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NEW INSIGHTS INTO THE BIOLOGY OF THE PERMIAN GENUS *CISTECEPHALUS* (THERAPSIDA, DICYNODONTIA)

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ABSTRACT—The taxonomy and paleobiology of the Upper Permian dicynodont *Cistecephalus* have been much debated over the last century. Fossils of *Cistecephalus* have been identified as belonging either to one species or up to six species and hypotheses concerning their lifestyle range from aquatic to arboreal and fossorial. Earlier studies of *Cistecephalus* focused mainly on macroanatomical characteristics, whereas the current assessment examines a combination of anatomical features, as well as bone histology and microanatomy to unravel its biology. The allometries of a skull growth series that were examined in the present study imply that all *Cistecephalus* specimens belong to a single species. Furthermore, our data suggest that the variability in the occurrence of supraorbital ridges, which are raised in some specimens and leveled in others, is a feature of sexual dimorphism. Histological thin-sections of a humerus, an ulna, a femur, and ribs from two *Cistecephalus* specimens were studied to evaluate life history traits of this taxon. The comparison of ribs from a subadult and a fully grown specimen allows an estimation that sexual maturity was attained when the skull length was between 5.9 and 6.5 cm. The compact microstructure of the sampled *Cistecephalus* bones implies aquatic and/or fossorial adaptations, refuting an arboreal lifestyle. We propose that the high degree of binocular vision evident in *Cistecephalus* developed in response to predatory (insectivory) and/or nocturnal habits and that it is unrelated to a scansorial lifestyle.

INTRODUCTION

The Beaufort Group in the Karoo Basin of South Africa is renowned for its rich Permian and Early Triassic tetrapod remains. Abundant therapsid taxa with restricted temporal appearances have been used to subdivide this sequence of fluviolacustrine sediments into 8–10 assemblage zones (Kitching, 1977; Rubidge, 1995; Smith et al., 2012). The biostratigraphic marker of the *Cistecephalus* Assemblage Zone (Wuchiapingian, Upper Permian), the genus *Cistecephalus*, is among the smallest representatives of the diverse and successful group of dicynodonts (Therapsida, Anomodontia), which were the dominant herbivores during the Middle and Upper Permian (King, 1990; Fröbisch, 2009; Smith et al., 2012; Fig. 1). Constituting about 9% of the fossil finds of the *Cistecephalus* Assemblage Zone of the Beaufort Group (Smith et al., 2012), but also known from the preceding *Tropidostoma* Assemblage Zone, as well as Upper Permian deposits of India (Ray, 1999, 2001), *Cistecephalus* is a well-recognized member of Upper Permian ecosystems. Curiously, despite several studies, *Cistecephalus* taxonomy is contested and its lifestyle and biology remain enigmatic.

Previous Work on *Cistecephalus*

Taxonomy—*Cistecephalus* was first described by Owen (1876). The genus name derives from the Greek terms ‘Kiste’ (‘box’) and ‘Kephalus’ (‘head’), referring to its diagnostic wide skull roof and the overall short skull, which is approximately as wide as it is long (Fig. 2A). Because postcranial material is rare for this genus, all species were described and distinguished on the basis of cranial features such as size, overall skull shape, and the presence or absence of raised supraorbital ridges (SR).

Owen (1876) recognized six species of *Cistecephalus*, though two of these were later assigned to other dicynodont genera. Subsequently, Broom (1932) considered only three *Cistecephalus* species as valid, but later added another three species in a revision of the Rubidge collection in South Africa (Broom, 1948).

More recently, Keyser (1973) discarded the concept of multiple species of *Cistecephalus* and assigned all known specimens to *C. microrhinus*. He argued that for most of the skulls, the shapes were altered by compression and distortion, concluding that many measurements were unreliable and that the overall skull shape could not be used to discriminate between species (Keyser, 1973, 1976). Keyser thus interpreted differences in skull size and the presence or absence of raised SR as ontogenetic.

Lifestyle Habits—The paleoecology of *Cistecephalus* has been subjected to much speculation over the last century. Broom (1948) and Brink (1950) proposed an aquatic or semiaquatic lifestyle. Keyser (1973) and later MacRae (1999) considered that the frontally positioned orbits of *Cistecephalus* implied binocular vision and possibly stereopsis, which they reasoned to be a scansorial adaptation. Keyser (1973) additionally proposed that the peculiarly broad skull could have housed a brain enlarged for optical processing. Moreover, he suggested that the front limbs were suitable for arboreality, because the distal phalanx of the first digit of the manus is elongated and curved and could have opposed the long phalanges of the second and third digits. However, considering the massive humeri and broad manus evident in *Cistecephalus*, Keyser included digging activities in the lifestyle interpretations.

Cluver (1978) was the first to reconstruct the whole skeleton of *Cistecephalus* (Fig. 2B). He identified a range of morphological specializations that he interpreted as adaptations for a digging or fossorial lifestyle, such as the broad skull that was probably associated with strong neck and shoulder musculature, the robust humerus, broad manus, mobile pes, and the outward rotation of

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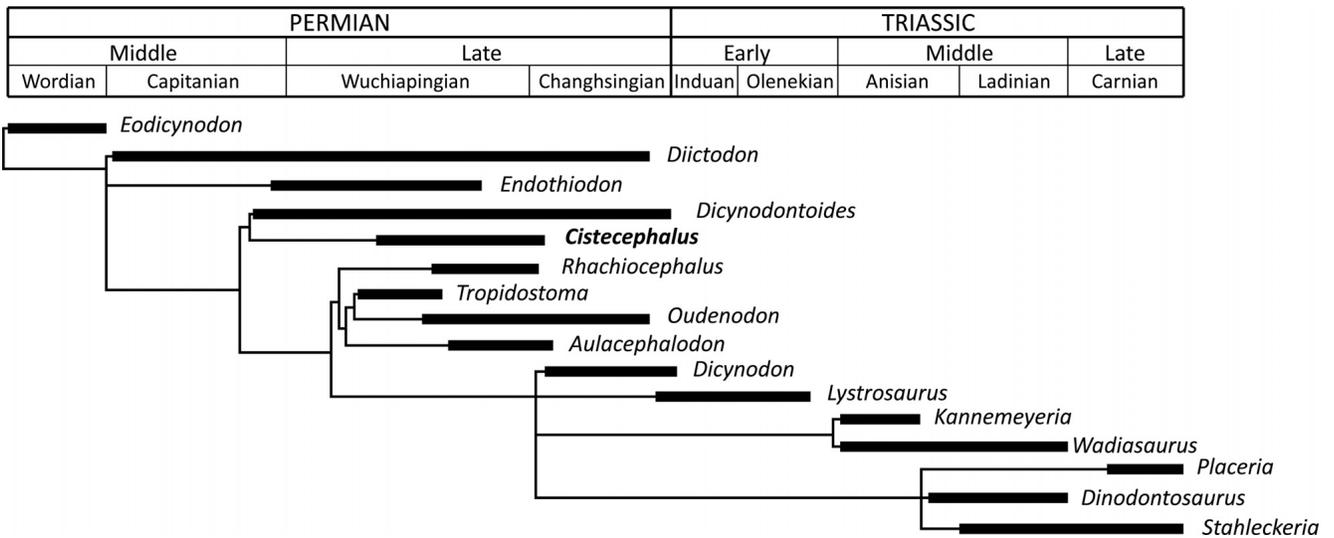


FIGURE 1. Cladogram showing the phylogenetic position of *Cistecephalus* among selected dicynodont genera for which histological studies have been conducted (see Appendix 1). Modified from Kemp (2012) and Botha-Brink and Angielczyk (2010).

the hind limbs. A fossorial lifestyle has also been proposed for the other members of the Cistecephalidae: for *Kawingasaurus* from the Late Permian deposits of Tanzania (Cox, 1972) and for *Cistecephaloides* from the *Cistecephalus* Assemblage Zone of South Africa (Cluver, 1978). Since Cluver’s study, a fossorial lifestyle for *Cistecephalus* has been generally accepted (King, 1990; Smith et al., 2012).

Paleobiological Inferences from Bone Microanatomy and Bone Histology

Previous lifestyle inferences for *Cistecephalus* were exclusively drawn from anatomical studies. However, today it is well recognized that aside from macromorphological studies, additional paleobiological information about extinct vertebrates can be inferred from microstructural and histological examination of fossil bones. The basic structure and histology of bone are

fairly consistent among tetrapods and are often preserved over millions of years in fossils (e.g., Ricqlès, 1977; Francillon-Vieillot et al., 1990; Chinsamy-Turan, 2005). The microanatomy of bones is determined by various factors, such as phylogeny, ontogeny, lifestyle, and biomechanics (e.g., Castanet et al., 2001). Extensive studies have shown how lifestyle influences the microstructure of bones and this relationship has been verified for a broad range of extant and extinct taxa (e.g., Wall, 1983; Currey and Alexander, 1985; Fisch and Stein, 1991; Chinsamy et al., 1998; Germain and Laurin, 2005; Gray et al., 2007; Canoville and Laurin, 2009, 2010). Amphibious and aquatic tetrapods living in shallow water, for example, show a higher degree of bone compactness than their terrestrial relatives (e.g., Ricqlès and Buffrénil, 2001; Ray et al., 2005; Houssaye, 2009; Canoville and Laurin, 2009, 2010; Buffrénil et al., 2010) in order to overcome buoyancy (Taylor, 1994, 2000). An increase of bone compactness has also been observed in fossorial animals (Magwene, 1993; Botha, 2002;

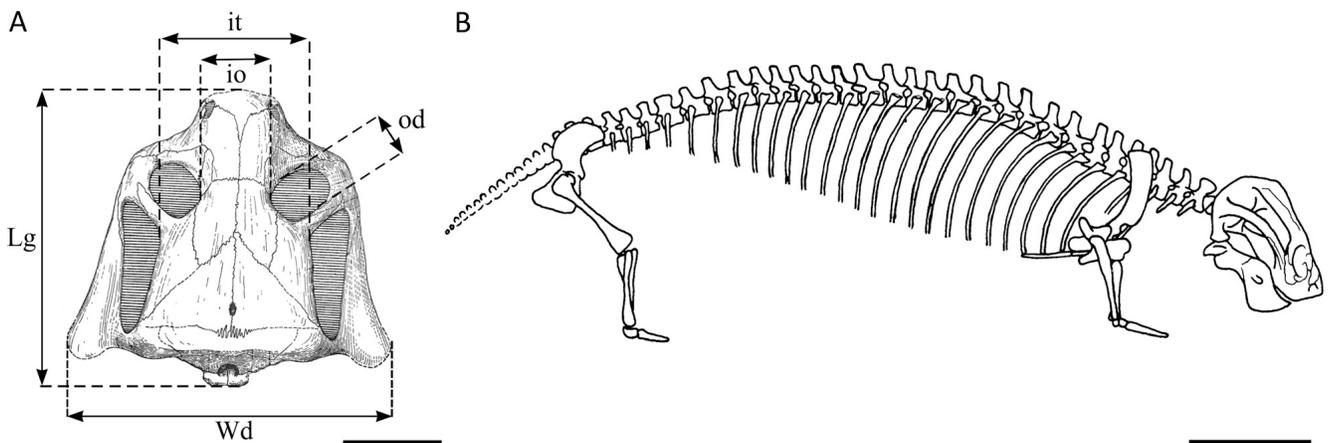


FIGURE 2. Reconstruction of *Cistecephalus* skeleton. **A**, skull in dorsal view (modified from Broili and Schröder, 1935), highlighting the measurements taken in the present study. **B**, skeleton in lateral view (reconstructed from BP/1/4086; total body length approximately 33 cm), from Cluver (1978) reproduced with permission from Iziko SAM. **Abbreviations:** **io**, minimal interorbital length; **it**, minimal intertemporal length; **Lg**, median length of the skull (tip of the snout to the foramen magnum); **od**, orbit diameter (mean of largest and smallest extent); **Wd**, maximal width of the skull. Scale bars equal 2 cm (**A**) and 5 cm (**B**).

Botha and Chinsamy, 2004; Ray et al., 2012). To the contrary, fully terrestrial, flying, and arboreal tetrapods usually feature more tube-like bones with compact cortices and large medullary cavities (Currey and Alexander, 1985; Casino and Cubo, 2001).

The relative rate at which bone tissues are deposited during ontogeny is also determinable from the resulting tissue types (e.g., Margerie et al., 2002). According to Amprino's law (Amprino, 1947), highly vascularized bone in a loosely woven-fibered matrix (fibrolamellar bone tissue) indicates fast depositional rate, whereas slowly deposited bone results in a more organized, lamellar structure. Moreover, growth marks that form in response to seasonal fluctuation in the bone depositional rates can be used as a biological chronometer (e.g., Castanet, 1985, 2006). Histology and microstructure of bones are thus valuable sources for paleobiological inferences (Ricqlès, 2011; Chinsamy-Turan, 2012).

Bone histology has been extensively examined in the diverse dicynodonts (Fig. 1, Appendix 1), but only two studies involving bone histology included *Cistecephalus* material. The first of these by Chinsamy and Rubidge (1993) comprised a single humerus and focused on comparisons among dicynodont subfamilies, whereas the more recent study by Botha-Brink and Angielczyk (2010) examined a radius and an ulna of a subadult specimen. Both studies revealed the presence of moderately vascularized fibrolamellar bone in the cortex interrupted by annuli. The sampled humerus had a dense microstructure with cancellous bone infilling the medullary region; but the radius and ulna were found to be relatively lightly built, with thin cortices and large medullary cavities. The contrasting results regarding bone compactness were considered as reflecting intraskeletal variability (Botha-Brink and Angielczyk, 2010), but they also highlighted the need for further investigations.

In the present study, we use anatomical, morphometric, and microstructural approaches to reevaluate previously proposed hypotheses pertaining to the biology and ecology of *Cistecephalus*. Bone histology of various skeletal elements is analyzed to deduce growth strategies, and examine intraskeletal variability and lifestyle adaptations. Furthermore, given that the presence or absence of prominent (or raised) SR has previously been used to discriminate between species (Broom, 1948) and later

been described as an ontogenetic feature (Keyser, 1973), here, we reassess these hypotheses. Through a comprehensive comparison of skull allometries of a skull series, we consider the possibility of (i) different species, (ii) ontogeny, and (iii) sexual dimorphism underlying the occurrence of leveled or raised SR.

MATERIALS AND METHODS

The *Cistecephalus* materials examined in the present study were obtained from the paleontological collections of the Iziko South African Museum (SAM) in Cape Town, the Bernard Price Institute for Paleontological Research of the University of the Witwatersrand in Johannesburg (BPI), and the Council for Geoscience in Pretoria (former Geological Survey: specimens with prefix numbers GS, RMS, or WB). As far as it could be determined, all the specimens were recovered from the *Cistecephalus* Assemblage Zone (Wuchiapingian, Late Permian) of the Beaufort Formation, South Africa.

Material for Skull Measurements

Skull Allometries (Sample 1)—Skull measurements of 21 fairly undistorted specimens, identified at the genus level as *Cistecephalus*, were taken (Table 1). Dimensions of SAM-PK-K8304 were complemented with measurements from Ray (2001). The skull sample represents a series with lengths ranging from 3.2 cm to almost 7.5 cm and comprises specimens without (e.g., Fig. 3A–E) and with (e.g., Fig. 3F–H; Table 1) raised SR. Although the sample obviously includes individuals at different ontogenetic stages, it is not representative of the overall size range for *Cistecephalus*. The largest skull described in the literature measures 10 cm in length and exhibits distinctly raised SR (see Broom, 1948).

Skull Size Distribution (Sample 2)—Another set of 54 skulls from the SAM were used to assess the size distribution of specimens of *Cistecephalus* in the fossil record (Appendix 2). Every skull with a determinable and undistorted length axis, which constitutes more than 80% of the SAM specimens, was included; however, most skulls were in poor condition. Because the

TABLE 1. Skull measurements taken from 21 specimens of *Cistecephalus* (see Fig. 2A).

| Specimen number | Lg | Wd | io | it | odw | ods | SR |
|-----------------|------|------|------|------|------|------|----------------------|
| BP/I/1260 | 7.44 | 8.43 | 2.36 | 5.62 | 1.89 | 1.63 | Leveled |
| BP/I/2450 | 5.87 | 5.48 | 1.82 | 4.16 | 1.38 | 1.38 | Raised |
| BP/I/4024 | 5.31 | 5.44 | 1.51 | 2.93 | 1.43 | 1.06 | Leveled |
| BP/I/4086 | 5.57 | 5.4 | 1.59 | 3.48 | 1.63 | 1.35 | Leveled |
| BP/I/4096 | 6.98 | 7.47 | 2.31 | 4.22 | 1.42 | 1.42 | Raised |
| BP/I/4111 | 5.01 | 5.85 | 1.15 | 3.26 | 1.41 | 0.81 | Raised |
| BP/I/503 | 5.77 | NA | 1.71 | 3.37 | NA | NA | Raised |
| BP/I/506 | 5.88 | 6.49 | 1.66 | 3.78 | 1.47 | 1.08 | Leveled |
| BP/I/580 | 6.10 | 7.12 | 1.84 | 4.00 | 1.82 | 1.28 | Leveled |
| BP/I/Fno-33 | 6.13 | 6.44 | 1.49 | 3.68 | 1.49 | 1.40 | Leveled |
| GS-225 | 3.71 | 2.15 | 0.84 | 1.73 | 0.84 | 0.73 | Individual too small |
| GS-K160 | 6.46 | 6.13 | 1.64 | 3.55 | 1.72 | 1.11 | Raised |
| SAM-PK-10665 | 4.46 | 4.02 | 1.08 | 3.23 | 1.28 | 0.96 | Individual too small |
| SAM-PK-7332 | 6.91 | 7.23 | 2.27 | 4.23 | NA | NA | Raised |
| SAM-PK-K11150 | 6.40 | NA | 1.69 | 3.93 | 1.87 | 1.38 | Leveled |
| SAM-PK-K6814 | 5.60 | 5.91 | 1.69 | 3.94 | 1.46 | 1.10 | Raised |
| SAM-PK-K7667 | 6.34 | 7.00 | 2.21 | 3.89 | 1.42 | 1.00 | Leveled |
| SAM-PK-K7852 | 4.27 | 3.70 | 1.01 | 0.25 | 0.99 | 0.74 | Individual too small |
| SAM-PK-K8068 | 5.61 | 7.21 | 1.59 | 4.11 | 1.52 | 1.00 | Leveled |
| SAM-PK-K8304 | 5.50 | 6.20 | 1.80 | 4.50 | 1.43 | 1.17 | Raised |
| WB-158 | 7.10 | 6.53 | 1.87 | 4.11 | 1.98 | 1.50 | Leveled |

All the measurements are in centimeters. **Abbreviations:** **io**, minimal interorbital length; **it**, minimal intertemporal length; **Lg**, median length of the skull (tip of the snout to the foramen magnum); **NA**, not available; **odw**, orbit diameter (widest); **ods**, orbit diameter (smallest); **SR**, supraorbital ridges; **Wd**, maximal width of the skull.

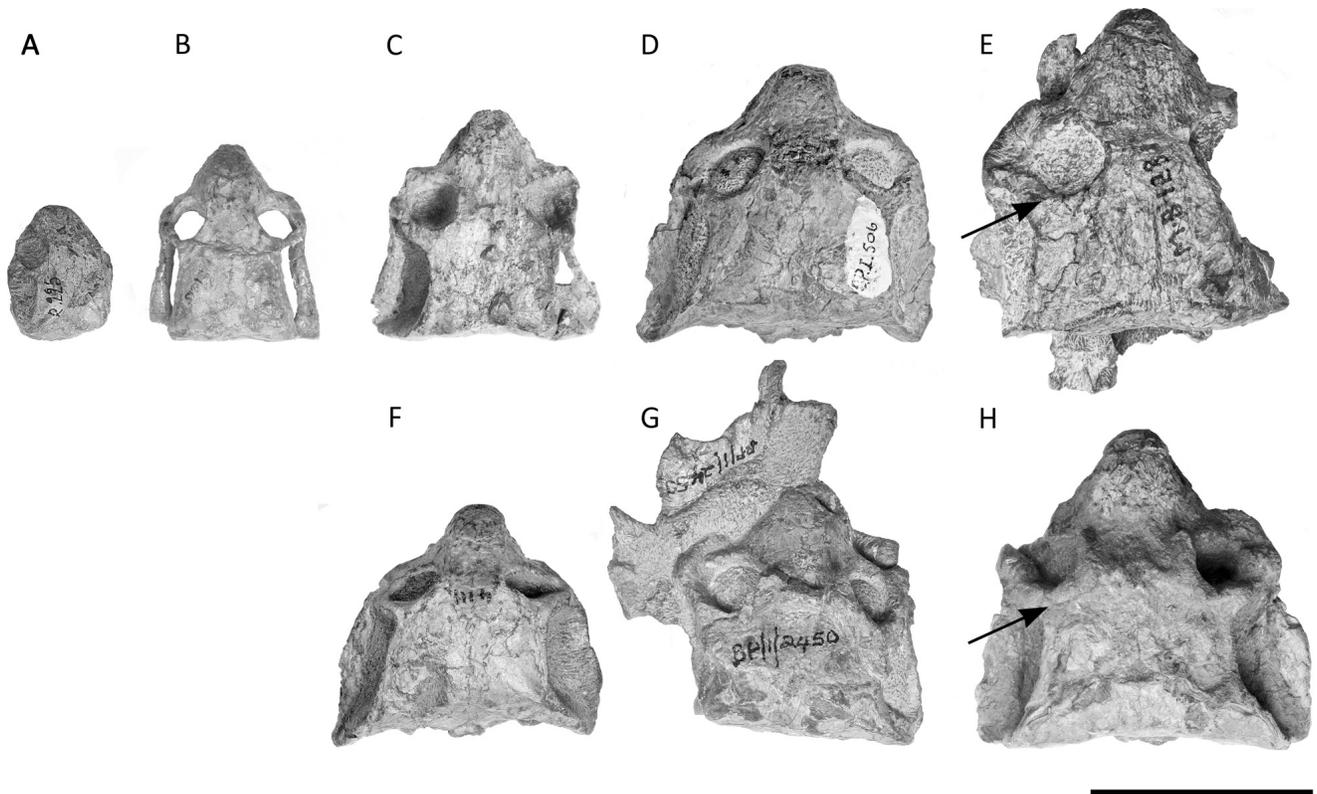


FIGURE 3. Growth series of skulls of *Cistecephalus*. Top row depicts skulls without raised supraorbital ridges, whereas the bottom row indicates skulls having raised supraorbital ridges (arrows). **A**, specimen GS-225; **B**, SAM-PK-10665; **C**, BP/I/4024; **D**, BP/I/506; **E**, WB-158; **F**, BP/I/4111; **G**, BP/I/2450; **H**, BP/I/4096. Scale bar equals 5 cm.

material derives from different localities and consists of a random sampling, they represent a good estimate of the skull length distribution of *Cistecephalus* in the fossil record.

Material for Thin-Sectioning (Sample 3)

Long bones and ribs from two different-sized specimens of *Cistecephalus* were sampled for thin-sectioning, thereby permitting an assessment of histovariability in the skeleton, as well as ontogenetic or specific variation in bone structure. Given that the microstructure of limb bones is generally considered to reveal the most significant ecological signal (e.g., Ricqlès et al., 2004; Canoville and Laurin, 2010), long bones were sampled where possible. In addition, because the compactness is subject to intrabone variability and the highest compactness is generally found in the midshaft region of long bones (Francillon-Vieillot et al., 1990), the thin-sections were made at this level. Non-weight-bearing bones such as ribs are usually less affected by bone remodeling and therefore considered good for deducing aspects of growth (Erickson et al., 2004; Horner and Padian, 2004). Hence, ribs from both specimens were included in the current study. Femora of the arboreal gray squirrel (*Sciurus carolinensis*) and the fossorial naked mole rat (*Heterocephalus glaber*) were sectioned for comparisons of lifestyle adaptations in bone compactness.

Specimen BP/I/2450—This *Cistecephalus* specimen consists of a 5.9-cm-long skull with disarticulated postcranial elements (Fig. 4A, B). The SR are prominent, though the skull is dorsoventrally compressed in the anterior region. Three ribs were sampled: two small ribs (probably from the anterior region of the rib cage), preserved in relative closeness to each other and in near-

parallel arrangement, and a larger third rib probably from the midregion of the rib cage.

Specimen RMS-410—This is an incomplete and semiprepared specimen comprising cranial and postcranial material (Fig. 4C, D) and a skull length of 6.5 cm. It includes a lower jaw and a fairly crushed skull without prominent SR. Two large ribs, one femur, one ulna, and a humerus were sampled for thin-sectioning.

Methods and Equipment

Skull Measurements—Measurements to determine allometries were taken with a digital calliper (Mitutoyo Absolute Digimatic Caliper Series 500). The notations for analyses are rounded to the nearest 0.1 mm.

Due to the high degree of distortion among fossils of *Cistecephalus* (Keyser, 1973), we considered that only few dimensions of the skull were valid for analyses. These measurements are the median length of the skull (from the tip of the snout to the foramen magnum; Lg; samples 1 and 2); the maximal width of the skull (Wd); the size of the orbits calculated as a mean of the largest and the smallest diameters; the minimal interorbital length (io); and the minimal intertemporal length (it) (sample 1; Fig. 2A). The latter dimensions (io and it) have previously been reported to be the least affected by distortion (Keyser, 1973).

Graphs and Statistical Analyses—Scatterplots and a histogram were drawn with Microsoft Excel 2010. All statistical tests, comprising χ^2 test for normality, nonparametric Mann-Whitney U-tests, regression functions, and coefficient of determination R^2 , were performed with Statsoft STATISTICA 10.

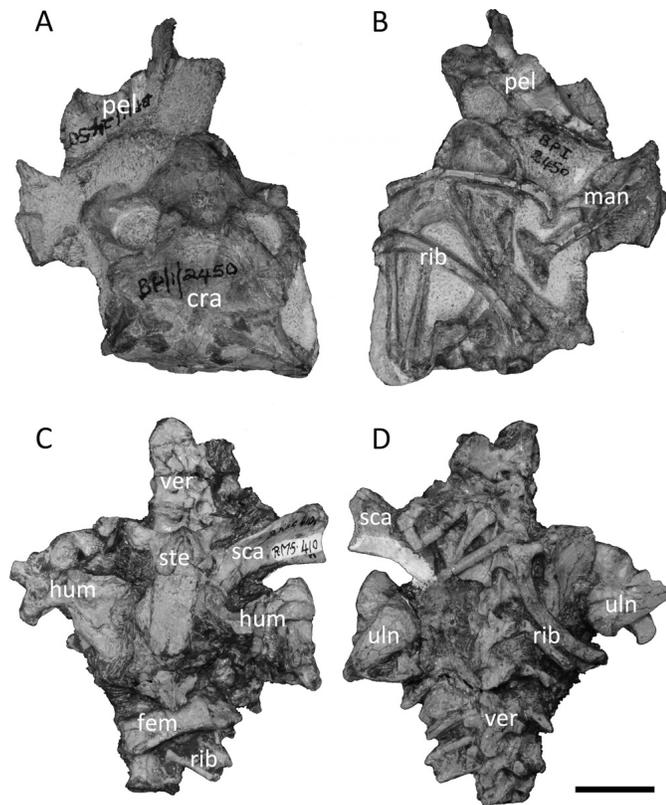


FIGURE 4. *Cistecephalus* specimens sampled for histological examination. **A**, BP/I/2450, dorsal view; **B**, BP/I/2450, ventral view; **C**, RMS-410, ventral view; **D**, RMS-410, dorsal view. **Abbreviations:** cra, cranium; fem, femur; hum, humerus; man, mandible; pel, pelvis; rib, ribs; ste, sternum; uln, ulna; ver, vertebrae. Scale bar equals 2 cm.

Microanatomical and Histological Descriptions—All bones were photographed before sampling and standard measurements were taken. Thin-sectioning was performed according to the protocol of Chinsamy and Raath (1992). The histological descriptions follow those from Francillon-Vieillot et al. (1990) and Chinsamy-Turan (2005).

Bone compactness is expressed as the relative bone wall thicknesses (RBT), determined by measuring the cortical and the medullary extent on the median length and width axes of the cross-section (Ray and Chinsamy, 2004). The mean is expressed as a percentage, whereas a RBT of 100% implies that there is only cortex and no medullary cavity. The RBT has previously been used to quantify the bone compactness of a radius and an ulna of a subadult specimen of *Cistecephalus* (Botha-Brink and Angielczyk, 2010). By choosing the same parameter, comparisons are possible.

Imaging and Microscopy—Microscopic examination of the thin-sections were performed with a Nikon ECLIPSE E200 microscope and micrographs were taken with a Nikon Digital Sight DS-Fi 1 camera in combination with the imaging software NIS Elements 3.0.

RESULTS

Total Body Length of *Cistecephalus*

Skulls of *Cistecephalus* are well represented in the collections, but postcranial elements are rare. It is of considerable use for paleobiological reconstructions to have an estimate of the to-

tal body size (from snout to the end of the tail) that a particular taxon could reach. Fortunately, a unique, nearly complete *Cistecephalus* skeleton (BP/I/4086) was available for measurement: the skull of 5.6 cm is associated with a postcranial length of 27.5 cm (following the spine length as preserved), giving a total body length of 33.1 cm and a head-to-body ratio of 1 to 4.9. The largest prepared skull from the Iziko SAM (SAM-PK-K8113) measures 8.8 cm in length, and assuming that the skull-to-postcranium ratio does not change in larger individuals, this results in an extrapolated body size of 52.1 cm. Furthermore, considering the largest skull found for *Cistecephalus* (10 cm in length; Broom, 1948), a full body length of 60 cm can be extrapolated for the largest individuals in the fossil record.

Occurrence of the Supraorbital Ridges

The raised SR are a distinctive feature of many skulls of *Cistecephalus*. According to Keyser (1973), the development of raised SR initiates when the skull size exceeds 5 cm. In the current study, over a hundred skulls of *Cistecephalus* were examined, and indeed we found that no specimen with a skull length less than 5 cm had raised SR. There are, however, several cases of larger skulls also lacking distinct SR (Fig. 3D, E; Table 1). In our sample 1, among the 18 fairly undistorted skulls larger than 5 cm, 8 have raised SR and 10 do not (Table 1). Figure 3E and H illustrate specimens WB-158 and BP/I/4096, which have comparable skull sizes (respectively 7.1 and 7.0 cm) but differ distinctly in the occurrence of SR. In BP/I/4096, the upper halves of the orbits have thick bony bulges (thickness of 4.6 mm) forming the SR, whereas no SR occur in WB-158.

Allometries in a Series of *Cistecephalus* Skulls (Sample 1)

The maximal skull width (Wd) is proportional to the median skull length (Lg) (sample 1; Fig. 5A). A linear regression of the data points is significant ($P < 0.05$), with a coefficient of determination (R^2) of 0.82. The skull length of the smallest specimen of our sample (GS-225; Fig. 3A; skull length 3.2 cm) is, however, almost 1.5 times greater than its width (ratio 1.47), whereas the second smallest skull of the sample (SAM-PK-K7852; skull length 4.27 cm) features a length-to-width ratio of 1.15. All the larger skulls exhibit ratios between 0.77 and 1.11 (average 0.95).

In our sample, the size of the orbits is also in linear correlation to the total skull length, irrespective of the presence or absence of raised SR (Fig. 5B). The correlation is significant ($P < 0.05$) and the linear regression function explains 79.2% of the variation that is observed. The interorbital width correlates to the intertemporal width ($P < 0.05$) with an R^2 of 0.70 (Fig. 5C).

If skulls with and without raised SR exhibit allometric differences, this would support the hypothesis of multiple species. Thus, nonparametric tests comparing two independent samples were chosen to evaluate if there are significant differences among skulls with and without distinct SR. The results are as follows: (i) there is no difference in the ratio of length to width among skulls with and without SR (Mann-Whitney U-test: n [with SR] = 7; n [without SR] = 9; $U = 33$; $P = 0.6806$); (ii) there is no difference in the ratio of intertemporal to interorbital widths between skulls with and without SR (Mann-Whitney U-test: n [with SR] = 8; n [without SR] = 10; $U = 38$; $P = 0.8968$); (iii) there is no difference in the ratio of orbital size to skull length among skulls with and without SR (Mann-Whitney U-test: n [with SR] = 6; n [without SR] = 10; $U = 16$; $P = 0.1471$). Thus, according to our data set, the dimensions of orbit sizes, skull lengths, skull width, and intertemporal and interorbital widths do not exhibit statistically significant differences among skulls with and without SR.

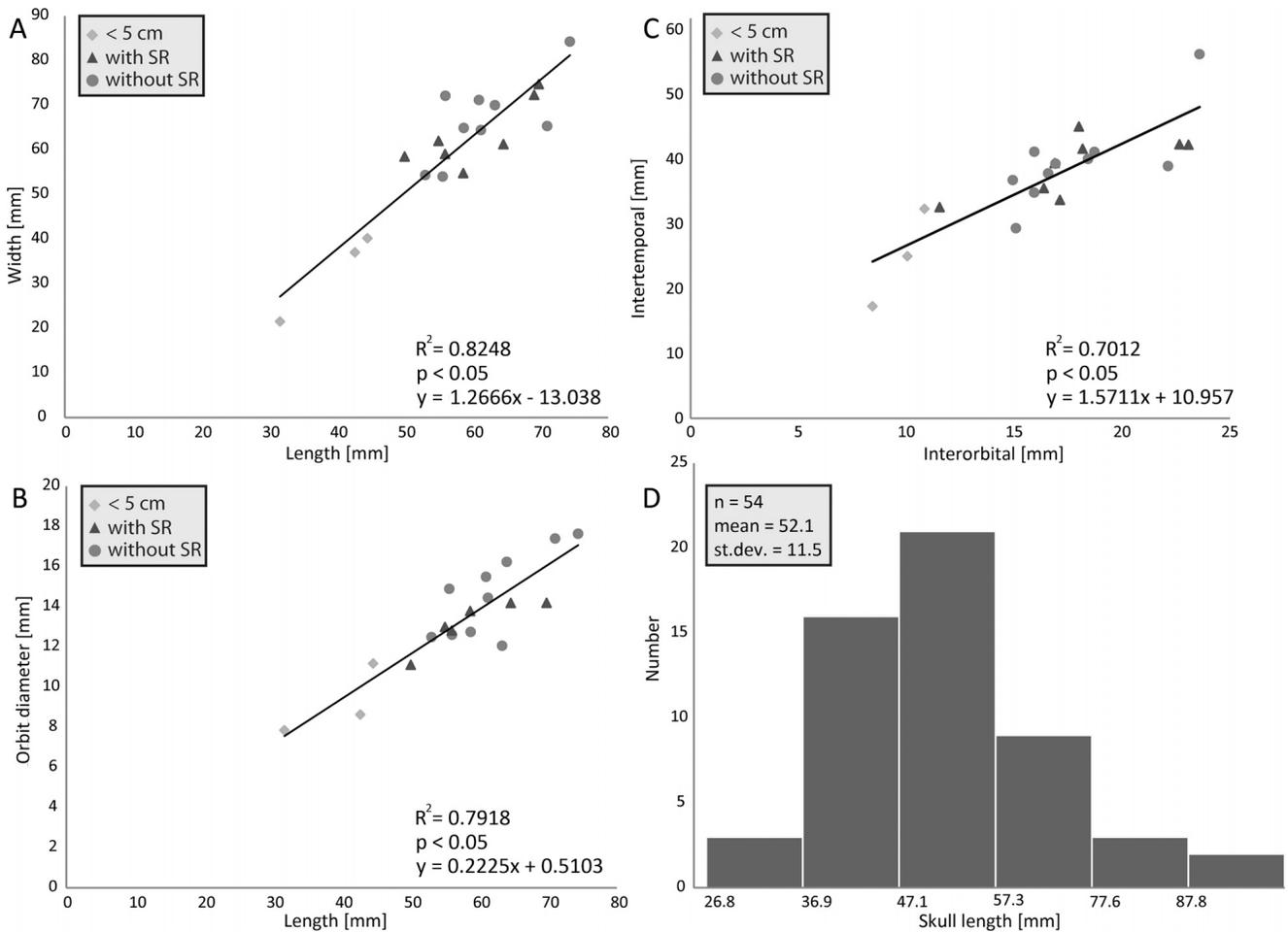


FIGURE 5. Scatterplots of dimensions on a skull growth series (with and without raised supraorbital ridges) of *Cistecephalus* (A–C) and a histogram of skull size distribution of the Iziko SAM collection (D). A, median length of the skull versus maximal width of the skull (n = 19 skulls); B, median length of the skull versus orbit diameter (n = 19 skulls); C, minimal interorbital length versus minimal intertemporal length (n = 21 skulls); D, histogram: n = 54; mean equals 52.1 mm; standard deviation equals 11.5 mm. The distribution diverges from a normal distribution (adjustment to normal distribution is insignificant; $\chi^2 = 7.7942$, df = 4 (adjusted), P = 0.0994) and is skewed to the left.

Skull Size Distribution in Iziko SAM Specimens (Sample 2)

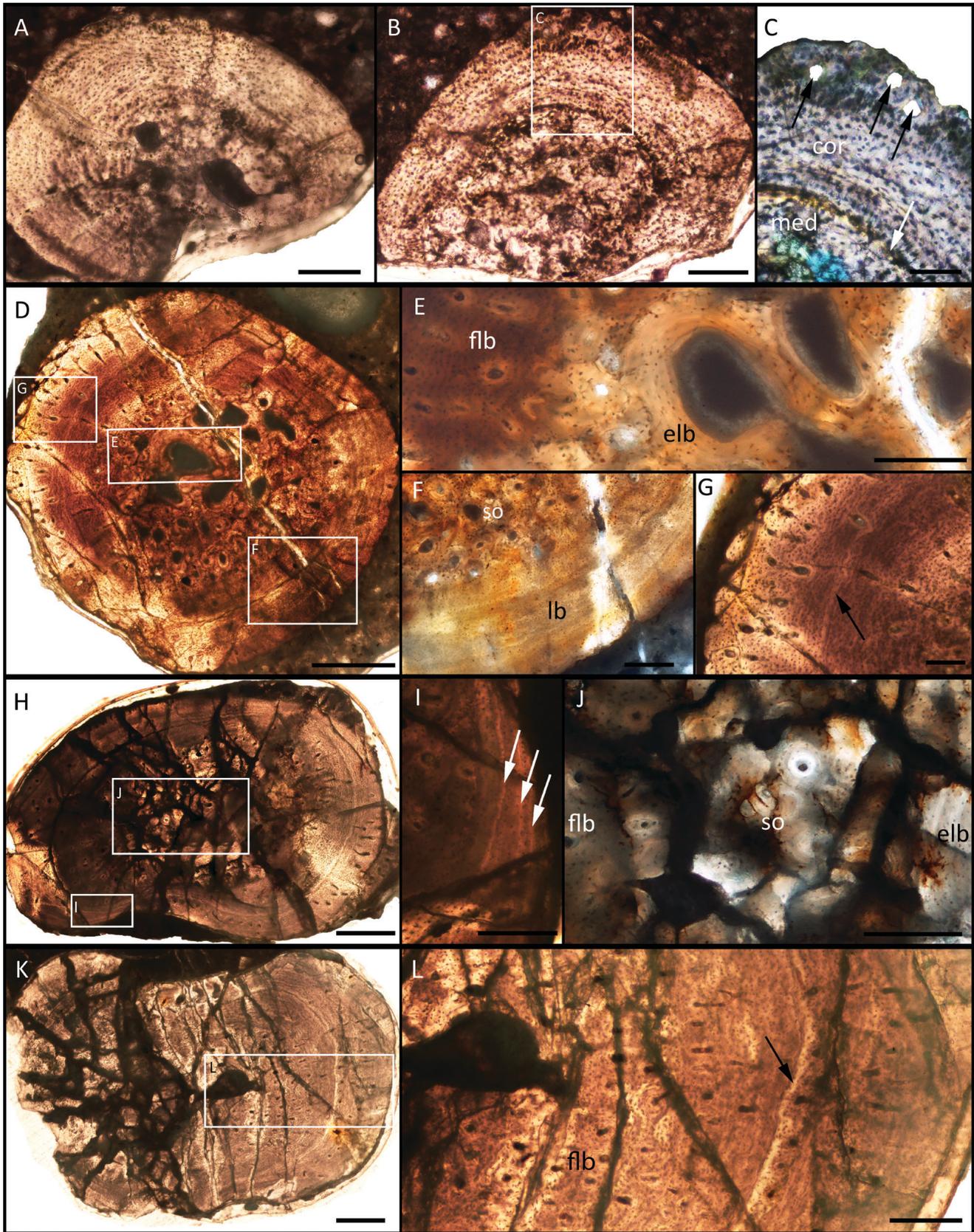
Figure 5D depicts a histogram that illustrates the size distribution of 54 skulls from the Iziko SAM (for raw data see Appendix 2). The distribution of the skull lengths peaks between 4.71 and 5.73 cm (mean equals 5.21 cm, standard deviation equals 1.15 cm) and is skewed to the left, i.e., there are relatively more smaller skulls than there are larger skulls in the fossil record (adjustment to normal distribution is insignificant on a 95% confidence interval; $\chi^2 = 7.79415$, df = 4 [adjusted], P > 0.05).

Microstructure and Histology of Long Bones and Ribs

Histological and microanatomical examinations of long bones and ribs were performed on thin-sections of the various *Cistecephalus* bones sampled. For some of the bones sampled, the preservation of the overall microanatomy and histology was not optimal and limited the histological descriptions.

Ribs—The midregions of three ribs of a medium-sized specimen (BP/I/2450) were sampled in transverse sections. Both smaller ribs are near complete in cross-section, but lack part of the cortices in the region where the bone was not surrounded by matrix (Fig. 6A, B). The ribs are osteosclerotic-like: the

medullary region is almost completely infilled by cancellous bone. A thin birefringent line that separates the cancellous bone from the compact cortex (Fig. 6C) could represent a line of arrested growth (LAG). The cortical region consists of avascular lamellar bone, suggesting a rather slow bone deposition and resulting in a circumferential lamellar organization of the numerous osteocyte lacunae. Few large longitudinal vascular channels occur in the periphery of the cross-sections. These canals are surrounded by large osteocytes, suggesting a localized asymmetric fast growth of the bone in this region or perhaps a zone of tendon attachment (Fig. 6C). The larger rib is complete in cross-section and also osteosclerotic-like (Fig. 6D). The remnant of the medullary cavity is bordered by endosteal lamellar bone (Fig. 6E). The cross-section of the bone is asymmetric in terms of bone deposition rate and remodeling. On one side, the inner cortex has been highly remodeled and consists of a dense Haversian bone tissue (Fig. 6E, F). The remaining two-thirds of the cortex consist of avascular lamellar bone highlighting a slow bone apposition rate (Fig. 6F). The other side of the cross-section consists of lamellar-zonal bone with numerous longitudinal and radial canals (Fig. 6G). The canals consist of simple vascular channels and primary osteons. This side of the rib apparently



grew faster than the other side. Numerous Sharpey's fibers, orthogonal to the bone surface and associated with the accumulation of osteocytes, are responsible for the gray-shaded areas in the cross-section. In this rib, at least one LAG is observed (Fig. 6G).

Both ribs of the specimen RMS-410 have major cracks that are infilled by a black deposit (Fig. 6H–L). The histology of the two elements is consistent and very similar to the structure of the large rib of the specimen BP/I/2450. The cross-section reveals a dense, osteosclerotic-like bone, with a compactness of almost 100% (Fig. 6H, K). The small medullary region is almost completely infilled by a thick layer of endosteal lamellar bone (Fig. 6J). The perimedullary region presents numerous secondary osteons on one side of the section (Fig. 6J). The cortex consists of lamellar zonal bone with alternating fast and slow growth. The channels consist of longitudinal and radial primary osteons and simple vascular canals. Two to three LAGs can be observed in the ribs of RMS-410 (Fig. 6I, L).

Long Bones—A femur, a humerus, and an ulna of specimen RMS-410 were sampled in cross-sections (Fig. 7A, D, F).

The diaphyseal cross-section of the femur is incomplete but displays a relatively high compactness (Fig. 7A–C). The large medullary region is partially infilled with trabecular bone (Fig. 7C). The innermost cortex consists of fast deposited fibrolamellar bone with longitudinal primary osteons. The osteocyte lacunae are globular. External to this layer a slow down in the rate of the bone deposition occurred followed by an annulus associated with a LAG. The simple vascular canals show a reticular orientation and the flat osteocyte lacunae have a sublamellar organization (Fig. 7B). The outermost cortex consists of slow lamellar deposited bone with few simple vascular canals and flat osteocyte lacunae (Fig. 7B).

The cross-section of the humerus is incomplete and large cracks affect histological preservation (Fig. 7D). Nevertheless, it is noticeable that the medullary cavity is small and compact bone occupies the major part of the cross-section. Some patches of fibrolamellar bone are observable in the inner cortex (Fig. 7E). An annulus associated with multiple LAGs marks the transition between the fast deposited fibrolamellar tissue and the outer poorly vascularized lamellar bone (Fig. 7E).

The overall structure of the sampled ulna of RMS-410 (Fig. 7F) is consistent with the femoral histology. The small medullary cavity is surrounded by a thick layer of lamellar endosteal bone. Two-thirds of the cortex consists of a fast deposited fibrolamellar bone with longitudinal and reticular canals (Fig. 7G). Contrary to the ulna previously sectioned by Botha-Brink and Angielczyk (2010; Fig. 7L), the outer periosteal bone consist of low vascularized lamellar bone interrupted by at least three LAGs that reveal periodic pauses in the generally slow bone depositional rate (Fig. 7H).

In contrast to the *Cistecephalus* bones sampled, the femur of the extant arboreal gray squirrel displays a thin bone wall and a large medullary cavity (Fig. 7I), whereas femora of the fossorial naked mole rat (Fig. 7J) and the digging dicynodont *Diictodon* (Fig. 7K) feature relatively thick bone walls.

DISCUSSION

Skull Allometries

Cistecephalus was named for its 'box-shaped' skull, which is approximately as long as it is wide. This is, however, not true for the smallest skull of our sample (GS-225, Fig. 3A; skull length 3.2 cm), which appears to be an exception (ratio of skull length to skull width of 1.47). The calculated linear regression function provides a fair estimate of this ratio for the larger skulls of *Cistecephalus* (the function explains 82% of the variation), but based on specimen GS-225, it is suggested that very young individuals feature narrow, elongated skulls that widen relatively quickly during ontogeny, until the width of the skull approximately equals its length.

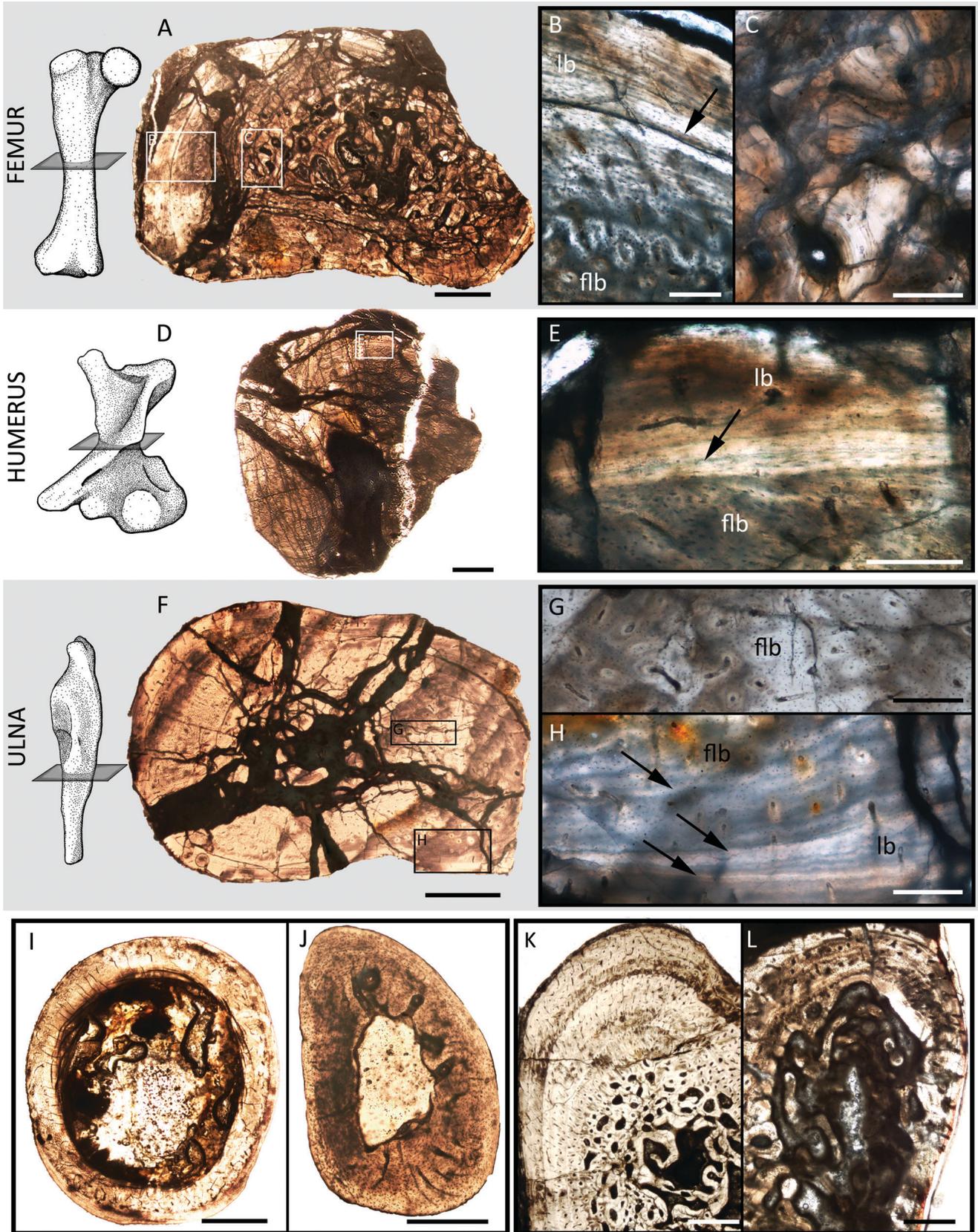
Our analysis suggests that the ratios of intertemporal to interorbital width and orbit size to skull length do not change during ontogeny, irrespectively of the presence or absence of SR. Moreover, the allometries of both groups of skulls (with or without SR) do not reveal significant differences (P-values >> 0.05). The results of this study, although based on a different methodology, support Keyser's (1973) hypothesis that all known specimens of *Cistecephalus* belong to a single species.

Interpretations for the Occurrence of Supraorbital Ridges

This study confirms Keyser's hypothesis (1973) that SR start to develop in individuals with skulls larger than 5 cm (corresponding to a body length of almost 30 cm, or 50% of the maximum body length found in the fossil record; Broom, 1948).

We considered the possibility that distortion and weathering may have caused a loss of SR in some specimens with skulls longer than 5 cm. However, Keyser (1976) noted that raised or leveled supraorbital margins are among the features least affected by distortion. Furthermore, some well-preserved specimens such as BP/I/506 (skull length 5.9 cm; Fig. 3D) clearly lack raised SR. If the occurrence of SR was dependent of ontogeny only, as suggested by Keyser (1973), the initiation of the development of this feature would be highly variable. Given the absence of raised SR in some specimens, even among the very large ones (Table 1), as an alternative hypothesis we suggest that the SR represent a sexually dimorphic character. Sexual dimorphism has previously been suggested for several dicynodonts (e.g., *Diictodon*: King, 1993; Sullivan et al., 2003; *Aulacephalodon*: Tollman et al., 1980; *Lystrosaurus*: Ray, 2005), based on cranial features. It is often the presence and absence

← FIGURE 6. Cross-sections of ribs of two specimens of *Cistecephalus*. **A–G**, specimen BP/I/2450; **H–L**, specimen RMS-410. **A–B**, two small ribs from the anterior region of the rib cage. The cortical region consists of an avascular lamellar bone with numerous osteocyte lacunae. The medullary cavity is infilled by cancellous bone; **C**, detail of **B**. Few large longitudinal vascular channels are found in the outermost cortex of one side of the cross-sections (black arrows). A partially preserved thin line in the compact cortex could be a LAG (white arrow); **D**, larger rib complete in cross-section; **E**, detail of the cross-section center of the large rib of specimen BP/I/2450. The remnant of the medullary cavity is bordered by endosteal lamellar bone; **F**, the inner cortex consists of dense Haversian bone. The outer part of the cortex consists of apposition of avascular lamellar bone interrupted by LAGs; **G**, the cortex consists of lamellar-zonal bone with numerous longitudinal and radial canals. At least one LAG is observable (arrow); **H**, rib 1 of the specimen RMS-410. At least two LAGs are distinct in the compacta; **I**, detail of **H** (bone surface on the right). Deposition of lamellar bone interrupted by three LAGs (arrows) in the outer-most cortex; **J**, detail of **H**. The small medullary cavity is almost completely infilled by a thick layer of endosteal lamellar bone. The perimedullary region presents dense Haversian bone. The inner cortex consists of fibrolamellar bone. The outer cortex is formed of poorly vascularized lamellar bone interrupted by LAGs; **K**, rib 2 of the specimen RMS-410. Two LAGs are observed in some parts of the cortex; **L**, the inner cortex consists of fibrolamellar bone. The outer cortex is formed of poorly vascularized lamellar bone interrupted by LAGs (arrow). **Abbreviations:** **cor**, cortex; **med**, medullary region; **lb**, periosteal lamellar bone; **elb**, endosteal lamellar bone; **flb**, fibrolamellar bone; **so**, secondary osteons. Scale bars in **A**, **B**, **E**, **F**, **G**, **I**, **J**, and **L** equal 200 μm , that in **C** equals 100 μm , that in **D** equals 1 mm, and those in **H** and **K** equal 500 μm .



of tusks that is attributed to sexual dimorphism (Botha and Angielczyk, 2007; Fröbisch, 2007:character 14). For the tuskless genus *Cistecephalus*, we propose that level or raised SR can be used to discriminate between the sexes. Although we cannot with certainty assert these sexual dimorphic features to a particular gender, given that among extant Reptilia and Mammalia, males are often more robust, it is likely that the ones with raised SR are males.

Indications for Indeterminate Growth and a High Natural Mortality Rate

The distribution of skull sizes from the Council for Geoscience (Keyser, 1973:fig. 3; n = 30) and the Iziko SAM (present study, Fig. 5D; n = 54) are near normally distributed, but skewed to the left. By applying the head-to-body ratio estimated from the complete specimen BP/I/4086, we deduce that individuals exceeding 45 cm in body length were rare, because skulls over 8 cm in length are few in the fossil record (2 out of 54 in the collection of the Iziko SAM, none in the Council for Geoscience). The few large specimens in the skull ranges distribution Fig. 5D) suggest an indeterminate growth strategy for *Cistecephalus*, an observation that is supported by histological examinations (see below). The largest skulls hence possibly represent the oldest individuals. Because most skulls in the fossil record are from relatively small individuals (skull length < 5.73 cm; Fig. 5D), it is assumed that the majority of the animals died before attaining sexual maturity or at an early adult stage (see following paragraph). The reason for this remains speculative, but because *Cistecephalus* was a small dicynodont, it seems probable that it was a favored prey of gorgonopsian and therocephalian predators of the time (Smith et al., 2012).

Growth Patterns and Sexual Maturity, Deduced from Bone Histology

All examined bones of the larger specimen RMS-410 (humerus, femur, ulna, ribs) exhibit LAGs. The occurrence of fast deposited bone in the inner cortex, followed by lamellar bone in the outermost cortex, indicates that the individual had reached an ontogenetic stage where growth had slowed down. The histological features (the relative decrease of the growth rate, apposition of lamellar bone in the periphery, and low or no peripheral vascularization) shown by specimen RMS-410 are characteristic of individuals that have already attained sexual maturity (Castanet et al., 1993). The slow and sustained apposition of periosteal lamellar bone is also indicative of indeterminate growth, which has previously been suggested to be a general growth strategy among the dicynodonts (Ray et al., 2009b) and is consistent with the pattern of the skull size distribution. In contrast to the sampled ribs of RMS-410, the ribs of specimen BP/I/2450 are less compact, exhibit higher peripheral vascularization, and an uneven bone surface, indicating that the growth had not slowed down at the time that the animal died. Furthermore, only one LAG can be observed in the largest

sampled rib of BP/I/2450, whereas up to three LAGs are found in the ribs of RMS-410. It is therefore likely that BP/I/2450 represents a sexually immature individual, probably a subadult considering its skull size, whereas RMS-410 represents an adult individual. The two specimens hence allow the estimation that sexual maturity occurred when individuals reached between 5.9 and 6.5 cm skull length (corresponding to an extrapolated body size of between 34.7 and 38.5 cm). Because BP/I/2450 exhibits SR, it suggests that this possible sexually dimorphic characteristic developed before the attainment of sexual maturity.

Lifestyle Adaptations of *Cistecephalus*, Inferred from Bone Microanatomy

All the examined bones (ribs, femur, humerus, ulna) of both *Cistecephalus* specimens are exceptionally compact, with thick bone walls and large amounts of cancellous bone infilling the medullary cavities. The bone compactness of an ulna of a subadult *Cistecephalus* (RBT of 27%) previously described by Botha-Brink and Angielczyk (2010; Fig. 7L), differs strikingly from the compactness of the adult ulna of specimen RMS-410 (RBT of 84%; Fig. 7F). A similar trend is observed in the ribs of the different-sized specimens sampled for this study, which indicates that the bone compactness of *Cistecephalus* increases during ontogeny, mostly by the infilling of the medullary cavity.

Arboreal animals generally have lightly built bones with thin cortices and large medullary cavities (e.g., Currey and Alexander, 1985), because these animals have to lift their body weight against the force of gravity. This is indeed well illustrated in the femur of the scansorial gray squirrel (Fig. 7I). Based on its overall dense thick-walled bone architecture, it is unlikely that *Cistecephalus* was an arboreal animal.

The microstructure of the bones of *Cistecephalus* supports the hypothesis of a digging lifestyle. It has been suggested that extant and extinct animals with high digging activities feature more compact bones than their non-digging relatives (Magwene, 1993; Botha, 2002; Botha and Chinsamy 2004; Chinsamy and Hurum, 2006), which is illustrated by the femoral cross-section of the naked mole rat in Figure 7J. This adaptation has also been observed in several small- to medium-sized digging dicynodonts such as *Diictodon* (Ray and Chinsamy, 2004; Fig. 7K) and also among the cynodonts *Trirachodon* (Botha and Chinsamy, 2004) and *Thrinaxodon* (Botha and Chinsamy, 2005), whose remains were found associated with burrows (Smith, 1987; Groenewald et al., 2001; Smith and Swart, 2002; Damiani et al., 2003).

The dense bone microstructure of *Cistecephalus* could also suggest an aquatic or amphibious adaptation, as found in many tetrapods inhabiting shallow water environments (e.g., Ricqlès and Buffrénil, 2001; Germain and Laurin, 2005, Canoville and Laurin, 2010). Because digging and aquatic adaptations cannot be discriminated from the bone microanatomy of the sampled bones, and a combination of both lifestyles is known from some extant mammals (e.g., the platypus, *Ornithorhynchus anatinus*),

← FIGURE 7. Mid-diaphyseal cross-sections of various long bones of *Cistecephalus* (A–H and L), the gray squirrel *Sciurus carolinensis* (I), the naked mole rat *Heterocephalus glaber* (J), and *Diictodon* (K), described in the present study (A–J) and in Botha-Brink and Angielczyk (2010; K–L). The long bone drawings with the plane of the cross-sections are modified from Cluver (1978) and are not to scale. A, femur of specimen RMS-410; B, detail of A (bone surface to the top). Annulus with a line of arrested growth (arrow); C, detail of A. Medullary region infilled by cancellous bone; D, humerus of the specimen RMS-410; E, detail of D. Annulus with multiple lines of arrested growth (arrow); F, ulna of the specimen RMS-410; G, detail of F. Fibrolamellar bone in the inner cortex; H, detail of F. Lamellar bone interrupted by at least three LAGs (arrows) in the outer cortex; I, femur of a gray squirrel. The bone microanatomy is typical of arboreal tetrapods, with a thin compact bone wall and a large medullary cavity; J, femur of a naked mole rat (ZOO/UCT/192); K, femur of a *Diictodon* subadult (SAM-PK-K7725), displaying a similar compactness to the sampled femur of specimen RMS-410 (A); L, ulna of a subadult specimen of *Cistecephalus* (NMQR1465b), displaying a less compact structure than the ulna of RMS-410 (F) and peripheral vascularization. **Abbreviations:** lb, periosteal lamellar bone; flb, fibrolamellar bone. Scale bars in A, D, F, I, and K equal 1 mm, those in B, C, E, G, and H equal 200 μm, and those in J and L equal 500 μm.

we discuss these hypotheses with regard to the skeletal features of *Cistecephalus*.

Lifestyle Adaptations of *Cistecephalus* Suggested by Skeletal Morphology

Arboreal—An arboreal lifestyle has previously been suggested for *Cistecephalus* (Keyser, 1973; MacRae 1999), mainly based on the prominent, frontally placed eyes and possible opposability of the digits. There are, however, anatomical features seemingly inconsistent with this hypothesis. The limbs of arboreal tetrapods are generally elongated and gracile (Dublin, 1903), such as in the scansorial basal anomodont *Suminia* from the Late Permian of European Russia (Fröbisch and Reisz, 2009, 2011). In contrast, the limbs of *Cistecephalus* are short and stout (Cluver, 1978) and the tail is short, whereas the tail of *Suminia* and other climbing tetrapods are often elongated, acting as a balancing or prehensile organ. In addition, the dense architecture of its bones precludes it from having an arboreal lifestyle.

Amphibious—The bone microstructure of *Cistecephalus* supports a (semi)aquatic habit for this dicynodont; however, its cranial features argue against such a lifestyle: many aquatic or amphibious animals have dorsally placed eyes and the ears, orbits, and external nares tend to be located in the same plane (Osburn, 1903). In *Cistecephalus*, the nares are situated well under the orbital openings and the orbits point frontally.

Fossorial—On the basis of a range of anatomical features, Cluver (1978) proposed a digging or fossorial lifestyle for *Cistecephalus*. These include the outward rotation of the hind limbs, as observed in the extant European mole *Talpa europaea* (Cluver, 1978); the rounded occiput bearing strong neck and shoulder musculature; the massive, short, and robust humeri; the strengthened manus; and the more gracile, mobile pes (which he proposed to be suitable for removing loose soil during digging activities). As described by Shimer (1903), the skull of burrowing mammals is often fusiform and the body diameter is greatest at the shoulders and diminishes gradually towards the tip of the snout. The heads of many burrowing animals therefore follow a triangular form, with the zygomatic arches not extending over the greatest width of the skull. The shape of the *Cistecephalus* skull (Fig. 2A), which features the greatest width at the back and the unusual lateral position of its temporal openings (most dicynodonts feature them dorsally), could therefore be explained as a digging adaptation. The observation of a rapid widening of the skull during ontogeny, probably associated with an increase of the neck and shoulder musculature, could indicate that very young individuals (such as specimen GS-225; Fig. 3A) were not active diggers; this activity being performed only by older animals. The short tail is a characteristic of many fossorial animals as well (Shimer, 1903).

The compact bones described in the current study support the previously proposed digging lifestyle for *Cistecephalus*. The heavily built bones could well be an adaptation to the mechanical forces the body withstands during digging activities (Currey, 2003). The proposed threshold of 30% RBT of the bones of digging animals (Botha, 2002; Botha and Chinsamy, 2004) is well exceeded by the adult *Cistecephalus* (RBT of the ulna equals 84%).

It is well established that digging adaptations characterize many (if not all) dicynodonts (Botha-Brink and Angielczyk, 2010). However, even though dicynodonts such as *Rhachiocephalus*, *Aulacephalodon*, *Dicynodon*, and *Kannemeyeria* “possessed spatulate ungual phalanges with large flexor tubercles, which are typical of many digging animals,” Botha-Brink and Angielczyk (2010:360) suggested that they were too large to be truly fossorial and that these adaptations may reflect a general foraging behavior among the group (such as digging for the subterrestrial parts of plants). Unlike its large relatives, *Cistecephalus* was relatively small and could have had a burrowing lifestyle. Curiously, how-

ever, although dicynodont burrows have been described from the *Tropidostoma* Assemblage Zone (Smith, 1987), none of these have remains of *Cistecephalus* associated (Ray and Chinsamy, 2003). To date, no burrows have been found in the *Cistecephalus* Assemblage Zone, where *Cistecephalus* is far more abundant (Smith et al., 2012). A possible explanation for the lack of burrows is that the preservation of burrows (and the animals inhabiting them) is often related to floods, followed by a sedimentation process (Smith, 1987). However, according to Smith et al. (2012), the floodplain tables during the *Cistecephalus* Assemblage Zone were lower than in the preceding and succeeding zones, indicating a time of relative aridity. It is therefore possible that the absence of burrows in the fossil record of the *Cistecephalus* Assemblage Zone may be simply the result of taphonomic bias.

Dicynodont Bone Microstructure in Phylogenetic Context

Recent studies have highlighted that lifestyle inferences from bone microstructure are limited when a phylogenetic signal is strong, i.e., differences in bone compactness are insignificant among closely related but ecologically diverse taxa. For example, fresh water and terrestrial testudines exhibit similar compactness in their long bones and their lifestyles are thus indeterminate from bone microstructure (Kriloff et al., 2008; Canoville and Laurin, 2010).

Chinsamy and Rubidge (1993), Botha-Brink and Angielczyk (2010), and Ray et al. (2012) described the bone microstructure of many dicynodont genera. A general trend among these dicynodonts is that although the compacta surrounding the medullary cavity is variable in thickness, in most cases cancellous bone infilled the medullary cavity, resulting in high bone compactness in adult specimens.

Because there appears to be a phylogenetic trend of compact bones with trabeculae infilling the medullary cavity among the Dicynodontia, caution is warranted in deducing lifestyle adaptations from bone microstructure alone. A similar conclusion was reached by Green et al. (2010), who found the dense, compact bone microstructure of the Triassic dicynodont *Placerias hesternus* inconsistent with an aquatic lifestyle when considering its anatomy and taphonomy. It is, however, notable that the adult *Cistecephalus* features exceptionally heavily built bones, when compared with other dicynodonts (Botha-Brink and Angielczyk, 2010:tab. 2), therefore making it likely that this species indeed shows an ecological signal in its bone microstructure.

The Function of Binocular Vision in *Cistecephalus*

Based on the frontally placed orbits and the wide skull of *Cistecephalus* that could house an enlarged brain suitable for processing stereoscopic vision, Keyser (1973) suggested a scansorial lifestyle. Because *Cistecephalus* was in all likelihood not arboreal (see above), the function of binocular vision deserves a reevaluation.

A high degree of binocular vision is essential for visual depth-of-field and distance estimations and is therefore widely found in predatory animals (e.g., Heesy, 2008), as opposed to the laterally placed orbits of many herbivores that benefit from a larger vision field. The dicynodonts are generally hypothesized to have been herbivorous (e.g., King, 1990), but the prominent position of the orbits in *Cistecephalus* could be interpreted as evidence of a predatory lifestyle. According to Keyser (1973), the shortened skull leads to a concentration of the bite force to the tip of the snout, because the adductor musculature could insert far forward on the mandible. Keyser (1973) interpreted it as an adaptation to a diet of hard plant materials, but the seemingly strong jaw musculature could also have been used to crack the exoskeletons of small invertebrates. Further, a combination of active hunting, involving the need for stereopsis, and extensive digging activities

to reach invertebrates could explain the specialized anatomy of *Cistecephalus*.

Alternatively, or in addition, the frontal location of the orbits could be an adaptation to a nocturnal way of life. A high degree of binocular vision characterizes many nocturnal animals, because the redundancy of optical inputs results in improved optical sensitivity (Pettigrew, 1986; Heesy, 2008). Cruickshank (1978) and Sullivan et al. (2003) hypothesized that the dicynodonts had tusks either for display or threat purposes; Cruickshank (1978) further inferred that the tuskless forms (which would include *Cistecephalus*) were either nocturnal or living subterrestrially. This hypothesis was treated with skepticism (Morato et al., 2008), but from the findings of this study, it could apply to *Cistecephalus*.

CONCLUSIONS

Cistecephalus skulls differ in the presence or absence of raised SR, but allometries of a skull growth series support the earlier deductions that all of the fossil remains of *Cistecephalus* belong to a single species (Keyser, 1973). Our findings that even some of the largest individuals do not exhibit raised SR contradict the previous hypothesis that the development of SR is a feature of ontogeny only. We therefore propose that the development of SR is an ontogenetic, as well as a sexual dimorphic feature.

Histological data, as well as the distribution of skull sizes in the fossil record, indicate that *Cistecephalus* had an indeterminate growth strategy. The comparison of two ribs of different-sized individuals with the smaller one exhibiting subadult characteristics allows the deduction that sexual maturity was attained when skull sizes were between 5.9 and 6.5 cm.

The compact bone microanatomy of the adult *Cistecephalus* could imply either an aquatic or a fossorial adaptation. However, anatomical features support digging adaptations. A burrowing lifestyle and other seek-or-hide behaviors of many dicynodonts and other therapsids have been suggested to be strategies to escape the harsh environmental conditions of the Late Permian and Early Triassic (e.g., Damiani et al., 2003; Botha and Chinsamy, 2004; Botha-Brink and Angielczyk, 2010; Fröbisch et al., 2010). Both bone microstructure and skeletal anatomy suggest that *Cistecephalus* was not an arboreal animal. We propose that the high degree of binocular vision is an adaptation for a predatory (insectivorous) and/or nocturnal lifestyle.

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APPENDIX 1. List of studies carried on dicynodont bone histology.

| Dicynodont genera | Histological studies |
|------------------------|--|
| <i>Eodicynodon</i> | Botha-Brink and Angielczyk, 2010; Ray et al., 2012 |
| <i>Diictodon</i> | Chinsamy and Rubidge, 1993; Ray and Chinsamy, 2004; Ray et al., 2009a, 2012; Botha-Brink and Angielczyk, 2010 |
| <i>Endothiodon</i> | Chinsamy and Rubidge, 1993; Ray et al., 2009a, 2012; Botha-Brink and Angielczyk, 2010 |
| <i>Dicynodontoides</i> | Botha-Brink and Angielczyk, 2010 |
| <i>Cistecephalus</i> | Chinsamy and Rubidge, 1993; Botha-Brink and Angielczyk, 2010 |
| <i>Rhachiocephalus</i> | Botha-Brink and Angielczyk, 2010 |
| <i>Tropidostoma</i> | Botha and Angielczyk, 2007 |
| <i>Oudenodon</i> | Ricqlès, 1972; Chinsamy and Rubidge, 1993; Botha, 2003; Botha and Angielczyk, 2007; Botha-Brink and Angielczyk, 2010; Jasinoski and Chinsamy-Turan, 2012; Ray et al., 2012 |
| <i>Aulacephalodon</i> | Ricqlès, 1972; Chinsamy and Rubidge, 1993; Botha-Brink and Angielczyk, 2010 |
| <i>Dicynodon</i> | Chinsamy and Rubidge, 1993; Kriloff et al., 2008; Botha-Brink and Angielczyk, 2010 |
| <i>Lystrosaurus</i> | Ricqlès, 1975; Chinsamy and Rubidge, 1993; Germain and Laurin, 2005; Ray et al., 2005, 2009b, 2012; Botha-Brink and Angielczyk, 2010; Canoville and Laurin, 2010; Jasinoski and Chinsamy-Turan, 2012 |
| <i>Kannemeyeria</i> | Gross, 1934; Enlow and Brown, 1957; Ricqlès, 1975, 1976; Chinsamy and Rubidge, 1993; Botha-Brink and Angielczyk, 2010; Ray et al., 2012 |
| <i>Wadiasaurus</i> | Ray et al., 2009a, 2009b, 2010, 2012 |
| <i>Placerias</i> | Green et al., 2010; Green, 2012 |
| <i>Siahleckeria</i> | Ricqlès, 1972 |
| <i>Dinodontosaurus</i> | Enlow and Brown, 1957 |
| Unidentified genera | Green, 2012 |

APPENDIX 2. Skull lengths of 54 specimens of *Cistecephalus* from the Iziko SAM of Cape Town (South Africa). All the measurements are in centimeters. **Abbreviation: Lg**, median length of the skull (tip of the snout to the foramen magnum).

| ID | Specimen number | Lg |
|----|-----------------|------|
| 1 | SAM PK-K8629 | 3.92 |
| 2 | SAM PK-K8517 | 5.11 |
| 3 | SAM PK-K8512 | 5.78 |
| 4 | SAM PK-K8510 | 4.50 |
| 5 | SAM PK-K8309 | 4.79 |
| 6 | SAM PK-K8117 | 4.50 |
| 7 | SAM PK-K8116 | 4.58 |
| 8 | SAM PK-K8115 | 6.30 |
| 9 | SAM PK-K8113 | 8.78 |
| 10 | SAM PK-K8068 | 6.03 |
| 11 | SAM PK-K8001 | 4.76 |
| 12 | SAM PK-K7852 | 4.27 |
| 13 | SAM PK-K7817 | 5.05 |
| 14 | SAM PK-K7667 | 5.65 |
| 15 | SAM PK-K7667 | 6.34 |
| 16 | SAM PK-K7602 | 3.91 |

(Continued on next page)

APPENDIX 2. Skull lengths of 54 specimens of *Cistecephalus* from the Iziko SAM of Cape Town (South Africa). All the measurements are in centimeters. **Abbreviation: Lg**, median length of the skull (tip of the snout to the foramen magnum). (*Continued*)

| ID | Specimen number | Lg |
|----|-----------------|------|
| 17 | SAM PK-K7561 | 5.00 |
| 18 | SAM PK-K7475 | 6.17 |
| 19 | SAM PK-K7419 | 5.67 |
| 20 | SAM PK-K7418 | 6.57 |
| 21 | SAM PK-K7416 | 6.90 |
| 22 | SAM PK-K7406 | 4.35 |
| 23 | SAM PK-K7393 | 2.68 |
| 24 | SAM PK-K7392 | 5.67 |
| 25 | SAM PK-K7362 | 4.05 |
| 26 | SAM PK-K7354 | 8.03 |
| 27 | SAM PK-K7337 | 6.95 |
| 28 | SAM PK-K7332 | 6.91 |
| 29 | SAM PK-K7331 | 5.56 |
| 30 | SAM PK-K7317 | 3.89 |
| 31 | SAM PK-K7009 | 5.22 |
| 32 | SAM PK-K7007 | 3.64 |
| 33 | SAM PK-K6814 | 5.60 |
| 34 | SAM PK-K6642 | 4.89 |
| 35 | SAM PK-K6058 | 4.36 |
| 36 | SAM PK-K5519 | 4.83 |
| 37 | SAM PK-K5517 | 3.58 |
| 38 | SAM PK-K5513 | 5.71 |
| 39 | SAM PK-K1686 | 4.90 |
| 40 | SAM PK-K1150 | 6.40 |
| 41 | SAM PK-K10901 | 4.01 |
| 42 | SAM PK-K10677 | 4.46 |
| 43 | SAM PK-K10665 | 4.46 |
| 44 | SAM PK-K10664 | 4.21 |
| 45 | SAM PK-K10652 | 3.82 |
| 46 | SAM PK-K10564 | 5.71 |
| 47 | SAM PK-K10561 | 4.87 |
| 48 | SAM PK-K10554 | 4.98 |
| 49 | SAM PK-K10553 | 6.00 |
| 50 | SAM PK-K10419 | 5.67 |
| 51 | SAM PK-K10400 | 6.43 |
| 52 | SAM PK-K10398 | 5.57 |
| 53 | SAM PK-K10393 | 4.62 |
| 54 | SAM PK-K10155 | 4.90 |