A Second *Anolis* Lizard in Dominican Amber and the Systematics and Ecological Morphology of Dominican Amber Anoles

KEVIN DE QUEIROZ,[1] LING-RU CHU,[2] AND JONATHAN B. LOSOS[3]

ABSTRACT

A fossil *Anolis* lizard in the collections of the American Museum of Natural History is the second anole preserved in amber from the Dominican Republic (Miocene epoch) to be studied. The fossil exhibits skeletal characters indicating that it is a juvenile member of a large clade of anoles that includes many extant Hispaniolan species and is characterized by close association between the clavicles and the lateral processes of the interclavicle. Standard external characters that can be scored in the fossil are identical to those of two of the four extant species in the *A. chlorocyanus* species group; however, because relatively few characters can be scored in the fossil, and because the polarities of the relevant characters are currently unknown, the fossil can be only tentatively referred to that group. The skeletal and external characters of the new fossil are also nearly identical to those of *A. dominicanus*, another Dominican amber anole; however, the latter fossil is relatively poorly preserved, and its currently known characters are identical to those of several extant species, including two species of the *A. chlorocyanus* species group. Body proportions and lamella counts of both amber fossils indicate that these lizards are trunk-crown anoles, that is, members of an ecologically and morphologically defined class of anoles specialized for life high on the trunks and in the crowns of trees. This finding is consistent with referral of the fossil anoles to the *A. chlorocyanus* species group, all extant members of which are trunk-crown anoles.

[1] Associate Curator, Department of Vertebrate Zoology, National Museum of Natural History, Smithsonian Institution, Washington, DC 20560.
[2] Undergraduate Honor Student, Department of Biology, Washington University, St. Louis, MO 63130.
[3] Associate Professor, Department of Biology, Washington University, St. Louis, MO 63130.

INTRODUCTION

Although amber is best known as a preservation medium for fossil arthropods (e.g., Larsson, 1962; Petrunkevitch et al. 1963, 1971; Davis, 1989; Poinar, 1992), it occasionally contains the remains of vertebrates, including bird feathers (Schlee, 1973; Poinar et al., 1985; Grimaldi and Case, 1995), mammal hair (Larsson, 1962) and bones (MacPhee and Grimaldi, 1996), and partial to nearly entire frogs (Poinar and Cannatella, 1987) and lizards (Lazell, 1965; Rieppel, 1980; Böhme, 1984; Kluge, 1995). The frog and lizard fossils are extraordinary in that they often consist not only of bones, but also of more delicate cartilaginous skeletal structures as well as other uncommonly preserved soft tissues (Poinar, 1992; Grimaldi, 1993).

Among the best known sources of amber fossils are mines in the Cordillera Septentrional of the Dominican Republic (Poinar, 1992), which have on several occasions yielded fossil *Anolis* lizards, the living representatives of which are both diverse and common in the extant fauna of the Dominican Republic (e.g., Cochran, 1941; Rand and Williams, 1969; Williams, 1983). Although at least a dozen anoles preserved in Dominican amber are currently known (D. Grimaldi, personal commun.; Schlee, 1980, 1990), most are in private collections, and only one, the holotype of *Anolis dominicanus* (Rieppel, 1980), has been studied previously. We report here on a second *Anolis* lizard preserved in Dominican amber, which was brought to our attention by David Grimaldi, curator of the amber fossil collection at the American Museum of Natural History (AMNH). This specimen is noteworthy in that it preserves aspects of morphology not found in the holotype of *A. dominicanus*, and thus provides further information about the Tertiary anole fauna of Hispaniola and the adaptive radiation of Caribbean *Anolis* lizards.

MATERIALS AND METHODS

We studied both the fossil and radiographs of it using binocular dissecting microscopes (magnification 7–30× and 8–64×). Stereo radiographs proved especially useful for ex-amining complex, three-dimensional skeletal structures, particularly the skull; they were viewed using two 7–30× dissecting microscopes placed side-by-side over a light table. The best images were obtained using Kodak Industrex R (SR 5) film with a 60-sec exposure at 38 kV and 2 mA. We studied the holotype of *Anolis dominicanus* using similar techniques. Our descriptions of both specimens are not intended to be exhaustive but instead focus on characters relevant to determining sex, ontogenetic stage, and phylogenetic relationships (e.g., Etheridge, 1959). Terminology follows Oelrich (1956) and de Queiroz (1987) for skeletal elements and Williams (1995) for squamation. Phalanges are numbered from distal to proximal so that the phalanges associated with the claws and toe pads of different digits have the same number.

We compared the amber fossil anoles with 66 preserved juvenile anoles of five extant Hispaniolan species, representing four ecologically specialized classes (e.g., Rand and Williams, 1969; Williams, 1983). These comparisons were based on eight measurements (snout–vent length and lengths of the humerus, radius, ulna, femur, tibia, fibula, and tail) and counts of the expanded subdigital lamellae under the third and fourth phalanges of pedal digit IV. Measurements of the limb bones were taken from radiographs using the computer package MORPHOSYS (Meacham and Duncan, 1990). Several of the specimens were preserved in positions that did not allow us to obtain accurate measurements of the forelimb elements from radiographs. Therefore, we estimated their values from external measurements using regression equations based on specimens for which accurate measurements could be obtained both externally and from radiographs.

We evaluated the similarity of the amber fossil anoles to the five extant species using visual inspection of ranges and bivariate plots and discriminant function analyses (DFAs) performed with the computer software package SYSTAT (vers. 5.2). Of the limb measurements, only the lengths of the humerus, ulna, femur, and tibia were used in the DFAs. Because the limb and tail measurements increase with increasing body size, each one was plotted against snout–vent

length, a commonly used estimate of body size (e.g., Losos 1990a, 1990b). The lamella counts did not increase with increasing size, permitting direct comparison of their values. Two DFAs were conducted—one on the raw values of the limb-bone measurements and lamella counts, and another on size-adjusted values. The effect of size on the lengths of the various limb elements was removed by calculating the residual value from a regression of the length of each element versus snout–vent length for all specimens. Residuals were not calculated for lamella counts, which did not change with increasing size. Tail length was not included in the DFAs because of the large number of specimens with incomplete or regenerated tails. Because the snout–vent length of the AMNH fossil anole could only be estimated, we calculated residuals based on its estimated snout–vent length as well as the estimate ± 2 mm.

DESCRIPTION OF THE AMNH AMBER SPECIMEN

GENERAL: The specimen, AMNH DR-SH-1 (fig. 1; see also Grimaldi, 1996: 109), consists of six fragments of amber that have been cemented together, ground down, and polished to form a single piece containing the remains of a lizard and several insects. It is said to be from the Dominican Republic, but the specific provenance is unknown. Although an earlier study (Lambert et al., 1985) proposed ages as great as 40 million years (i.e., upper Eocene) for Dominican amber, more recent estimates give the age as Oligocene or Miocene (Grimaldi, 1995) and Early to Middle Miocene (Iturralde-Vinent and MacPhee, 1996).

The piece of amber containing the lizard is ca. 59 mm long and 21.5 mm wide at the longest and widest points and 8.5 mm thick (measurements to the nearest 0.5 mm). The fossil lizard is contained within five of the six fragments that make up the entire piece. These five fragments are arranged more or less in a row through which passes the longitudinal axis of the lizard. Beginning anteriorly, the first fragment contains most of the head. The second contains the posteriormost part of the head, the neck, the anterior part of the trunk, and the forelimbs. The third

fragment contains the posterior part of the trunk, the anterior part of the tail, and most of the hindlimbs. The fourth contains a part of the tail, most of the left foot, and distal parts of the right foot. The fifth fragment contains only the posterior part of the tail. The sixth fragment is not in line with the others; it lies adjacent to the fifth and contains no lizard remains. This fragment is lighter in color and apparently was not part of the original amber piece containing the fossil lizard. The third and fourth fragments are each broken along a single fracture plane into two parts that have been cemented back together; the smaller parts appear to contain no lizard remains. Preserved along with the lizard are a planthopper nymph (D. Grimaldi, personal commun.) by the left side of the head, two ants near the base of the tail, and two flies, one above the right thigh and the other alongside the right foot.

The lizard is preserved as an almost complete skeleton with patches of dried skin and flesh adhering to it. The remains measure ca. 53 mm in total length and 24 mm from the snout to the vent, although the parts in different amber fragments are not perfectly aligned, and some are missing. Adherent skin is present on the anterior, anterolateral, and ventral surfaces of the head, the ventral and right lateral surfaces of the body and anterior part of the tail, the ventral surface of the left hindlimb, the entire right fore- and hindlimbs, and most of the posterior part of the tail (i.e., the part within the fourth and fifth amber fragments described above). In some places, the skin and flesh are sufficiently transparent for the skeleton to be seen clearly through them, but in others, the soft tissues obstruct the view of the skeleton, particularly in the regions of the anterolateral and anteroventral part of the head, the dorsomedial and the right posterolateral part of the trunk, the right hindlimb, and the right anterolateral and posterior part of the tail. The only parts of the skeleton that are missing are the posterodorsal part of the skull, the left hand, part of the right forearm and hand, a short segment of the trunk between the second and third amber fragments, the distal part of the left foot, a short segment of the tail between the fourth and fifth amber fragments, and the posteriormost part of the tail. The cross-sec-

Fig. 1. AMNH DR-SH-1, dorsal view of entire specimen. Scale bar equals 1 cm.

tional shape of the body could not be determined accurately, but the tail appears to be round or weakly compressed.

SQUAMATION: Scales cover the dorsal surface of the snout, except for the portion overlying the left nasal bone and posterior part of the premaxillary's nasal process and the posterior part of the right nasal bone. The scales are smooth and juxtaposed without evidence of striations or keels. The number of scales across the snout between the canthals could not be determined. There are four postrostrals between the anterior nasals. The anterior nasals are in contact with the rostral and are not divided transversely. The skin has been stripped away from the frontal bone, the dorsal part of the left orbit, and most of the dorsal part of the right orbit. The

supraorbital semicircles are not preserved, and it cannot be determined how many scales separate them medially. The skin of the anterior and anterolateral part of the right supraocular region is preserved. The supraoculars are at least partially differentiated, but the presence or number of distinctly enlarged scales could not be ascertained. There is at least one elongated anterior superciliary, but the exact number of such scales could not be determined. More posteriorly, both skin and bone have been ground away, prohibiting determination of the condition of the posterior superciliaries, the size of the interparietal, the number of scales separating the interparietal from the supraorbital semicircles, and the number of enlarged scales between the interparietal and the smaller scales of the nape. Most of the skin on the lateral surfaces of the snout is present, but it is difficult to see through the amber. There appear to be three rows of loreals, but the total number of loreals could not be determined. The ventral suboculars appear to contact the supralabials. The boundaries of the supralabials are difficult to discern, but there appear to be about seven between the rostral and the center of the eye. The skin of the mental and gular regions is more or less entire, although particles in the amber and separation of the oberhauchten make certain features difficult to see. There appear to be at least six postmentals (i.e., scales in contact with the mentals between the infralabials), but the exact number could not be determined. The lateralmost postmentals on each side are the anteriormost members of a row of differentiated sublabials, which consists of at least three enlarged scales on the left side. Gular folds are absent.

The dorsal and lateral skin of the body can be more or less clearly observed in the middle part of the trunk, just anterior to the crack separating the second and third amber fragments. The dorsals appear to be unkeeled, juxtaposed, and more or less homogeneous. There are 10–11 scales per millimeter as measured along a posterolaterally oriented diagonal, that is, the longest dimension of the scales. Although the dorsals closest to the midline appear to be somewhat enlarged, the number of enlarged rows could not be determined. There is no obvious crest of modified middorsal scales. The scales of the flank are somewhat smaller than the dorsals; they are juxtaposed and more or less homogeneous. Ventrally, scales can be observed over most of the thoracic region and the right side of the abdominal region. They are somewhat larger than the dorsals, numbering seven to eight per millimeter (measured longitudinally), juxtaposed to subimbricate, and unkeeled. The subdigital scales of several digits can be seen, and at least some are enlarged to form friction or toe pads. These toe pads can be seen most clearly in right manual digit II, right pedal digits II, III, and IV, and left pedal digits II, III, and V. The pads are well developed, with that of right pedal digit IV extending distally to partially overlap the penultimate (second) phalanx. There are 22 or 23 lamellae underlying the third and fourth phalanges of right pedal digit IV. Supradigitals could be observed on several digits, but whether they were keeled could not be determined. The scales of the tail are keeled and subimbricate. The caudal middorsal scale row is enlarged and relatively strongly keeled compared with adjacent scales, but there is no distinct caudal crest. If there are any enlarged whorls of caudal scales, they are only slightly enlarged, with perhaps six to eight whorls of smaller scales separating them. The presence or absence of enlarged postanal scales could not be determined.

SKELETON: The skull (fig. 2) is approximately 10 mm long and 4.5 mm wide, although the occipital portion has been displaced ca. 0.5 mm posteriorly after breakage and rejoining of the two amber fragments in which it is contained. The lengths of the preorbital, orbital, and postorbital portions of the skull are approximately 3.5, 3.5, and 3.0 mm, respectively. Nearly the entire skull is preserved. Because of its complex and three-dimensional nature and the presence of adherent skin, the details of its morphology are most clearly seen in stereo radiographs.

In the dermal skull roof, the premaxilla is preserved undamaged; it appears to bear eight tooth positions and has a narrow posterior (nasal) process that extends between the nasals but fails to contact the frontal. Both septomaxillae appear to be intact, but little could be discerned of their structure. The left septomaxilla appears to flare poste-
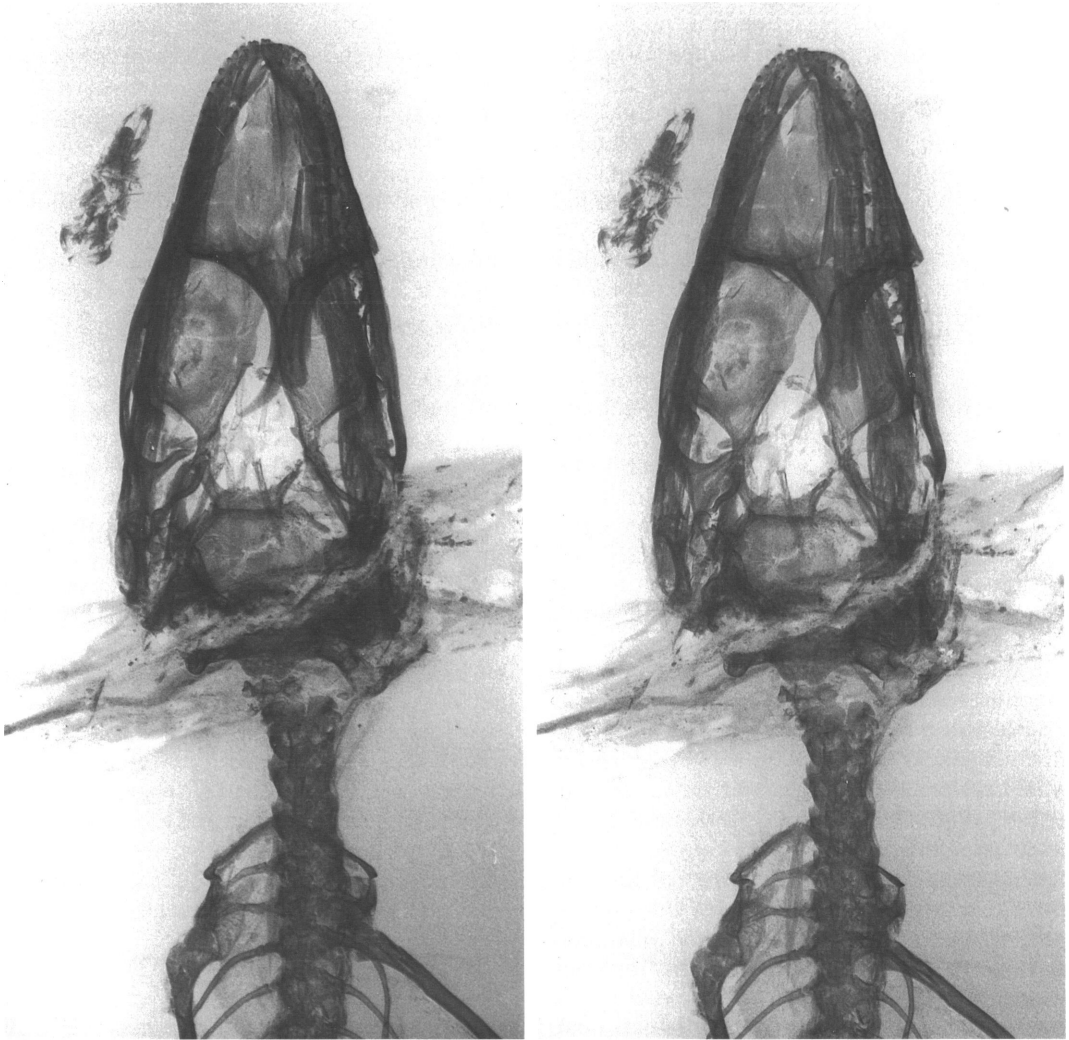
Fig. 2.   Stereo radiographs of the skull of AMNH DR-SH-1 (ca. 8.6 times actual size).

riorly and bear a pointed posterolateral pro-
cess that terminates anterior to the posterior
margin of the external nares. Both maxillae
are preserved undamaged; the right bears ca.
15 tooth positions, and the left bears ca. 17.
The maxillae fail to contact the frontal dor-
sally, being excluded by contact of the nasals
and prefrontals.

Both nasals are intact. Their anterior edges
form the posterior margins of the external na-
res. The two elements meet one another me-
dially posterior to the posterior terminus of
the posterior (nasal) process of the premax-
illa. The nasals are bordered laterally by the
maxillae anteriorly and the prefrontals pos-

teriorly, with which they form a relatively
straight longitudinal suture. Posteriorly, the
nasals form a W-shape suture with the fron-
tal. Both prefrontals are intact. They contact
the nasals anteromedially, excluding the
frontal from contact with the nasal (dorsal)
process of the maxilla. The prefrontals bear
distinct dorsal and lateral faces separated by
distinct canthal ridges, the posterior termini
of which form a posteriorly directed process
at the anterodorsal corner or the orbit.

Most of the single frontal is preserved, ex-
cept for its posteriormost part, which has
more missing on the right side than on the
left. It is bordered by the nasals anteriorly

and the prefrontals posterolaterally but fails to contact the maxillae anterolaterally. The frontal is strongly constricted between the orbits, where it measures ca. 0.62 mm at its narrowest point. On the left side, the posterolateral part of the frontal contacts the postfrontal anteriorly and the postorbital posteriorly. A small postfrontal is visible on the left side only. It is located along the anterior edge of the posterolateral part of the frontal. It closely approaches, but apparently fails to contact, the dorsal process of the postorbital, although this may be an artifact of preservation.

Very little of the parietal is preserved, although part of its right lateral (deep) portion and a small part of its left posterolateral portion, including the supratemporal process, can be observed. The location of the parietal foramen could not be determined, nor could the form of the parietal crests and roof or the extent of the parietal over the occipital region. The supratemporals appear to be preserved on both sides, along the lateral surfaces of the supratemporal processes of the parietal near the posterior termini of the squamosals and the dorsal articulations of the quadrates.

The lacrimal could not be located on either side; however, it is difficult to make out the details of the lacrimal region either through direct examination or with the aid of radiographs, so it is unclear whether the lacrimal is present or absent. The jugal is preserved in its entirety on both sides. Its temporal process runs along the anteroventral edge of the anterior process of the postorbital, but it fails to contact the squamosal along the dorsal margin of the lower temporal fenestra. A small but distinct posteriorly directed process is visible on the right side at the base of the temporal process.

Both postorbitals are present, although the posterior process of the right one is broken. Because the jugal and squamosal fail to contact along the dorsal margin of the lower temporal fenestra, a small portion of the postorbital contributes to this margin. The left squamosal is intact, but the right one is broken and its anterior end appears to be displaced laterally. On the left side the squamosal is separated from the jugal by a gap

of ca. 0.01 mm along the ventral margin of the temporal arch.

Of the palatal elements, both vomers are preserved but can be seen clearly only in radiographs and then only under the external nares where there are fewer layers of overlapping bones. Both palatines are preserved but can be seen clearly only in radiographs of the orbital region where there are no overlapping bones. Here their pterygoid processes form broad, flat surfaces. No palatine teeth are evident. The palatine–pterygoid suture runs more or less transversely, with the pterygoid having only a slight anterior extension along the posteromedial borders of the palatine, that is, the lateral margins of the pyriform recess (interpterygoid vacuities). Both pterygoids are present and mostly undamaged; their palatine processes are very broad. No pterygoid teeth are evident. Both ectopterygoids are preserved undamaged. They appear to form only small portions (if any) of the posterior margins of the suborbital fenestrae (inferior orbital foramina).

Of the palatoquadrate ossifications, the columelliform epipterygoids are present on both sides. They slope posteriorly and are bowed inward. The entire left quadrate is preserved, as is at least the dorsal part of the right one. The quadrate bears a strong posterior crest. The lateral (tympanic) crest is relatively narrow, being only slightly wider than the posterior crest, and the medial crest is virtually absent.

Of the braincase elements, approximately the anterior half of the parasphenoid process of the parabasisphenoid is preserved, but the portion that presumably extended from the body of the basisphenoid to the posterior end of the preserved portion is missing or unmineralized (nothing is evident in the radiographs, but its outlines can be seen in the amber under visible light). The part that is present appears to lie in its natural position between the orbits dorsal to the interpterygoid vacuity (pyriform recess). The remainder of the parabasisphenoid is more or less intact, although the right basipterygoid process appears to be damaged distally. The left basipterygoid process flares only slightly at its articulation with the pterygoid. The parabasisphenoid bears very short posterolateral

processes. The suture between the basisphenoid and the basioccipital is unfused.

The right prootic is badly damaged, but the left one is more or less intact. The osseous labyrinth housing the anterior semicircular canal forms a prominent bulge that forms the anterior margin of the bone; the crista alaris is not developed. The contacts of the prootics with the basisphenoid and basioccipital were observed on the right side of the specimen, but whether the sutures between the prootic and these other elements were fused could not be determined. The left exoccipital-opisthotic is badly damaged, but the right one is more or less intact. The osseous labyrinth housing the posterior semicircular canals forms prominent ridges on the posterior surfaces of both bones. The paraoccipital process is relatively short, only slightly larger than the ridges formed by the osseous labyrinth. It could not be determined whether the sutures between the exoccipital-opisthotic and either the prootic or the supraoccipital are fused.

At least the posteroventral part (if not most) of the supraoccipital is preserved. Its contact with the exoccipital-opisthotic was observed on the right side, but whether the suture between the two elements is fused could not be determined. The basioccipital is broken by the transverse crack separating the first and second amber fragments, which runs just anterior to the occipital condyle in the region of the spheno-occipital tubercles, which could not be observed themselves. The basioccipital is clearly unfused to the basisphenoid, with which it forms a posteriorly concave suture, but it could not be determined whether it is fused to the exoccipital-opisthotics or the prootics. Both orbitosphenoids are preserved, but the left one appears to be displaced to the right of its natural position. Each orbitosphenoid is narrow ventrally and flares dorsally, but its contacts with the planum supraseptale and the pila accessoria and pila antotica do not form separate processes. The stapes could not be located on either side of the specimen.

In the lower, jaw, both dentaries are preserved, but the right one is broken between tooth positions 12 and 13 and between positions 17 and 18. Both right and left dentaries bear ca. 22 teeth. There is no evidence of sculpturing on the labial or ventral surfaces. The coronoid is preserved in its entirety on both sides, while the surangular and prearticular are preserved undamaged on the left side but are damaged posteriorly on the right. Sutures could not be made out between any of the mandibular bones. Both retroarticular and angular processes of the prearticular are preserved on the left side of the specimen, and the anterior part of the angular process is preserved on the right. The two processes are subequal in size and are connected by a bony shelf. The presence or absence of a separate splenial and angular could not be determined. The right articular appears to be preserved and retains its articulation with the ventral condyle of the quadrate.

A more or less complete ring of scleral ossicles is preserved on left side of the specimen and probably also on the right, but neither the total number of individual ossicles nor their patterns of overlap could be determined. Much of the delicate hyoid apparatus is preserved, including at least parts of all major components, that is, the body of the hyoid, hypohyal (lingual process), ceratohyals, hyoid cornu, first ceratobranchials, and second ceratobranchials. The first ceratobranchials are ossified, but the remaining elements are cartilaginous. There appears to be a posterior median fontanelle ca. 0.22 mm in diameter in the body of the hyoid where it joins the second ceratobranchials. The lingual process is ca. 2.1 mm long. The lengths of the first and second ceratobranchials could not be determined because of breakage.

As noted above, teeth are present on the premaxilla, maxillae, and dentaries. Those on the premaxilla and the anterior portions of the maxillary and dentary rows are conical (i.e., with a single cusp). The teeth of the middle and posterior portions of the maxillary and dentary rows are tricuspid, with each tooth bearing a large central cusp and smaller anterior and posterior cusps.

In the postcranial skeleton (fig. 3), the total numbers of presacral and caudal vertebrae are not determinable because neither segment is complete, although at least 19 presacral and 25 caudal vertebrae are preserved. The first 11 presacrals are preserved more or less intact, although the intercentrum of the atlas (which is associated with the cranium) is sep-
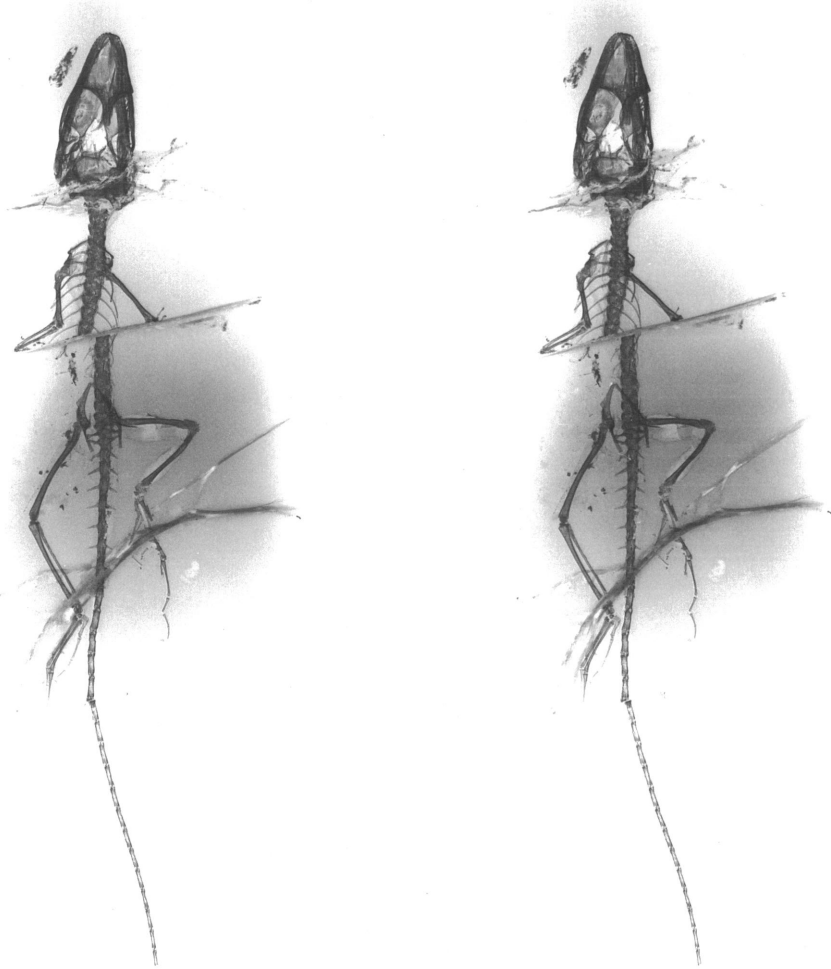
Fig. 3. Stereo radiographs of AMNH DR-SH-1 (ca. 2.3 times actual size).

arated from its neural arch (which is associated with the axis), and the posteriormost part of the 11th vertebra is missing. Short ribs articulate with vertebrae 5 and 6 and longer ones with vertebrae 7–11, although the distal ends of those articulating with the left sides of vertebrae 10 and 11 are missing. The eight vertebrae anterior to the sacrum are also preserved. The anterior four of these bear short ribs; the posterior four lack ribs and apparently also lack rib facets. The next two vertebrae bear stout fused ribs (sacral di-

apophyses) that articulate with the ilia. None of the presacral vertebrae have neural spines exceeding their centra in height. Cartilaginous extensions were observed on several of the longer ribs, but none retain their connections with the sternum or xiphisternum. The right side of the sternum, however, bears three short processes, indicating that three ribs were connected to it. The posterior ends of the xiphisterna are missing, but the lengths of the preserved portions are sufficient for connections to at least two ribs. Part of what

may be a postxiphisternal inscriptional rib is preserved on the right side of the specimen.

Assuming that the specimen was like other anoles in having two short and two long cervical ribs, there appear to have been eight cervical vertebrae (those anterior to the first bearing ribs that articulate with the sternum). Processes on the sternum and the length of the xiphisternal rods indicate that three of the thoracic vertebrae were connected via ribs to the sternum and at least two to the xiphisternum. There are four lumbar vertebrae (posterior presacrals lacking ribs) and two sacral vertebrae. The number of attached and free postxiphisternal inscriptional ribs could not be determined.

The first seven caudal vertebrae are continuous with the sacral and eight posterior presacral vertebrae; they are preserved more or less intact, although numbers 5, 6, and 7 all appear to have suffered damage. All seven vertebrae bear posterolaterally directed transverse processes. Autotomy septa (fracture planes) are not obvious in any of these vertebrae, although the last (number 7) may have a partial septum. Haemal arches begin between vertebrae 3 and 4 and continue to the end of this segment. The next segment consists of five entire vertebrae plus parts of two others at the anterior and posterior ends. The anteriormost of these appears to be the posterior part of vertebra 7; at least the part that is present (right posterior) corresponds with the part of number 7 that is absent. Only the first entire vertebra in this segment (inferred to be number 8 in the series) has transverse processes; the rest lack them entirely. All of the vertebrae in this segment have autotomy septa. The transverse process of vertebra 8 lies posterior to the fracture plane. The last segment consists of 13 more or less intact vertebrae, although small parts of the first and last may be missing. All of these vertebrae lack transverse processes. Autotomy septa are present in the anteriormost vertebrae in this segment, but they are reduced gradually posteriorly until they are entirely absent. None of the caudal vertebrae have their neural spines exceeding the centra in height. In summary, the caudal sequence fits the definition of the alpha type of Etheridge (1959); it has seven anterior aseptate caudals, eight anterior caudals bearing transverse processes, and autotomy septa are present in at least part of the series.

Most of the pectoral girdle is preserved intact. The left suprascapula is missing, but the right one is present. It flares dorsally and overlies the first two cervical vertebrae on that side. Both scapulae are preserved. On the right side, where the element can be seen most clearly, there is a single large emargination along the anteroventral border, part of the margin of the scapulocoracoid fenestra. Scapular fenestrae appear to be absent. Both coracoids are also preserved; there is a single large emargination anteriorly, ventromedial to a narrow anteriorly directed process that separates it from the scapulocoracoid fenestra. This is part of the margin of the anterior (primary) coracoid fenestra. There is no posterior (secondary) coracoid fenestra. Fusion of the scapula and coracoid could not be determined. Little of the epicoracoid cartilages could be seen either in the specimen (because of adherent tissue) or in radiographs.

Both clavicles are preserved. They appear to articulate dorsally very near the dorsal limit of scapular ossification (i.e., the boundary between scapulae and suprascapulae). The interclavicle is preserved intact. Its pointed posterior process extends to about the level of the widest part of the sternum. The lateral processes (arms) of the interclavicle are directed posterolaterally, forming an angle of 55–60° with the posterior process. They are in contact with the clavicles along their entire anterior margins. The sternum is at least partially preserved. Posteromedially, it contains a fontanelle measuring ca. 1.2 mm anteroposteriorly and 0.5 mm laterally (maximum dimensions).

The pelvic girdle is preserved more or less entirely. It could not be determined if any of the three elements on a single side were fused to one another. The ilia retain their articulations with the sacrum. They bear distinct anterior iliac processes. The ischia are loosely articulated with one another medially; a remnant of the proischiac and most of the hypoischiac cartilages can be seen in radiographs. The pubes are also loosely articulated medially; the epipubis is small or absent.

Both forelimbs are more or less intact. Except for the distal end of the right humerus,

both humeri are preserved entirely, although in both cases the shaft is fractured proximally. The three humeral epiphyses that are preserved (both proximal and left distal) are unfused to the diaphyses. Each humerus is ca. 4.0 mm long. The ulna and radius are preserved on the left side. The proximal epiphysis of the radius is unfused to the diaphysis; fusion of the other epiphyses could not be determined. The left ulna is ca. 3.5 mm long, and the left radius is ca. 3.2 mm long. The right radius is also preserved, but details of its structure are difficult to discern because of its orientation. Only a small part of the manus is preserved on each side, including what appears to be a metacarpal on the left side and three phalanges (presumably parts of digits I and II) on the right. These digits reach the surface of the amber, and their distal ends are no longer present.

Most of both hindlimbs are also preserved. The femora are both preserved, although the shaft of the left one is fractured proximally and that of the right is fractured both proximally and distally. The distal end of the right femur reaches the surface of the amber and its distalmost portion is missing. The left femur is ca. 6.4 mm long. Its distal epiphysis is unfused to the diaphysis. Proximal epiphyses are preserved on both sides; the right is difficult to see, but the left also appears to be unfused to the diaphysis. The tibia and fibula are preserved more or less entire on both sides, but the shaft of the right tibia is fractured proximally, and a break in the amber passes through the distal ends of both bones on the left. On the left side, both the proximal and distal tibial and fibular epiphyses can be seen clearly; they are unfused to the diaphyses. The left tibia is ca. 5.3 mm long, and the left fibula is ca. 5.4 mm long (these approximate measurements correct for separation at a break in the amber). The greater part of the pes is preserved on both sides. On the right, most of the elements are preserved, but they are partially disarticulated; on the left, they are articulated, but the distal elements are missing. The astragalocalcaneum is preserved on both sides, as well as a large distal tarsal proximal to metatarsal IV and a small one proximal to the epiphysis of metatarsal III on the left side. All five metatarsals are preserved on both sides, although several

of the central ones are broken on the right side. Their relative sizes are $5 < 1 < 2 < 3 < 4$. The fifth metatarsal is hooked proximally. Unfused epiphyses were observed both proximally and distally on left metatarsals II–IV as well as distally on right metatarsal IV. The number of phalanges could be determined for all pedal digits except III. The phalangeal formula is 2(both sides):3(L):–:5(R):4(L).

ESTIMATED SIZE

The snout–vent length (SVL) of the specimen was estimated based on the assumption that it had 24 presacral vertebrae. Most extant species of *Anolis* have a modal number of 23 or 24 presacrals, and 24 is the mode in all of the extant Hispaniolan species examined by Etheridge (1959). Our estimate was calculated as the sum (rounded to the nearest millimeter) of the following numbers: (1) tip of snout to break at posterior end of skull in first piece of amber (at midline) = 8.8 mm, (2) break at posterior end of skull in second piece of amber to condyle of vertebra 10 minus 0.2 mm for displacement of skull and vertebral column = 7.9 mm, (3) condyle of eighth vertebra anterior to sacrum to 0.1 mm beyond terminus of hypoischiac cartilage = 5.6 mm, (4) average of condyle-to-condyle distances for first complete segment anterior to break in column and first complete segment posterior to break multiplied by seven segments (two partial segments plus number needed to total 24) = 6.4 mm. The estimated SVL of the specimen is 29 mm.

ONTOGENETIC STAGE AND SEX

All available evidence indicates that the fossil lizard is a juvenile rather than an adult of a species with a small body size. Although many lizards reach sexual maturity before they attain maximum size, a maximum size of less than 35 mm SVL (compared with 29 mm for the fossil) is rare even for the smaller sex among extant anoles. Only 6 such species out of 132 are reported for the Caribbean and only 1 out of 40 for Hispaniola (Schwartz and Henderson, 1991). More significantly, several ossifications that characteristically fuse in lizards as they approach maximum size remain unfused in the fossil;

these include the basisphenoid and basioccipital of the braincase and the epiphyses and diaphyses of several limb bones (fusion of other elements could not be determined). Furthermore, the orbitosphenoid ossifications do not extend into the pila accessoria, and there are large uncalcified areas in the center of the hyoid body and sternum. Although the second ceratobranchials are broken, they do not appear greatly enlarged to support a dewlap, although in many anole species the second ceratobranchials are not enlarged in adult females, and in a few Cuban species they are not enlarged in either sex. The sex of the fossil is unknown because of its probable juvenile status and concomitant absence of secondary sex characters (such as a dewlap), and because the presence or absence of enlarged postanal scales could not be determined.

SYSTEMATIC POSITION

IDENTIFICATION OF THE FOSSIL AS AN ANOLE: Identification of the fossil as an anole (sensu Etheridge, 1959 and including the species commonly referred to *Anolis*, *Chamaeleolis*, *Chamaelinorops*, and *Phenacosaurus*) is based on two groups of characters. Etheridge and de Queiroz (1988) listed 14 hypothesized synapomorphies for the anole clade. Of the eight characters in this list for which the fossil can be scored, it possesses the derived condition of seven: slender clavicles, the absence of ribs on vertebrae 3 and 4, three sternal ribs, the absence of ribs from the posterior presacral (lumbar) vertebrae, transverse processes of the caudal vertebrae posterior to the fracture planes, lamellar subdigital scales that form a pad under phalanges 3 and 4 (not 2 and 3 contra Williams 1974; Peterson and Williams, 1981; Peterson 1983; Etheridge and de Queiroz, 1988; Frost and Etheridge, 1989; Williams, 1995) of digits 2–5, and absence of gular folds. Although it does not possess the ninth character (i.e., elongated second ceratobranchials supporting a dewlap), this can be attributed to the probable juvenile status of the specimen. It also possesses a character identified in the present study as a possible anole synapomorphy: lateral expansion of the pterygoid processes of the palatines and the palatine processes of the

pterygoids so that each palatal ramus is wider than the suborbital fenestra, and the lateral part of the palatine–pterygoid suture is oriented almost transversely. The corresponding parts of the palatines and pterygoids are unexpanded so that each palatal ramus is narrower than the suborbital fenestra, and the palatine–pterygoid suture is usually oriented obliquely in para-anoles (*Anisolepis* and *Urostrophus*), leiosaurs (*Enyalius*, *Pristidactylus*, *Leiosaurus*, *Aperopristis*, and *Diplolaemus*), and *Polychrus* (see Etheridge and de Queiroz, 1988; Frost and Etheridge, 1989; Etheridge and Williams, 1991, for discussions of anole outgroups and their relationships).

The fossil possesses several other characters that appear derived within Iguania and characterize anoles but are also found in some other anoloids (sensu Etheridge and de Queiroz, 1988; = polychrotids of Frost and Etheridge, 1989) and thus may be synapomorphies of more inclusive clades. The part of the quadrate medial to the posterior crest is reduced. This condition occurs also in *Polychrus*, but its distribution among other anoloids is not currently known. The posterolateral processes of the basisphenoid are short and do not extend along the ventrolateral processes of the basioccipital even half the distance to the spheno-occipital tubercles. This condition also occurs in some leiosaurs and para-anoles (drawings provided by R. Etheridge). The osseous labyrinth, particularly that part housing the posterior semicircular canals, is raised above the surface of the occipital bones. This condition occurs in most anoloids (Etheridge and de Queiroz, 1988), but it also occurs in many small lizards, including juveniles of species that lack the condition as adults. A bony shelf connects the angular and retroarticular process of the mandible. This condition occurs in at least some leiosaurs and para-anoles (drawings provided by R. Etheridge).

POSITION OF THE FOSSIL WITHIN ANOLES: A set of 13–16 characters based on variation in skeletal morphology (Etheridge, 1959) has been used to assess higher level phylogenetic relationships within anoles (Etheridge, 1959; Guyer and Savage, 1986, 1992; Cannatella and de Queiroz, 1989; Williams, 1989). The fossil anole can be scored for five of these

characters: (1) the interclavicular lateral processes are in close contact with the clavicles for more than half their lengths; (2) there are four lumbar vertebrae; (3) there are seven aseptate anterior caudal vertebrae; (4) autotomy septa are present in the caudal vertebrae; and (5) the caudal vertebrae conform to the first iguanid type of Etheridge (1959; see also Etheridge, 1967), in which transverse processes are lacking from most of the autotomic caudal vertebrae. The fossil also lacks the jaw sculpturing found in adult males of several West Indian taxa, but a juvenile would not be expected to exhibit this character.

The total set of skeletal morphological characters has been subjected to several different analyses using parsimony methods of phylogenetic reconstruction (Guyer and Savage, 1986, 1992; Cannatella and de Queiroz, 1989). These analyses consistently reconstruct a large clade composed of Etheridge's (1959) beta section and the *equestris, lucius, carolinensis, chlorocyanus, angusticeps, alutaceus, darlingtoni,* and *monticola* series of *Anolis* (all sensu Savage and Guyer, 1989). This large clade is hereafter called the T clade, based on Etheridge's shorthand description of the interclavicle morphology found in its members, although a similar condition also occurs in some members of the distantly related (and probably paraphyletic) *latifrons* series (Williams, 1989) and the *wattsi* species group of the *bimaculatus* series (personal obs.). The T clade is diagnosed by derived states of two characters—absence of a splenial bone in the lower jaw (reversed in a few taxa; see Williams, 1989), and extensive contact of the clavicles with the lateral process of the interclavicle (convergent in some members of the *latifrons* series). The fossil anole possesses the derived state for the second of these characters (it cannot be scored for the other), which suggests that it is part of the T clade. This placement is not contradicted by any of the other skeletal characters for which the fossil can be scored; the same states observed in the fossil occur in several other members of the clade. Moreover, the T clade contains all of the Hispaniolan anoles except the *cybotes* subseries and *distichus* subgroup (sensu Williams, 1976) and possibly *Chamaelinorops,* which

possesses the derived state of both characters but has been placed outside of the T clade in the phylogenetic analyses cited above.

Within the T clade, the remaining four characters for which the fossil anole can be scored allow limited further resolution of its phylogenetic position. Two of those characters are relatively uninformative. The amber anole has autotomy septa in its caudal vertebrae, an ancestral state for the T clade that has been lost convergently in several small subclades whose members have specialized tails. It also has seven anterior aseptate caudal vertebrae, a state of uncertain polarity that is present in various members of the T clade. The other two characters are somewhat more informative. The amber anole shares a derived increase in the number of lumbar vertebrae (i.e., more than three) with certain Cuban and Hispaniolan taxa (also seen in some anoles outside of the T clade), and it lacks the derived condition of the caudal vertebrae characteristic of beta anoles. In total, these characters indicate that the amber anole is a member of the T clade that is not a beta anole and may be closely related to certain Hispaniolan and/or Cuban taxa that have more than three lumbar vertebrae. In total, five of the skeletal characters used by Etheridge (1959) can be scored in the fossil anole; the same states present in the fossil are also present (data from Etheridge, 1959) in at least some members of the Hispaniolan *chlorocyanus* and *hendersoni* species groups (sensu Williams, 1976).

Although external morphological characters of anoles have not been analyzed phylogenetically, they are commonly used to diagnose extant anole species. A standard set of external characters has been described by Williams (1995) and used as the basis for a computer program designed to assist in the identification of anoles (Williams et al., 1995). We used the key in the *Anolis* handlist (O'Hara and Williams, 1994) to compare the external characters of the amber anole with extant Hispaniolan anole species, particularly those of the T clade. The amber anole could be scored for 20 (54%) of the 37 characters used in the key (1, 3–5, 8, 10, 15–18, 20, 22–28, 30, 31). When compared with the extant Hispaniolan species of the T clade for these 20 characters, it could be distinguished

from all species except *A. aliniger* and *A. singularis*. Both of these species are part of the Hispaniolan green anole (Williams, 1965) or *chlorocyanus* (Williams, 1976) species group, which is composed of four highly similar species. The other species of this group, *A. chlorocyanus* and *A. coelestinus*, differ from the fossil by one character each (as do *A. christophei* and *A. sheplani*)—the number of subdigital lamellae (character 28) for *chlorocyanus* (and *sheplani*), and the number of loreal rows (character 10) for *coelestinus* (and *christophei*). Of the characters used to distinguish between the species of the *chlorocyanus* species group by Williams (1965), the number of loreals and the number of subdigital lamellae are the only ones that can be scored in the fossil. It is noteworthy that *A. aliniger*, one of the two extant species from which the amber anole cannot be distinguished in either skeletal or external morphology, occurs in the Recent fauna of the Cordillera Septentrional (Schwartz and Henderson, 1991).

Although the characters that can be scored on the fossil anole suggest that it is part of the *chlorocyanus* species group, lack of information concerning polarity and homoplasy for many of those characters makes this assignment, as well as monophyly of the group itself, tentative. Furthermore, although the fossil cannot be distinguished from two of the extant species in this group (i.e., *A. aliniger* and *A. singularis*), lack of information concerning polarity and homoplasy in the characters that differ among the members of the *chlorocyanus* species group prohibits us from considering it conspecific with either of those species or even from considering it more closely related to them than to other members of the group.

RELATIONSHIP TO *ANOLIS DOMINICANUS*

The AMNH fossil anole is of comparable age and provenance to the only other fossil anole preserved in Dominican amber that has been studied previously, the holotype of *Anolis dominicanus* Rieppel (1980). Both are thought to be Oligocene or Miocene in age. The holotype of *A. dominicanus* is from the La Toca mine in the Cordillera Septentrional

(Rieppel, 1980), and although the specific provenance of the AMNH specimen is unknown, it is likely from one of the mines of the Cordillera Septentrional, the most common source of Dominican amber (Poinar, 1992). It is therefore possible that the two specimens are conspecific.

Rieppel considered *A. dominicanus* part of the green anole or *chlorocyanus* species group (Williams, 1965, 1976) and provided the following diagnosis: "A member of the α section of the genus *Anolis*: ventral scales hexagonal, subimbricate, smooth; scales on tail imbricate, keeled, arranged in verticils comprising 4–5 middorsal scales; 22–24 lamellae under fourth toe." This combination of characters, however, is found in all members of the *chlorocyanus* species group except *A. chlorocyanus*, which exhibits higher lamella counts (Williams, 1965). Rieppel described additional characters of *A. dominicanus*, but they do not indicate that the fossil differs from extant Hispaniolan green anoles. Therefore, we borrowed the holotype (Naturhistorisches Museum Basel [NMBA], Department of Entomology number P 52) to determine whether more information could be gained from the specimen. A redescription follows.

GENERAL: The piece of amber containing the type of *Anolis dominicanus* is ca. 59.5 mm long, 32.2 mm wide, and varies from 11.9 to 13.4 mm thick (fig. 4; Rieppel, 1980: fig. 1a). It appears more or less entire, although it contains several fractures, including one passing through the entire piece and transversely intersecting the lizard in the posterior trunk region. The block also contains the remains of at least four insects: one by the left forearm, one by the right hand, one by the right foot, and another about one-fourth of the way posteriorly along the tail.

The specimen consists of a substantial part of the skeleton with adherent skin on the ventral surface of the head, neck, and body/trunk, at least part of each limb, and most of the tail. Details of the skeleton are difficult to see with light microscopy because of the adherent tissues, but examination of radiographs (fig. 4) indicates that the following components are missing: most of the dermal roofing bones of the skull, the anterior and posterior portions of the palate, most of the
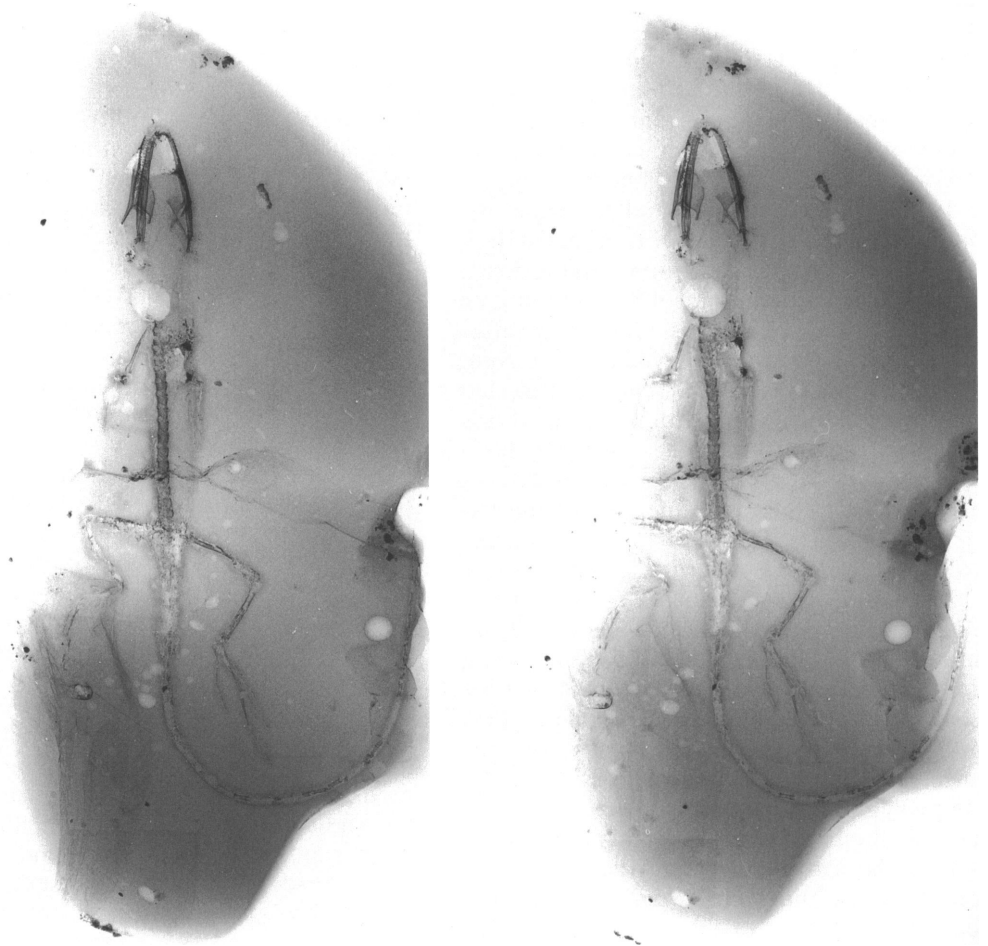
Fig. 4.   Stereo radiographs of NMBA Entomology P 52 (ca. 2.1 times actual size).

braincase, the anterior part of the vertebral column, a short segment of the distal part of the tail, and most of the right humerus, radius, and ulna. Parts are missing where the specimen reaches the surface of the amber and either decomposed or were removed during polishing. In addition, the skeletal remains are generally poorly preserved so that virtually nothing can be discerned concerning the morphology of the pectoral girdle, sternum, xiphisternum, bony and inscriptional ribs, and pelvic girdle. The missing elements do not disrupt the external form of the specimen ventrally, so that snout–vent and tail lengths can be measured directly, albeit with greater error than for fluid preserved specimens of extant anoles. The snout–vent length is ca. 26 mm, and the tail length is ca. 44 mm (including the missing segment). The cross-sectional shape of the body could not be determined, and the tail appears weakly compressed.

SQUAMATION: Scales can only be seen in sufficient detail to describe their morphology on the ventral surface of the head, neck, and body/trunk, parts of several limbs, and the distal three-fourths of the tail. Ventral scales in the gular region are juxtaposed and number 11–12 per mm; near midbody they are juxtaposed to subimbricate, apparently unkeeled, number ca. 8 per mm, and occur in transversely oriented rows. Digital friction

pads with laterally expanded subdigital lamellae can be seen on digits III–V of the right pes, digit III of the right manus, and digits II and III of the left manus. The lamellae are difficult to count because of cracks and other irregularities in the amber and degradation of the skin, but there appear to be 22–23 subdigital lamellae under the third and fourth phalanges of right pedal digit IV. The pad is well developed and extends distal to the proximal part of the penultimate (second) phalanx. There are 20–21 lamellae under the third and fourth phalanges of right pedal digit V. The caudal scales are keeled and arranged in whorls, with adjacent whorls subequal in size. There are six verticils in several caudal segments near the middle of the tail. The middorsal scale row of the tail appears enlarged relative to the adjacent scales, but it does not form a distinct crest.

SKELETON (fig. 4): The skull (premaxilla to condyle length) could not be measured accurately because the posterior part, including most of the braincase, is missing. It is very roughly 8.5 mm long and 4.5 mm wide. Preserved elements include both jugals, the ventral part of the left maxilla, the body of the left pterygoid and posterior part of the left palatine, the body of the right pterygoid, both rami of the lower jaws, the right basipterygoid process, the ventral part of the right quadrate, and most of the left quadrate. Approximately 20 tooth positions are visible on the left maxilla and at least 18 on the left dentary, although both series may be incomplete anteriorly. On the right dentary there are at least 16 tooth positions, and there may be as many as 23. At least some of the posterior maxillary and dentary teeth are tricuspid; the anterior teeth are unicuspid and at least some are slightly recurved. The palatine processes of the pterygoids are broad. Two or three teeth are possibly present along the medial edge of the left pterygoid. The basipterygoid process flares distally. Although the lower jaws are more or less entirely preserved, the presence or absence of splenial and angular bones could not be determined. Sculpturing is not evident on the dentary. Most of the hyoid apparatus is preserved, including at least parts of the body, hypohyal, ceratohyals, hyoid cornu, first ceratobranchi-

als, and the second ceratobranchials, the lengths of which could not be determined.

The numbers of vertebrae in various categories are largely undeterminable because of missing segments and poor preservation. Seventeen to 20 presacral vertebrae are preserved; the exact number is difficult to determine because of missing cervicals and poor preservation of sacral diapophyses. Caudal vertebrae are preserved to different degrees, with even relatively well-preserved elements sometimes immediately adjacent to very poorly preserved ones. In general, the vertebrae in the anterior third of the tail are poorly preserved relative to those in the posterior two-thirds. Transverse process are not evident in any of the vertebrae in the posterior two-thirds of the tail. Autotomy septa apparently are present in at least some of the posterior caudal vertebrae. No part of the tail is regenerated.

Virtually nothing can be discerned concerning the morphology of the pectoral girdle, and only the general shape of the pelvic girdle is determinable. Nor can anything be observed concerning the structure of the sternum, xiphisternum, or ribs, either bony or cartilaginous. All of the limb bones except the right humerus, radius, and ulna (which were exposed to the surface and apparently decomposed) appear to be present. All of the long bones (propodials and epipodials) are poorly preserved. We were unable to assess fusion of epiphyses and diaphyses for any of the elements, and we were able to measure them only very approximately: left humerus = ca. 4 mm, left anterior epipodium = ca. 3.1 mm, left femur = ca. 5 mm, left posterior epipodium = ca. 4.5 mm, right femur ca. = 5.3 mm, right posterior epipodium = 4.5 mm. Both hands and feet are preserved, although the right manus is poorly mineralized and the left pes is damaged and obscured by fractures in the amber. The phalangeal formula of the left manus is 2:3:4?:5?:–; that of the right pes is 2:3:4:5:4.

The NMBA specimen is even smaller than the AMNH specimen, but poor preservation of the former precludes us from determining whether various bony elements remain unfused. Assuming that the NMBA specimen is a juvenile, it can be scored for only 2 of the 13–16 skeletal characters that have been

used to analyze anole phylogeny. It exhibits the α type of caudal sequence and possesses caudal autotomy septa. Both of these conditions are likely ancestral for anoles, and even if the second is not, it diagnoses an enormous clade that includes more than 95% of the extant species and all currently recognized species of *Anolis* (with some reversals). The Basel specimen can also be scored for 7 (19%) out of the 37 external characters (25–28, 30, 31, 37) used in the key in the *Anolis* handlist (O'Hara and Williams, 1994). When compared with extant Hispaniolan anoles for these characters, it cannot be distinguished from five species, including *A. aliniger* and *A. singularis* (it can be distinguished from *A. chlorocyanus* and *A. coelestinus*).

Rieppel (1980) considered *A. dominicanus* most similar, on the basis of ratios of head length to snout–vent length (HDL/SVL) and hind limb length to head length (HLB/HDL), to the *A. chlorocyanus–A. coelestinus* subgroup of Hispaniolan green anoles, particularly to *A. coelestinus*. This conclusion seems at odds with our finding that the type of *A. dominicanus* (as well as the AMNH specimen) can be distinguished from *A. chlorocyanus* and *A. coelestinus* but not from *A. aliniger* and *A. singularis*. The apparent discrepancy is attributable to allometry. Although Rieppel examined specimens spanning a range of sizes for all four extant species, his conclusions about similarity were based on comparing the values of *A. dominicanus* with mean values for the other species. We examined an ontogenetic series of 18 *A. chlorocyanus* and found that both of the ratios in question are highly correlated with overall size (snout–vent length), which calls into question the significance of Rieppels comparisons. On the one hand, it is not clear that the four species differ in head and limb proportions; differences in the mean values of the ratios may result simply from sampling different frequency distributions in terms of body size. Even if differences in head and limb proportions exist, they most likely take the form of differences in parameters that define growth curves, in which case comparisons of mean values are likely to conflate those differences with the allometric consequences of differences in (mean) body size among the samples. Thus, Rieppel's data

should not be interpreted as indicating that *A. dominicanus* is more similar in head and limb proportions to *A. coelestinus* and *A. chlorocyanus* than to *A. aliniger* and *A. singularis*.

Direct comparison of the AMNH specimen with the type of *A. dominicanus* reveals only minor differences. Of the skeletal characters, pterygoid teeth are absent in the AMNH specimen but may be present in *A. dominicanus*; however, this character is known to vary within other lizard species (e.g., de Queiroz, 1987). The numbers of maxillary and dentary tooth positions may differ, but the counts are uncertain and the estimated differences are within the range of intraspecific variation seen in other anoles (e.g., Etheridge, 1964). Only six of the standard external characters (25–28, 30, 31) or 16% of the entire set can be scored for both specimens. They are indistinguishable in these characters. Indeed, the only difference is that the tail is either round or weakly compressed in the AMNH specimen, but it appears weakly compressed in *A. dominicanus*. The scales making up the enlarged caudal verticils are possibly larger in *A. dominicanus*, but they are difficult to see in the AMNH specimen.

In summary, poor preservation of the type and only known specimen of *A. dominicanus* makes it very difficult to determine whether the AMNH specimen is conspecific with the NMBA specimen or whether *A. dominicanus* is distinct from several extant species. Because Rieppel's diagnosis for *A. dominicanus* does not contain any characters that will distinguish the specimen from certain extant anole species, and because no such characters have been discovered in the present study, there is no evidence that justifies recognizing *A. dominicanus* as a separate species. Nevertheless, we also consider the evidence insufficient to synonymize the name with that of one of the extant species. We recommend that the type of *A. dominicanus* be referred to simply as "NMBA Entomology P 52" or "the Basel specimen" and assigned tentatively to the *A. chlorocyanus* species group. This assignment should be considered even more tentative than for the AMNH specimen, because fewer of the relevant characters can be scored.

AMBER GECKOS AND ANOLES

Böhme (1984) described the gecko *Sphae-rodactylus dommeli* from two fossil specimens preserved in Dominican amber, but Kluge (1995), citing Frost (personal commun.), suggested that *S. dommeli* is not a gecko but an anole, and he stated that this tentative identification is corroborated by better photographs of the paratype published by Schlee (1980, 1990). We will not judge whether the specimens of *S. dommeli* are geckos, but at least the holotype does not appear to be an anole. The toe pads of the holotype, illustrated in photographs by Böhme (1984: figs. 1, 3), are unlike those of anoles in that they are distally located, appearing broadest ventral to the ultimate (ungual) or penultimate phalanges. In anoles, the pads are more proximally located, being broadest ventral to the antepenultimate phalanges. The digits of the paratype cannot be seen clearly in the photograph published by Böhme (1984: fig. 4), and they are not visible at all in the photograph published by Schlee (1990). The paratype of *S. dommeli* was not illustrated in the earlier work by Schlee (1980), which includes several photographs of a different lizard preserved in amber. That specimen does appear to be an anole.

ECOLOGICAL MORPHOLOGY OF HISPANIOLAN AMBER ANOLES

Many extant species of Greater Antillean anoles are readily classified as members of one of six ecologically and morphologically defined categories based primarily on similarities in structural habitat use, coloration, and the proportions of various body parts (e.g., Williams, 1983; Losos and de Queiroz, 1997). These ecomorphs, named for the part of the structural habitat characteristically occupied by their members, are thought to have evolved largely independently on the different Greater Antillean islands and have been of considerable interest to students of ecology and evolution (e.g., Rand and Williams, 1969; Williams, 1972, 1983; Losos, 1992, 1994). We attempted to classify the fossil anoles ecomorphologically both to evaluate our systematic inferences and to gain insight into the evolution of anole ecomorphs on Hispaniola.
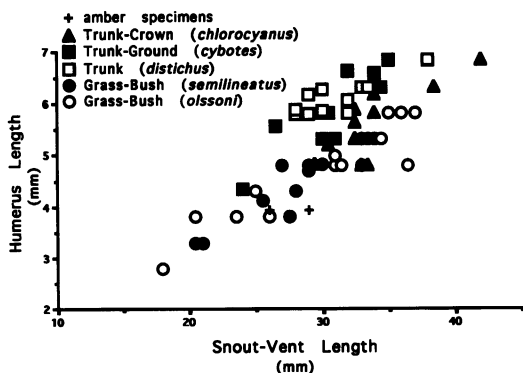

Fig. 5. Plot of humerus length versus snout–vent length for two amber fossil anoles and anoles of five extant Hispaniolan species representing four ecomorphs. The AMNH specimen is the larger of the two fossil specimens (SVL = 29 mm).

To do this, we compared the amber anoles with juveniles of five extant Hispaniolan species representing four of the six ecomorph classes: *A. chlorocyanus* (a member of the trunk-crown ecomorph class), *A. cybotes* (trunk-ground), *A. distichus* (trunk), and *A. olssoni* and *A. semilineatus* (grass-bush). Classification of the amber anoles as crown giants was ruled out on the grounds that even hatchlings of extant crown giant species are much larger than either of the fossil anoles (the smallest juvenile reported by Schwartz [1974] has a SVL of 40 mm compared with an estimated 29 mm for the larger of the two fossil anoles) and have higher lamella counts. Classification as twig anoles was ruled out on the basis of certain distinctive morphological characters not seen in the fossils, including short limbs and prehensile tails.

Relative lengths of the humerus (fig. 5) and ulna (fig. 6) are greater in the trunk and trunk-ground species than in the trunk-crown and grass-bush species. The values for both fossil anoles fall within the cloud of points for the trunk-crown and grass-bush group for both elements. Relative femur lengths (fig. 7) and relative tibia lengths (fig. 8) are greater in the trunk, trunk-ground, and grass-bush species than in the trunk-crown species. The values for both fossil anoles lie close to the line for the trunk-crown group. Relative tail length (fig. 9) is greater in the grass-bush species than in the trunk-ground and trunk-crown species, which are in turn greater than
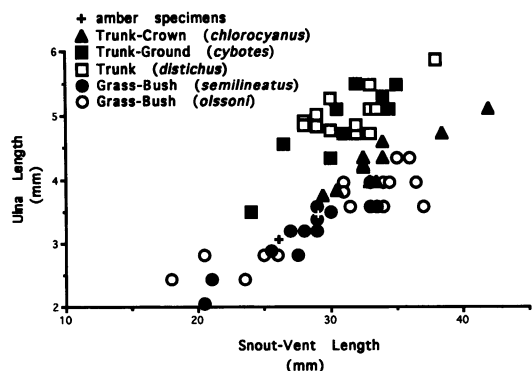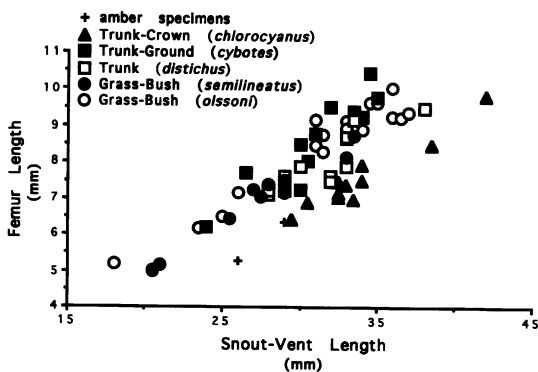
Fig. 6. Plot of ulna length versus snout–vent length for two amber fossil anoles and anoles of five extant Hispaniolan species representing four ecomorphs. The AMNH specimen is the larger of the two fossil specimens (SVL = 29 mm).

Fig. 8. Plot of tibia length versus snout–vent length for two amber fossil anoles and anoles of five extant Hispaniolan species representing four ecomorphs. The AMNH specimen is the larger of the two fossil specimens (SVL = 29 mm).
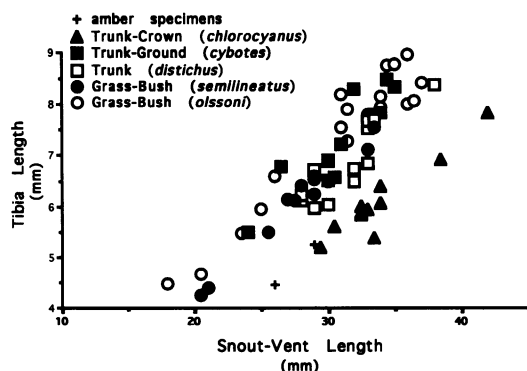
in the trunk species. The value for the one fossil for which tail length could be measured (Basel specimen) falls within the group with intermediate tail lengths. The numbers of lamellae in the two fossils do not lie within the range of any of the five extant Hispaniolan species examined, although they are closest to that of the trunk-crown species, *A. chlorocyanus* (table 1). Moreover, the three other Hispaniolan trunk-crown species in the *A. chlorocyanus* species group all have lower lamella counts than does *A. chlorocyanus* (Williams, 1965). The numbers in the two fossils fall within the ranges of two of these

species, *A. aliniger* (21–24) and *A. singularis* (21–23), and they are close to that of the third, *A. coelestinus* (23–32). Moreover, when a larger set of Greater Antillean species is used to represent the various ecomorphs (table 2), the numbers of lamellae for the fossils fall within the observed range of only the trunk-crown and twig anoles.

The DFA using non-size-adjusted data was highly significant (Wilks' $\lambda = 0.005$, $F_{20,189} = 36.37$, $P < 0.001$). Of the 66 specimens, only 3 were classified to the incorrect ecomorph category: two trunk-ground anoles (*A. cybotes*) were classified as trunk anoles (*A. distichus*), and one trunk anole was classified
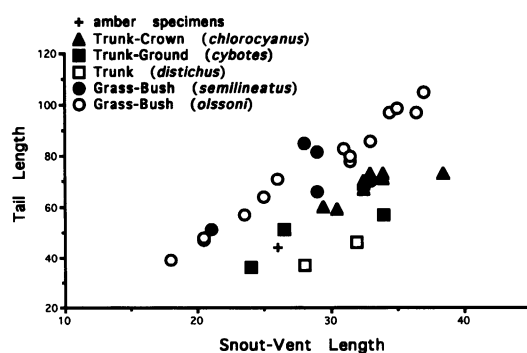

Fig. 7. Plot of femur length versus snout–vent length for two amber fossil anoles and anoles of five extant Hispaniolan species representing four ecomorphs. The AMNH specimen is the larger of the two fossil specimens (SVL = 29 mm).

Fig. 9. Plot of tail length versus snout–vent length for one amber fossil anole and anoles of five extant Hispaniolan species representing four ecomorphs. The AMNH specimen is not included because its tail length could not be measured.

TABLE 1

Numbers of Lamellae Underlying Third and Fourth Phalanges of Pedal Digit IV in Five Hispaniolan *Anole* Species Representing Four Ecomorph Classes

(The fossil anoles are both estimated to have 22–23 lamellae.)

Ecomorph (species)	Mean no. of Lamellae (±1 SE)	Range
Trunk-crown (A. chlorocyanus)	25.6 ± 0.3	24.0–27.0
Trunk-ground (A. cybotes)	16.4 ± 0.3	15.0–18.0
Trunk (A. distichus)	16.9 ± 0.5	15.0–20.5[a]
Grass-bush I (A. semilineatus)	17.0 ± 0.2	15.5–17.5[a]
Grass-bush II (A. olssoni)	16.8 ± 0.2	15.5–18.0[a]

[a] Counts of 0.5 result either from half-formed scales that do not extend the entire width of the pad or from averaging differing counts for right and left sides.

TABLE 2

Numbers of Lamellae Underlying the Third and Fourth Phalanges of Pedal Digit IV in 31 Greater Antillean Anole Species Representing Six Ecomorph Classes

(Data are from Losos (1990a, unpubl.) and Irshick and Losos (1996). The fossils are both estimated to have 22–23 lamellae.)

Ecomorph	Mean no. of Lamellae (±1 SE)	Range
Trunk-crown	24.8 ± 1.1	19.0–30.4
Trunk-ground	18.8 ± 0.5	17.5–21.3
Trunk	17.9 ± 0.4	17.6–18.2
Grass-bush	18.9 ± 0.6	17.1–20.5
Crown giant	31.0 ± 1.2	28.4–34.5
Twig	18.8 ± 1.8	15.0–22.6

as a trunk-ground anole (in addition, five grass-bush anoles were assigned to the wrong species). Both fossil anoles were classified as trunk-crown anoles (*A. chlorocyanus*) with a probability of 1.0. The results with size-adjusted data were very similar. The DFA was highly significant (Wilks' λ = 0.005, $F_{20,189}$ = 36.21, $P < 0.001$), and the same three specimens were misclassified to ecomorph category (although in this case only two grass-bush anoles were assigned to the wrong species). Again, both fossil anoles were classified as trunk-crown anoles (*A. chlorocyanus*) with a probability of 1.0. Classification and probability values for the AMNH specimen were identical regardless of whether an estimated SVL of 27, 29, or 31 mm was used to calculate residuals.

In short, morphometric analyses indicate that both amber anoles belong to the trunk-crown ecomorph. This result is consistent with our tentative systematic assignment of the fossils to the *A. chlorocyanus* species group, all extant members of which belong to the trunk-crown ecomorph class (Williams, 1983). It also indicates that the trunk-crown ecomorph (and possibly the *A. chlorocyanus* species group) has been present in

Hispaniola since the Early or Middle Miocene. The phylogeny of Hispaniolan anoles is currently poorly understood both in terms of the relationships of these taxa to one another and to other West Indian taxa and in terms of the ages of the various cladogenetic events. Furthermore, the composition of the Miocene anole fauna of Hispaniola is still poorly known in terms of both ecomorphs and species. With better understanding in both these areas, the fossil anoles of Hispaniola might ultimately provide evidence relevant to alternative hypotheses regarding anole faunal evolution in the Greater Antilles, specifically, whether the ancestral species (one or several) of the Hispaniolan radiation was an ecological generalist as opposed to a trunk-crown specialist (Losos and de Queiroz, 1997).

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