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The Use of Zygapophyseal Skeletochronology in Individual Age Determination of a Basal Mosasauroid (Squamata, Mosasauridae) from the Campanian of Saratov Region

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Abstract—Here we determine the individual age of a basal mosasaur (subfamily Halisaurinae) using zygapophyseal skeletochronology. This study is based on the cervical vertebra from the Late Cretaceous Beloe Ozero locality (Saratov Region). By of counting the zygapophyseal growth rings on the right prezygapophysis, it has been revealed that the age of the animal to which this vertebra belonged was at least 11 years. The absence of drastic reduction in the distance between the zygapophyseal growth rings is indicative of the fact that in the first 11 years of life, until the moment of death, the animal grew rapidly and evenly and reached a length of about 6 meters.

Keywords: Mosasauridae, Halisaurinae, skeletochronology, growth marks, zygapophyseal cyclical growth marks, Upper Cretaceous, and Campanian

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INTRODUCTION

Mosasaurs (Mosasauridae) were a group of large secondary aquatic marine Varanoidea that lived during the Late Cretaceous from the Turonian (possibly Cenomanian) to the end of the Maastrichtian. Mosasaurs inhabited the epicontinental seas and shelves adjacent to deep-sea basins. Their remains have been found on all continents, including Antarctica (Polcyn et al., 2014). In the European part of Russia and adjacent areas, scattered remains and incomplete skeletons of mosasaurs are common (Pervushov et al., 1999).

Most mosasaur remains from Russia were found in the Volga River basin: Penza, Saratov, and Volgograd regions. The best-preserved material was collected in the Campanian Beloe Ozero locality near the settlement of the same name, in the Lysogorsky District of the Saratov Region. The locality is a series of ravines exposing the deposits of the Rybushka Formation. The formation corresponds in stratigraphical volume to most of the Lower Campanian and lowermost Upper Campanian (Olferiev and Alekseev, 2005). The upper part of the formation contains a phosphorite horizon as an interbed consisting of phosphorite nodules with varying concentrations. The mosasaur vertebra described in this work was found in the phosphatic bed. Scattered fish and pterosaur remains (Averianov and Popov, 2014; Averianov et al., 2016; Averianov and Arkhangelsky, 2020), a frontal bone of the mosasaur *Clidastes propython* Cope, 1869 (Grigoriev et al., 2015), and fossil turtles and plesiosaurs (Ochev, 1976; Arkhangelsky et al., 2007; Danilov et al., 2018; Zverkov et al., 2018) were described earlier for this locality.

In 2017, during the excavation work at the locality, a student of the Saratov State Technical University A.A. Shchetinkin found a mosasaur cervical vertebra with an unusual morphology, assigned to a member of the subfamily Halisaurinae. Halisaurinae remains had not been described previously from Russia.

Concentric structures are visible to the naked eye on the anterior and posterior articular processes (pre- and postzygapophyses, respectively) of the studied mosasaur vertebra. Similar structures (zygapophyseal growth zones or zygapophyseal cyclic growth marks) were noted previously on the articular surface of zygapophyses in various tetrapods, including Squamata (Venczel et al., 2015; Petermann and Gauthier, 2018;

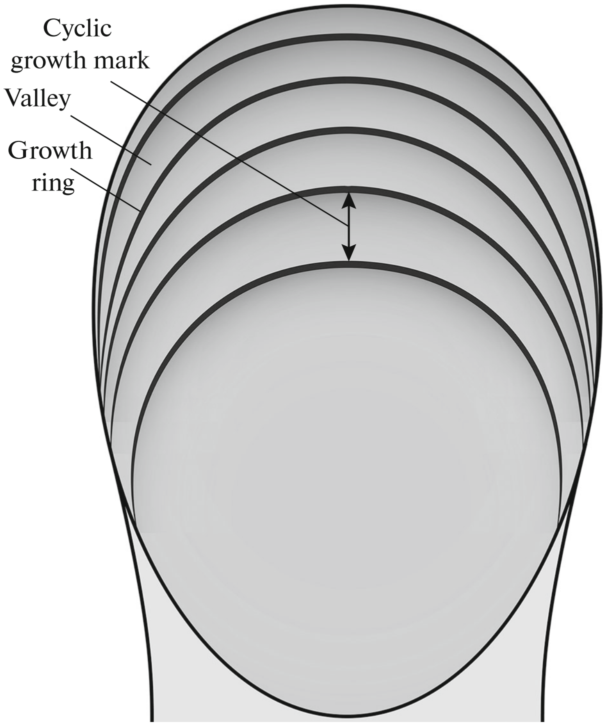

Fig. 1. Schematic representation of the zygapophysis explaining the terms used in the paper.

Skutschas et al., 2020) and were used to estimate individual age (using zygapophyseal skeletochronology).

This paper reports the morphological description of the mosasaur cervical vertebra from the Beloe Ozero locality, and its individual age is obtained by zygapophyseal skeletochronology. This data are obtained for the first time for a member of Mosasauridae.

The described specimen (ZIN PH no. 29/90) is housed in the paleoherpetological collection of the Zoological Institute, Russian Academy of Sciences, (ZIN) in St. Petersburg, Russia. Material from the collections of the Natural History Museum of Maastricht (NHMM, the Netherlands) and the Natural History Museum of Marrakech (MHNM.KH, Morocco) were used for the purposes of comparison.

ZYGAPOPHYSEAL SKELETOCHRONOLOGY

In skeletochronology, direct counting of cyclic annual growth marks is used to determine individual age (Woodward et al., 2013; Buffrenil and Quilhac, 2021). These cyclic growth marks can be observed inside skeletal structures (in bones and cement), and they are counted by a classical histological skeletochronology, when the number of growth marks is determined in thin sections. The growth marks which are taken into account in the analysis are either lines of arrested growth (LAGs) corresponding to a complete cessation of osteogenesis, or slow growth lines (annuli) as compact avascular bone tissue layers corresponding to a substantial slowdown in osteogenesis (Woodward et al., 2013; Buffrenil and Quilhac, 2021).

In addition to internal growth marks, there are annual growth marks formed on the bone surface, in particular, on pre- and postzygapophyses. According to earlier studies, zygapophyseal growth marks are formed during the ontogenesis and record seasonal cycles (usually annual) of bone growth, while correlating well with intraosseous growth marks (LAGs) (Petermann and Gauthier, 2018; Skutschas et al., 2020). Direct counting of their number can be used as an alternative (or as an addition) to the classical destructive skeletochronology which requires the preparation of thin bone sections and the subsequent counting of lines of arrested growth (LAGs) or growth retardation lines (annuli) (Petermann and Gauthier, 2018; Skutschas et al., 2020).

As no established terminology is provided for zygapophyseal skeletochronology, we introduce the main terms and concepts in this paper (by analogy with histological skeletochronology) (Fig. 1).

The annual growth mark in zygapophyseal skeletochronology is a zygapophyseal growth ring which is formed at the end of each growth cycle (when it slows down/stops). In histology, a zygapophyseal growth ring corresponds to lines of arrested growth (LAGs) and/or slow growth lines (annuli). Designating the zygapophyseal growth ring as a line of growth arrest (LAG), as was done by H. Petermann and J. Gauthier (2018), does not seem entirely correct, in our opinion, because these rings can be relatively wide and be formed when the growth is slowing down, rather than stopping completely [more consistent with slow growth lines (annuli) in histology], and also because the use of the same terms for internal and external growth marks will cause confusion when comparing the results of different skeletochronology methods.

Between the zygapophyseal growth rings there are lower areas corresponding to active bone growth; these structures will be designated as zygapophyseal valleys. The entire annual growth cycle includes the zygapophyseal valley and the growth ring and is designated as the zygapophyseal cyclic growth mark (corresponding to the annual growth cycle) in (Petermann and Gauthier, 2018). Counting the number of zygapophyseal growth rings and cyclic growth marks makes it possible to reconstruct individual age, while estimating the distance between the growth rings (=width of cyclic growth marks) makes it possible to reconstruct the growth pattern (with rapid growth, a distance between the growth rings will be large; with slow growth, it will decrease).

Zygapophyseal growth rings are composed of mineralized (calcified) cartilage (Skutschas et al., 2020). In fossil material, a calcified cartilage is not so well preserved as bone, and some zygapophyseal growth rings can be lost during burial or preparation. Accordingly, if the preservation of zygapophyses on one vertebra is different, then for analysis it is necessary to choose the zygapophysis (or zygapophyses) with the maximum number of preserved zygapophyseal growth rings. In our study, it is the best-preserved right prezygapophysis with 11 zygapophyseal growth rings.

MORPHOLOGICAL DESCRIPTION OF THE VERTEBRA

High vertical rib articulation facets suggest that the vertebra could be from the fourth to the seventh in the cervical region (Holmes and Sues, 2000).

The centrum (Fig. 2) is strongly elongated and dorsoventrally compressed (length-to-width ratio, 1.95; width-to-height ratio, 1.9). Its length is 74 mm. The condyle is ellipsoid, 38 mm in width, and 20 mm in height. Lateral processes are short, slightly protruding beyond prezygapophyses. The rib articulation facets are high and narrow; their ventral margins almost closely adjoin the cotyle. The hypapophyseal peduncle is drop-shaped without a pronounced cavity. The prezygapophyses are massive and strongly elongated anteriorly. Their length is 27 mm from the base at the spinal canal.

Articular surfaces are highly elongated ellipsoids. Zygosphenes and zygantra are absent. The neural spine has a pronounced posterior midsagittal crest which is absent, for instance, in *Mosasaurus hoffmannii* Mantell, 1829 (cervical vertebra, specimen NHMM 06696-4, D.V. Grigoriev's personal observations), but pronounced, for instance, in *Phosphorosaurus ponpetelegans* (Konishi et al., 2015).

COMPARISON

A highly flattened condyle is typical of the subfamiles Plioplatecarpinae and Halisaurinae, while it is almost round in most Mosasaurinae and Tylosaurinae (Russell, 1967; Caldwell and Bell, 1995). According to Caldwell and Bell (1995), the ratio of vertebra centrum length/condyle height to vertebra body length/condyle width in Plioplatecarpinae ranges from 1.18 to 1.47, while in Halisaurinae, it is from 1.46 to 2.16. In specimen ZIN PH no. 29/90, this value is 1.94, and it can be attributed to Halisaurinae with great confidence. The overwhelming majority of Halisaurinae were medium-sized mosasaurs of 2–3 m long (Polcyn et al., 2013). The exception was *Pluridens* Lingham–Soliar, 1998 which could reach 10 m and more in length (Longrich et al., 2021). In particular, the fourth cervical vertebra was approximately 81 mm in length (measured from a photograph) in MHNM.KH.262 referred to *Pluridens serpentis* Longrich, 2021 with an estimated length of about 6.5 m. In ZIN PH no. 29/90, the vertebra body is 74 mm in length, and, respectively, the body length could be approximately 6 m. Such large dimensions are indirectly indicative of the fact that the specimen ZIN PH no. 29/90 could belong to the genus *Pluridens*, but the available data are insufficient to justify this assumption.

ZYGAPOPHYSEAL SKELETOCHRONOLOGICAL ANALYSIS

Concentric growth marks (zygapophyseal rings recording the annual growth slowdown/stop stages) can be seen on the zygapophyses articular surface. These structures are well-seen under oblique illumination, and their maximum number is noted on the right prezygapophysis (Figs. 3a, 3d). The left prezygapophysis and the right postzygapophysis were slightly damaged at the base during the preparation, so the zygapophyseal growth rings are not fully visible on them. Up to 11 growth zygapophyseal rings can be counted on the best-preserved right prezygapophysis. The growth rings are not traceable over the entire articular surface and are arc-shaped.

A width of the zygapophyseal cyclic growth marks between the first and second and between the second and third zygapophyseal growth rings is approximately the same; further on, a width of the cyclic growth mark between the third and fourth growth rings slightly increases. From the fourth to the eleventh growth ring, a width of cyclic growth marks is slightly variable (visually, the cyclic growth marks between the seventh and eighth growth rings, as well as between the tenth and eleventh growth rings, are slightly wider than the neighboring ones and correspond in width to the cyclic growth marks between the first and second and between the second and third zygapophyseal growth rings). In general, no drastic reduction in a distance between the growth rings (i.e., a drop in the width of cyclic growth marks) is observed.

DISCUSSION

Histological skeletochronology is a method commonly used to determine an individual age of vertebrates by counting the lines of arrested growth (LAGs) (concentric lines formed annually under the growth arrest). This method is used to determine the age of recent (Matsuki and Matsui, 2009; Epova et al., 2016; Fornasiero et al., 2016; Guarino et al., 2016) and extinct (Buffrenil and Buffetaut, 1981; Horner et al., 1999; Erickson and Tumanova, 2000; Skutschas et al., 2020) vertebrates. In the case of extinct animals, this method is the main source of obtaining the data on an individual age of the animal and its growth rates. However, the method is subject to a number of limits.

For example, with aging, along with bone growing, the medullary cavity expands due to resorption of the cortex interior, “erasing” the early bone growth information (respectively, early growth marks are not preserved). Exactly for this reason, the reliable animal's individual age based on the classical skeletochronology data can be obtained only with the help of ontogenetic sampling sets using comparative material from

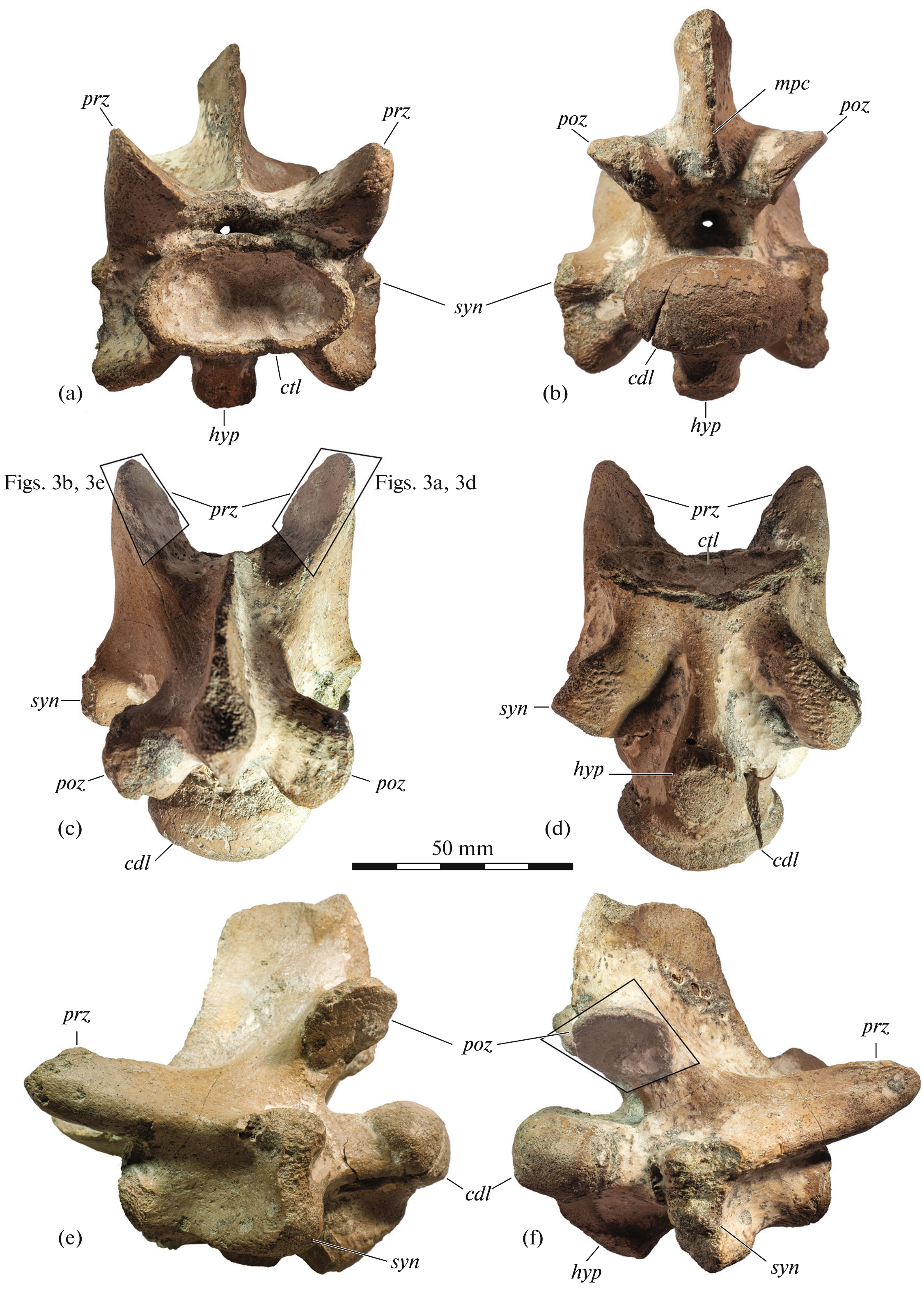

Fig. 2. Cervical vertebra of Halisaurinae gen. indet., specimen ZIN PH no. 29/90: (a) anterior view, (b) posterior view, (c) ventral view, (d) dorsal view, (e, f) lateral views; Saratov Region, Beloe Ozero locality; Upper Cretaceous, lower Campanian, Rybushka Formation. Semitransparent quadrangles indicate the areas on the zygapophyses with growth rings depicted large in Fig. 3. (*cdl*) condylus, (*ctl*) cotylus, (*hyp*) hypapophysis peduncle, (*mpc*) posterior midsagittal crest, (*poz*) postzygapophysis; (*prz*) prezygapophysis; (*syn*) synapophysis.

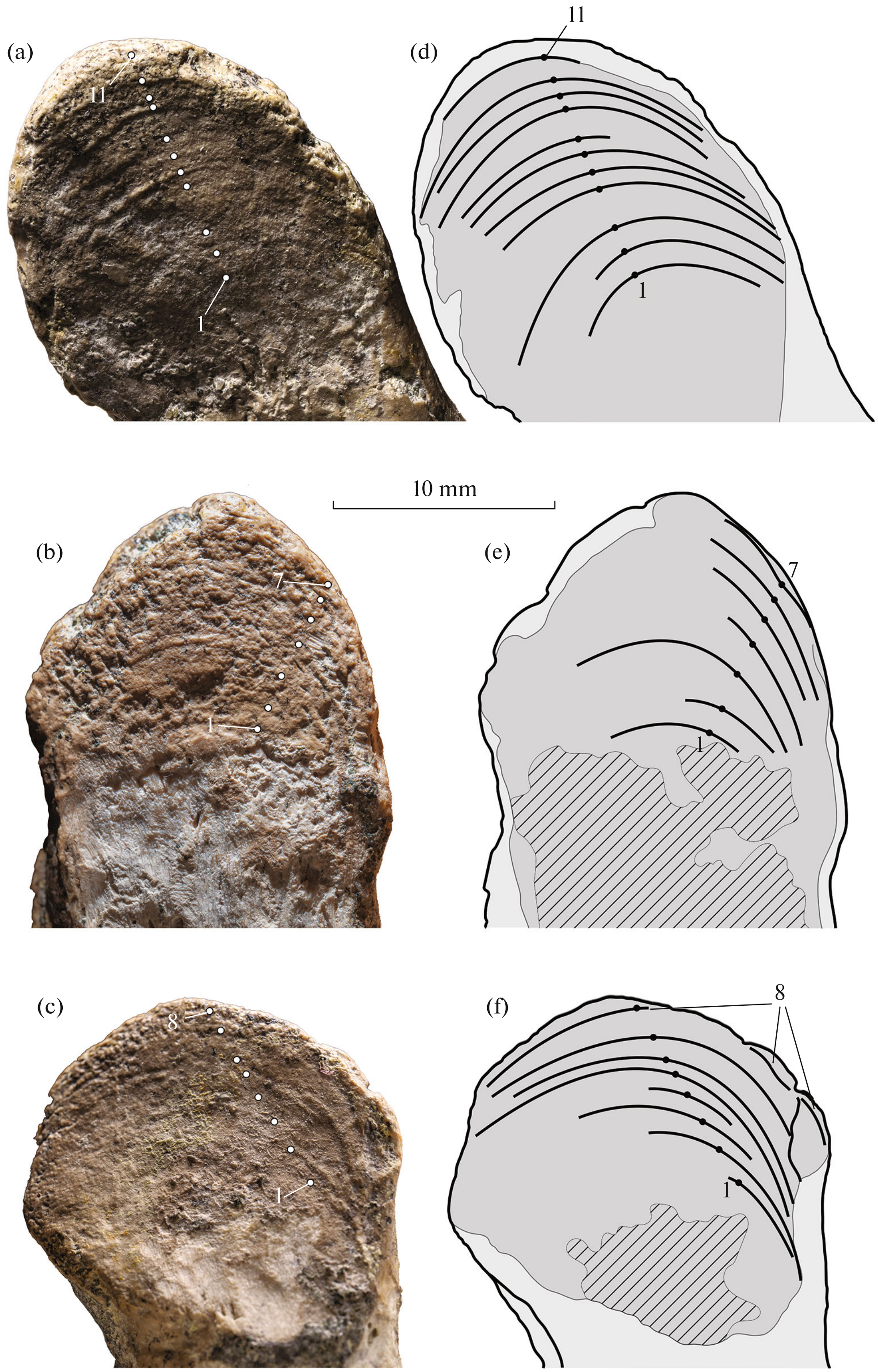

Fig. 3. Cervical vertebra of Halisaurinae gen. indet., specimen ZIN PH no. 29/90, articular surfaces of (a, d) right prezygapophysis, (b, e) left prezygapophysis, and (c, f) right postzygapophysis with growth rings, where d, e, and f are explanatory drawings of the growth rings. Articular surfaces are shown with dark gray. The numbering of growth rings on different zygapophyses do not correlate due to different state of preservation.

different skeleton parts (Chinsamy, 1990; Horner et al., 1999; Erickson and Tumanova, 2000). It is also proved with the help of the recent animal skeletons (Schucht et al., 2021) that different histological sample preparation methods give different numbers of growth arrest lines. Moreover, the number of these lines does not correspond to the real animal's age: in almost all cases, their number is slightly less than the age. Nevertheless, this study confirms that the number of lines of growth arrest does not exceed the animal's age.

Another limitation is related to the fact that this method is destructive and involves a damage (preparation of histological sections) of the material under study.

The zygapophyseal skeletochronology devoid of the limitations described above was applied in practice relatively recently. This method consists of counting the number of zygapophyseal growth rings, and makes it possible to reconstruct individual age, as well as the nature of growth. Petermann and Gauthier (2018) showed in extant and fossil snakes that zygapophyseal growth rings corresponded to the lines of arrested growth (LAGs) on histological sections. Hence, an individual age of some vertebrate groups can be determined by external signs on bone structures (based on isolated vertebrae). Zygapophyseal skeletochronology can be used for all tetrapods which retain zygapophyseal growth rings, such as salamanders, frogs, anthracosaurs, seymouriamorphs, pareiasaurs, lepidosaurs, and archosaurs (Petermann and Gauthier, 2018; Skutschas et al., 2020).

Based on the maximum number of visible zygapophyseal growth rings (11), it can be assumed that the age of the animal which the cervical vertebra ZIN PH no. 29/90 belonged to was 11 years. It was a relatively large animal reaching about 6 m in length. Considering that the last (eleventh) zygapophyseal growth ring is not located at the outermost edge of the zygapophysis (the zygapophysis outer edge corresponds to the zygapophyseal valley), it can be assumed that the animal's age was a little over 11 years at the time of death.

As the distance between the zygapophyseal growth rings is not drastically reduced throughout the zygapophysis, it can be assumed that the animal grew fairly quickly and evenly for the first 11 years of life until its death. The distance between the zygapophyseal growth rings in the zygapophysis exterior does not decline sharply. It means that the animal continued to grow steadily before its death, and that the animal did not reach a growth plateau and a maximum possible size.

A similar uniform arrangement of zygapophyseal growth rings and, accordingly, a similar uniform growth pattern during the first few years of life was noted earlier for recent scaled reptiles such as snakes and lizards (Petermann and Gauthier, 2018; Skutschas et al., 2020).

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CONFLICT OF INTEREST

The authors declare that they have no conflicts of interest.

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