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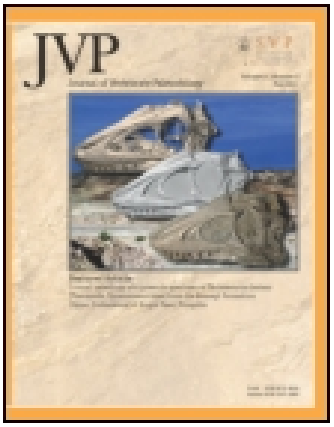

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Skeletal variation and ontogeny of the Late Triassic Dinosauriform Silesaurus opolensis

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ARTICLE

SKELETAL VARIATION AND ONTOGENY OF THE LATE TRIASSIC DINOSAURIFORM *SILESAURUS OPOLENSIS*

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ABSTRACT—A principal component analysis (PCA) performed for a set of 24 measurements on 33 femora and 15 measurements on 20 ilia of *Silesaurus opolensis* from the early Late Triassic of Krasiejów, southern Poland, shows that this sample is highly variable but probably monospecific. Most of the morphological variation is concentrated in the muscle attachments and proportions of bones, which significantly change in both size and position during ontogeny. Despite the small sample size, femora of smaller individuals have less flattened shafts and a more sinusoidal appearance. In many large specimens, proximal parts of muscle tendons are ossified at their attachment site on femora and remain attached to the bone in the largest specimens. The specimens with attached ossifications are interpreted as mature females that were statistically larger than proposed males. It is suggested that ossifications developed in females under calcitonin control. The intrapopulation variability of ilia is high, but less dependant on ontogeny. The population represented by a few specimens from the lower level at Krasiejów may represent a different stage in the evolution of the species than that from the upper horizon.

SUPPLEMENTAL DATA—Supplemental materials are available for this article for free at www.tandfonline.com/UJVP

INTRODUCTION

Among Triassic archosaurs closely related to the dinosaur clade, those in the family Silesauridae, which show herbivorous adaptations in their teeth and a horny beak in the lower jaw, seem to be geographically most widespread and temporally long-ranging (Ezcurra, 2006; Ferigolo and Langer, 2006; Nesbitt et al., 2010; Kammerer et al., 2012). The most completely known silesaurid is *Silesaurus opolensis* Dzik, 2003, from the late Carnian deposits exposed at Krasiejów in southern Poland. It is represented by several articulated partial skeletons and numerous isolated bones (Dzik, 2001, 2003; Dzik and Sulej, 2007; Mazurek and Słowiak, 2009; Piechowski and Dzik, 2010) that make it probably the largest available sample of a member of the dinosaur stem group. There is much variation among specimens, especially in femoral and iliac structures, presumably in connection with their important functional and sexual roles. The present paper attempts to explore this unique opportunity of having insight into variability and ontogeny of such a phylogenetically important animal. The crucial questions addressed are the morphological differences and taxonomic value of particular varying traits.

MATERIALS AND METHODS

The available material is generally well preserved, although shafts of long bones are usually crushed and some degree of deformation may alter the original proportions of the bones. Therefore, we did not use landmark-based shape analysis, restricting our analysis to simple measurements taken with a caliper. This allowed better control of deformational artifacts (especially in case of displacement or rotation of crushed bone segments) and to omit areas where deformation affected the dimensions of particular bone structures.

Thirty-three more-or-less complete femora were used in this study: ZPAL AbIII/361/23L, 361/21R, 1930L, 460/1L, 411/4R, 563/7R, 405L, 362R, 362L, 363L, 1914R, 457L, 2498L, 407/1L, 2514L?, 1266R, 403/5L, 1272R, 1263R, 1884L, 2063R, 2068R, 1155/1R, 458/1L, 2515R, 458/6L, 1269R, 2516R, 907/10R, 2380R, 907/11L, 907/9R, and 2534R. Their morphology has been quantified by measuring 38 linear traits (Fig. 1A).

A peculiar aspect of femoral variability in *Silesaurus opolensis* is the presence of additional bony structures (Fig. 2). The osseous structures of irregular rosette shape have distinct sharp margins and a fissure separating them from the bone proper at least near their margins. Their central elevated areas are truncated, and they represent the basal parts of muscle tendons, which sometimes ossify in vertebrates (Hutchinson, 2002). They are located on the muscle attachment site near to, or on, the trochanters (Fig. 2). In some smaller individuals, the bone surface on which such ossifications develop is marked by a rough area.

Incipient ossification of tendon heads cannot be confirmed in the material because the calcified parts apparently detached during decay. They remained attached only after the ossification had resulted in unification of the ossified tendon with the femur surface. This result suggests that ossification of the tendons was rapid. Hence, there are only two classes of specimens: those lacking ossifications and those with ossifications already well developed. We propose that the dorsolateral, lateral, and fourth trochanter ossifications probably appeared simultaneously in ontogeny (Fig. 2). Specimens with tendon ossifications have also developed a characteristic 'overhang structure' on the proximal femoral head (Fig. 2A) that is interpreted as a calcification of the articular cartilage (see Holliday et al., 2010).

In non-avian dinosaurs, tendon ossifications develop mostly in the tail, and we have not been able to trace in the literature any

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*Corresponding author.

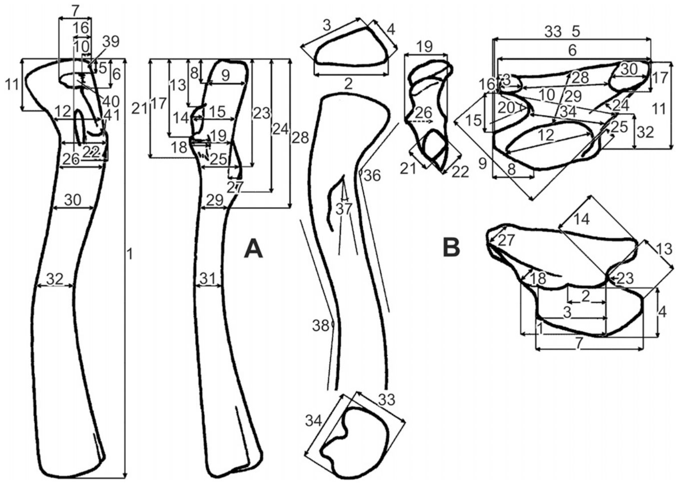

FIGURE 1. Characters measured on femora (1–38, **A**) and ilia (1–34, **B**) used in the first factor analysis. Characters 39–41 (**A**) mark ossifications on the femur that were not included in the factor analysis.

mention of these kinds of separate ossifications associated with hind limbs, although such structures are common in birds (e.g., Hutchinson, 2002). Their histology is similar to that of regular bone (Moodie, 1928; Organ and Adams, 2005; Zhou et al., 2010). It is possible that the trochanteric shelf in some dinosaurs is of such origin (Raath, 1990; Nesbitt et al., 2009).

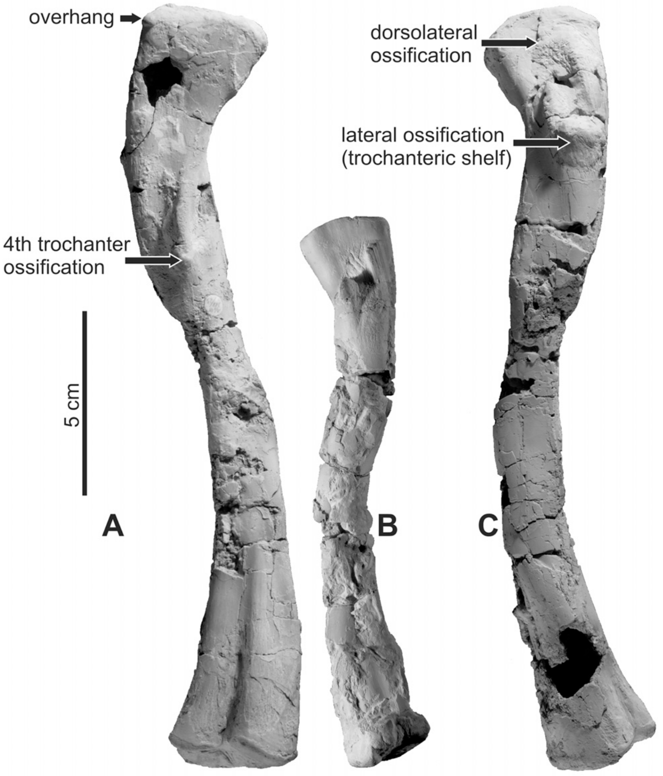

FIGURE 2. Femora of *Silesaurus opolensis* Dzik, 2003, from the late Carnian of Krasiejów. **A**, ZPAL AbIII/361/23 left femur of a large individual in posteromedial view; **B**, ZPAL AbIII/457L left femur of a small individual in anterolateral view; **C**, ZPAL AbIII/361/21 right femur of a large individual in lateral view (note that the proximal part of bone is a little twisted in relation to the distal part).

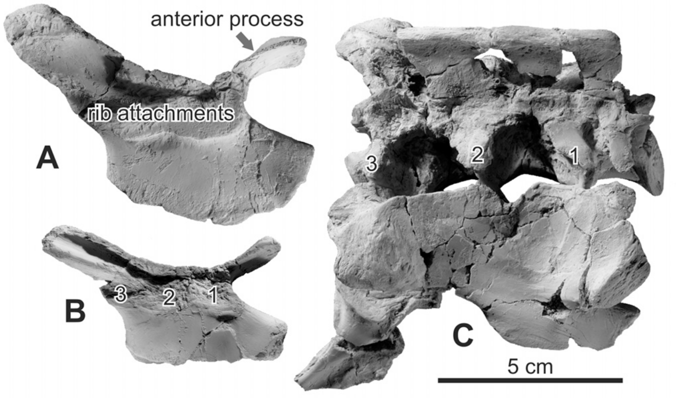

FIGURE 3. Ilia of *Silesaurus opolensis* Dzik, 2003, from the late Carnian of Krasiejów. **A**, ilium of a large individual ZPAL AbIII/404/2 in medial view; **B**, ilium of a small individual ZPAL AbIII/907/8 in medial view; **C**, pelvis of a large individual ZPAL AbIII/362R in lateral view. Note the shape of rib attachments (**A**, **B**) and width of anterior and posterior iliac processes.

Twenty ilia were available for measurement: ZPAL AbIII/404/2L, 2517L, 404/1R, 907/8L, 907R, 362R, 362L, 2518L, 400R, 2519R, 2520L, 1202L, 2521R, 1835R, 439/1L, 363R, 363L, 2522R, 361R, and 361L, and 34 linear traits have been measured (Fig. 1B, Fig. 3).

The objective of the analysis was to estimate the range of variation in the sample and identify its possible multimodal distribution or discrete groups of specimens. To determine this, we used principal component analysis (PCA). Due to incompleteness of the bones, the data matrix includes many missing measurements. There are many ways of replacing missing data. The simplest is to substitute missing values with the mean of the available data. However, if the amount of missing data is great, then their substitution requires a more sophisticated approach (Jackson, 1991). Most of the morphological characters we measured depend on size of the individual being measured. Therefore, we created a method of substituting a missing measurement by multiplying the arithmetic mean of a character by a coefficient of relative specimen size. The coefficient was based on characters 1, 2, 34, 33, 11, 25, 26, 9, 20, 15, 12, 31, and 32 (femur) and 5, 6, 13, 14, 34, 4, 19, 11, 1, 25, 16, and 17 (ilium) (Fig. 1). Bones of the same individual were analyzed together, so the same coefficient value was applied to each of them. Although this has introduced an artificial clustering of points in the center of the PCA plots, such procedure makes interpretation of incomplete specimens possible, although one has to be aware of resulting distortion of data.

For bivariate plots, we estimated relative specimen size for each individual by comparing available measurements of particular bones with those of more completely preserved specimens. The inferred specimen size was then standardized with respect to the mean.

We performed several Student's t-tests to check if the differences between observed groups of femora (e.g., with overhang structure or without it) are statistically significant.

Factor Analysis

Factor analysis is a technique of data exploration, which finds the hidden structure of the latent variables responsible for the observed relationships between the data. The analysis is limited to such factors that can be expressed as a sum of the weighted variables.

We used this method to reveal factors engaged in observed variation. We tried to check if factors are linked to ontogeny, intraspecific variation, or the presence of two separate species.

Factor analysis was performed for 38 femoral variables and 34 iliac variables (Fig. 1), as well as 24 (femoral) and 15 (iliac) variables (Tables 1 and 2) belonging to the values standardized and normalized in respect to the means of particular features. Main factors were identified by PCA. We created scree plots and applied the Kaiser criterion to determine the number of factors necessary to describe adequately the distribution: eight for the femur and five for the ilium (see supplementary data).

We applied multidimensional scaling for 24 variables of the femur and 15 of the ilium (Tables 1 and 2). The distance matrix of standardized measurements was figured for each animal. As the measure of the distance between each two animals, we used the root of the sum of squared differences in each individual variable (in Euclidean distance).

Student's t-Test

We performed 26 Student's t-tests for the whole femoral sample. The independent binary variable (grouping) was the presence of the 'overhang structure': (1) exists or (0) does not exist. We chose this character, because it is possible to trace its presence (or absence) on almost all specimens and it defines two distinct classes in the sample. The null hypothesis was the assumption that the average values of the dependent variable in both groups are the same. All 26 tests were performed at the significance level of 5%. Means and standard deviations were rounded to two figures and the standard error of the mean was estimated.

TABLE 1. Measurements used to calculate the morphological distance between femora.

No.	Name
1	Upper edge of femoral head compression (ratio of 2 and 9 in Fig. 1A)
2	Lower edge of femoral head compression (ratio of 15 minus 14 and 12 in Fig. 1A)
3	Femoral neck compression (ratio of 20 and 19 in Fig. 1A)
4	Compression below first ridge of fourth trochanter region (ratio of 25 and 26 in Fig. 1A)
5	Proximal part of femoral shaft compression (ratio of 29 and 30 in Fig. 1A)
6	Middle part of femoral shaft compression (ratio of 31 and 32 in Fig. 1A)
7	Distal end compression (ratio of 33 and 34 in Fig. 1A)
8	Femoral head curvature angle (measurement 36 in Fig. 1A)
9	Femoral shaft curvature angle (38 in Fig. 1A)
10	Distance between dorsolateral trochanter to proximal end (8 in Fig. 1A)
11	Anterior dorsolateral trochanter location (10 in Fig. 1A)
12	Dorsolateral tuber area (40 in Fig. 1A)
13	Anterior trochanter size (14 in Fig. 1A)
14	Distance between the anterior trochanter to proximal end (13 in Fig. 1A)
15	Anterior trochanter location (16 in Fig. 1A)
16	Lateral ossification size (18 in Fig. 1A)
17	Distance between proximal edge of lateral ossification to proximal end (17 in Fig. 1A)
18	Distance between distal edge of lateral ossification to proximal end (21 in Fig. 1A)
19	Anteroposterior muscle attachment of anterior trochanter and lateral ossification extent (22 in Fig. 1A)
20	Fourth trochanter size (27 in Fig. 1A)
21	Distance between first ridge of fourth trochanter to proximal end (23 in Fig. 1A)
22	Distance between second ridge of fourth trochanter to proximal end (24 in Fig. 1A)
23	Fourth trochanter angle (37 in Fig. 1A)
24	Overhang presence (39 in Fig. 1A)

Each of the measurements was standardized.

TABLE 2. Measurements used to calculate the morphological distance between ilia.

No.	Name
1	Anterior process length (measurement 14 in Fig. 1B)
2	Postacetabular process length
3	Preacetabular process length (13 in Fig. 1B)
4	Ischiatic process length (32 in Fig. 1B)
5	Distances between muscle attachments ratio (28 in Fig. 1B)
6	Angle between anterior and preacetabular processes (20 in Fig. 1B)
7	Distances from lower ridge to medial ridge and to brevis shelf ratio (24 in Fig. 1B)
8	Anteroposterior iliac blade extent (6 in Fig. 1B)
9	Lateromedial bone thickness (19 in Fig. 1B)
10	Lateromedial ischiatic process thickness (25 in Fig. 1B)
11	Distances from the anterior process to the preacetabular process and from the postacetabular process to ischatic process ratio (11 to 15 in Fig. 1B)
12	Acetabulum depth (26 in Fig. 1B)
13	Acetabulum width (12 in Fig. 1B)
14	Iliac median width (34 in Fig. 1B)
15	Area above attachment

Each of the measurements was standardized.

We also prepared several bivariate plots to display possible trends in the ontogeny of *Silesaurus*. The lack of histological data for each specimen forced us to choose total bone length as an age indicator. This seems defensible as the length of the bones engaged in locomotion is usually linked with body length mass (Klein and Sander, 2008). We are aware that this assumption may have resulted in introducing error into interpretations of the plots. Therefore, we figured and discussed only the most apparent trends. We use linear correlation and Spearman rank correlation tests to check the statistical significance. Unfortunately, the number of specimens is too small to reveal significant results in some cases.

RESULTS

The measurements of femora and ilia were used to perform the first PCA. Eight factors were identified in the matrix of 38 femur measurements, and five factors were identified in the matrix of 34 ilium measurements. The obtained plot shows the dominance of ontogenetic variability, which obliterates other factors. Apparently, the linear dimensions of bones express both population variability and directional ontogenetic change, whereas coefficients reflect only variability at each ontogenetic stage. To remove this bias, we created a covariance matrix of 15 iliac variables and 24 femoral variables, which are not directly dependent on size (see Supplementary Data). These are mainly angles between bone structures, the presence or absence of various features, and surface area or linear measurements in relation to specimen size (Fig. 1, Tables 1 and 2). They were used in the second PCA and Student's t-tests. Size dependence has ceased in the second data set and new significant factors emerge. Four factors appear essential for the femur and two factors for the ilium (see Supplementary Data).

Because of bone incompleteness the data matrix includes many missing measurements. Substitution of a missing measurements based on the coefficient of relative specimen size enabled use of incomplete specimens in the PCA, but this has resulted in an artificial clustering of such specimens in the center of the plots (Figs. 4, 5).

More complete specimens of femora form a ring around the central cluster of points (Fig. 4). Main characters (factor 1)

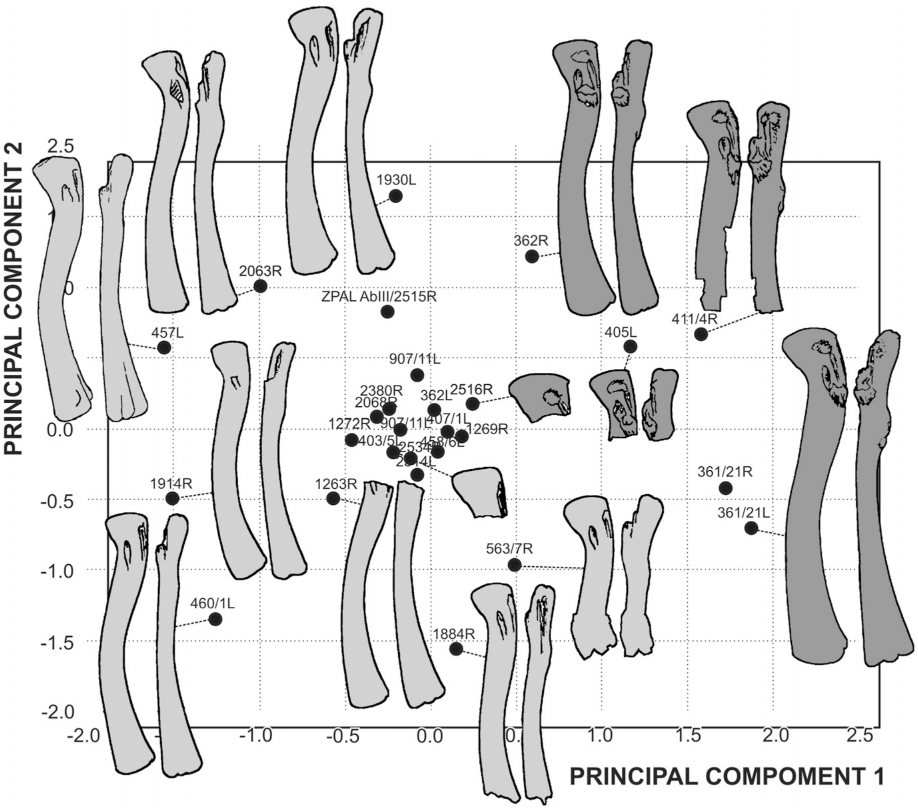

FIGURE 4. Principal component analysis plot for femora. The difference between any two animals is expressed by the root of the sum of squared differences among each of 24 different parameters. The total stress (sum of squared differences between the predefined distances and those that go on the chart) amounts to 37.069. The cluster of specimens in the center of the plot is an artifact of the method of supplementing missing data used in this study (see Materials and Methods). Darker color marks femora with ossifications.

responsible for the distribution of femoral in the PCA plot were linked to additional ossifications (Table 1, nos. 16, 17, 18, and 24). Other factors were connected with fourth trochanter variability, femoral head curvature, and femoral shaft compression (Table 1, nos. 4, 5, 8, 20, 21, 22, and 23).

The distribution of ilia on the PCA plot is more uniform (Fig. 5). The shallow ilia group at the bottom of the scattergram; small and high ones are above them. The total stress is also low. This shows that intraspecific variation dominates over ontogenetic differences. Main characters (factor 1) responsible for the distribution of the ilia were linked to the position of the brevis shelf, bone thickness, and width (Table 2, nos. 7, 9, 13, and 14). Other factors were connected with ischiadic process length, the angle between the anterior and preacetabular processes, anteroposterior iliac blade extent, and iliac height (Table 2, nos. 4, 6, 8, and 11).

Student's t-Test

The two recognized groups of femora (those with or without ossifications) significantly differ in a number of other variables (Table 3). This clearly shows that the ossifications developed with age, together with changing compression and curvature of the femur. Specimens with the overhang structure are statistically larger and bear extra ossifications.

However, there are no grounds to reject the null hypothesis of no difference for the other variables between groups with and without the overhang structure, and excluding the relative specimen size from the analysis did not change the results significantly.

Ontogenetic Changes in Bone Proportions

We used relative specimen size as an ontogenetic proxy. Size is not strictly correlated with ontogenetic age but approximates some trends. The small number of specimens means we are unable to obtain significant results for some trends on the bivariate plots.

The position of the dorsolateral trochanter (Figs. 1A, 6A, B) differs in larger and smaller individuals ($r = 0.8052$, $P = 0.0005$, $r_s = 0.7379$, $P = 0.0026$). Its distance from the posterior edge of the femur ranges from 6 to 13 mm (Fig. 6A), being located more anteriorly in larger individuals. The specimens with additional ossifications have the dorsolateral trochanter positioned distinctly further from the posterior edge of femur (8–13 mm). In contrast, femora without additional ossifications have this structure 6–9 mm from the posterior edge of the bone (Fig. 6A). Treating these two groups separately, trends are less visible: $r = 0.8024$, $P = 0.1023$, $r_s = 0.9$, $P = 0.0167$ and $r = 0.7195$, $P = 0.0289$, $r_s = 0.3347$, $P = 0.3747$, respectively. The distance from the dorsolateral trochanter to the end of the proximal femur ranges from 10 to 19 mm (Fig. 6B). Again, specimens with additional ossifications show a notably larger distance from the femoral edge to this structure (14–19 mm). There is also a positive relationship between the specimen size and this distance: $r = 0.6168$, $P = 0.0143$, $r_s = 0.6673$, $P = 0.0066$. However, no trends are visible in these separate groups alone: $r = 0.4614$, $P = 0.4341$, $r_s = 0.2052$, $P = 0.7333$ and $r = 0.2665$, $P = 0.4567$, $r_s = 0.3404$, $P = 0.3358$, respectively.

The femoral shaft angle (Fig. 6C) seems to be greater in larger individuals, but the trend is insignificant: $r = 0.7032$, $P = 0.1191$, $r_s = 0.7714$, $P = 0.1029$. It ranges from 139° to 151°. In contrast, the angle between femoral head and shaft (Fig. 6D) seems to be lower in larger specimens, but the trend is also insignificant: $r = -0.3187$, $P = 0.3395$, $r_s = 0.2145$, $P = 0.5265$. No positive or negative trend ($r = -0.0911$, $P = 0.8301$, $r_s = 0.0952$, $P = 0.8401$) can be observed from the fourth trochanter angle (Fig. 6E). All three angles (Fig. 1A) have notable variation but are not dependant on size (Fig. 6C–E).

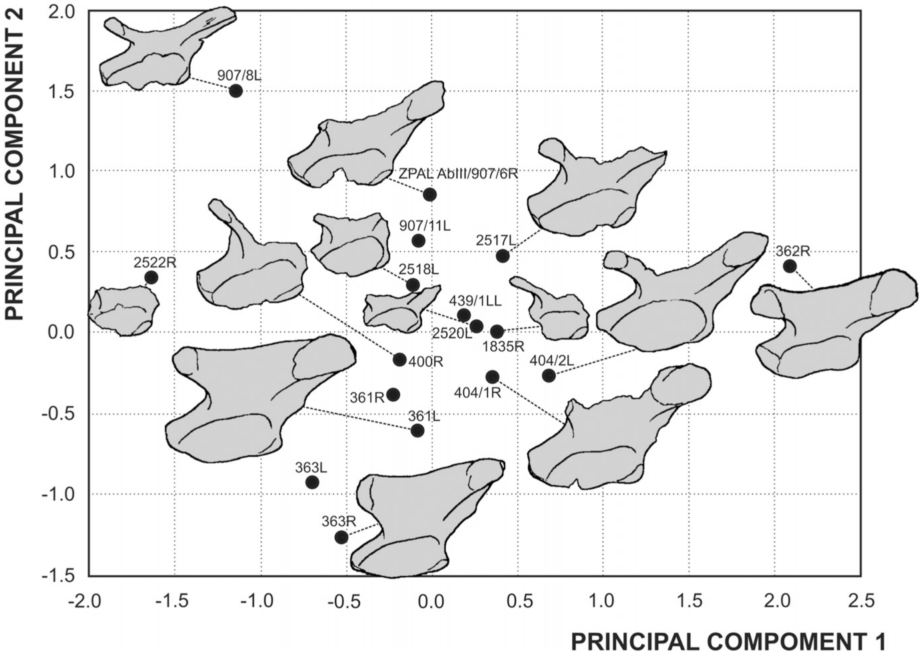

FIGURE 5. Principal component analysis plot for ilia. The difference between any two animals is expressed by the root of the sum of squared differences among each of 15 different parameters. The total stress (sum of squared differences between the predefined distances and those that go on the chart) is 4.612.

The ratio between femoral shaft length and width (measurement 32 and 31 in Fig. 1A) is larger in larger individuals (Fig. 6F). In the smallest specimen, this ratio is less than 1.2, whereas in the largest it is almost 1.6. Again, the change is insignificant probably due to small sample size: $r = 0.6577$, $P = 0.1084$, $r_s = 0.7143$, $P = 0.0881$.

Despite small number of specimens, we observed some possible ontogenetic changes. The femoral shaft changes its cross-sectional shape (Fig. 6F). It is circular and disproportionally narrower in small individuals and wide anteroposteriorly in larger specimens, which makes its cross-section more ovate. Also, the angle between the femoral shaft and the head changed during ontogeny (Fig. 6D). Heads are more erect in smaller individuals. The proximal part of femur is more curved in larger specimens (Figs. 2, 5), and they also have a larger fourth trochanter, but the angle between the fourth trochanter and the femoral shaft is variable (Fig. 6E). In smaller individuals, the femoral shaft is strongly curved, and it straightens in larger ones (Figs. 2, 4, 6C). The posteromedial tuber on the proximal femur head (tuberosity of Ezcurra, 2006) usually disappears with growth (Fig. 9), but it is retained in large femora without ossifications (unfortunately, this feature is not well preserved in several specimens).

The length and shape of muscle attachments on the anterior and posterior iliac processes (Figs. 1B, 5, 7A) are variable, and they are usually disproportionally longer in larger specimens ($r = 0.7816$, $P = 0.0379$, $r_s = 0.8469$, $P = 0.0246$ and $r = 0.6948$, $P = 0.0558$, $r_s = -0.0793$, $P = 0.8540$, respectively). In particular, the posterior iliac process is larger and reaches a length of almost 30 mm in the largest individual.

The distance between the ischiadic process and the attachment of the third sacral rib (Fig. 7B) is disproportionally greater in larger specimens: $r = 0.7495$, $P = 0.0126$, but $r_s = 0.6159$, $P = 0.0580$. The distance ranges from 11 to 26 mm.

The length of the iliac blade as well as the length of the lower part of the ilium (Fig. 7C) increase disproportionally in larger individuals: $r = 0.9778$, $P = 0.00002$, $r_s = 0.8434$, $P = 0.0137$ and $r = 0.9058$, $P = 0.00005$, $r_s = 0.8443$, $P = 0.0005$, respectively. The iliac blade is relatively longer in the largest specimens compared with the lower part of the ilium. Variation among individuals of similar size is low (Fig. 7C).

TABLE 3. Results of Student's t-tests.

Character	Group without the overhang structure	Group with the overhang structure	t	P
The index of size	1.065	0.946	t(21) = 3.12	0.005
The lower edge of femoral head compression	1.996	1.798	t(23) = 2.12	0.045
The level of femoral shaft curvature angle	−147.51	−145.44	t(23) = 2.2	0.038
The distance from dorsolateral trochanter to proximal end	0.3396	0.3126	t(23) = 2.29	0.031
The lateral ossification size	−0.82	0.37	t(11.08) = 0.52	0.009
The distance from proximal edge of lateral ossification to proximal end	0.2192	0.2322	t(9.20) = 0.01	0.018
The distance from distal edge of lateral ossification to proximal end	0.2602	0.2756	t(9.28) = 0.01	0.015

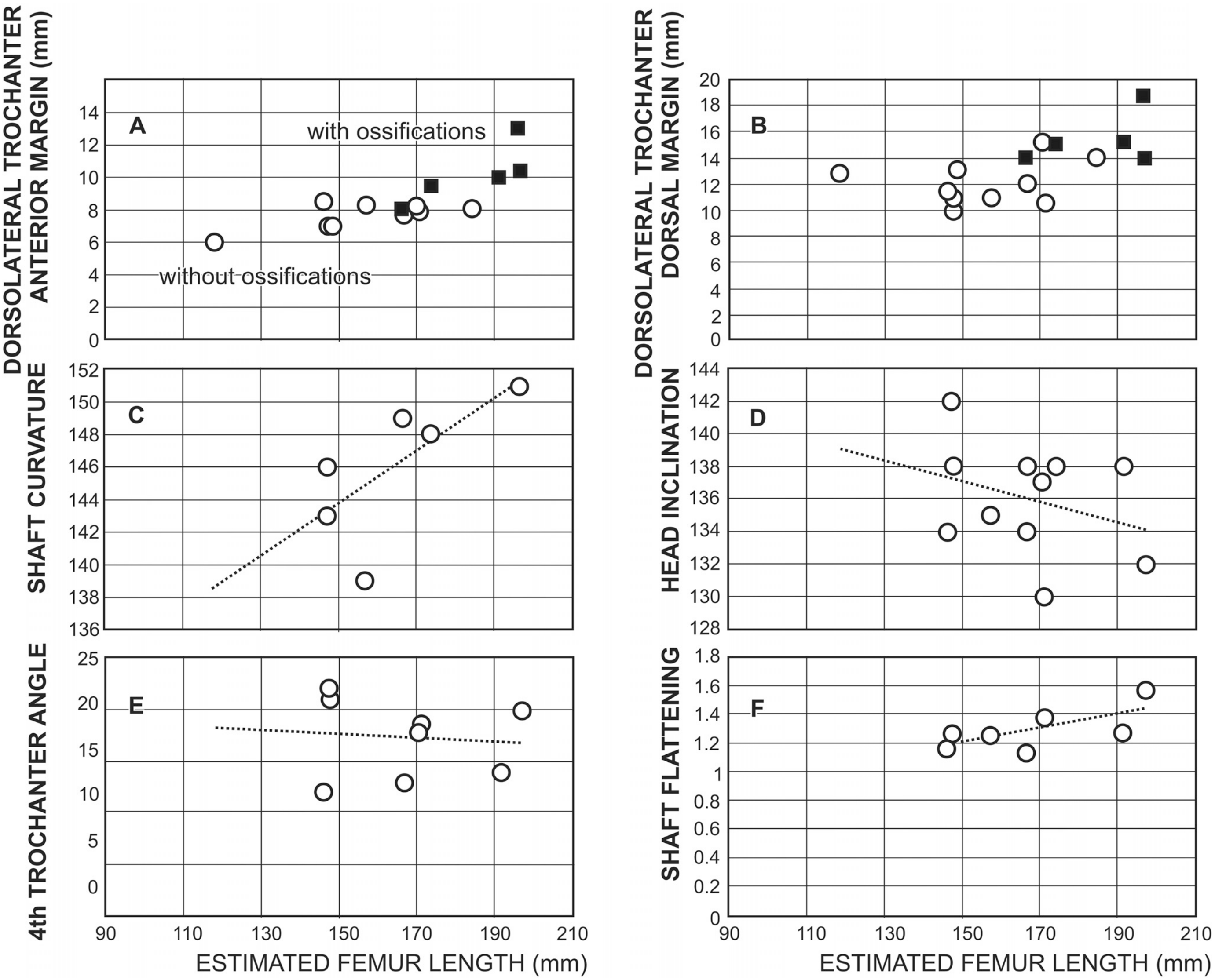

FIGURE 6. Ontogeny of femora. **A**, anterior dorsolateral trochanter location (measurement 10 in Fig. 1 A) plotted against specimen size as a measure of ontogenetic stage ($r = 0.8052$, $P = 0.0005$, $r_s = 0.7379$, $P = 0.0026$); **B**, distance from the dorsolateral trochanter to proximal femur end (measurement 8 in Fig. 1A) plotted against specimen size ($r = 0.6168$, $P = 0.0143$, $r_s = 0.6672$, $P = 0.0066$); **C**, femoral shaft curvature (measurement 38 in Fig. 1A) plotted against specimen size ($r = 0.7032$, $P = 0.1191$, $r_s = 0.7714$, $P = 0.1028$); **D**, angle between femoral head and shaft curvature (measurement 36 in Fig. 1A) plotted against specimen size ($r = -0.3187$, $P = 0.3395$, $r_s = 0.2145$, $P = 0.5264$); **E**, angle between fourth trochanter and femoral shaft (measurement 37 in Fig. 1A) plotted against specimen size ($r = -0.0911$, $P = 0.8301$, $r_s = 0.0952$, $P = 0.8401$); **F**, femoral shaft flattening (the ratio of measurement 32 and 31 in Fig. 1A) plotted against specimen size ($r = 0.6577$, $P = 0.1084$, $r_s = 0.7143$, $P = 0.0881$).

The height of the anterior iliac process and the whole ilium (Fig. 7D) has slightly different proportions in small and large individuals: $r = -0.4982$, $P = 0.2089$, $r_s = 0.0482$, $P = 0.9181$ and $r = 0.4885$, $P = 0.1821$, $r_s = 0.1958$, $P = 0.6123$, respectively. The height of the whole ilium increases slightly more than the height of the anterior iliac process, but the trend is insignificant.

The lengths of particular sacral rib attachments and their proportions are very variable (Fig. 8) and appear to be not related with specimen size.

Smaller ilia have prominent anterior and postacetabular processes. In larger individuals, these processes are proportionally longer. In contrast, the lower part of the bone grew proportionally slower during ontogeny (Fig. 7C). The muscle attachments grew faster on the anterior iliac process than on the posterior iliac process (Fig. 7A), but their shape is variable. The acetabulum depth increases with respect to the whole bone size. Small ilia are robust and their thickness increased slightly during growth, as did the height of ilium. The distance between the ischiadic process and the attachment of third sacral rib is variable (Fig. 7B).

DISCUSSION

Ontogeny

Histological sections of femora ZPAL AbIII/2380, 411, and 405 imply that they were probably skeletally mature (Fostowicz-Frelik and Sulej, 2010). We do not have histological data to determine the exact ontogenetic age of other specimens. However, the similar size and complete coossification of the vertebral centra of all examined individuals suggest that they were skeletally mature or close to it (Brochu, 1996; Irmis, 2007). Smaller femora are not represented in the sample, so we could only trace

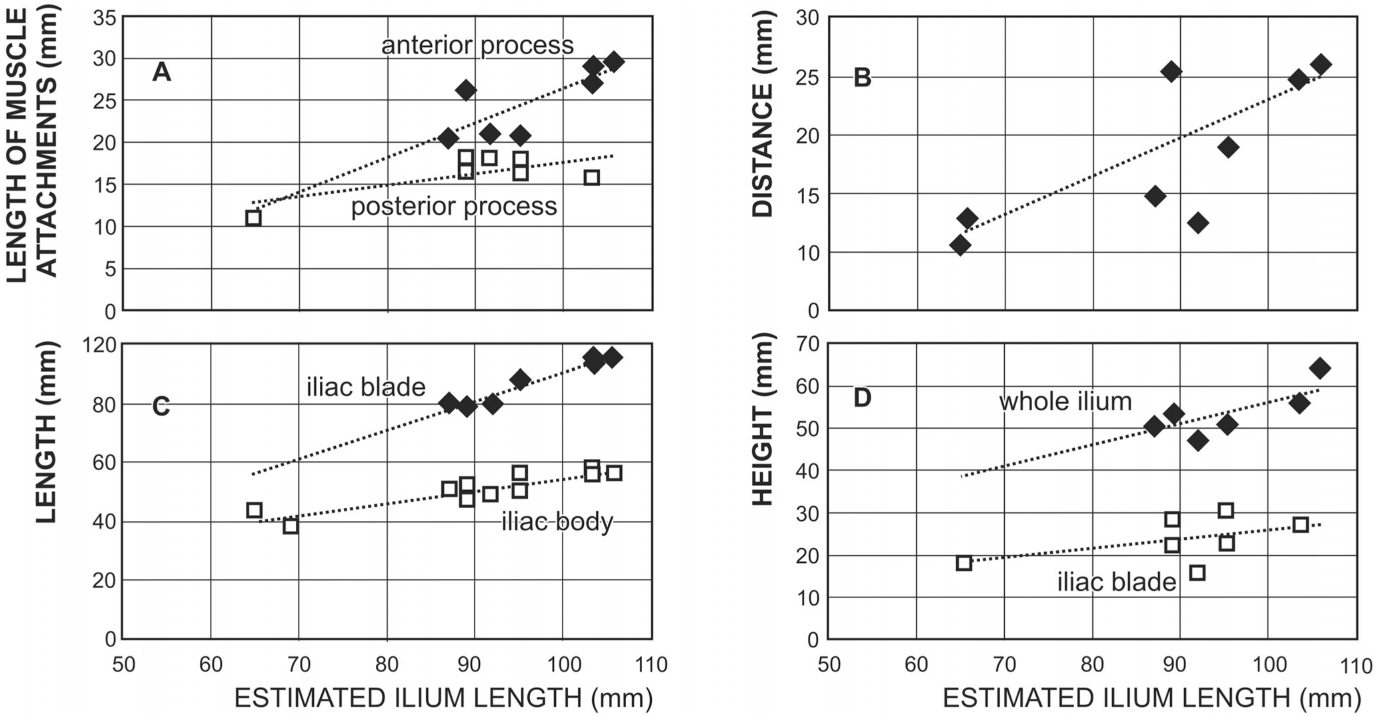

FIGURE 7. Ontogeny of ilia. **A**, length of muscle attachments on anterior and posterior iliac processes (measurement 30 and 31 in Fig. 1 B) plotted against the specimen size (measurement 30: $r = 0.7816$, $P = 0.0379$, $r_s = 0.8469$, $P = 0.0246$; measurement 31: $r = 0.6948$, $P = 0.0558$, $r_s = 0.0793$, $P = 0.8540$); **B**, distance between the ischiadic process and the attachment of the third sacral rib (measurement 32 in Fig. 1B) ($r = 0.7495$, $P = 0.0379$, $r_s = 0.6159$, $P = 0.0580$); **C**, length of iliac blade (measurement 5 in Fig. 1B) and the length of the ventral part of ilium (measurement 7 in Fig. 1B) (measurement 5: $r = 0.9778$, $P = 0.00002$, $r_s = 0.8434$, $P = 0.0137$; measurement 7: $r = 0.9058$, $P = 0.00005$, $r_s = 0.8443$, $P = 0.0005$); **D**, height of the anterior iliac process (measurement 15 in Fig. 1B) and ilium (measurement 11 in Fig. 1B) (measurement 11: $r = -0.4982$, $P = 0.2089$, $r_s = 0.0482$, $P = 0.9181$; measurement 15: $r = 0.4885$, $P = 0.1821$, $r_s = 0.1958$, $P = 0.6123$).

changes in late ontogeny. Some inferences on earlier stages of ontogeny are possible only by extrapolation of trends recognizable in the variability of medium- and large-sized specimens. These specimens differ significantly in size and thus, presumably, in their ontogenetic age. The ilia show a wider size distribution and presumably a larger span of ontogeny.

The femoral shaft widens anteroposteriorly and becomes oval in cross-section during the ontogeny of *Silesaurus* (Fig. 6F). A similar change was observed in the ontogeny of *Allosaurus* by Foster and Chure (2006). Presumably, juveniles had a more multidirectional load and stress on the hind limb because of their more agile running (Foster and Chure, 2006). However, data on bird locomotion suggest that there is no direct correlation between femoral shaft geometry and appendage movements (Habib and Ruff, 2008; Farke and Alicea, 2009). The femoral shaft also becomes increasingly straight (Fig. 6C), as in *Coelophysis*

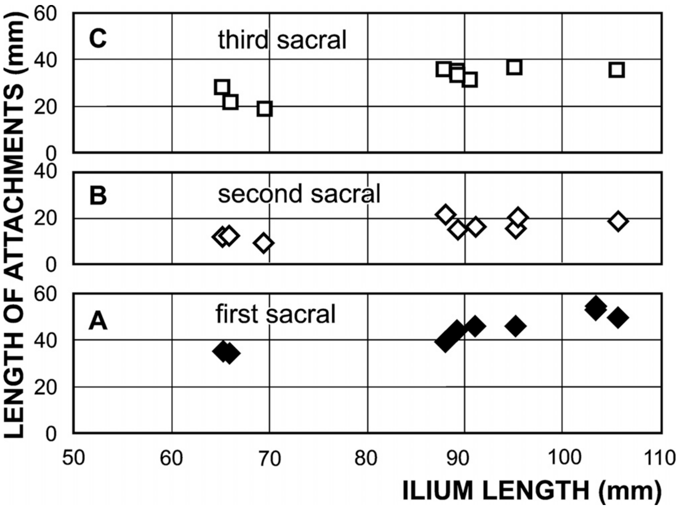

FIGURE 8. Length of sacral rib attachments to ilia of different size.

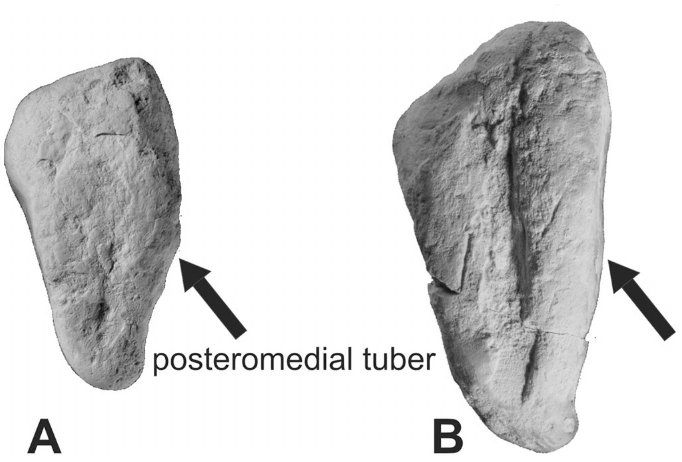

FIGURE 9. The proximal end of femora. **A**, small individual ZPAL AbIII/457L with posteromedial tuber (arrow); **B**, large individual ZPAL AbIII/361/23 without posteromedial tuber (arrow).

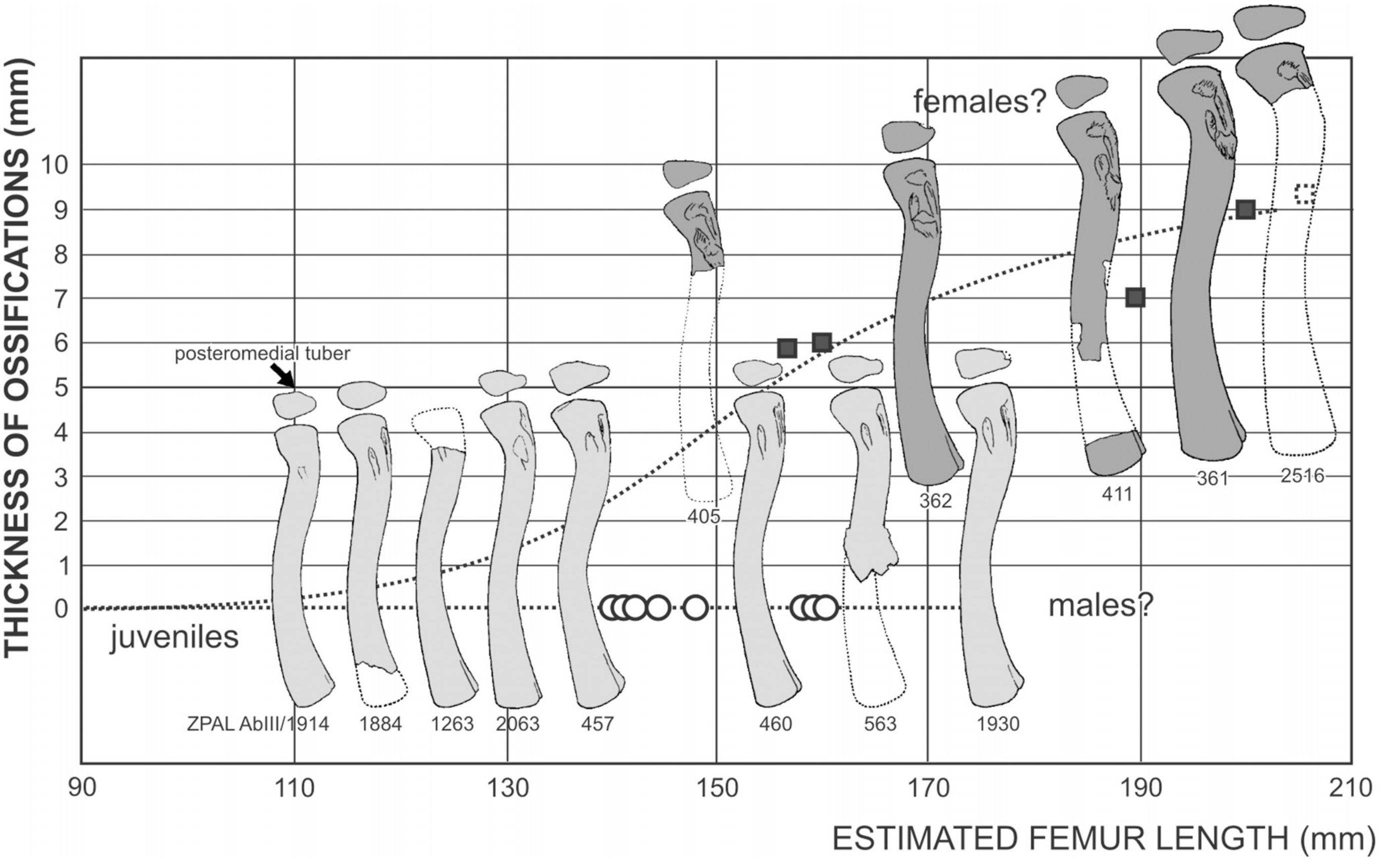

FIGURE 10. Proposed interpretation of the variability of *Silesaurus opolensis* femora as being an expression of sexual dimorphism. Males would be significantly smaller than females.

(Colbert, 1989). The femoral head is more curved anteriorly in larger specimens (Fig. 6D), and the fourth trochanter is higher. The depth of the acetabulum also increases slightly. All these changes may reflect adaptation to carrying a heavier body more efficiently and may also be a compensation for disproportionally shorter tibia, as a kind of trade-off.

Body proportions changed during the growth of *Silesaurus*, as suggested by the only two specimens preserved completely enough to offer a femur/tibia ratio. In specimen ZPAL AbIII/1930, the ratio is 1.13 (femur 16.0 cm, tibia 14.2 cm). In the larger individual ZPAL AbIII/361, the same ratio is 1.25 (femur 20.0 cm, tibia 16.0 cm). This suggests that the femur grew faster than the tibia and that smaller individuals might have run relatively fast for their size (Foster and Chure, 2006), but inferring cursoriality from bone proportions is a complex problem in extinct animals (Farlow et al., 2000). Our suggestion may be supported by the fact that smaller individuals are generally subjected to greater predatory pressures (Pounds et al., 1983), because relatively few carnivores are able to attack larger prey. Having a longer femur with respect to the tibia enables carrying a heavier body mass (Fechner, 2009). However, these two specimens were found in different layers and may represent morphologically different populations.

Ossifications of tendons on the femur developed late in ontogeny and simultaneously in different locations (Fig. 10). Presumably, as suggested by the rough surface of muscle attachment area, in smaller individuals a layer of cartilaginous tissue was developed there, such as on the epiphyses of crocodiles (Suzuki et al., 2003).

Calcified tendon attachments (Fig. 2) and articular cartilage (overhang structure) are associated with the lack of a posteromedial tuber (Fig. 9B) and a dorsolateral trochanter positioned relatively far from the bone margins (Fig. 6A, B). The posteromedial tuber is present in specimens lacking any additional ossifications, and these specimens have a dorsolateral trochanter positioned relatively close to the bone margin. As supported by t-tests, femora with ossifications are generally larger than those without them (Fig. 4). It would therefore seem apparent that femora with ossifications represent a later ontogenetic stage. Calcification of cartilaginous elements is induced by calcitonin in all vertebrates (Sasayama, 1999; Lyritis and Boscainos, 2001). In fishes (salmon), an increase of calcitonin level marks puberty in both sexes (Fouchereau-Peron et al., 1990). Secretion of this hormone is influenced by sex hormones: estrogens and androgens (Dacke et al., 1976).

In birds, living dinosaurs, ossifications in larger individuals are connected with a high level of calcitonin. In the Japanese quail (*Coturnix coturnix japonica*), castration of male birds considerably reduces the calcitonin level. This therefore indicates a relationship between calcitonin and gonadal hormone activity (Dacke et al., 1976) and that the possibly dimorphic pattern of ossification in *Silesaurus* may be an ancestral archosaur feature. As observed in *C. coturnix*, the females exhibit a three-fold increase in plasma calcitonin levels shortly before maturity, whereas males have more stable levels (Dacke et al., 1976). It is suggested that this surge in plasma calcitonin levels might be associated with the appearance of additional ossifications in the *Silesaurus* femora.

Size ranges of *Silesaurus opolensis* femora with and without ossifications overlap strongly (Fig. 10). Moreover, the range of variability in this respect seems to be largest among specimens of sizes close to the mean of the sample (Fig. 10; admittedly, the sample size is too small to prove this statistically). This may be an expression of limited correspondence between size and age (Brochu, 1996) or low precision of hormonal control of ossification. However, the largest specimen without ossification, ZPAL AbIII/1930, seems to belong to a series with a different trajectory of ontogenetic change than specimens of similar size with well-developed ossifications (Figs. 6A, B, 10). Two classes are recognizable at this stage of growth: the specimens with and without a posteromedial tuber. Again, the sample size is inconveniently low, but an appealing alternative to population variability is sexual dimorphism. Large specimens without additional ossifications (including a trochanteric shelf) and preserving the posteromedial tuber would then belong to males and specimens with additional ossifications to females (see Chinsamy, 1990; Raath, 1990). Also, the position and shape of the dorsolateral trochanter would be sex related. The distance between the dorsolateral trochanter and proximal end of femur and location of the anterior margin of dorsolateral trochanter are higher in the proposed females (Fig. 6A, B). The high value of this trait in ZPAL AbIII/563/7R may indicate that it belonged to an immature female (Fig. 4). This refers also to the posteromedial tuber (Fig. 9). A similar pattern was observed and interpreted as sexual dimorphism in *Megapnosaurus rhodesiensis* (Raath, 1990), with two morphotypes differing in size, presence or absence of the trochanteric shelf, and other ossified muscle insertions. The additional ossifications of these fossil forms appeared during maturity (Raath, 1990). This may correspond with an increase in calcitonin levels shortly before maturity, because it is observed in modern quail females (Dacke et al., 1976).

On the ilium, the anterior and postacetabular iliac processes grew proportionally faster than the acetabulum region (Fig. 7C). However, the difference is moderate. At the same time, the anterior and postacetabular iliac processeses became wider and more massive. Muscle attachments become more distinct, presumably as a result of ossification of tendon attachment sites on the bone (Figs. 3, 7A). This may have also resulted from increased body mass. Perhaps the height of ilia is related to sex or intraspecific variation.

The question emerges whether changes in bone proportions modified the body posture in *Silesaurus opolensis*. Generally, a straight femoral shaft follows the achievement of bipedal locomotion in the evolution of early dinosauromorphs (Fechner, 2009). However, in larger individuals of *Silesaurus*, ilia are disproportionally shorter than in smaller ones. This might suggest that older individuals had reduced abilities for bipedal locomotion. Fechner (2009) argued that *Silesaurus* was quadrupedal based on limb and trunk proportions. Indeed, this species has a long trunk (Piechowski and Dzik, 2010) as compared with the hind limbs and long (but disproportionally gracile) forelimbs. These proportions are known only for large individuals. However, body posture depends also on location of the center of gravity of the body. Piechowski and Dzik (2010) posited that center of gravity of the body was near sacrum in *Silesaurus*. This implies that it was able to stand on two limbs, even if quadrupedal posture dominated in large individuals.

Taxonomy

Many of the differences between individuals of *Silesaurus opolensis* that appear to be ontogenetic changes have been used to discriminate species in early dinosauromorphs (i.e., Ezcurra, 2006; Ferigolo and Langer, 2006). A distinct tuberosity on the proximal femoral head, and lack of a trochanteric shelf and other ossifications (Ezcurra, 2006; Ferigolo and Langer, 2006), suggests that fossils of *Eucoelophysis baldwini* and *Sacisaurus agudoensis* represent juvenile or male forms. The condition of *Eucoelophysis* (allegedly more basal than *Silesaurus*), *Diodorus*, or *Sacisaurus* (Kammerer et al., 2012) is in conflict with its younger geologic age (Norian). Similarly, the isolated femur from Woźniki (Sulej et al., 2011) may represent a juvenile individual or a male. The anterior trochanter is prominent during the whole known ontogeny of *Silesaurus opolensis* in both sexes. Surprisingly, young individuals of *Dromomeron gregorii* lack this feature (Nesbitt et al., 2009). It is therefore possible that this is an expression of their early ontogenetic stage.

We applied PCA to the measurable morphological traits of ilia and femora to test a possibility that two species are represented in the *Silesaurus* material from Krasiejów. As mentioned above, the plot of femora forms a ring surrounding the specimens in the center with incomplete data sets. The right half of the ring (Fig. 4) is composed of specimens with additional ossifications. As shown by Student's t-tests, specimens without ossifications on the left are usually smaller (Fig. 4). There is a continuity between these groups because the distinguishing characters develop gradually during ontogeny (Fig. 10). It cannot be asserted, based on the morphology of femur alone, whether these groups represent separate sexes (as proposed here) or species. The variance of ilia is more uniform, but it is dominated by intraspecific variation, with no signs of a bimodal frequency distribution (Fig. 5). The highly specific morphology of associated jaws of *Silesaurus* (Dzik, 2003; Kubo and Kubo, 2014) suggests that not more than one morphospecies is represented in the material.

Taking all the available evidence together, it seems likely that the material studied here probably represents one biological species with dimorphic femora developing in late ontogeny. Most of the morphological characteristics show wide intraspecific variability. There are few data regarding intraspecific variability in other closely related taxa to compare with *Silesaurus*. The presence of a trochanteric shelf in *Saturnalia tupiniquim* (Nesbitt et al., 2009) and *Megapnosaurus rhodesiensis* (Raath, 1990) varies within these species, which is observed also in *Silesaurus opolensis*. This calls for caution while using such characters in phylogenetic studies. It appears that the most variable characters within species are the shape and position of the dorsolateral trochanter, the contact of the ilium with the sacral ribs, the angle of the fourth trochanter, and the distance between the ischiadic process and the edge of fourth sacral rib articulation area. Also, the muscle attachments on the anterior and posterior iliac processes are variable in shape (more or less ossified). The presence of a lateral ossification fused with the femur shaft (trochanteric shelf) may be an aspect of late ontogenetic age (Nesbitt et al., 2009) or sexual dimorphism, as discussed above. This may explain the chaotic distribution of this character among dinosauromorphs (see Langer and Benton, 2006).

Evolution

Most *Silesaurus* material comes from a single lens of mudstone in the upper part of the Krasiejów clay-pit (Dzik, 2003; Dzik and Sulej, 2007; Piechowski and Dzik, 2010). Only a few specimens were collected from the lower fossiliferous horizon. Among them, ZPAL AbIII/1930 is the most complete, with preserved femora. There is no doubt that it represents an older population belonging to the same local continuum. The difference in age is difficult to estimate, but the sedimentation rate of the fluvial deposits in Krasiejów was probable high (Gruszka and Zieliński, 2008). It cannot be excluded that only thousands of years separate the two horizons.

The femur of ZPAL AbIII/1930 is located on the margin of the PCA plot (Fig. 4A). It is relatively large, but lacks the ossifications observed in other large individuals. Despite that it is very robust. It may represent a male individual, according to the interpretation proposed above.

Ilia are not preserved in ZPAL AbIII/1930, but other bones, including vertebrae, scapulocoracoids, the humerus, and dentary, seem to differ slightly in morphology and proportions from the specimens most common in the upper horizon. Such differences might be a result of microevolutionary changes, but the morphological distance is not large enough to preclude this single individual belonging to a population with the same range of variability.

Differences between populations of different geologic age may be influenced by directional evolution. If precise stratigraphic control is lacking, it is difficult to distinguish such differences from sexual dimorphism. Possibly, bimodal distribution of variables in *Kentrosaurus* (Barden and Maidment, 2011) may have resulted from differences between populations. However, the disparity in prominence of the greater trochanter supports the sexual dimorphism interpretation.

The fast rate of growth of young individuals of *Silesaurus opolensis* is a typical archosaurian pattern (Fostowicz-Frelik and Sulej, 2010). Selection pressure was focused on the hind limbs, which were the main locomotory organ. The intraspecific variability of *Silesaurus* ilia is higher than of femora, especially regarding sacral rib attachments (Fig. 8). Apparently, the functional aspects of femoral morphology were more important for survival.

CONCLUSIONS

This study suggests that the available material of *Silesaurus opolensis* represents populations of a single dimorphic species. Ontogeny was the main factor influencing variation in the sample. Presence or absence of tendinous ossifications on the femora may have been determined by the maturity and sex of individuals. The ossifications developed simultaneously and may have been controlled by raised levels of calcitonin during puberty in females (or by their ageing). Therefore, specimens with enlarged trochanteric shelves, and tendon ossification at this and other muscle attachments, are interpreted as mature females that were significantly larger than males. Specimens without ossifications belong to males and immature females. Femoral variations are more dependent on ontogeny than iliac variations. This is presumably because femoral morphology was more important for efficient locomotion and survival. Ontogenetic changes were influenced by the disproportionate increase of body mass and slightly different ecology of older individuals. Ilia show higher intrapopulation variability than femora. It remains a possibility that the population from the lower horizon within the Krasiejów exposure represents a different stage in the evolution of the species than that from the upper horizon.

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