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COMPUTED TOMOGRAPHY OF AN ANOLIS LIZARD IN DOMINICAN AMBER: SYSTEMATIC, TAPHONOMIC, BIOGEOGRAPHIC, AND EVOLUTIONARY IMPLICATIONS

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ABSTRACT

The cranial morphology of an **Anolis** lizard preserved in Dominican amber, observed using pseudo-three-dimensional reconstructed images derived from high-resolution X-ray computed tomography (CT) data, demonstrates the lack of a splenial in the lower jaw. The specimen is referred to T-clade anoles, the clade that includes the **A. chlorocyanus** species group, to which two other Dominican anoles in amber have been referred. The pattern of bone breakage and loss suggests trauma followed by decomposition prior to entombment. The trunk-crown ecomorph of **A. chlorocyanus** species group anoles was established on what was to become Hispaniola between approximately 33 and 20 million years ago.

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INTRODUCTION

Fossil vertebrates preserved in amber are rare. Although as many as a dozen lizards in amber may exist, most are in private collections (de Queiroz et al. 1998). Only two specimens of **Anolis** lizards preserved in Dominican amber have been described previously (Rieppel 1980, de Queiroz et al. 1998). Both descriptions are based on relatively complete skeletons retaining some soft tissue and squamation. We report here a third

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Figure 1. SMU 74976, **Anolis** lizard skull in Dominican amber. Oblique view of left side. Scale bar equals 5 mm.

Anolis lizard preserved in amber with details of skull osteology and taphonomy described and illustrated using digitally reconstructed images derived from high-resolution CT data. Application of CT imaging to the study of fossils is well documented (Cifelli et al. 1996, Rowe 1996, Brochu 2000, Kobayashi et al. 2002) and has obvious advantages in illustrating internal or hidden details through non-destructive means.

The earliest comprehensive study of the osteology of **Anolis** lizards was conducted by Etheridge (1959), utilizing radiographs of approximately 1800 specimens, and comparisons with skeletons. Radiographs were also employed in two later studies of amber-preserved **Anolis** specimens (Rieppel 1980, de Queiroz et al. 1998); the latter also utilized stereo-pairs. De Queiroz et al. (1998) tentatively referred both specimens to the **A. chlorocyanus** species group, based on postcranial characters and scale patterns.

Because these descriptions of amber-preserved anoles were based primarily on features of external morphology and skeletal characters that could be scored using binocular microscopes and stereo-radiographs, details of internal or visually obstructed morphology could not be described. For instance, neither study was able to determine the presence or absence of a splenial, a key diagnostic character of the T-clade anoles (de Queiroz et al. 1998), which includes the **A. chlorocyanus** species group.

MATERIALS AND METHODS

The specimen, SMU 74976 (Figure 1), was donated to the Shuler Museum of Paleontology at Southern Methodist University (SMU) by William S. Lowe of Granbury, Texas, who discovered it in a commercial shipment of amber containing plant and insect inclusions. The amber originated in the Dominican Republic, but was purchased through a broker without precise locality data. Dominican amber deposits are considered to be late Early to early Middle Miocene in age, approximately 15-20 million years old (Iturralde-Vinent and MacPhee 1996).

Preserved elements include a relatively complete skull, portions of the first six cervical vertebrae, some soft tissue, and limited squamation. The posterior-most vertebra is exposed to the polished amber surface; the remaining portion of the fossil is completely encapsulated. Because of the exposure of an articulated vertebra on the surface of the amber, we assume the fossil was originally more complete (e.g., not preserved only as a head and neck), but that the loss of an undetermined amount of the body occurred between fossilization and curation. The amber is dark, approximately 1.5 cm x 1 cm x .85 cm, and contains gas bubbles and organic detritus. Semi-opacity of the amber and optical distortion caused by its irregular, polished surface limits microscopic examination.

CT scanning was performed at the University of Texas High-Resolution X-ray CT Facility in Austin, Texas. The first scan used 3-slice-mode in two passes. Because of a computer error, the two passes did not line up correctly, corrupting the three- dimensional reconstruction. However, this scan provided enhanced detail on a slice-by-slice basis compared to the second scan series. Settings for the first scan were: 80 kV, 0.2 mA, no filter, air wedge, 160 per cent offset, slice thickness of 0.035 mm, standard outside diameter (S.O.D.) 19 mm, 2696 views, two samples per view, inter-slice spacing 0.06 mm, field of reconstruction 4.5 mm, reconstruction offset 190, reconstruction scale 7. Eight-bit export parameters were set to level 1600 and width 4095. The second scan was done using single-slice mode and thicker slices to provide data adequate for 3D reconstruction. Settings used were: 80 kV, 0.2 mA, no filter, air wedge, no offset, slice thickness 0.068 mm, S.O.D. 22 mm, 1800 views, 2 samples per view, inter-slice spacing 0.06 mm, field of reconstruction 4.5 mm, reconstruction offset 190, reconstruction scale 7. Eight-bit export parameters were set to level 1500 and width 3000.

The second scan resulted in 148 two-dimensional images that were used to reconstruct pseudo-three-dimensional images using Voxblast version 3.0 (Vaytek 2000). Two-dimensional images were analyzed using Scion Image for Windows version Beta 3b (Scion 1998). A polygon surface model was generated using the Voxblast iso-surface extraction function with a threshold value of 120. The polygon surface model was then imported into Lightwave version 6.5 (Newtek 2001) to produce the final renderings. Two artifacts of the iso-surface extraction algorithm are obvious. First, variability in the recorded density at the bone-amber interface manifests as occasional non-reconstruction of any bone that falls below the selected threshold value of 120, as in the void illustrated in Figure 5D. Any artifacts in the iso-surface reconstruction that could affect presence-absence or character state decisions (e.g., splenial, postfrontal) were checked against the original two-dimensional data. Surface texturing manifested as transverse raised ridges, most notably on curved surfaces, is due to sampling density in the longitudinal axis and does not reflect the state of the bone surface in the original specimen.

Descriptive nomenclature for osseous elements follows Estes et al. (1988). Institutional abbreviations are as listed in Leviton et al. (1985). A complete set of digital data is on file at the Shuler Museum of Paleontology at SMU and at the University of Texas High-Resolution X-ray CT Facility.

DESCRIPTION OF THE SKULL (SMU 74976)

The head appears to have been partially defleshed prior to encapsulation in the amber matrix (Figure 1). Skin is visible on the left side of the skull. Description of the scale pattern, as observed under a dissecting microscope, follows Williams et al. (1995). Taphonomic damage due to soft tissue decomposition adds uncertainty to some of the scale counts. The rostral is broad. There are seven supralabials to below the center of the eye. Three preoculars and three suboculars are preserved, although it is unclear whether the preserved series is an accurate reflection of the total number in life. The suboculars are in contact with the supralabials. Four canthals are clearly discernable. A minimum of 35 loreals are preserved with five loreal rows present. Ventrally, there are two sublabial and three postmental scales (including sublabials) on each side of the midline, for a total of six postmentals. The gular region, preserved as a semi-transparent membrane, lacks gular folds.

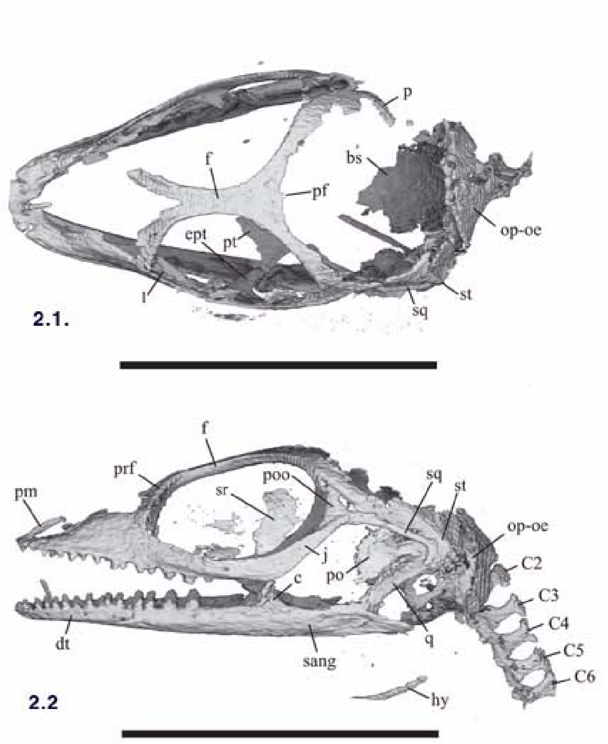

Figure 2. Iso-reconstruction of SMU 74976 in (**2.1**) dorsal and (**2.2**) left lateral views; bs = basisphenoid, c = coronoid, C1= atlas vertebra, C2 = axis vertebra, C3-C6 = cervical vertebrae, dt = dentary, ept = ectopterygoid, f = frontal, hy = hyoid fragment, j = jugal, l = lacrimal, op-eo = fused opisthotic and exoccipital, pf = pineal foramen, pm = premaxilla, po = prootic, poo = postorbital, prf = prefrontal, pt = pterygoid, q = quadrate, sang = surangular, sq = squamosal, sr = sclerotic ring, st = supratemporal. Scale bar equals 5 mm. See Appendix for a QuickTime VR movie of the skull. Click on image or number for enlargement.

The skull is 7.44 mm in length and 3.74 mm wide as measured across the jugals, similar in size and proportion to the two other amber- preserved specimens (10.5 x 4.5 for AMNH DR-SH-1, ~8.5 x 4.5 for the NMBA specimen; de Queiroz et al. 1998). It is relatively complete, with damage restricted primarily to the right lateral and posterodorsal regions.

The skull has a T-shaped, unpaired premaxilla with a narrow internarial bar that extends posteriorly to about the third or fourth maxillary tooth position (Figures 2-4). Lateral premaxillary processes form the anterior floor of the external nares. Two

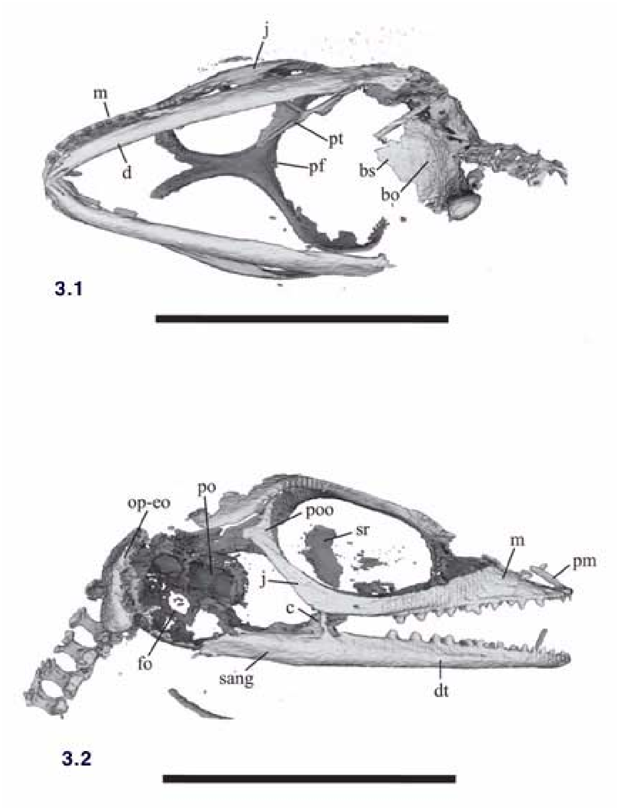

Figure 3. Iso-reconstruction of SMU 74976 in (**3.1**) ventral and (**3.2**) right lateral views; bo = basioccipital, fo = foramen ovalis, m = maxilla, other abbreviations as in Figure 2. Scale bar equals 5 mm.

sub-conical premaxillary teeth are preserved, one each in the lateral position of each side, with room for a total of five or six tooth positions. Articulation with the maxilla is oblique and loose. Septomaxillae and nasals are not preserved.

The maxillae are damaged along their dorsomedial margins. Maxillary palatine processes are well developed, protruding medially at about the seventh maxillary tooth position. The maxillae are depressed in lateral view to form the posterior floor of the external nares. Thirteen or 14 tooth positions are preserved in each maxilla, the tooth row extending posteriorly beyond the ectopterygoid contact. The left prefrontal is nearly complete, the right is badly damaged. The maxillary-prefrontal sutures are indistinct, but the junction presents a continuous surface. The prefrontals probably did not contact the nasal, as the apparently complete anterolateral process of the frontal appears to exclude this contact.

The anterior roof table is formed by the frontal, which is relatively complete. Diverging anterior processes extend anterolaterally to contact the prefrontals and medially exhibit a shelf-like facet for articulation with the nasals. There is no evidence of an anterior medial process as seen in **A. carolinensis** (Stimie 1966), but instead the frontal forms a v-shaped cleft. The frontal is strongly constricted between the orbits, forming their complete dorsal margin. Discernable parietal remnants occur only at the lateral frontal-parietal suture; however, an inverted cone-like notch is preserved at the midline of the suture (Figs 3.1, 4.2) and may represent the anterior wall of the pineal foramen. Postfrontals are not present as in the NMBA specimen. Although a left postfrontal is reported on the AMNH specimen, examination of the stereo-radiograph in de Queiroz et al. (1998) illustrates the element in a damaged portion of the skull and suggests it may as likely represent a fragment of the frontal.

Figure 4. Iso-reconstruction of SMU 74976 in (**4.1**) anterior and (**4.2**) posterior views. Abbreviations as in Figures 2 and 3. Scale bar equals 2 mm

The left lacrimal is present, forming the anteroventral margin of the orbit, and meeting the anterior margin of the jugal posteroventrally. The anterior terminus of the jugal is lateral to the posterior maxillary tooth position. The jugal forms the greater portion of the ventral and posterior orbital margin, and overlies the lateral face of the postorbital posteriorly. There is no contact of the jugal with the squamosal. The tri-radiate postorbitals are complete; the two anterior processes complete the posterodorsal orbital margin, while the third extends posteriorly to contact the squamosal, although this junction is not clearly defined. The rod-like squamosal lies lateral to the preserved left supratemporal and does not appear to have had contact with the parietal. It terminates posteriorly in a hook-like, ventrally directed process that extends into the tympanic recess of the quadrate.

Only the left quadrate is preserved. It is anteroventrally oriented and the main shaft is long and narrow (4:1 length/width). The tympanic rim is well developed, extending from the squamosal to the posterolateral shelf that lies dorsal to the articular facet of the mandibular fossa, forming a shallow concavity.

Of the palatal bones, the left and right ectopterygoids and left pterygoid are present. The left ectopteryogoid-pterygoid contact is unclear. The ectopterygoid contacts the jugal near the posterior terminus of the maxilla. Pterygoid teeth are not present, and there is no contact of the pterygoid (or ectopterygoid) with the lacrimal.

There is significant damage to the braincase and little of this region could be resolved. Of the basicranial elements, the parabasisphenoid is absent and the basioccipital is fragmentary. The left prootic and opisthotic are present, exposing the osseous labyrinth medially. Within the osseous labyrinth, the posterior semi-circular canals, which do not exhibit prominent ridges on their surfaces, are visible. Nothing could be discerned concerning fusion or suturing of contacts. Within the fenestra, ovalis there is the remnant of a ring-like ossification that may be the stapedial footplate.

The mandibles are relatively well preserved (Figure 5). The dentaries each bear 17-18 tooth positions. The anterior teeth are sub-conical, with tricuspid tooth morphology appearing at about the tenth tooth position. There is no sculpting of the dentaries. However, the left dentary displays a laterally and medially directed ossified protuberance that may represent a pathology. As many as six mental foramina are present on the lateral surface of each dentary. Meckel's groove is enclosed to the posterior tooth position. The posteromedial end of the dentary is divided into dorsal and ventral processes; the dorsal process terminates against the anterior process of the coronoid while the ventral process tapers posteriorly, terminating ventral to the apex of the coronoid. Laterally, the dentary meets the surangular in a poorly defined suture.

The ventral extension of the labial process of the coronoid is unclear. The anteromedial process extends ventrally to terminate without a posterior projection, and the posteromedial process contacts the articular. There is no splenial. It is unclear if the angular is present. The surangular forms the dorsal margin of the lower jaw posterior to the coronoid process. There is a well-developed medial angular process of the articular.

COMPARISONS AND SYSTEMATIC RELATIONSHIPS

The genus **Anolis** includes approximately 300 living species, more than 35 of which occur on the island of Hispaniola (Roughgarden 1995). This systematic diversity is accompanied by ecological diversity allowing as many as six species to coexist by segregating habitat from ground to canopy. The ecological adaptations of anole species are accompanied by morphological features. Species can thus be grouped into ecomorphs (Williams 1983), taking into account both their preferred perches, a reflection of habitat selection, and their body proportions: crown giant, twig dwarf, trunk-crown, trunk, trunk-ground, and bush grass. SMU 74976 falls within the size range of smaller extant species included in the twig dwarf ecomorph. However, while the adaptive significance of anole ecomorphs is clear, the systematic significance of anoles grouped into ecomorphs requires extended phylogenetic analysis (de Queiroz et al. 1998, Poe 1998). With respect to Hispaniolan amber-preserved fossils, de Queiroz et al. (1998) defined a T-clade within the **A. chlorocyanus** species group based on morphological characters.

The intra- and inter-specific variability of anoles emphasizes a consistent problem in paleontology because samples are often too small to allow evaluation of individual variation. In this case, not only is the sample size small, but SMU 74976 is incomplete with only cranial characters discernible. There are two further complications. The American Museum (AMNH) and Basel (NMBA) specimens of Hispaniolan amber anoles both present postcranial characters, which SMU 74976 does not. Moreover, only SMU 74976 has been CT scanned, providing enhanced resolution of cranial osteological features compared to the other specimens. Nevertheless, this is the sample available for study and it does present a view, however incomplete, of anoles in the Caribbean 15 to 20 million years ago.

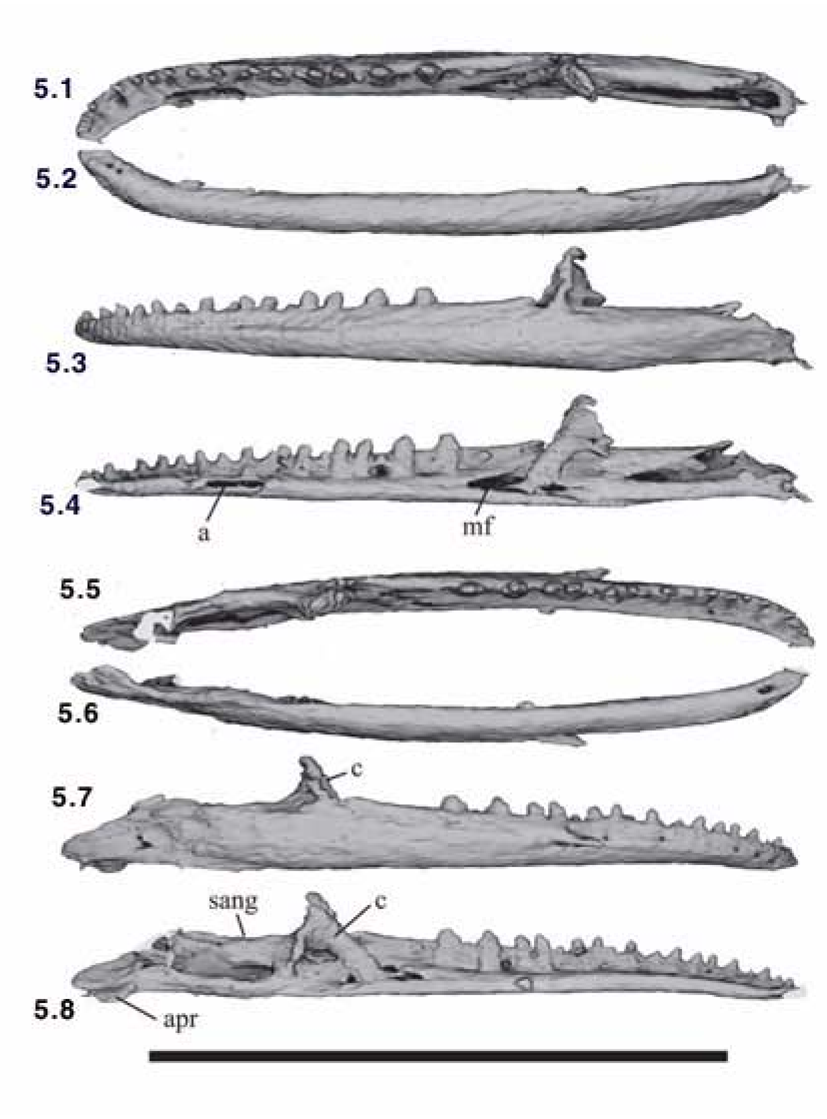

Figure 5. Iso-reconstruction of SMU 74976 mandibles. (**5.1**) right dorsal, (**5.2**) right ventral, (**5.3**) right lateral (image reversed for comparison), (**5.4**) right medial, (**5.5**) left dorsal, (**5.6**) left ventral, (**5.7**) left lateral (image reversed for comparison), (**5.8**) left medial, a = artifact of surface extraction algorithm; apr = angular process of the articular; mf = Meckelian fossa; other abbreviations as in Figures 2-4. Scale bar equals 5 mm.

Skull measurements, characteristics of the postcranial skeleton, and external morphology allowed Rieppel (1980) to place the NMBA specimen tentatively within the green anole species group, which includes **A. chlorocyanus** and **A. coelestinus**, among others (Williams 1965, 1976). De Queiroz et al. (1998), in their study of the American Museum specimen, re-examined the NMBA specimen, recognizing what were considered minor differences between the two. Pterygoid teeth are not present in AMNH DR-SH-1, but two or three are possibly present in the NMBA specimen. Maxillary and dentary tooth counts and positions differ slightly. These differences were attributed to intraspecific variation as seen in other anoles. They concluded that both of the specimens could be tentatively assigned to the **A. chlorocyanus** species group within the T-clade anoles (de Queiroz et al.1998). In addition, de Queiroz et al. (1998) considered the diagnosis of **Anolis dominicanus**, which has as its holotype the NMBA specimen, insufficient to distinguish it from certain extant **Anolis** species, yet inadequate to synonymize the name.

Direct comparisons among the three anoles in amber considered here are limited because of the condition of each specimen and the techniques used. One characteristic, absence of the splenial,

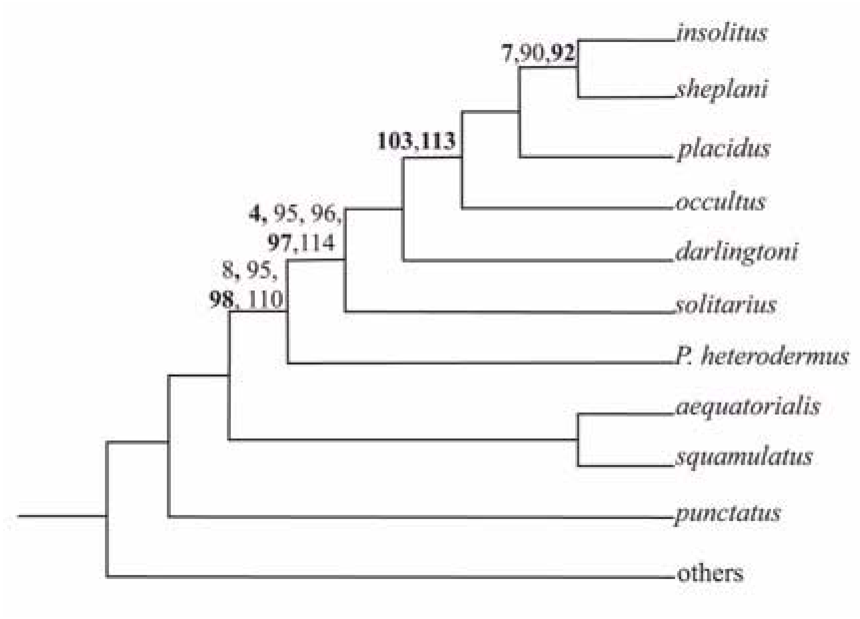

Figure 6. Cladogram of twig dwarf anoles (modified from Poe 1998). Numbers indicate characters from Poe for which SMU 74976 can be scored. Those in bold indicate derived attributes in SMU 74976. See Table 1 for referral to illustrations of significant cranial osteological characters in the phylogenetic interpretation of Hispaniolan twig dwarf anoles.

Table 1. Squamation and cranial osteological characters that could be scored for SMU 74976 (modified from Poe, 1998, which should be consulted for elaboration). Referred figures illustrate significant cranial osteological characters in the phylogenetic interpretation of Hispaniolan dwarf-twig anoles as placed in Figure 6.

Character no.	Character Description
4	Number of sublabials
7	Median number of postmental scales
8	Median number of loreal scale rows
90	Pineal foramen at parietal-frontal suture, or in parietal (Figures 3.1, 4.2)
92	Postfrontal present, or absent (Figure 2.1)
95	Dorsal process of jugal terminates on posterior or medial aspect of postorbital, or on later-alaspect of postorbital. (Two derived states are scored on Poe's cladogram, but the primitive attribute, jugal terminates on lateral aspect of postorbital, is exhibited by SMU 74976 relative to both; Figure 2.2.)
96	Jugal-squamosal contact absent, or present (Figure 2.2)
97	Pterygoid-lacrymal contact absent, or present (Figure 2.1)
98	Jugal extends superiorly to form anterior border of lacrimal, or abuts ventral edge of lacrimal (Figure 2.2)
101	Pterygoid teeth present, or absent
103	Maxilla extends posteriorly to ectopterygoid, or beyond ectopterygoid (Figure 2.1, 2.2)
106	Quadrate shelf absent, or present
107	Posteroventral process of the squamosal extendsventrally into auditory cup of quadrate, or squamosal excluded from auditory cup by dorsal surface of quadrate
108	Posterodorsal process of squamosal contacts supratemporal, or extends above supratemporal to contact parietal
110	Angular process of articular present, large, or reduced or absent (Figure 5.8)
113	Splenial present, or absent (Figure 5.4, 5.8)
114	Anteromedial process of coronoid extends anteriorly, or ventral aspect of anteromedial process projects posteriorly (Figure 5.4, 5.8)

is discernible through CT scanning of SMU 74976, but not observable in the others, to which the technique has not been applied. Absence of the splenial, along with long lateral interclavicular processes in contact with clavicles, define the T-clade anoles (de Queiroz et al. 1998). The pectoral girdle is not preserved in the SMU specimen.

SMU 74976 has two sublabial scales on each side and five loreal rows, as opposed to three sublabials, and three loreal rows in the AMNH specimen (de Queiroz et al. 1998). Both have at least six postmentals and lack gular folds. The AMNH specimen may have postfrontals, but they appear to be lacking in SMU 74976 (however, the relevant area is defleshed and we cannot rule out taphonomic loss). The NMBA specimen appears to lack postfrontals. It also appears to have pterygoid teeth, which are lacking in both the SMU and AMNH specimens.

Morphological characters in anoles, as demonstrated by Poe (1998), for example, are for the most part both variable and homoplastic. While Poe's (1998) phylogenetic analysis of Hispaniolan twig dwarf anoles utilizes more than morphological characters alone, he specifically addresses inherent variability of morphological characters by utilizing frequency, unscaled, and any-instance approaches to phylogenetic analysis. For two relevant skull characters of Poe (character 97, pterygoid-lacrimal contact, and 98, jugal extension) intraspecific variability is considered plesiomorphic.

In all, Poe used 116 characters. Table 1 lists the characters from Poe (1998) that could be scored for SMU 74976. Figure 6 is abstracted from Poe's figure 17 and shows the distribution of characters observed in SMU 74976 along that portion of the cladogram leading to the twig dwarf clade and which Poe specifically discusses. His analyses show monophyly of the Hispaniolan twig dwarf species **A. placidus**, **A. insolitus**, and **A. sheplani**, with the latter two being sister species. The Hispaniolan twig dwarf clade is diagnosed by two unique, unreversed synapomorphies of the parietal, neither of which could be scored in SMU 74976 because of damage to the back of the skull. The sister to the three Hispaniolan twig dwarf species is the Puerto Rican twig dwarf **A. occultus**. Two characters (103, maxilla extends to ectopterygoid, and 113, loss of splenial) are among the eight synapomorphies supporting the clade. **A. darlingtoni** and **A. solitarius**, twig species from Hispaniola and northern South America, and **Phenacosaurus heterodermus** from South America, are the closest relatives of twig dwarf species. This clade is supported by eleven unambiguous synapomorphies. Four of the characters defining the clade could be scored in SMU 74976. Of those four characters, one shows the derived character state, and three are primitive. Ten characters diagnose the next less inclusive clade, five of which can be scored for SMU 74976, two of those exhibiting the derived character state. The phylogenetic resolution for all the taxa in Poe's cladogram represented by "others" in our Figure 6 is weakly supported and represents deep branches. Poe's demonstration that the derived characters in his cladogram are homoplastic coupled with the mix of primitive and derived characters at relevant basal nodes reveal that SMU 74976 is not a twig dwarf species. Thus, absence of the splenial (character 113) in SMU 74976 is homoplastic with Hispaniolan twig dwarf anoles.

Given the variability seen in modern anoles, uncertainties in observation in the amber-preserved specimens, and differential preservation preventing comparison, we find ourselves in a similar situation to de Queiroz et al. (1998), in that we cannot satisfactorily demonstrate that the three specimens are not members of the same species, nor demonstrate apomorphic characters shared exclusively by all three. They may very well belong to the same species, or their variation may indicate specific diversity; it cannot be determined with certainty at this time. Nevertheless, some speculation is permitted based on characters we can observe and the composition of the modern Hispaniolan fauna. While we can rule out the loss of the splenial in SMU 74976 as an unambiguous synapomorphy with twig dwarf anoles, we cannot rule it out as a synapomorphy with T-clade anoles. If that proves valid, SMU 74976 is more likely to share a close relationship with the AMNH specimen, which exhibits the characteristic T-clade interclavicle morphology. Far less certain, but certainly plausible based on possible identity with the AMNH and NMBA specimens, is inclusion within the **A. chlorocyanus** species group, as indicated by characters of the caudal vertebrae in the AMNH and NMBA specimens. Morphometric analysis by de Queiroz et al. (1998) includes the AMNH and NMBA specimens within the trunk-crown anole ecomorph. **A. chlorocyanus** species group anoles are trunk-crown anoles, which inhabit Hispaniola and other Caribbean islands today.

DISCUSSION

E. E. Williams (1972) stated why West Indian anoles are well-suited subjects for the study of ecological principles: They are taxonomically well known. There are large museum collections providing a source for metric data. They are diverse. And they are distributed over a large number of islands with varying levels of diversity, which allows each island fauna to be used as an experiment of nature (his term) to test ecological hypotheses. While those attributes are valid, complicated issues relevant to longer time scales (e.g., the biogeographical stratification of island faunas and the phylogenetic relationships among scattered island species) are often difficult to resolve. Ecological, phylogenetic, and paleontological approaches have been applied, each elucidating some aspect of diversity, origin, biogeography, or ecology, but none alone or in aggregate is totally satisfactory. For example, Losos and de Queiroz (1997) proposed that the ancestral Greater Antillean anole may have been a trunk-crown ecomorph, which could be consistent with phylogenetic analysis, with a South American origin, and with the meager fossil record (de Queiroz et al. 1998). But the fossil record, while suggestive, is insufficient to test this hypothesis rigorously. Nevertheless, new data from this and other studies contribute to understanding the historical and ecological development of the Caribbean fauna.

Taphonomy

Iturralde-Vinent and MacPhee (1996) document an age of 15-20 Ma for Dominican amber. They further demonstrate the likelihood that amber-bearing deposits in Hispaniola are derived from a single sedimentary basin. Vegetation within the basin is known to include the resin-producing legume **Hymenaea protera**, which gave rise to the amber, **Acacia eocaribbeanensis**, half a dozen or so other angiosperms represented by flowers in amber, two genera of bamboo, an epiphytic fern (**Grammitis succinea)**, two genera of mosses, and 10 liverworts (Hueber and Langenheim 1986, Dilcher et al. 1992, Graham 1992, Poinar 1991, 1992). **Hymenaea courbaril**, an extant resin-producing species of Mexico, Central America, South America, and the Antilles, grows in a variety of habitats and reaches a height of 55 m (Poinar 1992). Resin is produced in all growing stages, but in mature trees resin issues from openings to resin cavities in the cambial zone. **Hymenaea courbaril** is pollinated by glossophagine bats.

The placement of the AMNH and NMBA specimens within the trunk-crown ecomorph is consistent with exposure to weeping sap from **Hymenaea** limbs, and therefore the ultimate incorporation of these particular lizards into amber as inclusions. An ecology that facilitates the association of sap and organisms is necessary because entombment must take place before introduction into a sedimentary environment. For animals larger than insects, but still too small to escape from the sticky sap, death and subsequent entombment is a possibility; especially if their ecology places them in proximity.

The SMU 74976 specimen, as observed under a dissecting microscope and with CT data, is substantially de-fleshed and has missing bony elements. The nasals, right prefrontal, and the majority of the palate are missing without damage to adjacent bones. In contrast, the damage to the parietal is accompanied by breaks and many adjacent bones are missing, including the right temporal arcade, right quadrate, and the right posterior mandible. The pattern of damage appears to indicate trauma that excised a portion of the right rear of the skull. None of the missing bones is present in the amber specimen, although a portion of the left hyoid arch is still in place, a delicate structure that could easily have been floated off. The pattern of bone damage and loss as illustrated by CT images suggests to us an initial trauma to the posterior portion of the head, followed by some degree of decomposition and loss of flesh, resulting in further loss of bones from the anterior and palatal regions. Subsequent total engulfment in resin preserved the head, albeit with an unknown degree of further decomposition. The pattern and orientation of air bubbles entrapped in the amber of SMU74796 indicate the specimens skull was in an upright position and out-gassing due to decompostion was primarily concentrated in the damaged rear portion of the skull as illustrated in Figure 7. All three of the amber anole specimens exhibit damage to the skull roof primarily in the region of the parietal and temporal arcade.

Damage to the skull roof could have been inflicted by predators. Documented predators of modern Caribbean anoles are predominantly birds, specifically American kestrels (**Falco sparverius**) and pearly-eyed thrashers (**Magarops fuscatus**) (Adolf and Roughgarden 1983, McLaughlin and Roughgarden 1989, Roughgarden 1995). Andrews (1990) noted that the kestrel **Falco tinnunculus** sometimes consumes only part of its prey, pulling flesh through a hole at the top of the thorax, leaving skin with some bone behind. Further, the damage exhibited in the three amber anoles is consistent with damage patterns documented in bird predation on small mammals (Andrews 1990). Birds have been identified from Dominican amber from preserved feathers. The only identified feather is tentatively referred to the Picidae, woodpeckers and their relatives (Poinar 1992). Nevertheless, it is reasonable to assume that predatory birds played a similar ecological role with respect to anoles in the Caribbean during the Miocene as they do now. Although not conclusive, the common pattern of

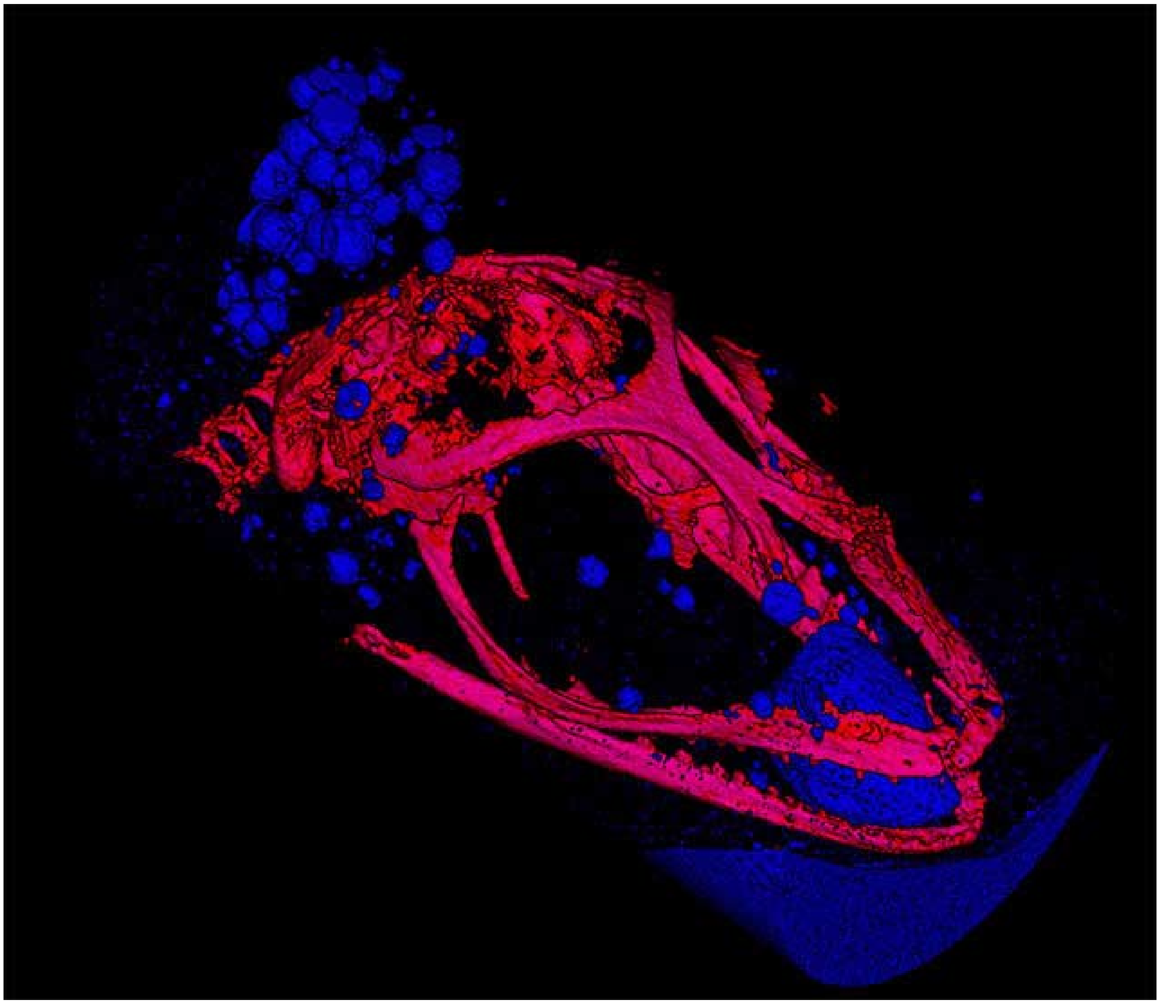

Figure 7. This figure illustrates the spatial relationship of the air bubbles to the skull. Two density ranges representative of bone (in shades of red) and air (in shades of blue) were rendered opaque with all other densities set to transparent. The large concentration of air in the oral cavity is likely due to entrapment of atmospheric gasses as the skull was entombed whereas bubbles in the rear portion of the skull are likely representative of out-gassing of decomposing organic material. The orientation of the bubbles indicate the skull was in an approximately upright position subsequent to entombment and while the resin was still sufficiently viscous to allow transport of air bubbles.

damage to the three amber-preserved anoles appears indicative of aborted avian predation. If so, their final entombment in resin occurred passively after death, followed by incorporation into the depositional system of a single sedimentary basin some 15 to 20 million years ago.

Historical Biogeography

The age of the sediments containing amber as determined by Iturralde-Vinent and MacPhee (1996) provides the younger age limit for the first occurrence of anoles on Hispaniola and also the oldest fossil evidence for anoles anywhere in the Caribbean. However, because the earliest fossil evidence does not necessarily correspond clearly to the time of introduction especially where the fossil record is poor, the Dominican anoles do not set an acceptable older age limit for anoles first entering the Caribbean region. Nor do they provide definitive information as to the biogeographical route or mechanism utilized. Evidence relevant to those issues must be garnered from other sources.

Iturralde-Vinent and MacPhee (1999 and references therein) elaborated a biogeographical model based on geological evidence, which provides both a mechanism and an older age limit for the introduction of anoles to Hispaniola. Fundamental to their model is the recognition that continual emergence of any current Caribbean island does not extend older than 35 million years ago. Before that time islands certainly existed, but subsidence and sea level rise prior to 35 million years ago drowned all existing land surfaces. The land fauna of early Cenozoic Caribbean islands would have been extirpated by inundation. Between 35 and 33 Ma, the Eocene-Oligocene transition, tectonic uplift coincided with a drop in sea level, which according to Iturralde-Vinent and MacPhee (1999) resulted in exposure of what they term the “GAARlandia landspan.” A landspan is simply a subaerial connection between a continent, in this case South America, and off-shelf islands, specifically the Greater Antilles joined by an emergent Aves Ridge, hence the name GAARlandia. Subsequent to 33 million years ago, general subsidence and sea level rise caused connections of GAARlandia to founder and existing islands to form. Originally, the landspan connection with South America provided a dispersal route to Hispaniola and other presumptive islands of the Greater Antilles, followed by the drowning of the connection, which facilitated alternately continent-island and island-island vicariance. This model is certainly extreme compared to concepts of Caribbean biogeography that attribute a greater permanency to islands and rely on overwater dispersal to distribute island fauna (e.g., Hedges 1996). However, the extremes are not mutually exclusive in the context of geologic time.

The important points for this study are that the uplift and sea level drop between 35 and 33 million years ago provide a maximum age for the introduction of anoles to any existing island. Subsequent biogeographical events would involve vicariance certainly and over-water dispersal possibly. In any event, anoles arrived on Hispaniola between 35 and 15 million years ago at most. Given the uncertainties involved, anoles could have colonized what is now Hispaniola between 33 and 20 million years ago. This represents a maximum span of 20 million years and a minimum of 13, which seems a rather long interval in which to constrain a biogeographical event except when compared to the previous less constrained interval that could accommodate 50 million years or more if the origin of Caribbean anoles was taken back into the Cretaceous.

Evolutionary Pattern

Within that 13 million-year interval, T-clade and probably **A. chlorocyanus**-group anoles became established, at least on that portion of Hispaniola where the amber-producing sedimentary basin is located. The three specimens available differ among themselves and may belong to more than one species. Moreover, they could belong to one or more living species. This extent of morphological variability is not limited to the fossils in question, but has long been recognized in extant anoles and is still not completely resolved even with large samples of living species. Nevertheless, phylogenetic analyses are contributing to defining clades. For example, Poe’s (1998) study focused on the twig dwarf clade, the geographic distribution of which does not appear to contradict the biogeographical model of Iturralde-Vinent and MacPhee (1999). Cladistic resolution of the other anoles considered in Poe’s study is less reliable and not well supported. His results are consistent with the molecular study of Jackman et al. (1999) that concluded the deep branches characteristic of **Anolis** phylogeny in their study reflected early and rapid diversification. That may well explain part of the complexity of anole evolution, but it cannot explain all of the inter- and intra-island evolution that has occurred in the Caribbean since the Miocene. Individual variation in anoles on islands apparently manifests rapidly and adaptively as shown by colonization experiments (Losos et al. 1997, see also Thomson 1997), bringing about morphological differentiation within a population in a matter of decades.

Anolis is a long-lived genus with a high degree of specific diversity, a confusing amount of inter- and intra-specific morphological variability and homoplasy, but a low level of morphological disparity. Those attributes combine to obfuscate the phylogenetic and biogeographical history of the group. But this same pattern of attributes contributed to the viability of the genus over time. The fossil anoles from the Dominican Republic, while few in number, suggest that the evolutionary-ecological strategy this pattern reflects has not changed significantly over the past 15 million years.

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Appendix. 240 images arranged in 20 columns (18 degrees offset) by 12 rows (15 degrees offset) were used to generate the linked Quicktime Virtual Reality Objects (QTVR), allowing 3d manipulation and viewing of the skull of SMU74976. After selecting the desired size object below, and allowing time for download, place the cursor in the window, press the left mouse button and drag the object to the desired viewing angle. You can also use the toolbar under the QTVR to zoom and pan the object.
QuickTime is required and available for download from Apple.