

Sexual and age size variation in the western Palaearctic populations of *Miniopterus* bats (Chiroptera: Miniopteridae)

Jan ŠRÁMEK^{1,2*} and Petr BENDA^{1,3}

¹ Department of Zoology, Faculty of Science, Charles University in Prague, Viničná 7, 128 44 Prague, Czech Republic

² Department of Cell and Molecular Biology, Third Faculty of Medicine, Charles University in Prague, Ruská 87, 100 00 Prague, Czech Republic; e-mail: jan.sramek@lf3.cuni.cz

³ Department of Zoology, National Museum (Natural History), Václavské nám. 68, 115 79 Prague, Czech Republic

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Abstract. Among populations of the *Miniopterus* bats of western Palaearctic, intraspecific variation has not been well documented. Herein we investigate sexual and age variation of these populations using two approaches – linear and geometric morphometrics. We analysed Moroccan (*M. maghrebnis*), western and eastern European (*M. schreibersii*), Levantine (*M. schreibersii*), and east-Afghanistani (*M. cf. fuliginosus*) specimens; variation was compared between sexes of the particular specimen sets of three above mentioned *Miniopterus* spp. and between four age cohorts of *M. schreibersii* samples. The results showed in all examined population sets males to be generally larger in size than females, the exception being the east-European animals. Significantly the most divergent sexes were those from eastern Afghanistan, the Levant and eastern Europe. The differences found between sexes in as well as between examined population sets can be attributed to different life histories and/or to food competition. Weak correlations between patterns of sexual dimorphism and the newly proposed western Palaearctic classification of the *Miniopterus* bats suggest only a limited contribution of sexual variation to morphological variation in general. Certain aspects of age variation were found in all examined morphological characters except the non-metric traits, which in turn indicates the importance of these traits for identification of the particular taxon across age categories.

Key words: *Miniopterus*, western Palaearctic, geometric morphometrics, morphology, sexual dimorphism, age variation

Introduction

Bent-winged bats, the genus *Miniopterus* Bonaparte, 1837, represent the only genus of the family Miniopteridae. It comprises some 20 species occurring mainly in the tropics and sub-tropics of the Old World (Simmons 2005). Morphometric as well as molecular phylogenetic analyses (e.g. Tate 1941, Maeda 1982, Appleton et al. 2004, Tian et al. 2004, Miller-Butterworth et al. 2005, Benda et al. 2006, Furman et al. 2008, 2010) indicate that identification of particular taxa (species/subspecies) of the genus is often difficult according to their similar or even cryptic phenotype.

In the western Palaearctic (North Africa and Eurasia to the west of Pakistan), at least four species of the genus have been documented: Schreibers' bat, *Miniopterus schreibersii* Kuhl, 1817; pallid bent-winged bat, *M. pallidus* Thomas, 1907; Indian bent-winged bat, *M.*

cf. fuliginosus Hodgson, 1835; and Maghrebian bent-winged bat, *M. maghrebnis* Puechmaille, Allegrini, Benda, Bilgin, Ibáñez & Juste, 2014. *M. schreibersii* occurs in southern Europe, coastal areas of North Africa and in the western areas of the Middle East (Furman et al. 2010, Šrámek et al. 2013, Puechmaille et al. 2014) while *M. pallidus*, morphologically almost identical with the *M. schreibersii* (Furman et al. 2010, Šrámek et al. 2013), occurs in the eastern portion of the Middle East (Furman et al. 2010, Šrámek et al. 2013). The Nangarhar Province of Afghanistan perhaps represents the westernmost occurrence area of another *Miniopterus* sp. whose taxonomic position is currently unclear; Maeda (1982) and Šrámek et al. (2013) proposed that this population is best attributed to *M. fuliginosus*. Recently another species, *M. maghrebnis*, morphologically very similar to *M. schreibersii* s. str., was described from the mountainous

* Corresponding Author

parts of the Maghreb (southern parts of Morocco and Tunisia). Its distribution range as well as the level of sympatry with *M. schreibersii* remain to be clarified. Sexual dimorphism in morphometric characteristics was shown in bats to be relatively an important factor of species variation (e.g. Findley & Traut 1970, Schmidt 1978, Maeda 1983); however, within the genus *Miniopterus*, it has not been broadly studied. Maeda (1982, 1983, 1984) analysed this variation in several Australasian species (*M. macrodens*, *M. magnetes*, *M. australis*, *M. fuliginosus*, and *M. solomonensis*). Goodman et al. (2008) studied variation in two cryptic species from Madagascar, *M. gleni* and *M. griffithsii*. Concerning the western Palaearctic populations of *Miniopterus*, Gaisler (1970) analysed bats from eastern Afghanistan (Jalalabad area) and found no sexual dimorphism. Crucitti (1976), Spitzenberger (1981) and Uhrin et al. (1997) examined specimens of *M. schreibersii* s. str. from Italy, Austria and Slovakia. In all these studies the authors found (with more or less high statistical significance) males to be larger than females in majority of their cranial or external dimensions. To our knowledge no dental as well as specific non-metric characters have been analysed yet in western Palaearctic *Miniopterus* populations. Little information is available on age variation in *Miniopterus* spp. Maeda (1977, 1982) studied populations from Japan and found presence of age variation in many skull characters. Van der Merwe (1978) analysed post-natal growth (body mass, hindfoot and forearm lengths) of *M. natalensis* (sensu Simmons 2005) from South Africa and Serra-Cobo (1987) investigated postnatal forearm growth of *M. schreibersii* s. str. from southern Spain.

Here, we present a detailed morphometric analysis (combination of traditional linear morphometrics, geometric morphometrics and non-metric data analyses) of cranial and dental characters of the above mentioned four western Palaearctic *Miniopterus* species to assess aspects of their sexual and age variation. Simultaneously, we attempt to ascertain the role of the sexual variation patterns of respective populations in their taxonomic classification (cf. Šrámek et al. 2013).

Material and Methods

To examine intrapopulation (sexual and age) variation in various cranial and dental metric or non-metric characters of western Palaearctic *Miniopterus* bats, we studied 342 skulls (see Appendix 1 and Material and Methods in Šrámek et al. 2013 for the list of specimens, their origin, species affiliation and determination). To

examine aspects of sexual dimorphism, the specimens were divided into five population sets based on previously published results (Šrámek et al. 2013): (1) Morocco (8 ♂♂, 10 ♀♀); (2) western Europe – specimens from Spain, France, Italy, Austria (14 ♂♂, 20 ♀♀, three unsexed); (3) eastern Europe – Slovakia, Romania, Bulgaria, and Greece (including Crete) (49 ♂♂, 89 ♀♀, 14 unsexed); (4) the Levant – Turkey, Syria, Cyprus, Lebanon (54 ♂♂, 37 ♀♀); (5) eastern Afghanistan (18 ♂♂, 9 ♀♀, one unsexed). Specimens lacking sex identification were not used for the sexual dimorphism analysis. According to identified rate of tooth wearing (Fig. 1) in the specimens of *M. schreibersii* s. str. (i.e. groups 2-4), these specimens were divided into four age groups for purpose of the age variation analysis: C0 – unweaned juveniles, no abrasion; C1 – weaned juveniles, slightly worn dentition; C2 – adults, middle worn dentition; C3 – adults, heavily worn dentition. All statistical analyses were performed using the Statistica 6.0 software.

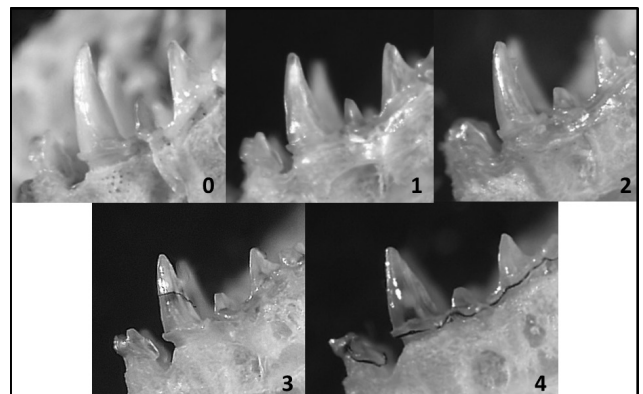


Fig. 1. Defined scale system of abrasion. Rate of abrasion is in ascending order.

Linear morphometrics

We recorded 24 cranio-dental measurements (11 skull or mandible measurements and 13 upper or lower tooth-row dimensions) taken with a mechanical calliper (by J. Šrámek) to the nearest 0.01 mm. Further, we recorded 57 dental measurements (width, length and height dimensions of respective teeth) using an optical calliper (by J. Šrámek) to the nearest 0.0125 mm. For complete list of all examined measurements, see Appendix S1, Figs. S1 and S2 in Šrámek et al. (2013).

Basic descriptive statistical parameters (mean [M], minimum value [min], maximum value [max], standard deviation [SD]) were calculated separately for each measurement of each geographical group (1-5) and sex, and of each age cohort (C0-C3). Sexual size variation was analysed via the one-way analysis

Table 1. Mean value and Storer's index (SI) of all crano-dental dimensions (in mm), CS and RW scores of the *Miniopterus* sexes in the respective populations. See methods for explanation of dimension abbreviations. * = P < 0.05, ** = P < 0.001, *** = P < 0.0001, df = degrees of freedom.

Character	Morocco			Western Europe			Eastern Europe			Levant			Jalalabad			
	♀	♂	df	♀	♂	df	♀	♂	df	♀	♂	df	♀	♂	df	
LCr	15.312	15.431	16	15.218	15.256	-0.252	32	15.293	15.107	1.222	127***	15.015	15.438	15.735	-1.901	25**
Lcb	14.900	15.019	16	14.723	14.871	-1.003	31**	14.819	14.664	1.052	127***	14.544	15.101	15.391	-1.896	25***
Laz	8.704	8.669	16	8.559	8.601	-0.488	31	8.555	8.557	-0.024	126	8.502	8.794	8.983	-2.118	25
Lal	3.781	3.773	16	3.712	3.714	-0.062	32	3.718	3.698	0.517	134	3.665	3.900	3.941	-1.047	25
Laln1	4.210	4.193	16	3.993	4.058	-1.625	32	3.981	3.967	0.352	132	3.974	4.038	4.158	-2.910	25*
Lan	8.051	8.158	16	8.056	8.069	-0.171	32	8.065	8.043	0.278	132	7.924	8.028	8.226	-1.759	25*
Lam	8.778	8.801	16	8.662	8.708	-0.533	31	8.748	8.666	0.936	127**	8.643	8.738	8.896	-1.785	25*
AnC	6.343	6.375	16	6.329	6.355	-0.425	31	6.283	6.298	-0.235	130	6.227	6.340	6.368	-2.704	25*
ACr	7.925	8.033	16	7.429	7.625	-2.603	26	7.728	7.733	-0.059	125	7.770	7.757	7.789	-0.421	25
LMd	10.955	11.029	16	10.826	10.903	-0.708	32	10.875	10.776	0.916	128**	10.747	11.173	11.373	-1.769	25**
ACo	2.589	2.609	16	2.589	2.614	-0.947	32	2.514	2.540	-1.046	129	2.560	2.633	2.646	-0.462	25
CC	4.677	4.630	16	4.525	4.471	1.194	23	4.508	4.501	0.143	124	4.544	4.569	4.617	-3.299	24***
Pp1	5.568	5.509	16	5.467	5.385	1.998	32	5.545	5.512	0.600	130	5.500	5.523	5.699	-2.143	25*
Mm1	6.409	6.385	16	6.281	6.241	0.647	28	6.317	6.299	0.282	128	6.286	6.308	6.626	-1.812	25*
Im1	6.918	6.981	16	6.951	6.949	0.018	30	6.937	6.890	0.676	132*	6.851	6.909	7.114	-2.669	25***
Cm1	5.877	5.933	16	5.853	5.853	0.011	29	5.890	5.853	0.625	132*	5.821	5.872	6.049	-1.698	25*
Pm1	4.282	4.328	16	4.291	4.253	0.881	31	4.297	4.299	-0.061	133	4.286	4.305	4.382	-1.332	25
Mm1	3.227	3.285	16	3.237	3.224	0.400	32	3.303	3.278	0.768	134	3.259	3.272	3.340	-1.285	25
CP1	2.864	2.893	16	2.918	2.890	0.973	22	2.875	2.842	1.155	133*	2.866	2.901	3.000	-1.595	25
Im1	7.256	7.321	16	7.171	7.252	-1.118	31	7.317	7.236	1.119	128**	7.159	7.185	7.537	-0.763	25
Cm1	6.166	6.226	16	6.159	6.234	-1.218	31*	6.187	6.155	0.510	127*	6.136	6.176	6.454	-1.246	25
Pm1	4.358	4.420	16*	4.419	4.485	-1.414	16*	4.449	4.454	-0.110	129	4.399	4.412	4.574	-0.036	25
Mm1	3.606	3.606	16	3.699	3.757	-1.563	32	3.753	3.752	0.020	130	3.676	3.668	3.778	0.703	25
CP1	2.351	2.393	16	2.369	2.386	-0.740	26	2.365	2.332	1.401	127*	2.373	2.394	2.507	-3.934	25*
CS1	11.093	11.262	16	11.084	11.174	-0.816	31	11.183	11.035	1.329	117*	10.920	11.061	11.538	-0.151	20
CS2	20.731	20.915	16	20.413	20.600	-0.909	28**	20.532	20.429	0.504	118	20.312	20.528	20.867	-1.497	25*
CS3	16.883	17.000	16	16.717	16.837	-0.720	28	16.740	16.622	0.704	121**	16.523	16.688	17.048	-1.546	25**
CS4	17.647	17.803	16	17.452	17.626	-0.991	30**	17.615	17.427	1.074	118***	17.189	17.409	18.022	-1.958	25**
GIRW1	-1.67E-03	2.09E-03	-	9.04E-04	-1.53E-03	-	31	-8.15E-04	3.49E-05	-	117	-8.19E-04	9.88E-04	6.45E-04	-	20
GIRW2	1.72E-03	-2.15E-03	-	-6.92E-04	-5.93E-04	-	31	-1.58E-03	2.63E-03	-	117	-1.34E-03	9.24E-04	3.25E-03	-	20
GIRW3	4.85E-04	-6.06E-04	-	-1.79E-03	2.78E-03	-	31	-1.69E-04	-2.18E-03	-	117	-9.61E-04	9.67E-04	-2.30E-03	-	20
GIRW4	-6.32E-04	7.90E-04	-	1.35E-03	-2.69E-03	-	31	1.68E-03	-3.21E-03	-	117**	7.70E-04	-6.44E-04	2.13E-03	-	20
G2RW1	-3.44E-04	4.30E-04	-	-1.03E-04	7.78E-04	-	28	1.77E-03	-3.43E-03	-	118*	-9.42E-04	1.54E-03	-4.62E-03	-	24
G2RW2	-1.16E-03	1.45E-03	-	-1.51E-03	1.94E-04	-	28	-8.46E-04	1.94E-03	-	118	9.43E-04	-4.46E-04	5.40E-05	-	25*
G2RW3	2.11E-03	-2.64E-03	-	-1.23E-03	7.81E-04	-	28	8.77E-04	-1.76E-03	-	118	8.99E-04	-1.06E-03	3.20E-04	-	25
G2RW4	-1.39E-03	1.73E-03	-	6.35E-04	-1.40E-03	-	28	-6.33E-04	1.45E-03	-	118	2.81E-04	-1.95E-04	-1.33E-03	-	25
G3RW1	8.40E-04	-1.05E-03	-	3.75E-03	-2.21E-03	-	28	3.64E-04	8.36E-04	-	121	-1.80E-03	9.45E-04	-2.64E-03	-	25
G3RW2	-1.74E-03	2.17E-03	-	-1.73E-03	3.37E-03	-	28*	-1.02E-03	7.84E-03	-	121	-1.14E-03	5.59E-04	1.05E-03	-	25
G3RW3	-1.40E-03	1.75E-03	-	-1.40E-03	5.49E-04	-	28	1.33E-03	-1.62E-03	-	121*	5.97E-04	-1.36E-04	2.06E-04	-	25
G3RW4	-1.87E-03	2.34E-03	-	-2.22E-03	3.31E-03	-	28**	1.38E-04	-9.77E-04	-	121	-2.02E-03	1.47E-03	-2.29E-04	-	25
G4RW1	-1.10E-04	1.37E-04	-	6.97E-04	5.60E-05	-	30	-4.29E-04	-4.83E-04	-	118	1.31E-03	-1.14E-03	3.13E-03	-	25*
G4RW2	-2.00E-03	2.50E-03	-	5.36E-04	-2.64E-04	-	30	2.55E-04	-7.89E-04	-	118	-1.41E-03	7.95E-04	-4.96E-05	-	25
G4RW3	-3.68E-04	4.60E-04	-	-2.34E-04	1.84E-04	-	30	4.42E-04	-1.50E-03	-	118	-3.06E-04	-4.62E-05	2.40E-04	-	25
G4RW4	-1.22E-03	1.52E-03	-	1.56E-03	-1.14E-03	-	30	-5.30E-04	4.86E-04	-	118	1.54E-03	-1.12E-03	-7.74E-04	-	25

Table 3. Cranio-dental dimensions (in mm) and CS scores of the examined *M. schreibersii* age cohorts. See methods for explanation of dimension abbreviations. *n* = number of specimens, *M* = mean, min = minimum value, max = maximum value, SD = standard deviation.

Character	Cohort 0					Cohort 1					Cohort 2					Cohort 3								
	<i>n</i>	<i>M</i>	min	max	SD	<i>n</i>	<i>M</i>	min	max	SD	<i>n</i>	<i>M</i>	min	max	SD	<i>n</i>	<i>M</i>	min	max	SD	<i>n</i>	<i>M</i>	min	max
LcR	61	15.134	14.54	15.88	0.223	120	15.213	14.68	15.83	0.224	69	15.245	14.48	15.82	0.257	15	15.274	14.88	15.61	0.235				
LcB	61	14.681	14.07	15.58	0.253	120	14.733	14.30	15.20	0.228	68	14.755	14.05	15.39	0.259	15	14.801	14.32	15.16	0.238				
LaZ	59	8.491	8.13	9.00	0.151	121	8.555	8.11	9.00	0.163	67	8.584	8.10	8.88	0.147	15	8.610	8.45	8.76	0.100				
LaI	63	3.677	3.49	4.02	0.096	125	3.700	3.41	3.98	0.094	69	3.711	3.48	3.97	0.091	16	3.749	3.57	3.89	0.091				
LaInf	62	3.958	3.45	4.24	0.120	123	3.982	3.45	4.29	0.110	69	4.020	3.67	4.16	0.098	15	4.027	3.89	4.18	0.076				
LaN	62	8.018	7.76	8.40	0.128	123	8.043	7.70	8.47	0.147	69	8.035	7.63	8.33	0.151	17	8.049	7.89	8.21	0.103				
LaM	59	8.684	8.40	9.21	0.150	121	8.689	8.10	9.05	0.185	68	8.739	8.27	9.04	0.150	17	8.778	8.60	8.97	0.123				
ANc	62	6.263	6.02	6.53	0.105	120	6.303	6.00	6.52	0.110	68	6.311	6.08	6.57	0.105	17	6.306	6.12	6.53	0.112				
ACr	57	7.698	6.92	8.04	0.261	113	7.709	6.66	8.13	0.328	69	7.781	6.86	8.15	0.295	17	7.814	7.10	8.21	0.239				
LMd	63	10.790	10.28	11.26	0.168	118	10.807	10.15	11.17	0.174	69	10.844	10.32	11.30	0.168	16	10.859	10.32	11.02	0.180				
ACo	61	2.517	2.04	2.85	0.129	120	2.538	2.35	2.84	0.093	69	2.578	2.38	2.93	0.113	16	2.569	2.41	2.93	0.136				
CC	58	4.474	4.14	4.73	0.110	112	4.526	4.28	4.81	0.105	65	4.554	4.29	4.77	0.102	15	4.560	4.40	4.74	0.099				
P ⁴ P ⁴	63	5.509	5.09	5.76	0.105	122	5.505	5.18	5.80	0.126	67	5.525	5.06	5.82	0.119	14	5.526	5.36	5.66	0.099				
M ³ M ³	62	6.294	6.00	6.61	0.118	117	6.295	5.78	6.56	0.127	67	6.313	6.14	6.63	0.094	15	6.331	6.16	6.44	0.076				
I ¹ M ³	62	6.895	6.56	7.13	0.108	121	6.908	6.59	7.20	0.106	69	6.923	6.54	7.16	0.110	16	6.949	6.81	7.10	0.091				
CM ³	62	5.851	5.66	6.03	0.085	121	5.862	5.58	6.13	0.097	69	5.868	5.64	6.06	0.092	16	5.877	5.72	6.05	0.089				
P ⁴ M ³	64	4.312	4.06	4.47	0.074	122	4.284	4.06	4.44	0.079	69	4.290	4.01	4.45	0.073	16	4.278	4.17	4.43	0.068				
M ¹ M ³	64	3.291	3.10	3.49	0.082	123	3.267	3.10	3.47	0.076	69	3.275	3.09	3.49	0.082	17	3.272	3.07	3.48	0.105				
CP ⁴	61	2.858	2.66	3.05	0.083	117	2.876	2.69	3.28	0.090	67	2.890	2.71	3.08	0.076	16	2.889	2.76	3.00	0.073				
I ₁ M ₃	62	7.274	6.95	7.54	0.147	118	7.213	6.87	7.51	0.141	69	7.239	6.96	7.60	0.139	16	7.307	7.06	7.54	0.143				
CM ₃	62	6.165	5.98	6.36	0.086	116	6.167	5.90	6.41	0.085	69	6.176	6.00	6.35	0.075	16	6.221	6.12	6.35	0.071				
P ₄ M ₃	62	4.460	4.29	4.65	0.073	117	4.426	4.24	4.72	0.077	69	4.429	4.18	4.61	0.085	17	4.457	4.32	4.57	0.063				
M ₁ M ₃	62	3.769	3.59	3.97	0.103	119	3.708	3.49	3.89	0.092	69	3.713	3.54	4.00	0.100	17	3.698	3.57	3.83	0.089				
CP ₄	61	2.346	2.19	2.50	0.076	113	2.363	2.20	2.56	0.074	69	2.390	2.22	2.55	0.087	15	2.389	2.26	2.49	0.078				
CSI	56	11.110	10.61	12.03	0.338	112	11.088	10.15	11.89	0.332	65	11.085	10.54	11.97	0.327	13	11.253	10.69	11.92	0.345				
CS2	55	20.389	20.00	21.19	0.241	114	20.478	19.79	21.11	0.293	67	20.527	19.72	21.37	0.312	12	20.559	20.18	20.96	0.222				
CS3	55	16.601	16.23	17.43	0.211	115	16.692	16.13	17.26	0.245	68	16.688	16.05	17.39	0.241	14	16.791	16.47	17.19	0.226				
CS4	56	17.425	16.86	18.44	0.258	115	17.475	16.56	18.17	0.301	66	17.492	16.64	18.08	0.299	15	17.573	17.15	18.04	0.304				

Table 4. Selected dental dimensions (in mm) of the examined *M. schreibersii* age cohorts. See methods for explanation of dimension abbreviations. *n* = number of specimens, *M* = mean, *min* = minimum value, *max* = maximum value, *SD* = standard deviation.

Character	Cohort 0					Cohort 1					Cohort 2					Cohort 3								
	<i>n</i>	<i>M</i>	<i>min</i>	<i>max</i>	<i>SD</i>	<i>n</i>	<i>M</i>	<i>min</i>	<i>max</i>	<i>SD</i>	<i>n</i>	<i>M</i>	<i>min</i>	<i>max</i>	<i>SD</i>	<i>n</i>	<i>M</i>	<i>min</i>	<i>max</i>	<i>SD</i>	<i>n</i>	<i>M</i>	<i>min</i>	<i>max</i>
LI ¹	60	0.502	0.40	0.63	0.036	118	0.498	0.41	0.63	0.030	65	0.482	0.40	0.54	0.029	16	0.473	0.43	0.50	0.023				
WI ¹	60	0.440	0.40	0.50	0.024	118	0.443	0.25	0.55	0.032	65	0.448	0.38	0.53	0.022	16	0.450	0.41	0.48	0.021				
LI ²	61	0.624	0.54	0.70	0.036	118	0.622	0.43	0.73	0.040	66	0.620	0.53	0.70	0.038	16	0.591	0.49	0.66	0.042				
WI ²	61	0.585	0.53	0.71	0.031	118	0.584	0.45	0.68	0.033	66	0.586	0.54	0.65	0.025	16	0.589	0.53	0.64	0.031				
LC ^{sup}	60	1.070	1.00	1.14	0.034	117	1.065	0.98	1.15	0.034	67	1.074	1.00	1.15	0.033	16	1.088	1.01	1.18	0.048				
WC ^{sup}	60	0.845	0.78	0.93	0.038	117	0.853	0.76	1.15	0.047	67	0.855	0.79	0.93	0.032	16	0.852	0.79	0.93	0.041				
LP ²	64	0.825	0.75	0.90	0.032	125	0.824	0.73	0.94	0.038	69	0.833	0.78	0.93	0.035	16	0.847	0.79	0.93	0.037				
WP ²	64	1.102	1.00	1.18	0.045	125	1.106	0.90	1.25	0.048	69	1.114	0.94	1.20	0.049	16	1.128	1.05	1.21	0.040				
WP ⁴	64	1.379	1.26	1.48	0.056	125	1.390	1.15	1.51	0.058	69	1.383	1.15	1.53	0.077	16	1.397	1.25	1.48	0.059				
LP ⁴	64	1.248	1.13	1.38	0.066	125	1.249	1.13	1.38	0.062	69	1.235	1.08	1.38	0.061	16	1.251	1.14	1.40	0.069				
LoM ¹	64	1.461	1.38	1.54	0.032	124	1.458	1.31	1.56	0.035	69	1.442	1.24	1.55	0.046	17	1.437	1.35	1.49	0.037				
LiM ¹	64	0.970	0.85	1.06	0.043	124	0.966	0.88	1.08	0.041	69	0.962	0.83	1.05	0.047	17	0.985	0.90	1.09	0.050				
WIM ¹	64	2.011	1.90	2.13	0.051	124	2.018	1.83	2.18	0.053	69	2.021	1.93	2.13	0.050	17	2.018	1.78	2.19	0.093				
LoM ²	64	1.426	1.29	1.58	0.044	124	1.417	1.35	1.50	0.032	69	1.412	1.33	1.48	0.035	17	1.419	1.38	1.49	0.027				
LiM ²	64	0.882	0.79	0.95	0.030	124	0.885	0.83	0.98	0.031	69	0.884	0.75	0.98	0.036	17	0.893	0.84	0.95	0.027				
WIM ²	64	1.943	1.85	2.03	0.038	124	1.947	1.85	2.06	0.045	69	1.952	1.88	2.06	0.037	17	1.971	1.88	2.03	0.038				
WM ³	64	1.750	1.70	1.83	0.032	123	1.746	1.65	1.83	0.035	69	1.743	1.65	1.83	0.040	17	1.745	1.69	1.80	0.031				
LM ³	64	0.792	0.75	0.89	0.024	123	0.789	0.75	0.85	0.020	69	0.793	0.76	0.85	0.019	17	0.796	0.78	0.84	0.016				
LI ₁	58	0.400	0.35	0.50	0.026	103	0.397	0.35	0.48	0.022	65	0.406	0.35	0.60	0.034	16	0.388	0.38	0.43	0.015				
WI ₁	59	0.241	0.20	0.28	0.016	104	0.247	0.20	0.30	0.020	65	0.245	0.23	0.29	0.017	16	0.247	0.23	0.28	0.017				
LI ₂	60	0.401	0.36	0.45	0.019	110	0.401	0.35	0.48	0.019	69	0.399	0.38	0.43	0.017	16	0.393	0.35	0.41	0.018				
WI ₂	60	0.394	0.35	0.43	0.017	110	0.393	0.35	0.55	0.025	69	0.392	0.35	0.43	0.017	16	0.409	0.38	0.45	0.017				
LI ₃	60	0.549	0.50	0.63	0.024	112	0.545	0.38	0.60	0.027	69	0.545	0.49	0.60	0.026	16	0.541	0.50	0.58	0.020				
WI ₃	60	0.536	0.50	0.58	0.017	112	0.528	0.38	0.63	0.025	69	0.531	0.49	0.58	0.020	16	0.536	0.50	0.56	0.016				
LC ^{inf}	60	0.734	0.64	0.80	0.034	112	0.736	0.65	0.85	0.033	69	0.730	0.63	0.80	0.035	16	0.725	0.68	0.75	0.022				
WC ^{inf}	60	0.799	0.74	0.85	0.025	112	0.807	0.75	0.86	0.025	69	0.807	0.75	0.86	0.022	16	0.813	0.78	0.85	0.021				
LP ₂	60	0.561	0.53	0.60	0.022	111	0.570	0.53	0.63	0.023	68	0.570	0.53	0.63	0.021	16	0.573	0.53	0.63	0.031				
WP ₂	60	0.642	0.60	0.70	0.024	111	0.632	0.58	0.71	0.024	68	0.632	0.58	0.68	0.025	16	0.644	0.60	0.68	0.024				
LP ₃	60	0.620	0.55	0.71	0.030	115	0.619	0.54	0.68	0.028	69	0.618	0.53	0.68	0.029	17	0.624	0.56	0.68	0.025				
WP ₃	60	0.653	0.58	0.73	0.028	114	0.638	0.54	0.75	0.036	69	0.648	0.60	0.70	0.026	17	0.646	0.54	0.69	0.034				
WP ₄	62	0.767	0.63	0.84	0.035	117	0.764	0.68	0.85	0.034	69	0.771	0.68	0.88	0.033	17	0.769	0.70	0.85	0.039				
LP ₄	62	0.600	0.50	0.68	0.048	117	0.605	0.50	0.71	0.045	68	0.621	0.51	0.75	0.042	17	0.625	0.55	0.70	0.039				
LM ₁	62	1.465	1.38	1.51	0.027	120	1.463	1.33	1.56	0.033	69	1.455	1.35	1.51	0.035	17	1.459	1.38	1.50	0.037				
WIM ₁	62	0.861	0.80	0.93	0.032	120	0.861	0.78	0.93	0.031	69	0.868	0.79	1.00	0.037	17	0.873	0.80	0.95	0.033				
LM ₂	62	1.408	1.35	1.48	0.029	120	1.394	1.30	1.56	0.032	69	1.384	1.30	1.48	0.034	17	1.378	1.31	1.43	0.036				
WIM ₂	62	0.831	0.75	0.91	0.034	120	0.830	0.73	0.93	0.034	69	0.831	0.78	0.93	0.033	17	0.845	0.75	0.93	0.037				
LM ₃	62	1.262	1.15	1.33	0.031	120	1.254	1.15	1.35	0.031	69	1.246	1.18	1.33	0.030	17	1.243	1.18	1.33	0.039				
WM ₃	62	0.640	0.60	0.70	0.023	120	0.643	0.59	0.88	0.034	69	0.643	0.58	0.78	0.031	17	0.645	0.63	0.70	0.021				

of variance (ANOVA), independent t-test and Storer's index. Storer's index is a value expressing relative difference of metric (or non-metric) character(s) between sexes (Storer 1966) and is calculated according to the formula $[(Mf - Mm)/Mn] \times 100$ (M = mean, f = female, m = male, n = all specimens). Negative values indicate the relatively larger size for males, positive values for females (cf. Bogdanowicz 1992, Benda 1994).

Geometric morphometrics and non-metric traits

Geometric morphometrics was used to analyse skull and mandible variation between sexes of the respective population sets (groups 1-5) and also partly (see below) between age cohorts. We used the same specimens as for the linear morphometrics.

Images of skulls (lateral, ventral and dorsal views), mandibles (lateral and occlusal views) and dentition (details of the upper and lower tooth-rows) were taken with a digital camera, archived in jpg format (1360 × 1200 pixels resolution) and processed with QuickPhoto 4.1 (Promicra, Prague). The centroid size (CS) as well as the relative warp (RW) scores of all types of view for each specimen (CS1 [G1 in case of RW] – lateral view of mandible, CS2 [G2 in case of RW] – lateral view of skull, CS3 [G3 in case of RW] – ventral view of skull, CS4 [G4 in case of RW] – dorsal view of skull) were calculated using the tpsRegr 1.36 (for CS calculation; Rohlf 2009) and tpsRelw 1.46 software package (for RW calculation; Rohlf 2008). For methodology details see Šrámek et al. (2013). The RW and CS scores were analysed by the same methods as the linear metric data (basic descriptive statistics, one-way ANOVA, independent t-test; Storer's index only for CS scores). The RW analysis as well as Storer's index calculation of the data of age cohorts was not performed.

Based on images of skulls, mandibles and teeth, 49 non-metric cranial and dental characters (44 dental and five skull or mandible; see Table S1 in Šrámek et al. 2013) were investigated for each geographical group (1-5) and sex, and for each age cohort (C0-C3). Statuses of these characters were evaluated using the defined scale system 1-5 in accordance to the character state (see Fig. S3 in Šrámek et al. 2013 for details). Non-metric data were analysed in the same manner as the linear metric data.

Results

Sexual variation

Linear morphometrics

Results of the analyses (ANOVA, t-test) as well as Storer's index values of cranio-dental and tooth

dimensions (Tables 1 and 2, and Tables S1 and S2) generally showed that the most significant differences associated with sexual dimorphism were found in populations from Afghanistan, the Levant and eastern Europe while those from Morocco and western Europe diverged only in a few variables. The results indicate that males are generally larger within a given population sets, with the exception of eastern Europe. In all cranio-dental measurements the Moroccan males showed larger values than females except for dimensions associated with skull and rostral width (LaZ, LaI, LaInf, CC, P⁴P⁴, and M³M³), but the sexes just slightly diverged ($P < 0.05$) in the length of upper tooth-row (P⁴M³). In dental characters, the Moroccan females were larger in 38 of 57 variables and the sexes highly diverged ($P < 0.001$) in the length of lower canine (LC_{inf}); slightly diverged in widths of the second lower incisor (WI₂), second upper molar (in central part, W2M²) and third lower molar (WM³). Males of the western European bats showed values larger than those of females in almost of all cranio-dental measurements, with the exception of all upper tooth-row dimensions. Sexes moderately diverged ($P < 0.01$) in the condylobasal length (LCb) and only slightly diverged in the length of upper tooth-row (CM₃). Teeth showed larger values more likely in males in 30 of 57 measurements; the sexes diverged (moderately) only in the first lower molar diagonal width (W3M₁).

In the eastern European bats, females showed values larger than those of males in most cranio-dental measurements, with the exception of zygomatic width (LaZ), skull heights (ACr, ANc, ACo) and partly in tooth-rows length (P⁴M³, P₄M₃). Sexes highly diverged in the length characters (LCr, LCb); moderately diverged in mastoidal width (LaM), mandible and lower tooth-row length (LMd, I₁M₃); and slightly diverged in length of tooth-rows (I¹M³, CM³, CP⁴, CM₃, CP₄). In the majority of dental characters (40 of 57) females showed larger values than in males, with the exception of most height dimensions. The sexes were highly divergent in the widths of the second upper molar (in central part, W2M₂) and the second lower incisor (LI₂); moderately diverged in the second upper molar diagonal width (W1M²), length and width of the third lower incisor (LI₃, WI₃), length of the second lower premolar (LP₂) and height of lower canine (HC_{inf}); and slightly diverged in some dimensions of the first upper incisor (WI¹, HI¹), molars (W2M¹, W3M², WM₃) and height of the second lower incisor (HI₂).

In all cranio-dental measurements males of the Levantine bats showed larger values than those of

females, with the exception of lower molar-row length (M_1M_3). They highly diverged in skull length (LCr, LCb), braincase dimensions (LaN, ANc); moderately diverged in mastoidal width (LaM) and length of upper tooth-row (I^1M^3 , CM^3); and slightly diverged in skull height (ACr) and partly in the tooth-rows lengths (CP^4 , CM_3). In dental characters males showed values larger than females in 38 of 57 dimensions. Sexes highly diverged in some canine dimensions (HC^{sup} , HC_{inf} , LC_{inf}); moderately in lower canine width (WC_{inf}); and slightly in upper canine width (WC^{sup}) and the dimensions of upper second premolar (WP^4 , HP^4).

Males of Afghanistan *Miniopterus* were larger than females in all cranio-dental characters (except of lower molar-row length, M_1M_3). The sexes were highly divergent in condylobasal length (LCb), rostral width across the upper canines (CC) and upper tooth-row length (I^1M^3); moderately divergent in the skull and mandible length (LCr, LMd); and slightly in some skull widths (LaM, LaN, LaInf, P^4P^4 , M^3M^3), neurocranium height (ANc) and some tooth-rows lengths (CM^3 , CP_4). Dental measurements were larger in males in 42 of 57 dimensions, particularly in height dimensions, and sexes highly diverged in height of lower canine (HC_{inf} , Fig. 2); moderately diverged in the length of upper canine (LC^{sup}) and height of first upper incisor (HI^1); and slightly diverged in the lengths of the first upper incisor (LI^1), lower canine (LC_{inf}) and the second premolar (LP_4), in the height of the upper canine (HC^{sup} , Fig. 2) and in the width of the first lower molar ($W2M_1$).

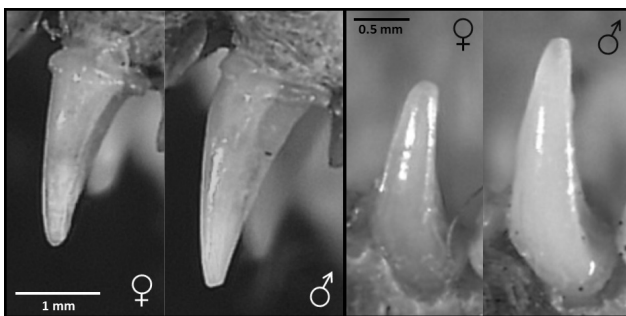


Fig. 2. Sexual size variation in upper (left) and lower (right) canines of bats from eastern Afghanistan.

Geometric morphometrics and non-metric traits

Cendroid size scores (see Table 1 and S1) showed larger values in males than in those of females in all views and examined population sets (significantly [$P < 0.05$] except for CS1 of the Afghanistani and western European sets, CS3 of the western European set, and for all views of the Moroccan set), except the

eastern European set, where females showed larger values in all views (significantly except CS2). The significance level for respective views and groups was rather variable (see Table 1 and S1).

Twenty-two RWs were generated for the lateral skull view for both sexes of each population set, 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 for subsequent analyses (ANOVA, t-test). These generally showed minimal shape differences between sexes of all examined population sets (Table 1 and S1).

Results of analyses (ANOVA, t-test), as well as Storer's index values, of non-metric traits showed various levels of sexual dimorphism in the respective population sets in size parameters as well as in notably variable levels of statistical significance (Table S3). The sexes of Moroccan bats only slightly diverged in $P2P4inf2$, $CingM2sup$ and $RmanW$. The sexes of the western European bats moderately diverged in $P4sup2$ and $CingCsup$, while only slightly in $Fmen$ and $M3sup$. The sexes of eastern European bats highly diverged only in $M1sup$, moderately in $Fmen$, and slightly in $P3inf2$, $M3sup2$, $M2sup$, $P4sup$, $P4sup8$, $CingCsup$, $ProcCW$ and $Isup$. The sexes of Levantine bats moderately diverged in $P4inf$ and slightly in $P3inf2$, $P2P4inf2$, $P3P4inf$, $FmenP2inf$, $M1sup5$ and $P4sup5$. The sexes of Afghanistan bats only slightly diverged in $M3sup$.

Age variation

Linear morphometrics

The values of all cranio-dental measurements of four age cohorts and their simple comparisons (Table 3 or Fig. S1) showed certain level of age variation. In most of these dimensions, the size of the respective character was found to increase with age. This pattern was found to be inverted (the dimensions decreased in size with age) only in some dimensions concerning molariform teeth (P^4M^3 , M^1M^3 , P_4M_3 and M_1M_3). In the dental dimensions (Table 4 and S4 or Fig. S2), the situation was markedly less expressive than in the cranio-dental measurements and in some (mainly tooth length) dimensions (LI^1 , LI^2 , LoM^1 , LI_3 , LM_2 and LM_3), the above mentioned pattern was found to be inverse, i.e. with dimensions smaller in older bats.

Geometric morphometrics and non-metric traits

CS scores showed considerable age variation and positive correlation between age and value of the respective centroid size, i.e. the higher cohort (older

bats) the larger the centroid size value. Only the mandibular CS scores showed an inverse pattern (except for the C3 cohort whose values were markedly highest among all cohorts). For details see Table 3 or Fig. S1.

The non-metric traits data did not show a general correlation between age and value of the particular character (Table S5). Differences in character values between the respective cohorts were largely not present, with the exception of P2P4inf.

Discussion

Synthesis of results of the sexual dimorphism analysis of the western Palaearctic *Miniopterus* bats, comprising the Moroccan, western and eastern European, Levantine and eastern Afghanistani populations, indicates that males are larger than females in all examined geographical sample sets, with the exception of eastern Europe. These results are in parallel to the majority of published studies of *Miniopterus* populations in different portions of the Palaearctic (Crucitti 1976, Spitzenberger 1981, Maeda 1982, 1983, 1984). Only Uhrin et al. (1997) who studied Slovakian populations, on the contrary to our results, found the males to be generally larger than females. Nevertheless, it is important to mention that the Slovakian specimens comprised a minority in our eastern European set (29 Slovakian vs. 109 Balkan samples) and individual populations thus could have different characteristics. Unfortunately, our samples were insufficient to test Slovakian bats separately as well as any other population within this sample set, with the exception of Bulgarian bats, in which males were generally larger than females. Moreover, our finding of sexual dimorphism in cranial dimension in *Miniopterus* bats from eastern Afghanistan is in contradiction with that by Gaisler (1970) who found no sexual differences in *Miniopterus* bats from the same locality. This dissimilarity may be the result of measuring specimens in different manners, as well as more precise statistical analyses of our data.

Sexual dimorphism is generally explained by several hypotheses. The most common being male-male competition for females (or selection by females; Darwin 1871, Trivers 1972) or male-female food competition (e.g. Selander 1966, Storer 1966, Earhart & Johnson 1970). Among chiropterans, there are also other proposed hypotheses, such as 'The Big Mother' hypothesis (Ralls 1976), which suggests that larger females give their offspring better conditions and this system subsequently lead to females of a given taxon being larger than males. Myers (1978) found

positive correlation between sexual dimorphism of vespertilionid bats and number of young per litter, similarly as Brunett (1983) in *Eptesicus fuscus*, and proposed that female body size (particularly wing size) is positively influenced by the need to carry in flight and nourish large foetus or carry young juveniles. Williams & Findley (1979) tested this hypothesis; however, did not find this correlation. They and some other authors (Findley & Traut 1970, Findley & Wilson 1982) explained the larger size of the vespertilionid females in relation to the gravidity process and some climatic conditions (temperature, humidity) – larger females are more resistant to hypothermia and associated perturbations in embryo development and, also, the larger size provides greater energetic efficiency in maintaining homeothermy during gestation while males are hypothermic. Climatic conditions in connection with different life history traits of the respective sexes were found in some small insectivorous bat species associated with sexual dimorphism (e.g. Egsbaek & Jensen 1963, Bogdanowicz 1992). In the case of *Myotis daubentonii*, the precise mechanism involved in the development of sexual dimorphism was connected with different periods of time spent in hibernacula; males fly out to foraging activities in early spring while females stay and are more exposed to climatic stresses (low temperature, high humidity) (Egsbaek & Jensen 1963, Stebbings 1977, Baagøe et al. 1988). Larger size then provides greater energetic efficiency in maintaining homeothermy and thus means benefit for females.

However, our results showed males of *Miniopterus* bats to be generally larger than females (with an exception of the eastern European populations). Hence, sexual dimorphism differences are presumably related to different factors or, to the same factors but affected by other mechanisms. We speculate that these factors involved may be in parallel to the case of *Myotis daubentonii*, specifically associated with different climatic conditions affecting differentially aspects between the sexes in life history traits at the population level, such as the use of seasonally different shelters (hibernacula) or different periods of their usage, forming of sex-specific colonies. These factors may also be directly related to differences in patterns of sexual dimorphism at the population level (i.e. females larger than males in eastern Europe vs. males larger than females in Morocco, western Europe, the Levant, and Afghanistan). Nevertheless, to elucidate the mechanisms leading to development of sexual dimorphism of the respective *Miniopterus* populations

concerning their life histories of their sexes remain to be studied, since they were generally not much explored yet (Spitzenberger 1981, Boye 2004). Another factor that might contribute to sexual dimorphism in *Miniopterus* may be associated with the feeding strategies (food competition). We documented in some sample sets (mainly in Levantine and Afghanistani sets) very marked dimorphism in dentition (positively correlating with the level of dimorphism in skull dimensions), particularly in canines and this finding may thus indicate intraspecific food competition that consequently led to male adaptations to different prey types of size than in females, and consequently the generally larger size in the former. However, this was not documented in other bat species (Krzanowski 1971) and this hypothesis is not corroborated with some of our other results, specifically weak dimorphism and larger dentition in females of eastern European and Moroccan populations. To conclude, the differences in patterns of sexual dimorphism between studied population sets might be best explained by different effects or combination of effects of two different factors – distinct life histories and feeding strategies. The level of sexual dimorphism found among the examined population sets does not fully correlate with the classification of the western Palaearctic bats of the genus *Miniopterus* as presented in recent revision (Šrámek et al. 2013). Most particularly, the different patterns of dimorphism found in the western (larger males) and eastern (larger females) European populations are surprising. In other areas, these patterns were quite similar to each other; however, the level of significance diverged. The most significant dimorphism was found in bats from

eastern Afghanistan (classified as *M. cf. fuliginosus*), the Levant (*M. schreibersii*) and eastern Europe (*M. schreibersii*). In Moroccan (recently defined as a new species, *M. maghrebensis*) and western European (*M. schreibersii*) populations, the rate of dimorphism was less pronounced and similar to each other. However, it may be important to mention that the rate of dimorphism found in the respective population sets could be affected by different sample sizes (n affects P value calculation). To conclude, results rather suggest that in this genus, sexual dimorphism probably has had a minor contribution to measurable aspects of morphological variation with little signal associated with recent phylogenetic evolution (cf. Šrámek et al. 2013).

Age variation was demonstrated to occur in all linear-metric characteristics and CS scores, while almost no age variation was found in non-metric traits. This finding clearly indicates importance of the non-metric traits for species identification of taxa across age categories. The negative correlation found between age and size in several linear-metric dimensions (e.g. P^4M^3 , M^1M^3 , LI^1 , LI^2) and one non-metric trait ($P2P4_{inf}$) can be attributed to abrasion or to the relative difference generated by mandible development, i.e. tooth size does not change with mandible development.

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Supplementary online materials

Fig. S1. Graphs of mean values of cranio-dental measurements and of mean CS values for respective cohorts. See methods for explanation of dimension abbreviations.

Fig. S2. Graphs of mean values of dental measurements for respective cohorts. See methods for explanation of dimension abbreviations.

Table S1. Cranio-dental dimensions (in mm), CS and RW scores of the *Miniopterus* sexes in the respective populations. See methods for explanation of dimension abbreviations. *n* = number of specimens, M = mean, min = minimum value, max = maximum value, SD = standard deviation, * = $P < 0.05$, ** = $P < 0.001$, *** = $P < 0.0001$, F = F-values from ANOVA and T-test, SI = Storer's index.

Table S2. Dental dimensions (in mm) of the *Miniopterus* sexes in the respective populations. See methods for explanation of dimension abbreviations. *n* = number of specimens, M = mean, min = minimum value, max = maximum value, SD = standard deviation, * = $P < 0.05$, ** = $P < 0.001$, *** = $P < 0.0001$, F = F-values from ANOVA and T-test, SI = Storer's index.

Table S3. Non-metric traits of the *Miniopterus* sexes in the respective populations. See methods for explanation of dimension abbreviations. *n* = number of specimens, M = mean, min = minimum value, max = maximum value, SD = standard deviation, * = $P < 0.05$, ** = $P < 0.001$, *** = $P < 0.0001$, F = F-values from ANOVA and T-test, SI = Storer's index.

Table S4. Dental dimensions (in mm) of the examined *M. schreibersii* age cohorts. See methods for explanation of dimension abbreviations. M = mean, min = minimum value, max = maximum value, and SD = standard deviation.

Table S5. Non-metric traits of the examined *M. schreibersii* age cohorts. See methods for explanation of dimension abbreviations. M = mean, min = minimum value, max = maximum value, and SD = standard deviation.

(URL: http://www.ivb.cz/folia/download/sramek_benda_supp.docx).