On the Palæontology of Sturgeons.

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The Acipenseroid Fishes, or the common Sturgeons and their allies, have been looked upon by naturalists ever with increasing interest as the minutiæ of their anatomy have been revealed and made the subject of comparative study. They are the links between cartilaginous fishes and those possessed of well-formed bones; and, such being the case, they are evidently the little modified descendants of a race dominant in very remote Palæozoic times. Their Palæontological History, if it could be fully deciphered, would thus be one of considerable significance in the discussion of the philosophical problems of Biology; and it is proposed on the present occasion briefly to review the few fragments of this history that are already available for consideration.

The members of the group existing at the present day are divisible only into four genera and two families,* and the most familiar genus, Acipenser (or the common Sturgeon), has the widest distribution and the greatest number of species. This fish, with its close ally, Scaphirhynchus, forms the family Acipenseridæ, characterized by the presence of five longitudinal series of bony scutes upon the trunk. The Polyodon (=Spatularia) of the Mississippi, and Psephurus of the Chinese rivers, form the family of Polyodontidæ, in which there are no large scutes upon the trunk, and only occasional small stellate ossifications.

An examination of Acipenser itself (Fig. 1) suffices to indicate the main characteristics of the order, so far as known. The roof and sides of the head are covered with dermal plates or membrane bones, and both these and the armature of the trunk have the microscopical structure of true bone, thus exhibiting an advance upon the dentinal dermal calcifications characteristic of Selachians and Chimæroids, and probably of some older groups. The cartilaginous cranium itself is almost entirely persistent, only two or three small lateral areas being converted

^{*} A. Günther, 'Catal. Fishes British Museum,' Vol. viii (1870), pp. 332-347.

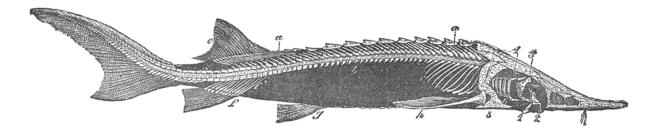


Fig. 1.—Skeleton of Sturgeon (Acipenser).

1, posterior extremity of cartilaginous cranium beneath the head-plates; 2, upper jaw; 3, hyomandibular bone; 4, lower jaw; 6, gill-arches; 8, pectoral arch; a, neural arches and spines, placed above the notochord; b, hæmal arches, placed below the notochord; c, dorsal fin; e, caudal fin; f, anal fin; g, pair of pelvic fins; h, pair of pectoral fins; r, ribs.

into bone,* and the base is covered with the well-known large membrane-bone, the parasphenoid, besides representatives of The jaws are entirely suspended by the upper part of the hyoid arch, which here consists of two pieces instead of one, as in the Selachii; and the uppermost of these suspensory elements, the hyomandibular (Fig. 1, 3) is considerably ossified. The two halves (palato-pterygo-quadrate cartilages) of the upper jaw (Fig. 1, 2) meet in the middle line in front, as in Selachii, each half exhibiting two small tracts of ossification, and slightly overlapped by two apposed membrane-bones, the maxilla and jugal. † Each half of the lower jaw (Fig. 1, 4) is also mostly ensheathed in one large membrane-bone (the dentary), with one of small size (coronoid, Parker). The opercular bones are incomplete, and only one (the operculum) is developed in the Sturgeon. In the figure, this element is removed to display the branchial arches (6), of which there are five on each side, and, like the ceratohyals, several of the cartilages of these are partially ossified.

In the axial skeleton of the trunk the notochord is persistent, but there are cartilaginous neural arches and spines (Fig. 1, a) above this rod, and hæmal arches, more or less complete, beneath.‡

the greater part of the cartilaginous (endoskeletal) base, and having become powerful dermal structures. The median fins, however, are less advanced, in the fact that, although the dermal fin-rays are powerful, they do not yet precisely correspond in number to the supporting cartilages or ossicles, but are slightly more numerous. Both the dorsal fin (Fig. 1, c) and the anal (f) possess a double series of supporting cartilages, as well shown in the figure. The caudal fin (e) is strongly heterocercal, the superior margin of the upper lobe being provided with a ridge of large over-lapping "fulcral" scales (i.e., A-shaped, though broadened at the apex), and the hæmal spines of the vertebral axis directly support the great inferior lobe of the terminal fin.

As characters of generic or family importance may also be noted-(i) the slight extension backwards of the dermal headplates beyond the skull; (ii) the fusion of the most anterior portion of the vertebral axis with the back of the skull: (iii) the absence of teeth in the adult;* (iv) the absence of branchiostegal rays; (v) the presence of a few ribs (r); (vi) the presence of fulcra upon the dorsal and anal fins, and the remote situation of the former; (vii) the presence of series of dermal scutes; and (viii) the presence of sensitive barbels upon the snout.

The amount of ossification in Polyodon and Psephurus is somewhat less than is observed in Acipenser, as just described; but a detailed recapitulation of their characters seems unnecessary for our present purpose, and the incidental allusions to them below will suffice. †

On turning to the paleontology of these fishes, it is interesting to note, in the first place, that the differentiation of the families Acipenseridæ and Polyodontidæ was almost certainly complete in Eccene times. Agassizt has already recognized the occurrence of dermal scutes indistinguishable from those of Acipenser in the London Clay of Sheppey; there is another similar fossil in the British Museum from the Upper Eccene of Hempstead

^{*} In the embryo and young sturgeon minute teeth have been observed (T. Knoch, "Ein Beitrag zur Entwickelungs-geschichte der Sterlette," 'Bull.

Anoch, "En Beldag 2dr Entwickenings-gescheide der Sterlete," Bull. Soc. Imp. Nat. Moscou, 1871, Pt. i, p. 281. Pl. vi, Fig. 7).

† A detailed description of Polyodon is given by T. W. Bridge, "On the Osteology of Polyodon folium," 'Phil. Trans.,' 1878, pp. 683-733, Pls. lv-lvii. For a figure of the skull, see also R. H. Traquair, "The Palæoniscidæ" ('Mon. Pal. Soc.,' 1877), Pl. vii, Fig. 1.

‡ A. Agassiz, "Recherches sur les Poissons fossiles," Vol. ii, Pt. ii (1843),

p. 280

(Pl. I, Fig. 2); and Cope* has discovered a fish only generically distinguishable from Polyodon in the Eocene Green River Shales of Wyoming, U.S.A.

The London Clay fossils have not hitherto been described and figured, but there is a small series in the British Museum, and one scute is shown, of the natural size, in Pl. I, Fig. 1. The narrow, smooth, overlapped area is indicated, and the exposed portion exhibits the characteristic pitted ornament. The form, so far as recognizable, also corresponds with that of one of the dorsal scutes of an existing Acipenser. It is quite impossible, however, to found upon a series of isolated fossils of this kind a scientifically-defined species; though it will be convenient, for reference, to adopt Agassiz' provisional name of Acipenser tolianicus.

The detached scute from the Hempstead Beds (Pl. I, Fig. 2) also pertains to a fish of about the same dimensions as the Sheppey species, and exhibits all the features observed in a lateral scute of some existing forms.

The fossils just noticed being so precisely similar to the corresponding parts of the living Acipenser, we approach, with all the more satisfaction, the discussion of some problematical fishspines, which do not appear to have been hitherto determined, and are in some respects suggestive of Siluroids and Scleroderm Plectognathi. So far as I have been able to discover, only one figure of such a fossil has been published, the specimen being derived from the Lower Pliocene of Montpellier, France; but a few examples are now preserved in the British Museum from the Upper Eocene of the Hampshire Basin, and still finer specimens occur in the Reed Collection in the York Museum.

Through the kindness of William Reed, Esq., F.G.S., we are able to append figures of one of the last-named specimens (Pl. I, Figs. 3, 3a).

The fossils in question are stout unsymmetrical spines, evidently originally occurring in pairs, and showing no trace of

† 'Premier rayon de la dorsale d'un Poisson, ayant quelque rapport avec celui des Balistes.' P. Gervais, "Zoologie et Paléontologie françaises" (1852), 'Explic. Planches, Poiss. foss.,' p. 5, Pl. lxviii, Fig. 33.

^{*} E. D. Cope, "A new Chondrostean from the Eocene," 'Amer. Nat.,' Vol. xvii (1883), p. 1152; "Eocene Paddle-fish," ibid., Vol. xix (1885), p. 1090; "On two New Forms of Polyodont and Gonorhynchid Fishes from the Eocene of the Rocky Mountains," 'Mem. Nat. Acad. Sci.,' Vol. iii (1886), pp. 161-163, Figs. 1-3.

proximal articular facettes, such as characterize the weapons of File-fishes and Siluroids. Posteriorly (Fig. 3a) there is a deep longitudinal groove, which becomes gradually widened towards the base, forming an extensive excavation; and the anterior border is compressed into a sharp and slightly wavy edge, with no denticles, but marked on each side, in unabraded specimens, with a series of small transverse striæ. The lateral ornamentation consists of a number of strong, irregular longitudinal rugæ, often raised at intervals into little nodose expansions; and these terminate at a short distance from the proximal extremity of the spine, thus leaving a smooth area, without any anterior keel, evidently more or less saddle-shaped when perfect

On comparing these spines with the large preaxial pectoral fin-ray of the common existing Sturgeon, they are found to agree in the most minute particulars. They may, therefore, be regarded as undoubtedly referable to an Acipenseroid fish, and, like the Sheppey scutes, may be provisionally assigned to the genus *Acipenser* itself.

Similar spines occur in the Red Crag of Suffolk (Reed Coll., York Museum); but the only other known evidence of *Acipenser* in beds above the Eocene is a typical scute described by Leidy* from the Miocene of Virginia, under the name of *A. ornatus*.

Prof. Cope's Eocene Polyodont fish is more completely known than the European Acipenser-like fossils just described, both the head and the caudal region having been discovered. It is remarkable on account of the presence of distinct scales upon the trunk, and has received the generic name of Crossopholis (fringe-scale), the single known species being C. magnicaudatus.† In many respects the cranial bones are very similar to those of Polyodon, but the snout is relatively shorter, and more closely corresponds in form to that of Psephurus. The body is long and slender, with short dorsal and anal fins, remotely situated, and the former commencing slightly in advance of the latter. The scales are numerous, in oblique series, not quite in contact; and each consists of a small subquadrate

† See references in footnote on p. 28.

^{*} J. Leidy, "Extinct Vertebrata of the Western Territories" ('Rep. U.S. Geol. Surv. Territ.,' Vol. i, Pt. i, 1873), p. 350, Pl. xxxii, Fig. 58. The supposed Acipenseroid scutes from the Molasse of Würtemberg, described by J. Probst ('Württ. Jahresh.,' 1882, p. 116, Pl. ii) are truly Selachian (K. A. von Zittel, Sitzungsb. k. bay. Akad. Wiss., 1886, Pt. ii, pp. 9-12).

disc, with a row of long, sharp, backwardly-directed spines arranged upon the posterior margin. In an individual measuring 0·170 m. from the anterior extremity of the dorsal fin to the notch of the caudal, the scales only measure one millimetre each way; the caudal fulcra are large and strong.

Below the Eocene, no satisfactory evidence of Acipenseroid fishes has hitherto been recorded from deposits later than the Lias*; and on this horizon, as might be expected, some of the forms exhibit a greater divergence from the existing family and generic types than is observed in the Eocene examples.

On the present occasion, however, it is interesting to be able to add that some slight traces of the order are gradually becoming revealed among the fossils of our English chalk. Since the reading of my paper last Session, I have succeeded in interpreting some specimens in the British Museum, which have long been among the most perplexing of undetermined chalk fossils; and these must undoubtedly be regarded as forming part of a typical Acipenseroid tail.

The specimens in question are three small blocks of chalk from the Upper Chalk of Gravesend, Kent, exhibiting five more or less fragmentary fulcral scales, and portions of robust finrays, probably all found together, and belonging to the tail of one individual. They are numbered 33221-4, and drawings are given in Pl. I, Figs. 4, 5.

One of the fulcral scales is shown of the natural size in Pl. I, Fig. 4, the bifurcating inserted portion being restored in outline from another specimen. A still larger example, however, measures 0.024 m. in maximum breadth, and 0.027 m. from the apex to the bifurcation of the base. These scales are all deeply-overlapping, relatively broad, and notably flat; and the backwardly-directed apex is rounded and obtuse. The small exposed portion is ornamented with thick ganoine in irregular dots and short wavy lines, more or less clustered, especially near the margin.

Like the fulcral scales, the caudal fin-rays (Pl. I, Fig. 5) are also very robust, and the superficial ganoine thick and rugose, not always completely covering the exposed faces of the successive joints. As usual, each ray is double, and for some dis-

^{*} The tail from the Cretaceous of Mount Lebanon named "Chondrosteus?" by J. W. Davis ('Trans. Roy. Dublin Soc.' [2], Vol. iii, p. 501, Pl. xxiv, Fig. 1) is truly Teleostean.

tance proximally it is not articulated; when reached, however, the articulations immediately become very numerous and approximated, the divisions being mostly shorter than broad.

No oat-shaped scales, such as might have covered the sides of the upper lobe of the tail, can be distinguished; and, although the British Museum collection comprises undetermined dermal bones from the Chalk, nothing appears to be referable with much probability to an Acipenseroid of the same character.

In the Willett collection at Brighton, however, there is the extremity of a snout, from the Chalk of Sussex, which exhibits so much superficial resemblance to that of the common Acipenser that it may quite possibly belong at least to the same order (Pl. I, Figs. 6, 6a). This fossil is merely an imperfect example of thin sculptured bone enveloping the termination of the snout, and it only seems to differ from the corresponding armature of Acipenser in the fact that it is very broad, shows no sutures, and overlaps the margin more completely. It is ornamented above (Pl. I, Fig. 6) by large, coarse, forwardly-directed rugæ, passing into a network in front; the anterior face of the overturned margin is more or less smooth, apparently by wear; and the narrow inferior face of this margin is finely reticulated.

The Cretaceous caudal fulcra (or ridge-scales) most closely resemble those of *Psephurus* among living Acipenseroids; but they are broader and flatter, less pointed, and evidently betoken a stout depressed fish. Mr. Willett's fossil might thus belong to the same form, and the genus would be well distinguished; but, in any case, it will be convenient to propose for the British Museum specimens a provisional name, and record them as *Pholidurus disjectus*.

There is some reason to hope that before long evidence of other Acipenseroids will also be definitely recognized in later Jurassic rocks. In the collection of Oxford Clay Vertebrates made by Alfred N. Leeds, Esq., of Eyebury, Peterborough, there are traces of a very large fish, having stiff branched finrays and irregular dermal bones; and these fossils are apparently most nearly paralleled by Acipenseroids, though no elements sufficiently like those of known genera have yet been found to render any determination certain.

In the Upper Lias of the neighbourhood of Whitby, Yorkshire, however, fragments of the skeleton of a very large fish of this order have long been known. They were briefly noticed (not described) by Agassiz,* who assigned them to the "Cœlacanths," under the name of Gyrosteus mirabilis; and there are many fine specimens in the British Museum, besides

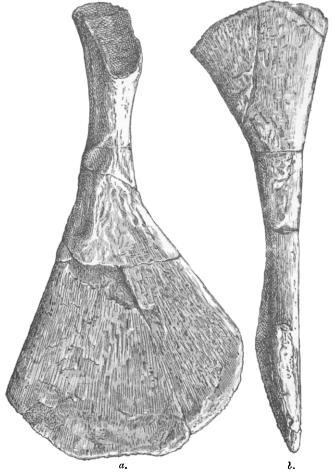


Fig. 2.—Right hyomandibular bone of Gyrosteus mirabilis, lateral aspect (a) and posterior aspect (b); one-third nat. size. (B.M., No. P. 3356a.)

^{*} L. Agassiz, tom. cit., Pt. ii, p. 179. Some desultory notes have subsequently been published by Prof. J. F. Blake in Tate and Blake, 'The Yorskhire Lias' (1876), p. 256, Pl. ii, Figs. 2, 3.