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

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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. maghrebesnis*), 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. Significatly 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 variaton 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. maghrebensis* 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. maghrebensis*, morphologicaly very similar to *M. schreibersii* s. str., was described from the mountainous

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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. magneter*, *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 dimorhism. 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-metrical 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) investegated 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.

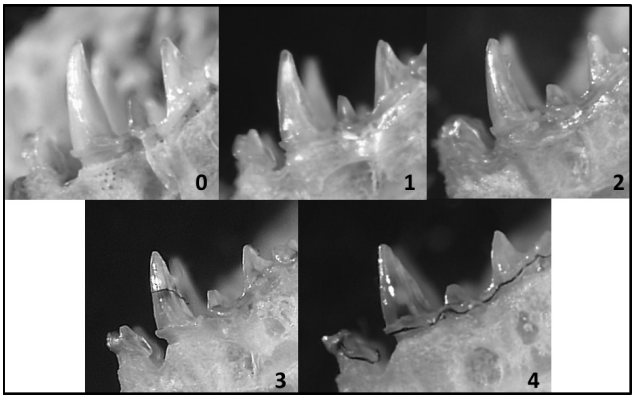


Fig. 1. Defined scale system of abrasion. Rate of abrasion is in ascending order.

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 heigh 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

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Table 1. Mean value and Storer's index (SI) of all cranio-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			
	♀	♂	SI	df	♀	♂	SI	df	♀	♂	SI	df	♀	♂	SI	df	♀	♂	SI	df
LCr	15.312	15.431	–0.776	16	15.218	15.256	–0.252	32	15.293	15.107	1.222	127***	15.015	15.244	–1.511	89***	15.438	15.735	–1.901	25**
LCb	14.900	15.019	–0.794	16	14.723	14.871	–1.003	31**	14.819	14.664	1.052	127***	14.544	14.732	–1.286	89***	15.101	15.391	–1.896	25***
LaZ	8.704	8.669	0.406	16	8.559	8.601	–0.488	31	8.555	8.557	–0.024	126	8.502	8.560	–0.686	88	8.794	8.983	–2.118	25
LaI	3.781	3.773	0.225	16	3.712	3.714	–0.062	32	3.718	3.698	0.517	134	3.665	3.689	–0.651	89	3.900	3.941	–1.047	25
LaInf	4.210	4.193	0.416	16	3.993	4.058	–1.625	32	3.981	3.967	0.352	132	3.974	3.999	–0.646	89	4.038	4.158	–2.910	25*
LaN	8.051	8.158	–1.315	16	8.056	8.069	–0.171	32	8.065	8.043	0.278	132	7.924	8.028	–1.298	89***	8.082	8.226	–1.759	25*
LaM	8.778	8.801	–0.265	16	8.662	8.708	–0.533	31	8.748	8.666	0.936	127**	8.643	8.739	–1.106	89**	8.738	8.896	–1.785	25*
ANc	6.343	6.375	–0.503	16	6.329	6.355	–0.425	31	6.283	6.298	–0.235	130	6.227	6.340	–1.798	89***	6.368	6.543	–2.704	25*
ACr	7.925	8.033	–1.348	16	7.429	7.625	–2.603	26	7.728	7.733	–0.059	125	7.770	7.850	–1.017	86*	7.757	7.789	–0.421	25
LMd	10.935	11.029	–0.854	16	10.826	10.903	–0.708	32	10.875	10.776	0.916	128**	10.747	10.788	–0.376	87	11.173	11.373	–1.769	25**
ACo	2.589	2.609	–0.760	16	2.589	2.614	–0.947	32	2.514	2.540	–1.046	129	2.560	2.579	–0.735	87	2.633	2.646	–0.462	25
CC	4.677	4.630	1.009	16	4.525	4.471	1.194	23	4.508	4.501	0.143	124	4.544	4.569	–0.550	87	4.617	4.772	–3.299	24***
P^4P^4	5.568	5.509	1.069	16	5.467	5.385	1.498	32	5.545	5.512	0.600	130	5.500	5.523	–0.424	87	5.699	5.823	–2.143	25*
M^3M^3	6.409	6.385	0.375	16	6.281	6.241	0.647	28	6.317	6.299	0.282	128	6.286	6.308	–0.359	88	6.626	6.747	–1.812	25*
I^1M^3	6.918	6.981	–0.911	16	6.951	6.949	0.018	30	6.937	6.890	0.676	132*	6.851	6.909	–0.839	88**	7.114	7.308	–2.669	25***
CM^3	5.877	5.933	–0.940	16	5.853	5.853	0.011	29	5.890	5.853	0.625	132*	5.821	5.872	–0.873	89**	6.049	6.153	–1.698	25*
P^4M^3	4.282	4.328	–1.058	16	4.291	4.253	0.881	31	4.297	4.299	–0.061	133	4.286	4.305	–0.450	89	4.382	4.441	–1.332	25
M^1M^3	3.227	3.285	–1.783	16	3.237	3.224	0.400	32	3.303	3.278	0.768	134	3.259	3.272	–0.380	89	3.340	3.383	–1.285	25
CP^4	2.864	2.893	–0.991	16	2.918	2.890	0.973	22	2.875	2.842	1.155	133*	2.866	2.901	–1.206	88*	3.000	3.048	–1.595	25
I_1M_3	7.256	7.321	–0.896	16	7.171	7.252	–1.118	31	7.317	7.236	1.119	128**	7.159	7.185	–0.365	86	7.537	7.594	–0.763	25
CM_3	6.166	6.226	–0.973	16	6.159	6.234	–1.218	31*	6.187	6.155	0.510	127*	6.136	6.176	–0.650	85*	6.454	6.536	–1.246	25
P_4M_3	4.358	4.420	–1.414	16*	4.419	4.485	–1.485	31	4.449	4.454	–0.110	129	4.399	4.412	–0.302	86	4.574	4.576	–0.036	25
M_1M_3	3.606	3.606	–0.007	16	3.699	3.757	–1.563	32	3.753	3.752	0.020	130	3.676	3.668	0.220	86	3.804	3.778	0.703	25
CP_4	2.351	2.393	–1.751	16	2.369	2.386	–0.740	26	2.365	2.332	1.401	127*	2.373	2.394	–0.890	85	2.507	2.608	–3.934	25*
CS1	11.093	11.262	–1.509	16	11.084	11.174	–0.816	31	11.183	11.035	1.329	117*	10.920	11.061	–1.288	82*	11.521	11.538	–0.151	20
CS2	20.731	20.915	–0.886	16	20.413	20.600	–0.909	28**	20.532	20.429	0.504	118	20.312	20.528	–1.058	87***	20.867	21.182	–1.497	25*
CS3	16.883	17.000	–0.689	16	16.717	16.837	–0.720	28	16.740	16.622	0.704	121**	16.523	16.688	–0.990	88**	17.048	17.314	–1.546	25**
CS4	17.647	17.803	–0.878	16	17.452	17.626	–0.991	30**	17.615	17.427	1.074	118***	17.189	17.409	–1.267	88***	17.671	18.022	–1.958	25**
G1RW1	–1.67E-03	2.09E-03	-	16	9.04E-04	–1.53E-03	-	31	–8.15E-04	3.49E-05	-	117	–8.19E-04	9.88E-04	-	87	–6.00E-05	6.45E-04	-	20
G1RW2	1.72E-03	–2.15E-03	-	16	–6.92E-04	–5.93E-04	-	31	–1.58E-03	2.63E-03	-	117	–1.34E-03	9.24E-04	-	87	–2.81E-03	3.25E-03	-	20
G1RW3	4.85E-04	–6.06E-04	-	16	–1.79E-03	2.78E-03	-	31	–1.69E-04	–2.18E-03	-	117	–9.61E-04	9.67E-04	-	87	5.05E-03	–2.30E-03	-	20
G1RW4	–6.32E-04	7.90E-04	-	16	1.35E-03	–2.69E-03	-	31	1.68E-03	–3.21E-03	-	117**	7.70E-04	–6.44E-04	-	87	–2.42E-03	2.13E-03	-	20
G2RW1	–3.44E-04	4.30E-04	-	16	–1.03E-04	7.78E-04	-	28	1.77E-03	–3.43E-03	-	118*	–9.42E-04	1.54E-03	-	82	8.34E-03	–4.62E-03	-	24
G2RW2	–1.16E-03	1.45E-03	-	16	–1.51E-03	1.94E-04	-	28	–8.46E-04	1.94E-03	-	118	9.43E-04	–4.46E-04	-	82	1.12E-03	5.40E-05	-	25*
G2RW3	2.11E-03	–2.64E-03	-	16	–1.23E-03	7.81E-04	-	28	8.77E-04	–1.76E-03	-	118	8.99E-04	–1.06E-03	-	82	8.01E-04	3.20E-04	-	25
G2RW4	–1.39E-03	1.73E-03	-	16	6.35E-04	–1.40E-03	-	28	–6.33E-04	1.45E-03	-	118	2.81E-04	–1.95E-04	-	82	2.13E-03	–1.33E-03	-	25
G3RW1	8.40E-04	–1.05E-03	-	16	3.75E-03	–2.21E-03	-	28	3.64E-04	8.36E-04	-	121	–1.80E-03	9.45E-04	-	88	4.40E-03	–2.64E-03	-	25
G3RW2	–1.74E-03	2.17E-03	-	16	–1.73E-03	3.37E-03	-	28*	–1.02E-03	7.84E-04	-	121	–1.14E-03	5.59E-04	-	88	–3.22E-03	1.05E-03	-	25
G3RW3	–1.40E-03	1.75E-03	-	16	–1.40E-03	5.49E-04	-	28	1.33E-03	–1.62E-03	-	121*	5.97E-04	–1.36E-04	-	88	–6.47E-04	2.06E-06	-	25
G3RW4	–1.87E-03	2.34E-03	-	16*	–2.22E-03	3.31E-03	-	28**	1.38E-04	–9.77E-04	-	121	–2.02E-03	1.47E-03	-	88***	7.57E-04	–2.29E-04	-	25
G4RW1	–1.10E-04	1.37E-04	-	16	6.97E-04	5.60E-05	-	30	–4.29E-04	–4.83E-04	-	118	1.31E-03	–1.14E-03	-	88	–6.66E-03	3.13E-03	-	25*
G4RW2	–2.00E-03	2.50E-03	-	16	5.36E-04	–2.64E-04	-	30	2.55E-04	–7.89E-04	-	118	–1.41E-03	7.95E-04	-	88	–1.18E-03	–4.96E-05	-	25
G4RW3	–3.68E-04	4.60E-04	-	16	–2.34E-04	1.84E-04	-	30	4.42E-04	–1.50E-03	-	118	–3.06E-04	–4.62E-05	-	88	–1.87E-03	2.40E-04	-	25
G4RW4	–1.22E-03	1.52E-03	-	16	1.56E-03	–1.14E-03	-	30	–5.30E-04	4.86E-04	-	118	1.54E-03	–1.12E-03	-	88***	1.78E-03	–7.74E-04	-	25

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Table 2. Mean value and Storer's index (SI) of dental dimensions (in mm) 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			
	♀	♂	SI	df	♀	♂	SI	df	♀	♂	SI	df	♀	♂	SI	df	♀	♂	SI	df
LI^1	0.484	0.497	–2.681	16	0.510	0.516	–1.191	23	0.495	0.495	–0.037	130	0.490	0.488	0.403	88	0.486	0.517	–6.107	23*
WI^1	0.446	0.447	–0.140	16	0.451	0.452	–0.306	23	0.448	0.438	2.179	130*	0.441	0.448	–1.510	88	0.459	0.451	1.898	23
HI^1	0.638	0.583	9.075	2	0.559	0.606	–8.146	17	0.556	0.586	–5.404	130*	0.550	0.561	–2.001	54	0.561	0.626	–10.697	23**
LI^2	0.603	0.631	–4.673	16	0.625	0.618	1.093	23	0.619	0.629	–1.569	131	0.625	0.619	0.817	88	0.634	0.615	3.157	23
WI^2	0.566	0.586	–3.424	16	0.592	0.590	0.370	23	0.582	0.577	0.741	131	0.588	0.591	–0.510	88	0.563	0.575	–2.189	24
HI^2	0.675	0.625	7.843	2	0.653	0.644	1.488	17	0.610	0.619	–1.508	131	0.629	0.640	–1.604	54	0.686	0.709	–3.245	24
LC^{sup}	1.055	1.055	0.030	16	1.080	1.088	–0.710	24	1.063	1.070	–0.636	130	1.069	1.076	–0.602	88	1.078	1.132	–4.865	23**
WC^{sup}	0.889	0.875	1.558	16	0.893	0.899	–0.644	24	0.832	0.834	–0.255	130	0.852	0.874	–2.612	88*	0.914	0.945	–3.335	23
HC^{sup}	1.650	1.654	–0.252	2	1.558	1.592	–2.120	19	1.512	1.530	–1.170	129	1.526	1.610	–5.347	54***	1.522	1.702	–10.901	23*
LP^2	0.856	0.822	4.088	16	0.818	0.810	1.018	32	0.830	0.822	0.906	135	0.831	0.833	–0.283	89	0.896	0.892	0.438	24
WP^2	1.144	1.114	2.626	16	1.141	1.137	0.353	32	1.092	1.089	0.278	135	1.117	1.130	–1.225	89	1.065	1.085	–1.783	24
HP^2	0.588	0.583	0.713	2	0.581	0.549	5.648	23	0.522	0.527	–1.001	134	0.568	0.586	–3.158	55	0.526	0.563	–6.500	24
WP^4	1.399	1.380	1.371	16	1.443	1.446	–0.167	32	1.366	1.370	–0.301	135	1.393	1.410	–1.224	89*	1.421	1.406	1.058	24
LP^4	1.215	1.227	–0.948	16	1.278	1.285	–0.571	32	1.228	1.220	0.655	135	1.256	1.273	–1.340	89	1.250	1.293	–3.384	24
HP^4	1.650	1.542	6.906	2	1.593	1.575	1.104	23	1.479	1.474	0.337	135	1.471	1.551	–5.309	55*	1.500	1.539	–2.545	24
LoM^1	1.434	1.444	–0.695	16	1.470	1.480	–0.677	31	1.448	1.452	–0.296	136	1.452	1.459	–0.490	89	1.471	1.500	–1.956	24
LiM^1	0.928	0.919	0.947	16	0.984	0.975	0.937	31	0.971	0.976	–0.525	136	0.949	0.960	–1.135	89	0.993	0.990	0.264	24
$W1M^1$	1.998	1.948	2.483	16	2.047	2.054	–0.335	31	2.017	1.997	0.985	136	2.024	2.024	0.007	89	2.026	2.005	1.054	24
$W2M^1$	1.649	1.608	2.511	16	1.689	1.688	0.064	31	1.642	1.624	1.095	136*	1.652	1.649	0.165	89	1.683	1.676	0.408	24
$W3M^1$	1.815	1.772	2.401	16	1.827	1.816	0.598	31	1.778	1.764	0.787	136	1.774	1.782	–0.446	89	1.772	1.748	1.400	24
LoM^2	1.440	1.439	0.065	16	1.428	1.432	–0.325	32	1.422	1.416	0.435	135	1.406	1.416	–0.684	89	1.460	1.479	–1.337	24
LiM^2	0.906	0.892	1.563	16	0.889	0.886	0.412	32	0.890	0.888	0.237	135	0.877	0.876	0.073	89	0.974	0.965	0.846	24
$W1M^2$	1.979	1.963	0.824	16	1.975	1.989	–0.721	32	1.953	1.930	1.204	135**	1.950	1.940	0.524	89	1.975	1.988	–0.630	23
$W2M^2$	1.828	1.792	1.949	16*	1.829	1.825	0.205	32	1.801	1.777	1.355	135***	1.792	1.792	–0.007	89	1.815	1.827	–0.654	23
$W3M^3$	1.951	1.903	2.494	16	1.949	1.958	–0.444	32	1.914	1.895	0.979	135*	1.906	1.890	0.816	89	1.938	1.944	–0.340	24
WM^3	1.768	1.723	2.521	16*	1.759	1.759	–0.010	32	1.749	1.735	0.852	134*	1.746	1.744	0.086	89	1.771	1.786	–0.852	24
LM^3	0.803	0.803	–0.078	16	0.796	0.796	0.011	32	0.792	0.788	0.578	134	0.793	0.792	0.127	89	0.801	0.811	–1.193	24
LI_1	0.403	0.397	1.406	16	0.399	0.403	–1.023	19	0.402	0.399	0.724	121	0.399	0.395	1.030	82	0.399	0.407	–1.983	24
WI_1	0.244	0.227	7.279	16	0.253	0.263	–3.856	20	0.244	0.242	0.983	121	0.244	0.241	1.497	83	0.264	0.257	2.800	24
HI_1	0.300	0.292	2.837	2	0.289	0.283	1.938	13	0.278	0.290	–4.143	122	0.284	0.290	–2.252	50	0.253	0.256	–1.213	24
LI_2	0.436	0.419	4.084	16	0.402	0.409	–1.781	24	0.405	0.394	2.852	125***	0.396	0.396	–0.142	86	0.415	0.421	–1.267	24
WI_2	0.384	0.405	–5.327	16*	0.396	0.408	–2.848	24	0.396	0.391	1.362	125	0.388	0.389	–0.220	86	0.386	0.387	–0.169	24
HI_2	0.313	0.317	–1.320	2	0.313	0.314	–0.570	15	0.290	0.305	–5.177	125*	0.299	0.304	–1.507	53	0.265	0.278	–4.597	24
LI_3	0.519	0.545	–5.007	16	0.553	0.532	3.876	26	0.555	0.541	2.521	125**	0.535	0.541	–0.967	86	0.543	0.560	–3.106	24
WI_3	0.534	0.525	1.651	16	0.528	0.528	–0.088	26	0.539	0.529	1.977	125**	0.523	0.525	–0.331	86	0.533	0.535	–0.230	24
HI_3	0.300	0.325	–7.843	2	0.347	0.347	0.000	18	0.319	0.331	–3.501	125	0.335	0.336	–0.149	53	0.311	0.310	0.263	24
LC_{inf}	0.714	0.742	–3.915	16***	0.753	0.759	–0.856	27	0.725	0.724	0.066	125	0.725	0.744	–2.564	85***	0.763	0.798	–4.470	23*
WC_{inf}	0.819	0.842	–2.827	16	0.813	0.832	–2.411	27	0.802	0.798	0.559	125	0.798	0.813	–1.941	85**	0.832	0.862	–3.489	23
HC_{inf}	1.500	1.504	–0.277	2	1.424	1.354	5.006	19	1.395	1.440	–3.181	125**	1.395	1.486	–6.294	52***	1.429	1.628	–12.738	22***
LP_2	0.593	0.597	–0.736	16	0.589	0.585	0.672	24	0.567	0.556	1.945	126**	0.569	0.567	0.402	85	0.575	0.573	0.407	23
WP_2	0.651	0.650	0.192	16	0.625	0.626	–0.182	24	0.645	0.635	1.478	126	0.631	0.625	0.902	85	0.650	0.652	–0.360	23
HP_2	0.600	0.567	5.797	2	0.522	0.516	1.203	18	0.500	0.494	1.152	126	0.489	0.492	–0.645	52	0.460	0.474	–3.071	23
LP_3	0.645	0.641	0.680	16	0.626	0.634	–1.263	28	0.618	0.609	1.488	129	0.623	0.621	0.200	85	0.657	0.657	0.050	24
WP_3	0.678	0.667	1.533	16	0.626	0.632	–1.044	27	0.651	0.651	0.046	129	0.639	0.635	0.658	85	0.622	0.625	–0.445	24
HP_3	0.675	0.600	12.121	2	0.580	0.578	0.420	19	0.542	0.535	1.171	129	0.563	0.572	–1.682	52	0.542	0.525	3.176	24
WP_4	0.795	0.786	1.146	16	0.756	0.771	–1.992	30	0.770	0.767	0.319	130	0.761	0.762	–0.197	86	0.763	0.770	–0.959	24
LP_4	0.600	0.616	–2.574	16	0.610	0.611	–0.162	30	0.615	0.615	0.017	129	0.596	0.603	–1.116	86	0.633	0.690	–8.548	24*
HP_4	0.975	0.908	7.207	2	0.894	0.850	5.007	20	0.822	0.832	–1.122	130	0.878	0.887	–1.091	52	0.864	0.879	–1.767	24
LM_1	1.436	1.428	0.567	16	1.476	1.477	–0.079	32	1.461	1.460	0.116	131	1.462	1.456	0.365	86	1.456	1.473	–1.174	24
$W1M_1$	0.895	0.889	0.665	16	0.849	0.864	–1.812	32	0.871	0.870	0.085	131	0.856	0.853	0.342	86	0.850	0.868	–2.054	24
$W2M_1$	0.904	0.888	1.813	16	0.864	0.871	–0.812	32	0.888	0.885	0.402	131	0.880	0.870	1.107	86	0.893	0.932	–4.289	24*
$W3M_1$	0.978	0.970	0.738	16	0.944	0.978	–3.542	32*	0.977	0.973	0.441	131	0.958	0.960	–0.184	86	0.990	1.001	–1.049	24
LM_2	1.390	1.403	–0.940	16	1.410	1.411	–0.051	32	1.394	1.384	0.730	131	1.393	1.394	–0.075	86	1.415	1.393	1.614	24
$W1M_2$	0.863	0.847	1.826	16	0.809	0.823	–1.775	32	0.841	0.835	0.684	131	0.831	0.825	0.715	86	0.826	0.840	–1.686	24
$W2M_2$	0.853	0.839	1.587	16	0.818	0.828	–1.162	32	0.840	0.840	–0.084	131	0.834	0.830	0.408	86	0.860	0.882	–2.508	24
LM_3	1.211	1.228	–1.385	16	1.276	1.278	–0.161	32	1.255	1.243	1.005	131	1.247	1.250	–0.289	86	1.264	1.268	–0.296	24
WM_3	0.666	0.666	0.094	16	0.633	0.637	–0.549	32	0.647	0.646	0.155	131	0.633	0.642	–1.404	86	0.676	0.696	–2.793	24

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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				
	n	M	min	max	SD	*n*	M	min	max	SD	*n*	M	min	max	SD	*n*	M	min	max	SD
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^4P^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^3M^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^1M^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^4M^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^1M^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_1M_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_4M_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_1M_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
CS1	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

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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				
	n	M	min	max	SD	*n*	M	min	max	SD	*n*	M	min	max	SD	*n*	M	min	max	SD
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
$W1M^1$	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
$W1M^2$	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
$W1M_1$	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
$W1M_2$	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] × 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 oclusal 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, P^4P^4, and M^3M^3), but the sexes just slightly diverged ($P < 0.05$) in the length of upper tooth-row (P^4M^3). 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 (WI_2), second upper molar (in central part, $W2M^2$) and third lower molar (WM^3).

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 (CM_3). 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 ($W3M_1$).

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 (P^4M^3, P_4M_3). Sexes highly diverged in the length characters (LCr, LCb); moderately diverged in mastoidal width (LaM), mandible and lower tooth-row length (LMd, I_1M_3); and slightly diverged in length of tooth-rows (I^1M^3, CM^3, CP^4, CM_3, CP_4). 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, $W2M_2$) and the second lower incisor (LI_2); moderately diverged in the second upper molar diagonal width ($W1M^2$), length and width of the third lower incisor (LI_3, WI_3), length of the second lower premolar (LP_2) and height of lower canine (HC_{inf}); and slightly diverged in some dimensions of the first upper incisor (WI^1, HI^1), molars ($W2M^1$, $W3M^2$, WM3) and height of the second lower incisor (HI_2).

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

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females, with the exception of lower molar-row length (M_1M_3). They highly diverged in skull length (LCr, LCb), braincase dimesions (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 ($W2M_1$).

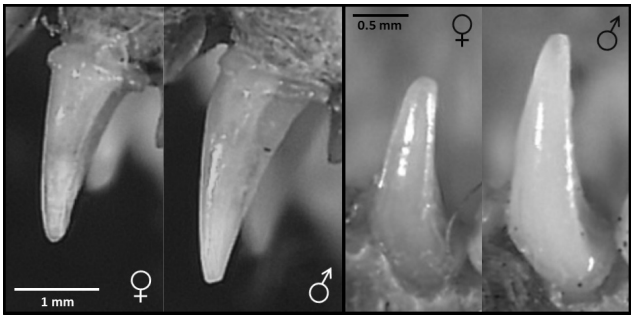


Fig. 2. Sexual size variation in upper (left) and lower (right) canines of bats from eastern Afghanistan.

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 (significantely 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 inversed (the dimensions descreased 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

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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 Europan 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 machanisms leading to development of sexual dimorphism of the respective *Miniopterus* populations

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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 measureable 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 (P2P4inf) 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.

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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.

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