

Palaeoenvironmental controls on the distribution of Cretaceous herbivorous dinosaurs

Richard J. Butler · Paul M. Barrett

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Abstract Previous attempts to determine palaeoenvironmental preferences in dinosaurs have generally been qualitative assessments based upon data from restricted geographical areas. Here, we use a global database of Cretaceous herbivorous dinosaurs to identify significant associations between clades and broad palaeoenvironmental categories ('terrestrial', 'coastal', 'marine'). Nodosaurid ankylosaurs and hadrosaurids show significant positive associations with marine sediments, while marginocephalians (Ceratopsia, Pachycephalosauria), saurischians (herbivorous theropods, Sauropoda) and ankylosaurid ankylosaurs are significantly positively associated with terrestrial sediments. These results provide quantitative support for the hypothesis that some clades (Nodosauridae, Hadrosauridae) were more abundant in coastal and/or fluvial environments, while others (e.g. Marginocephalia, Ankylosauridae) preferentially inhabited more distal environments.

Keywords Cretaceous · Dinosauria · Palaeoecology · Palaeoenvironments

Introduction

Macroevolutionary studies attempt to identify broad-scale patterns in the history of life, but detecting such patterns can be difficult due to the nature of the fossil record

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R. J. Butler (✉) · P. M. Barrett
Department of Palaeontology, The Natural History Museum,
Cromwell Road,
London SW7 5BD, UK
e-mail: r.butler@nhm.ac.uk

(Jablonski et al. 1996). Preservational biases, relating to both the structure and ecology of the organism and geological and environmental factors, exert a strong influence on the quality of the record and the accuracy of the information that it can provide. For example, the volume of fossiliferous rock deposited is known to vary through time (due to tectonic activity, changes in global sea level, etc.), thereby increasing sampling heterogeneity and undermining a simple reading of the palaeontological data (e.g. Smith 2001, 2007; Peters 2005). A thorough understanding of palaeoenvironmental biases is also necessary in order to underpin rigorous discussions of palaeoecology and macroevolution (Behrensmeyer et al. 1992).

Most attempts to determine palaeoenvironmental preferences for dinosaurs have assessed distribution within a single geological formation (e.g. Dodson 1971; Brinkman et al. 1998), a limited geographical area (e.g. Late Cretaceous North America; Horner 1979; Lehman 1987) or for supra-specific clades based on largely qualitative assessments (see chapters in Weishampel et al. 2004a). Only a few workers have attempted large-scale quantitative analyses of dinosaur palaeoenvironmental distribution at a global level (e.g. Lockley et al. 1994). We present such a study here, using a relational database of global dinosaur occurrences to test existing hypotheses of broad environmental preferences at the level of supraspecific clades. The majority of previously proposed hypotheses of palaeoenvironmental preferences in dinosaurs have focussed upon Cretaceous herbivores; we therefore limit our analyses to these taxa.

Materials and methods

Global occurrences of Cretaceous herbivorous non-avian dinosaurs were compiled as a relational database in Micro-

soft Access; data were collected from the primary literature, based upon references cited in Weishampel et al. (2004b). Additional data were obtained from more recent references and *The Palaeobiology Database* (www.paleodb.org). All Cretaceous ornithischians and sauropods, and several theropod clades (therizinosaur, oviraptorosaurs, ornithomimosaurs), are considered to be herbivorous (cf. Weishampel and Norman 1989; Barrett 2005). Taxonomic assignments generally follow Weishampel et al. (2004a, b), except where more recent information is available. Faunal information was collected for each locality and combined with data on the geological age, lithology and depositional environment, which was extracted from the primary literature (see Electronic Supplementary Material, S1; an EndNote database containing references used in compiling this database is available on request from the lead author).

Our Cretaceous dataset consists of 1,985 occurrences of herbivorous dinosaurs (an occurrence is the presence of a particular taxon at a particular locality), representing both ichnological and body fossil remains, although our dataset focusses in greater detail on the latter remains. Palaeoenvironmental data were simplified into broad categories termed ‘marine’ (136 occurrences), ‘coastal’ (225 occurrences; includes estuarine, deltaic, paralic environments, etc.) and ‘terrestrial’ (1,482 occurrences; includes fluvial, aeolian, fluviolacustrine, lacustrine environments, etc.). Although this categorisation of the data is coarse grained, it allows us to test the broad environmental preferences proposed for many supraspecific clades (e.g. Horner 1979, who discussed the apparent overrepresentation of certain clades in marine depositional environments). Occurrences lacking associated environmental data were excluded from the analyses, as were those collected from unusual or poorly defined environments that could not be assigned easily to one of the three environmental categories (e.g. cavern infills, “swamp”). This winnowed dataset contained 1,843 samples. Detailed palaeoenvironmental data were often unavailable; for example, no information beyond ‘terrestrial’ was available for 43% of occurrences, and it is possible that future sedimentological analyses will demonstrate that some of these represent more marginal, coastal environments. The accuracy of our results is therefore limited by the quality of available information in the primary literature.

Chi-squared tests (Waite 2000) were used to identify significant associations between specific dinosaurian clades (e.g. Ankylosauria) and environmental categories. Positive associations indicate that representatives of a clade are significantly overrepresented relative to those of other dinosaurian herbivores in that environment. Conversely, a negative association indicates underrepresentation of the clade in that environment relative to other dinosaurian herbivores. A positive–negative association does not imply

that a clade is only–never found in that environment; instead, it simply indicates that the number of occurrences of the clade in that environment is significantly greater–fewer than expected if all dinosaur clades are spread evenly across all environments. The lack of a significant association between a clade and an environment indicates that the faunal composition in that environment does not differ significantly from that predicted by simple probability models. Stegosaur could not be analysed separately due to small sample sizes; for similar reasons, it was not possible to conduct separate analyses for several individual subclades (e.g. Diplodocoidea, Centrosaurinae, Therizinosauoidea) although these were analysed as part of broader taxonomic categories (e.g. Sauropoda, Ceratopsia, Theropoda).

In order to assess whether conflicting signals are present in the body fossil and ichnological datasets, two different sets of Chi-squared tests were carried out. The first set of analyses focussed on the total-evidence dataset (body fossils and ichnology). The second excluded body fossil occurrences only (1,834 occurrences; 92.5%), and focussed on ichnology only (151 occurrences; 7.5%). The ichnological data are dominated by occurrences of ornithopods (57% of ichnological occurrences) and sauropods (28%), with only very rare ankylosaur, ceratopsian and stegosaur tracks. For this reason, and because footprints can generally only be assigned to relatively coarse taxonomic levels, we were only able to carry out ichnological Chi-squared tests for the clades Ornithopoda and Sauropoda. Ichnological Chi-squared tests were only carried out for ‘coastal’ and ‘terrestrial’ environments.

Results

Results are summarised in Table 1. No significant associations were discovered for the ichnological analysis. The rest of this section deals only with the results of the total-evidence analysis—this analysis identified significant ($p \leq 0.05$) associations for a number of clades.

Significant positive associations with marine environments and significant negative associations with terrestrial environments support previous qualitative suggestions that nodosaurid ankylosaur remains are more common than might be expected in marine sediments (Horner 1979; Coombs and Deméré 1996). By contrast, a positive association occurs between ankylosaurid ankylosaurs and terrestrial environments. The overall positive association between ankylosaurs and marine environments results from the numerous nodosaurid specimens found in marine sediments and the large number of marine localities yielding ankylosaur specimens—taxa that cannot be referred with confidence to either clade (Vickaryous et al. 2004; Weishampel et al. 2004b). Interestingly, many of these

Table 1 Results of the Chi-squared tests of association between depositional environments and dinosaur groups

	Marine (136)			Coastal (225)			Terrestrial (1,482)		
	χ^2	+/-	<i>p</i>	χ^2	+/-	<i>p</i>	χ^2	+/-	<i>p</i>
Ankylosauria (240)	7.46 ₍₂₈₎	+	0.006**	0.43 ₍₃₃₎	N/A	0.61	5.95 ₍₁₇₉₎	–	0.015*
Nodosauridae (90)	4.91 ₍₁₂₎	+	0.027*	2.74 ₍₁₆₎	N/A	0.098	7.98 ₍₆₂₎	–	0.005**
Ankylosauridae (79)	1.55 ₍₃₎	N/A	0.213	2.66 ₍₅₎	N/A	0.103	4.69 ₍₇₁₎	+	0.03*
Ornithopoda (ichnology) (72)	N/A	N/A	N/A	0.272 ₍₄₆₎	N/A	0.602	0.272 ₍₄₆₎	N/A	0.602
Non-hadrosaurid Ornithopoda (321)	0.03 ₍₂₃₎	N/A	0.872	11.17 ₍₅₇₎	+	0.008**	7.02 ₍₂₄₁₎	–	0.008**
Hadrosauridae (391)	43.17 ₍₅₉₎	+	<0.0001**	0.84 ₍₅₃₎	N/A	0.359	25.85 ₍₂₇₉₎	+	<0.0001**
Hadrosaurinae (111)	1.43 ₍₅₎	N/A	0.232	2.76 ₍₈₎	N/A	0.097	4.65 ₍₉₈₎	+	0.031*
Lambeosaurinae (59)	0.61 ₍₃₎	N/A	0.436	1.03 ₍₅₎	N/A	0.311	1.41 ₍₅₁₎	N/A	0.236
Pachycephalosauria (69)	5.71 ₍₀₎	–	0.017*	1.65 ₍₅₎	N/A	0.199	6.93 ₍₆₄₎	+	0.008**
Ceratopsia (353)	32.17 ₍₁₎	–	<0.0001**	1.65 ₍₃₆₎	N/A	0.2	22.99 ₍₃₁₆₎	+	<0.0001**
Chasmosaurinae (113)	7.43 ₍₁₎	–	0.006**	0.004 ₍₁₄₎	N/A	0.952	3.05 ₍₉₈₎	N/A	0.081
Sauropoda—ichnology only (27)	N/A	N/A	N/A	0.8 ₍₉₎	N/A	0.8	0.8 ₍₁₈₎	N/A	0.8
Sauropoda—total evidence (354)	1.34 ₍₂₁₎	N/A	0.247	4.87 ₍₃₁₎	–	0.027*	6.68 ₍₃₀₂₎	+	0.0097**
Macronaria (190)	3.11 ₍₈₎	N/A	0.08	14.36 ₍₇₎	–	0.0002**	18.38 ₍₁₇₅₎	+	<0.0001**
Herbivorous theropods (94)	4.00 ₍₂₎	–	0.046*	2.1 ₍₇₎	N/A	0.148	6.35 ₍₈₅₎	+	0.012*

Results that are significant at the 95% level ($0.01 < p < 0.05$) are marked by an asterisk; results that are significant at the 99% level ($p < 0.01$) are marked by a double asterisk. The table is divided into results for “marine”, “coastal” and “terrestrial” (sample size for each environment given in brackets) and the major dinosaur groups of interest (sample size for each group given in brackets). Within each of these subdivisions, three columns give the χ^2 value (number of occurrences of that dinosaur group in that environment indicated as subscript), whether the association (if significant) is negative or positive and the *p* value. Degrees of freedom for all tests=1.

latter specimens were previously assigned to Nodosauridae: e.g. *Texasetes pleurohalio* (Coombs 1995; Carpenter 2001), *Niobrariasaurus coleii*, “*Hierosaurus sternbergi*” and other Niobrara Chalk specimens (Carpenter et al. 1995) and *Antarctopelta* (Gasparini et al. 1996; but see Salgado and Gasparini 2006). A recent comprehensive phylogenetic analysis of Ankylosauria supports referral of *Texasetes* and *Niobrariasaurus* to Nodosauridae (Parish 2005). Reassignment of these specimens to Nodosauridae results in the identification of an even stronger positive association between ‘marine’ environments and nodosaurids ($\chi^2 = 19.16$, $p < 0.0001$). Only three occurrences of ankylosaurids in marine sediments are included in the database, but all are problematic; these occurrences include two specimens of *Minmi* in Australia (Molnar 1980, 1996) and the only known occurrence of *Aletopelta* in California (Coombs and Deméré 1996; Ford and Kirkland 2001). None of these occurrences can be incontrovertibly assigned to Ankylosauridae: *Minmi* has been considered the sister taxon of all other ankylosaurs by Kirkland (1998) and Carpenter (2001), while *Aletopelta* has been considered an ankylosaurid by Ford and Kirkland (2001) but a nodosaurid by Coombs and Deméré (1996) and an indeterminate ankylosaur by Vickaryous et al. (2004) and Parish (2005). When these three occurrences are completely removed from the dataset, a significant negative association between ankylosaurids and ‘marine’ environments is recovered ($\chi^2 = 6.57$; $p = 0.01$).

Non-hadrosaurian ornithopods are significantly positively associated with coastal deposits and significantly negatively associated with terrestrial deposits; a significant negative association with terrestrial deposits is also present in hadrosaurid ornithopods, which additionally show a significant positive association with marine deposits. Both groups of marginocephalian ornithischians (Pachycephalosauria, Ceratopsia) show significant negative correlations with marine environments and positive correlations with terrestrial environments.

Sauropods in general are significantly negatively correlated with coastal environments and positively associated with terrestrial environments; these associations hold at the less-inclusive taxonomic level of Macronaria. Herbivorous theropods are in general significantly negatively correlated with marine deposits and positively associated with terrestrial deposits.

Discussion

Ankylosauria

The significant negative association between nodosaurid ankylosaurs and marine environments cannot be easily explained by taphonomy and/or selective transportation: although nodosaurids may have been prone to post mortem ‘bloat and float’ scenarios (which might increase their

frequency in marine sediments), this should also have been true for their sister clade, Ankylosauridae, which contains animals built to the same basic *bauplan* and that are similar in size and mass to nodosaurids. Likewise, although amphibious habits have been previously proposed for nodosaurids (Mehl 1936), there is no anatomical evidence in favour of this hypothesis (Coombs and Deméré 1996). Instead, it is more likely that the statistical association between nodosaurids and marine sediments reflects a genuine palaeoecological signal, with two potential, although not mutually exclusive, explanations: (1) nodosaurids inhabited a broader range of palaeoenvironments than did their sister clade ankylosaurids, including coastal and shoreline habitats in addition to inland terrestrial environments (Coombs and Deméré 1996); (2) nodosaurids occurred preferentially (relative to ankylosaurids and other contemporaneous herbivores) in fluvial environments and were thus more prone to transport into marine sediments. Distinguishing between these alternatives requires finer-grained analyses that are beyond the scope of this paper; however, in either case, our results provide evidence for broad-scale habitat partitioning within Ankylosauria.

Ornithopoda

The suggestion of Horner (1979) that hadrosaurid remains are overrepresented in Cretaceous marine sediments relative to most other dinosaurian clades is supported by this analysis; as with ankylosaurs, we interpret this overrepresentation as a palaeoecological signal providing further evidence that many hadrosaurid taxa were most abundant in coastal plain environments (e.g. Horner et al. 2004) and/or suggesting that the group preferentially inhabited fluvial environments. The absence of significant association between either hadrosaurine or lambeosaurine hadrosaurids and marine deposits may be due to taphonomy; most hadrosaurids recovered from marine deposits are fragmentary and cannot be assigned with confidence to either clade. We find no statistical evidence to support the hypothesis of Horner (1979) that hadrosaurines are more common than lambeosaurines in marine sediments and had more coastal habitat preferences; by contrast, our results indicate a weak positive association between hadrosaurines and terrestrial environments, although it is plausible that this signal might be also taphonomic (better preservation of hadrosaurid fossils in terrestrial sediments allows more ready identification of fossils to the level of Hadrosaurinae or Lambeosaurinae). The identification of a positive association between non-hadrosaurid ornithopods and coastal depositional environments suggests that coastal plain environmental preferences may be a plesiomorphic palaeoecological signal for Ornithopoda as a whole, rather than a novel feature of hadrosaurids. Nevertheless, it should also be recognised

that some ornithopods occur in inland terrestrial settings, suggesting that the clade had a wide range of habitat preferences, even if they were significantly more abundant in coastal environments. The absence of significant associations for the ornithopod ichnological record may reflect the small size and/or the coarse-grained nature of the ichnological dataset—ornithopod footprints are often difficult to distinguish from those of contemporaneous theropods, as well as from other functionally tridactyl herbivores (e.g. pachycephalosaurs, basal ceratopsians; Olsen and Rainforth 2003). Moreover, it is not possible to consistently identify footprints belonging to less-inclusive taxonomic levels of Ornithopoda—e.g. it is not possible to carry out analyses of the hadrosaur ichnological record.

Marginocephalia

The palaeoenvironmental preferences of pachycephalosaurs were discussed by Dodson (1971) and Maryńska et al. (2004); they concluded that pachycephalosaurs generally inhabited inland environments, more distal to the coastal environments favoured by contemporaneous ornithischians. The results of this analysis are consistent with that hypothesis, identifying a positive association of pachycephalosaurs with fully terrestrial environments and a negative association with marine depositional environments, although there is no significant association with coastal environments. Similar associations are recovered for the sister group of Pachycephalosauria, Ceratopsia. Our results for Ceratopsia differ from some recent work that has suggested coastal plain habitat preferences in this group (e.g. Brinkman et al. 1998)—we find that ceratopsians are neither underrepresented or overrepresented in coastal environments, although like pachycephalosaurs they are significantly underrepresented in marine deposits. We know of no obvious taphonomic reason to expect pachycephalosaurian and ceratopsian fossils to be underrepresented in marine sediments (in fact, fossils of these clades are almost completely unknown in marine deposits), and we interpret this underrepresentation as a genuine palaeoecological signal indicating more distal, or inland (away from channels), palaeoenvironmental preferences for these clades when compared to contemporaneous clades such as Nodosauridae and Hadrosauridae.

Saurischia

Lockley et al. (1994) demonstrated, on the basis of a whole Mesozoic dataset, that sauropod ichnofossils are strongly associated with low-latitude carbonate deposits, in either coastal carbonate platform settings or lacustrine environments. Our database partially confirms this result: 32% of the Cretaceous sauropod ichnological record is found in coastal environments, as compared to only 7% of the

Cretaceous sauropod body fossil record. However, our statistical analysis of the ichnological data does not find that sauropod trackways are overrepresented in coastal environments relative to trackways of other herbivorous groups (Table 1). Analysis of the total-evidence dataset recovers a positive association between sauropods and terrestrial environments, which supports previous hypotheses of inland environmental preferences for the clade (e.g. Lehman 1987; Hunt et al. 1994). Therefore, body fossil evidence suggests more distal, or inland (away from channels), palaeoenvironmental preferences for sauropods, at least during the Cretaceous, when compared to contemporaneous clades such as Nodosauridae and Hadrosauridae. Sauropod footprints indicate that sauropods undoubtedly did enter coastal palaeoenvironments on occasion—preservation potential for footprints in coastal environments may have been higher than in contemporaneous inland habitats.

The positive association between herbivorous theropod clades and terrestrial environments is suggestive of inland environmental preferences—perhaps unsurprising given that virtually all known occurrences of these clades are from fluvial and aeolian deposits in Asia and North America (Weishampel et al. 2004a, b).

Conclusions

Analysis of palaeoenvironmental preferences in Cretaceous herbivorous dinosaurs reveals clear, statistically significant patterns in the broad-scale habitat preferences of most major clades, though it should be noted that no dinosaur clade is restricted exclusively to any particular environment. Future work should aim to determine whether such patterns hold at more restricted spatial or temporal scales. Such patterns can potentially offer useful information on the palaeoecology and palaeobiology of these animals (e.g. niche partitioning, preferred vegetation types, etc.). In addition, this study demonstrates the utility and potential of large datasets in palaeobiological analysis, which in this case provided quantitative tests for existing palaeoecological hypotheses (which were previously based almost entirely on qualitative data).

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