

Biology 356 - Major Features of Vertebrate Evolution

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Permo-Carb. Synapsids

Paleozoic synapsids (also called mammal-like reptiles, pelycosaurs and early therapsids) occupy a central position in amniote evolution. Paleozoic synapsids include some of the oldest known amniotes, and their fossil remains record the earliest successful adaptations of terrestrial vertebrates to herbivorous and active predatory modes of life. During the Paleozoic synapsids diversified greatly and became the most conspicuous terrestrial vertebrates of their time. Although both pelycosaurs and early therapsids are paraphyletic taxa at the base of the clade that includes advanced therapsids and mammals, these Paleozoic reptiles have played a pivotal role in considerations of synapsid evolution, including the origin of mammals. Recent cladistic analyses have shown that the synapsid clade (pelycosaurs, therapsids and mammals) is the sister taxon of all other amniotes. Thus, an understanding of pelycosaurian evolution has implications to many broad problems of amniote evolution, including the origin and interrelationships of all higher vertebrates.

The oldest known mammal-like reptiles have been found in sediments of Early and Middle Pennsylvanian age in Nova Scotia. The remains of Protoclepsydraps haplous, retrieved from upright Sigillaria stumps from Joggins, Nova Scotia (Reisz 1972) are too fragmentary to provide any useful information; even the identification of these remains as a pelycosaur has been questioned (Reisz 1986, Reisz and Modesto 1996). By the Late Pennsylvanian pelycosaurs become the most common amniotes in North American sediments. The fossil record of this group is most extensive during the Early Permian, representing nearly 70 percent of all amniote finds of this time; by the Late Permian, however, pelycosaurs disappear from the fossil record. Instead, the early therapsids become the most diverse and common amniotes.

Pelycosaurs have been distinguished from other synapsids mainly on geological and geographical grounds. Although easily recognizable, and readily separated from more advanced synapsids, pelycosaurs represents a paraphyletic grade of basal synapsids that includes the ancestors of advanced synapsids (therapsids and mammals). Nevertheless, it is worth discussing pelycosaurs as a group because they represent a major adaptive radiation that dominated the terrestrial landscape during the Late Pennsylvanian and Early Permian, and were replaced by the much more advanced therapsids only in the Late Permian. As primitive synapsids, pelycosaurs are characterized by the presence of an anteriorly inclined plate-like occiput, the small posttemporal fenestra is bordered by the supraoccipital, tabular, and opisthotic bones; the lateral temporal fenestra bordered is by jugal, squamosal and postorbital bones, the pillar-like septomaxilla has a broad base that straddles the maxilla-premaxillary suture. Pelycosaurs retain a number of features that appear in the derived condition in all other

amniotes, including therapsids. These features include the presence of broad, plate-like supratemporals on the dorsal surface of the skull, large tabulars, two coronoids on the lower jaw, and a medial centrate in the pes.

Recent phylogenetic studies of pelycosaurs have proposed that within this group six major clades (families) can be recognized: small insectivores (Eothyrididae), two different types of large, bulky herbivores (Caseidae and Edaphosauridae), and three different types of medium to large-sized carnivores (Varanopseidae, Ophiacodontidae and Sphenacodontidae).

Family Eothyrididae

This family was erected as a provisional group by Romer and Price (1940) for the small pelycosaur Eothyris, known from a single skull from the Lower Permian of Texas, and fragmentary remains of three large pelycosaurs. Other fossils were subsequently placed within this family, but at present only two genera, Eothyris, from the Early Permian of Texas, and Oedaleops, from the Early Permian of New Mexico, can be assigned with confidence into the Eothyrididae. Eothyris is known from a single skull, whereas Oedaleops is represented by three partial skulls and some limb elements. These specimens, although fragmentary, have revealed that eothyridids were small amniotes. The teeth are simple conical structures, and there are distinct caniniform teeth. In most respects eothyridids exhibit the most primitive known cranial morphology of any pelycosaur. For example, the postparietal is paired, the supratemporal is broad, the postorbital is large and extends far posteriorly, the jugal is excluded from the ventral margin of the skull, the parasphenoid ventral plate is broad, the quadrate ramus of the pterygoid has a ventral shelf, the ventral surface of the lower jaw is rounded, and there is no retroarticular process. There are, however, a few synapomorphies that unite this family with caseids into the Caseasauria (Reisz 1986).

Family Caseidae

The caseids were a widespread and diverse group of herbivorous pelycosaurs, with a fossil record that extended from the Early Permian of North America and western Europe to the Late Permian of eastern Europe. Although ranging in size from 1 to nearly 4 meter in body length, caseids are surprisingly conservative in their skeletal anatomy and body proportions. The skulls are distinctive in the presence of relatively large temporal fenestrae, enormous external nares, and large pineal foramen. The snout overhangs dramatically the tooth row to form an anteriorly projecting rostrum. The external surface of the skull has unusual rounded deep pits and sometimes crevice-like depressions that form a distinctive sculpturing pattern. The marginal teeth have spatulate crowns and are serrated along the edge, in some respects similar to the teeth of parelasaurs. In contrast to most other pelycosaurs, except Edaphosaurus, there are neither caniniform

teeth, not caniniform region on the maxilla. Instead, in caseids the largest teeth in the marginal series is located anteriorly, on both the premaxilla and dentary. The first premaxillary and dental teeth are therefore longer than all other marginal teeth, and there is a gradual decrease in the size of upper and lower jaw teeth posteriorly. Also, there is a general reduction in the number of marginal teeth in caseids, ranging from a minimum of 10 (Ennatosaurus) to a maximum of 20 (Cotylorhynchus) marginal cheek teeth. All caseids, whether modest in size, or enormous, are characterized by small cervical vertebrae, bulky, barrel-shaped bodies and relatively massive limbs. There is reduction in the phalangeal formula, ranging from 2-3-4-4-3 to 2-2-2-3-2. Two distinct types of terminal phalanges can be found in caseids. In Corylorhynchus the claw bearing element is very large and broad, with apparently sharp edges on the sides. In Angelosaurus the claw bearing phalanges are also massive, but more conservative in morphology, roughly triangular in outline.

Caseids and eothyridids share a number of derived characters associated with the morphology of the snout and external naris that support the hypothesis that these primitive pelycosaur form a clade, the Caseasauria. These pelycosaur share a significant number of primitive features that appear in derived form in all other pelycosaur. All other pelycosaur can be placed into the Eupelycosauria, a clade that also includes therapsids and mammals. Eupelycosaur are characterized by reduction in the width of the snout, reduction in the width supratemporal, increased contribution of the frontal to the dorsal orbital margin, posterior location of the pineal foramen along the interparietal suture, decrease in the length of the skull table and in the length of the parietal relative to the length of the frontal.

Family Varanopseidae

These faunivorous synapsids of small to moderate size are all characterized by slender, lightly built skulls with highly specialized marginal dentition. All varanopseids have mediolaterally flattened teeth with anterior and posterior cutting edges, and are strongly recurved. Both the premaxilla and maxilla are also highly modified, the tooth bearing portion of the premaxilla being enlarged, and the maxilla being greatly elongated in association with the posterior extension of the marginal dentition. Other diagnostic features of varanopseids includes enlargement of the temporal fenestra and the reduction of the subtemporal arch to a narrow bar. The lower jaw is slender, and the mandibular symphysis is reduced in size. The postcranial skeleton is also lightly built, giving varanopseids a sleek appearance, superficially similar to modern monitor lizards. It is therefore reasonable to suggest that varanopseid pelycosaur were probably the most agile predators of their time.

Mycterosaurus longiceps is the most primitive member of the family. This small pelycosaur has the varanopseid features listed above, but lacks several

autapomorphies of the advanced members of this family. The larger varanopseids, Varanops, Aerosaurus, and Varanodon are all characterized by the presence of a massive external maxillary buttress above the caniniform region, a dramatic anterior tilt of the occiput, and anteroposterior enlargement of the temporal fenestra. In these advanced varanopseids, the postfrontal is reduced in size, the pineal foramen is practically at the posterior edge of the skull table, and the squamosal has a long anterodorsal process that reaches the dorsal process of the jugal, excluding the postorbital from the margin of the temporal fenestra.

Varanopseids retain a number of primitive skeletal features that appear in derived form in all other eupelycosaurids, including the paired condition of the postparietals, the absence of an articulating facet along the ventral edge of the opisthotic for the dorsal process of the stapes, the retention of a maxillary-quadratojugal contact that excludes the jugal from the ventral edge of the skull, the retention of a nearly straight ventral skull margin, and the lack of a ventral keel on the angular.

The hypotheses of phylogenetic relationships of this group of pelycosaurids has changed dramatically as our knowledge of primitive synapsids has increased. Romer and Price (1940) associated varanopseids with the advanced sphenacodontids as a group of primitive carnivorous sphenacodonts, and even suggested that Varanops may have been close to the ancestry of sphenacodontids. The most recent hypothesis places varanopseids within the Eupelycosauria, as its most primitive member. Although retaining many primitive cranial and postcranial features that appear in derived form in edaphosaurs, ophiacodontids and sphenacodontids, it is obvious that varanopseids developed a number of autapomorphies, and the advanced members of this group, outlasted all other carnivorous pelycosaurids as highly specialized, agile predators. Varanodon is one of the youngest known pelycosaurids, and there is strong evidence to indicate that Elliotsmithia, from the Upper Permian strata of South Africa is also a varanopseid, making it the youngest known pelycosaur (Dilkes and Reisz 1996).

Family Ophiacodontidae

The oldest known pelycosaurids have been included in this family. Protoclepsydrops from the Middle Pennsylvanian of Joggins, Nova Scotia has been placed within the Ophiacodontidae, but its identity and taxonomic status is uncertain, partly because the known skeletal remains are fragmentary. Archaeothyris, from slightly younger sediments near Florence, Nova Scotia, is the oldest known diagnosable ophiacodontid.

Ophiacodontids include small to very large carnivorous pelycosaurids that have the following cranial autapomorphies: the posterodorsal process of the premaxilla is

long, slender, and separated at the midline by an anterior process of the nasal; the nasal is at least twice as long as the parietal; elongation of the snout is accompanied by the elongation of the lacrimal; the ossification of braincase elements is reduced; the tabular has a large medial process; there is a well developed lateral mandibular fenestra in a notch of the dentary. Among ophiacodontids there is a tendency towards increase in the skull to trunk ratio, larger taxa having unusually large, awkward looking, elongate skulls. In the postcranium, ophiacodontids have relatively large, massive shoulder girdles, with anteroposteriorly broad scapulocoracoids, but small headed interclavicles and clavicles.

Ophiacodon is the best known member of the family, represented by an extensive fossil record in North America, that has been subdivided, somewhat arbitrarily (based largely on stratigraphic position and size) into six species. There appears to be extensive variation on morphology among the known specimens, even to the presence of two lateral temporal fenestrae on each side in larger specimens. In one particular specimen of Ophiacodon retroversus, the second opening is apparently present on one side of the skull but not on the other. A particularly puzzling characteristic of the postcranial skeleton is its reduced level of ossification, even in very large specimens, and the lack sharp claws as indicated by the truncated tip of the terminal phalanges. It is largely because of these features that Ophiacodon has been considered as being amphibious. This hypothesis is supported by the location of the orbit high on the side of the face, but it is nevertheless difficult to imagine how this animal, with a tall skull, could be an effective aquatic predator.

Ophiacodontids, edaphosaurids, and sphenacodontids share a list of derived features that appear in primitive form in the other pelycosaurs: there is a distinct recess on the opisthotic for the dorsal process of the stapes, the ventral edge of the skull is concave in the postorbital region, the jugal contributes to the ventral edge of the skull, the nasal is longer than the parietal, and there is a well developed ventral keel on the angular.

Family Edaphosauridae

One of the most striking features exhibited by several pelycosaurs is the great elongation of the neural spines. The poorly known Middle Pennsylvanian Echinerpeton, the Lower Permian pelycosaur Lupeosaurus, at least three distinct genera of sphenacodontids, as well as all the edaphosaurs have large sails supported by tall neural spines above the presacral portion of the vertebral column. Among these, edaphosaurs have the most spectacular sail because the greatly elongated neural spines have lateral projections or tubercles along each side. It is generally accepted that this great elongation of neural spines must have occurred independently at least three times among pelycosaurs. The presumed function of such elongation is for support of the membrane that

spanned the space between successive spines. This membrane probably facilitated temperature control, but the sail and its associated spines may have also served in display behaviour, and in edaphosaurs it may have also served as protection against predators. This last hypothesis is supported by the presence of the lateral tubercles, as well as by the orientation of the neural spines; anteriorly tilted cervical and thoracic spines and posteriorly tilted lumbar spines probably provided protection in the neck and thigh region, respectively.

Edaphosaurus and lanthasaurus are the only pelycosaur that can be placed with confidence in this family (Modesto and Reisz 1990, Modesto 1995) . Both are characterized by the presence of greatly elongated neural spines that are rounded in traverse section, and by the presence of well-developed lateral tubercles. The arrangement of these tubercles along the height of the spines is similar in the two taxa, the proximal lateral tubercles being not only the largest of the set, but also paired. One distinctive cranial feature that is found in edaphosaurs is the loss of contact between the postorbital and supratemporal, probably because the posterior process of the postorbital is reduced in length.

lanthasaurus is a small edaphosaur from the Upper Pennsylvanian that lacks many of the spectacular specializations seen in Edaphosaurus. For example, the marginal dentition of lanthasaurus is similar to that of insectivorous reptiles, with slender conical teeth which are slightly recurved at the tips, and there is a slight development of a caniniform region. The palatal and mandibular dentition is unspecialized, and there are no batteries of teeth for crushing of plant materials. This is in contrast to the cranial morphology of Edaphosaurus where the palate has been greatly modified in order to carry a massive array of closely packed teeth that occluded against a similarly developed set of teeth on the medial surface of the mandible. The modifications of the skull include reduction in the length of the skull, loss of the caniniform region, the presence of a massive supraorbital shelf that probably formed a bony hood over the eyes. The lower jaws are also reduced in length, but have become massive, and especially deep where the large adductor muscles probably inserted. The two edaphosaurs are also quite distinct from each other in their postcranial morphology. Whereas lanthasaurus appears lightly built and was probably quite agile, Edaphosaurus possesses a combination of features that suggest that this animal was a heavy, relatively slow herbivorous reptile. For example, the cervical vertebrae are reduced in length in association with the reduced size of the skull, the dorsal vertebrae are massive, the tail is deep, the limbs are short and robust and the ribs form a wide ribcage. Nine species of Edaphosaurus have been described, ranging in size from small to very large, bulky animals. The largest species, Edaphosaurus cruciger and Edaphosaurus pogonias have modified their cervical and anterior thoracic spines into massive club-like processes. It is not unreasonable to suggest that the small, insectivorous lanthasaurus represents the primitive edaphosaur pattern from which the larger herbivorous Edaphosaurus may have been derived. lanthasaurus shows many similarities in its cranial morphology to another relatively small pelycosaur, the primitive

sphenacodont Haptodus. In fact edaphosaurs and sphenacodonts share a surprisingly large number of derived cranial features that appear in primitive form in all other pelycosaurs. In both edaphosaurs and sphenacodonts the subtemporal arch is formed by the jugal and the squamosal, the jugal contribution to the ventral edge of the skull is extensive, the anteroventral process of the quadratojugal is greatly reduced, the frontal has a lateral lappet, the postfrontal is anteroposteriorly enlarged; on the palatal surface the parasphenoid wings lack the anterior spanning shelf, and the quadrate ramus of the pterygoid lacks the lateral shelf.

Family Sphenacodontidae

Haptodus is a relatively small pelycosaur that has been included in the family Sphenacodontidae, as primitive member of that group (Laurin 1993). The better known sphenacodontids include the large carnivores Dimetrodon, Sphenacodon, Ctenospondylus, and Secodontosaurus (Reisz, Berman and Scott 1992). These reptiles were the dominant predators of their time, and their fossil record extends from the Late Pennsylvanian throughout the Early Permian. The significance of this group, however, lies with its phylogenetic relationships, because sphenacodontids are generally considered to be the nearest pelycosaurian relatives of therapsids. Sphenacodonts have a supracanine buttress on the medial surface of the maxilla, the first premaxillary and second dentary teeth are greatly increased in size, similar in length to the enlarged canine, the ventral edge of the premaxilla slopes anteroventrally, giving the snout a slightly hooked appearance, the supraorbital shelf terminates posteriorly on the concave lateral surface of the postorbital, the pineal foramen is located on a slightly raised area of the parietal, with a distinct ridge surrounding the foramen, and the ventral keel of the angular is reflected slightly from the long axis of the mandible. These synapomorphies support the hypothesis that Haptodus and the large sphenacodontids are closely related. Haptodus has been recovered from the Late Pennsylvanian and Early Permian of North America and Europe. Both small and medium sized individuals have been discovered, ranging between about one and two meters in total length. Their morphology suggests that members of this genus were probably effective predators, being able to feed on both arthropods and small vertebrates.

The better known advanced sphenacodontids (Dimetrodon, Sphenacodon, Secodontosaurus, and Ctenospondylus) are all large to very large predators that have tall neural spines, strongly excavated centra and neural arches, and long limbs making them relatively agile, fast moving animals, especially when compared to their slower, bulkier herbivorous relatives. Dimetrodon, Sphenacodon, and Ctenospondylus all have similarly constructed, massive skulls with extremely large anterior incisors and canines. Sphenacodon and Ctenospondylus have blade-like neural spines, whereas Dimetrodon has greatly elongated spines that are rounded in transverse section. Secodontosaurus is

greatly modified from the pattern seen in the other large sphenacodontids by reducing the width and height of the skull roof, while retaining the neural spine morphology of Dimetrodon. The cranial modifications of Secodontosaurus can only be interpreted as an adaptation to specialised feeding strategies, perhaps preying upon burrowing animals, or feeding on tetrapods that tried to evade capture by hiding in crevices.

Origin of Therapsids

A major morphological gap exists between pelycosaurs, which are mostly Pennsylvanian and Early Permian synapsids from North America and Europe and therapsids, which are Late Permian and Triassic advanced synapsids from South Africa and USSR. Previous attempts at bridging this gap have not been successful. Among pelycosaurs the haptodontine and sphenacodontine sphenacodontids have been proposed as the most likely candidates for sister-group status to therapsids. Romer and Price (1940) proposed that of all the known sphenacodontids Haptodus is the most likely ancestor of therapsids. More recently, however Reisz, Berman and Scott (1992) have shown that the pattern of distribution of synapomorphies in haptodontines, sphenacodontines, and therapsids supports the hypothesis that sphenacodontines are the sister group of therapsids. The morphology of the reflected lamina of the angular provides the strongest evidence for the latter hypothesis: in both primitive therapsids and sphenacodontids the reflected lamina is a prominent feature of the lower jaw, whereas in haptodontines the reflected lamina, if present at all, is a modest, slightly developed ventral projection with little or no lateral displacement (Laurin 1993).

Recent studies of Tetraceratops indicate that this enigmatic fossil from the Early Permian of Texas bridges the morphological and temporal gaps between the pelycosaurian and basal therapsid synapsids (Laurin and Reisz 1995). As the oldest known therapsid, this form shares with other early therapsids a number of derived cranial features, but numerous primitive features that appear in derived form in all other therapsids Tetraceratops is therefore the sister taxon to all other therapsids.

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