THE AFFINITIES OF *PIPISTRELLUS RIDLEYI* THOMAS, 1898 AND *GLISCHROPUS ROSSETI* OEY, 1951 (CHIROPTERA: VESPERTILIONIDAE)

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INTRODUCTION

In a recent study Hill (1969) examined four further specimens of *Glischropus rosseti* Oey, 1951, hitherto known in the literature only from the holotype and paratype from Cambodia, and concluded that the species should be transferred to *Pipistrellus*, being allied to the equally poorly known *P. ridleyi*, described from Malaya by Oldfield Thomas many years before. Four additional specimens of *rosseti* have now been found in the collections of the Hungarian Natural History Museum, obtained at Bangkok nearly one hundred years ago by the traveller J. Xantus. Not immediately recognized as *rosseti*, their external features in particular suggested to one of us (G.T.) that they might represent the genus *Myotis*, and one skull was sent to London where its identity with *rosseti* was established. There seemed sufficient grounds, however, to justify a further examination of the generic affinities of the two species, Hill (1969 : 138) having considered their features distinctive enough to warrant the establishment of a separate group (the *ridleyi* group) within *Pipistrellus*.

SYSTEMATIC SECTION

For many years it remained customary to separate the genera *Myotis*, *Pipistrellus* and *Eptesicus* on the basis (in part) of the premolar dentition, the premolar formula of *Myotis* being $pm\frac{3}{3}-\frac{3}{3}$, of *Pipistrellus* $pm\frac{2}{2}-\frac{2}{2}$ and of *Eptesicus* $pm\frac{1}{2}-\frac{1}{2}$. In *Myotis* the central teeth ($pm\frac{3}{3}$) are small and sometimes displaced from the toothrows: in *Pipistrellus* they are presumed to have disappeared and the anterior premolars ($pm\frac{2}{2}$) are frequently much reduced, the upper tooth often displaced. The extent of reduction and degree of displacement has been and is used as a diagnostic feature at the specific level in both *Myotis* and *Pipistrellus*, and some authors such as Tate (1942) employ these features as indicators of "primitive" or "specialised" species, a greater degree of reduction and displacement being presumed to indicate greater specialisation, reflecting as it does the extent of shortening of the rostrum from a "primitive" long-nosed condition.

Premolar dentition of *Pipistrellus* and *Eptesicus*

In the last three decades much doubt has been cast on the adequacy of the premolar dentition in *Pipistrellus* and *Eptesicus* as a diagnostic generic feature, although many years ago Leche (1875 : 34) mentioned a specimen of *Pipistrellus maurus* (=*P. savii*) in which pm^2 was rudimentary and barely pierced the gum, and its occasional absence in this species was noted by Miller (1912 : 221). More recently,

Tate (1942 : 232, 271) questioned the validity of a distinction based on the presence or absence of an obsolescent, disappearing structure, bearing in mind that pm^2 may be present or absent in another vespertilionid genus, *Scotoecus*, but nevertheless retained the conventional distinction between *Pipistrellus* and *Eptesicus*. Kuzyakin (1944 : 101, 1950 : 388 et seq., 1965 : 103) and Topál (1959 : 91) noted and discussed the occasional absence of pm^2 from the toothrows of *Pipistrellus savii*: Kuzyakin referred the Russian species of *Pipistrellus* and *Eptesicus* to the related genus *Vespertilio*, but Topál (1958) described and illustrated differences in the baculum or os penis of their European species. The occasional presence of pm^2 in *Eptesicus capensis* was noted by Hayman (1954 : 289, 290) and in *E. pumilus* by Hill (1966 : 303) who also (1972 : 33) has described a specimen of *Pipistrellus javanicus* from Malaya which has a small supernumerary premolar in the right upper toothrow, situated in a recess or shallow angle between the postero-internal face of the canine and the antero-internal face of the usual anterior premolar. It is clear that the presence or absence of pm^2 can have no universal validity in defining *Pipistrellus* or *Eptesicus*, but most authors, e.g. Miller (1912 : 303), Ellerman & Morrison-Scott (1951 : 152) or Rosevear (1965 : 243), who have discussed the point retain them as distinct on grounds of convenience.

Premolar dentition of *Myotis*

The absence from one or both sides of the jaw of the "diagnostic" second upper premolar (pm^3) in *Myotis* has been reported on a number of occasions and the loss of the corresponding lower tooth (pm_3) less frequently so: occasionally the anterior upper tooth (pm^2) may be absent. Allen (1908 : 45) recorded a specimen of *M. nigricans* which lacked the right pm^3 and another lacking the left pm_3. Ärnbäck-Christie-Linde (1909 : 578) discussed dental variation in the same species, noting a specimen without the left pm^3 and a second example lacking $pm\frac{3}{3}$ from both sides of the jaw. This author also (p. 579) drew attention to specimens of *M. muricola* with pm^3 so reduced and displaced as to be quite functionless: the right pm^3 is lacking from a specimen (B.M. 10.4.6.24) of *muricola* in the collections of the British Museum (Natural History).

Miller & Allen (1928 : 7, 99) found pm^3 frequently absent from the toothrows of *M. occultus* (=*M. lucifugus occultus*) and pm_3 occasionally so: in *M. lucifugus carissima* these authors reported (p. 53) a specimen without the right pm_3 and with (pp. 8, 53) the left pm^{2-3} coalesced, while in *M. thysanodes* they recorded (p. 124) a specimen lacking the left pm^{2-3} and with only pm^2 present in the right toothrow, another specimen (pp. 8, 124) having pm^{2-3} on one side coalesced. Findley & Jones (1967 : 432, fig. 3) indicated a geographical variation in the number of small premolars ($pm\frac{2}{2}$-$\frac{3}{3}$) in *M. lucifugus* and showed that in *M. fortidens* from Mexico the normal condition is the presence of but one small upper and lower premolar in each side of the jaw: in the holotype (B.M. 88.8.8.18) $pm\frac{3}{3}$ are lacking from both sides. A specimen referred to *fortidens* by Miller & Allen (1928 : 8, 55) had on each side in addition to the two small upper premolars (pm^{2-3}) common in *Myotis* a third small supernumerary tooth crowded beneath the inner anterior border of the large premolar (pm^4).

Status and records of *Pipistrellus annectans* Dobson, 1871

Topál (1970) has shown from an examination of the holotype that *Pipistrellus annectans* Dobson, 1871 from Assam (Nagaland), north eastern India is in fact synonymous with *Myotis primula* Thomas, 1920, from the northern part of the nearby province of West Bengal, the small $pm\frac{3}{3}$ being absent from both sides of the jaw in the holotype. This finding has been confirmed by Hill & Thonglongya (1972 : 188) who reported a further specimen (from Thailand) referable to *annectans* and who were able to compare it directly with the holotype of *Myotis primula*.

The existence of a species sharing some features of *Myotis* and of *Pipistrellus* was first indicated by Dobson (1871 : 214), who wrote of *Pipistrellus annectans* (=*Myotis annectans*): "This species unites the external form of a *Vespertilio* to the dentition of a *Pipistrellus*; the form of the ear and tragus is almost precisely similar to those of the next species which is a true *Vespertilio*". The next species described by Dobson is *Vespertilio nipalensis*, nowadays (Ellerman & Morrison-Scott, 1951 : 139) listed as a subspecies of *Myotis mystacinus*. Subsequently, Dobson (1876 : 117) reiterated this conclusion, transferring *annectans* to *Vesperugo*: "This species unites the external appearance of a *Vespertilio* to the dentition of a *Vesperugo*. In the form of the ear and tragus, and elevation of the roof of the skull above the face, it very closely resembles some species of the former genus".

Schneider (1905 : 80) reported three specimens from the Upper Langkat, Sumatra in the Zoological Institute of the University of Stockholm (now apparently transferred to the National Museum of Natural Sciences, Stockholm) identified by Leche as *Pipistrellus annectans*, but gave no diagnostic details. Subsequently, Ärnbäck-Christie-Linde (1909 : 574) gave a detailed description of these examples, noting (p. 575) that in the shape of the muzzle, ear and tragus, the absence of a post-calcarial lobe and height of braincase they corresponded with *Myotis* but in dental formula with *Pipistrellus*. A comparison (p. 575) of the length of the tibia with the length of the head and body led Ärnbäck-Christie-Linde to conclude that the tibia is relatively longer in *Myotis* than in *Pipistrellus*, the holotype of *Pipistrellus annectans* being close to *Myotis* in this respect while in the specimens from Sumatra referred to *annectans* the tibia proved longer than in any *Pipistrellus* examined, although not as long as in the holotype. Furthermore, Ärnbäck-Christie-Linde demonstrated (p. 577) that in the Sumatran examples the coracoid is not bifurcated at the tip so that in this respect they resemble *Myotis* rather than *Pipistrellus*, although this author also reported (pp. 578, 581) a specimen of *Myotis nigricans* with the coracoid showing a tendency to bifurcation but with the dental formula of *Pipistrellus*.

Ärnbäck-Christie-Linde concluded (pp. 578, 581) from the description of the holotype and from the Sumatran specimens referred to *annectans* that this species represented an example of transition between forms referred to different genera. However, the Sumatran specimens are much too small (length of forearm 29·9 mm) to represent *Myotis annectans* (length of forearm 45–47 mm) of which Ärnbäck-Christie-Linde (pp. 576, 580, 582) considered them to be a small form. From the size and description these specimens seem likely to represent the species known as *Pipistrellus ridleyi*, hitherto reported only from Malaya.

Generic affinities of *Pipistrellus ridleyi* and *P. rosseti*

Except in dental formula, there is no doubt that many of the features of *Pipistrellus ridleyi* and *P. rosseti* are those of *Myotis* rather than of *Pipistrellus*, to which Hill (1969 : 138) transferred *rosseti* from *Glischropus* where originally it had been placed. Both have long, rather narrow, slightly funnel-shaped ears with the tragus one half or almost one half as long as the ear, its outline narrowed distally to a blunt, anteriorly directed point. There is no post-calcarial lobe in *ridleyi* but a narrow lobe is present in *rosseti*. So far as can be determined from specimens in alcohol, the tibia in both *ridleyi* and *rosseti* is approximately one third of the length of the head and body, as in the specimens of "*Pipistrellus annectans*" from Sumatra described by Ärnbäck-Christie-Linde (1909 : 574). In both species the braincase is high and inflated, rising above the facial line in a smooth but sharp curve. The rostrum is narrow and low, especially in *ridleyi*, medianly slightly flattened, with a shallow median depression, and agrees more closely with that of *Myotis* than with the more elevated, wider rostrum of *Pipistrellus* which as a rule does not lie markedly lower than the braincase. The toothrows are parallel posteriorly but converge at the level of the front face of pm^4 to give the anterior palate a slightly "pinched-in" look very like the anterior palate of *Myotis*.

The peculiarities of the incisive dentition of both *ridleyi* and *rosseti* provide perhaps the most convincing indication of their affinity to *Myotis*. These features were commented upon by both Thomas (1898) and Oey (1951) in their descriptions of the two species. Thomas (p. 362) in particular noted of *ridleyi* that "This little Pipistrelle is readily distinguishable from all others by its short and peculiarly shaped incisors, for all the ordinary members of the genus have long styliform incisors, which may or may not have a small supplementary cusp near their tips, but which are never short, broad, and separated into two almost subequal cusps, as is the case in *P. ridleyi*". Oey (p. 3) noted that the upper dentition of *rosseti* differed from that of *Pipistrellus* in the position and size of i^2 (in fact the outer incisor, usually considered to be i^3). These anomalies are immediately explained if the incisive dentition is compared with *Myotis* rather than with *Pipistrellus*.

The inner upper incisor (i^2) of both *ridleyi* and *rosseti* is short and broad, anteriorly rather narrow, wider posteriorly, with a strong anterior cusp and small posterior cusp about one half the height of the anterior cusp: the base of the tooth is expanded posteriorly to form a low, cusp-like labial extension. The tooth is hollowed posteriorly through engagement with i_3 and in profile the anterior cusp is slightly hooked. It thus corresponds with i^2 of *Myotis*: in *Pipistrellus* i^2 is more linear, its base not expanded posteriorly but in fact often narrower posteriorly than anteriorly. In *ridleyi* and *rosseti* the principal cusp of i^3 is equal to or exceeds that of i^2 in height and is hooked so that its tip points very slightly posteriorly to give the tooth in profile the appearance of a reduced canine, again a condition corresponding more closely with *Myotis* than with *Pipistrellus* in which i^3 is usually much lower in height than i^2 and, like i^2, points forward rather than having a hooked appearance. The lower incisors in *ridleyi* and *rosseti* resemble those of *Myotis*, especially in the wide disparity in size between i_3 and i_{1-2}, the former being much larger, its bulk twice that of the latter teeth.

Apart from the absence of $pm\frac{3}{3}$ the premolar dentition of *ridleyi* and *rosseti* presents few diagnostic features: the anterior tooth (pm^2) is more or less circular in basal outline, with a narrow cingulum and central cusp. It is in the toothrow, in contact with the canine but separated from pm^4 by a short diastema. The anterior lower premolar (pm_2) is oval or sub-circular in basal outline, in the toothrow but not at all compressed between the canine and pm_4, in close agreement with pm_2 in *Myotis*: in *Pipistrellus* pm_2 is usually more angular in outline and is usually compressed in the toothrow.

Some emphasis is placed by Ärnbäck-Christie-Linde (1909 : 577, 581) on the structure of the coracoid as a diagnostic feature between *Myotis* and *Pipistrellus*. It has been possible to examine the coracoid of the paratype of *ridleyi* and of three specimens of *rosseti*: in all it is a plain, narrow shaft, not bifurcated or even expanded distally, and strongly curved. It thus satisfies the criteria set by Miller (1907 : 205) for the coracoid of *Myotis*.

It is our conclusion, therefore, that properly to reflect the evident similarities of *ridleyi* and *rosseti* to *Myotis* they must be transferred to that genus and that the dental formula must be disregarded in this instance for the purposes of generic classification. The only real features by which the two species may be allied to *Pipistrellus* are those concomitant with a shortening of the rostrum, a tendency already apparent in *Myotis*, which in *ridleyi* and *rosseti* has proceeded sufficiently far as to involve the disappearance of $pm\frac{3}{3}$. These teeth in some species of *Myotis* such as *nigricans*, *muricola* or *annectans* are greatly reduced or in some specimens completely lacking and in one species, *fortidens*, their absence is apparently a normal condition. In all of the recorded examples of *ridleyi* (six, if the specimens from Sumatra reported as "*Pipistrellus annectans*" by Ärnbäck-Christie-Linde (1909 : 574) represent this species) and of *rosseti* (ten, including two juveniles) these teeth are absent in both upper and lower jaws. The remaining $pm\frac{2}{2}$ are not at all compressed in the toothrows, and, indeed, pm^2 is separated from pm^4 by a small diastema.

Divisions within *Myotis* are uncertain, the most recent reviewer of the Asiatic species, Tate (1941), recognizing a number of weakly defined subgenera, some of which may not prove valid. *Myotis ridleyi* and *M. rosseti* are referable to the division to which Tate allocates *Selysius* as a subgeneric name. This subgenus includes a number of species such as *frater* and *siligorensis* with elevated, rounded braincase and also species in which reduction and displacement of $pm\frac{3}{3}$ has begun as it has in *nigricans* and *muricola*, also referred to *Selysius* by Tate. Both *ridleyi* and *rosseti* stand rather apart in *Selysius* by virtue of their shortened rostra: their nearest approach in the subgenus appears to be *muricola* which has a longer, slightly lower rostrum and in which $pm\frac{3}{3}$ are reduced and often displaced, the canines and remaining cheekteeth being more massive than in either *ridleyi* or *rosseti*.

The two species may be diagnosed:

Myotis ridleyi (Thomas, 1898)

Pipistrellus ridleyi Thomas, 1898 : 361 (Selangor, States of Malaya); Kloss, 1908 : 158 (listed, type locality given as Kepong); Chasen, 1940 : 51 (listed); Tate, 1942 : 240, 291 (notes, measurements of holotype); Medway, 1969 : 39 (description, measurements, Malayan

records); Hill, 1969 : 136 (notes, measurements of holotype, paratype and further example, allied to *rosseti*); Hill (1972:33) (incisive dentition, measurements of Malayan specimens repeated).

?*Pipistrellus annectans*, Schneider, 1905 : 80 (specimens from Sumatra); Ärnbäck-Christie-Linde, 1909 : 574 (description, measurements of Sumatran specimens).

Similar to *Myotis muricola* but smaller (length of forearm 28–30 mm) with slightly shorter ear; skull with similarly expanded braincase but with the frontal region more elevated; rostrum shorter and deeper, generally a little more massive; dentition less massive, the canines short, c^1 barely exceeding pm^4 in height and c_1 equal in height to pm_4. There is some resemblance to *M. siligorensis* which has similarly reduced canines but in which the braincase rises more abruptly from the rostrum, this itself lower, narrower and less massive than in *ridleyi*. There is no trace of $pm\frac{3}{3}$ in either side of the jaw in any of the three Malayan specimens examined, nor is it to be found in the specimens from Sumatra reported as "*Pipistrellus annectans*" by Ärnbäck-Christie-Linde, if correctly these should be referred to *ridleyi*. The species has been reported from lowland localities in the Malayan States of Perak, Pahang and Selangor (Medway, 1969 : 39) and possibly occurs also in Sumatra.

Myotis rosseti (Oey, 1951)

Glischropus rosseti Oey, 1951 : 4 (Cambodia).

Pipistrellus rosseti, Hill, 1969 : 133 (description, measurements of further specimens, transferred to *Pipistrellus*).

Externally like *ridleyi* but ears slightly longer, the base of the thumb expanded to form a fleshy, wrinkled pad, the soles of the feet similarly swollen to form a broad concave pad, and with a narrow post-calcarial lobe. Skull similar to that of *ridleyi* but braincase a little more swollen frontally; interorbital region shorter; rostrum slightly shorter and wider, its median depression shallower and less clearly defined; narial emargination more nearly U-shaped rather than V-shaped as in *ridleyi*, not extending as far posteriorly; basial depressions more pronounced. Lower canine (c_1) slightly exceeding pm_4 in height, the latter tooth a little less reduced than in *ridleyi*: no evidence of the presence of $pm\frac{3}{3}$ has been found in any of the ten known specimens. *Myotis rosseti* has been recorded so far only from Cambodia and Thailand (specimens in Hungarian Natural History Museum, Budapest).

Myotis ridleyi and *M. rosseti* may be readily recognised among *Myotis* by their expanded braincases and shortened, rather massive rostra, *rosseti* being the only described species of the genus to have enlarged basal thumb pads or to have the soles of the feet similarly swollen. The occurrence of pads on the thumbs and feet in the Vespertilionidae was discussed by Hill (1969 : 135). Such pads occur incipiently in *Pipistrellus* and characterize the related genus *Glischropus*, the genera *Eudiscopus* and *Tylonycteris*, and occur in one species of *Hesperoptenus*. All of these, however, are removed from any affinity with *rosseti* by a variety of features of the skull and dentition.

SUMMARY

The discovery of additional specimens of *Glischropus rosseti* Oey, 1951 has prompted a further examination of the generic affinities of this and the related species *Pipistrellus ridleyi* Thomas, 1898. Variations in the premolar dentition of *Myotis*, *Pipistrellus* and *Eptesicus* are reviewed and it is concluded that the numerical premolar formula is not always an adequate guide to the allocation of species within these genera. As a result of an examination of alternative features in both *ridleyi* and *rosseti*, both species are transferred to *Myotis* as components of the subgenus *Selysius*. Specimens from Sumatra first reported by Schneider (1905 : 80) as *Pipistrellus annectans* Dobson, 1871 (=*Myotis annectans*) and later described in detail under this name by Ärnbäck-Christie-Linde (1909 : 574) are thought in fact to represent *Myotis ridleyi*, known otherwise only from Malaya.

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