Lost, hidden, broken, cut - estimating and interpreting the shapes and masses of damaged assemblages of plesiosaur gastroliths (#97916)

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Lost, hidden, broken, cut - estimating and interpreting the shapes and masses of damaged assemblages of plesiosaur gastroliths

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Background. Gastroliths are stones of uncertain purpose that are commonly found inside the body cavity of plesiosaur fossils worldwide. Gastroliths from four Alberta plesiosaurs were studied to determine both their shapes and masses, and their mass fractions relative to body mass. One animal's set of gastroliths was 100% complete and fully visible, but the others showed varying degrees of loss, damage or obscuration, so estimations of their original states needed to be done. **Methods**. The studied animals were: *Albertonectes vanderveldei*, *Fluvionectes sloanae*, *Nichollssaura borealis* and *Wapuskanectes betsynichollsae.* The animals come from three different environments: open marine, near shore marine, and fluvial. Gastrolith shapes were classified as either xiphoid, cylindrical, discoidal or spherical based on observed and/or estimated dimensions. Although not all methods could be applied in all cases, gastrolith shapes and masses were estimated four different ways – 1) direct measurement and weighing of a subset and predicting the properties of the remaining obscured and hidden stones; 2) measuring triaxial ellipsoid dimensions of free stones to calculate volumes and multiplying by the mass density of chert; 3) measuring two visible triaxial dimensions of embedded stones, estimating the hidden third dimension three different ways, and then determining volumes and masses by calculation; and 4) predicting the density and mass of a densely packed cluster of small gastroliths using geometrical arguments. **Results**. Total gastrolith mass never exceeded 0.2% of body mass in any plesiosaur. The largest plesiosaur in the sample had the largest single gastrolith and total gastrolith mass increases with body size. The shape characteristics of the gastroliths were different for different environments, but compositionally they are dominated by black cherts. A possible common source for the gastroliths was identified for the two geographically close and near-contemporanous Nichollssaura and Wapuskanectes.

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2   masses of damaged assemblages of plesiosaur gastroliths

3

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9   <mark>**Abstract**</mark>

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11   inside the body cavity of plesiosaur fossils worldwide. Gastroliths from four Alberta

12   plesiosaurs were studied to determine both their shapes and masses, and their mass

13   fractions relative to body mass. One animal's set of gastroliths was 100% complete and

14   fully visible, but the others showed varying degrees of loss, damage or obscuration, so

15   estimations of their original states needed to be done.

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18   three different environments: open marine, near shore marine, and fluvial. Gastrolith

19   shapes were classified as either xiphoid, cylindrical, discoidal or spherical based on

20   observed and/or estimated dimensions. Although not all methods could be applied in all

21   cases, gastrolith shapes and masses were estimated four different ways – 1) direct

22   measurement and weighing of a subset and predicting the properties of the remaining

23 obscured and hidden stones; 2) measuring triaxial ellipsoid dimensions of free stones to

24 calculate volumes and multiplying by the mass density of chert; 3) measuring two visible

25 triaxial dimensions of embedded stones, estimating the hidden third dimension three

26 different ways, and then determining volumes and masses by calculation; and 4)

27 predicting the density and mass of a densely packed cluster of small gastroliths using

28 geometrical arguments.

29 **Results**. Total gastrolith mass never exceeded 0.2% of body mass in any plesiosaur.

30 The largest plesiosaur in the sample had the largest single gastrolith and total gastrolith

31 mass increases with body size. The shape characteristics of the gastroliths were

32 different for different environments, but compositionally they are dominated by black

33 cherts. A possible common source for the gastroliths was identified for the two

34 geographically close and near-contemporanous *Nichollssaura* and *Wapuskanectes*.

Introduction

36   Plesiosaurs were unusual animals with nothing like them living today which

37 makes them both very interesting and very frustrating animals to study ~~and try and~~

38 ~~understand~~. The last of plesiosaurs went extinct at the end of the Cretaceous, and their

39 evolutionary origins are obscure, but they are diapsid reptiles and maybe more closely

40 related to archosaurs than to lizards and snakes (Bardet et al, 2023), and were all

41 exclusively aquatic. They were among the first vertebrate fossils to be studied in a

42 rigorous, scientific fashion beginning in the early 19th century (Ellis 2003), and

43 gastroliths ("stomach stones") are frequently found with their body fossils. The purpose

44 of the stones has been controversial ever since they were first encountered, with the

45 most common suggestions being that they were either for digestion, ballast, or material

46 accidentally ingested. See Taylor (1993) and Wings (2007) for comprehensive reviews.

47   Several nearly complete plesiosaurs have been discovered in the western

48 Canadian province of Alberta over the past 30 years, with the most recent one being

49 from December 2012 – not counting more fragmentary specimens from 2019 and 2023.

50 These fossils come from two different time periods – Early Cretaceous (Aptian-Albian

51 boundary) and Late Cretaceous (late Campanian) – and from three very different

52 environments - open marine, near-shore marine, and fluvial. Within the intact body walls

53 of some of these specimens have been found collections of gastroliths, and it was

54 realized that a quantitative analysis of the stomach stones and the bodies that hosted

55 them could be done with the knowledge that the stones really did come from within the

56 specimens and were not washed into the body cavity after death. The rock units hosting

57 the fossils are devoid of any gravels, pebbles or cobbles, demonstrating that the

58 gastroliths within the bodies were genuinely allochthonous. However, the hosting fossils

59 were either subject to varying degrees of erosion prior to their discovery, or were

60 damaged when first exposed, leading to a loss of fossil material and often a partial loss

61 of any enclosed gastroliths. Additionally, in all but one case, decisions about the

62 preparation of the fossils resulted in bones and any enclosed gastroliths not being

63 removed, thus leaving quantities of stones incompletely exposed or fully hidden inside

64 the bodies.

65   Despite uncertainty about their actual biological function(s), any new analyses of

66 plesiosaur gastroliths and their relationship to other aspects of the bodies of the animals

67 have the potential to improve our understanding of these intriguing geological-biological

68 entities. ==This paper presents the results of using quantitative methods to make==

69 ==estimates of the original masses and shape characteristics of incompletely preserved,==

70 ==broken or obscured stomach stones found with plesiosaur fossils.== Lastly, the body

71 masses of these plesiosaurs, derived from three-dimensional, digital models of the

72 animals, are used to compare the relative mass fractions of the gastroliths to the bodies

73 that hosted them.

74 Institutional abbreviation: TMP - Royal Tyrrell Museum of Palaeontology.

75

Materials

==Body Fossils==

78 The geographic locations of the four species are shown in figure 1A. Three of the

79 studied specimens are based on single individuals: *Albertonectes vanderveldei*

80 TMP2007.11.1, *Fluvionectes sloanae* TMP2009.37.68, *Nichollssaura borealis*

81 TMP1994.122.1; while the analysis of *Wapuskanectes betsynichollsae* is based on two

82 separate specimens - TMP2011.88.1 and TMP2012.50.1. Three of the specimens were

83 found during open pit mining – *Albertonectes*, *Nichollsaura*, and the first

84 *Wapuskanectes* TMP2011.88.1. The second specimen of *Wapuskanectes*,

85 TMP2012.55.1, was exposed during roadworks, while *Fluvionectes* was discovered

86 during field prospecting. Figure 1B shows the chronostratigraphic positions of the four

87 genera.

88   *Albertonectes* (Fig. 2) was found in 2007 during open pit mining for gem quality

89   ammonite shells ("ammolite") south of the town of Lethbridge in the mine operated by

90   Korite International. It comes from the Late Cretaceous Bearpaw Formation and was

91   described and named as the elasmosaurid *Albertonectes vanderveldei* by Kubo *et al*.

92   (2012). This specimen is missing its head, its left forelimb and portions of the distal

93   regions of the hind limbs, and these losses happened prior to final burial. However, all

94   the vertebrae from the atlas-axis to the tip of the tail, and most of the ribs, were found in

95   articulation, although the neck had snapped into four sections. Gastroliths with this

96   specimen were first observed in the field, with more being revealed during preparation.

97   *Fluvionectes* (Fig. 3) was found during fossil prospecting in the extreme

98   southeast of the province in 2009 in an area known as the Porcupine Pocket of the

99   Sage Creek Grazing Preserve. It is another elasmosaur (Campbell et al., 2021) and was

100   found in rocks of the Lethbridge Coal Zone, a subdivision of the Dinosaur Park

101   Formation (DPF), and the Zone represents a near-coastal setting that was subject to

102   tidal influences (Eberth, 2005). The biozone defined by the ammonite *Baculites*

103   *compressus* is the same for Bearpaw Formation that produced the *Albertonectes* and

104   the Lethbridge Coal Zone (Tsujita 1995). *Fluvionectes* was found in fluvial sediments

105   along with many pieces of coalified wood in close association with the bones, and the

106   interpretation is that the carcass was caught in a log jam (Campbell et al., 2021). The

107   periphery of the outcrop which held the specimen was heavily eroded when found, and

108   much of the animal's extremities were lost – most of the tail, neck and distal limbs.

109   However, most the axial body from the proximal quarter of the tail to the proximal

110   quarter of the neck is preserved, with all the bones in close association, and this allows

111   an estimation of the animal's size to enable a body reconstruction. The presence of

112   gastroliths with this specimen was revealed during preparation.

113   *Nichollssaura* (Fig. 4) was uncovered during overburden removal in the Syncrude

114   Canada Ltd. tar sand mine north of Fort McMurray, and comes from the Wabiskaw

115   Member of the Early Cretaceous Clearwater Formation which is interpreted to be

116   earliest Albian in age (Caldwell et al. 1978). This specimen was almost complete except

117   for a missing left forelimb, the bones distal the tarsals on the right hindlimb, and the

118   proximal third of the cervical ribs on the left side, and the first few anterior dorsal ribs,

119   also on the left side. These missing elements were reconstructed for display purposes.

120   This animal is a leptocleidid plesiosaur and was described by Druckenmiller & Russell

121   (2008). The presence of its gastroliths was revealed during preparation.

122   The first *Wapuskanectes* specimen, TMP2011.88.1 (Fig. 5), is an early

123   elasmosaurid and comes from the same Syncrude Canada Ltd. tar sand mine and rock

124   unit that produced *Nichollssaura* – the Wabiskaw member of the Clearwater Formation.

125   The genus was described and named by Druckenmiller & Russell (2006), with the

126   holotype specimen being TMP1998.49.2 which also came from the same mine and rock

127   unit. The present specimen consists of proximal neck vertebrae, anterior dorsal

128   vertebrae, the pectoral region, a left humerus, some manual phalanges, and some

129   incomplete ribs and gastralia. This specimen has a substantial collection of gastroliths

130   visible at the posterior end of the pectoral girdle that was revealed during preparation.

131   The second *Wapuskanectes* specimen (Fig. 6) also comes for the Wabiskaw

132   Member of the Clearwater Formation, but was found during road construction for the

133 Parson's Creek Interchange on the north side of the town of Fort McMurray in

134 December of 2012. It was located about 30km south-southeast of the localities of the

135 earlier specimens from the Syncrude mine. Unfortunately, it was exposed when a

136 grader ploughed through the neck resulting in the destruction and loss of the skull and

137 most of the neck. Additionally, there was no trace of the right forelimb, and this loss is

138 interpreted to have occurred some time prior to the final burial of the animal. Despite

139 these missing pieces, the rest of the specimen is very well preserved. Preparation

140 revealed some small gastroliths visible between the posterior dorsal ribs of this

141 specimen. The relative completeness of this specimen enabled the generation of a 3D

142 body model for mass estimation. The maximum transverse widths of the pectoral girdles

143 of the two *Wapuskanectes* specimens, as measured at the postero-lateral margins of

144 the glenoids, are identical at 57cm, and it is assumed that the overall body sizes and

145 proportions of the two animals would have been very similar.

146

147 Stomach Stones

148   *Albertonectes* was first exposed when an excavator bucket unexpectedly struck

149 the fossil. Portions of the mid-trunk dorsal and ventral ribs, and an unknown quantity of

150 gastroliths, were lost when the excavator bucket smashed through the fossil. Some time

151 after death the carcass came to lie on the seabed on its back. As the internal organs,

152 and the stomach in particular, decayed and lost their ability to support themselves, the

153 gastroliths gravitated downwards towards the medial side of the dorsal body wall and

154 some came into direct contact with ribs. Subsequent compaction resulted in some

155 portions of the ribs being plastically deformed around the gastroliths. Except for four

156 stones that were knocked loose at the time of impact, the remainder were tightly

157 clustered together and held in the matrix in a roughly spherical volume and did not show

158 any degree of size or shape sorting. Given the uniqueness of the specimen, and its

159 excellent state of preservation, it was decided to leave it intact and not remove any

160 bones or gastroliths. 97 gastroliths were revealed in total, four in the field, with the rest

161 being exposed during preparation (Fig 2B). 52 stones could be reliably measured to

162 obtain three dimensional radial measurements. The remaining 45 were visible but were

163 either too deeply embedded in the hosting matrix, or were too obscured by ribs, to

164 enable the collection of reliable geometry data. The gastroliths are all gray to black, sub-

165 spherical, chert cobbles with some having a high polish.

166 For *Fluvionectes*, given the incomplete nature of its preservation, and its modest

167 level of disarticulation, it was decided to fully prepare its remains and remove all the

168 bones. During this preparation 75 gastroliths was discovered and removed (Fig 3B).

169 These gastroliths tend to be disk-shaped and are all black cherts. The complete

170 removal of these stones permitted the accurate measurement of their lengths, widths

171 and depths, and the direct determination of their masses. These data were used as a

172 basis for assessments of the reliability of the methods of estimation of missing gastrolith

173 data used with the other plesiosaurs (see Methods).

174 The gastroliths of the *Nichollsaura* were inadvertently exposed when a saw cut,

175 intended to cut away excess matrix from the ventral side of the block, went through the

176 trunk region at a level that intersected limb girdles, dorsal vertebrae, gastralia and

177 gastroliths (Fig. 4B). 165 stones, composed of cherts and quartzites, are exposed on

178 the cut surface as isolated, two-dimensional elliptic shapes with most of them arranged

179 along the left and right sides of the vertebral column, but with a substantial cluster

180 immediately in front of the left pubis. This entire collection of stones appears to be

181 spread out uniformly in a single layer. The visible co-occurrence of limb girdles,

182 vertebrae, gastralia and gastroliths on the frontal plane defined by the cut surface

183 demonstrates the substantial amount of dorso-ventral compaction that the fossil

184 experienced after burial.

185 The gastroliths associated with the first *Wapuskanectes* specimen,

186 TMP2011.88.1 (Fig. 5B), were found during preparation as an isolated, elliptical cluster

187 with semi-major and intermediate diameters of approximately 25 and 20cm, and a

188 thickness (semi-minor diameter) of roughly 5cm. The stones are almost exclusively

189 black, polished cherts with some minor quartzites. There are two regions within the

190 cluster comprising two different sets of stone sizes: a loosely packed region of 93

191 stones with an average maximum diameter of about 2-3cm and a densely packed

192 region with an unknown, but large, number of small stones with an average maximum

193 diameter of no more than 1cm. This latter collection is defined by a sharp, posterior

194 margin that may indicate the original boundary of the stomach (gizzard?) wall. The

195 collection of coarser gastroliths was sufficiently exposed by mechanical preparation to

196 obtain reliable lengths and widths for them, but not depths. It was not possible to obtain

197 reliable measurements from any of the densely packed, smaller stones.

198 With the second, Fort McMurray Parson's Creek roadworks specimen of

199 *Wapuskanectes*, TMP2012.50.1, there were no gastroliths visible initially. The specimen

200 came to rest on the seabed on its back, and during initial preparation a single, black

201 chert pebble was uncovered poking out between a pair of mid-trunk dorsal ribs on the

202 right side of the body. Similar to what occurred with the *Albertonectes* gastroliths (see

203 above), the stomach stones of TMP 2012.50.1 also settled towards the medial side of

204 the dorsal ribs in the posterior trunk region. Before preparation of the torso went any

205 further, the specimen was X-rayed at an industrial facility that analyses large metal

206 castings for defects where they can easily detect tiny fractures and voids. The hope was

207 that this technology would reveal the sizes and extents of other gastroliths within the

208 body cavity, but it was unable to detect anything resembling gastroliths (or even bones).

209 Subsequent preparation revealed more small, black chert pebbles lying between the

210 ribs, and close to the vertebral column, on both the left and right sides at a position just

211 posterior to the midpoint of the trunk (Fig. 6B). Given the overall quality of the fossil, it

212 was decided to leave all the bones in place, thus leaving an unknown number of

213 gastroliths hidden within. Despite the limited number gastroliths exposed with this

214 specimen, they are very similar in size, shape and composition to the small gastroliths

215 seen with TMP2011.88. As both specimens come from the same rock unit, the

216 Wabiskaw Member of the Clearwater Formation, it was assumed that the overall

217 gastrolith composition would be similar for the two specimens.

218

219 **Methods**

220 Gastrolith volume and mass estimates

221   Four of the gastroliths associated with the *Albertonectes* were free of the matrix

222 and could be confidently measured to obtain the three diameters, the remainder were

223   partially embedded within the matrix and some were also partly obscured by the ribs.

224   Ninety seven stones were observed in total, but reliable measurements in all three

225   dimensions could only be taken from 52 of them. These gastroliths were viewed as tri-

226   axial ellipsoids and their semi-major, intermediate and semi-minor diameters were

227   measured with digital calipers to the nearest tenth of a millimetre. The expression to

228   compute the volume of a tri-axial ellipsoid is $Volume = \frac{4}{3}\pi abc$, where 'a', 'b', and 'c' are

229   the semi-major, intermediate, and semi-minor radii, respectively, of the ellipsoid. Chert

230   has a density of 2.67 gm/cc (Deer et al., 1992), and the masses of these 52 chert

231   gastroliths were computed by multiplying their volumes by the density of chert. For the

232   remaining 45 stones only two diameters could be confidently measured. Lacking full

233   knowledge of their dimensions, and noting that no sorting by shape or size was

234   apparent with the fully measurable cluster of 52 stones, this latter assemblage was

235   taken to be a representative, and random, sample of the original full set of gastroliths. A

236   simple ratio was used to estimate the combined mass of the remaining stones: if the

237   measured 52 stones have a combined mass of 4.98 kg, then the mass of the remaining

238   45 will come from solving for '?kg' in the expression: $\frac{4.98\,kg}{52} = \frac{?kg}{45}$

239   Only with *Fluvionectes*, and its fully removed gastroliths, was it possible to get

240   the actual masses of all the stones. The stones were weighed to the nearest tenth of a

241   gram on electronic scales (Symmetry ED-150 by Cole-Parmer). As a check on the

242   gastrolith mass estimation schemes outlined above and below for the other plesiosaur

243   specimens, the three, tri-axial dimensions of the Sage Creek gastroliths were also

244   measured and their masses estimated by multiplying their calculated volumes by the

245   density of chert. The semi-major and intermediate diameters were also used to predict

246 the third diameter. The goal was to test the accuracy of the computed masses against

247 the observed mass.

248   The *Nichollssaura* gastroliths were exposed on the saw-cut surface as closed

249 contours of elliptic shape, from which the longitudinal and transverse diameters could

250 have been obtained by direct measurement. However, to properly estimate the volume

251 and shape of the gastroliths, the third diameter needs to be estimated, and it was

252 decided to use a computational method to do this and objectively determine the lengths

253 and widths of the exposed elliptical cross-sections at the same time. A digital image of

254 the cut surface exposing the gastroliths was imported into the drawing program Corel

255 Draw!, and all the visible perimeters of gastroliths were digitally traced, and the traces

256 were then exported as individual AutoCAD DXF files. These DXF files were reduced to

257 simple (X,Y) co-ordinate pairs defining the stone perimeters, and a computer program

258 was written to carry out the following processing of the data. The longest diameter of a

259 stone cross-section was found by determining the greatest distance between a pair of

260 points for a given stone perimeter. Using its perimeter data, the cut-exposed area of the

261 stone was computed using a triangular decomposition method (Henderson, 2002). The

262 formula for the area of an ellipse given by $Area = \pi\left(\frac{a}{2}\right)\left(\frac{b}{2}\right)$, where 'a' and 'b' are the semi-

263 major and semi-minor diameters of the visible ellipse, respectively. Using the observed

264 value for 'a' (the longest diameter) and the computed area, the value of 'b' can be

265 derived via the expression $b = 2 \cdot \frac{Area}{\left(\frac{\pi a}{2}\right)}$. These values of 'a' and 'b' are used in estimation

266 methods outlined in the next paragraph.

267 Like what was seen with the *Nichollssaura* gastroliths, those of *Wapuskanectes*

268 could only be reliably measured in two dimensions - length and width, with the third

269 dimension, depth, needing to be estimated. Three methods were used to estimate this

270 third dimension for the gastroliths of these two plesiosaurs: 1) depth = length ÷ 2; 2)

271 depth = average of length and width = (length + width) ÷2; and 3) depth = square root

272 of the product of length and width = √(length × width). These three methods were also

273 applied to the fully measured stones of *Albertonectes* and *Fluvionectes* using the

274 observed lengths and widths to estimate depths. These latter results were used to see

275 which of the three methods produced an estimated mass closest to the properly

276 measure ones.

277 For a long time, mathematicians have been interested in knowing the best way

278 pack spheres so as to have the least amount of space between them, and this became

279 known as the Kepler Conjecture (Kepler, 1611). Eventually, it was formally proven that

280 the most efficient method achieves a packing density of approximately 0.74048 (Hales,

281 2012). The spherical packing idea was applied to the densely packed cluster of small

282 gastroliths found with first *Wapuskanectes* specimen, TMP2011.88.1, in an attempt to

283 estimate the mass of the stones. The gastroliths visible on the surface of the cluster are

284 clearly touching all their neighbours, as posited by the sphere packing theorem, and this

285 packing configuration was assumed to be true for the entire cluster of small stones

286 inside. With an estimate of the volume of this cluster, multiplying the volume by the

287 density of chert, and then applying the packing density factor would give an estimate of

288 the cluster mass.

289

290   Body mass estimations

291   Three-dimensional meshes representing the axial body and limbs of the four

292   plesiosaurs were generated using the methods of Henderson (1999). The actual body

293   outlines were based on the preserved skeletal forms along with estimates of the soft

294   tissues that would have surrounded them. For the neck regions, the dorso-ventral

295   diameters were set so that space for an esophagus and trachea could be

296   accommodated. Given the great length of the trachea in these animals, it was assumed

297   that the tracheal lumen would have to be large to reduce the effects of the viscous drag

298   on air flow caused by the large amount of surface area of the trachea. It has been

299   shown that the resistance to flow decreases exponentially with increasing tracheal

300   diameter (Daniels and Pratt 1992). The outlines of the flippers were extended beyond

301   their known bony extents by comparison with the limbs of sea-turtles and penguins. The

302   bones forming the limbs of *Nicholssaura* and the *Wapuskanectes* road works specimen

303   (TMP 2012.50.1) were both much broader (greater fore-aft chordal lengths) than those

304   of the two elasmosaurs, and this resulted in their modelled limbs being broader than

305   those of the elasmosaurs. Lung volumes were estimated for each model, and were set

306   to represent between 8-10% of the axial body volume, based on observations of the

307   lungs of living reptiles (Tenney and Tenney 1970). Actual computation of the masses of

308   the body regions (axial and appendicular) involves multiplying the volumes of these

309   regions by a predefined value for the tissue density. The volumes were estimated using

310   the methods outlined in Henderson (1999). A uniform body density of 1,050 gm/L was

311   used for all the post-cervical body regions in all the models. This value is higher than

312   that of pure water at 1000 gm/l, but it was felt that given the dense, non-pneumatic

313 nature of the bones of the axial and appendicular skeletons, and in particular the high

314 proportion of bone relative to soft-tissue inferred for the limbs, that this denser value

315 was justified. The necks, with their large, air-filled trachea, were set to a lower density of

316 900 gm/l. Despite the main body density value being greater than that of water, when a

317 full body model is combined with its lung, the animals are still positively buoyant when

318 the lungs are fully inflated as observed in a study of buoyancy and equilibrium in

319 plesiosaurs that used digital models with the same densities and lung volume

320 proportions used here (Henderson 2006). The assumptions and methods that went into

321 the generation of the above models have been validated with accurate mass estimates

322 for similarly constructed models of extant, semi-aquatic reptiles – alligators (Henderson,

323 2003), sea turtles (Henderson, 2006) and penguins (Henderson, 2018) – and fully

324 terrestrial animals such as horses and giraffes (Henderson and Naish, 2010) and

325 elephants (Henderson, 2006).

326

Results

328   Figure 7 shows the four body models generated from the plesiosaur skeletons,

329 and Table 1 presents the physical attributes determined from the models. Two of the

330 models were based on nearly complete fossils – *Albertonectes* and *Nichollssaura* – and

331 their necks (grey coloured regions on models) are estimated to weigh 1100 kg and 10.6

332 kg, respectively. Relative to body mass, these necks represent 22.7% and 7.86% of

333 total body mass. The necks of the other two – *Fluvionectes* and *Wapuskanectes* – were

334 incompletely preserved, and this could lead to uncertainty regarding their actual body

335   mass. As restored, the necks for these two animals are estimated to have mass of 72.9

336   kg and 198 kg, respectively, and their relative mass fractions are 18.6% and 16.5%,

337   respectively. As these latter two animals are early elasmosaurids from close to the

338   Aptian/Albian boundary, they were given substantial necks and their relative neck mass

339   fractions approach that of the later and derived Campanian *Albertonectes*.

340   Table 2 presents observed and estimated gastrolith masses for the four

341   plesiosaurs. The 52 stones that could be fully measured for *Albertonectes* were found to

342   have a combined volume of 1,865 cm^3, and when multiplied by the density of chert at

343   2.67 gm/cm^2, to have a mass of 4,980 gm. From the calculated mass of the observable

344   52 stones, the remaining, unmeasured 45 stones are predicted via a simple ratio

345   expression to have a combined mass of 4,310 gm. Together, these two estimates give a

346   total gastrolith mass of 9,290 gm. Using the measured semi-major and intermediate

347   diameters of the first 52 gastroliths of *Albertonectes*, the three methods of predicting the

348   third diameter gave the following mass results - Half Length: 4,654 gm; Average of

349   Length and Width: 10,695 gm; RMS of Length and Width: 10,577 gm. The Half Length

350   method clearly produced the result closest to the one that used the three measured

351   diameters.

352   Direct weighing of the *Fluvionectes* gastroliths gave a total gastrolith mass of 359

353   gm. Determining the volumes of the stones from their measured diameters, and

354   multiplying them by the density of chert, gave a total mass estimate of 325 gm – a value

355   9.56% less than the directed weighed value. At first it might seem reasonable to apply

356   the 9.56% mismatch as a correction factor the stone masses calculated for

357   *Albertonectes* that were also based on geometry. However, the shape distributions of

358   the two assemblages are very different (see the histograms and pie charts below),

359   suggesting that the mismatch between observed and calculated mass for *Fluvionectes*

360   might be sample specific, and not be applied as a correction factor to the results

361   obtained for *Albertonectes*. Applying the three, third-dimension estimation methods to

362   the measured semi-major and intermediate diameters of the *Fluvionectes* gastroliths

363   gave the following mass estimates - Half Length: 337.7 gm; Average of Length and

364   Width: 780.7 gm; RMS of Length and Width: 770.8 gm. Again, the Half Length

365   estimation provides the estimate closest to the one derived from actually weighing the

366   gastroliths.

367   In light of the close agreement between gastrolith mass estimates produced

368   using the Half Length method and those from direct measurement of *Albertonectes* and

369   *Fluvionectes* gastroliths, the obscured depth dimensions for the gastroliths of

370   *Nichollssaura* and *Wapuskanectes* were estimated using the Half Length method. This

371   method gave a total mass for the cut *Nichollssaura* gastroliths of 105.4 gm, and a mass

372   of 186.7 gm for the scattered cluster of larger gastroliths from *Wapuskanectes*.

373   The densely packed cluster of small gastroliths found with *Wapuskanectes*

374   specimen TMP2011.88.1 has a shape similar to that of a flattened, tri-axial ellipsoid with

375   its length, width and depth being 20, 10 and 5 cm, respectively. This cluster has a

376   volume of 157.1 cm^3, and when multiplied by the density of chert and the spherical

377   packing density factor, has an estimated stone mass of 310.6 gm. Adding the mass

378   estimates of the loose and dense clusters give a total mass of 497.3 gm.

379   Histograms and pie charts were generated to aid visualization of the differences

380   and similarities between the shapes and masses of stomach stones. Figure 8 presents

381   histograms that show marked differences in the ranges and proportions of the masses

382   of stones ingested by the animals. *Albertonectes*, being the largest animal in the study,

383   also had the greatest range of stone sizes, with the largest stone being 1.13 kg. The

384   largest stones recovered from the other animals were all an order of magnitude smaller

385   (Table 2). To facilitate comparisons between the stones of all four animals, the

386   histogram for *Albertonectes* was done again but with the same smaller range of bin

387   sizes (0 – 16 gm) that was applied to the other specimens (Fig. 8B). The gastroliths of

388   the three smaller animals are dominated by stones in the 0 – 4 gm range, while these

389   stones represent a minor component for *Albertonectes*. Visual inspection of the

390   gastrolith size distributions for the smaller animals shows them to be skewed to the

391   right, but with *Fluvionectes* having less of a skew.

392   Pie charts were generated for all the gastrolith samples using four shape

393   categories – xiphoid ("blade-like"), discoid, spherical, and cylindrical based on the

394   classification scheme of Dobkins and Folk (1970). The pie charts only analyze those

395   gastroliths that could be fully or partly measured. The pie chart proportions were

396   computed two ways: 1) using the individual masses of the stones and seeing how the

397   masses of stones distributed across each category (Fig. 9), and 2) the absolute count of

398   how many stones were in each category (Fig. 10). For *Albertonectes* and *Fluvionectes*,

399   their pie charts demonstrate that the two different ways of looking at gastrolith shape

400   distribution can give very different results. This is especially noticeable with the blade-

401   like (xiphoid) class where *Albertonectes* would appear to have almost none (1.1%)

402 when their mass is considered (Fig. 9A), but almost 10 times as much when counted

403 (Fig. 10A). However, both measures are consistent in showing that the blade-like

404 gastroliths of *Albertonectes* make up the smallest fraction of the entire collection. The

405 differences in shape category fractions based on different methods of analysis also

406 apply to *Fluvionectes* (Fig 9B vs Fig. 10B). It should be noted that the present count

407 fraction pie chart for *Albertonectes* gastroliths differs slightly from the one originally

408 presented in the initial description by Kubo et al. (2012, Fig. 9) – a small error was

409 discovered in the earlier program used for calculating the shape fractions. The corrected

410 plot has slightly larger spheroid and smaller cylindrical fractions than were previously

411 presented.

412   Figure 11 summarizes the relationships between largest gastrolith and total

413 gastrolith mass relative to body mass. The 2 orders of magnitude differences seen in

414 the ranges of stone masses necessitated plotting the data on log-log plots. Although it is

415 just a sample of four plesiosaurs, and the gastrolith collections each have their

416 deficiencies, two trends are noticeable from the two plots. The first is that the largest

417 plesiosaur, *Albertonectes*, has both the largest single gastrolith and the most gastroliths.

418 A regression computed for the largest gastrolith vs. body mass has correlation of

419 0.8762, but the uncertainty on the computed slope (0.5474) is almost half the slope

420 value (1.40760. A better regression result comes from plotting total gastrolith mass

421 against body mass. The uncertainty on the computed slope (0.2446) is less than half

422 that seen with previous plot, and the correlation coefficient is ~~much~~ higher at 0.9606. In

423 both plots, the amounts of gastroliths estimated for *Wapuskanectes* lie below the fitted

424 line. The collection of stones found with the first specimen of *Wapuskanectes*,

425 TMP2011.88.1, was disturbed after death as shown by the "smeared-out" shape of the

426 collection, and suggests that an unknown number of gastroliths were lost prior to final

427 burial of the carcass. Of the four fossils studied, this one was also the most disrupted,

428 with the pectoral girdle being inverted relative to the rest of the body prior to final burial.

429 The specimen was discovered when some neck vertebrae were exposed by heavy

430 equipment. It was removed from the mine as a single, large, intact block with no chance

431 of any stones being lost during this process (pers. obs.).

432

433 **Discussion**

434   Although both are derived Late Cretaceous elasmosaurs, *Albertonectes* and

435 *Fluvionectes* come from rock formations that represent ~~very~~ different environments –

436 ==open marine vs. fluvial==, respectively, and this could explain the differences in their

437 respective gastrolith compositions. Support for this idea might come from the

438 observation that the other two plesiosaurs – *Nichollssaura* and *Wapuskanectes* – both

439 come from the Wabiskaw Member of the Clearwater Formation, and by both pie chart

440 measures their gastrolith composition are very similar. This is also remarkable because

441 the body sizes of the animals are ~~very~~ different in body proportions and size, with

442 *Wapuskanectes* being approximately ==ten time more massive== than *Nichollssaura* (Table

443 1).

444   The pie charts reveal that the discoid fractions of the stomach stones represent

445 either major (*Fluvionectes*) or substantial (*Albertonectes*) portions of the sample. The

446 strong discoid signal seen in these samples suggests that these animals were collecting

447   potential stomach stones mainly from beaches (discs), but also some from the mouths

448   of rivers (spheres), based on the observations of Dobkins and Folk (1970). The bias

449   towards crypto- and micro-crystalline quartz (chert) gastroliths for plesiosaurs of the

450   present study may indicate that the animals actively sought these rock types for their

451   hardness and durability. It could also be argued that we have biased samples of

452   stomach stones because any ingested limestone or carbonate-cemented clastic

453   pebbles would have been dissolved and/or disaggregated by stomach acids and the

454   small constituent grains excreted. However, if the gastrolith samples represent an

455   instantaneous, random "snap-shot" of the stone assemblages carried by the animals at

456   the time of their deaths, it is surprising that none of four gastrolith samples studied show

457   even the slightest trace of any sandstone or limestone pebbles.

458   As can be seen from Table 2, the masses of gastroliths represent extremely

459   small fractions of total body mass, with an average value being just one tenth of one

460   percent. The 9.29kg mass of stones estimated for *Albertonectes* is similar to the 8.84kg

461   mass of stones recovered from an elasmosaur from the Bearpaw Formation of Montana

462   (Darby and Ojakangas, 1980), but the largest stone from this latter animal was ~~just~~

463   662gm, approximately half the size of the largest stone from *Albertonectes*. In their

464   review of elamosaur gastroliths, Thompson et al. (2007) comment on the extremely

465   variable nature of the range of sizes and the total masses of the gastroliths recovered

466   from this group of plesiosaurs. A large Antarctic specimen examined by Thomson et al.

467   2007) was found to have 2,626 gastroliths, but their total mass was just 3.02kg, and the

468   largest was ~~only~~ 46.6gm. At the other extreme, Everhart (2000) reports on a total mass

469   of gastroliths from a Kansas elasmosaur being equal to 13.1kg with the largest weighing

470   1.49kg. If gastroliths were truly related to buoyancy control the expectation would be

471   that elasmosaurs of the same size should have the same amounts of gastroliths, but

472   this is ~~clearly~~ not the case. Similar what was argued for in modelling studies of

473   gastroliths in crocodilians (Henderson 2003) and plesiosaurs (Henderson 2006), and

474   the suspicions of other authors <mark>eg. (Cicimurri & Everhart 2001)</mark>, the effects of these

475   relatively tiny, and variable, masses of stones on the buoyancy and equilibrium of the

476   animals when they were alive are considered to be almost non-existent.

477   The stones found with *Nichollssaura* and *Wapuskanectes* are very similar in size,

478   shape and composition to the clasts found within the Cadomin Conglomerate, a Lower

479   Cretaceous rock formation which is found the length of the Rocky Mountain foothills in

480   Alberta from the 49th to the 60th parallels (Schultheis and Mountjoy,1978). This

481   identification was done with reference to a large sample of the conglomerate held in the

482   collections of the Royal Tyrrell Museum with specimen number TMP2016.38.4. This

483   conglomerate is early Aptian in age, while the Wabiskaw Member and its plesiosaurs

484   are earliest Albian, and this temporal gap represents an interval of proximately 8 – 10

485   million years (Alberta Geological Survey, 2015). It is hypothesized that *Nichollssaura*

486   and *Wapuskanectes*, living the northern Western Interior Seaway during the Albian,

487   could have swum westwards to beaches and river mouths along the west coast of the

488   Seaway to collect either uncemented, or <mark>eroding, Cadomin clasts.</mark>

489

490   CONCLUSIONS

491   Using samples of gastroliths from four plesiosaur fossils (two Early Cretaceous

492   and two Late Cretaceous) with varying degrees of completeness, it has been shown

493   that plausible estimates of the original masses of the stones can be made. Total body

494   masses were made for the four animals, and these can be used as a reference

495   standard for other plesiosaurs with similar body shapes. ==Consistent with earlier==

496   ==suspicions about the ineffectiveness of the relatively small amounts of stones found with==

497   ==plesiosaurs on their buoyancy, the total masses of the stones found with the present==

498   ==plesiosaurs was never more 0.2% of total body mass. With geometry== data from the

499   stones their shapes can be categorized and hypotheses made about where the animals

500   collected the stones. eg. river or beach setting. Lastly, the sizes, shapes and

501   compositions of the gastroliths found with the two different species of Early Cretaceous

502   plesiosaur that came from the same geographic area and time were found to be very

503   similar, and suggest a common origin.

504

505   ACKNOWLEDGMENTS

526

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598

Table 1(on next page)

Body model data (table 1) and gastrolith data (table 2)

1 Table 1. Summary of physical attributes of the four plesiosaur models. Ordering is alphabetical by genus.

	Body Length (m)	Total Body Mass (kg)	Lung Volume (L)[1]	Axial Body Mass (kg)	Single Arm Mass (kg)[2]	Single Leg Mass (kg)[2]	Centre of Mass (m)[3]
Albertonectes vanderveldei TMP2007.11.1	12.1	4810	43.8 (9.36%)	4480	115 (2.40%)	52.0 (1.08%)	(4.26, 0.579)
Fluvionectes sloanae TMP2009.37.68	5.21	392	24.2 (6.20%)	378	3.42 (0.875%)	3.54 (0.905%)	(1.84, 0.274)
Nichollssaura borealis TMP1994.122.1	2.86	135	10.7 (8.27%)	117	2.75 (2.17%)	2.19 (1.72%)	(1.26, 0.163)
cf. *Wapuskanectes* sp. Plesiosaur TMP2012.50.1	6.63	1120	84.3 (7.31%)	1090	32.0 (2.68%)	19.8 (1.67%)	(2.57, 0.356)

2 [1] Lung volume percentage expressed as a percentage of total axial body volume.

3 [2] Limb mass percentage expressed as a percentage of total body mass.

4 [3] Centre of mass expressed as (X,Y) where X is the distance from tip of tail and Y is the height above the
5 ventral-most part of the axial body.

6

7

8

9 Table 2. Observed and estimated gastrolith data for the plesiosaurs in the present study. See Methods

10 and Results for derivations of Predicted Missing Mass. Ordering is alphabetical by genus. Total Gastrolith

11 Mass as a percentage of Total Body Mass (Table 1) is shown in parentheses.

	Measured/Observed Mass (gm)	Predicted Missing Mass (gm)	Total Gastrolith Mass (gm)	Largest Single Gastrolith (gm)
Albertonectes vanderveldei TMP2007.11.1	4980	4310	9290 (0.193%)	1130
Fluvionectes sloanae TMP2009.37.68	359	†	359 (0.0916%)	15.3
Nichollssaura borealis TMP1994.122.1	††	105	105 (0.0778%)	9.96
Wapuskanectes sp. TMP2012.50.1	††	497	497 (0.0444%)	14.5

12 †All *Fluvionectes* stones could be weighed, so no estimate needed.

13 ††None of the stones were fully visible, so no sets of observable triaxial measurements possible.

Figure 1

Geographic locations of the four Cretaceous plesiosaurs from the province of Alberta, Canada discussed in the text.

Geographic locations of the four Cretaceous plesiosaurs from the province of Alberta, Canada discussed in the text. (A) *Albertonectes vanderveldei* TMP2007.11.1, Bearpaw Formation, late Campanian. (B) *Fluvionectes sloanae*, TMP2009.37.68, Dinosaur Park Formation, late Campanian. (C) *Nichollsaura borealis* TMP1994.122.1, Clearwater Formation, early Albian. (D) *Wapuskanectes* betsynichollsae TMP2011.88.1 and TMP2012.50.1, Clearwater Formation, early Albian. (B) Stratigraphic positions of the four plesiosaurs. Dorsal silhouettes are to scale with *A. vanderveldei* at 12m. Chronostratiphic chart after Cohen *et al*. (2013), with the numbers on the righthand side indicating boundary ages in millions of years.
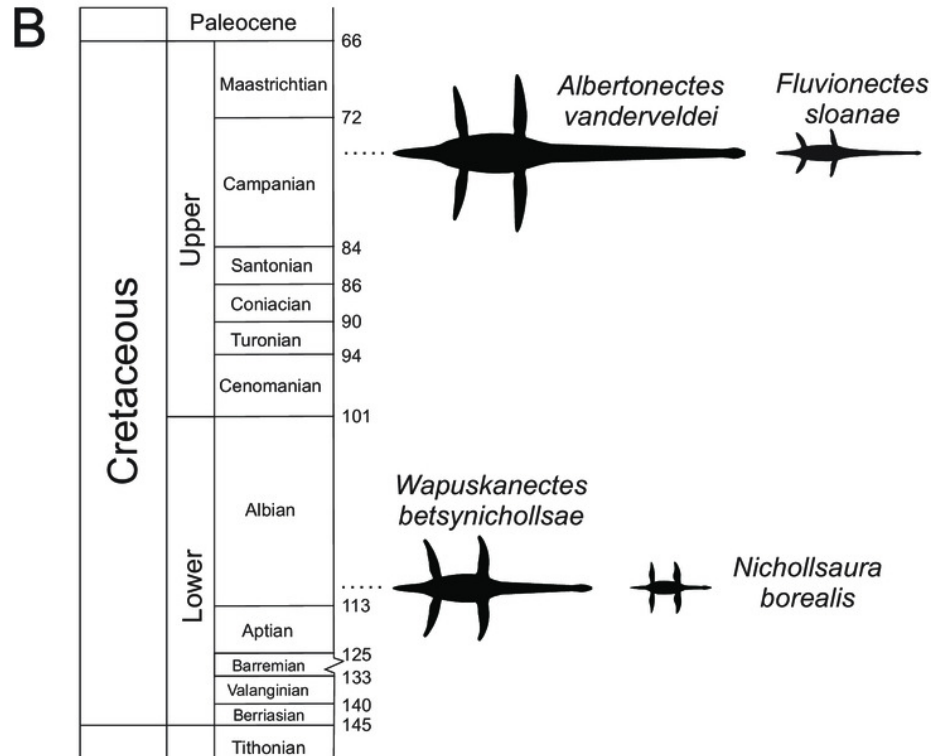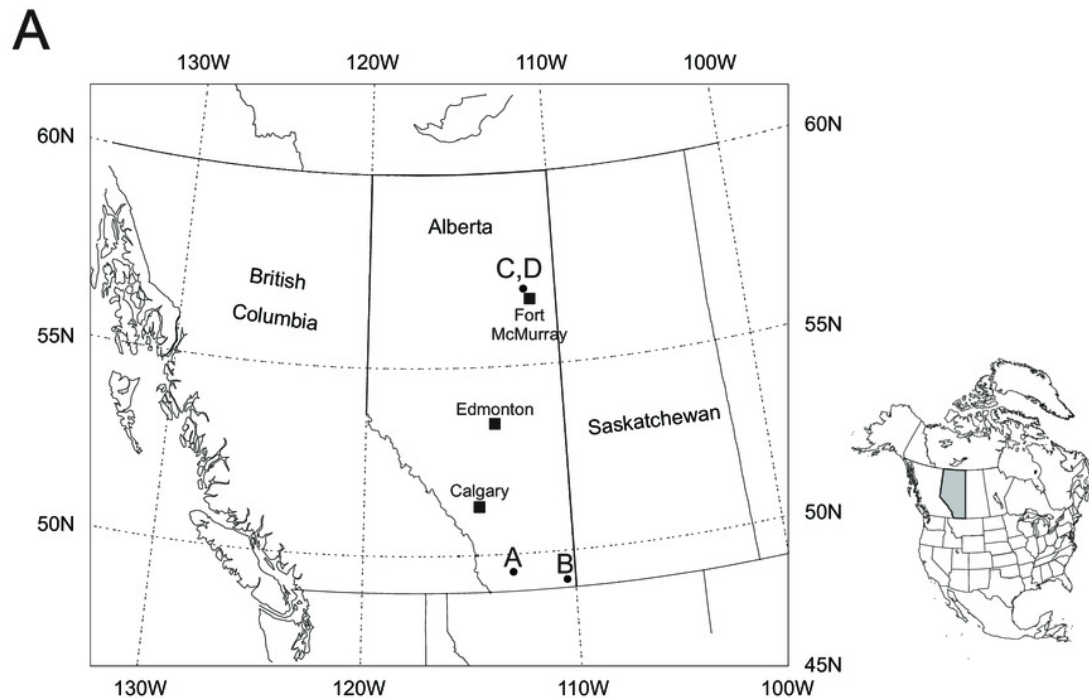
Figure 2

Albertonectes vanderveldei TMP2007.11.1 (Kubo et al., 2010).

(A) View of the original downside in the field and the best preserved side as it experienced the least disruption by scavenging sharks. (B) Detail of midbody region showing the large gastroliths that settled downwards onto the inside of the right, dorsal ribs. This region was hit by the excavator bucket with the partial loss of ribs and an unknown number of gastroliths. Fortuitously, the broken blocks hosting gastroliths can be removed and their contents inspected from several sides. Scalebar is 10cm.

Figure 3

Fluvionectes sloanae TMP2009.37.68 (Campbell et al.,2021).

(A) Recovered skeletal and gastrolith material with the gastroliths arranged in a grid at the lower right. (B) Full complement of gastroliths removed from inside the rib cage of TMP2009.37.68 during preparation. This view is an enlargement of the gastrolith grid seen in (A).

Figure 4

Nichollsaura borealis TMP1994.122.1 (Druckenmiller and Russell, 2009).

(A) Dorsal view of the specimen which was found intact with its limbs fully outstretched. The left fore flipper, the phalanges of the right pes, the left proximal third of the cervical ribs, and the left anterior dorsal ribs are restored. (B) Internal, ventral view of TMP1994.122.1 produced by a rock saw cut, originally intended to remove excess matrix, that fortuitously exposed the dorsal and ventral components of the axial skeleton and enclosed gastroliths (highlighted with white outlines).

Figure 5

An incomplete specimen of *Wapuskanectes betsynichollsae* TMP2011.88.1 that has a large number of gastroliths visible.

(A) Posterior cervical and anterior dorsal vertebrae in left lateral view, the pectoral girdle in ventral view and the left humerus, together with an intact collection of gastroliths located at the posterior end of the pectoral girdle (circled). Large scale bar at right glenoid is 10cm.The maximum pectoral width of this specimen, 57 cm, is identical that of TMP2012.50.1. (B) Close up the gastroliths found with TMP2011.88.1.

Figure 6

A more complete specimen of *Wapuskanectes betsynichollsae*. TMP2012.50.1.

(A) Dorsal view of the originally upside down remains recovered from north of the town of Fort McMurray, Alberta. The head and most of the neck were lost when intercepted by a grader during road construction. The right flipper was lost sometime in the Early Cretaceous prior to the final burial of the body. (B) The pelvic and abdominal regions of TMP2012.50.1 showing gastroliths (black arrows) within the body cavity that settled between the ribs of the inverted carcass and hint at a more substantial collection that is hidden inside the body cavity. Scale bars on body regions are 10cm.
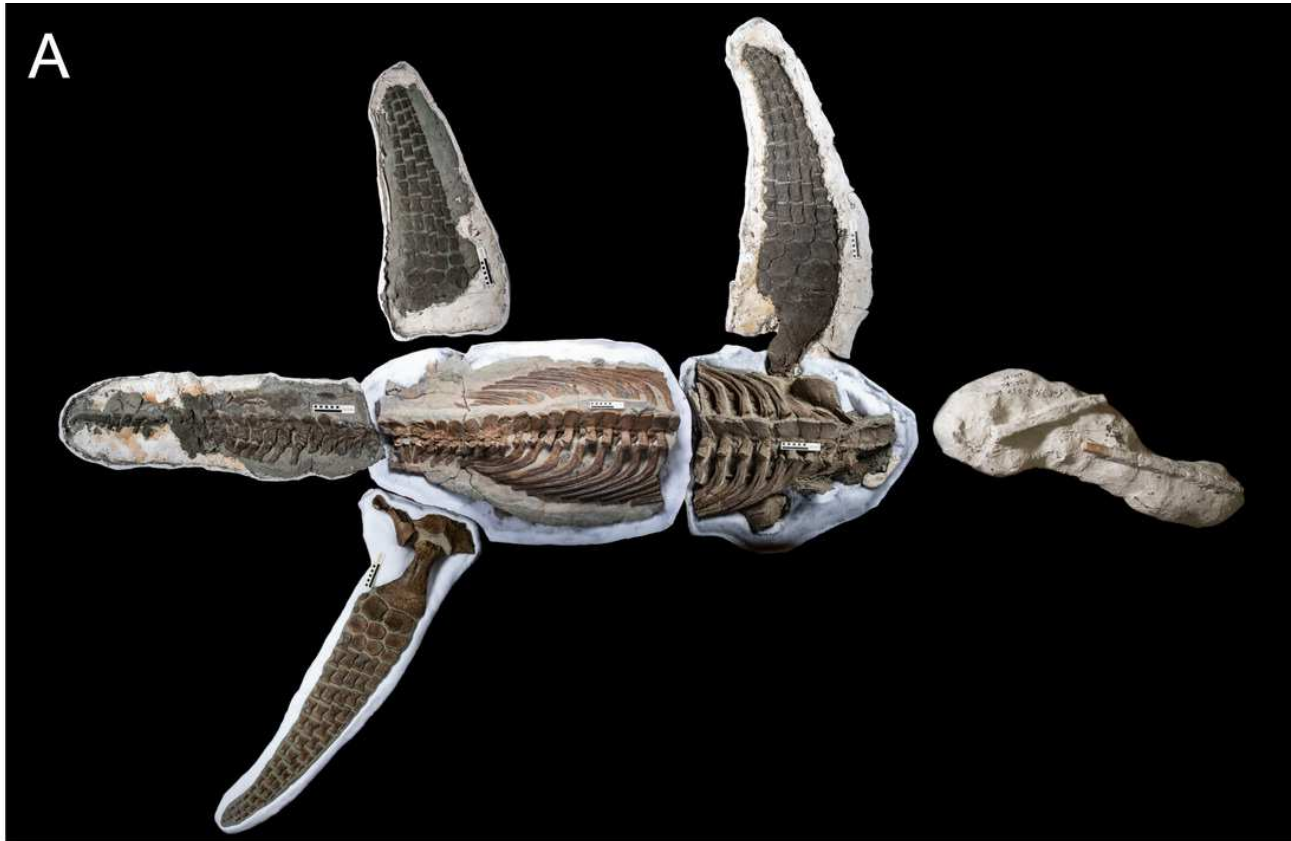
Figure 7

Three-dimensional, digital models of the four plesiosaurs analyzed in the present study.

The models were used for calculation of body mass estimates. The model of *Wapuskanectes* is based on the more complete TMP2012.55.1. The model of *Fluvionectes* is based on the full body outlines drawn by Campbell *et al*. (2021). Hollow lung volumes are indicated by the dark grey shapes in the chest regions. Limb and axial body densities were set to 1050 gm/l, except for the necks (medium grey) which were set to 900 gm/l to account for the empty space occupied by the tracheal and esophageal volumes. Black '+' signs indicate the centres of mass computed for the combined axial body, lungs and limbs and incorporates the regional density differences. See Table 1 for the physical parameters determined for the models.

Albertonectes vanderveldei

2 m

Fluvionectes sloanae

1 m

Nichollssaura borealis

50 cm

Wapuskanectes betsynichollsae

1 m
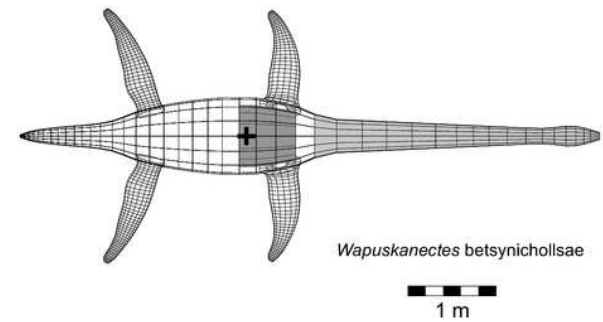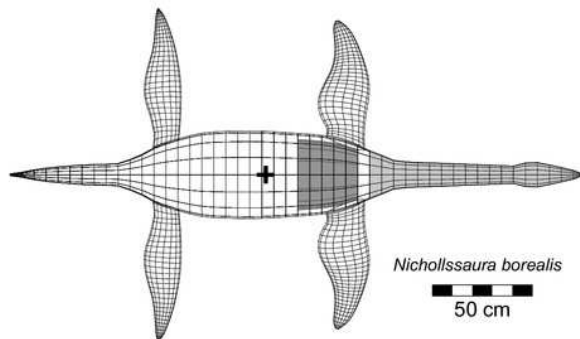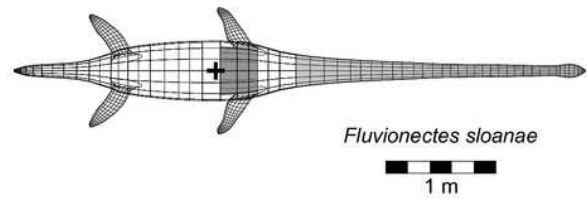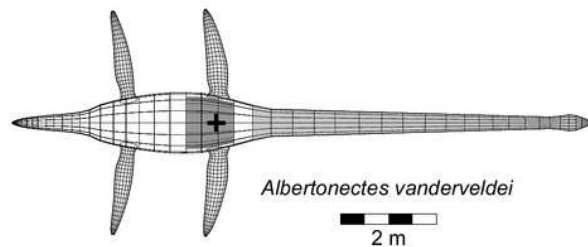
Figure 8

Histograms showing the very different mass distributions of the sets of gastroliths found with the plesiosaurs of the present study.
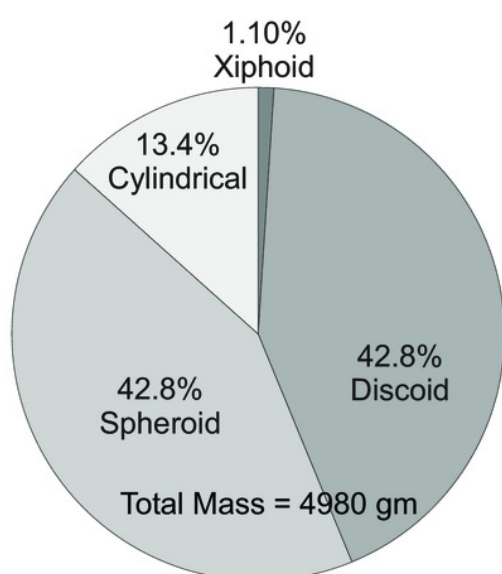
Note that the *Albertonectes* analysis is done twice: first encompassing the full mass range of its stones, and second only applying the smaller mass range of 0 – 16 gm that was also used with the other plesiosaurs. Only the stones masses of *Fluvionectes* were weighed directly. The other masses came from estimation techniques. See Methods and Results for details. Note that the maximum frequency range of each histogram plot is different to make the detailed counts visible.
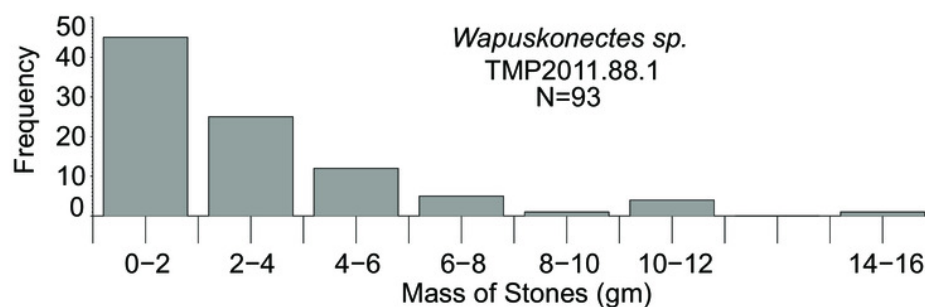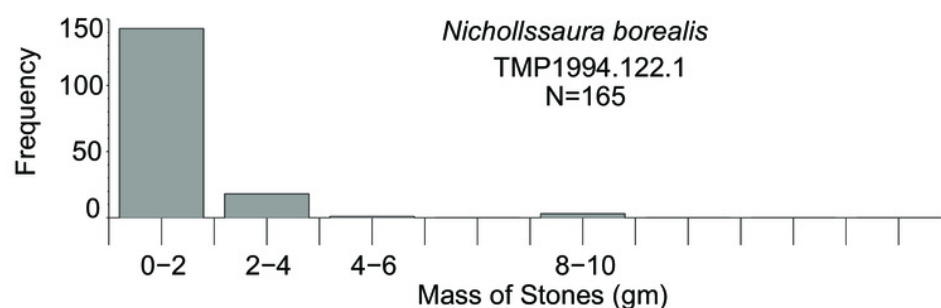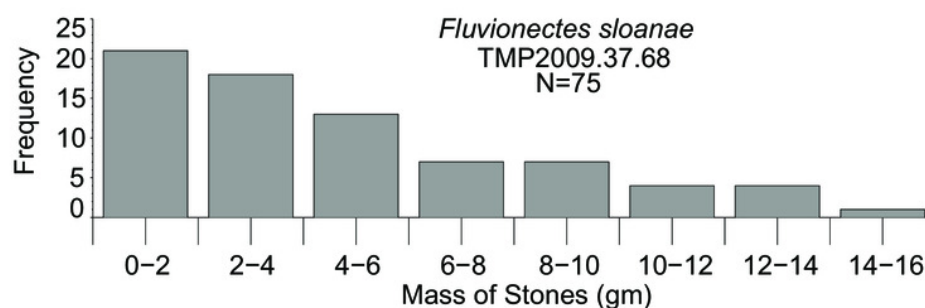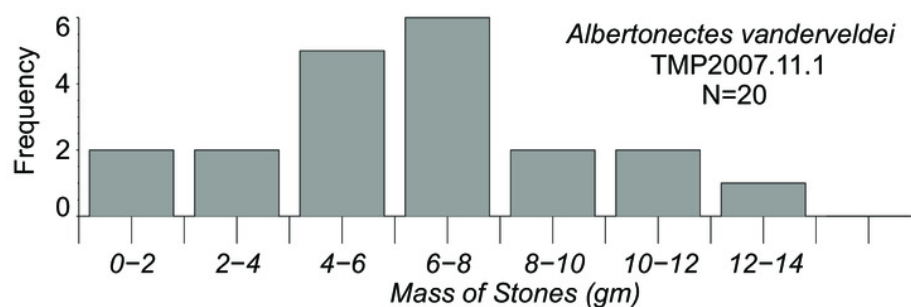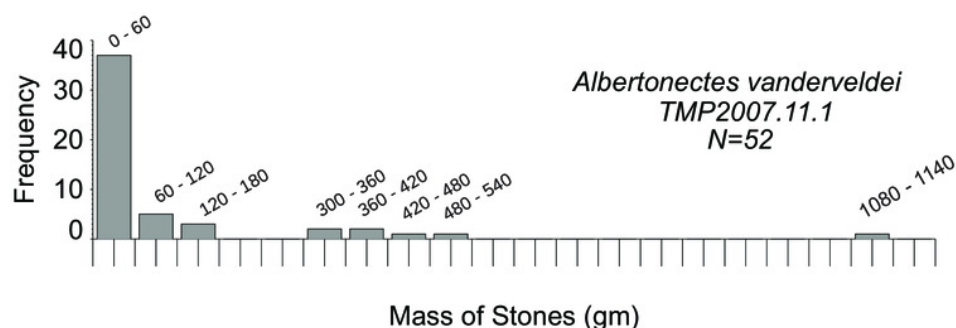
Figure 9

Pie charts showing the relative proportions by mass of the different shapes of the gastroliths recovered from the four plesiosaur specimens using the shape categories of Dobkins and Folk (1970).
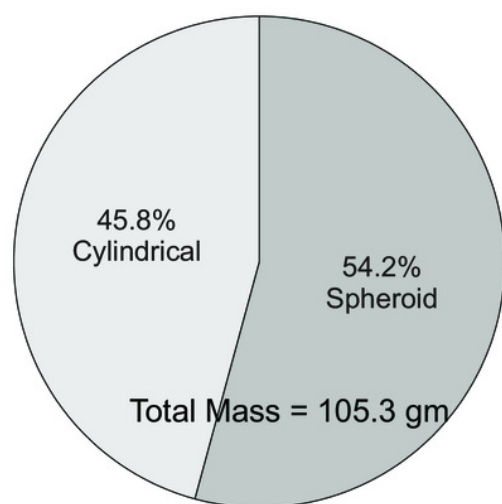
Fluvionectes is distinguished from the others by the high fraction of discoid gastroliths and may reflect its being found in fluvial sediments. *Nichollssaura* and *Wapuskanectes* both come from the same formation and show very similar gastrolith shape distributions that are dominated by spherical pebbles.
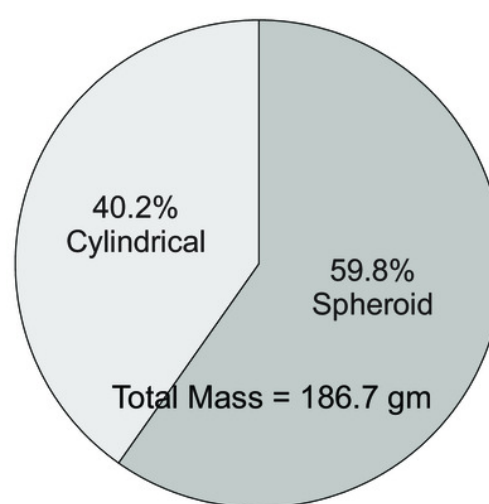
1.10%
Xiphoid

13.4%
Cylindrical

42.8%
Spheroid

42.8%
Discoid

Total Mass = 4980 gm

Albertonectes vanderveldei
TMP 2007.11.1
Bearpaw Fm.
U. Cretaceous
Southern Alberta

1.85% Cylindrical

4.59%
Spheroid

22.2%
Xiphoid

71.4%
Discoid

Total Mass= 359 gm

Fluvionectes sloanae
TMP 2009.37.68
Dinosaur Park Fm.
U. Cretaceous
Southern Alberta

45.8%
Cylindrical

54.2%
Spheroid

Total Mass = 105.3 gm

Nichollssaura borealis
TMP 1994.122.1
Clearwater Fm.
L. Cretaceous
Northern Alberta

40.2%
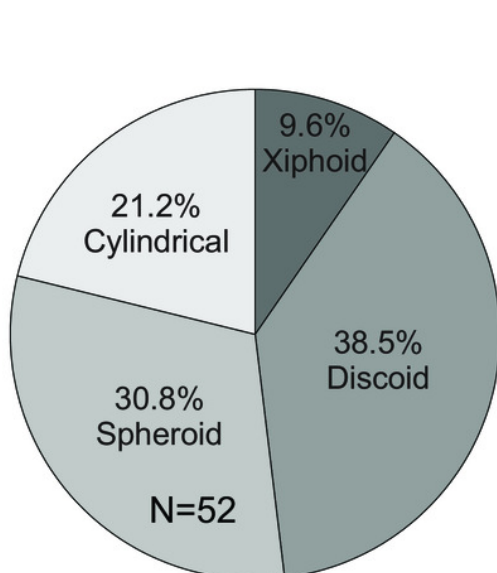Cylindrical

59.8%
Spheroid

Total Mass = 186.7 gm
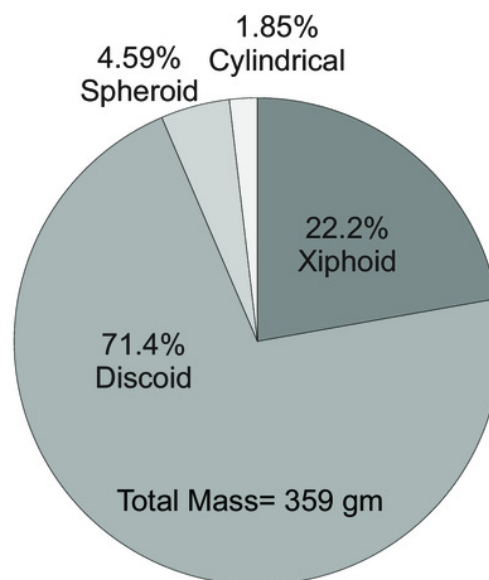
cf. Wapuskanectes sp.
TMP 2011.88.1
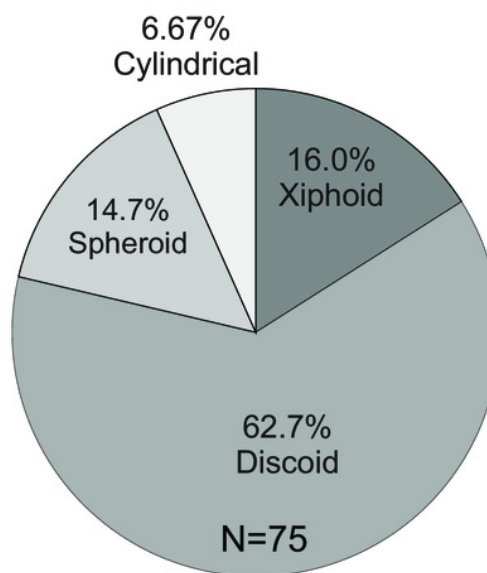Clearwater Fm.
L. Cretaceous
Northern Alberta

Figure 10

Pie charts showing the relative proportions by absolute counts of the different shapes of the gastroliths recovered from the four plesiosaur specimens using the shape categories of Dobkins and Folk (1970).
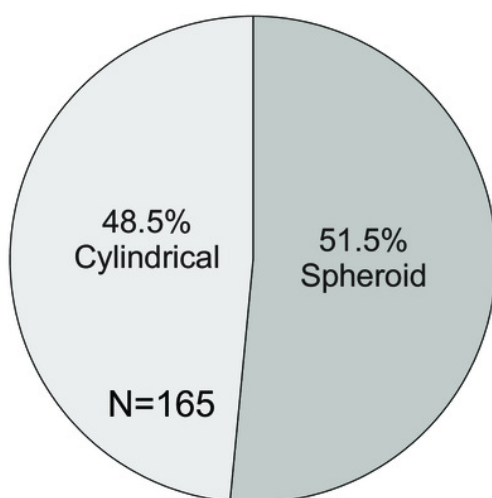
The higher number of xiphoid clasts with *Albertonectes* contrasts with their lower total mass

fraction (Fig. 9) and shows that these clasts tend to be small. *Fluvionectes* still shows a

majority of discoid gastroliths. *Nichollssaura* and *Wapuskanectes* continue to show the same

pattern of having mainly spherical gastroliths.

9.6%
Xiphoid

21.2%
Cylindrical

38.5%
Discoid

30.8%
Spheroid

N=52

Albertonectes vanderveldei
TMP 2007.11.1
Bearpaw Fm.
U. Cretaceous
Southern Alberta

6.67%
Cylindrical

14.7%
Spheroid

16.0%
Xiphoid

62.7%
Discoid

N=75

Fluvionectes sloanae
TMP 2009.37.68
Dinosaur Park Fm.
U. Cretaceous
Southern Alberta

48.5%
Cylindrical

51.5%
Spheroid

N=165

Nichollssaura borealis
TMP 1994.122.1
Clearwater Fm.
L. Cretaceous
Northern Alberta

40.9%
Cylindrical

59.1%
Spheroid

N=93
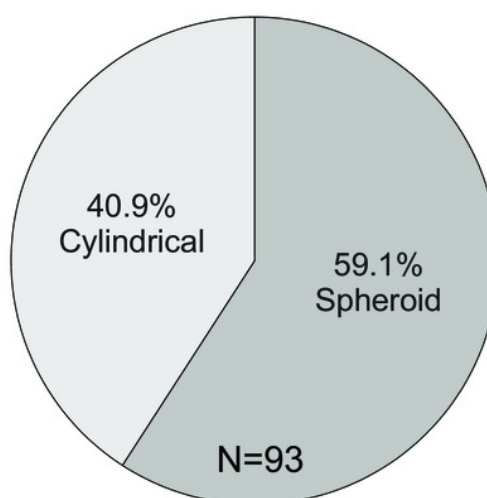
cf. Wapuskanectes sp.
TMP 2011.88.1
Clearwater Fm.
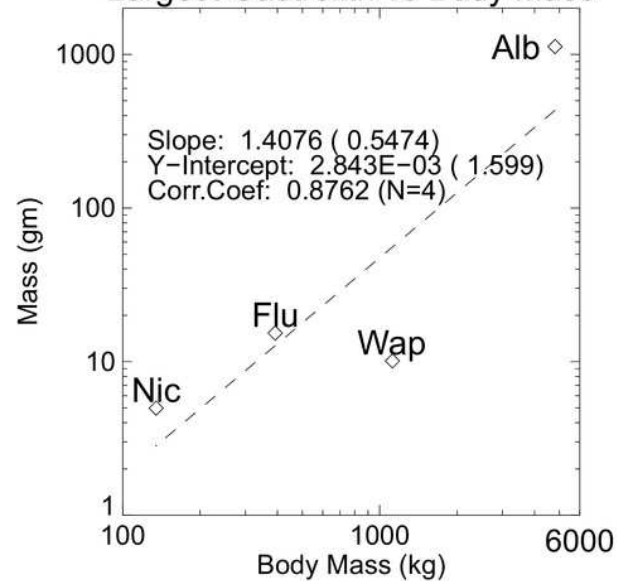L. Cretaceous
Northern Alberta

Figure 11

Maximum plesiosaur gastrolith size and total gastrolith mass plotted as functions of body mass for the four animals of the present study.

Although based on a sample of just four animals, larger plesiosaurs appear to have a larger maximum stone size and greater total mass of stones than smaller plesiosaurs. See Table 1 for body mass data and Table 2 for stone mass data. Logarithmic plotting is used as both body masses and stone masses span approximately two orders of magnitude. Abbreviations: Alb – *Albertonectes vanderveldei*, Flu – *Fluvionectes sloanae*, Nic – *Nichollssaura borealis*, Wap – *Wapuskanectes* betsynichollsae.

Largest Gastrolith vs Body Mass

Slope: 1.4076 (0.5474)
Y-Intercept: 2.843E-03 (1.599)
Corr.Coef: 0.8762 (N=4)

Total Gastrolith Mass vs Body Mass

Slope: 1.1961 (0.2446)
Y-Intercept: 0.243 (0.714)
Corr.Coef: 0.9606 (N=4)