SHORT NOTES

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A CONSIDERATION OF THE PHYLOGENETIC SIGNIFICANCE OF ACRODONTY

MARC AUGÉ

Laboratoire de Paléontologie des Vertébrés, Case 106, Université Paris VI, 4 Place Jussieu, 75252 Paris Cedex 05, France

It is widely held that the acrodont tooth implantation is the derived condition within Squamata. However, Witten (1994) has recently questioned the polarity of this character and he claims that acrodonty is primitive for Squamata. The definition of apical attachment is usually given to the term acrodont (Edmund, 1969). However, very few squamates bear truly apical teeth. The acrodont teeth of agamids and chamaeleontids are always both apical and mesial, not solely apical, although they may be attached closer to the apex than many pleurodont teeth. Thus, the traditional definition of acrodont teeth is rather misleading in squamates and needs a reappraisal. Robinson (1976) used another definition and she indicates that acrodont teeth are fused with the bone of attachment. Such a definition is equally applicable to a pleurodont dentition, because pleurodont teeth are also fused to the lingual surface of the jaw. Alifanov (1989) coined the term "subacrodont" to designate an intermediate condition between acrodonty and pleurodonty. Moreover, tooth attachment in varanids is on an obliquely sloping bony surface (subpleurodont teeth, after Hoffstetter, 1954). However, if the acrodont type of insertion is not clearly defined, it seems that there is an acrodont mode of tooth replacement, or more exactly, absence of replacement. Worn teeth are not replaced and new teeth appear at the rear of the tooth row. Acrodont teeth of squamates may also be characterized by morphological characters, such as the presence of lateral occlusal wear and acrodont dentition is generally associated with the lack of a true dental shelf which supports the tooth basis in most squamates (Moody, 1980). New fossil material assigned to the extinct genus *Tinosaurus*, from the earliest Eocene of Dormaal (Belgium), illustrates these ambiguities. The dentition of *Tinosaurus* has always been described as acrodont (Gilmore, 1928; Hecht & Hoffstetter, 1962; Augé, 1990). However, the attachment of its teeth is both lingual and apical, and *Tinosaurus* has a well defined subdental shelf on the dentary as in the members of the Cretaceous family (subfamily?) Priscagamidae (Borsuk-Bialynicka & Moody, 1984; Alifanov, 1989). Despite these facts, we can observe constant features on the dentition of *Tinosaurus*: on the labial surface of the dentary bone there are distinct vertical wear facets located on the bone, between two successive teeth. These facets extend somewhat below the level of the upper edge of the dentary. The presence of occlusal wear indicates that the acrodont teeth are permanent. The bases of acrodont teeth are merged with the lingual surface of the dentary but they do not reach the level of the subdental shelf unlike anterior pleurodont teeth that are present in most species of agamids. Hence, I suggest a definition for the acrodont dentition of lizards as follows: (1) tooth base not fused to the subdental shelf or subdental shelf absent; (2) presence of occlusal wear, mostly on the labial surface of both teeth and bone; (3) Teeth without replacement.

It seems established (Edmund, 1969; Cooper, Poole & Lawson, 1970; Cooper & Poole, 1973) on developmental data, that the acrodont tooth replacement has been derived from the continuous replacement which is regarded as plesiomorphic. Indeed, the contribution of pleurodont teeth to the main cheek series is more significant in early phases of ontogeny of the agamid dentition and decreases with increasing age. Subsequently, these teeth have lost their capacity for replacement in the postnatal stages of ontogeny.

Among lizards, acrodonty occurs only within the Iguania (Agamidae and Chamaeleonidae). The infraorder Iguania is the most primitive group of extant lizards, as shown by its basal position in recent cladograms depicting squamate phylogeny (Estes, de Queiroz & Gauthier, 1988). Acrodont teeth also occur in the Sphenodontia, the sister group to the Squamata (Evans, 1984; Gauthier, Estes & de Queiroz, 1988). Witten (1994) suggests applying the rule of parsimony to members of the Iguania and Sphenodontia. Hence, because of the presumed relationships, acrodonty is apparently primitive for Sphenodontia and Squamata, and, within Squamata, pleurodont teeth would be a derived character. The conflicting evidence resulting from the distribution of characters within taxa and early developmental stage of these characters is not easy to resolve. Some authors (e.g. DeBeer, 1930; Gould, 1977) deny the ontogenetic argument and believe that ontogeny is not a reliable source of information in phylogenetic studies. On the other hand, Nelson (1973) has re-formulated the ontogenetic argument. He considers the ontogenetic transformation of a character (*a-b*) in a species *X* and the lack of transformation in a species *Y* (noted *a-a*). If the normal rules of parsimony are applied to taxa *X* and *Y*, character state '*a*' is plesiomorphic (the most general) and state '*b*' is apomorphic (the least general). Within the Squamata, Acrodonta (Agamidae + Chamaeleonidae) are assumed to show the transformation pleurodont-acrodont (*p-a*) and other lizards are merely pleurodont (noted *p-p*). Sphenodontids are acrodont and an early pleurodont dentition is not observed in the Sphenodontid dentition. However, at least one fossil sphenodontid has anterior pleurodont teeth, the genus *Diphydontosaurus* from the Triassic of U.K. (Whiteside, 1986). The dentary and

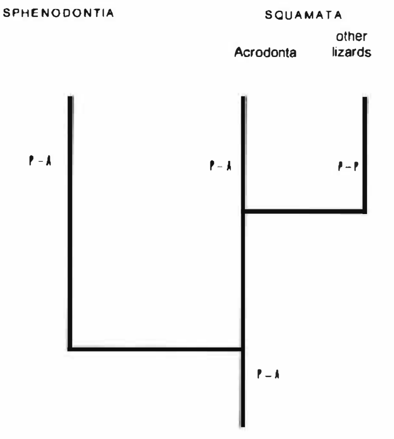

FIG. 1. Alternative interpretations of the ontogenetic transformation in Squamata and Sphenodontia.

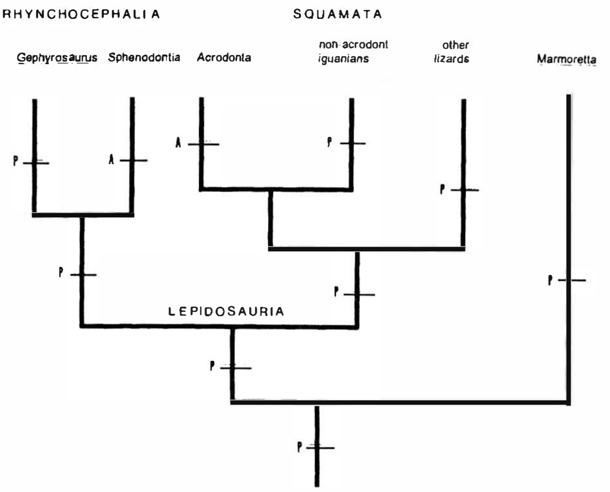

FIG. 3. Distribution of acrodonty (a) and pleurodonty (p) among Lepidosauria + *Marmoretta*.

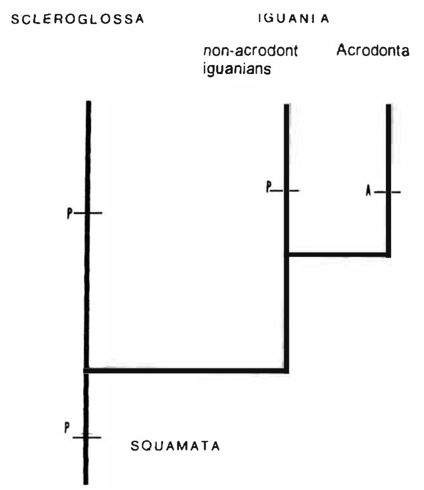

FIG. 2. Distribution of acrodonty (a) and pleurodonty (p) among Squamata. State (p) is more general than state (a).

the maxilla of *Sphenodon* bear anterior successional (replaced) teeth; moreover, those teeth are "canine-like" (Robinson, 1976). *Gephyrosaurus*, first described by Evans (1980) from the lower Jurassic of South Wales is now accepted to be the most primitive relative of the acrodont sphenodonts (Gauthier *et al.*, 1988; Fraser & Benton, 1989) and it is pleurodont. Thus, pleurodont teeth have been present in sphenodontid ancestors and their dentition gives a strong indication of the pleurodont-acrodont transformation (*p-a*). Hence, we admit that the sphenodontids show the transformation (*p-a*) and that this transformation is primitive within Squamata + Sphenodontia (Fig. 1). Moreover, within Squamata, the acrodont lizards (Agamidae + Chamaeleonidae) form a monophyletic taxon along with the Iguanidae, the Iguania (Estes, de Queiroz & Gautier, 1988). Perusal of the distribution of acrodonty and pleurodonty among Squamata leaves no doubt (Fig. 2): the pleurodont dentition is the primitive state for this character.

We may conclude that the transformation pleurodont-acrodont (i.e. acrodonty) seen in the Agamidae and the Chamaeleonidae is a derived condition for Squamata. Outgroup comparisons with the Sphenodontids entirely confirm the polarity of this character.

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