Arthropod remains in the oral cavities of fossil reptiles support inference of early insectivory

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Inference of feeding preferences in fossil terrestrial vertebrates (tetrapods) has been drawn predominantly from craniodental morphology, and less so from fossil specimens preserving conclusive evidence of diet in the form of oral and/or gut contents. Recently, the pivotal role of insectivory in tetrapod evolution was emphasized by the identification of putative insectivores as the closest relatives of the oldest known herbivorous amniotes. We provide the first compelling evidence for insectivory among early tetrapods on the basis of two 280-million-year-old (late Palaeozoic) fossil specimens of a new species of acleistorhinid parareptile with preserved arthropod cuticle on their toothed palates. Their dental morphology, consisting of homodont marginal dentition with cutting edges and slightly recurved tips, is consistent with an insectivorous diet. The intimate association of arthropod cuticle with the oral region of two small reptiles, from a rich fossil locality that has otherwise not produced invertebrate remains, strongly supports the inference of insectivory in the reptiles. These fossils lend additional support to the hypothesis that the origins and earliest stages of higher vertebrate evolution are associated with relatively small terrestrial insectivores.

Keywords: arthropod; cuticle; diet; insectivory; Palaeozoic; parareptile

1. INTRODUCTION

Inference of feeding preferences in early terrestrial vertebrates (tetrapods) has been drawn predominantly from craniodental morphology (Reisz & Sues 2000) and less so from spectacular, but incredibly rare specimens preserving direct evidence of diet in the form of oral (Eaton 1964) and gut contents (Romer & Price 1940; Munk & Sues 1993; Kriwet *et al.* 2008).

Among Palaeozoic amniotes, an insectivorous diet has been attributed to small, terrestrial taxa that are generally characterized as possessing unspecialized dentitions of sharp, peg-like teeth (Carroll 1969; Clark & Carroll 1973; Benton 2005). These include some of the oldest known taxa assigned to Amniota (the group containing mammals, birds, squamates, turtles and crocodiles, and their extinct relatives).

These oldest known amniotes (Reisz & Modesto 1996) have recently been recognized as eurentiles (Müller & Reisz 2006), suggesting that insectivory is the plesiomorphic diet in Eurentilia, the clade that contains modern reptiles (and birds).

Recently, the pivotal role of insectivory in early vertebrate evolution was emphasized by the identification of putative insectivores as the closest relatives of the oldest known herbivorous amniotes (Reisz & Sues 2000). An insectivorous diet was posited as a probable mechanism through which early herbivores acquired from herbivorous arthropods endosymbiotic cellulolytic microbes which are necessary for extracting energy from plant structural carbohydrates. The evolutionary innovation of high-fibre herbivory, seen initially in Palaeozoic terrestrial vertebrates, is recognized as a first step in the development of the modern terrestrial ecosystem, in which numerous primary consumers support relatively few large, top predators.

Despite the possible, crucial role of insectivory as the ecological gateway to high-fibre herbivory, material of putative insectivorous Palaeozoic amniotes rarely comes to light. The attribution of an insectivorous diet to taxa continues to rely on tentative comparisons with modern analogues (e.g. Modesto & Reisz 2008). A confounding factor is the observation that fossil insects are generally not preserved at the same localities as Palaeozoic vertebrates. Here, we describe a close association of arthropod and amniote material from the Lower Permian Richards Spur locality, which is renowned for preserving thousands of early tetrapod remains, yet has never before yielded invertebrate fossils.

2. MATERIAL AND METHODS

The study material (figure 1) includes two skulls and a mandibular ramus of a new species of parareptile from the Lower Permian (Artinskian) Richards Spur fissure-fill locality of Oklahoma, and is deposited in the collections of the Sam Noble Oklahoma Museum of Natural History as OMNH 73362–73364.

OMNH 73362 and 73364 are both superbly preserved skulls. They can be assigned to the parareptilian family Acleistorhinidae on the basis of a maxillary–prefrontal contact, upper marginal dentition that extends posterior to a frontal plane passing through the orbital midpoint, and dermal skull-roof sculpturing consisting of a diffuse field of shallow dimples (Modesto & Reisz 2008, p. 681). A right mandibular ramus, OMNH 73363 (figure 1a), was collected together with the skull OMNH 73362 (see Heaton 1979, p. 71 for summary of collecting practices at Richards Spur) and may belong to the same individual, because it is of the appropriate size and it articulates perfectly with that skull (figure 1a). It is regarded as assignable to the same (yet-to-be described) genus and species on the basis of tooth morphology and sculpture pattern, which is indistinguishable from that preserved in OMNH 73362 and 73364.

3. DESCRIPTION

OMNH 73362–73364 are characterized by homodont marginal dentition (figure 1a). The marginal teeth exhibit cutting edges on their mesial and distal surfaces, and the crown apices are slightly recurved. These teeth are indistinguishable in morphology from the small, simple (i.e. not folded) marginal teeth described for the acleistorhinid *Colobomycter pholeter* (Modesto 1999; Modesto & Reisz 2008). OMNH 73362 features 23 maxillary tooth positions that extend posteriorly as far as the temporal region. In this respect, the relative length of the maxillary dentition is similar to that of the acleistorhinid *Acleistorhinus*

Figure 1. Reptile and arthropod material from the Richards Spur fossil locality, specimens OMNH 73362–73364 in the Oklahoma Museum of Natural History. (a) OMNH 73362 and 73363, skull and mandible of reptile in right lateral aspect, illustrating homodont dentition suggestive of insectivory. (b) Close-up of palate of OMNH 73362, showing short section of antenna. (c) Close-up of palate of second skull, OMNH 73364, showing presumed cercal element. Cu, arthropod cuticle.

pteroicus (deBraga & Reisz 1996), but it differs in the greater number of maxillary teeth (23 versus 17 in both *A. pteroticus* and, presumably, *C. pholeter*). A further notable difference is that the teeth forming the maxillary series of OMNH 73362 do not exhibit a straightforward decrease in tooth height mesial and distal to the largest teeth. Instead, the teeth can be grouped into at least two distinct regions arranged in tandem: the first, anterior grouping consists of seven or eight teeth, the second and third being the largest, whereas the second, posterior series comprised the remaining teeth, the third and fourth in that series (i.e. maxillary tooth positions 11 and 12) being the largest and positioned ventral to the antorbital buttress. Both groups of teeth exhibit a gradual decrease in size mesially and distally to the largest teeth.

The palate is extensively denticulated with not only the three pairs of tooth fields characteristic of most early amniotes, but also with numerous small teeth between the tooth fields. Fragments of arthropod cuticle are stuck among the extensive palatal teeth in the two skulls. In OMNH 73362 (figure 1b), the cuticle sample consists of a short series of five segments that appears to be a section of antenna, whereas in OMNH 73364 (figure 1c) the cuticle fragment is an elongate element that progresses from rod-like at its

narrow end to compressed to its broader tip, and may be a part of a cercus (i.e. a posterior appendage).

4. DISCUSSION

The morphology of the marginal teeth of the new reptile described here is strongly suggestive of an insectivorous diet. Relatively small, sharp, marginal teeth of the type present in the new reptile are generally interpreted as forming an adaptation for gripping and piercing arthropod cuticle, and a densely denticulated palate is generally thought to have functioned for holding onto food items in the oral cavity (e.g. Benton 2005, p. 110). The presence of cutting edges on the marginal teeth is not necessarily suggestive of carnivory proper (i.e. a diet of primarily (terrestrial) vertebrates, as opposed to mainly invertebrates), because edged conical teeth have been demonstrated to be equally suitable for piercing arthropod cuticle and vertebrate flesh (Freeman & Lemen 2006). We envision the new acleistorhinid reptile as feeding primarily on small invertebrates, but also, as perhaps occasional opportunities arose, preying upon tetrapods that were small enough to swallow whole. Thus, the new parareptile is a Palaeozoic analogue of extant insectivorous lizards (Pough 1973), which subsist on a wide variety of small prey (Cooper & Pérez-Mellado 2001). Similarly, the acleistorhinids *A. pteroticus* and *C. pholeter* have been interpreted to be insectivorous, with the latter probably having specialized either on invertebrates with harder cuticles or on small tetrapods (Modesto & Reisz 2008).

It is astonishing to find the preservation of arthropod remains in the oral cavities of not one but two late Palaeozoic reptile fossils for which an insectivorous diet can be inferred from dental morphology. Since 1932, the Richards Spur locality has yielded tens of thousands of vertebrate fossils, mainly disarticulated elements, but also numerous articulated and semi-articulated skulls (Heaton 1979; Olson 1991; Sullivan *et al.* 2000). Arthropod remains, however, have not been reported heretofore from the Richards Spur fissures, despite the preservation of numerous, coeval insects in Oklahoma (Carpenter 1947; Beckemeyer & Hall 2007). It is, therefore, all the more surprising to discover the first invertebrate remains from this rich fossil locality preserved within the oral cavities of insectivorous reptiles. Accordingly, we conclude that the intimate association of this arthropod material with the reptiles strongly supports the inference of insectivory in these tetrapods.

The initial stages of amniote evolution are populated by small terrestrial vertebrates that have dentition similar to that seen in acleistorhinid parareptiles, such as the new form described here. The compelling evidence of insectivory in this fossil reptile provides strong support for the hypothesis that the origins and earliest stages of higher vertebrate evolution are associated with relatively small terrestrial insectivores. We can conclude, therefore, that the subsequent diversification of Palaeozoic amniotes and the rise of small and large omnivorous, herbivorous and predatory forms arose from these modest beginnings.

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