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Vergleichende Entwicklungsgeschichte — A Festschrift on the occasion of the 80th birthday of Prof. Dr. Wolfgang Maier, Tübingen

Festschrift in Honour of Professor Dr. Wolfgang Maier
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Abstract

Following the traditional and holistic concept of *Vergleichende Entwicklungsgeschichte*, Wolfgang Maier studied different aspects of vertebrate morphology, including dentition, the locomotor apparatus, nasal and ear regions. His work comprises investigations on pre- to postnatal stages of extant species as well as fossils and is mainly based on histological serial sections, but also on µCT data in recent years. This resulted in an integrative research agenda on the evolutionary biology of mammals and other vertebrates. Most of his studies are designed around the interrelationship of ontogenetic and functional adaptations and evolutionary transformations. The present collection in *Vertebrate Zoology* collates a series of research articles related to and in honor of Wolfgang Maier's work. Invited colleagues of Maier provide current insights to their own research, in many cases inspired by his scholarship, ranging from mammalian to reptilian and fish comparative anatomy. In total, this volume contains 19 publications. They apply modern and traditional techniques to investigate the diversity of biological form. In so doing, they integrate traditional conceptual frameworks from the earliest days of morphological research more than two centuries ago.

Keywords

Comparative anatomy (morphology), history of science, holistic organism concept, Mammalia, Vertebrata

Origin of "*Vergleichende Entwicklungsgeschichte*"

There is a direct line from Johann Wolfgang von Goethe (1749–1832, Weimar) and Johann Friedrich Blumenbach (1752–1840, Göttingen) to Carl Friedrich Kielmeyer (1765–1844, Tübingen), Karl Mayer (1787–1865, Bonn), Johannes Peter Müller (1801–1858, Berlin), Albert von Kölliker (1817–1905, Würzburg), Carl Gegenbaur (1826–1903, Jena, Heidelberg), Ernst Göppert (1866–1945, Heidelberg, Marburg), Dietrich Starck (1908–2001, Frankfurt am Main), and finally to Wolfgang Maier (*1942, Frankfurt am Main, Tübingen) as well as to most other present-day German comparative anatomists (https://academictree.org/evolution/tree.php?pid=776240, accessed October 25th, 2022). This academic tree of life, however, is merely a random construct neglecting the complexity of influences on academic careers, including many other teachers, individual scientific discoveries, personal fates, and philosophical outlooks, not to mention the Zeitgeist which shaped these researchers in many different ways. Their research spans idealistic to cladistic approaches to tackle anatomical diversity. Along the way, many scholars often dissociated from their supervisors.

Nevertheless, a holistic view of nature is a common theme in German morphology up to this day. It is basically an integrated view that takes into account not only adult anatomy (zoology and paleontology), but also embryology to formulate hypotheses on evolutionary changes. One of Gegenbaur's students, Max Fürbringer (1846–1920, Jena), framed this approach as follows: "*The question on the origin of mammals can only be solved by an exact comparative-anatomical and comparative-ontogenetic treatment with thorough consideration of the paleontological forms, and of course this comparison must be carried out on a sound morphological basis, whereby the homogeneity* [i.e., homology] *has to be determined with the effort of all the tools available to our research and are to be sharply distinguished from the analogies and isotimies. Reliable taxonomic results can only be expected with morphological materials obtained in this way*."[1] (Fürbringer 1904, p. 576). This view, of course, is also largely influenced by works of Gegenbaur's (Hoßfeld et al. 2003) close colleague and friend Ernst Haeckel (1834–1919, Jena), who propagated an evolutionary triad of 'paleontology, comparative anatomy, and embryology,' which was a direct and most comprehensive application of Darwin's (1859) evolutionary theories to comparative anatomy (Haeckel 1866; Hoßfeld et al. 2021; Werneburg et al. 2022a,b).

In personal discussions, Wolfgang Maier and his students use the term *Vergleichende* (= Comparative) *Entwicklungsgeschichte*. A direct English translation of *Entwicklungsgeschichte* is difficult because the German word "*Entwicklung*" comprises 'embryological' and 'evolutionary' change in one word. A literal translation as 'comparative embryological and evolutionary history' implies a separation between "embryological" and "evolutionary" which is less pronounced in German. Although correct, an English translation as 'comparative ontogeny' on the other hand shifts the emphasis to the embryological aspect, because postnatal life is commonly (but erroneously) recognized as a static process by many researchers (as we have personally experienced in many peer review debates). *Entwicklungsgeschichte*, however, implies an integrated epistemological approach from the very beginning, giving neither embryology nor adult anatomy a certain rank in the actual morphological observation in evolutionary research. A simple translation as "development" would be too vague.

In the 19th century the now antiquated term "*Entwickelung*" (with an additional "e" in the middle) was used instead of "*Entwicklung*". The old spelling preserved the historical preformistic understanding of embryology in which the embryo is unfolding ("ent-/auswickeln") toward adult anatomy, a view that was clearly falsified in terms of natural science methodology (Juncker and Hoßfeld 2009). As such, the term *Entwicklungsgeschichte* (without the extra "e") can now be confidently applied to both ontogenetic and phylogenetic evolutionary history in a modern comparative ("*vergleichend*") manner. Because of the semantic and historic subtlety, we would recommend using the German term rather than an English adaptation (which would somehow translate as "comparative evolutionary ontogeny" at the best).

With recent scientific developments leaving the merely descriptive anatomy of the 19th century behind, functional, genetic, and epigenetic aspects were also taken into consideration to formulate a refined version of the holistic view on evolution (e.g., Mayr 1988). Partly as a reaction to the overemphasis on genetics in the second part of the 20th century (comparable to the EvoDevo-approach these days), Wolfgang Maier – in a Festschrift (Zoologischer Anzeiger 238/1–2; Duncker 1999) to his doctoral advisor Dietrich Starck (Hoßfeld and Juncker 1998) – brought the organism back to the center of interest and formulated the "holistic organism concept" ("*Ganzheitliches Organismuskonzept*") (Maier 1999). Here, the organism is seen as a multidimensional entity in which, through time, structure, function, and genes constitute its morphological complexity. During individual development, in Maier's (1999) view, the organism is also influenced by external selective pressures and only the gametes transfer the "complete picture" of the organism to the next generation in evolution. This gradual evolutionary change can also

1 Our translation from: „Die Frage der Abstammung der Säugetiere ist nur durch eine genaue vergleichend-anatomische und vergleichend-ontogenetische Behandlung unter eingehender Berücksichtigung der paläontologischen Formen lösbar, und selbstverständlich muß diese Vergleichung auf gesicherter und gesichteter morphologischer Grundlage geführt werden, wobei die Homogenien mit Aufwand aller unserer Forschung verfügbaren Hilfsmittel zu bestimmen und scharf von den Analogien und Isotimien zu unterscheiden sind. Nur mit so gewonnenen morphologischen Materialien sind einigermaßen gesicherte taxonomische Resultate zu erwarten."

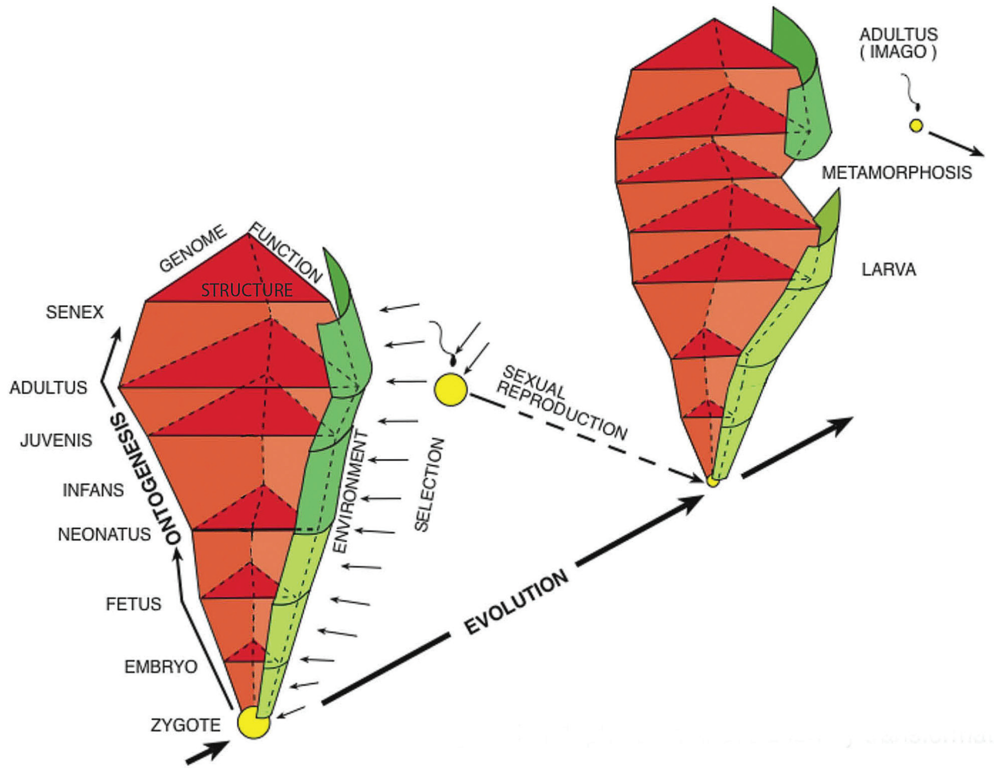

Figure 1. Holistic Organism Concept, after Maier (1999, 2021). Structure, function, and genome constitute the shape of an organisms throughout its whole life (ontogenesis). Natural selection acts on the organism and sexual reproduction transfers the organisms' construction through evolution, eventually reaching new morphotypes and life history modes. Through ontogeny and evolution, the shape of an organism is influenced by various biological aspects such as relative age, social role, loss of teeth in infant and adult, sexual maturity, secondary sexual characteristics, maturation of sexual organs, adolescence, skeletogenesis, tooth eruption, maturity of the neonate (altriciality vs. precocity), organ maturity, placentation and gastrulation mode, blastocyst and cleavage type, content of yolk (lecithal vs. polylecithal), structure of spermia, enzyme, fat and cholesterol, carbohydrate, DNA, RNA, and developmental genetics. Reproduction with kind permission of Scidinge Hall Verlag Tübingen.

include changes in life history, such as the emergence of metamorphosis, as an example (Fig. 1; see also Maier and Werneburg 2014a, b).

Methodology and the history of biological sciences

Wolfgang Maier (born August 4th, 1942) studied biology in Tübingen and conducted his doctorate in Frankfurt am Main (Fig. 2), where he later also became a professor of human anatomy. In 1987, he moved back to Tübingen as chair of evolutionary zoology. He retired in 2007 and is still an active researcher (Fig. 3). In honor of his contributions to the evolutionary morphology of various vertebrate taxa, the Society of Vertebrate Paleontology awarded him an 'Honorary Membership' at its annual meeting in Bristol (UK) in 2009. In 2015, Wolfgang Maier became an honorary research associate in the Mammalogy Section of the Senckenberg Research Institute and Natural History Museum (Frankfurt am Main, Germany). A scientific autobiography and a bibliography can be found in Maier (2017, 2021). In our editorial, we refer to only a few aspects of his scientific career.

In the following, we provide an overview of the articles published in this Festschrift. The sections of the Festschrift follow the main chapters of Maier's (2017, 2021) recent book "*Der Weg zum Menschen – Ausgewählte Schriften zur Evolutionsbiologie der Wirbeltiere*" ('Toward humans – contributions to the evolutionary biology of vertebrates'), which reflects the general structure of his wide research agenda (book reviewed by Sánchez-Villagra 2017).

The first section of his book (Maier 2017, 2021) comprises historical and methodological remarks aiming at locating his scientific approach in the history of evolutionary research – mainly relying on Charles Darwin, Ernst Haeckel, Dietrich Starck, and on Willi Hennig (1913–1976), who introduced 'phylogenetic systematics' (Hennig 1950, 1966; see also Schmitt 2013). Wolfgang Maier was among the first German biologists to apply this concept to his own research, whereas many other Germans of his generation were very skeptical about using this merely analytical approach in their analyses. Wolfgang Maier always cautions against the uncritical use of numerical character definitions, as frequently used in cladistics, which often neglect studies on primary homology and morphofunctional integration.

In his book "*Der Weg zum Menschen*", Wolfgang Maier (2017, 2021) provided a series of German chap-

Figure 2. Wolfgang Maier as doctoral student in winter semester 1965/66 (from Maier 2017, 2021). Photo by Manfred Steck. With kind permission of Scidinge Hall Verlag Tübingen.

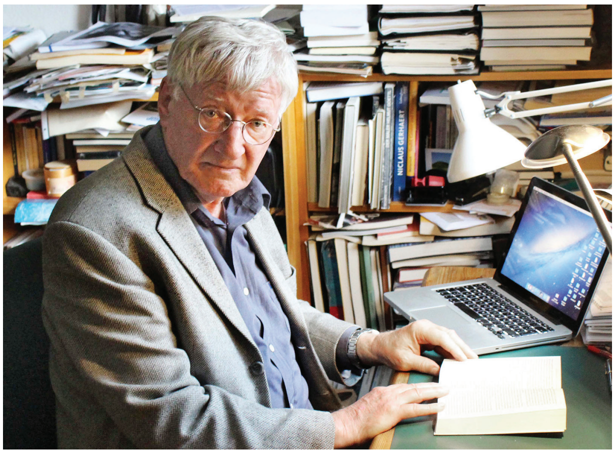

Figure 3. Wolfgang Maier on August 4th, 2021, photo by his son Johannes Karl Kleinknecht (with permission).

ters highlighting the long traditions of morphological research and advising to the scientific contributions of important researchers such as Johann Wolfgang von Goethe, George Cuvier (1769–1832), Karl Friedrich Kielmeyer, Carl Gegenbaur, Ernst Haeckel, and Ernst Gaupp (1865–1916), among many others. He discussed how their scientific conceptualizations influenced the interpretation of the observed material, including religious, idealistic, and Darwinian worldviews.

The roots of a holistic *Vergleichende Entwicklungsgeschichte* go back in evolutionary form to the famous Jena zoologist Ernst Haeckel. They were also evident among proto-evolutionary naturalists such as Lamarck, Kielmeyer, Meckel, and even Goethe. In the present Festschrift, ***Werneburg et al. (2022b)** report the discovery of rare lecture notes from 1866 that provide exceptional insights into the conceptualization and visualization of paleontology by Ernst Haeckel. In the same year, Haeckel (1866) published his famous "*Generelle Morphologie der Organismen*", in which he already propagated the integrated view on evolution taking paleontology, comparative adult anatomy, and embryology into account (Hoßfeld et al. 2021). Werneburg et al. (2022b) illustrate how, through the following decades, Haeckel's interest in paleontology decreased and how this influenced the split between paleontology and zoology typical for German history. Wolfgang Maier, also influenced by Wolf-Ernst Reif (1945–2009) in Tübingen (Levit and Hoßfeld 2013, Werneburg 2021), has helped to join these often disparate traditions in his own scientific contributions (e.g., Maier et al. 1996).

Wolfgang Maier was involved in the discussion of a "technomorph" organism view in the early 1990s, taking progress in physics and evolutionary epistemology into account (Maier and Zoglauer 1994). In our Festschrift, ***Drack and Betz (2022)** apply engineering approaches to biology. The authors discuss central concepts of 'function, working principles, and construction' to improve functional interpretations in organismic research. They show that 'design spaces' are comparable between engineering optimization and evolvability. Also, questions related to biomimetics (see Werneburg and Betz 2018a, b) are discussed. As in engineering, the general properties of organisms influence their constructional design while maintaining the performance of the relevant functions at a higher level.

Evolution of animal organisms

In addition to his scientific efforts, Wolfgang Maier influenced hundreds of students in courses on medical human anatomy and embryology (mainly in Frankfurt am Main) and comparative anatomy of animals (mainly in Tübingen). He was always dedicated to teaching and actually started his own study in Tübingen as teacher trainee. His book "*Der Weg zum Menschen*" (Maier 2017, 2021) includes some of his lectures on fundamental 'key innovations in organismic evolution' (see also Maier and Werneburg 2014) taking the major discoveries of the 19th and early 20th century into account. He himself contributed with studies on deep time-related questions on the evolution of animal organisms (e.g., Bonik et al. 1978; Schnell et al. 2008). In his lectures, he always referred to the general anatomy of sharks to understand original structural arrangements in vertebrate evolution, particularly regarding their cranial anatomy. At the same time, he also cautioned against the naive use of "ancestral types", as would be present in these animals, and inspired an unbiased study of anatomy.

In our Festschrift, ***Staggl et al. (2022)** studied the cranial morphology of the brownbanded bamboo shark *Chiloscyllium punctatum* in great detail using micro-computed tomography (µCT). The authors discovered sexual dimorphism in this species and highlighted the importance of accurate anatomical observation before providing major evolutionary hypotheses.

In Tübingen, Wolfgang Maier curates a comprehensive histological collection of mainly perinatal specimens of diverse vertebrate species, predominantly mammals. Dozens of doctoral and undergraduate theses are based on this material and many of them deal with different stages of cranial development and have great value as basic descriptive studies. Most of the material was collected and sectioned at the University of Tübingen and many visitors from all over the world come to this 'treasure house of embryology', comparable to the famous Hubrecht-Hill-collection (Richardson and Narraway 1999), which is now stored in the Museum für Naturkunde Berlin (Giere and Zeller 2006).

The Tübingen embryology collection even houses the late embryo of a coelacanth. This species is relevant to understand water-to-land transition (Molnar et al. 2022a, b). Using this Tübingen specimen, ***Johnston (2022)** studied the 'missing anatomy' of *Latimeria chalumnae* and made progress in understanding homologies in the spiracular organ, the ultimobranchial endocrine gland, and the musculus (m.) cucullaris. In addition, a muscle arising on the medial side of the pectoral girdle is identified and compared with a muscle in a similar location that attaches to the cranial rib in lungfish; these are proposed as homologs of the tetrapod m. omohyoideus.

A major focus of Wolfgang Maier's research lays on understanding the origin of mammals from early amniotes and comprehensive knowledge of 'fish', 'amphibian', and 'reptilian' anatomy is necessary for comparison. Together with Detlev Thies (Hannover), he translated Carroll's (1988) famous text book on "Vertebrate Paleontology and Evolution" into German (Carroll 1993) and thereby broadened the scope of German education in paleontology towards the more progressing aspects of US-American approaches at that time (Reif 1999; Levit and Hoßfeld 2013; Werneburg et al. 2022a, b).

While being head of the zoology department (Ordinarius) in Tübingen, Wolfgang Maier hired several assistants focusing on different major vertebrate taxa (e.g., for fish: Peter Bartsch, Ralf Britz, Sven Gemballa; for birds: Matthias Starck; for mammals: Martin S. Fischer, Marcelo R. Sánchez-Villagra, Irina Ruf). In this Festschrift, Marcelo R. Sánchez-Villagra (now Zürich, Switzerland), who has broad interests in vertebrate evolutionary morphology, provides a study on the macroevolutionary and developmental evolution of the turtle carapacial scutes: ***Ascarrunz and Sánchez-Villagra 2022**. The authors show that simple changes in embryogenesis may have a major impact on morphological change and diversification of clades. Patterns observed for turtle integumental appendages are also applied to structures found in the posterior head scales of squamates.

Another study of turtle anatomy concerns the so-called "cartilaginous rider" in the endocasts of the brain cavity. Using the classical approach of *Vergleichende Entwicklungsgeschichte*, taking extant adult and fossil specimens as well as embryos into consideration, ***Werneburg et al. (2021)** show that a cartilaginous process of the embryonic chondrocranium remains in postembyronic life and may even leave traces in the fossil. It is hypothesized that this structure takes a major role in taking up neck retraction forces (see Werneburg 2015) or even bite forces.

Digging even more into reptilian phylogeny and diving deep into the history of the Tübingen paleontology collection (acronym: GPIT, for the former Geologisch-paläontologisches Institut Tübingen), ***Regalado Fernandez and Werneburg (2022)** discovered an early sauropodomorph dinosaur, which was hidden as "*Plateosaurus*" for 100 years. It was unearthed at an excavation on the Swabian Alb near Tübingen in 1922. The authors re-analyzed the anatomy and found the specimen to represent a new massopodan genus and species closer to sauropods than to the more rootward plateosaurs. Compared to its bipedal ancestors, it already was quadrupedal. The authors named the species *Tuebingosaurus maierfritzorum* (GPIT-PV-30787), a homage to the city and inhabitants of Tübingen as well as to Wolfgang Maier and to Uwe Fritz (Dresden), the chief editor of *Vertebrate Zoology*, who enabled this Festschrift in his journal (Knauer 2022).

Evolutionary origin and diversification of mammals

Fossil data are always relevant in the discussion of structural changes through time. Wolfgang Maier contributed to the understanding of the secondary palate in therapsids (*Promoschorhynchus*, Therocephalia) and provided a new theory on the origin of the soft palate in mammals (Maier et al. 1996). Furthermore, he contributed to the detailed description of the nasal region of *Brasilitherium riograndensis*, the putative sister taxon of Mammaliaformes (Ruf et al. 2014). In honor of his studies on mammalian origins, Bonaparte et al. (2010) named a Late Triassic cynodont from Southern Brazil as *Minicynodon maieri* (UFRGS-PV-1030-T, Museu de Paleontología de la Universidade Federal do Rio Grande do Sul, Porto Alegre, Brasil).

Locomotion and other aspects of functional morphology also were of great interest to Wolfgang Maier. In the gelada baboon (*Theropithecus geleda*), he discovered a separate adductor muscle at the pollex, namely m. flexor pollicis longus (Maier 1971). In extant diprotodontian marsupials, Wolfgang Maier studied locomotory adaptations based on morphometric analyses of a locomotor proxy, the semicircular canals of the inner ear bony labyrinth (Schmelzle et al. 2007).

Also interested in evolution and functional morphology, ***Preuschoft et al. (2022)** discuss in our Festschrift the origin of the mammalian locomotory mode by tracing constructional changes that document the transition from sprawling to parasagittal walking in Therapsida. Again, material from the Tübingen paleontology collection, which houses a vast amount of therapsid material collected in South America and southern Africa, was used to provide inferences on evolutionary changes. Compared to more conventional, taxonomic studies that focus on very specific anatomical arrangements, the authors provide a more general view on animal evolution by discussing basic physical properties related to body posture (see also Preuschoft 2022).

Selected aspects of head morphology (in mammals)

Particular cartilages and bones

Wolfgang Maier is always interested in identifying homologies of animal structures and states that when "nature discloses itself that way, it is the highest cognition one could receive in life". For example, he identified cranial ribs and intercentra in turtles which clarified the processes of neck simplification in this taxon (Werneburg et al. 2013). Also in turtles, he observed the altering embryonic fusion of the palatoquadrate to the braincase (Werneburg and Maier 2019) as a potential adaptation to differing neck movement behaviors. For mammals, he traced the evolution of the dorsal spina scapulae (Sánchez-Villagra and Maier 2002) and, most importantly in our view, he clarified the homology of the reptilian epipterygoid with the therian alisphenoid (Maier 1989, 1993).

One of the most recent papers of Maier, published in *Vertebrate Zoology* and attached as a supplement to this Festschrift, provides an integrative approach to understanding the anatomy and ontogeny of the orbitotemporal region and jaw articulation in shrews (Soricidae) (Maier et al. 2022). It is, again, a paramount study that resembles many methodological and epistemological scientific approaches typical for Wolfgang Maier and his colleagues. For this reason, we have actually chosen the central image of that paper (Maier et al. 2022, fig. 1D) to illustrate the cover of our Festschrift (Fig. 4).

Using a similar integrated approach, in the Festschrift, ***Wible (2022)** presents some insights into the 200-year-old history and homology of the os paradoxum, the dumbbell-shaped bone, of the platypus *Ornithorhynchus anatinus* (Monotremata). A wide set of techniques, including µCT, are used to provide a comprehensive view angle on a specific structure. The author found that, at the choanae, the Miocene ornithorhynchid *Obdurodon dicksoni* has what appears to be a separate parasphenoid bone unknown in extant monotremes today.

Figure 4. Cover of the printed version of this Festschrift. The photo shows a histological cross-section through the mandibular joint and posterior nasal region of an adult common shrew (*Sorex araneus*) (from Maier et al. 2022). See text for further details.

Nasal region

Much of his research Wolfgang Maier has performed on the anatomy and evolution of the nasal cavity in mammals. In the external nasal cartilages of soricids, he discovered that the rostrum can be retracted via a m. retractor proboscidis in a telescope-like mechanism that, by resorption, only develops shortly after birth in postnatal life (Maier 2002). The short perinatal time window and the spatial transition between microscopic and macroscopic observation are rarely studied, but always was a focus of Maier's research, and he has coined for that the term mesoscopic anatomy, which would, in the future, deserve its own research agenda (Maier 2020).

Wolfgang Maier clarified the homologies of different ethmoidal structures in primates (e.g., Maier 2000; Maier and Ruf 2014) and demonstrated the persistence of the ductus nasopalatinus in Catarrhini (Cercopithecoidea, Hylobatidae, and some Hominidae) (Maier 1997). Moreover, he identified a cupula nasi posterior in Platyrrhini (Maier 1986).

Motivated by Wolfgang Maier's research on nasal structures, ***Ruf (2022)** provides the first comparative description of the turbinal skeleton of the Amami rabbit *Pentalagus furnessi* (Leporidae). These data contribute to our knowledge of this enigmatic insular species as well as to a deeper understanding of general cranial diversity in lagomorphs, which can serve as morphological model organisms (Kraatz et al. 2021).

***Smith and Bonar (2022)** describe the nasal cavity of agoutis (*Dasyprocta leporina* and *D. cristata*, Rodentia). The related structures are poorly studied in larger-bodied rodents. The authors used, like Wolfgang Maier in many of his publications, µCT data as well as histological serial sections. The latter also allow for the study of soft tissue like the distribution of respiratory and olfactory epithelia inside the nasal cavity.

Wolfgang Maier's research often deals with the development of the studied structures to detect homologies. The same approach is applied by ***Ito et al. (2022)** who found so far unobserved differences in the turbinal morphology of moles and shrews (Lipotyphla), that can be used for systematic purposes.

Ear region

In addition to studies on nasal anatomy, Wolfgang Maier is largely interested in the unique ear anatomy of mammals. For instance, by studying the jaw angle and the skull base of *Monodelphis*, Wolfgang Maier observed that the postnatal differentiation and ontogenetic translation of the middle ear is in fact a recapitulation of the evolution of this complex. He also provided a functional interpretation of the processus angularis in marsupials (Maier 1987). Wolfgang Maier studied the anterior attachment of the malleus and described a processus internus praearticularis in Artiodactyla; he observed that different proportions of this process exist in relation to the tegmen tympani in ruminants and non-ruminants (including Cetacea) (Maier and Ruf 2016). Such a process he also found in Lagomorpha, although different morphological patterns can be observed in both extant groups, Ochotonidae and Leporidae (Maier et al. 2018).

In a series of papers, Wolfgang Maier has described and identified the systematic relevance of the epitensoric course of the chorda tympani, i.e., the nerve runs dorsal to the attachment site of the m. tensor tympani. It is, together with the fissura petrotympanica (Glaser'sche Spalte), an apomorphy of Anthropoidea (Maier 2008). The epitensoric chorda tympani is also a synapomorphy of Herpestidae (Ruf and Maier 2010), some monophyletic subgroups of Rodentia (Ruf et al. 2009, Tröscher et al. 2015), and is also present in Equidae (Maier and Ruf 2011). Related to these discoveries, Maier found an entotympanicum in *Equus* (Maier et al. 2013) and in Artiodactyla (Maier 2013b).

The postnatal growth pattern of the middle ear in *Monodelphis domestica* is studied by ***Nummela et al. (2022)**. Based on statistical analyses of the size variation of selected middle ear structures, the authors reveal different growth trajectories and timing of maturity for the auditory ossicles which are interpreted as an improvement of hearing sensitivity during postnatal development.

***Wirkner et al. (2022)** provide the first comprehensive study on the ontogeny and comparative morphology of the inner ear bony labyrinth in Pantherinae taking all extant species into account. Based on µCT scans of different postnatal to adult stages of lion, tiger, and leopard, the authors support previous observations that inner ear size is not changing significantly after birth in placentals. In addition, several morphological characters that can be used for phylogenetic purposes are identified.

The petrosal bone comprises systematically relevant characters and can provide a deeper understanding of evolutionary transformations of the mammalian ear as demonstrated by ***Schultz et al. (2022)**. The authors describe the anatomy of a petrosal bone from the Lower Cretaceous of Yakutia (Russia). This specimen reveals a puzzling pattern of characters, each observed in different Mesozoic mammal clades, and is tentatively assigned to Eutriconodonta.

Chewing apparatus and dentition

Many of Wolfgang Maier's studies concern also the anatomy of teeth and the chewing muscles in mammals. For mole-rats (Bathyergidae), he observed a transitory appearance of a pars infraorbitalis of m. masseter medialis profundus. This finding demonstrated the anatomical hystricomorphy of these animals (Maier and Schrenk 1987). Other important discoveries were the pseudo-myomorphy in dormice (Gliridae) (Maier et al. 2002) and the different origins of m. levator veli palatini in Artiodactyla (Maier 2013a). Wolfgang Maier identified variable occlusal relationships in Zalambdodonta (Maier 1985). He provided a constructional morphological explanation for the bilophodonty in Cercopithecidae (Maier 1977a), studied intraspecific and intergeneric degrees of molar differentiation in Indriidae (Maier 1977b), found a specific molar facet pattern in Lemuridae (Maier 1980), and described the tooth formula of *Tarsius spectrum* with exhaustive details (Luckett and Maier 1982). Maier and Schneck (1981) identified a new pair of molar wear facets as apomorphies of the Hominoidea, and thereby showed that their postprotocrista is not a homolog of the crista obliqua.

In the Festschrift, based on µCT data, ***McKay et al. (2022)** elucidate the development and homology of the first premolar in afrotherians such as macroscelidids and hyracoids and carnivorans such as canids. Their results underpin previous hypotheses that Macroscelididae retains a deciduous first premolar, whereas in Canidae the first premolar is exclusively a permanent one without any precursor (Kindahl 1957; Williams and Evans 1978).

Detailed tooth anatomy is important for taxonomic and functional studies of extant and extinct species. ***Babot et al. (2022)** describe and analyze the morphology of the lower dentition and jaw of a new specimen of the carnivorous metatherian *Callistoe vincei* from the Eocene of northwestern Argentina. Based on mesowear, the authors conclude that the lack of cutting edges was compensated by the overeruption of antagonistic teeth in order to maintain functional occlusion.

Primatology and anthropology

In addition to the research topics mentioned above, Wolfgang Maier also published observations in primatology and anthropology. Shortly after his doctoral thesis, he conducted research in Brazil and South Africa to study living and extinct primates. For example, he described new fossil skulls of *Simopithecus* and *Parapapio* from the Plio-Pleistocene cave deposits of South Africa (Maier 1970). He studied the postnatal development of the interorbital fenestra in *Saimiri sciureus* (Maier 1983) and 'sap-feeding' in *Callithrix jacchus* (Maier et al. 1982).

In this research area, the work by ***Mano et al. (2021)** on the fetal and perinatal morphogenesis of the sphenoid bone in primates contributes to a deeper understanding of the skull base development of this clade. The study is based on histological and µCT data as well as immunohistological methods. The authors conclude that the orientation of orbits and midface is prenatally directed by active growth centers.

In his private life, Wolfgang Maier always shows great interest in cultural evolution, philosophy, classical music, and literature. In this regard, the study of ***Zeller and Göttert (2021)** in our Festschrift nicely fits his widespread interest. The authors provide an insight into the interrelationship of humans, megafauna, and landscape structure. They study rock engravings from Namibia and encourage a comparative approach to central Europe and southern Africa to better manage megafauna today.

Conclusion

It has been a pleasure to compile the Festschrift in honor of Prof. Dr. Wolfgang Maier, who has given us personally a valuable intellectual connection to the European tradition of holistic research in vertebrate morphology. Inspired by him, *Vergleichende Entwicklungsgeschichte* has enabled us to understand how the organism and its anatomical structures are the result of an evolutionary process.

Wolfgang Maier always distinguishes between quantitative patterns vs. qualitative morphological research. These days, there is a bit too much emphasis on quantitative patterns in evolutionary studies. Whereas qualitative research into structure helps to provide hypotheses on rare but exquisite material, the more quantitative approaches are valuable to statistically test larger samples. This Festschrift shows that both approaches should supplement each other to advance our understanding of evolutionary transitions in nature.

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Content of the Festschrift

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2. Werneburg I, Hoßfeld U, Levit GS (2022) Discovery of rare lecture notes from 1866 provides exceptional insights into the conceptualization and visualization of paleontology by Ernst Haeckel. Vertebrate Zoology 72: 577–597. https://doi.org/10.3897/vz.72.e84983
3. Drack M, Betz O (2022) A technomorphic conceptualisation of biological 'constructions' and their evolution. Vertebrate Zoology 72: 839–855. https://doi.org/10.3897/vz.72.e86968

Evolution of animal organisms

4. Staggl MA, Abed-Navandi D, Kriwet J (2022) Cranial morphology of the orectolobiform shark, *Chiloscyllium punctatum* Müller & Henle, 1838. Vertebrate Zoology 72: 311–370. https://doi.org/10.3897/vz.72.e84732
5. Johnston P (2022) The missing anatomy of the living coelacanth, *Latimeria chalumnae* (Smith, 1939). Vertebrate Zoology 72: 513–531. https://doi.org/10.3897/vz.72.e84274
6. Ascarrunz E, Sánchez-Villagra MR (2022) The macroevolutionary and developmental evolution of the turtle carapacial scutes. Vertebrate Zoology 72: 29–46. https://doi.org/10.3897/vz.72.e76256
7. Werneburg I, Evers SW, Ferreira G (2021) On the "cartilaginous rider" in the endocasts of turtle brain cavities. Vertebrate Zoology 71: 403–418. https://doi.org/10.3897/vz.71.e66756
8. Regalado Fernández OR, Werneburg I (2022) A new massopodan sauropodomorph from Trossingen Formation (Germany) hidden as '*Plateosaurus*' for 100 years in the historical Tübingen collection. Vertebrate Zoology 72: 771–822. https://doi.org/10.3897/vz.72.e86348

Evolutionary origin and diversification of mammals

9. Preuschoft H, Krahl A, Werneburg I (2022) From sprawling to parasagittal locomotion in Therapsida: A preliminary study of historically collected museum specimens. Vertebrate Zoology 72: 907–936. https://doi.org/10.3897/vz.72.e85989

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