



Neuroanatomy of the vertebral column of *Vegasaurus molyi* (Elasmosauridae) with comments on the cervico-dorsal limit in plesiosaurs



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ABSTRACT

The evolution of the axial skeleton of vertebrates, particularly regionalization and the changes in the limits of each region is yet to be completely understood. The features of this process are more difficult to follow in groups with strong changes in the number of vertebrae as is the case of plesiosaurs. In this work we record the osseous correlates of the nervous system housed in the neural channel along the vertebral column of the elasmosaurid *Vegasaurus molyi*, from the lower Maastrichtian levels of the Snow Hill Island Formation (Antarctica). The new data allows inference of the position of the brachial plexus (i.e. the innervation of the pectoral girdle and anterior limbs), which in turn allows identification of the position of the pectoral girdle and the homology of the transitional “pectoral” region and the anterior dorsal (=trunk) vertebrae. The results indicate that in *Vegasaurus molyi* the pectoral girdle is at the level of the so called “pectoral” region, and that the pectoral region is homologous to the anterior trunk vertebrae of other Sauropsida. Additionally, the comparison with other published results of polycotyliids showing differences with *V. molyi* suggesting an interesting difference in the pattern of vertebral column regionalization among plesiosaurs.

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1. Introduction

Elasmosaurids are Cretaceous marine reptiles characterized by an increase in the number of cervical vertebrae (O'Keefe, 2002; Vincent et al., 2011; Kubo et al., 2012; Sachs et al., 2013). As in all plesiosaurs, elasmosaurids are inferred to have four limb locomotion (O'Keefe and Carrano, 2005) without reduction of anterior or posterior limbs. Although recent advances in our understanding of the evolution of the neck of elasmosaurids have been made (see Otero, 2016), some aspects of the homology of different segments of their vertebral column (i.e. regionalization) are still unclear. In particular, since the 19th century (Seeley, 1877), the identity of the posteriormost cervical and anteriormost dorsal (=trunk) vertebrae, and particularly the use of the term “pectoral” for them, have been

strongly debated in scientific literature. Some authors disagree with the use of the term “pectoral” as it is not used in any other reptiles and consider them as the posteriormost cervicals (e.g. Carpenter, 1999). On the contrary, Sachs et al. (2013) proposed to continue using this term in order to differentiate the transitional zone between the cervical and dorsal (trunk) regions, where the ribs articulate on both the diapophysis and parapophysis (Seeley, 1877).

Apart from the issue of whether a particular term (i.e. pectoral) is used or not an important issue is to analyze its homology. That is, if this transitional region corresponds to the cervical or to the dorsal (trunk) series. The most commonly cited criteria to identify cervical and dorsal vertebrae involve the location of rib articulations on them. Here we use independent evidence including the location of relevant nerves and plexus in order to test the homology of the “pectoral” vertebrae of the elasmosaurid neck. This approach is based on Giffin (1990, 1995) contributions who explored the correlation between the gross spinal soft anatomy and the size of the neural canal in extant diapsids and two plesiosaurs.

In this contribution we use the neural canal as an osteological correlate of the neural tube; we explore the variations of this

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correlate along the vertebral column of *Vegasaurus molyi* O’Gorman et al. (2015) in order to infer the positions of the brachial and lumbo-sacral plexuses and thus the location of the anterior and posterior limbs. Additionally, we discuss the homology of the cervico-dorsal transitional region classically called the “pectoral” region.

Institutional abbreviations—ANSP, Academy of Natural Sciences of Philadelphia, Philadelphia, USA; MLP, Museo de La Plata, Buenos Aires Province, Argentina; YPM, Yale Peabody Museum, New Haven, USA.

Anatomical abbreviations—ABNC, anterior breadth measurement of neural canal; PBNC, posterior breadth measurement of neural canal; C, cervical; P, pectoral; D = T, dorsal = troncal region. Ap, area enclosed by the neural canal in posterior view.

2. Material and methods

2.1. Material

The specimen considered (MLP 93-I-5-1) is the holotype of the elasmosaurid *Vegasaurus molyi*, a postcranial skeleton composed on an almost complete vertebral column. This specimen comes from Cape Lamb, Vega Island, Antarctic Peninsula, James Ross Archipelago (Fig. 1), lower Maastrichtian levels of the Cape Lamb Member of the Snow Hill Island Formation (O’Gorman et al., 2015).

2.2. Methods

2.2.1. Measurements

Measurements of the breadth of the neural canal at its base on both the anterior (ABNC) and posterior (PBNC) views of vertebrae (Fig. 2) were made, using a caliper with 0.01 mm precision, in order to be used as a proxy of the area enclosed by the neural canal. Additionally the area enclosed by the neural canal in posterior view (Ap) of all vertebrae with the complete neural arch preserved was recorded using the Software ImageJ. The correlation between the PBNC and the Ap was evaluated using free PAST 3.13 software (Hammer et al., 2001). An additional evaluation of the relationship between PBNC and Ap using log transformation of both variables

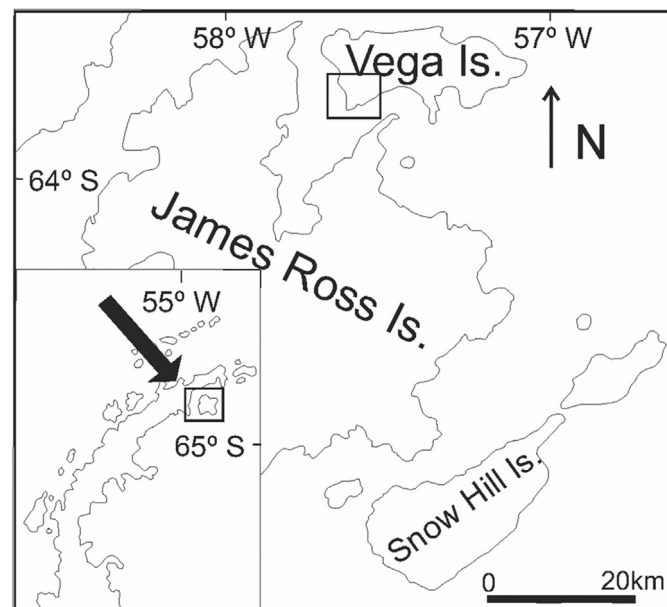


Fig. 1. Map of Cape Lamb, Vega Island, Antarctic Peninsula.

was performed in order to determine the allometric relation between the two measurements.

2.2.2. Osteological correlates of brachial and lumbosacral plexuses

The neuroanatomical methods employed here follow Giffin (1990, 1995) regarding osseous correlates of the neuroanatomy of diapsids: 1] the segmental extent and general organization of limb-level plexuses (Giffin, 1995; Burke et al., 1995). 2] the isosegmental relationship of vertebrae and spinal segments (Giffin, 1995) and 3] position of the plexuses relative to the cervical/dorsal and dorsal/sacral vertebral transitions (Giffin, 1995; Burke et al., 1995) and 4] the correlation between neural tube cross section and the neural canal size (Giffin, 1995: fig. 3). Although the percentage of canal filled with cord varied somewhat between taxa, the sizes of cord and neural canal of postatlantal segments were highly correlated in all cases (Giffin, 1990, 1995). Since the cross section of the neural arch, the osteological correlate of the neural tube, is not available for all the vertebrae in the holotype of *V. molyi*, a proxy of this value (PBNC) was considered. In order to validate this approach the correlation between the area enclosed by the neural canal in posterior view (Ap) and the PBNC is tested (see Section 3.2).

3. Results

3.1. General pattern of neural canal metrics

The measurements of the anterior and posterior breadth of the neural canal (ABNC and PBNC hereafter) taken from specimen MLP 93-I-5-1, were plotted against vertebral position (Fig. 3). The main features of this graph are described below.

The cervical series, following the classical definition of cervical in elasmosaurids as vertebrae where the ribs articulate only with the vertebral centrum (Fig. 2A, B), shows an increase in the ABNC and PBNC of the neural canal along the vertebral column to the 41st (last measurement available) and the 42nd cervical vertebrae (measurement not available). The values recorded between the 43rd and 54th vertebrae show a markedly different pattern between anterior and posterior breadth measurements. The ABNC shows slight increases, following the general trend observed in the anterior part of the neck, while PBNC shows an increase of about 20% (Fig. 3).

The pectoral region, a “transitional” region between the cervical and dorsal regions, where the ribs articulate across the centrum/neural arch suture (Fig. 2A, B), consists of three vertebrae. The 55th, 56th and 57th vertebrae (Fig. 3A, B), show a sharp decrease of the PBNC compared to the values of the posterior cervical vertebrae to values similar to those previously indicated for the 43rd vertebra. The dorsal vertebrae (where ribs articulate only on the diapophysis of the neural arch, Fig. 2A, B) show a decrease in both anterior and posterior breadth values up to the posteriormost dorsal vertebrae where an increase is observed. This continues into the sacral vertebrae (where the ribs articulate, as in pectoral vertebrae, on both the neural arch and vertebral centra, Fig. 2A, B). Both ABNC and PBNC values decreased posteriorly among the caudal vertebrae, where the exact position of each vertebra is not known. The last three caudals are only shown to indicate the general values.

3.2. Correlation of PBNC and neural canal section

A correlation analysis between the square root of the cross-sectional area of the posterior neural canal and the PBNC was performed (Fig. 4). The Pearson correlation value ($r = 0.883$), indicates a high and significant correlation ($p < 0.05$) and thus supports the use of the width of the basal part of the neural canal as a proxy for cross-sectional area (Giffin, 1995). Additionally an

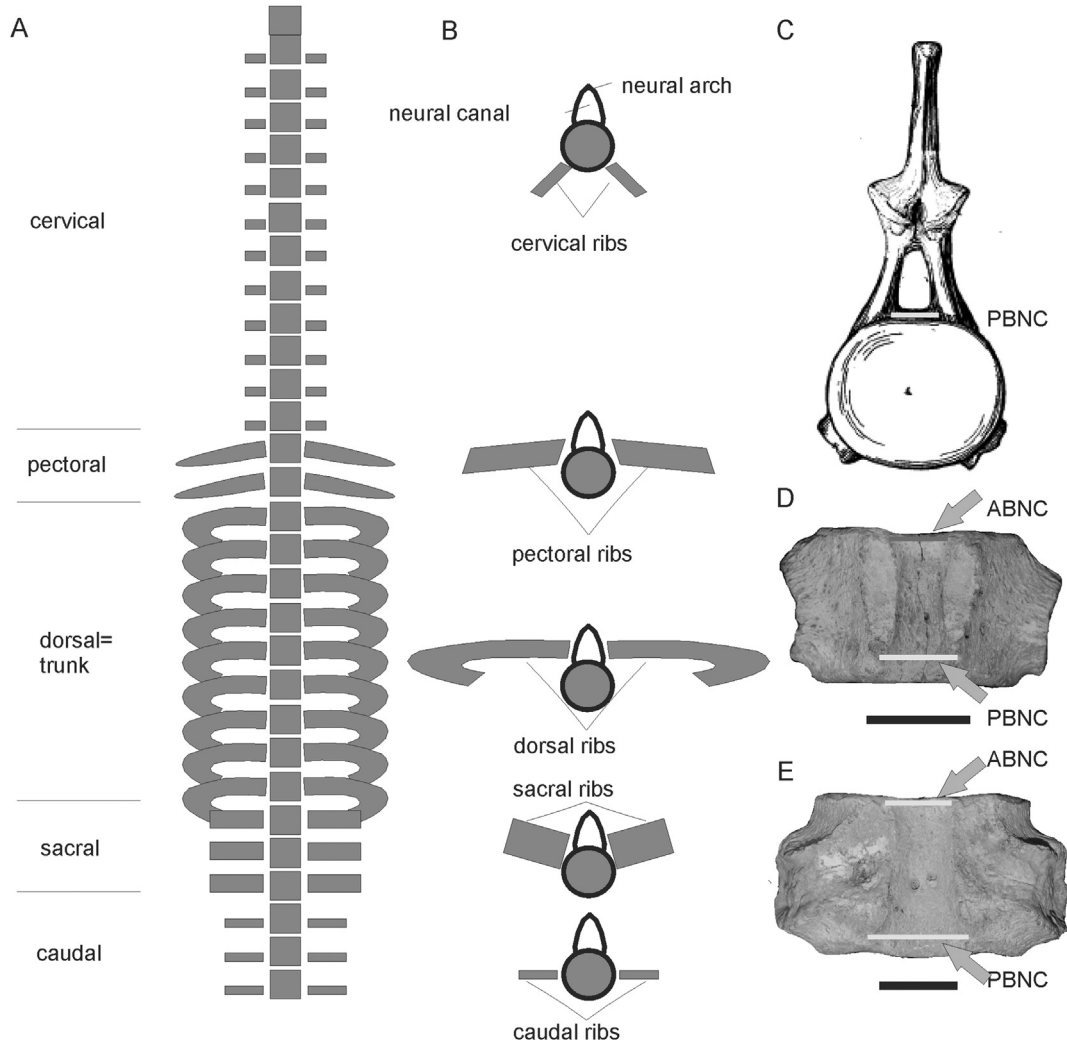


Fig. 2. A–B. Plesiosaur vertebral column and measurements taken. A, schematic diagram of generalized elasmosaurid and polycotyloid vertebral column. B, diagrams showing the main anatomical differences between vertebrae of each region. C, measurements of the PBNC in a vertebra with the neural arch preserved. D, E dorsal views of elasmosaurid vertebrae showing the positions of the ABNC and PBNC, D, cervical (MLP 93-XII-20-1) and E, sacral (MUC Pv 92). Scale bars = 20 mm. Schematic vertebra (C) after [Andrews \(1913\)](#).

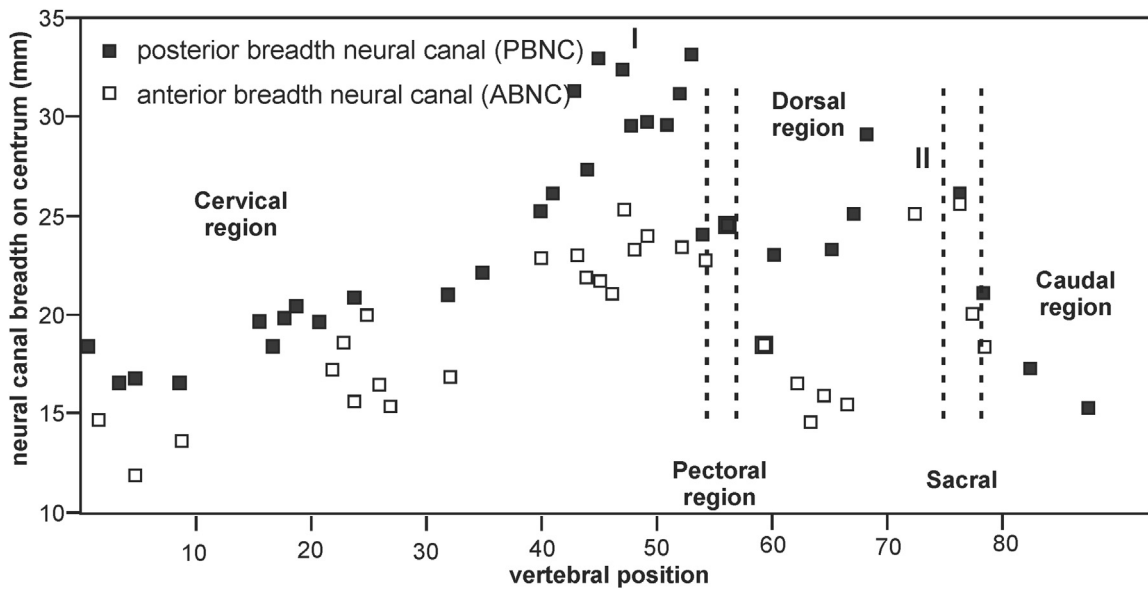


Fig. 3. Measurements of the anterior and posterior breadth of the neural canal ABNC (empty squares) and PBN (black squares). I, II, indicate position of the brachial (A) and lumbosacral (B) plexuses.

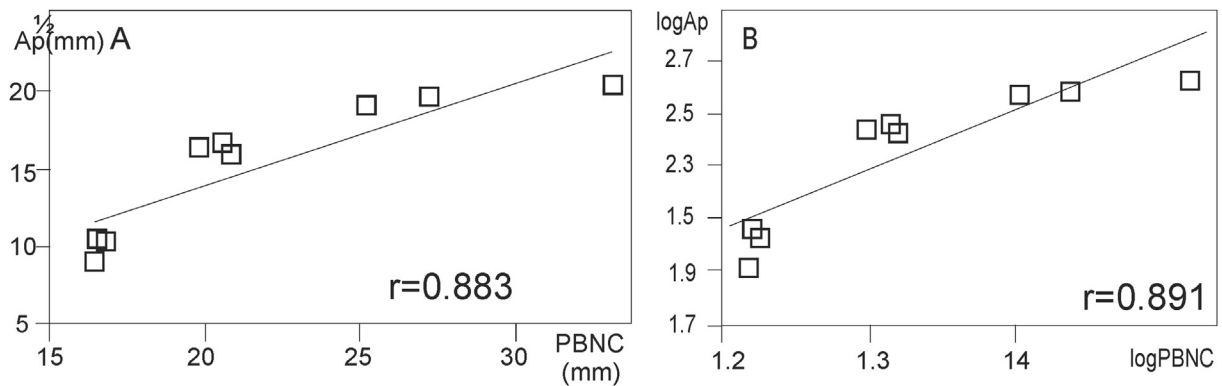


Fig. 4. A, Plot of section of neural canal in posterior view (A_p) and posterior broad measure of the base of neural canal (PBNA) and correlation coefficient. B, same with log transformation of variables.

allometry analysis was performed on the A_p and the PBNC. The relation obtained, $\log A_p = 2.2364 \cdot \log \text{PBNC} - 0.6275$, shows that A_p increases as an approximately quadratic function of PBNC. Therefore the changes observed in PBNC are even underestimating the variation of A_p at least along the cervical region.

4. Discussion

4.1. General ABNC and PBNC patterns

Figure 3 shows two features that need to be explained. One of the main patterns observed is the difference between the ABNC and PBNC (Fig. 3). This difference is connected with the position of the neural pedicels of elasmosaurids displaced toward the anterior limit of the dorsal surface, probably related to the anatomical position of the exit of the rachideal nerve. These nerves exit through the intervertebral foramen, which are mostly limited by the posterior part of the neural arch. The area of exit of the rachideal nerves is correlated with an increase of associations neurons and neuronal connections in this area that generates an increase of the section of the neural tube. This increase in section is more marked at limb levels (Streeter, 1904; Kusuma et al., 1979; Cruce, 1979).

The other feature of the plot in Fig. 3 is the presence of two zones; an anterior one and a less clear posterior one indicated as “I” and “II”. Both zones are characterized by an increase of both ABNC and PBNC, and increases in the difference between both their values. These two areas (Fig. 3) are inferred to indicate the locations of the brachial (I) and lumbosacral plexuses (II).

4.2. Brachial plexus, anterior limb position and the cervico-dorsal limit in elasmosaurids

Following Giffin (1995) lizards and crocodiles provide extant analogs for comparison with plesiosaurs (Fig. 5). Both lizards and crocodiles show the brachial plexus associated with the region from posteriormost third to fourth cervical to the first thoracic vertebrae, a feature recorded in all tetrapods (Burke et al., 1995: fig. 11). Extrapolating these results to the pattern shown in Fig. 3, the anterior enlargement is probably produced, at least in part, by the presence of the brachial plexus, although it is unclear why it comprises approximately ten segments, while there are only five segments in living diapsids (Fig. 5A, B). Here we consider that the posterior five segments of this area indicate the position of the brachial plexus. Therefore the pectoral girdle is located at the level of the pectoral vertebrae as was traditionally considered in classic reconstructions (Welles, 1943).

Additionally, the position of the posterior end of the brachial plexus in tetrapods coincides with the first dorsal vertebrae (Giffin, 1990, 1995; Burke et al., 1995). Our results indicate that the three pectorals of *Vegasaurus molyi* that are located posteriorly to the brachial plexus are homologous with (dorsal) trunk vertebrae of extant diapsids. The most extended zone of neural canal enlargement (ten segments versus five) recorded in *Vegasaurus molyi* is probably associated with innervation of cervical muscles other than those innervated by the brachial plexus. Although this inference requires a complete reconstruction of neck muscles, it seems to indicate the presence of important innervations of the muscles along the posterior part of the neck that may have important functional consequences.

Giffin (1995) analyzed the position of the brachial and lumbosacral plexus in two plesiosaurs (*Elasmosaurus platyurus* and *Polycotylus latipinnis*) based on the breadth measurements of the base of the neural canal, unfortunately no detailed explanation is given and therefore it is not clear if the measurements were taken on the posterior or anterior part of the neural canal. However a comparison of the results for *Vegasaurus molyi* with those obtained by Giffin (1995: fig. 15) for *Elasmosaurus platyurus* shows some unexpected differences. The sharp increase in the breadth of the neural canal of *Elasmosaurus* is located more posteriorly and it is only composed of the three posteriormost cervical segments (Fig. 6A), a significant difference with the patterns observed in *Vegasaurus molyi*. Additionally, the pattern recorded by Giffin (1995) for *Polycotylus latipinnis* (Fig. 6B) also shows differences with the pattern recorded here for *Vegasaurus molyi*, with a long anterior increase in the breadth of the cervical neural canal up to the pectoral vertebrae. These features probably represent evidence of the brachial plexus, which in this case, is located in a more posterior position. This comparison, although preliminary, reveals unexpected differences between the position of the brachial plexus and the classical anatomical limits and neck muscles innervations.

4.3. Cervico dorsal limit homology and expression of hox genes

One of the most perplexing aspects of the axial anatomy of elasmosaurids is the cervical count and the features of the cervico-dorsal limit (Carpenter, 1999; Sachs et al., 2013; Otero, 2016). This limit is usually determined by the position of the rib facets on the vertebral centra. However, this raises some problems with the transitional zone which has been called “pectoral” (Welles, 1943), a region not recognized in other diapsids (Carpenter, 1999). Although the term “pectoral” is well established in the descriptions of elasmosaurids (Welles, 1943, 1962), there has been some discussion

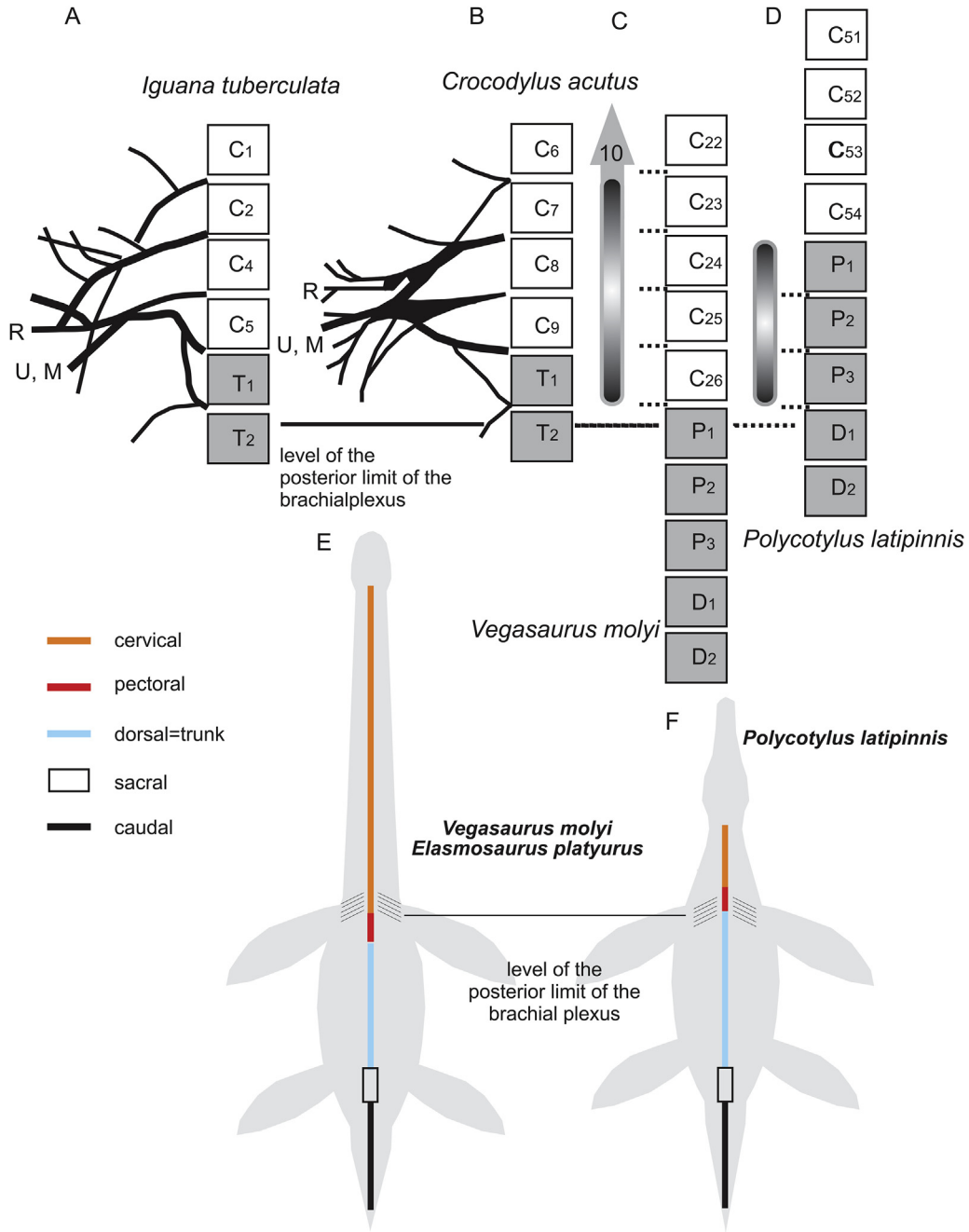


Fig. 5. A, B. Comparison between brachial plexus and cervico-dorsal limit in A, lizard (*Iguana tuberculata*) and B, crocodile (*Crocodylus acutus*) taken from Giffin, 1995. C, D inferred position of the brachial plexus in a cervico dorsal limit in C, *Vegasaurus molyi* and D, *Polycotylus latipinnis*. E, F, Diagram showing inferred position of the pectoral region in E, *Vegasaurus molyi* and *Elasmosaurus platyurus* and F, *Polycotylus latipinnis* (C, cervical; P, pectoral; T = D, dorsal vertebra; numbers in arrow indicate number of segments).

regarding its utility and anatomical consistency (Carpenter, 1999). The inferred position of the brachial plexus of *Vegasaurus molyi* provides new data regarding this point because the cervico-dorsal limit is controlled by Hoxc-6 located at the somites that map the first thoracic vertebra (that carry the last spinal nerve of the brachial plexus) in the chicken, the goose and the mouse (Burke et al., 1995). This correlation is clear in mammals with more or less than seven cervical vertebrae as observed in *Trichechus manatus*, *Choloepus hoffmanni* and *Bradypus tridactylus*, where the brachial plexus is also displaced in a caudal or cranial direction following the cervico-dorsal limit (Giffin and Gillett, 1996). Therefore, if we

consider that the brachial nerves exit anterior to the 55th cervical vertebra of *Vegasaurus molyi*, the pectoral vertebrae are homologous with dorsal (trunk) vertebrae. However, previous results suggest the same could not be true for other plesiosaurs such as *Polycotylus latipinnis*, where the brachial plexus seems to be located in the pectoral region (and not anterior to it as in *V. molyi*) thus at least part of the pectoral vertebrae in *Polycotylus latipinnis*, are homologous to the cervical vertebrae (Fig. 6C–F). Therefore the pectoral regions of these species are not homologous and show unexpected differences in the cervico-dorsal limit between elasmosaurids and polycotyliids.

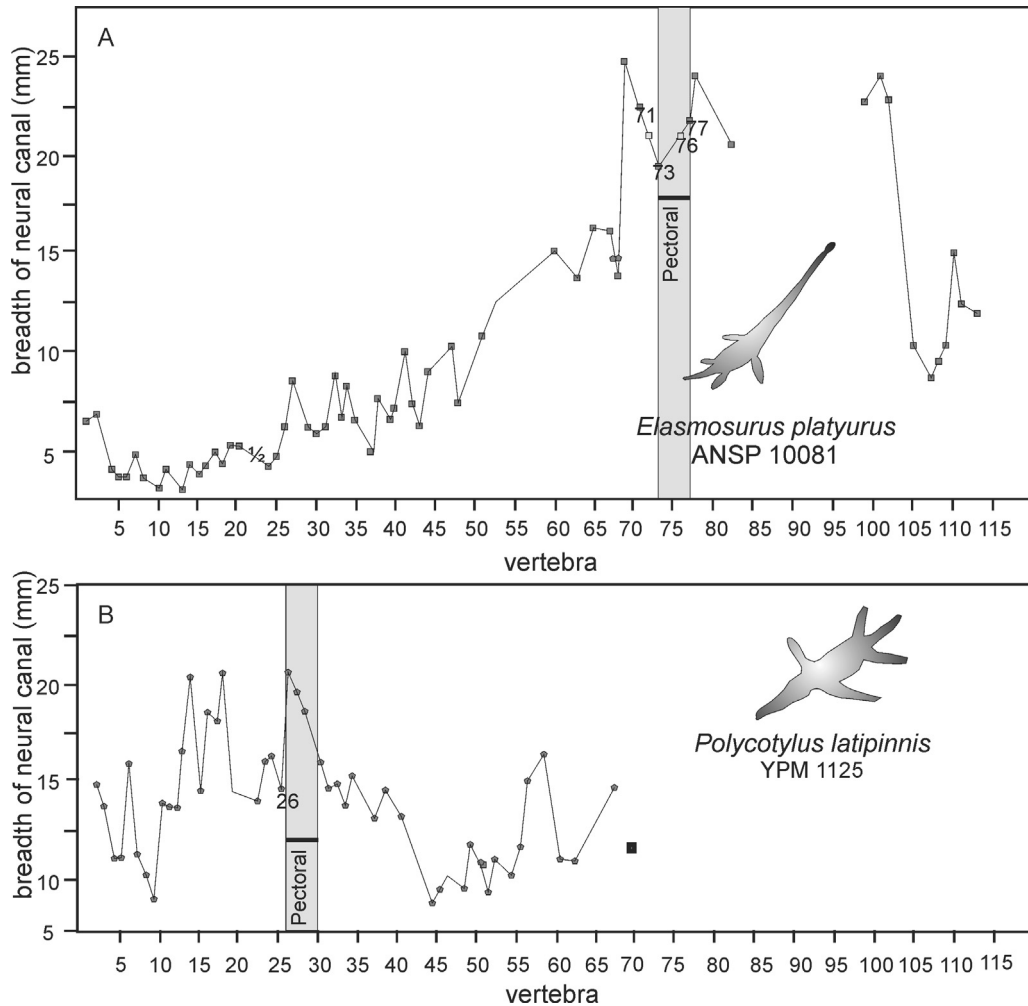


Fig. 6. Plots of the measurements of the breadth of the neural canal in A, *Elasmosaurus platyurus* (ANSP 10081) and B, *Polycotylus latipinnis* (YPM 1125). Modified from Giffin (1995).

5. Conclusions

Measurements of ABNC and PBNC of *V. molyi* show differences between them related to the position of the exit of the rachideal nerves, with the ABNC being smaller than the PBNC. The pattern recorded for *Vegasaurus molyi* shows two peaks that indicate the positions of the brachial and lumbosacral plexuses. As the brachial plexus is located at the posterior limit of the cervical region and indicates the cervico-troncal limit, the pectoral vertebrae of *Vegasaurus molyi* are homologous to trunk vertebrae of extant diapsids. Following the same criterion, the pectoral vertebrae of *Polycotylus latipinnis* are homologous to the cervical vertebrae of extant diapsids.

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