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Penile Morphology and Classification of Bush Babies (Subfamily Galagoninae)

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The penile morphologies of nocturnal prosimians are complex and vary considerably between genera and species. Accordingly, comparative morphology can be useful in taxonomic studies, particularly when assessing the status of newly discovered species. I measured features of penile morphology—surface area of the glans penis; shape and size of the keratinized spines on the glans—for populations representing 14 species within the subfamily Galagoninae. Intraspecific variations in penile morphology were relatively minor. By contrast, there are significant differences in several morphological features among closely related, sympatric species, e.g., in the greater bush babies (Otolemur crassicaudatus *and* O. garnettii) *and lesser bush babies* (Galago senegalensis *and* Galago moholi). *Assessment of glans area resulted in the recognition of a second needle-clawed form:* Euoticus pallidus. *Similar divisions exist in the dwarf and greater bush babies with respect to proportional spiny area and characteristics of spine size. I constructed a key based on the presence/absence of certain features—penile spines, dermal markings on the glans, penile lappets—as well as the shape of the baculum and possession of different spinal morphotypes. This key may be used to identify all 14 species of bush babies. Penile morphologies provide a useful guide to specific identity in the Galagoninae, which may be true also for other groups of nocturnal mammals.*

KEY WORDS: Galago; bush baby; classification; penis; morphology.

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INTRODUCTION

The study of the reproductive anatomy of primates has revealed that genitalia can be extremely specialized (Dixson, 1987a; Hill, 1958). This is especially true of penile morphology which may differ markedly even between closely related primate species (Anderson, 1998; Dixson, 1987b; Dixson, 1991; Hill, 1953). Primate penes are often extremely complex, but particular characteristics appear to exhibit little variation within any given species. Indeed, low levels of intraspecific variation and comparatively higher levels of interspecific variation are common. The study of such diversity is most useful in the assessment of taxonomy, wherein comparative morphological techniques can aid classification. Qualitative studies have revealed marked differences in penile morphology in several cryptic primate species (Dixson, 1989, 1995). Typically, they belong to nocturnal groups within the Prosimii (Napier and Napier, 1967).

Like Napier and Napier (1967), I consider the bush babies to be a subfamily (Galagoninae) of the family Loridae, with nomenclature amended in accordance with Jenkins (1987). They are a nocturnal group of arboreal clingers and leapers, which occupy several diverse niches (Bearder and Doyle, 1974; Bearder, Honess and Ambrose, 1995). They are especially interesting because their taxonomy has long been contentious (Nash, *et al.,* 1989). This is mainly due to an inherent crypsis and short falls in certain classical taxonomic approaches, such as the use of skeletal measurements and pelage coloration, for identification.

Comparison of penile morphologies in galagos might provide a new technique with which to reassess their taxonomy using both qualitative and quantitative approaches. The current classification recognizes four separate genera, comprising 14 species belonging to one of three body sizes (Kingdon, 1997) (Table I).

The greater bush babies (*Otolemur*) contain the largest species [734–1750 g]. The needle-clawed bush babies (*Euoticus*) [271–300 g] and lesser bush babies (*Galago*) [188–314 g] contain the medium-sized species, and the dwarf bush babies (*Galagoides*) contain the smallest and lightest species [69–149 g] (Jungers and Olson, 1985; Bearder, Honess and Ambrose, 1995; Kingdon, 1997; Rowe, 1996; Smith and Jungers, 1997; Bearder: Pers. Comm).

The bush baby penis has several distinctive characteristics which are seen to vary from species to species. Each particular characteristic may therefore be used to classify species. For example, the glandes differ in relative size and surface morphology. The penis can be either spineless or covered in keratinized spines to varying degrees (Dixson, 1995). Such initial gross differences can be analyzed further in terms of proportional spiny area

Table I. Current taxonomy (subfamily Galagoninae): genera and species examined

Common name (Genus)	Body weight range (species means)	Species	Numbers[a]	Sources[b]
Greater bush babies (*Otolemur*)	734–1750 g	*Otolemur crassicaudatus*	0/23	BMNH
		Otolemur garnettii	18/22	BMNH/University of Memphis
Needle-clawed bush babies (*Euoticus*)	271–300 g	*Euoticus elegantulus*	0/15	BMNH
		Euoticus pallidus	0/14	BMNH
Lesser bush babies (*Galago*)	161–315 g	*Galago alleni*	0/16	BMNH
		Galago matschiei	0/7	BMNH
		Galago senegalensis	16/16	BMNH/Foundation AAP: Netherlands
		Galago moholi	0/25	BMNH
Dwarf bush babies (*Galagoides*)	60–149 g	*Galagoides demidoff*	0/18	BMNH
		Galagoides granti	0/8	BMNH
		Galagoides thomasi	0/12	BMNH
		Galagoides udzungwensis	0/2	BMNH
		Galagoides rondoensis	0/1	BMNH
		Galagoides zanzibaricus	0/12	BMNH

[a]Living/preserved.
[b]BMNH: British Museum of Natural History.

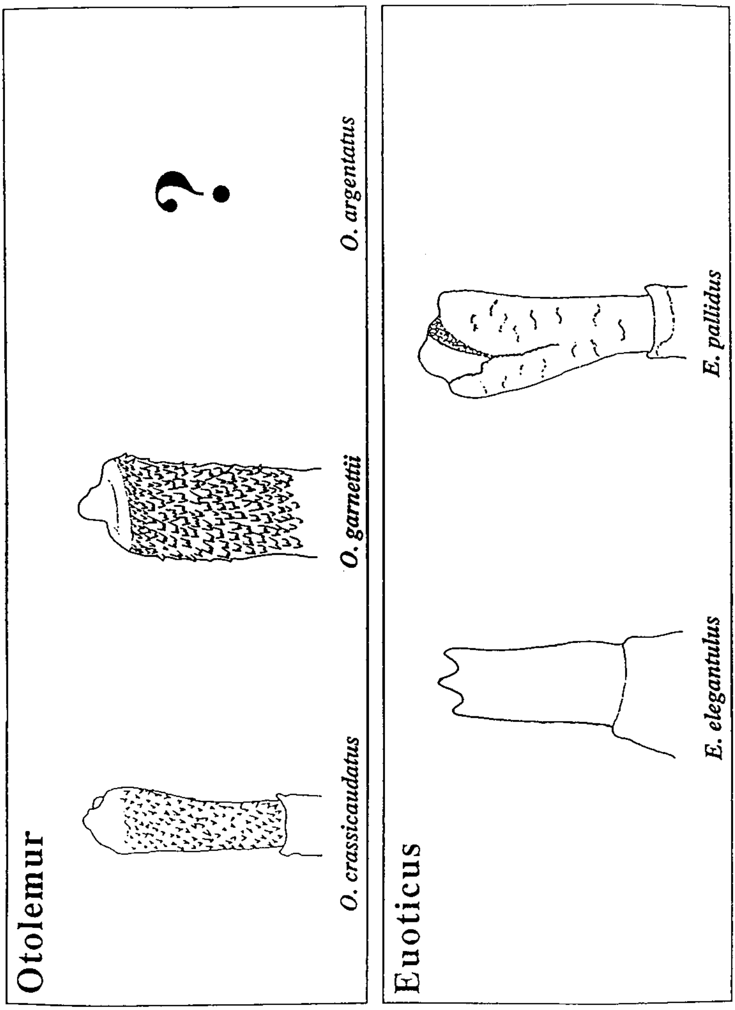

Fig. 1. Penile morphologies of the Galagoninae.

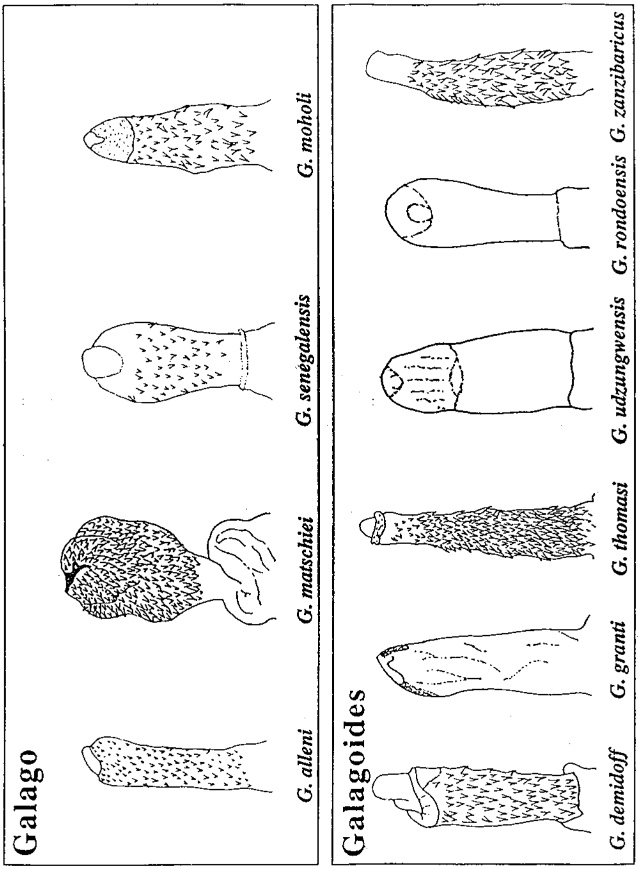

Fig. 1. (Continued).

and regional differences in spine size. The occurrence of dermal markings or of different spine types on the glans is informative. For example, penile spines can be simple (type 1: small, pointed structures of moderate length), robust (type 2: single-pointed enlarged structures often thickened at the base) or complex (type 3: multipointed) (Dixson, 1995).

I present quantitative data on penile morphologies of 14 bush baby species and assess the taxonomic value of the measurements. In addition, I constructed a key based on qualitative comparisons of penile morphology in galagos, in order to distinguish among the 15 currently identified species. Such morphological comparisons of penile morphology have not previously been attempted for galagos and are rare for other primates, e.g., macaques (Fooden, 1976).

METHODS

I examined 225 specimens, representing 14 bush baby species and four bush baby genera (Table I). I recorded details of penile morphology via a video camera with Hi8 video format tape and digitized the images using a Macintosh PowerPC with a digital image grabber board. All the images are right lateral views (Fig. 1). I used an image analysis package for the Apple Macintosh (IMAGE NIH) to measure the total area of the glans, overall spiny area, and mean and maximum spine size in different regions of the glans.

I measured total area of the glans penis in all specimens with or without spines. A calibration scale was set and the outline of the penis selected with the program (Fig. 2a). Then I recorded glans size on a spreadsheet for later statistical analysis.

I calculated proportional spiny area in all specimens exhibiting any kind of penile spine on the surface of the glans. A scale was set and the outline of each spine selected with the program. Then I measured each spine and calculated the total spiny area calculated (Fig. 2b). Proportional spiny area was then calculated as follows:

$$\text{Proportional spiny area} = \frac{\text{Total spiny area}}{\text{Total glans area}}$$

I recorded each specimen's glans size on a spreadsheet for later statistical analysis.

I analyzed regional measures of spine size within each galago species after setting the scale via splitting the glans image of each specimen into three sections. Each section was a third of the overall length of the glans. Differences in width along the length of the glans were controlled for by

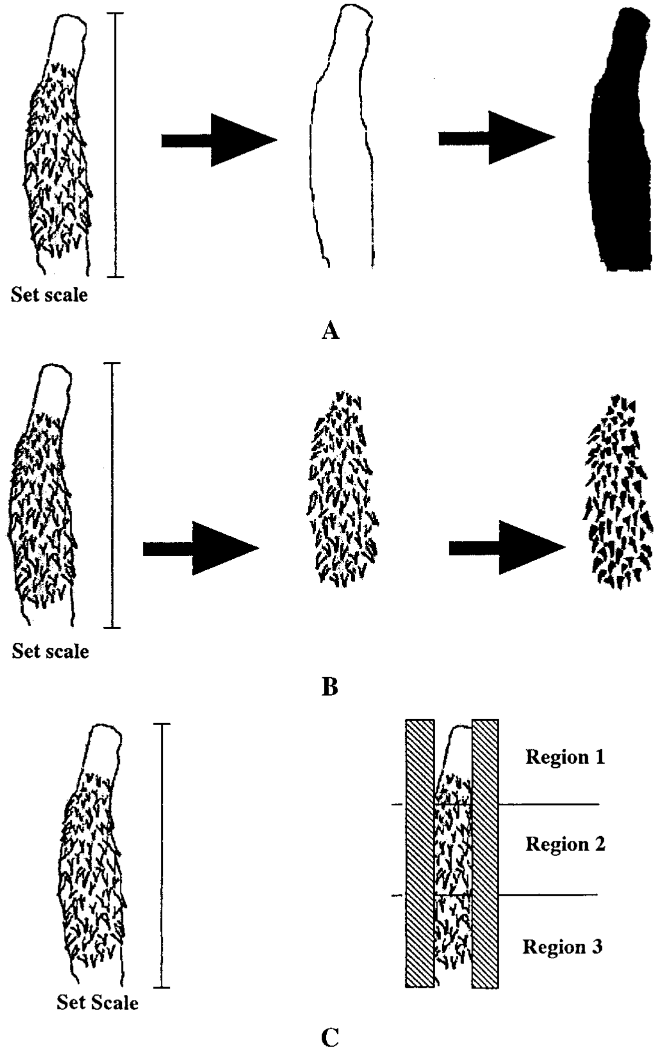

Fig. 2.(a) Area of glans (right lateral view) in *Galagoides zanzibaricus*; (b) overall area of spines (right lateral view) in *Galagoides zanzibaricus*; (c) spiny areas in different regions of glans.

overlaying a channel which is half the maximum overall width in each case (Fig. 2c).

I calculated two measures of spine size in each region:

a. Individual mean spine size $= \frac{\text{Total spiny area}}{\text{Number of spines}}$

b. Maximum spine size = largest individual spiny area in each region

As penile glans area is thought to be correlated with absolute body size, absolute differences in body size should be taken into account in comparisons of glans size. Relative glans size can then be calculated simply as a proportion or ratio, as follows:

$$\text{Penile glans area ratio} = \text{Ln}\,(\sqrt{\text{penile glans area}}) - \text{Ln}\,(\text{Head–Body length})$$

I used head–body length instead of absolute body weight because reliable measurements of individual weights were not available for many of the preserved specimens.

The ratios were then analyzed for homogeneity of variance and normality about the mean at genus and species levels, and where these assumptions were satisfied, I conducted an analysis of variance (ANOVA) (Zar, 1974). Where the ANOVA revealed significant differences between the different measures of penile morphology, I assessed them post hoc via Scheffé pair tests (Zar, 1974).

In addition to this quantitative analysis, I examined several other characteristics of penile morphology qualitatively. I noted spine presence/absence, baculum morphology, dermal markings on the glans, presence of penile lappets and possession of different spine types and constructed a key. Examples of these characteristics are in Fig. 3.

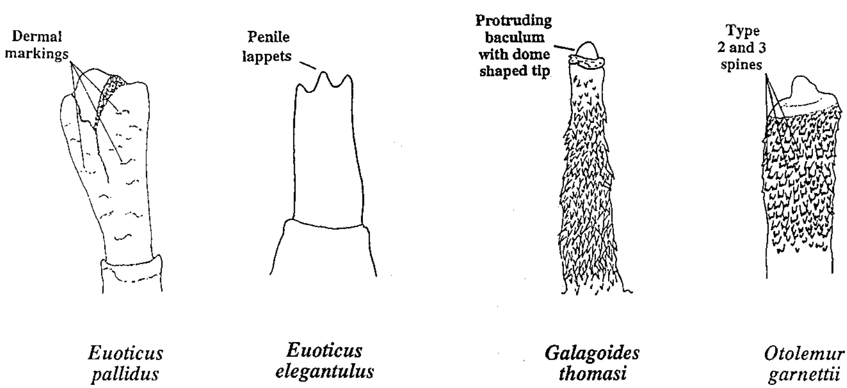

Fig. 3. Qualitative characteristics of galago penile morphology.

RESULTS

Comparisons of Glans Size Ratios

There is a strong correlation between glans size and head–body length (raw data: $r = 0.83$). Subsequent calculated ratios showed homogeneity of variance and normality about the mean. Further, there is a strong correlation between relative glans size and head–body length ($r = 0.80$), revealing an allometric relationship.

Analysis of variance of penile glans area ratios in the four genera of galagos revealed a statistically significant effect ($F = 8.724$; $p < 0.0001$). Post-hoc Scheffé pair tests revealed three intergeneric comparisons to be significant (*Otolemur* vs *Euoticus,* $p < 0.01$; *Otolemur* vs *Galagoides,* $p < 0.05$; *Galago* vs *Euoticus,* $p < 0.05$).

A second ANOVA test across all species analyzed using the mean glans area ratios revealed statistical significance in all cases ($F = 218.598$; $p < 0.0001$). Post-hoc Scheffé pair testing showed that most species are significantly different from one another ($p < 0.01$; Fig. 4), whilst levels of intraspecific variation are very low. However, two species of *Galago*—the Senegal bush baby (*Galago senegalensis*) and the mohol bush baby (*Galago moholi*)—do not differ significantly from each other. The same is true for two species of *Galagoides:* Demidoff's bush baby (*Galagoides demidoff*) and the Zanzibar bush baby (*Galagoides zanzibaricus*). However, species within *Otolemur* and *Euoticus* can be distinguished from one another via assessment of glans size. Differences were also revealed when species of either genus were compared. However, only some of the species within and between *Galago* and *Galagoides* could be distinguished using this measure.

Even given these exceptions, if species are split in respect to presence or absence of penile spines (shaded = spined species; Fig. 4), though exceptions exist in the spined species, all species with spineless glandes are significantly different from one another ($p < 0.01$).

Measurements of Penile Spinal Area

Percentages of spine cover on the glans penis in the different galago genera range from 40% (*Galago*) to between 50 and 60% (*Otolemur* and *Galagoides,* respectively). Specific level results mirror this variation in cover, with percentages ranging from 35% to >70%.

An ANOVA test using the mean proportional spiny area revealed statistical significance for all three spined genera ($F = 15.9$; $p < 0.001$). Post-hoc Scheffé pair testing revealed significant differences among all

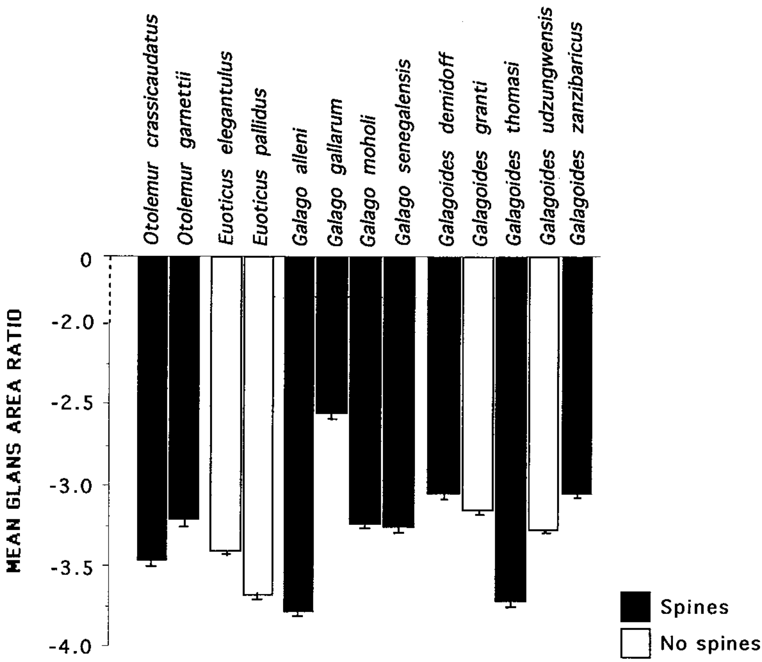

Fig. 4. Mean glans area ratios at the specific level (ANOVA: $p < 0.0001$; Scheffé: $p < 0.01$, except *G. moholi* vs *G. senegalensis* and *G. demidoff* vs *G. udzungwensis*).

three genera. Comparisons between *Otolemur* and *Galago,* and *Galago* and *Galagoides* showed very highly significant differences ($p < 0.01$).

The comparison of *Otolemur* and *Galagoides* is significantly different, albeit at a slightly lower level ($p < 0.05$).

A further ANOVA test across the 9 species types possessing spined glans via the mean residual glans area revealed statistical significance for all species ($F = 180.762$; $p < 0.001$). Post-hoc Scheffé pair testing revealed that all species are significantly different from one another ($p < 0.01$; Fig. 5). Levels of intraspecific variation are low and all species types are easily distinguished both within and between genera via the proportional spiny area.

Regional Variations in Sizes of Penile Spines

Regional variation in mean and maximum spine size in each galago species exhibits three distinct patterns. ANOVA tests across the three regions of the glans via the mean residual glans area achieved statistical

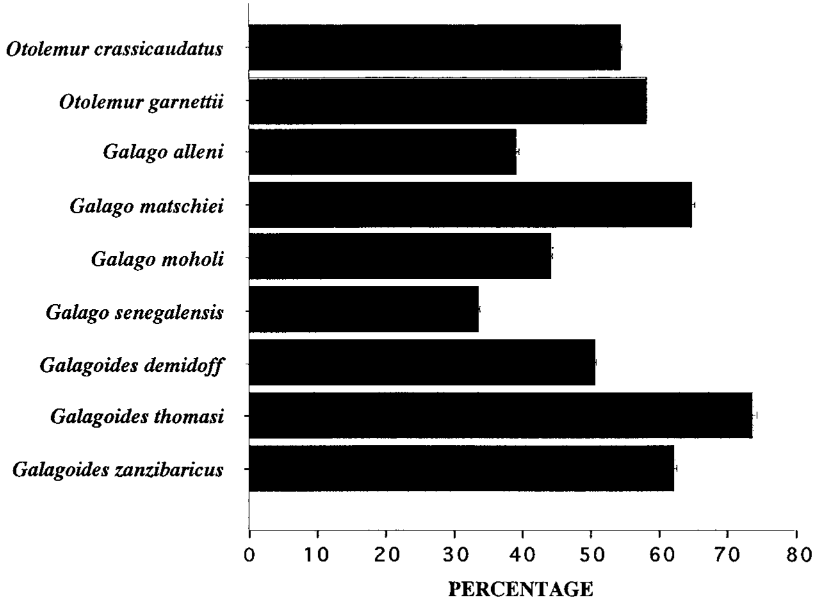

Fig. 5. Mean proportional spiny area at the specific level (ANOVA: $p < 0.001$; Scheffé: $p < 0.01$ between all species pairs).

significance for 5 of 9 species ($p < 0.001$). Post-hoc Scheffé pair testing revealed differences among regions using both measures in all the galago species ($p < 0.01$; Figs. 7 and 8).

Mean and maximum spine values for *Otolemur garnettii* showed no significant difference among any of the three regions on the glans (Fig. 6). There is no difference in spine pattern from base to tip (regions 1, 2, and 3). This pattern also characterizes two lesser galago species (*Galago matschiei* and *G. senegalensis*) and one dwarf galago species (*Galagoides thomasi*).

The mean and maximum spine values for *Otolemur crassicaudatus* show significant differences between the base and middle regions and middle and tip ($p < 0.01$; Fig. 7). However, spines at the base and tip show no significant difference. The spine pattern consists of small spines at the base and the tip and larger spines in the middle region. This second pattern also occurs in one lesser bush baby species (*Galago alleni*) and one dwarf bush baby species (*Galagoides zanzibaricus*).

The lesser galago (*Galago moholi*) has mean and maximum spine values that are significantly different in all regions ($p < 0.01$; Fig. 8). Typically, the spine pattern for both measures is for spines to be smallest at

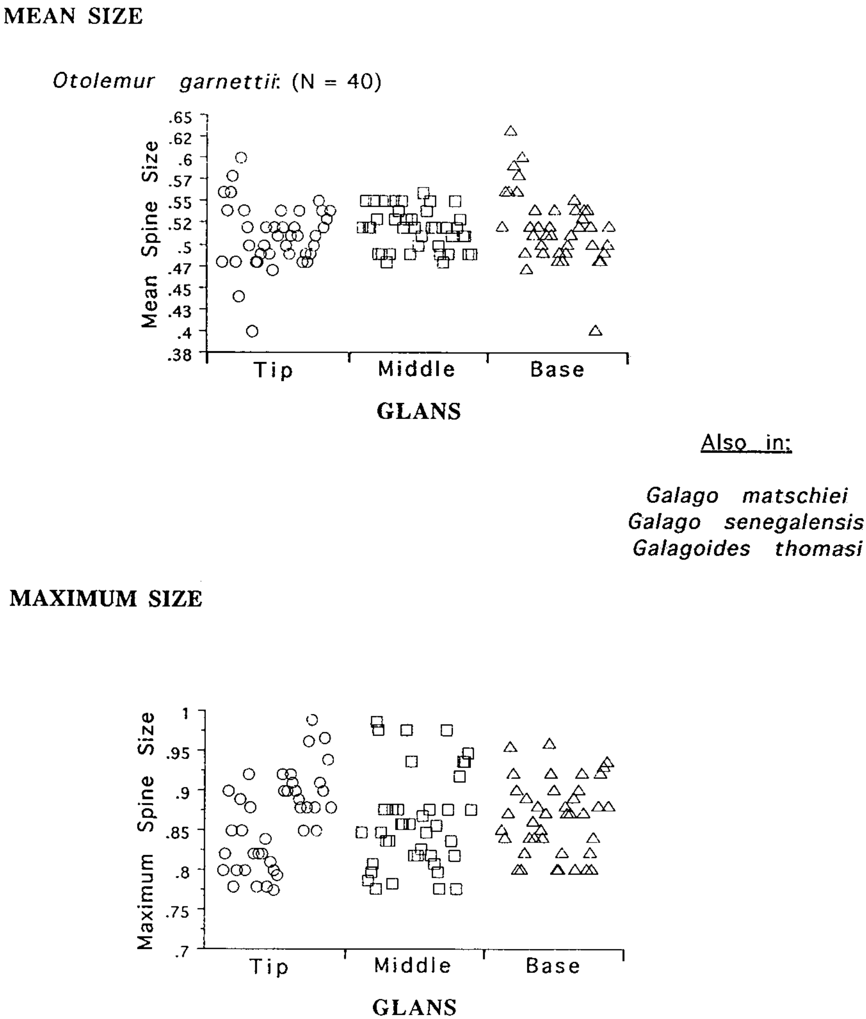

Fig. 6. Spine size on different regions of glans (no significant difference between regions).

the tip, largest in the middle and medium-sized at the base. This third pattern also occurs in one dwarf galago species; *Galagoides thomasi.*

Construction of a Taxonomic Key

Qualitative examination of the bush baby glans revealed several other features of taxonomic value. Gross characteristics such as possession of

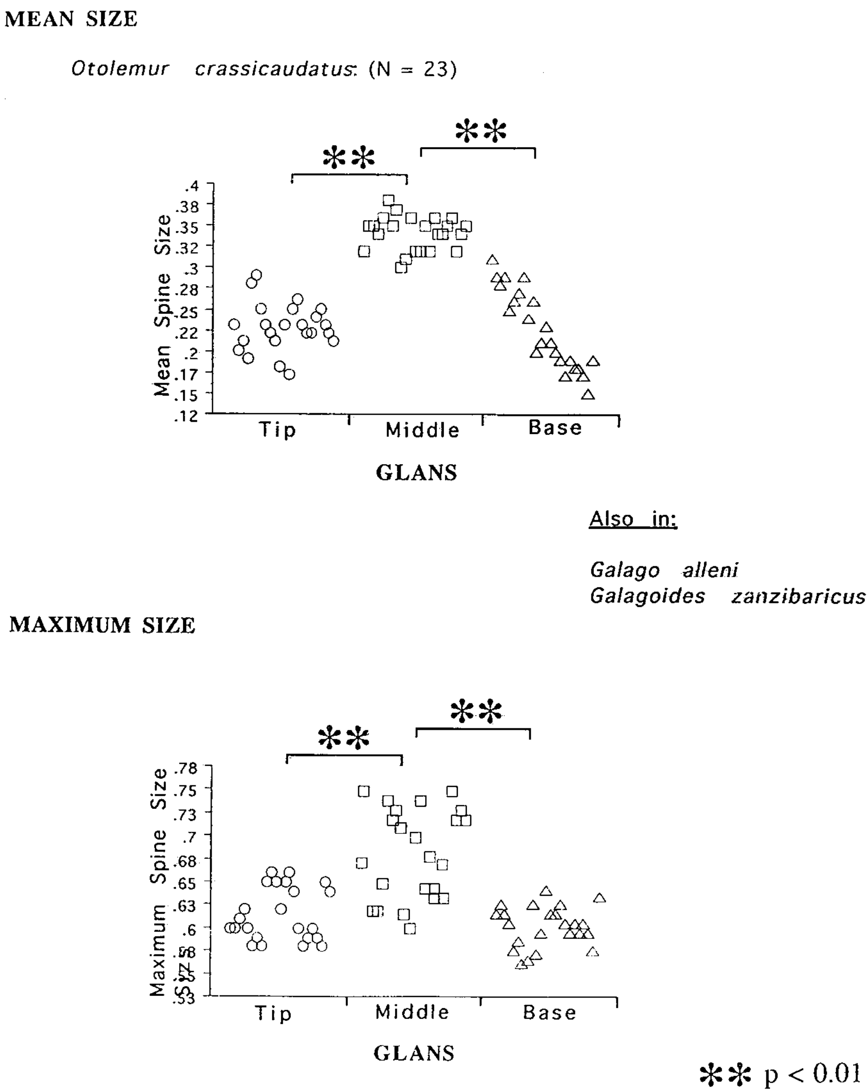

Fig. 7. Spine size on different region of glans (significant differences between middle region and base and middle section and tip. ANOVA: $p < 0.001$; Scheffé: $p < 0.01$).

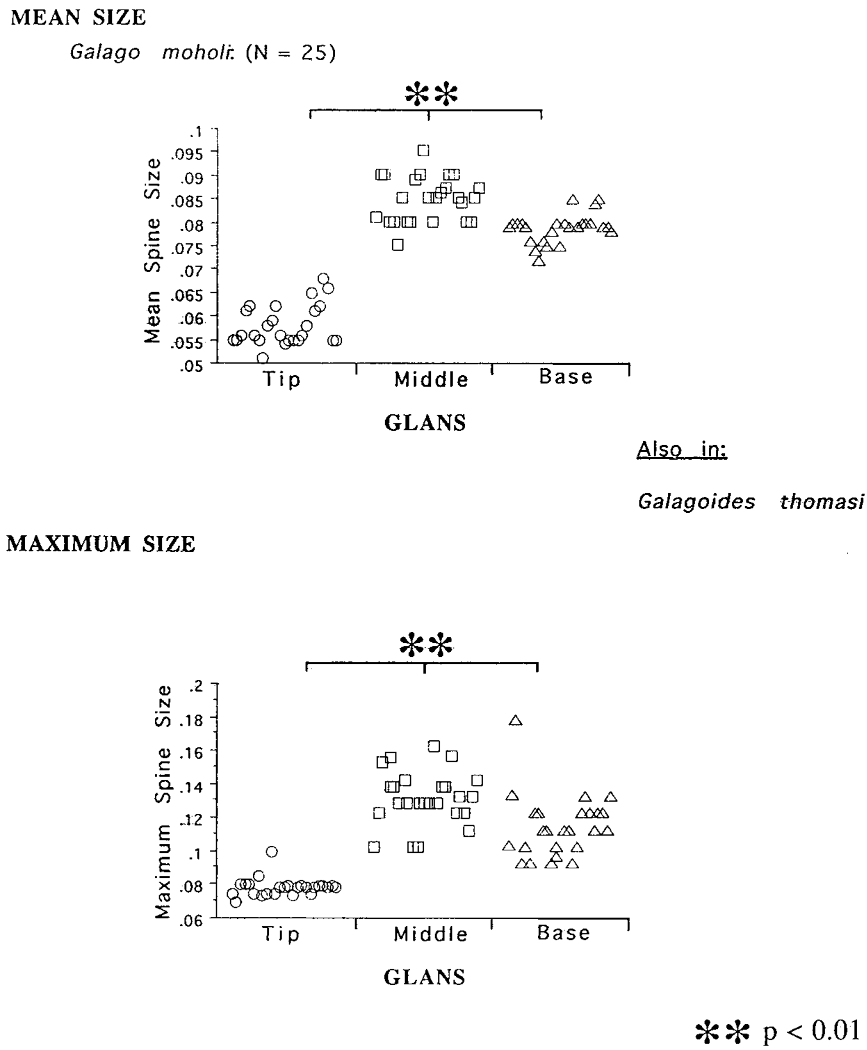

Fig. 8. Spine size on different region of glans (significant difference between regions. ANOVA: $p < 0.001$; Scheffé: $p < 0.01$).

dermal markings, a projecting baculum, penile lappets and certain spine types provided enough information to support a species key: Fig. 9a: species without spines; Fig. 9b: spined species. The key allows for pairwise decisions to be made in relation to the presence or absence of certain penile characteristics. For example, two bush babies with spineless glans—*Euoticus ele-*

gantulus and *Galagoides rondoensis*—can be distinguished because the former possesses penile lappets while the latter does not.

Additionally, I considered several species types, excluded from the quantitative study due to low sample sizes, in this qualitative examination. They could also be distinguished using these traits.

DISCUSSION

The traditional classification of the Galagoninae consists of 4 separate genera with 3 different body size ranges (Bearder, Honess and Ambrose, 1995). Allometric comparisons of penile glans area ratios test this classification. An ANOVA at genus and species level indicates how variance is distributed.

Initial results from these tests reveal very low levels of intraspecific variation and relatively high levels of interspecific variation at species level. This effectively supports the specific nominations in the current taxonomy.

However, analysis at genus level is more problematic, with the majority of variation within rather than between genera. Only 30% of the differences between species can be accounted for by differences between genera, with the remaining cases resulting from differences between species within a given genus. This is highlighted in the genus level post-hoc Scheffé tests wherein only 3 intergeneric comparisons are significant.

Further examination of data on relative glans size also reveals that sizing trends at genus level do not indicate the glans size possessed by constituent species. For example, greater bush babies (*Otolemur*), show larger than average glandes when compared to other genera, but between *O. crassicaudatus* and *O. garnettii* there is no similarity in size. *Euoticus,* which possesses a relatively smaller glans area in relation to body size than any of the other genera, also shows similar differences at the species level, with *E. elegantulus* having a much smaller relative size than that of its close relative *E. pallidus*. Further differences in genus and species glans size occur in lesser bush babies (*Galago*), especially between *G. alleni* and *G. matschiei,* and dwarf bush babies (*Galagoides*), most notably between *G. thomasi* and *G. zanzibaricus*.

Nevertheless, the marked differences in relative glans area between most bush baby species are useful for identification. This is especially true in species that possess glandes without spines wherein all comparisons are highly significant. However, presence or absence of spines on the glans penis doesn't appear to have a generic basis. The spineless species appear to be randomly distributed throughout the Galagoninae. The only exception

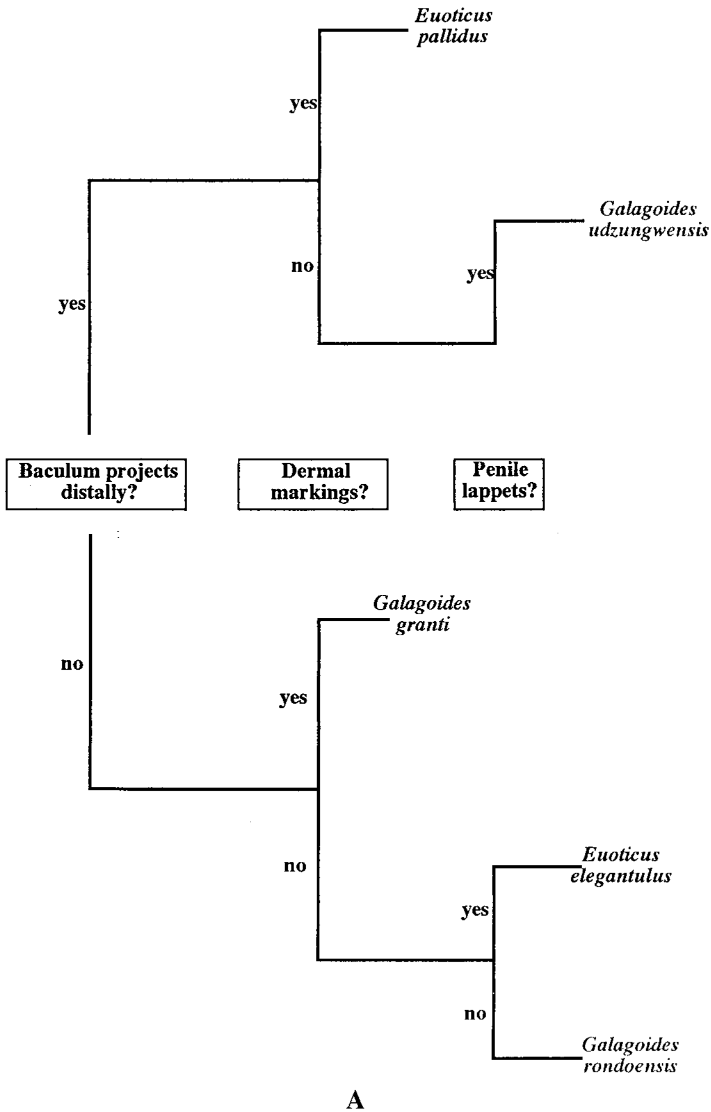

Fig. 9. (a) Key for species without penile spines; (b) key for species with penile spines.

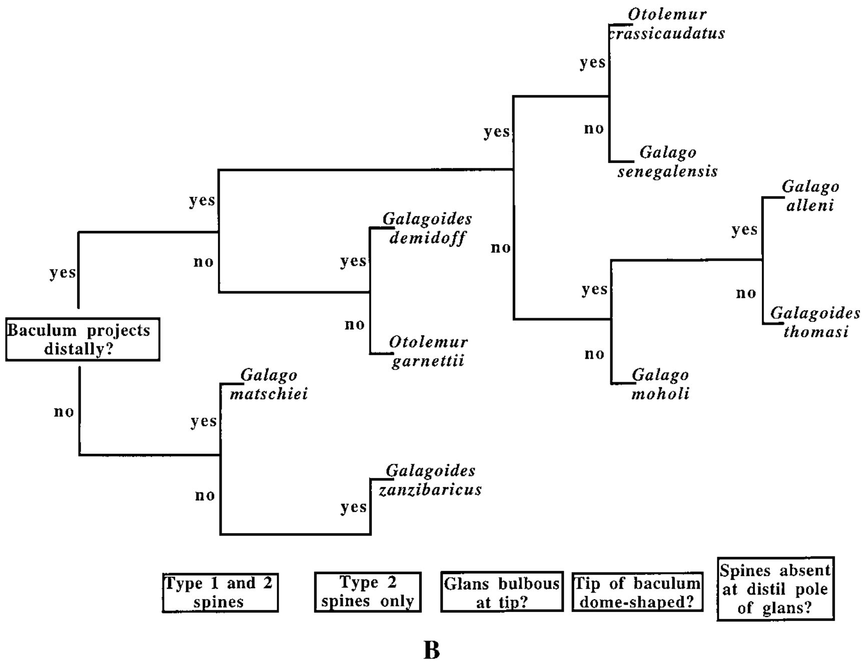

Fig. 9. (Continued).

appears within *Euoticus,* wherein both species lack spines. However, even in this case, the possible existence of a third spined form, thought to be related to *Euoticus elegantulus* (Dixson, pers. comm), shows that such generalizations cannot be made.

Mean proportional spiny area at genus and species level mirrors trends in variation in relative glans size. However, post-hoc Scheffé tests show many more significant differences at both levels. Comparisons between genera yield higher levels of significance, with only *Otolemur* vs *Galagoides* showing lower levels of significance at the 0.05 level, the same as that in comparisons of relative glans size.

Although this allows for different genera containing species with spined glandes to be distinguished effectively using proportional spiny area, it is at the specific level, where the majority of variation is observed, that the measure becomes extremely useful. As with relative glans size, intraspecific variation is relatively low whilst interspecific variation is high. Indeed, all bush baby species with penile spines are significantly different from one another in terms of mean proportional spiny area. This means that the species type of all specimens with spines can be determined using mean proportional spiny area.

Measurements of penile morphology facilitate the reliable identification of all bush baby species considered thus far. The dramatic differences observed in size and complexity of bush baby penes are most interesting when considering species that are very closely related and typically live sympatrically. For example, greater bush babies (*Otolemur*) contain well-established specific types, such as thick-tailed bush babies (*Otolemur crassicaudatus*) and Garnett's bush babies (*O. garnettii*), which differ markedly in both relative glans size and proportional spiny size. A third form, *Otolemur argentatus* also differs from *O. crassicaudatus* and *O. garnettii* in several ways, including an apparent lack of spines. However, more specimens are required before a full analysis can be undertaken, so I included no illustration. Comparable results characterize Demidoff's dwarf bush babies (*Galagoides demidoff*) and Thomas' dwarf bush babies (*G. thomasi*), which are also extremely similar in overall appearance and often occur sympatrically in parts of their range. Previously, vocalizations were the only means to recognize *Galagoides thomasi*, previously an Eastern subspecies of *G. demidoff* (Nash, Bearder and Olson, 1989; Bearder, Honess and Ambrose, 1995; Kingdon, 1997). However penile morphological markers can now also be utilized. For example, relative glans size and proportional spine size enables correct classification of the two forms. Such findings are supported via examination of type specimens: *G. demidoff phasma* (Zaire: ZD.1926.7.6.42) and *G. thomasi* (Zaire: ZD. 1906.12.4.58) at the Natural History Museum in London.

These new approaches allow for quantification of several species types whose taxonomy has remained uncertain. Two needle-clawed species provide an ideal case study. Analysis of relative glans size alone enables one to distinguish the northern needle-clawed form (*Euoticus pallidus*) from *E. elegantulus* and thereby support conclusions made in previous studies (Groves, 1989, 1993; Kingdon, 1997). The existence of this second form is further supported by similarities observed between the type specimen (Bioko, formerly Fernando Po) and other specimens of *E. pallidus* located at mainland sites (Cameroon and Nigeria). Additional penile characteristics along with other anatomical, behavioral and ecological evidence provide support for these findings. Most notable are differences in pelage with the northern form possessing a foxy-red fur, which contrasts with the dull yellow-brown color of the well-established southern needle-clawed form (*Euoticus elegantulus:* Kingdon, 1997). Habitat preferences also appear to differ with the newly nominated *Euoticus pallidus* preferring secondary forests only and *E. elegantulus* subsisting in both primary and secondary forests (Rowe, 1996). Although both species are predominantly gummivorous, the southern form has a much more widespread distribution throughout the moist forest belt between the river Sanaga and river Zaire. The northern species, by contrast, has a more fragmented distribution zoogeographically

(Kingdon, 1997). Recent studies also show that the two species differ significantly in various features of hand morphology (Anderson, 1999).

Quantification of different regions along the glans in terms of mean and maximum spine size shows three different patterns of spine distribution in bush babies. The first pattern is one of no significant difference in spine size between regions. The second pattern involves larger spines in the middle region of the glans (region 2) only, with size increasing significantly here. The third pattern is a significant increase in size from the base to the middle region (medium to large spines) and then a dramatic decrease in size at the tip (large to small spines). None of these patterns is characteristic of any genus as such, with species in different genera sharing the same regional characteristics. However, when the patterns of variation in spine size are used in conjunction with the measures outlined above, they provide a useful adjunct to specific classification. For example, the two lesser bush babies, *Galago senegalensis* and *G. moholi*, cannot be distinguished on the basis of relative glans area alone, but are found to display two different patterns of spine size. Regional differences are therefore useful for fine-grained species determinations, involving closely related, sympatric forms.

Regional differences in spine size also suggest functional differences, which may, in part, begin to explain the evolution of complexities observed in galago penile morphology (Dixson, 1987a; Eberhard, 1985, 1996, 1998).

I augmented the quantitative analysis of bush baby penile morphologies with qualitative consideration of other morphological characteristics. Dermal markings, shape of the distal baculum, possession of penile lappets and simple/complex spine types provide material for a key to various species. Initial consideration of presence or absence of spines in any given specimen allows for the simplification of the key, with species having spineless glandes considered separately from those with spines. Specimens without spines can be identified via consideration of three characteristics relating to bacula, dermal markings and penile lappets. Because of the qualitative nature of these data even species types with relatively small sample sizes can be considered. For example, the recently described dwarf bush baby species, *Galagoides rondoensis* Honess (Kingdon, 1997) can be distinguished from other well-established species. Likewise, the use of information collected on bacula, and spine types allows for the classification of bush baby species with spiny glandes. Again, small samples of species can be considered. For example, possession of ≥1 of the 3 different spine types (Dixson, 1995) (type 1: simple spines of moderate length; type 2: robust single pointed spines; and type 3: complex, multipointed spines) allows for the identification of three greater galago species. Kingdon (1997) proposed a third species, *Otolemur argentatus*, which would also be recognizable on the basis of its penile morphology.

The diversity observed in both the qualitative and quantitative characters of the penis presumably relate to function. However, in the absence of a true phylogeny, the identification of independant evolutionary events is problematic (Harvey and Pagel, 1991). Therefore, functional significance at species level should be treated with caution.

The majority of bush babies possess a nongregarious mating system, which is typically dispersed and complex. Overlapping ranges and relatively elongated periods of estrus may allow for females to mate with several males in one breeding season (Bearder, 1987; Charles-Dominique, 1977; Pullen, pers. comm). In such a mating system, there may be mechanisms allowing for the female to influence which male achieves conception. This peri- and/or postcopulatory cryptic female choice (Eberhard, 1985, 1996, 1998) relates to certain male sexual stimuli. Thus the male that presents the advantageous stimulus achieves fertilization and a reproductive advantage. In this manner, small adaptive features of penile morphology and male copulatory behavior become subject to sexual selection, which may, in turn, result in rapid divergence of penile characteristics.

The function of these complex morphologies may also relate to different roles in sexual behavior. For example, small tactile spines appear to help to achieve intromission (Dixson, 1989) and may also influence physiological feedback (Eberhard, 1985). Conversely, larger spines appear to relate to prolonged periods of intromission, possible mate-guarding and multiple ejaculations.

Overall, the morphological diversity of galago penile morphology may be a result of speciation events strongly influenced by sexual selection (Darwin, 1871), specifically cryptic female choice (Eberhard, 1985, 1996). Extremes of penile morphology might thereby result from runaway sexual selection for certain characteristics that differ initially as a result of founder effects, genetic drift and/or geographic isolation (Eberhard, 1985). This could explain differences in male traits that are apparently nonadaptive or random in relation to natural selection.

The techniques described in this report for quantifying penile morphologies have proven extremely useful in reassessing traditional taxonomies of the Galagoninae. These findings should encourage the use of similar techniques to study other nocturnal mammalian groups.

CONCLUSIONS

- Examination of penile morphologies enables classification of bush baby species.
- Glans size enables identification of species with spineless glandes.

- Proportional spine size enables identification of all species with spined glandes.
- Regional differences in the spine size may relate to function.
- Qualitative measures allow construction of a key to bush baby species.
- This new technique for examining penile morphologies is potentially useful in the classification of other nocturnal mammalian groups.
- Spines may play different roles in sexual behavior.
- Spines may affect female responses and cryptic female choice.

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