Syst. Biol. 64(2):294–306, 2015

DOI:10.1093/sysbio/syu107
Advance Access publication December 15, 2014

The More, the Better: The Use of Multiple Landmark Configurations to Solve the Phylogenetic Relationships in Musteloids

SANTIAGO A. CATALANO[1,2,*], MARCOS D. ERCOLI[1,3], AND FRANCISCO J. PREVOSTI[1,3,4]

[1]*Consejo Nacional de Investigaciones Científicas y Técnicas;* [2]*Unidad Ejecutora Lillo (UEL), Miguel Lillo 251, 4000 S.M. de Tucumán, Argentina;*
[3]*Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", División Mastozoología, Av. Angel Gallardo 470. C1405DJ Buenos Aires, Argentina; and*
[4]*Departamento de Ciencias Básicas, Universidad Nacional de Luján, Luján, Buenos Aires, Argentina*
**Correspondence to be sent to: Consejo Nacional de Investigaciones Científicas y Técnicas; Unidad Ejecutora Lillo (UEL), Miguel Lillo 251, 4000 S.M. de Tucumán, Argentina; Email: sacatalano@gmail.com*

Received 13 September 2014; reviews returned 3 November 2014; accepted 2 December 2014
Associate editor: Norm McLeod

Abstract.—Although the use of landmark data to study shape changes along a phylogenetic tree has become a common practice in evolutionary studies, the role of this sort of data for the inference of phylogenetic relationships remains under debate. Theoretical issues aside, the very existence of historical information in landmark data has been challenged, since phylogenetic analyses have often shown little congruence with alternative sources of evidence. However, most analyses conducted in the past were based upon a single landmark configuration, leaving it unsettled whether the incorporation of multiple configurations may improve the rather poor performance of this data source in most previous phylogenetic analyses. In the present study, we present a phylogenetic analysis of landmark data that combines information derived from several skeletal structures to derive a phylogenetic tree for musteloids. The analysis includes nine configurations representing different skeletal structures for 24 species. The resulting tree presents several notable concordances with phylogenetic hypotheses derived from molecular data. In particular, Mephitidae, Procyonidae, and Lutrinae plus the genera *Martes*, *Mustela*, *Galictis*, and *Procyon* were retrieved as monophyletic. In addition, other groupings were in agreement with molecular phylogenies or presented only minor discordances. Complementary analyses have also indicated that the results improve substantially when an increasing number of landmark configurations are included in the analysis. The results presented here thus highlight the importance of combining information from multiple structures to derive phylogenetic hypotheses from landmark data. [Landmark data, multiple configurations, Musteloidea, parsimony, phylogenetic analysis, shape characters.]

The idea of inferring phylogenies from morphogeometric data, landmarks in particular, was strongly discouraged during the years that followed the "geometric morphometric revolution." The concerns were mainly theoretical in nature. Although some researchers argued against the general use of landmark data in phylogenetics (e.g., Bookstein 1994), other studies criticized particular approaches developed to make use of this type of data (e.g., Adams et al. 1998; Monteiro 2000). However, this earlier position has moved toward a more open view: In recent years, several approaches have been proposed for the phylogenetic treatment of landmark data (Rohlf 2002; Lockwood et al. 2004; Caumul and Polly 2005; González-José et al. 2008; Catalano et al. 2010; Klingenberg and Gidaszewski 2010; Catalano and Goloboff 2012), and many empirical studies have been conducted (e.g., Cardini 2003; Lockwood et al. 2004; González-José et al. 2008; Panchetti et al. 2008; Chemisquy et al. 2009; Francoy et al. 2011; Scalici and Panchetti 2011; Cruz et al. 2012; Freitas et al. 2012; Maiorino et al. 2013; Voyta et al. 2013).

A common characteristic of most previous phylogenetic analyses of landmark data was the inclusion of only a single landmark configuration (i.e., a group of landmarks that describes the shape of a structure). Although in some cases the results obtained have presented some level of agreement with accepted phylogenies, such as in studies performed in elephant shrews (Panchetti et al. 2008; Scalici and Panchetti 2011) and in hominoids (González-José et al. 2008), the more general trend has been one of incongruence with alternative sources of evidence (Klingenberg and Gidaszewski 2010). The poor results generally obtained were interpreted by some authors (e.g., Klingenberg and Gidaszewski 2010) as indicating that landmark data may not be a suitable source of evidence for phylogenetic analyses. However, expecting to obtain a well-resolved and well-supported phylogeny from a single configuration may be too optimistic, especially when considering the number of structures required to derive phylogenetic hypotheses in traditional morphological analyses. Ultimately, the issue of whether or not the incorporation of multiple configurations into a single analysis can improve the results of a given study has not been previously evaluated. We, therefore, present here a phylogenetic analysis of 22 species of musteloids (Carnivora–Mammalia) that includes landmark data from nine different skeletal structures. No previous phylogenetic analysis has included this many landmark configurations. The phylogenetic analysis was performed using the approach described in Catalano et al. (2010), which extends the parsimony principle to the analysis of landmark data. The present study was designed to address two main questions:

1) Do landmark data present historical information that allows us to infer phylogenetic relationships in Musteloidea?
2) Do phylogenetic results improve—in terms of congruence with a reference phylogeny—when

an increasing number of skeletal structures are included in the analyses?

Musteloids as a case study.—Musteloidea is a diverse superfamily of the order Carnivora that includes approximately 80 species (Wilson and Mittermeier 2009; Sato et al. 2012). Musteloids include procyonids (coatis, kinkajou, olingos, and raccoons), mephitids (skunks and stink badgers), ailurids (red panda), and mustelids (grisons, weasels, martens, badgers, and otters). The systematics and phylogeny of this group have been extensively studied. Some of these analyses were based on morphological data (mostly dental and skeletal anatomy; see Wozencraft 1989; Decker and Wozencraft 1991; Bryant et al. 1993; Wyss and Flynn 1993; Finarelli 2008; Ahrens 2012) with general disagreement among those studies and also with the traditional taxonomy. The use of molecular characters has helped resolve some unsettled questions about musteloid phylogeny and has stabilized views on the internal relationships of Mustelidae and Procyonidae (e.g., Koepfli and Wayne 1998; Koepfli et al. 2007, 2008; Sato et al. 2012).

Members of Musteloidea present a wide range of habits, including terrestrial epigean, fossorial, semi-aquatic, scansorial, and fully arboreal (Ewer 1973; Taylor 1989; Schutz and Guralnick 2007; Wilson and Mittermeier 2009). A high degree of variation is also found in dietary types, with some species being herbivores (e.g., red panda), others frugivores (e.g., kinkajou), and others hypercarnivores (e.g., weasels) (Ewer 1973; Wilson and Mittermeier 2009). This ecological diversity is correlated with a wide range of morphologies, a fact that suggests that there is a strong morpho-functional relationship in several aspects of the anatomy of this group (Savage 1957; Ewer 1973; Riley 1985; van Valkenburgh 1987; Taylor 1989; Youlatos 2003; Schutz and Guralnick 2007; Fisher et al. 2008, 2009; Ercoli et al. 2013). The ample existing knowledge about the phylogenetic relationships and morphological variation for this group, together with the numerous specimens available for study in museum collections, make this group a good case study to evaluate the utility of landmark data for phylogenetic inferences.

Material and Methods

Sampling

A total of 22 species of musteloids were included in our analysis (Table 1). Taxon sampling included representatives of different taxonomic levels within Musteloidea—three families, seven subfamilies and 16 genera (representing 75%, 58%, and 48% of the total extant representatives of each of these taxonomic levels). This approach allowed us to evaluate the capability of landmark data to solve the phylogenetic relationships at different phylogenetic levels. Two species of Canidae were considered as functional outgroups. The selection of species was based on the availability of postcranial structures in the collections of the museums visited. Since the main premise of the present analysis was to include several skeletal structures representative of different anatomical regions, our taxon sampling was limited to those species that presented specimens with an almost complete skeleton. However, despite the existence of these limitations, the present phylogenic analysis of landmark data is one of the largest in terms of taxon sampling.

For each species, the number of specimens considered varied between one and 10 depending upon the species and structure, with an average of approximately three specimens per species/structure (Table 1; Supplementary Data 1 available on Dryad at http://dx.doi.org/10.5061/dryad.26m66). Landmarks were digitalized in two dimensions, and placed to represent the general shape of the structure analyzed while at the same time trying to capture most of the variation present in each structure (Fig. 1; Supplementary Data 2 available on Dryad at http://dx.doi.org/10.5061/dryad.26m66). Only the proximal portion of femur and the distal portion of the humerus were digitalized, since several museum specimens lacked the other parts of these bones. Two configurations (the axis and the sixth cervical vertebrae) were digitalized including semi-landmarks (Fig. 1). Landmark digitization and scaling were carried out using tpsDig 2.10 (Rohlf 2013).

Phylogenetic Searches

The complete procedure performed to obtain a phylogenetic hypothesis from landmark data is illustrated in Figure 2. First, all specimens from each species were superimposed using a General Procrustes Analysis (GPA; Gower 1975; Rohlf and Slice 1990). The consensus configurations derived from this step represent the shape of each species, and this procedure was repeated for all of the structures analyzed. Next, the consensus configurations representing each species were used to define a multiple superimposition by means of a new GPA, and this was again repeated for each structure. After a standardization step (see below), the multiple superimposition of each structure was incorporated into a matrix as a different character, generating a combined data set. Finally, the matrix was used to conduct the phylogenetic search.

The phylogenetic analyses were performed following the approach proposed by Catalano et al. (2010) for the analysis of landmark data in phylogenetics. This method is implemented in Tree Analysis using New Technology (TNT) phylogenetic software (Goloboff et al. 2008) and is a direct extension of the parsimony principle (*sensu* Farris 1983) for the analysis of landmark data. This approach maximizes the degree to which the similarity in landmark position in different taxa can be accounted for by common ancestry. The tree score is given by the sum of the landmark displacements along the tree. To allow all of the configurations to make an equal contribution to the selection of the phylogenetic hypothesis, a standardization procedure was conducted

TABLE 1. Species included in the phylogenetic analysis indicating the number of specimens per structure and species.

Species	Family, Subfamily	CV	LM	LAx	LVI	LEs	AHu	LUl	LIP	PFe
Aonyx cinerea	Mustelidae, Lutrinae	5	5	1	-	2	1	1	1	2
Conepatus chinga	Mephitidae	10	8	5	5	4	5	4	4	3
Eira barbara	Mustelidae, Guloninae	5	5	2	1	3	6	7	3	5
Galictis cuja	Mustelidae, Ictonychinae	4	4	11	7	10	4	8	10	9
Galictis vittata	Mustelidae, Ictonychinae	5	5	2	1	2	2	–	2	2
Ictonyx striatus	Mustelidae, Ictonychinae	4	4	1	–	2	3	1	–	2
Lontra canadensis	Mustelidae, Lutrinae	2	2	–	–	3	3	4	–	1
Lontra longicaudis	Mustelidae, Lutrinae	4	4	4	3	2	2	1	4	2
Lontra provocax	Mustelidae, Lutrinae	3	2	3	2	2	2	2	2	2
Lutra lutra	Mustelidae, Lutrinae	5	4	1	–	2	3	2	–	1
Lyncodon patagonicus	Mustelidae, Ictonychinae	4	3	3	1	4	3	4	3	4
Martes americana	Mustelidae, Guloninae	4	4	–	–	2	2	3	–	1
Martes martes	Mustelidae, Guloninae	1	1	1	–	1	2	2	1	1
Meles meles	Mustelidae, Melinae	4	4	1	1	1	1	1	1	1
Mustela frenata	Mustelidae, Mustelinae	3	5	1	1	4	4	2	2	1
Mustela vison	Mustelidae, Mustelinae	1	1	1	1	2	2	1	1	1
Nasua nasua	Procyonidae	5	3	2	3	3	3	3	2	2
Potos flavus	Procyonidae	4	4	1	1	4	5	4	1	2
Procyon cancrivorus	Procyonidae	4	4	5	3	4	4	3	5	5
Procyon lotor	Procyonidae	2	2	1	1	3	4	4	1	1
Pteronura brasiliensis	Mustelidae, Lutrinae	5	4	3	2	4	4	2	2	2
Spilogale putorius	Mephitidae	4	4	2	2	3	3	2	3	1
Canis lupus	Canidae (Outgroup)	3	1	1	1	3	4	2	1	2
Lycalopex griseus	Canidae (Outgroup)	1	1	1	1	1	1	1	1	1

Note: The assignment to families and subfamilies is based on Sato et al. (2012). CV = ventral view of the cranium; AHu = cranial view of the distal end of the humerus; LAx = lateral view of the axis; Les = lateral view of the scapula; LIP = lateral view of the pelvis; LUl = lateral view of the ulna; LVI = lateral view of the sixth cervical vertebra; LM = lateral view of the mandible; PFe = caudal view of the proximal end of the femur.

that downweights those configurations with more landmarks and/or a larger scale of change (Goloboff and Catalano 2011). A full description of the standardization procedure as well as a discussion of the standardization issue is included as Supplementary Data 3 (available on Dryad at http://dx.doi.org/10.5061/dryad.26m66).

The tree score and ancestral shapes were established using the algorithms described in Goloboff and Catalano (2011) to optimize landmark data on a tree. In summary, this approach consists of establishing the optimal ancestral positions of each landmark by means of a heuristic approximation, where a grid is placed over the space occupied by all of the observed positions for a given landmark. Each cell of the grid is considered as a possible state (i.e., position) for the inner nodes. A cost matrix is built where the costs between states are the distances between the centers of each of the cells. Once each of the observed positions has been assigned to the corresponding cell, the optimal positions are established using a cost matrix algorithm (Sankoff and Rousseau 1975). The score can then be improved by repeating this Sankoff step, but this time superimposing a new grid over the optimal cell and the neighboring cells for each node. This step is called "nested Sankoff." Finally, the score can also be improved by iteratively modifying the position of each landmark at each internal node. In the present study, the landmark optimization was run with the following settings: A 6 × 6 grid of cells, one level of nested Sankoff; observed landmark positions included as states, and a final iterative improvement of the positions.

Since phylogenetic searches for landmark data are not yet implemented natively in TNT, the searches were conducted using a script written in TNT macro language. The search strategy consisted of 50 Random Addition Sequences (RAS = Wagner trees) followed by TBR (Tree Bisection Reconnection algorithm). All of the analyses were run on a cluster of fourteen 4-core CPUs using the parallel version of TNT. Phylogenetic uncertainty in relation to configuration and landmark sampling was analyzed by means of two independent resampling analyses. The resampling was done in the same way as in the implementation of symmetric resampling (Goloboff et al. 2003) in TNT: Each configuration/landmark had a 0.33 probability of being deleted, a 0.33 probability of having its weight duplicated, and a 0.33 probability of remaining unaltered. A total of 100 pseudoreplicates were conducted, with a single run of RAS + TBR per pseudoreplicate.

A series of phylogenetic analyses were conducted to assess whether the results would be improved by the inclusion of an increasing number of skeletal structures. Data sets were generated by including from one to eight configurations, and in each case all possible combinations of configurations were considered (i.e., 9 data sets that included a single configuration, 36 data sets that included two configurations, 84 data sets that included three configurations, etc.) Then, a single RAS–TBR replicate was run in each case. Additional analyses were conducted to evaluate the performance of each configuration analyzed independently and also when each configuration was removed from the complete

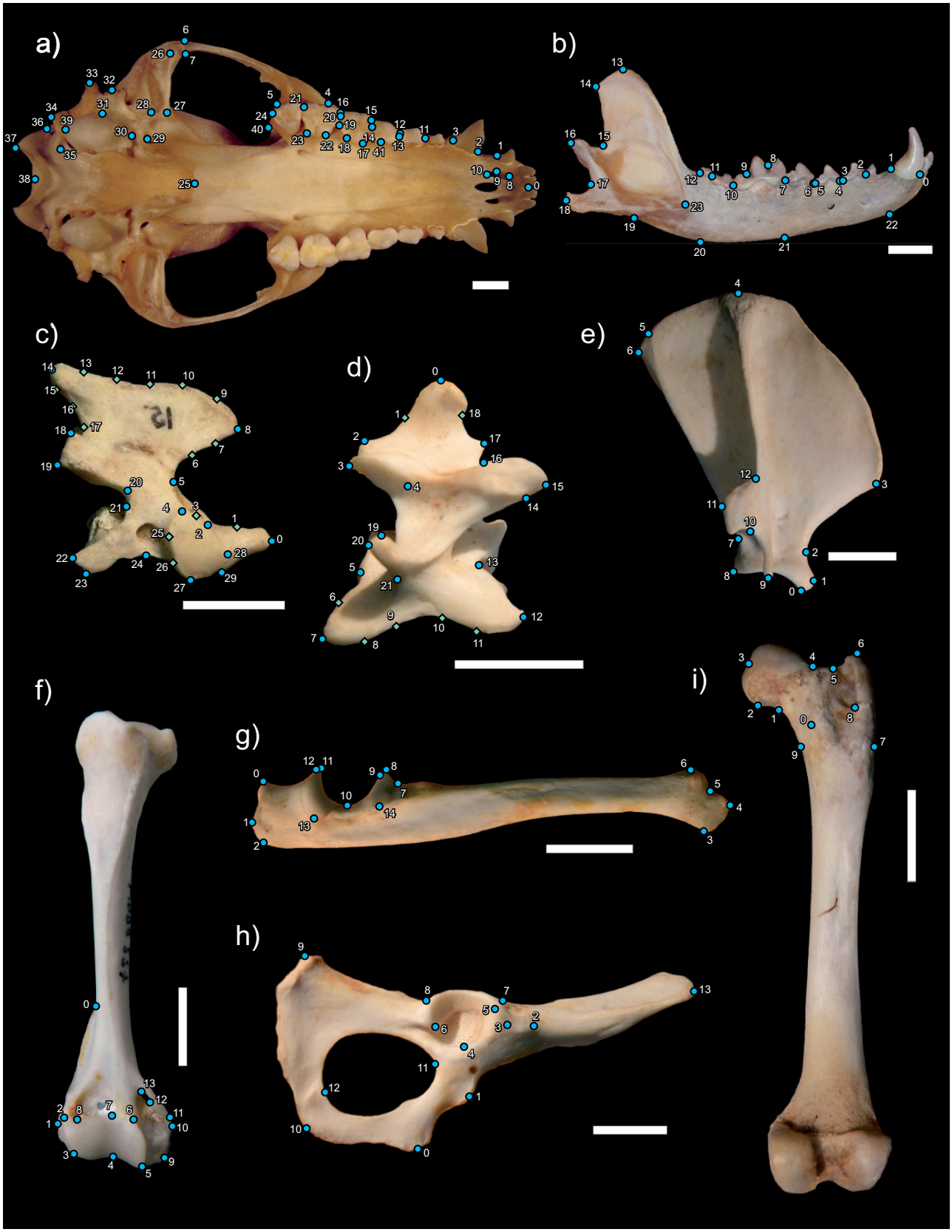

FIGURE 1. Skeletal structures analyzed, showing the position of each landmark: a) ventral view of cranium, b) lateral view of mandible, c) lateral view of axis, d) lateral view of sixth cervical vertebra, e) lateral view of scapula, f) anterior view of distal humerus, g) lateral view of ulna, h) lateral view of pelvis, and i) posterior view of proximal femur. Picture in (a) corresponds to *Nasua nasua*, picture in (b) corresponds to *Canis lupus*. All other images correspond to *Galictis cuja*. Diamonds in the axis and sixth cervical vertebra represent semi-landmarks. See Supplementary Data 2 (available on Dryad at http://dx.doi.org/10.5061/dryad.26m66) for a detailed definition of landmarks. Scale bar = 1mm.

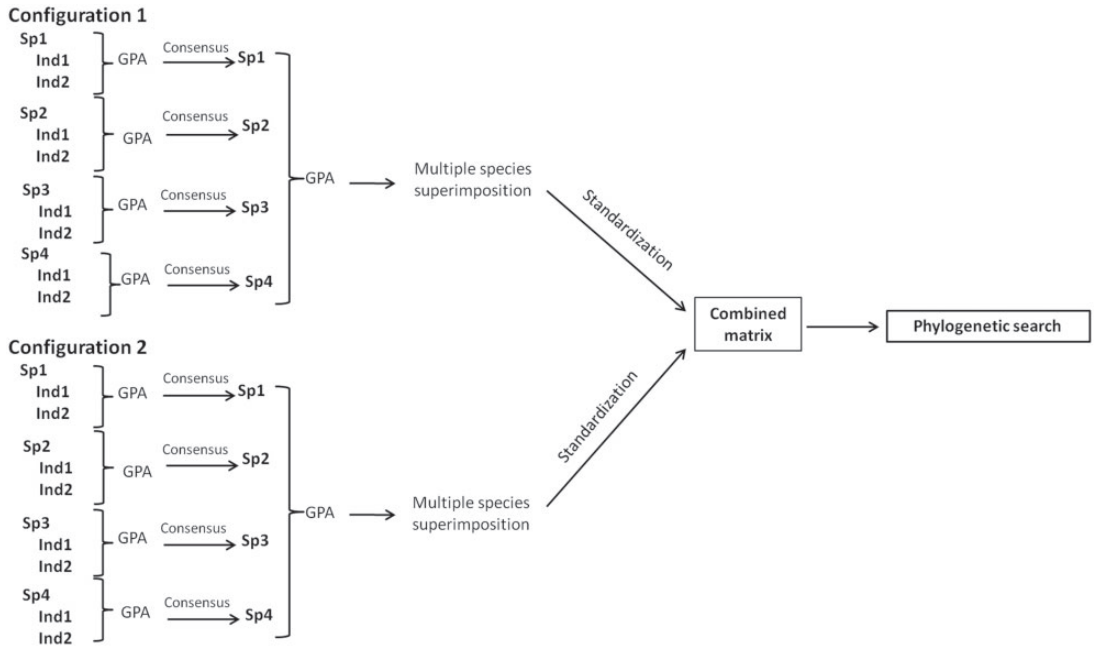

FIGURE 2. Schematic representation of the approach followed to derive phylogenetic hypotheses from multiple landmark configurations. GPA = generalized procrustes analysis; Sp = species; Ind = individual. For further explanation see text.

matrix. In this case, the search strategy involved five RAS + TBR.

The performance of each combination of configurations was evaluated by comparing the trees obtained against a reference topology derived from several recently published molecular phylogenetic analyses (Supplementary Data 4 available on Dryad at http://dx.doi.org/10.5061/dryad.26m66). We considered a topology based on molecular evidence as a reference for two reasons. First, molecular data offers a more independent source of evidence than traditional morphological characters, since some of the morphological characters considered in the published phylogenies for the group under study describe the shape of structures that are also included in the present analysis. Second, morphological phylogenetic analyses in musteloids present taxon samplings that are not very concordant with the one considered in the present study, making it difficult to compare results. The degree of concordance of the trees derived from landmark data and the reference tree was assessed by calculating a topological similarity measure based on the number of Subtree Pruning Regrafting (SPR) moves. This measure is the complement of the number of SPR moves required to convert one tree into the other, divided by $T - 2$, where T is the number of taxa (Goloboff 2007). The performance of each data set was also assessed by comparing the resulting trees with the accepted taxonomy for the group (trees included as Supplementary Data 5 available on Dryad at http://dx.doi.org/10.5061/dryad.26m66). We considered the familial and subfamilial groups proposed or followed by Sato et al. (2012). These analyses were automated using the new TNT tools for handling taxonomic information (Goloboff and Catalano 2012).

A series of complementary analyses were also conducted to evaluate if different methodological decisions made during the analysis (method of superimposition, standardization procedure, treatment of missing data, phylogeny used as reference, inclusion of semi-landmarks) may have affected the main conclusions obtained in the present study. A description of these complementary analyses as well as the results obtained is included in Supplementary Data 6 (available on Dryad at http://dx.doi.org/10.5061/dryad.26m66). Data matrix, best tree, and script used to run the phylogenetic search are included in Supplementary Data 7 (available on Dryad at http://dx.doi.org/10.5061/dryad.26m66).

RESULTS

The optimal (= shortest) tree obtained (Fig. 3) presents several congruencies with published taxonomic and phylogenetic studies (e.g., Flynn et al. 2005; Koepfli et al. 2007, 2008; Sato et al. 2009, 2012; Eizirik et al. 2010). Musteloidea, Mephitidae, Procyonidae, and Lutrinae were retrieved as monophyletic. In addition, four out of the five genera with more than one species included in the analysis were monophyletic (*Galictis*, *Martes*, *Mustela*, and *Procyon*), with the only exception being the genus *Lontra* since *Pteronura brasiliensis* appears intermingled with the three *Lontra* species included. The best tree obtained presents nine clades that correspond to accepted taxonomic categories, and 12 out of 21 nodes (57%) are shared between the best tree and the molecular reference tree. Although the optimal tree differs from the molecular reference tree in seven SPR moves, a

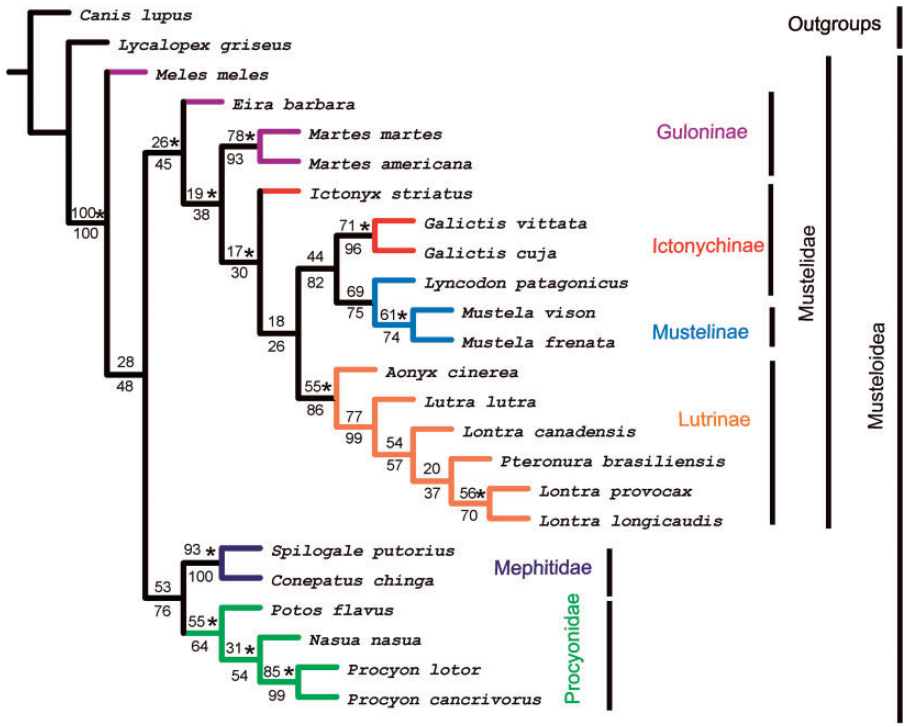

FIGURE 3. Optimal tree obtained in the combined analysis of nine different skeletal structures (score 34.180). Numbers above branches indicate support values when configurations were resampled. Nodes below branches indicate support values when landmarks were resampled. Asterisks indicate nodes shared with the molecular reference tree.

comparison of 10,000 randomly generated trees with the molecular reference tree yielded much higher numbers of SPR moves (average of 18.9 moves, minimum of 12 moves). Searching for the worst binary tree (that with the highest score in terms of the criteria considered in this study) produced a tree that did not share any group with the accepted taxonomy, and differed from the molecular tree in 21 moves. These comparisons strongly suggest that the correspondence between the tree obtained from landmark data and both the molecular reference tree and the taxonomy was by no means coincidental.

In general, the phylogenetic analyses based only on a single landmark configuration yielded poor results and in all cases these results were worse than those obtained when considering the complete data set (Table 2). The best performance was obtained for the scapula (six taxonomic groups retrieved), whereas the worst results were obtained for the ulnae (one taxonomic group retrieved). Searches were also conducted by excluding one configuration at a time. The number of taxonomic groups retrieved was similar regardless of which configuration was excluded (Table 2), although the resulting trees differed in terms of the particular groups obtained (Supplementary Data 5 available on Dryad at http://dx.doi.org/10.5061/dryad.26m66).

The phylogenetic searches conducted considering a variable number of configurations showed that inclusion of more landmark configurations clearly improves the results (Fig. 4). This trend was observed in terms of the number of taxonomic groups retrieved as well as in terms of topological similarity (according to the SPR metric and number of nodes shared), between the obtained trees and the reference molecular tree.

TABLE 2. Number of taxonomic groups retrieved when each configuration was analyzed individually (second column) and when each configuration was excluded from the complete matrix (third column)

	Single configuration	Configuration excluded from the matrix
Cranium	5	8
Humerus	4	9
Axis	2	9
Scapula	6	9
Pelvis	3	9
Ulnae	1	9
Sixth Cervical	4	9
Mandible	4	8
Femur	4	9

DISCUSSION

The results of the present study clearly show that landmark data can be an important source of evidence for phylogenetic analysis. Although not completely congruent with the accepted phylogeny for musteloids, several taxonomic groups were monophyletic and others were retrieved with low inaccuracy. Another relevant finding from the present study is that, at least for the analyzed data set, inclusion of a higher number of landmark configurations (representing the shapes

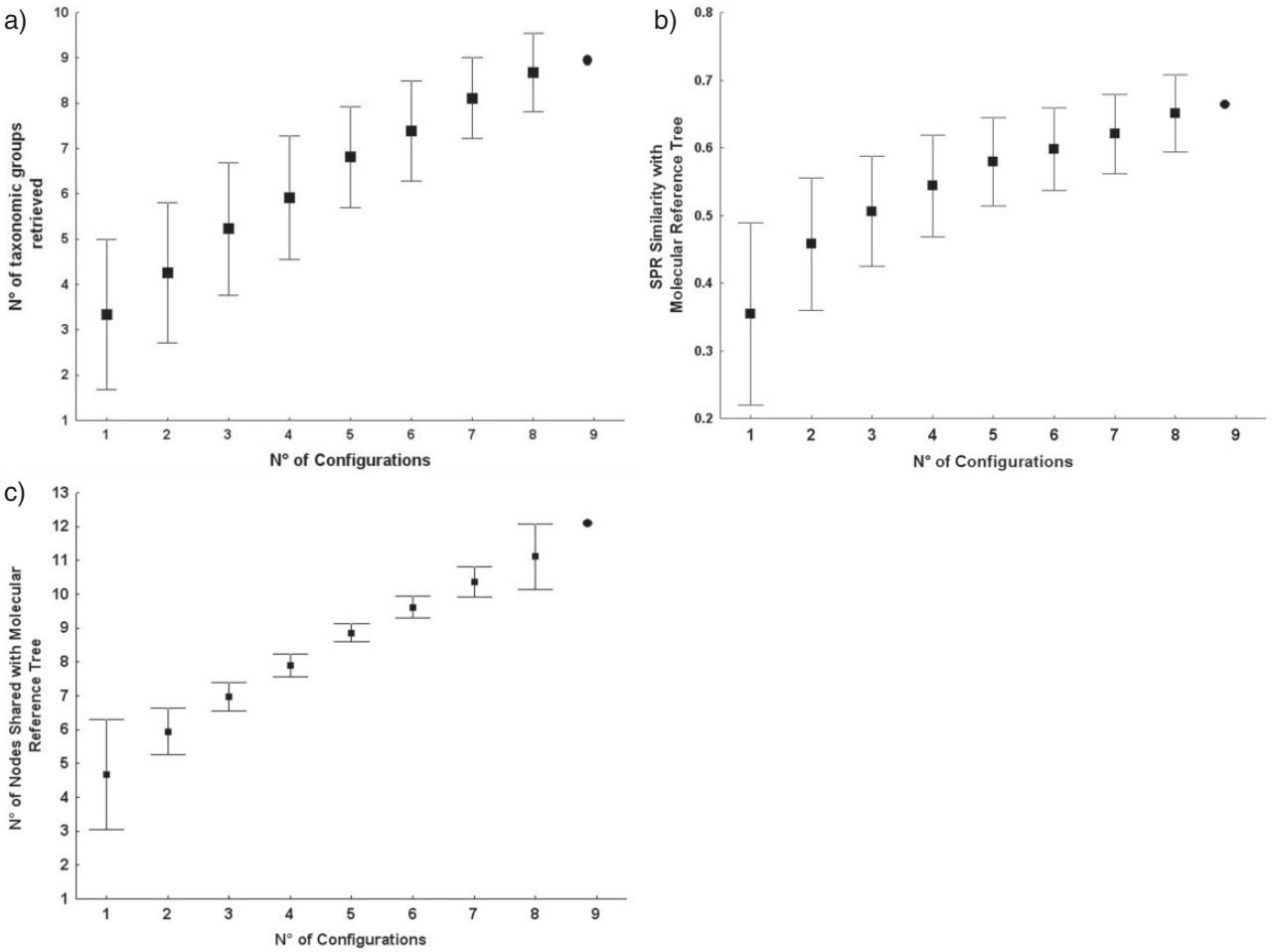

FIGURE 4. Correspondence between the trees obtained considering a variable number of landmark configurations and previous phylogenetic and taxonomic schemes. a) Number of clades in agreement with accepted taxonomy. b) SPR similarity between the obtained trees and the molecular reference tree. c) Number of nodes shared between the obtained trees and the molecular reference tree. The mean values (± SD) for the trees derived from all possible combinations of configurations (for a given number of configurations) are shown.

of different structures) clearly improves the results in terms of the congruence with alternative sources of evidence.

Comparison with Previous Phylogenetic Analyses

Current musteloid systematics are based mainly on molecular data generated during the last 10 years (e.g., Koepfli et al. 2007, 2008; Eizirik et al. 2010; Wolsan and Sato 2010; Sato et al. 2012). The results obtained in the present study, based on landmark data, are congruent in general with the relationships defined in those studies. Out of 21 nodes (57%), 12 were shared between the best tree obtained in the present analysis and the reference molecular tree. This congruence with previous analyses can be examined in greater detail by means of a group-by-group comparison. For example, Musteloidea, Mephitidae, Procyonidae, and Lutrinae were monophyletic in the present study. The internal relationships obtained for Procyonidae, as well as the monophyly of the genera *Martes*, *Mustela*, and *Galictis* are in agreement with previous analyses (Koepfli et al. 2007, 2008; Sato et al. 2012). The clade formed by Guloninae, Ictonychinae, Lutrinae, and Mustelinae was also recovered by recent DNA studies (Koepfli et al. 2008; Sato et al. 2012). The position of *Martes* species as sister taxa of Mustelinae + Ictonychinae + Lutrinae, is congruent with molecular analyses, although *Eira* appeared in a more basal position in our study rather than as a sister taxon of *Martes*, making Guloninae paraphyletic. The position of Mustelinae and Ictonychinae are congruent with DNA data, since these are closer to Lutrinae than to other mustelids, although Ictonychinae is paraphyletic since *Ictonyx* is the sister taxa of other Ictonychinae plus Mustelinae and Lutrinae, and *Mustela* unexpectedly falls into a clade with *Galictis* and *Lyncodon*. In contrast, some other groupings are incompatible or present less agreement with the molecular trees. For example, Mustelidae is not monophyletic since *Meles* appears at the base of Musteloidea, and mephitids and procyonids are sister taxa (but see Agnarsson et al. 2010). Also, with the exception of the clade formed by *Lontra longicaudis* and

Lontra provocax (Vianna et al. 2010), the relationships within Lutrinae are not compatible with previous analyses (Dragoo and Honeycutt 1997; Koepfli and Wayne 1998; Flynn et al. 2005; Arnason et al. 2007; Koepfli et al. 2008; Sato et al. 2009, 2012).

Some groups retrieved in the present study agree more closely with molecular data than with previous morphological analyses based on discrete characters. For instance, most morphological studies place the skunks (Mephitidae) within Mustelidae and closely related to Lutrinae (Wozencraft 1989; Bryant et al. 1993; Wyss and Flynn 1993; Finarelli 2008), whereas DNA data and landmark data presented here place the skunks in a separate clade outside of Mustelidae. In contrast, in our study the placement of other taxa, such as in the case of *Meles* being outside of Mustelidae, seems to be incorrect, given that both molecular and discrete morphological characters place *Meles* within this group. Finally, some relationships found in our analysis are in agreement with both molecular and discrete morphological characters. This is the case for example in the internal relationships within Procyonidae, which are in agreement with the results obtained by Decker and Wozencraft (1989), Ahrens (2012), Koepfli et al. (2007), and Eizirik et al. (2010).

Multiple Landmark Configurations in Phylogenetic Analyses

The results of the present study indicate that the inclusion of an increasing number of landmark configurations in the analysis improves the results obtained in terms of congruence with the accepted phylogeny for the group. Although our complete data set included a much greater amount of evidence than previous phylogenetic analyses based on landmark data, it seems that even more data should be included to obtain a well-supported and well-resolved phylogeny for musteloids. Extrapolation of the trend observed between the number of configurations and the number of taxonomic groups retrieved in Figure 4 supports this conclusion.

The support values derived from resampling configurations were highly variable along the tree (from 17% to 100%). Interestingly, the nodes that agree with the molecular reference tree present, on average, a much higher support value than those of incompatible nodes (69% vs. 34% when configurations were resampled and 78% vs. 50% when landmarks were resampled). This suggests that the retrieval of incorrect groupings is more closely related to a lack of information than to a strong phylogenetic signal supporting alternative groupings.

The results presented here are more promising than most of previous analyses that have empirically evaluated the phylogenetic utility of landmark data. Although some previous analyses have shown partial agreement with alternative sources of evidence, the results were generally poor (Klingenberg and Gidaszewski 2010). Given that almost all previous analyses were based on a single landmark configuration, the more encouraging results presented here are probably associated with the simultaneous analysis of multiple landmark configurations. This explanation is also strongly supported by the clear correlation found between the number of skeletal structures included in the analysis and the correspondence with the molecular reference topology (Fig. 4).

The advantage of including multiple landmark configurations as shown in the present analysis seems so predictable that in principle it is difficult to comprehend why most previous analyses have included only a single configuration. One possible explanation for this is the fact that most of the methods proposed to analyze landmark data in phylogenetics are only able to analyze one configuration at a time (at least as currently implemented). This has probably in turn led to conclusions about the utility of landmark data in phylogenetics that cannot be directly derived from the results obtained. For instance, Klingenberg and Gidaszewski (2010) found that although the configuration analyzed in their study presented a low level of homoplasy, the tree derived from landmark data was incongruent with a well-supported molecular tree. Based upon these results, the authors concluded that morphometric data may not provide reliable information for inferring phylogenies. However, the conclusion drawn by these authors only follows from their results if their wing shape data cannot be combined with data from other structures. The low homoplasy in wing shape found by Klingenberg and Gidaszewski (2010) may very well indicate that combining information from this structure with data from other structures may help to correctly define some groupings. It is again worth noting in relation to the present study that if we had based our conclusions on the analysis of a single configuration, the results would have been poor in most of the cases (Table 2). Since Klingenberg and Gidaszewski (2010) did in fact discuss the potential advantages of including several configurations in the same analysis, it seems likely that their conclusion that landmark data may not provide reliable information was driven by the assumption that phylogenetic methods can analyze only a single configuration.

Cardini and Elton (2008) also discussed the amount of information required to allow phylogenetic conclusions to be derived from landmark data. They cite Oxnard (2000) to support the inclusion of multiple characters in the analysis. However, the phylogenetic hypothesis they present was based on a single module (the one with the strongest phylogenetic signal). In this case, the approach considered for their analysis did not present a limitation in terms of incorporating multiple configurations into the same analysis: Since the characters they considered were the scores derived from a Principal Component Analysis (PCA). The authors could have combined the information from several modules into the same analysis as was done by González-José et al. (2008)—whether PCA scores are suitable for use in phylogenetic analysis is a different issue, Catalano et al. (2010) and Adams et al. (2011).

Selecting Landmark Configurations for Phylogenetic Analyses

One concern about the use of landmark data in phylogenetics is that these characters would present high levels of homoplasy (Klingenberg and Gidaszewski 2010). Since the structures analyzed are generally associated with processes of adaptation, they would be prone to reversals and parallelisms that would in turn complicate the inference of phylogenetic relationships from landmark data. The results obtained in the present study show that including structures associated with adaptive processes does not necessary lead to incorrect phylogenetic conclusions. For example, changes supporting Lutrinae include postcranial modifications such as a shorter and more caudally positioned symphysis of the pelvis, a longer ischial corpus, and a relatively dorsal projection of the iliac wing (Fig. 5a). These changes are probably associated with adaptation to aquatic locomotion, since as suggested by morpho-functional studies in otters these features would provide more maneuverability and propulsion strength in aquatic environments (Lewis 2008; Peigné et al. 2008). The inclusion of several skeletal units in a single analysis allows phylogenetic relationships to be correctly inferred even if similar changes occur in parallel in two groups. This can be illustrated in our analysis for the case of *Conepatus* and

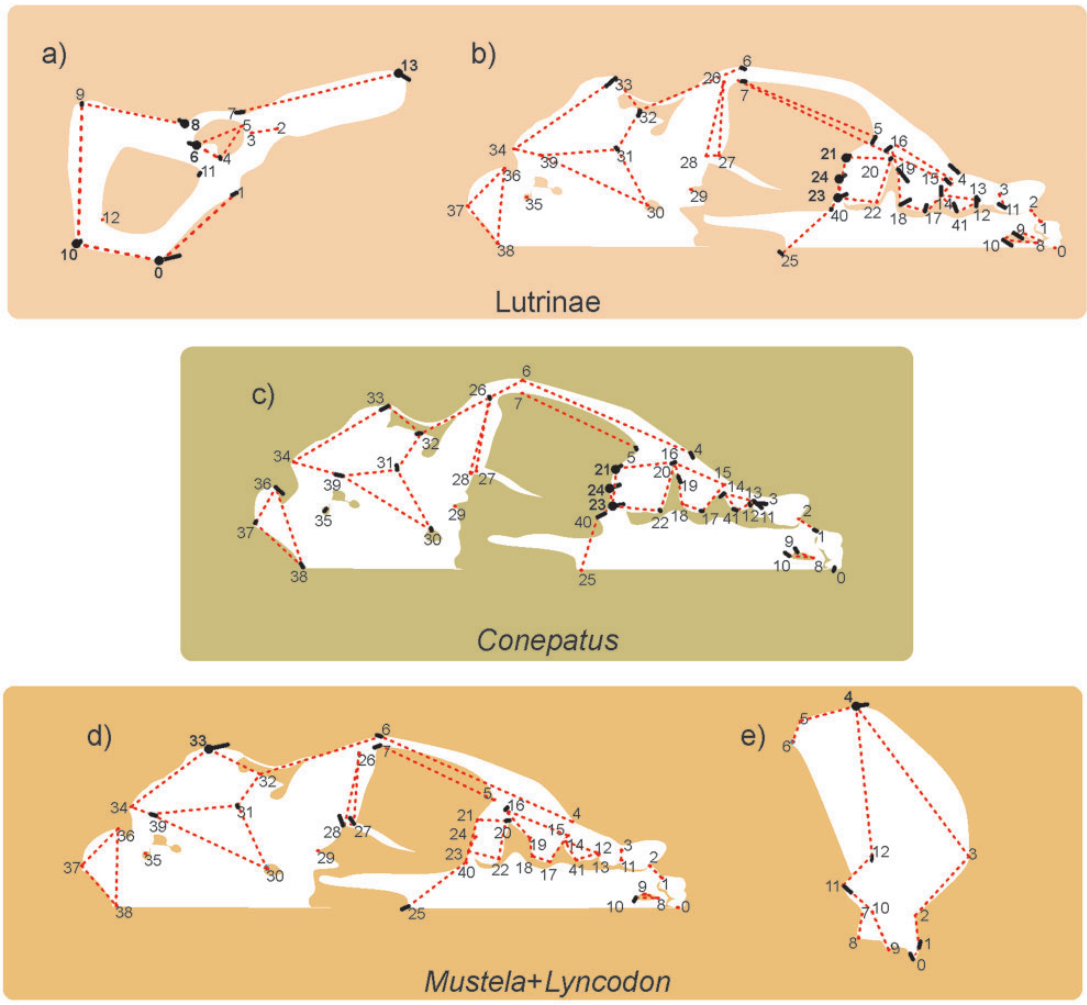

FIGURE 5. a) Optimization of landmark characters on the optimal tree (Fig. 3), suggests a probable adaptive nature of shape changes that support some groupings: A shortening and caudal positioning of the symphysis of the pelvis (lm 0 and lm 10), the enlargement of the ischial corpus (lm 6 and lm 8), and a dorsal projection of the iliac wing (lm 13) represent a unique reconfiguration of the hip of Lutrinae, probably associated to propulsion during aquatic locomotion. b, c) Other possible adaptive changes, convergent in lutrines and *Conepatus*, including the enlargement of the M1 (lm 21, lm 23 and lm 24), do not affect the phylogenetic position of these taxa. d, e) Morphological convergences may explain the incorrect placement of some taxa: The caudal position of the mastoid process (lm 33), and the reduction of the vertebral margin of scapula (lm 4), are features related to predatory habits and small sizes of *Lyncodon* and Mustelinae, two taxa that appear together in the phylogenetic tree. Ancestral shapes for Lutrinae (a, b); *Conepatus* (c); and Mustelinae+*Lyncodon* (d, e); pelvis in lateral view (a); cranium in ventral view (b–d); scapula in lateral view (e). Dashed lines represent reconstructed shapes. Solid lines indicate the change in position of each landmark from the ancestor to the corresponding node.

Lutrinae. Although both taxa present an enlargement of the M1 molar (Fig. 5b,c), a change associated with less carnivorous habits, they do not form a clade in the optimal tree. Nevertheless, it is still possible to recognize certain cases where the misplacement of some taxa is in fact related to this issue. For example, the position of both species of *Mustela* as a sister clade of *Lyncodon* is supported by a caudally positioned mastoid process (Fig. 5d), a trait that can be associated with similar predatory habits and hypercarnivorous diets. Other converging postcranial traits, such as reduction of the vertebral margin of the scapula (where weight-bearing muscles insert, Fisher et al. (2008); Fig. 5e) or the muscle attachments on the humerus and the femur, could be related to the similarities seen in these taxa in terms of their small size and specialization in predation of fossorial rodents. The incorrect placement of *Mustela* within this clade would, therefore, be a product of convergences related to these similar specializations (Ewer 1973; Prevosti and Pardiñas 2001).

The improved results obtained by inclusion of an increasing number of landmark configurations raises the question of whether any configuration available should be included in the analysis or whether, alternatively, some sort of quality control should be carried out before a particular configuration is selected for inclusion. Some researchers have proposed to analyze those configurations presenting a significant phylogenetic signal determined beforethe analysis (Cardini and Elton 2008). However, this reduces the utility of landmark data to cases where a reference phylogeny exists. One possible solution, rather than excluding certain configurations beforethe analysis, is to adopt methods that allow the weight of each character (configuration) to be defined during the analysis in accordance with its congruence with the rest of the characters. One such method is known as implied weighting (Goloboff 1993; Goloboff 2014), an approach that is already implemented in TNT (Goloboff et al. 2008) for the analysis of landmark data.

The results presented here indicate that no decisive judgment regarding the suitability of landmark data in phylogenetic analysis can be arrived at based on analysis of a single landmark configuration. As a direct consequence of this, any method that intends to evaluate the utility of landmark data for reconstructing phylogenies should be able to analyze multiple configurations simultaneously.

Landmark Data and Traditional Characters

The use of landmark data in phylogenetics has been the subject of much discussion (e.g., Bookstein 1994; Rohlf 1998; Monteiro 2000). Although the peculiarities of this type of data require special cautions to be exercised when treated in a phylogenetic context, the behavior of landmark data in the present analysis resembles, in several respects, that of traditional characters. First, the results presented here strongly suggest that, to obtain good results, the number of structures to be included in a phylogenetic analysis should be much higher than previously considered, probably including a similar numbers of structures as those included in the analysis of traditional morphological characters. Another point that highlights the similar behavior of landmark data and traditional characters is related to the sampling size within each species. A clear phylogenetic pattern was retrieved in the present study even when only a few specimens per species were considered and when the shape for each species was represented by a consensus configuration. An important conclusion that can be derived from the results presented here is that the amount of phylogenetic information found in the postcranial elements is far from negligible (Table 2), contrary to the traditional conception of previous morphological studies in this group (Wyss and Flynn 1993; Wesley-Hunt and Flynn 2005; but see Spaulding and Flynn 2012), where postcranial elements had been virtually obviated as a data source. One possible explanation for this previous disregard is that it is more difficult to describe the variation present in postcranial elements as discrete states, in contrast to the features of the cranium and mandible. In the latter case, the complexity of these elements is represented by many subunits (i.e., complexes of bones and teeth) and many specific, localized anatomical accidents (e.g., sutures, foramina), which may help to describe the variation in different discrete states. Landmark configurations can, therefore, provide better description of the morphological variability present in the postcranial elements and improve the performance of this source of data in phylogenetic analyses.

Concluding Remarks

In the age of phylogenomics, the importance of morphometric data for phylogenetic reconstruction may be disputed. However, the advantages of including morphological data in phylogenetic inferences have already been noted by several authors (e.g., Wiens 2004; Wheeler 2008; Assis 2009; Giribet 2010) and most of these advantages also apply to morphometric data. The most obvious advantage is the potential for including taxa known only from fossils as well as species that are rare or difficult to collect but that are present in museum collections. In addition, the analysis of morphological data also provides a potential source of alternative evidence that can be used to identify potential biases in molecular data. At last but not least, phylogenetic morphological studies generate a vast amount of biological knowledge—anatomical, morphological, etc.—presented in a systematized and ordered manner. This is the type of knowledge that at the end represents the most important data for systematists. Although the number of molecular characters will still overwhelm morphological characters, the new technologies and data processing methods currently at hand are allowing an increasing number of morphological characters to be available

for phylogenetic analysis (Beutel and Kristensen 2012; Friedrich et al. 2014). In particular, some recent technologies are now more readily available for use by systematists and morphologists (micro-computed tomography, 3D laser scanning, and confocal laser scanning microscopy) and are allowing morphological studies to be expanded into character systems seldom used in phylogenetics (e.g., soft parts). These new technologies are also complemented by new techniques for data acquisition (Schunke et al. 2012), automated processing (MacLeod 2007, 2008; Boyer et al. 2011), image storage, and data sharing (Berquist et al. 2012; Ziegler and Menze 2013), all of which can greatly improve the future contributions of morphometric characters to phylogenetics.

The use of landmark data to infer phylogenetic relationships is a relatively new area of research. Irrespective of any theoretical or methodological concerns, the degree to which such data will be used in the future as an additional source of evidence will depend upon its empirical performance. It is hoped that the present study will make a contribution in this direction.

Supplementary Material

Data available from the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.26m66.

Funding

This work was supported by CONICET Consejo Nacional de Investigaciones Científicas y Técnicas (PIP 0260 to S.A.C., PIP 164 to F.J.P.), ANPCyT Agencia Nacional De Promoción Científica y Tecnológica (PICT 2011-1679 to S.A.C., PICT 2011-309 to F.J.P.), and Universidad Nacional de Luján (to F.J.P.).

Acknowledgments

The authors thank the Willi Hennig Society for subsidizing the program TNT and making it freely available; the curators that helped during the visits to Museum Collections: Itatí Olivares, Diego Verzi, Ross MacPhee, Bruce Patterson, Min-Tho Schulenberg, William Stanley, Linda Gordon, Walter Joyce, Sergio Lucero, Valentina Segura, Mónica Diaz, Rubén Barquez, and David 'El Turko' Flores; and Mieczyslaw Wolsan, Ignacio Escapa, Rolando González-José, Iván Pérez, and three anonymous reviewers for critical reviews of an early version of the manuscript. M.D.E. wants to thank MACN for a PhD student Grant and F.J.P. to CONICET, FMNH, FLMNH, AMNH, CNRS, and JSPS for traveling grants. S.A.C. wants to thank the kind support of the German Science Foundation (DFG) for attending to the XXXII Meeting of the Willi Hennig Society (August 3–7, 2013 in Rostock) where this contribution was discussed.

References

Adams D., Rosenberg M. 1998. Partial warps, phylogeny, and ontogeny: a comment on Fink and Zelditch (1995). Syst. Biol. 47:168–173.
Adams D.C., Cardini A., Monteiro L.R., O'Higgins P., Rohlf F.J. 2011. Morphometrics and phylogenetics: principal components of shape from cranial modules are neither appropriate nor effective cladistic characters. J. Hum. Evol. 60:240–243
Agnarsson I., Matjaz K., May-collado L.J. 2010. Dogs, cats, and kin: a molecular species-level phylogeny of Carnivora. Mol. Phylogenet. Evol. 54:726–745.
Ahrens H.E. 2012. Craniodental characters and the relationships of Procyonidae (Mammalia: Carnivora). Zool. J. Linn. Soc. 164:669–713.
Arnason U., Gullberg A., Janke A., Kullberg M. 2007. Mitogenomic analyses of caniform relationships. Mol. Phylogenet. Evol. 45:863–874.
Assis L.C.S. 2009. Coherence, correspondence, and the renaissance of morphology in phylogenetic systematics. Cladistics. 25:528–544.
Berquist R.M., Gledhill K.M., Peterson M.W., Doan A.H., Baxter G.T. 2012. The digital fish library: using MRI to digitize, database, and document the morphological diversity of fish, PLoS ONE 7(4): e34499.
Beutel R.G., Kristensen N.P. 2012. Morphology and insect systematic in the era of phylogenomics. Arth. Struct. & Dev. 41:303–305.
Bookstein F.L. 1994. Can biometrical shape be a homologous character? In: Hall B.K., editor. Homology: the hierarchical basis of comparative biology. New York: Academic Press. p. 197–227.
Boyer D.M., Lipman Y., St. Clair E., Puente J., Patel B.A., Funkhouser T., Jernvall J., Daubechies I. 2011. Algorithms to automatically quantify the geometric similarity of anatomical surfaces. Proc. Natl Acad. Sci. USA. 108:18221–18226.
Bryant H.N., Russell A.P., Fitch W.D. 1993. Phylogenetic relationship within the extant Mustelidae (Carnivora): appraisal of the cladistic status of the Simpsonian subfamilies. Zool. J. Linn. Soc. 108:301–334.
Cardini A. 2003. The geometry of marmot (Rodentia: Sciuridae) mandible: phylogeny and patterns of morphological evolution. Syst. Biol. 52:186–205.
Cardini A., Elton S. 2008. Does the skull carry a phylogenetic signal? Evolution and modularity in the guenons. Biol. J. Linn. Soc. 93:813–834.
Catalano S.A., Goloboff P.A., Gianinni N. 2010. Phylogenetic morphometrics (I): the use of landmark data in a phylogenetic framework. Cladistics. 26:539–549.
Catalano S.A., Goloboff P.A. 2012. Simultaneously mapping and superimposing landmark configurations with parsimony as optimality criterion. Syst. Biol. 61:392–400.
Caumul R., Polly P.D. 2005. Phylogenetic and environmental components of morphological variation: skull, mandible, and molar shape in marmots (Marmota, Rodentia). Evolution. 59:2460–2472.
Chemisquy M.A., Prevosti F.J., Morrone O. 2009. Seed morphology in the tribe Chloraeeae (Orchidaceae): combining traditional and geometric morphometrics. Bot. J. Linn. Soc. 160:171–183.
Cruz, R.A.L., Pante, M.J.R., Rohlf, F.J. 2012. Geometric morphometric analysis of shell shape variation in *Conus* (Gastropoda: Conidae). Zool. J. Linn. Soc. 165:296–310.
Decker D.M., Wozencraft W.C. 1991. Phylogenetic analysis of recent procyonid genera. J. Mammal. 72:42–55.
Dragoo J.W., Honeycutt R.L. 1997. Systematics of mustelid-like carnivores. J. Mammal. 78:426–443.
Eizirik E., Murphy W.J., Koepfli K.-P., Johnson W.E., Dragoo J.W., Wayne R.K., O'Brien S.J. 2010. Pattern and timing of diversification of the mammalian order Carnivora inferred from multiple nuclear gene sequences. Mol. Phylogenet. Evol. 56:49–63.
Ercoli M.D., Busker F., Echarri S., Álvarez A., Morales M.M., Turazzini G.F. 2013. The functional and phylogenetic implications of the myology of the lumbar region, tail, and hindlimbs of the lesser grison (*Galictis cuja*). J. Mammal. Evol. 20:309–336.
Ewer R.F. 1973. The Carnivores. New York: Cornell University Press. p. 500.
Farris J. 1983. The logical basis of phylogenetic analysis. In: Platnick N.I., Funk V.A., editors. Advances in cladistics II. New York: Columbia University Press. p. 7–36.

Finarelli J.A. 2008. A total evidence phylogeny of the Arctoidea (Carnivora: Mammalia): relationships among basal taxa. J. Mammal. Evol. 15:231–259.
Fisher R.E., Adrian B., Elrod C., Hicks M. 2008. The phylogeny of the red panda (*Ailurus fulgens*): evidence from the hindlimb. J. Anat. 213:607–628.
Fisher R.E., Adrian B., Elrod C., Hicks M. 2009. The phylogeny of the red panda (*Ailurus fulgens*): evidence from the forelimb. J. Anat. 215:611–635.
Flynn J.J., Finarelli J.A., Zehr S., Hsu J., Nedbal M.A. 2005. Molecular phylogeny of the Carnivora (Mammalia): assessing the impact of increased sampling on resolving enigmatic relationships. Syst. Biol. 54:317–337.
Francoy T.M., Grassi M.L., Imperatriz-Fonseca V.L, May-Itzá W. de J., Quezada-Euán J.J.G. 2011. Geometric morphometrics of the wing as a tool for assigning genetic lineages and geographic origin in Melipona beecheii (Hymenoptera:Meliponini). Apidologie 42:499–507.
Freitas T.R.O., Fernandes F.A., Fornel R., Rorato P.A. 2012. An endemic new species of tuco-tuco, genus Ctenomys (Rodentia: Ctenomyidae) with a restricted geographic distribution in southern Brazil. J. Mammal. 95:1355–1367.
Friedrich F., Matsumura Y., Pohl H., Bai M., Hörnschemeyer T., Beutel R.G. 2014. Insect morphology in the age of phylogenomics: innovative techniques and its future role in systematic. Entomol. Sci. 17:1–24.
Giribet G. 2010. A new dimension in combining data? The use of morphology and phylogenomic data in metazoan systematics. Acta Zool. 91:11–19.
Goloboff P.A. 1993. Estimating character weights during tree search. Cladistics 9:83–91.
Goloboff P.A. 2007. Calculating SPR distances between trees. Cladistics 24:591–597.
Goloboff P.A. 2014. Extended implied weighting. Cladistics 30:260–272.
Goloboff P.A., Farris J.S., Källersjö M., Oxelman B., Ramírez M.J., Szumik C.A. 2003. Improvements to resampling measures of group support. Cladistics 19:324–332.
Goloboff P.A., Farris J.S., Nixon K.C. 2008. TNT, a free program for phylogenetic analysis. Cladistics 24:774–786.
Goloboff P.A., Catalano S.A. 2011. Phylogenetic morphometrics (II): algorithms for landmark optimization. Cladistics 27:42–51.
Goloboff P.A., Catalano S.A. 2012. GB-to-TNT: facilitating creation of matrices from GenBank and diagnosis of results in TNT. Cladistics 28:503–51.
González-José R., Escapa I., Neves W., Cúneo R., Pucciarelli N. 2008. Cladistic analysis of continuous modularized traits provides phylogenetic signals in Homo evolution. Nature 453:775–778.
Gower J.C. 1975. Generalized Procrustes analysis. Psychometrika 40:33–51.
Klingenberg C.P., Gidaszewski N.A. 2010. Testing and quantifying phylogenetic signals and homoplasy in morphometric data. Syst. Biol. 59:245–261.
Koepfli K.-P., Wayne R.K. 1998. Phylogenetic relationships of otters (Carnivora: Mustelidae) based on mitochondrial cytochrome b sequences. J. Zool. 246:401–416.
Koepfli K.-P., Gompper M.E., Eizirik E., Ho C., Linden L., Maldonado J. E., Wayne R. K. 2007. Phylogeny of the Procyonidae (Mammalia: Carnivora): molecules, morphology and the Great American Interchange. Mol. Phylogenet. Evol. 43:1076–1095.
Koepfli K.-P., Deere K. A., Slater G. J., Begg C., Begg K., Grassman L., Lucherini M., Veron G., Wayne R. K. 2008. Multigene phylogeny of the Mustelidae: resolving relationships, tempo and biogeographic history of a mammalian adaptive radiation. BMC Biol. 6:10.
Lewis M.E. 2008. The femur of extinct bunodont otters in Africa (Carnivora, Mustelidae, Lutrinae). Syst. Palaeontol. 7:607–627.
Lockwood C., Kimbel W., Lynch J. 2004. Morphometrics and hominoid phylogeny: support for a chimpanzee-human clade and differentiation among great ape subspecies. Proc. Natl Acad. Sci. USA. 101:4356–4360.
MacLeod N. 2007. Automated taxon identification in systematics: theory, approaches, and applications. Taylor & Francis Group London: CRC Press.
MacLeod N. 2008. Understanding morphology in systematic contexts: 3D specimen ordination and 3D specimen recognition. In: Wheeler Q., editor. The new taxonomy. Taylor & Francis Group, London: CRC Press. p. 143–210.
Maiorino L., Farke A.A., Kotsakis T., Piras P. 2013. Is torosaurus triceratops? Geometric morphometric evidence of late maastrichtian ceratopsid dinosaurs. PLoS ONE 8: e81608.
Monteiro L. 2000. Why morphometrics is special: the problem with using partial warps as characters for phylogenetic inference. Syst. Biol. 49:796–800.
Oxnard C.E. 2000. Morphometrics of the primate skeleton and the functional and developmental underpinnings of species diversity. In: O'Higgins P., Cohn M.J., editors. Development, growth and evolution. London: Academic Press. p. 235–263.
Panchetti F., Scalici M., Carpaneto G.M., Gibertini G. 2008. Shape and size variations in the cranium of elephant-shrews: a morphometric contribution to a phylogenetic debate. Zoomorphology. 127:69–82.
Peigné S., De Bonis L., Likius A., Mackaye H.T., Vignaud P., Brunet M. 2008. Late Miocene Carnivora from Chad: Lutrinae (Mustelidae). Zool. J. Linn. Soc. 152:793–846.
Prevosti F.J., Pardiñas U.F.J. 2001. Variaciones corologicas de lyncodon patagonicus (carnivora, mustelidae) durante el cuaternario. Mast. Neotrop. 8:21–39.
Riley M.A. 1985. An analysis of masticatory form and function in three mustelids (*Martes americana*, *Lutra canadensis*, *Enhydra lutris*). J. Mammal. 66:519–528.
Rohlf F.J. 1998. On application of geometric morphometrics to studies of ontogeny and phylogeny. Syst. Biol. 47:147–158.
Rohlf F.J. 2002. Geometric morphometrics and phylogeny. In: MacLeod N., Forey P.L., editors. Morphology, shape, and phylogeny. London: Taylor & Francis. p. 175–193.
Rohlf F.J., Slice D. 1990. Extensions of the Procrustes method for the optimal superimposition of landmarks. Syst. Zool. 39:40–59.
Rohlf F.J. 2013. TpsDig, ver. 2.17. Department of Ecology and Evolution, State University of New York at Stony Brook, Stony Brook.
Sankoff D., Rousseau P. 1975. Locating the vertices of a Steiner tree in an arbitrary space. Math. Program. 9:240–246.
Sato J. J., Wolsan M., Minami S., Hosoda T., Sinaga M.H., Hiyama K., Yamaguchi Y., Suzuki H. 2009. Deciphering and dating the red panda's ancestry and early adaptive radiation of Musteloidea. Mol. Phylogenet. Evol. 53:907–922.
Sato J.J., Wolsan M., Prevosti F.J., D'Elia G.D., Begg C., Begg K., Hosoda T., Campbell K.L., Suzuki H. 2012. Evolutionary and biogeographic history of weasel-like carnivorans (Musteloidea). Mol. Phylogenet. Evol. 63:745–757.
Savage R.J.G. 1957. The anatomy of *Potamotherium* an oligocene lutrine. Proc. Zool. Soc. Lond. 129:151–244.
Scalici M., Panchetti F. 2011. Morphological cranial diversity contributes to phylogeny in soft-furred sengis (Afrotheria, Macroscelidea). Zoology 114:85–94.
Schunke A.C., Bromiley P.A., Tautz D., Thacker N.A. 2012. TINA manual landmarking tool: software for the precise digitization of 3D landmarks. Frontiers Zool. 9:6.
Schutz H., Guralnick R.P. 2007. Postcranial element shape and function: assessing locomotor mode in extant and extinct mustelid carnivorans. Zool. J. Linn. Soc. 150:895–914.
Spaulding M., Flynn J.J. 2012. Phylogeny of the Carnivoramorpha: the impact of postcranial characters. J. Syst. Palaeontol. 10:653–677.
Taylor M.E. 1989. Locomotor adaptations by carnivores. In: Gittleman J.L., editor. Carnivore behavior, ecology, and evolution. Ithaca, New York: Cornell University Press. p. 382–409.
van Valkenburgh B. 1987. Skeletal indicators of locomotor behavior in living and extinct carnivores. J. Vertebr. Paleontol. 7:162–182.
Vianna J., Ayerdi P., Medina-Vogel G., Mangel J.C., Zeballos H., Apaza M., Faugeron S. 2010. Phylogeography of the marine otter (*Lontra felina*): historical and contemporary factors determining its distribution. J. Hered. 101:676–689.
Voyta L.L., Golenishchev F.N., Tiunov F.N. 2013. Analysis of shape and size variation of the first molar in Far-Eastern grey volves of genus *Alexandromys* (Rodentia:Cricetidae) from Russian fauna using geometric morphometrics. Russia J. Theriol. 12:19–32.
Wesley-Hunt G. D., Flynn J. J. 2005. Phylogeny of the Carnivora: basal relationships among the carnivoramorphans and assessment of the

position of 'Miacoidea' relative to crown clade Carnivora. J. of Syst. Palaeontol. 3:1–28.
Wheeler Q.D. 2008. Undisciplined thinking: morphology and Hennig's unfinished revolution. Syst. Entomol. 33:2–7.
Wiens J.J. 2004. The Role of morphological data in phylogeny reconstruction. Syst. Biol. 53:653–661.
Wilson D.E., Mittermeier R.A. 2009. Handbook of the mammals of the world, Vol. 1. Carnivores. Barcelona: Lynx Editions. p. 728.
Wolsan M., Sato J. 2010. Effects of data incompleteness on the relative performance of parsimony and Bayesian approaches in a supermatrix phylogenetic reconstruction of Mustelidae and Procyonidae (Carnivora). Cladistics 26:168–194.
Wozencraft W.C. 1989. The phylogeny of the recent Carnivora. In: Gittleman J.L., editor. Carnivore behavior, ecology and evolution. Ithaca, New York: Cornell University Press. p. 569–593.
Wyss A.R., Flynn J.J. 1993. A phylogenetic analysis and definition of the Carnivora. In: Szalay F.S., Novacek M.J., McKenna M.C., editors. Mammal phylogeny: placentals. New York: Springer. p. 32–52.
Youlatos D. 2003. Osteological correlates of tail prehensility in carnivorans. J. Zool. Lond. 259:423–430.
Ziegler A., Menze B.H. 2013. Accelerated acquisition, visualization, and analysis of zoo-anatomical data. In: Zander J., Mosterman J.P., editors. Computation for Humanity. Boca Ratón: CRC Press. p. 233–261.