



ECOLOGICAL SEGREGATION OF THE LATE JURASSIC STEGOSAURIAN AND IGUANODONTIAN DINOSAURS OF THE MORRISON FORMATION IN NORTH AMERICA: PRONOUNCED OR SUBTLE?

*John R. Foster**

*Curator of Paleontology
Museum of Western Colorado
P.O. Box 20000
Grand Junction, Colorado 81502-5020

jfoster@westcomuseum.org

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ABSTRACT

The Upper Jurassic Morrison Formation of western North America has yielded a number of specimens assigned to the ornithischian dinosaurs *Stegosaurus* and *Camptosaurus*, and many of these specimens come from channel sandstone deposits. Six new specimens are recorded mostly from channel sandstones as well. Indeed, early analyses of site occurrences (reducing the effects of large single-site samples) suggested that *Stegosaurus* and *Camptosaurus* were more often found in channel sandstone deposits than other common Morrison Formation dinosaurs such as *Camarasaurus* or *Diplodocus*. This also indicated the possibility of ecological segregation of the former two genera from other herbivorous dinosaurs of the Morrison. Revisiting this question with additional data suggests the pattern may not be as strong as it once appeared. Analysis of occurrence data indicates that *Stegosaurus* and *Camptosaurus* occur in channel sandstone deposits slightly more frequently than the two sauropods, but statistical analysis of this pattern by either localities or individuals indicates little significance to the trend. However, *Camptosaurus* appears more strongly associated with channel sandstone deposits relative to other dinosaurs than does *Stegosaurus*. These results suggest that any ecological segregation of these genera was moderate, but that, if present, the segregation was more pronounced in *Camptosaurus*.

Introduction

Ecological separation and habitat preference among co-occurring species are phenomena commonly observed in modern large-vertebrate faunas (e.g. Leuthold, 1978), but such trends are more difficult to demonstrate for ancient ecosystems. One of the best-studied paleofaunas of (very) large vertebrates is that of the Morrison Formation of Late Jurassic (150 mya) age in the western United States. Analyses of this biota (e.g. Dodson *et al.*, 1980; Coe *et al.*, 1987; Foster, 2003; Farlow *et al.*, 2010) have found only hints at paleoecological trends among dinosaurs and smaller vertebrates, probably mainly due to what is truly a limited data set for these ancient rocks. However, among the potential patterns revealed by these studies, one of the most intriguing is the possibility of paleoenvironmental preference that seemingly separated the ornithischians *Stegosaurus* and *Camptosaurus*, to some degree, from other elements of the large-vertebrate fauna (Dodson *et al.*, 1980). Closer study of this question is made possible now with additional data.

The first stegosaurian dinosaurs were found in the Morrison Formation by Arthur Lakes outside Morrison, Colorado, in the 1870s (Marsh, 1877), and in subsequent years several species attributed to *Stegosaurus* were named from the Morrison Formation in Wyoming and Colorado (Marsh, 1879, 1887; Galton, 2010). Gilmore (1914) named *S. longispinus* based on a specimen from near Alcova, Wyoming, and Galton (1982) described *Stegosaurus* elements belonging to juveniles from Wyoming and Utah. The primitive stegosaur *Hesperosaurus mjosi* from the lower Morrison Formation was described and named by Carpenter *et al.* (2001); this genus was suggested to be a junior subjective synonym of *Stegosaurus* by Maidment *et al.* (2008). Galton (2010) proposed that the type species of *Stegosaurus* (*S. armatus*) be reassigned to *S. stenops*. At least thirteen additional species of stegosaurs now have been found in Jurassic to Cretaceous rocks in Asia, Africa, and Europe (Zhiming, 1990; Galton, 1991; Galton and Upchurch, 2004).

Camptosaurus was described by Marsh (1879), and several species from the Morrison Formation were named subsequently (Marsh, 1894); most of these are likely synonymous with *C. dispar* (Foster, 2003; Carpenter & Wil-

son, 2008). *Camptosaurus* has also been found in England and possibly Portugal (Galton, 1980, 2009; Norman, 2004). *Camptosaurus aphanocetes* was recently named from parts of several individuals (previously assigned to *C. dispar*) from Dinosaur National Monument in Utah (Carpenter & Wilson, 2008); the same authors also determined in a biomechanical study in the same paper that *Camptosaurus* was probably primarily quadrupedal. McDonald (2011) assigned *C. aphanocetes* to the new genus *Uteodon* and suggested that this genus was a more derived ornithopod than *Camptosaurus*. An embryonic *Camptosaurus* has also been described from the Morrison Formation at Dinosaur National Monument (Chure *et al.*, 1994).

A total of approximately 100 stegosaurs and 54 camptosaurus have been collected from the Morrison Formation so far (MNI count; see Methods). Some quarries in channel sandstones in the Morrison Formation, such as Reed's Quarry 13, contain a significant number of *Stegosaurus* and/or *Camptosaurus* specimens; this association of the two genera with channel sandstones was noted by Dodson *et al.* (1980) in their landmark paleoecological study of the Morrison Formation. Those authors suggested that a possible ecological segregation of *Stegosaurus* and *Camptosaurus* from other herbivorous dinosaurs (sauropods) of the time may account for the pattern. If the large ornithischians are more commonly found in river channel deposits (as opposed to floodplain mudstones, and more so than the sauropods), then *Stegosaurus* and *Camptosaurus* may have preferred upland habitats and were more frequently washed in to the lowland floodplain settings by way of the river channels. The current study aims to investigate this association further with the 30 years worth of additional data now available to us. Many new specimens have been collected since 1980, and we have the opportunity to study the ecological distribution of *Stegosaurus* and *Camptosaurus* with a larger data set.

Previously unreported specimens listed here include four *Stegosaurus* and two *Camptosaurus*. In the 1970s Lance Eriksen collected a fragmentary stegosaur from the Fruita Paleontological area in western Colorado, and in the 1990s Cathleen May, Tony Fiorillo, and Kelli Trujillo led excavation of an *Apatosaurus* at the Blue Mesa Reservoir in central Colorado; although it was not recognized until after preparation

of the material, two vertebrae of a *Stegosaurus* were also found in with that specimen. In the 1980s, the Museum of Western Colorado collected a 42%-complete partial skeleton of *Stegosaurus* from the lower Brushy Basin Member of the Morrison Formation, found by Harold Bollen; this specimen was approximately 3 miles east of the Mygatt-Moore Quarry in Rabbit Valley, Colorado (Bollan, 1991). In 2002, a limb bone of a juvenile *Stegosaurus* was collected from the Kings View Quarry near Fruita, Colorado (on the opposite side of the hill from Riggs Quarry 15, which produced part of the *Apatosaurus* at the Field Museum of Natural History). New *Camptosaurus* material includes a partial skeleton collected in the 1980s at the Averett locality in Rabbit Valley and a tibia and other material of a juvenile collected from Moffat County, Colorado, in 2002.

Institutional Abbreviations

MWC, Museum of Western Colorado, Fruita.

Methods

Although there is little indication of major differences in the paleobiogeographic distributions of dinosaurs within the Morrison Formation by relative abundances (Foster, 2000), paleoenvironmental distributions of taxa may demonstrate a different pattern. In an important taphonomic study of the Morrison Formation, Dodson *et al.* (1980) noted several patterns in the distributions of dinosaurs in the unit. Nearly all six of the main, abundant dinosaurs (*Camarasaurus*, *Apatosaurus*, *Diplodocus*, *Allosaurus*, *Stegosaurus* and *Camptosaurus*) occur across the whole range of major lithofacies in the Morrison Formation; each genus occurred most often in Lithofacies A (channel sandstones) but was also represented in all or most of the others. Sauropods demonstrated a particularly similar distribution among themselves. *Allosaurus* was similar to the sauropods, and *Camptosaurus* had relatively few datum points and was difficult to interpret, but *Stegosaurus* was preserved far more often in Lithofacies A (Dodson *et al.*, 1980). Also, the distribution of *Stegosaurus* on the floodplain appeared to be far more similar to that of the rhinoceros in the Pleistocene of Kenya, than were those of *Diplodocus* and *Camarasaurus*, which more

resembled the distribution of elephants (Dodson *et al.*, 1980: fig. 6). Similarly, Dodson *et al.* (1980) noted the abundance of *Camptosaurus* at sites such as Cleveland-Lloyd and Reed's Quarry 13, which otherwise preserve relatively few sauropods. These factors led the authors to suggest possible ecological segregation of *Stegosaurus* and possibly *Camptosaurus* from the sauropods of the Morrison Formation, indicating that *Stegosaurus* in particular may have inhabited drier parts of the floodplain in a mode typical of more terrestrial animals. If these animals preferred drier, upland habitats their preservation in channel sandstones may reflect an association with fluvial environments due to being washed into the lowland Morrison floodplain areas from more proximal areas. At the time of the Dodson *et al.* (1980) study the data set included up to 12 localities for each dinosaur genus (Dodson *et al.*, 1980). The genera *Stegosaurus*, *Camptosaurus*, *Diplodocus* and *Camarasaurus* are now known from between 22 and 65 localities each, providing an opportunity to look at the issue of ecological segregation again in more detail.

The current study replicated Dodson *et al.* (1980) figures 5 and 6 (the latter in part), based on updated census data, to see how the new data compare and to test whether *Stegosaurus* and/or *Camptosaurus* still show signs of ecological segregation with a multi-fold increase in minimum available data. The results of the taxon-lithofacies associations were tested statistically to determine whether differences were significant. Binomial tests were conducted with the null hypothesis that there was no statistical difference between the occurrences of the respective taxon within Lithofacies A+B versus C+D. Given the number of observed occurrences in the more abundant of the two lithofacies associations for each taxon (k, 'event'), and the total number of occurrences (N, 'trials'), the binomial result gives the probability of there being that many observed occurrences or more (assuming the probability of the k 'event' on any particular occasion is 0.5, as it would be with only two combined lithofacies categories A+B and C+D; but see below). Rejection of the null hypothesis required binomial probability results less than 5%.

Chi-square analysis of the observed and expected occurrences of all four taxa (*Stegosaurus*, *Camptosaurus*, *Diplodocus* and *Camarasaurus*) by Lithofacies A–D was conducted to determine

if any taxon is significantly associated with any one lithofacies. The null hypothesis was that given the total numbers of sites in each lithofacies, and given the total numbers of each taxon, the genera occurrences in respective settings would be close to expected values. Given the number of observed occurrences of each taxon in each lithofacies, the chi-square test returns a number (X^2 , calculated from the differences between observed and expected values of each taxon-lithofacies association) that is compared to a critical value for the number of degrees of freedom. Chi-square results greater or lesser than the critical value at the $p=0.05$ or $p=0.95$ level, respectively, would reject the null hypothesis and suggest that at least one taxon is significantly more associated with a particular lithofacies than are the others. Binomial and Chi-square analyses of data were conducted in Excel and on the Vassar College math department website.

The project surveyed 289 quarries in the Morrison Formation, 159 of which contained one or more of the four genera being studied. Specimen counts for *Stegosaurus*, *Camptosaurus*, *Camarasaurus* and *Diplodocus*, along with locality counts and lithofacies data, were updated from census data in Foster (2003, 2007). Specimen counts were minimum number of individuals (MNI); in the case of multiple elements of disarticulated and disassociated skeletons in one quarry, counts were based on repetition of skull, limb, or girdle elements of the same side. Axial element samples were rarely large enough to indicate multiple individuals with certainty, but even without element overlap, a significant size difference between bones (i.e., presence of juvenile elements) was taken as a separate individual or individuals. All analyses were performed on locality occurrences, however, in order to minimize taphonomic and sampling effects. Lithofacies characterizations used the A-D system of Dodson *et al.* (1980) as summarized in Foster (2003, table 2).

Ornithischian taxa included in this analysis include species assigned to *Stegosaurus* (except *S. (Hesperosaurus) mjosi*), and those assigned to *Camptosaurus*. *Uteodon aphanocetes* (McDonald, 2011) is included within the counts of *Camptosaurus* in order to facilitate comparison with Dodson *et al.* (1980) and is not necessarily meant to imply rejection of the new assignments of those specimens; that, of course, is not

in the scope of this study. *Camptosaurus* and specimens assigned to *Uteodon* are morphologically rather similar overall, regardless of the potential systematic significance of their differences, and are here regarded as likely ecologically similar enough to each other to be compared collectively versus *Stegosaurus* and the sauropods.

In any analysis of this type, there are some assumptions that are unavoidable. The first in this case is that the channel lithofacies (A, fluvial along with B) are not significantly more time-averaged deposits than are the swampy plain to lake mudstones and limestones (C and D). Fluvial channel sandstones are naturally more time-averaged with vertebrate material than are mudstones, but splay sandstones (also A) would not be. In this study the amount of time averaging should be minimized by the fact that the occurrences are being analyzed by locality occurrences and not by MNI. A time-averaged assemblage may have more of a temporal window in which to sample a particular taxon; conceivably, however, any given site should have a reasonable chance of preserving dinosaurs of the size of the four studied here, and more time-averaged sites simply would preserve more of them. Because only occurrence or non-occurrence is being recorded for the analysis, time-averaging effects should be minimized. The vast majority of the material observed for this study lacks signs of entomological traces that would suggest longer pre-burial exposure times; most specimens seem to have been buried relatively quickly.

A second major assumption in this analysis is that the probability of taxon-lithofacies associations is equal (e.g. in the binomial analysis, that the probability of a Lithofacies A+B result versus C+D is 0.5). Of course, in looking for results that reject the null hypothesis and thus suggest that there is habitat preference that would make this probability something other than 0.5, we are testing whether or not this is true in all cases. Still, the initial assignment of a 0.5 probability to a given potential result, even in a trial with only two possible outcomes, is potentially problematic. We understandably know next to nothing, for example, about the perimortem behavior of dinosaurs in general (among the few data are those in Faux & Padian, 2007); would sick or injured dinosaurs reduce their home range and stay in (or move to) preferred areas

of their habitat, as injured elephants have been observed to do today (Woolley *et al.*, 2008)? If so, would some dinosaur species be more likely to be preserved in one habitat (lithofacies) versus another? This possibility demonstrates that the 0.5 probability assigned in the binomial analysis (above) is an assumption based solely on potential outcomes and would need to be modified if any data came to light suggesting unusual perimortem behavior in the taxa being studied.

Results

At least one specimen of one genus of the group being studied (two sauropods and two ornithischians) occurs at 159 sites in the Morrison Formation. Six new specimens of *Stegosaurus* and *Camptosaurus* are recorded here, and five of

these are from quarries in sandstone. Logging the occurrences of 385 individual specimens of the four genera at the 159 localities reveals that *Stegosaurus* is represented at 53 quarries, *Camptosaurus* at 22, *Camarasaurus* at 65, and *Diplodocus* at 34. The lithofacies occurrences for each genus are remarkably consistent, as Dodson *et al.* (1980) found, and the slightly more frequent occurrences of *Stegosaurus* and *Camptosaurus* in channel sandstone (Lithofacies A) is still apparent (figure 1). However, the pattern is somewhat different from what was found then; although these major dinosaur types are found in all paleoenvironments and channel sandstones are one of the dominant ones, drab mudstones (Lithofacies C) are far more important with the new data than they appeared originally. Lithofacies B and D are less important and preserve relatively few sites in general. Most

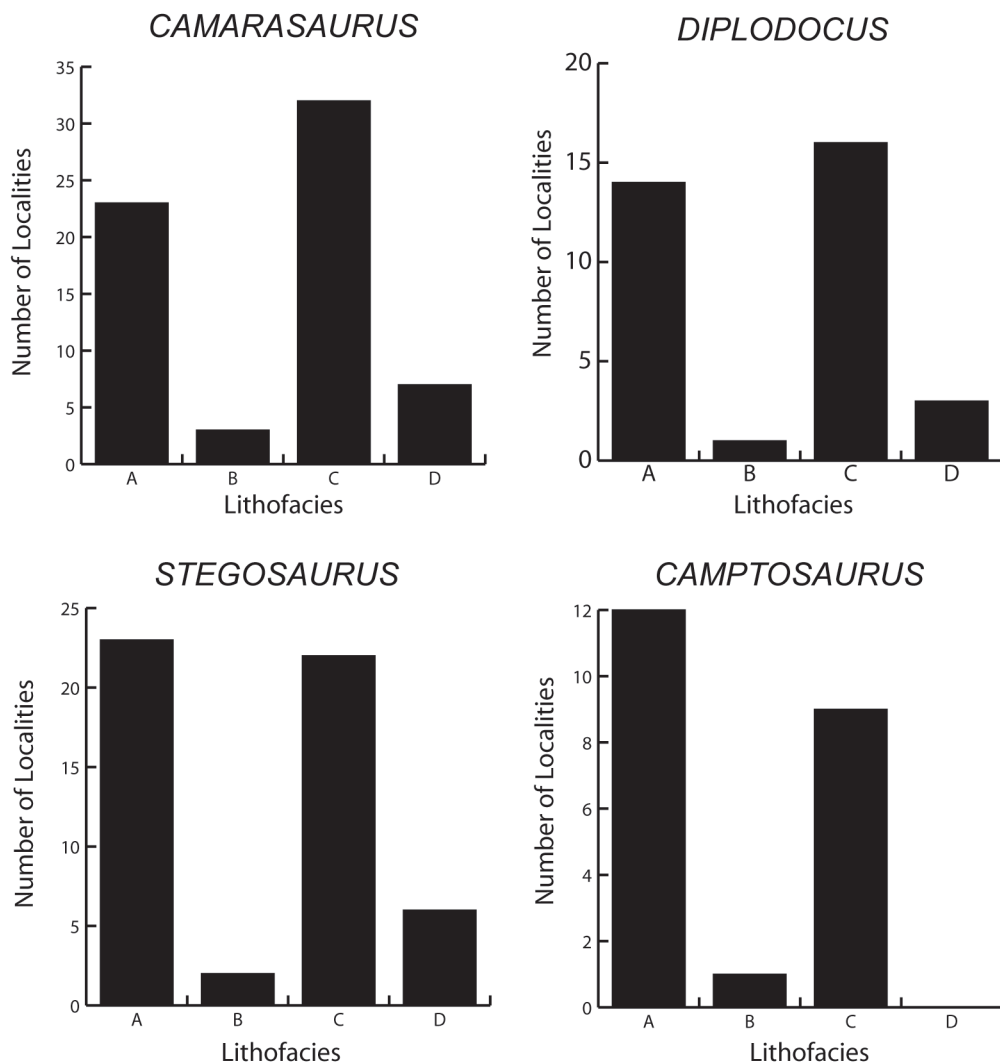


Figure 1. Occurrences of four dinosaurian genera studied here. By lithofacies of Dodson *et al.* (1980) and measured by number of localities. Same format as Dodson *et al.* (1980: figure 5), but with new data.

	<i>Stego O</i>	<i>Stego E</i>	<i>Campto O</i>	<i>Campto E</i>	<i>Cam O</i>	<i>Cam E</i>	<i>Dip O</i>	<i>Dip E</i>	<i>Totals</i>
Facies A	23	21.9	12	9.1	23	26.9	14	14.1	72
Facies B	2	2.1	1	0.9	3	2.6	1	1.4	7
Facies C	22	24.1	9	9.9	32	29.5	16	15.4	79
Facies D	6	4.9	0	2.0	7	5.9	3	3.1	16
<i>Totals</i>	53		22		65		34		174

Table 1. Data table for chi-square analysis of distributions of *Stegosaurus*, *Camptosaurus*, *Camarasaurus* and *Diplodocus* across the four lithofacies of Dodson *et al.* (1980) (A-D). Occurrences are numbers of localities. Observed numbers are fossil sample; expected values are part of the chi-square calculation based on totals of each row and column. Stego O = Observed number of localities with at least one *Stegosaurus* specimen; Stego E = *Stegosaurus* expected value; Campto O = *Camptosaurus* observed; Campto E = *Camptosaurus* expected; Cam O = *Camarasaurus* observed; Cam E = *Camarasaurus* expected; Dip O = *Diplodocus* observed; Dip E = *Diplodocus* expected. Chi-square value for the distribution is 4.68; degrees of freedom 9; critical value 16.9 at $p = 0.05$.

impressive, however, is the similarity displayed by the distributions among the four genera; there is little difference between the four, and little indication anymore that *Stegosaurus* or *Camptosaurus* are distributed differently from the sauropods (figure 1). Chi-square analysis of the locality occurrence data for the four genera across all four lithofacies (table 1) cannot reject the null hypothesis that all genera are distributed evenly across environments.

If we graph the distributions by grouped lithofacies so that A and B are together as a 'fluvial' category and C and D are combined as a 'swampy plain to lake' category we see very similar patterns between the sauropods and *Stegosaurus* (figure 2). Dodson *et al.* (1980) made this comparison in their figure 6 in order to facilitate comparisons of the Morrison fauna with that of the Pleistocene Koobi Fora Formation in Kenya. They noted that the sauropods were similar to elephant distributions in having a slightly higher percentage of fluvial occurrences (Lithofacies A and B) and that *Stegosaurus* was similar to the rhinoceros in having a dominance of fluvial occurrences, suggesting more dry-floodplain habits. We see from figure 2 that not only is *Stegosaurus* now rather similar to *Camarasaurus* and *Diplodocus* in its fluvial versus swampy plain occurrences, but that the pattern among the three is now somewhat different from what Dodson *et al.* (1980) found; the percentage occurrence of A+B versus C+D is still relatively even but the swampy plains (C+D) now have a slightly higher percentage occurrence. This is the reverse of the 1980 pattern. In this analysis, however, *Camptosaurus* does demonstrate a break from the other three genera (figure 2). Its distribution is the only one with a majority of fluvial occurrences, sug-

gesting it may have preferred drier parts of the floodplain more so than the other three genera. Binomial analyses of these four occurrences (as in figure 2), however, indicate no statistical significance to the patterns, even that of *Camptosaurus*, at the $p=0.05$ level.

Discussion

Possible reasons for the differences between the current study and that of Dodson *et al.* (1980) relate to the scales of available data and possible differences in lithofacies characterizations of newer sites. The original study included 19 localities, seven of which were primarily channel sandstone settings; of these, four were major quarries producing many individuals and a diversity of species (Bone Cabin, Reed's Quarry 13, Dinosaur National Monument, and Marsh-Felch quarries). Included in the 159 localities surveyed for this study were a much greater number of sites in drab mudstones, most often preserving one or a few individuals. In this analysis, approximately 47% of localities were in Lithofacies C, and about 38% were in Lithofacies A (Foster, 2003). By contrast, 26% of localities were in Lithofacies C and 37% in Lithofacies A in Dodson *et al.*'s (1980) data table.

The co-occurrence of the four dinosaurs studied here in the Morrison Formation overall and at many individual sites in the formation suggest that the group was part of a true living community of animals (Dodson *et al.*, 1980; Foster, 2000). Relative abundances of fossil occurrences and reconstructions of possible original populations, suggesting densities of 2-32 individuals of each genus, and of all sizes, per km² (Farlow *et al.*, 2010), also

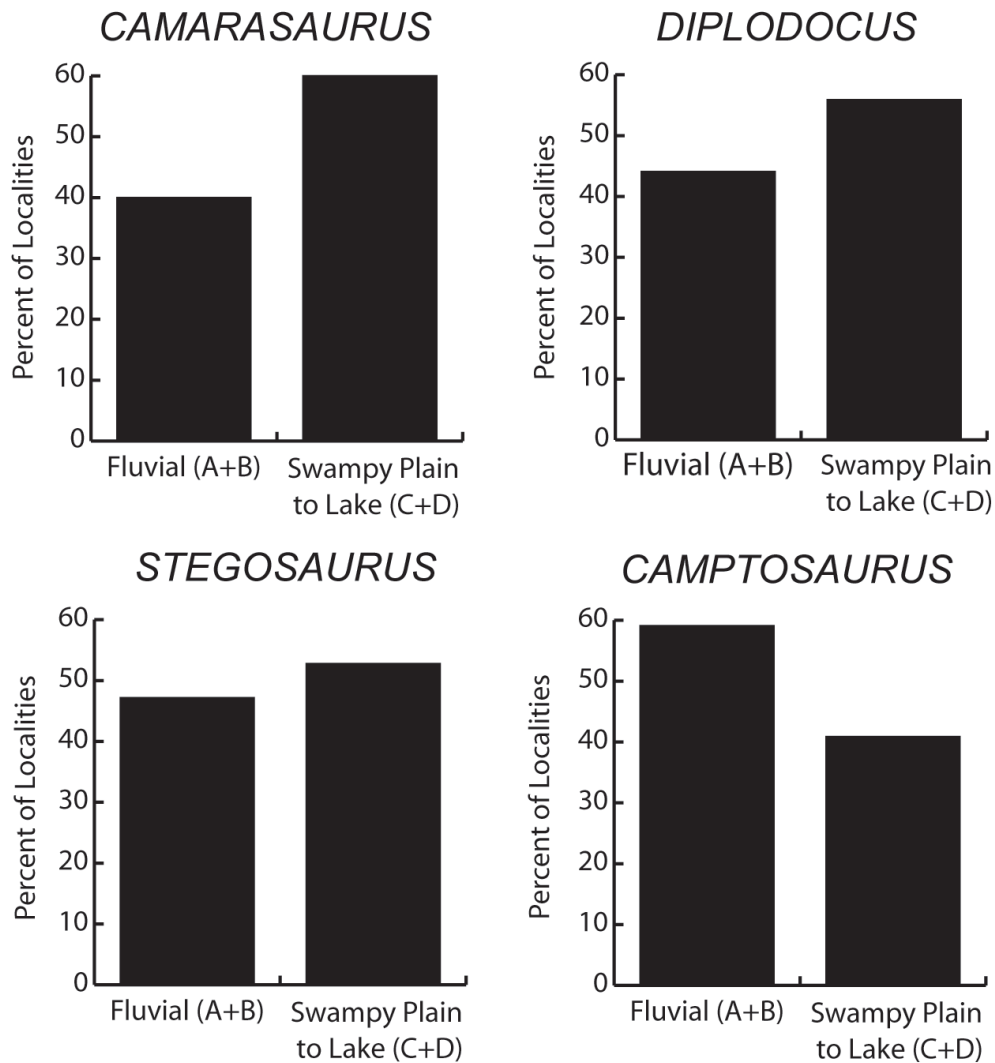


Figure 2. Occurrences of dinosaurian genera by combined lithofacies as in Dodson *et al.* (1980, fig. 6), measured by percent of localities.

suggest that the stegosaurs, camptosaurs, and sauropods were part of a consistent fauna of megaherbivorous dinosaurs in the Late Jurassic of North America. There appears to be no evidence for ecological separation of *Stegosaurus* from other large herbivores, as represented by *Camarasaurus* and *Diplodocus*. *Camptosaurus* may be more strongly associated with fluvial settings, but this evidence is equivocal (figures 1 & 2). If this trend for *Camptosaurus* was in fact present in the dinosaur fauna of the Morrison Formation, it appears to represent a subtle environmental preference, perhaps for upland areas, but not habitat separation. All four dinosaurs were preserved in the same environments and probably lived in the same areas, but *Camptosaurus* alone may have more commonly frequented areas that would preserve their carcasses in fluvial settings.

This suggests slight preferences within the same range of habitats and no longer appears to represent ecological segregation.

New Specimens: Systematic Palaeontology

Dinosauria Owen, 1842
Thyreophora Nopcsa, 1915
Stegosauridae Marsh, 1880
Stegosaurus sp. Marsh, 1877

Figures 3, 4A-D

Referred Specimens – MWC 81, partial skeleton including 1 cervical centrum, 6 dorsal centra, 35 caudal centra, 10 neural spines, 45 rib fragments, anterior blades of both ilia, left scapula, both humeri, both ulnae, both radii, 1 metacar-

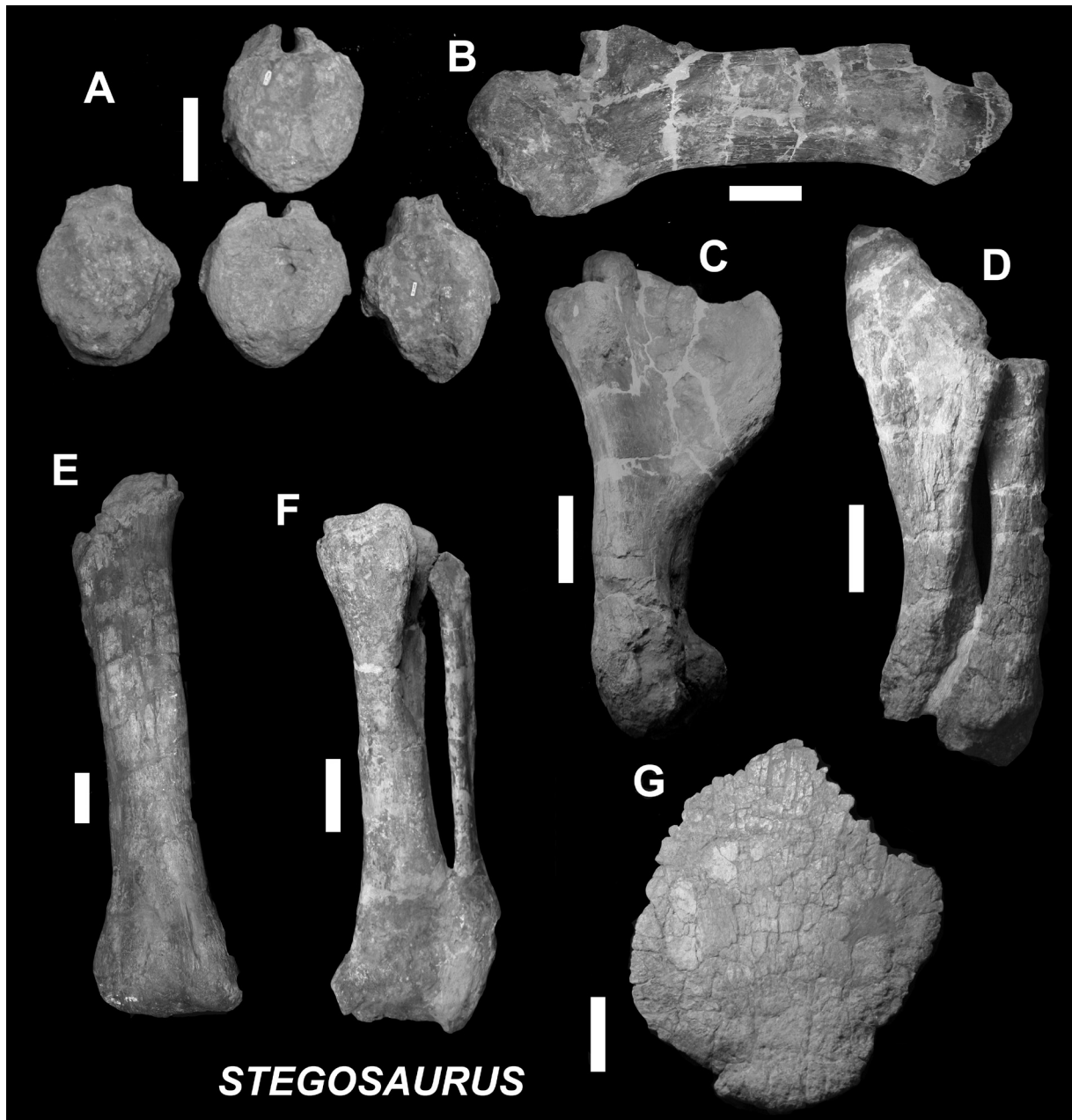


Figure 3. *Stegosaurus* sp., MWC 81, from the lower Brushy Basin Member, Morrison Formation, Rabbit Valley, Colorado. Selected elements. A) Four anterior caudal vertebrae; B) Left scapula in lateral view; C) Left humerus in medial view; D) Radius and ulna; E) Right femur in anterior view; F) Tibia and fibula; G) Dorsal plate. Scale bars = 10 cm.

pal, fragments of one pubis and one ischium, the right femur, both tibiae, both fibulae, 5 complete to partial plates, 4 tail spikes (a 5th tail spike comes from the same site but some distance away), and 2 dermal ossicles; from the Bollan Quarry, channel sandstone, ~5m above the base of the Brushy Basin Member of the Morrison Formation, Rabbit Valley, western Colorado.

MWC 5525, two caudal centra from the Blue Mesa Quarry, mudstone, Morrison Formation, Curecanti National Recreation Area, central Colorado.

MWC 7982, 4 caudal vertebrae, a pubis, rib fragments, one neural spine, and two limb elements; from the Fruita Paleontological Area, sandstone, Brushy Basin Member of the Morrison Formation, western Colorado.

MWC 5304, right tibia of juvenile from Kings View Quarry, sandstone, Brushy Basin Member of the Morrison Formation, near Fruita, Colorado.

Ornithopoda Marsh, 1881
Iguanodontia Sereno, 1986
Camptosaurus Marsh, 1885
Camptosaurus dispar (Marsh, 1879)

Referred Specimens – MWC 2, partial skeleton including predentary, both dentaries with teeth, 14 isolated teeth, 2 neural arches, caudal vertebra, partial scapula, partial femur, 3 articulated pedal digits, ungual of fourth pedal digit, and many fragments; from Averett Quarry, channel sandstone, Brushy Basin Member of

Figure 4F-I

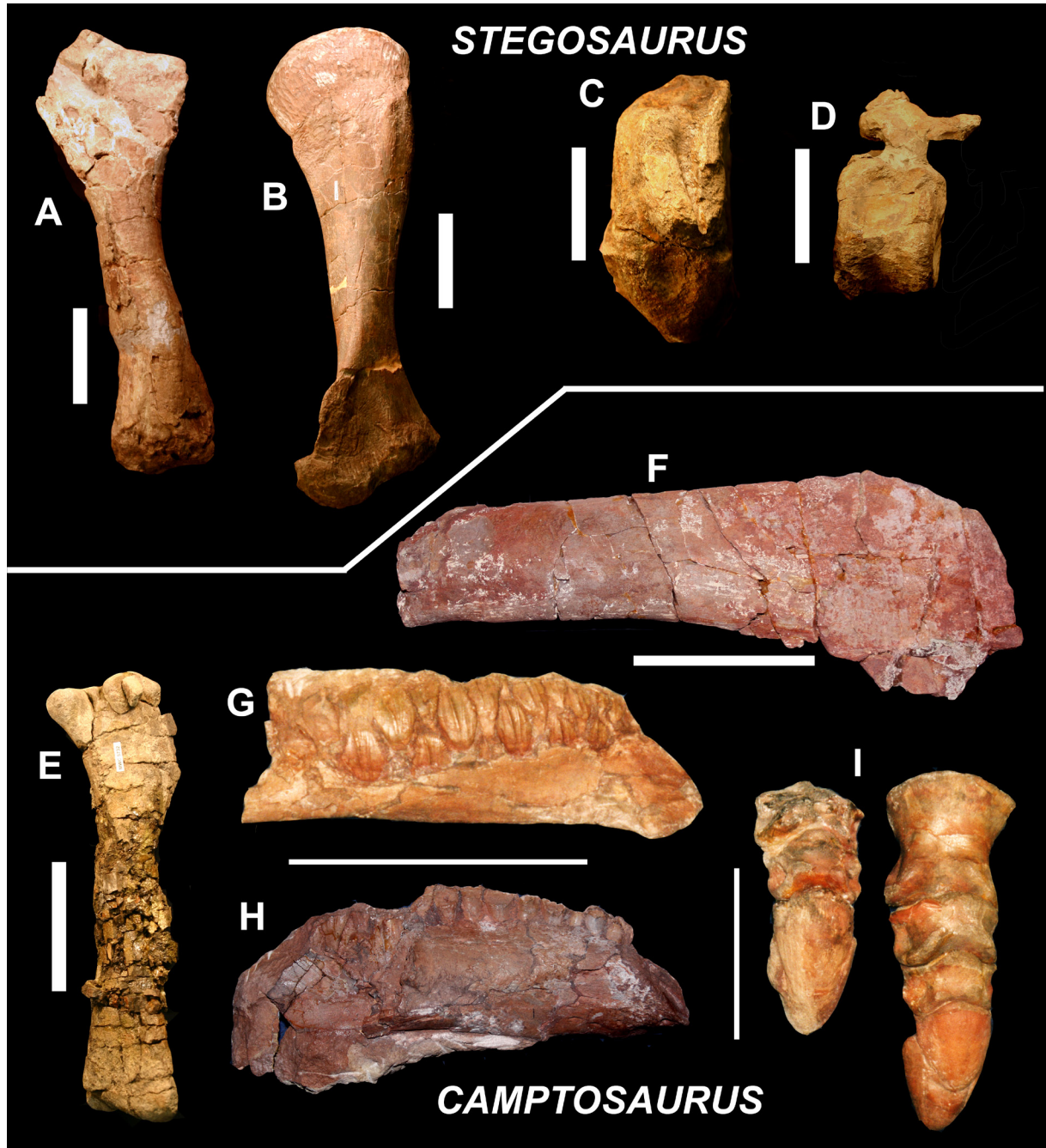


Figure 4. *Stegosaurus* and *Camptosaurus* specimens from the Morrison Formation of western Colorado. A) MWC 7982, radius of *Stegosaurus* from the Fruita Paleontological Area; B) MWC 5304, tibia of juvenile *Stegosaurus* from the Brushy Basin Member at the Kings View Quarry, near Fruita; C) MWC 5525, anterior caudal centrum of *Stegosaurus*, in right lateral view, from the Blue Mesa *Apatosaurus* Quarry at Curecenti National Recreation Area; D) MWC 5525, mid-caudal vertebra of *Stegosaurus*, in right lateral view, from same site as C; E) MWC 5732, tibia of juvenile *Camptosaurus* sp. from the Powder Ridge Quarry in Moffat County; F-I) MWC 2, *Camptosaurus dispar* from the Averett Quarry, Rabbit Valley. F) Partial left scapula; G) Lingual view of left dentary and teeth; H) Labial view of right dentary; I) Two articulated pedal digits. Scale bars = 10 cm.

the Morrison Formation in Rabbit Valley, western Colorado.

Discussion – The left scapula of MWC 2 is missing the proximal end and consists just of the shaft. The dorsal margin is straight and not bowed or convex as in *Uteodon aphanocetes*, better matching *Camptosaurus dispar*.

Camptosaurus sp.

Figure 4E

Referred Specimens – MWC 5732, right tibia; MWC 5733, right and left distal femur fragments; MWC 5734, proximal left tibia fragment; MWC 5735, pedal phalanx; MWC 5737, dorsal centrum; all associated and from the MF Amphitheater site, pebbly sandstone, Brushy Basin Member of the Morrison Formation southeast of Dinosaur National Monument, northwestern Colorado.

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Cited Literature

Bollan, H.R. 1991. The Bollan *Stegosaurus*. In: Averett, W.R. Ed. Guidebook for dinosaur quarries and tracksites tour. – Grand Junction Geological Society: 53-54.

Carpenter, K. & Y. Wilson. 2008. A new species of *Camptosaurus* (Ornithopoda: Dinosauria) from the Morrison Formation (Upper Jurassic) of Dinosaur National Monument, Utah, and a biomechanical analysis of its forelimb. – *Annals of Carnegie Museum* 76, 4: 227-263.

Carpenter, K., C.A. Miles & K. Cloward. 2001. New primitive stegosaur from the Morrison Formation, Wyoming. In: Carpenter, K. Ed. *The Armored Dinosaurs*. – Bloomington, Indiana University Press: 55-75.

Chure, D.J., C. Turner, & F. Peterson. 1994. An embryo of *Camptosaurus* from the Morrison Formation (Jurassic, Middle Tithonian) in Dinosaur National Monument, Utah. – In: Carpenter, K., K.F. Hirsch & J.R. Horner. Eds. *Dinosaur Eggs and Babies*. – New York, Cambridge University Press: 298-311.

Coe, M.J., D.L. Dilcher, J.O. Farlow, D.M. Jarzen, & D.A. Russell. 1987. Dinosaurs and land plants. – In: Friis, E.M., W.G. Chaloner & P.R. Crane. Eds. *The origins of Angiosperms and their biological consequences*. – New York, Cambridge University Press: 225-258.

Dodson, P., A.K. Behrensmeyer, R.T. Bakker & J.S. McIntosh. 1980. Taphonomy and paleoecology of the dinosaur beds of the Jurassic Morrison Formation. – *Paleobiology* 6: 208-232.

Farlow, J.O., I.D. Coroian & J.R. Foster. 2010. Giants on the landscape. Modelling the Abundance of megaherbivorous dinosaurs of the Morrison Formation (Late Jurassic, western USA). – *Historical Biology* 22: 403-429.

Faux, C.M. & K. Padian. 2007. The opisthotonic posture of vertebrate skeletons. Postmortem contraction or death throes? – *Paleobiology* 33: 201-226.

Foster, J.R. 2000. Paleobiogeographic homogeneity of dinosaur faunas during the Late Jurassic in western North America. – *New Mexico Museum of Natural History and Science Bulletin* 17: 47-50.

Foster, J.R. 2003. Paleocological analysis of the vertebrate fauna of the Morrison Formation (Upper Jurassic), Rocky Mountain region, U.S.A. – *New Mexico Museum of Natural History & Science Bulletin* 23: 1-95.

Foster, J. 2007. *Jurassic West. The dinosaurs of the Morrison Formation and their world*. – Bloomington, Indiana University Press.

Galton, P.M. 1980. European Jurassic ornithopod dinosaurs of the families Hypsilophodontidae and Camptosauridae. – *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen* 160: 73-95.

Galton, P.M. 1982. Juveniles of the stegosaurian dinosaur *Stegosaurus* from the Upper Jurassic of North America. – *Journal of Vertebrate Paleontology* 2: 47-62.

Galton, P.M. 1991. Postcranial remains of stegosaurian dinosaur *Dacentrurus* from Upper Jurassic of France and Portugal. – *Geologica et Palaeontologica* 25: 299-327.

- Galton, P.M. 2009. Notes on Neocomian (Lower Cretaceous) ornithomimid dinosaurs from England - *Hypsilophodon*, *Valdosaurus*, "*Camptosaurus*", "*Iguanodon*" - and referred specimens from Romania and elsewhere. – *Revue de Paléobiologie* 28: 211-273.
- Galton, P.M. 2010. Species of plated dinosaur *Stegosaurus* (Morrison Formation, Late Jurassic) of western USA. New type species designation needed. – *Swiss Journal of Geosciences* 103: 187-198.
- Galton, P.M. & P. Upchurch. 2004. Stegosauria. – In: Weishampel, D.B., P. Dodson & H. Osmólska. Eds. *The Dinosauria*. – Berkeley, University of California Press: 343-362.
- Gilmore, C.W. 1914. Osteology of the armored Dinosauria in the United States National Museum, with special reference to the genus *Stegosaurus*. – *United States National Museum Bulletin* 89: 1-143.
- Leuthold, W. 1978. Ecological separation among browsing ungulates in Tsavo East National Park, Kenya. – *Oecologia* 2: 241-252.
- Maidment, S.C.R., D.B. Norman, P.M. Barrett & P. Upchurch. 2008. Systematics and phylogeny of Stegosauria (Dinosauria: Ornithischia). – *Journal of Systematic Palaeontology* 6: 367-407.
- Marsh, O.C. 1877. A new order of extinct Reptilia (Stegosauria) from the Jurassic of the Rocky Mountains. – *American Journal of Science*, 3, 14: 513-514.
- Marsh, O.C. 1879. Notice of new Jurassic reptiles. – *American Journal of Science*, 3, 18: 501-505.
- Marsh, O.C. 1880. Principal characters of American Jurassic dinosaurs. Part 3. – *American Journal of Science* 3, 19: 251-259.
- Marsh, O.C. 1887. Principal characters of American Jurassic dinosaurs. Part 9. The skull and dermal armor of *Stegosaurus*. – *American Journal of Science* 3, 34: 413-417.
- Marsh, O.C. 1894. The typical Ornithopoda of the American Jurassic. – *American Journal of Science* 3, 48: 85-90.
- McDonald, A.T. 2011. The taxonomy of species assigned to *Camptosaurus* (Dinosauria: Ornithopoda). – *Zootaxa* 2783: 52-68.
- Norman, D.B. 2004. Basal Iguanodontia. In: Weishampel, D.B., P. Dodson & H. Osmólska. Eds. *The Dinosauria*. – Berkeley, University of California Press: 413-437.
- Woolley, L.A., J.J. Millsaugh, R.J. Woods, S.J. van Rensburg, R.L. Mackey, B. Page & R. Slotow. 2008. Population and individual elephant response to a catastrophic fire in Pilanesberg National Park. – *PLoS One* 3, 9: e3233.
- Zhiming, D. 1990. Stegosauria of Asia. In: Carpenter, K. & P.J. Currie. Eds. *Dinosaur systematics. Approaches and perspectives*. – New York, Cambridge University Press: 255-268.

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