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How much evidence is enough evidence for a new species?

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Voss et al. (this issue) took issue with our paper on a new species of *Tapirus* (Cozzuol et al. 2013), claiming that the evidence we presented was not “extraordinary” enough to support a new species of large mammal in the Amazon. We agree that a new large mammal species attracts more attention than a new smaller species; however, there is no real scientific reason for evidence requirements to be stricter due to animal size or popularity. We believe our evidence was sufficient to propose a new species and in this paper we counter point by point the objections raised by our colleagues. We revisit the phylogenetic analyses of molecular data, the multivariate analyses of morphometric data, the qualitative character differences, and indigenous knowledge.

We believe the key problem with the objections from Voss et al. (this issue) is found in the following sentence: “Have several generations of Neotropical mammalogists really failed to recognize a species of Recent megafauna that is said to be widely distributed in Amazonia?” The answer is, simply, yes. Specifically, they failed, as many others have done for many years, to listen to the local people more carefully; those people have been aware of the existence of this species for a long time. At the beginning of our research, which originally started with a single atypical skull, we verified information from the local population with several specialists. Many of the specialists knew that the locals recognized 2 species and considered their observations unreliable; however, none of them had taken the time to explore the possibility. How many times have we as scientists dismissed seemingly anecdotal information without even considering the possibility of its being accurate? This was just one of those cases.

PHYLOGENETIC ANALYSES OF MOLECULAR DATA

Voss et al. criticized our analysis of the molecular data supporting the new species, *Tapirus kabomani*, arguing that the support in the cytochrome *b* (*Cytb*)-based tree was too low to consider it as a separate species. They also said that the support from the concatenated sequences (*Cytb*, COI, and COII) was

also not more than a “moderate likelihood .” Voss et al. ran another analysis using only *Cytb* and “different methods” with the same sequences we used after downloading the data from GenBank. Unfortunately, they did not provide information about their methods (beyond indicating the use of Bayesian inference), software, or priors; therefore, we were not able to compare their results with our analyses.

The use of the sequences from GenBank is fine, although at Voss’s request we provided our complete data set, not just *Cytb*; however, Voss et al. did not use that data set in their reanalysis. They also used *T. indicus* as an outgroup instead of other Perissodactyla, as we did; they then argued that the use of *T. indicus* was more appropriate to resolve the shallow divergence between these species. This may be true; however, *T. indicus* has accumulated a large number of autapomorphies. Consequently, in the absence of a more external outgroup, these will be erroneously considered as plesiomorphies for the Neotropical tapirs, which may have a distorting effect in the results. Although using distant outgroups does risk producing the long-branch attraction effect, no long branch collapsed in our analysis. As we noted in the original paper, there was no



collapse in either the Bayesian tree or in the maximum-parsimony or maximum-likelihood trees, which match in all the significant clades with only minor differences.

In their result for the molecular phylogeny, Voss et al. found stronger support than we found for the *T. kabomani* clade, but they obtain a paraphyletic *T. terrestris*, which matches our own results and, quite surprisingly, also found a paraphyletic *T. pinchaque*. Besides the fact that reciprocal monophyly is not absolutely necessary to support a species, the most striking observation is that splitting *T. pinchaque* implies that this species should also be considered part of a *T. terrestris* clade. *T. pinchaque* is a well-established species that was never questioned before, and presents significant morphological differences with *T. terrestris* and all other *Tapirus* species. Besides its unique external morphology, the development of the skull in this species follows a comparatively primitive path, very different from that of *T. terrestris* (Holbrook 2002). In this respect, *T. kabomani* seems to follow a similarly primitive path, showing a relatively wide variation, resembling in part the extinct *T. polkensis* (Abernethy 2011, see below). Moreover, *T. pinchaque* differs from *T. terrestris* in the number of chromosomes, being $2n = 80$ in *T. terrestris* and $2n = 76$ in *T. pinchaque*, apparently due to 2 chromosome fusion events (Trifonov et al. 2008). Besides the number, the X chromosome of *T. pinchaque* is unique among tapirs and the Y chromosome of *T. terrestris* seems also to be unique (Houck et al. 2000).

Consequently, Voss et al. suggested that *T. pinchaque* may be just an ecomorph of *T. terrestris* or a recent species undergoing introgression by hybridization. The first assertion is difficult to maintain because of the above-mentioned differences. The second assertion seems to be because one of the clades that contains *T. pinchaque* specimens in its *Cytb* tree is linked to *T. terrestris*, which represents an individual haplotype from Rondonia State, Brazil; that location is about 1,500 km away in a straight line and 1,200 m of vertical offset. It is hard to explain how a haplotype that is known only from Rondonia makes its way to the high Andes. Besides, after consulting people who work on tapir ecology and conservation, we confirm that *T. terrestris* × *T. pinchaque* hybrids were never reported, either in nature or in captivity (P. Medici, pers. comm.). However, hybrids between *T. terrestris* and the more distant *T. bairdii* are known from captive animals, including an apparent F2 in the San Francisco Zoo (Anonymous 2009; McCarthy 2013).

We reran our analyses with *T. indicus* and also with *T. bairdii* as outgroups, but with the same methodology used in our original article, to determine if the outgroup choice influenced the results. *T. kabomani* still splits before *T. pinchaque* and *T. terrestris* in the *Cytb* tree with *T. indicus* as outgroup, but the clade reuniting the *T. pinchaque* and *T. terrestris* has low support. All species appear in a polytomy with *T. bairdii* as outgroup in the *Cytb* tree, whereas *T. kabomani* and *T. pinchaque* remain monophyletic. The discrepancies in topology we see may well be due to the effect of considering the *T. indicus* and *T. bairdii* autapomor-

phies as plesiomorphies for the ingroup. Despite these discrepancies, we obtained moderate support for the *T. kabomani* clade in the *Cytb* trees (Supporting Information S1 and S2) and strong support in the concatenated trees (Supporting Information S3 and S4). Besides, the *Cytb* trees show a well-supported *T. pinchaque* clade, and 4 well-supported clades containing *T. terrestris* specimens; these results were documented in our original paper with the Bayesian inference, and also with maximum-likelihood and maximum-parsimony methods. Since Voss et al. did not provide any information about the method they used in their analysis, we cannot ascertain the reasons for those discrepancies; however, we know now that the outgroup choice was not the reason.

We think the best conclusion is that there are 2 monophyletic species (*T. pinchaque* and *T. kabomani*) and a paraphyletic taxon called nominally *T. terrestris*, which is in need of more attention from both systematics and conservation perspectives.

The argument for small genetic divergence is debatable. If we use the limits proposed by Bradley and Bakker (2001), for example, not just *T. kabomani*, but also *T. pinchaque* and even *T. bairdii* should be considered conspecific with *T. terrestris*. However, as Ferguson (2002) noted: "Systematics needs tools that are parsimonious, have well-understood foundations, and that can be used consistently in a wide range of taxa. In terms of identification of new species, genetic divergence fails in all three of these criteria." Reciprocal monophyly has also not been considered necessary to recognize species (Kizirian and Donnelly 2004; Knowles and Carstens 2007).

We recognize that 2 of the *T. kabomani* specimens appearing in the *Cytb* tree were tissue samples derived from animals captured in nature without a voucher or morphological data about the external characteristics. However, it is common that samples obtained from nature (from local hunters or living animals in the wild) present no such data. For example, samples from living animals, specimens from which cannot be verified, were used recently to describe 2 new species of odontocete cetaceans (Charlton-Robb et al. 2011; Hrbek et al. 2014).

MULTIVARIATE ANALYSES OF MORPHOMETRIC DATA

Voss et al. criticized several points of our morphometric analysis. First, they focused on the supposed mix of ontogenetic states. It is important to note that all the *T. kabomani* are young adults or older. Of the 8 specimens, 4 have the M3 erupted and in use, and the remaining 4 had the P4 and M2 erupted. Thus, it cannot be argued that they may be just young or immature specimens of *T. terrestris*. The statement that individuals with erupted M1 are sexually mature was questioned for absence of reference, but this observation is our own. Among our collected specimens of *T. terrestris* from Acre and Rondonia states (Brazil), we found 3 females with DP4/M1 erupted that gave birth to at least 1 calf; consequently, these females are sexually mature.

Other specialists (i.e., Hulbert 2010; Gibson 2011) considered animals with P1–P3, DP4, M1, and p2–p3, dp4, m1 fully erupted and in use as subadults, not juveniles, as Voss et al. stated. Animals with P4, M2, p4, and m2 erupted and in use are considered young adults. In our reanalysis we removed all the individuals that belong to the subadult category, leaving only adults (young or older), to remove any doubts on this issue. Nonetheless, aside from suture closure, including subadult animals did not change the skull morphology or size significantly. A complete list of the specimens used, including locality, dental eruption state, sex, and collection number, can be found in Supporting Information S13.

This time we had the chance to include other important specimens that were not available in the original work. Noticeably, we included one of Theodore Roosevelt's specimens from Mato Grosso, Brazil (American Museum of Natural History [AMNH]36661), most likely the one mentioned in his book (Roosevelt 1914:142); he noted that it was a fully grown animal, but much smaller and the local people considered it a "different kind" (see Supporting Information S5 to S7 and S13). Roosevelt (1914) explicitly mentioned it was a "bull," so we consider it as male here, despite the sex being noted as unknown in the AMNH collection. This specimen is quite important because it comes from a locality more than 1,000 km from the type locality of *T. kabomani* in southern Amazonas State. The specimen also has the skin preserved and we requested a piece to try to obtain DNA from it, but we did not receive the sample.

Unfortunately, 2 other specimens also collected by Roosevelt from the same locality, clearly belonging to *T. terrestris* on the basis of discrete cranial features, could not be included in the multivariate analysis because they were badly broken and more than 30% of the measurements were missing. Furthermore, we included the holotype of *T. terrestris guianensis* Allen (AMNH36198) and 4 specimens of *T. terrestris* from the Karitiana indigenous land, the same locality where some *T. kabomani* paratypes were collected.

Voss et al. questioned how we identified the specimens "a priori." Our article stated that we relied on the morphology of the frontals between nasals and frontoparietal suture and the length and height of the crest, which are clearly visible key features. Invariably, in all the *T. terrestris* specimens we examined from several localities, including the ones from the same area where most *T. kabomani* skulls were collected, the crest extends into the frontals, a few centimeters behind the suture with the nasals, making the frontals in this region very narrow. *T. terrestris* has a significantly higher sagittal crest than *T. kabomani*, despite some degree of variation. As explained by Holbrook (2002), in *T. terrestris* the sagittal crest develops in a unique way, different from any other tapirs, being present and well formed already in neonates, and this difference cannot be attributed merely to a remodeling due to temporalis muscle development.

In *T. kabomani* the sagittal crest invariably stops at the frontoparietal suture in all the specimens we examined. This feature makes the crest shorter and it never develops as high as

in *T. terrestris*, but it is higher than in *T. pinchaque*. Since we do not have any very young animals in our sample, we do not know if, as in *T. pinchaque*, the 2 parasagittal ridges meet medially as the animal gets older, but the observation of 1 specimen (Universidade Federal de Minas Gerais [UFMG]33178, Supporting Information S16) that retained the sutures relatively open suggests that this may be the case. In any case, it should be noted that the character state in *T. kabomani* is a plesiomorphy for tapirs, and the state found in *T. terrestris* is the derived one.

Objections were made of the use of canonical variate analysis in our paper. We used this method because of a suggestion from a reviewer and in a previous version we used principal components analysis (PCA). To avoid this issue, we return to the PCA here, excluding the subadults and including the newly available specimens. The results are in Supporting Information S5 to S12. We excluded *T. indicus* to avoid the distortion that the larger size of this species may have in the results. For this analysis we used PAST 2.17 (Hammer et al. 2001), with an iterative imputation method to deal with missing data. Summary statistics, loadings, and specimen information can be found in the Supporting Information S11 and S12.

Component 1 represents mainly size; all the Neotropical species partially overlap along this axis (Supporting Information S5). A clear separation of *T. kabomani* from *T. terrestris* can be seen along component 2 (Supporting Information S5 and S7), for which major contributors are listed in order of importance, positive values for variables 11 (maximum width of the frontals at midpoint between the frontoparietal suture and the frontonasal suture) and 10 (maximum width of the frontals at the frontoparietal suture), and negative values for variables 3 (height from basioccipital to top of skull) and 20 (basicranium length from posterior palatine border to basioccipital). Component 3 separates *T. kabomani* from *T. pinchaque* with a minor overlap. Its major contributors are, in order of importance, negative values for variable 4 (an expression of the rostral length) and positive values for variables 3 (height of skull), 5 (orbit to occipital condyle), and 2 (height of sagittal crest). In Supporting Information S7 we plotted components 2 and 3, showing how all the Neotropical species separate along component 2, except *T. kabomani* and *T. pinchaque*, which separate along component 3. Biplots for components 1 versus 2 and 2 versus 3 can be found in Supporting Information S8 and S9.

In Supporting Information S5, S6, and S7 are shown the positions of relevant specimens in the multivariate space: the *T. kabomani* holotype UFMG3176 and paratype UFMG3176, for which we have both morphological and molecular data, and AMNH36661, Roosevelt's specimen collected in Mato Grosso, Brazil. Note that Roosevelt's specimen is positioned very distant from *T. terrestris*, along component 2, which reinforces our identification and contradicts the comments of Voss et al. (in press). They suggested that it matched more closely *T. terrestris*. We pointed out also that AMNH36198, the holotype of *T. terrestris guianensis* Allen, falls inside *T. terrestris* by size (component 1) and in component 2. It is marginal to the

variation of this species for component 3, but in all cases falls far away from the *T. kabomani* cloud.

We must recognize that we did not send our raw morphological data; however, in the AMNH mammal collection 75 skulls are listed as *T. terrestris* (74, because AMNH36661 belongs to *T. kabomani*), 11 as *T. bairdii*, and 7 as *T. pinchaque*, plus 58 as *T. terrestris*, 3 as *T. pinchaque*, and 55 as *T. bairdii* in the National Museum of Natural History (Smithsonian) collection of mammals. Thus, Voss et al. should have access to these skulls and measures to perform their own PCA analysis.

QUALITATIVE CHARACTER DIFFERENCES

Voss et al. questioned our description of external characters, particularly the data from camera-trap photos. Part of the problem is their suspicion about the ability of the local people to recognize the species, which will be discussed below, in the section “Indigenous Knowledge of Local People.”

Another issue they raised is the absence of some of the data of the photographed animals. We do not believe it is common to have data about the age of animals captured in camera-trap photos, but we do have data on the sex of the individuals. Regarding the scale, we included it at the side of one of the photos of the original publication (Supporting Information S14).

Most of the camera-trap photos were taken at night, which makes the coloration not as apparent, but we also have some daylight photos of the very same specimens. One of these photos can be found in Supporting Information S15 (right), showing that the skin color was quite dark (please note that the lighter color of the back of the animal in the front is due to the reflection of the flash). It is also possible to note the low mane in this photo. We also have photos in which the forehead is visible, like the one in Supporting Information S15 (left).

We tested a potential geographic variation structure of *T. terrestris* using specimens with known geographic data. As we mentioned above, 4 *T. terrestris* specimens in our data set are from Rondonia (actually from the Karitiana indigenous land) and 11 from Mato Grosso, Brazil. Thus, animals from the same or nearby localities to the *T. kabomani* specimens were included. A plot of component 2 versus 3 of the PCA including the Neotropical species with *T. terrestris* discriminated by localities, when available (specimens without geographic data were omitted), can be found in Supporting Information S10. *T. terrestris* specimens from the southwestern Amazon, which include those from the Karitiana indigenous land in Rondonia, are more distant in multivariate space from *T. kabomani* than other *T. terrestris* specimens. *T. terrestris* specimens from central Brazil, which include all of those from Mato Grosso State, are closer to the *T. kabomani* cloud than those from the southwestern Amazon. However, they are far from Roosevelt’s specimen (AMNH36661) that was hunted in Mato Grosso, which falls at the opposite side of the *T. kabomani* distribution. This clearly shows that there is no variation gradient across the geographic distribution of *T. terrestris* and *T. kabomani*

specimens in the multivariate analysis, even though these species are sympatric in part of their range. Although *T. kabomani* is found in a large area stretching from south Amazon (central Brazil) toward southwestern Amazon (Rondonia and south Amazonas states in Brazil, and in the border with Colombia), it is a quite restricted area when compared with the *T. terrestris* range, which is found in most of the tropical biomes of South America, including some where no *T. kabomani* is reported.

As mentioned previously, *T. terrestris* differs from any other tapir, living or fossil, including *T. kabomani*, by the development of the sagittal crest (Holbrook 2002). The crest is already present in the neonates and emerges from the middle of the skull, being quite high and always extending to the frontals, even in very young specimens (Holbrook 2002). In *T. indicus* and *T. bairdii* a single crest is never formed, having 2 separated parasagittal ridges. Young individuals of *T. pinchaque* present parasagittal ridges that meet medially as the animal grows, forming a true sagittal crest, but it is always low and limited to the parietals.

We do not have any very young *T. kabomani*, but the sagittal crest is never as developed, high, or long as in *T. terrestris*, never extending to the frontals. Actually, one of the *T. kabomani* specimens, UFGM3178, an adult with M3 erupted and in use, has a stage of sagittal crest development that resembles some individuals of the extinct *T. polkensis* that Abernethy (2011) calls “crest morphology 1” (see Abernethy 2011:figure 9 and our Supporting Information S16), in which the parasagittal ridges are proximal to one another in the midline of the skull. Other adult and subadult *T. kabomani* are like Abernethy’s “crest morphology 2” (Abernethy 2011: fig.10), which he calls a true sagittal crest. We conclude that the development of the sagittal crest of *T. kabomani* is closer to that of *T. pinchaque*, and quite different from *T. terrestris*.

The concerns of Voss et al. with our phylogenetic analysis of morphological data are confusing. First, the characters and character states we used followed those of Hulbert and Wallace (2005) and served as a basis for most of the recent morphological cladistics of tapirs (Hulbert and Wallace 2005; Hulbert 2010; Ferrero and Noriega 2007; Holanda and Ferrero 2012). We made a few modifications to this matrix by excluding several dental characters that could introduce a lot of ambiguity because of the high degree of homoplasy they exhibit, as seen, for example, in the work of Perini et al. (2011). We believe that to start from zero each time is not a good procedure because the results are hard to compare, so we chose to follow an already established character list with slight modifications and added our own data into it.

INDIGENOUS KNOWLEDGE OF LOCAL PEOPLE

Our statement regarding the local people’s knowledge about the new tapir species was not limited to indigenous groups. Certainly several indigenous communities from the Amazon recognize 2 different kinds of tapirs in their lands, but some others do not, like the Uru-Eu-Uau-Uau and Xavante (pers.

obs. MAC and FRS respectively). Despite the fact that Voss et al. do not personally disregard traditional knowledge, it has been common in Brazil for researchers to not pay attention to this information and to consider situations like this a simple case of overdifferentiation without checking it properly.

We agree with Voss et al. that specific methods are needed to establish a complete ethnozoological diagnosis for any traditional culture. However, it should be noted that we focused on a single ethnotaxonomic issue, based on several semi-structured and informal interviews, and we merely compared this information with the data from other lines of evidence (i.e., morphology and genetics). We did not accomplish a strong discussion about ethnoecology, hunting, or even ethnotaxonomy which would have required a more robust effort.

The recognition of 2 species of tapir is not the privilege of the Karitiana tribe (Fernandes-Ferreira, in press). Some historical documents already show that the kabomani tapir is widely described in the Amazon by indigenous and rural populations as “anta pretinha” (small-black-tapir). As we already mentioned, Theodore Roosevelt (1914) documented 2 species of tapir described by local hunters and indigenous people (Pareci indians) who joined the River of Doubt expedition.

In a doctoral dissertation in development about hunting in Brazil, HF-F shows that the popular description of the small-black-tapir is widely distributed in the Amazon. In localities of Rondonia State (western Brazilian Amazon), about 100 km from the type locality of *T. kabomani*, nonindigenous rural and fishing communities ($n = 132$ informants) cite the same morphological characteristics and name this species as anta-pretinha or “anta-pequena” (small-tapir), and all people recognize both nomenclatures for the same ethnospecies. In addition, these same citations were documented in localities of Para State (eastern Brazilian Amazon), about 1,500 km from Rondonia ($n = 34$ informants). In both areas, the hunting of anta-pretinha is accomplished with traps and active techniques. The species is used for food, medicinal, and magic-religious purposes, and reaches maximum use values. In addition, some people have mentioned that they prefer the little-black-tapir’s meat to that of the lowland tapir.

We agree that overdifferentiation in folk taxonomy must be common. The analysis of Voss et al. is very well structured regarding this subject. However, although an overdifferentiation cannot be ruled out completely, the high degree of utility this animal has for the local people and the wide distribution of this popular knowledge strongly decrease this possibility because people tend to assign more specific nomenclatures for useful animals such as game mammals (Diamond 1966; Craig 1986; Berlin 1973; Atran 1999), even in rural communities of Brazil (Lopes 2004; Mourão et al. 2006). Meanwhile, it is very clear that the recognition of this new species is widely supported by various ethnic groups (indigenous or not). Furthermore, we want to emphasize that all the specimens donated by the Karitiana and other nonindigenous local people and identified by them as either

anta-pretinha (*T. kabomani*) or “anta comum” (*T. terrestris*) coincided with the morphometric and molecular identification.

CONCLUSIONS

We have shown that the choice of outgroup does not affect the phylogenetic results significantly. The absence of data on the methodology that Voss et al. used makes it impossible to discover the reason for their divergent results. In any case, the chromosomal differences and skull development path make it difficult to support the possibility of considering *T. pinchaque* conspecific with *T. terrestris* as well as the possibility of introgression by hybridization.

As discussed above, the morphological issues of supposed age mixing and geographical variation were not supported. We have also shown that *T. kabomani* specimens cannot be considered young *T. terrestris*, since all of them were either young adults or older. On the basis of the available material we have a good indication that the path of skull development in *T. kabomani* is most likely similar to that of *T. pichaque* and some fossil species, such as *T. polkensis* (Abernethy 2011) and *T. cristatellus* (Holanda and Ferrero 2012). Skull development follows a relatively primitive path, quite different from the highly derived and unique skull development path of *T. terrestris* (Holbrook 2002). The morphological cladistics, despite not intending to support the species recognition, gave support to the tree topology, congruent with the one obtained with the *Cytb* tree.

Despite the absence of an extensive ethnozoological study, the discussion of local knowledge shows that the differentiation of 2 tapir species (and not multiple species) in the Amazon region and their descriptions are consistent throughout the region and not restricted to indigenous people, for which linguistic or other barriers can be problematic. Since the focus here is the recognition of a single taxonomic issue, we have shown that the local population is capable of differentiating both species successfully.

What we presented here is evidence from different sources (genetics, morphometrics, discrete morphology, morphological phylogeny, and folk taxonomy) that supports the existence of a separate species not previously recognized by scientists. We do not base our conclusions on just a single criterion but in the concurrent results of different lines of evidence. We agree with Sites and Marshall (2004) in that “... the fuzzy nature of species boundaries, requires an eclectic approach to delimiting species and caution against the reliance on a single data set or method when delimiting species.”

Many species were recently described with much less evidence than we presented (i.e., Jones et al. 2005; Davenport et al. 2006; Solari 2004, 2007; Solari et al. 2012; Voss et al. 2012; Hrbek et al. 2014), on the basis of very few specimens (some with just 1), sometimes without morphometry, and none with morphological cladistics. Some of the new taxa described cannot be checked for coalescence or genetic divergence of lineages because the sample is restricted to 1 individual, and obviously, monophyly is impossible to determine.

We want to comment on the following sentence in the Voss critique: “Given the potential flagship status of the alleged new species for rain-forest conservation efforts, timely assessment of the supporting evidence is important, before scarce resources (money, personnel, political capital) are expended on its behalf.” We honestly believe that, despite scarce resources or personnel, if a remote possibility of a new species like this exists, in an environment so endangered and under hunting pressure, efforts should be made to clarify both its taxonomic and conservation status. Not considering this possibility may condemn an important part of Amazonian mammalian diversity to extinction without even knowing it properly. We expect that our work and conclusions will generate more research, and we hope that scientists continue to examine the evidence and evaluate the taxonomic placement of the proposed new species.

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