Cretaceous Research 124 (2021) 104813

Contents lists available at ScienceDirect

Cretaceous Research

journal homepage: www.elsevier.com/locate/CretRes

Short communication

A new agamid lizard in mid-Cretaceous amber from northern Myanmar

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ARTICLE INFO

Article history:
Received 25 July 2020
Received in revised form
2 March 2021
Accepted in revised form 2 March 2021
Available online 11 March 2021

Keywords:
Squamata
Sauria
Agamidae
Cretaceous
Myanmar
Burmite
Herpetology

ABSTRACT

The first amber-embedded fossil representing the lizard family Agamidae, *Protodraco monocoli* gen. et sp. nov., is described in burmite of the lowermost Cenomanian (ca. 99 Ma; mid-Cretaceous) from northern Myanmar. It is among both the oldest known amber lizards and the oldest fossils of the family. The fossil is a well preserved left hind foot with shank, morphologically similar to basal taxa of modern Southeast Asian agamids. Because of the sparse Cretaceous fossil record it could provide a calibration point for divergence-time analyses and contradicts views that agamids colonized SE Asia during the Paleogene.
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1. Introduction

Five higher lizard taxa are currently known as amber embedded fossils (Wang and Xing, 2020). The youngest are found in Miocene amber from Hispaniola and Mexico and represent the extant genera *Anolis* Daudin, 1802 (Dactyloidae, two species) and *Sphaerodactylus* Wagler, 1830 (Sphaerodactylidae, two species). Eocene Baltic amber includes the fossil genera *Succinilacerta* Böhme & Weitschat, 1998 (Lacertidae, one species) and *Yantarogekko* Bauer, Böhme & Weitschat, 2005 (Gekkota, one species). However, numerous other Neo- and Paleogene amber fossil lizards, mostly referable to recognized genera, are known, but have not yet been thoroughly studied (Daza et al., 2014; Fontanarrosa et al., 2018). The oldest described fossil lizards in amber are of Cretaceous age and include *Cretaceogekko* Arnold & Poinar, 2008, (Gekkota, one species, 99 Ma) from Myanmar, and the *incertae sedis Baabdasaurus* Arnold, Azar, Ineich & Nel, 2002 (one species, 120 Ma) in Lebanese amber.

Early acrodontan lizards are described from the Cretaceous of Brazil (*Gueragama sulamericana* Simões et al., 2015, although its correct placement in Acrodonta is under discussion) and Morocco (*Jeddaherdan aleadonta* Apesteguía et al., 2016). Beside the likewise questionably allocated *Xianglong* Li et al., 2007 from the Early Cretaceous (see Bolet & Evans [2014] for discussion), the earliest unambiguous agamid records are *Mimeosaurus* Gilmore, 1943, *Pleurodontagama* Borsuk-Bialynicka & Moody, 1984 (both 84.9–70.6 Ma), and *Priscagama* Borsuk-Bialynicka & Moody, 1984 (125.45–70.6 Ma), all from the Cretaceous of China, Mongolia and Uzbekistan (Estes, 1983; Nessov, 1988; Alifanov, 1993). Other agamid fossil species are recognized from the Eocene of Europe (Estes, 1983) and Central and East Asia (Averianov & Danilov, 1996; Joshi & Kotlia, 2010). The initial divergence between Priscagaminae and modern subfamilies is hypothesized to have occurred at about 100 Ma (Bolet & Evans, 2014). Living agamids are believed to be of Gondwanan origin (Macey et al., 2000). The East Asian lineage has presumably been the result of more than one accretionary event and is thought to be of Indian origin (Macey et al., 2000).

Recent discoveries of squamate inclusions in Cretaceous amber from Myanmar (burmite) include a partial leg of a lizard (Fig. 1) which is assignable to the Agamidae. It is among the oldest agamid

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https://doi.org/10.1016/j.cretres.2021.104813
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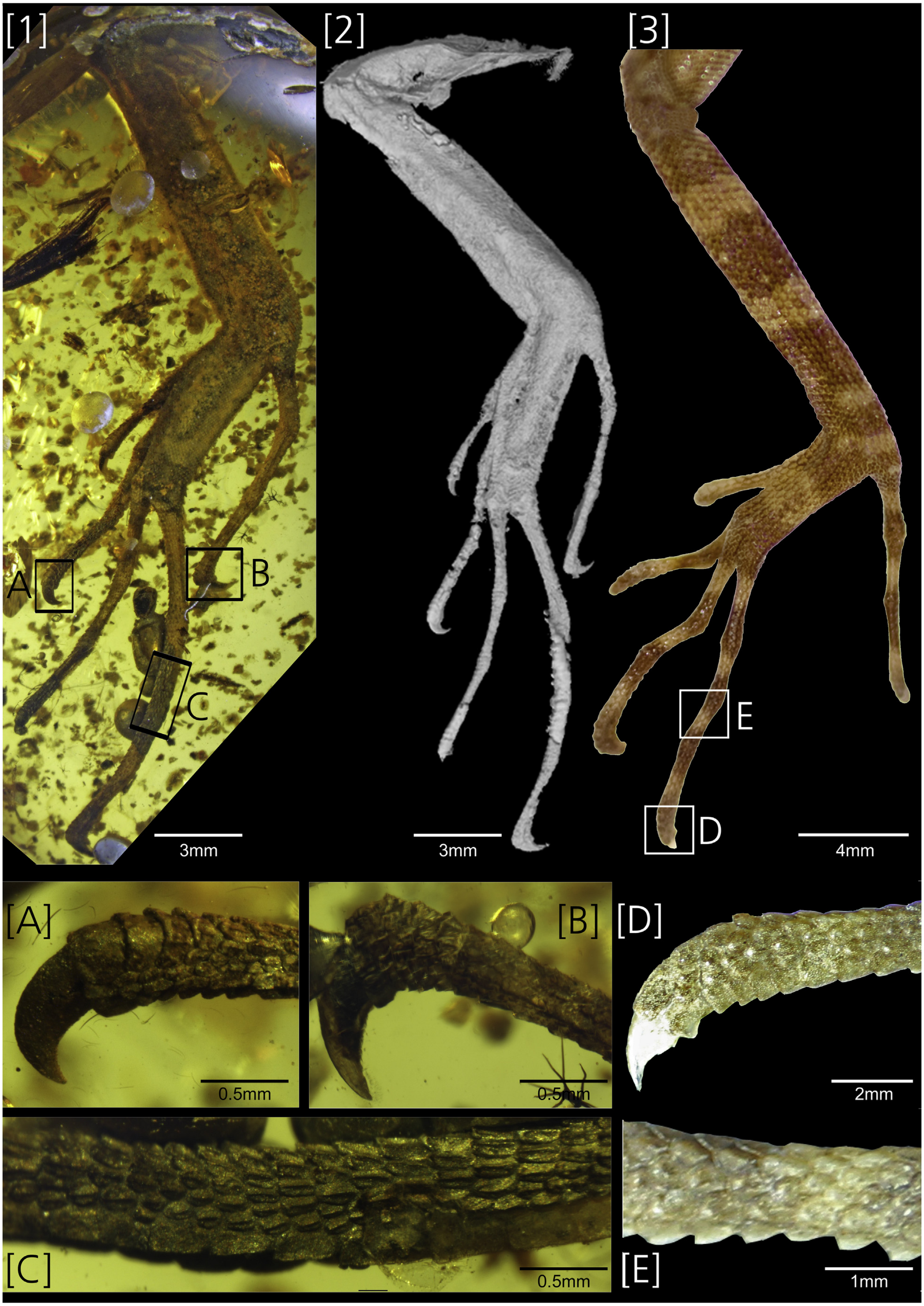
[1]
[2]
[3]
A
B
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D
3mm
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4mm
[A]
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[D]
0.5mm
0.5mm
2mm
[C]
[E]
0.5mm
1mm

fossils and was the first one to be reported from amber (Daza et al., 2016).

2. Material and methods

2.1. Methods

The fossil was photographed using a Nikon SMZ1500 stereomicroscope with 15MP digital camera and Nikon NIS Elements software. High-resolution x-ray computed tomography (HRXCT) was performed using a 2010 GE phoenix v| tome|x s240a microfocus system (General Electric, Fairfield, CT, USA). The scan was performed at 80kV and 170μA using a molybdenum target, with an output resolution of 21.6μm/voxel. The skeletal and dermal elements were reconstructed using VG Studiomax version 2.2. Skeletal elements are poorly conserved and only dermal elements could be meaningfully compared with modern specimens.

Principal component analyses (PCA, see Fig. 2), were done with the program PAST, version 2.12 (Hammer et al., 2001) using higher taxonomic levels as operational taxonomic units (OTU). The analyses were performed on a matrix of twelve binary characters (Table 1) retrieved from the fossil and additional 126 recent species in 104 genera of six higher taxonomic categories (Agamidae = 42 genera; Gekkota = 18, only padless geckos; pleurodont Iguania = 29; Lacertidae = 2; Scincidae s.l. = 8; Teiioidea = 5; see Supplemental Material).

2.2. Origin of amber

Cretaceous amber from Myanmar is well known for its numerous inclusions, especially invertebrate fossils representing more than 250 families of arthropods (Rasnitsyn et al., 2016). Moreover, this amber source also includes a high number of vertebrate species including various lizards (Daza et al., 2016). Our specimen originates from the Noije Bum 2001 Summit Site mine, Hukawng Valley, southwest of Maingkhwan, Kachin State, northern Myanmar. The site is dated to 98.79 ± 0.62 Ma (Cruickshank and Ko, 2003; Shi et al., 2012), which is according to the International Commission on Stratigraphy (see the International Stratigraohic Chart, version 2020/03) the earliest Cenomanian, of the mid-Cretaceous. The presence of araucaroid wood fibers and the results of Nuclear magnetic resonance (NMR) spectra (Poinar et al., 2007), indicate an araucarian tree as the source of the amber.

3. Results

Morphological comparisons place the fossil close to or within the morphospace of agamid OTUs. Four genera (*Bronchocela*, *Hydrosaurus*, *Mantheyus*, *Physignathus*) are always close in morphospace to the fossil (Fig. 2a−c). However, the character of the dorsal toe scales subtending the claw is only shared between the fossil and *Mantheyus* within the entire dataset.

The skin and soft tissues of the specimen are well preserved. In contrast, the skeleton is uninformative, although it does contain some indication of bone and hard tissue. Additionally, skin and soft tissues are present (Fig. 3). The enlarged white area on pedal digit IV is very likely to be calcified.

3.1. Systematics

Squamata Oppel, 1811
Iguanomorpha Sukhanov, 1961
Iguania, Cope, 1864
Acrodonta, Cope, 1864
Agamidae Spix, 1825

†***Protodraco*** gen. nov.
Type species: *Protodraco monocoli* sp. nov.
LSID: zoobank.org:act:EFB7BA60-B2AA-4F4D-8B51-B55E8FA7165D.

Diagnosis. The genus has the unique character among all known Cretaceous lizard fossils of having the first four scales behind claw of each digit distinctly larger than more proximal ones. Shank covered with small, smooth, granular scales. Fourth digit slightly longer than third. Distance between base of digit IV and that of digit V about three-fourths the length of digit V. Dorsal and lateral digit scales small, elongated, keeled and arranged in regular rows. Subdigital lamellae larger than upper scales of the digit. Claws strongly developed, curved, base nearly as wide as width of digit.
Etymology. The name is derived from the Greek word *protos* for "first" and *Draco*, the type genus of the SE Asian Draconinae.

Protodraco monocoli sp. nov.

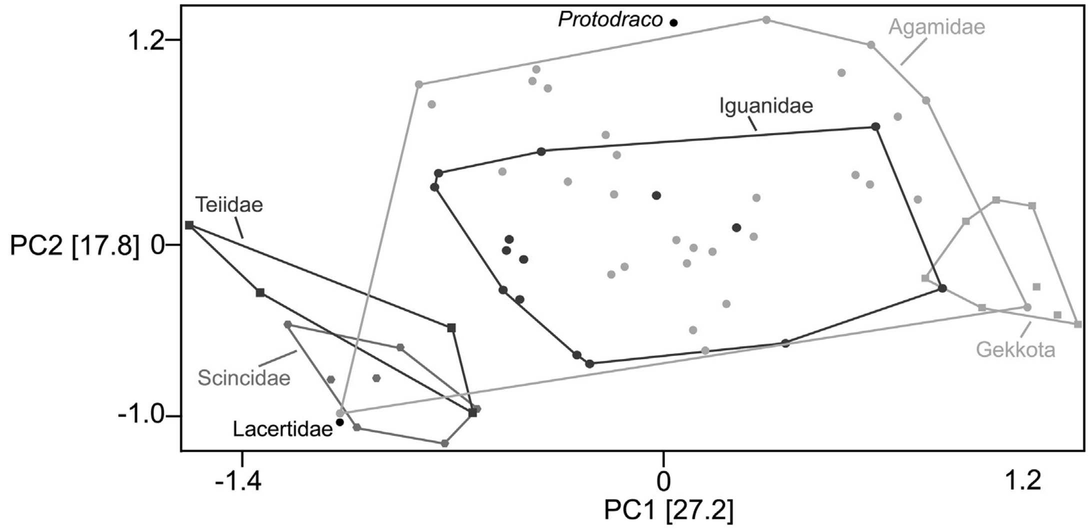
Holotype. James Zigras collection (JZC Bu266, housed at the American Museum of Natural History in New York, USA), obtained prior to 2017, an amber-embedded fossil consisting of a left foot with shank (Fig. 1).
LSID: zoobank.org:act:D204BF21-B55E-44EB-BC12-71B895BEC4C4.

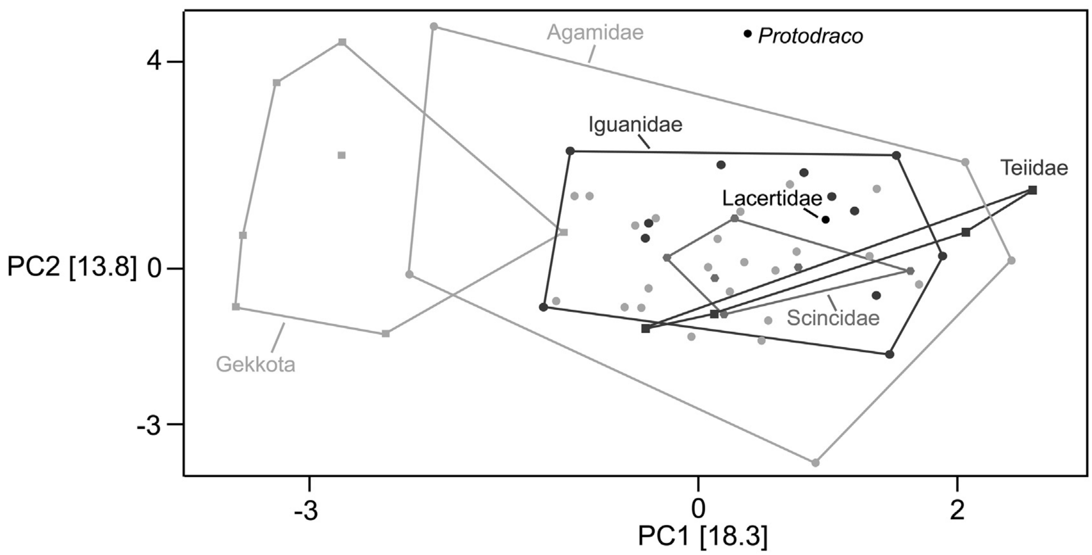
Tomograms of the fossil can be accsses online using the following link: https://doi.org/10.17602/M2/M351301.

Raw files and digital specimen can be accessed online using the following link: https://doi.org/10.17602/M2/M126219

Type locality and horizon. Derives from outcrops of the mine "Noije Bum 2001 Summit Site", Hukawng Valley, Kachin Province, Myanmar, approximately 100 km west of Myitkyina (26.335268, 96.602325) (Grimaldi et al., 2002; Dikow & Grimaldi, 2014). The source strata are assigned to the lowermost Cenomanian (99 Ma; mid-Cretaceous), based on U-Pb isotopes (Shi et al., 2012).
Description. The lizard leg is contained in an oval amber piece, clear dark yellow, about 18 mm long, 15 mm wide and, 5 mm thick with virtually no external distortion of the specimen; original surfaces polished, piece untrimmed.
The fossil is a partial left hind leg, including the distal portion of the stylopodium, zeugopodium and autopodium. Foot 18 mm from ankle to tip of ungual of digit IV. Shank shorter than length of foot, including digit IV. Scales are beautifully defined, and even have some of the color pattern preserved; shank and metatarsus covered with small, smooth, granular scales, not arranged in distinct rows. Longest digit 12 mm, rank of digit lengths I<II<V<III<IV; digit IV only slightly longer than III. Metatarsals of digits II−IV parallel and tightly bound, digit I moderately, digit V strongly offset. Distalmost interphalangeal joints strongly flexed. Claws curved, large and robust, bases about same widths as digits. Dorsal digital scales mainly small, imbricate, elongated, keeled and forming distinct rows; first four scales proximal to claw enlarged, imbricate and

Fig. 1. [1−2] Images of the holotype of *Protodraco monocoli gen. et sp. nov.* (JZC Bu266), including close-ups of several portions of the foot: A) claw of toe II; B) claw of toe V; C) mid-section of toe IV. [3] Foot of a specimen (ZFMK 95271) of *Mantheyus phuwuanensis* of about the same size as the holotype of *Protodraco monocoli*, including close-ups of several portions of the foot: D) claw of toe IV; E) mid-section of toe IV.


Protodraco
Agamidae
Iguanidae
Teiidae
Scincidae
Lacertidae
Gekkota
1.2
PC2 [17.8] 0
-1.0
-1.4
0
1.2
PC1 [27.2]


Agamidae
Protodraco
Iguanidae
Teiidae
Lacertidae
Scincidae
Gekkota
4
PC2 [13.8] 0
-3
-3
0
2
PC1 [18.3]

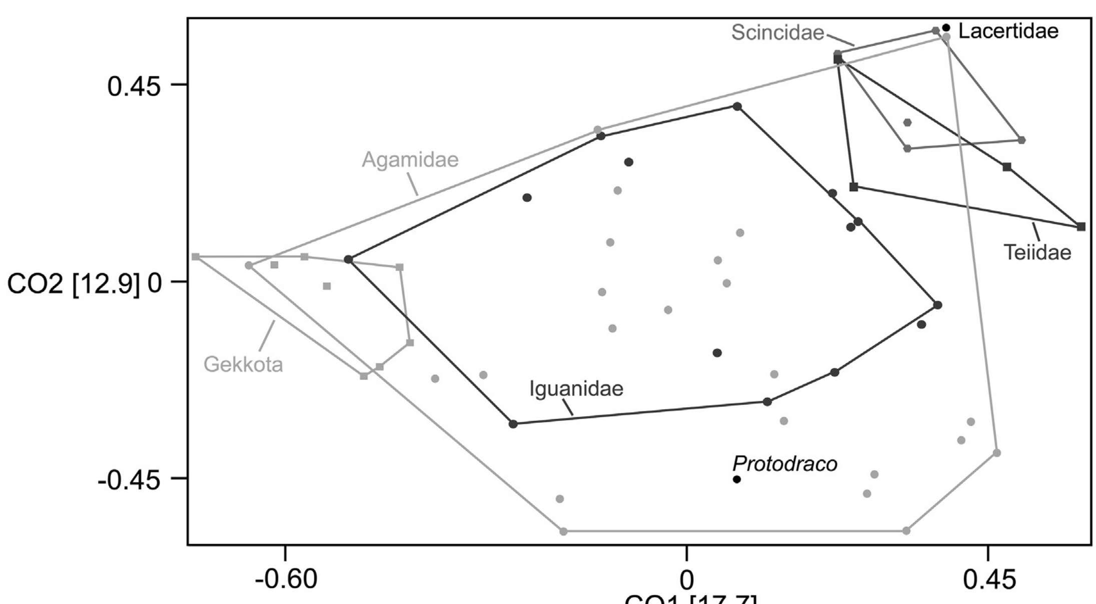

Scincidae
Lacertidae
Agamidae
Teiidae
Gekkota
Iguanidae
Protodraco
0.45
CO2 [12.9] 0
-0.45
-0.60
0
0.45
CO1 [17.7]

Table 1
Characters used for morphological comparison between the studied fossil, *Protodraco monocoli* gen. et sp. nov., and 126 extant species.

No.	Character
01	Uniform, granular scalation of the shank versus non-granular and heterogeneous.
02	First toe distinctly shorter than the fifth versus nearly as long as the fifth or longer.
03	First scales behind the claw enlarged and distinctly larger than the following upper toe scales versus uniform scalation of upper toe scales.
04	Long foot span, as long as or longer than half of the fourth toe versus shorter.
05	Upper toe scales directly in contact with the subdigital lamellae, or interjected by one, or two and more rows of lateral toe scales.
06	Scales on the lateral side of the toe small and keeled versus smooth or large and keeled.
07	Claws strongly developed versus weakly.
08	Number of digits of the left foot five versus four.
09	Fifth toe as long as or longer than the foot span versus shorter.
10	Fourth toe as long as or longer than the shank versus shorter.
11	Fifth toe as long as or longer than the fourth versus shorter.
12	Toe pads present versus absent.

smooth. Lamellae under digit much larger than upper scales; 34 lamellae under digit IV. Faint light brown coloration, with some darker transverse bands on shank.
Etymology. From *Monocoli*, a mythical one-legged creature reported by the Greek writer Pliny the Elder who also reported, probably for the first time, an amber-embedded lizard (Plinius, 77, see (König and Winkler, 1986)).

3.2. Associated material

In addition to the large hind leg, the amber also contains a layer of sand grains under the ventral surface of the foot, as well as small fragments of isolated wood/bark fibers, some stellate plant trichomes, and a small clump of five sporangia/fruiting bodies of a slime mold (the only Cretaceous fossil myxomycete; Rikkinen et al., 2019).

3.3. Additional material

Poinar et al. (2017) reported trematode metacercaria from a fossil lizard (Senckenberg Museum and Research Institute, Frankfurt am Main, Germany; F28461BUICJW) from the same locality. Based on characters given by Daza et al. (2016), Witten (1989) and Hutchinson et al. (2012) and the long tail, reduced claws, long 4th digits of both the manus and pes and configuration of the lateral scales the authors assigned the fossil to an adult sized lizard of the family Agamidae. Pending a further investigation of the specimen, the fossil can be at least placed within the genus here described.

4. Discussion

Agamids have a unique combination of skull characters (Moody, 1980; Estes et al., 1988), which unfortunately does not help identify fossil species represented exclusively by postcranial remains.

However, the unique combination of hindlimb characters of *Protodraco monocoli* —(I) shank covered with granular scales; (II) distance between digits IV and V relatively long (III); scales immediately proximal to claw enlarged, distinctly larger than more basal ones (IV); dorsum of digits covered by numerous small keeled scales; and (V) large claws— supports its classification as an agamid.

Characters (I) and (II) are found across all lizard families. Character (III) is rare, but phylogentically widespread. Character (IV) is only found in the Iguania and Gekkota. Character (V) is broadly distributed. Character (IV) places *Protodraco* within the Gekkota or Iguania, but because of character (II) most of the gekkotans examined herein can be ruled out. Synapomorphic characters are preferable for use in fossil classifications [Bell et al., 2010]. *Protodraco* does not bear any recognized apomorphic characters, but shows the unique character of the claw scalation. Additionally, we relied on a combination of very distinctive features and overall phenetic similarity to assess the identity of the fossil. The analysis shows *Protodraco* phenetically similar to *Hydrosaurus* (Fig. 2), but not sharing the rare character (III). The latter was only found in *Mantheyus* (Agamidae), *Gonatodes*, *Pristurus* and *Quedenfeldtia* (all Sphaerodactylidae), while most iguanids and agamids have an enlarged scale subtending the claw, followed by uniformly-sized scales which are distinctly smaller. *Mantheyus* is distinguished from *Protodraco* only in having smooth scales on the dorsal and lateral aspects of the digits, and in having the fourth digit not longer than the shank.

Morphological similarities could reflect similar life styles rather than phylogenetic affinity, but all genera, excluding *Bronchocela*, that are similar to *Protodraco* are in relatively basal positions among extant agamids (Macey et al., 2000). These taxa are distributed among several subfamilies and an allocation of *Protodraco* at this taxonomic rank is not possible. Moreover, Priscagaminae are only known from skulls and it is not possible to clarify the similarities of *Protodraco* with this group. The phenetic similarity of *Protodraco* to extant saxicolous and arboreal agamids occurring in SE Asia suggests that it may have had a similar lifestyle. However, the layer of sand and the presence of myxomycete sporangia in the amber piece suggest that the lizard also spent time on the ground.

Interestingly, *Protodraco* is approximately the same age as the hypothesized split between Priscagaminae and modern agamas (Bolet and Evans, 2014). A Gondwanan origin of Acrodonta has been suggested (Macey et al., 2000), but when Burmese amber was being formed India, Africa and Australia, Gondwanan fragments known to have harbored agamids, were not yet connected with Asia. This would support a Laurasian origin of extant agamid lizards in SE Asia, but as pointed out by Poinar (2019), based on geology, flora and invertebrate faunas, the area which is known as northwestern Myanmar today, has to be recognized as an island landmass with southern Gondwanan origins during the mid-Cretaceous.

Burmite contains the most diverse Cretaceous palaeobiota known from amber. More than 228 families of organisms are reported from burmite (Shi et al., 2012), compared with a range of 68–125 families for the other six major Cretaceous amber deposits (Shi et al., 2012). This applies as well for the herpetofauna, as a gekkotan (Estes et al., 1988), an agamid (this paper), a probable anguimorph (Daza et al., 2018), an albanerpetonid (Daza et al., 2020), the controversial lizard *Oculudentavis* (described as the smallest dinosaur by (Xing et al., 2020), but subsequently redetermined as a lizard by Li et al., 2020 and Bolet et al., 2020) and diverse undescribed fossils in burmite (Daza et al., 2016) provide a surprisingly rich picture of this Cretaceous community.

Fig. 2. Morphological comparison of *Protodraco* gen. nov. with 126 extant species of 104 genera within six higher taxonomic ranks (Agamidae, Gekkota, pleurodont Iguania (="Iguanidae"), Lacertidae, Scincidae *s. l.* (="Scincidae"), and Teiioidea. A: Principal Components Analyzes, Var Covar (Jolliffe cut-off = 0.11463) [PC1 Eigenvalue = 0.536349; % Variance = 27.293; PC2 0.351262; 17.875]. B: Principal Components Analyzes, Correlation (Jolliffe cut-off = 0.7) [PC1 2.19682; 18.307; PC2 1.66658; 13.888]. C: Principal Coordinates Analyzes, Euclidean (Transformation exponent c = 1) [CO1 17.722; 14.691; CO2 12.961; 10.744].

Fig. 3. HRCT of the left foot of *Protodraco monocoli* gen. et sp. nov. (JZC Bu266). Hard tissue (bone and calcified tissue) shown in white and soft tissue in green. A, ventral view; B, dorsal view. Enlarged white area on pedal digit IV is very likely to be calcified rather than a pathology.

Erroneous dating and identification of *Tikiguana estesi*, described as a primitive lizard related to Acrodonta and reported as the oldest squamate from the Late Triassic, introduced an excessively early calibration point into analyses of acrodontan diversification (Datta and Ray, 2006). As a result, several divergence-time analyses made erroneous assumptions of ancient diversification and extensive ghost lineages for all major squamate clades (Hutchinson et al., 2012; Parham et al., 2012). However, it was later shown that *Tikiguania* is almost indistinguishable from living draconines and is of Quaternary or Late Tertiary origin (Hutchinson et al., 2012). *Protodraco monocoli* could provide a calibration point for future dating studies that include agamids or iguanians more generally.

5. Conclusions

We are using a unique scalation character, only known from one extant species *Mantheyus phuwuanensis*, to describe the first amber-embedded agamid fossil, *Protodraco monocoli* gen. et sp. nov. The fossil from the lowermost Cenomanian (ca. 99 Ma; mid-Cretaceous) is a preserved left hind foot with shank, assigned to a new taxon due to the described character clearly diagnosable.

Funding statement

This research was supported by the Lemole Endowed Chair in Integrative Biology Fund at Villanova University.

Acknowledgements

We are especially thankful to James Zigras, who provided the amber fossil for detailed examination. We are grateful to David Grimaldi from the American Museum of Natural History (New York, NY, USA) who provided research facilities for this study. We are grateful to Andreas Schmitz (Genève, Switzerland) and one anonymous reviewer for comments which improved the manuscript.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.cretres.2021.104813.