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Phenetic analysis of Old World *Myotis* (Chiroptera: Vespertilionidae) based on dental characters

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Similarities between 42 taxa of genus *Myotis* were studied based on 11 dental characters. The most primitive conditions were found in subgenus *Leuconoe* and in most taxa of subgenus *Selysius*. No clear differences between subgenera *Leuconoe* and *Selysius* were found. Only *Myotis altarium*, *M. ikonnikovi*, *M. mystacinus*, and *M. hosonoi* were found to be distinct from the 13 species studied within subgenus *Selysius*. The subgenus *Myotis* was distinct from the other subgenera in having the most derived conditions.

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Key words: *Myotis*, dental morphology, discrete state characters, cluster analysis

Introduction

Taxonomy should be principally based upon all available metric and discrete-state characters (Findley 1993). However, studies of the Recent bats, which include discrete-state characters, use mainly external morphology, molecular data and only in few cases dental characters (eg Bogdanowicz 1992, Bogdanowicz and Owen 1992, Volleth and Heller 1994, Morales and Bickham 1995). This is contrasts with the paleontological taxonomy of bats, which is mainly based upon tooth morphology (eg Sevilla 1990, Sigé 1991, Czaplewski 1993). This lack of compatibility between neontological and paleontological taxonomy hinders evaluation of species coherence and definitions. A re-evaluation of the taxonomic value of dental morphology on Recent bats suggets that these characters have a higher power of discrimination than traditional external and skeletal characters (Sevilla and Lopez-Martinez 1986).

The aim of this study was to provide dental character distribution of the Recent taxa in the genus *Myotis*. Species of this genus are the most common among fossil microchiropteran remains and are therefore well suited for studies of taxonomy.

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A phenetic analysis of dental characters was used to compare the subgenera. Some phylogenetic suggestion are also given. Taxa from the Old World were selected because bats of genus *Myotis* likely originated there (Findley 1972). Classification of bats to subgenera follows Koopman (1994).

Material and methods

In totals 433 skulls of 42 taxa of the genus *Myotis* were examined (Appendix). Thirteen characters were coding using the terminology of Menu (1985, 1987) and Sevilla and Lopez-Martinez (1986). All characters were checked for intraspecific variability in *Myotis mystacinus* which included the largest number of specimens studied ($n > 50$). Two characters were excluded due to high variability: the number of grooves in upper canines and the shape of the cingulum of P^4 at labial view, leaving 11

Table 1. Morphological characters used in analysis and their coded conditions.

Character	Condition	Code	See Figure
1. First upper incisor I^1	condition 1	0	1
	condition 2	1	
	condition 3	2	
2. Cingular cusplet/cusp at margin of P^4	with well developed cusplet	0	2
	with little cusplet	1	
	absent	2	
3. Heel of P^4	well developed	0	3
	slightly developed	2	
4. First two upper molars M^1 and M^2	with paraloph	0	4
	without paraloph	2	
5. as above	with metaconule	0	4
	without metaconule	2	
6. as above	with metaloph	0	4
	without metaloph	2	
7. as above	with paraconule	0	4
	without paraconule	2	
8. as above	protofossa closed	0	4
	protofossa opened	2	
9. Cingular cusplet of lower C	present	0	5
	absent	2	
10. Cingular platform of lower C	well developed	0	6
	minimally developed	2	
11. Talonid of lower M_3	not reduced	0	7
	reduced	2	

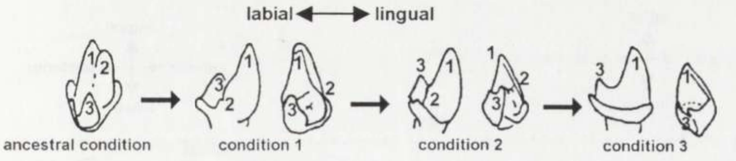

Fig. 1. Development of first upper incisor. Drawings on Figs 1–7 are after Menu (1985).

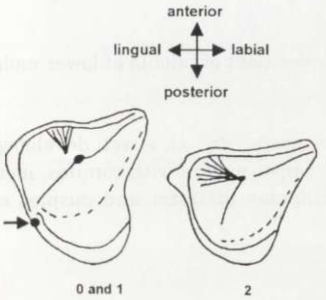

Fig. 2. Development of cusp at margin of P^4 (condition 0 and 1 together).

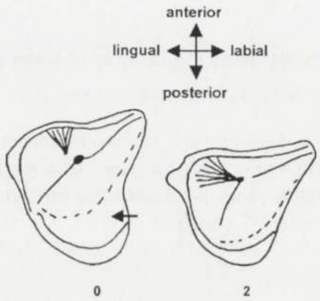

Fig. 3. Development of heel of upper premolar P^4.

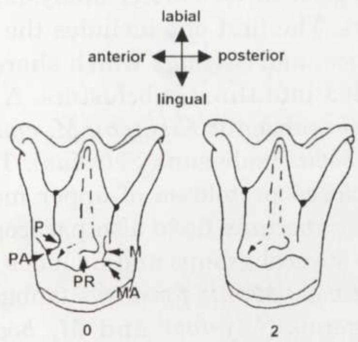

Fig. 4. Development of upper molars M^1 and M^2. PA – paraconule, MA – metaconule, P – paraloph, M – metaloph, PR – protofossa.

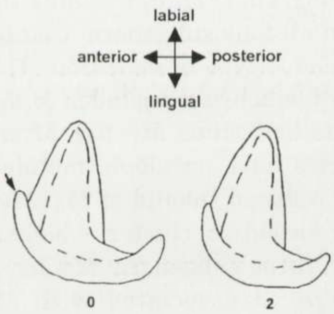

Fig. 5. Development of cingular cusplet of lower canine.

characters for remaining analyses (Table 1). Clustering of the taxa was done by unweighted pair-group using arithmetic averages (UPGMA, Sneath and Sokal 1973) based on simple matching coefficient. The cluster analysis was performed with the NTSYS-pc (version 1.80) sofware package. The cophenetic correlation was used as a measure of goodness of fit for a cluster analysis (Rohlf 1994). The following characters being characteristic for genus *Stehlinia* were defined as ancestral forms and

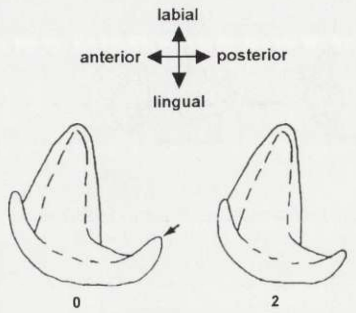

Fig. 6. Development of platform of lower canine.

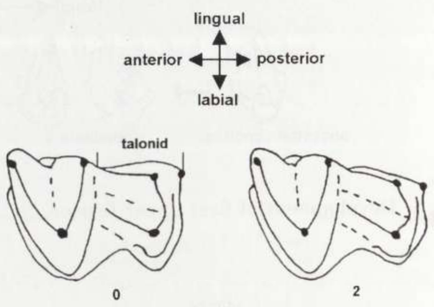

Fig. 7. Development of talonid of lower molar M_3.

checked for development in Recent forms: I^1 – condition 1 (three cusps; Fig. 1); a well developed heel and presence of cingular cusplet at margin of P^4 (Figs 2 and 3); upper molars with conules, metaloph and paraloph (Fig. 4); lower canine with a well developed cingular platform and cusplet on the cingulum (Figs 5 and 6).

Results

Phenetic procedure

The cophenetic correlation (r = 0.83) showed good fit for cluster analysis. The phenogram (Fig. 8) contains three major clusters. The first one includes the taxa from all four subgenera: *Cistugo*, *Myotis*, *Leuconoe*, and *Selysius* which share the *Leuconoe* type of dentition. This cluster is divided into three subclusters. A first small subcluster includes *M. lesueuri, M. seabrai* (subgenus *Cistugo*), *M. emarginatus* (subgenus *Myotis*), *M. annectans* and *M. scotti* (subgenus *Selysius*). These species have paraloph, metaloph, metaconule, closed protofossa of upper molars and reduced talonid of M_3. *Myotis scotti* and *M. annectans* have also paraconule. The second subcluster is bigger and divided into several groups and includes taxa from three subgenera: *Myotis*, *Selysius* and *Leuconoe*. *Myotis formosus* (subgenus *Myotis*) is associated with *M. muricola* (subgenus *Selysius*) and *M. bocagei* (subgenus *Leuconoe*). *Myotis formosus* has metaloph, paraloph and metaconule which is characteristic for subgenus *Leuconoe*. I^1 is provided with three cusps. *Selysius* species within the second subcluster (*M. muricola, M. ridleyi, M. rosseti, M. siligorensis*) have paraconule (the only exception being *M. muricola*), metaconule, paraloph and metaloph on upper molars. *Myotis ridleyi* and *M. rosseti* have the first upper incisor with three cups. *Leuconoe* taxa and one *Selysius* (*M. brandti*) belong to the third subcluster. *Myotis brandti* has good developed paraconule, metaconule, paraloph and metaloph on upper molars.

A second small cluster is formed by *M. bechsteini, M. frater* and *M. ater*. These three species have intermediate type of dentition.

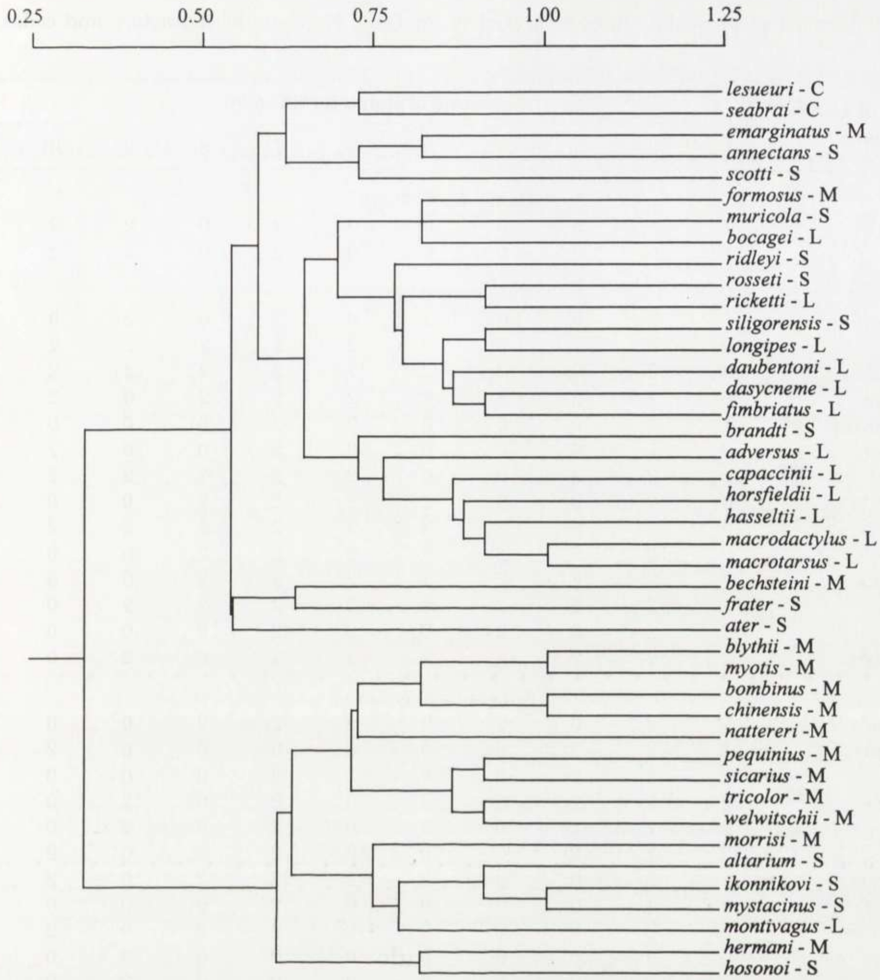

Fig. 8. Phenogram for average taxonomic distances between *Myotis* bat species based on matrix of simple-matching coefficient. Subgenera: C – *Cistugo*, L – *Leuconoe*, M – *Myotis*, S – *Selysius*.

The last third cluster contains the species of the subgenera *Myotis* and *Selysius*. One exception is *M. montivagus* which belongs to subgenus *Leuconoe*. This species has paraloph, but metaloph, metaconule and paraconule are absent. First upper incisor has two cusps. Taxa of this cluster are characteristic by a more derived type of dentition.

The matrix of dental characters (Table 2) shows differences between the subgenus *Myotis* and other subgenera. Most species of the subgenus *Myotis* have derived character states (eg different from those in the genus *Stehlinia*). Subgenus *Leuconoe* shows the most primitive states among all subgenera.

Table 2. Morphological dental characters used in analysis. Numbers of characters and codes as in Table 1.

Species of genus *Myotis*	State of character (in code)										
	1	2	3	4	5	6	7	8	9	10	11
					Subgenus *Cistugo*						
lesueuri	1	1	2	0	0	0	2	0	2	2	2
seabrai	1	0	0	0	0	0	2	0	2	2	0
					Subgenus *Myotis*						
bechsteini	1	2	0	0	2	0	2	0	2	0	0
blythii	0	2	2	2	2	2	2	2	2	2	2
bombinus	0	2	2	2	2	2	2	2	2	2	0
chinensis	0	2	2	2	2	2	2	2	0	2	0
emarginatus	1	2	2	0	0	0	2	0	0	0	2
formosus	0	1	0	0	0	0	2	0	0	2	0
hermani	2	2	2	0	0	2	2	2	2	2	2
morrisi	0	2	0	0	2	2	2	2	0	0	0
myotis	0	2	2	2	2	2	2	2	2	2	2
nattereri	0	2	2	2	0	2	2	2	0	0	0
pequinius	1	2	2	2	2	2	2	2	0	0	2
sicarius	1	2	2	2	2	2	2	2	2	0	2
tricolor	2	2	2	2	2	2	2	2	0	0	2
welwitschii	2	2	2	2	2	2	2	2	2	0	2
					Subgenus *Selysius*						
altarium	2	2	0	2	2	2	2	2	0	0	0
annectans	1	2	2	0	0	0	0	0	0	2	2
ater	2	2	2	2	0	0	2	0	0	0	0
brandti	2	0	2	0	0	0	0	0	2	0	0
frater	2	1	2	0	2	0	2	0	2	0	2
hosonoi	2	2	2	0	0	2	2	2	0	2	0
ikonnikovi	2	2	0	2	2	2	2	2	0	2	0
muricola	2	1	0	0	0	0	2	0	0	0	0
mystacinus	2	2	0	2	2	2	2	2	0	2	0
ridleyi	0	0	0	0	0	0	0	0	0	0	2
rosseti	0	2	0	0	0	0	0	0	0	0	0
scotti	2	1	2	0	0	0	0	0	0	2	2
siligorensis	0	0	0	0	0	0	0	0	2	0	0
					Subgenus *Leuconoe*						
adversus	0	2	2	0	2	0	0	0	2	0	0
bocagei	2	1	0	0	0	0	0	0	0	2	0
capaccinii	0	0	2	0	0	0	0	0	2	2	0
daubentoni	0	1	0	0	0	0	0	0	0	0	0
dasycneme	0	1	0	0	0	0	0	0	2	0	2
fimbriatus	0	1	0	0	0	0	0	0	2	0	0
horsfieldii	0	2	0	0	0	0	0	0	2	2	0
hasseltii	1	2	2	0	0	0	0	0	2	2	0
longipes	0	2	0	0	0	0	0	0	2	0	0
macrodactylus	0	2	2	0	0	0	0	0	2	2	0
macrotarsus	0	2	2	0	0	0	0	0	2	2	0
montivagus	2	2	0	0	2	2	2	2	0	2	0
ricketti	0	2	0	0	0	0	2	0	0	0	0

Discussion

Primitive state of characters

Menu (1987) proposed theoretical basic characters of dentition, which agree with dentition characters of *Stehlinia* (Sigé 1974). This genus, known from Quercy, France (late Eocene, early Oligocene) is assumed to have an ancient vespertlionid's type of dentition (Menu 1985, 1987). Further evolution of dentition can be studied in relation to this genus. Its first upper incisor has three well developed cusps (Fig. 1). The upper premolar P^4 has a cusp and a well developed heel (Figs 2 and 3). The upper molars M^1 and M^2 have well developed paraconule, metaconule with strong metaloph, and paraloph (Fig. 4). The lower canine bears a well developed cingular platform and cusp (Figs 5 and 6). A talonid of M_3 is larger than the trigonid, not reduced (Fig. 7). States of characters characteristic for *Stehlinia* are hence presumed to be primitive. The three cusps of first upper incisor make the most primitive state of character within the genus *Myotis*, but they are, however, different from that of the genus *Stehlinia*. Condition 1 of development of I^1 is called here a primitive state of character.

Description of subgenera

Subgenus *Myotis*: *Myotis myotis* (type species), *M. blythii* and *M. welwitschii* have the most modern type of dentition within subgenus. All characters (except the development of upper first incisors in *M. myotis, M. blythii*, and a well developed cingular platform in lower canine in *M. welwitschii*) are of derived state. *Myotis formosus* has only two derived states of characters, ie 7 and 10 (Table 1). Other characters look like in genus *Stehlinia*.

Subgenus *Selysius*: Development of I^1 (namely, the connection between third and first cusp, and space disappeared) distinguishes this subgenus from *Leuconoe*. Among *Leuconoe* taxa only *M. bocagei* and *M. montivagus* has I^1 in condition 3. *Myotis montivagus*, regarded as belonging to the subgenus *Selysius* by Corbet and Hill (1991), was transferred to the subgenus *Leuconoe* by Koopman (1994). *Myotis mystacinus* and *M. ikonnikovi* have generally the most derived character states within the subgenus. Only three characters have primitive states: a well developed heel on upper P^4, cingular cusplet of lower canine present, and not reduced talonid of lower third molar. Numerous species of the subgenus *Selysius* have dental characters similar to bats of the subgenus *Leuconoe*. For instance, *Myotis annectans, M. brandti, M. ridleyi, M. rosseti, M. scotti*, and *M. siligorensis* have paraconule and metaconule, which are characteristic for *Leuconoe* forms.

Subgenus *Cistugo*: Two African species, *Myotis lesueuri* and *M. seabrai*, belong to this subgenus. Both species have I^1 of intermediate condition 2, ie the second cusp disappears (Fig. 1: condition 2). The primitive character states of both species are: presence of metaconule, paraloph and metaloph, and protofossa closed. *Myotis seabrai* has two additional primitive characters: cusp at margin of P^4 and a well developed talonid. Dentition of *Cistugo* species is of the *Leuconoe* type.

Subgenus *Leuconoe*: Taxa of this subgenus have the most primitive type of dentition within the genus *Myotis*. Only two character states are derived in a majority of *Leuconoe* taxa: lack of cusp at margin of P^4 and at lower canine. All *Leuconoe* taxa have paraconule (except *M. montivagus* and *M. ricketti*). Without any doubt, the presence of conules is a primitive structure. Slaughter (1970) wrote that in course of evolution the bats of genus *Myotis* have lost conules of upper molars. Tate (1941) suggested, that presence of a paraconule is characteristic for *Leuconoe* forms and not for the subgenus *Selysius*. However, almost half of the taxa of subgenus *Selysius* examined here have paraconule (Table 2).

Conclusions

Taxa of subgenus *Myotis* could be separated from those of three other subgenera (Fig. 8, Table 2). Miller and Allen (1928) wrote that this subgenus "is not connected by intermediate stages of structure with any other members of the genus". Except for the development of first upper incisor, the other characters have derived character states in most species of this genus. Menu (1987) includes in the subgenus *Myotis* only two species: *M. myotis* and *M. blythii*. Species of this subgenus are very large, contrary to most species of other subgenera (excluding *M. ricketti*). All representatives of subgenus *Myotis* had lost the paraconule in upper molars. Almost all species are separated in the phenogram (excluding *M. bechsteini, M. formosus* and *M. emarginatus*). *Myotis hermani* is listed as subspecies of *M. formosus* by Koopman (1994), but these species are different in dentitition characters and general size of body.

Most species of subgenera *Selysius* and *Leuconoe* are mixed in the phenogram. Exceptions are *M. altarium, M. ikonnikovi, M. mystacinus, M. hosonai* (*Selysius*), and *M. montivagus* (*Leuconoe*). As was told above, representatives of both subgenera show similarities. Menu (1987) proposed to combine subgenera *Selysius* and *Leuconoe* into one subgenus *Leuconoe*, but his proposition has not been generally accepted. It is difficult to find sharp boundary between these two subgenera based solely on dental characters. *Leuconoe* "*daubentoni*" type of dentition is the most primitive among genus *Myotis*. There is no *Selysius* type of dentition; all *Selysius* species have more or less *Leuconoe* type. Among this subgenus only *M. altarium, M. hosonai, M. ikonnikovi,* and *M. mystacinus* have the more derived character states. *Myotis ikonnikovi* was included to "*muricola*" group by Koopman (1994), but this species is more similar to *M. mystacinus* in dentition structure and shape of skull. Both *Cistugo* species (*M. lesueuri, M. seabrai*) have *Leuconoe* type of dentition, but their wing-glands distinguish this subgenus from the others.

This is suggested to leave three subgenera in genus *Myotis: Myotis, Leuconoe* and *Cistugo*. Bats of subgenus *Selysius* should be included to subgenus *Leuconoe*.

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Appendix. List of examined specimens. Museum acronyms for specimens used in this study are defined in the acknowledgments section. Number in parentheses after localities indicates the number of specimens examined from that locality. Number in parentheses after species name indicates total number examined.

Myotis adversus (7) – Borneo (2): BMNH – 95.8.4.2, 95.8.41; Java (5): 9.1.5.396, 9.1.5.400, 9.1.5.398, 9.1.5.408, 15.2.21.3.

M. altarium (5) – China (5): BMNH – 11.2.1.7, 11.2.1.8, 11.2.1.10–11.2.1.12.

M. annectans (1) – Thailand (1): BMNH – 78.2355.

M. ater (2) – Siberut (2): BMNH – 28.2933, 78.2934.

M. bechsteini (19) – Hungary (9): HNHM – 56.611, 71.2.1, 2937, 73.110.1, 57.37.1, 55.17.1, 71.1.1, 57.89.1, 57.59.1; Germany (3): SMF – 9930, 47445, 3332; Holland (1): RNHL – 4260; France (3): MZP – 1975.730, 1962.1791, 1920.79; Sweden (1): MZL – L935/3995; Poland (2): ISEZ – M/1021/59, M/6235/84.

M. blythii (37) – Austria (13): NHW – 11580, 14328, 18815, 18844, 29410, 29411, 39170–39176; Italy (1): 12065; Slovenija (14): 28832–28845; Spain (9): MZB – 82-7273, 82-6761, 84-9322, 84-9323a, 84-9323b, 84-9324, 84-9326, 94-9328, 85-0226.

M. bombinus (4) – Japan (4): BMNH – 6.1.4.14 (type), 6.1.4.15, 6.1.4.13, 6.1.4.17.

M. brandti (27) – Austria (12): NMW – 29420–29423, 29826, 30395, 30396, 30381, 30404, 30418, 30420, 30429; Czechoslovakia (3): 11163; IZB – 1.187, 1.188; Poland (5): ZBS – 961091510; ISiW – M/15030/10, M/15040/90, M/14616/20, M/15031/10; Switzerland (2): MHNG – 1684.71, 943.71; Holland (3): RNHL – 12011, 12193, 3677; Russia (European part) (2): NMW – 15198, 30426.

M. capaccini (14) – Austria (1): NMW – 33298; Greece (1): 27559; Slovenija (12); 15715–15717, 18924, 30335–30337, 30339–30342, 30380.

M. chinensis (2) – China (1): BMNH – 54.2.8.2 (type); Vietnam (1): HNHM – 32.

M. dasycneme (30) – Hungary (9): HNHM – 56.84.1, 2460/1, 57.171.1, 56.85.1, 56.87.1, 71.3.1, 3741.2, 57.89.1, 54.87.1; Holland (10): RNHL – 12297, 12311, 12267, 11067, 29075, 12276, 11108, 12266, 12289, 12278; Russia (European part) (11): ZISP – 76452, 25770, 25772, 25771, 38540, 25765, 41717, 76453, 72426, 70312, 76451.

M. daubentoni (34) – Austria (19): NMW – 12026, 14630, 29042, 29044–29048, 29451, 29464, 29848, 30390, 30391, 30401, 30414, 30437–30439, 34221; Poland (15): ZBS – 146159, 146160, 150309, 150333–150335, 150338, 150342, 150344, 150345, 150347, 150348, 150391, 150397, 150404.

M. emarginatus (17) – Hungary (9): HNHM – 56.55.2, 2419.1, 71.7.1, 2419.9.3, 56.105.1, 2420/172, 2957.6, 58.41.1, 59.130.1; Bulgaria (1): ZISP – 48067; Holland (5): RNHL – 29061, 29059, 12159, 12173, 12335; Slovenija (1): ZISP – 31422; Italy (1): SMF – 12052.

M. fimbriatus (2) – China (2): BMNH – 70.7.18.9, 10.7.8.10.

M. formosus (11) – Formosa (1): BMNH – 66.6.17.1; India (3): 6.12.2.41, 79.11.21.175, 79.11.21.176; Tibet (1): 15.2.21.14; Taiwan (6): RNHL – 19705, 29021, 20923–20926.

M. frater (11) – Japan (2): ZISP – 59097, 72227; south-eastern Russia (9): 9295, 9303, 77171, 50710, 9309, 71988, 9293, 8888, 9301.

M. hasseltii (16) – Burma (1): BMNH – 78.154; Java (1): 60.319.1378; Thailand (1): 9.10.11.9; Thailand (1): 79.1414; Malaya (1): 68.842; Vietnam (11): HMNH – 73, 74, 76, 82-84, 205, 232, 286, 386, 387.

M. hermani (1) – Indonesia (1): BMNH – 23.12.13.

M. horsfieldii (5) – Celebes (1): BMNH – 73.1804; Java (1): 9.1.5.383; Malaysia (1): 73.616; Thailand (2): 79.1415, 79.1416.

M. hosonoi (3) – Japan (3): BMNH – 70.2523, IZSP: 59098, 59099.

M. ikonnikovi (8) – Baikal (1): IZSP – 5101; south-eastern Russia (5): 5375, 63809, 30451, 77632, 77142; Manchuria (1): 9254; Mongolia (1): 5190.

M. lesueuri (1) – South Africa (1): BMNH – 27.4.13.

M. longipes (22) – Afghanistan (2): IZSP – 58447, 58448; India (20): HNHM – 472–474, 476, 478, 480–483, 493, 499, 501, 502, 504-508, 510, 511.

M. macrodactylus (7) – Japan (7): HZM – 1.2563; BMNH – 6.1.4.6–6.1.4.11.

M. macrotarsus (1) – Philippines (1): BMNH – 978.4.3.

M. montivagus (2) – India (1): BMNH – 1.2563 (type); Malaysia (1) – 83.349.

M. morrisi (1) – Niger (1): BMNH – 84.840.

M. muricola (10) – Borneo (1): HNHM – 2869/23-2; Sumatra (1) – 2869/3; Java (4): BMNH – 6.1.4.7, 6.1.4.8, 9.15.375, 10.4.6.27; Malaysia (4): 1.3.9.6, 65.338–65.340.

M. myotis (30) – Poland (18): ISEZ – M/3024/66, M/3025/66, M/3028/66, M/5591/80–M/5594/80, M/5596/80, M/5597/80, M/5600/80–M/5604/80, M/5611/80, M/5612/80, M/5614/80, M/5617/80, M/5617/80, M/5618/80, M/5621/80, M/5622/80, M/5624/80, M/5626/80–M/5629/80, M/5631/80, M/5632/80, M/6281/85.

M. mystacinus (57) – Austria (23): NMW – 10100, 11578, 11584, 11585, 11894, 12019, 12117, 12121, 12883, 14324, 15128, 15708, 15983, 19951, 27477, 29122, 29125, 34208–34213; Germany (31): SMF – 3324, 3328–3334, 3339, 3528, 4595, 9059, 9065, 9064, 9066, 9068, 9073, 9075, 9076, 9092, 9094, 9066; MAK – 39.790, 46.413, 53.169, 57.195, 79.181–79.184, 79.240; Holland (3): NMW – 16836, 18884, 18884.

M. nattereri (12) – Spain (7): IZB – 84-9317–84-9320, 84-9318b, 84-9318c, 84-9318d; Poland (5): ZBS – 110207, 115826, 115822; NMW – 42510, 42511.

M. pequinius (2) – China (2): BMNH – 8.8.7.3, 26.2.3.4.

M. ricketti (4) – China (3): BMNH – 8.7.25.8, 88.326, 26.11.15.8, 94.1.1.22.

M. ridleyi (5) – Borneo (1): BMNH – 82.553; Malaysia (4): 84.1983, 67.16004, 98.3.13.6, 83.75.

M. rosseti (4) – Thailand (3): HNHM – 2869/5, 2869/51; BMNH – 74.336; Cambodia (1): 68.1194.

M. scotti (3) – Ethiopia (3): BMNH – 27.3.4.6, 60.340, 71.673.

M. seabrai (1) – South Africa (1): BMNH – 25.1.2.6.

M. sicarius (3) – India (1): BMNH – 91.10.7.56 (type); Nepal (2): 23.1.9.4, 23.1.9.5.

M. siligorensis (5) – India (1): HNHM – 763; Vietnam (1): 98; Malaysia (1): BMNH – 67.219; Thailand (2): 79.1417, 21.1.10.19.

M. tricolor (6) – Ethiopia (1): BMNH – 37.2.14.13; Malawi (1): 87.1082; South Africa (1): 14.5.4.2; Uganda (3): 40.741, 40.740, 64.172.

M. welwitschii (3) – South Africa (1): BMNH – 0.11.6.1; Malawi (2): 22.12.17.75, 22.12.17.76.