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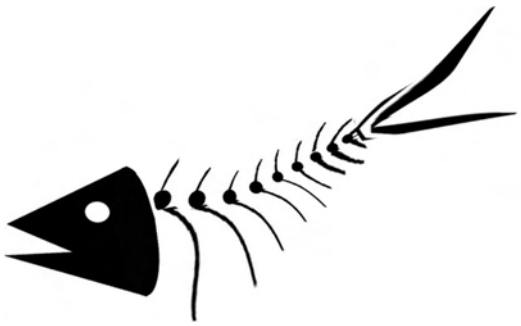

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GROWTH CHARACTERISTICS OF CRETACEOUS AND CENOZOIC NORTH AMERICAN ESOCIFORMES: IMPLICATIONS FOR SYSTEMATICS

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INTRODUCTION

Fossil esocoids, mostly consisting of isolated bones, centra, and scales, have a fossil record extending from the Cretaceous through the Quaternary (e.g., WILSON *et al.* 1992). The lack of complete fish hampers systematic and phylogenetic studies but incomplete specimens provide growth data.

We examined the growth patterns and the response of the various components of the von Bertalanffy growth equation to **M**ean **A**nnual **T**emperature (MAT) from extant esocids and umbrids to document the variation between the species. The variation and variable responses to temperature provide a context to classify growth patterns in the Cretaceous and Cenozoic fossil record. Specifically, we quantified and contrasted the growth characteristics of fossil and extant esociforms with regard to relationships between MAT and the: 1) total length (TL) at age four, 2) percentage of maximum observed TL attained by age four (PMTL), 3) K (Brody growth coefficient), 4) longevity, and 5) maximum observed total length (MTL).

RESULTS

Our analysis is primarily based on North American von Bertalanffy growth data, parameters, and regressions from the extant esocids and

umbrids, which include: *Esox masquinongy* (n = 23), *E. lucius* (n = 21), *E. reicherti* (n = 3), *E. niger* (n = 9), and *E. americanus* (n = 6); *Umbra limi* (n = 4), *Umbra krameri* (n = 1), and *Dallia pectoralis* (n = 1). Total length at age four was positively correlated with MAT for *E. masquinongy*, *E. lucius*, *E. niger*, and *U. limi*. The PMTL at age four is influenced by the effects of K and MTL and was positively correlated with MAT for *E. masquinongy*, and *E. lucius*, but was negatively correlated for *E. niger*. The responses of K, longevity, and MTL for *E. niger* are opposite to those for *E. masquinongy* and *E. lucius*. For *E. niger,* K is negatively correlated with MAT; however, longevity and MTL are positively correlated with MAT. *Esox americanus* has growth characteristics not significantly related to temperature, except with regard to MTL, which responds in a similar manner to MAT as that for *E. lucius*.

We found that esocid centra from the Cretaceous Dinosaur Park Formation (DPFm) of Alberta and Saskatchewan (BRINKMAN & NEUMAN 2002) were from fish up to 10 years old with a bimodal age distribution of ages one and five. Centrum diameters did not exceed 4.4mm (range 1.1 - 4.4mm) indicating that they remained small throughout their life. Growth was linear and moderately slow ($\overline{x}$ = 0.19, range 0.1 - 0.36 K). We would have expected growth to be faster given the high Cretaceous MAT (i.e., ~19°C). Centra reached their maximum diameters as early as four years in age. No differences existed in the growth patterns of the centra to suggest different species even though the deposits contain dentaries of *Estesesox* and *Oldmanesox* (WILSON *et al*. 1992).

The centra of incomplete *Esox* specimens from the Paleocene Bullion Creek Formation in North Dakota attained much larger sizes (i.e., 5.8 - 13.2mm diameter) and ages up to 12 years old. *Esox* of the Paleocene Sentinel Butte Formation in North Dakota lived at least as old as nine years, attaining an estimated total length of about 115cm. The largest centrum recorded was 13.5mm diameter for a specimen that was six years old. Examination of *Esox tiemani* WILSON 1980 of the Paleocene Paskapoo Formation indicated that the holotype and another specimen attained a TL of 26 to 32cm by age one, which is similar to one year old *E. masquinongy* in the southern end of their range today.

Scales of Paleocene *Esox* were similar in size and age to those from the Eocene Coalmont and Clarno Formations from Colorado and Oregon, respectively. Two *Esox* scales were aged from the Coalmont Formation at six and 10 years old. One scale was aged from the Clarno Formation at eight years old. *Esox kronneri* GRANDE, 1999 of the Eocene Green River Formation, age zero, has a TL of 11.8cm with centrum diameters similar in size to those of Paleocene esocids at age one and much larger that those of the Cretaceous specimens at age one.

A comparison of PMTL and MTL to MAT among extant and extinct fishes indicates values more comparable to those of *E. masquinongy* for most extinct taxa. The exception is the small Cretaceous esocids. The Cretaceous, Paleocene, and Eocene esocid centra have mean K values (0.175 - 0.338 K) more similar to those of the extant *E. masquinongy* and *E. americanus* at temperatures greater than 13°C. However, Paleocene esocids attained large sizes with a PMTL (>71% PMTL at >10°C) and MTL (>100 cm at >10°C) more equivalent to populations of *E. masquinongy* than to populations of *E. lucius*, *E. niger*, *E. americanus*, or to any of the extant umbrids. The individual longevity (>6 years old at >13°C) of Cretaceous to Eocene esocids appears more similar to the longevity of *E. niger* than to that of *E. masquinongy* at temperatures >13°C.

DISCUSSION

A comparison of the growth parameters of extant and extinct esocids suggests that *E. masquinongy* possesses three primitive growth characteristics (i.e., PMTL, K, MTL), *E. niger* possesses one (i.e., longevity), and *E. americanus* possesses two (i.e., PMTL, K). However, Cretaceous esocids appear to have small sizes, more comparable to those of extant umbrids, *Dallia* and *Umbra*. Our analyses show that the small Cretaceous esocids had a longevity and growth rate similar to those of the large esocids in the Paleocene and Eocene and that of extant esocids at >0°C. All extinct taxa show longevity more similar to that predicted for *E. niger* from 15–20°C.

Extant esocids show adaptations to cooler environments compared to their Paleocene and Eocene ancestors, manifested by lower K values, longer lives, and larger maximum sizes. Our data show a shift from small Cretaceous esocids inhabiting very warm environments to larger Paleocene esocids inhabiting cooler environments. As a matter of observation in living esocids, small esocid species inhabit warmer environments from 16 to 23°C; this leads us to speculate that the cooler climate associated with the Paleocene compared to that of the Cretaceous influenced the selection pressure for cold-tolerant, larger individuals. This hypothesis can be tested in two ways: future studies of esocids from arctic latitudes in the Cretaceous should show larger individuals than those observed in Alberta; and esocids living during the Early Eocene Climatic Optimum should show trends to shorter lengths.

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