the interpretation of the antorbital fenestra as an area of insertion of the *pterygoideus* D. muscle maintained by Dollo, Gregory and Adams, and Walker. She stresses the possibility that this fenestra might have housed a large salt gland, as suggested by Broom (1913). It is now well known that not only several marine vertebrates (Schmidt-Nielsen, 1958) but also desert lizards such as Ctenosaura and Sauromalus (see Templeton, 1964, 1966) have nasal salt glands that play an important role in removing chloride salts from the body, with a small loss of water, thus acting as an extrarenal mechanism for salt excretion and water economy. The known cases of the presence of nasal salt glands of this sort in living vertebrates do not show this gland housed in an antorbital fenestra, but we do not believe that this fact need be a serious challenge to the interpretation of Broom and Ewer. Though admittedly highly speculative, the following reasoning is presented as a possible explanation of the known facts concerning this problem.

As the mammals are urea-secreting animals derived from the pelycosaurs through the therapsids, it can be assumed that the pelycosaurian ancestors of the archosaurs were also ureotelic animals, and that uricotelism developed only later in their archosaurian descendants (the birds are typically uric acid-secreting animals). Uricotelism being related with water economy in animals living in dry conditions, the lack of this metabolic device in the increasingly upland dwelling archosaurs may have been balanced by the development of an extrarenal salt-secreting device. If the antorbital fenestra is actually the site for a salt gland, this may explain the characteristic development of such an opening in all the archosaurs. In this connection, Euparkeria clearly shows an improvement beyond the proterosuchian level, as it has a larger antorbital fenestra lodged in a basin-like depression, which indicates a bigger size, and hence, an intensification of the function of the salt gland. This intensification of function of an extrarenal salt-secreting organ can be thought of as an improvement of the adaptation to upland, dry environments, in ureotelic animals coming from a freshwater environment in which economy of water was not necessary. The presence of a small antorbital fenestra in *Proterochampsa* and later crocodiles agrees with this argument; the presence of a large antorbital fenestra in phytosaurs, however, is not consistent with it.

For all these reasons, it seems evident that Euparkeria has departed from the proterosuchian level of evolution in significant respects. As most of its innovations are also well developed in the pseudosuchian thecodonts, it is reasonable to think of it as a member of the group representing the early shift of the thecodonts towards the upland life to fulfill the roles of terrestrial carnivorous reptiles, a shift that triggered the radiation of the Middle and Upper Triassic pseudosuchians. In this sense, the new character-states shown by Euparkeria in locomotion, biting mechanism, hearing, and water economy are to be interpreted as key innovations opening up new evolutionary possibilities and enhancing the emergence of a new major taxon, which in this case is the suborder Pseudosuchia of the Thecodontia.

In spite of the fact that Euparkeria (with Browniella as a junior synonym) is the only Lower Triassic slightly-built pseudosuchian known from skeletal remains, the available evidence shows that thecodonts that had already attained the same level of evolution were widespread in upper Lower Triassic and lower Middle Triassic times. This evidence comes mainly from ichnological data, which indicates that quadrupedal, lightly built, and small-sized pseudosuchians flourished by that time in North America (Peabody, 1948). As contended by this and other authors, it is quite probable that the large manus footprints of the chirotheriids of small size were actually made by euparkeriid thecodonts. At the same time, it is also possible that some dubious skeletal remains of the same general age could in the future be demonstrated as belonging to the same family. *Wangisuchus*, a genus based on fragmentary remains of various individuals, has been referred by Young (1964) to this family. The basis for this assignment is not clear, however.

The known skeletal structure of Euparkeria makes it clear that this genus had not attained certain of the specializations that are full-fledged in the Middle and Upper Triassic pseudosuchians that are probably euparkeriid derivatives. This fact supports the splitting off of Euparkeria into a family of its own, distinct from the remaining families of the Pseudosuchia. As far as the relationships of the euparkeriids with the other pseudosuchians are concerned, one could say that with respect to the remaining pseudosuchians, the euparkeriids hold the same relationship that the Proterosuchians hold with respect to the whole of the non-proterosuchian archosaurs.

Relationships with the Pseudosuchia

The remaining Middle and Upper Triassic thecodonts are far from affording a clear-cut picture of their evolutionary relationships and classification. It has been said that the Pseudosuchia are a sort of waste-basket, a statement that seems to cast serious doubts about the naturalness of the group. The Pseudosuchia seem to be, however, a natural group, but it is evident that the whole taxon is in need of a thorough revision. Some recent papers by Krebs (1963, 1965), Reig (1961), Sill (1967), Walker (1961, 1964, 1966), and others have already contributed to a great extent to clearing up the status of parts of this taxon.

It is now agreed that the Elachistosuchidae must be ruled out of the Pseudosuchia, as *Elachistosuchus* has been demonstrated by Walker (1966) to belong to the rhynchocephalians. At the same time, Sill (1967, see also below) suggested that the crocodiloid thecodonts usually placed in the superfamily Sphenosuchoidea of the Pseudosuchia, are better considered as belonging to the protosuchian crocodiles. After these deletions, the main subordinate taxa of the Pseudosuchia are the Lower (and Middle?) Triassic Euparkeriidae, the Middle Triassic Rauisuchidae, the Middle and Upper Triassic Stagonolepididae (see below) and the probably related Upper Triassic Stegomosuchidae,¹ the Upper Triassic Ornithosuchidae, and the Upper Triassic Scleromochlidae. It will now be useful here to assess the main conclusions that can be drawn from present knowledge of the pseudosuchians (Fig. 10).

All pseudosuchian families share the following characters: possession of an otic notch; suspensorium shifted forward; Vshaped contour of the posterior border of the lower temporal opening; large antorbital fenestra lying in an extended basinlike depression (with the exception of *Rhadinosuchus* and *Clarenceia*, see later); fairly large nares close to the antorbital fenestra (same exceptions); pterygoids joined at the midline; palatal teeth absent (with the exception of *Euparkeria*); marginal teeth subheterodont and thecodont; intercentra absent (with the exception of Euparkeria); advanced quadrupedal or bipedal gait; posterior limbs somewhat longer than the front ones; propodials vertical in position; pes "crocodiloid," with astragalocrural-calcaneum-tarsal ankle joint (incipiently so in *Euparkeria*); calcaneum with a tuberosity; long pubis and ischium; well-developed dermal armor (except in Scleromochlus, surely a secondary loss). It seems clear that the above intension of the concept of Pseudosuchia makes this taxon a well-defined one with respect to the Proterosuchia.

The pseudosuchian character-states evolved seemingly as an adaptation to

¹Walker (1968), however, has recently maintained that the Stegomosuchidae are crocodiles; see Addendum.



Figure 10. Phylogenetic diagram of the suggested relationships among the various families of the Pseudosuchia and the other thecodonts.

terrestrial life, and for the most part they were already established in the euparkeriids. The rauisuchids probably evolved as a branch divergent from the euparkeriid stock in the early Middle Triassic or uppermost Lower Triassic. Their first welldocumented representative is *Ticinosuchus* from the Anisian of Europe (Krebs, 1965). Young (1964) referred to the same family the upper Lower Triassic Chinese genus *Fenhosuchus* because of some similarities in vertebral morphology, shape of the scutes, and other dubious characters. This genus is known from fragmentary bones of various individuals, and its status is far from clear. Nevertheless, the presence of rauisuchids in the Lower Triassic is suggested again by the ichnological evidence, as large-sized quadrupedal chirotheriids of probable rauisuchid relationships have been

found in beds of Scythian age in Germany, North America, and South America (see Peabody, 1948, 1955; Krebs, 1965). Apart from those mentioned above, rauisuchids are known in Middle Triassic (lower Ladinian?) beds of Africa (Stagonosuchus of the Manda beds of Tanganyika) and Brazil (Rauisuchus, Prestosuchus from the Santa Maria beds of Rio Grande do Sul) and in the upper Middle Triassic (upper Ladinian?) of Argentina (Saurosuchus from the Ischigualasto beds of San Juan Province). The rauisuchids seem to have been reptiles well adapted for terrestrial life, and they reached a great size. They were surely huge predators more active and efficient than the erythrosuchids, but they remained quadrupedal like the latter, perhaps because of the attainment of a bulky body and a great weight before the full acquisition of the necessary limb modifications for bipedal stance and locomotion. Advance beyond the euparkeriid level is shown, however, in the full development of a crurotarsal crocodiloid ankle joint, the great elongation of the ventral pelvic bones, the loss of palatal teeth, and the pterygoid union at the midline (as shown in Saurosuchus, unpublished personal data), the loss of postparietal and postfrontal bones, and large size. The rauisuchids became extinct at the end of the Middle Triassic, apparently without giving rise to any other group, and perhaps because of the competition of the carnosaurian saurischians. It is also probably meaningful that their spread and diversification from the beginning of the Middle Triassic can be correlated with the extinction of the ervthrosuchids at the end of the Lower Triassic.

Another well-defined family of pseudosuchians is the Stagonolepididae.¹ Reig

(1961), Walker (1961), and Krebs (1965) have demonstrated that the stagonolepidids are not as closely related to the rauisuchids as is maintained by some authors. Nevertheless, Reig's contention that the two families must be placed in different suborders now appears too exaggerated a view, as it is quite possible that the two families originated in the euparkeriids. The stagonolepidids are, of course, a very clear-cut group, as their specializations in bony armor and in skull and dentition are unique among the thecodonts. That the family was fully established in upper Middle Triassic times is demonstrated by Aëtosauroides from the Ischigualasto beds of Argentina (Casamiquela, 1961). They may have separated from the euparkeriid stock in early Middle Triassic times, evolving as an independent lineage that played its own distinct ecological role. Aëtosaurus from the German Keuper, Stagonolepis from the Elgin Sandstones of Scotland, and Typothorax, Desmatosuchus, Acompsosaurus, and Stegomus from the Upper Triassic of North America demonstrate that the family was rather widespread in Keuper times.

Though the way of life of the stagonolepidids is still a matter of controversy, it is evident at least that the members of this family were completely terrestrial pseudosuchians and that they are to be regarded as the first archosaurs that were not predators. Walker has supposed that they were mostly herbivorous, while Sawin (1947) maintained that they were scavengers. It is interesting to realize that the stagonolepidids share some general resemblance with the dasypodids, both in the possession of dermal armor and in the general shape of the skull and dentition, a point that would bolster the scavenger hypothesis, but which does not necessarily exclude the assumption of a rather com-

¹ I agree with Walker in including in one family all the genera of thecodonts currently referred to the families "Stagonolepidae," Aëtosauridae, and Desmatosuchidae. The correct familial name for this assemblage is Stagonolepididae Lydekker, July

^{1887,} a name that antedates Aëtosauridae Baur, September 1887. Von Huene's "Stagonolepidae" (1908), so frequently encountered in the literature, is etymologically incorrect.

posite and variable diet, with vegetables and arthropods as usual components.

Stegomosuchus and Dyoplax, from the Upper Triassic of North America and Europe, respectively, are rather poorly known genera showing several resemblances to the stagonolepidids in armor development and other features. They may be closely related to the aëtosaurids in origin, but if they are really related to each other, they should be placed in a separate family Stegomosuchidae.

The taxonomic status and the relationships of the remaining pseudosuchians are less clear. Most of the non-rauisuchid and non-stagonolepidid genera are commonly grouped in the family Ornithosuchidae, which is supposed to include small or medium-sized, bipedal predators, of which Ornithosuchus would be a typical example. However, this genus has been recently demonstrated by Walker (1964) to include fairly large animals, and the large Dasygnathus from the same Elgin Sandstones that yielded the original remains of Ornithosuchus is placed by him in its synonymy. Walker also arrives at the odd conclusion that Ornithosuchus is neither a pseudosuchian nor any other kind of thecodont, but that it is better placed within the order Saurischia. This latter view is rather difficult to agree with, and the present author has not found in Walker's new data and appraisals sufficient supporting reasons for such an astounding upheaval of the current arrangement.

It is true that *Ornithosuchus* looks like the carnosaurian dinosaurs in several respects, but the instances of resemblance are better ascribed either to the sharing of general archosaurian features or to the fact that *Ornithosuchus* and the carnosaurs attained, in parallel, specializations for bipedal locomotion and a predaceous way of life. On the other hand, Walker did not attempt to demonstrate that this genus is not a pseudosuchian, his argument being directed to support of the view that it is a carnosaur. We think that important reasons are at hand for keeping Ornithosuchus in the Pseudosuchia. One of them is the possession of the double line of paramedial scutes, a character-state shared by the euparkeriids, the rauisuchids, and some genera referred to the ornithosuchids, and which is to be considered as an original pseudosuchian feature from which evolved the armor of such heavily armored forms as the stagonolepidids. No certain evidence of dermal armor is known for the Carnosauria; the alleged carnosaurian scutes from the Upper Cretaceous of India are better referred to ornithischian dinosaurs (see Walker, 1964: 117-119). Another important point is that Ornithosuchus has, almost surely, a typical pseudosuchian ankle joint. The carnosaurs, like all the saurischians, have a completely different type of ankle joint, which is hardly derivable from such a specialized structure as the pseudosuchian-crocodiloid tarsus (see below). In other respects, Ornithosuchus agrees perfectly with the pseudosuchian character-states. It seems rather bizarre to claim that it is a carnosaur when it is not really separable from the thecodonts. Walker admits that "it might ultimately prove necessary to retain Ornithosuchus in the Pseudosuchia" (1964: 110), a statement that does not seem to fit very well with his previous affirmation that only the coelurosaurs and the carnosaurs "need be seriously considered in a discussion of the affinities of Ornithosuchus" (1964: 105).

Walker also maintains that Ornithosuchus lies morphologically close to the boundary between the pseudosuchians and the carnosaurs, and that phylogenetic relationships are more clearly expressed by placing it with the carnivorous dinosaurs. In fact, this seems not to be the case, as typical carnosaurian and other saurischian dinosaurs have been found in beds definitely earlier than the Elgin Triassic (see Reig, 1963a; Charig, Attridge and Crompton, 1965; Ellenberger and Ginsburg, 1966). These finds clearly prove that by the Middle Triassic several lineages of

saurischians were already differentiated, and this suggests that the origin of the group is to be sought as early as the Lower Triassic. The Upper Triassic Ornithosuchus cannot be considered as intermediate for temporal reasons, and there are no cogent grounds for placing it anywhere but in the Pseudosuchia. It is more reasonable to believe that within that suborder of thecodonts, one family attained bipedalism and other carnivorous specializations, paralleling some lineages of contemporary dinosaurs with which it entered in competition. If we retain the family Ornithosuchidae and include in it not only the large-sized Ornithosuchus, but also the tiny genera Saltoposuchus and Hesperosuchus, we may agree that the ornithosuchids paralleled both the coelurosaurs and the carnosaurs in general appearance and ecological roles.

The curious Scleromochlus may be considered as an arboreal derivative of the Ornithosuchidae, distinct enough to warrant familial separation. There remain, however, other pseudosuchian genera that are less clear as to family allocation. Erpetosuchus, from the Upper Triassic of the Elgin Sandstones, has been commonly classified with the ornithosuchids, but other opinions have resulted in the erection of a family of its own for this genus. Walker (1961) places Erpetosuchus, Dyoplax, and probably Stegomosuchus in the family Erpetosuchidae, an arrangement that seems unnatural to the present author. The place of this genus is better considered as unsettled until a modern revision is undertaken.

As far as *Cerritosaurus* (Price, 1946) from the Santa Maria Middle Triassic of Brazil is concerned, it is almost surely, as suggested by Hoffstetter (1955), a junior synonym of *Rhadinosuchus* von Huene. This genus is very peculiar in the small size of the antorbital fenestra, the size and the position of the external nares, the obliteration of the postemporal fenestra, and the straight posterior border of the

lower temporal opening. These features make this genus hardly derivable from the euparkeriids, and some of them are actually proterosuchian, non-pseudosuchian character-states. Nevertheless, it has acquired pseudosuchian status in such characters as the absence of postfrontal and postparietal bones, the presence of an otic notch, and the thecodont and subheterodont dentition. If Rhadinosuchus is actually a pseudosuchian, it could represent a family of its own, Rhadinosuchidae, as proposed by Hoffstetter (1955) and accepted by Kuhn (1961). This family might have originated independently within the proterosuchians, reaching the pseudosuchian level in its own way. Another poorly known genus from the Upper Triassic of South Africa, Clarenceia (see Brink, 1959), agrees with Rhadinosuchus in the structure of the antorbital fenestra and the form of the maxilla, and might belong to the same family (Romer, 1966b, makes this genus a dubious member of the Ornithosuchidae, a position that seems to lack relevant foundations). If our interpretation of Rhadinosuchus is right, the implication is that either we accept the Pseudosuchia as a polyphyletic assemblage, or we must allow for the inconvenience of erecting a new suborder to accommodate Rhadinosuchus and allies. Our knowledge of these forms is, however, too imperfect to support any formal proposal of changes in the system of the Thecodontia.

The origin of the crocodilia

The crocodiles have been classically considered as descendants of the Pseudosuchia. Within the latter, the Sphenosuchidae from the Upper Triassic of South Africa were considered to be the ancestral group. Primitive crocodilian archosaurs such as Notochampsa and Pedeticosaurus (from the Cave Sandstone beds of the Stormberg Series of South Africa), Erythrochampsa (from the underlying Red Beds, which also yielded Sphenosuchus), and Protosuchus (from the later Triassic or earliest Jurassic of Arizona), commonly grouped in the crocodilian suborder Protosuchia, have been regarded as transitional between the ancestral sphenosuchids and the later typical crocodiles (Mesosuchia, Sebecosuchia, Eusuchia). According to this conception, the assumption is made that the crocodiles evolved from primitively bipedal pseudosuchians, and that they returned to a quadrupedal gait as an adaptation to the amphibious way of life (for broader information on these ideas on crocodilian origins, see Haughton, 1924; von Huene, 1925; Colbert and Mook, 1951; Kälin, 1955).

Recently, Sill (1967) has made a thorough reappraisal of the question, on the basis of the bearing of *Proterochampsa* upon crocodilian origins. *Proterochampsa* (Reig, 1959) (Fig. 11) is an obvious crocodile from the late Middle Triassic Ischigualasto beds of Argentina, showing a remarkable combination of primitive, transitional, and advanced character-states. It is the earliest crocodile so far known, and it is definitely earlier than the sphenosuchids reported to be the pseudosuchian ancestors of the crocodiles.

The crocodilian nature of Proterochampsa is evident from the morphology of the dorsal surface of the skull, the presence of a rudimentary secondary palate built up by the premaxilla and the maxilla, the sculptured bones of the roof of the skull, and the structure of the vertebral apophyses. Besides this, it is noteworthy that the anterior foot shows the typical carpal specializations of modern crocodiles: elongated radiale and ulnare carpal bones. This is demonstrated by a nearly complete anterior leg found in association with the remains of a coelurosaurian dinosaur in the Ischigualasto beds (Reig, 1963a).¹ The femur and the humerus, known to the author through undescribed specimens associated with skull remains, are also typically crocodiloid. Unfortunately, bones of



Figure 11. Ventral and dorsal views of the skull of Proterochampsa barrionuevoi Reig. (After Sill.)

the girdles have not been found so far. As pointed out by Sill (1967), it is meaningful that *Proterochampsa* is in several respects more crocodilian than the later genus *Protosuchus*.²

The implication of the discovery of *Proterochampsa* is that the sphenosuchids can no longer be considered as the thecodont ancestors of the crocodilians, nor can *Protosuchus* and its allies be thought of as a transitional group between the pseudosuchians and the later full-fledged crocodiles. Sill has made a suborder Archaeosuchia to group together both the Middle Triassic monotypic family Proterochampsidae and the Upper Triassic Notochampsidae (including *Notochampsa* and

¹ See, however, the Addendum.

 $^{^{2}}$ For another view on the place of *Proterochampsa* and other early crocodiles, see Walker (1968) and the Addendum.



Figure 12. Phylogenetic diagram of the probable origin of crocodiles and the relationships among the various crocodilian and thecodontian suborders.

Erythochampsa). He believes that this suborder is the ancestral group of the Mesozoic and modern crocodiles of the suborders Mesosuchia, Sebecosuchia, and Eusuchia (Fig. 12). Protosuchus, on the other hand, would represent a suborder, the Protosuchia of Mook (1934) and later authors, that has departed from the main direction of crocodilian evolution by adaptating to a more terrestrial way of life. As Sill has proposed and Romer (1966b) has accepted, the Sphenosuchidae and such dubious genera as Pedeticosaurus and Platyognathus are better grouped within the Protosuchia, since they agree with Protosuchus in the sharing of an early crocodilian heritage with adaptations for a more terrestrial life. Referring to these animals, Sill uses an expression coined by Kermack: they are "crocodiles trying to be dinosaurs." This meaningful expression describes perfectly the evolutionary trend in these atypical crocodiles for a dinosaur-like (i.e. terrestrial and predaceous) way of life.

Sill advances two alternative hypotheses for crocodilian origins: either they originated from a non-pseudosuchian group of aquatic thecodonts, or they descended from a primitive group of terrestrial thecodonts, possibly early pseudosuchians. As we have already seen, the euparkeriids make perfect early pseudosuchians in their organization. Proterochampsa is, however, hardly derivable from euparkeriid ancestors for the following reasons: (1) it has not developed the typical pseudosuchian oticnotch; (2) it has a primitive and small antorbital fenestra; (3) it has not acquired the pseudosuchian V-shaped contour of the posterior border of the lower temporal opening; and (4) it has the suspensorium placed backwards. These are actually proterosuchian character-states, and *Proterochampsa* is also proterosuchian in the possession of palatal teeth and in the shape and proportional size of the temporal openings.

This gives support to the first of Sill's

two alternative hypotheses, suggesting that the Archaeosuchia (and through them, all the crocodiles) might have been derived from the aquatic proterosuchians of the Lower Triassic. It should be remembered that after the separation of the erythrosuchids, proterosuchids were represented in beds equivalent to the *Cynognathus* Zone. These late aquatic proterosuchians could have been the ancestors of other lines of aquatic archosaurs.

Nevertheless, one important point remains unexplained if we accept Sill's first alternative. Crocodiles and pseudosuchians (and probably phytosaurs) share the possession of a peculiar type of ankle joint, the so-called "crocodiloid" tarsus, in which the functional joint lies between the astragalus and calcaneum, these being articulated by means of a ball-and-socket type of joint. As we have already seen, this kind of tarsus is not a primitive archosaur characteristic, as both proterosuchids and erythrosuchids show quite another, more primitive, type of ankle. Walker's belief (1964: 110) that the crocodilian ankle-joint "may after all represent a basic archosaurian pattern," is therefore lacking a serious basis. Krebs (1963) has pointed out that the resemblance between pseudosuchians and crocodiles in tarsal structure is so great that it is difficult to think that such a tarsus arose independently in both groups by convergent evolution. It must be realized that the hypothetical common ancestral group for both crocodiles and pseudosuchians, required by tarsal structure, could not be identical with the euparkeriids, as Euparkeria has not reached full development of such a type of ankle joint. This means either that the supposed common ancestor should be sought at a post-euparkeriid level of thecodont evolution or that it must be accepted that the character-state under discussion developed independently in pseudosuchians and crocodilians. The first possibility seems to be ruled out, as the characteristics of the archaeosuchians do not permit thinking of a common ancestry even at the level of the euparkeriids. It would be very useful to have information about the structure of the ankle in *Proterochampsa*, which, unfortunately, is not available thus far.

In our present state of knowledge it seems best to adhere to the hypothesis of the proterosuchian origin of the crocodilians, and to accept the idea of the convergent evolution of the type of ankle found in both crocodiles and pseudosuchians. It must be admitted, however, that the evidence is still too incomplete to permit a fully satisfactory explanation of crocodilian origins, and that a better knowledge of Lower and Middle Triassic thecodonts may make it necessary in the future to introduce changes in the present explanation. At this point, it is interesting to recall the Rhadinosuchidae, a Middle Triassic group of scarcely known thecodonts that seem to have reached the pseudosuchian level from an ancestry distinct from the euparkeriids. It will not be surprising if a better understanding of these forms throws light on questions of the kind raised here.

Saurischian ancestry

The ancestry of the saurischian dinosaurs is also commonly explained by hypotheses that advocate that the pseudosuchian thecodonts were the ancestral group. Until recently, the first unquestionable saurischians were known only from beds of Upper Triassic age; indeed the presence of dinosaurs has been considered conclusive evidence for dating Triassic strata of dubious age as Upper Triassic. Coelurosaurs, carnosaurs, and prosauropods were known from the Upper Triassic, and all three groups were supposed to derive from a single source in the Upper Triassic, namely allegedly tiny, bipedal, carnivorous pseudosuchians similar to the ornithosuchids. According to this conception, the quadrupedalism of the sauropods was secondary and derived from a primitive bipedal condition.

Our intent here is not to essay an exhaustive look at the rather confusing situation of the Triassic saurischians. This task has been partially carried out by Charig, Attridge, and Crompton (1965), Colbert (1964), and Walker (1964), and work by these and other authors will surely contribute to a better understanding of the group. We need, however, to present a very general survey of the present status of knowledge about Triassic saurischians in order to frame the question of saurischian origins as coherently as possible in terms of its factual foundations, and thus to check to what extent the existing stereotyped opinions on saurischian origins are supported by the available evidence.

The Upper Triassic faunas of the world differ sharply from the Middle and Lower Triassic ones in the abundance and variety of their dinosaurs. Romer (1966a) recently made it clear that in spite of semantic discussions on the rather conventional question of the boundary between Middle and Upper Triassic, the faunas currently referred to the Middle Triassic are distinct from those usually referred to the Upper Triassic by the fact that their dominant groups are different. Gomphodonts and rhynchosaurs are dominant in the B assemblages (Middle Triassic); dinosaurs are the dominant group in the C faunas (Upper Triassic). The same synecological criterion has been used in Reig's (1963a) discussion of the age of the Ischigualasto beds, a criterion that seems not to have been sufficiently grasped by Bonaparte (1966) in his recent discussion of the Argentinian vertebrate-bearing Triassic. These Upper Triassic faunas are known in the European Keuper, the Red Beds and Cave Sandstones of South Africa, the Forest Sandstones of Southern Rhodesia, the Dockum and Chinle of North America, and the Lufeng Series of China. The Los Colorados beds and the El Tranquilo Formation of Argentina, the faunas of which are now being studied by Bonaparte and Casamiquela, probably belong to the same group. Faunas of the B type are known in South America (Santa Maria, Ischigualasto, Chañares), Africa (Manda beds, Molteno beds, Ntaware Formation), and India (Maleri beds). Some faunas, such as those from the Elgin Sandstones (Scotland) and Maphutseng (Basutoland), seem to be transitional between the B and C assemblages.

The saurischians of the late Triassic faunas belong to three different infraorders, which are clearly recognizable at the time of their first appearance in the Lower Triassic, namely the Coelurosauria, the Sauropoda, and the Palaeopoda (I use here Colbert's [1964] new name instead of Prosauropoda, as this last concept is confusing both in intension and in extension). The coelurosaurians are represented in the Upper Triassic by the family Podokesauridae, Hallopidae, and Segisauridae (the second not surely distinct from the first). They were slightly-built upland predators, distinguished from other contemporaneous dinosaurs by the "dolichoiliac" pelvis (Colbert, 1964), advanced bipedal gait, birdlike feet, calcaneum usually with a tuber, long neck, relatively elongated skull. It is now clear that the true Carnosauria of the Jurassic and Cretaceous are an offshoot of the Coelurosauria, with which they share the same type of pelvis, the birdlike feet, and many other features. Both infraorders are therefore grouped in the suborder Theropoda of Marsh, giving to this taxon-concept a narrower extension than that in the current conservative classification.

The Sauropoda are represented from the very beginning of the Upper Triassic by the Melanorosauridae. This family is usually placed within the "Prosauropoda" (= Palaeopoda). Recent work by Ellenberger and Ginsburg (1966) demonstrates that they are quadrupedal and very close to the true sauropods. These authors and Attridge (1963) suggested that the melanorosaurids should be considered true sauropods, a suggestion that seems very reasonable to me. Though disregarding the melanorosaurids as direct ancestors of the sauropods, Charig *et al.* have convincingly demonstrated that "the line of evolution which led from the pseudosuchians towards the sauropods was entirely quadrupedal; thus the sauropods were not, as commonly supposed, quadrupedal reversions from bipedal forebears.

"The various families of prosauropods were offshoots from this main, quadrupedal sauropodomorph line, representing adaptations to different habitats which differed especially in their degree of bipedality; none survived the Trias" (1965: 205). From the new evidence provided by Ellenberger and Ginsburg (1966), one arrives at the conviction that the melanorosaurids should belong to this "main, quadrupedal sauropodomorph line" which, from its very beginning, was part of the evolution of the true sauropods. Melanorosaurids are known from the Middle-Upper Triassic boundary, as represented by the remains referred to Euskelosaurus by Ellenberger and Ginsburg (1966), which come from the "Passage beds" of Basutoland (the "Maphutseng dinosaur" of Charig et al., 1965); a hind leg from the same beds described by Crompton and Wapenaar (in press) (reported by Charig et al. as the "Blikana dinosaur"); and the "Soebeng trackways," footprints of a big quadrupedal dinosaur, mentioned by the above authors and by Ellenberger and Ginsburg (1966). Besides these early finds, melanorosaurids are relatively abundant in the Red Beds of South Africa. The Melanorosauridae are likely to have been herbivores and swamp-dwellers; the possibility that the family would include carnivorous forms has been suggested by Charig et al. (1965), but there are good reasons to doubt this. The evidence supporting such a view is far from conclusive and it is not very likely that these enormous quadrupedal marshdwellers could have been sustained by any food other than large amounts of green matter.

The Palaeopoda are represented by the Thecodontosauridae, the Plateosauridae, and the "Triassic carnosaurs." This last group has been demonstrated (Colbert, 1964; Charig et al., 1965; Walker, 1964) not to have any relationships with the true, post-Triassic carnosaurs, and to be closely connected with (or even inseparable from, as maintained by Charig et al., 1965) the first two families. The thecodontosaurids are medium-sized bipedal or semi-bipedal upland herbivores, known from different levels of the Upper Triassic of South Africa, China, Europe, and North America. The plateosaurids are large European and Asiatic (probably also South American) bipedal plant-feeders dwelling in lowlands. The carnivorous palaeopods are here considered as belonging to one distinct family, for which the name Gryponychidae must be used.¹ Though the facts of association of skull and postcranial bones are scarce and dubious, there is enough evidence to show that carnivorous palaeopods were living in the Upper Triassic. The convenience involved in placing these forms in families containing herbivorous dinosaurs is not very great, as one of the current criteria for family separation is distinction in ecological type. It is therefore preferable to separate the gryponychids as a carnivorous offshoot of the palaeopods, though recognizing that they are close to the other two families with which they share the same type of pelvis, tarsus, and limb structure.

All the palaeopods are closely related, and they are also very similar to the melanorosaurids and later sauropods, so that it makes sense to group both palaeopods and sauropods in a suborder Sauropodomorpha as proposed by Charig *et al.* (1965) and accepted by Romer (1966b). Charig et al. make a convincing case in claiming that this term, coined by von Huene (1932), is preferable to Pachypodosauria of the same author, a name applied to the unnatural assemblage of sauropods, "prosauropods," and carnosaurs. Within the Sauropodomorpha, the distinction of palaeopods and sauropods as infraorders is meaningful, as it adequately expresses the evolutionary situation. The sauropods seem to have played a secondary role during Triassic times, only evolving to full-fledged diversity and abundance after the close of that period. The palaeopods, most probably derived from a quadrupedal promelanorosaurid or melanorosaurid stock, represent the main radiation of Triassic Sauropodomorpha, and they evolved into both upland and lowland plant-eaters, and upland bipedal carnivores.

What do we know about the probable origin of the three groups of dinosaurs already well established at the very beginning of the Upper Triassic? Not too much, but at least enough to reveal that the history of the sauropodomorphs and coelurosaurs must be traced well back into the Triassic. Saurischian remains are known from the Middle Triassic of Argentina (Reig, 1963a) and Brazil (von Huene, 1942). The Argentinian fossils are rather abundant, and they come from the Ischigualasto beds, a formation that, following Romer (1966a) and Reig (1963a), contains a fossil assemblage that clearly belongs to the B type of faunas representing, perhaps, an upper Ladinian stage (i.e., the latest Middle Triassic). The Brazilian remains occur from the Santa Maria beds, which are generally agreed to be older than the Ischigualasto and roughly equivalent to the Manda beds of Tanganyika.

According to our present knowledge, the Argentinian material represents at least four genera of saurischians, only three of which have been described (Reig, 1963a). One genus is a very small, undescribed coelurosaur. Another coelurosaur is repre-

¹ Both Walker (1964) and Charig *et al.* (1965) have indicated that the name Palaeosauridae cannot be used, as *Palaeosaurus* Riley and Stutchbury is preoccupied by *Palaeosaurus* Geoffroy; Kuhn (1959) created the name *Palaeosauriscus* to replace the first name.



Figure 13. Lateral view of the skull of Triassolestes romeri Reig. (From Reig.)

sented by a podokesaurid, Triassolestes (Figs. 13, 14), known from skull and postcranial bones of two individuals.¹ The remaining two genera are obviously palaeopods. The best known is Herrerasaurus, a fairly large genus with specialized carnivorous dentition and typical palaeopod pelvis and posterior limbs (Figs. 14, 15), but with a peculiarly expanded distal border of the pubis, very like the situation in megalosauroid carnosaurs. As indicated by Walker (1964: 107), this last characterstate does not necessarily imply a taxonomic or phylogenetic affinity between Herrerasaurus and the Upper Jurassic and Cretaceous true carnosaurs, and the genus must be placed in the Palaeopoda either as a member of the Gryponychidae or as a separate line. The other palaeopodan genus is Ischisaurus, known from incomplete remains of different individuals. It is thecodontosaurid-like in size and general appearance, and the small size of the humerus, which hardly exceeds half of the length of the femur, suggests that it was a definitely bipedal form.

A supposed Brazilian dinosaur has been described by von Huene as *Spondylosoma*, on the basis of isolated bones insufficient to allow of even ordinal assignment. Material recovered later, and being at present studied by Colbert, clearly indicates, however, that a saurischian of palaeopodian



Figure 14. Pes in Middle Triassic saurischians from Ischigualasto, Argentina: A, Herrerasaurus ischigualastensis Reig; B, Triassolestes romeri Reig. (From Reig.) [See Addendum for systematic position of Triassolestes.]

affinities was present in the Santa Maria fauna.

The Sauropodomorpha and the Theropoda were thus well differentiated in the Middle Triassic (Fig. 16). It has been suggested (Charig *et al.*, 1965: 215–216) that these two major divisions of the Saurischia originated independently within the Pseudosuchia of the Middle Triassic.

I believe that there are good reasons to doubt that the sauropodomorphs could have arisen from Middle Triassic pseudosuchians, and I am more inclined to look for their ancestry in the Lower Triassic thecodonts. One important argument for this is the timing, as the origin of the sauropodomorphs must necessarily be placed at least as early as the very beginning of the Middle Triassic. This is the only way to explain that in the upper Middle Triassic they have already split into at least three different families: melanoro-

¹ See, however, the Addendum.



Figure 15. Pelvis of Herrerasaurus ischigualastensis Reig. (From Reig.)

saurids, gryponychids, and thecodontosaurids (Fig. 16). The other important argument is ankle morphology. As Krebs (1963) pointed out, the mesotarsal type of ankle joint of the saurischians is hardly derivable from the crocodiloid ankle of the Pseudosuchia. Therefore, the only groups to be considered in sauropodomorph ancestry, as required by ankle morphology, are the euparkeriids and the erythrosuchids, both of which combine the possession of a reduced carpal set with the lack of crocodiloid specializations. In the case of the euparkeriids, Ewer (1965: 431) pointed out that the ankle of *Euparkeria*, in spite of not being specialized as in later pseudosuchians, is advanced a bit towards a pseudo-mesotarsal articulation, which involves eventual elimination of the calcaneum, a situation that could have been ancestral to the "prosauropods" and sauropods. Euparkeria is, moreover, slightly built, potentially bipedal, and has dermal armor, all features not to be expected in the ancestor of the originally quadrupedal, morphs. It is more likely that the ancestry of the latter would be within the erythrosuchids, both on ecological and morphological considerations. In fact, it is not difficult to think of the huge, marsh-dwellquadrupedal erythrosuchids, with ing, mesotarsal ankle and devoid of any armor, as the ancestors of the quadrupedal, largesized, unarmored, and marsh-dwelling melanorosaurids (Fig. 16). At the same time, the euparkeriids are likely to be the ancestors of the coelurosaurians, since the evidence indicates that the latter have from the very beginning been upland, rapidlymoving bipedal carnivores, possessing a type of ankle joint which, in spite of being of mesotarsal type, has a calcaneum with a tuber, a condition reminiscent of the crocodiloid pseudosuchian tendencies. At the same time, the fact that at least one coelurosaurian (Ceratosaurus) has dermal armor can also be taken as an indication of an early pseudosuchian ancestry.

But, as a matter of fact, it is necessary to realize that we are at the very beginning of an explanation of saurischian origin. The views here advanced on the probable origin of sauropodomorphs from erythosuchid proterosuchians are only to be considered as working hypotheses that, in our belief, match the known facts better than do alternative interpretations. We must admit that these facts are so far not sufficiently complete to warrant a thorough reconstruction of early saurischian history. They are, however, at least complete enough to make it necessary to discard such generally accepted views as that the common origin of all the saurischians lay in bipedal, Upper Triassic pseudosuchians. It is also evident now that the radiation of the saurischians did not start after the extinction of the thecodonts. During Middle and Upper Triassic times, both taxa had their own extensive radiations, apparently developing not only parallel and competitive similar forms, but also forms differing in ecological roles and habitat preferences. The herbivores are by far the less common of the



Figure 16. Phylogenetic diagram showing the suggested origins and the relationships of the major saurischian groups.

heavy-built, and unarmored sauropodo-Middle and Upper Triassic pseudosuchians and saurischians, being limited in fact to the stagonolepidids and the melanorosaurids. At these times gomphodonts and kannemeyeroid dicynodonts seem to have been competitors of plant-eating archosaurs.

The case of the phytosaurs and other archosaurian groups

In our present state of knowledge, the relevant evidence for advancing a serious hypothesis of the origin of the Pterodactyla and the Ornithischia is not available. The Pterodactyla, when first encountered in the Lower Jurassic, had already acquired the whole set of specializations for air locomotion. They were probably derived from lightly-built, arboreal pseudosuchians, and the fact that Scleromochlus is a genus with these characteristics supports the view that it was connected with the group from which those archosaurs adapted to flying could have arisen. This is as much as can be said at the moment.

As far as the Ornithischia are concerned. this order of dinosaurs, dominant in the Cretaceous, is rather obscure in origin. It has been maintained that the order had its first radiation prior to the Upper Triassic, because of the characteristics of incomplete remains from the Cave Sandstone beds of South Africa, which have been referred to two different genera: Geranosaurus and Heterodontosaurus (see Crompton and Charig, 1962). The evidence is, however, too fragmentary to support any such conclusion. Walker (1961) suggested that the stagonolepidids might be close to the ancestry of the ornithischians, but in this case also the evidence warrants only highly tentative speculations. The question of ornithischian origins is better considered an open problem until more information becomes available. The lack of relevant data on Triassic ornithischians could also be interpreted as an indication that their origin took place at a rather late stage of archosaurian evolution.¹

The case of phytosaur origins seems to be a little less obscure, since we are at least able to postulate a probable ancestral group: the proterosuchids. The phytosaurs are a typical Upper Triassic group, and their association with saurischians and metoposaurid labyrinthodonts is the characteristic feature of the C type of Triassic faunas. No certain phytosaur remains are known from the Middle Triassic, but the Lower Triassic of Europe has afforded one skull, which is the basis of the genus Mesorhinosuchus, currently referred to this group. Recent work by Gregory (1962) casts some doubts upon the stratigraphic provenance and taxonomic position of this skull, and it must be admitted that the isolation of the specimen with respect to the whole remaining phytosaur record, together with the date and conditions of its discovery, justify a skeptical attitude. The probable presence of a phytosaur in the European Bunter, however, is to be admitted if we assume that the proterosuchians are the most likely ancestors of this group. And this is likely to be the case, since the phytosaurs, aquatic and primitive in postcranial morphology, are hardly derivable from the pseudosuchians, a group that from the outset shows specializations in the appendicular skeleton for a terrestrial way of life that clearly went beyond the level attained by similar advances in the phytosaurs. Admittedly, the phytosaurs share with the pseudosuchians several improvements in general organization, such as the presence of an otic notch, pterygoids joined at the midline, absence of palatal teeth, large antorbital fenestra, absence of intercentra, propodials largely moving in a vertical plane, and well-developed osteoderms. All these features can be interpreted as acquisitions connected with a better

¹Casamiquela (1967), however, recently described ornithischian remains from the Ischigualasto (upper Middle Triassic) beds. See Addendum.

adaptation both for locomotion on land and for predation that may well have arisen independently in different groups evolving from a proterosuchian condition. Besides these character-states, the phytosaurs show several specializations connected with improvements for aquatic life and aquatic predation: a very long and narrow rostrum formed largely by premaxillaries; external narial openings placed far behind the tip of the snout, close to the midline, between or at a short distance in front of the antorbital fenestra; orbits situated high in the skull; choanae placed posteriorly, and palatines forming lateral shelves below them, etc. The phytosaurs are to be considered specialized proterosuchid derivatives that evolved as amphibious predators, able to live a more efficient aquatic life than their forebears, and at the same time able to move about on the firm land around the water. They were probably very close to the modern crocodiles in biological type.¹

SUMMARY OF THE MAJOR EVENTS IN EARLY ARCHOSAURIAN EVOLUTION

Improved knowledge of the organization of the first archosaurs, the proterosuchian thecodonts, and a re-examination of present evidence and interpretations of the phylogeny and taxonomy of the main archosaurian groups support the following reconstruction of the early events in the evolution of archosaurs:

1) The archosaurs arose during early Upper Permian times, probably from a branch of aquatic pelycosaurs, the Varanopsidae, which separated from the main line of pelycosaur evolution early in the Lower Permian.

2) During the uppermost Permian and the early Lower Triassic, the first recorded group of archosaurs, the proterosuchid proterosuchians, developed. These were primitive, aquatic predators, living mostly in permanent waters (lakes, ponds, and rivers), as important members of freshwater communities. They survived until the upper part of the Lower Triassic, but dwindled in number and diversity.

3) Some populations of proterosuchids became better adapted to living in shallow waters and improved as predators of large animals. The erythrosuchid proterosuchians arose from such populations, and became dominant in swamps during the upper Lower Triassic.

4) The Pseudosuchia are first represented by the Euparkeriidae of the upper Lower Triassic. These were mostly quadrupedal, rather tiny, upland predators. Their origin is to be sought in the transitional phase of the proterosuchid-erythrosuchid descent.

5) In the uppermost Lower Triassic, the euparkeriids evolved into the rauisuchids. These were the large, quadrupedal, upland predators of the Middle Triassic.

6) The stagonolepidids arose from the euparkeriids in the Middle Triassic, becoming an important group in the Upper Triassic. They were upland dwellers, either scavengers or omnivores.

7) The euparkeriids probably survived through the Middle Triassic, and their last populations gradually were transformed into the ornithosuchids, which became a rather important group in the Upper Triassic as bipedal, medium-sized and large predators.

8) Perhaps on the borderline between Middle and Lower Triassic, the coelurosaurian saurischians evolved from a pseudosuchian, euparkeriid-like source. They were from the beginning bipedal, lightly-built, rapid predators inhabiting the upland environments. They were well established by the upper Middle Triassic, and became diversified and rather abundant in the Upper Triassic.

¹Walker (1968) has recently advocated that *Proterochampsa* is a phytosaur ancestor (see Addendum).

9) The true carnosaurs evolved in the uppermost Triassic or lowermost Jurassic from a coelurosaurian ancestor.

10) The sauropodomorph saurischians arose as true sauropods in the uppermost Lower Triassic, probably from erythrosuchid proterosuchians, and were fourlegged, marsh-dwelling forms from the beginning. These first sauropods were a rather unimportant group in Middle and Upper Triassic times, represented only by the melanorosaurids in the known record.

11) The first important radiation of the sauropodomorphs developed within the framework of the infraorder Palaeopoda. Palaeopod saurischians probably evolved from the first sauropods and radiated in Middle and Upper Triassic times into herbivorous and carnivorous lowland and upland forms. They included partially bipedal and completely bipedal forms.

12) The first crocodiles were the Middle Triassic Archaeosuchia. They probably arose from the last proterosuchid populations of the uppermost Lower Triassic, within the framework of the freshwater communities, but evolved adaptations for a more amphibious way of life. They seem not to have been an important group in the freshwater environments of the Upper Triassic, perhaps because of the competition of the phytosaurs, dominant at this time.

13) During the Upper Triassic, an offshoot of the archaeosuchians became better adapted for terrestrial life and spread as a group of upland predators: the protosuchian crocodiles.

14) The phytosaurs probably evolved from the proterosuchids in the late Lower Triassic as members of the freshwater communities. They were unimportant in the Middle Triassic, perhaps because of the competition of the Archaeosuchia, and became dominant freshwater predators only in the Upper Triassic. 15) By the end of the Triassic, several groups of archosaurs had become extinct: pseudosuchians and protosuchians, and probably archaeosuchians, phytosaurs, and palaeopod saurischians. It was the beginning of the second phase of archosaurian evolution, a phase in which sauropods, carnosaurs, coelurosaurs, mesosuchian crocodiles, pterosaurs, and, later, ornithischians, deployed as full-fledged archosaurian groups.

EVOLUTIONARY AND TAXONOMIC CONCLUSIONS

The foregoing statement of the major events of the early phase of archosaurian evolution and the previous discussion of the evidence supporting such conclusions, are full of implications for the theoretical problems posed on pages 230ff. and 245ff. of this paper.

It will be of interest, now, to examine to what extent the described patterns of origin both of the archosaurs as a major group and of the groups within the archosaurs agree with the current concepts about the processes involved in the emergence of new major taxa. I have already said that a shift into a new adaptive zone, a speeding up of the evolutionary change in the transitional region between the original and the new adaptive zone, and the sudden appearance of key innovations opening new evolutionary possibilities are alleged to occur in the origin of new supraspecific taxa. This process would be responsible for the creation of apparent discontinuities that afford a clear-cut borderline between the original and the descendent groups. We have also seen that Bock (1965) claimed that this alleged pattern is an oversimplification; he emphasized the step-wise character of the process leading to the emergence of a new taxon, a process that he thought of as involving a more complex pattern than any single-phase change from one adaptive zone into another.

Let us examine, first of all, to what extent the shift into a new adaptive zone is exemplified by archosaur origins and the origin of the subordinate major taxa of archosaurs.

In fact, the origin of the archosaurs as a whole does not seem to be associated with a major shift between two different adaptive zones. The probable archosaur ancestors were water-adapted pelycosaurs, and the first known archosaurs were waterdwelling animals. Both ancestors and descendants seem to have been predaceous animals. Although it must be admitted that a considerable gap exists between the proposed ancestral group and the derived one, the process of the emergence of the archosaurs is likely to have been one of gradual improvement toward a more efficient life in the same general adaptive zone.

As far as the origins of the various archosaurian subordinate taxa are concerned, the pattern seems to have been a mixed one. There is an actual shift from lowland, marsh habitats toward upland environments in the passage from the proterosuchians to the pseudosuchians, but the passage from the proterosuchians to the crocodilians, phytosaurs, and sauropods does not seem to have involved any major departure from the general environments inhabited by the ancestral forms. The same is the case if the coelurosaurians were derived from the euparkeriid-like pseudosuchians. But a shift did occur from the archaeosuchians to the protosuchians. These various cases indicate that a major shift between two distinct general adaptive zones is not necessarily connected with the emergence of a major taxon, though it may occur in certain cases.

If we take a large scale approach, we could, however, agree that there is a major shift in general adaptive zone between the time of the appearance of the archosaurs and the time of their achievement of dominance at the beginning of the Jurassic. The first archosaurs were strictly watertied animals, swimming and feeding in lakes, ponds, and rivers; the post-Triassic ones were enormous swamp-dwellers and upland forms. The intermediate zone is, however, a long-lasting one, in which various minor radiations took place, and in which there is no reason to postulate any special acceleration of the evolutionary changes.

The hypothesis of an evolutionary speeding up in an alleged transitional zone is also not supported by the known cases of an actual shift. As already stated, the origin of the Pseudosuchia can be considered as one of the cases in which an actual switch seems to have occurred. Nevertheless, we can see here that the process was a gradual and long-term one, and that even the first definite pseudosuchians, the euparkeriids, were transitional in several respects.

Key innovations have arisen, as we have seen, several times in the early evolution of archosaurs. Character-states such as the development of an antorbital fenestra, the acquisition of an otic notch, the shifting forward of the mandibular articulation, the upright stance of the propodials, the pseudosuchian-crocodiloid ankle joint, to mention only some examples, can be safely regarded as being connected with improvements in general adaptability, thereby opening new evolutionary possibilities. It is interesting to realize, however, that features such as the above probably arose independently in different groups, and even that some of them, like the antorbital fenestra, had already evolved at a prearchosaurian level of evolution.

The general pattern of the emergence of major taxa, as exemplified by the case of the archosaurs, seems to be a pattern of gradual and long-lasting change. At least seven different processes are involved: (1) steady development of the typical characters of the emerging taxon; (2) exploratory radiations into new adaptive zones; (3) competition between lineages that achieve a similar ecological role from different ancestries; (4) steady acquisition of key characters opening new evolutionary possibilities in different lineages;

(5) improvement within the framework of a generally similar adaptive zone; (6) gradual shift into new adaptive zones; and (7) gradual replacement of successive groups until eventually a new, major taxon becomes established. No factors different from those involved at the species or infraspecies level need be involved. Although it may be convenient, for the sake of the description of the evolutionary events, to distinguish the different processes of evolution [as did Huxley (1958) and other authors], it must be stressed that the final agencies of evolutionary change are really the same for any of the processes distinguished in the description of large-scale evolutionary phenomena.

Thus, the emergence of a new taxon can be considered a phenomenon plainly involving only evolution governed by selection and by the known processes of change in gene frequency within populations; the regular processes of evolution at the species level therefore, are also those responsible for the gradual, progressive establishment of major taxonomic groups. On the other hand, the latter are to be considered not as artifacts of classification but as natural units, for they include subordinate entities connected by relationships of origin and descent. But they are not bounded by discontinuities, these being only imposed by the incompleteness of the record. The fact is that the better the evidence connected with the origins of a major group is known, the less apparent are the alleged discontinuities between the ancestral and the descendent groups.

The concepts having natural taxa as referents are hence necessarily polythetic concepts, and a fringe of vaguenesss seems to be unavoidable in the statement of the intension of taxonomic concepts at the supraspecific level. It also seems necessary to agree that vagueness can occur in the statement of the extension of these concepts, as intermediate forms can always be placed in either of the groups they connect.

RESUMEN

Nuevos conocimientos sobre la organización de los tecodontes proterosuquios, que son los más antiguos y los más primitivos reptiles conocidos de la subclase Archosauria, conjuntamente con un estudio crítico de los datos y las interpretaciones actuales sobre la filogenia y la clasificación de los principales grupos de reptiles arcosaurios, dan fundamento a la siguiente reconstrucción de los acontecimientos que tuvieron lugar durante el comienzo de la evolución de los arcosaurios:

1) Los arcosaurios surgieron durante el comienzo del Pérmico superior a partir, probablemente, de una rama de pelicosaurios acuáticos, los Varanopsidae, que se separaron de la línea principal de la evolución de los pelicosaurios en el Pérmico inferior.

2) Durante el Pérmico más superior y el comienzo del Triásico inferior se desarrolló el primer grupo conocido de reptiles arcosaurios, los tecodontes proterosuquios de la familia Proterosuchidae. Los proterosúquidos fueron predadores acuáticos primitivos que vivían en aguas dulces permanentes (lagos, pantanos y ríos) constituyendo una parte importante de las comunidades dulceacuícolas de la época. Sobrevivieron hasta la parte superior del Triásico inferior, aunque en menor número y más reducidos en diversidad.

3) Algunas poblaciones de proterosúquidos se hicieron mejor adaptados para vivir in aguas someras y se perfeccionaron como predadores de grandes herbívoros semiacuáticos. Los proterosuquios de la familia Erythrosuchidae surgieron de dichas poblaciones, tornándose dominantes en los pantanos de la parte superior del Triásico inferior.

4) Los primeros representantes del suborden Pseudosuchia de tecodontes fueron los euparkéridos de la parte superior del Triásico inferior. Eran predadores terrestres de tamaño pequeño y de locomoción cuadrúpeda. Su origen debe buscarse en la fase transicional de la transformación de los proterosúquidos en eritrosúquidos.

5) A finales del Triásico inferior, los euparkéridos dieron lugar a los rauisúquidos. Estos fueron predadores terrestres de gran tamaño y de andares cuadrúpedos que prosperaron principalmente en el Triásico medio, donde están representados por géneros como *Prestosuchus*, *Saurosuchus* y *Stagonosuchus*.

6) Los Stagonolepídidos (familia que incluye a aetosáuridos y stagonolépidos) surgieron probablemente de los euparkéridos en el Triásico medio, tornándose un grupo importante de las faunas terrestres del Triásico superior. Fueron reptiles terrestres acorazados, de hábitos alimentarios omnívoros, o carroñeros.

7) Es probable que los euparkéridos sobrevivieron durante el Triásico medio, época en la que se fueron transformando gradualmente en los ornitosúquidos. Estos constituyen un grupo de predadores bípedos de tamaño mediano y grande de importancia en las comunidades terrestres del Triásico superior.

8) Es posible que los dinosaurios saurísquios del grupo de los celurosaurios hayan surgido de una cepa pseudosuquia afín a los euparkéridos en la transición entre el Triásico inferior y el Triásico medio. Los celurosaurios fueron desde su origen predadores terrestres bípedos y esbeltos. Estaban ya bien representados en la parte final del Triásico medio, pero se hicieron más abundantes y diversificados en el Triásico superior, donde competían con los ornitosúquidos.

9) Los verdaderos dinosaurios carnosaurios evolucionaron en el Triásico más superior o en el Jurásico más inferior, a partir de un ancestro celurosaurio.

10) Los dinosaurios saurísquios del grupo de los Sauropodomorpha, surgieron como verdaderos saurópodos a finales del Triásico inferior, probablemente a partir de los proterosuquios de la familia Erythrosuchidae. Desde el comienzo fueron animales cuadrúpedos habitantes de los pantanos. Estos primeros saurópodos constituyen un grupo relativamente poco importante en el Triásico medio y en el Triásico superior, donde están representados solamente por los melanorosáuridos.

11) La primera radiación importante de los sauropodomorfos se desarrolló en el marco del infraorden Palaeopoda. Los saurisquios paleópodos surgieron probablemente de los primeros saurópodos y radiaron en el Triásico medio y superior en varias formas herbívoras y carnívoras que vivian tanto en los pantanos como en las tierras altas, entre los que se encontraban animales parcialmente bípedos y otros totalmente bípedos.

12) Los primeros cocodrilos fueron los Archaeosuchia del Triásico medio. Es probable que los arqueosuquios surgieran de las últimas poblaciones de proterosúquidos en la parte más superior del Triásico inferior, en el contexto de la comunidad dulceacuícola, pero desarrollando adaptaciones para una vida más anfibia. No parecen haber sido un grupo importante en los ambientes de agua dulce del Triásico superior, quizás por la competencia de los fitosaurios.

13) Durante el Triásico superior, una rama de los arqueosuquios se tornó mejor adaptada para la vida terrestre y se desarrolló como un grupo de predadores no acuáticos convergente con los pseudosuquios y los celurosaurios: los cocodrilos protosuquios.

14) Los fitosaurios probablemente se originaron en los proterosúquidos a finales del Triásico inferior, en el seno de las comunidades dulceacuícolas. Fueron poco importantes en el Triásico medio, posíblemente por la competencia con los arqueosuquios, pero se hicieron predadores dulceacuícolas dominantes durante el Triásico superior. 15) A finales del Triásico, se extinguieron varios grupos de arcosaurios: pseudosuquios, protosuquios, probablemente también los arqueosuquios, los fitosaurios y los saurisquios paleópodos. Estas extinciones marcan el comienzo de la segunda fase de la evolución de los arcosaurios, caracterizada por la expansión de los saurópodos, los carnosaurios, los cocodrilos mesosuquios, los pterosaurios y los ornitisquios.

Los enunciados anteriores sobre los acontecimientos probablemente suscitados en la fase temprana de la evolución de los arcosaurios tienen variadas implicaciones de interés en la cuestión de la clasificación y el origen de los grupos taxonómicos de rango superior.

El problema del origen de los arcosaurios y de los grupos subordinados de arcosaurios se relaciona con la cuestión ampliamente debatida del origen de los taxa de rango superior. La tesis más difundida para explicar el origen de los taxa de rango superior sostiene que en el proceso de evolución de tales taxa, se produce la invasión de una nueva zona adaptativa, la aceleración del ritmo evolutivo en la zona transicional entre la zona adaptativa original y la nuevamente conquistada, y el surgimiento súbito de innovaciones evolutivas que abren nuevas posibilidades de expansión en la nueva zona. A través de estos procesos, se originaría una clara discontinuidad entre el taxón original y el taxón descendiente, que haría relativamente fácil la distinción entre los mismos. Bock (1965) sostuvo que esa tesis implica una simplificación excesiva de la marcha real de los acontecimientos, y destacó el caracter gradual del proceso de la emergencia de un nuevo taxón, proceso que involucraría fenómenos más complejos que un cambio producido meramente al pasar de una zona adaptativa a otra.

La descripción que hemos hecho en lo que antecede de los principales acontecimientos vinculados con el origen y la primera diferenciación de los arcosaurios, confirma las objeciones señaladas por Bock. El origen de los arcosaurios como tales no parece estar asociado con un cambio adaptativo importante. Tanto los antecesores de los arcosaurios como los primeros arcosaurios (los proterosúquidos) eran animales acuáticos y carnívoros. Es muy probable que el origen de los proterosúquidos sólo haya involucrado un perfeccionamiento gradual hacia una vida más eficiente en la misma zona adaptativa general. El analisis del origen de los grupos subordinados de arcosaurios, indica que tampoco se puede postular un cambio brusco hacia distintas zonas adaptativas como fenómeno inseparable del surgimiento de nuevos grupos. Sin embargo, si observamos el proceso en su perspectiva general, podemos coincidir en la existencia de un cambio en la explotación de distintas zonas adaptativas desde la época de la primera aparición de los arcosaurios hasta la época de la culminación de su dominancia al comienzo del Jurásico. Los primeros arcosaurios eran creaturas estrictamente acuáticas y carnívoras, mientras que las formas jurásicas eran enormes herbívoros terrestres o anfibios y diversos tipos de carnívoros terrestres. La transición entre estos dos extremos, sin embargo, ocupó la mayor parte del Triásico, y durante ese período tuvieron lugar diversas radiaciones exploratorias en el marco de la competencia por la explotación de distintos recursos alimentarios. No queda lugar, entonces, para suponer un proceso en una solo fase ni una aceleración especial de los ritmos evolutivos.

El proceso general de la emergencia de un taxón de rango superior, como surge del ejemplo de los arcosaurios, parece más acorde con la idea de un proceso de cambio gradual y de larga duración, que involucra sencillamente el juego de las fuerzas evolutivas conocidas para la evolución al nível de la especie: cambios en la frecuencia génica en las poblaciones y selección natural.

BIBLIOGRAPHY

- ATTRIDGE, J. 1963. The Upper Triassic Karoo deposits and fauna of Southern Rhodesia. South Afr. J. Sci., **59**(5): 242–247.
- BAIRD, D., AND R. L. CARROLL. 1967. *Romeriscus*, the oldest known reptile. Science, **157**: 56– 59.
- BAUR, G. 1887. On the phylogenetic arrangement of the Sauropsida. J. Morph., 1(1): 93–104.
- BECKNER, M. 1959. The Biological Way of Thought. New York: Columbia University Press, 200 pp.
- BEER, G. R. DE. 1954. Archaeopteryx and evolution. Adv. Sci., 11: 160–170.
- Воск, W. 1965. The role of adaptive mechanisms in the origin of higher levels of organization. Syst. Zool., 14(4): 272–287.
- BONAPARTE, J. F. 1966. Chronological survey of tetrapod-bearing Triassic of Argentina. Breviora, Mus. Comp. Zool., No. **251**: 1–13.
 - ——. 1969. El primer y el cuarto grupo faunístico del Triásico de América del Sur. IV Congreso Lationoamericano de Zoología, Caracas, 1968.
 - ——. (In press). Dos nuevas "faunas" de reptiles triásicos de Argentina. I Simposio Intern. de Estrat. y Paleont. del Gondwana, Mar del Plata, 1967.
- BOONSTRA, L. D. 1953. A report on a collection of fossil reptilian bones from Tanganika Territory. Ann. South Afr. Mus., **42**: 5–18.
- BRINK, A. S. 1950. Notes on a second specimen of *Homodontosaurus kitchingi*. South Afr. J. Sci., 47: 118–119.
- . 1955. Notes on some thecodonts. Navors.
 Nasion. Mus. Bloemfontein, 1(6): 141–148.
 . 1959. A new small thecodont from the Red Beds of the Stormberg Series. Palaeont. Afr., 5: 109–115.
- BROILI, F., AND J. SCHRÖDER. 1934. Beobachtungen an Wirbeltieren der Karrooformation. V. Über Chasmatosaurus vanhoepeni Haughton. Sitzungsber. Bayer. Akad. Wiss. München (Math.-Nat. Abt.), **1934**(3): 225–264.
- BROOM, R. 1913. On the South African pseudosuchian *Euparkeria* and allied genera. Proc. Zool. Soc. London, **1913**: 619–633.
 - —. 1914. A new thecodont reptile. Proc. Zool. Soc. London, **1914**: 1072–1077.
 - . 1922. An imperfect skeleton of Youngina capensis Broom in the collection of the Transvaal Museum. Ann. Transvaal Mus., 8: 273–277.
 - ——. 1924a. On the classification of the reptiles. Bull. Amer. Mus. Nat. Hist., 52: 39–65.
 - . 1924b. Further evidence on the structure of the Eosuchia. Bull. Amer. Mus. Nat. Hist., **51**: 67–76.

——. 1925. On the origin of lizards. Proc. Zool. Soc. London, **1925**: 1–16.

- ——. 1938. On a new type of primitive fossil reptile from the Upper Permian of South Africa. Proc. Zool. Soc. London, (B) **108**: 535–542.
- ——. 1940. Some new Karroo reptiles from the Graaff Reinet District. Ann. Transvaal Mus., **20**: 71–87.
- ------. 1946. A new primitive proterosuchid reptile. Ann. Transv. Mus., 20(4): 343–346.
- ——. 1948. A contribution to our knowledge of vertebrates of the Karroo beds of South Africa. Trans. Roy. Soc. Edinburgh, **61**: 577– 629.
- ——. 1949. New fossil reptilian genera from the Bernard Price collection. Ann. Transvaal Mus., **21**: 187–195.
- BUNGE, M. 1959. Metascientific Queries. Springfield: Charles C. Thomas, 313 pp.
- CAMP, C. L. 1930. A study of the phytosaurs. Mem. Univ. California, 10: 1–161.
- CARROLL, R. L. 1964. The earliest reptiles. J. Linn. Soc. London, 45(304): 61-83.
- CASAMIQUELA, R. M. 1961. Dos nuevos estagonolepoideos argentinos (de Ischigualasto, San Juan). Rev. Asoc. Geol. Arg., 16(3–4): 143– 203.
- ——. 1967. Un nuevo dinosaurio ornitisquio triásico (*Pisanosaurus mertii*; Ornithopoda) de la formación Ischigualasto, Argentina. Ameghiniana, 4(2): 47–64.
- CHARIG, A. J. 1965. Stance and gait in the archosaur reptiles. British Assoc. Adv. Sci., Ann. Meet. 1965, Sect. C, Geology, 1–7.
- CHARIG, A. J., J. ATTRIDGE, AND A. W. CROMPTON. 1965. On the origin of the sauropods and the classification of the Saurischia. Proc. Linn. Soc. London, **176**(2): 197–221.
- CHARIG, A. J., AND O. A. REIG. In press. The classification of the Proterosuchia.
- COLBERT, E. H. 1964. Relationships of the saurischian dinosaurs. Amer. Mus. Novit., No. **2181**: 1–24.
- COLBERT, E. H., AND C. C. MOOK. 1951. The ancestral crocodilian *Protosuchus*. Bull. Amer. Mus. Nat. Hist., **97**: 149–182.
- Cox, C. B. 1965. New Triassic dicynodonts from South America, their origins and relationships. Phil. Trans. Roy. Soc. London, (B) 248: 457–519.
- CROMPTON, A. W., AND A. J. CHARIG. 1962. A new ornithischian from the Upper Triassic of South Africa. Nature (London), **196** (4859): 1074–1077.
- CROMPTON, A. W., AND M.-L. WAPENAAR (In press). Reptilian remains and trackways in

the Passage Beds (Stormberg Series of South Africa and Basutoland).

- EFREMOV, I. A. 1938. Novye permskie reptilii SSSR. Dokl. Akad. Nauk SSSR, **19**(9): 771– 776.
- ELLENBERGER, F., AND L. GINSBURG. 1966. Le gisement de dinosaurièns triassiques de Maphutseng (Basutoland) et l'origine des sauropodes. C. R. Acad. Sci. Paris, (D) **262** (4): 444–447.
- EWER, R. F. 1965. The anatomy of the thecodont reptile *Euparkeria capensis* Broom. Phil. Trans. Roy. Soc. London, (B) **248**: 379–435.
- GISIN, H. 1964. Synthetische Theorie der Systematik. Z. Zool. Syst. Evolutionsforsch., 2: 1–17.
- 1966. Signification des modalités de l'évolution pour la théorie de la systématique.
 Z. Zool. Syst. Evolutionsforsch., 4(1/2): 1–12.
- GOUDGE, T. A. 1961. The Ascent of Life. London: Allen and Unwin, 236 pp.
- GREGORY, J. T. 1962. The genera of phytosaurs. Amer. J. Sci., **260**: 652–690.
- HAUGHTON, S. H. 1924. The fauna and stratigraphy of the Stormberg Series. Ann. South Afr. Mus., **12**: 323–495.
- HEILMANN, G. 1926. The Origin of Birds. London: Witherly, 210 pp.
- HOFFSTETTER, R. 1955. Thecodontia. In: J. Piveteau, ed., Traité de Paléontologie, **5**: 665–694.
- HUENE, F. VON. 1908. Die Dinosaurier der europäischen Triasformation, mit Berücksichtigung der aussereuropäischen Vorkommnisse (part). Geol. Palaeont. Abh. Supplement-Band 1(6): 345–419.
- ——. 1911. Ueber *Erythrosuchus*, Vertreter der neuen Reptil-Ordnung Pelycosimia. Geol. Palaeont. Abh., N. F., **10**: 1–60.
- . 1914a. Das natürliche System der Saurischia. Zentralbl. Min. Geol. Paläont., 1914: 154–158.
- ——. 1914b. Beiträge zur Geschichte der Archosaurier. Geol. Palaeont. Abh., N. F., **13:** 1–53.
- —. 1920. Osteologie von Aëtosaurus ferratus
 O. Fraas. Acta Zool., 1: 465–491.
- ——. 1925. Die Bedeutung der Sphenosuchus Gruppe für den Ursprung der Krokodile. Z. Indukt. Abstamm. Vererbl., **38**(4): 307–320.
- ——. 1932. Die fossile Reptil-Ordnung Saurischia, ihre Entwicklung und Geschichte. Mon. Geol. Palaeont., Ser. 1, **4**: 1–361.
- ———. 1938. Ein grosser Stagonolepide aus der jüngeren Trias Ostafrikas. Neues Jahrb. Min. Geol. Palaeont. Abt. B, **80**(2): 264–278.
 - ——. 1942. Die fossilen Reptilien des Südamerikanischen Gondwanalandes. Lief. 3/4: 161–332, Munich.

—. 1956. Paläontologie und Phylogenie der niederen Tetrapoden. Jena: Gustav Fischer, 716 pp.

- —. 1960. Ein grosser Pseudosuchier aus der Orenburger Trias. Palaeontographica, Abt. A, 114(1/4): 105–111.
- ——. 1962. Die Pseudosuchier als Wurzelgruppe der meisten Landsaurier der Juraund Kreidezeit. Neues Jahrb. Geol. Paläont., **1962**(1): 1–6.
- HUGHES, B. 1963. The earliest archosaurian reptiles. South Afr. J. Sci., **59**(5): 221–241.
- HUXLEY, J. S. 1958. Evolutionary processes and taxonomy with special reference to grades. Uppsala Universitets Årsskrift, **6**: 21–39.
- KÄLIN, J. 1955. Crocodilia, In: J. Piveteau, ed., Traité de Paléontologie, **5**: 695–784.
- KREBS, B. 1963. Bau und Funktion des Tarsus eines Pseudosuchiers aus der Trias des Monte San Giorgio (Kanton Tessin, Schweiz). Paläont. Z., 37(1/2): 88–95.
- ———. 1965. Ticinosuchus ferox, nov. gen., nov. sp. Ein neuer Pseudosuchier aus der Trias des Monte San Giorgio. Schweiz. Paläont. Abh., 8: 1–140.
- KUHN, O. 1959. Die Ordnungen der fossilen "Amphibien" und "Reptilien." Neues Jahrb. Geol. Paläont., M. H., 337–347.
- ——. 1961. Die Familien der rezenten und fossilen Amphibien und Reptilien. Bamberg: Meisenbach K. G., 79 pp.
- KUHN-SCHNYDER, E. 1954. The origin of lizards. Endeavour, **13**(52): 213–219.
- ———. Ein weitere Schädel von *Macrocnemus* bassani Nopcsa aus der anisischen Stufe der Trias des Monte San Giorgio (Kanton Tessin, Schweiz). Paläont. Z., H. Schmidt Festband, 110–133.
- ——. 1963. Wege der Reptilien-Systematik. Paläont. Z., **37**(1.2): 61–87.
- LYDEKKER, R. 1887. Note on the Hordwell and other crocodilians. Geol. Mag. (N.S.) Decade III, 4(7): 307–312.
- MAYR, E. 1965. Numerical phenetics and taxonomic theory. Syst. Zool., 14: 73–97.
- Mook, C. C. 1934. The evolution and classification of the Crocodilia. J. Geol. 42: 295–304.
- OLSON, E. C. 1962. Les Problèms actuels de Paléontologie (Evolution des Vertébrés). Colloques Int. C. N. R. S., No. 104: 157–174.
 —. 1965. Chickasha vertebrates. Oklahoma Geol. Surv., Circular 70: 1–70.
- PARRINGTON, F. R. 1935. On *Prolacerta broomi*, gen. et sp. nov., and the origin of lizards. Ann. Mag. Nat. Hist., Ser. 10. **16**: 197–205.
 - ——. 1956. A problematic reptile from the Upper Permian. Ann. Mag. Nat. Hist., Ser. 12, **9**: 333–336.
 - —. 1958. The problem of the classification

of reptiles. J. Linn. Soc. London, Zool., 44 (295): 99–115.

- PEABODY, F. E. 1948. Reptile and amphibian trackways from the Lower Triassic Moenkopi Formation of Arizona and Utah. Univ. Calif. Publ. Bull. Dept. Geol. Sci., 27(8): 295–468.
 ——. 1952. Petrolacosaurus kansensis Lane, a Pennsylvanian reptile from Kansas. Univ. Kansas Paleont. Contrib., Vertebrata, 1: 1–41.
 —. 1955. Occurrence of Chirotherium in South America. Bull. Geol. Soc. Amer., 66: 239–240.
- PEARSON, H. S. 1924. A dicynodont reptile reconstructed. Proc. Zool. Soc. London, 1924: 827–855.
- PIVETEAU, J. 1955. Eosuchia. In: J. Piveteau, ed., Traité de Paléontologie, **5**: 545–557.
- POPPER, K. R. 1959. The Logic of Scientific Discovery. London: Hutchinson, 480 pp.
- PRICE, L. I. 1946. Sôbre um novo pseudosuquio do Triásico superior do Rio Grande do Sul. Minist. Agric. Div. Geol. Min., Bol. 120: 1–38.
- REIG, O. A. 1959. Primeros datos descriptivos sobre nuevos reptiles arcosaurios del Triásico de Ischigualasto. Rev. Asoc. Geol. Arg., 13 (4):257–270.
 - —. 1961. Acerca de la posición sistemática de la familia Rauisuchidae y del género Saurosuchus (Reptilia, Thecodontia). Publ. Mus. Munic. Cien. Nat. Trad. Mar de Plata, 1(3): 73–114.
 - ——. 1963a. La presencia de dinosaurios saurisquios en los "Estratos de Ischigualasto" (Mesotriásico superior) de las provincias de San Juan y La Riojo (República Argentina). Ameghiniana, **3**(1): 3–20.
 - —. 1963b. Anagenesis and the processes of evolutionary progress. Proc. XVI Internat. Cong. Zool., Washington, D. C., August 20– 27, 1963, Vol. **2**: 185.
 - . 1967. Archosaurian reptiles: a new hypothesis on their origins. Science, **157**: 565– 568.
 - ——. 1968. Los conceptos de especie en la biología. Ediciones Biblioteca Univ. Central de Venezuela. Caracas, 43 pp.
- RENSCH, B. 1947. Neuere Probleme der Abstammungslehre: die transspezifische Evolution. Stuttgart: Enke, 407 pp.
- ROMER, A. S. 1945. Vertebrate Paleontology. 2nd ed. Chicago: Univ. Chicago Press, 687 pp.
 - restudied. Amer. J. Sci., **244**: 149–188.
 - —. 1956. Osteology of the Reptiles. Chicago: Univ. Chicago Press, 772 pp.

—. 1966a. The Chañares (Argentina) Triassic reptile fauna. I. Introduction. Breviora, Mus. Comp. Zool., No. **247**: 1–14. —. 1966b. Vertebrate Paleontology. 3rd ed., Chicago: Univ. Chicago Press, 468 pp.

- ——. 1967. Early reptilian evolution reviewed. Evolution, **21**: 821–833.
- ——. In press. Middle Triassic tetrapod faunas of South America. IV Congreso Latinoamericano de Zoología, Caracas, 1968.
- ROMER, A. S., AND L. I. PRICE. 1940. Review of Pelycosauria. Geol. Soc. Amer. Spec. Pap., No. 28: 1–538.
- ROZHDESTVENSKII, A. K. 1964. Klass Reptilia. Reptilii, ili presmykaiushtchiesia. Obshtchaia chast. In: J. A. Orlov, ed., Osnovy Paleontologii. Zemnovodnye, presmykaiushtchiesia i ptitzy. Moscow, pp. 191–213.
- RUSCONI, C. 1951. Laberintodontes triásicos y pérmicos de Mendoza. Rev. Mus. Hist. Nat. Mendoza, **5**: 33–158.
- SATSANGI, P. P. 1964. A note on *Chasmatosaurus* from the Panchet series of Raniganj coalfield, India. Current Sci., **33**(21): 651–652.
- SAWIN, H. J. 1947. The pseudosuchian reptile Typothorax meadei. J. Paleont., 21: 201–238.
- SCHMIDT-NIELSEN, K. 1958. Salt glands in marine reptiles. Nature (London), 182(4638): 783– 785.
- SHAROV, A. G. 1965. Evolution and taxonomy. Z. Zool. Syst. Evol.-forsch. 3(3/4): 349–358.
- SILL, W. 1967. Proterochampsa barrionuevoi and the early evolution of the Crocodilia. Bull. Mus. Comp. Zool., 135: 415–446.
- SIMPSON, G. G. 1953. The Major Features of Evolution. New York: Columbia Univ. Press, 434 pp.
- ——. 1959. The nature and origin of supraspecific taxa. Cold Spring Harbor Symp. Quant. Biol., **24**: 255–271.
- New York: Columbia Univ. Press, 247 pp.
- SNEATH, P. H. A. 1962. The construction of taxonomic groups. In: G. C. Ainsworth and P. H. A. Sneath, eds., Microbial Classification. Cambridge: Cambridge Univ. Press, pp. 289– 332.
- SOKAL, R. R., AND P. H. A. SNEATH. 1963. Principles of Numerical Taxonomy. San Francisco and London: Freeman and Co., 359 pp.
- SUN, A. L. 1963. The Chinese kannemeyerids. Paleont. Sinica, (C) 17:1–109.
- TAKHTAJAN, A. 1959. Die Evolution der Angiospermen. Jena: Gustav Fischer.
- TATARINOV, L. P. 1959. Proishkhozhdenie presmykaiushtchiesia i nekotorye printzipy ikh klassifikatzii. Paleont. Zh. 1959, 4: 65–84.
 - _____. 1961. Materialy po psevdozukhiian S.S.S.R. Paleont. Zh. 1961, 1: 117–132.
 - ed., Osnovy Paleontologii: Zemnovodnye,

presmykaiushtchiesia i ptitzy. Moscow, pp. 444-446.

TEMPLETON, J. R. 1964. Nasal salt excretion in terrestrial lizards. Comp. Biochem. Physiol., 11: 223–229.

—. 1966. Responses of the lizard nasal salt gland to chronic hypersalemia. Comp. Biochem. Physiol., **18**: 563–572.

- VAUGHN, P. P. 1955. The Permian reptile Araeoscelis restudied. Bull. Mus. Comp. Zool., 113: 305–467.
- VERSLUYS, J. 1910. Streptostylie bei Dinosaurien, nebst Bemerkungen über die Verwandtschaft der Vögel und Dinosaurier. Zool. Jahrb., Abt. Anat., **30**(2): 175–260.
- ——. 1912. Das Streptostylie-Problem und die Bewegungen im Schädel bei Sauropsiden. Zool. Jahrb. Suppl. XV (Festschrift J. W. Spengel), 2: 545–716.
- WADDINGTON, C. H. 1960. The Ethical Animal. London: Allen and Unwin, 230 pp.
- WALKER, A. D. 1961. Triassic reptiles from the Elgin area: Stagonolepis, Dasygnathus and their allies. Phil. Trans. Roy. Soc. London, (B) 244: 103–204.
 - —. 1964. Triassic reptiles from the Elgin area: *Ornithosuchus* and the origin of carnosaurs. Phil. Trans. Roy. Soc. London, (B) **248:** 53–134.
 - —. 1966. *Elachistosuchus*, a Triassic rhynchocephalian from Germany. Nature (London), **211:** 583–585.
 - —. 1968. *Protosuchus*, *Proterochampsa*, and the origin of phytosaurs and crocodiles. Geol. Mag. **105**(1): 1–14.
- WATSON, D. M. S. 1954. On *Bolosaurus* and the origin and classification of reptiles. Bull. Mus. Comp. Zool., 111: 297–449.
 - ——. 1957. On *Millerosaurus* and the early history of the sauropsid reptiles. Phil. Trans. Roy. Soc. London, (B) **240**: 325–400.
 - —____. 1960. The anomodont skeleton. Trans. Zool. Soc. London, **29**(3): 131–208.
 - . 1962. The evolution of the labyrinthodonts. Phil. Trans. Roy. Soc. London, (B)
 245: 219–265.
- WILLISTON, S. W. 1914. The osteology of some American Permian vertebrates, I. Contrib. Walker Mus., 1: 107–182.
- WILSON, E. O. 1965. A consistency test for phylogenies based on contemporaneous species. Syst. Zool., 14: 214–220.
- WOODGER, J. H. 1952. Biology and Language. Cambridge: Cambridge Univ. Press, 364 pp.
- YOUNG, C. C. 1936. On a new *Chasmatosaurus* from Sinkiang. Bull. Geol. Soc. China, **15** (3): 291–311.

-. 1963. Additional remains of Chasmato-

saurus yuani Young, from Sinkiang, China. Vertebr. Palas. 7(3): 215–222.

Paleont. Sinica, (Ser. C) **19:** 1–205.

(Received 27 February 1968.)

ADDENDUM

After this paper was submitted for publication, some important contributions appeared that are relevant to several of the topics herein discussed.

The question of crocodile origins and the evolutionary meaning of Proterochampsa merited a paper by Walker (1968) that introduced radical changes in previous interpretations, including the views sustained in this paper. Walker affords a new look at the cranial structure of Stegomosuchus on the basis of casts procured by Dr. Romer, which allowed him to reinterpret the roof of the skull of Protosuchus as known from the photographs given by Colbert and Mook (1951). On the basis of these new interpretations, and of similarities in the dermal scutes, Walker concluded that Stegomosuchus is closely related to Protosuchus, and even that Stegomosuchus longipes could be a juvenile of Protosuchus richardsoni. Furthermore, in his view, the skull of Protosuchus indicates that this genus is much more closely related to Notochamsa than was previously maintained. Thus, his conclusion is that these three genera are to be placed in a single family of the suborder Protosuchia of crocodiles, a family that, by priority, should be named Stegomosuchidae.

Although I accept that some of these views might be proved as well substantiated by further work on the actual specimens of these forms, I hardly think it justified to propose such drastic changes without observing the original specimens. The same criticism applies to Walker's reappraisal of the phylogenetic place of *Proterochampsa*.

Walker analyzed 16 characters, most of which would afford "ample evidence for regarding *Proterochampsa* as a very primitive phytosaur, and not a crocodile" (1968: 11). This conclusion is, of course, of great interest, but here again the foundations might be suspected, due to the lack of direct observations of the several available specimens of the discussed genus. Moreover, Walker bases a part of his argument on my first description of *Proterochampsa* (Reig, 1959), a description which has been corrected by Sill's work (1967), based on broader comparisons and on more specimens, some of them better preserved.

There is not the space here to attempt a thorough discussion of Walker's arguments on the place of *Proterochampsa*. I wish to advance, however, my feeling that several parts of his analysis deserve serious consideration and a careful checking in the light of the actual specimens. Nevertheless, I am strongly convinced that, until this work is accomplished, it is wiser to maintain Sill's interpretation of *Proterochampsa* as the correct one, as, furthermore, it is the only one which is based on direct comparisons.

Another interesting suggestion in Walker's paper is his belief that Cerritosaurus (here considered as a probable junior synonym of Rhadinosuchus) possesses "some at least of the attributes one expects to find in a crocodile ancestor" (Walker, 1968: 11–12). We have already mentioned the isolated position of this genus among the Pseudosuchia, and the difficulties that arise in tracing its origins from the early and central Pseudosuchian family Euparkeriidae. Thus, Walker's suggestion seems to deserve serious consideration here, as it is likely to make more balanced the phylogenetic scheme of the Pseudosuchia.

Needless to say, new evidence might also be critical for the testing of Walker's views, and this evidence may already be available through Romer's and Bonaparte's new findings in the pre-Ischigualasto Chañares formation of La Rioja (Romer, 1966a, and *in press*). These two colleagues found excellent specimens of a small archosaurian showing significant resemblances to *Proterochampsa* (Romer and Bonaparte, pers. comm.). The animal, still undescribed, could be the key to the correct interpretation of *Proterochampsa* and other early crocodiloid forms, including the awkward "*Cerritosaurus*."

Furthermore, new light on the question of early crocodilian history will surely be shed by Bonaparte's recent findings in the Upper Triassic Los Colorados Beds of Ischigualasto (Bonaparte, 1969, in press.). These findings, still mostly undescribed, include two crocodiloid archosaurians. One of them is closely related to Sphenosuchus and Hesperosuchus, the other resembles Protosuchus. The former is also related to Triassolestes romeri from the Ischigualasto beds, an archosaur which I described (Reig, 1963) as a saurischian dinosaur. In that paper, I tentatively referred to *Proterochampsa* a fore-limb showing the typical carpal structure of crocodiles associated with the type skull of Triassolestes romeri. Now, the Sphenosuchus-like new archosaurian from Los Colorados found by Bonaparte (Pers. comm. and 1969), which include both cranial and postcranial material, allowed him to conclude that the fore-limb associated with Triassolestes' skull actually belongs to the same individual represented by the skull. Triassolestes is to be interpreted, therefore, as a primitive crocodilian of the group of "dinosaur-like crocodiles."

In all likelihood, after these new findings of the Argentinian Middle and Upper Triassic are described, we shall have a better understanding of the various crocodiloid forms currently classified as Protosuchids, Notochampsids, Sphenosuchids, etc. We can suppose, therefore, that a new appraisal of early crocodilian history will come in the near future.

A recent description of ornithischian dinosaur remains from the Ischigualasto beds (Casamiquela, 1967) makes it necessary to change some of the tentative conclusions of previous pages on the time of origin of this taxon. Although the new findings, described as *Pisanosaurus mertii*, are too fragmentary to afford precise observations on the problem of Ornithischian ancestry, they are conclusive first of all in proving the presence of a full-fledged ornithopod in the upper Middle Triassic of Argentina, and secondly, in tracing the origin of ornithischian dinosaurs well into the early Middle Triassic, that is to say, at the very beginning of the first diversification of the non-proterosuchian archosaurs.

Bulletin OF THE Museum of Comparative Zoology

New Fossil Pelobatid Frogs and a Review of the Genus Eopelobates

RICHARD ESTES

HARVARD UNIVERSITY CAMBRIDGE, MASSACHUSETTS, U.S.A. VOLUME 139, NUMBER 6 MAY 14, 1970

PUBLICATIONS ISSUED OR DISTRIBUTED BY THE MUSEUM OF COMPARATIVE ZOOLOGY HARVARD UNIVERSITY

BULLETIN 1863– BREVIORA 1952– MEMOIRS 1864–1938 JOHNSONIA, Department of Mollusks, 1941– Occasional Papers on Mollusks, 1945–

Other Publications.

- Bigelow, H. B., and W. C. Schroeder, 1953. Fishes of the Gulf of Maine. Reprint, \$6.50 cloth.
- Brues, C. T., A. L. Melander, and F. M. Carpenter, 1954. Classification of Insects. \$9.00 cloth.
- Creighton, W. S., 1950. The Ants of North America. Reprint, \$10.00 cloth.
- Lyman, C. P., and A. R. Dawe (eds.), 1960. Symposium on Natural Mammalian Hibernation. \$3.00 paper, \$4.50 cloth.
- Peters' Check-list of Birds of the World, vols. 2–7, 9, 10, 12, 14, 15. (Price list on request.)
- Turner, R. D., 1966. A Survey and Illustrated Catalogue of the Teredinidae (Mollusca: Bivalvia). \$8.00 cloth.
- Whittington, H. B., and W. D. I. Rolfe (eds.), 1963. Phylogeny and Evolution of Crustacea. \$6.75 cloth.
- Proceedings of the New England Zoological Club 1899–1948. (Complete sets only.)
- Publications of the Boston Society of Natural History.

Publications Office

Museum of Comparative Zoology Harvard University Cambridge, Massachusetts 02138, U. S. A.

© The President and Fellows of Harvard College 1970.

NEW FOSSIL PELOBATID FROGS AND A REVIEW OF THE GENUS EOPELOBATES

RICHARD ESTES1

CONTENTS

Abstract	293
Introduction and Acknowledgments	294
Abbreviations	294
The Status of the Genus Eopelobates	295
The Family Assignment of Eopelobates	298
Discussion of Anatomical Features	298
Frontoparietal-squamosal connection	298
Prootic foramen	299
Orbitotemporal opening	299
Squamosal angle	299
Ossified sternum	299
Ethmoid	300
Chronological Review of Described	
Eopelobates	304
Eopelobates anthracinus	304
Eopelobates hinschei	306
Eopelobates bayeri	307
Eopelobates grandis	308
Eopelobates sp	308
Description of New Material of Eopelobates	309
Eopelobates guthriei n. sp.	309
?Eopelobates sp.	315
The Relationships of Eopelobates	316
Intrageneric classification	322
Adaptation and intrafamilial classification	323
The Pelobatinae	324
Macropelobates osborni	324
Pelobates	326
Miopelobates robustus	328
Scaphiopus	328
S. skinneri, n. sp.	328
Species Removed from the Pelobatidae	333
Evolution and Zoogeography of the	
Pelobatidae	333
Appendix	337
References Cited	338

¹ Department of Biology, Boston University, and Museum of Comparative Zoology, Harvard University.

ABSTRACT

Eopelobates was a fossil pelobatid frog that lived in North America during the Eocene and early Oligocene, and may have been present in the Cretaceous as well. In Europe, it extended from middle Eocene through the middle Miocene. In many ways Eopelobates is intermediate between megophryine and pelobatine subfamilies, but is retained here in the Megophryinae because of absence of an enlarged prehallux, or spade. Two lines may be distinguished within the genus: a primitive, short-skulled group composed of the North American E. guthriei n. sp. and E. grandis, with the European E. anthracinus probably included here as well, and a long-skulled European lineage composed of E. hinschei (n. comb.) and E. bayeri.

The spadefoot toads were probably derived from Eopelobates, and the primitive E. guthriei shows some indications of The earliest true spadefoot relationship. spadefoot was Scaphiopus skinneri n. sp., from the early and middle Oligocene of North America. It has some primitive features but is already close to the modern S. holbrooki. A form close to Pelobates was also present in the early Oligocene of Europe, further implying at least an Eocene divergence of the spadefoots from the megophryines. The early or middle Oligocene Macropelobates from Mongolia links Eopelobates and the spadefoots in some

Bull. Mus. Comp. Zool., 139(6): 293–340, May 14, 1970 293

features, but the contemporaneous record of *Scaphiopus* described here indicates that it was too late to have been ancestral to the modern subfamily. *Macropelobates* is best interpreted as a relict of the spadefoot group that gave rise to both *Scaphiopus* and *Pelobates*. It seems to be most closely related to the primitive modern species *P. cultripes*, and also shows some similarity to the primitive *S. skinneri*. *Miopelobates*, a primitive pelobatine that lived in Europe in the middle Miocene and early Pliocene, may have been an early offshoot from the ancestral spadefoot.

The modern megophryines are tropical and subtropical and probably diverged from an *Eopelobates*-like form no later than the Cretaceous. *Leptobrachium* is the most primitive of the modern megophryines and is in some ways the most *Eopelobates*like of the group. Megophryines of modern type were probably restricted to the southern part of the Eurasian continent during the early Cenozoic; they have undergone a separate radiation and have developed both high- and low-altitude terrestrial forms from the more aquatic, primitive types.

The Pelobatidae probably differentiated from a discoglossid-like ancestor in the Holarctic middle-latitude tropics, and the primitive aquatic megophryine *Eopelobates* gave rise to the terrestrial spadefoots in response to early Cenozoic climatic deterioration in both Europe and North America. Similarities between the two modern pelobatines indicate that they probably had a common ancestry.

INTRODUCTION AND ACKNOWLEDGMENTS

Although fossil frogs are relatively rare, the pelobatid frogs are one of the most frequently encountered frog families in the Cenozoic fossil record, especially in the Oligocene and Miocene. Many different forms have been described from North American late Cenozoic deposits and have been recently reviewed by Kluge (1966) and Zweifel (1956). I am principally concerned here with the Eocene, Oligocene, and early Miocene forms and describe two new fossil finds that bear on the evolution of the Pelobatidae: (1) an early Eocene skull of *Eopelobates* from Wyoming, and (2) a skull and partial skeleton of a primitive *Scaphiopus* from the middle Oligocene of North Dakota.

I am especially grateful to Professor Zdeněk Špinar for discussion, for providing measurements, and for allowing me to utilize his new specimen of Eopelobates bayeri in this study. I also thank Dr. Alan Charig of the British Museum (Natural History); Dr. R. Hoffstetter (Muséum National d'Histoire Naturelle, Paris); Dr. H. Matthes (Geologisch-Paläontologisches Institut, Martin Luther University, Halle); Dr. H. Zapfe (Universität Wien); Dr. Donald Baird (Princeton University); Dr. Max Hecht (Queens University, N. Y.); and Dr. Arnold Kluge (University of Michigan) for allowing me to study specimens in their care. Dr. Daniel Guthrie (Pfitzer College, California) and Mr. Morris Skinner (Frick Laboratory, American Museum of Natural History) deserve special thanks for providing the new Eopelobates and Scaphiopus material described here. Mr. Walter P. Murphy, Jr. aided in the description of the latter as part of an Honors Program project in Biology, Boston University.

Drs. Špinar, Hecht, Ernest Williams (Harvard University), Charles Meszoely (Northeastern University), and J. A. Tihen (Notre Dame University) have offered helpful comments on the manuscript. Mr. Fred Maynard prepared Figures 14 and 30; Mrs. Patricia Kerfoot drew Figures 29 and 30.

This study was supported in part by National Science Foundation Grant GB-4303.

Abbreviations

AM = American Museum of Natural History, New York City.

- BM = British Museum (Natural History), London.
- CUPI = Charles University Paleontological Institute, Prague.
- FAM = Frick Laboratory, American Museum of Natural History, New York.
- MCZ = Museum of Comparative Zoology, Harvard University, Cambridge.
- MME = Museum für Mitteldeutsche Erdgeschichte, Geologisch-Paläontologisches Institut, Halle (Saale).
- PU = Princeton University Museum of Geology, Princeton.
- UCMP = University of California Museum of Paleontology, Berkeley.
- UMMZ = University of Michigan Museum of Zoology, Ann Arbor.

THE STATUS OF THE GENUS EOPELOBATES

Eopelobates anthracinus Parker (1929) is from the lignite beds of Rott, near Bonn, Germany. It lacks a spade (Fig. 1) and is unlikely to have been fossorial. Parker called the beds Lower Miocene, but Westphal (1958) states them to be middle Oligocene (Rupelian). Špinar (1952) noted the presence of a larger, related species, E. bayeri, from Bechlejovice, near Děčin, Czechoslovakia, in beds of Chattian or Aquitanian age (late Oligocene or early Miocene). The presence of a spade was not determinable in his specimen. Hecht (1963, p. 23) suggested that E. bayeri was in fact referable to Pelobates. Zweifel (1956) referred a spadeless early Oligocene specimen from the Chadron Formation of South Dakota to a new species, E. grandis.

I have recently examined all published material of *Eopelobates* and have also had the privilege of studying both a new complete specimen of *E. bayeri* and an associated series of tadpoles of this species collected by Professor Špinar. He will describe these in detail but he has kindly allowed me to figure (Fig. 2) and briefly discuss the adult animal in order to justify the generic assignment.

Except in a few cases in which the nature of the specimen precludes knowledge, material referred to Eopelobates shows the following features: (1) prominent, elongated sternal style; (2) strong posterior projection of the ischium; (3) spade absent; (4) long, relatively slender limbs; (5) urostyle either separate, partially, or completely fused with sacrum; (6) sacral diapophyses strongly dilated; (7) tibia longer than femur; (8) approximately subequal orbit and temporal openings; (9) dermal ossification well developed and fused to skull roof; (10) skull roof flat or concave dorsally; (11) ethmoid wide and blunt anteriorly, and with dorsal ethmoid roof over nasal capsules; (12) squamosal-frontoparietal connection absent; (13) prominent, well-ossified paroccipital processes on frontoparietal and occiput; (14) complete maxillary arcade; (15) femur-tibia length approaching or exceeding head-body length. Comparison with the two currently recognized subfamilies of pelobatids, the Pelobatinae and Megophryinae, indicates similarity of Eopelobates to both groups. The most clearcut megophryine resemblances are 2, 3, 4, 7, 8, 10, and 11. The only specific pelobatine feature is 9, but in a number of other features discussed below Eopelobates shows pelobatine resemblances. In 1, 6, 13, and 14 resemblance to both groups occurs. Character 5 is variable and useless as Zweifel (1956, p. 12) has suggested.

I believe that *in combination* characters 3, 7, 9, 10, 11, 12, and 15 validate *Eopelobates* as a distinct genus. In many ways, *Eopelobates* is intermediate between the two Recent subfamilies; this relationship will be discussed later in this paper. Zweifel's characterization of the genus (1956, p. 13) as extremely close to *Megophrys* is still valid, but it requires qualification. Hecht's contention (based only on the type) that *Eopelobates bayeri* is a



Figure 1. Eopelobates anthracinus, BM R-4841; X 3.

Pelobates is not supported by the new, complete specimen. There are indications, however, that an *Eopelobates*-like form gave rise to the spadefoot toads; these indications will be discussed below in the section on Scaphiopus and the new species of Eopelobates from Wyoming. Following Zweifel (1956), a revised

Following Zweifel (1956), a revised diagnosis of *Eopelobates* might read: pelobatid frogs with a fused encrustation



of dermal bone on the skull; skull roof concave or flattened medially; maxillary teeth present; eight procoelous presacral vertebrae; sacral diapophyses widely expanded; squamosal in wide contact with maxilla; no squamosal-frontoparietal contact; no bony prehallux or spade; tibia longer than femur; combined femur-tibiofibula length more than 90% of length from anterior tip of skull to tip of urostyle. This diagnosis differs from that of Zweifel in several respects. First, there is no frontoparietalsquamosal bar in Eopelobates, contrary to statements in the literature (see below under E. grandis and E. anthracinus). The term "postorbital bar" is confusing, since there is a possibility of "postorbital" contact both between maxilla and squamosal and between squamosal and frontoparietal. Neither Zweifel nor Parker were always specific in referring to this matter. Second, all species have a tibia either slightly or substantially longer than femur. Third, Zweifel (1956, p. 12) states that tibia and femur are "together somewhat shorter than the head-body length"; this is true of all Recent or fossil pelobatids measured by me, with the exception of E. bayeri and E. hinschei (see below).

THE FAMILY ASSIGNMENT OF EOPELOBATES

This has been discussed by Zweifel (1956). In the combination of procoelous vertebrae, imbricate neural arches, probable arciferal pectoral girdle, single coccygeal condyle, prominent sternal style, wide dilation of sacral diapophyses, long anterior and short posterior transverse processes, and the general aspect of the skull and skeleton, *Eopelobates* is referable to the Pelobatidae without much question.

DISCUSSION OF ANATOMICAL FEATURES

Before discussing the individual species of *Eopelobates*, a brief evaluation of selected anatomical features is necessary. Little or no attention will be given to features that have been treated adequately elsewhere or are not applicable to fossils.

Frontoparietal-Squamosal connection

Mertens (1923) believed Pelobates fuscus to be primitive because of the ligamentary frontoparietal-squamosal connection. Such a connection is not constant in either P. cultripes or P. syriacus. There is interpopulational variation as indicated by Başoğlu and Zaloğlu (1964; see also Fig. 27, this paper) and the connection may be absent in small individuals of P. cultripes (MCZ 15376). In most Recent megophryines, except Leptobrachium hasselti and Scutiger mammatus, a specialized connection of frontoparietal and squamosal occurs on the surface of the prootic, ventral to the temporal musculature (Fig. 11d).

Absence of the superficial, sculptured frontoparietal-squamosal connection in both *Eopelobates* and the Oligocene pelobatine *Macropelobates* probably indicates the primitive pelobatine condition. I believe, however, that Gislén (1936) was correct in suggesting that *Pelobates cultripes* is primitive, although my reasons for this decision are different from his (see section below on *Pelobates*).

In Megophrys, dermal ossification spans frontoparietal and squamosal, and Zweifel (1956, p. 15) has suggested that the presence of considerable dermal bone may be a primitive condition. While it is true that a complete bony head casque may develop in large individuals of Megophrys carinensis, M. monticola, and perhaps other species, this is not fused to the skull bones, but instead coalesces from peculiar, irregular dermal plaques that usually remain separate, even though they grow to meet each other. Dermal covering lacks discrete boundaries and may extend into the skin of the dorsum; it is therefore quite different from the sculptured, fused, and discrete ossifications of pelobatines and Eopelo*bates.* Whether it is an independently derived condition or a degeneration from a fused, Eopelobates-like condition cannot be determined. Many fossil frogs have secondary dermal sculpture on the skull roof, and these forms occur as far back as the late Jurassic; some other Jurassic frogs, however, lack dermal sculpture. Extensive dermal skull sculpture is present in some Hylidae, Leptodactylidae, Ranidae, Bufonidae, Rhacophoridae, and Discoglossidae; most of these groups have acquired this dermal covering independently.

Prootic Foramen

Kluge (1966, p. 13) has shown some apparent morphogenetic trends in the shape of the prootic foramen (= trigeminal foramen). There is a tendency for this to be surrounded by bone in some species, but in general, the foramen is open anteriorly (e.g. in *Megophrys* and in *Pelobates cultripes*). The foramen is narrow in both *Scaphiopus* (*Scaphiopus*) and the one species of *Eopelobates* in which this is known (*E. guthriei* n. sp.; see p. 309). In *Pelobates fuscus*, this foramen is elongated vertically and in some specimens may be surrounded by bone, as in *Scaphiopus* (*Spea*).

While a trend toward closure does seem to exist, this is quite variable throughout the pelobatid series, as might be imagined in a condition involving minor degrees of ossification. The actual shape variation is even greater within species than Kluge indicated (Fig. 16). Care should be taken in the use of this character. Study of the soft structures involved would be useful, as would a functional study of the correlation of closure of foramen with the loss of dermal roofing bone.

Orbitotemporal Opening

The proportions of orbit and temporal opening vary widely in pelobatids (Fig. 15). In *Megophrys* and *Eopelobates*, the skull is relatively broad and flat and the orbito-temporal openings are of about equal size. In pelobatines there is a tendency towards the enlargement of the orbit and the reduction of the temporal area and rear part of skull. This is most extreme in *Scaphiopus couchi* and *S. (Spea)*, and results in a major change in the squamosal angle (see below and Figs. 15, 17). Other skull changes accompany this one and result in the high, domed, toad-like skull of these species.

Squamosal Angle

Griffiths (1963, p. 248) gave three categories for the condition of the angle between squamosal and quadratojugal, and for the origin of the depressor mandibulae: (1) depressor mandibulae originating from the squamosal stem and otic arm; squamosal angle > than 55° (Bufonidae, Brachycephalidae); (2) muscle originating from squamosal and dorsal fascia, squamosal angle 45°-50° (Ranidae, Microhylidae, Rhacophoridae, Leptodactylidae, Hylidae); (3) muscle originating only from dorsal fascia, squamosal angle $< 45^{\circ}$ (Discoglossidae, Pelobatidae). He noted that all groups passed through condition (1) in their development and that care should be taken in using this character because of the possibility of parallel paedomorphy.

In specimens I measured, the squamosal angle was 45° or less only in *Megophrys*; but in *Eopelobates guthriei* nov. (see below), *E. hinschei*, and *Scaphiopus skinneri* nov. (see below), the angle fell between 45° and 50° . All other pelobatines were between 56° and 73° , the highest in *S. couchi*. This change in the squamosal angle suggests that the development of a higher skull and larger orbit in pelobatines (discussed above) may involve a paedomorphic trend.

Ossified Sternum

Kluge (1966, p. 17) noted that Griffiths (1963, p. 271) was incorrect in stating that all pelobatids have an ossified sternal apparatus. Zweifel (1956, p. 24) states that the sternum is cartilaginous in *Scaphiopus*. This seems to be true in general, but a specimen of *S. couchi* chosen at random



(MCZ 64374, cleared and stained) has an irregular sternal ossification (Fig. 9d) in the stylar region, and an ossified, paired omosternum as well. Although this condition has not yet been described in a fossil *Scaphiopus* and I have not checked it in *S. holbrooki*, it is possible that some ossification is the primitive condition in *Scaphiopus*.

Ethmoid

The ethmoid shows considerable intergeneric variation in general shape, and since it is often found in fossils it can be useful in identification. I lack sufficient material for a meaningful study on intrageneric variation, but the material available seems to be relatively consistent and to demonstrate that some species may be identifiable on this basis as well.

In *Megophrys* the ethmoid is pinched-in ventrally, but develops lateral wings dorsally, giving a rhombic shape to the dorsal surface of the bone. In *Leptobrachium* no lateral wings are present and the ethmoid is hour-glass shaped. The lateral processes (Fig. 3) are prominent, but are not strongly separated from the anterior process by emargination in the choanal region. The

palatines underlie the lateral processes and the vomers lie along the lateral sides of the anterior process. Internally there is only a faint development of a turbinal fold between lateral and anterior processes, if it is present at all (Fig. 4); however, a turbinal fold is present in cartilage. The internal surface is flattened dorsoventrally and the capsule area is completely roofed by the ethmoid; only at the anterior end is it covered by the nasal. In Pelobates cultripes and P. syriacus, the anterior process is moderately developed, but the end of the process is relatively blunt with only a slight median projection. The turbinal fold is moderately developed.

In *Pelobates fuscus* and especially in *Scaphiopus*, there is marked separation of the anterior and lateral processes by emargination. In the emarginated area between those processes, *P. fuscus* has a moderately developed turbinal fold, and *Scaphiopus* a very well developed one. In both species (except *S. holbrooki*), the turbinal fold projects strongly in ventral view as the capsular process (Fig. 5), and the anterior process itself has two separate projections. The capsular process is much better developed in *Scaphiopus* (again,



Figure 4. Ethmoids in anterior view; a, Megophrys monticola, AM 23964; b, Eopelobates grandis, PU 16441; c, Macropelobates osborni, AM 6252; d, Pelobates cultripes, UMMZ S-2630; e, Pelobates fuscus, MCZ 1012; f, Scaphiopus couchi, AM 56284; a-d, \times 3; e-f, \times 6; diagonal hatching \equiv broken surface, dashed line \equiv restoration, stippled area \equiv cartilage attachment surface; A \equiv anterior process; C \equiv capsular process; L \equiv lateral process; T \equiv turbinal fold.

except in S. holbrooki) and is somewhat different than in *Pelobates fuscus*.

In *Eopelobates* intermediate conditions prevail, so far as this can be determined in the fossil material. There is definite separation of lateral and anterior processes by emargination in *E. bayeri*, although the general configuration is more *Megophrys*like than pelobatine. The anterior process as shown in *E. guthriei* n. sp. and *E. bayeri* ossifies very little (see p. 312 and Fig. 6), and remains broad as in megophryines.



Figure 5. Pelobatine ethmoids in ventral view; a, Pelobates fuscus, MCZ 1012; b, Scaphiopus couchi, AMNH 56284; c, S. holbrooki, MCZ 25577; d, P. cultripes, UMMZ S-2730; e, P. varaldii, MCZ 31970, with ethmoid cartilage in stipple; all \times 2. Irregular line = depression; - . - . - . - = dorsal border of bony ethmoid; - . - . - . - = dorsal border of ethmoid cartilage. A = anterior process; C = capsular process; L = lateral process; P = palatine articulation surface; PM = premaxillary articulating surface.

This situation is approached in *P. varaldii* (separated from *P. cultripes* by Pasteur and Bons, 1959; Fig. 5e, this paper). A separate anterior process is not present on *E. grandis* (Fig. 7) and is not visible in the other species. In the ventral view of *E. bayeri*, a depression develops between lateral and anterior processes, reflecting a weak turbinal fold development like that of *Megophrys* and *Pelobates*, but not as distinct as in *Scaphiopus*. The ethmoid of *Macropelobates* is as in *P. cultripes*, as far as can be determined (*cf.* Figs. 7b; 5d).

In all pelobatines, the dorsal ethmoid roof of the nasal capsule is absent and the entire capsule is then roofed by the nasal (Fig. 5), but in *Megophrys* the ethmoid floor and roof are of about equal extent and the nasal provides cover for the capsules only anteriorly (Fig. 7). The extent of roofing by ethmoid in *Eopelobates* can be seen only in *E. grandis*, and is approximately as in the megophryines. In the subgenus *Spea* of *Scaphiopus*, the anterior process may become extremely large and



Figure 6. Ventral view of ethmoid of (A) Eopelobates guthriei, MCZ 3493, \times 3; (B) E. bayeri, CUPI 6.874, \times 5.5. Dashed line = restoration, dotted line = broken bone outline; P = palatine articulation; VB = boss for vomerine teeth.

flared anteriorly (e.g. S. *intermontanus*), producing the most extreme pelobatine condition.

The bony ethmoid is, of course, merely an ossified portion of the ethmoid cartilage and not coextensive with it. The cartilage itself is also quite different in the two modern subfamilies (cf. Figs. 3b, 5e) and within that cartilage, the above-noted variations in ossification occur. The retreat of the bony roof of the pelobatine ethmoid is accompanied by regression of the cartilage to a partial ring surrounding the naris and a thin, membranous cover over the main unossified part of the capsule.



Figure 7. (A) Eopelobates grandis, PU 16441, ventral view of ethmoid and vomer; (B) Macropelobates osborni, AM 6252, ventral view of ethmoid; both \times 3. Dashed line = restoration; dotted line = broken bone surface; __.___ = dorsal border of ethmoid; V = vomer; P = palatine articulation surface.



Figure 8. Eopelobates anthracinus, type, BM R-4841; left, restoration of dorsal and lateral views of skull; right, camera lucida drawing of vertebral column, posterior skull roof outline shown anteriorly; X 6.

Without the knowledge that the large rodlike anterior process is present in cartilage in *Pelobates cultripes*, the similarities of *Pelobates fuscus* and *Scaphiopus* in ethmoid construction might seem to indicate that the spadefoot genera are closely related through *P. fuscus*, but the latter is not likely to be ancestral to the North American spadefoots, as is discussed further below. *Scaphiopus holbrooki*, the most primitive member of the genus, is intermediate between *P. cultripes* (or *P. syria-cus*) and other *Scaphiopus* in this regard; *S. couchi*, *S.* (*Spea*), and *P. fuscus* have independently ossified the anterior process of the ethmoid as far anteriorly as the premaxillae.

It would be of considerable interest to study olfaction within the pelobatines; their nasal capsules indicate some strong adaptive trends not seen in the aquatic *Megophrys* and *Eopelobates*.



Figure 9. Scapulae and sternal styles of pelobatids. a, Pelobates cultripes, UMMZ S-2629; b, P. syriacus balcanicus, MCZ 50690, style only; c, Megophrys monticola, AM 23964; d, Scaphiopus couchi, MCZ 64374; e, Eopelobates hinschei, MME 6692, scapula only; f, E. grandis, PU 16441; g, E. anthracinus, BM R-4841, scapula only; h, E. bayeri, CUPI 6.874; a-g, \times 3; h, \times 4.5.

Chronological Review of Described Eopelobates

CLASS AMPHIBIA SUPERORDER LISSAMPHIBIA ORDER SALIENTIA Family Pelobatidae

Eopelobates anthracinus Parker 1929

Parker's account is good, but better knowledge of other species allows some additional discussion. In the skull, the pattern is approximately as Parker described it, but contrary to the implication of his figure, there is no process of the squamosal leading towards the frontoparietal; this is partly the result of the bone being underlain by the pterygoid and partly the result

of crushing in the area. Also, the squamosal is more hatchet-shaped posteriorly than in his figure. The frontoparietal shows prominent, well-defined pits on the lateral edges, and sculpture is more apparent laterally than medially. Because of crushing, the exact shape of the frontoparietal is difficult to determine, but it is about as indicated in Figure 8. There is a groove between the two halves of the frontoparietal that probably indicates a suture, but since all adult E. bayeri specimens appear fused, this cannot be certain. There is a complete maxillary arcade; the quadratojugal can be seen clearly on the photograph (Fig. 1), and there is a strong quadratojugal process of the maxilla. The teeth are pedicellate. The bone in the left orbit that



Figure 10. Eopelobates hinschei, MME 6692; X 3; see Table 1, 8a.

Parker thought was the dentary is actually the prearticular. The anterior tip of the parasphenoid appears to be visible near the anterior end of the left frontoparietal, but the impression is vague. In the postcranial skeleton, imprints of transverse processes on all vertebrae occur on the matrix, contrary to Parker's statement: these are long on the anterior vertebrae but short and anteriorly directed on the posterior ones (Fig. 8) in accord with other species of *Eopelobates*, *Pelobates*, and some *Megophrys*. Again contrary to Parker, the cleithrum is visible on the morphological left side.

Parker remarks (1929, p. 280) that the skull "appears to have been almost identical with that of the recent *Pelobates*." In fact, the skull differs from that of *Pelobates* and *Scaphiopus* and resembles that of other

TABLE 1 Synonymy of *Eopelobates hinschei*

Eopelobates hinschei (Kuhn)

- 1. Halleobatrachus hinschei, type, MME 1312, Kuhn, 1941, p. 353, pl. I, fig. 1.
- 2. Parabufella longipes, type, (unique specimen, no number?), ibid., p. 358, pl. 4, fig. 5.
- 3. Palaeopelobates geiseltalensis, type, MME 6695, ibid., p. 360, pl. 1, fig. 5.
- 4. Archaeopelobates efremovi, type, (no number), ibid., p. 361, pl. 3, fig. 6.
- A. eusculptus, type, MME 6728, ibid., p. 362, pl. 4, fig. 1.
- 6. Amphignathodontoides eocenicus, type, MME 6744, ibid., p. 364, pl. 6, fig. 1.
- 7. Germanobatrachus beurleni, type, MME 6719, ibid., p. 368, pl. 2, fig. 4.
- 8. The following specimens referred by Kuhn to the above genera are also referable to E. *hinschei*:
 - a. Palaeopelobates geiseltalensis, MME 6692, pl. 1, fig. 4.
 - b. P. geiseltalensis, pl. 2, fig. 5.
 - c. P. geiseltalensis, MME 6696, pl. 3, fig. 2.
 - d. P. geiseltalensis, pl. 3, fig. 7.
 - e. cf. Archaeopelobates eusculptus, pl. 2, fig. 1.
 - f. cf. A. eusculptus, MME 6762, pl. 4, fig. 3.
 - g. ?A. efremovi, MME 1572
 - h. Opisthocoelellus weigelti, pl. 4, fig. 2 (not the holotype).
 - i. O. weigelti, MME 4995, pl. 5, fig. 2 (not the holotype).

Eopelobates in having a flattened or concave skull table and in having approximately subequal orbit and temporal openings. The dermal sculpture is coarse and open, more or less as in the other European *Eopelobates*.

There is an anterior lamina on the scapula (Fig. 9). The urostyle is separate and there were two, perhaps three, post-sacral vertebrae, although crushing makes the exact number uncertain (Fig. 8).

The skull restoration of *Eopelobates* anthracinus (Fig. 8) was made from camera lucida tracings of the individual bones; the tracings were then fitted together. Since the bones were all flattened after burial, their somewhat different shape in the restoration results from curvature incorporated into the three dimensional



Figure 11. Right posterior half of pelobatid skulls, dorsal view. a, Scaphiopus h. holbrooki, MCZ 58003; b, Eopelobates guthriei, MCZ 3493; c, Pelobates fuscus, MCZ 1012; d, Megophrys lateralis, AM 23549; all \times 3. f = frontoparietal; p = prootic; s = squamosal; _____ = ____ = margin of prootic covered by squamosal; cartilage stippled.

model. The skull height (especially anteriorly) is the major feature in doubt, but as given it is approximately intermediate between the flattened skulls of Megophrys and the domed skulls of Pelobates and Scaphiopus. The bone outlines do not allow much deviation either way from the outline suggested here. There is a welldefined groove between the frontoparietals, but a distinct suture cannot be seen. The exact shape and placement of the nasals is conjectural, but the arrangement given is consistent with what remains of the bones. The photograph of the specimen (Fig. 1) does not allow confirmation of all bone outlines; this was only made possible by comparing many photographs taken with light coming from different angles and from drawings made at the time of study of the original specimen.

Eopelobates hinschei (Kuhn, 1941)

This species was originally described as *Halleobatrachus hinschei* by Kuhn (1941, p. 353) from the middle Eocene Geiseltal deposits near Halle, Germany. As Špinar (1967, p. 218) correctly pointed out, this species belongs to the Pelobatidae rather than to the Palaeobatrachidae. Much of the other material described by Kuhn also belongs to the genus *Eopelobates*. All the characters of the genus are clearly visible in this series of specimens. The photograph given here (Fig. 10) shows one of the best skulls available. Kuhn gave six generic and seven specific names to this sample, but on the basis of proportions alone, the fossils can easily be related and demonstrated as a growth series (Fig. 25). Hecht (1963, p. 23) has already commented accurately on the reliability of Kuhn's study, but contrary to Hecht, however, Spinar (1967) has shown the presence of palaeobatrachids at Geiseltal.

I think it unlikely that *Eopelobates* bayeri (Špinar, 1952) is conspecific with *E. hinschei*. As Figures 19 and 20 show, the squamosals are different, and there are proportional differences of the nasals. However, the two species are related and both have rather elongated frontoparietals, though that of *E. bayeri* is fused (Fig. 12). Their scapulae are also similar (Fig. 9e, h), as is their ratio of tibiofibula-femur to head-vertebral column length (Fig. 29). Prof. Špinar is presently studying the specimens of *E. hinschei* and *E. bayeri*, and his report will deal with this matter more fully.

Table I lists the synonymy of *Eopelo*bates hinschei as I interpret the Geiseltal remains.



Figure 12. Skull roof of (A) Eopelobates hinschei, MME 6692 (8a, Table 1), \times 4.5; (B) E. bayeri, CUPI 6.874; \times 4.8; dashed line \equiv restoration; dotted line \equiv broken bone outline.

Eopelobates bayeri Spinar 1952

As the figure shows, the late Oligocene -middle Miocene Czechoslovakian species E. bayeri has all of the characters of the genus noted above (Figs. 2, 12b). Variation may exist with respect to fusion of urostyle and sacrum; in the type specimen of E. bayeri, they appear to be separate (perhaps because of poor preservation), but in the new complete specimen are apparently fused. They are separate in E. bayeri tadpoles as in tadpoles generally. E. bayeri has a somewhat similar squamosal to E. anthracinus, but other features, such as frontoparietal shape and ratio of limb to body (Fig. 29), are different. Both species have more sculpture laterally than medially on the frontoparietal, but E. bayeri lacks the large pits seen in E. anthracinus. The two species seem quite clearly different. The Czechoslovakian

material confirms the absence of a spade, and the orientation and shape of the transverse processes is in accord with those of the other specimens of *Eopelobates*, some *Megophrys*, and *Macropelobates*.

Of special interest is the shape of the ethmoid, which is well shown on the new specimen of *Eopelobates bayeri* (cf. Figs. 2, 6). It is similar to that of *E. guthriei* n. sp. (see p. 312) but differs from that of *E. grandis.*

The exact contour of the nasals is conjectural. They have been thrust backward over the frontoparietals, and their relations to the latter in the restoration have been determined by triangulation with other skull parts and by comparison with other *Eopelobates* specimens (including the type of *E. bayeri*). On the left side of the restoration (morphological right; the specimen is an imprint), the two parts of the nasal thrust apart by crushing have been rejoined. Compensation for flattening of the nasals in preservation has been made laterally in the restoration in order to make all restorations comparable.

Eopelobates neudorfensis (Wettstein-Westersheimb, 1955) was based on disarticulated elements derived from a Middle Miocene (Helvetian) fissure filling in southern Czechoslovakia. Most of the diagnostic elements are preserved. The frontoparietal is fused except at the anterior margin and is indistinguishable from that of the new specimen of Eopelobates bayeri. The squamosal has a hatchet-shaped tympanic process as in E. bayeri and E. anthracinus (Fig. 19c). The maxilla has a strong posterior process for the quadratojugal. Urostyle and sacrum are separate. The close association of this species with E. bayeri in morphology, time, and geography indicates that it is a synonym of the latter.

Eopelobates grandis Zweifel 1956

A few additions and corrections can be made to Zweifel's excellent account of this early Oligocene North American species (Zweifel, 1956). Although the maxilla and squamosal are in firm contact, there is no contact of squamosal and frontoparietal as Zweifel indicated (1956, p. 5). The right squamosal, on which he apparently based this interpretation, has been rotated and displaced up against the frontoparietal. Normal relationships to the frontoparietal are retained by the left squamosal, as confirmed by Eopelobates anthracinus, E. bayeri, and E. guthriei n. sp. (see p. 311). The squamosal shape is more rounded than Zweifel's figure indicates, and is essentially a deeper version of the E. guthriei squamosal (cf. Figs. 19d and 20d). The frontoparietal differs from that of E. guthriei and E. anthracinus, but, except for being relatively short, it is in accord with that of other *Eopelobates* (Fig. 13a).

The quadratojugal (identified as stapes by

Zweifel) is present and is excavated for a posterior projection of the maxilla as in Megophrys. The vomer is now exposed (Fig. 7a) and is like that of Pelobates in having a rather expanded anterior wing, an almost transversely-oriented tooth row (rather than a patch), and a dorsal flange clasping the side of the ethmoid as in P. cultripes. The ethmoid is more megophryine than in any other *Eopelobates*. It is flattened and dilated anteriorly, and has prominent lateral processes that are deeply notched on their ventral surfaces for the palatines (Fig. 7a). The dorsal surface of the ethmoid is little emarginated. The order of difference from ethmoids of other Eopelobates is about the same as between those of the modern species Megophrys carinensis and M. robusta (Fig. 3). The scapula has a well-developed anterior lamina (Fig. 9f), which has a straight anterior border as in E. anthracinus.

The wide posterior extent of the nasal resembles that of E. guthriei n. sp. (see Fig. 13) and the pelobatines. This resemblance tends to link the two American species, but I believe it unnecessary to distinguish them generically. Zweifel's reference of this species to *Eopelobates* is undoubtedly correct; it is probably a distinct species because of ethmoid shape, wide frontoparietal, and rounded tympanic process of the squamosal. Hecht (1963, p. 23) has suggested that this animal is a distinct genus, but it differs no more from other Eopelobates than the Recent Megophrys carinensis differs from M. lateralis, for instance.

Eopelobates sp.

Hecht (1959, p. 131) described a megophryine sacrum from the middle Eocene Tabernacle Butte local fauna of Wyoming and correctly noted a close resemblance to *Eopelobates grandis* Zweifel. It is reasonable to refer the Tabernacle Butte specimen (AMNH 3832) to *Eopelobates* without specific designation.



Figure 13. Skull roof of (A) Eopelobates grandis, PU 16441, \times 1.8; (B) E. guthriei, MCZ 3493, \times 3. Dashed line = restoration; dotted line = broken bone outline.

Młynarski referred to *Eopelobates* sp. material from the Pliocene of Poland. The specimens consist only of sacra having separate urostyles. Other fused sacra and urostyles and characteristic skull elements he referred to Pelobates cf. fuscus. Since, however, Eopelobates is otherwise unknown later than middle Miocene, and since *Pelobates cultripes* often has partially or completely separated urostyles, it seems unlikely that *Eopelobates* is represented in the Polish material, at least in the absence of characteristic skull elements. These elements may be referable to Miopelobates (see below). Since the salamander Andrias is now known to occur in the European Pliocene (Westphal, 1967) there is no apparent reason why Eopelobates might not also have persisted, but at present there is insufficient reason to confirm its extension beyond the middle Miocene.

Description of New Material of Eopelobates

Eopelobates guthriei, n. sp.

Type: MCZ 3493, nearly complete skull and associated fragmentary scapula.

Diagnosis: Differs from other species of *Eopelobates* in having a narrow tympanic process of the squamosal combined with a triple emargination of the frontoparietal margins and a relatively short skull.

Etymology: Patronym for Dr. Daniel Guthrie, who collected the unique specimen in 1962.

Locality: NE 1/4, SE 1/4, Sect. 16, T 39 N, R 90 W, Fremont County, Wyoming.

Horizon: Upper part of the Lysite member, Wind River Formation.

Age: Early Eocene (Lysitean, late Sparnacian equivalent).

Preservation: Only the skull, portions of the prearticular region of the jaws, and an associated fragment of left scapula are present (Fig. 14). The slightly crushed skull is well preserved on the right side, but on the left the temporal region is missing. The premaxillae, the anterior portions of the nasals, and the anterior part of both maxillae are missing.

Although the skull is slightly flattened, distortion is limited for the most part to the peripheral tooth-bearing and temporal bones. The ventral borders of the maxillae



Estes, Richard. 1970. "New fossil pelobatid frogs and a review of the genus Eopelobates." *Bulletin of the Museum of Comparative Zoology at Harvard College* 139, 293–339.

View This Item Online: <u>https://www.biodiversitylibrary.org/item/25014</u> Permalink: <u>https://www.biodiversitylibrary.org/partpdf/31380</u>

Holding Institution Harvard University, Museum of Comparative Zoology, Ernst Mayr Library

Sponsored by Harvard University, Museum of Comparative Zoology, Ernst Mayr Library

Copyright & Reuse Copyright Status: In copyright. Digitized with the permission of the rights holder. License: <u>http://creativecommons.org/licenses/by-nc-sa/3.0/</u> Rights: <u>https://biodiversitylibrary.org/permissions</u>

This document was created from content at the **Biodiversity Heritage Library**, the world's largest open access digital library for biodiversity literature and archives. Visit BHL at https://www.biodiversitylibrary.org.