

Discovery of Cretaceous Arboreal Eutherians

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Mammalian phylogeny is undergoing a considerable renewal with regard to the interaction between molecular studies and the more traditional contributions of morphology and paleontology [1–3]. In spite of many advances, “higher mammalian phylogeny is still unclear” [1], and the adaptation of the earliest eutherians remain poorly documented. We report here the discovery of arboreal eutherians from the Cretaceous, found in India. These eutherians have palaeoryctid-like teeth. Their tarsals show a marked specialization to an arboreal way of life, which contrasts to the terrestrial adaptation found in previously studied Cretaceous eutherians [4]. Hence, the small insectivorous Late Cretaceous eutherians, which presented only limited skull and dental evolution [5–7], had already widely diverged in their locomotor adaptations.

The first Cretaceous eutherians found in India were isolated teeth of *Deccanolestes*, which were ascribed to the family Palaeoryctidae [8]. From the same locality in intertrappean beds near the village of Naskal (Andhra Pradesh), dated as Maastrichtian [9, 10], further matrix processing led to the recovery of additional dental and tarsal remains. The only eutherians present are two species of *Deccanolestes*, which differ in size. Eutherian tarsals of two different sizes are therefore confidently attributed to these two species. Only one astragalus was found for the larger species, whereas one calcaneum and two astragali correspond to the smaller species, *D. hislopi* Prasad and Sahni, 1988. The tarsals of

this last species are analyzed here. A longer description and functional analysis of all the material will be given elsewhere [11].

The astragalus has a broad body and a short neck set at an angle relative to the main direction of the tibial trochlea (Fig. 1). The trochlea is broad and shallow,

extends slightly on to the neck medially, and is proximally limited by a small astragalus foramen. The lateral trochlear crest is salient, distinctly curving distomedially, and slightly higher than the medial crest. Hence, dorsiflexion of the foot was accompanied by abduction and some conjunct inversion. This movement is the same as that described in primates, but deviation is guided by the lateral trochlear crest instead of the distomedial prolongation of the medial tibial facet as in primates [12]. On the calcaneum, the proximal astragalus facet is proximodistally elongated, and curved (Fig. 1). The smaller corresponding facet on the astragalus could slide on it, producing a helical movement between the two bones. Distally, the sustentacular facet of the astragalus is prolonged both proximally and distally, where it is confluent with

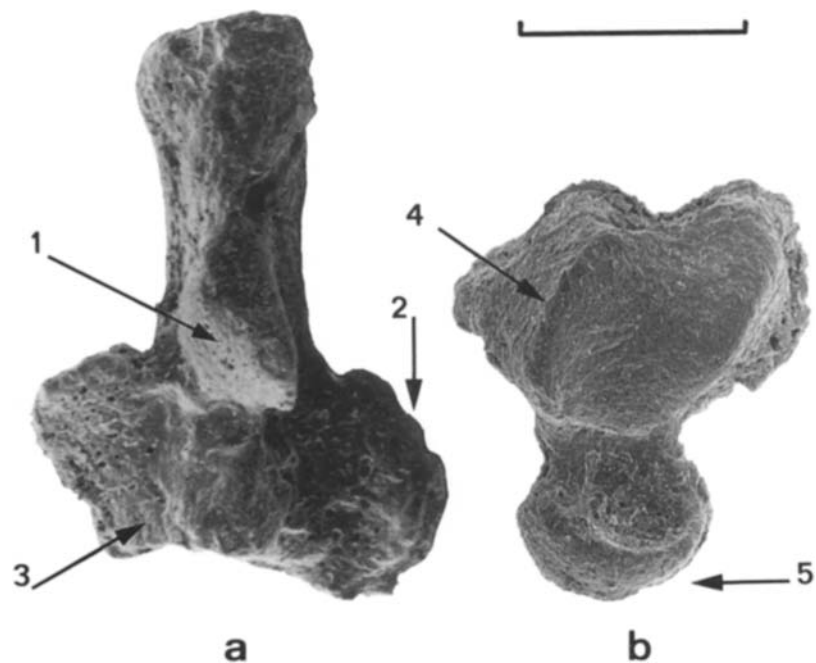


Fig. 1. Scanning electron micrographs of casts of tarsals from Late Cretaceous beds near Naskal (India), attributed to *Deccanolestes hislopi* and housed in the University of Jammu collection; a) left calcaneum in dorsal view (NKIM 50), b) right astragalus in dorsal view (NKIM 52); scale bar 1 mm (micrographs by A. Rossi). Arrows point toward characters typifying an arboreal adaptation: the elongated and curved proximal calcaneo-astragalus facet (1), the prominent peroneal tubercle (2), the distally extended sustentacular facet (3), the high and distomedially curved lateral trochlear crest (4), and the round navicular facet (5)

the navicular facet. Hence, the distal articulation between the two tarsals also reflects extensive sliding movements between them. The cuboid facet of the calcaneum is shallow and subcircular. It is well suited for sliding and conjunct rotation of the cuboid [13]. The head of the astragalus is mediolaterally very round (Fig. 1), and the extended navicular facet reflects good sliding capability of the navicular on the astragalus head. Mobility at the lower ankle joint and the transverse tarsal joint resulted in good rotational capability of the foot, as is known in living arboreal mammals and especially primates [13, 14].

The peroneal tubercle of the calcaneum laterally displaces the tendon of the peroneus longus, and dorsally provides space for the tendon of the peroneus brevis and plantarly the body of abductor digiti quinti [4, 15]. These three muscles are involved in movements of eversion-inversion of the foot. The very large size of the peroneal tubercle in *Deccanolestes* (Fig. 1) suggests that these tendons and muscles were large, permitting frequent foot rotation movements necessary in an arboreal way of life. The astragalus head, dorsoplantarily higher on the lateral side than in other known Cretaceous eutherians, points toward more frequent postures and movements with an inverted foot, as is usual in living arboreal mammals [4, 14]. Hence, the tarsal characters of *D. hislopi* indicate that this species was well adapted to an arboreal way of life, something which had never been found in Cretaceous eutherians until now.

Linked to this differing adaptation are a number of marked morphological differences between *Deccanolestes* and the other known Cretaceous eutherian tarsals, those of the condylarthran *Protungulatum* and the palaeoryctid *Procerberus* [4] (those of the older *Asioryctes* are very specialized [5, 16]). These differences will be detailed elsewhere [11]. Conversely, *Deccanolestes* shares a number of characters with Paleocene-Eocene Archonta, the superorder containing Chiroptera, Dermoptera, Scandentia, and Primates [1, 17–19]. In fact, *Deccanolestes* tarsals show almost all the characters listed by Szalay and Drawhorn [14] to define the archontan morphotype, providing a remarkable confirmation of their prediction. These characters are those analyzed above, and showing an arboreal adaptation. Among the

expected primitive characters of such an ancient fossil is the transverse orientation of the proximal calcaneal facet of the astragalus [14]. A difference to Szalay and Drawhorn's archontan morphotype is the lateral instead of medial merge between the sustentacular and the navicular astragalar facets. However, a similar lateral merge exists in dermopterans [14], showing that it does not exclude archontan affinities (a median merge can be observed in some primates [20]). Unsuspected in the archontan morphotype are the extreme breadth of the body and the distomedial curvature of the lateral trochlear crest of the *Deccanolestes* astragalus. These two characters are linked with its arboreal adaptation, and could as well represent the archontan morphotypic condition, or an early specialization of the genus. In any case, these differences do not alter the remarkable overall resemblance (mostly in shared derived characters) of the *Deccanolestes* tarsus with that of early archontans, which suggests that *Deccanolestes* is probably closely related to them, and could even represent an early member of this taxon.

The known teeth of *Deccanolestes* show a broad palaeoryctoid pattern [8], but they also differ from typical palaeoryctids. The upper molars are less transversely wide, have a less elongated parastylar area, lower labial cusps, and an anteroposteriorly broader protocone base. The lower molars have lower trigonids. These characters, which are advanced over those of North American palaeoryctids [6, 7], could indicate an incipient archontan dental pattern in *Deccanolestes*. However, this dental evidence consists of subtle differences, which will be reassessed elsewhere (based on the new material). More clearly than its teeth, *Deccanolestes* tarsals point toward archontan affinities, and suggest that archontans may have originated from primitive eutherians having palaeoryctid-like teeth. This agrees with recent studies discarding lepididaffinities for primates [18, 19, 21], which were advocated earlier [6, 22]. This also confirms the suspicion that "some of the phenetically similar members (of palaeoryctoids) relate to widely divergent groups of mammals" ([21], p. 76). We propose to include archontans in the group derived from "dental palaeoryctids". The discovery in India of early archontan relatives fits with the biogeographical evidence.

The most generalized living archontans, the treeshrews (Tupaiaidae, order Scandentia) live in Asia and their sole fossil relatives come from the Miocene of the Indian subcontinent [23–26]. An Asian origin for Archonta appears probable.

Some similarities exist between *Deccanolestes* tarsals and those of primitive marsupials, e.g., in extreme breadth of the astragalar body and some sloping of the medial tibial facet [16]. However, these are not enough to suggest a revival of the theory of the arboreal origin of Eutheria [16, 27]. *Deccanolestes* has a typical eutherian tenon-mortise upper ankle joint, interpreted as a terrestrial adaptation by anatomists [12, 16]. Hence, it seems to confirm a terrestrial heritage in archontans and other eutherians, even if Jurassic predecessors were scansorial [28] (unless another behavioral interpretation would be proposed for this tenon-mortise joint, as, e.g., rapid movements on any kind of support).

The differences between *Deccanolestes* and other Cretaceous eutherian tarsals emphasize a considerable amount of morphological and locomotor evolution having occurred prior to and during Maastrichtian time. This contrasts to limited skull and dental evolution in early eutherians [5–7]. It suggests that Cretaceous eutherians, which were small insectivorous animals, diverged first in habitat and locomotion. Hence, their postcranials should become more and more critical for deciphering the earliest dichotomies in the eutherian radiation, which took place during the Cretaceous.

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1. Novacek, M. J.: Nature 356, 121 (1992)
2. McKenna, M. C., in: Molecules and Morphology in Evolution: Conflict or Compromise?, p. 55 (C. Patterson, ed.). Cambridge: Cambridge Univ. Press 1987

3. Novacek, M. J., Wyss, A. R., McKenna, M. C., in: *The Phylogeny and Classification of the Tetrapods*, Vol. 2, p. 31 (M. J. Benton, ed.). Oxford: Clarendon 1988
4. Szalay, F. S., Decker, R. L., in: *Primate Locomotion*, p. 223 (F. A. Jenkins, ed.). New York: Academic Press 1974
5. Kielan-Jaworowska, Z., Bown, T. M., Lillegraven, J. A., in: *Mesozoic Mammals, the First Two-thirds of Mammalian History*, p. 221 (J. A. Lillegraven, Z. Kielan-Jaworowska, W. A. Clemens, eds.). Berkeley: Univ. of California Press 1979
6. Lillegraven, J. A.: *Univ. Kansas Paleont. Contr.* 50, 1 (1969)
7. Clemens, W. A.: *Univ. Calif. Pub. Geol. Sci.* 94, 1 (1973)
8. Prasad, G. V. R., Sahni, A.: *Nature* 332, 638 (1988)
9. Prasad, G. V. R.: *J. Geol. Soc. India* 34, 161 (1989)
10. Sahni, A., Venkatachala, B. S., Kar, R. K., Rajanikanth, A., Prakash, T., Prasad, G. V. R., Singh, R. Y.: *Cretac. Res.* (in press)
11. Prasad, G. V. R., Godinot, M.: *J. Paleont.* (in press)
12. Lewis, O. J.: *Functional Morphology of the Evolving Hand and Foot*. Oxford: Clarendon 1989
13. Jenkins, F. A., McClearn, D.: *J. Morphol.* 182, 197 (1984)
14. Szalay, F. S., Drawhorn, G., in: *Comparative Biology and Evolutionary Relationships of Tree Shrews*, p. 133 (W. P. Luckett, ed.). New York: Plenum 1980
15. Jouffroy, F. K.: *Mammalia Sup.* 26, 1 (1962)
16. Szalay, F. S.: *Evol. Biol.* 18, 215 (1984)
17. Gregory, W. K.: *Bull. Am. Mus. Nat. Hist.* 27, 1 (1910)
18. McKenna, M. C., in: *Phylogeny of the Primates*, p. 21 (W. P. Luckett, F. S. Szalay, eds.). New York: Plenum 1975
19. Szalay, F. S., in: *Major Patterns in Vertebrate Evolution*, p. 315 (M. K. Hecht, P. C. Goody, B. M. Hecht, eds.). New York: Plenum 1977
20. Godinot, M.: *Z. Morph. Anthropol.* 78, 387 (1991)
21. Novacek, M. J.: *Bull. Am. Mus. Nat. Hist.* 183, 1 (1986)
22. McKenna, M. C.: *Fol. Primatol.* 4, 1 (1966)
23. Chopra, S. R. K., Kaul, S., Vasishat, R. N.: *Nature* 281, 213 (1979)
24. Chopra, S. R. K., Vasishat, R. N.: *ibid.* 281, 214 (1979)
25. Jacobs, L. L., in: *Comparative Biology and Evolutionary Relationships of Tree Shrews*, p. 205 (W. P. Luckett, ed.). New York: Plenum 1980
26. Butler, P. M., in: *ibid.*, p. 171
27. Matthew, W. D.: *Am. Nat.* 38, 811 (1904)
28. Krebs, B.: *Berliner Geowiss. Abh. A* 133, 1 (1991)

Frequency Spectra of Atmospherics over the North Atlantic

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In a previous paper [1] variations of atmospheric activity in narrow frequency bands at 10 and 27 kHz, respectively, recorded during a ship voyage over the North Atlantic, have been described. It was found that the patterns of atmospheric activity are reproducibly correlated with the actual weather situation within the receiving range of the antenna system, i.e., 500 km around the ship's position.

In addition, integral frequency spectra of atmospheric activity were determined during selected time intervals at definite positions on the ship's route. The results are presented in this paper and compared with the frequency spectra, measured over land at our station in Pfaffenhofen, 45 km north of Munich [2].

The measurements were performed aboard a container cargo ship of Hapag-Lloyd on a voyage from Hamburg (FRG) to Norfolk (USA) and back. The electronic equipment for recording and analyzing atmospheric activity has been described in [1]. A description of the atmospheric frequency spectrometer, used in this investigation, has been presented in [2]. With this instrument the main spectral frequencies of each individual atmospheric impulse between 3 and 100 kHz could easily be detected.

The atmospheric analyzer contained a special electronic impulse-form recognition system which excluded original lightning signals as well as technically produced signals (technics) from being recorded. Such technics can, for

instance, be generated by crane motors or radar antennas of the ship.

The ship's route had a length of about 15000 km and led from Hamburg (start: 20.9.1984) to Greenock-Glasgow (24.9.), Halifax (30.9.), New York (2.10.), and Norfolk (3.10.). The stations on the way back were New York (7.10.), Halifax (8.10.), Southampton (14.10.), Calais (15.10.), Antwerpen (17.10.), and Hamburg (19.10.1984). This route covered 86° longitude and 22° latitude. The most northern point was 58°42'N and the most southern and simultaneously western point was 36°54'N and 76°19'W, respectively (Fig. 1).

During this voyage, on 12 days, more than 5000 measurements of single atmospheric impulse frequency spectra at selected ship positions were performed. Special positions for such measurements were chosen with respect to geographical viewpoints and the geological structure of the ocean's ground. Regions of interest were shelf areas, mountains and lines of faulting on the bottom of the sea, deep-sea areas, coastal districts and ports as sources of electrosmog. The numbers in Fig. 1 indicate the locations where frequency spectra of atmospheric activity were measured. The frequency spectra were compared with those obtained over land at the station in Pfaffenhofen [2].