Geol. Mag. **152** (*4*), *2015*, *pp. 694–710*. © *Cambridge University Press 2014*
doi:10.1017/S0016756814000636

Postcranium of the paradigm elasmosaurid plesiosaurian *Libonectes morgani* (Welles, 1949)

SVEN SACHS*† & BENJAMIN P. KEAR‡

*Im Hof 9, 51766 Engelskirchen, Germany
‡Palaeobiology Programme, Department of Earth Sciences, Uppsala University, Villavägen 16, SE-752 36 Uppsala, Sweden

(*Received* 17 June 2014; *accepted* 7 October 2014; *first published online* 20 November 2014)

Abstract – Elasmosauridae constitutes one of the most immediately recognizable plesiosaurian radiations. Their distinctive body plan represents the popular model for Plesiosauria, and is typified by an osteological morphology especially adapted for hyper-elongation of the neck. Nevertheless, many archetypal elasmosaurids are known only from incomplete and/or inadequately documented material, a problem that has contributed to their uncertain intra-clade relationships. A prime example of this is *Libonectes morgani* from the Upper Cretaceous of Texas, USA, which is frequently presented as an elasmosaurid structural proxy because of its three-dimensionally preserved holotype skull. Perplexingly though, both the taxonomic diagnosis and phylogenetic placement of *L. morgani* rely primarily upon the cervical vertebrae, together with the pectoral girdle and forelimb, yet most of these elements are now lost and figured only as line drawings. We therefore reviewed the remnant postcranial skeleton of *L. morgani* first-hand with the objective of clarifying its defining character states. Our observations showed that the existing diagnosis of *L. morgani* is indeed inadequate. Moreover, the only identifiable autapomorphies occurred within the axial skeleton. This concurred with an examination of character scores used in published plesiosaurian phylogenies, and highlights the persistent significance of postcranial elements for discriminating elasmosaurid taxa.

Keywords: Plesiosauria, axial skeleton, atlas-axis complex, systematics.

1. Introduction

Elasmosauridae constitutes one of the most immediately recognizable radiations of Mesozoic marine amniotes. Their distinctive body-shape encapsulates the popular concept of Plesiosauria, and via its selective tendency towards hyper-increase in the number of neck vertebrae, manifests one of the most extreme adaptive specializations evidenced in the vertebrate fossil record (see Sachs, Kear & Everhart, 2013). Yet despite this classic bauplan, the underlying intra-clade morphology of elasmosaurids is generally conservative, and in particular, incorporates numerous homoplastic traits within the diagnostic axial skeleton (see alternative datasets in Bardet, Godefroit & Sciau, 1999; Carpenter, 1999; O'Keefe, 2001; T. Sato, unpub. Ph.D. thesis, Univ. Calgary, 2002; Kear, 2005*a*; Großmann, 2007; Druckenmiller & Russell, 2008*a*; Ketchum & Benson, 2010; Vincent *et al*. 2011; Kubo, Mitchell & Henderson, 2012; Benson & Druckenmiller, 2014; Otero *et al*. 2014). Evidence of this structural ambiguity is discernible in fluid phylogenetic topologies and the persistent attribution of incomplete specimens, which have extended the chronostratigraphical distribution of putative elasmosaurids from uppermost Lower to uppermost Upper Cretaceous strata (Aptian–Maastrichtian, see synopses in Welles, 1962; Vincent *et al*. 2011), to the lowermost Cretaceous (Valanginian, *Brancasaurus brancai* Wegner, 1914, see O'Keefe, 2001, 2004), Lower–Middle Jurassic (Toarcian *Hydrorion brachypterygius* (von Huene, 1923) and *Occitanosaurus tournemirensis* Bardet, Godefroit & Sciau, 1999 to Callovian *Muraenosaurus leedsii* Seeley, 1874, see Bardet, Godefroit & Sciau, 1999; Großmann, 2007; Druckenmiller & Russell, 2008*a*) and even Upper Triassic (Norian, *Alexeyisaurus karnoushenkoi* Sennikov & Arkhangelsky, 2010).

Of the indisputably referred elasmosaurid taxa, *Libonectes morgani* from the lower Upper Cretaceous of Texas, USA, is one of the most frequently discussed, and has been repeatedly used as a structural archetype for elasmosaurid anatomy because of its three-dimensionally preserved holotype skull (SMU SMP 69120, see Carpenter, 1997; Araújo & Polcyn, 2013). Originally, however, the virtually complete cranium and mandible of SMU SMP 69120 were found in articulation with a continuous series of 62 vertebrae, ribs, the pectoral girdle and parts of the forelimbs (Fig. 1). These were excavated sometime prior to the 1940s by a tenant farmer near Dallas, Mr T. W. Tidwell, and eventually donated to the Department of Geology at Southern Methodist University (SMU) by the local landowner Mr Andy Anderson (Shuler, 1950). Welles (1949) formally described SMU SMP 69120 and established it as the type of a new species *Elasmosaurus morgani*, which was later reassigned to a separate genus, *Libonectes*

---

†Author for correspondence: sachs.pal@gmail.com

Figure 1. Original site photographs (reproduced from Shuler, 1950) of the holotype skeleton of *Libonectes morgani* (SMU SMP 69120) as it occurred *in situ* during excavation. The image on the left also shows the discoverer T. W. Tidwell.

Carpenter, 1997, by Carpenter (1997). Shuler (1950) also contributed a popular account of the discovery and reported on the preservational state of the skeleton. Sadly though, during relocation of the SMU palaeontology collection to a new storage facility, the caudal-most cervicals and appendicular skeleton of SMU SMP 69120 were unwittingly discarded (G. W. Storrs, unpub. M.Sc. thesis, Univ. of Texas, 1981). As a result, these elements are today represented only by the scant text and interpretive line drawings of Welles (1949), as well as the illustrations reproduced by Welles (1952, 1962), and Shuler's (1950) anecdotal summary. Moreover, this non-confirmable information has been unquestionably accepted as reliable data for phylogenetic analyses (e.g. Carpenter, 1999; O'Keefe, 2001; T. Sato, unpub. Ph.D. thesis, Univ. Calgary, 2002; Großmann, 2007; Druckenmiller & Russell, 2008*a*; Ketchum & Benson, 2010; Vincent *et al*. 2011; Benson & Druckenmiller, 2014). To test this assumption, we reassessed SMU SMP 69120 first-hand with the aim of confirming its postcranial character state manifestations. Our observations are presented herein, along with a critique of diagnostic traits, and a comprehensive descriptive synopsis of one of the world's most significant elasmosaurid plesiosaurians.

Institutional abbreviations: ANSP – Academy of Natural Sciences of Drexel University, Philadelphia, USA; NZGS – New Zealand Geological Survey, Lower Hutt, New Zealand; RSM – Royal Saskatchewan Museum, Regina, Canada; SMNK – Staatliches Museum für Naturkunde Karlsruhe, Germany; SMU SMP – Shuler Museum of Paleontology, Southern Methodist University, Dallas, USA; TMM – Texas Memorial Museum, Austin, USA.; TMP – Royal Tyrrell Museum of Paleontology, Drumheller, Canada; UCMP – University of California Museum of Paleontology, Berkeley, USA.

2. Systematic palaeontology

Superorder SAUROPTERYGIA Owen, 1860
Order PLESIOSAURIA de Blainville, 1835
Family ELASMOSAURIDAE COPE, 1869
Genus *Libonectes* Carpenter, 1997
Libonectes morgani (Welles, 1949)

Holotype. SMU SMP 69120, skull and mandible, atlas–axis complex, 48 successive cervical vertebrae, fragmentary thoracic ribs, gastralia and associated gastroliths. Welles (1949) also reported an additional 14 cervical vertebrae (potentially including an undetermined number of pectorals), both coracoids, scapulae, the clavicular complex, the right humerus, epipodials (two radii) and distal forelimb elements as components of the recovered skeleton, which are now lost.

Differential diagnosis. Characters follow the phylogenetically derived unambiguous elasmosaurid clade definitions of Druckenmiller & Russell (2008*a*), Ketchum & Benson (2010) and Vincent *et al*. (2011) with state distributions for *Libonectes morgani* determined from original fossils. Features differentiating *L. morgani* from non-elasmosaurid plesiosaurians are: loss of the pineal foramen and rostral interpterygoid vacuity; a 'massive' quadrate; a 'keyhole-shaped' foramen magnum; an oval tooth cross-section shape in the rostal-half of the premaxillary–maxillary tooth row; a high coronoid eminence on the mandible; the craniad and middle cervical centra longer than high; a longitudinal ridge present on the lateral surface of the craniad cervical centra; the combined width of cervical zygapophyses distinctly narrower than the centrum; and the presence of a caudad intercoracoid vacuity (inferred from the published description of Welles, 1949). *Libonectes morgani* can be distinguished within Elasmosauridae by: loss of the pineal foramen, which is retained in *Callawayasaurus colombiensis* (Welles, 1962) (see Welles, 1962) and species of *Aristonectes* Cabrera, 1941 (see Chatterjee & Small, 1989; Otero *et al*. 2014), as well as the putative elasmosaurids *Brancasaurus brancai* Wegner, 1914 (see Wegner, 1914), *Muraenosaurus leedsii* Seeley, 1874 (see Druckenmiller & Russell, 2008*a*), *Microcleidus homalospondylus* (Owen, 1865) (see Brown, Vincent & Bardet, 2013), *Seeleyosaurus guilelmiimperatoris* (Dames, 1895) and *Hydrorion brachypterygius* (von Huene, 1923) (see Großmann, 2007); a prominent dorsomedian ridge on the premaxillae unlike *Hydrotherosaurus alexandrae* Welles, 1943 and *Styxosaurus snowii* (Williston, 1890) (see Ketchum & Benson, 2010); five premaxillary teeth, differing from *Kaiwhekea katiki* Cruickshank & Fordyce, 2002 (see Cruickshank & Fordyce, 2002) and *Elasmosaurus platyurus* Cope, 1868 (see Sachs, 2005*a*); a heterodont maxillary dentition that incorporates teeth with an oval cross-section, as opposed to the distinctly homodont tooth arrangement occurring in *Futabasaurus suzukii* Sato, Hasegawa & Manabe, 2006 (see Sato, Hasegawa & Manabe, 2006), and the rounded tooth cross-sections of *Eromangasaurus australis* (Sachs, 2005*b*) (see Kear, 2005*a*), *Terminonatator ponteixensis* Sato, 2003 (see Sato, 2003) and the Early Jurassic taxon *Occitanosaurus tournemirensis* (see Bardet, Godefroit & Sciau, 1999); suturing of the pterygoids behind the caudal interpterygoid vacuity, and contact of the prezygapophyses for their entire transverse width, differing from the separated pterygoids and prezygapophyseal articular surfaces of *Thalassomedon haningtoni* Welles, 1943 (see Welles, 1943); amphicoelous craniad cervicals contrasting with the platycoelous centra of *Mauisaurus haasti* Hector, 1874 (see Hiller *et al*. 2005); and the presence of a ventral notch on the cervical centra unlike *Tuarangisaurus keyesi* Wiffen & Moisley, 1986 (see Wiffen & Moisley, 1986) and the referred elasmosaurids *Gronausaurus wegneri* Hampe, 2013 (see Hampe, 2013; Benson & Druckenmiller, 2014) and the ‘Speeton Clay plesiosaurian’ (see Benson & Druckenmiller, 2014). Finally, based solely upon the account of Welles (1949), *L. morgani* differs from *Aphrosaurus furlongi* Welles, 1943, *Morenosaurus stocki* Welles, 1943, *Hydralmosaurus serpentinus* (Cope, 1877) (see Welles, 1962), *Albertonectes vanderveldei* Kubo, Mitchell & Henderson, 2012 (see Kubo, Mitchell & Henderson, 2012) and *Zarafasaura oceanis* Vincent, Bardet, Pereda Suberbiola, Bouya, Amaghzaz & Meslouh, 2011 (see Lomax & Wahl, 2013) by the presence of a pectoral bar; and *Waputskanectes betsynichollsae* Druckenmiller & Russell, 2006 (see Druckenmiller & Russell, 2006) in its distinctly angled articulations for the epipodials.

Stratigraphical and geographical provenance. Welles (1949) listed the type locality as ‘Andy Anderson farm’, approximately 2 km (1.25 miles) NW of the TV tower, W of Cedar Hill, Dallas County, Texas, USA (see also G. W. Storrs, unpub. M.Sc. thesis, Univ. of Texas, 1981). McGowen *et al.* (1987) included this outcrop area within the Eagle Ford Group (their Eagle Ford Formation), although recent site surveys refer it to the Britton Formation (Jacobs *et al*. 2013), which constitutes the lower section of the Eagle Ford Group sequence (Dawson, 2000). In his unpublished thesis, Storrs (G. W. Storrs, unpub. M.Sc. thesis, Univ. of Texas, 1981, p. 101) noted that ammonites identified as ‘*Helicoceras pariense*’ had been found in association with SMU SMP 69120. Kennedy (1988) synonymized this nominal with *Allocrioceras annulatum* (Shumard, 1860), an anisoceratid heteromorph index species correlated with the lower upper Cenomanian *Sciponoceras gracile* Zone of the Western Interior succession (Cobban, 1984; Kennedy & Cobban, 1991; see also Kennedy, Walaszczyk & Cobban, 2005 for distribution relative to the Cenomanian–Turonian type section). Significantly, this is inconsistent with previous accounts of SMU SMP 69120 (e.g. Carpenter, 1997 and later papers), which usually ascribe the type specimen to Turonian strata but without justification (see Jacobs *et al*. 2013). We therefore suggest that SMU SMP 69120 might alternatively be late Cenomanian (early Late Cretaceous) in age, pending a detailed stratigraphical reassessment of the type locality.

3. Description and comparisons

3.a. Atlas–axis complex

The atlas–axis complex of SMU SMP 69120 (Fig. 2a–e) is very well preserved and shows complete co-ossification of its component elements without trace of sutures (consistent with osteological maturity, see Welles, 1949; Brown, 1981). The conjoined atlas intercentrum – axis centrum is cylindrical and distinctly longer than high (Fig. 2c, Table 1, an ontogenetic feature *sensu* Brown, 1981), as illustrated in a number of other elasmosaurids (e.g. Welles, 1943, p. 239, pl. 22, fig. a; Wiffen & Moisley, 1986, p. 212, fig. 4; Sachs, 2005*a*, p. 100, fig. 4A, B; Kubo, Mitchell & Henderson, 2012, p. 561, fig. 4A, B, D; Otero *et al.* 2014, p. 112, fig. 10A), and the atlantal cotyle is deeply concave (Fig. 2a). The cotylar rim is surrounded by a thin edge that is damaged along its right ventrolateral margin; its dorsal midline is incised by a tapered notch (Fig. 2a, d). Ventrally, the atlas intercentrum contributes to a prominent hypophyseal ridge (Fig. 2c, e) similar to that reported in *Elasmosaurus platyurus* (Sachs, 2005*a*), *Eromangasaurus australis* (Kear, 2005*a*) and *Albertonectes vanderveldei* (Kubo, Mitchell & Henderson, 2012). Its proximal extremity forms a ‘lappet-like’ projection; distally this is expanded into a prominent flattened tubercle (15.7/8 mm in maximum length/width: Fig. 2e), which is elliptical in outline and situated beneath the atlas intercentrum

Table 1. Measurements (mm) of the atlas–axis complex in SMU SMP 69120, the holotype of *Libonectes morgani*

Parameter	Measurement
Length of co-ossified atlas–axis centrum complex	69.35
Length from cranial edge of atlantal cup to caudal extremity of postzygapophysis	88.55
Width of atlantal cup (between inner lateral edges)	34.51
Width of cranial end of atlas	39.62
Height of atlas at atlantal cup	41.40
Length of atlas rib facet	21.13
Height of atlas rib facet	8.25
Craniocaudal diameter of axis rib at base	17.43
Length of axis rib long axis	25.93
Transverse diameter of axis rib in mid-section	11.07
Width of articular facet of axis centrum	48.27
Height of articular facet of axis centrum	39.36
Length of atlas neural arch at the base of the neural canal	20.09
Length of axis neural arch at the base of the neural canal	27.18
Internal width of neural canal at cranial end	21.82
Height of neural canal at cranial end	21.85
Internal width of neural canal at caudal end	18.08
Height of neural canal at caudal end	20.16
Length of neural spine long axis	59.84
Maximum width of neural spine caudally	11.26
Length of postzygapophysis long axis	21.74
Width of postzygapophysis	11.85

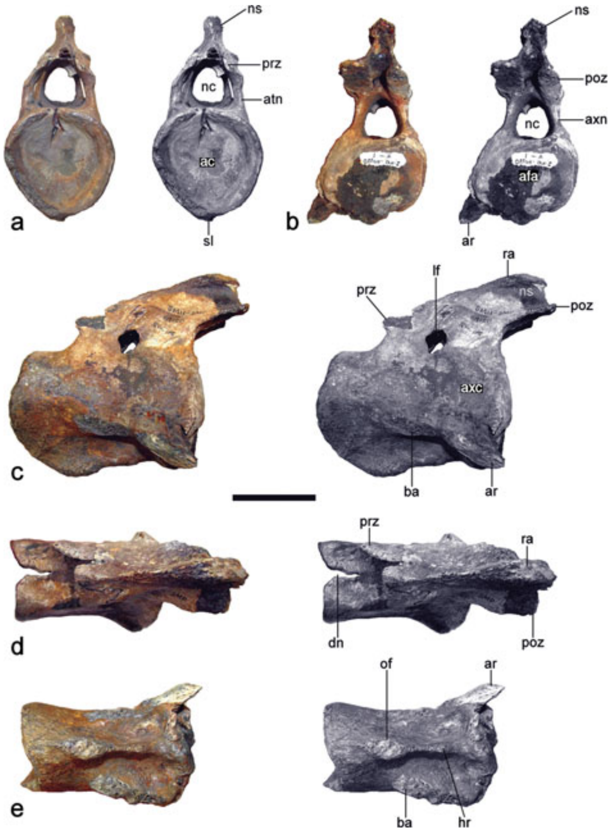

Figure 2. (Colour online) Atlas–axis complex of the *Libonectes morgani* holotype SMU SMP 69120 shown in (a) cranial, (b) caudal, (c) lateral, (d) dorsal and (e) ventral views (with labelled graphic restoration shown on right). Abbreviations: ac – atlantal cotyle; afa – articular facet of axis; ar – axis rib; atn – atlas neural arch; axc – axis centrum; axn – axis neural arch; ba – base of atlas rib; dn – dorsal notch in atlantal cup; hr – hypophyseal ridge; lf – lateral foramen; nc – neural canal; ns – neural spine; of – oval facet in hypophyseal ridge; poz – postzygapophysis; prz – prezygapophysis; ra – rugose area of neural spine; sl – sagittal lip. Scale bar equals 30 mm.

(17 mm from the craniad edge of the atlantal contyle). Noticeable transverse expansion of the craniad hypophyseal ridge has been recorded in *A. vanderveldei* (Kubo, Mitchell & Henderson, 2012, p. 561, fig. 4D), and a hypophyseal tubercle is also known in *Abyssosaurus nataliae* Berezin, 2011 (Berezin, 2011, p. 651, fig. 1d). Caudally, the hypophyseal ridge widens and merges with the articular face of the axis centrum, whose ventral surfaces are deeply excavated adjacent to the ventrolaterally oriented axial rib heads. The atlas ribs are broken off but their elongate oval bases (20.8/8.4 mm in maximum length/height) are still visible and situated at the approximate mid-section of the atlas–axis complex. Only the left axial rib is complete (Fig. 2c, e) and directly abuts the atlas rib remnant. In lateral view, the shaft of the axial rib tapers caudoventrally but does not project beyond the articular face of the axis centrum (Fig. 2c); this is in marked contrast to the elongate and backswept atlas–axis ribs of *Thalassomedon haningtoni* (Welles, 1943, p. 239, pl. 22a), *Libonectes atlasense* Buchy, 2006 (Buchy, 2006, p. 24, fig. 6b), *A. vanderveldei* (Kubo, Mitchell & Henderson, 2012, p. 561, fig. 4D) and *Aristonectes quiriquinensis* Otero, Soto-Acuña, O'Keefe, O'Gorman, Stinnesbeck, Suárez, Rubilar-Rogers, Salazar & Quinzio-Sinn, 2014 (Otero *et al.* 2014, p. 112, fig. 10A). The dorsolateral side of the axial rib in SMU SMP 69120 is distinctly concave, and its craniad surface is rugose, presumably for overlapping contact from the atlas rib as in other elasmosaurids (see Chatterjee & Small, 1989; Gasparini *et al.* 2003; Kear, 2005*a*; Kubo, Mitchell & Henderson, 2012; Otero *et al.* 2014).

The articular face of the axis centrum is wider than high (Table 1) and surrounded by a thickened convex rim (Fig. 2b). Its surface is partly obscured by matrix but was clearly shallowly concave with a slight notch in its dorsal margin.

The neural canal is arched and wider cranially than caudally. The cranial end is sub-circular in outline but becomes triangular caudally (Fig. 2a, b). The floor of the neural canal is perforated by a single elongate foramen near its caudal end. The atlas neural arch bases are craniocaudally shorter than those of the axis (20.9 mm versus 26 mm), and their contact is perforated by a large foramen (similar to that depicted in *Aristonectes parvidens* Cabrera, 1941, *E. platyurus* and *L. atlasense*, see Gasparini *et al*. 2003, p. 108, fig. 2C; Sachs, 2005*a*, p. 100, fig. 4A; Buchy, 2006, p. 24, fig. 6b; Fig. 2c this paper). A pronounced lateral ledge runs from the dorsocaudal edge of the atlas neural arch to the axis neural spine, and merges with the bone surface 22 mm from the top of the lateral foramen. The bone surface between this ledge and neural spine in gently dished.

The atlantal prezygapophyses (Fig. 2a) are incomplete. Likewise, the right axial postzygapophysis is damaged, but the preserved left postzygapophysis is gently dorsocaudally oriented in lateral view and has an elliptical outline with a weakly concave articular surface when observed in caudoventral aspect (Fig. 2b). The postzygapophyses protrude beyond the caudal edge of the axis centrum for their entire length (contrary to Buchy, 2006, p. 7; see Fig. 2c) and are separated by a deep medial excavation that is buttressed laterally against broad ledges converging towards the neural spine (Fig. 2b). The neural spine itself is dorsocaudally inclined at ~ 35° relative to the long axis of the centrum. The craniad side of the neural spine forms a sharp edge, and is transversely expanded dorsocaudally such that its apex expands into a rugose platform that is transversely broadest caudally (Fig. 2d).

3.b. Postaxial cervical vertebrae

Welles (1949, p. 15) reported an articulated series of 62 cervical vertebrae in SMU SMP 69120, with the 61st situated in the clavicular region, and the disarticulated 62nd lying on its side within the partly prepared block containing the pectoral girdle. Welles (1949) assumed that the 62nd vertebra was the last cervical, but it could have been the first pectoral (Welles, 1962). Welles (1949. pp. 15, 18) also calculated a maximum length for the neck at 5.618 m (‘18 feet 5 inches’). Presently, though, remnants of only 50 cervicals (including the atlas–axis complex) are preserved (this concurs with the count of G. W. Storrs, unpub. M.Sc. thesis, Univ. of Texas, 1981, p. 101). Some of these bear fused fragments of the neural spines and cervical ribs; unfortunately, though, most of these components were broken off and lost during the initial excavation (Welles, 1949, p. 15). Many vertebrae, especially from the craniad section of the neck, are likewise incomplete. However, their proportions clearly increased towards the caudal end of the column (centrum measurements in Welles, 1949, pp. 16–17, table 1), with the cranial-most cervicals being wider than long or high, and their length marginally greater than their height (Fig. 3 a–c; Welles, 1949, p. 16, table 1). This proportional trend changes from cervicals 26–36, where the maximum length increases substantially and exceeds both the height and width; from cervical 36 onwards the centra once more become broader (Fig. 3i–t; Welles, 1949 pp. 16–17, table 1). O’Keefe & Hiller (2006) established that cervical centrum proportions in elasmosaurids were subject to extreme variability, although a vague pattern of proportional length increase throughout the midsection of the neck was noticeable in many taxa. They also extrapolated that the complete caudad cervical series of SMU SMP 69120 would have had dimensions markedly dissimilar to the extremely long-necked morphotypes *Elasmosaurus platyurus* and *Styxosaurus snowii* (Williston, 1890) (the latter following synonymy of Carpenter, 1999).

The articular faces of the cervical centra in SMU SMP 69120 have thickened convex rims. These are pronounced in the cranial cervicals (Fig. 3b, f, j), but become less distinct caudally and are lost in the caudalmost cervicals. Brown (1981) considered this feature indicative of osteological maturity amongst plesiosaurians (e.g. ANSP 10081, the ‘adult’ type specimen of *E. platyurus*, see Sachs, 2005*a*; Sachs, Kear & Everhart, 2013). SMU SMP 69120 also displays distinct amphicoely throughout the cervical column, up until cervical 43 where it is reduced, and by cervical 50 the vertebrae become platycoelous. The presence of platycoelous craniad cervicals has long been considered a diagnostic trait of Elasmosauridae (e.g. Andrews, 1910; Welles, 1943, 1962; Persson, 1963; Brown, 1981, 1993; Bardet, Godefroit & Sciau, 1999; O’Keefe, 2001; T. Sato, unpub. Ph.D. thesis, Univ. Calgary, 2002; Großmann, 2007; Druckenmiller & Russell, 2008*a*; Ketchum & Benson, 2010; Vincent *et al*. 2011; Smith, Araújo & Mateus, 2012; Otero, Soto-Acuña & Rubilar-Rogers, 2012). Nevertheless, amphicoely is documented in the craniad centra of even the most classic elasmosaurid taxa including *E. platyurus* (Sachs, 2005*a*), *Hydrotherosaurus alexandrae* and *Callawayasaurus colombiensis* (Welles, 1962), as well as in *Albertonectes vanderveldei* (Kubo, Mitchell & Henderson, 2012), which is also known from a complete cervical series.

A shallow notch is evident in the preserved ventral margin of both the cranial and caudal articular faces of all the cervicals in SMU SMP 69120 (Fig. 3f, j, n, r). A more pronounced expression of this trait is often evident in Late Cretaceous elasmosaurids (e.g. Welles, 1943; Cruickshank & Fordyce, 2002; Gasparini *et al*. 2003; Hiller *et al*. 2005; Sachs, 2005*a*; Sato, Hasegawa & Manabe, 2006; Kubo, Mitchell & Henderson, 2012; Hiller, O’Gorman & Otero, 2014; Otero *et al*. 2014), but has also been observed in basal plesiosauroids (e.g. *Occitanosaurus tournemirensis*: see Bardet, Godefroit & Sciau, 1999). In contrast, Early Cretaceous elasmosaurid taxa including *C. colombiensis* (Welles, 1962), *Eromangasaurus australis* (Kear, 2005*a*; Sachs, 2005*b*), as well as other coeval indeterminate specimens (e.g. Kear, 2002, 2005*b*, 2006; Sachs, 2004) tend to lack this feature. A pronounced

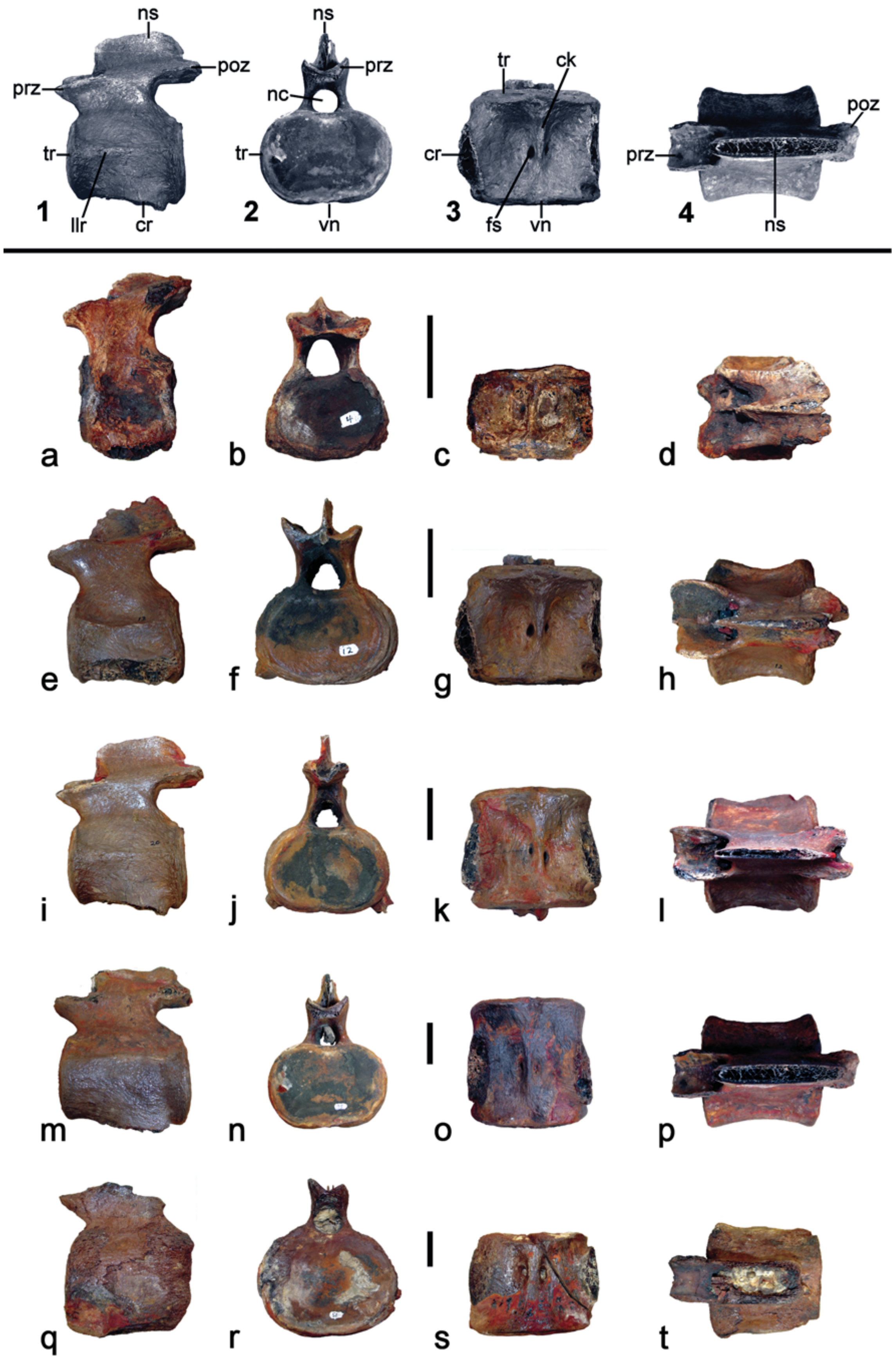

Figure 3. (Colour online) Selected cervical vertebrae of the *Libonectes morgani* holotype SMU SMP 69120. Labelled graphical restoration shown in (1) lateral, (2) articular, (3) ventral and (4) dorsal views. Photographs of cervical 4 in (a) lateral, (b) cranial, (c) ventral and (d) dorsal views; cervical 12 in (e) lateral, (f) cranial, (g) ventral and (h) dorsal views; cervical 20 in (i) lateral, (j) cranial, (k) ventral and (l) dorsal views; cervical 35 in (m) lateral, (n) cranial, (o) ventral and (p) dorsal views; and cervical 51 in (q) lateral, (r) cranial, (s) ventral and (t) dorsal views. Abbreviations: ck – central keel; cr – cervical rib; fs – foramen subcentrale; llr – lateral longitudinal ridge; nc – neural canal; ns – neural spine; poz – postzygapophysis; prz – prezygapophysis; tr – thickened rim of articular facet; vn – ventral notch in articular facet. Scale bars equal 30 mm.

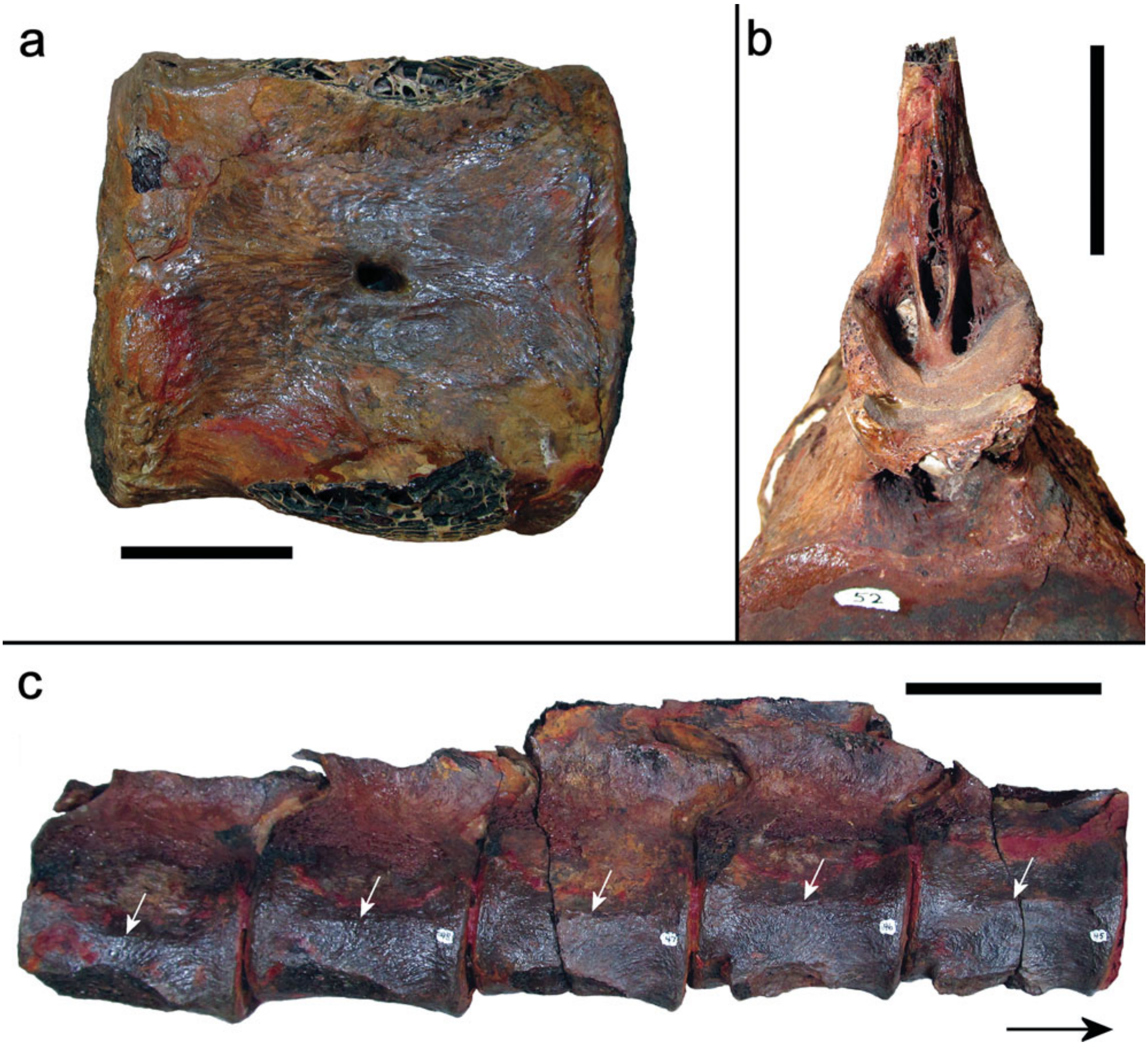

Figure 4. (Colour online) Diagnostic structures of the cervical vertebrae in the *Libonectes morgani* holotype SMU SMP 69120. (a) Conjoined *foramina subcentralia* in cervical 27 viewed in ventral aspect. (b) Divergent laminae at the craniad base of the neural spine in cervical 52. (c) Articulated cervicals 45–49 in lateral view indicating progressive migration of the longitudinal ridge (white arrows) across the lateral centrum surface (black arrow indicates craniad direction). Scale bars equal 30 mm in (a) and (b); 10 mm in (c).

longitudinal ridge is developed in between, and in contact with, the articular surface rims in most of the craniad cervicals of SMU SMP 69120 (Fig. 3a, e, i, m). It is not visible in the incomplete third cervical, and is only weakly expressed in the fourth, but is otherwise expressed on every centrum up until cervical 50. In the more craniad cervicals the longitudinal ridge is situated slightly dorsal to the lateral midline. However, by cervical 43 it progressively migrates down the lateral side of the centrum towards the rib facet and is eventually placed immediately dorsal to the rib facet on cervical 49, where it also loses contact with the articular surface rims (Fig. 4c). The presence of a longitudinal ridge is a phylogenetically defined synapomorphy for Elasmosauridae (Druckenmiller & Russell, 2008*a*; Ketchum & Benson, 2010), although it is barely developed in some taxa (e.g. *Aristonectes parvidens* and *A. quiriquinensis*, see Gasparini *et al.* 2003; O'Gorman, Gasparini & Salgado, 2013; Otero *et al.* 2014; caudad cervicals of *Futabasaurus suzukii* Sato, Hasegawa & Manabe, 2006), apparently absent in *Tuarangisaurus keyesi* (Wiffen & Moisley, 1986) and otherwise occurs widely in disparate long-necked plesiosaurians including *Seeleyosaurus guilelmiimperatoris* (Dames, 1895) (Fraas, 1910), *Muraenosaurus leedsii* (Andrews, 1910; Brown, 1981), *O. tournemirensis* (Bardet, Godefroit & Sciau, 1999) and *Spitrasaurus wensaasi* Knutsen, Druckenmiller & Hurum, 2012 (Knutsen, Druckenmiller & Hurum, 2012), where it probably correlates with convergent increase in the number of cervical vertebrae (Druckenmiller & Russell, 2008*a*). The adjacent lateral surfaces of the cervical centra are shallowly concave. The broken bases of the cervical ribs are ventrolaterally positioned and elliptical in basal outline throughout the column. They extend almost the entire length of the centrum in the cranial-most cervicals. The rib facets become longitudinally shorter towards the caudal end. In the mid-neck level, there is a gap between the rib facets and the craniad articular faces (e.g. in cervical 20). In the caudad cervicals (e.g. in cervical 54) the rib facets are placed about in the longitudinal mid-section of the centra (Fig. 3a, e, i, m).

A prominent midline keel transects between the paired *foramina subcentralia* (Storrs, 1991) on the ventral surfaces of all centra (Fig. 3c, g, k, o, s). This keel is narrow and rounded in the craniad cervicals, but becomes transversally broader and more flattened caudally (see cervical 51, Fig. 3s). It is also transversely flared at its terminal ends and more caudally expanded in the craniad cervicals. The elliptical *foramina subcentralia* are positioned directly adjacent to the midline keel. In the craniad cervicals they are situated within inset grooves (lost caudally), and may be offset relative to each other in cervical 19 and 20, but are fully conjoined in cervical 27 (Fig. 4a); a similar polymorphism has been detected in the holotype skeleton of *H. alexandrae* (UCMP 33912, see Welles, 1943) and indeterminate elasmosaurid specimens from the Maastrichtian of Morocco (Vincent *et al.* 2013). In the caudal-most cervicals the *foramina subcentralia* are very prominent and occupy about one-fifth of the length of the centra.

The cervical neural arches enclose a neural canal whose outline shape varies from nearly circular (at the cranial end) and triangular (at the caudal end) in the craniad cervicals (e.g. in 4, 11 and 20), to subtriangular (at the cranial end) and oval (at the caudal end) in the mid-neck (present in cervicals 27 to 35), and finally circular (at the cranial end) to oval (at the caudal end) in the caudal part of the neck (present in cervical 51). The prezygapophyses are not divided, but form a continuous concave articular surface (Fig. 3b, f, j, n, r: as described in many elasmosaurids, e.g. Welles, 1943; Sato, 2003; Sato, Hasegawa & Manabe, 2006; Kubo, Mitchell & Henderson, 2012; Vincent *et al.* 2013) whose width is distinctly less than the maximum transverse dimension of the centrum. The projecting cranial edge of the prezygapophyseal articular surface is embayed in dorsal view (most pronounced in cervical 4, Fig. 3d), and the lateral margins curve dorsolaterally when viewed in cranial aspect. In lateral perspective they also project well beyond the articular faces of the centra (Fig. 3a, e, i, m, q); this extends up to one-third of their articular surface length in the craniad cervicals (e.g. cervical 12, Fig. 3e), or approximately half in the mid-section of the neck (e.g. cervicals 20 and 35; Fig. 3i, m), and at around two-thirds in the caudal-most cervical vertebrae (e.g. cervical 52). The postzygapophyses are elliptical in shape in ventrolateral aspect, and dorsolaterally oriented in caudal view. Their articular surfaces are flattened. Unlike the prezygapophyses, the postzygapophyses diverge along their midline, but a transverse sheet of interconnecting bone is still evident caudally (Fig. 3l, p). The combined width of the postzygapophyses is less than that of the accompanying centrum. They also project beyond the caudal articular face by about half their length (e.g. cervicals 4 and 12; Fig. 3a, e); this reduces to around a third in the middle and caudal parts of the cervical column (e.g. cervicals 20 and 35; Fig. 3i, m). A rounded ledge runs from the caudal edges of the postzygapophyses to the base of the neural spine, and continues to contact the prezygapophyses in cervical 4; conversely this is less obvious in cervical 12 and disappears by cervical 20.

Only broken remnants of the neural spine bases are preserved. These suggest a transversely compressed cross-section that widens towards the caudal part of the column, and has a sharply tapered cranial edge (a corresponding rounded ridge is evident caudally). In lateral view, the cranial edge is dorsocaudally curved in the craniad cervicals. In cervical 4 it projects forward along the midline of the prezygapophyseal platform (Fig. 3d). In cervical 52 (and probably 58) the basal craniad edge of the neural spine bifurcates into paired lamellae that run parallel, and eventually merge (Fig. 4b). Deeply excavated cavities border these lamellae and are floored by prominent foramina opening into the spongiosa. Sato, Hasegawa & Manabe, (2006) and Vincent *et al.* (2013) described similar structures on the neural spines of other elasmosaurids and speculated that they might have served as attachments for connective tissue.

3.c. Ribs and gastroliths

Some sections of both the dorsal and gastral ribs, together with some gastroliths, are still preserved in SMU SMP 69120. Welles (1949) did not discuss these components in detail, but Shuler (1950) presented photographs of sectioned ribs (Shuler, 1950, pp. 10–11, figs 3, 4) and showed the gastralia in association with dispersed gastroliths (Shuler, 1950, pp. 19–21, figs 11–17). A few incompletely prepared gastralia are today evident in a large block of matrix and suggest an interlocking meshwork of dorsoventrally flattened elements similar to that found in other plesiosaurians (e.g. Sollas, 1881, pl. 23; Fraas, 1910, p. 114, fig. 3; Wegner, 1914, p. 281, fig. 9; Ketchum & Smith, 2010, p. 1077, fig. 5).

Shuler (1950, p. 18) mentioned that more than 70 gastroliths were originally present with the skeleton, and these ranged from around 10–80 mm (‘half an inch’ to ‘4 inches’) in maximum diameter. They were also apparently found enclosed within the ribcage, and lithologically composed of chert (‘flint’ *sensu* Shuler, 1950, p. 18).

3.d. Appendicular skeleton

Welles (1949, pp. 18–21) provided a brief description of the incompletely prepared pectoral girdle and partial right forelimb of SMU SMP 69120 (Fig. 5). The former incorporated the clavicle, possibly the interclavicle, both scapulae and the coracoids exposed in ventral view; these elements were articulated but somewhat distorted by crushing (Welles, 1949, pp. 18–19,

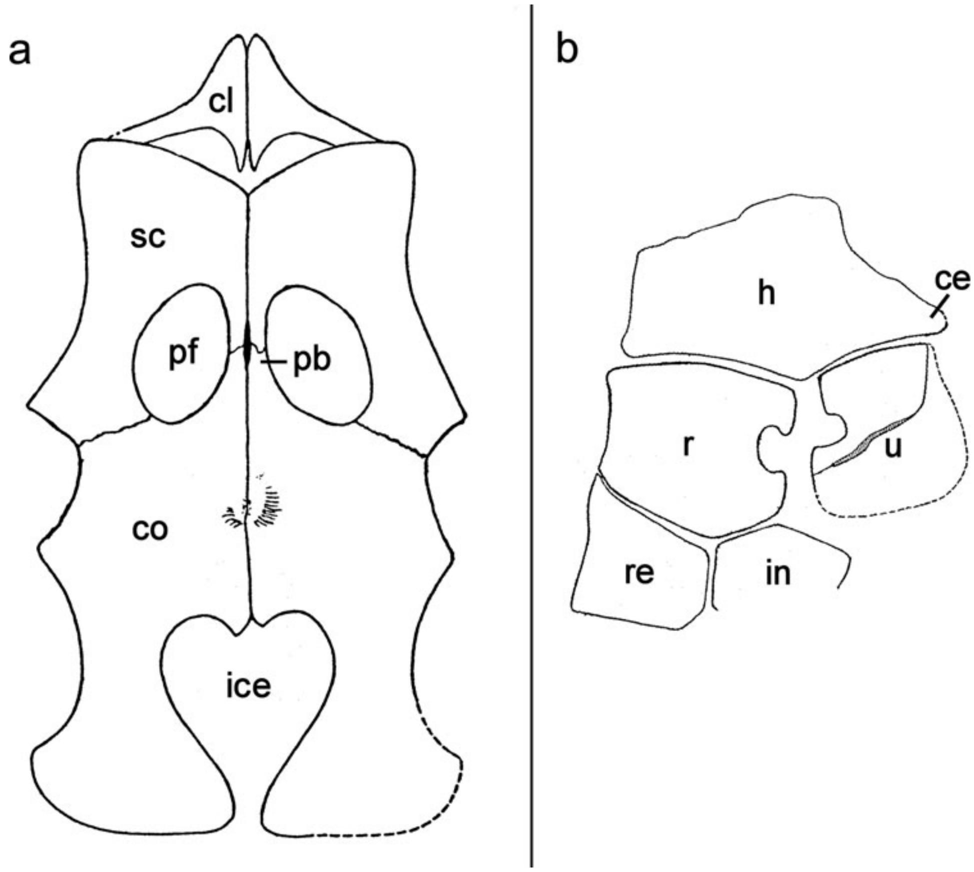

Figure 5. Schematic drawings (reproduced from Welles, 1949) of the now lost pectoral girdle and proximal forelimb elements of the *Libonectes morgani* holotype SMU SMP 69120. (a) Pectoral depicted in ventral view; (b) articulated proximal forelimb elements. Abbreviations: ce – caudal extension; cl – clavicle; co – coracoid; h – humerus; ice – intercoracoid embayment; in – intermedium; pb – pectoral bar; pf – pectoral fenestrum; r – radius; re – radiale; sc – scapula; u – ulna. The original restorations were not drawn to scale.

fig. 2). Welles (1949, 1962) examined the humerus, radius and radiale in his discussion of the limbs; however, part of the ulna and intermedium were also shown in his accompanying drawings, and a distal carpal and metacarpal were additionally mentioned. Furthermore, Shuler (1950, p. 9) stated that Welles (1949) measured the ‘pelvic area’, but this appears to be an error since there is no indication that the rear part of the skeleton was ever recovered.

According to Welles (1949, p. 18), the clavicles obscured part of an element that could have been the displaced interclavicle, but the exact arrangement of dermal bones along the craniad margin of the pectoral girdle was unclear. Nevertheless, the clavicles were apparently ‘fused along their midline’ (with greatest anteroposterior dimension along the central margin) and did not enclose a median fenestra (*sensu* Druckenmiller & Russell, 2008*a*, p. 19, characters 119–121, who scored these traits as present in the putative elasmosaurid *Muraenosaurus leedsii*). Welles (1949, p. 18) further reported that the scapulae met along the midline in a ‘long suture’ that excluded the clavicles from contact with the coracoids via a broad pectoral bar (‘ten centimeters wide and at least as deep’, but where these dimensions were measured was not stipulated). Development of the pectoral bar is known to have been ontogenetically variable in plesiosaurians (see Welles, 1952; Brown, 1981; Carpenter, 1999), yet it has been disparately incorporated into many phylogenetic character descriptions (e.g. O’Keefe, 2001; T. Sato, unpub. Ph.D. thesis, Univ. Calgary, 2002; Druckenmiller & Russell, 2008*a*; Ketchum & Benson, 2010; Benson & Druckenmiller, 2014). Amongst elasmosaurids, formation of the pectoral bar by the scapulae and coracoids seemingly occurred in the osteologically mature type specimens of *E. platyurus* (ANSP 10081: based upon the reconstruction by Cope, 1869, the original fossils are now lost) and *Waputskanectes betsynichollsae* (TMP 98.49.02, see Druckenmiller & Russell, 2006), as well as in indeterminate remains from the Maastrichtian of Morocco (Vincent *et al*. 2013). It has also been documented in *M. leedsii* and the reconstructed growth series of the Jurassic cryptoclidid *Cryptocleidus eurymerus* (Phillips, 1871) (Andrews, 1910; Brown, 1981; Carpenter, 1999).

According to the measurements published by Welles (1949, p. 21, table 2), the maximum parasagittal length of the coracoids exceeded that of the scapulae by a ratio of 1.5 (600 mm versus 400 mm). This does not comply with the proportions of the accompanying line drawing (yielding 1.36 for the same dimensional relationship, see Welles, 1949, p. 19, fig. 2), which we regard as schematic. Likewise, the redrafted diagram presented by Welles (1962, p. 58, fig. 12a) depicts different, albeit closer, parameters again (coracoid/scapula ratio = 1.48), and implies that the vaunted pectoral bar of SMU SMP 69120 was actually incomplete. Interestingly, O'Keefe (2001, 2002) proposed that 'plesiosauromorphs' generally trended towards shortening of the coracoid in comparison to the scapula, and especially elasmosaurids, of which SMU SMP 69120 purportedly possessed 'subequal' coracoid/scapula lengths. The doctoral thesis of Sato (T. Sato, unpub. Ph.D. thesis, Univ. Calgary, 2002), as well as Druckenmiller & Russell (2008*a*), Ketchum & Benson (2010) and other derivative analyses have subsequently followed this incongruous phylogenetic coding, although Benson & Druckenmiller (2014) alternatively introduced a subjective multistate subdivision that placed SMU SMP 69120 together with *W. betsynichollsae* (coracoid/scapula ratio = 1.38 based on Druckenmiller & Russell, 2006) in a derived ratio range of '< or equal to 1.6'.

Welles (1949, p. 18) stated that 'a heavy central thickening [was present] at the ventral centre of the midline suture' of the coracoids in SMU SMP 69120. This corresponds with the distinctive ventral process encountered in many elasmosaurids (e.g. Welles, 1943; T. Sato, unpub. Ph.D. thesis, Univ. Calgary, 2002; Hiller *et al.* 2005; Kubo, Mitchell & Henderson, 2012; Otero, Soto-Acuña & Rubilar-Rogers, 2012; Otero *et al.* 2014), some of which may elaborate the structure into a prominent midline projection (e.g. Hiller & Mannering, 2005; Druckenmiller & Russell, 2006). Traditional diagnoses of Elasmosauridae (e.g. Welles, 1962; Persson, 1963; O'Keefe, 2001) also usually list the presence of a substantial intercoracoid embayment that was 'cordiform' in outline in SMU SMP 69120 (Welles, 1962, p. 56) and 'almost closed [off]' behind the coracoids (Welles, 1949, p. 19). The intercoracoid embayment is often returned as an unequivocal synapomorphy for Cretaceous elasmosaurids (e.g. O'Keefe, 2001; T. Sato, unpub. Ph.D. thesis, Univ. Calgary, 2002; Ketchum & Benson, 2010), but has not yet been clearly differentiated from the coracoid perforations evident in polycotylids (see comments in T. Sato, unpub. Ph.D. thesis, Univ. Calgary, 2002; Druckenmiller & Russell, 2008*a*) or the proximally positioned coracoid fenestra occurring in the enigmatic 'pliosauromorph' *Leptocleidus superstes* Andrews, 1922 (Kear & Barrett, 2011). Furthermore, Sennikov & Arkhangelsky (2010) ascribed fragmentary Late Triassic sauropterygian material to Elasmosauridae because its coracoid remnants were reconstructed as being much wider proximally than distally (inferring an intercoracoid vacuity), but we consider this to be tenuous given the absence of tangible evidence (the only other noted elasmosaurid similarity was an extrapolated 'subtrapezoid' outline of the pubis, see Sennikov & Arkhangelsky, 2010, p. 569).

The right humerus of SMU SMP 69120 seems to have been preserved in two sections: the 'flat' proximal articular head, which was still in place in the glenoid, and the broken distal extremity that Welles (1949, p. 20) reconstructed as having a 'long postero-distal extension', but was damaged in the area of its 'anterior knee'. Little unambiguous information can be gleaned from these remarks, although Carpenter (1999) did list caudal expansion of the humerus as a distinguishing feature of *Hydralmosaurus serpentinus* (Cope, 1877), and Welles (1949) also identified the discrete epipodial facets on SMU SMP 69120 as being concave (a convex ulnar facet is known in *Terminonatator ponteixensis*: Sato, 2003).

The epipodials of SMU SMP 69120 were represented by part of the right ulna and both radii, which according to Welles (1949, p. 21, table 2) were noticeably broader than long (unspecified right or left radius craniocaudal width = 180 mm; proximodistal length = 150 mm). This conforms to the typical epipodial proportions found in most elasmosaurids, except for some aberrant taxa such as *Callawayasaurus colombiensis* and *Aristonectes quiriquinensis* in which the radii are longer than broad (left/right craniocaudal width = 180/175 mm; proximodistal length = 16.5/150 mm, see Welles, 1962, p. 33, table 2; Otero *et al.* 2014, pp. 115, 118, fig. 15A, C). Phylogenetic analyses of SMU SMP 69120 have also pointedly scored both the presence of an epipodial foramen (the development of which is intraspecifically variable in elasmosaurids, see T. Sato, unpub. Ph.D. thesis, Univ. Calgary, 2002, character 208; Benson & Druckenmiller, 2014, character 261) and a preaxial concavity on the radius (T. Sato, unpub. Ph.D. thesis, Univ. Calgary, 2002, character 204; Benson & Druckenmiller, 2014, character 256). We assume that these interpretations were made from Welles's (1949, p. 20, fig. 3) diagram since his only written reference to such structures is a 'very deep notch on the ulnar surface' of the right radius. Critically, the drawing of SMU SMP 69120 produced by Welles (1962, p. 58, fig. 2b) showed different epipodial foramen proportions, with the same preaxial margin of the right radius depicted as convex (coded '0/1' by T. Sato, unpub. Ph.D. thesis, Univ. Calgary, 2002, p. 286, appendix D).

The only comment that Welles (1949, p. 21) made about the distal components of the limbs in SMU SMP 69120 was the occurrence of an 'anteroproximal projection' on the radiale, which he surmised to be a 'completely fused supernumerary ossicle'. Postaxial accessory ossicles are certainly preserved in some elasmosaurids, but where identifiable, form discrete elements that often lack obvious synarthrotic facets (see *T. ponteixensis*, *W. betsynichollsae*, *A. quiriquinensis* Sato, 2003; Druckenmiller & Russell, 2006; Otero *et al.* 2014).

4. Diagnostic features of *Libonectes morgani*

The type specimen of *Libonectes morgani*, SMU SMP 69120, is one of the most famous elasmosaurid fossils, but has hitherto been examined almost exclusively in terms of its exceptionally preserved cranium and mandible (e.g. Carpenter, 1997; Araújo & Polcyn, 2013). Paradoxically, the formal diagnoses published for this taxon (Welles, 1949; Carpenter, 1997, 1999) rely upon postcranial traits, most of which are equivocal in terms of their preservation and/or phylogenetic significance.

4.a. Atlas–axis complex

Welles (1949) listed complete fusion of the atlas and axis, and the presence of a hypophyseal ridge as distinguishing features of SMU SMP 69120. Carpenter (1997, p. 214) also added a qualitatively determined 'short and deep' atlas–axis centrum, a low axis neural spine, and caudad projection of the atlas postzygapophyses beyond the centrum articular face. Relative external fusion of the various atlas–axis complex components is clearly ontogenetic (see Brown, 1981), and a hypophyseal ridge is expressed in a variety of long-necked plesiosaurians (Andrews, 1910; Welles, 1943; Druckenmiller & Russell, 2008*a*), although its expansion into a transversely broad craniad tubercle does appear to be distinctive.

The length/height dimensions of the atlas–axis complex in SMU SMP 69120 yield a ratio of 1.76. Carpenter (1997, 1999) described this as 'short and deep' similar to *Tuarangisaurus keyesi* (1.89, see Wiffen & Moisley, 1986, p. 211, table 2) and *Thalassomedon haningtoni* (1.51, see Welles, 1943, p. 162, table 4). *Elasmosaurus platyurus* was alternatively classified as 'long and low' (1.83, see Sachs, 2005*a*, p. 95, table 2), despite its lack of coherent proportional differentiation. Other elasmosaurids produce disparate ratio values, and are influenced by ontogeny (Gasparini *et al*. 2003): *Aristonectes parvidens* = 1.44 (Gasparini *et al*. 2003, p. 110); *A. quiriquinensis* = 1.43 (Otero *et al*. 2014, p. 111); *Eromangasaurus australis* = 1.6 (Kear, 2005*a*, p. 799); and *Albertonectes vanderveldei* = 2.2 (Kubo, Mitchell & Henderson, 2012, p. 560).

Buchy (2006, p. 7) diagnosed the type specimen of *Libonectes atlasense* (SMNK-PAL 3978) by its axis neural arch being '1.5 times higher' than the accompanying centrum. Our personal inspection of SMNK-PAL 3978, however, showed the axial neural spine to be highly distorted. Moreover, Buchy (2006) did not provide measurements to support this proportional relationship, which we find misleading given that the equivalent ratio of SMU SMP 69120 is virtually identical (1.4).

Carpenter (1999) discriminated SMU SMP 69120 from *T. keyesi* and *T. haningtoni* by its 'low' neural spine. Conversely, Wiffen & Moisley (1986, p. 211) described this structure as 'long' and 'low' in the holotype of *T. keyesi* (NZGS CD426), but no precise measurements were given. On the other hand Welles (1943, p. 162, table 4) explicitly recorded a craniocaudal length for the axial neural spine of *T. haningtoni* as 91 mm and a dorsoventral height of 61 mm. According to Carpenter (1999), this represented a 'tall' category relative to SMU SMP 69120 (preserved craniocaudal length = 59.84; dorsoventral height = 19.97 mm) and *E. platyurus*, despite the neural spine in the *E. platyurus* type specimen (ANSP 10081) being incomplete (Sachs, 2005*a*). Furthermore, we found that the neural spine apex of SMU SMP 69120 was transversely expanded, forming a platform. This resembles the squat axial neural spine of *A. parvidens* (Chatterjee & Small, 1989, p. 207, fig. 10A, B), but has not been documented in other elasmosaurids and appears to be diagnostic (e.g. compare with Kubo, Mitchell & Henderson, 2012).

Carpenter (1997, 1999) cited projection of the atlas postzygapophyses beyond the centrum articular face as identifying SMU SMP 69120 in comparison to *T. haningtoni* and *E. platyurus*. Incongruously, though, Welles (1943) did not mention the condition of the postzygapophyses in his scant report on the atlas–axis of *T. haningtoni*. Indeed, his only figure shows that the caudal half of the postzygapophyseal facets extends past the axis articular facet (see Welles, 1943, p. 239, pl. 22a). Likewise, Sachs (2005*a*, p. 97) reported that the postzygapophyses of *E. platyurus* 'reach over the level of the centrum' in the cervical series, but are missing from the atlas–axis complex (see Sachs, 2005*a*, p. 100, fig. 4A–C). Based on our observations, caudal projection of the axial postzygapophyses seems to be universal amongst elasmosaurids (e.g. Wiffen & Moisley, 1986; Chatterjee & Small, 1989; Gasparini *et al*. 2003; Kubo, Mitchell & Henderson, 2012), and also manifests in a variety of other plesiosaurians (e.g. Andrews, 1910; Wegner, 1914; Druckenmiller, 2002; Druckenmiller & Russell, 2008*b*).

As an extension of this character, Buchy (2006, p. 7) noted projection of the axial postzygapophyses to 'entirely overhang the centrum of the third cervical' in *L. atlasense* (SMNK-PAL 3978). However, our re-examination not only confirmed that the axial postzygapophyses of SMU SMP 69120 extend beyond the centrum for their entire length, but also that the supposed 'overhang' of the third cervical in SMNK-PAL 3978 only affects two-thirds of the length of the succeeding vertebra (see Buchy, 2006, p. 24, fig. 6a). We therefore find no discriminative veracity in this trait and do not consider it sufficient grounds (on its own) for separating the species of *Libonectes* (currently under study by BPK and SS).

An additional diagnostic character state of SMU SMP 69120 is the presence of a rounded foramen enclosed laterally between the atlas and axis neural arches. Gasparini *et al*. (2003), Sachs (2005*a*) and Buchy (2006) illustrated similar foramina in *A. parvidens*, *E. platyurus* and *L. atlasense*, respectively, but compatible examples also occur in some cryptoclidids (Andrews, 1910; Gasparini, Bardet & Iturralde-Vinent, 2002).

4.b. Postaxial cervical vertebrae

Welles (1949), Carpenter (1997, 1999) and Buchy (2006) all listed the occurrence of > 62 cervical vertebrae as a key discriminant of SMU SMP 69120 amongst elasmosaurids. The absence of a complete cervical series for this specimen, however, renders this count as little more than an estimate (Welles, 1949, p. 7 even stated this fact). Limited understanding of intraspecific variability in elasmosaurid cervical vertebra number (O'Keefe & Hiller, 2006), together with conflicting approaches towards weighting (Carpenter, 1999), scoring (T. Sato, unpub. Ph.D. thesis, Univ. Calgary, 2002; Druckenmiller & Russell, 2008*a*) and delimitation (Sachs, Kear & Everhart, 2013), further renders its use problematic.

The merged *foramina subcentralia* and bifurcating lamellae at the craniad bases of the caudad cervical neural spines identified during our inspection of SMU SMP 69120 are obviously polymorphic and of uncertain diagnostic value. However, the number and relative size of the *foramina subcentralia* have been used elsewhere as independent discrete character states (Benson & Druckenmiller, 2014, characters 156, 191); we alternatively consider them to be inconsistent and only applicable when a substantial number of cervical vertebrae are preserved in articulated sequence.

4.c. Appendicular bones

Welles (1949, p. 7) incorporated the presence of a median pectoral bar, transverse midline constriction and subsequent distal expansion of the coracoids, a pronounced caudal projection on the distal articular extremity of the humerus, and a 'large' epipodial foramen into his definition for *Libonectes morgani*. Unfortunately, none of these features can be confirmed from SMU SMP 69120 as it is preserved today. Indeed, the occurrence of a pectoral bar is currently substantiated in only one elasmosaurid taxon, *Waputskanectes betsynichollsae* (Druckenmiller & Russell, 2006), and is otherwise an ontogenetically plastic trait (Brown, 1981). The shape of the coracoid in SMU SMP 69120 is influenced by formation of the intercoracoid vacuity, which is a widely advocated synapomorphy for Elasmosauridae (Welles, 1962; Persson, 1963; O'Keefe, 2001; T. Sato, unpub. Ph.D. thesis, Univ. Calgary, 2002; Ketchum & Benson, 2010; Otero *et al*. 2012). Sato (T. Sato, unpub. Ph.D. thesis, Univ. Calgary, 2002, p. 43) also employed distocaudal expansion of the humerus to assign Campanian–Maastrichtian elasmosaurid remains (RSM P625.1) to '?*Libonectes morgani*', yet this condition is present (albeit in an incrementally more extreme form, see T. Sato, unpub. Ph.D. thesis, Univ. Calgary, 2002, p. 346, character 187) in the stratigraphically proximal taxon *Hydralmosaurus serpentinus* (Carpenter, 1999). Unfortunately, the distocaudal extremity of the humerus was reported as missing in *L. atlasense* (Buchy, 2006).

Sato (T. Sato, unpub. Ph.D. thesis, Univ. Calgary, 2002) additionally recorded the presence of an epipodial foramen (variable in elasmosaurids, see T. Sato, unpub. Ph.D. thesis, Univ. Calgary, 2002), gradational variation in the length/width ratio of the radius (uniformly broader than long in most elasmosaurids, see e.g. Ketchum & Benson, 2010) and the outline of the caudal edge of the ulna (not figured by Welles, 1949) as additional diagnostic features of *L. morgani*. However, we alternatively treat them as ambiguous, and note that minor proportional differences have also been advocated for the classification of other elasmosaurids from the Eagle Ford Group (e.g. TMM 42245–1: G. W. Storrs, unpub. M.Sc. thesis, Univ. of Texas, 1981, p. 102).

4.d. Accompanying cranial features

Welles (1949, p. 7) enigmatically noted '[t]eeth 9/16' in SMU SMP 69120, which appears to refer to his maximum count of alveoli on the right maxilla versus dentary (see Welles, 1949, p. 15). Carpenter (1997, 1999) alternatively concluded that these numbers were incorrect (we confirmed 14/18 teeth in the right maxilla/dentary, see Carpenter, 1999, p. 157), and that the dental arrangement of SMU SMP 69120 was generally comparable to that of other elasmosaurids (e.g. *Hydrotherosaurus alexandrae*: Welles, 1943). Furthermore, Carpenter (1997, 1999) attributed Welles's (1949) erroneous description of a pineal foramen to inadequate preparation, and additionally corrected his anomalous identification of the 'nasal' and 'prefrontal' (see Welles, 1949, pl. I) as the prefrontal and frontal (corroborated by SS and BPK, pers. obs.). Finally, Carpenter (1999) introduced differential placement of the external bony nasal opening over the third–fourth alveolus in the maxillary tooth row to distinguish SMU SMP 69120 from *Tuarangisaurus keyesi*, in which the bony nasal opening was supposedly situated over the second–third maxillary tooth, and *Thalassomedon haningtoni*, which had a positioning over the fourth–fifth tooth, or proximally over the sixth tooth in *Styxosaurus snowii*. Our examination of the bony nasal openings in SMU SMP 69120 showed that their elongate margins actually commenced at the alveolar edge between the third–fourth maxillary tooth on the right side, or at the midline of the third alveolus on the left side, and extended proximally to a point parallel with either the fifth or fourth maxillary alveolus, respectively. Based on the undistorted left side of the holotype skull of *T. keyesi* (NZGS CD425), the bony nasal opening (as preserved) is delimited between the second and fourth maxillary alveolus (Wiffen & Moisley, 1986, p. 208, fig. 3). Similarly, the crania representing both *T. hanington*i (Carpenter, 1999) and *S. snowii* (Storrs, 1999; Everhart, 2006) are crushed but again accord with SMU SMP 69120 (see Carpenter, 1999, p. 164, fig. 12A), or have inconsistent restorations of their damaged external nasal regions as is the case in *S. snowii* (see Williston, 1890, p. 174; Welles & Bump, 1949, p. 525, fig. 3A; Carpenter, 1999, p. 161, fig. 10A, B).

5. Conclusions

Libonectes morgani is one of the most famous and best-documented elasmosaurid plesiosaurians, yet its

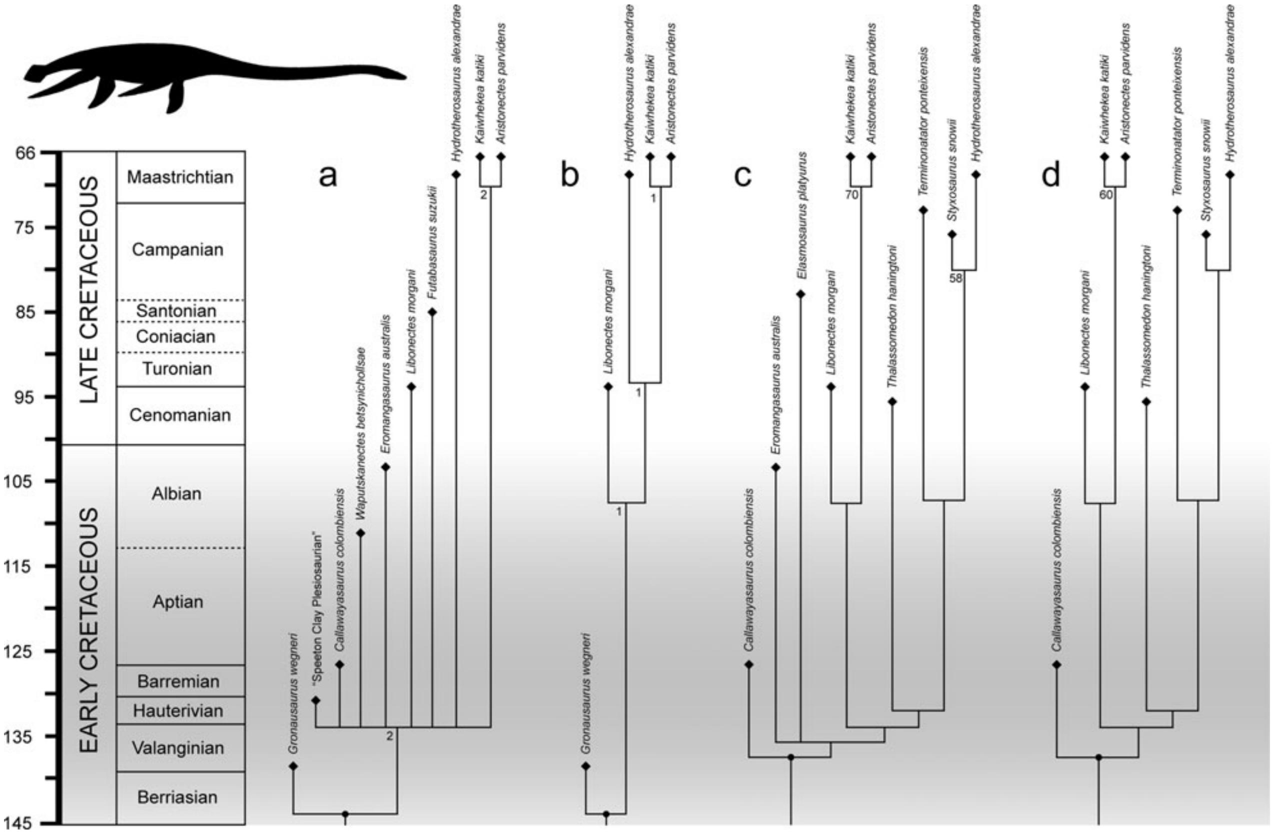

Figure 6. Phylogenetic placements of *Libonectes morgani* amongst Elasmosauridae derived using modified code lines within the published datasets of Benson & Druckenmiller (2014) and Benson *et al*. (2013): strict consensus (a, c), and strict reduced consensus (b, d). Calculation of Bremer index (depicted where > 0) and bootstrap values followed the original parameters described in Benson & Druckenmiller (2014) and Ketchum & Benson (2010), respectively. Chronostratigraphical branch lengths were scaled according to Gradstein *et al*. (2012) for all trees.

postcranial skeleton has not been re-evaluated since its initial description. Moreover, the unfortunate loss of key skeletal elements (the pectoral girdle and partial right forelimb) that were not fully prepared (Welles, 1949) has hindered confirmation of phylogenetically critical data. Irrespectively, these components have been repeatedly scored from the scant text and line diagrams of Welles (1949), information that was contradicted by his later reproductions (Welles, 1962) and subsequently found to contain errors (see Carpenter, 1999). The reliability of Welles's (1949) account is therefore open to question, but should not be dismissed off-hand. Rather, we advocate judicious selectivity of only those states that are explicitly mentioned and/or supported by photographic evidence (e.g. the vertebrae depicted in Welles, 1949, pl. 6; Shuler, 1950, p. 12, fig. 7). With this premise in mind, we rescored the code lines for *L. morgani* and ran topological tests using two recent phylogenetic datasets compiled for Plesiosauria: Benson *et al*. (2013), which was modified from Benson, Evans & Druckenmiller (2012) and derived a well-resolved consensus tree using a mixed series of discrete and continuous characters (the latter constructed from Ketchum & Benson, 2010); and Benson & Druckenmiller (2014), which applied qualitative criteria to all states and returned less resolution, but included a larger sample of Early Cretaceous elasmosaurid taxa.

We re-ran both these matrices independently using *PAUP*4.0b10* (Swofford, 2002), and with a Parsimony Ratchet search strategy (Nixon, 1999) in *PAUPRat* (Sikes & Lewis, 2001). The Benson *et al*. (2013) matrix processed rapidly using standard *PAUP** searches. The 15 gap-weighted (*sensu* Thiele, 1993) characters employed by Benson *et al*. (2013) were treated as ordered. All non-quantitative characters, on the other hand, were unordered by default and each assigned a weight of 26 corresponding to the maximum number of states designated by Ketchum & Benson (2010). All characters examined in Benson & Druckenmiller (2014) were unordered and unweighted. Our *PAUPRat* simulations of this dataset proceeded with the random number seed set to 'seed = 0', thus enabling a different seed selection for each run, and with 'wtmode = uniform' activated for equal weighting of discrete characters. Ratchet implementation in PAUP* undertook 200 iterations with 15 % characters perturbed per iteration. Most parsimonious tree islands were achieved in four batch files. These were subjected to heuristic searches in *PAUP** with TBR (tree-bisection-reconnection) branch swapping activated and zero length branches collapsed ('amb-' setting). The resulting strict consensus trees (Fig. 6) differed from those generated by Benson *et al*. (2013, p. 241, fig. 5A) and Benson & Druckenmiller (2014, p. 8, fig. 2) in their contrasting positions for *L.*

morgani within Elasmosauridae. This is not surprising given that we altered 19 % (42/216) to 26 % (70/270) of the state scores for this taxon in each respective dataset (see Appendix), and derived weak support at all elasmosaurid ingroup nodes (Fig. 6). Such ambiguity was presumably driven by missing data and/or homoplasy in the parent matrices but is beyond the scope of evaluation here. Rather, the more pertinent issue concerns the diagnostic traits for *L. morgani*, which do not hold up to scrutiny. Our solution has been to employ character transformation lists from published elasmosaurid-rich phylogenies (e.g. Druckenmiller & Russell, 2008*a*; Ketchum & Benson, 2010; Vincent *et al*. 2011; Kubo, Mitchell & Henderson, 2012; Benson & Druckenmiller, 2014) to compile a simple differential framework for distinguishing the remnant holotype material (the diagnosis employed in herein). However, this process also revealed a dearth of unequivocal autapomorphies that might render *L. morgani* unique. Certainly some conspicuous features are evident in the axial column, including the hypophyseal ridge on the atlas–axis complex bearing a prominent flattened tubercle at its distal apex, a rounded foramen enclosed laterally between the atlas and axis neural arches, the axis neural spine apex manifesting expansion into a rugose platform, the polymorphic presence of either merged or paired *foramina subcentralia* that were offset longitudinally relative to each other, and the equally variable occurrence of bifurcating lamellae at the cranial base of the caudad cervical neural spines. These can be tentatively coupled with components of the original diagnosis from Welles (1949), namely the distinctive pectoral bar formed by the scapulae and coracoids, pronounced caudal projection on the distal articular extremity of the humerus, and the epipodial foramen formed between the ulna and radius, to provide a viable definition for the taxon. Importantly, though, this inventory highlights the sparse postcranium as the more informative skeletal data source, despite its accompanying one of the most completely known elasmosaurid skulls. Such implications warrant exploration as a driver of plesiosaurian tree topologies, and offer a classical but still clearly discriminative basis for delineating taxonomic boundaries.

Acknowledgements. The authors are grateful to D. Winkler and M. Polcyn (Shuler Museum, Southern Methodist University) and E. Frey (Staatliches Museum für Naturkunde Karlsruhe) for their generous assistance with access to the various specimens of *Libonectes* housed in museum collections. N. van Vranken (University of Texas, Odessa) provided stratigraphical information on the type locality of *L. morgani*. BPK acknowledges funding from the Australian Research Council and Swedish Research Council. Finally we want to thank both anonymous reviewers.

References

ANDREWS, C. W. 1910. *A Descriptive Catalogue of the Marine Reptiles of the Oxford Clay, Part I*. London, England: British Museum (Natural History), 202 pp.

ANDREWS, C. W. 1922. Description of a new plesiosaur from the Weald Clay of Berwick (Sussex). *Quarterly Journal of the Geological Society of London* **78**, 285–95.

ARAÚJO, R. & POLCYN, M. J. 2013. A biomechanical analysis of the skull and adductor chamber muscles in the Late Cretaceous plesiosaur *Libonectes. Palaeontologia Electronica* **16**, 1–25.

BARDET, N. P., GODEFROIT, P. & SCIAU, J. 1999. A new elasmosaurid plesiosaur from the Lower Jurassic of Southern France. *Palaeontology* **42**, 927–52.

BENSON, R. B. J. & DRUCKENMILLER, P. S. 2014. Faunal turnover of marine tetrapods during the Jurassic–Cretaceous transition. *Biological Reviews* **89**, 1–23.

BENSON, R. B. J., EVANS, M. & DRUCKENMILLER, P. S. 2012. High diversity, low disparity and small body size in plesiosaurs (Reptilia, Sauropterygia) from the Triassic–Jurassic boundary. *PLoS ONE* **7**, e31838.

BENSON, R. B. J., KETCHUM, H. F., NAISH, D. & TURNER, L. E. 2013. A new leptocleidid (Sauropterygia, Plesiosauria) from the Vectis Formation (Early Barremian–early Aptian; Early Cretaceous) of the Isle of Wight and the evolution of Leptocleididae, a controversial clade. *Journal of Systematic Palaeontology* **11**, 233–50.

BEREZIN, Y. A. 2011. A new plesiosaur of the family Aristonectidae from the Early Cretaceous of the center of the Russian Platform. *Paleontological Journal* **45**, 648–60.

DE BLAINVILLE, H. D. 1835. Description de quelques espèces de reptiles de la Californie, précédée de l'analyse d'un système général d'Erpétologie et d'Amphibiologie. *Nouvelles Annales du Muséum (national) d'Histoire Naturelle de Paris* **4**, 233–96.

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 Series* **35**, 253–347.

BROWN, D. S. 1993. A taxonomic reappraisal of the families Elasmosauridae and Cryptoclididae. *Revue de Paléobiologie* **7**, 9–16.

BROWN, D. S., VINCENT, P. & BARDET, N. 2013. Osteological redescription of the skull of *Microcleidus homalospondylus* (Sauropterygia, Plesiosauria) from the Lower Jurassic of England. *Journal of Paleontology* **87**, 537–49.

BUCHY, M.-C. 2006. An elasmosaur (Reptilia: Sauropterygia) from the Turonian (Upper Cretaceous) of Morocco. *Carolinea* **63**, 5–28.

CABRERA, A. 1941. Un plesiosaurio nuevo del Cretáceo del Chubut. *Revista del Museo de La Plata* **2**, 113–30.

CARPENTER, K. 1997. Comparative cranial anatomy of two North American plesiosaurs. In *Ancient Marine Reptiles* (eds J. M. Callaway & E. L. Nicholls), pp. 191–216. San Diego: Academic Press.

CARPENTER, K. 1999. Revision of North American elasmosaurs from the Cretaceous of the Western Interior. *Paludicola* **2**, 148–73.

CHATTERJEE, S. & SMALL, B. J. 1989. New plesiosaurs from the Upper Cretaceous of Antarctica. In *Origins and Evolution of the Antarctic Biota* (ed. J. A. Crame), pp. 197–215. Geological Society of London, Special Publication no. 47.

COBBAN, W. A. 1984. Mid-Cretaceous ammonite zones, Western Interior, United States. *Bulletin of the Geological Society of Denmark* **33**, 71–89.

COPE, E. D. 1868. [Remarks on a new large enaliosaur]. *Proceedings of the Academy of Natural Sciences of Philadelphia* **20**, 92–3.

COPE, E. D. 1869. Synopsis of the extinct Batrachia and Reptilia of North America. Part 1. *Transactions of the American Philosophical Society* **14**, 1–235.

COPE, E. D. 1877. Report on the geology of the region of the Judith River, Montana, and on the vertebrate fossils obtained on or near the Missouri River. *Bulletin of the United States Geological and Geographical Survey of the Territories* **3**, 565–97.

CRUICKSHANK, A. R. I. & FORDYCE, R. E. 2002. A new marine reptile (Sauropterygia) from New Zealand: further evidence for a Late Cretaceous austral radiation of cryptoclidid plesiosaurs. *Palaeontology* **45**, 557–75.

DAMES, W. 1895. Die Plesiosaurier der süddeutschen Liasformation. *Abhandlungen der Königlich Preussischen Akademie der Wissenschaften zu Berlin* **1895**, 1–81.

DAWSON, W. C. 2000. Shale microfacies: Eagle Ford Group (Cenomanian-Turonian) north-central Texas outcrops and subsurface equivalents. *Gulf Coast Association of Geological Societies Transactions* **50**, 607–21.

DRUCKENMILLER, P. S. 2002. Osteology of a new plesiosaur from the Lower Cretaceous (Albian) Thermopolis Shale of Montana. *Journal of Vertebrate Paleontology* **22**, 29–42.

DRUCKENMILLER, P. S. & RUSSELL, A. P. 2006. A new elasmosaurid plesiosaur (Reptilia: Sauropterygia) from the Lower Cretaceous Clearwater Formation, northeastern Alberta, Canada. *Paludicola* **5**,184–99.

DRUCKENMILLER, P. S. & RUSSELL, A. P. 2008*a*. A phylogeny of Plesiosauria (Sauropterygia) and its bearing on the systematic status of *Leptocleidus* Andrews, 1922. *Zootaxa* **1863**, 1–120.

DRUCKENMILLER, P. S. & RUSSELL, A. P. 2008*b*. Skeletal anatomy of an exceptionally complete specimen of a new genus of plesiosaur from the Early Cretaceous (Early Albian) of northeastern Alberta, Canada. *Palaeontographica* **A283**, 1–33.

EVERHART, M. 2006. The occurrence of elasmosaurids (Reptilia: Plesiosauria) in the Niobrara Chalk of western Kansas. *Paludicola* **5**, 170–83.

FRAAS, E. 1910. Plesiosaurier aus dem oberen Lias von Holzmaden. *Palaeontographica* **57**, 105–40.

GASPARINI, Z., BARDET, N. & ITURRALDE-VINENT, M. 2002. A new cryptoclidid plesiosaur from the Oxfordian (Late Jurassic) of Cuba. *Geobios* **35**, 201–11.

GASPARINI, Z., BARDET, N., MARTIN, J. E. & FERNANDEZ, M. 2003. The elasmosaurid plesiosaur *Aristonectes* Cabrera from the latest Cretaceous of South America and Antarctica. *Journal of Vertebrate Paleontology* **23**, 104–15.

GRADSTEIN, F. J., OGG, J. G., SCHMITZ, M. D. & OGG, G. M. 2012. *The Geologic Time Scale 2012*. Volume 2. Amsterdam: Elsevier, 1176 pp.

GROßMANN, F. 2007. The taxonomic and phylogenetic position of the Plesiosauroidea from the Lower Jurassic Posidonia Shale of south-west Germany. *Palaeontology* **50**, 545–64.

HAMPE, O. 2013. The forgotten remains of a leptocleidid plesiosaur (Sauropterygia: Plesiosauroidea) from the Early Cretaceous of Gronau (Münsterland, Westphalia, Germany). *Paläontologische Zeitschrift* **87**, 473–91.

HECTOR, J. 1874. On the fossil reptiles of New Zealand. *Transactions of the New Zealand Institute* **6**, 333–58.

HILLER, N. & MANNERING, A. A. 2005. An unusual new elasmosaurid plesiosaur (Sauropterygia) from the Upper Haumurian (Maastrichtian) of the South Island, New Zealand. *Memoirs of the Queensland Museum* **51**, 27–37.

HILLER, N., MANNERING, A. A., JONES, C. M. & CRUICKSHANK, A. R. I. 2005. The nature of *Mauisaurus haasti* Hector, 1874 (Reptilia: Plesiosauria). *Journal of Vertebrate Paleontology* **25**, 588–601.

HILLER, N., O'GORMAN, J. P. & OTERO, R. A. 2014. A new elasmosaurid plesiosaur from the lower Maastrichtian of North Canterbury, New Zealand. *Cretaceous Research* **50**, 27–37.

HUENE, F. VON. 1923. Ein neuer Plesiosaurier aus dem oberen Lias Württembergs. *Jahreshefte des Vereins für Vaterländische Naturkunde in Württemberg* **79**, 3–23.

JACOBS, L. L., POLCYN, M. J., WINKLER, D. A., MYERS, T. S., KENNEDY, J. G. & WAGNER, J. B. 2013. Late Cretaceous strata and vertebrate fossils of North Texas In *Late Cretaceous to Quaternary Strata and Fossils of Texas, Field Excursions Celebrating 125 Years of GSA and Texas Geology, GSA South-Central Section Meeting, Austin, Texas, April 2013* (eds B. B. Hunt & E. J. Catlos), pp. 1–13. Geological Society of America Field Guide no. 30.

KEAR, B. P. 2002. Reassessment of the Early Cretaceous plesiosaur *Cimoliasaurus maccoyi* Etheridge, 1904 (Reptilia, Sauropterygia) from White Cliffs, New South Wales. *Australian Journal of Zoology* **50**, 671–85.

KEAR, B. P. 2005*a*. A new elasmosaurid plesiosaur from the Lower Cretaceous of Queensland, Australia. *Journal of Vertebrate Paleontology* **25**, 792–805.

KEAR, B. P. 2005*b*. Marine reptiles from the Lower Cretaceous (Aptian) deposits of White Cliffs, southeastern Australia: implications of a high-latitude cold-water assemblage. *Cretaceous Research* **26**, 769–82.

KEAR, B. P. 2006. Marine reptiles from the Lower Cretaceous of South Australia: elements of a high-latitude cold-water assemblage. *Palaeontology* **49**, 837–56.

KEAR, B. P. & BARRETT, P. M. 2011. Reassessment of the Early Cretaceous (Barremian) pliosauroid *Leptocleidus superstes* Andrews, 1922 and other plesiosaur remains from the nonmarine Wealden succession of southern England. *Zoological Journal of the Linnean Society* **161**, 663–91.

KENNEDY, W. J. 1988. Late Cenomanian and Turonian ammonite faunas from northeast and central Texas. *Special Papers in Palaeontology* **39**, 1–131.

KENNEDY, W. J. & COBBAN, W. A. 1991. Stratigraphy and interregional correlation of the Cenomanian-Turonian transition in the Western Interior of the United States near Pueblo, Colorado, a potential boundary stratotype for the base of the Turonian stage. *Newsletters on Stratigraphy* **24**, 1–33.

KENNEDY, W. J., WALASZCZYK, I. & COBBAN, W. A. 2005. The global boundary stratotype section and point for the base of the Turonian Stage of the Cretaceous; Pueblo, Colorado, USA. *Episodes* **28**, 93–104.

KETCHUM, H. F. & BENSON, R. B. J. 2010. Global interrelationships of Plesiosauria (Reptilia, Sauropterygia) and the pivotal role of taxon sampling in determining the outcome of phylogenetic analyses. *Biological Reviews* **85**, 361–92.

KETCHUM, H. F. & SMITH, A. S. 2010. The anatomy and taxonomy of *Macroplata tenuiceps* (Sauropterygia, Plesiosauria) from the Hettangian (Lower Jurassic) of Warwickshire, United Kingdom. *Journal of Vertebrate Paleontology* **30**, 1069–81.

KNUTSEN, E. M., DRUCKENMILLER, P. S. & HURUM, J. H. 2012. Two new species of long-necked plesiosaurians (Reptilia: Sauropterygia) from the Upper Jurassic (Middle Volgian) Agardhfjellet Formation of central Spitsbergen. *Norwegian Journal of Geology* **92**, 187–212.

KUBO, T., MITCHELL, M. T. & HENDERSON, D. M. 2012. *Albertonectes vanderveldei*, a new elasmosaur (Reptilia, Sauropterygia) from the Upper Cretaceous of Alberta. *Journal of Vertebrate Paleontology* **32**, 557–72.

LOMAX, D. R. & WAHL, W. R. 2013. A new specimen of the elasmosaurid plesiosaur *Zarafasaura oceanis* from the Upper Cretaceous (Maastrichtian) of Morocco. *Paludicola* **9**, 97–109.

MCGOWEN, J. H., PROCTOR, C. V., HAENGGI, W. T., REASER, D. F. & BARNES, V. E. 1987. Geologic atlas of Texas, Dallas sheet (Gayle Scott Memorial Edition). *Geologic Atlas of Texas. Bureau of Economic Geology, University of Texas at Austin, Austin* **1**, no. 250,000.

NIXON, K. C. 1999. The parsimony ratchet, a new method for rapid parsimony analysis. *Cladistics* **15**, 407–14.

O'GORMAN, J. P., GASPARINI, Z. B. & SALGADO, L. 2013. Postcranial morphology of *Aristonectes* (Plesiosauria, Elasmosauridae) from the Upper Cretaceous of Patagonia and Antarctica. *Antarctic Science* **25**, 71–82.

O'KEEFE, F. R. 2001. A cladistic analysis and taxonomic revision of the Plesiosauria (Reptilia, Sauropterygia). *Acta Zoologica Fennica* **213**, 1–63.

O'KEEFE, F. R. 2002. The evolution of plesiosaur and pliosaur morphotypes in the Plesiosauria (Reptilia: Sauropterygia). *Paleobiology* **28**, 101–12.

O'KEEFE, F. R. 2004. Preliminary description and phylogenetic position of a new plesiosaur (Reptilia, Sauropterygia) from the Toarcian of Holzmaden, Germany. *Journal of Paleontology* **78**, 973–88.

O'KEEFE, F. R. & HILLER, N. 2006. Morphologic and ontogenetic patterns in elasmosaur neck length, with comments on the taxonomic utility of neck length variables. *Paludicola* **5**, 206–29.

OTERO, R. A., SOTO-ACUÑA, S. & 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. E., RUBILAR-ROGERS, D., SALAZAR, C. & QUINZIO-SINN, L. A. 2014. *Aristonectes quiriquinensis*, sp. nov., a new highly derived elasmosaurid from the upper Maastrichtian of central Chile. *Journal of Vertebrate Paleontology* **34**, 100–25.

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, London* **29**, 153–66.

OWEN, R. 1865. *Monograph on the Fossil Reptilia of the Liassic Formations. Part I: Sauropterygia*. London: The Palaeontographical Society, 40 pp.

PERSSON, P. O. 1963. A revision of the classification of the Plesiosauria with a synopsis of the stratigraphical and geographical distribution of the group. *Lunds Universitets Årsskrift* **59**, 1–59.

PHILLIPS, J. 1871. *Geology of Oxford and the Valley of the Thames*. Oxford: Clarendon Press, 523 pp.

SACHS, S. 2004. Redescription of *Woolungasaurus glendowerensis* (Plesiosauria: Elasmosauridae) from the Lower Cretaceous of Northeast Queensland. *Memoirs of the Queensland Museum* **49**, 713–31.

SACHS, S. 2005*a*. Redescription of *Elasmosaurus platyurus* Cope 1868 (Plesiosauria: Elasmosauridae) from the Upper Cretaceous (lower Campanian) of Kansas, USA. *Paludicola* **5**, 92–106.

SACHS, S. 2005*b*. *Tuarangisaurus australis* sp. nov. (Plesiosauria: Elasmosauridae) from the Lower Cretaceous of Northeastern Queensland, with additional notes on the phylogeny of the Elasmosauridae. *Memoirs of the Queensland Museum* **50**, 425–40.

SACHS, S, KEAR, B. P. & EVERHART, M. J. 2013. Revised vertebral count in the "longest-necked vertebrate" *Elasmosaurus platyurus* Cope 1868, and clarification of the cervical-dorsal transition in Plesiosauria. *PLoS ONE* **8**, e70877.

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

SATO, T., HASEGAWA, Y. & MANABE, M. 2006. A new elasmosaurid plesiosaur from the Upper Cretaceous of Fukushima, Japan. *Palaeontology* **49**, 467–84.

SEELEY, H. G. 1874. On *Muraenosaurus leedsii*, a plesiosaurian from the Oxford Clay. Part I. *Quarterly Journal of the Geological Society of London* **30**, 197–208.

SENNIKOV, A. G. & ARKHANGELSKY, M. S. 2010. On a typical Jurassic sauropterygian from the Upper Triassic of Wilczek Land (Franz Josef Land, Arctic Russia). *Paleontological Journal* **44**, 567–72.

SHULER, E. W. 1950. A new elasmosaur from the Eagle Ford Shale of Texas. Part II. The elasmosaur and its environment. *The Fondren Science Series* **1**, 1–32.

SHUMARD, B. F. 1860. Descriptions of new Cretaceous fossils from Texas. *Academy of Science St Louis Transactions* **1**, 590–610.

SIKES, D. S. & LEWIS, P. O. 2001. *PAUPRat: PAUP* Implementation of the Parsimony Ratchet*. Storrs: University of Connecticut, Department of Ecology and Evolutionary Biology.

SMITH, A. S, ARAÚJO, R. & MATEUS, O. 2012.A new plesiosauroid from the Toarcian (Lower Jurassic) of Alhadas, Portugal. *Acta Palaeontologica Polonica* **57**, 257–66.

SOLLAS, W. J. 1881. On a new species of *Plesiosaurus* (*P. conybeari*) from the Lower Lias of Charmouth; with observations on *P. megacephalus*, Stutchbury, and *P. brachycephalus*, Owen. *Quarterly Journal of the Geological Society of London* **37**, 440–81.

STORRS, G. W. 1991. Anatomy and relationships of *Corosaurus alcovensis* (Diapsida: Sauropterygia) and the Triassic Alcova Limestone of Wyoming. *Bulletin of the Peabody Museum of Natural History* **44**, 1–163.

STORRS, G. W. 1999. An examination of Plesiosauria (Diapsida Sauropterygia) from the Niobrara Chalk (Upper Cretaceous) of Central North America. *The University of Kansas Paleontological Contributions* **11**, 1–15.

SWOFFORD, D. 2002. *Phylogenetic Analysis using Parsimony *4.0b10*. Sunderland, MA: Sinauer Associates, Inc.

THIELE, K. 1993. The holy grail of the perfect character: the cladistic treatment of morphometric data. *Cladistics* **9**, 275–304.

VINCENT, P., BARDET, N., PEREDA SUBERBIOLA, X., BOUYA, B., AMAGHZAZ, M. & 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**, 1062–73.

VINCENT, P., BARDET, N., HOUSSAYE, A., AMAGHZAZ, M. & MESLOUH, S. 2013. New plesiosaur specimens from the Maastrichtian Phosphates of Morocco and their implications for the ecology of the latest Cretaceous marine apex predators. *Gondwana Research* **24**, 796–805.

WEGNER, T. H. 1914. *Brancasaurus brancai* n. g. n. sp., ein Elasmosauride aus dem Wealden Westfalens. In *Festschrift für Wilhelm Branca zum 70. Geburtstage 1914*, pp. 235–305. Leipzig: Borntraeger.

WELLES, S. P. 1943. Elasmosaurid plesiosaurs with a description of new material from California and Colorado. *University of California Publications in Geological Sciences* **13**, 125–215.

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**, 47–143.

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.

WELLES, S. P. & BUMP, J. 1949. *Alzadasaurus pembertoni*, a new elasmosaur from the Upper Cretaceous of South Dakota. *Journal of Paleontology* **23**, 521–35.

WILLISTON, S. W. 1890. A new plesiosaur from the Niobrara Cretaceous of Kansas. *Transactions of the Kansas Academy of Science* **12**, 174–8.

WIFFEN, J. & 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**, 205–52.

Appendix

Revised character scores (NEXUS format) for cranial/postcranial holotype material (SMU SMP 69120) of *Libonectes morgani*.

Benson *et al.* (2013)

```
Libonectesmorgani_Revised
BAB0010002102200100?-0??101010?2??2-?110???10000
10001000100–11011001??0110001120100110000000 1K0211
0110101111115400110P11111120221????????????0011?1?11?
???????1???????????????????001?100?110????????????000?
00101??????
```

Benson & Druckenmiller (2014)

```
Libonectes_morgani_Revised
00?0???011?00020102001001000000?001?00?10??1????0??1
??1?1?00?10?01012120101 1000?1?22110010100000?122?
1300???0?11000?01020???01200010100 11000?01011011126
2111???320?210111??01?01???????????????????210?1??????
?11???0?????????????????????????????????1??????2??????
(01)?????????
```