# The smallest of the largest: a new look at possible dwarfing in sauropod dinosaurs

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## Abstract

Franz Baron Nopcsa recognised that the Late Cretaceous titanosaurid sauropod from Transylvania, *Magyarosaurus dacus*, was much smaller than the better known sauropods from the Upper Jurassic of the United States and even from Late Cretaceous deposits elsewhere in the world. In keeping with his biogeographic interpretations, Nopcsa viewed this difference as a consequence of body-size effects via island habitation. We present a preliminary re-evaluation of Nopcsa's claims and their heterochronic consequences using two approaches, viz. (1) regression analysis of humeral data as a means of establishing patterns in body size among titanosaurids, and (2) optimisation of humeral data onto titanosaurid cladograms to evaluate evolutionary trends within the clade. Our regression analysis is based on twenty species distributed among fourteen genera of neosauropods and uses length and mid-shaft mediolateral width of the humerus of presumed fully adult forms, and of growth samples that consist of postnatal to adult individuals. Linear regression analysis suggests that, among adult neosauropods, *M. dacus* appears to be represented by the smallest individuals; that *M. dacus* humeri appear to be more similar to those of subadults than to adults of other taxa; and that this 'juvenile' morphology may constitute dwarfing in *M. dacus* by paedomorphosis. In order for these regressions to reflect their evolutionary context more fully, we also present optimisation analyses of humeral form within Titanosauroidea. Although many aspects of the phylogeny of this clade are relatively poorly resolved, preliminary results of our analyses are consistent with the conclusion that *M. dacus* was a heterochronic dwarf.

## Introduction

Sauropods have long been known to be the largest of all terrestrial animals ranging upward of 50 tonnes in *Brachiosaurus* (Alexander 1985) and, according to Gillette (1994), possibly as much as 100 000 kg in *Seismosaurus*. Yet, not all sauropods reached the 'super-gigantic' status for which the group is famous. In particular, Nopcsa (1914) recognised that the titanosaurid sauropod from the Upper Cretaceous of Transylvania, later named *Magyarosaurus* by von Huene (1932), was relatively small by sauropod standards. In keeping with his biogeographic interpretations of the Transylvanian region as a Late Cretaceous island, Nopcsa viewed dwarfing as a consequence of body-size effects via insular habitation. In this way, the dwarfed sauropod of Transylvania represents the same phenomenon as the dwarfing seen in elephants that lived on Corfu and the dwarfed hippos that inhabited Sumatra during the Pleistocene (Boekschoten & Sondaar 1972, Sondaar 1976, Roth 1992).

With these claims in mind, we here present a preliminary re-evaluation of Nopcsa's identification of dwarfing in *Magyarosaurus* and its heterochronic consequences. This re-evaluation takes two approaches: a regression analysis of humeral data as a means of establishing patterns in body size among closely related sauropods, and an optimisation analysis of humeral data onto sauropod phylogeny to evaluate evolutionary trends within the clade.

*Figure 1.* A reconstruction of the titanosaurid sauropod *Saltasaurus* from the Upper Cretaceous of Argentina (reproduced by courtesy of Brian Franczak).

## *Magyarosaurus*, Titanosauridae and Sauropoda

Nopcsa (1915) provided the first description of Hațeg titanosaurid material, referring it to *Titanosaurus*, a taxon otherwise known at the time only from India and Argentina. This material was later restudied and revised by von Huene (1932), who renamed it *Magyarosaurus* and who recognised three species, *M. dacus*, *M. transsylvanicus*, and *M. hungaricus*. At present, all species are tacitly grouped together as *M. dacus* (Weishampel et al. 1991, Le Loeuff 1993), but this situation clearly requires further taxonomic and systematic research (Weishampel et al. in prep.).

From the outset, what was to become *Magyarosaurus* was considered a titanosaurid sauropod, a clade of poorly known taxa known principally from the southern hemisphere (McIntosh 1990, Dodson 1990). The first named titanosaurid, *Titanosaurus indicus* (Lydekker 1877), provided a poor sense of the *Gestalt* of these sauropods, but later discoveries have helped refine our understanding of them (Figure 1).

We know that titanosaurids arose by the Late Jurassic (i.e., the age of *Janenschia robusta* from Tendaguru, Tanzania: Wild 1991) and remained very common in parts of Gondwana up to the end of the Cretaceous (Jacobs et al. 1993, 1996). The best known of these is *Saltasaurus loricatus* from the Upper Cretaceous of Argentina (Powell 1993). Titanosaurids are also known from the southwestern United States (*Alamosaurus sanjuanensis*; Lucas & Hunt 1989). Besides *Magyarosaurus*, other titanosaurids are known from Europe (Le Loeuff 1993).

The fossil record of titanosaurids, as is generally true of nearly all sauropods (Dodson 1990), suffers from relatively high taphonomic bias. Most species are based on disarticulated, dissociated, and often isolated material. In addition, descriptions of a complete, articulated titanosaurid skeleton or skull are still lacking, although forthcoming studies of new material from the Upper Cretaceous of Madagascar (D. Krause, pers. comm.) and of roughly contemporary beds of Argentina (R. Coria, pers. comm.) should act to change
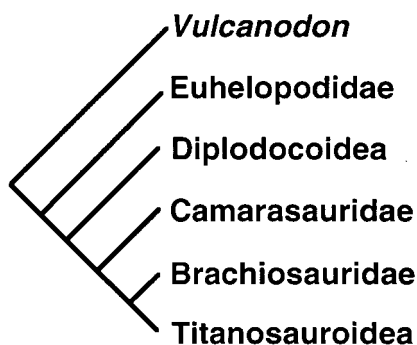
Figure 2. Simplified cladogram of Sauropoda, after Upchurch (1998).
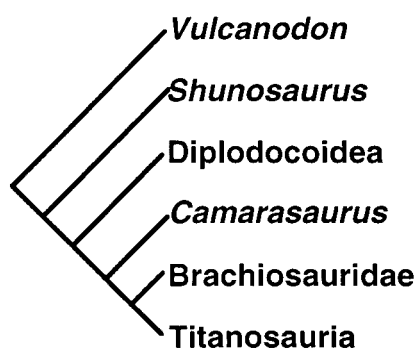
Vulcanodon
Euhelopodidae
Diplodocoidea
Camarasauridae
Brachiosauridae
Titanosauroidea

*Figure 2*. Simplified cladogram of Sauropoda, after Upchurch (1998).

Vulcanodon
Shunosaurus
Diplodocoidea
Camarasaurus
Brachiosauridae
Titanosauria

*Figure 3*. Simplified cladogram of Sauropoda, after Wilson & Sereno (1998).

this situation. Despite these inadequacies associated with their skeletal record, it is clear that titanosaurids ranged in size from a 7-m length (*Saltasaurus*; Powell 1993) to 25–30 m length (*Argentinosaurus*; Bonaparte & Coria 1993). The long, thin teeth of these sauropods were chisel-like and restricted to the rostrum (Calvo 1994). Ingestion (and perhaps slight oral processing) appears to have been limited to orthal (up-and-down) motion of the lower jaw. Finally, eggs and embryonic remains referable to titanosaurid sauropods have recently been discovered in the Upper Cretaceous of Argentina (Chiappe et al. 1998).

Since their original discovery and through the fulsome years of the exploration of the American west, the excavations at Tendaguru, and the newer finds in Sichuan (China), the systematics of sauropods have been anything but clear. Sauropods have long been considered a monophyletic group, but it was only recently that the Gordian knot of their internal relationships has been cut with the first comprehensive use of phylogenetic analysis. In one of these works, Upchurch (1998) recognised euhelopodids, diplodoc-

oids, camarasaurids, brachiosaurids and titanosauroids as monophyletic clades, with other taxa interpolated among them (Figure 2). For the purposes of the present study, titanosaurids are positioned more closely to brachiosaurids and camarasaurids than to diplodocoids. Upchurch called this clade – comprising titanosaurids, brachiosaurids and camarasaurids – Brachiosauria. In the other major study (Wilson & Sereno 1998), three of these clades (diplodocoids, brachiosaurids and titanosaurids) were also identified, but their study advocated different relationships among them and between them and other taxa (Figure 3). It is not our purpose to assess the relative merits of the Upchurch and Wilson-Sereno studies in what follows. We will rather use Upchurch's phylogenetic analyses in our analyses, leaving the Wilson-Sereno cladogram and its implications for dwarfing to another study.

**Heterochrony**

Heterochrony is evolutionary change in the developmental timing of features (such as changes in body size, age of reproductive maturity, etc.) from the primitive condition in ancestors to the derived condition in descendants (Gould 1977, Alberch et al. 1979, McKinney 1988, McKinney & McNamara 1991). Six kinds of heterochrony can be assessed in terms of only three timing parameters: onset timing, offset timing, and growth rate (Figure 4). Early growth onset produces descendant predisplacement, whereas late descendant onset produces postdisplacement. In contrast, early growth offset between descendant and ancestor produces progenesis, a truncated or arrested condition. Hypermorphosis is the contrasting condition of late offset in which development is continued beyond the ancestral condition. Finally, elevated growth rates (acceleration) increase the rate at which features develop during the ontogeny of descendants relative to the rate of development in ancestors. In contrast, decreased growth rates (deceleration) produce what is known as neoteny, in which the appearance of features in descendants is protracted relative to their appearance in ancestral ontogenies.

In many cases, particularly with extinct organisms, it is not possible to evaluate these six discrete kinds of heterochrony (McKinney 1988). Instead, we can speak of overdevelopment of features as peramorphosis, which is attained via early onset, late offset, or acceleration (Figure 4). Paedomorphosis, or juvenilisation, is produced by opposing parameters: late onset, early
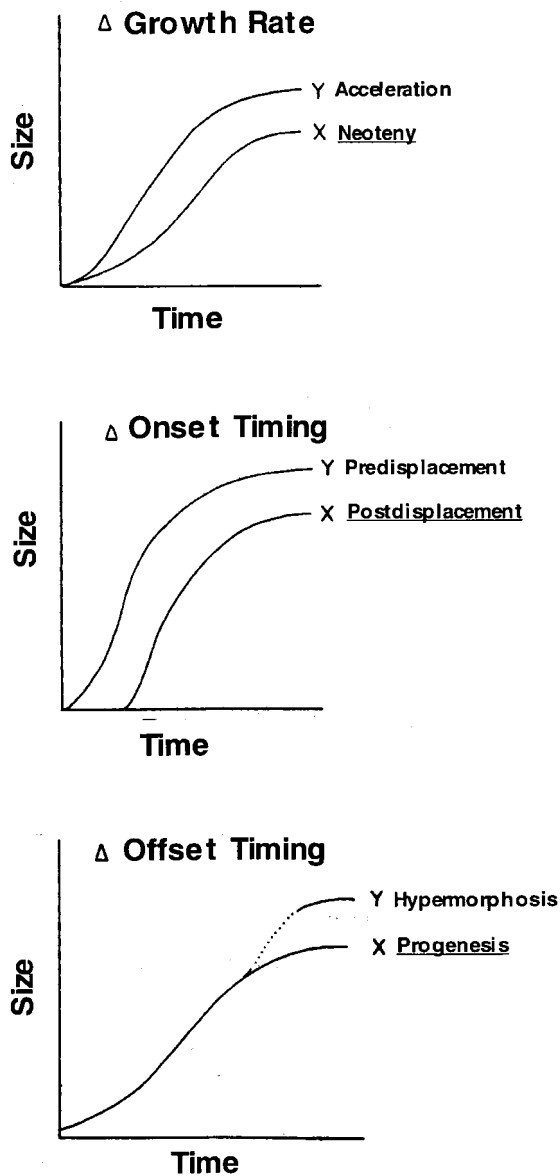
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*Figure 4.* The six outcomes of heterochronic processes due to differences in growth rate, onset timing, and offset timing. The peramorphic patterns are indicated without underlining, whereas the paedomorphic patterns are indicated by underlining.



*Figure 5.* Selected specimens of *Magyarosaurus dacus*; bottom left: braincase (Faculty of Geology and Geophysics, University of Bucharest R1007); bottom right: left radius and ulna (Muzeul Civilizaţiei Dacice şi Romane Deva 61, 62); middle: left humerus (Magyar Állami Földtani Intézet v.13492); top: left femur (Faculty of Geology and Geophysics, University of Bucharest R1046).

Nopcsa's notion of sauropod dwarfing gave rise to our re-examination of *Magyarosaurus*.

**Material**

*Magyarosaurus* (Figure 5) is now known from considerable material originally collected from the Haţeg Basin, now kept in the Natural History Museum, London (where the type resides; Le Loeuff 1993), the University of Bucharest, the Hungarian Geological Institute (Budapest), and the Muzeul Civilizaţiei Dacice şi

offset, or deceleration (Figure 4). Of these two heterochronic patterns, it is peramorphosis that has been implicated as one of the chief driving forces in dinosaur evolution (Weishampel & Horner 1994, Long & McNamara 1995), although paedomorphosis has also been identified in the origin of hadrosaurid ornithopods (Weishampel et al. 1993). This claim about the importance of heterochrony in dinosaur evolution and

*Table 1.* Taxa used in regression and optimisation analyses.

| | | |
|---|---|---|
| *Saltosaurus loricatus* | *Magyarosaurus dacus* | *Camarasaurus lewisi* |
| *Saltosaurus australis* | *Alamosaurus sanjuanensis* | *Camarasaurus supremus\** |
| *Saltosaurus robustus\** | *Phuwiangosaurus sirindhornae\** | *Dicraeosaurus sattleri* |
| *Antarctosaurus wichmannianus* | *Aegyptosaurus baharijensis* | *Dicraeosaurus hansemanni\** |
| *'Antarctosaurus' septentrionalis* | *Malawisaurus dixeyi* | *Apatosaurus excelsus\** |
| *Titanosaurus colberti* | *Opisthocoelicaudia skarzynskii* | *Apatosaurus louisae* |
| *Titanosaurus indicus* | *Brachiosaurus africanus\** | *Diplodocus longus* |
| *Laplatasaurus araukanicus* | *Brachiosaurus brancai\** | |
| *Ampelosaurus atacis* | *Camarasaurus grandis\** | |

\* indicates source of growth series data.



*Figure 6.* Humeral measurements. HL = humeral length; MSW = mediolateral midshaft width.

Romane Deva (Romania). For comparative and phylogenetic purposes, our analyses were based on twenty-five species of neosauropods (Table 1), sampled principally from titanosaurids, brachiosaurids and camarasaurids within the Brachiosauria clade. We restricted our observations to one of the commonest elements available to us (the humerus; Figure 6), and data were obtained from original specimens, from literature (Lydekker 1877, 1897, Gilmore 1922, von Huene 1929, 1932, von Huene & Matley 1933, Stromer 1932, Janensch 1961, Borsuk-Bialynicka 1977, Bonaparte & Powell 1980, Powell 1993, Martin 1994, Carpenter & McIntosh 1994, Jain & Bandyopadhyay 1997) and from personal communications (J. Le Loeuff, pers. comm.; E. Gomani, pers. comm).

## Regression analyses

For our regression analysis of intra- and interspecific differences in humeral form, we first divided the neosauropod sample into individuals thought to be adult, and individuals that could be assembled into a growth series. Age classing of the humeral samples was based on comments in the literature, joint-surface maturity, and overall body size. In nearly all cases, the largest individuals of a species were identified as adults. Data on these adults are readily available. Data on growth series, on the other hand, were more difficult to obtain. Because sauropod ontogenies are known only in small part, we instead assembled a combined growth series drawn from closely related brachiosaurian sauropods under the assumption that ontogenetic trajectories should be more similar intra-cladally than extra-cladally. These included very small humeri of *Camarasaurus*, *Brachiosaurus*, *Saltasaurus*, and *Phuwiangosaurus* (see Carpenter & McIntosh 1994, Janensch 1961, Powell 1993, Martin 1994).
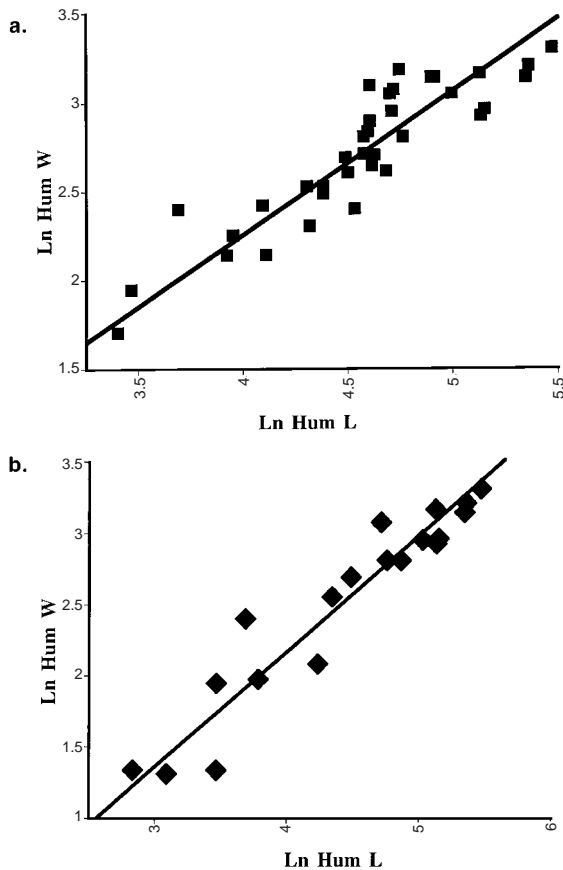
**a.**

**b.**

*Figure 7.* Reduced major axis regressions. a = adult sample. b = growth sample.



*Figure 8.* Combined reduced major axis regressions of adult and growth samples, with *Magyarosaurus*, *Phuwiangosaurus* (a titanosaurid from the Lower Cretaceous of Thailand), and *Ampelosaurus* (a titanosaurid from the Upper Cretaceous of France) added to the analysis.

Linear regression analysis consisted of both least-squares and reduced major axis (RMA) methods (see Hofman 1988, Clarke 1980) applied to measurements of the length and mid-shaft mediolateral width of the humerus. Other skeletal measurements will be included in a future study. Because of the relatively low correlation coefficients of the former, we report here only on the RMA analyses.

In order to identify differences, if any, RMA regressions were separately run on the adult and growth samples (Figure 7(a, b)). Regression of the adult data (transformed into natural logarithms) produced a line with a slope of 0.80, an intercept of –0.97, and a correlation coefficient of 0.90. Regression of the logged growth data produced a line with the same slope (0.80), but an intercept of –1.06; the correlation coefficient was 0.95.

*Magyarosaurus* was then added to the mix in order to evaluate whether it is more similar to the growth series or the adult sample (Figure 8). By inspection,
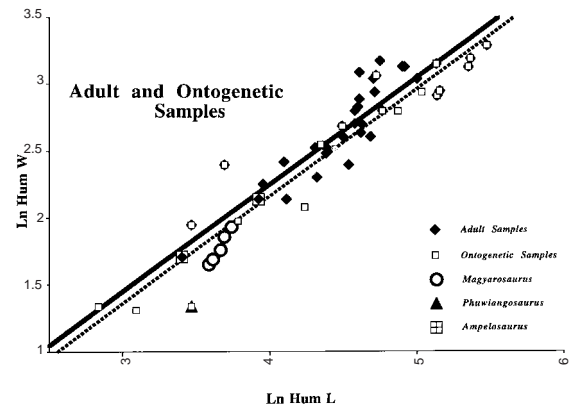
*Magyarosaurus* plots closest to the growth regression, but because scatter about these lines is high, we applied Tsutakawa & Hewett's (1977) 'quick test' to our problem. This simple non-parametric test is useful in testing the equality of two populations when the observations are bivariate. Pooled data are subjected to a reduced major axis analysis and, on the basis of this linear regression, the number of points above and below the resulting line are counted for each of the two populations, in this case, adults and *Magyarosaurus*, and growth series and *Magyarosaurus*. These counts are then assembled into a 2 × 2 table, the sampling probabilities of which are obtained from Fisher's exact test.

In our study, the probability that the *Magyarosaurus* data were obtained from the adult sample is 0.035, but this same probability for the growth series data increases to 0.24, nearly an order of magnitude higher. Humeral form in our sample of *Magyarosaurus*, at least as expressed by our data, has a greater probability of coming from, and therefore is more similar to that of, juvenile than adult brachiosaurians. As a result, we can conclude the following, based on regression and quick-test analyses:

– among adult neosauropods, *Magyarosaurus* appears to be represented by the smallest individuals, as Nopcsa foresaw;

– *Magyarosaurus* humeri appear to be more similar to those of subadults than to adults of other taxa;

– this 'juvenile' morphology may constitute dwarfing in *Magyarosaurus* by paedomorphosis, i.e., retention of juvenile features into adulthood.
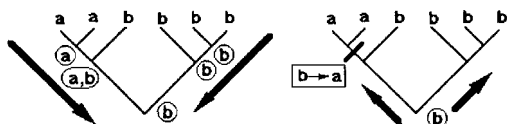
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*Figure 9.* Optimisation of characters (a) and (b) onto a phylogenetic tree (see text for explanation).

## Phylogenetic analyses

In order for these 'ahistorical' regressions to reflect their evolutionary context more fully, we also conducted optimisation analyses of the humeral form within Titanosauroidea. As developed by Farris (1970) and summarised by Wiley et al. (1991) and Brooks & McLennan (1991), optimisation analysis begins with an explicit phylogenetic hypothesis and data to be optimised onto it. The best-supported sequence of transformations (using Wagner parsimony) can then be determined by reference to the phylogenetic tree. For our study, data on heterochrony are generalised down the tree from terminal taxa node by node to the base of the tree. In doing so, both unambiguous and ambiguous characters are identified at the nodes. Finally, character transformations are predicted up the tree from the basally-resolved node. This prediction/optimisation of the data resolves any ambiguity from the generalising phase of analysis by comparing the value of the ambiguous node with the value of the node directly below it. For example, optimisation of characters (a) and (b) in Figure 9 involves first mapping them down a cladogram by pair-wise comparisons of terminal taxa, terminal taxa and nodes, and nodes and nodes. Once the basal node is resolved, as (b), character ambiguities are resolved back up the tree, such that the shift from (b) to (a) is readily identified.

Although a robust phylogenetic hypothesis of Titanosauridae that includes *M. dacus* is not available, we nevertheless qualitatively optimised body size at adulthood onto Upchurch's (1988) cladogram of Titanosauroidea, modified to cover additional although unresolved taxa (Figure 10). In the same way as previously described, our analysis indicates that *Magyarosaurus* exhibits an apomorphic shift to small, juvenilised morphology, at least for the humerus. The same seems to be true of *Ampelosaurus*, although it falls between the adult and growth curves provided by the regression analyses, rather than beneath the growth curves, as does *Magyarosaurus*. It may be that both *Magyarosaurus* and *Ampelosaurus* have a close rela-
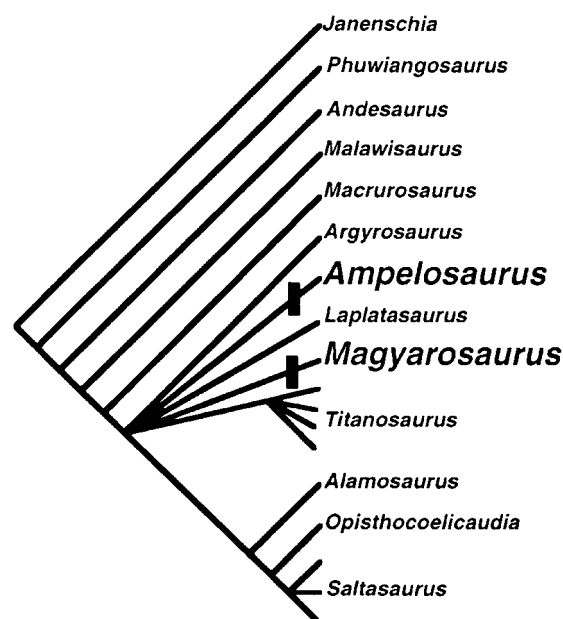


*Figure 10.* Optimisation of humeral form onto a cladogram of Titanosauroidea (modified after Upchurch 1998).

tionship based on some degree of dwarfing, but we are not ready yet to make such a claim, as it would be based on lack of phylogenetic resolution of these two forms, and many others among titanosauroids. From both a phylogenetic and a regression perspective, however, the smallness of *Magyarosaurus* appears to represent an apomorphic shift in body size, the basis for which may be dwarfing by heterochronic paedomorphosis, i.e., retention of juvenile features into adulthood.

## Discussion

Nopcsa (1914) claimed that the Haţeg Basin was insular in nature, in part on the basis of geological evidence, but also through his identification of members of the fauna as dwarfs. The basin as an island or part of an island is of interest, particularly because insular evolution is often regarded as a microcosm of larger-scale evolutionary dynamics (MacArthur & Wilson 1967, Case 1978, Lomolino 1985, 1986, Roth 1992, Wagner & Funk 1995, Grant 1998, Losos et al. 1998). The geological, palaeogeographical, and palaeoecological aspects of the Haţeg Basin as an island or as an outpost are now under investigation (Jianu & Boekschoten in press). From a taxonspecific perspective and regardless of environmental

context, however, *Magyarosaurus dacus* (and the had-rosaurid *Telmatosaurus transsylvanicus*; Weishampel et al. 1993) provide evidence of dwarfing, at least in terms of the paedomorphic changes in the humeral dimensions under consideration. This interpretation is borne out in both the regression and optimisation analyses described here.

Whether it can be argued that heterochrony in *M. dacus* was involved in the evolution of major morphological features (i.e. evolutionary novelties), as appears to be the case in hadrosaurids and the origin of their dental battery, is far from clear. To be pursued in further research, we can nevertheless state that our optimisation analyses, together with our linear regression analysis, provide a consistent interpretation for heterochrony in *Magyarosaurus dacus*. It appears to have been a paedomorphic dwarf.

## Acknowledgements

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