

Considerations of the neural laminae of sauropod dinosaurs and their morphofunctional meaning*

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Abstract: Considerations of the neural laminae of sauropod dinosaurs and their morphofunctional meaning. The axial skeleton of sauropod dinosaurs is distinguished by the presence of vertebral laminae that connect different points between the neural arch and the centrum. Previous exhaustive studies have conferred phylogenetic value to the array and organization of these structures. These studies, among others, have also explored the function of the laminae. Many authors suggested that the characteristic cross-shaped transverse section of the sauropod dorsal neural spine (resulting from the axial prespinal and postspinal laminae and the lateral structures formed by the fusion of the spinodiapophyseal and the spinopostzygapophyseal laminae) is a function of four large pneumatic grooves. In this study, we associate the pattern of the sauropod (especially of the titanosaur) neural laminae with soft anatomy structures such as aerial diverticula and interneural and other epaxial muscles; we consider surfaces and spaces bounded by these laminae, and how they vary in the dorsal sequence. The inferred musculature, especially the transversospinalis group, is based on myology of extant lepidosauromorphs and archosauromorphs.

Key words: Sauropoda, vertebral anatomy, neural laminae, pneumaticity.

One of the most notable characteristics of the presacral axial skeleton of sauropod dinosaurs is the existence of bony laminae that connect, between each other and with the vertebral centrum, different points of the neural arch. Some investigators, among whom Bonaparte (1986, 1999) and Wilson (1999) stand out, have studied in detail their disposition and organization, reaffirming their phylogenetic strength (at a time when it was doubted by some paleontologists, e.g. Curtice, 1998). Also, these and other authors have reflected on the probable function of these structures. Britt (1997) suggested that the laminae of complex origin and of axial orientation (formed beginning with the union of the pre- and postspinal laminae with the spinoprezygapophyseal and medial spinopostzygapophyseal laminae) and lateral (formed beginning with the union of the distal segments of the spinodiapophyseal and lateral spinopostzygapophyseal laminae), separating four pneumatic diverticulae. According to this author, during ontogeny, the contact with the epithelium that would have covered those pneumatic organs would have induced the bony remodeling of the structures that originally were placed

between contiguous diverticulae, reducing them to thin laminae of bone. It should be noted that, generally, soft tissues have morphogenetic primacy over the skeletal tissue, in that the form of the bones (in this case, of the neural spines) will be largely governed by specific soft tissues (Witmer, 1997, p. 2).

In turn, Wilson (1999) agreed in that the neural laminae are primarily pneumatic structures, although he admitted that a secondary structural function was possible. In this case, the orientation of the laminae would be the result of *stress* generated about the bony structure by certain tendons or ligaments during ontogeny. Bonaparte (1999) has been openly contrary to the pneumatic hypothesis. According to him, “the vertebral complexity of the sauropods was totally tied to a very specialized system of axial muscles and support and of control of movements, and not of a system for lightening the weight of the bones as has been frequently hypothesized” (Bonaparte, op. cit., p. 116). Finally, Wedel (2003a, 2003b), like Britt and Wilson (in part), interpret the bony laminae of sauropod dinosaurs as septa that separate contiguous pneumatic diverticulae.

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Of course, these diverticula have not been preserved as fossils, but rather they have been inferred to leave morphological structures or osteo-histological markers; it has not been possible in this case to apply the criterion of the “Extant Phylogenetic Bracket” of Witmer (1997), because the above mentioned diverticulae have been found in one of the reference taxa (Aves), but are absent in the other (crocodiles).

In this work, we interpret the pattern of some of the neural laminae that extend along the neural spine of sauropods, with special emphasis on titanosaurs, beginning with the presence of certain soft tissues such as pneumatic diverticulae and muscular bundles. It is not our intention here to revise or discuss the pneumaticity of the axial skeleton of sauropods, we understand that, in general, this hypothesis is solid, and valid by the arguments of Britt, Wilson, Wedel, and other authors. Simply we want to demonstrate a way that one can understand, in the framework of a hypothesis of pneumaticity, the distribution and orientation of the principle neural laminae of sauropods (above all those located on the neural spines).

Mostly, the authors that have investigated this matter have put their interest in the laminae themselves, and in their probable function of connectors or as structural supports. Here we focus more in the areas or surfaces bounded by those structures, and in how those bony surfaces (about which, according to our interpretations, are arranged a series of soft tissues) vary along the length of the dorsal column.

GENERAL MORPHOLOGY OF THE PRESACRAL NEURAL SPINES OF SAUROPODS

The neural spines of sauropod cervical vertebrae are found extended along four principal laminae: two spinoprezygapophyseal (sprl, spinoprezygapophyseal laminae) and two spinopostzygapophyseal (spol, spinopostzygapophyseal laminae) (we maintain the abbreviations of the English, in accordance with the terminology proposed by Wilson, 1999). In lateral view (Fig. 1A-C), generally there is a wide and deep parallelogram-shaped surface (named by Bonaparte [1999, fig. 1] the “lateral dorsal zone”), bounded by the postzygodiapophyseal lamina (podl, postzygodiapophyseal lamina), the prezygodiapophyseal lamina (prdl, prezygapopdiapophyseal lamina), in addition to the two laminae mentioned above (the sprl and the podl that

correspond, precisely, to the long sides of that parallelogram). Generally, the sprl are found nearer to the axial plane than the spol, so that these are completely visible in the anterior view (Fig. 1A).

In dorsal vertebrae there is, apomorphically, an important lamina, the spinodiapophyseal (spd1, spinodiapophyseal lamina) (Fig. 1D-I). In accordance with Wilson (2002), the presence of this lamina constitutes a synapomorphy of the clade *Barapasaurus* + [(Omeisauridae + *Jobaria* + Neosauropoda)] (Wilson 2002, his character 99).

In the members of the clade *Barapasaurus* + more derived eusauropods, each spol is divided longitudinally into two branches: lateral and medial (Fig. 1E, F). Towards the posterior dorsal vertebrae, the lateral branch of the spol tends to unite distally with the spd1, constituting a lateral composite lamina (that Janensch [1929] called “lateralspinalleiste”, although Wilson [1999], precisely because of this composite condition did not give it a formal name), while the medial branch (designated the “suprahyposphential” by Osborn and Mook, 1921), tended to unite (at least in some groups, like diplodocoids) into a new posterior lamina, the postspinal lamina (posl, postspinal lamina) (Wilson, 1999) (Fig 1H, I).

In some groups (e.g., *Camarasaurus*), this pattern is maintained along the entire dorsal series. In others (e.g., diplodocoids), the sprl begins to close coming near each other until the other lamina is fused in the posterior dorsals subsuming the other into a unique anterior axial lamina, which is also an apomorphy: the prespinal (prsl, prespinal lamina, Wilson, 1999) (Fig. 1G, H).

Certainly, there is important variation in relation to this general design, even within the same taxonomic group. For example, in the posterior dorsals of the basal titanosaur *Andesaurus* (lower Cenomanian of Neuquén Province), the spol seems to divide (normally) into the two aforementioned branches (personal observation), that does not continue in more derived titanosaurs like *Malawisaurus* (Lower Cretaceous of Africa, Gomani, 2005), *Neuquensaurus* (lower Campanian of Río Negro, Salgado et al., 2005), and *Saltasaurus* (Maastrichtian of Salta, Powell, 2003) (the longitudinal division of the spol is not clear in the basal titanosaur *Epachthosaurus*, lower Upper Cretaceous of Chubut, Martínez et al., 2004). Wilson (2002: p. 268) consigned “middle and posterior dorsal vertebral neural arches with divided spinopostzygapophyseal lamina” as a synapomorphy of the clade Nemegtosauridae +

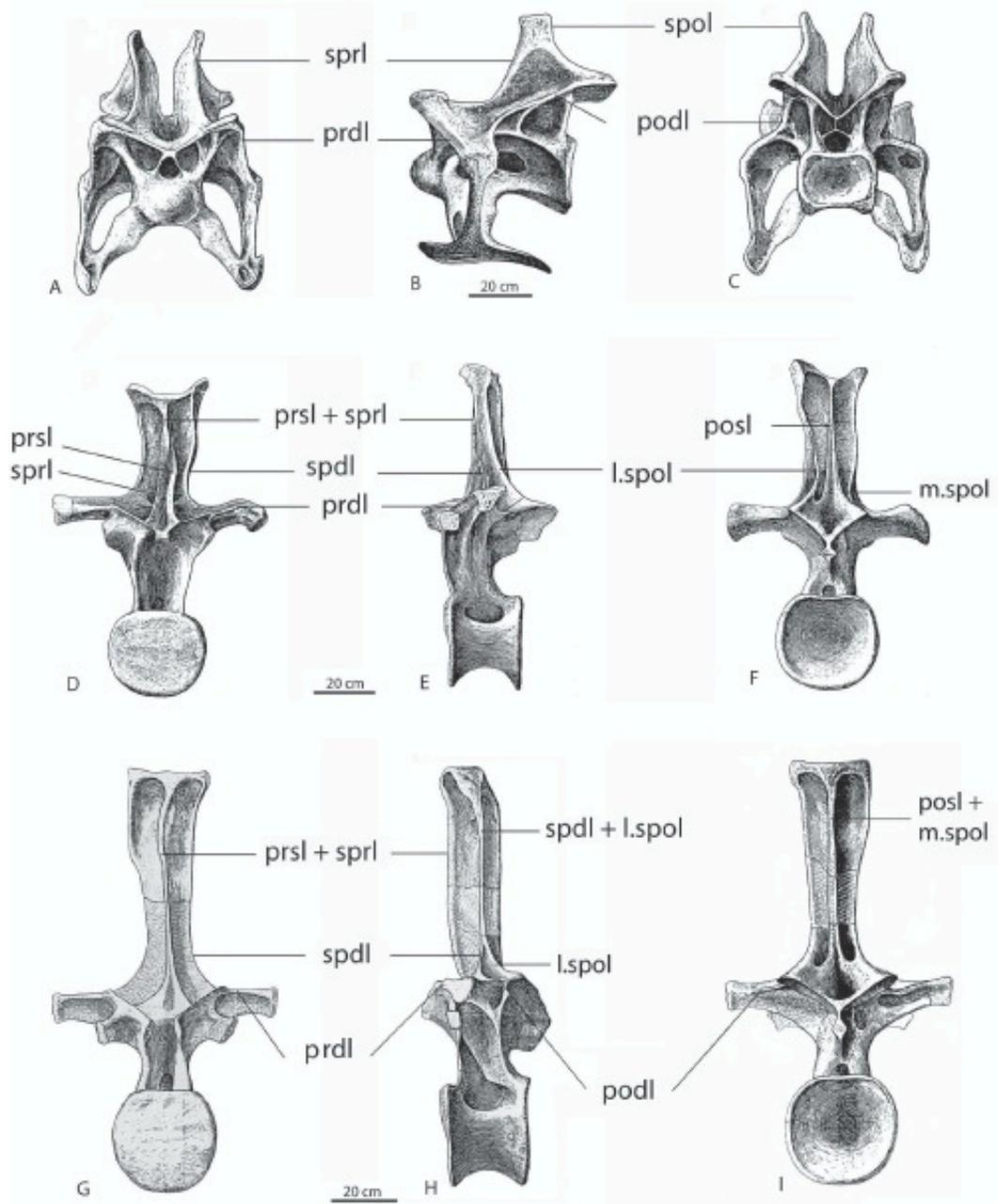


Fig. 1: Axial skeleton of *Apatosaurus*, CM (Carnegie Museum) 563 (*A. excelsus*): A-C, 8th cervical vertebra in anterior, lateral, and posterior views. CM 3018 (*A. louisae*): D-F, dorsal vertebra in anterior, lateral, and posterior views; G-I, 7th dorsal vertebra in anterior, lateral, and posterior views (from Gilmore, 1936). Abbreviations: l.spol, lateral spinopostzygapophyseal lamina; m. spol, medial spinopostzygapophyseal lamina; podl, postzygodiapophyseal lamina; posl, postspinal lamina; prdl, prezygodiapophyseal lamina; spd, spinodiapophyseal lamina; sprl, spinoprezygapophyseal lamina.

“*Titanosaurus*” [= *Isisaurus*] *colberti*) + Saltasauridae. It is likely that this was an error, because in his own matrix of characters it is noted (correctly) that the representatives of this clade have the plesiomorphic

condition (Wilson, 2002, appendix 1, p. 257). The synapomorphic revision of the clade Nemegtosauridae + “*Titanosaurus*”

[=*Isisaurus*] *colberti*) + Saltosauridae is, in reality, “middle and posterior dorsal neural arches with spinopostzygapophyseal lamina undivided.” In the same way, Bonaparte [1999, p. 148] indicates that, within Diplodocidae, the longitudinal division of the spol occurs in *Apatosaurus* but not in *Diplodocus*, although Wilson (2002, p. 256) is contrary to that opinion. The recently described Spanish sauropod *Galvesaurus herreroi* (Barco et al., 2005), also has an undivided spol, that unites distally with the spdl (Barco, 2005, p. 32).

There are also important differences in how the spdl manifests itself and develops progressively along the length of the sequence of dorsal vertebrae. In general, this lamina begins modestly as a posterior longitudinal division from the base of the sprl. In *Amargasaurus* (lower Barremian of Neuquén Province), this splitting begins from the 3rd-4th dorsal (personal observation). In some diplodocoids (e.g., *Apatosaurus*), the more conspicuous lamina that results from this doubling is, apparently, the posterior (Gilmore, 1936, plate XXV), while in others (e.g., *Diplodocus*, *Amargasaurus*), the anterior (Hatcher, 1901, plate VIII).

In titanosaurs there seem to be two modes of sequential differentiation of neural laminae, especially in relation to the spdl and podl. In some cases (*Neuquensaurus*), the spinodiapophyseal lamina is manifest and expands normally following as mentioned above, although, as I have indicated, without reaching to connect the spinopostzygapophyseal lamina distally (that at the same time is not split). Here, the podl is normally developed. In other cases, as in DGM (Divisão Geología y Mineralogía) “Series B”, material on which was recently erected the genus *Trigonosaurus pricei* (Campos et al., 2005) and in *Opisthocoelicaudia*, the spinodiapophyseal lamina is incipiently developed in anterior dorsals, and immediately is reduced to one anterior lamina (which Borsuk-Bialynicka [1977, p. 12] calls “supradiapophyseal lamina”) (Fig. 2). Normally, this lamina, which we call here a “relict spdl”, contacts the anterior axial lamina (prsl + sprl), or, in the case of *Opisthocoelicaudia*, at the base of the “metapophysis” (Borsuk-Bialynicka, 1977, p. 12). More posteriorly in the dorsal sequence, in the second case, the podl extends caudodorsally, surpassing the postzygapophysis, until practically reaching the neural spine (which, invariably, is strongly inclined posteriorly), it is transformed from the task of a true lateral neural spine lamina (which could be easily

confused with a spinodiapophyseal (Fig. 2). Borsuk-Bialynicka calls this lamina “horizontal posterior”; Bonaparte (1999, fig. 34), “diapophyseal posterior”; Powell (2003, p. 61), “supra-diapophyseal.” In some cases (*Trigonosaurus pricei*), the relict spdl and the lateral lamina that result in the caudodorsal expansion of the podl are fused at their base (Fig. 2, dorsals 5-7); Powell (2003, p. 61) interprets the configuration resulting from this union as a special architecture of the “supradiapophyseal” lamina (to which he implies it is “bifurcated towards the top/front”).

Bonaparte (1999, p. 165) has demonstrated that the lateral lamina that is present in the neural spines of some titanosaurs (precisely, in *Opisthocoelicaudia* and in *Trigonosaurus*) do not correspond to the “supradiapophyseal,” but probably to a true structure of a certain “vertebral morphotype” (his “titanosaur type”). We add that the “posterior diapophyseal” lamina of Bonaparte (1999) and “postzygodiapophyseal” of Wilson (1999) are homologous, in agreement with the sequential variation observed in *Trigonosaurus*. Reciprocally, in those cases in which posterior dorsals present a typical development of the podl, that is to say, connecting the diapophysis with the postzygapophysis (as in *Neuquensaurus*), the lamina that travels along the neural spine is invariably the spdl (Salgado et al., 2005, fig. 4).

Bonaparte (1999, p. 170) mentions that “in *Camarasaurus*, the cited posterior dorsal lamina connects the posterior border of the spine,” although in his description of the “camarasaurid type” he does not mention this lamina (pp. 152-154).

The condition in *Saltasaurus loricatus* cannot be established with certainty, because some of those materials assigned by Powell (2003) to this species are dissimilar, in which the some of the posterior dorsal vertebrae present a podl (PV [Paleovertebrado, Instituto Miguel Lillo] 4017-137; PV 4017-135), while others do not (PV 4017-42, PV 4017, 14). In agreement with this author (op. cit.), the vertebrae that lack the postzygodiapophyseal laminae are anterior in relation to those that have them (an interpretation made, apparently, from observations of *Trigonosaurus*), although still there may be the possibility that the material assigned to *Saltasaurus* correspond to more than one species of titanosaur. In this sense, it isn't possible to know if the podl that is observed in vertebrae PVL 4017-135 and PV 4017-137, and the incipient lamina observed in the medial dorsals of

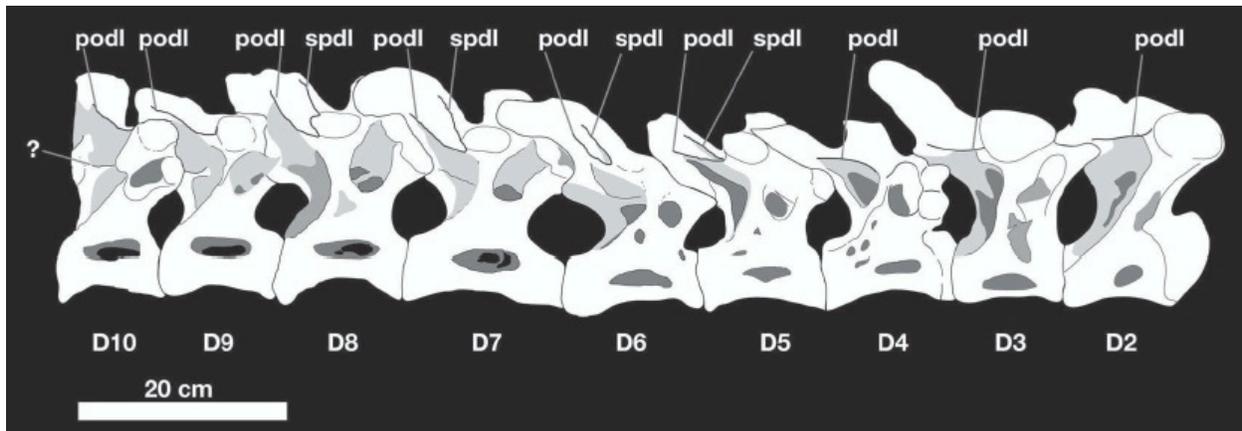


Fig. 2: Schematic of the sequence of dorsal vertebrae of *Trigonosaurus*. (Redrawn from Powell, 1987). Observe how the podl of the first five dorsal vertebrae ends continues to form a lateral spinal lamina in the last dorsals. The spdl retains a relict form from dorsals 5-8. In dorsal 10, the question mark indicates a new lamina that occupies a position similar to the podl in other sauropods. Abbreviations as in Fig. 1.

Trigonosaurus (that occupy a position coincident with the podl, and which towards dorsal 10 are important, the spine acquiring a vertical orientation, Fig. 2) are homologous structures. The same can be presented in relation to the lamina that, in *Saltasaurus*, extends laterally from the neural spine: does it correspond to the spdl or is it treated as the original podl, expanded caudodorsally? Powell (2003, plate 29, p. 117) calls this lateral lamina “spinodiapophyseal.” Bonaparte (1999, fig. 32F) designates it as “posterior diapophyseal lamina” (LDP). It was explained above that, according to this last author, the LDP lamina and spdl are not homologous.

Salgado et al. (1997) interpreted the presence of “accessory spino-diapophyseal laminae” (their character 30) as a synapomorphy of a subgroup of titanosaurs (their “unnamed taxon III”) that was made up of *Argentinosaurus huinculensis*, *Opisthocoelicaudia skarzynskii* and Titanosaurinae indet. [DGM “Series B”, *Trigonosaurus pricei*]. Nevertheless, in light of the aforementioned evidence, this should be revised: said accessory laminae seem to be, in reality, relict spinodiapophyseal laminae. In the case of *Argentinosaurus huinculensis* they do not even seem to be treated as true laminae, but as simple rugosities that extend along the anterior face of the spine (see fig. 6G in Salgado et al., 1997).

Of the differences present in certain groups of sauropods, in particular some titanosaurs, it is evident that the development and expansion of the spdl posteriorly in the dorsal sequence, and the proximity of

the sprl following the dorsal vertebrae, produces a new anterolaterally oriented surface, without correspondence in the cervical dorsals (Fig. 3). In the same way, the division of the spol into two branches (in the majority of sauropods, except *Galvesaurus herreroi* and derived titanosaurs), produces a new face, oriented posteriorly and laterally. In some groups, the first surface mentioned above acquires the condition of a true cavity: what Osborn and Mook (1921, fig. 39) called “supraprezygapophyseal cavity.”

EPAXIAL MUSCULATURE AND PNEUMATICITY

As mentioned above, Bonaparte (1999) has advocated an alternative interpretation to the pneumatic hypothesis: according to him, the system of neural laminae in sauropods has evolved as a result of an increase in the complexity of axial musculature. According to this author (op. cit.), the cavities or depressions bounded by laminae would have been occupied by packets of muscles. So, in *Plateosaurus*, the “infradiapophyseal central cavity” in the dorsal vertebrae (bounded by the anterior and posterior centrodiapophyseal laminae), would have been occupied by hypaxial musculature. In sauropods, that musculature would have extended into the neck, because of the existence of the same cavity in the cervical series. In the anterior dorsals of dicraeosaurids, the central infradiapophyseal cavity is very deep, according to Bonaparte, such that it could have been linked to the absence of “pleurocoels” in the dorsal

centra (p. 156) (according to Bonaparte, the “pleurocoels” were also occupied by hypaxial musculature). Behind the “central infradiapophyseal cavity,” sauropods have a depression in the area posterolateral to the prezygapophysis (p. 129). The development of this last cavity in the cervicals of these dinosaurs would indicate, according to Bonaparte, an advance of the epaxial musculature, particularly the *longissius*. In the laterodorsal area, in turn, would be arranged epaxial muscular packets (p. 129). In *Plateosaurus* and in sauropods (p. 131), in the prespinal area, there would be intervertebral epaxial musculature, while in certain circumneural depressions, the *longissimus* and part of the *interrans-versari* (p. 131). In the postspinal area (p. 131), in turn, there would be strong musculature linking the prespinal region of the subsequent vertebra.

With respect to the type of soft tissue that, in dinosaurs, would have been situated on both sides of the neural spine, Bonaparte thinks that it should be treated as epaxial musculature. Specifically, in the sauropod *Patagosaurus*, this author mentions that the lateral space of the spine is made up of the sprl and the spol, which would have been occupied by packets of muscle (Bonaparte, 1999, p. 140-141). While Bonaparte takes note of the important differences in posterior dorsals of the “typical diplodocoid” (in + and in that of *Patagosaurus* (in X), he does not explain if those osteological differences are (as we think here), a reflection of differences in soft tissues (p. 144).

Finally, in titanosaurs, “the space bounded by the anterior border of the neural spine and the internal faces of the transverse processes (...) should have been a place to harbor muscular intervertebral connections, and that corresponds in part to the space that accommodates the posterior region of the spine of the preceding vertebra (Bonaparte, 1999, p. 165).

The works of Britt (1997) and Wedel (2003a, 2003b) about sauropod postcranial pneumaticity have centered on the internal spaces of the vertebrae and other postcranial elements, finished as a result of the invasion of pneumatic diverticulae, and as in how the external fossae/foraminae via those diverticulae had penetrated to the interior of the bone. The “pleurocoels,” that, according to Bonaparte, held hypaxial musculature, are true pneumatic fossae according to Britt and Wedel. The infradiapophyseal cavities (the anterior and posterior cavities occupied by epaxial musculature according to Bonaparte, and the central cavity occupied

by hypaxial musculature), also are, according to Britt (1997), natural pneumatic spaces.

Until today, the correspondence between pneumatic diverticulae and neural spine laminae (posl, prsl, spdl, sprl, and spol) suggested by Britt (1997) has been poorly investigated, beyond the cited function of the laminae as divisions between contiguous diverticulae. In this sense, and although the pneumatic hypothesis enjoys a relatively wide consensus, there still lacks an interpretation that gives the precise location of those diverticulae (and other soft tissues) along the length of the sequence of presacral vertebrae. Our intention is, in this section, to offer some elements of analysis to contribute to that interpretation.

The inference of epaxial musculature that we present, in particular of the muscles of the *transversospinalis* group, is based on the myology of actual forms in lepidosauromorphs and archosauromorphs. Diverging in the Early Permian, (Benton, 2004, 2005), these groups show an important change in the plane of flexion in the axial skeleton. In some lepidosauromorphs, as it has been demonstrated experimentally, the flexion of the body is produced primarily by the action of hypaxial muscles (Carrier, 1990), which suggests that the epaxial musculature, whose function in this group is to provide rigidity and strengthen the vertebral column (Zug et al., 2001), would be more conservative in this group. On the contrary, the archosauromorphs seem to have experienced a major transformation of their epaxial musculature.

In the presacral vertebrae of tetrapods, particularly in reptiles, a series of epaxial muscles corresponding to the aforementioned *transversospinalis* group (containing the *multifidus*, *spinalis*, and *semispinalis*), inserts itself above the lateral face of the neural spine directing itself forward, upward and slightly inside, until reaching the neural spine of one vertebra anterior, located two or three elements anteriorly (Gasc, 1981). Other muscles in this group, the *interneuralis*, connect contiguous vertebrae, filling the space between the zygapophyses ad the neural spine (the “prespinal” and “postspinal” areas, according to the terminology proposed by Bonaparte for sauropods (1999, fig. 10) (Gasc, 1981; Rockwell et al., 1938, fig. 2).

While, as we note, the distribution and relationship between those muscles are very inconsistent, especially within the group of archosauromorphs,

it is still possible to recognize a common pattern in reptiles. In general, as observed in crocodiles (Gasc, 1981), the *semispinalis*, whose area of insertion is located near the postzygapophysis, equal to the *multifidus*, is the most lateral of the muscles of the group. The *spinalis*, on the other hand, generally occupies a medial position relative to the anterior, originating normally on the base of the neural spine, above its lateral face.

Differing from what is known in other diapsids [reptiles and in aves], the distribution of the principal muscular bundles of sauropod cervical vertebrae can be inferred (Wedel and Sanders, 2002), taking into account the profound musculoskeletal modifications that are found in the axial skeleton of archosauromorphs from the hypothetical ancestor of Archosauria to the hypothetical ancestor of Neornithes, such as the shortening and the augmentation of the rigidity of the post-cervical column (Gatesy, 2002). In those dinosaurs, as in reptiles, the area of origin for the *transversospinalis* group would have been located in the posterior section of the area bounded by the spinoprezygapophyseal, spinopostzygapophyseal, and postzygodiapophyseal laminae (although in some cases, as in the brachiosaurid *Sauroposeidon proteles*, this area is profoundly excavated and possibly invaded and occupied in large part by a pneumatic diverticula [Wedel et al., 2000a, 2000b], leaving little space to the epaxial musculature. From there, those muscles that would have been anterodorsomedially directed, until reaching the neural spine of an anterior vertebra, as it occurs in the majority of reptiles. It is likely that the notable development of the *podl* in sauropods owes not only to the increase in the volume of the muscles that are homologous to the *transversospinalis* group, but also to the insertion of fibers of a muscle homologous to the *intercostalis externus*, as it occurs in some groups of reptiles (e.g., in the infraorder Scolecophidia), Gasc, 1981, fig. 51). If this last lamina is found present in all saurischians (Wilson, 1999), it is in sauropods where it reached its greatest expansion. Even in basal sauropodomorphs, like *Riojasaurus* (Triassic of La Rioja, Argentina) and *Plateosaurus* (Triassic of Europe) that lamina is conspicuous, although recently splitting from the 9th cervical (Bonaparte, 1999, figs. 7 and 10).

From the *spol* and posteriorly there would have been a series of muscles homologous to the *intercristales* developed as in aves (Wedel and Sanders, 2002).

In cervical vertebrae, the space bounded by both *sprls* and the *spols* of the vertebra immediately anterior would have always been occupied by a muscle homologous to the *interneuralis*, as found in other reptiles (Fig. 3). This space is singularly extensive in sauropods, because this organ should have reached an important development in this region of the axial skeleton.

Very likely, the notable anatomical modifications that are observed in the neural spines of the dorsal vertebrae in relation to the cervical vertebrae are principally due to changes in the soft tissue anatomy between one and another region of the axial skeleton. In our opinion, these modifications would consist in an augmentation of the volume of certain pneumatic diverticulae (precisely in those that would have been distributed on the neural spine) and in a progressive decrease in the epaxial musculature, as has been demonstrated in aves, and identified in non-avian theropods and pterosaurs (which in turn has been suggested as a possible synapomorphy of ornithomirans) (O'Connor and Claessens, 2005). In sauropods particularly, the expansion of the spinodiapophyseal lamina after the first dorsals, and the doubling of the *spol* that characterizes the majority of eusauropods, would have been observed in the creation and extension of new bony surfaces, which would have resulted in the bony remodeling induced during embryogenesis by four large pneumatic diverticulae (whose location in posterior dorsals would have been, in agreement with Britt [1997], on both sides of the axial laminae), and would have caused reduction of the area of insertion of epaxial musculature (Fig. 3). This last area, following our interpretation, would have been circumscribed into two principal areas. 1. Between axial laminae of complex origin in successive vertebrae, and 2. in the lateral region of the base of the neural spine, dorsal to the transverse processes, in an area bounded anteriorly by the *spdl*, posteriorly by the lateral *spol*, and ventrally by the *podl*; an area that Osborn and Mook (1921, fig. 39) classify as the “supraprezygapophyseal cavity”. Osborn and Mook’s “supraprezygapophyseal cavity” (1921, fig. 39), as indicated, doesn’t have a corresponding area in the cervical vertebrae. It is this space that would have been occupied, according to our interpretation, by the large pneumatic diverticulae referred to by Britt (1997). Included in some cases (*Neuquensaurus*, Salgado et al., 2005, fig. 5), the area made up of the *prsl* + *sprl* and *spdl* that resulted in an extension of the

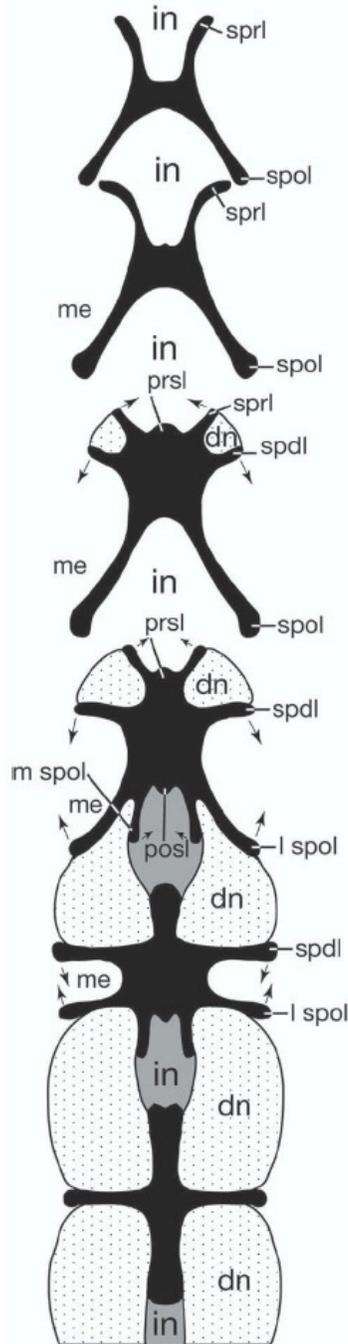


Fig. 3: Interpretive scheme of the neural laminae and their relation to the presence of soft tissues in sauropods, based principally on the specimens CM 563 of *Apatosaurus excelsus* and CM 3018 of *Apatosaurus louisae*. From top to bottom, the two first sections correspond to cervical vertebrae; the others to dorsal vertebrae. The sections have been made about half-way along the spine (the sections are not to the same scale). Abbreviations: dn, pneumatic diverticulae; in, interneural musculature; me, other epaxial muscles. Other abbreviations as in Fig. 1.

“supraprezygapophyseal cavity” as a result of the formation of an anterior axial lamina, shown as a series of orifices (supposedly pneumatic), that communicate with the interior of the neural spine.

In some groups (e.g., *Camarasaurus*, Osborn and Mook, 1921, and in general, in all of the sauropods that do not have “axial laminae”), the surface above that which would have supported the pneumatic diverticulae is relatively narrow. In these cases, the sprl and medial spol don't fuse into an anterior and posterior axial lamina, respectively. In other groups (in diplodocoids and in many titanosauriformes), the pneumatic diverticulae would have had a larger size, such that the sprl and the spol would have been fused medially in the posterior dorsals, resulting in the amplification of the bony surface occupied by pneumatic structures. In this last case, the *interneuralis* muscles would have been reduced to an interspinous ligament (Wilson, 1999) (Fig. 3).

Bonaparte (1999: p. 131) understands that the interneural musculature would have been reduced already in the first dorsals of *Plateosaurus*. It is possible that he includes the prespinal lamina (or simple rugosity) that is normally observed between the sprl, has developed as a result of the decrease in the area bounded between the sprls, and the consequential need to account for a larger area of insertion for the interneural musculature. In this way the habitual form of the prsl of the dorsal vertebrae that is manifested, just as in the reduction of space bounded by both, can be explained. In the case of sauropods with bifid cervical and dorsal neural spines, it is possible that during ontogeny, the expansion of pneumatic diverticulae accompanied (produced?) the closing of the dorsal neural spines (see Salgado, 1999).

In some cases, the spdl begins to manifest itself in a vertebra anterior to that in which the longitudinal doubling of the spol has begun (see, for example, *Diplodocus*, Hatcher, 1901, plate VIII; *Apatosaurus*, Gilmore, 1936, plates XXIV and XXV; *Camarasaurus*, Osborn and Mook, 1921, plate LXX). A possible explanation for this is the following. In the anterior and middle dorsals, the pneumatic diverticulae would have been arranged on the anterior face of the neural spine. To augment their volume posteriorly in the sequence, the diverticulae would have caused a modification to the posterior face of the preceding spine consistent with the doubling of the spol (Fig. 3).

In posterior dorsal vertebrae of some titanosaurs (e.g. *Saltasaurus*, *Neuquensaurus*), the area bounded by the *spdl*, the *spol* and the *podl* is very expanded, owing, on the one hand, to the development (lateral) of the first, and on the other hand, to the second (that does not divide into lateral and medial branches) that do not unite dorsally to the *spdl*, as is found in the majority of eusauropods (Wilson, 2002). If, as we suppose, this is the area that would have been occupied by the *transversospinalis* group, then those muscles would have had an important development in this part of the column. Conversely, in the cases in which a lateral and expansive lamina is developed dorsocaudally of the *podl*, as in *Trigonosaurus*, the epaxial musculature would have been restricted to the space bounded by the *podl* (or “posterior diapophyseal lamina” of Bonaparte, 1999) and the relict *spdl*. Possibly, the space between the axial lamina (*prsl* + *sprl*) and the (relict) *spdl* would have been occupied by pneumatic diverticulae, as in other sauropods. This interpretation differs from that of Bonaparte, who found in this same region of the vertebra, musculature “linked to intervertebral connections” (Bonaparte, 1999, p. 165).

Finally, the extension of the space located between the postzygapophyses and the *podl* (the area that Bonaparte called “lateral anterior to the postzygapophysis” (Bonaparte, 1999, fig. 1B), would have been occupied, following this author, by hypaxial musculature.

Notably, the area that is occupied by the epaxial musculature according to our interpretation is oriented posteriorly in the titanosaurs of the first group and anteriorly in the second.

CONCLUSION

The prespinal, postspinal, and “lateral” neural laminae probably separated four contiguous pneumatic diverticulae (Wedel, 2003a, 2003b; Britt, 1997; Wilson, 1999). The differences observed in the sequential development and ultimate location of the neural laminae of dorsal vertebrae are due principally to the rearward expansion of those pneumatic organs, and the consequent reduction of the space for the epaxial musculature (Fig. 3). In the case of some titanosaurs, that musculature was probably greatly developed, including in the posterior dorsals. This could be inferred as resulting from the fact that the spinopostzygapophyseal laminae (that do not split into

two branches, medial and lateral), never were lateral, at least in derived forms (*Neuquensaurus*, *Rocasaurus*, *Saltasaurus*, and included in *Malawisaurus* Gomani, 2005, fig. 10), and in none of which the fusion between the spinodiapophyseal laminae and the union of the spinopostzygapophyseal laminae occurs. In other titanosaurs (*Opisthocoelicaudia*, *Trigonosaurus*), on the other hand, it is possible that the epaxial musculature would have diminished posteriorly in the dorsal sequence, to the impairment of the hypaxial, as affirmed by Bonaparte (1999, p. 165).

In the anterior caudal vertebrae of some titanosaurs, it is very probable that the pneumatic diverticulae would have been arranged above the neural spine and both sides of the *prsl*. This can be inferred by the presence of orifices (probably pneumatic) in this area (*Bonatitan*, Martinelli and Forasiepi, 2004, fig. 16; *Neuquensaurus*, Salgado et al., 2005:fig. 6; *Rocasaurus*, Salgado and Azpilicueta, 2000, fig. 8).

While in this work we have focused our attention on the surfaces established by the neural laminae and their probable morphofunctional significance, we do not rule out that the same laminae have other functions such as structural support, or that they performed some other function. Logically, both structures (laminae and surfaces), are the result of the same morphofunctional transformation, and because of this should not be mutually independent.

If the neural pneumatic diverticulae of the dorsal vertebrae increase in volume posteriorly (as we interpret here), it could be thought that the pneumatization of the dorsal vertebrae would have been produced as a result of an abdominal air sac, and not from a simple extension of the cervical diverticulae (see Wedel, 2003a, 2003b).

Although historically it has been considered that the epaxial musculature serves a predominantly locomotor function (e.g., producing a torsion of the trunk in salamanders and some reptiles), today it is thought that the role of these muscles is to counter the effects of the strong reactive forces of the ground when the animal walks (Ritter, 1995), or to stabilize the trunk during locomotion (Ritter et al., 2001). In sauropods, the important development of the epaxial musculature of the neck contrasts notably with its scarce development in the dorsal region (Bonaparte, 1999). This can be explained by the relative immobility of the trunk region, or by functional differences in the epaxial musculature in those regions of the skeleton. In

titanosaurs, it is possible that the role of this musculature was different.

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