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

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Abstract. Additional preparation of the holotype of the Maastrichtian aristonectine elasmosaurid *Aristonectes parvidens* Cabrera from Chubut Province, Argentina, permits new observations and reveals features that were not previously described and allows new interpretations of those that were previously described. Quantitative comparison with non aristonectine elasmosaurids shows that the increase in the number of alveoli in the premaxilla, maxilla and mandible is not a consequence of increase in skull size increase. Instead, decrease in alveolar size and interalveolar space, compared with that seen in non-aristonectine elasmosaurids, is at least as important. Increase in skull length compared with non-aristonectine elasmosaurids is not as marked as classically considered: skull length is equivalent to the length of the first 8–10 cervical vertebrae in non-aristonectines and the first 10–12 in aristonectines. The ratio of atlas-axis complex length to skull length shows no significant difference between aristonectine and non-aristonectine elasmosaurids. An aristonectine autapomorphy not mentioned previously is the decrease in premaxilla anteroposterior length. This may be correlated with the shortening of the mandibular symphysis. The cervical region is characterised by a rapid increase in the BI index of the vertebral centra, indicating 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 and mouth aperture. These are probably related to change in prey size and capture strategy compared with that of non-aristonectine elasmosaurids, such as a change to smaller fishes or invertebrates and/or a change from ambushing one prey individual to ambushing multiple simultaneous prey individuals.

Keywords. *Aristonectes parvidens*. Aristonectinae. Elasmosauridae. Late Cretaceous

Resumen. NUEVAS OBSERVACIONES SOBRE EL HOLOTIPO DE *ARISTONECTES PARVIDENS* (PLESIOSAURIA, ELASMOSAURIDAE), NOVEDADES SOBRE UN ANTIGUO ESPÉCIMEN. Nuevas observaciones y una re-preparación del holotipo del elasmosáurido aristonectino Maastrichtiano *Aristonectes parvidens* Cabrera colectado en la provincia de Chubut, Argentina, indican características que no se han descrito anteriormente y permite nuevas interpretaciones de las previamente mencionadas. La comparación cuantitative con elasmosauridos no-aristonectinos muesta que el incremento en el número de alvéolos del premaxilar, maxilar y la mandíbula no es únicamente consecuencia del aumento de tamaño del cráneo. En su lugar, la disminuciones del tamaño alveolar y del especio interalveolar en comparación con aquellos de otros elasmosáuridos no aristonectinos tienen al menos la misma importancia en el incremento total. El aumento de la longitud relativa del cráneo en relación a otros elasmosauridos no aristonectinos es relativamente menos importante que lo considerado clásicamente: longitud cráneo equivalente a 8-10 primera vértebra cervical (no-aristonectinos) y 10-12 (aristonectinos). El cociente entre la longitud del cráneo y el complejo- atlas axis no muestra diferencias entre aristonectinos y no aristonectinos. Una autapomorfía de los aristonectinos previamente no mencionada es la disminución de la longitud anteroposterior del premaxillar que posiblemente está correlacionada con el acortamiento de la sínfisis mandibular. La región cervical se caracteriza por el rápido aumento del índice BI de los centros vertebrales que indican la reducción de la movilidad lateral del cuello. El aumentos de número de alvéolos logrado debido a una sumatoria de cambios parecen indicar la importancia de la función biológica del incremento de la longitud de la hilera dentaria, lo que probablemente están relacionados 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

82 más pequeños o invertebrados y/o un cambio de una estrategia de emboscada a captura de
83 presas múltiples y simultáneas.
84 **Palabras clave**. *Aristonectes parvidens*. Elasmosauridae. Aristonectinae. Cretácico Tardío.

ARISTONECTINES are bizarre elasmosaurids that flourished in the last part of the Cretaceous (Gasparini *et al*., 2003; O'Gorman *et al*., 2013, 2014; Otero *et al*., 2014) and they 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; Araujo et al., 2015). One of the most important results to come 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* Cuickshank and Fordyce, 2002), a topic discussed for the previous 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, Salazar, 2014 from the upper Maastrichtian of central Chile, and the recognition of new and previously misinterpreted aristonectine records (O'Gorman *et al*., 2013; 2014a, b) that have added information about the anatomy anddistribution of these elasmosaurids. However, despite these new results, the internal phylogenetic relationships among the aristonectines are poorly understood (Otero *et al*., 2014; O'Gorman *et al.*, 2015).

New preparation of the *Aristonectes* holotype (MLP 40-I-14-6; MLP: *Museo de La Plata*, Buenos Aires Province, Argentina) and the subsequent increases of knowledge about its anatomy shows new features previously unknown or not completely discussed about this historical and systematically relevant specimen and allows to see the aristonectine classical features under a new light. Additionally two explanation about how the

aristonectine cranium accommodate the increases 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* (MLP 40-XI-14-6) 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 during September of 1940 as a donation of the *Dirección de Minas y Geología del Ministerio de Agricultura* (Cabrera, 1941). The identification of the material followed only after the preparation of the cranium and mandible by Lorenzo Parodi. An incomplete vertebra and phalanges from the same area had been previously donated to the *Museo de La Plata* (MLP) by Mario Reguiló and carried to the MLP by Dr. Joaquin Frenguelli. These were later added to the holotype because, as was 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 (Fig. 1.1; 2.1, 2). The features of *Aristonectes* have generated doubts about its affinities since the first description and throughout the 20th century (Welles, 1962; Pearsson, 1963; Brown, 1981). Two parts of the specimen were later re-prepared: the skull and the atlas-axis complex, in order to show more sutures and alveoli for the revision of Gasparini *et al.* (2003), and the caudal vertebrae, for the revision by O'Gorman (2013). Both preparations were carried out by the fossil preparator Lic. Javier Posik.

***Institutional Abbreviations*. ANSP**, Academy of Natural Sciences of Drexel University, Philadelphia, USA; **CIT**, California Institute of Technology, Pasadena now in the Natural History Museum of Los Angeles County; **CM**, Canterbury Museum, Christchurch, New

Zealand; **DMNH**, Denver Museum of Natural History, Denver County, USA; **GNS**, Institute of Geological and Nuclear Sciences, Lower Hutt, New Zealand; **MACN**, Museo Argentino de Ciencias Naturales Bernardino Rivadavia, Ciudad Autónoma de Buenos Aires, Argentina; **MLP**, Museo de La Plata, Buenos Aires Province, Argentina; **OU**, Otago Museum, Dunedin, New Zealand; **SMU SMO**, Southerns Methodist University, Shuler Museum of Paleontology, Dallas. University of California Paleontological Museum, California University, San Francisco, USA; **TTU P**, Museum of Texas Tech University, Lubbock, Texas, U.S.A; **TMP**, Royal Tyrrell Museum of Palaeontology, Drumheller, Alberta, Canada; **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; **axna**, axis neural arch; **axc**, axis centrum; **axr**, axis rib; **cr**, cervical rib; **de**, dentary, **dt I**, distal tarsal I; **dt II+III**, distal tarsal, 2+3; **hf**, hemal facet; **in**, internal nares; **j**, jugal; **lk**, lateral keel; **kl**, 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**, scuamosal; **ti**, tibiale; **vf**, ventral foramina; **vk**, vetral keel; **vn**, ventral notch; **v**, vomers.

MATERIAL AND METHODS

The linear measurements were taken using an electronic calliper that allows 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), the ratio between height (H) and length of the centrum (100*H/L), and the ratio between breadth (B) and length of the centrum (100*B/L). In addition, the ratio between the breadth and height (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 about the relationship between the number of alveoli and the skull length, the ratio (Ar) between the cranium length (from rostrum tip to occipital condyle= Cl) and the number of mandibular alveoli (Al) of several elasmosaurids (Table 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 is explained only by the increase in the cranial and mandibular size. The nomenclature used for alveoli measurements follows Smith (2003: fig. 7; see Fig. 7.1). Particularly the mesodistall measurement was considered used to compare alveolar sizes. Two ratios were used to compare the ratio between the cranium and the cervical region of the aristonectine and non-aristonectine elasmosaurids: 1] the ratio between the cranium length (Cl) and atlas-axis complex length and 2] the number of cervical vertebrae from the atlas that form a neck sector as long as the cranium lenght (Cl).

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, an at least slightly flattened and broad skull without premaxillary–maxillary constriction, which differs 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), but slightly higher than those of *Kaiwhekea katiki*. Additional features showing differences between *Aristonectes* and *Kaiwhekea*, although they are not found/ in all of the representative skulls: 13 premaxillary teeth (not preserved in *A. quiriquinensis*), differing from the seven premaxillary teeth of *Kaiwhekea*; 50 or more teeth in the maxilla (not found in *A. quiriquinensis*), differing from the 36 teeth recorded in *Kaiwhekea*.

Aristonectes parvidens Cabrera, 1941

Figs. 2; 3; 4.1; 8; 9.1,2; 10, 1–9; 11. 1–9

Type material. MLP 40-XI-14-6, part of a skull 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 (42º 40" S70 º 00" W), northwestern Chubut Province, Patagonia, Argentina (Cabrera, 1941); Lefipán Formation, Maastrichtian (Lesta and Ferello, 1972; Page *et al*., 1990).

Diagnosis. *Aristonectes* species with symphyseal lingual groove; mandible higher than in *A. 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.

Description

The specimen MLP 40-XI-14-6 was originally described by Cabrera, 1941 and then carefully re-described by Gasparini *et al*. (2003). Here, only specific features previously not

reported or reinterpreted are described, carefully illustrated and discussed and measurement (Tables 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 while Gasparini *et al*. (2003) indicated a number of 10 to 13. The difference is due to the different interpretation about where the premaxilla-maxilla suture is located (Fig. 2.6). Careful observation of the specimen and a comparison with *Kaiwheke katiki* indicates the most probable number of premaxillary alveoli is 13. The number of maxillary teeth indicated by Cabrera (1941) was 26 whereas Gasparini *et al*. (2003)counted 51–53 maxillary alveoli. The new observations confirm the presence of 37 clearly visible alveoli and at least 14 inferred by a sulcus on the counterpart in the lower jaw and, therefore, the presence of at least 51 maxillary alveoli. Cabrera (1941) indicated the presence of 58 mandibular teeth and 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 and the number could be between 63 and 65. Additionally, the lateral inclination of the alveoli series is confirmed (Fig. 2.3, 4, 6), a feature mentioned by Gasparini *et al*. (2003) and recently observed in *A*. *quiriquinensis* but difficult to determine in *Kaiwhekea* (Otero *et al*., 2014; J.P. O'G. pers. obs.).

Internal naris. Gasparini *et al*. (2003: fig. 3D) did not attempt to identify the 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 but 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 relating to

228 the anterior structure of the palate is that the suture between the vomer and premaxilla
229 seems to be asymmetrical, as was figured by Gasparini *et al*. (2003: fig. 3). However,
230 careful observation indicates that the probable suture is located as shown in figure 3.3, 4.
231 Unfortunately, the posterior border of the naris is not preserved (although a posterior bone
232 wall is preserved, it is not clear if it is natural). A comparison between *Aristonectes*
233 *parvidens* and a non aristonectine elasmosaurid such as *Libonectes morgani* (Welles,1949)
234 (Fig. 6.11, 12) indicates that the vomer of *A. parvidens* has two lateral depressions that
235 limit the vomeronasal fenestra recorded by Gasparini *et al*. (2003), giving a premaxilla-
236 vomer suture with the premaxilla presenting the "M" shape mentioned by Gasparini *et al*.
237 (2003) and a long anterior process (Fig. 3.3, 4), features absent in other elasmosaurids
238 (Carpenter, 1997: fig. 2D; Sato *et al*., 2006: fig. 4C; Vincent *et al*., 2011:fig. 2E). The
239 posteriormost part of the vomer shows an open suture between both lateral vomeral
240 elements (Fig. 3.1, 3), usually fused or with a strong suture in adults (Carpenter, 1997; Sato
241 *et al*., 2006). This open suture is congruent with the only other palate known from an
242 aristonectine (Chatterjee and Small, 1989: fig. 4), where the vomers are only anteriorly and
243 medially fused but posteriorly they show a wide intervomerial space generated by the
244 absence of a medial suture. If the vomer of *Aristonectes* has the same morphology, the
245 vomer had to expand laterally and generate a relatively small and anterioposteriorly long
246 internal naris (Fig. 3.4) which differs from the morphology inferred by O'Gorman (2013)
247 and gives a reconstruction which is more consistent with the morphology observed in other
248 elasmosaurids (Carpenter, 1997). Another interesting feature of the *Aristonectes parvidens*
249 holotype regards the probable dorsal overlapping of medial element that projects dorsally
250 to the vomer. This element was interpreted as part of the vomer by Gasparini *et al*. (2003)
251 and O'Gorman (2013). However, careful observation shows a possible suture between both

252 elements and, therefore, the dorsal and posterior elements could not be part of the vomer
253 (Fig. 3.1, 2). By its medial position, this element is possibly the anteriormost part of the
254 pterygoid that overlaps part of the vomer dorsally and is visible in palatal view due to the
255 absence of the posterior part of the vomer.
256 ***Mandibular symphysis*.** The mandibular symphysis of MLP 40-XI-14-6 is short and, as
257 was mentioned by Otero *et al*. (2014) bears a depression, the "deep groove" of Otero *et al*.
258 (2014) on its internal surface (Fig. 3.2). The ventral side of the symphysis does not show
259 the mental boss observed by Otero *et al*. (2014) in the symphysis of *A*. *quiriquinensis* (Fig.
260 3.1; 4.1). However, the mandible surface of the holotype of *A*. *parvidens* has suffered the
261 loss of the external layer of bone and, therefore, it is possible that at least weak mental boss
262 was originally present. This is even probable because the mental spines of *A*.
263 *quiriquinensis* are located in the lateral margins of a wide symphyseal sulcus, which is
264 present in *A*. *parvidens* (Fig. 4.1). Comparison between the ventral surface of the
265 symphysis of *A*. *parvidens* and those of non aristonectine elasmosaurids (Fig. 4.1–4) shows
266 that they share the symphyseal sulcus but that of *Aristonectes parvidens* is much wider,
267 following the general widening of the symphysis. Another interesting feature of the
268 symphysis is the reduced symphyseal post alveolar surface similar to that observed on *A*.
269 *quiriquinensis* but different from other elasmosaurids (Carpenter, 1997:fig. 2E). All this
270 corroboratess the observations of Gasparini *et al*. (2003) and Otero *et al*. (2014) about the
271 presence of a relatively weak symphysis compare to non-aristonectine elasmosaurids (Fig,
272 5.1–4).
273 ***Glenoid cavity*, *retroarticular processand coronoid process*.** Only the right glenoid cavity
274 and the proximal part of the retroarticular process is preserved. The glenoid cavity is deep
275 (42 mm antero-posterior 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 process to the limit to the posterior limit of the glenoyd cavity (Fig. 4.5, 6). The medial view of the right mandible (Fig. 3.5) shows a relatively high and rounded coronoid and additionally it is observed the suture between the angular and surangular and splenial remains open.

Atlas-axis complex. The atlas axis was carefully described by Gasparini *et al*. (2003). The description focused on the elements that formed it and its distribution. Here, other features that appear distinctive among elasmosaurids are recorded and shown in figures. 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, as 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). Although part of this phenomenon could be consequence of the preparation, it seems to be at least partially natural feature (Fig 8.1, 2), probably connected to some difference in the relative time of suture closure among elasmosaurids. The second mentioned feature, the absence of a developed ventral keel (Fig. 8.6) is unusual among elasmosaurids (Welles, 1943; Kubo *et al*., 2012; O'Gorman *et al*., 2015; Sachs and Kear, 2014) but it seems to be present in *Tuarangisaurus keyesi* (Wiffen and Moisley, 1986). Finally, the presence of a circular atlantal cup (Fig. 7.4) is also unusual among elasmosaurids, in which they are usually higher than broad (Fig. 9). Another feature recorded for atlas-axis of *A*. *parvidens* is the absence of ventral foramina (Fig. 8.6), which are present in some other 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: fig. 2A, 3E). Detailed observation

300 reveled that the observed “ventral projection” (Fig. 8.1, 2, 5) is part prezygapophysis of the
301 third vertebra which remains attached to the postzygapophysis of the atlas-axis complex
302 and, therefore, it is not a natural feature. Finally the posterolateral process of the atlas
303 seems to be broken in its distalmost part (Fig. 8. 4) although it was probably not as long as
304 that recorded for *A*. *quiriquinensis* (Otero *et al*., 2014).
305 ***Lateral keel.*** The holotype preserves a cervical series that belong to the anterior part of the
306 neck (Fig. 9.1). This was described by Gasparini *et al*. (2003) but the question of the lateral
307 keel needs some clarification. In the original description Cabrera (1941) did not record or
308 include figures of any lateral keel in the cervical vertebrae of the holotype (Cabrera, 1941:
309 figs 3, 4). Afterwards Gasparini *et al*. (2003) described “scarcely visible lateral crests that
310 can occur only on a single side”. The present revision indicate tha the only constant
311 convexity observed in the cervical vertebrae of MLP 40-XI-14-6 is a distinctive convex
312 area located above the parapophysis (Fig. 10.2, 8) which is evident in the specimen because
313 the cervical ribs are displaced. However, the dorsal margin of the parapophysis seems to be
314 more prominent than in other elasmosaurids (see Fig 10.10 of non elasmosaurid specimens,
315 CIT 2832, referred to *Afrosaurus furlongi* by Welles, 1943). It is likely that the dorsal
316 margin of the parapophysis, together with the capitulum of the cervical rib, has produced an
317 even larger convex zone. Therefore, direct observation of the holotype indicates that there
318 are not well developed lateral keels independent of the dorsal margin of the parapophyses.
319 Another possibility is that a faint lateral ridge was erased during the original preparation,
320 but there is no way to test this.
321 **Caudal centra.** Cabrera (1941) indicated that only two caudal vertebrae were preserved.
322 These are indeed caudal vertebrae but Cabrera misidentified eight caudal vertebrae as
323 posterior cervicals and was later corrected by Gasparini *et al*. (2003) , Figure 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). This is very surprising considering that one vertebral foramen (or two in anteriormost caudals) is the most frecuent number of foramina among elasmosaurids (Benson and Druckenmiller, 2014) and the presence of five large and well defined ventral foramina has been recorded only for the specimen considered here**.** Another interesting feature of the caudal vertebrae is their proportions. The figure 11.10 compares the HI and BI indexes of the caudal vertebrae of MLP 40-XI-14-6 and non aristonectine elasmosaurids. The comparison shows thatthe caudals of MLP 40-XI-14-6 show relatively high HI and BI indexes.

***Caudal ribs*.** No caudal ribs were described by Cabrera (1941), probably because they were wrongly identified. Gasparini *et al*. (2003) failed to mentioned them as well. However, in the material, there are several damaged caudal ribs similar to the caudal ribs of other elasmosaurid (J.P.O'G. per. obs) but with a slightly larger proximal expansion in the capitulum (Fig. 11.6, 7), related to the large parapophysis 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 only one paddle but he stated that he was not certain that all the elements 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 11.8 and 11.9 show the original interpretation of Cabrera (1941) and the ones ofO'Gorman (2013) and Otero *et al*. (2014) respectively. The interpretation of the elements given here follows the last of theese.

CALCULATIONS

Correlation between mandibular alveoli and skull size.

Table 4 shows the cranial lengths (from premaxilla tip to occipital condyle) of six elasmosaurids and the ratio number of mandibular alveoli/cranium length (alveolar rate=Ar). For calculation *Tuarangisaurus* (20 alveoli); *Aristonectes* (64 alveoli) and *Kaiwhekea* (43 alveoli) were considered. The last column "predicts" the alveoli number of a non-aristonectine elasmosaurid if it had 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 aristonectine only partly "explains" the increases of alveoli number (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 measurements of the alveoli of MLP 40-I-14-6 were recorded and are plotted in Figure 7.2. Additionally, Figure 7.2 plots the alveoli size of *Tuarangisaurus keyesi* Wiffen and Moisley, 1986, a non-aristonectine elasmosaurid from the Campanian–Maastrichtian of New Zealand in order to compare them with those of *Aristonectes parvidens*. The comparison of both alveolar series shows a marked difference in mesodistal length of the alveoli.

Skull/neck proportion

Table 5 shows the ratio between the cranium length (from premaxilla tip to occipital condyle) and the atlas-axis complex length. It indicates that the values for *Aristonectes* falls within the range of values calculated for other elasmosaurids.

DISCUSSION AND CONCLUSION

371 ***Alveoli number and size***. The recognition of the elasmosaurid affinities of aristonectines
372 raised the question about how this group achieved its classically mentioned distinctive
373 features among elamsoaurids, such as the relatively large skull, high number of alveoli and
374 short neck. The question about of how an elasmosaurid skull could accommodate increase
375 in the number of alveoli, is a relevant issue that has not been previously discussed. The
376 number of alveoli among non-aristonectine elasmosaurids has been largely recognised to be
377 lower than that of the aristonectines and the same is true for the skull size (Table 4).
378 However, no attempt to look for some correlation between skull size and alveoli number
379 was previously undertaken, therefore, it was not discussed if wheather the increase in
380 alveoli number is a direct effect of the increase in cranial size and the retention of teeth size
381 or if other factors are involved. In order to test this, two analyses were carried out. Table 4
382 shows the ratio mandibular alveoli nunmber/cranium length. The last column "predicts" the
383 alveoli number of a non-aristonectine elasmosaurid with an aristonectine-like cranium size.
384 This column shows that the increase in length of the skull of aristonectines only partly
385 "explains" the increases of alveoli number (between 21 and 34 for *Aristonectes parvidens*
386 and 18 and 30 for *Kaiwhekea katiki*). Therefore, the enlarged number of alveoli is only
387 partially explained by the enlargement of the skull compared with non-aristonectine
388 elasmosaurids.

389 The previous result indicates that other features, such as the small size of the alveoli
390 and the absence of large interalveolar spaces and/or diastemata, generate the space for the
391 additional alveoli. In order to investigate the difference in the alveoli size between
392 aristonectines and non aristonectine, the meso-distal measurements of the alveoli of MLP
393 40-I-14-6 were recorded and plotted in Figure 7.2. Additionally, Figure 7.2 includes the
394 alveoli sizes for *Tuarangisaurus keyesi* Wiffen and Moisley, 1986, a non-aristonectine

elasmosaurid. The comparison of both alveolar series shows a marked difference between the size of the alveoli, indicating that this sizes difference is the second feature that allows to accommodation of the high alveolar account. Therefore, these two mentioned features together with the small interalveolar spaces (between 1–2 mm), the ogival shape that increases the cranial and mandibular alveolar margin, and the absence of diastema generate the difference in the alveolar count compared with that of non- aristonectine elasmosaurids.

Vomer-perygoid contact. The position of the anteriormost end of the pterygoid overlapping the vomer has not been previously recorded for elasmosaurids. However a dorsal view of articulated specimens of these two elements has not been described among elasmosaurids and therefore it could be a widespread features. 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 and the idea that this is a widepread feature among Plesiosauria was pointed out because, as was mentioned by Schumacher (2008) and Schumacher *et al*. (2013), the common two-dimensional observation in palate view does not negate the possible 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 usual feature among Plesiosauria.

***Cranial proportions*.** Skull proportions of *Aristonectes* have been previously mentioned as low and ogival shaped. This is produced partially by the increase in transverse width near the rostrum and mandibular symphysis. Additionally, the holotype of *A*. *parvidens* shows another interesting feature which was not previously mentioned and is shared with *Kaiwhekea*: the low ratio between premaxilla and maxilla anteroposterior length. This is

419 evident when the cranial proportions are compared among aristonectine and non-
420 aristonectines (Figure 5.7–10). The same proportion is observed in palatal view (Fig. 5.5,
421 6). Therefore, the relatively shorter premaxilla appears to be a feature of the aristonectines.
422 Additionally, a short mandibular symphysis is also present, a feature known since the
423 original description of Cabrera (1941; see Fig. 5.1–4). It is interesting that both the
424 anteroposterior length of the premaxilla and the length of the symphysis show both a
425 shortening. The functional reason for this correlation is currently unknown.
426 ***Large cranium or large body?: skull/ cervical vertebrae proportions.*** Another feature also
427 cited since Cabrera (1941) for *Aristonectes* is the large skull. It is clear that among the
428 distinctive small skulled elasmosaurids the aristonectines *Aristonectes parvidens*;
429 *Aristonectes quiriquinensis* and *Kaiwhekea katiki* stand out with their large skulls (Fig. 6.1,
430 2). However, the relationship between skull size and vertebral length has not been
431 previously considered. Figure 6.1 indicates that the skull is as long as the sum of the
432 lengths of the first eleven to twelve cervical vertebrae. Similar values are recorded for
433 *Kaiwhekea* (~10 to 11) but other elasmosaurids show slightly lower values. Therefore,
434 although the skull is relatively larger than in other elasmosaurids, the difference is not as
435 big as was classically pointed out. The ratio between the skull length and the atlas-axis
436 length (Tab. 5) shows that this is even among the ratio of other elasmosaurids.
437 ***The problem of the lateral keel.*** The apparent absence of a lateral keel on the cervical
438 vertebrae of MLP 40-XI-14-6 is surprising because it is a typical elasmosaurid feature. The
439 only constant convexity observed in the cervical vertebrae of the specimen is a distinctive
440 convex area located above the parapophysis (Fig. 10.2, 8) which is more evident in the
441 specimen because the cervical ribs are displaced. However, the dorsal margin of the
442 parapophysis seems to be more prominent than in other elasmosaurids (see Fig 10.10 of

443 non elasmosaurid specimens, CIT 2832, referred to *Afrosaurus furlong* by Welles, 1943). It
444 is evident that the dorsal margin of the parapophysis, together with the capitulum of the
445 cervical rib, produced an even larger convex zone. Therefore, direct observation of the
446 holotype indicates that there are no well developed lateral keels independent of the dorsal
447 margin of the parapophysis. The other preserved aristonectines also show complex patterns
448 of features regarding the lateral margins of their cervical vertebrae. *Kaiwhekea* was
449 described as lacking a lateral ridge (Cruickshank and Fordyce, 2002) and a personal
450 observation of the holotype also failed to record this feature. On the other hand, *A*.
451 *quiriquinensis* shows lateral keel. Juvenile aristonectine specimens show a convex area
452 dorsal to the parapophysis called "lateral keel" but not a completely independent distinctive
453 lateral keel (Chaterjee and Small, 1989: fig.10D; Otero *et al*., 2012: fig. 3C, D). Therefore,
454 more complete and well prepared specimens are necessary to answer the question about the
455 nature and distribution of the lateral keel among aristonectines.
456 ***Cevical ribs.*** Some of the cervical vertebrae preserve the cervical ribs attached, although
457 most are displaced (Fig. 10.2, 5). A comparison between the cervical ribs of the 9th cervical
458 vertebra of *Aristonectes parvidens* and the 10th of the non aristonectine *Vegasaurus molyi*
459 O'Gorman, Salgado Olivero and Marenssi, 2015 indicates that the cervical ribs of
460 *Aristonectes* were probably relatively longer and wider than those of the non aristonectine.
461 ***Skull and neck features: integrated interpretation.*** Aristonectines show several
462 features that indicate marked differences with other elasmosaurids. The comparisons based
463 on *A. parvidens* carried out in this contribution confirm and improve our knowledge about
464 theses differences. The analysis of the alveolar number seems to indicate that the large
465 number of alveoli of *Aristonectes parvidens* was achieved, not only by the absolute and
466 relative enlargement of the skull (which only partly "explains" the increases in the alveoli

number), but also by the small alveolar size and reduced interalveolar spaces. Therefore, there are at least three ways of accommodating the phylogenetical increases of alveoli number: increases of skull size, decreases of alveolar size and a reaccommodation modifications due to diastema elimination and reduction of interalveolar spaces. This could indicate that the increases of alveoli and the teeth located in them was achieved by a complex process that involved several factors and, therefore, was probably favoured by the importance of the biological role of the length of the tooth line and mouth aperture. These suggest a change of prey and/or strategy of capture, such as moving to smaller fishes or invertebrates and/or/ changing from ambush one-by-one prey to multiple simultaneous prey individuals.These conclusions are consistent with the type of prey indirectly inferred for aristonectines. The exactly prey preference of *Aristonectes parvidens* or any other aristonectine is not known by direct evidence as the only gut contents are recorded until now are gastrolithscollected associated with a specimen referred to *Aristonectes* sp. (O'Gorman *et al*., 2014) and *Aristonectes quiriqinensis* (Otero et al., 2014). However some inferences have been made based on tooth morphology. Although tooth morphology of *Aristonectes parvidens* is not known, some teeth of *A*. *quiriquinensis* were described by Otero et al. (2014: fig. 7B). These show 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). Following 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) belong to the 'Trap guild', which used its specialized tooth occlusion as a device for straining and trapping preys 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*). This inference seems to be correlated with the features of the skull and neck previously discussed because 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. Also the configuration of skull and neck characters seems to be correlated because large skull used in ram feeding, requires greater support from the cervical region and the support area is related to the neck transverse section, therefore, the increases in height and width of the cervical centra could represent a mechanical necessity. However, increases in width and a relative increase of height relative to length compared with other elasmosaurids generate a restriction in the lateral and dorsoventral movements of the neck (Massare and Sperber, 2001). Restriction of the mobility 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 (Masare and Sperber, 2001; Zamit et al., 2008). The difference observed for the aristonectines is a major restriction compared with other elasmosaurids precluding ambush hunting based on quick lateral movement, but give 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, it seems probable that increases in skull length increases in the total number of teeth changes in cervical proportions compared with other elasmosaurids and the type of prey and/or capture strategy were highly correlated.

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Figure captions

Figure 1. 1, Original display of the holotype; **2,** artistic representation of *A*. *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).

Figure 2. *Aristonectes parvidens* holotype (MLP 40-XI-14-6). **1–2,** skull with plaster reconstruction in **1,** dorsal and **2,** ventral views. Scale bars= 40 mm. **3,** cranium and mandible in anterior view. Scale bar= 20 mm. **4,** cranium and mandible in right lateral view. Scale bar= 100 mm. **5,** posterior part of cranium and mandible. Scale bar= 20 mm. **6,** anterior part of cranium and mandible in anterior-right view showing alveoli disposition. Scale bar= 20 mm.

Figure 3. *Aristonectes parvidens* holotype (MLP 40-XI-14-6). **1,** cranium and mandible in ventral view. Scale bar= 100 mm. **2,** mandibular symphysis in posterior view, showing the "deep groove" of Otero *et al*., (2014). **3–4,** anterior palate **3,** photo and **4,** interpretative drawing. Scale bar= 20mm. **5,** medial view of the middle and posterior part of the right mandible. Scale bar = 50 mm.

Figure 4. 1–4, mandibular symphysis of elasmosaurids in ventral view. **1,** *Aristonectes parvidens* (MLP 40-XI-14-6). **2,** *Tuarangisaurus keyesi* (NZGS, CD425). **3,** *Callawayasaurus colombiensis* (UCMP 38349) and **4,** CIT 2749, referred to *Morenosaurus stocki* Welles, 1943. **5, 6**, cuadrate and glenoyd cavity of *Aristonectes parvidens* (MLP 40-XI-14-6). Scale bar = 20mm.

Figure 5. *Aristonectes parvidens* comparative cranial and mandibular proportions and palatal structure. **1–2,** relative symphyseal length in ventra view **1,** *Aristonectes parvidens*, **2,** *Libonectes mogani*. **3–4,** relative symphyseal length in medial view **3,** *Aristonectes parvidens*, **4,** *Libonectes morgani*. Scale bar= 100 mm**. 5–6,** relative premaxillar length in

palatal view **5,** *Aristonectes parvidens* **6,** *Libonectes morgani*. Not in scale. **7–10,** comparison of premaxilla anteroposterior lateral length **7,** *Kaiwhekea katiki* **8,** *Aristonectes parvidens* **9,** *Libonectes morgani* and **10,** *Terminonatator ponteixensis* Sato, 2003. **11–12,** palatal structures of **12,** *Aristonectes* and **11,** *Libonectes morgani*. Not in scale (**2**, **4**, **6**, **9**, modified from Carpenter, 1997; **7** modified from Cruickshank and Fordyce, 2002; 10, modified from Sato, 2003).

Figure 6. Cranial and cervical feature of *A*. *parvidens*. **1,** relation between the cranium length and the accumulative cervical length. **2,** cranium lengths. Data taken from Weles, 1943, 1952; Wiffen and Moysley, 1986; Cruickshank and Fordyce, 2002.

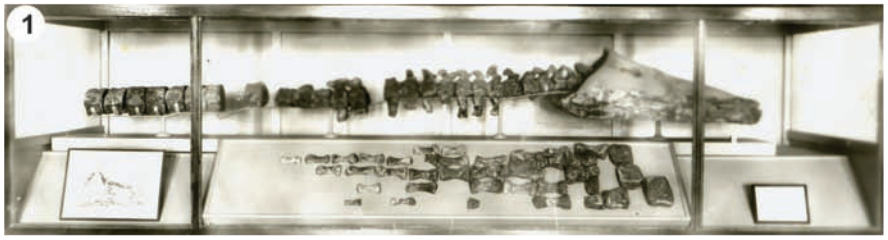
Figure 7. 1, scheme indicating the mesodistal length measure of alveoli; **2**, alveolar mesodistal length of A. *parvidens* and *Tuarangisaurus keyesi*. **3,** BI measurement of the anterior cervical centra of *A*. *parvidens* and three non-aristonectine elasmosaurids. Data taken from Weles, 1943, 1952.

Figure 8. *Aristonectes parvidens* holotype (MLP 40-XI-14-6). **1–4** atlas-axis complex in **1,** left lateral, **2,** detail of axis neural spime, **3**, anterior, **4,** axis rib**5,** posterior and **6,** ventral views. Scale bar= 20 mm.

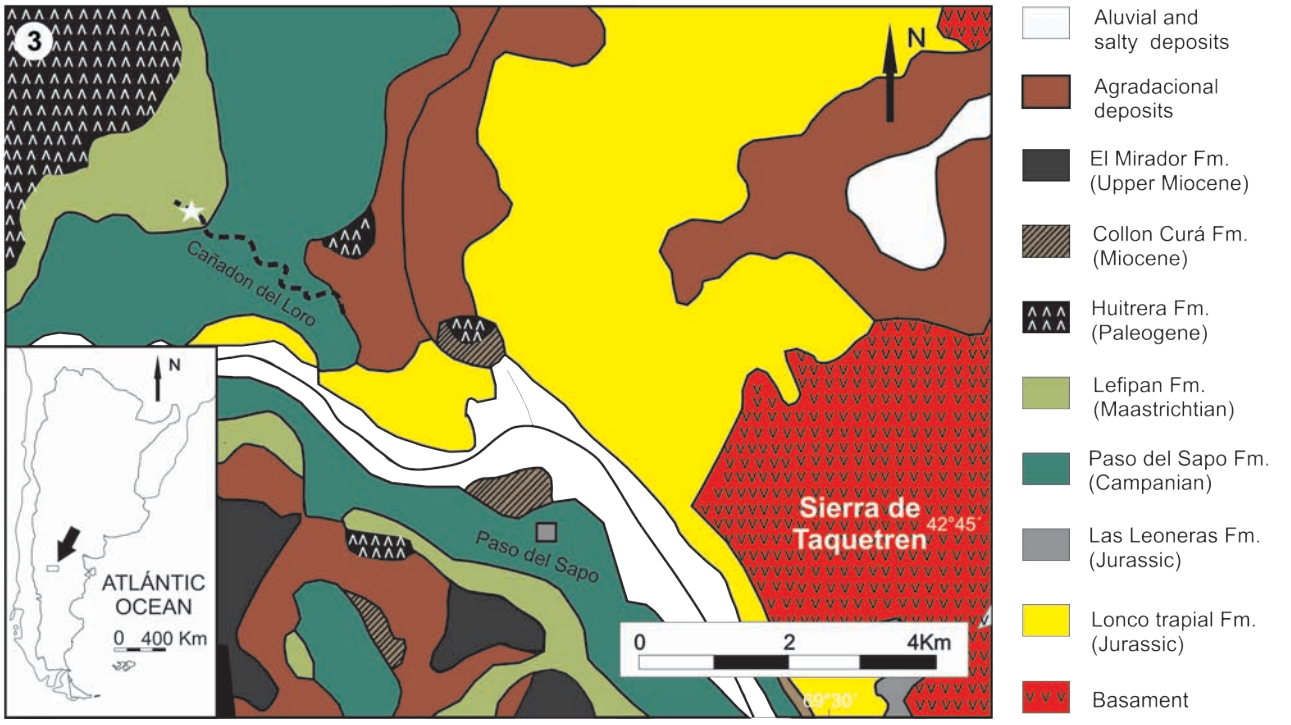
Figure 9. Atlas-axis complex of elasmosaurids. **1–2,** *Aristonectes parvidens* (holotype, MLP 40-XI-14-6) in **1,** anterior and **2,** ventral views. **3–4,** *Vegasaurus molyi* (holotype, MLP 93-I-5-1) in **5,** anterior and **6,** ventral views. **5–6,** *Tuarangisaurus keyesi* (holotype, NZGS,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

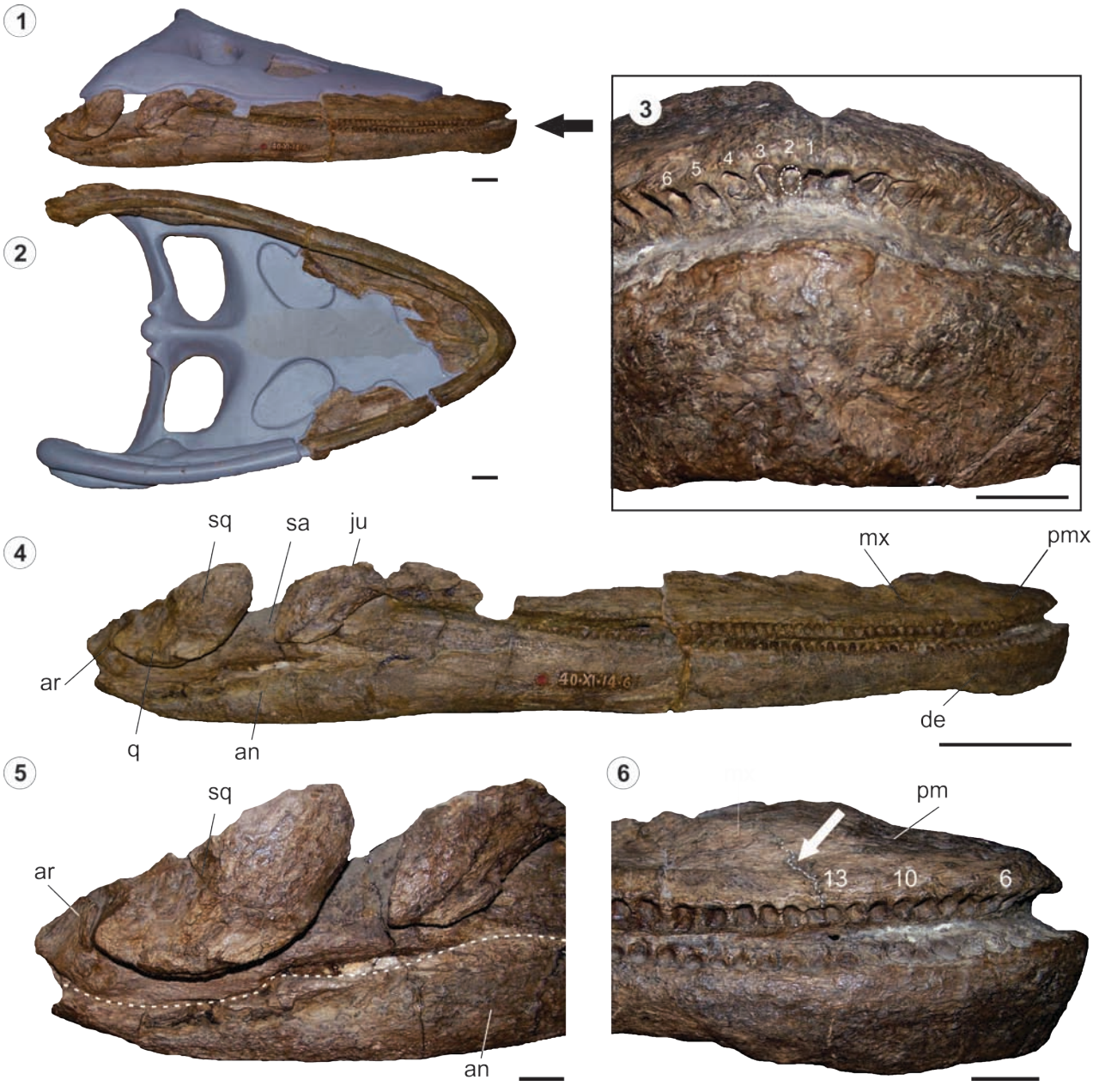
Figure 10. *Aristonectes parvidens* holotype (MLP 40-XI-14-6). **1,** sequence composed by 3^{th} to 19^{th} cervical vertebrae. Scale bar = 100 mm. **2,** cervical vertebrae 11^{th}–12^{th} in left lateral view. **3,** 11^{th} vertebrae in anterior view. **4,** 11^{th}–12^{th} vertebrae in ventral view. **5-6,**

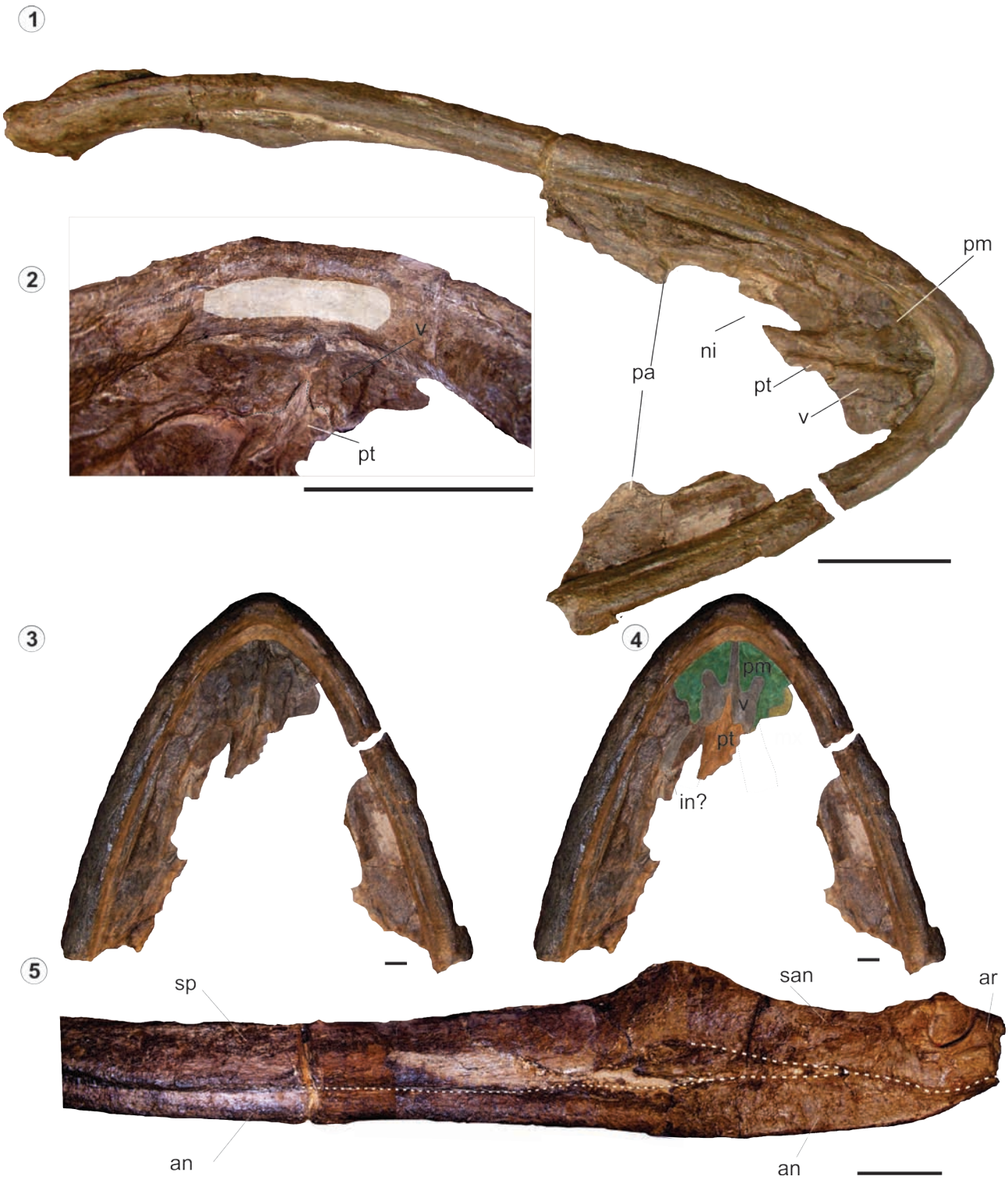
703 9th cervical vertebrae in **5,** anterior view and **6,** reconstruction of cervical ribs in the 9th
704 cervical vertebrae. **7,** 10th cervical vertebrae of *Vegasaurus molyi* (MLP 93-I-5-1) in
705 posterior view. **8–9,** 17th–19th cervical vertebrae in **8,** left lateral and **9,** ventral view. **10,**
706 cervical vertebrae of the non aristonectine *Afrosaurus furlongi* in left lateral view. Scale
707 bars = 20 mm.
708 **Figure 11.** *Aristonectes parvidens* holotype (MLP 40-XI-14-6). **1–4** caudal centra in **1,**
709 anterior; **2,** left lateral; **3,** ventral and **4,** dorsal views. **6–7,** caudal rib in **6,** posterior? and **7,**
710 dorsal? views. **8–9**, posterior? limb **8,** original display and **9,** reconstruction. Scale bars =
711 40 mm. **10,** plot of the HI and BI index of the caudal vertebrae of MLP 40-XI-14-6 and non
712 aristonectine elasmosaurids.


1

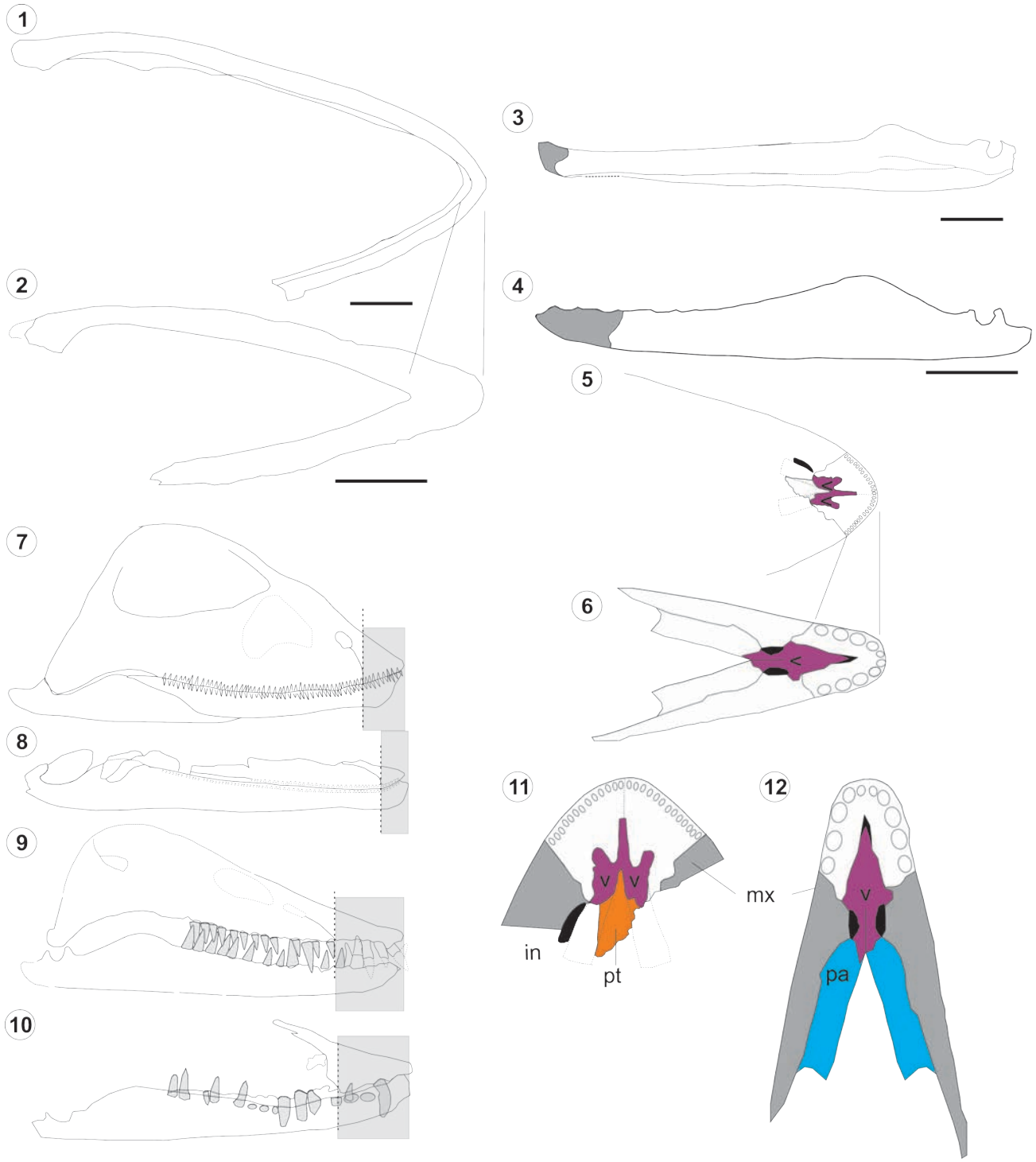

2


3
N
Cañadon del Loro
Paso del Sapo
Sierra de Taquetren
42°45'
69°30'
0 2 4Km
N
ATLÁNTIC OCEAN
0 400 Km
Aluvial and salty deposits
Agradacional deposits
El Mirador Fm. (Upper Miocene)
Collon Curá Fm. (Miocene)
Huitrera Fm. (Paleogene)
Lefipan Fm. (Maastrichtian)
Paso del Sapo Fm. (Campanian)
Las Leoneras Fm. (Jurassic)
Lonco trapial Fm. (Jurassic)
Basament


1
2
3
6 5 4 3 2 1
4
sq
sa
ju
mx
pmx
ar
q
an
de
5
sq
ar
an
6
pm
13
10
6


1
2
v
pt
pm
ni
pa
pt
v
3
4
pm
v
pt
in?
5
sp
san
ar
an
an


1
2
3
4
337
2749
5
6
ar
kl


1
2
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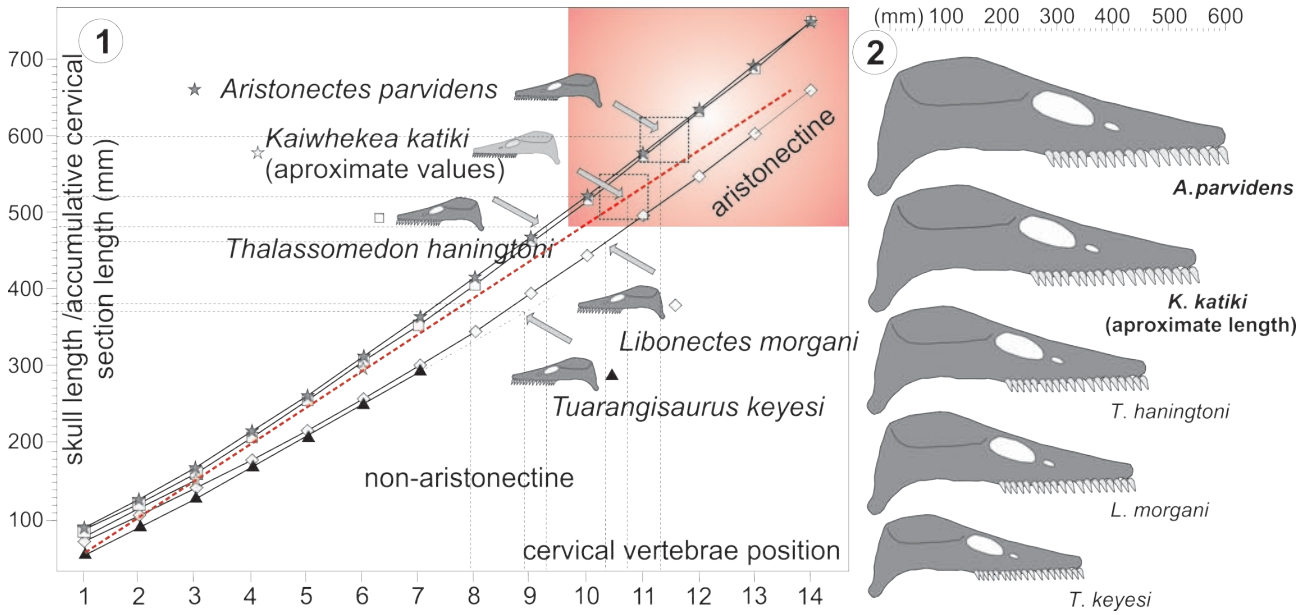
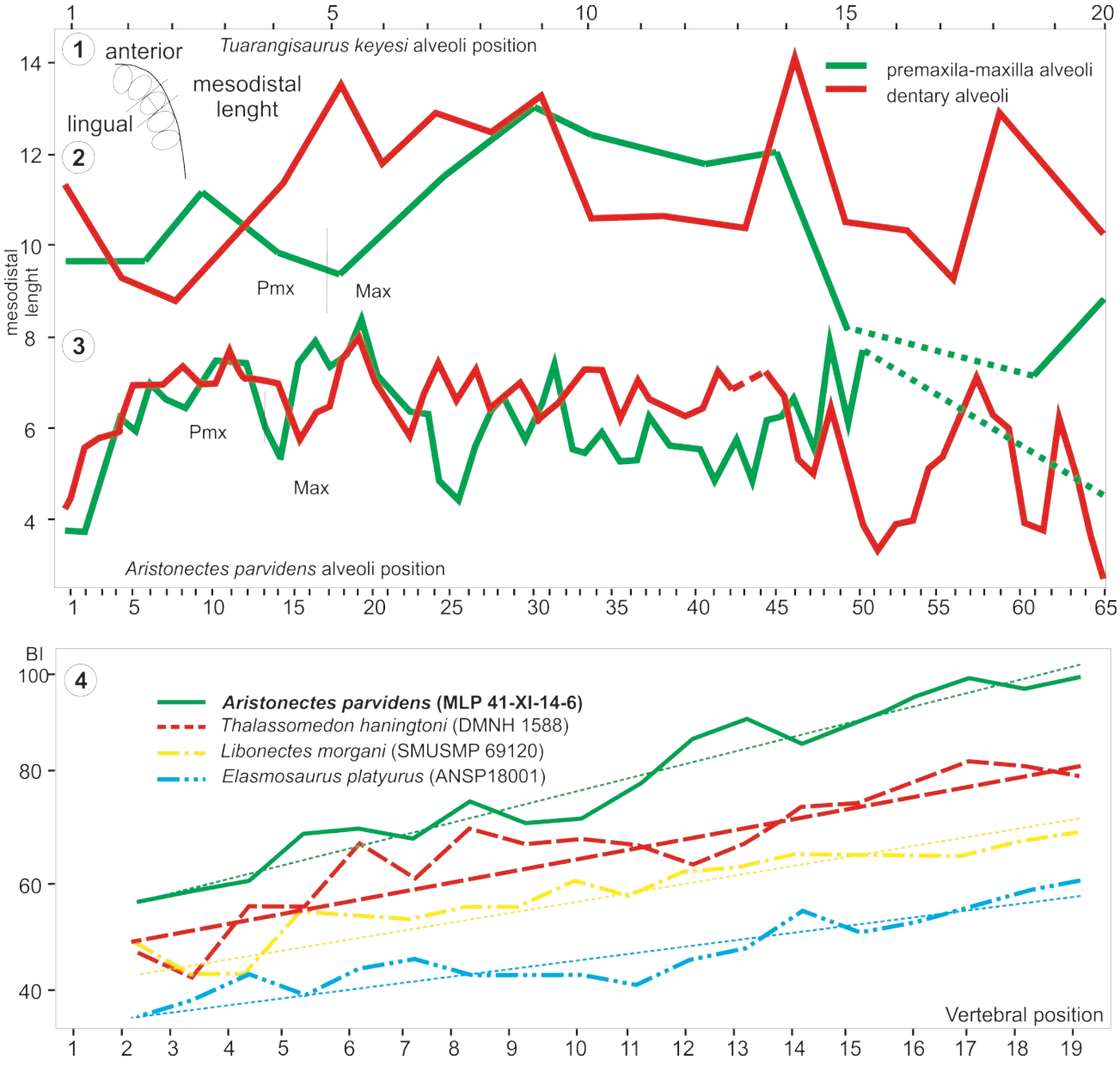
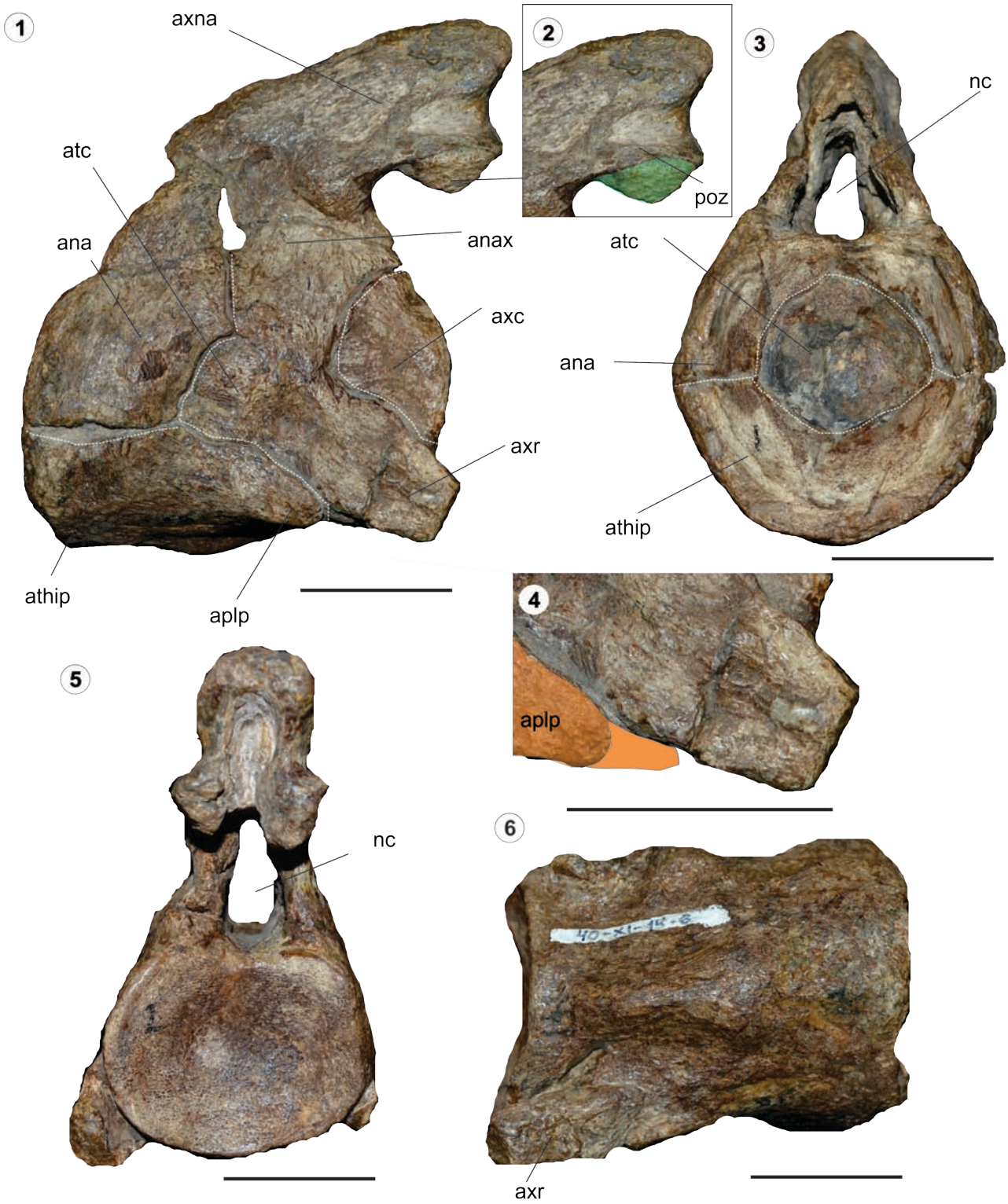
4
5
6
7
8
9
10
11
12
v
v
v
v
in
pt
mx
pa


1
skull length /accumulative cervical section length (mm)
700
600
500
400
300
200
100
Aristonectes parvidens
Kaiwhekea katiki
(aproximate values)
Thalassomedon haningtoni
aristonectine
Libonectes morgani
Tuarangisaurus keyesi
non-aristonectine
cervical vertebrae position
1 2 3 4 5 6 7 8 9 10 11 12 13 14
2
(mm) 100 200 300 400 500 600
A.parvidens
K. katiki
(aproximate length)
T. haningtoni
L. morgani
T. keyesi


1
anterior
lingual
mesodistal
lenght
2
Tuarangisaurus keyesi alveoli position
premaxila-maxilla alveoli
dentary alveoli
mesodistal lenght
Pmx
Max
3
Pmx
Max
Aristonectes parvidens alveoli position
4
BI
Aristonectes parvidens (MLP 41-XI-14-6)
Thalassomedon haningtoni (DMNH 1588)
Libonectes morgani (SMUSMP 69120)
Elasmosaurus platyurus (ANSP18001)
Vertebral position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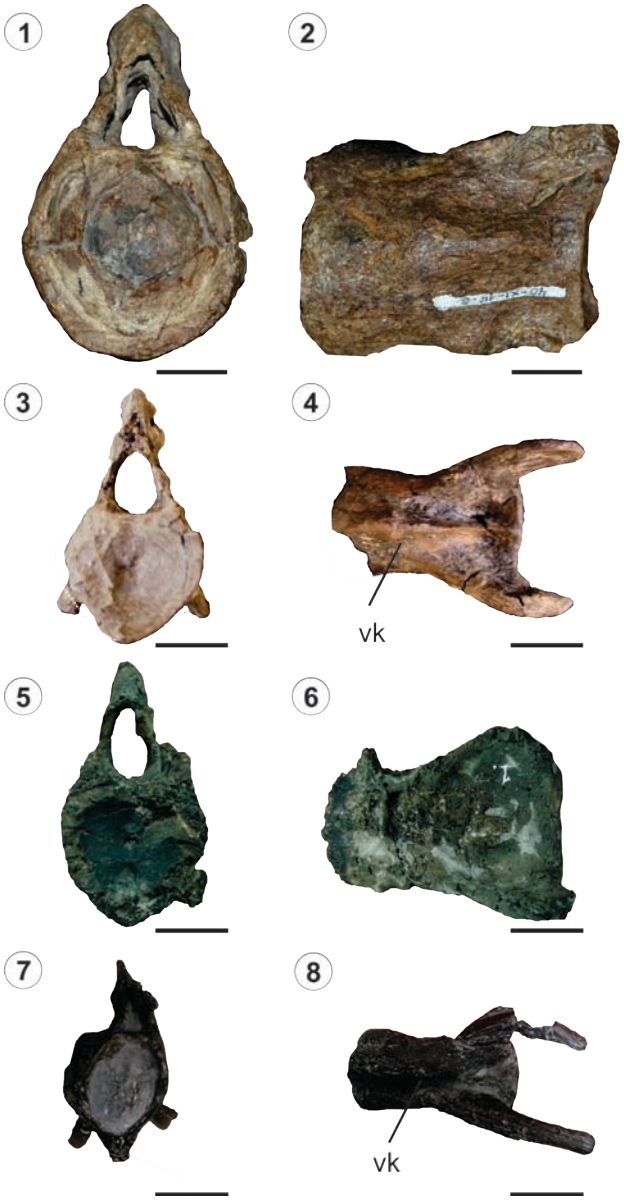
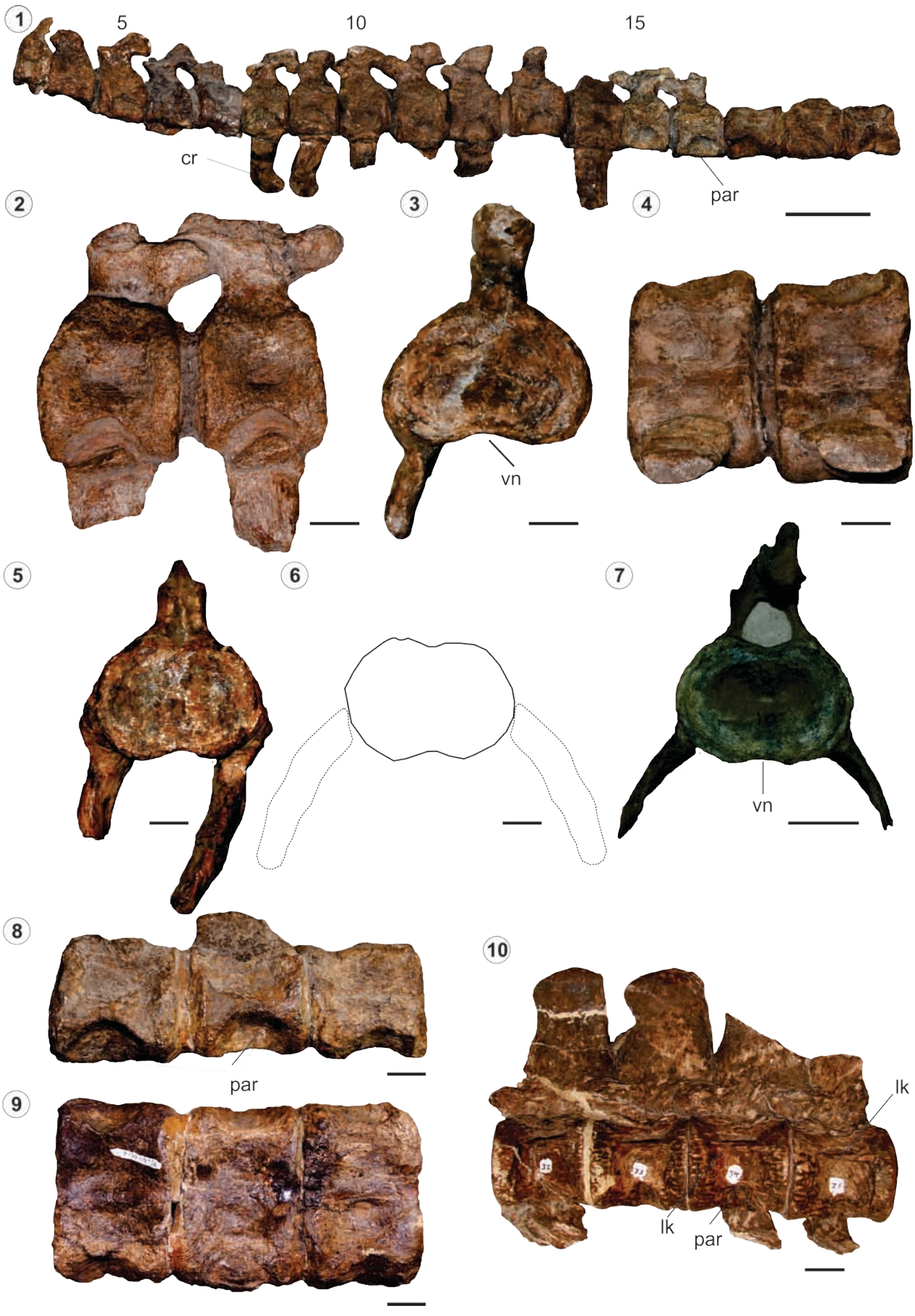
axna
atc
ana
anax
axc
axr
athip
aplp
2
poz
3
nc
atc
ana
athip
4
aplp
5
nc
6
axr


1
2
3
4
vk
5
6
7
8
vk


1
5
10
15
cr
par
2
3
vn
4
5
6
7
vn
8
par
9
10
lk
lk
par

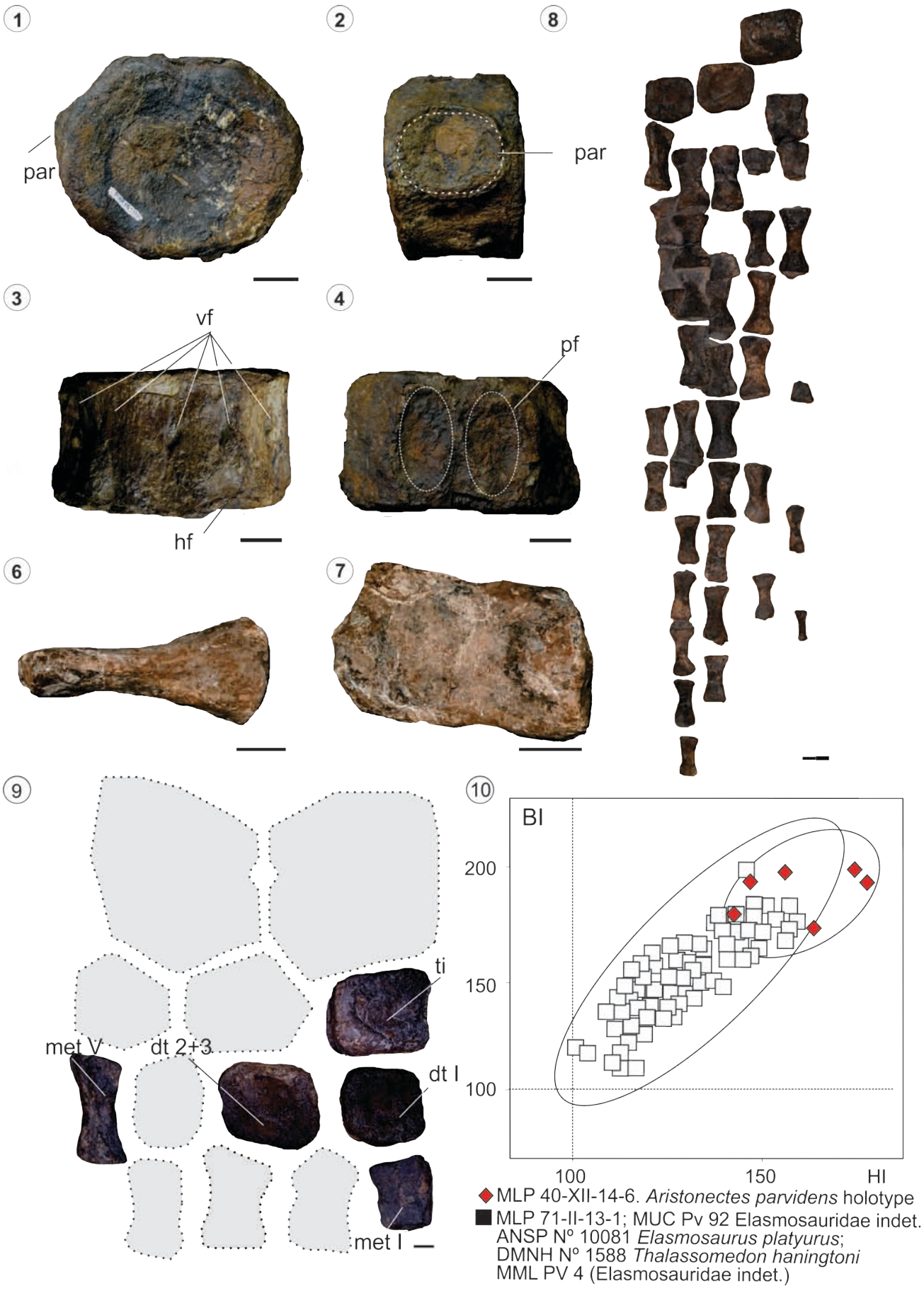

1
par
2
par
8
3
vf
hf
4
pf
6
7
9
ti
met V
dt 2+3
dt I
met I
10
BI
200
150
100
100
150
HI
MLP 40-XII-14-6. Aristonectes parvidens holotype
MLP 71-II-13-1; MUC Pv 92 Elasmosauridae indet.
ANSP Nº 10081 Elasmosaurus platyurus;
DMNH Nº 1588 Thalassomedon haningtoni
MML PV 4 (Elasmosauridae indet.)

TABLE 1- Elasmosaurid taxa considered on the cuantitative comparison with Aristonectes parvidens. Data taken from (Cabrera, 1941; Welles, 1943; Wiffen and Moysley, 1986; Carpenter, 1999; Cruickshank and Fordyce, 2002; Sach and Kear, 2014).

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, CD425	Mangahouanga Stream, inland Hawke's Bay, New Zealand/ Tahora Formation. upper Campanian-lower Maastrichtian
Callawayasaurus colombiensis (Welles) Carpenter, 1999	UCMP 38349	Villa de Leyva, Colombia/Paja Fm. upper Aptian
Libonectes morgani Welles,1949	MU SMP 69120	Dallas County, Texas, USA/ Britton Fm. upper Cenomanian
Aristonectes parvidens Cabrera, 1941	MLP 40-XI-14-6	Paso del Sapo, Cubut Province, Argentina/Lefipan Fm. Maastrichtian.
Kaiwhekea katiki Cruickshank and Fordyce, 2002	OU 12649	Shag Point, North Otago, New Zealand. Katiki Fm. boundary between Upper and Lower Maastrichtian

TABLE 2-Aristonectes parvidens MLP 40-XI-14-6, cranium and mandible measurements (in mm). ~ indicates approximate measurements.

Measurement	*value (mm)*
skull length	*~600*
pre-glenoid length	*674*
premaxilla anteroposteriorly length	*74*
premaxilla transversely length	*135*
symphysis anterioposterior length	*45.33*
mandible height at coronoid process level	*124*
coronoid-symphysis distance	*534*

TABLE 3- Aristonectes parvidens MLP 40-XI-14-6 vertebral measurements (in mm): L, length; H, height and B, breadth, indexes HI, height (H)/length (L) ratio (HI=100*H/L), BI, breadth (B)/length (L) ratio (BI=100*B/L), BHI, breadth/height ratio (BHI=100*B/H) and VLI, Vertebral Length Index [VLI= 100*L / (0.5*(H + B))].

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*

TABLE 4- Number of dentary alveoli (Al), skull length (SL, in mm), and ratio between both values(Ar) and the predicted number of aristonectine alveoli number based on a non elasmosaurid mandible sizes. Values in italics are approximate. 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'G. pers. obs).

Taxon	*Dentary alveoli (Al)*	*Skull length (SL)*	*AR= SL/Al*	*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*, CD425)	*19-21*	*370*	*0.05405*	32	28
Libonectes *(SMU SMP 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*		

TABLE 5- Indicates the ratio between skull length and atlas axis length in aristonectine and non-aristonectine elasmosaurids. Values in bold are approximate. Data taken from (Welles, 1943, 1962; Wiffen and Moisley, 1986; Carpenter, 1999; J.P.O'G pers Obs.).

Taxon	*Skull length (mm)*	*Atlas-axis complex length (mm)*	*Radio skull length/atlas axis length*
Thalassomedon haningtoni (UNSM 50132)	*480 mm*	*77*	*6.23*
Tuarangisaurus keyesi (NZGS CD425)	*370 mm*	*55*	*6.72*
Libonectes morgani (SMU SMP 69120)	*466 mm*	*60.3*	*7.72*
Aristonectes parvidens (MLP 40-XI-14-6)	***600** mm*	*82*	*7.31*