

MORPHOLOGICAL VARIATION IN THE SEQUENCE OF CAUDAL VERTEBRAE OF SOME TITANOSAUR SAUROPODS¹

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ABSTRACT

[original English]

In the proximal caudal vertebrae of many titanosaurs a variation in centrum morphology is observed, here interpreted as the result of a change in the distribution of caudofemoralis muscles. These changes involve the inclination and development of the lateral surfaces and the width of the ventral surface of the centrum. The lateral surfaces of caudals 7-8 of *Titanosaurus araukanicus* are inclined dorsolaterally, resulting in a narrow ventral surface. In caudals 8-9, the primary lateral surface is restricted to the ventrolateral corners of the centrum. The lateral surface of caudal 10 and those distal to it, named the secondary lateral surface, is nearly vertical and replaces the primary lateral surface. Although this morphological pattern is present in several titanosaurs, its phylogenetic significance must still be established. Musculature may have been important in the evolution of caudal morphology in titanosaurs.

Keywords: Titanosaurs, caudal morphology, musculature.

INTRODUCTION

Powell (1986) recognized the existence of two basic types of caudal vertebral centra in titanosaurs: the first of these consists in tall centra, with lateral surfaces slightly concave dorsoventrally and ventral surface narrow; this vertebral type is typical, according to this author (Powell, *op. cit.*) of the Subfamily Titanosaurinae. The second type, diagnostic of the Subfamily Saltasaurinae, is represented by short centra with dorsoventrally convex lateral surfaces and wide ventral surfaces.

Salgado et al. (1997) interpreted the condition proposed by Powell (*op. cit.*) to characterize Titanosaurinae to be plesiomorphic for Titanosauridae, as other titanosaurs seem to present identical caudal morphology. In fact, *Andesaurus*, a basal

titanosaur from the Cenomanian of Neuquén Province (Argentina), and *Epachthosaurus*, a basal titanosaurid from the Cenomanian of Chubut Province (Argentina), have anterior and middle caudal vertebrae that maintain similarity with the Titanosaurinae, taking into account the characterization proposed by Powell.

In this paper, some anatomical features are briefly described that were included in the caudal categorization established by Powell, which vary along the caudal sequence, at least in some titanosaurs. On one hand, we try to make a contribution to the knowledge of the anatomy of the soft tissues of these animals; on the other, we discuss the taxonomic and morphofunctional value of the modifications that we recognize.

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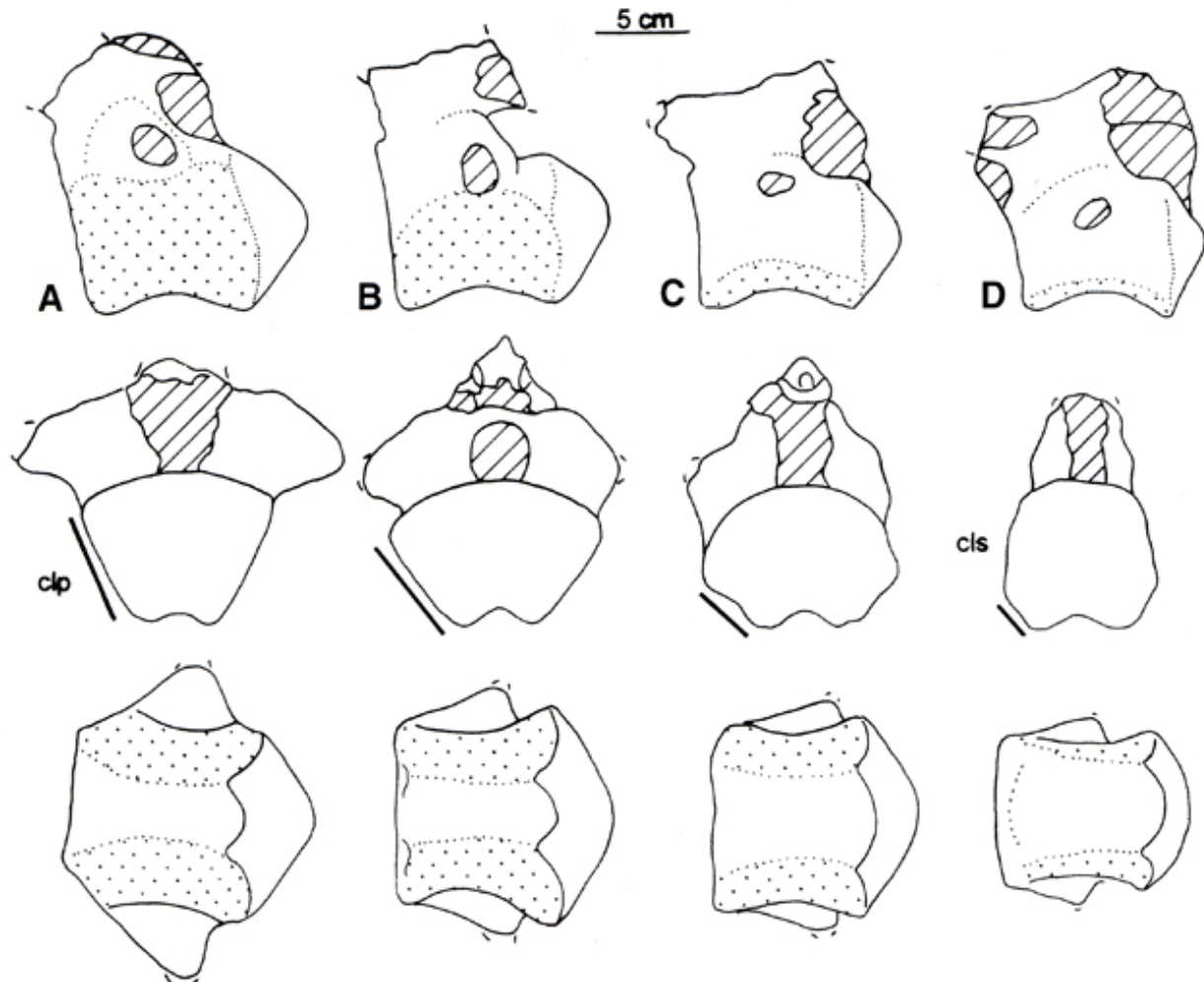


Figura 1. MPCA-1501. *Titanosaurus araukanicus*. Secuencia caudal 7-10 (A-D), en vistas lateral, posterior y ventral, en donde se muestra el relativo desarrollo de las caras laterales primarias (clp) y su reemplazo por las caras laterales secundarias (cls).
Caudal sequence 7-10 (A-D), in lateral, posterior and ventral views, where is shown the relative development of the primary lateral faces (clp) and its replacement by the secondary lateral faces (cls).

ABBREVIATIONS

MCS: Museo de Cincos Saltos, Río Negro, Argentina; MLP: Museo de La Plata, Provincia de Buenos Aires, Argentina; MPCA: Museo Provincial "Carlos Ameghino" de la Ciudad de Cipolletti, Río Negro, Argentina; MUCPv: Colección de Paleovertebrados del Museo de Geología y Paleontología de la Universidad Nacional del Comahue, Neuquén, Argentina; SMU: Southern Methodist University, Dallas, USA; USNM: United States National Museum, Washington USA.

MATERIALS

We refer principally to two vertebral series: MPCA-1501 (Figure 1), a continuous sequence of 27 vertebrae that form the hypodigm of *Titanosaurus araukanicus* Huene, 1929 (Powell, 1986) y MUCPv-204 (Figure 2), a series of 13 caudal vertebrae of a Titanosauridae indet., described by Salgado and Calvo (1993). In the latter case, we have numbered the vertebrae sequentially from 1 to 13, although it should be noted that with the exception of the segment 9-12 (Figure 2a-d) it is not certain that the whole series represents a continuous sequence.

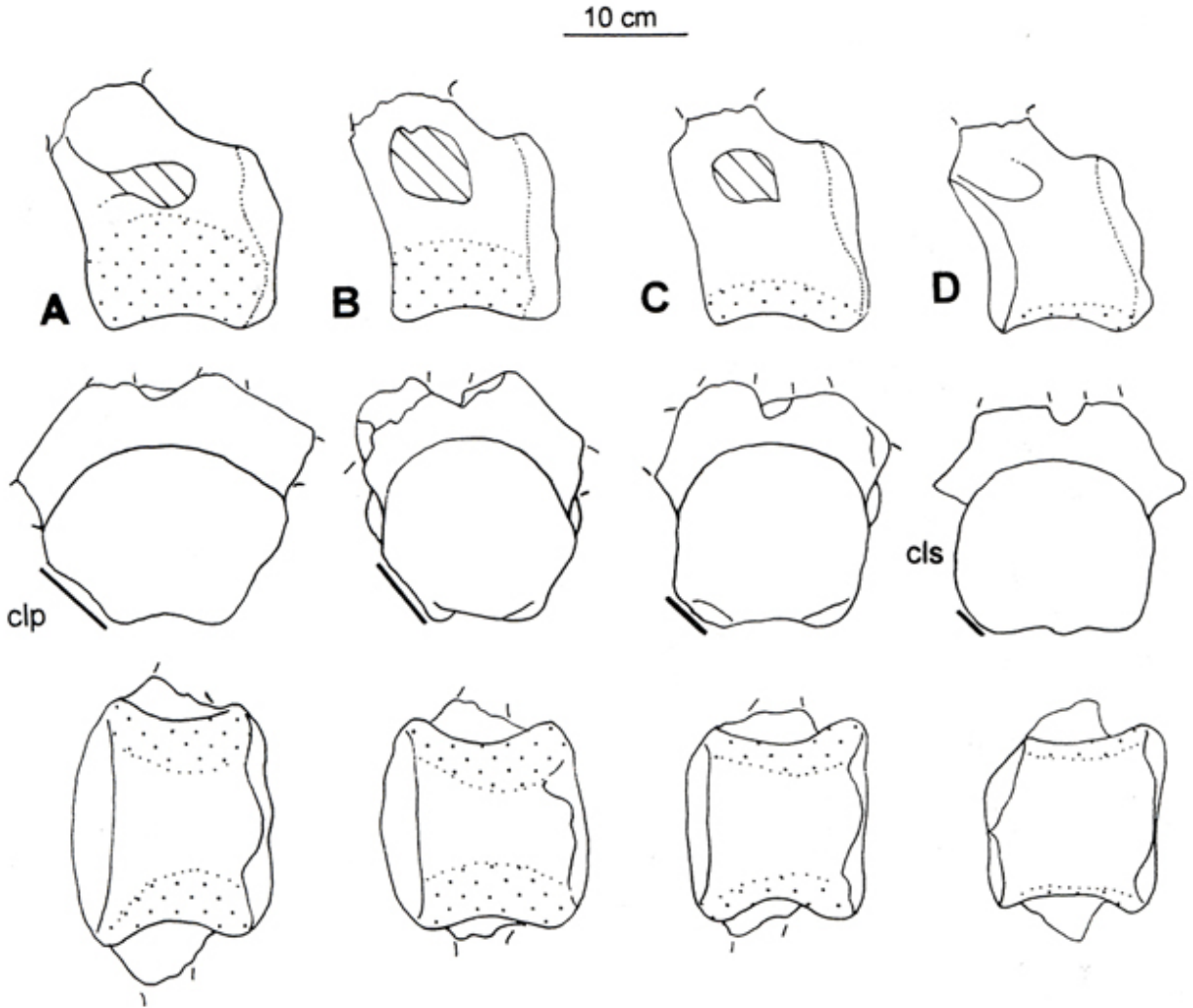


Figura 2. MUCPv-204. Secuencia caudal 9-12 (A-D), en vistas lateral, posterior y ventral, en donde se muestra el relativo desarrollo de las caras laterales primarias (clp) y su reemplazo por las caras laterales secundarias (cls).
Caudal sequence 9-12 (A-D), in lateral, posterior and ventral views, where is shown the relative development of the primary lateral faces (clp) and its replacement by the secondary lateral faces (cls).

DESCRIPTION

In MPCA-1501, the width of the first caudals of the series is approximately equal to the height of the centra, the ventral surface is wide, and the lateral surfaces are dorsoventrally convex. In the first vertebra of the series, chevron facets are not observed, although in the others these are well developed. In the 3rd-6th caudals of the series, the lateral surfaces are inclined slightly outwards, in a manner that the ventral centrum becomes relatively narrow. These vertebrae correspond well to the characterization of the Titanosaurinae made

by Powell (1986). In the following four vertebrae (caudals 7-10, Figure 1a-d), the lateral surfaces (which hereafter we will call *primaries*) become shorter, leaving room for new lateral surfaces (or *secondaries*) to progressively replace the primary surfaces, which are left as facets on the ventrolateral corner of the centrum. The line of contact between the primary and secondary surfaces culminates posteriorly in a lateral protuberance. Precisely, these vertebrae of a transitional character (7-9) have a markedly wide centrum. Although the transverse processes were incompletely preserved, it is possible to observe that those of the 7th

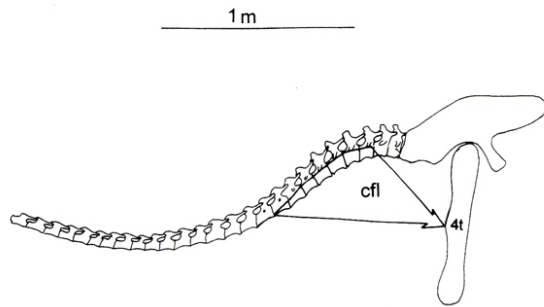


Figura 3. MPCA-1501. *Titanosaurus araukanicus*. Reconstrucción de la secuencia caudal y de las relaciones anatómicas sugeridas para el músculo *caudofemoralis longus* (cfl). 4t.: Cuarto trocánter del fémur.
Reconstruction of the caudal sequence and the proposed anatomical relationships for the caudofemoralis longus muscle (cfl). Fourth trochanter of the femur (4t).

caudal were well developed and those of the 10th were notably reduced.

MUCPv-204 has similar morphological variation, although with certain important differences. The first 6 caudals, which are procoelous, have an anteroposteriorly short centrum and lateral surfaces that are tall and slightly concave dorsoventrally. The seventh and eighth vertebrae are also procoelous, although they are very short and wide. Continuing backwards, the centra become amphiplatyan, although it is possible to observe a subtle dorsal border on the posterior articular surface (9-12, Figure 2a-d). In vertebra 9 (Figure 2a), the lateral surfaces are inclined outwards, in a manner that can be clearly observed in ventral view; their body is significantly wider than tall. In fact, the caudal centra of the vertebrae considered here as 7 and 8, which are somewhat procoelous, also have their lateral surfaces inclined outwards. In the vertebrae immediately posterior to the sequence shown in Figure 2 (10-12), the primary surface becomes progressively narrower, being relegated in the 11th and for the most part in the 12th to the ventrolateral corners of the centrum (Figure 2). These facets can still be observed in ventral view in vertebra 12. The new or secondary surfaces are also, in this case, slightly concave dorsoventrally, which differs from MPCA-1501, in which they are more flat. In posterior view, one can see that as in vertebrae 9-11 the maximum width of

the vertebra becomes displaced ventrally. This point precisely marks the boundary between the primary and secondary surfaces. In the last vertebra of the series in Figure 2 (12), the primary surface has almost completely disappeared. In this part of the tail, the chevron facets are more separated than in the anterior caudals, consequently the ventral surface of the centrum is exceptionally wide. As in *Titanosaurus araukanicus*, the vertebrae posterior to 9-10 become approximately as tall as wide, taking into account the posterior articulation. The transverse processes are not completely preserved, except for that of the 12th, in which are very reduced.

DISCUSSION

Our interpretation of the variation presented in the series of caudal vertebrae that we described is based on the distribution of muscle packets corresponding to the *caudofemoralis* group (*coccygeo-femoralis*, after the terminology of Romer, 1923: 606), which connects the hind limb and tail (Figure 3). Numerous authors have referred to the influence of these soft tissues on the formation of bone, not of cartilage, which can be genetically determined (Herring, 1993: 156). In this case, the muscle masses have influenced, possibly, the morphology of the caudal vertebrae, in particular that of the lateral and ventral surfaces.

In our opinion, on the primary lateral surfaces of the anterior caudals (3-7 of *Titanosaurus araukanicus*, 3-9, 19 of MUCPv-204), below the transverse processes would be positioned the *caudofemoralis longus* muscle, which has its origin in the fourth trochanter of the femur (Figure 3, see Romer, 1923, fig. 6). In the way that the muscle mass continues diminishing in volume posteriorly, the lateral face of the vertebra is reduced, giving way to a new lateral surface that replaces it: the secondary surface. Possibly, this vertebra is where the last trace of the primary face is observed (in the cases that we studied, the 10th caudal of *T. araukanicus* and the 12th of MUCPv-204) marking the end of the *caudofemoralis longus* muscle (Figure 3).

In *Titanosaurus araukanicus*, the 7-9 caudal vertebrae, in which the

caudofemoralis longus muscle begins to reduce its volume, are significantly broad, more broad than tall. As we said, posterior to caudal 10 of *Titanosaurus araukanicus* and 11 of MUCPv-204, the width of the centrum is approximately equal to the height of the centrum. In *T. araukanicus*, the vertebral centra become subcylindrical through the distalmost caudals. In MUCPv-204, vertebra 9 is not the widest in the series, although it is significantly wider than the vertebra located immediately after it (the 10th). Also in this segment, we see variation in the width of the ventral surface. In the first, 9-10, the ventral face becomes narrow, but it becomes broad again in the following (11-12). Evidently, the outward inclination of the primary lateral surfaces in the 9th and 10th vertebra produces a narrowing in the ventral surface of these vertebrae.

With respect to the location of the *caudofemoralis brevis* muscle (*coccygeofemoralis* in the terminology of Romer, 1923: 606), it is possible that it was originating from the *brevis fossa* of the ilium (reduced in the case of sauropods) and the two first caudals until the femur, although it has not been possible to establish this with precision.

The morphological changes that can be observed along the length of the tail of *Titanosaurus araukanicus* and MUCPv-204 indicate the risk of making taxonomic characterizations from isolated vertebrae. In effect, the characters mentioned by Powell (1986) as those of the Subfamily Titanosaurinae are restricted in this case to vertebrae 1-8 of *Titanosaurus araukanicus* and 1-9 of MUCPv-204.

In the second place, and keeping in mind that the *caudofemoralis longus* musculature is a femoral retractor (Carrano, 2000), it is possible to think that the morphology of the titanosaurs had been, in a way, similar to that suggested by some authors for crocodiles and theropods (Wu and Russell, 1997). In this sense, we propose another form of establishing the posterior extension of the *caudofemoralis longus* musculature than that referred to by Wu and Russell (*op. cit.*), who considered the relative development of the transverse processes. In effect, it is possible that the transverse processes still persist in the cases in which the muscle mass that is arranged below them has seen significant

reduction. In turn, the modifications that we described are, according to our interpretation, the *direct result* of the presence of these muscle masses. In fact, in MUCPv-204, the transverse processes persist, although reduced, after the primary lateral surfaces have disappeared completely (Figure 2d).

Morphological variations similar to those described in this paper can be found in other titanosaurs and related sauropods. In the paratype of *Alamosaurus sanjuanensis* Gilmore, 1922 (USNM 10487), a distinct rim begins to be observed in the center of caudal 13 (personal observation) and is retained until the 16th, although its position is lower. The rim practically disappears in the distal caudals of *Alamosaurus sanjuanensis*, whose morphology resembles that of saltasaurines (Salgado et al., 1997). In caudal 19 of specimen USNM 10487 of *Alamosaurus sanjuanensis*, it can be observed that the lateral surface of the vertebra, below the imaginary prolongation of the osseous rim that is developed solely in the posterior part of the vertebral centra, becomes practically ventral. In this case, if our interpretation is correct, the *caudofemoralis* extends further posteriorly in *Alamosaurus sanjuanensis* than in *Titanosaurus araukanicus* and MUCPv-204. Also, in the vertebra figured by Lull (1911: pl. 19, figs. 2,3) pertaining to *Pleurocoelus altus* Marsh, a probable titanosaur, the lateral border that delimits the two planes of the vertebra can be observed.

In *Pelligrinisaurus powelli*, Salgado, 1996, the sixth caudal vertebra (Salgado, 1996, fig. 4) shows a morphology similar to the seventh of *Titanosaurus araukanicus*, with lateral surfaces outwardly inclined and a relatively narrow ventral surface. At the same time, the centrum of the seventh caudal (Salgado, *op. cit.*, fig. 5) bears a lateral protuberance that, according to our interpretation, marks the border of the primary and secondary surfaces. Possibly, this vertebra corresponds to the ninth caudal of *Titanosaurus araukanicus* and the 10th-11th caudal MUCPv-204 (in materials deposited in the collections of the Museo Regional de Cincos Saltos, possibly referable to *Pelligrinisaurus*, one can see morphology equivalent to the 8th-9th vertebrae of *Titanosaurus araukanicus*). Nonetheless, it should be

mentioned that the vertebrae of *Pelligrinisaurus*, not only the caudals, are notably deformed, as such it is not possible to know with certainty if they have in this species same modifications that we describe in this paper. On the other hand, it is clear that some of the morphological variation that was observed in the sequence MPCA-1501 of *Titanosaurus araukanicus* is not distinct in the specimen MLP-26-28 (a series of 11 caudals, Powell, 1986, pl. 6,7). In the latter, nevertheless, some of the vertebrae have lateral faces that are inclined outwards, as in the sequence MPCA-1501. At the same time, in MLP-26-28 a variation with relation to the width of the ventral centrum is observed (personal observation). Possibly, vertebrae 6-9 are not represented in series MLP-26-28, because it is not possible to notice the replacement of the primary surface by the secondary surface.

In *Neuquensaurus australis* (MCS-5) identical variation as that described here can be observed. In the fifth and sixth, the rim that separates the two surfaces is very robust and separates two deep depressions. The transverse processes are little pronounced until the sixth caudal, after which they become pronounced ridges. The definitive disappearance of the last trace of the primary face is in vertebrae 6-7. The principle difference that is observed with the other taxa is that the process of replacing the lateral faces does not produce a narrowing of the ventral surface. In fact, along the length of the sequence 2-8, the distance separating the posterior chevron facets does not vary significantly in *Neuquensaurus australis*.

Recently, Kellner and Azevedo (1999) described a new titanosaur, *Gondwanatitan faustoi*, from the Upper Cretaceous of Álvarez Machado in São Paulo (Brazil). One of the proposed autapomorphies for this species by the authors (*op. cit.*: 115, figs. 12, 14) is the following: "distal articulation surface of proximal and middle caudals heart-shaped". The particular morphology described by Kellner and Azevedo in *Gondwanatitan faustoi* is very similar to caudal 8 of MPCA-1501 and, to a certain point, the ninth caudal of MUCPv-204. In keeping with variation observed in the caudal vertebrae of these two Patagonian titanosaurs, it is possible to recognize that

the "heart-shaped" form, which in posterior view is adopted by the fifth vertebra of *Gondwanatitan faustoi*, responds to the inferred function of the morphological variations described in this paper. At the very least, this characterization should not be used as an autapomorphic character of *G. faustoi*, as suggested by those authors (Kellner and Azevedo, *op. cit.*).

Lastly, the same variation has been observed in the caudal vertebrae of the titanosaur SMU 61732, assigned by Langston (1974) to *Pleurocoelus sp.* (personal observation).

CONCLUSION

Although the available evidence remains insufficient, the idea that has been proposed is that the evolution of the caudal musculature was an important factor in the evolution of vertebral morphology in titanosaurs. The morphology of the lateral surfaces of caudal vertebrae 3-7 or 3-9 of some titanosaurs, especially those of the vertebral type attributed by Powell to titanosaurines, can be explained functionally by the presence of the *caudofemoralis longus* muscle. In particular, the caudal segment 7-10 or 9-12, at least in the aforementioned forms, presents a transitional state; there the primary lateral surface can be observed giving way to the secondary lateral surface. Posterior to caudal 10 or 12, the lateral surfaces of the caudal vertebrae are invariant, at least with respect to the aspects we examined.

It is not improbable that the vertebral type that characterizes the saltasaurines, and in general the proportional variations observed in various titanosaurs, have arisen as a result of modifications of the tail musculature in relation to changes in the mechanics of locomotion, although these aspects require more thorough study. In closing, this hypothesis should be tested with studies of caudal musculature and their relation to the vertebral morphology in Aves and different crocodile groups. Similarly, the distribution of this character should be known to establish its phylogenetic significance.

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