Molecular phylogeny and morphological revision of *Myotis* bats (Chiroptera: Vespertilionidae) from Taiwan and adjacent China

MANUEL RUEDI¹ ², GÁBOR CSORBA³, LIANG-KONG LIN³ & CHENG-HAN CHOU³,⁴

¹Department of Mammalogy and Ornithology, Natural History Museum of Geneva, Route de Malagnou 1, BP 6434, 1211 Geneva (6), Switzerland. E-mail: manuel.ruedi@ville-ge.ch
²Department of Zoology, Hungarian Natural History Museum, Budapest, Baross u. 13., H-1088. E-mail: csorba@nhmus.hu
³Laboratory of Wildlife Ecology, Department of Biology, Tunghai University, Taichung, Taiwan 407, R.O.C. E-mail: lklin@mail.thu.edu.tw
⁴Division of Zoology, Endemic Species Research Institute, Nantou, Taiwan 552, R.O.C. E-mail: shockhouau@gmail.com

¹Corresponding author

Abstract

In taxonomic accounts, three species of *Myotis* have been traditionally reported to occur on the island of Taiwan: Watase’s bat (*M. formosus watasei* Kishida), the Formosan broad-nosed bat (*M. muricola latirostris* Kishida) and the Formosan mouse-eared bat (*M. adversus taiwanensis* Linde). The discovery in 1997 of an unknown taxon not fitting to the description of any of these species encouraged us to re-examine more thoroughly the systematics and phylogeny of *Myotis* bats inhabiting Taiwan. We used a combination of morphologic and molecular methods to aid the identification of the different taxa from this island and reconstruct their phylogenetic relationships. Multivariate analyses based on 17 craniodental characters of 105 specimens caught across Taiwan and further external characters allowed us to discriminate eight taxa of *Myotinae* co-occurring on this island. A subset of 80 specimens were further sequenced for the cytochrome b gene (1140 bp) and subjected to phylogenetic reconstructions including representative species from adjacent China and from all main lineages of the worldwide *Myotis* radiation. These molecular reconstructions showed that the Myotinae from Taiwan are phylogenetically diverse and are issued from several independent clades. The genetic results were completely congruent with the phenetic groupings based on craniodental and external morphology, as each of the eight Taiwanese taxa proved to be reciprocally monophyletic. Two unnamed taxa that did not fit into any of the known species were described as species new to science. Furthermore the taxon *latirostris* usually associated to the Asian *M. muricola*, was phylogenetically and morphologically distant from any other known *Myotis* and was assigned here to the fossil (Miocene) genus *Submyotodon*. Sub-
myotodon latirostris, M. secundus sp. n. and M. soror sp. n. are endemic species from Taiwan, whereas the other five Myotis are more widespread and also found in the mainland. An identification key is provided to ease the discrimination of these Myotinae species in Taiwan and adjacent China.

**Key words:** Myotinae, Submyotodon, cryptic species, multivariate analysis, cytochrome *b*, taxonomy

**Introduction**

The spectacular discoveries of several new, large mammal species in the Asian fauna during the last decades (Dung et al. 1993; Jenkins et al. 2005; Dawson et al. 2006; Kitchener et al. 2006) indicate that even in well-studied groups, the current biodiversity of this region is underestimated. Bats are a diverse group and comprise a fifth of all extant species of mammals of the world (Simmons 2005), but because many groups are morphologically rather conservative, the exact number of biological species is not well known. The regular discovery of new cryptic species of bats (Csorba & Lee 1999; Kuo et al. 2009; Ruedi et al. 2012; Thong et al. 2012; Kruskop & Borisenko 2013) has been facilitated by the use of molecular methods, which opened access to many valuable characters that could complement traditional morphologic approaches (Goodman et al. 2009; Francis et al. 2010). The underestimate of taxonomic diversity is potentially more severe in such large radiation like *Myotis* bats (more than 103 species recognized; Simmons 2005), that involves karyotypically conservative species (Bickham et al. 2004) but which evolved convergent or parallel morphologies (Ruedi & Mayer 2001; Fenton & Bogdanowicz 2002). Recent global molecular surveys of the phylogenetic relationships of *Myotis* species, indicated that East Asia was not only the probable center of origin for that genus (Ruedi et al. 2013), but is also home to a number of unnamed or taxonomically uncertain taxa (Francis et al. 2010; Ruedi et al. 2013). Taiwan in particular harbors at least three divergent and unnamed forms (Chou 2004; Lin et al. 2004; Ruedi et al. 2013), and one species that could represent even a new genus (Stadelmann et al. 2007; Lack et al. 2010; Ruedi et al. 2013), indicating the need for further taxonomic studies.

Historically, Tate (1941) made one of the first comprehensive taxonomic surveys of Eurasian *Myotis*, which included both continental and insular forms such as those from Taiwan (Formosa at that time). He recognized four species occurring on this island: two belong to the subgenus *Selysius* and were classified in the *mystacinus* section under the name *M. mystacinus orii* Kuroda, 1935, and *M. latirostris* Kishida, 1932, respectively. Tate (1941) further placed *M. taiwanensis* Ärnback-Christie-Linde, 1908 in the subgenus *Leuconoe*, in the *adversus* section and finally classified *M. watasei* Kishida, 1924 in the subgenus *Chrysopterion*. He subsequently (Tate 1947) added *M. flavus* Shamel, 1944 to the latter distinctive subgenus, without commenting whether it was specifically or subspecifically distinct from *M. watasei*. In their major contribution to the classification of Palearctic and Indian mammals, Ellerman and Morrison-Scott (1966) essentially followed the arrangement proposed by Tate, except that *orii* was considered as a junior synonym of *M. mystacinus latirostris* and *watasei* as a subspecies of *M. formosus* (Hodgson, 1835), while *flavus* was considered *incertae sedis*. Corbet and Hill (1992) largely retained this systematic arrangement, but they distinguished *M. muricola* (Gray, 1846) from *M. mystacinus sensu stricto* (s.s.) and transferred *latirostris* and *orii* to junior synonyms of *M. muricola*. They further synonymized *taiwanensis* with the widespread *M. adversus* (Horsfield, 1824).

Until recently, the prevailing classification thus recognized three valid species of *Myotis* for Taiwan, *M. formosus watasei*, *M. muricola latirostris*, and *M. adversus taiwanensis* (Corbet & Hill 1992; Koopman 1994; Simmons 2005). This view was however challenged by recent surveys (Lin et al. 1997) as at least one *Myotis* taxon found in the mountain areas did not fit into any of the three recognized species, and was later referred to as *Myotis* sp. 1 (Chou 2004; Lin et al. 2004). A lowland and mountain form of *M. formosus* were also distinguished and referred to *M. flavus* and *M. watasei*, respectively (Lin et al. 2004; Jiang et al. 2010), suggesting that the current taxonomy and species assignments in Taiwanese *Myotis* do not reflect the real diversity. Molecular studies further challenged the classical taxonomy by showing that *taiwanensis* was inadequately assigned to *M. adversus* and should rather be considered as a species on its own (Han et al. 2010), and that *latirostris* was not related to *M. muricola*, not even to any other species of *Myotis* (Stadelmann et al. 2007; Lack et al. 2010; Ruedi et al. 2013). However, none of these molecular surveys referred the analyzed specimens directly to available type material for a proper systematic arrangement, implying that their taxonomic recommendation could be questionable, as demonstrated in a recent review of species in the *Chrysopterion* subgenus (Csorba et al. 2014; Kuo et al. 2014).
Acknowledgments

We wish to thank authorities from the Yushan National Park, Shei-Pa National Park Taroko National Park and the National Taiwan University for facilitating the collecting permits. We are also grateful to H.-C. Cheng, K.-L. Huang, C.-H. Chang and H.-C. Kuo for their assistance during the field work. The following people kindly provided access to specimens under their care: N. Simmons, E. Westwig (AMNH), P. Jenkins, R. Portela Miquez (BMNH), J.-M. Pons (MNHN), S-I. Kawada, S. Shimoinaba (NSMT), L.-L. Lee (NTU), H.-C. Cheng, S.-W. Chang (TESRI), K. Helgen, D. Lunde (USNM), F. Mayer and N. Lange (ZMB). We thank D. Lunde and R. Moratelli (USNM) for their expert advice. Photo illustrations in this study were prepared by P. Wagneur (MHNG); the drawings were finally elaborated by A. Honfi and Tamas Göröfö (HNHM). We appreciate the very useful comments made by two anonymous reviewers to improve an early version of this manuscript. The research of GC received support from the SYNTHESES Project which is financed by the European Community Research Infrastructure Action under the FP7 "Capacities" Program. Part of this research was also funded by the Yushan National Park, National Taiwan University, and Ministry of Science and Technology, Taiwan ROC.

References


---

**MYOTIS FROM TAIWAN AND ADJACENT CHINA**

*Zootaxa* 3920 (1) © 2015 Magnolia Press · 339