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Body Form and Behavioural Types in Fish

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Introduction

Towards the end of the 19th century the characteristics of fish form aroused interest from a mechanical point of view. Parsons[1] examined the maximal cross sections of teleosts and cetaceans: a similar approach was taken by Amans[2], who selected certain distinctive fishes for analysis. Earlier, the classic work of Marey[3] demonstrated the element of anguilliform motion. A later notable study was that of Houssay[4], who related body form to dynamic equilibrium: about the same time Alliaud and Vlès[5] also studied the natural stability of fish by an electrocutory technique.

The literature is indeed somewhat diffuse, in that the problem of form belongs to no single discipline, and apart from the above investigations developmental studies need consideration, such as those of Meek[6], Fulton[7], and Hecht[8]. In this connection special mention must be made of Sir D'Arcy Wentworth Thompson[9], and in particular of his application of the theory of transformations. He wrote: '...if...diverse and dissimilar fishes can be referred as a whole to identical functions of very different co-ordinate systems, this fact will of itself constitute a proof that variation has proceeded on definite and orderly lines, that a comprehensive "law of growth" has pervaded the whole structure in its integrity, and that some more or less simple and recognizable system of forces has been in control.'[10] It is precisely by starting with a relatively undifferentiated type, such as the Salmonid, and applying the principles of (1) extension along a single axis, (2) tapering, (3) simple shear, and (4) the conversion of rectilinear into radial co-ordinates, that one may trace divisions and equations among fish forms, establishable by correlated behavioural or biological observations.

Magnan's excellent experiments[11] continued research along the lines of Houssay, providing data on the dimensions of a large number of fish, on equilibrium, and on power of swimming. Meanwhile, in a completely different field, Breder[12] examined the type of locomotion shown by particular species of fish, classifying it into anguilliform, ostraciiform, or carangiform. Later Gregory[13] provided extensive classificatory schemata for the analysis of body form. Apart from the important work of Gray[14-16], Bainbridge[17,18], and others, which considered locomotion per se, little explicit investigation was undertaken relevant to the problems of shape, neural organization, and behaviour as interconnected factors. A certain amount of evidence, however, may be gained from a consideration of mainly zoological studies, particularly those dealing with evolutionary questions such as the function of the tail and fins.

Unfortunately, several Russian references relevant to this survey proved to be unobtainable, but they are listed below for completeness[19-24].

The sensitivities of the organism – visual, olfactory, and tactile – relate to morphology if they are to be developed in a given environment; this implies that they must be capable of increased performance; in other words, sensitivity precedes adaptation. A principle of concomitance is at work which ensures that when sensitivities are in the process of becoming attached to

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[1] H. de B. Parsons, Trans. Am. Soc. Mech. Engineers *9*, 679 (1888).

[2] P. C. Amans, Ann. Sci. Nat., Zool. 7 sér. *6*, 1 (1888).

[3] J. Marey, *Le Mouvement* (Masson, Paris 1884).

[4] Fr. Houssay, *Forme, Puissance et Stabilité des Poissons* (Coll. de morphologie dynamique *4*, 1912).

[5] M. C. Alliaud et F. Vlès, C. r. Acad. Sci. (Paris) *1911*. 1627.

[6] A. Meek, Sci. Invest. Northumberland Sea Fish Comm. *1903*, 40.

[7] T. W. Fulton, Fisheries Board for Scotland *part 3*, 141 (1904).

[8] S. Hecht, J. Morph. *27*, 379 (1916).

[9] D'Arcy Wentworth Thompson, *On Growth and Form* (1916, new edn. CUP 1942).

[10] D'Arcy Wentworth Thompson, *On Growth and Form* (1942 edn.), p. 1037.

[11] A. Magnan, Ann. Sci. Nat., Zool. 10 sér. *12*, 5 (1929); Ann. Sci. Nat., Zool. 10 sér. *13*, 355 (1930).

[12] C. M. Breder jr., Zoologica, N.Y. *4*, 159 (1923–1926).

[13] W. K. Gregory, Zoologica, N.Y. *8* (1928).

[14] J. Gray, J. exp. Biol. *6*, 126 (1928).

[15] J. Gray, J. exp. Biol. *13*, 170, 181 (1936).

[16] J. Gray, Symp. Soc. exp. Biol. *4*, 112 (1950).

[17] R. Bainbridge, New Scientist *4*, 476 (1958).

[18] R. Bainbridge, Symp. Zool. Soc. Lond. *5*, 13 (1961).

[19] Yu. G. Aleev, Dokl. Akad. Nauk SSSR (Biol.) (trans.) *120*, 299 (1958).

[20] Yu. G. Aleev, Dokl. Akad. Nauk SSSR (Biol.) (trans.) *120*, 484 (1958).

[21] Yu. G. Aleev, *Functional Bases of the External Structure of Fish* (Akad. Nauk SSSR, Moscow 1963).

[22] V. V. Barsukov, Dokl. Akad. Nauk SSSR (Biol.) (trans.) *129*, 1076 (1959).

[23] M. Dzumaliev, Tr. Inst. Fiziol. Akad. Nauk Kaz. SSR *4*, 148 (1963).

[24] M. N. Kuerepina, Bull. Acad. Sci. URSS (Biol.) *1*, 4 (1946).

developing functions which exploit environmental conditions, they are increased if they are interlocked with morphological changes permitting the above exploitations. Gross morphology in fish followed the exigencies of life in water because morphological plasticity either allowed changes of sensitivity to the conditions of the medium to dictate possibilities in activity or acquired purely mechanical perfections which increased mobility. Adaptations, however, must not proceed to a too specific degree or the potentialities of structure are so reduced that the conditions of a particular environment dominate the organism. Behaviour has a certain superabundance: it presents to the environment a variety of possibilities for synchronization with sensitivities, which act as criteria limiting the range of activity.

There are certain problems universal to fish structure and it is proposed to examine these prior to the consideration of certain typal solutions to these structural constraints.

Geometric framework for the analysis of form

As mentioned above, GREGORY drew up classificatory schemata and a fundamental geometric framework to cover the variations of the main body shapes and their parts. Throughout this discussion of the mechanics displayed in a variety of fish this framework will be used as the basis of analysis.

In this schema the foremost point of the snout P is connected with a central point in the tail where the caudal peduncle is narrowest. Lines are then drawn from the frontal point P to the highest point on the dorsal contour A and the deepest ventral point G. This construction describes the entering angle, and is completed by joining A to a point vertically above the previously calculated central point of the caudal peduncle, on the dorsal contour, and extending this line so that it intersects the main horizontal axis to form the point O. G is then connected to O and the verticals are dropped from A (ad) and from G (av) onto the horizontal axis (Figure 1a).

The variations within this quadrilateral are intimately related to variations in the pattern of locomotion. It is also apparent that the first two categories of locomotion as described by BREDER are not entirely susceptible to analysis according to GREGORY's paradigm, since this presupposes a certain internal rigidity optimally adjusted to a minimum of external plasticity. This arrangement allows the pivot of strike (situated as a fixture at the base of the skull for eels and at the caudal peduncle for *Ostracion*) which initiates the contractions inducing forward propulsion to proceed backward along the arc of carangiform motion.

Body form appears to have resulted from the subtle interplay of the type of locomotory system, skeletal framework, the internal systems, and behavioural habits. The outcome of these factors determined the degree of necessity on the one hand, or behavioural tendency on the other, in the final structural endowment of any particular fish. This is illustrated by GREGORY and RAVEN[25] who, to explain the existence of spines in acanthodians during the transition from bottom-living to free-swimming habits, quoted the suggestion of SMITH[26] that changes in the renal and vascular systems provided for a waterproof covering for the surface of the body when the ancestors of chordates came from the ocean into the estuaries: the first stages of a skeleton were a chemical result of this adjustment: continuation of the same process led to the deposition of spikes and other forms of armour which became adapted as locomotory organs.

The principle of form by necessity is seen in the locomotory possibilities of *Cephalaspis* (HEINTZ[27]); its broad flattened skull of shell confined it to bottom life, as its balance was achieved by external construction on the glider principle, its heterocercal tail providing the force to lift and propel the anterior portion. The initial problem for this type of form was to internalize the seat of equilibrium by the internalization of stresses, enabling its abandonment of extermal armature: in other words, the problem was to achieve GREGORY's paradigm. As HEINTZ points out, the reduction of external armature was associated with the perfection of the internal skeleton, and it is interesting to note that this ossification proceeded from the tail forward, centrally, and dorsally. If this is so, then equilibrium developed in close association with the type of propulsion used by a particular fish, ensuring stable motion by sensitizing itself to erratic forces prior to the perfection of the muscular system, and using them to produce ordered movement.

Certain of the features of body form characterized by the quadrilateral of Figure 1a are critical and lay a basis for the analysis of the major shape variations. Firstly, as the early investigator PARSONS discovered, the maximal area of cross sections in teleosts, as plotted against their distance from the snout, is fixed at approximately 36% of the total length. It is clearly seen from calculations on the data provided by MAGNAN that the centre of gravity also tends to be fixed between 36 and 38% of the total length. Further, examination of MAGNAN's data shows that the above maximal area has its highest point situated by definition at A in Figure 1a; this is more posteriorly placed than the maximal point in the transverse plane, so that the entering angle of the fish tends to be an oval-shaped wedge (see Figure 1b). It is here observable that the majority of teleosts improve on anguilliform movement by minimizing their

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[25] W. K. GREGORY and H. C. RAVEN, Ann. N.Y. Acad. Sci. *42*, 273 (1941–1942).

[26] H. W. SMITH, *Studies in the Physiology of the Kidney* (Porter Lectures ser. 9, Univ. Kansas Sch. Med. 1939).

[27] A. HEINTZ, Smithson Report 223 (1934).

use of the lateral angle as they proceed forward, and optimize the value of the vertical entering angle.

Secondly, the increasing acuteness of this wedge-shaped contour reflects the increasing customary speed at which a fish travels. The simpler the lateral contour, the less the fish is likely to show specializations of form; contrarily, the more vagaries the lateral contour shows, the slower the fish appears to become. The points of maximal depth or height, marked by perpendiculars dropped from A and G onto the horizontal, are in general preceded or followed by a smooth plateau, indicating that as far as possible fishes evolved in such a way as to reduce the resistance offered by sharp angles in movement. As will be shown below, wherever such a sharp angle occurs on the dorsal contour it is due to the mechanical problems of the posterior musculature, and is marked on the caudal side of the maximal point by a pronounced dorsal fin (bottom-dwelling fish).

Thirdly, HECHT's belief that the special form of fish is due to variations mainly in depth still seems to be borne out, but one must modify this notion by noting that it is not simply $ad + av$ that is critical, but the relative length of each to the other in the vertical plane, the relative point at which each occurs on the horizontal, and finally the relation of both summated to overall body length, corrected for comparability by scaling according to weight. Although it is hazardous to generalize when dealing with variations in body shape, the Table indicates the main relations between the verticals. For example, from this Table one might deduce that no fish has a form in which ad approaches P and is small, while av approaches O and is relatively large. All the trends indicated here are relative in that they define that, when ad or av are found approaching either horizontal extremity, they may have a characteristic length. In other words, the application of GREGORY's paradigm is only valid if one works within certain typal forms of fish. It is possible that these typal lengths correlate with ecological conditions and behavioural tendencies, as is suggested below.

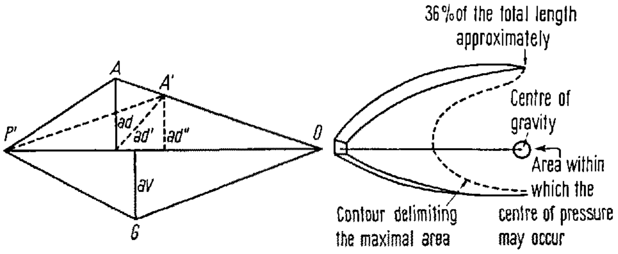

Fig. 1a. Basic framework for the analysis of body form (after GREGORY[13]) incorporating a transformation of the upper and posterior part of the quadrilateral to which it is confined (after D'ARCY WENTWORTH THOMPSON[9]) to show how continuity might be achieved for various forms despite their seeming disparateness. P = prosthion, or the foremost part of the snout. G = gasterion, or the lowest ventral point. A = apex, or the highest dorsal point. O = opisthion, or the point of intersection with the horizontal of a line drawn from A and passing through a point immediately above the centre of the caudal peduncle where it is narrowest. av = a ventral vertical dropped onto the horizontal. ad, ad', ad'' = successive modifications of the dorsal vertical dropped onto the horizontal. Fig. 1b. The frontal entering angle depicted as an oval shaped wedge, the contour delimiting the maximal lateral area showing that the same principle is at work on the flanks. These contours are related to the centre of gravity as shown, and to total body length.

Fourthly, the position of the frontal head segment may be varied in the vertical plane: as KYLE[28] noticed, perches tilt it back on the vertebral column to keep it in a horizontal position. Variation of this segment causes the direction of the mouth to change with an alteration in the entering angle, giving an automatic bias to forward movement and a corresponding change in feeding habits may result.

The relation of fins to form

An examination of the fins of fishes seems to reveal quite clearly that not only do they serve a variety of purposes, such as equilibrators, aids to locomotion, elements of display, and defensive camouflage, but they may also be vestigial, reduced, and apparently functionless. It is not, therefore, surprising that early experiments on the ablation of fins did not produce clear cut results showing disequilibrium. In considering them as accessories of form, one must also take into account the fact that to a certain extent their functions are interchangeable: nevertheless, common conditions of adaptation may produce assemblies of fins with apparently similar characteristics.

A seemingly universal need among fishes both in locomotion and static equilibrium is that of a median or frontally placed pair of equilibrators. The Anaspid as a structural glider, the Palaeoniscid pectorals, and the Elasmobranch lateral keels illustrate this necessity. That it is a primitive solution is seen from its taking precedence over body muscles, yet it is a fundamentally persistent problem which may be due to the conditions of static equilibrium. The early researches of ALLIAUD and VLÈS revealed that *Crenilabrus* and certain Gobies turned upside down when subjected to the passage of electric current through sea water, whereas other fish did not. According to MAGNAN this tendency to instability is due to a condition in which the centre of pressure does not lie in the same horizontal or vertical axis as the centre of gravity. Clearly, although this phenomenon occurs when the fish is approximately stationary and is therefore ruled out in locomotion, it affects the position of the pectorals and ventrals along the body contour. It is precisely these fins which characterize the slow fish both by their size and position (see below): both *Crenilabrus* and the Gobies are slow fish.

It might be concluded that this difficulty was to some extent mitigated in evolution, because the development

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[28] H. M. KYLE, *The Biology of Fishes* (Macmillan, New York 1923).

The relationships between the various parameters of body shape

	ad in 1st $^1/_3$ of horizontal axis, and $^1/_4$–$^1/_5$ of total length	*ad* in 1st $^1/_3$ of horizontal axis, and c. $^1/_6$ of total length	*ad* in 2nd $^1/_3$ of horizontal axis, and $^1/_4$–$^1/_5$ of total length	*ad* in 2nd $^1/_3$ of horizontal axis, and c. $^1/_6$ of total length	*ad* in 3rd $^1/_3$ of horizontal axis, and $^1/_4$–$^1/_5$ of total length	*ad* in 3rd $^1/_3$ of horizontal axis, and c. $^1/_6$ of total length
av in 1st $^1/_3$ of horizontal axis, and $^1/_4$–$^1/_5$ of total length		*Chalcinus elongatus* *Uranoscopus inermis*	*Selene vomer*	*Pristogaster*	*Sternopteryx*	*Gasteropelecus sternicla* *Thoracocharax stellatus*
av in 1st $^1/_3$ of horizontal axis, and c. $^1/_6$ of total length	*Trachypterus* (possibly) *Steatocranus casuarius* *Aequidens pulcher*	The *Garra* species *Lepidocephalus thermalis* *Teleogramma* *Scartelaos vindis*		*Gephyroglanis longipinnis* *Doras asterifrons* *Kryptopterus macrocephalus*		*Pseudocorynopoma heterandria* (possibly)
av in 2nd $^1/_3$ of horizontal axis, and $^1/_4$–$^1/_5$ of total length	*Cichlasoma coryphaenoides* (possibly) *Pygocentrus piraya*		*Metynnis calichromus*	*Ephippicharax orbicularis*		
av in 2nd $^1/_3$ of horizontal axis, and c. $^1/_6$ of total length	Certain *Cichlids* (possibly)	*Heterotis niloticus*	*Distichodus sexfasciatus* *Synodontis batensoda* *Callichthys*	*Scomber scombrus* the *Salmonids* *Gadus gadus* numerous others		*Luciocharax* *Esox lucius* *Scleropages formosus*
av in 3rd $^1/_3$ of horizontal axis, and $^1/_4$–$^1/_5$ of total length			*Citharinus citharus* *Mylossoma argentum*		*Gyrodus wagneri*	
av in 3rd $^1/_3$ of horizontal axis, and c. $^1/_6$ of total length	*Tilapia* (possibly)	*Mystus vittatus* *Polypterus bichir*	*Cyclocheilicthys apogon* *Corydoras aeneus*	*Botia lecontei*		*Petrocephalus bovei* *Gnathonemus macrolepidotus* *Lepisosteus osseus*

may be traced from primitive pectorals, acting like median fins, which had an unconstricted base and an endoskeleton consisting of a uniform series of basals, as in the sturgeon, to a comparatively mobile pectoral in which the number of radials is reduced (WATSON[29], WHITE[30]). With this increased mobility the pectorals show a tendency towards a more dorsal site and a vertically held broad surface, as in the carp, thus reflecting a change in function, viz. from lateral keels used at speed to effectors operative in manipulation and suppressed at speed. Thus this development of more mobile pectorals may have gone some way to solving problems of equilibrium in the above type of fish. Concomitant with this change, there is a tendency for the ventrals to progress forward to a position in front of the centre of gravity, directly below the pectorals, indicating that the ventrals now replace the pectorals as equilibrators, as in *Ambloplites rupestris*.

A great deal has been written on the function of the caudal fin (LAVOCAT[31], KYLE, WATSON, GRAHAM-SMITH[32], GROVE and NEWELL[33], AFFLECK[34], BARSUKOV). It is here necessary only to note the effects on behaviour and active equilibrium associated with change in tail form. According to ABEL[35] the heterocercal tail marked a change in swimming habits from wave-like undulations to an action which took place in the tail shaft: in addition, WATSON notes the enlargement of the eyes and mid-brain in the Palaeoniscid and a reduction of the olfactory apparatus, suggesting that it was increased activity due to this improvement in vision which led to this form of tail. Commenting on this process, GARSTANG[36] observed that this affects the number of dorsal fins: two fins being required to balance the body when it is thrown into sinuous curves, but only one when it is kept straight and the caudal fin does the work. HARRIS[37] maintained that the heterocercal tail vanished with the introduction of the air bladder which

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[29] D. M. S. WATSON, Proc. Zool. Soc. Lond. *5*, 815 (1925).

[30] E. I. WHITE, Proc. Zool. Soc. Lond. *109*, 41 (1939).

[31] M. LAVOCAT, Mém. Acad. Sci. Toulouse 9 sér. *8*, 193 (1896).

[32] W. GRAHAM-SMITH, Proc. Zool. Soc. Lond. *106*, 595 (1936).

[33] A. J. GROVE and G. E. NEWELL, Ann. Mag. Nat. Hist. *4*, 401 (1939).

[34] R. J. AFFLECK, Proc. Zool. Soc. Lond. *120*, 349 (1950).

[35] O. ABEL, referred to in D. M. S. WATSON[29].

[36] W. GARSTANG, Proc. Leeds Philos. Lit. Soc. (Sci.) *2*, part 5 (1931).

[37] J. E. HARRIS, Pap. Tortugas Lab. *31*, 171 (1936).

made the specific gravity of the fish more equal to that of water, and **Affleck** notes that the two developments to the diphercal (characteristic of *Dipnoi* and *Crossopterygii*) and homocercal tails (in teleosts) were by no means comparable temporally. The latter form of tail was achieved by the development of an anterior ventral part of the caudal fin, in such a way that the degree of inclination of the heterocercal form was directly related to the size and position of the ventral and dorsal parts: that is, the larger the ventral in relation to the dorsal, the greater the angle of inclination. Curiously, although this does not support **Houssay**'s theory that body form is moulded by fluid pressures and currents, it does support that part of his theory which held that the correction of the upward motion caused by the inequilobate heterocercal tail led to a redistribution of forces around the caudal area, causing homocercy. Associated with this correction, achieved by the pectorals (by their positioning to slant downwards and to the front), was a depression of the head, thus also bringing about terminal mouth and lateral compression, this latter being chiefly due to the redirection of currents by the pectorals in their new position.

Much of this argument may be seen to support the idea that fish do not entirely aim at keeping their longitudinal axis horizontal and controlling their body movements so that they cancel out deviations from the upright position, though indeed they do this to a certain extent, but that they create biases or forces in given directions in the medium and then use these forces to generate co-ordinated locomotion; in other words, they use unstable positions of their bodies to initiate subsequent reflex movements. Thus, for example, the sinusoidal movement of the shark as it swims, or the fact that *Sphaerides splengeri* after bilateral labyrinthectomy achieved upright swimming only by the inhibition of body and tail movements (**Sperry**[38]): these suggest that something of this kind of principle is at work. Another indication may come from the following consideration: a smooth body of a relatively oval shape creates behind itself an area of low pressure in a current of water, which would tend to act as a suction force stretching the body in a backward direction. Given a strong muscle mass sloping to a narrow caudal peduncle, as in Scombrids, the screw-type propeller tail is ideal to disperse this area of low pressure to greatest locomotory advantage. Here again may be observed the creation and use of a force to achieve enduring swimming capacity.

Typal forms

Broad dimensions in the population of fishes may be delineated, which, if they do not define exactly a certain correlation between habitat, behaviour, and morphological structure, appear to suggest it. This correlation is mediated by a constellation of mutually reinforcing factors, such as the originators of trophic tendencies and sensory abilities, and the availability of food and defence. The subject does not appear to be extensively documented, and therefore seems to open up a new area of research. One might illustrate the complexity of interacting factors by noting as an example certain elements which might enter the complexity of controlling or controlled components. **Black**[39] observed that in phylogeny all motor nuclei tend to be situated originally on the segmental level of the emergent roots in the spinal cord, describing a reflex specificity in behaviour. **Healey**[40] suggested that in development the centre of motor control passes upward to the anterior medulla. This may have been stimulated by morpho-locomotory problems set the organism by the environment. Such a problem appears to be raised by **Shterba**[41], who relates that on the transition to the carnivorous state there is an exceptionally rapid growth rate in lampreys, from 15 cm (in the course of four years) to 35–50 cm in the following 1.5–2 years, with a weight increase by a factor of 15–20. The type of solution for problems of this sort, or others like it in the fish population, might account for gradients of relative growth, such as slow longitudinal growth compared with the rate for posterior parts (**Martin**[42]). The following typal forms suggest that the environmental potentialities may not only pose the problem but also control the effectiveness of the solution.

Type 1. The rover (Figure 2): This type is best illustrated by the Salmonids and Clupeids. The former do not show morphological specializations such as the auditory connections with the air bladder retained by Clupeids from freshwater Ostariophysian stock, which makes them to a certain extent more purely typical than the Clupeids (**Garstang**), but they tend to maintain their equilibrators at the beginning of the second third of the horizontal axis, the dorsal occurring almost directly above the centre of gravity, the pelvics below it and slightly posterior. Thus the entering angle *APG*

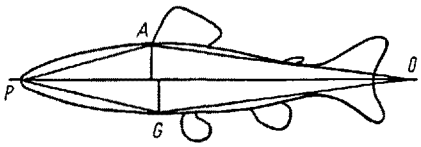

Fig. 2. The Salmonid type, characteristically simple in design, the centre of gravity being at the base of the dorsal vertical below the median fin; the caudal peduncle is thick; the locomotory orientation tends to the rectilinear; these are features of a fish that is constantly active.

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[38] R. W. Sperry, J. comp. Physiol. Psychol. *43*, 482 (1950).

[39] D. Black, J. comp. Neurol. *27*, 467 (1916–1917).

[40] J. Healey, in *The Physiology of Fishes* (Ed., M. E. Brown; Academic Press, New York 1957), vol. 2, p. 1.

[41] G. Shterba, Vest. Leningradsk. Univ. *15*, 58 (1962).

[42] W. R. Martin, Univ. Toronto Studies, Biol. Ser. 58. Publ. Ontario Fisheries Res. Lab. *70* (1949).

marking the point of maximal depth, which is about a sixth of the length, is closely related to these controlling elements, while the direction of power as defined by Magnan is approximately horizontal, receiving its impetus from a thick caudal peduncle. This structure is mechanically sound and simple and obviously built to pursue long-term activity rhythms, which demand a great amount of cruising in pursuit of the controlling environment factors.

Type 2. The predator (Figure 3): This type defines the *Lepisosteidae*, *Esocidae*, *Aphredodorus*, *Alepocephalidae*, etc. According to Garstang, the conversion of the salmon to the pike has occurred frequently in teleost history; behaviourally, the change is dramatic, and the way in which it was achieved is reflected perhaps in the structural adaptation and imperfection of the pike. Structurally, *ad* and the dorsal fin, previously a centrally placed equilibrator of the oscillations of the stern propeller, migrate towards the caudal peduncle, displacing the adipose fin. A dissociation occurs between *ad* and the dorsal fin which may be a function of the amount by which *ad* is greater than *av*, so that *ad*, when it follows this function, proceeds forward leaving the dorsal aft as a propeller. The depression of the head taken with *ad* renders more acute the entering angle and counteracts the tendency to rise in the vertical plane during motion, this being caused by the posterior fin configuration, and the relatively median placing of the centre of gravity, it being situated at a point which is 46% of the length (this point being measured from the snout), as opposed to 36–38% for fish of comparable speed. Behavioural factors corresponding to the streamlined form induced vigilance based on rapidity of scanning, which is perhaps a replacement of locomotor by sensory activity. An interesting fact is that owing to the forward and slightly ventral position of its centre of pressure (Magnan) as related to the centre of gravity, it must constantly use its pectoral fins to prevent its inversion; thus is apparent the structural stimulation of this type of fish's predatory vigilance.

Type 3. The surface fish (Figure 4): These fishes have a ship-like bow due to the angling of the mouth; there is a dorsal flattening with a posteriorly placed dorsal fin balanced by an anal fin immediately below it. Here, *av* is almost universally greater than *ad*, which leads to an upward slanting of the horizontal axis and therefore entering angle. It is interesting to note that dorsal reshaping of the depressed contour establishes a deep-bodied fish, thus enabling one to distinguish between an active fish with this structure and a sedentary one if some surface swimmers originated from certain deep-bodied forms. There are innumerable surface fish; generally they are small in size and follow the cycle of life of shallow waters, where fly populations, temperature, and light often determine their occurrence.

Type 4. Bottom-living fish (Figure 5a, b): These interesting forms (*Cobitidae*, *Doradidae*, *Siluridae*, *Mochokidae*, *Callichthyidae*, etc.) show that with the sharp increase in *ad* and its frontal position compared with *av* a sharp dorsal angle is introduced which, in free swimming, demands extensive posteriorly placed sails: in locomotion close to the bottom they seem to follow the principle of a horizontally positioned wedge, using either a minimal degree of lateral compression or dorso-ventral depression to minimize the resistance offered to water. Those tending to dorso-ventral depression also use a large clear dorsal. These fish combine a complex thigmotactic searching of their habitat with a gliding principle of movement. They often receive their adaptational characteristics either from attempts to leave the water to mount muddy banks or from the needs of life in flowing water. A possible typal form for fish living in mountain streams is indicated in the Table.

Hora[43] showed that in fish inhabiting fast flowing waters the lower lobe of the caudal fin is larger than the

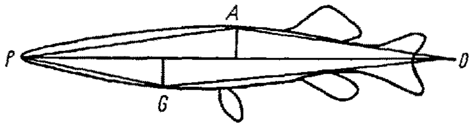

Fig. 3. The pike or predatory type: the centre of gravity is set far back along the body: basically instable, it continuously moves its fins, preserves sensory vigilance and motor readiness.

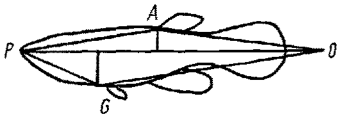

Fig. 4. The surface fish, e.g. *Fundulus dispar dispar*.

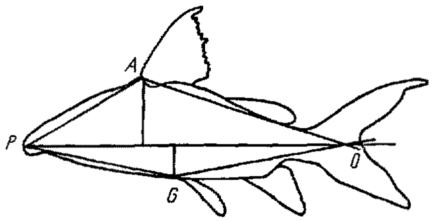

Fig. 5a. *Synodontis clarias* exemplifies the bottom-living fish (the pectorals are omitted for clearer demonstration of the essential relationships).

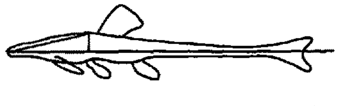

Fig. 5b. *Loricaria microlepidogaster* shows the dorso-ventral compression, and a modification of the bottom-living form due to flowing water.

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[43] S. L. Hora, Philos. Trans. Roy. Soc. (B) *218*, 171 (1930).

dorsal lobe, giving a whip-like character to the tail's stroke, which raises the head; this obviates any difficulties arising from a rough river bed since the fish is automatically raised just above it. HORA also argued that the size of fishes (the *Garra* species) is automatically governed by the rapidity of the current, since at velocities below the critical where the flow is streamlined, resistance is due to velocity, to viscous shear of the adjacent layers of fluid, and, in bodies of similar form, to the length of corresponding dimensions. Recent investigations by LYAGINA and SPANOVSKAYA[44] seem to indicate that changes in size as a function of rapidity of flow are due to a potential of growth available, as it were, to the organism over and above any genetic regulation of size. They found that transfer of roach (*Rutilis rutilis*) and bleak (*Culter alburnus*) from river life to slower water currents resulted in increased body depth and added length of the caudal peduncle and base of the anal fin. The well-known fact that the number of vertebrae vary with the temperature of the water also suggests this marginal potential of growth. Although the rates of change would be much slower, more stable developments between typal forms may have occurred in this way. This argument will be further illustrated in Type 5.

It was also noted by HORA that the resistance of a sphere may be reduced at certain speeds by roughening its surface, since this slows the velocity in the neighbourhood of the body: this would explain the function of dorsal spines and to some extent the large collapsible dorsal, though its median position suggests that it acts as a rudder to angle the body longitudinally in fast currents. It may be seen that *Farlowella* (Figure 6) exhibits all these characteristics, as well as a suction disc under the snout, which is protruding, depressed, yet terminally bent upwards, so that it gains the advantage of depression, which reduces resistance, and at the same time forces the disc to the bottom while the body drags a little due to the upward angling of the end of the snout. In this way this fish seems to combine almost contradictory mechanical virtues.

Type 5. The deep-bodied fish (Figure 7): Where *ad* and *av* range from a quarter to a half of the total body length certain structural problems arise which do not always lead to slow swimming, but do to a certain extent impair stability. Thus, *Beryx*-like fish, according to GREGORY, by attaching the pelvic arch onto the base of the pectoral arch, increase the stability of functioning of these fins (pelvic and pectoral) and add to the lateral caudal sweep without adding to the length. It is clear, however, as HOUSSAY remarked, that as the suppleness of the body in the vertical plane decreases, the ventral fin advances towards the head. This is borne out below. *Balistid*-type anguilliform undulation of the anal and dorsal fins then apparently aids locomotion. The pectorals tend to rise, acting as active stabilizers. Lacking a defined axle propeller and a concomitant dorsal keel, the deep-bodied fish is labile about the vertical axis, as is shown by *Scatophagidae* and *Chaetodontidae* (indicated in Figure 1a). Lateral compression and the tendency of *av* to maintain its comparative length to advance, especially with the shortening of *ad*, both decrease the equivocal state of affairs holding at the centre of the body mass.

In attempting to determine the development of the deep-bodied fish, certain suggestions may be relevant. AMANS noted that the maximal entering area offers initial resistance to water, which then, once this resistance has been overcome, moves more quickly towards the tail. Additionally, certain forms of contour influence speed: thus contours ideal for 7–9 knots become disadvantageous at 16–18 knots. If one also takes into account the notion of OEHMICHEN[45] that lateral undulation achieves the same effect as a revolving screw, so that water moving between the undulations is responsible for acceleration, then the deep body might originate in a fairly short fish of moderate speed which did not rely completely on the above principle for its acceleration. This incomplete application would not merely be due to increasing rigidity with shortening of total length but to the assumption of propulsion by the fins, correctly positioned (aft, for example, in many surface dwellers). These two factors, loss of length with rigidity and a consequent repositioning of fins, would lead to deviation from the rectilinear in movement. Increased vertical depth of the muscular wall would, as shown

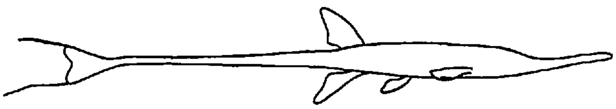

Fig. 6. *Farlowella gracilis* shows a tilted snout with an initial depression. A suction disc is located underneath the head. The large dorsal balances the long body. This combination of factors holds it in a free swimming position in rapid water.

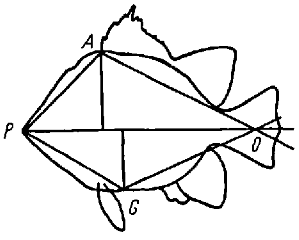

Fig. 7. *Scatophagus tetracanthus:* a deep-bodied unstable form. (The pectorals are omitted.) The entering angle is greater than the posterior angle: the pectoral has moved vertically upwards possibly among other things to correct the central instability.

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[44] T. N. LYAGINA and V. D. SPANOVSKAYA, in *Uchinskoye i Mozhaiskoye vodokhranilislicha* (Mosk. Univ., Moscow 1963), p. 337.

[45] E. OEHMICHEN, in *Traité de Zoologie* (Ed., P.-P. GRASSÉ), vol. 13, 1er fasc., *Agnathes Poissons* (Masson, Paris 1958).

above, add to caudal sweep and correct deviation from the rectilinear, but would not be able to sustain enduring locomotion. This, however, would increase the distance between the centre of gravity and the pectorals, which would consequently rise to act as equilibrators. Thus one would obtain a fish of uncertain balance but accurate rectilinear motion in sudden bursts of speed.

Body form and its relationship to speed of swimming

MAGNAN's work dealt largely with the physical characteristics of fish from the hydrodynamic point of view. Calculations were performed on his data to underline certain conclusions concerned with the subject under discussion. These are presented in Figures 8 and 9.

Based on a sample of 150, Figure 8 reveals that the length of fishes tends to vary in relation to the weight only within a very narrow range, and that only in extremely fast fishes is this range extended in favour of a higher length value (the overall frequency curve for length). If this is compared with the relationship of length to maximum height, it is seen that extremely fast fishes (N = 10) prevent a relative increase in weight by a higher length to height ratio, or at least the two appear to be correlated. The component curves for moderately fast and moderately slow fish may be taken to show that it is a critical decrease in the length to height ratio which accounts for their loss of speed. The curve for very slow fish (N = 45) indicates that it is not the just mentioned ratio which accounts for their speed. This can be best explained by turning to a consideration of the trends shown in Figure 9. The values for the relative surface area of the fins of very fast fish tend to be comparatively low, while they are sited on the body in a relatively posterior position. With loss of speed, complications of the locomotory accessories become increasingly apparent; thus the dorsal and pectoral fins assume a greatly enlarged relative surface area, the dorsal moving forward along the horizontal axis. The ventrals follow a closely parallel path forward, but there appears to be a point at which, owing to the pectorals' enlargement, their surface area is reduced. They now not only act as a ventral keel working with the dorsal, but also acquire the function of controlling the direction of the entering angle. Their exact function is not entirely clear, however, especially as the anal fin becomes enlarged and migrates or extends forward, possibly partly replacing the ventral in operation. At this point the ventrals are sited below the pectorals, which have migrated upward (cf. the intersection of the forward paths of the ventral and pectoral fins along the horizontal axis: this could take place only if the pectorals actually showed this migration). Thus one obtains a radically new configuration of fins, which make for better manoeuvrability of the frontal part of the body, at the same time increasing its stability. In particular, the

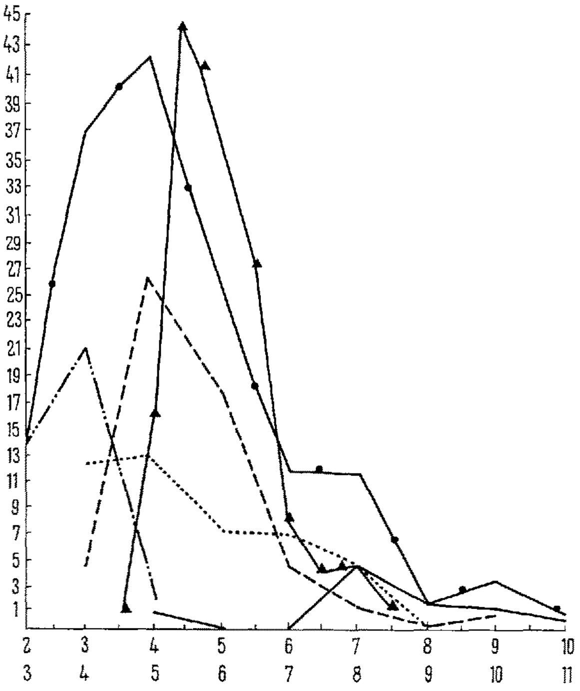

Fig. 8. The frequency curves expressing the relationship between height and length in fish. Key: -·-·-·- medium to slow fish (N = 37). – – – – – medium fast fish (N = 57). —— extremely fast fish (N = 11). · · · · · slow fish (N = 45). ●——● the overall frequency curve for the relation length/maximal height (N = 150). ▲——▲ the overall frequency curve for the function length/$\sqrt[3]{\text{weight}}$ (N = 150).

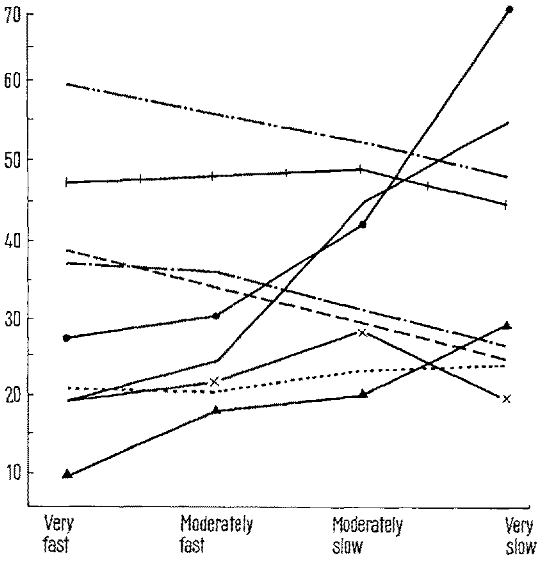

Fig. 9. Relations between the fins of fish classified according to speed (N = 130). ●——● relative surface area of the pectoral fins. —— relative surface area of the dorsal fin. x——x relative surface area of the ventral fins. |——| relative surface area of the caudal fin. ▲——▲ relative surface area of the anal fin. —··—··— relation between distance from snout to the anal fin/length. – – – – – relation between distance from the snout to the ventral fins/length. —·—·— relation between distance from the snout to the dorsal fin/length. ·········· relation between distance from the snout to the pectoral fins/length.

higher situation of the pectorals characterizes a slower type of fish which paddles, inducing habits compatible with a system of orientation different from that of the more agile fish. The simple lined fish tends on the whole not to be concerned with the subtleties of the aquatic environment, while morphological changes and specializations, in so far as they reduce viability, enlarge the value of the particular ambient sphere of the animal, so that it focuses its sensory capacities and its reactions onto more minute and detailed aspects of its environment.

The work of EVANS[46] suggests that the orientation of fishes is governed by the dominant sensory system, and it has been pointed out above that a change in sensory dominance can radically alter fish shape and locomotory potentialities. Clearly, such dominance at the same time ties the organism to particular natural conditions in such a way as to prevent a successful rapid change to other more flexible environmental conditions. This inability is probably connected with the characteristic stereotyped behaviour exhibited in fishes, since, as PRIBRAM points out[47], it is only with multiple sensory control over drives that behaviour becomes capable of flexible sequences, and this is certainly not present at this level. It is possible that the complicated changes such as occur in migration keep open the possibility for the organism to free itself from too close an adaptation. It is also possible that fishes found in extreme conditions actively sought these conditions, looking for a more exacting environment. In fact, the theme throughout seems to indicate that when the organism is not forcedly active, its development is not apparently controlled, so that there appears a spontaneity which creates adaptations[48].

Résumé. Il existe un lien très étroit entre la morphologie des poissons et les capacités sensorielles et motrices de l'organisme, en sorte que les modifications qui apparaissent dans l'une affectent les autres et réciproquement. En outre, les poissons semblent rechercher activements des contrôles dans le milieu même, ce qui permet d'établir une distinction entre des processus adaptatifs guidés par la nécessité et d'autres guidés par le choix. Les premiers sont réduits au minimum par l'action de l'organisme lui-même. Ainsi, à l'équilibre réalisé par la structure extérieure est venu se substituer un équilibre dynamique contrôlé de l'intérieur qui a résulté en la locomotion active orientée. Ce processus a entraîné des changements notables dans la forme du corps. Les formes corporelles des poissons récents qui en sont résultées, montrent que la conquête de cet équilibre actif a dépendu d'un certain nombre de facteurs essentiels. Pour atteindre ce but, les forces erratiques developpées pendant la locomotion ont dû être progressivement asservies à un type de mouvement coordonné à la forme; elles n'ont donc pas simplement été éliminées au titre de déviations par rapport à la position primaire du corps dans le milieu.

Les facteurs en cause semblent être les suivants: (1) La forme et la grandeur de l'angle locomoteur d'impact, et l'aire frontale du corps couverte par celui-ci. Plus simple est cet angle, plus le poisson tend à devenir hydrodynamique. L'aire frontale maximum tend à se concentrer en un point situé à 36% de la longeur totale mesurée à partir de l'extrémité buccale. (2) La position du centre de gravité. Celui-ci se situe également à 36% environ de la longeur totale, et tend à s'établir au centre du plan vertical du poisson. (3) Le centre de pression. Celui-ci est en relation critique avec le centre de gravité, en sorte que le moindre écart par rapport à ce dernier, détermine des gênes locomotrices non-négligeables. (4) La relation entre la longeur et la hauteur maximum. Cette relation semble être une variable importante à prendre en considération lorsque l'on cherche à expliquer la forme des poissons. Notons que la hauteur maximum dépend des facteurs précédemment cités.

Ces facteurs attirent l'attention sur la partie frontale du second tiers de la longeur totale. Celle-ci se situe juste derrière le pivot initial de l'effort dans le type de locomotion carangiforme. C'est également dans ce segment que l'on trouve le caractère principal permettant de distinguer les poissons rapides des poissons lents. De plus, c'est dans ce segment que l'on observe les modifications essentielles dans la configuration des nageoires, non seulement en relation avec la vitesse spécifique, mais aussi avec certains aspects évolutifs importants.

Ces remarques tendent à montrer qu'il est probablement illusoire de prétendre établir une relation simple entre forme et équilibre en ne tenant compte que des nageoires, comme certains auteurs l'ont tenté antérieurement.

En plus des modifications précitées, des altérations notables de la forme doivent être attribuées à des changements dans la dominance sensorielle. Nous avons discuté, entre autres, sous ce rapport, le rôle du passage de la dominance olfactive à la dominance visuelle. De telles dominances sont toujours susceptibles de se modifier en fonction du développement particulier d'une sensibilité parmi d'autres. Les formes typiques de poissons que nous avons décrites mettent en évidence les relations existant entre le comportement, les aspects de l'habitat et les potentialités structurales des poissons. Ces formes typiques peuvent en outre être analysées à partir du paradigme proposé par GREGORY, et il est possible de montrer, de cette manière, comment les

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[46] H. M. EVANS, *The Brain and Body of Fish* (Technical Press, London 1940).

[47] K. H. PRIBRAM, in *Evolution and Behavior* (Ed., G. G. SIMPSON; Yale Univ., Newhaven 1958).

[48] Acknowledgment: The author is indebted to Professor Dr. G. THINÈS for his help and encouragement in the preparation of this paper.

diverses voies d'adaptation exploitent au mieux les possibilités offertes par l'environnement.

Enfin, l'analyse des relations entre la vitesse de nage et la forme du corps nous a amené à conclure que les poissons rapides étaient les moins spécialisés au point de vue mécanique, tandis que les poissons lents révèlent, selon leur type, des complications diverses, probablement en lien avec leur milieu, mais certainement pas avec la vitesse considérée isolément.

Nous suggérons, en manière de conclusion, que les poissons se fixent dans certaines conditions de milieu qu'ils cherchent à exploiter par leur développement même, sans toutefois que celui-ci puisse mener à la suradaptation.

Brèves communications – Kurze Mitteilungen – Brevi comunicazioni – Brief Reports

Mast Cells, Tryptophan and 5-Hydroxytryptamine in Precancerous Mouse Skin

It has previously been shown that the golden-brown fluorescence of the numerous mast cells in precancerous mouse skin, fixed in formaldehyde, is due to their high content of 5-hydroxytryptamine (5-HT)[1-3]. It was thus of interest to look for precursors of 5-HT in such material.

40 young female white mice were divided into 2 groups. Half were painted twice, nape to tail, 7 days apart with a carcinogen, 0.5% 9,10-dimethyl-1,2-benzanthracene (DMBA) in acetone. The remainder were painted with 5% ethylphenylpropiolate (EPP) in acetone, which causes epilation and epidermal hyperplasia, but is neither carcinogenic nor co-carcinogenic for mouse skin[4,5]. EPP was applied twice a week for the first month, three times a week for the second month and on alternate days for the third month, by which time the EPP mice had acquired a patch of epilation and epidermal hyperplasia grossly resembling that of the DMBA series. Papillomas in the DMBA mice were excised, and the remaining treated areas of both groups were subjected to histological and chromatographic examination.

Paraffin sections from skin fixed in 10% formaldehyde, or fresh frozen sections cut on a cryostat and fixed overnight in formaldehyde vapour, were first examined for fluorescence in UVL (Leitz Panphot) and then stained with toluidine blue at pH 3 for mast cells. This showed that initial painting with DMBA, or continuous treatment with EPP, both produce epidermal hyperplasia and a mast cell reaction. Following fixation in formaldehyde, the mast cells in both groups fluoresced golden-brown (maximal under a papilloma) and the hyperplastic epidermis showed a deep blue, alkali-resistant fluorescence. The small new mast cells in precancerous skin develop *immediately* under the hyperplastic epidermis: in EPP skin they lie at a deeper level.

The substances responsible for the two types of fluorescence were identified by paper chromatography. Epidermis and dermis were separated either by stretching and scraping or by immersion in alkaline trypsin at 4°C[6]. Pooled epidermis, dermis and the excised papillomas, were extracted twice with acetone and the residues re-extracted with $0.01\,N$ HCl. Ascending chromatograms were run in isopropanol, ammonia, water (20:1:2 by volume), with tryptamine (T), tryptophan (TP), 5-hydroxytryptophan (5-HTP) and 5-HT as reference markers. Spraying with formaldehyde and heating the papers revealed that 5-HT was present only in the acetone extract of papillomas (Rf = 0.63, blue colour with *p*-dimethylaminocinnamaldehyde, golden brown fluorescence with formaldehyde). The separated epidermis of both groups contained TP (Rf = 0.16, violet colour with *p*-dimethylaminocinnamaldehyde, blue fluorescence resistant to spraying with alkali). Only a trace of TP was present in any specimen of dermis.

It has recently been shown that neoplastic mast cells in the mouse can convert TP into 5-HT via the intermediate, 5-HTP[7,8]. It would thus appear that the high content of 5-HT in the mast cells of both groups is derived from TP in the overlying, hyperplastic epidermis[9].

Zusammenfassung. Nach Formaldehydfixation und Vorbehandlung mit dem Carcinogen DMBA oder Äthylphenylpropiolat (das nicht cancerogen oder co-cancerogen wirkt) wird in der Epidermis der Maus eine Tryptophan-bedingte blaue Fluoreszenz gefunden. Die gelbe Fluoreszenz in den Mastzellen beruht auf 5-HT.

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[5] Our thanks are due to Dr. F. L. ROSE for the sample of EPP.

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[8] W. LOVENBERG, R. J. LEVINE, and A. SJOERDSMA, Biochem. Pharmacol. *14*, 887 (1965).

[9] This research programme has been supported by a grant from the Scottish Hospital Endowments Research Trust.