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Brief report

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Convergent evolution of jaws between spinosaurid dinosaurs and pike conger eels

ROMAIN VULLO, RONAN ALLAIN, and LIONEL CAVIN

Spinosaurs represent a group of peculiar theropod dinosaurs that have often been described as "crocodile-mimic", predominantly fish-eating predators, and recently claimed to have been semi-aquatic animals. Here we report a suite of craniodental characters unexpectedly shared by spinosaurs and pike conger eels. Pike conger eels are predatory, mainly piscivorous bottom-dwelling anguilliform fishes that inhabit marine and brackish environments. These two groups of dinosaurs and fishes show a mediolaterally compressed, elongated rostrum, a terminal "rosette" bearing enlarged teeth in both upper and lower jaws, and a notch posterior to the premaxillary "rosette" characterized by the presence of reduced teeth. The morphological convergence observed in the jaws of these two distantly related groups of vertebrates may result from similar feeding behaviours. This typical jaw morphology likely represents an effective biomechanical adaptation for biting and grabbing elusive prey items in low-light aquatic environments. Associated with this specialized snout morphology, numerous integumentary mechanoreceptors involved in prey detection are present in both spinosaurs and pike congers. Our new observations provide an additional convincing argument regarding the decades-long and widely debated lifestyle of spinosaurs.

Introduction

Outstanding examples of convergent evolution are regularly reported, showing how similar selective pressures can drive to common morphofunctional features in unrelated taxa, extinct or extant (e.g., Donley et al. 2004; Ji et al. 2006; Field et al. 2011; O'Brien et al. 2016). In this short communication, we present preliminary observations concerning a previously unrecognized case of convergent adaptation between spinosaurs (Archosauria: Spinosauridae), an iconic group of bizarre theropod dinosaurs, and pike congers (Actinopterygii: Muraenesocidae), a modern group of anguilliform fishes.

During the Cretaceous period, spinosaurs were a highly specialized group of megalosauroid theropods with a craniodental morphology clearly distinct from those known in all other carnivorous dinosaurs (Charig and Milner 1986, 1997; Sereno et al. 1998; Dal Sasso et al. 2005; Rayfield 2011). Moreover, the palaeoecology of spinosaurs is widely considered to have also been radically different. Spinosaurs have been early recognized as piscivorous animals (Taquet 1984; Charig and Milner 1986, 1997; see also Dyke 2010: fig. 1), although it has subsequently been shown that the diet of these theropods also included items other than fishes (Buffetaut et al. 2004). Furthermore, a semi-aquatic lifestyle has recently been proposed for these theropods on the basis of isotopic data (Amiot et al. 2010) or anatomical features (e.g., retraction of the fleshy nostrils, downsized pelvic girdle and short hindlimbs) (Ibrahim et al. 2014), and a new, hydrodynamic hypothesis regarding the function of the huge dorsal sail of *Spinosaurus* has been formulated accordingly (Gimsa et al. 2016).

Despite its strong mediolateral compression, the rostrum of spinosaurids has usually been compared with the snout of modern crocodilians (Taquet 1984; Charig and Milner 1997; Holtz 1998; Sereno et al. 1998). It is true that the crocodile (*Crocodylus* spp.) and alligator (*Alligator* spp.) skulls, in particular, share dental characters with spinosaurids, such as size heterodonty (anisodonty) and sinuous tooth rows. However, the alligator skull is strongly dorsoventrally compressed, and some biomechanical analyses have shown that the closest functional analogues to spinosaurids are the African slender-snouted crocodile (*Mecistops cataphractus*) and the Indian gharial (*Gavialis gangeticus*), which have a long tubular snout (Rayfield et al. 2007; Cuff and Rayfield 2013). In the latter, however, the straight jaw margins and the homodont condition make it morphologically very different from spinosaurids. Lastly, Foffa et al. (2014a) found that the snout-bending and torsion resistances of the spinosaurid *Baryonyx* closely match those of the Nile crocodile (*Crocodylus niloticus*) and the Late Jurassic marine reptile *Pliosaurus kevani*. Nevertheless, the general morphology of the rostrum of pliosaurids remains clearly distinct from that of spinosaurids. Although the dentition of *Pliosaurus* is similarly anisodont, tooth rows are almost rectilinear in lateral view and terminal "rosettes" are not so well defined (Benson et al. 2013).

The narrow jaws of spinosaurids actually appear strikingly similar to those of pike conger eels, a small and relatively poorly known family of tropical/subtropical anguilliform fishes (Castle and Williamson 1975; Smith 1999). Pike congers, such as the Indo-Pacific *Muraenesox* and *Congresox*, live over soft bottoms from estuaries down to about 100 m deep, and shallow species are apparently nocturnal (Smith 1999). These medium- to large-sized eels (up to 2.5 m long), recognized for their aggressiveness, feed mostly on small demersal fishes and crustaceans (George 1980; Smith 1999).

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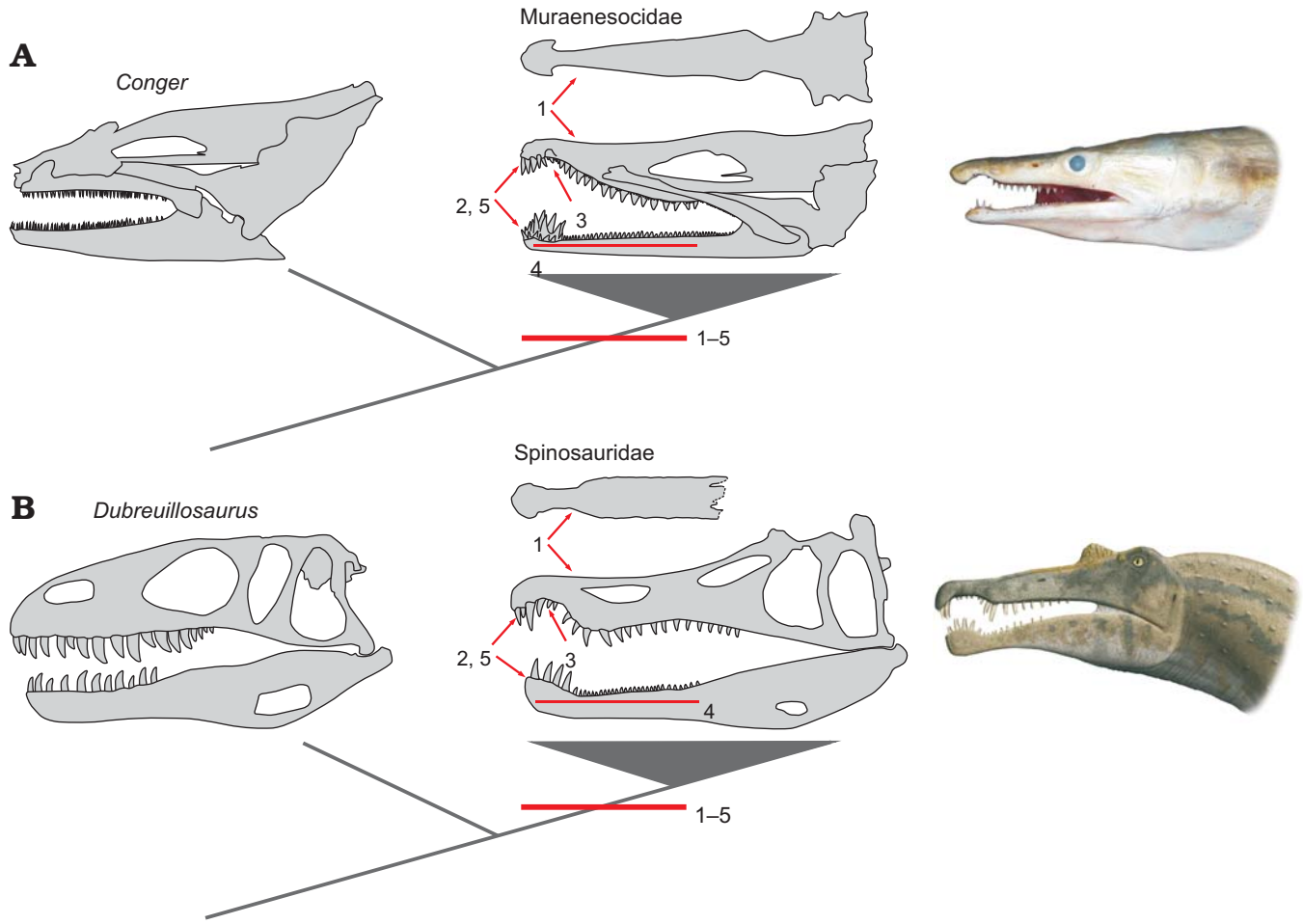


Fig. 1. Comparative evolution of jaws between Muraenesocidae (**A**) and Spinosauridae (**B**). Craniodental morphologies of Recent pike conger eels and Cretaceous spinosaurid theropod dinosaurs are convergently similar, likely resulting from similar feeding habits. In the sister groups of Muraenesocidae and Spinosauridae, here represented respectively by *Conger* (Congridae) and *Dubreuillosaurus* (Megalosauridae), skulls exhibit the plesiomorphic condition (i.e., rostrum not markedly elongated, absence of premaxillary and dentary "rosettes", dentition homodont). The derived condition observed in both pike congers and spinosaurs, which seems to be associated with an enhanced sensitivity, can be interpreted as an adaptation to forage efficiently in aquatic environments and to grab evasive prey items such as fishes. Muraenesocidae are represented here by *Muraenesox bagio* (skull and head), and Spinosauridae by *Baryonyx walkeri* (skull) and *Spinosaurus aegyptiacus* (head reconstruction; courtesy of Stephen O'Connor). Characters: 1, elongated rostrum; 2, terminal "rosette" in both upper and lower jaws; 3, deep notch posterior to the upper jaw "rosette"; 4, strong heterodonty (in size); 5, "rosettes" bearing enlarged teeth. Illustrations not to scale.

Results

The main common morphological features observed in spinosaurid dinosaurs and muraenesocid eels are: (i) snout elongated and mediolaterally compressed; (ii) rostral end of premaxilla and dentary rounded ("rosettes"); (iii) upper jaw showing in lateral view a notch posterior to premaxillary "rosette", bearing reduced teeth and receiving the dentary "rosette" when mouth is closed; (iv) strong heterodonty (in size), particularly well marked in the lower dentition; and (v) "rosettes" bearing enlarged, slender conical teeth (Takai 1959; Charig and Milner 1997; Smith 1999; Dal Sasso et al. 2005) (Fig. 1). In the upper jaw of pike congers, the fused medial bone corresponding to the robust premaxillo-ethmo-vomerine complex (Eagderi and Adriaens 2010), which is traditionally regarded as autapomorphic for the Anguilliformes, reinforces the analogy with the solid snout of spinosaurs. The main difference consists in the nature of the largest tooth-bearing element of the upper jaw, which corresponds to the maxilla in spinosaurids (paired, laterally placed, tooth rows) (Dal Sasso et al. 2005) and to the vomer in muraenesocids (a single medially placed tooth row) (Takai 1959; Smith 1999). In addition, the dentition posterior to the "rosettes" shows laterally compressed, blade-like teeth in *Muraenesox* (Castle and Williamson 1975; Smith 1999). This condition differs from the conidont condition observed in *Congresox* (Castle and Williamson 1975; Smith 1999) and spinosaurs (Dal Sasso et al. 2005; Hendrickx et al. 2015). It is worth noting that the specialized craniodental morphology of spinosaurids and muraenesocids (Fig. 1) represents a derived condition with respect to the more generalized morphology of their sister groups (here referred to as megalosaurids and congrids, respectively), whose members are medium-snouted forms with non-sinuous jaws and homodont dentitions (Takai 1959; Allain 2002; Eagderi and Adriaens 2010; Rayfield 2011).

Discussion

The acquisition of an elongated snout improving prey capture is observed in many groups of aquatic predators (e.g., trematosaurs within temnospondyls; Fortuny et al. 2011). Snout elongation in both spinosaurids and muraenesocids is apparently correlated to the acquisition of a greater sensitivity. Interestingly, it has recently been suggested that the jaw elongation observed in long-snouted anguilliforms, such as muraenesocid and nettastomatid eels, confers some advantages in prey detection and prey capture kinematics (Eagderi and Adriaens 2010). In such benthic, biting predators, the premaxillo-ethmo-vomerine complex seems to enhance the grasping and maintaining capacity, and an enlarged space for the olfactory organ would improve foraging efficiency in dark and muddy environments. In addition, long, mediolaterally compressed jaws may increase biting speed and reduce drag during prey capture. In *Spinosaurus*, fleshy nostrils were retracted to a posterior position to facilitate breathing at the water-air interface when the head was in vertical position (Ibrahim et al. 2014). Unlike in pike congers, olfaction was probably not involved in prey detection in spinosaurids. On the basis of the presence of snout neurovascular foramina (Dal Sasso et al. 2005), it has been suggested that *Spinosaurus* had a sensory integumentary system similar to that of other groups of long-snouted predators such as crocodilians (Dal Sasso et al. 2009, 2014; Ibrahim et al. 2014) and pliosaurs (Foffa et al. 2014b). Pressure receptors and the enhanced tactile sensitivity would have helped in localizing and biting aquatic prey items under low-light conditions (i.e., in turbid waters or during crepuscular/nocturnal feeding activity), similarly to mechanoreceptive neuromasts present in the pored canals of the cephalic lateral line system of pike congers.

The previously unreported convergence described here between spinosaurs and predatory fishes such as pike conger eels indicates that the former had a snout particularly well adapted to forage in water over sediments, thus providing further evidence for riparian (possibly semi-aquatic) habits and predominant piscivory in these intriguing theropod dinosaurs. This remarkable case of trophically driven convergent evolution involving two phylogenetically and temporally disparate taxa adds to the few known examples of behavioural and morphofunctional similarities between fishes and reptiles (Pettigrew et al. 1999). However, further studies and new data on foraging tactics (i.e., prey detection and capture) and jaw biomechanics of pike congers, for which very little is known, would be required to achieve a more detailed comparison between spinosaurids and muraenesocids.

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