OUTLINE GUIDE TO THE CLASSIFICATION AND EVOLUTION OF
LEPIDOSAURS by ROGER MEEK

One of the problems in attempting an article on classification or evolution is the amount
of controversy that exists as to whether one group of animals is related to another, or
whether one is an ancestor of a related type. Not least amongst these is the status of the
Lepidosauria as a sub-class. Colbert in his 'Evolution of the Vertebrates' proposes that
they be regarded as infraclass allied with the infraclass Archosauria to form the sub class
Archosauria. However, other workers, notably Romer, argue that there is no such close
relationship (particularly from the fact that they are both reptiles) exists between the two,
and that the Diapsid condition, commonly shared by them is a result of convergence
rather than a direct relationship. He therefore differs from the long-held belief that
both groups have arisen from early Eusuchian ancestors, saying that the Archosauria
already developed the beginnings of a Diapsid condition. Reviewing both theories I
propose to follow Romer and regard the Lepidosauria as a sub class of the Reptilia.

Lepidosauria then are a sub-class of the Reptilia which contain three recognised orders,
the Eusuchia, the oldest and most primitive of the three, the Rhynchocephalia abundant
during past ages, but today represented by one living form the well known Tuatara
(Sphenodon punctatus) and the Squamata with two sub orders the Sauria (lizards) and
Serpentes (snakes).

All reptiles past and present can be divided into four main types using the skull condition
as a basis. The criteria for these divisions is the presence of positions of temporal fenestra
of vacuities in relation to the postorbital and squamosal bones. The purpose of these
fenestrae is to give room for additional jaw musculature allowing greater pressure to be
applied when closing the mouth.

In the earliest reptiles, the Cotylosaurs, there are no fenestrae and with the Orders
Chelonia (turtles, tortoises etc) and Mesosauria (extinct) these reptiles are termed Anapsid.
Following this is the Synapsid condition found in two orders now extinct, the Polycsauria
and Therapsida in these there is a single temporal fenestrae bound above by the post-
orbital and squamosal bones. The third condition, Eurypapsid is found in four reptilian orders
all extinct, these are the Protorosaurus, Sauropeterygia (marine) Placodontia (Marine) and
Ichthyosaurus (marine) in these reptiles there is a single temporal fenestrae bounded below
by the post orbital squamosal bones. Lastly, the diapsid condition found in no less than
eight orders of reptiles. With the three orders of Lepidosauria, all the members of the sub
class Archosauria (Ruling Reptiles) show this condition. These are the Theropodia,
Protosaurus, Crocodilia, Ornithischia and Saurischia. In these there are two temporal
fenestrae one above the post orbital squamosal one below the post orbital squamosal.

Lepidosauria then are diapsid reptiles, although as we shall see in one order of this group
the Squamata, there have been certain modifications to this condition. However, if
the evolution of the skull condition in the Rhynchocephalia and Squamata are to be
understood, then it is necessary to begin these notes with the most primitive of the orders,
the Eusuchia.

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The history of the Eusuchia, stretches back some 230 million years into geological time to the Permian Period. At this time the first of the four Geological Periods, which make up the 'Age of Reptiles', the first Diapsid reptiles in the form of Eusuchians make their appearance. One of these early forms was Youngina (see fig 2). In this reptile the skull, as would be expected is comparatively primitive. In addition to the usual marginal teeth, there was also present a set of teeth on the palatal bones. The primitive nature of the Youngina can be seen in the lower fenestra by the Squamosal and Quadratojugal. The pineal eye was present and at the back of the skull there were bones that had been retained from their Cynosaursian ancestors. However, Youngina is a true Diapsid, and it was from forms similar to this that the other Lepidosauriforms arose.

During the early Triassic are found more advanced forms of the Eusuchia amongst these is one known as Proacerta (see fig. 3). Proacerta differs from Basal Eusuchians in that the lower temporal arch is much reduced. Moreover, the Squamosal which in Youngina tappped downwards over the quadrate has also undergone a marked reduction in size. The effect of these developments are that the quadrate has freed itself from the lower bar giving potentialities of an increased jaw scope. Furthermore, certain bone elements absent in lizards have in Proacerta undergone notable reduction. These developments in Proacerta point it in an evolutionary direction towards lizards. However, with the advent of these features the problem of classification arises.

Mainly, is Proacerta an advanced Eusuchian or a primitive lizard? Romer and Robinson propose that only those reptiles in which a fully moveable quadrate has been evolved should be classified as lizards. Using this criteria, Proacerta and its allies should be regarded as Eusuchians. Lastly, mention must be made of the Champsaurs, a family of reptiles which stretched Eusuchian history into early Tertiary times. These Lepidosaurus were remarkable for their resemblance to long nosed crocodiles, and indeed, it would seem they lived alongside and competed with the surviving Archaeosaurs. In the Champsaurs skull, apart from the elongation of the snout region, the temporal region is greatly expanded possibly to allow for stronger jaw muscles, further, unlike, most other Lepidosaurus the teeth are set in sockets, rather than the typical pleurodont-acrodont dentition found in subclass. The Champsaurs are another examples of the remarkable adaptability and diversity that the Lepidosaurus have shown throughout their history. With the extinction of the Champsaurs, we come to the end of Eusuchian history.

Developing from Youngina-like Eusuchians during the lower Triassic, the Rhynchocephalians rose in the mid Triassic to become a major element of the fauna. Since then, however, they have dwindled in numbers and importance. Today only one form survives, Sphenodon Punctatus, living in isolated populations on islands off the coast of New Zealand. The most prominent family of this group were
the Rhynchosaur, variants from the typical Rhynchocephalian condition. The Rhynchosaur were large reptiles up to the size of a cow and seem to have been specialised for a diet of hard shelled fruits abundant at that time. The skull was broad and massive and on the maxillary bones a formidable battery of crushing teeth were present. However, it is in forms of which Sphenodon is a typical example that generalised diagnostic features of the whole order can be seen.

The Rhynchocephalians or beak-heads, are so named for the peculiar development of the premaxillary bones which have a downward projection over the front of the dentary on the lower jaw, the general condition however is similar to that of the Eosuchia. The true diapsid form is still retained with the quadratojugal still present and there is also a well developed pineal eye in the skull roof. It differs from Eosuchians in mainly the presence of the 'beak' and a specialised acrodont dentition. Furthermore, the supratemporal, tabular and lacrimal bones have disappeared giving a degree of bone consolidation. Sphenodon itself seems to be a persistent survivor from the Jurassic.

It can be seen then that while the Rhynchocephalians may be morphologically intermediate between Eusuchians and the Squamata, they are not in linear descent with each other. Rather the Rhynchocephalians and Squamata are separate evolutionary offshoots from different Eusuchian stock.

The most abundant Lepidosaurus today are the lizards and snakes which make up the order Squamata. During the Mesozoic when they first appeared, they rapidly (geologically speaking) established themselves in a variety of ecological niches, probably at the expense of their fellow Lepidosaurus. Indeed, it would seem that the decline of these related orders has been brought about by the morphologically more advanced lizards.

Their adaptability can be seen in the success of the group under the intense ecological pressure exerted by the Archosaurs, the ruling reptiles who dominated the Mesozoic and the endothermic mammals who inherited the earth from the reptiles at the end of the Mesozoic and have been the major element of the land faunas to the present day. Indeed, there seems to be more species of lizards and snakes alive today than at any time in the past.

Most Paleontologists agree that the success of the Squamata has been the result of the remarkable modifications to the basic diapsid skull structure.

The lizards appear in Triassic times as small reptiles in which the skull has lost the quadratojugal and lower temporal bar. This has resulted in the quadrate becoming freely movable swinging back and forward on its contact with the squamosal, consequently the lower jaw can then be opened by pivoting at the quadrate-articular junction, then dropped further by retraction of the quadrate on its squamosal junction.
FIG 1

Diagrammatic side views of reptilian skulls to show divisions based on temporal fenestra position in relation to postorbital-squamosal bones;

(A) Anapsid - no temporal fenestra;

(B) Synapsid, a single temporal fenestra bound above by the postorbital-squamosal;

(C) Euryapsid, a single temporal fenestra bound below by the post orbital-squamosal

(D) Diapsid, two temporal fenestra one above the post orbital-squamosal, one below the post orbital squamosal. All the three orders of Lepidosaurus show the Diapsid condition.

FIG 2

Skull of Youngina a primitive Eosuchian from the upper permian of South Africa showing the true diapsid condition.

FIG 3

Skull of Prolacerta a progressive Eosuchian from the early Triassic of South Africa. In this reptile features antecedent to that of the lizards can be seen. In addition to the reduction of the Quadratojugal (absent in lizards), a gap has formed at the base of the Quadrate and Jugal bones, thus giving the Quadrate potentialities of freedom of movement (as in lizards).
FIG 4

Side view of the skull of Kuehneosaurus, an early lizard from the upper Triassic. Kuehneosaurus is classed as a lizard on the basis that the lower temporal bar and quadratojugal have disappeared. The quadratojugal fits into a rounded depression in the squamosal enabling it to swing to and fro on that junction.

FIG 5

Side view of the skull of a python, a primitive living snake. The relatively heavy skull with its short quadrates and teeth on the premaxillary are characteristic of early members of the sub order.

FIG 6

Diagrammatic drawings of side views of Lepidosaur skulls to show stages in the evolution of the sub class. (A) Primitive type with the quadrates tightly united to the squamosal and both temporal bars present. (B) Condition found in lizards. The lower temporal bar has gone leaving the quadrates freely moveable on its squamosal junction. (C) Condition found in snakes. The upper temporal bar has also gone and bone reduction has occurred over the whole skull area.

FIG 7

Side view of the skull of the pit-viper Crotalus, an advanced snake. In addition to the elongation of the quadrates, these forms have reduced the maxillary to a nodule which bears only the venom conducting teeth. The maxillary is movable allowing the fangs to be folded against the roof of the mouth, thus they can be greatly lengthened.
Further refinements were brought about by a loosening of the bone attachments in the skull thus aiding the animal to swallow larger prey.

In many specialised lizards the temporal fenestra is greatly reduced, or in some cases absent altogether. In the Amphibianidae these highly specialised burrowing lizards not only has the temporal fenestra been lost, but the characteristic mobility of the skull roof has also been abandoned. In addition to this, the brain, by expansion of the parietal and frontal bones has been fully enclosed.

The Squamosal which as a progressive feature in lizards has undergone reduction has in the Amphibianidae disappeared altogether. In contrast with Triassic lizards, Iguanodon, Kuenringsaurus etc. which had a cup-shaped depression in the squamosal for the attachment of the quadrate, the squamosal of the more recent forms is a peg-like element which fits into a notch in the quadrate and by a dorsal process that abuts the skull roof. In the more advanced families the dorsal process is lost and the squamosal is represented by a narrow bar. With the Amphibianidae, the Goodeos and Helodermis have carried the whole process further by a reduction of the squamosal to its end point - that is to say the condition where it no longer exists.

The skull of the Sauria is further characterised by a condition known as Kinesis. A process in which various bones are connected by cartilage. This allows for the independent movement of large areas of the skull and it is known that lizards when feeding involve the kinetic process to a large degree although this is more apparent in snakes.

Morphologically lizards can be divided into four major groups. The most primitive being those that form the infraorder Iguania. The family Iguanidae are mostly new world reptiles and fossil forms are known as early as the Jurassic. The family Agamidae are the old world counterparts of the Iguanidae and are probably derived from them. The Chameleonidae are also old world forms and seem to be specialised off-shoots from the Agamid stem, this event occurring some time during the early Cretaceous. Judging from the fossil record the Iguanids were once widely distributed in the old world, but were seemingly replaced by their descendants the Agamids around Miocene times. However, relics of the Iguanid stock can still be found on the island of Madagascar.

The primitive nature of the skull of the Iguania can be seen in its resemblance to that of the advanced Eocarchian Prolacerta, in which the lower temporal bar has separated due to a retreat of the jugal. In a typical Iguanid the skull is high and laterally compressed and the remaining temporal fenestra is greatly enlarged. There is, however, a contrast in dental arrangements with the infra order. In the Iguania the dentition is pleurodont, that is, the teeth are fused to the inner surface of the jaw bones, while in the old world Agamidae and Chameleonidae, the condition is acrodont, that is, fused to the surface of the jaw bone. Furthermore, the Agamidae show a parallelism to the mammals in that the teeth can be divided into incisors, canines and molars.

Competing with the Iguania for the position of most primitive forms are the two families of the Gekkota - the Gekkonidae and the snake-like Pygopodidae. The skull of the Gekkota is more flattened than that of the Iguanids, and differs in having undergone a great deal of bone reduction. The upper temporal bar has, in most forms, disappeared
as have also the postorbital, squamosal, lacrimal and supra orbital bones - moreover, the
ejugal which in some forms has undergone a reduction, has in others become rudimentary.
In typical Gekkos the dentition is pleurodont, however, in the Australian Pygopods,
which seem to be specialised, derivatives from the main line of Gekko evolution, the
teeth are recurved and seated in sockets, a condition known as subpleurodont.

The reptiles which can be appropriately termed 'middle lizards' are those families
that form the infra order Skincomorpha. Composed of the families Xantusiidae
Teiidae, Skinkidae, Lacertidae, Cordylidae and Dibamidae they seem to be inter-
mediate between the primitive Iguanidae and Gekko on one hand and the advanced
Diplaglossine lizards on the other.

The skincomorpha have their origins in the genera Archaeosaurus from the upper Jurassic
of Europe, which when viewed from the temporal region of the skull seem to have been
primitive members of the group. In typical Skincomorpha the lacrimal is either absent
or fused with the prefrontal. The temporal fenestra is in all but one family, closed. In
many forms the postorbital and postfrontal bones are fused to form a single element.
Although in some forms the postorbital may be absent. The Teiidae alone amongst the
Skincomorpha have the upper temporal fenestra normally developed, that is the region
is open. In the Xantusiidae and Cordylidae it is closed by the union of the Squamosal, post
orbital and parietal bones. In the Skinkidae and Lacertidae it is roofed by a backward
growth of the postfrontal. Osteoderms which in the lacertidae and cordylidae are well
developed are in skinks hardly present at all. The dibamidae differ from other Skincomorpha
in reduction of kinetic movement over the whole skull area. Plus the absence of the post-
orbital, squamosal, supraorbital and jugal bone. The old world lacertids and new world
tellids are so alike superficially that it is difficult to distinguish between them. A method
used by many workers is based on the condition of the skull roof. In tellids the head shields
are loosely connected with the skull bones whereas in Lacertids, the head shield are under-
lain by bony elements, which in turn are fused to the bones of the skull roof. These
features plus the normal development of the temporal region of the skull, suggest that the
tellids are the most primitive of the Skincomorpha and may lie close to the basal stock from
which the other families arose. The Xantusiidae however are problematical whereas the skull
shows a large measure of bone consolidation and is therefore regarded as progressive,
the vertbral characters of the body are primitive.

The lizard families that form the infraorder Diplaglossa, in many ways show intermediate
structures between typical lizards and primitive snakes. Composed of two superfamilies,
the Anguinaidea and Varanidea, they are the most advanced of the sub-order. The
Anguinaidea seem to be the more primitive of the two, having their origins in the Cretaceous.
At this time relatively advanced forms were already present and it may be that the groups
history stretches back much further, possibly into the Jurassic. Amongst these early forms
from the Cretaceous were the Placosaurines, lizards with well developed limbs and heavily
covered in osteoderms. They inhabited both the old and new world continents, reaching
their peak during Eocene times then, their distribution reduced to North America by the
Oligocene, became extinct by the end of that period. Present day forms such as
Ophisaurus the 'Glass Snake' appeared during the Oligocene in Europe. Anguis the
'slow worm' appeared during the Miocene also in Europe.

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In typical Anguoids the temporal fenestra is usually retained, although in some forms it is roofed by Osteoderms. Osteoderms are a major characteristic of Anguoids, generally being present on both head and body. In the skull the frontal bones send out descending flanges which partly enclose the brain but never meet below it. The jaws are solidly constructed never showing the development of the joint found in Varanoids. The dentition is Pleurodont, the teeth in addition to the normal marginals are usually present on the palatal bones. The family Anniellidae differ from other Anguoids in that the skull bones are tightly united, with the brain-case much enlarged. Further, unlike other members of the Anguidea the frontals meet below the brain, enclosing it. It would seem then that the Anniellidae are a divergent off-shoot from the main Anguoid stock, convergent to the Amphisbaenids. Typical Anguoids are themselves of Skin cosmorphic origin.

Derived from Anguoids, the Varanoidea are the super-family which contain such notable families as the Monitors (Varanus), the venomous Helodermas and the extinct Marine Lizards, the Mosasours. Appearing during the early Cretaceous in the form of Aigialosaurs, they became, during the upper Cretaceous a prominent reptile group. Amongst all lizard families the Varanoidea show a tendency towards gigantism. Some mosasaurs grew to lengths of up to 40 feet, while several fossil monitors (Varanus and Megalania) exceeded 15 feet. One family, the Paleophiidae from the Cretaceous and Eocene, were limbless and may have been closely related to the ancestral snakes.

The skull of these lizards is usually long and slender with elongate external nares. The temporal fenestra is, in most cases, normally developed with the frontals meeting ventrally below the olfactory bulb. The lower jaw has developed a joint in midline, although the degree of development varies within families. In Helodermas it is primitively present on the outer surface only. The Mosasours showing it as its most advanced stage. Osteoderms are in the most advanced families absent, but are present on head and body of Helodermas. The dentition is Pleurodont, with teeth in some forms being present on the palatal bones. In Mosasours however, the condition is subthecodont, the teeth in these lizards being lodged in shallow pits (alveoli). From this it would seem that the Helodermas are the most primitive of the Group, branching off from ancestral forms at an early stage in the groups history.

The Amphisbaenids conclude this review of the lizards. It has been suggested by many workers that this family, based on the many modifications to the skull which are a result of the burrowing habits of these lizards, should be given the status of suborder. The skull bones are tightly united with the resultant loss of kineticism, the temporal fenestra has gone as are the postfrontal, postorbital (usually), Squamosal, Supratemporal and Jugal (usually). Furthermore, there has undergone a great deal of fusion between bone elements. Dentition is usually Pleurodont, although in one family the Crocodiles the condition is Acrodont, there are no palatal teeth. Developments of the parietal and frontal bones completely encloses the brain. Although an early form from the Eocene is known the history and origins of the Amphisbaenids are obscure. Because of the highly modified structure of the skull, no relationships with any other lizard family can be established.
Derived from the lizards sometime during the Jurassic-Cretaceous transition. The snakes are the last Lepidosauria and indeed the last of all reptiles to evolve. In form and structure the snakes do not exhibit the diversity that can be seen in lizards. However other features, namely the evolution of venom conducting teeth and constriction to overcome their prey, are unique amongst the vertebrates. The origins of snakes are obscure, many workers classify the Paleophidae from the early Cretaceous as the first members of the sub order (Chudinov, Hoffstetter and Tatarinov), although Romer points to the varanoid nature of the remains of these reptiles. Therefore, it would be that the Paleophidae are a specialised group of varanoid lizards, paralleling the early snakes rather than ancestral to them. Yet many morphological features found in the varanoid lizards foreshadow or resemble those found in snakes, and some workers (McDowel and Bogert) believe in a varanoid ancestry for the snakes. However, G.L. Walls in his research on the Ophidian Eye has shown that this organ differs in many important ways from the eyes of lizards and thus, snakes could not have originated from lizards similar to those living today. He proposes that the snake eye with its tinted lens and unique retinal cells is the result of changes in the unusual history of these animals. He believes that snakes for the early part of their career lived a life underground. He goes on to say that here their eyes degenerated almost to the point where they were non-existent then they re-emerged on the surface and redeveloped their eyes from the parts that were left and that once visual efficiency had been regained they radiated into the many forms found today. Romer adds to this, he feels that all the snakes from the Cretaceous were fossorial and that the re-emergence to the surface took place during the early tertiary. Bellairs reviewing the arguments believes that the ancestors of snakes when they are found are likely to be lizards of Jurassic times belonging to varanoid stock and modified for burrowing.

If Walls and Romer are correct in their assumptions of early snake developments and history, why did snakes for the 65 million years of Cretaceous history live a fossorial life? Could it have been that the first snakes as primitive limbless predators, were unable to compete with the small agile carnivorous dinosaurs, so successful at that time, and that while these reptiles were dominant the snakes had to be content with their subterranean existence.

The Cretaceous was the time when the Archosaurian reptiles were at the pinnacle of their career and snakes would not have been alone in being unable to compete. Other reptiles were also under pressure, some had taken to living a marine life others had remained small, while the turtles survived by clinging conservatively to their early innovations in body armour. Even the mammals had only survived by living in the undergrowth, snakes survived by living underground.

Whatever the nature of the causes of the unusual structure and early history of the snakes, it is clear that the Eocene a typical serpent condition had been achieved. From rocks of this age, two large forms Gigantophis Garstoni and Madsolda Bat are known (the former estimated at nearly 60 ft). The known remains of these reptiles
are of a boid-like nature and this had led some workers to believe that they belonged to the early stock from which the modern boas and pythons have arisen. Remains of the higher snakes (Colubridae) are not known until the Miocene. Those of the Elapidae and Viperidae forms which synthesize venom for delivery through modified teeth at the front of the mouth are also known from the Miocene. Certain differences in structure between these advanced types and boid like forms suggest that snakes may have evolved in part from lizards. Indeed some workers suggest a polychyletic origin from the lizards with the Typhlopidae as a third radiation. Therefore it may be that the snakes as a group represent a structural rather than a natural grade in reptilian organisation.

The rise of the venomous snakes during the Miocene coincides with the upheavals within the mammalian class occurring at that time. Whole orders of these vertebrates were undergoing extinction and were being replaced by more advanced forms with larger brains. It seems likely then that the upgrading in serpentine organisation was a progressive response to the new ecological conditions of those days.

In common with all other reptile groups, the major diagnostic features of snakes are to be found in the skull. Although snakes are diapsids the cranial skeleton is a highly mobile structure developed to overcome certain mechanical problems resulting from their unusual feeding patterns. To attain this increased mobility the snake skull has lost the upper temporal bar which bounded the remaining temporal fenestra in lizards. Also gone are the lacrimal, postfrontal, squamosal and jugal bones. Thus the quadrates is now an elongate element lying forward on the skull roof, there joined to the supra temporal and with the pterygoid on the palate by fibrous tissue. The resultant condition being that a forward movement of the lower end of this element greatly increases the gape. In addition, the palatal bones have freed themselves from the braincase, that element now a fully enclosed structure by ventral expansion of the frontals and parietals. In advanced snakes there is no premaxilla-maxilla contact. The maxilla in the Viperidae being a mobile element for fang movement. The lower jaws are also modified. Similar to the condition found in Mosasaurs, the two anterior ends of the lower jaws are connected only by ligament bonds with the dentary moveable on the posterior jaw bones. Dentition is acrodont, the teeth always recurved, with some higher forms showing modifications in the form of grooves, or closed channels for the passage of venom. From the osteological characteristics of the skull, snakes can be shown to form a threefold division on a super family level (Romer) The Boidea, primitive forms including the Boas and Pythons. The Colubroidea, advanced forms amongst whom the familiar grass snakes, ratsnakes, cobras and vipers are found, and lastly the Typhlopidae 5, specialised borrowing types of unsure relationships.

The Typhlopidae seem to represent a group of snakes that have retained the fossorial habits of the ancestral forms. Indeed, the structure of these reptiles is highly modified for this end. In the skull, the various bone elements are solidly united, with the dentary and maxilla bearing only a few teeth, with no teeth at all being present on the palatal bones. The supratemporal is usually
absent or at best a rudimentary element. In contrast with higher snakes the quadrate slants forward ventrally. Vestiges of the pelvic girdle are usually present. The earliest known forms (Typhlops) are from the Eocene of Europe.

In conjunction with the Columbroidea the Boaidea probably represent a series of radiations to the surface which took place at the end of the Cretaceous. However, some members of the Boaidea still live a fossorial life, although they are not as specialised as members of the Typhlopidae for this purpose. Amongst the Boaidea are the largest living snakes past and present. Most forms are constrictors, some feeding on fairly large prey. The skull in these snakes is comparatively primitive in a general way showing relationships with the varanoid lizards. The quadrate lies vertically being a much shorter element than that of the Columbroidea, with the pterygoid extending back to meet it. The supratemporal is usually present, as is the supraorbital in primitive forms and the premaxilla sometimes articulates with the maxilla. A formidable dentition is present on the dentary, maxilla, premaxilla, palatine and pterygoids, although in the most advanced types there are none present on the premaxilla. The tail is short and vestiges of hind limbs and a pelvic girdle are usually present. The most primitive of the three families which make up the superfamily is the single fossil form Dinilysia (Dinilysiidae) from the upper Cretaceous which seems to be the oldest definite snake. The family Aniliidae contains the new world 'Python' Loxocamus which based on the presence of the supraorbital bone, seems to represent a transitional stage between the Aniliidae and the Pythons (Pythonidae). The most advanced family are the Boidea (Pythons, Boas, Anacondas) amongst whom the Boaidea (Boas and Anacondas) show progressive features, such as the loss of the supraorbital and the premaxillary teeth. Furthermore, the prefrontals are in contact with each other, with the palatines reduced. These features are not found in the Pythonidae.

The rise of the colubrid snakes and their derivatives during the Miocene was an important chapter in the history of snakes. Today they constitute the vast majority of snake forms, being found on almost every continent. Genera abundant today, coluber, elaphe and thamnophis, existed at that time. The Heterodon and Malpolon genera appeared during the Pliocene other forms Drymarchon, Natrix, Pityophis and Ptyas arose in the Pleistocene. However, the majority of remaining genera are of recent date, suggesting that these snakes are still undergoing evolutionary radiations.

The family Colubridae is the largest of snakes families containing a host of non-venomous (aglyphous) forms in addition to a large number of venomous back fanged (opisthoglyphous) types. The Colubrid skull has lost the coronoid bone normally found in the lower jaw of booids. This being a major feature of their classification. However, other features mainly in the development of a more flexible structure have taken place. There is no contact between the premaxillary-maxillary or prefrontal-nasal bones and the maxillary is a movable element on the prefrontal. Areas of flexibility have also occurred between the supratemporal and the braincase and between the braincase and the palatal bones. Numerous teeth are usually present on
the maxillary and dentary and also on the palate, but never on the premaxillary. No trace of a pelvic girdle remains.

Much debate has taken place on the classification of the colubrid snakes indeed as yet no definite conclusions have been arrived at. The Opisthoglyphous snakes, mostly grouped together as a sub-family - The boidinae were once believed to have formed a natural grouping. Now however they are seen to represent an artificial assemblage and that this dental condition has evolved independently on a number of occasions. Morphologically the colubrids are the logical outcome of a progressive boid evolutionary trend, yet some workers doubt this validity of a boid ancestry for these forms, feeling that they may have arisen from some obscure lizard forms independent of the booids. The family Elapidae (cobras, Mambas, coral snakes, Kraits etc) contain all those forms which show the proteroglyphous condition in fangs, structure, that is - fixed venom conducting teeth at the front of the upper jaw. Basically they are structurally similar to the Colubridae, differing in that the maxillary is a much shortened element bearing the large venom conducting fangs, followed by only a few smaller normal teeth. However the sub-family Dendroaspinae (Mambas) differ in that apart from the fangs, no other teeth are present on the maxillary, which is a longer element than that of other members of the Elapidae. Moreover, there is on the dentary a large anterior tooth. These features have led to the suggestion by some workers that the Dendroaspinae be elevated to the rank of family, distinct from the elapidae. The elapid snakes may have developed from Opisthoglyphous Colubrids by the loss of the anterior portion of the maxillary, this bringing to the fore the grooved teeth of these forms, which then developed as the enclosed fangs of the elapidae. Only one fossil elapid is known, that of Cobra (Naja) from the Miocene of Europe and Pliocene of Asia.

The family Hydrophidae (sea snakes) show strong resemblances to the elapids and differ only in the condition of the spinal structure, there developments have taken place as an adaptation for swimming. The close relationships to the elapids suggest that they may have a common ancestry but that they split from one another early in their history. The family Viperidae (vipers and pit vipers) have taken the evolution of the venom apparatus to its end point. The skull is similar to that of the elapidae but has a higher appearance. It is in the condition of the maxillary bone that the major diagnostic feature is found. In the Viperidae the maxillary has been reduced to a nodule which bears only the venom conducting teeth and its replacements (solenoglyph). Furthermore, it is a movable element and under control from movements of the ectopterygoid, pterygoid, palatine complex. Movements of these elements can either erect the fangs or fold them, against the roof of the mouth when not in use. In addition, each side of the jaw is independent of the other as herpetologists who have had experience with these reptiles will know. The chemical make-up of the venom is another major difference between the elapidae and viperidae, the former producing mainly a neurotoxic type, the latter mainly of hemotoxic content. The sub-family Crotalinae (rattlesnakes, bushmasters and lance-heads) differ from the sub-family Viperinae only in that the maxillary is hollowed to house the amazing heat sensory device.
The Viperidae are the end point in Lepidosaurian evolution and are presumably the last family to evolve; fossils are reported from the Miocene of Europe from where they presumably spread to Asia and there gave rise to the pit vipers (crotalinae) who in turn spread to the New World. Rattlesnakes and their relations are known from the Pliocene onwards on that continent. From the osteological features it would seem that the Viperidae are derived from the Elapidae. However, studies on the musculature of the skulls show that this is not so. It would appear from this research that both groups have arisen independently from one another from the Colubridae.

NOTES TO THE TEXT

1. Initially, Watson attempted to show that the Millerettid Cotylosaurs had fathered the whole Diapsid assemblage, based on the condition of the quadrate and its attachment to the squamosal, which was similar to that of the early Archosaurs and Lepidosausrs and also on the presence of a single temporal fenestra below the post-orbital squamosal. He believed that in view of the generalised nature of the skull, the appearance of a second fenestra above the post-orbital squamosal would have transformed it into an early Diapsid type. Romer has since shown that the condition or absence of an otic notch may be decisive. An Otic Notch was present in Millerettiids and early Lepidosausrs and this probably does all these reptiles. However, although all later Archosaurs have an Otic notch, it is not present in earlier forms (Chasmatosaurus etc.) therefore, it is impossible for the Archosaurs to have arisen from the Millerettiids.

2. Tatarinov has upgraded these two suborders of the Squamata to ordinal rank. Hoffstetter followed this view but also raised the Amphisbaenids to ordinal status. Later however, he reversed his earlier views and downgraded them to three suborders - Sauria, Serpentes and Amphisbaenidae. I have followed Romer in his original classification as two suborders - Sauria and Serpentes. However he later felt that he may have been over conservative in this and should have given them ordinal status.

3. Chelonians show this condition in modified form, that is emarginations have developed from the posterior region of the skull.

4. Piveteau has also classified them in this manner, but Tatarinov regards them as primitive lizards.

5. Hoffstetter and Tatarinov have retained the views of earlier workers and retained these reptiles on the basis of the dental condition, as members of the Archosauira. However, others believe that this is a result of retention of a primitive condition (a socketed dental condition was present in Youngina and its allies). I have followed the latter view.
6. Earlier workers classified the Helodermas on the presence of Osteoderms as advanced Anquoids.

7. Although of a somewhat later date during this period than the Colubridae.

8. Formed by two families the Typhloidae and Leptotyphloidae (Romer).

**ABBREVIATIONS TO DRAWINGS**

(Skull)

<table>
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<th>SQ</th>
<th>Squamosal</th>
<th>PO</th>
<th>Postorbital</th>
<th>J</th>
<th>Jugal</th>
<th>ST</th>
<th>Supratemporal</th>
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<tr>
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<td>Frontal</td>
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<td>Prefrontal</td>
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<tr>
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(Lower Jaw)

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<td>Surangular</td>
<td>C</td>
<td>Coronoid</td>
<td>PL</td>
<td>Palatine</td>
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</tbody>
</table>

Drawings by A.J. Rowell-Burton.

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