

The baculum in the Vespertilioninae (Chiroptera: Vespertilionidae) with a systematic review, a synopsis of *Pipistrellus* and *Eptesicus*, and the descriptions of a new genus and subgenus

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Synopsis

Current classification of the Vespertilioninae rests chiefly on a suite of mainly adaptive characters, among which facial shortening throughout the subfamily with consequent changes in the structure, size, relative position and number of the incisors and premolar teeth features prominently. Such characters may not necessarily reflect relationships or phyletic diversity, and sometimes do not serve properly to distinguish the genera that they purport to define, as in the distinction of *Pipistrellus* and *Eptesicus*, where generic boundaries remain unclear. The search for possibly less strongly adaptive features suggested the possibility that the morphology of the os penis or baculum might prove valuable in the study of the systematics of these genera and perhaps in the subfamily as a whole.

This paper reviews earlier studies of the baculum in the Chiroptera and their relevance to systematics in the Order, with an examination of its gross morphology throughout the Vespertilioninae, especial attention being given to species currently allocated either to *Pipistrellus* or to *Eptesicus*. A synoptic review of the species

content of these genera is presented, with the recognition and definition of subgenera and included species groups: three such (*pumilus*, *capensis* and *tenuipinnis*) currently referred to *Eptesicus* on dental grounds seem instead more closely related to *Pipistrellus* to which they are here transferred. One subgenus of *Pipistrellus* is described as new (p. 250).

The Vespertilioninae as a whole display a wide range of bacular variation, which falls into two major and several minor groups. This has suggested a revision of the current classification of the subfamily, combining bacular features with those conventionally in use. Bacular morphology provides a clear indication that the 'Nycticeini' (or 'Nycticeiini') is an artificial grouping and that the genus *Nycticeius* as presently understood is composite. Currently it is held to include two species, the North American *humeralis* and the African *schlieffenii*: these are here thought to be sufficiently characterised to justify generic separation and a new generic name is proposed for *schlieffenii* (p. 254).

A suggested classification of the subfamily is presented, with a tabulated review of earlier classifications; possible relationships between the constituent genera are discussed and the zoogeography of the bacular types within the subfamily is examined.

Introduction

A penial bone is known to occur among mammalian Orders in the Insectivora, Chiroptera, Primates, Rodentia and Carnivora. Various called the os penis, os priapi or os glandis, it was first named the baculum by Thomas (1915*a*), the corresponding structure in the female, the os clitoridis, being later called the baubellum by Shortridge (1934: 327, footnote). The features of the baculum have been used extensively in attempts to determine phyletic relationships at various systematic levels (Patterson & Thaler, 1982). Thomas (loc. cit.), for example, suggested that the baculum might provide evidence valuable in the subfamilial classification of the Sciuridae and indeed pointed out that in this connection there were no bacular features to support the association of the dwarf squirrels in a separate subfamily, the Nannosciurinae. More commonly, bacular features have been used to indicate or determine relationships within genera in the Sciuridae, among New World rodents, and in the Mustelidae. Such characteristics have been employed in species descriptions, especially where bacular variation is pronounced, and also for age determination. Numerous examples of these uses of the baculum are summarised by Patterson & Thaler (loc. cit.) while Burt (1960) gave an account of the earlier of such studies. Similar early accounts of the baculum in the Chiroptera are reviewed by Hamilton (1949).

The presence of a baculum in some at least of the Chiroptera has been long established. Daubenton (1760) described and illustrated (in part) the baculum of *Nyctalus noctula* and Blainville (1840) similarly studied the baculum of *Rhinolophus ferrumequinum*, *R. hipposideros*, *Vespertilio murinus* and again of *Nyctalus noctula*, the latter author providing perhaps the first accurate and quite detailed drawings of this structure. Later workers such as Ercolani (1868), Robin (1881), Gilbert (1892), Rauther (1903), Gerhardt (1905) and Chaine (1926) provided further details of penial and bacular morphology in the Chiroptera, Chaine in particular discussing and illustrating the baculum in several species and to some extent summarising earlier work in the field. However, none attempted to use the structure of the baculum for systematic purposes.

The first use of the baculum in chiropteran systematics appears to be by Thomas (1915*b*) who employed bacular characteristics in defining the species of *Nyctophilus*. This worker clearly foresaw the value of bacular features in the definition of some at least of the species of bats, beginning from that time a collection of vespertilionid bacula at the British Museum (Natural History) although subsequently making little use of the material that was accumulating, except in 1928 employing bacular characters to separate Indo-Chinese species of *Pipistrellus* (Thomas, 1928*a, b*). Since then the baculum has been utilised in a variety of taxonomic studies of bats, for example by Krutzsch (1959, 1962) and Lanza (1969) to examine its value in indicating relationships in the Megachiroptera, by Topál (1970*a*) in determining the affinities of *Ia*, or by Heller & Volleth (1984) as an indicator of relationship among the species of *Pipistrellus* and *Eptesicus*. The baculum of *Plecotus* was found valuable by Lanza (1960) in discriminating between *P. auritus* and *P. wardi* (= *P. austriacus*): the subsequent use of the baculum in distinguishing these species is summarised by Corbet (1964). Genoways & Jones (1969) found that bacular features distinguished closely

related species of North American *Myotis*, LaVal (1973a) employing bacular characters for the same purpose among the Neotropical species of this genus.

The emphasis placed on bacular characters in chiropteran systematics is perhaps best illustrated by the number of studies devoted chiefly to bacular structure, often on a regional or faunal basis, as for instance the work by Hamilton (1949) and Krutzsch & Vaughan (1955) on North American species, by Brown *et al.* (1971) on Neotropical bats, by Topál (1958) on central European species, by Bhatnagar (1967), Agrawal & Sinha (1973), Sinha (1976) and Khajuria (1979, 1980, 1982) on Indian bats, or by Wassif & Madkour (1972) and Wassif, Madkour & Soliman (1984) on Egyptian bats. Bacula are sometimes studied in discrete taxonomic groupings, as for example those of New World molossid by Brown (1967) or of Malaysian *Hipposideros* by Zubaid & Davison (in press). Thus among the Chiroptera the baculum has been employed as a source of taxonomic features at several systematic levels, but primarily to indicate degrees of relationship or for separation at the specific and sometimes the generic grades, or especially for distinguishing closely related, often sympatric species whose conventional morphological characters are otherwise very similar, as in *Myotis* and *Plecotus*.

Functional and systematic significance of the baculum

Conflicting hypotheses for bacular variation were reviewed in detail by Patterson & Thaeler (1982). These authors proposed that among rodents at least the probability was that the baculum has a precise reproductive purpose and functions primarily as a device contributing to species isolation. Bacular differences among closely related taxa might well then take an exaggerated form. As such, the baculum would be therefore a poor basis for supra-specific classification, but an excellent structure for species diagnosis. Thus they would not consider a phyletic basis for bacular variation to be appropriate. They admit, however, that while in some rodent groups there are patterns of bacular morphology that do not agree with phyletic divergence as indicated by other morphological features, there exist also gross patterns of bacular variation in other groups that do in fact conform with accepted phyletic relationships. Indeed, they remarked that there can be little doubt that the baculum exhibits phyletic weight and consequently may serve as a valuable taxonomic tool. Moreover, taxa that differ in external and cranial characters may have similar bacula, while others that are similar in such features may exhibit highly distinctive genitalia. Patterson & Thaeler (loc. cit.) suggested that although bacular morphology reflects phyletic history on a gross scale, discordance between patterns of bacular and phyletic divergence supports a functional interpretation of bacular variation, especially at the species level.

Similarly, opinions vary as to the value of bacular morphology in chiropteran systematics. Hamilton (1949) examined the baculum in North American vespertilionids and concluded that in this family the baculum was useful in defining relationships when considered with skull and other skeletal characteristics. Thus he was able to suggest that the close similarity between the bacula of *Myotis* (Fig. 19i, j) and *Pizonyx* (Fig. 19k) indicated their close relationship, and that the dissimilarity between the bacula of *Pipistrellus subflavus* (Fig. 2d) and *P. hesperus* (Fig. 8d) suggested generic or at least subgeneric difference. This author also noted that in most instances among North American vespertilionids there were marked generic differences in the baculum. He considered that further study was needed to determine the usefulness of the baculum in chiropteran systematics and that with time and sufficient material the bone might be utilised in classification. These conclusions were reinforced by Krutzsch & Vaughan (1955) who examined the bacula of further North American species. They remarked that in the case of those that are closely related the baculum can serve as a criterion in judging relationship when other clear cut distinguishing characters are lacking. These authors found bacular variation in closely related bat species to be chiefly in shape, detail of outline, and gross size: their study led to the belief that in at least some superficially similar species well marked and consistent bacular differences reinforced the more subtle external and cranial dissimilarities.

Krutzsch (1959) accepted the view that the baculum can provide additional evidence for classification, or, in the absence of other clearly defined characters, can serve as a criterion in judging

relationship. He added in relation to the Pteropodidae that by virtue of its relative simplicity and structural stability the baculum might well serve to help place entities of doubtful relationship in their natural position, although they might be otherwise morphologically contradictory. Among pteropodids he found that infrageneric differences in the baculum involved minor details of shape, outline and size. Genera, however, might be separated by more profound differences. His study suggested that although within the genus well marked and consistent differences existed between the bacula of individual species, there was nevertheless a basic similarity in pattern throughout the genus, leading to the suggestion that marked variants from this morphological standard in a single genus might provide grounds for a reappraisal of the affinities of the variant. A further study (Krutzsch, 1962) confirmed these opinions, especially in the broad agreement of bacular variation in pteropodids with the taxonomic arrangement of this family by Andersen (1912) and by Tate (1942*b*). Krutzsch concluded that strong intrageneric similarities exist among the bacula of pteropodids, but that representative bacula of different genera differ distinctly: although serving well as a source of diagnostic features for the genus, the baculum does not seem to offer exceptional insight into suprageneric relationships. The large genus *Pteropus*, however, to some extent proves to be an exception, with various of its many species demonstrating considerable variation in bacular structure: on occasion differences between species equal those between some megachiropteran genera.

Lanza (1969) examined the baculum of *Pteropus* in detail and found that its bacular morphology did not conform to the classification proposed by Andersen (1912), a conclusion also reached by Davis (1947) who examined only five species. Lanza found that in many cases bacula of an identical size and shape could be found among species belonging to the same group as well as to different groups; or that the baculum could be extremely different among forms apparently otherwise very closely related. Thus in this genus he found the baculum to be of limited value in phyletic analysis. Similarly, LaVal (1973*b*) found that with one exception the bacula of the various species of the vespertilionid *Rhogeessa* are not sharply differentiated from each other: although in shape they show substantial geographic and individual variation within species they seem nevertheless to differ between species in areas of sympatry or near sympatry. Harrison & Brownlow (1978) found that individual variation in the baculum of adults of another vespertilionid, *Scotophilus*, was such that it rendered this structure of little or no value in species diagnosis in this difficult genus.

Martin (1978) discussed the adaptive value of the baculum in bats, having found a wider range of structural variation among several pteropodid species than was previously thought. He considered that the baculum may have a number of roles of varying adaptive significance in supporting the penis, as a stimulatory structure, or in preventing urethral closure during the pressures of copulation. Although these might allow the baculum to maintain morphological stability within certain taxonomic units, this possible variability of function he thought tended to reduce its value in classification at the specific and subspecific levels.

Despite these possible limitations, many authors admit at least the species-specificity of bacular variation among bats, using the baculum to provide additional characters to separate species that sometimes otherwise closely resemble each other. Some examples have been mentioned: others include Wallin (1969) who drew attention to bacular differences in Japanese *Pipistrellus* and who used such differences to define two species groups in *Vespertilio*, or Baagøe (1973) who utilised bacular characters in comparing sibling species of European *Myotis*. Zubaid & Davison (in press) found the baculum to be specifically diagnostic among Malaysian *Hipposideros*. In some genera authors have routinely described and illustrated the baculum of new species: for instance Sinha (1969) in describing *Pipistrellus peguensis* compared its baculum with the bacula of the related species. Similarly, McKean *et al.* (1978) described and illustrated the baculum of '*Eptesicus sagittula*', comparing it with the bacula of other Australian '*Eptesicus*', while Kitchener (1976) employed the baculum of '*Eptesicus douglasorum*' in the same way. Bacular characters sometimes form an essential part of revisionary study, as by Kitchener *et al.* (1986) in defining and keying the Australo-Papuan representatives of *Pipistrellus* and *Falsistrellus*. The baculum has also featured in generic revision, Hill (1966*a*) for example describing and illustrating that of *Philetor* in the course of such a study, or (1976) that of the majority of the species of *Hesperoptenus*.

Bacular variation has also been employed for generic and subgeneric distinction within the

Vespertilioninae. Wallin (1969) used penial characters in establishing *Vespertilio* as a genus distinct from *Eptesicus* and in recognising *Hypsugo* as a subgenus within *Pipistrellus*, while Topál (1970a) noted that bacular morphology allied the aberrant genus *Ia* more closely to *Eptesicus* than to *Pipistrellus* with which it had been associated by some authors. Heller & Volleth (1984) summarised published illustrations of the bacula of *Pipistrellus*, *Eptesicus* and some of their associated genera, drawing attention to their taxonomic implications. At a further systematic level, Pine *et al.* (1971) discussed the penial and bacular morphology of *Antrozous* and *Bauerus* in relation to the presumed affinities of these North American genera to the Australian and New Guinea genera *Nyctophilus* and *Pharotis* with which they have been associated in the subfamily Nyctophilinae.

It is clear from the foregoing account that the baculum is regarded as a valuable source of diagnostic information by many students of chiropteran systematics. This seems especially true in the Vespertilioninae, a subfamily in which diagnosis and definition at both specific and generic levels is sometimes difficult if only the orthodox morphological characters of external, cranial and dental structure are to be relied upon.

Nature and scope of this study

The basis of the current classification of the Vespertilioninae was first set out in detail by Miller (1907), who recognised a total of thirty-two genera in the group, with diagnoses and short descriptive accounts. The classification of Miller was based chiefly on external, cranial and dental features. Tate (1942a) reviewed the characters used for diagnosis in some detail, dividing the subfamily into four main (tribal) aggregations, and attempting to quantify the interrelationships of its many genera. The major outlines of his classification have since been followed, sometimes with local modification as for instance by Koopman (1984a, b, 1985) who subsumed the subfamily Nyctophilinae into the Vespertilioninae. Hill (1966) pointed out that the subfamily comprises a complex of closely interrelated genera separated in some instances by comparatively slender or even rather arbitrary distinctions, the patterns of relationship often obscured by parallelism or convergence.

The narrowness of the orthodox distinctions that define many of the constituent genera of the Vespertilioninae has led to much taxonomic combination and recombination since Tate wrote. This situation is exemplified by the more extreme variants of classification that have been proposed. For example, Kuzyakin (1944, 1950, 1965) included *Pipistrellus* and *Eptesicus* in *Vespertilio* while Simpson (1945) included *Glischropus*, *Scotozous*, *Nyctalus* and *Ia* in *Pipistrellus* and *Rhinopterus*, *Hesperoptenus*, *Tylonycteris*, *Mimetillus*, *Philetor*, *Histiotus* and *Laephotis* in *Eptesicus*. A yet more extreme viewpoint was adopted by Sokolov (1973) who considered that *Vespertilio* should include not only *Pipistrellus* and *Eptesicus* as was thought by Kuzyakin, but also all of the other above mentioned genera except *Nyctalus*. Horáček & Hanák (1985a, b) commented that the concepts of Kuzyakin and Sokolov (with the inclusion of *Nyctalus*) might be provisionally accepted, at least until factual proof of paraphyly in the group was forthcoming. Nevertheless, they considered this to be a retrograde solution since it expresses nothing of the factual diversity of the group, proposing instead that the problematic taxa should be arranged in separate genera, their diagnoses then making their content clearer though narrower. Both Simpson and Sokolov also included *Scotoecus* and *Scotomanes* in *Nycticeius* as then understood, *Baeodon* in *Rhogeessa*, *Glauconycteris* in *Chalinolobus* and *Dasypterus* in *Lasiurus* to produce a heavily 'lumped' classification. The status of some such as *Scotoecus*, *Dasypterus* and *Idionycteris* has varied from one author to another for decades: in the Australian region *Scoteanax* and *Scotorepens* have recently achieved generic rank after many years as nominal subgenera (Kitchener & Caputi, 1985) while *Ia* has once again reverted to *Pipistrellus* (Koopman 1984a, b, 1985) after a brief spell with *Eptesicus*. The major variants of vespertilionine classification are summarised in Table 1.

Many of the characters used to define taxa and relationships among the Vespertilioninae appear strongly adaptive and of equivocal value in generic and suprageneric systematics. Most concern

ear size and shape, tragal structure, the architecture of the skull, and the number and formation of the teeth. Zima & Horáček (1985) pointed out that the use of the morphological characters employed hitherto in the classification of the Vespertilionidae as a whole might not lead invariably to correct taxonomic conclusions, their degree of differentiation perhaps reflecting the orientation and intensity of selection pressure rather than actual phyletic relationships. These authors indicated an urgent need for new, sufficiently reliable and taxonomically useful criteria based on features that did not possess a direct adaptive significance, including among these the morphology of the reproductive organs and the baculum.

Much weight has been placed in the past upon the progressive shortening of the muzzle apparent throughout the Vespertilioninae with concomitant reduction and loss of the incisors and premolars (Tate, 1942a). In the incisive dentition the first upper tooth (i^1)^a is absent, as in all bats. Reduction results in the remaining inner tooth (i^2) becoming peg-like and unicuspid, although sometimes quite massive, in a reduction in size of the outer tooth (i^3), its displacement inwards or outwards, or in its eventual obsolescence or loss. In the mandible, the first (i_1) and second (i_2) incisor teeth are invariably present, but exceptionally the third (i_3) may be absent. The process also involves the reduction and loss of the second upper and lower premolars (pm^3) and then of the anterior upper premolar (pm^2): thus the premolar formula ranges from $pm \equiv \frac{2}{2} \frac{3}{3} \frac{4}{4}$ to $pm \equiv \frac{2}{2} \frac{4}{4}$ the first upper and lower premolars (pm^1) being presumed to be those that are absent from all bats. Seven different combinations of incisors and premolars occur in the subfamily, if *Antrozous* and *Bauerus* are included. The full complement is usually taken as the primitive condition, the reduction and disappearance of teeth as derived. These are summarised in Table 2, which gives the incisive and premolar formulae usually attributed to each of the various genera. However, *Myotis* occur in which pm^3 or pm^2 are absent (Hill & Topál, 1973), thus in the first instance producing the formula typified by *Lasionycteris* or *Plecotus*, in the second the formula for *Pipistrellus* or *Nyctalus*; pm^2 may be absent from *Pipistrellus* to give the arrangement for *Eptesicus*, or may be present in *Eptesicus* to produce the formula for *Pipistrellus* (Hill & Topál, loc. cit.); i^3 is variable in *Scotozous* (of 45 examined, present in 34, absent from one side or the other in 8, completely absent from 3), when totally absent to produce the incisive formula that usually characterises *Nycticeius* and its associates (but Thomas & Wroughton (1908) report an example of '*Nycticeius*' *schlieffenii* in which the left i^3 is present); pm^2 is variable in *Scotoecus* (Hill, 1974) and in *Chalinolobus* (Ryan, 1966; Koopman, 1971), and very rarely may be present in '*Nycticeius*' *schlieffenii* (Dobson, 1878; Thomas, 1890).

Most genera of Vespertilioninae can be defined by other features besides those of the incisive and premolar dentition, although sometimes only in differing combinations. Thus although some species exist that combine the external features of *Myotis* with the dental formula of *Pipistrellus* to the extent that initially they (*annectans*, *ridleyi*) were described in the latter genus, other characters such as the form and structure of the tragus and the structure of the incisors enable them to be referred confidently to *Myotis* (Topál, 1970b; Hill & Topál, 1973). Another (*rosseti*) was first described in *Glischropus*, subsequently removed to *Pipistrellus* by Hill (1969) and finally (with *ridleyi*) to *Myotis* by Hill & Topál (loc. cit.). However, the genera *Pipistrellus* and *Eptesicus* do not offer further conventional characters in this way and are separated for the most part by the presence of pm^2 in the former and its absence in the latter. Wallin (1969) and Hill & Topál (loc. cit.) discussed the variability of this tooth in *Pipistrellus* and *Eptesicus* in detail, the latter authors concluding that the presence or absence of pm^2 can have no universal validity in defining the two genera. Heller & Volleth (1984) also examined the relevance of pm^2 in separating *Pipistrellus* and *Eptesicus* and concluded that it does not seem to be a reliable characteristic, a classification based on it perhaps misrepresenting true relationship. Tate (1942a) recognised this difficulty but adhered to the conventional practice of separating the two genera by this feature, and indeed the majority of authors have retained the distinction as a matter of convenience, often using the extent of reduction and degree of displacement of pm^2 from the line of the tooththrow as a diagnostic feature between the species of *Pipistrellus*.

^aDental notation of Miller (1907)

Koopman (1975) has commented upon this problem. This author examined African species allocated variously to *Pipistrellus* and *Eptesicus* in an attempt to find some other character that would divide this large assemblage into two major groups. He could find none among the usual suite of morphological features. Although he found no African *Pipistrellus* species that closely resembled the *hottentotus*, *tenuipinnis* or *floweri* groups of *Eptesicus* and no African member of the latter genus that was similar to the *pipistrellus*, *hesperus*, *savii* or *rueppellii* groups of *Pipistrellus* as he defined them, he did find a resemblance amounting in some cases to virtual identity (if pm^2 was ignored) between the *kuhlii* group of *Pipistrellus* and the *Eptesicus capensis* group. Expanding a view first expressed by Tate (1942a) in his account of *Eptesicus*, Koopman commented that it is probable that the anterior upper premolar has been lost more than once here, and that true phyletic relationships run across the 'generic' line. He thought that it is even possible that in some cases a '*Pipistrellus* species' and an '*Eptesicus* species' are actually conspecific, but was of the opinion that the available material was insufficient to establish this with certainty for any such pair at the present time. Although retaining *Pipistrellus* and *Eptesicus* as separate genera since he believed that the problem should be attacked on a cosmopolitan basis, he remarked that such an arrangement is almost certainly wrong. More recently, Horáček & Hanák (1985–1986) have offered further definitions of *Pipistrellus*, *Hypsugo* and *Eptesicus*.

Many varying interpretations can be placed upon external, cranial and dental morphology or on karyological data in the Vespertilioninae. These range from the relationship of one species to another to suprageneric relationships, even to the view that *Pipistrellus* and *Eptesicus* may be polyphyletic. Menu (1984), for example, remarked that an exhaustive odontological study of the Vespertilioninae indicated that *Pipistrellus* includes species wrongly associated by reason of their identical dental formula, but which are not related. Williams & Mares (1978) discussed the karyology of *Eptesicus*, which as currently defined they thought seemed to be a composite taxon, encompassing perhaps several phyletic lines of pipistrelloid species with reduced numbers of premolars. Heller & Volleth (1984) suggested that *Pipistrellus* may be a very heterogeneous assemblage and after reviewing the relevance of pm^2 in separating this genus from *Eptesicus* considered the baculum to be a more reliable guide to the phylogeny of the species of *Pipistrellus* and *Eptesicus*, using its features to supplement their findings from karyological data. Many years before this Tate (1942a) remarked that it seemed probable that study of the baculum in the Microchiroptera would yield valuable results, with the implication that this might have significance in the classification of the Vespertilionidae. Indeed, Tate records that G. M. Allen had gathered together a number of bacula representing many of the species of *Pipistrellus* which he intended to employ in revising the genus. Moreover, relatively few species of the nominal genera *Pipistrellus* and *Eptesicus* have so far been studied: the impression gained from the literature is that *Pipistrellus* as currently understood is dignified chiefly by a long, slender shafted baculum and most *Eptesicus* as it is presently classified by a small, triangular structure, which we have found not to be the case.

Initially our intention was to examine the bacula of as many species of *Pipistrellus* as possible to establish the pattern of bacular variation within the genus, and to compare it with the species groupings proposed by Tate (1942a) and by Koopman (1973, 1975). As the work progressed, however, it became increasingly apparent that its implications extended far beyond the limits of this nominal genus and that it was necessary in addition to study the bacula of *Eptesicus* so far as we were able, and to examine the boundary between these two conventional groupings. Finally, to place our findings in proper perspective, we have surveyed the bacula of most of the remaining genera of the Vespertilioninae and have attempted to assess the generic significance of bacular variation in the subfamily. We have also examined the bacula of *Nyctophilus* and *Pharotis*, both usually referred to the closely related subfamily Nyctophilinae. This has been united recently with the Vespertilioninae (Koopman, 1984a, b, 1985) and is thus relevant to our study.

We have made no detailed examination of the gross morphology of the chiropteran penis except insofar as it is reflected by bacular structures. Nor have we attempted to study its histomorphology. These features are discussed by Smith & Madkour (1980) in an effort to elucidate their relevance to interordinal and infraordinal phylogenetic relationships, and who review earlier studies of penial morphology.

Materials and methods

We have been able to examine bacula from the majority of species currently listed in *Pipistrellus* and from most of those presently assigned to *Eptesicus*. In a few instances we have relied upon illustrations and descriptions from the literature. Similarly, for the other genera of the Vespertilioninae our study material has been drawn chiefly from specimens and to a much lesser extent from the published works of others. The specimens that we have examined are listed in Appendix 1. Our aim as far as genera other than *Pipistrellus* and *Eptesicus* are concerned has been to provide illustrations of representative bacula, but in those instances where bacular structure has not before been studied we have endeavoured to examine as many species within each genus as the available specimens permitted. Clearly, the material available to us has been quite inadequate to establish the extent of individual variation in any one species or subspecies. While only adult specimens (wing epiphyses fully fused) have been used, we have necessarily had to accept that for the majority of species our data is limited. We have concentrated therefore on studying and comparing the gross morphology (size, shape, gross structure) of the bacula that we have examined in an attempt to identify similarities, differences and general trends. The finer details perhaps more valuable in species distinction have received much less attention, although where it is known that species are difficult to separate by conventional means attention has been drawn to bacular features that may assist in identification.

The specimens used in this study have been drawn almost entirely from the collections of the British Museum (Natural History), London (BM(NH)) and the Harrison Zoological Museum, Sevenoaks, Kent (HZM). Apart from these we have been able to examine one from the Naturhistorisches Museum, Wien (NMW), by courtesy of Dr K. Bauer, and one from the Carnegie Museum of Natural History, Pittsburgh (CMNH), an anomalous specimen loaned for identification by Dr D. A. Schlitter, while Dr K. F. Koopman generously brought to London an example of *Nycticeius humeralis* from the American Museum of Natural History, New York (AMNH) from which a much needed baculum was obtained. Specimens prepared many years ago at the British Museum (Natural History) are dry, sometimes mounted on card: the remainder have been prepared in the course of this study. This has been accomplished by maceration for a short period in a 5% solution of potassium hydroxide to which a small quantity of alizarin red has been added, after which the grosser macerated tissue was removed by dissection, the specimen then being cleared and stored in glycerin.

Drawings have been prepared using either a stereoscopic microscope with graticule scale and attached camera lucida, or freehand using a similar instrument. A few were drawn freehand using a stereo projection microscope with travelling micrometer stage. The wide range of size variation among vespertilionine bacula (for example from a length of 1 mm or less to as much as 9 or 10 mm in *Pipistrellus*) has necessitated the use of several scales of magnification. So far as possible all drawings on any one page of figures are at the same magnification, with an appropriate scale: to facilitate comparison the varying magnifications used follow an arithmetic progression whereby each successive larger value is twice its predecessor. It has not always been possible to conform to this arrangement, especially where drawings have been prepared from published illustrations. As a rule dorsal (D) and right lateral (RL) views of each baculum are provided: rarely through damage the left lateral (LL) aspect is given. Occasionally where it is of especial interest a half ventral (RVL or LVL) drawing has been made, and in a few instances where drawings have been taken from the literature it has been necessary to give the ventral (V) rather than the dorsal aspect.

Authorship and responsibility

We take joint responsibility for the results and opinions put forward and expressed in this paper, and for the new names proposed therein.

The baculum of *Pipistrellus*

Four bacular types have been identified within the nominal genus *Pipistrellus*. With some exceptions, modification and combinations, these are in broad agreement with the groupings of species

proposed by Tate (1942a) and Koopman (1973, 1975). The classifications of Tate and Koopman are summarised in Table 3.

(1) An elongate structure (Fig. 1a) with a slender shaft and paired basal flanges (e.g. Figs 2a–c, 3, 4, 5), the ventral surface of the proximal part of the shaft transversely concave, its distal part cylindrical or nearly so; in profile the base in line with the shaft or more or less deflected downward at an angle to it; the shaft may be more or less straight, flexed or variously curved in the vertical plane, while the tip is generally bifid or forked and may be directed ventrally to a greater or lesser extent.

Species aggregations in which this type of baculum is found include the *abramus*, *pipistrellus*, *coromandra* and *tenuis* groups of Tate (1942a); Koopman (1973) amalgamated these to form a *pipistrellus* group to which he added (1975) the African *nanus* and *permixtus*. However, *nanus* (Fig. 6b) proves to have a very different baculum, as does *imbricatus* (Fig. 9a), included by Tate in the *coromandra* group and thus by Koopman (1973) in the *pipistrellus* group. *Pipistrellus babu* (Fig. 4a), provisionally placed by Tate in the *kuhlii* group, also has the long, relatively straight baculum characteristic of this part of the division, as do *endoi* (Imaizumi, 1959) (Fig. 3b) and *peguensis* (Sinha, 1969) (Fig. 15c), both described since Tate wrote. The more recently described *westralis* (Koopman, 1984c) (Fig. 10d), *adamsi* (Fig. 10c) and *wattsi* (Fig. 10g) (Kitchener *et al.*, 1986) also belong with *tenuis* (Fig. 9d) and its allies in this grouping. Taxa referred to the *ceylonicus* group by both Tate and Koopman (1973) prove to have this bacular structure, as do those that have been examined of the *rueppellii* group (Figs 7e, f, 10a, b) of Koopman (1975). *Pipistrellus kuhlii* and its associates (Figs 5a–d, 6c) also belong in this division. In these, however, the basal lobes of the baculum are sharply angled to the shaft in the vertical plane, and this bacular profile is very characteristic of *kuhlii* and its relatives. The shaft is straight, without flexion, and the tip is usually bifid and not directed ventrally. Koopman (1975) included *anchietae* (Fig. 6e) in the *kuhlii* group, but this proves to have a very different bacular configuration.

A long-shafted baculum of this type occurs with little modification in the majority of the Australian species (Figs 11a–f, 12k) currently referred to *Eptesicus*, in *Nyctalus* (Fig. 10f), in *Scotozous* (Fig. 16d) (to which *rueppellii* and its immediate associates have sometimes been referred) and in *Scotoecus* (Fig. 20a–e), in which the ‘horns’ of the bifid tip extend in some instances almost to form a ring, a condition foreshadowed in *Pipistrellus paterculus* (Fig. 3c). The Australian *Scoteanax* (Fig. 16i) and *Scotorepens* (Figs 16g, h, 21e, f) also share this bacular type: in *Scoteanax* the ‘horns’ at the tip have become a transverse bar, but the species of *Scotorepens* retain the bifid or slightly bifid tip. A similar long-shafted baculum but with a simple tip occurs in the genera *Hesperoptenus* (Fig. 21a–c, g) and *Chalinolobus* (Fig. 17a–e). The baculum of *Glischropus* (Fig. 18a), although very small, is also of this type, with paired basal lobes, a slender shaft, and bifid tip.

(2) A very small structure (Fig. 1b), consisting of a broad base with two basal lobes (e.g. Figs 2d, e, 9c, h), supporting a short, very slightly hollowed shaft. This bacular type is found in *subflavus* (Fig. 2d), *circumdatus* (Fig. 2e), *societatis* (Fig. 9c) and the more recently described *cuprosus* (Hill & Francis, 1984) (Fig. 9h).

(3) A relatively short, stout shafted baculum (Fig. 1c), sometimes with expanded base and tip (e.g. Figs 6a, b, 7a, h, 8e, f), the base on occasion divided into paired lobes, sometimes angled vertically to the line of the shaft, which is fluted ventrally rather than mostly cylindrical; tip when expanded having its anterior edge sometimes divided into several irregular serrations and on occasion downwardly directed.

Such bacula are found in the *savii* group of Tate (1942a) and Koopman (1973, 1975) but not in *maderensis* (Fig. 5b) which was put into the *savii* group by both authors. Its baculum is however quite different and is like that of *kuhlii* and its associates. *Pipistrellus anchietae* (Fig. 6e), referred to the *kuhlii* group by Koopman (1975) also belongs with *savii*, and the same bacular type occurs in *nanus* (Fig. 6b), allocated with *permixtus* to the *pipistrellus* group by the same author. We have been unable to examine the baculum of *permixtus* but that of *nanus* and of *helios* (Fig. 6d) is of the type characteristic of this division, with its basal part quite sharply flexed to the shaft although not especially deep, and with an expanded, downwardly directed distal part. *Pipistrellus eisentrauti*

(Fig. 9g), referred to the *rueppellii* group by Koopman (1975) also shares this bacular type. The North American *hesperus* (Fig. 8d) was placed by this author in a *hesperus* group, with the African *musculus*. It has a robust baculum of the type found in this division, somewhat flattened, without basal lobes but broadened just beyond the base, the shaft narrowing towards the tip; the ventral surface is shallowly fluted throughout its length. Unfortunately, no baculum has been available for *musculus* but provisionally it is referred to this division on other grounds.

This bacular class also includes *imbricatus* (Fig. 9a), referred to the *coromandra* group by Tate (1942a) and by Koopman (1973), and *pulveratus* (Fig. 8c), *lophurus* (Fig. 8f), and *kitcheneri* (Fig. 8e) which Tate placed in the *affinis* group (vide infra). Koopman (loc. cit.) followed this lead with respect to *kitcheneri* but did not include *pulveratus* and *lophurus* since these were extralimital to his study. *Pipistrellus bodenheimeri* (Fig. 9f), described (Harrison, 1960) since Tate wrote and extralimital to Koopman (loc. cit., 1975) also belongs in this group. Tate referred *macrotis*, *vordermanni* and *curtatus* to the *savii* group on account of their reduced pm² but indicated that this allocation might not be tenable: however, the baculum of *macrotis* shows that it should be placed in this group. This author also created the *joffrei* group to include *joffrei*, *anthonyi*, *brachypterus*, and *stenopterus*: *brachypterus* has since proved to be a *Philetor* (Hill, 1971). We have been unable to examine the baculum in either *joffrei* or *anthonyi* but that of *stenopterus* (Fig. 7h) indicates that it belongs here. Both *joffrei* and *stenopterus* have been referred variously to *Nyctalus* (Chasen, 1940; Ellerman & Morrison-Scott, 1951) or to *Pipistrellus* (Tate, 1942a; Hill, 1966a) but the baculum of *stenopterus* has no resemblance to the long-shafted structure of the former genus.

(4) A relatively large, short but strong baculum (Fig. 1d), broad, with little or no proximal or distal expansion (e.g. Figs 8a, b, g, 10h), the ventral surface transversely deeply concave so that it is strongly arched or fluted throughout its length. This grouping includes *affinis* (Fig. 8a) and *petersi* (Fig. 8b), placed in the *affinis* group by Tate (1942a) and in the case of *petersi* in the same group by Koopman (1973), *affinis* being extralimital to his study, together with the Australian *tasmaniensis* (Fig. 8g) for which Tate maintained a *tasmaniensis* group. A further Australian form, *mackenziei* (Kitchener *et al.*, 1986) (Fig. 10h) is very like *tasmaniensis* and also belongs here. To some extent this grouping is linked to the previous division by *pulveratus*, *imbricatus*, *lophurus*, *kitcheneri* and their immediate associates: Tate allocated all except *imbricatus* to the *affinis* group.

The baculum of *Eptesicus*

We have been able to identify three bacular types among the species currently referred to the nominal genus *Eptesicus*. There is no single reference for species groupings in this aggregation of species, but for African forms these bacular types agree almost exactly with the species groups defined by Koopman (1975).

(1) A more or less triangular structure (Fig. 1e), its apex occasionally drawn out into a slight, short shaft, the base widened and sometimes slightly lobed but the tip not expanded, usually more or less pointed or gently rounded (e.g. Figs 13, 14a, c). This type of baculum is flattened, with little ventral fluting or concavity: there is little vertical flexion either of the base or of the more distal part, and the tip is not deflected downwards. So far as we have been able to establish, this bacular class occurs in all of the forms that are currently referred to *Eptesicus* from the New World, Europe and Asia, and in the African forms that Koopman (1975) included in the *serotinus* and *floweri* groups.

(2) The structure in a small group of species, wholly Australian, in which the baculum has usually a long cylindrical or slightly fluted shaft with paired expanded basal lobes (Fig. 1f) and usually a blunt tip (e.g. Fig. 11a–e), very similar in fact to the first of the bacular types that we have described for *Pipistrellus*. This grouping includes *pumilus* (Figs 11a, b, 12k), *vulturinus* (Fig. 11c), *douglasorum* (Fig. 11d) and *regulus* (Fig. 11e): in *pumilus* and *douglasorum* the shaft and base may be flexed rather like those of *Pipistrellus kuhlii* and its immediate relatives, while in *regulus* the shaft has an expansion just behind the tip (McKean *et al.*, 1978; Kitchener, 1976). A further species, *sagittula* (Fig. 11f), also appears to belong here, its baculum being perhaps a shorter-shafted version of this type.

(3) A slender-shafted baculum (Fig. 1g), usually with distinct paired basal lobes, sometimes angled or flexed to the line of the shaft, which is cylindrical, with variously expanded tip, the distal expansion varying from a downwardly directed spatulate plate to a large, anteriorly directed, downwardly deflected lobed structure (e.g. Figs 12a–j, 14b). Taxa with this type of baculum are wholly African and the grouping comprises those forms referred to the *capensis* and *tenuipinnis* group by Koopman (1975).

The baculum in other Vespertilioninae

Before considering the implications of bacular morphology in relation to the systematics of *Pipistrellus* and *Eptesicus*, a brief review of bacular types in the remaining genera of the Vespertilioninae will serve to place these nominal genera in the perspective of bacular structure in the subfamily as a whole.

Myotis (Fig. 19i, j). The baculum of *Myotis* has been figured and described by numerous authors. Palaearctic species have been studied by Topál (1958), Hanák (1965, 1970, 1971), Wallin (1969), Atallah (1970) and Baagøe (1973), among others. Nearctic and Neotropical species have been examined by Hamilton (1949), Wimsatt & Kallen (1952), Krutzsch & Vaughan (1955), Davis & Rippey (1968), Genoways & Jones (1969), LaVal (1973a) and Warner (1982). In this genus the baculum is much like a small saddle. In profile the base and tip are slightly elevated, the baculum ventrally slightly concave. In dorsal aspect the baculum is more or less triangular or projectile-shaped, anteriorly bluntly or sometimes more sharply pointed, the base divided to a greater or lesser extent into two lobes, the ventral surface deeply fluted. In some instances at least there is evidently distinctive variation between species and it is possible that some clear infrageneric division into bacular types might be made. There is also apparently considerable individual variation in some species, leading LaVal (1973a) in the case of *nigricans* to suggest the possibility that the material that he studied was a composite of sibling species. However, for so large a genus there seems to be a surprising degree of broad homogeneity in gross bacular structure. We have examined relatively few bacula from such a well known genus, but it is of some interest to note that the baculum of *ridleyi* (Fig. 19i), described and retained for many years in *Pipistrellus* on account of its dentition which corresponds to that genus (Hill & Topál, 1973) is undeniably of the type characteristic of *Myotis*.

Pizonyx (Fig. 19k). Figured and described by Hamilton (1949). The baculum is similar to that of *Myotis*, but lacks much of the saddle-like appearance, and is more triangular in dorsal aspect, tapering distally to a flattened, slightly elevated tip; it is also elevated proximally so that in profile the base inclines slightly upwards. Ventrally the baculum is slightly fluted.

Lasionycteris (Fig. 17f). Figured and described by Hamilton (1949). The baculum has a large, swollen, bilobed base, a long cylindrical shaft, and a slight distal enlargement, the tip and base elevated dorsally. Proximally, there is sometimes a flattened dorsal prominence on the base, its bilobed extremity projecting beyond the main bulbous part.

Plecotus (including *Corynorhinus*). The Old World forms (*Plecotus*, Figs 14d, 19g, h) are figured and described by Topál (1958), Lanza (1960) and Ibáñez & Fernández (1986), American taxa (*Corynorhinus*, Fig. 15f–h) by Nader & Hoffmeister (1983). In most the baculum is arrow-head-shaped, slightly saddle-like, with basal lobes and broad, short distal part, the base elevated dorsally, the ventral surface deeply fluted: in two taxa (*auritus*, Fig. 19g, *teneriffae*, Fig. 14d) it has a longer, more slender shaft with paired basal lobes and is less saddle-like.

Idionycteris (Fig. 15e). Figured and described by Nader & Hoffmeister (1983). An elongate baculum, with triangular basal plate, its apex directed posteriorly, and narrow shaft, curved dorsally and ventrally shallowly grooved.

Euderma. The baculum in this genus is so far apparently unknown.

Barbastella (Fig. 18j). Figured and described by Topál (1958). A small, saddle-like baculum similar in many ways to that of *Plecotus*, with elevated base, narrowed distal part which is upwardly curved, and with slightly raised, elevated tip.

Rhogeessa (Fig. 18k). Figured and described by LaVal (1973b). A small baculum with expanded, bilobed base and short, stubby shaft lacking any distal modification, the shaft ventrally fluted.

Baeodon (Fig. 15b). Figured and described by Brown *et al.* (1971) and LaVal (1973b). Baculum very like that of *Rhogeessa* but with shorter shaft.

Nycticeius. Australian forms hitherto referred to *Nycticeius* have been recognised as *Scoteanax* and *Scotorepens* by Kitchener & Caputi (1985). As therefore it is currently understood, *Nycticeius* includes two species, *humeralis* from North America and *schlieffenii* from Africa. These have widely differing bacula. In *humeralis* (Fig. 17k) the baculum is blade-like, with short, narrow shaft, the base thickened, proximally forming a prominent angle which inclines towards the ventral surface, the distal portion deep, with convex walls which terminate in an ascending point. This structure is figured by Hamilton (1949) who remarked that it differed markedly from the bacula of other [North American] genera: in fact it is not closely approached by any other vespertilionine. The baculum of *schlieffenii* (Fig. 16e), by contrast, has a broad bilobed base with tapering, fluted shaft, its tip unmodified, bluntly pointed, and unexpanded. Moreover, the bacular morphology of the Australian species formerly referred to *Nycticeius* supports their separation from this genus. This matter is discussed more fully below.

Otonycteris (Fig. 16a). Figured and described by Wassif & Madkour (1972), Fairon (1980) and Wassif, Madkour & Soliman (1984). An unusual baculum, mostly a more or less parallel-sided narrow shaft, the base and tip not expanded, both strongly elevated dorsally, the shaft tapering distally to a raised tip.

Lasiurus (Fig. 19l). Figured and described by Hamilton (1949). A slipper-like baculum with broad, dorsally elevated base, a short shaft, fluted ventrally, and with slightly expanded and elevated tip.

Dasypterus (Fig. 18f). Figured and described by Brown *et al.* (1971) and Hamilton (1949). Baculum like that of *Lasiurus* but tip as a rule not upturned.

Antrozous (Fig. 18b). Figured and described by Krutzsch & Vaughan (1955) and Pine *et al.* (1971). Baculum broadly triangular in dorsal view, tapering to broad, blunt point, fluted ventrally, and with the base elevated dorsally. It is very different from the baculum in *Nyctophilus* and *Pharotis*, and from that of *Otonycteris*, with which genera *Antrozous* has been associated in the past.

Bauerus (Fig. 15i). Figured and described by Pine *et al.* (1971). Baculum like that of *Antrozous* but smaller and narrower, the distal part not upcurved.

Scotomanes (Fig. 18g). A short baculum with broad, bilobed base merging into a very narrow, short cylindrical shaft with no distal expansion, lacking any upward deflection either proximally or distally.

Scotophilus (Fig. 17g–j). Figured and described by Harrison & Brownlow (1978). Baculum irregularly sub-rectangular or sub-triangular, flattened, anteriorly usually bluntly rounded, slightly concave in ventral transverse section, with slight basal lobes.

Vespertilio. Figured and described by Topál (1958) and Wallin (1969). In two species (*murinus* and *orientalis*) the baculum is situated at the base of the penis, which is supported by a cartilaginous pseudobaculum. In the third (*superans*) the baculum is situated not at the base of the penis but midway along the shaft, and there is no pseudobaculum. The baculum in *orientalis* (Fig. 21j) and *superans* is flattened and triangular, with a broad, bilobed base, tapering anteriorly to a narrow point and with slight vertical flexion. The baculum of *murinus* (Fig. 21i) is broad but less triangular in outline, and has a wide, bluntly rounded distal part. The bacula of *orientalis* and *superans* in particular are similar in many respects to those of the *Eptesicus serotinus* group (vide supra).

Histiotes (Fig. 18c–e). A very small baculum, with expanded bilobed base and short, narrow cylindrical shaft, its tip unexpanded, the base and tip deflected slightly upwards.

Ia (Fig. 21d). Figured and described by Topál (1970a). A large, flattened, triangular baculum similar to those of the *Eptesicus serotinus* group (vide supra).

Tyloncyteris (Fig. 18h, i). Baculum small, similar to that of *Histiotes* or to those of the *Eptesicus serotinus* group (vide supra), but with the distal part extended into a narrowed shaft and with relatively wider, expanded base with a slight trace of basal lobes.

Glaucocyteris (Fig. 19a–f). Baculum very small and somewhat variable within the genus, but mostly more or less triangular, with some modification, usually as reduction, to a deeply lobed base with a short, blunt distal portion. However, on occasion the base is slightly or considerably expanded and the distal portion lengthened to a short shaft.

Mimetillus. We have been unable to establish the presence of a baculum in this monotypic genus, from which it appears to be lacking.

Eudiscopus. The baculum of *Eudiscopus* (if present) is apparently unknown.

Nyctalus (Fig. 10f). Figured and described by Topál (1958) and Lanza (1959). A long, slender baculum with narrow basal lobes, a long cylindrical shaft, and slightly bifurcated tip.

Laephotis (Fig. 16f). Baculum with expanded, bilobed base, narrow fluted shaft and broadly expanded tip with slight downward deflection, a small protuberance on its upper surface. Similar in many respects to the baculum in the *Eptesicus capensis* and *E. tenuipinnis* groups (vide supra).

Glischropus (Fig. 18a). A very small baculum, with paired basal lobes, narrow cylindrical shaft and slightly expanded, bifid tip.

Scotozous (Fig. 16d). Figured and described by Sinha (1976). A long baculum with slight basal lobes, a narrow, fluted shaft, and slightly bifid tip, the shaft slightly flexed.

Scoteanax (Fig. 16i). Figured and described by Kitchener & Caputi (1985). A long baculum with strong, expanded bilobed base, a slender cylindrical shaft, and with the tip embellished into a short, transverse bar.

Scotorepens (Figs 16g, h, 21e, f). Figured and described by Kitchener & Caputi (1985). A long baculum with expanded, bilobed base and slender, cylindrical shaft, the tip slightly expanded and bifid, the ‘horns’ deflected ventrally.

Scotoecus (Figs 20a–e, 21h). A long, slender baculum with slightly expanded and bilobed base, long cylindrical shaft and an expanded, bifurcated tip, the ‘horns’ extending ventrally and sometimes curving to form an almost complete ring.

Philetor (Fig. 16b). Figured and described by Hill (1966a). A strong but relatively short baculum with paired basal lobes, a short, fluted shaft, and expanded rugose tip, the base and tip elevated and deflected upwards.

Hesperoptenus (Fig. 21a–c, g). Figured and described by Hill (1976) and Hill & Francis (1984). Baculum long and slender, with paired basal lobes, a flattened, ventrally fluted shaft, and unmodified, rounded tip.

Chalinolobus (Fig. 17a–e). Baculum long, with clearly defined basal lobes, a long cylindrical shaft, and an expanded tip, the expansion sometimes slight, considerable, or bifid with two obtuse projections.

Although the two genera are commonly referred to a separate subfamily, the Nyctophilinae, for purposes of comparison we have also examined the baculum in *Nyctophilus* and *Pharotis*.

Nyctophilus (Figs 16c, 22a–g). Figured by Churchill *et al.* (1984). A long, rather broad baculum with scarcely expanded, bilobed base and a broad shaft tapering distally to a blunt point, or wider

terminally with a median emargination to produce a shallowly bifid tip; shaft ventrally deeply fluted.

Pharotis (Fig. 22h). Baculum similar to that of *Nyctophilus* but shaft narrower, tapering to slightly expanded tip.

Systematic considerations

The majority of genera in the Vespertilioninae have bacula which overall display a wide range of variation in their gross morphology. Most have a distinctive baculum: where closely similar bacula occur in genera currently recognised as distinct, as for example in *Scotozous* and *Pipistrellus*, then close relationship has been presumed on other morphological grounds. We are thus persuaded that in this subfamily the baculum can be used as a guide to infrageneric and intergeneric classification, although it seems that its value as a suprageneric indicator may be less. In the same way, although we have not explored the point in detail, it has become apparent that in many genera the minor details of bacular morphology can be used to assist in species distinction. These considerations have led us to the view that the very dissimilar bacular types that we have been able to identify and define within *Pipistrellus* and *Eptesicus* do indeed reflect natural groupings and show that *Eptesicus* as it is currently defined is a composite. Certainly it seems true to say that the current classification of both nominal genera does not properly reflect the relationships that we believe bacular morphology suggests exist within and between them.

Genus *Pipistrellus* Kaup, 1829

Pipistrellus Kaup, 1829: 98. *Vespertilio pipistrellus* Schreber.

Romicia Gray, 1838: 495. *Romicia calcarata* Gray = *Vespertilio kuhlii* Kuhl.

Romicius Blyth, 1840: 75. Variant of *Romicia* Gray.

Hypsugo Kolenati, 1956: 131. Included *Vespertilio maurus* Blasius = *Vespertilio savii* Bonaparte, and *Vespertilio krascheninnikowii* Eversmann. Type species fixed as *Vespertilio savii* Bonaparte by Wallin (1969). Valid as a subgenus.

Nannugo Kolenati, 1856: 131. Included *Vespertilio nathusii* Keyserling & Blasius, *Vespertilio kuhlii* Kuhl and *Vespertilio pipistrellus* Schreber.

Alobus Peters, 1868: 707. *Vespertilio temminckii* Cretzschmar = *Vespertilio ruppellii* Fischer. Preoccupied by *Alobus* Le Conte, 1856 (Coleoptera).

Euvesperugo Acloque, 1899: 35. Included six species, one being *Vespertilio pipistrellus* Schreber.

Eptesicops Roberts, 1926: 245. *Scotophilus rusticus* Tomes.

Neoromicia Roberts, 1926: 245. *Eptesicus zuluensis* Roberts. Valid as a subgenus.

Vansonina Roberts, 1946: 304. *Pipistrellus vernayi* Roberts = *Vespertilio ruppellii* Fischer.

Vespadelus Iredale & Troughton, 1934: iii, 95. *Scotophilus pumilus* Gray. Nomen nudum.

Vespadelus Troughton, 1943: 348. *Scotophilus pumilus* Gray. Valid as a subgenus.

Registrellus Troughton, 1943: 349. *Pipistrellus regulus* Thomas (see Hill, 1966b).

Falsistrellus Troughton, 1943: 349. *Vespertilio tasmaniensis* Gould. Valid as a subgenus.

Perimyotis Menu, 1984: 409, 415. *Vespertilio subflavus* F. Cuvier. Valid as a subgenus.

Parastrellus Horáček & Hanáček, 1985a: unpaginated; 1985b: 62; 1985–1986: 15, fig. 4. *Pipistrellus hesperus* H. Allen. Nomen nudum.

The genus *Pipistrellus* cannot be diagnosed by conventional morphological characters that are individually exclusive. Its current definition rests on Miller (1907) who based his diagnosis on the structure of i^2 which is simple or has a well developed secondary cusp; on the reduction of i^3 which is smaller than i^2 but nevertheless extends beyond the cingulum of that tooth; on rather short canines, c^1 often but not invariably with incipient secondary cusp on its posterior edge; and on the absence of pm^3 to give the dental formula $i_1^1 \frac{2}{2} \frac{3}{3}$, c_1^1 , $pm_1^2 \frac{2}{2} \frac{4}{4}$, $m_1^1 \frac{2}{2} \frac{3}{3} = 34$, with pm^2 barely or not in the toothrow. He remarked that the members of the genus were recognisable by their dental formula, large i^3 , unmodified skull and ears, and the normally long fifth finger.

The definition of the genus is briefly discussed by Tate (1942a), Ellerman & Morrison-Scott (1951) and Kitchener *et al.* (1986). All recognised the unreliability of the presence or absence of pm^2 as a prime diagnostic character, Ellerman & Morrison-Scott also remarking that 'strictly

speaking *Pipistrellus* is not more than a subgenus of *Eptesicus*, which itself might be referred to *Vespertilio*, but for convenience they and most other recent authors have followed the conventional distinction. It is clear from the foregoing account of the baculum in the Vespertilioninae that the species allocated to *Pipistrellus* can be separated from most other vespertilionine genera by their bacular morphology: those genera which have bacula similar to those of some *Pipistrellus* species (e.g. *Nyctalus*, *Scotozous*) can be defined by other morphological features of the skull and dentition, as they were by Miller (loc. cit.).

Species groups in *Pipistrellus* are difficult and in some instances almost impossible to define on external, cranial and dental characters: most (Tate, 1942a; Koopman, 1973, 1975) are brought together by combinations of characters with few or sometimes no exclusive features. Some species of *Pipistrellus*, moreover, appear difficult to separate from some of *Eptesicus* (Koopman, 1975; Heller & Volleth, 1984) except by the presence or absence of pm^2 which is itself evanescent. Bacular morphology appears to offer at least a partial solution to this difficulty, at the same time indicating that the genus as currently understood is a composite of several different groups of species, as suggested by Heller & Volleth (loc. cit.) on the basis of its known karyology.

Chromosomal features so far as they have been established in *Pipistrellus* are reviewed by Heller & Volleth (1984) and Zima & Horáček (1985). Their summaries demonstrate that karyologically *Pipistrellus* as currently constituted is a very heterogeneous and diverse group, with $2N$ varying from 26–44 and FN from 44–60. At this stage we have been unable to find any consistent correlation between the chromosome formulae that these authors quote for various species and the groupings that we recognise on bacular and other grounds. However, many species remain to be studied karyologically and it appears from Zima & Horáček that for the present karyotype variability in the Vespertilioninae may be only of limited value as a taxonomic criterion.

While at present we would not support the generic division of *Pipistrellus* as has been indicated or suggested by Menu (1984), Horáček & Hanák (1985a, b) or Kitchener *et al.* (1986) since besides bacular features there appear to be few or no characters reported for its constituent groups that would support this wider separation, we consider that the divisions apparent within the genus justify subgeneric recognition. Wallin (1969) has already anticipated this view to some extent, employing *Hypsugo Kolenati*, 1856 for *P. savii*, in part on bacular grounds. Horáček & Hanák (1985–1986) recognised *Hypsugo* as a distinct genus. The gross morphology of the baculum also indicates that the Australian taxa formerly referred to *Eptesicus* should be transferred to *Pipistrellus*, as Heller & Volleth (1984) suggested, and that the African forms hitherto allocated to the *capensis* and *tenuipinnis* groups of *Eptesicus* also represent *Pipistrellus* as these authors inferred on account of their known karyology. Thus we would classify *Pipistrellus* in the following manner, listing included taxa without distinction as to taxonomic rank: some are not necessarily valid species or subspecies and for obvious reasons we have been unable to examine every named form in the genus.

Subgenus *Pipistrellus* (*Pipistrellus*)

Baculum long, with strong, extended shaft, well developed basal lobes, nearly always with a bifid tip. Braincase high, rounded, not flattened, sometimes globose; postorbital region usually wide; cranial profile generally straight or nearly straight from occiput to nares; interdental palate longer than wide; maxillary tooththrows parallel or only slightly convergent anteriorly; i^2 generally bicuspid; pm^2 usually large, pm_2 not greatly reduced, usually about $3/4$ crown area of pm_4 . *Pipistrellus kuhlii* and its associates differ slightly in almost unicuspid i^2 ; greatly reduced i^3 , much reduced pm^2 and more reduced pm_2 although some of these features occur in isolation in other species of the subgenus.

(a) *pipistrellus* group

Basal lobes of baculum more or less in line with the bacular shaft in the vertical plane; i^2 bicuspid, but not strongly so, cusps not deeply divided.

(a) (i) *pipistrellus* subgroup. Braincase high, rounded; postorbital region wide; supraorbital region not widened or swollen; rostrum long, not greatly broadened, with shallow median rostral

depression; cranial profile almost straight from occiput to nares, slightly depressed over anterior part of orbit; premaxillae not shortened; zygomata slender, lacking any jugal eminence; interdental palate longer than wide; maxillary tooththrows parallel for most of their length, anteriorly slightly convergent; short bony post-palate; slight basal pits; i^2 bicuspid, posterior cusp $1/2-3/4$ the height of anterior cusp; i^3 about the same in crown area or a little larger than i^2 , about $1/2$ or a little more its height, with larger central and smaller lateral accessory cusps, lying postero-externally to that tooth, separated from c^1 by a small diastema; pm^2 large, unreduced, its crown area similar to that of i^2 or a little less, slightly intruded but separating c^1 and pm^4 ; i_{1-3} not much imbricated, i_3 about twice the bulk of i_{1-2} ; pm_2 not usually much reduced, about $1/2-3/4$ or more the crown area of pm_4 .

Included taxa: *aladdin*, *bactrianus*, *lacteus*, *nathusii* (Fig. 2b); *mediterraneus*, (?) *permixtus*, *pipistrellus* (Fig. 2a).

Among African *Pipistrellus* we have been unable to examine the baculum of *permixtus* (Aellen, 1957) compared by its describer chiefly with *nathusii*. Its dentition, with bicuspid i^2 , the posterior cusp $2/3$ the height of the anterior cusp, i^3 with lateral accessory cusps, its main cusp equal in height to the posterior cusp of i^2 , large, slightly intruded pm^2 which is about as big as i^3 , and unreduced pm_2 , its crown area about $3/4-4/5$ the crown area of pm_4 suggests that it should be referred to the *pipistrellus* subgroup. Koopman (1975) referred it to the *pipistrellus* group.

(a) (ii) *javanicus* (*abramus*) subgroup. Braincase slightly globular, elevated posteriorly; post-orbital region wide; supraorbital region distinctly broadened to produce abruptly incurving lateral margins to the anterior part of the postorbital area; rostrum broad, dorsally flattened, with no more than an indication of a median rostral depression; cranial profile almost straight from occiput to nares, slightly flattened over the occiput and a little depressed over the anterior part of the orbits; premaxillae not shortened; zygomata slender but not weak, lacking any jugal eminence; interdental palate only little longer than wide; palate strongly domed with broad anterior emargination; maxillary tooththrows more or less parallel, scarcely convergent anteriorly; short bony post-palate; shallow basal pits; i^2 well developed, bicuspid, posterior cusp sometimes small, usually about $3/4$ height of anterior cusp; i^3 similar in size to i^2 or slightly larger, about as high as its posterior cusp, with larger central and smaller lateral accessory cusps, lying postero-externally to that tooth, separated from c^1 by a narrow diastema; pm^2 little reduced, equal to or rather less than i^3 in crown area, in recess between c^1 and pm^4 which approach but do not touch; i_{1-3} scarcely imbricated, i_3 as a rule similar in size to i_2 , both a little more massive than i_1 ; pm_2 about $1/2-3/4$ the size of pm_4 , very slightly intruded from tooththrow.

Included taxa: *abramus* (Fig. 3a), *akokomuli*, *babu* (Fig. 4a), *bancanus*, *camortae* (Fig. 15d), *endoi* (Fig. 3b), *irretitus*, *javanicus* (Fig. 10e), *meyeni*, *peguensis* (Fig. 15c), *paterculus* (Fig. 3c), *pumiloides*.

Current treatments of Asian *Pipistrellus* usually include *abramus* in *P. javanicus* (*tralatitius*, Laurie & Hill, 1954) as a valid subspecies. There appear to be few conventional features that clearly separate *javanicus* from *abramus* but their bacula differ quite sharply in the high degree of vertical flexion of the shaft evident in the latter. This difference was used by Thomas (1928a) who examined Indo-Chinese *Pipistrellus* and differentiated *abramus* from *raptor*, *javanicus* (as *tralatitius*) and *coromandra* by virtue of the double curvature of its baculum, the others being straight. Van Peenen *et al.* (1969) recorded *coromandra*, *javanicus* and *mimus* from Vietnam but the baculum that they illustrate for *javanicus* is clearly that of *abramus*. This bacular difference suggests that *javanicus* and *abramus* should be considered specifically distinct even although there seem to be few cranial and dental characters to separate them. The braincase in *javanicus* is slightly more inflated than in *abramus* and its rostrum narrower, the palate is usually a little wider in relation to its length and is slightly more excavated and domed, while pm^2 is a little less reduced and less intruded, tending rather more to separate c^1 and pm^4 . Both occur in Vietnam (Thomas, 1928a; specimens listed below). It seems likely that *bancanus* and *camortae*, which has an unflexed baculum, are more closely related to *javanicus* than to *abramus*.

Soota & Chaturvedi (1980) remarked that Thomas (1915c) had pointed out that the baculum of *abramus* is doubly curved and that in *paterculus* it is straight, but they stated further that material of

paterculus in the collections of the Zoological Survey of India revealed that its baculum is doubly curved. However, specimens in the collections of the British Museum (Natural History) referred to *paterculus* (some the original material seen by Thomas) have relatively straight bacula when compared with the sinuous baculum of *abramus*. We have found this sinuous baculum to be characteristic of *abramus*, to which perhaps the specimens seen by Soota & Chaturvedi should be referred.

The very elongate baculum of *paterculus*, with its strongly bifid tip, the 'horns' of which are deflected ventrally and extend to some extent to form a ring (Thomas, 1915c) is reminiscent of the baculum of *Scotoecus*. A very long baculum is also found in *endoi*, but in this species the tip is less strongly bifid and the 'horns' are deflected dorsally. Both, however, are clearly referable to *Pipistrellus* on cranial and dental characters, *Scotoecus* being distinguished especially by a massive unicuspid i^2 , the loss of i^3 , a grooved c^1 , and usually by the absence of pm^2 .

(a) (iii) *coromandra* subgroup. Small, with small, rounded braincase, elevated posteriorly and slightly so frontally; postorbital region wide; rostrum short, relatively narrow; no median rostral depression; cranial profile straight or nearly so from occiput to tip of rostrum; premaxillae exceptionally short; zygomata slender, without jugal projection; interdental palate about as long or a little longer than wide; short bony post-palate: no basal depressions; i^2 usually bicuspid, posterior cusp sometimes very small or rarely absent, when present about 1/2 or a little more the height of the anterior cusp; i^3 equal or greater than i^2 in crown area, reaching to tip of its posterior cusp, with larger principal cusp and smaller lateral accessory cusps, lying postero-externally to the inner tooth; pm^2 not much reduced, nearly as great or as great in crown area as i^3 , with well developed, slightly inwardly directed pointed cusp, in recess between c^1 and pm^4 ; i_{1-3} not much imbricated, i_3 a little larger than i_{1-2} ; pm_2 about 1/2 crown area and height of pm_4 , slightly extruded.

Included taxa: *adamsi* (Fig. 10c), *afghanus*, *angulatus*, *collinus* (Fig. 4b), *coromandra* (Fig. 7c), *glauacillus*, *mimus* (Fig. 7g), *murrayi* (Fig. 4c), *nitidus*, *papuanus* (Fig. 2c), *ponceleti* (Fig. 4d), *portensis*, *principulus*, *sewelanus*, *sturdeeii*; possibly *subulidens* which may however represent *javanicus*; *tenuis* (Fig. 9d), *tramatus* (Fig. 7b), *wattsi* (Fig. 10g), *westralis* (Fig. 10d).

(a) (iv) *ceylonicus* subgroup. Large, with rather short, broad braincase; wide postorbital region; some degree of supraorbital expansion; rostrum broad, rather long; weak, diffuse median rostral depression; cranial profile slightly convex, raised over the frontal region; premaxillae normal, not shortened; zygomata moderate, without jugal eminence or process, interdental palate longer than wide; maxillary tooththrows parallel; short bony post-palate; slight basal pits; i^2 large and massive, bicuspid to almost unicuspid, with moderate to small posterior cusp about 2/3 height of anterior cusp; i^3 massive, as large or larger than i^2 , extending to or a little beyond posterior cusp of that tooth, with large principal cusp and smaller lateral accessory cusps, lying postero-laterally to i^2 , narrowly separated from c^1 ; pm^2 large, nearly as great or greater in crown area than i^3 , usually filling the recess between c^1 and pm^4 into which it is intruded, these almost in contact labially; i_{1-3} slightly imbricated, i_3 a little larger than i_{1-2} ; pm_2 almost as large in crown area as pm_4 , very slightly extruded from the tooththrow.

Included taxa: *borneanus*, *ceylonicus* (Fig. 7d), *chrysothrix*, *indicus*, (?) *minahassae*, *raptor* (Fig. 3d), *shanorum*, *subcanus*.

An account of *minahassae* is given by Tate (1942a) who referred it to a *minahassae* group of which it was the sole member. The skull of the holotype has never been described and Tate's remarks are based on a referred specimen in the American Museum of Natural History, New York (AMNH 102359). It has a short, high braincase with rudiments of a sagittal crest, prominent supraorbital tubercles and slender zygomata; i^2 is long, with well developed posterior cusp, c^1 slender, lacking an accessory cusp, pm^2 only slightly intruded, its crown area greater than that of i^3 , and i_{1-3} scarcely imbricated. These features suggest that if this specimen represents *minahassae* the taxon should be allocated to *Pipistrellus* (*Pipistrellus*) and provisionally we place it in the *ceylonicus* subgroup of the *pipistrellus* group, but clearly these decisions can only be speculative.

(b) *rueppellii* group

Baculum as in *pipistrellus* group; braincase high, broadened, rounded and globose; postorbital

region wide; supraorbital region slightly expanded; rostrum short; with shallow, ill-defined median depression; cranial profile almost straight, a little raised over frontal region, a little depressed over rostrum; premaxillae not shortened; zygomata slender, without jugal projection; interdental palate a little longer than wide; maxillary tooththrows slightly convergent; short bony post-palate; no basal pits, instead a shallow depression; i^2 strongly bicuspid, posterior cusp about 3/4 height of anterior cusp; i^3 usually very small or minute, its crown area less than 1/2 that of i^2 , its tip sometimes barely rising above the cingulum of the inner tooth, on occasion (e.g. *nanulus*) larger, equal to or slightly exceeding i^2 in crown area, about 1/2 or a little more the height of that tooth; i^3 lying sublaterally to i^2 , separated from c^1 by a wide diastema; pm^2 not usually greatly reduced, its crown area similar to that of i^2 , with strong cusp, separating c^1 and pm^4 , occasionally (*crassulus*) much reduced, similar in size to i^3 in its much reduced condition, or (*crassulus*, *nanulus*) recessed between these teeth; i_{1-3} little imbricated, i_3 slightly the largest as a rule; pm_2 about 3/4 or more as large in crown area as pm_4 and about 3/4 its height, rarely (*coxi*, *crassulus*) more reduced, about 1/2 crown area and height of pm_4 .

Included taxa: Probably *coxi*; *crassulus* (Fig. 7e), *fuscipes*, *leucomelas*, *nanulus* (Fig. 7f), *pulcher* (Fig. 10a), *rueppellii* (Fig. 10b), *senegalensis*, *vernayi*.

Vansonia Roberts, 1946 is available should further separation of the *rueppellii* group be thought justified: an earlier name, *Alobus* Peters, 1867 is preoccupied.

(c) *kuhlii* group

Baculum of moderate length with narrow cylindrical shaft and paired basal lobes as in *pipistrellus* and *rueppellii* groups but basal lobes strongly angled to line of shaft in vertical plane; braincase low but not flattened, rounded, only slightly elongate; postorbital region wide; supraorbital region not widened or swollen; rostrum long, unwidened, with very slight median flattening; cranial profile almost straight from occiput to nares, slightly raised over frontal region, slightly depressed over front of orbits; premaxillae slightly shortened; zygomata slender, weak, without jugal eminence; interdental palate longer than wide; maxillary tooththrows almost parallel; short bony post-palate; small, narrow basal pits; i^2 usually unicuspid, at best only slightly bicuspid; i^3 small, its crown area 1/2 or less that of i^2 , its tip extending only slightly beyond the cingulum of that tooth, to which it lies laterally or sublaterally, separated from c^1 by a moderate or narrow diastema; pm^2 small, similar in crown area to i^3 , intruded to lie in recess between c^1 and pm^4 , these more or less in contact; i_{1-3} moderately imbricated, i_3 slightly the largest; pm_2 reduced, about 1/2 or less the crown area and height of pm_4 .

Included taxa: Probably *aero*; *deserti* (*aegyptius*, Qumsiyeh, 1985) (Fig. 5c), *fuscatus*, *ikwanius*; probably *inexpectatus*; *kuhlii* (Fig. 5a), *maderensis* (Fig. 5b), *marrensis*, *rusticus* (Figs 5d, 6c).

We have been unable to examine the baculum of *inexpectatus* (Aellen, 1959) but this taxon was placed in the *kuhlii* group by Koopman (1975) who also referred *maderensis* to the *savii* group. However, an example of *maderensis* in the collections of the British Museum (Natural History) has a baculum clearly of the *kuhlii* type.

Romicia Gray, 1838 is available for the *kuhlii* group should this be thought worthy of further separation.

Subgenus *Pipistrellus* (*Vespadelus*)

Baculum usually with long cylindrical or ventrally slightly fluted shaft, paired basal lobes and a blunt tip; shaft shorter and wider in *sagittula*; basal lobes sometimes flexed to line of shaft in vertical plane; braincase slightly broadened, flattened and elongated; postorbital region wide; supraorbital region slightly broadened; rostrum short but not greatly widened; shallow median rostral depression; cranial profile almost straight from occiput to nares, a little depressed over rostrum; premaxillae not shortened; zygomata slender, without jugal process; interdental palate a little longer than wide; maxillary tooththrows slightly convergent anteriorly; short bony post-palate; no basal pits: i^2 bicuspid, posterior cusp almost as high as anterior cusp; i^3 much reduced, its crown area 1/2 or less that of i^2 , its tip barely extending beyond the cingulum of that tooth, to which i^3 lies postero-laterally, separated from c^1 by a narrow diastema; pm^2 almost invariably absent,

when present a small spicule in recess between c^1 and pm^4 : i_{1-3} moderately imbricated, i_3 slightly the largest, pm_2 greatly reduced, in crown area about 1/2 or more usually less the crown area of pm_4 , and 1/2 its height.

Included taxa: *caurinus* (Fig. 11b), *douglasorum* (Fig. 11d), *pumilus* (Figs 11a, 12k), *regulus* (Fig. 11e), *sagittula* (Fig. 11f), *vulturinus* (Fig. 11c).

Formerly referred to *Eptesicus*, the transfer of these taxa to *Pipistrellus* was first suggested by Heller & Volleth (1984), purely on bacular grounds. The bacular, cranial and dental features of this group suggest that it represents *P. (Pipistrellus)* in Australia, the few members of this subgenus (*adamsi*, *westralis* and perhaps *javanicus*) that also occur there being possibly slightly less differentiated by virtue of their relatively slightly less shortened skulls and their retention of pm^2 . The *pipistrellus* group of the subgenus extends widely through the islands of Indo-Australia to New Guinea, the Solomon Islands and Australia, chiefly as the *coromandra* subgroup, to which *adamsi* and *westralis* belong. The *javanicus* subgroup reaches at least to Java and Sulawesi and may extend to Australia (Hill, 1983) but the Australian record of *javanicus* is based on two old examples and has never been confirmed. Possibly the slightly differentiated *pumilus* and its allies result from a further perhaps earlier invasion of Australia. Bacular differences in this subgenus (Figs 11, 12k) suggest that it may consist of two groups: it has been possible to examine only *pumilus*.

There has been hitherto a wide geographical hiatus in the Indo-Australian distribution of *Eptesicus* as formerly understood. Beyond these Australian forms, no other taxon attributed to this nominal genus has been reported further east in Indo-Australia than southern Thailand, other than an unconfirmed record from Sarawak of *Eptesicus* sp. (Pirlot, 1968) which provided no details.

Subgenus *Pipistrellus (Perimyotis)*

Baculum very small, Y-shaped, with paired basal lobes and very short shaft; braincase slightly elongate, rounded, almost globose; postorbital region wide; supraorbital region slightly broadened; rostrum long, elevated, slightly widened; shallow median frontal depression; a very slight lateral depression on each side just anterior to the orbital rim; cranial profile sinuous, raised over frontal region, a little depressed over front of orbits; premaxillae not shortened; zygomata moderate, a slight jugal eminence; interdental palate longer than wide with wide anterior palatal emargination; maxillary tooththrows convergent anteriorly; very short bony post-palate; slight basal depressions; i^2 bicuspid with well developed posterior cusp about 3/4 height of anterior cusp; i^3 massive, its crown area exceeding that of i^2 , in height reaching or exceeding the height of anterior cusp of that tooth, with larger principal cusp and smaller lateral accessory cusps, lying postero-externally to inner tooth, separated from c^1 by a wide diastema; pm^2 large, its crown area equal to that of i^3 , in tooththrow, sometimes separated from pm^4 by a slight diastema; i^2-3 and pm^2 almost identical to those of *P. nathusii*; i_{1-3} not imbricated, i^3 only slightly bulkier than i_{1-2} ; pm_2 not greatly reduced or compressed in tooththrow, its crown area about 1/2 or more that of pm_4 , about 1/2-3/4 its height; tragus myotine, about 1/2 height of ear, tapering to blunt point.

Included taxon: *subflavus* (Fig. 2d).

Menu (1984) proposed the genus *Perimyotis* for *P. subflavus*, chiefly on account of the features of the canine and post-canine dentition in which he believed this species to approach *Myotis*. However, Hill & Topál (1973) in discussing *Myotis rosseti* and *M. ridleyi* which also combine the tragal features of *Myotis* with the *Pipistrellus* dentition (pm_3^3 absent) noted that in *Myotis* i^2 is short and broad, its posterior cusp wider basally than the anterior cusp, while in *Pipistrellus* this tooth is linear, often narrower posteriorly than anteriorly. Also, in *Myotis* the principal cusp of i^3 is equal to or exceeds that of i^2 in height and the tooth is often hooked to produce a caniniform appearance while in *Pipistrellus* it is lower and is not hooked. In *Myotis* i_3 is usually much larger than i_{1-2} but in *Pipistrellus* there is as a rule no such great distinction in size. The incisive dentition of *subflavus* corresponds closely with that of *Pipistrellus*.

The baculum of *subflavus* is of a type not found in *Myotis*. Menu (1984) stated on the basis of published figures that the baculum approached that of certain *Myotis* and more particularly that of *Plecotus auritus*. We find no significant resemblance to the morphologically rather stable, saddle-

like baculum of *Myotis* and although there are some similarities with the bacula of *Plecotus auritus* (Fig. 19g) and *P. teneriffae* (Fig. 14d), that of *P. austriacus* (Fig. 19h) is nearer in structure to the myotine baculum. The bacular type found in *subflavus* occurs in a similar form in *Pipistrellus circumdatus* (Fig. 2e), *P. societatis* (Fig. 9c) and *P. cuprosus* (Fig. 9h). There are considerable differences, however, between *subflavus* and *circumdatus* and its allies, not least in the degree of reduction of pm^2 , this tooth in these three species being very small or absent.

The unshortened rostrum and the dental features of *subflavus* suggest that it is nearest to *P. (Pipistrellus)*, which it appears to represent in North America. We find *hesperus*, the other North American species of *Pipistrellus*, to belong on bacular and dental grounds to *P. (Hypsugo)*. Thus we do not support Menu's view (p. 410, footnote) that *Pipistrellus* is limited to the Old World and that the lines leading to this genus did not enter the North American continent. The marked differences between *subflavus* and *hesperus* indicate two quite different pipistrelline groups, as Hamilton (1949) remarked in relation to their bacula, but bacular and dental evidence suggests alliance to established Old World groupings, the baculum of *subflavus* being perhaps a reduced form of the shafted structure found in *P. (Pipistrellus)*, that of *hesperus* a modification of the type found in *P. (Hypsugo)*.

Subgenus *Pipistrellus (Hypsugo)*

Baculum usually short, stout, sometimes with expanded base and tip; base rarely bilobed, sometimes dorsally elevated; shaft generally flattened dorso-ventrally, sometimes wide, its underside transversely concave or fluted; tip ventrally hollowed as an extension of ventral fluting of shaft, when expanded anteriorly sub-square or slightly rounded, its anterior edge sometimes irregularly serrated, tip sometimes downwardly directed, its lateral margins on occasion forming two broadly based, ventrally directed projections; pm^2 generally much reduced, small, minute, or rarely absent.

Wallin (1969) considered *Hypsugo* a valid subgenus within *Pipistrellus* but included only *P. savii*: Horáček & Hanák (1985a, b) added *cadornae* and *pulveratus* and suggested the elevation of *Hypsugo* to generic rank, subsequently (1985–1986) widening its possible content and considering it generically distinct.

(a) *savii* group

Postorbital region, supraorbital region and rostrum not greatly widened; supraorbital tubercles if present small and undeveloped.

(a) (i) *pulveratus* subgroup. Braincase elongate, inflated; postorbital region wide, supraorbital area not broadened; rostrum long, not widened; shallow frontal depression; no median rostral depression; broad, shallow lateral depressions above anterior part of orbit; cranial profile somewhat sinuous, depressed over front of orbits; premaxillae not shortened; zygomata robust, with very slight jugal eminence; interdental palate longer than wide; maxillary tooththrows almost parallel; moderate bony post-palate; no basal pits; i^2 bicuspid, posterior cusp about 3/4 height of anterior cusp; i^3 large, wide, its crown area equal to or slightly exceeding that of i^2 , reaching to tip of the posterior cusp of that tooth, with moderate lateral accessory cusps, lying postero-externally to the inner tooth, separated from c^1 by a moderate diastema; pm^2 about equal or nearly equal to i^3 in crown area, in recess between c^1 and pm^4 which are closely approximated; i_{1-3} slightly imbricated, i_3 a little the largest; pm_2 a little less than 1/2 the crown area of pm_4 , 1/2–3/4 its height.

Included taxon: *pulveratus* (Fig. 8c).

(a) (ii) *nanus* subgroup. Braincase elevated, slightly inflated, more or less globose but a little elongated; postorbital region wide; supraorbital area slightly widened with small supraorbital swellings; rostrum not especially shortened or broadened; shallow median rostral depression; slight lateral depressions just anterior to supraorbital region; cranial profile sinuous, strongly depressed and concave over rostrum; premaxillae not shortened; zygomata slender, lacking jugal projection; interdental palate longer than wide; maxillary tooththrows slightly convergent; short bony post-palate; no basal pits; i^2 unicuspid or with small posterior cusp extending to about 3/4 of

its height; i^3 wide, its crown area slightly exceeding that of i^2 , about 1/2–3/4 the height of that tooth, extending almost to the tip of its posterior cusp, with slight lateral cusps, lying postero-externally to the inner tooth, separated from c^1 by a wide diastema; pm^2 about 1/2–2/3 or a little more the crown area of i^3 , intruded into recess between c^1 and pm^4 , these sometimes in contact or nearly so; i_{1-3} not or only very slightly imbricated, i^3 slightly the largest; pm_2 about 1/2 the crown area and height of pm_4 .

Included taxa: *arabicus* (Fig. 7a), *culex*, *helios* (Fig. 6d); probably *musculus*; *nanus* (Fig. 6b), *stampflii*.

Current listings (i.e. Hayman & Hill, 1971; Koopman, 1975) unite *helios* with *P. nanus* as a synonym or possibly as a valid subspecies. However, the bacular features of this pale form suggest that it may represent a species distinct from *nanus* with which it may be sympatric in northern and eastern Kenya and in the Sudan. No baculum has been available for *musculus*, which was placed in a *hesperus* group by Koopman (loc. cit.). Although its incisive and premolar dentition agrees with the *nanus* subgroup its placement here remains speculative.

(a) (iii) *savii* subgroup. Braincase rather low and flat, elongate rather than globose; postorbital region not especially widened; supraorbital region unwidened or only slightly widened; rostrum of moderate length; a shallow median rostral depression; usually slight lateral rostral depressions just anterior to supraorbital and anterior orbital rim; cranial profile straight or slightly concave; premaxillae not shortened; zygomata robust, often with slight jugal process; interdental palate a little longer than wide; maxillary tooththrows more or less parallel; short bony post-palate; shallow or no basal pits; i^2 unicuspid or with posterior cusp, when present about 3/4 height of anterior cusp; i^3 similar to or exceeding i^2 in crown area, about 1/2–3/4 the height of i^2 , with strong central cusp flanked by smaller lateral accessory cusps, lying postero-externally or more laterally (*anchietae*) to the inner tooth, separated from c^1 by a strong diastema; pm^2 much reduced, minute or absent, when present crown area less than 1/2 that of i^3 , in recess between c^1 and pm^4 , these as a rule in contact; i_{1-3} slightly or more strongly imbricated, similar in size or i_3 slightly the bulkiest; pm_2 reduced, about 1/2 or less in crown area than pm_4 and about 2/3 its height.

Included taxa: *anchietae* (Fig. 6e); probably *ariel*; probably *austenianus*; *bodenheimeri* (Fig. 9f), *caucasicus*, *darwinii*, *maurus*, *savii* (Fig. 6a).

We have been unable to examine the baculum of *ariel*. The baculum of a small *Pipistrellus* from the Naturhistorisches Museum, Wien (from Sayala, Upper Egypt) tentatively identified as *ariel* is illustrated by Gaisler *et al.* (1972) but is evidently of the *kuhlii* type. Qumsiyeh (1985) employs the description of this baculum in his account of *ariel*. However, Dr K. Bauer informs us (in litt.) that the specimen (NHW 10351) of which the baculum is figured by Gaisler *et al.* (loc. cit.) is not referable to *ariel* but is instead a small *deserti*, an identification clearly supported by its bacular structure. Moreover, Dr Bauer has loaned three similarly small specimens, one male, the others female (NHW 27501–3) (length of forearm 29.2, 28.9, 28.2; condylobasal length 11.0, 10.5, 10.9; $c-m^3$ 4.0, 3.8, 3.9) apparently from Upper Egypt, that also represent *deserti*: a baculum from this sample is again exactly of the *kuhlii* type. The cranial (narrow braincase, unexpanded rostrum, short broad narial and anterior palatal emarginations, narrow basioccipital) and dental (long i^3 , minute pm^2) features of *ariel* clearly indicate that it belongs with *savii*, to which group Koopman (1975) referred it.

A syntype of *Eptesicus bicolor* (Bocage, 1889) (BM(NH) 89.5.1.3) (Fig. 9e) proves to be identical cranially, dentally and in bacular morphology with *Pipistrellus anchietae* (Seabra, 1900) (vide infra, p. 249). However, the point needs confirmation or otherwise by examination of the other syntype in the Museu Nacional de Lisboa. It should be noted that *bicolor* is the prior name (Honacki *et al.*, 1982).

The relationship between the *pulveratus*, *nanus* and *savii* subgroups is illustrated by *arabicus* and *bodenheimeri*, the bacula of which are compared directly by Harrison (1982). The baculum of *arabicus* (Fig. 7a) approaches that of *anchietae* (Fig. 6e) yet cranially and dentally this species is nearer to *nanus* (Fig. 6b), while that of *bodenheimeri* (Fig. 9f) is like the baculum of *pulveratus* (Fig. 8c) but cranially and dentally the species is close to *savii* (Fig. 6a). These combinations of features link the three subgroups.

(a) (iv) *hesperus* subgroup. Baculum a fluted structure, much like that of *pulveratus* or *bodenheimeri*. Braincase low but broad, elongated; postorbital region wide; supraorbital area slightly widened; rostrum short, not greatly broadened; a shallow median frontal depression; slight lateral rostral depressions just above anteorbital foramina; cranial profile almost straight, slightly depressed above anterior root of zygomata; premaxillae not shortened; zygomata slender, a little widened anteriorly, lacking any jugal eminence; interdental palate about as wide as long; maxillary tooththrows convergent; short bony post-palate; no basial pits; cochlear bullae inflated with narrow basioccipital; i^2 unicuspid; i^3 slightly greater in crown than i^2 but about 1/2 its height, with little trace of lateral accessory cusps, lying postero-externally, separated from c^1 by moderate to small diastema; pm^2 small to minute, at best about 1/2 or less in crown area than i^3 , in recess between c^1 and pm^4 which are closely approximated; i_{1-3} scarcely or not imbricated, similar in size; pm_2 reduced, about 1/2 the crown area of pm_4 , a little less than 1/2 its height.

Included taxon: *hesperus* (Fig. 8d).

Horáček & Hanák (1985a, b, 1985–1986) have indicated that they intend to propose generic status for *hesperus* and indeed have suggested that it be referred to *Parastrellus* which they offer as a new name. It is however a nomen nudum in these publications. There seem good grounds for considering *hesperus* the North American representative of *P. (Hypsugo)* to which its bacular, cranial and dental features ally it. Like *bodenheimeri* (Fig. 9f) its baculum approaches that of *pulveratus* (Fig. 8c) but cranially and dentally it is nearer to *savii* and its immediate allies. Koopman (1975) referred *hesperus* to a *hesperus* group in which he also included the African *musculus*, here provisionally allocated to the *nanus* subgroup.

(a) (v) *eisentrauti* subgroup. Braincase broad, elevated and globular; inflated frontally; postorbital region wide; supraorbital region broadened, with small supraorbital tubercles; rostrum short, deep, wide and massive; slight median rostral depression; cranial profile straight or slightly convex; premaxillae not shortened; zygomata strong, lacking any jugal projection; interdental palate very slightly longer than wide; maxillary tooththrows almost parallel; short bony post-palate; slight basial pits usually present; i^2 long, narrow, bicuspid, posterior cups about 3/4 height of anterior cusp; i^3 short, wide, similar to or slightly greater in crown area than i^2 , about 1/2 or a little more its height, with larger central cusp and smaller lateral accessory cusps, lying laterally and slightly posteriorly to the inner tooth, separated from c^1 by a moderate diastema; pm^2 small, about the same in crown area as i^3 , sandwiched into recess between c^1 and pm^4 , these almost in contact; i_{1-3} slightly imbricated, i_{2-3} similar in size, both larger than i_1 ; pm_2 about 1/2 crown area and height of pm_4 .

Included taxon: *eisentrauti* (Fig. 9g).

Koopman (1975) places *eisentrauti* in a *rueppellii* group, no doubt on account of its elevated, inflated braincase and its bicuspid i^2 , but its bacular features do not associate it with this species and its immediate allies. Its baculum is very similar to that of *imbricatus* (Fig. 9a) or *macrotis* (Fig. 9b).

(a) (vi) *imbricatus* subgroup. Braincase inflated, globular, raised posteriorly; postorbital region wide; supraorbital area slightly widened with very small supraorbital tubercles; rostrum short, not especially broadened; no median rostral depression; cranial profile almost straight; slightly concave above supraorbital region; premaxillae not shortened; zygomata moderate to strong, sometimes with a trace of a jugal eminence; interdental palate about as wide as long, not domed; maxillary tooththrows almost parallel; very short bony post-palate; well developed basial pits; i^2 bicuspid, posterior cusp about 3/4 height of anterior cusp; i^3 similar in crown area to i^2 , about 1/2 its height, with larger central cusp and smaller lateral accessory cusps, lying laterally to the inner tooth, separated from c^1 by a narrow diastema; pm^2 greatly reduced, 1/4 or less the crown area of i^3 , in recess between c^1 and pm^4 , these in contact; i_{1-3} scarcely imbricated, i_{2-3} of similar size, a little larger than i_1 ; pm_2 about 1/2 the crown area and height of pm_4 .

Included taxa: *curtatus*, *imbricatus* (Fig. 9a), *macrotis* (Fig. 9b), *vordermanni*.

(a) (vii) *lophurus* subgroup. Braincase inflated, rounded, slightly elongate, raised posteriorly; postorbital region wide; supraorbital area little widened; at best only a trace of supraorbital

tubercles; rostrum moderate in length, longer than in *imbricatus* subgroup, not broadened; no median rostral depression; cranial profile almost straight, slightly depressed or concave above supraorbital region; zygomata strong with distinct jugal eminence; interdental palate a little longer than wide; maxillary tooththrows slightly convergent; moderate bony post-palate; deep basal pits; incisor and premolar dentition closely similar to that of *imbricatus* subgroup but i^3 lying more postero-laterally to i^2 , and pm^2 sometimes (*lophurus*) slightly larger, about 1/2 crown area of i^3 .

Included taxa: *cadornae*, *kitcheneri* (Fig. 8e), *lophurus* (Fig. 8f).

The baculum of *kitcheneri* is unusual in the presence distally of two anterior dorso-lateral, posteriorly directed processes, with ventrally a more or less tapered median gutter. As in *lophurus*, the tip is directed slightly ventrally.

(b) *stenopterus* group

Braincase large, rounded and globular; postorbital region very wide; supraorbital region much widened to include well developed supraorbital tubercles; rostrum short, wide; shallow median rostral depression anterior to frontal region; cranial profile slightly convex, elevated over frontal area; premaxillae not shortened; zygomata rather weak, lacking jugal process but usually with small descending process external to m^3 ; palate short and broad, the interdental palate as wide as long; maxillary tooththrows parallel or nearly so; short bony post-palate; shallow basal pits; i^2 small, bicuspid, posterior cusp 1/2–3/4 height of anterior cusp; i^3 a little smaller in crown area than i^2 , its tip reaching almost to tip of the posterior cusp of that tooth, with large central cusp and smaller lateral accessory cusps, lying postero-laterally to the inner tooth, only narrowly separated from c^1 or almost in contact with it; c^1 with distinct, well defined posterior accessory cusp; pm^2 small or minute, about equal in crown area or a little larger than i^3 (*stenopterus*) or about 1/3–1/4 the crown area of this tooth (*joffrei*, *anthonyi*), in recess between c^1 and pm^4 , which touch; i_{1-3} not much imbricated, all of similar size; crown area of pm_2 slightly exceeding that of pm_4 , pm_2 similar in height to the second tooth (*stenopterus*), or crown area of pm_2 about 1/2 that of pm_4 , pm_2 almost as high as that tooth (*joffrei*, *anthonyi*).

Included taxa: *anthonyi*, *joffrei*, *stenopterus* (Fig. 7h).

The baculum of *stenopterus* is unusual, although of the *savii* type: it has a narrow lobed base, hollowed shaft, and expanded tip the lateral margins of which project ventrally as two broadly based 'horns'. The *stenopterus* group as here understood is the *joffrei* group of Tate (1942a) and (in part) of Koopman (1973). Both *joffrei* and *stenopterus* have been referred in the past to *Nyctalus* but as mentioned above (p. 234) the baculum of *stenopterus* has no resemblance to the long-shafted baculum of that genus (Fig. 10f). Tate (1942a) referred both to *Pipistrellus* with the comment that the group approached Oriental members of the *savii* group, and might at a later time be accorded generic rank.

Subgenus *Pipistrellus* (*Falsistrellus*)

Baculum a broad, proximally widened and ventrally deeply fluted structure with no distal expansion; braincase elongate; postorbital region wide; supraorbital area not expanded; rostrum long, not broadened; zygomata moderate to strong; and palate rather narrow, the interdental palate longer than wide.

Pipistrellus (*Falsistrellus*) appears to be related to *P. (Hypsugo)* of which it may be the eastern representative. It is approached in bacular morphology by some of the latter subgenus such as *imbricatus* (Fig. 9a), *macrodis* (Fig. 9b), *kitcheneri* (Fig. 8e) and *lophurus* (Fig. 8f), and indeed the baculum in *P. (Falsistrellus)* appears to be an extreme variant of the broad, ventrally fluted structure of many of *P. (Hypsugo)*.

Kitchener *et al.* (1986) raised *Falsistrellus* to generic rank but did not include *affinis* and *petersi*, confining their comparisons to the Australasian *Pipistrellus* (i.e. *adamsi*, *angulatus*, *collinus*, *papuanus*, *wattsi* and *westralis*) here referred to the *coromandra* subgroup of *P. (Pipistrellus)*. These authors drew attention to its larger size; to its small i^3 which is anteriorly displaced and swivelled or rotated outwards to lie alongside i^2 , its concavity facing outwards (a feature which may have influenced Iredale & Troughton, 1934 in placing it in *Glischropus*); and to its combination of

unicuspid i^2 , tiny pm^2 and pronounced occipital crest, which as Tate (1942a) noted gives the rear of the skull a 'helmeted' appearance. Excepting the large size and the presence of a strong occipital crest, these features occur elsewhere in the various groups of *Pipistrellus*: the extent of the occipital crest may be a function of the large size of the skull.

(a) *affinis* group

Braincase rather narrow, mastoid width markedly less than zygomatic width; postorbital region wide; slight, rather poorly developed supraorbital ridges; very shallow median rostral depression just anterior to frontal region; dorso-lateral margin of rostrum more or less straight from post-orbital constriction to anterior edge of orbit; cranial profile almost straight, slightly elevated frontally, depressed over supraorbital region; premaxillae not shortened; zygomata moderate to robust with jugal eminence; maxillary tooththrows slightly convergent; moderate bony post-palate; no basal pits; i^2 strongly bicuspid, posterior cusp 3/4 or more the height of the anterior cusp; i^3 larger in crown area than i^2 , its height about equal to the height of the posterior cusp of that tooth, with strong central cusp and smaller lateral accessory cusps, lying postero-laterally to the inner tooth, separated from c^1 by a moderate diastema; pm^2 almost as great in crown area as i^3 (*affinis*) or about 3/4 its crown area (*petersi*), in recess between c^1 and pm^4 ; i_{1-3} moderately imbricated, i_3 the largest; pm_2 about 1/2 the crown area of pm_4 and about 2/3–3/4 its height.

Included taxa: *affinis* (Fig. 8a), (?) *mordax*, *petersi* (Fig. 8b).

It has not been possible to examine *mordax*. Indian records of this species appear to be based on specimens in the collections of the British Museum (Natural History) tentatively labelled as such. These, however, agree closely with the description of *P. affinis* by Dobson (1871) and with the account of a specimen referred to this species from Likiang, Yunnan by Tate (1942a). If correctly allocated, *mordax* (Peters, 1867) is the earliest name in the group.

(b) *tasmaniensis* group

Large and distinctive; braincase high, with well developed sagittal crest; postorbital region wide and strong; no median rostral depression; cranial profile straight; premaxillae slightly shortened; zygomata strong with slight jugal process and small inferior process; maxillary tooththrows nearly parallel; short bony post-palate; slight basal depressions; i^2 large, unicuspid; i^3 small, its crown area about 1/4 that of i^2 , barely extending above the cingulum of that tooth to which it lies laterally, its hollowed face outwardly directed, separated from c^1 by a moderate diastema: pm^2 very small, about 1/3 the crown area of i^3 , in recess between c^1 and pm^4 , which touch; i_{1-3} much imbricated, i_3 twice the bulk of i_{1-2} ; pm_2 much reduced, about 1/4 the crown area of pm_4 and about 1/2 its height.

Included taxa: *mackenziei* (Fig. 10h), *tasmaniensis* (Fig. 8g)

Subgenus *Pipistrellus* (*Neoromicia*)

Baculum with distinct paired basal lobes, slender cylindrical shaft and variously expanded tip; braincase broad, sometimes slightly elongate, rather flattened; postorbital region wide; supra-orbital area unwidened or only slightly broadened; rostrum moderate or slightly lengthened; cranial profile straight; premaxillae shortened; zygomata moderate, no jugal process; maxillary tooththrows only slightly convergent; short bony post-palate; no basal pits; i^2 unicuspid or with small posterior cusp extending for about 3/4 its height; i^3 smaller than i^2 , its crown area 3/4–1/2 or less that of the inner tooth, about 1/2 its height, with usually a larger central cusp and slight lateral accessory cusps, the inner cusp as a rule very small, the tooth anteriorly displaced to lie alongside or almost alongside i^2 , separated from c^1 by a moderate to wide diastema; pm^2 almost invariably absent, when present very small, in recess between c^1 and pm^4 , i_{1-3} slightly to moderately imbricated, of similar size of with i_{2-3} a little the larger; pm_2 reduced, its crown area 1/2 or less that of pm_4 and its height 1/2–3/4 of the height of that tooth.

This subgenus is wholly African and hitherto its members have been referred to *Eptesicus*, although there is karyological evidence (vide infra) suggesting that one at least should be moved to *Pipistrellus*. It incorporates the *Eptesicus capensis* and *E. tenuipinnis* groups of Koopman (1975).

These can be recognised readily by the structure of the baculum, *capensis* and its allies (Fig. 12a–d, f–i) having the distal part of the baculum spatulate and ventrally deflected, *tenuipinnis* and its associates (Fig. 12e, j) having the baculum modified distally into a lobed, almost vertical plate-like structure.

Published karyological data refers only to *capensis*, although studies of other members of the subgenus are in progress (Rautenbach & Schlitter, 1985a, b). Peterson & Nagorsen (1975) found that *capensis* has a diploid number of 32 and a fundamental number of 50: Williams & Mares (1978) discussed the possible composite nature of *Eptesicus* as suggested by Koopman (1975) and pointed out that the species fitted karyologically within the variation exhibited by *Pipistrellus*. This genus has a diploid number varying from 26 to 44, and fundamental numbers from 44 to 60, these findings apparently supporting Koopman's observations. These authors remarked, however, that the karyotype of *capensis* is more similar to that of *Pipistrellus nanus* ($2N = 36$, $FN = 50$) than to *P. kuhlii* ($2N = 44$, $FN = 50$), Koopman having thought *capensis* nearer to the *kuhlii* group than to the *pipistrellus* group in which he placed *nanus*. Williams & Mares (loc. cit.) also found, in contrast, that small *Eptesicus* from the New World (*diminutus*, *furinalis*) have the typical 'eptesticoid' karyotype ($2N = 50$, $FN = 48–50$), and added that the karyotypic differences between *Eptesicus* (sensu stricto) and *Pipistrellus* might prove more useful for separating these genera than other structural features.

Our study of the bacula of African '*Eptesicus*' confirms these observations and indicates the isolation of *capensis*, *tenuipinnis* and their relatives from *Eptesicus* sensu stricto (vide infra): Heller & Volleth (1984) also transferred *capensis* to *Pipistrellus*, entirely on account of its published karyology. It is interesting to note also that the baculum of *P. nanus* indicates that this species should be referred to *P. (Hypsugo)* rather than to *P. (Pipistrellus)* where Koopman (1975) effectively allocated it. The bacular morphology of *capensis*, *tenuipinnis* and their allies suggests strongly that these former groupings of *Eptesicus* are most closely allied to *P. (Hypsugo)* as the karyological similarity of *capensis* to *P. nanus* indicates. The anterior upper premolar (pm^2) is very small, vestigial or absent in *P. savii* and is very small in most other members of *P. (Hypsugo)*: very rarely it is present in *capensis* (Wallin, 1969; Hill & Topál, 1973). On the same point, we have been able to examine a specimen (MJS 2846) from Somalia, in the Carnegie Museum of Natural History, which has a small pm^2 on both sides of the jaw, leading to its erstwhile identification as *Pipistrellus deserti*. The baculum, however, is characteristically that of '*Eptesicus somalicus*', which in fact the specimen represents.

Koopman (1975) suggested that *Vesperus bicolor* Bocage, 1889 (= *Eptesicus bicolor*) and *Pipistrellus anchietae* (Seabra, 1900), both from Angola, may be conspecific, having examined syntypes of both at the British Museum (Natural History). This author thought that *bicolor* might be a form of '*Eptesicus tenuipinnis*' as Hayman & Hill (1971) suggested, or that it might be based on a specimen of *Pipistrellus anchietae* with missing anterior upper premolars. Bocage (loc. cit.) says 'pas de trace de la premiere premolaire a la machoire superieure'. Further study of the syntype (BM(NH) 89.5.1.3) in London shows it to have a small pm^2 in a recess between c^1 and pm^4 on each side: cranially it agrees exactly with the syntype of *anchietae* (♀ BM(NH) 6.1.3.1) and its baculum is exactly as in that species. Curiously, Bocage states that both original specimens of *bicolor* are female. The specimen in London is quite clearly listed as a 'Co-type' by Thomas in the relevant accession register.

(a) *capensis* group

Tip of baculum flattened, deflected ventrally, sometimes a small sub-apical dorsal projection; braincase flattened, slightly elongate; rostrum not especially broadened; palate long, narrow, interdental palate longer than wide; i^3 1/2 or less the crown area of i^2 .

Included taxa: *capensis* (Fig. 12b, g); probably *brunneus*, *garambae*, *grandidieri*; *guineensis* (Fig. 12c), *matroka* (Fig. 12a), *melckorum* (Fig. 12f); *minutus* (?) (Fig. 12i); probably *rectitragus*; *somalicus* (Fig. 12h); probably *vansoni*; *zuluensis* (Fig. 12d).

The baculum of *brunneus* sensu stricto has not been examined. That (Fig. 14b) of a Nigerian specimen (BM(NH) 48.702) collected by I.T. Sanderson and hitherto referred to this species is very similar to that of *rendalli* (Fig. 12e), with which this example agrees in cranial and ventral

characters. The series whence this specimen comes is discussed by Koopman (1965) and Hayman & Hill (1971).

Our study of bacula in this group shows clearly that *matroka* belongs with *capensis*: we have been unable to examine the baculum of *humbloti*. We find too that *capensis* and *somaticus* can be separated by bacular features: the baculum of *capensis* has distally a downwardly directed, plate-like expansion, while in *somaticus* the distal part of the baculum is more spatulate, depressed just below the line of the shaft. Moreover, *zuluensis* is very clearly of the *somaticus* type, and the two appear to be very closely related, as Koopman (1975) suggested. Bacular morphology also confirms the observation by this author that *melckorum* is like a giant *capensis*: Rautenbach & Schlitter (1985a, b) suggested that these are synonymous.

(b) *tenuipinnis* group

Tip of baculum expanded into an almost vertical, lobed, plate-like structure; braincase similar to *capensis* group, but broader and less elongate; rostrum slightly widened; palate short and broad, interdental palate about as long as wide; i^3 about $1/2-3/4$ the crown area of i^2 .

Included taxa: Probably *angolensis*, *faradjius*, *flavescens*, *phasma*; *rendalli* (Fig. 12e), *tenuipinnis* (Fig. 12j).

Pipistrellus (Arielulus) subgen. nov.

TYPE SPECIES: *Vespertilio circumdatus* Temminck, 1840. Java.

REFERRED SPECIES: *Pipistrellus societatis* Hill, 1972; *Pipistrellus cuprosus* Hill & Francis, 1984.

DISTRIBUTION: Burma to Java (*circumdatus*, Fig. 2e); Malaya (*societatis*, Fig. 9c); Borneo (*cuprosus*, Fig. 9h).

DIAGNOSIS: Differs from most other subgenera of *Pipistrellus* in very small, Y-shaped baculum which has paired basal lobes and a short shaft; baculum similar to that of *P. (Perimyotis)* but differing from this subgenus in greatly reduced i^3 and pm^2 , the former displaced anteriorly to lie alongside i^2 , the latter sometimes absent.

DESCRIPTION: Size small to medium (length of forearm 34.7–43.6); muzzle short, broad and blunt; ears large, rounded, with blunt tip, anterior margin with prominent, posteriorly directed basal lobe, posterior margin with wide quadrate lobe at insertion just behind angle of mouth; tragal margin concave anteriorly, rising to anteriorly directed point, upper margin of tragus nearly horizontal, posterior margin strongly convex; ears and upper margin of tragus edged to a greater or lesser extent with dull white or yellowish white; dorsal pelage black or blackish brown, the hairs tipped with yellowish, orange, russet, copper or bronze.

Braincase high, inflated, globose; postorbital region wide; supraorbital area broadened, with small supraorbital projections or tubercles; rostrum short, widened, sometimes a shallow median rostral depression; cranial profile almost straight, elevated frontally, slightly depressed behind and above supraorbital region; premaxillae not shortened; zygomata strong, no jugal eminence; interdental palate longer than wide; short to moderate bony post-palate; shallow to moderate basal pits; i^2 almost unicuspid, posterior cusp if present insignificant; i^3 very small, about $1/4$ the crown area of i^2 , $1/3$ or less its height, lying almost alongside this tooth, separated from c^1 by a narrow to moderate diastema; pm^2 very small or absent, when present similar in size to i^3 , recessed into angle between c^1 and pm^4 which are in contact; i_{1-3} considerably imbricated, i_{1-2} tricuspid or incipiently quadricuspid, i_{2-3} bulkier, larger than i^1 , similar in size to each other, their cusps indistinct; pm_2 $1/2-1/4$ size of pm_4 , compressed in tooththrow.

ETYMOLOGY: The new subgeneric name is a diminutive of Ariel, a little sprite.

REMARKS: Heller & Volleth (1984) transfer *circumdatus* and *societatis* to '*Eptesicus*' on karyological, bacular and dental grounds. However, the baculum in these species does not resemble closely any of those found either in *Eptesicus* sensu lato or *Eptesicus* sensu stricto. Possibly the unusual baculum in *P. (Arielulus)*, similar to that of *P. (Perimyotis)*, is a reduced form of the *P.*

(*Pipistrellus*) type, but the species allocated to *P. (Arielulus)* differ widely cranially and dentally from *P. subflavus*, the sole species referred to *P. (Perimyotis)*.

Genus *Eptesicus* Rafinesque, 1820

- Eptesicus* Rafinesque, 1820: 2. *Eptesicus melanops* Rafinesque = *Vespertilio fuscus* Palisot de Beauvois.
Cnephaeus Kaup, 1820: 103. *Vespertilio serotinus* Schreber.
Noctula Bonaparte, 1837: fasc. xxi. *Noctula serotina* Bonaparte.
Cateorus Kolenati, 1856: 131. *Vespertilio serotinus* Schreber.
Amblyotus Kolenati, 1858: 252. *Amblyotus atratus* Kolenati = *Vespertilio nilssonii* Keyserling & Blasius.
Pachyomus Gray, 1866: 90. *Scotophilus pachyomus* Tomes.
Nyctiptenus Fitzinger, 1870: 424. *Vespertilio smithii* Wagner = *Vespertilio hottentota* A. Smith.
Rhinopterus Miller, 1906: 85. *Glauconycteris floweri* De Winton. Valid as a subgenus.
Scabrifer Allen, 1908: 46. Substitute for *Rhinopterus* Allen, thought preoccupied by *Rhinoptera* Kuhl, 1841, Pisces.
Pareptesicus Bianchi, 1917: lxxvii. *Vesperugo pachyotis* Dobson.
Rhyneptesicus Bianchi, 1917: lxxvii. *Vesperugo nasutus* Dobson.
Rhineptesicus Horáček & Hanák, 1985–1986: 16. Lapsus.

Baculum more or less triangular, its apex occasionally extended into a short shaft, basally rather wide, sometimes base expanded into small lobes, tip not expanded, usually more or less pointed or gently rounded. There is little flexion in the vertical plane and the tip is not depressed ventrally; transversely the base is sometimes slightly arcuate. Externally and cranially not essentially different from *Pipistrellus* but pm^2 invariably absent, the premolar formula being $\frac{2}{2} = \frac{4}{4}$.

The karyological features of *Eptesicus* are summarised by Heller & Volleth (1984) and Zima & Horáček (1985). Such as have been examined (*andinus*, *bottae*, *brasiliensis*, *diminutus*, *furinalis*, *fuscus*, *guadeloupensis*, *hottentotus*, *japonensis*, *lynni*, *nilssonii*, *parvus*, *serotinus*, *turcomanus*) are homogeneous in this respect, with $2N = 50$, $FN = 48-50$. On present published knowledge only *capensis* differs with $2N = 32$, $FN = 50$. It is transferred to *Pipistrellus* by Heller & Volleth (loc. cit.) on this account and in the present paper, with others, on bacular grounds. *Pipistrellus societatis* in which $2N$ is also apparently 50 and FN 48 is transferred to *Eptesicus* by Heller & Volleth (loc. cit.) on account of its karyology and bacular structure, these authors considering it conspecific with *P. circumdatus* (but see Hill & Francis, 1984). Both species are here retained in *Pipistrellus*, with the closely related *P. cuprosus*.

Subgenus *Eptesicus* (*Eptesicus*)

Postorbital region not widened, evident postorbital constriction; rostrum not especially shortened, its dorsal margins not sharply angular; cranial profile straight or slightly concave, not elevated over frontal region; maxillary tooththrows almost straight, only slightly convergent; upper surface of forearm, tibia and tail lacking horny excrescences.

(a) *nilssonii* group

Cranially large, the skull rather elongate; braincase flattened, elongate, no cranial crests; post-orbital region slightly widened; supraorbital area unwidened but with very small supraorbital projections; margins of supraorbital region almost straight from postorbital constriction to front of orbit, no prominent supraorbital ridges delimiting upper surface of rostrum; the rostrum long, not widened, rounded dorsally, its upper surface not flattened but transversely convex above; a shallow median rostral depression; slight lateral rostral depressions on each side just above front of orbit; cranial profile straight or almost straight, slightly concave over supraorbital region; premaxillae not shortened; zygomata moderate with slight jugal process; palate long, narrow, interdental palate longer than wide; maxillary tooththrows parallel or only slightly convergent; very short bony post-palate; prominent basal pits; tympanic bullae not enlarged, not completely covering cochleae; i^2 bicuspid, posterior cusp about $1/2-3/4$ height of anterior cusp; i^3 wide, as large or larger than i^2 in crown area, almost reaching tip of posterior cusp of inner tooth, with very small lateral accessory cusps, not displaced anteriorly, lying postero-laterally to i^2 and separated from c^1 by a moderate diastema; m^3 not greatly reduced, with trace of fourth commissure, the tooth quite

long; i_{1-3} slightly imbricated, i_3 a little the largest; pm_2 about 1/2 the crown area and height of pm_4 , not compressed in toothrow.

Included taxa: *bobrinskoi* (Fig. 13e), *gobiensis*, *nilssonii* (Fig. 15a).

If subgeneric recognition is thought justified for this group then *Amblyotus* Kolenati, 1858 is available. The *nilssonii* group was recognised as subgenerically valid by Tate (1942a) who however included within it a number of taxa here allocated to the *nasutus* group (vide infra). Strelkov (1986) illustrated the bacula of *nilssonii*, *bobrinskoi* and *gobiensis*, considering the last to be a valid species.

(b) *nasutus* group

Cranially small, the skull not especially elongate, braincase flattened, only slightly elongate, broad; postorbital region relatively narrower than in *nilssonii* group; supraorbital area slightly widened; margins of supraorbital region nearly straight from postorbital constriction to front of orbit, supraorbital ridges sometimes prominent; rostrum shortened, its upper margins slightly angular, its upper surface flattened dorso-ventrally, transversely flat, not convex as in *nilssonii* group; a shallow or sometimes more pronounced median rostral depression, slight lateral rostral depressions above front of orbit, small lateral rostral elevations above c^1-1 ; cranial profile straight or nearly so, sometimes slightly concave above supraorbital region; premaxillae sometimes slightly shortened; zygomata moderate, on occasion a slight jugal eminence; interdental palate longer than wide; maxillary toothrows slightly convergent; short bony post-palate; no basal pits; tympanic bullae very large, completely covering cochleae; i^2 large, unicuspid; i^3 small, about 1/2 crown area and height of i^2 , with larger main cusp and smaller lateral accessory cusps, anteriorly displaced to lie alongside or almost alongside the inner tooth, separated from c^1 by a moderate diastema; m^3 sometimes reduced, usually with three commissures, no trace of the fourth, antero-posteriorly rather short, compressed, platelet-like; i_{1-3} moderately or well imbricated, similar in size or with i_3 slightly the largest; pm_2 very small, 1/3–1/4 the crown area and 1/2–1/3 the height of that tooth, compressed in toothrow.

Included taxa: *batinensis*, *matschiei*, *nasutus* (Fig. 14c), *pellucens*, *walli*.

Tate (1942a) included *walli*, *matschiei* and *pellucens* in the *nilssonii* group but these agree more appropriately with *nasutus* as De Blase (1980) and Honacki *et al.* (1982) recognised: Ellerman & Morrison-Scott (1951) listed *matschiei* and *pellucens* as subspecies of *nasutus*. Indeed, Tate (loc. cit.) noted the large tympanic bullae of *walli* and the absence of basal pits from this taxon. *Rhynptesiscus* Bianchi, 1917 is available if subgeneric recognition is thought justified for this group.

(c) *serotinus* group

(c) (i) *serotinus* subgroup. Cranially large, the skull elongate; braincase flattened, elongate, often with lambdoid and sagittal crests forming a distinct occipital 'helmet'; postorbital region slightly widened; supraorbital area not widened or only slightly so, with well developed supraorbital ridges in many instances; rostrum long, not broadened, its upper surface flattened but less so than in *nasutus* group; very shallow or shallow median frontal depression, shallow to moderate lateral frontal depressions just above front of orbit; cranial profile almost straight, a slight concavity above front of orbits; premaxillae sometimes a little shortened; zygomata usually robust with moderate jugal projection, on occasion slender to moderate, the projection lacking; palate long and narrow, the interdental palate longer than wide; maxillary toothrows slightly convergent; short bony post-palate; shallow basal pits; tympanic bullae not covering cochleae; i^2 bicuspid, posterior cusp about 3/4 height of anterior cusp; i^3 small to very small, 1/2–1/4 or less the crown area and height of i^2 , its tip 1/2 or less the height of the posterior cusp of that tooth, with very small lateral accessory cusps, the tooth displaced anteriorly to lie alongside or almost alongside i^2 , separated from c^1 by a moderate to small diastema, sometimes almost in contact with that tooth; m^3 sometimes much reduced, its third commissure obsolescent or obsolete, its second commissure short, the tooth platelet-like; i_{1-3} often massive, much imbricated, i_3 the largest; pm_2 about 1/3–1/2 the crown area and 1/2 the height of pm_4 .

Included taxa: *andinus* (Fig. 13d), *argentinus*, *bottae*, *brasiliensis* (Fig. 13k), *dorianus*, *fidelis*,

furinalis (Fig. 13c), *fuscus* (Fig. 13a), *hingstoni*, *hispaniolae* (Fig. 13i), *hottentotus*, *inca*, *innesi* (Fig. 13j), *imoxius*, *isabellinus* (Fig. 13h), *megalurus* (Fig. 13b), *melanopterus*, *montosus*, *omanensis* (Fig. 14a), *pachyomus*, *peninsulae*, *platyops*, *punicus*, *serotinus* (Fig. 13g), *shirazensis*, *sodalis*, *tatei*, *turcomanus*.

Tate (1942a) has pointed out that the Old World members of this subgroup fall into two categories, one of larger taxa, the other of smaller members of the subgroup. This is also true of the New World taxa: however, here the larger forms are found chiefly in North America, extending only slightly into South America to which the smaller taxa are entirely confined (Thomas, 1920). Material available to us is quite inadequate to attempt any detailed revision and we have followed the lead provided by Tate (loc. cit.) in our allocation of all to the one category. Cranial differences between large and small members of the subgroup appear chiefly to be those associated with size.

The subgroup does not extend substantially into Africa. It is represented in Egypt by *Eptesicus bottae* (*innesi*) and in northwestern Africa by *E. serotinus* (*isabellinus*). Ibáñez & Valverde (1985) consider the West African *platyops* to be a subspecies of *serotinus*, as may be the South African *hottentotus* and also *loveni* from Kenya.

(c) (ii) *demissus* subgroup. *Eptesicus demissus* Thomas, 1916 from Thailand appears to be known only from the holotype, which has a damaged skull. It is very similar to the larger members of the *serotinus* subgroup but has a long bony post-palate, prominent basal pits, i^3 about the same in crown area as i^2 and about 1/2 its height, m^3 not especially reduced, its third commissure complete, and with i_{1-3} moderately imbricated, i_3 the largest. We follow Tate (1942a) in referring it to a separate subgroup although it is likely that more adequate material might enable its status to be determined more precisely.

(c) (iii) (?) *pachyotis* subgroup. We have been unable to examine *Eptesicus pachyotis* (Dobson, 1871) from Assam. Little is known of the species, of which the holotype is in the Indian Museum, Calcutta, and as Tate (1942a) pointed out, most of the characters given by Dobson in the original description might apply to almost any species of *Eptesicus*. The generic epithet *Pareptesicus* Bianchi, 1917 was proposed for this taxon.

Subgenus *Eptesicus* (*Rhinopterus*)

Cranially small; braincase low, flattened and elongate, inflated anteriorly; postorbital region wide; supraorbital area widened with very small supraorbital tubercles; anterior margin of orbit flange-like; rostrum short, flattened dorso-ventrally, its dorsal margins angular; very shallow median rostral depression, shallow lateral depressions just above front of orbit; cranial profile convex, raised above frontal region; premaxillae not shortened; zygomata slender, no jugal projection; palate short, broad, interdental palate about as long as wide; maxillary tooththrows convergent; short to moderate bony post-palate; no basal pits; i^2 bicuspid, posterior cusp 3/4 or more the height of the anterior cusp; i^3 small or minute, about 1/4 or less the crown area of i^2 , about 1/3–1/2 its height, its lateral accessory cusps very small or obsolete, lying postero-laterally or almost alongside the inner tooth, separated from c^1 by a moderate or small diastema; m^3 not much reduced, its third commissure complete; i_{1-3} strongly imbricated, i_2 the smallest, i_1 and i_3 of similar size; pm_2 very small, about 1/2 crown area and height of pm_4 , strongly compressed in row; horny excrescences on upper surface of forearm, tibia and tail.

Included taxa: *floweri* (Fig. 13f), *lowei* (Fig. 13l).

The status of the 'Nycticeiini'

An especially interesting feature emerges from our survey of bacular morphology in the Vespertilioninae. The structure of the baculum suggests very strongly that the 'Nycticeiini' (or 'Nycticeiini') as presently accepted is not a natural group. Defined chiefly on dental characters (i^2 generally unicuspid, i^3 and pm^2 absent), this group was assembled by Tate (1942a) to include *Baeodon*, *Rhogeessa*, *Otonycteris*, *Nycticeius* (i.e. *N. humeralis*, including *cubanus*), 'Scoteimus' (then including among others the Australian species now referred to *Scoteanax* and *Scotorepens*), *Scotoecus*, *Scotomanes* and *Scotophilus*. Tate, however, made no mention of the African species *schlieffenii*

which was extralimital to his study but which by then had been variously referred either to *Scoteinus* (Miller, 1907) or to *Nycticeius* (Hollister, 1918; Braestrup, 1935). More recently, the type species of *Scoteinus* (the Indian *emarginatus*) has proved to be a *Scotomanes* (Sinha & Chakraborty, 1971) and the other Indian species (*pallidus*) formerly referred to it a *Scotoecus* (Hill, 1974). The Australian *Scoteanax* and *Scotorepens* have been considered to be subgenera of *Nycticeius* (Laurie & Hill, 1954; Koopman, 1978; Corbet & Hill, 1980) but recently have been accorded generic rank (Kitchener & Caputi, 1984; Corbet & Hill, 1986). Thus the current concept of *Nycticeius* is of two species, *N. humeralis* from North America and *N. schlieffenii* from Africa and southwestern Arabia.

The bacula of *Rhogeessa* (Fig. 18k) and *Baeodon* (Fig. 15b) are quite distinctive and are variants of the saddle-like or slipper-like structure found in *Myotis* and *Plecotus* or their allies, as are the very characteristic bacula of *Otonycteris* (Fig. 16a) and *Nycticeius humeralis* (Fig. 17k), the type species of *Nycticeius*. *Scotomanes* (Fig. 18g) and *Scotophilus* (Fig. 17g–j) have bacula reminiscent of the flattened, triangular structure of *Eptesicus* and its immediate associates. In contrast, the bacula of *Scotoecus* (Fig. 20a–e), *Nycticeius schlieffenii* (Fig. 16e), *Scoteanax* (Fig. 16i), and *Scotorepens* (Figs 16g, h, 21e, f) are closely similar to those of *Pipistrellus* (*Pipistrellus*). Thus in bacular terms this supposed group appears to be a composite of different elements, so dissimilar among themselves that its unity seems very unlikely. Kitchener & Caputi (1984) contended on the grounds of a phyletic analysis that *Otonycteris* and *Scotophilus nigrata* fitted poorly into the then current concept of the 'Nycticeini' and moreover on similar considerations that *Nycticeius humeralis* and *Nycticeius schlieffenii* are not congeneric. This view contrasts sharply with that of Koopman (1978) who remarked that the latter are similar in all important characters and should be retained together in the subgenus *Nycticeius* (*Nycticeius*).

The sharp bacular difference between the American *humeralis* and the African *schlieffenii* suggests wider separation and indicates that their congeneric association is wrong, despite their morphological similarities in some other ways. We propose therefore to dissociate *schlieffenii* from *Nycticeius* as generically distinct. The newly proposed genus may be called:

Nycticeinops gen. nov.

TYPE SPECIES: *Nycticeius schlieffenii* Peters, 1860.

REFERRED SPECIES: None.

DISTRIBUTION: Mauretania to Egypt, Namibia and Mozambique; SW Arabia.

DIAGNOSIS: Baculum (Fig. 16e) distinctive, with expanded base and long fluted shaft, very different from that of *Nycticeius humeralis* (Fig. 17k) which is slipper-like, elevated proximally and distally; cranially similar to *Nycticeius* sensu stricto but rostrum shorter, more narrowed anteriorly, the maxillary tooththrows much more convergent, not nearly parallel, with correspondingly narrower narial and anterior palatal emarginations; mandible similarly narrowed anteriorly, with i_{1-3} strongly imbricated, thrust further anteriorly into an arc; narial emargination more clearly U-shaped, not prolonged posteriorly; anterior palatal emargination extending further posteriorly; basal depressions absent or only very slight; pm_2 more reduced. Similar to Australian *Scoteanax* and *Scotorepens* but differing sharply in bacular morphology, the baculum with a more flanged and fluted shaft and lacking the modification of the tip found in these genera, and in less reduction of m_3^3 .

Differs from *Pipistrellus* in massive, unicuspid i^2 which has no trace of a secondary cusp, in contact or nearly so with c^1 , the premaxillae greatly shortened, combined with the almost invariable absence of i^3 and pm^2 . Similar in some respects to *Scotozous* but differing in bacular morphology; in the presence of a small, posteriorly directed lobe at the base of the inner margin of the ear; tip of tragus anteriorly directed; pm^2 almost invariably absent; pm_2 more reduced. Similar also in some ways to *Scotoecus* but penis not greatly lengthened, baculum similarly shorter, its tip not expanded and bifid; rostrum narrower, uninflated; narial and anterior palatal emarginations not extensively deepened; and anterior face of c^1 rounded, not flattened and grooved.

DESCRIPTION: Small (length of forearm about 29–33 mm); muzzle flattened, anteriorly sparsely haired, nares opening obliquely; ear rounded with broadly rounded tip, anterior or medial margin with small, posteriorly directed basal lobe, anterior margin slightly convex for most of its length; posterior margin nearly straight distally, more convex proximally with well developed, thickened antitragal lobe; tragus with bluntly pointed, anteriorly directed tip, the anterior margin strongly concave basally, straight distally, upper margin nearly horizontal, posterior margin strongly convex, with prominent basal lobe; calcar extending along a little more than one half of the uropatagial border; well developed, rounded post-calacarial lobe or epiblemma. Dorsal surface of head and body brown to pale brown, the pelage unicolored; ventral surface paler brown to greyish white, the pelage usually unicolored but in the darker subspecies faintly bicolored, the hair bases darker than the tips.

Skull low, with broad, flattened braincase, not elevated frontally; very low cranial crests and very slight occipital 'helmet'; postorbital region wide; supraorbital area a little broadened; rostrum not expanded laterally, narrow anteriorly; cranial profile almost straight, a little depressed over front of orbits; narial emargination U-shaped, extending posteriorly one half of distance from tip of maxillae to a line joining front of orbits; premaxillae much shortened; anteorbital foramen moderate to large; zygomata slender, no jugal projection; palate rather short, the interdental palate little longer than wide, narrowed anteriorly, maxillary tooththrows convergent, anterior palatal emargination narrow, extending posteriorly to a line joining the posterior faces of c^{1-1} , not extending laterally beyond the inner faces of i^{2-2} ; short to moderate bony post-palate, a narrow median post-palatal spine; basal depressions at best only very slight.

Dental formula normally i_{1-2}^{1-3} , pm_{1-2}^{2-4} , m_{1-2}^{3-3} = 30. Upper incisor i^2 massive, unicuspid, usually separated from c^1 by a very short diastema, sometimes in contact with this tooth; i^3 and pm^2 almost invariably absent (Thomas, 1890; Thomas & Wroughton, 1908); pm^4 in contact with c^1 , with small protocone; lingual shelves of m^{1-3} widely separated, m^3 not reduced, with three commissures and mesostyle, about 1/2 crown area of m^1 or m^2 ; i_{1-3} strongly imbricated to one half of their width, thrust forward, i_1 clearly tricuspid, i_{2-3} less obviously so, i_1 longest, i_{2-3} more massive; pm_2 much reduced, 1/2–1/4 crown area of pm_4 and 1/2 its height, compressed in tooththrow; m_3 slightly reduced, posterior triangle smaller than anterior triangle, hypoconid and entoconid lower than protoconid, paraconid and metaconid.

Thomas & Wroughton (1908) reported a specimen (BM(NH) 8.4.3.23) from Tette, Malawi in which a well developed i^3 is present in the left side of the jaw. Dobson (1878) remarked of two specimens in the Muséum National d'Histoire Naturelle, Paris that pm^2 is present on one side in one, on both sides in the other, but Thomas (1890) who examined these noted that pm^2 is completely absent from one and present on both sides in the other, Dobson having in the first instance perhaps mistaken a grain of sand for the tooth. Allen (1914) remarked of a specimen that he identified as *schlieffenii* from Bados, Blue Nile Province, Sudan that pm^2 was present on both sides of the jaw and that 'in common with *Scotoecus*, it has a large penial bone, 12 mm long' but Koopman (1965) pointed out that in fact this specimen is a *Scotoecus* (not *Scotophilus* as Qumsiyeh, 1985 avers) and that *schlieffenii* has a very much smaller penis.

INCLUDED TAXA: The genus is monospecific, its sole species *N. schlieffenii* Peters, 1860. Taxa allocated to it either as valid subspecies or synonyms include *adovanus* Heuglin, 1877; *africanus* Allen, 1911; *albiventer* Thomas & Wroughton, 1908; *australis* Thomas & Wroughton, 1908; *bedouin* Thomas & Wroughton, 1908; *cinnamomeus* Wettstein, 1916; *fitsimmonsii* Roberts, 1932; *minimus* Noack, 1887.

ETYMOLOGY: The name of the new genus is derived from νύξ, νυκτός or νυκτιος, night, and οψ aspect.

REMARKS: The type species *schlieffenii* has undergone a wide variety of generic allocations and taxonomic change since Peters (1860) first described it as a *Nycticejus*. Dobson (1876, 1878) placed it in *Scotozous* with *dormeri* while under the impression that this genus lacked i^3 , and considered (1878) *Scotozous* to be a subgenus of *Vesperugo*. Noack (1877) and Thomas (1890) referred it to *Scotophilus*, the latter author discussing this genus in relation to *Scotozous*, which following

Dobson he thought to have but one pair of upper incisors. Trouessart (1897) initially followed Dobson (1878) in allocating *schlieffenii* to *Scotozous* as a subgenus of *Vesperugo*, but later (1904) changed this opinion to consider *Scotozous* a subgenus of *Scotophilus*. Miller (1907) referred *schlieffenii* to *Scoteinus*, although in fact the species does not display the reduction of m_3^3 that he considered diagnostic for this genus and which occurs in the Australian species (*balstoni*, *greyii*, now incorporated into *Scotorepens*) that he allocated to it. Miller's view was adopted by Thomas & Wroughton (1908) and in differing ways by many subsequent authors. However, Allen (1911) when describing *africanus* referred it to the hitherto American genus *Nycticeius*, commenting on its similarity to *N. humeralis* and Hollister (1918) remarked that Old World bats usually placed in the genus *Scoteinus* did not seem to differ generically from the American species of *Nycticeius*, to which he also referred *africanus*. Since then *africanus* has been relegated to subspecific status or synonymy in *schlieffenii* (Braestrup, 1935; Allen, 1939; Aellen, 1952). Braestrup (loc. cit.) also employed *Nycticeius* for *schlieffenii* in preference to *Scoteinus*, and pointed out that its last upper molar was not reduced in the way that Miller (1907) had described for that genus. This author drew attention to the affinity thus established between the Ethiopian and American faunas, but did not exclude the possibility of convergent evolution from different *Pipistrellus*-like forms. Tate (1942a) maintained *Nycticeius* and *Scoteinus* as distinct genera but Simpson (1945) united them, a lead followed by many modern authors who have considered *Scoteinus* a subgenus of *Nycticeius*. Thus Ellerman & Morrison-Scott (1951) and Ellerman *et al.* (1953) referred *schlieffenii* to *Scoteinus* as a subgenus of *Nycticeius*, while Laurie & Hill (1954) listed the Australian species before then allocated to *Scoteinus* in *Scoteanax* and *Scotorepens* as further valid subgenera of *Nycticeius*. On the other hand, Rosevear (1965) considered *Nycticeius* and *Scoteinus* synonymous. Koopman (1965) referred *schlieffenii* to *Scoteinus* as a subgenus of *Nycticeius* but later (in litt. in Hayman & Hill, 1971) revised this opinion to allocate it to *Nycticeius* (*Nycticeius*), since then (1978) reinforcing this view.

The classification of the Vespertilioninae

Earlier classifications of the Vespertilioninae (Miller, 1907; Tate, 1942a) rely heavily on the pattern of reduction of the incisor and premolar teeth, chiefly on the presence or absence of the outer upper incisor (i^3), of one or both of the first (pm^2) or second (pm^3) upper premolars, and on the presence or absence of the second (pm_3) of the lower premolars, as Tate's 'phyletic' diagrams (loc. cit.) indicate. These dental features have been discussed in more detail above (p. 230): they reflect the degree of shortening that forms an evident trend within the subfamily. When combined with the relative size of one or more of these teeth and the position of the relevant tooth or teeth in the toothrow such factors form an important element in generic identification and diagnosis (cf. Miller, loc. cit.). The many different combinations of incisive and premolar formula in the subfamily (Table 2), the evanescence in some genera of some of the teeth involved, the extreme tendencies towards reduction seen in some such as *Pipistrellus*, and the variety of positions within the toothrow adopted by i^3 and pm^2 in particular reinforce the conclusion that such features reflect a universal trend that may have occurred more than once within the group and which as a result may not provide a totally reliable yardstick by which relationship may be judged.

In addition to these dental features, Tate (1942a) reviewed a number of other characters used in the classification of the subfamily. These include the presence or absence of accessory canine cusps; the form and shape of the braincase and rostrum; the degree of reduction of the zygomata; the structure of the palate, its anterior emargination and accessory anterior and posterior spines; the presence or absence of basal pits; enlargement of the ears and their associated bony structures; the presence or absence of adhesive pads on the thumb or foot; and the nature of other minor structures such as the calcar. These features, however, seem of greater value in the distinction of species and species groups, that is, for infrageneric classification, or for the diagnosis of individual genera.

The value of such characters has been discussed at some length by Zima & Horáček (1985) who pointed out that there are grounds for thinking that some of the traditional morphological

characters may not provide unequivocally reliable criteria for the establishment of a classification based on presumed phyletic relationship, and that their taxonomic significance may be limited. They also remarked that such characters may reflect parallelism or convergence, or result from selection pressure rather than relationship. These reasons led them to suggest that the baculum might provide one of several alternative sources of reliable, taxonomically useful criteria based on characters that do not have a direct adaptive significance.

The structure of the baculum in the Vespertilioninae suggests some modifications to tribal classification within the subfamily, although clearly other morphological characters need to be given equivalent or greater weight. Provisionally, therefore, we offer an arrangement of the Vespertilioninae in which bacular morphology is used in association with the traditional diagnostic features to suggest possible relationship. This classification is presented in Table 1.

There appear to be two major bacular types in the Vespertilioninae, each with numerous variations as might be expected in such a large and diverse subfamily. A classification that includes a major consideration of bacular morphology shows significant resemblances to earlier arrangements based on traditional and conventional morphological features. However, there are some wide divergences, as for example the seemingly artificial nature of the 'Nycticeiini' or the associations of the various genera of big-eared bats. Tate (1942a) commented upon the latter and pointed out that very large ears and their associated auditory specialisations in the skull occurred independently in three sections of the subfamily: indeed, if *Antrozous* and *Bauerus* are included, these features occur four times in the group. In particular, both Miller (1907) and Tate (loc. cit.) associated *Laephotis* with *Histiotus* on cranial and dental morphology but its bacular structure shows a clear affinity with *Pipistrellus* (*Neoromicia*) as here recognised. *Otonycteris*, another big-eared bat, was allied by Tate (loc. cit.) to the 'Nycticeiini' but proves to have a baculum much more like those of the plecotine genera.

One major bacular type is 'saddle-like' or 'slipper-like' and is exemplified by *Myotis* and *Pizonyx*. Their bacula are very similar, emphasising the close relationship that is generally accepted between these genera. The baculum of *Lasionycteris* is somewhat different in the presence of a lengthened shaft. However, in comparison with the long-shafted bacula found in the Pipistrellini the baculum of *Lasionycteris* is relatively short, and it retains indications of the more characteristic myotine type in its upraised proximal and distal portions. The occasional presence of a flattened dorsal prominence on its base also recalls the condition found in *Idionycteris*. The genus, although having some specialised features, is allied firmly to *Myotis* by Miller (1907) and Tate (1942a). It has slightly hooked upper incisors, i^3 with a slightly caniniform profile as in *Myotis*; pm^2 is in the line of the tooththrow; m^3 is unreduced; pm_{2-3} are exactly as in *Myotis*, much smaller than pm_4 , with pm_3 not removed from the line of the other teeth. Although pm^3 has been lost, this appears to be a specialisation; as Tate (loc. cit.) pointed out, pm_{2-3} still agree closely with those of the less specialised species of *Myotis* not only in relation to each other but also in their proportional size relative to pm_4 . Although associated with *Myotis*, this genus is considerably specialised in other ways (Miller, loc. cit.) and its bacular structure may well reflect this divergence. Its baculum might be regarded as derived from the more typical myotine structure.

Bacula variously reminiscent of the saddle shaped structure found in *Myotis* occur in a number of other genera. Such bacula characterise *Plecotus* (including *Corynorhinus*), *Idionycteris*, *Barbastella*, *Rhogeessa*, *Baeodon*, *Nycticeius*, *Otonycteris*, *Lasiurus*, *Dasypterus*, *Antrozous* and *Bauerus*, and possibly may be found in *Euderma*. Tate (1942a) postulated the grouping 'Plecotini' for *Plecotus*, (*Corynorhinus*), *Idionycteris* and *Euderma*, allying it to the Myotini but not employing the term in a formal taxonomic or systematic sense. Bacular morphology thus lends support to his hypothesis that the plecotine genera should be associated with *Myotis*. Also, the baculum of *Barbastella* suggests that it too belongs here: Miller (1907) postulated such a relationship, despite several morphological differences. *Rhogeessa*, *Baeodon*, *Nycticeius* and *Otonycteris* also seem allied to this grouping. Tate (1942a) referred these genera to the 'Nycticeiini' with *Scotoecus*, *Scotomanes* and *Scotophilus* on account of their incisive and premolar dentition. However, the bacula of *Rhogeessa*, *Baeodon*, *Nycticeius* and *Otonycteris* are variants of the saddle-like type; that of *Scotoecus* is like that of *Pipistrellus* (*Pipistrellus*), and the bacula of *Scotomanes* and *Scotophilus* are broadly similar to those of *Eptesicus* and its allies. *Lasiurus*, *Dasypterus*, *Antrozous* and *Bauerus*

have further variants of this bacular type, but are quite distinctive on other morphological grounds.

The bacula of *Antrozous* and *Bauerus* are not at all like that of *Otonycteris*, with which these genera have been tentatively associated (Pine *et al.*, 1971), nor do their bacula have any significant resemblance to those of *Nyctophilus* or *Pharotis*, thus supporting the view (Koopman, 1984*b*, 1985; Breed & Inns, 1985) that these North American genera should not be associated with the Australian *Nyctophilus* and *Pharotis* in the subfamily Nyctophilinae. Bacular morphology suggests instead an association with those genera that have the myotine type of baculum, to which the bacula of *Antrozous* and *Bauerus* have many resemblances. The bacula of *Nyctophilus* and *Pharotis* (Fig. 22a–h) are consistently homogeneous and differ in many ways from those of the genera usually referred to the Vespertilioninae. For the present we would place these two genera in a separate subfamily, the Nyctophilinae, rather than merge them into the Vespertilioninae as is done by Koopman (1984*a*, 1984*b*, 1985).

A further basically triangular and flattened variant of the saddle-like baculum characterises the genera *Eptesicus*, *Vespertilio* (if the pseudobaculum is ignored), *Ia* and *Histiotus*. Miller (1907) remarked that the skull of *Vespertilio* showed a strong likeness to that of *Lasionycteris* but that the former was in all respects a typical *Eptesicus*. *Vespertilio* and *Lasionycteris* are separated by marked dental and bacular differences: the bacular morphology of *Vespertilio* allies it with *Eptesicus* as Miller suggested. It is perhaps not unreasonable to speculate that *Lasionycteris* which has a strongly myotine dentition has diverged among the Myotini in the same way as *Vespertilio* has diverged among the Vespertilionini, the latter genus supporting a long penis either by a centrally situated baculum or perhaps more effectively by the development of a cartilaginous pseudobaculum, this function in *Lasionycteris* by a short shaft. The genera *Tylonycteris* and *Mimetillus* also belong here. The African *Glauconycteris* has been associated (Ryan, 1966; Koopman, 1971) with the Australian *Chalinolobus* but their bacula differ widely. Although structurally variable within the genus, the bacula of *Glauconycteris* are more like the vespertilionine or eptesicine type: those of *Chalinolobus* are long-shafted and like the bacula of *Pipistrellus* (*Pipistrellus*). Finally, the baculum of *Scotomanes* appears to be a derivative of the saddle-like type, leading to the distinctive baculum of *Scotophilus*.

The genus *Pipistrellus* seems to stand more or less at the centre of the second major grouping. It has broadly two divisions in bacular terms, one characterised by a long baculum with well developed basal lobes and a relatively long, mostly cylindrical shaft, its tip often bifid or with similar elaboration. The second division includes those species in which the basal lobes are sometimes small or obsolete and which have a shorter, flatter, ventrally fluted shaft, its tip sometimes elaborated into a spatulate or platelet-like structure.

These groupings have been used in this study to support subgeneric division of this large genus. The first division includes *Pipistrellus* (*Pipistrellus*), *P. (Vespadelus)*, *P. (Perimyotis)* and *P. (Arielulus)*. Reduction and loss of pm^2 occurs in *P. (Arielulus)* and the tooth is almost invariably absent in *P. (Vespadelus)*. The second division contains *P. (Hypsugo)* in which pm^2 may be very small or absent, *P. (Neoromicia)* from which it is again almost invariably absent, and *P. (Falsistrellus)*. Although primarily Old World in distribution, both of these divisions are represented in the New World, each by a single species. The Australian *P. (Vespadelus)* seems on bacular features to represent *P. (Pipistrellus)*; the wholly African *P. (Neoromicia)* is apparently similarly related to *P. (Hypsugo)*, of which *P. (Falsistrellus)* appears to be an eastern representative.

The majority of the genera here allocated to the Pipistrellini show strong bacular affinities to *Pipistrellus* (*Pipistrellus*): some such as *Glischropus* and *Scotozous* have been considered congeneric with *Pipistrellus* in the past. Besides *Glischropus* and *Scotozous* these include *Nycticeinops*, *Scoteanax*, *Scotorepens*, *Scotoecus*, *Nyctalus*, *Hesperoptenus* and *Chalinolobus*, all with long-shafted bacula. Of the remainder, *Laephotis* in bacular structure is similar to *P. (Neoromicia)*, while *Philetor* has a baculum that appears to be an elaboration of the bacular structure found in some of *P. (Hypsugo)*. Tate (1942*a*) postulated a relationship between *Philetor*, *Tylonycteris* and perhaps *Mimetillus* but the bacula of the first two are totally dissimilar and the structure is apparently absent from *Mimetillus*: it is very small in *Tylonycteris*. Hill (1966*a*) drew attention to the unusual genitalia of *Philetor* and following Tate's (loc. cit.) suggestion of affinity with *Pipistrellus joffrei* and

its associates allied *Philetor* with this group. Unfortunately, excepting for the aberrant species *stenopterus* the bacula of the *stenopterus* subgroup (including *P. joffrei*) of this present study remain unknown.

Bacular morphology suggests that the conventional view that *Eptesicus* and its immediate allies derive from or are closely related to *Pipistrellus* can be questioned. Cranially and dentally there are many similarities between 'Eptesicus' as formerly defined and *Pipistrellus* and as Koopman (1975) has pointed out, the loss of pm^2 enables a species to cross the boundary between the two genera as then understood, a process which in his view might have occurred more than once. Our conclusions do not challenge this opinion: those 'Eptesicus' species in which pm^2 has been found occasionally to occur prove on bacular grounds to be closer to *Pipistrellus* than to *Eptesicus* as we understand it, while *Pipistrellus* as formerly defined has long been known to include some species from which on occasion this 'diagnostic' tooth is absent. Clearly, our findings support Koopman's (loc. cit.) opinion that this process may have occurred several times and indeed may be occurring in some species, but all belong to the one genus, *Pipistrellus*.

As we understand its composition, *Eptesicus* is now a more restricted genus in which the triangular, flattened baculum is basically closer in structure to the saddle-like grouping than to the long-shafted group, although some *Eptesicus* do indeed have bacula that suggest the beginnings of basal lobulation or of a very short shaft. We suggest therefore that in bacular terms the Vespertilionini to which we refer *Eptesicus* may represent a transitional stage between the saddle-like baculum and the predominantly basally lobed and long-shafted type. *Tylonycteris* and *Glauconycteris* also show this tendency.

Dental reduction proceeds throughout both of the major bacular groups. In the grouping with broadly myotine or saddle-like bacula the dentition varies in number of teeth from a total of 38 (*Myotis*, *Pizonyx*) through 36 (*Lasionycteris*, *Plecotus* and allies), 34 (*Barbastella*, *Eptesicus* and allies), 32 (*Lasiurus*), 30 (*Dasypterus*, *Rhogeessa*, *Baeodon*, *Nycticeius*, *Otonycteris*, *Scotomanes*, *Scotophilus*) to 28 (*Antrozous*, *Bauerus*). In the second of the two major bacular groups, dental reduction varies from *Eudiscopopus* with a total of 36 teeth (its association here is presumed) through 34 (*Pipistrellus*, *Glischropus*, *Scotozous*, *Nyctalus*, *Chalinolobus*), 32 (*Laephotis*, *Philetor*, *Hesperoptenus*) to 30 (*Nycticeinops*, *Scoteanax*, *Scotorepens*, *Scotoecus*). Thus this trend occurs concurrently in the two major groupings, taking the same form in each by increasing the size and bulk of i^2 , the reduction, transposition and loss of i^3 , and the progressive reduction, transposition and loss of pm^2 , pm^3 and pm_2 .

Zoogeographical considerations

The saddle-shaped or slipper-like baculum characteristic of the Myotini, Plecotini, Lasiurini and Antrozoini as here understood is cosmopolitan in but one genus, *Myotis*. It occurs in one Holarctic genus, *Plecotus*, in one Palaearctic genus, *Barbastella*, itself probably closely related to *Plecotus*, and in one other Old World genus, *Otonycteris*, that occurs in southwestern Asia and northern Africa. Otherwise this bacular type is limited to the New World. *Lasionycteris*, exclusively North American, has a baculum apparently derived from this type, as does *Nycticeius*, also North American, although in this genus the baculum is considerably modified to the extent that Hamilton (1949) commented upon its unique character among the genera that he had examined. Thus although the saddle-shaped baculum or its derivatives is represented about equally in number of species in the Old and New Worlds, genera with bacula of this type predominate in the latter, its extension into the Old World being primarily through the many species of *Myotis*, with a lesser contribution from *Plecotus*, *Barbastella*, and *Otonycteris*.

A further variety of this bacular type is found in the Vespertilionini, that is, in *Eptesicus* and its close relatives. In these, the baculum is less strongly saddle-shaped or slipper-like, flatter, and often more triangular in outline. This bacular type is primarily Old World in numbers of genera and species, only *Eptesicus* among Old World genera extending to the New World where there is a closely related genus, *Histiotus*. In the Old World, *Vespertilio* is also closely related to *Eptesicus*. Another Old World genus, *Ia*, is a giant representative of this same bacular type. The southeastern

Asian *Tylonycteris* and the African *Glauconycteris* have bacula that are modified variants of this type: *Mimetillus*, in which no baculum has been found, also appears to belong here. Two further Old World genera, *Scotomanes* and *Scotophilus*, also have bacula that are similar in many respects to the vespertilionine type.

The shafted or long-shafted bacular type is confined almost exclusively to the Old World, and is represented in the New World by no more than two species of *Pipistrellus* in the Nearctic region, one of these with a highly modified baculum. This bacular type is restricted to the Pipistrellini and within that grouping to those genera that for the most part can be shown on other grounds to cluster around *Pipistrellus*. Indeed, some such as *Scotozous*, *Glischropus*, *Scoteanax*, *Scotorepens* and perhaps even *Nyctalus* might on bacular grounds be regarded as subgenera of this widespread genus. In a reduced form this bacular type appears in two of the subgenera of *Pipistrellus*, *P. (Perimyotis)* and *P. (Arielulus)*. Widespread in the Palaearctic region and in southeastern Asia, this bacular type is represented in Australia by five distinct groupings: *Pipistrellus (Pipistrellus)*, *P. (Vespadelus)*, *Scoteanax*, *Scotorepens*, and *Chalinolobus*. This type of baculum also occurs in Africa among *Pipistrellus kuhlii* and its associates, which might in fact be considered to warrant recognition as a further subgenus of *Pipistrellus*.

A further variant of the shafted bacular type is found in *Pipistrellus (Hypsugo)* and *P. (Falsistrellus)*. In these the shaft is shorter and is ventrally fluted, often with expansion of the tip. *Pipistrellus (Hypsugo)* is confined chiefly to Asia and Africa, where in the latter region it appears to be closely associated with *P. (Neoromicia)* in which pm^2 is generally lost. Thus as in Australia where *P. (Vespadelus)* in which pm^2 is also generally absent appears to derive from *P. (Pipistrellus)*, so in Africa *P. (Neoromicia)* is apparently similarly related to *P. (Hypsugo)*. Of the two North American pipistrelles, *P. subflavus* has a reduced form of the *P. (Pipistrellus)* baculum, the shaft very short and stubby: this species has a myotine tragus and has been considered (Menu, 1984) to have a myotine dentition. However, on the balance of features it appears to be clearly referable to *Pipistrellus* and indeed to be cranially and dentally close to *P. (Pipistrellus)*, which apparently it represents in North America. There do not appear to be sufficient grounds to justify its generic separation from *Pipistrellus* as has been recently effected (Menu, loc. cit.), although subgeneric recognition within that genus seems appropriate. The second North American species of *Pipistrellus*, *P. hesperus*, should evidently be referred to *P. (Hypsugo)* with which it has close bacular and dental similarities, although recently generic separation (Horáček & Hanák, 1985a, b, 1985–1986) has been proposed for it. Finally, *P. (Falsistrellus)* is restricted to southeastern Asia, Australasia and Tasmania: the deeply ventrally fluted baculum of this subgenus, lacking basal and distal modification but massive and substantial appears to be an extreme of the *P. (Hypsugo)* type: possibly *P. (Falsistrellus)* represents *P. (Hypsugo)* which seems to be linked to it by several of its Asian species.

One corollary of the removal of the African *capensis* and *tenuipinnis* groups of '*Eptesicus*' to *Pipistrellus*, and of the similar transfer of the Australian species formerly referred to '*Eptesicus*' is that in the Old World *Eptesicus* now becomes primarily Palaearctic, with outliers, perhaps all closely connected to *E. serotinus*, in Africa while in the New World it extends over both North and South America. In southeastern Asia the genus becomes restricted to no further east than southern Thailand, the former enormous hiatus in its distribution between this part of southern Asia and Australia having been removed.

Conclusions

(1) The current classification of the Vespertilioninae is based chiefly on adaptive characters with considerable emphasis on facial shortening and concomitant dental reduction and loss. Several authors have drawn attention to the deficiencies and dangers of any classification that relies heavily on such features. A review of bacular morphology within the subfamily suggests that this structure provides indications of relationship that in many respects support the existing classification but which also indicate several changes to the current arrangement. In particular, bacular morphology suggests a number of major and minor changes in the systematics of the nominal genera *Pipistrellus*

and *Eptesicus*, separated hitherto only by dental formula, itself subject to variation in both 'genera' as they are currently understood.

(2) The presence or absence of the anterior upper premolar (pm^2) in *Pipistrellus* and *Eptesicus*, used formerly as their principal diagnostic character, has little taxonomic significance. The tooth is variable in *Pipistrellus* as here understood, being reduced or lost in three of its subgenera, and is absent from *Eptesicus* as we envisage it.

(3) Bacular morphology in *Pipistrellus* and *Eptesicus* provides groupings that largely agree in species content with those proposed by earlier authors such as Tate (1942a) and Koopman (1973, 1975) although in basing their studies on 'conventional' morphological characters neither considered these genera in their entirety. The bacular morphology of '*Eptesicus*' as it is currently understood provides a clear indication that as such it is not a natural group, but that three species aggregations, the Australian *pumilus* group and the African *capensis* and *tenuipinnis* groups, should be transferred to *Pipistrellus*.

(4) It has been possible to recognise and define subgenera for the major species groups in both *Pipistrellus* and *Eptesicus* and to suggest possible relationships between them. One subgenus is described as new as *Pipistrellus* (*Arielulus*) for *P. circumdatus* and its allies.

(5) There appear to be clear links between certain of the pipistrelline subgenera: *Pipistrellus* (*Vespadelus*) in Australia seems to represent *P. (Pipistrellus)* in bacular terms while *P. (Hypsugo)* is apparently represented in Indo-Australia by *P. (Falsistrellus)* and is related to the African *P. (Neoromicia)*. Although the features of the two Nearctic species of *Pipistrellus* have been thought to justify their recognition in separate, individual genera we consider that the characters of one (*subflavus*) merit no more than subgeneric status as the sole species of *P. (Perimyotis)*, which itself perhaps represents *P. (Pipistrellus)*, while the other (*hesperus*) is perhaps more appropriately referred to *P. (Hypsugo)*.

(6) The examination of bacula in *Pipistrellus* has suggested that some taxa hitherto ranked as subspecies, for example *abramus*, *paterculus* or *helios*, might in fact be distinct species.

(7) As we now understand the species content of *Pipistrellus* and *Eptesicus* the former remains primarily an Old World genus where it is widespread and diverse in the tropics and subtropics, extending into the temperate zones and just to North America. In contrast, our concept of *Eptesicus* limits this genus to the New World and in the Old World primarily to the Palaearctic, with outlying representatives in Africa. It does not extend significantly into Australasia.

(8) Bacular morphology suggests the informal recognition of two major groupings within the subfamily Vespertilioninae. The first includes the Myotini, Plecotini and Lasiurini; *Antrozous* and *Baeurus*, which in bacular terms have no relation to *Nyctophilus* and *Pharotis* (the Nyctophilinae); the Scotophilini to include *Scotomanes* and *Scotophilus*; and finally the Vespertilionini, here reduced in content to include *Eptesicus* and its close relatives *Histiotus*, *Ia* and *Vespertilio*, with *Tylonycteris*, *Mimetillus* and *Glauconycteris*.

(9) The second grouping consists of *Pipistrellus* and those genera which cluster round it. All with the possible exception of *Philetor* appear to relate quite closely in bacular terms to one or other of the subgenera that we recognise in *Pipistrellus*, principally to *P. (Pipistrellus)*. *Laephotis*, formerly considered related to *Histiotus*, is instead in bacular terms closely associated with *P. (Neoromicia)*. The bacula of *Chalinolobus* and *Glauconycteris* are widely dissimilar although these genera have been closely allied in the past; *Chalinolobus* is of the pipistrelline type while the baculum of *Glauconycteris* apparently associates it more appropriately with *Eptesicus* and its allies.

(10) Bacular morphology provides clear indications that the 'Nycticeini' of Tate (1942a) and Koopman (1984, 1985) is not a natural group, its constituent members despite cranial and dental similarities having widely different bacula. Thus *Rhogeessa*, *Baeodon*, *Nycticeius* sensu stricto, and *Otonycteris* have been here allied to the plecotine bats on bacular grounds, while *Scoteanax*, *Scotorepens* and *Scotoecus* are quite clearly associates in bacular terms of *Pipistrellus*. '*Nycticeius*', at one time thought to include the Australian *Scoteanax* and *Scotorepens* as well as its North

American type species *humeralis* and the African *schlieffenii*, has recently been restricted only to the American and African forms. These prove to have widely different bacula; *humeralis* has been associated with the plecotine bats on this account, while generic status has been accorded to *schlieffenii* with the proposal of a new generic name, *Nycticeinops*.

(11) The two broad bacular types that we discern in the subfamily Vespertilioninae have definite geographical patterns: the saddle-like baculum and its variants that characterise the first group noted above is primarily New World and Palaearctic, extending less significantly into the Old World tropics or Australasia, while the shafted baculum of the second group is chiefly confined to the Old World.

Addendum

A phenetic analysis of the relationships of selected vespertilionine species (chiefly those currently referred to *Pipistrellus* and *Eptesicus*) by Horáček & Hanák (1985–1986) appeared while this paper was in press. These authors provided definitions of *Pipistrellus*, *Hypsugo* (which they considered generically valid) and *Eptesicus*, based on the morphology of the penis and baculum, the upper molars, the basisphenoid pits, the pelvic girdle, and the tibia, tail and epiblema.

Horáček & Hanák suggested that the classification of pipistrelloid bats might be clarified by the recognition of additional subgenera or genera for those species or species groups that do not conform precisely with those that they included within these three generic groupings. To some extent such recognition is provided in several instances by the classification here proposed and although some major differences exist between the informal assessments and species groups of Horáček & Hanák and the formal arrangement put forward in this paper there is nevertheless a broad measure of agreement. Horáček & Hanák did not attempt any classification of the Vespertilioninae as a whole, but '*Nycticeius*' *schlieffenii*, here considered to represent a distinct monospecific genus (*Nycticeinops* gen. nov.) was thought by these authors to be referable either to *Eptesicus* (*Rhyneptesicus*), or possibly to justify the establishment of a new subgenus within *Eptesicus*.

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Appendix 1. Specimens examined

AMNH = American Museum of Natural History, New York

BM(NH) = British Museum (Natural History), London

CMNH = Carnegie Museum of Natural History, Pittsburgh

HZM = Harrison Zoological Museum, Sevenoaks, Kent

NMW = Naturhistorisches Museum, Wien

Vespertilioninae*Myotis nattereri*

HZM 26.11254 Leany Cave, Pilis Heights, Hungary. (Fig. 19j)

Myotis ridleyi

BM(NH) 98.3.13.5 Selangor, Malaya. Holotype. (Fig. 19i)

Pizonyx vivesi

HZM 3.10284 Isla Cordonosa, Bahia de Los Angeles, Baja Norte, Mexico. (Fig. 19k)

Lasionycteris noctivagans

BM(NH) 7.7.7.2319 Raleigh, North Carolina, USA. (Fig. 17f)

HZM 2.3708 Delta, Manitoba, Canada

Plecotus auritus

HZM 19.1227 Near Godstone, Surrey, England. (Fig. 19g)

Plecotus austriacus

BM(NH) 91.10.5.4 Duirat, Tunis

HZM 3.4867 St. Pierre de Varenne, Saone et Loire, France.

HZM 4.8337 Mont de Lans, Les Deux Alpes, Isere, France.

HZM 5.8467 Chateau de Salse, Salse, Rousillon, France. (Fig. 19h)

Barbastella barbastellus

HZM 13.11222 Kiralyret, Borzsony Heights, Hungary. (Fig. 18j)

Rhogeessa tumida

HZM 1.12080 Airport Camp, Belize. (Fig. 18k)

Nycticeius humeralis

AMNH 249144 Sierra de Tamaulipas, Acuna, Tamaulipas, Mexico, 2890 ft. (Fig. 17k)

Otonycteris hemprichii

BM(NH) 14.8.17.1 Syrian Desert.

HZM 6.8174 17 km N of Hufoof, Saudi Arabia. (Fig. 16a)

Lasiurus cinereus

HZM 1.3695 S Fork, Cave Creek, near Portal, Cochise County, Arizona, USA. (Fig. 19l)

Dasypterus argentinus

BM(NH) 33.6.24.3 Bonifacio, Argentina. (Fig. 18f)

Antrozous pallidus

BM(NH) 50.767 California, USA. (Fig. 18b).

HZM 3.3692 S Fork, Cave Creek, near Portal, Cochise County, Arizona, USA.

Scotophilus borbonicus

BM(NH) 89.1.11.2 E coast of Africa.

Scotophilus dinganii

BM(NH) 79.513 Tokadeh, Nimba, Liberia, 600 m.

Scotophilus heathii

BM(NH) 14.7.19.19 Mount Popa, Burma.

BM(NH) 14.7.19.28 Kyauk Inyaung, Irrawaddy, Burma.

BM(NH) 60.257 Tori, Pakistan. (Fig. 17h)

BM(NH) 70.1488 Bang Phra, Cholburi, Sriracha, Thailand.

BM(NH) 76.787–788 Nhatrang, Annam, Vietnam.

Scotophilus kuhlii

BM(NH) 75.2955 Chiang Mai, Thailand (Fig. 17i)

Scotophilus nigrata (gigas)

BM(NH) 22.12.17.55a Mtondo, Ruo, Malawi. (Fig. 17g)

Scotophilus nigritellus

BM(NH) 78.189 Numan, Gongola, Nigeria. (Fig. 17j)

Scotomanes ornatus

BM(NH) 94.9.1.21 Foochow, China. (Fig. 18g)

*Eptesicus (Eptesicus)**Eptesicus bobrinskoi*

BM(NH) 63.1187 Guter Su, N of Mount Sabalan, NW Iran. (Fig. 13e)

*Eptesicus nasutus*HZM 3.4571 Harmul, 10 m N of Sohar, Oman (*batinensis*).HZM 12.11172 Jamma, near Rostaq, Oman (*batinensis*). (Fig. 14c)HZM 1.1623 Shaiaba, Iraq (*pellucens*).*Eptesicus bottae*

HZM 18.1616 Ser'Amadia, Kurdistan, Iraq.

HZM 5.1628 Basrah, Iraq (*hingstoni*).BM(NH) 3.12.8.9 Cairo, Egypt (*innesi*). (Fig. 13j)HZM 12.8075 Birkat Sharaf al Wadi Sahtan, Jebel al Akhdar, Oman (*omanensis*). (Fig. 14a)*Eptesicus brasiliensis*

BM(NH) 85.6.26.10 San Lorenzo, Rio Grande do Sul, Brazil. (Fig. 13k)

BM(NH) 0.6.29.4 Palmeira, Parana, Brazil.

BM(NH) 98.10.3.32 Valdivia, Colombia (*andinus*). (Fig. 13d)*Eptesicus furinalis*

BM(NH) 4.8.8.5 La Plata, Argentina. (Fig. 13c)

Eptesicus fuscus

BM(NH) 89.6.1.4 Sing Sing, New York, USA. (Fig. 13a)

BM(NH) 52.551 Chinchona, Jamaica (*hispaniolae*). (Fig. 13i)*Eptesicus hottentotus*BM(NH) 81.7.11.1 Drakenburg Mountains, Natal, South Africa (*megalurus*). (Fig. 13b)*Eptesicus serotinus*

BM(NH) 53.555 Blandford, Dorset, England. (Fig. 13g)

HZM 3.629 Shepreth, Cambridgeshire, England.

BM(NH) 66.1150 Defilia Oasis, Figuig, Morocco (*isabellinus*). (Fig. 13h)*Eptesicus (Rhinopterus)**Eptesicus floweri*

BM(NH) 0.8.6.20 Abu Zeit, White Nile, Sudan. (Fig. 13f)

BM(NH) 1.5.5.78 Shendy, Sudan (*lowei*). (Fig. 13l)*Vespertilio orientalis*

BM(NH) 8.7.25.6, BM(NH) 8.8.11.2 Kuatun, NW Fokien, China

Histiotus macrotis

BM(NH) 71.1123 Antofagasta, Lake Miniques, Chile, 1450 m. (Fig. 18e)

Histiotus (?) macrotis

BM(NH) 6.5.8.3 Jafi, Tucuman Province, Argentina. (Fig. 18d)

Histiotus velatus

BM(NH) 0.6.29.2 Palmeira, Parana, Brazil. (Fig. 18c)

Tylonycteris pachypus

BM(NH) 9.1.5.954 Buitenzorg, Java. (Fig. 18h)

Tylonycteris robustula

BM(NH) 60.1499 Bukit Lagong Forest Reserve, Kepong, Selangor, Malaya. (Fig. 18i)
 HZM 3.7444 15th mile Ulu Gombok, Selangor, Malaya.

Mimetillus moloneyi

BM(NH) 93.1.7.2 Leckie, Nigeria
 BM(NH) 54.862 Irumu, Zaire.
 BM(NH) 60.154 Bo, Sierra Leone.
 BM(NH) 64.1788 Liwale, Tanzania.
 HZM 2.7802 Near Babeke, River Isai, Ituri, Zaire.

Glauconycteris argentata

BM(NH) 54.863 Banana, Zaire.
 BM(NH) 59.510 Ikela, Ikela Territory, Zaire. (Fig. 19d)

Glauconycteris beatrix

BM(NH) 48.713 Eshobe, Mamfe, Cameroun. (Fig. 19c)

Glauconycteris humeralis

BM(NH) 30.11.11.173 River Wasa, Semliki Valley, Uganda. (Fig. 19e)

Glauconycteris poensis

BM(NH) 96.12.31.2 Sierra Leone.
 BM(NH) 69.26 Abidjan, Ivory Coast. (Fig. 19a)

Glauconycteris variegata

BM(NH) 76.780 Mole National Park, Ghana. (Fig. 19b)
 BM(NH) 55.409 Mongue, near Inhambane, Mozambique (*papilio*). (Fig. 19f)

*Pipistrellus (Pipistrellus)**Pipistrellus pipistrellus*

HZM 94.6807 Rabat, Malta.
 HZM 116.8549 Sevenoaks, Kent, England. (Fig. 2a)
 HZM 117.8650 Aylesford, Kent, England.
 BM(NH) 73.689 Kululai Rest House, Northwest Frontier Province, Pakistan (*bactrianus*)
 BM(NH) 14.5.10.19 BM(NH) 14.5.10.22 Djarkent, Semiretschenskoi, USSR (*lacteus*).

Pipistrellus nathusii

BM(NH) 8.8.4.128 BM(NH) 62.1368 St Giles, France (Fig. 2b)

Pipistrellus abramus

BM(NH) 89.6.17.3–4 Kin Kiang, Yangtse Kiang, China (seen by Thomas, 1928a).
 BM(NH) 5.1.4.8 Tokyo, Japan.
 BM(NH) 7.7.3.26 Nanking, China (seen by Thomas, 1928a). (Fig. 3a)
 BM(NH) 14.10.1.1 Lokow, Hunan, C China.
 BM(NH) 26.10.4.18 Hue, Annam, Vietnam (seen by Thomas, 1928a)
 BM(NH) 66.3469–3470 Chihli, China.
 BM(NH) 86.529 Chusan, China (Syntype *irretitus*).
 BM(NH) 86.532 Canton, S China.

Pipistrellus babu

BM(NH) 45.1.8.403 Nepal.
 BM(NH) 16.3.25.8 Pashok, Darjeeling, India. (Fig. 4a)

Pipistrellus camortae

BM(NH) ——— Car Nicobar (Original No. 3/76). (Fig. 15d)

Pipistrellus endoi

BM(NH) 70.2522 Horobe, Tayama, Ajiro-Machi, Minohe-Gun, Iwate Prefecture, Japan. (Fig. 3b)

Pipistrellus javanicus (tralatitius)

BM(NH) 0.8.2.9 Sumatra.
 BM(NH) 9.1.5.295 Tjilatjap, Java.
 BM(NH) 9.1.5.997–998 W Java.
 BM(NH) 16.4.21.3 Sungei Penoh, Korinchi, Sumatra.

- BM(NH) 27.12.1.37 Tam Dao, Tonkin, Vietnam, 3000 ft (No. 411 of Thomas, 1928a).
 BM(NH) 28.7.1.20 Phu Qui, Annam, Vietnam, 100 ft (No. 866 of Thomas, 1928b, who identified the specimen as *P. coromandra tramatus*, but with a longer baculum than those previously examined).
 BM(NH) 83.76 Silau Silau Trail, Mount Kinabalu, Sabah, Borneo. (Fig. 10e)

Pipistrellus paterculus

- BM(NH) 14.7.8.62 Pyaunggaung, N Shan States, Burma, 2794 ft.
 BM(NH) 14.7.19.241 Kyauk Myaung, Irrawaddy, W Burma.
 BM(NH) 14.7.19.242 Mount Popa, Upper Burma (Holotype). (Fig. 3c)
 BM(NH) 14.7.19.240 Mandalay, Burma.

Pipistrellus angulatus

- BM(NH) 67.2125 Schoolmaster's House, Nuhu, Guadalcanal I, Solomon Is (*ponceleti*). (Fig. 4d)

Pipistrellus collinus

- BM(NH) 50.983 Baiyanka, Purari-Ramu Divide, SE Bismarck Range, Papua New Guinea. (Fig. 4b)

Pipistrellus coromandra

- BM(NH) 32.11.1.7 Nam Tamai, Upper Burma.
 BM(NH) 50.478 Ningma, Upper Burma.
 BM(NH) 76.1263 Sumka Uma, Upper Burma.
 HZM 1.7317, HZM 2.7318 Near Mirzapur, India. (Fig. 7c, HZM 2.7318)
 HZM 4.7320 Dalatpur, near Mirzapur, India.
 BM(NH) 4.6.8.1 Annam, Vietnam (*tramatus*). (Fig. 7b)
 BM(NH) 27.12.1.40 Bac-kan, Tonkin, Vietnam (*tramatus*) (Original No. 444, seen by Thomas, 1928a).

Pipistrellus mimus

- BM(NH) 98.5.5.20 Dangs, Bombay, India.
 HZM 1.10456 Vikas Vidyalaya, near Ranchi, Bihar, India. (Fig. 7g)

Pipistrellus murrayi

- BM(NH) 99.8.6.34 Christmas I, Indian Ocean (Holotype). (Fig. 4c)
 BM(NH) 9.1.16.7 Flying Fish Cove, Christmas I, Indian Ocean.

Pipistrellus papuanus

- BM(NH) 22.2.2.3 Fredrik Hendrik I, Irian Jaya. (Fig. 2c)
 BM(NH) 34.1.14.8 Kokoda, Papua New Guinea.

Pipistrellus tenuis

- BM(NH) 85.912 Coast of Sabah, Borneo (*nitidus*). (Fig. 9d)

Pipistrellus ceylonicus

- BM(NH) 95.6.12.1 Pundibiya, India.
 BM(NH) 2.4.2.8 Astoli, Belgoum, India. (Fig. 7d)
 BM(NH) 11.4.5.5 Lanje, Konkan, India.
 BM(NH) 13.9.8.102 Gujarat, India.
 BM(NH) 9.1.4.73 Mangalore, Malabar Coast, India (Holotype *indicus*)
 BM(NH) 4.6.8.7-8 Tonkin, Vietnam (*raptor*). (Fig. 3d, BM(NH) 4.6.8.7 Holotype).

Pipistrellus crassulus

- BM(NH) 4.2.8.1 Efulen, Cameroun (Holotype). (Fig. 7e)

Pipistrellus nanulus

- BM(NH) 4.2.8.8 Efulen, Cameroun (Holotype). (Fig. 7f)
 BM(NH) 79.508 South Nimba, Liberia.

Pipistrellus rueppellii

- BM(NH) 68.12.22.3 Zanzibar (Holotype *pulcher*). (Fig. 10a)
 BM(NH) 99.9.9.20 Egypt.
 BM(NH) ——— Uganda. (Fig. 10b)
 HZM 3.3170 Kabompo Boma, Zambia.
 HZM 7.12109 Suez, Egypt.

Pipistrellus deserti

- BM(NH) 79.987 Hoggar Plateau, Algeria. (Fig. 5c)
 NMW 27503 (?) Upper Egypt.

Pipistrellus kuhlii

- BM(NH) 92.9.9.25 Upper Egypt.
BM(NH) Argostoli, Cephaloni, Greece. (Fig. 5a)
BM(NH) 63.335 Sangha, Malya Khola, E Nepal.
HZM 5.11607 Horefto, near Volos, Greece.
HZM 11.1016 Rapallo, N Italy.
HZM 138.4563 Yal bu Hillal, Batinah, Oman.
HZM 154.4619 Saham, Batinah, Oman.
HZM 203.7232 Dig Dagga, Ras al Khaima, United Arab Republic.
HZM 218.7402 Benghazi, Libya.
HZM 227.9110 Kapsowat, Marakwat, Kenya.

Pipistrellus maderensis

- BM(NH) 86.528 Madeira. (Fig. 5b)

Pipistrellus rusticus

- BM(NH) 35.9.1.108 Okavango-Omatako Junction, Grootfontein District, Namibia.
BM(NH) 79.1731 Oli River, Borgu G.R., Nigeria. (Fig. 6c)
HZM 4.3285 Sentinel Ranch, River Limpopo, Zimbabwe. (Fig. 5d)

*Pipistrellus (Vespadelus)**Pipistrellus pumilus*

- BM(NH) 70.1093 E Bonithon Range, C Australia 23°42'S, 129°02'E, 1400 ft.
BM(NH) 71.1497 Westwood, near Rockhampton, Queensland, Australia. (Fig. 12k)

*Pipistrellus (Perimyotis)**Pipistrellus subflavus*

- HZM 1.2422 Big Wyandotte Cave, Crawford County, Indiana, USA. (Fig. 2d)

*Pipistrellus (Hypsugo)**Pipistrellus anchietae*

- BM(NH) 69.1248 Ngoma, Zambia.
BM(NH) 70.2632 Balovale, Zambia. (Fig. 6e)
BM(NH) 89.5.1.5 Caconda, Angola (Syntype of *Vesperus bicolor* Bocage, 1889). (Fig. 9e)

Pipistrellus bodenheimeri

- HZM 3.3786 Jazirat al Abid, Aden, South Yemen.
HZM 5.8279 Ein Gedi, Israel. (Fig. 9f)

Pipistrellus savii

- BM(NH) 31.11.11.13, BM(NH) 66.4644 E slope of Mount Olympus, Greece.
BM(NH) 61.395 Ainab, Lebanon. (Fig. 6a)

Pipistrellus arabicus

- HZM 4.10060 Wadi Sahtan, Oman.
HZM 5.11625 Wadi Fidah, Dank/Ibri, Oman. (Fig. 7a)

Pipistrellus helios

- BM(NH) 39.133 N Guaso Nyiro, Kenya. (Fig. 6d)
BM(NH) 69.207 Kangatet, S Turkana, Kenya.
HZM 2.4086 Archer's Post, Northern Frontier District, Kenya.

Pipistrellus nanus

- BM(NH) 49.484 Kontaur, Gambia.
HZM 3.2778 Sokoto, N Nigeria.
HZM 3.4026, HZM 4.4027 Near Monrovia, Liberia.
HZM 83.4387 Haroni-Lusitu Beacon 74, Zimbabwe.
HZM 107.3212 Kabompo Boma, Zambia.
HZM 146.5161, HZM 147.5162 Rondo, Lindi, Tanzania.
HZM 165.5321 Liwale, Tanzania.
HZM 200.6581 Karonga, Malawi.
HZM 258.11469 Kunyale Stream, Mwinilunga District, Zambia.

HZM 260.12175 Lamto, Ivory Coast.

HZM 261.12176 Ivory Coast.

HZM 263.12451, HZM 264.12452 Kamuani Area, Machakos District, Kenya. (Fig. 6b, HZM 263.12451)

Pipistrellus pulveratus

BM(NH) 79.702 Near Nicholson Goat Bungalows, Hong Kong I.

BM(NH) 79.903 Peace Mansion, Tai Hang Road, New Territories, Hong Kong (Fig. 8c)

Pipistrellus hesperus

BM(NH) 98.3.1.8 Sierra Laguna, Baja California, Mexico.

BM(NH) 29.11.7.10 Panamint Mts, California, USA.

HZM 4.11219 Sycamore Well, Hidalgo County, New Mexico, USA. (Fig. 8d)

Pipistrellus eisentrauti

BM(NH) 84.1684, BM(NH) 84.1686 Mount Cameroun, Cameroun. (Fig. 9g, BM(NH) 84.1684)

Pipistrellus imbricatus

BM(NH) 9.1.5.286 Buitenzorg, Java. (Fig. 9a)

Pipistrellus macrotis

BM(NH) 23.1.2.12 Sabang, NW Sumatra. (Fig. 9b)

Pipistrellus kitcheneri

BM(NH) 10.4.5.47 Boentok, Barito River, Kalimantan, SC Borneo. (Fig. 8e)

Pipistrellus lophurus

BM(NH) 14.12.1.6 Maliwun, Victoria Province, Tenasserim, Burma (Holotype). (Fig. 8f)

Pipistrellus stenopterus

BM(NH) 60.1537 Institute of Medical Research Compound, Kuala Lumpur, Malaya.

BM(NH) 65.135 Pasir Road, Kuala Lumpur, Malaya. (Fig. 7h)

Pipistrellus (Falsistrellus)

Pipistrellus affinis

BM(NH) 83.3.3.2 Wynaard, India. (Fig. 8a)

BM(NH) 72.4224 Argarawa, Nevrawa Elwa, Central Province, Sri Lanka.

Pipistrellus petersi

BM(NH) 23.1.2.3. Buru I, Molucca Is (Fig. 8b)

Pipistrellus tasmaniensis

HZM 1.8712 Barrington Tops National Park, New South Wales, Australia. (Fig. 8g)

Pipistrellus (Neoromicia)

Pipistrellus capensis

BM(NH) 32.9.1.249 Broken Hill, Zambia.

BM(NH) 54.859 Elizabethville, Zaire.

BM(NH) 61.1078 Doddieburn Ranch, West Nicholson, Zimbabwe, 2300 ft, 21°24'S, 29°21'E.

BM(NH) 72.4383 E of Lake Margharita, Bulcha Forest, Ethiopia, 1800 m, 06°11'N, 36°10'E.

BM(NH) 72.4391 Didessa River, Wollega Province, Ethiopia, 1190 m, 09°02'N, 36°09'E. (Fig. 12g)

BM(NH) 75.561 Mole National Park, Ghana. (Fig. 12b)

BM(NH) 83.200 Mcheni Gorge, Chizarira National Park, Binga Province, Zimbabwe, 17°40'S, 27°52'E.

HZM 36.4514 40 m NW of Serowe, Botswana.

BM(NH) 66.6057 Ambositra, Madagascar (*matroka*). (Fig. 12a)

BM(NH) 77.2.19.6 Anzahameru, Madagascar (*minutus*). (Fig. 12i)

Pipistrellus guineensis

BM(NH) 70.2224, BM(NH) 70.2228, BM(NH) 72.4373 Gambela, Ethiopia, 8°15'N, 34°35'E (BM(NH)

72.4373 at 515 m) (Fig. 12c, BM(NH) 70.2224)

BM(NH) 76.293 Shagamu, Nigeria.

BM(NH) 84.1019 Bontioli, Bougouriba River, Burkina Faso (Upper Volta).

Pipistrellus melckorum

BM(NH) 83.216 Mcheni Gorge, Chizarira National Park, Binga Province, Zimbabwe, 17°40'S, 27°52'E.

(Fig. 12f)

Pipistrellus somalicus

BM(NH) 70.484 Mouth of Fincha River, Blue Nile Gorge, Ethiopia, 10°03'N, 37°20'E. (Fig. 12h)

BM(NH) 76.814 S bank of Ganale Doria, Sidam-Bale Bridge, Sidamo Province, Ethiopia, 5°45'N, 39°37'E.

BM(NH) 84.1016 Comoe River, Burkina Faso (Upper Volta), 260 m, 9°57'N, 4°38'W.

CMNH MJS 2846 Snai Sugar Plantation, 1½ km S, ½ km E of Giohar, Somalia, 2°46'N, 45°31'E.

Pipistrellus zuluensis

BM(NH) 83.212 Mchesu River, Chizarira National Park, Binga Province, Zimbabwe, 17°47'S, 27°39'E.

BM(NH) 83.215 Singama, Sibuwu, Binga Province, Zimbabwe, 17°36'S, 27°51'E. (Fig. 12d)

Pipistrellus rendalli

BM(NH) 89.12.12.1 Bathurst, Gambia.

BM(NH) 7.12.17.1–2 Gondokoro, White Nile, Sudan.

BM(NH) 23.4.12.1–2 Bugala, Sesse Is, Victoria Nyanza, Uganda. (Fig. 12e, BM(NH) 23.4.12.2)

BM(NH) 48.702 N'ko, Obubra Division, S Nigeria (?*brunneus*). (Fig. 14b)

Pipistrellus tenuipinnis

BM(NH) 47.350 Umuahia, E Nigeria.

BM(NH) 54.917 Bonthe, Sierra Leone.

BM(NH) 67.1734 Bota, Victoria, Cameroun, 4°00'N, 9°05'E. (Fig. 12j)

*Pipistrellus (Arielulus)**Pipistrellus circumdatus*

BM(NH) 73.618 Telecommunications Tower, Fraser's Hill, Pahang, Malaya. (Fig. 2e)

Pipistrellus cuprosus

BM(NH) 83.351 Sepilok, Sabah, Borneo, 5°52'N, 117°56'E (Holotype). (Fig. 9h)

Pipistrellus societatis

BM(NH) 67.1605 Base Camp, Gunong Benom, Pahang, Malaya, 800 ft (Holotype). (Fig. 9c)

Nyctalus noctula

BM(NH) ———— Locality unknown.

HZM 10.613 Bottisham, Cambridgeshire, England.

HZM 33.8888 Winchelsea Beach, Sussex, England. (Fig. 10f)

Laephotis botswanae

BM(NH) ———— Zomba, Malawi (original No. 2269; damaged).

Laephotis wintoni

HZM 1.3020 Nyeri, Mount Kenya, Kenya. (Fig. 16f)

Glischropus tylopus

BM(NH) 10.4.5.136 Upper Barito River, Kalimantan, SC Borneo. (Fig. 18a)

Scotozous dormeri

BM(NH) 12.3.8.30 Furdapur, Ajanta, Khandesh, India.

BM(NH) ———— Kathiawar, India (Original No. BNHS 2007). (Fig. 16d)

Scoteanax rueppellii

BM(NH) 80.3.25.1 Richmond River, New South Wales, Australia. (Fig. 16i)

Scotorepens balstoni

BM(NH) 10.6.21.9 Hermannsburg, Northern Territory, Australia. (Fig. 16g)

Scotorepens greyii

BM(NH) 75.2261 Pine Creek, 20 m ESE of Gandy's Hill, Northern Territory, Australia, 13°49'S, 131°49'E.
(Fig. 16h)

Nycticeinops schlieffenii

BM(NH) 14.7.31.14 Wei Wei River, Kenya.

BM(NH) 15.3.6.66 Kamisu, Dinda River, Sudan.

BM(NH) 71.675 Awash, Filhoa, Ethiopia, 09°00'N, 38°58'E.

HZM 5.2120 Ikau, Rukwa, Tanzania. (Fig. 16e)

Scotoecus albigula

BM(NH) 63.1042 Calundo, Lunda, Angola. (Fig. 20a)

Scotoecus albofuscus

BM(NH) 96.12.31.1 Sierra Leone. (Fig. 20e)

Scotoecus hindei

BM(NH) 14.7.31.13 30 m NW of Baringo, Kenya. (Fig. 20d)

BM(NH) 66.1466 Jos, Nigeria (*falabae*). (Fig. 20b)*Scotoecus hirundo*

BM(NH) 76.771 Mole National Park, Ghana. (Fig. 20c)

Scotoecus pallidus

BM(NH) 86.531 Afghanistan (damaged).

Philetor brachypterus

BM(NH) ——— New Guinea. (Fig. 16b)

*Hesperoptenus (Militronycteris)**Hesperoptenus blanfordi*

BM(NH) 83.853 Sepilok, Sabah, Borneo, 5°52'N, 117°56'E. (Fig. 21g)

Hesperoptenus tickelli

BM(NH) 71.12.26.1 Sri Lanka. (Fig. 21b)

Hesperoptenus tomesi

BM(NH) 7.1.1.428 Malacca, Malaya (Holotype). (Fig. 21a)

Chalinolobus gouldi

BM(NH) 71.1504 Westwood, near Rockhampton, Queensland, Australia. (Fig. 17b)

Chalinolobus morio

BM(NH) 6.8.1.60 (King River, Western Australia. (Fig. 17a)

*Chalinolobus nigrogriseus*BM(NH) 44.6.13.2 Port Essington, Northern Territory, Australia (*rogersi*).BM(NH) 75.2260 Pine Creek, 20 m ESE of Gandy's Hill, Northern Territory, Australia, 13°49'S, 131°49'E. (*rogersi*). (Fig. 17c)*Chalinolobus picatus*

BM(NH) 9.3.7.2 Gunnamulla, Queensland, Australia. (Fig. 17d)

Chalinolobus tuberculatus

BM(NH) 89.10.27.1 Outlying islands near Stewart I, New Zealand. (Fig. 17e)

Nyctophilinae*Nyctophilus bifax*

BM(NH) 67.5.6.5 Cape York, Queensland, Australia.

BM(NH) 77.3.28.1 Islands of Torres Straits, Australia.

BM(NH) 86.11.8.12 Somerset, Cape York, Queensland, Australia.

BM(NH) 15.3.13.1 Cloncurry, Queensland, Australia.

BM(NH) 15.3.13.3 Herberton District, Queensland, Australia (Holotype). (Fig. 22a)

Nyctophilus daedalus

BM(NH) 47.7.21.16, BM(NH) ——— Port Essington, Northern Territory, Australia. (Fig. 22g, BM(NH) 47.7.21.16)

BM(NH) 97.4.12.5 Daly River, Northern Territory, Australia.

Nyctophilus gouldi

BM(NH) 15.3.13.7 Ash I, Hunter River, New South Wales, Australia (damaged, part lost).

BM(NH) 15.3.13.8 Sydney, New South Wales, Australia.

BM(NH) ——— Botany, Sydney, New South Wales, Australia (Original No. 164) (Fig. 22d)

HZM 1.12085 Werrikimbe, Hastingsshire, New South Wales, Australia. (Fig. 16c)

BM(NH) 52.1.15.30 Tasmania (*sherrini*). (Fig. 22f)*Nyctophilus geoffroyi*BM(NH) 15.3.13.11 Kosciusko, New South Wales, Australia (*pacificus*).BM(NH) ——— Tasmania (*pacificus*) (Original No. M.1735).

BM(NH) ———— Launceston, Tasmania (*pacificus*) (Original No. M.168) (Fig. 22e)

BM(NH) 7.1.4.3 Alexandria, Northern Territory, Australia (*pallescens*). (Fig. 22b)

Nyctophilus microtis

BM(NH) 88.4.18.1 Sogeri, Papua New Guinea (Holotype). (Fig. 22c)

Pharotis imogene

BM(NH) 97.8.7.21 Kamali, Papua New Guinea. (Fig. 22h)

Table 1 Classification of the Vespertilioninae and Nyctophilinae.

Miller (1907)	Tate (1942a)	Simpson (1945)	Sokolov (1973)	Koopman (1984a, b, 1985)	Hill & Harrison
Vespertilioninae	Vespertilioninae	Vespertilioninae	Vespertilionidae (part)	Vespertilioninae	Vespertilioninae
<i>Myotis</i>	Myotini	<i>Myotis</i>	<i>Myotis</i>	Myotini	Myotini
<i>Pizonyx</i>	<i>Myotis</i> (Including <i>Pizonyx</i>)	(Including <i>Pizonyx</i>)	(Including <i>Pizonyx</i>)	<i>Myotis</i> (Including <i>Pizonyx</i>)	<i>Myotis</i> (Including <i>Cistugo</i> and <i>Anamygdon</i>)
<i>Lasionycteris</i>	<i>Lasionycteris</i>	<i>Lasionycteris</i>	<i>Lasionycteris</i>	<i>Pizonyx</i>	<i>Cistugo</i>
<i>Pipistrellus</i>	'Plecotini'	<i>Pipistrellus</i>	<i>Vespertilio</i>	<i>Cistugo</i>	<i>Anamygdon</i>
<i>Glischropus</i>	<i>Plecotus</i>	(Including <i>Pipistrellus</i>)	(Including <i>Vespertilio</i>)	<i>Anamygdon</i>	<i>Lasionycteris</i>
<i>Scotozous</i>	<i>Corynorhinus</i>	<i>Glischropus</i>	(Including <i>Eptesicus</i>)	<i>Lasionycteris</i>	<i>Lasionycteris</i>
<i>Pterygistes</i>	<i>Idionycteris</i>	<i>Scotozous</i>	<i>Rhinopterus</i>	Vespertilionini	Plecotini
[= <i>Nyctalus</i>]	<i>Euderma</i>	<i>Nyctalus</i>	<i>Eptesicus</i>	<i>Eudiscopus</i>	<i>Plecotus</i>
<i>Eptesicus</i>	<i>Pipistrellini</i>	<i>Idionycteris</i>	<i>Rhinopterus</i>	<i>Pipistrellus</i>	(Including <i>Corynorhinus</i>)
<i>Vespertilio</i>	<i>Eudiscopus</i>	<i>Idionycteris</i>	<i>Hesperoptenus</i>	(Including <i>Ia</i>)	<i>Idionycteris</i>
<i>Rhinopterus</i>	<i>Pipistrellus</i>	<i>Eptesicus</i>	<i>Tylonycteris</i>	<i>Ia</i>	<i>Euderma</i>
<i>Hesperoptenus</i>	<i>Glischropus</i>	<i>Eudiscopus</i>	<i>Mimetillus</i>	<i>Nyctalus</i>	<i>Barbastella</i>
<i>Tylonycteris</i>	<i>Nyctalus</i>	(Including or closely allied to <i>Rhinopterus</i> and <i>Hesperoptenus</i>)	<i>Philetor</i>	<i>Philetor</i>	<i>Rhogeessa</i>
<i>Mimetillus</i>	<i>Ia</i>	<i>Philetor</i>	<i>Histiotus</i>	<i>Histiotus</i>	<i>Baeodon</i>
<i>Philetor</i>	<i>Scotozous</i>	(Including or closely allied to <i>Rhinopterus</i> and <i>Hesperoptenus</i>)	<i>Laephotis</i>	(Including <i>Rhinopterus</i>)	<i>Otonycteris</i>
<i>Laephotis</i>	<i>Chalinolobus</i>	<i>Rhinopterus</i>	<i>Pipistrellus</i>	<i>Vespertilio</i>	<i>Lasiurini</i>
<i>Otonycteris</i>	<i>Glauconycteris</i>	<i>Hesperoptenus</i>	<i>Scotozous</i>	<i>Laephotis</i>	<i>Lasiurus</i>
<i>Nycticeius</i>	<i>Barbastella</i>	<i>Tylonycteris</i>	<i>Ia</i>	<i>Histiotus</i>	<i>Dasypterus</i>
<i>Scotoceus</i>	<i>Philetor</i>	<i>Mimetillus</i>	<i>Glischropus</i>	<i>Philetor</i>	<i>Antrozoini</i>
<i>Scoteinus</i>	<i>Mimetillus</i>	<i>Histiotus</i>	<i>Nyctalus</i>	<i>Tylonycteris</i>	<i>Bauerus</i>
[= <i>Scotomanes</i>]	<i>Tylonycteris</i>	<i>Laephotis</i>)	<i>Eudiscopus</i>	<i>Mimetillus</i>	<i>Scotophilini</i>
[<i>Scoteanax</i>]	<i>Hesperoptenus</i>	<i>Vespertilio</i>	<i>Rhinopterus</i>	<i>Hesperoptenus</i>	<i>Scotomanes</i>
[<i>Scotorepens</i>]	<i>Eptesicus</i>	(Including <i>Otonycteris</i>)	<i>Scotoceus</i>	<i>Chalinolobus</i>	[<i>Scoteinus</i>]
<i>Scotomanes</i>	<i>Rhinopterus</i>	<i>Nycticeius</i>	<i>Scoteinus</i>	(Including <i>Glauconycteris</i>)	<i>Scotophilus</i>
<i>Rhogeessa</i>	<i>Laephotis</i>	(Including <i>Scoteinus</i>)	[= <i>Scotomanes</i>]	<i>Scoteinus</i>	Vespertilionini
<i>Pachyotus</i>	<i>Histiotus</i>	<i>Scoteinus</i>	[<i>Scoteanax</i>]	<i>Nycticeini</i>	<i>Eptesicus</i>
[= <i>Scotophilus</i>]	<i>Nycticeini</i>	<i>Scoteinus</i>	[<i>Scoteanax</i>]	<i>Nycticeius</i>	

Table 1—cont.

Miller (1907)	Tate (1942a)	Simpson (1945)	Sokolov (1973)	Koopman (1984a, b, 1985)	Hill & Harrison
<i>Chalinolobus</i>	[= <i>Scotomanes</i>]	[= <i>Scotomanes</i>]	[<i>Scotorepens</i>]	[<i>Scoteanax</i>]	(Including
<i>Glauconycteris</i>	[<i>Scoteanax</i>]	[<i>Scoteanax</i>]	<i>Rhogeessa</i>	[<i>Scotorepens</i>]	<i>Rhinopterus</i>)
<i>Lasiurus</i>	[<i>Scotorepens</i>]	[<i>Scotorepens</i>]	(Including	<i>Rhogeessa</i>	<i>Vespertilio</i>
<i>Dasypterus</i>	<i>Nycticeius</i>	<i>Scotomanes</i>)	<i>Baeodon</i>)	(Including	<i>Histiopus</i>
<i>Barbastella</i>	<i>Rhogeessa</i>	(Including	<i>Scotophilus</i>	<i>Baeodon</i>)	<i>Ia</i>
<i>Plecotus</i>	<i>Baeodon</i>)	<i>Baeodon</i>)	<i>Chalinolobus</i>	<i>Scotoecus</i>	<i>Tylonycteris</i>
<i>Corynorhinus</i>	<i>Scotoecus</i>	(Including	(Including	<i>Scotomanes</i>	<i>Mimetillus</i>
<i>Euderma</i>	<i>Scotophilus</i>	<i>Scotophilus</i>	<i>Glauconycteris</i>)	[<i>Scoteinus</i>]	<i>Glauconycteris</i>
Nyctophilinae	<i>Scotomanes</i>	<i>Chalinolobus</i>	<i>Lasiurus</i>	<i>Scotophilus</i>	Pipistrellini
<i>Antrozous</i>	<i>Otonycteris</i>	(Including	(Including	<i>Otonycteris</i>	(?) <i>Eudiscopus</i>
<i>Nyctophilus</i>	<i>Lasiurini</i>	<i>Glauconycteris</i>)	<i>Dasypterus</i>)	<i>Lasiurini</i>	<i>Pipistrellus</i>
	<i>Lasiurus</i>	<i>Cistugo</i>	<i>Barbastella</i>	<i>Lasiurus</i>	<i>Laephotis</i>
	<i>Dasypterus</i>	<i>Lasiurus</i>	<i>Plecotus</i>	(Including	<i>Glischropus</i>
		(Including	(Including	<i>Dasypterus</i>)	<i>Scotozous</i>
	Nyctophilinae	<i>Dasypterus</i>)	<i>Corynorhinus</i>	<i>Dasypterus</i>)	<i>Scoteanax</i>
	<i>Nyctophilus</i>	<i>Barbastella</i>	<i>Idionycteris</i>)	<i>Plecotini</i>	<i>Scotorepens</i>
	<i>Pharotis</i>	<i>Plecotus</i>	<i>Euderma</i>	<i>Barbastella</i>	<i>Nycticeinops</i>
	<i>Antrozous</i>	(Including	<i>Antrozous</i>	<i>Plecotus</i>	
		<i>Corynorhinus</i>)	<i>Nyctophilus</i>	(Including	<i>Scotoecus</i>
		<i>Idionycteris</i>	(Including	<i>Corynorhinus</i>	<i>Nyctalus</i>
		<i>Euderma</i>	<i>Pharotis</i>)	<i>Idionycteris</i>)	<i>Philetor</i>
	Nyctophilinae			<i>Euderma</i>	<i>Hesperoptenus</i>
	<i>Antrozous</i>			<i>Antrozoini</i>	<i>Chalinolobus</i>
	<i>Nyctophilus</i>			<i>Bauerus</i>	
				<i>Antrozous</i>	
					Nyctophilinae
					<i>Nyctophilus</i>
					(Including
					<i>Lamingtona</i>)
					<i>Pharotis</i>

Table 2 Usual incisor and premolar dental formulae in the Vespertilioninae and Nyctophilinae. Total number of teeth (including four canines and twelve molars) in parentheses. Dental notation of Miller (1907).

$i_{\overline{1}} \frac{2}{2} \frac{3}{3}$, pm = $\frac{2}{2} \frac{3}{3} \frac{4}{4}$	(38)	<i>Myotis</i> , <i>Pizonyx</i>
$i_{\overline{1}} \frac{2}{2} \frac{3}{3}$, pm = $\frac{2}{2} \frac{3}{3} \frac{4}{4}$	(36)	<i>Lasionycteris</i> , <i>Plecotus</i> , <i>Idionycteris</i> , <i>Eudiscopus</i>
$i_{\overline{1}} \frac{2}{2} \frac{3}{3}$, pm = $\frac{2}{2} \frac{3}{3} \frac{4}{4}$	(34)	<i>Euderma</i> , <i>Barbastella</i> , <i>Ia</i> , <i>Pipistrellus</i> , <i>Glischropus</i> , <i>Scotozous</i> , <i>Nyctalus</i> , <i>Chalinolobus</i>
$i_{\overline{1}} \frac{2}{2} \frac{3}{3}$, pm = $\frac{2}{2} \frac{4}{4}$	(32)	<i>Eptesicus</i> , <i>Vespertilio</i> , <i>Histiotus</i> , <i>Tylonycteris</i> , <i>Mimetillus</i> , <i>Glauconycteris</i> , <i>Pipistrellus</i> , <i>Laephotis</i> , <i>Philetor</i> , <i>Hesperoptenus</i>
$i_{\overline{1}} \frac{2}{2} \frac{3}{3}$, pm = $\frac{2}{2} \frac{4}{4}$	(32)	<i>Lasiurus</i>
$i_{\overline{1}} \frac{2}{2} \frac{3}{3}$, pm = $\frac{2}{2} \frac{4}{4}$	(30)	<i>Rhogeessa</i> , <i>Baeodon</i> , <i>Nycticeius</i> , <i>Otonycteris</i> , <i>Dasypterus</i> , <i>Scotomanes</i> , <i>Scotophilus</i> , <i>Scoteanax</i> , <i>Scotorepens</i> , <i>Nycticeinops</i> , <i>Scotoecus</i> , <i>Nyctophilus</i> , <i>Pharotis</i>
$i_{\overline{1}} \frac{2}{2}$, pm = $\frac{2}{2} \frac{4}{4}$	(28)	<i>Antrozous</i> , <i>Bauerus</i>

Table 3 Classifications of the Vespertilioninae and Nyctophilinae. That of Tate (1942a) is concerned primarily with Oriental and Australasian taxa, those of Koopman with Australasian (1973) and predominantly African (1975) forms.

Tate (1942a)	Koopman (1973, 1975)	Hill & Harrison
<i>Pipistrellus</i>	<i>Pipistrellus</i>	<i>Pipistrellus</i>
<i>abramus</i> group	Amalgamates <i>pipistrellus</i> , <i>abramus</i>	<i>Pipistrellus</i> (<i>Pipistrellus</i>)
<i>abramus</i>	(= <i>javanicus</i>), <i>coromandra</i> and	<i>pipistrellus</i> group
<i>akomomuli</i>	<i>tenuis</i> groups of Tate (1942a)	<i>pipistrellus</i> subgroup
<i>bancanus</i>	<i>pipistrellus</i> group	<i>pipistrellus</i> (Including <i>aladdin</i> ,
<i>camortae</i>	<i>imbricatus</i>	<i>bactrianus</i> , <i>lacteus</i> ,
<i>irretitus</i>	<i>javanicus</i> (Including	<i>mediterraneus</i>)
<i>paterculus</i>	<i>abramus</i>)	<i>nathusii</i>
<i>pumiloides</i>	<i>meyeni</i>	<i>permixtus</i>
<i>pipistrellus</i> group	<i>nanus</i> (Including	<i>javanicus</i> subgroup
<i>pipistrellus</i> (Including	(?) <i>helios</i>)	<i>abramus</i> (Including
<i>bactrianus</i>)	<i>permixtus</i>	<i>akomomuli</i> , <i>irretitus</i> ,
<i>nathusii</i>	<i>tenuis</i> (Including <i>angulatus</i> ,	<i>pumiloides</i>)
<i>coromandra</i> group	<i>collinus</i> , <i>nitidus</i> , <i>papuanus</i> ,	<i>babu</i>
<i>aladdin</i>	<i>ponceleti</i> , <i>murrayi</i> , <i>sewelanus</i> ,	<i>endoi</i>
<i>angulatus</i>	<i>subulidens</i> , <i>westralis</i> [Koopman,	<i>javanicus</i> (Including <i>bancanus</i> ,
<i>collinus</i>	1984c)]	<i>camortae</i> , <i>meyeni</i> ,
<i>coromandra</i>		' <i>tralatitius</i> ')
<i>imbricatus</i>		<i>paterculus</i>
<i>meyeni</i>		<i>peguensis</i>
<i>micropus</i>		<i>coromandra</i> subgroup
<i>murrayi</i>		<i>adamsi</i>
<i>ponceleti</i>		<i>angulatus</i> (Including <i>ponceleti</i>)
<i>portensis</i>		<i>collinus</i>
<i>regulus</i>		<i>coromandra</i> (Including <i>afghanus</i> ,
<i>sturdeeii</i>		<i>portensis</i> , <i>tramatus</i>)
<i>subulidens</i>		<i>mimus</i> (Including
<i>tramatus</i>		<i>glaucillus</i> , <i>principulus</i>)
<i>tenuis</i> group		<i>murrayi</i>
<i>mimus</i> (Including		<i>papuanus</i>
<i>glaucillus</i>)		<i>sturdeeii</i>
<i>nitidus</i>		<i>tenuis</i> (Including <i>nitidus</i> ,
<i>papuanus</i> (Including		<i>sewelanus</i> , <i>subulidens</i>)
<i>orientalis</i>)		<i>wattsi</i>
<i>principulus</i>		<i>westralis</i>
<i>tenuis</i>		<i>ceylonicus</i> subgroup
<i>ceylonicus</i> group	<i>ceylonicus</i> group	<i>ceylonicus</i> (Including <i>borneanus</i> ,
<i>ceylonicus</i> (Including	<i>ceylonicus</i>	<i>chrysothrix</i> , <i>indicus</i> , <i>raptor</i> ,
<i>chrysothrix</i> , <i>indicus</i> ,		<i>shanorum</i> , <i>subcanus</i>)
<i>subcanus</i>)		(?) <i>minahassae</i>

Table 3—cont.

Tate (1942a)	Koopman (1973, 1975)	Hill & Harrison
<i>minahassae</i> group <i>minahassae</i> <i>rueppellii</i> group <i>coxi</i>	<i>minahassae</i> group <i>minahassae</i> <i>rueppellii</i> group <i>rueppellii</i> (Including (?)) <i>fuscipes</i> ; <i>pulcher</i>)	<i>rueppellii</i> group <i>crassulus</i> <i>nanulus</i> <i>rueppellii</i> (Including <i>coxi</i> , <i>fuscipes</i> , <i>leucomelas</i> , <i>pulcher</i> , <i>senegalensis</i> , <i>vernayi</i>)
<i>kuhlii</i> group <i>babu</i> <i>canus</i> <i>kuhlii</i> (Including <i>ikhwanius</i> , <i>lepidus</i>) <i>leucotis</i> <i>lobatus</i>	<i>kuhlii</i> group <i>aero</i> <i>anchietae</i> <i>deserti</i> <i>inexpectatus</i> <i>kuhlii</i> (Including (?)) <i>aegyptius</i> ; <i>fuscatus</i>) <i>rusticus</i> (Including <i>marrensis</i>)	<i>kuhlii</i> group <i>aero</i> <i>deserti</i> <i>inexpectatus</i> <i>kuhlii</i> (Including (?)) <i>aegyptius</i> ; <i>fuscatus</i> , <i>ikhwanius</i>) <i>maderensis</i> <i>rusticus</i> (Including <i>marrensis</i>)
<i>Eptesicus</i> <i>pumilus</i> group <i>pumilus</i> (Including <i>caurinus</i> , <i>darlingtoni</i> , <i>vulturmus</i>) <i>pygmaeus</i>		<i>Pipistrellus</i> (<i>Vespadelus</i>) <i>douglasorum</i> <i>pumilus</i> (Including <i>darlingtoni</i>) <i>regulus</i> <i>sagittula</i> <i>vulturmus</i>
<i>Pipistrellus</i> <i>savii</i> group <i>austenianus</i> <i>cadornae</i> <i>curtatus</i> <i>macrotis</i> <i>savii</i> <i>vordermanni</i>	<i>savii</i> group <i>ariel</i> <i>macrotis</i> <i>maderensis</i>	<i>Pipistrellus</i> (<i>Perimyotis</i>) <i>subflavus</i> <i>Pipistrellus</i> (<i>Hypsugo</i>) <i>savii</i> group <i>savii</i> subgroup <i>anchietae</i> (= 'bicolor'?) <i>ariel</i> <i>austenianus</i> <i>bodenheimeri</i> <i>savii</i> (Including <i>caucasicus</i> , <i>darwini</i> , <i>maurus</i>) <i>nanus</i> subgroup <i>arabicus</i> <i>helios</i> <i>musculus</i> <i>nanus</i> (Including <i>culex</i> , <i>stampflii</i>) <i>pulveratus</i> subgroup <i>pulveratus</i> <i>hesperus</i> subgroup <i>hesperus</i> <i>eisentrauti</i> subgroup <i>eisentrauti</i> <i>imbricatus</i> subgroup <i>curtatus</i> <i>imbricatus</i> <i>macrotis</i> <i>vordermanni</i> <i>lophurus</i> subgroup <i>cadornae</i> <i>kitcheneri</i> <i>lophurus</i>
<i>joffrei</i> group <i>anthonyi</i> <i>joffrei</i> <i>stenopterus</i>	<i>joffrei</i> group <i>stenopterus</i>	<i>stenopterus</i> group <i>anthonyi</i> <i>joffrei</i> <i>stenopterus</i>

Table 3—cont.

Tate (1942a)	Koopman (1973, 1975)	Hill & Harrison
<i>affinis</i> group <i>affinis</i> <i>kitcheneri</i> <i>lophurus</i> <i>petersi</i> <i>pulveratus</i> <i>tasmaniensis</i> group <i>tasmaniensis</i> (Including <i>krefftii</i>)	<i>affinis</i> group <i>kitcheneri</i> <i>petersi</i> <i>Eptesicus</i> <i>capensis</i> group <i>brunneus</i> <i>capensis</i> (= <i>notius</i>) (Including <i>garambae</i> , <i>grandidieri</i>) <i>guineensis</i> (Including (?) <i>rectitragus</i>) <i>melckorum</i> <i>somaticus</i> (Including <i>ugandae</i> , <i>vansoni</i> , <i>zuluensis</i>)	<i>Pipistrellus (Falsistrellus)</i> <i>affinis</i> group <i>affinis</i> (?) <i>mordax</i> <i>petersi</i> <i>tasmaniensis</i> group <i>mackenziei</i> <i>tasmaniensis</i> (Including <i>krefftii</i>) <i>Pipistrellus (Neoromicia)</i> <i>capensis</i> group <i>brunneus</i> <i>capensis</i> (Including <i>garambae</i> <i>grandidieri</i> , <i>notius</i> , <i>matroka</i>) <i>guineensis</i> (Including <i>rectitragus</i>) <i>melckorum</i> <i>somaticus</i> (Including <i>ugandae</i>) <i>zuluensis</i> (Including <i>vansoni</i>)
<i>circumdatatus</i> group <i>circumdatatus</i> <i>mordax</i>	<i>tenuipinnis</i> group <i>flavescens</i> (= <i>angolensis</i>) <i>rendalli</i> (Including <i>faradjius</i> , <i>phasma</i>) <i>tenuipinnis</i> (Including <i>ater</i>) <i>Pipistrellus</i> <i>circumdatatus</i> group <i>circumdatatus</i> <i>mordax</i>	<i>tenuipinnis</i> group <i>flavescens</i> (Including <i>angolensis</i>) <i>rendalli</i> (Including <i>faradjius</i> , <i>phasma</i>) <i>tenuipinnis</i> (Including <i>ater</i>) <i>Pipistrellus (Arielulus)</i> <i>circumdatatus</i> <i>cuprosus</i> <i>societatis</i>
<i>Eptesicus</i> <i>Eptesicus (Amblyotus)</i> <i>alashanicus</i> <i>bobrinskoi</i>	<i>Eptesicus</i>	<i>Eptesicus</i> <i>Eptesicus (Eptesicus)</i> <i>nilssonii</i> group <i>bobrinskoi</i> <i>gobiensis</i> (Including <i>centrasiaticus</i> , <i>kashgaricus</i>) <i>nilssonii</i> (Including <i>japonensis</i> , (?) <i>parvus</i> , <i>propinquus</i>) <i>nasutus</i> group <i>nasutus</i> (Including <i>batinensis</i> <i>matschiet</i> , <i>pellucens</i> , <i>walli</i>)
<i>matschiet</i> (Including <i>pellucens</i>) <i>nilssonii</i> (Including <i>caucasicus</i> , <i>centrasiaticus</i> , <i>gobiensis</i> , <i>kashgaricus</i> , <i>pallescens</i> , <i>tamerlani</i> , <i>velox</i>) <i>tauricus</i> <i>walli</i> [<i>alashanicus</i> , <i>caucasicus</i> , <i>pallescens</i> , <i>tamerlani</i> , <i>tauricus</i> , <i>velox</i> allocated to <i>Pipistrellus savii</i> by Kuzyakin, 1950]	<i>serotinus</i> group <i>bottae</i> (Including <i>innesi</i>) <i>hottentotus</i> (= <i>megalurus</i>) (Including <i>smithi</i>) <i>loveni</i> <i>platyops</i> <i>serotinus</i> (Including <i>isabellinus</i>)	<i>serotinus</i> group <i>serotinus</i> subgroup <i>bottae</i> (Including <i>anatolicus</i> , <i>hingstoni</i> , <i>innesi</i> , <i>ognevi</i> , <i>omanensis</i>) <i>brasilienis</i> (Including <i>andinus</i> , <i>argentinus</i> , <i>chiriquinus</i> , <i>melanopterus</i>) <i>diminutus</i> (Including <i>dorianus</i> , <i>fidelis</i>) <i>furinalis</i> (Including <i>inca</i> , <i>montosus</i>) <i>fuscus</i> (Including <i>hispaniolae</i> , <i>peninsulæ</i>) <i>guadeloupensis</i> <i>hottentotus</i> (= <i>megalurus</i>)
<i>Eptesicus (Rhyneptesicus)</i> <i>nasutus</i> group <i>nasutus</i> <i>Eptesicus (Eptesicus)</i> <i>fuscus</i> group <i>bottae</i> <i>hingstoni</i> <i>serotinus</i> (Including <i>andersoni</i> , <i>brachydigitus</i> , <i>mirza</i> , <i>pachyomus</i> , <i>pallens</i> , <i>shirazensis</i> , <i>sinensis</i>)		

Table 3—cont.

Tate (1942a)	Koopman (1973, 1975)	Hill & Harrison
<i>sodalis</i> (Including <i>ognevi</i>)		(Including <i>smithi</i>) <i>innoxius</i> (Including <i>punicus</i>) <i>loveni</i> <i>lynni</i> <i>serotimus</i> (Including <i>andersoni</i> , <i>brachydigitus</i> , <i>horikawai</i> , <i>intermedius</i> , <i>isabellinus</i> , <i>mirza</i> , <i>pachyomus</i> , <i>pallens</i> , <i>pashtomus</i> , <i>platyops</i> , <i>shirazensis</i> , <i>sinensis</i> , <i>sodalis</i> , <i>turcomanus</i>)
<i>demissus</i> group <i>demissus</i> <i>Eptesicus</i> (<i>Pareptesicus</i>) <i>pachyotis</i> group <i>pachyotis</i>		<i>tatei</i> <i>demissus</i> subgroup <i>demissus</i> (?) <i>pachyotis</i> subgroup <i>pachyotis</i>
	<i>floweri</i> group <i>floweri</i> (= <i>lowei</i>)	<i>Eptesicus</i> (<i>Rhinopterus</i>) <i>floweri</i> (Including <i>lowei</i>)

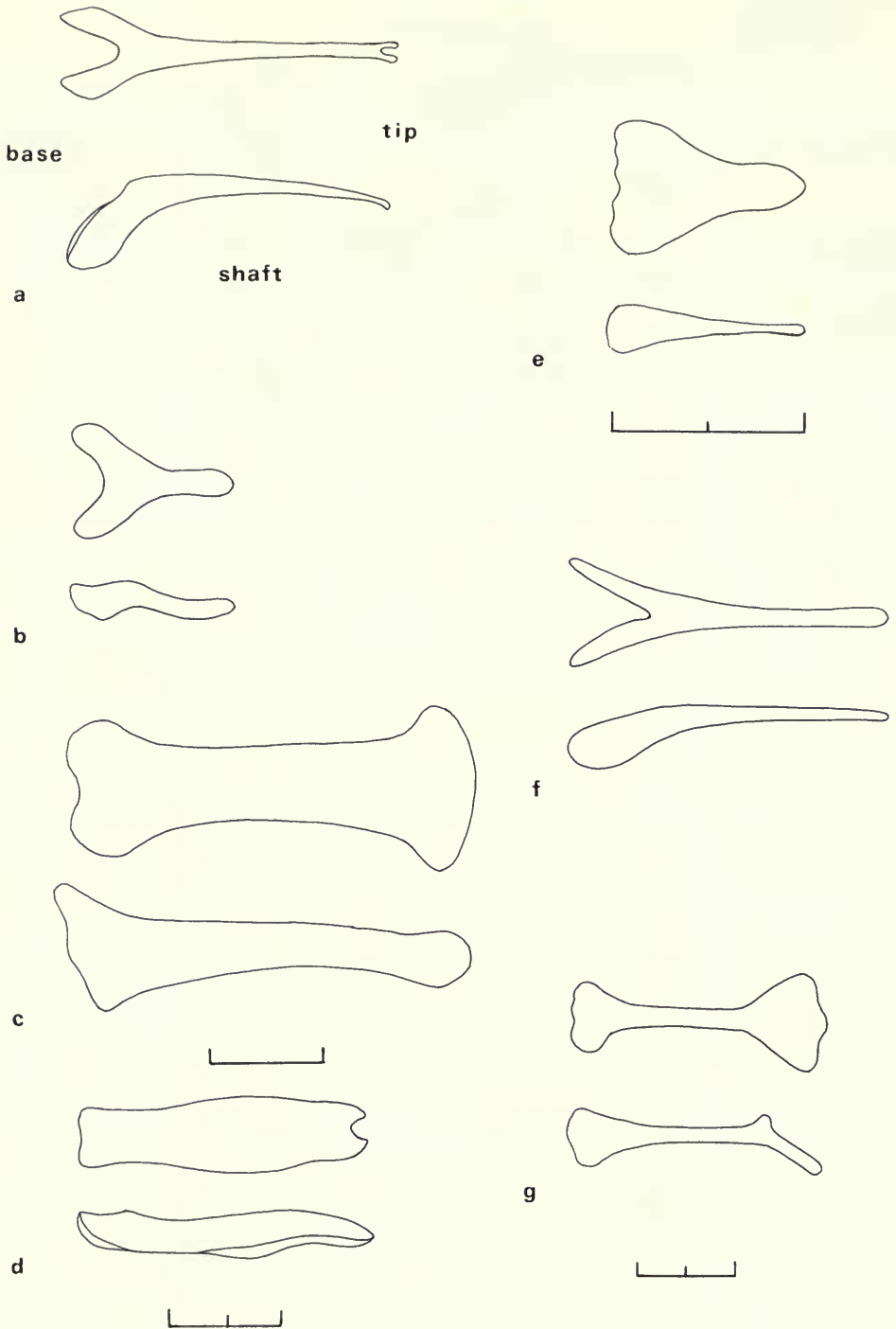


Fig. 1 Bacular types in *Pipistrellus* and *Eptesicus* (see text). Scale a-c=0.5 mm; d-g=1 mm.

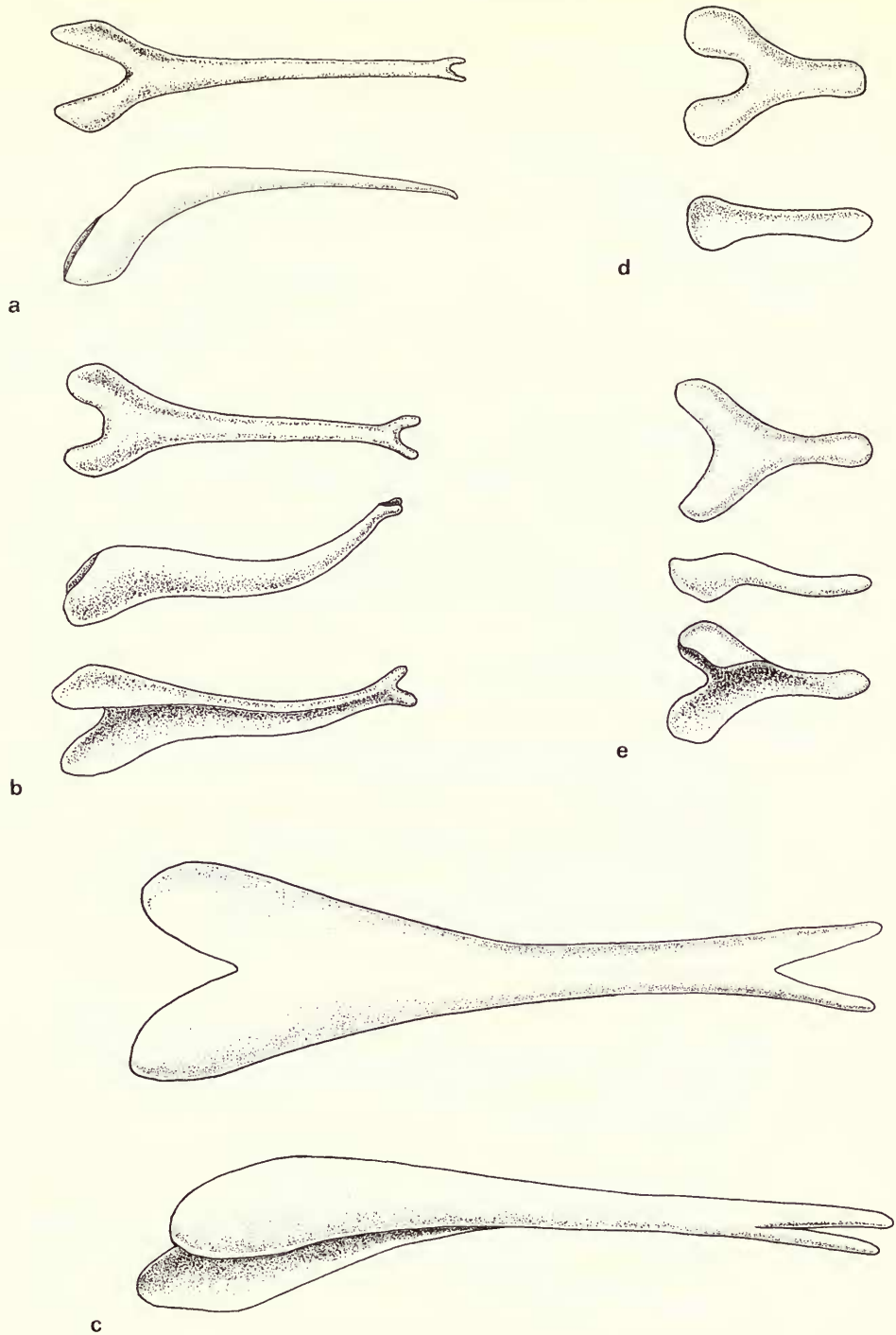


Fig. 2 Baculum of a, *Pipistrellus pipistrellus* (D, LL, reversed); b, *P. nathusii* (D, RL, RVL); c, *P. papuanus* (D, RL); d, *P. subflavus* (D, RL); e, *P. circumdatus* (D, LL, RVL). Scale = 0.5 mm.

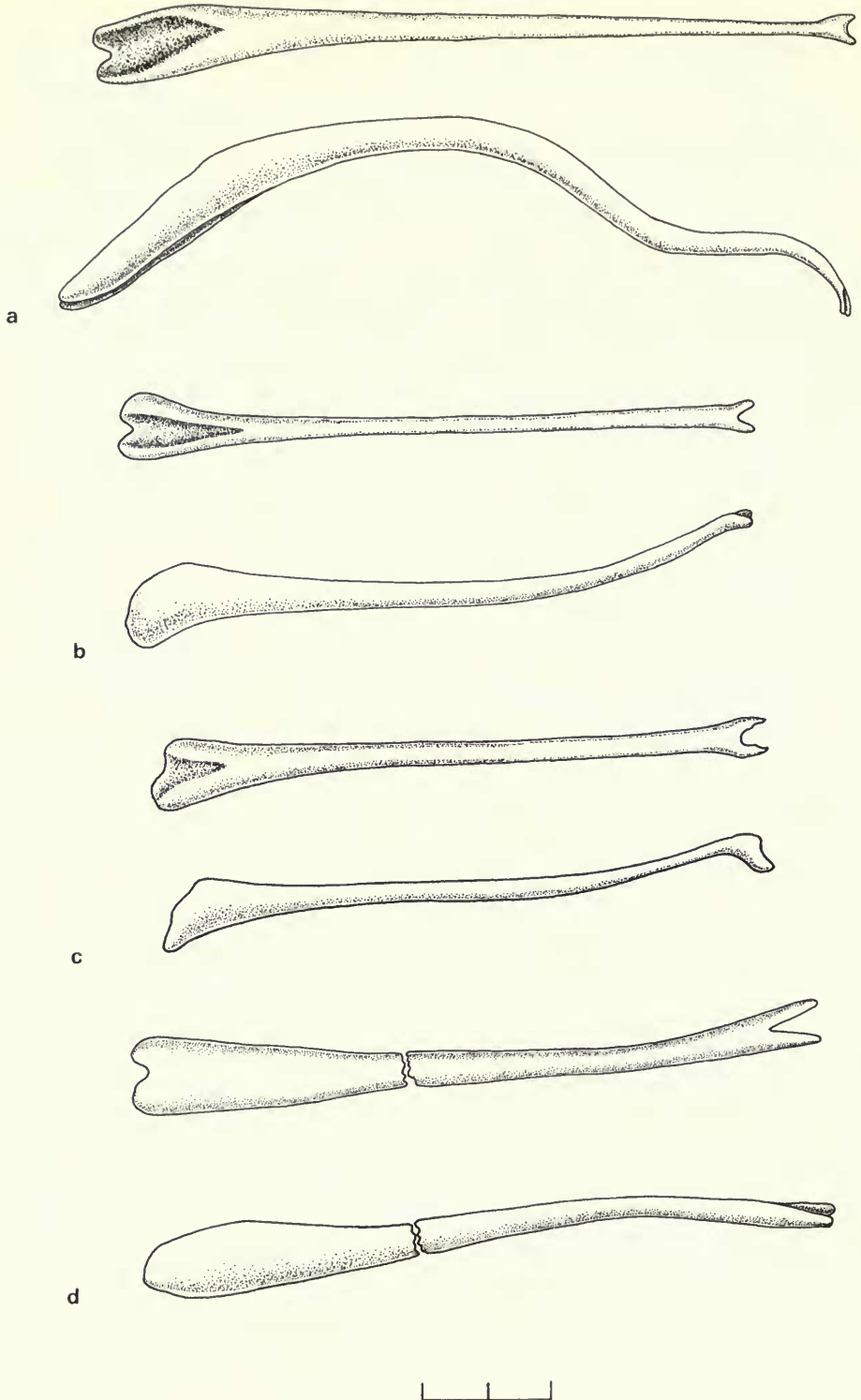


Fig. 3 Baculum (D, RL) of a, *Pipistrellus abramus*; b, *P. endoi*; c, *P. paterculus*; d, *P. ceylonicus* (*raptor*).
Scale = 2 mm.

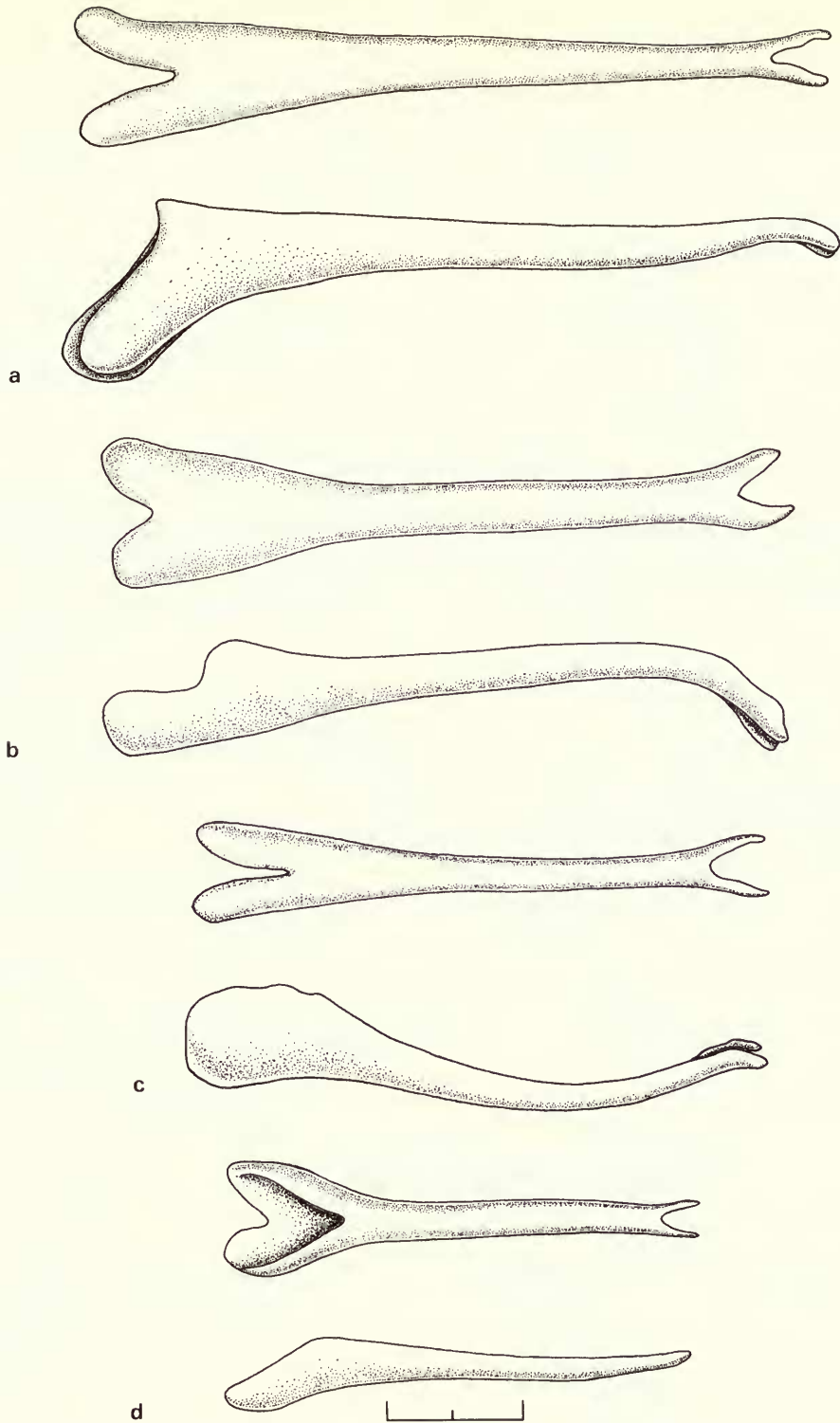


Fig. 4 Baculum (D, RL) of a, *Pipistrellus babu*; b, *P. collinus*; c, *P. murrayi*; d, *P. angulatus (ponceleti)*.
Scale = 1 mm.

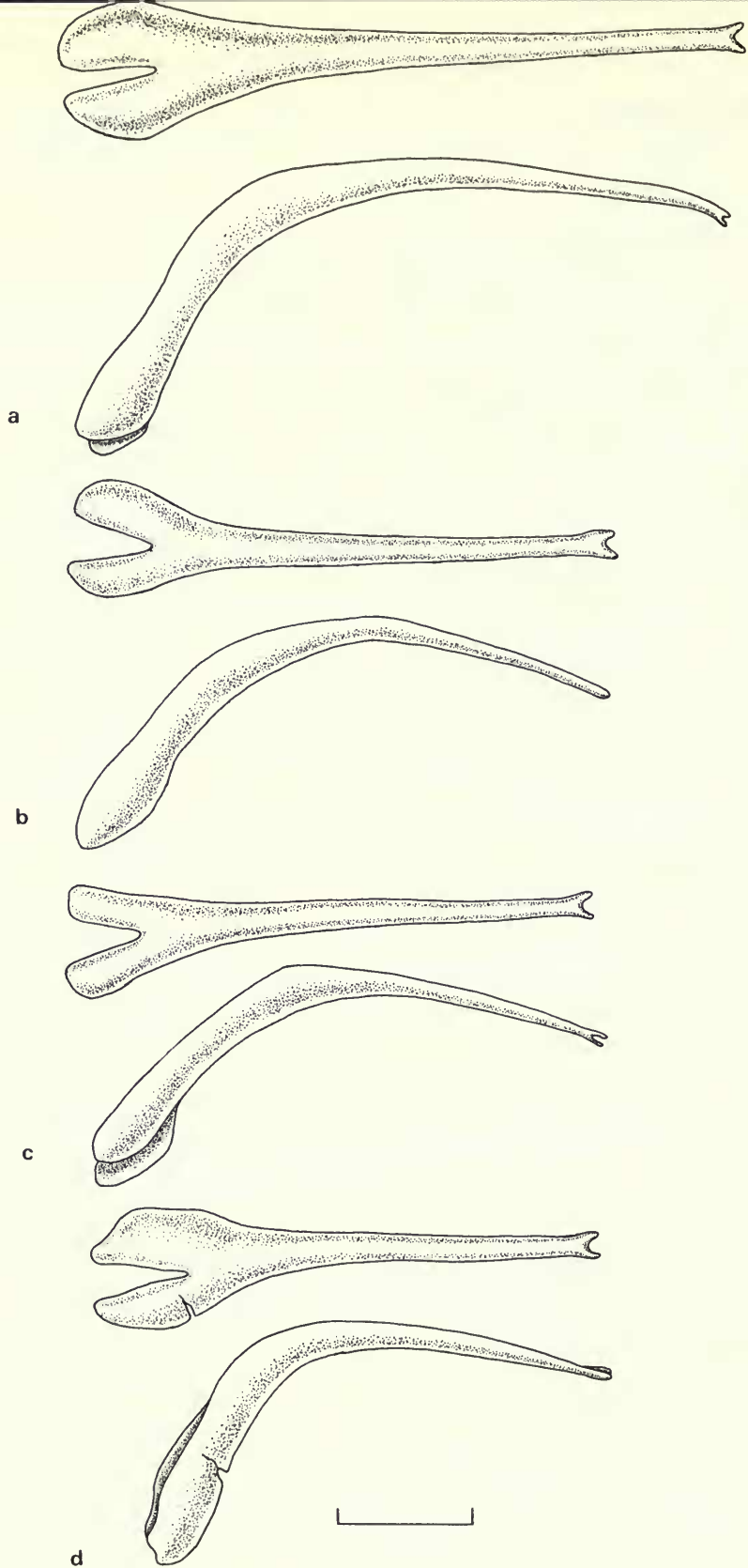


Fig. 5 Baculum (D, RL) of a, *Pipistrellus kuhlii*; b, *P. maderensis*; c, *P. deserti*; d, *P. rusticus*.
Scale = 0.5 mm.

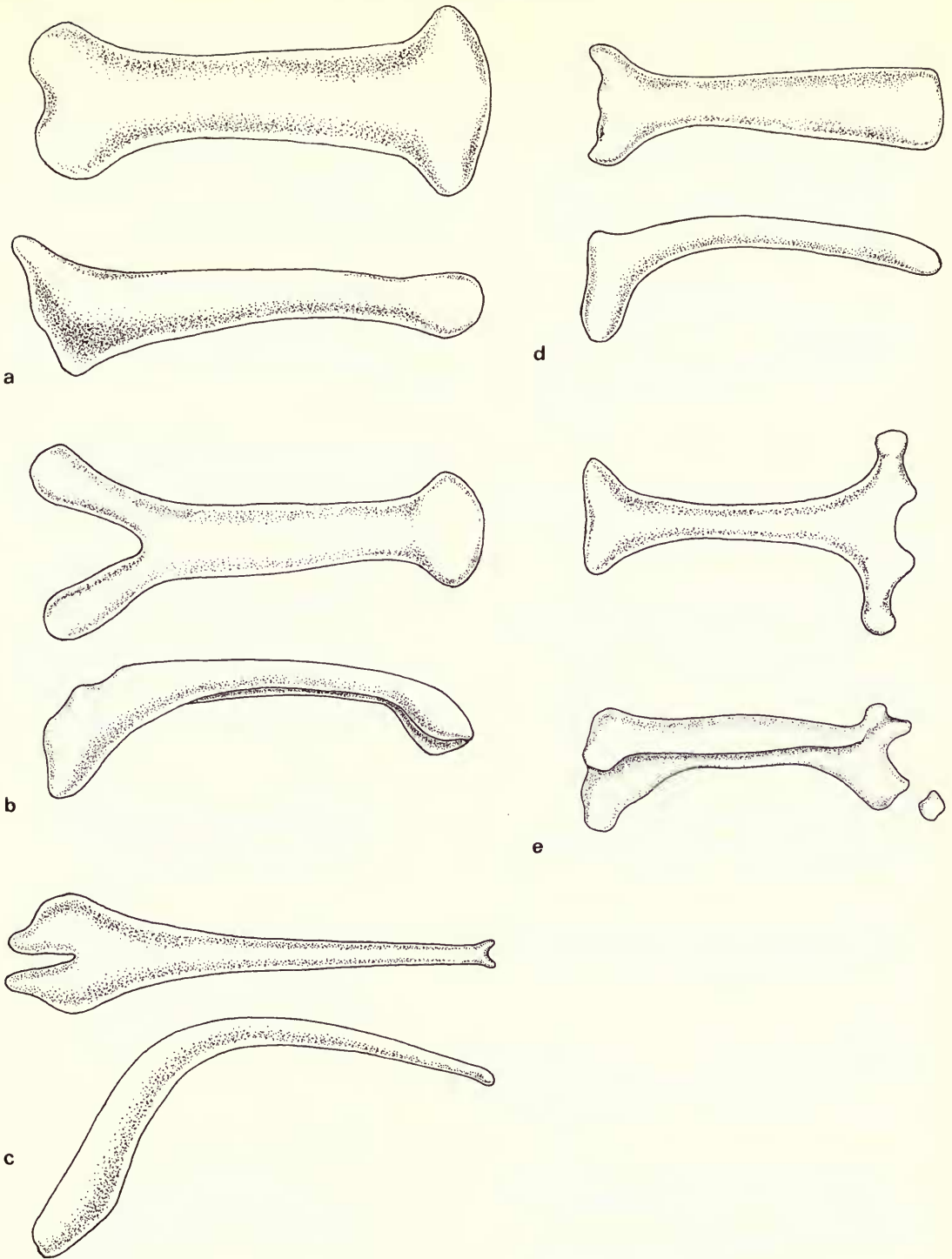


Fig. 6 Baculum of a, *Pipistrellus savii* (D, RL); b, *P. nanus* (D, RL); c, *P. rusticus* (D, RL); d, *P. helios* (D, RL); e, *P. anchietae* (D, LVL, reversed). Scale = 0.5 mm.

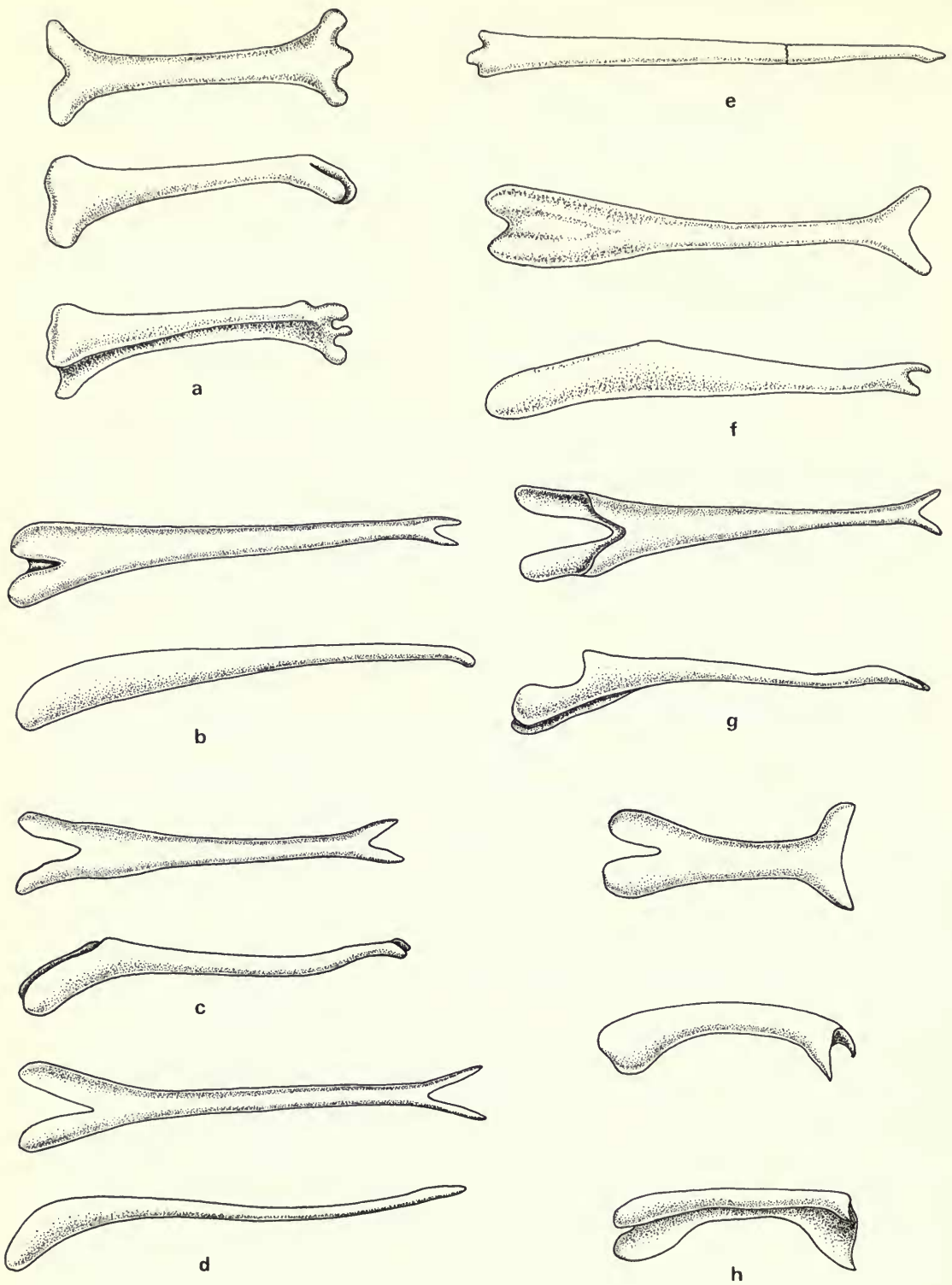


Fig. 7 Baculum of a, *Pipistrellus arabicus* (D, RL, RVL); b, *P. coromandra (tramatus)* (D, RL); c, *P. coromandra* (D, RL); d, *P. ceylonicus* (D, RL); e, *P. crassulus* (D); f, *P. nanulus* (D, RL); g, *P. mimus* (D, RL); h, *P. stenopterus* (D, RL, RVL). Scale = 1 mm.

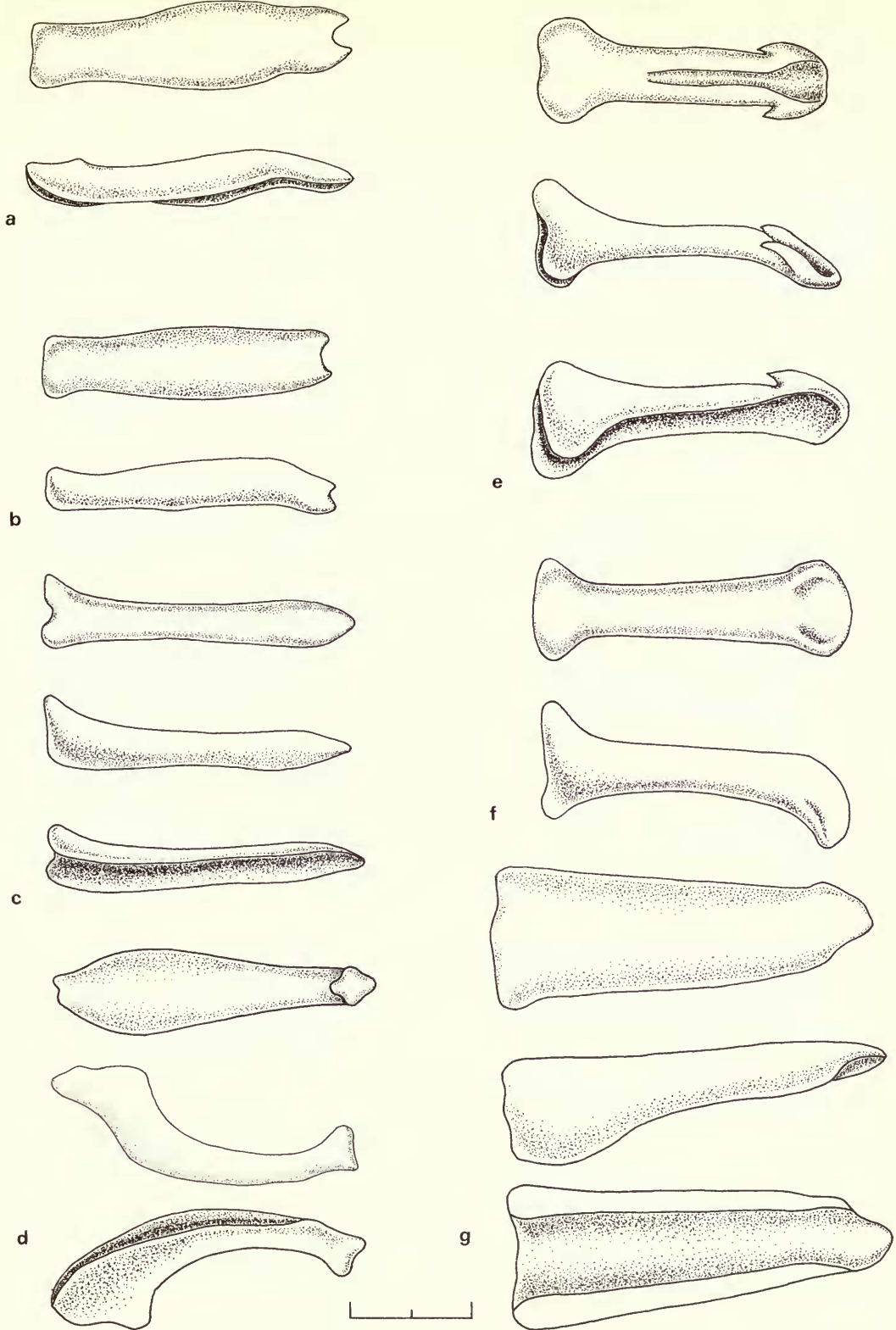


Fig. 8 Baculum of a, *Pipistrellus affinis* (D, RL); b, *P. petersi* (D, RL); c, *P. pulveratus* (D, RL, RVL); d, *P. hesperus* (D, LL, reversed, LVL); e, *P. kitcheneri* (D, RL, RVL); f, *P. lophurus* (D, RL); g, *P. tasmaniensis* (D, RL, V). Scale = 1 mm.

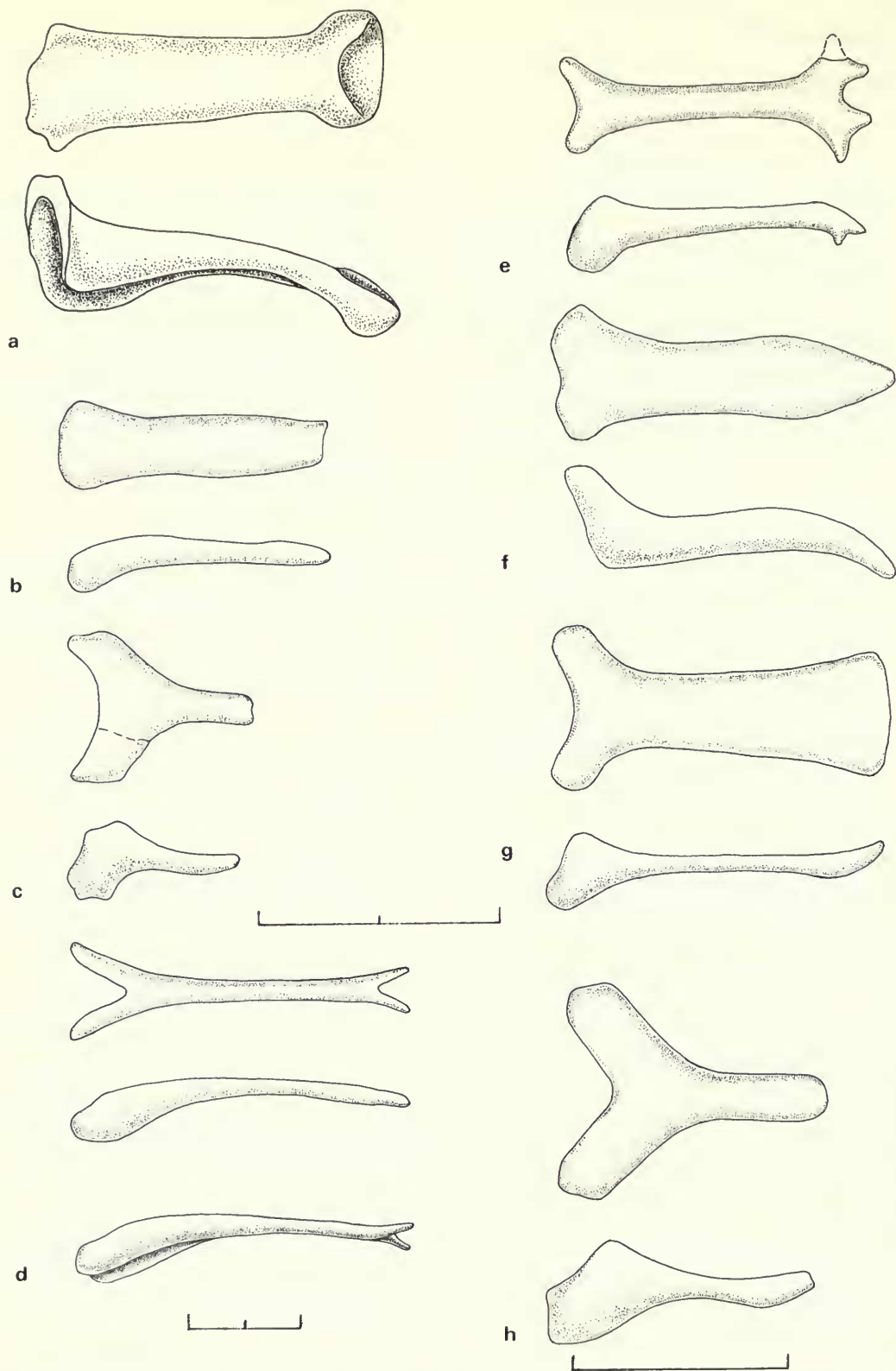


Fig. 9 Baculum (D, RL except where stated) of a, *Pipistrellus imbricatus*; b, *P. macrotis*; c, *P. societatis*, d, *P. tenuis* (*nitidus*) (D, RL, RVL); e, *P. anchietae* ('*Vesperus*' *bicolor*); f, *P. bodenheimeri*; g, *P. eisentrauti*; h, *P. cuprosus*. Scales a-g=1 mm; h=0.5 mm.

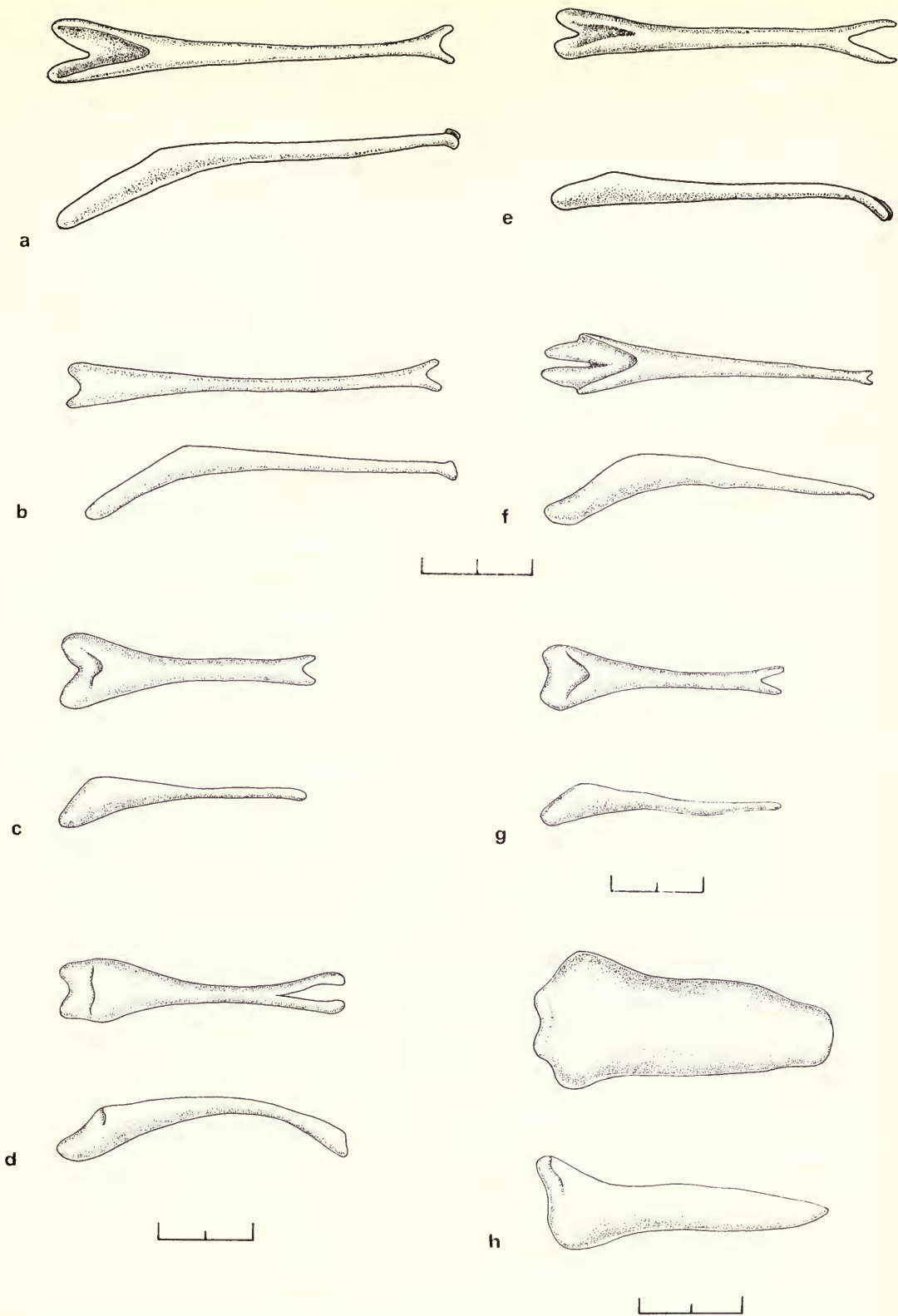


Fig. 10 Baculum (D, RL) of a, *Pipistrellus rueppellii* (*pulcher*); b, *P. rueppellii*; c, *P. adamsi*; d, *P. westralis*; e, *P. javanicus*; f, *Nyctalus noctula*; g, *P. wattsi*; h, *P. mackenziei* (c, d, g, h from Kitchener *et al.*, 1986). Scales = a, b, e, f = 2 mm; c, d, g, h = 1 mm.

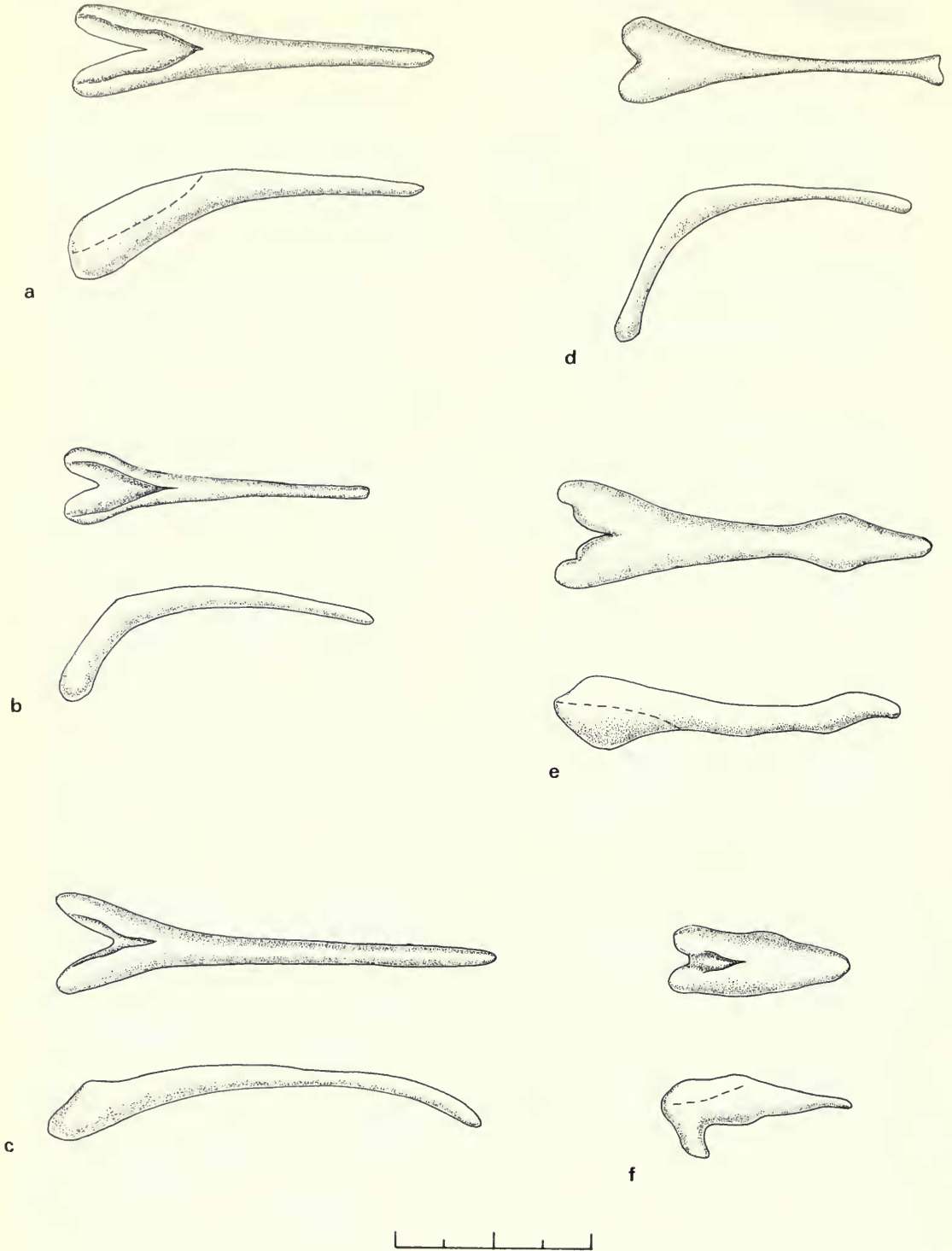


Fig. 11 Baculum (V, RL) of a, *Pipistrellus pumilus pumilus*; b, *P. pumilus (caurinus)*; c, *P. vulturinus*; d, *P. douglasorum*; e, *P. regulus*; f, *P. sagittula* (a-c, e, f from McKean *et al.*, 1970; d from Kitchener, 1976). Scale = 2 mm.

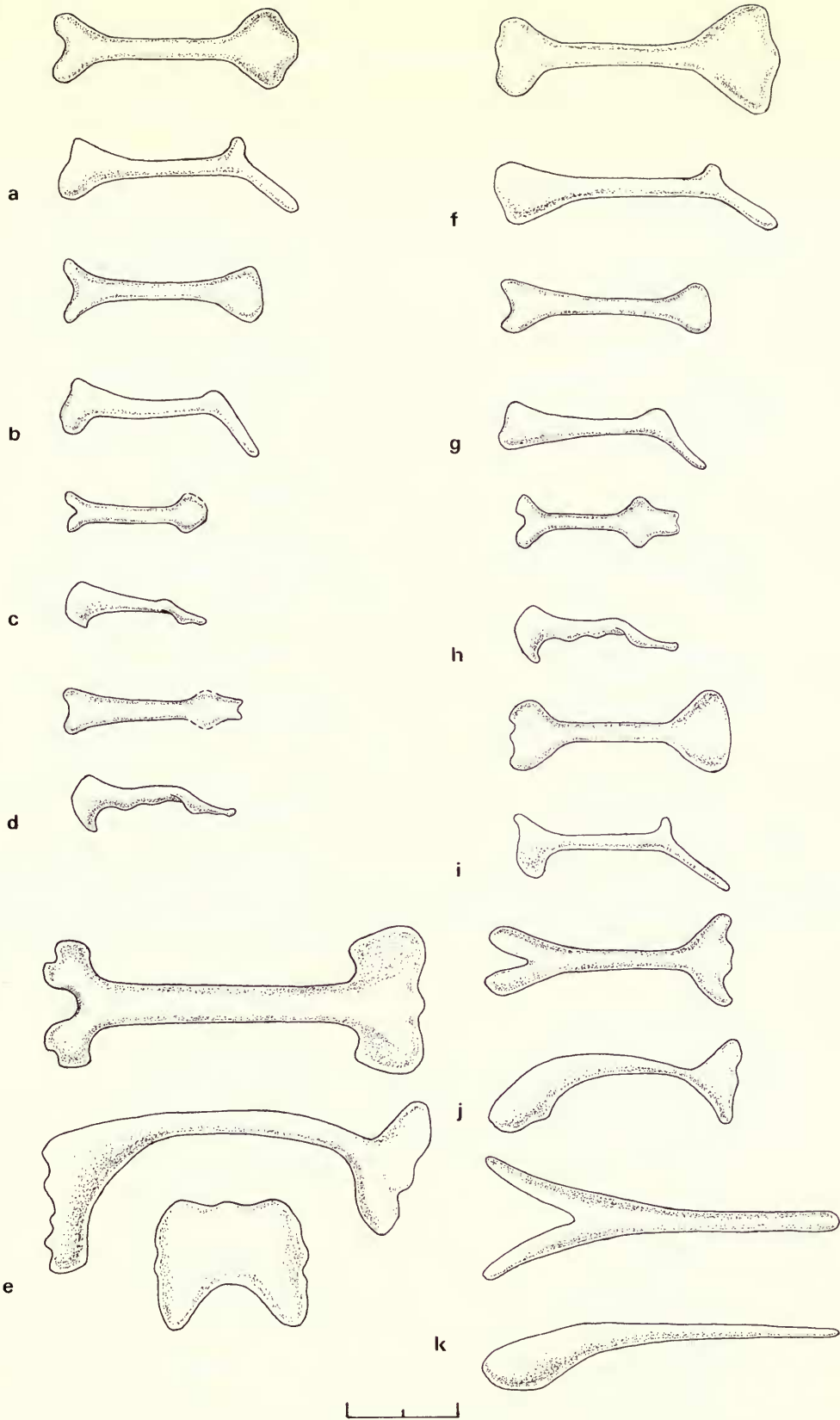


Fig. 12 Baculum (D, RL) of a, *Pipistrellus capensis (matroka)*; b, *P. capensis*; c, *P. guineensis*; d, *P. zuluensis*; e, *P. rendalli* (with anterior view); f, *P. melckorum*; g, *P. capensis*; h, *P. somalicus*; i, *P. capensis ('minutus')*; j, *P. tenuipinnis*; k, *P. pumilus*. Scale = 1 mm.

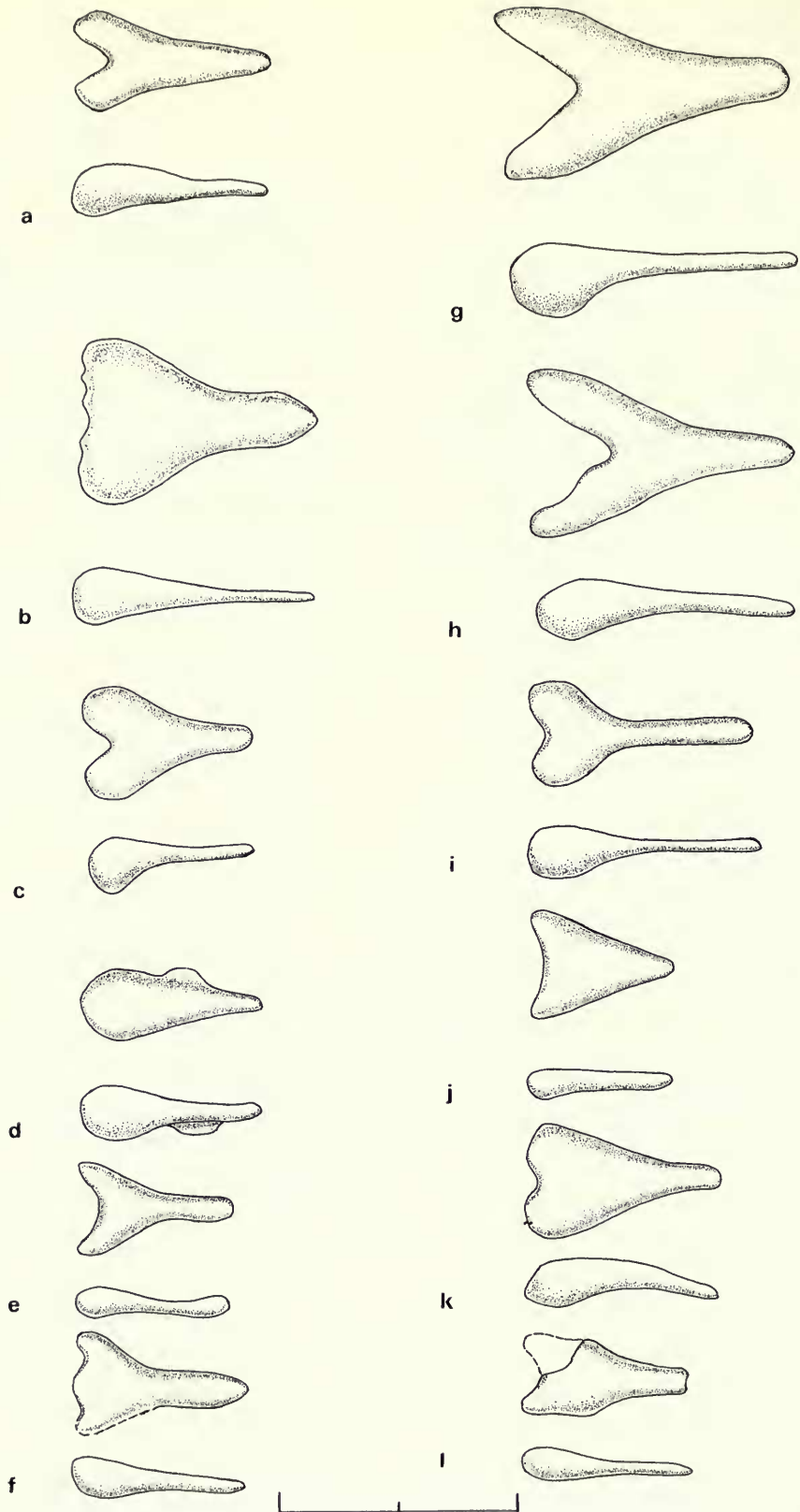


Fig. 13 Baculum (D, RL) of a, *Eptesicus fuscus*; b, *E. hottentotus (megalurus)*; c, *E. furinalis*; d, *E. brasiliensis (andinus)*; e, *E. bobrinskoi*; f, *E. floweri*; g, *E. serotinus*; h, *E. serotinus (isabellinus)*; i, *E. fuscus (hispaniolae)*; j, *E. bottae (innesi)*; k, *E. brasiliensis*; l, *E. floweri (lowei)*. Scale = 1 mm.

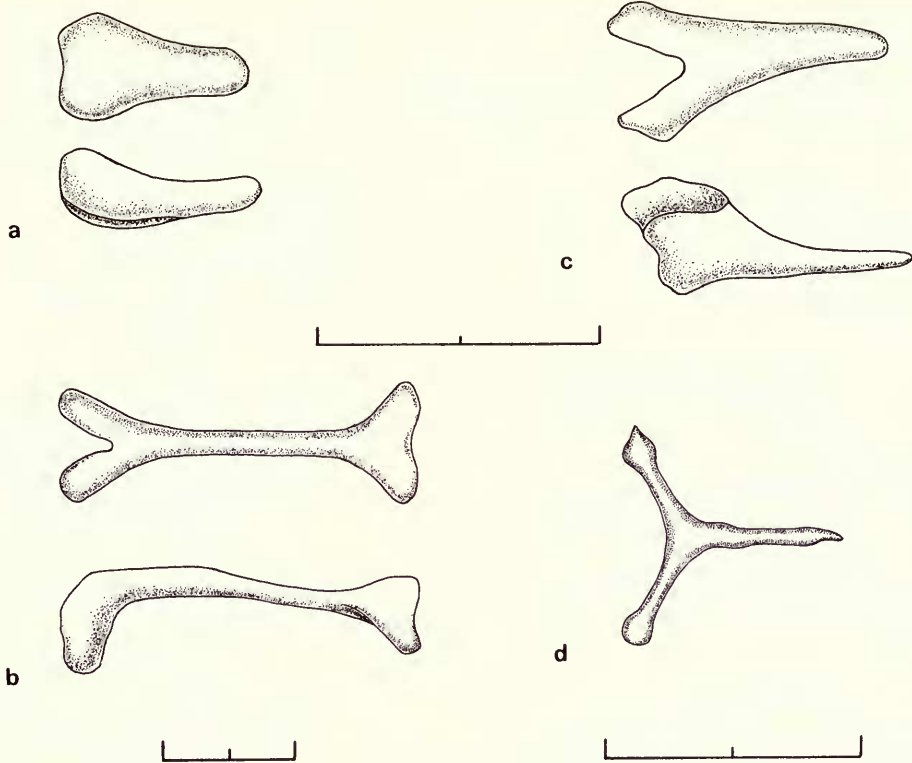


Fig. 14 Baculum (D, RL except where stated) of a, *Eptesicus bottae (omanensis)*; b, *Pipistrellus rendalli* (? *brunneus*); c, *Eptesicus nasutus*; d, *Plecotus teneriffae* (D) (from Ibanez & Fernandez, 1986). Scales = 1 mm.

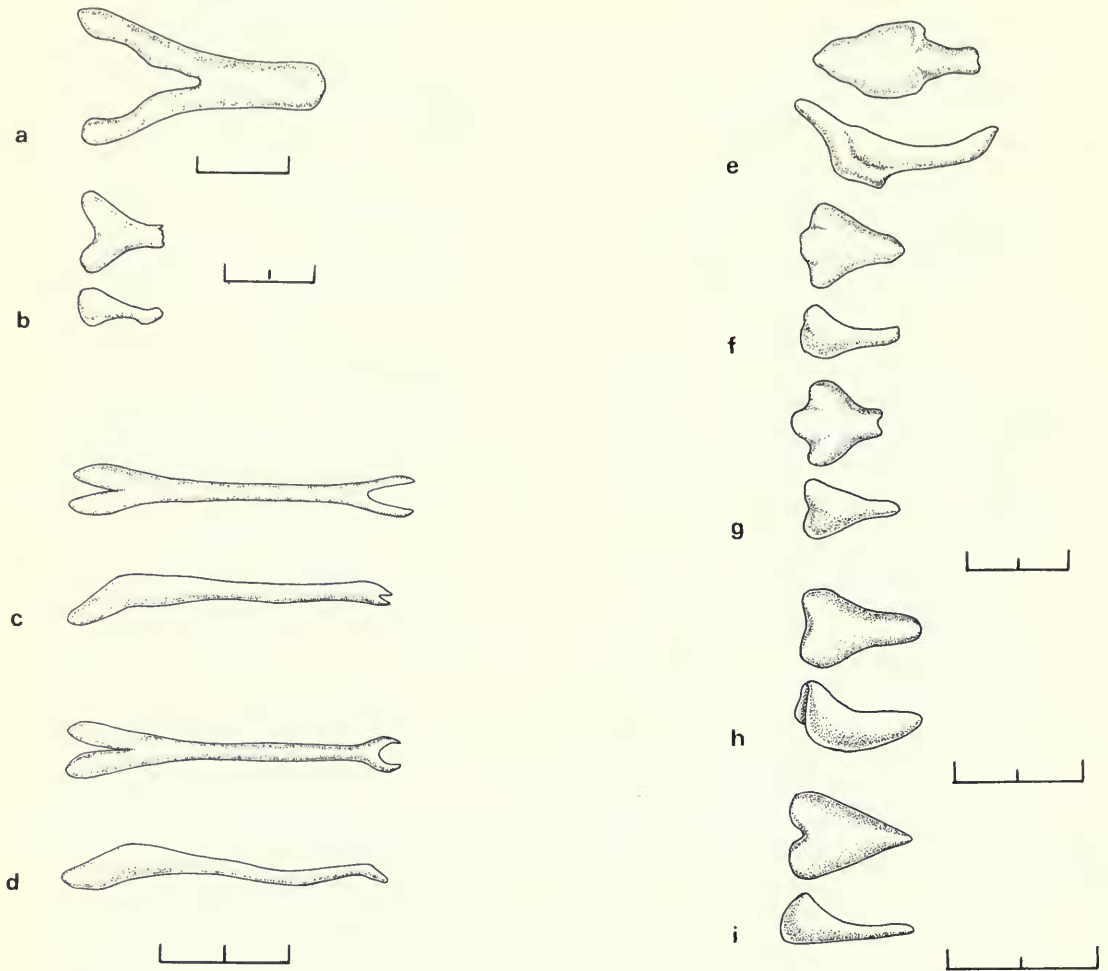


Fig. 15 Baculum (D, RL except where stated) of a, *Eptesicus nilssonii* (D) (from Topal, 1958); b, *Baeodon alleni* (from Brown *et al.*, 1971); c, *Pipistrellus peguensis* (from Sinha, 1969); d, *P. camortae*; e, *Idionycteris phyllotis*, f, *Plecotus townsendii* (*pallescens*), g, *P. rafinesquii* (e-g from Nader & Hoffmeister, 1983; h, *P. rafinesquii* (*macrotis*) (from Hamilton, 1949); i, *Bauerus dubiaquercus* (from Pine *et al.*, 1971). Scales a = 0.5 mm; b, e-i = 1 mm; c, d = 2 mm.

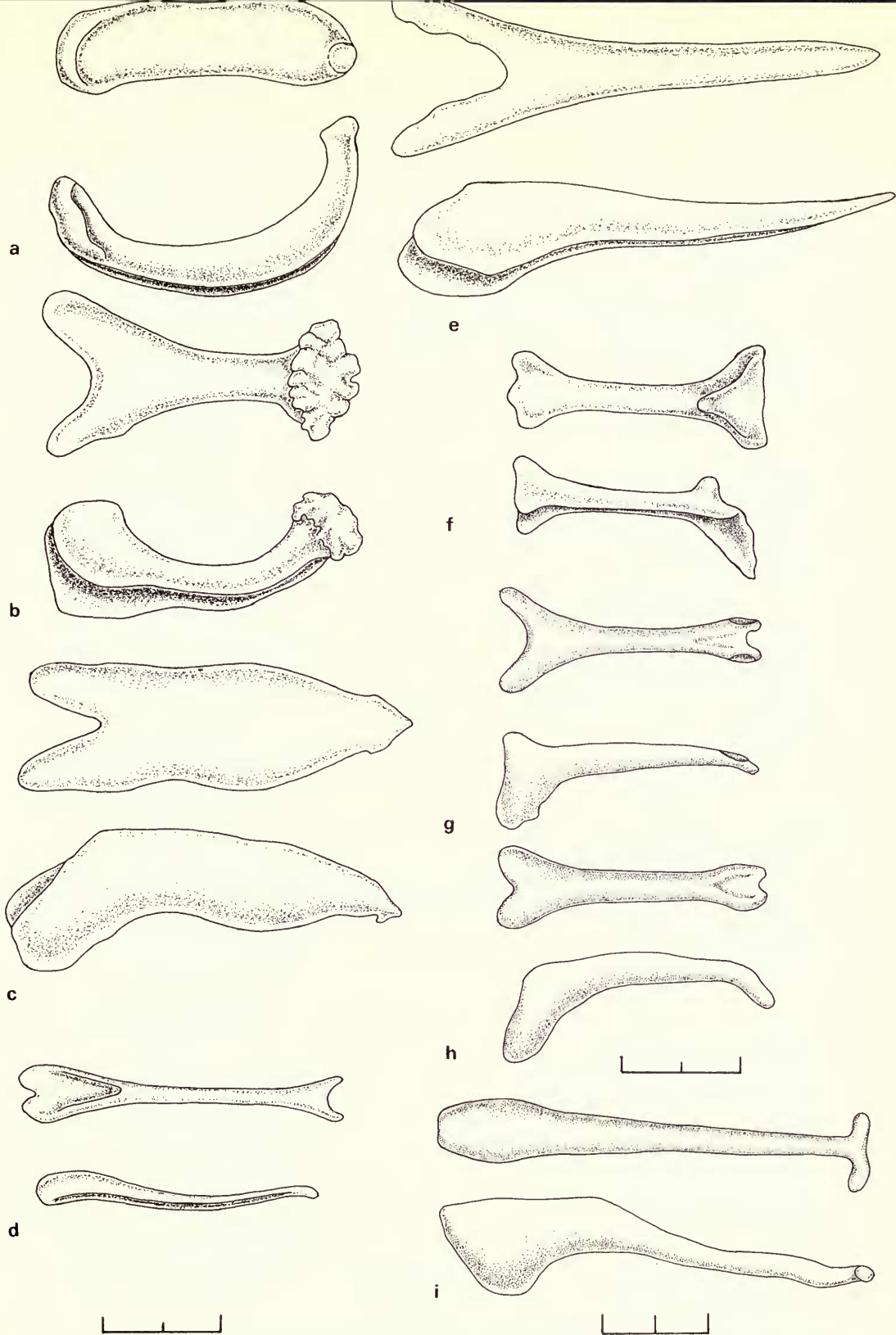


Fig. 16 Baculum (D, RL except where stated) of a, *Otonycteris hemprichii*; b, *Philetor brachypterus* (D, RVL); c, *Nyctophilus gouldi*; d, *Scotozous dormeri*; e, *Nycticeinops schlieffenii*; f, *Laephotis wintoni*; g, *Scotorepens balstoni*; h, *S. greyii*; i, *Scoteanax rueppellii*. Scales a–h = 1 mm; i = 2 mm.

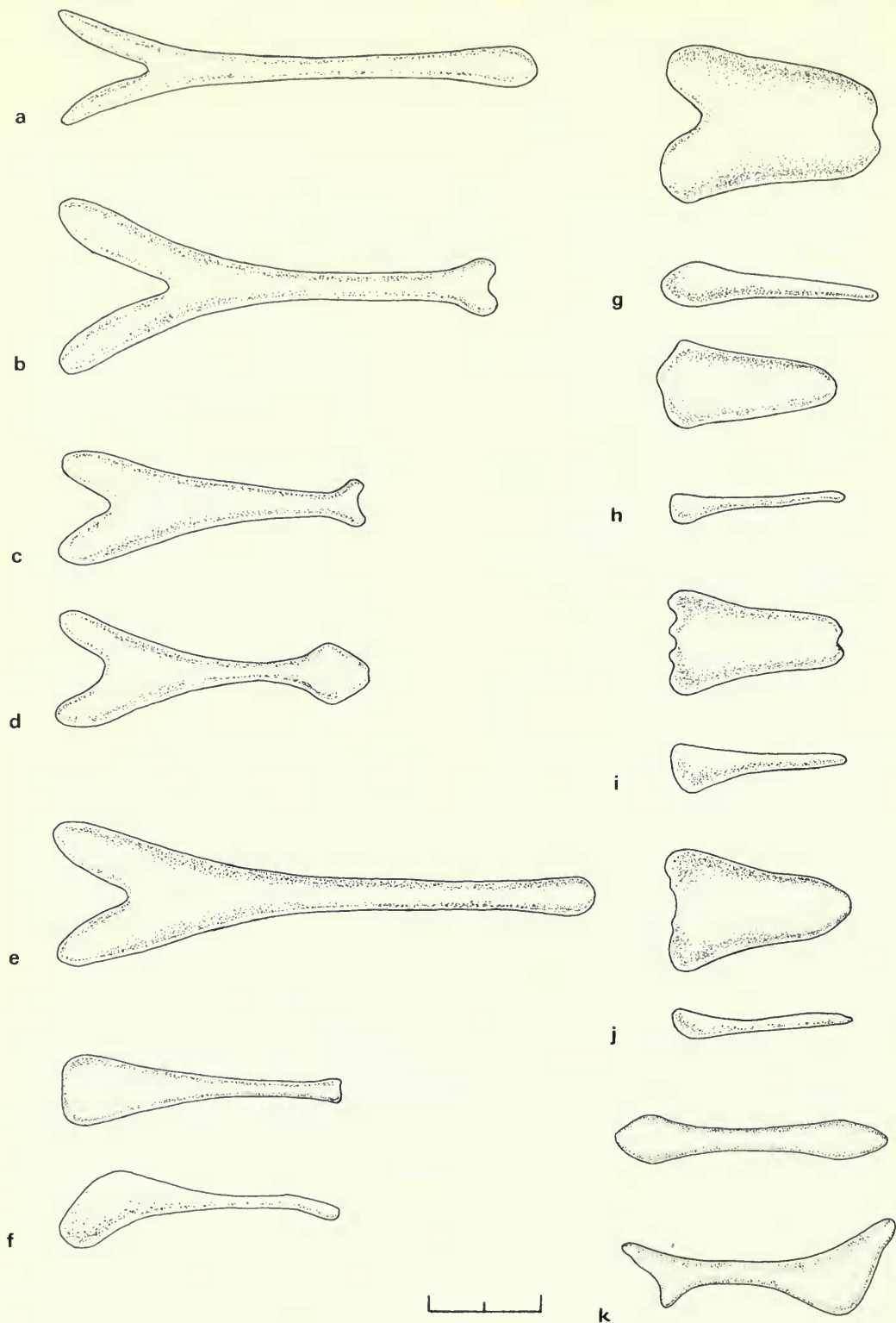


Fig. 17 Baculum of a, *Chalinolobus morio* (D); b, *C. gouldi* (D); c, *C. nigrogriseus (rogersi)* (D); d, *C. picatus* (D); e, *C. tuberculatus* (D); f, *Lasionycteris noctivagans* (D, RL); g, *Scotophilus nigrita (gigas)* (D, RL); h, *S. heathii* (D, RL); i, *S. kuhlii* (D, RL); j, *S. nigritellus* (D, RL); k, *Nycticeius humeralis* (D, LL, reversed). Scale = 1 mm.

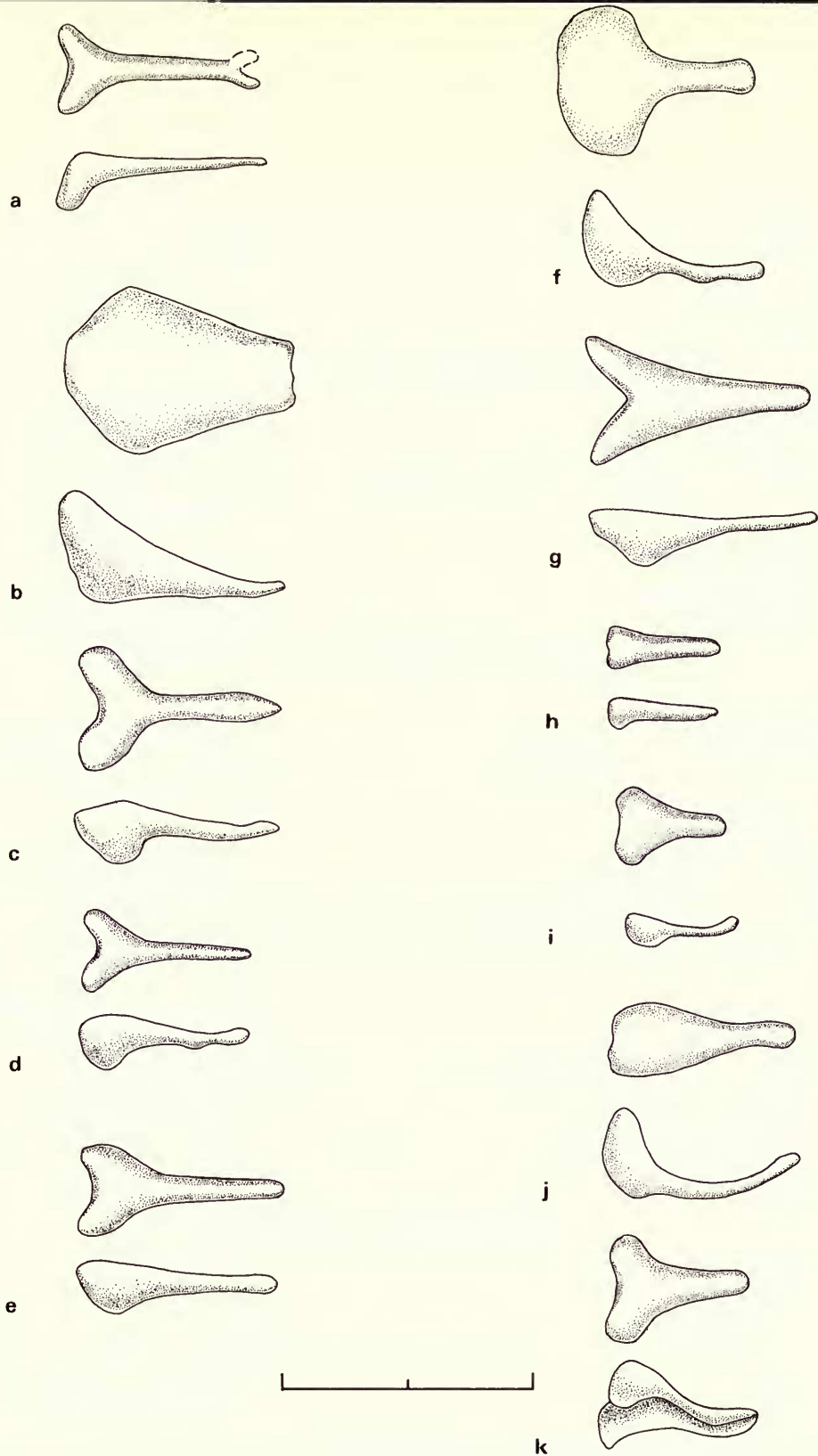


Fig. 18 Baculum (D, RL) of a, *Glischropus tylopus*; b, *Antrozous pallidus*; c, *Histiotus velatus*; d, *H. (?) macrotis*; e, *H. macrotis*; f, *Dasypterus argentinus*; g, *Scotomanes ornatus*; h, *Tyloncyteris pachypus*; i, *T. robustula*; j, *Barbastella barbastellus*; k, *Rhogeessa tumida*. Scale = 1 mm.

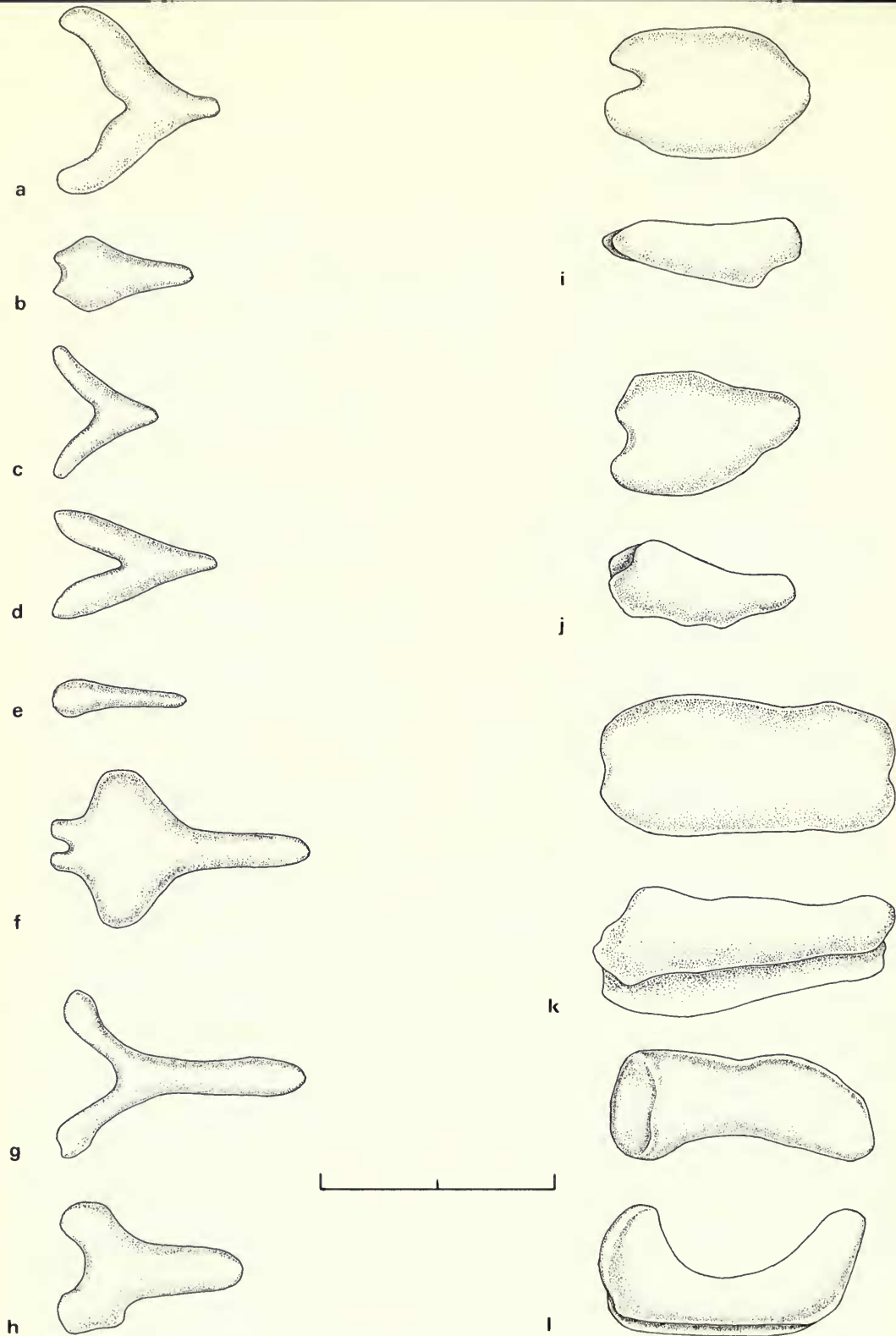


Fig. 19 Baculum of a, *Glauconycteris poensis* (D); b, *G. variegata* (D); c, *G. beatrix* (D); d, *G. argentata* (D); e, *G. humeralis* (D); f, *G. variegata (papilio)* (D); g, *Plecotus auritus* (D); h, *P. austriacus* (D); i, *Myotis ridleyi* (D, RL); j, *M. nattereri* (D, RL); k, *Pizonyx vivesi* (D, RVL); l, *Lasiurus cinereus* (D, RVL). Scale = 1 mm.

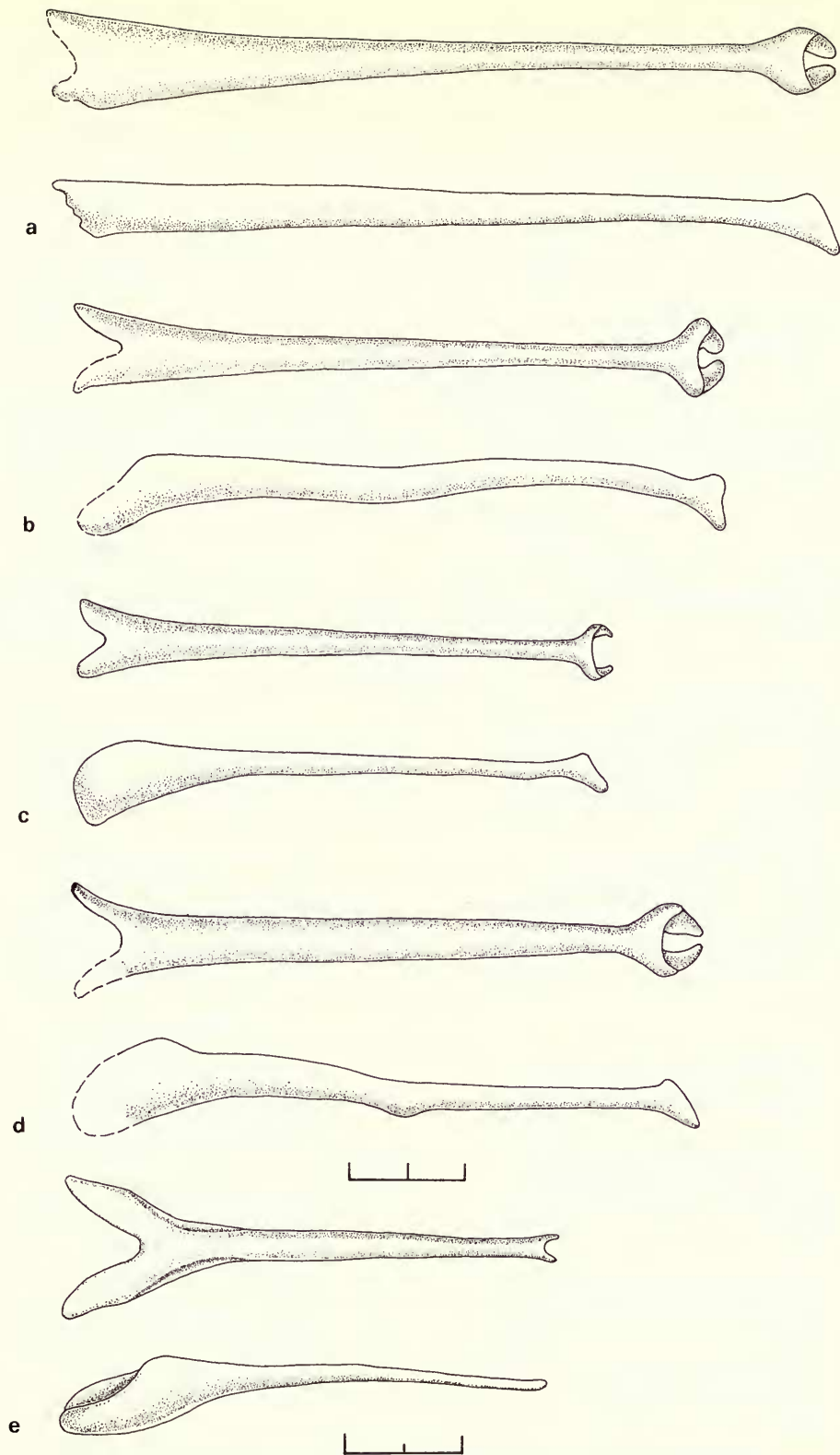


Fig. 20 Baculum (D, RL) of a, *Scotoecus albigula*; b, *S. hindei* (*falabae*) c, *S. hirundo*; d, *S. hindei*; e, *S. albofuscus*. Scales a-d = 2 mm; e = 1 mm.

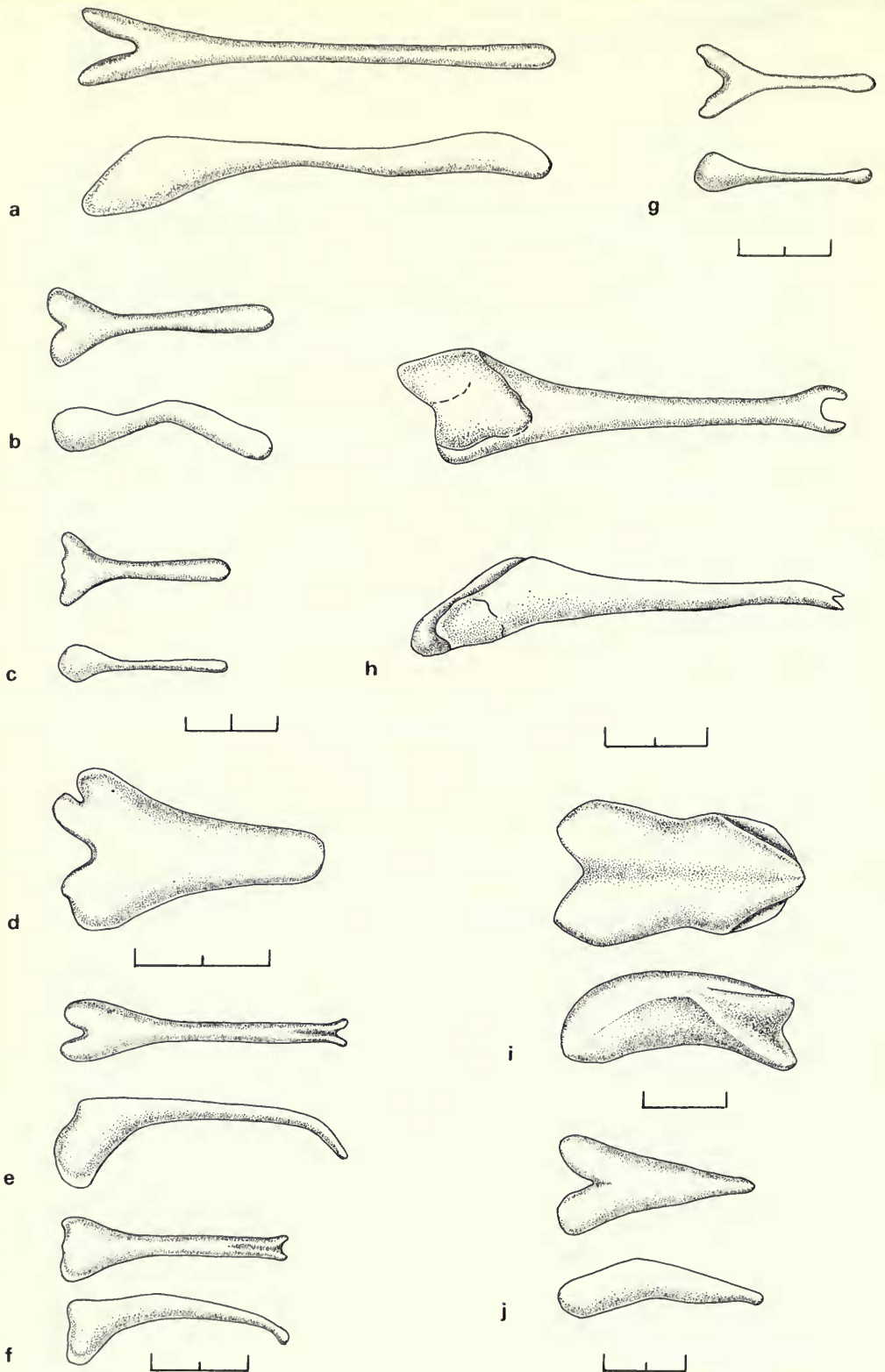


Fig. 21 Baculum (D, RL except where stated) of a, *Hesperoptenus tomesi*, b, *H. tickelli*, c, *H. doriae* (a-c from Hill, 1976); d, *Ia io* (D) (from Topal, 1970); e, *Scotorepens orion*, f, *S. sanborni* (e, f from Kitchener & Caputi, 1985); g, *Hesperoptenus blanfordi* (from Hill & Francis, 1984); h, *Scotoecus pallidus* (from Agrawal & Sinha, 1973); i, *Vespertilio murinus* (V, RL) (from Topal, 1958); j, *V. orientalis* (from Wallin, 1969). Scales a-c=2 mm; d-h, j=1 mm; i=0.5 mm.

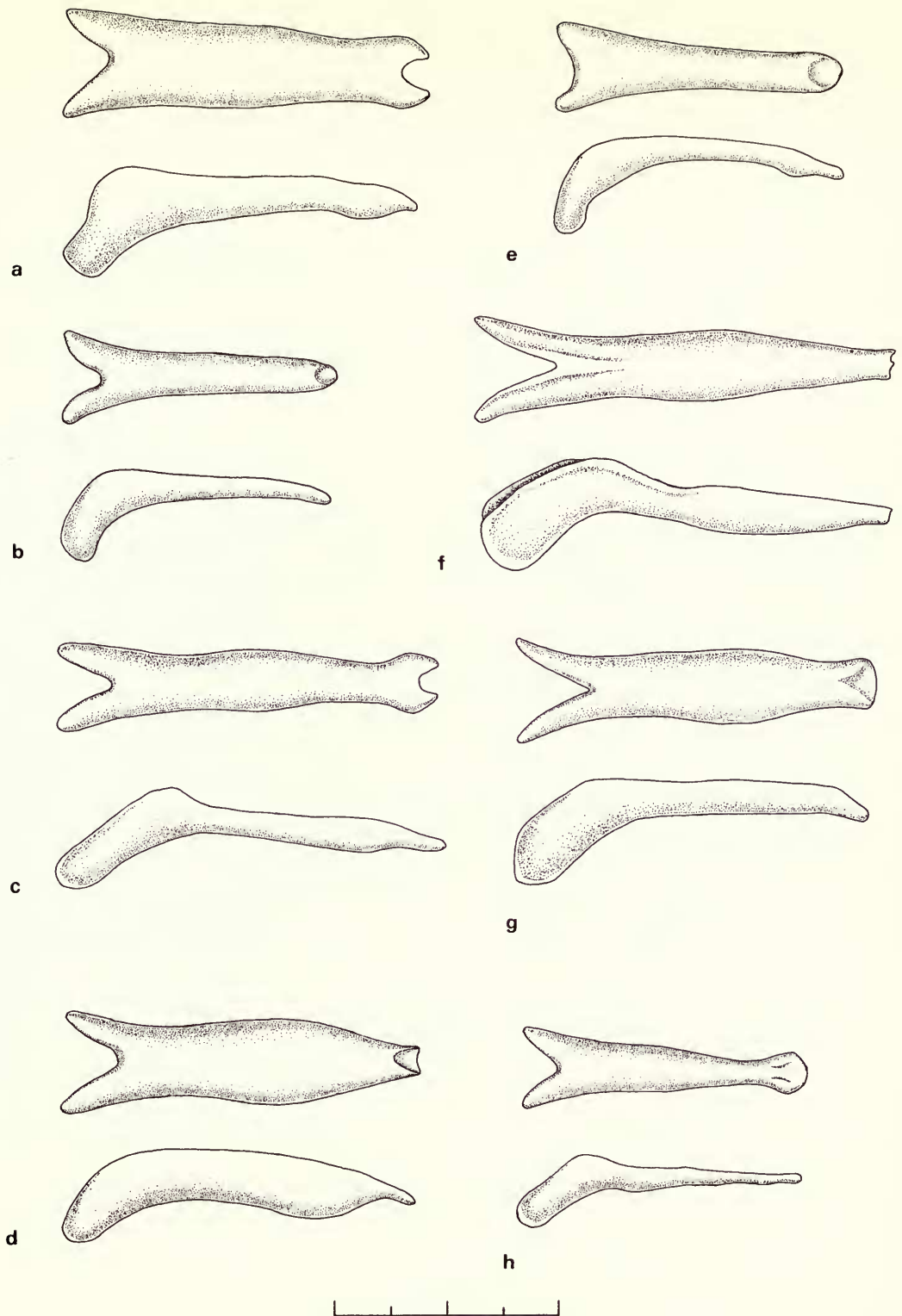


Fig. 22 Baculum (D, RL) of a, *Nyctophilus bifax*; b, *N. geoffroyi (palescens)*; c, *N. microtis*; d, *N. gouldi*; e, *N. geoffroyi (pacificus)*; f, *N. gouldi (sherrini)*; g, *N. daedalus*; h, *Pharotis imogene*. Scale = 2 mm.