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### *Dyoplax* O. FRAAS, a Triassic sphenosuchian from Germany

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With 5 Figures

#### Summary

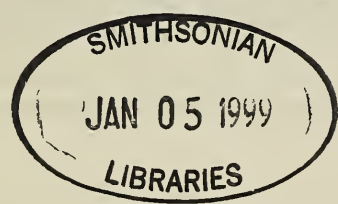
We redescribe the holotype and only known specimen of *Dyoplax arenaceus* O. FRAAS, 1867 and reinterpret its affinities to conclude it is the oldest sphenosuchian crocodylomorph. The sphenosuchian fossil record is very incomplete but indicates a pre-Carnian origination and rapid diversification during the late Carnian-Norian.

#### Zusammenfassung

Das nur durch den Holotypus bekannte Reptil *Dyoplax arenaceus* O. FRAAS, 1867, wird neu beschrieben. Aufgrund seiner Verwandtschaftsbeziehungen wird *Dyoplax* als geologisch ältester crocodylomorpher Sphenosuchier gedeutet. Die Fossilüberlieferung der Sphenosuchier ist sehr unvollständig; sie weist jedoch auf eine prä-karnische Entstehung und eine rasche Diversifizierung der Sphenosuchier im oberen Karn bis Nor hin.

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## 1. Introduction

In 1867, O. FRAAS described a new Keuper fossil reptile, *Dyoplax arenaceus*, based on the natural cast of most of a skeleton found in Stuttgart-Feuerbach, Germany. FRAAS clearly was puzzled by the affinities of *Dyoplax*, stating that it has the head of a lizard and the armor of a gavial. Since FRAAS, *Dyoplax* has either been assigned to the Aetosauria or to the Crocodylomorpha, usually as a protosuchian. Here, we re-describe the holotype and only known specimen of *Dyoplax* and reinterpret its affinities to conclude it is the oldest sphenosuchian crocodylomorph.

## 2. Locality and Stratigraphical Context

The type locality of *Dyoplax arenaceus* was the “LEINS quarry” in the Schilfsandstein of Stuttgart-Feuerbach. The quarry was named after its owners, the LEINS family of Stuttgart. Using the town archives of Stuttgart and old topographic and geological maps, we could not exactly locate this quarry in the former quarry area of the Feuerbacher Heide. However, O. FRAAS (1867: 108–109) notes that the ‘Leins quarry’ was located “... hart vor den Thoren Stuttgarts am Fuss des Sonnenbergs...”

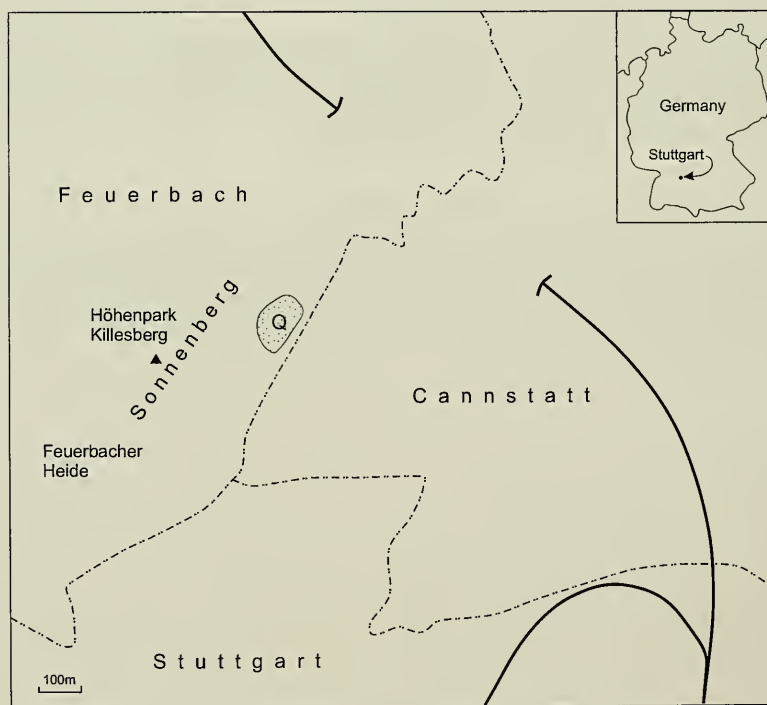


Fig. 1. Topographic map of Stuttgart-Northeast with the railway line Stuttgart-Feuerbach and the district borders of the formerly independent communities Feuerbach and Cannstatt (dash-point-dash). East of Sonnenberg, the Schilfsandstein quarry area (Q), from which the holotype of *Dyoplax arenaceus* came, is indicated.

This means the quarry was located in the area of the community of Feuerbach, which was not integrated into today's Stuttgart, the capital of the Land Baden-Württemberg. On the topographic map at a scale of 1:25000 (in Württembergian feet), Stuttgart und Umgebung, 1877, three quarries are mapped which lie close together near the district border of Feuerbach, Stuttgart and Cannstatt. One of these three quarries must have been the "LEINS quarry". This area now belongs to the "Höhenpark Killesberg", a park ground with botanical garden, tree-covered meadows, old, partly overgrown quarry walls and small lakes that indicate the former Schilfsandstein quarrying area. Its coordinates are approximately: R = 3512675 to 3512750 and H = 5407625 to 5407750, referring to topographic sheet Nr. 7121 Stuttgart-Nordost 1985 (scale 1:25000) (Fig. 1).

O. FRAAS (1867: 109) reported that the holotype of *Dyoplax* was found in the upper (about 3-m-thick), red-coloured, platy sequence of the Schilfsandstein, which was quarried to produce building stone for walls. Indeed, the holotype of *D. arenaceus*, SMNS 4760, is a natural cast in grayish red, micaceous sandstone (Fig. 2). The lower two-thirds of the 9-m-thick Schilfsandstein in the area of the Feuerbacher Heide, still exposed by the quarry walls in the "Höhenpark Killesberg", consist mainly of green, thick-bedded sandstone. It is the fine-grained, and often crossbedded sandstone which was quarried to obtain large blocks used for private and state buildings in Stuttgart until the beginning of this century. It was formerly called the "Bausandstein" of Stuttgart.

### 3. Description

The holotype of *Dyoplax arenaceus*, SMNS 4760, is the sandstone cast of the dorsal surface of a nearly complete axial skeleton missing the tip of the tail, and lacking most of the limb bones (Figs. 2–3). O. FRAAS (1867: 110–112, pl. 1) described and illustrated this specimen. We reproduce O. FRAAS' (1867: pl. 1) illustration here as Figure 3; note that his lithograph is a mirror image of the specimen. The holotype of *D. arenaceus* preserves no bone, but it is a remarkably detailed cast that provides significant anatomical information.

Total length (tip of snout to last preserved caudal scute) is 530 mm. Skull length is 80 mm. The skull is long and narrow; the rostrum represents more than 50 % of skull length. This long, narrow rostrum terminates in a blunt, rounded, narrow anterior edge. The small external naris is nearly round and at the anterior tip of the rostrum. The rostrum has a distinctly flattened dorsal surface with two lateral faces that are

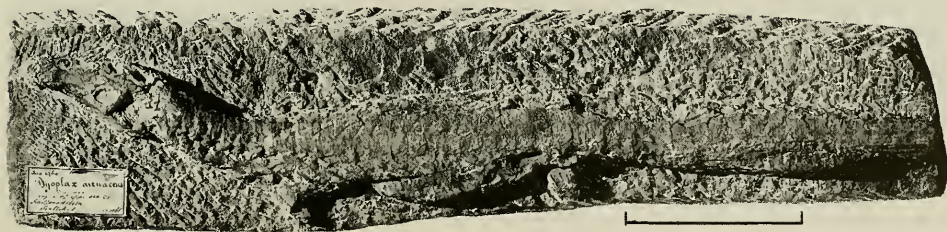


Fig. 2. The holotype of *Dyoplax arenaceus* FRAAS, SMNS 4760; bar scale = 100 mm.



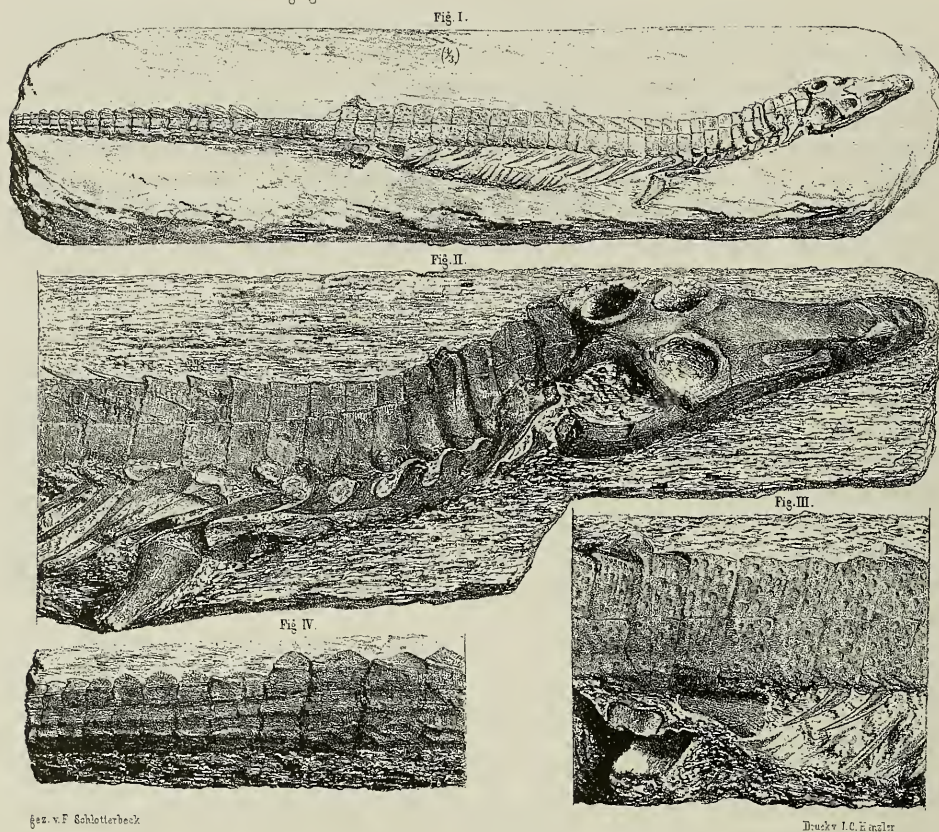


Fig. 3. Original lithographic illustration of the holotype of *Dyoplax arenaceus*, from O. FRAAS (1867: pl. I). Fig. I shows the dorsal aspect of the entire specimen, Fig. II is a closer view of the dorsal aspect of the anterior portion of the specimen, Fig. III is a close-up of a portion of the dorsal armor and Fig. IV is a close-up of part of the caudal armor. Note that because of the printing process these are mirror images of the specimen.

angled slightly ventrally and laterally away from this surface. These lateral surfaces bear long, nearly rectangular antorbital fenestrae set in longer, more shallow depressions.

The nasals cover the dorsal aspect of the rostrum and extend at least as far forward as the external nares, though their anterior tip apparently is broken. Posteriorly, these long, narrow bones come to a triangular posterior edge that projects backward into the frontal. The frontal extends backward to form a small part of the medial rim of the orbit and a larger part of the antero-medial margin of the supratemporal fenestra.

The prefrontal, visible on the antero-medial edge of the left orbit dorsal margin, excludes the nasal and maxillary from contacting the orbit. Its suture with the lachrymal is not clear, but both(?) bones separate the orbit and antorbital fenestra. The jugal forms a prominent convex bone that sweeps under the orbit back to posterior



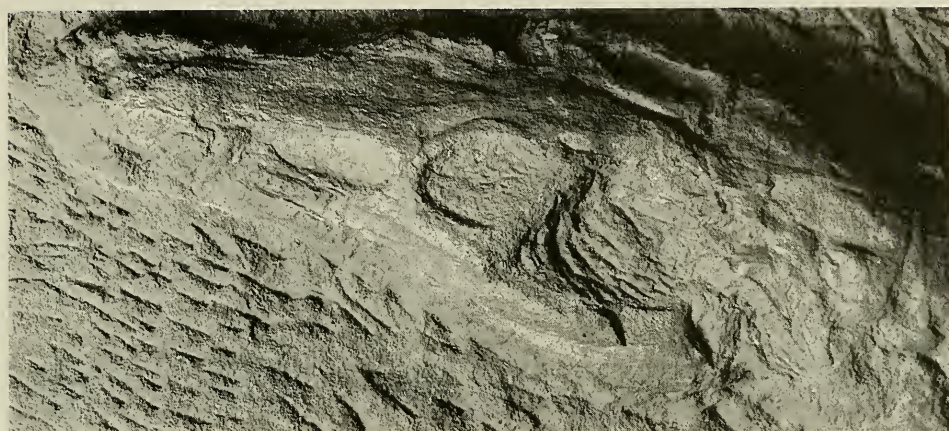
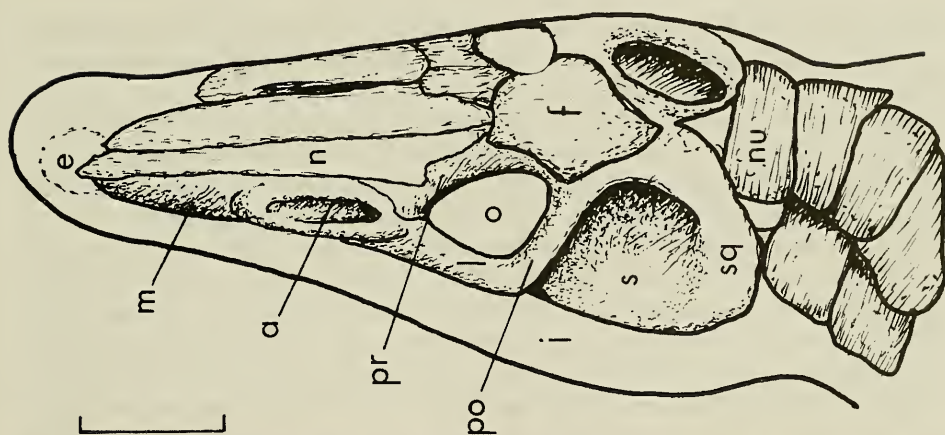


Fig. 4. Stereophotograph and drawing of skull of *Dyoplax arenaceus*. Abbreviations are: a = antorbital fenestra, e = external nares, f = frontal, j = jugal, l = lachrymal, m = maxillary, n = nasal, nu = nuchal scute, o = orbit, po = postorbital, pr = prefrontal, s = supratemporal fenestra, sq = squamosal. Bar scale = 25 mm.

to the supratemporal fenestra. Details of the back of the skull roof are obscured by crushing, a lack of preservation and overlap of the anterior dorsal (nuchal) scutes on to that part of the skull.

The body is long, narrow and of essentially unvaried width from the back of the skull to the hindlimbs. The dorsal surface of the back is covered by two parallel rows of osteoscutes. There are 28 such rows between the back of the skull and the hindlimbs. At least 23 osteoscuterows covered the tail, which is incomplete.

The dorsal osteoscutes are square to slightly rectangular (the long axis is medio-lateral) and sutured to each other along the midline. Regular to irregular, shallow round pits cover their dorsal surfaces, and they overlap each other anteroposteriorly. The postero-lateral edge of each osteoscuterow is produced into a short, angular, projecting process.

The proximal part of the left forelimb is preserved, including the proximal end of the humerus. This is a conical bone fragment that tapers rapidly distally. It has a rounded proximal end and a flat proximal articular surface. The positions of both hindlimbs are recorded by rock infilling – probably of the tissues surrounding the proximal ends of the femora.

The left side of the body wall protrudes laterally. Double-headed cervical ribs and longer dorsal ribs, as well as some gastralia, are visible on the left side of the body wall.

#### 4. Affinities of *Dyoplax* – Previous Ideas

ZITTEL (1890) and HUENE (1902) assigned *Dyoplax* to the Pseudosuchia, including it in the “Aetosauridae”. MCGREGOR (1906) also listed *Dyoplax* as an aetosaur. ROMER (1945: 597) assigned *Dyoplax* to the “Aëtosauridae”, but subsequently listed it as Notochampsidae? (=Protosuchidae) (ROMER, 1956: 560) and as Erpetosuchidae? (ROMER, 1966: 368; also see CARROLL, 1988: 619). BENTON (1994: 393) identified *Dyoplax* as possibly the oldest member of the Protosuchidae, following a suggestion by WALKER (1968).

#### 5. *Dyoplax* not an Aetosaur

PARRISH (1994: 206; also see HECKERT et al., 1997) distinguished a monophyletic Aetosauria based on the following synapomorphies: (1) edentulous anterior portion of premaxilla consisting of an anteroventrally projecting, mediolaterally expanded “shovel” with an “upturned”, anteriorly flattened dentary that lacks teeth anteriorly; (2) teeth that are reduced in size and nearly conical; (3) a complete dorsal and ventral carapace; (4) paramedian scutes that are markedly wider than long, sculptured and lack anterior or posterior projections; and (5) limb bones that are disproportionately robust with “hypertrophied trochanters” on the humerus, femur, tibia and fibula.

*Dyoplax* appears to lack an upturned, shovel-like dentary that is medio-laterally expanded, though it could be argued that this feature simply is not completely preserved by SMNS 4760. No teeth can be seen on the holotype of *D. arenaceus*, so the second synapomorphy of the Aetosauria cannot be evaluated. *D. arenaceus* only has



paired dorsal, median scutes, no lateral scutes, so it lacks a complete dorsal carapace. No evidence of a ventral carapace can be seen in the abdominal region where it is possible to observe part of the ventrum of *D. arenaceus*. Furthermore, the dorso-median scutes of *D. arenaceus* have postero-lateral projections. The preserved impressions of the proximal ends of the humerus and femur of *D. arenaceus* are not robust and lack hypertrophied trochanters. They are very different from the humeri and femora of aetosaurs (compare LONG & MURRY, 1995: figs. 62c–f, 63b–d, 67a–c, 81, 83, 89c, 90, 93, 94a–d, 105c–e, 110). Thus, in four of five observable characters, *D. arenaceus* lacks synapomorphies of the Aetosauria.

The question remains whether *D. arenaceus* is the sister taxon of the Aetosauria *sensu* PARRISH, or whether the Aetosauria could be expanded to include *Dyoplax*. We argue against these possibilities simply by demonstrating that *Dyoplax* is a sphenosuchian crocodylomorph and therefore well removed phylogenetically from the Aetosauria.

## 6. *Dyoplax* as a Sphenosuchian

We rely here on cladistic definitions of the Crocodylomorpha and Sphenosuchia recently published by SERENO & WILD (1992; also see BENTON & CLARK 1988). They listed six synapomorphies of the Crocodylomorpha: (1) nasal excluded from margin of antorbital fossa; (2) postfrontal absent; (3) jugal excluded from margin of antorbital fossa and fenestra; (4) anterior process of squamosal transversely broad; (5) squamosal and paroccipital process form tongue-and-groove articulation; and (6) ulnare and radiale with elongate shafts. Our interpretation of the skull of *D. arenaceus* (Fig. 4) indicates the nasal and jugal are excluded from the margin of the antorbital fossa, the postfrontal is absent, and the anterior process of the squamosal is broad transversely. The articulation of the squamosals and paroccipital processes cannot be observed, and the ulnare and radiale are not preserved. However, those characters that can be observed indicate *Dyoplax* is a crocodylomorph.

*D. arenaceus* has a prefrontal with a posterior process deflected under the frontal, an arcuate squamosal in dorsal view, and a squamosal margin of the supratemporal fossa that is bounded in part by a rim, three of the four synapomorphies of the Sphenosuchia listed by SERENO & WILD (1992). The fourth character – forked posterior process of squamosal – cannot be observed. Assignment of *Dyoplax* to the Sphenosuchia thus seems certain.

## 7. Sphenosuchian Distribution and Evolution

Assignment of *Dyoplax* to the Sphenosuchia extends the temporal range of the Sphenosuchia back to the early Carnian (Julian). Previously, the oldest known sphenosuchians were late Carnian (Fig. 5). At present, sphenosuchian distribution can be grouped into six temporal intervals:

1. *Dyoplax* is from the Schilfsandstein of Germany. *Metoposaurus diagnosticus* is also known from the Schilfsandstein/Lehrbergschichten, as is a trematosaur and a phytosaur (e.g., BENTON 1986; HUNT 1993). Non-German *Metoposaurus* records are generally regarded as late Carnian (HUNT 1993), but trematosaurs are otherwise

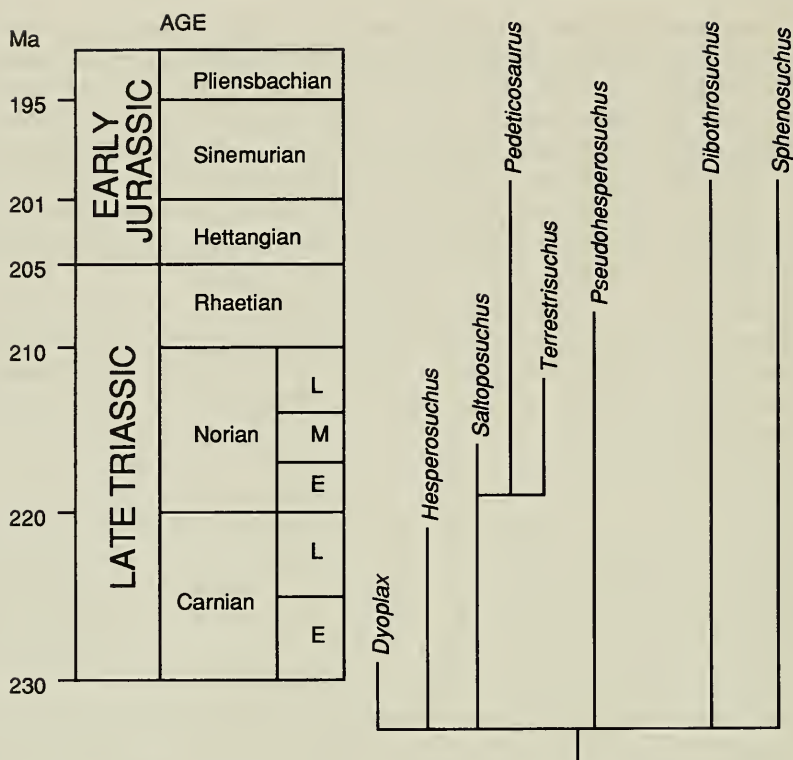


Fig. 5. Temporal distribution of sphenosuchians with the phylogenetic hypothesis of SERENO & WILD (1992) slightly modified to accommodate *Dyoplax* and *Hesperosuchus*. See text for discussion.

known from Lower-Middle Triassic strata across Pangea. We resolve the discrepancy by correlating the Schilfsandstein as early Carnian (Julian), which is also the correlation advocated by palynologists and sequence stratigraphers (e.g., MADER 1990; AIGNER & BACHMANN 1992).

2. LONG & MURRY (1995; also see PARRISH 1991) tentatively assigned *Hesperosuchus* from the upper Carnian – lower Norian (Adamanian-Revueltian) and *Parrishia* from the upper Carnian (Adamanian) interval of the Chinle Group in the western United States to the Sphenosuchia. The ages of these records are well-established (e.g. LUCAS et al. 1997; LUCAS & HUBER 1998), but the sphenosuchian affinities of *Parrishia* are uncertain, so it is not shown on Figure 5.

3. *Saltoposuchus* is from the Middle Stubensandstein of Germany (HUENE 1921). The Carnian-Norian boundary has been placed at the base of the Stubensandstein, largely based on palynostratigraphy. Indeed, a significant reorganization of the tetrapod fauna occurs at this contact, with the best known and most diverse Keuper assemblage being that of the Lower Stubensandstein. This assemblage includes the temnospondyl *Cyclotosaurus*, the earliest turtle (*Proterochersis*), *Pseudopalatus*-grade phytosaurs (*Nicrosaurus*), the aetosaurs *Aetosaurus* and *Paratypothorax*, rauisuchians (*Teratosaurus*) and the oldest European dinosaurs, and the prosauropods *Sellosaurus* and *Thecodontosaurus* (see BENTON 1993 for bibliography). The phyto-



saurs, aetosaurs, and rauisuchians provide a strong basis for a Stubensandstein-Revueltian correlation (LUCAS & HUNT 1993; HUNT 1993).

The younger, Middle and Upper Stubensandstein produce a similar, but less diverse assemblage, so we also correlate them to the Revueltian. Palynostratigraphy, vertebrate biostratigraphy, and sequence stratigraphy suggest the Stubensandstein is of early to middle Norian age (BRENNER 1973; BRENNER & VILLINGER 1981; VISCHER & BRUGMAN 1981; WILD 1989; BENTON 1986, 1993; AIGNER & BACHMANN 1992; KOZUR 1993; LUCAS & HUBER 1994). The most precise correlation available suggests the Lower Stubensandstein is early Norian, whereas the Middle Stubensandstein is middle Norian (e.g., BENTON 1993).

4. *Terrestrisuchus* is from fissure fill deposits in Wales (CRUSH 1984). The fissure-fill assemblages occur in paleokarst features developed in Carboniferous limestones at a number of quarries in the Bristol Channel region. Two broad groups of assemblages can be distinguished, of Norian-Rhaetian and of Sinemurian-Pliensbachian age (e.g., BENTON 1986; FRASER 1994; EVANS & KERMACK 1994; STORRS 1994; BENTON & SPENCER 1995). The Late Triassic fissure fill assemblages include procolophonids (?*Tricuspisaurus*), isolated teeth of phytosaurs, a possible, undescribed aetosaur (based on one scute), the prosauropods *Thecodontosaurus* and *Camelotia*, indeterminate theropods (includes possible *Syntarsus*) and pterosaurs, one or more sphenosuchians including *Terrestrisuchus* and two enigmatic archosaurs (termed "suchian A" and "B" by FRASER 1994). The sphenodontids, which numerically dominate the Triassic assemblages, are represented by numerous species of *Clevosaurus*, *Sigmala*, *Planocephalosaurus*, and *Diphydontosaurus*. The diapsid glider *Kuehneosaurus* and several taxa of mammals are also present, including *Kuehneotherium*, *Haramiyia*, and *Morganucodon* (FRASER 1994; BENTON & SPENCER 1995).

The precise ages of all the Triassic fissure fill assemblages have not been adequately defined. Detailed study of the Cromhall Quarry by WALKDEN and FRASER (1993) and FRASER (1994) determined a temporal sequence of the various fill-deposits, and based on the similarity of fossil content of immediately overlying marls with basal Penarth Group assemblages, they considered most of the fissures to predate the Westbury Formation. However, a maximum age-constraint is lacking, and assertions have been made that certain fissures are as old as Carnian, based on SIMMS & RUFFELLS (1989, 1990) concept of a Laurusian "middle Carnian pluvial episode".

BENTON (1991) and BENTON & SPENCER (1995) thought the collective Triassic fissure-fill fauna at least superficially resembles that of the Lower and Middle Stubensandstein and Elgin faunas. The only potential independent age control is provided by the palynomorphs (MARSHALL & WHITESIDE 1980), which were thought to be indicative of the "early" or "late Sevatian". However, we believe such refined biostratigraphy is well beyond the resolving power of palynomorphs in delimiting intervals of Late Triassic time, so we regard the microflora to indicate a Norian (undivided) age. Furthermore, the chronostratigraphic ordering of the fill sequences shown most recently by FRASER (1994) suggests that the development and infilling of paleokarst features at the Cromhall quarry was an ongoing process for 20–30 million years, depending on which Triassic numerical time scale is used. We doubt that active karst solution and sediment-infilling would actively persist for such an extended length of time, and furthermore believe sediment filling of the fissures that contain Triassic age faunas in the southwest UK are contemporaneous with deposition of the upper Mercia Mudstone Group. Therefore, we believe that the Triassic fissure fill sedi-

ments were deposited either during the marine transgression recorded by the uppermost Blue Anchor Formation (WARRINGTON et al. 1980) or are homotaxial with the basal Penarth Group (Westbury Formation). Their age thus ranges from late Norian to Rhaetian, and we tentatively assign *Terrestriisuchus* a late Norian age.

5. *Pseudohesperosuchus* is from the Los Colorados Formation in Argentina (BONAPARTE 1978). The Los Colorados Formation is siliciclastic red beds approximately 800 m thick. Near its base, a single tetrapod fossil – a dicynodont skull, the holotype of *Jachaleria colorata* BONAPARTE 1970 – was collected. The remainder of the tetrapod fossils from the Los Colorados Formation are from its middle and upper parts but have not been stratigraphically organized. The assemblage includes the turtle *Palaeochersis talampayensis*, the ornithosuchid *Riojasuchus tenuisiceps*, the aetosaur *Neoetosauroides engaeus*, the sphenosuchid *Pseudhesperosuchus jachaleri*, the protosuchid *Hemiprotosuchus leali*, the prosauropod dinosaurs *Riojasaurus incertus* and *Coloradisaurus brevis*, a theropod dinosaur and the tritheledontid cynodont *Chalimnia musteloides* (e.g. BONAPARTE 1970, 1971, 1978, 1980; LUCAS & HUNT 1994; ROUGIER et al. 1995). This assemblage clearly is of Late Triassic age and must be post-late Carnian, which is the age of the Ischigualasto Formation below the Los Colorados. However, the endemism of the Los Colorados vertebrate assemblage makes it difficult to correlate precisely. We tentatively consider it late Norian/Rhaetian based on prosauropod abundance, though admittedly this provides a weak basis for correlation.

6. Early Jurassic sphenosuchians are *Dibothrosuchus* from the Lufeng Formation in Yunnan, China, *Sphenosuchus* from the upper Elliot Formation in South Africa and *Pedeticosaurus* from the lower Clarens Formation in South Africa (e.g., VAN HOEPEN 1915; KITCHING & RAATH 1984; WALKER 1990; WU & CHATTERJEE 1993). The Early Jurassic (Sinemurian) age of the Lufeng vertebrates is well established (e.g., LUCAS 1996).

The Middle and Upper Elliott Formation contains a diverse tetrapod assemblage that KITCHING & RAATH (1984) defined as the “*Massospondylus* range zone”. The combined assemblage is dominated by the tritylodontid *Tritylodon*, which occurs with rare brachyopid? amphibian remains, a proganochelyid turtle, sphenosuchian archosaurs ( *Sphenosuchus* and “pedeticosaurids”), a variety of dinosaurs (the prosauropod *Massospondylus*, a coelurosaur referred to cf. *Syntarsus*, and several ornithischians), other cynodonts including *Pachygenelus* and *Tritheledon*, and the mammal *Erythrotherium* (KITCHING & RAATH 1984). The *Tritylodon* acme zone is interpreted as a reworked paleosol (SMITH & KITCHING 1996), and is widely, and we believe correctly assigned an Early Jurassic age. The age of the *Massospondylus* range zone is unclear and we conservatively assign it an Early Jurassic age, possibly Sinemurian (Fig. 5). The overlying Clarens Formation contains a limited fauna that mostly includes taxa of ornithischian dinosaurs and cynodonts common to the underlying Upper Elliott assemblage (KITCHING & RAATH 1984) and also is of Early Jurassic age, possibly Sinemurian.

We have plotted the phylogenetic hypothesis of sphenosuchian relationships of SERENO & WILD (1992) against the revised ages of sphenosuchians reviewed here (Fig. 5). *Dyoplax* and *Hesperosuchus* are added to this phylogenetic hypothesis as part of its basal multichotomy; both taxa are not well enough known to be placed elsewhere. This analysis suggests a pre-Carnian origin of sphenosuchians and a rapid, largely undiscovered late Carnian-Norian diversification of the group.

## 8. Acknowledgements

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