

ties representatives, and social work professionals to initiate discussions on the status of fauna and to reach consensus recommendations for its conservation. Improvements of existing laws was one goal, but not the exclusive points to deal with. During four years, public-open working groups included several topics: awareness and education, hunting practices and regulation, forest management, non extractive uses of forest (e.g., tourism), etc. After hundreds hours of discussions, often getting lively since conflicting points of view were addressed, some consensus points were reached. The necessity to retrieve the tapir and three frugivorous birds (*Psophia crepitans*, *Crax alector* and *Penelope marail*) from the list of commercial species was one of those points, and the first approved with a decree. Forthcoming working groups sessions will be focused on hunting periods, quotas, and other management details. Indeed, the status of many sensitive species remains precarious: despite the National Park, only 3% of the territory is under strong protection, where hunting is totally prohibited. Elsewhere, subsistence hunting is allowed, and several species are under a strong risk of overharvesting (e.g., monkeys and tapirs, de Thoisy & Vogel 2002; de Thoisy et al. 2005).

The weakness of the legal status of the tapir in French Guiana was highlighted during the TSG meeting at Sorocaba, 2007 (Working group "Human conflicts", objective 2, action 2.2). The involvement of, and implications for many Guianan peoples has to be acknowledged for this first but indispensable review step for large vertebrate conservation in French Guiana.

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New Fossil Discoveries and the History of Tapirus

By Matthew Colbert

Fossil tapirs tell a fascinating tale of intercontinental dispersal, extinction, and evolution. While their current geographic range is confined to Southeast Asia, South America, and Central America, fossil tapirs prove that as recently as a few thousand years ago they ranged across North America, Europe, and Asia. Fossil evidence also suggests that tapirs were not present in South America until at most a few million years ago.

But how did this geographic pattern emerge? And what is the relationship of these ancient tapirs to living species? Recent discoveries of fossil tapirs in South and North America, and an improved understanding of their evolutionary relationships, have started to shed some light on these questions. Here I briefly review some of these new discoveries of fossil *Tapirus*, and discuss some of the outstanding issues related to the evolution of *Tapirus*.

In North America, major fossil discoveries of tapirs have recently been reported from the southeastern United States. These studies have shown the existence of new species of *Tapirus*, and have also provided material for a much more thorough documentation of formerly poorly known species. Most of the description and interpretation of these has been the work of paleontologist Richard Hulbert from the Florida Museum of Natural History.

Hulbert's work suggests that there were at least six extinct species of *Tapirus* from the late Miocene to

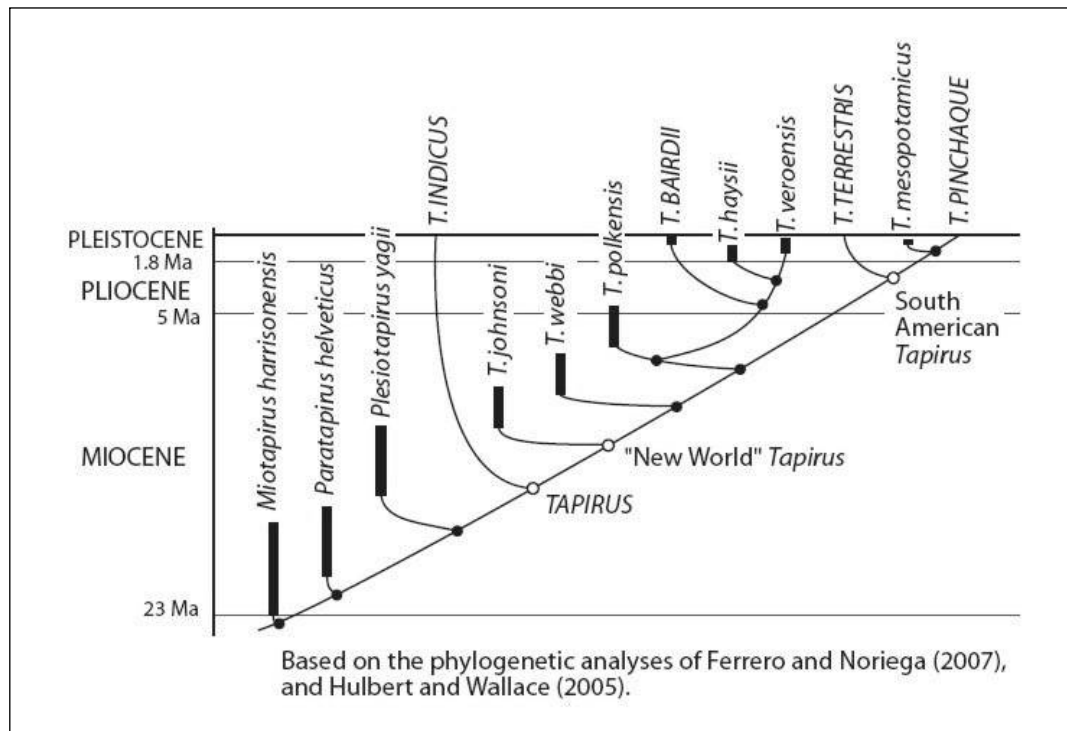


Figure 1. The South American tapirs define a monophyletic cluster.

Pleistocene of the eastern United States (about 9.5 million years ago to about 10,000 years ago). This tally does not include several fossil species that had been named based on material that was not diagnostic (in other words, the identification cannot be conclusive), or that have been synonymized with other species (the same is true for the extant tapir species!). Additionally there are a couple named species from the western United States that are in need of taxonomic revision, and that may actually pertain to earlier named eastern species.

One of the newly-described species is *Tapirus webbi*, from the late Miocene (about 9.5 to 7.5 million years ago) of Florida (Hulbert 2005). This tapir was about the size of the living *T. terrestris*, but with longer legs, and is also characterized by having several primitive features for *Tapirus*. Most importantly the appearance of *T. webbi* signals a period of time in which tapirs seem to have been diversifying in North America, following an earlier period in which they are extremely rare.

This diversification is exemplified recent discoveries of a small-bodied tapir called *Tapirus polkensis*, from the early Pliocene (7 to 4.5 million years old) Gray Fossil Site in eastern Tennessee. This tremendous site has yielded abundant remains of *Tapirus polkensis*, as well as many other fossil vertebrates. The tapirs there are currently being studied by Steve Wallace and Richard Hulbert, and have already provided data for preliminary phylogenetic analyses and an improved

understanding the evolutionary relationships among the species of *Tapirus*. More about this below.

Recent reports of late Pleistocene fossil tapirs have also come from South America. These include several isolated jaw bones from southwestern Amazonia, Brazil (Hollanda and Cozzuol, 2006), and the skull of a new species from the Entre Rios Province of Argentina (Ferrero and Noriega, 2007). Although the Brazilian sample is small, and is not diagnostic to the species level, the fossils document two markedly different size classes that suggest the presence of

at least two fossil species at that time (as there are today in South America - notably, these two fossil forms are both lowland species). Note, while several species of fossil tapirs have been named from South America, they are all based on scanty material, and are probably not diagnostic (as is the case with several fossil species from North America).

The skull from Argentina, however, is relatively complete, and was placed into a new species, *T. mesopotamicus* by Ferrero and Noriega (2007). Ferrero and Noriega also performed a phylogenetic analysis, which indicated to them that their new species is more closely related to *T. pinchaque* than to *T. terrestris* (see Figure 1). Although I am not entirely convinced of this relationship, it is clear that *T. mesopotamicus* is closely related to, or belongs to, a group that includes both *T. terrestris* and *T. pinchaque*. The results are also consistent with an earlier molecular analysis of mitochondrial DNA that independently supports a close relationship between *T. pinchaque* and *T. terrestris* (Ashley et al., 1996). Ferrero and Noriega's work builds on the preliminary analysis of Hulbert and Wallace (2005) that incorporates the new Gray Fossil Site tapirs.

The close evolutionary relationship between the two living South American tapirs and *T. mesopotamicus* is also concordant with the geologically relatively recent appearance of tapirs in South America. Available evidence suggests that tapirs, together with many other North American biotic elements, dispersed to South

America from North America when the Isthmus of Panama emerged from the sea about 3 million years ago (of course, there were also South American biota that dispersed northwards). Furthermore, the close relationship between the South American tapirs is also consistent with a hypothesis that they arose from a single dispersal event that sent the ancestor of these two over the Panamanian Isthmus. This hypothesis will be tested with future fossil discoveries, and with additional phylogenetic analyses.

But how are the South American tapirs related to *T. bairdii* (Baird's tapir), and to other fossil North American *Tapirus*? And how are all these New World tapirs related to *T. indicus* (the Malayan Tapir), and all the fossils from Europe and Asia? The recent analyses of Hulbert and Wallace (2005), and Ferrero and Noriega (2007), as well as the earlier molecular analysis of Ashley et al (1996) have greatly improved our understanding of these evolutionary relationships within *Tapirus*, and have begun to shed some light on these questions.

Before proceeding, I would like to present definitions for the name *Tapirus* and for the word tapir. *Tapirus* is here considered to comprise all of the descendants of the most recent common ancestor of the four living species (see Colbert, 2005). Thus, by definition, all living tapir species belong to the genus *Tapirus*. Note that this differs from a definition presented by Hulbert (2005), and although I would love to debate the merits of the different definitions here, it would be extremely boring to most of you. Please email me if you really interested (colbert@mail.utexas.edu). The informal name 'tapir' is here used to refer to a more general group consisting of all species closer to *Tapirus* than to the rhinoceroses. In addition to *Tapirus*, tapirs also include a number of extinct genera (such as *Paratapirus*, *Plesiotapirus*, and *Miotapirus*, shown in Figure 1).

The South American tapirs define a monophyletic cluster (that is, a group having a single common ancestral species) in the phylogenies of both Hulbert and Wallace (2005), and Ferrero and Noriega (2007; and see Figure 1). The Central American *T. bairdii*, however, is more closely related to *T. polkensis* and to other Pleistocene North American tapirs. The earliest divergence of the "New World" *Tapirus* is *T. johnsoni* which is from the Miocene of the state of Nebraska in the United States (about 11 to 9 million years ago).

Tapirus indicus is shown here (Figure 1) as the sister to all the "New World" tapirs, which are resolved as a monophyletic group. This result implies a scenario involving a single dispersal event between the Old and the New World. Indeed because *Plesiotapirus* and *Paratapirus* are from China and Europe, respectively, this dispersal event would parsimoniously be considered to have been from the Old to the New

World. *Miotapirus* is from North America, and implies yet another (earlier) intercontinental dispersal. In other words, there was a dispersal of *Miotapirus* (or a related species) from North America to Europe and Asia giving origin to *Paratapirus* and *Plesiotapirus*, and then a dispersal of a derived Asian species back to North America that gave rise to both *T. indicus* and all extant forms in the Americas.

These dispersal scenarios are dependent upon the tree topology shown in Figure 1. But while the analyses represent a great start, they are still far from complete. They do not include any fossil species of *Tapirus* from Asia and Europe, and would benefit from the inclusion of species from other genera of fossil tapirs. Indeed, a global analysis comprising all known species of tapirs (including fossil species outside of *Tapirus*) is the ultimate goal for interpreting tapir evolution. Such an analysis would test these results reviewed here, allow a greater appreciation of rates and modes of morphological change, and a refined scenario of dispersal and evolutionary radiation. The exciting thing is that the rate of discovery of fossil species is increasing, and the pieces are being put in place for undertaking such a global analysis.

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