LOWER PERMIAN PELYCOSAURS FROM THE ENGLISH MIDLANDS

by ROBERTA L. PATON

ABSTRACT. Three dentigerous bones from sandstones in the Kenilworth area are described and allocated to different genera of pelycosaurs. One of the specimens, the holotype of *Oxyodon britannicus* von Huene, 1908, is a sphenacodontine, but the generic name *Oxyodon* is preoccupied and the species is assigned to the genus *Sphenacodon* Marsh. The second specimen is designated as a new sphenacodontid species, *Haptodus grandis*; and the third is identified as belonging to the genus *Ophiacodon* Marsh—previously known only from North American deposits. The palaeoecological and stratigraphical significance of the specimens is discussed; they provide additional evidence of an Autunian age for the Kenilworth Sandstones.

PELYCOSAURS are the dominant reptiles of the early Permian; they are also among the oldest known fossil reptiles. Several genera have been described from Upper Carboniferous (Upper Pennsylvanian) deposits in North America and western Europe. These include *Clepsydrops*, a primitive ophiacodont from Illinois (Cope 1875); *Stereorhachis*, an ophiacodont from Autun in France (Gaudry 1880); some species of *Edaphosaurus* from North America (Peabody 1957); *Petrolacosaurus* from North America, tentatively assigned by Romer (1966, p. 372) to the Edaphosauria; *Macromerion*, an advanced sphenacodont from the Stephanian (Upper Pennsylvanian) of Kuonova, Bohemia (Romer 1945); and *Milosaurus*, a primitive sphenacodont from Illinois (DeMar 1970). Thus members of all three suborders of pelycosaurs were present in Upper Carboniferous deposits and it is obvious that the order itself must have originated at an earlier date, possibly Middle Pennsylvanian (Westphalian A) or earlier. Carroll (1964) has described the earliest known pelycosaur, *Protoclepsydrops*, an ophiacodont from near the base of the Pennsylvanian at Joggins, Nova Scotia (Westphalian A and B), although in a later paper (Carroll 1969) he has cast doubts upon its assignation to the Pelycosauria.

The vast majority of pelycosaurs come from localities in North America, only a few remains having been collected from western European localities, and two genera of caseids from Russia (Olson 1962). Nothing definitely assignable to the Pelycosauria has been found in other areas. The only pelycosaur previously reported from England is *Oxyodon britannicus* von Huene (1908), based upon part of a maxilla from probable Lower Permian rocks near Kenilworth. Von Huene (1908, 1925) thought that '*Dasygnathus*' from the Trias of Findrassie near Elgin in Scotland, might be pelycosaurian but Walker (1964) showed that this specimen belonged to the archosaur *Ornithosuchus*. No other pelycosaurian bones have been described from the British Isles. In the present study, two more fragments from approximately the same horizon as *Oxyodon* and which can be definitely identified as pelycosaurian are also described. Their interest lies in the scarcity of pelycosaur material from England, and in showing that a range of different types of pelycosaur was in fact present in English deposits. All the specimens were collected during the nineteenth century. Unfortunately the

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localities are not precisely known but it is believed that there were two—one very close to Kenilworth and the other, one mile north-west of Coventry (grid ref. SP 327 797). Both are probably now obscured by buildings. Abbreviations preceding specimen numbers: GSM = Geological Survey Museum; Gz = Warwick County Museum.

SYSTEMATIC PALAEONTOLOGY

Order PELYCOSAURIA
Suborder SPHENACODONTOIDEA
Family SPHENACODONTIDAE
Subfamily SPHENACODONTINAE
Genus SPHENACODON Marsh, 1878
Sphenacodon britannicus (von Huene)

Plate 84, figs. 1, 2; text-fig. 1

1908 *Oxyodon britannicus* von Huene, p. 431, fig. 1.

Holotype. GSM 22893 (text-fig. 1B) and GSM 22894 (text-fig. 1A); part and counterpart of a left maxilla.

Locality. Kenilworth.

Horizon. Kenilworth Sandstone, probably Autunian, Lower Permian.

Description. The two specimens, though part and counterpart, do not preserve identical portions of the left upper jaw. GSM 22894 shows an impression of the external surface of part of the left maxilla while 22893 shows the left maxilla itself, and part of the premaxilla, but with the external surface badly broken.

The specimens were first noted in the 74th Annual Report of the British Association (Lomas 1904) as 'Dinosaurian jaws, Trias? Kenilworth'. Von Huene described them in 1908 and recognized that they belonged to a pelycosaur, but he considered that they were from a form closely related to *Clepsydrops* or *Ophiacodon*. His description was very brief and several features which he did not mention are visible. *Oxyodon* was next dealt with by Romer and Price (1940) in their definitive review of the order and they identified it as a member of the Sphenacodontinae. The specimens are embedded in a coarse, red, loosely cemented sandstone containing pellets of red clay.

The preserved portion of the maxilla measures 89 mm in length and has a maximum depth of 42 mm. The anterior 10 mm of 22893 are missing from the counterpart. 22893 shows a single small precanine tooth followed by a pair of large canine teeth, these being succeeded by nine postcanine teeth. In addition, anterior to the precanine tooth the impression of another tooth is clearly visible, about the same size as the preserved one. The bone above this impression is broken but it shows traces of the

EXPLANATION OF PLATE 84

Figs. 1, 2. *Sphenacodon britannicus* (von Huene). Kenilworth. Left maxilla, × 1. 1, Institute of Geological Sciences, GSM 22893. 2, Silastomer cast, GSM 22894.
Fig. 3. *Haptodus grandis* sp. nov. Kenilworth. Left maxilla, × 1. Warwick County Museum Gz 1071.
Fig. 4. *Ophiacodon* sp. Coventry. Left lower jaw, × 1. Warwick County Museum Gz 41.

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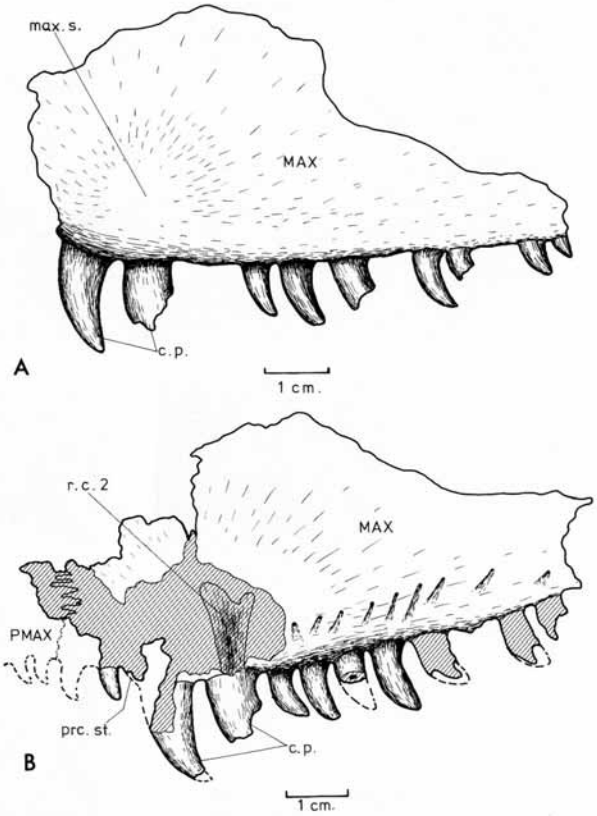
PATON, pelycosaurs



TEXT-FIG. 1. *Sphenacodon britannicus* (von Huene). A. Silastomer cast of GSM 22894. B. GSM 22893. c.p.—canine pair; MAX—maxilla; max. s.—maxillary swelling; PMAX—premaxilla; prc. st.—precanine step of maxilla; r.c. 2—root of second canine tooth.

maxillary/premaxillary suture and therefore the animal had only two precanine maxillary teeth. At the anterior extremity of the specimen there appears to be an impression of a small tooth—the last premaxillary tooth—situated at a slightly higher level than the first maxillary tooth, and separated from it by a gap of about 11 mm. Impressions of all the teeth except the precanines can be seen on 22894. The length of the precanine tooth is approximately 8 mm, that of the canines is roughly 19 mm, and that of the postcanines, which do not show any decrease in size posteriorly, is about 10 mm. All the teeth show the typical sphenacodont features of being laterally compressed, much recurved, and with a sharp posterior cutting edge which is unserrated. The base of the last precanine tooth is situated about 6 mm above the base

of the first canine—this height may have been even greater as at some time the piece of matrix containing the precanines has been broken off and replaced in a slightly lower position. The bone is badly damaged in this region and this led von Huene (1908) to believe that the last precanine was just erupting and was on the same level as the other teeth. However, the length of the precanines and their height above the rest of the tooth row are sufficiently great to show that the edge of the maxilla curved upwards in the typically sphenacodontine step anterior to the first canine. The maxilla above the two canines is broken, exposing the extremely long roots of these teeth, and it can be seen from 22894 that the surface of the maxilla bulged outwards overhanging the canines in the characteristically sphenacodont swelling which accommodates the enlarged roots of these teeth.

No empty sockets were present in the tooth row—two appear to be present in 22893, but in fact the teeth in them are broken off and preserved on the counterpart. The 1st, 3rd, 5th, and 7th postcanine teeth are smaller than the 2nd and 4th. No bones other than the maxilla and a very small part of the posterior end of the premaxilla are visible on the specimen. The maxilla is incomplete posteriorly and thus the tooth count is unknown.

Discussion. The teeth and general structure of the maxilla are typically sphenacodont and the precanine step seen here is a feature found only in members of the Sphenacodontinae. Romer and Price (1940) correctly placed *Oxyodon* in this subfamily. As they pointed out, the size and proportions of the specimen are very similar to those in *Sphenacodon ferox*, a large animal with a skull length of 297 mm from the Lower Permian of New Mexico. Unfortunately, the imperfect nature of the specimen and the lack of more material prevent any further comparison with similar American forms. The only other European sphenacodontine known is *Neosaurus cynodus* (Gervais 1869) from the Autunian of France. This is a small, slightly aberrant form with a slight maxillary step, and as *Oxyodon britannicus* is from a large animal which had a pronounced maxillary step it is unlikely that the two can be placed in the same genus. The name *Oxyodon* proposed by von Huene (1908) is unfortunately preoccupied by a fish of the family Acropomatidae (Brauer 1906, p. 287) although this fact has just been noticed. It was, therefore, necessary to assign the specimens to either a new, or an existing genus. As pointed out above, the size and proportions of the animal are very close to those of *Sphenacodon* and the canine teeth of the specimens are also of roughly the same proportions as in this genus (those of *Dimetrodon* are relatively much more prominent). It seems very likely that North America was joined to Europe in the Lower Permian so that the present geographical separation carries little weight. For these reasons it is probable that '*Oxyodon*' von Huene, 1908 is a junior synonym of *Sphenacodon* Marsh, 1878. It was therefore considered appropriate to assign the specimens to the genus *Sphenacodon* while retaining them for convenience in a separate species, *S. britannicus*, although no diagnostic characters can be given for this species. The discovery of more complete material might make it possible to assign the material to one of the North American species of the genus.

Subfamily HAPTODONTINAE
Genus HAPTODUS Gaudry, 1886

Diagnosis. Primitive sphenacodontids of small size. Skull high and moderately elongated; lower edge of maxilla convex; ventral margin of cheek region strongly curved; quadrate in low position; quadrate region wide; maxilla unexpanded dorsally; lachrymal extends forward to naris; no maxillary step. Palate of sphenacodont pattern. Lower jaw deep; angular apparently notched. Dentition typically sphenacodontid but canines not greatly enlarged.

Haptodus grandis sp. nov.

Plate 84, fig. 3; text-fig. 2A

Holotype. Gz 1071; part of the left maxilla (text-fig. 2A).

Locality. Kenilworth.

Horizon. Kenilworth Sandstone, probably Autunian, Lower Permian.

Diagnosis. As for generic diagnosis with in addition, the following points: a large haptodont with skull length about 280 mm; maxilla slightly swollen antero-laterally above canines; at least three precanine maxillary teeth present; canine teeth large, with poorly developed roots; postcanine teeth large and few in number.

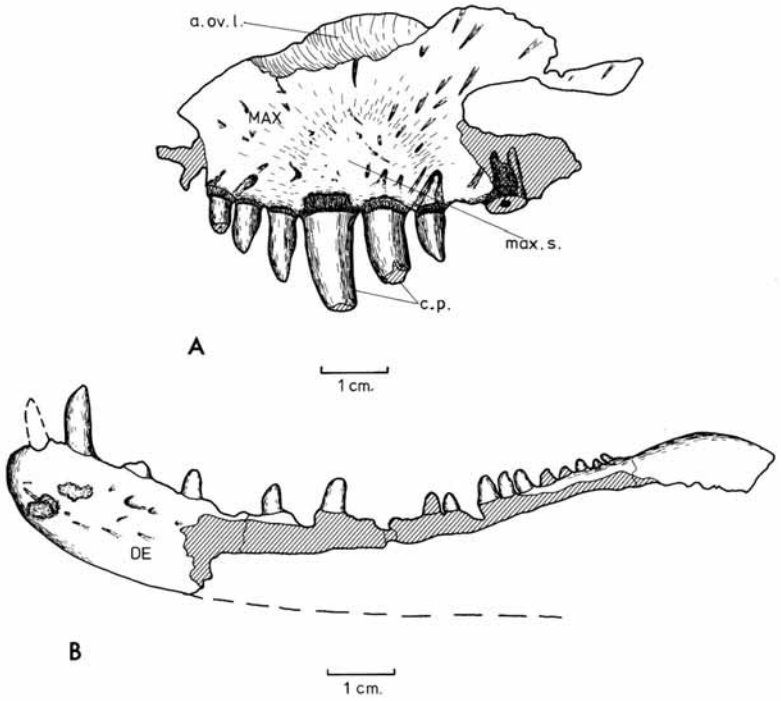
Description. This specimen has not been previously described and was identified as ?*Mastodonsaurus*. It comes from Kenilworth and is preserved in a coarse, red sandstone. As in *Sphenacodon britannicus*, it shows part of the left maxilla with a pair of large canine teeth, but more of the precanine and less of the postcanine tooth row is preserved. The maxilla appears to have been partially disarticulated prior to fossilization as dorsally it bears a large area of overlap for the lachrymal bone.

The length of the preserved part of the tooth row is 51 mm and the specimen has a maximum depth of 34 mm. Indications of eight teeth are preserved: three precanines which decrease in size anteriorly; a pair of large canine teeth (length about 16 mm), the first apparently loosening in its socket; and spaces for three postcanine teeth. The first postcanine is small and had probably just erupted; the second postcanine is missing; and the third is broken off at its base, but the maxillary surface is broken here and the root of this tooth is visible still firmly fixed to the bone—it was obviously a fairly large tooth with a length of about 10 mm. The teeth are all slightly recurved and laterally compressed with sharp, unserrated posterior edges, and the tips, where preserved, are pointed and laterally compressed, i.e. the teeth are typically sphenacodont. The lower edge of the maxilla is gently convex in side view, the first precanine thus being at a slightly higher level than the canines (about 2 mm above them) but there is no definite step such as occurs in the Sphenacodontinae, and the precanines, although smaller than the postcanines, are not greatly reduced in size. Above the canine pair the maxilla is swollen to accommodate their roots but this swelling is not as pronounced as in *Sphenacodon britannicus* and other sphenacodontines. Neither is the maxilla greatly expanded dorsally as occurs in the latter forms—its greatest depth in this specimen is 34 mm above the 2nd and 3rd postcanines; above the canines it has a depth of 26 mm.

The surface of the maxilla is pitted with foramina for nerves and blood vessels and in many places grooves lead outwards from these foramina. Figures in the literature on pelycosaurs indicate that these foramina and grooves may possibly be more widespread in sphenacodonts than in other pelycosaurs.

Discussion of Gz 1071. The laterally compressed, pointed teeth with sharp posterior cutting edges; the maxilla with its lateral swelling above the canine teeth; the convex maxillary margin; the large size of the postcanine teeth; and the much pitted maxillary surface are features which show that this specimen belonged to the family Sphenacodontidae. However, several features exclude it from the subfamily Sphenacodontinae: the lack of a precanine step in the dentition; the number and size of the precanine teeth (3+); the dorsally unexpanded maxilla which indicates (*a*) that the roots of the canine teeth were not exceptionally long as they are in sphenacodontines—this is confirmed by the maxillary swelling being only slight—and (*b*) that the lachrymal reached the naris.

It thus seems likely that the specimen belongs to an animal of the genus *Haptodus*



TEXT-FIG. 2. A. *Haptodus grandis* sp. nov. Warwick County Museum Gz 1071. B. *Ophiacodon* sp. Warwick County Museum Gz 41. a. ov. l.—area of overlap on maxilla for the lachrymal; c.p.—canine pair; DE—dentray; MAX—maxilla; max s.—maxillary swelling.

first described in 1886 by Gaudry and also known from several other specimens originally described as *Palaeohatteria* (Credner 1888), *Callibrachion* (Boule and Glangeau 1893), *Datheosaurus* (Schroeder 1904), and *Pantelosaurus* (von Huene 1925) but all now considered to be congeneric with *Haptodus*. Romer and Price (1940) give the characters of the subfamily Haptodontinae as primitive sphenacodontids with a high, moderately elongated skull, a moderately convex tooth row, slightly developed canines, and with the lachrymal reaching the naris. The subfamily contains only the genus *Haptodus*, the species contained in this being all from western European localities of Autunian age—none, however, have been previously described from England. All known haptodonts are of small size.

Two characteristics thus distinguish Gz 1071 from other haptodonts: (*a*) The size suggests that it is only slightly smaller than *Sphenacodon britannicus* which had a skull length of approximately 300 mm. The skull length estimated from Gz 1071 is approximately 280 mm. *Haptodus saxonicus*, which is the largest known haptodont, has a maximum skull length of 180 mm. (*b*) All known haptodonts have only slightly developed canines. Those of Gz 1071 are fairly well developed, being only slightly smaller than those of *Sphenacodon britannicus*.

There is not, however, a great deal of material representing the Haptodontinae and it is probably accidental that so far no large forms have been discovered. There appears to be no reason why a large species of *Haptodus* should not have existed. Remains of pelycosaurs in Europe suggest that *Haptodus* is the commonest genus and it is therefore likely that it would have developed forms of different sizes adapted to different modes of life. The relatively large size of the canines in the present specimen is probably correlated with this larger size. It is therefore suggested that Gz 1071 represents a previously unknown species of *Haptodus* which, in view of its large size, is here named *Haptodus grandis*.

Suborder OPHIACODONTIA
Family OPHIACODONTIDAE
Genus OPHIACODON Marsh, 1878
Ophiacodon sp.

Text-fig. 2B

Figured Specimen. Gz 41.

Locality. One mile north-west of Coventry.

Horizon. Kenilworth Breccia, probably Autunian, Lower Permian.

Description. Murchison and Strickland (1840) noted the occurrence of this specimen and figured it rather poorly (pl. 28) as the maxillary bone of a fish. The matrix is a coarse, red, loosely cemented sandstone containing pellets of red clay.

It shows part of a poorly preserved left dentary. The anterior part extends to the symphysis and the complete tooth row is present, but most of the ventral part is missing and the specimen ends 24 mm posterior to the last tooth. The total length is 122 mm. The impression of the missing ventral part of the jaw remains, permitting the general shape to be seen. The jaw is slender, very shallow dorso-ventrally at the front, and deepening gradually posteriorly. The dorsal edge of the dentary is moderately concave; posterior to the tooth row it becomes convex.

The tooth row has spaces for about 34 teeth, many of which are missing—the state of preservation makes it difficult to distinguish empty sockets from broken bases, but as far as can be determined, the tooth arrangement is as follows:

anterior																														posterior
1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34
?	1	1	—	1	—	—	1	1	—	1	—	1	—	—	1	—	1	—	1	—	1	1	—	1	1	1	1	1	1	1	1	1	—

Because of the curvature of the bone, tooth 1 cannot be seen, but it was probably a large tooth as are teeth 2 and 3. Tooth 3 is complete and is 11 mm long. Position 4 probably also contained a large tooth. Teeth 5 to 26 are all roughly equal in size with a height of 5 mm. Teeth 27 to 34 are very much smaller, diminishing in size posteriorly to a minimum of 2 mm. The teeth are not laterally compressed and do not have posterior cutting edges, and teeth 5 to 34 are conical pegs with blunt tips. The complete and enlarged tooth 3 is slightly recurved, however, and has a definite point.

Discussion. The slender structure of the jaw and the nature of the teeth are typical of conditions found in the ophiacodont lower jaw whose structure is entirely different to that of sphenacodonts. The group of enlarged teeth at the anterior end of the lower jaw is characteristic of pelycosaurs. The teeth of Gz 41 are smaller and more numerous than those in sphenacodonts and there are many gaps in the tooth row. This is also a feature found in ophiacodonts, probably caused by a slow rate of tooth replacement (Romer and Price 1940, p. 91).

The jaw is closest in its structure to pelycosaurs of the genus *Ophiacodon*. This is interesting as previously ophiacodontids, even the primitive Carboniferous forms, are known only from North American deposits. The portion of jaw preserved indicates a skull length of about 185 mm. This is considerably smaller than any of the known American forms. The number of teeth in the jaw is also lower than that normally occurring in the American species, although the number exceeds that which is characteristic for sphenacodonts. Apart from the smaller size and number of teeth, the jaw most closely resembles that of *Ophiacodon uniformis*, a form from the Wichita Beds which are generally held to be Autunian in age (Romer 1966). The specimen unfortunately does not show sufficiently diagnostic characters to enable it to be established as a separate species, or to be assigned to one of the already described species of the genus. It is quite possible that it could have belonged to a young individual and size is therefore irrelevant.

General discussion

Various 'Upper Coal Measures' deposits including red continental sediments in the Midlands Coalfields have in the past been thought to be Permian in age, but over the years there has been a general tendency to push these red beds, the upper part of which is the Keele Group, down into the Carboniferous giving them a Westphalian D age. The Keele Group is succeeded by a series of red mudstones, sandstones, and conglomerates known as the Bowhills Group, the Calcareous Conglomerate Group, and the Gibbet Hill Group according to their locality. These beds have been assigned by various authors (Boulton 1933; Shotton 1929; Whitehead and Eastwood 1927) to either the Carboniferous or the Permian, but it is now generally considered that

a Stephanian age is possible although Haubold (1970, 1971, 1972) believes that, on the evidence of footprints, the beds are of early Permian age. These conglomerate-bearing strata are overlain unconformably by the Clent and Enville Breccias which have been shown (Shotton 1929) to pass laterally into the Kenilworth Breccia Group (which includes the Kenilworth Sandstone) which rests conformably on the conglomerates of the Gibbet Hill Group. These breccias have all been tentatively assigned (Hains and Horton 1969) to the Lower Permian. They are, as a whole, virtually barren, the only other fossils found in them being the zatracheid labyrinthodont *Dasyceps bucklandi* (Lloyd 1850; Huxley 1859; von Huene 1910; Romer 1947) from roughly the same horizon as the pelycosaurs—this fossil (currently under study by the author) is believed to be a specialized member of a family of amphibians whose more advanced species are limited to Lower Permian sediments of Autunian age; some amphibian and reptilian footprints (Haubold 1970, 1971, 1972); and a species of the conifer *Lebachia* (*Walchia*) (Hains and Horton 1969) which also supports a Lower Permian age for these beds.

Because of the rarity of other fossils, the pelycosaur remains described here assume some importance in the determination of the age of the Kenilworth Sandstones. The subfamily Sphenacodontinae includes specimens from North America and Europe and is mainly Autunian in age, the genus *Sphenacodon*, to which GSM 22893 and 22894 are here assigned, being found only in Autunian (Lower Permian) sediments (Romer and Price 1940). The subfamily Haptodontinae in which Gz 1071 is included is known only from specimens found in western European localities which are all of Autunian age (Romer and Price 1940). Specimen Gz 41 is believed to belong to the genus *Ophiacodon* which is known only from North American deposits of late Stephanian and early Autunian age (Romer and Price 1940).

The above evidence thus points to an Autunian (Lower Permian) age for the Kenilworth Breccia Group. The beds are thought to have accumulated under arid conditions because of the presence in them of pellet rocks, footprints, raindrop impressions, and suncracks. They were produced from material eroded from the near-by Mercian Highlands and were deposited in a series of interconnecting basins, in one of which was formed the Kenilworth Breccia, the others receiving the Clent and the Enville Breccias.

In view of these conditions it is hardly surprising that fossils are rare in these deposits. Those which do occur, however, suggest that the fauna of the Mercian Highlands was fairly varied. There must have been plenty of food to support two species of carnivorous pelycosaurs (*Ophiacodon* is believed to have been piscivorous). A similar instance occurs in the 'Lower Keuper' Sandstone which, near Warwick and Bromsgrove, has a relatively rich fauna of amphibians and reptiles plus invertebrates, plants, and fish, and which contrasts with the barrenness of most of the Trias over considerable thicknesses and wide areas. Many different sorts of tracks thought to have been made by amphibians and reptiles of various sizes occur in the Permian deposits, and it is interesting to note that Haubold (1971) has suggested that the reptilian track known as *Ichniotherium* found in the English beds corresponds to a member of the suborder Edaphosauria. If this is true, all three suborders of pelycosaurs found in North America are represented in the English Autunian deposits, and there can be no basis for suggestions that the fauna of the latter is restricted.

The occurrence of the hitherto solely North American genera *Sphenacodon* and *Ophiacodon* in the English Lower Permian provides additional evidence of the close land links between North America and Europe at this time.

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