



# A distinctive Late Triassic microvertebrate fissure fauna and a new species of *Clevosaurus* (Lepidosauria: Rhynchocephalia) from Woodleaze Quarry, Gloucestershire, UK

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## ABSTRACT

During the Late Triassic and Early Jurassic, diverse terrestrial vertebrates were preserved in fissures formed in Carboniferous Limestone on an island archipelago spanning from the south of Wales to the north and south of Bristol. Here we report the faunas of two new fissures in Woodleaze quarry, near to Tytherington quarry, where the vertebrate fauna is already well known. The new site extends the lateral distribution of fissures in this vicinity to over 900 m, and fissures sampled along that transect show a southerly change in the dominant species and a reduction in diversity. The Woodleaze fissure fauna is nearly monofaunal, comprising >98% of a new *Clevosaurus* species, as well as some *Diphydontosaurus* fragments, a possible undescribed lepidosaur and a few fish fossils. The new clevosaur is distinguished from the type species *Clevosaurus hudsoni* by its dentition, and by being smaller (average long bones are 40–80% the length of *C. hudsoni*). In addition, the collection also includes individual skeletal elements that were not previously well described, thus expanding our knowledge of clevosaur anatomy. The Woodleaze bones are preserved as black or dark grey, rather than white, and this preservation mode and single-species dominance occurs elsewhere only in the Windsor Hill fissure where *Oligokyphus* predominates. Together with Tytherington, this location offers an exceptional opportunity to study a Triassic terrestrial biota across an extended distance, and to compare near-littoral niches with more inland island habitats.

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## 1. Introduction

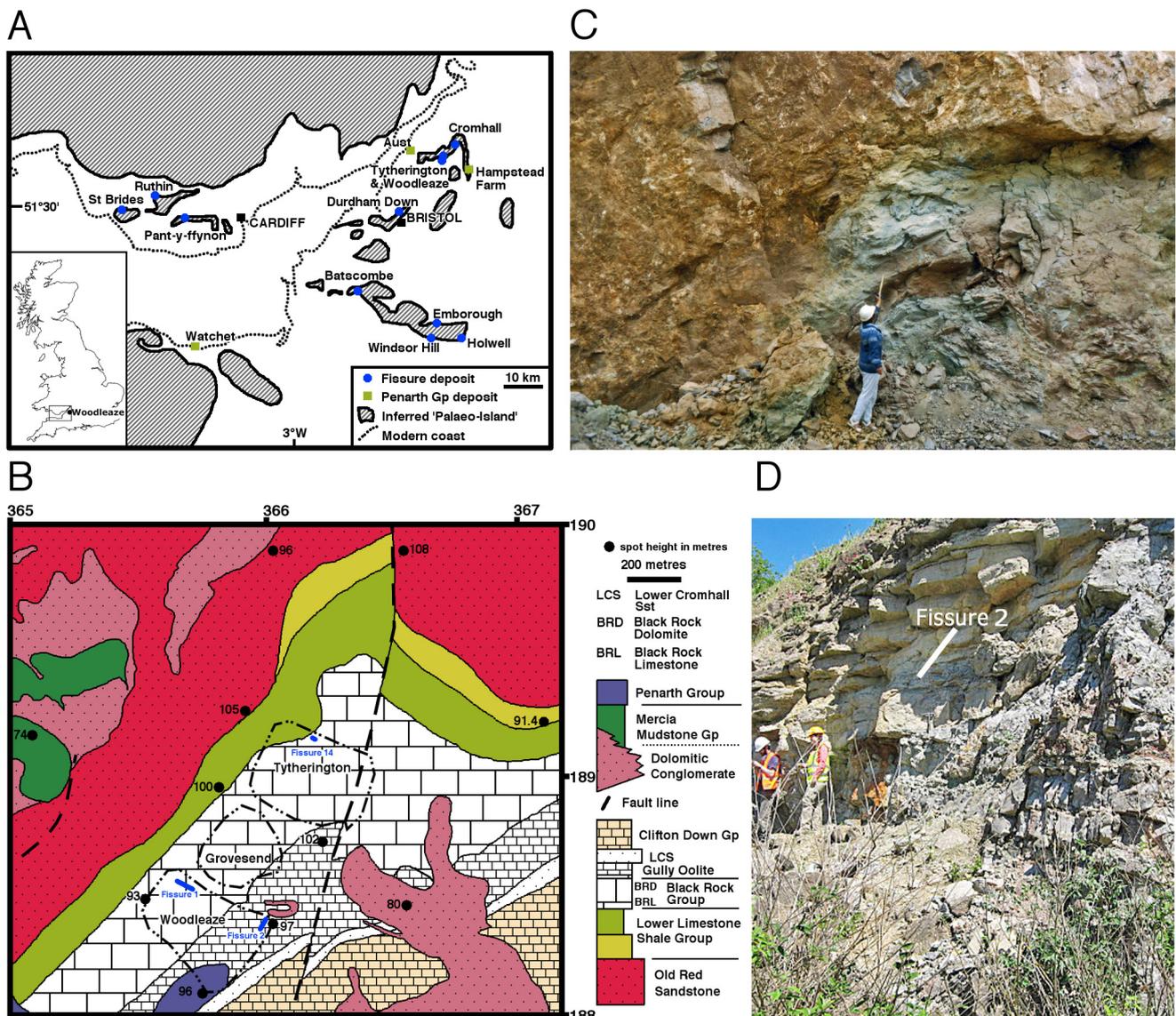
Upper Triassic and Lower Jurassic fissures in South Wales and in the region around Bristol have yielded internationally important terrestrial reptiles and mammalian morphs that shed light on the origins of both clades (e.g. Evans, 1980; Whiteside, 1986; Gill et al., 2014). The Upper Triassic fissure deposits to the north of Bristol have yielded reptiles such as the sauropodomorph dinosaur *Thecodontosaurus* and the rhynchocephalians *Clevosaurus*, *Diphydontosaurus* and *Planocephalosaurus*. The fissures formed by solution, and were filled by sediments in an archipelago (Fig. 1A) of limestone and sandstone palaeo-islands (Robinson, 1957; Whiteside and Marshall, 2008). The principal tetrapod-yielding localities are Tytherington quarry (Whiteside, 1983; Whiteside and Marshall, 2008; Van den Berg et al., 2012), Cromhall

(Fraser, 1994) and Durdham Down (Foffa et al., 2014). The chronological succession of the fissures is not certain, but the most common view is that the earliest tetrapod biota consisted of reptiles only, and therefore these fissures were termed 'sauropsid', whereas the younger deposits include mammalian morphs such as *Morganucodon* and *Oligokyphus* (Robinson, 1957).

The fissures around Bristol are noted for their documentation of early rhynchocephalians. This group of lepidosaurian reptiles is known today only from *Sphenodon*, the New Zealand tuatara, often termed a 'living fossil' because it is apparently the solitary surviving genus from a lineage that extends back to the Late or Middle Triassic (Jones et al., 2013), and has seemingly changed little morphologically. The epithet 'living fossil' is misleading, and has been disputed (Whiteside, 1986; Meloro and Jones, 2012). The Bristol fissure rhynchocephalians were first notified by Swinton (1939), who reported the type species of *Clevosaurus*, *C. hudsoni*, from Cromhall quarry, and the extensive material was described by Fraser (1988). The genus is now known from Durdham Down (Foffa et al., 2014), Cromhall, Tytherington, Emborough, Highcroft

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**Fig. 1.** Geology of Woodleaze quarry. (A) Palaeogeographical map of the Bristol area in the Late Triassic showing fissure deposits and inferred palaeo-highs with superimposed modern geography. Modified from Whiteside and Marshall (2008). (B) Simplified geological map of Tytherington and Woodleaze quarries. Geology mapping and column derived from BGS map 264. Modified from Whiteside and Marshall (2008). (C) Photograph of fissure 1 with Jennifer Rogers indicating the position of the fossils in the cavernous void. (D) Photograph of fissure 2 showing linear morphology of the deposit.

(Whiteside and Marshall, 2008) and Holwell (Fraser, 1994), all near Bristol; it is also probably present in the 'sauropsid' fissures of Ruthin and Pant-y-ffynon in South Wales (Fraser, 1994). *Clevo-saurus* is additionally found in the presumed Lower Jurassic mammalian-bearing fissures of St. Brides palaeo-island (Säilä, 2005; Whiteside and Marshall, 2008). In addition, further species of *Clevo-saurus* have been reported from the eastern United States, Canada, South Africa, Brazil, Luxembourg, Belgium, and China, from similarly aged latest Triassic and earliest Jurassic sediments. The Bristol fissures have also yielded abundant remains of other rhynchocephalian taxa, such as *Planocephalosaurus* and *Diphydontosaurus* (Fraser, 1982; Whiteside, 1986; Fraser, 1994).

Here we describe microvertebrate material recovered from a new quarry within the Tytherington quarry complex: Woodleaze quarry. These were collected in 1989, and we have since been able to examine and prepare the specimens as well as visiting Woodleaze on a number of occasions to find more fossils.

Institutional abbreviations: BRSMG, Bristol City Museum and Art Gallery collection; BRSUG, Bristol University, School of Earth Sciences collection; NHMUK, Natural History Museum, London.

## 2. Geological setting

Woodleaze quarry is the southernmost, and most recently excavated, of a three-quarry complex that lies to the west of the village of Tytherington and east of the town of Thornbury, South Gloucestershire (Fig. 1B). The most northerly, Tytherington quarry, is the location of the find of the 'Bristol dinosaur', *Thecodontosaurus antiquus*, in 1975 by the amateur geologists Mike Curtis and Tom Ralph (Whiteside, 1983; Benton et al., 2000, 2012; Whiteside and Marshall, 2008). The middle and oldest quarry, Grovesend, has not yielded any Triassic fossils, perhaps because the fissure infillings were largely eroded away before fieldwork started in the mid-1970s.

The location of Woodleaze, about 400 m to the south of the margin of Tytherington quarry, significantly increases the sampled area of fissures in these Carboniferous Limestones. Whiteside and Marshall (2008) noted that the proportions of the rhynchocephalians *Planocephalosaurus*, *Diphydontosaurus* and *Clevo-saurus* changed from the north-west to south-east of Tytherington quarry, with the south-easternmost fissures yielding only *Clevo-saurus* and

*Diphydontosaurus*. These authors also noted that fissures where *Planocephalosaurus* is the dominant sphenodontian, namely in the fissures at Cromhall quarry and in fissure 14 at Tytherington, have the greatest diversity of tetrapods. Examining the fossils from Woodleaze quarry enables a further scrutiny of the line of trend, which is extended from 450 m within Tytherington to over 900 m.

The field relationships of the fissures in Woodleaze are similar in some key respects to those in Tytherington quarry; both have cavern development (Fig. 1C) in the massive Black Rock Limestone which succeeds the Lower Limestone Shales. Also, both show Carboniferous Limestone dipping at about 22° or more towards the south-east. However there are differences; for example, the eastern part of Woodleaze lies in the Gully Oolite in which we have found fissure deposits that linearly follow the bedding planes of the host Carboniferous Limestone (Fig. 1D). There is only a very modest expansion of the void in this outcrop and nothing comparable to the caverns developed in the Black Rock Limestone, figured by Simms (1990) from the west of Woodleaze, or by Whiteside and Robinson (1983) from Tytherington quarry. The mapped geological relationships of the fissures are similar overall to those at Tytherington reported by Whiteside and Marshall (2008) and at Durdham Down by Foffa et al. (2014). Evidence for the dissolution process that formed the Woodleaze fissures includes a single heavily weathered chimaeroid ('bradyodont') tooth derived from the surrounding Carboniferous Limestone.

The rocks from fissures 1 and 2 at Woodleaze differ in variety from Tytherington. The Tytherington fissures include conglomerates, breccias, and recrystallised limestones, as well as calcareous red, green and black mudstones and sandstones. Tetrapod bones are found mainly in conglomerates in the Tytherington fissures, such as those described by Van den Berg et al. (2012). The Woodleaze deposits are more consistent, comprising bedded green, yellow and (some) red calcareous mudstones or siltstones. The rock from fissure 1 at Woodleaze also contains significant quantities of gypsum. Importantly, the bones of the rhynchocephalian *Clevosaurus* from the Woodleaze fissures are almost always black or dark grey in colour, which indicates deposition in an anoxic environment such as that described by Macquaker (1999) for the marine Westbury Formation. The suggestion is also in accord with the presence of black bones of *Oligokyphus* found in Windsor Hill fissure, ascribed to deposition in a marine environment by Kühne (1956). Black bones of terrestrial tetrapods are known from Tytherington quarry, but are most abundant in the southern part, particularly from fissures 12 and 16 of Whiteside and Marshall (2008). Whiteside and Marshall (2008) proposed that the Cromhall palaeo-island in the vicinity of Tytherington would have had anoxic conditions around the halocline, and we suggest that the bones in the Woodleaze fissures were deposited under similar conditions.

We interpret the Woodleaze fissures as broadly contemporaneous with the others in the Tytherington quarries complex, and this relies on direct and circumstantial evidence of geological age, as well as the detailed overview of local topography that indicates the fissures formed in a limestone island emerging from the early Rhaetian sea. For all these fissures, the surface of the host Carboniferous Limestone lying directly above is near to or at a higher altitude than the nearest outcrop of the bedded, marine Westbury Formation of the Penarth Group. Preserved scree deposits, the Dolomitic Conglomerate, which are the products of the eroded Triassic limestone hills, lie close to the quarries and on the eastern downslope side of the Carboniferous Limestone.

Dissolution and karstification of the Carboniferous Limestone around Bristol predominantly took place in the early Rhaetian (Whiteside and Marshall, 2008) based on two lines of evidence. First, early Rhaetian palynomorphs have been identified from fissure sediment fills at Tytherington (Marshall and Whiteside, 1980;

Whiteside and Marshall, 2008). We searched for palynomorphs in the Woodleaze sediments, but so far found none. Second, seawater around the palaeo-island is required to maintain cavernous fissures. The cavernous fissure 1 (Fig. 1C) indicates that the palaeo-island possessed a freshwater lens, and such large voids formed in either the body of the lens or in a fluctuating freshwater/saline water mixing zone around the halocline (Whiteside and Marshall, 2008). To maintain the freshwater lens the sea level would have had to be high, and this points to the Rhaetian transgression at the time of the Westbury Formation, thus giving a date of early Rhaetian for the formation of the cavern.

The Woodleaze fissure reptile-bearing beds lie approximately 12 m below the base of the nearest outcrop of the marine Westbury Formation, and we have found a few fish elements associated with the *Clevosaurus* bones. This suggests that the anoxic conditions during deposition of the bones were similar to features of the palaeoenvironment described for Tytherington by Whiteside and Marshall (2008), which resulted from a saline water intrusion from the Rhaetian sea into the Carboniferous Limestone.

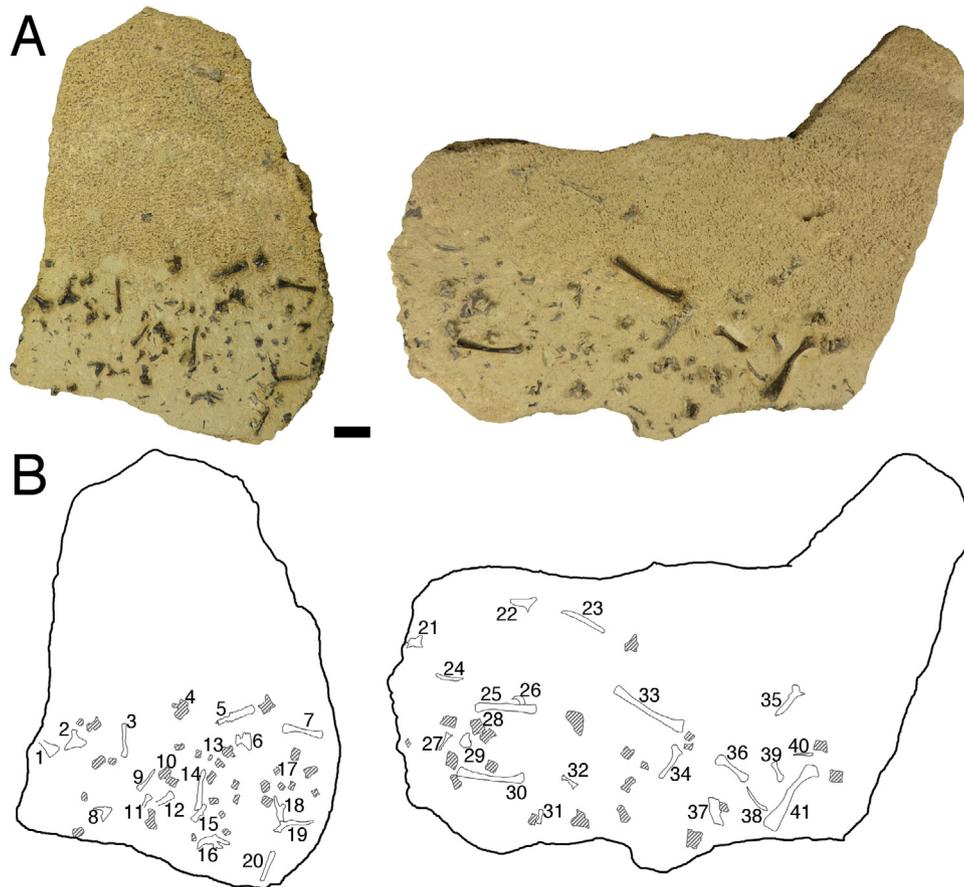
The field relationships of the nearest Penarth Group outcrop to Woodleaze quarry suggest that the reptiles lived on the marginal edge of the land. The modern day topography in the Bristol area is regarded as essentially an exhumed Triassic landscape (Robinson, 1957), and the Carboniferous Limestone of Woodleaze quarry would have formed the margin of the small 'Cromhall palaeo-island' in the early Rhaetian (Fig. 1A). The highest areas of this palaeo-island lay to the north and the immediate west, with steep slopes to the east and further west (Fig. 1B) that would have been inundated by the Rhaetian sea. Tytherington quarry Carboniferous limestones would have formed slightly higher land further from the shoreline of the Rhaetian sea, whereas the Woodleaze limestones formed a land surface closer to that sea.

### 3. Materials and methods

#### 3.1. The rocks and fossils

Material from the original fissure 1 was collected by Chris Alabaster, Liz Loeffler, Andrew Hook and Jennifer Rogers in 1989. The fissure had been exposed just two weeks prior to collection. More material was collected later in 1989 by Mike Simms and colleagues and was given to BRSMG in 1994. That material appears to have come from the lower boundary of fissure 1 (Fig. 1C), and although a long bone was manually prepared, little more was processed, as sufficient material had been prepared from the BRSMG collection. Several trays of fossiliferous Woodleaze rock remain for comparative and reproducibility purposes in BRSMG and BRSUG. The microvertebrate fossils are mostly *Clevosaurus* sp., but fragments of *Diphydontosaurus avonis* and a possible new lepidosaur named lepidosaur B by Whiteside (1983) were also found. Whilst two of the rocks from the sample showed a particularly high concentration of fossiliferous material (Fig. 2), the long bones on these slabs revealed that the bones come from a number of individuals through variation in length of comparable bones. Hence, the carcasses must have undergone some transport and mixing after becoming disarticulated, although the transport distance following disarticulation may have been short. Some preferential orientation can be seen when observing the long bones, revealing a likely influence by water at the time of deposition. The fissure 1 material represents three or four individual *clevosaurs*.

Material from the currently exposed fissure 2 (Fig. 1D) was collected in 2012 by Pedro A. Viegas and David I. Whiteside. The faunal assemblage, despite being found more than 100 m away, is almost the same as that of fissure 1, as is the rock type. This is an extremely unusual finding, as nearby fissures in Tytherington (Whiteside and Marshall, 2008) and other localities such as Cromhall (e.g. Fraser, 1994), differ greatly in the species present



**Fig. 2.** The fossiliferous material from Woodleaze; left BRSUG 29381-1, right BRSUG 29381-2. (A) Photographs of the two most fossiliferous slabs from fissure 1, showing some preferred orientation of long bones. (B) Diagrammatic representations of the slabs, highlighting the range of bones preserved: (1) tibia fragment; (2) pterygoid flange; (3) humerus; (4) dorsal vertebra; (5) pterygoid; (6) pterygoid flange; (7) humerus; (8) jugal or squamosal; (9) fibula, proximal end; (10) cervical vertebra; (11) tibia?; (12)?; (13) mid-caudal vertebra; (14) femur; (15) ischium; (16) pterygoid; (17) end-caudal vertebra; (18) ilium; (19) pterygoid; (20) long bone fragment; (21) dentary; (22) postorbital or prefrontal; (23) prearticular?; (24) long bone fragment; (25) femur; (26) claw; (27) cervical rib; (28) cervical vertebra; (29) nasal; (30) tibia; (31) long bone fragment; (32) tarsometatarsal; (33) tibia; (34) humerus; (35) pterygoid; (36) humerus; (37) ilium; (38) clavicle; (39) metacarpal; (40) rib; (41) femur. All shaded specimens are vertebrae, most of which are caudal. Scale bar equals 1 cm.

and their relative abundances. The similarity of the tetrapod faunas in fissures 1 and 2 at Woodleaze suggests that the assemblages are coeval. Further material from fissure 2 was collected by David I. Whiteside, Victor Selles de Lucas and Pedro A. Viegas in 2013. These samples proved to be fossil-poor, yielding only three fossils. Subsequent visits in 2014 with students from Bristol University did not yield any further bone-bearing matrix from this fissure. The fissure 2 clewsaur material may well come from a very few individuals.

### 3.2. Rock and fossil processing

Preparation followed the methods described in [Viegas and Benton \(2014\)](#). Any exposed bones were cleaned with acetone and a pin vice. The brittle specimens were then coated with a thin layer of 5% by volume Paraloid™ B-72 solution (B72). This coating kept the fragile material intact throughout the acid cycling and sieving steps, consolidating the bones as well as preventing the acid from etching them from the inside.

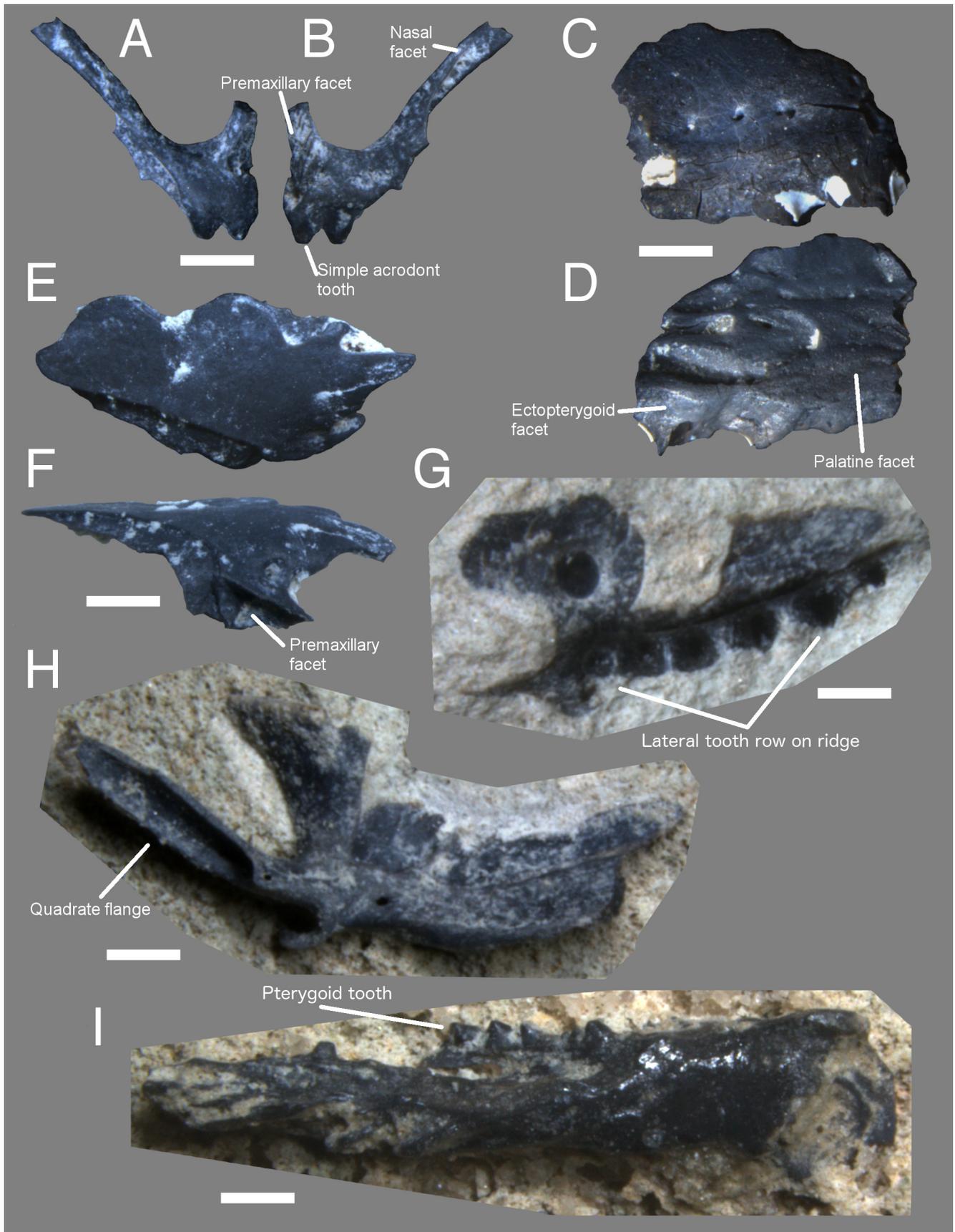
The bulk samples were put in separate buckets for easier handling. The buckets were filled with a 5% acetic acid solution, buffered with tri-calcium orthophosphate to prevent acid digestion of fossil material. After two days in the acid solution, the acid was drained as much as possible whilst leaving loosened fossils and sediment. The samples were then rinsed three to four times, depending on the sample size and amount of loose sediment, before being immersed in the neutralising solution. This consisted

of water and a small amount of alkaline dishwashing soap. They were then left for at least twice the number of days they had spent in acid to make sure all the acid was fully neutralised.

To recover the microfossil-rich sediments, five sieves with mesh sizes ranging from 1180 to 63  $\mu\text{m}$  were used. Sediments from the different mesh fractions were transferred to fine filter papers standing in funnels to allow for rapid drying. A minimum amount of interference with the brush was used to reduce the amount of mechanical stress on the fossils, and the sediment was then left to completely dry. Once dry, the sediment was poured into small crystal polystyrene (Styron 678E) lidded boxes.

If any rock was seen still to be fossiliferous, freshly exposed fossils were micro-prepared using a binocular microscope and a pin vice. Once the surface was cleared of debris, the fossils were cleaned with acetone and thinly coated with B72. This was done before putting the rock through a new acid cycle.

We wish to caution future researchers working on similar material. A preliminary study was conducted by Whiteside in 2007 using formic acid instead of acetic acid. This stained the enamel from black teeth white, and caused greater fragility and cracking in the specimens. The effects can be seen in [Fig. 3C](#). Furthermore, Paraloid™ B72 should be left to fully cure before being exposed to acid (usually overnight suffices), or the interaction of the poorly cured consolidant with the acidic solution will cause it to become opaque, as seen in [Fig. 6S](#). This makes it difficult to monitor the specimen and the amount of etching occurring around it.



**Fig. 3.** Jaw elements and snout bones of *Clevosaurus sectumsemper*. (A and B) BRSUG 23381-9, right premaxilla in anterior (A) and posterior (B) views; (C and D) BRSUG 29381-11, posterior fragment of left maxilla in lateral (C) and medial (D) views; (E and F) BRSUG 29381-15, right nasal in dorsal and lateral views; (G) BRSUG 29381-3, right palatine in ventral/occlusal view, showing row of six teeth and anterior single tooth medially; (H) BRSUG 29381-1, right pterygoid in ventral view; (I) BRSUG 29381-1, right pterygoid in medial view. Scale bars equal 1 mm.

### 3.3. Identification and photography

Collected sediment was spread onto a standard microfossil grid, and every fossil observed through a binocular microscope was hand-picked. Unidentifiable fossils were grouped roughly according to morphotype, whilst identifiable fossils were placed into separate Styron boxes. To reduce damage from the rattling of fossils in their separate boxes, thin layers of conservation-grade Plastazote<sup>®</sup> were cut out to fit the boxes using the custom-made tool and padding system developed and described by Viegas and Clapham (2012), and placed above and below the specimens. To prevent crushing of the fossils by the Plastazote<sup>®</sup>, a pin vice under a binocular microscope was used to carve an area with the approximate shape of each specimen in the foam, this would allow for a custom snug fit of each individual bone into its protective housing. The boxes were subsequently arranged by bone type, and are stored as part of the BRSUG collection.

Pictures of key specimens were taken using a Leica 205C stereomicroscope with the Leica Application Suite LAS v3.7 software that produces automatic stacking microphotography. Despite the dark colour of the fossils, using a light background was not possible, as articulation surfaces were blended out. A glass background with no lighting from below was used instead. Backgrounds were removed from the fossil photographs using Adobe Photoshop<sup>®</sup>, and the specimen images were moved to a light grey background to optimise visibility of both dark pits and bright articulation surfaces.

The maximum length of complete long bones was measured using a digital vernier caliper. Whilst measurements were given in millimetres to two decimal places, the values were rounded up to one decimal place. This is because the calliper was applied loosely, in order to prevent the delicate fossils from shattering, which might have happened if we had closed the calliper more tightly.

### 3.4. Fossils

The processed rocks yielded over 4100 fossil elements with unidentifiable bone shards predominant. The 504 identifiable fossils (417 in fissure 1, 87 in fissure 2; including reworked material and wood) comprise 474 *Clevosaurus* elements, revealing the near complete monofaunality of the sites.

### 3.5. Comparative study

We compared the new rhynchocephalian fossils with published data on other Late Triassic and Early Jurassic materials, as well as personal inspection. In addition, we studied specimens of the modern tuatara, *Sphenodon*, NHMUK 1861, NHMUK1985.212, NHMUK Unnumbered (Oct. 1828), BRSMG Aa 3831, and BRSUG Ost111.

## 4. Systematic palaeontology

### 4.1. *Clevosaurus sectumsemper* sp. nov

Superorder: Lepidosauria Duméril and Bibron, 1839 (sensu Evans, 1984)

Order: Rhynchocephalia Günther, 1867 (sensu Gauthier et al., 1988)

Suborder: Sphenodontia Williston, 1925 (sensu Benton, 1985)

Family: Clevosauridae (sensu Bonaparte and Sues, 2006)

Genus *Clevosaurus* Swinton, 1939

Type species. *Clevosaurus hudsoni* Swinton, 1939

Included species. *C. minor* Fraser, 1988; *C. bairdi* Sues et al., 1994; *C. latidens* Fraser, 1993; *C. convallis* Säilä, 2005; *C. brasiliensis* Bonaparte and Sues, 2006, and possible species *C. wangi*, *C. mcgilli* and *C. petilus* Wu, 1994.

**Remarks.** The premaxilla of *Clevosaurus* has a lateral forked flange that connected with the nasal and excluded the maxilla from the posterior margin of the external naris (Fraser, 1988). As pointed out by Säilä (2005) and Jones (2006a), this feature had been considered diagnostic of *Clevosaurus* (Sues et al., 1994; Wu, 1994) but is also present in *Pamizinsaurus* (Reynoso, 1997) and *Godavarisaurus* (Evans et al., 2001).

Most cladograms produced by recent authors (e.g. Rauhut et al., 2012) demonstrate that clevosaurs form a distinct clade, although *Clevosaurus latidens* may pair with opisthodontians (e.g. Martínez et al., 2013). The apomorphic features described by Bonaparte and Sues (2006) to diagnose the Clevosauridae are: length of antorbital region one-quarter or less of total skull length; length of lower temporal fenestra more than one-quarter of skull length; anterior (premaxillary) process of maxilla small or absent. Jones (2006a) added: the presence of a lateral ectopterygoid-palatine contact that excludes the maxilla from the suborbital fenestra, and a jugal with a long dorsal process that extends far enough backward to contact the squamosal.

We cannot use many of these features, as the bones from Woodleaze are disarticulated and do not include the anterior part of the maxilla. However, the maxillary facet of the premaxilla (on the left side of Fig. 3A) demonstrates that the anterior process of the maxilla is the same as that found in *C. hudsoni*. The posterior part of the maxilla shown in Fig. 3D displays ectopterygoid and palatine facets of the same type as *C. hudsoni* (see Fraser, 1988, Fig. 6). There are, however, many dental features, notably the flanges on the maxillary and additional dentary teeth, development of premaxillary teeth, as well as conical palatine teeth with an isolated tooth lying medially to the anterior of the lateral row, which are characteristic of *Clevosaurus* species and especially the type species *C. hudsoni*.

*Clevosaurus sectumsemper* sp. nov.

**Derivation of species name.** Latin meaning 'always cut', an allusion to the self-sharpening teeth that remain sharp by cutting against each other and the lower jaw throughout the animal's life.

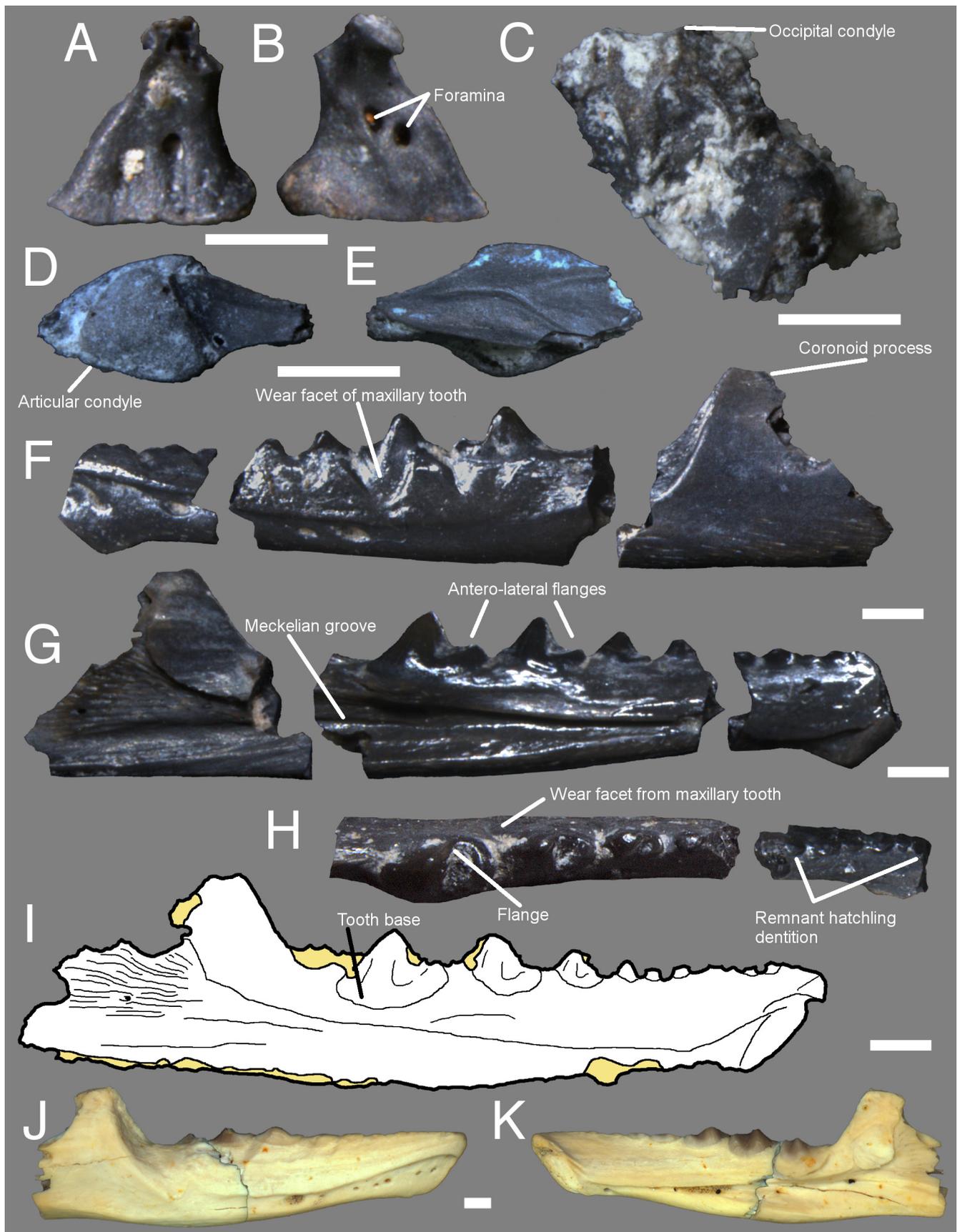
**Holotype.** A left dentary, showing additional teeth each with a more ventral base in a progressively posterior position. BRSUG 29381-56

**Referred specimens.** Many of these specimens are on two slabs, numbered BRSUG 29381-1 and BRSUG 29381-2, both from fissure 1. The BRSUG 29381 numbers refer to fissure 1 material, whereas BRSUG 29382 numbers refer to fissure 2 material. Right premaxilla (BRSUG 29381-9); right maxilla (BRSUG 29381-11); right palatine (BRSUG 29381-3); right nasal (BRSUG 29381-15); right pterygoid (BRSUG 29381-1); humeri (BRSUG 29381-2); radiale (BRSUG 29381-85); ulnare (BRSUG 29382-20); claw (BRSUG 29381-87); ilium (BRSUG 29381-69); pubis (BRSUG 29382-16); femur (BRSUG 29381-2); tibia (BRSUG 29381-2); vertebrae (BRSUG 29381-1); 5th metatarsal or tarsometatarsal (BRSUG 29382-23).

**Type locality and horizon.** Rhaetian fissure fill in Lower Carboniferous Limestone, Fissure 1 in Woodleaze Quarry, South Gloucestershire (NGR ST 657 886).

**Diagnosis.** Distinguished from other *Clevosaurus* species by five characters: (1) caudad, the additional teeth bases on the dentary are more ventrally positioned with the final tooth base close to the upper edge of the Meckelian groove (see Fig. 4G and I); (2) the pronounced antero-lateral flanges do not overlap or barely overlap the posterior flanges of the preceding tooth on the dentary (Fig. 4G and H); (3) the premaxillae each have two or three teeth (Fig. 3A and B), compared to the three or four of *C. hudsoni*; (4) a premaxillary chisel structure is not observed in any specimen; and (5) all the bones are small, no more than 80% the size of those in *C. hudsoni*.

**Remarks.** *Clevosaurus sectumsemper* differs from other *Clevosaurus* species in a number of unique features or a combination of



**Fig. 4.** Brainscase and mandibular elements of *Clevosaurus sectumsemper*. (A and B) BRSUG 29381–48, right exoccipital in postero-lateral (A) and antero-medial (B) views; (C) BRSUG 29381–51, basioccipital in dorsal view; (D and E) BRSUG 29382–14, left articular in dorsal-lateral (D) and ventral (E) views; (F to H) BRSUG 29381–56 left dentary in lateral (F) and medial (G) occlusal view of middle and anterior region (H); reconstruction (I); (J and K) reconstructed right dentary of *Clevosaurus* sp. from Tytherington in lateral (J) and medial (K) views. Scale bars equal 1 mm. Specimens in J and K from Van den Berg (2012).

features. The tail-ward sequence of increasingly more ventral bases of the additional teeth of the dentary (Fig. 4I) is a particular characteristic of the species. The pronounced antero-lateral flanges of the dentary additional teeth are similar to those that were otherwise unique to *C. hudsoni* (Jones, 2006a) but do not overlap the preceding tooth as in that species; indeed there are pronounced gaps between the last four teeth (Fig. 4F and G); like *C. hudsoni* (Jones, 2006a), the new species has dentary teeth that noticeably increase in size posteriorly. It has two to three premaxillary teeth unlike the three to four of juvenile and sub-adult *C. hudsoni*, but does have the distinct dorso-posterior flange that contacts the maxilla and nasal of that species, excluding the maxilla from the external naris. We have found no evidence of even a partial development of the premaxillary 'chisel' tooth formed on each premaxilla by overgrowth of bone and dentine in all other clevosaurus; this includes worn specimens.

The lateral edge of the palatine of *C. sectumsemper*, *C. hudsoni* (Fraser, 1988), *C. convallis* (Säilä, 2005) and *C. mcgilli* (Wu, 1994) is relatively straight compared to that of *C. wangi* and *C. petilus*, where it is noticeably curved (Wu, 1994; Jones, 2006a). The number of teeth in the palatine row is five or six in *C. hudsoni* and *C. convallis*, six in *C. sectumsemper* (Fig. 3G) and possibly *C. petilus* (Wu, 1994). It is at least seven in *C. mcgilli* and over eight in *C. wangi* (Wu, 1994) and *C. brasiliensis* (Bonaparte and Sues, 2006). The palatine teeth are emplaced on a ventral ridge in *C. sectumsemper* and in *C. hudsoni*, but not in *C. minor* (Fraser, 1988). The dentary teeth of *C. latidens*, which may not even be a clevosaur (Jones, 2006a), are much broader than in *C. sectumsemper*.

Calculations of skull length using ratios found in *C. hudsoni* (Fraser, 1988) and based on the dentary, maxilla and palatine indicate that *C. sectumsemper* from Woodleaze ranged from 1.4 cm to 1.8 cm. This is smaller than *C. minor* from Cromhall described by Fraser (1988), which had an estimated skull length of about 2 cm. The dentary of another example (Fig. 4J and K) from fissure 2 in Tytherington indicates a skull length of approximately 2.4 cm.

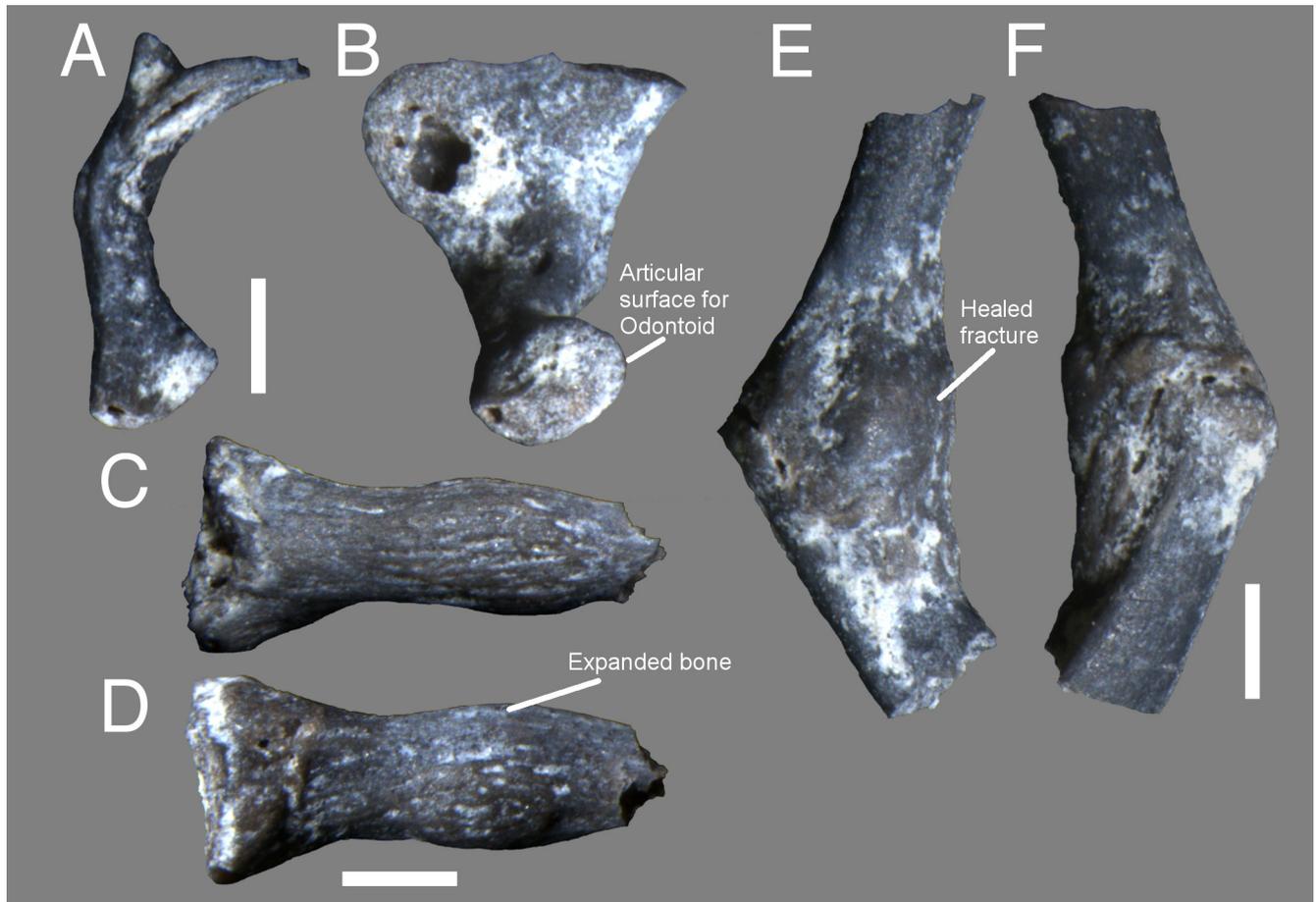
Calculations using proportions found in *C. hudsoni* (Fraser, 1988) based on head length to body length ratio and an average of body length predicted from average lengths of humeri and femora suggest that *C. sectumsemper* had a mean size of about 11 cm (range 8.5–17.8 cm). This is just under half the length of adult *C. hudsoni* from Cromhall. It is therefore the smallest clevosaur known.

We consider the Woodleaze clevosaur to be an adult, despite its small size, because all specimens are the same size, with no larger examples at the site, and the jaws and teeth show wear, sometimes substantial wear, in similar distributions to what is seen in samples of *C. hudsoni*.

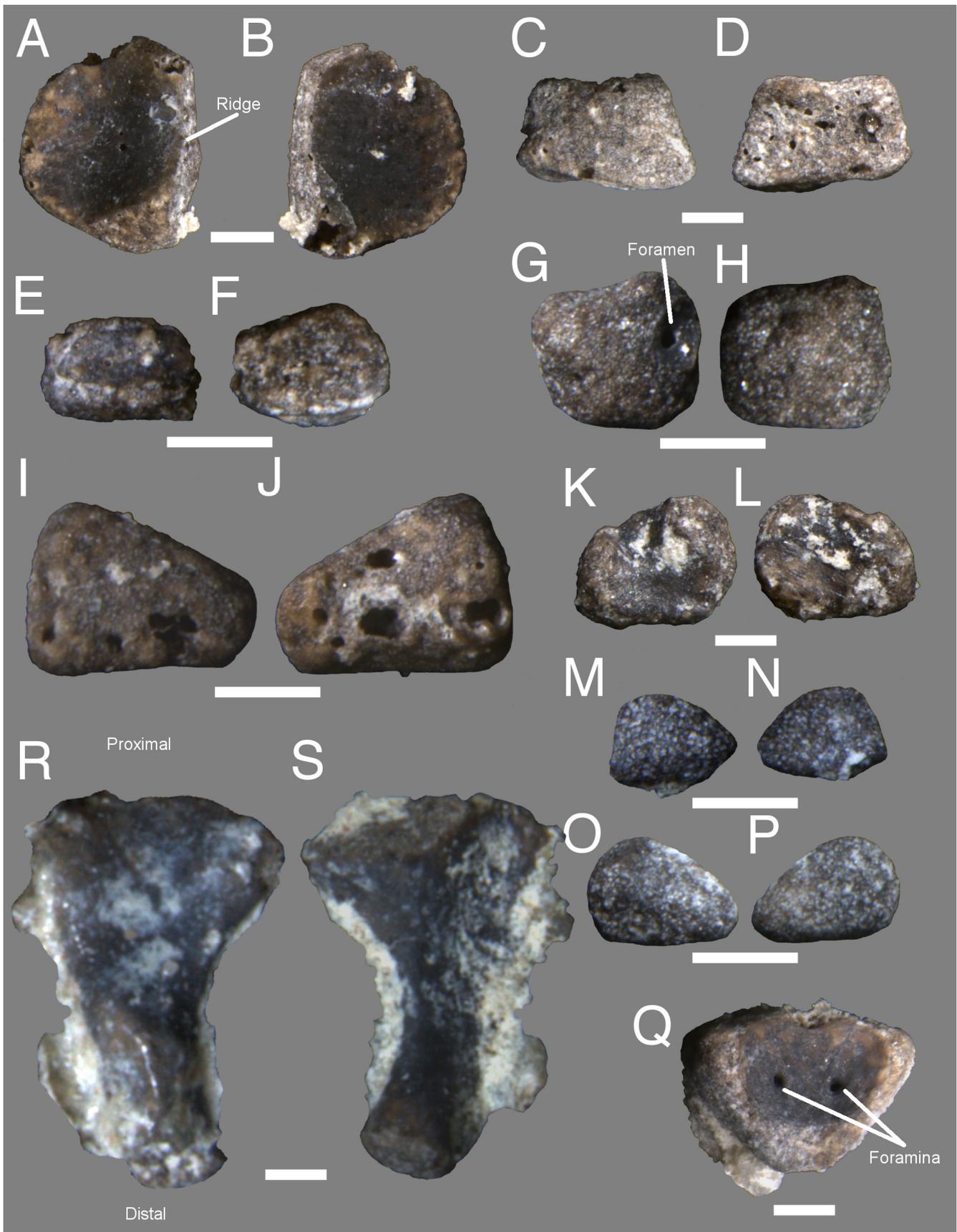
#### 4.1.1. Descriptions of bones

The type clevosaur, *Clevosaurus hudsoni*, was described in detail by Fraser (1988). Here we will focus on bones that are identifiable to genus or species level, and bones not treated in that paper but found in our study (Figs. 3–6).

Whilst the *Clevosaurus sectumsemper* fossils from Woodleaze are in many ways similar to *C. hudsoni*, some significant species-level differences were seen, particularly in terms of dentary dentition, the number of additional and premaxillary teeth and the



**Fig. 5.** Vertebral element and pathologies of *Clevosaurus sectumsemper*. (A and B) BRSUG 29381–61, atlas in posterior (A) and medial (B) views; (C and D) BRSUG 29381–94, metatarsal with pathology in two views (C) and (D); (E and F) BRSUG 29381–89, healed rib in medial (E) and lateral (F) views. Scale bars equal 500  $\mu\text{m}$ .



**Fig. 6.** Elements of the wrist and ankle of *Clevosaurus sectumsemper*. (A and B) BRSUG 29381-85, right? radiale in proximal (A) and distal (B) views; (C and D) BRSUG 29382-20, left ulnare in anterior (C) and posterior (D) views; (E and F) BRSUG 29381-82, distal carpal 3 in ?posterior (E) and ?anterior (F) views; (G and H) BRSUG 29382-19, distal carpal 4 in posterior (G) and anterior (H) views; (I and J) BRSUG 29381-80, distal carpal 5 in anterior (I) and posterior (J) views; (K and L) BRSUG 29381-76, left astragalocalcaneum in anterior (K) and posterior (L) views; (M and N) BRSUG 29381-81, ?distal tarsal 2 in two views (M) and (N) views; (O and P) BRSUG 29381-78, distal tarsal 3 in anterior (O) and posterior (P) views; (Q) BRSUG 29382-22, right distal tarsal 4 in dorsal (proximal) view; (R and S) BRSUG 29382-23, right tarsometatarsal in ventral (R; with an extensive B72 layer) and dorsal (S) views. Scale bars equal 500  $\mu\text{m}$ .

**Table 1**

Lengths of *C. sectumsemper* humeri, femurs and tibiae recorded from complete specimens from the sieved material, slabs BRSUG 29381-1 and 29381-2, and the BRSUG collection, their average lengths, and the average lengths recorded for *C. hudsoni* long bones (Fraser, 1988).

	Humerus	Femur	Tibia
Bone lengths recorded from complete specimens (mm)	8.6	19.1	19.2
	9.6	10.5	15.5
	8.5	8.4	–
	6.2	14.6	–
	–	25.6	–
Mean length in <i>C. sectumsemper</i> (mm)	8.2	15.6	17.4
Mean length in <i>C. hudsoni</i> (mm)	20.4	29.0	22.1

long bone mean length and size ranges (Table 1). Based on small long bones, small dentaries and maxillae, Whiteside (1983) recognised a small morph of *Clevosaurus* from Tytherington, which he termed *Clevosaurus hudsoni* var. *tytheringtonensis*. Specimens from this locality also have the characteristic two-to-three-tooth premaxilla and additional teeth dentition of *C. sectumsemper*, but the dentary is larger. It is possible that a specialist diet, a relative paucity of prey or genetic drift due to the isolation of island living resulted in selection for dwarfism, and the characteristic dentary and premaxillary dentition at Woodleaze. Furthermore, it should be noted that, analogously, a great deal of variation can be seen in dental elements of the extant *Sphenodon*, such as heavily worn versus prominent teeth.

#### 4.1.2. Cranial elements

The Woodleaze *Clevosaurus* premaxillae have two or three small teeth (Fig. 3A and B), a feature found in Tytherington specimens (see Whiteside, 1986, pl. 7) but in contrast with the three or four 'incisors' found by Fraser (1988) for *C. hudsoni* from Cromhall. Also, we have found no evidence of the development of a single chisel tooth such as that found in *C. hudsoni* and in Tytherington specimens (Whiteside, 1986, Fig. 32). The simple teeth at the front of the *C. sectumsemper* jaw would be ideal for puncturing and holding arthropod prey whilst the posterior maxillary and dentary teeth precision-sliced the exoskeleton in a scissor-like action, in contrast to the proal movement of modern *Sphenodon* (Jones et al., 2012) and as postulated for Early Jurassic *Gephyrosaurus* (Evans, 1980).

Maxillae are relatively rare and predominantly from older individuals with the teeth worn to the bone. One specimen (Fig. 3C and D) shows a posterior maxilla fragment with distinct foramina on the labial side above the teeth. As this specimen was prepared in formic acid, the enamel became stained white. On the medial side (Fig. 3D) the facets for the jugal, ectopterygoid and palatine are clearly seen. The enamel, stained white, was broken during preparation but the characteristic posterior flange on the maxillary teeth is visible, confirming the clevosaur identification.

A single complete nasal (Fig. 3E and F) has facets for both processes extending upwards from the pre-maxilla, behind which two foramina are situated. As described for *C. hudsoni* by Fraser (1988), the nasal continues for a short distance underneath the pre-maxilla and maxilla, whilst it overlaps with the frontal posteriorly.

Although no clear example of a *Clevosaurus* vomer was found, several examples of the palatine and pterygoid are present. The palatine (Fig. 3G) is identifiable through its row of relatively large, conical palatine teeth that sit on a ridge, and a single tooth located medially. A deep groove runs medially to the tooth row. In this specimen, the maxillary process could not be prepared out, but it would lie near the first two, and largest, teeth. The pterygoid (Fig. 3H and I) has two rows of smaller conical teeth, and a large, triangular flange that extends dorsally. Interestingly, BRSUG 29381-2 shows three relatively complete pterygoids and flanges, often preserved separately.

The exoccipital and basioccipital were found as discrete elements typical of *Clevosaurus* (Fraser, 1988) and these distinguish the specimen from the fused unit found in *Planocephalosaurus* (Fraser, 1982). The exoccipital (Fig. 4A and B) shows large foramina that would have transmitted the hypoglossal nerve. The dorsal view of the basioccipital (Fig. 4C) shows the exoccipital facets at the top and in the mid lower section. The middle section is a basin that formed the posterior floor of the braincase.

An almost complete left dentary from a probable young adult (Fig. 4F–H) shows about seven hatchling teeth, most being broken off at the tip, but not yet worn down. It also has four additional teeth with high crowns and the last tooth has the relatively undeveloped posterior flange found in adult *C. hudsoni*. In contrast to the tooth pit of a juvenile *C. hudsoni* described by Fraser (1988), where the fourth additional tooth would erupt, no tooth pit is seen here, thus suggesting that no more teeth will erupt. Unlike in the dentary of *C. wangi* and *C. petilus* (Wu, 1994), and *C. convallis* (Säilä, 2005), no further teeth are found posterior to the standard series of additional teeth. *C. mcgilli* (Wu, 1994) has five additional teeth, one more than the maximum found for *C. hudsoni* by Fraser (1988) and for *Clevosaurus sectumsemper*.

Despite the small size of the specimen, deep scouring of the teeth and jawbone on the lateral side of the dentary by maxillary teeth can be seen (Fig. 4F and H), and this reveals the immense precision and strength of the bite. The change in wear at particular places demonstrated by repeated cut marks, such as on and below the penultimate and most posterior tooth (Fig. 4F), provides a history of occlusion of the teeth during ontogeny. The teeth are sharpened by cutting against each other analogous to the function of mammalian carnassials (Whiteside, 1983; Jones, 2006b). The large forces that would have been produced by the apex of the cones with a broad base would have enabled prey such as arthropods, for example amphipods or isopods, with hard exoskeletons, and smaller sphenodontians, to be rendered into small pieces quickly. We postulate that the increasingly lower bases of the progressively more posterior additional teeth allowed, during maximum gape, a greater gap between the dentary and maxillary tooth crowns than would be expected for an animal of this size, particularly near the jaw articulation where the forces were greatest. Therefore this species could dismember larger prey than would otherwise be possible.

Although smaller, the specimen is strikingly similar to a dentary from Tytherington (Van den Berg et al., 2012; Fig. 4J and K). Another dentary fragment from Woodleaze is heavily worn but in a rounded way; the individuals appear to replicate some of the variation in wear found in the living tuatara, which has very different patterns in individuals of the same size (Robinson, 1976; Jones et al., 2012). The diet of the tuatara has been recorded to include crustaceans (Meyer-Rochow, 1988), insects, snails, small shore skinks, sea bird chicks and even rats (Robb, 1977). Having different preferential prey items explains the differential tooth wear found in our observations of the NHMUK individual tuataras.

The clevosaur articular (Fig. 4D and E) is distinguishable from that of some other sphenodontians such as *Diphydontosaurus*, as it has a clearly defined two-part condylar surface that articulated with the quadrate. These restricted the lateral movement of the jaw, aiding the maintenance of a precise orthal shearing bite (Robinson, 1976; Fraser and Walkden, 1983) and ensuring that the teeth self-sharpened.

#### 4.1.3. Postcranial elements and pathologies

Part of the atlas (Fig. 5A and B) was identified from its similarity to the atlas of *D. avonis*.

Although *C. hudsoni* usually has a fused scapulacoracoid (Fraser, 1988), a separate coracoid was found here with clean, unbroken edges. We propose that juveniles or sub-adults may have had an unfused scapula and coracoid, which became fused in the adults.

Overall, pectoral girdle bones were underrepresented compared to pelvic girdle bones, possibly because the former are more fragile.

A large number of pathologies were observed on long bones and ribs. These include (Fig. 5C and D), an expanded metatarsal or metacarpal that looks tumorous, and many healed breaks (Fig. 5E and F). Fraser (1988) also noted substantial pathologies in his sample of *Clevosaurus* remains. Likewise, Evans (1983) previously noted the high incidence of fractures in Lower Jurassic British *Gephyrosaurus bridensis* mandibles, suggesting intraspecific competition as a likely cause. The remodelled fractures seen here are on long bones and ribs, probably caused either by a different form of intraspecific competition, predation, or by accident. The individuals must have survived long enough for the fractures to completely remodel, suggesting that they successfully avoided predators at least during recovery periods. The absence of archosauriforms in the Woodleaze collection suggests that those predators may have been rare in the habitat above the fissure. This is probably not a result of sorting during transport, as archosaur fossils, mainly teeth, are similar in size and found in good numbers with sphenodontians in other fissure microvertebrate assemblages, and they are the second most numerous taxa in fissure 2 at Tytherington (Van den Berg et al., 2012) and at Durdham Down (Foffa et al., 2014).

#### 4.1.4. Carpals and tarsals

Sixteen presumed carpals or tarsals were found in the material, and these are generally difficult elements to assign with certainty as, excepting the tarsometatarsal and a few other examples (in e.g. Evans, 1981), there is little in the scientific literature on early Mesozoic isolated rhynchocephalian bones from this region of the skeleton. Nine could be identified with a variable degree of probability by comparison with *S. punctatus* skeletons stored at the NHMUK. From the manus, the radiale, ulnare and elements ascribable to distal carpals 3, 4 and 5 were found. The radiale (Fig. 6A and B) is a flattened disc with a ridged margin. The ulnare (Fig. 6C and D) is box-like, with undulating sides; it is superficially similar to a fourth distal tarsal of *Sphenodon*, but lacks the dorsal slope seen on the latter. Distal carpal 3 (Fig. 6E and F) is identifiable through its small, box-like shape in anterior and posterior views. Distal carpal 4 (Fig. 6G and H) is larger, as is the case with *S. punctatus*. Both distal carpal 3 and 4 have a distinctive single dorsal foramen. Distal carpal 5 (Fig. 6I and J) is flattened proximo-distally, trapezoidal-shaped bone with a ventral expansion, which is a larger protrusion in the observed *S. punctatus* manus.

Clevosaurs have a fused astragalocalcaneum (Fig. 6K and L). It is identifiable through its many articulation surfaces, as it articulates with the tibia, fibula and distal tarsals. All other distal tarsals or carpals being larger and more complex, it is highly likely that two small, featureless, triangular elements (Fig. 6M–P) represent distal tarsals 2 and 3 respectively. Distal tarsal 4 (Fig. 6Q) is box-like, and has two dorsal foramina, as seen on cleaner *S. punctatus* specimens. It articulates with the tarsometatarsal, although this articulation surface is obscured by Paraloid™ in our specimen. The 5th metatarsal–tarsometatarsal (Fig. 6R and S), is shorter than the other metatarsals. It is proximally wider where it fused with the 5th distal tarsal, and has a dorsal protrusion near the distal end.

#### 4.2. *Diphydontosaurus avonis*

Two consecutive parts of a left dentary (Fig. 7A–D) were identified through the elongated, straight shape of the teeth, with a slightly rounded tip, a deep Meckelian groove, and by having pleurodont dentition in the anterior part of the jaws (Whiteside, 1986). The teeth are smaller and have a greater number per unit length of dentary than the pleurodont jaw region of *Gephyrosaurus*.

A small damaged articular (Fig. 7E) is also assigned to *Diphydontosaurus* because of its relatively uniform condylar

surface, as opposed to the two-part surface with a pronounced ridge found in *Clevosaurus* (Fraser, 1988).

A vomer was also assigned to *D. avonis* because it is much smaller than would be expected from *C. sectumsemper* (~250 µm). The single tooth is conical and straight, and thus not assigned to Lepidosaur B.

#### 4.3. *Lepidosaur B?*

A single fragment of bone with three conical teeth (Fig. 7F–H) is distinguishable from *C. sectumsemper* and typical *D. avonis* dental elements as the teeth curve in a posterior direction.

The fragment is comparable to the fragment assigned to lepidosaur B by Whiteside and Marshall (2008), which has backwardly curving teeth. However, some specimens of *Diphydontosaurus* are known with posteriorly directed palatal teeth such as on the vomer (Whiteside, 1986).

#### 4.4. Marine fossils

Two coeval marine fossils could be identified. One (Fig. 7I) is a conical tooth with a constricted base. The lack of an acrodine cap would indicate it is not from an actinopterygian fish, although it is likely the cap has been worn off. Its exact affinities are not clear, but the general shape is more characteristic of fish than any other organism. It is here tentatively identified as a *Severnichthys* tooth (C.J. Duffin, pers. comm.). A heavily abraded fish scale with a faint ridge running across one of the flat surfaces (Fig. 7J and K) is a common morphotype among microvertebrates from bedded marine Rhaetic sediments (Westbury Formation) of Hampstead Farm quarry, Chipping Sodbury (A. Weir, pers. comm.).

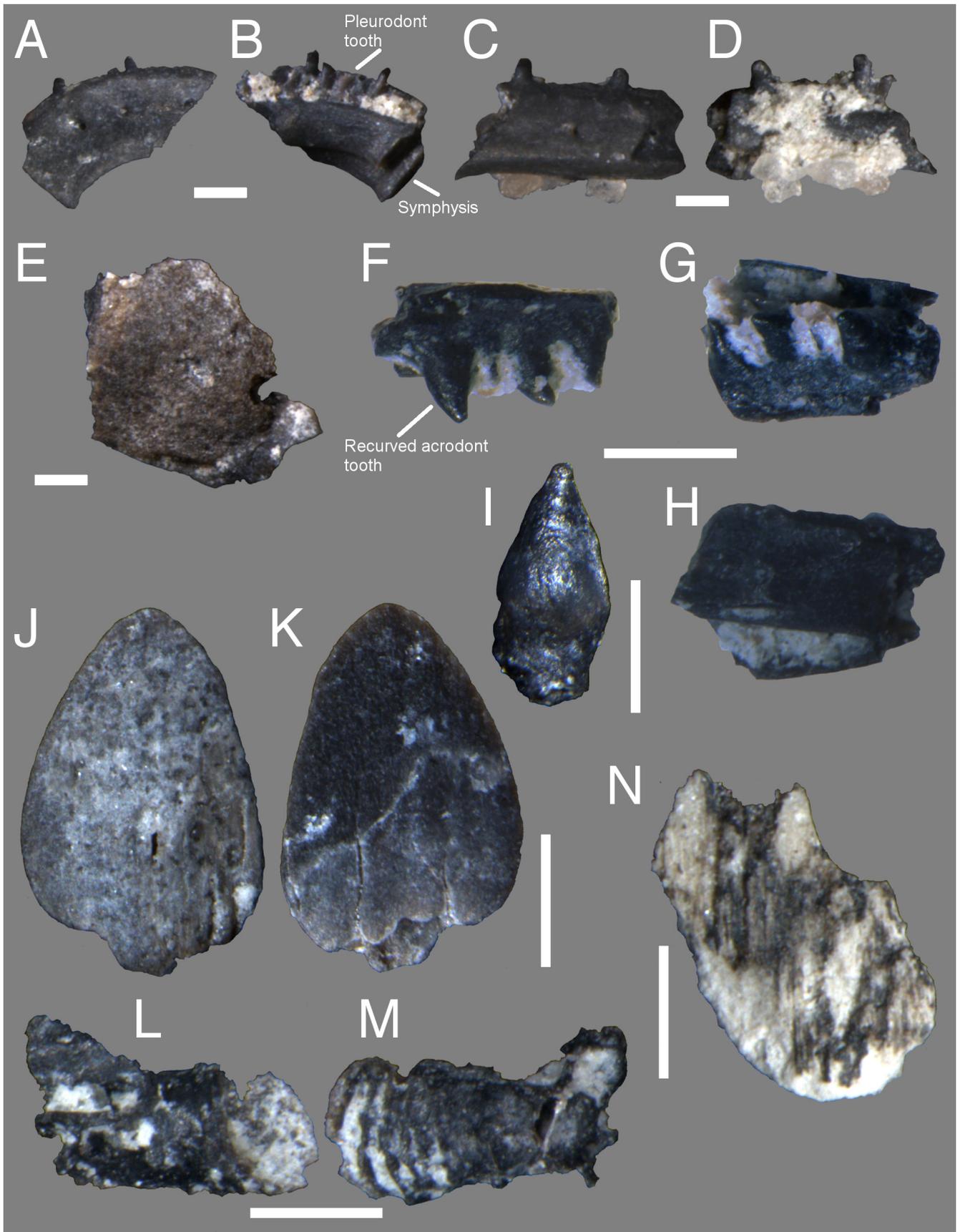
#### 4.5. Other

Only one fragment of wood was found (Fig. 7N), distinguishable by the striations on the irregular surface with oval gaps. Several small fragments of what could be amber were found in the 63 µm mesh size sediment, identified using their colour and how they reflected light. Four fragments of ichnofossils were also discovered. They may be agglutinated tubes of an invertebrate, or could be casts of plant rootlets (Fig. 7L and M).

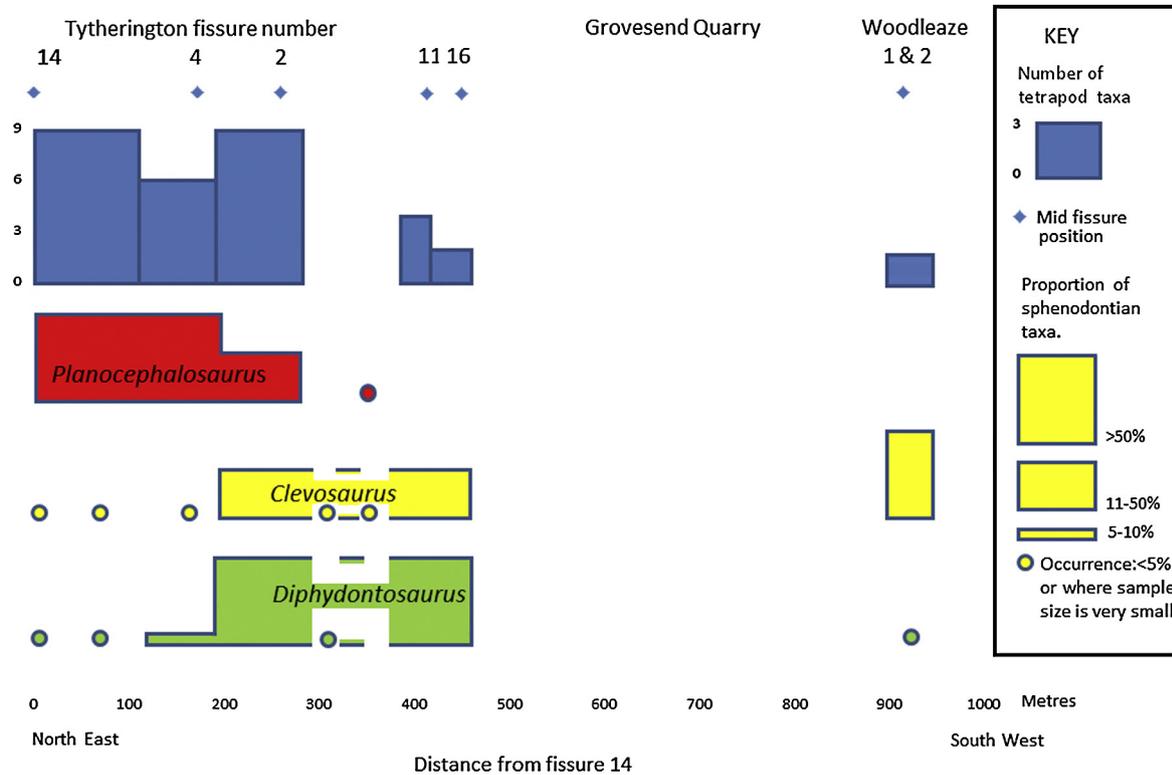
### 5. Faunal composition, associations and discussion

Unlike the diverse Triassic-aged fissure faunas of nearby Durdham Down, Cromhall and Tytherington, Woodleaze represents a unique, almost monofaunal ecosystem. With over 98% of the identifiable material belonging to *Clevosaurus sectumsemper*, as seen in Fig. 9, the Woodleaze tetrapod assemblage differs vastly from those localities, which have archosauromorphs and sometimes procolophonids in addition to other sphenodontians. Near-monofaunal deposits are known at Emborough and Batscombe, with a mainly kuehneosaur assemblage (Fraser, 1994) but these are preserved as white or pale coloured bones typical of the Triassic fissures. The dark blackened bone preservation at Woodleaze is found in the near-monofaunal Lower Jurassic *Oligokyphus* fossils at Windsor Hill, but, this is the first time it has been noted in a typical Upper Triassic fissure fauna and indicates a subterranean marine influence at deposition.

As well as Tytherington and Durdham Down, *Clevosaurus* species are ubiquitous in Holwell (Fraser, 1994), Cromhall, Emborough, Highcroft, Ruthin, Pant-y-ffynon (Whiteside and Marshall, 2008), and quarries on the St Brides palaeo-island (Säilä, 2005). Sphenodontians are common in these faunas, but different genera vary overall in relative abundance; Tytherington and



**Fig. 7.** Remains of diverse taxa from Woodleaze. (A and B) BRSUG 29381-98, anterior portion of left dentary of *Diphydontosaurus*, in lateral (A) and medial (B) views, showing the symphysis; (C and D) BRSUG 29381-99, mid portion of dentary of *Diphydontosaurus*, in lateral (C) and medial (D) views; (E) BRSUG 29382-29, articular of *Diphydontosaurus* in dorsal (E) view; (F to H) BRSUG 29381-101, portion of palate (pterygoid?) of possible 'Lepidosaur B', in lateral (F), ventral (G), and dorsal (H) views; (I) BRSUG 29381-102 *Severnichthys?* tooth; (J and K) BRSUG 29381-103, fish scale, in external (J) and internal (K) views; (L and M) BRSUG 29381-109, ?burrow or plant rootlet; (N) BRSUG 29382-30, wood fragment. Scale bars equal 500  $\mu\text{m}$ .



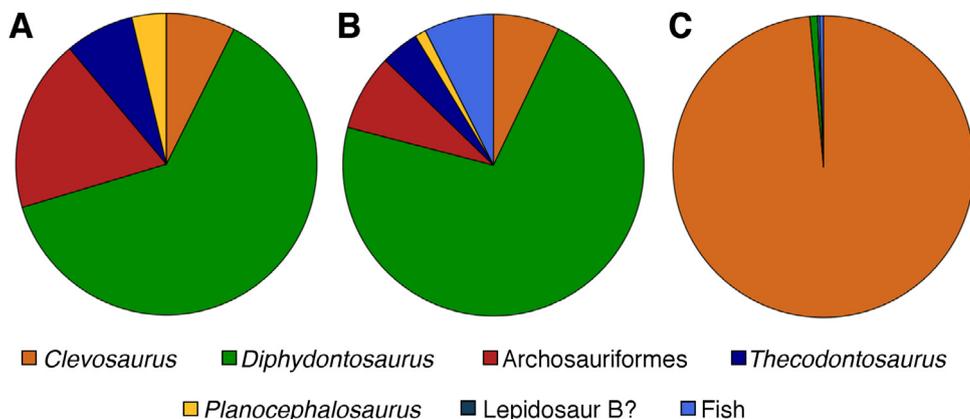
**Fig. 8.** Chart showing the trend in tetrapod diversity from sampling of fissure infillings in Tytherington quarry and Woodleaze quarry, separated by 400 m. The key sphenodontian taxa in the seven fissures are also shown, as well as occurrences in a further three Tytherington sites. Note that taxonomic diversity is greatest where *Planocephalosaurus* is a significant component of the tetrapod assemblage. *Diphydontosaurus* is the dominant sphenodontian in the middle fissures whereas *Clevosaurus* is most prevalent in Woodleaze. Sample sizes for the sphenodontian assemblages in Woodleaze and Tytherington fissures 2, 4, 11, 14, 16 vary from 14 to 623 recognisable bones. Infilled circles show either sphenodontian proportions below 5% or their presence in fissures 1, 8 and 10 that have fewer than 10 recognisable specimens. Data are from Whiteside and Marshall (2008) and from the Woodleaze study in this paper.

Durdham Down are dominated by *Diphydontosaurus*, whereas Cromhall has a preponderance of *Planocephalosaurus*.

Continuing the pattern suggested for Tytherington by Whiteside and Marshall (2008), our findings indicate that the relative dominance of the common sphenodontians across Tytherington and Woodleaze in the Lower Rhaetian is related to geographical position on the palaeo-island as shown in Fig. 8. *Planocephalosaurus* is predominant in the north part of Tytherington with *Diphydontosaurus* dominant in the middle of that quarry (particularly in fissure 2) and the proportion of *Clevosaurus* is greatest in the south, in Woodleaze quarry. The diversity of terrestrial reptiles drops from nine genera in the north part of Tytherington quarry to

two, or possibly three taxa, in Woodleaze (Fig. 8). In this regard it is equally striking that the two Woodleaze fissures have near identical faunal composition, even though they are located well over 100 m apart, and especially when compared to the significant amount of variation between fissures in Tytherington identified by Whiteside and Marshall (2008).

It is likely that the many fissures at Tytherington do represent different ages of infilling in the Lower Rhaetian, but the resemblance of the Woodleaze *Clevosaurus sectumsemper* specimens to some of those from the palynologically precisely dated fissure 2 at Tytherington (Whiteside and Marshall, 2008) suggests that these localities are broadly similar in age. The presence of a



**Fig. 9.** Faunal composition of (A) Durdham Down, (B) Tytherington fissure 2, and (C) all Woodleaze acid digested material, based on identifiable non-reworked vertebrate material from the respective sites. Sample size totals 481 from Woodleaze fissures 1 and 2.

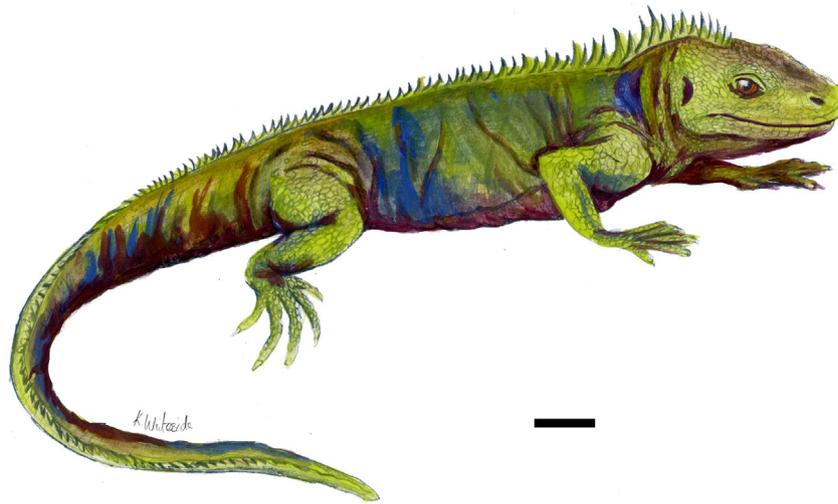


Fig. 10. Artist's impression, with guidance from the authors, of how *Clevosaurus sectumsemper* may have looked in life. Scale bar is 10 mm. Copyright Katharine Whiteside.

few marine fossils, the blackened nature of the *Clevosaurus* fossils and the palaeogeographical relationships of the limestone, indicate that the Woodleaze fissures, like Tytherington fissure 2, were infilled below the Rhaetian sea level. In this environment, at the very margin of the palaeo-island, the limestone surface in the Woodleaze area would be partially inundated with saline water, providing a restricted/sparse, species-poor habitat in which perhaps only a few or one species such as *Clevosaurus sectumsemper* could thrive. This would also explain the remarkable consistency between the assemblages in fissures 1 and 2. It is possible that the area of limestone above the fissures was isolated from the rest of the palaeo-island but there is no evidence either way. A reconstruction of how *C. sectumsemper* may have looked in life is shown in Fig. 10.

The assemblage that we have prepared contains examples of nearly all skeletal elements with little sorting, indicating that we have a representative sampling of the biota from the limestone surface directly above the fissures. The variation in tooth wear seen in different similarly sized specimens could be explained by their differing food choices, some having fed on arthropods whereas others may have chosen shelled molluscs or smaller tetrapods. The unusual dentition, particularly the relatively large dorso-ventral gap at the back of the dentary tooth row, would have enabled *Clevosaurus sectumsemper* to maximise the size range of possible food it could eat. The dentition of *C. sectumsemper* provides further information on the great adaptability of the Triassic sphenodontians, and the differences from *C. hudsoni* may have evolved rapidly, possibly due to genetic drift on the isolated population of the palaeo-island. In a poorly resourced habitat, some individuals were successful intraspecific competitors and it may have been this competition that resulted in the healed bones and bones with prominent pathologies.

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collection, and Claudia Hildebrandt for help with accessing and documenting the BRSUG collection. We thank Chris Duffin for suggesting a possible identification of the fish remains, and two anonymous referees for their very helpful comments. We are also grateful to Katharine Whiteside who painted the reconstruction of *C. sectumsemper* in Fig. 10.

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