

GEORGE R. ZUG

*The Distribution and
Patterns of the Major
Arteries of the Iguanids
and Comments on the
Intergeneric Relationships
of Iguanids
(Reptilia: Lacertilia)*

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ABSTRACT

Zug, George R. The Distribution and Patterns of the Major Arteries of the Iguanids and Comments on the Intergeneric Relationships of Iguanids (Reptilia: Lacertilia). *Smithsonian Contributions to Zoology*, 83: 1-23. 1971.—The spatial arrangement of the major arteries, i.e., systemic arches, carotid arches and major branches, subclavians, coeliac, and mesenterics, are described for 42 genera of iguanid lizards. The arterial patterns are relatively uniform in iguanids. All of iguanids examined had carotid ducts, lacked a primary common carotid, and with the exception of *Iguana*, the coeliac arose anterior to or adjacent to the mesenterics. Variation was observed in the type of origin of the external carotid and sternohyoid, subclavians, and mesenterics. These pairs of vessels could arise separately, contiguous, or form a common trunk.

Ten arterial characters were analyzed to determine their taxonomic value. Comparison of similarly generated phenograms, one for arterial data and the other for extant iguanid data, showed the arterial characters to be of little value for intrafamilial classification. The arterial data can function only as a weak indicator of relationships.

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The Distribution and Patterns of the Major Arteries of the Iguanids and Comments on the Intergeneric Relationships of Iguanids (Reptilia: Lacertilia)

Introduction

The current systematic revolution revolves around the search for new characters and methods of character analysis. The saurian arterial system possesses a diversity of patterns, yet it has remained unanalyzed. Diversity is a prerequisite for determining phylogenetic relationships. Uniformity indicates only the possibility of taxon derivation from a common ancestor but not the degree and form of intragroup relationships which are provided by diversity (Throckmorton, 1968; Wake and Ozeti, 1969). Diversity, however, must be balanced with uniformity, for excessive and discordant variation within the taxon will mask the relationships. My objectives have been to determine the patterns and amounts of variation in the arterial system of lizards. The iguanids were selected for a critical analysis of pattern variation, since the recent investigations of Etheridge, e.g., 1959, 1964, 1967, show them to be a natural assemblage of lizards and provide a basis for an interpretation of intragroup relationships.

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Saurian Arterial System: A Selective Literature Review

Corti's 1847 thesis on the circulatory system of *Varanus griseus* generally is accepted as the first detailed description of the saurian circulatory system. His description was based on two specimens, one with the arteries injected. In 1857, Rathke published a survey of the aortic arches and its branches in approximately fifty species of lizards and of the visceral arteries of a similar number of lizards in 1863. Rathke's investigations were the first and most valuable comparative surveys of the saurian arterial system. His work clearly illustrated the existence of different arterial arrangements, although his attempt to examine representatives of most saurian families caused his data to be too superficial for purposes of classification.

In 1886, two articles on the saurian arterial system appeared. Mackay described the arterial system of *Chamaeleo vulgaris*. He noted that it was very different from that of other lizards, although he did not mention which other lizards. Van Bemmelen compared the aortic arches of *Lacerta muralis* to those of a snake and birds. Shufeldt

(1890) provided a brief description of the arterial system of *Heloderma* in his anatomical investigation of this genus.

At the beginning of the twentieth century, Beddard published a series of articles, e.g., 1904, 1905, 1906, 1907, on the vascular system of lizards. His interest in the classification of lizards led him to draw some systematic conclusions based on the vascular system. Shindo's (1914) survey of reptilian cranial arteries contains data on the saurian condition and is of particular interest for its topographic details. In 1920, O'Donoghue presented a detailed study of the circulatory system in *Sphenodon*. Although his study was not concerned primarily with lizards, he synthesized the published data on lizards and provided the framework and terminology for most subsequent investigations.

Three Indian genera of lizards were examined in the 1920s and 1930s. Thapar (1923) compared the arterial system of *Varanus* to those of *Uromastix* and *Hemidactylus*. Bhatia and associate (1929, 1933) extended and corrected Thapar's data on *Uromastix* and *Hemidactylus*. Additional information on the lizards of this region was published by Meinertz (1952) on *Varanus*, de Silva (1956a and b) on *Calotes*, and Kashyap and Nigwekar (1964) on *Riopa*.

Adams published a series of articles (1952, 1953, 1957a and b) on the carotid arch—all contain valuable information on the saurian condition. Sidky (1967) described carotid sinus of *Chalcides* and *Scincus*. Oelrich (1956) gave topographic details for the cranial arteries of the iguanid *Ctenosaura*. Burda (1966) described the development of intracranial arteries in *Lacerta*.

Material and Methods

IGUANID ARTERIAL SYSTEM.—The following description serves two purposes: (1) To familiarize the reader with the topographic relationships of the saurian arterial system and to indicate the vessels examined, i.e., the names in this section that are printed in bold type; (2) to provide sufficient details so that concise repetitive descriptions are possible. Figure 2 provides a stylized illustration of arterial arrangement.

The heart lies at the anterior end of the body cavity between the forelimbs. Externally two large vessels originate from the anterior end of the ven-

tricle. Both are displaced dextrally of the ventricle's midline. The pulmonary arch arises ventrally and the systemic arch dorsally. Both extend anteriorly between the atria. The pulmonary arch curves dextrally and dorsally. Concurrently the systemic arch curves sinistrally and ventrally. As the two arches diverge, the systemic bifurcates into right and left branches. The branches cover ventrally the pulmonary arch and its bilateral bifurcation. Each systemic arch curves laterally along the anterior edge of its adjacent atrium.

The common carotid arteries arise paired from the right systemic (systemocarotid of some authors) as the latter begins its lateral course. A primary carotid artery does not exist. The common carotids pass laterally along the anterior margins of their respective systemic arches and continue dorsolaterally to the ventral side of the internal jugular veins. The common carotid divides beneath the internal jugular. Three arteries, **sternohyoid**, **external carotid** and **internal carotid**, arise from this division in several different arrangements. The small sternohyoid extends ventrolaterally and bifurcates into an anterior branch to the ventral throat musculature and frequently to the thyroid gland and the posterior branch to the pectoral girdle. The external carotid passes anteriorly along the ventral surface of the internal jugular vein to the level of the thyroid gland and bifurcates. A small branch supplies the anterior part of the esophagus and thyroid gland. The major arterial supply of the thyroid gland, however, is derived from the paired laryngotracheal arteries, which arise from the pulmonary arches. The larger lateral branch of the external carotid, **hyomandibular artery**, passes to the posterior base of the mandible and divides into numerous branches.

The internal carotid artery extends dorsally along the medial surface of the internal jugular. Its posteriomedial face is continuous with the carotid gland. Dorsally at the body wall, the internal carotid bifurcates. The posterior branch, **carotid duct**, passes caudally and joins the systemic arch at the beginning of the latter's posterior course. The anterior branch, the internal carotid, extends anteriorly along the medial edge of the internal jugular and enters the base of the skull. It is accompanied on its anterior course by a branch of the musculocervical artery. The musculocervical artery arises from the dorsal surface of the carotid duct

and has numerous small branches supplying the cervical muscles, glands, and digestive tract.

At the lateral edge of the atria, the systemic arches curve sharply dorsally. They pass medial to the internal jugular and curve posteriorly as they reach the body wall. The left systemic arch gives off several small esophageal arteries before joining with the right systemic to form the dorsal aorta. The left and right subclavian arteries arise from the right systemic near the axillary plane. If they arise separately, the left is usually displaced posteriorad of the right. A vertebral artery may arise dorsally from the right systemic near the subclavians or proximally from the left subclavian. The vertebral artery has a number of branches to the esophagus and a major branch extending dorsally into the neck. Posterior to the subclavians, the paired parietal arteries appear in every segment. The first pair of parietals may originate from their respective subclavians. An irregular number of small gastric arteries extend ventrally from the aorta to the dorsal surface of the stomach.

Three large arteries arise from the aorta and extend to the digestive tract. The sequence of origin—anterior to posterior—is usually **coeliac**, **inferior mesenteric**, and **superior mesenteric**. The inferior mesenteric supplies the posterior end of the small intestine, the caecum, and the large intestine. The superior mesenteric extends to the middle and anterior end of the small intestine, the posterior part of the pancreas, the pyloric region of the stomach, and generally to the liver in the region of the gall bladder. Unlike the former two arteries, the coeliac originates from the sinistral surface of the aorta rather than the ventral surface. The coeliac supplies most of the stomach, the spleen, and the anterior part of the pancreas.

SPECIMENS EXAMINED.—All specimens listed below with the exception of an *Iguana* from a biological supply-house, did not have the arteries injected and are a part of the United States National Museum of Natural History herpetological collection. The number in parentheses denotes the number of specimens examined.

Anolines: *Anisolepis undulatus* (1), *Anolis frazeri* (Alpha Group) (1), *Anolis petersi* (Beta Group) (3), *Anolis vermiculatus* (Alpha Group) (2), *Chamaeleolis chamaeleontides* (1), *Chamaeleolis porcus* (1), *Phenacosaurus heterodermus* (2), *Polychrus marmoratus* (3).

Basiliscines: *Basiliscus basiliscus* (2), *Basiliscus galeritus* (2), *Basiliscus plumifrons* (1), *Basiliscus vittatus* (1), *Corytophanes hernandesi* (2), *Lacmanctus longipes* (2).

Iguanines: *Amblyrhynchus cristatus* (2), *Brachylophus fasciatus* (1), *Ctenosaura acanthura* (1), *Ctenosaura hemilopha* (1), *Ctenosaura similis* (1), *Cyclura carinata* (2), *Cyclura macleayi* (1), *Dipsosaurus dorsalis* (2), *Iguana iguana* (4), *Sauromalus obesus* (2).

Sceloporines: *Callisaurus draconoides* (2), *Crotaphytus collaris* (3), *Gambelia wislizeni* (2), *Holbrookia maculata* (1), *Holbrookia texana* (2), *Petrosaurus mearnsi* (1), *Petrosaurus thalassinus* (2), *Phrynosoma asio* (1), *Phrynosoma coronatum* (2), *Phrynosoma douglassi* (1), *Phrynosoma orbiculare* (1), *Sceloporus cyanogenys* (2), *Sceloporus magister* (2), *Uma notata* (1), *Urosaurus ornatus* (2), *Uta stansburiana* (3).

Tropidurines: *Ctenoblepharis jamesi* (1), *Leiocephalus carinatus* (3), *Liolaemus elongatus* (1), *Liolaemus fitzingeri* (2), *Ophryoessoides guentheri* (2), *Plica plica* (3), *Plica umbra* (1), *Stenocercus crassicaudatus* (2), *Tropidurus delanonis* (2), *Tropidurus hispidus* (1), *Tropidurus peruvianus* (1), *Uracentron azureum* (1), *Uranoscodon superciliaris* (2).

Malagasian iguanids: *Chalarodon madagascariensis* (2), *Oplurus quadrimaculatus* (1), *Oplurus sebae* (2).

Incerta sedis: *Cupriganus spatulata* (1), *Enyalioides heterolepis* (1), *Enyalioides microlepis* (1), *Enyalius iheringii* (2), *Leiosaurus paronae* (1), *Morunasaurus annularis* (2).

CHARACTERS EXAMINED.—Typically, the variation within the circulatory system is presented qualitatively. Such a presentation is usually by necessity rather than by choice. Nonetheless, it makes accurate analysis of variation impossible. Since many vessels have their origin along the dorsal midline of the peritoneal cavity, they share a common axis with the longitudinal body axis. This linear arrangement enabled me to take the succeeding measurements with a high degree of accuracy. All measurements were taken with Helios dial caliper to the closest millimeter. It was necessary to pin out all specimens to ensure that the longitudinal axis was straight.

Snout to ventricle length (SVR): Distance from the

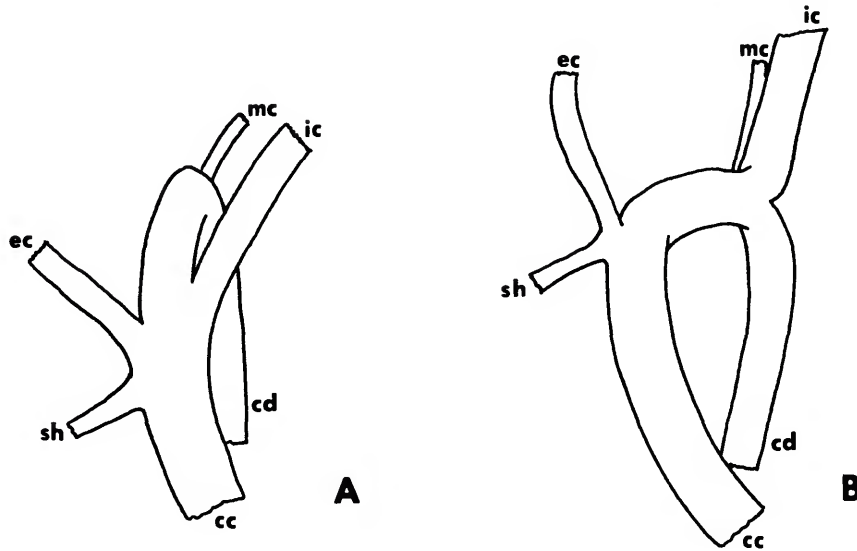


FIGURE 1.—The two divergent patterns of carotid arches in iguanids. A, The tropidurine type. B, The iguanine type. Abbreviations: cc, common carotid; cd, carotid duct; ec, external carotid; ic, internal carotid; mc, musculocervical; sh, sternohyoid.

anterior end of the lower jaw to the posterior tip of the ventricle.

Snout to vent length (SV): Distance from the anterior end of the lower jaw to the anteromedial edge of the vent.

Ventricle length (VR): Distance from the origin of the pulmonary trunk to the posterior tip of the ventricle.

Snout to axilla length (SA): Distance from the anterior end of the lower jaw to the transverse axillary plane.

Snout to subclavian length (SS): Distance from the anterior end of the lower jaw to the anterior edge of right subclavian or common subclavian at its origin.

Snout to dorsal aorta (SD): Distance from the anterior end of the lower jaw to the dorsal junction of the right and left systemic arches.

Snout to coeliac length (SC); Snout to inferior mesenteric length (SIM); Snout to superior mesenteric length (SSM); Snout to common mesenteric length (SCM): Distance from the anterior end of the lower jaw to the anterior edge of the aforementioned arteries at their origin.

A number of other arterial characteristics were noted but could not be quantified. The origins of the external carotid and the sternohyoid may be separated, contiguous, or from a common trunk. The relative diameter of the carotid duct is extremely variable and difficult to record. Generally it is nearly equal to the internal carotid. Two types of carotid arches are recognizable. In the tropidurine type (Figure 1A), the carotid duct originates in common with the internal carotid and external carotid as a trifurcation of the common carotid. In contrast, the carotid duct and internal carotid of the iguanine type bifurcate distal to the origin of the external carotid (Figure 1B). These two types are the extremes of a continuous range, thus it is impossible to designate two separate classes. The subclavians may arise widely separated, contiguous, or from a common trunk. As the subclavian extends laterally, it passes beneath a thin ligament or the muscular bundle of a subvertebral muscle (longus colli?). The coeliac is usually present; only in one species was it absent. The inferior and superior mesenteric may originate separately, contiguous, or from a common trunk.

CHARACTER ANALYSIS.—The mensural data were

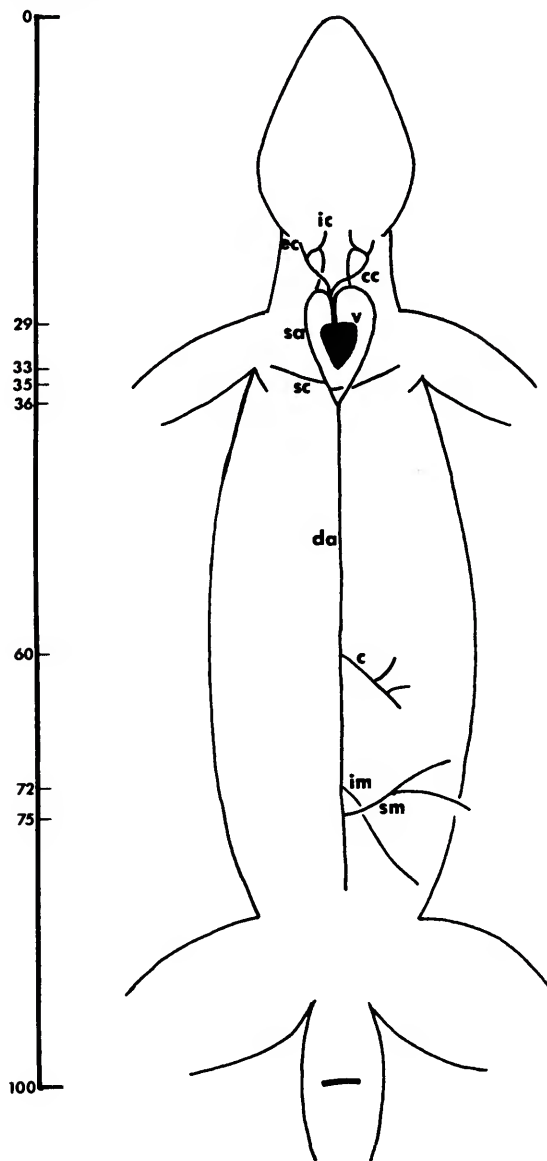


FIGURE 2.—The arterial arrangement and their positions in the hypothetical lizard. The numerical column provides the values (in millimeters) assigned to the different measurements. The value assigned to the common mesenteric is 75 mm. Abbreviations: c, coeliac; cc, common carotid; da, dorsal aorta; ec, external carotid; ic, internal carotid; im, inferior mesenteric; sa, systemic arch; sc, subclavian; sm, superior mesenteric; v, ventricle.

analyzed by ratio diagrams (Simpson, 1941). Rather than plot a ratio diagram for each single specimen,

the data for each genus were combined and a mean was determined for each measurement. Usually one of the taxa examined is selected as a standard, and all other taxa are compared to this standard. I have constructed, however, a hypothetical lizard (Figure 2) to be used as a standard. A hypothetical specimen has several advantages over an actual specimen: (1) In a hypothetical specimen the positions of the arteries can be set so that the proportions are evident, i.e., as percentages. (2) Interpretation of the diagram is enhanced, since all lizards are compared to a single standard of known proportions. (3) Selection of an actual specimen implies a certain significance attached to that taxon and it is difficult to compare the proportions within this species since all the measurements have been standardized to zero.

Only the means are plotted in the ratio diagrams. The sample sizes are too small for the range, standard deviation, or 95-percent confidence interval to be meaningful. It is to be expected that the amount of variation reflects the range of body length instead of interspecific differences. *Iguana* has the greatest range of body size and would be expected to have the highest standard deviations.

Observations and Comparisons of the Arterial System

ANOLINES.—Compared to the hypothetical lizard (Figure 3) the body proportions of the anolines differ by having the heart more posteriorly, i.e., beyond 33 percent of the body length. The latter is indicated by SVR greater than SV. The heart lies at the extreme anterior end of the body cavity and anterior to the transverse axillary plane. In all genera, the heart is nearly 4 percent of the body length, $SV \cong VR$.

The carotid arches of *Anisolepis* and *Phenacosaurus* are of the tropidurine type, whereas the other genera have a more iguanine type of arch. *Anisolepis* and *Phenacosaurus* have the origins of the sternohyoid and external carotid separate but contiguous. The two vessels originate by a common trunk in *Chamaeleolis*. *Anolis* (Alpha and Beta Groups) and *Polychrus* possess both of the previously mentioned conditions.

The subclavians arise widely separated in all genera except *Anisolepis* and one specimen of *Phenacosaurus*. The former has a long common

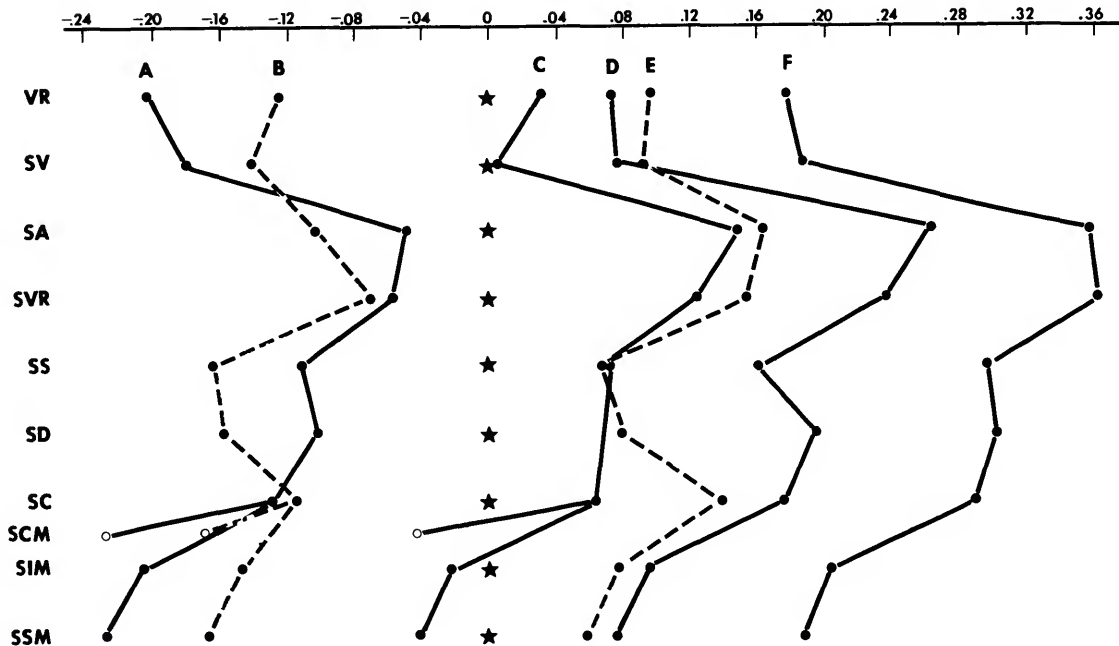


FIGURE 3.—Ratio diagram of arterial characters for anolines. A, *Phenacosaurus*. B, *Anisolepis*. C, *Anolis* (Beta). D, *Anolis* (Alpha). E, *Polychrus*. F, *Chamaeleolis*. The stars indicate the position of the hypothetical lizard. An open circle denotes the presence of a common mesenteric. The abbreviations on the left are explained in the characters examined section.

subclavian trunk, the latter a short one. In *Anolis* (Alpha and Beta Groups) and *Chamaeleolis*, the subclavians do not pass beneath a muscular bundle as in the other genera. The origins of the anoline subclavians and dorsal aorta are clearly separated and lie beneath the heart in all genera.

The origin of the coeliac is variable. In *Anisolepis* and *Polychrus*, it arises anterior to and well separated from the mesenterics. The remaining genera has the coeliac arising in close association with the mesenterics, both anterior and posterior to them in *Phenacosaurus*, posterior to them in *Anolis* (Alpha and Beta) and *Chamaeleolis*, and laterally contiguous in one *Anolis* (Alpha). The relative position of its origin is greater than 60 percent of body length in all genera.

In *Anolis* (Alpha), *Chamaeleolis*, and *Polychrus* the inferior and superior mesenterics arise separately, although only in *Chamaeleolis* are the two mesenterics not contiguous at their origin. The mesenterics arise as a common trunk in *Anisolepis*,

Anolis (Beta), and *Phenacosaurus*. In the genera with two mesenterics, they arise at approximately 72 percent of the body length, i.e., the point of origin of the inferior mesenteric in the hypothetical lizard. In the genera with a common mesenteric, the origin is less than 72 percent of body length.

BASILISCINES.—The body proportions of the basiliscines are very similar (Figure 4). The heart and the axilla are located posterior to the anterior third of the body. The entire heart lies anterior to the transverse axillary plane. The heart is clearly greater than 4 percent of the body length.

The carotid arches are of the iguanine type. The external carotid and sternohyoid arise distinctly separated in all specimens examined.

The subclavians arise paired, one on each side of the right systemic. The subclavians extend laterally beneath a thin ligamentous muscle attachment. The origin of the dorsal aorta is well removed from the origin of the subclavians. Both lie dorsal to the heart.

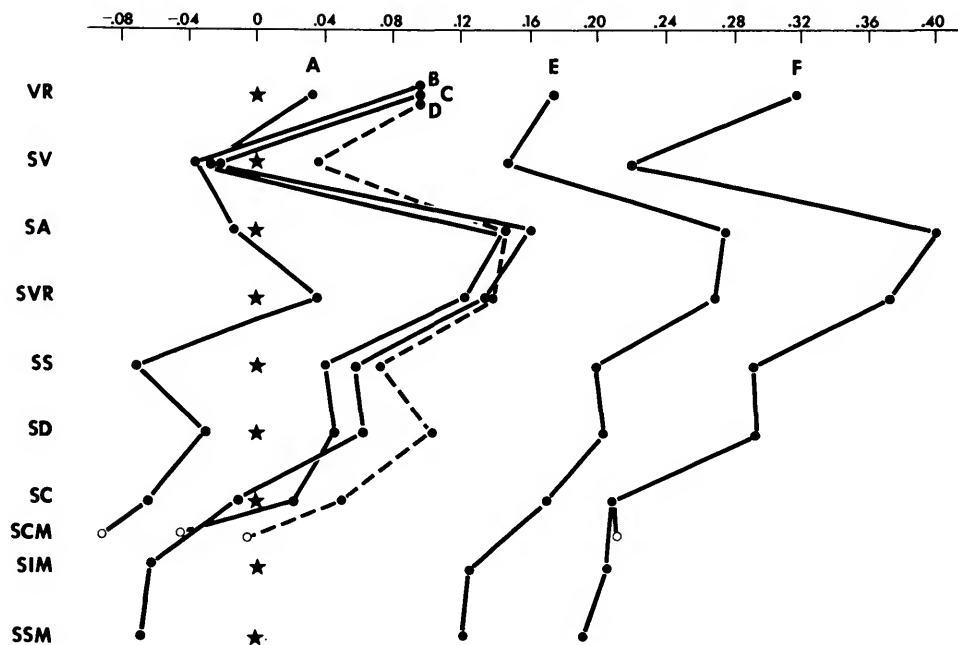


FIGURE 4.—Ratio diagram of arterial characters for basiliscines and sceloporine allies. A, *Crotaphytus*. B, *Phrynosoma*. C, *Corytophanes*. D, *Gambelia*. E, *Laemanctus*. F, *Basiliscus*. The stars indicate the position of the hypothetical lizards. An open circle denotes the presence of a common mesenteric. The abbreviations on the left are explained in the characters examined section.

The coeliac is present and anterior of the mesenterics in *Basiliscus galeritus*, *B. plumifrons*, *B. vittatus*, *Corytophanes*, and *Laemanctus*. The coeliac, however, is small and supplies only the anterior part of the spleen and the stomach in that region. The superior mesenteric has a branch which supplies the visceral region usually supplied by the coeliac. In *B. basiliscus*, the coeliac is absent, and the superior mesenteric has completely taken over the functions of the coeliac.

Both the inferior and superior mesenterics are present in all basiliscines. The inferior mesenteric precedes the superior, and both are anterior of the site of origin in the hypothetical lizard, SIM and SSM less than SV.

IGUANINES.—Like the anolines and basiliscines, the heart lies further posterior in the iguanines than in the hypothetical lizard (Figure 5). The heart extends posteriorad to the transverse axillary plane only in *Sauromalus*. All other genera have their hearts anterior to the axillary plane. Heart size is variable. It is larger than the hypothetical

lizard's heart in all genera except *Brachylophus* in which it is smaller.

The carotid arches are of the iguanine type. The origins of the external carotid and sternohyoid are variable. All three types of origins are present, and two different ones may occur in an individual, i.e., left and right sides.

The subclavians arise paired, one on each side of the right systemic. In all the genera except *Brachylophus* and *Dipsosaurus*, the subclavian passes laterally beneath a muscle bundle. In the *Brachylophus* and *Dipsosaurus*, only a thin flat ligament covers the subclavian. The origins of the dorsal aorta and the subclavians are clearly separated. In *Dipsosaurus* and *Brachylophus*, the origins of both lie dorsal to the heart. Only the subclavians' origins lie above the heart with the aorta's origin posterior to the heart in the remaining genera.

The position of the coeliac's origin in relation to the mesenterics is variable, whereas its relative position in the body is always very similar to that of the hypothetical lizard. In all genera except *Iguana*, the

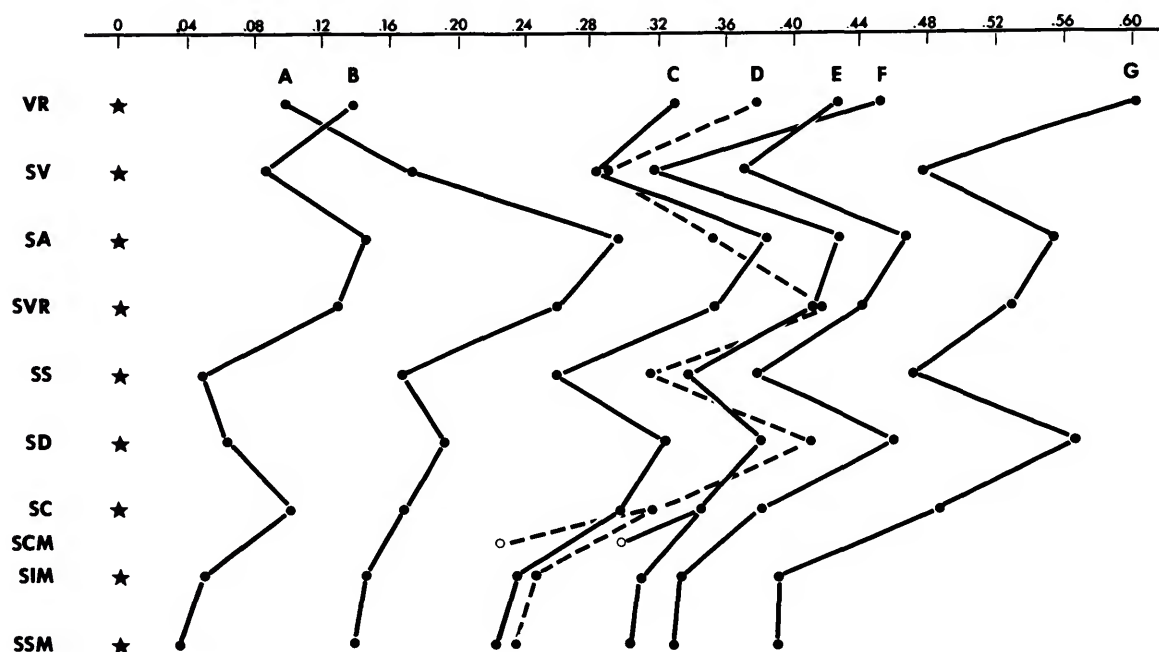


FIGURE 5.—Ratio diagram of arterial characters in iguanines. A, *Brachylophus*. B, *Dipsosaurus*. C, *Amblyrhynchus*. D, *Sauromalus*. E, *Cyclura*. F, *Ctenosaura*. G, *Iguana*. The stars indicate the position of the hypothetical lizard. The open circle denotes the presence of a common mesenteric. The abbreviations on the left are explained in the characters examined section.

coeliac arises anterior to and separate from the mesenterics. In *Iguana*, the coeliac may arise posterior to and separated from the mesenterics, contiguous with the superior mesenteric or nearly so, between the mesenterics, or contiguous with the inferior mesenteric.

An inferior and a superior mesenteric are present in all the genera; however, in one *Ctenosaura* and one *Sauromalus*, the mesenteric arises from a common trunk. When paired, the inferior mesenteric always arises anterior of the superior. The mesenterics always arise more anterior than those of the hypothetical lizard.

SCELOPORINES.—The heart of sceloporines lies posterior to that of the hypothetical lizard (Figures 4 and 6). Only in *Phrynosoma*, does the heart lie near to the anterior third of the body. The heart in *Crotaphytus*, *Gambelia*, *Holbrookia*, *Uta*, *Callisaurus*, *Petrosaurus*, and *Sceloporus* lies anterior to the transverse axillary plane. In *Urosaurus*, *Uma*, and *Phrynosoma*, it extends posteriorly beyond the axillary plane. The size of the heart is nearly equivalent to that of the hypothetical lizard in

Urosaurus, *Uta*, *Petrosaurus*, and *Sceloporus*, much smaller in *Callisaurus*, *Uma*, *Crotaphytus*, and *Gambelia*, and much larger in *Phrynosoma* and *Holbrookia*.

The carotid arches of the sceloporines are of an intermediate type. The arches of *Sceloporus* approach closest to the iguanine type, whereas those of *Callisaurus* are more tropidurine in appearance. The origins of the sternohyoid and external carotid display the three possible patterns. Although the pattern of origin tends to be symmetrical, some individuals display different patterns on the left and right sides.

The subclavians arise paired in all genera except *Phrynosoma*. *Phrynosoma* has a short, but distinct, common subclavian trunk. A muscle bundle covers the initial lateral extension of the subclavian in all genera. The origins of the subclavians and dorsal aorta are usually separated, although in a few specimens they were nearly contiguous. These origins lie above the heart in all genera.

The coeliac is the first major visceral artery to originate. Its origin is well anterior to the mesen-

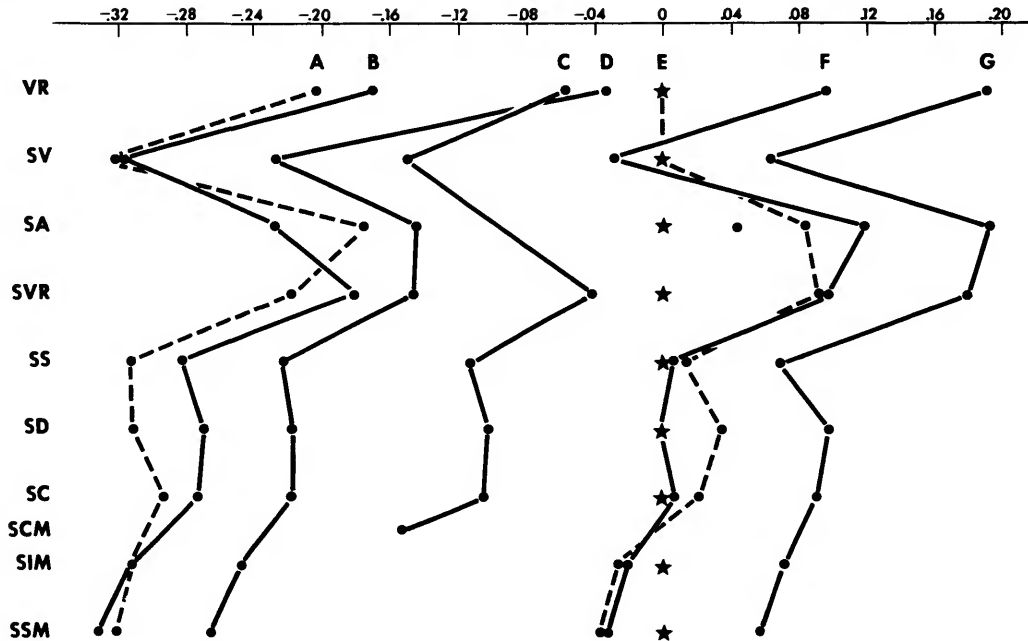


FIGURE 6.—Ratio diagram of arterial characters in sceloporines. A, *Uta*. B, *Urosaurus*. C, *Callisaurus*. D, *Holbrookia*. E, *Uma*. F, *Petrosaurus*. G, *Sceloporus*. The stars indicate the position of the hypothetical lizard. The abbreviations on the left are explained in the characters examined section.

terics' origins. Excluding *Phrynosoma* and *Holbrookia*, the origin is posterior to that in the hypothetical lizard. In *Holbrookia*, the origin is nearly identical to that of the hypothetical lizard; whereas the origin in *Phrynosoma* is anterior.

Crotaphytus, *Gambelia*, *Callisaurus*, and *Phrynosoma* have a common mesenteric. *Holbrookia*, *Petrosaurus*, *Sceloporus*, *Uma*, *Urosaurus*, and *Uta* have an inferior and a superior mesenteric. In *Uta*, *Urosaurus*, and *Holbrookia*, the mesenterics are contiguous. The inferior mesenteric of *Petrosaurus* and *Uma* is anterior to the superior mesenteric and is separated from it by a short interval. *Sceloporus* possesses both of the above conditions. *Holbrookia*, *Uma*, *Gambelia*, and *Phrynosoma* are the only taxa which have the mesenterics' origins lying well anterior to that in the hypothetical lizard. The other genera have origins slightly anterior to that of the hypothetical lizard.

TROPIDURINES.—As in all preceding iguanids, the heart of tropidurines lies further posterior than does that of the hypothetical lizard (Figure 7). The posterior tip of the heart reaches the transverse

axillary plane in *Ctenoblepharis*, *Plica*, and *Uracentron*. The other genera have the heart completely anterior to the axillary plane. The hearts of all tropidurines are proportionately bigger than that of the hypothetical lizard.

All genera possess carotid arches of the tropidurine type, but of various degrees of development. The arches are definite tropidurine in *Ctenoblepharis* and *Tropidurus*, less so in the other genera. All three types of sternohyoid-external carotid origins are present. The type of origin is usually symmetrical within the individual, but there is considerable intrageneric variation.

The subclavians arise from a common trunk in *Ctenoblepharis*, *Ophryoessoides*, *Plica*, *Stenocercus*, and *Uracentron*. In *Leiocephalus* and *Liolaemus*, their origins are either contiguous or joined and only contiguous in *Tropidurus*. The subclavians of all tropidurines pass laterally beneath a thick muscle bundle. The origins of the subclavians and dorsal aorta are usually separate, although in *Stenocercus* they are contiguous, and separated by a small interval in some of the other tropidurines. They lie

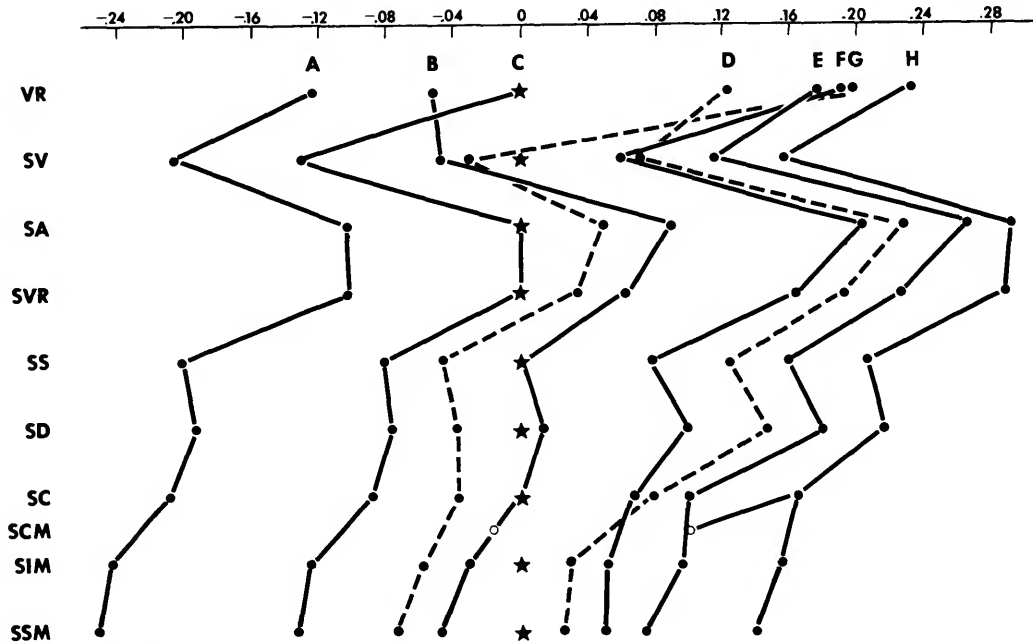


FIGURE 7.—Ratio diagram of arterial characters for tropidurines. A, *Ctenoblepharis*. B, *Ophryoesoides*. C, *Uracentron*. D, *Leiocephalus*. E, *Uranoscodon*. F, *Tropidurus*. G, *Liolaemus*. H, *Plica*. The stars indicate the position of the hypothetical lizard. The abbreviations on the left are explained in the characters examined section.

dorsal to the heart and not posterior to it.

The coeliac arises anterior of the mesenterics and distinctly separated from them. *Ctenoblepharis*, *Leiocephalus*, *Liolaemus*, *Plica*, and *Tropidurus* have their coeliacs originate from approximately the same body position as that of the hypothetical lizard. In *Uracentron*, *Stenocercus*, and *Ophryoesoides*, the origin lies more posteriorly and slightly anterior in *Uranoscodon*. All the tropidurines, except *Plica umbra*, *Ophryoesoides*, and *Stenocercus* have the inferior mesenteric arise separately and anterior to the superior mesenteric. In *Stenocercus*, *Uranoscodon*, and one specimen of *Ophryoesoides*, the mesenterics are contiguous. A common mesenteric is present in the other specimen of *Ophryoesoides* and *P. umbra*. The relative position of the mesenterics' origin is similar to that of the hypothetical lizard in *Plica*, *Tropidurus*, *Ophryoesoides*, and *Uracentron*. The origins are more anterior in *Ctenoblepharis*, *Liolaemus*, and *Leiocephalus*, and more posterior in *Stenocercus*.

MALAGASIAN IGUANIDS.—The ratio diagram (Figure 8) shows the two Malagasian iguanid genera to be very similar. The heart lies further posterior than in the hypothetical lizard. The posterior tip of the heart reaches the transverse axillary plane in *Chalarodon* and nearly so in *Oplurus*. The heart is proportionately larger in *Chalarodon* and proportionately smaller in *Oplurus* than that of the hypothetical lizard.

The carotid arches are of the iguanine type. The sternohyoid and external carotid arise contiguously.

In *Oplurus*, there is a common subclavian trunk. The subclavians are paired but nearly contiguous in *Chalarodon*. The origins of the subclavians and the dorsal aorta's origin lie dorsal of the heart in *Chalarodon*. The dorsal aorta's origin of *Oplurus* lies posterior to the heart.

The coeliac arises anterior to the mesenterics in both genera. Its origin is posterior to that in the hypothetical lizard. The mesenterics arise separately. The inferior mesenteric appears first. In *Chalarodon*, they originate anterior to the position in the

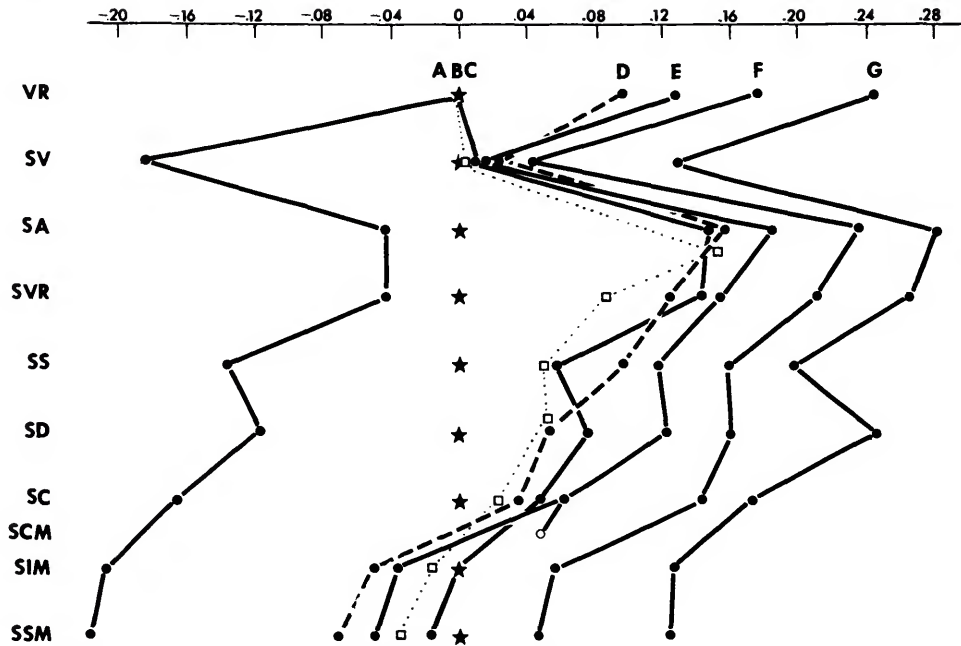


FIGURE 8.—Ratio diagram of arterial characters of iguanids of uncertain affinities. A, *Chalarodon*. B, *Leiosaurus*. C, *Cupriganus*. D, *Enyalioides*. E, *Enyalius*. F, *Morunasaurus*. G, *Oplurus*. The stars indicate the position of the hypothetical lizard. The abbreviations on the left are explained in the characters examined section.

hypothetical lizard and are nearly the same as the hypothetical in *Oplurus*.

IGUANIDS OF UNCERTAIN AFFINITIES.—All of these genera have their hearts farther posterior than in the hypothetical lizard (Figure 8). The heart is always anterior to the transverse axillary plane. The heart is proportionately smaller than that of the hypothetical lizard in *Cupriganus* and *Leiosaurus* and proportionately larger in *Enyalioides*, *Enyalius*, and *Morunasaurus*.

The carotid arches are distinctly tropidurine in *Cupriganus*. The arches of the other genera appear iguanine in form. The origins of the sternohyoid and external carotid are from a common trunk in *Enyalioides*, *Enyalius*, *Leiosaurus*, and *Morunasaurus*. *Enyalius* and *Morunasaurus* have a very short common trunk. In *Cupriganus*, the origins are contiguous or nearly so.

The subclavians arise separately and paired in *Cupriganus*. A common subclavian trunk is present in the other genera. One of the *Enyalius* had a paired but contiguous origin of the subclavians.

The origins of the subclavians and dorsal aorta are separate. The origin of dorsal aorta lies posterior to the heart in only *Enyalius*, *Cupriganus*, and *Leiosaurus*.

The coeliac originates well anterior to the mesenterics in *Cupriganus*, *Enyalius*, and *Leiosaurus*. In *Enyalioides heterolepis*, the coeliac arises first but is contiguous with the mesenterics. In *Enyalioides microlepis*, the coeliac arises posterior to and separated from the mesenterics. The coeliac of *Morunasaurus* is posterior to and contiguous with the superior mesenteric. The relative body position is similar to that of the hypothetical lizard in *Enyalius*, and posterior in the remaining genera.

The mesenterics are paired and clearly separated in one *Enyalius*, *Enyalioides*, and *Morunasaurus*. They are paired and contiguous in *Cupriganus* and *Leiosaurus*. In the other *Enyalius*, there is a short common mesenteric trunk. The mesenterics lie anteriorly relative to their position in the hypothetical lizard in all except *Morunasaurus* and the *Enyalius* with a common mesenteric. *Morunasaurus*

has the origin nearly identical to that of the hypothetical lizard, whereas it is more posterior in the *Enyalius*.

COMMENTS.—The primary carotid (carotis primaria) is absent in all iguanids. This condition is common to most lizards with the exception of varanids and possibly anguids and scincids. Rathke (1857), Thapar (1923), and Meinertz (1952) report its presence in varanids. A short one is reported in *Anguis* by Rathke. Likewise the illustrations of Kashyap and Nigwekar (1964) show a short but distinct primary carotid in *Riopa*, a scincid. A short one is reported in *Hemidactylus*, a gekkonid, by Bhatia and Dayal (1933), although their illustration suggests that the carotids arise paired. It is absent in amphisbaenids (Rathke, 1857), *Chamaeleo* (Mackay, 1886), *Heloderma* (Beddard, 1906), *Uromastix* (Bhatia, 1929), and *Calotes* (de Silva, 1956a and b). I did not observe a primary carotid in *Dicrodon* or *Tupinambis*, teiids.

Carotid ducts were observed in all iguanids. Poor preservation and different degrees of development, however, occasionally made them difficult to locate. The level of my observations prevents any decision on whether the ducts were functional vessels in all iguanids. Adams (1953) states that the ducts are absent in amphisbaenids, chamaeleonids, helodermatids, and varanids.

Intraspecific variation was most prevalent in the origins of the sternohyoid and external carotid and the origin of the coeliac relative to the mesenterics. Occasionally the type of subclavian origin would display intraspecific variation. As a whole, however, the pattern of vessel origin is relatively stable within a genus and commonly within groups of related genera.

The functional significance of this stability and its selective value is difficult to explain. Embryologically, the large blood vessels appear before circulation begins and will continue development even if circulation is impeded (Copenhaver, 1955). Yet there is also evidence that vessel formation is strongly influenced by the growth and metabolism of adjacent tissues. These factors suggest that perhaps the vessel pattern is established by the pattern of the other body organs, although growth is inherent within the circulatory system and free from mechanical influence. Iberall (1967) provides two facts which further suggest that one pattern is me-

chanically no more efficient than another: (1) The cross-sectional area of the cardiovascular system does not change significantly from the aorta to the major arteries. (2) High blood pressure does not fall until the terminal levels of the arterial tree, i.e., below 100 μ diameter. Thus different arterial patterns do not indicate that one pattern is any more efficient than another one.

Analysis of the Arterial Characters

Several sets of interrelated questions should be asked of each new character before it is incorporated into general taxonomic usage. (1) What is the character's range of variation? Is the range of variation continuous or discontinuous? At what level, i.e., intraspecific, interspecific, etc., does the variation occur? Can the variation be traced to specific causes, e.g., ontogenetic, environmental, genetic? (2) Does the new character or particularly the set of new characters provide evidence of genetic relationships among the compared taxa? If new relationships are indicated, how valid is the new interpretation? (3) How is the character related to other characters? Is the character a primary or secondary character (sensu Kendrick, 1965)? How many states does the character possess? Can the polarity, i.e., primitive to derived, of the character states be determined? Are the character states uniquely derived (sensu Wilson, 1965 or Le Quesne, 1969)? In the following sections, I will attempt to answer for the arterial characters some of the questions proposed in sets one and two.

CHARACTER VARIATION.—Of the characters described in the anatomical section, only ten are considered sufficiently distinct and nonredundant for further analysis (Table 1). The presence of the carotid ducts or the absence of the primary carotid trunk are useless characters in iguanids, for they are invariable. Other characters, e.g., origin of sternohyoid and external carotid, type of carotid arch, or size of carotid duct, either show considerable intraspecific variation or are difficult to record accurately.

Seven distance measurements (SA, SVR, SS, SD, SC, SSM, SIM) display intergeneric variation and can, thus, be analyzed to determine their value as indicators of intergroup relationships. Although the sample size for each genus is too small for statistical analysis of variation, the consistently narrow range of variation within each genus suggests that the

TABLE 1.—The arterial characters of the iguanids used to generate the shortest connection networks. Columns A through G are proportions. A, SA/SV. B, SVR/SV. C, SS/SV. D, SD/SV. E, SIM/SV. F, SSM/SV. G, SC/SV. H, Muscle covering subclavians: 0, absent; 1, ligamentous; 2, muscular. I, Type of subclavian origin: 0, separate; 1, contiguous; 2, common trunk. J, Type of mesenteric origin: 0, separate; 1, contiguous; 2, common trunk.

TAXON	A	B	C	D	E	F	G	H	I	J	TAXON	A	B	C	D	E	F	G	H	I	J
ANISOLEPIS	.96	.99	.99	.95	.71	.71	.64	2	2	2	PETROSAURUS	.46	.44	.98	.98	.79	.74	.65	2	0	0
PHENACOSAURUS	.45	.44	.41	.49	.67	.67	.67	2	0	2	SCELOPORUS	.45	.49	.96	.99	.74	.74	.64	2	0	0
ANOLIS (Beta)	.46	.43	.41	.42	.67	.67	.66	0	0	2	PHRYNOSOMA	.95	.99	.92	.97	.66	.66	.56	2	2	2
POLYCHRUS	.99	.98	.99	.95	.70	.70	.67	2	0	1	CROTAPHYTUS	.48	.45	.41	.49	.72	.72	.68	2	0	2
ANOLIS (Alpha)	.51	.48	.46	.44	.74	.74	.75	0	0	1	GAMBELIA	.42	.41	.98	.42	.68	.68	.62	2	0	2
CHAMAELIOLIS	.49	.49	.45	.47	.74	.75	.76	0	0	0	URANOSCODON	.46	.42	.98	.41	.67	.67	.57	1	0	1
CORYTOPHANES	.51	.47	.47	.44	.66	.68	.62	1	0	0	CTENOBLEPHARIS	.42	.42	.95	.97	.66	.68	.60	2	2	0
LAEMANCTUS	.44	.49	.99	.41	.68	.71	.69	1	0	0	URACENTRON	.45	.45	.99	.41	.79	.74	.66	2	2	0
BASILISCUS	.50	.47	.42	.49	.70	.71	.62	1	0	0	LIOLAEMUS	.40	.98	.94	.95	.66	.68	.60	2	1	0
DIPSOSAURUS	.98	.97	.92	.94	.66	.68	.62	1	0	0	OPHRYOESBOIDES	.45	.42	.99	.41	.74	.74	.66	2	2	1
BRACHYLOPHUS	.44	.40	.94	.98	.67	.69	.59	1	0	0	TROPIDURUS	.46	.42	.97	.40	.71	.79	.61	2	1	0
SAUROMALUS	.99	.46	.98	.48	.66	.66	.64	2	0	0	STENOCCERCUS	.48	.47	.40	.40	.78	.78	.68	2	2	1
AMBLRYHYNCHUS	.41	.99	.99	.99	.64	.65	.62	2	0	0	LEIOCEPHALUS	.48	.44	.40	.49	.66	.67	.62	2	0	0
CTENOSAURA	.44	.41	.97	.42	.71	.72	.64	2	0	0	PLICA	.45	.44	.99	.41	.69	.70	.60	2	2	1
CYCLURA	.41	.99	.96	.44	.66	.68	.49	2	0	0	CHALARODON	.46	.46	.99	.42	.68	.69	.69	2	0	0
IQUANA	.99	.97	.95	.44	.59	.62	.61	2	0	0	OPLURUS	.47	.45	.41	.46	.71	.74	.67	2	2	0
UROSAURUS	.41	.42	.95	.96	.79	.79	.64	2	0	1	LEIOSAURUS	.49	.99	.98	.42	.67	.67	.61	2	2	1
UTA	.46	.45	.98	.41	.79	.75	.67	2	0	0	CUPRIGUANUS	.48	.47	.41	.44	.79	.79	.68	2	0	1
CALLISAURUS	.41	.41	.96	.98	.71	.71	.64	2	0	2	ENYALIOIDES	.48	.44	.40	.41	.65	.65	.65	2	2	0
HOLBROOKIA	.40	.40	.96	.96	.69	.69	.62	2	0	1	ENYALIUS	.49	.45	.45	.47	.72	.79	.67	2	2	1
UMA	.40	.41	.96	.99	.68	.69	.69	2	0	0	MORUNASAURUS	.51	.48	.45	.47	.74	.75	.75	2	2	0

intraspecific and interspecific variation is small. In addition, the distance measurements were converted to proportions to eliminate the influence of body size, thereby also slightly reducing ontogenetic variation. The proportions were obtained by dividing each distance measurement of a specimen by the specimen's snout-vent length. The proportions of each character were summed and the arithmetic mean recorded for each genus. Since some genera lack separate mesenteric arteries, the mean proportion of the common mesenteric was used for both the inferior and superior mesenteric.

Each of the three remaining characters possess three states, which are designated by 0, 1, and 2, respectively. The states for the subclavian enclosed by a muscle are muscle absent, small and/or ligamentous, and large. The states for the type of subclavian origin and mesenteric origin are paired and

separate, paired but contiguous, and a single trunk. Although the latter two character states were discrete and easily recognizable, there was occasional intrageneric variation. Variation of the subclavian occurred in *Crotaphytus*, *Enyalius*, *Leiocephalus*, *Liolaemus*, and *Stenocercus*, of the mesenteric in *Anolis*, *Ophryoesoides*, *Sauromalus*, *Sceloporus*, and *Uta*. The most prevalent state in the taxa was recorded.

The proportions, SSM/SV, and SIM/SV, and the type of mesenteric origin are not redundant characters. The type of origin does not influence the relative body position of the origin. The type of origin, however, does affect the position of the mesenterics in relation to one another. Since the proportions indicate relative body position, the occasional fusion of the two mesenterics has a minor effect. Of the ten characters, the SA/SV and the

muscle enclosing the subclavian do not reflect arterial patterns. Nonetheless they are incorporated, since they have not previously been analyzed for taxonomic purposes.

IGUANID RELATIONSHIPS.—The incorporation of new characters into an extant taxonomic framework must be done judiciously. Otherwise, the new characters may be disruptive without adding any alternative or new interpretations of intergroup relationships. The following steps are utilized herein to test the significance and validity of the arterial characters.

(1) Select the taxonomic level, e.g., intrafamilial, intrageneric, at which the classification information of the new character set is to be compared. Assemble as completely as possible the extant character set which is currently used to define the stated taxonomic level.

(2) Select an objective and repeatable procedure for generating relationship diagrams, i.e., phenograms, cladograms, etc.

(3) Generate a relationship diagram for each of the character sets and compare the two diagrams. If the two diagrams are strongly divergent, return to step 1.

The preceding steps are based on several assumptions. A primary assumption is that the relationship diagram generated by the extant character set will conform closely to the current interpretation of intergroup relationships. If this assumption is not obtained, a valid comparison of the two character sets cannot be made. The current interpretation may be in error, the extant character set may be too small or lack the diagnostic characters, or the analysis procedure may be inadequate. Comparison of the two sets assumes that the general pattern of intergroup relations is fairly well understood. It is necessary, however, to avoid circular reasoning. Since the goal of obtaining new characters is to increase the accuracy of our current interpretation, a new character set should not be discarded simply because its diagram does not match that of the extant character set. The degree of discordance must be weighed. Strong discordances imply that the new character set or at least part of it is not usable at the chosen taxonomic level. There is also the possibility, however, that the extant character set and its implied relationships are in error. The zoogeographic implications of the relationship diagram provide valuable criteria for evaluation.

Suggestions of unusual or irregular zoogeographical patterns suggest an invalid set of characters. If clusters of taxa in a relationship diagram have a strong correlation with ecological or behavioral groups, body form or shape, etc., the relationships are probably not phylogenetic. The character set may be reflecting a single adaptation system, and the likelihood of convergence is great.

To test the arterial data, I have used a shortest connection network computer program developed by James S. Farris while at the University of Michigan. The program was used on the United States National Museum of Natural History time-share computing facilities. The network is entirely phenetic. Each taxon is linked to its most similar taxon, and in turn linked segments or clusters are linked together through the most similar member of each cluster. None of the characters were weighted, nor were they transformed. The character set (Table 2) for the extant classification was extracted mainly from articles of Etheridge.

The network (Figure 9), based on the extant character set, clusters the genera similarly to the groups proposed by Etheridge (1967:717). Actually there is only one disagreement. The *Crotaphytus* complex is clustered with the iguanines. This linkage appears to result from the presence of zygosphenes and zygantra, variable presence of pterygoid teeth, presence of a secondary coracoid fenestra, and number of sternal rib and presacral vertebrae. Savage (1958) was the first to formally group *Crotaphytus* with the iguanines. Etheridge (1964) placed *Crotaphytus* in the sceloporine-tropidurine lineage and showed it to be more similar to *Petrosaurus* than to any other Nearctic and Central American iguanid. The difference between the phenogram and Etheridge's interpretation is largely due to Etheridge weighting characters and evaluating a larger character set. Etheridge showed that zygosphenes and zygantra probably appeared independently in several iguanid lineages. Perhaps such an occurrence is also true for the secondary coracoid fenestra. The presence of pterygoid teeth may reflect nothing more than the retention of a primitive character state. Thus, Etheridge's allocation of *Crotaphytus* to the sceloporine-tropidurine lineage should be accepted.

Although the arrangement of genera within clusters should be noted, the limitations of the data set and the manner of constructing the network medi-

TABLE 2.—Some of the characters currently used to classify iguanids. This set of characters was derived from the investigations of Etheridge (1959, 1964, 1965, 1966, 1967) and Savage (1958). A, Femoral pores: absent, 0; present, 1. B, Caudal vertebra fracture plane: absent, 0; absent or present, 0.5; present, 1. C, Transverse process of caudal vertebra: absent, 0; single, 1; double, 2. D, Inscription ribs: all joined to dorsal ribs, 0; one or more floating, 1. E, Inscription ribs: opposites not fused on ventral midline, 0; one or more fused, 1. F, Scapular fenestra: absent, 0; present, 1. G, Secondary coracoid fenestra: absent, 0; absent or present, 0.5; present, 1. H, Sternal fontanelle: absent, 0; absent or present, 0.5; present, 1. I, Clavicular fenestra: absent, 0; absent or present, 0.5; present, 1. J, Number of sternal ribs. K, Number of xiphisternal ribs. L, Number of presacral vertebrae minus 20. M, Number of cervical ribs. N, Zygosphenes-zygantra: absent, 0; present, 1. O, Pterygoid teeth: absent, 0; absent or present, 0.5; present, 1. P, Palatine teeth: absent, 0; present, 1. Q, Meckel's groove: open, 0; closed, 1; fused, 2. R, Calcified endolymphatic glands: absent, 0; present, 1. The underlined values are questionable and should be confirmed.

TAXON	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R
ANISOLEPIS	0	0	1	1	1	0	0	0	0	<u>3</u>	<u>2</u>	<u>4</u>	<u>4</u>	<u>0</u>	0	<u>0</u>	<u>2</u>	1
PHENACOSAURUS	0	0	0	1	1	0	0	0	0	2	2	2	4	0	1	0	2	1
ANOLIS (Alpha)	0	0.5	0	1	1	0	0	0	0	<u>3</u>	2	4	4	1	1	0	2	1
ANOLIS (Beta)	0	1	1	1	1	0	0	0	0	<u>3</u>	2	4	4	1	1	0	2	1
POLYCHRUS	1	0	0	1	1	0	0	0	0	2	2	6	4	1	1	0	2	1
CHAMAEOLEOLIS	0	0	0	1	1	0	0	0	0	<u>3</u>	<u>2</u>	<u>4</u>	4	0	1	1	2	1
CORYTOPHANES	0	0	0	0	0	0	0	1	1	4	2	4	4	1	1	0	2	0
LAEMANTUS	0	0	0	0	0	0	0	1	1	4	2	4	5	1	1	0	0	0
BASILISCUS	0	1	0	0	0	1	1	1	1	4	2	4	4	1	1	0	1	0
OIPSOSAURUS	1	1	2	0	0	1	0	1	0	4	2	4	4	1	0.5	0	2	0
BRACHYLOPHUS	1	0	2	0	1	1	0	1	0	4	2	4	4	1	1	0	2	0
SAUROMALUS	1	1	2	0	0	1	1	0.5	0	4	2	4	4	1	0.5	0	2	0
AMBLYRHYNCHUS	1	0	2	0	1	1	1	1	0	4	2	4	4	1	0.5	0	2	0
CTENOSAURA	1	1	2	0	1	1	1	0.5	0	4	2	4	4	1	0.5	0	2	0
CYCLURA	1	1	2	0	1	1	1	0.5	0	4	2	4	4	1	0.5	0	2	0
IGUANA	1	0.5	2	0	1	1	1	0.5	0	4	2	4	4	1	1	0	2	0
UROSAURUS	1	1	1	0	0	0	0	1	0	<u>3</u>	<u>2</u>	<u>3</u>	5	0	0	0	1	0
UTA	1	1	1	0	0	0	0	1	0	<u>3</u>	<u>2</u>	<u>3</u>	5	0	0	0	1	0
CALLISAURUS	1	1	1	0	0	1	0	1	0	2	3	3	4	0	0	0	1	0
HOLBROOKIA	1	1	1	0	0	1	0	1	0	<u>3</u>	<u>2</u>	<u>3</u>	4	0	0	0	1	0
UMA	1	1	1	0	0	1	0	1	0	<u>3</u>	<u>2</u>	<u>3</u>	5	0	0	0	1	0
PETROSAURUS	1	1	1	0	0	0	0	1	0	4	2	3	5	0	0	0	0	0
SCELOPORUS	1	1	1	0	0	1	0	1	0	<u>3</u>	<u>2</u>	<u>3</u>	5	0	0	0	1	0
PHRYNOSOMA	1	0	1	0	0	1	0	1	0	<u>3</u>	0	<u>3</u>	5	0	0	0	1	0
CROTAPHYTUS	1	0	1	0	0	1	1	0.5	0	4	2	4	4	1	0.5	1	0	0
GAMBELIA	1	1	1	0	0	1	1	0.5	0	4	2	4	6	1	0.5	1	0	0
URANOSCODON	0	0	0	0	0	1	1	1	0	<u>3</u>	<u>2</u>	<u>4</u>	5	1	1	0	2	0
CTENOBLEPHARIS	0	1	1	0	0	0	<u>0.5</u>	1	<u>0</u>	<u>3</u>	<u>2</u>	<u>4</u>	<u>5</u>	<u>0</u>	1	0	2	0
URACENTRON	0	0	1	0	0	1	<u>1</u>	1	0.5	<u>3</u>	1	4	6	<u>0</u>	0	0	2	0
LIOLAEMUS	0	1	1	0	0	0	0.5	1	0	<u>3</u>	<u>2</u>	<u>4</u>	5	0	0.5	0	2	0
OPHYROSSOIDES	0	0.5	1	0	0	1	1	1	0	<u>3</u>	<u>2</u>	<u>4</u>	5	0	1	0	2	0
TROPIOURUS	0	1	1	0	0	1	1	1	0.5	<u>3</u>	<u>2</u>	<u>4</u>	5	0	1	0	2	0
STENOCERCUS	0	1	1	0	0	0	1	1	0	<u>3</u>	<u>2</u>	<u>4</u>	5	0	0.5	0	2	0
LEIOCEPHALUS	0	1	1	0	0	1	0	1	0	<u>3</u>	<u>2</u>	<u>4</u>	5	0	0.5	0	2	0
PLICA	0	1	1	0	0	1	1	1	0.5	4	2	4	5	1	0.5	0	2	0
CHALARODON	0	1	1	1	0	1	0	0	0	4	2	3	4	1	0	0	1	0
OPLURUS	0	1	1	1	0	1	<u>0</u>	<u>0</u>	<u>0</u>	4	2	3	4	1	0	0	1	0
LEIOSAURUS	0	0.5	1	1	1	<u>0</u>	<u>0</u>	1	0	4	2	4	5	<u>0</u>	1	0	2	0
ENYALOIDES	1	0.5	0	1	1	0	0	1	0	4	2	4	5	1	1	0	0	0
ENYALIUS	0	0	0	1	1	<u>0</u>	<u>0</u>	1	0	4	2	4	5	<u>0</u>	1	0	1	0
MORUMSAURUS	1	1	0	<u>1</u>	0	<u>0</u>	<u>0</u>	1	0	4	2	4	5	<u>0</u>	1	0	1	0

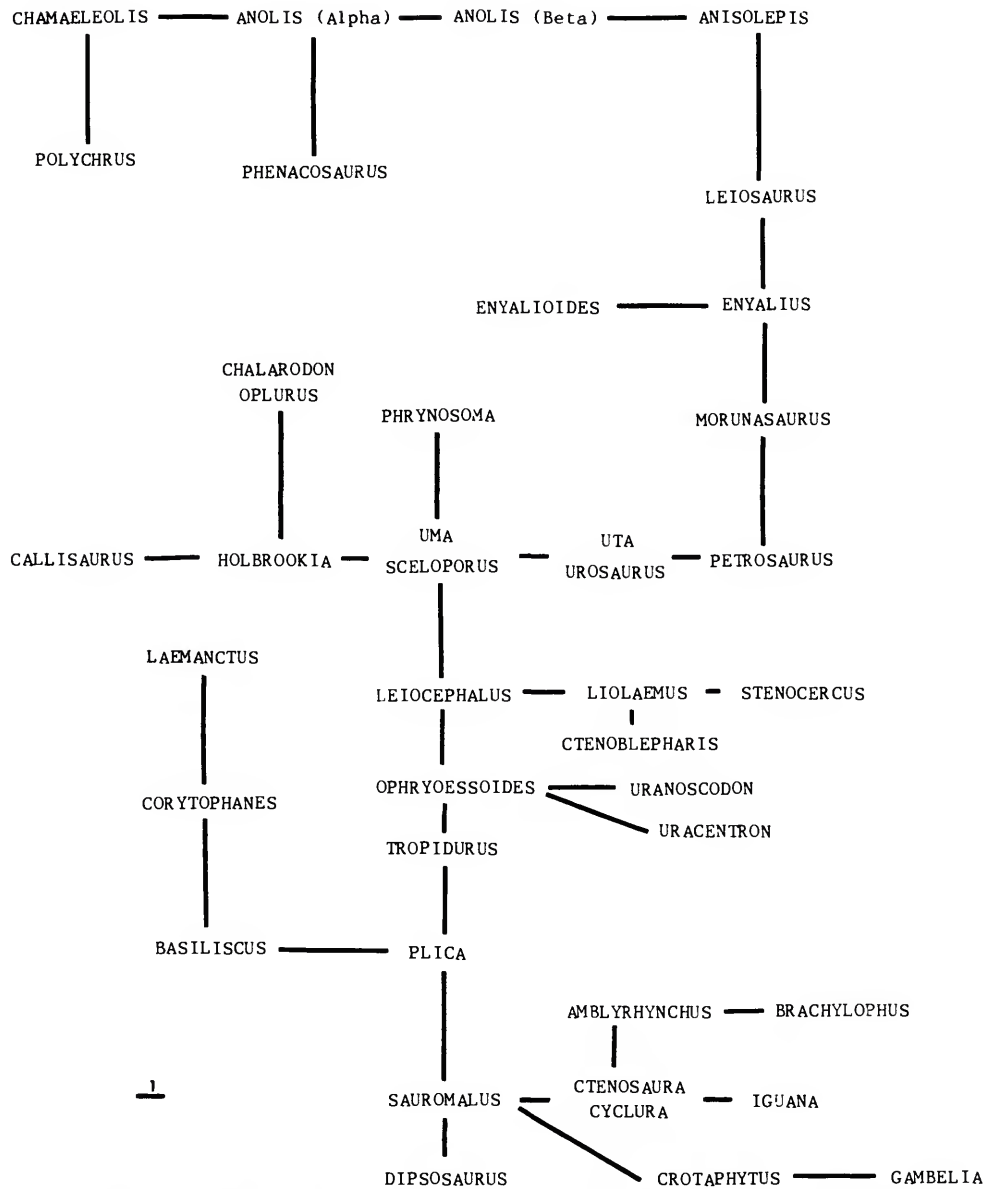


FIGURE 9.—A shortest connection network for iguanids based on the characters in Table 2. The bar equals one unit of difference. The mean difference for this network is 2.5.

ate against any "absolute" statement of phylogenetic relationships. In other words, I do not propose that the Malagasian iguanid are derived from sceloporine stock or that *Brachylophus* is derived from an ancestral *Amblyrhynchus*. The relative position and distribution of the clusters may provide clues

to the relationships of certain genera. Etheridge's iguanids of uncertain affinities lie between the anoline and the tropidurine, so a search for their affinities should be with those groups. Also these incerta sedis iguanids form a loose cluster. Perhaps this is a natural assemblage. Likewise, what is the signifi-

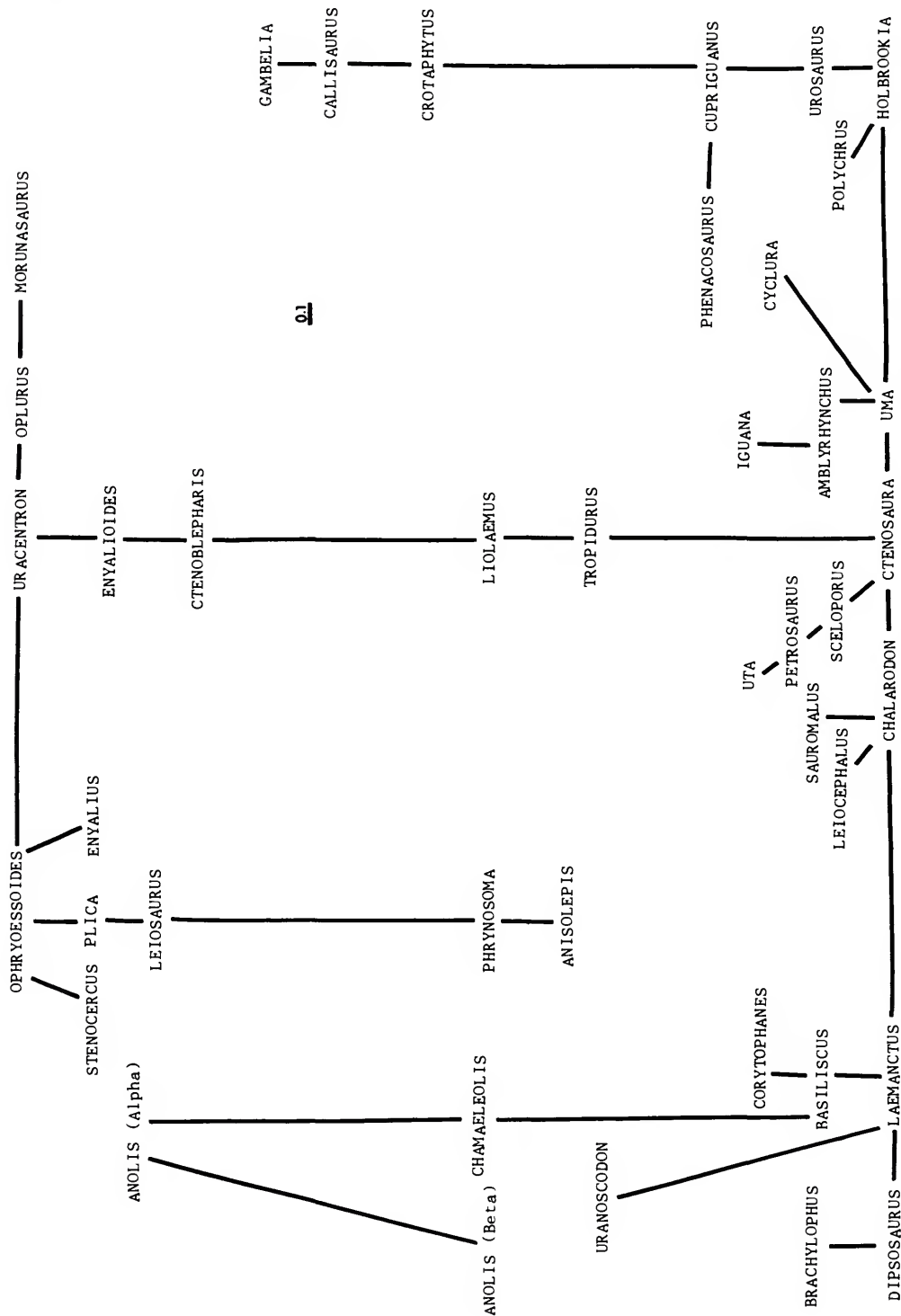


FIGURE 10.—A shortest connection network for iguanids based on the arterial characters in Table 1. The bar equals one unit of difference. The mean difference for this network is 2.7.

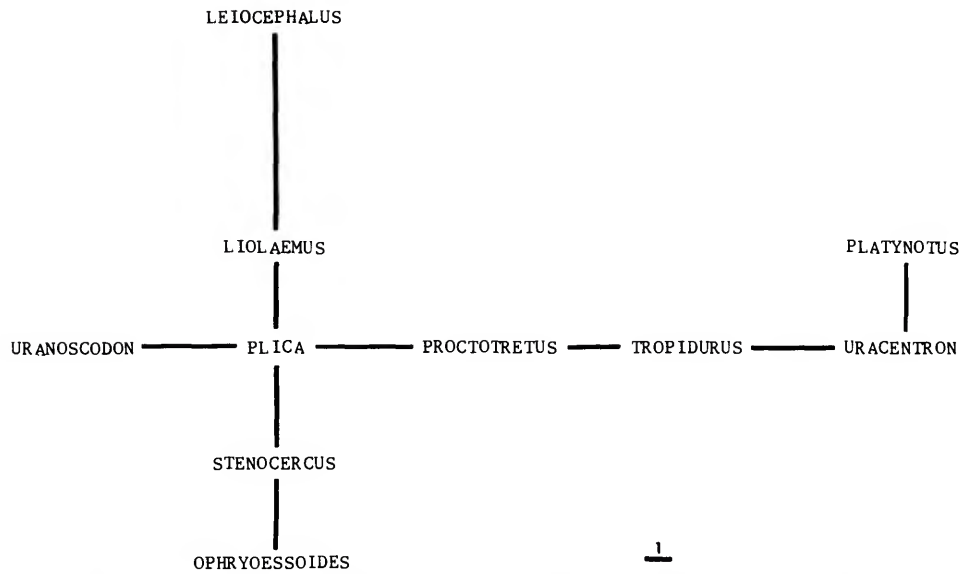


FIGURE 11.—A shortest connection network for tropidurines based on the characters in Table 3. The bar equals one unit of difference. The mean difference for this network is 3.3.

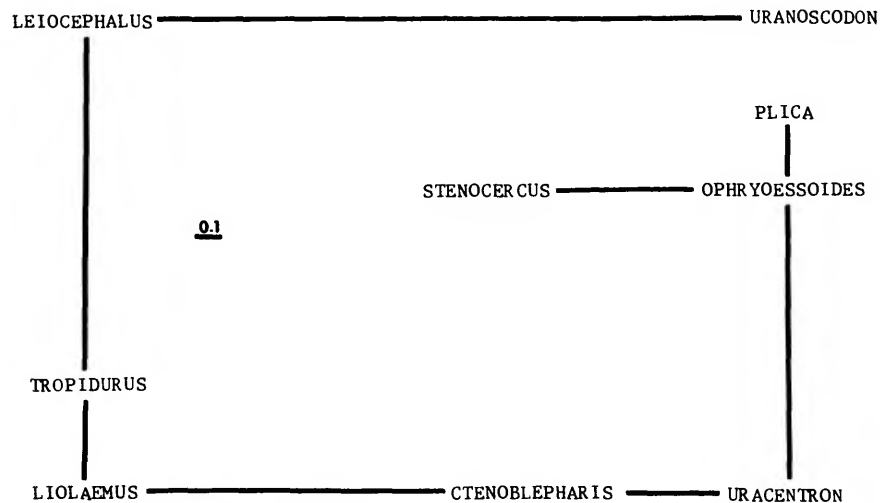


FIGURE 12.—A shortest connection network for tropidurines based on the arterial characters in Table 1. The bar equals one tenth of a unit of difference. The mean difference for this network is 0.8.

cance of *Plica* forming a pivoting point for the basiliscines, iguanines, and tropidurines?

Comparison of the former network (Figure 9) with the arterial network (Figure 10) shows a high degree of discordance. Of the clusters delimited by

a linkage of less than the mean of the coefficient of similarity, only three of the clusters in the arterial network contain a natural assemblage of genera, i.e., based on Etheridge's groups. Three clusters are composed of members of two groups, and two clus-

TABLE 3.—A series of characters for tropidurines taken from Etheridge (1966). A, Tricuspid teeth: sharp cutting edge, 0; blunt edge, 1. B, Pterygoid teeth: absent, 0; absent or present, 0.5; present, 1. C, Lower jaw: coronoid over dentary, 0; coronoid not over dentary, 1. D, Premaxillary-nasal overlap: nasal process of premaxillary covered dorsally, 0; not covered dorsally, 1. E, Parietal: lateral borders narrowly separated, 0; borders widely separated, 1. F, Interclavicle: lateral process widely separated from clavicle, 0; process contacts clavicle, 1. G, Xiphisternon: xiphisternal rods extend posterior, 0; variable, 0.5; rods do not extend posterior, 1. H, Parasternal ribs: absent, 0; one pair, 1; two pairs, 2; three or more pairs, 3. I, Caudal vertebrae: spine above fracture plane, 0; above entire arch, 1. J, Nasal-rostral contact: broad contact, 0; variable, 0.5; separated or slight contact, 1. K, Dorsal head scales: smooth, 0; smooth and rugose, 0.5; rugose, 1. L, Enlarged anterior auricular scales: absent, 0; absent and present, 0.5; present, 1. M, Middorsal crest: absent, 0; present, 1. N, Subdigital lamellae: enlarged to form comb, 0; do not form comb, 1. O, Scale organs: five or less per dorsal scale, 0; six or more per dorsal scale, 1.

TAXON	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O
LEIOCEPHALUS	0	0.5	0	0	0	0	0	2	0	0	0.5	0.5	1	0	1
OPHRYOESSOIDES	1	1	1	1	1	1	1	3	1	1	0.5	0.5	1	1	0
LIOLAEMUS	0	0.5	0	0	1	1	1	1	1	0.5	0.5	0.5	1	1	0
PLICA	0	0.5	1	1	1	1	1	1	1	1	0.5	0.5	1	1	0
PROCTOTRETUS	1	1	1	1	1	1	0.5	1	1	0.5	0.5	0.5	0	1	0
STENOCERCUS	1	0.5	1	1	1	1	1	3	1	1	0.5	0.5	1	1	0
TROPIDURUS	1	1	1	1	1	1	0.5	1	1	0.5	0.5	0.5	1	0	0
URANOSCODON	1	1	1	1	1	1	1	0	1	1	1	0	1	1	0
URACENTRON	0	1	1	1	1	1	0.5	0	1	1	0	0.5	0	1	0

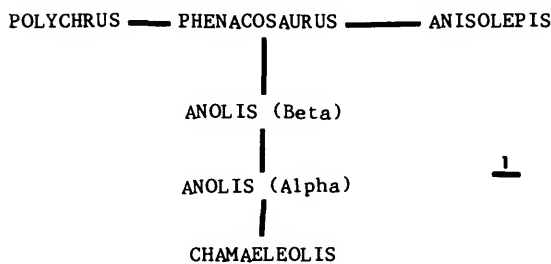


FIGURE 13.—A shortest connection network for anolines based on the arterial characters in Table 1. The bar equals one unit of difference. The mean difference for this network is 1.7.

ters possess members of three groups. The two Malagasian genera are widely separated. Certain linkage patterns, such as the closeness of *Phrynosoma* and *Anisolepis* or the dichotomy of the two

Anolis groups, cast additional doubt on the validity of using the arterial character set at this taxonomic level. A network generated by using only the proportions (first seven characters in Table 1) produces an even more discordant network. The following linkages were, however, retained: *Cupri-guanus* to *Crotaphytus*, *Uracentron* to *Ophryoes-soides*, *Sceloporus* to *Petrosaurus*, *Iguana* to *Amblyrhynchus*, *Holbrookia* to *Uma*, *Liolaemus* to *Ctenoblepharis*, *Corytophanes* to *Basiliscus*, *Cteno-saurus* to *Tropidurus*, *Laemanctus* to *Chalarodon* to *Sauromalus*.

Although the two networks (Figures 9 and 10) are dissimilar, certain linkage patterns occur in both. The basiliscines are linked, as are also *Anolis* (Alpha and Beta) and *Chamaeleolis*. *Ctenoblepharis* and *Liolaemus*, *Ophryoesoides* and *Leiosaurus*, *Tropidurus* and *Liolaemus*, and *Petrosaurus* and

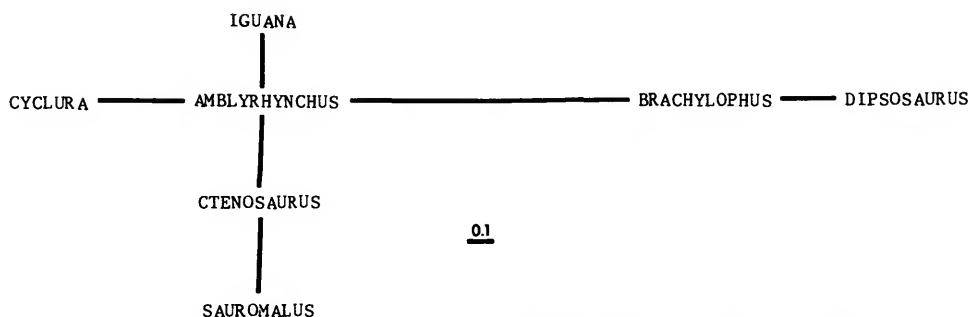


FIGURE 14.—A shortest connection network for iguanines based on the arterial characters in Table 1. The bar equals one unit of difference. The mean difference for this network is 0.4.

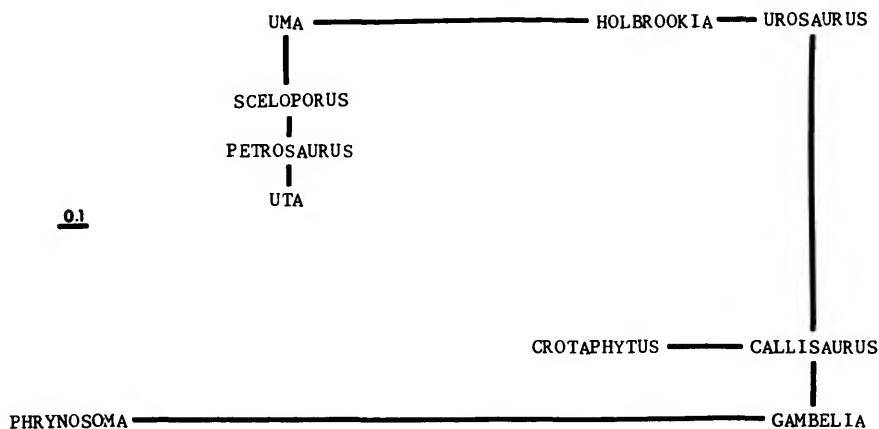


FIGURE 15.—A shortest connection network for sceloporines based on the arterial characters in Table 1. The bar equals one tenth of an unit of difference. The mean difference for this network is 0.6.

Uta are linked. The occurrence of these linkage patterns in two widely different data sets suggest that these linkages may be natural.

Comparison of the arterial data at a lower taxonomic level, i.e., within Etheridge's "subfamilies" (Figures 11 and 12) again shows discordance. Evaluation of the discordance is difficult at this level. Each network has one or two genera not included in the other. There is no obvious correlation with ecology, size, etc. Thus neither network can be rejected or accepted on any logical criterion. Only a single linkage group, *Plica*, *Stenocercus*, and *Ophryoessoides*, is shared by the two networks. This linkage suggests that *Plica* should be removed from the *Strobilurus*, *Uracentron*, *Tropidurus*, and *Platynotus* group (Etheridge, 1968). *Uracentron*,

Tropidurus, and *Platynotus* are linked in Figure 11; *Strobilurus* was not included in the analysis.

Figures 13, 14, and 15 are not compared to phenograms derived from an extant character set. Both the iguanine and anoline networks are very compact. Their members differ only slightly from one another. The anoline network does not agree with Etheridge's 1967 divisions, although *Phenacosaurus* and *Polychrus* are linked. The tropidurine and sceloporine networks show the same degree of dispersion, i.e., a higher degree of arterial diversity. Comparison of the sceloporine network with Etheridge's phylogenetic tree (1964: fig. 6) shows few similarities. The extreme divergence of *Phrynosoma* is the only point of close agreement. Although *Gambelia* and *Crotaphytus* are separated in the

network, I do not believe that this information is of sufficient merit to be used in the *Gambelia* controversy (see Montanucci for additional details).

The arterial characters employed herein appear to be of minimal value in iguanid classification. At the intrafamilial level, they are disruptive and form groups of questionable zoogeographical unity. Some of their implied relationships bear additional investigation, but definitely should not be accepted on the basis of arterial data alone.

Summary

Anatomically, the major arteries of iguanids show a fairly uniform pattern. A single primary carotid and a pair of carotid ducts are always present. The subclavians always arise from the right systemic arch and usually above the heart. With the exception of *Iguana*, the coeliac originates anterior to or adjacent to the mesenterics. The inferior and superior mesenterics are always present, although they may arise initially from the dorsal aorta in a common trunk.

Variation was observed in the type of origin of the sternohyoid and external carotid, the subclavians, and the mesenterics. The two vessels can arise independently, separately but contiguous, or from a common trunk. The carotid arch showed two extremes, an iguanine and a tropidurine type, of a continuous pattern. Within the genus *Basiliscus*, the manner of the coeliac loss is displayed by a morphological series.

The anatomical observations are reduced to ten characters by discarding those observations with a large amount of intrageneric variation. Seven of these are distance measurements which are converted to proportions to eliminate the influence of body size. Each of the remaining three characters exist in three discrete character states. The taxonomic information content of the arterial characters is determined by generating a phenogram from the arterial data. Another phenogram is produced from the extant data on iguanids. When the two phenograms are compared, they are very dissimilar, and cluster of genera in the arterial phenogram shows little correlation with zoogeographical, taxonomical, ecological, or behavioral groups. Thus the arterial characters employed herein may be useful as indicators of relationships but should not

be incorporated in our extant character set for determining iguanid relationships.

As an indicator the different structure of the carotid arch in iguanines and tropidurines supports their separation into two groups. The basiliscines are clustered in both phenograms, attesting to their close relationships. Both the anolines and iguanines form compact groups in the phenograms. Other relationships are implied among the iguanids but require more data than that provided by the arterial characters.

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