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The Nature of the So-Called Electric Organs in Ostracoderms

By GEORGE M. ROBERTSON

There seems to be something about working with fossils which loosens the imagination, and one of the ways in which the emancipated imagination goes to work is in trying to determine the functions of problematic structures. In general we believe we are justified in assuming that the structures we identify as orbits in the skulls of fossil fishes housed eyes. Most of us would also agree to accept and use identification of structures closely resembling what we find in modern forms, such as otic capsules, nasal organs, lateral line systems, portions of the brain-case, etc. Other structural features are not so readily homologized with those of modern forms. Hypotheses regarding the functions of these structures we regard with skepticism.

Ostracoderms were the bony-armored vertebrates which furnish us with the earliest records of vertebrate life. Remains of these creatures have been found in rocks dating from the Upper Ordovician, some 400 million years ago, to the end of the Devonian, a time range of about 100 million years. They are widely distributed. Their range of form and body plan was sufficiently wide to justify subdivision of the Class into at least two Sub-classes and four or more Orders. In fundamentals of body plan they are so closely similar to the modern Cyclostomes that we place them in the same Class. This enables us to make additional comparisons of structure with a modern group, and the larval lamprey (*Ammocoetes*) has contributed much to our understanding and interpretation of ostracoderm structure.

One Order, the *Osteostraci*, has furnished us with a great amount of detail, form of the brain-case, distribution of some of the nerve trunks and blood vessels, etc. It is in this group that the features commonly designated "electric organs" have been found. In the *Osteostraci* a bony dorsal shield covered the head and more or less of the trunk. On this shield, immediately posterior to the orbital region, between the otic capsules, is a small area which is usually seen as a depression filled with matrix. When the matrix is cleaned out the depression is seen to have a bony floor. An occasional specimen has the bony plates which covered this area preserved. Along

the lateral margins of the dorsal field, roughly dorsal to the branchial region, lie the paired lateral fields. The general structure of these areas is similar to that of the dorsal field. There may be a single pair or two or more separated by areas of normal shield surface. These structures have been variously designated, my preference being for the non-committal terms "dorsal field" and "lateral fields".

In *Tremataspis*, the form in which I have studied them most extensively, the basal portion of the field, when the covering plates are removed and the matrix has been cleared out, has a fenestrated appearance due to ramifying of small channels up through the bony base, channels which probably housed blood vessels and nerves. Just below the shield is a plexus of small vessels, some of which penetrate into the base of the fields. The dorsal field lies between the otic capsules and the most basal portion of that field communicates with a channel which leads into the otic vestibule on either side, that portion of the base being divided into two cup-like spaces.

The plates over-lying the fields are separated from the base by a thin layer of matrix, which presumably represented the extent of the space which in life would have been occupied by any special structure these fields might have housed. Wängsjö (1952) gives the depth in *Tremataspis* as 0.06 mm. The covering plates have the same histologic structure as the general shield (Robertson 1938, Denison 1947). Wängsjö states that in a specimen of *Tremataspis* which he sectioned through these plates the basal layer of the shield was adherent to the underlying bony surface, the matrix-filled space thus being between the middle layer and the basal layer of the exoskeleton, rather than below the basal layer.

Stensiö (1927) succeeded in dissecting a surprising amount of detail of the brain-case, cranial nerves, and blood vessels in Cephalaspids. Subsequently similar work has been described by a number of workers on this same group (Cf. especially Wängsjö 1952). In *Tremataspis* similar findings have been reported (Robertson 1938, Denison 1951), although less detail is available. The dorsal field lies immediately dorsal to the brain-case. Presumably some of the channels which enter its base and ramify in it transmitted nerves. The nerve and vascular channels out to the lateral fields are very striking. Their general resemblance to the nerve channels leading to the electric organs in *Torpedo* was largely responsible for Stensiö's original suggestion (1927) that they might have been electric organs. Certainly, whatever their functional

significance may have been, they were abundantly supplied with both nerves and blood vessels.

The number of nerve channels leading out toward the lateral field or fields on either side differs somewhat in different forms, and certain details of their distribution have been used as criteria for separation of taxonomic groups. In general the number ranges from 3 or 4 to 6. Their origin as a group indicates that probably all were branches of the *Facialis* (Stensiö 1927, Wängsjö 1952). A detailed description of their distribution would be simply a repetition of the accounts of these workers.

Various speculations regarding the function of the fields have been advanced, most of which, as Westoll (1945) says "are invalidated by our present detailed knowledge of their structure." The two which seem most to be favored are that they must have been sensory or that they were electric organs. Stensiö's 1927 monograph, the first detailed account of ostracoderm structure which went into nerve and blood vessel distribution in any thorough fashion, suggested the electric organ hypothesis as follows: "The possibility is not quite out of question of course, that the organs described here as electric fields might have been sensory organs with a special function. But since it is very difficult to understand what this special function could have been, and since the organs in question undoubtedly have certain superficial resemblance to electric organs, especially to those in *Torpedo*, I feel inclined to think that in reality they were electric organs, and because of that they have been referred to as electric fields throughout this work."

He pointed out, however, that they could hardly have been developed in the same manner as those of most electric fishes, such as *Torpedo*, since in these the functional units of the electric organs are derived from skeletal muscle. These "electroplaxes", as they are called, are stacks or series of flattened plates, each innervated by a nerve fiber, the whole series resembling the old-fashioned voltaic pile. In the *Osteostraci* the terminations of the nerves to the fields are too superficial to be located in trunk or tail musculature, and if some equivalent of electroplaxes were developed the source must have been within or immediately beneath the corium, certainly superficial to the fascia. As Stensiö writes "the *Cephalaspids* would in this respect be nearest comparable to *Malopterus electricus* which, as is well known, has an electric organ which perhaps has been derived from the corium."

Against the view that these structures were electric organs two types of argument have been used. One is simply the point that if the only basis for regarding them as electric organs is the resemblance of nerve channels to that of the electric nerves in *Torpedo*, plus the difficulty of imagining any other function for them, it is better to use a non-committal term such as "dorsal and lateral fields." This has been a major consideration in my consistent use of such terms. The other type of argument is that anatomical considerations do not support the view that they could have been electric organs.

Stensiö (1927) pointed out that the "electric nerves" in the cephalaspids "alternated in a certain regular way with the ordinary branchial nerves and that accordingly they had a metameric arrangement." This would, of course, support the idea that the structures innervated were related to metameric features such as the trunk musculature. These nerves traversed the labyrinth cavity in common with the branchial nerves. As somatic motor branches they would presumably not be ganglionated and Stensiö goes on to state: "If they had any ganglionic formations, which cannot be positively decided, these formations must have been situated in the middle portion of the vestibular division of the labyrinth cavity, probably on or close to the bottom." Wängsjö (1952) described and discussed these nerves in cephalaspids, presenting what looks like convincing evidence that they were in fact ganglionated, therefore sensory. He sums up this portion of the argument: "Now we have previously seen that the nerves for the lateral fields must have been provided with a basal ganglionated mass in the proximal part of their canals or in the vestibulum . . . This furnishes, I think, independently of other indications, definite proof for the view that the lateral (and consequently also the dorsal) fields cannot have been electric organs but must have been special sensory organs."

A second anatomical consideration is the extremely small size of the space which the electroplaxes (or their dermal equivalent) must have occupied. Wängsjö gives measurements of the distance between the covering plates and the endoskeletal base as ranging from 0.06 mm. to 0.48 mm. Compared with this, the electric organs in present-day forms occupy very large spaces. Moreover, as Bohlin (1941) comments, "there must have been a very remarkable disproportion between the quantity of electric tissue and nerves connected with it."

If these fields were not electric organs, what might have been

their functional significance? The most widely advocated view is that they were "sensory" in function. Wängsjö (1952) analyzes some of the sensory possibilities and concludes "that they were not electric organs but lodged special sensory organs, possibly (or probably) belonging to the lateralis system," and adds in parenthesis "their function is however wholly unknown and will so remain."

Westoll (1945) raises similar criticisms of the "electric field" hypothesis. He suggests that these fields were "special receptor organs, probably receptors of vibratory stimuli, consisting of invaginated pockets probably derived from placodes, richly supplied with neuromast organs, innervated by important nerves of the acoustico-lateralis system, and roofed by a flexible skin which was largely ossified but remained flexible because of the loose mosaic-structure" of the plates. He closes his discussion with the statement "It is therefore proposed that the non-committal terms, lateral and dorsal fields, should be used, as suggested by Robertson (1938), and that the term "electric field" be discarded."

Denison (1947) criticized Westoll's suggestion that the fields were receptors for vibratory stimuli, but based this criticism largely on what I regard as a mistaken concept of the "mucous canals" found in the exoskeleton. He concluded that the network of canals within the exoskeleton of *Tremataspis* was actually a diffuse sensory canal system, a view which I do not regard as tenable (Robertson 1950). His argument is essentially that since *Tremataspis* already has "its entire body entirely covered, even on the scale-covered tail, with a net-work of canals whose function was to receive vibratory stimuli" the possession of another set of organs to do a similar job was unreasonable.

We seem thus to be driven to reaffirm the usage which I adopted in earlier papers (Robertson 1935) and advocated in my 1938 paper, the use of names which imply nothing regarding function but simply serve to designate the structures.

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