THE BODY-FORMS OF FISHES AND THEIR INSCRIBED RECTILINEAR FIGURES.

By

WILLIAM K. GREGORY

(New York).

(*Eingelangt am 11. Mai 1927.*)

It seems appropriate to dedicate to Professor LOUIS DOLLO the present article because of his justly famous studies on the evolution of the body-forms of dipnoans and other fishes.

The *Arcturus* Oceanographic Expedition of The New York Zoological Society in 1925 made large collections of deep-sea and pelagic fishes in the Sargasso Sea and in the Central Pacific, and of inshore fishes in the Galapagos Archipelago and Cocos Islands. I desire to thank the director of the expedition, Mr. WILLIAM BEEBE, not only for the priceless opportunity of being a member of it, but also for the privilege of accompanying him in many of his numerous descents, by means of diving apparatus, into the teeming inshore waters of the Galapagos and Cocos Islands, where we were able to study the movements and habits of fishes in their own environment. In the laboratory of the *Arcturus* my assistant, Miss ELIZABETH S. TROTTER, and I made over ten thousand measurements on the body forms of fishes as well as many dissections of the locomotor apparatus. The data thus secured form the chief basis of the present paper, which is partly a summary of fuller reports to be published in *Zoologica*.

The body forms of normal fishes in the lateral view have certain relations to quadrilateral figures of varying proportions that may be inscribed within them. The anatomically constant points of reference and axes of these figures may be named as follows:

1. *prosthion (P):* the most anterior point of the snout (or of either jaw when the latter protrude beyond the snout);
2. *pygidion (p):* the mid-point of the caudal peduncle. The line from the prosthion through the pygidion is called the *horizontal* or anteroposterior axis;
3. *apex (A):* the summit of the dorsal curvature. The vertical from the apex to the horizontal is here called the *antero-dorsal vertical (ad);*

4. *gasterion (G):* the lowest point of the ventral contour. The vertical from the gasterion to the horizontal is called the *antero-ventral vertical (av);*
5. *opisthion (O):* the point of intersection of the horizontal with a line drawn from the apex through the epipygidion *(e)*;
6. *epipygidion (e):* the lowest point on the dorsal border of the caudal peduncle above the pygidion;
7. *hypopygidion (h):* the highest point on the ventral border of the caudal peduncle often immediately below the pygidion;

   The vertical from the pygidion to the epipygidion is the *postero-dorsal vertical (pd);* that from the hypopygidion to the horizontal is the *postero-ventral vertical (pv)*;
8. *uranion (u):* the point where the posterior border of the tail crosses the horizontal.

The four sides or boundaries of the quadrilateral are:

1. *Antero-dorsal (PA)* from prosthion to apex;
2. *Postero-dorsal (AO)* from apex to opisthion;
3. *Antero-ventral (PG)* from prosthion to gasterion;
4. *Postero-ventral (GO)* from gasterion to opisthion.

The angles of the quadrilateral are named as follows:

1. *Anterior* or *entering angle (APG):* at the prosthion between the antero-dorsal and antero-ventral slopes. This angle may be divided into two parts, an antero-dorsal *(L α)* and an antero-ventral angle *(L α').*
2. *Dorsal angle (PAO):* at the apex between the antero-dorsal and the postero-dorsal. Subdivided by the *antero-dorsal vertical (ad)* into two, usually unequal, angles *PAQ* and *OAQ;*
3. *Posterior angle (AOG):* at the opisthion, between the postero-dorsal and the postero-ventral slope. Includes a *dorso-posterior* angle (β) and a *ventro-posterior* angle *(β');*
4. *Ventral angle (PGO):* at the gasterion, between the postero-ventral and the antero-ventral boundaries. Subdivided by the *antero-ventral vertical* into two angles *PGQ'* and *Q'GO.*

The ventral, dorsal and front views likewise have definite relations to inscribed rectilinear figures, which are usually quadrilaterals. In the ventral view the four principal points of reference are the prosthion and the hypopygidion, defining the longitudinal axis, and the opposite points of the greatest diameter across the entrance (usually above the preopercular) which may be named the *dexiterion (D)* and the *aristerion (Ar).* In the front view the four points of reference are the prosthion and the apex, fixing the vertical, and the *dexiterion* and *aristerion* fixing the transverse diameter. In the top view the four points of reference are the prosthion, epipygidium, dexiterion and aristerion. In the back view the axes would be drawn through the apex and gasterion, dexiterion and aristerion.

The principal kinds of rectilinear figures that may be drawn within or near to the body forms of fishes in the side view are as follows:

1. Inscribed rectilinear figures quadrilateral:
   a) Dorsal and ventral verticals in line. (*e. g.*, many sharks, sturgeons, Protospondyli, Isospondyli, Ostariophysi, Scombridae, *Micropterus dolomieu*, etc.);
   b) Ventral vertical behind dorsal vertical. (*e. g.*, *Upeneus*, *Chaetodipterus*);
   c) Ventral vertical in front of dorsal vertical. (*e. g.*, *Tarpon atlanticus*, *Sphyraena barracuda*).
2. Inscribed rectilinear figure incompletely quadrilateral:

   Postero-dorsal and postero-ventral angles both = 180° and the postero-dorsal and postero-ventral boundaries meeting only at infinity. This case is rarely met with (*e. g.*, *Schilbeodes insignis*).
3. Inscribed rectilinear figure pentagonal:

   When the ventral fins are shifted forward below the pectorals the simple quadrilateral is often transformed into a pentagon, as in *Chaetodon*, *Xystema* and many other Acanthopts.

The variable relations of the parts of the rectilinear figures to each other, of the form and position of the median and paired fins, etc., are given below in the list of variable factors of body form, which also contains the new descriptive terms used in the present paper.

The highly variable forms of the bodies of fishes and the position and proportions of the fins, can be analysed and described very effectually in relation to the primary points and axes of reference and to the inscribed quadrilaterals as defined above, especially by means of the following set of new terms, which are somewhat similar to those used in anthropometry. If we consider the varying relations of total body height (anterior dorsal vertical plus anterior ventral vertical) to body length (prosthion to pygidion) we can arrange the resulting indices in the following progressive series:

In *hyperdolichosomatic* forms the greatest body height (measured on the vertical through the apex) is equal to or less than one tenth of the body length *(Pp);* in dolichosomatic forms it varies from one tenth to one fifth (both inclusive); in *mesosomatic* fishes the height is greater than one fifth to one third (inclusive) of the length; in *hypsisomatic* forms the height is greater than one third of the length.

In *hyperdolichonotic* forms the anterior dorsal vertical *(ad)* = or $<$ $^1/_{20}$ body length; in *dolichonotic* $^1/_{20}$ to $^1/_{10}$ inclusive; *mesonotic* $>$ $^1/_{10}$ to $^1/_6$ inclusive; in *hypsinotic* $>$ $^1/_6$.

In *hyperdolichogastric* forms the antero-dorsal vertical = or $<$ $^1/_{20}$ body length; in *dolichogastric* $^1/_{20}$ to $^1/_{10}$ inclusive; in *mesogastric* $>$ $^1/_{10}$ to $^1/_6$ inclusive; in *bathygastric* $>$ $^1/_6$.

Similarly if we compare maximum transverse diameter of body (between dexiterion and aristerion) with body height, we have:

Stenothoracic fishes, body width $<$ $^{45}/_{100}$ body heigth; *mesothoracic* $^{45}/_{100}$ to $^1/_1$ (inclusive); *eurythoracic* $>$ $^1/_1$.

If we compare the greatest width across the extended pectoral fins with the body heigth, we have the following: *stenobrachial*, greatest pectoral width < $^1/_1$ body heigth; *mesobrachial*, $^1/_1$ to $^4/_1$ inclusive; *eurybrachial* > $^4/_1$.

The standard points and axes of reference also afford a ready means of describing, within defined limits, the relative positions of various parts. Thus the gasterion is *postapical*, when it is behind the vertical of the apex, *subapical* when it is directly beneath the apex, and *preapical* when in front of that line. The apex is said to be *anterior* when its vertical falls in the anterior third of the horizontal, *middle* when it falls in the middle third and *posterior* when in the posterior third.

So, too, the relative positions of the opisthion to the uranion may be described as *opisthion posturanic* when the former is behind the uranion, *uranic* when it coincides with the uranion, or *preuranic* when it is in front of that point.

The relative size of various parts of the body is described in the following terms: —

Considering head length (prosthion to posterior border of operculum) in comparison with body length (prosthion to pygidion) we have *microcephalic* forms in which the head length is less than $^1/_5$ of the body length; *nomocephalic* $^1/_5$ to $^1/_3$ (both inclusive); *macrocephalic* > $^1/_3$.

If we compare the depth of the head (supraoccipital to isthmus) with its length, we have *platycephalic* forms in which the head depth is < than one half its length; *mesocephalic* ½ to $^1/_1$ (both inclusive); *hypsicephalic* > $^1/_1$.

Considering transverse diameter of head to its height, we have *stenocranial* forms in which the greatest head width is less than forty percent of the head height; *mesocranial* ½ to $^1/_1$ (both inclusive); *hypsicephalic* > $^1/_1$.

Similarly snout length to total head length gives *microrhynchal* (< ¼ length); *nomorhynchal* ¼ to ½ (both inclusive); *macrorhynchal* (> ½). Snout width to snout depth (at nares), *stenorhynchal* (< $^1/_1$ depth); *mesorhynchal* ($^1/_1$ to $^3/_1$ both inclusive); *euryrhynchal* (> $^3/_1$).

Considering the relative proportion of maxillary (functional upper jaw) length to head length, we have *micrognathic*, in which the maxillary length is less than one third the head length; *mesognathic*, $^1/_3$ to $^1/_2$ inclusive; *macrognathic*, > $^1/_2$.

Anteroposterior diameter of eye to head length *microphthalmic* (< $^1/_5$ head length); *mesophtalmic* ($^1/_5$ to $^1/_3$ both inclusive); *megophtalmic* (> $^1/_3$).

Proportion of antero-posterior diameter of gill chamber (anterior border of preoperculum to posterior border of operculum) to heod depth (supraoccipital to isthmus), *microcameral* (< $^1/_3$ head depth); *mesocameral* ($^1/_3$ to ¾ both inclusive); *macrocameral* (> ¾).

In *leptopygidial* forms the minimum vertical diameter of the caudal peduncle (pd + pv) is less than one fourth the body height (ad + av); in *nomopygidial* ¼ to < ½; *macropygidial* ½ or > ½.

Comparing the transverse width of the caudal peduncle to its vertical diameter, we have: *stenopygidial* forms with a transversely or narrow peduncle (width $=$ or $< 1/3$ depth); *mesopygidial* $1/3$ to $3/4$; *eurypygidial* $> 3/4$.

In considering the actions of the various fins, we need to know their locations with reference to the antero-posterior and vertical axes, the extent of their bases, the length of their longest rays, the shapes of their distal borders, their areas, the distance of their centroids from the center of gravity of the body and other factors.

Thus, considering the first dorsal fin, the middle of its base may fall in either the first, second, third or fourth quarter of the body length (prosthion to pygidion). With reference to the relative extent of the base of the first dorsal, this fin is termed *brevibasic* if its length is $< 1/10$ the body length; *medibasic* $1/10$ to $1/4$ (both inclusive); *longibasic* $> 1/4$ to $1/2$; *perlongibasic* $> 1/2$.

Height of dorsal fin from its summit to its base (measured along the longest ray excluding filaments), *breviradial* length $< 1/3$ body depth (adv + avv); *mediradial* $1/3$ to $3/4$ (both inclusive); *altiradial* $> 3/4$. The distal or postero-superior border of the first dorsal may be either concave, flat, convex (spatulate) or emarginate. The first and second dorsals may be either *continuous*, *notched* or *separate*.

As to the second dorsal fin its mid-point may be in either the second, the third or the fourth quarter of the horizontal. It is *perbrevibasic* if its base is $< 1/12$ body length; *brevibasic* $1/2$ to $< 1/7$; *medibasic* $1/7$ to $< 1/3$; *longibasic* $1/3$ to $1/2$ or $> 1/2$. It is *breviradial* if its longest ray is $< 1/2$ the body depth; *mediradial* $1/3$ to $1/2$ inclusive; *longiradial* $> 1/2$ to $1/1$; *perlongiradial* $> 1/1$. Its postero-superior border may be *convex* (spatulate), *flat*, *concave*, or *produced* into a long filament.

The anal fin may have its mid-point below the third or fourth quarters of the body length; its posterior border may be *postdorsalic* (with reference to the posterior border of the dorsal); *subdorsalic* or *predorsalic;* its spinous portion may be variously developed and the extent of its base compared to body length may be *brevibasic* when $< 1/10$ body length; *medibasic* $1/10$ to $1/3$ (both inclusive); *longibasic* $> 1/3$ to $1/2$ inclusive; or *perlongibasic* $> 1/2$. With regard to its depth, the anal fin, measured on its longest ray, may be *breviradial* ($< 1/3$ body depth); *mediradial* ($1/3$ to $1/2$ both inclusive); *longiradial* ($> 1/2$ to $1/1$); or *perlongiradial* $> 1/1$. Its postero-inferior border *concave*, *flat*, *convex*, *pointed* or *produced*.

The pectoral fins may have the center of their base either in the first or in the second quarter of the body length; the dorsal axial border of the pectoral fin, with respect to the horizontal line may be *inferior*, *median* or *superior*. Comparing the magnitude of the pectoral fin spread to the total body depth, the pectorals may be either *parviareal* (greatest spread of pectoral fin $< 1/3$ body depth); *mediareal* ($1/3$ to $1/2$); *latiareal* ($< 1/2$). As to length of the pectorals in comparison with body length they may be *breviradial* (base to end of longest ray $< 1/6$ body length; *mediradial* ($1/6$ to $1/3$ inclusive); *longiradial* ($> 1/3$ to $1/2$ inclusive); *perlongiradial* ($> 1/2$). In form the pectorals may be *spatulate* (rounded), *intermediate* to *pointed*, or *falcate*.

The ventral fins may have their anterior borders beneath any one of the first three quarters of the body length; with regard to the fin spread of one ventral, they may be *parviareal* (< $^1/_{10}$ body length); *mediareal* ($^1/_{10}$ to $^1/_6$ inclusive); or *magniareal* (> $^1/_6$); as to length, the ventrals may be *breviradial* (longest ray < $^1/_{10}$ body length); *mediradial* ($^1/_{10}$ to $^1/_5$ inclusive); *longiradial* (> $^1/_5$); while their postero-external borders may be either *concave, flat, convex,* to *spatulate* or *pointed* in the middle.

The caudal fin may have its vertebral axis either *superior, median* or *inferior,* with reference to the horizontal line; in *homocercal* forms, the uranion may be at varying distances behind the pygidion, the tail being *dolichocercal* when *pu* (basal length) > *tt'* (maximum vertical spread); *mesocercal* ($^1/_1$ to $^1/_2$ inclusive); or *brachycercal* < $^1/_2$. Similarly the varying relations of the maximum spread of the caudal fin to the body depth gives rise to *microcercal* (< $^1/_3$); *nomocercal* ($^1/_3$ to $^3/_4$ both inclusive); or *macrocercal* (> $^3/_4$) conditions.

From a morphological point of view caudal fins may be either *hypocercal* (reversed heterocercal), *heterocercal, tristichopterous, diphycercal, hemiheterocercal, homocercal* or *gephyrocercal.* The varieties of these fundamental types will be discussed elsewhere.

The foregoing analysis while exposing the great complexity of the problem, also reveals a vast field for fruitful research.

Broadly speaking the body forms of fishes may be divided into two main categories: —

I. Nomosomatic, with primitive bilateral symmetry, the median sagittal plane being vertical.

II. Heterosomatic, with a secondary twisting, which overlies the primitive bilateral symmetry, the median sagittal plane being horizontal. The heterosomatic forms being confined to one order (the Heterosomata) and comparatively recent, show but little further adaptive radiation in body form, the less specialized ones being hypsisomatic rhomboid, some of the more specialized genera being secondarily meso- to dolichosomatic.

On the other hand the nomosomatic group, comprising the vast majority of the swarming hosts of recent and fossil fishes, shows the utmost diversity of body forms and methods of locomotion which, however, may be referred to the following descriptive groups: —

1. eurythoracic (body depressed);
2. mesosomatic (fusiform);
3. dolichosomatic (elongate fusiform);
4. hyperdolichosomatic (anguilliform);
5. hypsisomatic (disciform).

The bodies of fishes may also be described as flexible, intermediate, loricate and rigid. Any of the five primary body forms may be combined with several degrees of flexibility so that we may have eurythoracic-loricate („*Flachboot-Typus*"), mesosomatic-loricata, dolichosomatic loricata, hyperdolichosomatic-loricate or hypsisomatic-loricate; or, we may have eurythoracic-rigid, eurythoracic-flexible, eurythoracic-intermediate and so forth. Again each of these combinations (*e. g.*, hypsisomatic-loricate) may be realized among different fishes in which the placement and form of the fins differ widely, so that as the number of variables is large, the conceivable number of combinations becomes extremely great.

Owing to the *different chronological* order in which new characters have been acquired in different groups, almost every family of fishes has its own diagnostic combination of body form and of locomotion. Hence also, pure convergence between fishes of widely different stocks can effect only relatively few characters or series of characters and even the resemblances due to parallelism between more nearly related stocks should be recognized as such, if our analysis can be sufficient close.

The objects of investigations on the body forms of fishes will usually be: first, to discover the immediate relations between structure and function and secondly to trace the evolutionary steps by which a given body form was reached as in the brilliant essays of Professor DOLLO.

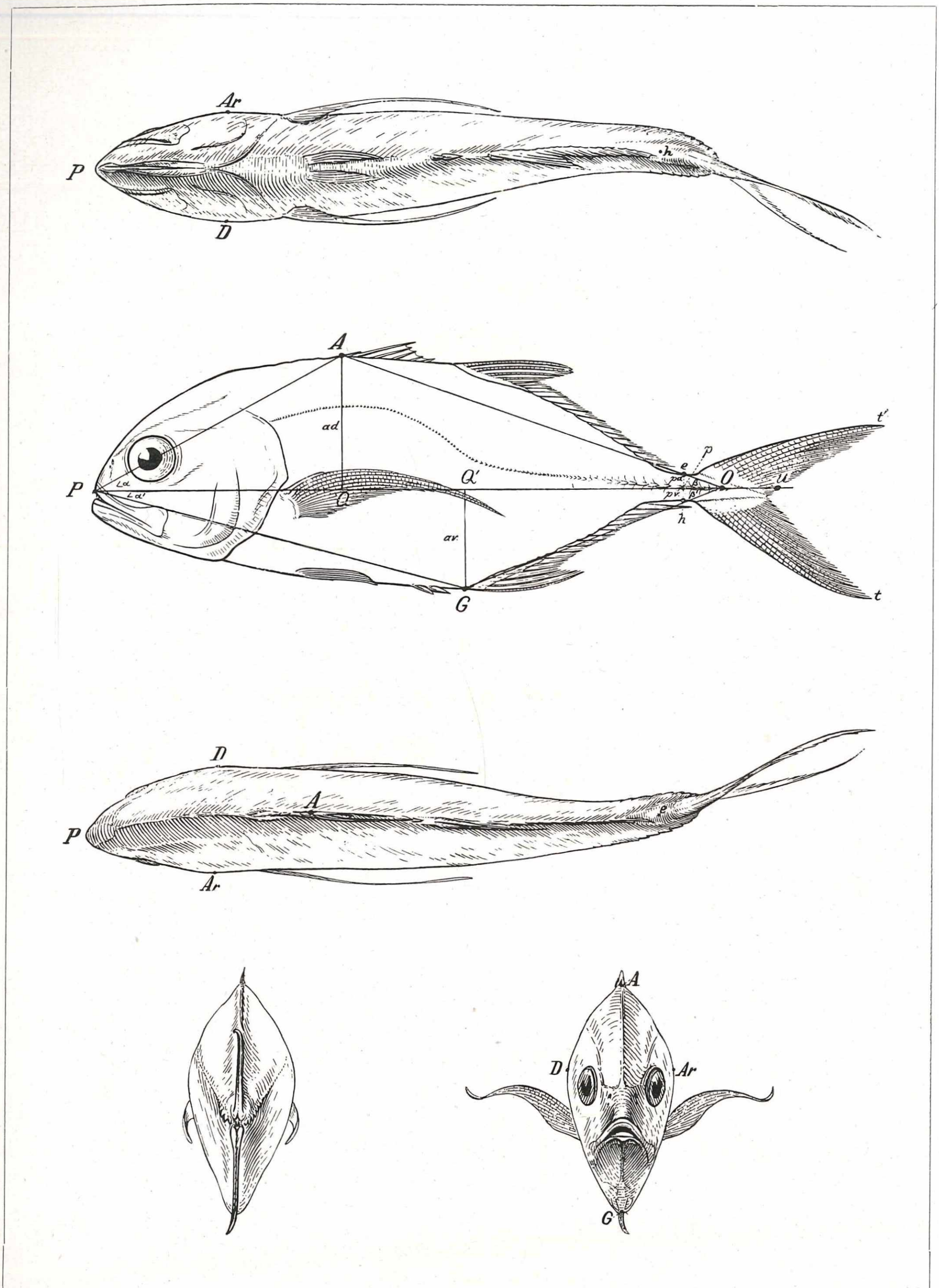
In either case I have found that the present system of analysing the body form of fishes has proved useful. In the first place, it has made me realize the significance of the obvious facts that bilateral symmetry and the relations of the primary points and axes of reference are an expression of the results of locomotion in a gravity-pervaded medium, *i. e.*, that the dorso-ventral differentiation and vertical axis lie in the directions of the earth's radii, while the antero-posterior differentiation and horizontal axis are more or less parallel to the earth's surface. A fish, however, must maintain both horizontal and vertical balance not only with reference to the constant directions and pressures due to gravity under relatively stable conditions but also to the variable and unexpected thrusts and pressures due to the indirect effects of gravity in rapidly shifting streams. In addition, in order to capture sufficient energy from the environment to carry on the game of life, the fish must adjust itself to the varying velocities both of its food and of its enemies. Moreover the medium in which typical fishes move is most efficiently cleaved by stream-line forms, which have accordingly been adopted by animals that either move through the water, or resist the flow of a stream.

The jointed body of a fish with its various appendages comprises a complex mechanism of simple and compound levers, each of which may serve either as an active lever for pushing the water or as a fulcrum for turning other parts. Thus predatory pike-like fishes have a low entering wedge and a posteriorly placed strong axis of lateral turning (running vertically through the dorsal and anal fins) which permits sudden lateral displacements of the head and fore-part of the body. Hence the apex and the gasterion are placed far back, the downward slope of the base of the dorsal fin is slight, and the vertical diameters are very small. The long body is thrown into eel-like undulations, the amplitude of which increases posteriorly. In this case forward locomotion results from the longitudinal summation of the contractions of a long series of myomeres. At the other extreme such deep-bodied forms as the pomacentrids and angel-fishes have a high entering wedge, requiring short and very powerful muscles to push it through the water. The powerful posterior axis of lateral turning, by reason of the shortness of the body, is far nearer to the principal fulcrum than is the case in long-bodied fishes. Hence the vertical diameters are relatively great, the pygidion is relatively near to the prosthion and the postero-ventral boundary, forming the base of the dorsal fin, slopes downward at a sharp angle. These differences in leverage make the pike efficient in quick dashes and sudden snatches while many deep-bodied fishes have a firm stance and purchase in order to tear their food from the rocks.

Erklärung zu Tafel VIII.

Fig. 1. Body form of young *Caranx hippos*. Locality: Panama. For abbreviations, see pages, 93—95.

The fish is nomosomatic, hypsisomatic, hypsinotic, mesogastric, mesothoracic, mesobrachial; gasterion, decidedly postapical, opisthion preuranic; head nomocephalic (length), barely hypsicephalic (depth), mesocranial (width); snout microrhnychal (length), stenorhynchal (width); maxillary mesognathic (length); eye mesophthalmic (length), gill chamber mesocameral; caudal peduncle decidedly leptopygidial (depth) and eurypygidial (width). First dorsal medibasic (length), breviradial (height); second dorsal longibasic, mediradial. Anal subdorsalic, medibasic, mediradial. Pectorals median, parviareal, longiradial, falcate. Ventrals subpectoral, parviareal, breviradial. Caudal homocercal, mesocercal (length), nomocercal (spread).



Verlag von **Emil Haim & Co.,** Wien und Leipzig.