The Beginning of Carl Gegenbaur´s Career:
A Forgotten Early Paper on Axolotl Skull Morphology

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In the year 2003, we celebrate the centennial of Carl Gegenbaur´s death, and in preparing a special issue of the journal "Theory in biosciences" devoted to Carl Gegenbaur and his influence on the development of comparative morphology[1], we came across Gegenbaur´s earliest publication sefely buried a volume of his collected works. Perhaps the leading figure in 19th century evolutionary morphology, Carl Gegenbaur (1826-1903), started out as an axolotl researcher already when he was a medical student in Würzburg, Germany. Together with a fellow student, he made a detailed description of the skull of the Mexican axolotl (then with the latin name *Siredon pisciformis*) that was published by their teacher Albert Kölliker in 1849[2]. The paper, which is reprinted here in facsimile, is very detailed and beautifully illustrated with a plate in colour. Upon reading it, one gets the feeling that it corresponds to just the "Results" parts of a modern paper, because it lacks a proper introduction and discussion, and the methods used are not described. This was, however, not unusual at the time. The methods were standard methods used by morphologists and anatomists, and the reader was supposed to be knowledgeable about the scientific tradition and debates to which such "data papers" contributed, and to know the anatomical terminology, which is not explained at all. The paper starts with a division of the axolotl skull into 4 main parts: the occipital, sphenoid, nasal and jaw regions. Then the bones in each of the four regions are described, as well as the foramina for the cranial nerves. In the colour plate, the numbers refer to the list of anatomical terms on pages 8 and 9. Figures 1-9 on the colour plate are listed on page 9. They are:

Fig. 1. Carl Gegenbaur at 35, Jena 1861.

[1] To be published as volume 122, issue 2-3, 2003.

[2] The reference is "Der Schädel des Axolotl (*Siredon pisciformis*). Beschrieben von N. Friedrich and C. Gegenbaur, Studirenden der Medicin aus Würzburg. Berichte von der Königlichen Zootomischen Anstalt zu Würzburg. Zweiter Bericht für das Schuljahr 1847/48 von Dr. Albert Kölliker", pp. 28-34. Reprinted in Gegenbaur, C. (1912). Gesammelte Abhandlungen I. Fürbringer, M., Bluntschli, H. (eds.) W. Engelmann. Leipzig, pp. 1-9 + 1 plate.

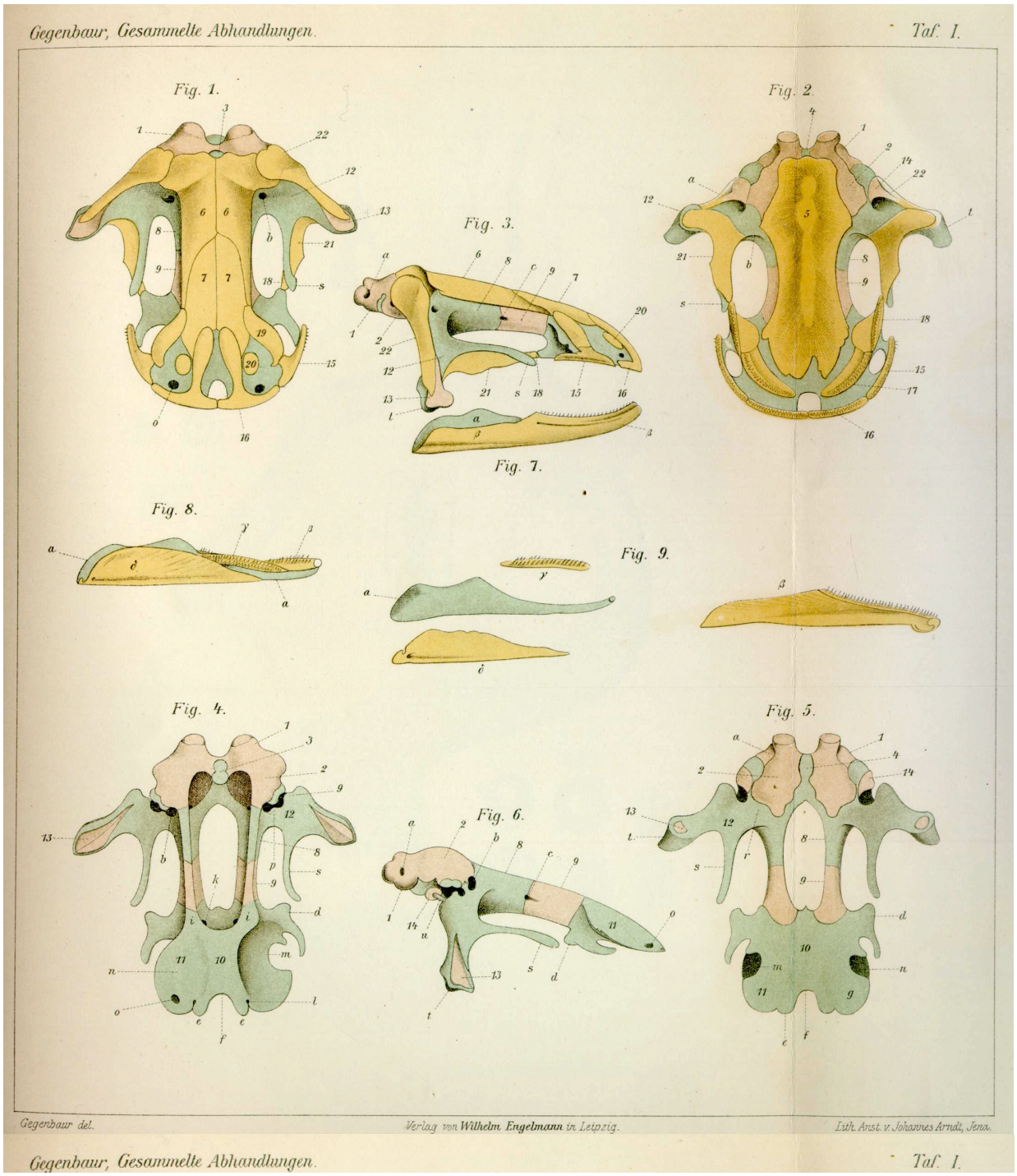

Fig. 1. The entire skull from above
Fig. 2. The entire skull from below
Fig. 3. The entire skull from the side
Fig. 4. The primordial skull from above
Fig. 5. The primordial skull from below
Fig. 6. The primordial skull from the side

Fig. 7. The lower jaw from the outside. Terms as for figure 7:a = Meckel´scartilage; b = Outer toothbearing part; g = Inner toothbearing part; d = Angular part. Terms as for figure 7. Cartilage is blue, dermal bones yellow, and other bones brownish.
Fig. 8. The lower jaw from the inside.
Fig. 9. The single parts of the lower jaw.

Erklärung der Abbildungen auf Tafel I.

Die folgenden Bezeichnungen gelten für alle Abbildungen.

1. *Occipitalia lateralia.*
2. *Ossa petrosa.*
3. Knorpeliges *Occipitale superius.*
4. Knorpeliges *Occipitale basilare.*
5. *Os sphenoidale basilare.*
6. *Ossa parietalia.*
7. *Ossa frontalia.*
8. Grosse Keilbeinflügel (knorpelig).
9. Kleine Keilbeinflügel (knöchern).
10. Mittlerer Nasalknorpel.
11. Seitliche Nasenknorpel oder Nasenkapseln.
12. Quadratknorpel.
13. Knöchernes Quadratbein.

[34] 14. *Columella.*

15. Oberkieferbeine.
16. Zwischenkieferbeine.
17. *Os palatinum primum.*
18. *Os palatinum secundum.*
19. *Os nasale majus.*
20. *Os nasale minus.*
21. *Os pterygoideum.*
22. *Os tympanicum* (Reichert).

a. Loch für den *Vagus.*
b. Loch für den *Trigeminus.*
c. Loch für den *Opticus.*
d. *Processus palatinus* des Keilbeins oder der *Alae parvae.*
e. Fortsätze des mittlern Nasalknorpels.
f. Ausschnitt zwischen diesen.
g. Boden der Nasenkapsel.
h. Hintere Fortsetzung der unteren Fläche des mittleren Nasenknorpels.
i. Senkrechte Knorpelwand, welche den mittleren Nasenknorpel mit den *Alae parvae* verbindet.
k. Loch für den Durchtritt des Riechnerven.
l. Loch für den Nasenast des *Trigeminus.*
m. Hintere Incisur im Boden der Nasenkapsel.
n. Decke der Nasenkapsel.
o. Aeussere Nasenöffnung.
p. Oberer vorderer Gelenkfortsatz des Quadratknorpels.
q. Unterer hinterer Gelenkfortsatz des Quadratknorpels.
r. Querer Fortsatz des Quadratknorpels zu den *Alae magnae.*
s. *Processus pterygoideus* des Quadratknorpels.
t. Gelenkfortsatz, durch den der Quadratknorpel mit dem Unterkiefer artikulirt.
u. Fibröses Bändchen, durch welches die *Columella* sich mit dem Quadratknorpel verbindet.

Fig. I. Ansicht des vollständigen Schädels des *Siredon pisciformis* von oben.
Fig. II. Dieselbe von unten.
Fig. III. Dieselbe von der Seite.
Fig. IV. Ansicht des Primordialschädels von *Siredon* von oben.
Fig. V. Dieselbe von unten.
Fig. VI. Dieselbe von der Seite.
Fig. VII. Unterkiefer von aussen. α. Meckel'scher Fortsatz; β. Aeusseres zähnetragendes Stück; γ. Inneres zähnetragendes Stück; δ. Winkelstück.
Fig. VIII. Unterkiefer von innen.
Fig. IX. Die einzelnen Stücke des Unterkiefers. Die Bezeichnung wie bei Fig. VII. Die Knorpel sind blau, die Deckknochen gelb, die übrigen Knochen bräunlich.

Carl Gegenbaur, the leading morphologist of his time

Carl Gegenbaur was born on August 21, 1826 in Würzburg, Germany. He became a medical student at the local university in 1845, completed the preparatory *biennium philosophicum* in 1847, and received the Dr. med. in 1851 with the dissertation "De limacis evolutione". In 1854, after some travels and a eighteen-month research period in Messina, he presented his Habilitationsschrift "Zur Lehre vom Generationswechsel und der Fortpflanzung bei Medusen und Polypen"[3]. In 1855, he came to Jena University as an associate (Extraordinarius) professor of zoology and comparative anatomy in the medical faculty. In 1858, Gegenbaur got the chair in comparative anatomy at Jena University. In addition, he was the director of the Zoological Museum at Jena University between 1855 and 1861. In 1865, Ernst Haeckel became the first full professor of zoology in Jena and also took over the museum duties. Gegenbaur was instrumental in seeing to that his friend Haeckel was brought to Jena. In 1873 Gegenbaur accepted the chair of anatomy at Heidelberg University, where he remained for the rest of his career. He retired in 1901, and died on June 14, 1903 in Heidelberg.

Carl Gegenbaur had a great reputation as a scientist, teacher and founder of the "Gegenbaur school" of comparative morphology during his lifetime and beyond[4]. The Berlin anatomist Wilhelm Waldeyer wrote. "Gegenbaur is a man worthy of the highest admiration ... he is without any doubt the most important morphologist in the world [and has been] for many years now, [the one] who first created a scientific comparative anatomy."[5]. This reputation was based on Gegenbaur´s syntetic views more than on just his research in anatomy. He wanted to found a comparative morphology based on Darwin´s theory of evolution, and could build upon the comparative method already developed earlier by George Cuvier, Johannes Müller and others. Through critical comparisons, Gegenbaur tried to develop descriptive anatomy into an explanatory science, which he liked to call morphology – in contrast to physiology. Gegenbaur wrote a number of research monographs and textbooks, which were seen as a model of critical investigation based on an extensive collection of facts. Maybe the most important was the monograph on the development of the head skeleton in sharks, which appeared in 1872. This was an important step in the investigation of comparative vertebrate head development. The old ideas of a segmented skull, stemming from Lorenz Oken and Johann Wolfgang von Goethe around 1800, were developed by Gegenbaur into a segmental theory of the head in light of the new theory of evolution and encompassing not only the skeleton, but all organ systems in the head region of vertebrates. In addition to being a productive and successful scientist, Carl Gegenbaur was also a highly esteemed teacher and textbook author. His textbooks were an expression of his intention to improve the standards of education prevailing at the time.

Important books by Carl Gegenbaur include: *Grundzüge der vergleichenden Anatomie* [6](Leipzig 1959; 2nd ed., rev. 1870) ; *Das Kopfskelet der Selachier. Ein Beitrag zur Erkenntnis der Genese des Kopfskeletes der Wirbelthiere* [7](Leipzig 1872); *Grundriss der vergleichenden Anatomie* [8](Leipzig 1874; 2nd ed. 1878); *Lehrbuch der Anatomie des Menschen* [9](Leipzig 1883; 7th ed., 2 vols. 1898-1899); *Vergleichende Anatomie der Wirbelthiere mit*

[3] In English: "The theory of alternating generations and the reproduction of medusas and polyps".

[4] For a review of the development of morphology and comparative anatomy in Germany in the 19th century , see Nyhart, L. (1995) Biology Takes Form: Animal Morphology and the German Universities, 1800-1900. Univ. of Chicago Press. Chicago.

[5] German original. "Gegenbaur ist ein Mann der höchsten Verehrung werth; er ist ja ausser allem Zweifel schon seit vielen Jahren der bedeutendste Morphologe der Welt, der eine wissenschaftliche vergleichende Anatomie erst geschaffen hat." Waldeyer to Fürbringer, 2 April 1897. Senckenbergische Bibliothek, Nachlass Max Fürbringer, A. 1. 2752. We thank Dr. Lynn K. Nyhart for bringing this quote to our attention.

[6] In English: "An outline of comparative anatomy".

[7] In English: "The skeleton of the shark head. A contribution to the understanding of vertebrate head skeleton development".

[8] In English: "A survey of comparative anatomy".

[9] In English: "Textbook of human anatomy".

Berücksichtigung der Wirbellosen[10], 2 vols. (Leipzig 1898-1901). Gegenbaur`s articles have been collected and published as *Gesammelte Abhandlungen von Carl Gegenbaur*, M. Fürbringer and H. Bluntschli, eds., 3 vols., Leipzig 1912.

The evolution of evolutionary morphology into evolutionary developmental biology

Carl Gegenbaur and Ernst Haeckel both found it necessary to study development in order to understand evolution. It was clear to them that a better understanding of the processes and regulation of ontogeny could throw light upon phylogeny. This new approach was often referred to as "evolutionary morphology". Now at the centennial of Gegenbaur´s death, research trying to connect developmental and evolutionary biology is experiencing a renaissance. Developmental biology is increasingly seen as relevant to evolution after a long period in which evolutionary and developmental biology progressed along diverging paths. Changes in developmental processes and, ultimately, in the mechanisms that regulate development underlie the morphological changes in adult organisms seen over evolutionary timescales. The increasing interest in comparative approaches to animal development is largely due to the accelerating use of molecular genetics in elucidating the mechanisms of development, and the incorporation of the methods for reconstructing phylogenies, which have been developed by systematists. The development of new morphological methods, such as confocal laser scanning microscopy and improved fate mapping methods have contributed to making detailed studies on a wide range of organisms possible. In this perspective, organisms like the Mexican axolotl might become more popular as an experimental animal again. We should not forget that a lot of research has been performed on the axolotl since they were first seen in the lab in the 1860s, including fundamental descriptive anatomy relevant also today.

[10] In English: "Comparative anatomy of vertebrates with a consideration of invertebrates".