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C. S. Sherrington

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STRUCTURE AND FUNCTIONS OF THE EAR OF THE SQUETEAGUE

By G. H. Parker, Ph. D.
Professor of Zoology, Harvard University

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STRUCTURE AND FUNCTIONS OF THE EAR OF THE SQUETEAGUE.

By G. H. PARKER, Ph. D.,
Professor of Zoology, Harvard University.

INTRODUCTION.

Although fishes have no external ears, they have long been known to possess internal ears which in complexity of structure often approach even those of the higher vertebrates. It is therefore natural to expect that the functions ascribed to the internal ears of birds, mammals, etc., would be found in one form or another among the fishes. These functions are chiefly three—first, hearing, which is historically the earliest function to be ascribed to the internal ear; second, an influence on bodily equilibrium both when the body is at rest and when it is in motion, a view founded upon the experimental investigations of Flourens (1828); and, third, an influence on tonus or strength of contraction of the skeletal muscles, as demonstrated first by Ewald (1892).

The ear of the squeteague (*Cynoscion regalis*) is a well-developed organ and shows in a striking way all the essential parts of the ears in fishes. The male squeteague, moreover, is well known to produce sounds through a special mechanism not possessed by the female (Tower, 1908). Because of these structural conditions and of the highly specialized habit of sound production in these fishes, I was led to make an investigation of their ears. The only objection to this species for such study is its lack of vitality. It can not be kept many days in confinement, even in large fish boxes in the open sea, and it is not resistant to the effects of operations. Nevertheless, the exceptionally favorable conditions at the Woods Hole Laboratory of the Bureau of Fisheries made it possible to overcome these obstacles sufficiently to carry out the proposed work.

ANATOMY OF THE EAR.

The internal ears of the squeteague are relatively large organs and are lodged in the lateral walls of the posterior part of the skull. In a dry preparation of the skull their position is indicated on the ventral side by two smooth elongated bony capsules (fig. 4, pl. CXXII), whose posterior ends lie close together near the occipital condyle and whose anterior ends diverge as they approximate the regions of the orbits. These capsules form a part of the bony roof of the mouth and are separated from this cavity by only a thin covering of mucous membrane. In an adult fish the capsules are nearly an inch and a half (3.5 cm.) in length and their longitudinal axes diverge from each other anteriorly at an angle of a little over 40°. The internal ears lie partly in these capsules and partly in the bony wall of the skull dorsal to the capsule (fig. 2). Each ear consists of a sacculus with its appended lagena, and a utriculus and its semicircular canals.

The sacculus is an elongated, thin-walled structure which lies in the cavity of the bony capsule. It has the shape of a long flattened bean, and measures in an adult fish a little over 1¼ inches (3.5 cm.) in length by almost ½ inch (1.1 cm.) in width. The walls of the sacculus are very thin and conform closely to the shape of the inner surface of the bony capsule, to which they seem to be molded. Much of the median wall of the sacculus is occupied by a large sensory patch, the macula acustica sacculi, which receives the most considerable branch of the eighth nerve. This patch is in the form of an elongated band of moderate width extending lengthwise of the sacculus; its anterior end spreads out into a very considerable oval area; its posterior end is marked by a smaller expansion. The lateral wall of the sacculus is smooth and without special nerve terminals.

Each sacculus contains a large ear stone or otolith, the sagitta (1, 2, 3, pl. CXXII), to use the term employed by Webb (1905), which almost completely fills its cavity. In full-grown squeteagues these otoliths are conspicuous structures; they may measure 1¼ inches (3.2 cm.) in length by ⅜ inch (1 cm.) in width. Their dry weight may exceed 25 grains (1.7 gm.). They are white and hard and, excepting for a small organic residue, dissolve completely with effervescence in dilute acetic acid. They are chiefly carbonate of lime, and their specific gravity, 2.84, is between those of the minerals calcite and aragonite. Their concentric structure favors the belief that they are secretions from the sacculus. Their lateral faces are irregularly concave (fig. 1, C–F, pl. CXXII) with a dorsal blade-like edge and a ventral blunt one. Posteriorly they are roughly pointed; anteriorly they are flattened out into an almost spatula-like ending. Their median faces (fig. 1, A–B) are relatively smooth with a slightly depressed figure on them corresponding to the form of the macula acustica sacculi, against which they are well adapted for resting lightly.

At the posterior end of the sacculus is a small triangular pocket, the lagena, which contains a flattened otolith, the asteriscus, and a single sensory patch, the papilla acustica lagenæ, to which a branch of the eighth nerve is distributed.

Although the sacculus communicates freely with the lagena, it does not connect with the utriculus. A careful search in fresh and in well-preserved material for a communication between these two parts failed to reveal the least trace of such a structure. This condition has been reported already by Retzius (1881, p. 215) for 20 of the 33 species of teleosts that he studied. Among these there were 15 that belonged to the same order as the squeteague, the Acanthopteri, and in only 1 of these 15, *Gasterosteus*, was the sacculus found to communicate with the utriculus. In this respect, then, the squeteague is like the great majority of the acanthopterous fishes thus far examined.

The utriculus is a slender sac which lies dorsal to the sacculus and is of about half the length of that structure. From near its middle a large duct, the sinus superior, extends dorsally, and from the upper end of this sinus pass off the anterior and the posterior semicircular canals. Each canal bends ventrally and after enlarging into an ampulla, connects with an end of the utriculus. Close to the region at which the ampulla of the posterior canal unites with the utriculus, the horizontal canal arises and, after a semicircular course, it enlarges to form an ampulla and then unites with the utriculus near the place where the ampulla of the anterior canal joins that organ. In the utriculus close to its anterior end is a sensory patch, the macula acustica recessus utriculi, over which a small otolith, the lapillus, is found. Each of the three ampullæ of the semicircular canals contains a sensory patch, the crista acustica, but these are unprovided with otoliths. No macula neglecta could be found. Unlike the sacculus and the lagena, which are mostly surrounded by bone, the utriculus and the semicircular canals lie for the most part in the loose tissue between the brain and the wall of the skull. The horizontal canal and the posterior vertical canal are in part surrounded by bone, but the anterior vertical canal merely rests against the bone that forms the inner surface of the skull.

It is thus clear that the ear of the squeteague is not a single sense organ, but two organs structurally distinct—what may be called the saccular organ including the sacculus with its outgrowth, the lagena, and its two sensory patches and two otoliths, and the utricular organ including the utriculus and its three semicircular canals, with four sensory patches and one otolith.

FUNCTIONS OF THE EAR.

As was stated at the outset, three chief functions have been ascribed to the vertebrate ear. The sense of hearing has long been associated with the cochlea and adjacent parts of the internal ear, and recent discoveries confirm this view. The bodily equilibrium of vertebrates was shown by Flourens (1828) to be seriously interfered with on cutting the semicircular canals, and though there has been opposition to this view, the work of Mach (1874a, 1874b), Breuer (1874), and many recent investigators has added much in support of it. Finally, Ewald (1892) has pointed out, in a most elaborate study, that the internal ear exerts an influence on the tonus of skeletal muscles—i. e., the vigor of an animal's movements is largely dependent upon the integrity of this sense organ.

Since the ear of the squeteague is really double, in that the saccular and utricular organs are anatomically separate, and since these organs are large and fairly accessible, it seemed reasonable to expect that experiments upon them might be devised which would lead to a more definite knowledge as to the localization of function in these parts.

UTRICULAR ORGAN.

After some practice on the heads of dead squeteagues it was found possible to destroy the utriculus and semicircular canals of live fishes by cutting them with a long, narrow knife blade inserted through a small incision on each side of the head, and yet to leave the sacculus and its appended parts uninjured. This operation could be performed without serious bleeding and without injury to the brain. The slight opening thus made through the skin and subcutaneous parts closed of itself, and even after the death of the fish it showed no tendency to gap open. It was expected that these operations would be followed by a loss of equilibrium, but it was soon clear that the squeteague could still keep its upright position. Since this fish, like many others, is in unstable equilibrium (Monoyer, 1866) when in its so-called resting posture, I suspected that the retention of its upright position after the loss of the utricular organ was dependent upon the eyes, and to eliminate the action of these sense organs a set of blinders was devised. These were attached to the head of the squeteague by means of a cord harness. A single loop of cord was tied snugly round the body of the fish just posterior to the pelvic fins, and from the point at which this loop crossed the dorsal line a cord was run over the median dorsal line of the head to the large premaxillary teeth, where it was made fast. To this median dorsal cord were attached two cloth flaps that could be turned down over the eyes and held there by a cord, passed from one flap to the other under the jaws. In this way the eyes could be covered without interfering with the freedom of movement of the mouth and gills, for unless these parts are entirely free the animal is extremely restive and may even lose its balance.

Five sets of four fishes each were tested for the effects of destroying the utriculus and the semicircular canals. Before operating upon the fishes each was tried to see that it responded to sound vibrations and that it swam normally with the eyes covered. In testing the reactions to sound, the fish was placed in a large wooden tank of sea water, and after it had become quiet the side of the tank was tapped once or twice with a mallet in such a way that the fish could not see the movements. At each tap the fish almost invariably made a slight spring forward. To test the relation of the eyes to equilibrium, the harness was put on the fish and the eyes covered by the blinders. The majority of fishes immediately swam away slowly, though in normal equilibrium, but a few lost orientation and would even rest on their sides on the bottom of the aquarium. In only such fishes as responded to the tapping and swam upright after the blinders had been put on them were the utriculus and the semicircular canals destroyed. The following records from one of the five sets of fishes tested will give a fair idea of the results of these experiments:

Fish No. 1 was operated upon for the destruction of the right and left utriculi and the semicircular canals. After the operation the fish swam irregularly, often revolving on its long axis. It died about three hours after the operation. Dissection showed extensive hemorrhages within the cranium.

Fish No. 2 was subjected to the same operation as No. 1. After the operation the fish swam irregularly for about half an hour. It then reassumed normal equilibrium both in resting and in swimming. Five hours after the operation it still swam normally. The blinders were then put on it and it lost equilibrium and swam in irregular spirals, but it regained its equilibrium as soon as the blinders were removed. This test was repeated several times during the next few hours and always with the same results. During this period the fish was also placed several times in the wooden aquarium; it always responded normally to the taps of the mallet on the aquarium wall. At all times after the operation the locomotor movements of the fish were weaker than they had been before the utriculus was destroyed, a condition that made it much easier to catch the fish in a hand net after the operation than before it. The fish retained its power of orientation till about the time of its death, thirty-two hours after the operation. On dissection the utriculi and semicircular canals were found to be cut through in many places, but the sacculi and brain were intact.

Fish No. 3 was subjected to the same operation as No. 1. The fish swam irregularly and rested in unusual positions; it never regained its equilibrium. It died in about twenty hours after the operation. A post-mortem examination showed that the medulla had been partly cut.

Fish No. 4 was subjected to the same operation as No. 1. The fish at first swam irregularly, but twenty minutes after the operation it had regained its equilibrium. In its response to tapping, its method of swimming when blinded, and in its muscular weakness it resembled No. 2. It lived for about two days after the operation. On examination, its utriculi and semicircular canals were found much cut to pieces, but the sacculi and brain had not been injured.

Of the total of twenty fishes in which the utriculi and semicircular canals had been destroyed, 11 through early death or other unfavorable conditions proved to be useless for experimentation. The remaining 9 reacted much the same as No. 2 and No. 4 in the set just described. In all 9, so far as I could judge, the animals were as sensitive after the operation as before it to the noise produced by tapping on the side of the aquarium. Immediately after the operation all swam with disturbed equilibrium, but within an hour, and often in even less time, they reassumed their equilibrium. This was persistently retained up to about the time of death, except when their eyes were temporarily covered. With the blinders on, they invariably swam irregularly. All 9 fishes after the operation were noticeably weaker in their responses than before it. Most of these fishes lived only a few days and only one lived for as long as five days after the operation.

These observations show that the utriculus and the semicircular canals of the squeteague are not essential for the responses of these animals to sounds. They show also that though these organs are concerned with equilibrium, they share this function with the eye, for it is only after both sets of sense organs have been rendered ineffective that permanent disturbances in equilibrium occur.

There is, however, no reason to assume that in this relation the utriculus and its canals stand second to the eye. They are certainly of prime importance as sense organs in which impulses originate for the reflexes of equilibrium. In this respect my results fully confirm those of Loeb (1891a, 1891b), Ewald (1891, 1907), Kreidl (1892), Lee (1892, 1893, 1894, 1898), Bethe (1894, 1899), Gaglio (1902), Quix (1903), and Fröhlich (1904b) on various fishes. They also agree with those of Tomaszewicz (1877), Kiesselbach (1882), Sewell (1884), and Steiner (1886, 1888) in that they make evident that the destruction of the utriculus and the semicircular canals is not necessarily followed by permanent disturbances in equilibrium. Had these investigators, however, taken steps to eliminate the influence of the eyes of the fishes on which they worked, it is probable that they would have found these animals incapable of retaining their equilibrium. I therefore can not agree with their conclusion, briefly put by Ayers (1892), that the ear has nothing to do with equilibrium. The utriculus and the semicircular canals of the squeteague are one or both certainly concerned with this function, and this conclusion probably holds good for other fishes, but whether the sense organs involved are the cristæ acusticæ of the semcircular canals or the macula acustica recessus utriculi with its otolith, or both, I can not say. These parts are also concerned with muscular tonus, as is seen by the weakness of the fish after their destruction, a condition already observed by Ewald (1891, p. 5; 1907, p. 191) for *Anguilla* and by Bethe (1894, p. 575) for *Perca* and *Sardinius*.

SACCULAR ORGAN.

The sacculus and lagena each contain sensory patches, i. e., on the median face of the sacculus is the very large macula acustica sacculi, and on the corresponding side of the lagena the much smaller papilla acustica lagenæ. The sacculus, as already mentioned, contains a very large otolith, the sagitta, which rests on the macula acustica sacculi, and the lagena contains a much smaller one, the asteriscus, which covers the papilla acustica lagenæ. For experimental purposes the sacculus is scarcely accessible from the dorsal or lateral aspects of the head, but it is so near the roof of the mouth that I determined to approach it from that side. As already stated, it is separated from the mouth by only a thin layer of bone and mucous membrane. It was not difficult to hold the mouth of a squeteague open and, by means of long bone forceps, to cut through this thin wall and thus gain access to the sacculus, but this operation was attended with so much loss of blood that it was finally abandoned.

Since the lateral wall of the sacculus is essentially nonnervous, it occurred to me that I might force the sagitta off the sensory patch on which it rested and against the nonnervous lateral wall by driving a pin in an appropriate direction through the thin roof of the mouth. A little practice on the heads of dead fishes showed that this could be accomplished with comparative ease. The pins used were long steel hat pins about 8 inches (20 cm.) in length. These could be easily manipulated in the open mouth of the fish, and after they had been forced into place against the sagittæ they could be cut off short next the roof of the mouth. Apparently they offered no obstacle to the breathing and other mouth movements of the fish. Squeteagues that had thus been operated upon lived about as long as normal squeteagues do in confinement. Of 10 fishes in which it was attempted to pin off the otoliths in this manner, 7 survived for nearly a week and were used in the following experiments. The 3 others died during the experiments, and hence their records were omitted as incomplete. In all 10 cases, final dissection showed that the otoliths had been pinned against the nonnervous side of the sacculus as was intended. The tests carried out on the 7 vigorous fishes gave very uniform results.

Before the otoliths were pinned down, each squeteague was tested with the blinders for equilibrium and in the wooden aquarium for responses to sound. After pinning down the otoliths the fishes swam at first irregularly, but in ten minutes at most they regained their equilibrium, and they retained this even when the blinders were put on them. After the immediate effects of the operation of pinning down the otoliths had disappeared, the equilibrium of these fishes was indistinguishable from that of normal fishes. The vigor of their movements was likewise unimpaired by this operation. After it they were about as difficult to catch with a hand net as before it. On testing them with sound stimuli they were found to be only slightly responsive as compared with their former condition. Thus a fish that before the pinning of the sagittæ had responded to every tap of the mallet on the wooden wall of the aquarium, reacted to only 3 in 30 taps after the sagittæ were anchored laterally. This considerable reduction in reactiveness was also noticed in the other 6 fishes. When, moreover, a squeteague with the otoliths pinned down was placed in the aquarium with a normal fish and the wall of the aquarium was tapped, it was quite easy to determine from the movements of the 2 fishes which was the normal one, for the normal fish almost invariably responded by a slight leap forward to every tap, while the other fish only very rarely reacted. The same was true when normal *Fundulus heteroclitus* were put in the aquarium and compared with squeteagues whose ear-stones had been pinned. I therefore believe that the larger otolith of the sacculus, the sagitta, is concerned with the squeteague's sensitiveness to sound, and further, for reasons already given, that it has nothing to do with equilibrium or with muscle tonus.

These conclusions are in accord with the observations of several other investigators. Thus, so far as hearing is concerned, Smith (1905) has pointed out that in all sciænid fishes which drum, as the squeteague does, the sagittæ are very large, but in *Menticirrhus*, which does not drum, these otoliths are relatively small. Hence, the size of the otolith seems to be related to the drumming habit, as might be expected if the otoliths are concerned with hearing. Further, Piper (1906a) has demonstrated that a negative variation is observable in the eighth nerve of *Esox* when that portion of the ear of *Esox* which contains the otoliths is subjected to sound vibrations. From the standpoint of equilibrium Laudenbach (1899) has already shown that the removal of the otoliths from the ears of *Siredon* and the frog has no effect on the subsequent success of these animals in keeping themselves upright, a state of affairs in agreement with my experience in pinning down the otoliths in the squeteague. These observations therefore confirm me in the belief that the sagitta of the fish's ear is in some essential way concerned with the responses of these animals to sounds, as surmised by Scott (1906), and has nothing to do with equilibrium or muscle tonus. So far as equilibrium is concerned this conclusion is rather the reverse of what would be anticipated, for in the invertebrates, at least, the otoliths have been clearly shown to be concerned with equilibrium, and this function has been definitely ascribed by Breuer (1891), Sherrington (1906), and others to these bodies in the vertebrates; but this opinion is not supported by my observations.

The sagittæ in the ears of vertebrates are certainly not merely tolerated foreign bodies, as Ayers (1892, p. 309) has maintained, but, as has just been pointed out, they are of real functional significance. How they act in the reception of sound is not known with certainty; but since in the squeteague they have a specific gravity of 2.84 and that of the whole head is about 1.8, it is quite probable that when sound vibrations influence the normal fish they induce the relatively lighter parts of the head, including the macula acustica sacculi, to vibrate against the relatively heavier otolith; in other words, the otolith is a relatively stable body against which the auditory hairs of the macula acustica sacculi may strike. In my opinion sound stimulates the auditory hairs in some such mechanical way as this.

That the sagitta and its underlying sensory patch is not the only sound-receptive mechanism in the squeteague may be inferred from the fact that after both sagittæ are pinned down the squeteague will still respond occasionally to sound, but whether this response is through the sensory patch in the lagena or even in the utriculus, or through the skin, can not be stated. That it is from an organ far inferior to that in the sacculus is plain from its character, and hence, though there may be other parts of the body of the squeteague than the macula acustica sacculi that are sensitive to sound, this structure is certainly the chief organ in this respect.

It also seems fair to me to class the reactions of the squeteague to sound, when these reactions are mediated by the ear, under the head of hearing. While no sharp line can be drawn between touch and hearing, it seems to me that when any vertebrate can be shown to possess an ear which is stimulated by the vibrations of material particles it is fair to ascribe hearing to such an animal, and, for reasons already given, I believe this to be the case in the squeteague. I therefore reaffirm my former statement that certain fishes can hear, a statement that was based originally upon the conditions found by me in *Fundulus heteroclitus* (Parker, 1903a, 1903b) and confirmed in certain respects in other fishes by Zenneck (1903) and in the goldfish by Bigelow (1904). It does not seem to me that the very inadequate tests by Körner (1905) on some 25 fishes, with negative results so far as hearing was concerned, as well as the similar results of Lafite-Dupont (1907) can have great weight against positive results such as have already been obtained by other investigators, for it is comparatively easy in certain tests to find animals irresponsive to sounds by which they are certainly stimulated as shown by other methods (Yerkes, 1905). From the observations given in this section, I conclude that in the squeteague the sacculus with its contained sagitta is the chief organ of hearing and that these parts have nothing to do with equilibrium or muscle tonus. Although I agree with Hensen (1904) in ascribing hearing to fishes, I believe, for reasons already given, that the ears of these animals are also directly concerned with equilibrium.

SUMMARY.

1. The ear of the squeteague (*Cynoscion regalis*) is anatomically double in that it consists of (1) a utricular organ with its semicircular canals and (2) a saccular organ with its lagena. There is no utriculo-saccular canal.

2. The utriculus possesses a macula acustica recessus utriculi covered by an otolith, the lapillus, but no macula neglecta. Each of the three semicircular canals has a crista acustica without an otolith.

3. The sacculus possesses a macula acustica sacculi covered by a large otolith, the sagitta, and the lagena has a papilla acustica lagenæ covered by a small otolith, the asteriscus.

4. Squeteagues whose eyes have been covered with blinders usually swim with normal equilibrium. Squeteagues whose utriculi and semicircular canals

have been destroyed soon recover normal equilibrium. When the utriculi and semicircular canals are destroyed and the eyes are covered, the squeteagues swim with great irregularity and have all the appearances of having lost their equilibrium completely. Such fishes show marked muscular weakness, but respond to sounds as do normal individuals.

5. Squeteagues whose sagittæ have been pinned down against the non-nervous sides of their sacculi retain normal equilibrium and show no diminution of muscular strength, but they respond to sound to a slight degree only.

6. The utricular organ has to do with equilibrium and muscular tonus, and possibly, but not probably, with hearing.

7. The saccular organ has nothing to do with equilibrium or muscle tonus, but is the chief organ of hearing, a function in which the sagitta plays an essential part.

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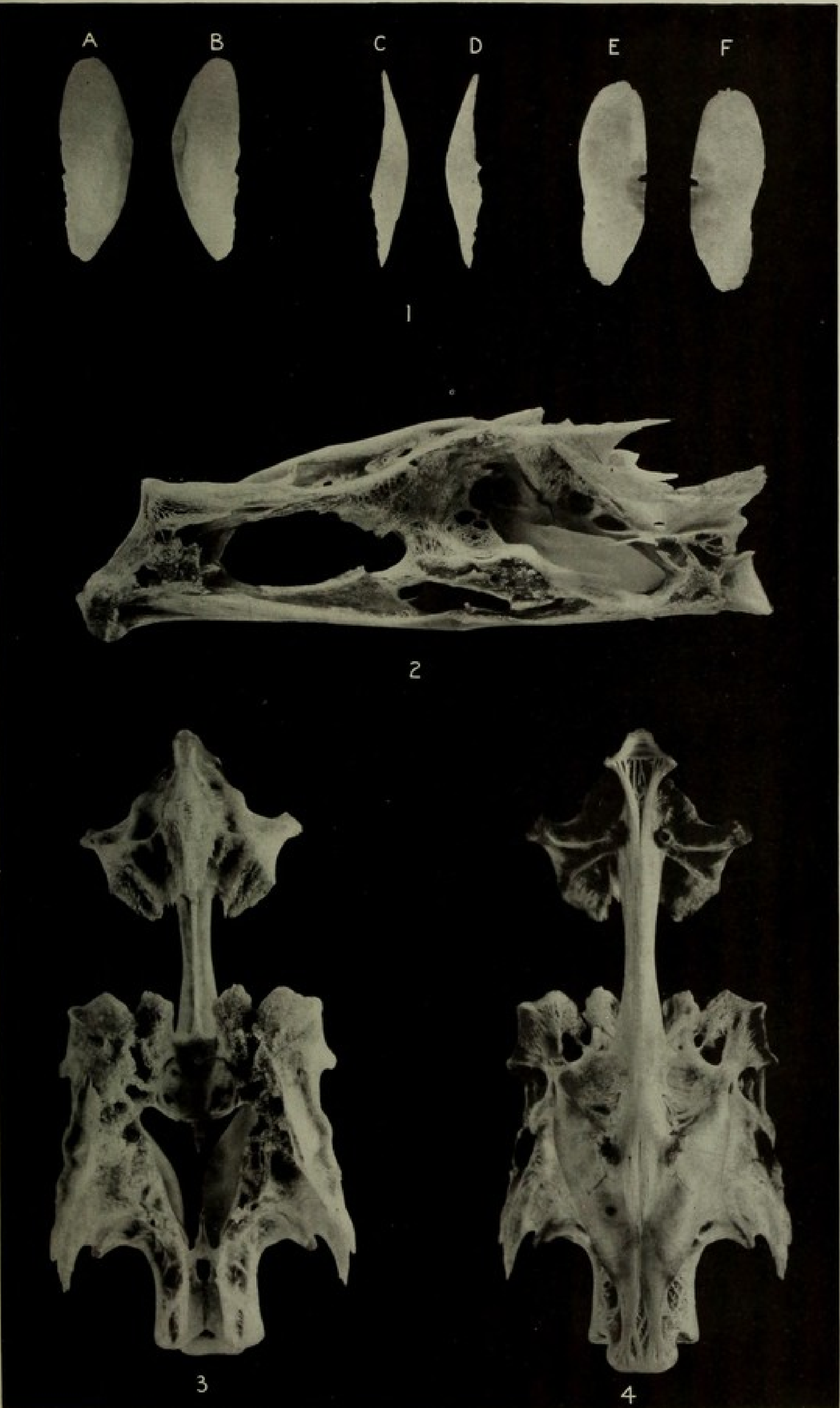
EXPLANATION OF PLATE.

FIG. 1.—Saccular otoliths (sagittæ) from the squeteague. All figures are placed with the anterior ends uppermost. *A*, *B*, median faces of a right (*A*) and of a left (*B*) otolith. *C*, *D*, dorsal edges of a left (*C*) and of a right (*D*) otolith. *E*, *F*, lateral faces of a left (*E*) and of a right (*F*) otolith.

FIG. 2.—Right half of the cranium of a squeteague viewed from the median face. The sagitta is shown in the bony capsule that partly surrounds the sacculus.

FIG. 3.—Dorsal view of the cranium of a squeteague. Much of the dorsal wall has been cut away to show the two bony capsules in which the sagittæ lie; the right sagitta is in normal position; the left one is turned out against what would be the nonnervous lateral wall of the sacculus.

FIG. 4.—Ventral view of the cranium of a squeteague, to show the bony capsules in which the sacculi are lodged.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