

Extraordinary claims require extraordinary evidence: a comment on Cozzuol et al. (2013)

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The recent description of a new species of Amazonian tapir is inadequately supported by the genetic, morphological, and ethnographic information provided by the authors.

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The late Carl Sagan's aphorism, that extraordinary claims require extraordinary evidence, expresses a fundamental principle of scientific skepticism. The recent description of a new species of living tapir (Cozzuol et al. 2013) definitely rates as extraordinary, so the taxonomic community has a right to expect that it is backed up by compelling data. Have several generations of Neotropical mammalogists really failed to recognize a species of Recent megafauna that is said to be widely distributed in Amazonia? 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.

The alleged new species, which Cozzuol et al. (2013) named *Tapirus kabomani*, is said to be distinct from *T. terrestris*, the only Recent species of Amazonian tapir previously recognized as valid. This hypothesis is based on several lines of evidence, including phylogenetic analyses of molecular sequence data, multivariate analyses of morphometric data, qualitative character differences, and the traditional knowledge of local people. The following assessment concerns the adequacy of this evidence as summarized in the published article and its Supporting Information, supplemented by our reanalyses of the molecular data of Cozzuol et al. (2013) and by our examination of tapir specimens at the American Museum of Natural History, New York (AMNH) and the National Museum of Natural History, Washington, DC (USNM).

PHYLOGENETIC ANALYSES OF MOLECULAR DATA

Cozzuol et al. (2013) analyzed 2 molecular data sets, one consisting of 960 base pairs (bp) of cytochrome *b* (*Cytb*) and another consisting of *Cytb* sequences concatenated with sequences from cytochrome oxidase I (COI, 617 bp) and cytochrome oxidase II (COII, 690 bp). Analyses of both data sets—which included representatives of all currently recognized species of Recent tapirs (with other perissodactyls as outgroups)—recovered a haplotype group that the authors identified as *T. kabomani*. However, nodal support for this group was weak in their *Cytb* analysis and only moderate likelihood support was recovered from their concatenated-gene data set (Bayesian posterior probabilities were less than 0.95 in both analyses). Furthermore, the mean distance between *Cytb* sequences attributed to *T. kabomani* and those identified as *T. terrestris* is only 1.3% (Supporting Information S13), which is well within the range of sequence divergence values routinely reported among conspecific mammalian haplotypes (reviewed by Baker and Bradley 2006). Therefore, the published genetic evidence for recognizing *T. kabomani* can only be described as inadequate.

Cozzuol et al. (2013) analyzed 53 new *Cytb* sequences from *T. bairdii*, *T. kabomani*, *T. pinchaque*, *T. terrestris*, and *Acrocodia indica* (the Malayan tapir, a distinctive Old World species formerly classified in *Tapirus*—Groves and Grubb



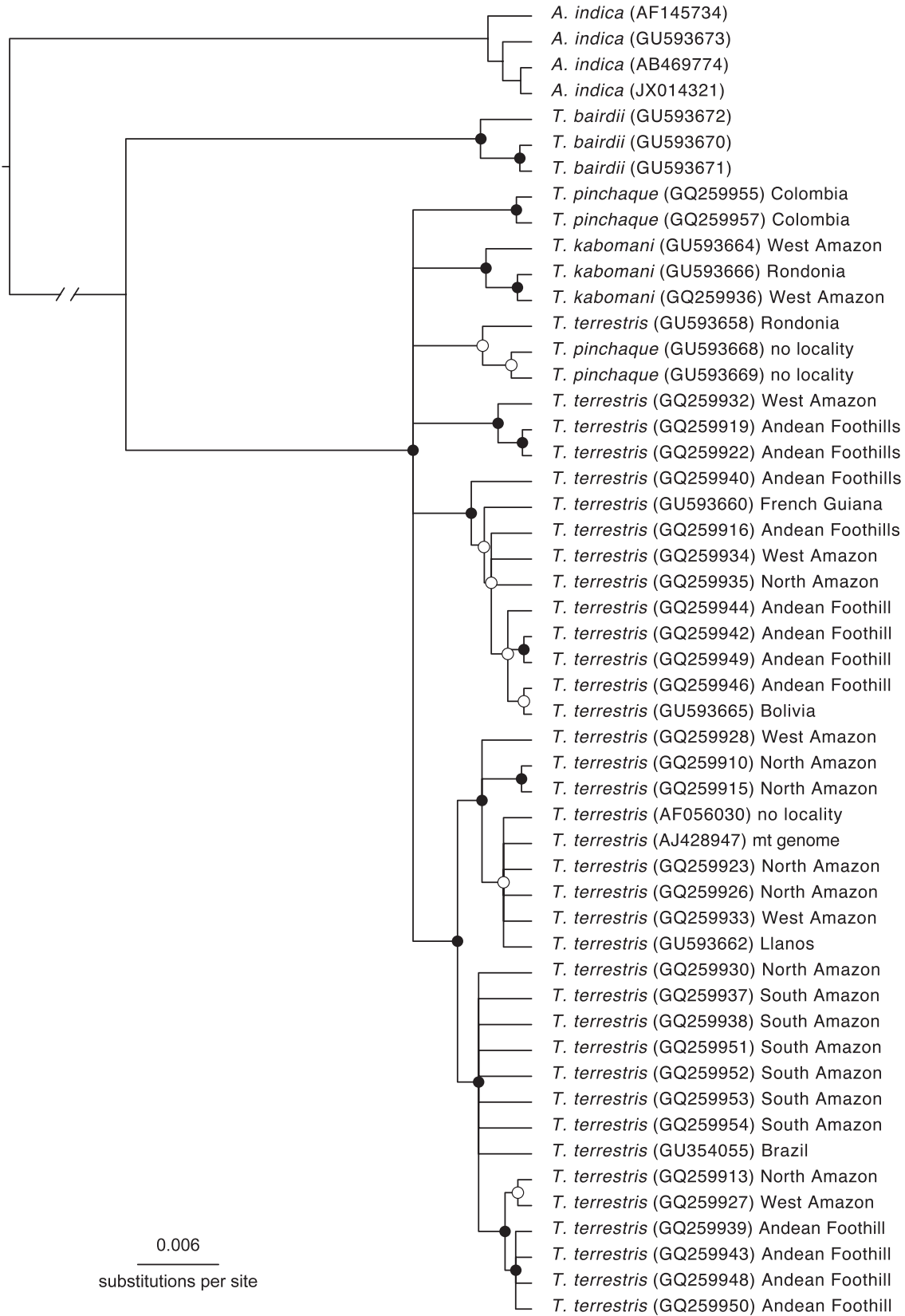


FIG. 1.—The 50% majority rule consensus tree resulting from Bayesian analysis of cytochrome *b* sequences from Malayan and Neotropical tapirs. Terminals are labeled with Latin binomials, followed by GenBank numbers (in parentheses) and locality information. Nominal taxon names and localities follow Cozzuol et al. (2013) or de Thoisy (2010). Nodes supported with posterior probability values ≥ 0.95 are indicated with black circles; those with posterior probability values between 0.50 and 0.94 are indicated with white circles. The analysis was based on a matrix of

2011) plus other sequences from *T. pinchaque* and *T. terrestris* previously analyzed by de Thoisy et al. (2010). We downloaded these data from GenBank and reanalyzed them to see if more robust support for *T. kabomani* could be obtained by using different methods. Whereas Cozzuol et al. (2013) fitted models of sequence evolution to a data set that included distant outgroups (nontapirid perissodactyls), we used only *A. indica* (sister genus to *Tapirus*) as the more appropriate outgroup for resolving shallow divergence patterns among Neotropical tapirs, and we analyzed only unique haplotypes. Using Bayesian inference (Fig. 1) we obtained strong support (posterior probability = 0.99) for the haplotype clade alleged to correspond to *T. kabomani*. However, this reanalysis conspicuously fails to resolve *T. kabomani*, *T. pinchaque*, and *T. terrestris* as reciprocally monophyletic groups, nor does stronger nodal support for *T. kabomani* alter the fact that this nominal taxon is minimally divergent from other South American tapir haplogroups.

Vouchering is also problematic. The mitochondrial (mt) DNA sequences that the authors attributed to *T. kabomani* were obtained from 4 tissue samples, 2 of which were collected in SW Amazonia (in the Brazilian states of R ndonia and Amazonas), and the other 2 from NW Amazonia (one collected in Colombia and the other from near the Colombian–Brazilian border). However, morphological voucher material was apparently examined only for the 2 SW Amazonian sequences, so the morphological traits associated with sequences from NW Amazonia are unknown. In effect, the correlation between mtDNA sequence characteristics and allegedly diagnostic phenotypic attributes (see below) is not convincingly established, and the most that can be said from these results is that the same minimally divergent mtDNA haplogroup seems to occur in both SW and NW Amazonia.

MULTIVARIATE ANALYSES OF MORPHOMETRIC DATA

The authors' multivariate morphometric analyses—based on samples that included males, females, unsexed specimens, and specimens with incompletely erupted dentitions—are not accompanied by any substantive discussion of sexual size dimorphism or ontogenetic variation. Although sexual size dimorphism in tapirs is thought to be unimportant (Simpson 1945), ontogenetic variation is potentially problematic. Cozzuol et al. (2013:1333) assert that “Tapirs with M1 erupted are already sexually mature and the skull and size subsequently changes [sic] little or not at all,” but they provide no evidence that this is really true. In fact, the 1st upper molar (M1) of tapirs erupts while the deciduous premolar dentition (dP2–dP4) is still in place. Specimens that retain dP2–dP4 are considered

juveniles by most tapir taxonomists (e.g., Simpson 1945; Hulbert et al. 2009; Hulbert 2010), who consider only specimens with erupted P4/p4 to be fully grown. Cozzuol et al. (2013), however, mention neither premolar eruption nor any other ontogenetic criterion for sample membership in the context of their multivariate morphometric analysis. This is hard to understand because, to score sagittal crest height for cladistic analysis, they only measured adults (which they defined as having fully erupted P4 and M3; see Supporting Information S4: character 1).

Although a canonical variates analysis showed a cluster that the authors identified as *T. kabomani* to be widely separated from *T. terrestris* (see Cozzuol et al. 2013:1337, figure 5), this discriminant method requires groups to be identified a priori, so the criteria by which specimens were sorted into groups are crucial to avoid circular inference. The authors do not state how specimens were identified a priori as *T. kabomani* and *T. terrestris*, but if this were done on the basis of size or cranial proportions (for example), then their analyses merely show that samples predefined by morphometric traits are, in fact, morphometrically different. Unfortunately, there is no summary table of measurement data from which to assess the magnitude of univariate species differences (if any), and there is no table of canonical coefficients to indicate which measurements contribute to group separation. Absent crucial information about sample age structure, ontogenetic variability, taxonomic sorting, and the relationship between canonical variate scores and the original measurement data, these morphometric results are uninterpretable, and they are effectively useless for identification of new material. Although we requested the original measurement data, these were not provided by the authors, so we are currently unable to further evaluate this aspect of their study.

QUALITATIVE CHARACTER DIFFERENCES

External characteristics that Cozzuol et al. (2013:1336) attribute to *T. kabomani* were based on information from local hunters who “identified the animals in camera-trap photos ... from the type locality as belonging to the new species.” The traits in question (dark pelage, low mane, broad forehead, small size) are not, therefore, unambiguously associated either with mtDNA sequences or with examined cranial material. If local hunters are taxonomically unreliable (see below), then these characteristics might simply represent phenotypic (possibly ontogenetic) variation within a local population of *T. terrestris*. Additionally, none of the allegedly diagnostic external traits of *T. kabomani* can be evaluated from the camera-trap photographs published by the authors (Cozzuol et al. 2013:1335,

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unique haplotypes that comprised 960 base pairs of unambiguously aligned sequence. The best-fitting model of nucleotide substitution (as assessed with an hierarchical likelihood-ratio test implemented by MrModelTest) was GTR+G, and a molecular clock for these sequences could not be rejected ($\Delta\ln L = 37.15$; $d.f. = 49$; $P = 0.89$). Phylogenetic analyses were implemented by specifying this model in MrBayes ver. 3.2 (Huelsenbeck and Ronquist 2001) and performing 2 runs of 5×10^6 generations, each with 1 cold and 3 heated chains. The resulting runs were assessed for convergence, the first 10% of the trees in each run were trimmed as burn-in, and the 50% majority rule consensus tree was calculated from the remaining trees.

figure 3), which show 2 animals of unknown age with no scale for assessing size and no view from which forehead breadth is apparent; if their pelage is darker and their manes shorter than those of *T. terrestris*, there is nothing in these images to document such claims (no comparative views of sympatric *T. terrestris* are provided).

Qualitative craniodental differences alleged to distinguish *T. kabomani* from *T. terrestris* are reported in the text (Cozzuol et al. 2013:1334–1336) and in a morphological data matrix (op. cit.: Supporting Information S3). Craniodental characters mentioned in the text include a “lower, shorter, and wider” sagittal crest that does not extend anteriorly onto the frontals; shallower fossae for the meatal diverticulum; and a less “upturned” rostrum. However, no measurements are provided to document these alleged differences, and not all of them are easily appreciated in the accompanying photographs (Cozzuol et al. 2013:1336, figure 4), where the holotype skull of *T. kabomani* and an exemplar skull of *T. terrestris* do not seem to differ very much in length or width of the sagittal crest. Similarly, neither the depth of the fossae that house the meatal diverticulum (a mucocartilagenous pouch of unknown function, peculiar to tapirs—Witmer et al. 1999) nor rostral inclination seem to be visibly different in these photographs.

Two described character differences that correspond plausibly with these photographic images concern frontal morphology and the relationship between the sagittal crest and the frontal–parietal suture. As illustrated, the dorsal surface of the frontals between the nasals and the beginning of the sagittal crest—approximately corresponding to the “dorsal table” of Hulbert et al. (2009:242)—is conspicuously larger and broader in the holotype of *T. kabomani* than in the accompanying exemplar skull of *T. terrestris*. (The authors claim that this region is also more inflated in *T. kabomani* than in *T. terrestris*, but inflation is hard to judge from the photographs.) Additionally, the sagittal crest of the holotype of *T. kabomani* appears to start at or near the frontal–parietal suture, whereas the sagittal crest of the photographed specimen of *T. terrestris* seems to begin well anterior to the frontal–parietal suture. We don’t dispute that these skulls look different.

In our experience, however, it is seldom hard to find different-looking skulls in any large population sample, and the exemplar skulls photographed by Cozzuol et al. (2013:1335, figure 3) are not even from the same region. One (the holotype of *T. kabomani*) is from Rondônia, the other (MCN 2750) is from Rio Grande do Sul; therefore, they represent populations separated by about 2,000 km, and geographic variation—an alternative hypothesis that is never mentioned by the authors—is a possible explanation for any apparent differences (similar morphological differences among regional samples of *T. terrestris* were illustrated by Haggmann 1908). On the basis of information provided in the article, we have no way to be sure that illustrated exemplars represent distinct taxa rather than conspecific variants selected from a continuous range of intermediate phenotypes.

The same uncertainties apply to morphological traits that Cozzuol et al. (2013) scored for phylogenetic analysis.

According to their matrix (Supporting Information, S3), *T. kabomani* and *T. terrestris* exhibit fixed differences in no fewer than 12 characters, including several that were not mentioned in the authors’ diagnosis and description of *T. kabomani*. In our experience, closely related mammalian species seldom differ unambiguously in so many phenotypic characters, so we examined specimens of South American tapirs in the collections of the AMNH and the USNM to determine whether or not the traits that Cozzuol et al. (2013) scored as distinct character states are unambiguously distinguishable in practice.

Although the specimens we examined exhibit variation in all of the characters that Cozzuol et al. (2013) scored for phylogenetic analysis, we were unable to confidently replicate their observations due to the ambiguity of many character-state definitions (e.g., “relatively narrow” versus “relatively broad” frontals) and the presence of intermediate morphologies. Our strong impression is that Amazonian tapirs, in particular, exhibit an unappreciated range of both ontogenetic and geographic variation in the characters alleged to distinguish *T. kabomani* from *T. terrestris*. Additionally, we note that some morphological descriptions and character scores of Cozzuol et al. (2013) are inconsistent with those in other recent publications with overlapping authorship. For example, Cozzuol et al. (2013) described *T. kabomani* as having more inflated frontals than *T. terrestris*, and they scored *T. terrestris* (Supporting Information S3) as having uninflated or weakly inflated frontals. However, in a contemporaneous article on South American tapir systematics (Holanda and Ferrero 2013), *T. terrestris* was described and scored as having strongly inflated frontals. Such inconsistencies contribute to our assessment that much of the character scoring in these (and other) recent analyses of tapir taxonomy are based on subjective criteria.

Among the specimens we examined was AMNH 36661, a paratype of *T. kabomani* that was collected by the Roosevelt Brazilian Expedition in Mato Grosso. Roosevelt (1914) himself remarked that this adult individual seemed unusually small by comparison with other tapirs collected by the expedition. In fact, AMNH 36661 agrees with the diagnosis of Cozzuol et al. (2013) of *T. kabomani* in having broader and somewhat more inflated frontals than are usual in Amazonian tapirs, and in having a sagittal crest that begins close to the frontal–parietal suture. However, both of these traits could reflect cranial remodeling as a function of temporalis development, and this specimen is notably divergent from the alleged phenotype of *T. kabomani* in other characters that the authors scored for cladistic analysis (e.g., by having an exceptionally deep supraorbital groove for the meatal diverticulum). We are not persuaded that AMNH 36661, which otherwise resembles most other Amazonian material of *T. terrestris*, represents a taxonomically distinct form. In this respect, we agree with Allen (1914), who examined AMNH 36661 and other tapirs collected by the Roosevelt Brazilian Expedition and concluded that all were referable to *T. terrestris*.

INDIGENOUS KNOWLEDGE OF LOCAL PEOPLE

Cozzuol et al. (2013) imply—but do not actually state unambiguously—that local people (possibly the Karitiana, who are said to have collected several paratypes of *T. kabomani*) recognize *T. kabomani* and *T. terrestris* as distinct species. From this, the authors conclude that their genetic and morphological analyses validate “often-denigrated traditional knowledge” of biodiversity. For the record, we have never denigrated the traditional knowledge of indigenous cultures, having written at length about the potential value of mammalian natural history information obtained from carefully conducted interviews with local hunters (e.g., Voss and Fleck 2011; Heyes and Helgen 2014). However, much linguistic and ethnographic effort is required to establish what, in fact, is actually known by local people, versus what they may say in response to leading questions, or what is inferred from imperfectly understood or inaccurately translated statements.

Among other relevant complexities, knowledge of mammalian biodiversity is imperfectly correlated with linguistic labeling by native Amazonian cultures. Indigenous people are often aware of many species that they do not name, especially of small mammals that are not culturally important and do not need to be talked about (Fleck et al. 2002). By contrast, game species and other large mammals are often overdifferentiated, resulting in several local names for the same biological species. The Aguaruna Jívaro, for example, recognize 4 named kinds of coatis (all of which correspond to *Nasua nasua*) and 4 named kinds of tamanduas (all referable to *Tamandua tetradactyla*—Patton et al. 1982). Among speakers of Panoan languages, multiple synonyms for large game species seem to be the rule rather than the exception (Fleck and Voss 2006).

On occasion, local informants can be very convincing about the reality of the named varieties (folk species) that they recognize. Matses hunters, for example, unanimously distinguish 2 named kinds of saki monkeys—bëshudu and mamu—that they consistently assert to have different pelage traits, to live in different habitats, and to not interbreed. Nevertheless, morphological and molecular analysis of numerous specimens identified by the Matses as either bëshudu or mamu showed that both correspond to *Pithecia monachus*, and that their distinguishing morphological traits probably represent maturational differences between younger and older adults (Fleck et al. 1999).

Tapirs are not exempt from overdifferentiation by indigenous Amazonians. The Kakataibo, for example, recognize 7 folk species of tapir (Zariquiey and Fleck 2014), so it would not be surprising if the Karitiana (or other indigenous cultures whom Cozzuol et al. [2013] might have consulted) were to have multiple names for *Tapirus terrestris* based on ontogenetic or other phenotypic variants in local populations. Molecular data from multiple voucher specimens of each folk taxon—if any are really distinguished (Cozzuol et al. [2013] do not provide even rudimentary documentation of linguistic labeling)—would contribute some credibility to the notion that 2 biological species of tapir occur in Karitiana territory, as

would a careful morphological analysis (taking ontogenetic variation into account) of skulls or other trophy material identified by local hunters. If such information really is available, the essential link between biological research results and folk-taxonomic labeling is not effectively documented by Cozzuol et al. (2013).

DISCUSSION

In our opinion, the description of *T. kabomani* by Cozzuol et al. (2013) fails to provide compelling evidence for a new species of Amazonian tapir. However, their results—together with the more appropriately restrained interpretation of many of the same sequence data by de Thoisy et al. (2010)—do suggest that South American tapir taxonomy deserves additional scrutiny. In particular, there seems to be little support for the genetic distinctness of the mountain tapir (*T. pinchaque*) despite its traditional recognition on the basis of morphology (e.g., by Hershkovitz 1954). Striking ecogeographic variation is well known among other widespread large mammals (e.g., Rausch 1963; Patterson 2007; Terada et al. 2012), and it is not impossible that mountain tapirs might be a high-altitude ecomorph or subspecies of *T. terrestris*. Alternatively, *T. pinchaque* might be a valid species harboring introgressed *T. terrestris* mitochondria from relatively recent hybridization events. Nuclear-gene sequencing and more detailed assessments of morphological variation would provide a welcome additional source of information for distinguishing these alternative interpretations of the data currently at hand.

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