A NEW DICRAEOSAURID SAUROPOD, *AMARGASAURUS CAZAUI* GEN. ET SP. NOV., FROM THE LA AMARGA FORMATION, NEOCOMIAN OF NEUQUÉN PROVINCE, ARGENTINA

Leonardo SALGADO and José F. BONAPARTE

ABSTRACT: The material is represented by the basicranial and temporal region of the skull and most of the postcranium. The comparative discussion of this new species suggests it is more derived than *Dicraeosaurus hansemanni* from the Late Jurassic Tendaguru beds, in the more elongate and pronounced bifurcation of the presacral vertebrae, and in the longer basipterygoid processes. The comparison of the genera *Dicraeosaurus-Amargasaurus* with other clades of sauropods, in particular with Diplodocidae, suggests they correspond to a family of their own: Dicraeosauruse, which is more derived than and with significant differences to Diplodocidae.

INTRODUCTION

The discovery of the majority of the skeleton of a sauropod in the Lower Cretaceous (Neocomian) of the Neuquén Basin, reveals the existence, in South America, of a clade of sauropod dinosaurs not previously recognized on the continent. It is of a representative of the family Dicraeosauridae (Huene, 1956) previously recognized by well preserved specimens only in the Late Jurassic of Tanzania (Janensch, 1914, 1929a, 1929b, 1936).

This material from the Neuquén Basin will contribute to the better understanding of one of the many lineages of Late Jurassic-Lower Cretaceous sauropods. In general, sauropods from this period are recorded mostly from the Morrison Formation of the USA, the Shaximiao beds of China, and from the Tendaguru beds of Tanzania. The conditions of the discovery that we communicate and its good preservation has allowed us to analyze, briefly in this case, the anatomy of the basicranium and an articulated sequence of presacral vertebrae in which are found diagnostic characters for the interpretation of its probable phylogenetic relationships within the sauropods (Bonaparte, 1986a).

Until now, the record of South American sauropods from the Cretaceous was limited to representatives of the family Titanosauridae *sensu* Powell (1986), and to poorly preserved remains of indeterminate sauropods (Huene, 1929, del Corro, 1975), upon which studies of sauropods, particularly titanosaurs, from the Late Cretaceous could be based.

In the case of the present material, not only is it from a different and older stage in the history of South American sauropods, the available anatomical characteristics allow insight into systematic and phylogenetic interpretations that can augment the knowledge of this varied group of dinosaurs.

Generally, sauropods, despite their great dimensions and their supposed grotesque aspect, don't merit sufficient attention from specialists in vertebrate evolution, especially in South America. Nevertheless, the studies that we have carried out (Bonaparte 1986a, 1986b), and some modern interpretations (Bakker, 1971, 1972, 1986; Ostrom, 1986) tend to show that the gigantism of sauropods required unique and very elaborate physiological, osteological, and behavioral adaptations (Coria, in press), that allowed them

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Figure 1. *Amargasaurus cazaui*. Posterior view of the preserved portion of the cranium. Abrev.: BO, basioccipital; CPR, crista prootica; EO, exoccipital; P, parietal; PBT, basipterygoid process; PO, postorbital; PPO, paroccipital process; SO, supraoccipital; SQ, squamosal; TBS, basal tubera.

to evolve and dominate the continental scene during singularly prolonged periods of time.

The study the Neuquén sauropod, and of other sauropods of the Argentinean Cretaceous, provides an opportunity to better know the South American record and to evaluate, in some measure the balance of the faunas in which they existed, and through this some aspects of evolution and relationships among the distinctive sauropod groups. The discovery of the specimen that is herein briefly described was discovered during the 8th Paleontological Expedition to Patagonia, directed by one of the authors (J.F.B.), by means of the Lic. Guillermo Rougier, in February of 1984, as part of the research program "Continental Vertebrates from the Jurassic and Cretaceous of South America", begun in 1976 with the support of the National Geographic Society.

SYSTEMATICS AND DESCRIPTION Order SAURISCHIA Seeley, 1887 Suborder SAUROPODOMORPHA Huene, 1932 Infraorder SAUROPODA Marsh, 1878 Family DICRAEOSAURIDAE, Huene, 1956

Amargasaurus gen. nov.

ETYMOLOGY: In reference to La Amarga, in Neuquén Province, that produced the holotype: the lizard of La Amarga.

TYPE SPECIES: Amargasaurus cazaui sp. nov., figures 1-13

DISTRIBUTION: Lower part of the La Amarga Formation, Lower Cretaceous (Hauterivian), in south-central Neuquén Province, Argentina.



Figure 2. *Amargasaurus cazaui*. Lateral view of the preserved portion of the cranium. Abrev.: in addition to those from the anterior figure, F, frontal; FST, supratemporal fenestra; OS, orbitosphenoids; PF, prefrontal; PS, parasphenoid; I, olfactory nerve foramen; II, optic nerve opening.

DIAGNOSIS: Dicraeosauridae of size comparable to Dicraeosaurus hansemanni, with taller presacral vertebrae than in Dicraeosaurus, with the split in the neural spines more accenutuated than in this genus, extending to the penultimate presacral. Cervical neural spines substantially longer than in Dicraeosaurus and subcylindrical in cross section; pleurocoels secondarily obliterated as in Dicraeosaurus; 5 fused sacral vertebrae; pelvis and appendicular elements comparable to those of Dicraeosaurus. Temporal region of the skull with parietal and postparietal fenestrae as in Dicraeosaurus; basal tubera fused. Position and shape of the external nares comparable to Dicraeosaurus hansemanni; robust orbitosphenoids with the opening of the olfactory nerve large, bounded by a bony process.

Amargasaurus cazaui sp. nov.

Figures 1 to 13

ETYMOLOGY: In recognition of Dr. Luis B. Cazau, of Y.P.F. Exploration who, in 1983, interested us in the paleontological exploration of the La Amarga Formation, offering data on discoveries.

HOLOTYPE: Specimen MACN-N 15 consisting of a great part of an skeleton composed of the temporal region and basicranium of the skull, 22 articulated presacral vertebrae and articulated with the cranium and sacrum, relatively complete and associated with some ribs; sacrum with 5 fused vertebrae, affected partially by erosion before being buried, 3 anteriormiddle caudal vertebrae, 1 posterior caudal, 3 haemal arches, 1 proximal end of a cervical rib, numerous incomplete dorsal ribs,



Figure 3. A, B. Crania of *Amargasaurus cazaui* in posterior and dorsal views. abrev.: FP, parietal foramen; FPP, postparietal foramen. C, D. Posterior and dorsal views of the cranium of *Diplodocus* for comparison. C and D, from Holland. 1906.

fragments of ribs and caudal vertebral centra; scapulocoracoid from the right side, humerus, radius and ulna from the left side, ilium, femur, tibia and fibula from the same side. 1 astragalus and 2 metatarsals.

STRATIGRAPHIC AND GEOGRAPHICAL PROVENANCE: lower part of the La Amarga Formation, in layers of small arenaceous conglomerates, 2.5 km SE of the bridge of the La Amarga Arroyo on National Route No. 40: Department of Picún Leufú. Neuquén Province, Argentina.

DESCRIPTION: **Skull** (figures 1, 2, 3 and 13). The preserved portion of the skull includes the complete occipital region and its continuation in the basicranial region, including both basipterygoid processes. The temporal region is complete, except the ventral border of the infratemporal fenestra. The narial region is well preserved, with the prefrontals and frontals framing

the opening; the nasals are missing. The braincase is intact, up to the parasphenoid. It lacks the whole rostral and mandibular parts of the skull. No teeth were found.

BASICRANIUM: The occipital condyle is subspherical with a wide neck in its ventral region. The basioccipital forms the major part of the condyle and is elongate until the tubera that are united to each other, forming a wide bony process. From there the basisphenoids form two very long basipterygoid processes, separated slightly between them

OCCIPITAL REGION: The exoccipitals form a limited dorsolateral part of the condyle. The paroccipital processes are curved back and down, ventroanteriorly surpassing the position of the condyle. A thick, robust crest of the supraoccipital extends from the foramen magnum upward to support the postparietal fenestra from behind. On each



Figure 4. *Amargasaurus cazaui*. Atlas and axis in lateral and anterior views. Abrev.: A, atlas: D, diapophysis; EN, neural spine; PTZ, postzygapophysis.

side of this crest are marked depressions that correspond to sites of muscular insertion.

SKULL ROOF: The parietals have a short contact with each other and are separated in the axial plane forward, defining the rear border of the wide parietal fenestra. Laterally, each parietal shows topographic relief in the form of a semicircular, bony rim. The frontals define the anterior limit of the parietal fenestra and extend laterally to border the orbit. The prefrontals are robust: they bound the region anterior and dorsal to the orbits and they terminate anteriorly in the shape of a wedge. The nasals are not preserved.

LATERAL VIEW: The preserved portion of the orbit is high, with rugosities in its dorsal and posterodorsal regions. The postorbital forms the posteroinferior angle of the orbit and is elongate anteriorly and ventrally, framing the narrow infratemporal opening superiorly. The supratemporal opening is exposed laterally as a vertical fissure. The squamosal displays a wide contact with the postorbital, and is elongate ventroanteriorly where it becomess wedge-shaped, with an articular surface for the quadrate covered by an external sheet.

ANTERIOR VIEW: The anterior view of the preserved portion preserves a massive bony midline, with wide bony plates

in the posterior region of the external nares. The prefrontals possess a crest that topographically widely separates the nares from the orbit.

The dorsal part of the orbitosphenoids presents a bony rim that surrounds the wide opening of the olfactory nerve. These bones and their continuation in the parasphenoid rostrum are thick and robust. The parasphenoid rostrum is laminate but rather thick; it possesses an anterior process that does not exceed half the length of the of the long basipterygoid processes. The aspect of the external nares, the robustness of the bones that bound it, and its proximity to the robust occipital region recalls the interpretation of Bakker (1986) concerning the existence of a proboscis, it may have significant indications in this specimen.

COMPARISONS OF THE SKULL: The general characteristics of this cranial portion coincide well with those of *Dicraeosaurus hansemanni* Janensch (1914), but it differs in some important respects. The smaller relative size of the postparietal fenestra with respect to parietal fenestra is more accentuated in the Patagonian species; the basal tubera of the basioccipital are united in *Amargasaurus cazaui*; and the proportional length



Figure 5. *Amargasaurus cazaui*. 6th cervical vertebra in anterior and lateral views. Abrev.: CN, neural canal; D, diapophysis; PP, parapophysis; PRZ, prezygapophysis; PTZ, postzygapophysis.

of the basipterygoid processes it is greater in A. cazaui.

We believe that the aforementioned features represent derivative characters of the skull of *Amargasaurus cazaui* with regard to that of *Dicraeosaurus hansemanni*. In the Neuquén specimen, the parietal and postparietal fenestrae are very obvious, confirming their existence in the Tanzanian species illustrated by Janensch (1935-36, figures 95, 197 and 98) whose existence was doubted by some authorities.

The most posterior position of the external nares indicates that this sauropod lineage is more derived in that character than the Camarasauridae. Diplodocidae and Brachiosauridae. The supposed relationship between the Dicraeosauridae and Diplodocidae. suggested by Berman and McIntosh (1978). it is not endorsed by diverse cranial characters, such as the existence of parietal and postparietal fenestrae, the extreme elongation of the basipterygoid processes, and the presence of a supraoccipital crest of the Dicraeosauridae are all nonexistent in the Diplodocidae.

POSTCRANIAL SKELETON

Cervical vertebrae, figs. 4, 5 and 6. The species that we describe possesses 13 cervical vertebrae that are characterized, except the atlas and the axis, by a deep partition of the neural spine that extends to the roof of the neural canal. As in other sauropods, the centra are opisthocoelous, longer than tall, and with characteristic pendant parapophysis. The lateral depressions of the centra are very light, except in the most anterior part above the parapophysis. The diapophysis possess on their dorsal surfaces strong lateral depressions that penetrate almost to the axial plane. The double neural spines are directed up and backward, show wide separation at their bases and, according to our observations in distinct vertebrae, this separation is reduced upward by a probable contact between each branch of the neural spine. Each branch of the spine



Figure 6. *Amargasaurus cazaui*. 8th. cervical vertebra in anterior and lateral views. Abrev.: as in previous figures.



Figure 7. Amargasaurus cazaui. 1st.dorsal vertebra in anterior and lateral views. Abrev.: as in previous figures.

is rather laminate near its base and subcircular for most of its length. They are approximately 4 times the length of the vertebral body in the posterior cervicals.

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Dorsal vertebrae, figs. 7, 8 and 9. *Amargasaurus cazaui* possesses 9 dorsals. They are characterized by deeply cleft neural spines, except the last two dorsals. The anterior dorsals are opisthocoelous, a character that changes beginning in the middle dorsals backward to amphiplatyan. The vertebral bodies are somewhat longer than high and without lateral depressions, except in the first 3 dorsals where a depression is observed that, incidentally, does not resemble a pleurocoel. The first dorsals differ from the cervicals by the presence of a prominent and robust diapophysis that suggests the existence of strong ribs.

Sacrum. The sacrum is incompletely preserved since it lacks most of the vertebral centra.

It seems to have consisted of 5 vertebrae equipped with very tall and undivided neural spines. The neural arches of the sacrals are fused in two groups: sacrals 1 and 2 to each and across the entirety of the neural spines, and sacrals 3, 4 and 5 to each other in the same manner. Thus, the neural arches of sacrals 2 and 3 are separate. Each neural spine extends a short lateral lamina, more expanded at its dorsal end-, beside a short anterior lamina and another posterior one. The transverse processes have been preserved in their dorsal parts; they are long and indicate a very wide pelvic structure, with widely separated ilia.

Caudal vertebrae, figure 13. The few conserved caudals are amphiplatyan, with slight opisthocoely manifested by a modest convexity in the anterior face. The middle caudals are quite amphiplatyan, with low and long bodies, and with the neural arch directed backward.

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Table I

Amargasaurus-Dicraeosaurus Fused frontals Parietal fenestra present Postparietal fenestra present Narrow supraoccipital; doesn't participate in posttemporal fossa Robust supraoccipital crest Basipterygoid processes very long Cervical vertebrae without pleurocoels or system of bony trabeculae Dorsal vertebrae secondarily without pleurocoels Proximal caudals robust, heavy, without pleurocoels

Haemal arches. The available haemal arches have their proximal region strongly fused and very concave. The haemal foramen is large and the shaft axially expanded.

Pectoral girdle. The scapula united with the coracoid from the right side has been preserved. The scapula is relatively narrow and elongate

Diplodocus Unfused frontals Parietal fenestra absent Postparietal fenestra absent Wide supraoccipital; participates in posttemporal fossa Vestigial supraoccipital crest Basipterygoid processes moderately long Cervical vertebrae with marked pleurocoels and system of bony trabeculae. Dorsal vertebrae with marked pleurocoels Proximal caudals light, with pleurocoels

In the center of the scapular blade, the external face is convex and the internal flat. The acromial expansion is modest and the glenoid cavity presents a slight anterior expansion.

The coracoid has a marked edge in the glenoid part, with a light posterior projection. The coracoid foramen



Figure 8. Amargasaurus cazaui. 21st.presacral vertebra in anterior and lateral views. Abrev.: as in previous figures.



Figure 9. *Amargasaurus cazaui*. Last dorsal (= 22nd. presacral) vertebra in anterior and lateral views. Abrev.: LPE, prespinal lamina; LPTE, postspinal lamina; LL, lateral lamina.



Figure 10. *Amargasaurus cazaui, left* ilium in lateral view. Abrev.: PI, ischiadic peduncle; PP, pubic peduncle.

is rather large. Length of the scapula greater than the coracoid, 1180 mm.

Pelvic girdle, figure 10. Of the pelvic girdle, only the left ilium is preserved. It is characterized by an extensive pubic peduncle and only a short projection as the ischiadic peduncle. The anterior part of the iliac blade projects anterolaterally forming an angle with the rest of the blade. The acetabulum is completely open in the medial side and proportionally large.

Humerus, figure 11. The left humerus is preserved. Torsion between the proximal and distal parts is not very pronounced. Its aspect is robust and rather heavy, with an appreciable expansion in the proximal half. The deltoid crest is pronounced, persisting half the length of the humerus, forming a strong ventral concavity on the dorsal half of this bone. The length of the humerus: 720 mm; minimum circumference: 380 mm.

Radius and ulna, figure 11. Both bones of the left side are conserved in their entireties. The proximal part of the ulna is triradiate, provided with three very simple crests. The olecranon is barely discernible. The distal end has an appreciable transverse expansion with rugosities for ligaments conjoining it with the radius. It is roughly the same length as the ulna and it has both ends slightly expanded. No better details are observable because of the type of preservation of the piece.

Length of the ulna: 440 mm. Length of the radius: 470 mm.

Femur, figure 12. Only the left femur is relatively complete but has some preservational alteration. It is a rectangular, robust bone, with the strong femoral head slightly projected medially. The 4th trochanter is blunt, thick, and it is positioned somewhat below the midpoint of the femur. The distal condyles are well separated and they present a marked posterior projection. The femur/humerus ratio is 1.45. Length of the

femur: 1050 mm; minimum circumference 530 mm.

Tibia and fibula, figure 12. Both have been preserved articulated to the left femur. The tibia is robust with a wide proximal region and modest cnemial crest. The torsion of the lower end doesn't reach 90° with regard to the proximal end. The well preserved, distal articular surface possesses a posterior projection in a more ventral position than the anterior one. The length of the tibia is 640 mm. The fibula is proportionally thick, with modest proximal and distal expansions. There is a pronounced anterolateral process in proximal half. The length of the fibula is 640 mm. The femur/tibia ratio is 1.64.

Astragalus. It is transversely quite narrower than the tibia. The internal part is low and the external high, suggesting the presence of a calcaneum.

COMPARISONS AND DISCUSSION

Amargasaurus cazaui is a dicraeosaurid with diverse derived characters in relation to Dicraeosaurus hansemanni and D. sattleri (Janensch, 1929, 1935-36), both from the Late Jurassic of Tanzania. Of these African species, only in D. hansemanni is the skull known. The main anatomical features that distinguish A. *cazaui* from *D. hansemanni* are: in the skull the fusion of the basal tubera of the basioccipital; the better development of the basipterygoid processes, and of the parietal fenestra with respect to the postparietal fenestra. In the postcranial skeleton, the persistence of split neural spines until the penultimate dorsal, the remarkable elongation and sharpening of the cervical spines, and the robustness of the diapophyses of the first dorsals, seem to be autopomorphies of the vertebral column of A. cazaui. The more derived characters that A. cazaui presents compared to D. hansemanni agree with the younger age in the species that we describe, (approximately 15-20 million years), that is to say that at least certain evolutionary aspects of the Dicraeosauridae, such as the increasing length of the neural spine and their progressive bifurcation, would have been in the midst of development between the Jurassic and the Early Cretaceous.

The Dicraeosauridae shares some characters with the Diplodocidae. In the skull, the general shape of the muzzle, the type of teeth, the lengthening and forward and downward orientation the basipterygoid processes, and the retraction of the nares to a position practically between the orbits. Nevertheless, there are also strong differences, mentioned above. The postcranial anatomy is basically different, as much in the vertebral morphology as in the main features of the long bones. For that reason,



Figure 11. *Amargasaurus cazaui*. A, left humerus in ventral or anterior view; B, left radius in internal view; C, left ulna in proximal and lateral views. Abrev.: CD, deltoid crest: O, olecranon.

we consider that *Diplodocus* and *Dicraeosaurus* pertain to families with different evolutionary histories, presumably starting from the level of the Cetiosauridae or even before. We don't believe that *Diplodocus* and *Dicraeosaurus* can be referred to the same family, Diplodocidae, as Berman and McIntosh have suggested (1978). In Table I, the principal differences have been summarized that, from our perspective, distinguish the specified genera and their respective families.

The long skulls with retracted nares and cylindrical teeth, commonly known as skulls of the "*Diplodocus* type" (Berman and McIntosh, 1978) are found in clades that are well differentiated systematically, such as the families

Diplodocidae, Titanosauridae and Dicraeosauridae. This type of skull, with marked differences in detail between the different groups, would have taken place as an adaptive response to relatively similar diets.

The "Diplodocus type" skulls are readily distinguished from the other type of skull, which is short, has wide nares separated from each other by a bony arch formed by the premaxillae and nasals, and with spatulate teeth. These skulls are called the "*Camarasaurus* type" (Berman and McIntosh, 1978), and are found in the Cetiosauridae, Camarasauridae. Brachiosauridae and Euhelopodidae. It is probable that these cranial types, and the families

to which they belong, originated prior to the Late Jurassic, beginning from primitive cetiosaurid species. This interpretation corresponds to studies on the anatomy of the presacral vertebrae (Bonaparte, 1986a) that allowed that author to postulate a phylogenetic relationship between the Cetiosauridae and Diplodocidae. The family Dicraeosauridae seems to have been geographically limited to the supercontinent of South America-Africa, and temporally to the Late Jurassic-Early Cretaceous. This family constitutes a sauropod group that Gondwana differentiated in and that. for paleogeographic reasons, could not colonize Laurasia. This hypothesis, advanced by Bonaparte (1986b) implies that, in the Late Jurassic, corresponding to the dinosaurian fauna of the Morrison Formation from North America and the Tendaguru beds of Tanzania, the endemic characters would already be found in both faunas. This presumption is partly confirmed by the presence in Tendaguru of Dicraeosaurus and Tornieria, not represented in North America; similarly, Haplocanthosaurus and Camarasaurus from North America are not found in Africa.

RECONSTRUCTION OF THE SKELETON OF AMARGASAURUS CAZAUI

The reconstruction of A. cazaui, figure 13, is based on the posterior region of the skull, the articulated vertebral column through last sacral vertebra, isolated caudal vertebrae, a good portion of the bones of the pelvic girdles (lacking the pubis and ischium), and the majority of the appendicular elements bones, (lacking carpals and parts of the feet and the hands). In summary, we believe that it is based on a very good proportion of associated material, corresponding to a single specimen. The only significant elements that are lacking are those of the preorbital region of the skull, all of the jaws, and proximal caudal vertebrae. The missing pieces have been reconstructed based on the materials of Dicraeosaurus hansemanni Janensch (1929), a species that shows enough basic morphological affinities to provide reliable interpretations of the few missing pieces of A. cazaui.

The diagnostic features of this Patagonian species refer to the organization of the vertebral column that shows a notable and unique hypertrophy of the height of the neural arches, accompanied by a marked bifurcation of the neural spines along almost all of the presacral vertebrae (except the atlas, axis, and two last presacrals). The girdles and both extremities, although possessing features characteristic of the sauropod family Dicraeosauridae, recorded in Tanzania and in our country, don't reveal exceptional characters as do the vertebrae.

The length and orientation of the neural spines has allowed us to reconstruct the curvature of the column in the



Figure 12. *Amargasaurus cazaui*. A, left femur in posterior view; B, left tibia in medial view; and C left tibia in external view.

cervical region. Although it may have some error in this respect, we interpret the position achieved is the result of characters of those vertebrae that don't allow any other position, except when flexed downward or upward in which case the spines tend to touch each other or separate distally. The position that we have given it is what we interpret as the "neutral" position, without flexion.

We interpret that A. cazaui was a permanently quadrupedal sauropod, and we don't perceive anatomical qualities that would permit it to rise on its hind feet as has been postulated for some titanosaurids (Powell, 1986). Nor do we notice in the organization of its extremities qualities for speed: the epipodials are too short with respect to the length of femur and humerus, a feature that seems to characterize giant species with slow movements. In and of itself we think that the great development of the neural spines, especially the sharpened one in the cervical region, would represent adaptations for defense. They could also function in other aspects of behavior, such as to intimidate or impress rivals, for "territoriality," for social hierarchy, and possibly for mating rituals. Nevertheless, we find it more reasonable to interpret a defense function



Figure 13. Amargasaurus cazaui. Reconstruction of the skeleton in lateral view.

for the strong bony structures that are the neural spines.

It is worthwhile to point out that the process of hypertrophy of the neural spines is manifested in less accentuated form in Dicraeosaurus hansemanni from the Late Jurassic of Tanzania. and that the character in A. cazaui, from the Hauterivian, is logically more derived than in the Tanzanian species, perhaps representing an extreme, terminal form. Among the members of the Sauropoda, that have given rise to strongly differentiated adaptive types in their presacral vertebral structure (Bonaparte, 1986), the Dicraeosauridae is exceptional for the notable dorsoventral development (not lateral), of the neural arch, at the same time exhibiting proportionally small vertebral bodies, and secondarily deprived of pleurocoels or lateral cavities in the middle and posterior dorsals.

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