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# MORPHOLOGICAL VARIABILITY AND EVOLUTION OF THE BACULUM (OS PENIS) IN MUSTELIDAE (CARNIVORA)

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We examined morphological variability and evolution of the baculum (os penis) across the Mustelidae through allometric analyses and character mapping. Fifty-four species and 26 genera (including 2 fossil forms) were examined with numerous caniform out-group species. Allometric analyses showed that bacular length is relatively constant across mustelids and caniforms; only a tendency to a slightly shortened baculum in mephitines was observed. Character mapping revealed the ancestral mustelid baculum to be an elongated rod-shaped bone that lacks a urethral groove and possesses a simple, nondistinct distal tip. This form is largely retained in mephitines and, to a lesser degree, in lutrines. From the ancestral condition, it is possible to derive forms with a more complicated head that has projections and openings (e.g., melines, *Eira barbara*, *Galictis*, *Gulo gulo*, *Martes*) or spoon-shaped and cup-shaped processes (e.g., *Ictonyx*, *Mellivora capensis*). Another evolutionary trajectory involves the distal tip of the baculum becoming hook-shaped and the urethral groove well developed (e.g., *Mustela*, *Vormela peregusna*). Although the structure of the baculum distinguishes closely related species, many features are derived independently in more distantly related forms. Therefore, bacular structure provides restricted phylogenetic information and should be analyzed in concert with other data sources (e.g., morphology of the basicranial region).

Key words: allometry, baculum, independent contrasts, morphology, Mustelidae, phylogeny

The baculum (os penis) is a heterotopic bone (Romer and Parsons 1986) that is derived from connective tissue and is situated dorsal to the urethra and medial to the corpora cavernosa. It is found across a diverse range of mammals—carnivores, bats, rodents, insectivores, flying lemurs, and some primates (Weber 1928)—and often shows great morphological diversity among even closely related species. This especially is true among rodents and carnivores.

The reason for the high degree of morphological variation is unclear; no single interpretation of bacular function seems satisfactory and well supported (Dixson 1995; Larivière and Ferguson 2002; Long and Frank 1968). Two primary hypotheses exist (Patterson and Thaeler 1982). One explanation is that the variation is simply a pleiotropic by-product of phylogenetic divergence (Burt 1936; Contreras et al. 1993; Hafner 1978; Hamilton 1949). Conversely, other hypotheses explain bacular differences as proceeding from the functional role of the os penis in copulation (e.g., as a supporting or stimulating structure—Ewer 1973; Long and Frank 1968) and may extend to a potential role as a reproductive isolating mechanism. For example, Meczynski (1974) suggested that the bacular

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teeth in ground squirrels (*Spermophilus citellus* and *S. suslicus*) apparently interdigitate with the rugae vaginalis of the female during copulation, providing functional specificity of genital morphology. However, in Carnivora at least, such functional explanations do not seem to pertain (Larivière and Ferguson 2002).

Baryshnikov and Abramov (1997, 1998) described bacular morphology in the majority of genera of Mustelidae. Herein, we present a comprehensive comparative analysis of bacular length and morphology across all mustelids with a view toward elucidating the evolution of the os penis within the family. Specifically, we examine the relationship between changes in the baculum as an internal heterotopic structure and the major pathways of adaptive evolution of mustelids (Sokolov 1968). We also clarify whether only unique divergence of its structural characters has occurred or whether there also have been convergent changes in different phylogenetic lineages.

## MATERIALS AND METHODS

*Data sources*.—Data on mustelid bacular length and morphology were obtained primarily from museum specimens. Three hundred and two bacula, representing 46 extant species and 22 genera, were examined. Data for 8 additional mustelid species from 4 genera (including 2 fossil forms) were obtained from the literature. Data on the bacular morphology of other species of caniforms (‘‘dog-like carnivores’’: canids, mustelids, pinnipeds, procyonids, and ursids) also were collected personally or obtained from the literature. A list of all species studied, together with museums visited or literature sources appears in Appendix I. Unless stated otherwise, all observations are for bacula of adults.

Taxonomy of the family follows Wozencraft (1993) except for the following changes. We recognize 2 species of *Meles*: the European badger, *Meles meles*, and the Asian badger, *Meles anakuma* (Abramov 2001; Baryshnikov 2001; Baryshnikov and Potapova 1990). Also, we recognize *Mustela subpalmata* as distinct from *Mustela nivalis* (Abramov and Baryshnikov 2000; van Zyll de Jong 1992) and *Mustela itatsi* as separate from *Mustela sibirica* (Abramov 2000a; Masuda and Yoshida 1994).

*Allometry*.—We investigated the allometry of bacular length in mustelids and in caniforms (Appendix II) using both simple cross-species analysis and the method of independent contrasts to account for possible phylogenetic effects. Measurements of maximum bacular length (L) without considering the curvature of the shaft were made on pertinent specimens. Body size was estimated using condylobasal length (CBL) of the skull of adult males.

Although cross-species analysis provides an accurate estimate of the regression coefficient for any relationship (Pagel 1993), it is generally invalid because it assumes that species are independent (Harvey and Pagel 1991; Pagel 1993; Purvis et al. 1994). This assumption especially is problematic when trying to ascertain functional reasons for any observed trends. Hierarchical descent with modification during evolution means that species that share a common ancestor are likely to be more similar than distantly related species. For example, 2 sister species might share relatively long bacula simply because they both inherited it from their common ancestor. Independent contrasts account for this potential ‘‘phylogenetic inertia’’ and provide answers independent of the phylogenetic relationships among species, thereby allowing true functional trends to be explored.

Independent contrasts were obtained using the ‘‘crunch’’ procedure in the computer program Comparative Analysis Using Independent Contrasts (CAIC—Purvis and Rambaut 1995) based on the complete and dated (‘‘best estimate’’ branch lengths) phylogeny for all extant carnivores of Bininda-Emonds et al. (1999). Based on a phylogeny, branch length information, and some specified predictor variable (CBL here), CAIC estimates nodal values for both the predictor and dependent (L) variables from their values in the node’s descendent taxa and then generates ‘‘contrasts’’ (i.e., differences) between independent nodes or species.

We excluded the species *Meles anakuma*, *Mustela itatsi*, *Mustela subpalmata*, *Plesiogulo marshalli*, and *Sardolutra ichnusae* from the analyses because they are not present on the phylogeny of Bininda-Emonds et al. (1999). Other species were excluded because data for either L or CBL were unavailable: *Galictis cuja*, *Melogale moschata*, and *Mustela felipei*. Both L and CBL were log-transformed (base e) to accord better with the underlying random walk model of evolution used in CAIC (Felsenstein 1985; Purvis and Rambaut 1995) and also to reduce heterogeneity of variances for the regression analysis, improve normality, and convert the allometric relationship into a predicted linear one (Harvey 1982). Various diagnostic tests indicated that this transformation was appropriate, that the branch lengths were standardized adequately, and that the Brownian motion model was appropriate for the data (Purvis and Rambaut 1995).

We used cross-species analysis largely to calculate ''relative bacular length'' (with respect to skull length, CBL) for the subsequent character-mapping analysis. Relative bacular length was characterized by using the residuals derived from fitting raw species data to the regression equation obtained using the species data for mustelids. Species with residuals $>1$ *SD* above or below the regression line were held to possess relatively long or short bacula (compared with the mustelid average), respectively; the remaining species were defined as having bacula of average length. Species with residuals $>1.96$ *SD*s above or below the regression line were held to have significantly longer or shorter bacula, respectively.

*Character analysis*.—Fifty-two mustelids species were scored, as well as several out-group species (Appendix II) for the following 10 characters, described here with their alternative states (Fig. 1 and Appendix III). Character 1—abrupt upward bend in distal tip: 0, absent; 1, weak or slightly curved; 2, well marked or pronounced (Fig. 1a). Character 2—presence of a distal hook: 0, absent; 1, present (Fig. 1b). Character 3—shape of median portion of stem in cross section: 0, triangular, dorsal crest well pronounced; 1, rounded/triangular, dorsal crest not pronounced; 2, rounded, dorsal crest absent. Character 4—pronounced urethral groove: 0, long; 1, short, only present distally; 2, absent (Fig. 1c). Character 5—pronounced head: 0, absent; 1, slightly pronounced; 2, well marked (Fig. 1d). Character 6—opening on head: 0, absent; 1, present (Fig. 1e). Character 7—subdivision of distal tip in ventral plane: 0, absent; 1, present (Fig. 1f). Character 8—shape of distal tip: 0, symmetrical; 1, asymmetrical (Fig. 1g). Character 9—complexity of distal tip: 0, additional projections absent; 1, additional projections present beyond those formed by subdivision of distal tip (Fig. 1h). Character 10—relative length of baculum (compared with mustelid average): 0, shorter; 1, average; 2, longer.

Evolutionary transformations of these characters (Appendix III) were examined by mapping them on the carnivore phylogeny of Bininda-Emonds et al. (1999; Fig. 2). This phylogeny is a supertree (Sanderson et al. 1998) derived from 274 individual estimates of carnivore phylogeny (including 31 for mustelids alone); as such, it probably represents the best current estimate of the evolutionary relationships of all extant (mustelid) species. For each character, the ancestral state for mustelids was reconstructed using parsimony methods. Except for character 10, the out-group consisted of a restricted set of caniform species representing all major caniform lineages; for character 10, the ancestral state was inferred using a broader selection of species from the allometry analysis (Appendix II).

## RESULTS

### *Allometry Using Independent Contrasts*

Although there are clear differences in size between the different groups, caniforms are remarkably homogeneous in the relative length of their bacula (Fig. 3a). When ln(L) is regressed on ln(CBL), most species cluster relatively tightly around the regression line, with only a few being $>1$ *SD* away (Appendix II). However, some clade-specific trends are apparent. Most canid and ursid species fall below the line, whereas most pinniped and procyonid species are located above the line; however, these trends generally are not significant. Species in the various mustelid subfamilies are scattered equally on either side of the line, although mephitines do possess relatively short bacula compared with other mustelids (Fig. 3b).

Analyzing the species data using independent contrasts confirmed that a significant linear relationship exists between the length of the os penis and size across caniforms (Fig. 4a). This also revealed significant trends that would have been missed if only the raw species data were examined. Although the regression is highly signifi-

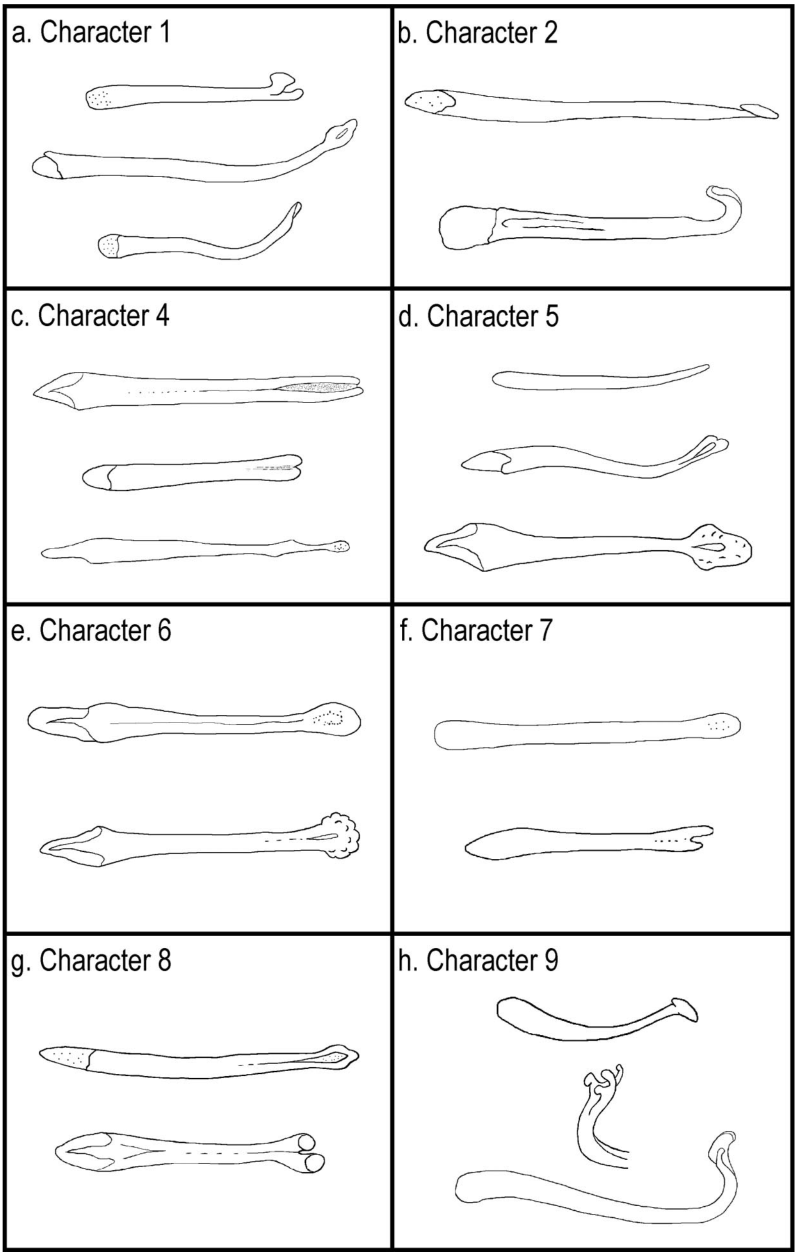

FIG. 1.—Characters examined, as shown by representative bacula of mustelids. Bacula are shown in lateral view from right side (lat), ventral view (vent), or as distal tip from left side (dist). a) Character 1, bend of tip—*Melogale personata* (top, lat); *Martes pennanti* (middle, lat); *Mustela erminea* (bottom, lat). b) Character 2, presence of hook—*Eira barbara* (top, lat); *Mustela eversmanii* (bottom, lat). c) Character 4, presence of urethral groove—*Lontra canadensis* (top, vent); *Pteronura brasiliensis* (middle, vent); *Mydaus javanensis* (bottom, vent). d) Character 5, size of head—*Mephitis mephitis* (top, lat); *Martes foina* (middle, lat); *Meles anakuma* (bottom, vent). e) Character 6, presence of opening in head—*Arctonyx collaris* (top, vent); *Meles meles* (bottom, vent). f) Character 7, division of tip—*Lyncodon patagonicus* (top, vent); *Lutrogale perspicillata* (bottom, vent). g) Character 8, shape of tip—*Enhydra lutris* (top, vent); *Lutra lutra* (bottom, vent). h) Character 9, complexity of tip—*Ictonyx libyca* (top, lat); *Martes flavigula* (middle, dist); *Mustela strigidorsa* (bottom, lat). (Not illustrated—character 3, cross-sectional shape and character 10, relative length.)

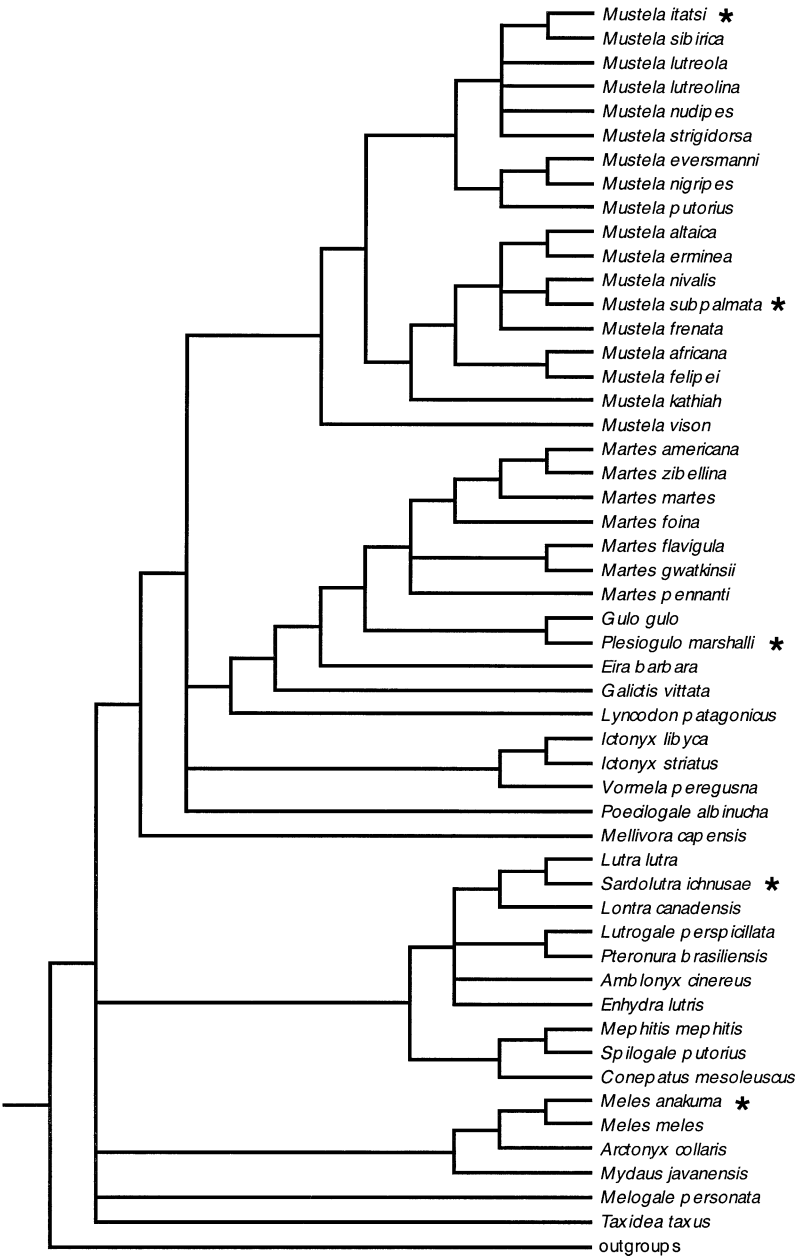

FIG. 2.—A recent estimate of mustelid phylogeny used for the independent contrasts analysis and character mapping. The tree is a simplified version of the supertree in Bininda-Emonds et al. (1999) showing only those species examined in the current study. Taxa marked with asterisks do not appear in the original study but were placed with their putative sister species based on other sources; they were included for the character mapping only. Branch lengths are not proportional to time.

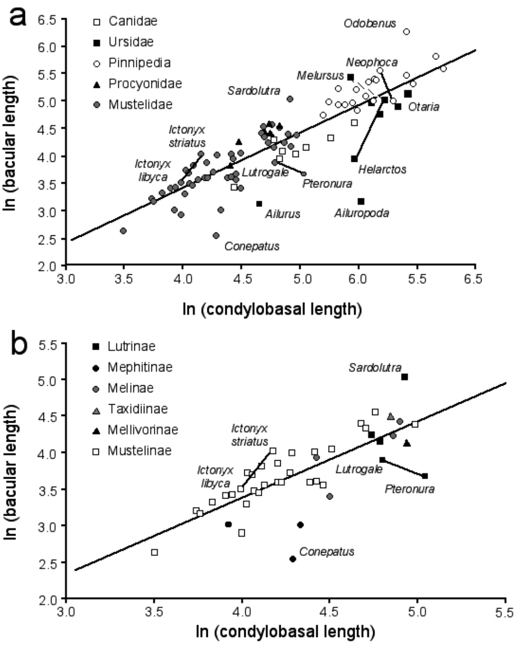

FIG. 3.—Regression of ln bacular length on body size (ln condylobasal length) using raw species points a) across caniforms and b) within mustelids. Named species are those with significantly shorter or longer bacula or those that contribute to the outliers in Fig. 4.

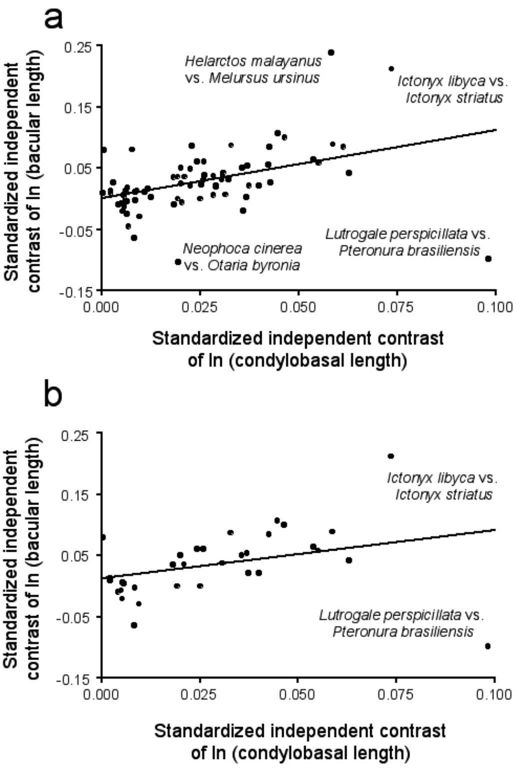

FIG. 4.—Independent standardized contrasts for ln bacular length regressed on standardized contrasts of body size (ln condylobasal length) a) across caniforms and b) within mustelids. Significant outliers are labeled.

cant ($P < 0.0001$), the coefficient of determination is rather low ($r^2 = 0.366$) due to 4 contrasts, all of which are significant outliers (i.e., possess residuals $>1.96$ *SD*s from the regression line): *Helarctos malayanus* versus *Melursus ursinus* (ursids), *Neophoca cinerea* versus *Otaria byronia* (otariids), *Lutrogale perspicillata* versus *Pteronura brasiliensis* (lutrines), and *Ictonyx libyca* versus *I. striatus* (mustelines). The removal of these 4 points improves the fit of the regression equation dramatically ($r^2$ increases to 0.582). Similarly, a highly significant linear relationship is present within mustelids (Fig. 4b). Again, the coefficient of determination is low (0.356) due to the *Lutrogale–Pteronura* and *Ictonyx* contrasts being significant outliers. Removal of these outliers raises $r^2$ to 0.662.

Each outlier reveals significant deviations away from the general tendency among caniforms (and within mustelids) for the baculum to increase in length as size increases. For instance, although this positive relationship holds when *H. malayanus* and *M. ursinus* are contrasted, connecting the species points yields a line with a much more positive slope than that for all caniforms (Fig. 3a), thereby emphasizing the relatively short os penis of *H. malayanus* compared with its sister species *M. ursinus*. In contrast, the highly negative residual for the node connecting *Lutrogale perspicillata* and *P. brasiliensis* indicates a trend in the opposite direction. Thus, although *P. brasiliensis* is larger than its close relative *Lutrogale perspicillata*, its baculum is relatively (and absolutely) shorter (Fig. 3b).

### *Character Analysis*

The 10 bacular characters are highly incongruent with the carnivore phylogeny of Bininda-Emonds et al. (1999), showing an ensemble consistency index (CI) of 0.147 and individual CIs for each character of 0.500 or less (and often <0.200). This is reflected by numerous parallel derivations of the different states and reversals within each character. Below, we discuss each of the 10 characters described in the ''Materials and Methods'' and illustrated in Fig. 1.

*Character 1*.—A baculum without an abrupt distal bend is primitive for caniforms and mustelids. Any upward bend in the distal tip is peculiar to mustelids and is derived independently on several occasions. A weak bend is found independently in *Meles anakuma*, *Spilogale putorius*, *Poecilogale albinucha*, and the clade of *Gulo gulo*, *P. marshalli*, and *Martes*. Within the latter clade, the bend is more prominent (state 2) in *Martes gwatkinsii* and *Martes flavigula*. Independent derivations of this morphology also occur in *Lontra*, *Mustela*, *Taxidea taxus*, and *Vormela peregusna*.

*Character 2*.—A hook on the distal part of the os penis is a derived feature present only within mustelids. It unites *Mustela* with independent reversals to the primitive condition occurring in *Mustela erminea* and *Mustela frenata*. However, note that the latter would be a synapomorphy for the 2 species under the phylogeny of Abramov (2000b).

*Character 3*.—Shape of the stem in cross section varies among out-group taxa. Most species possess a purely triangular shape. Only the 2 procyonid species examined (state 2) and several pinniped species (state 1) display the 2 derived conditions. As such, although the ancestral mustelid form differs from the plesiomorphic caniform condition (state 0), it is equivocal between the 2 apomorphic states (1 and 2). This uncertainty, combined with the polytomy at the base of the mustelid radiation, makes tracing the evolution of this character difficult. The ancestral condition for most lineages is equivocal. Only *Mustela* clearly reverse primitively to rederive the triangular morphology, which universally is present in all the species examined (also independently in *Lontra* and *V. peregusna*). Both lutrines and mephitines display the apomorphic conditions, as do ''badgers'' (i.e., *Arctonyx*, *Meles*, *Mellivora*, *Melogale*, *Mydaus*, *Taxidea*). However, the intermediate morphology (state 1) does diagnose the clade of *Arctonyx collaris*, *Meles*, and *Mydaus javanensis*. Most of the remaining species, notably the clade of *G. gulo*, *P. marshalli*, and *Martes*, possess a baculum with a rounded stem.

*Character 4*.—The urethral groove shows a complicated evolutionary history, with a number of gains and losses in mustelids to which it is largely confined; only the canids *Canis lupus* and *Vulpes vulpes* (state 0) and the procyonid *Procyon lotor* (state 1) possess a urethral groove among the out-group taxa. Lack of a groove also is ancestral for mustelids. The polytomy at the base of the mustelids prevents an exact reconstruction of these characters, but the absence of a groove is found primitively in most of major lineages: mephitines, all the badgers with the exception of *Mellivora capensis* (state 0), *P. albinucha*, and from *Lyncodon patagonicus* to *Eira barbara*. Except for *S. ichnusae*, all lutrines possess a groove of some form, although there is no apparent pattern. *G. gulo*, *P. marshalli*, and most species of *Martes* possess a short, distal groove, which becomes increasingly pronounced in the sister species *Martes gwatkinsii* and *Martes flavigula* (state 0). All species of *Mustela* also have a long, strongly formed groove.

*Character 5*.—The primitive condition among caniforms is the absence of a distinct head on the baculum. Only otarioids, procyonids, and mustelids derive a head of some description. Unfortunately, the distribution of this character makes the ancestral condition for all mustelids and the major lineages within mustelids equivocal between states 0 and 2. Mephitines and lutrines lack a distinct head ancestrally, as does *Mustela*. This condition remains in most species within the 2 clades. The lutrines *Enhydra lutris* and the sister species *Lutra lutra* and *S. ichnusae* together with *Mustela felipei*, *Mustela nudipes*, and *Mustela strigidorsa* independently derived the intermediate state 1. The remaining mustelid species generally possess a bacular head. This includes all badgers (except *Mydaus javanensis*), which possess a well-marked head. The clade spanning from *Galictis vittata* to *Martes* primitively has a pronounced bacular head, before it weakens to become only slightly pronounced in *G. gulo*, *P. marshalli*, and most species of *Martes*.

*Character 6*.—The absence of an opening is primitive in mustelids. Derived occurrences of an opening are found independently in *Meles* and within *Martes* (all species except *Martes gwatkinsii* and *Martes flavigula*). The polytomy within *Martes* prevents a more exact reconstruction of this character within the genus.

*Character 7*.—The primitive condition among caniforms is of an undivided tip, which is found in all species except *Phoca vitulina*, in both procyonid species examined (*Potos flavus* and *P. lotor*), and among mustelids. The ancestral condition for mustelids is equivocal; however, most lineages are characterized primitively by an undivided tip (e.g., lutrines plus mephitines, most badgers, and within mustelines). Bacula with subdivided tips occur independently in most lutrine species, *Melogale personata*, *Mellivora capensis*, throughout the clade spanning from *L. patagonicus* to *Martes*, *Mustela nudipes*, *Mustela strigidorsa*, *Mustela felipei*, and *Mustela africana*.

*Character 8*.—An asymmetrical bacular tip is found only within mustelids and independently is derived a number of times within the family. It occurs among the majority of lutrines, including the clades of *Lutra lutra* plus *S. ichnusae*, and *Lutrogale perspicillata* plus *P. brasiliensis*. Other derivations of an asymmetrical tip include *Melogale personata*, *T. taxus*, *V. peregusna*, all species of *Mustela*, and the clade of *G. gulo*, *P. marshalli*, and *Martes*, with *Martes pennanti* regaining the ancestral condition.

*Character 9*.—The derived condition where the bacular head has additional projections occurs infrequently among caniforms: some otariids, *P. flavus*, and mustelids. Within mustelids, *V. peregnusa*, *G. gulo*, *G. vittata*, *Mustela felipei*, and *Martes gwatkinsii* plus *Martes flavigula* all possess the derived condition independently.

*Character 10*.—The distribution of this character is shown in Appendix II. Of the species listed as having relatively short or long bacula, this difference was significant (>1.96 *SD* from the regression line) in only a few species. Those with significantly shorter bacula were *Ailuropoda melanoleuca*, *Ailurus fulgens*, *Conepatus mesoleucus*, and *H. malayanus*. Only *Odobenus rosmarus* and *S. ichnusae* had significantly elongated bacula.

Bacula of average length are ancestral for caniforms and for all the caniform families examined herein. For nonmustelid species, relatively shorter bacula are derived independently in *A. melanoleuca*, *A. fulgens*, and *H. malayanus*. Relatively longer bacula are limited to independent appearances in *P. lotor* and several pinnipeds, *N. cinerea*, *O. rosmarus*, and *Phoca groenlandica*.

Most mustelids maintain the ancestral state of a baculum of average length. Relatively shorter or longer bacula are derived independently a number of times. Shorter bacula occur in *Mydaus javanensis*, *P. albinucha*, *P. brasiliensis*, and the mephitines *C. mesoleucus* and *Mephitis mephitis*. A relatively short baculum may represent a synapomorphy for all mephitines, followed by a reversal back to the ancestral conditions in *S. putorius* (accelerated transformation optimization). However, parallel derivations in the 2 mephitine species are equally parsimonious (delayed transformation optimization—Swofford and Maddison 1987). Relatively long bacula are found independently in *I. striatus*, *P. marshalli*, and the lutrines *E. lutris*, *Lontra canadensis*, and *S. ichnusae*. *Mustela felipei*, for which we lacked data on bacular length, was inferred by parsimony to possess bacula of average length.

Overall, we infer the ancestral mustelid baculum to be a remarkably simple structure. It is of average length (relative to that found in extant mustelids), with a straight, not triangular, stem that likely lacks a urethral groove and has a simple distal end that is for the most part not distinct from the rest of the bone (it may possess a distinct head, however).

## DISCUSSION

*Functional correlates of baculum length (size)*.—The general uniformity in length of the os penis observed in this study, whether across caniforms or across mustelids only, belies an important dichotomy present within Carnivora. To some extent, the uniformity is an artifact of examining only caniforms, which all possess the putative ancestral condition among carnivores of a much-elongated baculum (Dixson 1995). In contrast, some families within the other major carnivore clade, the Feliformia (‘‘cat-like carnivores’’: felids, herpestids, hyaenids, and viverrids), are characterized by an os penis that is sharply reduced or incompletely ossified (felids) or is lost completely (hyaenids and some viverrids). This length dichotomy is thought to be related to the duration of copulation, with a correlation between extended copulation times and an elongated os penis being observed, suggesting a structural or functional role for this bone such as protecting the urethra (Dixson 1995; also Ewer 1973; Long and Frank 1968). Fractures of the baculum have been reported in mustelids (Laidler 1982; Ruprecht 1994), which points to a large load being placed on the penis during the prolonged intromission pattern of copulation.

Caniforms are remarkably similar in relative bacular length. Most species have a baculum that is not significantly different from the average length found in mustelids. Even measuring bacular lengths relative to the caniform average did not alter this pattern much. When we performed this calculation, only *V. zerda* shifted categories (from having an average-sized to relatively short baculum). Therefore, it is probably not worthwhile seeking a functional explanation for what we believe is largely random variation in baculum length in mustelids or across caniforms as a whole. Our view is substantiated by the analyses of Larivière and Ferguson (2002), who found a lack of support in carnivores for various functional explanations of bacular length variation. Willemsen (1992) associated the relatively elongate baculum in otters with their aquatic lifestyle, but this observation is at best only weakly substantiated by our data. Only *E. lutris*, *Lontra canadensis*, and *S. ichnusae* have elongate bacula, whereas *P. brasiliensis* possesses a relatively short os penis; all remaining otters have ones of average length. A similar relation between elongate bacula and aquatic copulation in pinnipeds (Scheffer and Kenyon 1963) also is not supported by our data (also Dixson 1995). Finally, although some significant shortenings or lengthenings of the bacula do occur, they arise independently in diverse lineages with no obvious functional connection between the species. Otherwise, there is no consistent phylogenetic pattern for changes in baculum length among caniforms except possibly for mephitines where it is shorter in 2 of the 3 species examined.

Instead, functional explanations are perhaps more profitably directed at variation in qualitative bacular morphology. However, even here, different explanations may apply to different taxa (Dixson 1995). Therefore, we concentrate on possible evolutionary transformations of bacular morphology in mustelids.

*Evolution of the mustelid baculum*.—It is clear that a large os penis (compared with that found in feliforms) is primitive for caniforms and mustelids. Furthermore, we infer that the baculum of the mustelid common ancestor was a remarkably simple rod-like structure resembling the morphology found in extant species of mephitine. Unfortunately, paleontological evidence to support this latter assessment is lacking. Bacula for Oligocene and early Miocene ‘‘palaeomustelids,’’ which are diagnosed as such by the retention of a carnassial notch on the upper carnassial tooth (Wolsan 1993), are virtually unknown. A fragment of the baculum from *Megalictis* (=*Aelurocyon*) from the early Miocene of North America (Matthew 1907) does reveal that this archaic group had a relatively large os penis. The succeeding group of ‘‘neomustelids,’’ which are characterized by having lost the carnassial notch on the upper fourth premolar, already possessed a baculum with a complex head (e.g., *P. marshalli* from Pliocene of North America; Harrison 1982).

From the ancestral mustelid condition, it is possible to derive what we consider to be the major bacular forms in mustelids. One form is characterized by the presence of a distinct head with projections. These projections are usually paired, although the distal tip often is also divided into 3 (e.g., *G. gulo*, *Melogale moschata*), which also is observed in juvenile *E. lutris*. To some extent, we can place *G. vittata* and *G. cuja* in the same group because the small-paired knobs (‘‘horns’’) and a large central lobe of their bacula resemble the trifid tip in the above-mentioned forms. *E. barbara* also can be considered to belong to this group.

The paired projections can fuse to form an opening (e.g., most badgers and *Martes*) or not (e.g., *Melogale personata*, *P. marshalli*, and *S. ichnusae*). In the former case, a putative transformation sequence for the os penis is observable (Fig. 5). The fork-shaped distal tip in *Martes zibellina* (also present in juvenile specimens of badgers and lutrines) is closed to form a ring in *Martes martes*, *Martes americana*, and *Martes foina* (the projections are always fused in the latter species, but not necessarily in some specimens of the former 2 species), with the foramen thus formed becoming smaller in *Martes pennanti*. Continuation of this sequence would result in the complete closure of the foramen and possibly a flat, nearly triangular shaped head as in *T. taxus*. We base the polarity for this sequence on ontogenetic data where it is noteworthy that young individuals of badgers and lutrines also possess a bifurcated head. However, the reverse polarity makes more sense according to the tree of Bininda-Emonds et al. (1999) and the times of divergence that it presents.

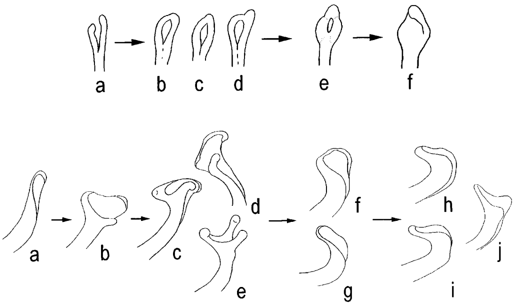

FIG. 5.—Putative evolution of the head of the baculum. Top—in *Martes* and *Taxidea taxus*: a) *Martes zibellina*, b) *Martes martes*, c) *Martes americana*, d) *Martes foina*, e) *Martes pennanti*, f) *Taxidea taxus*. All views are of the distal tip in dorsal view. Bottom—in *Mustela*: a) *Mustela erminea*, b) *Mustela africana* (from Izor and Peterson 1985), c) *Mustela nudipes*, d) *Mustela strigidorsa*, e) *Mustela felipei* (from Izor and de la Torre 1978), f) *Mustela lutreola*, g) *Mustela sibirica*, h) *Mustela putorius*, i) *Mustela vison*, j) *Mustela nivalis* (abnormal specimen from the Netherlands). All views are of the distal tip from the left side.

A different evolutionary pathway is demonstrated by *Mellivora capensis*, *Ictonyx*, *V. peregusna*, and *Mustela* in which the head is either absent or flattened, spoon-shaped or cup-shaped. In those cases where the head is not pronounced, the distal tip of the os penis is hook-shaped. *V. peregusna* and *Mustela* are further characterized by a strongly developed urethral groove. Finally, a tendency toward complication of the baculum by the formation of a distal hook is observed within *Mustela* (Fig. 5). From a simple, weakly curved baculum (*Mustela erminea* and *Mustela frenata*), the distal tip is flattened (*Mustela africana*) with small projections developing on it (*Mustela felipei*, *Mustela nudipes*, and *Mustela strigidorsa*), which are subsequently lost while the tip is bent upward (*Mustela itatsi*, *Mustela lutreola*, and *Mustela sibirica*) to finally form an actual hook (*Mustela altaica*, *Mustela eversmanii*, *Mustela kathiah*, *Mustela nigripes*, *Mustela nivalis*, *Mustela putorius*, *Mustela subpalmata*, *Mustela vison*). Evidence for this series, with a late appearance of hook in the evolution of the baculum in *Mustela*, again derives from ontogenetic information; it is not easily reconcilable with the phylogeny of Bininda-Emonds et al. (1999). In immature males of the last group, the hook is not yet developed and baculum is a rod-like, slightly curved structure resembling that of *Mustela erminea* and *Mustela frenata* (e.g., *Mustela vison*; Tarasov 1984).

Therefore, 3 major apomorphies are apparent in the development of the mustelid os penis: a slight reduction in length, increased complication of the head, and development of the urethral groove. Although the baculum as a whole is highly diagnostic of most genera, these pathways have probably occurred independently in all adaptive lineages to varying extents. Some parallels are particularly noteworthy. The division of the distal tip in *Mustela felipei* is reminiscent of that in *Melogale moschata* or *G. gulo*. The characteristic wide, leaf-shaped lobe and opposing finger-shaped outgrowth of the bacular head of *P. marshalli* is also found in *Mustela strigidorsa* and *Mustela nudipes*. Special attention also should be given to the similarity in structure between the distantly related genera *G. gulo* and *Melogale moschata*, or *P. marshalli* and *S. ichnusae*, in which the cranial and dental characters otherwise differ considerably.

Analogous examples of morphological parallelism also are observed with species from other caniform families, notably procyonids. For example, the bifurcated head in *P. lotor* resembles that of *Lutra lutra*, and the distal trifid tip of *P. flavus* is quite similar to that in *G. gulo*. *Nasua nasua* also has a trifid tip on its baculum. In contrast, *Bassariscus astutus* has a simple rod-shaped baculum with a slightly extended and flattened distal tip (Burt 1960), which partly resembles the bacula of *L. patagonicus* and some mephitines.

*Systematic value of the baculum.*—The taxonomic importance of bacular structure among closely related forms has long been appreciated. The species-specific nature of bacular morphology causes it to be an excellent character for species diagnosis and taxonomy, assessing the affinity of fossil species, and elucidating relationships among closely related genera (Baryshnikov and Abramov 1997, 1998; Lavrenchenko and Baskevich 1996; Packard 1960; Patterson and Thaeler 1982 and references therein; Pocock 1918; Rabeder 1976; White 1953). This especially has been the case in Carnivora (e.g., Abramov 2000b; Baryshnikov 2001; Burt 1960; Chaine 1926; Didier 1947a, 1947b, 1948; Morejohn 1975; Pocock 1941; Tumlinson and McDaniel 1984; van Zyll de Jong 1972). This utility may derive from the fact that many proposed functional hypotheses to explain variation in bacular morphology (e.g., a pleiotropic side effect or a mechanism for prereproductive isolation) relate to species-level phenomena.

Despite this, 2 factors limit the utility of using bacular characters to elucidate phylogeny. First, there is the high amount of convergence that we noted, both within mustelids and across caniforms as a whole. Second, even on a more restricted scale, notable differences in the shape of os penis can occur between closely related species. This potentially hinders the discovery of shared derived features. For example, strong differences occur between *S. ichnusae* and other lutrines, between *Lutra lutra* and *Lontra*, or between the sister species *Martes flavigula* and *Martes gwatkinsii* and remaining species in *Martes*. These differences could have arisen either due to an early phylogenetic separation or rapid changes in the structure of the os penis during a short period of time. The latter supposition appears to be more realistic in case of the insular isolation of *S. ichnusae*, where its separation from the Eurasian genus *Lutra* occurred relatively recently (Middle Pleistocene—Willemsen 1992).

Still, we feel that the os penis can provide useful phylogenetic information. Much of the convergence we observed results from defining our characters too generally so that they were applicable across all mustelids. However, gross bacular structure is informative at very inclusive levels within Carnivora, where it distinguishes the clades Canidae (large bacula consisting of 2 bony plates grown together), Arctoidea (large, rod-shaped baculum), and Feliformia (reduced bacula that are lost entirely in some groups). Bacular morphology also should be informative at less inclusive levels, particularly around the generic or subgeneric levels, with more specific coding schemes individually tailored for each genus and when combined with other data sources such as morphology of the basicranial region.

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## APPENDIX I

*Specimen list.*—The following species (with sample sizes in parentheses; extinct species are preceded by †) were examined from the following museum collections: American Museum of Natural History in New York; Biological and Soil Research Institute of the Far East Division, Russian Academy of Sciences, Vladivostok, Russia; Field Museum of Natural History in Chicago, Illinois; Illinois State Museum in Springfield, Illinois; Illinois University Champaigne-Urbana in Urbana, Illinois; Muséum National d'Histoire Naturelle, Paris, France; Natural History Museum, London, United Kingdom; Naturhistoriska Riksmuseet, Stockholm, Sweden; National Science Museum, Tokyo, Japan; Zoological Institute, Russian Academy of Sciences, St. Petersburg, Russia; Zoological Museum, Helsinki, Finland; Zoological Museum of Moscow University, Moscow, Russia; and Zoological Museum, Siberian Branch of Russian Academy of Sciences, Novosibirsk, Russia. Eight additional species where information was obtained from the literature are listed with the sources. Subfamily taxonomy again follows Wozencraft (1993) for convenience.

Lutrinae.—*Amblonyx cinereus* (4), *Enhydra lutris* (8), *Lontra canadensis* (2), *Lontra longicaudis* (1), *Lutra lutra* (2), *Lutrogale perspicillata* (1), *Pteronura brasiliensis* (1), †*Sardolutra ichnusae* (from Malatesta 1977).

Melinae.—*Arctonyx collaris* (2), *Meles anakuma* (10), *Meles meles* (8), *Melogale moschata* (from Pocock 1941), *Melogale personata* (2), *Mydaus javanensis* (1).

Mellivorinae.—*Mellivora capensis* (from Pocock 1918).

Mephitinae.—*Conepatus mesoleucus* (1), *Mephitis mephitis* (2), *Spilogale putorius* (from Mead 1967).

Mustelinae.—*Eira barbara* (3), *Galictis cuja* (5), *Galictis vittata* (from Mondolfi 1987), *Gulo gulo* (9), *Ictonyx striatus* (5), *Ictonyx libyca* (3), *Lyncodon patagonicus* (2), *Martes americana* (4), *Martes flavigula* (4), *Martes foina* (6), *Martes gwatkinsii* (1), *Martes martes* (17), *Martes pennanti* (2), *Martes zibellina* (45), *Mustela africana* (from Izor and Petersen 1985), *Mustela altaica* (5), *Mustela erminea* (29), *Mustela eversmanii* (8), *Mustela felipei* (from Izor and de la Torre 1978), *Mustela frenata* (3), *Mustela itatsi* (10), *Mustela kathiah* (2), *Mustela lutreola* (5), *Mustela lutreolina* (1), *Mustela nigripes* (2), *Mustela nivalis* (31), *Mustela nudipes* (1), *Mustela putorius* (11), *Mustela sibirica* (25), *Mustela strigidorsa* (2), *Mustela subpalmata* (1), *Mustela vison* (5), †*Plesiogulo marshalli* (from Harrison 1982), *Poecilogale albinucha* (1), *Vormela peregusna* (5).

Taxidiinae.—*Taxidea taxus* (3).

Caniformia excluding Mustelidae (outgroups).—*Ailuropoda melanoleuca* (1), *Ailurus fulgens* (1), *Callorhinus ursinus* (3), *Canis lupus* (10), *Eumetopias jubatus* (4), *Leptonychotes weddellii* (1), *Odobenus rosmarus* (6), *Phoca groenlandica* (3), *Phoca vitulina* (4), *Potos flavus* (1), *Procyon lotor* (2), *Ursus arctos* (3), *Vulpes vulpes* (8), *Zalophus californianus* (2).

## Appendix II

Condylobasal length of skull and baculum lengths for adult male caniforms. Relative length refers to length of baculum relative to the mustelid average (see text): 0 = shorter by 1 *SD*, 1 = average, 2 = longer by 1 *SD*. Those species with an asterisk were significantly shorter or longer than the mustelid average (i.e., residuals greater than 1.96 *SD* from the regression line). Data for condylobasal and bacular lengths not collected by the authors were obtained from the following sources, as indicated: 1, Burt (1960); 2, Didier (1946); 3, Didier (1950); 4, Gittleman and Van Valkenburg (1997); 5, Hall and Kelson (1959); 6, Harrison (1982); 7, Heptner et al. (1976); 8, Izor and Petersen (1985); 9, Malatesta (1977); 10, Mead (1967); 11, Mondolfi (1987); 12, Ognev (1931); 13, Pocock (1918); 14, Scheffer and Kenyon (1963); 15, Vaz-Ferreira (1968). Nonmustelid taxa in boldface were used as outgroups for the parsimony analysis and for the mapping of characters 1–9; mapping of character 10 used all taxa listed.

| Family, species | Condylobasal length (mm) | Source | Baculum length (mm) | Relative bacular length | Source |
|---|---|---|---|---|---|
| Canidae | | | | | |
| *Alopex lagopus* | 127.90 | 12 | 59.30 | 1 | 1 |
| *Canis aureus* | 156.20 | 12 | 62.67 | 1 | 2 |
| *Canis latrans* | 193.60 | 3 | 76.80 | 1 | 1 |
| ***Canis lupus*** | 237.10 | | 100.83 | 1 | 1, 2 |
| *Nyctereutes procyonoides* | 119.20 | | 72.50 | 1 | 2 |
| *Urocyon cinereoargenteus* | 125.30 | 4 | 53.10 | 1 | 1 |
| *Vulpes vulpes* | 145.50 | | 57.60 | 1 | 1, 2 |
| ***Vulpes zerda*** | 84.70 | | 31.00 | 1 | 2 |
| Otariidae | | | | | |
| *Arctocephalus tropicalis* | 240.60 | | 128.00 | 1 | 14 |
| ***Callorhinus ursinus*** | 232.30 | 7 | 142.00 | 1 | 14 |
| ***Eumetopias jubatus*** | 389.70 | 7 | 206.00 | 1 | 14 |
| *Neophoca cinerea* | 295.38 | | 260.00 | 2 | 14 |
| *Otaria byronia* | 330.41 | | 146.00 | 1 | 15 |
| ***Zalophus californianus*** | 279.20 | | 148.50 | 1 | 1, 14 |
| Odobenidae | | | | | |
| ***Odobenus rosmarus*** | 369.00 | 7 | 528.68 | 2* | 1, 14 |
| Phocidae | | | | | |
| *Cystophora cristata* | 271.50 | 7 | 210.00 | 1 | 14 |
| *Erignathus barbatus* | 220.50 | 7 | 140.00 | 1 | 14 |
| *Halichoerus grypus* | 261.90 | | 163.00 | 1 | 14 |
| *Hydrurga leptonyx* | 374.04 | | 233.00 | 1 | 14 |
| ***Leptonychotes weddellii*** | 284.81 | | 218.00 | 1 | 14 |
| *Lobodon carcinophagus* | 281.37 | | 220.00 | 1 | 14 |
| *Mirounga angustirostris* | 503.98 | | 274.00 | 1 | 14 |
| *Mirounga leonina* | 479.98 | | 331.00 | 1 | 14 |
| *Monachus schauinslandi* | 238.55 | | 183.00 | 1 | 14 |
| *Phoca fasciata* | 191.70 | 7 | 142.00 | 1 | 14 |
| ***Phoca groenlandica*** | 210.60 | 7 | 185.00 | 2 | 14 |
| *Phoca hispida* | 185.70 | 7 | 118.00 | 1 | 14 |
| ***Phoca vitulina*** | 205.00 | 7 | 137.00 | 1 | 14 |
| Procyonidae | | | | | |
| ***Potos flavus*** | 87.80 | 4 | 71.30 | 1 | 1, 3 |
| *Bassariscus astutus* | 82.00 | 5 | 46.80 | 1 | 1 |
| *Bassariscus sumichrasti* | | | 47.00 | 1 | 1 |
| *Nasua narica* | 115.00 | 5 | 82.53 | 1 | 1, 3 |
| *Nasua nasua* | 109.50 | 4 | 85.00 | 1 | 1, 3 |
| *Procyon cancrivorus* | 125.80 | 5 | 94.65 | 1 | 1, 3 |
| ***Procyon lotor*** | 114.60 | 4 | 98.68 | 2 | 1, 3 |

APPENDIX II.—Continued.

| Family, species | Condylobasal length (mm) | Source | Baculum length (mm) | Relative bacular length | Source |
|---|---|---|---|---|---|
| Ursidae | | | | | |
| ***Ailurus fulgens*** | 105.40 | | 23.00 | 0* | |
| ***Ailuropoda melanoleuca*** | 251.00 | | 24.00 | 0* | |
| *Helarctos malayanus* | 238.40 | | 52.00 | 0* | 3 |
| *Melursus ursinus* | 307.30 | | 151.00 | 1 | 3 |
| *Ursus americanus* | 272.20 | | 145.23 | 1 | 1, 3 |
| ***Ursus arctos*** | 340.00 | | 134.00 | 1 | 3 |
| *Ursus maritimus* | 375.00 | | 168.00 | 1 | 3 |
| *Ursus thibetanus* | 291.60 | | 118.25 | 1 | 3 |
| Mustelidae | | | | | |
| *Amblonyx cinereus* | 86.00 | | 39.00 | 1 | |
| *Enhydra lutris* | 137.50 | | 155.00 | 2 | |
| *Lontra canadensis* | 110.00 | | 95.00 | 2 | |
| *Lontra longicaudis* | 114.80 | | 69.60 | 1 | |
| *Lutra lutra* | 119.50 | | 65.00 | 1 | |
| *Lutrogale perspicillata* | 122.10 | | 50.00 | 1 | |
| *Pteronura brasiliensis* | 154.80 | | 39.20 | 0* | |
| *Sardolutra ichnusae* | 102.00 | 9 | 152.00 | 2* | 9 |
| *Arctonyx collaris* | 134.00 | | 82.00 | 1 | |
| *Meles meles* | 130.80 | | 70.00 | 1 | |
| *Meles anakuma* | 125.50 | | 68.30 | 1 | |
| *Melogale personata* | 84.00 | | 52.00 | 1 | |
| *Mydaus javanensis* | 90.10 | | 30.30 | 0 | |
| *Taxidea taxus* | 125.00 | | 92.00 | 1 | |
| *Mellivora capensis* | 138.00 | | 65.50 | 1 | 13 |
| *Conepatus mesoleucus* | 73.00 | | 13.00 | 0* | |
| *Mephitis mephitis* | 75.70 | | 20.60 | 0 | |
| *Spilogale putorius* | 50.70 | 4 | 20.50 | 1 | 10 |
| *Eira barbara* | 110.00 | | 78.00 | 1 | |
| *Galictis vittata* | 72.00 | | 55.80 | 1 | 11 |
| *Gulo gulo* | 144.70 | | 80.10 | 1 | |
| *Plesiogulo marshalli* | 169.50 | 6 | 182.00 | 2 | 6 |
| *Ictonyx libyca* | 54.00 | | 33.90 | 1 | |
| *Ictonyx striatus* | 65.00 | | 57.00 | 2 | |
| *Lyncodon patagonicus* | 55.60 | | 27.50 | 1 | |
| *Martes americana* | 85.20 | | 36.00 | 1 | |
| *Martes flavigula* | 108.00 | | 82.00 | 1 | |
| *Martes foina* | 83.00 | | 55.50 | 1 | |
| *Martes gwatkinsii* | 90.00 | | 57.30 | 1 | |
| *Martes martes* | 81.00 | | 37.00 | 1 | |
| *Martes pennanti* | 117.20 | | 96.70 | 1 | |
| *Martes zibellina* | 82.70 | | 37.40 | 1 | |
| *Mustela africana* | 51.20 | 8 | 31.00 | 1 | 8 |
| *Mustela altaica* | 43.00 | | 24.00 | 1 | |
| *Mustela erminea* | 42.00 | | 25.00 | 1 | |
| *Mustela eversmanii* | 71.00 | | 41.00 | 1 | |
| *Mustela frenata* | 46.00 | | 28.00 | 1 | |
| *Mustela itatsi* | 53.00 | | 29.00 | 1 | |
| *Mustela kathiah* | 50.10 | | 30.50 | 1 | |

APPENDIX II.—Continued.

| Family, species | Condylobasal length (mm) | Source | Baculum length (mm) | Relative bacular length | Source |
|---|---|---|---|---|---|
| *Mustela lutreola* | 63.00 | | 36.00 | 1 | |
| *Mustela lutreolina* | 58.50 | | 32.70 | 1 | |
| *Mustela nigripes* | 68.00 | | 37.00 | 1 | |
| *Mustela nivalis* | 33.00 | | 14.00 | 1 | |
| *Mustela nudipes* | 60.70 | | 46.00 | 1 | |
| *Mustela putorius* | 67.00 | | 37.00 | 1 | |
| *Mustela sibirica* | 60.00 | | 32.00 | 1 | |
| *Mustela strigidorsa* | 57.40 | | 40.70 | 1 | |
| *Mustela subpalmata* | 50.20 | | 25.90 | 1 | |
| *Mustela vison* | 67.00 | | 48.00 | 1 | |
| *Poecilogale albinucha* | 54.20 | | 18.80 | 0 | |
| *Vormela peregusna* | 56.40 | | 42.05 | 1 | |

APPENDIX III

Character states for the 10 morphological characters of the os penis used for cladistic analysis. (See ''Materials and Methods'' for descriptions of characters and states.) Missing value (character 10 for *Mustela felipei*) is indicated by a question mark.

| | Character | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 |
| *Canis lupus* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| *Vulpes vulpes* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| *Callorhinus ursinus* | 0 | 0 | 0 | 2 | 1 | 0 | 0 | 0 | 1 | 1 |
| *Eumetopias jubatus* | 0 | 0 | 1 | 2 | 2 | 0 | 0 | 0 | 0 | 1 |
| *Zalophus californianus* | 0 | 0 | 1 | 2 | 1 | 0 | 0 | 0 | 1 | 1 |
| *Odobenus rosmarus* | 0 | 0 | 1 | 2 | 2 | 0 | 0 | 0 | 0 | 2 |
| *Leptonychotes weddellii* | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 1 |
| *Phoca groenlandica* | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 2 |
| *Phoca vitulina* | 0 | 0 | 1 | 2 | 0 | 0 | 1 | 0 | 0 | 1 |
| *Potos flavus* | 0 | 0 | 2 | 2 | 2 | 0 | 1 | 0 | 1 | 1 |
| *Procyon lotor* | 2 | 0 | 2 | 1 | 1 | 0 | 1 | 0 | 0 | 2 |
| *Ailurus fulgens* | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Ailuropoda melanoleuca* | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Ursus arctos* | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 1 |
| *Amblonyx cinereus* | 0 | 0 | 2 | 1 | 0 | 0 | 1 | 1 | 0 | 1 |
| *Lontra canadensis* | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 |
| *Lontra longicaudis* | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| *Lutra lutra* | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 1 |
| *Lutrogale perspicillata* | 0 | 0 | 2 | 0 | 0 | 0 | 1 | 1 | 0 | 1 |
| *Enhydra lutris* | 0 | 0 | 2 | 0 | 1 | 0 | 0 | 0 | 0 | 2 |
| *Pteronura brasiliensis* | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 0 |
| *Sardolutra ichnusae* | 0 | 0 | 1 | 2 | 1 | 0 | 1 | 1 | 0 | 2 |
| *Conepatus mesoleucus* | 0 | 0 | 1 | 2 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Mephitis mephitis* | 0 | 0 | 2 | 2 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Spilogale putorius* | 1 | 0 | 2 | 2 | 0 | 0 | 0 | 0 | 0 | 1 |
| *Arctonyx collaris* | 0 | 0 | 1 | 2 | 2 | 0 | 0 | 0 | 0 | 1 |
| *Meles meles* | 0 | 0 | 1 | 2 | 2 | 1 | 0 | 0 | 0 | 1 |
| *Meles anakuma* | 1 | 0 | 1 | 2 | 2 | 1 | 0 | 0 | 0 | 1 |

APPENDIX III.—Continued.

| | Character | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 |
| *Mellivora capensis* | 0 | 0 | 1 | 0 | 2 | 0 | 1 | 0 | 0 | 1 |
| *Melogale personata* | 0 | 0 | 2 | 2 | 2 | 0 | 1 | 1 | 0 | 1 |
| *Mydaus javanensis* | 0 | 0 | 1 | 2 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Taxidea taxus* | 2 | 0 | 2 | 2 | 2 | 0 | 0 | 1 | 0 | 1 |
| *Eira barbara* | 0 | 0 | 1 | 2 | 2 | 0 | 0 | 0 | 0 | 1 |
| *Galictis vittata* | 0 | 0 | 1 | 2 | 2 | 0 | 1 | 0 | 1 | 1 |
| *Gulo gulo* | 1 | 0 | 2 | 1 | 1 | 0 | 1 | 1 | 1 | 1 |
| *Ictonyx libyca* | 0 | 0 | 2 | 2 | 2 | 0 | 0 | 0 | 0 | 1 |
| *Ictonyx striatus* | 0 | 0 | 2 | 0 | 2 | 0 | 0 | 0 | 0 | 2 |
| *Lyncodon patagonicus* | 0 | 0 | 2 | 2 | 0 | 0 | 0 | 0 | 0 | 1 |
| *Martes americana* | 1 | 0 | 2 | 1 | 1 | 1 | 0 | 1 | 0 | 1 |
| *Martes flavigula* | 2 | 0 | 2 | 0 | 1 | 0 | 1 | 1 | 1 | 1 |
| *Martes foina* | 1 | 0 | 2 | 1 | 1 | 1 | 0 | 1 | 0 | 1 |
| *Martes gwatkinsii* | 2 | 0 | 2 | 0 | 1 | 0 | 1 | 1 | 1 | 1 |
| *Martes martes* | 1 | 0 | 2 | 1 | 1 | 1 | 0 | 1 | 0 | 1 |
| *Martes pennanti* | 1 | 0 | 2 | 1 | 2 | 1 | 0 | 0 | 0 | 1 |
| *Martes zibellina* | 1 | 0 | 2 | 1 | 1 | 1 | 1 | 1 | 0 | 1 |
| *Mustela africana* | 2 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 |
| *Mustela altaica* | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 |
| *Mustela erminea* | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 |
| *Mustela eversmanii* | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 |
| *Mustela felipei* | 2 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | ? |
| *Mustela frenata* | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 |
| *Mustela itatsi* | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 |
| *Mustela kathiah* | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 |
| *Mustela lutreola* | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 |
| *Mustela lutreolina* | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 |
| *Mustela nigripes* | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 |
| *Mustela nivalis* | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 |
| *Mustela nudipes* | 2 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 1 |
| *Mustela putorius* | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 |
| *Mustela sibirica* | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 |
| *Mustela strigidorsa* | 2 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 1 |
| *Mustela subpalmata* | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 |
| *Mustela vison* | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 |
| *Plesiogulo marshalli* | 1 | 0 | 2 | 1 | 1 | 0 | 1 | 1 | 0 | 2 |
| *Poecilogale albinucha* | 1 | 0 | 2 | 2 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Vormela peregusna* | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 |