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Source: Acta Palaeontologica Polonica, 59(1) : 81-98

Published By: Institute of Paleobiology, Polish Academy of Sciences

URL: https://doi.org/10.4202/app.2011.0095

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A morphometric approach to the specific separation of the humeri and femora of *Dicraeosaurus* from the Late Jurassic of Tendaguru,Tanzania

DANIELA SCHWARZ-WINGS and NICO BÖHM



Schwarz-Wings, D. and Böhm, N. 2014. A morphometric approach to the specific separation of the humeri and femora of *Dicraeosaurus* from the Late Jurassic of Tendaguru, Tanzania. *Acta Palaeontologica Polonica* 59 (1): 81–98.

The two species of dicraeosaurid dinosaurs *Dicraeosaurus*, *Dicraeosaurus hansemanni*, and *Dicraeosaurus sattleri*, have been distinguished mainly by their differences in size and geological age, as they occur in different members of the Late Jurassic Tendaguru Formation of Tanzania. Linear and geometric morphometric measurements distinguish between the humeri and femora of both species. Linear measurements and Principal Component Analysis of Thin-plate Splines reveal strong differences in size and shape between their humeri and weak differences between their femora, also supported by a Discriminant Factor Analysis. Generally, the humerus and femur of *D. hansemanni* are slightly longer and more robust than those of *D. sattleri*. Further, the humerus is shorter in relation to the femur in *D. sattleri*, related to its more distally positioned deltopectoral crest, resulting in differences in its arc of movement and mechanical power. Thus, a morphological separation between the humeri and femora of *D. hansemanni* from the Middle Dinosaur Member and *D. sattleri* from the Upper Dinosaur Member of the Tendaguru Formation can be confirmed. Morphometric comparisons of the humeri and femora of *Dicraeosaurus* with the single known humerus and femur of *Amargasaurus cazaui* reveal many shape differences between the two genera, which are especially well marked in the Thin-plate Splines analysis and affect in particular the humerus. These results suggest a closer relationship between *D. hansemanni* and *D. sattleri* than between *D. sattleri* and *A. cazaui*, and a clear separation between the two genera.

Key words: Dinosauria, Sauropodomorpha, *Dicraeosaurus*, *Amargasaurus*, morphometry, taxonomy, statistic, humerus, femur, Jurassic, Tendaguru, Tanzania.

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Received 17 August 2011, accepted 5 July 2012, available online 9 July 2012.

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Introduction

The Dicraeosauridae, an exclusively Gondwanan family of Late Jurassic and Early Cretaceous diplodocoid sauropods (Salgado and Bonaparte 1991; Rauhut et al. 2005; Harris 2006), is named for the sauropod genus *Dicraeosaurus* Janensch, 1914 from the Late Jurassic of Tendaguru (Tanzania, Eastern Africa). The Dicraeosauridae are relatively small-sized (10–13 m total body length) and short-necked sauropods with significantly high presacral, sacral and anterior caudal neural spines (Janensch 1929a; Wilson 2002; Rauhut et al. 2005) and a presumed low-browsing dietary habit (Stevens and Parrish 2005a, b).

Remains of *Dicraeosaurus* were collected, together with a plethora of other dinosaur bones, around Tendaguru hill in Tanzania by the German Tendaguru Expedition of the Institute for Palaeontology of the Humboldt University in Berlin between 1909 and 1912 (Branca 1914; Janensch 1914a; Zils et al. 1995; Heinrich et al. 2001). The locality represents a partially marine and partially limnic coastal area with tidal flats and a forested hinterland (Heinrich et al. 2001; Aberhan et al. 2002; Bussert et al. 2009) (Fig. 1). According to Janensch (1914b, 1929a, b), two species, *Dicraeosaurus hansemanni* and *Dicraeosaurus sattleri*, can be separated from each other, based on more robust hindlimbs in *D. hansemanni* and lighter and smaller vertebral centra with longer neural spines in *D. sattleri*. Additionally, both species are restricted to separate strata, *D. hansemanni* from the Middle Dinosaur Member (Late Kimmeridgian), and *D. sattleri* from the Upper Dinosaur Member (Tithonian) (Fig. 1). Because of the longer neural spines of *D. sattleri*, Salgado (1999) postulated a closer relationship of this species to the Early Cretaceous (Barremian–Aptian) dicraeosaurid *Amargasaurus* from Argentina, a view that was not widely adopted. *Dicraeosaurus* remained the only known dicraeosaurid taxon for an extended period of time, and although all dicraeosaurid taxa known

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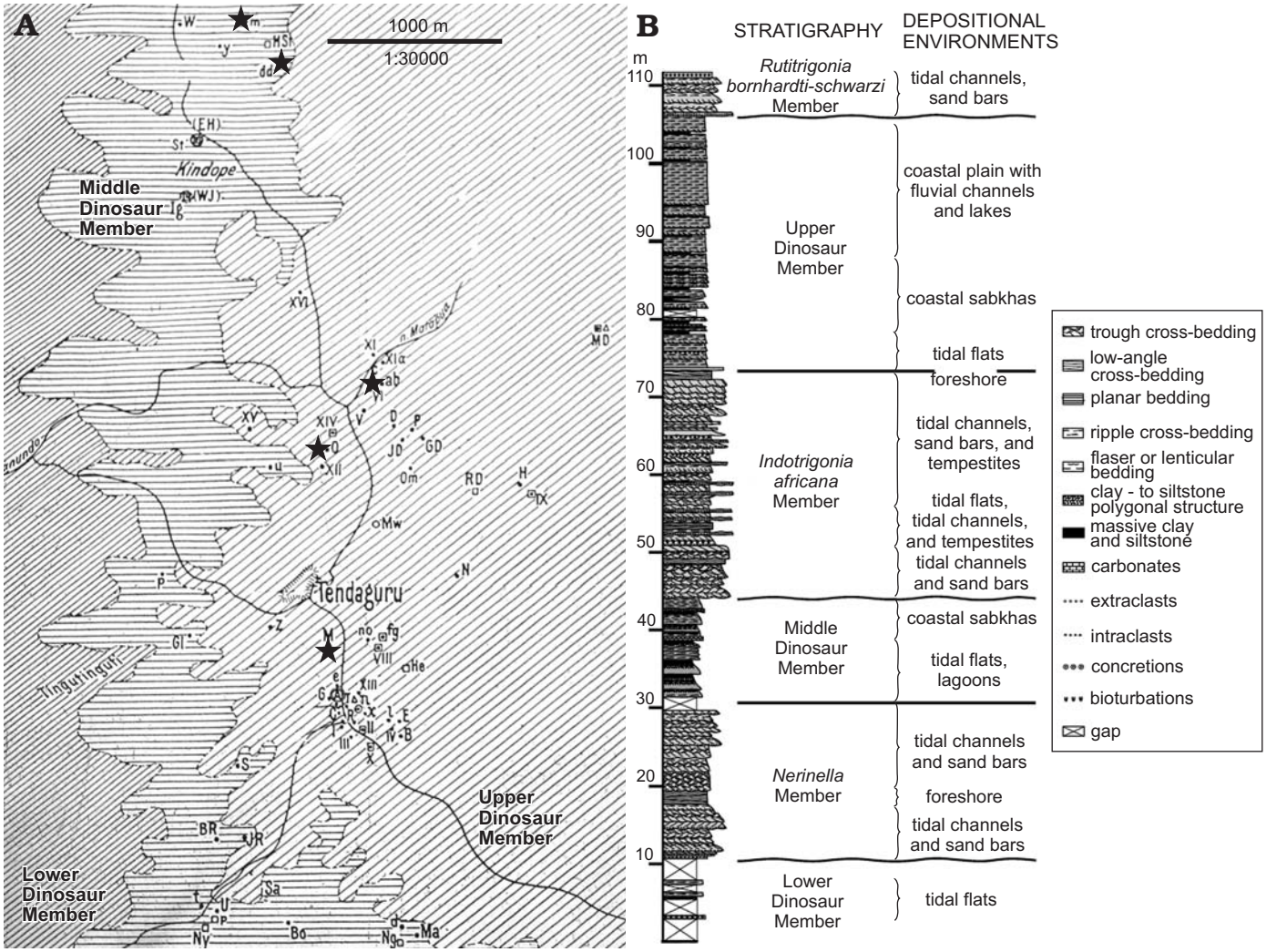


Fig. 1. Localities and stratigraphy of the excavation area in Tendaguru, Tanzania. **A**. Originally published field map with dinosaur yielding localities excavated between 1909 and 1912, slightly modified from Janensch (1929). Localities of *Dicraeosaurus hansemanni* from the Middle Dinosaur member (m, dd) and localities of *Dicraeosaurus sattleri* from the Upper Dinosaur member (ab, M, O) are marked by an asterisk. **B**. Recently published stratigraphy of Tendaguru, showing position of Middle and Upper Dinosaur members in the stratigraphic column, from Bussert et al. 2009.

today have been coded and included in recent phylogenetic analyses, the genus needs a detailed re-description and discussion of the taxonomic status of its two species with regard to the other two dicraeosaurids *Amargasaurus* Salgado and Bonaparte, 1991 and *Brachytrachelopan* Rauhut, Remes, Fechner, Cladera, and Puerta, 2005.

As indicated by Janensch (1914b, 1929b), one main difference between *D. hansemanni* and *D. sattleri* might be a difference in robustness of the hindlimbs. This study explores differences in the size and morphology of their humeri and femora by morphometric methods. Because known distal limb elements of *Dicraeosaurus* are poorly preserved, studies are restricted to humerus and femur. The only known humerus and femur of *Amargasaurus cazaui* were included in the study as the closest related taxon and because of its hypothesized close relationship to *D. sattleri* (Salgado, 1999). From the latest described dicraeosaurid *Brachytrachelopan*, no proximal limb elements are preserved completely, so this taxon is excluded.

Institutional abbreviations.—MB.R., Collection of fossil reptiles in the Museum für Naturkunde Berlin, Germany; MfN, Museum für Naturkunde Berlin, Germany; MACN, Museo Argentino des Ciencias Naturales, Buenos Aires, Argentina.

Other abbreviations.—DFA, Discriminant Factor Analysis; GI, gracility index (ratio of shaft length to shaft diameter; Taylor 2009); PC, Principal Component; PCA, Principal Component Analysis; TPS, Thin-plate Spline.

Material and methods

Material and preservation.—The dinosaur fossils from Tendaguru hill are preserved partially as articulated skeletons and partly as accumulations of smaller skeletal units or disarticulated single bones (Heinrich 1999). The type specimen of *D. hansemanni* is an articulated incomplete skeleton

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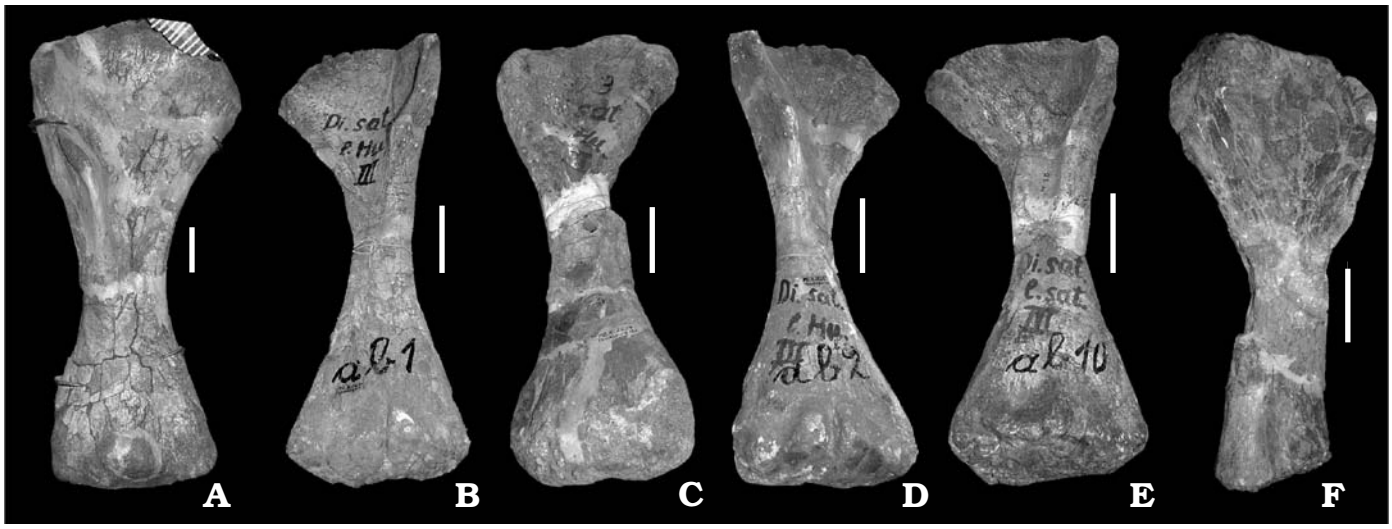


Fig. 2. Studied sample of humeri of dicraeosaurid dinosaurs *Dicraeosaurus* and *Amargasaurus* in anterior aspect. *Dicraeosaurus hansemanni* (**A**), *Dicraeosaurus sattleri* (**B**–**E**), and *Amargasaurus cazaui* (**F**). **A**. MB.R.4912, right humerus. **B**. MB.R.2631, right humerus. **C**. MB.R.2634, right humerus. **D**. MB.R.2655, left humerus. **E**. MB.R.2657, left humerus. **F**. MACN-N 15, right humerus. Scale bars 10 cm.

from the locality "m" in the Middle Dinosaur member, the most complete articulated dinosaur skeleton from Tendaguru hill (Fig. 1A). *D. hansemanni* is also represented by a large quantity of isolated skeletal elements (mostly vertebral fragments) from locality "dd" in the Middle Dinosaur member. *D. sattleri* is known from an incomplete partial skeleton from the locality "M" in the Upper Dinosaur member, as well as by further isolated remains from different localities in the Upper Dinosaur Member (Heinrich 1999) (Fig. 1A).

Five humeri and 7 femora of *Dicraeosaurus* are housed in the collection of the MfN. Material of *D. hansemanni* comprises a right humerus (MB.R.4912, field number Q11), included in the mounted skeleton "m" (MB.R.4886) of *D. hansemanni* on display in the exhibition of the MfN (Fig. 2), a right (MB.R.4886.92) and a left (MB.R.4886.93) femur belonging to the mounted skeleton "m", and two isolated right femora (MB.R.2695, field number dd3032; and MB.R.2696, field number dd3040) (Fig. 3). The humerus MB.R.4912 is well preserved, but shows some fractures and cracks in the surface of the compacta. Although parts of its deltopectoral crest seem to be displaced medially and are distally modelled with plaster, the overall preservation of this bone is good enough for a comparison. Landmarks and surface structures in the four femora of *D. hansemanni* are better preserved than in the three femora of *D. sattleri* (see below). The exception is a lateral displacement of the femoral shaft in MB.R.2695 and MB.R.2696, and in particular the medial curvature of the shaft of MB.R.2696. MB.R.4886.92 and MB.R.4886.93 have smooth ends and are polished. The 4th trochanter of MB.R.4886.93 is displaced to the medial margin of the shaft. Because both MB.R.4886.92 and MB.R.4886.93 belong to one skeleton, these two bones are counted as one and any differences measured are considered preservational. For the comparisons, all values from these two femora were added and divided by 2 for the total mean values.



Fig. 3. Studied sample of femora of dicraeosaurid dinosaurs *Dicraeosaurus* in posterior aspect. *Dicraeosaurus hansemanni* (**A**, **B**), *Dicraeosaurus sattleri* (**C**–**G**), and *Amargasaurus cazaui* (**H**). **A**. MB.R.4886.92, right femur. **B**. MB.R.4886.93 left femur. A and B belong to the mounted skeleton "m". **C**. MB.R.2695, right femur. **D**. MB.R.2696, right femur. **E**. MB.R.2697, right femur. **F**. MB.R.2638, left femur. **G**. MB.R.2915, left femur. **H**. MACN-N 15, left femur. Scale bars 20 cm.

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Material of *D. sattleri* comprises two right (MB.R.2631, field number ab1; and MB.R.2634, field number O3), and two left (MB.R.2655, field number ab2; and MB.R.2657, field number ab10) humeri (Fig. 2), and one right (MB.R.2697, field number M1) and two left (MB.R.2638, field number O2; and MB.R.2915, field number M1) femora (Fig. 3). The humerus MB.R.2634 is badly preserved and most of its surface structures, especially its actual deltopectoral crest and the lateral and the medial ridge, are lost. The femoral heads of MB.R.2638 and MB.R.2697 have strongly reduced surface marks (such as vertical notches around the femoral head or the rugosity of the proximal articular area) and are more or less polished and fractured, resulting in a different shape than the femoral head of MB.R.2915. The femoral condyles are only well preserved in MB.R.2697, whereas they are anteriorly and posteriorly partly lost in MB.R.2915 and MB.R.2638. Consequently, the evaluation of mean values for the femora *D. sattleri* is problematic, thanks to the damage.

The left humerus *Amargasaurus cazaui* (MACN-N 15) (Fig. 2F) possesses surface structures that are mostly fragmented but, except a lost medial shaft, most of the bone is preserved. The left femur (Fig. 3H) shows some fractures and is slightly anteroposteriorly compressed. Exceptions are the mostly polished and thus lost proximal articulation surface, the femoral head, which also misses surface structures, and a part of the medial end, which is reconstructed on the bone in plaster.

In addition to *A. cazaui*, a complete and well preserved humerus (MB.R.2911) and femur (MB.R.2633) of *Giraffatitan brancai* (ex "*Brachiosaurus*" *brancai*, see Taylor 2009) were used for the TPS and PCA to check the significance of potential differences in the humeri and femora of *Dicraeosaurus*. Each taxon sample was tested first intraspecifically, then intragenerically, and then combined in a reference shape to be tested against *Giraffatitan* and *Amargasaurus*. Because of the small group sizes for *Dicraeosaurus*, sample size had been extended further for the DFA to include more groups (see below). Additional bones comprised the well preserved humeri MB.R.2181.73, MB.R.2181.74, MB.R.2658, MB.R.2674, MB.R.2679, MB.R.2680, MB.R.2681, MB.R.2682, MB.R.2683, MB.R.2684, MB.R.2910 of *Giraffatitan brancai*, and the femora MB.R.2181.83, MB.R.2633, MB.R.2640, MB.R.2668, MB.R.2693, MB.R.2694, MB.R.2699, MB.R.2914, MB.R.2916, and MB.R.5016 of *Giraffatitan brancai*; MB.R.2672 and MB.R.2673, two humeri of *Tornieria africana* (Remes 2006), the humeri MB.R.2632, MB.R.2639, MB.R.2642, MB.R.2643, MB.R.2646, MB.R.2649, MB.R.2650, MB:R.2652, MB.R.2653, MB.R.2656, and MB.R.2709 and the femora MB.R.2637, MB.R.2641, MB.R.2660, MB.R.2661, MB.R.2662, MB.R.2663, MB.R.2665, MB.R.2666, MB.R.2667, MB.R.2670, MB.R.2671, MB.R.2685, and MB.R.2700; all originally attributed to "*Barosaurus*" (Janensch 1961).

Measurements.—Bones were measured with a tape measure for the linear morphometric comparisons. All measurements of *Dicraeosaurus* and *Giraffatitan* were taken by NB, those of *Amargasaurus* by DSW. The bending angle of the humeral deltopectoral crest was documented by a set square. It is important to mention that there were only three (anterior) or four (posterior) humeri of *D. sattleri* and one humerus of *D. hansemanni* humerus available for measurements, so especially in the case of the humerus of *D. hansemanni* it is not absolutely clear how much minor diagenetic effects altered its representative shape.

For the geometric morphometric measurements, bones were photographed with a digital camera, with all of them positioned in the same distance and orientation to the camera focus. Landmarks were taken for the anterior and posterior face of the humeri and the posterior face of the femora (Fig. 4). Landmarks from the anterior face of the femora presented no supplements to the posterior landmarks and therefore were abandoned. The humerus MB.R.2634 (*D. sattleri*) was excluded from the anterior landmarks of the humeri because of its badly preserved deltopectoral crest. The femur MB.R.2915 (*D. sattleri*) was excluded from the geometric morphometric analysis because of the loss of its distal condyles. An artificial long axis for the femora, extend-

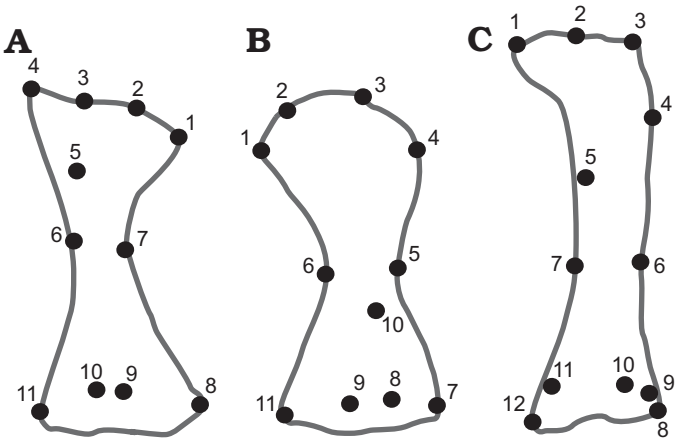


Fig. 4. Landmark positions used for the bones of *Dicraeosaurus* and *Amargasaurus*. **A**. Left humerus in anterior aspect, 1. and 4. maximum width of proximal extremity, measured on medial and lateral margin of proximal extremity; 2. and 3. latero-medial width of articular surface of humeral head (3. is also proximal border of deltopectoral crest); 5. peak (highest elevation) of deltopectoral crest; 6. and 7. medial and lateral margin of shaft at distal end of deltopectoral crest; 8. and 11. maximum width of distal extremity, measured on medial and lateral margin of distal extremity; 9. distal medial ridge; 10 distal lateral ridge. **B**. Left humerus posterior aspect. 1. and 4. maximum width of proximal extremity, measured on medial and lateral margin of proximal extremity; 2. and 3. latero-medial width of articular surface of humeral head ; 5. and 6. minimum shaft diameter measured at the medial and lateral margin of the shaft; 7. and 11. maximum width of distal extremity, measured on medial and lateral margin of distal extremity; 8–10. boundary of olecranon fossa. C. Left femur posterior aspect. 1. medial margin of femoral head; 2. lateral margin of femoral head; 3. greater trochanter; 4. lesser trochanter (lateral end); 5. peak (maximum elevation) of 4th trochanter; 6. and 7. minimum shaft diameter measured at the medial and lateral margin of the shaft (7. is also distal end of 4th trochanter); 8. and 12. maximum width of distal extremity, measured on medial and lateral margin of distal extremity; 9. centre of fibular condyle; 10. maximum elevation of lateral condyle; 11. maximum elevation of tibial condyle.

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ing from the base of the femoral head over the 4th trochanter as far as the intercondylar fossa, was used for checking if the landmarks were set correctly. With the help of this axis, the orientation and twisting of the femoral shaft could be detected and potential compression was revealed.

Numerical analysis.—Digitisation was done in the program tpsDig (Rohlf 2008), which allowed also saving of landmarks as coordinates in a two-dimensional plane to be used for Thin-plate Splines (TPS) and Principal Components Analysis (PCA). To attain similar landmark positions for all bones, the landmark positions of all left bone elements (MB.R.4886.93, MB.R.2631, MB.R.2657, and MB.R.2915) were entered mirror-reversed in tpsDig. The single images were then merged into groups with tpsDig, and a mean value for the landmark positions of the single bones was calculated with TpsSuper (Rohlf 2004b). Mean values allowed building reference shapes for the humeri and femora of *D. sattleri* and *D. hansemanni* for use in the following comparisons.

TPS were performed with the tpsSplin program (Rohlf 2004a). In a TPS, landmarks of a comparison object are positioned above a reference shape by Procrustes superimposition. Then, the landmarks of the reference shape are displaced to the position of the corresponding landmark of the object. TpsSplin calculates then the needed bending energy (i.e., the theoretical energy consumption, if the landmarks of the reference shape were on a thin flexible plate deformed into the shape of the comparison object) and the Procrustes distance between the correlated landmarks (i.e., the distance between two points in Kendall's shape space, given here as the sine value of the angle of the geodesic distance) (Bookstein 1991; Birch 1997; Bonnan 2004, 2007; Zelditch et al. 2004; Slice 2005). The TPS analysis can also be performed using TPSRelw (Rohlf 2010), which has the advantage of allowing export of the partial warp scores for use in other statistics programs and yielded essentially similar results as tpsSplin. Nevertheless, in the case of this analysis, tpsSplin proved to be better suited for the analysis of shape changes than TPSRelw. After the export of partial warp scores via TPSRelw, SPSS 17.0 (2008) was used for a MANOVA to test for potentially significant differences between both groups. For the humeri and femora of *Dicraeosaurus* and *Amargasaurus* all X coordinates (X1–X9, Uniform X) of the partial warps were compared between each other as variables, and the same was repeated with the Y.

To test by TPS if the shape differences are sufficient to separate the investigated bones of both *Dicraeosaurus* taxa or if they are mainly artificial (e.g., caused by diagenetic processes), each humerus and femur was compared to a reference shape humerus of the same and one of the other species. Differences between *D. sattleri* and *D. hansemanni* would be indicated by a higher shape difference to the other than to the same species. Because only one humerus of *D. hansemanni* is known, the humeri of *D. sattleri* were compared to their own species reference shape and the humerus of *D. hansemanni* was compared only to the reference shape of *D. sattleri*. An additional test of the hypothesis of shape differences between the humeri and femora of *Dicraeosaurus* was their comparison to another sauropod taxon, for which the macronarian *Giraffatitan brancai* was chosen. In a case where MB.R.2911 and MB.R.2633 show the same degree of difference from the reference shape as the single humeri and femora of *D. hansemanni* and *D. sattleri*, the TPS analysis is regarded as ambiguous in terms of a shape difference between the two *Dicraeosaurus* species. Another test with the phylogenetically closest relative *Amargasaurus* was made to evaluate potential morphometric similarities and differences in these long bones. For these calculations, the landmark positions of both *Dicraeosaurus* species were re-calculated to fit those of *A. cazaui* (taken later and by DSW instead of NB), so that their values differ slightly from those of the first calculation. However, the relationships between the different landmarks were not changed so that the results of these tests are comparable.

The programs CordGen6 and PCAGen6 (Sheets 2004) were used to transfer the landmark data into CS data format and to perform the PCA. The PCA was conducted to show how much the single objects differed from each other and the importance and dimension of each variation. The PCs are depicted as straight lines, which pass through the shapes of the superimposed single bones in a way that their strongest deviating opposite landmarks have exactly the same distance to the straight line. The PCs are the eigenvectors of the changed Principal Warps variance/covariance matrix of the single objects and chosen in a way that their eigenvalues (factors multiplied with the original eigenvectors) are as small as possible. PC 1 is always the eigenvector with the highest eigenvalue (Sheets 2004; Zelditch et al. 2004). Group encoding in PCAGen6 made it possible to display all of the compared bones with different colours in a Procrustes superimposition, which facilitated recognition of possible shape differences between the taxa and single objects. Another feature of the program PCAGen6 is to illustrate the changes of the reference shape performed by PC scores as a TPS diagram.

Eighteen PC scores per object are erected for each of the 11 anterior and 11 posterior landmarks of each humerus (number of landmarks * 2 minus 4 [the four non shape-changing aspects of size, position in the two dimensional room and orientation of the object]; Zelditch et al. 2004) and 20 PC scores per object are erected for the 12 posterior landmarks of each femur. The PC scores with the highest eigenvalues result in the strongest deformation, which is specified here as the percentage of the whole deformation performed on the reference shape. In this work, only PCs explaining more than 5% of the whole deformation are considered.

Finally, a Discriminant Factor Analysis (DFA) was conducted by SPSS 17.0 (2008) to test if assigned groups of sauropod bones differ significantly from one another based on differently developed conditions of character variables, and so to check the affiliation of single cases with a certain group. In a DFA, groups are separated from each other by different ranges of values of their dicriminant functions. The partial warps of the single bones were used, with

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their single coordinates representing the character variables and the bones representing the cases. Three groups were formed from the 30 humeri and 30 femora. Group 1 comprised diplodocids (*Tornieria* and "*Barosaurus*"), with the humeri MB.R.2639, MB.R.2642, MB.R.2643, MB.R.2646, MB.R.2649, MB.R.2650, MB.R.2652, MB.R.2653, MB.R.2656, MB.R.2672, MB.R.2673, MB.R.2709, and MB.R.2632, and the femora MB.R.2637, MB.R.2641, MB.R.2660, MB.R.2661, MB.R.2662, MB.R.2663, MB.R.2665, MB.R.2666, MB.R.2667, MB.R.2670, MB.R.2671, MB.R.2685, and MB.R.2700 respectively. Group 2 comprised *Giraffatitan brancai* with the humeri MB.R.2910, MB.R.2911, MB.R.2181.73, MB.R.2181.74, MB.R.2658, MB.R.2674, MB.R.2679, MB.R.2680, MB.R.2681, MB.R.2682, MB.R.2683, and MB.R.2684, and the femora MB.R.2181.83, MB.R.2633, MB.R.2640, MB.R.2668, MB.R.2693, MB.R.2694, MB.R.2699, MB.R.2914, MB.R.2916, and MB.R.5016, respectively. In Group 3 all used bones of Dicraeosauridae were assembled. Group 3 humeri were from *Amargasaurus cazaui* (MACN-N 15), *Dicraeosaurus hansemanni* (MB.R.4912), and *D. sattleri* (MB.R.2631, MB.R.2655, and MB.R.2657). Group 3 femora were from *Amargasaurus cazaui* (MACN-N 15), *Dicraeosaurus hansemanni* (MB.R.4886.92, MB.R.4886.93, MB.R.2695; and MB.R.2696), and *D. sattleri* (MB.R.2697, and MB.R.2638). It must be mentioned that "*Barosaurus*" long bones from Tendaguru most probably belong to more than one diplodocid taxon (Remes 2009), but their close phylogenetic relationship makes it justifiable to use them together for the DFA in a supplementary group. Additionally, the group 3 with Dicraeosauridae comprises different taxa.

Each character variable was first separately tested for its qualification to separate the groups from each other (Figs. 1, 6; Supplementary Online Material available at http://app.pan.pl/SOM/app59-Schwarz-Wings_Bohm_SOM.pdf). The resulting four character variables each for the humeri and for the femora were then chosen for the DFA, meeting the criteria that no more variables than different cases per group should occur, and that more variables than groups should be included. A Box's M test for the homogeneity of covariance matrices was used to check the hypothesis that the chosen groups are different from each other, which would be the case with a significance value higher than 0.05. The Log determinant for a group of all humeri/all femora together was calculated, showing the amount of variability of the cases within a group. Afterwards, the discriminant functions could be calculated, which had to be two for three groups.

These two discriminant functions were then subjected to a Chi-squared test to check their suitability to discriminate between the groups: The critical discriminant function value should be able to separate the groups clearly into all cases with a higher value belonging to one group and all cases with a lower value belonging to the other group. In the case of two discriminant functions, the relation between the two values is important. The higher the value of the Chi-squared test, the more different are the groups, and the Chi-squared value should also be larger than the number of degrees of freedom. Finally, the structure matrix shows the correlation between the variables and the discriminant functions: the higher the value, the better the variable can be distinguished. After the single groups have been positively tested for significant differences, the single cases (i.e., the particular bones) can be tested for their group membership, first as included within the group, and second by excluding the single tested case for each calculation from the group (cross-validation). In another test, the a priori probabilities for group memberships were adjusted to the real group sizes. Instead of a probability of 0.333 for each group, the distribution is then corrected by group size.

Results

Morphological and linear morphometrical comparison

Humeri.—The humeri of *D. sattleri* are very similar in size to each other, and small morphological differences represent natural variation and preservational effects. An exception is the difference in gracility between the approximately 4 cm longer humeri MB.R.2631 (GI 7.88) and MB.R.2655 (GI 8.27) and the two shorter humeri MB.R.2634 (GI 6.94) and MB.R.2657 (GI 6.5). The difference in gracility is associated with differences in the values depending on shaft diameter, especially the ratio of shaft diameter to proximal width (Table 1). Shape differences exist at the humeral head and at the deltopectoral crest. The humeral head widens posteriorly in a rather small area for MB.R.2631 and MB.R.2657, but widens more broadly posteriorly in MB.R.2634 and MB.R.2655. In MB.R.2631 and MB.R.2655, the deltopectoral crest is more narrow and steeper elevating than in MB.R.2634 and MB.R.2657, which is most probably the result of poor preservation.

The humerus of *D. hansemanni* (MB.R.4912) is longer than the humeri of *D. sattleri*, but comparative values of the total length of the bone and the shaft diameter are rather similar in both species. An exception is the size ratio of proximal width to shaft diameter (Table 1): MB.R.4912 has a narrower proximal width in relation to its shaft diameter than the humeri of *D. sattleri*. Additionally, the GI of both species indicates that MB.R.4912 is more robust than the humeri of *D. sattleri* (Table 1). Although the proximal articular area is quite broad in *D. hansemanni*, its humeral head widens posteriorly in a rather small area as in MB.R.2631 and MB.R.2657 and the deltopectoral crest is rather small and steeply elevating, as in MB.R.2631 and MB.R.2655. The turning angle between the deltopectoral crest and the shaft, measured at the distal end of the deltopectoral crest, is 34° for *D. hansemanni* and for *D. sattleri* ranges between 32° and 37°. A distinctive shape difference is a sharp transition between the shaft and the medial humeral margin of the expanded proximal extremity of *D. sattleri*, which is more gradual in *D. hansemanni*.

In conclusion, the humerus of *D. hansemanni* is longer, less gracile and has a proximally less expanded head than

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Table 1. Measurements (in cm) and linear morphometric comparisons for the humeri of *Dicraeosaurus sattleri* (SAT) and *Dicraeosaurus hansemanni* (HAN). Abbreviations: X, mean; σ, standard deviation; L, length; Wp, proximal width; Wd, distal width; Sd, shaft diameter; Ldc, length of deltopectoral crest; Bp, proximal breadth (anteroposterior); Bd, distal breadth (anteroposterior); Pb, length of proximal broadening of the shaft (anterior); Db, length of the distal broadening of the shaft (anterior); GI, gracility index; R1, proximal width/shaft diameter; R2, distal width/shaft diameter; R3, proximal width/distal width; R4, length/length of dpc; R5, length/length of the prox. broadening; R6, length/length of the dist. broadening.

	L	Wp	Wd	Sd	Ldc	Bp	Bd	Pb	Db	GI	R1	R2	R3	R4	R5	R6
MB.R.2631, SAT	63	27	18	8	33.8	9.1	8.5	21.6	18	7.88	3.40	2.25	1.5	1.86	2.92	3.5
MB.R.2634, SAT	59	23	18	8.5	29.1	9.4	9.1	21.5	16	6.94	2.71	2.12	1.27	2.03	2.74	3.69
MB.R.2655, SAT	62	26	18	7.5	31.8	9.3	8.7	23.5	18	8.27	3.47	2.4	1.44	1.95	2.64	3.44
MB.R.2657, SAT	58.5	24	19	9	29.4	8.8	8.4	22.8	16	6.5	2.67	2.11	1.26	1.99	2.57	3.66
X	60.6	25	18.25	8.25	31.0	9.15	8.68	22.4	17	7.40	3.01	2.22	1.37	1.96	2.71	3.57
σ	1.92	1.58	0.43	0.56	1.91	0.23	0.27	0.84	1	0.71	0.17	0.12	0.10	0.06	0.22	0.11
MB.R.4912, HAN	74	33.5	26.5	13	40.4	10	11	29	20	5.7	2.58	2.04	1.26	1.83	2.55	3.7

Table 2. Comparison of mean values for humeri of *Dicraeosaurus sattleri*, *Dicraeosaurus hansemanni*, and *Amargasaurus cazaui*. Abbreviations: X, mean; σ, standard deviation; L, length in cm; Wp, proximal width in cm; Wd, distal width in cm; Sd, shaft diameter in cm; Ldc, length of deltopectoral crest; GI, gracility index; R1, proximal width/shaft diameter; R2, distal width/shaft diameter; R4, shaft length/length of deltopectoral crest.

	L	Wp	Wd	Sd	Ldc	GI	R1	R2	R4
X *Dicraeosaurus sattleri*	60,6	25	18.25	8.25	31.0	7.4	3.01	2.22	1.96
σ *Dicraeosaurus sattleri*	1.92	1.58	0.43	0.56	1.91	0.71	0.17	0.12	0.06
Dicraeosaurus hansemanni	74	33.5	26.5	13	40.4	5.7	2.58	2.04	1.83
Amargasaurus cazaui	69.4	31.3	18.9	15.5	32	4.47	2.01	1.21	2.17

the humeri of *D. sattleri*. Under the assumption of a normal distribution around a mean value, significant differences between both species are confirmed for length and gracility, but the small number of measurements restricts the significance of the applied statistical tests (Shapiro-Wilk test, Gaussian test, Kruskal-Wallis-Test).

A morphological comparison of the humeri of *D. sattleri* and *D. hansemanni* with the humerus of *Amargasaurus cazaui* (MACN-N 15) shows that the distal shaft of the latter is slightly broader than its medial part. The humerus of *A. cazaui* is longer than those of *D. sattleri*, but its deltopectoral crest is relatively shorter than the mean value of *D. sattleri* (Table 2). The humeral shaft of MACN-N 15 has an absolutely broader diameter than those of both *Dicraeosaurus* species, but also a lower GI. In the humerus of *A. cazaui*, the hemicondyles of the distal extremity broaden less than in *D. hansemanni* and *D. sattleri*. In absolute size and gracility, the humerus of *A. cazaui* is more similar to *D. hansemanni* than to *D. sattleri* (Table 2), but in the ratio of proximal and distal width to total shaft diameter and shaft length to deltopectoral crest, the humerus of *A. cazaui* differs both from *D. hansemanni* and *D. sattleri* (Table 2). Thus, the humerus of MACN-N 15 is more robust than in *Dicraeosaurus* species, with a shorter deltopectoral crest and a narrower distal end.

Femora.—The evaluation of mean values of the femora of *D. sattleri* is problematic, because of major fractures on each specimen. A direct comparison of MB.R.2697 and MB.R.2915 demonstrates that with nearly the same lateromedial length (3 cm difference only), the anteroposterior length of the femoral head of MB.R.2697 is only half that of MB.R.2915. The 4th trochanter is weakly elevated and positioned along the longitudinal axis of the shaft in MB.R.2638 and MB.R.2697, whereas in MB.R.2915 it is sharply elevating and more medially displaced. The femoral shaft of MB.R.2915 is anteroposteriorly one third shorter than the comparably sized femur MB.R.2697 (6.3 cm in MB.R.2915; 9.6 cm in MB.R.2697), but this does not seem to influence the positions of landmarks on the anterior and posterior sides. The mean values are reduced by the small femoral heads of MB.R.2638 and MB.R.2697, and the lost distal condyles of MB.R.2915 (Table 3). The small length of MB.R.2638 also influences the overall size of the shaft, the shaft diameter and the means of the proximal/distal width. Although MB.R.2638 is apparently smaller, the positions and size proportions of landmarks fit with those positions in the bigger femora (Table 3). MB.R.2638 has the highest GI, which might be a result of partly lost surface structures.

Landmarks and surface structures in the femora are better preserved in *D. hansemanni* than in *D. sattleri*. In intraspecific comparisons, the femoral condyles are similar in shape, except for MB.R.2696, in which the tibial condyle and the intercondylar fossa are curved laterally. This curvature might be a result of the total curvature of the shaft to the medial side. The curvature changes also the shape of the 4th trochanter, which shows a sharply elevated ridge and is displaced towards the middle of the femoral shaft. In contrast, the 4th trochanter of the other femora of *D. hansemanni* is rather broad and descends more gradually onto the femoral shaft. Except for a slight difference in shaft diameter (Table 4), the individual femora show no big differences in their proportions. Whereas the curvature of MB.R.2696 seems to have no influence on the calculated values, a displacement of the

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Table 3. Measurements (in cm) and ratios for the femora of *Dicraeosaurus sattleri*. Abbreviations: X, mean; σ, standard deviation; L, length; Wp, proximal width; Wd, distal width; Sd, shaft diameter; Tr, distance from centre of 4th trochanter to proximal end of the femoral shaft; GI, gracility index; R7, length/proximal width; R8, proximal width/distal width; R9, shaft length/distance of 4th trochanter from proximal end.

	L	Wp	Wd	Sd	Tr	GI	R7	R8	R9
MB.R.2638	97	26	22	12.5	43	7.76	3.73	1.18	2.26
MB.R.2697	114	28	26	15.5	52	7.35	4.07	1.08	2.19
MB.R.2915	111	31.5	23	16.5	52	6.73	3.52	1.37	2.13
X	107.3	28.5	23.7	14.8	49	7.28	3.77	1.21	2.19
σ	7.41	2.27	1.7	1.7	4.24	0.41	0.23	0.17	0.05

Table 4. Measurements (in cm) and ratios for the femora of *Dicraeosaurus hansemanni*. Abbreviations: X, mean; σ, standard deviation; L, length; Wp, proximal width; Wd, distal width; Sd, shaft diameter; Tr, distance from centre of 4th trochanter to proximal end of the femoral shaft; GI, gracility index; R7, length/proximal width; R8, proximal width/distal width; R9, shaft length/distance of 4th trochanter from proximal end.

	L	Wp	Wd	Sd	Tr	GI	R7	R8	R9
MB.R.2695	112	36	31	17	51	6.6	3.2	1.13	2.20
MB.R.2696	117	35	29	16.5	50	7.3	3.34	1.21	2.34
MB.R.4886.92	120	36	30.5	21	51.5	5.71	3.33	1.15	2.33
MB.R.4886.93	119	34	31	21	53	5.71	3.5	1.15	2.25
X	116.2	35.3	30.25	18.2	51.1	6.54	3.32	1.16	2.28
σ	3.12	0.47	0.89	2.01	0.92	0.65	0.09	0.03	0.04

Table 5. Comparison of mean values for the femora of *Dicraeosaurus sattleri*, *Dicraeosaurus hansemanni*, and *Amargasaurus cazaui*. Abbreviations: X, mean; σ, standard deviation; L, length in cm; Wp, proximal width in cm; Wd, distal width in cm; Sd, shaft diameter in cm; Tr, distance from centre of 4th trochanter to proximal end of the femoral shaft in cm; GI, gracility index; R7, length/proximal width; R8, proximal width/distal width; R9, shaft length/distance of 4th trochanter from proximal end.

	L	Wp	Wd	Sd	Tr	GI	R7	R8	R9
X *Dicraeosaurus sattleri*	107.3	28.5	23.7	14.8	49	7.28	3.77	1.21	2.19
σ *Dicraeosaurus sattleri*	7.41	2.27	1.7	1.7	4.24	0.41	0.23	0.17	0.05
X *Dicraeosaurus hansemanni*	116.2	35.3	30.25	18.2	51.1	6.54	3.32	1.16	2.28
σ *Dicraeosaurus hansemanni*	3.12	0.47	0.89	2.01	0.92	0.65	0.09	0.03	0.04
Amargasaurus cazaui	104	24.2	26	17.2	6.05	4.44	0.93	59.5	1.75

4th trochanter of MB.R.4886.93 influences the comparative position of the 4th trochanter (Table 4).

The femora of *D. hansemanni* are slightly longer and more robust than the femora of *D. sattleri*. Excluding the small femur MB.R.2638 from the *D. sattleri* group, the length difference between the mean values of *D. sattleri* and *D. hansemanni* would be only 4 cm (Table 5), and the differences in shaft diameter as well as the distance between the proximal shaft end and the 4th trochanter would also be smaller (Table 5). Thus, the total length difference should, regarding the small sample size, not be overrated. The femoral head of MB.R.2915 (*D. sattleri*) is comparable in shape to the femoral heads of *D. hansemanni*, and the well-preserved distal condyles of MB.R.2697 (*D. sattleri*) compare to those of *D. hansemanni*. Between *D. sattleri* and *D. hansemanni*, there are no significant differences in position of the greater, smaller and 4th trochanters, and the measured differences are most probably the results of fractures during fossilisation. An apparent difference between the species is the lateromedial width of the proximal shaft end, which is significantly higher in *D. hansemanni* than in *D. sattleri*. Even with MB.R.2638 and MB.R.2697 excluded (because their femoral heads show a large amount of surface structure loss), the proximal shaft width of MB.R.2915 is smaller than the mean proximal shaft width in *D. hansemanni* (Table 5). The same size difference applies for the ratio of proximal width to total length. The different sizes for the distal width are considered preservational, and probably caused by the material loss at the femoral condyles of *D. sattleri*. The values for total lengths of the shaft are not significantly different. There is also a difference in the GI, even with MB.R.2638 excluded (Table 5), although because of the high standard deviation in *D. sattleri*, no significant difference in GI can be noted between both species. In summary, the femora of *D. sattleri* are possibly shorter and less robust, and possess a shorter femoral head than those of *D. hansemanni*.

The femur of *Amargasaurus cazaui* is slightly shorter than the femora of both species of *Dicraeosaurus*, but remains within the standard deviation of the femora of *D. sattleri* (Table 5). Being of comparable length and distal width to the femora of *D. sattleri*, the femur of *A. cazaui* has a wider diameter, resulting in a GI more similar to that of *D. hansemanni* (Table 5). A remarkable difference is the distance from the proximal extremity to the 4th trochanter, which is 57% of the total length in *Amargasaurus*, but 44% in *D. hansemanni* and 46% in *D. sattleri* (Table 5). Additionally, the ratio of proximal width to femoral length in *A. cazaui* is less broad

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than in *Dicraeosaurus*, based on a total lateromedial width of 24.2 cm, but a length of 104 cm and a distal width of 26 cm. The ratio of proximal width to shaft length for *A. cazaui* is outside the standard deviation and every single value for the femora of *D. sattleri* and especially for *D. hansemanni*. The ratio of proximal to distal width is even smaller in *Amargasaurus* (Table 5), whereas in *Dicraeosaurus*, the distal width of the femora is always less than the proximal width. In conclusion, the femur of *A. cazaui* has a 4th trochanter placed more distally and is more robust with a relatively shorter femoral head than both *Dicraeosaurus* species.

Thin-plate Spline deformation grids

Humeri.—The humeri of *D. sattleri* differ only little from each other in their single landmark positions, as the shape differences between them are small (Fig. 5). MB.R.2655 differs from the reference shape by a smaller minimum shaft diameter and a wider distance between the lateral end of the humeral head and the proximolateral end of the shaft. In contrast, MB.R.2657 possesses a slightly broader shaft diameter and a more proximally shifted deltopectoral crest than the reference shape.

In comparison with the humerus of *D. sattleri*, that of *D. hansemanni* (MB.R.4912) has a broader shaft diameter, but a smaller distal width and a humeral head slightly elevated from the proximal shaft end (Fig. 5). In the reference shape of all anterior landmark configurations, the humerus of *D. hansemanni* increases the similarity towards its own shape and decreases the similarity to the shape of *D. sattleri*. When turned into the shapes of MB.R.2631 or MB.R.2655 (both *D. sattleri*), there is a decrease in the shaft diameter, an increase in the distal width and a lowering of the humeral head with respect to the reference shape of *D. hansemanni* (Fig. 5). Turning the reference shape into the humerus of *D. hansemanni* shows the opposite effects, with a broadening of shaft diameter, elevation of the humeral head and a decrease of distal width. These effects indicate true shape differences between the humeri of *D. hansemanni* and *D. sattleri*.

In contrast, the posterior landmarks do not show similarly clear differences. The humerus of *D. hansemanni* differs only in the landmark positions of the shaft diameter and the olecranon fossa, the latter being more proximally positioned than in *D. sattleri*. These landmark modifications increase the distance between the proximomedial end of the shaft and the medial shaft boundary, leading to a more gradual widening of the proximal shaft of *D. hansemanni* (Fig. 5) whereas the shaft of *D. sattleri* widens more abruptly in a proximal direction.

Testing the humerus of *Giraffatitan brancai* (MB.R.2911) against the anterior reference shape of *Dicraeosaurus* and *D. sattleri* reveals that the landmarks of MB.R.2911 differ in similar ways from the reference shape as in *D. hansemanni* (see above), but indicates a more narrow shaft diameter for *G. brancai* in comparison with *Dicraeosaurus*. More landmarks need to be displaced in *G. brancai* than in *D. hansemanni*, demonstrating that the humerus of MB.R.2911 has a different shape than both species of *Dicraeosaurus*. This supports the hypothesis of a possible differentiation between the humerus of *D. hansemanni* and *D. sattleri* (see also PCA for Procrustes superimposition of anterior landmarks of all humeri).

To turn the reference shape into the shape of the humerus of *Amargasaurus cazaui*, the landmarks for the medial and the lateral ridge move farther away from each other, those for the distal width approach each other, those of the shaft diameter widen, the deltopectoral crest is displaced distally and the humeral head is proximally elevated (Fig. 5). Although these changes resemble those of MB.R.4912, they are many times higher. Both the humerus of *A. cazaui* and *D. hansemanni* change the reference shape in a similar direction by increasing the difference between proximal and distal width and elevation of shaft diameter, whereas the humeri of *D. sattleri* witness a decrease in proximal width and shaft diameter and displace the deltopectoral crest proximally. With regard to the magnitude of the values, humeri of *D. hansemanni* differ in shape from *D. sattleri*, but not as much as *A. cazaui*, which differs from both *Dicraeosaurus* species. The differences between the values of the humeri of both *Dicraeosaurus* species in the calculation with *A. cazaui* compared to those obtained without *Amargasaurus* (see above) are related to the re-calculation of the landmarks of both *Dicraeosaurus* species for the comparison with *Amargasaurus* (see Material and Methods). The values for *A. cazaui* are high when compared to the TPS graphics or the Procrustes superimposition (see below), which is consistent with the many differences already measured with linear morphometrics. Thus, the humerus of *A. cazaui* is clearly different in shape to *D. hansemanni* and *D. sattleri*.

Femora.—The *Dicraeosaurus* femora are more similar in shape to the reference shape of their own species, than to that of the other species. The reference shape of the femora of *D. sattleri* contains only two specimens, MB.R.2638 and MB.R.2697, which are very similar to each other, even in damage to the femoral head. MB.R.2697 differs in its slightly shorter femoral head from the reference, whereas MB.R.2638 shows no particular differences (Fig. 6).

Larger intraspecific shape differences are present in the femora of *D. hansemanni*, resulting from deviating single landmarks, which are strongly displaced compared to its reference shape (Fig. 6). In MB.R.2695, the 4th trochanter is shifted proximally and the greater trochanter lies closer to the femoral head and lesser trochanter. In MB.R.4886.92, the 4th trochanter is displaced medially and distally, and the distal landmarks at the condyles are weakly compressed in comparison to the reference shape (Fig. 6). Abrasion of some areas of the femoral head and the distal condyles and a medial displacement of the 4th trochanter explain major deviations from MB.R.4886.93 in all comparisons (Fig. 6). MB.R.2696 differs, despite its stronger curved shaft, only slightly from the reference shape of *D. hansemanni*. Apparently, differences among the *D. hansemanni* femora are the result of individual preservation, making it difficult to understand the significance of differences of the femora of *D. sattleri*

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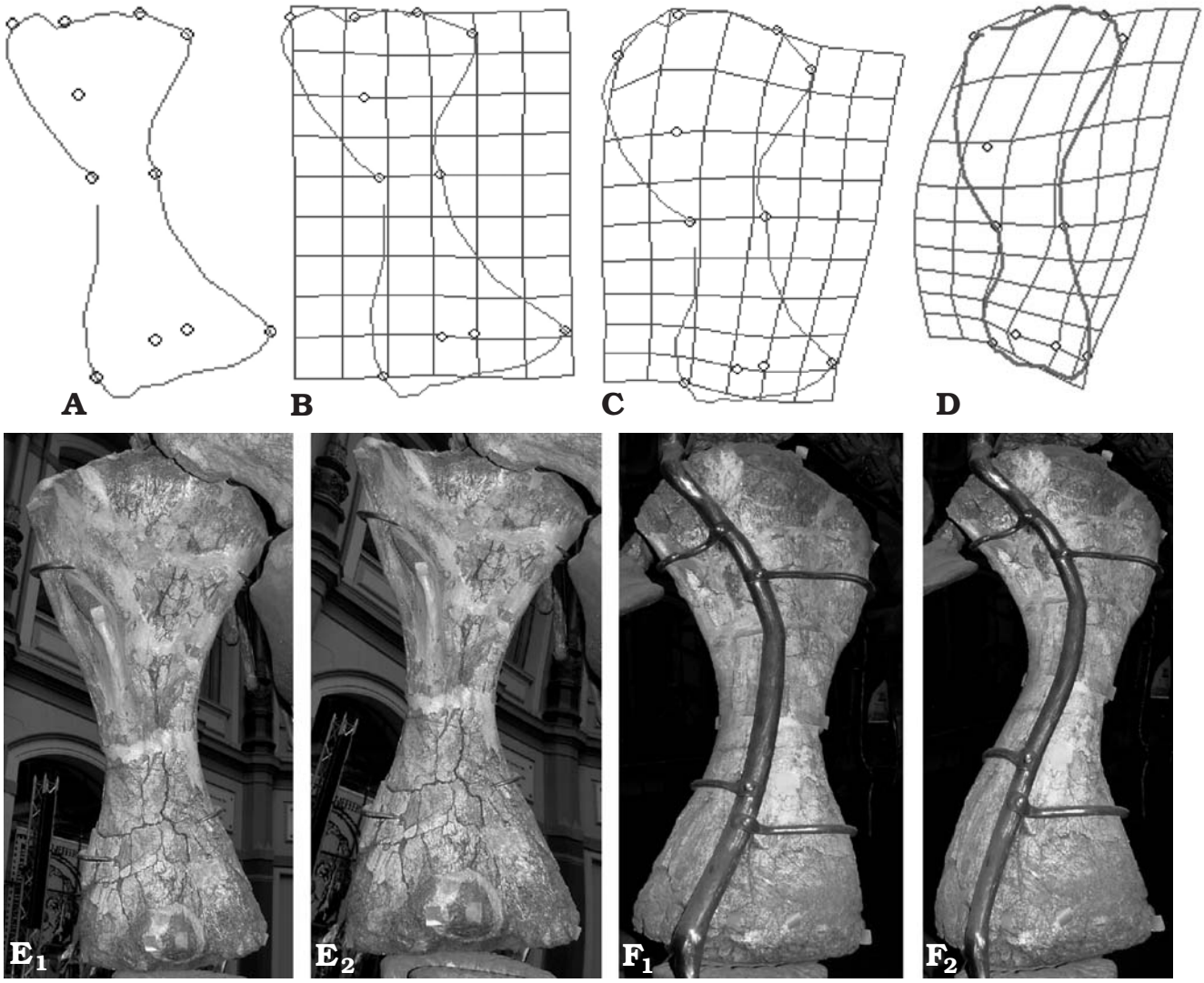


Fig. 5. Thin-plate Splines of humeri of dicraeosaurid dinosaurs *Dicraeosaurus* and *Amargasaurus*. **A**. Reference shape of humeri of *Dicraeosaurus sattleri*. **B**. Same reference shape adjusted onto the landmark positions of MB.R.2631 (*Dicraeosaurus sattleri*). **C**. Same reference shape adjusted onto the landmark positions of MB.R.4912 (*Dicraeosaurus hansemanni*). **D**. Reference shape of humerus of *Amargasaurus cazaui*, MACN N-15. Only landmarks are displaced, whereas outlines are left for better overview of shape; printouts from tpsSplin (Rohlf 2004a). **E**, **F**. Right humerus MB.R.4912 of *D. hansemanni*, photograph in comparison with shape-changes when fitted onto reference shape of *D. sattleri*. Photographs (E_1, F_1) and shape of anterior (E_2) and posterior (F_2) faces modified by tpsSuper. Not to scale.

from the reference shape of *D. hansemanni*. When comparing the femora of *D. hansemanni* to the reference shape of *D. sattleri*, only MB.R.4886.92 is not markedly changed, which probably relates to the medial curvature of the shaft of MB.R.2696. The landmarks for the 4th trochanter, the lesser trochanter, the lateral and the fibular condyle and the shaft diameter are all shifted laterally in comparison with the reference shape of *D. sattleri*.

Two shape-relevant features were detected in the femoral comparisons. First, the landmark position for the femoral head (medial) always lies more medially in the femora of *D. hansemanni*, because the femoral head of *D. sattleri* is shortened (Fig. 6). Second, the shaft diameter is broader in the femora of *D. hansemanni* than in *D. sattleri*. To test the possibly shorter femoral head in *D. sattleri*, one more TPS analysis was conducted, focusing only on the five landmarks of the proximal extremity and therefore including MB.R.2915 with its well-preserved femoral head. This analysis yielded clearly smaller bending energy values correlated with high Procrustes distances, presumably because only five landmarks per object are displaced, increasing the vectors of displacement in relation to the energy consumption for the displacement. MB.R.2915 differs in its proximal shape from the other two femora of *D. sattleri*, but also from the femora of *D. hansemanni*, mainly because of its medially shifted 4th trochanter. Additionally, the femoral head of MB.R.2915 is shorter than the femoral head of the reference shape of *D. hansemanni*. The shortest femoral head of MB.R.2697 shows the second highest agreement with the reference shape of *D. hansemanni*. In summary, shape differences between the femora of *D.*

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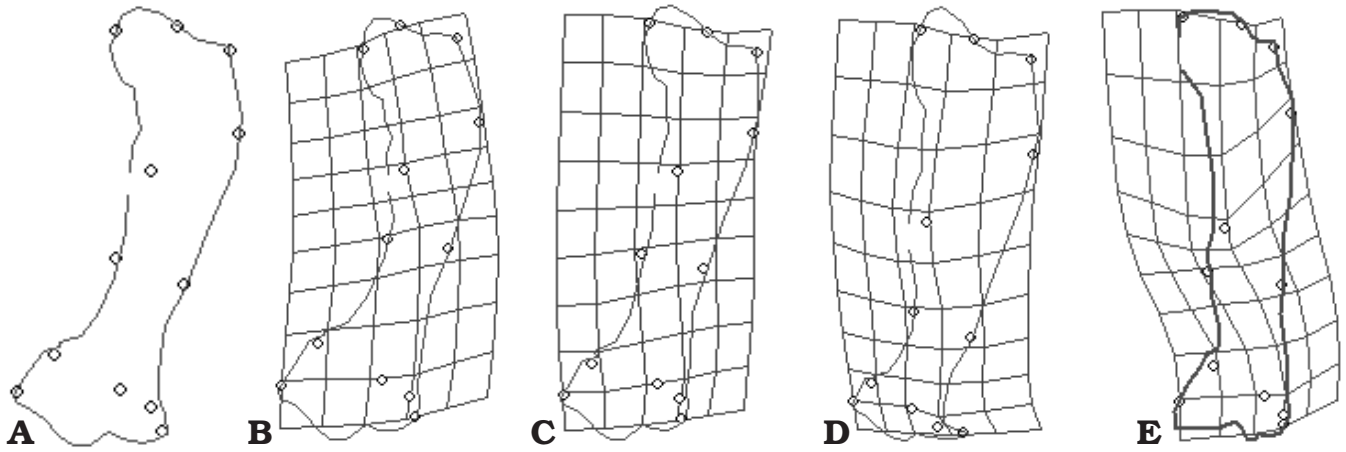


Fig. 6. Thin-plate Splines of femora of dicraeosaurid dinosaurs *Dicraeosaurus* and *Amargasaurus*. **A**. Reference shape of femora of *Dicraeosaurus*. **B**. MB.R.2638, *Dicraeosaurus sattleri* in comparison with reference shape slightly shortened femoral head, 4th trochanter proximally displaced and longer tibial condyles. **C**. MB.R.4886.92, *Dicraeosaurus hansemanni* in comparison with reference shape femoral head slightly medially and proximally enlarged and distal condyli approaching each other. **D**. MB.R.4886.93, *D. hansemanni* in comparison with reference shape 4th trochanter displaced distally and medially, and distal condyles approaching each other. **E**. Reference shape of femur of *Amargasuarus cazaui*, MACN N-15. Printouts from tpsSplin (Rohlf 2004a). Not to scale.

sattleri and *D. hansemanni* exist, although a few diagenetic landmark displacements probably have a higher influence on the shape analyses than the potential taxon specific shape differences. The femoral head of *D. sattleri* is shorter and the shaft diameter is smaller.

The comparison with the femur of *Giraffatitan brancai* (MB.R.2633) does not facilitate a species differentiation within *Dicraeosaurus*. Most of the landmarks in *G. brancai* do not differ strongly from each of the three reference shapes, except for the medially displaced 4th trochanter. Whereas it is possible to separate the femora of *D. sattleri* and *D. hansemanni* by excluding those femora with large preservational damage, it is not possible to differentiate between the femur of *Dicraeosaurus* and *Giraffatitan*. The more medially displaced 4th trochanter of the femur of *G. brancai* is apparently not sufficient to separate it by a TPS analysis from the femora of *Dicraeosaurus*.

To turn the reference shape into the femur of *A. cazaui*, the distal width is reduced by displacing the laterodistal end ventral to the fibular condyle, stretching the shaft diameter, and most importantly displacing the 4th trochanter far more distally and moving the medial landmark of the femoral head proximally to produce a higher proximal inclination of the medial femoral head in comparison with *Dicraeosaurus*. Landmarks in *A. cazaui* are probably less displaced than the few landmarks of MB.R.4886.93 (*D. hansemanni*), so that the shape difference between *A. cazaui* and both *Dicraeosaurus* species may not be caused by one or two single landmarks, but by a completely differently shaped femur of *A. cazaui* (Fig. 6). The landmarks of MB.R.4886.93 (*D. hansemanni*) differ from the reference shape in the same way as the landmarks of *A. cazaui* (see above). In contrast, the shape modifications of MB.R.2695 (also *D. hansemanni*), a broadened distal width and a more proximally displaced 4th trochanter, are opposite to those in MB.R.4886.93. The opposing effects of *A. cazaui* and MB.R.4886.93 on one side and MB.R.2695 on the other change the reference shape in a way that those femora with a mean distal width or position of the 4th trochanter (in particular, MB.R.4886.92) are more similar to the reference shape, as in those calculations without *A. cazaui*. The reference shape thus changes towards a more robust shaft diameter and a slightly broader femoral head. Overall, the femur of *A. cazaui* can be separated very well from the femora of *D. sattleri* and *D. hansemanni* with the TPS analysis.

Principal Components Analysis

Humeri.—In all PCAs of the humeri, at least 84% of deformation can be explained by the first and second PC scores (Fig. 7). A first PCA is performed with the humeri of *D. sattleri* only, to account for possible intraspecific variation. According to PC 1 (89% of variance), the shaft diameter is reduced, the deltopectoral crest is proximally displaced, and the lateral and medial ridge and the mediodistal end of the humerus are medially displaced. MB.R.2655 supports these changes, MB.R.2657 opposes them and MB.R.2631 does not differ at all from the reference shape in PC 1. According to PC 2 (10.8% of variance), the humeral head narrows considerably, which is weakly supported by MB.R.2631. All these differences are small in comparison to those differences in the PCA including *D. hansemanni* (see below).

The PCA including the humeri of *D. sattleri* and *D. hansemanni* results in a Procrustes superimposition in which the landmarks of all humeri are positioned close together (Fig. 7), except for the height of the humeral head and the smaller width of the distal extremity of *D. hansemanni*. There is no evidence for a difference in gracility between the humeri of both taxa, but in comparison with the mean values of the humerus of *D. sattleri*, the shaft diameter of *D. hansemanni* is slightly broader and more distally positioned, and the deltopectoral crest is shifted more distally. According to PC 1 and PC 2, the

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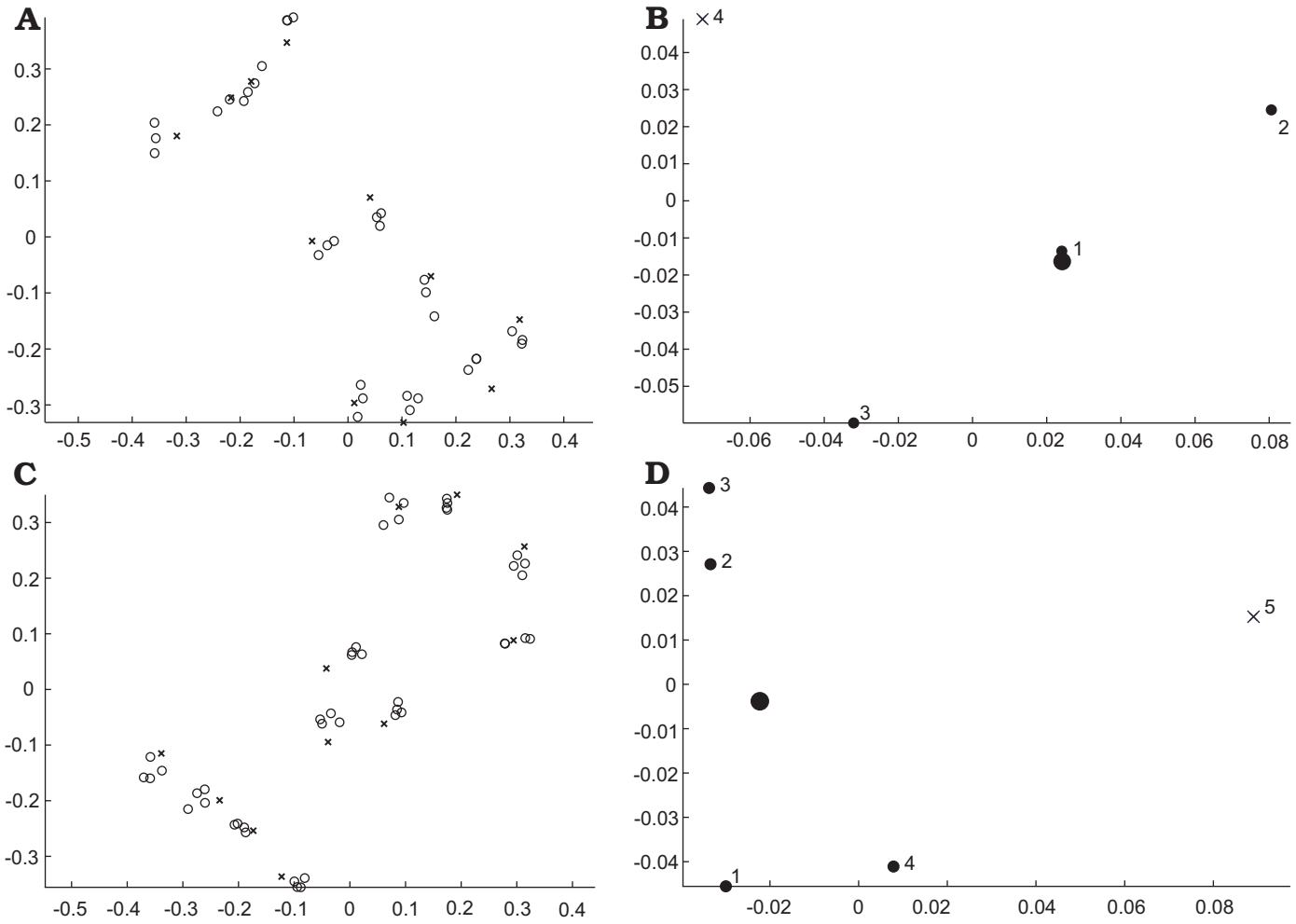


Fig. 7. Procrustes fits (**A**, **C**) and PCA values (**B**, **D**) of *Dicraeosaurus* humeri. **A**. Procrustes fits of *Dicraeosaurus sattleri* (open circles) and *Dicraeosaurus hansemanni* (crosses), anterior face. **B**. PCA values of same taxa, large circle is mean value of deviance for *D. sattleri*; 1, MB.R.2631; 2, MB.R.2655; 3, MB.R.2657; 4, MB.R.4912. **C**. Procrustes fits of *D. sattleri* (open circles) and *D. hansemanni* (crosses), posterior face. **D**. PCA values of same taxa, large circle is mean value of deviance for *D. sattleri*; 1, MB.R.2631; 2, MB.R.2634; 3, MB.R.2655; 4, MB.R.2657; 5, MB.R.4912.

humeri of both species differ from each other. MB.R.2631 is very close in its landmark positions to the reference shape of *D. sattleri* (see also above). The humerus of *D. hansemanni* (MB.R.4912) generates a proximal displacement of the humeral head, a distal displacement of the deltopectoral crest, a decrease of the distal width and an increase of the shaft diameter, which is consistent with the TPS analysis and the Procrustes superimposition. In support of PC 1, the reference shape of *D. sattleri* changes exactly in the opposite way to *D. hansemanni*, placing MB.R.4912 on the outer left side of PC 1. PC 2 changes the reference shape of *D. sattleri* by displacing the humeral head proximally and reducing the distal width, so that these changes are supported by MB.R.4912. The humerus of *D. hansemanni* changes the reference shape of all *Dicraeosaurus* humeri in a different way than the humeri of *D. sattleri*, implying that it has a distinct shape (Fig. 7).

The posterior landmarks of the humeri of *Dicraeosaurus* coincide better than the anterior landmarks (Fig. 7). Exceptions are the landmarks for the shaft diameter and the olecranon fossa, which are located more distally on the humerus of *D. hansemanni* than in *D. sattleri.* The displacement of the medial shaft diameter landmark away from the proximomedial shaft end results in a more gentle proximal expansion of the humeral head of *D. hansemanni*, whereas the same expansion in *D. sattleri* is sharply bent (see also above). In PC 1, *D. hansemanni* is clearly separated from *D. sattleri*, whereas in PC 2–4 the taxon lies between the values of *D. sattleri* (Fig. 7). PC 1 changes the reference shape by displacing the landmarks for the olecranon fossa and the shaft diameter distally. The remaining deformations are all very small and insignificant, as are the deformations performed by the other PCs. PCs 2–4 have a relatively large (47%) amount of variance, but they represent only very small differences. Thus, the PCA of the posterior landmarks supports only small differences between the *Dicraeosaurus* humeri. Even the differences between the two species concerning PC 1 are smaller than at the anterior landmarks.

In a PCA with inclusion of the humerus of *Giraffatitan brancai* (MB.R.2911), the Procrustes superimposition shows the deviation of nearly all landmarks from *Dicrae-*

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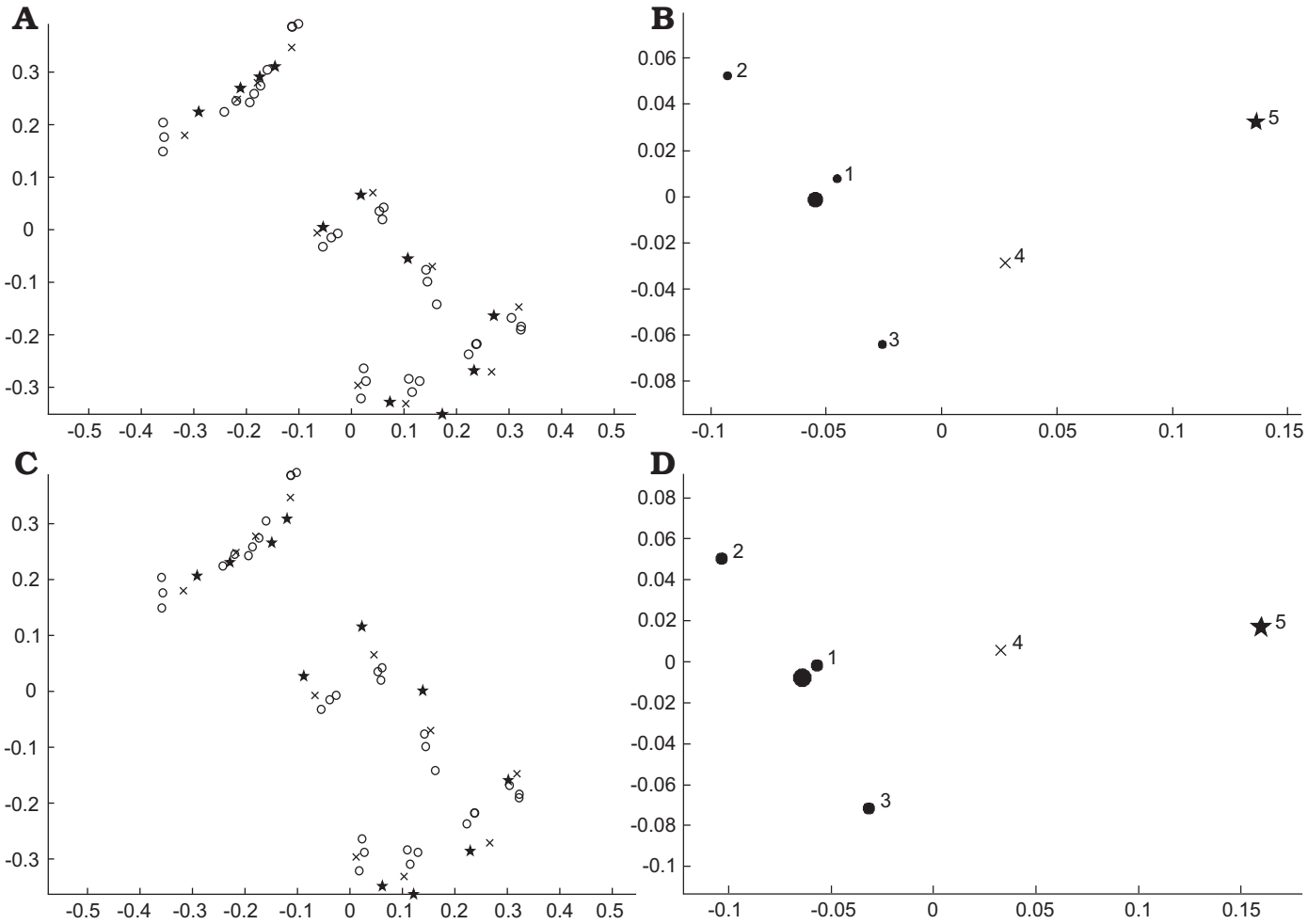


Fig. 8. Procrustes fits (**A**, **C**) and PCA values (**B**, **D**) of *Dicraeosaurus*, *Giraffatitan*, and *Amargasaurus* humeri. **A**. Procrustes fits of *Dicraeosaurus sattleri* (open circles), *Dicraeosaurus hansemanni* (crosses), and *Giraffatitan brancai* (stars) anterior face. **B**. PCA values of same taxa, large circle is mean value of deviance for *Dicraeosaurus sattleri*; 1, MB.R.2631; 2, MB.R.2655; 3, MB.R.2657; 4, MB.R.4912; 5, MB.R.2911. **C**. Procrustes fits of *D. sattleri* (open circles), *D. hansemanni* (crosses), and *Amargasaurus cazaui* (stars) anterior face. **D**. PCA values of same taxa, large circle is mean value of deviance for *D. sattleri*; 1, MB.R.2631; 2, MB.R.2655; 3, MB.R.2657; 4, MB.R.4912; 5, MACN-N 15.

osaurus, except those of the lateral and medial ridge (Fig. 8). In MB.R.2911, the deltopectoral crest is more distally displaced, the humeral head is medially elevated, the shaft diameter is reduced, and the distal width is very small compared to *Dicraeosaurus*. Except for the proximal width, the landmarks of *G. brancai* are mostly closer to *D. hansemanni* than to *D. sattleri*. In PC 1, the humerus of *G. brancai* is separated from *Dicraeosaurus*, in PC 2 and 3 it is within the values of *D. sattleri*, whereas the humerus of *D. hansemanni* stands alone in PC 3. PC 1 and MB.R.2911 deform the reference shape similarly by reducing the distal width markedly, moving the deltopectoral crest more distally and elevating the humeral head on the medial side. The changes in the humerus of *D. hansemanni* are similar but weaker. PC 2 reduces the shaft diameter and the proximal width. Thus, MB.R.2911 differs significantly from the *Dicraeosaurus* humeri, and changes the reference shape in many different ways (Fig. 8).

Including the humerus of *Amargasaurus cazaui* in the PCA yields some distinctive dispositions (Fig. 8). The humerus of *A. cazaui* has a far distally positioned deltopectoral crest, a reduced distal width, and its lateral and medial ridges are positioned relatively far away from each other compared to *Dicraeosaurus*. Overall, the humerus of *A. cazaui* differs from that of both *Dicraeosaurus* species like the humerus of *Giraffatitan brancai*, but even more extremely. On PC 1, the humeri can be separated into the three species. PC 1 decreases the distal width, moves the deltopectoral crest and the shaft diameter more distally, and positions the humeral head more proximally. The humerus of *D. hansemanni* follows the changes induced by PC 1, that of *A. cazaui* follows them even more extremely. PC 2 exposes only differences within the humeri of *D. sattleri*. PC 2 moves the lateral and the medial ridge medially and the deltopectoral crest proximally and decreases the shaft diameter. There are no differences between the taxa, their mean values being neutral to PC 2, and only MB.R.2655 and MB.R.2657 differ from each other. Another test with *A. cazaui* and the humeri of only *D. sattleri* yields no differences compared to the test performed with both *Dicraeosaurus* species.

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Only the percentage of the PC values changes with one object less. The PCA results confirm that the humerus of *Amargasaurus* is a different shape from that of *Dicraeosaurus* (Fig. 8).

Femora.—Because the reference shape of all posterior landmarks of *D. sattleri* is composed by MB.R.2638 and MB.R.2697 only, both differ to the same amount in opposite directions and PC 1 explains 100% of variation.

For *D. hansemanni*, in PC 1 the 4th trochanter is displaced far medially and distally, the landmarks on the tibial condylus are positioned more laterally and closer to each other, the shaft diameter is smaller and the medial end of the femoral head is positioned more proximally. In PC 2, the landmarks of both the medial and lateral distal end are positioned closer together and the landmarks for the shaft diameter are proximally displaced. The left femur MB.R.4886.93 shows the same deformations compared to the reference, whereas landmark positions of MB.R.2695 are the opposite. Therefore the femora of *D. hansemanni* differ in their PC scores from each other (Fig. 9).

In a comparison of the femora of *D. hansemanni* and *D. sattleri* in one PCA, the Procrustes superimposition demonstrates that the landmarks of *D. sattleri* are closer together than those of *D. hansemanni*, but positioned very close to or even within the *D. hansemanni* landmark group (Fig. 9). The landmarks for the lesser trochanter scatter least. The mean values for each landmark of the two species yield a shorter femoral head and a more proximally positioned shaft diameter (therefore a more proximal distal end of 4th trochanter) for *D. sattleri* than for *D. hansemanni*. The other mean values are very close together. According to PC 1 and 3, the two groups blend, whereas PC 2 and 4 separate the femora of *D. sattleri* and *D. hansemanni*. The PC 1 values for *D. hansemanni* are highly scattered, and MB.R.2696 and MB.R.4886.93 differ strongly. MB.R.4886.92 is placed closer to the *D. sattleri* plot in PC 2. PC 1 and 2 taken together (79% of variance) would separate the two taxa. PC 1 moves the tibial condyle laterally, the shaft diameter and the fourth trochanter are distally displaced and the medial end of the femoral head moves proximally. In PC 2, the laterodistal end of the femur is displaced ventrally to the fibular condyle, the shaft diameter moves proximally and the femoral head shortens. PC 3 moves both the lesser and the 4th trochanter in the direction of the femoral head. For *D. hansemanni*, MB.R.4886.93 follows PC 1 with its smaller distal width and the distally placed 4th trochanter, whereas MB.R.2695 with a more proximally placed 4th trochanter and MB.R.2696 with a broader distal width are opposite to PC 1. The femora of *D. sattleri* follow PC 2, especially with their shortened femoral heads. MB.R.4886.92, a right femur of *D. hansemanni*, shows a displaced laterodistal end as induced by PC 2, but as its femoral head is still larger than in the femora of *D. sattleri*, is placed closer to the own species mean value in the PC 1 plot (Fig. 9).

Adding the femur of *Giraffatitan brancai* (MB.R.2633) to the PCA reference shape yields no outstanding differences to the *Dicraeosaurus* landmarks (Fig. 10). Most landmarks of *G. brancai* lie closer to *D. sattleri*, as they have a smaller proximal width in comparison with *D. hansemanni*. For PC1, PC 2 and PC 4, MB.R.2633 lies close to the femora of *D. sattleri* bones with a near zero distance to their mean value for the PC 1 score. For PC 3, MB.R.2633 is closer to the *D. hansemanni* group mean value. Thus, the PCs including *G. brancai* change the reference shape in a similar way as those without *G. brancai* and it is not possible to separate the femur of *Giraffatitan* from the femora of *Dicraeosaurus* (Fig. 10).

A PCA including only the proximal landmarks and MB.R.2915 added to the *D. sattleri* group reference shape also shows no clear separation of the two *Dicraeosaurus* species. Neither with PC 1 nor with PC 2 (together more than 90% of variance) is it possible to separate the two species. Besides the medially larger femoral head, the proximally displaced 4th trochanter of MB.R.2915 raises the variability within *D. sattleri* and follows the same trend as the femora MB.R.2695 and MB.R.2696 of *D. hansemanni*. So the results of the PCA are a possible way to separate the femora of *D. sattleri* and *D. hansemanni* based mainly on a different size of the femoral head. However, it is impossible to separate the *Dicraeosaurus* femora as a group from a femur of a different sauropod clade, so the intrageneric differences are weaker than the individual deformations.

The femur of *Amargasaurus cazaui* is tested against all *Dicraeosaurus* femora (Fig. 10). The Procrustes superimposition shows that the landmarks for the medial end of the femoral head are displaced proximally, resulting in a shortened proximal width of *A. cazaui*. The distal landmarks, especially the lateral end ventral to the fibular condyle approach each other. The 4th trochanter is placed distally in comparison to *Dicraeosaurus*, but not more distally than in MB.R.4886.93, and the landmarks of the shaft diameter approach the 4th trochanter more in *A. cazaui* than in any *Dicraeosaurus* femur. By PC 1 it is possible to separate the femur of *Amargasaurus* from those of *Dicraeosaurus*, although the difference is not very pronounced, probably because of the highly strained values of *D. hansemanni*. MB.R.4886.93 is nearly on the same PC 1 position as *A. cazaui*. PC 1 changes the reference shape by elevating the femoral head and decreasing its proximal width at the same time and by moving the 4th trochanter more distally. The mediodistal landmarks move to the shaft centre, decreasing the distal width. *A. cazaui* and MB.R.4886.93 follow these changes similarly. In contrast, MB.R.2695 and MB.R.2696 have a broader distal width and a more proximally positioned deltopectoral crest. The femora of *D. sattleri* and MB.R.4886.92 follow the changes of PC 1 only a little. The femora are not well separated by PC 2, which decreases the width of the femoral head and moves the landmarks of the shaft diameter proximally. The opposite positions of MB.R.4886.93 and *A. cazaui* demonstrate that the 4th trochanter of MB.R.4886.93 is displaced, but in contrast to *A. cazaui* not more closely positioned to the distal landmarks (Fig. 10).

When *Amargasaurus cazaui* is compared to the *D. hansemanni* or the *D. sattleri* femora only, the results are nearly the same with only the percentages having changed. Although shape differences between the femora of *A. cazaui* and *Di-*

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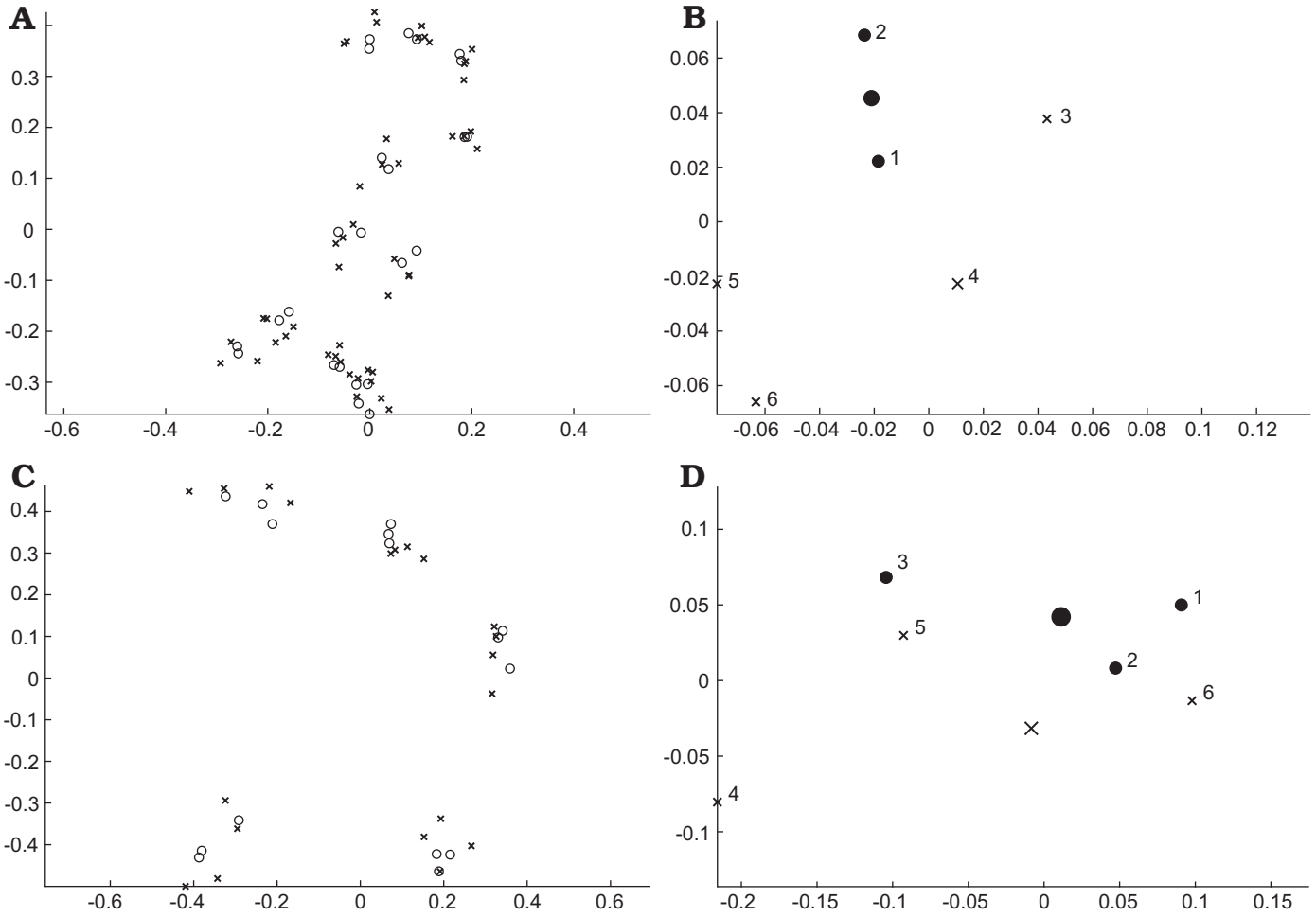


Fig. 9. Procrustes fits (**A**, **C**) and PCA values (**B**, **D**) of *Dicraeosaurus* femora. **A**. Procrustes fits of *Dicraeosaurus sattleri* (circles) and *Dicraeosaurus hansemanni* (crosses), posterior face. **B**. PCA values of same taxa, larger symbols denoting mean values for each group; 1, MB.R. 2697; 2, MB.R.2638; 3, MB.R.4886.92; 4, MB.R.4886.93; 5, MB.R.2696; 6, MB.R.2695. **C**. Procrustes fits of *D. sattleri* (circles) and *D. hansemanni* (crosses), femora proximal, posterior face. **D**. PCA values of same taxa, larger symbols denoting mean values for each group; 1, MB.R.2638; 2, MB.R.2697; 3, MB.R.2915; 4, MB.R.2695; 5, MB.R.2696; 6, MB.R.4886.92; 7, MB.R.4886.93.

craeosaurus are clearly induced by the Procrustes superimposition and the TPS analysis, the PCA results are equivocal. Even though it is possible to separate the femur of *D. sattleri* from *A. cazaui*, the differences in landmark preservation within *D. hansemanni* are a persistent problem, as long as there are only 5 to 7 different bones available.

Discriminant Factor Analysis

Humeri.—Each character variable is first separately tested by Wilk's Lambda about its qualification to separate the groups from each other, yielding four significantly different variables X3, Y4, X8, and UniformX out of 18 (SOM: table 1). Box's M Test yields for the three groups a significance value of 0.273, demonstrating unambiguously that the group matrices are not similar to each other (SOM: table 2). Thus, this test supports the hypothesis that the chosen characters make the groups separable from each other. The log determinant is 223,181 for the group of all humeri (groups 1–3 together), showing the presence of a roughly similar distribution of variability within the groups and less scattering than with all variables (log determinant then 995.316).

Of the two discriminant functions, the first function with the highest eigenvalue explains 95% of the variance, and the second function explains only 5% (SOM: table 3). The Chi-squared test yields significance values of 0.000 for the first function, and 0.117 for the second function, demonstrating that only the first function can be used to separate the three groups from each other (SOM: table 4). However, because the second function has a higher Chi-squared value than the degrees of freedom, it can be used for the analysis. In the structure matrix, those variables with significantly different group mean values (X3, Y4 and uniform X for discriminant function 1, and X8 for discriminant function 2) are most distinguishable.

In the original classification, 80% of cases are ordered into the predicted group (SOM: table 5). Cases with the squared Mahalanobis distance to the group centroid of another group smaller than to its predicted group are put into wrong categories: MB.R.2642, MB.R.2649, MB.R.2650, and MB.R.2653 (all from group 1) are ordered into group 3 instead, MB.R.4912

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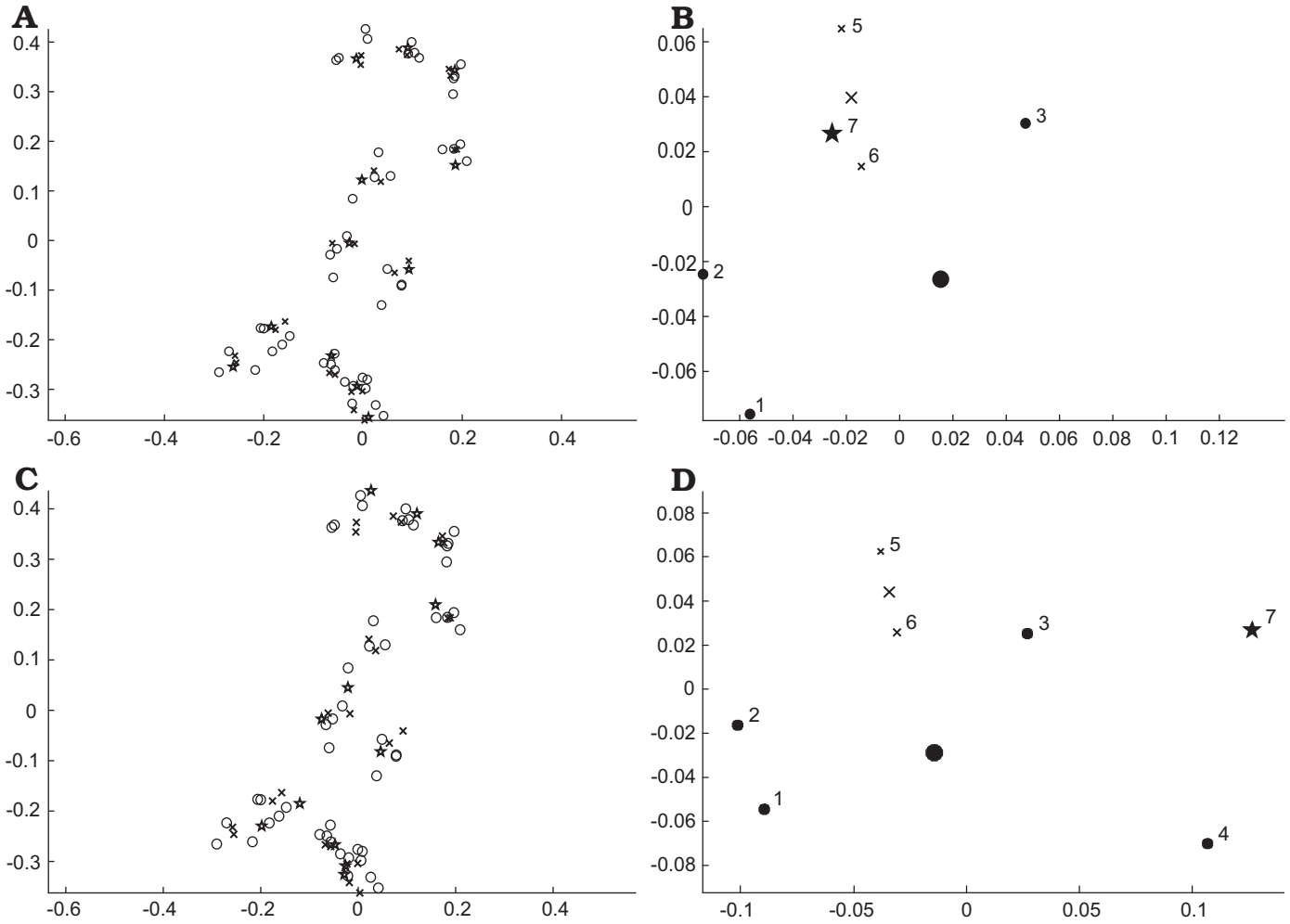


Fig. 10. Procrustes fits (**A**, **C**) and PCA values (**B**, **D**) of *Dicraeosaurus*, *Giraffatitan*, and *Amargasaurus* femora. **A**. Procrustes fits of *Dicraeosaurus sattleri* (circles), *Dicraeosaurus hansemanni* (crosses), and *Giraffatitan brancai* (stars), posterior face. **B**. PCA values of same taxa, larger symbols denoting mean values for each group; 1, MB.R.2695; 2, MB.R.2696; 3, MB.R.4886.92; 4, MB.R.4886.93; 5, MB.R.2638; 6, MB.R.2697; 7, MB.R.2633. **C**. Procrustes fits of *D. sattleri* (circles), *D. hansemanni* (crosses), and *Aicraeosaurus cazaui* (stars), posterior face. **D**. PCA values of same taxa, larger symbols denoting mean values for each group; 1, MB.R.2695; 2, MB.R.2696; 3, MB.R.4886.92; 4, MB.R.4886.93; 5, MB.R.2638; 6, MB.R.2697; 7, MACN-N 15.

(*D. hansemanni*) into group 1, and MACN-N 15 (*Amargasaurus cazaui*) into group 2 (*Giraffatitan*). Cross-validation yields 73.3% of the cases classified correctly, as in addition to the wrong cases mentioned above, MB.R.2632 (group 1) is ordered into group 3, and MB.R.2657 (*D. sattleri*) into group 1.

Adjusted a priori probabilities are for group 1 0.433, for group 2 0.4 and for group 3 0.167. Testing with the adjusted a priori probabilities yields an incorrect original classification for MB.R.2642 (group 1, but ordered into group 3), MB.R.2657 (group 3, but ordered into group 1), MB.R.4912 (group 3, but ordered into group 1), and for MACN-N 15 (group 3, but ordered into group 2). Cross-validation categorises additionally MB.R.2650 and MB.R.2653 (group 1) as group 3, and MB.R.2631 (group 3) as group 1. *Amargasaurus* is determined as group 2 (*Giraffatitan*). Therefore, only MB.R.2655 (*D. sattleri*) is correctly categorised as group 3 (SOM: table 5). In total, the proportion of assignments to the correct group is 86.7% for an original classification and 76.7% for the cross-validation.

Femora.—Separate tests of each character variable by Wilk's Lambda yield the four significantly different variables X3, X4, X6, and X7 out of 20 (SOM: table 6). Box's M Test for the three groups yields a significance value of 0.105, proving that the group matrices are not similar to each other and supporting that the chosen characters make the groups separable from each other. The log determinant is 220.701 for the group of all femora (groups 1–3 together) (SOM: table 7). Of the two discriminant functions, the first function with the highest eigenvalue explains 79.5% of the variance, and the second function explains the remaining 20.5%. The Chi-squared test yields significance values of 0.000 for the first function, and 0.003 for the second function, demonstrating that both discriminant functions are suitable to separate the three groups from each other (SOM: tables 8, 9). In the structure matrix, those variables with significantly different group mean values (X4 and X7 for discriminant function 1, and X3 and X6 for dicriminant function 2) are most distinguishable.

In the original classification, 86.7% of cases are ordered

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into the predicted group (SOM: table 10). Incorrect classifications are: MB.R.2661 and MB.R.2667 (both group 1) are categorised as group 3, MB.R.2696 (group 3) as group 1, and MB.R.4886.93 (group 3) as group 2. Cross-validation yields 80% of the cases classified correctly. Additionally to those cases above, MB.R.2638 (group 3) is ordered into group 1. In the test with the a priori probabilities for the group memberships adjusted to the real group sizes, MB.R.2661 (group 1) is categorised correctly as group 1 in a case-by-case categorisation, whereas all other cases are ordered similarly to the other analyses. In total, the proportion of correct identifications is 90% for case-by-case categorisation, and 80% for the cross-validation.

Discussion

Implications for species separation. —Shape differences between *D. sattleri* and *D. hansemanni* are detected by linear and geometric morphometric measurements most convincingly for the humeri, but less so for the femora. These differences are not only produced by individual preservation of the bones, but appear to be genuine and sufficient to separate both groups. Still, a problem in these analyses and especially for the geometric analyses of landmark positions is the partially very variably preserved surface of the bones. Lost bone fragments, such as the distal condyles of MB.R.2915 and the displaced 4th trochanter of MB.R.4886.93, strongly affect the values and therefore should be treated carefully. Another problem is the very low sample size, which meant that damaged elements could not be excluded.

The morphometric measurements corroborate a significant difference between humerus and femur of *D. sattleri* and *D. hansemanni*, which supports their taxonomic separation. The clear shape differences between the humeri and femora of the two species of *Dicraeosaurus* on the one side and *A. cazaui* on the other contradict the hypothesis of a close relationship between *A. cazaui* and *D. sattleri* (Salgado 1999), at least with respect to humerus and femur. Moreover, based on humeri and femora, a non-ambiguous generic separation between *Amargasaurus* and *Dicraeosaurus* seems possible. The differentiation of the two species of *Dicraeosaurus* from the Middle and Upper Dinosaur members by humeri and femora is a first step towards species separation, which requires also a comparison of the axial skeletons.

Functional implications.—The observations of a stronger differentiation of the humeri of the *Dicraeosaurus* species, but only modest differences in the femur, are consistent with the observation of a general trend in neosauropods to have a more plastic humerus than femur (Bonnan 2007; Bonnan et al. 2010). Indeed, the humerus in neosauropods may be generally subject to more extensive morphological changes than the femur because of its less pronounced role in locomotion (Bonnan 2007; Bonnan et al. 2010).

The elevated position of the humeral head and more proximally positioned deltopectoral crest in *D. hansemanni* would move the muscles attaching to the deltopectoral crest ("scapular deltoids", see Bonnan 2004, 2007) slightly more in the direction of the humeral articular joint. This would result in a slightly increased range of movement of the humerus around its articular joint, but a slight reduction of the relative mechanical power and torque of these muscles in *D. hansemanni* in comparison to *D. sattleri* (see Bonnan 2007 for explanations).

Because of the slight difference in femur lengths, but the clear difference in humerus lengths, the ratio between these two elements in *D. hansemanni* and *D. sattleri* must diverge. Specifically, the humerus is relatively shorter in relation to the femur in *D. sattleri*, and this would lead to differences in its arc of movement and mechanical power as implied by the different position of the deltopectoral crest. This compromising of humeral mobility would be offset by the increased power for forelimb movement. Unfortunately, only a few elements of the antebrachium are known for *Dicraeosaurus*, making it impossible to investigate the relative length of its whole forelimb. The measured morphometric difference between the fore and hindlimb would have consequences for the anatomy and skeletal reconstruction of *D. sattleri*, resulting in a slightly more anteriorly declining line of the presacral vertebral column in comparison to *D. hansemanni*.

Comments on numerical methods.—In the linear and geometric morphometric measurements including *Amargasaurus cazaui*, the humerus and femur of the latter differ clearly from *D. sattleri* and *D. hansemanni*. Whereas the TPS analyses run by TPS Splin result in large differences between *A. cazaui* and *Dicraeosaurus*, the PCA differences run by PCAGen6 are smaller. Both programs give the same conclusions about shape differences, but dimensions differ. These dimensional differences could be caused by a higher sensitivity of the TPS analysis for displaced landmark groups resulting in high bending energy values. The PCA values are results of changed eigenvalues, thus they are produced by a completely different way of measuring, which nevertheless leads finally to the same shape differences.

The very low number of objects per measurement makes it nearly impossible to use statistics for mean values or tests of significance like a MANOVA for differences. Consequently, MANOVA results were non-significant, e.g., for six tested femora (yielding five degrees of freedom for femur distribution) for both X and Y coordinates, a clearly non-significant distribution of the partial warp scores resulted. This is because the sample size was too small to meet the criterion of the MANOVA that a minimum of 20 values per variable should be used (Bookstein, 1991).

DFA results confirmed a single group for the humeri and femora of *Dicraeosaurus*. The shape similarities between the humeri and femora of *Dicraeosaurus* and those of diplodocids (here "*Barosaurus*" and *Tornieria*) might be consistent with the closer phylogenetic relationship between these two groups than to *Giraffatitan*. However, it should be considered that the *Giraffatitan* group is the only monophyletic group used here, whereas both other groups are more het-

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erogeneous. Interestingly, the humerus of *Amargasaurus* was, because of its partial warps values, sorted away from *Dicraeosaurus* and into group 2 (*Giraffatitan*) instead. It can be assumed that also in respect to the relatively narrow shaft, the humerus of *Amargasaurus* resembles more that of *Giraffatitan* than that of Diplodocidae and Dicraeosauridae.

Acknowledgements

We are indebted to the preparators Markus Brinkmann and Lutz Berner (both MfN) for helping us with transport and manipulation of the humeri and femora of *Dicraeosaurus* in the MfN. DSW thanks Alejandro Kramarz (MACN) cordially for the possibility of examining the femur and humerus of *Amargasaurus cazaui*. We are indebted to Wolfgang Kiessling and Oliver Hampe (MfN) for giving valuable hints and help on the morphometric analyses, as well help in the Bachelor thesis of NB. We are very grateful to an anonymous referee and Matt Bonnan (Richard Stockton College, New Jersey, USA) for their helpful comments and generous advice especially on the improvement of the statistics and the interpretation of our data. Finally, we thank cordially the editor Michael Benton (Bristol University, UK), whose work very much improved the quality of the manuscript and made it more concise.

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