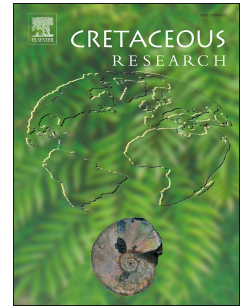


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Living alone or moving in herds? A holistic approach highlights complexity in the social lifestyle of Cretaceous ankylosaurs

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1 **Living alone or moving in herds? A holistic approach highlights complexity in the social**
2 **lifestyle of Cretaceous ankylosaurs**

3

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21 **ABSTRACT**

22 Gregarious behaviour of large bodied herbivorous dinosaurs, such as ceratopsians, hadrosaurs
23 and sauropods, has received much attention due to their iconic mass death assemblages
24 (MDAs). Yet, social lifestyle of ankylosaurs, a highly specialized group of armoured
25 herbivores that flourished predominantly during the Cretaceous Period, remains largely
26 ambiguous. Whereas most ankylosaurs are found as isolated individuals, which may suggest a
27 dominantly solitary lifestyle, the few examples of ankylosaur MDAs indicate that some
28 members of this clade could have been gregarious. In this review, we assess taphonomic
29 history, ontogenetic composition of the MDAs, defence system and other comparative
30 anatomical attributes, and inferred habitat characteristics of ankylosaurs; aspects that may
31 indicate and/or influence group formation in extant herbivores and can also be studied in
32 fossils. We show that the ankylosaurian gross anatomy, such as their heavy armour, barrel-
33 shaped body and usually stocky limbs, combined with the rarity of their MDAs and multiple
34 parallel trackways, all suggest a solitary adult life with efficient anti-predator defence system,
35 limited agility, and confined foraging range. However, characteristics of the known MDAs of
36 *Pinacosaurus*, *Gastonia*, and the Iharkút nodosaurids evaluated in this study imply that at
37 least some ankylosaurs formed groups. Nevertheless, we found no common and consistent set
38 of features to explain why these particular ankylosaurs were gregarious. While inefficient
39 anti-predator defence along with likely higher agility of juvenile *Pinacosaurus* living in open
40 habitats could account for their gregarious behaviour, such ontogenetic, anatomical and
41 habitat features are not combined either in *Gastonia* or in the Iharkút nodosaurid MDAs.
42 Instead, members of each MDA likely had their own specific conditions driving them to form
43 relatively small herds, indicating a more complex social structuring in ankylosaurs than
44 previously acknowledged. Studying morphological and functional disparity within
45 Ankylosauria may help explain the repertoire of their social behaviour. Our holistic approach

46 shows that combining palaeontological and biological information is essential and can provide
47 new insights into the behavioural ecology of long extinct vertebrates.

48

49 Keywords: ankylosaur, social lifestyle, gregarious, solitary, mass death assemblages,
50 comparative anatomy.

51

52

53 **1. INTRODUCTION**

54 The fossil record generally provides limited information on behavioural aspects of extinct
55 animals. Still, gregarious behaviour has been postulated for a number of dinosaurian clades,
56 including ceratopsians (e.g. Currie and Dodson, 1984; Rogers, 1990; Ryan et al., 2001; Eberth
57 and Getty, 2005; Qi et al., 2007; Mathews et al., 2009; Eberth et al., 2010; Fastovsky et al.,
58 2011; Hone et al., 2014), ornithopods (e.g. Horner and Makela, 1979; Norman, 1986; Winkler
59 and Murry, 1989; Forster, 1990; Varricchio and Horner, 1993; Van Itterbeeck et al., 2005;
60 Lauters et al., 2008; Gangloff and Fiorillo, 2010; Scherzer and Varricchio, 2010; Bell and
61 Campione, 2014; Evans et al., 2015; Botfalvai et al., 2017; Ullmann et al., 2017),
62 sauropodomorphs (e.g. Sander, 1992; Coria, 1994; Heinrich, 1999; Bandyopadhyay et al.,
63 2002; Sander et al., 2006; Myers and Fiorillo, 2009), and even herbivorous and predatory
64 theropods (Schwartz and Gillette, 1994; Currie, 1998; Kobayashi and Lu, 2003; Coria and
65 Currie, 2006; Varricchio et al. 2008; Ibiricu et al. 2013; Funston et al. 2016). The majority of
66 body fossil evidence for herd formation comes from taphonomical investigations which can
67 identify mass death assemblages; that is, accumulation of remains of animals that died over a
68 brief time span due to a single agent of death (e.g. Haynes, 1988). This scenario indirectly
69 suggests that multiple animals congregated before their death (Haynes, 1988; Behrensmeyer,
70 2007; Rogers and Kidwell, 2007), and hence mass death assemblages are most frequently
71 referred to as the strongest evidence of herding behaviour in extinct animals (e.g. Currie and

72 Dodson, 1984; Rogers, 1990; Sander, 1992; Coria, 1994; Ryan et al., 2001; Eberth and Getty,
73 2005; Rogers and Kidwell, 2007; Myers and Fiorillo, 2009; Gangloff and Fiorillo, 2010;
74 Ullmann et al., 2017). In addition, the unidirectional and subparallel trackways attributed to
75 certain dinosaurian clades are also often interpreted as indirect proof that those dinosaurs
76 lived and moved in groups, including large herds (Ostrom, 1972, 1985; Lockley et al., 1986,
77 1994; Lockley and Hunt, 1995; Day et al., 2004; McCrea et al., 2001 Myers and Fiorillo,
78 2009; Castanera et al., 2011).

79 Compared to the aforementioned herbivorous dinosaurs, the social lifestyle of
80 ankylosaurs, heavily armoured, medium-sized herbivores with a peak diversity in the
81 Cretaceous Period, is less clear. Adult ankylosaurs are often assumed to have been largely
82 solitary animals because their skeletons are almost always found as isolated individuals (e.g.
83 Vickaryous et al., 2004; Arbour and Mallon, 2017). However, the few known cases in which
84 multiple ankylosaur individuals are concentrated in a single horizon and form true mass death
85 assemblages suggest that the social structuring in ankylosaurs may have been more diverse
86 than previously thought. Several factors influence social behaviour of extant animals,
87 including the diverse, dynamically changing costs and benefits of group formation
88 (Alexander, 1974; Troyer, 1982; Rogers, 1985; Owen-Smith, 1988; Vermeij, 1994; Conrad,
89 1998; Lombardo, 2008; Owen-Smith and Mills, 2008; Romano and Farlow, 2018 and
90 references therein), but only a few among these can potentially be inferred in fossils.
91 Nevertheless, besides the traditional taphonomical and trace fossil evidences, assessing other
92 important aspects that can be studied in fossils is essential in order to get a more complete
93 understanding of the social behaviour of extinct herbivores, including ankylosaurs.

94 The main purpose of this review is to survey the available palaeontological information
95 and current concepts from related biological fields to provide new insights into the debated
96 social behaviour of ankylosaurs (Fig. 1). We consider the complex interactions of important

97 internal and external factors and other characteristics that can be predictive of gregarious or
98 solitary lifestyle in large bodied herbivores, while also drawing attention to the general need
99 for similar holistic approaches in reconstructing social behaviour in extinct vertebrates.

100

101

102 **2. ANKYLOSAURIAN MASS DEATH ASSEMBLAGES**

103 Mass death assemblages (hereafter referred to as MDAs) usually, if not exclusively, consist of
104 animals that tend to aggregate in groups which generally reflects true gregarious behaviour.
105 However, spontaneous aggregation of animals, irrespective of their social behaviour, also
106 occurs under sudden or prolonged, mostly unpredictable and unfavourable circumstances. For
107 instance, a prolonged drought can keep gregarious and non-gregarious animals together close
108 to temporary waterholes prior to their death (Alexander, 1974; Rogers and Kidwell, 2007).

109 Even though most aspects of social interactions cannot be reconstructed from the fossil
110 record, monodominant MDAs indicate that at least temporary associations of conspecific
111 animals into larger groups existed in some ancient populations. Still, taphonomical
112 circumstances, including time-averaging, mode of death, and deposition have to be carefully
113 considered in these aggregations to conclude gregarious behaviour in fossils (Varricchio,
114 2011). Necessary characteristics of a true MDA supporting the inference that a monospecific
115 group of animals was killed in a relatively confined area and over a brief time span are 1)
116 taxonomic exclusiveness, 2) high frequency of associated and/or articulated skeletons
117 preserved relatively close to each other, and 3) bones with similar taphonomic characteristics
118 enclosed in a sediment that shows signs of rapid deposition (e.g. Turnbull and Martill, 1988;
119 Haynes, 1988; Capaldo and Peters, 1995; Eberth and Getty, 2005; Qi et al., 2007).

120 Concerning ankylosaurs, the overwhelming majority of their fossils seems to represent
121 solitary animals, especially in the case of North American taxa. For instance, dozens of

122 associated and articulated ankylosaur skeletons unearthed from the Dinosaur Park Formation
123 and belonging to different taxa (e.g. *Euoplocephalus tutus*, *Edmontonia rugosidens* or
124 *Scolosaurus cutleri*) were discovered as isolated carcasses (Fig. 1A) representing only one
125 individual per site or bonebed (Currie and Russell 2005; Arbour and Currie 2013, and see
126 Supplementary Table S1). The rare occasions where skeletons of multiple ankylosaur
127 individuals were concentrated in a single bonebed horizon have been interpreted as resulting
128 from natural catastrophes (Fig 1B) (Britt et al., 2009; Currie et al., 2011; Botfalvai et al.,
129 2015; Kinner et al., 2016).

130 Currently, six fossil sites are known where enough taphonomical information exists to
131 conclude that the multiple individuals of ankylosaurs preserved within the same bonebed
132 represent true MDAs and not attritional accumulations (Table 1). Besides these Cretaceous
133 MDAs, there are a few other similar sites with multiple ankylosaur individuals, like the
134 Mongolian Bayn Shire locality providing six specimens of *Talarurus plicatospineus*((Arbour
135 and Currie, 2016, see Table 2). However, in the lack of sufficient data about the depositional
136 history and the precise position of the skeletons relative to each other, the taphonomical
137 situation of these assemblages and the probability that they represent MDAs cannot be
138 evaluated (Table 2).

139 We discuss each of the six, well-characterized ankylosaurian MDAs (sections 2.1 – 2.4,
140 in chronological order) to assess the degree to which these assemblages support or refute the
141 occurrence of gregarious behaviour in these ankylosaurs. Thereafter, we also consider their
142 assumed ontogenetic composition (section 2.5) which might be informative of the social
143 behavioural background triggering group formation.

144

145 **2.1 Cedar Mountain Formation (Utah, USA)**

146 There are three Lower Cretaceous sites in the Yellow Cat and Ruby Ranch members of the
147 Cedar Mountain Formation (USA, Utah) where many individuals of the ankylosaur genus
148 *Gastonia* were discovered within the same bonebed horizons (Kirkland, 1998; Kinner et al.,
149 2016). All three of these sites show characteristics of MDAs suggesting that *Gastonia* moved
150 in herds (Kinner et al., 2016).

151

152 *2.1.1 The Yellow Cat Quarry*

153 The Yellow Cat Quarry (also known as the Gaston Quarry), containing well preserved
154 ankylosaur material from minimum five individuals, is the type locality of *Gastonia burgei*,
155 and lies in the upper portion of the Yellow Cat Member (Kirkland, 1998; Kirkland et al.,
156 2008). The bone-bearing horizon is a pale green, sandy siltstone situated between two beds of
157 diagenetically altered sandy limestone (carbonate nodules) (Kinner et al., 2016). Based on a
158 preliminary sedimentological investigation, the bonebed was deposited in an ephemeral lake
159 or pond (Kirkland et al., 2008; Kinner et al., 2016). This multitaxic bonebed is dominated by
160 the mostly disarticulated and scattered bone material of *Gastonia burgei*.

161 Unfortunately, no detailed taphonomical study was conducted in the Yellow Cat Quarry,
162 thus the mass mortality origin of this material is assumed based on the following features: (1)
163 the ankylosaur individuals were discovered in a thin siltstone layer (Kirkland et al., 2008); (2)
164 the skeletal parts were situated close to each other within an area of approximately 30 m²
165 (Kinner et al., 2016); (3) the bonebed is clearly dominated by *Gastonia*, whereas other
166 vertebrate remains are only subordinate (Kirkland et al., 1999); (4) the bone-bearing strata
167 were deposited in an ephemeral lake or pond under arid to semiarid conditions with
168 monsoonal overprinting (Kirkland et al., 2016), which conditions often result in MDAs during

169 the seasonal drought events (e.g. Conybeare and Haynes, 1984; Rogers, 1990; Fiorillo et al.,
170 2000; Gates, 2005; Varrichio et al. 2008).

171

172 2.1.2 *The Dalton Wells Quarry*

173 This quarry is situated at the base of the Yellow Cat Member of the Cedar Mountain
174 Formation, where the bone-bearing horizons are interpreted as debris-flow sediments
175 deposited in a seasonally dry, alluvial-lacustrine setting (Eberth et al., 2006; Britt et al., 2009).

176 At least eight individuals of *Gastonia burgei* were discovered in the Dalton Wells Quarry.

177 The skeletons were at least partially articulated at the time of debris-flow reworking, which
178 indicates an immediate skeleton transportation after death (Britt et al., 2009). Britt et al.

179 (2009) suggest that the associated materials of *Gastonia burgei* were added to the

180 thanatocoenose as an MDA implying a herding lifestyle for this dinosaur.

181

182 2.1.3 *Lorrie's Quarry*

183 The bonebed is located in the Ruby Ranch Member of Cedar Mountain Formation, lying

184 below and within a sequence of crevasse splays that overlies a purple and green mottled

185 paleosol (Kinneer et al., 2016). The bone-bearing horizon at Lorrie's Quarry site includes

186 different skeletal parts of *Gastonia lorriemcwhinneyae* representing several individuals (exact

187 minimum number of individuals is unknown). Based on the preliminary taphonomical

188 investigation, Kinneer et al. (2016) suggested two hypotheses for the cause of formation of

189 this monospecific *Gastonia* assemblage: (1) congregation at a waterhole during a drought

190 period; or (2) mass drowning of a migrating herd that tried to cross a flooding river. Both

191 hypotheses suggest a gregarious lifestyle for this species of *Gastonia*, as well.

192

193 2.2 Csehbánya Formation (Iharkút, Hungary)

194 With more than thousand isolated bones, and at least twelve associated and/or articulated
195 partial skeletons, the Late Cretaceous (Santonian) dinosaur locality at Iharkút, Hungary,
196 provided the richest ankylosaur assemblage from Europe (Ósi et al., 2019). Taphonomical
197 investigation of the vertebrate material from this locality showed that ankylosaurs were the
198 most dominant dinosaurs at Iharkút with a minimum number of 21 individuals and with their
199 remains representing more than 25% of the total bone assemblage discovered to date
200 (Botfalvai et al., 2015; Ósi et al., 2019). The bone-bearing layers (site SZ-6) were deposited
201 by ephemeral, high-density flash-flood events probably triggered by episodic heavy rainfalls
202 (Botfalvai et al., 2016).

203 Uniquely, ankylosaurs represent the only vertebrates in Iharkút which are also known
204 from associated and/or articulated partial skeletons; all other taxa recovered from the locality
205 occur exclusively as isolated elements or fused multi-element complexes (Botfalvai et al.,
206 2015). The twelve partial and incomplete ankylosaurian skeletons were recovered from an
207 area of approximately 600 m² (Ósi et al., 2019). Their taphonomy (i.e. skeletons found close
208 to each other in the same layer having almost identical taphonomic features) supports uniform
209 depositional history and suggests that these remains record the simultaneous death of some
210 members of a herd that attempted to cross the flooding river (Fig. 1B) (for further details, see
211 Botfalvai et al., 2015). The significant dominance of the ankylosaur material as well as the
212 presence of associated/articulated skeletal parts indicate that these armoured dinosaurs
213 represent a parautochthonous element of the local community (Botfalvai et al., 2016).

214 This MDA may not be monospecific, as skeletal parts of two different nodosaurid
215 ankylosaurian taxa, *Hungarosaurus* and cf. *Struthiosaurus*, have been identified in this
216 material (Ósi and Pereda-Suberbiola, 2017; Ósi et al., 2019). Even though the precise
217 taxonomic composition of this assemblage is not yet fully understood, these two nodosaurids
218 are closely related taxa (Ósi and Makádi, 2009, Thompson et al., 2012), and have similar size

219 and ecological role. Therefore, we consider these potentially sympatric nodosaurid
220 ankylosaurs (Ósi and Prondvai, 2013) as equivalent representatives of a single, functional
221 group (hereafter referred to as ‘Iharkút nodosaurids’) within the herbivore palaeocommunity
222 of Iharkút. This approach follows the ecological concept of functional diversity (distribution
223 of functional traits in a community; see e.g. Hooper et al., 2006; Cadotte et al., 2011), which
224 circumvents the taxonomic uncertainties regarding the Iharkút MDA and is also in line with
225 the functional context of social behaviour used in this study.

226

227 **2.3 Alag Teeg Formation (Southern Gobi, Mongolia)**

228 The rich vertebrate material of the Upper Cretaceous Alag Teeg beds in Mongolia was
229 discovered in 1969 by the Soviet-Mongolian expedition which found several specimens of
230 *Pinacosaurus grangeri* in the mudstone-rich lower section of Alag Teeg (Tumanova, 1987,
231 2000; Currie et al., 2011; Burns et al., 2015). The enclosing sediment was interpreted as
232 deposits of ephemeral ponds or a lake situated in the floodplain area of a braided river system
233 (Hasegawa et al., 2009). The Mongolian-Japanese Expedition also excavated at Alag Teeg
234 between 1995-1996 and collected more than thirty skeletons of juvenile *Pinacosaurus*.
235 However, it is possible that some of these are the same specimens that had been discovered
236 but left behind by the Soviet-Mongolian expedition in 1969 (Currie et al., 2011).

237 The rich bone accumulation in the Alag Teeg beds, including the *Pinacosaurus* skeletons,
238 is referred to as a mass burial site (Fastovsky and Watabe, 2000). Based on sedimentological
239 and preliminary taphonomical observations, the ankylosaur assemblage at Alag Teeg is most
240 likely composed of animals that have concentrated around and within drying ponds during
241 drought, and their carcasses may have been buried by a subsequent ephemeral flood event
242 (e.g. Currie et al., 2011).

243

244 **2.4 Bayan Mandahu Formation (Inner Mongolia, China)**

245 Approximately twelve, mostly articulated skeletons of *Pinacosaurus grangeri* were
246 discovered from a single site at Bayan Mandahu (quarries 100 and 101), the Campanian-aged
247 Djadokhta-correlative beds in Inner Mongolia, China (Currie et al., 2011; Burns et al., 2011,
248 2015). Taphonomical investigations have suggested that most of the individuals discovered at
249 this site died *in situ* and were buried by sand fans during rain storms within a stabilized dune
250 field (Loope et al., 1999) rather than during wind storms in an active dune field (Jerzykiewicz
251 et al., 1993).

252

253 **2.5 Ontogenetic composition of ankylosaurian MDAs**

254 All *Pinacosaurus* MDAs are generally reported as being composed entirely of juveniles of
255 similar sizes, which has led to the suggestion that *Pinacosaurus* was gregarious when
256 immature (Currie et al., 2011; Burns et al., 2011, 2015). The juvenile assignment of the
257 specimens was partially based on size and phalangeal proportions (Currie et al., 2011), but
258 most importantly on visible cranial sutures (Burns et al., 2011) and unfused postcranial
259 elements (Burns et al., 2015).

260 The MDAs of *Gastonia* spp. are described as comprising five adults in the Yellow Cat
261 Quarry (Kirkland, 1998) and eight subadults in the Dalton Wells Quarry. In the latter quarry,
262 a ninth specimen referred to as an adult was located farther away from the subadults (Britt et
263 al., 2009; Kineer et al., 2016) and hence may not have belonged to the subadult group. The
264 adult assignment of the *Gastonia* individuals in the Yellow Cat Quarry was based on the fused
265 sutures in the holotype skull recovered from the locality, where all other associated
266 homologous bones originating from at least five individuals were about the same size. On the
267 other hand, the ankylosis of the dorsal ribs to the last dorsal vertebrae, typically seen in
268 ankylosaurs (Coombs and Maryanska, 1990), is not present in *Gastonia* (Kineer et al., 2016).

269 The subadult status of the Dalton Wells Quarry *Gastonia* specimens was exclusively based on
270 size, but no further specifications were given concerning their size difference from adults.

271 The incomplete, disarticulated nature of the skeletons in the Iharkút nodosaurid MDA has
272 so far prevented their proper ontogenetic assessment. For this study, we specifically address
273 this question using bone histology, the best approach for the ontogenetic assignment of such
274 fragmentary material. Multiple samples of ribs, which were the only homologous elements
275 present in all partial skeletons, and of a single femur of skeleton 2007.25.27 were taken and
276 prepared as ground sections (reposited at the Hungarian Natural History Museum). These
277 sections consistently reveal that the ontogenetic composition of the Iharkút nodosaurid MDA
278 ranges from still growing subadults being close to their final size to skeletally mature, fully
279 grown adults (Fig. 2). The lack of juvenile individuals in this assemblage is further supported
280 by the presence of osteoderms with well-developed keels and spikes, and by the complete
281 fusion of vertebral neural arches, of dorsal ribs to the last dorsal vertebrae, and of the
282 synsacrum (Ősi et al., 2019); i.e. those preserved elements of the skeletons which could show
283 unfused sutures, were any of the animals juveniles. Thus, morphological as well as
284 histological evidence indicate the advanced developmental stage of the specimens composing
285 the Iharkút nodosaurid MDA. For further details on the sampled bones and skeletal maturity
286 categories of each skeleton, see Supplementary Table S2.

287 Because the methods used to assess the ontogenetic composition of these MDAs are so
288 diverse, the indicated ontogenetic categories, even if referred to by the same terms, such as
289 juvenile, subadult and adult, do not necessarily represent corresponding stages of
290 development across these studies. For now, the unstandardized ontogenetic categorization,
291 along with the incompleteness of the available data, makes comparative evaluation of the
292 inferred social structure behind group formation in these ankylosaurian MDAs very difficult.

293 Nevertheless, *Pinacosaurus* MDAs were suggested to represent family groups or crèche-
294 like aggregations of young animals (Burns et al., 2011). However, these biological terms refer
295 to a sort of communal care for youngsters by the reproductively immature and mature
296 members of the family or by the adults of a colony, none of which notions seems to be
297 supported in these MDAs. Instead, the apparent lack of both very young and adult individuals
298 (Currie et al., 2011), and the assumed age of the specimens (several years old) forming the
299 MDAs (Burns et al., 2011) rather imply segregation of immature individuals from the
300 reproductively active portion of the population, similarly to bachelor groups in extant
301 mammals (Owen-Smith, 1988). The incomplete armour ossification characterizing juvenile
302 ankylosaurs (Hill et al., 2003; Burns et al., 2015) could have been an important drive leading
303 to the congregation of young animals as an anti-predator response (see ‘Herds against
304 predators’ below).

305 In *Gastonia*, the undefined, size-based ontogenetic assessment of the ‘subadult’ category
306 prevents interpretation of the underlying social structure of the Dalton Wells MDA because
307 size in itself has proven to be a weak predictor of ontogenetic maturity in several dinosaurs
308 (Prondvai, 2014, 2017; Griffin and Nesbitt, 2016), most likely including ankylosaurs as well
309 (Burns et al., 2015). However, the presence of the adult holotype skull with fused sutures
310 among the similarly sized remains of at least five individuals in the Yellow Cat Quarry
311 (Kirkland, 1998) suggests that individuals close to and/or being fully grown may have formed
312 small groups.

313 Although apparent size differences exist among the specimens of the Iharkút nodosaurid
314 assemblage (Ősi et al., 2019), which may also be attributable to its potentially paucitaxic
315 composition, the morphological and histological maturity degree of the preserved bones of the
316 skeletons imply that this MDA was primarily composed of the reproductively mature portion
317 of the population(s) which apparently moved in a small herd.

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3. HERDS AGAINST PREDATORS

One of the most frequently cited selective pressures leading to the formation of groups or larger herds in herbivores is predation. Herbivore groups may be more efficient in deterring predators by aggressive group defence, but they may also provide cover for the individuals which can blend in the group (Alexander, 1974; Owen-Smith, 1988; Hayward and Kerley, 2005).

Nevertheless, there are many other ways to significantly reduce predation pressure. For example, extant mammalian megaherbivores with an adult body mass exceeding 1000 kg experience lower predation risk compared to the smaller and more abundant prey animals that are generally favoured by carnivores (such as large felids) (Sinclair et al., 2003; Owen-Smith and Mills, 2008). Besides large body size, animals possessing defensive weapons (e.g. spikes, horns, armour) are less frequently attacked by predators than those without (Hayward and Kerley, 2005; Brown et al., 2017). During prey selection, besides nutritional value and vulnerability, predators also assess the risk of injuries associated with the prey's defensive weapons and size-related strength. Still, numerous other factors, such as physical threats and barriers in the prey's habitat or the potential to hunt in packs, may alter a predator's prey choice (Lendrem, 1986; Hayward and Kerley, 2005; Azevedo and Verdade, 2011; Mukherjee and Heithaus, 2013).

Below, we consider how ankylosaurian body size and armour can be interpreted in the context of efficient antipredator adaptation that may or may not allow a solitary lifestyle. We also discuss how the reconstructed ankylosaurian defence efficacy compares to that of other iconic herbivorous dinosaurs and whether this can be related to gregarious or solitary lifestyle in general.

344 3.1 Body mass

345 Adult ankylosaurs are characterized by a body mass usually exceeding 1000 kg (Benson et al.,
346 2014; Arbour and Mallon 2017; Brown et al., 2017). With an adult body mass of about 7-
347 8000 kg, and length of at least 7 m, *Ankylosaurus* is the largest and bulkiest ankylosaur
348 known to date (Carpenter, 2004). *Euoplocephalus* reached about 2.000 kg, and the skeleton of
349 *Borealopelta* indicates a similar body mass as that of *Sauropelta*, weighing about 1.300-1.500
350 kg (Carpenter, 1984; Arbour and Mallon, 2017; Brown et al., 2017). Skeletons of *Saichania*,
351 *Struthiosaurus* and *Hungarosaurus* indicate smaller body masses between 300 and 650 kg
352 (Pereda-Suberbiola, 1992; Ósi and Makádi, 2009; Benson et al., 2014). Thus, alongside the
353 true contemporary giant herbivores of the Cretaceous, like hadrosaurids, ceratopsians and
354 sauropods with adult body masses ranging from 2000 kg up to 90000 kg (e.g. Horner et al.,
355 2004; Benson et al., 2014), ankylosaurs represented medium-sized herbivorous dinosaurs,
356 with the exception of the largest genus, *Ankylosaurus*. The apex predators in most Cretaceous
357 terrestrial ecosystems were gigantic theropod dinosaurs, such as carcharodontosaurians and
358 tyrannosaurids, weighing up to ~15000 kg (Therrien and Henderson, 2007; Zanno and
359 Makovicky, 2013).

360 When put into this general context of Cretaceous giants, ankylosaurian body size alone
361 seems insufficient for deterring larger predators, which could speak against their solitary
362 lifestyle. However, large body size and the tendency to be solitary do not correlate positively
363 either, as evidenced by the great herds of several extant and fossil megaherbivores (e.g.
364 Alexander, 1974; Currie and Dodson, 1984; Owen-Smith, 1988; Eberth and Getty, 2005;
365 Myers and Fiorillo, 2009; Gangloff and Fiorillo, 2010; Bell and Campione, 2014; Evans et al.,
366 2015; Ullmann et al., 2017). Furthermore, in a more local context, the largest terrestrial
367 predators known from the localities of the MDAs of *Gastonia burgei* and the Iharkút
368 nodosaurids are not giants but medium-sized theropods (e.g. Senter et al., 2012; Ósi et al.,

369 2012), and the remains of gigantic predators are rare at the *Pinacosaurus* MDA sites as well
370 (Dingus et al., 2008). This pattern also weakens the hypothesis that group formation in these
371 ankylosaurs was driven by the presence and/or abundance of large-bodied predators. Thus,
372 medium body size of most ankylosaurs in itself provides clues neither for, nor against
373 gregarious/solitary behaviour.

374

375 **3.2 Ankylosaurian defence structures**

376 The dermal armour characterizing all thyreophoran dinosaurs shows high variation in
377 complexity among the different groups (Coombs, 1971; Vickaryous et al., 2004; Arbour,
378 2009), but in most taxa the armour complex covered most of the body dorsally from the neck
379 to the tip of the tail. In basal thyreophorans (*Scutellosaurus*, *Scelidosaurus*) the system of
380 osteoderms was still quite uniform with similarly shaped and sized, usually flat to low-keeled,
381 oval to subcircular osteoderms (Colbert, 1984; Norman, 2000). As for its potential functional
382 significance in defence, this type of armour could be deployed only as a passive defence
383 structure, in many ways similar to the relatively conservative system of osteoderms seen in
384 crocodyliforms. In stegosaurs, this extensive armour became quite reduced and modified,
385 consisting only of the parasagittally positioned, plate-like osteoderms and huge (up to 1 m)
386 spikes at the end of the tail (Galton, 1985; Czerkas, 1987). In ankylosaurs, on the other hand,
387 a significant differentiation of the armour complex, composed of cervical, thoracic/dorsal,
388 pelvic and caudal regions, appears already in the basalmost, Jurassic forms (e.g.
389 *Gargoyleosaurus*, Kilbourne and Carpenter, 2005).

390 Nodosaurids, one of the two major clades within Ankylosauria (Thompson et al., 2012),
391 generally show this complex, segmented armour configuration (Ford, 2000). The osteoderms
392 of the cervical region are usually co-ossified into quarter- or half-rings and bear spikes or
393 pointed plates (max. height up to 60 cm) oriented anterolaterally (e.g. *Edmontonia*, Carpenter,

394 1990), posterodorsally (e.g. *Hungarosaurus*, Ósi and Makádi, 2009) or posterolaterally (e.g.
395 *Borealopelta*, Brown et al., 2017). The thoracic and caudal armour in nodosaurids are
396 composed of closely packed bands of oval to circular, low crested (few cm in height)
397 osteoderms. On the lateral side of the body, however, as a continuation of the cervical plates
398 or spikes, highly crested (up to 20 cm) osteoderms frequently occur (e.g. *Gastonia*, Blows,
399 2001) reaching posteriorly to the tip of the tail. The pelvic armour is the most solid part of the
400 nodosaurid armour, frequently forming a fused or semi-fused shield in some basal
401 nodosaurids (Coombs and Demere, 1996; Arbour et al., 2011; Ósi and Pereda-Suberbiola,
402 2017). Tail club or spike at the tip of the tail, as seen in ankylosaurids and stegosaurs,
403 respectively, is not present in nodosaurids, so the most potent defensive structures in
404 nodosaurids were rather situated on the anterior and lateral sides of the body.

405 Ankylosaurids, forming the other major ankylosaurian clade, are characterized by an
406 armour that is still segmented into the four main regions seen in nodosaurids. However, it
407 becomes lighter with less numerous and thinner osteoderms (Scheyer and Sander, 2004) that
408 are shallow and oval to subcircular in shape (e.g. *Ankylosaurus*, Carpenter, 2004; Arbour and
409 Mallon, 2017; *Scolosaurus*, Brown et al., 2017). The pelvic armour is not fused into a shield,
410 and osteoderms on the lateral sides of the pelvic and caudal regions may bear higher crests
411 (Arbour and Mallon, 2017). In contrast to nodosaurids, ankylosaurids had their defensive
412 structures augmented posteriorly by possessing a massive, dorsoventrally flattened tail club
413 that, in later ontogeny, fused with the interlocking distal vertebrae (Coombs, 1995; Arbour,
414 2009).

415 It has generally been assumed that plate-like osteoderms provide passive protection,
416 whereas spike-shaped osteoderms and tail clubs of ankylosaurs were used actively as
417 defensive weapons against predators (Fig. 1C) (Padian and Horner, 2010; Coombs, 1995;
418 Thulborn, 1993; Kirkland, 1998; Burns and Currie, 2014; Brown et al., 2017; Arbour and

419 Zanno, 2018). As the plates covered almost the entire dorsolateral surface of the body from
420 the skull to the tail, and dermal ossification was more extensive than in any other dinosaurs,
421 such as ceratopsians or stegosaurs, Padian and Horner (2010) suggested that the ankylosaurian
422 armour represents the least controversial example of a defensive function in dinosaurs.

423 Recently, the armour of the largest known taxon, *Ankylosaurus*, has been revised as being
424 composed of more sparsely distributed osteoderms with larger intermittent patches of skin
425 creases than presented in most previous life restorations (Arbour and Mallon, 2017). Although
426 still hypothetical until the discovery of more complete specimens, this revised armour
427 reconstruction may imply a lower degree of defence efficacy. However, osteoderms that are
428 not stiffly connected could still bear extensive keratinous spiny extensions, as suggested for
429 the spiny osteoderms at the anterolateral region and over the cephalic notch of the dorsal
430 carapace in two *Glyptodon* species (Zurita et al., 2010). If these dermal structures in
431 *Ankylosaurus* had been spatially adjustable by cutaneous muscles (e.g. panniculus carnosus),
432 the spikes could have been elevated and exposed to predators, as seen in the echidna (Naldaiz-
433 Gastesi et al., 2018). Furthermore, the lighter armour construction composed of scattered
434 osteoderms in *Ankylosaurus* could be indicative of a considerable weight constraint on a
435 confluent armour at this body size. On the other hand, the large body size of *Ankylosaurus*
436 could have also compensated for a potentially inferior defence efficacy of its loosely
437 organized osteoderms when compared with the more extensive, confluent armour of smaller-
438 bodied ankylosaur taxa.

439 Still, the efficiency of the defensive function of different armour elements has been
440 questioned in some taxa and for some ontogenetic stages in ankylosaurs based on histological,
441 computed tomographic (CT) and finite element analyses of these structures (Arbour, 2009;
442 Arbour and Snively, 2009; Hayashi et al., 2010).

443 Hayashi et al., (2010) argued that the spikes of nodosaurids, being fairly compact bony
444 structures, had more likely a weapon function, while the highly cancellous and thin bone-
445 walled polacanthid spikes and ankylosaurid plates may have been used more for display
446 and/or thermoregulation rather than for defence. However, mammalian antlers that are well
447 known for their role in intra- and interspecific fight, are also highly porous (e.g. Rolf and
448 Enderle, 1999; Hall, 2005). Furthermore, the many types of porous osteoderms of
449 crocodylians form a biomechanically efficient light-weight armour. This crocodylian armour is
450 stiff as well as flexible due to its mineral and collagen content, respectively, and resists
451 penetration by teeth and/or claws (Chen et al., 2014). The mechanical testing of the body
452 armour of nine-banded armadillo consisting of osteoderms ('hard mineralized tiles')
453 connected by soft connective tissue has led to the same conclusion concerning its protective
454 efficacy against predators (Chen et al., 2011). Computational simulations and mechanical
455 testing of *Glyptotherium* osteoderms also showed that the combination of compact bone layer
456 and porous lattice core is biomechanically optimized for strength and high energy absorption,
457 and hence evolved to provide a protective armour (Plessis et al., 2018). The same protective
458 function of the thyreophoran osteoderms has been concluded by histological studies. These
459 showed that the special arrangement of integrated structural fibres greatly strengthens even
460 the thin cortex of ankylosaurid osteoderms (Scheyer and Sander, 2004; Burns and Currie,
461 2014).

462 The multi-functionality of osteoderms, such as thermoregulation, musculoskeletal
463 stiffening, calcium storage and protection against acidosis, in various animals are well known
464 (e.g. Seidel, 1979; Vickaryous and Sire, 2009, Burns et al., 2013; Broeckhoven et al., 2015).
465 Trade-offs, such as that shown between the strength and thermal capacity of osteoderms in
466 cordylid lizards (Broeckhoven et al., 2017), and also known to characterize relationships
467 between these functions and other morphological and physical constraints (e.g. Rivera and

468 Stayton, 2011), are expected. However, the importance of the protective role of dermal
469 armour has not been questioned in any of these cases, either.

470 Thus, the hypothetical deductions that some ankylosaurian armour elements were too
471 weak to be used as passive protection or active weapons based on the relative thinness of bone
472 wall and high porosity (Hayashi et al., 2010) are supported neither by biomechanical data in
473 extant and extinct animals (Chen et al., 2011, 2014; Plessis et al., 2018), nor by other
474 histological studies of ankylosaurian osteoderms (Scheyer and Sander, 2004; Burns and
475 Currie, 2014). Furthermore, the significant reinforcing role of keratinous sheaths (e.g. Zhang
476 et al., 2018), the so-called exaggerated epidermal structures, which must have covered the
477 osteoderms, especially the spikes, to a great extent in all ankylosaurs (Burns and Currie, 2014;
478 Brown et al., 2017), are not considered in these claims of inefficient defence, either.

479 Function of the tail clubs (Coombs, 1995) and their biomechanical efficiency as weapons
480 have been extensively investigated by Arbour (2009) and Arbour and Snively (2009),
481 although with somewhat contradicting final implications. Calculating impact force generation
482 using CT-scan-based models, Arbour (2009) concluded that tail clubs of juveniles with
483 relatively small-sized knobs could not have exerted enough impact force and hence were
484 unfunctional as defence weapons up to adulthood. The inferred lack of defence function in
485 juveniles has led to the suggestion that tail clubs were used in intraspecific combat and/or as a
486 display feature (Fig. 1D) rather than as defensive weapons against predators. On the other
487 hand, using finite element modelling of differently sized *Euoplocephalus* tail clubs, Arbour
488 and Snively (2009) concluded that whereas small and average sized tail clubs were unlikely to
489 fail from maximum calculated impact force, large clubs would have been in danger of
490 fracture. They did, however, consider that these results are largely influenced by the choice of
491 parameter settings in the FEA model as well as by other factors that could hardly be
492 incorporated in these simplified models.

493 Regardless of its initial evolutionary drive, a structure being used in conspecific fights is
494 expected to be effectively deployed in defence against predators, as well (Fig. 1C,D) (Bro-
495 Jørgensen, 2007; Emlen, 2008; Stankowich, 2012). Furthermore, the late ontogenetic
496 appearance of skeletal and integumentary defensive/offensive structures, including weapons,
497 does not exclude their importance in defence and/or agonistic behaviour. For instance, bovine
498 calves with no or underdeveloped horns engage in butting/pushing behaviour as part of their
499 social activities (e.g. Reinhardt et al., 1978; Bouissou et al., 2001). Crocodylians perform a
500 wide range of agonistic behaviours among each other, including biting with their tiny teeth
501 from hatching on (Brien et al., 2013). In these activities, the osteoderms, which start
502 developing only a year after hatching (Vickaryous and Hall, 2007), are thought to be
503 important for preventing serious injuries (Brien et al., 2013), as the bite-force of crocodiles
504 increases with positive allometry to body size through ontogeny (Erickson et al., 2003).
505 Finally, how efficient a structure is in passive or active defence always depends on the
506 relative strength and performance of the opponent, be it a predator or a conspecific rival. A
507 defensive/offensive structure may be fairly efficient against one type or size category of
508 predators, whereas useless against another. Hence, the relative abundance relationships and
509 frequencies of encounters with different types of predators also strongly influence the anti-
510 predator selection pressure and functional efficacy of any structure (Stankowich, 2012).

511 The lack of extant analogues, i.e. medium to large bodied herbivores possessing body
512 armour combined with a tail club, prevents definite assessments on the efficiency of
513 ankylosaur weaponry. However, phylogenetic analysis of tail weaponization in amniotes
514 suggests that initial predation pressure is necessary in evolving tail weapons as an adaptive
515 response (Arbour and Zanno, 2018). Thus, the combination of elaborate body armour and tail
516 club of ankylosaurids and the complex co-ossified armour elements and spikes of nodosaurids

517 seem to have provided efficient defence against predators to theoretically allow a solitary
518 diurnal lifestyle.

519

520 **3.3 Comparative defence efficacy and sociality among herbivorous dinosaurs**

521 As efficient as the ankylosaurian armour may be, a comparative approach is needed to assess
522 whether it represents a defence system of outstanding efficiency among herbivorous
523 dinosaurs, that would thus allow a solitary lifestyle. For this, the defensive importance of
524 'bizarre' structures seen in other medium to large sized herbivores, such as the plates and
525 spikes of stegosaurs, the horns and frills of ceratopsians, and the cephalic dome of
526 pachycephalosaurs, need to be discussed and interpreted in the context of possible social
527 behaviour.

528 The parasagittal plates of stegosaurs are generally considered to show little evidence of a
529 biomechanical function in defence because their thin, highly vascularized cortex and
530 cancellous interior could have been easily penetrated and crushed by the teeth of any large
531 predator (Main et al., 2005). However, as in ankylosaurs, a keratinous sheath that certainly
532 covered these osteoderms could have provided sharp edges and extra mechanical protection
533 (Christiansen and Tschopp, 2010). Furthermore, the iconic large, flat and blunt dorsal plates
534 characteristic of *Stegosaurus stenops*, that are almost stereotypically associated with
535 stegosaurs, are more the exception rather than the rule concerning general stegosaurian
536 osteoderm morphology. Most known stegosaurs show osteoderms of diverse transitional
537 morphologies between plates and spines. These include plates that strongly taper towards their
538 tip in *Lexovisaurus*, spike-like flat dorsal osteoderms in *Tuojiangosaurus*, and definite spines
539 on the shoulder region and in the parasagittal series of *Huayangosaurus* and *Kentrosaurus*
540 (Galton and Upchurch, 2004). Osteoderms form spines towards the tip of the tail in all
541 stegosaurs. Such spiny structures are undoubtedly important in deterring predators, either

542 passively if they are positioned on the girdle region and along the dorsal aspect of the neck
543 and trunk, or actively if they are on the mobile tail and can be deployed by swinging the tail
544 towards the enemy. Thus, stegosaurian flat spikes and spines seem to provide efficient anti-
545 predator defence, comparable with that of the ankylosaurian armour. This could have allowed
546 a solitary lifestyle for these medium to large sized thyreophoran herbivores. The lack of
547 known stegosaurian monodominant MDAs is also in line with this hypothesis (Galton and
548 Upchurch, 2004).

549 In ceratopsid dinosaurs, the orbital and nasal horns and frills of various sizes are all
550 positioned cranially, whereas the entire postcranial region is void of such structures,
551 contrasting the fairly complete body armour seen in ankylosaurs. The cranial horns and frill of
552 ceratopsids could have functioned as weapons and passive defence structures, respectively,
553 against predators or rivals in intraspecific combat (Padian and Horner, 2010; Farke, 2004;
554 Farke, et al., 2009). On the other hand, the vulnerable postcranial body could have been
555 protected from predators by adults cooperatively closing ranks and presenting powerfully
556 backed horns towards the enemy. In contrast, lone individuals would have been at much
557 higher risk of being attacked in their unprotected postcranial region. Hence, the distribution
558 pattern of potential defence structures in ceratopsians seems to favour highly social behaviour
559 which is in line with the numerous examples of monotaxic MDAs of various ceratopsids
560 suggesting gregarious behaviour (Currie and Dodson, 1984; Rogers, 1990; Dodson et al.,
561 2004). Nevertheless, some taxa may have been less gregarious than others, as indicated by the
562 relative scarcity of bonebeds with generally smaller number of individuals in chasmosaurines,
563 as compared with the bonebeds of the co-existing centrosaurines (Hunt and Farke, 2010).
564 These two ceratopsian clades show similar ontogenetic structuring in their bonebeds (Hunt
565 and Farke, 2010) and, as all known ceratopsids, have a conservative postcranial body (Forster
566 and Sereno, 1997) that appears equally defenceless. This raises the question whether their

567 general skull construction, in which lies the only remarkable anatomical difference between
568 these clades, could have differed in interspecific combat/defence performance, and hence in
569 predation-related group-forming tendency. However, several other possible factors have been
570 considered that could explain this diverging pattern in the frequency and size of the
571 centrosaurine and chasmosaurine bonebeds (e.g. Hunt and Farke, 2010; Ryan et al. 2010;
572 Maiorino et al. 2107). Furthermore, no objective measure of the predator-deterring efficacy of
573 the centrosaurine *versus* chasmosaurine skull construction has been proposed to date to assess
574 whether it could have led to potential differences in gregariousness between these two
575 ceratopsid clades.

576 The functional interpretation of the domed skull roof of pachycephalosaurs is also
577 controversial. Whereas some morphological and histological studies argued against head-
578 strike behaviour (Goodwin et al., 1998; Goodwin and Horner, 2004), other histological, FEA,
579 and cranial pathological studies favoured it (Lehman, 2010; Snively and Cox, 2008; Snively
580 and Theodor, 2011; Peterson and Vittore, 2012; Peterson et al., 2013). Nevertheless, various
581 types of evidence predominantly support intraspecific butting matches, with either head-to-
582 head or head-to-body strikes depending on species-specific dome morphologies. This
583 agonistic behaviour, if characteristic of pachycephalosaurs, could have also been used in
584 defence against predators. However, the lack of specific defence structures in the postcranial
585 body, just like in ceratopsians, would have made these small to medium-sized herbivores
586 more vulnerable, and hence poorly armoured for a solitary lifestyle compared to thyreophoran
587 dinosaurs. Still, no pachycephalosaurian MDA has been reported so far which may either
588 reflect the incompleteness of the fossil record or their genuine solitary lifestyle. If
589 pachycephalosaurians were indeed solitary, it would imply that a small- to medium-sized
590 body with an apparently insufficient structural defence system is a weak predictor of
591 gregarious lifestyle.

592 In conclusion, we suggest that the extensive armour of adult ankylosaurs composed of
593 plates, spikes and tail clubs indicate a superior role in agonistic behaviour compared to the
594 'bizarre' structures found in other medium to large sized herbivorous dinosaurs. Bearing in
595 mind that the osteoderms could have performed multiple functions, such as thermoregulation
596 or display, the ankylosaurian armour complex is the most clear-cut case of efficient passive
597 defence system which is further elaborated to active defence in ankylosaurids with the
598 appearance of a tail club (Fig. 1C,D). This could have significantly reduced the predation
599 pressure theoretically allowing a solitary lifestyle at least for adult individuals. However, it
600 has to be noted that the absence of a heavy body armour does not necessarily imply
601 gregariousness, and vice versa, possessing a well-developed armour does not exclude it.

602

603

604 **4. ANATOMY FOR A HERD**

605 Depending on the ecological carrying capacity of their habitat, medium to large bodied
606 herbivores living in larger herds tend to travel long distances to forage for adequate amounts
607 of essential resources (Owen-Smith 1988, 2014). To cover long distances in a foraging herd,
608 energy efficient trekking is needed that requires certain anatomical features mainly
609 concerning body size, shape and limb proportions.

610 As for body size, the metabolic cost of transport is relatively lower in larger animals,
611 because muscles consume energy at a much lower rate in larger than in smaller animals
612 during locomotion (Alexander, 2002, 2005). Body shape and relative limb length influence
613 trekking abilities in a more direct way: animals with proportionately shorter legs are
614 characterized by higher stride frequencies than long-legged animals, and hence also consume
615 more energy while covering the same distance (Heglund and Taylor, 1988). Most ankylosaurs
616 were broad and flat bodied animals, and their limbs were relatively short suggesting a barrel-

617 shaped, hippo- or rhino-like body (Carpenter, 1982; Paul, 1997; Kirkland, 1998; Vickaryous
618 et al., 2004). The heavily built, armoured body and short limbs of ankylosaurs indicate that
619 they must have had a relatively short stride (Maidment et al., 2012) and were poorly adapted
620 to running or long distance trekking (Paul, 1997). Other skeletal features, such as the
621 morphology of the pectoral apparatus, and the muscular reconstruction of the hind limbs are
622 also suggestive of a sluggish locomotion for ankylosaurs (Coombs, 1979).

623 Extant animals characterized by similar body proportions and likely comparable
624 locomotor capacities to ankylosaurs, such as rhinoceros, have relatively small home ranges.
625 These typically cover 10 – 100 km² depending on habitat characteristics, and the animals are
626 generally solitary or live in small family groups (Owen-Smith, 1988). Thus, the general
627 ankylosaurian bauplan is inefficient for long distance trekking and migration typical of larger
628 herds of meso- and megaherbivores.

629 In comparison with other Cretaceous meso- and megaherbivores that are believed to have
630 moved in larger herds, hadrosaurs seem to have had the best locomotor energetics allowing
631 long distance migrations (Fiorillo and Gangloff, 2001; Bell and Snively, 2008). Adult
632 hadrosaurs were most likely quadrupedal animals (facultatively bipedal for running), because
633 their anatomical and osteological features suggest that they used their forelimbs for weight-
634 bearing (e.g. Dilkes, 2001; Maidment et al., 2012). Their limb bone morphology suggests that
635 hadrosaurs had higher locomotor performance than ankylosaurs and other quadrupedal
636 ornithischians (Maidment et al., 2012), and thus they could have migrated over great distances
637 (Fiorillo and Gangloff, 2001; Bell and Snively, 2008). Ceratopsians have often been
638 considered as the dinosaurian equivalent of rhinoceros being graviportal rather than cursorial
639 animals (e.g. Carrano, 1999; Thompson and Holmes, 2007). However, they were likely able
640 to attain full gallop with a maximum running speed exceeding that of extant elephants (Paul
641 and Christiansen, 2000). In addition, just like hadrosaurs, ceratopsians also seem to have

642 migrated long distances based on their bonebed records which indicate the formation of
643 massive herds that must have needed large home ranges and constant trekking to forage (e.g.
644 Currie and Dodson, 1984; Eberth and Getty, 2005).

645 Besides the presence of an extensive, heavy armour and the difference in limb
646 proportions (Fig. 1E), ankylosaurs also have more massive femora with proportionally wider
647 midshaft than other ornithischians, and their humeri tend to be more robust as well
648 (Maidment et al., 2012; Barrett and Maidment, 2017). Such stocky limbs probably indicate
649 that ankylosaurs had a greater body mass than other ornithischians with the same femoral
650 length (Maidment et al., 2012). These comparative data imply that medium to large sized
651 dinosaurian herbivores with strong taphonomic support for gregarious behaviour, like
652 hadrosaurs and ceratopsians, also show better suited anatomy for energy efficient long range
653 locomotion than do ankylosaurs (Fig. 1E), and possibly thyreophorans in general (Bell and
654 Snively, 2008; Maidment et al., 2012; Barrett and Maidment, 2017). This in turn speaks
655 against gregarious behaviour in ankylosaurs, although formation of small family groups
656 foraging in moderate-size home ranges, as seen in modern day rhinoceros (Owen-Smith,
657 1988), is still conceivable with the general ankylosaurian bauplan.

658 Nevertheless, the nodosaurid *Hungarosaurus* might represent an exception concerning
659 the generalized restrictions on ankylosaurian locomotor efficiency summarized above. First,
660 *Hungarosaurus* is characterized by quite elongate and gracile fore- and hind limb elements
661 compared to other ankylosaurs. This includes a humerus with an unusually small deltopectoral
662 crest, which suggests a more erect posture of the forelimbs than usually reconstructed for
663 ankylosaurs (Maidment and Barrett, 2012). Furthermore, the forelimb to hind limb length
664 ratio in *Hungarosaurus* is 1.0, as opposed to ≤ 0.75 seen in other ankylosaurs. This results in a
665 more elevated anterior portion, i.e. a more horizontal major axis of the body and a relatively
666 longer stride than is generally reconstructed for ankylosaurs (Ósi and Makádi, 2009). Second,

667 *Hungarosaurus* possessed paravertebral elements – ossified tendons fused with osteoderms –
668 along the epaxial musculature, which served to stiffen the axial skeleton of the animal, as it
669 was also suggested for *Minmi* (Molnar and Frey, 1987). These elements could have aided to
670 keep the posture and decrease the energetic cost of locomotion. Third, in contrast to most
671 ankylosaurs but similar to *Struthiosaurus*, *Hungarosaurus* had a dorsally hypertrophied
672 cerebellum that indicates a more sophisticated cerebral coordination of posture and
673 locomotion (Ósi et al., 2014). The combination of these features suggests that *Hungarosaurus*
674 could have been more agile and cursorial than is typically reconstructed for ankylosaurs (Ósi
675 et al., 2014).

676

677

678 **5. HABITAT-DEPENDENT GROUP FORMATION**

679 Habitat heterogeneity, including spatiotemporal distribution of resources and structural
680 diversity providing potential cover, strongly influences the complex dynamics of herd
681 formation in extant meso- and megaherbivores (e.g. Winnie et al., 2008; Bercovitch and
682 Berry, 2010; Owen-Smith, 2014; Anderson et al., 2016). However, the most straightforward
683 relationship between habitat and gregarious behaviour is the increasing tendency for group
684 formation as habitat openness increases (e.g. Owen-Smith, 1988; Gerard and Loisel, 1995;
685 Taggart and Cross, 1997; Apollonio et al., 1998; Pays et al., 2007 and references therein).
686 Conversely, medium to large-sized herbivores inhabiting areas of dense vegetation are largely
687 solitary, while groups of habitually gregarious herbivores tend to split up into smaller groups
688 or single individuals if entering structurally more complex landscapes (Owen-Smith, 1988;
689 Fortin et al., 2009).

690 For example, antelope species occupying wooded habitats tend to form smaller groups
691 than grazer species which live in open habitats (Owen-Smith, 1988). Similarly, the white

692 rhinoceros (*Ceratotherium simum*) living in open, short-grass plains often congregate in small
693 groups, (Owen-Smith, 1988), whereas the Sumatran rhino (*Dicerorhinus sumatrensis*) or the
694 Javan rhino (*Rhinoceros sondaicus*) which live in rainforests are exclusively solitary animals
695 (Laurie, 1982). Even different ecotypes of a single species, such as the woodland, tundra, and
696 mountain forms of caribou (*Rangifer tarandus*), inhabiting areas of different structural
697 characteristics show this trend of being solitary or aggregating in smaller groups in woody
698 areas, while forming vast herds of hundreds to thousands of animals in open landscapes
699 (Tryland and Kutz, 2018).

700 The positive relationship between group size and habitat openness is mostly regarded as a
701 predator-mediated response whereby individual predation risk can be decreased (e.g. Jarman,
702 1974; Apollonio et al., 1998; Fryxell et al., 2004; Fortin et al., 2009). Nevertheless, other
703 studies have questioned the primary importance of predator avoidance and favour more
704 spontaneous drives. These studies consider open habitats as providing better visual conditions
705 for the inherent attraction to emerge between conspecifics as their perception radius increases
706 in open areas. This phenomenon is referred to as ‘fusion-by-attraction’, and regarded as the
707 main drive leading to group formation (e.g. Gerard et al., 1993, 2002; Gerard and Loisel,
708 1995; Creel and Winnie, 2005; Pays et al., 2007). Group cohesion is an inherent force in
709 highly social species that restrains individuals from leaving the group more and more the
710 larger the group gets, which in return correlates positively with habitat openness (Pays et al.,
711 2012).

712 Solitary lifestyle and group fission in woody and thicket landscapes were also associated
713 with predator evasion, as crypsis would be less effective with multiple individuals nearby
714 attracting the attention of predators (Jarman, 1974; Owen-Smith, 1988). However, this might
715 also be explained by the changes in density, quality and spatial distribution of resources and
716 related intraspecific competition in a heterogeneous habitat (Anderson et al., 2016) that also

717 presents physical obstacles passively splitting up groups. Although most likely a complex
718 interplay of all these factors account for the observed patterns (Bercovitch and Berry, 2010),
719 the general phenomenon that meso- and megaherbivores tend to aggregate in open habitats
720 and less so in woody and bushy areas seems to hold true across a variety of species and
721 environments.

722 Accordingly, reconstruction of the ancient habitat of ankylosaurs is an important step in
723 assessing their social behaviour. Inferring preferred habitat of extinct animals might be
724 difficult because remains of carcasses can be transported long distances crossing different
725 environments before deposition. This may result in the remains being buried in an area that
726 may not represent the actual environment the animal inhabited. Although ichnofossils record
727 *in situ* presence of living animals, their taxonomical assignment can be very difficult (see
728 below). Furthermore, they do not necessarily reflect habitual residence of the animal in that
729 particular region, either (e.g. footprints left behind during migration). Still, combining
730 information about the ancient depositional and preservation environments of body fossils and
731 ichnofossils is the best available method to reconstruct palaeohabitats of any extinct animal.
732 Thus, we also use this approach to decipher the preferred habitat of ankylosaurs occurring in
733 MDAs to see how favourable, permissive or aggravating the habitat conditions might have
734 been for a potentially gregarious lifestyle.

735

736 **5.1 Body fossil-related habitat reconstruction**

737 MDAs of *Pinacosaurus* from the Alag Teeg and Bayan Mandahu formations were formed in
738 slightly different palaeohabitats. Sedimentological characteristics of the Alag Teeg Formation
739 indicate sandy braided river, flood-plain and ephemeral lake environments under sub-humid
740 climate. Relatively rich vegetation is presumable around the ephemeral streams and lakes
741 based on the abundant occurrence of rhizoliths (Hasegawa et al., 2009). However, this type of

742 vegetation structure represents a low-growing thicket or shrub-like vegetation rather than a
743 permanent and extensive closed forest that could not have developed due to the prolonged
744 drought periods (Jerzykiewicz et al., 1987). The sedimentary rocks of the Bayan Mandahu
745 Formation were deposited at the margin of a dune desert field including structureless
746 sandstones with mature *in situ* calcrete and large fossil burrows. This lithofacies implies dry
747 steppe environments under semi-arid climate (Hasegawa et al., 2009). Based on these
748 palaeoenvironmental and vegetation reconstructions, *Pinacosaurus* lived in relatively open
749 habitats (Fig. 1F) known to favour congregation of herbivores (see previous section above).

750 Concerning *Gastonia*, all three MDAs recovered from the Cedar Mountain Formation
751 were deposited around ephemeral lakes or ponds under arid to semiarid conditions
752 characterized by sparse vegetation (Kirkland and Madsen, 2007; Kirkland et al., 2008;
753 Kinneer et al., 2016). This comparatively open habitat apparently allowed group formation in
754 *Gastonia*. In contrast, other ankylosaurs that were discovered in the uppermost part (the
755 Mussentuchit Member) of the Cedar Mountain Formation, such as *Animantarx*, *Peloroplites*,
756 *Cedarpetta* and probably *Sauropelta* individuals (Carpenter et al., 2001, 2008; Kinneer et al.,
757 2016), are known from partial, usually single individuals which may indicate solitary lifestyle.
758 However, these remains were deposited on a broad coastal plain with a high water table. This
759 suggests a relatively wet and densely vegetated palaeoenvironment characterizing the
760 Mussentuchit Member (Kirkland and Madsen, 2007) that is in line with the implied solitary
761 lifestyle of the latter ankylosaurian taxa.

762 Similarly, the palaeoenvironments of the Dinosaur Park Formation in Alberta, Canada,
763 were characterized by closed and dense vegetation of low gradient, alluvial to costal settings
764 that developed under subtropical conditions (Eberth, 2005). Here, dozens of partial
765 ankylosaur skeletons, including *Edmontonia*, *Anodontosaurus*, *Dyoplosaurus*,
766 *Euoplocephalus*, and *Panoplosaurus*, were found as isolated individuals (Currie and Russell,

2005; Arbour and Currie, 2013; Arbour and Mallon, 2017). Such a complex habitat of dense, subtropical forests is concordant with the solitary lifestyle of these ankylosaurs, which could also imply that solitariness was the norm for large herbivore inhabitants. However, at least twenty ceratopsian MDAs were found in the same palaeoenvironmental settings in the lower part of the Dinosaur Park Formation. This suggests gregarious behaviour in these large bodied herbivores (Currie and Dodson, 1984; Eberth and Getty, 2005), despite the reconstructed dense subtropical forest. Thus, gregarious lifestyle of ceratopsians and apparently solitary lifestyle of ankylosaurs is equally detectable in this palaeohabitat, which seems to undermine the prediction power of habitat openness when assessing the probability of herd formation in various large bodied herbivorous dinosaurs.

Although the general lack of detailed, small-scale and high-resolution palaeobotanical data of the depositional environments may account for these apparent discrepancies in the habitat-dependence of social lifestyles, this does not apply to the exceptionally well documented case of the Iharkút nodosaurid MDA. Here, the ankylosaur remains were accumulated under a subtropical climate that was characterized by seasonal but dominantly humid conditions (Botfalvai et al., 2016). Based on the abundant micro-, meso- and macrofossils of plants collected from the embedding deposits, the reconstructed vegetation type of the Iharkút palaeoenvironment is a closed-canopy floodplain forest composed of ferns, Sabiaceae, and Normapolles group representing Fagaleaceae, as well as gymnosperms that probably lived in more distal upland territories (Bodor and Baranyi, 2012; Botfalvai et al., 2016). Thus, even though such a habitat is believed to interfere with group formation of larger herbivores, the Iharkút nodosaurids seem to have moved in groups in this dense, forested habitat (Fig. 1G). Although the Iharkút nodosaurid MDA reveals an incomparably smaller group than the vast ceratopsian herds of the Dinosaur Park Formation, their case adds to the peculiarities related to the habitat dependency of group formation in fossil herbivores.

792

793 **5.2 Ichnofossil-related habitat reconstruction**

794 Ostrom (1972) was the first to suggest that the numerous unidirectional and subparallel
795 dinosaurian trackways, which have been reported from all around the world (e.g. Ostrom,
796 1972, 1985; Lockley et al., 1986; Thulborn, 1990), were left behind by groups and/or herds of
797 dinosaurs. Ostrom (1972) regarded such tracks as the most convincing evidence available that
798 several forms of dinosaurs moved in groups and were gregarious animals. These trackways
799 are characterized by a relatively small intertrackway space where the individual trackways
800 produce similar speed estimates and exhibit little overlap (Ostrom, 1972; Myers and Fiorillo,
801 2009). Such trackways were assigned to sauropods (e.g. Lockley et al., 1994, 2002; Day et al.,
802 2004; Myers and Fiorillo, 2009; Castanera et al., 2011), hadrosaurs (Currie, 1983),
803 ceratopsians (Lockley and Hunt, 1995) and ankylosaurs (Kurtz et al., 2001; McCrea et al.,
804 2001), and they were all interpreted as evidence for gregarious lifestyle. However, several
805 questions still remain related to the difficulties of time-averaging, i.e. whether traces were
806 produced simultaneously (Myers and Fiorillo, 2009), and to the problematic taxonomical
807 identification of the track-makers (see Thulborn, 1990).

808 Despite the abundant skeletal remains of ankylosaurs, their inferred footprints are
809 relatively rare in the fossil record, so far being restricted to 22 localities (Carpenter, 1984;
810 McCrea and Currie, 1998; McCrea et al., 2001; Kurtz et al., 2001; Dal Sasso, 2003; Gangloff
811 et al., 2004; Stanford et al., 2007; Sacchi et al., 2009; Petti et al., 2008, 2010; Kappus et al.,
812 2011; Apesteguía and Gallina, 2011; Hornung and Reich, 2014). The reason for this low
813 frequency, however, partially lies in the uncertainty of the taxonomical assignment of the
814 footprints, because hand and foot morphology of ankylosaurs are very similar to that of
815 ceratopsians (Lockley and Hunt, 1995; McCrea et al., 2001).

816 Most of the trackways considered as ankylosaurian are solitary and isolated (Fig. 1A),
817 including single and/or partial footprints (Carpenter, 1984; Thulborn, 1990; Gangloff et al.,
818 2004; McCrea et al., 2001; Dal Sasso, 2003; Sacchi et al., 2009; Petti et al., 2010). There are
819 only a few cases where the orientation and abundance of footprints might indicate that several
820 animals were walking together at the same time (McCrea and Currie, 1998; McCrea et al.,
821 2001). McCrea et al. (2001) mentioned five *Tetrapodosaurus* tracksites from the Smoky River
822 Coal Mine near Grande Cache (Alberta, Canada) which, based on the footprint sizes, were
823 most probably produced by adult ankylosaurs. These parallel trackways indicate that several
824 animals were travelling together in the same direction, and hence could hint at gregarious
825 behaviour of adult ankylosaurs (see also McCrea and Currie, 1998). Kurtz et al. (2001)
826 reported an abundant trackway assemblage from the Lower Cretaceous Skyline Drive site of
827 Dakota Group of the Cañon City area, where at least ten of the better preserved tetradactyl
828 tracks were attributed to ankylosaurs and show similar parallel orientations.

829 The richest ankylosaurian (*Tetrapodosaurus*) footprint assemblages, including parallel
830 trackways in the Smoky River ichnofauna of Gates Formation, were preserved in non-marine
831 sandstones originally deposited on a coastal plain or in a deltaic environment (McCrea and
832 Currie, 1998). McCrea et al. (2001) mentioned several ankylosaurian footprints from North-
833 America (e.g. in the Blackhawk, Cedar Mountain, Dunvegan, and Gething formations),
834 South-America (El Molino Formation; Bolivia) and Europe (Wealden Beds; Germany) that
835 were all preserved in coal-bearing and floodplain facies. This indicates that ankylosaurs lived
836 in freshwater-dominated environments most likely characterized by lush vegetation of
837 ginkgoes, cycads, ferns, conifers and angiosperms (see also Carpenter, 1984; Hornung and
838 Reich, 2014; Gangloff et al., 2004). A moderately well preserved ankylosaur trackway from
839 shallow-marine carbonate deposits of Puglia, southern Italy, suggests that some ankylosaurs
840 lived on carbonate coastal-plain (inner carbonate platform) environments with sparse

841 vegetation (Petti et al., 2010). Sacchi et al. (2009) also reported an ankylosaur trackway that
842 was discovered in carbonate platform deposits near Bisceglie, southern Italy. Ankylosaur
843 footprints from the fluviolacustrine deposits of the Djadokhta Formation (Abdrant Nuru
844 locality) of Mongolia indicate that some Mongolian ankylosaurs also lived along the margins
845 of freshwater bodies (Ishigaki et al., 2009).

846 The ankylosaurian track record, as all other fossil footprints, is strongly related to water-
847 saturated and possibly well-vegetated lowland facies (McCrea et al., 2001). However, based
848 on their abundant body fossils in arid to semi-arid environments, this overrepresentation of
849 footprints in wetlands is likely a preservational bias that is difficult to correct for when
850 assessing preferred – open or closed (woodland) – habitat of ankylosaurs. Nevertheless, the
851 limited number of unidirectional, subparallel ankylosaurian trackways, as opposed to other
852 major dinosaurian clades (Ostrom, 1972; Myers and Fiorillo, 2009; McCrea et al., 2001) may
853 indicate a lower tendency for gregarious behaviour in ankylosaurs.

854

855

856 **6. DISCUSSION**

857 The combined evaluation of all the aspects considered in this review that may be informative
858 of gregarious vs. solitary lifestyle in fossil meso- and megaherbivores outlines a fairly
859 complex, in some ways even counterintuitive, image of ankylosaurs (Fig. 1). The comparative
860 rarity of MDAs and multiple parallel trackways, the heavy armour built up by passive and
861 active defence structures, and the generally barrel-shaped body and stocky limbs all suggest
862 that the majority of ankylosaurs lived a mostly solitary life with limited agility, confined
863 home- and foraging range, but possessing an efficient anti-predator defence system at least in
864 adulthood. The known instances of multiple MDAs of *Pinacosaurus* and *Gastonia*, and the
865 single known MDA of *Iharkút nodosaurids* (possibly comprising two taxa) contrast with this

866 generalized pattern and imply that at least some ankylosaurs show stronger tendency to form
867 groups (Table 1). However, as extreme circumstances may also result in aggregation of non-
868 gregarious animals (Alexander, 1974; Rogers and Kidwell, 2007), MDAs do not necessarily
869 indicate habitual group formation.

870 MDAs of *Gastonia* and *Pinacosaurus* were deposited under semi-arid to arid climate
871 (Britt et al., 2009; Currie et al., 2011), where the seasonal prolonged drought could have
872 driven the animals to assemble in the vicinity of persistent reserves of food and water
873 irrespective of their social behaviour, as it happens in modern arid ecosystems (Rogers and
874 Kidwell, 2007). For example, the Dalton Wells bonebed, which yielded one of the *Gastonia*
875 assemblages, also contains clusters of partial carcasses of other dinosaurs (the sauropod
876 *Venenosaurus* and an iguanodontid; Britt et al., 2009), suggesting a drought-related
877 congregation. However, MDAs of *Gastonia* are present in two different horizons of the
878 Yellow Cat Member, as well as at Lorrie's Site in the Ruby Ranch Member of the Cedar
879 Mountain Formation. These localities are characterized by different depositional
880 environments and ages indicating that group formation was the typical lifestyle of *Gastonia*.
881 The multiple MDAs of juvenile *Pinacosaurus* individuals known from different localities and
882 formations of Mongolia and China also support the hypothesis that these are not random
883 aggregations but reflect true gregarious behaviour in these ankylosaurs.

884 By contrast, the Iharkút nodosaurid MDA was deposited in a subtropical environment
885 that lacked prolonged drought periods (Botfalvai et al., 2016). The taphonomical history of
886 their MDA was reconstructed as a mass drowning event (Botfalvai et al., 2015; Ósi et al.,
887 2019), similar to that of wildebeest during the annual migrations through the Serengeti plains
888 (e.g. Capaldo and Peters, 1995; Myers and Storrs, 2007; Chiba et al., 2015; Subalusky et al.,
889 2017). However, a severe flooding can result in local concentrations of individual carcasses
890 from true herds as well as in coincidental aggregations of otherwise non-gregarious animals

891 which all tend to withdraw from the flood and concentrate on higher ground refuges.
892 Nevertheless, the Iharkút nodosaurid MDA contains the only associated skeletons out of all
893 vertebrate groups known from the locality. This speaks against a disaster-related random
894 aggregation of animals, where associated/articulated remains of other taxa would also be
895 expected in the assemblage. Furthermore, the clear dominance of ankylosaur remains even
896 among the isolated material of this locality suggests that they were permanent inhabitants of
897 these floodplain forests. As floods in such a habitat must have been periodically recurring and
898 hence predictable events, residents are expected to have evolved movement patterns that are
899 adapted to these conditions (Riotte-Lambert and Matthiopoulos, 2020) making them less
900 likely to be driven into spontaneous catastrophic assemblages. This further supports the
901 hypothesis that this ankylosaurian MDA originated from a coordinated but fatal move of a
902 group indicating genuine gregarious behaviour in the Iharkút nodosaurids as well.

903 In sum, we conclude that the *Pinacosaurus*, *Gastonia* and Iharkút nodosaurid MDAs
904 reflect true gregarious behaviour. However, unlike the spectacular MDAs of ceratopsians,
905 which sometimes consist of over 1000 individuals indicating formation of vast herds (Eberth
906 et al., 2010), ankylosaurian MDAs typically consist of maximum a few dozens of individuals
907 (Table 1) suggesting smaller groups. Small as these groups appear to be, the question still
908 remains whether a common set of inherent features and external factors can be identified in
909 these MDAs that could explain why these particular ankylosaurs were found in aggregation,
910 as opposed to the solitary specimens comprising the majority of the ankylosaurian fossil
911 record.

912 The social structure and behavioural background underlying these small ankylosaurian
913 groups remains contentious. Uncertainties related to the ontogenetic composition of these
914 MDAs set back proper inferences, although the apparent lack of mixed-aged ankylosaurian
915 MDAs containing early and late juveniles along with adults speaks against family groups and

916 crèche-like aggregations. Instead, the all-juvenile status of *Pinacosaurus* MDAs (Currie et al.,
917 2011; Burns et al., 2011, 2015), and the subadult to adult composition assumed for *Gastonia*
918 assemblages (Kirkland, 1998; Kinner et al., 2016) and confirmed for the Iharkút nodosaurid
919 MDA in this study by osteohistology imply a certain level of age-segregation in the group
920 formation pattern of these ankylosaurs. Nevertheless, the notion that juvenile ankylosaurs
921 were gregarious, while adults were solitary (Arbour and Mallon, 2017) is an oversimplified
922 generalization based on the *Pinacosaurus* material and is apparently not supported by the
923 other ankylosaurian MDAs.

924 All ankylosaurian MDAs consist of small to medium sized animals relative to other
925 contemporary herbivorous dinosaurs. However, this does not necessarily imply the need to
926 form groups as an antipredator strategy because (1) body size in itself does not correlate with
927 gregarious antipredator response (Owen-Smith and Mills, 2008); and (2) some other
928 ankylosaurs known exclusively from isolated specimens also represent the same size range
929 (Vickaryous et al., 2004). In addition, *Hungarosaurus* was the largest known terrestrial
930 herbivore in the Iharkút palaeohabitat (Ósi et al., 2012) which further weakens a size-related
931 explanation for their gregarious behaviour.

932 Nevertheless, the small to medium ankylosaurian body sizes may well correlate with the
933 evolution of their extensive armour (Arbour and Zanno, 2018). The relative development of
934 defence structures, another clue to predator avoidance strategy and related trends in
935 gregarious vs solitary lifestyle, can be a distinctive feature of different ankylosaurian taxa and
936 different ontogenetic stages. For instance, although it is a persistent trait state in *Gastonia* and
937 the Iharkút nodosaurids, and only a temporary deficiency in the armour of juvenile
938 *Pinacosaurus*, the lack of a predator-detergent tail club is a common feature among the
939 specimens forming these MDAs. However, all nodosaurid ankylosaurs lack tail clubs (e.g.
940 Coombs, 1978; Vickaryous et al., 2004), still only the Iharkút nodosaurids were so far found

941 in unequivocal MDAs. Comparative assessment of the antipredator efficiency of the armour
942 between specimens and taxa that form MDAs or are found as isolated individuals could
943 provide deeper insight into this aspect. However, the disarticulated and incomplete nature of
944 the armour in most ankylosaurs makes such comprehensive endeavours difficult.

945 Unlike in *Hungarosaurus*, the better characterized member of the Itharkút nodosaurids, no
946 striking anatomical modifications can be detected in *Pinacosaurus* and *Gastonia* that would
947 reflect increased relative agility and capability of long-distance, energy-efficient locomotion;
948 features characterizing animals moving in herds. Nevertheless, due to their underdeveloped
949 armour, juvenile *Pinacosaurus* must have been lighter and more agile than their adults. This
950 notion is also supported by the allometric changes detectable in their forelimbs which change
951 from more elongate to increasingly robust through ontogeny (Burns et al., 2015). Due to the
952 scantiness of proper ontogenetic data, these aspects cannot be evaluated in the *Gastonia*
953 MDAs. The anatomical peculiarities related to the limbs, posture and brain of *Hungarosaurus*
954 (Ősi et al., 2014) could imply that they were better adapted to trekking than other ankylosaurs.
955 However, the yet unknown size of the island the Itharkút nodosaurids inhabited could have
956 limited the range of a potential long distance travel. Furthermore, these anatomical features
957 may equally indicate adaptations to browsing higher level vegetation in their woodland
958 habitat. Finally, the long-distance trekking constraint related to the ecological carrying
959 capacity of the habitat, and hence the selection pressure on anatomical adaptations, were most
960 likely incomparably weaker for any of these small ankylosaur groups than for the vast herds
961 of ceratopsians and hadrosaurs.

962 Even though habitat openness seems to be one of the strongest predictors of gregarious
963 behaviour among extant medium- and large-sized herbivores, inferring the structure of
964 palaeohabitats in which ankylosaurs roamed proves extremely challenging. It requires
965 tremendous amount of small-scale but high-resolution data collected from a variety of

966 sources, such as palaeoclimatology, sedimentology, taphonomy, palynology and
967 palaeobotany; a combination of extensive background information that most fossil localities
968 lack. Nevertheless, the deposits yielding the *Pinacosaurus* and *Gastonia* MDAs were formed
969 in an overall arid, semi-arid palaeoenvironment with vast open areas of low and sparse
970 vegetation. Such environments are suitable for the aggregation of multiple individuals, as
971 opposed to the palaeohabitat of the Iharkút nodosaurids which apparently lived in dense
972 floodplain forests under a subtropical humid climate.

973 The open palaeohabitat reconstructed for *Pinacosaurus* and *Gastonia* could have allowed
974 a more spontaneous, emergent group formation aided by the extended visual perception
975 radius, as it frequently occurs in extant meso- and megaherbivores occupying open habitats
976 (Gerard et al., 1993, 2002; Gerard and Loisel, 1995; Pays et al., 2007; Bercovits and Berry,
977 2009; Fortin et al., 2009). Such flexible social systems result in fusion-fission societies with
978 variable spatial cohesion and individual group membership over time (e.g. Aureli et al., 2008;
979 Couzin and Laidre, 2009). However, the uniformity of similarly sized juveniles in multiple
980 *Pinacosaurus* MDAs strongly contrasts the dynamically changing composition characterizing
981 fusion-fission societies (Aureli et al., 2008; Couzin and Laidre, 2009). This implies that these
982 *Pinacosaurus* individuals had a high affinity for gregarious behaviour, even if it was
983 temporarily confined to a juvenile ontogenetic window, as may be the case in several other
984 non-avian dinosaur taxa (Varricchio et al. 2008; Varricchio, 2011). Nevertheless, it cannot be
985 excluded that they represented a more cohesive, age-segregated subgroup of a larger-scale
986 fusion-fission society, also seen in modern animals (e.g. Sueur et al., 2011; Fishlock and Lee,
987 2013). The currently available data on *Gastonia* does not allow such hypothetical evaluation
988 to account for their MDAs. On the other hand, as loosely organized fusion-fission groups tend
989 to break up to smaller subgroups or even to single individuals when entering forests (Fortin et
990 al., 2009; Pays et al., 2012), the woodland palaeohabitat of the Iharkút nodosaurids suggests

991 they had strong inherent tendency for gregarious behaviour even in a habitat generally
992 unfavourable for group cohesion.

993 Clearly, only a small portion of the diverse internal and external factors influencing social
994 behaviour of animals can potentially be inferred from the fossil record. This deficiency
995 undoubtedly encumbers conclusions drawn on ankylosaurs or any other extinct animals that
996 lack both, modern-day descendants and ecomorphological analogues. Our review, however,
997 also shows that combining all sources of available palaeontological information with up-to-
998 date findings and concepts of related biological fields is essential and can provide new
999 insights into the behavioural ecology of long-extinct vertebrates. With this holistic approach
1000 we also demonstrated that the social structuring in ankylosaurs was likely more complex than
1001 previously thought. Even though the degree of morphological and functional disparity within
1002 Ankylosauria has not yet been assessed, it may be one of the key components in deciphering
1003 the repertoire of social behaviour in this highly specialized group of dinosaurs.

1004

1005

1006 **7. CONCLUSION**

1007 In our review, we have collected, combined and discussed palaeontological and biological
1008 data to provide the best supported interpretation of the social lifestyle of ankylosaurs. We
1009 focused particularly on those taxa for which MDAs have been reported raising the possibility
1010 that these animals were gregarious. While the general ankylosaurian anatomy as well as the
1011 rarity of their MDAs and multiple parallel trackways imply that most ankylosaurs lived a
1012 largely solitary life, holistic assessment of the *Pinacosaurus*, *Gastonia*, and the Iharkút
1013 nodosaurid MDAs strongly supports habitual group formation in these ankylosaurs. Despite
1014 that, no common set of internal and external factors and other characteristics investigated in
1015 this study could be identified that would distinguish these likely gregarious ankylosaurs from

1016 other ankylosaurian taxa considered to have been solitary. This lack of conclusive set of traits,
1017 however, only draws more attention to the diversity of the underlying drivers and mechanisms
1018 of group formation that likely led to a complex social structuring both, within and among
1019 different ankylosaur taxa. Addressing the degree of within-clade morphological and
1020 functional disparity may hold further clues to ankylosaurian social lifestyle, and hence can be
1021 a useful addition to the holistic approach demonstrated in this review. Future studies are also
1022 encouraged to apply similar integrative palaeontological and biological approaches to
1023 investigate social lifestyle in other clades of extinct terrestrial vertebrates.

1024

1025

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1683 **CAPTIONS**

1684 **Figure 1. General ankylosaurian bauplan and the conceptual representation of major**
 1685 **aspects considered for inferring ankylosaurian social behaviour. A and B,** Taphonomical
 1686 information drawn from **A**, an isolated carcass indicating solitary lifestyle and **B**, a mass death
 1687 assemblage (MDA) resulting from a drowning herd. A single trackway left behind by the
 1688 solitary individual is also depicted in **A**. **C and D,** Efficiency of body armour deployed **C**,
 1689 against predators and **D**, in intraspecific combat and/or display. **E,** Comparative anatomy of
 1690 ankylosaurs, ceratopsians and hadrosaurids scaled to the same size suggests poor adaptation
 1691 of ankylosaurs to running or long distance trekking, as opposed to ceratopsians and
 1692 hadrosaurids that are known to have formed massive herds. **F and G,** Ankylosaur gregarious
 1693 behaviour in the context of their habitat. **F,** Open habitat generally favours group formation.
 1694 **G,** Although closed, densely vegetated habitat usually promotes group fission, the Iharkút
 1695 nodosaurids moved in groups in forested habitats. (Illustration by Márton Szabó)

1696
 1697 **Figure 2. Representative histological sections of the subadult (A-C) and adult (D-E)**
 1698 **skeletal maturity range present in the Iharkút nodosaurid MDA.** All sections are cut
 1699 transversely. **A,** The first sacral rib and **B,** the femur of MTM 2007.25.27. **C,** Proximal
 1700 section of an anterior dorsal rib of MTM 2016.16.1 under cross polarized light. Composition
 1701 of large areas of primary bone (**pb**), abundant vascular canals (**vsc**) and closely spaced lines
 1702 of arrested growth (white arrowheads) in the outer cortex suggests still ongoing but slow
 1703 diametric growth. **D,** Proximal section of a dorsal rib of MTM 2007.26.20. **E,** Mid-shaft
 1704 section of a dorsal rib of MTM 2018.4.1. **F,** Distal section of a dorsal rib of MTM 2018.3.1
 1705 under cross polarized light. Avascular primary bone with stacked lines of arrested growth
 1706 forming an external fundamental system (**EFS**) in the outermost cortex and secondary bone
 1707 (**sb**) formed by multiple generations of secondary osteons (**mso**) up to the periosteal surface

1708 **(ps)** indicate cessation of diametric growth. Further abbreviations: **eps**, eroded periosteal
1709 surface; **mc**, medullary cavity; **po**, primary osteon. Scale bars: 300 μm in **A, B, D** and **F**; 600
1710 μm in **C**; 30 μm in **E**.

1711

1712 **Table 1:** Depositional settings and taphonomical attributes of the well-described ankylosaur
1713 mass death assemblages.

1714

1715 **Table 2:** Summary of other known but taphonomically insufficiently characterized sites
1716 yielding at least two ankylosaur individuals. These ambiguous cases have mostly low number
1717 of identifiable individuals and, along with other parameters, lack the crucial information about
1718 the distances between the skeletons, except for *Europelta*. Abbreviations: **MNI**, minimum
1719 number of individuals.

1720

1721 **Supplementary Table S1:** Dataset of ankylosaur material worldwide summarizing
1722 taxonomic, geological, taphonomical, ontogenetic and environmental characteristics of the
1723 fossil occurrences.

1724

1725 **Supplementary Table S2:** Histological ontogenetic assessment of the skeletons composing
1726 the Iharkút nodosaurid MDA. Histological sections of the sampled elements in boldface italics
1727 are depicted in Figure 2.

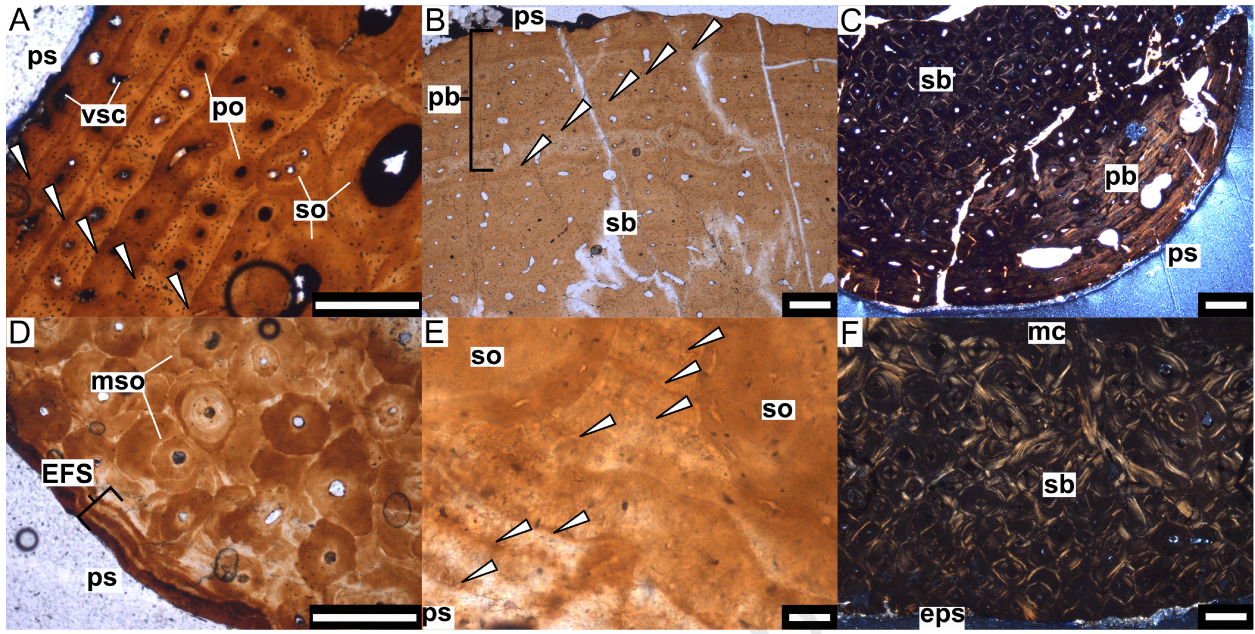
Species/Taxon	Family	Country & region	Formation	Age and stage	Site	Material	MNI	Ontogenetic stage	Sediments / environment	References
<i>Shamosaurus scutatus</i> (PIN N 3779/1 and 3779/2)	Ankylosauridae	Mongolia, Gobi Desert	Zuunbayan Formation	Early Cretaceous; Aptian-Albian	Khamryn-Uus	A complete skull, skull fragment, lower jaws, partial postcranial skeleton with armor elements	2?	NA	Lacustrine depositional environment	Tumanova, 1985; Arbour and Currie, 2016
<i>Jinyunpelta sinensis</i> (ZMNH M8960 and M8963)	Ankylosauridae	China; Jinyun County	Liangtoutang Formation	Early Cretaceous; Albian–Cenomanian	Lijin Industrial Park	Skull and postcranial elements	2	Adult	Shallow lacustrine environment	Zheng et al., 2018
<i>Talarurus plicatospineus</i> (PIN 557, holotype)	Ankylosauridae	Mongolia, Gobi Desert	Bayan Shireh Formation	Late Cretaceous; Cenomanian-Santonian	Bayn Shire locality	Skull and postcranial elements	6	NA	Sandy, red calcareous claystone deposited in meandering fluvial system	Arbour and Currie, 2016
<i>Europelta carbonensis</i> (AR-1/10 and AR-1/31)	Nodosauridae	Spain, Teruel	Escucha Formation.	Late Cretaceous; Early Albian	Arino site	Associated skeletons	2	NA	Coal-bearing beds; swamp	Kirkland et al., 2013
<i>Invictarx zephyri</i> (WSC 16505, holotype)	Nodosauridae	San Juan Basin, northwestern New Mexico	Menefee Formation	Late Cretaceous; Early Campanian	Outcrops of the Juans Lake Beds	Postcranial elements	3	NA	Fluvial mudstones and sandstones	McDonald and Wolfe, 2018
<i>Pinacosaurus grangeri</i> (IVPP 050790-1a; IVPP 050790-1b)	Ankylosauridae	China, Inner Mongolia	Bayan Mandahu Formation	Late Cretaceous; Campanian	Site 63	Skull and mandible with several associated osteoderms, atlas and axis.	2	Juvenile	Facies of subaerial deposition interfingering with water-lain interdune / ephemeral facies	Currie et al., 2011
<i>Struthiosaurus</i> sp. (MCNA L1 A and B)	Nodosauridae	Spain; Basque-Cantabric basin	Sobrepena Formation	Late Cretaceous; Maastrichtian	Laño	Isolated bones from attritional vertebrate assemblage	>2	Juvenile and adult	Alluvial system composed primarily of fluvial sands and silts	Pereda-Suberbiola et al., 1995

Cf <i>Struthiosaurus</i> sp / Nodosauridae indet. (e.g. UBB VP 12;16;17)	Nodosauridae	Romania; Transylvanian Basin	Şard Formation	Late Cretaceous; Maastrichtian	Vurpăr; F1	Associated and isolated postcranial remains	2	Adult	Floodplain deposits of braided and mending fluvial system	Ősi et al., 2014
<i>Tianzhenosaurus</i> <i>youngi</i> (HBV-10001- holotype, HBV- 10002-10003)	Ankylosauridae	China; Shanxi Province	Huiquanpu Formation	Late Cretaceous	Kangdailiang	Three skulls, one lower jaw and disarticulated postcranial region	3	NA	NA	Pang and Cheng, 1998

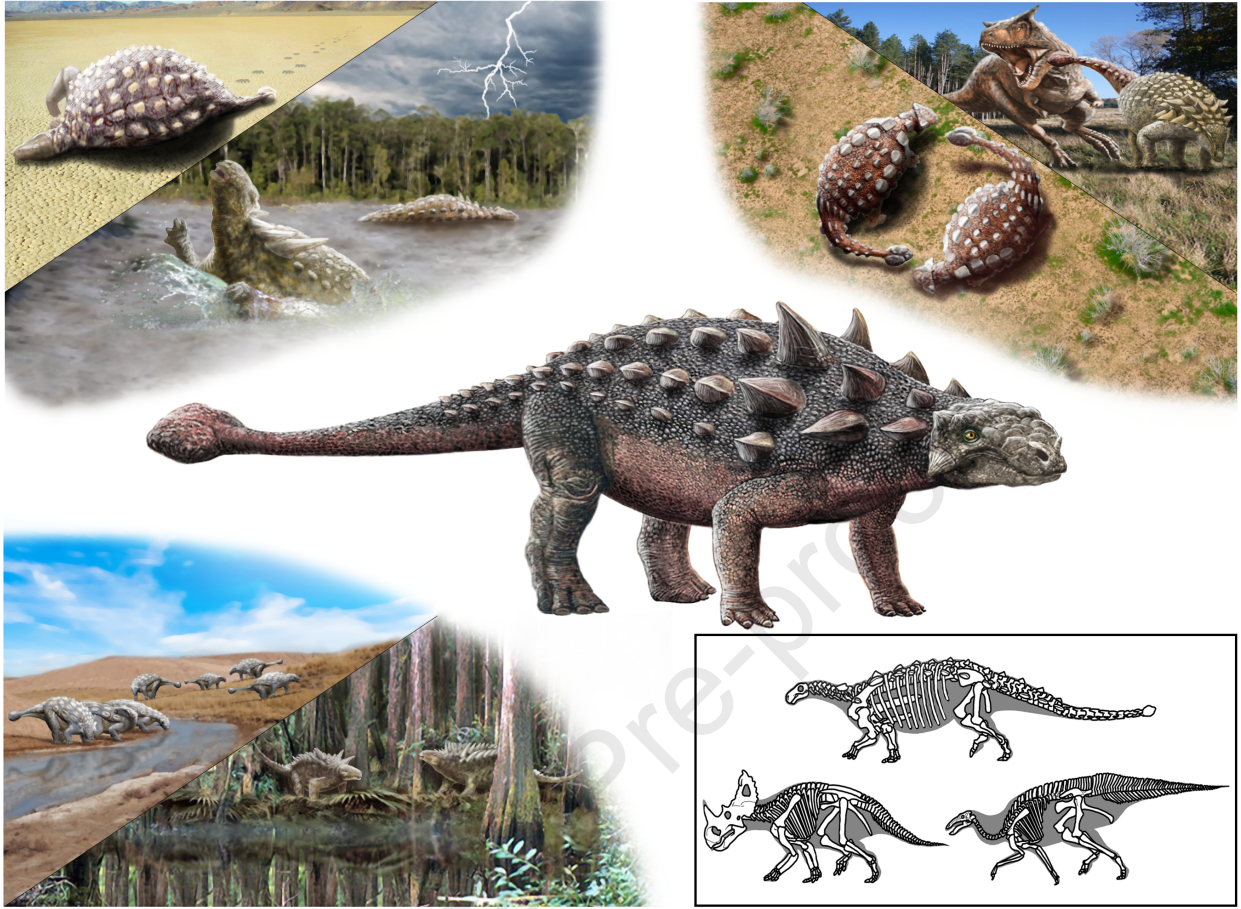
Mass death assemblages of ankylosaurs

	Yellow Cat Quarry	Dalton Well	Lorrie's site	Iharkút	Bayan Mandahu; Querry 100 and 101	Alag Teeg
Clade (Family)	Ankylosauridae	Ankylosauridae	Ankylosauridae	Nodosauridae	Ankylosauridae	Ankylosauridae
Ankylosaur taxon/taxa in the bonebed	<i>Gastonia burgei</i>	<i>Gastonia burgei</i>	<i>Gastonia lorriemcwhinneyae</i>	<i>Hungarosaurus tormai</i> ; Cf <i>Struthiosaurus</i> ;	<i>Pinacosaurus grangeri</i>	<i>Pinacosaurus grangeri</i>
Country, state/region	USA, Utah	USA, Utah	USA, Utah	Hungary, Bakony Mts	China, Inner Mongolia	Mongolia, Gobi Desert
Formation	Cedar Mountain Formation; Yellow Cat Member	Cedar Mountain Formation; Yellow Cat Member	Cedar Mountain Formation; Ruby Ranch Member	Csehbánya Formation	Bayan Mandahu Formation	Alag Teeg Formation
Geological age and stage	Early Cretaceous; Barremian	Early Cretaceous; Barremian	Early Cretaceous; Aptian	Late Cretaceous; Santonian	Late Cretaceous; Campanian	Late Cretaceous; ?late Santonian or early Campanian
Climating setting	Warm-to-hot and seasonally wet-and-dry climate	Warm-to-hot and seasonally wet-and-dry climate	Semiarid climate; strongly seasonal	Subtropical climate, dominantly humid, but seasonal	Unstable semiarid climate	Arid condition with fluvial influence
Burial setting	Ephemeral lake or pond	Alluvial/lacustrine setting	Floodplain setting	Fluvial overbank setting	Alluvial and/or aeolian environment	Floodplain of a braided system
Sediment	Diagenetically altered sandy limestones and interbedded pale green, sandy siltstone	Debrish-flows deposit	Crevasse splay deposit	High density flash flow deposit	Structureless sandstone	Red mudstone
Estimated number of individuals	5 or 6	8 or 9	monospecific assemblage of several individuals	12	12	more than 30
Ontogenetic composition	Adults	8 subadults and 1 adult	NA	2 subadults and 10 adults	Juveniles	Juveniles

Inferred taphonomical situation and cause of death	Drought-induced death around an ephemeral pond	Drought followed by ephemeral flooding	Drought and/or mass drowning of a migrating herd	Mass drowning of a migrating herd in a flash-flood event	Drought-induced death followed by sand fan burrial during rain storms	Drought-induced death around drying ponds
Other vertebrate material	Present	Present	Absent	Present	Present	Present
References	Kirkland, 1998; Kinneer et al., 2016	Britt et al., 2009; Kinneer et al., 2016	Kinneer et al., 2016	Botfalvai et al., 2015; Ósi et al., 2019	Burns et al., 2011	Currie et al., 2011



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Highlights

to the manuscript titled '**Living alone or moving in herds? A holistic approach highlights complexity in social lifestyle of Cretaceous ankylosaurs**'

by

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Highlights

- We use palaeontological and biological data to infer social lifestyle in ankylosaurs
- Six ankylosaurian mass death assemblages are known indicating gregarious lifestyle
- No common set of traits for gregariousness could be identified in these ankylosaurs
- Most likely a specific set of drivers led to group formation in each taxon
- This diversity indicates an unexpectedly complex social structuring in ankylosaurs

Declaration of interests

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

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