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SPOTLIGHT

ASPIRATION OR EXPIRATION: HYPOXIA AND THE INTERPRETATION OF FISH PREDATION IN THE FOSSIL RECORD

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Accurate interpretation of fossils of one organism inside another is essential for understanding predator-prey relationships, food-web structure, and energy flows in ancient ecosystems. Fossils of a fish inside the mouth or stomach of another fish are thought to represent examples of normal predation in such ecosystems (Viohl 1990; Maisey 1994; McAllister 2003; Ebert et al. 2015). Further, so-called "aspiration" fossils of a relatively large fish partly inserted headfirst into the mouth of another fish (Fig. 1A) often are considered to be the result of ingestion of over-sized normal prey leading to the death of the predator (Grande 1984, 2013; Viohl 1990; McAllister 2003; Ebert et al. 2015), which is known to happen with modern predatory fishes (e.g., Viohl 1990). However, there are other plausible explanations for some such fish fossils.

Collectively we have used hundreds of small rotenone stations over several decades of research in all three tropical oceans aimed at collecting cryptic reef fishes, a major component of reef-fish faunas (Robertson and Smith-Vaniz 2008; Brandl et al. 2018). Rotenone kills fishes by blocking cellular uptake of oxygen (Robertson and Smith-Vaniz 2008). Consequently our rotenone stations often led to fish dying with gaping mouths and flared gill covers, a response to hypoxia known as tetany that is often seen in fossils (Ferber and Wells 1995; Marramà et al. 2016). When those rotenone specimens became locally concentrated, e.g., in a sandy depression, an affected fish skittering rapidly around on the substratum amongst other fishes sometimes entered the mouth chamber via the gills or rammed itself headfirst into and became caught in the gaping mouth of another fish, with the recipients in such cases including herbivores as well as large-mouthed planktivores and predators. In other instances the churning action of waves led to a dead fish passively sifting headfirst into the gape of another fish. The orientation of the teeth of many large-mouthed predatory fishes, pointing back towards the throat, facilitates entry and hinders exit of prey, and also allows them to act as passive fish traps once dead with mouth agape. In addition, piscivorous fishes regularly were attracted to rotenone stations by the dead and dying fishes, and we observed various species of belonids, carangids, labrids, lutjanids, muraenids (Fig. 2), serranids, sphyraenids, and synodontids exploiting such stations, and, on occasion, succumbing with bellies engorged with prey, or prey in their mouths. Sometimes that piscivory involved unusual predator-prey interactions, e.g., schooling carangids that roam in midwater diving down to consume small cryptic fishes that, under the effects of rotenone, had emerged onto the surface of sand in which they normally were buried and hidden from view. As a result of these various behaviors we routinely checked inside the mouths of fishes obtained from rotenone stations for hidden specimens, and sometimes extracted specimens caught headfirst in the mouth of another fish.

Fishes are notably sensitive to but vary in their tolerance of hypoxia, which is common in aquatic habitats (Rogers et al. 2016). Some aspiration fossils may be the result of natural situations analogous to rotenone stations, when mortality due to hypoxia produced accumulations of dying fish that inevitably led to individuals becoming inserted headfirst into the gapes of other individuals. This process could be referred to as "expiration" as distinct from aspiration. Further, rather than arising through normal feeding, some fossils of a predator preserved (by anoxia) with another fish in its mouth or with articulated, hence recently consumed, fish in its stomach (Viohl 1990; Ferber and Wells 1995; Schmid et al. 2001; Marramà et al. 2016) could reflect "anomalous predation", the consumption of unusual types of prey or of unusual quantities of normal prey among fish killed by hypoxia that subsequently claimed the predator. Both expiration and anomalous predation need to be taken into consideration when interpreting the ecological significance of fossils of fishes killed by hypoxia.

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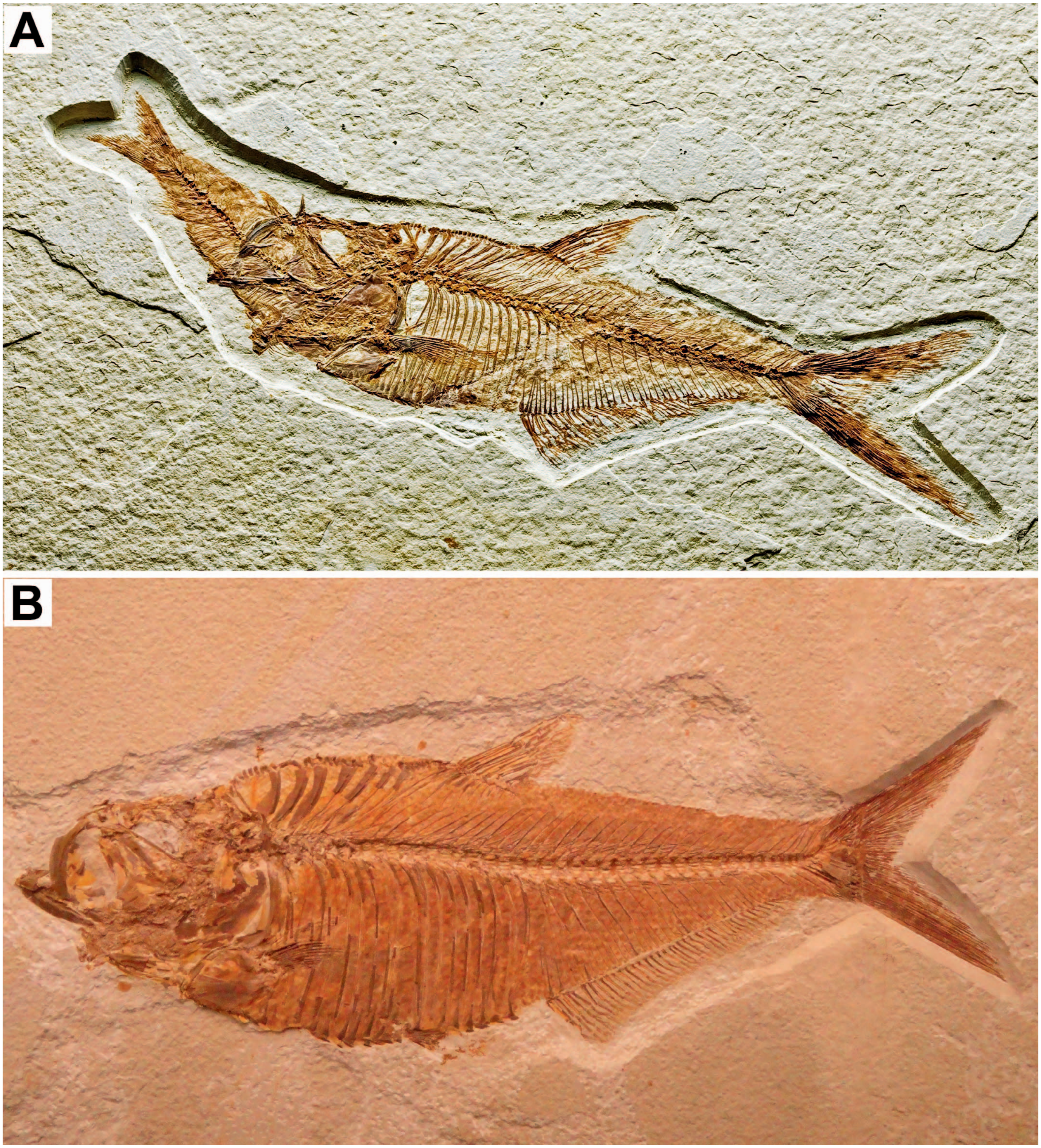

FIG. 1.—Two fossils of the extinct Eocene freshwater clupeiform *Diplomystus* with mouth agape, one with fish and one without. **A**) Fish inserted headfirst partway in its mouth. **B**) Fossil without a fish in mouth. Like most modern clupeiforms, large-mouthed *Diplomystus* may have been a planktivore, although there are some predatory clupeids that consume small fishes. Fossils such as view A are consistent with expiration. Image credits: A, Heritage Auctions, HA.com, with permission; B, Wikimedia, Naturmuseum Senckenberg, Creative Commons CC0 1.0.

FIG. 2.—A predatory moray eel, *Muraena clepsydra*, with a damselfish, *Chromis atrilobata*, that it has seized at a rotenone station in Pacific Panama. Moray eels are more resistant to rotenone than most other reef fishes, and, although mainly nocturnal, opportunistically consume less resistant fishes killed in rotenone stations during the day. *Chromis atrilobata* is a planktivore active in midwater, where it would be inaccessible to morays during the day. Although the ordinary diet of *M. clepsydra* is not known, other species of *Muraena* do normally consume reef-fishes. Photo by G.R. Allen, used with permission.

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