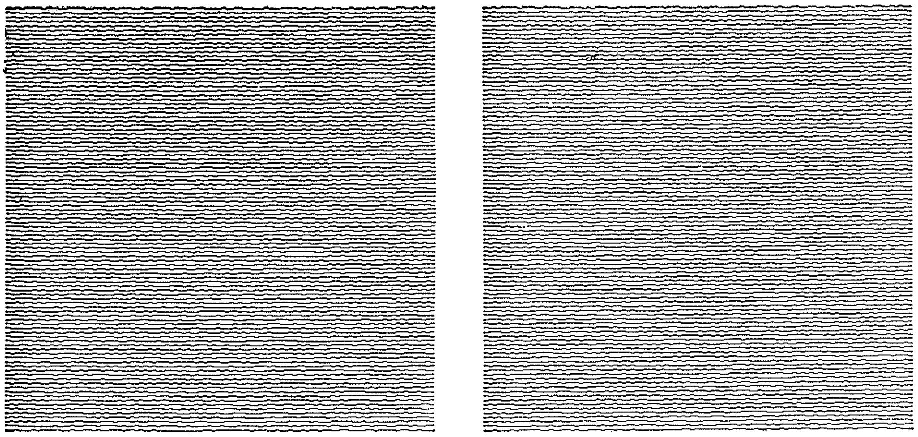

Fig. 3. Random-line stereogram similar to Fig. 1 except composed of horizontal line segments. Figure 3 yields stronger stereopsis than Fig. 1 under laboratory conditions.

ceived in a depth plane with zero disparity. Moreover, 25 percent of the picture elements (A-B) could have easily been fused with two-dot (16 seconds of arc) disparity as a lace-like transparent plane slightly in front of the zero-disparity plane, while 25 percent (B-A) could have been fused with a minus-two-dot disparity (behind the transparent zero disparity plane). This possible organization would have been an easy solution to the problem of fusing the two images. The fact that a more global organization is actually perceived (center square above the background) indicates that the central nervous system searches for a particular solution even if it is more unlikely. In this case, the ten-dot disparity of the center square is 5 times more than the two-dot disparity between the A-B and B-A picture elements. We have found that stereopsis can be obtained even for 20-dot global disparity (fully 10 times the local disparity). Thus the fusional process apparently favors a solid (densely packed) organization with a large disparity in preference to a transparent (lace-like) organization, even if the latter has much smaller disparity. It seems likely that this weighting process between various organizations occurs higher than the local binocular fusion of similar picture elements.

When the same experiments are tried with horizontal line segments, shown in Fig. 3, one would predict a different outcome, because of the anisotropy of stereopsis. When two vertical line segments are horizontally displaced by a small amount, as in Fig. 1, local stereopsis occurs with great ease; however, for horizontal line segments with a vertical displacement of even a few dots, local stereopsis would require that the fusional mechanism shift the entire line segment (ten dots long in Fig. 3). Therefore, local fusion of horizontal line segments should be more difficult and the global organization (that is, the center square) should be more likely. Because of the difficulty of reproducing patterns with this detail, the actual viewing of the stereograms illustrated here may deviate from the reported findings.

Stereoscopic viewing of Fig. 3 bore out this expectation. In spite of having the same local and global disparities as Fig. 1, Fig. 3 yields stronger global stereopsis. Even with 60-dot disparity the center square was perceived in depth, while the limit for the vertical case was 20-dot disparity.

The perceptual difference between global stereopsis with horizontal and with vertical line segments has another implication. The anisotropy of stereopsis (that is, vertical disparity does not yield stereopsis, while horizontal disparity does) has to be contrasted with the isotropy of binocular fusion. Panum's fusional area is about the same for horizontal and vertical disparities, and disparities under 6 minutes of arc should be easily fused in any direction. The finding that horizontal line segments yield stronger global stereopsis than vertical ones suggests that global stereopsis does not depend on local fusion, but rather on local stereopsis.

In these and similar experiments the local elements resemble the simple receptive field shapes found by Hubel and Wiesel (*6*), while the global percept is obtained by searching for the binocular organization. The study of how local features yield local stereopsis and how local stereopsis affects global stereopsis may be a bridge linking neurophysiological findings with perceptual psychology.

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18 May 1967

Archosaurian Reptiles: A New Hypothesis on Their Origins

Abstract. *The characteristics of the first archosaurs, the proterosuchian thecodonts, show that neither of the supposed common ancestors of archosaurs and lepidosaurs could actually be an ancestor of archosaurs. Instead, the evidence seems to indicate that the archosaurian ancestors are probably in the ophiacodont-varanopsid group of the pelycosaurian synapsids. In particular, the Varanopsidae are strongly indicative of proterosuchian relationships, as they have evolved some characters which are elsewhere found only in archosaurs. Archosaurs and lepidosaurs apparently have different origins; the former come from the pelycosaurs, and the latter come from the captorhinomorph cotylosaurs through the Millerettiformes.*

Dinosaurs, crocodiles, pterodactyls, and thecodonts are members of the reptilian subclass Archosauria—the ruling reptiles—a group of vertebrates (including the ancestors of birds) highly diversified and greatly expanded during Mesozoic times.

From the lower Triassic to the Recent, the history of the archosaurs is fairly well represented in the fossil record. Though many points are still controversial, there is much evidence to support the hypothesis that all the post-Triassic archosaurian orders (Saurischia, Ornithischia, Crocodilia, and Pterosauria) originated from the Thecodontia, about whose origin little is known, however.

It is generally assumed that the subclass Archosauria is more closely related to the subclass Lepidosauria (lizards, snakes, and rhynchocephalians) than to any other reptilian group, and that both taxa had a common ancestor in Permian times. Members of these subclasses have a two-arched type of skull; from this comes the name Diapsida, which is used in current phylogenetic discussions. Goodrich (*1*) advanced the hypothesis, further developed by Watson (*2*), that the Archosauria and the Lepidosauria are the basis for a larger group, the Sauropsida, in contrast to the mammal-like reptiles and their alleged relatives (the Theropsida) and that this separation into two major groups took place during an anthracosaurian, prereptilian level of evolution. Although this view has been criticized (*3*), the idea of an early differentiation of the archosaur-lepidosaur complex from the mammal-like reptiles prevails (*4*) and is one of the main assumptions of the generalizations of Olson (*5*) on the ecological factors in mammalian origins.

Broom (*6*) and others (*7*) proposed that the upper Permian younginiform reptiles of the family Younginidae (*Youngina, Youngopsis,* and *Youngoides*), which are the basis of the order Eosuchia of the Lepidosauria, are probably the group from which both the archosaurs and the later lepidosaurs evolved. There is evidence for a younginid ancestry of the rhynchocephalians, but the Squamata (lizards and snakes) are definitely derivable from another taxon among the Eosuchia—the prolacertids (*8, 9*). Moreover, Romer (*10, 11*) seriously questioned the idea of an eosuchian origin of the archosaurs, on the basis of striking differences in skull morphology.

Watson (*12*) proposed the millerettiform hypothesis as an alternative and suggested that the upper Permian millerettids (*Milleretta* and *Millerosaurus*) and their older relatives represented the origin of younginids, prolacertids, and archosaurs. The millerettids make a good link between the captorhinomorphs and the eosuchians (*13*), but they are more highly evolved than the first archosaurs and hence cannot be archosaur ancestors.

Romer (*10*) advocated the captorhinomorph hypothesis, which suggested that the common ancestor of lepidosaurs and archosaurs might be the captorhinomorph cotylosaurs and that the two-arched type of skull evolved twice from the anapsid condition. Kuhn-Schnyder (*14*) claimed that the separation of archosaurs and lepidosaurs from a common ancestor went back to the labyrinthodont amphibians.

Studies on the first archosaurs, the thecodonts of the suborder Proterosuchia, suggested a possible close relationship between archosaurs and synapsids. The Proterosuchia (*15–17*) are the stem thecodonts, representing a first step in archosaurian evolution, which took place in uppermost Permian and early Triassic times. They are incipiently archosaurian only in certain characteristics; in others, they are plainly atypical archosaurs. Archosaurs are described as reptiles which typically and originally had an upright stance and a bipedal gait. The proterosuchians were clearly quadrupedal animals with sprawled legs. In the early proterosuchians, the triradiate pelvis of the archosaur is only incipient, and the femur has the primitive intertochanteric fossa and a trochanter minor. The pes lacks the various archosaurian specializations; the vertebral intercentra are commonly retained in the neck region and occasionally also in the back (*16*). The skull retains primitive reptilian characters, lost or modified in later archosaurs, such as acrodont or subthecodont teeth, postparietal and postfrontal bones, the presence in some genera of a pineal foramen and palatal teeth on the pterygoid flanges, the absence of a typical otic notch and of a V-shaped contour in the posterior border of the lower temporal opening, the suspensorium lying well behind the occipital level, and the presence of a well-developed epipterygoid bone. At the same time, it shows such well-developed typical archosaurian skull characteristics as the two-arched temporal region, the developed antorbital fenestra, laterosphenoid ossifications, movable articulation between quadrate and squamosal, mandibular fenestra, and loss of posttemporal and tabular bones.

This association of primitive and advanced characteristics is expected in such an early archosaurian group; on the other hand, the proterosuchians do not have any characteristic that would preclude them as ancestors of later archosaurian groups. Actually, the presence of such intermediate forms as *Euparkeria* (*18*) (linking the Proterosuchia with the Pseudosuchia) and *Proterochampsa* (*19*) (connecting them with the Crocodilia) suggests that they certainly are stem archosaurs—a conclusion that also agrees with the time factor. But some of the skull characteristics, in which the Proterosuchia are more primitive than the Pseudosuchia and the remaining archosaurs, indicate that they are also more primitive than some of the supposed common ancestors of lepidosaurs and archosaurs, namely, the Younginiformes and the Millerettiformes. Even though they possess a typical diapsid skull, the Younginiformes have already developed an otic notch and have the suspensorium close to the level of the occipital condyle. The absence of an otic notch and the posterior position of the suspensorium in the Proterosuchia rule out the younginiform eosuchians as their possible ancestors, because absence of an otic notch and long-jawed skulls are primitive reptilian characteristics. This also excludes the Millerettiforms which, in addition, are not diapsid in type of skull.

Apparently, the captorhinomorph hypothesis is not contradicted by proterosuchian characteristics. However, such a hypothesis is too general, as the very primitive characteristics of the captorhinomorphs make it possible to propose them as ancestors of most of the reptilian groups. Moreover, the gap between the captorhinomorphs and the proterosuchians is really very wide; there must be a new and unknown intermediate reptilian major group to fill it. Furthermore, trends in the direction of some of the archosaurian specializations are not known in any of the captorhinomorph genera.

Olson's description (*20*) of the new varanopsid pelycosaur *Varanodon* suggested to me the concept of a pelycosaur origin for archosaurs. The ancestors of the archosaurs are probably to be found among the primitive varanopsid pelycosaurs, or in the ophiacodont-varanopsid group of pelycosaurs, rather than among any other reptilian group.

In skull morphology, these pelycosaurs agree with the requirements for proterosuchian ancestry in the absence of the otic notch and in the presence of a posterior suspensorium, intertemporal and postfrontal bones, and pineal foramen. They have also the synapsid lower temporal fenestra which is very large in the Varanopsidae, as it is in the more primitive proterosuchians. The development of the lower temporal opening is first in the development of the diapsid skull (*9*). This association of characteristics is in itself strongly indicative of proterosuchian-pelycosaur relationships; the probability of this ancestry is increased by the fact that an antorbital fenestra is present in *Varanodon* and probably also in *Varanops* (*20*) and the fact that the mandibular fenestra is well developed in *Ophiacodon* and apparently also in *Varanops* (*21*). Antorbital and mandibular fenestrae are typical of archosaur characters, only found elsewhere in the reported pelycosaur genera. Details of the palate, the occiput, and the prefrontal bones add more points of affinity; the differences in skull morphology between both groups are precisely of the type expected in a group from which the proterosuchians originated.

Postcranial morphology also supports the same conclusion. In spite of the more primitive, notochordal type of centra, the vertebrae of the ophiacodonts suggest archosaurian ancestry in the presence of lamellae connecting the two facets for dichocephalous ribs, and those of the Varanopsidae suggest this ancestry in the elongated cervical centra and the tendency of the dorsal rib-facets to be closer in succession from the front. The scapula is closely comparable in *Ophiacodon* and *Varanops* and in such primitive proterosuchians as *Chasmatosaurus* and *Cuyosuchus*. The coracoid is single in the archosaurs; in typical pelycosaurs, it is double.

Here again the facts that *Varanops* lacks the posterior coracoidal element and that the sphenacodonts in general show a lag in the ossification of that element (see *21*) are very suggestive. The ilia of *Chasmatosaurus* and *Shansisuchus* are very similar to those of *Varanops*, while the pelvis of the latter shows characteristics in the pubis and ischium that strongly indicate a very primitive stage in the triradiate trend already shown in the proterosuchians. Ophiacodonts and Varanopsids show the archosaurian limb disparity, suggesting that this trend developed from the primitive pelycosaurs as an adaptation to semiaquatic locomotion. The humerus of the proterosuchians shows many similarities to that of *Varanops*, such as the expanded and twisted ends and the well-developed deltopectoral crest. A humerus of *Chasmatosaurus* (*15*) also shows indications of the pelycosaurian entepicondylar foramen. The femur of the proterosuchians is most like the femur of *Varanops* and *Varanosaurus*; additional similarity is found in the structure of the posterior and anterior epipodials and the morphology of the feet.

All the evidence thus indicates that the proterosuchians are easily derivable from the generalized pelycosaurs of the ophiacodont-varanopsid group. Within them, the Varanopsidae have the closest relationships and show some trends (such as the evolution of the antorbital fenestra, the triradiate pelvis, the single coracoid, elongated cervical vertebrae, and enlargement of the lower temporal opening) which are well established in the early proterosuchians. Olson (*19*) pointed out that the specializations in skull morphology, when examined separately, suggest that the Varanopsidae "have departed rather far from the main lines of pelycosaur evolution." This departure could well have been the beginning of the evolutionary shift which started the emergence of the archosaurs.

This hypothesis implies that archosaurs and lepidosaurs are far apart in origin, the former derived from a special lineage of pelycosaurs, and the latter stemmed with the captorhinomorph cotylosaurs through the Millerettiformes (Fig. 1). But at the same time, these conclusions disagree with Olson's contention (*5*) that archosaurs and synap-

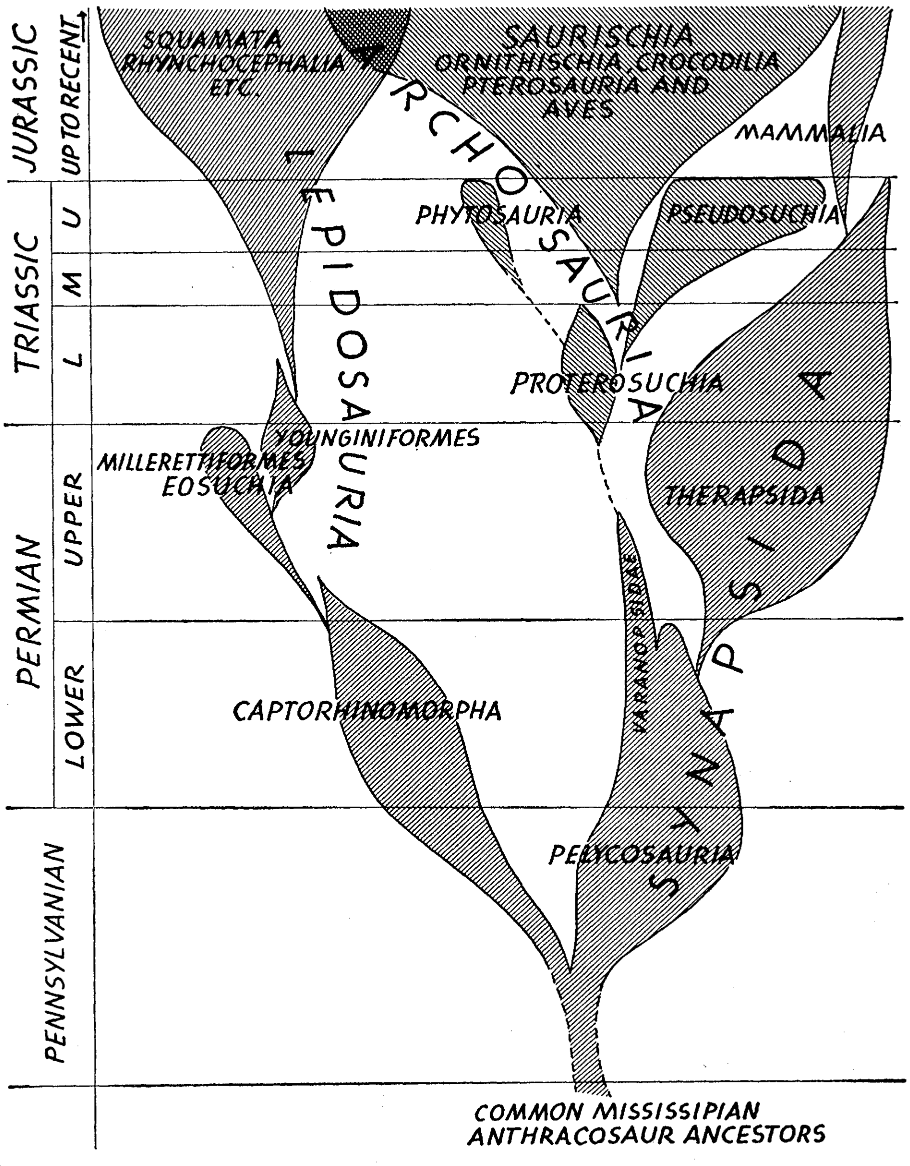

Fig. 1. Tentative dendrogram of the relationships and origins of archosaurian and lepidosaurian reptiles (not to scale).

sids evolved as members of separate communities. The history of archosaurs seems to have been closely linked with the history of synapsids, not only because they are considered to be derived from pelycosaurs, but also because the fossil record indicates that the first archosaurs were found in the same deposits that yield various synapsids as part of the same general faunal associations.

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Molecular Size of Hagfish Muscle Lactate Dehydrogenase

Abstract. *In contrast to an earlier report, we find that the primitive vertebrate* Eptatretus *possesses a muscle lactate dehydrogenase whose molecular size is like that of lactate dehydrogenases from higher vertebrates. The molecular size of lactate dehydrogenase appears to have remained constant during evolution.*

Hagfishes belong to the most primitive class of vertebrates, the Cyclostomata (*1*). The lactate dehydrogenases (*2*) of the hagfish *Eptatretus* have been studied with respect to their electrophoretic mobility, thermostability, immunological reactivity, and subunit hybridization (*3–5*).

It was recently reported that hagfish lactate dehydrogenases are unusually small molecules, possibly monomers (*6*), and it was suggested (*6*) that the common ancestor of vertebrates may have had a monomeric lactate dehydrogenase that was the evolutionary precursor of the tetrameric form found in all contemporary vertebrates examined, with the exception of the hagfish (*3, 7*). We, however, present evidence that the muscle lactate dehydrogenase of the hagfish is not a small molecule; it appears to have a molecular size like that of lactate dehydrogenase from other species. The molecular weight of lactate dehydrogenase has been previously determined to be approximately 140,000 in several species (*3, 7*).

Hagfishes (*Eptatretus stouti*) were caught off the coast of Southern California in April 1963, by Dr. David Jensen (*8*) and stored at −10°C. Owing to their large size, tongue muscles were used as a major source of lactate dehydrogenase. Portions (1 g) of tissue were ground in 3 ml of $0.25M$ sucrose at 4°C. The homogenates were clarified by centrifugation at $30{,}000g$ for 15 minutes, and the extracts were stored at −10°C.

Lactate dehydrogenase activity was estimated spectrophotometrically (*9*). The muscle extracts contained 150 enzyme units/ml (*10*), a value which is close to that which we have observed for muscle extracts from other vertebrates. In apparent contrast to certain earlier findings (*6*), hagfish muscle lactate dehydrogenase is rather stable, surviving for 4 years at −10°C with little loss of activity either in tissues or in sucrose extracts. The enzyme is also relatively resistant to denaturation by heat; 50 percent of its activity persists for 20 minutes at 64°C (*5*). No change in heat stability was observed after the enzyme's storage for 4 years at −10°C.

In order to estimate the molecular size of lactate dehydrogenase from hagfish muscle, we carried out gel-filtration studies with a Sephadex G-100 column (53 by 1.5 cm). The degree to which the column separated compounds differing in molecular size was determined by preliminary experiments with proteins of known molecular weight (*11, 12*). Table 1 presents the published molecular weights of the proteins that were used and the elution volumes that were observed in our experiments. Details concerning the experimental conditions are also given in Table 1.

Lactate dehydrogenase from extracts of hagfish muscle was eluted from the Sephadex column as a single symmetrical peak. More than 90 percent of the enzyme activity that was applied to the column was recovered. The elution volume for hagfish lactate dehydrogenase was 38 ml (*13*). The same elution volume was observed in another experiment with crystalline lactate dehydrogenase from chicken H_4; the molecular weight of this enzyme is approximately 140,000 (*7*). No evidence for the existence of a smaller form of lactate dehydrogenase was obtained in either case.

To check whether the elution profiles of these two enzymes were identical, we applied a mixture containing 65 enzyme units of hagfish lactate dehydrogenase from a muscle extract and 4.0 enzyme units of crystalline H_4 lactate dehydrogenase from chicken to the column. Samples of the material eluted from the column were assayed for enzyme activity before and after heating for 20 minutes at 72°C in the presence of 0.05 percent bovine serum albumin. The activity of chicken H_4 lactate dehydrogenase is unaffected