

Synapsida (Extinct Mammal Relatives)

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Based in part on the previous version of this eLS article 'Synapsida (Mammal-like Reptiles)' (2001) by Hans-Dieter Sues.

In the phylogenetic system, the Synapsida include Mammalia and all other amniotes more closely related to Mammalia than to Reptilia. The most characteristic feature is the presence of a single large opening behind the orbit on either side of the skull. This opening is small in basal synapsids but increases in size in later, more derived forms including mammals. Nonmammalian synapsids form an extensive series of taxa that are successively more closely related to mammals and thus are now often referred to as stem-mammals or ancient mammal relatives. They range from the Late Carboniferous to the Early Cretaceous. Crown-group mammals (which include all present-day mammals) are first known from the Middle Jurassic. Synapsida and Reptilia are now considered two entirely distinct evolutionary lineages of Amniota with a common ancestor in the Carboniferous.

Basic Features

The most diagnostic feature of Synapsida, which is retained in extant mammals, is the presence of a single temporal opening behind the orbit on either side of the skull (**Figure 1**). This opening is typically bounded by the jugal, postorbital and squamosal bones. In more derived nonmammalian synapsids and in mammals, this opening becomes greatly enlarged and the jaw-closing muscles insert along the margins of and on the connective tissue (fascia) covering the opening. Early-diverging synapsids (pelycosaurs) are readily distinguished from other early amniotes by various features of the skull, especially the forward-sloping, plate-like occiput and the presence of a single postparietal bone.

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Diversity

The oldest synapsids currently known are from the Late Carboniferous (Pennsylvanian) of Nova Scotia (Canada), over 310 million years ago (Angielczyk and Kammerer, 2018). By the early Permian, nonmammalian synapsids were already the most diverse group of terrestrial vertebrates, and they reached the acme of their diversity and abundance in the late Permian. The number of synapsid taxa dropped significantly during the mass extinction at the end of that period when several major lineages of therapsids vanished. During the Triassic, some groups of therapsids diversified again, but diapsid reptiles soon came to outnumber synapsids in communities of land-dwelling vertebrates. In the latter part of the Triassic, the closest relatives of mammals such as *Morganucodon* first appeared (Kielan-Jaworowska *et al.*, 2004). Mammals that are part of the group that includes all extant species first appeared in the Middle Jurassic. **See also:** [Extinction: End-Permian Mass Extinction](#); [Biotic Recoveries after Extinction](#)

Habitats and Abundance

Nonmammalian synapsids are known only from continental settings. Most of them were clearly land-dwellers. Fossils of these animals have been discovered on every present-day continent including Antarctica as well as in Greenland, Japan and Madagascar. 'Pelycosaurs' and therapsids probably occupied all major habitats on land, but appear most abundant in lowland floodplain settings. However, this distribution reflects, at least in part, the fact that skeletal remains of vertebrates are much more likely to be preserved in sedimentary rocks deposited by rivers and in lakes. By far the greatest diversity of therapsids is known from the Permo–Triassic continental strata of the Beaufort Group of the Karoo in South Africa; some species are documented by thousands of fossils (Rubidge and Sidor, 2001; Angielczyk and Kammerer, 2018). The Karoo therapsids apparently lived in temperate, fairly moist climates at relatively high palaeolatitudes. **See also:** [Fossil Record: Quality](#)

Habits and Life Histories

As for most extinct vertebrates, there is scant evidence concerning the life histories of nonmammalian synapsids. They probably hatched from possibly soft-shelled eggs as this mode of

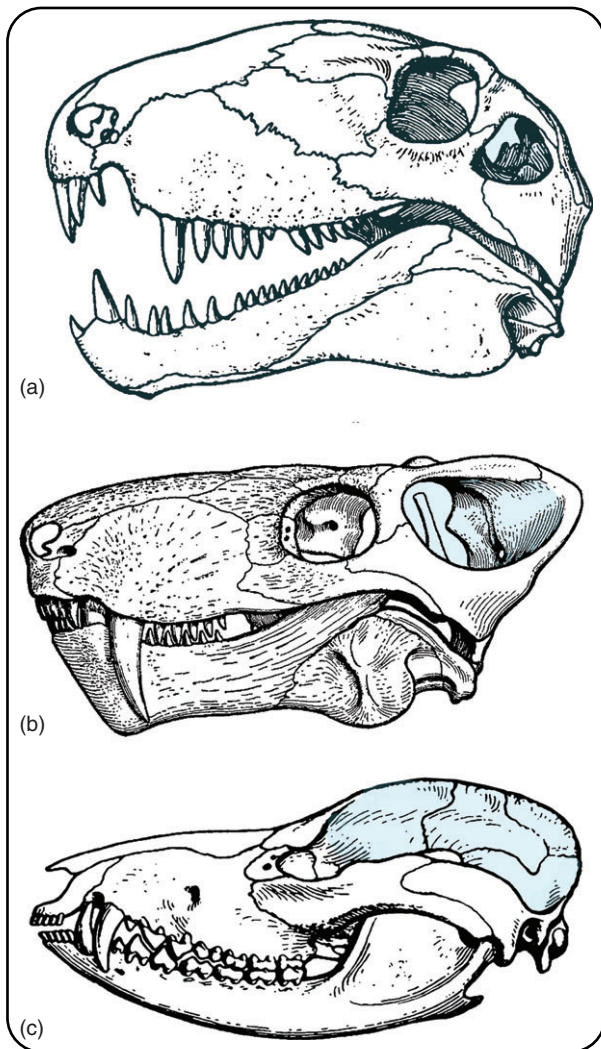


Figure 1 Evolution of the key feature of Synapsida – the temporal opening (highlighted in light blue) – from small temporal opening to fully developed temporal fossa (which is confluent with the orbit in many mammals). (a) sphenacodontid ‘pelycosaur’ *Dimetrodon*; (b) gorgonopsian therapsid *Sauroctonus*; (c) opossum (*Didelphis*). Not to scale. Modified from Bystrov (1957).

reproduction is primitive for amniotes and still retained by the most primitive living mammals, the monotremes. Known juveniles of ‘pelycosaurs’ and therapsids appear to differ little in skeletal structure from adult conspecifics. It is likely that, as in extant nonmammalian amniotes, most of them received little if any parental care and started fending for themselves soon after hatching. Nothing is known about the lifespan of nonmammalian synapsids. Most early synapsids were likely ectotherms, dependent on external sources of heat to raise their body temperature above ambient temperature. Therapsids more closely related to mammals show bone microstructure suggestive of higher growth and thus higher metabolic rates.

Early synapsids were insectivorous or carnivorous, but herbivory developed repeatedly and independently in several

lineages. During the late Palaeozoic, nonmammalian synapsids included both the dominant carnivores and herbivores in communities of land-dwelling vertebrates. One herbivorous lineage, the dicynodont therapsids, became especially diverse and abundant and included some large-bodied forms as well as small, superficially rather mole-like animals specialised for subterranean digging. Some therapsids built and lived together in burrows.

Fossil History and Phylogeny

Nonmammalian synapsids have a long, rich fossil history that extends from the Late Carboniferous (Pennsylvanian) to the Early Cretaceous, spanning some 200 million years. Indeed, they have one of the most extensive fossil records of any major group of vertebrates, and this record illustrates in remarkable detail the evolutionary transition from nonmammalian amniotes to mammals. Traditionally, palaeontologists distinguished three ‘grades’ of body plan among Synapsida – the basal ‘Pelycosauria’, the intermediate Therapsida, and the derived Mammalia (Angielczyk and Kammerer, 2018; **Figure 1**). ‘Pelycosaurs’ were the first to appear in the fossil record (Late Carboniferous), and mammals are the geologically youngest group to appear (Middle Jurassic). Since the 1980s, the application of phylogenetic methods has elucidated the evolutionary history of Synapsida. However, the relationships of many groups, especially the oldest therapsids, are still poorly understood. **See also: Fossil Record; Fossils in Phylogenetic Reconstruction**

‘Pelycosaurs’

The Late Carboniferous and Permian ‘pelycosaurs’ represent a series of basal synapsids that are successively more closely related to therapsids (which include mammals as a derived clade) and thus are no longer considered a monophyletic group in phylogenetic classifications (Angielczyk and Kammerer, 2018). The most basal clade, Caseasauria, includes the Caseidae, which represented the first major radiation of plant-eating tetrapods on land and are known from the Late Carboniferous to middle Permian of Europe and North America. The skull of caseids is unusually small relative to the massive body, especially in more derived forms such as the early Permian *Cotylorhynchus*. The snout has a pointed end that extends forward beyond the tooth rows and much enlarged external narial openings. The teeth of the more derived forms have spatulate crowns with apical denticles.

In all other ‘pelycosaurs’, the snout is deep dorsoventrally and rather narrow transversely, and the frontal bone enters broadly into the dorsal margin of the orbit. The Varanopidae comprise lightly built carnivorous forms with highly specialised skulls and rather long, slender limbs and range into the mid-Permian; they include the only ‘pelycosaurs’ known so far from South Africa. The Ophiacodontidae, from the Late Carboniferous and early Permian of North America and Europe, are characterised by a proportionately large skull. The best-known form, *Ophiacodon*, has a deep, long snout, and the small orbits and temporal opening are placed high on the sides of the skull. The Edaphosauridae, from the Late Carboniferous and early Permian of Europe and

North America, are characterised by the presence of a large ‘sail’ supported by greatly elongated neural spines on the cervical and dorsal vertebrae that are studded with short lateral protuberances. *Edaphosaurus*, the best-known representative, has a proportionately small skull with massive crushing tooth plates on the palate and lower jaws. It is considered one of the oldest known herbivorous tetrapods. Edaphosaurids are the sister-group of the most derived ‘pelycosaurs’, the carnivorous Sphenacodontidae. The latter are known from the Late Carboniferous and early Permian of Europe and North America and include the top predators in the early Permian continental ecosystems of these regions, including *Dimetrodon*. Sphenacodontids are closely related to the Therapsida, with which they share the presence of a posteriorly notched bony sheet (reflected lamina) on the angular bone of the lower jaw and the possession of a deflected retroarticular process of the articular bone. The skulls of *Dimetrodon* and its relatives further resemble those of therapsids in having a tall maxilla that excludes the lacrimal from the margin of the external narial opening and the presence of large canine-like teeth in the upper and lower jaws. *Dimetrodon* is best known for its ‘sail’ supported by tall, slender neural spines along much of the vertebral column.

Therapsids

Whereas ‘pelycosaurs’ are mainly known from North America and Europe, the oldest undisputed therapsids date from the middle Permian of China, Russia, and South Africa (Angielczyk and Kammerer, 2018). The latter forms still closely resemble sphenacodontid ‘pelycosaurs’ in much of their skeletal structure, but their skulls have proportionately much larger temporal openings, which become fossae for the jaw-closing muscles, and the occiput slopes backwards rather than forwards. The dentition comprises fewer teeth, and the upper canines are much enlarged. The shoulder and pelvic girdles are less massive and the limbs are more slender than those in sphenacodontids such as *Dimetrodon*. The bones of the shoulder girdle become reduced in size and, in most therapsids, mobility at the shoulder joint increased.

More derived therapsids (Eutherapsida) show even greater expansion of the temporal openings. The most primitive group of eutherapsids are the Dinocephalia (Angielczyk and Kammerer, 2018). They are large-bodied animals with massively built skeletons. The enlarged upper and lower incisors met in a precise, interlocking fashion. Dinocephalians include both carnivores (Anteosauridae) and herbivores (Tapinocephalidae). The latter are particularly noteworthy for the great thickening of the bones forming the skull roof, which may have been used as a battering ram in head butting.

Another major group of eutherapsids are the Anomodontia, which include the dominant terrestrial herbivores during the latter part of the Permian and part of the Triassic (Fröbisch, 2007). The most diverse group of anomodonts were the Dicynodontia. They are distinguished by their highly modified skull, which has a short snout and a long temporal region behind the orbits. The tips of the snout and mandible usually lack teeth. Instead, the jawbones form sharp cutting edges, which were probably covered by a keratinous beak in life. In most dicynodonts, the upper canines are the only remaining teeth. The facet for the jaw joint on the articular bone is nearly twice as long as that on the quadrate; this indicates that

the mandible could be retracted to cut or grind fodder between the edges of the upper and lower beaks. Although dicynodonts suffered a massive loss in species diversity at the end of the Permian, one lineage evolved very large plant-eating forms that survived until the end of the Triassic.

The Theriodontia comprise the most derived group of eutherapsids (Rubidge and Sidor, 2001; Angielczyk and Kammerer, 2018). They are characterised by the presence of a distinct, free-standing coronoid process on the dentary, which served as the site of attachment for jaw-closing muscles. The quadrate and quadratojugal bones are no longer suturally connected to the squamosal but sit loosely in a depression on the anterior surface of that bone. The earliest theriodonts, the middle to late Permian Gorgonopsia, have rather slender limbs that were more vertically oriented than those in more basal synapsids. Their predatory habits are reflected by the presence of enormous, blade-like canines and large incisors. The skull of more derived theriodonts (Eutheriodontia) is characterised by the possession of a wide, dorsally completely open temporal fossa and the anteroposterior expansion of the epipterygoid bone to form the anterior portion of the sidewall of the braincase. Both features already occur in the late Permian to Middle Triassic Therocephalia but became most prominently developed in the Cynodontia.

Cynodonts, which include mammals as a subgroup in phylogenetic classifications, first appear near the end of the Permian in Africa and Europe and diversified during the Triassic (Rubidge and Sidor, 2001; Angielczyk and Kammerer, 2018). Their dentition comprises incisors, canines, and increasingly complex post-canine (cheek) teeth with cingula and smaller cusps in addition to the main cusp. In some derived, omnivorous or herbivorous cynodonts (Gomphodontia), the crowns of the upper and lower post-canines are transversely expanded and met in precise occlusion. A secondary bony palate formed by mid-line fusion of the premaxillary, maxillary and palatine bones and separated the nasal passage from the oral cavity. The zygomatic arches curve outwards, and a superficial slip of the jaw-closing musculature, which developed into the masseter muscles in mammals, passed through the space between the zygomatic arch and the coronoid process of the dentary to insert on the lateral surface of that bone (Lautenschlager *et al.*, 2017). The dentary is the largest bone of the lower jaw. The quadrate, quadratojugal and postdentary bones are much reduced, and the latter were only loosely attached to the dentary. They probably functioned as part of a sound-transmitting mechanism involving a tympanic membrane at the back of the lower jaw. In mammals, these bones became completely separated from the lower jaw and integrated into the middle ear. Whereas the forelimb of nonmammalian cynodonts retained a sprawling posture similar to that in earlier synapsids, the femur was already held in a much more vertical position.

A recently discovered group of small-bodied derived cynodonts, the Middle to Late Triassic Brasilodontidae, is noteworthy for the presence of certain mammalian features like postcanine teeth with divided roots and the presence of a promontory on the prootic (which encloses the cochlea of the inner ear) (Bonaparte, 2012). Traditionally, mammals were defined based on features such as the development of a jaw joint between the dentary and squamosal bones (Kielan-Jaworowska *et al.*, 2004), but these features have a much wider distribution

than traditionally assumed. Following Rowe (1988), most researchers now distinguish between Mammaliaformes and Mammalia. Mammaliaformes comprises the last common ancestor of *Morganucodon* and Mammalia and all its descendants. Mammalia, the crown group, comprises the last common ancestor of monotremes, marsupials and placentals and all its descendants. *Morganucodon* and its close relatives have already numerous features found in present-day mammals but, for example, the novel dentary-squamosal jaw joint still existed side-by-side with the primitive articular-quadratoquadrate jaw joint. An exceptionally preserved skeleton of a Middle Jurassic mammaliaform from China provides the oldest known record of fur (although hair probably evolved earlier). *Morganucodon* is known from the Late Triassic and Early Jurassic of Europe, China, and North America. The oldest known representatives of crown-group mammals in the fossil record date from the Middle Jurassic (Luo *et al.*, 2011).

Glossary

- Amniote** A vertebrate that produces eggs that contain a membrane (amnion) enclosing the developing embryo in a fluid-filled chamber. Amniotes include reptiles, birds, and mammals.
- Cingulum (pl. cingula)** A band of small cusps encircling the principal cusps on a tooth crown.
- Crown-group** An assemblage comprising the last common ancestor of all present-day members of a group of organisms and all of its extant and extinct descendants.
- Epipterygoid** Bone in the anterior portion of the bony sidewall of the braincase.
- Fossa** Depression or hollow in a bony structure.
- Lacrima** Bone in the front wall of the eye socket (orbit) enclosing the tear (lacrimal) duct.
- Naris (pl. nares)** Opening of the nasal passage. The external opening is the nostril.
- Occiput** Back of the skull.
- Prootic** Bone in the wall of the braincase that bounds part of the inner ear.
- Zygomatic arch** Bony bridge extending from the orbit to the back end of the skull and enclosing the temporal fossa for the jaw-closing muscles on the side of the skull.

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