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# TAXONOMIC REVISION OF THE GENUS *TRIAENOPS* (CHIROPTERA: HIPPOSIDERIDAE) WITH DESCRIPTION OF A NEW SPECIES FROM SOUTHERN ARABIA AND DEFINITIONS OF A NEW GENUS AND TRIBE

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## Abstract

The genus *Triaenops* has been considered monospecific in its African and Middle Eastern range (*T. persicus*), while three other species have been recognised as endemic to Madagascar (*T. menamena*, *T. furculus*, and *T. auritus*), and another to the western Seychelles (*T. pauliani*). We analysed representative samples of *T. persicus* from East Africa and the Middle East using both morphological and molecular genetics approaches and compared them with most of the available type material of species of this genus. Morphological comparisons revealed four distinct morphotypes in the set of examined specimens; one in Africa, the others in the Middle East. The Middle Eastern morphotypes differed mainly in size, while the allopatric African form showed differences in skull shape. Two of three Arabian morphotypes occur in sympatry. Cytochrome *b* gene-based molecular analysis revealed significant divergences (K2P distance 6.4–8.1% in complete cyt *b* sequence) among most of the morphotypes. Therefore, we propose a split of the current *T. persicus* rank into three species: *T. afer* in Africa, and *T. persicus* and *T. parvus* sp. nov. in the Middle East. The results of the molecular analysis also indicated relatively close proximity of the Malagasy *T. menamena* to Arabian *T. persicus*, suggesting a northern route of colonisation of Madagascar from populations from the Middle East or north-eastern Africa as a plausible alternative to presumed colonisation from East Africa. Due to a considerable genetic distance (21.6–26.2% in 731 bp sequence of cyt *b*) and substantial morphological differences from the continental forms of *Triaenops* as well as from Malagasy *T. menamena*, we propose generic status (*Paratriaenops* gen. nov.) for the group of Malagasy species, *T. furculus*, *T. auritus*, and *T. pauliani*. We separated the genera *Triaenops* and *Paratriaenops* gen. nov. from other hipposiderid bats into Triaenopini trib. nov. recognising their isolated position within the family Hipposideridae Lydekker, 1891.

**Key words**: *Triaenops parvus* sp. nov., *Paratriaenops* gen. nov., Triaenopini trib. nov., morphological analysis, genetic analysis, cytochrome b, Middle East, Afrotropics, Madagascar

**Contents**

## Introduction

The hipposiderid genus *Triaenops* Dobson, 1871 is well known for its characteristic noseleaf structure. Its most distinctive features are four tall pointed processes on the strongly cellularised posterior leaf (Fig. 1A–E). Three of them form a trident-like structure on its caudal margin, which is combined with the strap-like projection extending forward from the internarial region of the anterior leaf (D o b s o n 1878, D o r s t 1948, H i l l 1982). The distributional range of this genus covers mostly the Afrotropics including Madagascar, extending marginally into the southern Palaearctic (Fig. 2). The genus occurs from Iran and Pakistan through southern Arabia to East Africa, from Eritrea and Somalia to Zimbabwe and Mozambique, and to Madagascar and some islands of the western Indian Ocean (H a r r i s o n 1955, 1963, 1972, D a l q u e s t 1965, F u n a i o l i & L a n z a 1968, K i n g d o n 1974, L a r g e n et al. 1974, D e B l a s e 1980, K o c k & F e l t e n 1980, H a r r i s o n & B a t e s 1991, H a p p o l d & H a p p o l d 1998, C o t t e r i l l 2001, P e a r c h et al. 2001, T a y l o r 2005, R a n i v o & G o o d m a n 2006, G o o d m a n & R a n i v o 2008, etc.). Isolated records were reported from south-western Congo (Brazzaville) and north-western Angola (A e l l e n & B r o s s e t 1968, C r a w f o r d - C a b r a l 1989).

Within the genus *Triaenops*, five species are currently recognised (S i m m o n s 2005, G o o d m a n & R a n i v o 2008), including a recently described species from southwestern

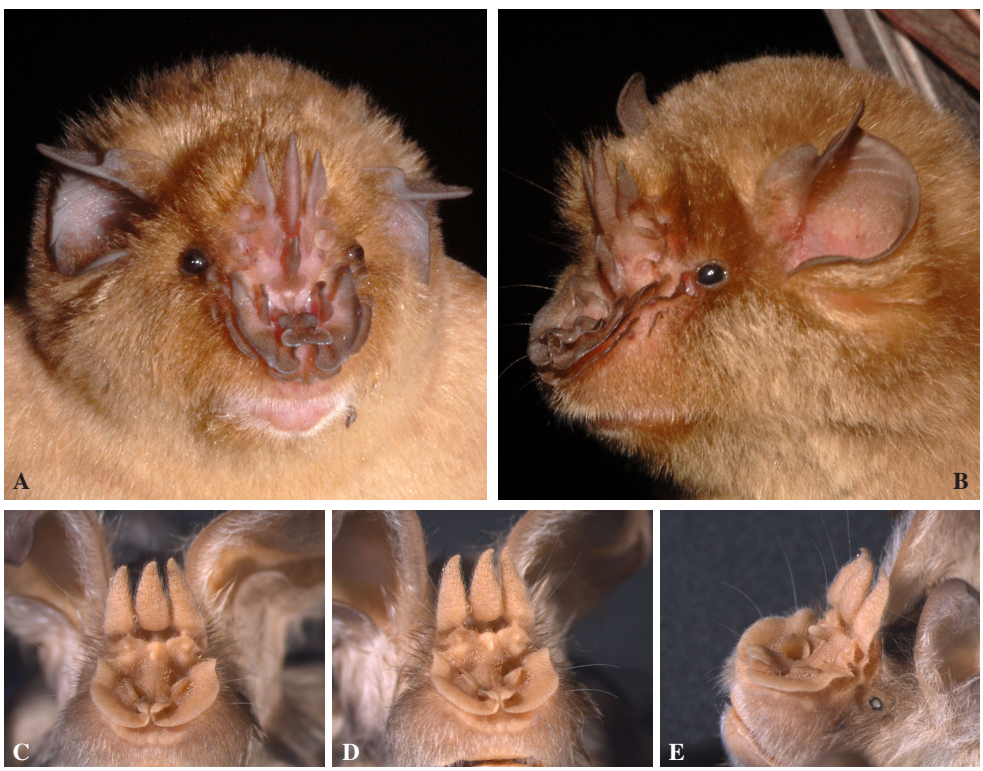


**Fig. 1.** Structure of the noseleaf in two representatives of the genus *Triaenops* s.l. Above – portraits of alive *T. persicus* from Wadi Tuban, SW Yemen, in frontal and lateral views (photos by A. R e i t e r). Below – detailed frontal, lateral and semi-lateral views on the noseleaf in fixed *T. furculus* (MSNG 44891) from Grotte de Sarondrana, SW Madagascar.

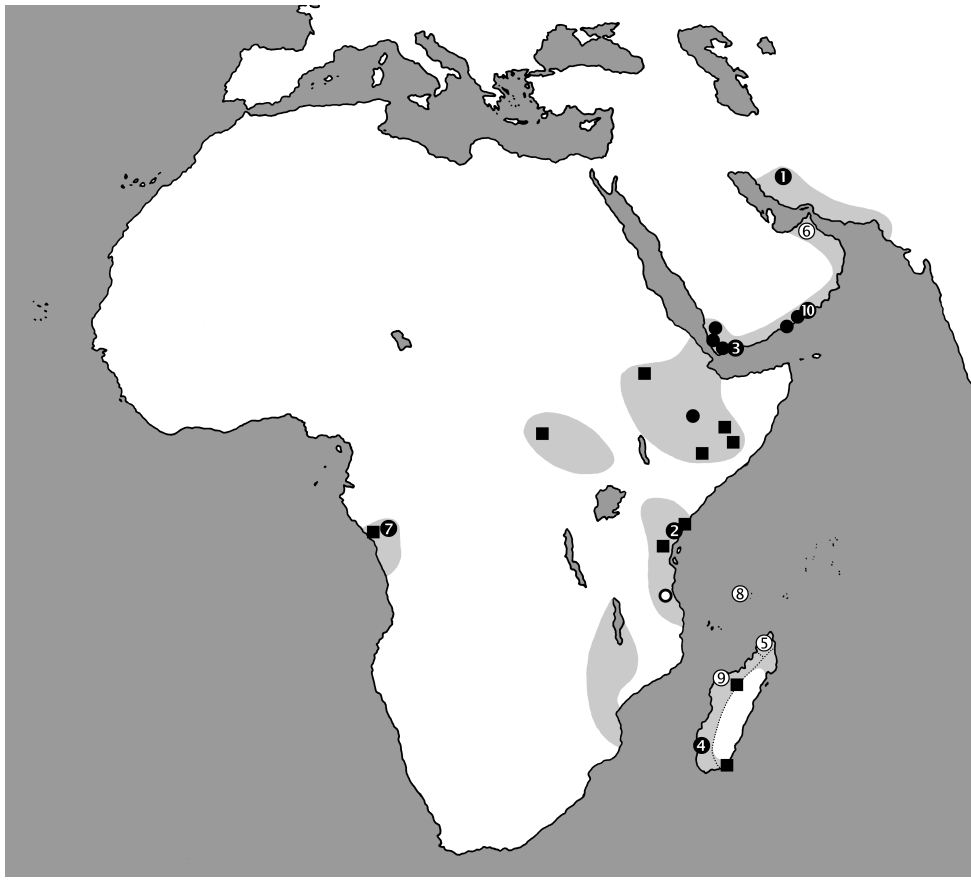


**Fig. 2.** Map of approximate distribution of *Triaenops* bats (after Harrison & Bates 1991, DeBlase 1980, Kock & Felten 1980, Taylor 2005, Russell et al. 2007, and own records) with the sampling sites denoted (in Madagascar, the margins of distribution ranges of *furculus* and *auritus* are delimited by dotted lines). Full circles stay for morphologic and genetic samples, open circle for genetic samples retrieved from the GenBank (except for those from Madagascar – see Russell et al. 2007) and full squares for morphologic samples only. Circles with number show type locality for described forms of the genus *Triaenops* Dobson, 1871; full circles with white number denote those of type material included in the analysis, open circles with black number those not included. Legend: 1 – *persicus* Dobson, 1871; 2 – *afer* Peters, 1877; 3 – *rufus* Milne-Edwards, 1881 and *humbloti* Milne-Edwards, 1881 (type locality uncertain); 4 – *furculus* Trouessart, 1906; 5 – *auritus* Grandidier, 1912; 6 – *macdonaldi* Harrison, 1955; 7 – *majusculus* Allen et Brosset, 1968; 8 – *pauliani* Goodman et Ranivo, 2008; 9 – *menamena* Goodman et Ranivo, 2009; 10 – *parvus* sp. nov.

Seychelles. Three species have been noted to inhabit western and northwestern portions of Madagascar (Simmons 2005, Ranivo & Goodman 2006, Russell et al. 2007): *T. rufus* Milne-Edwards, 1881, *T. furculus* Trouessart, 1906 and *T. auritus* Grandidier, 1912. Since the name *T. rufus* as well as *T. humbloti* Milne-Edwards, 1881 were just recently found unavailable for designation of any Malagasy population of *Triaenops* (Goodman & Ranivo 2009), the respective taxon was described under a new name, *T. menamena* Goodman et Ranivo, 2009. From the extensive belt of savannas of East Africa as well as from Congo and southern parts of the Middle East, only one species is reported, *Triaenops persicus* Dobson, 1871 (Hill 1982, Koopman 1993, 1994, Duff & Lawson 2004, Simmons 2005).

**Table 1.** Review of published opinions on the taxonomic content of the genus *Triaenops* Dobson, 1871. In parentheses are subspecies of the preceding species, in brackets are taxa separated into a genus other than *Triaenops*. Question mark denotes taxonomic position not expressed properly by the respective author

| author | species (subspecies) | | | | | | |
|---|---|---|---|---|---|---|---|
| Dorst (1948) | *furculus* | | | *rufus* | *persicus* | *afer* | *humbloti* |
| Aellen & Brosset (1968) | *furculus* | | | *rufus* | *persicus* (*persicus*, *macdonaldi*, *afer*, *majusculus*) | | |
| Hayman & Hill (1971) | *furculus* | | | *rufus* | *persicus* | | *humbloti* |
| Hill (1982) | *furculus* | | | ? *rufus* | *persicus* (*persicus*, *afer*, *majusculus*, ? *rufus*) | | |
| Koopman (1994) | *furculus* | | | | *persicus* (*persicus*, *afer*, *majusculus*, *rufus*) | | |
| Ranivo & Goodman (2006) | *furculus* | *auritus* | | *rufus* | *persicus* | | |
| Goodman & Ranivo (2008, 2009) | *furculus* | *auritus* | *pauliani* | *menamena* | *persicus* | | |
| present view | [*furculus*] | [*auritus*] | [*pauliani*] | *menamena* | *persicus* | *afer* | *parvus* sp. nov. |

Within the rank of the latter species, *persicus*, four names were proposed and/or synomised and three of them were accepted as those of separate subspecies (H i l l 1982, S i m m o n s 2005). *T. afer* Peters, 1877, described and for a long time considered a separate species (D o b s o n 1878, T r o u e s s a r t 1904, M i l l e r 1907, A l l e n 1939, T a t e 1941, D o r s t 1948, A e l l e n 1957, H a r r i s o n 1961, 1963), is currently regarded a subspecies of *T. persicus* inhabiting the East African part of its range (A e l l e n & B r o s s e t 1968, F u n a i o l i & L a n z a 1968, H a y m a n & H i l l 1971, K i n g d o n 1974, L a r g e n et al. 1974, C o r b e t 1978, H i l l 1982, A g g u n d e y & S c h l i t t e r 1984, K o o p m a n 1994, etc.). Some authors (H a r r i s o n 1964, A e l l e n & B r o s s e t 1968, C o r b e t 1978, H i l l 1982, N a d e r 1990, H a r r i s o n & B a t e s 1991, K o o p m a n 1994, A l - J u m a i l y 1998) also assigned individuals found in the former Aden Protectorate (= SW Yemen) to this subspecies (cf. Y e r b u r y & T h o m a s 1895), however, such opinion does not conform with some earlier authors (e.g., T h o m a s 1900, M i l l e r 1907, D o r s t 1948, E l l e r m a n & M o r r i s o n - S c o t t 1951). *T. p. persicus* is reported to inhabit the Middle East, including Pakistan, Iran, United Arab Emirates (U. A. E.), Oman and possibly Yemen. The subspecies named *T. p. macdonaldi* Harrison, 1955, described from U. A. E., is considered a junior synonym of the former name by majority of the recent authors (D e B l a s e 1980, H i l l 1982, K o o p m a n 1994, S i m m o n s 2005, contra H a r r i s o n 1955, 1956, 1964, A t a l l a h & H a r r i s o n 1967, N a d e r 1990, H a r r i s o n & B a t e s 1991). The geographically well isolated Congolese population of *T. persicus* was described as a separate subspecies, *T. p. majusculus* Aellen et Brosset, 1968. H i l l (1982) and K o o p m a n (1994) regarded also the population of Uganda as belonging to this subspecies. H i l l (1982) discussed a possible subspecific position of the Malagasy form *T. rufus* (= *T. menamena*) under *T. persicus*, this suggestion was, however, not accepted by modern authors (P e t e r s o n et al. 1995, E g e r & M i t c h e l l 2003, D u f f & L a w s o n 2004, S i m m o n s 2005, R a n i v o & G o o d m a n 2006, R u s s e l l et al. 2007, G o o d m a n & R a n i v o 2008, 2009), with the exception of K o o p m a n (1993, 1994).

The subspecies of *T. persicus* were separated by minute differences in pelage coloration and body size (H i l l 1982). Indeed, a clinal trend to an increase in body size from the northeast to the southwest is evident within this species. *T. p. persicus* was reported to be on average the smallest and *T. p. majusculus* the largest form among its subspecies; moreover, the Arabian populations of *T. persicus* were reported to demostrate the largest size variation among all the subspecies (H i l l 1982, H a r r i s o n & B a t e s 1991).

Intrageneric taxonomy of the genus *Triaenops* has been reviewed several times (Table 1), and from two to five species have been recognised within this genus. Here, we present results of analysis of mostly newly collected *Triaenops persicus* (sensu e.g. S i m m o n s 2005 = *T. persicus* s.l.) samples from the northern part of its distribution range, conducted with the aim of defining the intraspecific variation of this variable species and evaluating the validity of the current intraspecific, intrageneric and partly also intrafamilial taxonomy.

## Abbreviations

COLLECTIONS. BCSU = Biological Collection of the Sana'a University, Sana'a, Yemen; DNSM = Durban Natural Science Museum, Durban, South Africa; IVB = Institute of Vertebrate Biology AS CR, Brno, Czech Republic; MNHN = National Museum of Natural History, Paris, France; MSNG = Civil Natural History Museum Giacomo Doria, Genoa, Italy; MZUF = Natural History Museum, Florence, Zoology Section "La Specola", Italy; NMP = National

Museum (Natural History), Prague, Czech Republic; ZMB = Zoological Museum, Humboldt University, Berlin, Germany.

MEASUREMENTS. **External**: LC = head and body length; LCd = tail length; LAt = forearm length; LA = auricle length; LaFE = horseshoe width; G = body weight. **Cranial**: LCr = greatest length of skull incl. praemaxillae; LOc = occipitocanine length of skull; LCc = condylocanine length of skull; LaZ = zygomatic width; LaI = width of interorbital constriction; LaN = neurocranium width; LaM = mastoidal width of skull; ANc = neurocranium height; LBT = largest horizontal length of tympanic bulla; CC = rostral width between upper canines (incl.); $M^3M^3$ = rostral width between third upper molars (incl.); $CM^3$ = length of upper tooth-row between $CM^3$ (incl.); LMd = condylar length of mandible; ACo = height of coronoid process; $CM_3$ = length of lower tooth-row between $CM_3$ (incl.). **Bacular**: LBc = total length of baculum; LBcB = basal length of baculum (i.e. without proximal appendices); LaMin = least width of baculum diaphysis; LaProx = largest width of proximal epiphysis; LaDist = largest width of distal epiphysis (across arms); LArBc1 = length of the longer distal arm; LArBc2 = length of the shorter distal arm; AnBc = angle of bacular arms.

OTHER ABBREVIATIONS. A = alcoholic preparation; f = female; M = mean; m = male; min, max = dimension range margins; S = skull; SD = standard deviation.

## Material and Methods

We analysed representative set of museum specimens of *T. persicus* sensu lato from East Africa, Congo, Madagascar and the Middle East (Yemen) using morphological and molecular genetic approaches. This material was compared with type specimens of the genus *Triaenops* (see also Fig. 2); viz. ZMB syntypes of *Triaenops persicus* Dobson, 1871 (type locality: Shiraz, Persia); ZMB holotype of *Triaenops afer* Peters, 1877 (type locality: Mombaça [= Mombasa, Kenya]; see T u r n i & K o c k 2008); MNHN type series of *Triaenops rufus* Milne-Edwards, 1881 (type locality: Madagascar [= east coast of Madagascar sensu e.g. H i l l 1982, but apparently incorrect, see G o o d m a n & R a n i v o 2009]); MNHN type series of *Triaenops humbloti* Milne-Edwards, 1881 (type locality: Madagascar [= east coast of Madagascar sensu e.g. H i l l 1982, but apparently incorrect, see G o o d m a n & R a n i v o 2009]); MNHN type series of *Triaenops furcula* Trouessart, 1906 (type locality: Grotte de Sarondrana [Sarodrano], [S]W Madagascar); and MNHN type series of *Triaenops persicus majusculus* Aellen et Brosset, 1968 (type locality: Grotte de Doumboula, Loudima (Kouilou), Congo). For material used in the morphological analysis see Appendix 1; for material used in the genetic analysis see Appendix 2.

For morphological comparisons, the museum specimens were examined in the same way as described in our previous studies (e.g. B e n d a et al. 2004a, b). For the morphological analysis, we used mainly the skull metric dimensions in order to describe morphological trends in particular populations rather than individual variation. The specimens were measured in a standardised way with the use of mechanical or optical calipers. The evaluated external, cranial and bacular measurements are listed in the Abbreviations. With exception of the MNHN, MSNG, MZUF and ZMB specimens, the external dimensions were taken from freshly collected material. Bacula were extracted into 6% solution of KOH and coloured with alizarin red. Statistical analyses were performed using Statistica 6.0 software.

In the genetic analysis, we used a subset of museum specimens of *Triaenops persicus* from Ethiopia and Yemen, along with specimens of another two African hipposiderids *Cloeo-*

*tis percivali* Thomas, 1901 and *Asellia tridens* (Geoffroy, 1913), and three African rhinolophid bats *Rhinolophus alcyone* Temminck, 1853, *R. fumigatus* Rüppell, 1842 and *R. landeri* Martin, 1838. We retrieved sequences of East African (Tanzanian) *T. persicus*, Malagasy *T. menamena*, *T. furculus* and *T. auritus*; as well as sequences of *Hipposideros abae* Allen, 1917, *H. caffer* (Sundevall, 1846), *H. jonesi* Hayman, 1947, *Aselliscus stoliczkanus* (Dobson, 1871), *A. tricuspidatus* (Temminck, 1835) and *Coelops frithii* Blyth, 1848 from the GenBank database (cf. R u s s e l l et al. 2007, V a l l o et al. 2008, and L i et al. 2007). Sequences of vespertilionid bats *Vespertilio murinus* (Linnaeus, 1758), *Myotis nattereri* (Kuhl, 1817) and *Myotis schaubi* Kormos, 1934, which were used as an outgroup, were also taken from the GenBank (cf. R u e d i & M a y e r 2001). For specimens and sequences see Appendix 2.

Sequences for phylogenetic analysis were obtained by standard laboratory procedures. Genomic DNA was extracted from alcohol preserved tissue samples with a DNA Blood and Tissue Kit (Qiagen) following the manufacturer's protocol. A complete sequence of the mitochondrial gene for cytochrome *b* (cyt *b*) was PCR amplified using primers F1 (modified; 5'-CCACGACCAATGACAYGAAAA-3') and R1 (5'-CCTTTTCTGGTTTACAAGACCAG-3') from S a k a i et al. (2003) in 50 $\mu$l reaction volume containing 800 $\mu$M dNTP, 200 $\mu$M of each primer, 1U of HotMaster *Taq* DNA polymerase with an appropriate 10× buffer (Eppendorf), and 2–5 $\mu$l of extracted DNA. Reaction conditions were 3 min initial denaturation at 94 °C, 35 cycles of 40 s denaturation at 94 °C, 40 s annealing at 50 °C and 90 s extension at 65 °C, and 5 min final extension at 65 °C. Products were purified using QIAquick PCR Purification Kit (Qiagen), and sequenced commercially in both directions on an ABI 3730XL sequencing machine with the same primers and BigDye Terminator Sequencing Kit (Applied Biosystems). Two ca. 800 bp-long partially overlapping fragments obtained were assembled in Sequencher (GeneCodes) into complete sequences of cyt *b* (1140 bp). Final sequences were submitted to the GenBank database under accession numbers EU798748–EU798758 and FJ457612–FJ457617.

Sequences were aligned in BioEdit 7.0 (H a l l 1999). Alignment of 1140 bp was built from newly obtained sequences of *Triaenops persicus* and *Cloeotis percivali*, and was used for assessment of the genetic variation. Sequences of *Triaenops* species retrieved from the GenBank were then added to the new 1140 bp haplotypes and the alignment was trimmed to 731 bp, which was the length of the GenBank *Triaenops* sequences. Redundant 731 bp haplotypes, which appeared after trimming the new 1140 bp sequences, were omitted. This *Triaenops* dataset was used for inferring phylogenetic relationships within current content of the genus *Triaenops*. After this analysis, *Triaenops* sequences were reduced to one of each phylogroup and sequences of the other species were added. This extended dataset was used for inferring phylogenetic position of *Triaenops* species within the family Hipposideridae. Percent genetic divergences among haplotypes were based on Kimura two-parameter (K2P; K i m u r a 1980) distances, which are considered to be a 'standard' measure for comparison with other studies on bats (B r a d l e y & B a k e r 2001).

Phylogenetic trees were computed in programs PAUP* 4.10b (Sinauer Associates) and MrBayes 3.1.2 (R o n q u i s t & H u e l s e n b e c k 2003). The *Triaenops* dataset was analysed using maximum parsimony (MP), maximum likelihood (ML) and Bayesian methods. MP and ML trees were heuristically searched with 100 random additions of sequences and tree bisection-reconnection branch-swapping algorithm (TBR). MP tree was originally searched with all characters equally weighted. ML tree was computed under the Hasegawa-Kishino-Yano model of evolution (H a s e g a w a et al. 1985) with a proportion of invariable sites

and Γ-distributed among-site rate variation (HKY+I+Γ; transition to transversion ratio ts/tv=6.4205, proportion of invariable sites I=0.5205, shape parameter of the Γ-distribution α=1.5379), as suggested by the program Modeltest 3.7 (P o s a d a & C r a n d a l l 1998) under AIC criterion. Support for MP tree was checked by 1000× bootstrapping, for ML tree by 300× bootstrapping of 20 sequence additions only. Bayesian analysis was carried out in two simultaneous MCMC runs with default heating values and flat priors. Each run consisted of 4 Metropolis-coupled chains run for $10^6$ generations and sampled each 100 generations, with burn-in set to 25%. For testing of alternative topologies, Templeton (T e m p l e t o n 1983) and Shimodaira-Hasegawa (SH; S h i m o d a i r a & H a s e g a w a 1999) tests were conducted as implemented in the PAUP*. The SH test was carried out using RELL resampling algorithm and 1000 replicates. Relevant constraints were used in heuristic searches of trees under the same conditions as in the unconstrained ones.

Analysis of the extended dataset, which included other species of families Hipposideridae and Rhinolophidae, also started with the MP method. To cope with a high sequence variability in the dataset and assumed transition bias, transversions were weighted 5 times to transitions based on the ML estimate of ts/tv on MP tree. Both MP and weighted MP (wMP) trees were searched as in the analysis of the *Triaenops* dataset, including support of topology. Phylogeny was further inferred using maximum likelihood (ML) and Bayesian methods. The ML tree was heuristically searched with 100 random additions of sequences and the TBR swapping algorithm under the HKY+I+Γ model of evolution (ts/tv=6.8762, I=0.4984 and α=0.8119). This model was chosen as a simpler but reasonable alternative to more complex models (3rd in order after TVM+I+Γ and GTR+I+Γ) suggested under the AIC criterion in Modeltest 3.7, because of less parameters (6; in the two more complex models 9 and 10, respectively) needed to be estimated from a rather low number of sites analyzed (731 bp). Support for its topology was assessed by 300× bootstrapping of 20 random sequence additions only. Bayesian analysis was carried out under the same model of evolution as ML, and under the same conditions as given for the *Triaenops* dataset.

Approximate dates of evolutionary splits were estimated from a linearized tree (T a k e z a k i et al. 1995), computed under ML criterion with molecular clock enforced. The assumption of clock-like evolution for the dataset was tested with the likelihood ratio test between trees with and without molecular clock. Calibration of the molecular clock was based on the split of Rhinolophidae and Hipposideridae set approximately to 40 MA (= Mega Annum), according to estimation range of 43–37 MA (R e m y et al. 1987, S i m m o n s & G e i s l e r 1998).

## Results

### M o r p h o l o g i c a l c o m p a r i s o n

Analysis of body and skull dimensions showed several more or less distinct morphotypes within the examined set of samples. According to a mere comparison of skull dimensions, three size types appeared among the examined geographical samples of specimens, however, they mostly overlapped in their measurement ranges (Fig. 3, Table 2); (1) small-sized bats from Madagascar (LAt 42.5–52.6 mm; LOc 16.9–18.7 mm; $CM^3$ 5.9–6.5 mm) composed of two nominate species, *T. furculus* and *T. menamena*, (2) large-sized bats from Africa (LAt 50.9–57.5 mm; LOc 17.9–20.5 mm; $CM^3$ 6.3–7.5 mm), and (3) the Middle Eastern bats with an extreme size variation stretching over the ranges of the two preceding groups (LAt 44.7–

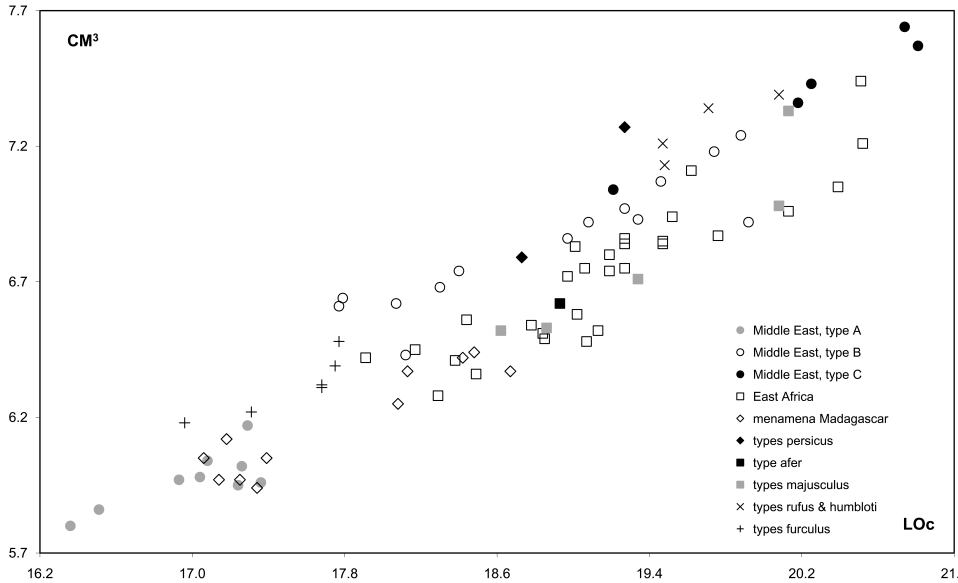


**Fig. 3.** Bivariate plot of compared *Triaenops* samples: occipitocanine length (LOc) against rostral length of the upper tooth-row ($CM^3$).

57.3 mm; LOc 16.3–20.8 mm; $CM^3$ 5.8–7.7 mm). The Malagasy and African size types do not vary much in size, showing just one third and two thirds of the size variation range shown by the Middle Eastern size type, respectively.

The bats of the African size type showed relatively short and wide rostra ($CM^3$/LOc 0.34–0.36 [M 0.351]; CC/LOc 0.24–0.28 [M 0.262]; CC/$CM^3$ 0.67–0.79 [M 0.747]) and relatively and absolutely rather large tympanic bullae (LBT/LOc 0.15–0.17 [M 0.158]). The dimensions and ratios of the type specimen of *T. afer* Peters, 1877 from Kenya as well as of the type specimens of *T. persicus majusculus* Aellen et Brosset, 1968 from Congo (Figs. 3 and 4; Tables 2 and 3) fall well into the dimensional ranges of the African morphotype. Some specimens from the *majusculus* type series showed rather larger forearm lengths (up to 59.5 mm), however, average length in that series was 56.0 mm, i.e. a lower value than the average value in the African group as a whole (Table 2).

The bats of the Malagasy size type showed relatively short but rather narrow rostra ($CM^3$/LOc 0.34–0.37 [M 0.353]; CC/LOc 0.23–0.26 [M 0.252]; CC/$CM^3$ 0.67–0.76 [M 0.714]) and also relatively and absolutely large tympanic bullae (LBT/LOc 0.15–0.18 [M 0.162]). However, the samples (type series) of *T. furculus* showed relatively longer and on average also narrower rostra than those of *T. menamena*.

Within the Middle Eastern set there were bats with both relatively short and rather narrow rostra (the specimens were absolutely smaller in size) and also with relatively long and rather wide rostra (the specimens absolutely larger in size) ($CM^3$/LOc 0.34–0.37 [M 0.360]; CC/LOc 0.24–0.28 [M 0.256]; CC/$CM^3$ 0.67–0.75 [M 0.712]; Fig. 4, Table 2); this group of samples as a whole showed relatively small tympanic bullae (LBT/LOc 0.14–0.17 [M 0.157]).

The Middle Eastern group was, however, represented by specimens of three size groups according to their geographic origin with either no dimensional overlap or very small dimensional overlap, respectively (Fig. 3, Table 2). (1) Group of six individuals collected in western Yemen (NMP 92275–92279, BCSU pb3123) were of the largest skull size within the whole

**Table 2.** Body and skull dimensions (in millimetres) of the examined samples. External dimensions other than forearm length were taken only from Middle Eastern samples. See Abbreviations for explanation of dimension abbreviations

| | Middle East, morphotype A | | | | | Middle East, morphotype B | | | | | Middle East, morphotype C | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | *n* | **M** | min | max | SD | *n* | **M** | min | max | SD | n | **M** | min | max | SD |
| LC | *10* | **55.2** | 52 | 57 | 1.476 | *16* | **61.25** | 56.0 | 64.0 | 2.864 | *6* | **69.2** | 63 | 72 | 3.189 |
| LCd | *10* | **31.8** | 30 | 34 | 1.317 | *16* | **33.25** | 29.0 | 35.0 | 1.693 | *6* | **35.7** | 33 | 38 | 1.862 |
| LAt | *10* | **46.98** | 44.7 | 48.1 | 1.029 | *16* | **51.73** | 48.0 | 55.1 | 1.949 | *6* | **56.08** | 54.7 | 57.3 | 0.911 |
| LA | *10* | **12.69** | 11.4 | 13.9 | 0.758 | *16* | **14.74** | 13.6 | 16.2 | 0.804 | *6* | **15.73** | 14.4 | 17.4 | 1.258 |
| LaFE | *10* | **7.90** | 7.4 | 8.3 | 0.291 | *16* | **9.36** | 8.6 | 9.8 | 0.329 | *6* | **9.92** | 9.2 | 10.9 | 0.643 |
| LCr | *9* | **17.57** | 16.83 | 17.97 | 0.369 | *14* | **19.61** | 18.38 | 20.92 | 0.850 | *5* | **21.06** | 19.97 | 21.76 | 0.744 |
| LOc | *9* | **17.01** | 16.36 | 17.36 | 0.354 | *14* | **18.87** | 17.77 | 19.92 | 0.774 | *5* | **20.24** | 19.21 | 20.81 | 0.640 |
| LCc | *9* | **14.95** | 14.41 | 15.25 | 0.310 | *14* | **16.63** | 15.62 | 17.61 | 0.694 | *5* | **17.81** | 16.68 | 18.27 | 0.656 |
| LaZ | *9* | **7.80** | 7.66 | 7.93 | 0.094 | *14* | **8.85** | 8.44 | 9.57 | 0.343 | *5* | **9.42** | 8.76 | 9.84 | 0.398 |
| LaI | *9* | **2.37** | 2.27 | 2.48 | 0.072 | *14* | **2.68** | 2.52 | 2.89 | 0.121 | *5* | **2.78** | 2.68 | 2.91 | 0.109 |
| LaN | *9* | **6.80** | 6.68 | 7.00 | 0.100 | *14* | **7.42** | 7.05 | 7.67 | 0.166 | *5* | **7.80** | 7.59 | 8.11 | 0.213 |
| LaM | *9* | **7.85** | 7.59 | 8.02 | 0.138 | *14* | **8.64** | 8.14 | 9.18 | 0.263 | *5* | **9.16** | 8.81 | 9.42 | 0.228 |
| ANc | *9* | **6.10** | 5.88 | 6.32 | 0.139 | *14* | **6.84** | 6.41 | 7.36 | 0.285 | *5* | **7.23** | 6.85 | 7.37 | 0.221 |
| LBT | *9* | **2.75** | 2.64 | 2.87 | 0.079 | *14* | **2.93** | 2.68 | 3.14 | 0.147 | *5* | **3.16** | 3.04 | 3.36 | 0.124 |
| CC | *9* | **4.29** | 4.14 | 4.47 | 0.109 | *14* | **4.83** | 4.33 | 5.20 | 0.287 | *5* | **5.34** | 4.82 | 5.73 | 0.365 |
| $M^3M^3$ | *9* | **5.90** | 5.74 | 6.03 | 0.081 | *14* | **6.66** | 6.40 | 7.24 | 0.219 | *5* | **7.18** | 6.66 | 7.54 | 0.339 |
| $CM^3$ | *9* | **5.97** | 5.80 | 6.17 | 0.105 | *14* | **6.84** | 6.43 | 7.24 | 0.234 | *5* | **7.41** | 7.04 | 7.64 | 0.234 |
| LMd | *9* | **10.53** | 10.02 | 10.92 | 0.288 | *14* | **11.97** | 11.26 | 12.88 | 0.500 | *5* | **12.93** | 11.88 | 13.46 | 0.637 |
| ACo | *9* | **2.21** | 2.11 | 2.29 | 0.063 | *14* | **2.67** | 2.44 | 2.94 | 0.162 | *5* | **2.94** | 2.64 | 3.13 | 0.192 |
| $CM_3$ | *9* | **6.43** | 6.21 | 6.58 | 0.135 | *14* | **7.34** | 6.92 | 7.89 | 0.273 | *5* | **7.93** | 7.41 | 8.17 | 0.308 |
| $CM^3$/LOc | *9* | **0.351** | 0.343 | 0.357 | 0.005 | *14* | **0.363** | 0.347 | 0.373 | 0.006 | *5* | **0.366** | 0.364 | 0.368 | 0.002 |
| CC/LOc | *9* | **0.252** | 0.244 | 0.262 | 0.006 | *14* | **0.256** | 0.239 | 0.267 | 0.007 | *5* | **0.264** | 0.251 | 0.276 | 0.010 |
| CC/$CM^3$ | *9* | **0.718** | 0.690 | 0.743 | 0.018 | *14* | **0.706** | 0.670 | 0.739 | 0.022 | *5* | **0.720** | 0.685 | 0.750 | 0.027 |
| LBT/LOc | *9* | **0.162** | 0.153 | 0.167 | 0.005 | *14* | **0.155** | 0.143 | 0.161 | 0.005 | *5* | **0.156** | 0.152 | 0.161 | 0.004 |
| LaI/LOc | *9* | **0.139** | 0.132 | 0.149 | 0.006 | *14* | **0.142** | 0.127 | 0.154 | 0.007 | *5* | **0.138** | 0.129 | 0.144 | 0.006 |
| LaN/LOc | *9* | **0.400** | 0.390 | 0.411 | 0.008 | *14* | **0.394** | 0.376 | 0.418 | 0.012 | *5* | **0.386** | 0.369 | 0.395 | 0.010 |
| LaM/LOc | *9* | **0.462** | 0.455 | 0.470 | 0.006 | *14* | **0.458** | 0.439 | 0.472 | 0.008 | *5* | **0.453** | 0.447 | 0.459 | 0.004 |
| ANc/LOc | *9* | **0.359** | 0.346 | 0.371 | 0.009 | *14* | **0.363** | 0.352 | 0.373 | 0.007 | *5* | **0.357** | 0.354 | 0.365 | 0.005 |

set of compared *Triaenops* bats (LAt 54.7–57.3 mm; LOc 19.2–20.8 mm; $CM^3$ 7.0–7.7 mm); this group overlapped in longitudinal skull dimensions with the largest individuals of the African morphotype (Fig. 3, Table 2). (2) Group of medium-sized to large specimens (NMP 92253–92263, 92266, 92271, 92273, BCSU pb3037, pb3038) from south-eastern Yemen (LAt 48.0–55.1 mm; LOc 17.7–19.9 mm; $CM^3$ 6.4–7.3 mm; Table 2) conformed in size with the syntypes of *T. persicus* Dobson, 1871 from Iran (Table 3) and also with published dimensions of *T. persicus* from the Middle East (see H a r r i s o n 1955, 1964, D e B l a s e 1980, H i l l 1982, H a r r i s o n & B a t e s 1991, etc.). The dimensions of the type specimens of *T. rufus* Milne-Edwards, 1881 and *T. humbloti* Milne-Edwards, 1881 (LAt 51.5–56.1 mm; LOc 19.4–20.1 mm; $CM^3$ 7.1–7.4 mm) fitted into the range of dimensional overlap of these medium-sized bats with the largest ones. (3) Group of small individuals coming from the south-eastern part of Yemen (NMP 92264, 92265, 92267–92270, 92272, 92274, BCSU pb3009, pb3010), i.e. an area of sympatry with the medium-sized bats, demonstrated the smallest dimensions within the compared set of bats (LAt 44.7–48.1 mm; LOc 16.4–17.4 mm; $CM^3$ 5.8–6.2 mm) (Table 2).

**Table 2.** continued

| | East Africa | | | | | Madagascar (*T. menamena*) | | | | | Madagascar (*T. furculus*) | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | *n* | **M** | min | max | SD | *n* | **M** | min | max | SD | n | **M** | min | max | SD |
| LAt | *27* | **54.01** | 50.9 | 57.5 | 1.791 | *5* | **49.70** | 47.6 | 52.6 | 1.926 | *15* | **44.90** | 42.5 | 47.3 | 1.435 |
| LCr | *28* | **19.75** | 18.69 | 21.05 | 0.652 | *11* | **18.18** | 17.38 | 19.28 | 0.628 | *5* | **18.05** | 17.52 | 18.33 | 0.350 |
| LOc | *30* | **19.17** | 17.91 | 20.52 | 0.654 | *11* | **17.74** | 17.06 | 18.67 | 0.617 | *6* | **17.53** | 16.96 | 17.77 | 0.324 |
| LCc | *30* | **16.72** | 15.61 | 18.13 | 0.644 | *11* | **15.39** | 14.74 | 16.13 | 0.573 | *5* | **15.34** | 14.59 | 15.74 | 0.444 |
| LaZ | *29* | **8.97** | 8.49 | 9.72 | 0.330 | *11* | **8.32** | 7.69 | 8.78 | 0.333 | *6* | **8.48** | 8.13 | 8.60 | 0.177 |
| LaI | *30* | **2.71** | 2.38 | 3.12 | 0.188 | *11* | **2.50** | 2.22 | 2.65 | 0.127 | *6* | **2.04** | 1.88 | 2.28 | 0.141 |
| LaN | *30* | **7.36** | 7.04 | 7.85 | 0.223 | *11* | **7.15** | 6.88 | 7.45 | 0.198 | *6* | **7.50** | 7.33 | 7.72 | 0.165 |
| LaM | *30* | **8.68** | 8.32 | 9.21 | 0.245 | *11* | **8.21** | 7.94 | 8.65 | 0.228 | *6* | **8.69** | 8.37 | 8.87 | 0.178 |
| ANc | *30* | **6.75** | 6.36 | 7.41 | 0.252 | *10* | **6.05** | 5.51 | 6.49 | 0.302 | *5* | **5.29** | 5.08 | 5.49 | 0.192 |
| LBT | *30* | **3.02** | 2.78 | 3.38 | 0.126 | *11* | **2.90** | 2.69 | 3.30 | 0.161 | *4* | **2.76** | 2.66 | 2.92 | 0.118 |
| CC | *30* | **5.03** | 4.52 | 5.53 | 0.257 | *11* | **4.46** | 4.08 | 4.76 | 0.221 | *11* | **4.44** | 4.11 | 4.73 | 0.165 |
| $M^3M^3$ | *30* | **6.66** | 6.22 | 7.34 | 0.252 | *11* | **6.23** | 5.89 | 6.56 | 0.214 | *5* | **6.23** | 5.99 | 6.37 | 0.148 |
| $CM^3$ | *30* | **6.73** | 6.28 | 7.44 | 0.269 | *11* | **6.18** | 5.94 | 6.44 | 0.196 | *6* | **6.32** | 6.18 | 6.48 | 0.110 |
| LMd | *30* | **11.90** | 11.21 | 12.93 | 0.463 | *11* | **11.03** | 10.57 | 11.69 | 0.420 | *6* | **11.17** | 10.54 | 11.42 | 0.320 |
| ACo | *30* | **2.76** | 2.46 | 3.18 | 0.164 | *11* | **2.52** | 2.21 | 2.75 | 0.154 | *6* | **2.44** | 2.31 | 2.51 | 0.079 |
| $CM_3$ | *30* | **7.20** | 6.74 | 7.96 | 0.301 | *11* | **6.62** | 6.36 | 7.02 | 0.243 | *6* | **6.63** | 6.44 | 6.78 | 0.109 |
| $CM^3$/LOc | *30* | **0.351** | 0.340 | 0.363 | 0.006 | *11* | **0.348** | 0.341 | 0.356 | 0.005 | *6* | **0.360** | 0.357 | 0.365 | 0.003 |
| CC/LOc | *30* | **0.262** | 0.237 | 0.281 | 0.010 | *11* | **0.252** | 0.221 | 0.263 | 0.011 | *5* | **0.250** | 0.242 | 0.256 | 0.006 |
| $CC/CM^3$ | *30* | **0.747** | 0.670 | 0.791 | 0.025 | *11* | **0.723** | 0.634 | 0.760 | 0.033 | *5* | **0.692** | 0.665 | 0.714 | 0.020 |
| LBT/LOc | *30* | **0.158** | 0.146 | 0.171 | 0.006 | *11* | **0.163** | 0.155 | 0.177 | 0.006 | *4* | **0.158** | 0.152 | 0.165 | 0.006 |
| LaI/LOc | *30* | **0.142** | 0.125 | 0.156 | 0.009 | *11* | **0.141** | 0.128 | 0.153 | 0.007 | *6* | **0.116** | 0.109 | 0.129 | 0.007 |
| LaN/LOc | *30* | **0.384** | 0.368 | 0.409 | 0.011 | *11* | **0.403** | 0.384 | 0.413 | 0.009 | *6* | **0.428** | 0.417 | 0.437 | 0.009 |
| LaM/LOc | *30* | **0.453** | 0.426 | 0.477 | 0.010 | *11* | **0.463** | 0.452 | 0.483 | 0.009 | *6* | **0.496** | 0.491 | 0.502 | 0.004 |
| ANc/LOc | *30* | **0.352** | 0.332 | 0.373 | 0.009 | *10* | **0.342** | 0.317 | 0.356 | 0.012 | *5* | **0.303** | 0.288 | 0.314 | 0.012 |

While the latter group of the smallest specimens (hereafter called morphotype A of the Middle Eastern samples) showed relatively short and narrow rostra ($CM^3$/LOc 0.34–0.36 [M 0.351]; CC/LOc 0.24–0.26 [M 0.252]; $CC/CM^3$ 0.69–0.74 [M 0.718]) and relatively very large tympanic bullae (LBT/LOc 0.15–0.17 [M 0.162]) although they were the smallest ones (Table 2), the group of medium-sized bats from south-eastern Yemen (Middle East morphotype B) and large specimens from western Yemen (Middle East morphotype C) exhibited relatively smaller bullae (LBT/LOc in morphotype B: 0.14–0.16 [M 0.155]; in morphotype C: 0.15–0.16 [M 0.156]) and relatively long and wide rostra ($CM^3$/LOc in morphotype B: 0.35–0.37 [M 0.363]; in morphotype C: 0.36–0.37 [M 0.366]; CC/LOc in B: 0.24–0.27 [M 0.256]; in C: 0.25–0.28 [M 0.264]; $CC/CM^3$ in B: 0.67–0.74 [M 0.706]; in C: 0.69–0.75 [M 0.720]). To summarise, the Middle Eastern samples were composed of at least two clearly distinct morphotypes differing in size, rostrum shape and relative size of bulla, A vs. B+C, where later B and C differed in size.

Size exclusivity of the skull morphotype A among the Middle Eastern bats was confirmed also by principal component analysis based on nine of the most variable skull dimensions (see below for their selection); the first principal component (representing some 89.89% of the whole metric variance) clearly separated the morphotype A (PC1>1.2) from the common cluster of remaining two morphotypes B+C (PC1<–0.5) according to skull size expressed by the large skull dimensions (not figured).

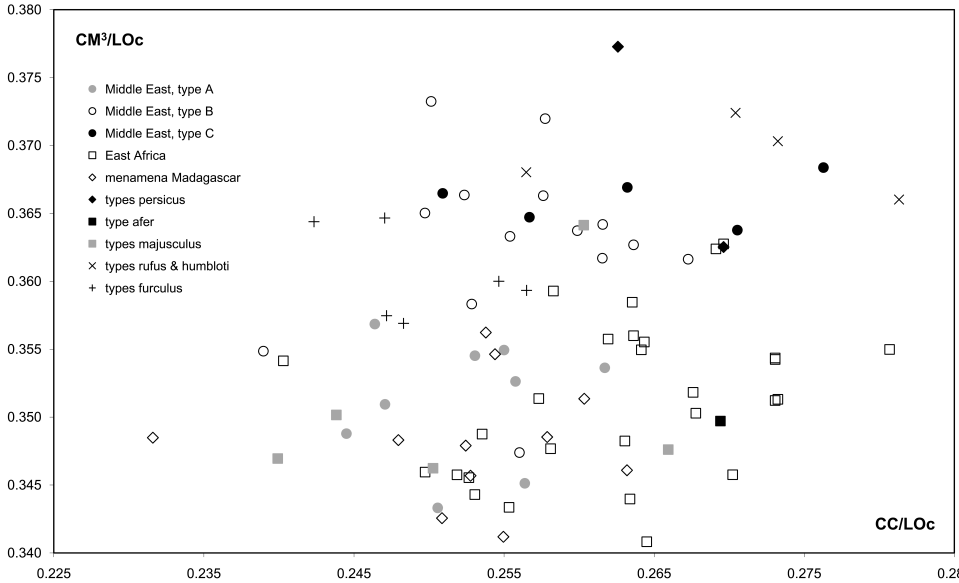


**Fig. 4.** Bivariate plot of compared *Triaenops* samples: relative width of rostrum (rostral width across upper canines vs. occipitocanine length – CC/LOc) against relative length of rostrum (length of the upper tooth-row vs. occipitocanine length – $CM^3$/LOc).

**Table 3.** Forearm and skull dimensions (in millimetres) of the examined holotype (syntype in *T. persicus*) specimens. The holotype of *T. furcula* represents alcoholic specimen with skull not extracted – for cranial measurements of the paratype series of *T. furcula* see Table 2. See Abbreviations for explanation of dimension abbreviations. * two alcoholic specimens are associated with the holotype skull (one of them should be a paratype, see also G o o d m a n & R a n i v o 2009)

| | *persicus* | *persicus* | *afer* | *rufus* | *humbloti* | *furcula* | *majusculus* | *parvus* sp. nov. |
|---|---|---|---|---|---|---|---|---|
| coll. | ZMB | ZMB | ZMB | MNHN | MNHN | MNHN | MNHN | NMP |
| No. | 4370/1 | 4370/2 | 5074 | 1997-1854 | 1962-2659 | 1912-40 | 1968-412 | 92270 |
| sex | m | f | m | – | m | m | m | m |
| LAt | 51.4 | 50.7 | 52.7 | 55.5 | 54.0/54.5* | 44.4 | 55.6 | 48.0 |
| LCr | – | – | – | 20.21 | 19.88 | – | 20.64 | 17.97 |
| LOc | 19.27 | 18.73 | 18.93 | 19.48 | 19.47 | – | 20.08 | 17.36 |
| LCc | 16.98 | 16.31 | 16.67 | – | – | – | 17.74 | 15.16 |
| LaZ | 8.87 | 9.02 | 9.19 | 9.13 | 9.61 | – | 9.27 | 7.92 |
| LaI | 2.78 | 2.61 | 2.76 | 2.88 | 2.89 | – | 2.76 | 2.38 |
| LaN | 7.61 | 7.49 | 7.74 | 7.56 | 7.89 | – | 7.46 | 6.83 |
| LaM | 8.75 | 8.71 | 8.58 | 8.73 | 9.21 | – | 8.82 | 7.93 |
| ANc | 6.41 | 6.64 | 6.58 | – | 7.17 | – | 6.92 | 6.12 |
| LBT | 2.93 | 2.87 | 2.95 | – | 3.38 | – | 3.22 | 2.65 |
| CC | 5.06 | 5.05 | 5.10 | 5.48 | 5.32 | – | 5.34 | 4.35 |
| $M^3M^3$ | 6.83 | 6.91 | 6.77 | 7.10 | 7.12 | – | 6.69 | 6.03 |
| $CM^3$ | 7.27 | 6.79 | 6.62 | 7.13 | 7.21 | – | 6.98 | 5.96 |
| LMd | 12.16 | 11.67 | 11.82 | – | 12.87 | – | 12.74 | 10.67 |
| ACo | 2.75 | 2.67 | 2.64 | – | 2.98 | – | 3.07 | 2.23 |
| $CM_3$ | 7.73 | 7.28 | 7.03 | – | 7.83 | – | 7.75 | 6.49 |

The *Triaenops* skull morphotypes were defined above according to the absolute size of the skull, the relative size of the tympanic bullae and the shape of the rostrum as well as by their affinities to the examined type material; their mutual positions were shown by discriminant function analyses (Figs. 5 and 6). The analysis of the whole set of examined skulls selected nine most variable dimensions (LCr, LOc, LaI, LaM, ANc, CC, $CM^3$, LMd, ACo; CV1=57.68% of variance; CV2=25.50%). This analysis of the selected dimensions clearly separated the most differing samples (Fig. 5), the type series of *Triaenops furculus* from Madagascar (CV1>8), apart from all other samples (CV1<5). In the common cluster of the remaining samples, it was possible to distinguish three groups of specimens; (1) a group (CV1<–0.1;5.0>; CV2<–1.3) composed of small individuals of *T. persicus* from the Middle East (morphotype A) and of *T. menamena* from Madagascar; (2) a group (CV1<–3.4;0.4>; CV2<–3.0;1.6>) composed of African specimens from Ethiopia, Somalia, Central African Republic, Kenya and Tanzania as well as the type specimens of *T. afer* and *T. persicus majusculus*; and (3) a group (CV1 <–4.3;–0.3>; CV2 <–0.9;4.7>) composed of remaining Middle Eastern samples (morphotypes B and C) and type series of *T. persicus*, *T. rufus* and *T. humbloti* (Fig. 5).

The discriminant function analysis of all 15 skull measurements of the whole set of examined skulls with exception of those of *T. furculus* (separated as most different by the previous analysis) clustered four groups of samples (CV1=57.23% of variance; CV2=26.28%; Fig. 6). Like the previous analysis, it indicated the same group of African samples (CV1 <–1.8;–2.4>; CV2 <0;3.8>), but the rest of specimens clearly clustered according to their geographic origin and also to their belonging to the above defined skull morphotypes – these groups almost did not overlap. A group of *T. menamena* from Madagascar (CV1 <2.9;6.6>; CV2 <–1.0;2.9>), a close up positioned group of smallest individuals (Middle East morphotype A) from south-eastern Yemen (CV1 <1.5;3.4>; CV2 <–4.0;–2.4>), and two groups of larger individuals from the Middle East (western and south-eastern Yemen, morphotypes B and C) partly overlapped with each other and also with the group of type specimens of *T. persicus*, *T. rufus* and *T. humbloti* (CV1 <–6.0;–0.6>; CV2 <–2.5;2.4>). Although Middle Eastern bats of the morphotype C were on average the largest ones according to the first canonical variable (CV1), they overlapped widely in the first two variables with the cluster of the specimens of morphotype B.

Bats of the four morphotypes of *Triaenops* coming from northern part of the genus range (samples of African bats from Ethiopia and of three Middle Eastern morphotypes A, B, C from Yemen) were additionally examined for noseleaf, baculum, and coloration variation. Among these compared samples, the noseleaf was of identical form, differing only in size, which, however, depended on the body size of the respective specimen (Table 2). Small individual variation was found only in noseleaf pigmentation (see below).

Examination of bacula extracted from the examined specimens (two bacula per skull morphotype) showed nearly uniform shape of bone, an elongated stick (length 1.5–2.1 mm) extended to broad pyramid in proximal epiphysis and bifurcated at distal epiphysis (Fig. 7). Besides the slight differences in size, we found minute differences in baculum shape. Most distinct bacula came from the Ethiopian bats showing slightly more robust diaphysis (relative width of diaphysis 0.12 and 0.16%), longer and robust distal arms (relative length of arm 0.27–0.29%) and more robust proximal epiphysis (relative width of the basis 0.44 and 0.48%) than in other samples. Another distinct baculum shape was demonstrated in the samples of the SE Yemeni morphotype A, in which it was gracile (relative width of diaphysis 0.08 in both bones) with short arms (relative length of arm 0.17–0.20%) and narrow proximal epiphysis (relative width of the basis 0.23 and 0.31%). In both bones a distinct proximal projection was

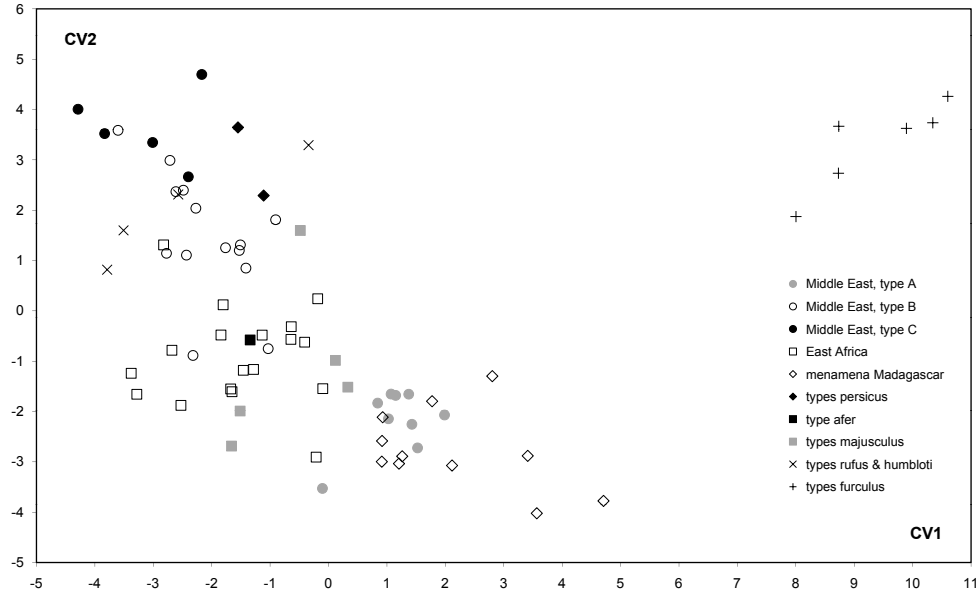


**Fig. 5.** Bivariate plot of compared *Triaenops* samples: results of discriminant analysis of nine skull dimensions of the whole compared set of specimens (see text for details).

also observed (possibly an ossified distal part of the erectile body), which was present only in one of the rest of examined bacula. Bats of the Yemeni morphotypes B and C exhibited similar structures of bacula, as the shapes and relative dimensions fall in between the two baculum morphotypes characterised above (Fig. 7, Table 4). Principal component analysis

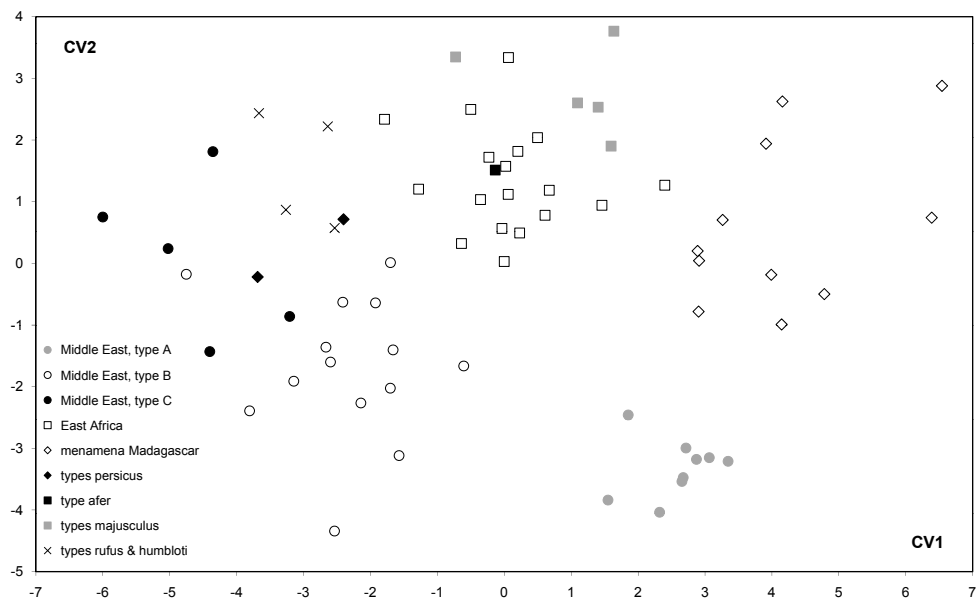


**Fig. 6.** Bivariate plot of compared *Triaenops* samples: results of discriminant analysis of all skull dimensions of the whole compared set with an exception of *Triaenops furculus* (see text for details).

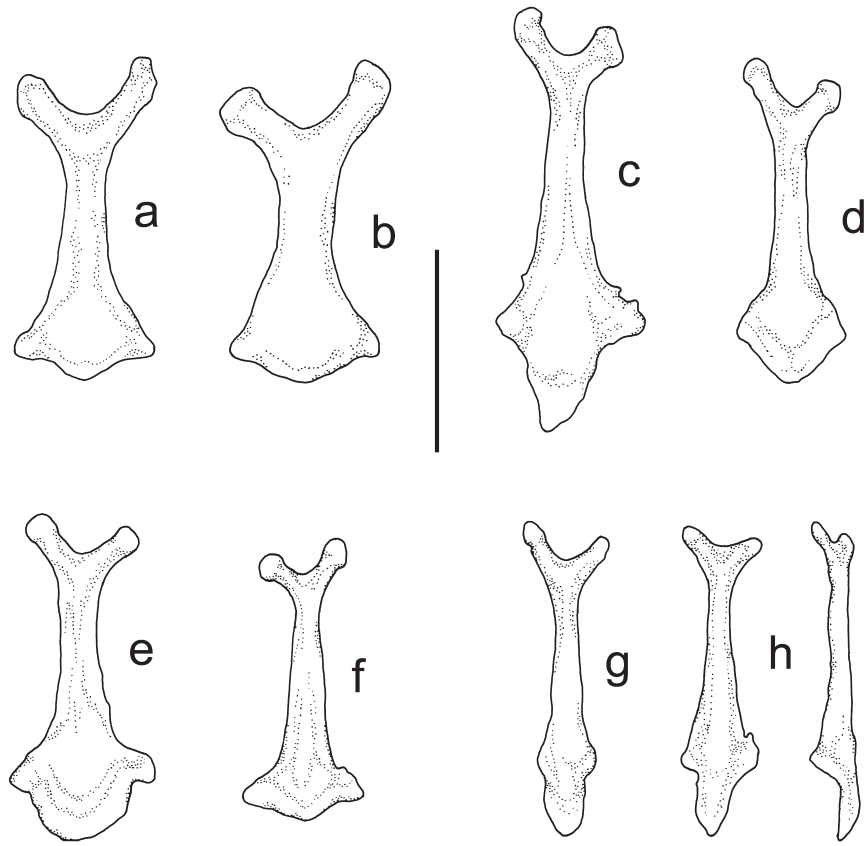


**Fig. 7.** Baculum preparations of the *Triaenops* morphotypes from northern part of distribution range (see text for details). Explanations: a – Sof Omar Caves, Ethiopia, NMP 92164; b – Sof Omar Caves, Ethiopia, NMP 92166; c – Wadi Zabid, W Yemen [morphotype Middle East C], NMP 92279; d – Jebel Bura, W Yemen [morphotype Middle East C], NMP 92275; e – Hawf, SE Yemen [morphotype Middle East B], NMP 92262; f – Damqawt, SE Yemen [morphotype Middle East B], NMP 92271; g – Hawf, SE Yemen [morphotype Middle East A], NMP 92264; h – Sayhut, SE Yemen [morphotype Middle East A], NMP 92274. Scale bar = 1 mm.

of eight bacular dimensions clearly separated three clusters of samples conforming with the above mentioned three groups (PC1=57.22% of variance; PC2=18.98%); (1) a pair of African samples (PC1<1; PC2<0), (2) a pair of Yemeni samples of the morphotype A (PC1>1; PC2<0) and (3) a common cluster of the Yemeni morphotypes B and C (PC2>0) (not figured).

Pelage coloration of the compared samples from Ethiopia and Yemen exhibited wide variation mostly depending on the sample size, with an exception of the Yemeni morphotype A. In this morphotype, the coloration was uniformly beige or pale brownish-grey above without any tinge of reddish or rusty colours (which was present in some individuals of all the remaining morphotypes), very pale beige to pale greyish-brown below and with a pale (in alcohol fixed specimens, i.e. unpigmented) to pale greyish-brown coloured noseleaf (see Fig. 8 for face coloration of two pairs of syntopically collected individuals of south-eastern Yemeni morphotypes A and B). The brightest pelage was found in Ethiopian bats, in which it was deep greyish-brown, dark brown or reddish-brown above, pale beige to brown below, with pale (unpigmented) to greyish-brown noseleaf. In the most numerous samples of the SE Yemeni morphotype B the dorsal pelage varied from pale greyish-brown over reddish-brown

**Table 4.** Dimensions (in millimetres) of examined baculum preparations (see text for details and Fig. 5). See Abbreviations for explanation of dimension abbreviations

| skull morphotype | No. | LBc | LBcB | LaMin | LaProx | LaDist | LArBc1 | LArBc2 | AnBc |
|---|---|---|---|---|---|---|---|---|---|
| Middle East A | NMP 92264 | 1.56 | 1.33 | 0.11 | 0.30 | 0.43 | 0.26 | 0.24 | 78 |
| Middle East A | NMP 92274 | 1.52 | 1.25 | 0.10 | 0.39 | 0.40 | 0.21 | 0.18 | 97 |
| Middle East B | NMP 92262 | 1.61 | 1.61 | 0.17 | 0.72 | 0.56 | 0.30 | 0.29 | 89 |
| Middle East B | NMP 92271 | 1.39 | 1.39 | 0.11 | 0.60 | 0.44 | 0.25 | 0.25 | 88 |
| Middle East C | NMP 92275 | 1.59 | 1.59 | 0.16 | 0.55 | 0.48 | 0.32 | 0.25 | 71 |
| Middle East C | NMP 92279 | 2.10 | 1.77 | 0.16 | 0.74 | 0.54 | 0.34 | 0.29 | 87 |
| Ethiopia | NMP 92164 | 1.59 | 1.59 | 0.19 | 0.70 | 0.69 | 0.43 | 0.43 | 75 |
| Ethiopia | NMP 92166 | 1.59 | 1.59 | 0.26 | 0.76 | 0.85 | 0.46 | 0.44 | 86 |

**Fig. 8.** Faces of two *Triaenops* morphotypes from Hawf, eastern Yemen. Above: left = morphotype A [= *Triaenops parvus* sp. nov.], right = morphotype B [= *Triaenops persicus* s.str.]; below: left = morphotype B [= *Triaenops persicus* s.str.], right = morphotype A [= *Triaenops parvus* sp. nov.]. Note the differences in coloration of noseleaf and head pelage.

to dark greyish-brown, ventral pelage beige, pale grey or pale rusty to greyish-brown and/or deep grey, with pale grey (almost unpigmented) to brown or dark grey noseleaf. In the western Yemeni morphotype C the dorsal pelage was greyish brown to dark reddish-brown, ventral pelage pale grey to dark greyish-brown, and noseleaf pale beige (unpigmented) or dark greyish-brown. Wing membranes were found to be dark brown in all samples, without any well observable distinctions of the colour.

### Genetic comparison

We processed 20 samples of *T. persicus* and obtained 17 complete sequences of cyt *b* (1140 bp). From three samples, only an initial portion of cyt *b* ca. 600 bp long could be recovered but these matched to other complete sequences obtained (Appendix 2). The obtained sequences corresponded to 11 *Triaenops* haplotypes and two unique haplotypes were recovered from the two *Cloeotis* samples. Genetic divergences among *Triaenops* haplotypes ranged 0.1–8.1%, among *Triaenops* and *Cloeotis* 22.4–24.9% (Table 5). Bats of the two Middle Eastern *Triaenops* skull morphotypes B and C showed a minute genetic distance of 0.0–0.2% from each other (i.e. an identical haplotype, ME1, was found in both the morphotypes and geographical regions, respectively, see Appendix 2), while genetic difference between either of these two sample sets and the Middle Eastern skull morphotype A ranged from 6.4 to 6.7%. The East African group of samples differed from all three Middle Eastern morphotypes at 7.1–8.1%.

After appending sequences of *Triaenops* from the GenBank and trimming them to 731 bp, the number of unique *Triaenops* haplotypes shrunk to eight and *Cloeotis* to one (Appendix 2). The 731 bp dataset thus contained 17 ingroup sequences, of which 248 positions were variable and 196 parsimony informative. Approximately 19% of substitutions occurred at 1st, 5% at 2nd, and 76% at 3rd codon position. Base composition did not differ among ingroup sequences ($\chi^2$=17.645792, d.f.=48, P=0.999) and mean values for base frequencies were A=0.27231, C=0.29621, G=0.16062, and T=0.27086. MP analysis revealed 12 shortest trees (length=667, consistency index=0.6747, retention index=0.7953) with well supported monophyletic clades corresponding to the respective species or geographical forms of *Triaenops persicus* (Fig. 9). These equally parsimonious trees differed in relationships among the *T. persicus* clades and *T. menamena*, in which the latter taxon mostly appeared in monophyly with *T. persicus* from the Middle East but without a significant bootstrap support. ML and Bayesian methods revealed the same well supported monophyletic clades as MP with slight differences in relationships among these clades. Especially, *T. menamena* haplotypes in the ML tree (–lnL=3724.69385) did not form a monophyletic clade and were placed as sisters to other African and Middle Eastern haplotypes. This relationship of *T. menamena* haplotypes, however, was not supported by bootstrap. In all analyses, *Cloeotis percivali* diverged as the

**Table 5.** Percent genetic distances among lineages of *Triaenops* Dobson, 1871 and *Cloeotis* Thomas, 1901 computed under Kimura's two-parameter model of evolution (K2P; Kimura 1980) based on complete sequences (1140 bp) of cyt *b* (for the naming of lineages see text)

| K2P [%] | Middle East A | Middle East B | Middle East C | Ethiopia | Cloeotis |
|---|---|---|---|---|---|
| Middle East A | – | | | | |
| Middle East B | 6.4–6.7 | – | | | |
| Middle East C | 6.5–6.7 | 0.0–0.2 | – | | |
| Ethiopia | 7.7–8.1 | 7.1–7.3 | 7.2–7.3 | – | |
| *Cloeotis* | 24.7–24.9 | 22.5–22.7 | 22.4–22.7 | 23.4–23.5 | – |

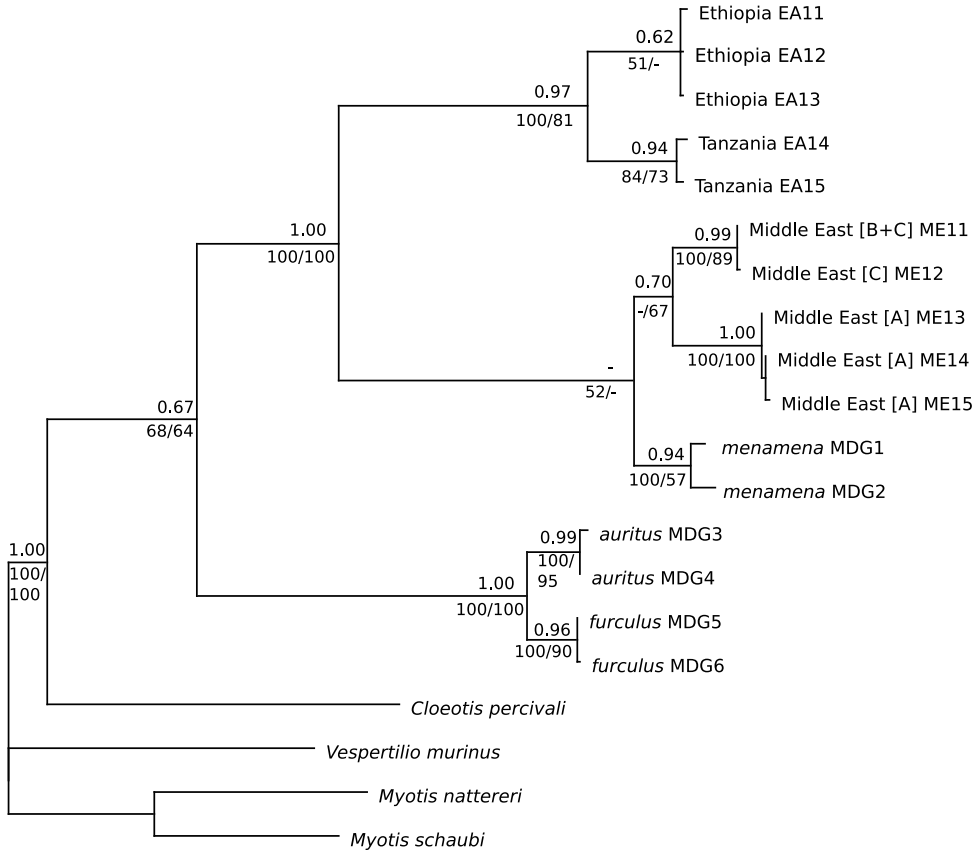


**Fig. 9.** One of the maximum parsimonial trees showing phylogenetic relationships within the genus *Triaenops* Dobson, 1871. Nodal support expressed as Bayesian posterior probabilities is indicated above branches, bootstrap values for MP and ML methods, respectively, are indicated below branches. Labelling of *Triaenops* haplotypes follows Appendix 2, in brackets the morphotype designation used throughout Results.

first taxon from the basal node differing 22.5–26.9% from the *Triaenops* haplotypes. A deep split divided the *Triaenops* haplotypes into two main lineages, differing 21.6–26.2%. These two main lineages were well supported but their sister relationship was not. One lineage represented the Malagasy sister species *T. furculus* and *T. auritus*, which differed at 4.1–4.6%. The other lineage comprised four clades: East African *T. persicus*, Middle Eastern *T. persicus* morphotype A, Middle Eastern *T. persicus* morphotypes B+C and the Malagasy *T. menamena*. Within the East African clade, Ethiopian haplotypes differed 1.1–1.4% from Tanzanian ones. Genetic divergences among the Middle Eastern morphotypes A and B+C of *T. persicus*, and Malagasy *T. menamena* ranged 6.8–8.4% (Table 6). Relationships among the four clades remained unresolved under all three phylogenetic methods, although MP suggested affinity of *T. menamena* to the Middle Eastern clades A and B+C. Therefore, this hypothesis (MP) was tested against the hypothesis represented by the ML tree (Fig. 10). Also, we tested two other alternative hypotheses assuming affinity of *T. menamena* to the African clade and basal position of monophyletic *T. menamena* clade to other African and Middle Eastern clades (alt. 1 and alt. 2; Fig. 10). The SH test showed that monophyly of the Middle Eastern haplotypes and *T. menamena* as suggested by the MP topology was not significantly different

**Table 6.** Percent genetic distances among morphotypes of *T. persicus* and other *Triaenops* species computed under Kimura's two-parameter model of evolution (K2P; K i m u r a 1980) based on partial sequences (731 bp) of cyt *b* (for the naming of lineages see text)

| K2P [%] | Middle East A | Middle East B+C | Ethiopia | Tanzania | *menamena* | *auritus* | *furculus* | *Cloeotis percivali* | *Vespertilio murinus* | *Myotis nattereri* |
|---|---|---|---|---|---|---|---|---|---|---|
| Middle East B+C | 6.2–6.7 | – | | | | | | | | |
| Ethiopia | 7.6–8.2 | 7.4–7.8 | – | | | | | | | |
| Tanzania | 8.3–8.7 | 7.4–7.6 | 1.0–1.4 | – | | | | | | |
| *T. menamena* | 7.6–8.4 | 7.1–7.6 | 6.8–7.3 | 7.8–7.9 | – | | | | | |
| *T. auritus* | 25.3–26.2 | 23.3–23.9 | 22.7–23.1 | 22.5–23.3 | 23.9–24.3 | – | | | | |
| *T. furculus* | 23.9–24.5 | 21.9–22.3 | 21.7–22.0 | 21.6–22.1 | 22.6–23.1 | 4.1–4.6 | – | | | |
| *C. percivali* | 26.0–26.2 | 22.5–22.7 | 24.4–24.7 | 23.8–24.6 | 23.3–23.7 | 25.9–26.3 | 26.7–26.9 | – | | |
| *V. murinus* | 30.0–30.5 | 30.7 | 30.0–30.2 | 29.6–30.0 | 30.7–31.1 | 29.6 | 28.3 | 30.0 | – | |
| *M. nattereri* | 30.6–31.0 | 29.3 | 30.3–30.8 | 30.5–30.6 | 30.5 | 30.4 | 30.5–30.7 | 29.6 | 25.1 | – |
| *M. schaubi* | 28.5–28.8 | 27.3 | 26.8–27.2 | 27.0 | 28.7–29.0 | 27.1–27.5 | 27.9–28.1 | 24.8 | 23.7 | 17.9 |

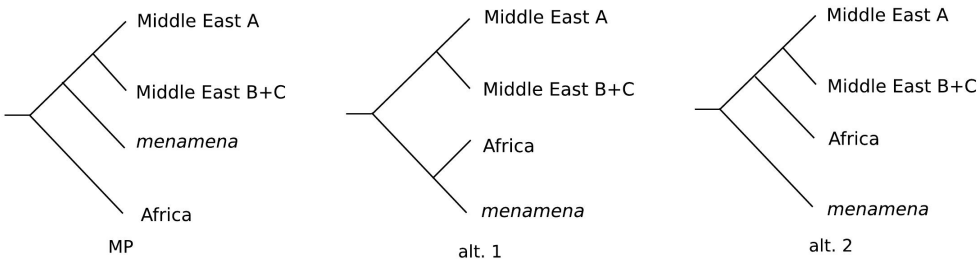


**Fig. 10.** Alternative phylogenetic hypotheses expressing possible relationships among Malagasy *T. menamena* to *T. persicus* from the Middle East and Africa (for details see text).

from the ML tree (diff. –lnL=0.62802, d.f.=17, P= 0.637), and could not be rejected. The other two alternative hypotheses also did not differ significantly from both the ML and MP topology (alt. 1: diff. –lnL=1.34594, P=0.549 and diff. –lnL=0.71792, P=0.461; alt. 2: diff. –lnL=1.26968, P=0.604 and diff. –lnL=0.64166, P=0.486). Templeton test showed significant difference between MP and ML topology (diff. length=13, P=0.007), and the ML topology thus could be rejected. Differences between MP and the alt. 1 and alt. 2 topologies were not

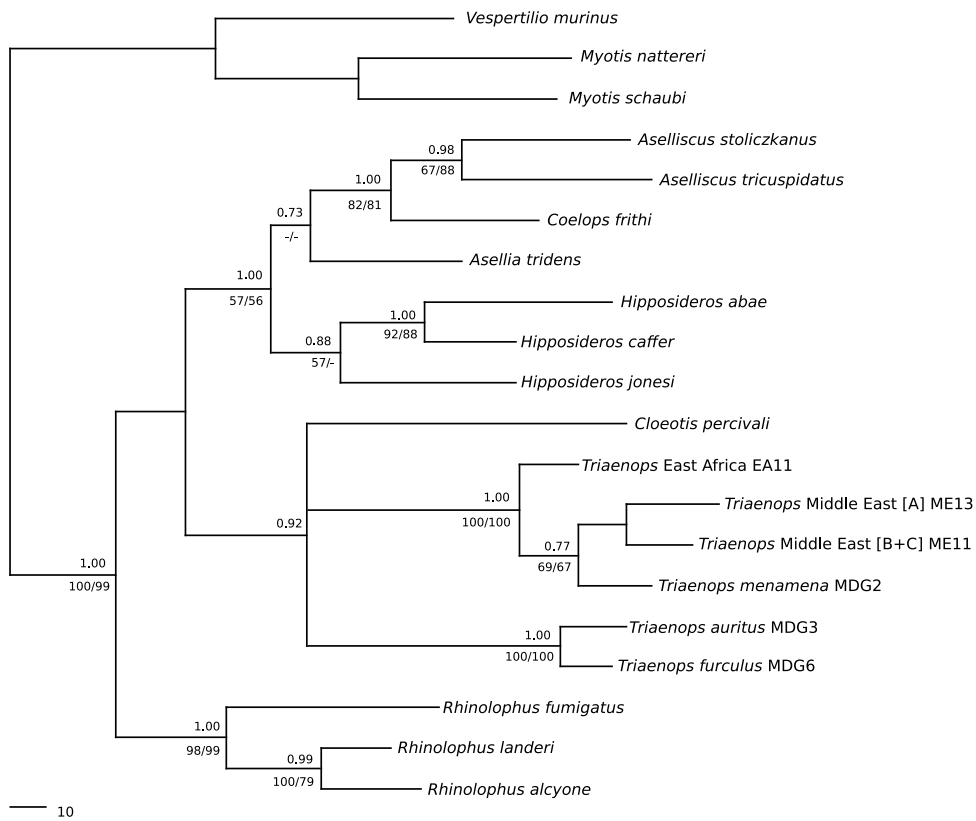


**Fig. 11.** Bayesian consensus tree showing phylogenetic relationship of the genus *Triaenops* to other Hipposideridae and to the sister family Rhinolophidae. Nodal support expressed as Bayesian posterior probabilities is indicated above branches, bootstrap values for weighted MP and ML methods, respectively, are indicated below branches. Labelling of *Triaenops* haplotypes follows Appendix 2, in brackets the morphotype designation used throughout Results.

significant (alt. 1: diff. length=1, P=0.763; alt. 2: diff. length=4, P=0157), and these alternative hypotheses could not be rejected.

The extended 731 bp dataset of hipposiderids and rhinolophids contained 18 ingroup sequences, of which three haplotypes of *T. persicus* represented the morphotypes/phylogroups from the Middle East A, B+C and East Africa from previous analysis. In the alignment, 336 positions were variable, 289 of them parsimony informative. Approximately 22% of substitutions occurred at 1st, 8% at 2nd, and 70% at 3rd codon position. Base composition did not differ among ingroup sequences ($\chi^2$=24.437, d.f.=48, P=0.998) and mean values for base frequencies were A=0.272, C=0.306, G=0.153, and T=0.268. Weighted MP yielded two most parsimonious trees with a length of 2832 steps. These two trees topologically differed in the position of *Triaenops* clade, which was sister either to other hipposiderids or to rhinolophids, without significant bootstrap support for either hypothesis. Two lineages of *Triaenops* were highly supported but their sister relationship was not. *Cloeotis percivali* clustered with other hipposiderids instead of *Triaenops* but its position also was not supported. ML tree (–lnL=5890.55931) and Bayesian consensus tree exhibited basically the same topology, differing in the position of *Cloeotis percivali*, which clustered as sister to Malagasy *Triaenops* in ML tree and as sister to all *Triaenops* in Bayesian tree. However, ML and Bayesian trees were congruent with wMP trees in grouping rhinolophids, African and Middle Eastern *Triaenops*,

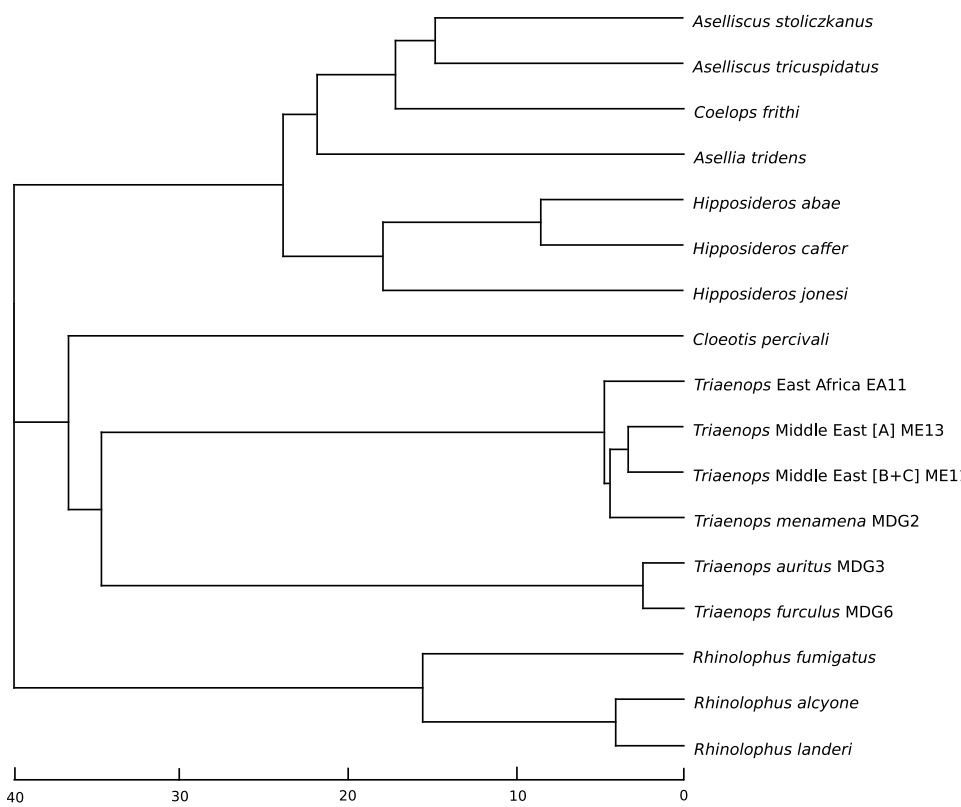


**Fig. 12.** Clock-like ML tree constructed under constraints reflecting current assumptions on phylogeny of hipposiderid bats. The tree is calibrated according to basal split of Rhinolophidae/Hipposideridae, set to approximately 40 MA. Labelling of *Triaenops* haplotypes follows Appendix 2, in brackets the morphotype designation used throughout Results.

Malagasy *Triaenops*, and other hipposiderids into respective monophyletic clades (Fig. 11). Sister relationship of the two main *Triaenops* lineages was not supported by bootstrap or posterior probability, and unsupported was also the sister position of *C. percivali* to *Triaenops* species. Similarly as in wMP trees, relationships of *Triaenops* to other hipposiderids and rhinolophids remained unresolved. An alternative phylogeny, which considered sister position of *Cloeotis* to *Triaenops* within Hipposideridae (i.e. currently acknowledged phylogeny), did not differ significantly from wMP (Templeton test; diff. length=8, z=–0.5252, P=0.5994) and ML (SH test; diff. –lnL=0.60680, P=0.342) trees and thus could not be rejected.

Because we could not reject the traditional phylogeny of Hipposideridae, we kept that assumption in a rough assessment of divergence times in molecular dating of the phylogeny. A clock-like phylogenetic tree was computed under topological constraints of assuming monophyly of the genus *Triaenops*, monophyly of *Triaenops* and *Cloeotis*, and monophyly of Hipposideridae. Vespertilionid outgroup taxa were excluded from this clock-like tree, as these negatively affected stationarity of base frequencies ($\chi^2$= 82.825173, d.f.=57, P=0.014). A likelihood-ratio test of the ML tree with (–lnL=4881.69411) and without a molecular clock (–lnL=4870.69325) could not reject the molecular clock assumption (diff. –lnL=11.00086, d.f.=15, P=0.1077) under HKY+I+Γ model of evolution. According to the assumed monophyly of Hipposideridae, three rhinolophids were used for rooting the tree. However, the most basal branch was collapsed to the root and the topology remained unresolved with three lineages emanating from the root: (1) Rhinolophidae, (2) *Triaenops* and *Cloeotis*, and (3) other Hipposideridae. Estimates of approximate minimal dates of splits among lineages are visualised in the linearised tree (Fig. 12).

## Discussion

The combination of results of the above morphological and molecular genetic analyses revealed existence of six distinct evolutionary units within the genus *Triaenops* (*sensu* S i m m o n s 2005 = *Triaenops* s.l.). They differed a lot in size and skull morphology and in genetic traits as well as in geographic distribution. The largest distance, both in morphology and genetics, was present between the pair of Malagasy species *T. furculus* and *T. auritus* and the remainder of the genus. These two distant groups were formerly distinguished as two species by H i l l (1982) and K o o p m a n (1993, 1994), differing in skull structure and shape, ear shape and significantly also in structure of the noseleaf (D o r s t 1948, H a y m a n & H i l l 1971, H i l l 1982, K o o p m a n 1994, R a n i v o & G o o d m a n 2006). However, within these 'species' deeper hidden distinctions were found in clearly different and finer morphological value than H i l l (1982) described as sufficient for specific level. The extraordinary genetic distance between these two groups exceed the intergeneric distance among other hipposiderids (e.g. 17.2% between *Hipposideros* Gray, 1831 and *Aselliscus* Tate, 1941; see W a n g et al. 2003) and even interfamilial distance among rhinolophids and hipposiderids and overlap the range of distances between the presumably sister genera *Cloeotis* and *Triaenops* s.l. Such a considerable distance as well as double categorial morphological differences, suggest the separation of the Malagasy forms (except for *T. menamena*) in a separate genus. The new genus, however, shows most similarities with the genus *Triaenops* s.str. and both these genera evidently compose a natural evolutionary unit, constituting a sister lineage to the remaining hipposiderid taxa. For this unit we therefore propose a new tribe (see Taxonomic Part below), while we consider the other hipposiderid taxa members of the tribe Hipposiderini Lydekker,

1891 (with an exception of the genus *Cloeotis* Thomas, 1901; for resolving its position within the family, a thorough genetic analysis using a marker with a lower mutational rate, needs to be done). In the Taxonomic Part of this paper, morphological and genetic differences among the taxa mentioned are specified in detail.

The assessment of phylogenetic relationships of *Triaenops* s.l. to other members of the family Hipposideridae brought additional interesting results. Although none of the methods used could fully resolve the phylogeny, our results indicate that the family Hipposideridae is not a monophyletic group as already suggested by e.g. H u l v a & H o r á č e k (2002) or H o o f e r & V a n D e n B u s s c h e (2003). A rather compact lineage comprising genera *Asellia*, *Aselliscus*, *Coelops* and *Hipposideros* stays separately from the genera *Triaenops* s.l. and *Cloeotis*, which form a loosely defined phylogroup showing larger genetic divergencies to the other members of Hipposideridae than the divergences among the other hipposiderids to Rhinolophidae. In contrast, a close relationship of two distinct lineages of *Triaenops* s.l. and *Cloeotis* could not be confirmed by bootstrapping in any of the phylogenetic methods used. Similarly, resolution at the basal node of the phylogeny remained obscure suggesting trichotomic evolution of the family Rhinolophidae, consisting of the lineages; (1) rhinolophids, (2) a lineage comprising *Triaenops* s.l. and *Cloeotis* (delimited mostly on morphologic traits, see e.g. H i l l 1982), and (3) other hipposiderids. Such a weak resolution can be undoubtedly influenced by a high saturation in cyt *b* sequences at large genetic distances. Nevertheless, it may also indicate a rapid radiation of the respective forms, as wMP and ML methods can handle the effect of saturation by adopting a proper weighting scheme and model of nucleotide substitution. Testing of the best hypotheses resulting from different phylogenetic methods against currently accepted systematic perception of Hipposideridae provided an ambiguous solution. The alternative hypothesis assuming monophyly of the genus *Triaenops* s.l. and a sister relationship of *Triaenops* and *Cloeotis* within monophyletic Hipposideridae could not be rejected based on our limited sequence data. Genetic markers with a lower mutational rate should be employed to obtain a definite resolution of this issue.

Within the current *Triaenops persicus* content (*sensu* S i m m o n s 2005), three evolutionary units were revealed. The first unit is represented by Yemeni bats of the morphotype A, extremely small individuals (absolutely smallest within the examined set of *Triaenops*; see Fig. 3 and Table 2, as well as the data by H i l l 1982, R a n i v o & G o o d m a n 2006, and/or G o o d m a n & R a n i v o 2008), living in sympatry and even syntopy with bats of the morphotype B in south-eastern Yemen, which are medium-sized to large. The morphotype C coming from westernmost Yemen was characterised by the largest size among the compared bats, however, in most of the characters (skull structure, baculum) it was close to or just overlapping with morphotype B. These two morphotypes (B+C), differing in size but not differing or almost imperceptibly differing in the examined genetic traits (four haplotypes differing in one substitution from each other, i.e. in 0.1%), represent the second unit. The types of *T. persicus*, *T. rufus* and *T. humbloti* fell also into ranges of dimensions of this unit. On the other hand, the sympatric morphotypes A and B, besides their size and morphologic differences, diverged by 6.4–6.7% of the complete sequence of cyt *b* gene. Such a value lies within the range of interspecific genetic divergences seen for Hipposideridae and other bat families (B r a d l e y & B a k e r 2001, V a l l o et al. 2008). Thus, these two units (morphotypes A and B+C) could be considered separate species. The third phylogenetic unit is composed of the fourth morphotype, found in the African samples (Ethiopian, Somalian, Central African, Kenyan and Tanzanian specimens and the types of *T. afer* from Kenya and *T. persicus*

*majusculus* from Congo-Brazzaville), differing in the structure of skull and baculum from the Middle Eastern morphotypes A, B and C and markedly in size from the Middle Eastern morphotype A and Malagasy *T. menamena*. This last unit composed of African continental samples also diverges in genetic traits from the Yemeni group of morphotypes (7.1–8.1% at 1140 bp and 7.4–8.7% at 731 bp of cyt *b*, respectively), i.e. by a larger distances than the sympatric A and B morphotypes. This situation suggests that all three here-defined phylogenetic units currently enclosed into the species rank of *T. persicus* (S i m m o n s 2005) represent three separate species.

From the area of the Middle East and Africa, five names of the genus *Triaenops* are presumably available; *T. persicus* Dobson, 1871 (type locality: Shiraz, Iran), *T. afer* Peters, 1877 (t.l.: Mombasa, Kenya), *T. rufus* Milne-Edwards, 1881 (t.l. unknown [east coast of Madagsacar sensu e.g. H i l l 1982, but apparently incorrect – the correct collections site lies in SW Yemen or E Somalia, see G o o d m a n & R a n i v o 2009]), *T. humbloti* Milne-Edwards, 1881 (t.l. unknown [east coast of Madagascar sensu e.g. H i l l 1982, but apparently incorrect, identically as in the previous name, see G o o d m a n & R a n i v o 2009]), and *T. persicus macdonaldi* Harrison, 1955 (t.l.: Al Ain, U. A. E.). Bats of the African morphotype from our set corresponded in their traits with those of the holotype of *T. afer*; haplotypes of the Ethiopian samples were shown to be closest to the Tanzanian ones (*sensu* R u s s e l l et al. 2007), i.e. to bats from an area more distant from Ethiopia than is the Kenyan coast of the Indian Ocean, the type locality of *T. afer.* The type series of *T. p. majusculus* did not show any remarkable difference from other examined African samples than partly in forearm size and in statistic analyses it was placed among other bats from Africa. It suggests that all African populations belong to one form and therefore, we consider the name *T. afer* appropriate for African *Triaenops* populations including those formerly assigned as separate subspecies *majusculus*: this name we therefore consider a junior synonym of *afer.* A separate position for *afer* is in accordance with previously mentioned opinions of various authors, however, we suggest for these populations a separate species status based also on genetic traits, not only morphological or geographical differences. Such a taxonomic view conform with the original and several traditional taxonomic opinions (P e t e r s 1877, D o b s o n 1878, T r o u e s s a r t 1904, M i l l e r 1907, A l l e n 1939, T a t e 1941, D o r s t 1948, A e l l e n 1957, H a r r i s o n 1961, 1963, etc.). In other words, we consider *Triaenops afer* Peters, 1877 the only member of the genus occurring in continental Africa.

Two names originated from the Middle East, *persicus* and *macdonaldi*, (H i l l 1982, S i m m o n s 2005) as well as two names suggested to originate in the SW Middle East and/or Somalia, *rufus* and *humbloti* (G o o d m a n & R a n i v o 2009) all seem to be appropriate for the species above designed as the 'second unit' within *Triaenops*, composed by the Middle Eastern morphotypes B and C. Since the above analyses indicate a close proximity of this species and the pair of syntypes of *T. persicus* from Iran, there is good reason to consider this name for this larger sized Middle Eastern species. The types of *rufus* and *humbloti* were shown by our morphologic analysis to be closest to the morphotype C originating in western Yemen, and therefore, we suggest the origin of these types in Aden area (south-western Yemen) as already proposed by G o o d m a n & R a n i v o (2009). The origin in Somalia is less probable since in continental Africa such a morphotype (nor any close one) was not found, even among Somalian samples, although it is not possible to disprove its presence there due to the geographical proximity of these areas. The synonymy of the names *rufus* and *humbloti* with *persicus* as already suggested by G o o d m a n & R a n i v o (2009) seems to be confirmed in our analysis.

The name *macdonaldi* was proposed by H a r r i s o n (1955) for the populations of south-eastern Arabia, from the oasis of Buraimi on the present border of Oman and U. A. E. as a form of similar size as *T. persicus* from Iran (LAt 47.1–51.6 mm; LCc 16.2–17.2 mm; $CM^3$ 6.3–6.6 mm [H a r r i s o n 1955: 903]; cf. Table 2, Middle East morphotype B), but of a slightly paler pelage colour. Since the pelage coloration, both its tinge and intensity, was found to be extremely variable within *Triaenops*, we regard this name to be a junior synonym of the name *T. persicus*. This opinion is also more convenient from the biogeographical point of view as the Iranian and Pakistani populations seem to be only small projections from an Arabian centre of the range of this form across the Strait of Hormuz, Persian Gulf. The validity of this subspecies was doubted already by D e B l a s e (1980), who examined and compared both type series (of *persicus* and *macdonaldi*) in detail, and this was accepted by subsequent authors (H i l l 1982, K o o p m a n 1994, S i m m o n s 2005).

Anyway, if the Omani populations really differ from the Iranian ones as tentatively suggested by H a r r i s o n & B a t e s (1991), this difference has never been expected on the species level and moreover, the name *macdonaldi* – although we did not have an opportunity to examine its type series – is absolutely not applicable for the smaller Yemeni species, referred here as Middle East morphotype A. This form, characterised by very small body size, cannot be attributed to the name *macdonaldi* as its type series fully conform with Iranian *persicus* in size (H a r r i s o n 1955, D e B l a s e 1980, H i l l 1982) as well as with our Yemeni morphotype B. Therefore, we propose a new name for the newly recognised species of morphotype A from south-eastern Yemen, see the Taxonomic Part of this paper. The area of eastern Yemen belongs to the most arid parts of the range inhabited by the genus *Triaenops*. From the ecological point of view, it is rather startling to find two species living there in sympatry as in other more fertile parts of genus range (*Triaenops* s.str.), only monospecific populations are known (with an exception of Madagascar).

From the above comparison it remains clear that the western Yemeni populations of *T. persicus* formerly assigned to the African form *afer* (for the first time suggested by H a r r i s o n 1964) is a part of the Middle Eastern form *T. persicus* s.str. (in the sense of the present review), although their representatives are larger than those of the typical *T. persicus* (of the morphotype B). However, this difference in just size could be explained by a clinal shift of the size characters along the southern Arabian coast. Although the geographic distance between the collection areas comprises nearly 1 000 km and the size variation ranges of both forms overlap only minutely, gene flow among them seems to be present as in both areas identical haplotypes in 1140 bp of the mitochondrial genome were found.

The topologies obtained by all methods exhibited rather low bootstrap and posterior probability supports for mutual positions of the six distinct clades of *Triaenops*, obtained from the analysis of 731 bp portion of cytochrome *b*. In particular, the position of *T. menamena* appeared questionable after comparison of the MP tree, suggesting a sister position of *T. menamena* to the Middle Eastern clades, and the ML tree, which did not corroborate monophyly of *T. menamena* and placed *T. menamena* haplotypes at the base of the Afro-Arabian lineage. According to R u s s e l l et al. (2007, 2008), *T. menamena* is a sister taxon to the African group of haplotypes (= *T. afer*, see above). This form represents a result of the second colonisation event ca. 0.66 MA to Madagascar from Africa, following the first colonisation 2.25 MA, which resulted in a pair of the other currently recognised Malagasy species *T. auritus* and *T. furculus* (here separated to a new genus, see below). Testing of alternative hypotheses assuming either a sister relationship of *T. menamena* and the Middle Eastern forms, a sis-

ter relationship of *T. menamena* and the African form or a basal position of *T. menamena* in the Afro-Arabian lineage (Fig. 10), however, suggested that *T. menamena* is also closely related to the Middle Eastern populations. As an alternative to the hypothesis of the second colonisation of Madagascar from neighbouring East African regions suggested by R u s s e l l et al. (2007, 2008), this colonisation may thus have occurred via a northern route from north-eastern Africa or the Arabian Peninsula as well. Our results further suggest that this colonisation occurred much more in the past, ca. 4 MA. Similarly much older, ca. 35 MA, appears the split within the genus *Triaenops* leading to the first colonisation of Madagascar. Order-of-magnitude discrepancies between R u s s e l l ' s et al. (2008) dating of these splits and ours probably can be attributed to the different approaches used, i.e. coalescent analysis and traditional phylogenetic inference. Although we admit inaccuracy of our clock-like ML tree, sequence divergencies on generic level between the two main *Triaenops* lineages (Table 6) suggest the estimate of 2.25 MA to be too low. It is beyond discussion that additional independent evidence from other molecular markers and more extensive sampling should be included to fully resolve true geographic origin of Malagasy *T. menamena* and reliable dating of important evolutionary split events within the current genus *Triaenops*.

## Taxonomic Part

### *Triaenops parvus* sp. nov.

Holotype. Adult male (NMP 92270 [S+A]), Hawf, Yemen, 15 October 2005, leg. P. B e n d a. Paratypes (7). Four adult males, three adult females (NMP 92264, 92265, 92267, 92269 [S+A], 92268 [A], BCSU field Nos. pb3009, pb3010 [S+A]), Hawf, Yemen, 14 October 2005, leg. P. B e n d a.

Type Locality. Republic of Yemen, Province of Al Mahra, oasis of Hawf (easternmost edge of the country), 16° 39' N, 53° 03' E, 410 m a. s. l.

Description and Diagnosis. Smallest representative of the genus *Triaenops* Dobson, 1871 s.str. (= *T. persicus*, *T. menamena*, *T. afer*, and *T. parvus* sp. nov.). It is in most respects very similar to other species of the genus *Triaenops* s.str., including the structure and relative size of noseleaf (Figs. 8 and 14). In body and skull size, *T. parvus* sp. nov. clearly differs from *Triaenops persicus* (Fig. 13) and *T. afer*, but overlapping dimensionally with *T. menamena* (Fig. 3). Forearm length 44.7–48.1 mm, occipitocanine length of skull 16.3–17.4 mm, length of the upper tooth-row 5.8–6.2 mm. *T. parvus* sp. nov. shares the shape of rostrum with *T. menamena*; it is relatively short and narrow, and in this character differs from *T. afer* (with broad and short rostrum) and *T. persicus* (with broad and long rostrum). *T. parvus* sp. nov.

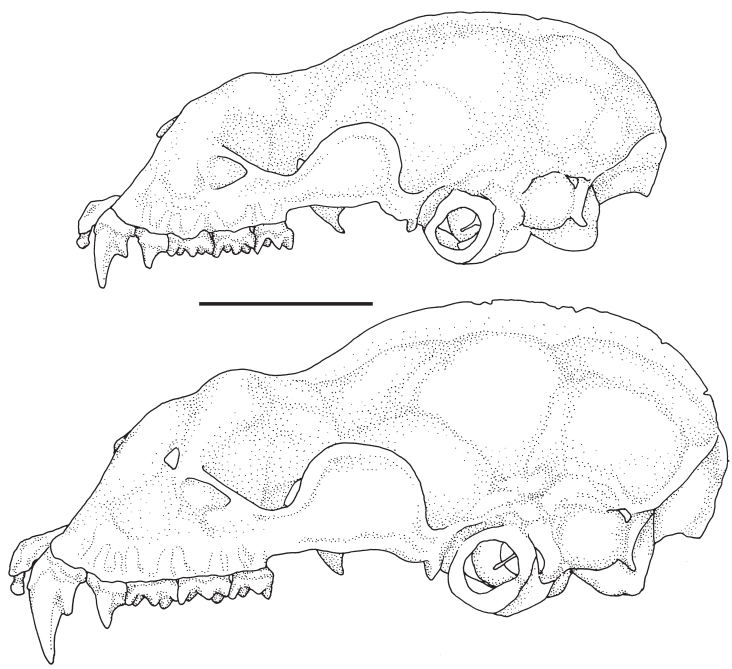

**Fig. 13.** Skulls of two *Triaenops* morphotypes from Hawf, south-eastern Yemen: above = morphotype A, female, NMP 92267 [= *Triaenops parvus* sp. nov.]; below = morphotype B, male, NMP 92254 [= *Triaenops persicus* s.str.]. Scale bar = 5 mm.

has relatively high braincase (character shared with *T. afer* and *T. persicus* and differing from *T. menamena*). *T. parvus* sp. nov. has relatively large tympanic bullae (character shared with *T. menamena*) – their large horizontal diameters represent 15–17% of the occipitocanine length of skull, although absolutely they are comparatively small (2.6–2.9 mm). From *T. persicus* s.str. living in sympatry with *T. parvus* sp. nov., the latter form differs by less dorsally prominent posterior nasal swellings and a much less pronounced sagittal crest on the skull (Fig. 13).

*T. parvus* sp. nov. is similar to members of the genus *Paratriaenops* gen. nov. in size, but it differs by having larger wings (forearms relatively longer) and totally different rostral shape and noseleaf structure (see Fig. 14 and the description of *Paratriaenops* gen. nov. below).

The baculum of *T. parvus* sp. nov. is a long gracile bone roughly 1.5 mm long, with broad basal epiphysis and bifurcated distal epiphysis; it has a relatively very narrow diaphysis (ca. 8% of the baculum length) with relatively short arms at its distal epiphysis (length of arm represent ca. 17–20% of the baculum length) and relatively narrow proximal epiphysis (width of the basis 23 and 31% of the baculum length). In two examined bones, there were distinct proximal projections in their bases, possibly representing an ossified distal part of the erectile penial body, however, this character is hardly typical for *T. parvus* sp. nov. without examination of a sufficiently numerous series of bacula.

The coloration of the dorsal pelage of *T. parvus* sp. nov. is beige or pale brownish-grey (without reddish or rusty tinges), ventral pelage is very pale beige to pale greyish-brown. Noseleaf is unpigmented to pale greyish-brown. Wing membranes are dark brown.

**Genetics**. Within the genus *Triaenops* s.str. (except for *T. menamena*, i.e. 11 haplotypes from *T. parvus* sp. nov., *T. persicus* and *T. afer*; see Appendix 3), *T. parvus* sp. nov. showed unique base positions within the complete mitochondrial gene for cytochrome *b* (1140 bp) at 39 sites: 231, 405, 408, 423, 462, 585, 609, 685, 711, 753, 759, 813, 816, 960 (A→G), 42, 180, 285, 312, 569, 644, 789, 924, 969, 993 (C→T), 18, 129, 138, 640, 898, 907, 1105, 1131 (G→A), 351, 456, 498, 858, 979 (T→C), 696 (C/A→T), and 750 (G/C→A).

*Triaenops parvus* sp. nov. shares identical unique base positions within the complete mitochondrial gene for cytochrome *b* (1140 bp) with *T. persicus* Dobson, 1871 at 41 sites (Appendix 3): 168, 171, 352, 486, 552, 576, 697, 720, 864, 873, 888, 915, 996, 1023 (A), 5, 54, 135, 207, 354, 396, 432, 459, 558, 561, 636, 708, 717, 732, 906, 939, 999 (C), 111, 429, 483, 984 (G), 87, 186, 291, 724, 744, 819 (T); and with *T. afer* Peters, 1877 at 28 sites (Appendix 3): 93, 117, 234, 297, 450, 861, 897, 1069 (A), 309, 321, 473, 478, 633, 718, 846, 891, 948, 990 (C), 369, 480, 1026 (G), 261, 286, 327, 579, 666, 672, and 840 (T). Within the 731 bp partial sequence of the mitochondrial gene for cytochrome *b*, *Triaenops parvus* sp. nov. shares identical unique base positions with *T. menamena* at three sites only (Appendix 4): 138 (A), 231 and 711 (G).

DIMENSIONS OF THE HOLOTYPE. See Table 3.

MITOCHONDRIAL SEQUENCE OF THE HOLOTYPE (complete sequence of the mitochondrial gene for cytochrome *b*; GenBank Accessite Number EU798754; haplotype ME8 [Appendix 2], 5' end). atg acc aac ata cga aaa tcc cac cca cta ttc aaa att att aac gac tca ttc gta gac ctc cca gcc cca tcc agc atc tca tct tga tga aac ttt ggc tca cta ctg ggc gta tgc tta gca gta cag atc tta act ggc cta ttc cta gcc ata cac tac aca gca gac aca gct acc gct ttc caa tca gtc acc cat atc tgc cga gac gtt aat tac ggt tgg gta ctg cgc tat ctc cac gcc aac gga gct tcc ata ttc ttc atc tgc cta ttt tta cat gta gga cgt ggc atc tac tat gga tcc tac aca ttt aca gaa aca tga aac att ggc atc atc ctc cta ttc gcg gtg ata gca aca gca ttc atg ggc tat gtc cta cca tgg ggg cag ata tcc ttc tgg ggg gcg acc gtc att act aac tta

cta tcc gcc atc ccg tac atc gga aca agc ctg gtg gaa tga gta tga ggc ggc ttc tca gta gac aaa gcc act cta aca cga ttt ttc gcc cta cac ttc cta ctc ccc ttc atc atc gta gcc cta gtt atg gtg cac ctc tta ttc cta cac gaa acg gga tcc aac aac cca aca gga atc ccc tca aat gtg gac ata atc ccg ttc cac cct tat tat aca atc aaa gac gtc ctc ggc ctt atc cta ata atc atg gct ctc cta tct tta gta ctc ttt tca cca gat tta cta ggg gac ccg gat aac tac acc cca gcc aac cca cta aat aca ccc cca cat att aaa cca gag tgg tat ttc ctc ttt gcc tac gcc att cta cgc tca att ccc aac aaa cta gga ggc gta gta gcc tta gta tta tcc atc cta atc ctt gcc atc atc cca cta cta cat aca tca aaa caa cgc agc atg acc ttc cga cca ctg agc cag tgt cta ttt tga ctc ctg gta gcc gat cta gcc aca ctc acc tga atc gga gga caa ccg gtt gaa cac cca ttt atc atc atc ggc caa ata gcc tca att atc tac ttc tta atc atc cta gta ctc ctc cca cta aca agt atc gca gaa aac cgc cta tta aaa tga aga.

Derivatio nominis. The name *parvus* (= small in Latin) reflects the extraordinary small size of the species representatives, the main character which distinguishes the new species from all other species within *Triaenops* sensu stricto.
Distribution. *Triaenops parvus* sp. nov. is known from three sites in the easternmost part of Yemen, all in the province of Al Mahra; Hawf, Damqawt, and 25 km WSW of Sayhut, distant for ca. 270 km from each other at maximum.

### *Paratriaenops* gen. nov.

Type species. *Triaenops furcula* Trouessart, 1906: *Bulletin du Muséum d'Histoire Naturelle, Paris 7*: 446.
Description. Medium-sized bats, forearm length 42–51 mm, greatest length of skull 15.9–18.8 mm, condylocanine length of skull 14.1–16.2 mm (R a n i v o & G o o d m a n 2006). Ears large, internal border of ear is not notched.
**Noseleaf** (Figs. 1C–E and 14b). Noseleaf relatively simple and large, bearing three long trident-like posterior projections and a medial process. Anterior leaf lacks lateral supplementary leaflets; the internarial projection (leaflet) is narrow, forked in mesial direction, its lateral margins are parallel and its mesial projections are broad and nearly pointed. Lateral margins of the posterior leaf are parallel or slightly convex; the posterior leaf composed of eleven cells, five cells surrounding the caudal margin of the intermediate leaf; their dividing septa are thin, most lateral cells basally without septa. Posterior medial cell very large, wider than the base of medial posterior projection and almost as wide as the intermediate leaf, sagitally incompletely divided by a low septum. Medial process of the intermediate leaf is small and laterally flattened. The posterior projections are long, almost as long as the anterior leaf; the medial projection wider than the lateral ones, which are slightly shorter. The projections extend across the whole width of caudal margin of the posterior leaf. Lateral margins of the projection bases extend ventrally to form the lateral walls of the adjacent cells.
**Skull** (R a n i v o & G o o d m a n 2006: 972, Fig. 3A, B; 973, Fig. 4A, B). Skull is typical with dorsally projecting and posteriorly tapered nasal swellings, their anterior margins are nearly vertical. In the interorbital region, a deep post-nasal concavity is present and in frontal region there is a low sagittal crest. In the dorsal view, nasal swellings are triangular-shaped with extremely short anterior celullae and extensive posterior celullae, in the mesio-distal direction they are twice as long as the anterior ones. The dorsal margin of nasal openings stretches mesially to a level of tips of the second upper premolars ($P^4$). Interorbital constriction is relatively narrow (mostly below 12% of the occipitocanine length of skull). Premaxil-

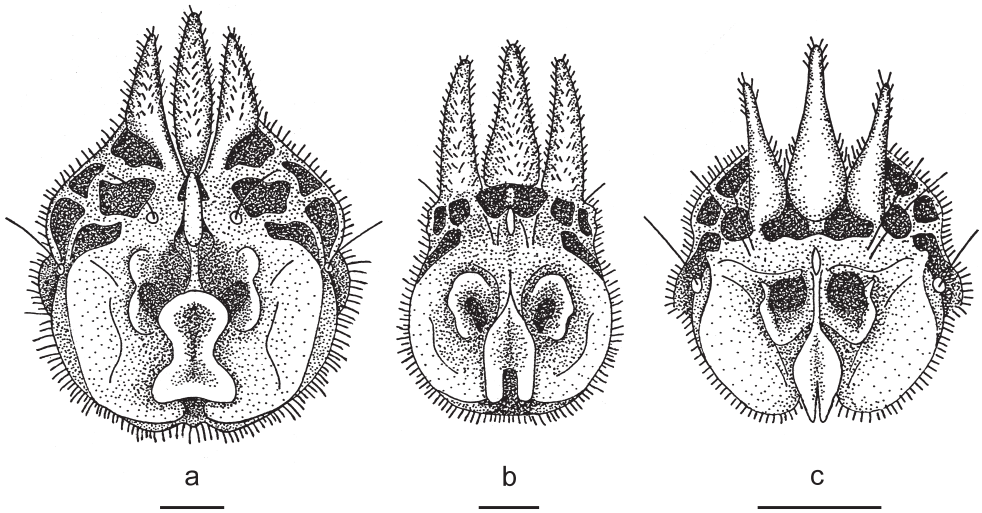


**Fig. 14.** Noseleafs of three close related genera of trident bats (after H i l l 1982); a – *Triaenops* Dobson, 1871; b – *Paratriaenops* gen. nov.; c – *Cloeotis* Thomas, 1901. Scale bars = 2 mm.

lae are mesio-distally relatively short, shorter than the palate, sphaenoidalia as broad as the interorbital part of frontalia. Zygomata bear high postorbital processes. Bullae tympanicae are mediolaterally narrow.

**Genetics**. *Paratriaenops* gen. nov. showed unique base positions in 731 bp partial sequence of the mitochondrial gene for cytochrome *b* at 72 sites (9.8% of the sequence, 29.0% of the variable sites; Appendix 4; haplotypes of the NCBI Accessite Numbers DQ005787, DQ005795, DQ005843, and DQ005849) within the group of close genera *Triaenops* s.str. (12 haplotypes), *Cloeotis* (one haplotype) and *Paratriaenops* gen. nov. (four haplotypes): 330, 402, 630 (A→C), 258, 617 (A→G), 336, 624 (A→T), 63, 183, 201, 555, 694 (C→A), 120, 125, 150, 156, 174, 198, 276, 303, 323, 355, 365, 384, 417, 420, 573, 597, 660, 700 (C→T), 67, 387 (G→A), 331 (G→C), 712 (G→C/T), 39, 345, 441, 534, 669, 670 (T→C), 522 (T→A/C), 492 (A/C→G), 12, 195, 687 (A/C→T), 138, 147, 171, 333, 429, 645, 657, 720 (A/G→C), 66 (A/G→T), 480, 582, 675 (A/G→C/T), 57, 105, 594, 729 (A/T→C), 48, 264, 357, 501, 579 (C/T→A), 228 (C/T→G), 399 (A/C/G→T), 234, 297 (A/G/T→C), and 87, 141 (C/G/T→A).

*Paratriaenops* gen. nov. shares identical unique base positions with *Triaenops* Dobson, 1871 at 47 sites (6.4% of the sequence, 18.9% of the variable sites; Appendix 4) of the examined part of cyt *b*: 27, 213, 294, 324, 328, 375, 381, 466, 471, 472, 474, 475, 507, 525, 580, 612, 705 (A), 6, 69, 75, 190, 244, 246, 252, 280, 318, 342, 358, 453, 465, 468, 477, 537, 540, 541, 549, 564, 688, 693 (C), 127, 232, 476, 643 (G), and 99, 136, 222, 393 (T); and with *Cloeotis* Thomas, 1901 at 29 sites (4.0% of the sequence, 11.7% of the variable sites; Appendix 4): 55, 114, 124, 132, 219, 237, 300, 348, 364, 483, 574, 615, 690, 699, 714 (A), 177, 192, 204, 315, 369, 438, 585, 592, 642, 710 (C), and 81, 96, 178, 713 (T).

DIFFERENTIAL DIAGNOSIS. *Paratriaenops* gen. nov. is very similar to *Triaenops* Dobson, 1871 and *Cloeotis* Thomas, 1901, it differs from both the genera mainly in the shape and mor-

phology of the noseleaf (Fig. 14), and by lacking of lateral supplementary leaflets; it differs from *Triaenops* by its narrow internarial projection forked in the mesial direction (character shared with *Cloeotis*, in which is rather diamond-shaped). *Paratriaenops* gen. nov. has relatively the longest trident-like pointed processes on the posterior leaf, being as long as or even longer than the anterior leaf. The medial process of the intermediate leaf is smaller in *Paratriaenops* gen. nov. than in *Triaenops* Dobson, 1871. The skull of *Paratriaenops* gen. nov. has triangular-shaped nasal swellings (when viewed dorsally) with extremely short anterior celullae (in mesio-distal direction) and extensive posterior celullae; in *Triaenops* there are broad and rather rectangular nasal swellings, and anterior and posterior celullae are equally long mesio-distally (see R a n i v o & G o o d m a n 2006: 973, Fig. 4). In the lateral view, the skull of *Paratriaenops* gen. nov. has a deep post-nasal concavity and dorsally prominent nasal swellings, rather similar to state in the genus *Rhinolophus* Lacépède, 1799, and completely differing from that in *Triaenops* Dobson, 1871. *Paratriaenops* gen. nov. differs from *Cloeotis* Thomas, 1901 in having dorsal vertical processes on zygomata (sharing with *Triaenops* Dobson, 1871, and also with somer other hipposiderids); *Cloeotis* has relatively much smaller and more rounded ears.

Derivatio Nominis. The name refers to close similarity of *Paratriaenops* gen. nov. with the genus *Triaenops* Dobson, 1871; Greek prefix *para-* means beside, next to. Masculinum.
Content. *Paratriaenops* gen. nov. contains three named species, *Triaenops furcula* Trouessart, 1906 [= *Paratriaenops furculus* comb. nov.], *Triaenops aurita* Grandidier, 1912 [= *Paratriaenops auritus* comb. nov.], and *Triaenops pauliani* Goodman et Ranivo, 2008 [= *Paratriaenops pauliani* comb. nov.]. (Although we had not an opportunity to examine any individual of *P. pauliani* comb. nov., we accept its separation from the species rank of *P. furculus* comb. nov. by G o o d m a n & R a n i v o 2008.)
Distribution. Western and northern parts of Madagascar and southwestern islands of Seyechelles (Aldabra and Cosmoledo Atolls) (H a y m a n & H i l l 1971, H i l l 1982, R u s s e l l et al. 2007, G o o d m a n & R a n i v o 2008).

Affiliation. Although substantially distant for the generic level, *Paratriaenops* gen. nov. is systematically positioned close to the genus *Triaenops* Dobson, 1871. According to the above genetic analyses, this pair of genera is a sister group to the most of the remaining content of the family Hipposideridae Lydekker, 1891 (see above). For these closely related genera we here propose a new tribe within that family:

**Triaenopini trib. nov.**

Type genus. *Triaenops* Dobson, 1871: *Journal of the Asiatic Society of Bengal 40*: 455.

Description. Hipposiderid bats with a noseleaf bearing four tall pointed projections on the strongly cellularised posterior leaf, three of them forming a trident-like structure on the caudal margin. A strap-like projection extending forward from the internarial region is typical for the anterior leaf (Figs. 1 and 14).
Content. *Triaenops* Dobson, 1871 and *Paratriaenops* gen. nov. Most probably, Triaenopini trib. nov. also includes genetically and mainly morphologically closely related genus *Cloeotis* Thomas, 1901, however, for its inclusion, more robust genetic evidence must be gathered.

## Conclusions

The above presented revision we summarise into the following review of the classification of *Triaenops* (*sensu* S i m m o n s 2005):

Triaenopini trib. nov.

- *Triaenops* Dobson, 1871
  - *Triaenops persicus* Dobson, 1871 (SE Middle East from SW Yemen to S Iran and Pakistan)
    - = *T. rufus* Milne-Edwards, 1881
    - = *T. humbloti* Milne-Edwards, 1881
    - = *T. persicus macdonaldi* Harrison, 1955
  - *Triaenops afer* Peters, 1877 (East Africa from Eritrea to Mozambique, SW Congo, NW Angola)
    - = *T. persicus majusculus* Aellen et Brosset, 1968
  - *Triaenops parvus* sp. nov. (SE Yemen)
  - *Triaenops menamena* Goodman et Ranivo, 2009 (Madagascar)
- *Paratriaenops* gen. nov.
  - *Paratriaenops furculus* (Trouessart, 1906) comb. nov. (Madagascar)
  - *Paratriaenops auritus* (Grandidier, 1912) comb. nov. (Madagascar)
  - *Paratriaenops pauliani* (Goodman et Ranivo, 2008) comb. nov. (SW Seychelles)

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**Appendix 1**
List of the material examined in morphologic analysis (in alphabetical order)

***Triaenops afer* Peters, 1877**

**Central African Republic**: 2 m, 1 f (MNHN 1985-1198, 1985-1199, 1985-1366 [S+A]), La Maboké, leg. R. P u j o l. – **Congo (Brazzaville)**: 3 m, 2 f (MNHN1968-412 [S+A], holotype of *Triaenops persicus majusculus* Aellen et Brosset, 1968; MNHN 1985-1348a, 1985-1348b, 1985-1349, 1985-1497 [S+A]), Grotte de Doumboula, Loudima (Kouilou), 19 June 1964, leg. J. P. A d a m; – 2 f (MNHN 1985-1350, 1985-1351 [S+A]), Grotte de Meya-Nzouari (Kouilou), 22 November 1966, leg. J. P. A d a m. – **Ethiopia**: 1 m (MZUF 6031 [S+A]), Gorgorà, Lago di Tana, 25 March 1937, leg. C a s t e l l i; – 1 m (MZUF 7863 [S+A]), Migiurtinia, Oasi di Galgalo, 8 October 1973, collector unlisted; – 8 m, 6 f (NMP 92150–92152, 92161, 92163–92167 [S+A], 92153, 92160, 92162, pb2497, pb2521 [A]), Sof Omar Caves, 2 and 3 May 2003, leg. P. B e n d a & J. O b u c h. – **Kenya**: 1 f (MZUF 4361 [S+A]), Kilifi, 3 November 1968, leg. B. L a n z a; – 1 m (ZMB 5074 [S+A], holotype of *Triaenops afer* Peters, 1877), Mombaca, leg. J. M. H i l d e b r a n d t. – **Somalia**: 6 m, 4 f (MZUF 13074, 13086, 13088, 15719, 15721, 15725–15727, 15729 [S+A]), Grotta di Showli Berdi, 14 March 1984, leg. L. C h e l a z z i & G. M e s s a n a, 24–25 November 1985, leg. M. B o r r i & L. C h e l a z z i; – 1 f (MZUF 2233 [S+A]), Pozzi di Mahas, 9 August 1959, leg. A. S a m m i c h e l i; – 1 m (MSNG 44301 [A]), Pozzi Meddo Erelle, 9–11 February 1896, leg. V. B o t t e g o. – **Tanzania**: 6 inds. s.i. (MNHN 1911-730/3–5, 8, 10 [S+A]), Tanga, Grotte de Kulumuzi, 1909, coll. M. A l l u a u d.

***Triaenops menamena* Goodman et Ranivo, 2009**

**Madagascar**: 1 m (MZUF 6185 [A]), Fort Dauphin, leg. S c h n e i d e r; – 1 m, 1 f (MNHN 1947-861, 1947-862 [S+B]), Lac Tsimanompetsoa, 20 February 1930, leg. Mission F. A. A.; – 2 inds. s.i. (MNHN 1996-352, 1996-353 [S+B]), Tsaratanana, 16° 46' N, 47° 40' E, November 1966; – 2 m, 1 f (MNHN1985-487–1985-489 [S+A]), Madagascar, February 1959, leg. A. R o b i n s o n; – 1 ind. s.i. (MNHN 1947-312 [S+A]), Madagascar, October 1938, leg. R. D e c a s y; – 1 m, 2 f (MNHN 1985-480–1985-482 [S+A]), Madagascar, September 1952, leg. R. P a u l i a n .

***Triaenops parvus* sp. nov.**

**Yemen**: 1 m (NMP 92272 [S+A]), Damqawt, 16 October 2005, leg. P. B e n d a; – 5 m, 3 f (NMP 92270 [S+A], holotype of *Triaenops parvus* sp. nov.; BCSU pb3009, pb3010 [S+A], NMP 92264, 92265, 92267, 92269 [S+A], 92268 [A]), Hawf, 14 and 15 October 2005, leg. P. B e n d a; – 1 m (NMP 92274 [S+A]), 25 km WSW of Sayhut, 17 October 2005, leg. P. B e n d a.

***Triaenops persicus* Dobson, 1871**

**Iran**: 1 m, 1 f (ZMB4370/1–2 [S+A], syntypes of *Triaenops persicus* Dobson, 1871), Shiraz. – **Yemen**: 1 m, 1 f (NMP 92271, 92273 [S+A]), Damqawt, 16 October 2005, leg. P. B e n d a; – 9 m, 5 f (NMP 92253, 92254, 92256–92262, 92266 [S+A], 92255, 92263 [A], BCSU pb3037, pb3038 [S+A]), Hawf, 12, 14 and 15 October 2005, leg. P. B e n d a; – 2 m, 1 f (NMP 92275, 92276 [S+A], BCSU pb3123 [S+A]), Jebel Bura, W of Riqab, 30 October 2005, leg. P. B e n d a; – 1 f (NMP 92277 [S+A]), Wadi Tuban, Kadamat al'Abali, 24 October 2007, leg. P. B e n d a & A. R e i t e r; – 1 m (NMP 92279 [S+A]), Wadi Zabid, ca. 10 km SE of Al Mawkir, 30 October 2007, leg. P. B e n d a & A. R e i t e r; – 1 f (NMP 92278 [A]), Wadi Zabid, ca. 15 km SE of Al Mawkir, 29 October 2007, leg. P. B e n d a & A. R e i t e r. – **Yemen (?)**: 4 inds. s.i. (MNHN 1997-1854 [S+A], holotype of *Triaenops rufus* Milne-Edwards, 1881; MNHN 1997-1856, 1997-1857 [S+A], 1997-1857 [A]), Madagascar [incorrect locality], 1880, leg. L. H u m b l o t; – 3 m, 3 f, 4 inds. s.i. (MNHN 1962-2659 [S], holotype of *Triaenops humbloti* Milne-Edwards, 1881; MNHN 1985-836–1985-842, MSNG 44521a, b [A]), Madagascar, cote est [incorrect locality], 1880, leg. L. H u m b l o t.

***Paratriaenops furculus* (Trouessart, 1906) comb. nov.**

**Madagascar**: 10 m, 5 f (MNHN 1912-40 [A], holotype of *Triaenops furcula* Trouessart, 1906; MNHN 1912-40b, 1912-40c [S+A], 1997-1859, 1997-1864–1997-1866 [S+A], MNHN 1997-1860–1997-1863, 1997-1867, MSNG 44891a, b [A]), Grotte de Sarondrana [= Sarodrano], 19 May 1898, leg. G. G r a n d i d i e r.

**Appendix 2**
List of the material used in the genetic analysis

| No. Coll. | haplotype [1140] | [731] | accession No. | species | state | site / [author] |
|---|---|---|---|---|---|---|
| NMP 92150 | EA1 | EA11 | EU798748 | *Triaenops afer* | Ethiopia | Sof Omar Caves |
| NMP 92152 | EA2 | EA12 | EU798749 | *Triaenops afer* | Ethiopia | Sof Omar Caves |
| NMP 92167 | EA2 | EA12 | | *Triaenops afer* | Ethiopia | Sof Omar Caves |
| NMP 92163 | EA3 | EA13 | EU798750 | *Triaenops afer* | Ethiopia | Sof Omar Caves |
| – | – | EA14 | DQ005799 | *Triaenops afer* | Tanzania | [R u s s e l l et al. 2007] |
| – | – | EA15 | DQ005807 | *Triaenops afer* | Tanzania | [R u s s e l l et al. 2007] |
| NMP 92254 | ME1 | ME11 | EU798751 | *Triaenops persicus* | Yemen | Hawf |
| NMP 92266 | ME1 | ME11 | | *Triaenops persicus* | Yemen | Hawf |
| BCSU pb3038 | ME1 | ME11 | | *Triaenops persicus* | Yemen | Hawf |
| NMP 92277 | ME1 | ME11 | | *Triaenops persicus* | Yemen | Wadi Tuban |
| NMP 92273 | ME1 582bp | – | – | *Triaenops persicus* | Yemen | Damqawt |
| NMP 92278 | ME1 610bp | – | – | *Triaenops persicus* | Yemen | Wadi Zabid |
| NMP 92271 | ME2 | ME11 | EU798755 | *Triaenops persicus* | Yemen | Damqawt |
| NMP 92276 | ME3 | ME12 | EU798757 | *Triaenops persicus* | Yemen | Jebel Bura |
| NMP 92279 | ME3 610bp | – | – | *Triaenops persicus* | Yemen | Wadi Zabid |
| BCSU pb3123 | ME4 | ME11 | EU798758 | *Triaenops persicus* | Yemen | Jebel Bura |
| NMP 92265 | ME5 | ME13 | EU798752 | *Triaenops parvus* sp. nov. | Yemen | Hawf |
| NMP 92267 | ME6 | ME14 | EU798753 | *Triaenops parvus* sp. nov. | Yemen | Hawf |
| NMP 92269 | ME6 | ME14 | | *Triaenops parvus* sp. nov. | Yemen | Hawf |
| NMP 92272 | ME7 | ME14 | EU798756 | *Triaenops parvus* sp. nov. | Yemen | Damqawt |
| NMP 92274 | ME7 | ME14 | | *Triaenops parvus* sp. nov. | Yemen | WSW of Sayhut |
| NMP 92270 | ME8 | ME15 | EU798754 | *Triaenops parvus* sp. nov. | Yemen | Hawf |
| – | – | MDG1 | DQ005766 | *Triaenops menamena* | Madagascar | [R u s s e l l et al. 2007] |
| – | – | MDG2 | DQ005771 | *Triaenops menamena* | Madagascar | [R u s s e l l et al. 2007] |
| – | – | MDG3 | DQ005787 | *Paratriaenops auritus* comb. nov. | Madagascar | [R u s s e l l et al. 2007] |
| – | – | MDG4 | DQ005795 | *Paratriaenops auritus* comb. nov. | Madagascar | [R u s s e l l et al. 2007] |
| – | – | MDG5 | DQ005843 | *Paratriaenops furculus* comb. nov. | Madagascar | [R u s s e l l et al. 2007] |

**Appendix 2**
List of the material used in the genetic analysis (continued)

| No. Coll. | haplotype [1140] | [731] | accession No. | species | state | site / [author] |
|---|---|---|---|---|---|---|
| – | – | MDG6 | DQ005849 | *Paratriaenops furculus* comb. nov. | Madagascar | [R u s s e l l et al. 2007] |
| NMP 90351 | – | – | FJ457617 | *Asellia tridens* | Egypt | Siwa Oasis |
| – | – | – | DQ888677 | *Aselliscus stoliczkanus* | China | [L i et al. 2007] |
| – | – | – | DQ888675 | *Aselliscus tricuspidatus* | New Hebrides | [L i et al. 2007] |
| DNSM 8026 | – | – | FJ457615 | *Cloeotis percivali* | Swaziland | Wylesdale |
| DNSM 8021 | – | – | FJ457616 | *Cloeotis percivali* | Swaziland | Wylesdale |
| – | – | – | DQ888674 | *Coelops frithi* | Taiwan | [L i et al. 2007] |
| – | – | – | EU934448 | *Hipposideros abae* | Senegal | [V a l l o et al. 2008] |
| – | – | – | EU934452 | *Hipposideros caffer* | Senegal | [V a l l o et al. 2008] |
| – | – | – | EU934472 | *Hipposideros jonesi* | Senegal | [V a l l o et al. 2008] |
| IVB S004 | – | – | FJ457613 | *Rhinolophus alcyone* | Senegal | Assirik |
| IVB S817 | – | – | FJ457614 | *Rhinolophus fumigatus* | Senegal | Dindéfélo |
| IVB S826 | – | – | FJ457612 | *Rhinolophus landeri* | Senegal | Dindéfélo |
| – | – | – | AF376863 | *Myotis nattereri* | Europe | [R u e d i & M a y e r 2001] |
| – | – | – | AF376868 | *Myotis schaubi* | Europe | [R u e d i & M a y e r 2001] |
| – | – | – | AF376834 | *Vespertilio murinus* | Europe | [R u e d i & M a y e r 2001] |

**Appendix 3**
Polymorphic sites identified in the complete cyt *b* (1140 bp) sequenced in *Triaenops* Dobson, 1871 s.str.

| species | haplotype | .....1111111112222222223333333333344444444444444455555556 |
|---|---|---|
| | | .1345891122336788023368899012255566990022355567788895566778 0 |
| | | 5812473171958810678141561792171246969583920692380368281969 59 |
| *T. afer* | EA1 | TGTCTCAAATGTGGGCCTCAATCTCACCCTTGTTGTGAAAAAATTACCGCGTCATCGTAA |
| *T. afer* | EA2 | .....G..... |
| *T. afer* | EA3 | .....T.....G..A..... |
| *T. persicus* | ME1 | C...CTGGCC.C.AA.TC..GC.CTGT.TC.ACGACA...GCG.C.TTAGA.ACC.AC.. |
| *T. persicus* | ME2 | C...CTGGCC.C.AA.TC..GC.CTGT.TC.ACGACA...GCG.C.TTAGA.ACC.AC.. |
| *T. persicus* | ME3 | C.C.CTGGCC.C.AA.TC..GC.CTGT.TC.ACGACA...GCG.C.TTAGA.ACC.AC.. |
| *T. persicus* | ME4 | C...CTGGCC.C.AA.TC..GC.CTGT.TC.ACGACA...GCG.C.TTAGA.ACC.AC.. |
| *T. parvus* sp.n. | ME5 | CA.TCT.G.CACAAATTCTG..T.T..T..CACG.CAGGGGC.CCG...GACACCTA.GG |
| *T. parvus* sp.n. | ME6 | CA.TCT.G..ACAAATTCTG..T.T..T..CACG.CAGGGGC.CCG...GACACCTA.GG |
| *T. parvus* sp.n. | ME7 | CA.TCT.G..ACAAATTCTG..T.T..T..CACG.CAGGGGC.CCG...GACACCTA.GG |
| *T. parvus* sp.n. | ME8 | CA.TCT.G..ACAAATTCTG..T.T..T..CACG.CAGGGGC.CCG...GACACCTA.GG |

| | | .....1111111 |
|---|---|---|
| | | 6666666666777777777777778888888888888999999999999990001111 |
| | | 3344567899001112234555589111445667899900123466789999226002 3 |
| | | 3604762567281780424036998369068143817867549809940369369252 1 |
| *T. afer* | EA1 | CTGCATTACGGTAACGCACGACACAAACTCTAGGGCAGTGCCTCACTACCGTGGAAGCG |
| *T. afer* | EA2 | ..... |
| *T. afer* | EA3 | ..... |
| *T. persicus* | ME1 | TC..GCC.AA.C.CTATCTC.....TCT.GAAAGG.C.A.CT...GT.ACAAGC.T. |
| *T. persicus* | ME2 | TC..GCC.AA.C.CTATCTC....G..TCT.GAAAGG.C.A.CT...GT.ACAAGC.T. |
| *T. persicus* | ME3 | TC..GCC.AA.C.CTATCTC.....TCT.GAAAGG.C.A.CT...GT.ACAAGC.T. |
| *T. persicus* | ME4 | TC..GCC.AA.C.CTATCTC.T.....TCT.GAAAGG.C.A.CT...GT.ACAAGC.T. |
| *T. parvus* sp.n. | ME5 | .CATG..GTA.CGC.ATCTAG.GT.GGT..C.AAA..ACAATC.GTCG.TACA..CA.A |
| *T. parvus* sp.n. | ME6 | .CATG..GTA.CGC.ATCTAG.GT.GGT..C.AAA..ACAATC.GTCG.TACA..TATA |
| *T. parvus* sp.n. | ME7 | .CATG..GTAACGC.ATCTAG.GT.GGT..C.AAA..ACAATC.GTCG.TACA..CA.A |
| *T. parvus* sp.n. | ME8 | .CATG..GTA.CGC.ATCTAG.GT.GGT..C.AAA..ACAATC.GTCG.TACA..CA.A |

**Appendix 4**

Polymorphic sites identified in the partial cyt *b* (731 bp) sequenced in Triaenopini trib. nov., including *Cloeotis* Thomas, 1901

| species | haplotype | .....1111111111111111111111111111111122<br>..1122334445555666677889990011122222233334455566777788899999 00<br>5628781925814573679571736956147014579256817036281478036025 6814 |
|---|---|---|
| *T. afer* | EA11 | TCAGACTTCCCATGACAGCCGCCACTACACACTGCGGGTTGTACACCGGCAGCCCCAAGCCT |
| *T. afer* | EA12 | ..... |
| *T. afer* | EA13 | ..... |
| *T. afer* | EA14 | ..... |
| *T. afer* | EA15 | ..... |
| *T. persicus* | ME11 | C.....C.....TG....G.C.C.....C.....AA.....T..... |
| *T. persicus* | ME13 | C.....C.....C.....TG....G.C.C.....C.....AA.....T..... |
| *T. parvus* sp.n. | ME14 | C..A....T...C.....T.....G...C...A.C.A.....AA...T.T..... |
| *T. parvus* sp.n. | ME15 | C..A....T...C.....T.....G.....A.C.A.....AA...T.T..... |
| *T. parvus* sp.n. | ME16 | C..A....T...C.....T.....G.....A.C.A.....AA...T.T..... |
| *T. menamena* | MDG1 | .....T...TT.C...G.....T.....T.....AC..G.T.A.....T.G..... |
| *T. menamena* | MDG2 | .....T...TT.C...G.....T.....T.....AC..G...A.....T.G..... |
| *P. auritus* | MDG3 | ..TA.T.C..AG.ACATA...TA.T.C..A.T.AT.AAC.CACT.T.ACTCT.A..CTATAC |
| *P. auritus* | MDG4 | ..TA...C..AG.ACATA...TA.T.C..A.T.AT.AAC.CACT.T.ACTCT.A..CTATAC |
| *P. furculus* | MDG5 | ..TA...C..A..ACATA..ATAGT.CT.A.T.AT.AA..CACT.T.ACTCT.AT.CT.TAC |
| *P. furculus* | MDG6 | ..TA...C..A..ACATA..ATAGT.CT.A.T.AT.AA..CACT.T.ACTCT.AT.CT.TAC |
| *Cloeotis percivali* | | CACAG.C.AT.C.AT...TA.TG.TCT..A..CA.ATACC.GG.G..AA.CT...TCC...C |

**Appendix 4**
Polymorphic sites identified in the partial cyt *b* (731 bp) sequenced in Triaenopini trib. nov., including *Cloeotis* Thomas, 1901 (continued)

| species | haplotype | 222222222222222222222222222233333333333333333333333333333333333 |
|---|---|---|
| | | 011222333344444556677888899900001112222223333344455555566666667 |
| | | 739258124703469281436056814703692581346780136925812457803456 92 |
| *T. afer* | EA11 | TATTCCAGAGCTCCCCATCCCCCTACAATCCCCACCCATTAAGAAACTCTGTCCCACGCTGA |
| *T. afer* | EA12 | .....G.. |
| *T. afer* | EA13 | .....T.....G.. |
| *T. afer* | EA14 | .....T.....G....C.....G.. |
| *T. afer* | EA15 | .....T.....G.. |
| *T. persicus* | ME11 | C.....G.....C.....C.T.G...T...T...C.....AC.....GA. |
| *T. persicus* | ME13 | C.....G.....C.....C.T.G...T...T...C.....AC.....GA. |
| *T. parvus* sp.n. | ME14 | C....TG.....T..T.....T.....CAC.....G.. |
| *T. parvus* sp.n. | ME15 | C....TG.....T..T.....T.....CAC.....G.. |
| *T. parvus* sp.n. | ME16 | C....TG.....T..T.....T.....CAC.....G.. |
| *T. menamena* | MDG1 | C....TG.G..C..T...T....C.T.....T.....CAC.....A.. |
| *T. menamena* | MDG2 | C....TG.G.....T...T....C.T.....T.....G.....AC.....A.. |
| *P. auritus* | MDG3 | C.A.TG..CATC....GCA.T..CG..CATTT.C..T.A..CCCT..CA.ACTA...ATAC. |
| *P. auritus* | MDG4 | C.A..G..CATC....GCA.T..CG..CATTT.C..T.A..CCCT..CA.ACTA...ATAC. |
| *P. furculus* | MDG5 | C.A..G..CA.C....GCA.T..C...CAT.T.C..T....CCCT..CA.ACTA..TATACG |
| *P. furculus* | MDG6 | C.A..G..CA.C....GCA.T..C...CAT.T.C..T....CCCT..CA.ACTA.GTATACG |
| *Cloeotis percivali* | | CGAC...ATA.CTATT.C.T.T.CC.GTA.TT.CG..GACT.....T.ACAC.TT..A.AC. |

**Appendix 4**
Polymorphic sites identified in the partial cyt *b* (731 bp) sequenced in Triaenopini trib. nov., including *Cloeotis* Thomas, 1901 (continued)

| species | haplotype | 333333334444444444444444444444444444444444455555555555555555555 |
|---|---|---|
| | | 788899990001122223344555566667777777788899001223344445555666666 |
| | | 514703692581703692815036925681234567803628179254701390258124 79 |
| *T. afer* | EA11 | AACGCTTGAAAGCCAGAATTTACTTACACAACAAGCCGCGATCACTATCCCACCCCATACCC |
| *T. afer* | EA12 | ..... |
| *T. afer* | EA13 | .......A..... |
| *T. afer* | EA14 | .....G..... |
| *T. afer* | EA15 | .....G...G... |
| *T. persicus* | ME11 | ......CA........GC...G..C......T....TAGA..............A.CC.... |
| *T. persicus* | ME13 | ......CA........GC...G..C......T....TAGA..............A.CC.... |
| *T. parvus* sp.n. | ME14 | ......CA.GG...G.GC.....CCG.............GA.C.............A.CC...T |
| *T. parvus* sp.n. | ME15 | ......CA.GG...G.GC.....CCG.............GA.C.............A.CC...T |
| *T. parvus* sp.n. | ME16 | ......CA.GG...G.GC.....CCG.............GA.C.............A.CC...T |
| *T. menamena* | MDG1 | ....T.AA.........C..C...C.............AG.................CC.... |
| *T. menamena* | MDG2 | ....T.AA...A.....C..C...C.............AG..............G.TC.... |
| *P. auritus* | MDG3 | ..TA..ATC..ATT.ACCCCC.................TAAG.A..C.C...T.TAA.C.... |
| *P. auritus* | MDG4 | ..TA..ATC..ATT.ACCCCC.................TAAG.A..C.C...T.TAA.C.... |
| *P. furculus* | MDG5 | ..TA..ATCG.ATT..CCCCC.................CAAG.A.TA.C......AA.C..T. |
| *P. furculus* | MDG6 | ..TA..ATCG.ATT..CCCCC.................CAAG.A.TA.C......AA.C..T. |
| *Cloeotis percivali* | | GC..TC.C...A...A.CC.CCA.CCTGTGGTCGAT.AA.CGTCT.C.TTT.T...CCGT.. |

**Appendix 4**
Polymorphic sites identified in the partial cyt *b* (731 bp) sequenced in Triaenopini trib. nov., including *Cloeotis* Thomas, 1901 (continued)

| species | haplotype | 5555555555555666666666666666666666666666666666677777777777777777<br>7777788899999001112233344444456667778889999990000011111112222<br>0346902512478092574703602345870690255780346790256801234780346 9 |
|---|---|---|
| *T. afer* | EA11 | ACCGTAGACTACCAAACAAAACTGTGCGCACTTTTAACCCCCCGCCGAATTAGCTACGTCAA |
| *T. afer* | EA12 | ..... |
| *T. afer* | EA13 | ..... |
| *T. afer* | EA14 | .....T..C.....TA.... |
| *T. afer* | EA15 | .....T..C.....C.....A.... |
| *T. persicus* | ME11 | ...AC.....TC.....G.C..C.....AA.....C.....CTA.T.. |
| *T. persicus* | ME13 | ...AC.....TC.....G.C..C.....AA.....C.....CTA.T.. |
| *T. parvus* sp.n. | ME14 | ...A...G.....G.....CA..T..G.....G.....TA.....C.G...C.A.T.. |
| *T. parvus* sp.n. | ME15 | ...A...G.....G.....CA..T..G.....G.....TA.....C.G...C.A.T.. |
| *T. parvus* sp.n. | ME16 | ...A...G.....G.....CA..T..G.....G.....TA..A..C.G...C.A.T.. |
| *T. menamena* | MDG1 | G..A.....T.TC.....T...A.....G...C.A.T.. |
| *T. menamena* | MDG2 | G..A.....G..T..T.TA.....A.....G...C.A.T.. |
| *P. auritus* | MDG3 | .TAAA.CCACCTT...AGT.C.A.C..CTCTCCCCT.T.A.A.AATA.GCC.TTA..CC.GC |
| *P. auritus* | MDG4 | .TAAA.CCACCTT...AGT.C.A.C..CTCTCCCCT.T.A.A.AATA.GCC.TTA..CC.GC |
| *P. furculus* | MDG5 | .TAAA.TCGCCT....AGT.C.A.C..CTCTCCCCC.T.A.A.AATA..CC.CTA..C...C |
| *P. furculus* | MDG6 | .TAAA.TCGCCT....AGT.C.A.C..CTCTCCCCC.T.A.A.AATA..CC.CTA..C...C |
| *Cloeotis percivali* | | G.AA.GACACT..C.CA.....A.CA.A...C..CG.ATAA.AAA.AG.CC..TAC.A...T |