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Theropod dinosaurs in the trees: a historical review of arboreal habits amongst nonavian theropods

Zusammenfassung
Darstellungen nicht-vogelhafter theropoder Dinosaurier, die in Bäumen klettern, werden zunehmend populär, zum einen wegen ihrer ästhetischen Wirkung, zum anderen wegen der aktuellen Theorien über die Verwandtschaft von Theropoden und Vögeln. Vorstellungen über eine baumbewohnende Lebensweise bei Theropoden sind jedoch nicht neu und reichen bis in das Jahr 1866 zurück. Sowohl die Theropoden-Morphologie als auch die Mannigfaltigkeit heutiger Taxa, die Bäume erklettern können, zeigen an, dass Baumklettern bei den meisten kleinwüchsigen Theropoden-Arten (mit weniger als 100 kg) möglich, vielleicht wahrscheinlich, war. Einige fossile Säugetiere werden weithin als Baumkletterer angesehen, sie erscheinen jedoch an diese Lebensweise schlecht angepasst, wenn man sie mit kleinen Theropoden vergleicht.

Abstract
Depictions of non-avian theropod dinosaurs climbing in trees are becoming increasingly popular due to both their aesthetic appeal and current theories on the affinities of theropods and birds. However, notions of arboreality in theropods are not new and date to as early as 1866. Both theropod morphology, and the diversity of extant taxa that can climb trees, indicate that tree-climbing in most small-bodied theropod species (less than 100 kg) was possible, perhaps probable. Some fossil mammals are widely regarded as tree climbers, yet appear poorly adapted for this lifestyle when compared with small theropod dinosaurs.

A history of climbing theropods

The idea that small theropod dinosaurs may have been capable of climbing trees is currently popular in the non- and semi-technical palaeontological literature, a fact we owe to the highly artistic members of the 'dancing dinosaur' school (cf. BAKKER 1986, 1987), to the protagonists of heterodox theories concerning avian origins (PAUL 1984, 1988a,b, OLSHEVSKY 1991, 1994, CHATTERJEE 1997), and to the influence of science fiction stories (CRICHTON 1991, BAKKER 1995). Life restorations of small coelurosaurs increasingly depict the animals in tree-climbing postures. This tradition has its recent genesis in PAUL's (1988a) famous depiction of the Morrison Formation coelurosaur *Ornitholestes hermanni* in the branches of a tree; a scene regarded as a 'wild speculation' by FEDUCCIA (1996).

However, suggestions that small theropods may have been scansorial or arboreal are by no means new. Writing in 1866 about *Calamospondylus oweni*, a taxon based on some pelvic elements found in the Wessex Formation (Wealden Group, Lower Cretaceous) of the Isle of Wight, England, FOX (1866a,b) opined that it may have been in the habit of 'leaping from tree to tree'. Based upon the apparent pneumaticity of the *C. oweni* type specimen (now of unknown whereabouts – new investigation indicates that this name does not pertain to BMNH R178, the holotype for *Aristosuchus pusillus* (NAISH in prep.)), this may constitute the earliest suggestion of arboreal habits in a specific non-avian dinosaur.

Reviewing the Isle of Wight's fossil dinosaur fauna, SWINTON (1936a) looked upon FOX's (1866a,b) idea in a favourable light, and in fact even elaborated on it. With regard to small coelurosaurs, SWINTON (1936a) wrote that 'their own safety lay in their running abilities and they may have been able to climb rocks and trees to some extent' and 'the long claws on the hands suggest some powers of grasping that would be useful in tearing the flesh of prey and of holding branches when climbing' (both p. 207). SWINTON's propensity to picture small dinosaurs as scansorial clearly dominated his thoughts on the lifestyle of the ornithopod *Hypsilophodon* as well (SWINTON 1936b).

Thereafter, notions of a scansorial lifestyle for small theropods went essentially unmentioned, despite GALTON's (1971a,b, 1974) discussion and refutation of ABEL's (1912) arboreal *Hypsilophodon*. GALTON (1971a,b) did mention the possibility that hypsilophodonts, small theropods and other dinosaurs of similar size may infrequently have climbed trees. However, the idea that small theropods may have been able to utilise trees as foraging, vantage or refuge points was essentially resurrected by PAUL in the wake of BAKKER's 'dinosaur renaissance' (BAKKER 1972). In considering the possible lifestyles of a number of dinosaur taxa, BAKKER (1993) regarded the tree-climbing skills of a variety of small dinosaurs, including the theropods *Procompsognathus* and *Velociraptor*, as highly proficient.

PAUL (1988a) has stated that 'small advanced theropods were good climbers ... their long arms and long, big-clawed fingers show that they were' (p. 196). He went on to suggest that some small Jurassic theropods may have become bush-climbing specialists that lengthened their forelimbs and essentially reverted to part-time quadrupedalism (PAUL 1988a). Speculating that some as-yet-undiscovered small theropods may have been predominantly arboreal, PAUL effectively created a hypothetical direct ancestor for *Archaeopteryx* and other birds. Recognising that it is probably unwise to dichotomise between a strict 'ground up' or 'trees down' hypothesis, PAUL coined this the 'trees up' hypothesis (PAUL 1988a).

Inspired by PAUL's (1984, 1988a,b) suggestion that some coelurosaurian theropods were descended from volant archaeopterygid ancestors, OLSHEVSKY (1991, 1994) argued that all theropods, and even all dinosaurs and all archosaurs (OLSHEVSKY 1994), were terrestrial descendants of small, scansorial archosaurs, themselves predisposed toward the evolution of flight and the direct ancestors of birds. OLSHEVSKY's theory, popularly dubbed 'Birds Come First' (BCF), requires the existence of numerous small-bodied climbing dinosaurs and dinosaur ancestors.

In an exception to the rule that speculations on tree-climbing theropods have been restricted to forms of small size, ROZHDESTVENSKY (1970) proposed that some large theropod taxa might have been scansorial or arboreal. Noting OSBORN's (1917) comparisons between ornithomimosaur and sloth forelimbs, ROZHDESTVENSKY (1970) suggested that ornithomimosaurs might have been tree-climbers. By extension, such comparisons also apply to other theropods with elongate forelimbs and proportionally large manual unguals – namely, amongst the Upper Cretaceous Mongolian taxa, *Chilantaisaurus tashuikouensis*, therizinosauroids and *Deinocheirus mirificus*. While ROZHDESTVENSKY (1970) regarded *Chilantaisaurus* and the therizinosauroids to be too large, and with hindlimbs too proportionally elongate, to be potential scansors, he suggested that *Deinocheirus* was an arboreal, sloth-like ornithomimosaur that might have had shortened hindlimbs. The medial orientation of the palms in *Deinocheirus* (an orientation currently thought to be common to most theropods) was suggested as an adaptation for a branch-climbing lifestyle. In essence, ROZHDESTVENSKY (1970) regarded *Deinocheirus* as a gigantic arboreal 'sloth-dinosaur'.

Following ROZHDESTVENSKY's speculations about *Deinocheirus*, NESSOV (1995) proposed that the large, fully terrestrial therizinosauroids of the Cretaceous were descendants of small, arboreal therizinosauroids which, again, were 'sloth-dinosaurs'. NESSOV (1995) suggested that the small size and arboreal habits of these hypothetical pre-Cretaceous therizinosauroids explained their absence from the fossil record. What appears to be a pre-Cretaceous therizinosauroid has now been reported (ZHAO & XU 1998). However, as this specimen consists only of a lower jaw, the arboreal or scansorial abilities of primitive therizinosauroids, and therefore NESSOV's scenario, remain untestable.

CHATTERJEE (1997) proposed that scansoriality was primitive for coelurosaurs (but not for Theropoda), being the primary mode of life in all basal members of this clade. According to this scheme, large-bodied coelurosaurs, including all known ornithomimosaurs and dromaeosaurids, are again secondarily terrestrial and have descended from small arboreal ancestors (CHATTERJEE 1997). Though he

had earlier characterised ornithomimosaurs as cursorial and entirely terrestrial, like extant ratites (CHATTERJEE 1993), CHATTERJEE (1997) more recently regarded and illustrated ornithomimosaurs as scansorial herbivores. Intriguingly, CHATTERJEE (1997) suggests that several unusual features of dromaeosaurid morphology, including the wrist with its restricted movement, the strongly hooked manual claws, the opisthopubic pelvis (NORELL & MAKOVICKY 1997), and the stiffened rod-like tail, may have originally evolved as specialisations for climbing.
Identical arguments and an identical model for dromaeosaurid evolution were proposed by PALM (1997). PALM's theory has remained poorly known and little discussed: it has been published in two booklets and was presented in 1989 as part of an ornithological convention at Cologne, Germany. Like CHATTERJEE (1997), PALM suggests that dromaeosaurids clambered up tree trunks using their hooked manual and pedal claws, but it is suggested that they were specifically suited for vertical ascent and descent on the trunks of cycadophytans.

Obstacles to tree-climbing theropods

For as long as theropods were not regarded as potential avian ancestors, there was no scientific *need* to create a tree-climbing theropod. Today, as the theropodan origin of birds is increasingly well supported, and as climbing abilities are often regarded as at least somehow intuitively 'useful' in the origin of birds and of flight, popularisers of dinosaur palaeontology often point to the possibility of scansorial abilities in non-avian theropods.
Conversely, supporters of the 'ground up' or cursorial theory for the origin of bird flight have never favoured arboreal habits amongst non-avian theropods – indeed, they also regard *Archaeopteryx* as cursorial and entirely terrestrial – as they are not required for this model. For example, OSTROM (1979) argued that the (possibly) reversed hallux of non-avian theropods was 'certainly ... not for arboreal activity' and that the strongly clawed, grasping hands of theropods were for prey capture, rather than climbing. Evidence for the predatory habits of many such theropods indicates that the primary use of sharp claws, grasping hands and elongate fingers was indeed predatory. Nevertheless, structures are rarely of single function.
OSTROM (1974, 1979) also argued that arboreal habits in bird ancestors were unlikely as, given that such ancestors were the obligatorily bipedal theropods, the invasion of the arboreal realm by obligatory bipeds was, excepting volant birds, effectively improbable. MARTIN (1983) argued similarly. OSTROM (1979) pointed out that tree kangaroos, a possible exception to this observation (CHATTERJEE (1997) employed them as such) were not obligate bipeds, but, with fore- and hindlimbs of equal size, were actually quadrupedal in the trees. PADIAN & CHIAPPE (1998) argue that theropods were 'ground-dwelling cursorial bipeds with no obvious scansorial or arboreal adaptations'.
PADIAN & CHIAPPE (1998) assert that the hallux of *Archaeopteryx* is too short and too proximal on the metatarsus to be an effective aid in perching. While they are certainly correct in that *Archaeopteryx* does not exhibit the proportionally large, distal and fully opposable hallux of passerines or other arboreal and scansorial birds, and does not therefore seem to have been a specialised percher or climber (BOCK & MILLER 1959, GALTON 1970, OSTROM 1974), the opposable hallux of this taxon appears more than adequate to have functioned during climbing. Similarly, despite current controversy concerning the orientation of the nonavian theropod hallux (OSTROM 1991, NORELL & MAKOVICKY 1997), the medial and somewhat elevated position of this structure would still appear beneficial in branch climbing. Furthermore, a retroverted hallux or other opposable digit is not necessarily required for climbing as many extant animals that are proficient or very proficient at climbing lack such structures. Many mustelids and even one canid, for example, are adept climbers, yet are conspicuously devoid of large, opposable digits or other climbing specialisations (Fig. 1).
Critics of the theropodan ancestry of bird theory have also argued that tree-climbing theropods were impossible or non-existent, in this instance because it is insisted both that bird flight evolved in the trees, and that theropods were wholly unsuited for a climbing lifestyle (TARSITANO 1989, FEDUCCIA 1996). FEDUCCIA has repeatedly made the incorrect assertion that all theropods were too large, and with forelimbs too small, to be potential bird ancestors (and, by extension, to be potentially scansorial). A number of theropod groups do indeed appear ill equipped to be potential climbers, and at least some such taxa appear to have inhabited environments where trees were rare or absent (e.g. JERZYKIEWICZ

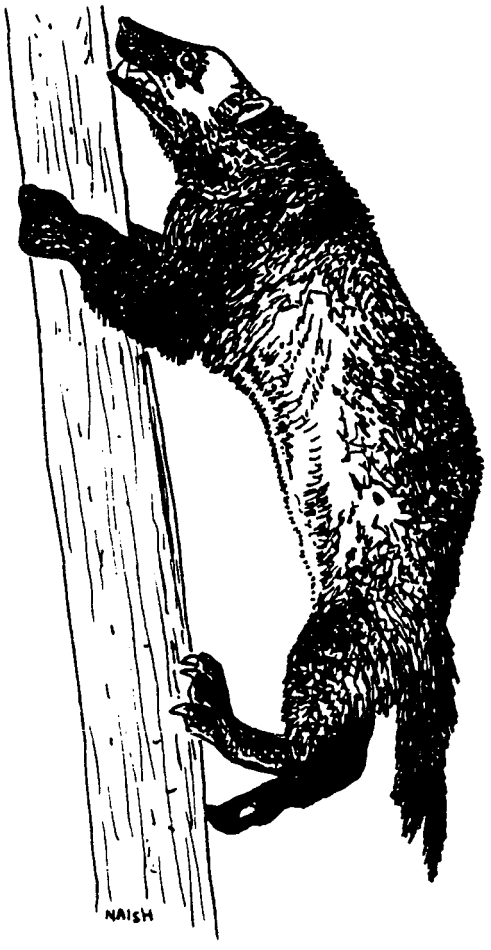

Fig. 1.
How a wolverine *(Gulo gulo)* climbs a tree. Note that the palms face medially to grasp the trunk while the feet are held in line with the long axis of the body. A similar mode of climbing seems entirely appropriate for smaller theropod dinosaurs given the morphology of their hands and feet. Based on a photograph taken by T. McHUGH/B. COLEMAN.

Abb. 1.
Wie ein Vielfraß *(Gulo gulo)* einen Baum erklimmt. Beachte, dass die Vorderfußflächen sich medial gegenüberstehen, um den Stamm zu ergeifen, während die Hinterfüße in einer Linie mit der Längsachse des Körpers gehalten werden. Eine ähnliche Klettermethode erscheint vollkommen angemessen für die kleineren Theropoden bei der bekannten Morphologie ihrer Hände und Füße. Nach einer Fotografie von T. McHUGH/B. COLEMAN.

et al. 1994). Theropods with markedly cursorial hindlimbs, such as ornithomimosaurs, appear ill suited for tree climbing. This makes ROZHDESTVENSKY's (1970) and CHATTERJEE's (1997) scansorial ornithomimosaur somewhat unlikely. It is similarly implausible that theropods with strongly reduced forelimbs, or of very large size (>150 kg), were capable of climbing.

In extant felids, *Panthera* species of 60 kg are able climbers (NOWAK 1983, KINGDON 1997) and even fully adult male *P. leo* of 180 kg or more are capable of climbing and do so regularly at some localities (e.g. Lake Nakuru National Park). The small size of many of the coelurosaur taxa that also possess the characteristics required for climbing is therefore fully in agreement with their possible scansorial abilities. ROZHDESTVENSKY's (1970) proposal of arboreality in *Deinocheirus* seems remarkably unlikely given that this dinosaur was enormous: PAUL (1988a) estimates its mass at between 6 and 12 tons.

A number of features are seen in extant taxa that may be regarded as specialised climbers. Prehensile tails and reversible ankles are common to many lineages of arboreal marsupial, eutherian and squamate, and the recognition of such features in fossil members of these groups has resulted in interpretation of them as arboreal or scansorial (e.g. GINGERICH & GUNNELL 1989). That all described nonavian theropod taxa lack these features indicates that no known nonavian theropod was truly specialised for arboreal life. The issue therefore becomes one of whether or not theropods were capable of facultative arboreality. The oft-cited scansorial skills of feral goats *(Capra hircus)* require that we exercise caution in setting constraints on the climbing abilities of extinct animals.

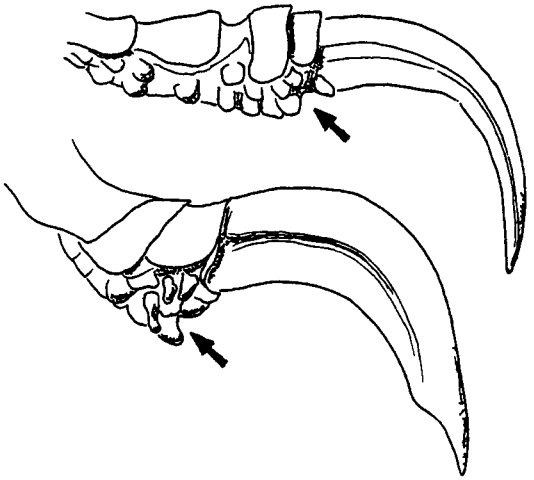

Fig. 2.
Notches in the distal toe pads of the certhiid *Certhia* and the parulid *Mniotilta*. Both taxa climb vertically on tree trunks and both have unusual distal notches on their toe pads. After CLARK (1973).

Abb. 2.
Kerben in den distalen Zehenpolstern des Baumläufers *Certhia* und des Waldsängers *Mniotilta*. Beide Taxa klettern vertikal an Baumstämmen, und beide haben ungewöhnliche distale Kerben an ihren Zehenpolstern. Nach CLARK (1973).

Small theropods were well equipped for facultative climbing

Amongst extant tetrapods, the ability to climb is common and widespread in taxa that have flexible digits and sharp claws. A limited ability to climb is even allegedly recorded for such ill-adapted animals as some chelonians (specifically *Platysternon*) (ALDERTON 1988) and crocodiles (FREY 1988). In palaeomammalogy, scansoriality is generally accepted as likely for agriochoerine merycoidodontoids as these animals combined an enlarged manus with clawed unguals and an opposable pollex (LANDER 1998). The opposable or semi-opposable medial digits of some theropods, their sharp, recurved unguals, their elongate phalanges, and their probably highly developed balancing abilities, make small theropods entirely suited for a scansorial lifestyle and, in fact, probably far better adapted for it than agriochoerines.

Comments on vertical trunk-climbing in theropods

CHATTERJEE (1997) and PALM (1997) illustrated dromaeosaurids of a *Deinonychus*-like morphology clinging to vertical trunks. Though the animals they illustrated were essentially hypothetical, at present no known non-avian theropod appears to have been a specialist trunk-clinger. Extant trunk-clingers such as campephilin woodpeckers and *Micropsitta*, the pygmy parrots, though exhibiting stiffened rectrices that function as props, and therefore as possible analogues to the stiffened, prop-like dromaeosaurid tail, possess pamprodactyl feet where all four toes point cranially (BOCK & MILLER 1959, WINKLER et al. 1995). The fact that these birds almost certainly have zygodactyl ancestors, and are the most specialised trunk-clinging taxa in their respective groups, indicates that pamprodactyly is selectively advantageous for trunk-clinging taxa. Certhiids (treecreepers) and some other trunk-climbing passerines are not pamprodactyl, but are very small and with tremendously recurved, hook-like pedal claws (NOSKE 1985).

CLARK (1973) noted that some trunk-climbing passerines possessed unusual notches in some of their toe pads (Fig. 2), the function or purpose of which was difficult to evaluate, but their absence in taxa that are not vertical climbers, and their prevalence in taxa that are, suggests that they are either structurally advantageous for this habit, or a result of it. Lacking soft tissue from the pedal digits of possible trunk-climbing non-avian theropods, the presence or absence of this feature cannot yet be tested in these animals. The above considerations may make it unlikely that known non-avian theropods were specialised for a trunk-climbing lifestyle.

Conclusions

Speculations that small theropods may have been scansorial or arboreal are currently popular and are integral to a number of speculative scenarios erected to explain the evolution of bird flight (PAUL

1988a, OLSHEVSKY 1994, CHATTERJEE 1997). Among the earliest speculations on scansoriality in an extinct theropod were those of FOX (1866a,b) on *Calamospondylus*, a small Wealden Group dinosaur known only from the sacral region. In the 1930s, SWINTON (1936a) elaborated on FOX's idea at the same time as he likewise pictured small ornithopods as tree-dwellers.

Regardless of where and how bird flight evolved, the presence of sharp claws borne on elongate, flexible digits indicates that some small theropods were capable of climbing. The absence within theropods of mobile ankles and/or prehensile tails indicates that no known taxon was specialised for arboreal life. The absence of pamprodactyl feet or of small body size coupled with strongly recurved pedal claws borne on all digits indicates that no known theropod was a specialised trunk climber.

Schlussfolgerungen

Spekulationen, dass kleine Theropoden möglicherweise eine kletternde oder arboreale Lebensweise hatten, sind gegenwärtig populär und wesentlicher Bestandteil einer Reihe von Szenarios zur Erklärung der Evolution des Vogelfluges (PAUL 1988a, OLSHEVSKY 1994, CHATTERJEE 1997). Zu den frühesten Spekulationen über das Klettern bei einem ausgestorbenen Theropoden gehören jene von FOX (1866a,b) über *Calamospondylus*, einen kleinen Dinosaurier aus dem Wealden, bekannt nur durch Knochen der Sakralregion. In den 1930er Jahren behandelte SWINTON (1936a) ausführlich den Gedanken von FOX, zu selben Zeit, als er ebenfalls kleine Ornithopoden als Baumbewohner darstellte.

Ungeachtet wo und wie der Vogelflug sich entwickelte, das Vorhandensein von scharfen Krallen auf langen und dünnen, flexiblen Fingern zeigt an, dass einige kleine Theropoden kletterfähig waren. Die Abwesenheit von beweglichen Fußgelenken und/oder Greifschwänzen innerhalb der Theropoden weist darauf hin, dass kein bekanntes Taxon für ein Baumleben spezialisiert war. Das Fehlen von pamprodactylen Füßen (Zehen I-IV nach vorn gerichtet) oder einer kleinen Körpergröße gekoppelt mit stark gekrümmten Fußkrallen auf allen Zehen lässt erkennen, dass kein bekannter Theropode ein spezialisierter Stammkletterer war.

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