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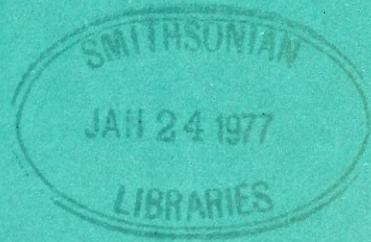
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FISCHER, P.-H., DUVAL, M. & RAFFY, A. 1933. Études sur les échanges respiratoires des littorines. — *Archs Zool. exp. gén.* 74: 627–634.

KOHN, A. J. 1960a. Ecological notes on *Conus* (Mollusca: Gastropoda) in the Trincomalee region of Ceylon. — *Ann. Mag. nat. Hist.* (13) 2: 309–320.

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(continued inside back cover)

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GALESPHYRUS CAPENSIS,
A YOUNGINID EOSUCHIAN FROM
THE *CISTECEPHALUS* ZONE OF SOUTH AFRICA

By

ROBERT L. CARROLL

Cape Town Kaapstad

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By

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Redpath Museum, McGill University, Montreal, Canada

(With 3 figures)

[MS accepted 5 May 1976]

ABSTRACT

Galesphyrus capensis, a primitive eosuchian reptile, is represented by two partial skeletons from the *Cistecephalus* zone of South Africa. Little is known of the skull. The teeth are smaller and more numerous than those of *Youngina* from the overlying *Daptocephalus* zone. Postcranial features of the skeleton are similar in the two genera, although the metatarsals are relatively longer in *Youngina*. The tarsus of *Galesphyrus* is very well preserved, providing a basis for comparison with those of more advanced diapsids. Neither of these younginid genera appear to be closely related to the Upper Pennsylvanian diapsid *Petrolacosaurus*, and may represent a distinct line of persistently small forms.

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INTRODUCTION

Reptiles first appear in the fossil record in the early Upper Carboniferous. Primitive groups remain dominant through the Lower Permian. Early members of all the living orders (Chelonia, Crocodylia, Squamata and Rhynchocephalia) are known by the late Triassic. Little specific evidence is yet available linking the advanced reptiles with their Palaeozoic predecessors. A number of forms from the Upper Permian and Lower Triassic, collectively termed eosuchians, has long been felt to represent an intermediate level of reptilian evolution. Eosuchians are generally accepted as being ancestral to lizards and rhynchocephalians, and have frequently been suggested as being ancestral to the archosaurs as well. Despite their significance, much remains to be learned of the anatomy and phylogeny of eosuchians.

The earliest diapsid, and so apparently the oldest recognizable ancestor of

the eosuchians, is *Petrolacosaurus* (Reisz 1975) from the Upper Pennsylvanian of North America. Aside from the configuration of the temporal region, *Petrolacosaurus* is quite primitive in cranial morphology, but rather specialized in the nature of the limbs and girdles. It is not obviously closely related to any of the known Upper Permian or Lower Triassic genera. For information on the differentiation of the advanced reptilian orders, more knowledge of middle and late Permian genera is necessary.

The family Younginidae has long been considered central to the eosuchian concept (Broom 1914*b*; Watson 1957; Romer 1966). Descriptions of the skull and postcranial skeleton of *Youngina* have recently been published (Gow 1975). This work goes far toward establishing the general proportions of late Permian eosuchians. Unfortunately, anatomical details of many of the elements appear poorly preserved, so that supplemental information would be desirable. All the known specimens of *Youngina* come from the *Daptocephalus* zone (Kitching 1970) at the top of the South African Permian. Since both archosaurs (Hughes 1963) and fairly advanced lizard-like genera (Carroll 1975) occur in the same or equivalent horizons, it is important to learn more of earlier eosuchians.

In 1914, Broom (1914*a*) described as the type of a new therapsid species, *Galesphyrus capensis*, a specimen in the South African Museum, SAM-2758, collected from Oorlog's Kloof, Calvinia, Cape Province. Romer (1956) subsequently included this species among the Younginidae. According to J. W. Kitching (pers. comm.), this specimen comes from the base of the *Cistecephalus* zone, considerably below the horizon from which *Youngina* is known. The specimen (Fig. 1) consists of most of a skeleton except the skull, preserved primarily as an impression of the dorsal surface in a water-worn cobble of fine-grained sandstone. Some of the remaining bone was removed with hydrochloric acid, but this technique appeared to be weakening the surface of the block and so was terminated prior to complete removal of the vertebral column. The resultant mould was cast with liquid latex. Where acid preparation was completed, excellent surface detail is evident. This is particularly important in the area of the carpus and tarsus.

A second eosuchian specimen, also from the *Cistecephalus* zone, may pertain to *Galesphyrus*. It is a partial skeleton in the collection of the Bernard Price Institute (No. 4286), from Meerderyk, Colesberg, Cape Province (Fig. 2). It also is preserved as a natural cast, in a small block of rather coarse sandstone. It includes part of the lower jaw, a large fragment of the maxilla, much of the vertebral column and ribs and elements of both girdles and limbs.

Identification of this material as belonging to the Younginidae is based on comparison with *Youngina* from the overlying *Daptocephalus* zone. In as far as comparable elements are present, there is little to differentiate the specimens from the two horizons, except for the larger number and smaller size of the maxillary teeth in the older form, and the relatively greater length of the metatarsals in *Youngina*. The vertebrae are similar in having short neural spines, with the zygapophyses widely spaced and relatively flat, as in the captorhinomorph

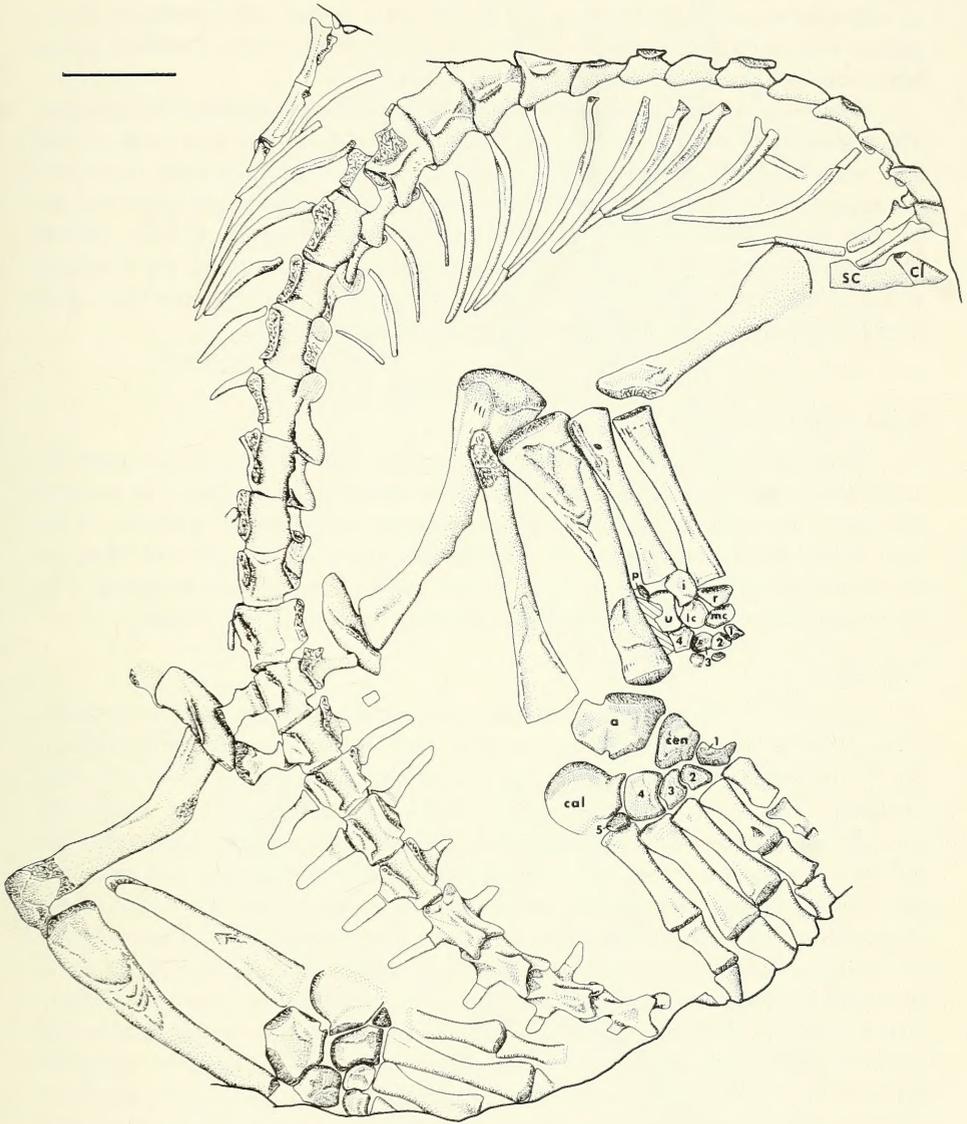


Fig. 1. *Galesphyrus capensis*, type, South African Museum 2758; Oorlog's Kloof, Calvinia, Cape Province; $\times 1.5$. Abbreviations: a, astragalus; cal, calcaneum; cen, centrale; cl, clavicle; i, intermedium; lc, lateral centrale; mc, medial centrale; p, pisiform; r, radiale; sc, scapula; u, ulnare; 1, 2, 3, 4, 5, distal carpals and tarsals.

Captorhinus. There is no evidence of dermal armour associated with the vertebrae of *Galesphyrus*, as has been described in the more specialized eosuchian *Heleosaurus*, also from the *Cistecephalus* zone (Carroll 1976). Isolated armour plates have been recognized in *Youngina* (Gow 1975).

Relatively little of the skeleton is preserved in both specimens of *Galesphyrus*. Their identity is based primarily on overall similarity in size and proportions, and particularly the similarity of vertebral structure. Although both specimens are rather incomplete and their specific identity subject to some question, the extreme rarity of eosuchians from this horizon makes it worth while to publish a complete description. It is of particular importance to document the structure of the tarsus because of the very important changes in foot structure that occur in the many derived diapsid lines during the Triassic.

DESCRIPTION

SKULL AND LOWER JAW

The only cranial remain is the right maxilla, lacking the anterior portion, in the Bernard Price Institute specimen. Eight blunt, peg-like teeth can be seen, with room for at least four more in this segment of the bone. Relative to the size of the maxilla, the teeth are smaller and more numerous than those of *Youngina capensis*. Unlike the teeth in that genus, they are not recurved. The associated lower jaw shows the dorsal posterior margin of the dentary.

VERTEBRAE

In the South African Museum specimen, 22 vertebrae are present in articulation anterior to the sacrum. The eosuchian *Heleosaurus*, from the same horizon, has 25 presacral vertebrae, suggesting that approximately 3 are missing in this specimen. There are 2 sacrals and 8 caudals in sequence. Three additional caudals can be seen adjacent to the 15th–17th trunk vertebrae. Presumably the tail curved around most of the body. The observed caudals may not be at the very end of the tail, but the tail was apparently at least twice the length of the trunk region. The cervical and trunk vertebrae have widely spaced zygapophyses, giving the neural arches an appearance closely comparable to those of *Youngina* described by Watson (1957, fig. 20). This is in strong contrast to the medially placed, sharply tilted zygapophyses of the dromosaurs, with which Broom had originally allied this species. The neural spines are short and roughly triangular in lateral view. Those in the anterior portion of the column, particularly vertebrae 9 and 11 (assuming only three cervicals are missing), are expanded laterally and flattened at the top. Presumably, such specialization would serve to strengthen the column, as would the dermal scutes of thecodonts and *Heleosaurus*. The transverse processes are short and angle anteroventrally from the anterior portion of the pedicle. Where the arches have not been prepared, the neural canal is exposed dorsally. The ventral and lateral margins are essentially flat. There are two sacral vertebrae; as exposed, they are not distinguishable from those of the posterior trunk except by the larger size of the transverse processes.

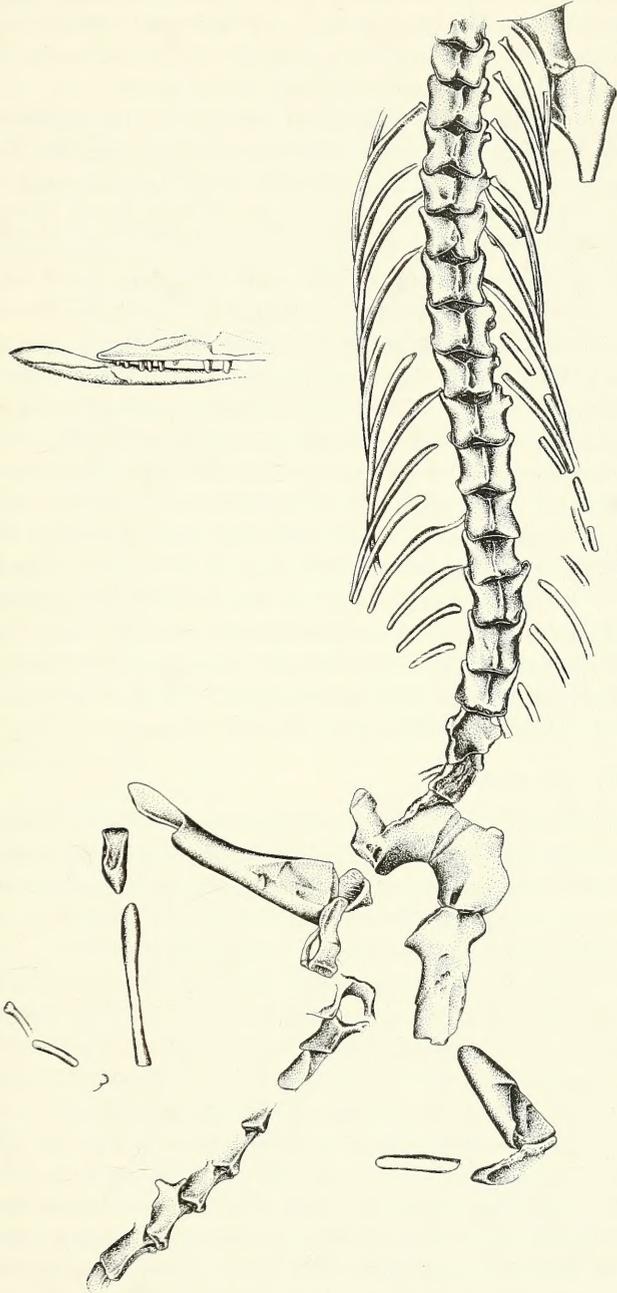


Fig. 2. *Galesphyrus capensis*, Bernard Price Institute 4286; Meerderyk, Colesberg, Cape Province; $\times 1,5$. Jaws were oriented at right angles to the plane of the remainder of the skeleton; they are illustrated to the left of the skeleton to save space.

Behind the sacrum, the neural arches narrow rapidly, with the zygapophyses approaching the midline. The first six bear well-developed transverse processes. The most distal caudals visible have very long, narrow, notochordal centra with closely integrated and very much abbreviated neural arches.

Because of the manner of preservation, neither haemal arches nor trunk intercentra are exposed. In dorsal view, the trunk centra can be seen to fit closely. Presumably, as in other eosuchians, they were deeply notochordal.

RIBS

Ribs are present from the fourth (the most anteriorly preserved) vertebra posteriorly. The most anterior appears considerably shorter than those succeeding it. On this basis it may be considered a cervical. The fifth rib resembles those more posterior. The trunk ribs have long narrow shafts, and at least the more anterior have clearly separate tubercular and capitular heads. The length remains constant to the sixteenth, and then decreases rapidly. Only fragments of ribs 21–25 are visible. There are two pairs of sacral ribs, suturally attached rather than fused to the transverse processes. They apparently had distinct capitular heads as well, but this area is incompletely exposed. The end of each rib expands ventrally as well as anteriorly and posteriorly from a constricted shaft to form a large surface for articulating with the ilium. The first six caudal vertebrae have short ribs which, like the sacrals, are suturally attached rather than fused to the vertebrae. They extend straight out from the pedicle, rather than extending posteriorly, as in captorhinomorph cotylosaurs and *Petrolacosaurus*. The length of the last three diminishes rapidly.

PECTORAL GIRDLE AND LIMB

Of the shoulder girdle, only the dorsal portion of the right clavicular stem and the scapulocoracoid are visible. What little there is is comparable to this region in other primitive reptiles, but does not permit more specific comparison. No cleithrum is visible, although remains would be expected in an animal preserved in this manner if the element were originally present.

Most of the right humerus is visible in more or less its normal position. As in other small primitive reptiles, the ends are expanded to an approximately equal extent and set at a considerable angle to one another. Neither articulating surface is well exposed. Not even the presence of the entepicondylar foramen can be established. The bone is equal in length to approximately four trunk vertebrae. The radius and ulna, of approximately equal length (80% that of the humerus), have fairly simple, lightly built shafts, with the two ends of both expanded to an approximately equal extent. The ulna is distinguished by the presence of a number of grooves and ridges on the posterior margin just beneath the area where the olecranon might have developed. Comparisons of limb proportions with those of *Youngina capensis* are indicated in Table I. The humerus is longer, relative to the femur in *Galesphyrus*, but shorter, relative to the ulna and radius.

TABLE I

	H	r	u	$\frac{r}{H}$	F	t	f	$\frac{t}{F}$	$\frac{H}{F}$
<i>Youngina capensis</i>	23	18	16	75%	34	—	—	—	68%
<i>Galesphyrus capensis</i>	21	17	16,5	81%	27	25	26	92%	78%

TABLE I. Limb measurements and proportions of *Galesphyrus* and *Youngina*, in mm. Measurements of *Youngina* courtesy of C. E. Gow, based on Bernard Price Institute specimen 3859. *Galesphyrus* measurements based on South African Museum specimen 2758.

H—humerus; r—radius; u—ulna; F—femur; t—tibia; f—fibula.

The carpals are preserved in almost normal articulation, although the lateral margin of the area was weathered somewhat prior to discovery, resulting in the loss of the fifth distal carpal, the lateral margin of the ulnare and most of the pisiform. The configuration of the carpus is generally similar to that of the captorhinomorph *Paleothyris* (Carroll 1969). The only conspicuous difference is the simpler pattern of the intermedium, without a sharp constriction between the area of ulnar and radial articulation. Of the hand, only the proximal ends of metacarpals 2 and 3 are visible. The carpus of *Youngina* (Gow 1975) is not sufficiently well preserved for detailed comparison.

In the earliest diapsid, *Petrolacosaurus*, the ulnare and intermedium are much longer bones than in either *Galesphyrus* or captorhinomorphs, presumably in relationship to the greater length of the ulna and radius. The proximo-distal length of the entire carpus is reduced in the ancestors of squamates, but remains long in crocodiles.

PELVIC GIRDLE AND LIMB

Only the dorsal portion of the pelvis is exposed in the South African Museum specimen. Most of the rather narrow iliac blades are visible, but only the dorsal rim of the acetabulum and the dorsal portion of the left pubis are preserved. In the Bernard Price Institute specimen, the anterior portion of the pelvic girdle can be seen in mediodorsal view. The anterior margin of the pubis is quite thick, with an anteriorly facing pubic tubercle, and an opening for the obturator foramen adjacent to the base of the ilium. The pubis appears to be recessed posteriorly for a thyroid fenestra, but this is probably an artefact of preservation. The apparent posterior margins are not smooth or symmetrical on the two sides. It is probable that the posterior portion has been weathered away, or had been slow to ossify. Only fragments of the ischia are preserved. The blade of the ilium is in the shape of a narrow rectangle, ending abruptly distally. The medial surface shows areas for the attachment of two sacral ribs.

Both femora are preserved in the South African Museum specimen, but little can be seen of the ventral surface which would be expected to show the most diagnostic features. The head appears to occupy the entire proximal surface of the bone, as in most other primitive reptiles, but in strong contrast to the con-

temporary eosuchian *Heleosaurus*. The shaft is approximately the length of five trunk vertebrae. The tibia and fibula are relatively much longer and more robust than their counterparts in the forelimb. The distal end of the tibia is relatively much larger than that of the captorhinomorph *Paleothyris*, suggesting firmer union with the astragalus. *Petrolacosaurus* shows a pattern similar to that of *Galesphyrus*. The fibula is somewhat longer than the tibia. The proximal end is not well exposed on either side but can be seen to be roughly cylindrical. The distal end is flattened and expanded in the same plane as the tarsals and would have articulated equally with the astragalus and calcaneum.

The tarsals are well exposed. In both feet they are visible dorsally. The pattern and relative position of the elements are broadly similar to those of primitive captorhinomorphs and pelycosaurs. The large astragalus bears facets for both the tibia and fibula, separated by a notch. This bone is clearly a unitary structure, but presumably it developed, as did that of *Captorhinus* (Peabody 1951), from primitively separate tibiale, intermedium and proximal centrale. The calcaneum, with the astragalus, forms the margin of the perforating foramen, and supports the fibula. Below the astragalus is a single, large, triangular centrale. There are five distal tarsals. The fourth is the largest and supports both the astragalus and calcaneum. The fifth is the smallest, a tiny oval bone, apparently not as wide as the proximal end of the fifth metatarsal. The surface of the fifth distal tarsal is completely unfinished bone, indicating very free movement of the fifth digit. Although it may normally have assumed a divergent position, all the digits are closely aligned on both sides in this specimen. The proximo-medial border of the first distal tarsal is missing, but this bone probably had an oval outline. The second and third are somewhat interlocked and may have functioned as a unit. The metatarsals follow the pattern of captorhinomorphs in increasing their length from the first to the fourth, with the fifth slightly shorter than the

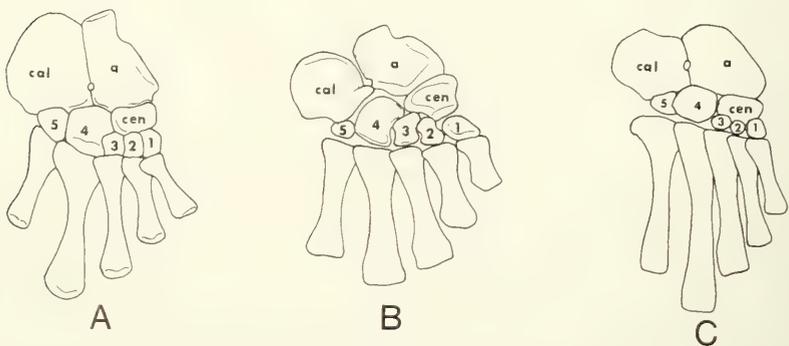


Fig. 3. Tarsus of primitive eosuchians. A. *Petrolacosaurus*, Upper Pennsylvanian of Kansas, $\times 1$ (from Reisz 1975). B. *Galesphyrus*, *Cistecephalus* zone, South Africa; $\times 1,5$. C. *Youngina*, *Daptocephalus* zone, South Africa; $\times 1,5$ (from Broom 1921).

third. The fifth shows no evidence of incipient hooking. The entire tarsus appears essentially flat, as that of romeriids and captorhinids.

Comparison with the romeriid *Paleothyris*, in which the foot is well known, shows several differences. The astragalus and calcaneum are somewhat smaller relative to the distal elements in *Galesphyrus*. In *Paleothyris*, there is a small medial centrale that is lost in *Galesphyrus*, and the lateral centrale is more elongate. The fifth distal tarsal is relatively smaller in the latter form.

The tarsus of *Petrolacosaurus* (Fig. 3A) is generally similar to that of *Galesphyrus*, except for the relatively larger size of the proximal elements. This feature is a primitive characteristic, common also to pelycosaur. The astragalus and calcaneum are closely integrated in *Petrolacosaurus*, but may have become more movable relative to each other in *Galesphyrus*. The centrale is larger in *Galesphyrus* and may have been more closely integrated with the astragalus, a tendency that is emphasized in some later diapsids, particularly the squamates.

The tarsus of *Youngina* (Fig. 3C) has been described by Broom (1921) and Goodrich (1942), but this material can no longer be located. Broom's reconstruction (1921, fig. 20) shows the centrale (identified by Broom as a tibiale) as a narrow oblong element, but his specimen drawing (Fig. 19) shows an oval shape comparable to that of *Galesphyrus*. In as far as can be judged from these illustrations, the arrangement and configuration of the bones are essentially similar in the two genera. The metatarsals are substantially longer, relative to the tarsus, in *Youngina*. Broom restores the fifth metatarsal in *Youngina* as slightly longer than the third. In *Galesphyrus* the fifth is slightly shorter.

No dermal scales are associated with either specimen of *Galesphyrus*.

DISCUSSION

Galesphyrus was a small primitive eosuchian resembling *Youngina* in most features of the skeleton. It is more advanced than *Petrolacosaurus* in having the proximal caudal ribs extending directly laterally, rather than posteriorly, and in the reduction of the relative size of the proximal tarsals.

The structure and proportions of the limbs and vertebrae are less specialized than those of *Petrolacosaurus*, possibly because of the smaller size of *Galesphyrus*, assuming these specimens are near to adult size as is suggested by the high degree of ossification of carpus and tarsus.

Aside from *Youngina*, *Galesphyrus* shows no specific affinities with other eosuchians, or any of the more specialized, derived diapsid lineages. These two genera may represent a persistently primitive group of generalized habits, from which, at a somewhat earlier time, the more specialized eosuchian families arose. Close affinities with the earliest known diapsid, *Petrolacosaurus*, are not apparent. Since the two genera are separated by the length of an entire geological period, one might postulate a considerable remodelling of the skeleton to produce the pattern of the postcranial skeleton evident in *Galesphyrus*, perhaps related to the

smaller size of the latter form. It might also be argued that *Galesphyrus* had evolved from a separate lineage of eosuchians, already distinct in the Upper Carboniferous, which had remained more primitive in its postcranial anatomy in relationship to a persistently smaller body size.

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6. SYSTEMATIC papers must conform with the *International code of zoological nomenclature* (particularly Articles 22 and 51).

Names of new taxa, combinations, synonyms, etc., when used for the first time, must be followed by the appropriate Latin (not English) abbreviation, e.g. gen. nov., sp. nov., comb. nov., syn. nov., etc.

An author's name when cited must follow the name of the taxon without intervening punctuation and not be abbreviated; if the year is added, a comma must separate author's name and year. The author's name (and date, if cited) must be placed in parentheses if a species or subspecies is transferred from its original genus. The name of a subsequent user of a scientific name must be separated from the scientific name by a colon.

Synonymy arrangement should be according to chronology of names, i.e. all published scientific names by which the species previously has been designated are listed in chronological order, with all references to that name following in chronological order, e.g.:

Family Nuculanidae

Nuculana (Lembulus) bicuspidata (Gould, 1845)

Figs 14–15A

Nucula (Leda) bicuspidata Gould, 1845: 37.

Leda plicifera A. Adams, 1856: 50.

Laeda bicuspidata Hanley, 1859: 118, pl. 228 (fig. 73). Sowerby, 1871: pl. 2 (figs 8a–b).

Nucula largillierti Philippi, 1861: 87.

Leda bicuspidata: Nicklès, 1950: 163, fig. 301; 1955: 110. Barnard, 1964: 234, figs 8–9.

Note punctuation in the above example:

comma separates author's name and year

semicolon separates more than one reference by the same author

full stop separates references by different authors

figures of plates are enclosed in parentheses to distinguish them from text-figures

dash, not comma separates consecutive numbers

Synonymy arrangement according to chronology of bibliographic references, whereby the year is placed in front of each entry, and the synonym repeated in full for each entry, is not acceptable.

In describing new species, one specimen must be designated as the holotype; other specimens mentioned in the original description are to be designated paratypes; additional material not regarded as paratypes should be listed separately. The complete data (registration number, depository, description of specimen, locality, collector, date) of the holotype and paratypes must be recorded, e.g.:

Holotype

SAM-A13535 in the South African Museum, Cape Town. Adult female from mid-tide region, King's Beach, Port Elizabeth (33.51S, 25.39E), collected by A. Smith, 15 January 1973.

Note standard form of writing South African Museum registration numbers, date and geographical positions.

7. SPECIAL HOUSE RULES

Capital initial letters

- (a) The Figures, Maps and Tables of the paper when referred to in the text
e.g. '... the Figure depicting *C. namacolus* ...'; '... in *C. namacolus*(Fig. 10) ...'
- (b) The prefixes of prefixed surnames in all languages, when used in the text, if not preceded by initials or full names
e.g. Du Toit but A. L. du Toit; Von Huene but F. von Huene
- (c) Scientific names, but not their vernacular derivatives
e.g. Therocephalia, but therocephalian

Punctuation should be loose, omitting all not strictly necessary

Reference to the author should be expressed in the third person

Roman numerals should be converted to arabic, except when forming part of the title of a book or article, such as

'Revision of the Crustacea. Part VIII. The Amphipoda.'

Specific name must not stand alone, but be preceded by the generic name or its abbreviation to initial capital letter, provided the same generic name is used consecutively.

Name of new genus or species is not to be included in the title: it should be included in the abstract, counter to Recommendation 23 of the Code, to meet the requirements of Biological Abstracts.



ROBERT L. CARROLL
GALESPHYRUS CAPENSIS,
A YOUNGINID EOSUCHIAN FROM
THE *CISTECEPHALUS* ZONE OF SOUTH AFRICA