

The subspecific taxonomic rank of the taxon *pallidus* has been applied, particularly by Russian authors (e.g. Ellerman & Morrison-Scott, 1951; Kuzâkin, 1965; Strelkov, Sosnovcena & Babaev, 1978; Rahmatulina, 2005), for populations occurring in some areas of the former Soviet Union (currently the Caucasus region and southern Turkmenistan; Ognev, 1927, 1928; Gazaryan, 2005). Distribution of this form has also been reported from the Levant (Syria, Lebanon, Israel, Jordan), Iraq, Iran, Afghanistan and from the inland/highland areas of central and eastern Turkey (e.g. Lay, 1967; Gaisler, 1970; Maeda, 1982; Horáček, Hanák & Gaisler, 2000; Boye, 2004; Benda *et al.*, 2006; Furman *et al.*, 2010c); Ferguson (2002), however, reported the occurrence of a subspecies, *schreibersii*, for Israel. Populations from the European distribution range of *M. schreibersii*, s.s. as well as populations from North Africa and the larger Mediterranean islands, have traditionally been attributed to the nominotypical subspecies (e.g. Aellen & Strinati, 1970; Spitzenberger, 1981; Gaisler, 1983; Cruicitti, 1989; Kowalski & Rzebik-Kowalska, 1991); the situation in Cyprus, however, remains unclear. Boye (2004), for example, mentions the occurrence of subspecies *pallidus*, while others assume the island to be inhabited by the nominotypical form (e.g. Horáček *et al.*, 2000).

In the Middle East, a morphologically distinct population of *M. schreibersii* s.l. has been suggested as present in the Nangarhar province of eastern Afghanistan, on the border of the Palaearctic and Oriental regions (Gaisler, 1970), and was thought to represent *M. s. fuliginosus* Hodgson, 1835 (t.l.: Nepal) (Gaisler, 1970; Hill, 1983; Koopman, 1994; Bates & Harrison, 1997). A further population traditionally assigned to *M. schreibersii* s.l. occurs at the border of the Palaearctic in south-western Arabia (Harrison & Bates, 1991). These populations were originally classified as *M. s. arenarius* Heller, 1912 (t.l.: Nanyuki, Kenya) (Nader & Kock, 1987; Harrison & Bates, 1991; Koopman, 1994). This taxon, however, is currently considered as part of *M. natalensis* Smith, 1834 (t.l.: Durban, South Africa), which was recently revalidated to species level within *M. schreibersii* s.l. and is reported to occur in sub-Saharan Africa and south-western Arabia (Koopman, 1994; Simmons, 2005).

To summarise, the taxonomic status and distribution ranges of particular taxa/populations of Palaearctic *Miniopterus* bats have tended to be reported more-or-less intuitively (mainly on a geographic basis) and its status remains unclear in most of the respective areas. Classification of the Levantine,

Middle Eastern, North African and, especially, European populations remains in need of revision. Delimitation of the geographical margins and contact zones between respective taxa, especially in the light of new findings (cf. Furman *et al.*, 2010c), is also necessary.

Here, we present a revision of the taxonomy of *Miniopterus* populations of Western Palaearctic and some adjacent regions, based on a synthesis of results from morphological and molecular analysis of a rich museum-material collection from all principal parts of the *Miniopterus* distribution range (i.e. southern Europe, south-west Asia and North Africa). In doing so, we aim to answer two main questions arising from several recent studies (e.g. Appleton *et al.*, 2004; Miller-Butterworth *et al.*, 2005; Bilgin *et al.*, 2008; Furman *et al.*, 2010b, c): (1) what are the phylogenetic and phenotypic relationships between particular Western Palaearctic *Miniopterus* populations (as well as their taxonomic status), and (2) is *M. pallidus* [demonstrated as representing a separate species in a recent study (Furman *et al.*, 2010c)] morphologically well differentiated and what is its present distribution range?

MATERIAL AND METHODS

In order to assess the taxonomic status of *Miniopterus* populations from the Western Palaearctic and adjacent regions (i.e. Afghanistan, Yemen and Ethiopia), we examined 352 skulls morphologically (Appendix 1) and 52 samples genetically. Fifty-seven additional sequences of *Miniopterus* spp. from around the Old World were retrieved from GenBank (Table 1). A review of the geographic origin of all the material investigated is displayed in Figure 1A.

MOLECULAR ANALYSIS

Total genomic DNA was extracted from tissue samples (c. 1 mm² of wing membrane) using the Genomed JetQuick Tissue DNA Spin Kit (Löhne, Germany), following the manufacturer's protocol. A segment of extracted mitochondrial DNA (mtDNA), the complete gene for the second subunit of NADH dehydrogenase (*ND2* – 1044 bp), was amplified by Polymerase Chain Reaction (PCR) using the primers ND2-1 and ND2-2 (Kirchman *et al.*, 2001) under the following thermal profile: initial denaturation of 93 °C for 3 min, 35 subsequent cycles of 93 °C for 30 s, 52 °C for 40 s and 72 °C for 1 min, and a final extension of 72 °C for 10 min. Sequencing was carried out by Macrogen Inc. (Seoul, South Korea, <http://www.macrogen.com>) using a combination of the above mentioned PCR primers, one formerly published internal forward primer (mmND2.1; Osborne

& Christidis, 2001), and one newly developed *Miniopterus*-specific internal reverse primer (mND2inR: 5'-TGAATRACYGCCGTACTA-3'). New sequences of different haplotypes were deposited in GenBank (see Table 1 for Accession Nos.). Fifty-seven additional sequences from various *Miniopterus* species were added to our dataset from GenBank (AY169435–46, AY169448–71, Appleton *et al.*, 2004; GU290290–310, Furman *et al.*, 2010b), as well as four outgroup taxa: *Myotis muricola* (AY504566; J. M. Worthington Wilmer, C. J. Schneider & M. D. Sorenson, unpubl. data), *Chalinolobus tuberculatus* (AF321051; Lin & Penny, 2001), *Chalinolobus nigrogriseus* (AY504561; J. M. Worthington Wilmer, C. J. Schneider & M. D. Sorenson, unpubl. data), and *Chalinolobus morio* (AY169472; Appleton *et al.*, 2004). For phylogenetic analysis, we shortened the new sequences from this study to 1034 bp in order to match the additional GenBank sequences. All sequences were aligned in BioEdit 7.0 (Hall, 1999) and examined by translation into amino acids with the vertebrate mitochondrial genetic code using DnaSP 5.10 (Librado & Rozas, 2009); no stop codons were detected.

Phylogenetic trees were constructed using a dataset of 89 sequences that comprised only unique haplotypes (haplotype dataset). The trees were constructed using the maximum likelihood (ML), Bayesian approach (BA), and neighbour-joining (NJ) methods. For ML and BA, the jModelTest 0.1.1 software package (Posada, 2008) was employed prior to analysis to calculate the best-fit model of nucleotide evolution (selected according to the Akaike information criterion for the whole sequence length in ML, and each codon position separately in BA). ML analysis was performed using PhyML 3.0 (Guindon *et al.*, 2010). The best-fit substitution model corresponded with the transitional model with a proportion of invariant positions and gamma distribution of rate heterogeneity (TIM2 + I + G). The best branch-swapping approach was applied, which combines nearest neighbour interchanges with subtree pruning and regrafting, and optimisation of topology and branch length settings. Bootstrap branch support was calculated based on 1000 resampled datasets. The BA was carried out using MrBayes 3.2 (Huelsenbeck & Ronquist, 2001; Ronquist & Huelsenbeck, 2003), with partitions for codon positions and parameters optimised during runs. The likelihood settings corresponded with the general time-reversible model, which was the closest approximation of the best-fit substitution model for each partition available in MrBayes (we applied GTR + G/GTR + G/GTR + I + G for codon position 1/2/3). BA analysis was performed for six million generations with two runs (to check convergence) and four coupled chains for each run,

Table 1. Specimens examined genetically

Species	Haplotype	Lineage/ sublineage	Country	Locality	Coordinates	GenBank Acc. No.	Voucher/Reference
<i>M. schreibersii</i>	MSC1	WM	Italy	Etna, Sicily	37.72 N, 14.92 E	JX012135	biopsy
<i>M. schreibersii</i>	MSC1	WM	Italy	Etna, Sicily	37.72 N, 14.92 E	JX012135	biopsy
<i>M. schreibersii</i>	MSC1	WM	Italy	Etna, Sicily	37.72 N, 14.92 E	JX012135	biopsy
<i>M. schreibersii</i>	MSC1	WM	Romania	Betfia	46.98 N, 22.02 E	JX012135	biopsy
<i>M. schreibersii</i>	MSC1	WM	Romania	Betfia	46.98 N, 22.02 E	JX012135	biopsy
<i>M. schreibersii</i>	MSC1	WM	Slovakia	Drienovec	48.62 N, 20.95 E	JX012135	NMP pb4261
<i>M. schreibersii</i>	MSC1	WM	Slovakia	Drienovec	48.62 N, 20.95 E	JX012135	NMP pb4260
<i>M. schreibersii</i>	MSC2	WM	Romania	Dubova	47.62 N, 22.25 E	JX012136	NMP pb4419
<i>M. schreibersii</i>	MSC2	WM	Romania	Betfia	46.98 N, 22.02 E	JX012136	NMP pb4256
<i>M. schreibersii</i>	MSC3	WM	Romania	Betfia	46.98 N, 22.02 E	JX012137	NMP pb4258
<i>M. schreibersii</i>	MSC4	WM	Greece	Milatos, Crete	35.30 N, 25.58 E	JX012138	NMP 91116
<i>M. schreibersii</i>	MSC4	WM	Greece	Milatos, Crete	35.30 N, 25.58 E	JX012138	NMP 91113
<i>M. schreibersii</i>	MSC4	WM	Greece	Omalos, Crete	35.35 N, 23.90 E	JX012138	NMP 91166
<i>M. schreibersii</i>	MSC4	WM	Greece	Vreikos Cave, Crete	35.08 N, 26.00 E	JX012138	NMP 92316
<i>M. schreibersii</i>	MSC5	WM	Greece	Lefkogia, Crete	35.18 N, 24.47 E	JX012139	NMP 92311
<i>M. schreibersii</i>	MSC5	WM	Greece	Omalos, Crete	35.35 N, 23.90 E	JX012139	NMP 91172
<i>M. schreibersii</i>	MSC6	EM	Cyprus	Kakopetria	34.97 N, 32.87 E	JX012140	NMP CH108
<i>M. schreibersii</i>	MSC6	EM	Cyprus	Kakopetria	34.97 N, 32.87 E	JX012140	NMP CH46
<i>M. schreibersii</i>	MSC7	EM	Cyprus	Akamas Peninsula	35.05 N, 32.33 E	JX012141	NMP CH123
<i>M. schreibersii</i>	MSC7	EM	Cyprus	Kakopetria	34.97 N, 32.87 E	JX012141	NMP 90406
<i>M. schreibersii</i>	MSC7	EM	Cyprus	Kakopetria	34.97 N, 32.87 E	JX012141	NMP 90405
<i>M. schreibersii</i>	MSC7	EM	Cyprus	Kalavassos	34.80 N, 33.27 E	JX012141	NMP 90434
<i>M. schreibersii</i>	MSC8	EM	Syria	Qala'at al-Hosn	35.65 N, 40.73 E	JX012142	NMP pb49989
<i>M. schreibersii</i>	MSC8	EM	Syria	Talsh'hab	32.70 N, 35.96 E	JX012142	NMP 48861
<i>M. schreibersii</i>	MSC9	EM	Turkey	Akbez	36.51 N, 36.30 E	JX012143	NMP tr099
<i>M. schreibersii</i>	MSC10	EM	Lebanon	Aaqura	34.12 N, 35.92 E	JX012144	NMP 91778
<i>M. schreibersii</i>	MSC10	EM	Syria	Safta	34.83 N, 36.12 E	JX012144	NMP 48883
<i>M. schreibersii</i>	MSC11	EM	Syria	Qala'at al-Hosn	35.65 N, 40.73 E	JX012145	NMP 48873
<i>M. schreibersii</i>	MSC11	EM	Syria	Safta	34.83 N, 36.12 E	JX012145	NMP 48881
<i>M. schreibersii</i>	MSC12	EM	Cyprus	Kakopetria	34.97 N, 32.87 E	JX012146	NMP CH45
<i>M. schreibersii</i>	MSC12	EM	Lebanon	Aamchite	34.15 N, 35.67 E	JX012146	NMP 91808
<i>M. schreibersii</i>	MSC13	EM	Lebanon	Aaqura	34.12 N, 35.92 E	JX012147	NMP 91777
<i>M. schreibersii</i>	MSC14	MO	Morocco	Tazouguerte	32.02 N, 03.78 W	JX012148	NMP pb3906
<i>M. schreibersii</i>	MSC14	MO	Morocco	Tazouguerte	32.02 N, 03.78 W	JX012148	NMP pb3908
<i>M. schreibersii</i>	MSC15	MO	Morocco	Sebt-des-Ait-Serhrouchen	34.03 N, 04.57 W	JX012149	NMP 90103
<i>M. schreibersii</i>	MSC15	MO	Morocco	Talkout	31.68 N, 07.28 W	JX012149	NMP 90047
<i>M. schreibersii</i>	MSC16	MO	Morocco	Talkout	31.68 N, 07.28 W	JX012150	NMP 90051

<i>M. schreibersii</i>	MSC17	WM	Bulgaria	Pazardziik	AY169446	Appleton <i>et al.</i> (2004)
<i>M. schreibersii</i>	MSC18	WM	Bulgaria	Sofia	AY169445	Appleton <i>et al.</i> (2004)
<i>M. schreibersii</i>	MSC19	WM	Georgia	Ghliana	GU290307	Furman <i>et al.</i> (2010b)
<i>M. schreibersii</i>	MSC20	WM	Georgia	Ghliana	GU290308	Furman <i>et al.</i> (2010b)
<i>M. schreibersii</i>	MSC21	WM	Morocco	Agadir	AY169450	Appleton <i>et al.</i> (2004)
<i>M. schreibersii</i>	MSC21	WM	Morocco	Agadir	AY169449	Appleton <i>et al.</i> (2004)
<i>M. schreibersii</i>	MSC22	WM	Spain	Cadiz	AY169448	Appleton <i>et al.</i> (2004)
<i>M. schreibersii</i>	MSC23	WM	Turkey	Hizar	Furman <i>et al.</i> (2010b)	Furman <i>et al.</i> (2010b)
<i>M. schreibersii</i>	MSC24	WM	Turkey	Horataş 1	GU290302	Furman <i>et al.</i> (2010b)
<i>M. schreibersii</i>	MSC25	EM	Turkey	Karanlık	GU290304	Furman <i>et al.</i> (2010b)
<i>M. schreibersii</i>	MSC26	EM	Turkey	Karanlık	GU290305	Furman <i>et al.</i> (2010b)
<i>M. schreibersii</i>	MSC27	EM	Turkey	Karanlık	GU290309	Furman <i>et al.</i> (2010b)
<i>M. schreibersii</i>	MSC28	EM	Turkey	Obruk	GU290310	Furman <i>et al.</i> (2010b)
<i>M. schreibersii</i>	MSC29	EM	Turkey	Obruk	GU290310	Furman <i>et al.</i> (2010b)
<i>M. schreibersii</i>	MSC30	EM	Turkey	Zindan	GU290303	Furman <i>et al.</i> (2010b)
<i>M. schreibersii</i>	MSC30	EM	Turkey	Zindan	GU290306	Furman <i>et al.</i> (2010b)
<i>M. pallidus</i>	MPA1	ME	Iran	Dorud	JX012151	Furman <i>et al.</i> (2010b)
<i>M. pallidus</i>	MPA2	ME	Iran	Bisotun	NMP 48154	NMP 48154
<i>M. pallidus</i>	MPA3	ME	Iran	Bisotun	JX012152	NMP 48151
<i>M. pallidus</i>	MPA3	ME	Iran	Mina	JX012153	NMP 90825
<i>M. pallidus</i>	MPA4	ME	Iran	Mina	JX012153	NMP 90826
<i>M. pallidus</i>	MPA5	ME	Iran	Bisotun	JX012154	NMP 48149
<i>M. pallidus</i>	MPA6	ME	Jordan	Khashibah	JX012155	NMP 92532
<i>M. pallidus</i>	MPA6	ME	Azerbaijan	Azix	GU290293	Furman <i>et al.</i> (2010b)
<i>M. pallidus</i>	MPA7	ME	Azerbaijan	Azix	GU290290	Furman <i>et al.</i> (2010b)
<i>M. pallidus</i>	MPA8	ME	Azerbaijan	Azix	GU290295	Furman <i>et al.</i> (2010b)
<i>M. pallidus</i>	MPA8	ME	Turkey	Epeçik	GU290296	Furman <i>et al.</i> (2010b)
<i>M. pallidus</i>	MPA9	ME	Iran	Karafu	GU290292	Furman <i>et al.</i> (2010b)
<i>M. pallidus</i>	MPA10	ME	Iran	Karafu	GU290294	Furman <i>et al.</i> (2010b)
<i>M. pallidus</i>	MPA11	ME	Turkey	Delikli	GU290299	Furman <i>et al.</i> (2010b)
<i>M. pallidus</i>	MPA12	ME	Iran	Sarin Ab-Garma	GU290291	Furman <i>et al.</i> (2010b)
<i>M. pallidus</i>	MPA13	ME	Turkey	Delikli	GU290300	Furman <i>et al.</i> (2010b)
<i>M. pallidus</i>	MPA14	ME	Turkey	Epeçik	GU290297	Furman <i>et al.</i> (2010b)
<i>M. pallidus</i>	MPA14	ME	Turkey	Epeçik	GU290298	Furman <i>et al.</i> (2010b)
<i>M. africanus</i>	MAF1		Ethiopia	Sof Omar	JX012161	NMP 92129
<i>M. africanus</i>	MAF2		Ethiopia	Sof Omar	JX012162	NMP 92127
<i>M. 'australis'</i>	MAU1		Australia	Cape York	AY169453	Appleton <i>et al.</i> (2004)
<i>M. 'australis'</i>	MAU2		Australia	Shoalwater Bay	AY169452	Appleton <i>et al.</i> (2004)
<i>M. 'australis'</i>	MAU3		Indonesia	Java	AY169444	Appleton <i>et al.</i> (2004)
<i>M. 'australis'</i>	MAU4		Philippines	Leyte Island	AY169458	Appleton <i>et al.</i> (2004)
<i>M. 'australis'</i>	MAU5		Philippines	Negros Island	AY169457	Appleton <i>et al.</i> (2004)

Table 1. Continued

Species	Haplotype	Lineage/ sublineage	Country	Locality	Coordinates	GenBank Acc. No.	Voucher/Reference
<i>M. 'australis'</i>	MAU6		Vanuatu	Aore Island		AY169454	Appleton <i>et al.</i> (2004)
<i>M. 'australis'</i>	MAU7		Vanuatu	Tegua Island		AY169455	Appleton <i>et al.</i> (2004)
<i>M. 'australis'</i>	MAU8		Vanuatu	Toga Island		AY169456	Appleton <i>et al.</i> (2004)
<i>M. bassanii</i>	MBA		Australia	Naracoorte		AY169435	Appleton <i>et al.</i> (2004)
<i>M. fuliginosus</i>	MFU1		China	Yunan		AY169468	Appleton <i>et al.</i> (2004)
<i>M. fuliginosus</i>	MFU2		Japan	Wakayama		AY169469	Appleton <i>et al.</i> (2004)
<i>M. inflatus</i>	MIN		Uganda	Rwenzori Mountains		AY169465	Appleton <i>et al.</i> (2004)
<i>M. magnater</i>	MMA		Papua New Guinea	Nong River		AY169443	Appleton <i>et al.</i> (2004)
<i>M. manavi</i>	MMN		Madagascar	Andringitra Reserve		AY169464	Appleton <i>et al.</i> (2004)
<i>M. 'medius'</i>	MME1		Papua New Guinea	Magidobo		AY169441	Appleton <i>et al.</i> (2004)
<i>M. 'medius'</i>	MME2		Papua New Guinea	Sol River		AY169442	Appleton <i>et al.</i> (2004)
<i>M. cf. arenarius</i>	MAR1	YE	Yemen	Halhal	15.73 N, 43.62 E	JX012156	NMP pb3747
<i>M. cf. arenarius</i>	MAR2	YE	Yemen	Riqab	14.87 N, 43.42 E	JX012157	NMP pb3127
<i>M. cf. arenarius</i>	MAR3	YE	Ethiopia	Masha	07.87 N, 35.48 E	JX012158	NMP 92178
<i>M. cf. arenarius</i>	MAR4	YE	Ethiopia	Masha	07.87 N, 35.48 E	JX012159	NMP 92177
<i>M. cf. arenarius</i>	MAR5	YE	Yemen	Riqab	14.87 N, 43.42 E	JX012160	NMP pb3128
<i>M. natalensis</i>	MNA1		South Africa	Steenkampskraal		AY169467	Appleton <i>et al.</i> (2004)
<i>M. natalensis</i>	MNA2		South Africa	Sudwala		AY169466	Appleton <i>et al.</i> (2004)
<i>M. oceanensis</i>	MOC		Australia	Nowa Nowa		AY169436	Appleton <i>et al.</i> (2004)
<i>M. orianae</i>	MOR1		Australia	Darwin		AY169437	Appleton <i>et al.</i> (2004)
<i>M. orianae</i>	MOR2		Australia	Kimberley Ranges		AY169438	Appleton <i>et al.</i> (2004)
<i>M. propritristis</i>	MPR		Papua New Guinea	Waro		AY169440	Appleton <i>et al.</i> (2004)
<i>M. sp.</i>	MSP1		Papua New Guinea	Waro		AY169439	Appleton <i>et al.</i> (2004)
<i>M. sp.</i>	MSP2		Philippines	Negros Island		AY169451	Appleton <i>et al.</i> (2004)
<i>M. sp.</i>	MSP3		Solomon Islands	Santa Isabel		AY169459	Appleton <i>et al.</i> (2004)
<i>M. sp.</i>	MSP4		Solomon Islands	Santa Isabel		AY169460	Appleton <i>et al.</i> (2004)
<i>M. sp.</i>	MSP5		Solomon Islands	Santa Isabel		AY169461	Appleton <i>et al.</i> (2004)
<i>M. sp.</i>	MSP6		Tanzania	Gonja Forest Reserve		AY169462	Appleton <i>et al.</i> (2004)
<i>M. sp.</i>	MSP7		Tanzania	Usambara Mountains		AY169463	Appleton <i>et al.</i> (2004)
<i>M. tristis</i>	MTR1		Philippines	Leyte Island		AY169471	Appleton <i>et al.</i> (2004)
<i>M. tristis</i>	MTR2		Philippines	Negros Island		AY169470	Appleton <i>et al.</i> (2004)
<i>Myotis muricola</i>						AY504566	Worthington Wilmer <i>et al.</i> (unpubl.)
<i>Chalinolobus morio</i>						AY169472	Appleton <i>et al.</i> (2004)
<i>Chalinolobus nigrogriseus</i>						AY504561	Worthington Wilmer <i>et al.</i> (unpubl.)
<i>Chalinolobus tuberculatus</i>						AF321051	Lin & Penny (2001)

NMP = National Museum in Prague, Czech Republic.

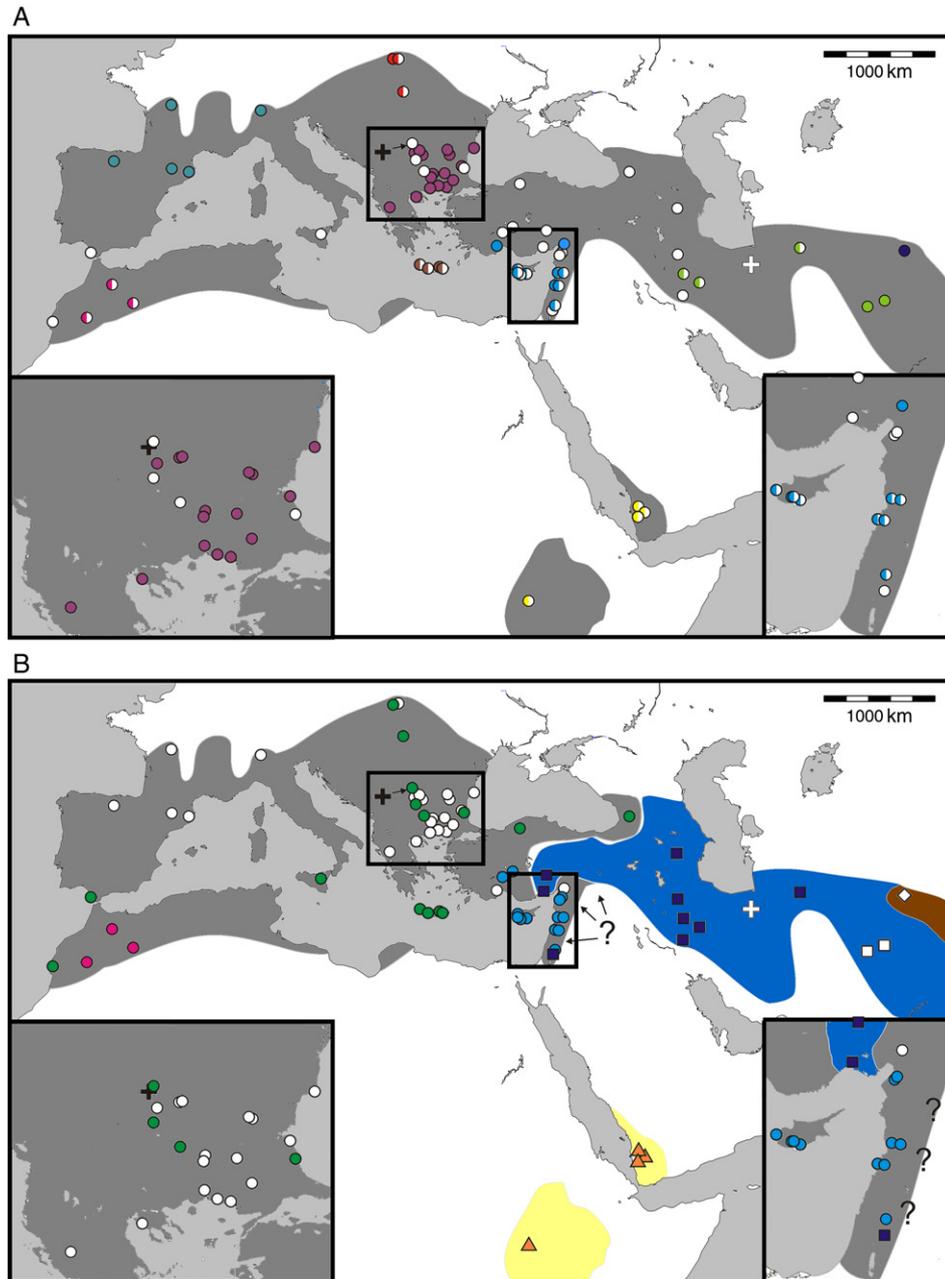


Figure 1. **A.** Map showing the origin of specimens investigated in this study and their sorting to nine groups defined for morphometric analysis. (1) Morocco = purple, (2) Western Europe = bluish green, (3) Pannonia = red, (4) Balkans = violet, (5) Crete = brown, (6) Levant = light blue, (7) Middle East = light green, (8) Eastern Afghanistan (Jalalabad) = dark blue, (9) Yemen and Ethiopia = yellow. Colours correspond to those in Figures 4A–4D, S4 and S5. Circles with any colour except white = samples used for morphometric analysis, white circles = samples used for molecular analysis, two-coloured circles = samples using both methods; grey shading delimits the distribution of *Miniopterus* spp.; black cross = type locality of *M. schreibersii*, white cross = type locality of *M. pallidus*. **B.** Geographic representation of the Western Palaeartic and Yemeni-Ethiopian lineages/sublineages, and approximate distribution of the respective species. Species and type localities (t.l.) are represented by different symbols (circles = *M. schreibersii* s.str.; squares = *M. pallidus*; triangles = *M. cf. arenarius*; diamond = *M. cf. fuliginosus*; black cross = t.l. of *M. schreibersii*; white cross = t.l. of *M. pallidus*). Coloured symbols indicate genetic, or both genetic and morphological, approaches used; white symbols represent morphological approach only used (colours of symbols correspond to different species/lineage/sublineage as indicated in Fig. 2 and to haplotypes presented in the haplotype network in Fig. 3). Coloured shading delimits the approximate distribution of species occurring in the Western Palaeartic and adjacent regions: grey = *M. schreibersii* s.str.; blue = *M. pallidus*; yellow = *M. cf. arenarius*; brown = *M. cf. fuliginosus*.

and parameter and tree samples saved every 100 generations. A 50% majority-rule consensus tree was constructed from the sampled trees after discarding the first 20 000 (two million generations) as burn-in, which included samples before attainment of the stationarity plateau on the log-likelihood score plot according to Tracer 1.4 (Drummond & Rambaut, 2007). Posterior probabilities were calculated as the frequency of samples recovering any particular clade (Huelsenbeck & Ronquist, 2001). The NJ tree was inferred using PAUP* 4.0b10 (Swofford, 2003), based on uncorrected *p*-distances and calculating the bootstrap branch support based on 1000 resampled datasets. Haplotype networks were prepared using the statistical parsimony algorithm implemented in TCS 1.21 (Clement, Posada & Crandall, 2000) under a 95% limit of parsimony. Based on the results obtained through phylogenetic analysis, ingroup haplotypes for bent-winged bat populations were divided into seven sets and average uncorrected *p*-distances between them calculated using MEGA 4.0 (Tamura *et al.*, 2007). In the text, we always refer to uncorrected *p*-distances as they are easily comparable with most previous molecular-taxonomic studies.

MORPHOLOGICAL ANALYSIS

Morphometric analysis was based on skull traits. The complete set of specimens was divided into nine groups (Fig. 1A) based on the results of both published (Appleton *et al.*, 2004; Bilgin *et al.*, 2006, 2008; Furman *et al.*, 2009, 2010b, c) and our own preliminary genetic analysis, geographic origin of the samples, and obvious differences observed in biometric data (cranial and dental metrics and non-metric traits): viz. (1) Morocco – specimens from the Atlas Mountains ($N = 18$); (2) Western Europe – specimens from Spain, France, Italy, and Austria ($N = 37$); (3) Pannonia – specimens from Slovakia and Romania ($N = 49$); (4) Balkans – specimens from Bulgaria and continental Greece ($N = 84$); (5) Crete ($N = 19$); (6) Levant – specimens from southern Turkey, western Syria, Cyprus, and Lebanon ($N = 93$); (7) Middle East – specimens from Iran and southern Afghanistan ($N = 14$); (8) Eastern Afghanistan (Jalalabad area) ($N = 28$); and (9) Yemen and Ethiopia – including one specimen from Sudan ($N = 11$). Only individuals morphologically assignable to *M. schreibersii* s.l. were included. Group 6 (Levant) contained some samples from the area of the zone of sympatry of *M. schreibersii* and *M. pallidus*. These samples were classified according to the prevailing genotypes present in the place of origin. Explanation of some geographic terms used in this study (considering the grouping of the examined material): Levant = western Syria and Lebanon, but including southern Turkey and Cyprus;

Middle East = central and eastern Turkey, southern Azerbaijan, Iran, southern Afghanistan and north-western Jordan. The Statistica 6.0 software package (StatSoft) was used for all morphological statistical analyses.

Linear morphometrics

We recorded 24 cranio-dental measurements (11 skull or mandible measurements and 13 upper or lower tooth-row dimensions) taken using a digital calliper (by JŠ) to the nearest 0.01 mm (Fig. S1). Further, we recorded 57 dental measurements (width, length and high dimensions of respective teeth; Fig. S2) to the nearest 0.0125 mm using an optical calliper (for a complete list of all measurements, see Appendix S1).

Basic descriptive statistical parameters (mean, minimum, maximum, and standard deviation) were calculated for each measurement and for each group (1–9). We further used the morphometric data to perform factor (FA) and discriminant function (DFA) analyses to test: (1) grouping and/or separation of the above groups (1–9); (2) similarity/dissimilarity of particular populations/taxa; and (3) the importance of particular dimensions for intrageneric, inter-specific and intraspecific variation and differentiation. FA and DFA were first performed on samples from all groups (1–9), and subsequently on groups 1–7, in order to better demonstrate differences between geographically and morphologically close populations. Cranial and dental characteristics were divided into six datasets (maxillary, mandibular, cranial, cranio-dental, all dental, and all cranial characteristics) and these tested separately in consecutive FAs and DFAs to assess the influence of different character sets on the grouping/separation of individuals in morphospace. The FA and DFA canonical scores were plotted to show relationships among the examined groups of samples. Morphological data of the Balkan (with addition of genotyped samples of the Levantine group) and Middle Eastern sample sets were analysed by analysis of variance (ANOVA).

Geometric morphometrics and non-metric traits

Geometric morphometrics were used to analyse geographic variation in *Miniopterus* skulls and mandibles. This technique has been demonstrated to be both objective and efficient compared to traditional methods (e.g. Zelditch, Fink & Swiderski, 1995; Rohlf, Loy & Corti, 1996; Rohlf, 1998), including in studies on bats (e.g. Velazco, Gardner & Patterson, 2010). The same material was used as for linear morphometrics (Appendix 1).

Images of skulls (lateral, ventral and dorsal view), mandibles (lateral and occlusal view) and dentition (details of the upper and lower tooth-row) were taken with a digital camera, archived (jpeg format;

1360 × 1200 pixels resolution), and processed using QuickPhoto 4.1 software (Promicra, Prague). Images of mandibles were taken separately. All images were taken at an identical angle. Images of skulls and mandibles were converted to thin-plate spline format (tps) using tpsUtil 1.46 software (Rohlf, 2010). Homologous and topologically equivalent landmarks were plotted on the skull (lateral, dorsal, and ventral views) and mandible (lateral view) images using the tpsDig 1.40 program (Rohlf, 2004) in order to describe size and shape variation (for landmark definitions see Appendix S1).

Landmark coordinates were converted into millimetres using an established conversion factor (pixel/mm) and the original scale. The centroid size (CS) scores of all view types for each specimen (CS1 – lateral view of mandible, CS2 – lateral view of skull, CS3 – ventral view of skull, and CS4 – dorsal view of skull) were calculated using the tpsRegr 1.36 program (Rohlf, 2009), and subsequently plotted to show size differences between the groups examined. In order to compare the shape of specimens from different groups, the coordinates for each specimen were scaled, aligned and transformed by general procrustes alignment (which generates a consensus configuration based on the landmark coordinates of all specimens) using the tpsRelw 1.46 software package (Rohlf, 2008) with $\alpha = 0$, and orthogonal projection and uniform component included. Shape differences between the consensus landmark configuration and each individual specimen were obtained and used to compute a matrix of partial warp (PW) scores. Relative warp (RW) scores were computed over the covariance matrix of the PW scores; these are, therefore, analogous to a principal components analysis (PCA) in the sense that they describe the axes of greatest variation in shape for all specimens investigated. The PW matrix was used in a DFA to describe differences between the studied groups and to confirm patterns previously suggested by the RW scores. The scores from canonical variant 1 of the DFA (of partial matrix data) and the CS of skull and mandible were plotted in order to visualise and evaluate how size and shape contributed to the arrangement of these groups. Data obtained by geometric morphometrics (RW scores) of the Balkan (with addition the genotyped Levantine samples) and Middle Eastern sample sets were analysed by ANOVA.

The status of 49 non-metric cranial and dental characteristics (44 dental and five skull or mandible; see Table S1) were investigated based on images of skulls, mandibles and dentition. Each characteristic was evaluated based on a pre-defined scale system 1–5 (see Fig. S3). Non-metric data were analysed in the same way as the linear metric data (basic descriptive statistics, FA and DFA computed).

RESULTS

MOLECULAR ANALYSIS

Eighty-nine haplotypes were registered from 111 shortened (1034 bp) sequences (including GenBank and outgroup sequences) of the mitochondrial ND2 gene. Within this haplotype dataset, 591 characters were variable and 527 parsimony-informative. Topologies from all analyses performed (ML, BA, NJ), as well as the log likelihood values ($\ln L$), were similar (Fig. 2; ML $\ln L = -10614.95$; BA mean $\ln L = -10316.71$). Three well supported *Miniopterus* bat clades were identified within the complete data set: (A) an Australian-Oriental clade (Australasian, Oriental and Eastern-Palaeartic regions) in the basal position; (B) an Afro-Arabian clade (sub-Saharan Africa and south-western Arabia); and (C) a West Palaeartic clade (Europe, North Africa, Asia Minor and the Middle East). The Western Palaeartic clade could be further divided into three well separated lineages: a Middle Eastern lineage (ME) (Iran, inland Turkey, Azerbaijan, Jordan) in the basal position, differing by 4.3 and 5.4% from the remaining two lineages; a Moroccan lineage (MO) from the Atlas Mts.; and a Mediterranean lineage (M) identified from Spain, Sicily, Slovakia, Romania, Bulgaria, Crete, the Atlantic coast of Morocco, the eastern Mediterranean region (southern Turkey, Cyprus, Syria, Lebanon), and the Black Sea region (northern Turkey, Georgia). The latter two lineages differed from each other by 2.5%. Within the third lineage, we detected a further subdivision into two seemingly parapatric sublineages with 1.2% divergence: a West Mediterranean sublineage (WM) from Europe, the Atlantic coast of Morocco, and the Black Sea region; and an East Mediterranean sublineage (EM) from southern Turkey, Cyprus, Syria and Lebanon. The mutual relationships between the West Palaeartic clade samples are also demonstrated through the parsimony haplotype network (Fig. 3). All the above-mentioned *Miniopterus* clades/lineages/sublineages were highly supported by ML bootstrap values ($\geq 80\%$), NJ bootstrap values ($\geq 85\%$), and BA posterior probabilities (≥ 0.98), except for clade A and lineage MO by ML bootstrap (62% and 71%), and sublineage WM by BA posterior probabilities (0.81).

All samples from south-western Arabia and Ethiopia, border areas of the Palaeartic and Afro-tropic regions, were embedded within clade B, where they formed two lineages (Fig. 2), one represented by a morphologically distinct Afro-tropic species, *M. africanus* Sanborn, 1936, collected from Ethiopia (and initially used as an outgroup species); and the other formed by individuals from Yemen and western Ethiopia [hereafter known as the Yemeni-Ethiopian lineage/group (YE)]. Representatives of the YE

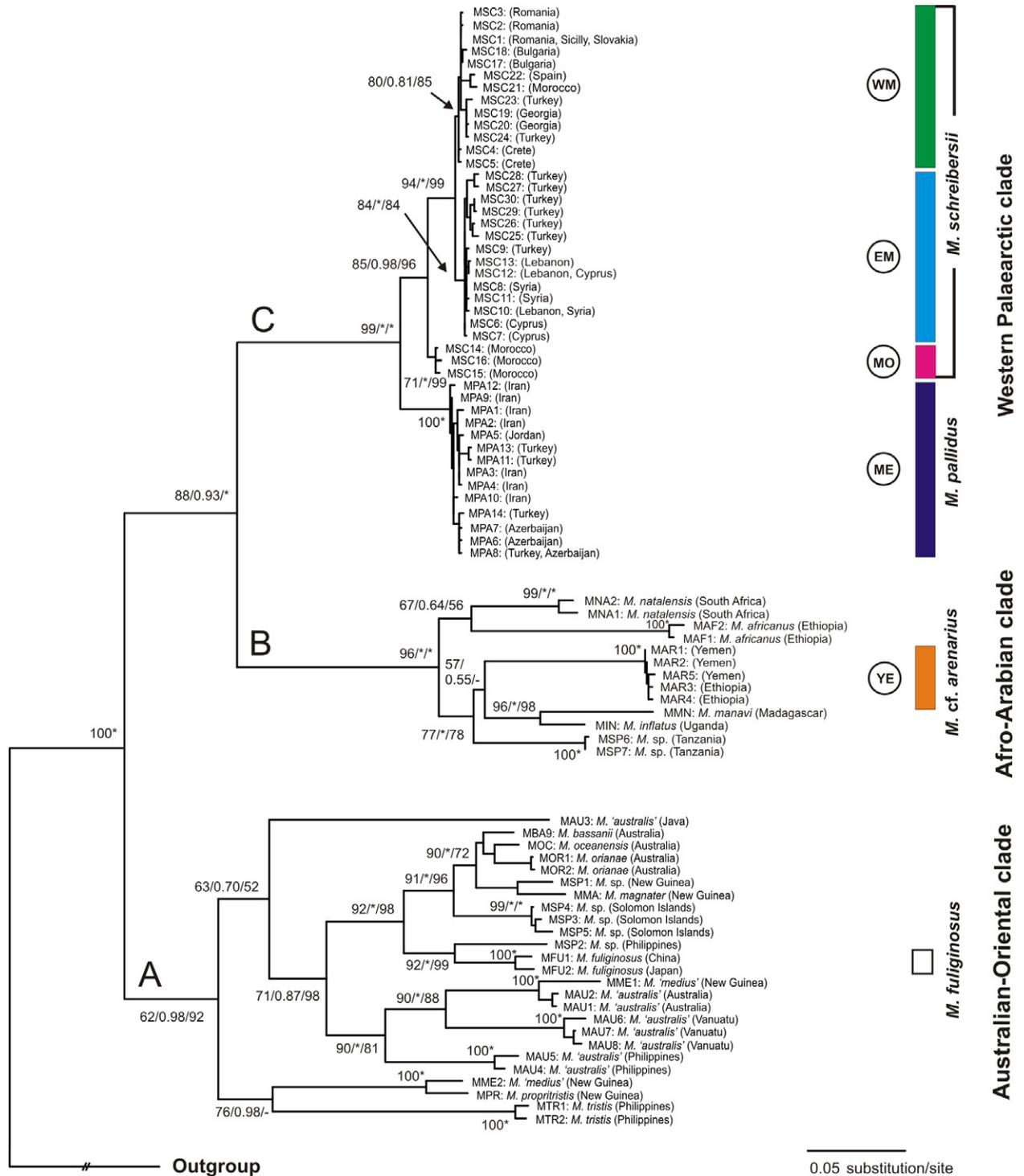


Figure 2. Maximum likelihood tree demonstrating phylogeny of *Miniopterus* as inferred from mitochondrial *ND2* (based on different haplotypes only). Numbers at the nodes represent bootstrap support or posterior probability values for maximum likelihood (ML), bayesian approach (BA), and neighbour joining (NJ) analyses. An asterisk (*) indicates full support (100 or 1.00) for a particular clade and analysis, 100* indicates full support in all analyses, – = clade not inferred in the respective analysis, // = branch length shortening in respect to outgroup. Capital letters and letters in circles represent respective clade/lineages/sublineage, as discussed in the text. Vertical bars indicate Western Palaearctic species that are the subject of this study (*M. fuliginosus* is represented only by sequences originating outside the Western Palaearctic retrieved from GenBank). Haplotype codes are identical to those listed in Table 1. Colours correspond to those in Figures 1B and 3.

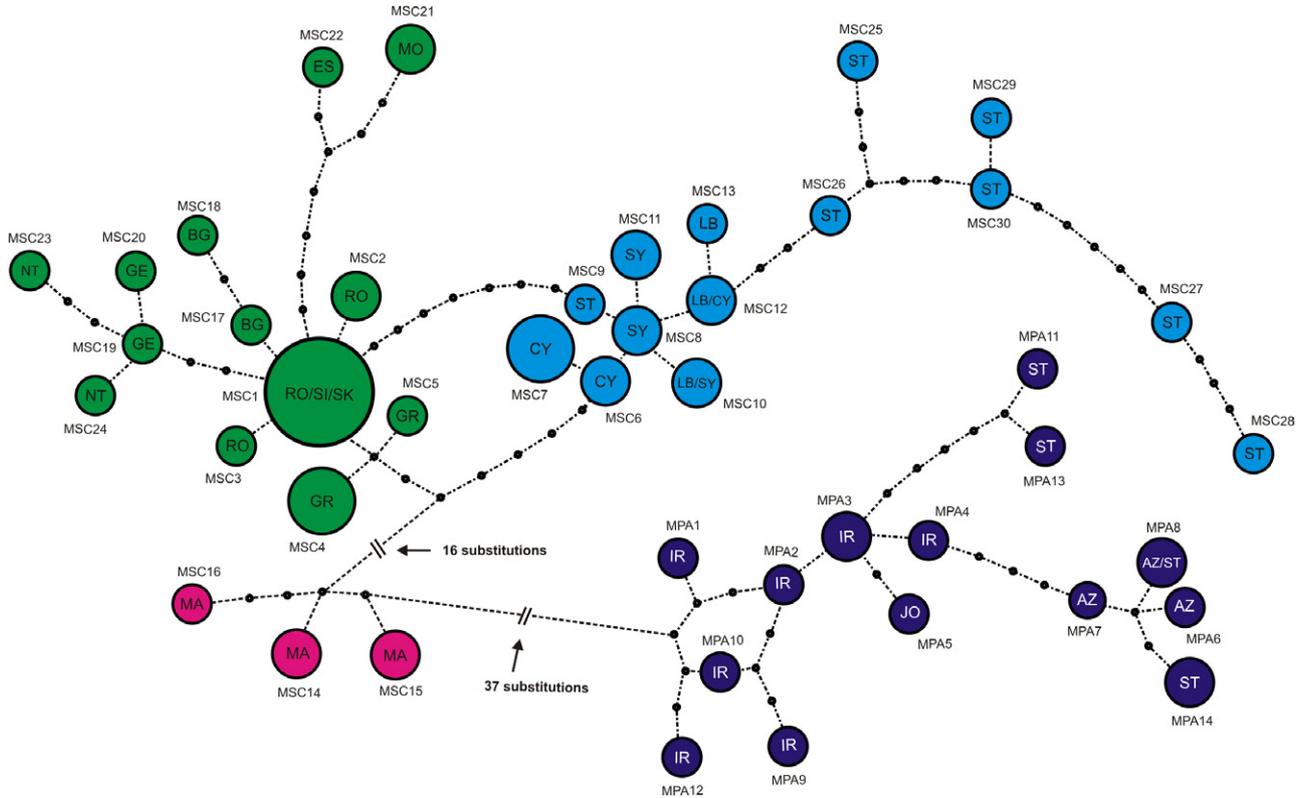


Figure 3. Graphic illustration of relationships between *ND2* haplotypes of *M. schreibersii* s.str. (green, light blue, purple) and *M. pallidus* (dark blue), as inferred through the maximum parsimony network approach. Size of circles corresponds to the number of samples within a particular haplotype (1, 2, 4 or 7 samples). Small dots between haplotypes indicate hypothetical haplotypes (or number of substitutions between them). Geographic abbreviations: MO – Morocco, Agadir (coast); MA – Morocco, Atlas Mts.; ES – Spain; SI – Sicily (Italy); SK – Slovakia; RO – Romania; BG – Bulgaria; CR – Crete (Greece); CY – Cyprus; NT – northern Turkey; ST – southern Turkey; GE – Georgia; AZ – Azerbaijan; LB – Lebanon; SY – Syria; JO – Jordan; IR – Iran. Colours correspond to those in Figures 1B and 2. Haplotype codes are identical to those listed in Table 1.

lineage morphologically resemble *M. cf. schreibersii* but have been recently assigned to *M. natalensis* (e.g. Simmons, 2005). The latter lineage, however, was differentiated by 11.5% from populations in South Africa, where the type locality of *M. natalensis* is registered. Moreover, the South African haplotypes were not in sister position to the YE lineage, with other species, such as *M. manavi* Thomas, 1906; *M. inflatus* Thomas, 1903; and *Miniopterus* sp. from Tanzania, being interspersed.

Genetic distances within and between selected populations/taxa are presented in Table 2; while a geographic representation of the Western Palaearctic and YE lineages/sublineages, and the approximate distribution of the respective species, is presented in Figure 1B.

MORPHOLOGICAL ANALYSIS

Linear morphometrics

All CS values, and all cranial and dental measurements for the nine different groups and their simple

comparisons (Table 3; Tables S2 and S3), indicated the same size patterns. Bats from eastern Afghanistan (Jalalabad area) were markedly larger in comparison to European and Levantine samples (size differences between the latter two bat groups were very small). Specimens from Crete, Yemen and Ethiopia were clearly the smallest; while samples from the Middle East were slightly smaller than those from eastern Afghanistan, but markedly larger than bats from Europe and the Levant, and similar in size to Moroccan bats. Both skull and dentition shape differences (expressed by ratios of cranial or dental dimensions) were much less expressive than differences in general size. This pattern was more pronounced in cranial than dental characteristics.

The results of FA and DFA analysis of skull and dental dimensions generally showed similar following patterns (results of FA not shown; for DFA see Fig. 4A, B; and Fig. S4), as did the comparison of raw skull and tooth dimensions and their ratios: (1) samples from eastern Afghanistan, the YE group and

Table 2. Uncorrected *p*-distances between and within different species/(sub)lineages of *Miniopterus* based on the haplotype dataset (in percentage; mean in parentheses)

	<i>M. schreibersii</i> , Western- Mediterranean sublineage (WM)	<i>M. schreibersii</i> , Eastern- Mediterranean sublineage (EM)	<i>M. schreibersii</i> , Moroccan lineage (MO)	<i>M. pallidus</i> , Middle Eastern lineage (ME)	<i>M. cf.</i> <i>arenarius</i> , Yemeni- Ethiopian lineage (YE)	<i>M. natalensis</i> , South Africa
<i>M. schreibersii</i> , Western-Mediterranean sublineage (WM)	0.1–1.4 (0.6)					
<i>M. schreibersii</i> , Eastern-Mediterranean sublineage (EM)	0.8–2.2 (1.2)	0.1–1.1 (0.5)				
<i>M. schreibersii</i> , Moroccan lineage (MO)	2.0–3.0 (2.4)	2.2–3.1 (2.5)	0.3–0.5 (0.4)			
<i>M. pallidus</i> , Middle Eastern lineage (ME)	4.9–6.3 (5.4)	4.7–5.9 (5.3)	3.9–4.7 (4.3)	0.1–1.1 (0.6)		
<i>M. cf. arenarius</i> , Yemeni-Ethiopian lineage (YE)	14.1–15.1 (14.6)	13.9–15.0 (14.4)	14.2–14.9 (14.5)	14.8–15.8 (15.2)	0.1–0.5 (0.4)	
<i>M. africanus</i> , Ethiopia	15.5–16.1 (15.7)	15.5–16.0 (15.8)	15.0–15.7 (15.3)	15.1–16.2 (15.6)	12.8–13.4 (13.1)	1.0
<i>M. natalensis</i> , South Africa	12.8–13.6 (13.2)	12.8–13.9 (13.2)	12.9–13.3 (13.2)	14.0–15.0 (14.5)	11.2–11.8 (11.5)	10.6–10.9 (10.8)
						1.5

Morocco clustered separately from the European, Levantine and Middle Eastern groups, however, in case of Morocco markedly less distinct; (2) samples from the Balkans and Pannonia formed a common cluster, as did samples from Crete and the Levant; (3) Middle Eastern samples overlapped substantially with the West European and Levantine samples, and were positioned close to the Pannonian and Balkan samples; (4) samples from western Europe were grouped together with other groups from Europe, the Middle East and the Levant (based on cranial dimensions), and very closely with samples from the Levant (based solely on dental traits). Using factor loading values, we were able to identify the 10 cranial and 13 dental dimensions that affected observed variation most significantly (DFA, $P < 0.0001$), i.e. LaZ, LaInf, LaM, ACr, ACo, CC, M³M³, I₁M₃, CM₃, M₁M₃; and LI², WC^{sup}, WP², WP⁴, LiM¹, W2M¹, LiM², W3M², LI₂, LI₃, LD_{inf}, WD_{inf} and LP₂, respectively. For a description of morphometric differentiation between the *Miniopterus* groups examined, see Appendix S2.

Results of ANOVA (Table S4) showed significant differences in 34 of 85 of the examined characteristics (mainly cranial) between the Balkan (with addition of the genotyped Levantine samples) and Middle Eastern samples.

Geometric morphometrics and non-metric traits

Twenty-two RWs were generated for the lateral skull view, 18 for the ventral view, 14 for the dorsal view, and 14 for the lateral view of the mandible. The first four RWs, which together represented more than 50% of total variation for each view, were used in all subsequent analyses (Table S5).

Results of PCA and DFA demonstrated a number of differences between the sample sets examined, and particularly in the lateral view of the skull; however, neither PCA nor DFA were able to demonstrate any clear separation between most of the groups examined (results of PCA not shown; for DFA see Fig. 4C), with the European and Middle Eastern samples in particular frequently showing a substantial overlap. Nevertheless, distinctive separations were observed in the samples from eastern Afghanistan when plotting the first two DFA canonical variables considering all views of skull (Fig. 4C); the YE group considering the dorsal and ventral views of skull; the Moroccan samples in the skull ventral view; and in the Pannonian samples for the skull lateral view. While the relationships between the groups differed for individual views, some general patterns were observable: (1) Pannonian and Levantine samples were distinct from each other; (2) samples from Crete were mostly similar to those from the Levant; and (3) Middle Eastern samples were mostly grouped together with samples from Western Europe. In general, all analy-

Table 3. Selected cranial and dental dimensions (in mm) of *Miniopterus* examined in this study

Character	Morocco (MO)										Western Europe (WM)										Pannonia (WM)										Balkans (WM)										Crete (WM)									
	N		M		min		max		SD		N		M		min		max		SD		N		M		min		max		SD		N		M		min		max		SD											
LCr	18	15.365	15.12	15.65	0.164	36	15.229	14.80	15.49	0.173	45	15.392	14.94	15.88	0.206	76	15.229	14.54	15.83	0.216	19	14.916	14.48	15.19	0.185	18	15.365	15.12	15.65	0.164	36	15.229	14.80	15.49	0.173	45	15.392	14.94	15.88	0.206	76	15.229	14.54	15.83	0.216	19	14.916	14.48	15.19	0.185
LaI	18	3.777	3.63	3.98	0.089	36	3.711	3.57	3.88	0.071	47	3.761	3.53	4.02	0.108	82	3.710	3.52	3.93	0.087	19	3.621	3.48	3.77	0.084	18	3.777	3.63	3.98	0.089	36	3.711	3.57	3.88	0.071	47	3.761	3.53	4.02	0.108	82	3.710	3.52	3.93	0.087	19	3.621	3.48	3.77	0.084
LaI _{inf}	18	4.202	4.02	4.32	0.086	36	4.023	3.74	4.29	0.104	45	4.025	3.85	4.24	0.088	80	3.974	3.45	4.18	0.136	19	3.894	3.78	4.05	0.091	18	4.202	4.02	4.32	0.086	36	4.023	3.74	4.29	0.104	45	4.025	3.85	4.24	0.088	80	3.974	3.45	4.18	0.136	19	3.894	3.78	4.05	0.091
LaM	18	8.788	8.64	8.97	0.105	35	8.675	8.10	8.99	0.190	46	8.757	8.10	9.21	0.180	76	8.746	8.12	9.04	0.155	19	8.524	8.40	8.67	0.091	18	8.788	8.64	8.97	0.105	35	8.675	8.10	8.99	0.190	46	8.757	8.10	9.21	0.180	76	8.746	8.12	9.04	0.155	19	8.524	8.40	8.67	0.091
ACr	18	7.973	7.73	8.34	0.185	30	7.497	6.66	8.01	0.420	43	7.672	6.79	8.04	0.325	77	7.743	6.83	8.21	0.324	19	7.765	7.36	7.99	0.154	18	7.973	7.73	8.34	0.185	30	7.497	6.66	8.01	0.420	43	7.672	6.79	8.04	0.325	77	7.743	6.83	8.21	0.324	19	7.765	7.36	7.99	0.154
LMd	18	10.977	10.80	11.28	0.144	36	10.852	10.56	11.15	0.143	48	10.923	10.28	11.30	0.175	75	10.847	10.15	11.07	0.154	19	10.622	10.32	10.88	0.118	18	10.977	10.80	11.28	0.144	36	10.852	10.56	11.15	0.143	48	10.923	10.28	11.30	0.175	75	10.847	10.15	11.07	0.154	19	10.622	10.32	10.88	0.118
ACo	18	2.598	2.48	2.81	0.077	36	2.594	2.40	2.93	0.109	48	2.583	2.17	2.93	0.120	75	2.508	2.04	2.93	0.109	19	2.538	2.41	2.69	0.076	18	2.598	2.48	2.81	0.077	36	2.594	2.40	2.93	0.109	48	2.583	2.17	2.93	0.120	75	2.508	2.04	2.93	0.109	19	2.538	2.41	2.69	0.076
CSI	18	11.168	10.84	11.52	0.189	34	11.130	10.67	11.97	0.298	44	11.431	10.94	12.03	0.278	66	11.103	10.64	11.90	0.261	19	10.730	10.15	11.02	0.211	18	11.168	10.84	11.52	0.189	34	11.130	10.67	11.97	0.298	44	11.431	10.94	12.03	0.278	66	11.103	10.64	11.90	0.261	19	10.730	10.15	11.02	0.211
CS2	18	20.813	20.39	21.21	0.228	32	20.478	20.15	20.89	0.199	42	20.659	20.04	21.19	0.276	68	20.502	19.87	21.11	0.261	19	20.163	19.72	20.59	0.205	18	20.813	20.39	21.21	0.228	32	20.478	20.15	20.89	0.199	42	20.659	20.04	21.19	0.276	68	20.502	19.87	21.11	0.261	19	20.163	19.72	20.59	0.205
CS3	18	16.935	16.73	17.33	0.159	32	16.760	16.37	17.09	0.173	40	16.738	16.30	17.43	0.250	73	16.756	16.23	17.19	0.186	19	16.394	16.05	16.75	0.173	18	16.935	16.73	17.33	0.159	32	16.760	16.37	17.09	0.173	40	16.738	16.30	17.43	0.250	73	16.756	16.23	17.19	0.186	19	16.394	16.05	16.75	0.173
CS4	18	17.716	17.44	18.03	0.193	34	17.515	17.18	17.93	0.194	37	17.762	17.18	18.44	0.264	74	17.580	17.14	18.10	0.204	19	17.179	16.84	17.51	0.221	18	17.716	17.44	18.03	0.193	34	17.515	17.18	17.93	0.194	37	17.762	17.18	18.44	0.264	74	17.580	17.14	18.10	0.204	19	17.179	16.84	17.51	0.221
LC ^{sup}	18	1.055	1.00	1.10	0.031	28	1.084	1.03	1.13	0.026	44	1.062	0.98	1.15	0.036	81	1.071	1.00	1.15	0.037	19	1.052	1.00	1.13	0.031	18	1.055	1.00	1.10	0.031	28	1.084	1.03	1.13	0.026	44	1.062	0.98	1.15	0.036	81	1.071	1.00	1.15	0.037	19	1.052	1.00	1.13	0.031
WC ^{sup}	18	0.883	0.81	0.93	0.035	28	0.896	0.81	0.98	0.032	44	0.840	0.78	0.90	0.030	81	0.833	0.76	0.93	0.033	19	0.825	0.78	0.85	0.024	18	0.883	0.81	0.93	0.035	28	0.896	0.81	0.98	0.032	44	0.840	0.78	0.90	0.030	81	0.833	0.76	0.93	0.033	19	0.825	0.78	0.85	0.024
HC ^{sup}	4	1.653	1.63	1.71	0.041	21	1.573	1.45	1.93	0.106	29	1.547	1.33	1.69	0.074	56	1.550	1.15	1.70	0.092	15	1.520	1.30	1.63	0.097	4	1.653	1.63	1.71	0.041	21	1.573	1.45	1.93	0.106	29	1.547	1.33	1.69	0.074	56	1.550	1.15	1.70	0.092	15	1.520	1.30	1.63	0.097
LP ²	18	0.841	0.75	0.90	0.046	36	0.816	0.78	0.88	0.027	48	0.829	0.73	0.93	0.047	82	0.829	0.78	0.94	0.036	19	0.818	0.78	0.88	0.025	18	0.841	0.75	0.90	0.046	36	0.816	0.78	0.88	0.027	48	0.829	0.73	0.93	0.047	82	0.829	0.78	0.94	0.036	19	0.818	0.78	0.88	0.025
WP ²	18	1.131	1.03	1.20	0.048	36	1.138	1.08	1.19	0.031	48	1.087	0.90	1.16	0.051	82	1.094	1.00	1.20	0.040	19	1.083	1.04	1.13	0.027	18	1.131	1.03	1.20	0.048	36	1.138	1.08	1.19	0.031	48	1.087	0.90	1.16	0.051	82	1.094	1.00	1.20	0.040	19	1.083	1.04	1.13	0.027
HP ²	4	0.584	0.55	0.63	0.031	25	0.568	0.48	0.65	0.047	33	0.535	0.43	0.63	0.049	58	0.561	0.43	0.65	0.053	15	0.521	0.45	0.60	0.045	4	0.584	0.55	0.63	0.031	25	0.568	0.48	0.65	0.047	33	0.535	0.43	0.63	0.049	58	0.561	0.43	0.65	0.053	15	0.521	0.45	0.60	0.045
WP ⁴	18	1.390	1.31	1.46	0.041	36	1.444	1.38	1.51	0.032	48	1.328	1.15	1.48	0.083	82	1.377	1.23	1.50	0.053	19	1.389	1.26	1.45	0.046	18	1.390	1.31	1.46	0.041	36	1.444	1.38	1.51	0.032	48	1.328	1.15	1.48	0.083	82	1.377	1.23	1.50	0.053	19	1.389	1.26	1.45	0.046
LP ⁴	18	2.220	1.10	1.38	0.068	36	1.283	1.18	1.35	0.042	48	1.231	1.13	1.38	0.066	82	1.231	1.13	1.38	0.057	19	1.181	1.15	1.23	0.023	18	2.220	1.10	1.38	0.068	36	1.283	1.18	1.35	0.042	48	1.231	1.13	1.38	0.066	82	1.231	1.13	1.38	0.057	19	1.181	1.15	1.23	0.023
HP ⁴	4	1.569	1.48	1.65	0.072	25	1.586	1.44	1.71	0.065	33	1.497	1.35	1.60	0.071	58	1.543	1.28	1.68	0.071	15	1.407	0.83	1.65	0.279	4	1.569	1.48	1.65	0.072	25	1.586	1.44	1.71	0.065	33	1.497	1.35	1.60	0.071	58	1.543	1.28	1.68	0.071	15	1.407	0.83	1.65	0.279
LoM ¹	18	1.438	1.35	1.50	0.039	35	1.473	1.43	1.55	0.034	48	1.447	1.35	1.53	0.039	83	1.452	1.24	1.55	0.043	19	1.439	1.40	1.48	0.021	18	1.438	1.35	1.50	0.039	35	1.473	1.43	1.55	0.034	48	1.447	1.35	1.53	0.039	83	1.452	1.24	1.55	0.043	19	1.439	1.40	1.48	0.021
LiM ¹	18	0.924	0.88	1.03	0.035	35	0.983	0.93	1.05	0.031	48	0.947	0.83	1.04	0.049	83	0.984	0.85	1.09	0.041	19	0.970	0.90	1.03	0.036	18	0.924	0.88	1.03	0.035	35	0.983	0.93	1.05	0.031	48	0.947	0.83	1.04	0.049	83	0.984	0.85	1.09	0.041	19	0.970	0.90	1.03	0.036
LC _{inf}	18	0.726	0.70	0.76	0.020	31	0.821	0.79	0.86	0.022	45	0.736	0.63	0																																				

Table 3. Continued

Character	Levant (EM)			Middle East (ME)			Eastern Afghanistan			Yemen & Ethiopia (YE)				
	N	M	SD	min	max	SD	N	M	SD	min	max	N	M	SD
LCr	93	15.148	0.217	14.71	15.74	0.222	28	15.636	0.222	15.03	16.13	10	15.058	0.254
LaI	93	3.675	0.084	3.41	3.97	0.096	28	3.928	0.096	3.76	4.15	11	3.711	0.083
LaInf	93	3.987	0.086	3.74	4.18	0.080	28	4.124	0.080	3.82	4.43	12	3.712	0.141
LaM	93	8.697	0.142	8.27	9.05	0.092	28	8.840	0.092	8.51	9.21	10	8.299	0.168
ACr	90	7.819	0.188	7.14	8.11	0.188	28	7.779	0.188	6.99	8.36	11	7.504	0.434
LMd	91	10.763	0.32	10.32	11.17	0.155	28	11.304	0.155	11.00	11.60	11	10.645	0.166
ACo	91	2.568	0.113	2.35	2.93	0.113	28	2.647	0.113	2.44	3.04	11	2.412	0.117
CS1	85	11.005	0.312	10.45	11.89	0.312	23	11.551	0.312	11.03	12.29	11	10.677	0.291
CS2	91	20.437	0.291	19.85	21.37	0.291	28	21.076	0.291	20.42	21.74	10	20.073	0.311
CS3	92	16.621	0.245	16.13	17.39	0.245	28	17.227	0.245	16.80	17.70	10	16.548	0.243
CS4	92	17.321	0.260	16.56	17.99	0.260	28	17.902	0.260	17.25	18.39	11	17.278	0.293
LC ^{sup}	92	1.072	0.034	1.00	1.18	0.034	26	1.114	0.034	1.03	1.20	12	1.056	0.048
WC ^{sup}	92	0.865	0.041	0.80	1.15	0.041	26	0.933	0.041	0.85	1.00	12	0.860	0.042
HC ^{sup}	57	1.579	0.088	1.25	1.73	0.088	26	1.645	0.088	1.28	2.00	3	1.629	0.178
LP ²	93	0.832	0.034	0.78	0.93	0.034	27	0.895	0.034	0.79	1.00	12	0.850	0.055
WP ²	93	1.124	0.051	0.91	1.25	0.051	27	1.081	0.051	0.90	1.19	12	1.028	0.061
HP ²	58	0.580	0.052	0.45	0.70	0.052	27	0.556	0.052	0.38	0.70	3	0.596	0.077
WP ⁴	93	1.403	0.039	1.30	1.53	0.039	27	1.413	0.039	1.33	1.58	12	1.350	0.057
LP ⁴	93	1.266	0.064	1.08	1.40	0.064	27	1.282	0.064	1.23	1.45	12	1.200	0.057
HP ⁴	58	1.514	0.088	1.31	1.56	0.088	27	1.531	0.088	1.35	1.75	3	1.533	0.104
LoM ¹	93	1.455	0.035	1.31	1.56	0.035	27	1.491	0.035	1.38	1.55	12	1.447	0.050
LiM ¹	93	0.957	0.042	0.85	1.05	0.042	27	0.991	0.042	0.90	1.10	12	0.951	0.044
LC _{inf}	89	0.736	0.026	0.68	0.80	0.026	26	0.787	0.026	0.71	0.86	12	0.745	0.040
WC _{inf}	89	0.807	0.025	0.75	0.86	0.025	26	0.853	0.025	0.75	0.93	12	0.780	0.045
HC _{inf}	55	1.452	0.088	1.15	1.55	0.088	25	1.557	0.088	1.29	1.80	3	1.425	0.148
LP ₂	89	0.569	0.022	0.53	0.63	0.022	26	0.575	0.022	0.53	0.63	12	0.567	0.032
WP ₂	89	0.627	0.021	0.58	0.68	0.021	26	0.651	0.021	0.61	0.68	12	0.610	0.019
HP ₂	55	0.490	0.025	0.43	0.55	0.025	26	0.472	0.025	0.36	0.55	3	0.463	0.056
WP ₄	90	0.761	0.030	0.68	0.85	0.030	27	0.767	0.030	0.73	0.83	12	0.751	0.027
LP ₄	90	0.601	0.037	0.50	0.68	0.037	27	0.668	0.037	0.58	0.76	12	0.633	0.058
HP ₄	55	0.883	0.050	0.75	0.95	0.050	27	0.879	0.050	0.75	1.03	3	0.900	0.076
LM ₃	90	1.249	0.031	1.15	1.33	0.031	27	1.268	0.031	1.20	1.31	12	1.221	0.029
WM ₃	90	0.638	0.034	0.58	0.88	0.034	27	0.688	0.034	0.64	0.75	12	0.665	0.032

Codes in brackets stand for the respective genetic lineage or sublineage (see text). See Appendix S1 for explanation of dimension abbreviations. Data for all dimensions are presented in Tables S2 and S3.

M = mean, min = minimum value, max = maximum value, and SD = standard deviation.

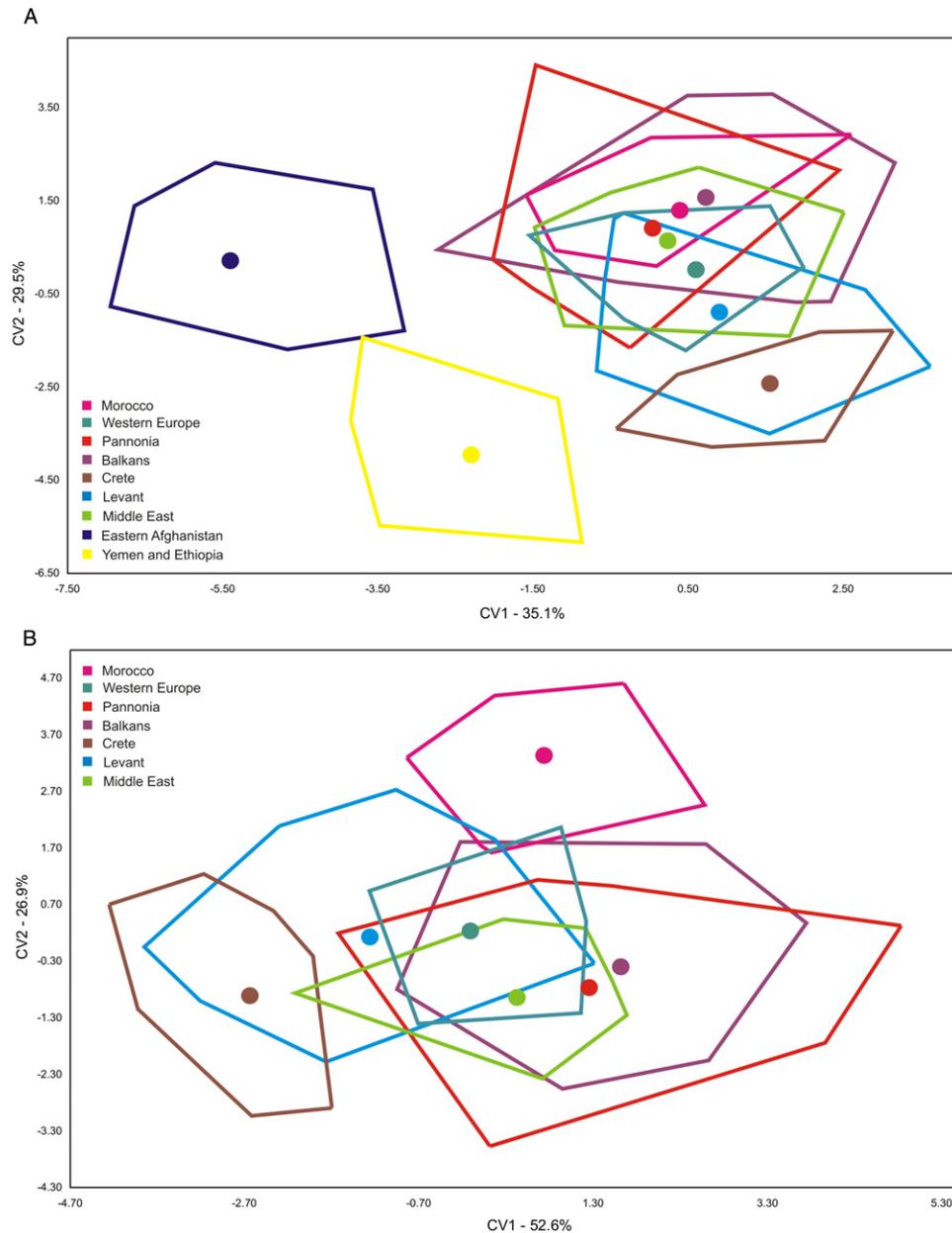


Figure 4. A, B. Results of discriminant function analysis based on linear morphometric data of skull dimensions – first two canonical axes. Polygons follow marginal points of particular groups, with coloured dots as centroids. **A** – all specimens; **B** – separate analysis excluding individuals from marginal areas (i.e. Eastern Afghanistan, Arabia and Ethiopia). **C.** Results of discriminant function analysis based on relative warp scores obtained from geometric morphometric analysis of 11 landmarks on the ventral view of the skull – first two canonical axes. Polygons and coloured dots are as in Figure 4A. **D.** Polygon plot of the first and second axes from factor analysis of all non-metric traits. Polygons and coloured dots are as in Figure 4A.

ses indicated that the most distinct groups were those originating from eastern Afghanistan, Yemen and Ethiopia; and from the Moroccan Atlas Mts.

Both bivariate plots of the main shape variable (RW1) and the CS for the respective view showed differences between the groups for all views; however,

these tended to be related to shifts in size rather than shape. This pattern was especially applicable within the eastern Afghanistan samples, and was most pronounced in results for the ventral and dorsal views of the skull. The shape-size plots provided very similar results for all views (see Fig. S5 for the skull lateral

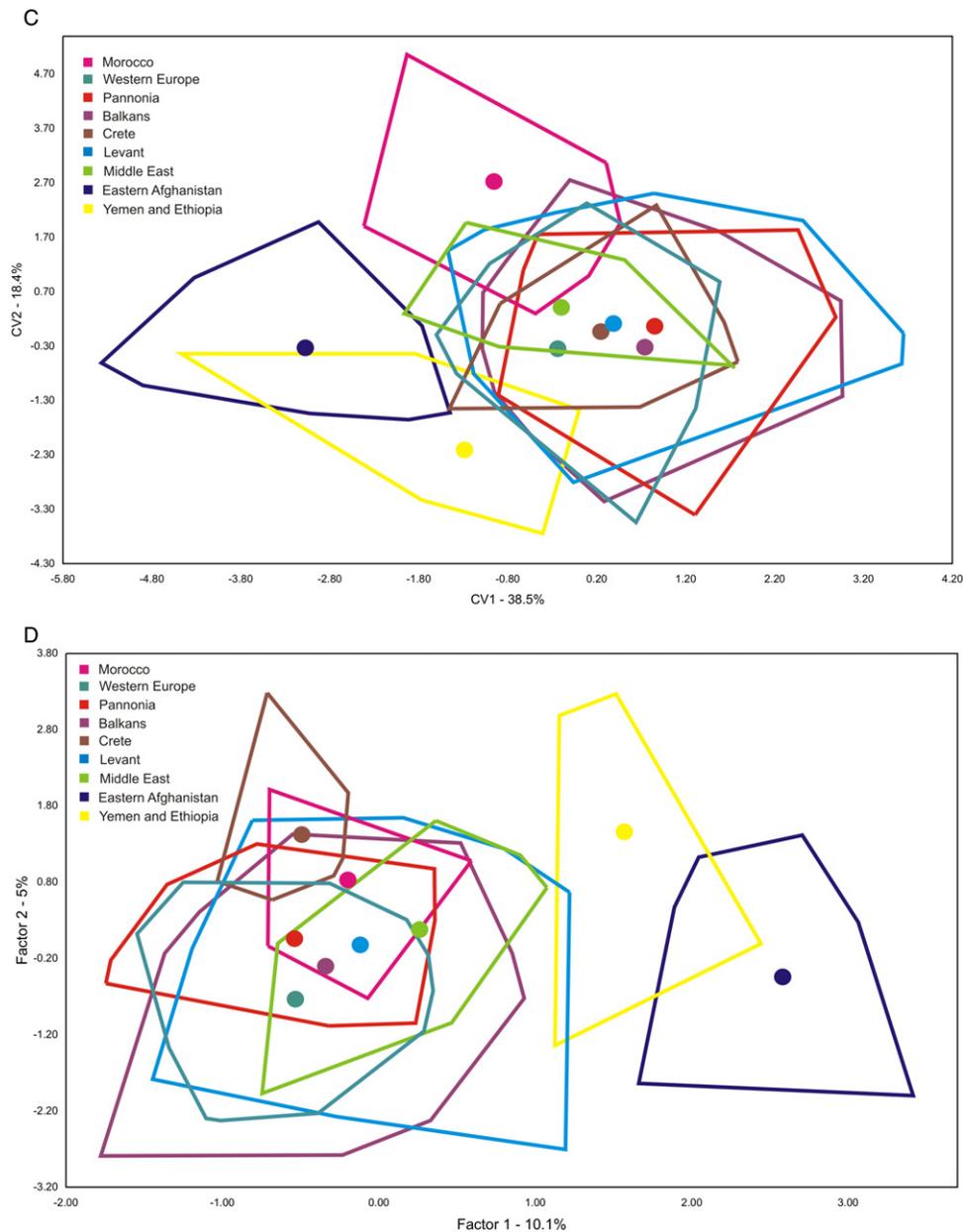


Figure 4. *Continued*

view) and may be summarised as follows: (1) the East Afghanistan samples were generally the most distinctive in both shape and size; (2) the YE group was positioned close to the Cretan group, and both were most distant from the eastern Afghanistan group by size dimension; (3) the Levantine samples were beside those from eastern Afghanistan the most distinctive to Pannonian samples by shape dimension; (4) the Moroccan group was positioned close to the Middle Eastern group, and both overlapped substantially with the Balkan and West European groups, especially by shape dimension; and (5) the Balkan and

West European samples were grouped very close to each other and were positioned centrally in the morphospace; for this reason they partially overlapped with all the other groups. In general, all the geometric morphometric results conformed well to the results of linear morphometric analyses.

Results of ANOVA (Table S4) showed four of 16 characteristics to be statistically different between the Balkan (with addition of the genotyped Levantine samples) and Middle Eastern samples.

The 49 non-metric cranial and dental traits (Table S6) examined through FA and DFA demonstrated

pronounced differentiation of the eastern Afghanistan group from the other groups. Similar differentiation was noted for the YE group, while all other groups formed a cluster of broadly overlapping samples (for FA see Fig. 4D; results of DFA not shown). These analyses also enabled selection of maxilla characteristics that most affected observed variation in the non-metric traits ($P < 0.0001$ in DFAs). For a description of non-metric differentiation between the *Miniopterus* groups see Appendix S2.

DISCUSSION

Revision of particularly Western Palaearctic bent-winged bat populations over their whole range (i.e. from the Maghreb to Afghanistan, and from Central Europe to Arabia) revealed unexpected hidden diversity, even in the light of recent discoveries by Furman *et al.* (2009, 2010c). Synthesis of the results from two different analytical approaches suggests that *M. schreibersii* s.l. (sensu, e.g. Corbet, 1978), a traditionally polytypic species, should be split into several allopatric or parapatric population groups, differing from each other in genetic and morphological traits. These groups can be delimited geographically as follows: (1) Europe, northern Turkey and Georgia; (2) the Levant, including southern Turkey and Cyprus; (3) the mountains of Morocco; (4) the Middle East (except for the Levant and Turkish coastal areas); (5) south-western Arabia and Ethiopia; and (6) eastern Afghanistan (Jalalabad area). This order mirrors the degree of relatedness of the respective populations to those of Europe (i.e. group two is closer related to the European population than group three). Although the geographical groupings may, at first, appear surprising, the findings are in general accordance with the opinions of earlier authors (namely Tate, 1941 and Maeda, 1982) who stressed morphological similarities among individual species of the genus *Miniopterus* and presumed the existence of more species, rather than a single universal morphotype. These conclusions have also recently gained support through several molecular studies (Appleton *et al.*, 2004; Tian *et al.*, 2004; Miller-Butterworth *et al.*, 2005; Furman *et al.*, 2009, 2010b, c), and we supplement these findings with additional molecular phylogeny and new morphological evidence.

Our results indicate that, though the populations differ only slightly in skull size, these differences were more pronounced than differences in skull shape. These findings are in accordance with those of previous authors (Tate, 1941; Maeda, 1982). Differences in cranial measurements were also more expressive than differences in dental measurements. Levels of significance for differentiation between populations were then followed by the results of non-metric

cranial and dental characteristics. Genetic differences between populations were markedly more expressive for some groups (i.e. the Middle East, Morocco, Yemen and Ethiopia) than differences observed for morphological traits. No clinal shift in size or other morphological data was found between populations, contrary to morphometric analysis results for other bat species occurring in the Western Palaearctic (Hanák & Horáček, 1984; Bogdanowicz, 1990; Benda & Horáček, 1995; Benda *et al.*, 2006).

EUROPE AND EASTERN MEDITERRANEAN

European, Black Sea region and eastern Mediterranean *Miniopterus* populations evidently represent identical taxa that can be co-identified with the species *M. schreibersii* s.str. (sensu Furman *et al.*, 2010c). Our results support the opinions of most previous authors (e.g. Spitzenberger, 1981; Crucitti, 1989; Fernandez & Ibañez, 1989; Appleton *et al.*, 2004; Boye, 2004; Gazaryan, 2005; Furman *et al.*, 2009, 2010b, c) who suggest that all European populations of *M. schreibersii* (in its traditional concept) belong to the nominotypical form.

Samples of the WM sublineage (that includes samples from Europe, coastal Morocco, coastal areas of northern Turkey and Georgia) showed relatively low genetic variation (0.1–1.4%). Only one sample from Spain and two from the Atlantic coast of Morocco showed more differentiation from the cluster of other European haplotypes (0.8–1.3%). This divergence could correspond to the ‘isolation by distance’ model suggested for other bat species in the region (e.g. *Pipistrellus* – Hulva *et al.*, 2004, 2007a, 2010). In order to confirm this genetic pattern, however, additional samples from less distant localities of Western Europe (e.g. France, the Italian peninsular, other Iberian samples) need to be studied. Morphometric data did not show any clinal pattern, and only shallow morphological variation. Bent-winged bats from Crete represented the only exception, these being significantly smaller. Ondrias (1978) and Iliopoulou-Georgudaki (1986), who studied bats from the Greek islands, including Crete, found similar morphological evidence and suggested that smaller size in island *Miniopterus* populations could have resulted from climatic influence, i.e. strong winds. These authors, however, did not take account of the general ecological factors associated with island biogeography (MacArthur & Wilson, 1967), which we consider a more likely explanation for this morphological effect. Interestingly, genetic divergence between Cretan and mainland populations is minute compared to morphometric divergence. Morphometric differentiation, however, appears to relate to skull size rather than skull shape. This suggests that

size-based morphological evidence does not correlate with genetic evidence in *Miniopterus* bats, as has been demonstrated for other bat groups (e.g. Hulva, Horáček & Benda, 2007b; Benda, Vallo & Reiter, 2011).

Levantine populations (including Cyprus), for which taxonomic position has hitherto been unclear, belong to the same taxon as European populations, i.e. *M. schreibersii* s.str. However, they formed a distinct clade under mtDNA genealogy, the EM sublineage, which diverged by 0.8–2.2% from the European and Black Sea region samples that formed their sister clade. Our genetic results thus support the opinions of Horáček *et al.* (2000) and Karataş & Sözen (2004), i.e. that the Mediterranean parts of the Levant are inhabited by the European form. When comparing Levantine bent-winged bats to the population more to the east, i.e. *M. pallidus* (see below), there was a substantial divergence in genetic traits (5.3%) but, interestingly, almost no distinction in cranial or dental morphology. It appears, therefore, that both *M. schreibersii* and *M. pallidus* are conservative in their morphology, and especially in skull shape. A further interesting point is that Miller-Butterworth *et al.* (2005) uncovered, and Furman *et al.* (2010b) consequently re-analysed, another genetic lineage from northern Israel (Alma Cave), based on the mitochondrial cytochrome *b* gene of the only sample. This was, however, completely outside the species ranks of both *M. schreibersii* s.str. and *M. pallidus* (c. 6–8% genetic distance; cf. Miller-Butterworth *et al.*, 2005; Furman *et al.*, 2010b; see also the phylogenetic tree topology in the latter paper). This lineage was most closely related to an Afro-tropical species, *M. natalensis*, and thus suggests the possible presence of the Arabian species *M. cf. arenarius* (see below) in southern Levant [if the sequence (AY614736) is correct – several ambiguity codes are present]. A similar disjunct distribution can be seen in the Arabian tree frog, *Hyla felixarabica* (Gvoždík *et al.*, 2010). Considering the high systematic and biogeographic importance of this possible Israeli lineage, it is necessary to confirm the finding with more numerous samples in future analyses. [Considering the apparent absence of this lineage in our rich dataset, which covers surrounding areas of the Levant (Lebanon, south-western Syria, north-western Jordan), a mislabelling of the sample would appear to be a more probable explanation of this curiosity.]

MOROCCO

Our results show that a unique evolutionary lineage of *M. schreibersii* s.str. inhabits the Atlas Mountains of Morocco. The inland Moroccan samples formed

a clade that diverged by 2.4–2.5% from the M lineage. Similar evidence was also provided by the morphometric analysis results. On the other hand, a published haplotype from Agadir (Atlantic coast of south-west Morocco; Appleton *et al.*, 2004) represented part of the M lineage (WM sublineage). The haplotype most similar to this was one detected from Spain and published by the same author (Appleton *et al.*, 2004). Unfortunately, we were unable to obtain samples from the Atlantic coast in order to investigate their morphological characteristics. Moroccan samples that separated into two genealogical lineages were also found by Furman *et al.* (2010b), based on mitochondrial cytochrome *b* sequences taken from García-Mударra, Ibáñez & Juste (2009), although exact locations of the samples were, unfortunately, not published. The available results, however, clearly suggest that there are two distinct lineages present in Morocco, the West Mediterranean *M. schreibersii*, occurring along the Atlantic coast, and an unnamed Moroccan form of *M. schreibersii* s.str., occurring in inland areas of the Atlas Mts. A similar geographic pattern of haplotype distribution was also documented in Morocco for the vespertilionid bats *Myotis mystacinus* (García-Mударra *et al.*, 2009) and *Pipistrellus pipistrellus* (Hulva *et al.*, 2010), as well as for the freshwater terrapin *Mauremys leprosa* (Fritz *et al.*, 2005). *Miniopterus* populations from the Atlas Mts. may thus represent a separate taxon. This suggestion contradicts the traditional view on taxonomic affiliation of Maghrebian populations, which are considered to represent the nominotypical form by most authors (e.g. Ellerman & Morrison-Scott, 1951; Aellen & Strinati, 1970; Qumsiyeh & Schlitter, 1982; Gaisler, 1983; Kowalski & Rzebik-Kowalska, 1991; Boye, 2004). An in-depth study of the North African *Miniopterus* population is necessary in order to reveal the phylogenetic and taxonomic position of the respective sub-populations.

MIDDLE EAST

Miniopterus populations of the Middle East, including those of southern Afghanistan, Iran, Azerbaijan, inland plateau areas of central and eastern Turkey, and north-western Jordan, represent a further distinct evolutionary lineage. This ME lineage, traditionally considered a subspecies *M. schreibersii pallidus* (e.g. Corbet, 1978; Koopman, 1994), displayed marked genetic divergence (5.4% distance to the M lineage and 4.3% distance to the MO lineage). The 5% value set as a species level indicator according to the genetic species concept in mammals, and particularly in bats, was, therefore, exceeded [the 5% value was originally suggested for mitochondrial markers with similar mutation rates, i.e. genes for cytochrome

b (Baker & Bradley, 2006) and ND1 (Mayer, Dietz & Kiefer, 2007)]. Cranial and dental morphological traits investigated in this study as well as performed analyses (FA, DFA, ANOVA), however, indicated that individuals of this group were in shape almost identical to those from Europe and the Levant, whereas in size were slightly bigger. ANOVA results otherwise showed many significant mainly cranial size characteristics (in shape minimum) between the Balkan (with addition of genotyped samples of the Levant; M lineage; representing *M. schreibersii* species) and Middle Eastern samples (ME lineage; representing possible *M. pallidus* species), nevertheless, these differences were at the same level or even smaller than differences between populations of *M. schreibersii* (see Table S4). Found significant morphological differences between representative samples of *M. schreibersii* and possible *M. pallidus* species in a way correspond to those found by Furman *et al.* (2010c) (and partly by Bilgin *et al.*, [2012]) between the Turkish inland (ME lineage) and Turkish coastal (M lineage) populations, based on forearm length, body mass and wing shape. Any of these three characteristics (particularly forearm length data – a possible important diagnostic character [see Furman *et al.*, 2010c]) were not analysed in our study thus comparison with data obtained by Furman *et al.* (2010c) and Bilgin *et al.* (2012) was not possible. Following a series of molecular studies (Bilgin *et al.*, 2006, 2008; Furman *et al.*, 2009, 2010b), Furman *et al.* (2010c) suggested the raising of Middle Eastern bent-winged bats to species level. Support for this came from Maraci *et al.* (2010) and Bilgin *et al.* (2012), who found the two taxa in sympatry, and even in syntopy, in the same roosts. Considering all these and ours findings, we agree that the ME lineage represents a separate species, *M. pallidus*, a sister species to *M. schreibersii* s.str., though this remains rather cryptic morphologically (i.e. not easily distinguishable in the field).

Genetic comparison of the Al Wardeh Cave population from north-western Jordan indicates that this population belongs to *M. pallidus*. Up to now, however, representatives of this taxon are known only from the belt of mountainous habitats that stretch from central Turkey to Afghanistan. The record from Jordan, therefore, represents a significant extension of this taxon's range southward to the Levant. Unfortunately, we had an insufficient number of specimens to provide a well-founded morphological analysis of the Jordanian population. The Jordanian site is geographically very close (c. 55 km) to Talsh'hab, south-west Syria, where an individual of *M. schreibersii* was found. A transition zone between *M. schreibersii* and *M. pallidus* may run along the Great Rift in the north-south transect of the Levant, therefore, and both taxa may be present there in sympatry [simi-

larly as in Turkey (Maraci *et al.*, 2010; Bilgin *et al.*, 2012)] or in close parapatry, as in the case of tree frogs or geckos (Gvoždik *et al.*, 2010; Moravec *et al.*, 2011).

EASTERN AFGHANISTAN

The Jalalabad (Nangarhar Province of Afghanistan) population, usually considered as representing *M. s. fuliginosus* (e.g. Ellerman & Morrison-Scott, 1951; Gaisler, 1970; Hill, 1983; Yoshiyuki, 1989; Corbet & Hill, 1992; Koopman, 1994; Bates & Harrison, 1997; Simmons, 2005), differed strongly from all other Western Palaearctic populations in both linear and geometric morphometrics, as well as in non-metric traits. These findings, therefore, support a hypothesis previously put forward by Maeda (1982), i.e. that this subspecies should be regarded as a separate species, *M. fuliginosus*. Regrettably, there were no genetic samples available to us to back-up the morphological findings through molecular analysis. Nevertheless, according to the published phylogenetic analyses of Chinese and Japanese populations affiliated to *M. fuliginosus* (Appleton *et al.*, 2004; Furman *et al.*, 2010b), the species status of this form appears to have been demonstrated sufficiently as it has been shown to be genetically very distant from species of the C (West Palaearctic) clade (Fig. 2). A complex morphological and molecular genetic analysis of Indian subcontinent *Miniopterus* populations is needed, however, to confirm taxonomic assignation of East Afghanistan and other Oriental region populations formerly co-identified with *M. schreibersii* s.l. (cf. Gaisler, 1970; Bates & Harrison, 1997). Here, we tentatively suggest using the name *M. cf. fuliginosus* for the Jalalabad populations, in accordance with previous authors, but as a full species.

SOUTH-WESTERN ARABIA AND ETHIOPIA

Of the Western Palaearctic *Miniopterus* populations examined, that of south-western Arabia (Yemen) was one of the most distinct. These bats demonstrated substantial similarities to African populations, and yet genetically were very close to the samples examined from Ethiopia. Yemeni and Ethiopian samples appear to represent an identical taxon with regard to both genetic data (a low distance of 0.1–0.5%) and morphology. Previously assigned to *M. schreibersii* s.l. (Nader & Kock, 1987; Harrison & Bates, 1991), these populations have more recently been regarded as part of *M. natalensis* (Simmons, 2005). The separation of African populations from *M. schreibersii*, suggested previously by Koopman (1994), has been confirmed through molecular analysis (Appleton *et al.*, 2004; Miller-Butterworth *et al.*, 2005), and our results

further support this conclusion. *M. natalensis*, however, is a species described as from South Africa, and bats of that origin represent a genetic lineage substantially distant from the YE lineage (11.5%). As the level of genetic differentiation clearly exceeds the 5% level recommended for species recognition according to the genetic species concept (Baker & Bradley, 2006; Mayer *et al.*, 2007), and the two lineages (*natalensis* s.str. and YE) are clearly not in a sister phylogenetic relationship, it may be appropriate to consider the YE lineage as a species distinct from the South African *M. natalensis*. Nader & Kock (1987), the first to attempt taxonomic determination of south-west Arabian *Miniopterus* populations, identified these bats as *M. schreibersii arenarius*, based on morphological and parasitological evidence. According to earlier classification, and in the light of our new results, we regard south-west Arabian and Ethiopian *Miniopterus* bats, formerly assigned to *M. schreibersii arenarius* or *M. natalensis arenarius* (see Harrison & Bates, 1991; Koopman, 1994), as representing a separate species tentatively named *M. cf. arenarius* Heller, 1912. As the name originates from Kenya, a genetic and/or morphologic comparison with type/topotypic material is needed to confirm this.

HISTORICAL BIOGEOGRAPHY OF *MINIOPTERUS SCHREIBERSII*

Observed genetic variation in *M. schreibersii* s.str. also brings new insights into the species' phylogeography. Furman *et al.* (2010a) suggested that shallow genetic differentiation between the western and eastern European colonies, and the relatively high genetic diversity observed in the eastern colonies, may indicate a re-colonisation of Europe from a single glacial refugium located in north-western Anatolia. Alternatively, Bilgin *et al.* (2008) localised such a possible refugium in Turkish Thrace, while Pereira *et al.* (2009) suggested either southern Iberia or North Africa. Furman *et al.* (2010a) further speculated on the existence of another glacial refugium in Italy. Our results, however, do not support such a hypothesis as a widely distributed haplotype was detected in southern Italy (Sicily; WM sublineage). To confirm such a hypothesis, an in-depth analysis of both Italian and surrounding populations is needed. Moreover, according to the available evidence, *M. schreibersii* fossils are absent in Pleistocene-Holocene transition cave-deposits in Italy (Tata & Kotsakis, 2005). Taking all the intraspecific genetic data available (Bilgin *et al.*, 2008; Pereira *et al.*, 2009; Furman *et al.*, 2010a; this study) into consideration, it would appear that, in addition to the apparent existence of a refugium in the Atlas Mts. of Morocco (see above) dating from the Middle Pleistocene (cf. molecular clock by Furman

et al., 2010b), the presence of three or four additional glacial refugia can also be detected within the M lineage. Based on the genetic structure observed in this study (e.g. Fig. 3), we hypothesise, in accordance with Furman *et al.* (2010a), that the main refugium of the WM sublineage was in the east in the Black Sea region. However, as the Spanish and coastal Moroccan samples form a distinct clade within the WM sublineage, we cannot exclude the possibility of a further, western refugium in south-western Europe or lowland North Africa (cf. Pereira *et al.*, 2009). Two distinct haplotype clusters observed within the EM sublineage, comprising southern Turkish and Levantine samples (including Cyprus), appear to correspond with the locations of glacial refugia in southern Turkey and the Levant (western Syria, Lebanon). The haplotypes of the Cypriot population do not form a monophyletic lineage, which suggests that colonisation of Cyprus from the adjacent mainland probably occurred recently and through repeated episodes (as also suggested for some other Cypriot bats; see Benda *et al.*, 2007). Considering the supposed migratory nature of *M. schreibersii* (cf. Rodrigues & Palmeirim, 2008; Pereira *et al.*, 2009), and the fact that geographic barriers do not appear to have a substantial effect on the evolutionary history of the species (Dobson, 1998; Appleton *et al.*, 2004; Ibáñez *et al.*, 2006; Bilgin *et al.*, 2008; García-Mударra *et al.*, 2009; Furman *et al.*, 2010c), one could also speculate on the existence of additional *Miniopterus* refugia. It would appear, therefore, that the genetic structure of *M. schreibersii* is a result of complex ecological-evolutionary causalities that may be diverse in different regions of the Western Palaearctic.

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APPENDIX 1

Specimens examined morphologically. Abbreviations: NMP = National Museum in Prague, Czech Republic; ZFMK = Zoological Research Museum Alexander Koenig in Bonn, Germany; AUB = American University of Beirut, Lebanon. *Mare* = *Miniopterus* cf. *arenarius*; *Mful* = *M.* cf. *fuliginous*; *Msch* = *M. schreibersii* s.str.; *Mpal* = *M. pallidus*; *Msp* = unidentified taxon of *M.* cf. *schreibersii*; f = female; m = male; x = unidentified sex.

GROUP 1: MOROCCO

Morocco: Azigza Cave (Tazouguerte) 6f (NMP: pb3910, pb3912–pb3914, pb3916, pb3917 – 26. 4. 2008), 4m (pb3907–pb3909, pb3911 – 26. 4. 2008), *Msch*, leg.: P. Benda; Oued Tessaout Valley (Talkout) 3f (NMP: 90046, 90049, 90054 – 30. 8. 2003), 4m (NMP: 90050–90052, 90055 – 30. 8. 2003), *Msch*, leg.: P. Benda; Oued El-Ammar River (Sebt-des-Ait-Serhrouchen) 1f (NMP: 90103 – 9. 9. 2003), *Msch*, leg.: P. Benda.

GROUP 2: WESTERN EUROPE

Spain: Bei Tremp (Pyrenees) 3f (ZFMK: 56.735, 56.737, 56.738 – 28. 5. 1955), 4m (ZFMK: 56.1068, 56.733, 56.734, 56.736 – 28. 5. 1955), *Msch*, leg.: J. Niethammer; Ramales de la Victoria 1m (ZFMK: 97.246 – 19. 4. 1963), *Msch*, leg.: J. Niethammer. **France:** Grotte de Povade (Banyuls) 9f (ZFMK: 59.120, 59.124, 59.127–59.131, 59.133, 59.134 – 8. 4. 1959), 7m (NMP: 59.121–59.123, 59.125, 59.126, 59.132 – 8. 4. 1959, 59.350 – 23. 5. 1959), *Msch*, leg.: A. Heymer; Chateau de Collioure (Banuyls) 2f (ZFMK: 59.348, 59.349 – 11. 5. 1959), 1m (ZFMK: 59.347 – 11. 5. 1959), *Msch*, leg.: A. Heymer; St. Remy 3f (ZFMK: 59.531b, 59.531c, 59.531d – 5. 11. 1959), 1m (ZFMK: 59.531a – 5. 11. 1959), *Msch*, leg.: H. Roer. **Italy:** Gargano 2f (ZFMK: 66.338 – 2. 8. 1961, 66.360 – 4. 8. 1961), 2x (ZFMK: 66.359 – 2. 8. 1961, 66.357 – date unspecified), *Msch*, leg.: G. Witte. **Country not stated:** Kaiserstuhl 1x (ZFMK: 84.529 – 27. 3. 1952), *Msch*, leg.: Eisentraut.

GROUP 3: PANNONIA

Slovakia: Čertova diera Cave (Dornica) 16f (NMP: 70/58, 76/58, 85/58, 89/58, 92/58, 94/58, 96/58, 100/58 – 3. 2. 1958; J – 114, J – 117, J – 118, J – 123, J – 176, J – 177, J – 178, J – 180 – 10. 12. 1956), 4m (NMP: 93/58, 99/58 – 3. 2. 1958; J – 174, J – 181 – 10. 12.

1956), 9x (NMP: 80/66 – date unspecified; ČD, ČD 1, ČD 2, ČD 3, ČD 4, ČD 5, ČD 6, ČD-NX – 5. 11. 1958), *Msch*, leg.: V. Hanák; Drienovecká vyvierka Cave (Drienovec) 6f (NMP: 150/58, 155/58 – 6. 2. 1958; 246/61 – 17. 2. 1961; 613/59 – 1. 6. 1959; pb4260, pb4261 – 17. 7. 2009), 2m (NMP: 156/58 – 6. 2. 1958; 570/59 – 31. 5. 1959), *Msch*, leg.: V. Hanák; P. Benda. **Romania:** Betfia Cave (Betfia) 11f (NMP: pb4247–pb4254, pb4256–pb4258 – 13. 7. 2009), *Msch*, leg.: P. Benda.

GROUP 4: BALKANS

Bulgaria: Maslen nos (Primorsko) 21f (NMP: 49191, 49198, 49205, 49206, 49214, 49220, 49222, 49227, 49228, 49341 – 5. 6. 1957; 49686 – 27. 8. 1961; 49688 – 7. 8. 1961; 49690, 49692–49698, 49700 – 27. 8. 1961), 12m (NMP: 49186, 49192, 49197, 49207, 49226, 49229, 49231, 49232 – 5. 6. 1957; 49691, 49699, 49703 – 27. 8. 1961), *Msch*, leg.: V. Hanák; Zmejovi Dupki Cave (Sliven) 7f (NMP: 49148, 49151, 49152, 49165 – 25. 5. 1957; 49177, 49178, 49180 – 27. 5. 1957), 4m (NMP: 49150, 49166 – 25. 5. 1957; 49179, 49181 – 27. 5. 1957), *Msch*, leg.: V. Hanák; Karlukovo 5f (NMP: 49351 – 3. 7. 1976; 49356, 49361, 49362 – 5. 7. 1976; 49367 – 6. 7. 1976), 1m (NMP: 49357 – 5. 7. 1976), *Msch*, leg.: M. Braniš *et al.*; Gardina Dupka Cave (Mostovo) 3f (NMP: 50059, 50061, 50062 – 22. 8. 1987), 3m (NMP: 50040 – 22. 6. 1984; 50058, 50060 – 22. 8. 1987), *Msch*, leg.: P. Musil; Hajduška Peštera Cave (Devenci) 3f (NMP: 49647–49649 – 14. 6. 1977), *Msch*, leg.: V. Bejček *et al.*; Nirica Peštera Cave (Kotel) 1f (NMP: 49799 – 15. 7. 1979), 1m (NMP: 49798 – 15. 7. 1979), *Msch*, leg.: P. Donát *et al.*; Kamen Brjag 2f (NMP: 50049, 50050 – 12. 7. 1986), *Msch*, leg.: V. Hanzal *et al.*; Ivanova voda Cave (Dobrostan) 1m (NMP: 49806 – 23. 7. 1979), *Msch*, leg.: P. Donát *et al.*; Ražiškata Cave (Lakatnik) 1m (NMP: 50143 – 21.12. 1956), *Msch*, leg.: J. Figala *et al.* **Greece:** Didimotichon (Thrakia) 1x (ZFMK: 97.247 – 3. 8. 1971), *Msch*, leg.: J. Niethammer; Xánthi (Kimmeria) 3f (NMP: 48622–48624 – 16. 6. 1989), 1m (NMP: 48625 – 16. 6. 1989), *Msch*, leg.: V. Hanák & V. Vohrálik; Evros Cave (Didimotihó) 2f (NMP: 48665, 48667 – 22. 6. 1989), 1m (NMP: 48666 – 22. 6. 1989), *Msch*, leg.: V. Hanák & V. Vohrálik; Polyphemos (Maronia) 2f (NMP: 48632, 48633 – 18. 6. 1989), 1m (NMP: 48642 – 19. 6. 1989), *Msch*, leg.: V. Hanák & V. Vohrálik; Petralona 1f (NMP: 48611 – 28. 9. 1988), 1m (NMP: 48610 – 28. 9. 1988), leg.: V. Hanák & V. Vohrálik *et al.*, 1x (ZFMK: 77.51 – 25. 5. 1962), leg.: Wolf, *Msch*; Ioánnina Cave (Papigo) 2f (NMP: 48578, 48579 – 26. 9. 1988), *Msch*, leg.: V. Hanák & V. Vohrálik *et al.*; Avas 1m (NMP: 48657 – 20. 6. 1989), *Msch*, leg.: V. Hanák & V. Vohrálik.

GROUP 5: CRETE

Greece – Crete: Spilion Tsanis Cave (Omalos) 1f (NMP: 91055 – 1. 10. 2006), 11m (NMP: 91054, 91056–91064, 91069 – 1. 10. 2006), *Msch*, leg.: P. Benda; Spilia Milatou Cave (Milatos) 2f (NMP: 91115, 91118 – 7. 10.), 3m (NMP: 91112–91114 – 7. 10. 2006), *Msch*, leg.: P. Benda; Vreikos Cave (Crete) 1f (NMP: 92316 – 12. 10. 2007), *Msch*, leg.: unspecified; Moni Kato Preveli (Lefkogia) 1m (NMP: 92311 – 11. 10. 2007), *Msch*, leg.: unspecified.

GROUP 6: LEVANT

Syria: Safita (Hama) 4f (NMP: 48880–48883 – 29. 5. 2001), *Msp*, leg.: P. Benda; Qala' *et al.* Hosn (Hama) 2f (NMP: 49989 – 10. 5. 2001, pb1904 – 29. 5. 2001), *Msp*, leg.: R. Lučan, P. Benda; Talsh'hab (Der'a) 1m (NMP: 48861 – 25. 5. 2001), *Msp*, leg.: P. Benda. **Lebanon:** Er Rouais Cave (Aaqura) 3f (NMP: 91778, 91779 – 22. 1. 2007; LE 86 – 26. 6. 2006), 7f (NMP: 91776, 91777 – 22. 1. 2007; LE 87–LE 91 – 26. 6. 2006), *Msp*, leg.: P. Benda *et al.*; I. Horáček *et al.*; Saleh Cave (Amchite) 22f (NMP: LE 77 – 25. 6. 2006, 91808 – 28. 1. 2007; AUB: M – 085–M – 089 – 13. 10. 1960; M – 091 – 14. 8. 1960; M – 108–M – 111 – 13. 10. 1960; M – 113 – 13. 10. 1960; M – 1162, M – 1165 – 17. 4. 1960; M – 119, M – 124, M – 127, M – 129, M – 133, M – 139, M – 140 – 18. 3. 1961), 31m (NMP: LE 78 – 25. 6. 2006; AUB: M – 084 – 13. 10. 1960; M – 092–M – 094 – 14. 8. 1960; M – 097 – 13. 10. 1960; M – 101–M – 105, M – 112 – 13. 10. 1960; M – 115 – 18. 3. 1961; M – 1163, M – 1164 – 17. 4. 1965; M – 120–M – 123, M – 125, M – 126, M – 128, M – 130–M – 132, M – 134–M – 138, M – 142 – 18. 3. 1961), *Msp*, leg.: I. Horáček *et al.*; P. Benda, R. E. Lewis. **Turkey:** Indigu Majarasi Cave (Antalya) 1f (ZFMK: 66.626 – 11. 4. 1966), 6m (ZFMK: 66.619 – 20. 4. 1966, 66.625, 66.627–630 – 11. 4. 1966), *Msch*, leg.: K. Dobat; Haruniye 2x (ZFMK: 58.282, 58.283 – 1953 (unspecified), *Msch*, leg.: unspecified. **Cyprus:** Smigies Trail (Akamas Peninsula) 5f (NMP: CH 32, CH 33, CH 35, CH 38 – 27. 3. 2005; CH 129 – 12. 10. 2005), 3m (NMP: CH 34, CH 36, CH 39 – 27. 3. 2005), *Msp*, leg.: I. Horáček *et al.*; Troodos forest – valley N of Kako-

petria (Kakopetria) 5m (NMP: pb2805–pb2807 – 11. 4. 2005), *Msp*, leg.: P. Benda; Troodos Forest – valley 4 km SW of Kakopetria (Kakopetria) 2m (NMP: CH 45, CH 46 – 29. 3. 2005), *Msp*, leg.: I. Horáček *et al.*; Kalavastos 1m (pb2836 – 19. 4. 2005), *Msp*, leg.: P. Benda.

GROUP 7: MIDDLE EAST

Afghanistan: Samphshir Ghor (Kala bust) 1f (ZFMK: 97.237 – 29. 3. 1972), 2m (ZFMK: 97.235, 97.236 – 29. 3. 1972), *Mpal*, leg.: J. Niethammer; Kandahar 1f (ZFMK: 97.245 – 28. 2. 1965), *Mpal*, leg.: J. Niethammer. **Iran:** Mina 7m (NMP: 90825 – 90830 – 22. 5. 2006), *Mpal*, leg.: P. Benda; Bisotun (Kermanshah) 1f (NMP: 48150 – 10. 8. 1998), 2m (NMP: 48149, 48151 – 10. 8. 1998), *Mpal*, leg.: P. Benda; Dorud (Lorestan) 1m (48154 – 10. 8. 1998), *Mpal*, leg.: P. Benda.

GROUP 8: EASTERN AFGHANISTAN
(JALALABAD AREA)

Afghanistan: Jalalabad 9f (ZFMK: 97.226, 97.227, 97.228, 97.229, 97.232, 97.234 – 1. 3. 1966; 97.238 – 14. 5. 1965; 97.243, 97.243 – 4. 3. 1966), 16m (ZFMK: 97.215, 97.216, 97.218, 97.220, 97.221, 97.222, 97.224, 97.225, two samples without number – 14. 5. 1965; 97.231, 97.233 – 1. 3. 1966; 97.239, 97.240, 97.241 – 14. 5. 1965; 97.244 – 4. 3. 1966), 1x (ZFMK: 97.230 – 1. 3. 1966), *Mful*, leg.: J. Niethammer.

GROUP 9: YEMEN AND ETHIOPIA

Yemen: Jebel Bura (Riqab) 1f (NMP: pb3129 – 30. 10. 2005), 5m (NMP: pb3126–pb3128, pb3130, pb3131 – 30. 10. 2005), *Mare*, leg.: P. Benda; At Tur (Hajjah) 1m (ZFMK: 85.64 – 1. 3. 1985), 1x (ZFMK: 85.63 – 1. 3. 1985), *Mare*, leg.: F. Schutte, H.P. Fritéz; Halhal (Haja) 1m (NMP: pb3747 – 2. 11. 2007), *Mare*, leg.: P. Benda. **Ethiopia:** Baro River (Masha) 2f (NMP: 92177, 92178 – 5. 9. 2003), *Mare*, leg.: P. Benda. **Sudan:** (unspecified) 1x (ZFMK: 212 – date unspecified), *Mare*, leg.: unspecified.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Figure S1. Cranio-dental measurements and landmarks used in the linear and geometric morphometric analyses.

Figure S2. Dental measurements used in the linear morphometric analyses.

Figure S3. Non-metric dental and cranial characters.

Figure S4. Results of the discriminant function analyses based on the linear morphometric data of dental dimensions.

Figure S5. The main shape variable (RW1) plotted against the centroid size (CS2) of the lateral view of skull.

Table S1. Non-metric dental and cranial characters. Letter codes are associated to those in Fig. S3.

Table S2. Skull dimensions of the examined *Miniopterus*.

Table S3. Dental dimensions of the examined *Miniopterus*.

Table S4. Results of ANOVA analyses of Middle Eastern (representing *M. pallidus*) and Balkan (containing sequenced samples from the Levant) (representing *M. schreibersii*) sample sets.

Table S5. Percentage share-values of the total variation of the first four relative warps of the examined sample sets for the respective view of skull and mandible.

Table S6. Non-metric dental and cranial characters of the examined *Miniopterus*.

Appendix S1. Supporting information to the methods. List of cranio-dental measurements. List of dental measurements. Landmark definitions for respective views of skull and mandible.

Appendix S2. Supporting information to the results. Description of morphometric cranial and dental differentiation among the examined groups of *Miniopterus*. Description of non-metric dental and cranial differentiation among the examined groups of *Miniopterus*.