

Long Bone Morphology and Histology of the Stem Salamander *Kulgeriherpeton ultimum* (Caudata, Karauridae) from the Lower Cretaceous of Yakutia

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Abstract—The morphology and histological structure of the humerus and femora of the stem karaurid salamander *Kulgeriherpeton ultimum* Skutschas et al., 2018, from the Lower Cretaceous Teete locality, Republic of Sakha (Yakutia) is described. The microanatomical and histological structure of *K. ultimum* is characterized by the presence of a thick compact primary cortex formed by a parallel-fibered bone; the absence (in the humerus) or presence of a small medullary cavity in the mid-diaphysis; the presence of a medullary cavity expanding towards the epiphyses, which continues in the proximal and distal parts as a complex network of branching canals, partially replaced by erosion bays; the presence of primary vascular canals and growth marks in the primary cortex; the presence of remnants of unresorbed cartilage and the Kashchenko's line; active secondary remodeling with the formation of erosion bays similar to those in large-sized salamanders (other stem karaurid salamanders and cryptobranchids). Skeletochronological analysis of the humerus of *K. ultimum* showed that, at the time of the animal's death, its individual age was 13–16 years, and the absence of a reduction in the distance between cyclic growth marks in the peripheral part of the cortex indicates that it belonged to an actively growing individual that had not reached its maximum possible size. The similarity in the morphology of the humerus and femur of *K. ultimum* and extant aquatic neotenic salamanders (absence of a dorsal crest on the humerus for the attachment of m. subcoracoscapularis, lower, forward-displaced trochanter of the femur, and shallow ventral fossa (fossa trochanterica) on the femur), as well as the presence of remnants of cartilage and preservation of Kashchenko's line in the internal structure of limb bones, confirm conclusions about aquatic life style and neotenic nature of stem karaurid salamanders.

Keywords: Kulgeriherpeton, stem salamanders, Karauridae, paleohistology, Early Cretaceous, Yakutia

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INTRODUCTION

Study of stem-group members is important for reconstructing the early stages of salamander evolution, including the emergence of the crown group, as well as for documenting character states and patterns of character state transformations in Caudata. One of the groups of stem salamanders is the Karauridae, basal neotenic salamanders with a number of primitive features, including relatively large size (20–40 cm), the presence of a well-developed sculpture on the skull roof bones, the presence of a sculptured dorsal part of the squamosal, which prevents the muscles of the internal adductor from getting on the dorsal surface of the frontal and parietal bones, the presence of a posterolateral process of the prefrontal bone, the absence of an opening for the exit of the spinal nerves in the

atlas, and strongly ossified (i.e., with an extensive endochondral component) trunk vertebrae (Skutschas and Martin, 2011; Skutschas, 2016; Jones et al., 2022).

Karaurid salamanders include Jurassic representatives (e.g., Middle Jurassic *Kokartus* (Kyrgyzstan), *Marmorherpeton* (United Kingdom), *Urupia* (West Siberia, Russia), and Late Jurassic *Karaurus* from Kazakhstan) and younger, Early Cretaceous forms, known from West Siberia (*Caudata* indet.) and Yakutia (*Kulgeriherpeton*) (Skutschas, 2016; Skutschas et al., 2018; Jones et al., 2022).

The karaurid salamander *Kulgeriherpeton ultimum* from the Lower Cretaceous Teete locality, Republic of Sakha (Yakutia), is of particular interest because (1) it is one of the latest stem salamanders in the fossil record and (2) it is a component of the fauna that

Table 1. List and dimensional characteristics of the studied specimens

No.	Skeletal element	Total bone length, mm	Diameter of the central part of the diaphysis, mm	Width of the proximal epiphysis, mm	Width of the distal epiphysis, mm	Maximum thickness of the cortex, mm	Maximum diameter of the medullary cavity, mm
ZIN PH 38/246	Humerus	16.5	2.4	5.0	6.5	1.1	—
ZIN PH 35/246	Femur	—	1.6	—	4.8	0.5	1.0
ZIN PH 37/246	Femur	—	2.4	4.6	—	0.4	1.5
ZIN PH 39/246	Femur	24.5	2.4	6.0	7.0	1.8	3.6

formed in the polar latitude region of the Early Cretaceous (Rich et al., 2002; Skutschas et al., 2018). Despite this, many aspects of the biology of *K. ultimum* remain unknown. To obtain data on the lifestyle, character and rate of growth, individual age, and other biological characteristics of *K. ultimum*, a histological analysis of the limb bones was performed. Additionally, the morphological structure of the humeri and femora of this species was described.

MATERIALS AND METHODS

To identify the internal and external structure in detail, the most complete studied specimens (humerus specimen ZIN PH 38/246 and femur specimen ZIN PH 39/246) were scanned using a Skyscan 1172 microtomograph (at 80 kV and 0.1 mA, resolution of the obtained images 1.94 μm per pixel, image size 1672 \times 1672 pixels) at the Resource Center for X-Ray Diffraction Studies (St. Petersburg State University) and visualized using the Amira 6.3.0 software (FEI-VSG Company). Then, to study the histological structure, standard thin petrographic (hereinafter, histological) sections of these two specimens (humerus specimen ZIN PH 38/246 and femur specimen ZIN PH 39/246), as well as two additional fragments of femurs, specimens ZIN PH 35/246 and ZIN PH 37/246, were prepared (Table 1).

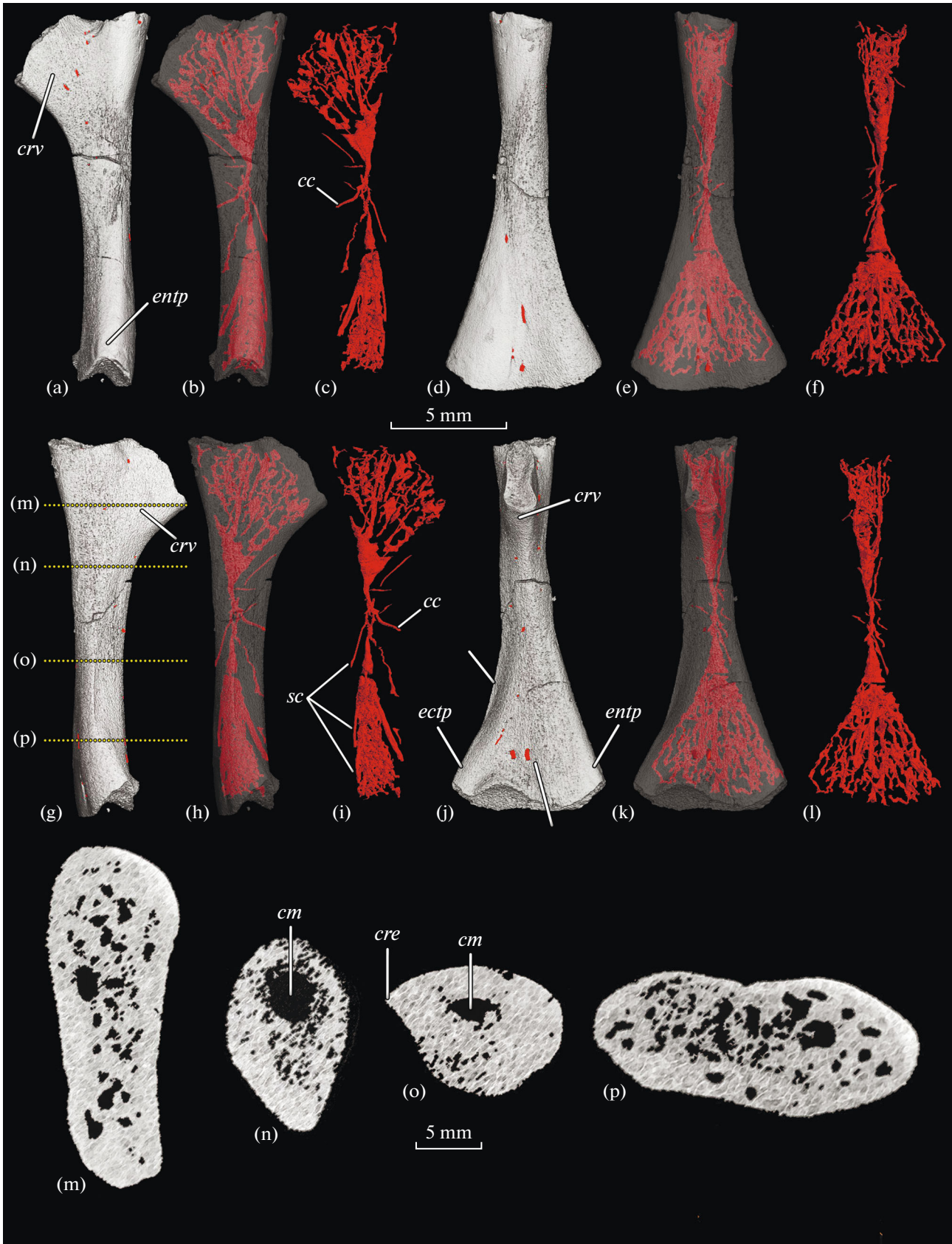
All sections were studied using a Leica 4500 optical polarizing microscope (Leica Microsystems, Wetzlar, Germany) at the Resource Center for X-Ray Diffraction Studies (St. Petersburg State University).

The skeletons of extant members of the genera *Cryptobranchus* (Cryptobranchidae), *Salamandrella* (Hynobiidae), *Ambystoma* (Ambystomatidae), and *Triturus* (Salamandridae), stored in the collection of the Department of Vertebrate Zoology, St. Petersburg State University, as well as CT-scans of the limb bones of *Necturus* (Proteidae), available in the Morpho-source repository (<https://www.morphosource.org>), were used as comparative materials in studying the morphology of the humerus and femur of *Kulgeriherpeton ultimum*. Here, we use the histological terminology from the work by Francillon-Vieillot et al. (1990). To designate the muscles of the limbs and interpret the attachment points of individual muscles, we use the terminology and results of the studies by Gurtovoi et al. (1978), Ashley Ross (1992), and Molnar et al. (2018, 2020). The studied material is stored in the paleoherpetological collection of the Zoological Institute of the Russian Academy of Sciences (ZIN PH), St. Petersburg, Russia.

MORPHOLOGICAL DESCRIPTION OF MATERIAL

The humerus of *Kulgeriherpeton ultimum* (specimen ZIN PH 38/246) is massive, with a relatively short diaphysis with narrow central part and widened proximal and distal ends located at an angle of approximately 90° to each other (Fig. 1). At both ends, there are depressions in which non-ossifying cartilaginous epiphyses were located during the life of the animal. The proximal end of the bone bears a well-defined wide deltopectoral crest (crista ventralis) for attaching

Fig. 1. *Kulgeriherpeton ultimum* Skutschas et al., 2018, 3D reconstruction of the right humerus (specimen ZIN PH 38/246) and reconstruction of its vascular canals: (a) reconstruction of the humerus, view from the medial side; (b, c) reconstruction of the circulatory system, medial view; (d) reconstruction of the humerus, dorsal view; (e, f) reconstruction of the circulatory system, dorsal view; (g) reconstruction of the humerus, lateral view, with indication of locations of virtual sections; (h, i) reconstruction of the circulatory system, lateral view; (j) reconstruction of the humerus, ventral view; (k, l) reconstruction of the circulatory system, ventral view; (m–p) internal structure of the humerus on virtual sections. Designations: *cc*, central canal; *sc*, subvertical canals extending to the bone surface; *cm*, medullary cavity; *cre*, crest for attachment of the humeral extensor muscles; *crv*, ventral crest; *ectp*, ectepicondyle; *entp*, entepicondyle; *fc*, fossa cubitalis.



a significant number of muscles that control the movements of the humerus. These are mainly the pectoral (m. pectoralis), procoracohumeral (m. procoracohumeralis), short coracobrachial (m. coracobrachialis brevis), and supracoracoid (m. supracoracoideus) muscles. In the area of attachment of the short coracobrachial muscle (in the proximal part of the ventral crest, on its medial side) and in the area of attachment of the supracoracoid muscle (in the proximal part of the ventral process, on its lateral side), there are clearly visible large openings of the vascular canals. The dorsal crest (crista dorsalis) is absent. The cubital fossa (fossa cubitalis, a depression on the ventral surface of the distal end, immediately in front of the epiphysis) is relatively small and shallow; several vascular canals open on its surface. On the anterior surface of the diaphysis, there is a low crest that extends approximately from the level of the base of the ventral crest to the level of the posterior edge of the cubital fossa, fusing proximally with the surface of the bone in the region of the lateral epicondyle (ectepicondyle). The distal part of this crest is noticeably thinner and higher; most likely, strong extensor muscles of the forearm (mainly m. brachioradialis) were attached to this area. The surface of the bone in the medial epicondyle (entepicondyle) area has a small triangular elevation, limited dorsally and ventrally by small depressions. Most likely, the flexor muscles of the forearm were attached to this area.

The femur of *Kulgeriherpeton ultimum* (specimen ZIN PH 39/246) is massive and short, with a significantly widened distal end (Fig. 3). The bone is sigmoidally curved when viewed anteriorly or posteriorly. The proximal end is thickened, triangular in cross-section, with the apex directed caudoventrally in the normal position of the limb (when it is laterally abducted). The dorsal surface of the proximal end has a small depression in the posterior part, most likely for the attachment of ligaments or the ischiofemoralis muscle (m. ischiofemoralis). On the ventral side of the proximal end, there is a small ventral fossa (fossa trochanterica), limited anteriorly by the trochanter. The trochanter is large. The crest of the trochanter is high, fairly thin, reaching the distal part of the diaphysis. The posterior surface of the crest is flatter, and bears a weak sculpture in the form of small ridges in the proximal part, probably for attaching the distal sections of the external puboischiofemoralis muscle (m. puboischiofemoralis externus). The distal end is greatly expanded and bean-shaped in cross section. The anterior edge of its dorsal surface has a pronounced depression into which numerous vascular canals open; most likely, this is the attachment site of the tibial extensor tendon (m. extensor cruristibialis). A similar depression, probably for the attachment of the femorofibular muscle (m. femorofibularis), is also present on the ventral side. Numerous vascular canals also open on the surface of this depression.

MICROANATOMICAL AND HISTOLOGICAL DESCRIPTION OF MATERIAL

The internal structure of the humerus (specimen ZIN PH 38/246) is characterized by the presence of a complex system of branched vascular canals and cavities connected with the medullary cavity (Figs. 1n, 1o). The medullary cavity in the central region of the diaphysis is small, but noticeably widens in the distal and proximal directions, gradually turning into a branched network of winding canals, partially transformed into erosion bays. This network is connected with the bone surface through several subvertical canals extending to the ventral and dorsal sides in the distal part and to the lateral and medial sides in the proximal part. On each side of the bone, these canals run almost parallel to each other towards the epiphysis, at an acute angle relative to the length of the bone (Fig. 1, sc). In the central part of the diaphysis, on the ventral side, another large more vertical canal comes to the surface of the bone (Fig. 1, cc). Most likely, this canal is the entry point of the vessel that feeds the bone, whereas the subvertical canals that come to the surface in the area of the epiphyses are its terminal sections that feed the periosteum, ligaments, and muscles adjoining the humerus.

The histological structure of the humerus at the level of the mid-diaphysis is characterized by a thickened primary periosteal cortex and the absence of a pronounced medullary cavity (Figs. 2b, 2c). The primary cortex is compact, almost avascular (with singular vascular canals in the deep parts of the cortex), formed by a parallel-fibered bone matrix. The primary cortex contains numerous cyclical growth marks represented by annuli and lines of arrested growth (LAGs) (see section Skeletochronological Analysis below). Double and triple LAGs are found (Fig. 2b).

Bone remodeling is expressed in the presence of erosion bays and secondary osteons in the central part of the bone (Figs. 2c, 2e).

Osteocyte lacunae are large, round in the primary cortex (Fig. 2d) and oval in the lamellar bone of secondary osteons (Fig. 2e). Osteocyte lacunae in the primary cortex are located in an orderly, cyclical manner, in the zones between growth marks.

The femur (specimen ZIN PH 39/246) has an internal structure pattern similar to that of the humerus, which is characterized by the presence of a medullary cavity (including in the mid-diaphysis), expanding towards the epiphyses and turning into a complex network of winding canals, partially replaced by erosion bays, in the proximal and distal sections (Fig. 3). As in the case of the humerus, this network opens onto the surface of the femur through subvertical canals directed towards the epiphyses and running parallel to each other on each side of the bone (Fig. 3, sc). In the area of the diaphysis, these canals have a significantly smaller diameter and are directed more vertically. An interesting feature is the presence of large

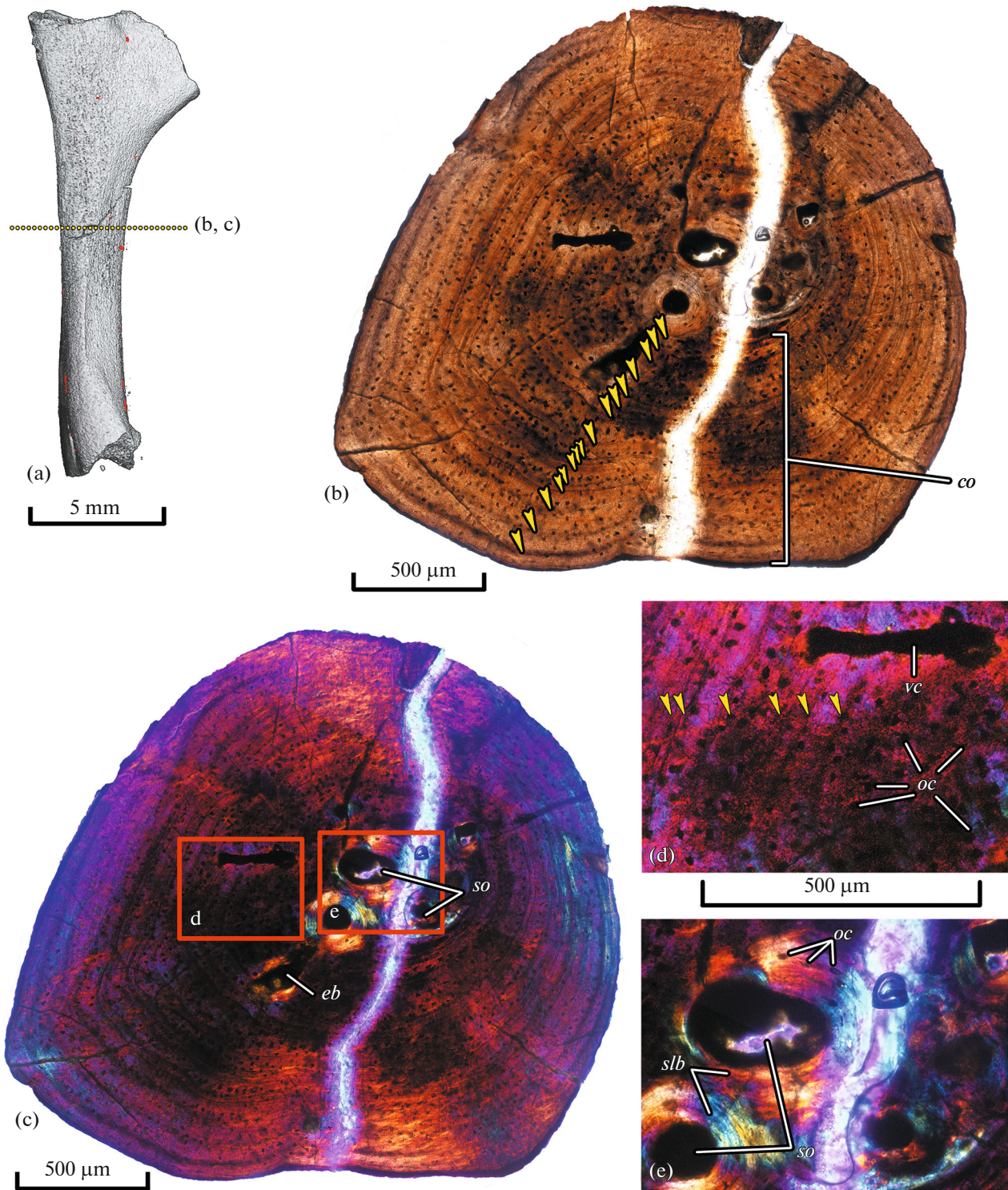
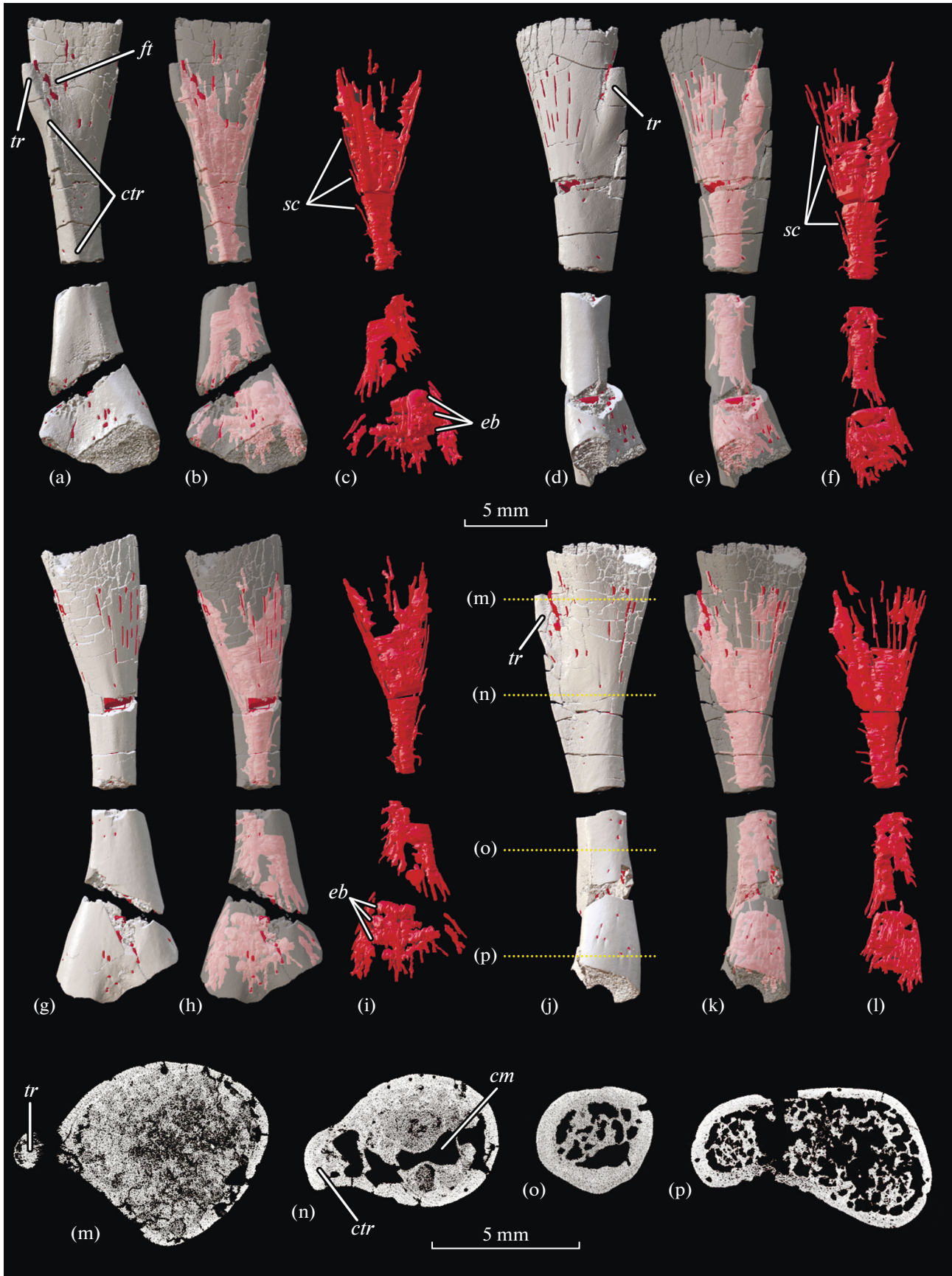


Fig. 2. *Kulgeriherpeton ultimum* Skutschas et al., 2018, transverse histological section of the humerus at the level of the mid-diaphysis (specimen ZIN PH 38/246): (a) reconstruction of the humerus, lateral view, with indication of the location of the section; (b) section of the humerus in transmitted light; (c) section of the humerus in polarized light, with indication of the boundaries of the areas shown under high magnification; (d, e) fragments of the section in polarized light under high magnification. Designations: *co*, cortex; *eb*, erosion bay; *oc*, osteocytes; *slb*, secondary lamellar bone; *so*, secondary osteon; *vc*, vascular canal. Yellow arrows indicate lines of arrested growth (LAGs).



flattened erosion bays in the distal epiphysis area, located one above the other at a relatively equal distance (Fig. 3, eb). The formation of these structures may be associated with cyclical arrests in bone growth, the presence of which is confirmed by the histological structure. In this case, these cavities may correspond to the position where the epiphyseal plate was located during periods of arrested growth of the bone.

All histologically studied femurs (specimens ZIN PH 35/246, ZIN PH 37/246, and ZIN PH 39/246) at the level of the diaphysis are characterized by the presence of a thick, compact primary cortex (Figs. 4, 5). The primary periosteal cortex is almost avascular (with sparse, longitudinal primary vascular canals in some sections). The primary cortex is formed by a parallel-fibered bone matrix and contains cyclical growth marks represented by annuli.

Areas of unresorbed calcified cartilage remain around the medullary cavity (=perimedullary), (Fig. 5, *car*). Kashchenko's line is present between the cartilage and the periosteal bone. Above the cartilage, a layer of endosteal lamellar bone may be present.

Bone remodeling is expressed in the presence of erosion bays (in the periosteal cortex, at the boundary of the primary cortex and cartilage, and in the cartilage itself), in the presence of secondary osteons in the perimedullary part (the initial stages of the formation of the secondary osteon are shown in Fig. 4h), as well as in the resorption of deep layers of the primary cortex with expansion of the medullary cavity and subsequent deposition of endosteal bone. In the medullary cavity, endochondral bone trabeculae formed by lamellar bone appear.

Osteocyte lacunae are large, round and oval in the primary cortex (Fig. 4e) and oval in the secondary lamellar bone (Fig. 4h).

COMPARISON

The microanatomical and histological structure of the limb bones of *Kulgeriherpeton ultimum* is similar to that of other stem karaurid salamanders (*Kokartus*, *Marmorherpeton*; see Buffr enil et al., 2015; Skutschas and Stein, 2015) in the following features: (1) the presence of a thick compact primary cortex formed by parallel-fibered bone matrix; (2) the medullary cavity in the mid-diaphysis area is narrow or not pronounced; (3) the presence of growth marks in the primary cortex; (4) the presence of remnants of unresorbed cartilage and Kashchenko's line; (5) the presence of pri-

mary vascular canals; and (6) active secondary remodeling with the formation of erosion bays. In addition, the common histological features of the structure of the long bones of *Kulgeriherpeton ultimum* and *Kokartus honorarius* are the presence of secondary osteons and the formation of endosteal perimedullary bone from lamellar bone matrix (Skutschas and Stein, 2015).

Among the crown salamanders, similar features of the microanatomical and histological structure of limb bones, namely, the thick compact primary cortex formed by a parallel-fibered bone matrix, the presence of growth marks and primary vascular canals, and the presence of erosion bays (secondary remodeling), are characteristic of representatives of giant salamanders (cryptobranchids) (Canoville et al., 2018; Skutschas et al., 2019; Buffr enil and Laurin, 2021). This similarity is apparently due to the relatively large size of karaurid stem salamanders and cryptobranchids (see Skutschas et al., 2019). In small salamanders, the primary cortex, even if thickened, is avascular and usually does not have signs of remodeling (erosion bays) (Canoville et al., 2018; Buffr enil and Laurin, 2021).

SKELETOCHRONOLOGICAL ANALYSIS

The preservation of cyclic growth marks (annuli, LAGs) in the primary cortex of the humerus of *Kulgeriherpeton ultimum* (specimen ZIN PH 38/246) allowed us to directly count them and determine the individual age and growth characteristics of the animal. At the level of the mid-diaphysis, 16 cyclic growth marks are observed, represented mainly by the lines of growth retardation (annuli). In two cases, contiguous double and triple lines of arrested growth (LAGs) were formed. The large distance between the cyclic growth marks in the outer parts of the cortex indicates that the animal was still growing at the time of death (at least 13 years of age).

Growth marks are also observed in the cortex of the femurs (Fig. 5), but due to the nature of their preservation, it is impossible to accurately count them.

DISCUSSION

Data on the morphology, microanatomy, and histology of the limb bones of *Kulgeriherpeton ultimum* make it possible to reconstruct some paleobiological features of both this salamander and karaurid stem salamanders in general.

Fig. 3. *Kulgeriherpeton ultimum* Skutschas et al., 2018, 3D reconstruction of the right femur (specimen ZIN PH 39/246) and reconstruction of the canals of its circulatory system: (a) reconstruction of the femur, ventral view; (b, c) reconstruction of the circulatory system, ventral view; (d) reconstruction of the femur, anterior view; (e, f) reconstruction of the circulatory system, anterior view; (g) reconstruction of the femur, dorsal view; (h, i) reconstruction of the circulatory system, dorsal view; (j) reconstruction of the femur, posterior view, with indication of locations of virtual sections; (k, l) reconstruction of the circulatory system, posterior view; (m–p) internal structure of the femur on virtual sections. Designations: *ctr*, trochanter crest; *cm*, medullary cavity; *eb*, erosion bays; *ft*, ventral fossa; *sc*, subvertical canals extending to the surface of the bone; *tr*, trochanter.

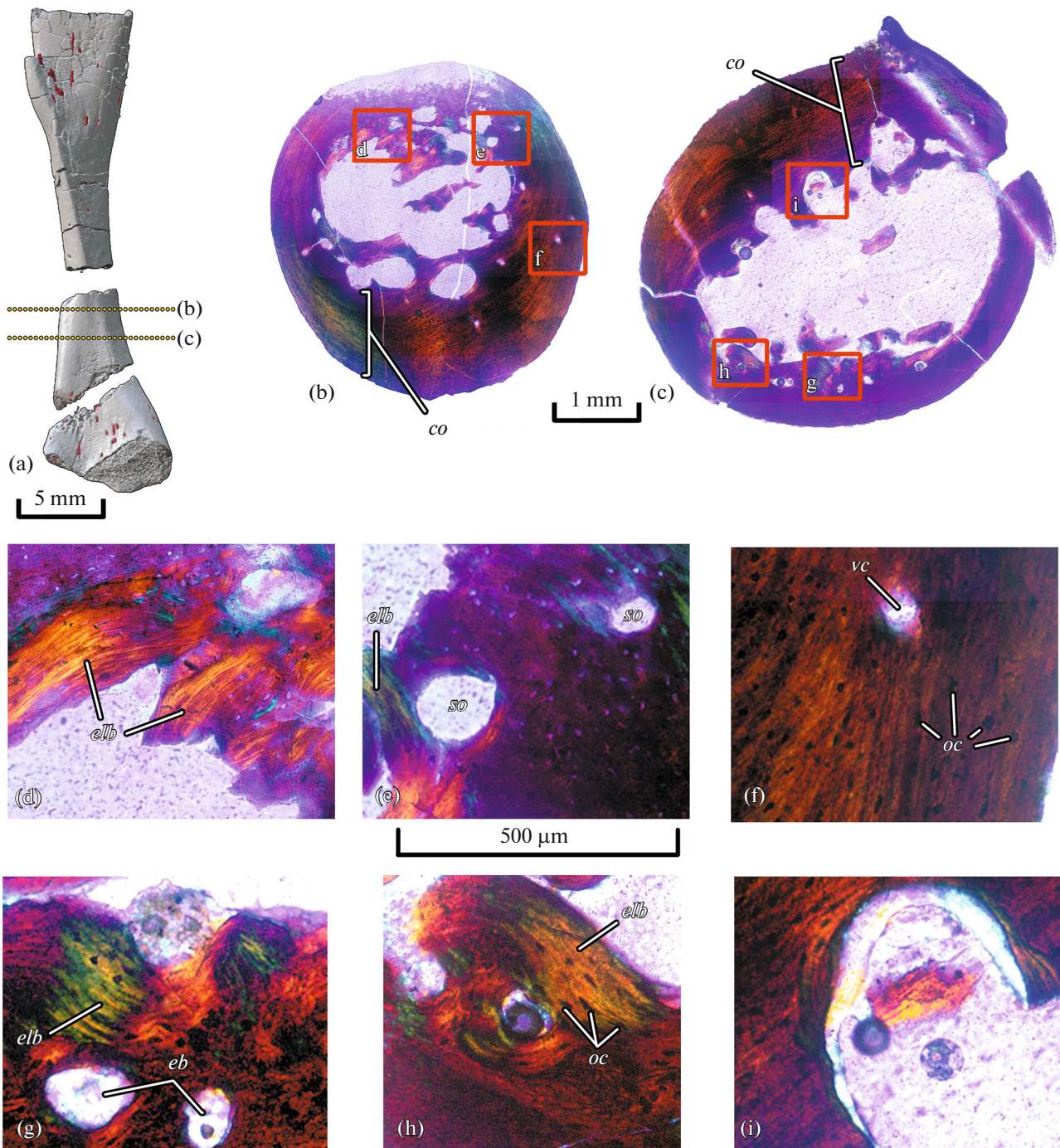


Fig. 4. *Kulgeriherpeton ultimum* Skutschas et al., 2018, transverse histological section of the femur at the level of the mid-diaphysis (specimen ZIN PH 39/246): (a) reconstruction of the femur, ventral view, with indication of the locations of the sections; (b, c) sections of the femur in polarized light, with indication of the boundaries of the areas shown under high magnification; (d–i) fragments of sections in polarized light under high magnification. Designations: *co*, cortex; *eb*, erosion bay; *elb*, endosteal lamellar bone; *oc*, osteocytes; *slb*, secondary lamellar bone; *so*, secondary osteon; *vc*, vascular canal.

The morphology of the humerus of *Kulgeriherpeton ultimum* is characteristic of permanently aquatic neotenic salamanders (e.g., *Cryptobranchus* and proteid *Necturus*) or the larval stages of representatives of more terrestrial groups. The absence of the dorsal

crest, to which the enlarged subcoracoid-scapular muscle (m. subcoracoscapularis, which pulls the limb backward in walking), is attached in terrestrial salamanders, indicates that this salamander is unable to move effectively on land. The presence of a prominent

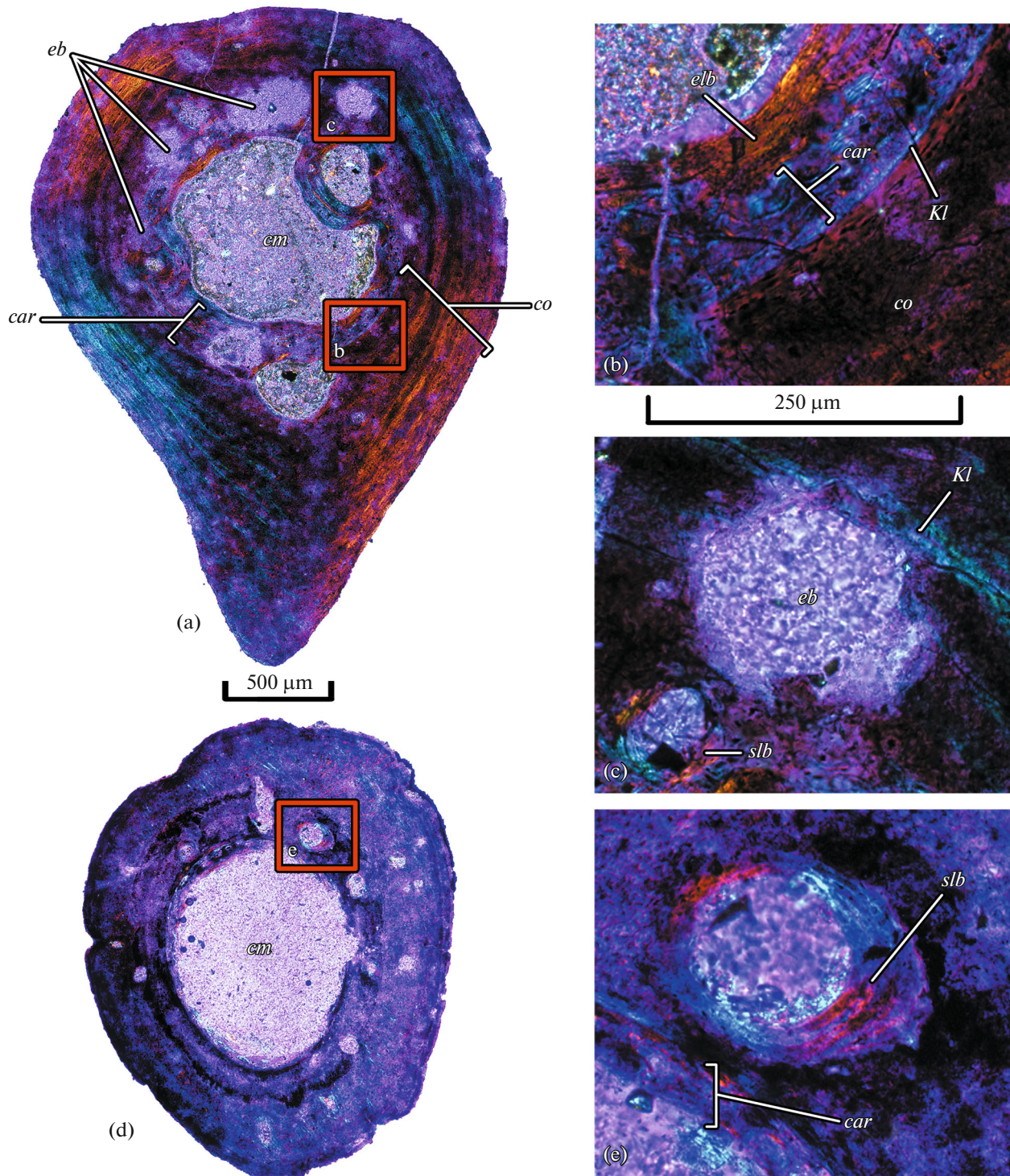


Fig. 5. *Kulgeriherpeton ultimum* Skutschas et al., 2018, transverse histological sections of femurs. (a–c) Specimen ZIN PH 37/246: (a) section in the proximal part of the diaphysis in polarized light, with indication of the boundaries of the areas shown under high magnification; (b, c) fragments of the section in polarized light under high magnification. (d, e) Specimen ZIN PH 35/246: (d) section at the level of the mid-diaphysis in polarized light, with indication of the boundaries of the area shown under high magnification; (e) fragments of a section in polarized light under high magnification. Designations: *car*, calcified cartilage; *co*, cortex; *cm*, medullary cavity; *eb*, erosion bay; *elb*, endosteal lamellar bone; *slb*, secondary lamellar bone; *Kl*, Kashchenko's line.

crest (or sculpture, in the case of *Cryptobranchus*) in the area of the lateral epicondyle and proximal to it indicates the presence of a strong forearm extensor muscles that are attached to this area. The development of this group of muscles indicates their active use, most likely during swimming.

The morphology of the femur is also similar to that of extant aquatic salamanders in the presence of a shorter trochanter displaced to the anterior surface of the bone and a smaller size of the ventral fossa (fossa trochanterica) as compared to more terrestrial salamanders. The displacement of the trochanter is most likely associated with the characteristically altered position of the limb in aquatic salamanders (at rest limbs are retracted and elevated), and the small size of the ventral fossa may indicate poor development of the muscles (in particular, m. puboischiofemoralis externus) that are used to support the body above the surface while moving on land. At the same time, the large size of the depressions in the area of the distal end of the bone and significant vascularization of these areas may indicate the presence of developed extensor and flexor muscles of the tibia, which could be actively used during swimming.

The presence of cartilage remains and the preservation of the Kashchenko's line are signs of neoteny (= "skeletal neoteny"; see, e.g., Buffr n l and Laurin, 2021) and confirm the conclusions about the neotenic nature of stem karaurid salamanders (Buffr n l et al., 2015; Skutschas, Stein, 2015).

Skeletochronological analysis showed the presence of 16 cyclic growth marks (annuli, LAGs) in the cortex of the large humerus of *Kulgeriherpeton ultimum* (specimen ZIN PH 38/246). Most of these cyclic growth marks are represented by lines of growth retardation (annuli); in the middle of the cortex, there are contiguous (double or triple) lines of arrested growth (LAGs).

Cyclic growth marks are formed annually and can be used to determine the individual age of an animal. Contiguous LAGs are formed under unfavorable conditions and in the case of slower growth. Accordingly, the animal repeatedly experienced stress throughout its life, as a result of which growth slowed down and osteogenesis stopped completely.

The presence of double LAGs often indicates two phases of growth during the year (and two phases of cessation of osteogenesis) associated with environmental fluctuations, such as climatic changes with pronounced seasonality (Caetano et al., 1985). Studies of extant amphibians, such as the salamander *Triturus marmoratus*, indicate that the frequency of occurrence of double LAGs in a population increases with increasing altitude (Caetano and Castanet, 1993). In the frogs *Scaphiopus coachii*, double LAGs are correlated with monsoon precipitation (Tinsley and Tocque, 1995). The presence of double LAGs may also be

associated with the lack of food resources (Sagor et al., 1998).

Double LAGs are often observed in lissamphibians (Caetano and Castanet, 1993; Smirina, 1994); however, they are also known in Permian and Triassic amphibians—temnospondyls *Apateon* and *Rhinesuchus* (Sanchez et al., 2010; McHugh, 2014), as well as *Doleserpeton* (Gee et al., 2020).

It is unclear whether the double and triple LAGs in *Kulgeriherpeton* formed during one year (then the age of the animal was 13 years), or each of them formed annually (in which case, the age of the animal was 16 years).

An important feature noted on a section of the humerus (specimen ZIN PH 38/246) is the absence of a reduction in the distance between the cyclic growth marks in the outer cortex. A sharp reduction in the distance between growth marks in the peripheral part of the cortex and the formation of an external fundamental system correspond to the cessation of the active growth phase (Woodward et al., 2011). The absence of closely spaced growth marks in the peripheral part of the cortex indicates that the large humerus (specimen ZIN PH 38/246) belonged to an actively growing animal that had not yet reached its maximum individual age.

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ETHICS APPROVAL AND CONSENT TO PARTICIPATE

This work does not contain any studies involving human and animal subjects.

CONFLICT OF INTEREST

The authors declare that they have no conflicts of interest.

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