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THE LATE CARBONIFEROUS VERTEBRATE FAUNA OF KOUNOVA (BOHEMIA) COMPARED WITH THAT OF THE TEXAS REDBEDS.

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ABSTRACT. The late Carboniferous vertebrate fauna from Kounova, Czechoslovakia, originally described by Fritsch, is redescribed and compared with the essentially contemporary fauna of the Texas redbeds. The assemblages from the two areas are strikingly similar, suggesting intimate geographical connections between Europe and North America in late Paleozoic times.

A SERIES of vertebrates from a late Carboniferous deposit at Kounova, Czechoslovakia, was described by Fritsch in his "Fauna der Gaskohle" (1879-1904). Little attention has been paid to this material by later writers (except for brief notes on certain of the species by Steen, 1938). Restudy of this fauna which I had undertaken in connection with a survey of Paleozoic amphibians indicates that it is worthy of re-description. Recent advances in our knowledge of early vertebrates makes it possible to interpret these fragmentary remains in a much more satisfactory fashion than could be done in Fritsch's day; the fauna, restudied, seems closely comparable to that of the nearly contemporaneous Texas redbeds assemblage, a situation with suggestive palaeogeographic implications.

The Kounova locality. Kounova lies some 35 miles northwest of Prague in the Rakonitz coal basin. The material studied by Fritsch appears to have come from a single mine, operated for a relatively few years, which supplied coal to the gas-works at Prague and other towns. The fossils were found in blocks of an impure shaly coal of the sort usually (although incorrectly) called a "cannel-coal" in North America. Fritsch (1879, vol. I, pp. 21-22) gives the general section and also the details of the layers normally present in the "cannel."

Kounova lies close to the Carboniferous-Permian boundary (cf. Broili 1908; Case 1926, 53-66; Nemejc 1932; Steen 1938, 266-269). In earlier years it was frequently considered as Permian. The flora, however, appears to be technically a Stephanian one, and hence Kounova must be classed as Carboniferous, although very close to the period boundary.

The Wichita group of Texas,[1] with which comparison is made, likewise lies in disputed Carboniferous-Permian territory. The writer (1935, pp. 1642-1657, etc.) has in the past argued that much of the Wichita should be considered as late Carboniferous rather than Permian. The most important criteria in this connection, however, are those derived from paleobotanical data. Recent work by Read, although not as yet published, is cited by King (1942) to show that *Callipteris*, diagnostic of the Autunian stage of the lower Permian, makes its appearance at the level currently considered as the base of the Wichita.

The Wichita is thus later than the stage represented by Kounova; but although the two are arbitrarily separated by an arbitrary period boundary, the actual time interval need not have been very great. I have repeatedly pointed out that the Wichita fauna was not one newly evolved at the time, but appears to have its roots in the Carboniferous, and similarities between an early Autunian fauna and one from the late Stephanian are thus to be expected. In North America vertebrates of pre-Wichita age, which are probably closer in time to those of Kounova, are known from the Pennsylvania-West Virginia-Ohio region and possibly other areas, but these faunas are as yet too poorly known to make comparison profitable.

Certain differences which exist between the Kounova and Wichita vertebrate assemblages are correlated with the nature of the deposits and the nature of the conditions under which deposition occurred. The Kounova remains are preserved on the surface of slabs of the "cannel." The characteristic Wichita matrix, on the other hand, is a clay, with little lamination, from which the fossils are excavated as three dimensional structures. The Kounova locality suggests deposition in the bottom of a quiet pool; much of the Texas material appears to have undergone considerable transportation. Thus at Kounova there was a better chance for the preservation and recovery intact of remains of smaller animals than in the Wichita clays.

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[1] The "classic" Wichita faunas are from the Belle Plains and Admiral formations; lower formations were long considered as pertaining to the Cisco group. In recent years, however, there has been a general tendency toward lowering of the boundary, so that the underlying Putnam, Moran and (most recently) Pueblo formations are included in the Wichita.

The Kounova environment seems to have been that of a coal-swamp region in which fishes and aquatic amphibians would be abundant and terrestrial animals rare; the Wichita deposits appear to have been formed by streams whose "catch" included a considerable percentage of terrestrial types. In sum, the Kounova fauna would be expected to include a greater representation of small vertebrates, particularly fishes and amphibians than the Wichita beds; in the latter, a greater percentage of large animals, including more terrestrial amphibians and reptiles, would be expected.

Original faunal list. Below are listed the vertebrates from Kounova as described by Fritsch. It appears unnecessary to refigure this material; full references are given to Fritsch's plates which are extremely valuable despite some inaccuracies. Part of the Fritsch material was studied by me during a visit to Prague a number of years ago, but I have in this revision relied in great measure upon these plates. Not included are several forms from other Bohemian localities which may be of comparable age but are not members of the actual Kounova fauna. Brief discussions of some of the amphibians are given by Steen (1938), but I am not aware of the description of any new forms from Kounova since Fritsch's work.

ACANTHODIAN FISHES.

Acanthodes punctatus III pp. 61-62, fig. 256, pl. 107, figs. 7-9.

SHARK-LIKE FISHES.

Orthacanthus kounoviensis II pp. 107-109, fig. 185; pls. 83, fig. 1; 84; 85; 86, figs. 1-4; 87, figs. 1, 2, 5, 7; 90.

Orthacanthus pinguis II p. 109; pl. 87, figs. 3, 4, 6.

Pleuracanthus ovalis III pp. 13-15, figs. 201-205; pl. 91, figs. 7-10, ? 11.

Brachiacanthus semiplanus II p. 113; pl. 83, fig. 10.

Platyacanthus ventricosus II p. 113; pl. 86, fig. 5.

Tubulacanthus sulcatus II p. 113; pl. 88, fig. 14.

Hybodus vestitus II pp. 97-98; pl. 73, fig. 14.

Vertebrae ? II pp. 113-114; pl. 88, fig. 17.

LUNGFISH.

Ctenodus obliquus II pp. 66-84, figs. 144-148, 164; pls. 71; 72, figs. 4-12; 73, figs. 1-13; 74-79; 80, figs. 5-12.

Ctenodus applanatus II p. 85; pl. 72, figs. 1-3.

CROSSOPTERYGIANS.

Megalichthys nitens III p. 75, pl. 88, figs. 15, 16.

PALAEONISCOID FISHES

Trissolepis kounoviensis III pp. 76-80, figs. 277, 278; pls. 109-112.

Acentrophorus dispersus III pp. 81-83, fig. 279; pls. 113, 114.
Progyrolepis speciosus III pp. 118-120, fig. 308; pl. 131.

AMPHIBIANS.

Ophiderpeton pectinatum I p. 122; pl. 20, figs. 1-10.
Ophiderpeton vicinum I pp. 123-124; pl. 19, figs. 2-8; pl. 24, fig. 2.
Ophiderpeton corvinii I p. 124; pl. 20, figs. 11, 12.
Sparodus crassidens I pp. 86-88; fig. 40; pls. 9, figs. 1, 2, 4. 8, 9; 10, figs. 1-8.
Hylonomus pictus I p. 89; pl. 12, figs. 14, 15.
Porierpeton nitens II p. 42; pl. 70, figs. 9-11, 13.
Macromerion schwarzenbergii II pp. 37-40, fig. 140; pls. 65; 66; 67, figs. 3-14, ? 16-24, ? 26; 68, figs. 10-15; 69.
Macromerion simplex II p. 41; pl. 67, figs. 1, 2.
Keraterpeton gigas II p. 42; pl. 69, fig. 8.
Branchiosaurus ? robustus I p. 84; pl. 10, figs. 9, 10.
Branchiosaurus ? venosus I p. 83; pl. 9, figs. 5, 6, ? 7; ? 10, fig. 8.
Dawsonia polydens I, pp. 90-92, figs. 42, 43; pls. 11; 12, figs. 1-13.
Limnerpeton dubium I p. 157; pl. 33, figs. 4, 5.
Dendrerpeton ? foveolatum II pp. 8-9, fig. 128; pl. 49, figs. 10-13; 51, figs. 2-9.
Macromerion ? abbreviatum II p. 40; pl. 68, fig. 2.
Macromerion ? bicolor II p. 41; pl. 67, fig. 15; 70, figs. 1-8.
Macromerion ? juvenile II p. 41; pl. 68, fig. 1.
Macromerion ? pauperum II p. 41; pl. 68, figs. 6-9.

REPTILE.

Naosaurus mirabilis III p. 121; IV pp. 86-87, fig. 386.

These groups may be reviewed in turn. As will be seen, many revisions of Fritsch's lists are necessary, and many of the tetrapod forms are to be re-interpreted in the light of newer knowledge of other faunas.

Acanthodian fishes. The "spiny sharks," mainly characteristic of the Devonian, survived into the Permian, in Europe at least, but because of their typically delicate structure and small size are preserved in the late Paleozoic only under particularly favorable circumstances (such as those at Lebach). From Kounova only a few spines of *Acanthodes* are reported, in Texas none has been positively identified.

Shark-like fishes. The Pleuracanthodii were apparently common inhabitants of fresh waters in the late Carboniferous and early Permian. Their remains are common at Kounova;

much of the material illustrated in Fritsch's plates 83-87 and 91 are Kounova specimens belonging to this group. Some of the material consists of the calcified cartilages of jaws, visceral arches and braincase; spines, usually with the characteristic double row of denticles, are not uncommon; teeth, showing variants of the characteristic three-pronged pleuracanth pattern are abundant. Fritsch attempted to distinguish three genera—*Pleuracanthus*, *Orthacanthus*, *Xenacanthus*—among his specimens of Carboniferous and Permian pleuracanths from Bohemia. Most of the material from Kounova is placed by him in a single species, *O. kounoviensis*, a large form with spines of the *Orthacanthus* type. A second supposed species of *Orthacanthus*, *O. pinguis*, is distinguished by the fact that the two rows of "teeth" on the spines are more widely separated than in *O. kounoviensis*. However, this character seems to be a variable one (note, for example, the variations between specimens included by Fritsch in *O. bohemicus* of Nyran, pl. 83, etc.) and does not seem to be valid. On the other hand, *Pleuracanthus ovalis*, in which the "teeth" are set on the lateral margins of the spine, appears to be a valid although relatively rare form.

Fritsch gave several other names to fragmentary specimens which are apparently pleuracanthid in nature; it is probable—although impossible to determine definitely — that they are synonymous with *O. kounoviensis* as the common pleuracanth in the deposit. *Brachiacanthus semiplanus* from Kounova is represented by a single unornamented spine of a sort which Fritsch elsewhere ascribes without hesitation to *Orthacanthus* (cf. pl. 83, fig. 10, with pl. 82, fig. 18, etc.). *Platyacanthus ventricosus* of Kounova (pl. 86, fig. 5) is a spine very closely comparable to the type of "*Anodontacanthus*" *americanus* of Hussakof (1911, pl. 26, fig. 5). As I have recently pointed out (1942, p. 227) this latter form is probably a pleuracanth. *Tubulacanthus sulcatus* is known only from a spine tip, apparently much weathered, seemingly indeterminate, but possibly pleuracanth in nature. *Porierpeton nitens* is a name given by Fritsch to certain "porous" skeletal elements which he included among the Amphibia. However, certain of the Texas pleuracanth specimens have a similar texture, and the visceral arch material from Texas includes an element (which I have not identified) comparable to that figured by him as *Porierpeton* in his plate 70, figure 10.

The Kounova pleuracanth material is very similar to that of the Texas redbeds, more especially that in the Wichita formations. Calcified cartilages are not uncommon and may be locally abundant; teeth are very common in many localities. The spines are less common. The few available to me are all of the *Orthacanthus* type; I have not seen the *Pleuracanthus* type of denticulation. The only remains in the Kounova materials indicative of the presence of sharks typical of saline waters is a single tooth described as "*Hybodus*" *vestitus.* In the Wichita such materials are quite rare, but are occasionally found in localities which lie close to marine sediments laterally or vertically and thus may be suspected of having been laid down in brackish waters.[2] Included are several specimens of spines of the *Hybodus* type.

Actinopterygian fishes. The Carboniferous and early Permian were times in which there flourished a great variety and abundance of palaeoniscoids, mainly of small size. In certain deposits their remains are abundant, in other localities (as at Kounova and in the Texas redbeds generally) they are relatively rare. Their rarity as fossils may be attributed in great measure to the fact that they were presumably a staple food supply for many of the contemporary predators as well as to the fact that unusual circumstances must be present for their adequate preservation. At Kounova only three palaeoniscoids were described by Fritsch—*Sphaerolepis* (*Trissolepis*) *kounoviensis*, "*Acentrophorus*" *dispersus*, *Progyrolepis speciosus*. Obviously this is not a fauna adequately representing the assemblage of palaeoniscoids present in Europe at the time, but merely an inadequate "random sample." Of the three forms, *Sphaerolepis* is represented by a fairly good set of materials and appears to be a good generic type without close relationships. The other two are inadequately known; I am not aware of any recent discussion of their nature or relationships by students of the palaeoniscoids except for Gill's note (1923, p. 38) that "*Acentrophorus*" *dispersus* does not belong to that genus.

In the Wichita (cf. Dunkle, 1939) we find likewise a sparse and not too representative assortment of palaeoniscoids, most of them also inadequately known; only five species are reported from both the Wichita and the overlying Clear Fork beds com-

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[2] I have recently reviewed such finds (1942, 220-227); in addition to the forms then known there has since been discovered in the Wichita a tooth of cochliodont type (cf. *Deltodus*).

bined. Two of the three Kounova genera may be present. *Sphaerolepis* is reported but doubtful. *Progyrolepis* is not recorded in the American literature, but Dr. D. H. Dunkle informs me that he is currently studying Wichita material of this genus.

Lungfish. A large percentage of the Kounova material consists of tooth plates and other bones of lungfishes. Most were first described by Fritsch as *Ceratodus barrandei* but later ascribed by him to *Ctenodus obliquus* (the type material of which is from the Westphalian of Newsham). This material has been discussed by Watson and Gill, (1923) who identified many of the elements figured by Fritsch. As these authors note, the Kounova lungfish belongs to the genus *Sagenodus.* It is none too likely that the species is the same as that found in England at a much earlier time, and the Kounova lungfish may be appropriately termed *Sagenodus barrandei.* Two specimens of dental plates from Kounova were smaller and differed in various points from the majority of the finds and hence were regarded by Fritsch as a separate species, *Ctenodus applanatus.* Similar plates in American materials have been found to be nearly immature specimens of "normal" *Sagenodus* plates and, *applanatus* can be confidently regarded as a synonym of *barrandei.* Certain bones included by Fritsch among the supposed amphibian material seem also to pertain to *Sagenodus.* Thus his plate 67, figure 14 is a *Sagenodus* quadrate (cf. Watson and Gill, fig. 11), and figure 20 of the same plate is perhaps a second specimen of this nature; plate 70, figures 6 and 7 may be a lungfish jaw element, as Fritsch himself suggested.

In Europe the genus *Sagenodus* is unknown beyond the time at which the Kounova sediments were deposited; indeed, as far as I am aware, no later Paleozoic (Permian) dipnoans are known from that continent except for the rare and very aberrant *Conchopoma* from Lebach and two specimens from beds regarded as basal Permian and hence only slightly later than Kounova. These last include a single specimen from Koschtialov, Bohemia, named "*Ctenodus*" *tardus* (Fritsch, pl. 80b) and another from Igornay in the Autun basin — *Megapleuron rochei* (Gaudry 1883, fig. 246). Both are nearly complete fishes, but cranial and dental features are obscure and generic assignment is impossible. This paucity of Permian lungfishes is in strong contrast to their abundance in earlier deposits and again in the Triassic.

A somewhat different situation is found in the North American Permian. There are few traces of lungfishes in the Clear Fork beds, but in the middle and lower parts of the Wichita *Sagenodus* is present and abundant despite the definite palaeobotanical evidence of the Permian age of these beds. Earlier Wichita finds (some then considered as Cisco) were reviewed by Romer and Smith (1934, 711-714); during the past decade a wealth of *Sagenodus* plates and teeth have been found as the result of work by the Museum of Comparative Zoölogy in the lower levels of the Wichita. This material is strikingly similar to that from Kounova pictured by Fritsch, both as to its general nature and the range of variation present; if we did not know otherwise, the Kounova material could be readily accepted as derived from a Texas locality.

Crossopterygians. Of the two major types of late Paleozoic crossopterygians, coelacanths are as yet unidentified from Kounova and, while definitely present in the Texas beds, are rare and were not identified there until recent years (Westoll, 1937). Of the typical crossopterygians (Rhipidistia) the last known representative in Europe is *Megalichthys* of the Carboniferous; none are known there in the Permian. Fritsch reports and figures scales of this genus from Kounova. In America the rhipidistians (like *Sagenodus*) persisted later than in Europe, for there have been found at several localities in the middle and lower portions of the Wichita specimens of *Ectosteorhachis*, a genus close to *Megalichthys* and often considered synonymous.

Amphibians. Fritsch lists from Kounova eighteen species of amphibians, assigned to ten genera. The deposit is especially rich in amphibian material, but this list needs considerable revision.

Most of the amphibian material pertains to members of the important labyrinthodont group. Apart from several rhachitomes there is positive evidence of the presence of an embolomere highly comparable, in such respects as are known, to the Wichita form usually termed *Cricotus* but apparently more properly called *Archeria*.[3] The most distinctive material consists of two typical embolomere pelves (pl. 66, figs. 1, 2; pl. 67,

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[3] The genus *Cricotus* was based upon embolomere vertebrae from the lower Stephanian of Illinois. It is very improbable that the embolomerous form or forms from the Texas deposits of considerably later age are generically identical. However the humerus described by Case (1915, 170) under the name of *Archeria* is that of the Texas "*Cricotus*" and it appears unnecessary to coin a new term.

figs. 1, 2). Fritsch correctly identified them as pelves, but misinterpreted their structure. They are very similar to the pelvis of *Archeria*. The first is somewhat larger than any complete Wichita specimen of that genus, but there are fragmentary remains of Texas embolomeres of this size; the second specimen is somewhat small and apparently somewhat immature. Apart from the pelves, other definitely embolomere remains are few. Plate 66, figure 5 is a typical embolomere intercentrum; figure 4 of the same plate is a femur with incomplete ends (? immature, or weathered?) which as far as preserved compares well with that of "*Cricotus*." I cannot be sure of the nature of plate 66, figure 3. The spine-like structure of plate 69, figure 8, called *Keraterpeton giganteum* by Fritsch appears to be, as he suggested, a tabular ("epioticum"), but of an embolemere, not a nectridian. Apart from this, however, I am unable to identify with confidence any embolomere material among the remains of skulls and jaws from this locality; most of them appear to belong to rhachitomes. *Archeria* is distinguished generically by the possession of closely-crowded slender teeth with somewhat chisel-like tips; no such teeth are known from Kounova, and none of the jaw fragments preserved is sufficiently complete to show whether other characteristic embolomere features were present.

The Kounova embolomere material was included by Fritsch in his genus *Macromerion*. This, however, included a melange of various amphibian and reptilian remains, as recognized by Steen (1938, p. 262), and it seems best to utilize the name for the reptile. In default of any proof of identity with *Archeria* it seems inadvisable to refer it to the American genus. *Memonomenos* (Steen, 1938, p. 240) is a Bohemian genus of approximately the same age which is probably an embolomere, and the Kounova form may be provisionally referred to it as *Memonomenos simplex* (the specific name has as a holotype a characteristic pelvis).

Rhachitomous amphibians were at one time believed to be almost entirely confined to the Permian; we now know, however, that they were abundant well back in the Pennsylvanian, and they appear to have formed a large percentage of the amphibians present at Kounova as in the Texas Wichita. There are apparently nine names (the last nine of the list given above) applicable to Kounova rhachitomes. The material, however, is so fragmentary that it is difficult to get any adequate idea of the nature of the forms concerned or to compare them with Texas genera. The situation is complicated by the fact that the type of fossilization at Kounova favors the preservation of larval or immature specimens as much or more than adults, so that size is not useful as a criterion for distinguishing one form from another. There are certainly two or three rhachitomes present; possibly a few more; but it is probable that many of the available names are synonyms.

Evidence of the presence of a rhachitome of rather good size comparable in nature to *Eryops* of the Texas deposits and to *Onchiodon* and *Actinodon* of Europe is afforded particularly by the partial jaws shown by Fritsch in plate 68, figures 2 to 9, to which the names *Macromerion ? abbreviatum* and *M. ? pauperum* were given. As may be seen (cf. Sawin, 1941; pl. 5) these jaws appear highly comparable to materials of *Eryops* of the Wichita and presumably to the closely related European Lower Permian genus *Onchiodon*. The jaw fragments indicate a form with a skull length of perhaps 22 cm., that is, about half the size of the familiar Middle Wichita specimens of *Eryops*. To this same form belong some or all of the teeth and jaw fragments of plates 67 and 70 referred to *M. schwarzenbergii* and *M. bicolor*; to it may also belong the *Eryops*-like scales of plate 65, figures 4 and 5; plate 67, figure 13; plate 69, figure 7; and such foot material as plate 67, figures 19, 21 and 22. There are, however, no other remains of any large amphibian which can be referred here, and the only other possible material is such "larval" specimens as appear to be of the general *Eryops-Onchiodon* type. One small form of this sort is "*Dendrerpeton*" *foveolatum*, founded on several specimens from Kounova, among which we here specifically designate that figured on plate 51, figure 2 (no. 108) as the holotype. This specimen includes part of the skull and postcranial elements of a small and obviously immature rhachitome, with a supratemporal but no intertemporal bone present in the skull table; particular attention is called to a clavicle (directly back of the left orbit) of the narrow, distally striate type characteristic of *Eryops* and its close kin. Whether or not several other specimens assigned to this species by Fritsch are generically or specifically identical is not certain. The interclavicle figured by Fritsch in plate 10, figure 9 as "*Branchiosaurus?*" *robustus*[4]

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[4] As I have pointed out elsewhere (Romer, 1939) *Branchiosaurus* is a term used for small, larval specimens of various rhachitomes.

is a small specimen of the type seen in the *Eryops* group; with this was associated a partial jaw of appropriate size. "*Branchiosaurus*" *venosus* is the name given by Fritsch to a number of parasphenoids[5] from Kounova (pl. 9, figs. 5-7; cf. also pl. 10, fig. 8). One or more of these may well belong to the type of rhachitome here discussed, and we may note a similar parasphenoid forming part of the type of "*Dendrerpeton*" *foveolatum.*

There is a considerable amount of Kounova material representing both upper and lower jaws of small amphibians. We may note specimens seen on plate 49, figures 10-13; plate 51, figure 3 ("*Dendrerpeton*" *foveolatum*); plate 67, figure 15 (*Macromerion bicolor*); the angular of plate 67, figure 12. Some of this material may belong to the present form, but certainty is impossible. It must be remembered that little diagnostic value can be placed on the distribution of teeth in a labyrinthodont jaw ramus because the type of tooth replacement (in alternating waves) would give the same jaw seemingly very different types of dental equipment at different periods.

There is thus considerable probability—although in individual points little certainty—that much of the Kounova amphibian material pertains to varied growth stages of a rhachitome similar to *Eryops* of the Wichita.

The first specific name applied to any of the material discussed is *foveolatum.* Generic assignment is difficult; no generic name used at Kounova is available. Geographical "propriety" suggests the use of a European name; *Onchiodon* is a seemingly closely related form of somewhat later date. We may therefore term this rather synthetic amphibian *Onchiodon? foveolatum.*

Dawsonia polydens was founded by Fritsch on the basis of a number of fragmentary specimens of small amphibians illustrated in plates 11 and 12. The most important single specimen is his No. 106, which may be specifically designated as the holotype. It is by no means sure that all these materials belong to the same animal. The holotype includes a rhachitomous neural arch (pl. 12, fig. 5); a feebly ossified scapula; some inadequate remains of limb and girdle elements; sculptured elements (pl. 12, fig. 6) which may be an expanded clavicle and interclavicle; some well sculptured skull bones; a parietal

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[5] Bulman and Whittard (1926, 558) consider them as interclavicles, but they are surely incorrect in this statement.

viewed from the ventral surface; an interclavicle. Fritsch associated with the type several other specimens in which the most characteristic element is the pterygoid. This is a puzzling element (it will be noted that although several pterygoids are figured by Fritsch on plate 11, none is present on the holotype). There appears to be a very deep quadrate (and otic) ramus, but the nature of the braincase articulation is not clear, and there is no evidence of the normal labyrinthodont pterygoid flange. The palatal ramus as preserved is a long, slender structure, heavily denticulate. I know of no well-known labyrinthodont comparable in respect to the pterygoid. Two of the pterygoids figured by Fritsch show along the lateral margin a row of teeth at right angles to the pterygoid's palatal surface. Possibly these may be a row of teeth on palatine and ectopterygoid.

There is no conclusive evidence that this palatal material belongs to the same amphibian as the holotype. The association rests on the fact that the parasphenoid associated with one of the palatal specimens appears to be similar to the holotype parasphenoid. The "microsaurs" *Pantylus* and *Sparodus* (the latter apparently present at Kounova) have a comparable pterygoid structure, and it is not impossible that the palatal material belongs to the latter genus.

No confidence can be placed on Fritsch's restoration of the skull roof from isolated elements, some of them of questionable nature. In this connection we may note the skull table named *Macromerion ? juvenile* (pl. 68, fig. 1). This is of appropriate size for *Dawsonia*. The upper surface, where seen, is strongly sculptured. The skull table is relatively long and narrow, as compared with eryopids. There are typical otic notches; cheek elements appear to have been firmly united to the table as in rhachitomes and in contrast with typical embolomeres. The sutures surrounding the postparietals ("oberes Hinterhauptbein") indicate that the tabulars were small in diagnostic rhachitomous fashion. Sutures are not readily seen in the temporal region in Fritsch's figure, but Steen (1938, 262) states that (in contrast with the *Eryops* group and most Permian genera) both intertemporal and supratemporal were present; it will be noted that the parietal of the *Dawsonia* holotype (pl. 12, fig. 3) is incised along its lateral margin as if for the reception of this element. It is, hence, possible that this skull table is that of *Dawsonia*, and that the form is a primitive rhachitome of the *Trimerorhachis* type known in the Texas Wichita.

Of the second major division of Paleozoic amphibians—forms with "holospondylous" vertebral centra, i.e., the lepospondyls in a broad use of that term—two types are clearly present at Kounova. *Ophiderpeton*, a snake-like aistopod common in earlier Pennsylvanian deposits, is represented, apparently by a single specimen. This is described as *O. vicinum*. Two other specific names are given to specimens of the "kammplatten" which Fritsch believed to belong to *Ophiderpeton*; I have nothing to add to the controversy regarding the nature of these structures. *Ophiderpeton* is not reported from the Wichita; a small and delicate form of this sort is not likely to be preserved there.

A second, and very different, lepospondyl is *Sparodus crassidens*. As I hope to point out at another time, *Sparodus* is closely related to *Pantylus*, known only from the Clyde Formation of the Wichita group. *Pantylus* is not, as usually stated, a cotylosaurian reptile but a lepospondylous amphibian of the "microsaur" group. *"Hylonomus" pictus* is the name given to an amphibian jaw fragment with blunt teeth; it is indeterminate, but may well belong to *Sparodus*.

Reptiles. In his earlier descriptions no reptiles of any sort were recognized by Fritsch at Kounova. Later he recognized a single specimen as reptilian. It now seems clear that at least two are actually present in the material.

A small spine fragment from Kounova was at first thought by Fritsch to pertain to a fish. Later, with the publication of descriptions of American specimens of the *Edaphosaurus-Naosaurus* type, he realized its identity (cf. Romer and Price 1940, pp. 388-389) with them. *Edaphosaurus* is one of the common pelycosaurs of the Wichita, but the American species of this age are larger; the smallest Wichita specimen known to me has a length of centrum twice that of Fritsch's. The somewhat earlier age of Kounova may account for at least part of the size difference; there appears to have been a steady increase in the size within the *Edaphosaurus* "phylum" during Wichita time.

The name *Macromerion schwarzenbergii* seems properly applicable to a large pelycosaur which can be definitely identified as such in the Kounova cannel although only a small percentage of the material described under this name belongs here.

I am embarrassed to find that this material was overlooked by Price and the writer in our recent review of pelycosaurs (1940) due to its "burial" in Fritsch's work amongst a series of amphibian remains. The most characteristic piece is the upper jaw fragment figured by Fritsch on plate 65, figures 6 to 9. This is an inner view of a right maxilla which in almost every respect is very closely comparable to that of *Dimetrodon* and other typical American sphenacodonts (cf. Romer and Price 1940, pl. 9). The anterior portion is missing, and with it the large pair of "canines" characteristic of sphenacodonts; Fritsch, however, notes that the base of a large canine is present. There are eight post-canine teeth preserved, whereas 12 or 13 are common counts for Wichita sphenacodonts; the bone is, however, incomplete posteriorly and several additional small teeth may have been present in life. There is a thick supracanine swelling of the type characteristic of sphenacodonts and even an indication of the antero-posterior groove seen to cross this swelling in well preserved sphenacodonts. The dorsal margin of the bone is, as in American sphenacodonts, thin and irregular along its line of suture with the lacrimal. At the lower left hand margin of the specimen is seen the deep recess into which fitted the anterior end of the palatine, a bone which here formed the posterior margin of the choana. The teeth are, as in American sphenacodonts, somewhat recurved and compressed at their tips. The size of the maxilla is appropriate for a sphenacodont little smaller than *Dimetrodon limbatus*, the typical Wichita form.

A second specimen which may well belong to the same animal is an interorbital region of a skull roof, seen in plate 65, figure 1. This bears a somewhat rugose surface as in large sphenacodonts. It seems probable that the whole central portion of the specimen consists of a pair of elongate sphenacodont frontals and that the apparent diagonal lines crossing these two elements are cracks rather than sutures. On the left side is a clear suture outlining the prefrontal. Posterior to this, it would seem that the postfrontal excludes the frontal from the orbit, an unusual (although not impossible) condition for a pelycosaur; however, the apparent inner border of the postfrontal may be a crack rather than a suture.

The bone in figure 2 of the same plate, which Fritsch thought might be a fish vomer, is a reptilian pterygoid, probably although not certainly pelycosaurian. The teeth crowning the flange are only preserved in part and are rather small, relatively, for a sphenacodont; and as an isolated structure the pterygoid could be interpreted equally well as an ophiacodont. In size it is a bit small for the other skull material just described, but it might nevertheless pertain to the same animal. The vertebra of plate 65, figure 3 is an appropriate pelycosaur caudal. The limb bone of plate 69, figures 2 and 3 is the proximal part of a left tibia, identifiable in every particular as that of a sphenacodont. Except that it is slightly immature and that, hence, the articular surfaces are less completely ossified, it can be directly compared with a tibia figured by Romer and Price (1940, pl. 32); it is somewhat small for an animal such as that to which the maxilla belonged. Plate 69, figure 6 is a crushed radius of similar size to the last (cf. Romer and Price, pl. 33). Not improbably the ribs seen in plate 68, figure 10 and plate 69, figures 4 and 5 are of sphenacodont type with the tuberculum broken off—a frequent occurrence in American material.

Of interest is the left pelvic girdle seen from the inner surface in plate 69, figure 1. One's first impression is that it is another embolomere pelvis; but, as far as preserved, it agrees perfectly with those of sphenacodonts (cf. Romer and Price 1940, pl. 28). This similarity is particularly true of the imperfect pubis, seen at the right in lateral view. The ilium as preserved differs from such a species as *Dimetrodon incisivus* in the length and rod-like character of its posterior extension and in the seemingly slight development of the blade. However, a comparable posterior development is seen in other American dimetrodons (as, for example, *D. loomisi*, Romer and Price 1940, fig. 27); the blade is rather variable in its development in American forms.

Certain of the unidentified bones on Fritsch's plate 67 may also belong to this pelycosaur as, for example, figure 18, which appears to be a metatarsal of sphenacodont type. We thus have, in the material here retained or included in *Macromerion schwarzenbergii*, evidence of the presence at Kounova of a good-sized pelycosaur closely comparable to *Dimetrodon* and related sphenacodonts of the Wichita and other American deposits. Since, however, the nature of the spines and other diagnostic features are not known, generic identification with American forms is not at present possible or advisable.

Taxonomic notes. The taxonomy of a series of fragmentary materials such as this is a difficult matter, and the situation is rendered worse in this instance because Fritsch in general failed to designate genotypes or species holotypes. Some points in this regard are here noted as related to the reptiles and amphibians.

Much of the tetrapod material from Kounova was included by Fritsch in the genus *Macromerion*, with a number of species.[6] No genotype was fixed by Fritsch, but Lydekker (1890, 160), properly, I think, fixed *M. schwarzenbergii* as the type. The material of the species, however, included elements of a lungfish, an embolomerous amphibian, at least one rhachitome, a reptile, and possibly other animals. The holotype is hereby designated as the specimen shown in Fritsch's plate 65, figure 6—a maxilla of a sphenacodont reptile. *M. simplex* is available as a specific (but not generic) term for the Kounova embolomere. *Macromerion bicolor*, *M.? juvenile*, *M.? abbreviatum*, *M.? pauperum* are, as noted above, terms available for rhachitomes from this locality. They date, however, only from 1885 (or 1886?) when pages 33-64 of Volume II of Fritsch's monograph were published; earlier available Kounova names which possibly or probably apply to rhachitomes are those which appeared in earlier portions of that work. These are, in order: *Branchiosaurus? venosus*, *B.? robustus*, *Dawsonia polydens*, *Dendrerpeton? foveolatum*, *Limmerpeton dubium*. These have been discussed above. Except for *Dawsonia polydens* none of these species is a genotype or should be considered as such.

Sytematic summary. As a result of our review of the Kounova material, the original list of forms given by Fritsch must be considerably modified. There appear to be about 16 forms whose presence at Kounova seems certain. The other species named by Fritsch are in all probability synonyms of those listed below and are given in brackets in the tabulation:

ACANTHODII.

1. *Acanthodes punctatus.*

SHARKS.

2. *Orthacanthus kounoviensis* [*O. pinguis*, *Brachiacanthus semiplanus*, *Platyacanthus ventricosus*, *Tubulacanthus sulcatus*].

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[6] *M. bayeri* was described from Nyran; part, at least of the material (Fritsch, pl. 64) is that of a good-sized rhachitome. It has an *Eryops*-like shoulder girdle, which Fritsch, followed by Lydekker (1890, 161), mistook for a pelvis (see Steen 1931, 7; Broili 1908, 52-53).

3. *Pleuracanthus ovalis.*
4. *"Hybodus" vestitus.*

ACTINOPTERYGII.

5. *Trissolepis kounoviensis.*
6. *"Acentrophorus" dispersus.*
7. *Progyrolepis speciosus.*

CROSSOPTERYGII.

8. *Megalichthys nitens.*

DIPNOI.

9. *Sagenodus barrandei* [*Ctenodus applanatus*].

LABYRINTHODONT AMPHIBIA.

10. *Memonomenos ? simplex* [*Keraterpeton gigas*]
11. *Onchiodon ? foveolatum* [*Macromerion abbreviatum, M. bicolor, M. ? pauperum, Branchiosaurus, ? robustus B. ? venosus, Limnerpeton dubium, Porierpeton nitens*].
12. *Dawsonia polydens* [*Macromerion ? juvenile*].

LEPOSPONDYLOUS AMPHIBIA.

13. *Ophiderpeton vicinum.*
14. *Sparodus crassidens* [*Hylonomus pictus*].

PELYCOSAURIA.

15. *Macromerion schwarzenbergii.*
16. *Edaphosaurus mirabilis.*

This fauna is, in its general aspects, one representative of the type expected in any European or North American assemblage of the late Carboniferous or early Permian, although the relatively restricted and fragmentary material from this single coal-swamp pool deposit presumably includes but a small part of the total fauna then present in the region. Among the fishes, pleuracanth sharks, the lungfish *Sagenodus* and palaeoniscoids are plentiful. Of the amphibians, there are both embolomeres and rhachitomes, labyrinthodonts and lepospondyls—the latter group nearing the close of their Paleozoic developmental period and not too abundant. Reptilian remains are not expected in any numbers in a coal-swamp deposit of this type, but the presence of *Edaphosaurus* and a typical sphenacodont indicate that the drier land areas may have had a varied fauna of primitive reptiles.

The Kounova fossil material is strikingly similar to that from the Texas Wichita. Many points of similarity have been noted in our discussion of the various groups and forms concerned. The material as a whole is of such a nature that if one familiar with Texas collections were presented with it without knowledge of its origins, he would consider it, with little or no question, as of Wichita origin. Most of the material could be assigned without difficulty to Texas genera (and even species); the relatively few exceptions would not be disturbing since it is common, even today, for any fairly extensive collection from a new Wichita locality to make some new addition to the fauna.

This similarity, however, does not appear in the faunal list as given above. None of the species as listed is a Texas species; relatively few of the generic names used are those of Texas forms. The reasons for this have been implied or stated more than once in our discussion of the various forms concerned. Texas and Bohemia are today regions remote from one another—about 5,700 miles by direct great circle distance across the North Atlantic, 10,000 miles along the shortest land route *via* Northern Asia.

In default of good proof to the contrary, one hesitates to claim generic or specific identity for two animals living in areas so remote geographically from one another.

Despite this conscientious attempt on my part to conceal the similarity of the faunas, their close relationship is still apparent. Of the sixteen genera listed from Kounova, four are definitely Texas Wichita forms and eight others might be generically identical as far as the evidence goes; four are unreported from Texas, but two, at least are based on rare and fragile materials readily overlooked there. Of the sixteen genera, thirteen are reasonably assignable to families known from the Texas deposits, and it is not improbable that further work in the Wichita may lead to future recognition of a complete identity of the faunas on the family level.

Palaeogeographical implications. This remarkable faunal similarity naturally leads to a reconsideration of the palaeogeographic situation. Vertebrate paleontologists have in recent years tended to be, on the whole, conservative in their views on earlier continental connections and relationships. As Matthew (1915) pointed out, nearly all Cenozoic faunal problems are best interpreted on the basis of fixed continents with none but the obvious "natural" connections above continental shelf boundaries between them; Simpson (1943) has recently reviewed the situation and affirmed Matthew's conclusions.

Concerning older geologic periods, however, the geographic picture is less clear as regards the vertebrate evidence. For the Mesozoic in general, continental vertebrate faunas are too few in number and too scattered to give any strong verdict on inter-continental relationships.[7] As regards the late Paleozoic the evidence is not decisive. It is unfortunate that until Permian times our knowledge of fossil vertebrates is almost entirely confined to Europe and North America. There is, however, a considerable body of data which suggests that at that time geographic relationships between these two continents were of a more intimate nature than was the case in the Cenozoic. The Kounova fauna is a case in point.

To explain the Kounova-Wichita similarities on the basis of "normal" continental relationships, one might point out, of course, that Eurasia and North America are today so similar in their faunas that they are often regarded as constituting a single Holarctic region, and argue that the similarities cited here between Texas and Bohemian forms are due to a continental configuration in the late Paleozoic similar to that of the Cenozoic, with intermigration between Europe and North America *via* Asia.

Upon closer examination, this argument loses much of its force. We do have, today, many resemblances between Eurasian and North American faunas. But how great are the resemblances between the two extremes, between North America and Europe—not Asia? Further, many of the faunal resemblances have to do with higher vertebrate groups, the mammals and birds, which can migrate with relative ease and rapidity. How great are, actually, the European — North American resemblances as regards lower vertebrates?

To answer this question I have tabulated and compared the amphibian and reptilian faunas of the two regions.[8] As perhaps the fairest method of formulation, I have put the question in this fashion: Of the genera and families present in Europe, what percentage are present in North America? This treatment is comparable to that given our discussion of the fossil faunas.

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[7] Von Huene and Nopcsa, notably, have argued ably for various "unorthodox" Mesozoic land connections. It is inappropriate to discuss the data on the present occasion, but I do not feel that their evidence is conclusive.

[8] My colleague, Curator Arthur Loveridge, has aided me in this compilation. I have not attempted to extend this comparison to the freshwater fishes, since I do not feel competent to deal with the systematic problems involved.

The modern European fauna comprises some 51 genera of reptiles and amphibians. Of these, only 12, or about 24 per cent, are also present in North America. There are 21 families present in Europe. Of these only 10, or about 48 per cent, are common to both continents.[9] It is obvious that the Kounova-Wichita resemblances were much greater. Generic identities are at a minimum 25 per cent, and may be as high as 75 per cent; family identities are not improbably as great as 87 per cent, and may prove to be still higher. At the end of the Carboniferous, resemblances between the lower vertebrate faunas of Europe and North America were, thus, roughly twice as marked as they are today, if the Kounova assemblage is representative.

If we cling to the concept that late Paleozoic continental relations were similar to those of later periods, how are we to account for the much greater resemblances between Europe and North America at that time? Several possible arguments come to mind. It might be claimed (1) that in the late Paleozoic the migration route *via* Asia was more readily traversed than in the Cenozoic; (2) that a longer period of time had been available for faunal diffusion; and, related to the last assumption, (3) that the Paleozoic groups concerned were old established and stable ones as compared with those involved in the Cenozoic faunal picture.

None of these suppositions appears to carry conviction.

1. We have almost no knowledge regarding the nature of possible land connections *via* Asia in the late Paleozoic, but the Cenozoic connection appears to be about as satisfactory a one as might be desired. The history of mammalian faunas indicates that, although, occasionally interrupted, it was freely open for migration for considerable lengths of time at various stages of the Cenozoic. For a relatively short period in very late Tertiary and Pleistocene days, the establishment of sharp climatic gradients would have hampered interchange of American and Eurasian amphibians and reptiles, but during the

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[9] The reverse formulation, i.e., compiling the larger North American list and determining the percentages of genera and families also found in Europe, gives, as expected, a distinctly lower percentage of common forms. If, however, African occurrences be added to European, the figures are about the same as those given above. It might be argued that the low percentage of common genera might be due to the work of taxonomic "splitters" of genera. However, in most of the types concerned, the genera are apparently broadly drawn.

greater part of the Tertiary, climatic conditions, as indicated both by the type of mammal migrants and by the flora (Chaney 1940), were favorable.

2. There is ample evidence that free communications between Eurasian and North American regions were in existence at least as far back as the beginning of the Tertiary, a span of time currently estimated, on the basis of radioactive phenomena, at about 70,000,000 years, and may have existed still earlier. We could not desire any longer span for a similar connection to account for the Kounova situation, for the simple reason that most of the groups concerned would not have been in existence at such an early date. Using a current estimate of 60,000,000 years for the Carboniferous, 70 millions would carry us back well into the late Devonian. Of about 11 orders and 15 families represented at Kounova, only 4 orders are known to have been in existence at such an early time, and not more than two or three of the families had been as yet developed.

3. It might be assumed that the relative lack of similarity between the modern faunas discussed is due to the fact that the types concerned have been in a rapid evolutionary phase, with consequent lack of thorough diffusion. This is not the case. Apart from the snakes, the major amphibian and reptilian groups now present were in existence by the beginning of the Cretaceous, and numerous and varied families representative of all of them were established by late Cretaceous or Eocene times. The snakes are poorly represented in the fossil record and appear to have undergone much of their differentiation during the Tertiary, and in their case alone late Tertiary climatic changes may have been a bar to free intermigration. In the Kounova-Wichita comparison, nine groups of ordinal rank include the common forms. One, that of the hybodont sharks, appears to have inhabited salt waters (although probably littoral) and hence affords unsatisfactory evidence. Two—rhipidistian crossopterygians and lung-fishes — were groups which were established well back in the Devonian and which appear to have evolved but slowly during the Carboniferous; their distribution at the end of that period may be adequately explained on the basis of "normal" continental construction. Three other groups — pleuracanth sharks, lepospondylous amphibians and embolomeres—appear to constitute an intermediate category as regards rate of evolutionary development. There is no reason to believe that any one of them was in

existence before the beginning of the Carboniferous.[10] We know little of them in the lower part of the Carboniferous and hence can say little about the rate of their evolutionary development. It is, however, quite possible that, once established, their development during this period was slow and that, hence, the similarities here between America and Europe could be attributed to communications *via* Asia.

Far different is the case of the three remaining groups—palaeoniscoid fishes, rhachitomous amphibians, pelycosaurian reptiles. Palaeoniscoids appear in the Middle Devonian, but were rare both in numbers and in variety of forms present until the end of the Devonian. Recent work has shown that at about the beginning of the Carboniferous there began within this group an explosive evolutionary phase which continued throughout the remainder of the Paleozoic. The oldest definitely known rhachitomes are mid-Pennsylvanian; there is abundant evidence that they were in a stage of rapid evolutionary advance and deployment during late Pennsylvanian times. The paucity of Carboniferous fossiliferous continental deposits other than those of coal-swamp type is responsible for the fact that we have little idea as to the time at which reptilian evolution began; but the development before the end of the Pennsylvanian of such specialized reptiles as the pelycosaur *Edaphosaurus* and the sphenacodonts is adequate evidence that the early evolution of the reptiles was a very rapid one. Close similarity—in some cases positive generic identity—between representatives in two regions of rapidly evolving groups strongly suggests intimate geographical connections between the areas involved.

The discussion above strongly suggests that in late Carboniferous times the possibilities of intermigration between Europe and North America were much greater than was the case in the Cenozoic *via* the Alaskan-Siberian bridge, and that, therefore, some more intimate type of connection was then present. Were the instance cited the only one leading toward this conclusion, the argument might be dismissed with relative ease. It is not, however, an isolated example. Throughout the later Paleozoic we find that in every case in which faunas of the same age and from the same general environment are known from the two sides of the Atlantic, they are remarkably similar in nature (cf. Nopcsa 1934).

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[10] Citations of Devonian pleuracanths are, as far as I know them, based on very fragmentary and systematically doubtful material.

The earliest faunas in which adequate material is available are those of Devonian fresh water fishes. Here every advance in our knowledge demonstrates increasingly the great similarity between the two continents. At one time this similarity was masked by the nomenclature. This is still true to a degree, and there are many rare, obscure, or doubtful genera reported only from one or the other of the two continents. It appears, however, that in almost every instance a form abundant in one continent can be proved present in the other. The crossopterygian *Eusthenopteron* is a case in point. This is common in the Upper Devonian of Quebec, but was thought to be a diagnostic American form, absent in Europe. During the last decade, however, it has been positively identified in collections from the "Old Red" of both Scotland and the Baltic region (Westoll 1937; Jarvik 1937).

American Mississippian continental vertebrates are inadequately known; our next opportunity for comparison comes in the Pennsylvanian, where both Steen and the writer have studied with some care the coal-swamp tetrapods of both continents. Both of us have been strongly impressed by the remarkable similarities of the faunas. Many of the genera are identical, and certain of the differences remaining are attributed in part to inadequate material and to the fact that the best faunas available on either side of the Atlantic (Linton, Nyran) are somewhat different in age (Romer 1930, Steen 1931, etc., cf. Westoll 1944, pp. 105-108). Westoll (1944) has studied the Pennsylvanian fish faunas of the two continents with particular reference to the Haplolepidae. His careful analysis of the situation leads him to believe that very free intermigration must have been possible, and that the most satisfactory explanation is afforded by the hypothesis of continental drift.

In the Permian, comparison can be made only in the earliest part of the period, for continental vertebrates disappear from the American record after the deposition of the lower Clear Fork. The faunas of the American redbeds and those of the Rotliegende were once thought to differ markedly. This, however, was due in part to inadequate knowledge of the faunas (particularly that of Europe) and in part to the fact that the type of sediments tended to the preservation of animals of different sorts in the two regions—small pool-dwellers in Europe, more of the larger and more terrestrial types in America. Increasing knowledge of the faunas tends to emphasize the basic similarity of the two regions (cf. Romer 1925, etc.). However the resemblances here are somewhat less marked than in the late Carboniferous. In some cases identical genera are present; in others, we are sure that although closely related forms were present, the genera were distinct. There is hence less evidence for direct contemporaneous connection of the continental areas. But, even so, it may be remarked that the comparisons between the Texas redbeds fauna and that of central Europe, which even on a Wegnerian basis cannot have been less than 2,000 miles apart, are just as close as they are between the Texas fauna and that of the supposedly contemporaneous Abo fauna of New Mexico, only a few hundred miles away!

Consideration of Paleozoic vertebrate faunas as a whole thus leads to the conclusion that during this time North America and Europe were connected in such fashion that extremely free and relatively rapid faunal interchange was possible among the rapidly evolving vertebrate groups. Discussion of the type of connection involved is handicapped by the fact that until Middle Permian times we know almost nothing of the vertebrates of any regions except Europe and North America. It is possible that the similarities between these two continents were due merely to a condition in the Paleozoic in which vertebrate faunas were similar throughout the world, with extremely easy interdiffusion between all areas, by way of normal intercontinental connections and that the faunas of other regions, if known, would also be similar in composition. This assumption cannot at present be proved or disproved, but it assumes, because of the rapidity of the evolution undergone by many of the groups concerned, an ease of intermigration difficult of belief. The available evidence strongly suggests (although it does not prove) intimate and direct connection in the later Paleozoic between Europe and North America, whether by apposition of the two continental masses under a Wegnerian interpretation or, with fixed continental positions, by a substantial North Atlantic bridge since destroyed.

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