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吉林桦甸盆地中始新世端生齿鬣蜥类（有鳞目）化石及对响蜥属的评述

Krister T. SMITH[1]　Stephan F. K. SCHAAL[1]　孙　巍[2]　李春田[2]
（1 德国森肯贝格研究所和自然历史博物馆古人类学与麦塞尔研究部　法兰克福　60325）
（2 吉林大学古生物学与地层学研究中心　长春　130026）

摘要：中国吉林省中始新世桦甸组的两种端生齿鬣蜥类化石突显出端生齿类（Acrodonta）在第三纪早期的分化。第一种化石的特征为具有多个（6个）前侧生齿位及单尖且侧扁的颊齿。其牙齿与牙齿缺失附尖的主要端生齿类（如鬣蜥亚科 Agaminae 的海蜥属 *Hydrosaurus*）无特别相似之处，其亲缘关系也并不清楚。第二种的牙齿与很多现生有三尖齿的鬣蜥类（即蜡皮蜥属 *Leiolepis* 和飞蜥亚科 Draconinae）以及化石响蜥属的许多种相似；一个骨骼特征显示其可能与包括鬣蜥亚科、海蜥属、飞蜥亚科和须鬣蜥亚科（Amphibolurinae）的支系有关，但尚需更多更完整的标本以做结论。与现生鬣蜥类的比较研究表明，与响蜥属牙齿相似的三尖型齿很可能是蜡皮蜥属及飞蜥亚科中大约200个现生种的典型特征。相对于这些支系，响蜥属的鉴定特征并不充分。由于端生齿类的分化被认为始于新生代早期，因而东亚的化石材料很可能有助于阐明这一支系的演化历史，尤其是结合分子遗传学的研究方法。然而仅基于破碎颌骨材料的新分类单元名称的成倍增加并不能使我们更接近这一目标，尽力采集标本并研究可对比的现生骨骼材料应是第一位的。

关键词：中国吉林；始新世；桦甸组；端生齿类；鬣蜥科；响蜥属；衍征

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ACRODONT IGUANIANS (SQUAMATA) FROM THE MIDDLE EOCENE OF THE HUADIAN BASIN OF JILIN PROVINCE, CHINA, WITH A CRITIQUE OF THE TAXON "*TINOSAURUS*"

Krister T. SMITH[1]　Stephan F. K. SCHAAL[1]　SUN Wei[2]　LI Chun-Tian[2]
(1 *Department of Palaeoanthropology and Messel Research, Senckenberg Research Institute and Natural History Museum* Senckenberganlage 25, 60325 Frankfurt am Main, Germany　krister.smith@senckenberg.de)
(2 *Research Center for Paleontology and Stratigraphy, Jilin University* Changchun 130026, China)

Abstract　Two acrodont iguanians from the middle Eocene Huadian Formation, Jilin Province, China, highlight the diversity of Acrodonta early in the Tertiary. The first is characterized by a high number (six) of anterior pleurodont tooth loci and by unicuspid, labiolingually compressed cheek teeth. These teeth, however, show no special similarity to those of major acrodontan clades in which the accessory cusps are absent (e.g., *Hydrosaurus*, Agaminae). Its relationships are poorly constrained. The dentition of the second taxon is similar to that of a number of living tricuspid agamids (viz., *Leiolepis* and Draconinae) and species of the fossil taxon *Tinosaurus*; one osteological feature suggests it may be related to a clade including Agaminae, Hydrosaurinae, Draconinae and Amphibolurinae, but more numerous and

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complete specimens are required before conclusions are drawn. A comparative examination of living agamids demonstrates that tricuspid teeth similar to those of *Tinosaurus* spp. are probably characteristic of some 200 living species in *Leiolepis* and Draconinae. *Tinosaurus* is inadequately diagnosed with respect to these clades. Because Acrodonta is thought to have been diversifying in the early Cenozoic, fossils from eastern Asia have great potential to elucidate the evolutionary history of the clade, particularly in combination with molecular-genetic methods. However, the multiplication of new taxon names based only on jaw fragments brings us no closer to this goal. Considerable effort must first be dedicated to the collection and study of modern comparative skeletal material.

Key words Jilin, China; Eocene; Huadian Formation; Acrodonta; Agamidae; *Tinosaurus*; apomorphies

1 Introduction

Acrodont iguanians are a diverse group of Old World lizards, the sister-taxon to the mostly New World Iguanidae (Estes et al., 1988; Macey et al., 1997; Schulte and Cartwright, 2009). The stem of the clade is recognized in the fossil record beginning in the Upper Cretaceous of Asia (Alifanov, 1989; Borsuk-Białynicka and Moody, 1984; Conrad, 2008; Conrad and Norell, 2007; Gao and Norell, 2000). Taxonomically more numerous are the 15 fossil species from the Paleogene of Asia, which are distributed among ten genera: *Qianshanosaurus huangpuensis*, *Anhuisaurus huainanensis*, and *Tinosaurus doumuensis* from the Paleocene of China (Hou, 1974), *Ti. postremus* from the Paleocene of Central Asia (Averianov, 2001), *Vastanagama susani* and *Ti. indicus* from the early Eocene of India (Prasad and Bajpai, 2008), *Zephyrosaurus hypsochorosus*, *Talosaurus tribolosus*, *Mergenagama paurosa*, *Pseudotinosaurus asiaticus* and *P. ascriptivus* from the middle Eocene of Mongolia (Alifanov, 1991; Gao and Dashzeveg, 1999), *Brevidensilacerta xichuanensis* and *Huadiansaurus sunjiatunsis* from the middle Eocene of China (Li, 1991a; Zhang et al., 1986), and *Ti. lushihensis* and *Ti. yuanquensis* from the late Eocene of China (Dong, 1965; Li, 1991b). Additionally, unnamed agamids have also been identified in other locations (Averianov and Danilov, 1996; Rage, 1987). Most of these Paleogene taxa are known only from jaw fragments, and their relationships are consequently poorly understood. The sole exception in the latter respect is an unnamed form from Central Asia, which Averianov and Danilov (1996) convincingly argued is related to the living mastigure lizards, *Uromastyx*.

Recent work in the middle Eocene deposits of the Huadian Basin, Jilin Province, China, has turned up the remains of two specimens representing two species of Acrodonta. Together, these specimens provide a fuller picture of the diversity of acrodont lizards in the early Tertiary of Asia. Here, we describe and compare them with fossil and living acrodontans. We also present observations on the dentition of tricuspid agamid lizards in order to test the diagnostic value of described dental characters in fossil agamid lizards.

2 Geologic setting

Huadian Basin is a half-graben situated in the Jilin Province, northeastern China (Fig. 1; Wang et al., 2005), whose Paleogene sediments are rich in oil-shale and coal. Thus far, most vertebrate finds come from the mine of Gonglangtou, which is situated at N43°00.1′, E126°51.4′. This mine obtains sediments of Member III of the Huadian Formation, which is overlain by the conglomeratic Tumenzi Formation. The Huadian Formation has a thickness of about 500 m and consists of oil-shale, gray and black layers of sandstone, siltstone, mudstone, and seams of coal. Wang et al. (2005) interpreted the oil-shale units as representing a semi-deep to deep lacustrine environment.

Although reports of fossils from the Huadian Formation date back to the 1940s (e.g., Su-

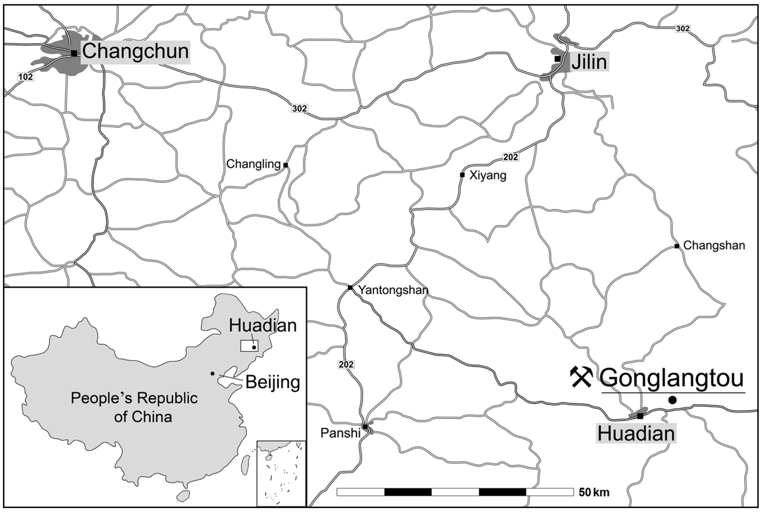

Fig. 1　Huadian and the mine of Gonglangtou located in northeastern China
The cities of Changchun and Jilin are shown for orientation (courtesy: M. Morlo)

zuki, 1946), the first detailed report on the vertebrate fossils is that of Zhang et al. (1986). The fossils from Gonglangtou now include plant pollen, leaves and fruits (Manchester et al., 2005), at least two species of snail, fishes, turtles, lizards, mammals, and birds (Beard and Wang, 1991; Hou and Ericson, 2002; Liu and Chang, 2009; Wang and Li, 1990; Zhang et al., 1986; Zhou and Sun, 1985). The mammals are represented by erinaceids, soricids, rodents, and the primate *Asiomomys*. *Asiomomys* speaks for an age of the Gonglangtou fauna slightly younger than early Uintan, probably corresponding to the late Uintan, or late middle Eocene (Beard and Wang, 1991). This age estimation is supported by the morphology of the other small mammals (Wang and Li, 1990).

During field work in the years 2006 to 2008, the oil-shale was extracted by miners underground and then transported to the surface in small carts. The rock could then be examined by the field team (S. Schaal, Sun W., M. Müller, Wu W-H., Chen F.) for fossils before the carts conveyed the oil-shale chunks to the crusher. Fossil remains of plants, snails, fishes, reptiles and mammals were found during the three field seasons. The jaws described herein were recovered in 2006; they are housed at the Research Center for Paleontology and Stratigraphy (RCPS), Jilin University, Changchun, China. The taphonomy of the Gonglangtou assemblage and additional information obtained from new fossil specimens found during field work conducted by Senckenberg in conjunction with the International Center for Geoscience Research and Education at Jilin University will be discussed elsewhere.

3　Systematic paleontology

Informal taxonomy follows Smith (2006), where "HD" refers to Huadian.

Squamata Oppel, 1811
Iguania Cope, 1864
Acrodonta Cope, 1864
Acrodontan HD-1
(Fig. 2)

Material　Partial left dentary (RCPS-CAMHD06-011; Fig. 2).

Description This partial dentary lacks an unknown portion of the posterior end (Fig. 2). The teeth are fairly well preserved, but the bone is not. Parts of the supra- and infra-Meckelian lip have also been broken away, especially near the anterior end of the bone (Fig. 2A). The lateral surface of the bone has been stripped away in places (Fig. 2B).

The dentition is divisible into three distinct regions. The first region consists of six successional teeth (sensu Robinson, 1976), all of which retain tooth bases but only one of which has a complete tooth (Fig. 2). The teeth are only shallowly pleurodont as a consequence of the relatively low dental parapet. The shafts of the five anterior teeth are nearly circular in cross-section, and the completely preserved tooth maintains this circularity almost to the very tip (Fig. 2C). The tip is slightly lingually inflected. Weak, asymmetric carinae are developed on the mesial and distal surfaces of the crown, beginning abruptly half-way up the tooth crown (as measured from the top of the parapet) and extending to the tip. The carinae bow slightly labially on both sides before curving lingually again to follow the inflected tip. In cross-section, the labial surface of each carina is smoothly continuous with the labial surface of the tooth, but lingually the carina is set off by a weak groove from the lingual surface (Fig. 2A). The tooth has a relatively blunt tip, because for much of its height it tapers only very gradually, then abruptly near the tooth tip. The tooth projects nearly parallel to the parapet. It shows no evidence of wear, except possibly at the very tip. No obvious nutritive foramina are present at the bases of the teeth. Nutritive foramina are closely related to the development of replacement pits in lizards (Zaher and Rieppel, 1999), and Cooper et al. (1970) indicate that replacement of anterior pleurodont teeth ceases with age in *Agama agama*. Possibly, then, the lack of nutritive foramina indicates that no more replacement would have taken place in this individual. The teeth become incrementally smaller toward the anterior end of the region (Fig. 2C). They also acquire a weakly triangular outline because of mesiolabial and distolabial planes of compression.

The second dentigerous region consists of three small, remnant hatchling teeth (sensu Robinson 1976; Fig. 2). These are fully acrodont and heavily worn. They are labiolingually compressed (Fig. 2C) but without distinct carinae mesially or distally. In labial or lingual profile they are triangular, with blunt, rounded tips. The first of these appears slightly more worn than the second. The third tooth is almost completely missing. Its irregular basal surface suggests it possibly was broken during life and then worn before the animal's death.

The third dentigerous region consists of four large, acrodont additional teeth (sensu Robinson 1976; Fig. 2). These teeth increase in absolute size from the first to the third; the fourth tooth is partly broken. These teeth are labiolingually compressed (Fig. 2C). No distinct carinae are formed, even at the tips, only blunt edges. These edges are slightly oblique to the axis of the jaw on the first and second teeth; that is, they pass just labial to the jaw parapet on the mesial side of the tooth and just lingual to it on the distal side of the tooth (Fig. 2C). This obliquity is lost on the third and fourth teeth. The bases of the teeth are everywhere convex in cross-section; that is, there is no place where the margin of the tooth in cross-section is concave (although on the anteromesial face of the second tooth it is nearly straight for a distance). Although the teeth are predominantly acrodont, their bases are ankylosed to a small part of the lingual surface of the parapet. The bases bulge slightly distolingually (Fig. 2A). Only the third tooth shows any trace of accessory cuspation. On the mesial margin of that tooth, approximately half-way up the crown, is a tiny cuspule (Fig. 2); it is distinguished from the main body of the tooth by a tiny groove lingually and an even tinier groove labially. The enamel of the tips of especially the third and fourth teeth is slightly roughened, but it is unclear to what process this texture may owe its existence.

Evidence of occlusally related wear is present on both teeth and bone. The very tip of the first through third of the additional teeth is very slightly worn (Fig. 2A, B). Moreover, weak longitudinal grooves on the mesial and distal edges of the crowns of the first two teeth testify to

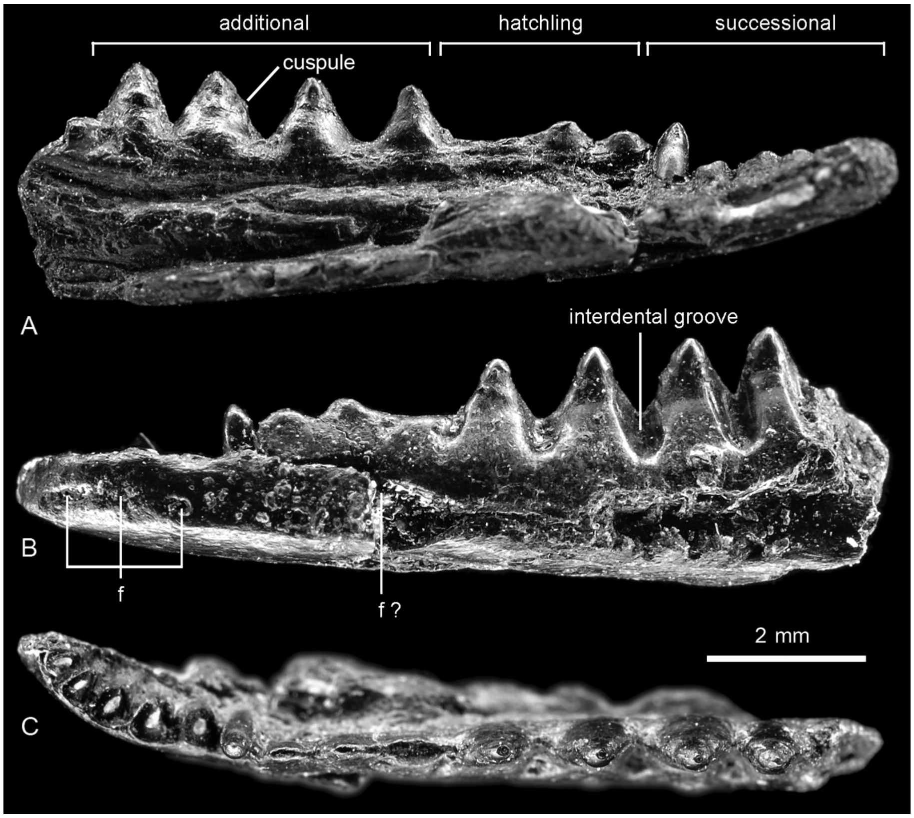

Fig. 2　Partial left dentary of Acrodontan HD-1 (RCPS-CAMHD06-011)
Photographs of specimen in A. medial, B. lateral, and C. dorsal views
Abbreviation: f. mental foramen

use. The lateral surface of the dental parapet also evinces interdental grooves (Fig. 2B). The first of these is weak and occurs between the anteroposterior level of the second and third hatchling teeth. The second groove, between the third hatchling tooth and the first additional tooth, is slightly deeper and more ventrally extensive. The next three grooves, between the additional teeth, are deep and more ventrally extensive still. The grooves are V-shaped both in labial profile (Fig. 2B) and in coronal cross-section (having flat walls; Fig. 2C). The grooves are especially deep (ventrally and medially) at their base, where the tip of the maxillary teeth inserted (Fig. 2B).

The dentary curves weakly medially at its anterior-most end (Fig. 2C). The symphysis appears to have been weak (Fig. 2A). At the anterior end of the bone, the Meckelian groove is located on the ventral margin of the bone, but elsewhere it is unrecognizable due to breakage.

As preserved, the dentary is nearly square in cross-section. The weakly convex labial surface turns strongly medially, forming a broad, nearly horizontal ventral surface (Fig. 2B). There is no evidence that this morphology is artifactual; more likely, the bend marks the extent of *M. genioglossus*, which inserts on the inferior margin of the anterior portion of the dentary (Oelrich, 1956). The medial deflection of the lateral surface of the dentary is sharpest and most pronounced beneath the hatchling and additional dentition. At least three labial (mental) foramina were present (Fig. 2B, f). They are located on the lateral surface, closer to its ventral margin than its dorsal one. The first one is the largest, a mesiodistally elongated opening at the level of the second pleurodont tooth. The second and third foramina, located at the levels of the third and fifth pleurodont teeth, respectively, are small and circular. It is conceivable that one more mental foramen was located beneath the posterior end of the hatchling dentition, where the lateral wall of the dentary is damaged. However, despite some inward crushing of the lateral wall beneath the additional teeth, it does not appear that additional mental foramina were present there.

Comparisons The morphology of the cheek teeth of Acrodontan HD-1 distinguishes the taxon from almost all examined agamids (Appendix). Most saliently, the acrodont teeth are unicuspid, which distinguishes them from those of *Draco*, (some) *Calotes*, *Japalura*, *Lyriocephalus*, *Gonocephalus*, and *Bronchocela*-in short, probably most of Draconinae (subfamilial taxonomy of Agamidae following Macey et al., 2000). In *Leiolepis* (Leiolepidinae) as well the teeth are all tricuspid. Tricuspid teeth are furthermore present in many Chamaeleonidae, including *Chamaeleo* and basal (Rieppel and Crumly, 1997; Townsend and Larson, 2002) *Brookesia*. Other agamid clades (Agaminae, *Hydrosaurus*, Amphibolurinae, *Uromastyx*) have more or less unicuspid teeth, but these differ in detail. The teeth of *Hydrosaurus amboinensis* (pers. obs.), *Uromastyx* (Cooper and Poole, 1973), and some Agaminae (generally on the posteriormost teeth) have a complicated labial and lingual surface morphology that is not seen in Acrodontan HD-1. The unicuspid teeth in *Uromastyx*, Agaminae, Amphibolurinae and *Hydrosaurus* moreover have distinct and fairly sharp mesial and distal carinae, unlike Acrodontan HD-1. The only fossil Paleogene taxa with unicuspid teeth are those plausibly referred to the *Uromastyx* lineage (Averianov and Danilov, 1996); their teeth differ from those of Acrodontan HD-1 in having convex mesial and distal margins and in being closely appressed.

The only examined species with tooth morphology approaching that of Acrodontan HD-1 is the draconine *Calotes mystaceus*. In this species, the anterior teeth in the additional series are unicuspid and lack mesial and distal carinae. They are also tall with respect to the hatchling series, so that the triangular lateral profile is acute. The anterior teeth in the additional series are more like flattened ovals in cross-section.

Acrodontan HD-1 differs, however, from *Calotes mystaceus* and all other examined acrodontans in possessing a greater number of anterior pleurodont teeth on the dentary (six). Many draconines (*Calotes*, *Japalura*, *Draco*, *Gonocephalus*, *Bronchocela*) as well as (many) *Physignathus cocincinus* (Amphibolurinae) have three such teeth, although *Lyriocephalus scutatus* possessed but a single pleurodont tooth, and *Acanthosaura armata* only two. Species of the African-West Asian clade Agaminae have no more than two. *Leiolepis belliana* has only two on the dentary, but the posterior of the two is extremely large; some *Uromastyx* show caniniform teeth on the dentary (Cooper and Poole, 1973; Robinson, 1976). Chamaeleons have no pleurodont teeth (Moody and Roček, 1980). Of all acrodontans surveyed, *Hydrosaurus amboinensis*, with five, has the largest number of pleurodont teeth on the dentary. Among Tertiary fossil acrodontans, *Tinosaurus europeocaenus*, with five, has the greatest number of anterior pleurodont loci (Augé and Smith, 1997). Other taxa — *T. yuanquensis*, *Vastanagama susani* and *Tinosaurus indicus* — have four (Li, 1991b; Prasad and Bajpai, 2008); still others — *Quercygama galliae* — even fewer (Augé and Smith, 1997). The number of pleurodont loci on the dentary of *T. doumuensis* is unclear (Hou, 1974; translation: W. Sun); figure 6 of Hou (op. cit.) suggests there may have been as many as five.

This situation in living and known Tertiary acrodontans contrasts with that seen in the earliest fossil record of the group. *Priscagama gobiensis* and *Pleurodontagama aenigmatodes* (if it is distinct from the former: Gao and Norell, 2000) have six or more pleurodont teeth anteriorly (Borsuk-Białynicka and Moody, 1984). Yet, it is far from clear that this ought to be considered the primitive condition for crown Acrodonta. The pleurodont dentition of acrodontans does not represent simply a failure of acrodont implantation to extend fully to the front of the jaws. The anterior dentigerous region of the dentary and maxilla in living acrodontans is secondarily pleurodont, a number of pleurodont tooth loci effacing anterior acrodont teeth after hatching (Cooper et al., 1970; Robinson, 1976). The rate of replacement at individual loci of these pleurodont teeth is thought to decrease with age, and it is possible that replacement eventually ceases (Cooper et al., 1970). Whether the anterior teeth of Cretaceous stem-acrodontans are primarily or secondarily pleurodont is unknown. Thus, whether the high number of pleurodont teeth in Acrodontan HD-1 is a primitive feature cannot be determined before the primary homology of anterior pleurodont teeth in the total clade of Acrodonta has been established.

Other minor features in the dentition distinguish Acrodontan HD-1. First, the region of hatchling teeth is relatively short by comparison with living acrodontans, but this may be related to the loss of more hatchling acrodont teeth to pleurodont loci. Second, the preserved pleurodont tooth in Acrodontan HD-1 is relatively small. The tooth is namely no higher than adjacent hatchling acrodont teeth. In this respect it differs from many living acrodontans, in which the pleurodont teeth of the dentary, particularly the ultimate one, are taller. But there are numerous exceptions even among living Acrodonta — for instance, *Acanthosaura armata* and Agaminae — where the pleurodont teeth on the dentary are relatively short.

In summary, Acrodontan HD-1 differs from all examined living and published Paleogene fossil acrodontans in having six pleurodont teeth on the dentary. It is also distinguished from *Leiolepis* and most Draconinae in having tall unicuspid teeth in the anterior part of the additional series. Furthermore, it differs from all extant unicuspid taxa in lacking mesial and distal carinae and flutings. The anterior part of the additional series of Acrodontan HD-1 shows great similarity to *Calotes mystaceus*, but further taxon sampling and more complete specimens of the Huadian form are necessary to determine the significance of the similarity.

Acrodontan HD-2

(Figs. 3, 4)

Material Partial left maxilla (RCPS-CAMHD06-004; Figs. 3, 4).

Description The specimen is largely complete, lacking small portions of the premaxillary process, the distal part of the facial process, and part of the palatal flange together with an unknown but probably small number of posterior teeth (Fig. 3). The specimen lay nearly on its side and was strongly compressed, so that the palatine process of the maxilla was folded to lie parallel to the facial process. This specimen represents a distinctly larger animal than RCPS-CAMHD06-011.

The dentition is clearly divisible into only two regions. Anteriorly are spaces for four pleurodont teeth (Fig. 3). The third tooth is completely preserved, together with the base of the first. The second and fourth are represented only by empty loci and appear to have been shed. This is consistent also with the presence of a large nutritive foramen (possibly an incipient resorption pit) at the lingual base of the third tooth (matrix obscures the base of the first tooth). The base of the third tooth is lingually expanded, giving it an elliptical cross-section; apically, the tooth decreases more strongly in a labiolingual direction than a mesiodistal one, such that the crown of the tooth is approximately circular in cross-section. 40% of the height of the tooth projects below the parapet of the jaw (Fig. 3A, B). Weak, blunt mesial and distal carinae descend the crown beginning at approximately half the distance below the parapet; the mesial carina appears much stronger than it is on account of a thin, irremoveable portion of lignite on the mesial margin (cf. Fig. 3A and B). The tip of the tooth is slightly lingually and distally decurved. The tip is unicuspid and acute.

The second dentigerous region consists of nine pleuracrodont teeth, which are very small anteriorly but grow rapidly in size posteriorly (Fig. 3). The first three teeth possibly represent the hatchling dentition, although they do not obviously differ morphologically from more posterior teeth. The bases of the first three teeth are fully in contact, but the third tooth is separated

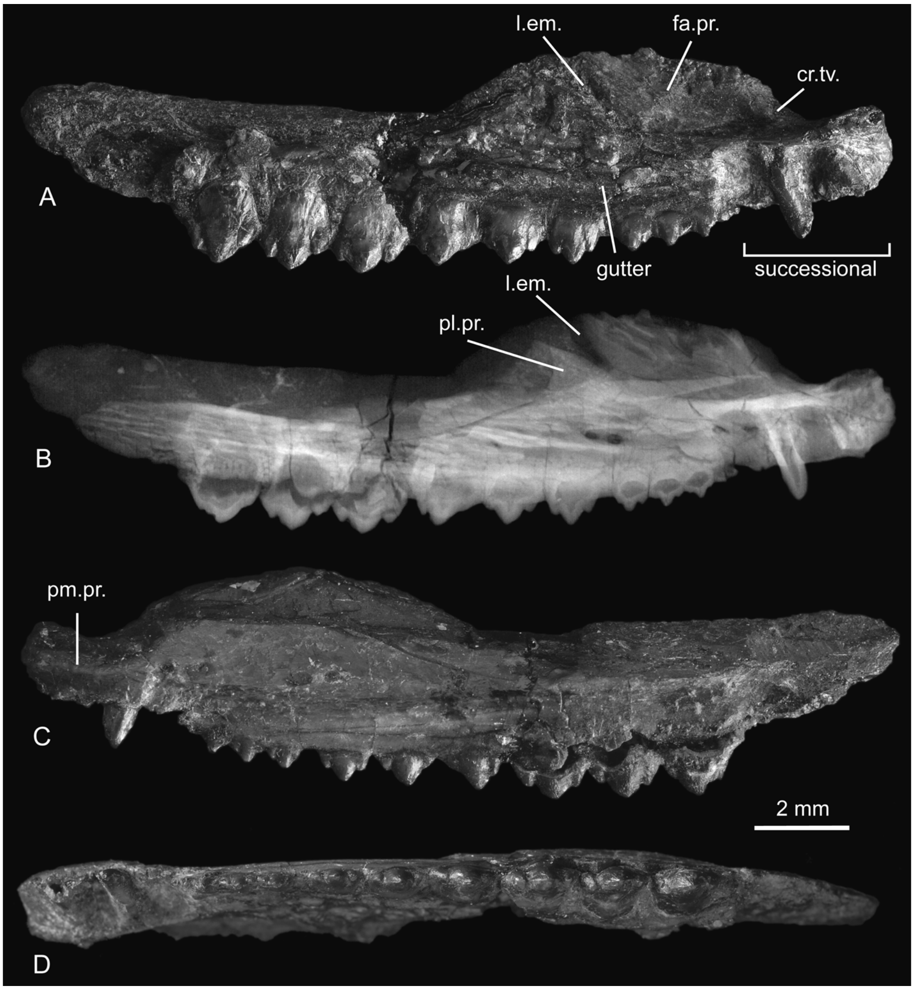

Fig. 3 Partial left maxilla of Acrodontan HD-2 (RCPS-CAMHD06-004)
Photographs of the specimen in A. medial, C. lateral, and D. ventral views; B. X-radiograph of same specimen (courtesy: J. Habersetzer); note that lignite could not be removed from several places due to the fragility of the specimen, and it obscures the osteology in parts A and C; the lignite is distinct from the bone in the X-radiograph (part B)
Abbreviations: cr. tv. crista transversalis; fa. pr. facial process; l. em. lacrimal embayment; pl. pr. palatine process; pm. pr. premaxillary process

from the remaining teeth by a space more than twice as wide as that separating posterior teeth. Moreover, the second and third of these teeth are slightly more lingually directed than the posteriorly succeeding teeth (although this could also be artifactual). Finally, the largest absolute and proportional increase in (mesiodistal) tooth length occurs at the boundary between the third and fourth teeth (cf. Robinson, 1976). It is also notable that two tiny bulges, perhaps covered by enamel, are present anterior to the first tooth; these small lumps possibly represent highly worn remnants of the hatchling dentition as well and in any case separate the first distinct acrodont tooth from the anterior pleurodont region.

The first three teeth appear to have been tricuspid (Fig. 3). Accessory cusps are separated from the central cusp by both lingual and labial grooves. On the first two teeth, the mesial and distal cusps are located relatively lower on the tooth, a little more than half-way up its total height (viewed lingually); on the third and more posterior teeth the cusps are located higher up, approximately two-thirds up the total height. The lingual surface of the central cusp of the first and second tooth appears 'pinched', bulging more acutely lingually; this is probably a consequence of interdental wear resulting from occlusion with the dentary teeth (it is also seen on the mesiolingual face of the sixth tooth in association with extensive wear).

Like the first three teeth, the six more posterior teeth, presumably additional teeth sensu Robinson (1976), are labiolingually compressed (Fig. 3D). They increase progressively in size, more so mesiodistally than labiolingually, so that the teeth appear more compressed posteriorly. Their implantation is less fully acrodont than that of anterior teeth. The accessory cusps on posterior teeth are strongly developed and nearly circular in cross-section. There is a progressive longitudinal change in the shape of the central cusp. Anteriorly, the central cusp, when viewed lingually or labially, has more or less straight (that is, uniformly inclined) mesial and distal margins; thus, the central cusp is triangular in form. Posteriorly, however, the mesial and distal margins begin to rise more steeply at first (i. e., more vertically) before turning toward the apex (Fig. 4). The mesial accessory cusp has a tendency to be located slightly more basally on the crown than the distal accessory cusp, as in some species of *Tinosaurus* (e. g., Smith, 2006). The central cusp bears mesial and distal carinae, approximately equally developed; these are not present on the accessory cusps. The carinae contribute to but do not wholly account for the change in shape of the central cusp posteriorly. The labial and lingual surfaces of the central cusp is coarsely striated, bearing impersistent, apicobasal irregularities that are almost but not quite linear; these striations are thus distinct from the straight, parallel, regular striations seen in Anguidae, for instance. They do not appear to be artifactual. Wear facets are weakly developed on the very tips of acrodont teeth four, six and seven. Lingual interdental wear facets are not clearly developed in the region of additional teeth, except between teeth five and six, where the mesial accessory cusp of tooth six is almost completely obliterated (Fig. 3A).

Dorsal to the bases of the teeth is a supradental gutter, as seen above the first six teeth in the acrodont series (Fig. 3A). This gutter appears to be especially deep above the first three teeth. The palatal shelf is approximately $1\frac{1}{4}$ mm wide medial to the presumed hatchling dentition. Immediately posterior to the third it begins to increase in width, forming a broad palatine process (Fig. 3B, pl. pr.) that is maximally about twice as wide as the shelf is anteriorly. The distal end of the palatine process appears to form a strong, hooked corner, but the sharpness of the corner and the severity of the concavity on the posterior edge of the palatine process might be exaggerated in the X-radiograph by damage of the posterior portion of the process (cf. Fig. 3A). The palatal shelf then decreases drastically in width posteriorly, as in living acrodontans. The dorsal surface of the palatal shelf appears to have had an elongate excavation posterior to the anterior base of the facial process (Fig. 3A, fa. pr.), but only the anterior-most end of the depression is exposed, and no foramina are visible. Anteriorly, the palatal shelf becomes thicker; the low, thick, rounded crista transversalis (Fig. 3A, cr. tv.) decreases rapidly in height as it extends anteromedially from the anterior base of the facial process. The dorsal surface of the premaxillary process (Fig. 3C, pm. pr.) appears to be both transversely and longitudinally concave, but it is largely obscured by irremovable sediment. At its anterior end, the premaxillary process begins to curve dorsally; because it is broken, it is not clear how tall the resultant dor-

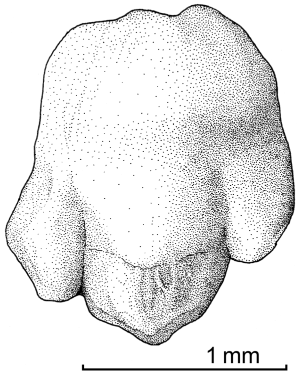

Fig. 4 Close-up illustration of dental morphology of Acrodontan HD-2: penultimate tooth of RCPS-CAMHD06-004 in lingual view

sal process would have been, but a groove near the mediolateral midpoint at the anterior end suggests that this dorsal process would have been bifurcated by the subnarial artery, as in some living acrodontans. On the ventral surface of the anterior end of the premaxillary process is a broad articulation facet that would have overlapped the lateral process of the premaxilla.

The lateral surface of the maxilla is smooth and, as preserved, laterally convex (Fig. 3C). The lateral surface of the jaw parapet appears to have been inclined slightly ventromedially. There are four clear labial foramina, all located well above the parapet: two closely spaced foramina at the level of the boundary between the pleurodont and acrodont regions, and two closely spaced foramina at the level of the presumed boundary between hatchling and additional teeth. The posterolateral corner of the facial process, which forms the dorsal limit of the lacrimal embayment (Fig. 3A, B, l. em.), is medially convex, and as in many acrodontans it was probably thickened. Additionally, it evinces oblique striations presumably related to the articulation of the prefrontal. This corner of the facial process is deeply undercut by the broad lacrimal embayment. The dorsal edge of the posterior remnant of the facial process then runs posteriorly before turning distinctly toward the ventral and then curving posteriorly again, forming a further embayment for the jugal (Fig. 3C); the posterior remnant of the facial process appears still to be developed even near the posterior end of the bone. Whether a maxillary reentrant on the jugal (Smith, 2009) was present cannot be determined, even with the aid of the X-radiography.

Comparisons Comparison of RCPS-CAMHD06-004 with 06-011 suggests they represent two different species. The former differs from the latter in having only four teeth in the anterior pleurodont region, in lacking a distinct region of hatchling dentition, in having tricuspid, less labiolingually compressed, more pleurodont teeth posteriorly, and in being distinctly larger. If the continued replacement of the anterior pleurodont teeth is taken to indicate that the animal producing 06-004 was not yet fully grown, and the apparent cessation of replacement of the anterior pleurodont teeth in 06-011 indicates that the animal was fully grown, then it is expected that the difference in adult size of the species was greater than these two specimens would suggest. Finally, the pleurodont teeth in 06-004 are relatively mesiodistally expanded, in comparison with those of 06-011, which are circular in cross-section. This variation exceeds that seen in any examined living acrodontan. Therefore, although only two specimens are known, they are taken to represent different species.

The strongest indication of the affinity of Acrodontan HD-2 is the extent of the lacrimal embayment. In Chamaeleonidae, *Uromastyx* and *Leiolepis*, as well as in Iguanidae, the edge of the facial process either runs ventrally or posteroventrally from its posterodorsal-most extent. In contrast, in Agaminae and especially in *Hydrosaurus*, Draconinae, and Amphibolurinae, the edge first runs anteroventrally, and the embayment that arises is deep enough to undercut the posterodorsal corner of the facial process, as in Acrodontan HD-2. This possibly suggests that Acrodontan HD-2 pertains to that clade of Agamidae, which contains the bulk of the family's diversity (see Macey et al., 2000; Schulte and Cartwright, 2009).

The significance of other features is less clear. As with Acrodontan HD-1, the pleurodont tooth count of Acrodontan HD-2, four, is relatively high. The number of dentary and maxillary pleurodont teeth cannot be directly compared, because they usually differ: the maxillary count being one fewer than the dentary count in almost all surveyed acrodontans except Agaminae. Most taxa have only two pleurodont teeth in the upper arcade, although *Lyriocephalus scutatus* and *Leiolepis belliana* are notable for having only one, and *Physignathus cocincinus* for having three. *Hydrosaurus amboinensis* is the only examined living acrodontan with as many as four pleurodont teeth in the maxilla, but four also appear to be present in *Tinosaurus doumuensis* (Hou, 1974). This number is not equalled by any other described Paleogene acrodont iguanian, but the Cretaceous taxon *Priscagama gobiensis* is thought to have three to five such teeth, and *Pleurodontagama aenigmatodes* four (Gao and Norell, 2000). As discussed above with regard to character polarity in tooth count, it is unclear whether the anterior pleurodont teeth of Cretaceous outgroups to Acrodonta and of most living agamids are homologous.

The primitive morphology of the facial process of the maxilla in Squamata is a flat, vertical blade extending parallel to the long axis of the bone (Smith, 2009). In many iguanians, the anterior edge of the process is inturned, partially exposing it in anterior view. In a few iguanians (*Anolis*, most phrynosomatines, some tropidurines) this inturn is abrupt, forming a well-developed canthal crest that extends to the base of the maxilla and an extensive, anterodorsally directed face (Smith, 2009). This is also true of certain agamids, namely Agaminae. On account of the strong medial inturning of the facial process in that clade, the palatal shelf of the maxilla is interrupted by a transverse wall that is the posterior face of the anterior base of the facial process. In the primitive state, also shown by Acrodontan HD-2, the dorsal surface of the palatal shelf is gradually restricted anteriorly by the obliquely trending base of the facial process.

In some taxa (e.g., *Physignathus cocincinus*, *Bronchocela cristatella*, *Pogona vitticeps*) the anteromedial edge of the facial process is markedly thickened and broadly rounded in coronal cross-section. This is presumably a derived feature and is lacking in Acrodontan HD-2.

A strong palatine process, as seen in Acrodontan HD-2, is also found in members of many major clades, including some chamaeleonids, *Leiolepis belliana*, and agamines. It is much less well developed in others, especially *Uromastyx* and Draconinae and most especially *Pogona vitticeps*, *Physignathus cocincinus*, and *Hydrosaurus amboinensis*. While this distribution might suggest that a strong process is derived in Acrodonta, some Late Cretaceous acrodontans appear to have a strong palatine process (Alifanov, 1989; Borsuk-Białynicka and Moody, 1984). In a phylogenetic analysis of Iguania, Smith (2009) found a strong process to be primitive for the clade.

In not all acrodontans do the anterior-most cheek teeth differ so substantially from the posterior ones in size as in Acrodontan HD-2. Among taxa at our disposal, a similar size difference is seen in *Leiolepis belliana*, *Physignathus cocincinus*, *Hydrosaurus amboinensis*, *Calotes mystaceus* and *C. versicolor*, *Lyriocephalus scutatus*, and *Pogona vitticeps*. This is particularly surprising insofar as a greater number of the anterior-most hatchling teeth have been replaced by pleurodont teeth in Acrodontan HD-2, *P. cocincinus*, and *H. amboinensis*. The primary reason for the size disparity is the increased height of posterior cheek teeth (≥2.5× the height of anterior teeth), not their length (which is only twice as great). In other taxa – particularly *Agama mossambica*, *Acanthocercus cyanogaster*, *Trapelus* spp., *Phrynocephalus* spp. – the posterior teeth are relatively shorter (only twice as tall). *Bronchocela cristatella*, *Japalura polygonata*, and *Gonocephalus grandis* have posterior cheek teeth of intermediate size. Many Late Cretaceous acrodontans are also characterized by relatively taller (more pleurodont) posterior teeth (Borsuk-Białynicka and Moody, 1984), which, in combination with the wide distribution of tall posterior teeth in crown Acrodonta, suggests this is primitive. The presence of tall posterior teeth in Acrodonta HD-2 merely suggests it is outside some part of Agaminae.

Acrodontan HD-2 possibly represents the same taxon as *Huadiansaurus sunjiatunsis*, also from the Huadian Formation (Zhang et al., 1986). This taxon was described as having tricuspid teeth and differentiated from Paleocene *Tinosaurus doumuensis* by its larger caniniform teeth, more distinct accessory cusps on posterior teeth, and "exposure" of the Meckelian groove (Zhang et al., 1986: trans. W. Sun). The material was not available for independent examination. The strength of the accessory cusps (particularly the distal one) on posterior cheek teeth of Acrodontan HD-2 appears to distinguish it from the Asian agamids *T. yuanquensis* (Li, 1991b: fig. 1A) and *T. indicus* (Prasad and Bajpai, 2008: fig. 6.3–9). Acrodontan HD-2 also differs from *T. lushihensis* in lacking significant "imbrication" of the posterior cheek teeth (Dong, 1965), which character, however, does occur in many living agamids, although it is generally not as highly developed. In respect of the strength of accessory cusps, however, Acrodontan HD-2 is not markedly different from *Tinosaurus* cf. *T. lushihensis* (Li, 1991a:fig. 2), *T. postremus* (Averianov, 2001), or (probably) *Vastanagama susani* (Prasad and Bajpai, 2008, where only anterior teeth are known) or *T. lushihensis* (Dong, 1965). The posterior teeth of Acrodontan HD-2 are also very similar to many European and North American species of *Tinosaurus* (e. g., Augé and Smith, 1997; Smith, 2006).

Despite the similarity in tooth form of Acrodontan HD-2 to many species of *Tinosaurus*, a measure of taxonomic caution is called for (cf. Estes, 1983). In particular, as discussed in some detail below, a similar tooth form is also found in a large number of living agamids.

4 Discussion

Tinosaurus was first recognized in the middle Eocene of the Bridger Basin, Wyoming (Leidy, 1872, 1873; Marsh, 1872). Beginning with Gilmore (1943), a large number of new species has been named from the fossil record of Asia (e. g., Averianov, 2001; Dong, 1965; Hou, 1976; Li, 1991b; Li and Xue, 2002; Prasad and Bajpai, 2008), and *Tinosaurus* has become the most species-rich acrodontan lizard genus in the fossil record, even after the removal of *T. asiaticus* Gilmore to *Pseudotinosaurus* (Alifanov, 1991). Yet, it has long been recognized that the diagnosis and the monophyly of the genus are problematic (e. g., Camp, 1923; Estes, 1983). Estes (1983:54) noted that "general similarity of teeth and geological age are the only criteria" for referral to *Tinosaurus*.

As of August, 2009, there were 416 species in the family Agamidae (TIGR Reptile Database: Uetz et al., 2007), and that number is steadily rising with continued herpetofaunal exploration of Southeast Asia (e. g., Ananjeva et al., 2007; Grismer, 2009; Hallermann and Böhme, 2000; McGuire and Alcala, 2000; Stuart and Emmett, 2006; Vindum et al., 2003). Few of these species are represented in modern skeletal collections, which is a serious hindrance to the phylogenetic allocation of fossil material. The articulation of a robust diagnosis of *Tinosaurus* with respect to living species of Agamidae has scarcely been possible. Yet, if *Tinosaurus* is to be a useful concept, it must be shown to be distinct from both extinct and extant representatives of Agamidae. What follows is a brief examination of tooth morphology among tricuspid agamids (Draconinae and *Leiolepis*).

The teeth of six species from six genera are shown in Fig. 5. The draconines (Fig. 5B–F) account for five of the 28 recognized genera of the subfamily (TIGR Reptile Database: Uetz et al., op. cit.; accessed Aug. 2009). In all of these species, the accessory cusps are separated by both labial and lingual grooves from the main cusp (see Smith, 2006 on "distinctively tricuspid"). All but one of the illustrated genera have numerous species (currently as many as 24 in *Calotes* and 26 in *Japalura*). Additionally, species in other genera of Draconinae have tricuspid teeth, notably *Draco* (with 39 species). In total, *Leiolepis* and Draconinae account for 197 species, most or all of which may have tricuspid teeth. Thus, it should not be considered that the comparisons below are exhaustive with respect to individual tooth morphology, nor is intraspecific variation explored here.

Numerous features vary among these tooth forms. Relative tooth height in *Leiolepis belliana* is usually similar to that of Acrodontan HD-2 (Fig. 5A), but in some specimens (e. g., SMF 57471) the posterior-most teeth are very tall. The posterior-most teeth of *Calotes versicolor* (Fig. 5B) and *Gonocephalus grandis* (Fig. 5C) are also relatively tall. In the first two taxa, increased tooth height is mediated by extension of the base of the tooth, whereas in *G. grandis* the main cusp is distinctively elongated but the base (judged from the tips of the accessory cusps) is unremarkable. The tall main cusps of *G. grandis* were not encountered in other agamids studied. Although the exact margin of the tooth with respect to bone of attachment (see Zaher and Rieppel, 1999) can be difficult to distinguish in acrodontans, it appears that the base of the posterior-most teeth in large *Le. belliana* is also more squared off in lingual view than in other agamids. The posterior dentary teeth as a whole are strongly distally inclined in *C. versicolor* (but, surprisingly, the maxillary teeth are not, or only slightly, mesially inclined), a feature not encountered in other taxa. The mesial and distal accessory cusps are approximately equally developed in most agamids, although there may be a slight tendency for the mesial cusp to be weaker or at least lower, and in *Lyriocephalus scutatus* the mesial cusp is indistinct (Fig. 5D), but not necessarily much lower. In cross section, the lingual surface of the central cusp has the shape of a broad V in *G. grandis*, *Ly. scutatus* and *Le. belliana*, where as it is closer to a U (i. e., it is more bulbous or rounded) in *C. versicolor* and *Bronchocela cristatella* (Fig. 5B, E).

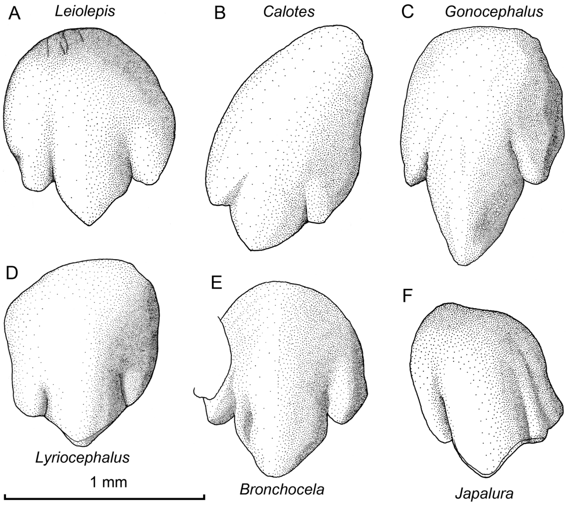

Fig. 5 Dental morphology in exemplary specimens of tricuspid members of Agamidae, in lingual view
A. penultimate left maxillary tooth of *Leiolepis belliana*, UF 62046; B. penultimate right dentary tooth (inverted) of *Calotes versicolor*, UF 68490; C. penultimate left maxillary tooth of *Gonocephalus grandis*, UF 62344; D. posterior right dentary tooth (inverted) of *Lyriocephalus scutatus*, UF 68088; E. penultimate left maxillary tooth of *Bronchocela cristatella*, UF 42346; F. penultimate right dentary tooth (inverted) of *Japalura polygonata*, UF 63381

The lingual profile of the central cusp also varies. In some tricuspid agamids, it has an inflection point that divides the mesial and distal margin into a more steeply trending and a more gently trending segment. For instance, in *Bronchocela cristatella* (Fig. 5E), as in Acrodontan HD-2 (Fig. 4), the inflection point is quite distinct; in the former, the steeply trending segment is effectively vertical (Fig. 5E), while in the latter it is oblique (Fig. 4). In other tricuspid agamids, the inflection point is located so close to the base of the central cusp that it can scarcely be distinguished (e. g., *Leiolepis belliana* and *Gonocephalus grandis*: Fig. 5A and C, respectively), and the inflection point may be entirely absent (e. g., *Calotes versicolor* and *Lyriocephalus scutatus*: Fig. 5B and D, respectively). The angle with respect to the tooth's long axis of the lingual grooves separating the mesial accessory cusp from the main cusp varies from about 0° to 10° in Acrodontan HD-2, *B. cristatella*, and *Le. belliana* to >20° in *C. versicolor* and *G. grandis*. In *G. grandis*, a weak lingual impression parallel to the mesial edge of the tooth contributes to a slight carina on that edge. A similar impression was found on the distal edge in *B. cristatella*.

Although the polarity of the evolution of these features is not understood at present, the identification of ten dental features, which despite their subtle nature nevertheless show considerable consistency within a jaw, might suggest that new phylogenetic data can still be won from detailed comparisons. Yet, the number of these features is very low compared to the number of species being considered. Thus, there is a serious risk that naming fossil agamids solely on the basis of jaw fragments will be an exercise in naming form taxa.

Diagnoses of *Tinosaurus* are apparently adequate to differentiate the species attributed to it from other fossil agamids, but they describe equally well many of the draconine species examined above, and *Leiolepis belliana*. It is probable that the same could be said of other species of the genera examined as well as those of other draconine genera. Thus, *Tinosaurus* is a form taxon, as Estes (1983) suggested, whose monophyly or even paraphyly is very far from demonstrated, and evolutionary conclusions based on the diversity or temporal or geographic distribution of "*Tinosaurus*" will not be well supported.

More importantly, the continued recognition of "*Tinosaurus*" outside of North America may mask the true phylogenetic diversity of Cenozoic agamids, a problem that the mere multiplication of new generic names will do nothing to solve. If *Uromastyx* (Averianov and Danilov, 1996) and especially *Leiolepis* were clearly distinct from other acrodontans by the early Eocene, then more deeply nested clades of Agamidae may have been diversifying as well (cf. Hugall and Lee, 2004; Macey et al., 2000; Schulte and Cartwright, 2009). An approach based on comparative study of modern forms is necessary if the fossil record is to help elucidate the evolutionary history of Acrodonta, but this will require that much more effort be devoted to the collection and study of skeletons of living agamids. Attention to non-dentigerous skeletal elements may prove particularly fruitful.

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Appendix List of specimens examined for this study

Institutional abbreviations for modern comparative osteological material: CM. Carnegie Museum of Natural History, Pittsburgh, Pennsylvania, USA; SMF. Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt am Main, Germany; UF. University of Florida Museum of Natural History, Gainesville, Florida, USA

Agamidae: *Acanthocercus cyanogaster* (UF 50556), *Acanthosaura armata* (UF 69015), *Bronchocela cristatella* (UF 42346, 51820), *Calotes mystaceus* (SMF 69754), *C. versicolor* (UF 68490, 71577), *Draco volans* (UF 53599), *Gonocephalus grandis* (UF 61548, 62344), *Hydrosaurus amboinensis* (SMF 70930), *Japalura polygonata* (UF 63381, 63382), *Laudakia stellio* (CM 39115, 39116, UF 68087), *Lyriocephalus scutatus* (UF 68088), *Phrynocephalus maculatus* (UF 71573, 71574), *Phrynocephalus interscapularis* (UF 80248), *Physignathus cocincinus* (SMF 61415, UF 71685, 71686), *Pogona vitticeps* (SMF 71829), *Pseudotrapelus sinaitus* (UF 13934), *Trapelus agilis* (UF 74674, 74675), *T. megalonyx* (UF 67819), *T. pallidus* (CM 41289), *T. ruderatus* (UF 71720, 71721); Uromastycidae: *Leiolepis belliana* (SMF 57471, UF 62046–62048), *Uromastyx acanthinurus* (UF 54136), *U. geyri* (UF 144229), *U. hardwickii* (CM 145030, 145031, 145037), *U. princeps* (CM 145043, 145044); Chamaeleonidae: *Chamaeleo hoehneli* (CM 144863, 144865)