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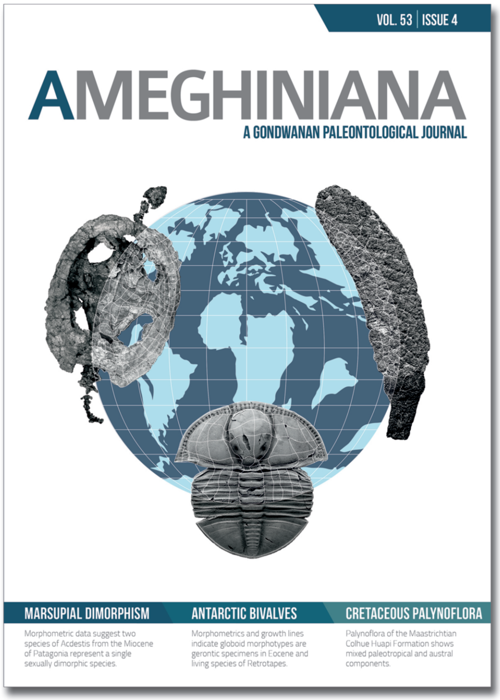

NEW INSIGHTS ON THE *ARISTONECTES PARVIDENS* (PLESIOSAURIA, ELASMOSAURIDAE) HOLOTYPE: NEWS ON AN OLD SPECIMEN

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ARTICLES

NEW INSIGHTS ON THE *ARISTONECTES PARVIDENS* (PLESIOSAURIA, ELASMOSAURIDAE) HOLOTYPE: NEWS ON AN OLD SPECIMEN

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Abstract. New observations on the holotype of the Maastrichtian aristonectine elasmosaurid *Aristonectes parvidens* Cabrera from Chubut Province, Argentina, reveals features that were not previously described while resulting in new interpretations. Quantitative comparison with non-aristonectine elasmosaurids demonstrates that the increase in the number of alveoli in the premaxilla, maxilla and mandible is not a consequence of skull size increase. Instead, decrease in alveolar size and interalveolar space, compared with that observed in non-aristonectine elasmosaurids, is at least as important. Increase in skull length compared with non-aristonectine elasmosaurids is not as marked as typically considered: skull length is equivalent to the summatory of length of the first 8–10 cervical vertebrae in non-aristonectines and the first 10–12 in aristonectines. The cervical region is characterized by a rapid increase of the relative broadness of the vertebral centra, which indicates a reduction in lateral mobility of the neck. Increase in alveoli number is achieved as a result of a number of changes that seem to indicate the importance of the biological role of the length of the alveolar row, this is probably related to changes in prey size and capture strategy such as trading for smaller fishes or invertebrates and/or a upgrading from ambushing one individual prey to simultaneously ambushing multiple prey individuals.

Key words. *Aristonectes parvidens*. Elasmosauridae. Aristonectinae. Late Cretaceous.

Resumen. NUEVAS OBSERVACIONES SOBRE EL HOLOTIPO DE *ARISTONECTES PARVIDENS* (PLESIOSAURIA, ELASMOSAURIDAE): NOVEDADES SOBRE UN ANTIGUO ESPÉCIMEN. Nuevas observaciones sobre el holotipo del elasmosáurido aristonectino maastrichtiano *Aristonectes parvidens* Cabrera, colectado en la provincia de Chubut, Argentina, muestran características no descriptas anteriormente y permiten nuevas interpretaciones. La comparación cuantitativa con elasmosáuridos no-aristonectinos muestra que el incremento del número de alvéolos del premaxilar, maxilar y mandíbula no es únicamente consecuencia del aumento de tamaño del cráneo. En su lugar, la disminución del tamaño alveolar y del espacio interalveolar, en comparación con lo observado en elasmosáuridos no aristonectinos, tienen al menos la misma importancia en el incremento total. El aumento de la longitud del cráneo en comparación con elasmosáuridos no aristonectinos es relativamente menos importante que lo considerado clásicamente ya que la longitud del cráneo es equivalente a la sumatoria de la longitud de las primeras 8–10 vértebras cervicales en los no-aristonectinos y a la sumatoria de la longitud de las primeras 10–12 vértebras cervicales en los aristonectinos. La región cervical se caracteriza por el rápido aumento del ancho relativo de los centros vertebrales que indican una reducción en la movilidad lateral del cuello. El aumento del número de alvéolos, causado por una sumatoria de cambios, parece indicar la importancia de la función biológica del incremento de la longitud de la hilera dentaria. Este cambio probablemente esté relacionado con un cambio de tamaño de la presa y/o de la estrategia de captura, en comparación con la de los elasmosáuridos no aristonectinos, tales como un cambio a peces más pequeños o invertebrados y/o un cambio de una estrategia de emboscada a captura simultánea de presas múltiples.

Palabras clave. *Aristonectes parvidens*. Elasmosauridae. Aristonectinae. Cretácico Tardío.

Aristonectines are bizarre elasmosaurids that flourished in the latest Cretaceous (Gasparini *et al.*, 2003; O'Gorman *et al.*, 2013, 2014b; Otero *et al.*, 2014) and only achieved a distribution restricted to the Weddellian Biogeographical Province (*i.e.,* Patagonia, Western Antarctica and New Zealand) and Angola (Cruickshank and Fordyce, 2002; Gasparini *et al.*, 2003; O'Gorman *et al.*, 2013; Otero *et al.*, 2014; Araújo *et al.*, 2015). One of the most important results springing from research on the Late Cretaceous plesiosaurs from the Weddellian Province is the inference of the elasmosaurian affinities of the aristonectines (*Aristonectes* Cabrera, 1941; *Kaiwhekea* Cruickshank and Fordyce, 2002), which had already been in discussion for 70 years (Cabrera, 1941; Welles, 1962; Cruickshank and Fordyce, 2002; Gasparini *et al.*, 2003; Benson and Druckenmiller, 2014; Otero *et al.*, 2014). The aristonectines remained poorly known until the recent recognition of *Kaiwhekea katiki* Cruickshank and Fordyce, 2002, as an aristonectine (Ketchum and Benson, 2011; Otero *et al.*, 2012), the description of the new aristonectine species *Aristonectes quiriquinensis* Otero, Soto-Acuña, O'Keefe, O'Gorman, Stinnesbeck, Suárez, Rubilar-Rogers, Quinzio-Sinn and Salazar, 2014, from late Maastrichtian rocks in central Chile, and the recognition of new and previously misinterpreted aristonectine records (O'Gorman *et al.*, 2013, 2014a, b) adding information about the anatomy and distribution of these elasmosaurids. However, in spite of these new results, the internal phylogenetic relationships among the aristonectines are still poorly understood (Otero *et al.*, 2014; O'Gorman *et al.*, 2015).

New preparation of the holotype of *Aristonectes parvidens* (MLP 40-XI-14-6) and the subsequent more detailed knowledge on its anatomy reveal features of this historical and systematically relevant specimen that were previously unknown or not completely discussed, therefore enabling researchers to consider the aristonectine typical features under a new light. Additionally, two explanations as to how the aristonectine cranium accommodates the increased number of teeth are tested and a possible correlation between the skull and neck features of the aristonectines is proposed.

Historical Background

The holotype of *Aristonectes parvidens* Cabrera, 1941 (MLP 40-XI-14-6) has a long history since its discovery to its display in the Museo of La Plata (Fig. 1.1–2). The holotype and only specimen was collected from Cañadón del Loro, near Paso del Sapo locality, Chubut Province (Fig. 1.3), by Cristian S. Petersen with the collaboration of a local resident, Victor Saldivia. The specimen was sent to the Museo de La Plata (Buenos Aires Province, Argentina) by Pablo Groeber in September of 1940 as a donation of the Dirección de Minas y Geología del Ministerio de Agricultura (Cabrera, 1941). After Lorenzo Parodi's preparation of the cranium and mandible, the identification of the material followed. An incomplete vertebra and phalanges from the same area had been previously donated to the Museo de La Plata by Mario Reguiló and transferred there by Dr. Joaquin Frenguelli. These were later added to the holotype because, as mentioned by Cabrera (1941), they probably belonged to the same specimen. The MLP 40-XI-14-6 was described by Ángel Cabrera, reconstructed with plaster and mounted for exhibition (Figs. 1.1, 2.1–2). Since its first description and throughout the 20th century (Welles, 1962; Persson, 1963; Brown, 1981), the features of *Aristonectes* have generated uncertainties about its affinities. Both the skull and the atlas-axis complex of the specimen were later re-prepared in order to display more sutures and alveoli for the revision by Gasparini *et al.* (2003) and the caudal vertebrae for the revision by O'Gorman (2013). Both preparations were carried out by the fossil technician Lic. Javier Posik (MLP).

Institutional abbreviations. **ANSP,** Academy of Natural Sciences of Drexel University, Philadelphia, USA; **LACM (CIT),** California Institute of Technology, Pasadena now housed in the LACM (Natural History Museum of Los Angeles County), Los Angeles, USA; **DMNH,** Denver Museum of Natural History, Denver County, USA; **NZGS CD,** Institute of Geological and Nuclear Sciences, Lower Hutt, New Zealand; **MLP,** Museo de La Plata, Buenos Aires, Argentina; **MML,** Museo Municipal de Lamarque, Río Negro, Argentina; **MUC,** Museo de la Universidad del Comahue, Neuquén, Argentina; **OU,** Otago Museum, Dunedin, New Zealand; **RSM,** Royal Saskatchewan Museum, Regina, Saskatchewan, Canada; **SMUSMP,** Southerns Methodist University, Shuler Museum of Paleontology, Dallas, USA; **TMP,** Royal Tyrrell Museum of Palaeontology, Drumheller, Canada; **UCMP,** University of California Paleontological Museum, San Francisco, USA; **UNSM,** University of Nebraska State Museum, Lincoln, USA.

Anatomical abbreviations. **an,** angular; **ana,** atlas neural arch; **aplp,** atlas posterolateral process; **ar,** articular; **atc,** atlas centrum; **athip,** atlas hipocentrum; **axc,** axis centrum; **axna,** axis neural arch; **axr,** axis rib; **cr,** cervical rib; **de,** dentary, **dt I,** distal tarsal I; **dt II+III,** distal tarsal II+III; **hf,** haemal facet; **in,** internal nares; **ju,** jugal; **kl,** keel; **lk,** lateral keel; **met V,** metatarsal V; **mx,** maxilla; **nc,** neural canal; **pa,** palatine; **par,** parapophyses; **pf,** pedicellar facet; **pmx,** premaxilla; **poz,** postzygapophyses**, pt,** pterygoid; **q,** quadrate; **sa,** surangular; **sp,** splenial; **sq,** squamosal; **ti,** tibiale; **v,** vomer; **vf,** ventral foramina; **vk,** ventral keel; **vn,** ventral notch.

MATERIALS AND METHODS

The linear measurements were taken using an electronic calliper that provides an accuracy of 0.01 mm. The indices considered in the description are those proposed by Welles (1952), which take into account the centrum length (**L**) and the ratio between height (**H**) and length of the centrum (**HI**=100*H/L) as well as the ratio between breadth (**B**) and length of the centrum (**BI**=100*B/L). Additionally, the ratio between the breadth and height (**BHI**=100*B/H) was considered. In this work, both breadth and height were measured on the posterior articular face. The vertebral length index [**VLI**= L/(0.5*(H+B))] was also considered. In order to test the hypothesis of the relationship between the number of alveoli and the cranium length, the ratio between the cranium length (**Cl**= from rostrum tip to occipital condyle) and the number of mandibular alveoli (**Al**) of several elasmosaurids (Tab. 1) was calculated as the alveolar ratio (**Ar**= Al/Cl). The Ar value (for each considered elasmosaurid)*Cl (*Aristonectes parvidens*; *Kaiwhekea katiki*) was used to calculate increases in alveoli number that can be explained by the expansion in the cranial and mandibular size. The nomenclature used for alveoli measurements follows Smith and Dodson (2003: fig. 7; see Fig. 7.1). To compare alveolar sizes, the mesodistal measurement was considered particularly useful. Two criteria were used to compare the Cl and the cervical region of aristonectine and non-aristonectine elasmosaurids: 1) the ratio between Cl and atlas-axis complex length and 2) the number of cervical vertebrae, counting from the atlas, that forms a neck sector as long as the Cl.

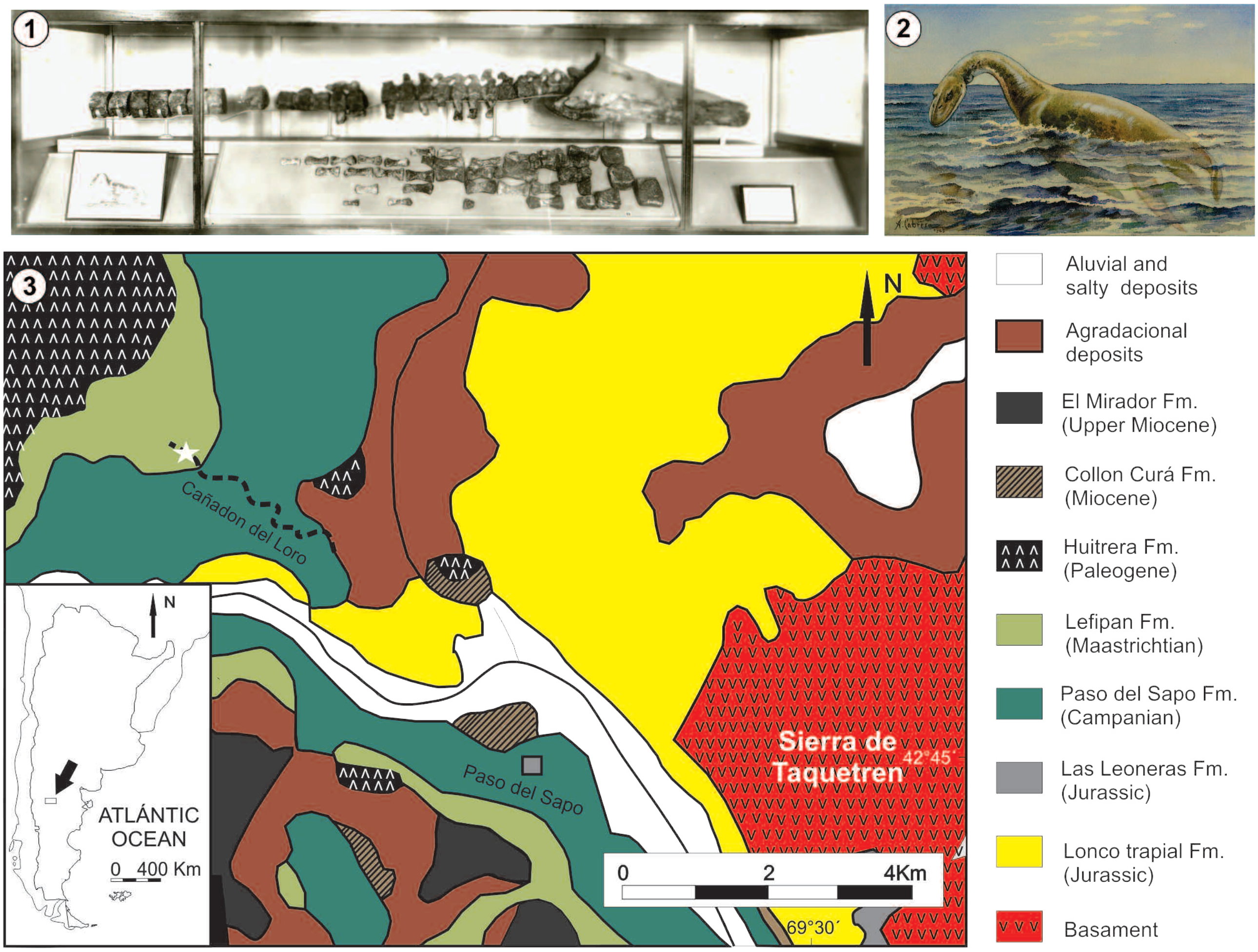


Figure 1. 1, Original display of the holotype; **2,** artistic representation of ***Aristonectes parvidens*** made by Ángel Cabrera; **3,** approximate locality where the **MLP** 40-XI-14-6 (holotype of *A. parvidens*) was collected. Modified from Lizuaín and Silva-Nieto (1996).

Table 1 – Elasmosaurid taxa considered in the quantitative comparison with* Aristonectes parvidens*.

Taxa	*Specimen*	*Locality/stratigraphy*
Thalassomedon haningtoni *Welles, 1943*	*UNSM 50132*	*Baca County, Colorado, USA/ Graneros Shale, lower Cenomanian*
Tuarangisaurus keyesi *Wiffen and Moysley, 1986*	*NZGS, CD 425*	*Mangahouanga Stream, inland Hawke's Bay, New Zealand/ Tahora Fm. Late Campanian-early Maastrichtian*
Callawayasaurus colombiensis *(Welles) Carpenter, 1999*	*UCMP 38349*	*Villa de Leyva, Colombia/Paja Fm. Late Aptian*
Libonectes morgani *Welles,1949*	*SMUSMP 69120*	*Dallas County, Texas, USA/ Britton Fm. Late Cenomanian*
Aristonectes parvidens *Cabrera, 1941*	*MLP 40-XI-14-6*	*Paso del Sapo, Chubut Province, Argentina/Lefipán Fm. Maastrichtian.*
Kaiwhekea katiki *Cruickshank and Fordyce, 2002*	*OU 12649*	*Shag Point, North Otago, New Zealand. Katiki Fm. boundary between early and late Maastrichtian*

Data taken from Cabrera (1941); Welles (1943); Wiffen and Moysley (1986); Carpenter (1999); Cruickshank and Fordyce (2002); Sachs and Kear (2014).

SYSTEMATIC PALEONTOLOGY

Subclass Sauropterygia Owen, 1860
Order Plesiosauria de Blainville, 1835
Superfamily Plesiosauroidea Welles, 1943
Family Elasmosauridae Cope, 1869
Subfamily Aristonectinae O'Keefe and Street, 2009 (*sensu* Otero *et al*., 2012)

Genus ***Aristonectes*** Cabrera, 1941

Type species. *Aristonectes parvidens* Cabrera, 1941.

Emended Diagnosis (modified from Gasparini *et al*., 2003; Otero *et al*., 2014). Aristonectine elasmosaurid with large, at least slightly flattened and broad skull without premaxillary–maxillary constriction, differing from the high skull of *Kaiwhekea katiki*; gracile mandible with very short symphysis; homodont dentition with more than 50 mandibular procumbent alveoli. Anterior and middle cervical vertebrae with low average VLI (~80) though slightly higher than those of *Kaiwhekea katiki*. Additional features, although not found in all of the representative skulls, display differences between *Aristonectes* and *Kaiwhekea*: 13 premaxillary teeth (not preserved in *A. quiriquinensis*) as opposed to the seven premaxillary teeth of *Kaiwhekea* and 50 or more teeth in the maxilla (not found in *A. quiriquinensis*) differing from the 36 teeth recorded in *Kaiwhekea*.

Aristonectes parvidens Cabrera, 1941
Figures 2–4.1, 5–6, 8–9.1–2, 10.1–9, 11.1–8

Type material. MLP 40-XI-14-6, part of a cranium attached to the mandible, atlas-axis complex, anterior and middle cervical vertebrae, anterior caudal vertebrae and one posterior caudal vertebrae, caudal ribs and an incomplete limb (Cabrera, 1941: figs. 1–6; Gasparini *et al*., 2003: figs. 1–3).

Type Locality and Horizon. Cañadón del Loro, middle Chubut River (42° 40" S; 70° 00" W), northwestern Chubut Province, Patagonia, Argentina (Cabrera, 1941); Lefipán Formation, Maastrichtian (Lesta and Ferello, 1972; Page *et al*., 1999).

Diagnosis. *Aristonectes* species with symphyseal lingual groove, mandible higher than in *Aristonectes quiriquinensis*, keel on the dorsal surface of the retroarticular process, short projection of the atlas along the axis rib. Absence of lateral keel independent of the dorsal margin of the parapophysis.

Comments. The specimen MLP 40-XI-14-6 was originally described by Cabrera (1941) and then carefully re-described by Gasparini *et al*. (2003). Herein, only specific features reinterpreted or previously not reported are described and carefully illustrated while discussion and measurements (Tabs. 2–3) are added.

Alveoli. The high number of alveoli in the aristonectine skull has been recorded since the description by Cabrera (1941), who indicated the presence of 15 premaxillary alveoli. Conversely, Gasparini *et al*. (2003) indicated a number of 10 to 13. The difference is due to the diverse interpretations as to where the premaxilla-maxilla suture is located (Fig. 2.6). Careful observation of the specimen and a comparison to *Kaiwhekea katiki* indicate that the most likely number of premaxillary alveoli is 13. As for the number of maxillary teeth, Cabrera (1941) indicated 26 while Gasparini *et al*. (2003) counted 51–53 maxillary alveoli. New observations confirm the presence of 37 clearly visible alveoli and at least another 14 that can be inferred by a sulcus on the counterpart in the

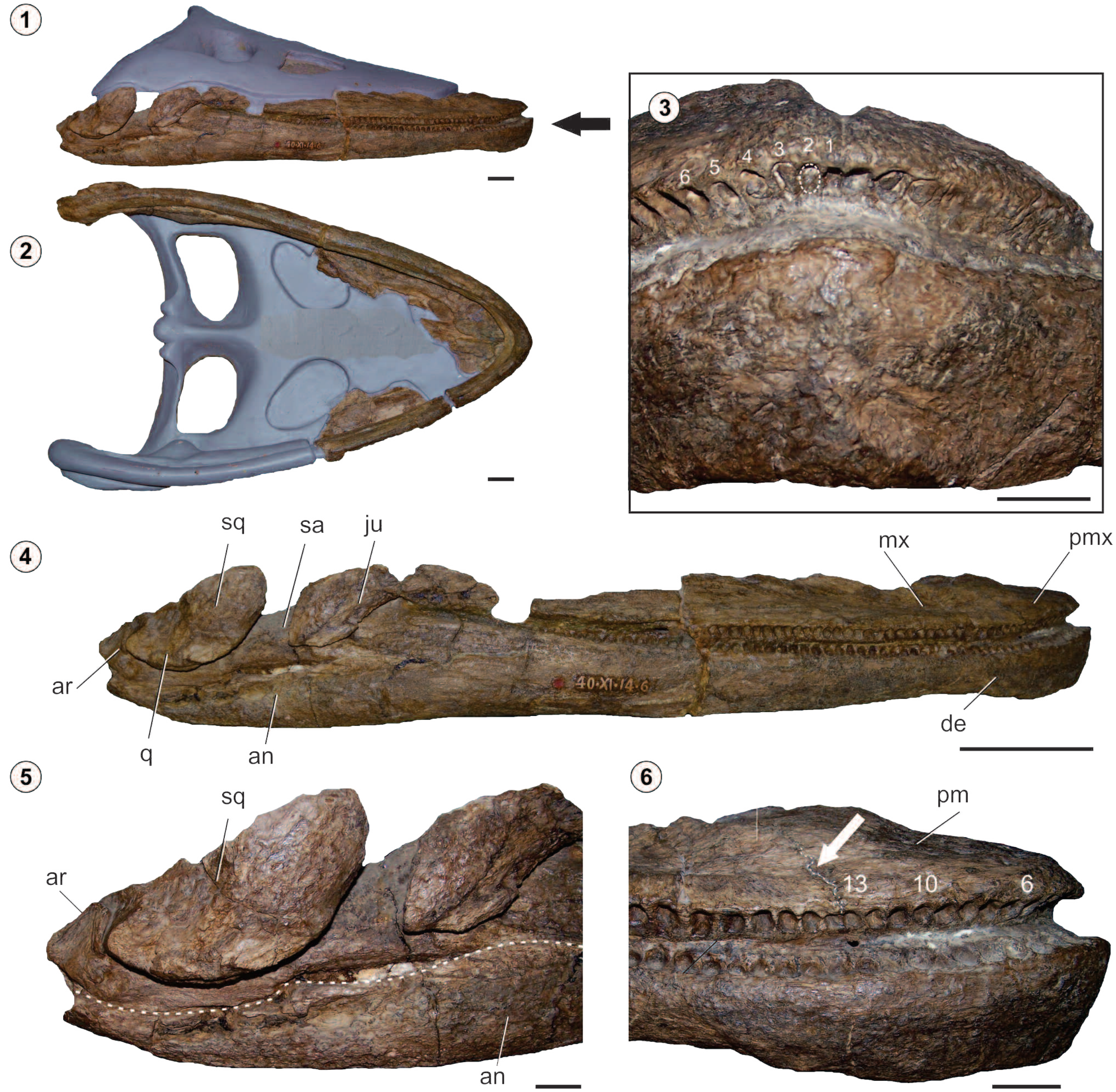


Figure 2. ***Aristonectes parvidens*** holotype, **MLP** 40-XI-14-6; **1–2,** skull with plaster reconstruction in **1,** dorsal and **2,** ventral views; **3,** cranium and mandible in anterior view, dot line indicates alveolar margin and white numbers indicate alveoli position; **4,** cranium and mandible in right lateral view; **5,** posterior part of cranium and mandible, dot line indicate dorsal limit of angular; **6,** anterior part of cranium and mandible in right view showing alveoli disposition, white numbers indicate alveoli position and white arrow and dot line indicate premaxilla-maxilla suture. See anatomical abbreviations section. Scale bars= 40 mm (**1, 2**); 20 mm (**3, 5, 6**); 100 mm (**4**).

Table 2* – Aristonectes parvidens *MLP 40-XI-14-6, cranium and mandible measurements (in mm).

Measurement	***value***
cranial length	*~600*
pre-glenoid length	*674*
premaxilla anteroposteriorly length	*74*
premaxilla transversely length	*135*
symphysis anteroposterior length	*45.33*
mandible height at coronoid process level	*124*
coronoid-symphysis distance	*534*

~ indicates approximate measurements

Table 3* – Aristonectes parvidens *MLP 40-XI-14-6 vertebral measurements (in mm).

Cervical vertebrae	***L***	***H***	***B***	***HI***	***BI***	***BHI***	***VLI***
1+2	*82*	*43*	*56*	*52*	*68*	*130*	*-*
3	*40*	*45*	*58*	*113*	*145*	*129*	*78*
4	*44*	*49*	*60*	*111*	*136*	*122*	*81*
5	*46*	*51*	*69*	*111*	*150*	*135*	*77*
6	*49*	*55*	*70*	*112*	*143*	*127*	*78*
7	*52*	*50*	*68*	*96*	*131*	*136*	*88*
8	*51*	*55*	*75*	*108*	*147*	*136*	*78*
9	*52*	*55*	*71*	*106*	*137*	*129*	*83*
10	*52*	*54*	*72*	*104*	*138*	*133*	*83*
11	*55*	*55*	*78*	*100*	*142*	*142*	*83*
12	*56*	*56*	*87*	*100*	*155*	*155*	*78*
13	*56*	*60*	*91*	*107*	*163*	*152*	*74*
14	*56*	*57*	*86*	*102*	*154*	*151*	*78*
15	*55*	*60*	*90*	*109*	*164*	*150*	*73*
16	*68*	*68*	*95*	*100*	*140*	*140*	*83*
17	*58*	*62*	*99*	*107*	*171*	*160*	*72*
18	*63*	*62*	*97*	*98*	*154*	*156*	*79*
19	*63*	*64*	*99*	*102*	*157*	*155*	*77*
Caudal vertebrae							
1	*71*	*-*	*-*	*-*	*-*	*-*	*-*
2	*70*	*110*	*121*	*157*	*173*	*110*	*61*
3	*70*	*99*	*121*	*141*	*173*	*122*	*64*
4	*63*	*-*	*-*	*-*	*-*	*-*	*-*
5	*58*	*97*	*116*	*167*	*200*	*120*	*54*
6	*66*	*89*	*118*	*135*	*179*	*133*	*64*
7	*61*	*91*	*121*	*149*	*198*	*133*	*58*
8	*65*	*91*	*127*	*140*	*195*	*140*	*60*
9	*55*	*77*	*98*	*140*	*178*	*127*	*63*

***Abbreviations: B**, breadth index; **BHI,** B/H ratio (BHI=100*B/H); **BI,** B/L ratio (BI=100*B/L); **H**, height index; **HI,** H/L ratio (HI=100*H/L); **L,** length index; **VLI**, vertebral length index [VLI= 100*L / (0.5*(H + B))].*

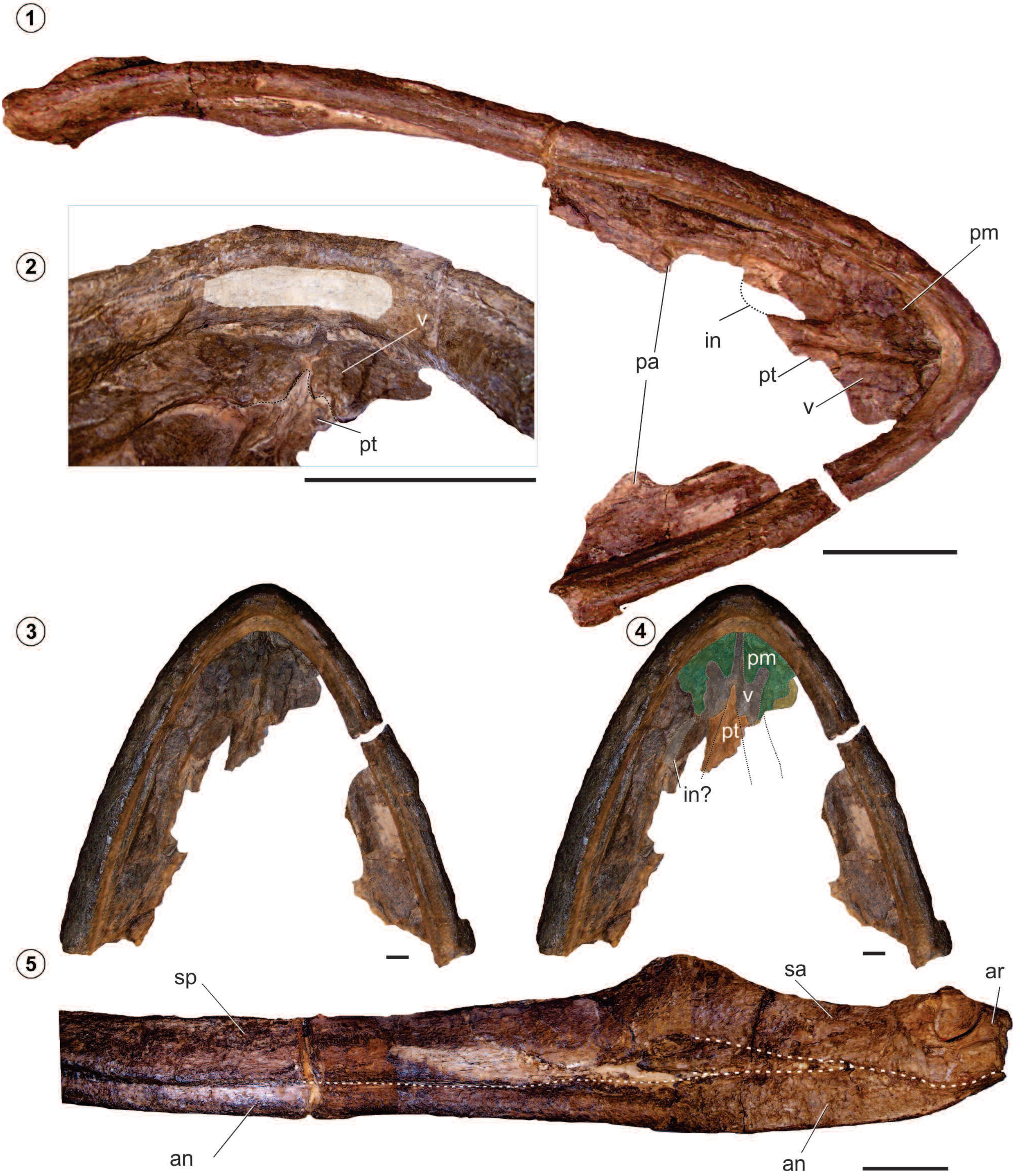


Figure 3. ***Aristonectes parvidens*** holotype, **MLP** 40-XI-14-6; **1,** cranium and mandible in ventral view; **2,** mandibular symphysis in posterior view, showing in grey the "deep groove" of Otero *et al.* (2014); **3–4,** anterior palate **3,** photo and **4,** interpretative drawing; **5,** medial view of the middle and posterior part of the right mandible. See anatomical abbreviations section. Scale bars= 1000 mm (**1**); 20 mm (**2–4**); 50 mm (**5**).

lower jaw. Therefore, the presence of at least 51 maxillary alveoli can be upheld. Cabrera (1941) indicated the presence of 58 mandibular teeth while 60–65 mandible alveoli were observed by Gasparini *et al*. (2003). This revision of the specimen indicates that the number is probably at least 63, but uncertainty remains as the number could actually be between 63 and 65. Additionally, the lateral inclination of the alveolar series is confirmed (Fig. 2.3–4, 6). Such feature was mentioned by Gasparini *et al*. (2003) and recently observed in *Aristonectes quiriquinensis* but difficult to determine in *Kaiwhekea* (Otero *et al*., 2014; J.P. O'Gorman. pers. obs.).

Internal naris. Gasparini *et al*. (2003: fig. 3D) did not attempt to identify elements that limit the internal naris other than the vomer and the maxilla. O'Gorman (2013) only mentioned the elements that could participate: vomer, maxilla and palatine. However, no attempt at a detailed reconstruction or discussion was made. The preserved elements of the anterior part of the palate are: premaxilla, anterior half of the vomer, maxilla, palatine and a previously not mentioned anterior part of the pterygoids. One of the problems related to the anterior structure of the palate is, as understood by Gasparini *et al*. (2003: fig. 3D), that the suture between the vomer and premaxilla seems to be asymmetrical. However, careful observation reveals that the probable suture is located as shown in Figure 3.3–4. Unfortunately, the posterior border of the naris is not preserved (although a posterior bone wall is preserved, it is not clear whether it is natural). A comparison between *Aristonectes parvidens* and a non-aristonectine elasmosaurid such as *Libonectes morgani* (Welles, 1949) (Fig. 5.5) indicates that the vomer of *A. parvidens* has two lateral depressions. These limit the vomeronasal fenestra recorded by Gasparini *et al*. (2003), thus resulting in a premaxilla-vomer suture with the premaxilla presenting the "M" shape mentioned by Gasparini *et al*. (2003) and a long anterior process (Fig. 3.3–4). Both these features are absent in other elasmosaurids (Carpenter, 1997: fig. 2D; Sato *et al*., 2006: fig. 4C; Vincent *et al*., 2011: fig. 2E; Fig. 5.6). The posteriormost part of the vomer presents an open suture between both lateral vomeral elements (Fig. 3.1, 3–4), which are usually fused or display a strong suture in adults (Carpenter, 1997; Sato *et al*., 2006). This open suture is congruent with the only other palate known from an aristonectine (Chatterjee and Small, 1989: fig. 4), where the vomers are only anteriorly and medially fused though posteriorly exhibiting a wide intervomerial space generated by the absence of a medial suture. If the vomer of *Aristonectes* presents a parallel morphology, the vomer had to expand laterally and generate a relatively small and anteroposteriorly long internal naris (Fig. 3.4). This reconstruction, which differs from the morphology inferred by O'Gorman (2013), is more consistent with the morphology observed in other elasmosaurids (Carpenter, 1997). The probable dorsal overlapping of a medial element that projects dorsally to the vomer is another interesting feature of the *Aristonectes parvidens* holotype. This element was interpreted as part of the vomer by both Gasparini *et al*. (2003) and O'Gorman (2013). However, careful observation reveals a possible suture between both elements and, hence, the dorsal and posterior elements could not be part of the vomer (Fig. 3.1–2). Judging by its medial position, this element is possibly the anteriormost part of the pterygoid that overlaps with part of the vomer dorsally and is visible in palatal view due to the absence of the posterior part of the vomer.

Mandibular symphysis. The mandibular symphysis of MLP 40-XI-14-6 is short and bears a depression on its internal surface (Fig. 3.2), mentioned by Otero *et al*. (2014) as a "deep groove". The ventral side of the symphysis does not exhibit the mental boss observed by Otero *et al*. (2014) in the symphysis of *Aristonectes quiriquinensis* (Figs. 3.1, 4.1). However, the mandible surface of the holotype of *A. parvidens* has suffered the loss of the external layer of bone and, therefore, it is possible that at least weak mental spines were originally present. This is plausible because the mental spines of *A. quiriquinensis* are located on the lateral margins of a wide symphyseal sulcus present in *A. parvidens* (Fig. 4.1). Comparison between the ventral surface of the symphysis of *A. parvidens* and that of non-aristonectine elasmosaurids (Fig. 4.1–4) suggests that they share the symphyseal sulcus. Nevertheless, the ventral surface of *A. parvidens* is much wider, following the general widening of the symphysis. Another interesting feature of the symphysis is the reduced symphyseal post alveolar surface similar to that observed in *A. quiriquinensis* but different from that of other elasmosaurids (Carpenter, 1997: fig. 2E). All of these data corroborate the observations of Gasparini *et al*. (2003) and Otero *et al*. (2014) about the presence of a relatively weak symphysis compared to that of non-aristonectine elasmosaurids (Fig. 5.1–2).

Figure 4. 1–4, Mandibular symphysis of elasmosaurids in ventral view. **1,** ***Aristonectes parvidens*****, MLP** 40-XI-14-6, double arrow indicates the wide symphyseal sulcus. **2,** ***Tuarangisaurus keyesi*****, NZGS CD** 425. **3,** ***Callawayasaurus colombiensis*****, UCMP** 38349. **4,** LACM **(CIT)** 2749, referred to ***Morenosaurus stocki*** Welles, 1943, arrow indicates symphyseal sulcus. **5–6,** ***Aristonectes parvidens*****, MLP** 40-XI-14-6, quadrate and glenoid cavity, dotted in green area indicate the quadrate. See anatomical abbreviations section. Scale bars= 20 mm.

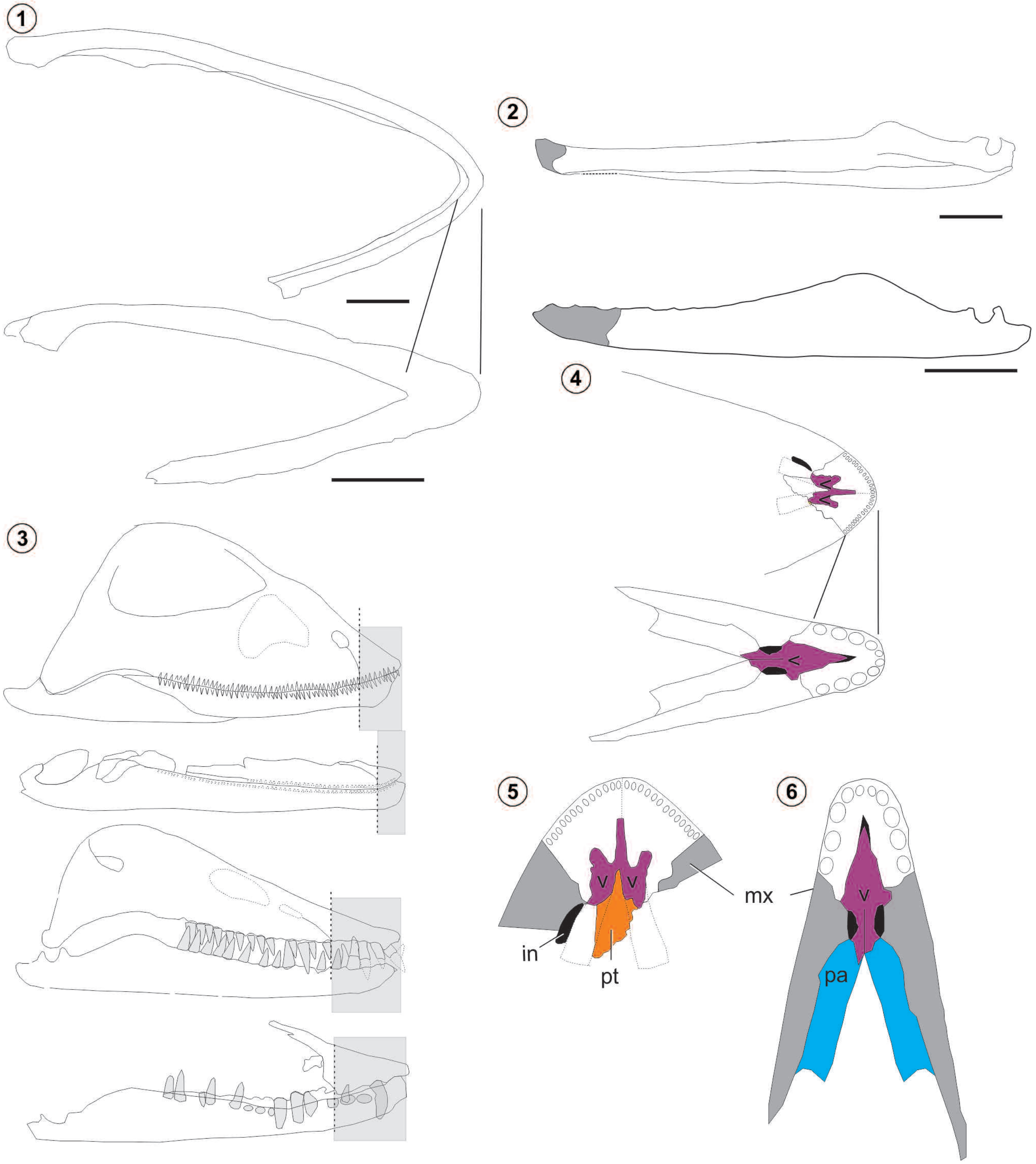


Figure 5. ***Aristonectes parvidens***, **MLP** 40-XI-14-6, comparative cranial and mandibular proportions and palatal structure. **1,** relative symphyseal length in ventral view: ***Aristonectes parvidens*** (top), ***Libonectes morgani***, **SMU SMO** 69120 (bottom). **2,** relative symphyseal length in medial view: ***Aristonectes parvidens*** (top), ***Libonectes morgani***, **SMU SMO** 69120 (bottom). **3,** comparison of premaxilla anteroposterior extension in lateral view (from top to botton): ***Kaiwhekea katiki***, **OU** 12649, ***Aristonectes parvidens***, ***Libonectes morgani***, **SMU SMO** 69120, ***Terminonatator ponteixensis*** Sato, 2003, **RSM** P2414.1. **4,** relative premaxillar length in palatal view: ***Aristonectes parvidens*** (top), ***Libonectes morgani***, **SMU SMO** 69120 (bottom). **5–6,** palatal structures of **5,** ***Aristonectes parvidens***, **MLP** 40-XI-14-6, and **6,** ***Libonectes morgani***, **SMU SMO** 69120. **1, 2, 3, 4,** in part modified from Carpenter (1997), 3, modified from Cruickshank and Fordyce (2002) and in part modified from Sato (2003). Scale bars = 100 m (**1–2**), not in scale (**3–6**).

Glenoid cavity, retroarticular process and coronoid process. Only the right glenoid cavity and the proximal part of the retroarticular process are preserved. The glenoid cavity is deep (42 mm anteroposterior length in dorsal view; 32 mm dorsoventral length) and strongly posteromedially directed (Fig. 4.5–6). As Otero *et al.* (2014) mentioned, a marked keel projects from the tip of the reotroarticular process to the posterior limit of the glenoid cavity (Fig. 4.5–6). The medial view of the right mandible (Fig. 3.5) shows a relatively high and rounded coronoid process. Additionally, it can be observed that the suture between the angular, surangular and splenial remains open (Figs. 2.5, 3.5).

Atlas-axis complex. The atlas axis complex was carefully described by Gasparini *et al.* (2003). The description focused on the elements that formed it and their distribution. Herein, other features that seem distinctive among elasmosaurids are recorded and illustrated. Three main features of the atlas-axis of *Aristonectes parvidens* are: the presence of open sutures, the absence of a developed ventral keel and the circular anterior atlantal cup. The presence of open sutures is quite interesting given the fact that sutures are usually fully closed in the atlas-axis of adult elasmosaurids (Wiffen and Moisley, 1986; Carpenter, 1999; Kubo *et al.*, 2012; Sachs and Kear, 2014; O'Gorman *et al.*, 2015). Admittedly, part of this phenomenon could be consequence of the preparation process it underwent. However, probably is related to some difference in the relative time of suture closure among elasmosaurids, suggesting that the open sutures are, at least, a partially natural feature (Fig. 8.1–2). Secondly, the absence of a developed ventral keel (Fig. 8.5), although atypical among elasmosaurids (Welles, 1943; Kubo *et al.*, 2012; Sachs and Kear, 2014; O'Gorman *et al.*, 2015), seems to be a feature shared with *Tuarangisaurus keyesi* Wiffen and Moisley, 1986. Finally, the presence of a circular atlantal cup is also a feature unusual among elasmosaurids, which usually present higher than broad atlantal cups (Fig. 9), is yet another significant trait. Another feature recorded for the atlas-axis of *A. parvidens* is the absence of ventral foramina (Fig. 8.5) typically present in elasmosaurids (Sachs and Kear, 2014; O'Gorman *et al.*, 2015). Also, the postzygapophysis of the axis appears to be ventrally projected in the figure of Cabrera (1941: fig. 2B) and Gasparini *et al.* (2003: figs. 2A, 3E). Detailed observation revealed that the observed "ventral projection" (Fig. 8.1–2, 6) is partly a

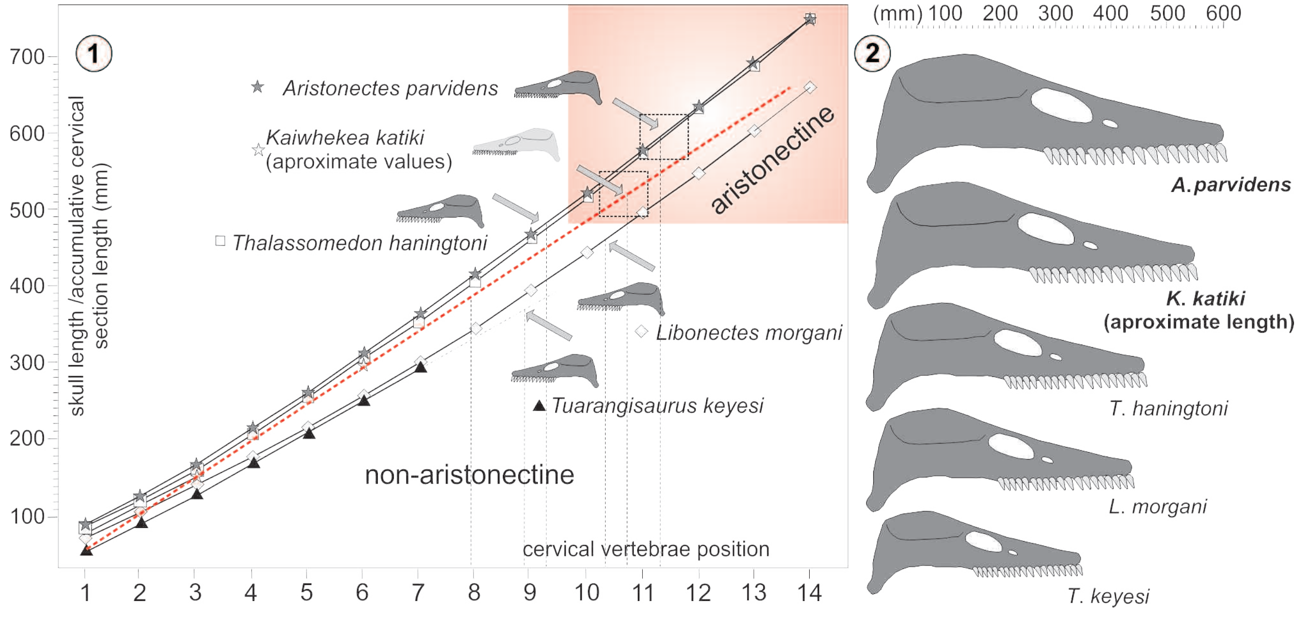


Figure 6. Cranial and cervical feature of ***Aristonectes parvidens*** and other elasmosaurids. **1,** Relation between the cranium length and the accumulative cervical length, dot line indicates approximate values. **2,** cranium lengths. Data taken from Welles (1943, 1952); Wiffen and Moysley (1986); Cruickshank and Fordyce (2002); Pers. Obs.

prezygapophysis of the third vertebra which remains attached to the postzygapophysis of the atlas-axis complex and, therefore, is not a natural feature. The posterolateral process of the atlas, although probably not as long as that recorded for *Aristonectes quiriquinensis* (Otero *et al*., 2014), seems to be broken in its distalmost part (Fig. 8.4).

Cervical vertebrae 3th–19th. The holotype preserves a cervical series that belongs to the anterior part of the neck (Fig. 10.1–4, 9). Such vertebrae were described by Gasparini *et al*. (2003); nevertheless, the matter of the lateral keel calls for some clarification. In the original description, Cabrera (1941) did not record or include figures of any lateral keel in the cervical vertebrae of the holotype (Cabrera, 1941: figs. 3–4). Gasparini *et al*. (2003) later described "scarcely visible lateral crests that can occur only on a single side". The present revision indicates that the only constant convexity observed in the cervical vertebrae of MLP 40-XI-14-6 is a distinctive convex area located above the parapophysis (Fig. 10.2, 8). This convexity is evident in the specimen because the cervical ribs are displaced. Therefore no well-developed lateral keels independent of the dorsal margin of the parapophyses are present in *Aristonectes parvidens*. Another possibility, unfortunately beyond testing, is that a faint lateral ridge was erased during the original preparation.

Caudal centra. Although Cabrera (1941) indicated that only two caudal vertebrae were preserved, he misidentified eight caudal vertebrae as posterior cervicals and was later corrected by Gasparini *et al*. (2003) (Fig. 11.1–4). Cabrera did not mention any ventral foramina in his "posterior cervicals" (=caudals) and neither did Gasparini *et al*. (2003). Additional preparation shows the presence of at least five ventral foramina in one vertebra (Fig. 11.3). Considering that one vertebral foramen (or two in anteriormost caudals) is the most frequent number of foramina among elasmosaurids (Benson and Druckenmiller, 2014), the fact that the presence of five large and well defined ventral foramina has been recorded only in the specimen considered here seems all the more remarkable. Other interesting features of the caudal centra are their proportions. Figure 11.9 compares the HI and BI indexes of the caudal vertebrae of MLP 40-XI-14-6 and non-aristonectine elasmosaurids. The comparison reveals that the caudals of MLP 40-XI-14-6 display relatively high HI and BI indexes.

Caudal ribs. Probably because they were wrongly identified, no caudal ribs were described by Cabrera (1941). Gasparini *et al*. (2003) failed to mention them as well. However, in the material, there are several damaged caudal ribs similar to the ones of other elasmosaurid (J.P. O'Gorman per. obs.) but exhibiting a slightly larger proximal expansion in the capitulum (Fig. 11.5–6) related to the large parapophyses of the caudal vertebrae (Fig. 11.2).

Limb. The only preserved limb elements of MLP 40-XI-14-6 were reconstructed by Cabrera (1941) as part of a single

Table 4 – Number of dentary alveoli, cranium length, and ratio between both values and the predicted number of aristonectine alveoli number based on a non elasmosaurid mandible sizes. Values are in mm.

Taxon	*Al*	*Cl*	*AR*	*Predicted alveoli number*	
				Aristonectes *(63-65)*	**Kaiwhekea** *(42-44)*
Callawayasaurus *(UCMP 38349)*	*20*	*350*	*0.05714*	*34*	*30*
Thalassomedon *(UNSM 50132)*	*17*	*480*	*0.03541*	*21*	*18*
Tuarangisaurus (*NZGS*, CD 425)	*19–21*	*370*	*0.05405*	*32*	*28*
Libonectes *(SMUSMP 69120)*	*18*	*466*	*0.03862*	*23*	*20*
Aristonectes *(MLP 40-XI-14-6)*	*63–65*	*~600*	*0.10416*		
Kaiwhekea *(OU 12649)*	*42–44*	*520*	*0.08269*		

Abbreviations: Al, *dentary alveoli;* ***Cl,*** *skull length;* ***AR,*** *ratio between both SL and AL. ~ indicates approximate measurements. For calculation* Tuarangisaurus *(20 alveoli);* Aristonectes *(64 alveoli) and* Kaiwhekea *(43 alveoli) were considered. Data taken from Welles (1943, 1962); Wiffen and Moisley (1986); Carpenter (1999); Cruickshank and Fordyce (2002); Sato (2002); J.P.O'Gorman. pers. obs.*

TABLE 5 – Ratio between cranium length and atlas-axis length in aristonectine and non-aristonectine elasmosaurids.

Taxon	*Craniaum length (mm)*	*Atlas-axis complex length (mm)*	*Radio skull length/atlas-axis length*
Thalassomedon haningtoni (UNSM 50132)	*480*	*77*	*6.23*
Tuarangisaurus keyesi (NZGS CD 425)	*370*	*55*	*6.72*
Libonectes morgani (SMUSMP 69120)	*466*	*60.3*	*7.72*
Aristonectes parvidens (MLP 40-XI-14-6)	*~600*	*82*	*7.31*

~indicates approximate measurements. Data taken from Welles (1943, 1962); Wiffen and Moisley (1986); Carpenter (1999); J.P.O'Gorman pers. obs.

paddle for which, he stated, there was no certainty that all the elements actually belonged to the same limb. Therefore, the dimensions are not adequate to calculate aspect ratios. The proximal limb elements were arranged in different ways by different authors. Figures 11.7 and 11.8 illustrate the original interpretation of Cabrera (1941) and the ones of O'Gorman (2013) and Otero *et al*. (2014) respectively. In this contribution the latter interpretation is followed.

CALCULATIONS

Correlation between mandibular alveoli and cranium length. Table 4 shows the cranial lengths of six elasmosaurids and alveolar rate. For calculation, *Tuarangisaurus* (20 alveoli), *Aristonectes* (64 alveoli) and *Kaiwhekea* (43 alveoli) were considered. The last column of the table "predicts" the alveoli number of a non-aristonectine elasmosaurid if it presents an aristonectine-like cranium size=[(non-aristonectine mandibular alveoli number/non-aristonectine cranium length)*aristonectine cranium length]. This column shows that the increase in length of the skull of aristonectines only partially "explains" the increase in the number of alveoli (between 21 and 34 for *Aristonectes parvidens* and 18 and 30 for *Kaiwhekea katiki*).

Alveoli size. In order to test the hypothesis of the relatively small alveoli of *Aristonectes parvidens* compared with non-aristonectine elasmosaurids, the meso-distal (see Fig. 7.1) measurements of the alveoli of MLP 40-XI-14-6 were recorded and then plotted in Figure 7.2–3. Additionally, Figure 7.2–3 illustrates the alveoli size of *Tuarangisaurus keyesi*, a non-aristonectine elasmosaurid from the Campanian–Maastrichtian of New Zealand, in order to compare the measurements with those of *Aristonectes parvidens*. The comparison of both alveolar series lays bare a marked difference in the mesodistal length of the alveoli.

Skull/neck proportion. Table 5 depicts the ratio between the cranium length and the atlas-axis complex length. It indicates that the values for *Aristonectes* fall within the range of values calculated for other elasmosaurids.

DISCUSSION

Alveoli number and size. The recognition of affinities between aristonectines and elasmosaurids raised the question about how the former achieved classically distinctive features of elamosaurids such as the relatively large skull, high number of alveoli and short neck. The question about how an elasmosaurid skull could accommodate such increase in the number of alveoli is a relevant issue that has not been previously discussed. The number of alveoli among non-aristonectine elasmosaurids has been largely recognised to be lower than that of the aristonectines. Furthermore, the same is true for skull length (Tab. 4). However, no attempt to look for some correlation between skull size and alveoli number was previously undertaken and, therefore, whether the increase in alveoli number is a direct effect of the increase in cranial length and the retention of teeth size or whether other factors are involved was not discussed. In order to test this, two analyses were carried out (see calculations and Table 4). Table 4 shows that the increase in length of the skull of aristonectines only partially "explains" the rise in the number of alveoli. Therefore, the elevated number of alveoli is only somewhat explained by the enlargement of the skull compared with non-aristonectine elasmosaurids.

The previous result indicates that other features, such as the small size of the alveoli and the absence of large interalveolar spaces and/or diastemata, generate the space for the additional alveoli. The comparison of the alveolar series of *Tuarangisaurus* and *Aristonectes* (Fig. 7) brings to light a marked difference in the size of the alveoli which can be considered the second feature that enables the accommodation of such high alveolar concentration. Therefore, the former two features together with the small interalveolear spaces (between 1–2 mm), the ogival shape that increases the cranial and mandibular alveolar margin, and the absence of diastema generate such difference in the alveolar count when compared to that of non-aristonectine elasmosaurids.

Vomer-pterygoid contact. The position of the anteriormost end of the pterygoid, overlapping the vomer, has not been previously recorded for elasmosaurids. However, dorsal

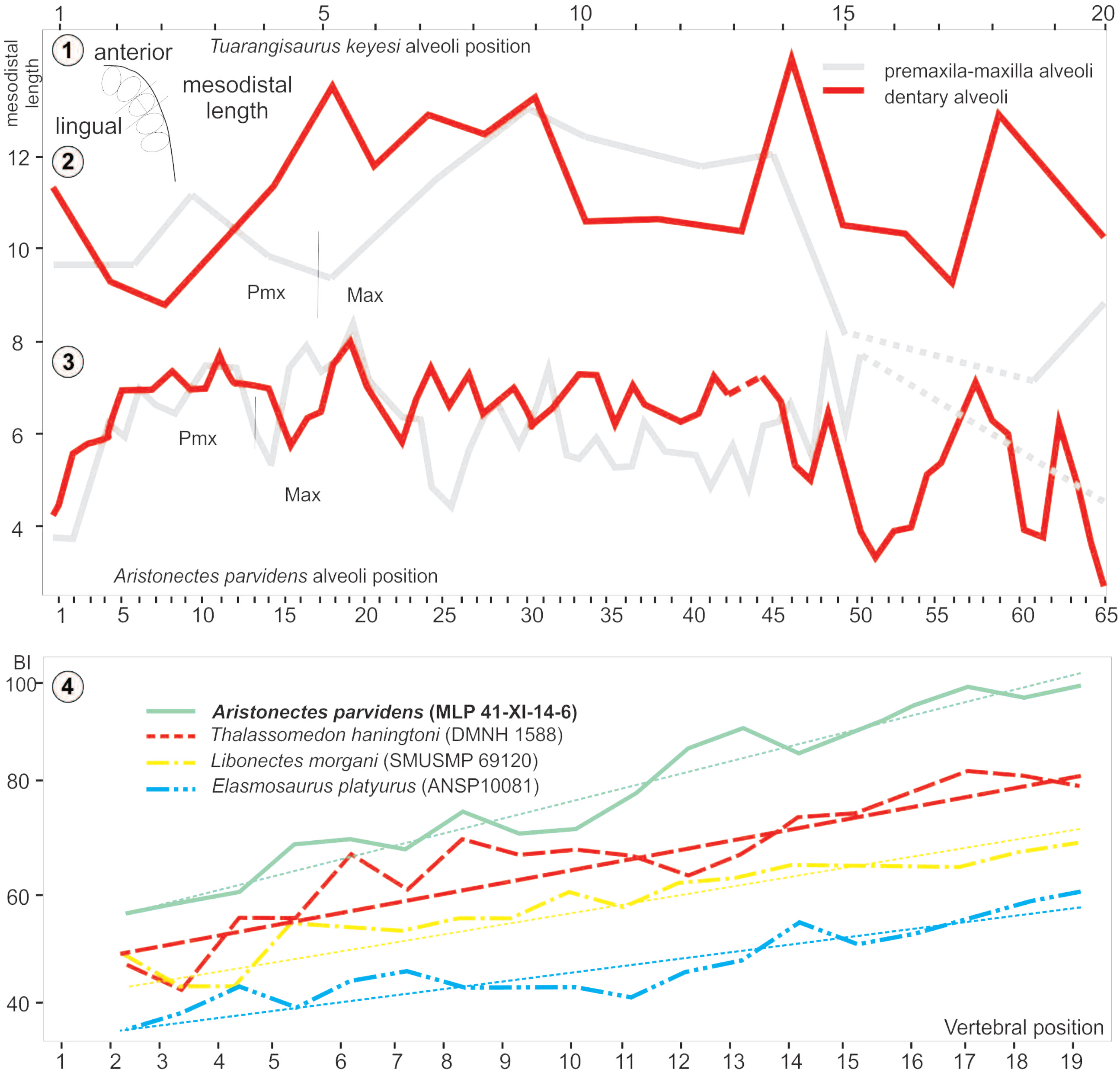


Figure 7. 1, Scheme indicating the measured mesodistal length of the alveoli; **2–3,** alveolar mesodistal length of **2,** ***Tuarangisaurus keyesi***, **NZGS CD** 425 and 3, ***Aristonectes parvidens***, **MLP** 40-XI-14-6; **4,** BI measurement of the anterior cervical centra of ***A. parvidens*** and three non-aristonectine elasmosaurids. See anatomical abbreviations section. Data taken from Welles (1943, 1952).

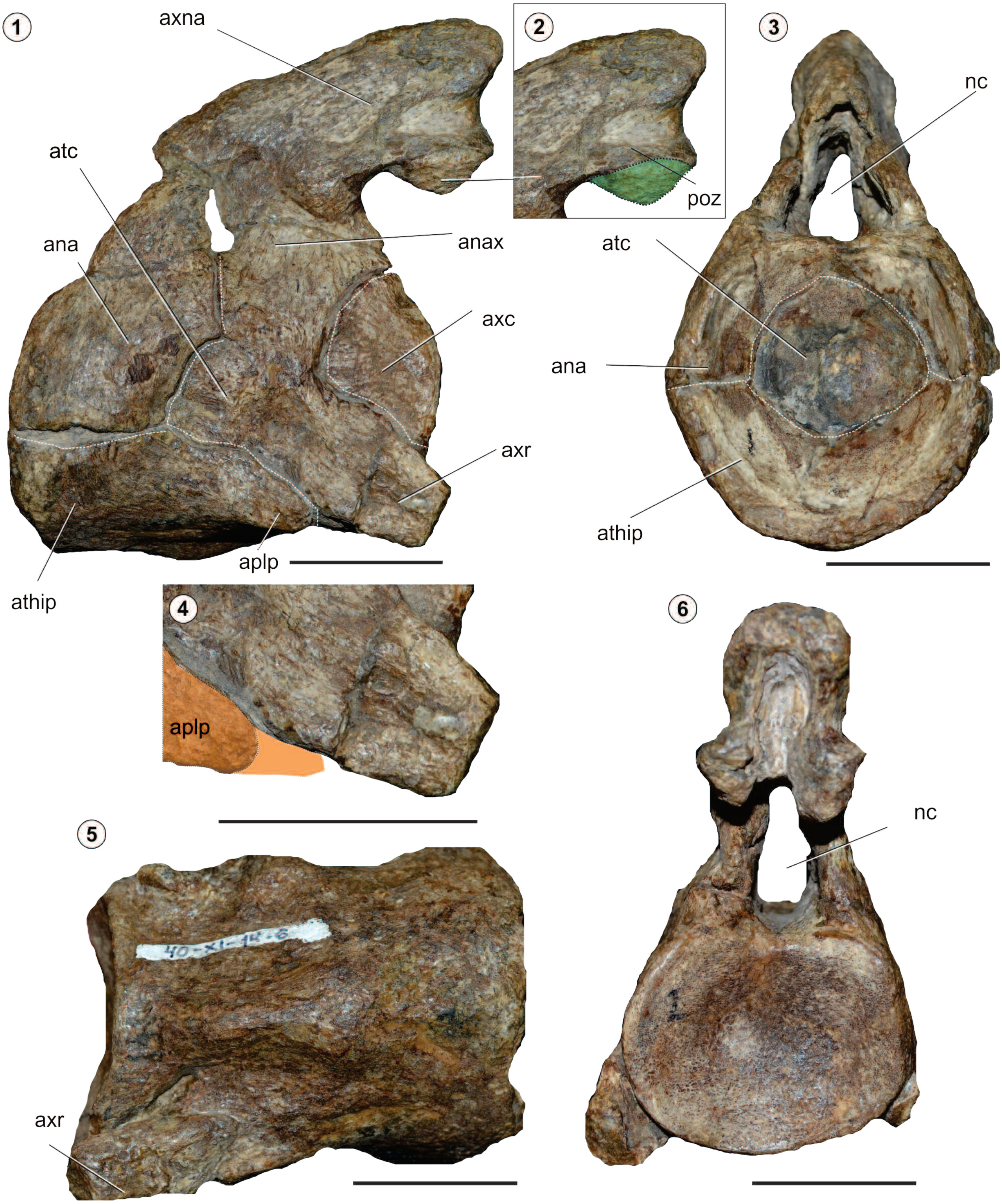


Figure 8. ***Aristonectes parvidens*** holotype, **MLP** 40-XI-14-6. **1–4,** Atlas-axis complex in **1,** left lateral view, **2,** detail of axis neural spine, **3,** anterior view, **4,** axis rib, **5,** ventral and **6,** posterior views. See anatomical abbreviations section. Scale bars= 20 mm.

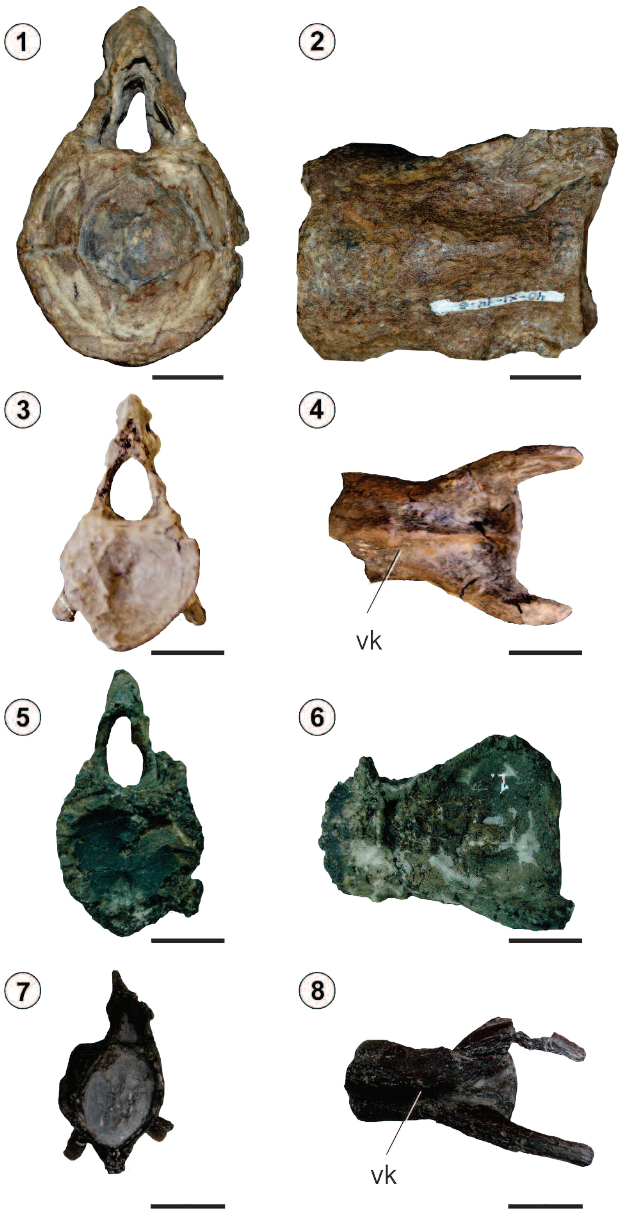
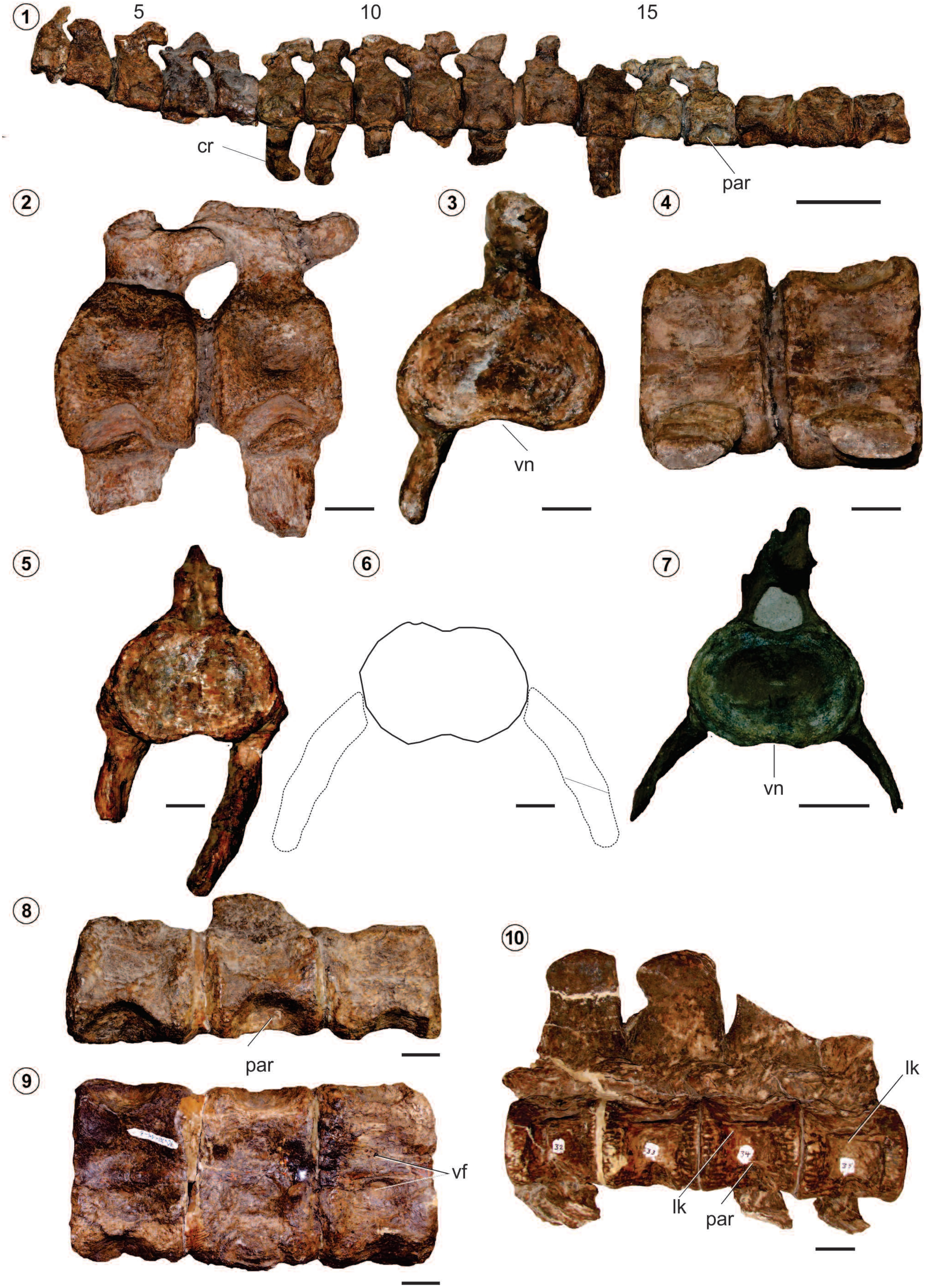


Figure 9. Atlas-axis complex of elasmosaurids. **1–2,** ***Aristonectes parvidens***, MLP 40-XI-14-6, **1,** anterior and **2,** ventral views; **3–4,** ***Vegasaurus molyi***, MLP 93-I-5-1, **3,** anterior and **4,** ventral views; **5–6,** ***Tuarangisaurus keyesi***, NZGS, CD 426, **5,** anterior and **6,** ventral views; **7–8,** ***Albertonectes vanderveldei***, TMP 2007.011.0001, **7,** anterior and **8,** ventral views. See anatomical abbreviations section. Scale bars= 20 mm.

views of articulated specimens of pterygoids and vomer has not been described among elasmosaurids because they are often covered by other elements. Therefore, this particular type of pterygoid-vomer contact could have a broader distribution than currently known. A similar condition was discussed by Schumacher (2008: fig. 2B) and Schumacher *et al.* (2013) for other plesiosaurs such as *Megacephalosaurus eulerti* Schumacher, Carpenter and Everhart, 2013, and *Dolichorhynchops osborni* Williston, 1903. The notion that this is a widespread feature among Plesiosauria was pointed out because, as mentioned by Schumacher (2008) and Schumacher *et al.* (2013), the common two-dimensional observation in palate view does not deny the possibility of an overlapping of the vomer with anterior extensions of the pterygoids in different plesiosaur taxa. The presence of this feature in the elasmosaurid *Aristonectes parvidens*, a highly derived elasmosaurid, reinforces the idea that this could be a frequent feature among Plesiosauria.

Cranial proportions. Skull proportions of *Aristonectes* spp. have been previously described as low and ogival-shaped. This is partially produced by the increase in transverse width near the rostrum and mandibular symphysis. Additionally, the holotype of *A. parvidens* exhibits yet another interesting feature which was not previously mentioned and is shared with *Kaiwhekea*: the low ratio between the premaxilla and maxilla anteroposterior length. Such trait becomes evident when the cranial proportions of aristonectines are compared to those of non-aristonectines (Fig. 5.3). The same proportions are observed in palatal view (Fig. 5.4). Therefore, the relatively shorter premaxilla appears to be a feature of the aristonectines. Additionally, a short mandibular symphysis known since the original description of Cabrera (1941; Fig. 5.1–2) is also present. It is interesting that both the anteroposterior length of the premaxilla and the length of the symphysis present a shortening. The functional reason for this correlation is currently unknown.

Figure 10. 1–6, 8–9, ***Aristonectes parvidens***, MLP 40-XI-14-6; **7,** ***Vegasaurus molyi***, MLP 93-I-5-1; **10,** ***Afphrosaurus furlongi***, LACM(CIT) 2748. **1,** sequence composed by 3th to 19th cervical vertebrae; **2,** 11th–12th cervical vertebrae in left lateral view; **3,** 11th vertebrae in anterior view; **4,** 11th–12th vertebrae in ventral view; **5–6,** 9th cervical vertebrae in **5,** anterior view and **6,** reconstruction of cervical ribs in the 9th cervical vertebrae. **7,** 10th cervical vertebrae in posterior view. **8–9,** 17th–19th cervical vertebrae in **8,** left lateral and **9,** ventral view. **10,** cervical vertebrae in left lateral view. See anatomical abbreviations section. Scale bars= 20 mm.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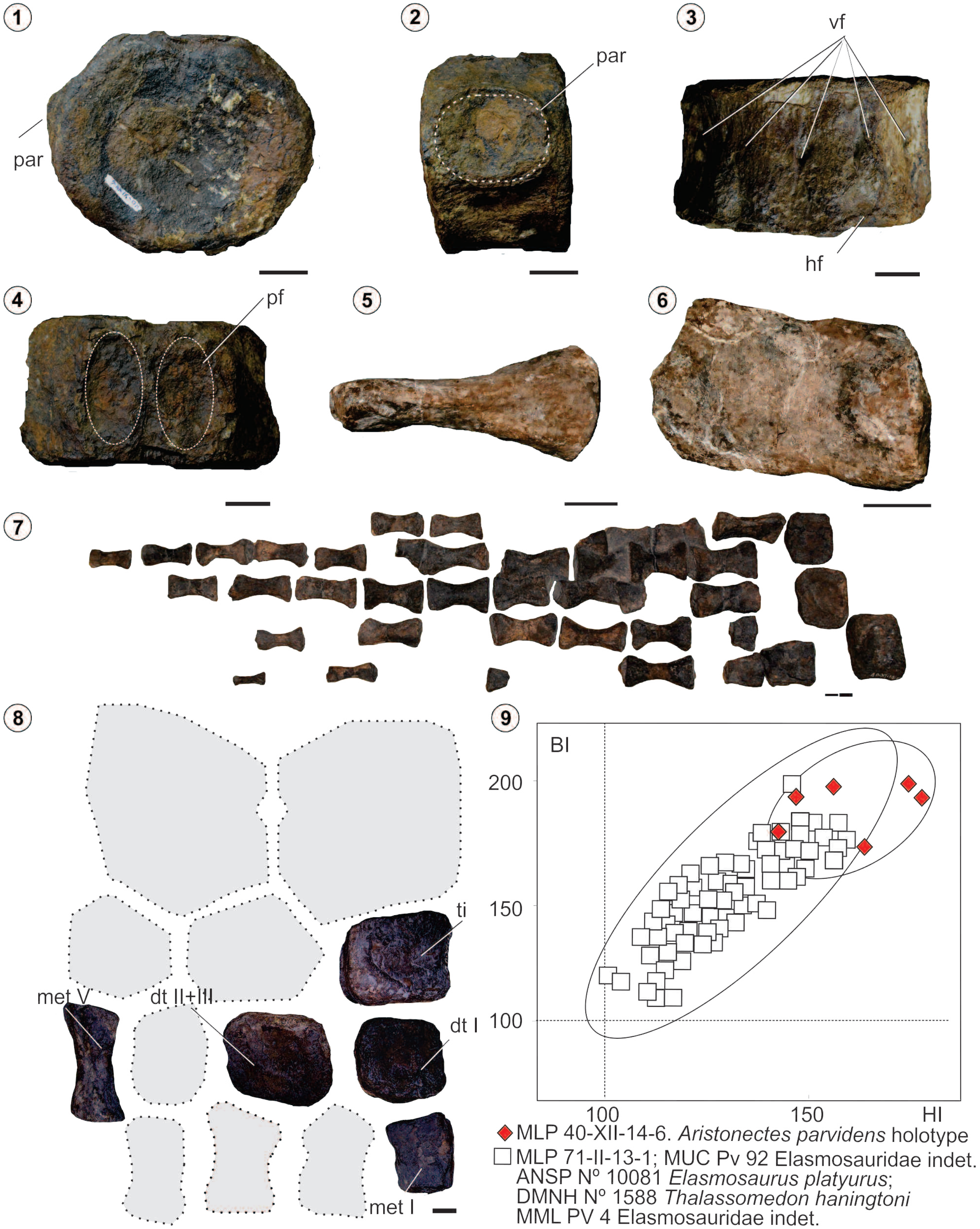

Figure 11. ***Aristonectes parvidens*** holotype, **MLP** 40-XI-14-6; **1–4,** caudal centra in **1,** anterior, **2,** left lateral, **3,** ventral and **4,** dorsal views; **5–6,** caudal rib in **5,** posterior? and **6,** dorsal? views; **7–8,** posterior? limb **7,** original display and **8,** reconstruction of the position of the proximal elements; **9,** plot of the HI and BI index of the caudal vertebrae of **MLP** 40-XI-14-6 and some non-aristonectine elasmosaurids. See anatomical abbreviations section. Scale bars= 40 mm.

Large cranium or large body?: skull/cervical vertebrae proportions. The large skull is another feature that was also initially mentioned by Cabrera (1941) for *Aristonectes parvidens.* It is clear that, among the distinctive small skulled elasmosaurids, aristonectines *Aristonectes parvidens*, *Aristonectes quiriquinensis* and *Kaiwhekea katiki* stand out for presenting large skulls (Fig. 6). However, the relationship between skull size and vertebral length has not been previously considered. Figure 6.1 indicates that the skull is as long as the sum of the lengths of the first 11 to 12 cervical vertebrae. Similar values are recorded for *Kaiwhekea* (~10 to 11). Conversely, other elasmosaurids present slightly lower values. Therefore, although the skull is relatively larger than in other elasmosaurids, the difference is not as big as was typically pointed out. The ratio between the cranium length and the atlas-axis length (Tab. 5) is even among the ratio of other elasmosaurids.

The problem of the lateral keel. The apparent absence of a lateral keel on the cervical vertebrae of MLP 40-XI-14-6 is unexpected given that it is a typical elasmosaurid feature. The only constant convexity observed in the cervical vertebrae of the specimen is a distinctive convex area located above the parapophysis (Fig. 10.2, 8) which, in this case, is even more evident because the cervical ribs of the specimen are displaced. However, the dorsal margin of the parapophysis seems to be more prominent than in other elasmosaurids (see Fig 10.10 of non-aristonectine elasmosaurid specimens, LACM (CIT) 2832, referred to *Aphrosaurus furlongi* by Welles, 1943). It is evident that the dorsal margin of the parapophysis together with the capitulum of the cervical rib produced an even larger convex zone. Therefore, direct observation of the holotype indicates that there are no well developed lateral keels independent of the dorsal margin of the parapophysis. The other preserved aristonectines also exhibit complex patterns of features regarding the lateral margins of their cervical vertebrae. *Kaiwhekea* was described as lacking a lateral ridge (Cruickshank and Fordyce, 2002) and a personal observation of the holotype also failed to record this feature. On the other hand, *Aristonectes quiriquinensis* does present a lateral keel. Juvenile aristonectine specimens display a convex area dorsal to the parapophysis called "lateral keel" but not a completely independent and distinctive lateral keel (Chatterjee and Small, 1989: fig. 10D; Otero *et al.*, 2012: fig. 3C, D). Therefore, more complete and well prepared specimens are necessary to further explore the matter of the nature and distribution of the lateral keel in aristonectines.

Cervical ribs. A comparison between the cervical ribs of the 9th cervical vertebra of *Aristonectes parvidens* and the 10th of the non-aristonectine *Vegasaurus molyi* O'Gorman, Salgado Olivero and Marenssi, 2015, indicates that the cervical ribs of *Aristonectes* were probably relatively longer and wider than those of the non-aristonectine (Fig. 10.5–7).

Skull and neck features: integrated interpretation. Aristonectines present several features that indicate marked differences with other elasmosaurids. The comparisons based on *Aristonectes parvidens* carried out in this contribution confirm and improve our knowledge on these differences. The analysis of the alveolar number seems to indicate that the large number of alveoli of *A. parvidens* results from two variables: 1) the enlargement of the skull (which only partly "explains" the increase in alveolar number) and 2) the small alveolar size and reduced interalveolar spaces. Therefore, there are at least three ways of accommodating the phylogenetic increase of alveoli number: 1) increase of skull size, 2) decrease of alveolar size and reaccommodation modifications due to diastema elimination and 3) reduction of interalveolar spaces. This could indicate that the increase of alveoli and the teeth located in them came about by means of a complex process involving several factors and that, therefore, it was probably favoured by the importance of the biological role of the length of the tooth line. This suggests a change of prey and/or strategy of capture; namely, progressing towards smaller fishes or invertebrates and/or evolving from ambushing single preys to simultaneously cornering multiple prey individuals. These conclusions are consistent with the type of prey indirectly inferred for aristonectines. The exact prey preference of *A. parvidens* or any other aristonectine is not confirmed by means of direct evidence since the only gut contents recorded so far are gastroliths collected associated with a specimen referred to *Aristonectes* sp. (O'Gorman *et al.*, 2014c) and *Aristonectes quiriquinensis* (Otero *et al.*, 2014). However, some inferences have been made based on tooth morphology. Although tooth morphology of *A. parvidens* is not known, some teeth of *A. quiriquinensis* were described by Otero *et al.* (2014: fig. 7B). These display the features described by Massare (1987) for the tooth crown morphology of the guild "Pierce I":

pointed apex, no wear apex, no cutting edges and shape of preserved tooth (height/ basal diameter higher than 3.0). According to Massare (1987), this type of tooth was used for piercing soft prey items such as small fish and soft cephalopods. Chatterjee and Small (1989) proposed that the teeth of *Morturneria seymourensis* (considered a junior synonym of *Aristonectes* by Gasparini *et al*., 2003) correspond to the "Trap guild", characterized by the usage of specialized tooth occlusion as a device for straining and trapping prey such as small fish and crustaceans. A similar prey preference was proposed by Cruickshank and Fordyce (2002, *K. katiki*) and Gaspaini *et al*. (2003, *A. parvidens*). Considering that a trap strategy could be related to a larger mouth aperture and an increase in absolute cranium size, which is a feature of the aristonectines, this inference seems to correlate to the features of the skull and neck previously discussed. Also, the configuration of skull and neck characters seems to be related to the fact that large skulls used in ram feeding require greater support from the cervical region. The support area is in turn related to the neck transverse section and, therefore, the increase in height and width of the cervical centra could represent a mechanical necessity. Then again, increase in cervical width (and a relative increase of cervical height relative to length compared with other elasmosaurids) generates a restriction in the lateral and dorsoventral movements of the neck (Massare and Sperber, 2001). A mobility restriction of the posterior part of the neck of elasmosaurids related to the change of centra proportions and increased height of neural spines has been suggested by previous authors (Massare and Sperber, 2001; Zammit *et al*., 2008). Comparison between the aristonectines and other elasmosaurids results in the observation of a major restriction marked by systematic preclusion of ambush hunting based on quick lateral movement. Conversely, this very same feature provides the specimen with additional support against the drag forces produced by the large skull. Finally, the absence of a lateral keel (*Kaiwhekea*) or the absence of an independent lateral keel (*A. parvidens*) could be related to changes in neck movements.

Although these are preliminary conclusions, the fact that increases in skull length or in the total number of teeth, changes in cervical proportions compared with other elasmosaurids and variations in the type of prey and/or capture strategy are highly correlated seems probable.

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REFERENCES

Araújo, R., Polcyn, M.J., Lindgren, J., Jacobs, L.L., Schulp, A.S., Mateus, O., Gonçalves, A.O., and Morais, M.L. 2015. New aristonectine elasmosaurid plesiosaur specimens from the Early Maastrichtian of Angola and comments on paedomorphism in plesiosaurs. *Netherlands Journal of Geosciences* 94: 93–108.

Benson, R.B., and Druckenmiller, P.S. 2014. Faunal turnover of marine tetrapods during the Jurassic–Cretaceous transition. *Biological Reviews* 89: 1–23.

Blainville, H.D. de 1835. Description de quelques espèces de reptiles de la Californie, précédée de l'analyse d'un système général d'herpétologie et d'amphibiologie. *Nouvelles Archives du Museum d'Histoire Naturelle* 4: 233–296.

Brown, D.S. 1981. The English Upper Jurassic Plesiosauroidea (Reptilia) and a review of the phylogeny and classification of the Plesiosauria. *Bulletin of the British Museum (Natural History), Geology* 35: 253–347.

Cabrera, A. 1941. Un Plesiosaurio nuevo de Cretáceo del Chubut. *Revista del Museo de la Plata (Nueva Serie)* 2: 113–130.

Carpenter, K. 1997. Comparative cranial anatomy of two North American Cretaceous plesiosaurs. In: J.M. Callaway, and E.L. Nicholls (Eds.), *Ancient Marine Reptiles*. Academic Press, San Diego, p. 191–216.

Carpenter, K. 1999. Revision of North American elasmosaurs from the Cretaceous of the Western Interior. *Paludicola* 2: 148–173.

Chatterjee, S., and Small, B.J. 1989. New plesiosaur from the Upper Cretaceous of Antarctica. *Special Publications of the Geological Society* 47: 197–215.

Cope, E.D. 1869. Synopsis of the extinct Batrachia, Reptilia and Aves of North America. *Transactions of the American Philosophical Society (new series)* 14: 1–252.

Cruickshank, A.R.I., and Fordyce, R.E. 2002. A new marine reptile (Sauropterygia) from New Zealand: Further evidence for a Late Cretaceous Austral radiation of cryptoclidid plesiosaur. *Palaeontology* 45: 557–575.

Gasparini, Z., Bardet, N., Martin, J.E., and Fernández, M. 2003. The elasmosaurid plesiosaur *Aristonectes* Cabrera from the Latest Cretaceous of South America and Antarctica. *Journal of Vertebrate Paleontology* 23: 104–115.

Ketchum, H.F., and Benson, R.B. 2011. A new pliosaurid (Sauropterygia, Plesiosauria) from the Oxford Clay Formation (Middle Jurassic, Callovian) of England: evidence for a gracile, longirostrine grade of Early-Middle Jurassic pliosaurids. *Special Papers in Palaeontology* 86: 109–129.

Kubo, T., Mitchell, M.T., and Henderson, D.M. 2012. *Albertonectes vanderveldei*, a new elasmosaur (Reptilia, Sauropterygia) from the Upper Cretaceous of Alberta. *Journal of Vertebrate Paleontology* 32: 557–572.

Lesta, P., and Ferello, R. 1972. Región Extrandina del Chubut y norte de Santa Cruz. In: A.F. Leanza (Ed.), *Geología Regional Argentina*. Academia Nacional de Ciencias de Córdoba, Córdoba, p. 601–654.

Lizuaín, A., and Silva-Nieto, D. 1996. Estratigrafía mesozoica del río Chubut medio (Sierra de Taquetrén). Provincia de Chubut. *13°*

Congreso Geológico Argentino y 3° Congreso de Exploración de Hidrocarburos (Buenos Aires), *Actas* 1: 479–493.

Massare, J.A. 1987. Tooth morphology and prey preference of Mesozoic marine reptiles. *Journal of Vertebrate Paleontology* 7: 121–137.

Massare, J.A., and Sperber, S.T. 2001. Vertebral morphology and swimming styles in Cretaceous plesiosaurs (Reptilia: Sauropterygia). *Paludicola* 3: 95–103.

O'Gorman, J.P. 2013. [Plesiosaurios del Cretácico Superior de Patagonia y Península Antártica, Tomos I y II. Tesis Doctoral, Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, Argentina. 527 p. Unpublished.]. http://sedici.unlp.edu.ar/bitstream/handle/10915/26140/Tomo_I Documento completo.pdf?sequence=4 http://sedici.unlp.edu.ar/bitstream/handle/10915/26140/Tomo_II Documento completo.pdf?sequence=4

O'Gorman, J.P., Gasparini, Z., and Salgado, L. 2013. Postcranial morphology of *Aristonectes* Cabrera, 1941 (Plesiosauria, Elasmosauridae) from the Upper Cretaceous of Patagonia and Antarctica. *Antarctic Science* 25: 71–82.

O'Gorman, J.P., Gasparini, Z., and Salgado, L. 2014a. Reappraisal of *Tuarangisaurus*? *cabazai* (Elasmosauridae, Plesiosauria) from the Upper Maastrichtian of northern Patagonia, Argentina. *Cretaceous Research* 47: 39–47.

O'Gorman, J.P., Otero, R.A., and Hiller, N. 2014b. A new record of an aristonectine elasmosaurid (Sauropterygia, Plesiosauria) from the Upper Cretaceous of New Zealand: implications for the *Mauisaurus haasti* Hector, 1874 hypodigm. *Alcheringa* 38: 504–512.

O'Gorman, J.P., Olivero, E.B., Santillana, S., and Everhart, M.J., and Reguero, M. 2014c. Gastroliths associated with an *Aristonectes* specimen (Plesiosauria, Elasmosauridae), López de Bertodano Formation (upper Maastrichtian) Seymour Island (*Is. Marambio*), Antarctic Peninsula. *Cretaceous Research* 50: 228–237.

O'Gorman, J.P., Salgado, L., Olivero, E., and Marenssi, S. 2015. *Vegasaurus molyi* gen. et sp. nov. (Plesiosauria, Elasmosauridae) from the Cape Lamb Member (lower Maastrichtian) of the Snow Hill Island Formation, Vega Island, Antarctica, and remarks on Wedellian Elasmosauridae. *Journal of Vertebrate Paleontology* (DOI: 10.1080/02724634.2014.931285).

O'Keefe, F.R., and Street, H.P. 2009. Osteology of the cryptocleidoid plesiosaur *Tatenectes laramiensis*, with comments on the taxonomic status of the Cimoliasauridae. *Journal of Vertebrate Paleontology* 29: 48–57.

Otero, R.A., Soto-Acuña, S., and Rubilar-Rogers, D. 2012. A postcranial skeleton of an elasmosaurid plesiosaur from the Maastrichtian of central Chile, with comments on the affinities of Late Cretaceous plesiosauroids from the Weddellian Biogeographic Province. *Cretaceous Research* 37: 89–99.

Otero, R.A., Soto-Acuña, S., O'Keefe, F.R., O'Gorman, J.P., Stinnesbeck, W., Suárez, M.A., Rubilar-Rogers, D., Quinzio-Sinn, L.A., and Salazar, C. 2014. *Aristonectes quiriquinensis* sp. nov., a new highly derived elasmosaurid from the late Maastrichtian of central Chile. *Journal of Vertebrate Paleontology* 34: 100–125.

Owen, R. 1860. On the orders of fossil and recent Reptilia, and their distribution in time. *Reports of the British Association for the Advancement of Science* 29: 153–166.

Page, R., Ardolino, A., de Barrio, R.E., Franchi, M., Lizuain, A., Page, S., and Silva Nieto, D. 1999. Estratigrafía del Jurásico y Cretácico del Macizo de Somún Curá, provincias de Río Negro y Chubut. In: R. Caminos (Ed.), *Geología Argentina*. SEGEMAR, Buenos Aires, p. 460–488.

Persson, P.O. 1963. A Revision of the classification of the Plesiosauria with synopsis of the stratigraphical and geographical distribution of the group. *Lunds Universitets Årsskrift* 59: 1–60.

Sachs, S., and Kear, B.P. 2014. Postcranium of the paradigm elasmosaurid plesiosaurian *Libonectes morgani* (Welles, 1949). *Geological Magazine* 152: 694–710.

Sato, T. 2002. [Description of plesiosaurs (Reptilia: Sauropterygia) from the Bearpaw Formation (Campanian-Maastrichtian) and a phylogenetic analysis of the Elasmosauridae. Phd thesis disertation, University of Calgary, Canada. 391 p. Unpublished.].

Sato, T. 2003. *Terminonator ponteixensis*, a new elasmosaur (Reptilia; Sauropterygia) from the Upper Cretaceous of Saskatchewan. *Journal of Vertebrate Paleontology* 23: 89–103.

Sato, T., Hasegawa, Y., and Manabe, M. 2006. A new elasmosaurid plesiosaur from the Upper Cretaceous of Fukushima, Japan. *Palaeontology* 49: 467–484.

Schumacher, B.A. 2008. On the skull of a pliosaur (Plesiosauria; Pliosauridae) from the Upper Cretaceous (early Turonian) of the North American Western Interior. *Transactions of the Kansas Academy of Science* 111: 203–218.

Schumacher, B.A., Carpenter, K., and Everhart, M.J. 2013. A new Cretaceous pliosaurid (Reptilia, Plesiosauria) from the Carlile Shale (Middle Turonian) of Russell County, Kansas. *Journal of Vertebrate Paleontology* 33: 613–628.

Smith, J.B., and Dodson, P. 2003. A proposal for a standard terminology of anatomical notation and orientation in fossil vertebrate dentitions. *Journal of Vertebrate Paleontology* 23: 1–12.

Vincent, P., Bardet, N., Suberbiola, X.P., Bouya, B., Amaghzaz, M., and Meslouh, S. 2011. *Zarafasaura oceanis*, a new elasmosaurid (Reptilia: Sauropterygia) from the Maastrichtian Phosphates of Morocco and the palaeobiogeography of latest Cretaceous plesiosaurs. *Gondwana Research* 19: 1062–1073.

Welles, S.P. 1943. Elasmosaurid plesiosaurs with description of new material from California and Colorado. *Memoirs of the University of California* 13: 125–234.

Welles, S.P. 1949. A new elasmosaur from the Eagle Ford Shale of Texas. Part I. Systematic description. *Fondren Science Series* 1: 1–28.

Welles, S.P. 1952. A Review of the North American Cretaceous Elasmosaurs. *University of California Publications in Geological Sciences* 29: 1–144.

Welles, S.P. 1962. A new species of Elasmosaur from the Aptian of Colombia and a review of the Cretaceous plesiosaurs. *University of California Publications in Geological Sciences* 44: 1–96.

Wiffen, J., and Moisley, W.L. 1986. Late Cretaceous reptiles (Families Elasmosauridae and Pliosauridae) from the Mangahouanga Stream, North Island, New Zealand. *New Zealand Journal of Geology and Geophysics* 29: 205–252.

Williston, S.W. 1903. North American plesiosaurs, Part 1. *Field Columbian Museum Publication (Geology)* 73: 1–77.

Zammit, M., Daniels, C.B., and Kear, B.P. 2008. Elasmosaur (Reptilia: Sauropterygia) neck flexibility: Implications for feeding strategies. *Comparative Biochemistry and Physiology Part A: Molecular and Integrative Physiology* 150: 124–130.

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