

A NEW SPECIES OF THE SPHENODONTIAN REPTILE *CLEVOSAURUS* FROM THE LOWER JURASSIC OF SOUTH WALES

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Abstract: Small reptiles from the Early Jurassic Pant 4 fissure fill in Glamorgan, South Wales (St. Bride's Island, Pant Quarry), were formerly provisionally attributed to three species of sphenodontian lepidosaurs. A re-analysis, aided by new material, has found this herpeto-fauna to consist almost exclusively of a single new species, *Clevosaurus convallis* sp. nov., with only one specimen referable to *Sphenodontia incertae sedis*. *Clevosaurus* is known from the Upper Triassic and Lower Jurassic in various parts of the world, but *C. convallis*

represents the first occurrence of the genus in the Jurassic of Britain. The material is fragmentary but includes numerous premaxillae, maxillae, dentaries and palatines, and the new species is distinguished by the unique combination of six large additional dentary teeth and a very short nasal process of the premaxilla, along with the diagnostic *Clevosaurus* features.

Key words: *Clevosaurus*, Sphenodontidae, Lepidosauria, Reptilia, Jurassic, St. Bride's Island.

THE sphenodontian remains from Pant 4 fissure in South Wales, one of several fissures associated with the Lower Jurassic of St. Bride's Island, were originally excavated in the early 1970s by a team from University College, London. A preliminary description of three new species of sphenodontians was made by Pacey (1978) in his unpublished thesis, and was mentioned later by Evans and Kermack (1994) in their review of the small Early Jurassic tetrapods of Britain. Fraser (1994) also briefly mentioned these sphenodontians and their possible close resemblance to Canadian and Chinese clevosaurus. The sphenodontians and other taxa from Pant 4 (yet to be formally described) were an important addition to the tetrapod assemblage found in other fissures of St. Bride's Island, showing that the island's fauna was not depauperate (Evans and Kermack 1994), as had been suggested earlier (Fraser 1989).

Thorough re-analysis of the original sphenodontian material, consisting of fragmentary jaw parts, aided by some new material, has resulted in their assignment to a new species of *Clevosaurus*, a genus currently known from the Upper Triassic of England, China and Belgium (Fraser 1988; Wu 1994; Duffin 1995) and the Lower Jurassic of China, Canada, South Africa and possibly Mexico (Reynoso 1993; Sues *et al.* 1994; Wu 1994; Sues and Reisz 1995).

GEOLOGICAL BACKGROUND OF ST. BRIDE'S ISLAND

Geological setting

In South Glamorgan, the area of South Wales between Porthcawl in the west and Cardiff in the east, there were three main upland zones in the Late Triassic landscape. The first was a long east–west strip between the Coal Measures and Millstone Grit to the north and the Old Red Sandstone to the south. The other two were islands, St. Bride's Island in the Porthcawl-Bridgend area and Cowbridge Island further east. These islands were formed from Carboniferous Limestone and they contain cave and fissure systems dating from the Late Triassic and Early Jurassic.

St. Bride's Island (named by Robinson 1957) was a small island of about 20 km². Shortly after the onset of the Rhaetian marine transgression, it formed a part of a small archipelago before becoming an isolated island distant from the mainland (Simms 1990; Evans and Kermack 1994). The island lay at a palaeolatitude of about 15°N and the climate was tropical to subtropical, with heavy seasonal rain. It was finally inundated early in the Sinemurian (Trueman 1922; Robinson 1957; Evans and Kermack 1994). (Evans and Kermack 1994, fig. 15.2, and Benton and Spencer 1995, pp. 80–95, give fuller locality details.)

Many methods have been used in attempts to date the St. Bride's fissures. Littoral deposits of early Sinemurian age around the island give a minimum age to the deposits (Trueman 1922; Cope *et al.* 1980). The maximum age is not as easily obtainable because there was no marine transgression over the plateau of St. Brides Island between the Lower Carboniferous and Hettangian (Strahan and Tiddeman 1904; Kermack *et al.* 1973). Consequently, fossils have been used as a dating tool.

Fossils and dating

The first tetrapod remains from St. Brides's Island were found by Walter Kühne in 1947 in a fissure fill in Duchy Quarry, Glamorgan (National Grid Reference, NGR, SS 906757; Kermack *et al.* 1973). Several other fissures have since been excavated in this and other quarries in close proximity. The most abundant plant remains in these fissures belong to the conifer *Hirmeriella muensteri* (Schenk) Jung, 1968, which has not been found in any other fissures in the Bristol Channel area (Harris 1957; Lewarne and Pallot 1957). Consequently, the whole faunal and floral association has been named 'The *Hirmeriella* association' (Kermack *et al.* 1973).

Three tetrapod genera normally characterize the *Hirmeriella* association. Most material (60 per cent) is referable to the pleurodont lepidosaur *Gephyrosaurus bridensis* Evans, 1980 and the rest consists of the mammals *Morganucodon watsoni* Kühne, 1949 and *Kuehneotherium praecursoris* Kermack, Kermack and Mussett, 1968, *Morganucodon* being the dominant form (Kermack *et al.* 1973, 1981). In addition, some isolated remains of other genera, including a possible amphibian, coelurosaur theropods, a pterosaur and unclassified archosaurs, have been reported (Kermack *et al.* 1973; Fraser 1989; Evans and Kermack 1994). The sphenodontians described here belong to an assemblage that includes the characteristic members of the *Hirmeriella* association and additionally the remains of sphenodontians, the tritylodontid *Oligokyphus*, archosaurs, and several mammals (Pacey 1978; Evans and Kermack 1994).

The most abundant plant fossil in the fissures, the conifer *Hirmeriella muensteri*, is also found in southern Germany and can be correlated with a series of Lower Liassic plant-bearing beds. Microflora (including *Bacutritetes tylotus* Harris, 1937 and *Kraeuselisporites*) have been dated as 'Rhaetian' but floral zones containing these fossils have been found to extend into the Hettangian (Morbey 1975; Evans and Kermack 1994). A 'latest Rhaetian' or early Jurassic age is also supported by the absence of latest Triassic palynomorphs (Waters and Lawrence 1987; Evans and Kermack 1994).

Some of the vertebrate fossils can also be used in dating but the mammals of the *Hirmeriella* association and the sphenodontians described in this paper are of little use, because of their long time-range (Benton 1991; Evans *et al.* 2001). Similarly, *Gephyrosaurus bridensis*, the most abundant reptile of the *Hirmeriella* association, is the only known species of its genus and has not been found elsewhere (Evans 1980, 1981). However, fragmentary remains of a very similar morphology have emerged from the Early Jurassic Kota Formation of India (Evans *et al.* 2001). More support for an Early Jurassic age comes from the *Oligokyphus* material excavated from the Pant 4 fissure (Pacey 1978; I. Corfe in prep.). The famous *Oligokyphus* material from Windsor Hill was dated as Charmouthian (Pliensbachian), owing to its association with Jurassic brachiopods, belemnites and ammonites (Kühne 1956). Other findings of *Oligokyphus* have also been dated as Early Jurassic, partly due to the age of the Windsor Hill specimens (Sues 1985; Luo and Sun 1993). Thus, an Early Jurassic age is generally accepted for the St. Brides Island's fissures (Robinson 1957; Kermack *et al.* 1973; Whiteside 1986; Simms 1990; Evans and Kermack 1994).

Pant 4 fissure

Material described in this paper comes from a fissure fill in Pant Quarry, South Glamorgan (NGR SS 896760). It was the fourth bone-bearing fissure found in this quarry and was therefore named Pant 4. Previous fissures in the quarry yielded material referable to the *Hirmeriella* association (Kermack *et al.* 1973). Pant 4 was a narrow slot-like fissure, never exceeding a width of 1.2 m. About 37 m of the fissure was excavated from 1968 to 1978 (Pacey 1978). Seventy-five per cent of the fissure filling is red, mainly consisting of haematite pellets cemented into a calcareous clay matrix, and almost all the remainder is grey marl. There was great variation in the mean grain size, both horizontally and vertically, throughout the whole length of the fissure, while graded stratification was strictly confined to local pockets. From this, Pacey (1978) concluded that the sediments were washed into the fissure on separate occasions, probably after heavy rainstorms. The fossils occur almost exclusively in the red deposits.

MATERIAL AND METHODS

Sphenodontian material

Pacey (1978) obtained thousands of bone fragments from the red deposits of the Pant 4 fissure. Most of them consisted of sphenodontian specimens (65–70 per cent) and around 600 sphenodontian jaw fragments are stored in

the collections of the Natural History Museum, London. Additional material is housed in the Department of Anatomy and Developmental Biology, University College, London. All of these specimens were examined. New material, including sphenodontian teeth and jaw fragments, obtained from previously unstudied sediment blocks, was also used in this re-analysis.

All specimens are fragmentary and represent mainly jaws (with some individual vertebrae and skull bones). This is in stark contrast to some of the other *Hirmeriella* fissures where the recovery of disarticulated bones has enabled the reconstruction of *Gephyrosaurus bridensis* (Evans 1980, 1981) and the skull of *Morganucodon watsoni* (Kermack *et al.* 1973, 1981). The fossils of Pant 4 are not only fragmentary but also heavily water-worn, indicating that they were transported for some distance prior to deposition in the fissure (Pacey 1978).

Preparation

The breakdown of 1.3 tonnes of the fossil-bearing, haematite-rich red deposits was completed by David Pacey at UCL during a 9-month period after its initial collection in 1972, using the 10 per cent acetic acid solution technique described by Toombs (1948). Breakdown of small amounts was continued throughout the study, until 1978.

After the cement was broken down, the residual matrix had a particle size varying from 0.5 to 10 mm. Pacey (1978) used four different mesh sizes to divide the material into size groups that were then examined under the microscope. However, a great deal of solid and unsorted material excavated from Pant 4 in 1973 and 1978 still remains unprocessed. Some of this material was sorted during this study. Initially, no division into size groups was made. However, all useful specimens were found to be in the 2-mm size category or larger. Consequently, approximately 17.5 kg of new matrix was sieved with a 1.68-mm sieve and all fossils were picked out.

Specimens were studied under a binocular microscope and a scanning electron microscope (SEM). Line drawings were produced using a camera lucida and measurements (Text-figs 9, 12) were taken from digital images using Image Pro Plus software.

Anatomical abbreviations

A1–A8, additional teeth; b, bump; cpr, coracoid process; fl, tooth flange; f, foramen; g, groove; htt, hatchling teeth; mkg, meckelian groove; mxf, maxillary facet; mxpr, maxillary process; npr, nasal process; ob, orbital border; palf, palatine facet; palfo, palatal foramen; prff, prefrontal facet; pmf, premaxillary facet; ppr, posterior process; sb, secondary bone; sy, symphyseal region; wf, wear facet.

Institutional abbreviations

BMNH, Natural History Museum, London; NSM, Nova Scotia Natural History Museum, Halifax; UCL, University College, London.

SYSTEMATIC PALAEOLOGY

Subclass DIAPSIDA Osborn, 1903

Infraclass LEPIDOSAURIA Haeckel, 1866

Order RHYNCHOCEPHALIA Günther, 1876

Suborder SPHENODONTIA Williston, 1925

Family SPHENODONTIDAE Cope, 1870

Genus CLEVOSAURUS Swinton, 1939

Type species. *Clevosaurus hudsoni* Swinton, 1939

Included species. *C. minor* Fraser, 1988; *C. wangi*, *C. mcgilli* and *C. petilus* Wu, 1994; *C. bairdi* Sues *et al.*, 1994.

Remarks. The premaxilla of *Clevosaurus* has a large lateral flange, which presumably excluded the maxilla from the margin of the external naris. This kind of premaxilla has been considered a diagnostic feature of *Clevosaurus* (Sues *et al.* 1994; Wu 1994) but at least one other sphenodontian genus, *Godavarisaurus* (Evans *et al.* 2001), and possibly also *Pamizinsaurus* (Reynoso 1997) possess a similar kind of premaxilla. However, many dental features, notably the flanges on the maxillary and additional dentary teeth, ontogeny of premaxillary teeth, and conical palatine teeth, are shared by all *Clevosaurus* species, while the dentition of *Godavarisaurus* and *Pamizinsaurus* is notably different (see comparison in Evans *et al.* 2001). Thus *Clevosaurus* is still a valid genus based on those characters but the structure of the premaxilla can no longer be used as its diagnostic feature.

Clevosaurus convallis sp. nov.

Text-figures 1A–E, 3–8

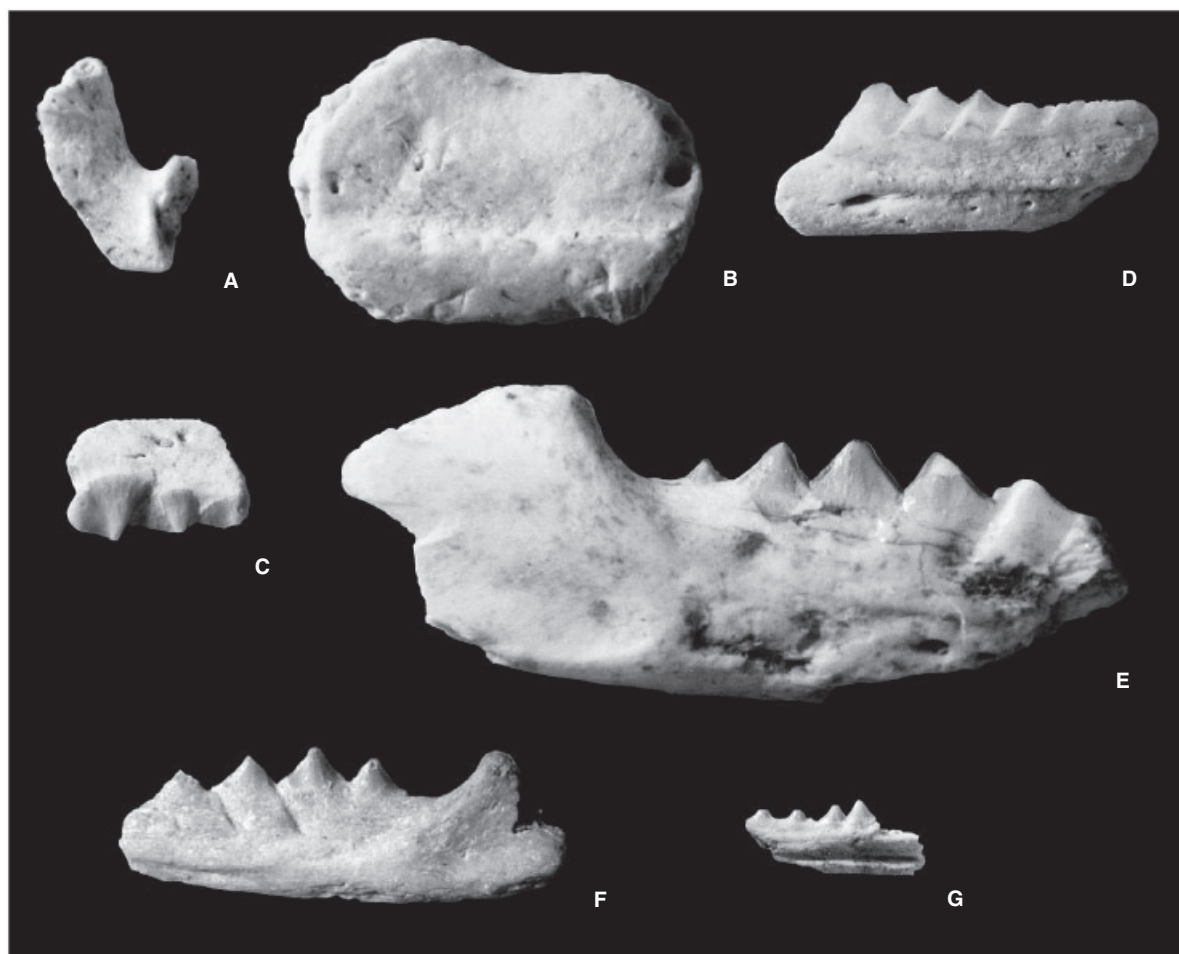
1978 sphenodontid A (sp. nov.); Pacey, p. 24.

1994 sphenodontian; Fraser, p. 220.

1994 sphenodontian sp. nov.; Evans and Kermack, p. 277.

Derivation of name. Latin *convallis*, enclosed valley, chosen to describe the location (Pant is Welsh for valley) and to indicate that the material comes from a fissure-fill.

Holotype. A left premaxilla showing a short nasal process, a long maxillary process, and the fusion of premaxillary teeth; BMNH R7530.



TEXT-FIG. 1. A–F, *Clevosaurus convallis* sp. nov. A, BMNH R7530, partial left premaxilla, in medial view. B, BMNH R7533, middle region of left maxilla, in lateral view. C, BMNH R7536, part of the tooth-bearing region of right maxilla, in lateral view. D, BMNH R7540, anterior end of mature right dentary, in lateral view. E, BMNH R7541, posterior end of mature right dentary, in lateral view. F, BMNH R7543, posterior end of left dentary, in lateral view. G, *Sphenodontia incertae sedis*, BMNH R7547, partial right dentary, in medial view. All $\times 8$.

Referred specimens. Left premaxillae (BMNH R7531, R7550); right premaxilla (BMNH R7532); left maxilla (BMNH R7533); right maxillae (BMNH R7534–7537); left palatine (BMNH R7538); right palatine (BMNH R7551); left dentary (BMNH R7539); right dentaries (BMNH R7540–7541, R7552).

Type locality and horizon. Pant 4 fissure in Pant Quarry, Glamorgan, South Wales, one of a series of Lower Jurassic fissure fills (NGR SS 896760).

Diagnosis. Distinguished from other *Clevosaurus* species by three characters: (1) it lacks the horizontal posterior flange of the long lateral process of the premaxilla; (2) the nasal process of the premaxilla is very short; and (3) it has six large, additional teeth on both the dentary and the maxilla, followed by one or two smaller ones on the dentary and up to four on the maxilla.

Remarks. *Clevosaurus convallis* differs from other *Clevosaurus* species most markedly in having a unique combination of characters previously seen in different species, as well as some unique features. It has 3–4 premaxillary teeth like *C. hudsoni* but it lacks the horizontal posterior flange attached to the long lateral process of the premaxilla in *C. hudsoni* (Fraser 1988). The short nasal process of the premaxilla of *C. convallis* is clearly different from the long and slender nasal process in *C. hudsoni* (Fraser 1988). The length of the nasal process is somewhat unclear in other *Clevosaurus* species. *C. convallis* has six large, additional teeth on both the dentary and the maxilla, followed by one or two smaller ones on the dentary and up to four on the maxilla. This is more than has been reported in any other *Clevosaurus* species. Many of these features are uncertain in *C. wangi* and *C. petilus*,

but the palatine of these two species is highly curved (Wu 1994), whereas the palatine of *C. convallis* and *C. hudsoni* (Fraser 1988) is straight.

Description

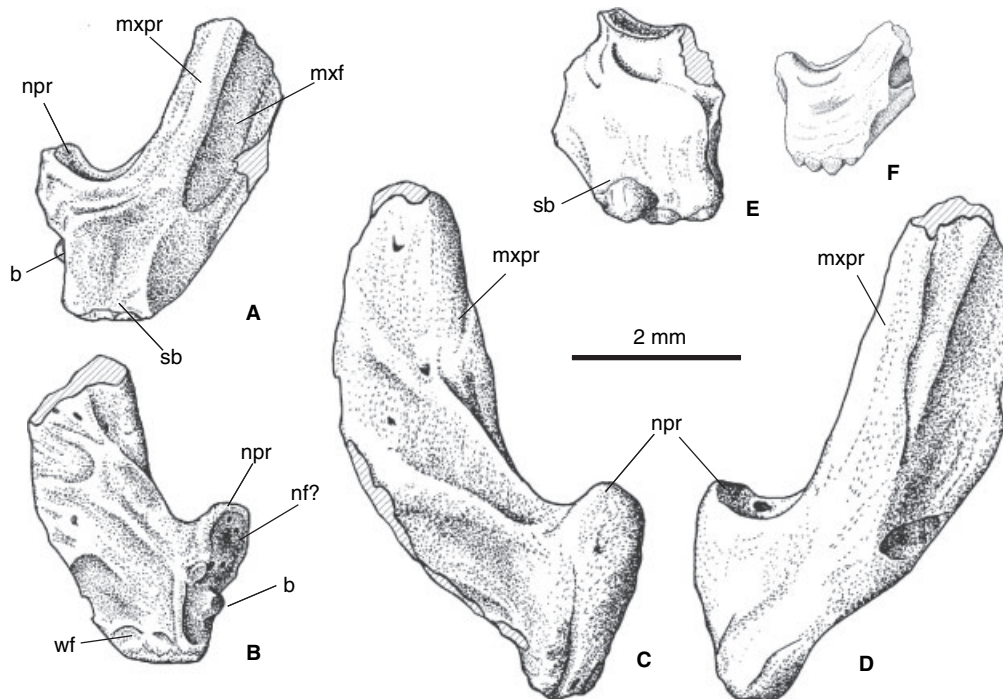
Premaxilla. The tooth-bearing portion of the premaxilla is U-shaped with quite a broad alveolar margin. In most specimens the teeth are completely (Text-fig. 2C–D) or partially worn down and they form a continuous cutting edge with the bone to which they are ankylosed. This is caused by secondary bone (*sensu* Harrison 1901; ‘secondary dentine’ of Fraser 1988) growing over and between the teeth (Text-fig. 2A). Two specimens, BMNH R7531 and R7532, show individual teeth. BMNH R7531 is the smallest premaxilla found, with four smallish, conical teeth that are all unworn (Text-fig. 2F). In contrast, BMNH R7532 has two small teeth followed by one large one, which is considered to be a replacement for two smaller teeth. BMNH R7532 is a medium-sized premaxilla and there is secondary bone growth over the worn teeth (Text-fig. 2E).

The lateral margin of the bone has developed into a long, broad maxillary process. This process is broken in all specimens, but the length of the process in BMNH R7550 (Text-fig. 2C–D) implies that it excluded the maxilla wholly from the margin of the external nares. The process also bears a deep, groove-like facet for the maxilla on its lateral surface (Text-fig. 2A). There is no sign of a horizontal, posterior flange of the maxillary process in any of the 31 premaxillae studied. The nasal process is short

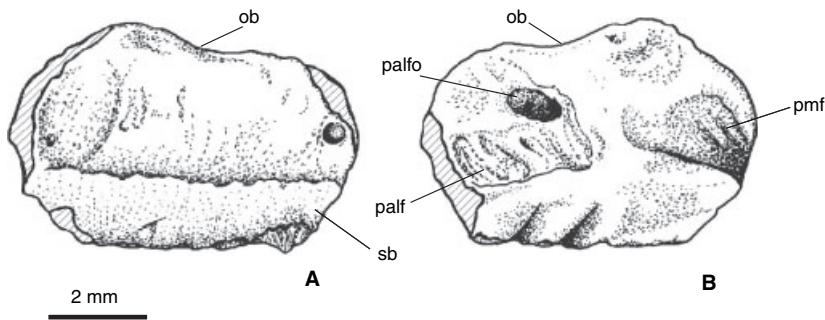
and relatively narrow in all specimens. In most cases it is heavily abraded, but in the holotype premaxilla BMNH R7530 it appears intact, revealing a concave outer surface with four small foramina, accompanied by a large ‘bump’ of bone below them (Text-figs 1A, 2B). It is uncertain whether this is just the junction of the two premaxillae or, possibly, a facet for the nasal bone. In any case, the nasal process of *Clevosaurus convallis* does not appear to be part of a longer process, implying that the nasals extended far anteriorly to meet the premaxillae.

The size-range of the premaxillae, measured as the depth of the tooth-bearing portion below the external opening, is quite extensive, being 1.3–3.4 mm (Text-fig. 9A).

Maxilla. The maxilla is represented by several fragments but most preserve only a small stretch of the dentition. Reconstruction of the whole maxilla is therefore not possible, but several features can be identified. Parts of the palatal facet can be seen on the medial side of numerous specimens close to the alveolar margin, and in BMNH R7533 it is accompanied by a large palatal foramen (Text-fig. 3B). BMNH R7533 is one of the largest, best-preserved maxillary fragments, showing also parts of the premaxillary facet and some of the ventral border of the orbit (Text-fig. 3A–B). The shape of the partial premaxillary facet matches the large maxillary process of the premaxillae. Some fragments also show parts of the jugal facet that, with the palatal and premaxillary facets, is nearly identical with the same features in *C. hudsoni* (Fraser 1988). On the lateral side there is extensive secondary bone growth, like a bony lip, that covers most of the worn teeth (Text-figs 1B, 3A).



TEXT-FIG. 2. Premaxilla of *Clevosaurus convallis*. A–B, BMNH R7530, holotype, partial left premaxilla, in A, lateral, and B, medial, views. C–D, BMNH R7550, partial left premaxilla, in C, medial, and D, lateral, views. E, BMNH R7532, tooth-bearing portion of a right premaxilla, in lateral view. F, BMNH R7531, tooth-bearing portion of a left premaxilla, in lateral view.

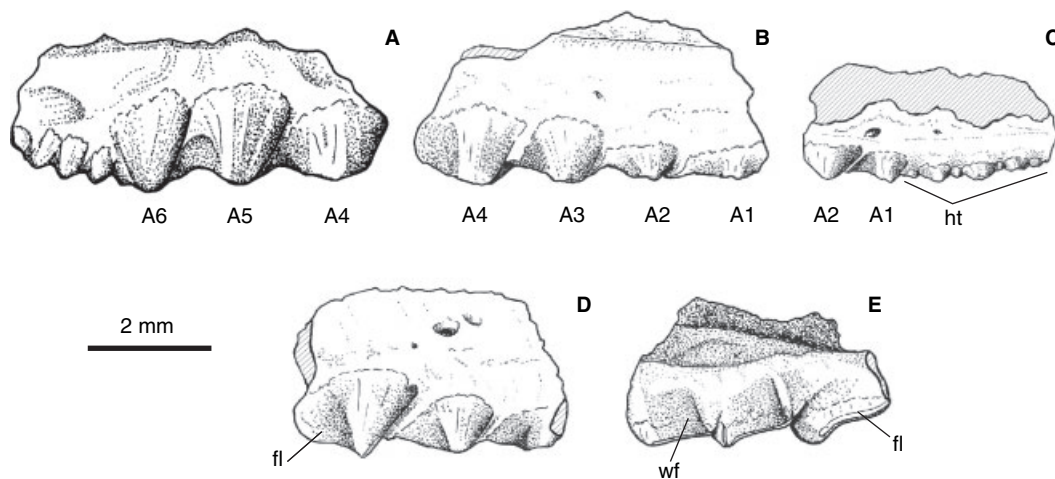


TEXT-FIG. 3. *Clevosaurus convallis*, BMNH R7533, middle region of left maxilla in A, lateral, and B, medial, views.

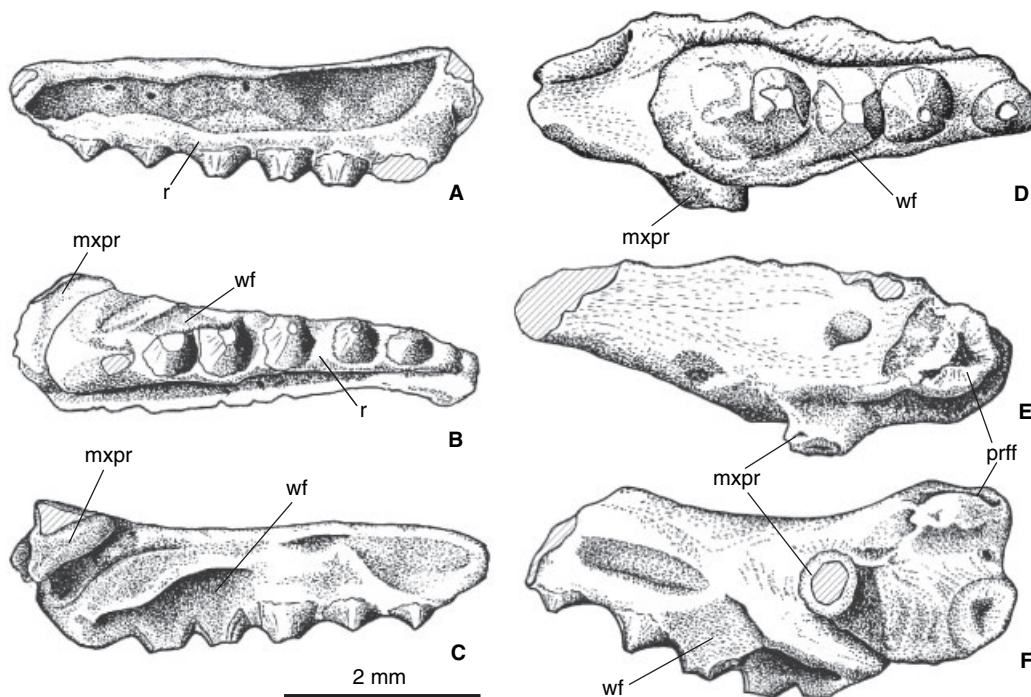
No maxilla with the complete tooth row is preserved, but information combined from several fossils permits a reconstruction. The maxillary dentition is fully acrodont and can be divided into a small hatchling dentition and a larger additional dentition, two sphenodontian tooth categories identified by Robinson (1973). The small, conical hatchling teeth have even smaller denticles between them (Text-fig. 4C). All are flattened on the lingual side. The tooth number is uncertain, but at least four teeth and four denticles are present. There is no sign of tooth replacement with successional teeth, the third sphenodontian dental category (Robinson 1973), present on the maxillae of many sphenodontians. Larger teeth, with very distinctive posteromedial flanges that overlap the succeeding tooth slightly, follow the hatchling dentition. BMNH R7536 shows the finest preserved flanges (Text-figs 1C, 4D–E). Wear facets on the dentary suggest that there was a corresponding maxillary tooth for every large additional dentary tooth (see below). BMNH R7534–R7535 and R7537 illustrate the large, additional teeth (A1–A6), showing their size and position following the hatchling teeth (Text-fig. 4A–C). The basal length of the large, additional teeth increases only slightly posteriorly but the increase in height is significant. The last large tooth, A6, bears a shorter flange than the previous teeth. After A6 there are up to four smaller, conical additional teeth without significant flanges (Text-fig. 4A).

Palatine. One of the best preserved palatines, BMNH R7538, clearly shows the existence of a single acrodont tooth row with five teeth and an indication of one more anteriorly (Text-fig. 5A–B), running parallel to the maxillary teeth. The teeth are conical, although most are heavily worn (Text-fig. 5B–C), probably as a result of contact with the dentary teeth. The tooth row is straight and raised on a bony ridge (Text-fig. 5A–B), causing it to hang lower than the rest of the palatine and possibly also lower than the maxillary tooth row. The palatal bone has broken off quite near the tooth row in all specimens, making it impossible to predict whether there were any solitary teeth or tooth rows medial to the main tooth row. The maxillary process seems short and quite robust in all specimens (Text-fig. 5B–F). However, there is an extensive palatine facet on the medial side of the maxilla (Text-fig. 3B), comparable with *C. hudsoni* (Fraser 1988), and this would imply that the process was larger in life. BMNH R7551, a partial right palatine, shows the prefrontal facet on the anter-dorsal edge of the palatine (Text-fig. 5E–F).

Dentary. Numerous fragmentary specimens of dentaries, representing different age groups and degrees of preservation, make it possible to reconstruct the basic shape of almost the entire dentary bone (Text-fig. 8). The anterior part of the dentary curves



TEXT-FIG. 4. Maxillary dentition of *Clevosaurus convallis*. A, BMNH R7535, posterior end of dentition, right maxilla, in lateral view. B, BMNH R7534, middle region of dentition, right maxilla, in lateral view. C, BMNH R7537, anterior end of dentition, right maxilla, in lateral view. D–E, BMNH R7536, part of right maxilla, showing three teeth with large posteromedial flanges, in D, lateral, and E, medioventral, views.

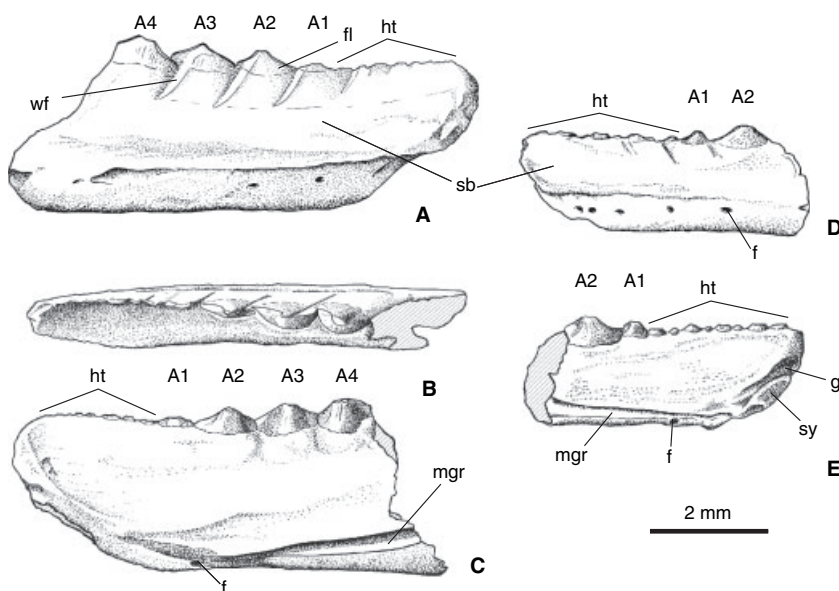


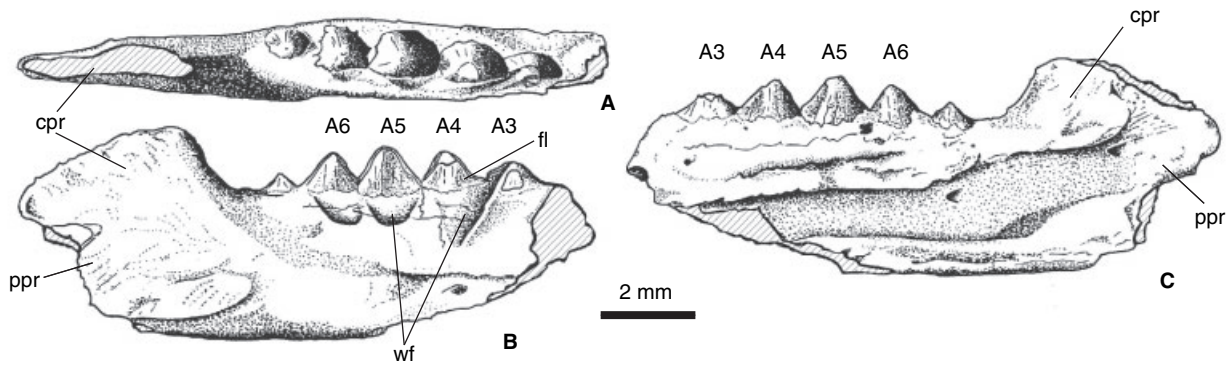
TEXT-FIG. 5. *Clevosaurus convallis*. A–C, BMNH R7538, left palatine, in A, medial, B, palatal, and C, lateral, views. D–F, BMNH R7551, right palatine in D, palatal, E, dorsal, and F, lateral, views.

somewhat medially, emphasized by the concave upper medial surface below the tooth row (Text-fig. 6B–C). The Meckelian groove is very broad posteriorly but thins to a delicate groove when approaching the anterior end, where it is interrupted by a foramen (Text-fig. 6C, E). The depth of the dentary, especially between the teeth and the Meckelian groove, increases with size. Consequently, most of the smaller and less worn specimens seem very narrow (Text-fig. 6D–E) in comparison with larger and/or

more worn specimens (Text-fig. 6A, C). Similarly the teeth seem relatively larger in the smaller specimens. The anterior symphyseal region is broad and divided from the alveolar margin by a distinctive U-shaped groove (Text-fig. 6E). On the lateral side there is a prominent ridge formed by secondary bone. Below this there are several foramina for blood vessels and nerves (Text-figs 1D, 6A, D). The coronoid process is high and the posterior process continued behind it, although neither is fully preserved

TEXT-FIG. 6. *Clevosaurus convallis*. A–C, BMNH R7540, anterior end of mature right dentary in A, lateral, B, dorsal, and C, medial, views. D–E, BMNH R7539, anterior end of immature left dentary, in D, lateral, and E, medial, views.





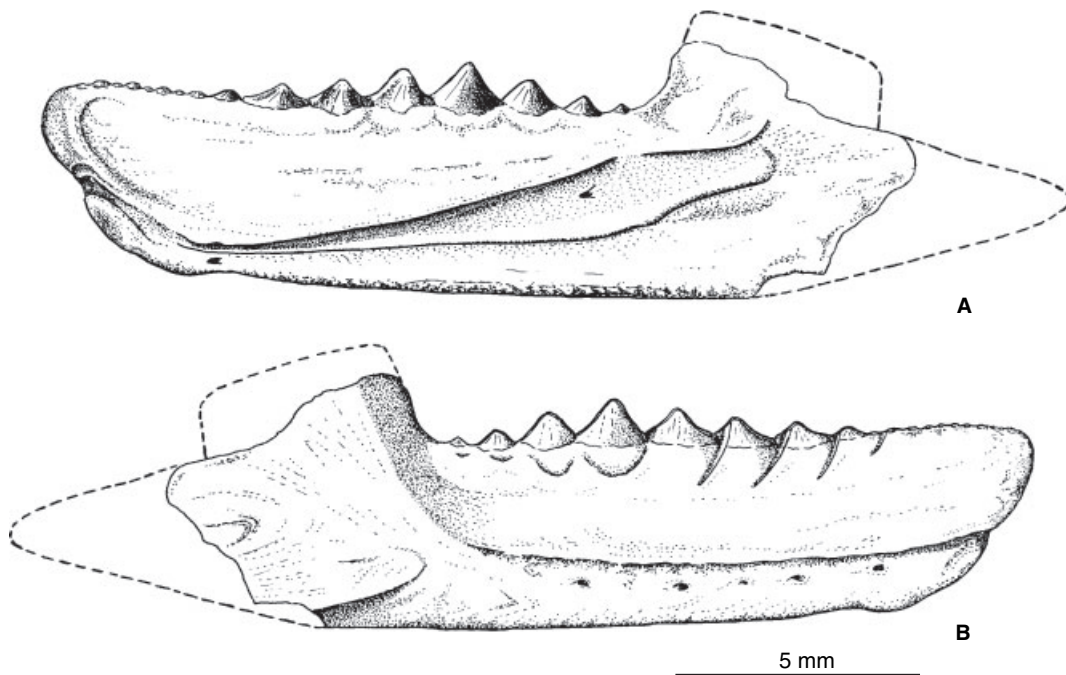
TEXT-FIG. 7. *Clevosaurus convallis*, BMNH R7541, posterior end of mature right dentary, in A, dorsal, B, lateral, and C, medial, views.

in any specimen (Text-figs 1E, 7). Size distribution in the bone depth below A1 is unimodal, ranging from 1.7 to 3.7 mm (Text-fig. 9B).

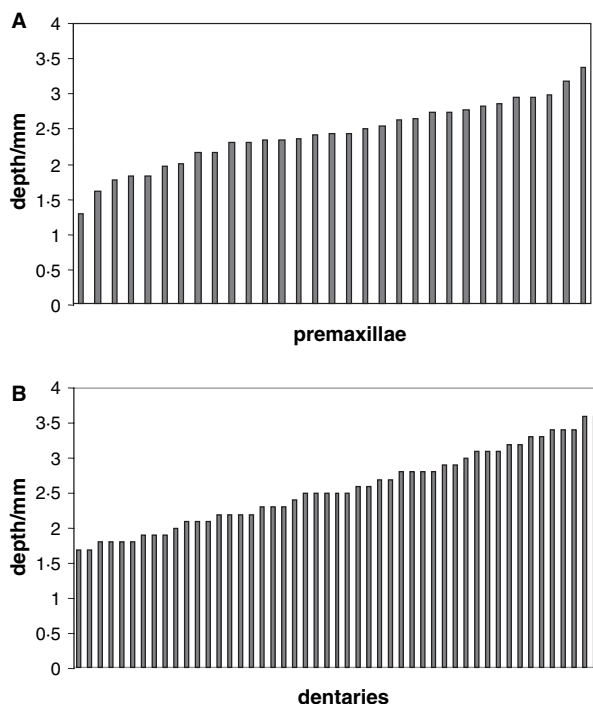
The dentary dentition is fully acrodont and falls into the same categories as the maxillary dentition; small hatchling dentition and larger additional dentition (Robinson 1973). No specimens display the whole tooth row but a complete hatchling dentition, composed of nine small, conical, buccally flattened teeth is well preserved in BMNH R7552. In most cases, however, the first tooth is completely worn away (Text-fig. 6C–E), presumably by the premaxillary teeth, but the rest of the teeth remain visible. Although there is variation in the size of these teeth, smaller and larger alternating, the difference is not

as marked as in the maxillary teeth. As in the maxilla, there is no sign of successional teeth at the anterior end of the dentition in any specimens.

The first additional tooth, A1, is quite small but visibly larger than any tooth of the hatchling series (Text-figs 1D, 6A–E). It has a broader base and is somewhat flattened on the buccal side, a character that is obvious in the following teeth. It has small anterior and posterior flanges. The anterior flanges of A2, A3 and A4 are elongated, making them overlap with the tooth in front (Text-fig. 6A–C). A5 is more pyramidal in side view, owing to a greater similarity in length of the anterior and posterior flanges. The size of the teeth increases posteriorly up to A5, but the last large additional tooth, A6, is usually slightly



TEXT-FIG. 8. Reconstruction of right mature dentary of *Clevosaurus convallis*, in A, medial, and B, lateral, views. Outline of the posterior and coronoid processes after *C. hudsoni* (Fraser 1988).



TEXT-FIG. 9. A, size distribution of *Clevosaurus convallis* premaxillae, measured as the depth of the teeth-bearing region below the narial opening in 31 premaxillae. B, size distribution of *Clevosaurus convallis* dentaries, measured as the depth of the bone below the first additional tooth (A1) in 49 dentaries.

smaller than A5 and lacks the elongated anterior flange (Text-fig. 7). After A6 there is often one (Text-fig. 7), and sometimes two, smaller additional teeth.

Dentition and wear patterns. Wear facets can be seen on the teeth and adjacent bone on the premaxilla, maxilla, palatine and dentary. On the premaxilla the groove-like wear facets are on the lingual side above the teeth. They are present even in the smallest specimen (BMNH R7531) and become more pronounced with size (Text-fig. 2B). They are presumably produced by contact with the most anterior dentary teeth. All maxillary teeth, up to the distal end of the tooth row, are heavily worn on their lingual side (Text-fig. 4E). In contrast, in the case of the posterior dentary, the maxillary teeth occluded only with the bone, leaving the last additional dentary teeth totally unworn (Text-fig. 7). In more anterior dentary teeth, the heaviest wear is on the tips of the anterolateral and posterior flanges of the teeth (Text-fig. 6A–B). This has resulted in a shortening of flanges and loss of tooth overlap in some of the more mature specimens (Text-fig. 7).

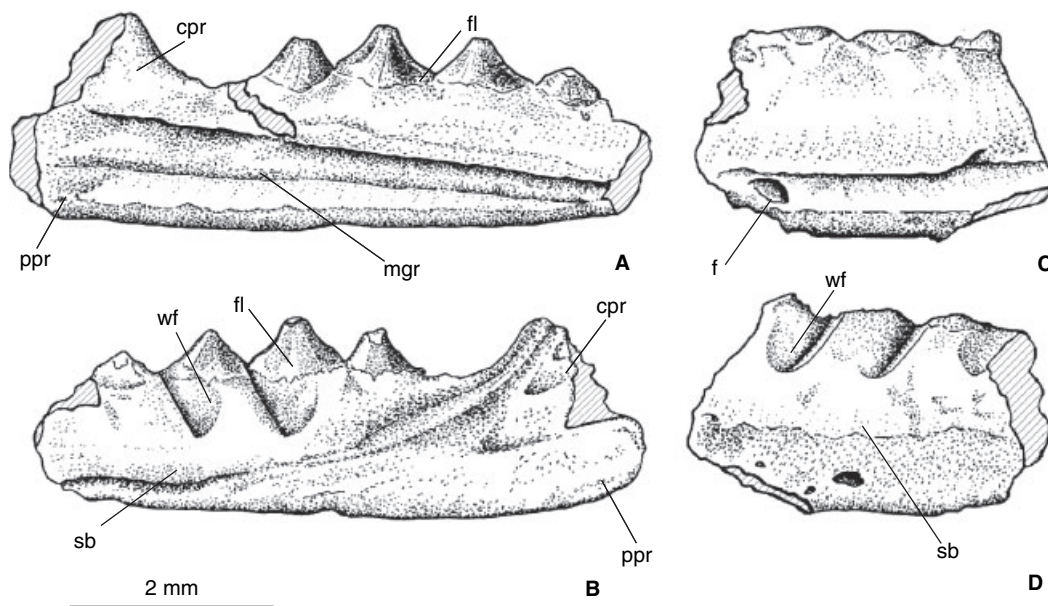
There is also heavy wear on the crowns of the large posterior additional dentary teeth, A4 in particular (Text-figs 6A–C, 7). This is interpreted as a result of occlusion with anterior palatine teeth that have heavy wear facets on their lateral side (Text-fig. 5B–C, F). However, some of the wear on the palatine could be from abrasive food material forced between the palatal and mandibular tooth rows, as speculated by Fraser (1988) in the case of palatal wear in *Clevosaurus hudsoni*.

OTHER MATERIAL

BMNH R7542–7546

Text-figures 1F, 10

Description. Pacey (1978) interpreted two specimens, BMNH R7542 and R7543, both posterior parts of dentaries, as belonging to a species distinct from his sphenodontid A (here *Clevosaurus convallis*). He came to this conclusion because of their small size,



TEXT-FIG. 10. *C. convallis*. A–B, BMNH R7543, posterior end of left dentary, in A, medial, and B, lateral, views. C–D, BMNH R7544, middle region of right dentary, in C, medial, and D, lateral, views.

high degree of wear and lack of non-functional additional teeth (Text-figs 1F, 10A–B). However, some of the smaller specimens of *C. convallis* lack the small additional teeth as well. In other respects than size they are nearly identical to *C. convallis*, although the tooth wear on the lateral side makes it impossible to determine whether the teeth overlapped in life. Three new specimens (BMNH R7544–7546) that match BMNH R7542 and R7543 in size and distribution of wear facets, but represent the middle region of the dentary, were found during this study. BMNH R7544 adds the fossa interrupting the Meckelian groove to the similarities with *C. convallis* (Text-fig. 10C). As in BMNH R7542 and R7543, the three new specimens seem to be more eroded and porous than most of the more abundant specimens.

Size comparisons between these dentaries and *C. convallis* were made by measuring the depth of the dentary beneath A5 and the height of A5 in *C. convallis*, and the height of the tallest tooth (possibly A5) and the depth of dentary beneath it in the smaller dentaries. Because of the fragmentary nature of the dentaries, these measurements could be obtained from only 19 *C. convallis* dentaries and from BMNH R7542 and R7543. Results show that BMNH R7542 and R7543 have the same depth of dentary as the young, less worn specimens of *C. convallis* and the tallest tooth is slightly smaller (Text-fig. 12).

Remarks. There have been other cases where specimens of different sizes, but which are similar in other ways, show the same amount of wear. Indeed, Robinson (1973) mentions small specimens with a high degree of tooth wear and large specimens with a lower degree in the only living sphenodontian, the Tuatara (*Sphenodon*). This was attributed to differences in diets between individuals. Similarly, Whiteside (1986) stated that some of the small (juvenile) specimens of *Clevosaurus hudsoni* from Tytherington quarry show a high degree of wear.

Two species of *Clevosaurus*, *C. hudsoni* and *C. minor*, have been described from Cromhall Quarry (Fraser and Walkden 1983; Fraser 1988). There are some differences in the structure of the palatines and in the successional and additional marginal dentition but the main difference between them is that highly worn *C. minor* specimens are considerably smaller than similar *C. hudsoni* ones. This

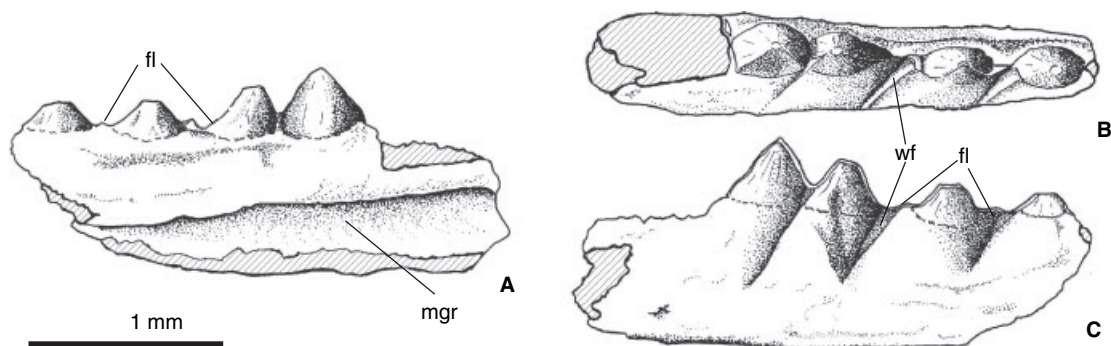
alone, however, could be a reflection of sexual dimorphism (Fraser 1988) or they could represent juveniles with a different, more abrasive diet (Fraser and Walkden 1983). The most important factor in separating them into two species, in addition to size, is their occurrence in different deposits, albeit at the same locality. Occasionally *C. minor* occurs with *C. hudsoni*, but generally they are mutually exclusive and could possibly have been separated in time (Fraser 1988).

Clevosaurus convallis dentaries and Pant 4 BMNH R7542–7546 do show some differences in tooth size but the main difference is that the highly worn BMNH R7542–7546 are smaller than *C. convallis* dentaries with the same amount of wear. However, as they are found in the same deposit, it is impossible to rule out other explanations, such as differences in diets between individuals, variation between successional years, or sexual dimorphism. Furthermore, there are only five specimens representing the smaller form; a larger sample would be needed to confirm whether there really were two distinctive size groups. On present evidence, BMNH R7542–7546 are considered to represent a variant of *C. convallis*.

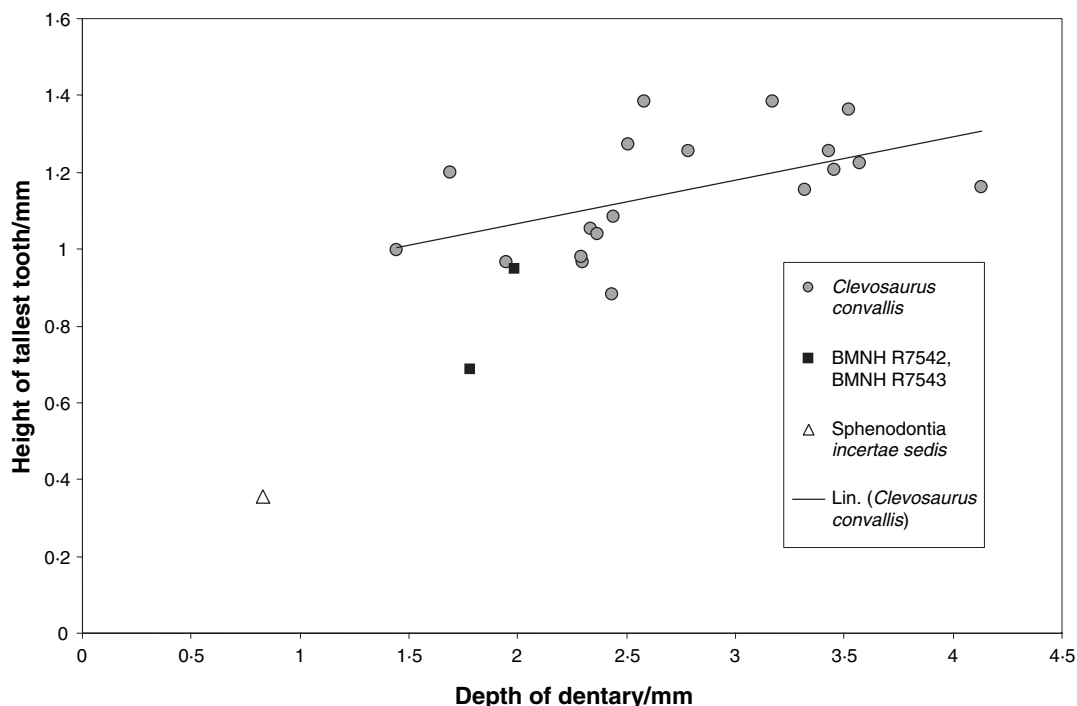
BMNH R7547

Text-figures 1G, 11

Description. Dentary BMNH R7547 is different from all other sphenodontian specimens found in Pant 4, mainly because of its minuscule size, both in bone depth and in tooth size (Text-figs 1G, 12). However, the tooth size is not really comparable with the other specimens because BMNH R7547 clearly had some teeth, possibly larger than those preserved, behind its largest preserved tooth, as indicated by a small fragment of enamel (Text-fig. 11B). The depth of the dentary is a more reliable measurement, although the dorsal border of BMNH R7547 is clearly somewhat eroded. Another difference between BMNH R7547 and *C. convallis* (including BMNH R7542–7546) is that the anterior flange of the third tooth of BMNH R7547 seems to be more elongated than in any teeth of the larger dentary



TEXT-FIG. 11. Sphenodontia *incertae sedis*, BMNH R7547, middle region of right dentary, in A, medial, B, dorsal, and C, lateral, views.



TEXT-FIG. 12. Size comparison of *Clevosaurus convallis* and *Sphenodontia incertae sedis* dentaries; the depth of the bone below the tallest tooth against the height of the tallest tooth.

specimens. This may, however, be due partly to the high dental wear that is, in itself, somewhat different from that of the other specimens. The wear facets differ from those of *C. convallis* (Text-figs 6A–B, 10B) in that they are not situated between the teeth but are more on the middle of the anterior flange in the second and third tooth (Text-fig. 11). This does not cause the flanges to shorten as it does in *C. convallis* specimens, but divides them into two parts. Additionally, teeth of BMNH R7547 lack the posterior flanges that are present in teeth of *C. convallis*. Considering all these differences, it is most likely that BMNH R7547 does not represent *C. convallis* but another species or even genus; however, as there is only one fragmentary specimen, this cannot be confirmed.

RELATIONSHIPS

General comparisons

At the time of his original study, Pacey (1978) had only two species of sphenodontians, *Clevosaurus hudsoni* and *Sphenodon punctatus*, available as comparative material. He came to the conclusion that the most common sphenodontian at Pant 4 (here described as *Clevosaurus convallis*) did not belong to either genus, although it resembled *C. hudsoni* more than *S. punctatus*. Pacey (1978) used descriptions of *C. hudsoni* by Swinton (1939) and Robinson (1973), aided by personal observations, in his analysis. Many details of *C. hudsoni* were unknown at that

time but now, after the description of the full cranial and postcranial skeleton of *C. hudsoni* (Fraser 1988) and the discovery of numerous new sphenodontians around the world, it is possible to make more extensive comparisons. There are many recent systematic analyses of the Rhynchocephalia (Fraser and Benton 1989; Sues *et al.* 1994; Wu 1994; Reynoso 1996, 1997; Wilkinson and Benton 1996; Evans *et al.* 2001) but the Pant 4 sphenodontian, like many other taxa from microsites (Fraser 1986; Evans 1992; Evans and Sigogneau-Russell 1997; Evans *et al.* 2001), is too fragmentary to be included in a cladistic analysis. Therefore, it is necessary to rely on comparison of the features of the tooth-bearing bones and dentition when trying to resolve its phylogenetic position.

Rhynchocephalia, as determined by Gauthier *et al.* (1988), consists of *Gephyrosaurus* and Sphenodontia. All rhynchocephalians share the features of enlarged teeth on the palatine and a posterior process of the dentary underlying the glenoid fossa (Rieppel 1994). *Gephyrosaurus* is the most primitive member with fully pleurodont dentition (Evans 1980). A fully acrodon dentition evolved within the Sphenodontia, *Diphydontosaurus* (Whiteside 1986) having the intermediate condition of both pleurodont and acrodon dentition. *Clevosaurus convallis* displays the rhynchocephalian features, although the elongated posterior process of the dentary is broken off in all cases, and it has a fully acrodon dentition. Therefore it belongs to the Sphenodontia.

There are many jaw bone and dentition types in different rhynchocephalian genera. The primitive premaxilla of *Gephyrosaurus*, similar to that of generalized lepidosaurs, is a shallow bone with a long nasal process and numerous small teeth. Many sphenodontians share this kind of premaxilla with *Gephyrosaurus*, although there is a reduction in tooth number (Evans *et al.* 2001). Another sphenodontian premaxilla type, seen in *Clevosaurus* (Fraser 1988), *Godavarisaurus* from the Lower Jurassic of India (Evans *et al.* 2001) and possibly in *Pamizinsaurus* from the Middle Jurassic of Mexico (Reynoso 1997), has a long, posterolateral maxillary process that excludes, or nearly excludes, the maxilla from the border of the external naris. The tooth-bearing portion of this type of premaxilla also differs from other sphenodontians in being deep and U-shaped. The premaxilla of *C. convallis* is of this latter type (Text-figs 1A, 2). The nasal process of the premaxilla in *C. convallis* is short (Text-figs 1, 2A–B), rather like that of *Godavarisaurus* (Evans *et al.* 2001), whereas *C. hudsoni* (Fraser 1988) has a long nasal process as in other sphenodontians. However, the teeth on the premaxilla of *Godavarisaurus* are spatulate (Evans *et al.* 2001), whereas those of *C. convallis* are more conical and become fused by secondary bone in more mature individuals (Text-fig. 2), as in *C. hudsoni* (Fraser 1988).

The shape of the maxilla seems to vary in rhynchocephalians mainly with regards to the length and the depth of premaxillary and jugal processes (Evans *et al.* 2001), both unknown in *C. convallis*. A more variable feature is the dentition, specifically the degree of posteromedial flanging in additional teeth. Four different degrees, namely (1) no flanges, (2) small flanges, (3) medium flanges and (4) large flanges, were identified by Evans *et al.* (2001). By this definition, *Godavarisaurus* has small, distinctive flanges on its posterior maxillary teeth, while *Clevosaurus* has large flanges (Evans *et al.* 2001). The flanges on the posterior maxillary teeth of *C. convallis* (Text-figs 1C, 4D–E) are very similar in size to those of *C. hudsoni* (pers. obs. on BMNH R9249, a mature left maxilla).

The palatines of rhynchocephalians fall into two categories. *Gephyrosaurus* and some basal sphenodontians, including *Diphydontosaurus*, have several tooth rows (Evans 1980; Whiteside 1986). Other sphenodontians have only one enlarged palatine tooth row, although additional individual palatine teeth can be found in, for example, *Clevosaurus* (Fraser 1988). The teeth in the single row of most sphenodontians are conical and unflanged, but they bear small posterolateral flanges in *Godavarisaurus* (Evans *et al.* 2001). There are also small flanges on the anterior palatine teeth of *C. hudsoni* (pers. obs. on BMNH R5939, a left palatine). The presence of flanges on the anterior palatine teeth of *C. convallis* is uncertain owing to the heavy wear on the lateral side of

the tooth row (Text-fig. 5). However, the general tooth shape resembles more the conical form of *C. hudsoni* (Fraser 1988) than the mediolaterally flattened and recurved form of *Godavarisaurus* (Evans *et al.* 2001).

There are two types of dentaries in rhynchocephalians. *Gephyrosaurus* and *Diphydontosaurus* have long and narrow dentaries with a distinctively oval and flat symphyseal surface (Evans 1980; Whiteside 1986). In other sphenodontians the dentary is shorter and deeper, with reduced tooth numbers and a vertical symphyseal surface divided from the alveolar margin by a notch (Evans *et al.* 2001). The dentary of *C. convallis* is of the latter kind, although in the unworn juvenile specimens the symphyseal surface is divided from the alveolar margin by a long, U-shaped groove (Text-fig. 6E) rather than a notch. In older specimens, however, the groove becomes unclear, resembling a notch.

The dentary dentition has not been stressed in the systematic analysis of the relationships of Rhynchocephalia, while maxillary and premaxillary dentition have been considered more important (e.g. Fraser and Benton 1989; Wu 1994; Reynoso 1996). There are, however, distinctive differences in the degree of flanging in the dentary dentition, just as in the posterior maxillary dentition. In *Gephyrosaurus* the teeth are simple cones without flanges (Evans 1980). The teeth of many sphenodontians, including *Godavarisaurus*, resemble half cones with a concave anteromedial surface, which in *Godavarisaurus* have faceted anteromedial and posteromedial borders (Evans *et al.* 2001). Enlarged anterolateral flanges are found on the dentary teeth of *Clevosaurus* (Fraser 1988), *Sigmala sigmala* from the Upper Triassic of England (Fraser 1986) and the Early Cretaceous *Tingitana* from South Africa (Evans and Sigogneau-Russell 1997). These flanges overlap with the tooth in front, forming a continuous cutting edge. Small posterior flanges are also present. The dentary teeth of *C. convallis* have elongated anterolateral flanges that overlap the tooth in front (Text-figs 1D, 6A–B). The flanges are not quite as long as in *C. hudsoni* (Fraser 1988) but they are longer than the flanges in *S. sigmala* (Fraser 1986). *S. sigmala* usually has eight flanged additional teeth, all roughly the same size (Fraser 1986). There are six functional additional dentary teeth that increase in size until the fifth tooth in *C. convallis* (Text-figs 6–7). The first and last teeth do not have an elongated anterior flange. This structure is very similar to that in *C. hudsoni* (Fraser 1988), although the tooth number is slightly higher in *C. convallis*. *C. convallis* lacks anterior successional teeth, as does *S. sigmala* (Fraser 1986); these are present in *C. hudsoni* (Fraser 1988) and many other sphenodontians. However, there is a distinctive sigmoid flexure in the dentary of *S. sigmala* in dorsal aspect (Fraser 1986), whereas *C. convallis* (Text-figs 6B, 7A) and *C. hudsoni* (Fraser 1988) have straight dentaries.

In conclusion, the bone structure and dental features of *C. convallis* clearly support its inclusion in the genus *Clevo-saurus*.

Comparison with other clevo-saurs

Currently known *Clevo-saurus* species are *C. hudsoni* and *C. minor* from the Upper Triassic of England (Fraser 1988), *C. bairdi* from the Lower Jurassic of Nova Scotia (Sues *et al.* 1994) and *C. mcgilli*, *C. wangi* and *C. petilus* from the Upper Triassic–Lower Jurassic of China (Wu 1994). *Clevo-saurus* sp. from the Lower Jurassic of South Africa is known from a crushed skull, and is indistinguishable from *C. bairdi* (Sues and Reisz 1995). Other new finds classified as possible clevo-saurs are either only brief mentions without descriptions (Evans and Kermack 1994; Benton and Spencer 1995) or fragmentary material with brief descriptions (Crush 1984; Fraser 1988; Reynoso 1993; Duffin 1995).

Based on the work of Pacey (1978), Fraser (1994) mentioned that the fragmentary sphenodontian material of Pant 4 seems to resemble the Chinese and Canadian clevo-saurs more than the English clevo-saurs. Systematic analysis of the relationships of sphenodontians, including *C. hudsoni*, *C. bairdi*, *C. mcgilli* and *C. petilus* (*C. wangi* was considered to be a junior synonym of *C. petilus*) was conducted by Sues *et al.* (1994; text-fig. 19). Unfortunately, none of the cranial characters used to group *C. bairdi* with *C. mcgilli* or *C. hudsoni* with *C. petilus* by Sues *et al.* (1994) can be scored from the fragmentary remains of *C. convallis*.

However, some similarities can be seen between the material from Pant 4 and China. The nasal process of the premaxilla of *Clevo-saurus convallis* is very short and some tendency towards this can be seen in *C. wangi* (Wu 1994, text-fig. 3.6A), although it is still clearly longer than the process of *C. convallis* (Text-fig. 2A–B). The nasal process is not preserved in *C. mcgilli* and *C. petilus*. The number of teeth in the Chinese clevo-saur skulls is uncertain because of their incompleteness but *C. mcgilli* has at least five large additional teeth on the dentary and *C. wangi* most probably four, followed by smaller teeth (Wu 1994). This resembles the condition of six large teeth followed by one or two smaller ones in *C. convallis*. The shape of the large flanged teeth, especially the length of the flanges, appears to be similar in *C. convallis* and the Chinese clevo-saurs, as the flanges seem shorter than in *C. hudsoni* (Wu 1994), but the poor preservation of dentary teeth in the Chinese specimens makes this feature uncertain. The anterior dentition is also poorly preserved in the Chinese specimens, but *C. mcgilli* lacks successional teeth on the maxilla, a feature that is shared with *C. convallis* but not with *C. hudsoni* (Fraser 1988; Wu 1994). However, there are also differences. There are two premaxillary teeth in

C. mcgilli (unknown in the other Chinese clevo-saurs; Wu 1994), but 3–4 in *C. convallis*, *C. hudsoni* and *C. minor* (Fraser 1988). The palatines of *C. convallis* and *C. hudsoni* are nearly identical, with straight tooth rows of six teeth raised on a bony ridge, and with tooth size increasing anteriorly, whereas *C. mcgilli* has seven teeth of equal size and *C. wangi* and *C. petilus* have very curved palatine tooth rows (Fraser 1988; Wu 1994).

Similarly, comparison with *Clevo-saurus bairdi* from Nova Scotia (Sues *et al.* 1994; pers. obs. on NSM 988GF2.1) reveals that it shares some features with *C. convallis*. Like *C. convallis*, *C. bairdi* lacks successional teeth on both dentary and maxilla (Sues *et al.* 1994), and in both species the dentary seems to be deeper than that of *C. hudsoni* (Fraser 1988). However, *C. bairdi* has only three large and perhaps no small additional dentary teeth (pers. obs. on NSM 988GF2.1 and 988GF4.1) and a single large premaxillary tooth (Sues *et al.* 1994), both conditions very different from *C. convallis*. Additionally, the anterior teeth of *C. bairdi* become completely worn away early in ontogeny (Sues *et al.* 1994), whereas in *C. convallis* the teeth remain visible (at least on the dentary). In summary, *C. convallis* shares several features with other clevo-saur species but with the available jaw material it is difficult to determine which is its sister species. The unique features of *C. convallis* are the short nasal process of the premaxilla and the six large additional teeth on both the dentary and the maxilla.

CONCLUSION

The reptilian fauna of Pant 4 fissure of St. Bride's Island is diverse, consisting of *Clevo-saurus convallis* and possibly another sphenodontian (sphenodontian *incertae sedis*), several different archosaurs, possibly including a pterosaur, a sphenosuchid crocodyliform and a small theropod dinosaur (Säilä, in prep.), one or more species of the tritylodontid *Oligokyphus* (Pacey 1978; I. Corfe, in prep.) and *Gephyrosaurus bridensis* (Säilä, in prep.). In addition to the reptiles, Pant 4 yields the mammals *Kuehneotherium praecursoris*, *Morganucodon watsoni*, a larger morganucodontid and haramiyids (Pacey 1978). It is therefore clear that the fauna of St. Bride's Island was not depauperate, as suggested by Fraser (1989).

The new sphenodontian, *Clevo-saurus convallis*, represents the first record of the genus *Clevo-saurus* in the Jurassic of Britain. Furthermore, the faunal components of St. Bride's Island (namely *Oligokyphus*, *Morganucodon*, crocodyliform archosaurs and *Clevo-saurus*) are comparable with other contemporaneous assemblages in North America, China and South Africa, lending further support to the idea of an unusually homogeneous composition of continental tetrapod communities globally during the Early Jurassic (Sues and Reisz 1995).

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