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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. 1960*a*. Ecological notes on *Conus* (Mollusca: Gastropoda) in the Trincomalee region of Ceylon. *Ann. Mag. nat. Hist.* (13) **2**: 309–320.
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THIELE, J. 1910. Mollusca: B. Polyplacophora, Gastropoda marina, Bivalvia. *In:* SCHULTZE, L. *Zoologische und anthropologische Ergebnisse einer Forschungsreise im westlichen und zentralen Süd-Afrika* **4**: 269–270. Jena: Fischer. *Denkschr. med.-naturw. Ges. Jena* **16**: 269–270.

(*continued inside back cover*)

ANNALS OF THE SOUTH AFRICAN MUSEUM

ANNALE VAN DIE SUID-AFRIKAANSE MUSEUM

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NEW PROCOLOPHONIDS FROM THE TRIASSIC *CYNOGNATHUS* ZONE OF SOUTH AFRICA

By

C. E. GOW

Cape Town Kaapstad

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NEW PROCOLOPHONIDS FROM THE TRIASSIC *CYNOGNATHUS* ZONE OF SOUTH AFRICA

By

C. E. Gow

Bernard Price Institute for Palaeontological Research, Johannesburg

(With 9 figures)

[*MS. accepted 11 August 1976*]

ABSTRACT

Previously only scraps of procolophonids have been known from the Cynognathus zone. One is redescribed here and four new species are described: *Thelegnathus oppressus*, *T. perforatus*, *T. contritus* and *T. spinigenis*. Taxonomy is based on tooth morphology, the species being adapted for specialized herbivorous diets. One of the new species exhibits *Captorhinus*-like tooth replacement. The suggestion is made that procolophonids were upland animals.

CONTENTS

INTRODUCTION

Broom (1905) described a new genus and species of procolophonid from the *Cynognathus* zone which had been collected by Alfred Brown; this he named *Thelegnathus browni*. The specimen was reconsidered and illustrated thirty years later (Broom 1936). Since that time the specimen has been further prepared and will be illustrated and further described in detail below.

Recently Kitching has collected ten more procolophonids from three localities in the *Cynognathus* zone; these are all skulls or partial skulls, some with a little associated postcranial skeleton. Detailed examination of particularly the teeth of these animals leads to the conclusion that there is a group of species present all broadly related to *Thelegnathus*. Owing to the small number of specimens this overall relationship will be assumed to be at the generic level for present purposes. The species exhibit various specializations for an herbivorous diet.

In this paper maxillary teeth are referred to as molars. Tooth replacement terminology follows Edmund (1960).

Ann. S. Afr. Mus. **72** (6), 1977: 109–124, 9 figs.

SYSTEMATICS AND DESCRIPTION

Class REPTILIA
Subclass ANAPSIDA
Order COTYLOSAURIA
Family **Procolophonidae**

Thelegnathus

Diagnosis

Procolophonids in which the maxillary teeth exhibit progressive mesio-distal broadening posteriad.

Thelegnathus browni Broom, 1905

Fig. 1

Holotype

SAM-5869, a left maxilla containing six teeth.

Locality

Unknown, but from a *Cynognathus* zone bone breccia.

Revised diagnosis

The curve of the occlusal plane and the nature of tooth wear are specifically distinctive.

Etymology

Named for the collector, Alfred Brown.

Description

The six molar teeth progressively increase in size posteriad. The teeth have undergone some polishing *post mortem* and before incorporation in the breccia.

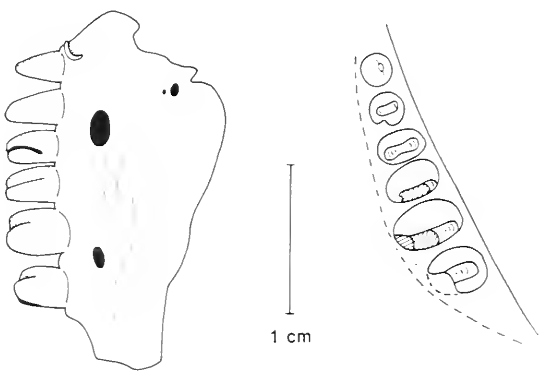

Fig. 1. *Thelegnathus browni* SAM-5896. The type maxilla in labial and occlusal views.

In occlusal view the tip of M1 is seen to lie in line with the labial cusps of the following teeth. Posterior teeth are more heavily worn, particularly on the lingual cusp, with M6 having actually been broken some time well before death. The occlusal plane, i.e. the best fit curve linking the occlusal surfaces of the teeth, is slightly convex ventrally.

Thelegnathus oppressus sp. nov.

Figs 2–4, 8A, C

Holotype

BPI 155, a small, nearly complete but distorted skull with well-preserved dentition.

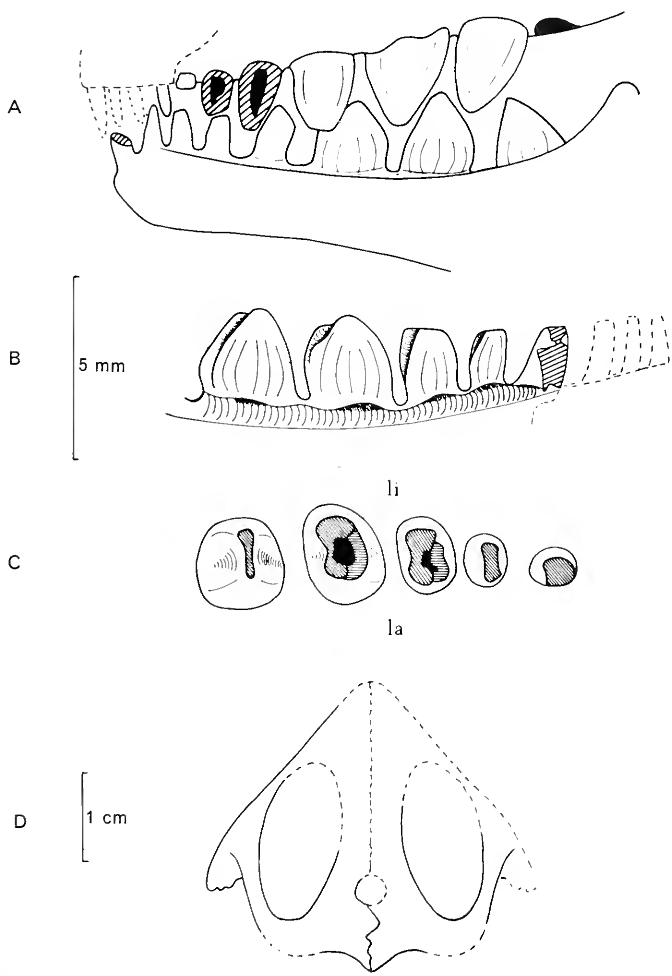

Fig. 2. *Thelegnathus oppressus* BPI 115. A. Labial view of left dentition. B. Labial view of right dentary teeth. C. Occlusal view of same. D. Dorsal outline of the skull.

Paratypes

BPI 4586, a beautifully preserved small skull with teeth occluded, and BPI 4584, the left half of a skull, somewhat larger and with good molar teeth. Both from the same locality.

Locality

The farm Hugoskop, district Rouxville, from the *Cynognathus* zone.

Diagnosis

Molar teeth bulbous at the base with the crowns pinched up to present a small occlusal area.

Etymology

From the Latin *apprimo* = crush, refers to the powerful crushing teeth.

Description

BPI 155 is a small skull found high in the *Cynognathus* zone (J. W. Kitching, pers. com.). Preservation is patchy, apart from the dentition. The roughened quadratojugal projects very slightly obliquely backwards. A subhorizontal break has exposed the right dentary teeth (Fig. 2B–C) and facilitated their preparation. The left dentition (Fig. 2A) has only been developed in external aspect. The dental formula of $I\frac{4}{3}$ $M\frac{6}{5}$ is what would be expected in *Procolophon* of this size (Gow, in press), however, the teeth are much more massive and differently shaped. They are broad and bulbous at the base, and the crowns, although still transversely widened, are pinched to present a much smaller occlusal surface.

The pattern of wear on the dentary teeth (C) produces a short, narrow, flat, transverse terminal facet set off from a deep facet on the anterior surface of the tooth (facets demarcated by a solid line). In molars three and four, wear is so heavy that a dark discoloration caused by the pulp cavity is visible at the centre (black areas).

Especially interesting is the groove which deeply undercuts the molar row on the labial surface, forming the curious sulci at the base of each tooth first reported by Ivachnenko (1974) in *Contritosaurus*.

The paratype BPI 4686 is shown in outline in Figure 3. A notable feature is that the teeth are set well in from the jaw margins. No suture detail is visible. Lateral views of the teeth of this specimen (A) and the type (B) are shown in Figure 4, from which it can be seen that they are substantially the same.

Thelegnathus perforatus sp. nov.

Figs 4–5, 8B, 9

Holotype

BPI 4585, a small, badly crushed skull with well-preserved teeth.

Locality

The farm Hugoskop, district Rouxville, from the *Cynognathus* zone.

Diagnosis

Dentary incisiform teeth large and robust. Occlusal plane forms distinct angle with the tooth-bearing surface of the dentary. Multiple tooth rows present in maxillae and dentaries.

Etymology

From the Latin *perforo* = pierce, refers to the piercing molars.

Description

This is a badly crushed skull with well-preserved dentition. The right maxilla is covered by the right lower jaw, which is displaced and closely applied against the exterior surface of the maxilla, which has thus not been prepared at this stage.

The full left maxillary dentition is preserved (Fig. 5A, D), and contains elements of three *Zahnreihen*. The labial row comprises one large incisiform tooth followed by five molars of which the last, and youngest, is the only unworn tooth. These teeth are massive pointed cones; wear is due to tip-to-tip pounding, and there is also a slip-wear facet on the lingual surface of the three central molars caused by rubbing against the corresponding lower teeth—hence we know that the lower teeth occluded within the uppers.

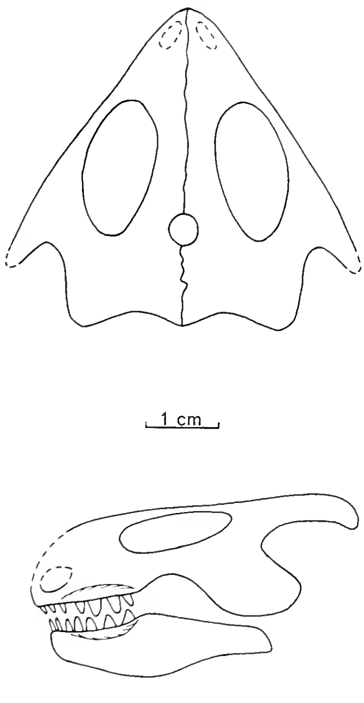

Fig. 3. *Thelegnathus oppressus* BPI 4586.
Paratype: outline drawings of the skull.

In the left dentary (Fig. 5B, E–F), there are two mature incisors followed by a tooth space, followed by three worn and two unworn molars comprising a *Zahnreihe*. The three anterior (therefore oldest) incisors of the next *Zahnreihe* are preserved in position. One or two tooth buds have probably been lost behind these.

The right dentary dentition (Fig. 5C, G) differs in having the first incisor broken off and in having only four molars in the oldest *Zahnreihe*; the second *Zahnreihe* is also more advanced.

The teeth of this specimen are shown in Figure 4C. The relatively enormous size of the incisors compared with those of *T. oppressus* is clear. In *T. oppressus* the slope of the occlusal plane is parallel to the tooth-bearing surface of the dentary, whereas in *T. perforatus* the occlusal plane forms a pronounced angle with the surface of the dentary.

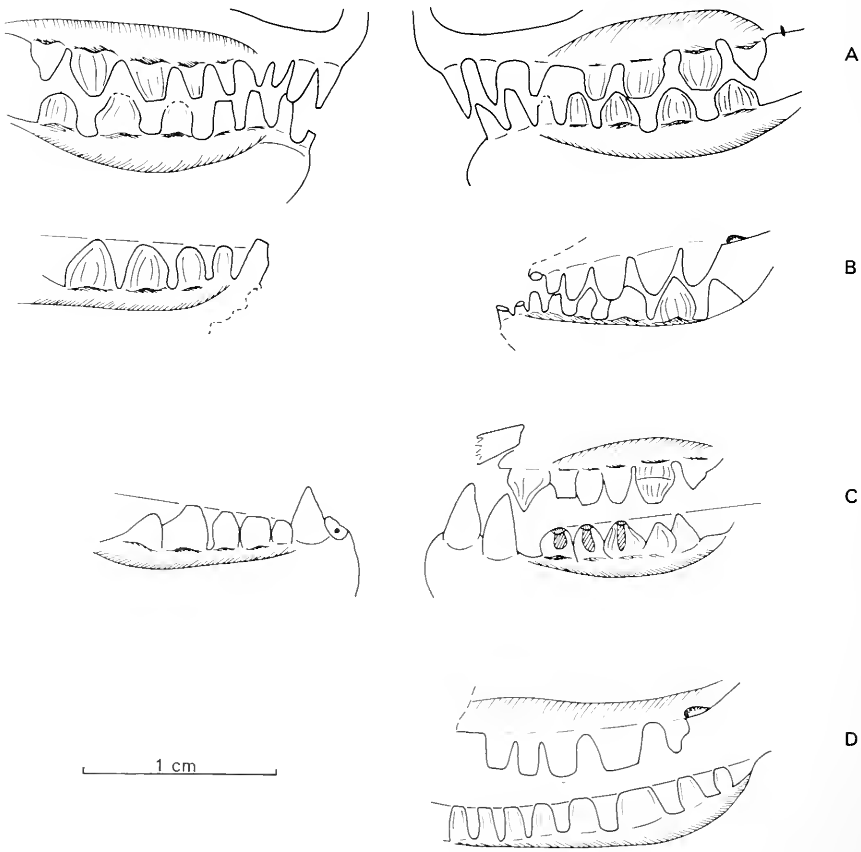

Fig. 4. Comparisons of the teeth of several new species in labial view. A. *Thelegnathus oppressus* BPI 4586. B. *Thelegnathus oppressus* BPI 155. C. *Thelegnathus perforatus* BPI 4585. D. *Thelegnathus contritus* BPI 3512.

Thelegnathus contritus sp. nov.

Figs 4, 6, 8D

Holotype

BPI 3512, a skull with some associated post-cranial bones, lacking the snout and with the right side of the skull weathered away.

Locality

The farm Winnaarsbaken, district Burghersdorp, from the *Cynognathus* zone.

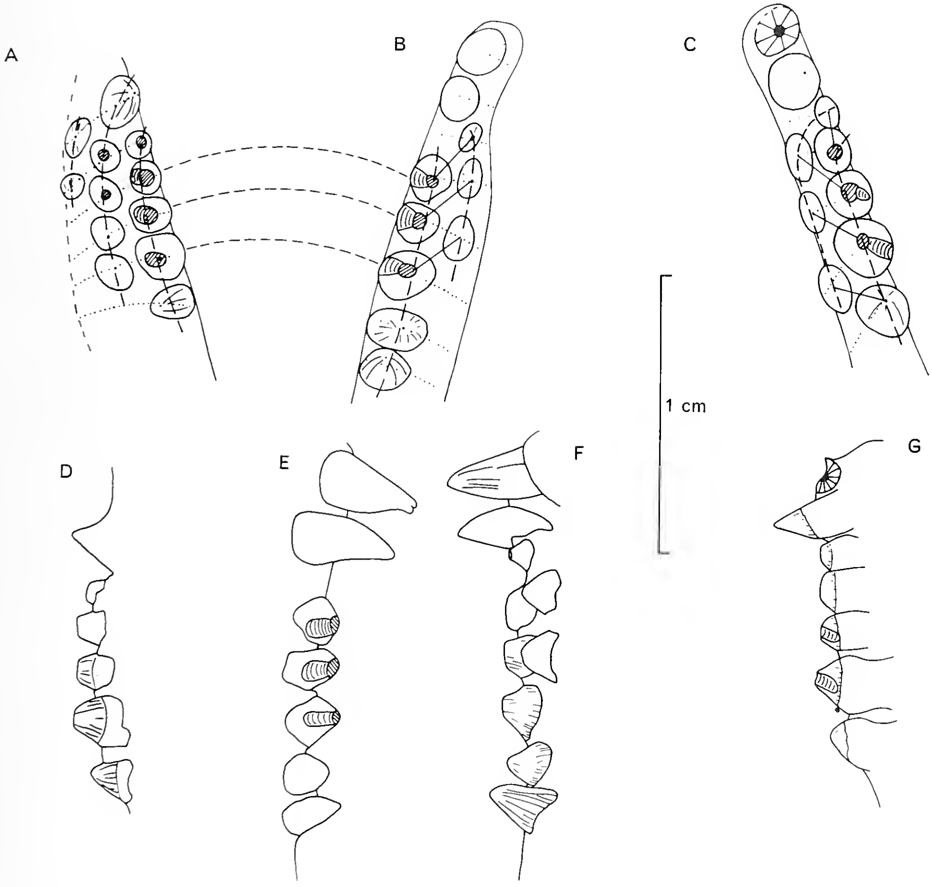

Fig. 5. *Thelegnathus perforatus* BPI 4585. Details of the dentition of the type. A. Left maxillary dentition in occlusal view. D. The same in labial view. B. Left dentary dentition in occlusal view. E. The same in labial view. F. The same in lingual view. C. Right dentary dentition in occlusal view. G. The same in labial view. *Zahnreihen* are indicated by dashed lines. Teeth of younger *Zahnreihen* replace those to which they are joined by dotted lines. Occluding teeth are linked by dashed arcs.

Diagnosis

One tooth of the molar series almost twice as broad in lateral aspect as any other. (The position of this tooth in the row will vary with the age of the individual. Tooth replacement is demonstrated in another paper (Gow, in press).)

Etymology

From the Latin *contero* = pound.

Description

All the preserved teeth are probably molars, though there could be some doubt about the anterior dentary teeth. Posterior molars are all broadened mesiodistally, but the second of these thickened teeth in both jaws is almost twice as

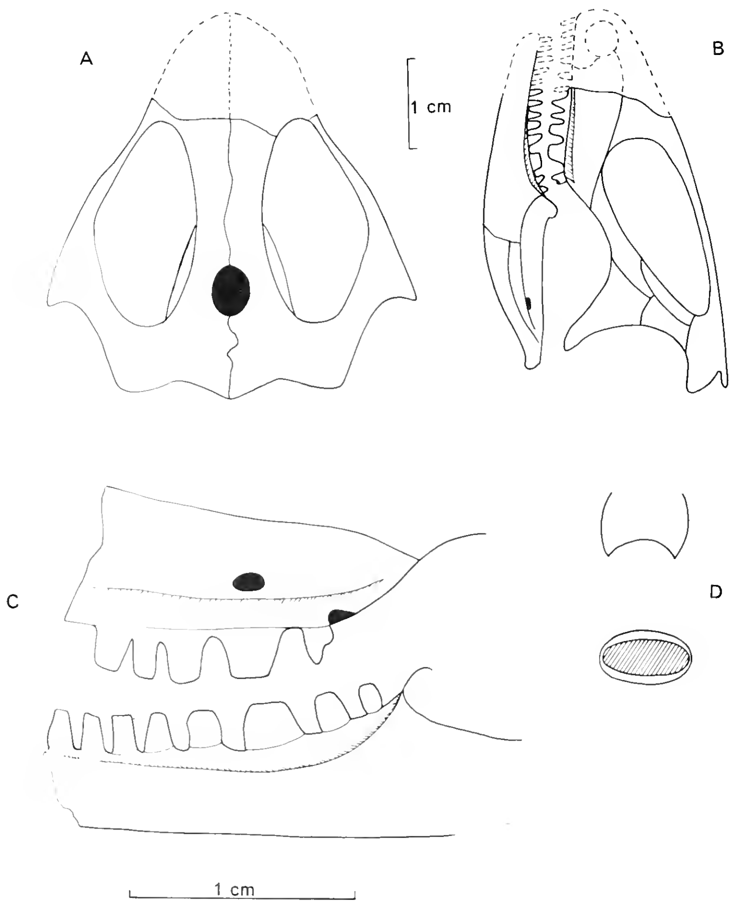

Fig. 6. *Thelegnathus contritus* BPI 3512. A. The skull in dorsal outline. B. The skull in lateral view. C. Labial outline of the dentition. D. Sketches of crown shape in mesiodistal and occlusal aspects.

thick as any other. In this feature this species differs substantially from those described above. The occlusal plane is curved and the molars are all heavily worn to the form sketched in Figure 6D. The quadratojugal of this specimen is small and smooth, but the taxonomic significance of this is unknown. (In *Procolophon* the morphology of the quadratojugal varies with the age of the individual.)

Thelegnathus spinigenis sp. nov.

Fig. 7

Holotype

BPI 4299, a reasonably complete and undistorted skull.

Paratypes

BPI 3894, 4300, 4587 and 4588, all skulls.

Locality

The farm Lemoenfontein, district Rouxville, from the *Cynognathus* zone.

Diagnosis

Quadratojugal produced postero-laterally in the form of a large blunt spine. (No species diagnostic dental information available.)

Etymology

From the Latin *spina* = spine, and *gena* = cheek.

Description

The five skulls from one locality all clearly belong to one species. Drawings are taken from the type except for the teeth, which are those of 4300. In all cases bone is soft and the nodular red rock matrix extremely hard, thus, while the teeth are seen to broaden posteriad and to be heavily worn, no detail of the occlusal surfaces is available. There is no suture detail that is anything but typically procolophonid. What all the skulls have, however, is the enormous quadratojugal which extends the line of the cheek backwards in the form of a large, blunt spine which in life may have borne a sharp keratinous spine protecting the neck and shoulder region.

Remarks

This form must be regarded as a distinct palaeontologic species. There is the possibility that it might be the adult form of *T. oppressus*; however, 4300, the smallest of the five, is not much bigger than *T. oppressus* so the inclination is to believe that *T. spinigenis* is a true biologic species.

DISCUSSION

The multi-rowed dentition of Thegnathus perforatus

In the left maxilla (Fig. 5A, D), initiation of *anlagen* at each tooth position clearly followed rapidly on the formation of their predecessors, as lingual to the marginal row of teeth the next row is nearly completely formed. This can be stated another way, by saying that the *Zahnreihe* slope (dashed lines connecting teeth, Fig. 5) is roughly parallel to the jaw. Of the oldest *Zahnreihe* the incisor has already been shed, while the interesting point about the second *Zahnreihe* is that the first two molars are already partially worn. A third *Zahnreihe* is represented by an incisor and first molar. In the maxillary dentition, wear on molars of the second *Zahnreihe* is interesting. The only way this wear could have

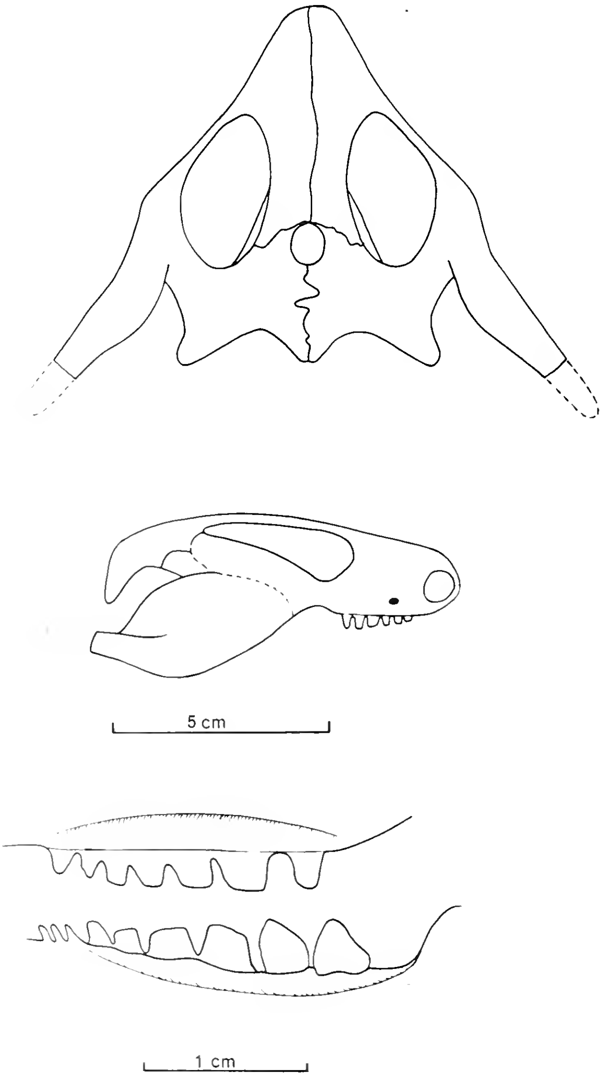

Fig. 7. *Thelegnathus spinigenis* BPI 4299.
Skull in dorsal and lateral views.
BPI 4300. Labial outline of teeth.

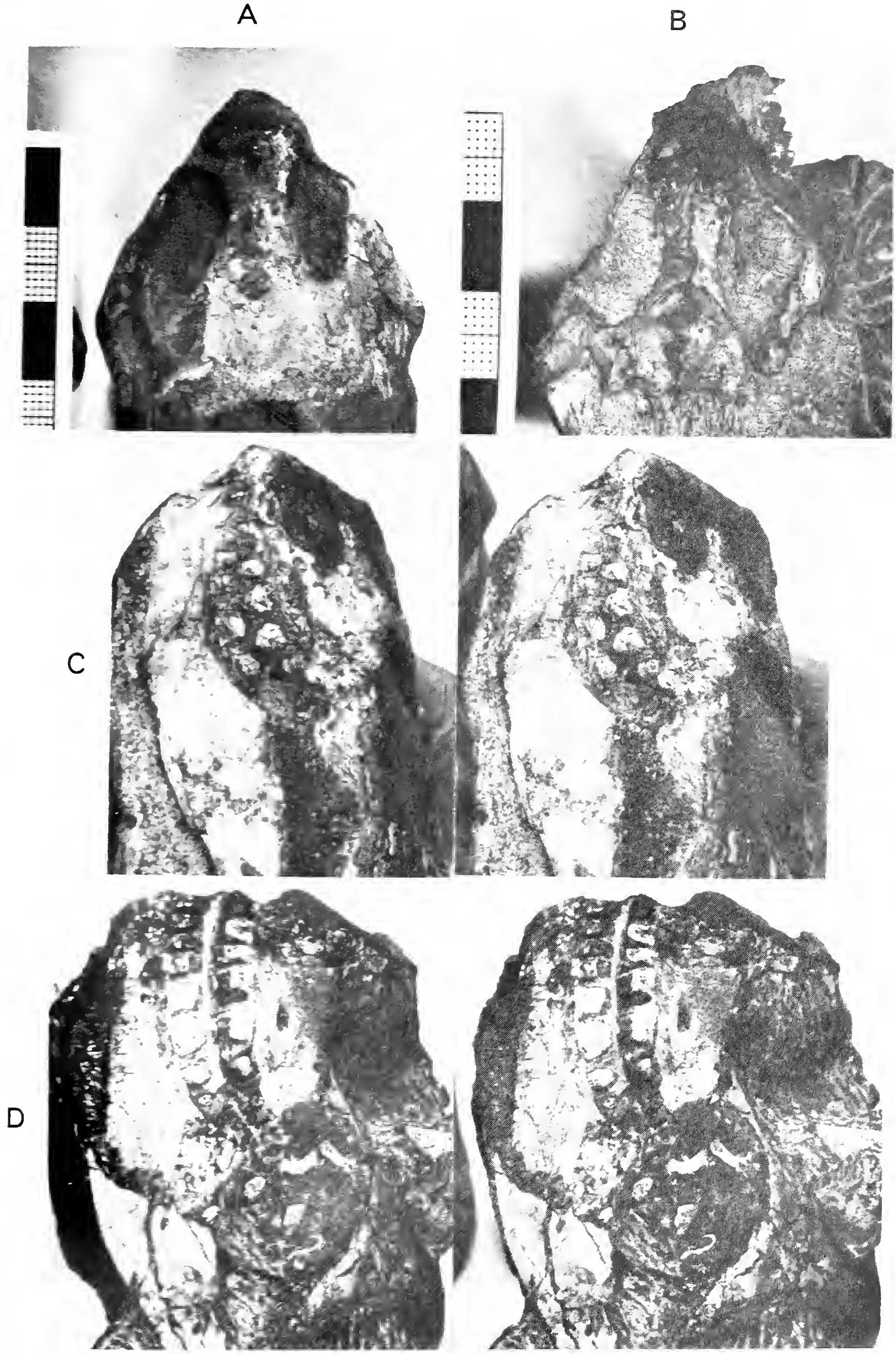

Fig. 8. A. *Thelegnathus oppressus* dorsal view of paratype BPI 586; ×1. B. *Thelegnathus perforatus* dorsal view of type BPI 4585; ×1. C. *Thelegnathus oppressus* BPI 586. Stereophotographs of left dentition; ×2. D. *Thelegnathus contritus* BPI 3513. Stereophotographs of left dentition; ×2.

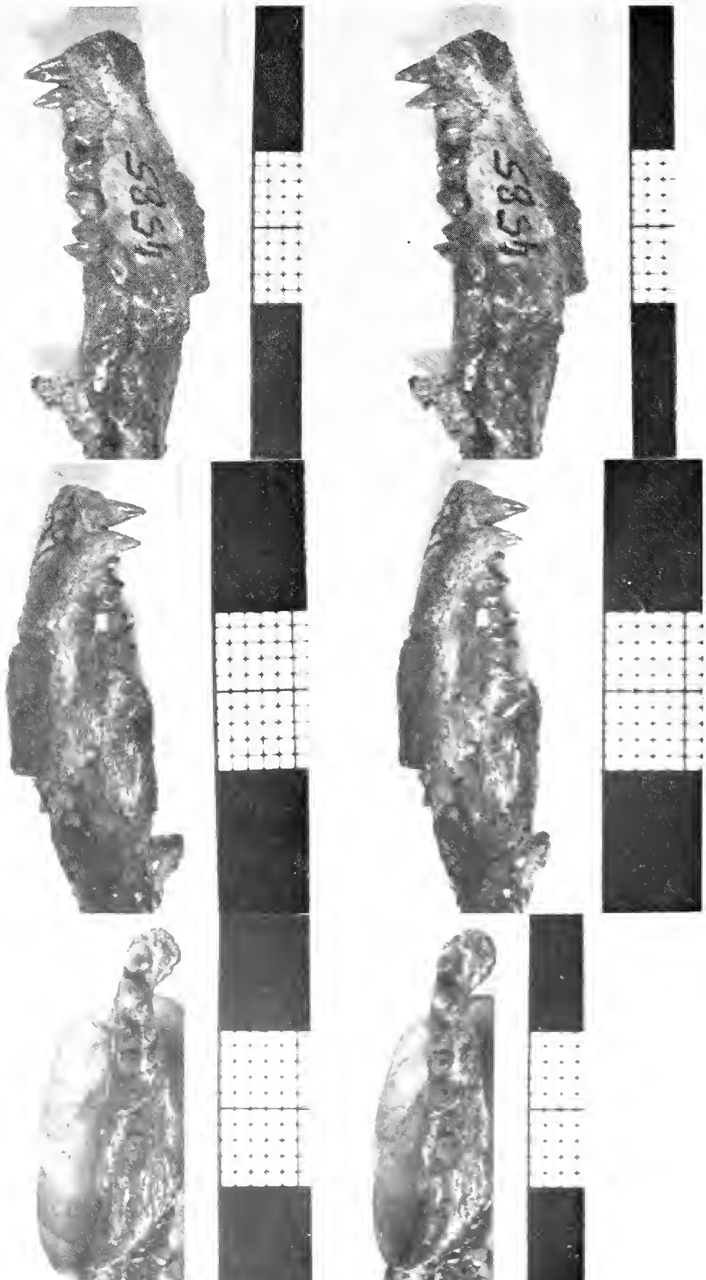

Fig. 9. *Thelegnathus perforatus* BPI 4585. Stereophotographs of the left lower jaw and teeth.

occurred would have been by contact with the first two lower molars before the latter reached their present position, hence the wear on a tooth may be due in part to contact with another long since replaced.

With respect to the dentary dentitions and due probably to the marked heterodonty as between molars and incisors, it is not possible to incorporate both types of teeth within the same *Zahnreihe* and it seems probable that replacement operated independently (as appears to be the case in *Procolophon* (Gow, in press)). Replacing teeth in the dentary are interpreted as having formed beside the teeth to which they are linked by dotted lines (Fig. 5), but replacing those to which they are linked by solid lines. This means that the functional teeth moved antero-labiad before being finally shed.

The dentition of *T. perforatus* as described above is strikingly similar to that of *Captorhinus aguti* (Bolt & De Mar 1975). One inference from this is that multiple rowed dentitions in cotylosaurs are a Permian specialization retained in *T. perforatus*. The alternative possibility is that the same dental arrangement has been evolved independently at different times in these two animals, i.e. that there is a genetically inherent predisposition to the attainment of this condition in cotylosaurs.

The teeth of most known procolophonids are labio-lingually broadened and distinctly bilobate (this is described elsewhere (Gow, in press)). Exceptions to this are some of the primitive Russian forms and *Owenetta*. It is becoming clear from much data on tooth replacement in reptiles by various workers, including the present writer, that rate of replacement is often variable with the age of the individual (typically, it seems, slowing with age). This affects *Zahnreihen* spacing and the number of teeth in a replacement sequence. These remarks are necessarily condensed as this is primarily a taxonomic paper; they lead to the following tentative statement.

Captorhinus and procolophonids presumably share common ancestry from romeriid captorhinomorphs. *Captorhinus* has attained a multiple tooth-rowed state by lengthening of *Zahnreihen*, and the same condition is seen in *Thelegnathus perforatus*; what then is the odontological history of the more typical broadened bilobate procolophonid tooth? At this stage one can suggest no more than a possibility, and this is done here in the hope of generating further interest, that possibility being that the bilobate molar may represent a fusion of two tooth buds from *adjacent Zahnreihen*.

One is not, in fact, faced with a choice between direct relationship between *T. perforatus* and *C. aguti* or the development much later in time of a *Captorhinus*-like condition in *Thelegnathus*. Rather, these apparently dramatic dental patterns are achieved through the plasticity inherent in the reptilian dental replacement cycle.

General

The sudden appearance in the *Cynognathus* zone of five species of procolophonid is most unexpected. That one of these should in addition possess a pattern of tooth replacement apparently more primitive than that in any other known procolophonid regardless of age, is remarkable.

Several points arise, but perhaps the overriding consideration is the inference that some aspect of procolophonid biology has mitigated against their preservation in the fossil record except under certain peculiar circumstances.

Hotton & Kitching (1963) suggested that what was then known as the *Procolophon* zone, and indeed the overlying *Cynognathus* zone as well, may have been laid down discontinuously on an erosion surface of considerable relief. Unfortunately this important concept still remains to be tested by a regional geological study. What is certain is that procolophonids from both these zones occur in hard red rocks typical of terrestrial redbeds.

Colbert (1946) discusses the geological setting of *Hypsognathus* in some detail. *Hypsognathus* was found in sandstone of the Newark Series. Taking a closer look at this series we find that it was laid down in a block-faulted area of high relief. Deposition of the Newark was very rapid, hence the lower section is nearly all sandstone, but redbeds towards the top (over part of the area of deposition) are cited by Pettijohn (1957) as a classic terrestrial redbed sequence. Newark plant fossils correlate floristically with those of the southern African Molteno formation (J. T. Brown, pers. com.).

Procolophonids are also known from the Triassic fissure fillings of Britain (Robinson 1967); these are as yet undescribed. These fillings contain an upland fauna.

These few observations suggest that the reason procolophonids occur only sporadically in the fossil record is that they were upland animals and would not have occurred in large depositional basins.

All the broad-toothed procolophonids were almost certainly plant-eaters. If it can be assumed that the large, well-known anomodonts were by and large lowland forms, then the procolophonids as upland herbivores would have had little competition from other known reptiles between the disappearance of the edaphosaurs and the arrival of the gomphodonts and bauriamorphs, with the exception of some of the rhynchosaurs and possibly small anomodonts like *Myosaurus* (this might also account for the extreme rarity of the latter). Thus it is possible that for much of the Permian and Triassic the procolophonids were not offered any serious competition as the only upland herbivorous reptiles. However, their depredations on particularly the reproductive parts of the vegetation very likely resulted in an interaction producing evolutionary responses on both sides.

This last observation seems particularly to hold good for the late Triassic as regards both plant (J. T. Brown, pers. com.) and animal. *Thelegnathus browni* clearly had powerful crushing teeth (even to the extent of the most recently erupted molar in the type having broken in use). Such an animal would make a very efficient seed-eater. *T. oppressus* was an even better crusher of hard seeds with its large, bulbous, sharp-pointed molars. In *T. perforatus* the incisors are large and powerful, such as might be used for grabbing and wrenching off the seed of a particularly tough plant. The first maxillary tooth is a piercing tooth which does not meet in tip-to-tip occlusion with any other. Other molars, although the tips do wear, seem to be primarily piercing teeth. On this basis it is suggested that this animal utilized only the soft outer coating of certain seeds. Molar tip wear would then simply be due to contact with the hard seed. *T. contritus* has well-worn pounding teeth rather like those of *Procolophon*: this species may have been a foliage feeder. Nothing can be said concerning the diet of *T. spinigenis* until a specimen turns up which is more amenable to preparation.

SUMMARY

The description of the procolophonid *Thelegnathus browni* from the *Cynognathus* zone is expanded and four new species referable to this genus are described.

Taxonomic separation is based entirely on details of tooth morphology, the various species being specialized for different herbivorous diets. *T. browni* and *T. oppressus* are thought to have been crushers of hard seeds. *T. perforatus* may have lived on the softer outer coatings of seeds. *T. contritus* was a foliage eater.

One of the new species, *T. perforatus*, had multi-rowed marginal teeth. The *Zahnreihen* are parallel to the jaw and follow in rapid succession, which suggests the possibility that the specialized broadened bicuspid teeth of typical procolophonids may represent a fusion of two *anlagen* in adjacent *Zahnreihen*.

Preliminary evidence is presented in the discussion which suggests that procolophonids were upland animals. Aside from fissure fillings they are typically associated with discontinuous redbed facies. This may account for the patchy appearance of these animals in the fossil record. It may also account for their success as they would then be removed from competition with most known anomodonts.

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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°51'S 25°39'E), collected by A. Smith, 15 January 1973.

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

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.

C. E. GOW

NEW PROCOLOPHONIDS
FROM THE TRIASSIC *CYNOGNATHUS* ZONE
OF SOUTH AFRICA