



<http://dx.doi.org/10.11646/zootaxa.3920.2.6>

<http://zoobank.org/urn:lsid:zoobank.org:pub:8B991675-0C48-40D4-87D2-DACA524D17C2>

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

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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-muzzled 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* Ärnäck-Christie-Linde, 1908 in the subgenus *Leuconoe*, in the *adversus* section and finally classified *M. watasei* Kishida, 1924 in the subgenus *Chrysopteron*. 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 Palaearctic 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 *Chrysopteron* 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), Y.-J. Chen (NMNS), 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 Görföl (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 SYNTHESYS 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

- Allen, G.M. (1923) New Chinese bats. *American Museum Novitates*, 85, 1–8.
- Allen, G.M. (1938) *The mammals of China and Mongolia. Vol. II. Part. 1.* The American Museum of Natural History, New York, 620 pp.
- Anderson, J. (1881) *Catalogue of Mammalia in the Indian Museum, Calcutta.* Indian Museum, Calcutta, 223 pp.
- Ärnback-Christie-Linde, A. (1908) A collection of bats from Formosa. *Annals and Magazine of Natural History*, 2, 235–238.
<http://dx.doi.org/10.1080/00222930808692477>
- Bates, P.J.J. & Harrison, D.L. (1997) *Bats of the Indian Subcontinent (Vol. 43).* Harrison Zoological Museum, Sevenoaks, 258 pp.
- Bates, P.J.J., Hendrichsen, D.K., Walston, J.L. & Hayes, B. (1999) A review of the mouse-eared bats (Chiroptera: Vespertilionidae: *Myotis*) from Vietnam with significant new records. *Acta Chiropterologica*, 1, 47–74.
- Benda, P., Faizolâhi, K., Andreas, M., Obuch, J., Reiter, A., Ševčík, M., Uhrin, M., Vallo, P. & Ashrafi, S. (2012) Bats (Mammalia: Chiroptera) of the Eastern Mediterranean and Middle East. Part 10. Bat fauna of Iran. *Acta Societatis Zoologicae Bohemicae*, 76, 163–582.
- Bickham, J.W., Patton, J.C., Schlitter, D.A., Rautenbach, I.L. & Honeycutt, R.L. (2004) Molecular phylogenetics, karyotypic diversity, and partition of the genus *Myotis* (Chiroptera: Vespertilionidae). *Molecular Phylogenetics and Evolution*, 33, 333–338.
<http://dx.doi.org/10.1016/j.ympev.2004.06.012>
- Blyth, E. (1863) *Catalogue of the Mammalia in the Museum Asiatic Society.* Savielle and Cronenburgh, London, 187 pp.
- Borisenko, A.V., Kruskop, S.V. & Ivanova, N.V. (2008) A new mouse-eared bat (Mammalia: Chiroptera: Vespertilionidae) from Vietnam. *Russian Journal of Theriology*, 7, 57–69.
<http://dx.doi.org/10.1515/mamm.2001.65.1.63>
- Bradley, R. & Baker, R. (2001) A test of the genetic species concept: cytochrome b sequences and mammals. *Journal of Mammalogy*, 82, 960–973.
[http://dx.doi.org/10.1644/1545-1542\(2001\)082<0960:atotgs>2.0.co;2](http://dx.doi.org/10.1644/1545-1542(2001)082<0960:atotgs>2.0.co;2)
- Cheng, H.C., Fang, Y.P. & Chou, C.H. (2010) *A photographic guide to the bats of Taiwan.* The Agriculture Committee Taiwan Endemic Species Research Institute, Taipei, 144 pp. [in Chinese]
- Chou, C.-H. (2004) *Taxonomic status of the genus Myotis (Chiroptera: Vespertilionidae) in Taiwan.* Department of Wildlife Ecology, Tunghai University, Tunghai, 115 pp. [in Chinese]
- Corbet, G.B. & Hill, J.E. (1992) *The mammals of the Indomalayan region: a systematic review.* Oxford University Press, Oxford, 488 pp.
<http://dx.doi.org/10.1017/s0030605300020718>
- Csorba, G., Chou, C.-H., Ruedi, M., Görföl, T., Motokawa, M., Wiantoro, S., Thong, V.D., Son, N.T., Lin, L.-K. & Furey, N. (2014) The reds and the yellows: a review of Asian *Chrysopteron* Jentink, 1910 (Chiroptera: Vespertilionidae: *Myotis*). *Journal of Mammalogy*, 95, 663–678.
<http://dx.doi.org/10.1644/13-mamm-a-200>
- Csorba, G. & Lee, L.L. (1999) A new species of vespertilionid bat from Taiwan and a revision of the taxonomic status of *Arielulus* and *Thainycteris* (Chiroptera: Vespertilionidae). *Journal of Zoology*, 248, 361–367.
<http://dx.doi.org/10.1017/s0952836999007086>
- Dawson, M.R., Marivaux, L., Li, C.K., Beard, K.C. & Metais, G. (2006) *Laonastes* and the "Lazarus effect" in recent mammals. *Science*, 311, 1456–1458.

- Dobson, G.E. (1871) Notes on nine new species of Indian and Indo-Chinese Vespertilionidae, with remarks on the synonymy and classification of some other species of the same family. *Proceedings of the Asiatic Society of Bengal*, 1871, 210–215. <http://dx.doi.org/10.1126/science.1124187>
- Dobson, G.E. (1878) *Catalogue of the Chiroptera in the collection of the British Museum*. Taylor & Francis, London, 567 pp. <http://dx.doi.org/10.5962/bhl.title.55341>
- Dung, V.V., Gioa, P.M., Chinh, N.N., Tuoc, D., Arctander, P. & MacKinnon, J. (1993) A new species of living bovid from Vietnam. *Nature*, 363, 443–445. <http://dx.doi.org/10.1038/363443a0>
- Ellerman, J.R. & Morrison-Scott, T.C.S. (1966) *Checklist of Palaearctic and Indian mammals, 1758 to 1946. 2nd Edition*. Alden Press, Oxford, 810 pp. <http://dx.doi.org/10.1126/science.115.2990.431>
- Fenton, M.B. & Bogdanowicz, W. (2002) Relationships between external morphology and foraging behaviour: bats in the genus *Myotis*. *Canadian Journal of Zoology*, 80, 1004–1013. <http://dx.doi.org/10.1139/z02-083>
- Findley, J.S. (1972) Phenetic relationships among bats of the genus *Myotis*. *Systematic Zoology*, 21, 31–52. <http://dx.doi.org/10.2307/2412256>
- Francis, C., Borisenko, A., Ivanova, N., Eger, J., Lim, B., Guillen-Servent, A., Kruskop, S., Mackie, I. & Hebert, P. (2010) The role of DNA barcodes in understanding and conservation of mammal diversity in Southeast Asia. *Plos One*, 5, e12575. <http://dx.doi.org/10.1371/journal.pone.0012575>
- Goodman, S.M., Maminirina, C.P., Weyeneth, N., Bradman, H.M., Christidis, L., Ruedi, M. & Appleton, B. (2009) The use of molecular and morphological characters to resolve the taxonomic identity of cryptic species: the case of *Miniopterus manavi* (Chiroptera: Miniopteridae). *Zoologica Scripta*, 38, 339–363. <http://dx.doi.org/10.1111/j.1463-6409.2008.00377.x>
- Gray, J.E. (1846) *Catalogue of the specimens and drawings of Mammalia and birds of the Nepal and Thibet presented by B.H. Hodgson, Esq. to the British Museum*. Trustees of the British Museum, London, 156 pp. <http://dx.doi.org/10.5962/bhl.title.32709>
- Han, N.J., Zhang, J.S., Reardon, T., Lin, L.K., Zhang, J.P. & Zhang, S.Y. (2010) Revalidation of *Myotis taiwanensis* Ärnäck-Christie-Linde 1908 and its molecular relationship with *M. adversus* (Horsfield 1824) (Vespertilionidae, Chiroptera). *Acta Chiropterologica*, 12, 449–456. <http://dx.doi.org/10.3161/150811010x538016>
- Hodgson, B.H. (1835) Synopsis of the Vespertilionidae of Nepal. *Journal of the Asiatic Society of Bengal*, 4, 699–701.
- Horsfield, T. (1824) *Zoological researches in Java, and the neighbouring islands*. Kingsbury, Parbury & Allen, London, 328 pp. <http://dx.doi.org/10.5962/bhl.title.44848>
- Howell, A.B. (1926) Three new mammals from China. *Proceedings of the Biological Society of Washington*, 39, 137–140.
- Ibáñez, C., García-Mударra, J.L., Ruedi, M., Stadelmann, B. & Juste, J. (2006) The Iberian contribution to cryptic diversity in European bats. *Acta Chiropterologica*, 8, 277–297. [http://dx.doi.org/10.3161/1733-5329\(2006\)8\[277:tictcd\]2.0.co;2](http://dx.doi.org/10.3161/1733-5329(2006)8[277:tictcd]2.0.co;2)
- Imaizumi, Y. (1962) List of type specimens of mammals which are present or had been present in the past in Japan. *Proceedings of the Japanese Society of Systematic Zoology*, 27, 6–10.
- Irwin, D.M., Kocher, T.D. & Wilson, A.C. (1991) Evolution of the cytochrome *b* gene of mammals. *Journal of Molecular Evolution*, 32, 128–144. <http://dx.doi.org/10.1007/bf02515385>
- Jenkins, P.D., Kilpatrick, C.W., Robinson, M.F. & Timmins, R.J. (2005) Morphological and molecular investigations of a new family, genus and species of rodent (Mammalia: Rodentia: Hystricognatha) from Lao PDR. *Systematics and Biodiversity*, 2, 419–454. <http://dx.doi.org/10.1017/s1477200004001549>
- Jiang, T.L., Sun, K.P., Chou, C.H., Zhang, Z.Z. & Feng, J. (2010) First record of *Myotis flavus* (Chiroptera: Vespertilionidae) from mainland China and a reassessment of its taxonomic status. *Zootaxa*, 2414, 41–51.
- Jones, G., Parsons, S., Zhang, S.Y., Stadelmann, B., Benda, P. & Ruedi, M. (2006) Echolocation calls, wing shape, diet and phylogenetic diagnosis of the endemic Chinese bat *Myotis pequinus*. *Acta Chiropterologica*, 8, 451–463. [http://dx.doi.org/10.3161/1733-5329\(2006\)8\[451:ecwsda\]2.0.co;2](http://dx.doi.org/10.3161/1733-5329(2006)8[451:ecwsda]2.0.co;2)
- Kaneko, Y. & Maeda, K. (2002) A list of scientific names and the types of mammals published by Japanese researchers. *Honyurui Kagaku (Mammalian Science)*, 42, 1–21.
- Kawai, K., Nikaido, M., Harada, M., Matsumura, S., Lin, L.K., Wu, Y., Hasegawa, M. & Okada, N. (2003) The status of the Japanese and East Asian bats of the genus *Myotis* (Vespertilionidae) based on mitochondrial sequences. *Molecular Phylogenetics and Evolution*, 28, 297–307. [http://dx.doi.org/10.1016/s1055-7903\(03\)00121-0](http://dx.doi.org/10.1016/s1055-7903(03)00121-0)
- Kim, Y.M., Choi, E.H., Kim, S.K., Jang, K.H., Ryu, S.H. & Hwang, U.W. (2011) Complete mitochondrial genome of the Hodgson's bat *Myotis formosus* (Mammalia, Chiroptera, Vespertilionidae). *Mitochondrial DNA*, 22, 71–73. <http://dx.doi.org/10.3109/19401736.2011.624598>
- Kishida, K. (1924) On the Formosan Chiroptera. *Zoological Magazine*, 36, 30–49. [Tokyo, in Japanese]
- Kishida, K. (1932) Notes on a Formosan whiskered bat. *Lansania*, 4, 153–160.

- Kitchener, A.C., Beaumont, M.A. & Richardson, D. (2006) Geographical variation in the clouded leopard, *Neofelis nebulosa*, reveals two species. *Current Biology*, 16, 2377–2383.
<http://dx.doi.org/10.1016/j.cub.2006.10.066>
- Koopman, K.F. (1994) Chiroptera: Systematics. In: Niethammer, J., Schliemann, H. & Starck, D. (Eds.), *Handbuch der Zoologie*. de Gruyter, Berlin, pp. 100–109.
- Kruskop, S.V. & Borisenko, A.V. (2013) A new species of South-East Asian *Myotis* (Chiroptera: Vespertilionidae), with comments on Vietnamese ‘Whiskered bats’. *Acta Chiropterologica*, 15, 293–305.
<http://dx.doi.org/10.3161/150811013x678937>
- Kruskop, S.V., Borisenko, A.V., Ivanova, N.V., Lim, B.K. & Eger, J.L. (2012) Genetic diversity of northeastern Palaearctic bats as revealed by DNA barcodes. *Acta Chiropterologica*, 14, 1–14.
<http://dx.doi.org/10.3161/150811012x654222>
- Kruskop, S.V. & Tsytsulina, K.A. (2001) A new big-footed mouse-eared bat *Myotis annamiticus* sp. nov. (Vespertilionidae, Chiroptera) from Vietnam. *Mammalia*, 65, 63–72.
<http://dx.doi.org/10.1515/mamm.2001.65.1.63>
- Kuo, H.C., Chen, S.F., Fang, Y.P., Flanders, J. & Rossiter, S.J. (2014) Comparative rangewide phylogeography of four endemic Taiwanese bat species. *Molecular Ecology*, 23, 3566–3586.
<http://dx.doi.org/10.1111/mec.12838>
- Kuo, H.C., Fang, Y.P., Csorba, G. & Lee, L.L. (2009) Three new species of *Murina* (Chiroptera: Vespertilionidae) from Taiwan. *Journal of Mammalogy*, 90, 980–991.
<http://dx.doi.org/10.1644/08-mamm-a-036.1>
- Kuroda, N. (1922) Notes on the mammal fauna of Tsushima and Iki Islands, Japan. *Journal of Mammalogy*, 3, 42–45.
- Kuroda, N. (1935) Formosan Mammals preserved in the collection of Marquis Yamishina. *Journal of Mammalogy*, 16, 277–291.
<http://dx.doi.org/10.2307/1374636>
- Lack, J.B., Roehrs, Z.P., Stanley, C.E. Jr., Ruedi, M. & Van den Bussche, R.A. (2010) Molecular phylogenetics of *Myotis* indicate familial-level divergence for the genus *Cistugo* (Chiroptera). *Journal of Mammalogy*, 91, 976–992.
<http://dx.doi.org/10.1644/09-mamm-a-192.1>
- Lin, L.K., Lee, L.L. & Cheng, H.C. (1997) *Bats of Taiwan (1st ed.)*. National Museum of Natural Sciences, Taipei, 165 pp. [in Chinese]
- Lin, L.K., Lee, L.L. & Cheng, H.C. (2004) *Bats of Taiwan (2nd ed.)*. National Museum of Natural Sciences, Taipei, 177 pp. [in Chinese]
- Mao, X., Zhang, J., Zhang, S. & Rossiter, S.J. (2010a) Historical male-mediated introgression in horseshoe bats revealed by multilocus DNA sequence data. *Molecular Ecology*, 19, 1352–1366.
<http://dx.doi.org/10.1111/j.1365-294x.2010.04560.x>
- Mao, X.G., Zhu, G.J., Zhang, S. & Rossiter, S.J. (2010b) Pleistocene climatic cycling drives intra-specific diversification in the intermediate horseshoe bat (*Rhinolophus affinis*) in Southern China. *Molecular Ecology*, 19, 2754–2769.
<http://dx.doi.org/10.1111/j.1365-294x.2010.04704.x>
- Menu, H. & Sigé, B. (1971) Nyctalodontie et myotodontie, importants caractères de grades évolutifs chez les chiroptères entomophages. *Comptes Rendus de l'Académie des Sciences de Paris*, 272, 1735–1738.
- Milne-Edwards, A. (1872) Mémoire de la faune mammalogique du Tibet Oriental et principalement de la principauté de Moupin. In: Milne-Edwards, H. (Ed), *Recherches pour servir à l'histoire naturelle des mammifères comprenant des considérations sur la classification de ces animaux*. G. Masson, Paris, pp. 231–304.
<http://dx.doi.org/10.5962/bhl.title.59889>
- Mori, T. (1928) Four new species of bats (Vespertilionidae) from Korea. *Annotationes Zoologicae Japonensis*, 11, 389–395.
- Nylander, J.A.A. (2004) MrModeltest v. 2.3. Program distributed by the author. Evolutionary Biology Centre, Uppsala University. Available from: <https://github.com/nylander/MrModeltest2> (accessed 21 October 2011)
- Peters, W. (1870) Catalogue of Mammals of China. In: Swinhoe, R. (Ed.), *Proceedings of the Zoological Society of London*, 3, 615–653.
- R-Core-Team (2014) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. Available from: <http://www.R-project.org> (accessed 11 November 2014)
- Rambaut, A. & Drummond, A.J. (2009) Tracer v1.5. Available from: <http://beast.bio.ed.ac.uk/Tracer> (accessed 17 September 2012)
- Ronquist, F., Teslenko, M., van der Mark, P., Ayres, D.L., Darling, A., Höhna, S., Larget, B., Liu, L., Suchard, M.A. & Huelsenbeck, J.P. (2012) MrBayes 3.2: Efficient Bayesian phylogenetic inference and model choice across a large model space. *Systematic Biology*, 61, 539–542.
<http://dx.doi.org/10.1093/sysbio/sys029>
- Ruedi, M., Biswas, J. & Csorba, G. (2012) Bats from the wet: two new species of Tube-nosed bats (Chiroptera: Vespertilionidae) from Meghalaya, India. *Revue suisse de Zoologie*, 119, 111–135.
- Ruedi, M. & Mayer, F. (2001) Molecular systematics of bats of the genus *Myotis* (Vespertilionidae) suggests deterministic ecomorphological convergences. *Molecular Phylogenetics and Evolution*, 21, 436–448.
<http://dx.doi.org/10.1006/mpev.2001.1017>

- Ruedi, M., Stadelmann, B., Gager, Y., Douzery, E.J.P., Francis, C.M., Lin, L.-K., Guillén-Servent, A. & Cibois, A. (2013) Molecular phylogenetic reconstructions identify East Asia as the cradle for the evolution of the cosmopolitan genus *Myotis* (Mammalia, Chiroptera). *Molecular Phylogenetics and Evolution*, 69, 437–449.
<http://dx.doi.org/10.1016/j.ympev.2013.08.011>
- Sambrook, J.E., Fritsch, F. & Maniatis, T. (1989) *Molecular cloning: a laboratory manual (2nd ed.)*. Cold Spring Harbor Laboratory, Cold Spring Harbor, 888 pp.
- Shamel, H.H. (1944) A new *Myotis* from Formosa. *Journal of Mammalogy*, 25, 191–192.
- Shamel, H.H. (1942) A collection of bats from Thailand (Siam). *Journal of Mammalogy*, 23, 317–328.
<http://dx.doi.org/10.2307/1375002>
- Sikes, R.S. & Gannon, W.L. (2011) Guidelines of the American Society of Mammalogists for the use of wild mammals in research. *Journal of Mammalogy*, 92, 235–253.
<http://dx.doi.org/10.1644/10-mamm-f-355.1>
- Silvestro, D. & Michalak, I. (2012) raxmlGUI: a graphical front-end for RAxML. *Organisms Diversity & Evolution*, 12, 335–337.
<http://dx.doi.org/10.1007/s13127-011-0056-0>
- Simmons, N.B. (2005) Order Chiroptera. In: Wilson, D.E. & Reeder, D.M. (Eds.), *Mammal species of the world. A taxonomic and geographic reference*. Johns Hopkins University Press, Washington, pp. 312–529.
- Stadelmann, B., Herrera, G., Arroyo-Cabrales, J. & Ruedi, M. (2004a) Molecular systematics of the piscivorous bat *Myotis (Pisonyx) vivesi*. *Journal of Mammalogy*, 85, 133–139.
[http://dx.doi.org/10.1644/1545-1542\(2004\)085<0133:msotfb>2.0.co;2](http://dx.doi.org/10.1644/1545-1542(2004)085<0133:msotfb>2.0.co;2)
- Stadelmann, B., Jacobs, D., Schoeman, C. & Ruedi, M. (2004b) Phylogeny of African *Myotis* bats (Chiroptera, Vespertilionidae) inferred from cytochrome *b* sequences. *Acta Chiropterologica*, 6, 177–192.
<http://dx.doi.org/10.3161/001.006.0201>
- Stadelmann, B., Kunz, T.H., Lin, L.K. & Ruedi, M. (2007) Molecular phylogeny of New World *Myotis* (Chiroptera, Vespertilionidae) inferred from mitochondrial and nuclear DNA genes. *Molecular Phylogenetics and Evolution*, 43, 32–48.
<http://dx.doi.org/10.1016/j.ympev.2006.06.019>
- Stamatakis, A. (2006) RAxML-VI-HPC: Maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. *Bioinformatics*, 22, 2688–2690.
<http://dx.doi.org/10.1093/bioinformatics/btl446>
- Swinhoe, R. (1870) Catalogue of the mammals of China (south of the River Yangtze) and of the island of Formosa. *Proceedings of the Zoological Society of London*, 42, 615–652.
- Tamura, K., Peterson, D., Peterson, N., Stecher, G., Nei, M. & Kumar, S. (2013) MEGA6: Molecular Evolutionary Genetics Analysis version 6.0. *Molecular Biology and Evolution*, 30, 2725–2729.
<http://dx.doi.org/10.1093/molbev/mst197>
- Tate, G.H. (1941) A review of the genus *Myotis* (Chiroptera) of Eurasia, with special reference to species occurring in the East Indies. *Bulletin of the American Museum of Natural History*, 78, 537–565.
- Tate, G.H. (1947) *Mammals of Eastern Asia*. MacMillan Co, New York, pp. 45–66.
- Thong, V.D., Puechmaillie, S.J., Denzinger, A., Dietz, C., Csorba, G., Bates, P.J.J., Teeling, E.C. & Schnitzler, H.U. (2012) A new species of *Hipposideros* (Chiroptera: Hipposideridae) from Vietnam. *Journal of Mammalogy*, 93, 1–11.
<http://dx.doi.org/10.1644/11-mamm-a-073.1>
- Tiunov, M.P., Kruskop, S.V. & Feng, J. (2011) A new mouse-eared bat (Mammalia: Chiroptera, Vespertilionidae) from South China. *Acta Chiropterologica*, 13, 271–278.
<http://dx.doi.org/10.3161/150811011x624758>
- Tomes, R.F. (1858) On the characters of four species of bat inhabiting Europe and Asia, and the description of a new species of *Vespertilio* inhabiting Madagascar. *Proceedings of the Zoological Society London*, 1858, 78–90.
- Tomes, R.F. (1859) Descriptions of six hitherto undescribed species of bats. *Proceedings of the Zoological Society of London*, 1859, 68–79.
- Topál, G. (1997) A new mouse-eared bat species, from Nepal, with statistical analyses of some other species of subgenus *Leuconoe* (Chiroptera, Vespertilionidae). *Acta Zoologica Academiae Scientiarum Hungaricae*, 43, 375–402.
- Trouessart, E.-L. (1878) Catalogue des mammifères vivants et fossiles. Chiroptera. *Revue et magazine de zoologie pure et appliquée*, 3, 200–254.
- Trouessart, E.-L. (1897) *Catalogus mammalium tam viventium quam fossilium. Fasciculus I.-II.* Friedländer and Sohn, Berlin, 1469 pp.
- Tsytulina, K., Dick, M.H., Maeda, K. & Masuda, R. (2012) Systematics and phylogeography of the steppe whiskered bat *Myotis aurascens* Kuzyakin, 1935 (Chiroptera, Vespertilionidae). *Russian Journal of Theriology*, 11, 1–20.
- Tsytulina, K. & Strelkov, P.P. (2001) Taxonomy of the *Myotis frater* species group (Vespertilionidae, Chiroptera). *Bonner zoologischer Beiträge*, 50, 15–26.
- Weyeneth, N., Goodman, S.M. & Ruedi, M. (2011) Do diversification models of Madagascar's biota explain the population structure of the endemic bat *Myotis goudoti* (Chiroptera: Vespertilionidae)? *Journal of Biogeography*, 38, 44–54.
<http://dx.doi.org/10.1111/j.1365-2699.2010.02393.x>
- Worthington-Wilmer, J. & Barratt, E. (1996) A non-lethal method of tissue sampling for genetic studies of Chiropterans. *Bat Research News*, 37, 1–3.
- Yoshiyuki, M. (1989) A systematic study of the Japanese chiroptera. *National Science Museum monographs*, 7, 1–242.

- Zhang, Z.Z., Tan, X.Y., Sun, K.P., Liu, S., Xu, L.J. & Feng, J. (2009) Molecular systematics of the Chinese *Myotis* (Chiroptera, Vespertilionidae) inferred from cytochrome-b sequences. *Mammalia*, 73, 323–330.
<http://dx.doi.org/10.1515/mamm.2009.058>
- Ziegler, R. (2003) Bats (Chiroptera, Mammalia) from Middle Miocene karstic fissure fillings of Petersbuch near Eichstätt, Southern Franconian Alb (Bavaria). *Geobios*, 36, 447–490.
[http://dx.doi.org/10.1016/s0016-6995\(03\)00043-3](http://dx.doi.org/10.1016/s0016-6995(03)00043-3)