

THE SKULL AND PECTORAL GIRDLE OF THE PARASEMIONOTID FISH
WATSONULUS EUGNATHOIDES FROM THE EARLY TRIASSIC
SAKAMENA GROUP OF MADAGASCAR, WITH COMMENTS ON
THE RELATIONSHIPS OF THE HOLOSTEAN FISHES

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ABSTRACT—*Watsonulus eugnathoides* (Piveteau, 1935) is a parasemionotid fish from Early Triassic rocks of Madagascar. The skull and pectoral girdle of this holostean are described from new material. The braincase retains a number of primitive chondrosteian-like characters such as an open lateral cranial fissure and frequently open vestibular fontanelle, presence of an endochondral intercalar without membranous outgrowths, and fusion between most of the the endochondral bones in the adult, but is otherwise similar to "caturids" such as *Heterolepidotus*. The dermal skull retains one major, putatively primitive, feature shared with chondrosteans, a preopercular with a broad dorsal edge. The dermal shoulder girdle retains a chondrosteian-style clavicle, but the endochondral shoulder girdle is most similar to teleosts among actinopterygians. *Watsonulus* also has an *Amia*-style jaw joint. The non-reduced clavicle and dorsally expanded preoperculum are lost in all other non-parasemionotid neopterygians (the reductions being synapomorphies), and the combination of these two primitive characters with an *Amia*-style jaw in *Watsonulus* shows that gars and teleosts are more closely related to each other than either is to *Amia*.

DEDICATION AND INTRODUCTION

Fourteen years ago I was introduced to Bobb Schaeffer in the old preparation room in the American Museum of Natural History. I was 15 years old and had with me my first fossil fish, a fragment of a semionotid from the Early Jurassic of New Jersey. Bobb spent a long time with me that day working out an identification. In the subsequent two years he made available to me the Osborn Library and fossil fish collection at the American Museum, and spent scores of hours with me during my frequent, totally unannounced visits. His continuous tutelage and encouragement in my early years opened up for me the door to professional scientific inquiry. Thus, it is to Bobb Schaeffer that I dedicate this paper, the first in a planned series of papers on the origin, relationships, and significance of the holostean fishes.

Here I describe the skull and shoulder girdle of the fish *Watsonulus eugnathoides* (Piveteau, 1935), and attempt to place that taxon within a phylogenetic framework of holosteans and teleosts suggested by the combination of characters seen in *Watsonulus*. *Watsonulus* has always been considered a representative of a group of Triassic fishes called parasemionotids, which have been variously hypothesized to be a basal grade within the holosteans or ancestral to *Amia*-like fishes and/or teleosts (Brough, 1939; Gardiner, 1960; Patterson, 1973; Nybelin, 1966). The new material of *Watsonulus* and the material described in the literature

reveal character combinations completely incompatible with all previously proposed schemes of relationships for the neopterygians and suggest a new hypothesis in which *Amia* is regarded as the primitive sister group of all living neopterygians.

MATERIAL AND METHODS

All the specimens described in this paper were collected during 1961 by Professor Bernard Kummel of the Harvard Museum of Comparative Zoology from the famous nodule-bearing beds in the Early Triassic of Madagascar (Piveteau, 1935; Lehman, 1952) at Ambilombe Bay. These units belong to "Bed 5" of the Middle Sakamena Group of probable Scythian age (Anderson and Anderson, 1973).

The utility of this new material of *Watsonulus* rests in the virtually uncrushed nature of the bones, the partial disarticulation of the skulls, and the preservation of fine surface detail. However, these specimens are preserved as hard siltstone nodules in which virtually all the bone has been leached out. During collection, each nodule was split into two halves exposing a hole which is the natural mold of the bones. Therefore, for their exceptional utility to be fully realized, the nodules must be cast in a flexible molding compound such as latex, Smooth-On, or silicone as described by Baird (1951, 1974) and used with great success by Schaeffer (1967, 1978). After much

