THE FUNCTIONAL SIGNIFICANCE OF THE HYPOCERCAL TAIL IN *PTERASPIS ROSTRATA*

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(With Five Text-figures)

It is now many years since Kiaer (1924) demonstrated the existence of the hypocercal tail in the Anaspida, and subsequently it has been found to be universally present in the Heterostraci (Stetson, 1931; Kiaer, 1932; White, 1935). No experimental attempt seems to have been made, however, to investigate its functional significance (see Harris, 1936), although it has been realized for a considerable time that the hypocercal tail would tend to depress the hinder end of the body during swimming (Ahlborn, 1896; Grove & Newell, 1936). An attempt is made in this paper to determine, by experimental methods, this functional significance.

For this purpose experiments were performed upon a scale model of the animal in the wind tunnel of the Cambridge Zoological Laboratory.

The model was constructed from copies, in the Zoological Laboratory, Cambridge, of White's drawings of the type of *Pteraspis rostrata* var. *Toombsi* (White). The drawings were enlarged photographically to the required size, and the model carved out of wood, the surface details being put in afterwards with 'plastic wood'. The finished model was painted with cellulose lacquer to give the requisite smooth finish, and any slight surface irregularities faired with plasticine. The model was of an overall length of 30 in., this being the most convenient size for the wind tunnel available. The balance system employed required a three-point suspension. The main balance frame was fastened to a 15 in. steel rod passing through the anterior end of the model, the moment balance wire being attached to a brass cleat 12 in. behind the rod.

The experimental technique of the wind tunnel may be found in any standard text-book on aerodynamics, and will not be dealt with here.

The balance system resolves the resultant force produced by the air stream on the model into two component forces: the lift (*L*) and the drag (*D*), acting respectively vertically to and tangentially to the air stream. The *X* axis is taken as the longitudinal axis of the wind tunnel, the positive direction being along the air stream. The *Y* axis is horizontal and normal to the *X* axis. The *Z* axis is vertical and normal to the *X* axis, the positive direction being upwards. The lateral force component acting parallel to the *X* axis is not dealt with in the present paper. The origin (*O*) of the axes is placed at the centre of gravity of the model. Rotation of the model about the *X*, *Y* and *Z* axes constitutes respectively rolling, pitching and yawing, the direction of positive roll, pitch and yaw being indicated by the arrows in the quadrants of the diagram. The angle between the projection on the *X*, *Z* plane of the longitudinal axis of the model and the *X* axis is known as the angle of pitch (*a*). In the experimental work only the forces and moments due to static changes in this angle were measured.

The model was tested at air speeds of 26.5, 36.7, and 50.6 ft./sec., the corresponding Reynolds'
numbers being $4.16 \times 10^4$, $5.75 \times 10^4$ and $7.96 \times 10^4$. The drag, lift and the pitching moment of the model were determined at the above values at angles of pitch (taken from an arbitrary point) of from $-20$ to $+17\degree$. The results are recorded as the drag, lift and moment coefficients, in accordance with usual aeronautical practice:

$$C_L = \frac{2L}{\rho A v^2},$$

where $\rho =$ fluid density, $v =$ relative fluid velocity, $A =$ maximum cross-sectional area, $L =$ lift—similar expressions apply for the drag and moment coefficients.

It should be noted that any observation made in the wind tunnel is only applicable to aquatic conditions if the Reynolds' number be the same in both cases. Unfortunately, as will be seen later, it has been found necessary to make calculations for the $Pteraspis$ in water at considerably lower Reynolds' numbers than those obtained in the experiments on the model. This was unavoidable, the length of the model (30 in.) being more or less fixed by the requirements of the balance system. The minimum steady air speed of the tunnel was about 26 ft./sec., and it was therefore impracticable to obtain results for Reynolds' numbers lower than about $4 \times 10^5$. It is necessary to assume that the divergence between the living fish in water and the model in air is small enough to render the results comparable.

The volume of the model was determined by measuring its liquid displacement and found to be $0.1114$ cu. ft. The maximum cross-sectional area was found from the working drawings to be $0.15$ sq. ft. Since the length of the actual $Pteraspis$ was $7.7$ in., and the length of the model 30 in., the corresponding values of volume and area may be found by the application of the appropriate scale factors.

**DISCUSSION OF EXPERIMENTAL RESULTS**

It appears that all craniates which are both primitively aquatic and lack a swim bladder, are denser than the water in which they live. The exceptions to this rule are highly specialized forms such as $Scambert$, which have developed large masses of oil that give buoyancy. Nearly all tissues have a specific gravity greater than unity, and the existence of a bony skeleton still further increases the density of the animal. $Pteraspis$, lacking a swim bladder, and having a heavy exoskeleton of bony scales and plates, must have been denser than the water in which it lived. This means that there would be a downward force ($W$) acting on the animal through its centre of gravity, such that

$$W = \rho V (\sigma - \rho),$$

where $W =$ downward force due to the weight of $Pteraspis$ in water, $V =$ the volume of the animal, $\sigma =$ its average density, $\rho =$ the density of the medium in which it lived, $g =$ $32.2$.

The work of Magnan (1929) suggests that it is very rare for the specific gravity of any living fish to exceed 1.1 with respect to the medium in which it lives, and this value will be assumed for $Pteraspis$. Substituting in equation (2):

$$W = \rho V \frac{\sigma}{10}.$$  

For $Pteraspis$ to be able to rise from the bottom and swim freely in the water, an upward force (lift), numerically equal to $W$ plus the downward component of thrust ($\xi$) due to the hypocercal tail, would be required. This lift could only have been generated by the forward motion of the animal through the water. Since $Pteraspis$ lacked paired fins this involved the inclination of the whole body of the animal to a positive angle of pitch, enabling it to function as a hydrofoil.

When the lift ($L$) equaled the downwardly acting forces, steady swimming at any given level would become possible. Putting this into the form of an equation:

$$L = W + \xi,$$  

where $\xi$ is unknown. In the case of the dogfish (see Harris, 1936), taking into account the relative positions of the tail, pectoral fins, and the centre of gravity, it seems that to give equilibrium the lift due to the action of the heterocercal tail must be something like a quarter or a fifth of that due to the pectoral fins. The heterocercal tail of the Selachii and the hypocercal tail of $Pteraspis$ being to some extent comparable, $\xi$ will be assumed for this calculation to have the value $\frac{1}{4}W$.

Substituting these values in equation (4) gives

$$L = g V \frac{\sigma}{8},$$  

and substituting for $L$ in equation (1) gives

$$v = \sqrt{\frac{g V}{4AC_L}},$$

With the data obtained, the value of $v$ can be obtained for any given value of $a$. This is shown in the form of a graph in Fig. 5, where the angle of pitch $\alpha$ is measured relative to the zero lift position.

In calculating $v$ the values used for $C_L$ are those obtained at the lowest Reynolds' number ($4.16 \times 10^4$). From this graph it can be seen that both small positive values of $a$ and low speeds would suffice to give the required lift.

Since solution of equation (6) gives reasonable values of $v$ and $a$, this is strong evidence for the view put forward here that in $Pteraspis$ the lift necessary for free swimming was produced by the inclination of the whole animal to a positive angle of pitch.

This method of obtaining lift was rather inefficient, since, as may easily be verified from Figs. 2 and 3, the $CL/CD$ ratio, which is a measure of the
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Fig. 2. Drag coefficient of model.

Fig. 3. Lift coefficient of model.

Fig. 4. Moment coefficient of model.
efficiency, never exceeds a value of 1.8 in *Pteraspis*. From the results of Harris (1936) it appears that in the case of *Mustelus canis* a maximum $CL/CD$ ratio of about 4 was obtained.

To enable the animal to incline its body to the required positive angles of pitch, some mechanism must have existed which could apply a positive pitching moment, since under certain conditions, e.g. when feeding on the bottom, *Pteraspis* would have been at a negative angle of pitch. Such a positive pitching moment was produced by the downward force due to the tail. Thus the tail must have been responsible for initially raising the head from a horizontal or downwardly inclined position.

Since the presence of the hypocercal tail appears always to be associated with the absence of paired fins, the above hypothesis would apply to all Ostracoderms with that form of tail.

While the animal was swimming in the manner indicated, the pitching moments about the centre of buoyancy would be: the positive pitching moment due to the forward motion of the animal through the water (Fig. 4);* the positive pitching moment due to the action of the hypocercal tail, and the moment due to the force $W$ acting through the centre of gravity.

For *Pteraspis* to be in pitching equilibrium, the force $W$ should act ahead of the centre of buoyancy, and should produce a negative pitching moment equal in magnitude to the sum of the positive pitching moments specified. The forward position of the centre of gravity which this would entail is suggested, in any case, by the heavily armoured nature of the head region of *Pteraspis*.

Assuming the values of the forces to be as estimated above, it seems that for this mechanism to be effective the centre of gravity in the actual animal would need to be some 0.5 in. ahead of the centre of buoyancy. Such estimates are, of necessity, very approximate; but the value obtained seems not unreasonable.

The mechanism suggested above is essentially similar to that outlined by Harris (1936) for the swimming equilibrium of the closely related Anaspida. He suggested 'that these animals were surface swimmers, and not bottom living, as were almost all of their relatives. If this were so, and the front end of the body were to be just "awash" when swimming, the extra weight of this region out of water might compensate by a negative pitching moment for the positive moment produced by the reversed heterocercal tail.' While this may well have been true of the Anaspida, which do not appear to possess a heavy head shield and have a terminal mouth, it can scarcely apply to *Pteraspis* whose ventrally placed mouth and general shape indicate a bottom-living form (White, 1935).

**SUMMARY**

1. An attempt has been made to determine the functional significance of the hypocercal tail in the swimming of one of those Ostracoderms which possessed it, *Pteraspis rostrata*.
2. Since *Pteraspis* was almost certainly denser than the medium in which it lived, a dynamic upthrust (lift) would have to be generated by forward motion. It is suggested that this lift was obtained by an inclination of the whole body of the animal to act as a lifting plane during forward movement.
3. The hypocercal tail would depress the hinder end of the body, so giving rise to the required inclination. This, it is suggested, was its functional significance in *Pteraspis*.
4. The above would apply to all those Ostracoderms (Anaspida and Heterostraci) with the hypocercal form of tail.

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REFERENCES


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