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## Short Communication

The epitensoic chorda tympani of *Laonastes aenigmamus* (Rodentia, Diatomyidae) and its phylogenetic implicationsAdrian Tröscher<sup>a,\*</sup>, Wolfgang Maier<sup>b,1</sup>, Irina Ruf<sup>c,2</sup>, Jean-Pierre Hugot<sup>d,3</sup>, Madelaine Böhme<sup>a,4</sup><sup>a</sup> Senckenberg Center for Human Evolution and Paleoenvironment, HEP Tübingen, Terrestrische Paläoklimatologie, Sigwartstrasse 10, 72076 Tübingen, Germany<sup>b</sup> Institut für Evolution und Ökologie, Universität Tübingen, Auf der Morgenstelle 28, 72076 Tübingen, Germany<sup>c</sup> Senckenberg Forschungsinstitut und Naturmuseum, Abteilung Paläoanthropologie und Messelforschung, Sektion Mammalogie, Senckenberganlage 25, 60325 Frankfurt a.M., Germany<sup>d</sup> Muséum National d'Histoire Naturelle, UMR CNRS 7205, 55, rue Buffon, 75231 Paris, France

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## ABSTRACT

Earlier studies have shown that the epitensoic position of the *chorda tympani* is a systematically useful apomorphic character in some mammalian orders (primates, carnivores, rodents). Newly made histological serial sections of a fetal stage now reveal that *Laonastes aenigmamus* (Diatomyidae), a rodent species first described in 2005, is epitensoic as well. Because *Ctenodactylus gundi* is the only other taxon within the Ctenohystrica having this derived character state, we conclude that this is an additional synapomorphy substantiating a sister group relationship between Diatomyidae and Ctenodactylidae.

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*Laonastes aenigmamus*, the Laotian rock rat, an enigmatic rodent from karstified limestone mountains of Laos and Vietnam, was first described by Jenkins et al. (2005) and immediately gained interest from the scientific community. The original describers placed the new and monotypic taxon in its own family Laonastidae belonging to the Hystricognathi. However, Dawson et al. (2006) concluded that *Laonastes aenigmamus* belongs to the otherwise extinct Asian family Diatomyidae; they also recognized that the masseter muscle

is hystricomorphous but the lower jaw is sciurognathous (see also Hautier et al., 2011). Therefore, they classified the new taxon in the Ctenohystrica clade (see also Hautier and Saksiri, 2009; Hautier, 2010; Hautier et al., 2011; Hautier et al., 2012; Herrel et al., 2012; Huchon et al., 2007; Churakov et al., 2010). Available systematic conclusions were based on both morphological and molecular evidence – but it was admitted by all cited authors that the database is still unsatisfactory.

Histological serial sections provide superior insight into vertebrate's soft tissue morphology to any other available technique like micro computed tomography ( $\mu$ CT), magnetic resonance imaging (MRI) or macroscopic preparation. Here we provide a report on a sectional series of a late fetal *Laonastes aenigmamus* (CRL = 72 mm, HL = 28.5 mm), allowing a refined understanding of the head morphology. In the present paper we point out that in the fetal *Laonastes* the *chorda tympani* crosses above the insertion of the *musculus tensor tympani* and therefore it is epitensoic (Fig. 1a).

The *chorda tympani* is a posttrematic branch of the facial nerve that leads we would prefer to use British English from taste buds and to salivary glands of the lower jaw. Its very peculiar course has raised the interest of comparative anatomists for a long time, and Goodrich (1915) convincingly put it into an evolutionary context by

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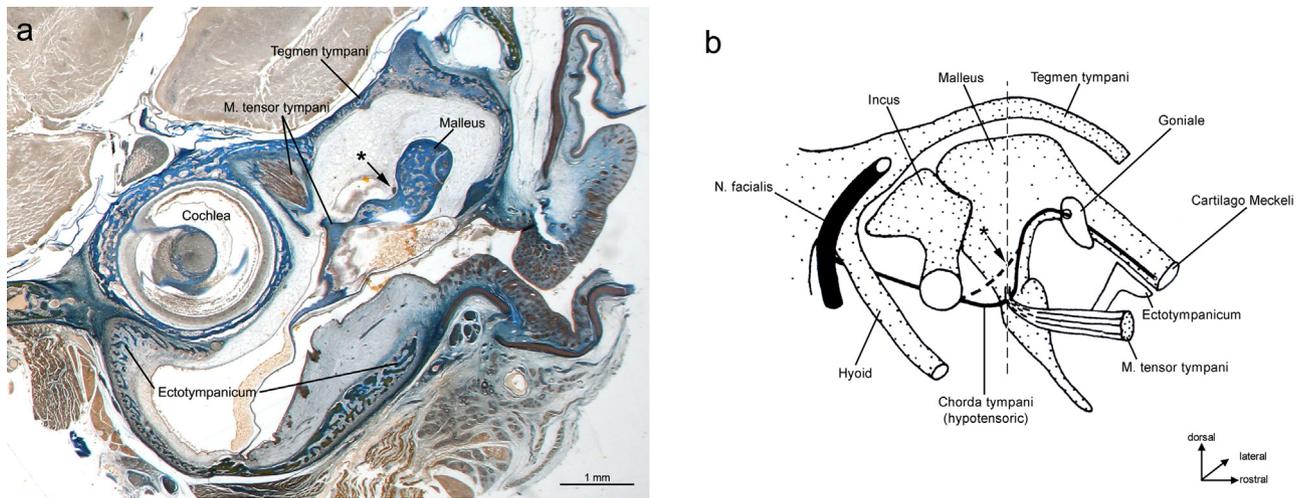
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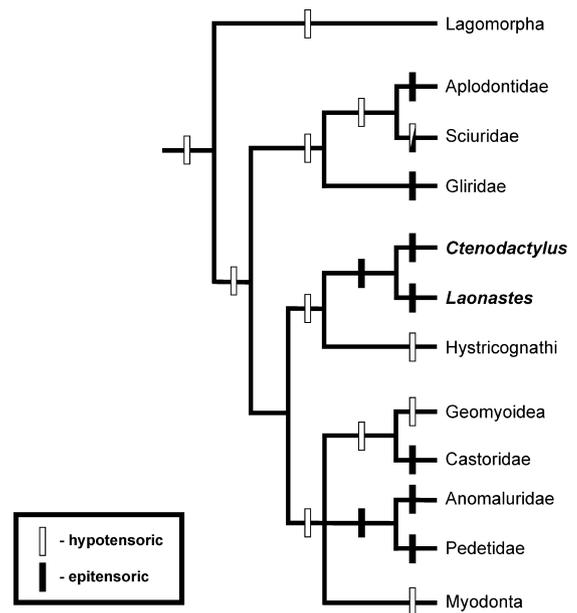
**Fig. 1.** (a) Histological section of the left ear region of the fetal specimen of *Laonastes aenigmamus* (Section no. 1040; Slice thickness 20  $\mu\text{m}$ ; staining: Azan after Heidenhain, cf. Romeis et al., 1989, frontal view). The asterisk and arrow indicate the position of the chorda tympani nerve; because it is situated dorsal to the insertion of the tensor tympani muscle, it is epitensoric. (b) Semi-schematic drawing of structures of the left middle ear seen from the medial side (modified after Voit, 1909 and Maier, 2008). The solid line shows the plesiomorphic condition of the chorda tympani nerve passing underneath the tensor tympani muscle (hypotensoric state); the stippled line shows the derived epitensoric state that is found in *Laonastes aenigmamus* and *Ctenodactylus gundi*. The arrow indicates the crossing point of the epitensoric chorda tympani with the transversal section plane shown in Fig. 1a.

spotting the neomorphic nature of the outer ear duct of amniotes (Fig. 1b).

Bondy (1907) studied the middle ear region of about 50 species of mammals, and he showed that in the overwhelming majority of these species, the chorda tympani passes below the insertion of the *m. tensor tympani* (Fig. 1b, the solid line represents this state). Many subsequent studies of skull development in various mammal species made more or less explicit remarks on the course of the chorda tympani, but only Maier (2008) established its systematic relevance: He showed that in all strepsirrhine primates and in tarsiers the chorda passes underneath the *m. tensor tympani*, whereas in all anthropoids it passes above; he called the former plesiomorphic state “hypotensoric” and the latter apomorphic state “epitensoric”. Further studies confirmed the notion of Bondy (1907) that the overwhelming number of mammal species have retained the hypotensoric situation, whereas the epitensoric state had been acquired only by a few well defined taxonomic groups. For instance, in carnivores, Ruf and Maier (2010) demonstrated that the epitensoric chorda occurs only in the family Herpestidae, thus confirming them as a monophyletic unit.

Ruf et al. (2009) studied a great number of rodents by means of histological serial sections and found the apomorphic state only in seven monophyletic groups: Aplodontidae, Gliridae, Castoridae, Ctenodactylidae, Anomaluridae, and Pedetidae; it is also found in the Sciuridae, but this is the only family for which we have good evidence that epitensoric conditions developed within the group (Fig. 2). Considering that Anomaluridae and Pedetidae are sister groups, as indicated by a number of molecular studies (Huchon et al., 2007; Churakov et al., 2010), their epitensoric chorda may be considered as a synapomorphy. As far as known, all of the speciose hystricognaths and myodonts are hypotensoric. Because lagomorphs as sister group are hypotensoric as well, we have to conclude that the ancestral morphotype (“Grundplan” sensu Hennig, 1982) of rodents and all the suprafamilial units is hypotensoric – and that the apomorphic epitensoric states developed independently in several rodent clades (Fig. 2).

Within this framework, the discovery of an epitensoric chorda tympani in *Laonastes aenigmamus* (Diatomyidae) gains specific relevance: the only other member of Ctenohystrica that shows an epitensoric chorda tympani is *Ctenodactylus gundi* (Ctenodactylidae) from Northern Africa (Ruf et al., 2009; Schrenk, 1989; Fig. 2), and



**Fig. 2.** Simplified cladogram of extant rodents into which the two different character states of the chorda tympani are mapped (modified from Ruf et al., 2009). A sister group relationship of Diatomyidae and Ctenodactylidae (Dawson et al., 2006), as supported by a synapomorphic epitensoric chorda tympani, is indicated.

ctenodactylids have been found on quite different evidence to be the sister group of diatomyids (Dawson et al., 2006; Hautier et al., 2011, Huchon et al., 2007). Therefore, it is likely that an epitensoric chorda tympani can be considered as a synapomorphy in the sense of Hennig (1982) further supporting a sister group relationship between the two taxa.

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