SPECIAL ISSUE on Recent Advances in Chondrocranium Research | Guest Editor: Ingmar Werneburg

Editorial to the Special Issue (Virtual Issue) 2019/2020
Recent Advances in Chondrocranium Research

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Introduction

In early May 1790, the famous poet and natural scientist Johann Wolfgang von Goethe (1749 – 1832) discovered a decomposed goat skull at the Jewish cemetery in Venice. He interpreted the separate skull elements as segments that continue the homonomy of the bones in the vertebral column (GOETHE, 1824; PEYER, 1950). Goethe understood the skull as the "crown" of the body, similarly to the flower of a plant. The plant was indeed the subject to which the majority of his research was dedicated (GOETHE, 1790). He envisioned the involvement of holistic principles (i.e., 'Platonic ideas') in the organization and formation of all organisms in nature (BREIDBACH, 2006; BUCHWALD, 1960; LEVIT & MEISTER, 2006). Generations of vertebrate comparative anatomists have discussed the value, originality, and shortcomings of his idea. Nowadays, our understanding of skull development is so complex that the principles which Goethe recognized can be interpreted with a fresh mind (ZIEMKE, 2015). Hox gene expression early in development, for example, patterns the postotic region of the head in the same way it does the vertebral column (ALEXANDER et al., 2009). Secondary segmentations appear, formed by spatial barriers, such as the eyes and ear capsules, and by the visceral arches (COULY et al., 2002; ZIERMANN et al., 2018). The posterior part of the braincase is actually formed by fused vertebrae (BRITZ & JOHNSON, 2010; GEGENBAUR, 1871; MITGUTSCH, 2003; WERNEBURG et al., 2013).

The vertebrate skull is composed of an internal, endocranial and an external, ectocranial part (Fig. 1A) (KARDONG, 2008; STARCK, 1979 – 1982). The external part, the dermatocranium, is easily recognizable, even in fossils, whereas the internal part is often less apparent and less well preserved. It has only been possible to understand the complex structure of the internal skull by deciphering its formation, and a kind of "hermetic" research agenda focussed on trying to understand the development of the internal skull for over 150 years (e.g., PARKER, 1879; RATHKE, 1839). This research has seen the publication of comprehensive textbooks on the enormous diversity of embryonic skulls and the discussion of fundamental questions of homology (BELLAIRS & KAMAL, 1981; DE BEER, 1937; GOODRICH, 1930; STARCK, 1965, 1979 – 1982). The focus of the research has always been the chondrocranium, itself a fused product of many early embryonic cartilages, which partly or fully ossifies – as neurocranium – in late embryonic or post-delivery stages.

In 2007 at the 8th International Congress of Vertebrate Morphology (ICVM) in Paris, the first scientific meeting I ever attended, I was impressed by modern developments in ontogenetic and phylogenetic studies of the skull. I also came into contact with Wolfgang Maier, a retired professor from Tübingen university, who had supervised dozens of student projects describing the embryonic skulls of various different vertebrates (MAIER, 2017), something which has a long tradition in German universities (e.g., FRICK, 1954). Furthermore, my Ukraine colleague Oleksandr Yaryhin drew me even further into the fascinating cosmos of embryonic skulls, bringing new perspectives from the former Soviet territory to my understanding of morphology (SEWERTZOFF, 1931).

Chondrocranium Symposium

At the 12th ICVM meeting in Prague, I then organized a symposium on "Recent Advances in Chondrocranium Research", held on July 25th 2019 (Fig. 2; for abstracts

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Fig. 1. Two cover pictures related to the Special (Virtual) Issue. **Left)** Cover of the issue as a whole with illustration of the embryonic skull of a tuatara, *Sphenodon punctatus* (Gray, 1842) (Reptilia, Rhynchocephalia), with a total body length of 58 mm (left skull side; redrawn by Margret Roser after Werner (1962: fig. 11), using the manual air brush technique; with kind permission of Prof. Dr. Wolfgang Maier, Tübingen, Germany). The image highlights the mutual developmental and morphological integration of the three major skeletal components of the vertebrate skull. In its centre is the primordial cartilaginous skull, the chondrocranium, in blue (known with the braincase as the neurocranium when ossified). It is surrounded by the dermatocranium (i.e., dermal bones), in brown. Both partly articulate with the viscerocranium (syn. splanchnocranium, pharyngeal elements), shown in pink (palatoquadrate and Meckel's cartilage) and yellow (hyoid apparatus, i.e. branchial arches). For further details on general skull construction and intracranial mobility, see Werneburg & Maier (2019). An updated account of tuatara chondrocranial anatomy and its importance for understanding orbitotemporal diversity in lepidosaur reptiles can be found in Yaryhin & Werneburg (2019). **Right)** Cover of *Vertebrate Zoology* issue 69(2). See Werneburg & Maier (2019, fig. 4B). Plate reconstruction of the right palatoquadrate, the otic, and the occipital region of a pleurodire turtle embryo (*Emydura subglobosa*) with a carapace length of 21 mm in ventral view. Cartilage is blue, ossification is purple, blood vessels are red, nerve structures are yellow, bone is brown.

see Starck, 2019). That symposium eventually resulted in this Special Issue, which is actually a virtual issue, meaning that directly after acceptance papers appeared online and were published in regular issues of *Vertebrate Zoology* over the last two years[1]. Quickly it became clear that focussing on the chondrocranium alone is a major limitation because the complexity of the skull can only be understood in a holistic research program considering early gene expression patterns and precartilaginous stages, the development and integration of tissues surrounding the chondrocranium, and the biomechanical characteristics of particular elements. The embryonic chondrocranium is "merely" an intermedial condition. For a better understanding, both earlier and later ontoge-

netic stages – up to adulthood – need to be studied in order to obtain a more complete picture of the contribution of the chondrocranium to skull formation. Furthermore, the diversity of different animals needs to be considered. As such, this Special Issue, which includes significantly more papers than originally presented in Prague, has a very wide conceptual, anatomical, and taxonomic scope and successfully mirrors the current diversity of chondrocranium research worldwide, featuring contributions from researchers from Argentina, Austria, Germany, Switzerland, Ukraine, the United Kingdom, and the USA.

From genes to structures

The contributions in the Special Issue can be ordered by the sequence of events in skull ontogeny. Using the African clawed-frog *Xenopus laevis* as a model, *Schmidt

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[1] Contributions to this Special Issue of *Vertebrate Zoology* are highlighted by asterisks.

Fig. 2. Speakers at the chondrocranium symposium at the 12th ICVM meeting in Prague on July 25th 2019. From left to right: Irina Ruf, Marketa Kaucka, Juan T. Richtsmeier, Casey M. Holliday, Kazuhiko Kowasaki, Oleksandr Yaryhin, Kai Ito, Marc E. H. Jones, and Ingmar Werneburg (other registered presenters at the symposium, but not on the photo, were Dominique Adriaens, Wolfgang Maier, Benjamin Naumann, and Marcelo R. Sánchez-Villagra; for further information see M. STARCK, 2019). Photo taken with a camera belonging to Marc E. H. Jones.

et al. (2020) ask "what is the gene regulatory network underlying the morphogenesis of the vertebrate head skeleton?" The authors identify the *FoxN3* gene in a key position for the regulation of cranial cartilage, joint, and muscle formation, highlighting that the development of hard and soft cranial tissues derived from neural crest and mesodermal precursors. It helps explaining major morphological transitions from an evolutionary perspective.

On a genetic level, the knockout of particular candidates in selected parts of the complex gene regulatory network helps to identify the origin of proposed evolutionary novelties. Conducting *zax* gene knockout in *X. laevis*, *LUKAS et al.* (2019) find that rather than the infrarostrals in the frog being a newly acquired character in anuran tadpoles, a joint inside Meckel's cartilage must actually be considered the true novelty.

Cartilage differentiation

The lower jaw cartilage (cartilago Meckeli) does not belong to the chondrocranium *sensu stricto* (Figs 1A, 3) but is an element of the anterior part of the viscerocranium (syn. splanchnocranium). Unlike the third part of the skull, the dermatocranium, chondrocranial and viscerocranial elements initially appear as cartilaginous structures which exhibit a high degree of integration right from their earliest stages. From a biomechanical point of view,

the elements are connected via muscles and ligaments and should be considered as one entity. Traditionally, whole mount skeletal preparation of embryonic skulls includes soft tissue bleaching (clearing) and staining against cartilages and bones only (YARYHIN & WERNEBURG, 2017). Depending on preservation, fixation, and degree of development, every species – indeed, every specimen – requires a unique laboratory manual for clearing and staining. *BLANCO & WITMER (2020) provide as an example a detailed protocol for staining crocodilian embryos. The protocol has resulted in very accurate resolution of late chondrocranial structures in different species.

Whole mount staining of skeletal structures has been widely used in recent decades (MAISANO, 2008) and provides a comprehensive data basis for modern analytical techniques (HUGI *et al.*, 2012; MITGUTSCH *et al.*, 2011; SÁNCHEZ-VILLAGRA, 2002; SÁNCHEZ-VILLAGRA *et al.*, 2008; WERNEBURG *et al.*, 2009) which even permit proper character comparisons in a phylogenetic framework (GERMAIN & LAURIN, 2009; LAURIN & GERMAIN 2011). In this tradition, *KLINGER-STROBEL *et al.* (2020) study the development of the skeleton of the dwarf clawed frog *Pseudhymenochirus merlini* and find clade-distinguishing differences in the timing of the appearance of certain cartilages and bones. General developmental plasticity in anatomy is apparent in a specific spatial shift in skeletal formation. It results in a differing number of cartilaginous elements in particular body regions among different species.

Tracing back anatomical differences between species is sometimes very difficult given the lack of comprehensive ontogenetic series and key material. *YARYHIN & WERNEBURG (2019) re-discovered historical histological sections of the rare tuatara *Sphenodon punctatus*, which is the sister taxon of Squamata (EVANS & JONES, 2010), the group with the greatest diversity in chondrocranial anatomy (BELLAIRS & KAMAL, 1981). Despite a number of apomorphic traits, a relatively archaic (see WERNEBURG, 2019) but still well-differentiated lateral side wall of the chondrocranium is described, helping us to understand – as a "material source" – the derived diversity of squamate chondrocrania from a craniogenetic perspective. The largely akinetic tuataran skull leads, in association with the robust chondrocranium, back to the discussion of structural and functional complexity and the integration of the skull as a whole. Using *Mus musculus* as a model, *PITTIRI et al. (2020) reviewed and illustrated the role which the chondrocranium plays throughout embryonic development in providing a structural framework for the developing exoskeleton to integrate the (eventually mainly ossified) neuro- and dermatocranial bones.

Cranial kinesis and biomechanics

In contrast to most other vertebrates, mammals (incl. mice) and crocodiles possess akinetic skulls which evolved as a response to changes in feeding behaviour. Secondary side walls in the braincase buffer high biting forces while maintaining the stability of the skull (KLEMBARA, 2005; MAIER, 1989). The formation of these new side walls demanded the integration of chondrocranial, dermatocranial, and viscerocranial elements. *WERNEBURG & MAIER (2019) describe two different modes of secondary side wall formation in turtles and show that embryonic neck movements – and not feeding – might be responsible for major rearrangements of primordial skull elements in these akinetic animals. From a paleontological point of view, the authors illustrate how increasing capacity for neck retraction in turtle evolution resulted in fundamental transformations in turtle skull morphology (see also FERREIRA et al., 2020).

Most vertebrates, including fishes, birds, and squamates, possess highly kinetic skulls. The vast diversity of cranial movements which exists ranges from the intracranial kinetism found in *Latimeria chalumnae* (BEMIS & NORTHCUTT, 1991) to kinetism between viscerocranial and neurocranial elements (IORDANSKY, 2000, 2011) and to the internal elasticity of otherwise fully sutured dermal bones (NATCHEV et al., 2016). As most research into cranial kinesis has been performed on ossified skull parts in the past, the contribution of the cartilaginous chondrocranium has been largely neglected (JONES et al., 2017). In most vertebrates the chondrocranium is mainly ossified in adults, but in squamates it widely persists until adulthood (OELRICH, 1956) and is an integral part of the complex skull. This complexity concerns not only the number and shape of skull elements, but also internal bone and cartilage structure. *JONES et al. (2020) discuss the material properties of the adult chondrocranium and conclude that, beyond general load absorption, the function of adult chondrocrania is far from being understood. The authors provide suggestions for future research including live force measurements, Finite Element Analyses, and broad taxonomic and ontogenetic sampling in order to further our understanding of the material properties of the cartilaginous parts of the adult cranium.

As mentioned above, only an integrated view taking all three compartments of the skull into account can provide a comprehensive picture of chondrocranial evolution and development. The suspensoric is a composite of viscero- and dermatocranial elements that articulate, via the pterygoid and the quadrate, with the more interior, neurocranium-related parts of the skull. Using five disparate sauropsid species, *WILKEN et al. (2020) demonstrate the way the biomechanics of the suspensoric change in relation to their osteology, their connection to the jaw musculature, and the orientation of the latter. This complexity must be understood as a result of evolutionary and ontogenetic integration.

Except in a few cases (see the remarks on turtles above), feeding behaviour must be understood as the major driver of skull evolution. As such, knowledge on specific feeding modes helps to interpret the selective regimes which lead to unique bone anatomy. Such knowledge is provided by *ACOSTA HOSPITALECHE et al. (2020), who illustrate that the specific feeding habits of highly specialized birds (penguins, albatrosses, and petrels) led to the development of a novel articulation between the lower jaw and the endocranium, namely the mandibulosphenoidal joint. To facilitate this novel feature, the chondrocranial precursors of the sphenoid region needed to become more strongly developed. A simple correlation between feeding habits and mandibulosphenoidal joint anatomy, however, is difficult to draw, as the shape of the novel jaw joint is correlated to that of the primary jaw joint, again highlighting the need for a holistic research agenda (MAIER & WERNEBURG, 2014). In fact, specific jaw joint anatomy is often only formed in postdelivery stages, because feeding behaviour may radically change over the course of ontogeny.

Transition to adulthood

The condition of skull morphology around birth or hatching provides the greatest insights into the circumstances leading to adult morphology because it is at this point in development that the animals are forced to actively interact with their wider environment (i.e., outside the egg or the uterus) for the first time, and they need to be adapted in order to survive (MAIER, 1999). By studying altricial and precocial rodents, *RUF (2020) discovers major differences and temporal shifts in the transformation of the ethmoid region of the chondrocranium. Tracing structural changes in this biologically relevant period of time
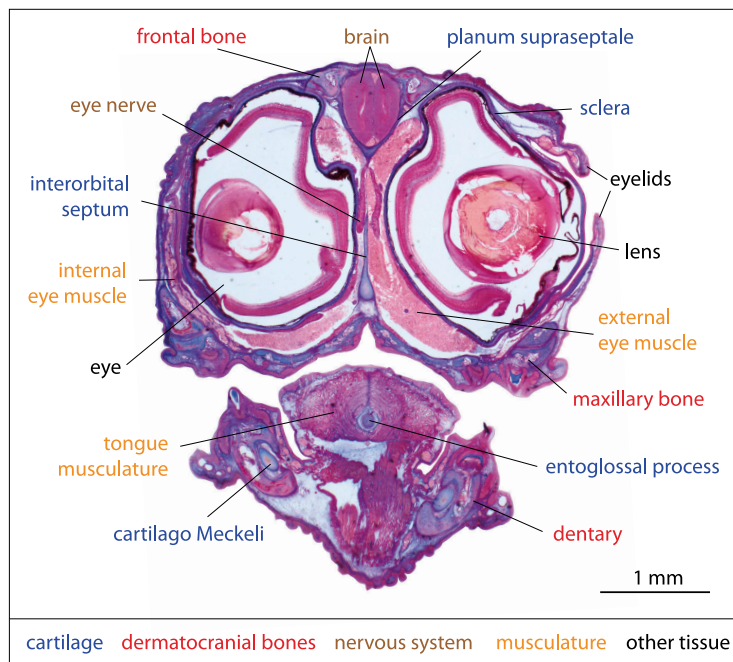
Fig. 3. The chondrocranium (visible here: interorbital septum, planum supraseptale, sclera) should be studied in the context of surrounding tissue. Meckel's cartilage is part of the viscerocranium, which interacts with the chondrocranium (see Fig. 1A). Histological slide section through the eye region of a tuatara embryo, *Sphenodon punctatus* (GRAY, 1842) (Reptilia, Rhynchocephalia), with a total body length of 52 mm. Collection of Phyletisches Museum Jena, Germany (Inv.-Nr.: Rept 1216, leg. coll. Dietrich Starck Nr. 152, "*Sphenodon punctat*. II", "Serie A", slide no. 9-1-1, Azan-staining). Photo taken by Zitong Zhang, student in Tübingen.

helps to clarify homologies between chondrocranial elements. Postdelivery stages (i.e., after birth or hatching) are difficult to handle using traditional histology. Modern μCT-scans, however, permit the visualization of ossified or highly calcified elements and help to document further transformations of the chondrocranium towards the adult neurocranium. The destiny of the endocranium, for example, can be monitored into adulthood, as shown by *Ruf et al.* (2020) who investigate the ontogeny and morphofunctional implications of the ethmoid region in the semiaquatic *Potamogale velox* (Mammalia), identifying and tracing a number of apomorphic features of this afrotherian species. The study illustrates how biological adaptations in the adult, such as those related to the semiaquatic behaviour of this species, are largely already presaged in the fetus. Once again, a holistic understanding of prenatal chondrocranium shape requires the observation of postdelivery stages and their functional adaptations.

Although most of the chondrocranium ossifies, postnatal differentiations and proliferations of some cartilaginous skull elements may still appear. This is particularly evident in the rostrum of many mammals, where it is connected with the importance of the olfactory sense. *Maier* (2020) provides unique data on the formation of external nasal cartilages in different placental mammals. As a highlight of this study, the author shows how in the elephant shrew the 'proboscis' is fragmented by the epigenetic influence of a facial muscle, which eventually results in a telescope-like, highly mobile rostrum.

Reaching adult anatomy

The diversity of adult skull anatomy is foreshadowed in early ontogenetic stages. The degree to which variation in early chondrocranial anatomy is directly mirrored

in adult skull characters is investigated by *Hüppi et al.* (2019), who review all the available literature on cranial cartilage formation in the domestic chicken. A number of intraspecific differences are recorded in the literature, but some of them might be distorted by the methodological and conceptual restrictions of the studies in question (for discussion, see also *Werneburg & Yaryhin*, 2019; *Yaryhin & Werneburg*, 2017). Adult chicken skulls exhibit great interbreed diversity and bilateral asymmetry in the number of hypoglossal foramina. Understanding this diversity, i.e. in relation to the atrophy of hypoglossal nerve roots, would require detailed interbreed studies on early ontogenetic skull differentiation.

The plasticity of certain ontogenetic features is stunning (*Yaryhin & Werneburg*, 2018). As such, a notion of a one-to-one correlation between embryonic and adult skull shape must be handled with care. Both embryonic and adult variation needs to be recorded, as recognized by *Mayr* (2019), who concentrates on the posterior part of the skull in adult birds, namely the otic region, which derives from a major part the embryonic chondrocranium. His detailed survey reveals a number of previously overseen morphological features in a variety of neognathous birds. An understanding of the homology and physiological significance of these variable features will only be achieved through a comprehensive craniogenetic study which takes into account inter-tissue correlations and biomechanic aspects of the developing skull.

Conclusions

For over 100 years, chondrocranium research was mainly descriptive; homology aspects were discussed extensively, but mainly without a robust phylogenetic framework

(e.g., Fuchs, 1915; Gaupp, 1902). Recent attempts to conduct broad evolutionary surveys using phylogenetic systematics (Hennig, 1966) and restricted character definitions (Hüppi *et al.*, 2018; Werneburg & Yaryhin, 2019; *Yaryhin & Werneburg, 2019) help to organize the available literature, which is mainly old, but it remains difficult to detect major transitions in evolution because of the conservative nature and plasticity of chondrocranial anatomy. The chondrocranium is a developmentally complex construction which acts primarily as the architectural base of the skull (*Pittiri *et al.*, 2020). Its taxonomic alterations and intraspecific variations, however, can only be understood by reflecting on peri-delivery (*Ruf, 2020) and adult (*Hüppi *et al.*, 2019; *Ruf *et al.*, 2020) functional adaptations, even going back to the genetic level (*Lukas *et al.*, 2019; *Schmidt *et al.*, 2020). As such, exploring the functional properties (*Jones *et al.*, 2020) and functional correlations (*Werneburg & Maier, 2019; *Wilken *et al.*, 2020) of the chondrocranium in a comprehensive morphological framework is currently a high priority for researchers, and comparative analyses depend on methodological clarity (*Blanco & Witmer 2020; *Klinger-Strobel *et al.*, 2020). Finally, the diversity of osteological correlates of the chondrocranium in the adult neurocranium, has been shown to comprise a number of features that still require detailed description and phylogenetic consideration (*Acosta Hospitaleche *et al.*, 2020; *Mayr, 2019). Only as part of a holistic research agenda can development, homology, and functionality be adequately discussed (Maier, 1999). Ontogeny has to be understood as a continuum from conception to death, not simply as the leaving of transitory juvenile (*Maier, 2020) or other stages behind. In a colourful histological slide section (Fig. 3) or in modern contrast stainings, the chondrocranium might serve as a fruitful starting point of research: nerves, muscles, tendons, vessels, and dermal and visceral skull elements are all associated with it. As an anchor of cranial differentiation, it is intrinsically connected with the rest of the head, and reflecting on the developmentally earliest aspects of the skull will, in the end, give us a better understanding of skull evolution in general.

Acknowledgements

References

*Contributions to this Special Issue of *Vertebrate Zoology* are highlighted by asterisks

*Acosta Hospitaleche, C. A., Piro, A. & Sosa, M. A. (2020). The mandibulosphenoidal joint in penguins, albatrosses, and petrels: comparative anatomy and functional implications. *Vertebrate Zoology*, **70**, 263–274.

Alexander, T., Nolte, C. & Krumlauf, R. (2009). Hox genes and segmentation of the hindbrain and axial skeleton. *Annual Review of Cell and Developmental Biology*, **25**, 431–456.

Bellairs, A. d'A. & Kamal, A. M. (1981). The chondrocranium and the development of the skull in recent reptiles, pp. 1–263 *in:* Gans, C. (ed.) *Biology of the Reptilia. Morphology F.* London, New York, Toronto, Sydney, and San Francisco, Academic Press.

Bemis, W. E. & Northcutt, R. G. (1991). Innervation of the basicranial muscle of *Latimeria chalumnae*. *Environmental Biology of Fishes*, **32**, 147–158.

*Blanco, M. V. F. & Witmer, L. M. (2020). A clearing-and-staining procedure for the study of the chondrocranium and other aspects of skeletal development in crocodilian embryos. *Vertebrate Zoology*, **70**, 447–454.

Breidbach, O. (2006). *Goethes Metamorphosenlehre*. München, Wilhelm Fink Verlag.

Britz, R. & Johnson, G. D. (2010). Occipito-vertebral fusion in actinopterygians: conjecture, myth and reality. Part 1: Non-teleosts, pp. 77–93 *in:* Nelson, J. S., Schulze, H. P. & Wilson, V. H. (eds), *Origin and Phylogenetic Interrelationships of Teleosts. Honoring Gloria Arratia*. München, Verlag Dr. Friedrich Pfeil.

Buchwald, E. (1960). *Naturschau mit Goethe*. Stuttgart, W. Kohlhammer Verlag.

Couly, G., Creuzet, S., Bennaceur, S., Vincent, C. & Le Douarin, N. M. (2002). Interactions between Hox-negative cephalic neural crest cells and the foregut endoderm in patterning the facial skeleton in the vertebrate head. *Development*, **129**, 1061–1073.

de Beer, G. R. (1937). *The Development of the Vertebrate Skull*. New York, Oxford University Press.

Evans, S. E. & Jones, M. E. H. (2010). The origin, early history and diversification of lepidosauromorph reptiles, pp. 27–44 *in:* Bandyopadhyay, S. (ed.) *New Aspects of Mesozoic Biodiversity, 27*. New York, Springer.

Ferreira, G. S., Lautenschlager, S., Evers, S. W., Pfaff, C., Kriwet, J., Raselli, I. & Werneburg, I. (2020). Feeding biomechanics suggests progressive correlation of skull architecture and neck evolution in turtles. *Scientific Reports*, **10**, 5505.

Frick, H. (1954). *Die Entwicklung und Morphologie des Chondrocraniums von* Myotis Kaup. Stuttgart, Georg Thieme Verlag.

Fuchs, H. (1915). *Über den Bau und die Entwicklung des Schädels der* Chelone imbricata *– Ein Beitrag zur Entwicklungsgeschichte und vergleichenden Anatomie des Wirbeltierschädels. Erster Teil: Das Primordialskelett des Neurocraniums und des Kieferbogens*. Stuttgart, E. Schweizerbart'sche Verlagsbuchhandlung, Nägele & Dr. Sproesser.

Gaupp, E. (1902). Ueber die Ala temporalis des Säugerschädels und die Regio orbitalis einiger anderer Wirbeltierschädel. *Anatomische Hefte*, **19**, 155–230.

Gegenbaur, C. (1871). Über die Kopfnerven von *Hexanchus* und ihre Verhältniss zur „Wirbeltheorie" des Schädels. *Jenaische Zeitschrift für Medizin und Naturwissenschaft*, **6**, 497–599.

Germain, D. & Laurin, M. (2009). Evolution of ossification sequences in salamanders and urodele origins assessed through event-pairing and new methods. *Evolution & Development* **11**(2): 170-190.

Goethe, J. W. v. (1790). *Versuch die Metamorphose der Pflanzen zu erklären*. Gotha, Ettingersche Buchhandlung.

GOETHE, J. W. V. (1824). *Schädelgerüst aus sechs Wirbelknochen aufgebaut. Zur Morphologie, Band 2*. Stuttgart, Tübingen, Cotta' sche Buchhandlung.

GOODRICH, E. S. (1930). *Studies on the Structure and Development of Vertebrates*. London, MacMillan and Co.

GRAY, J. E. (1842). Description of two hitherto unrecorded species of reptiles from New Zealand; presented to the British Museum by Dr. Dieffenbach. *Zoological Miscellany*, **2**, 8–14.

HENNIG, W. (1966). *Phylogenetic Systematics*. Urbana, University of Illinois Press.

HUGI, J., HUTCHINSON, M. N., KOYABU, D. & SÁNCHEZ-VILLAGRA, M. R. (2012). Heterochronic shifts in the ossification sequences of surface- and subsurface-dwelling skinks are correlated with the degree of limb reduction. *Zoology*, **115**, 188–198.

*HÜPPI, E., NÚÑEZ-LEÓN, D., NAGASHIMA, H. & SÁNCHEZ-VILLAGRA, M. R. (2019). Development of the chondrocranium in the domesticated fowl (*Gallus gallus* f. *domestica*), with a study on the variation of the of hypoglossal foramina. *Vertebrate Zoology*, **69**, 299–310.

HÜPPI, E., SÁNCHEZ-VILLAGRA, M. R., TZIKA, A. C. & WERNEBURG, I. (2018). Ontogeny and phylogeny of the mammalian chondrocranium: the cupula nasi anterior and associated structures of the anterior head region. *Zoological Letters*, **4**, 29.

IORDANSKY, N. N. (2000). Cranial kinesis in the amphibia: a review. *Zhurnal Obshchei Biologii*, **61**, 102–118.

IORDANSKY, N. N. (2011). Cranial kinesis in lizards (Lacertilia): origin, biomechanics, and evolution. *Biological Bulletin*, **38**, 852–861.

*JONES, M. E. H., GRÖNING, F., ASPDEN, R., DUTE, H., SHARP, A., FAGAN, M. & EVANS, S. E. (2020). The biomechanical role of the chondrocranium and the material properties of cartilage. *Vertebrate Zoology*, **70**, 699–715.

JONES, M. E. H., GRÖNING, F., DUTEL, H., SHARP, A., J., F. M. & EVANS, S. E. (2017). The biomechanical role of the chondrocranium and sutures in a lizard cranium. *Interface*, **14**.

KARDONG, K. V. (2008). *Vertebrates: Comparative Anatomy, Function, Evolution*. New York, NY, McGraw–Hill Primis.

KLEMBARA, J. (2005). Ontogeny of the partial secondary wall of the otoccipital region of the endocranium in prehatching *Alligator mississippiensis* (Archosauria, Crocodylia). *Journal of Morphology*, **266**, 319–330.

*KLINGER-STROBEL, M., OLSSON, L., GLAW, F. & MÜLLER, H. (2020). Development of the skeleton in the dwarf clawed frog *Pseudhymenochirus merlini* (Amphibia: Anura: Pipidae). *Vertebrate Zoology*, **70**, 435–446.

LAURIN, M. & GERMAIN (2011). Developmental characters in phylogenetic inference and their absolute timing information. *Systematic Biology*, **60**, 630–644

LEVIT, G. S. & MEISTER, K. (2006). Goethes langer Atem: „Methodologische Ideologien" in der Deutschen Morphologie des 20. Jahrhunderts. *Verhandlungen zur Geschichte und Theorie der Biologie*, **12**, 209–232.

*LUKAS, P., SCHMIDT, J. & OLSSON, L. (2019). Knockdown of zax in *Xenopus laevis* leads to craniofacial malformations and the absence of the intramandibular joint. *Vertebrate Zoology*, **70**, 9–22.

MAIER, W. (1989). Ala temporalis and alisphenoid in therian mammals, pp. 396–400 *in:* SPLECHTNA, H. & HILGERS, H. (eds), *Trends in Vertebrate Morphology. Progress in Zoology 35*. Stuttgart, G. Fischer Verlag.

MAIER, W. (1999). On the evolutionary biology of early mammals – with methodological remarks on the interaction between ontogenetic adaptation and phylogenetic transformation. *Zoologischer Anzeiger*, **238** (*Festschrift D. Starck*), 55–74.

MAIER, W. (2017). *Der Weg zum Menschen. Ausgewählte Schriften zur Evolutionsbiologie der Wirbeltiere*. Tübingen, Scidinge Hall Verlag.

*MAIER, W. (2020). A neglected part of the mammalian skull: The outer nasal cartilages as progressive remnants of the chondrocranium. *Vertebrate Zoology*, **70**, 367–382.

MAIER, W. & WERNEBURG, I. (2014). Einführung: Zur Methodik der organismischen Evolutionsbiologie, pp. 11–17 *in:* MAIER, W.

& WERNEBURG, I. (eds), *Schlüsselereignisse der organismischen Makroevolution*. Zürich, Scidinge Hall Verlag.

MAISANO, J. A. (2008). A protocol for clearing and double-staining squamate specimens. *Herpetological Review*, **39**, 52–54.

*MAYR, G. (2019). The otic region of the skull of neognathous birds: on the homology and comparative morphology of some neurovascular and muscular foramina and other external skeletal structures. *Vertebrate Zoology*, **70**, 69–85.

MITGUTSCH, C. (2003). On Carl Gegenbaur's theory on head metamerism and the selection of taxa for comparisons. *Theory in Biosciences*, **122**, 204–229.

MITGUTSCH, C., WIMMER, C., SÁNCHEZ-VILLAGRA, M. R., HAHNLOSER, R. & SCHNEIDER, R. A. (2011). Timing of ossification in duck, quail, and zebra finch: lntraspecific variation, heterochronies, and life history evolution. *Zoological Science*, **28**, 491–500.

NATCHEV, N., HANDSCHUH, S., LUKANOV, S., TZANKOV, N., NAUMOV, B. & WERNEBURG, I. (2016). Contributions to the functional morphology of caudate skulls: kinetic and akinetic forms. *PeerJ*, **5**, e2392.

OELRICH, T. M. (1956). The anatomy of the head of *Ctenosaura pectinata* (Iguanidae). *Miscellaneous Publications, Museum of Zoology, University of Michigan*, **94**, 1–22.

PARKER, W. K. (1879). On the development of the skull and its nerves in the green turtle (*Chelone midas*), with remarks on the segmentation seen in the skull of various types. *Proceedings of the Royal Society of London*, **28**, 329–346.

PEYER, B. (1950). *Goethes Wirbeltheorie des Schädels*. Zürich, Gebrüder Fretz AG.

*PITTIRI, M. K., KAWASAKI, K. & RICHTSMEIER, J. T. (2020). It takes two: Building the vertebrate skull from chondrocranium and dermatocranium. *Vertebrate Zoology*, **70**, 587–600.

RATHKE, H. (1839). *Entwickelungsgeschichte der Natter* (Coluber Natrix). Königsberg, Verlag der Gebrüder Bornträger.

*RUF, I. (2020). Ontogenetic transformations of the ethmoidal region in Muroidea (Rodentia, Mammalia): new insights from perinatal stages. *Vertebrate Zoology*, **70**, 383–415.

*RUF, I., BEHRENS, H. & ZELLER, U. (2020). Ontogeny and morphofunctional implications of the ethmoidal region in the semiaquatic *Potamogale velox* (Afrosoricida, Mammalia). *Vertebrate Zoology*, **70**, 679–697.

SÁNCHEZ-VILLAGRA, M. R. (2002). Comparative patterns of postcranial ontogeny in therian mammals: an analysis of relative timing of ossification events. *Journal of Experimental Zoology*, **294**, 264–273.

SÁNCHEZ-VILLAGRA, M. R., GOSWAMI, A., WEISBECKER, V., MOCK, O. & KURATANI, S. (2008). Conserved relative timing of cranial ossification patterns in early mammalian evolution. *Evolution & Development*, **10**, 519–530.

*SCHMIDT, J., SCHUFF, M., NAUMANN, B. & OLSSON, L. (2020). FoxN3 knock-down alters spatio-temporal expression patterns of genes involved in cranial cartilage and muscle development in the African clawed-frog *Xenopus laevis*. *Vertebrate Zoology*, **70**, 455–472.

SEWERTZOFF, S. A. (1931). *Morphologische Gesetzmäßigkeiten der Evolution*. Jena, Gustav Fischer.

STARCK, D. (1965). *Embryologie*. Stuttgart, Thieme.

STARCK, D. (1979–1982). *Vergleichende Anatomie der Wirbeltiere – auf evolutionsbiologischer Grundlage, Band 1–3*. Berlin, Heidelberg, New York, Springer.

STARCK, M. (2019). Supplement: International Congress of Vertebrate Morphology (ICVM). *Journal of Morphology*, **280**, S9–S13.

WERNEBURG, I. (2019). Morphofunctional categories and ontogenetic origin of temporal skull openings in amniotes. *Frontiers in Earth Science, Section Paleontology* **7**, 1–7.

WERNEBURG, I., HUGI, J., MÜLLER, J. & SÁNCHEZ-VILLAGRA, M. R. (2009). Embryogenesis and ossification of *Emydura subglobosa* (Testudines, Pleurodira, Chelidae) and patterns of turtle development. *Developmental Dynamics*, **238**, 2770–2786.

*WERNEBURG, I. & MAIER, W. (2019). Diverging development of akinetic skulls in cryptodire and pleurodire turtles: an ontogenetic and phylogenetic study. *Vertebrate Zoology*, **69**, 113–143.

WERNEBURG, I., MAIER, W. & JOYCE, W. G. (2013). Embryonic remnants of intercentra and cervical ribs in turtles. *Biology Open*, **2**, 1103–1107.

WERNEBURG, I. & YARYHIN, A. (2019). Character definition and tempus optimum in comparative chondrocranial research. *Acta Zoologica*, **100**, 376–388.

WERNER, G. (1962). Das Cranium der Brückenechse, *Sphenodon punctatus* Gray, von 58 mm Gesamtlänge. *Zeitschrift für Anatomie und Entwicklungsgeschichte*, **123**, 323–368.

*WILKEN, A. T., SELLERS, K. C., COST, I. N., ROZIN, R. E., MIDDLETON, K. M. & HOLLIDAY, C. M. (2020). Connecting the chondrocranium: Biomechanics of the suspensorium in reptiles. *Vertebrate Zoology*, **70**, 275–290.

YARYHIN, A. & WERNEBURG, I. (2017). Chondrification and character identification in the skull exemplified for the basicranial anatomy of early squamate embryos. *Journal of Experimental Zoology B*, **328**, 476–488.

YARYHIN, O. & WERNEBURG, I. (2018). Tracing the developmental origin of a lizard skull: chondrocranial architecture, heterochrony, and variation in lacertids. *Journal of Morphology*, **279**, 1058–1087.

*YARYHIN, O. & WERNEBURG, I. (2019). The origin of orbitotemporal diversity in lepidosaurs: insights from tuatara chondrocranial anatomy. *Vertebrate Zoology*, **69**, 169–181.

ZIEMKE, A. (2015). *Alle Schöpfung ist Werk der Natur*. Offenbach, Brüll & Heisterkam KG.

ZIERMANN, J. M., DIOGO, R. & NODEN, D. M. (2018). Neural crest and the patterning of vertebrate craniofacial muscles. *Genesis*, **56**, 1–39.

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