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A NEW SPECIES OF THE RHYTIDOSTEIDAE FROM THE *LYSTROSAURUS* ZONE AND A REVIEW OF THE RHYTIDOSTEOIDEA

by

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ABSTRACT

Pneumatostega potamia, a new rhytidosteid temnospondyl from the *Lystrosaurus* Zone, is described and compared with the other species of the family. Its evolutionary relationships and adaptive morphology are considered. The closest affinity is with the species of *Deltasaurus* from the Lower Triassic of Australia, the next closest with the species of *Peltostega* from the Lower Triassic of Spitsbergen and the most distant with *Rhytidosteus capensis*, a Karoo species which is probably also from the *Lystrosaurus* Zone. As with other species of Rhytidosteidae, for which both taphonomic and adaptive morphologic evidence is available, *P. potamia* was, apparently, a fluviatile, subsurface, piscivorous temnospondyl regarding its primary and preferred habitat.

Proceeding from information contributed by the new species, the taxonomic structure of the Rhytidosteoidea is reorganised and expanded and new diagnoses are provided for both this superfamily and its contained families. The family Rhytidosteidae now includes *Deltasaurus kimberleyensis, D. pustulatus, Peltostega erici, P. wimani, Pneumatostega potamia* and *Rhytidosteus capensis*. A new family, Indobrachyopidae, is created to include *Derwentia warreni* (removed from the Rhytidosteidae), *Indobrachyops panchetensis, Mahavisaurus dentatus, Mahavisaurus (Lyrosaurus) australis* and *Rewana quadricuneata*. *Laidleria gracilis* is removed from the Rhytidosteoidea. *Latiscopus disjunctus* and *Almasaurus habbazi* possess some features in common with members of the superfamily but are too distinct in most features to be considered rhytidosteoids.

Taxonomic distances among the rhytidosteids and indobrachyopids are established by a computer program. A phylogeny of the superfamily is constructed and this is consonant with the stratigraphic and geographic occurrences of the species. A southern origin for the superfamily with a generally northward dispersal is proposed.

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INTRODUCTION

In 1975, while inspecting the collection of Permian and Triassic labyrinthodonts at the Bernard Price Institute for Paleontology and the South African Museum, the senior author found in each collection an unidentified and unreported specimen from the *Lystrosaurus* Zone. Both specimens bore immediate resemblances to members of the family Rhytidosteidae, particularly to two of its Australian species, *Deltasaurus kimberleyensis* and *D. pustulatus*. Both were contained in sandy pebble conglomerate matrix, unusual for the *Lystrosaurus* Zone which is most productive of fossil vertebrates in its common red shale and red sandstone facies. The BPI specimen consisted of approximately two-thirds of a skull roof, exposed on its inner surface and consisting of actual bone over most of its extent but weathered down to the external impression in places. This specimen was collected by Dr. J. W. Kitching in 1950 on the Tafelberg property, near Middelburg, Cape Province. The SAM specimen consisted of various portions of the cranial and

postcranial skeleton, mostly broken and incomplete, of a single individual. The portions were disarticulated and randomly placed within a 130 × 130 × 40 mm rounded cobble of pebble conglomerate matrix. Locality information in the SAM catalogue states that it was collected in the *Lystrosaurus* Zone on the Goede Hoop property near Colesberg, Cape Province by A. J. Hesse and C. W. Thorpe in 1935.

Although the skull portion of the SAM specimen is less complete than the BPI specimen, enough remains to indicate that the original complete skull closely approximated the BPI specimen in shape, i.e. it presented an equilateral triangle in dorsal view. This feature, together with exact correspondence of the sculpturing on the dermal bones (a variant of the highly characteristic rhytidosteid pattern) suggests strongly that the two specimens are homotaxial. The BPI specimen is nominated the holotype as it has yielded the larger number of taxonomically important characters.

The BPI specimen was prepared by Dr. Kitching through careful mechanical removal of remaining bone from the well-preserved external impression of the skull roof. A series of photographs and peels were taken from the specimen prior to removal of the bone. Upon completion of preparation, peels were taken of the external impression.

The SAM specimen was placed on loan to the authors for preparation and study. Formic acid reacted well with the matrix and produced excellent results. The various skeletal fragments were completely freed of matrix and delicate surface features such as the dentition of the cranial fragments and surface sculpturing on dermal bones survived largely undamaged.

The new taxon constitutes an important addition to the labyrinthodont component of the fauna from the *Lystrosaurus* Zone. Previously described and taxonomically valid species of this component include:

Family Capitosauridae
Kestrosaurus dreyeri Haughton, 1925
Family Lydekkerinidae
Limnoiketes paludinatans Parrington, 1948
Lydekkerina huxleyi (Lydekker, 1889)
Lydekkerina kitchingi Broom, 1950
Family Micropholidae
Micropholis stowi Huxley, 1859
Family Rhytidosteidae
Rhytidosteus capensis Owen, 1884
Family Uranocentrodontidae
Uranocentrodon senekalensis (Van Hoepen, 1911)

Rhytidosteus capensis, based on a single partial skull found near Beersheba, Orange Free State, has always been cited as questionably deriving from the *Cynognathus* Zone (e.g. Romer, 1947, p. 190) but Kitching (pers. comm.) believes it more likely that the site lies within the basal Triassic *Lystrosaurus* Zone.

Broom (1930) nominated three further species of the Lydekkerinidae, *Lydekkerina dutoiti, Lydekkerina putterilli* and *Putterillia platyceps.* Romer (1947) changed the generic designation of the first to *Broomulus.* Cosgriff (1974) removed all three from the Lydekkerinidae, and placed them *incertae sedis* among the Temnospondyli. However, in 1975, the senior author had the opportunity to inspect the holotype skulls at the Bernard Price Institute and concluded that they are all distorted specimens of *Lydekkerina huxleyi.*

Although Von Huene (1920, p. 458) nominated the then monotypic family Rhytidosteidae for *Rhytidosteus capensis* Owen (1884, p. 333–338, pls. XVI and XVII), this was not accepted by other authorities and the species was for long included in the Trematosauridae (e.g. Romer, 1947, pp. 190–191 and 314). Cosgriff (1965, pp. 67–68) revived the family to include not only *R. capensis* but also *Peltostega erici* Wiman (1916, pp. 210–216, text figs. 1–3, pl. XV, figs. 1–3, pl. XVI, fig. 1), *P. wimani* Nilsson (1946, pp. 4–34, figs. 11–18), and two new species, *Deltasaurus kimberleyensis* Cosgriff (pp. 68–80, figs. 1–9) and *D. pustulatus* Cosgriff (pp. 80–83, figs. 10 and 11). In this same paper, the taxonomic relationships of two further labyrinthodont species, *Laidleria gracilis* Kitching (1958, pp. 67–82, figs. 16–19) and *Latiscopus disjunctus* Wilson (1948, pp. 359–361, pl. 59), were also considered. Kitching placed *L. gracilis* provisionally in the Trematosauridae but suggested, as an alternate allocation, that it be considered "as the type of a new family, the Laidleriidae". Cosgriff adopted Laidleriidae and provisionally included it as a family in the superfamily Rhytidosteoidea. Wilson created a new family, Latiscopidae, for *L. disjunctus,* not attempting a superfamily allocation. Cosgriff, although noting certain similarities of *L. disjunctus* to the rhytidosteids, followed Wilson in regarding the family as *incertae sedis.*

Subsequently, a sixth species, *Derwentia warreni* Cosgriff (1974, pp. 74–78, figs. 48–55) was added to the Rhytidosteidae.

In the present research, comparisons of the new species from the *Lystrosaurus* Zone with the six established species of the family led to a reconsideration of *Laidleria gracilis* and *Latiscopus disjunctus* and, further, to a review of five other temnospondyl species from the Lower Triassic of various parts of the world, each of which bears certain resemblances to the rhytidosteid species. These are: *Indobrachyops panchetensis* Von Huene and Sahni (1958, pp. 1–17, text figs. 2–5, pls. I and II); *Mahavisaurus dentatus* Lehman (1966, pp. 4–9, text figs. 1 and 2, pls. I, II and IIIa, c and d); *Lyrosaurus australis* Lehman (1966, pp. 11–15, text fig. 3, pl. IVa); *Rewana quadricuneata* Howie (1972, pp. 51–64, text figs. 1–6, pl. I); and *Almasaurus habbazi* Dutuit (1972, pp. 73—77, figs. 1 and 2). Gross comparisons of all of these with each other, with the rhytidosteid species and with *Laidleria gracilis* and *Latiscopus disjunctus* has produced alterations in the diagnoses of the superfamily Rhytidosteoidea and the family Rhytidosteidae. It has also produced changes in the contents of these taxa. *Derwentia warreni* is removed from the Rhytidostei-

dae. The Rhytidosteoidea is expanded to include a new family, Indobrachyopidae, which receives *Derwentia warreni* as well as *Indobrachyops panchetensis, Mahavisaurus dentatus, Lyrosaurus australis* and *Rewana quadricuneata.*

Following the description and consideration of the new form from the *Lystrosaurus* Zone and comparisons of this with the other species of the Rhytidosteidae, all related and possibly related species are reviewed. *Laidleria gracilis, Latiscopus disjunctus* and *Almasaurus habbazi* are excluded from the superfamily. Next, the reordered composition of the Rhytidosteoidea is presented, together with new diagnoses of its contained families. Finally, through employment of a computer program, taxonomic distances among all of the contained species are determined, a phylogeny is constructed and this phylogeny is shown to be consonant with geographic and stratigraphic distribution.

Superfamily RHYTIDOSTEOIDEA
Family RHYTIDOSTEIDAE
PNEUMATOSTEGA, n. gen.

Etymology. Pneumato from Greek *pneumatos*, lung; *stega* from Greek *stegos*, plate. Name given in reference to the highly vascular and, hence respiratory, bones of the dermal cranial and pectoral skeleton.

Diagnosis. The skull, in dorsal view, approximates an equilateral triangle. Snout tip acute. Occiput very broad relative to skull length, B : L index 1,41 (indices and letter symbols follow the convention of Welles and Cosgriff, 1965, fig. 1). Orbits circular. Interorbital area narrow, A : L index 0,34. Palatal tooth row on palatine and ectopterygoid bones well developed; teeth in this row twice as long as those on maxilla. Interpterygoid vacuities elongate, Y : L index 0,53. Dermal bones appear highly vascular. Nodes surmounting points of junction and bifurcation on dermal sculpture ridges very high and prominent. Frontal bones long and narrow, contrasting with square frontal of *Deltasaurus* and *Derwentia.* Lateral line canals better developed and more continuous than those of *Peltostega* and *Rhytidosteus*, less so than those of *Deltasaurus* and *Derwentia.*

Distribution. Lystrosaurus Zone, Beaufort Series of Cape Province, South Africa.

Type Species. Pneumatostega potamia.

PNEUMATOSTEGA POTAMIA, n. sp.

(figs. 1–7, 8a and 10; pls. I–V)

Etymology. Potamia from Greek *potamios.* Name given in reference to the stream channel habitat of the species.

Holotype. BPI F.no.981, impression on conglomerate matrix of the dorsal surface of a skull.

Type locality. Tafelberg property near Middelburg, Cape Province; *Lystrosaurus* Zone.

Paratype. SAM 11188, portions of the skull, lower jaw, dermal shoulder girdle and vertebral column of a single individual; material disarticulated and scattered through a rounded cobble of conglomerate matrix.

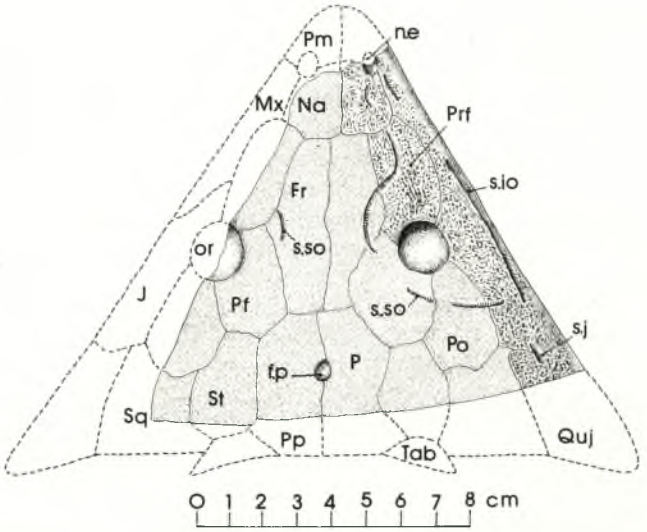


Figure 1. *Pneumatostega potamia*, n.g. and sp., reconstruction of dorsal surface of skull, based on holotype, BPI F.no.981. Shaded area indicates portion of skull roof impression retained on the specimen. Only right lateral bones of the impression have sculpture pattern indicated in this drawing although sculpture extends over the entire impression. Abbreviations for Figure 1 and following figures: a.p.v., anterior palatal vacuity; dia, diapophysis; fa.cl., clavicular facet; fo.st., subtemporal fossa; f.p., parietal foramen; Fr, frontal; Ic, intercentrum; i.p.v., interpterygoid vacuity; J, jugal; Mx, maxillary; Na, nasal; n.a., neural arch; n.e., external naris; n.i., internal naris; or, orbit; P, parietal; par, parapophysis; Pc, pleurocentrum; p.c., cultriform process; p.cl. cleithral process; Pf, postfrontal; Pm, premaxillary; Po, postorbital; Pp, postparietal; Prf, prefrontal; Ps, parasphenoid; Pt, pterygoid; Qu, quadrate; Quj, quadratojugal; S.io., infraorbital groove; s.j., jugal groove; Sq, squamosal; s.so., supraorbital groove; St. supratemporal; Tab, tabular; z.a., anterior zygapophysis.

Paratype locality. Goede Hoop property, near Colesberg, Cape Province; *Lystrosaurus* Zone.

Diagnosis. Same as for genus.

Description

Observations and interpretations concerning the dorsal surface of the skull are based on the holotype. Those concerning the palatal surface of the skull, the lower jaw, the dermal shoulder girdle and the vertebral column are all based on the fragmentary skeleton which comprises the paratype.

Skull, dorsal surface (figs. 1 and 8a; pl. I)

Removal of the residual bone of the skull roof of BPI F.no.981 by Kitching exposed the minutely detailed external impression on matrix of the larger part of the surface. A latex peel was taken from this for study purposes. The portions represented (pl. I) include: most of the right lateral and central areas and part of the posterior left lateral area; most of the right lateral edge; the entire right orbit and the inner margin of the left orbit; the posterior margin

of the right external naris; and the parietal foramen. Unfortunately, both the snout tip and the occipital edge with otic notches are missing, but the specimen is extensive enough to allow a confident restoration of its original complete shape. The peel reflects the highly unusual surface sculpture (to be described under a following subheading, together with the sculpture on the dermal bones of the paratype) and clearly portrays the courses of the sutures and lateral line canals.

The complement of bones forming the skull roof conforms for the most part with the standard for the Order Temnospondyli. The sutural relationships among these bones and their shapes and relative sizes agree in most respects with conditions observed in other members of the family. Those sutures visible on the peel are shown in solid line on Figure 1; the hypothetical ones are shown in dashed line.

As detailed bone by bone description would serve no purpose, only the particularly notable features are mentioned here. Lachrymal bones are absent as in all other rhytidosteids for which the snout region is known. The central bones of the skull roof, including nasals, frontals, prefrontals, postorbitals, parietals and supratemporals are all large relative to the more lateral series; this, also, is a universal rhytidosteid feature. The frontal bones are excluded from the orbits as in all members of the family but are longer and narrower than in the Australian genera, *Deltasaurus* and *Derwentia.* As in many temnospondyl skulls, asymmetry is marked; the internasal suture is offset to the right relative to the interfrontal suture and the latter is offset to the right relative to the interparietal suture. Although the occipital edge of the skull is not retained, its transverse level has been closely approximated by joint inferences from the trend of the right posterior portion of the skull roof and the construction and dimensions of the palatal surface provided by the paratype. Placing the occipital edge at the level shown in Figure 1 allows for fairly extensive supratemporals, squamosals and quadratojugals but yields relatively small postparietals and tabulars which are broader than long.

The orbits are almost perfectly circular, inset somewhat from the lateral edges of the skull and face dorsally; those of other rhytidosteids are either elongately oval or irregular in shape, are placed closer to the lateral edges and face dorsolaterally.

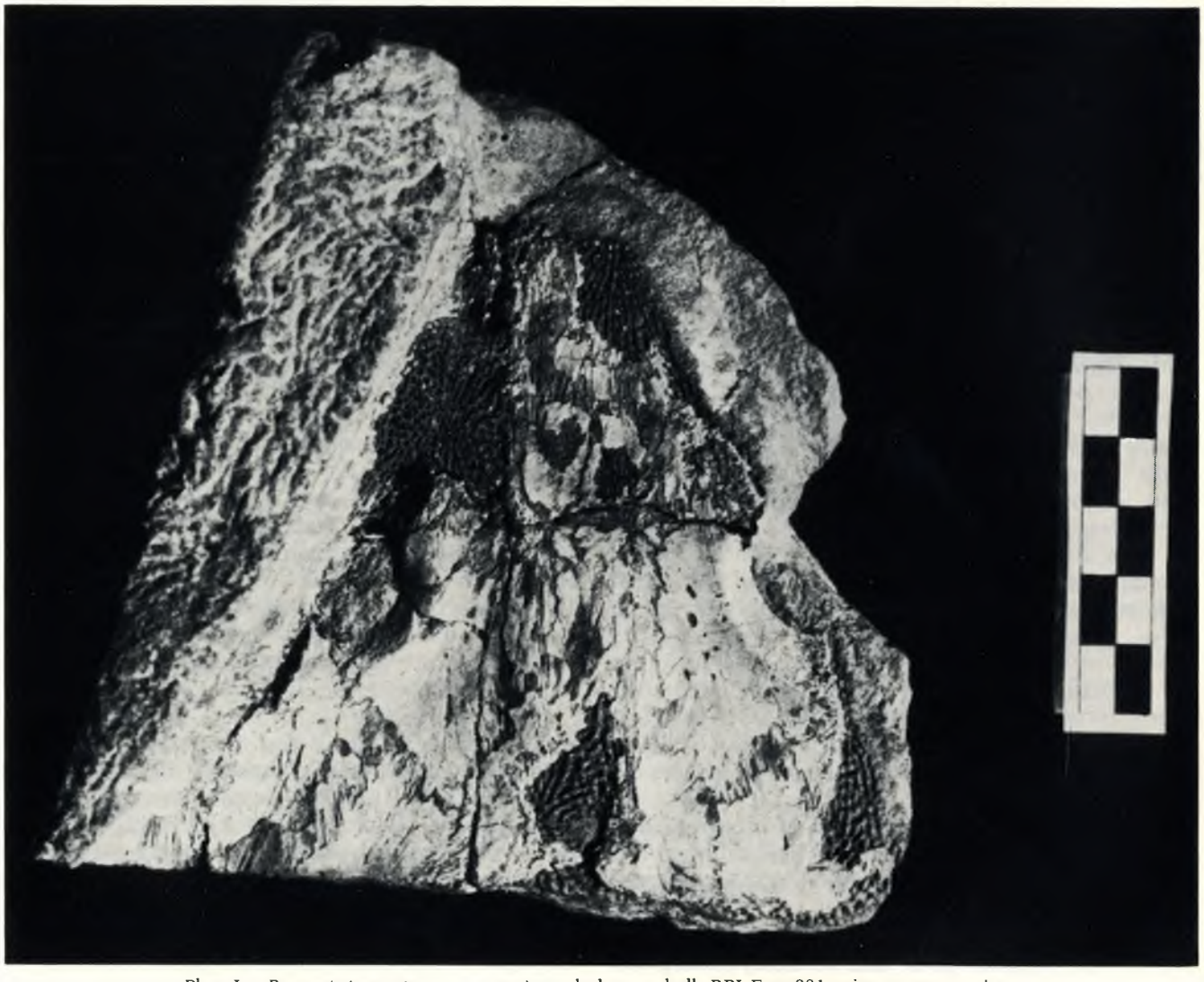


Plate I. *Pneumatostega potamia*, n.g. and sp., holotype skull, BPI F.no.981 prior to preparation.

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BERNARD PRICE INSTITUTE FOR PALAEONTOLOGICAL RESEARCH, UNIVERSITY OF THE WITWATERSRAND, JOHANNESBURG

REPORT OF THE DIRECTOR FOR 1978

By M. A. Raath

STAFF MATTERS

In mid 1978 Professor S. P. Jackson, who had been Honorary Director since 1974, handed over to me as the new Director. The Staff of the Institute wish to record their appreciation to Prof. Jackson for his wise and patient leadership during a difficult period.

Dr. A. R. I. Cruickshank, Assistant Director since 1967, resigned and returned to the United Kingdom. Dr. Cruickshank's contribution to the Institute's activities has been noteworthy and he will be missed by his colleagues on the Staff. Dr. B. R. Turner was promoted to the position of Senior Research Officer.

Apart from those senior changes, the staff of the Institute has remained static. The most serious problem in the Institute's staff complement remains the lack of a specialist palaeobotanist, and urgent steps are being taken to fill the vacancy. Drs. John and Heidi Anderson of the Botanical Research Institute, Pretoria, have kindly continued to assist with palaeobotanical matters in the meantime. Dr. Rosemary M. S. Falcon joined the staff as a major-time Research Officer to run the Coal Petrography laboratory with support from the Richard Ward Endowment Fund of the University. Her work in this new laboratory will be largely concerned with a co-operative project for the characterisation of South African coals under the auspices of the University's Bureau for Mineral Studies.

Dr. J. W. Kitching visited the Institute of Geoscience at Porto Alegre, Brazil, as the guest of Prof. Mario Barbarena in April 1978. During his stay he was able to visit exposures of the Santa Maria and Rio do Rasto Formation from which he collected a considerable number of vertebrate fossils. The University's Conference Fund kindly assisted Dr. Kitching's visit.

Dr. B. R. Turner attended a symposium on sedimentary geology in Israel in September 1978.

The micropalaeontological laboratory of SOEKOR (Southern Oil Exploration Corporation) continued to operate within the Institute building, and the laboratory's director, Mr. I. R. McLachlan, once again assisted in the post-graduate teaching programme of the Institute.

The Attendant at Makapansgat, Mr. Zava Maluleka, retired after many years of loyal service to the University but we confidently predict that "retirement" to Zava is an abstraction without basis in fact, and that for years to come he will continue to fuss and supervise anyone appointed to succeed him!

STUDENTS AND TEACHING

The year's end saw a comparative flood of higher degree students graduate, including:

ISERNHINKE, Dr. Sharon. — Ph.D. topic: "Review of South African fossil Amphibia with special reference to the Brachyopidae and Capitosauridae".

FALCON, Dr. Rosemary M. S. — Ph.D. topic: "A palynological comparison of Karoo sediments on opposite sides of the Rhodesian watershed with stratigraphic application".

MALLESON, Dr. Anna K. — Ph.D. topic: "The Sphenopsida of the South African Upper Permian".

MAGUIRE, B. — M.Sc. topic: "Food plants of the !Khu Bushmen of northeastern South West Africa". (Graduated with distinction)

SMITHIES, Mrs. Shirley M. — M.Sc. topic: "Description of a Permocarboniferous plant assemblage from Hammanskraal, north of Pretoria". (Graduated with distinction)

MACRAE, C. S. — M.Sc. topic: "Palaeozoic palynology of Botswana".

Since then one other M.Sc. student has submitted his dissertation for examination: I. M. Macgregor.

The following students are continuing their higher degree studies:

MAKRIDES, Marina. (M.Sc.: "Foraminifera of the Mzamba Formation").

SMITH, R. (M.Sc.: "Biostratigraphy of the Adelaide Subgroup").

WHATELEY, M. K. G. (M.Sc.: "Ecca coals in Zululand").

The Institute continues to offer courses in palaeontology at third-year and Honours level mainly to students from the Zoology Department wishing to read palaeontology as one option in their topic system. It is hoped that once the position of palaeobotanist is filled students from the Botany Department will also come forward.

STAFF RESEARCH PROGRAMMES

Research work within the Institute continues to concentrate largely on the mode of accumulation of fossil bone in the Grey Breccia (Member 3) of the Makapansgat Limeworks, and on aspects of Karoo vertebrate palaeontology and sedimentology. The commissioning of the coal laboratory has initiated a new research interest which brings the long-standing interests of the Institute into closer contact with one of the "applied" aspects of palaeontology and

allows the Institute to make a contribution to one of South Africa's pressing national priorities — energy.

A major field collecting programme was initiated during the year when Dr. J. W. Kitching, accompanied by Professor J. A. Hopson and Mr. A. Busbey of the University of Chicago, visited upper Stormberg exposures in the northern Orange Free State to collect fossils from the Elliot and Clarens Formations. This is the first systematic attempt to sample these formations since the publication of Haughton's paper on the Stormberg in 1924. After a relatively short visit to the Clarens and Fouriesburg districts the expedition returned with excellent material representing, among others, saurischian dinosaurs and tritylodontid therapsids. In fact, the tritylodontid material recovered more than tripled the total known world holdings of this family of advanced cynodonts. It is planned to extend collecting activities to as many exposures of the upper Stormberg as possible in a systematic sampling programme which is expected to last for several years.

Generally, staff were committed to finalising their several investigations for papers they were planning to offer to two conferences due to take place in 1979 — the first biennial Conference of the Palaeontological Association of Southern Africa and the 5th Conference of the South African Society for Quaternary Research (SASQUA). The latter conference will be held in the Institute, and its proceedings will be published in this journal.

PUBLICATIONS

Volume 21 of *Palaeontologia africana* was issued in 1978, containing the proceedings of the Karoo palaeontology symposium held at the Institute in June 1977.

Members of staff and students published the following additional papers:

CRUICKSHANK, A. R. I. The pes of *Erythrosuchus africanus* Broom. *Zool. J. Linn. Soc.*, **62**(2), 161–177.

———— and CHERNIN, S. The myth of the bottom-dwelling capitosaur amphibians. *S. Afr. J. Sci.*, **74**, March, 1978, pp. 111–112.

GOW, C. E., GRINE, F. E. and HAHN, B. D. Allometric growth in the skull of *Diademodon*. *S. Afr. J. Sci.*, **74**(2), 50–58.

TURNER, B. R. Palaeohydraulics of clast transport during deposition of the Upper Triassic Molteno Formation in the main Karoo Basin of South Africa. *S. Afr. J. Sci.*, **74**, 171–173.

ACKNOWLEDGEMENTS

It is a pleasure to record our gratitude to the C.S.I.R., and especially to its University Research Division, for continued generous financial support of the Institute following its triennial review of the position in 1978. The Department of National Education awarded a grant toward publication costs of this volume of *Palaeontologia africana*, and its continued support is gratefully acknowledged.

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Proceeding from information contributed by the new species, the taxonomic structure of the Rhytidosteoidea is reorganised and expanded and new diagnoses are provided for both this superfamily and its contained families. The family Rhytidosteidae now includes *Deltasaurus kimberleyensis, D. pustulatus, Peltostega erici, P. wimani, Pneumatostega potamia* and *Rhytidosteus capensis*. A new family, Indobrachyopidae, is created to include *Derwentia warreni* (removed from the Rhytidosteidae), *Indobrachyops panchetensis, Mahavisaurus dentatus, Mahavisaurus (Lyrosaurus) australis* and *Rewana quadricuneata. Laidleria gracilis* is removed from the Rhytidosteoidea. *Latiscopus disjunctus* and *Almasaurus habbazi* possess some features in common with members of the superfamily but are too distinct in most features to be considered rhytidosteoids.

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INTRODUCTION

In 1975, while inspecting the collection of Permian and Triassic labyrinthodonts at the Bernard Price Institute for Paleontology and the South African Museum, the senior author found in each collection an unidentified and unreported specimen from the *Lystrosaurus* Zone. Both specimens bore immediate resemblances to members of the family Rhytidosteidae, particularly to two of its Australian species, *Deltasaurus kimberleyensis* and *D. pustulatus*. Both were contained in sandy pebble conglomerate matrix, unusual for the *Lystrosaurus* Zone which is most productive of fossil vertebrates in its common red shale and red sandstone facies. The BPI specimen consisted of approximately two-thirds of a skull roof, exposed on its inner surface and consisting of actual bone over most of its extent but weathered down to the external impression in places. This specimen was collected by Dr. J. W. Kitching in 1950 on the Tafelberg property, near Middelburg, Cape Province. The SAM specimen consisted of various portions of the cranial and

postcranial skeleton, mostly broken and incomplete, of a single individual. The portions were disarticulated and randomly placed within a 130 × 130 × 40 mm rounded cobble of pebble conglomerate matrix. Locality information in the SAM catalogue states that it was collected in the *Lystrosaurus* Zone on the Goede Hoop property near Colesberg, Cape Province by A. J. Hesse and C. W. Thorpe in 1935.

Although the skull portion of the SAM specimen is less complete than the BPI specimen, enough remains to indicate that the original complete skull closely approximated the BPI specimen in shape, i.e. it presented an equilateral triangle in dorsal view. This feature, together with exact correspondence of the sculpturing on the dermal bones (a variant of the highly characteristic rhytidosteid pattern) suggests strongly that the two specimens are homotaxial. The BPI specimen is nominated the holotype as it has yielded the larger number of taxonomically important characters.

The BPI specimen was prepared by Dr. Kitching through careful mechanical removal of remaining bone from the well-preserved external impression of the skull roof. A series of photographs and peels were taken from the specimen prior to removal of the bone. Upon completion of preparation, peels were taken of the external impression.

The SAM specimen was placed on loan to the authors for preparation and study. Formic acid reacted well with the matrix and produced excellent results. The various skeletal fragments were completely freed of matrix and delicate surface features such as the dentition of the cranial fragments and surface sculpturing on dermal bones survived largely undamaged.

The new taxon constitutes an important addition to the labyrinthodont component of the fauna from the *Lystrosaurus* Zone. Previously described and taxonomically valid species of this component include:

Family Capitosauridae
Kestrosaurus dreyeri Haughton, 1925
Family Lydekkerinidae
Limnoiketes paludinatans Parrington, 1948
Lydekkerina huxleyi (Lydekker, 1889)
Lydekkerina kitchingi Broom, 1950
Family Micropholidae
Micropholis stowi Huxley, 1859
Family Rhytidosteidae
Rhytidosteus capensis Owen, 1884
Family Uranocentrodontidae
Uranocentrodon senekalensis (Van Hoepen, 1911)

Rhytidosteus capensis, based on a single partial skull found near Beersheba, Orange Free State, has always been cited as questionably deriving from the *Cynognathus* Zone (e.g. Romer, 1947, p. 190) but Kitching (pers. comm.) believes it more likely that the site lies within the basal Triassic *Lystrosaurus* Zone.

Broom (1930) nominated three further species of the Lydekkerinidae, *Lydekkerina dutoiti, Lydekkerina putterilli* and *Putterillia platyceps.* Romer (1947) changed the generic designation of the first to *Broomulus.* Cosgriff (1974) removed all three from the Lydekkerinidae, and placed them *incertae sedis* among the Temnospondyli. However, in 1975, the senior author had the opportunity to inspect the holotype skulls at the Bernard Price Institute and concluded that they are all distorted specimens of *Lydekkerina huxleyi.*

Although Von Huene (1920, p. 458) nominated the then monotypic family Rhytidosteidae for *Rhytidosteus capensis* Owen (1884, p. 333–338, pls. XVI and XVII), this was not accepted by other authorities and the species was for long included in the Trematosauridae (e.g. Romer, 1947, pp. 190–191 and 314). Cosgriff (1965, pp. 67–68) revived the family to include not only *R. capensis* but also *Peltostega erici* Wiman (1916, pp. 210–216, text figs. 1–3, pl. XV, figs. 1–3, pl. XVI, fig. 1), *P. wimani* Nilsson (1946, pp. 4–34, figs. 11–18), and two new species, *Deltasaurus kimberleyensis* Cosgriff (pp. 68–80, figs. 1–9) and *D. pustulatus* Cosgriff (pp. 80–83, figs. 10 and 11). In this same paper, the taxonomic relationships of two further labyrinthodont species, *Laidleria gracilis* Kitching (1958, pp. 67–82, figs. 16–19) and *Latiscopus disjunctus* Wilson (1948, pp. 359–361, pl. 59), were also considered. Kitching placed *L. gracilis* provisionally in the Trematosauridae but suggested, as an alternate allocation, that it be considered "as the type of a new family, the Laidleriidae". Cosgriff adopted Laidleriidae and provisionally included it as a family in the superfamily Rhytidosteoidea. Wilson created a new family, Latiscopidae, for *L. disjunctus,* not attempting a superfamily allocation. Cosgriff, although noting certain similarities of *L. disjunctus* to the rhytidosteids, followed Wilson in regarding the family as *incertae sedis.*

Subsequently, a sixth species, *Derwentia warreni* Cosgriff (1974, pp. 74–78, figs. 48–55) was added to the Rhytidosteidae.

In the present research, comparisons of the new species from the *Lystrosaurus* Zone with the six established species of the family led to a reconsideration of *Laidleria gracilis* and *Latiscopus disjunctus* and, further, to a review of five other temnospondyl species from the Lower Triassic of various parts of the world, each of which bears certain resemblances to the rhytidosteid species. These are: *Indobrachyops panchetensis* Von Huene and Sahni (1958, pp. 1–17, text figs. 2–5, pls. I and II); *Mahavisaurus dentatus* Lehman (1966, pp. 4–9, text figs. 1 and 2, pls. I, II and IIIa, c and d); *Lyrosaurus australis* Lehman (1966, pp. 11–15, text fig. 3, pl. IVa); *Rewana quadricuneata* Howie (1972, pp. 51–64, text figs. 1–6, pl. I); and *Almasaurus habbazi* Dutuit (1972, pp. 73—77, figs. 1 and 2). Gross comparisons of all of these with each other, with the rhytidosteid species and with *Laidleria gracilis* and *Latiscopus disjunctus* has produced alterations in the diagnoses of the superfamily Rhytidosteoidea and the family Rhytidosteidae. It has also produced changes in the contents of these taxa. *Derwentia warreni* is removed from the Rhytidostei-

dae. The Rhytidosteoidea is expanded to include a new family, Indobrachyopidae, which receives *Derwentia warreni* as well as *Indobrachyops panchetensis, Mahavisaurus dentatus, Lyrosaurus australis* and *Rewana quadricuneata.*

Following the description and consideration of the new form from the *Lystrosaurus* Zone and comparisons of this with the other species of the Rhytidosteidae, all related and possibly related species are reviewed. *Laidleria gracilis, Latiscopus disjunctus* and *Almasaurus habbazi* are excluded from the superfamily. Next, the reordered composition of the Rhytidosteoidea is presented, together with new diagnoses of its contained families. Finally, through employment of a computer program, taxonomic distances among all of the contained species are determined, a phylogeny is constructed and this phylogeny is shown to be consonant with geographic and stratigraphic distribution.

Superfamily RHYTIDOSTEOIDEA
Family RHYTIDOSTEIDAE
PNEUMATOSTEGA, n. gen.

Etymology. Pneumato from Greek *pneumatos*, lung; *stega* from Greek *stegos*, plate. Name given in reference to the highly vascular and, hence respiratory, bones of the dermal cranial and pectoral skeleton.

Diagnosis. The skull, in dorsal view, approximates an equilateral triangle. Snout tip acute. Occiput very broad relative to skull length, B : L index 1,41 (indices and letter symbols follow the convention of Welles and Cosgriff, 1965, fig. 1). Orbits circular. Interorbital area narrow, A : L index 0,34. Palatal tooth row on palatine and ectopterygoid bones well developed; teeth in this row twice as long as those on maxilla. Interpterygoid vacuities elongate, Y : L index 0,53. Dermal bones appear highly vascular. Nodes surmounting points of junction and bifurcation on dermal sculpture ridges very high and prominent. Frontal bones long and narrow, contrasting with square frontal of *Deltasaurus* and *Derwentia.* Lateral line canals better developed and more continuous than those of *Peltostega* and *Rhytidosteus*, less so than those of *Deltasaurus* and *Derwentia.*

Distribution. Lystrosaurus Zone, Beaufort Series of Cape Province, South Africa.

Type Species. Pneumatostega potamia.

PNEUMATOSTEGA POTAMIA, n. sp.
(figs. 1–7, 8a and 10; pls. I–V)

Etymology. Potamia from Greek *potamios.* Name given in reference to the stream channel habitat of the species.

Holotype. BPI F.no.981, impression on conglomerate matrix of the dorsal surface of a skull.

Type locality. Tafelberg property near Middelburg, Cape Province; *Lystrosaurus* Zone.

Paratype. SAM 11188, portions of the skull, lower jaw, dermal shoulder girdle and vertebral column of a single individual; material disarticulated and scattered through a rounded cobble of conglomerate matrix.

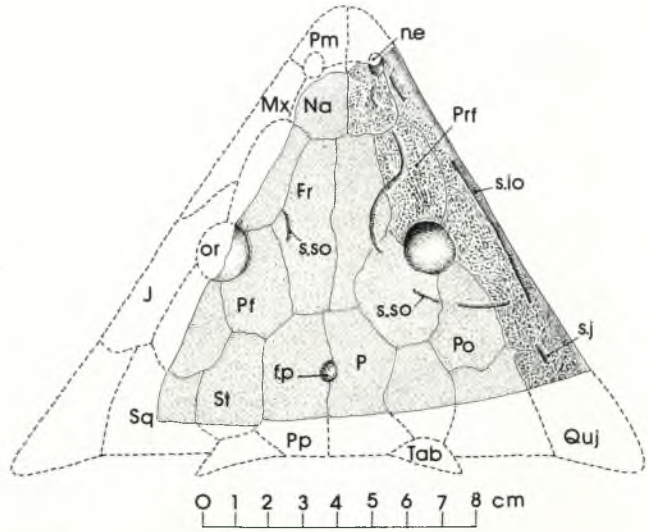


Figure 1. *Pneumatostega potamia*, n.g. and sp., reconstruction of dorsal surface of skull, based on holotype, BPI F.no.981. Shaded area indicates portion of skull roof impression retained on the specimen. Only right lateral bones of the impression have sculpture pattern indicated in this drawing although sculpture extends over the entire impression. Abbreviations for Figure 1 and following figures: a.p.v., anterior palatal vacuity; dia, diapophysis; fa.cl., clavicular facet; fo.st., subtemporal fossa; f.p., parietal foramen; Fr, frontal; Ic, intercentrum; i.p.v., interpterygoid vacuity; J, jugal; Mx, maxillary; Na, nasal; n.a., neural arch; n.e., external naris; n.i., internal naris; or, orbit; P, parietal; par, parapophysis; Pc, pleurocentrum; p.c., cultriform process; p.cl. cleithral process; Pf, postfrontal; Pm, premaxillary; Po, postorbital; Pp, postparietal; Prf, prefrontal; Ps, parasphenoid; Pt, pterygoid; Qu, quadrate; Quj, quadratojugal; S.io., infraorbital groove; s.j., jugal groove; Sq, squamosal; s.so., supraorbital groove; St. supratemporal; Tab, tabular; z.a., anterior zygapophysis.

Paratype locality. Goede Hoop property, near Colesberg, Cape Province; *Lystrosaurus* Zone.

Diagnosis. Same as for genus.

Description

Observations and interpretations concerning the dorsal surface of the skull are based on the holotype. Those concerning the palatal surface of the skull, the lower jaw, the dermal shoulder girdle and the vertebral column are all based on the fragmentary skeleton which comprises the paratype.

Skull, dorsal surface (figs. 1 and 8a; pl. I)

Removal of the residual bone of the skull roof of BPI F.no.981 by Kitching exposed the minutely detailed external impression on matrix of the larger part of the surface. A latex peel was taken from this for study purposes. The portions represented (pl. I) include: most of the right lateral and central areas and part of the posterior left lateral area; most of the right lateral edge; the entire right orbit and the inner margin of the left orbit; the posterior margin

of the right external naris; and the parietal foramen. Unfortunately, both the snout tip and the occipital edge with otic notches are missing, but the specimen is extensive enough to allow a confident restoration of its original complete shape. The peel reflects the highly unusual surface sculpture (to be described under a following subheading, together with the sculpture on the dermal bones of the paratype) and clearly portrays the courses of the sutures and lateral line canals.

The complement of bones forming the skull roof conforms for the most part with the standard for the Order Temnospondyli. The sutural relationships among these bones and their shapes and relative sizes agree in most respects with conditions observed in other members of the family. Those sutures visible on the peel are shown in solid line on Figure 1; the hypothetical ones are shown in dashed line.

As detailed bone by bone description would serve no purpose, only the particularly notable features are mentioned here. Lachrymal bones are absent as in all other rhytidosteids for which the snout region is known. The central bones of the skull roof, including nasals, frontals, prefrontals, postorbitals, parietals and supratemporals are all large relative to the more lateral series; this, also, is a universal rhytidosteid feature. The frontal bones are excluded from the orbits as in all members of the family but are longer and narrower than in the Australian genera, *Deltasaurus* and *Derwentia*. As in many temnospondyl skulls, asymmetry is marked; the internasal suture is offset to the right relative to the interfrontal suture and the latter is offset to the right relative to the interparietal suture. Although the occipital edge of the skull is not retained, its transverse level has been closely approximated by joint inferences from the trend of the right posterior portion of the skull roof and the construction and dimensions of the palatal surface provided by the paratype. Placing the occipital edge at the level shown in Figure 1 allows for fairly extensive supratemporals, squamosals and quadratojugals but yields relatively small postparietals and tabulars which are broader than long.

The orbits are almost perfectly circular, inset somewhat from the lateral edges of the skull and face dorsally; those of other rhytidosteids are either elongately oval or irregular in shape, are placed closer to the lateral edges and face dorsolaterally.

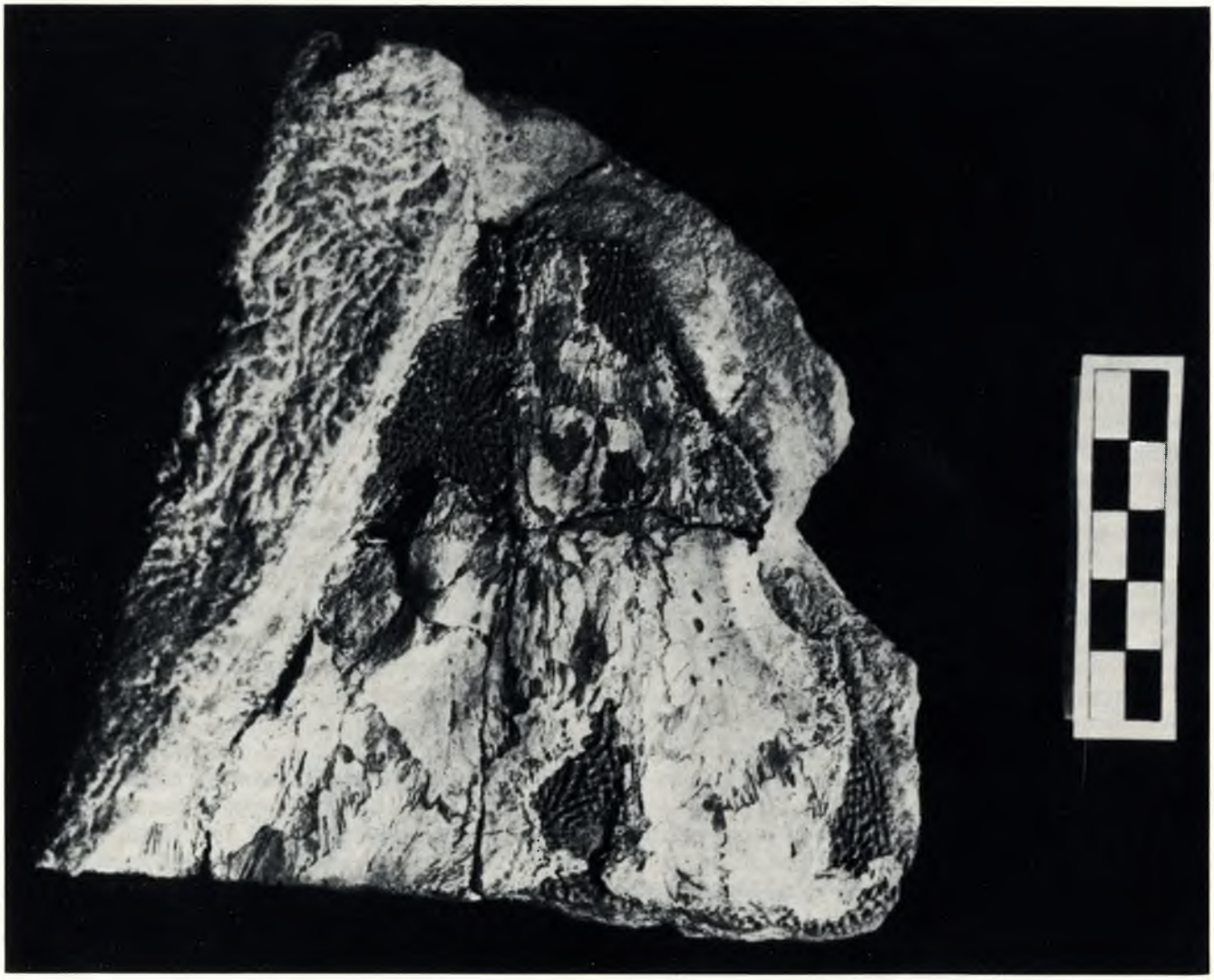


Plate I. *Pneumatostega potamia*, n.g. and sp., holotype skull, BPI F.no.981 prior to preparation.

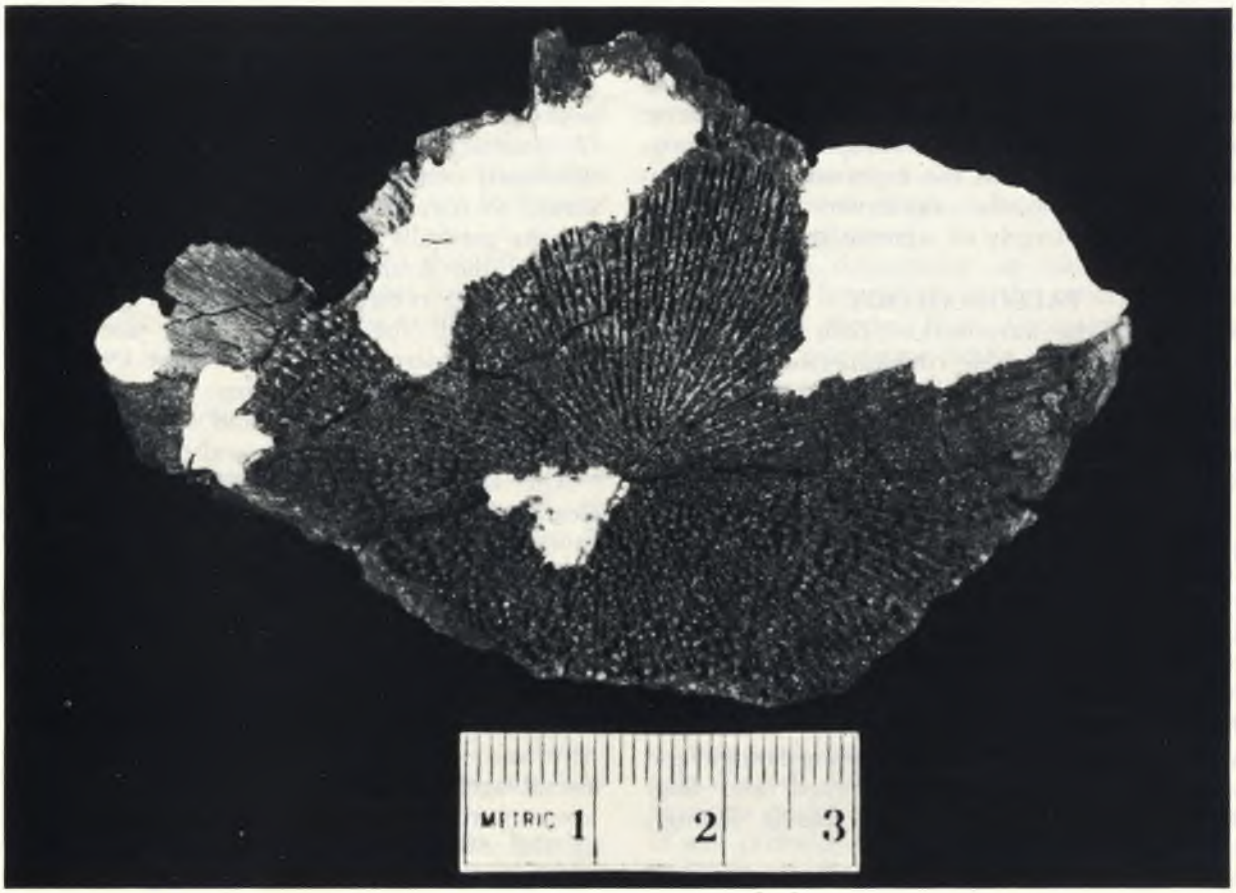


Plate V. *Pneumatostega potamia*, n.g. and sp., paratype interclavicle, SAM 11188: ventral view.

of the surface sculpture. The entire network carried a copious blood supply through the bone to the lower surface of a thin, mucous-covered skin through which gas exchange was efficiently conducted.

Probably, the lungs, if present, were secondary centres of respiration. They may even, as in plethodontid salamanders, have been entirely absent. This is a strong possibility as the lithologic context of rhytidosteids — stream channels and deltaic and lagoonal deposits — are areas of flowing water, not normally oxygen deficient. Lungs, among amphibians, are more normal to, and functionally more appropriate to, ponds and swamps where stagnant

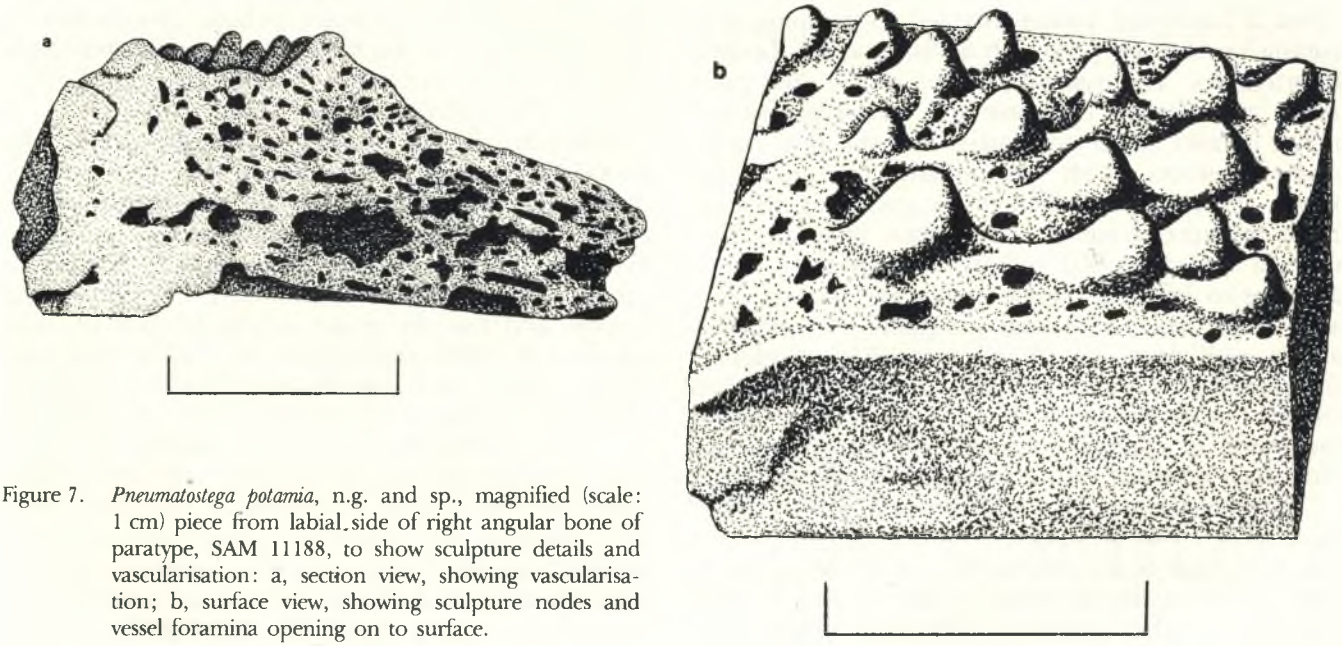


Figure 7. *Pneumatostega potamia*, n.g. and sp., magnified (scale: 1 cm) piece from labial side of right angular bone of paratype, SAM 11188, to show sculpture details and vascularisation: a, section view, showing vascularisation; b, surface view, showing sculpture nodes and vessel foramina opening on to surface.

conditions periodically occur. An analogous feature among living stagnant water amphibians is, of course, external gills, as seen in axolotls and others.

A well-developed cutaneous respiratory system as reflected in dermal bone structure is not unique to rhytidosteids and Triassic temnospondyls. Bystrov (1947) demonstrated that the capitosaurid, *Benthosuchus sushkini*, has heavily vascularised dermal bone and was, thereby, largely an aqueous respirator.

PALEOECOLOGY

As noted in the introduction, both specimens of *P. potamia* occur in pebble conglomerate matrix deriving from the *Lystrosaurus* Zone and, no doubt, representing stream channel environment. This provides strong corroborative evidence for the interpretations previously advanced (Cosgriff, 1974) regarding the habitat preferences and correlated adaptive morphology characteristic of the family. In this construct, the prime and central habitats for rhytidosteids were the lagoons and distributaries of river deltas and the lower reaches of river systems; they peripherally extended into upstream portions of the rivers but were sparse as individuals in these. Further, they seem to have been rather active, subsurface swimming piscivores. Both morphologic and taphonomic evidence, previously cited and augmented by the particulars of *P. potamia*, strongly support the interpretations.

First, regarding morphology: dentition, skull construction and shape and bone structure coupled with surface sculpture are indicative of a subsurface swimming piscivore which inhabited environments characterised by flowing water. The dentition, as noted, is appropriate to a piscivore and, further, is quite analogous to that found in the fish-eating modern gar, *Lepisosteus osseus*. The internal surfaces of the mouth are extensively lined with pavements of denticles and the marginal teeth are small and closely spaced. Together, these dental particulars provided a functional system adapted to grasping and cutting up slippery prey such as fish and soft-bodied invertebrates. The triangular shape of the skull provided an effective cut-water for subsurface swimming, parallel to the triangular skull shape in *Diplocaulus brevirostris* which was similarly interpreted by Olson (1951). As described in the preceding section, bone structure, coupled with surface sculpture, signifies a well-developed cutaneous respiratory system adaptive to life in a regime of flowing, well-oxygenated water. The very lateral placement of the orbits agrees with Wiman's (1915) hypothesis, developed from studies on the Spitsbergen trematosaurids, that lateral outward-facing orbits correlate with active swimming in contrast to dorsal, upward-facing orbits which correlate with a benthonic mode of life.

The only feature, in a consideration of the family as a whole, that seemingly conflicts with the above interpretations is the state of the lateral line system. This is well marked in terms of the grooves on dermal bone surfaces only in *Deltasaurus kimberleyensis* and *D. pustulatus*. In these species, the grooves of the skull roof are well-defined, deeply incised and continuous. In the remaining species of the family, the grooves are either entirely lacking *(Rhytidosteus capensis)* or are ill-defined, shallow and discontinuous *(P. potamia, Peltostega erici* and *P. wimani)*. A well-developed complete lateral line system can be presumed to correlate with an aquatic mode of life so that its generally poor development in most members of the family is anomalous. The explanation may be that, in the species where the grooves are not fully formed, the system ran for the most part through the dermis, well above bone level, so that it was not reflected by grooving. Or, alternatively, it may have been suppressed and compensated for by more highly developed sight and olfaction.

The taphonomic record of the family, which clearly and cogently supports the indications from functional morphology, may be summarised briefly as follows: *D. kimberleyensis* is an abundant, indeed the most common, taxon in the Blina Shale of Western Australia which was deposited in a deltaic-lagoonal setting (McKenzie, 1961). *D. kimberleyensis* also occurs in the upland stream channels of the Knocklofty Formation of Tasmania but it is rare here and, definitely, a subordinate member of the assemblage. The monotypic skulls of *P. erici* and *P. wimani* were collected in the near shore marine facies of the Sticky Keep Formation of Spitsbergen (Romer, 1947). Their rarity in comparison with the trematosaurs found at the same sites indicates that they were exotics in the assemblages and, likely, transported in from another, more distal, environment. This could well have been stream or deltaic distributaries emptying on to the shore platform. This interpretation is probably also applicable to the partial skull of *D. pustulatus* which was found associated with marine invertebrates and land derived pollen in the well core from the Kockatea Formation of Western Australia. *P. potamia*, as stated, is known only from stream channel pebble conglomerates. No information is available regarding the lithologic context in which the other rhytidosteid from the *Lystrosaurus* Zone, *R. capensis*, was found.

Returning to the matter of the grooves of the lateral line system, it is possible that their varying degrees of development through the species of the family are correlated with environmental and adaptive differences. The observations that the full set of grooves may be observed only in the species of *Deltasaurus* and that the prime habitat for one of these species, *D. kimberleyensis*, was the deltaic lagoonal regime, may have significance. Perhaps a fully-developed lateral system in the family was adaptive to the less turbulent waters of the lagoons and deltaic distributaries as it would have been more functional in this context. Obversely, it may have been less functional and, therefore, suppressed in species adapted to the more turbulent, farther upstream sites. Thereby, *P. potamia, P. erici* and *P. wimani* may have been upstream species. Inasmuch as infor-

mation on depositional environment is incomplete this explanation is purely speculative.

COMPARISONS

Figure 8 provides outline drawings with sutures of the dorsal skull surfaces of the rhytidosteid species, *P. potamia, D. kimberleyensis, D. pustulatus, R. capensis* and *P. erici*. The skull of *P. wimani* is too incomplete to allow a meaningful restoration; also, it is very close in most important respects to that of *P. erici*. Figure 10 is a largely parallel series for the palatal surfaces except that *D. pustulatus*, whose holotype lacks a palate, is omitted.

Deltasaurus kimberleyensis (figs. 8b and 10b) and D. pustulatus (fig. 8c)

Within the Rhytidosteidae, *P. potamia* is most closely allied, on distinctive heritage features, to these species of the Australian Lower Triassic. In *Deltasaurus*, as in the new African genus, the skull approximates an equilateral triangle with width across the occiput exceeding skull midline length. In all three species the lateral margins are nearly straight from snout tip to quadrate corner. The orbits are positioned very similarly in all; the index preorbital length:skull midline length (O:L index) is 0,48 in *P. potamia*, 0,51 in *D. kimberleyensis* and 0,45 in *D. pustulatus*.

The most striking similarity, however, between *Pneumatostega* and *Deltasaurus* and the one on which greatest taxonomic stress should be placed lies in the surface sculpture of the dermal bones. This is most marked between *P. potamia* and *D. kimberleyensis*. In these, the spider web ornamentation surmounted by prominent nodes exhibits its fullest expression. The sculpture of *D. pustulatus* is derived, as here the bone surface carries only radiating rows of nodes and the protean ancestral ridges underlying them have been completely suppressed.

Numerous distinctions in cranial construction necessitate a separation on the generic level of the new African species from *Deltasaurus*. The frontal bones of *P. potamia* are nearly twice as long as broad while those of the *Deltasaurus* species are nearly square. *P. potamia* has circular orbits whereas those of *Deltasaurus* are long-oval and indented on their anterior margins. The lateral line grooves of *Deltasaurus* are fully developed but those of *P. potamia* are discontinuous. The interpterygoid vacuities of *P. potamia* are markedly more elongate than those of *D. kimberleyensis*. In the former, the index interpterygoid vacuity length:skull midline length (Y:L) is 0,53 and in the latter only 0,36. Differences in shape of the vacuities is shown in Figure 10; those of *P. potamia* are oval but those of *D. kimberleyensis* are more nearly circular and have indented anterior margins. The palatal tooth row, present in *P. potamia* as in most temnospondyls, is definitely absent in *D. kimberleyensis* and probably so in *D. pustulatus*, as indicated by a fragment of the palate surface remaining with the

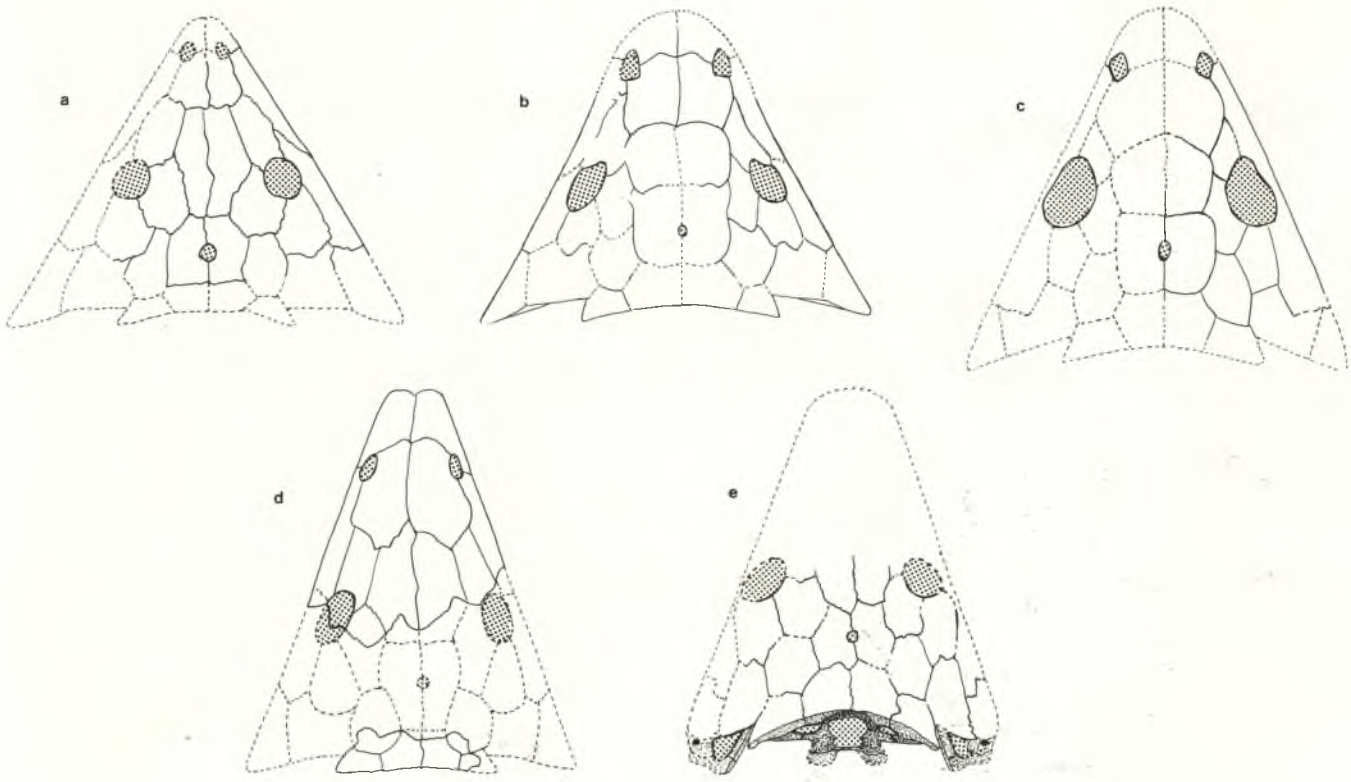


Figure 8. Restorations of dorsal views of rhytidosteid skulls (not to scale): a, *Pneumatostega potamia;* b, *Deltasaurus kimberleyensis* (after Cosgriff, 1965); c, *Deltasaurus pustulatus* (after Cosgriff, 1965); d, *Rhytidosteus capensis* (after Cosgriff, 1965); e, *Peltostega erici* (after Nilsson, 1946).

skull of this species. The elongately oval posterior meckelian foramen of the lower jaw of *P. potamia* is much larger than this opening in *D. kimberleyensis*.

Rhytidosteus capensis (figs. 8d and 10c)

This species, apparently also from *Lystrosaurus* Zone, resembles those discussed in having: straight lateral skull margins; small, triangular otic notches; and a fairly elongate preorbital region (O:L index 0,50). The elongate frontal bones resemble those of *P. potamia*. The oval orbits, however, are close in shape to those of *D. kimberleyensis* and *D. pustulatus*.

In most of its features the holotypic and only skull of *R. capensis* is quite distinctive. As reconstructed, it is quite narrow; the index greatest width across the occiput:skull midline length (B:L) is only 0,89 whereas in *P. potamia* it is 1,41, in *D. kimberleyensis* 1,32 and in *D. pustulatus* 1,16. The interptyergoid vacuities are comparatively small (Y:L index 0,27). The sculpture has been reduced to the radiating ridges which are much larger and coarser than those of the other species; pits, concentric ridges and nodes are all totally absent. No portion of the lateral line system is impressed on the skull surface in the form of grooves. The snout tip carries a prominent notch at the midline suture.

Peltostega erici and P. wimani (figs 8e and 10d)

The genus *Peltostega* repeats the prime family characters of: straight lateral skull margins; small, triangular otic notches; and an elongate preorbital region (O:L index 0,54). The interpterygoid vacuities are greatly enlarged as in *Pneumatostega* with a Y:L index of 0,51; further, they are similar in shape, being elongately oval with the greatest width near their posterior borders. The grooving of the lateral

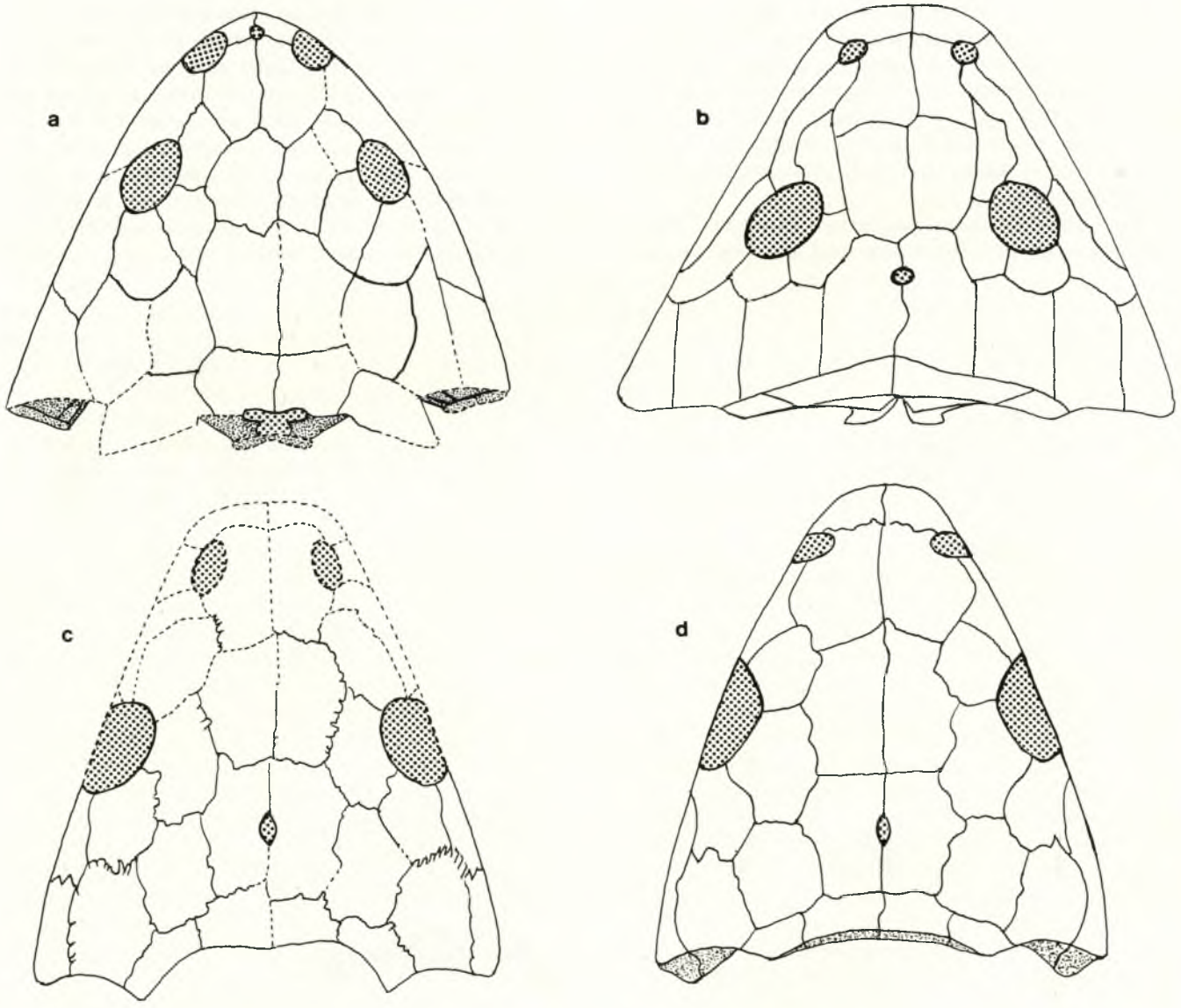


Figure 9. Restorations of dorsal views of indobrachyopid skulls (not to scale): a, *Derwentia warreni* (after Cosgriff, 1974); b, *Indobrachyops panchetensis* (after Von Huene and Sahni, 1958); c, *Mahavisaurus dentatus* (after Lehman, 1966); d, *Mahavisaurus (Lyrosaurus) australis* (after Lehman, 1966).

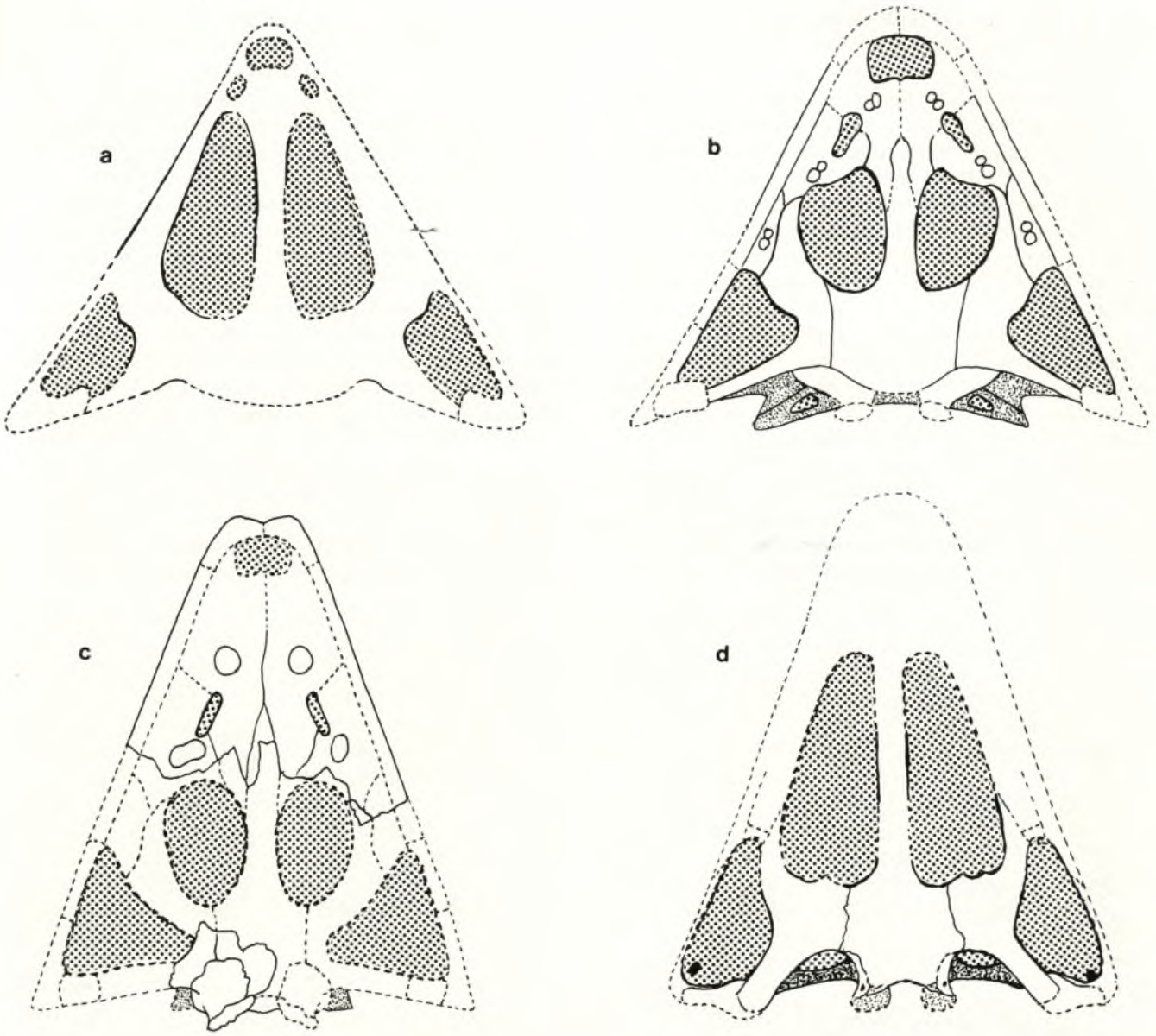


Figure 10. Restorations of palatal views of rhytidosteid skulls (not to scale): a, *Pneumatostega potamia;* b, *Deltasaurus kimberleyensis* (after Cosgriff, 1965); c, *Rhytidosteus capensis* (after Cosgriff, 1965); d, *Peltostega erici* (after Nilsson, 1946).

line system is poorly developed and discontinuous as in *Pneumatostega* rather than fully developed as in *Deltasaurus* or totally absent as in *Rhytidosteus*.

The sculpture pattern observed in *P. erici* and *P. wimani* appears to be a basic version of the rhytidosteid pattern which finds its most extreme expression in *P. potamia* and next most in *D. kimberleyensis*. The pronounced components, as usual, are the radiating ridges which give each dermal bone the characteristic spider web appearance. The texture, however, is coarser than that of *P. potamia* and *D. kimberleyensis* and the individual pits much larger. Also, the concentric ridges are more elevated, possessing a relief nearly equal to that of the radiating ridges. Low nodes are present at points where ridges join and diverge but these are not nearly so prominent as in the aforementioned species.

The *Peltostega* species share a comparatively narrow skull with *R. capensis* and, in this respect, differ from *P. potamia*. The B:L index is estimated at 0,99 in both *P. erici* and *P. wimani*, much closer to index of 0,89 of *R. capensis* than to the index of 1,41 of *P. potamia*. The orbits of both species of *Peltostega* appear to be elongately oval in shape, as in most rhytidosteids, rather than circular as in *P. potamia*.

P. erici is the only species of the family for which the palate is known that does not have the bones of this surface covered with a pavement of denticles. However, a few scattered denticles are present on the pterygoids of the holotypic skull (Nilsson, 1946, fig. 6) and these may be the remnants of an extensive pavement that was largely removed by erosion prior to fossilisation. Unfortunately, there is no palate surface with the holotypic and only skull of *P. wimani* so further information that might clarify the point is lacking.

REVIEW OF OTHER SIMILAR SPECIES

Indobrachyops panchetensis (figs 9b and 11b)

This form, known from a single fairly complete skull, derives from the Upper Panchet series (Lower Triassic) near Genu, Raniganj coalfield, India. Von Huene and Sahni (1958) described the species and referred it to the Brachyopidae. Both Cosgriff (1969) and Welles and Estes (1969) pointed out the lack of most of the definitive brachyopid characters in the specimen, removed it from this family but declined to place it elsewhere in the classification of the Temnospondyli.

In 1975, the senior author inspected the specimen at the University of Tubingen and noted many features in agreement with those observed on rhytidosteid skulls. The skull, although more rounded in dorsal view than a typical rhytidosteid skull, approximates an equilateral triangle. The occiput is quite broad relative to skull length (B : L index 1,47). The orbits are widely spaced (A : L index 0,46). The basal plate of the palate (between the subtemporal fossae) is wide (Q : R index 0,21). Although the cultriform process of the parasphenoid is missing, remaining adjacent parts of the palate show that it was wide and, no doubt, had a flat ventral surface. Denticles are retained on the pterygoids and ectopterygoids and the corpus of the parasphenoid is marked by small pits which are probably denticle sockets. The marginal teeth are small and closely spaced. The lateral line system is particularly similar to that of *Deltasaurus kimberleyensis*; it is completely incised on the skull roof and the grooves are deep, narrow and uniform.

In other respects, however, *I. panchetensis* is divergent from rhytidosteids. The preorbital portion of the skull roof is relatively much shorter (O : L index 0,39). Lachrymal bones, as shown by Von Huene and Sahni (1958, fig. 2), seem to be present with borders on both the orbits and the external nares. Rather than small triangular otic notches, the skull has broad, shallow embayments on the occipital edge for the anterior attachments of the tympani. This last feature parallels brachyopid conditions and was a feature contributing to the original inclusion

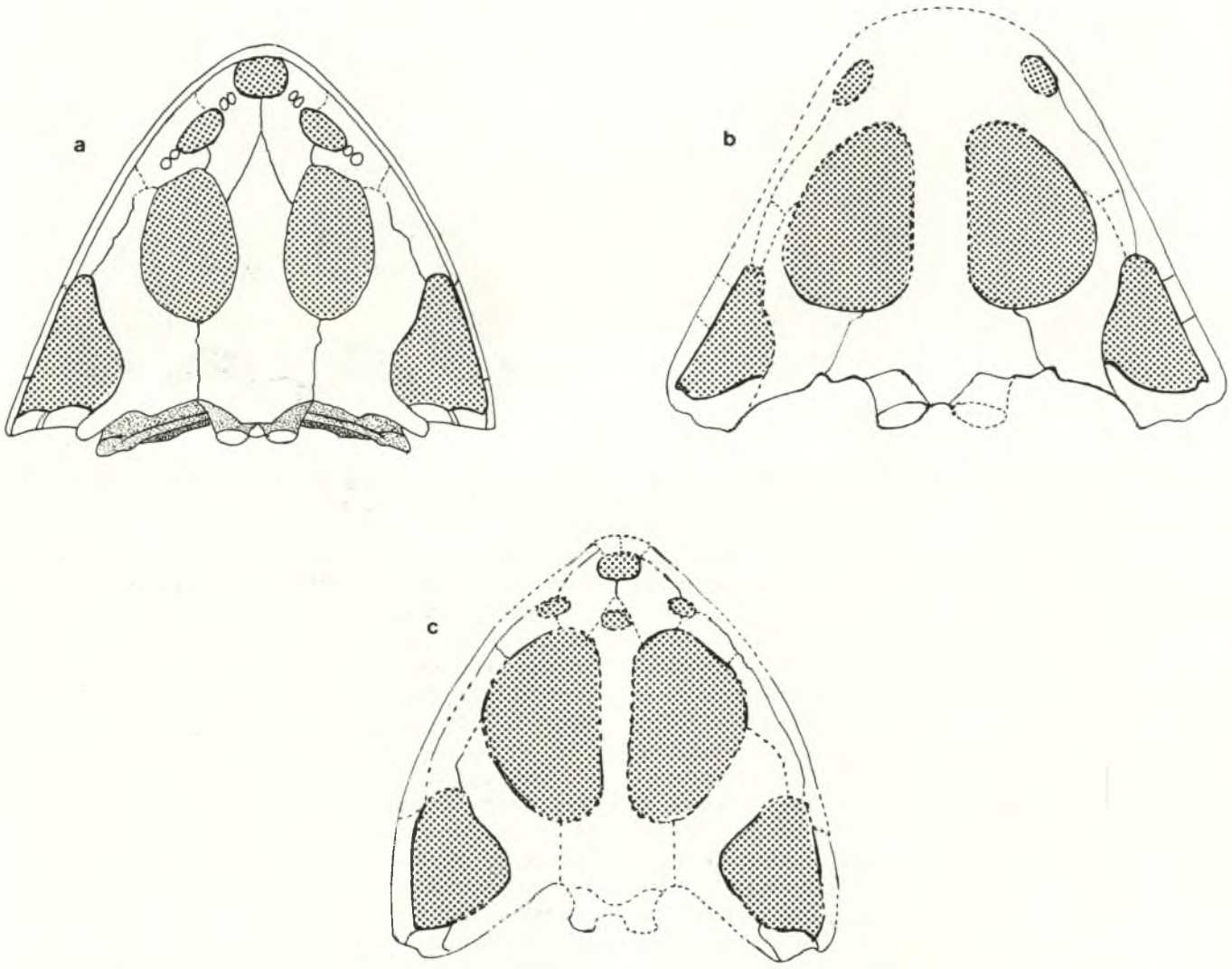


Figure 11. Restorations of palatal views of indobrachyopid skulls (not to scale): a, *Derwentia warreni* (after Cosgriff, 1974); b, *Indobrachyops panchetensis* (after Von Huene and Sahni, 1958); c, *Rewana quadricuneata* (after Howie, 1972).

of the species in that family. The sculpture pattern is that common to a number of temnospondyl families, including the Brachyopidae, Capitosauridae and Trematosauridae. This pattern, in contrast to rhytidosteid sculpture, is rather irregular in texture; it is composed of wavy, broad, round-crested ridges, which tend to bifurcate in a random fashion and which enclose and delineate pits and grooves; the pits, which tend to be concentrated around ossification centres in the middle of bones, vary in size and shape; the grooves, which occupy the peripheries of bones, are sinuous and discontinuous. A narial tooth row, lining the medial rim of the choana, is present; this feature is absent in those rhytidosteids in which the anterior part of the plate is preserved, namely *Deltasaurus kimberleyensis* and *Rhytidosteus capensis*.

Mahavisaurus dentatus (fig. 9c) and Lyrosaurus australis (fig. 9d)

These species were nominated by Lehman (1966) for specimens collected from the early Triassic Lower Sakamena Series of north-eastern Malagasy. The first is based on: a nearly complete skull roof with a few associated palatal fragments (holotype); a second, less complete and somewhat smaller skull roof; and, the entire right ramus of a mandible. The holotype and only specimen of the second species is the nearly complete external impression of a skull roof. Lehman (1961, pl. XX) had earlier described a palatal portion of a temnospondyl skull, also from the Lower Sakamena Series of north-eastern Malagasy, and placed it as "brachyopoide indetermine", but, in his 1966 paper (p. 6), referred it with question to *M. dentatus*. This fragment is from the base of the palate and includes the corpus of the parasphenoid, the posterior part of the cultriform process and large parts of both pterygoids.

Lehman separated the two species on a high categorical level. He referred *L. australis* to the Trematosauria, partly through its resemblances to *Peltostega erici*, and *M. dentatus*, with question, to the Rhinesuchoidea. Howie (1972, p. 61), however, offered the opposed interpretation that: *"Mahavisaurus* and possibly *Lyrosaurus* . . . should probably be added to the Rhytidosteidae." In 1975, while visiting the Institut de Paléontologie, the senior author had the opportunity to inspect all of the material in question and reached the following three conclusions. First, it seems apparent that the two species are closely related and should be regarded as congeneric and, possibly, conspecific. Therefore, on page priority, *Lyrosaurus australis* should be changed to *Mahavisaurus australis*. Second, as recognised by Howie, *Mahavisaurus* shows rhytidosteid affinities; it is either a rhytidosteid or a member of a closely related family. Actually, Lehman's interpretations were correctly based and pointed to the solution of the problem. *M. dentatus* does resemble rhinesuchids and this is a reflection of the rather certain derivation of rhytidosteids and their relatives from this family. *M. australis* does concur with *P. erici* (included by Lehman in the Trematosauria) in many features of cranial construction, indicating a true evolutionary relationship to this rhytidosteid genus. The third conclusion is that Lehman's surmise that his 1961 palatal fragment may be derived from a skull of *M. dentatus* is correct. This fragment not only is thoroughly rhytidosteid in all particulars but also matches the proportions of the holotype skull of *M. dentatus*.

Regarding the congeneric status of the two species, almost all features of the skull roofs of the two holotypes support this. The concurrences include: skull outlines; shapes and sutural relationship of all bones; extremely lateral positions of the orbits; sculpture pattern; and very broad, shallow otic embayments. The major differences to be observed are the somewhat narrower skull outline and the broad, well-defined and continuous grooves of the lateral line system in *M. australis*. It is possible that these are ontogenetic differences as the *M. australis* holotype is a considerably smaller skull than the *M. dentatus* holotype and, if so, the two forms are conspecific as well. Support for this possibility lies in the paratypic skull of *M. dentatus* which is intermediate in size and shows a rather intermediate development of the lateral line grooves. However, as identity cannot be conclusively demonstrated, it is better for the present to maintain the specific separation.

Most of the diagnostic cranial characters of the Rhytidosteidae are repeated in the Malagasy species. The orbits are widely spaced (O:L index 0,50 in both *M. dentatus* and *M. australis*). Indeed, the orbits are closer to the skull margins and face more laterally than in any of the rhytidosteids. The width across the occiput is nearly equal to skull midline length (B:L index 0,98 in *M. dentatus* and 0,89 in *M. australis*). Denticles probably covered much of the palate surface as they are preserved densely packed on the ectopterygoid fragment associated with the holotype skull of *M. dentatus*. Marginal teeth are small as shown by the paratypic lower jaw of *M. dentatus* which also carries a dense pavement of denticles over the entire surfaces of the three coronoid elements.

The basipalatal fragment of Lehman (1961) is, as noted above, typically rhytidosteid in structure. Its central part (corpi of the pterygoids and parasphenoid) is broad relative to length (Q:L index 0,38). The retained posterior stump of the cultriform process is broad with a flat ventral surface. Almost the entire expanse of the ventral surfaces, both of the parasphenoid and of the pterygoids, is covered with closely packed denticles. As further corroboration, the outlines of the entire fragment are strikingly similar to the corresponding portion of the holotype of *Peltostega erici*; the posterior borders of the interpterygoid vacuities form broad arcs and are indented by small projections on the pterygoid bones; the preserved outlines indicate that, just as in *P. erici*,

the vacuities narrowed anteriorly and possessed generally oval outline.

The Malagasy species share all of the above rhytidosteid characters with *I. panchetensis* and, quite significantly, further share with this species several of the important characters that set it off from the Rhytidosteidae s.s. The surface sculpture on both *M. dentatus* and *M. australis* is the normal, coarsely reticulate variety that *I. panchetensis* possesses. The skull margins are convex rather than straight as in the rhytidosteids. The preorbital regions of all of the Malagasy skulls are comparatively short (O:L index 0,39 in *M. dentatus* and 0,40 in *M. australis*). Lastly, and perhaps most importantly, there are shallow, broad otic embayments rather than sharply incised, triangular notches as in the rhytidosteid species.

Overall, the skulls of *M. dentatus, M. australis* and *I. panchetensis* correspond remarkably and these species should be united, at the least, on the family level. Generic separation, however, is assured by such features as the broader snout and smaller tabular bones of *I. panchetensis*, by the more laterally directed orbits of *M. dentatus* and *M. australis* and by the contrasting states of the lateral line grooves between all three species.

Rewana quadricuneata (fig. 11c)

Howie (1972) described this new species from the Lower Triassic Rewan Formation of Queensland, compared it in detail with various groups of Triassic temnospondyls and commented on certain notable similarities to the rhytidosteids, particularly to the genus *Deltasaurus*. Some equally important distinctions, however, obviated placing it in this family and, as the species did not show marked affinity for any other group of Triassic temnospondyls, Howie left its allocation to superfamily unresolved. She suggested, however, that all of the mainly short-faced temnospondyls, including the Trimerorhachoidea, Trematosauroidea, Brachyopoidea, Metoposauridae and *Rewana*, may constitute a single, large radiation with roots far back in the Paleozoic.

The holotype of *R. quadricuneata* is an incomplete skull and postcranial skeleton. The preserved portions of the skull are mainly from the palate and enough remained to allow Howie to provide an accurate restoration of this surface. Very little of the skull roof is present but some of the pieces contain margins of both orbits and the left external naris. These determined the shapes and locations of these openings on the skull roof. Some tabular horns in the Rewan collection may pertain to *R. quadricuneata* and, from these, Howie tentatively restored this structure on the skull, together with the flanking otic notch.

The features of *R. quadricuneata* noted by Howie as suggesting relationships to the rhytidosteids include the generally triangular outline of the skull and "the smallness and position of its orbits, well foward near the lateral margins of the skull and . . . its pointed snout." To these should be added: the nearly complete covering of denticles over the palate surface; the relatively broad basipalatal plate; the broad, flat cultriform process; the small size of the marginal teeth; and the poor development of the palatal tooth row. A correspondence with *Pneumatostega potamia* of uncertain significance is the paired condition of the neural arches; unlike *P. potamia*, however, *R. quadricuneata* also has paired intercentra.

Among the more important characters cited by Howie to exclude *R. quadricuneata* from the Rhytidosteidae are: the more anterior position of the orbits; normal reticulate sculpture rather than the characteristic rhytidosteid variety; and the presence of lachrymal bones. It is particularly germane to the evolutionary and systematic interpretations being developed in the present paper that *R. quadricuneata* shares these distinctions from rhytidosteids with *Indobrachyops* and (except perhaps for the lachrymal bones) with *Mahavisaurus*. The preorbital portion of the skull is even shorter (O:L index 0,29) than in the Indian and Malagasy genera. Regarding the lachrymal bone, it is significant that it possesses an orbital border, rare in Triassic temnospondyls, in both *Rewana* and *Indobrachyops*. Further concurrences between the two include: convex lateral skull margins; interpterygoid vacuities of similar size and shape; and similar sculpture on the lateral portions of the pterygoid corpi.

Several features distinguish *R. quadricuneata* from *I. panchetensis, M. dentatus* and *M. australis*, features indicative of at least generic separation. The snout is pointed rather than broadly rounded. The tympani seem to have been enclosed by otic notches rather than anchored only on their anterior edges to shallow otic embayments. And, the exoccipital condyles appear to be on a level far in advance of the level of the quadrate condyles. This last condition is decidedly more typical of Permian temnospondyls than their Triassic descendants. Howie, however, notes of her restoration of the palate: "the condyles may have been positioned more posteriorly, nearer the level of the quadrates."

In summary, then, the present analysis proffers the view that the similarities between *R. quadricuneata* and the rhytidosteids noted by Howie are more important for taxonomic purposes than the differences and that they should be grouped together on the superfamily level. The additional and superimposed resemblances to *Indobrachyops* and *Mahavisaurus* suggest that it be grouped with these on the family level.

Derwentia warreni (figs. 9a and 11a)

A discussion of this form, described by the senior author (1974) and assigned in that paper to the Rhytidosteidae, is included at this point as reappraisal points to a closer alliance with *Indobrachyops, Mahavisaurus* and *Rewana* than with the Rhytidosteidae s.s. As in these three genera, characters definitive on the superfamily level are exhibited on the skull of *D. warreni:* the skull is roughly triangular in outline; the orbits are widely spaced; the cultriform process is

broad and flat; the basipalatal plate is broad (Q:L index 0,27); the marginal teeth are small and closely spaced; the palatal tooth row is incomplete; and the pavement of denticles appears to have covered most of the palatal surface.

More restricted affinity with *Indobrachyops, Mahavisaurus* and *Rewana* is indicated by the anteriorly placed orbits, the equilateral shape of the skull in dorsal view with its convex lateral margins and the nature of the surface sculpture. Regarding the anterior placement of the orbits, the preorbital length (O:L index 0,34) is proportionately somewhat smaller than that of *Indobrachyops* and *Mahavisaurus* but somewhat greater than that of *Rewana.* The sculpture, although much eroded on the holotype skull, is observed to consist of small, irregular pits bounded by irregular ridges; the straight, prominent radiating ridges, surmounted by nodes, a feature of the Rhytidosteidae s.s., are not developed. In general, the sculpture of *D. warreni* appears to be a very finely textured variant of the normal reticulate pattern, somewhat similar to that observed in the lydekkerinids *Lydekkerina huxleyi* and *Cryobatrachus kitchingi* (Colbert and Cosgriff, 1974, fig. 1b).

One feature of the skull roof shared by *D. warreni* with the rhytidosteids but not with *Indobrachyops* and its allies is the absence of lachrymal bones. This may be of phyletic significance, indicating that the genus *Derwentia* lies closer to a divergence point from the Rhytidosteidae than do *Indobrachyops, Mahavisaurus* and *Rewana;* or, it may be that loss of the lachrymal bone occurred randomly in the superfamily and has no particular taxonomic significance.

The holotype skull of *D. warreni* demonstrates enough distinction from skulls of related genera in the *Indobrachyops* complex to insure its allocation to a separate genus. Features distinguishing it from *Indobrachyops* and *Mahavisaurus* are mainly localised on the dorsal surface. The presence of otic notches is a character shared with *Rewana* if Howie's (1972, fig. 2) restoration of this structure is correct; at any rate, it is a feature which contrasts *Derwentia* and *Indobrachyops* and *Mahavisaurus*, both of which have embayments rather than notches. The lateral line canals are fully developed as in *Indobrachyops* but in contrast to both species of *Mahavisaurus*. The entire skull surface of *D. warreni* has an irregular topography due to an elevated ossification centre on each dermal bone and to a central trough which extends from the occipital border anteriorly through the interorbital region. This irregularity is not present in *Indobrachyops*, in *Mahavisaurus*, or, for that matter, in any of the other rhytidosteoids. Also, the tabular bones of *D. warreni* occupy a much larger part of the dorsal surface than is the case in any of the other rhytidosteoids.

Comparisons of *D. warreni* with *R. quadricuneata* are, of necessity, largely limited to the palatal surface as this is the only part of the skull of the latter that is extensively preserved. Sufficient differences are observed on the palates, however, to confirm generic separation. The snout tip of *Rewana* is more pointed and the quadrate condyles are more posterior relative to the exoccipital condyles. *Derwentia* lacks the sculpture observed on the lateral parts of the pterygoids in *Rewana* (and, also *Indobrachyops*). The choanae of *Derwentia* are relatively much larger (more so than can be accounted for by ontogenetic factors even though the holotypic skull of *D. warreni* is considerably smaller than that of *R. quadricuneata*). The interpterygoid vacuities differ markedly in shape, those of *Rewana* having greater convexity of the lateral margins and those of *Derwentia* being indented on their anterior borders by swollen edges of the palatine bones. Finally, the differing character of the sculpture of the dorsal surfaces confirms allocation to separate genera; the sculpture of *Derwentia* is, as noted, very fine in texture whereas that of *Rewana* resembles, in its coarseness, that seen in *Indobrachyops* and *Mahavisaurus.*

Laidleria gracilis

This species, based on a single skull from the Karoo Series of South Africa and probably from the *Cynognathus* Zone, was described by Kitching (1957) and commented on by the senior author (1965). Kitching offered two solutions for its taxonomic position, either an allocation to the Trematosauridae or a placement in its own family, Laidleriidae. The senior author concurred with the latter and placed the family provisionally in the Rhytidosteoidea. The characters cited in support of this action were the triangular skull shape, the position of the orbits near the lateral edges, the wide occiput, the short postorbital region and the broad cultriform process. However, in the course of the present new assessment of the Rhytidosteoidea, the total case has come to seem much weaker than in 1965. Although the skull shape and proportions approach those of the superfamily, other characters argue that it is taxonomically quite removed. The cultriform process, although broad and flat, is not so extreme in these respects as in the rhytidosteoid genera. Also, as the senior author noted (1965), an assortment of specialised cranial characters distinguished *L. gracilis* from the then known rhytidosteid genera, *Deltasaurus, Peltostega* and *Rhytidosteus*. These characters, which constitute valid differences from *Pneumatostega* and the *Indobrachyops* complex as well, include: exceptionally large and widely-spaced marginal teeth; absence of the palatal pavement of denticles except for a few small patches on the pterygoids; very large orbits which, although lying close to the lateral skull margins, also lie close to each other so that the interorbital region is quite constricted; and otic foramina (as in the capitosaurid genus *Cyclotosaurus*) rather than otic notches or otic embayments.

Through the present reconsideration it seems best to maintain *L. gracilis* in its own family but to list this family, Laidleriidae, as *incertae sedis* among the Temnospondyli.

Latiscopus disjunctus

The only recorded specimen of this species is a poorly-preserved skull from the Upper Triassic Dockum Formation of Texas (Wilson, 1948). In 1965, the senior author compared this skull with the rhytidosteid species and concluded that, except for the laterally placed orbits and the short distance between the orbits and parietal foramen, there were no significant resemblances to this family. The family Latiscopidae was thus considered *incertae sedis* among the superfamilies of the Triassic Temnospondyli. The present reconsideration of the Rhytidosteoidea, with its consequent expansion of taxonomic content, prompted a reassessment of *L. disjunctus*. This, however, did not serve to elucidate the phylogenetic relationships of the species as it bears no more similarity to the *Indobrachyops* complex than it does to the Rhytidosteidae proper. Hence, this monotypic family must continue as *incertae sedis*.

Almasaurus habbazi

This species (Dutuit, 1972) is based on five cranial specimens from the Upper Triassic of Morocco. Dutuit considered it to represent a lineage separately derived from the Upper Permian Rhinesuchoidea and distinct from all other groups of Triassic temnospondyls; he placed it in its own superfamily, Almasauroidea, and own family, Almasauridae. It is considered in the present discussion at this point as Dutuit's restoration of the dorsal, palatal, occipital and lateral view of the skull show, at least superficially, strong resemblances to these views of the *Latiscopus disjunctus* skull provided by Wilson (1948). In both forms the skull is generally triangular in shape, the orbits are very laterally placed about midway along skull length and skull depth is quite large relative to skull breadth and length. A detailed comparison of the two species, beyond the scope of this paper, would be worth undertaking. The general time equivalence in the Upper Triassic, coupled with the wide geographic separation, furthers the interest of this possible relationship.

As for *L. disjunctus*, the Moroccan species has no features of taxonomic importance on the superfamily level in common with Rhytidosteoidea other than skull shape and orbit position. None of the distinctive characters of the palatal surface, dentition or skull ornamentation are present.

CLASSIFICATION OF THE RHYTIDOSTEOIDEA

The following classification summarises the morphologic comparisons and conclusions regarding taxonomic relationships that are accomplished in the two preceding sections. As the superfamily is now divided into two families, as its taxonomic content is nearly doubled and as its morphologic diversity is expanded, new diagnoses of the superfamily and the contained families are necessitated. This section also provides short résumés of the stratigraphic ranges of the families.

SUPERFAMILY RHYTIDOSTEOIDEA Cosgriff, 1965

As with most taxa on a high categorical level, only a limited number of features may be cited which are universal to it and which serve to define it. These are, of necessity in the present case, all skull characters. The following diagnosis is largely the same as that provided by the senior author (1965) but with certain additions and deletions necessitated by the reassortment of species among the contained families. The characterisation provided by this diagnosis underscores the fact that there are no valid arguments for allocating rhytidosteoid species to the superfamily Trematosauroidea as appears in certain classifications (e.g. Romer, 1966).

Diagnosis

Triassic temnospondyls with broad, triangular skulls and very wide occiputs. Orbits, external nares and otic notches (or embayments) very lateral in position with least interorbital width equal to one third to one half of skull midline length. Orbits face dorsolaterally. Cultriform process of parasphenoid bone exceptionally wide with flat ventral surface. Marginal teeth of premaxillaries, maxillaries and dentaries quite small and closely spaced as compared to other temnospondyls. Ventral surfaces of palatal bones almost entirely covered by dense pavements of denticles (except in *Peltostega* where, perhaps, removed by erosion). No lachrymal flexure of infraorbital canal and no oblique ridge on pterygoid in species where portions containing these structures are preserved. Palatoquadrate fissure present in specimens where the occiput is preserved.

Quadrate condyles on same hinge line as exoccipital condyles (except, perhaps, in *Rewana*) rather than posterior to them as in rhinesuchids, lydekkerinids and uranocentrodontids. Skulls lack: parabolic outlines, U-shaped palates and modifications of occipital processes of squamosals and pterygoids characteristic of brachyopids; elongate postorbital regions of skull roofs, high narrow cultriform processes, high narrow occiputs and extensive parasphenoid corpi underplating exoccipitals of trematosaurids; posterior slope of occiputs, as viewed from above, long postorbital portions and anterior positions of orbits of metoposaurids; and posterior, closely spaced orbits of capitosaurids, rhinesuchids and uranocentrodontids.

FAMILY RHYTIDOSTEIDAE, Huene, 1920

The contents of the family have been altered from Cosgriff (1965 and 1974) to include *Pneumatostega potamia* and to exclude *Derwentia warreni* (removed to the *Indobrachyopidae*). With these changes the family diagnosis and contents are as follows:

Diagnosis

Skull outline, in dorsal and palatal views, that of an isosceles triangle. Lateral skull margins straight. Preorbital portion of skull roof relatively long, distance from snout tip to orbit anterior margins: skull

midline length (O:L index) ranging from 0,45 to 0,55. Both otic notch and tabular horn relatively small and triangular in shape. No lachrymal bones. Sculpture of dermal bones dominated by straight ridges radiating from ossification centres with cross ridges suppressed or eliminated; total effect usually a spider-web pattern on each bone; in most species, points of junction and bifurcation of sculpture ridges surmounted by prominent nodes.

Contents

Deltasaurus kimberleyensis Cosgriff, 1965, *Deltasaurus pustulatus* Cosgriff, 1965, *Peltostega erici* Wiman, 1916, *Peltostega wimani* Nilsson, 1946, *Pneumatostega potamia* n. gen. and sp. and *Rhytidosteus capensis* Owen, 1884.

Stratigraphic range

Lower to Middle Scythian (Induan–Olenekian). All of species except for those of *Peltostega* occur in the Lower Scythian. The *Lystrosaurus* Zone which has produced *P. potamia* and, probably, *R. capensis,* lies within the lower part of the Scythian Stage (e.g. Kitching, 1970). *Deltasaurus kimberleyensis* includes a large hypodigm from the Blina Shale of Western Australia, a few specimens from the Knocklofty Formation of south-eastern Tasmania and one specimen from the Cluan Formation of central Tasmania. *Deltasaurus pustulatus* is based on a single partial skull from a well core in the Kockatea Formation of the Perth Basin, Western Australia. The fossiliferous sites in the Blina Shale and Knocklofty, Cluan and Kockatea Formation are, as assessed by the senior author (1965 and 1974) through consideration of all available palynologic, invertebrate and vertebrate fossil evidence, all restricted to the basal portions of the Scythian. *P. erici* and *P. wimani*, each known only from a single, incomplete skull, both derive from the Sticky Keep Formation of Spitsbergen, the former from Mt. Anderson and the latter from Mt. Wallenburg. The horizon at each locality lies, on the basis of invertebrate fossil evidence (Kummel, 1961), within the Owenitan Division of the mid-Scythian (approximately Induan–Olenekian boundary).

Paleoecology

See the previous section on the paleoecology of *Pneumatostega potamia.*

FAMILY INDOBRACHYOPIDAE, n. fam.

This grouping for the short-faced rhytidosteoids brings together five species comprising four genera. One of the species, *Rewana quadricuneata*, has not previously been placed in a family but all of the remaining four were allocated to different families by the authors first describing them.

Diagnosis

Skull outline, in dorsal and palatal views, generally that of an equilateral triangle but with convex lateral margins. Preorbital portion of skull relatively short, distance from snout tip to orbit anterior margins:skull midline length (O:L index) ranging from 0,30 to 0,40. Tympanic border of skull roof either in form of distinct notch *(Derwentia* and *Rewana)* or broad embayment *(Indobrachyops* and *Mahavisaurus)*. Lachrymal bone present in three genera *(Indobrachyops, Mahavisaurus* and *Rewana)*. Sculpture pattern of the reticulate variety usual to temnospondyls; irregular pits occupy ossification centre of each dermal element and elongate grooves form peripheral zone around pitted area; sculpture ridges delineating pits and grooves sinuous and irregular; no nodes at points of ridge junction and bifurcation.

Contents

Derwentia warreni Cosgriff, 1974, *Indobrachyops panchetensis* Von Huene and Sahni, 1958, *Mahavisaurus dentatus* Lehman, 1966, *Mahavisaurus (Lyrosaurus) australis* (Lehman, 1966) and *Rewana quadricuneata* Howie, 1972.

Stratigraphic Range

Lower to ?Upper Scythian (Induan through Olenekian?) *D. warreni*, known from a nearly complete skull and a few isolated skull fragments, occurs in the Knocklofty Formation with *D. kimberleyensis*. This unit, as noted above, is basal Triassic. The fossiliferous horizons of the Panchet Formation (Robinson, 1967), which produced the skull of *I. panchetensis*, and the Sakamena Series (Besairie, 1957), which produced the four specimens of species of *Mahavisaurus*, also lie in the lower part of the Scythian. The horizon in the Rewan Formation which produced the partial skull of *R. quadricuneata* certainly lies within the Scythian (Howie, 1972), but its position cannot be more firmly determined at this time.

Paleoecology

The Indobrachyopidae is composed of species which attained a smaller adult size than that seen among the Rhytidosteidae and which are characterised by a more generalised morphology, less modified from ancestral rhinesuchoid conditions. In particular, the dentition of this group appears to be much less specialised. These considerations suggest that the Indobrachyopidae may have been more euryphagic, feeding on a variety of invertebrates and smaller fish and amphibian larvae. The larger rhytidosteids, from their specialised dentition, may have been more restricted to larger fish as the main dietary component.

Taphonomic evidence, however, is equivocal and demonstrates no habitat distinction between the two families. *D. warreni* is found associated with *D. kimberleyensis* in the stream channel conglomerates of Tasmania. *M. dentatus* and *M. australis* occur in the littoral zone context of the Sakamena Series of Malagasy, a context perhaps parallel in part to that of *D. kimberleyensis* in the Blina Shale. No clear evidence is obtainable for the taphonomics of *I. panchetensis* in the Panchet Formation or of *R. quadricuneata* in the Rewan Formation.

EVOLUTION OF THE RHYTIDOSTEOIDEA

Phylogenetic relationships within the Rhytidosteoidea are represented cladistically in Figure 12. These relationships were arrived at solely on the basis of comparative morphology. The computer techniques of Farris (1970) for constructing Wagner networks through the principle of maximum parsimony (minimal morphologic change between taxa), were employed to compute the initial branching pattern. A more parsimonious pattern, within the limits imposed by the initial network topology, was achieved by the branch swapping methods discussed by Moore (1976). Tables 1 and 2 list the characters and character states employed in the computer constructed cladogram (fig. 12).

The cladogram suggests a subdivision of the group by contemporaneous radiation, as per the variant of phylogenetic pattern proposed by Simpson (1961, figs. 24E, 25C). Subdividing the Rhytidosteoidea into two families which experienced roughly contemporaneous radiation is thus substan-

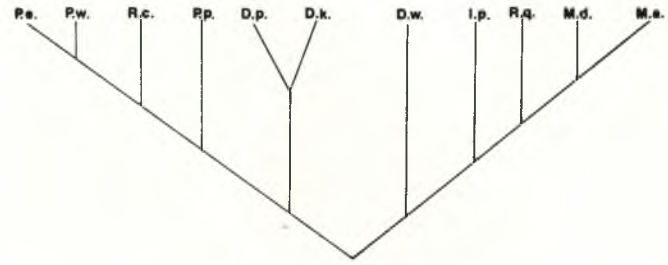


Figure 12. Cladistic relationships among the Rhytidosteoidea, based on computer processed morphologic data.

TABLE 1

Characters and character states used in computer analysis of rhytidosteoid phylogeny

Character I (B/L = greatest W/midline L)
State 1: 0,85–0,89
2: 0,96–1,2
3: 1,3–1,47
Sequence: 1–2–3

Character II (O/L = preorb. L/midline L)
State 1: 0,48–0,56
2: 0,39–0,45
3: 0,29–0,34
Sequence: 1–2–3

Character III (A/L = interorb. W/midline L)
State 1: 0,30–0,34
2: 0,39–0,41
3: 0,46–0,51
Sequence 1–2–3

Character IV (C/L = interotic W/midline L)
State 1: 0,30–0,35
2: 0,54–0,58
3: 0,60–0,69
4: 0,73–0,83
Sequence: 1–2–3–4

Character V (D/L = post orb. L/midline L)
State 1: 0,31–0,32
2: 0,34–0,40
3: 0,49–0,56
Sequence: 1–2–3

Character VI (orb. L/midline L)
State 1: 0,1–0,17
2: 0,2–0,3
Sequence: 1–2

Character VII (sculpture pattern)
State 1: coarse reticulate
2: fine regular pitting
3: fine spider-web and nodes
4: coarse spider-web and nodes
5: nodes only
6: ridges
Sequence: 1–2–3–4–5–6

Character VIII (snout tip)
State 1: rounded
2: pointed
3: notched
Sequence: 1–2–3

Character IX (lateral line canals)
State 1: broad shallow continuous
2: not present
3: narrow even continuous
4: narrow even discontinuous
Sequence: 1–3–4, 1–2

Character X (lateral skull margins)
State 1: convex
2: straight
3: concave
Sequence: 1–2–3

Character XI (orbit shape)
State 1: long oval
2: circular
3: indented anterior margin
Sequence: 1–2–3

Character XII (otic region)
State 1: triangular
2: otic embayment
Sequence: 1–2

Character XIII (breadth vs length — frontals and parietals)
State 1: breadth < length
2: breadth ≤ length
Sequence: 1–2

Character XIV (palatal tooth row)
State 1: present
2: absent
Sequence: 1–2

Character XV (Y/L = interptery. va. L/midline L)
State 1: 0,45–0,53
2: 0,27–0,36
Sequence: 1–2

Character XVI (Q/R = pt. bar L/ps. pt. W)
State 1: 0,48–0,53
2: 0,27–0,36
Sequence: 1–2

Character XVII (lachrymals)
State 1: present
2: absent
Sequence: 1–2

TABLE 2
Data matrix used in computer analysis of rhytidosteoid phylogeny

Character	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII	XIII	XIV	XV	XVI	XVII
D. kimberleyensis	3	1	3	3	2	1	3	1	3	2	3	1	2	2	2	2	2
D. pustulatus	2	2	3	2	2	2	5	1	3	2	3	1	2	2	—	—	2
P. erici	2	1	2	2	1	1	4	—	4	2	1	1	1	2	1	3	2
P. wimani	2	1	2	2	1	1	4	—	4	2	—	1	1	2	—	—	2
M. dentatus	2	2	3	4	1	2	1	1	2	1	1	2	1	—	—	2	1
M. australis	1	2	3	3	2	2	1	1	1	1	1	2	1	—	—	—	1
P. potamia	3	1	1	2	2	1	3	2	4	2	2	1	1	1	1	3	2
R. quadricuneata	2	3	—	—	3	—	1	2	—	1	1	—	—	1	1	2	1
I. panchetensis	3	2	3	4	2	2	1	1	3	1	1	2	1	1	1	3	1
R. capensis	1	1	2	1	2	1	6	3	2	2	1	1	1	2	2	1	2
D. warreni	3	3	3	4	3	1	2	1	3	1	1	1	1	2	1	3	2

tiated by the evolutionary branching sequence of the group.

Based on overall morphological considerations, the Indobrachyopidae is the more primitive of the two families, reflecting more closely the conditions of the ancestral Rhinesuchoidea. Within the family, *M. dentatus, M. australis* and *R. quadricuneata* represent states more derived than *I. panchetenesis* and *D. warreni*, the latter forms lying closer to the indobrachyopid-rhytidosteid divergence.

D. kimberleyensis and *P. potamia* are the most basic, unmodified species of the Rhytidosteidae and probably lie, at least morphologically, closest to its source. *D. pustulatus* obviously represents a closely allied derivative of *D. kimberleyensis*, differing from it principally in sculpture pattern. *R. capensis* and the species of *Peltostega* are the most modified, derived species of the family.

When extrinsic data, stratigraphy and geographic distribution are superimposed on the morphologic evidence further implications become apparent. Figure 13 suggests an austral origin for the superfamily as *D. kimberleyensis* and *D. warreni* are both found in Australia and are both close to the initial diverging point in the phylogenetic pattern. The subsequent radiation of the rhytidosteids and indo-

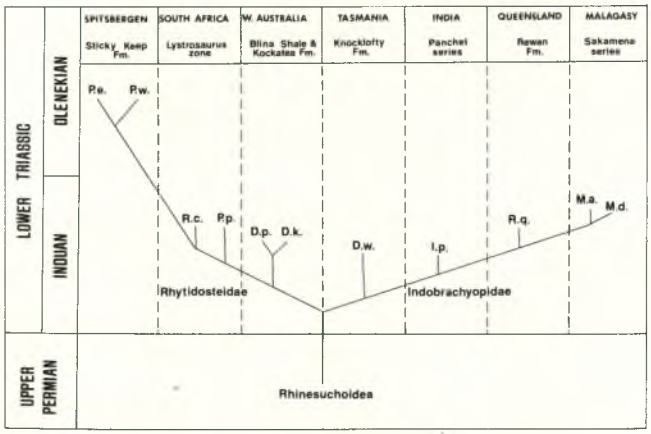


Figure 13. Phylogeny of the Rhytidosteoidea plotted against stratigraphic and geographic data. Note: *D. kimberleyensis* is also found in the Knocklofty Formation of Tasmania.

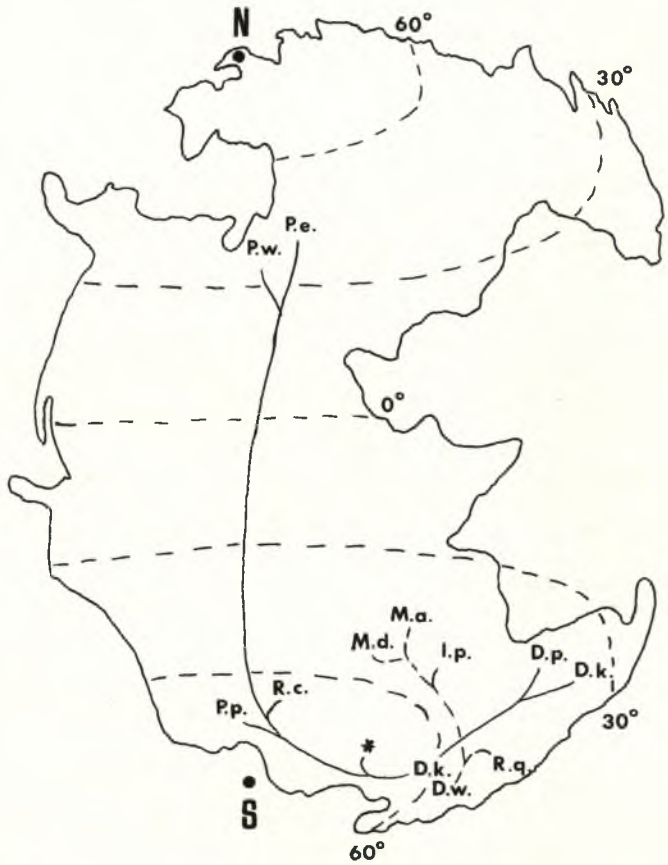


Figure 14. Proposed dispersal pattern of the Rhytidosteidae (solid line) and Indobrachyopidae (dashed line) across the Pangaean continent during the lower Triassic. Note, the asterisk indicates the new undescribed rhytidosteid from Antarctica. Continental outlines, paleolatitudes and polar positions are from Smith and Briden (1977, map 52).

brachyopids and a speculation on migratory pathways is shown in Figure 14.

The Rhytidosteidae were widely distributed across the Pangaean supercontinent, with forms such as *P. erici* and *P. wimani* ranging as far north as Spitsbergen by Olenekian times. Secondary centres of evolution along the implied migration route were located within Australia, South Africa and Spitsbergen. New rhytidosteid material recently collected from the Fremouw formation (Induan) of Antarctica in-

dependently corroborates the proposed dispersal route. This material, acquired during the 1977–78 season by the Wayne State University–Ohio State University field party, of which the authors were both members, derives from the Cumulus Hills area of the Queen Maud Mountains. As yet undescribed, the fragments pertaining to a rhytidosteid have close affinities in dermal sculpturing with *D. kimberleyensis* and *P. potamia*. Contrasting with the Pangaean distribution of the Rhytidosteidae, the Indobrachyopidae were restricted to Gondwanaland, with a major secondary centre of evolution in the India–Malagasy region.

The main ecological factor involved in the adaptive divergence within the superfamily was probably a switch in feeding preference. As noted previously, the indobrachyopids were generalised, mixed-feeders, preying on small fish and invertebrates. The rhytidosteids, conversely represent a more stenophagic, strictly piscivorous feeding strategy. More complete knowledge of depositional environments, perhaps derivable from the Fremouw formation and its contained vertebrate fauna, will allow for a more detailed analysis of the selection pressures involved in this radiation.

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