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A NEW GENUS AND SPECIES OF MARINE DIPNOAN FISH, FROM THE UPPER DEVONIAN OF CANADA

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INTRODUCTION

Our understanding of the evolutionary history of the lungfishes (Osteichthyes, Dipnoi) is based almost exclusively upon fossil material of freshwater forms. Indeed, everything we know about the fossil and living Dipnoi suggests that this group mostly has a freshwater habitat. It is of the greatest interest, therefore, to learn that the two earliest, and most primitive, lungfish species that we know of, *Dipnorhynchus sussmilchi* (Etheridge) and *D. lehmani* Westoll, were fully marine forms (see Westoll, 1949 and especially Campbell, 1965). The discovery and study of further marine lungfishes has thus become a matter of some importance, both in elucidating the variously primitive and advanced characters of *Dipnorhynchus* and in establishing more fully the evolutionary history of the Dipnoi as a whole.

The subject of this short paper is a specimen of lungfish from the marine Upper Devonian of Canada. The fish clearly belongs in a new genus and species, and seems to be more primitive than the typical and well-known freshwater dipnoans of the same age.

DESCRIPTION

Family uncertain

Sunwapta genus novum**grandiceps** species novum

"Coelacanth remains" (Gardiner 1966, p. 93)

DIAGNOSIS. A very large dipnoan fish: estimated length of skull approximately 22 cm., estimated standard length approximately 1 metre. Marine in occurrence. Tooth plates large and lacking separate denticles. Lower tooth plates differentiated peripherally by the presence of grooves separating approximately parallel ridges that show faint signs of becoming subdivided into small denticles. Dorsal surfaces of the ridges covered with enamel similar to that covering the dermal bones. Central and posterior portions of the tooth plates smooth and lacking the enamel covering (in all probability this is lost through wear during the life of the animal). Dermal bones of the lower jaw massive and bearing an external covering of enamel identical with that found in typical *Dipterus* Sedgwick and Murchison.

OCCURRENCE. Sunwapta Pass, Mount Athabasca, Alberta, Canada. Upper Devonian. Precise locality unknown.

TYPE SPECIMEN. Specimen number 477, University of Alberta Geological Museum, Edmonton, Alberta. Collected by "Mr. M. Bleuler," date unknown.

REMARKS. Unfortunately only a single specimen of this fish is known. The specimen is well preserved (Fig. 1) and consists of the symphysis and the anterior portions of the rami of the lower jaws. The specimen shows no sign of pronounced weathering or rolling and there can be virtually no doubt but that it derives from the marine environment in which it was deposited rather than having been transported before or after fossilization from some distant freshwater locality. The nature of the tooth plates also tends to confirm the conclusion that the fish lived in a marine environment, the structure suggesting that the fish was adapted to feeding on molluscs or other hard-shelled invertebrates. It has



FIGURE 1. *Sunwapta grandiceps* gen. et sp. nov. Holotype, symphyseal region of the lower jaws in occlusal and anterior view. Natural size.

been difficult to assess the familial status of the fish. The general structure shows a clear affinity with the families Dipteridae and Dipnorhynchidae, but the fish probably does not correctly belong in either of these families. The problem is discussed further below.

DISCUSSION

A search through the literature pertaining to the Dipnoi reveals that fragmentary remains of large lungfish have been found in a wide variety of Devonian marine or semi-marine deposits. Among such forms may be included *Palaeodaphus* van Beneden and Koninek, possibly *Grossipterus* Obruchev (formerly *Holodus*), *Conchodus* McCoy, *Holodipterus* White and Moy-Thomas (formerly *Archaeotylus*) in addition to *Dipnorhynchus susmilchi* and *D. lehmani*. These fishes are mostly imperfectly known; in the majority of cases only portions of the mandibles and tooth plates have been preserved. Nonetheless, we may see that they all have in common a marine origin, moderately large to very large size, and tooth plates which lack separate denticles and bear only a small number of broad, faintly ornamented, ridges radiating from a point near the postero-medial corner of the plate. Naturally, it is highly important in this analysis to be sure that the patterns of denticulation (particularly the lack of denticulation) are not simply caused by wear of the specimen. Usually, as in the present case, this can be determined quite readily.

It is of considerable interest to speculate upon the phylogenetic history of these marine forms. Since, in the majority of cases, only the tooth plates are known to us, it is impossible at the present time to determine with accuracy the morphological resemblance and taxonomic relationship of these fishes to the better-known freshwater Dipnoi of the Devonian. It seems reasonable to categorize them as separate genera and species close to but quite distinct from the family Dipteridae; it is probably most economical to assign them as Dipnoi *incertae sedis*.

A more important question than the taxonomic relations of these marine forms concerns their relative primitiveness. Are they secondarily derived from freshwater forms similar to the Dipteridae etc., or do they represent remnants of an ancestral *marine* radiation of Dipnoi from which all the freshwater forms have later evolved? At present we are only able to discuss the question with

respect to the evidence afforded from the structure of the tooth plates.

The studies of White (1965, 1966) have cleared up a good deal of the confusion concerning the nature of the dentition in Dipnoi. As he states, the *Dipterus*-type of dentition "is formed from specialized areas of the dentine-covered bone surface (of the jaws) and . . . the denticles arise subsequently to the development of the crushing plate" (1966, p. 7). According to this view the relatively unspecialized dentition of *Dipnorhynchus* (White, 1964; Campbell, 1965) is strictly primitive and has not been preceded by any denticulated stage.

Since, as the evidence stands at present, it is difficult to interpret the nature of the tooth plates in *Dipnorhynchus* as other than primitive, the characteristic denticulation of the tooth plates of the freshwater Dipnoi such as *Dipterus*, *Fleurantia* Graham-Smith and Westoll, *Scaumenacia* Traquair, or *Rhinodipterus* Säve-Söderbergh must be interpreted as having arisen secondarily, probably in accordance with adaptation to a new feeding requirement in a new habitat. These freshwater fishes seem to be adapted for dealing with a less brittle food; the difference between feeding upon arthropods and upon molluscs. (No doubt, of course, *Dipterus* and its relatives also fed on smaller freshwater shellfish and the marine forms probably fed on larger crustaceans too.) It is clear, however, that the denticulation of the *Dipterus*-type of tooth allows for the fish to deal with a wider range of food than the simple crushing plates of *Dipnorhynchus*. In a previous study (Thomson, 1965) I have discussed the possibilities that exist for differentiation of the dental battery in various Dipnoi — for example, by the development of a central crushing area quite distinct from the peripheral denticulation which may be used for "chopping."

If this interpretation is correct then *Sunwapta* and the similar large marine forms that we have listed above most probably belong to a group intermediate between the early Dipnorhynchidae and the later Dipteridae. They may represent part of an early radiation of Dipnoi from which the freshwater forms later evolved. The simplest interpretation of the pattern of the tooth plates in the forms like *Sunwapta* or *Palaeadaphus* is that they represent the earliest stage towards the development of the *Dipterus*-type of

tooth plate. According to this hypothesis, therefore, in the phylogenetic history of the Dipnoi the initial stage of the tooth plate from the coarsely tubercular *Dipnorhynchus*-stage is the differentiation of a series of marginal ridges, formed by the excavation of deep grooves in the peripheral portion of the plate. Thus the ridges are not *added* to the plate but are formed by the development of the grooves. The curvature and location of the opposing plates apparently allows the upper and lower ridges to interdigitate. We may extend this hypothesis to suggest that the formation of discrete denticles on the tooth plate occurs through subdivision of the ridges on the tooth plate. This hypothesis would accord well with White's observations on the nature of the denticles in Dipnoi since the denticles would essentially represent the original enamel-covered surface of the tooth plate.

In view of the marine affinities of *Dipnorhynchus* itself (the earliest dipnoan that is currently known), the alternative viewpoint — that the tooth plates in these fishes represent a secondary adaptation to marine life that has evolved from an ancestral freshwater dipterid stock — is less satisfactory. We may note, however, that the marine (or estuarine) *Dipterus digitatus* Eastman, *D. mordax* Eastman, *D. pectinatus* Eastman and *D. costatus* Eastman from the Upper Devonian of Iowa (Eastman, 1908) most probably do have just such a derivation from more advanced freshwater forms. Their exact taxonomic position is uncertain and will not be discussed here. They are clearly different from the *Sunwapta* — *Palaeadaphus* type in that, although the main body of the tooth plate is frequently not denticulated, distinct denticles are present nearer the periphery. Another feature that may be important is that in these apparently secondary forms the tooth ridges "radiate" from a point in the mid-section of the tooth plate, whereas in the more primitive forms the ridges are more parallel to the antero-posterior axis. On the whole, it seems most likely that these forms have arisen from more typical advanced dipnoans by the loss of denticles from the median portion of the tooth plate. Again, this development of a crushing type of dentition is associated with a marine or estuarine environment.

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