PHYLOGENETIC RELATIONSHIPS OF THE EUROPEAN TRILOPHOSAURIDS
TRICUSPISAURUS THOMASI AND VARIODENS INOPINATUS

SOFIA A. V. CHAMBI-TROWELL, DAVID I. WHITESIDE, MATTHEW SKINNER, MICHAEL J. BENTON, and EMILY J. RAYFIELD

1School of Earth Sciences, University of Bristol, Life Sciences Building, Tyndall Avenue, Bristol BS8 1TQ, United Kingdom; 2Palaeontology Section, Earth Science Department, Natural History Museum, Cromwell Road, London SW7 5BD, United Kingdom.

ABSTRACT—Trilophosauridae are an extinct group of archosauromorphs from the Upper Triassic of western North America and Nova Scotia. Possible trilophosaurids Tricuspisaurus thomasi and Variodens inopinatus have also been reported from Upper Triassic fissure fills in the southwestern United Kingdom, based on their multi-cuspid dentitions. Here, we provide an updated description of V. inopinatus and add to the description of T. thomasi, including re-examining CT scans of its holotype dentary. We confirm that the apparent gap on the dentary of T. thomasi is pathological, with the dentine of the teeth on either side of the gap asymmetrically thick, and that heavy vascularization of the anterior part of the dentary confirms if likely had a keratinous rhamphotheca. Our cladistic analyses, to which we add nine new characters, confirm that T. thomasi and V. inopinatus are closely related taxa and the youngest known trilophosaurids. Further, we support a previous suggestion that the relatively small size of these two European trilophosaurids results from insular dwarfism.

SUPPLEMENTAL DATA—Supplemental materials are available for this article for free at www.tandfonline.com/ujvp.


INTRODUCTION
Trilophosauridae are an extinct group of lizard-like, herbivorous reptiles included in the archosauromorph clade Archosauria, all known for their diverse dental morphologies (Nesbitt et al., 2015; Kligman et al., 2020). Trilophosaurids, characterized by their transversely broadened, bicuspid/tricuspid dentition, are known from the Upper Triassic of western North America and Nova Scotia (Gregory, 1945; Mueller and Parker, 2006; Spielmann et al., 2008; Kligman et al., 2020). Trilophosaurus was described as Carnian–Norian in age (e.g., Heckert et al., 2006), but radiometric and biochronological age estimations for the Chinle Formation and Dockum Group have been revised upwards, so that the genus Trilophosaurus is not recorded before the early Norian (Kligman et al., 2020). There are six currently accepted species of trilophosaurids, all from North America: Trilophosaurus buettneri, T. jacobi, T. dornorum, T. phasmatolophos, Teraterpeton hrynewichorum, and Spinoucas sasaeus (Murry, 1987; Heckert et al., 2006; Mueller and Parker, 2006; Kligman et al., 2020). Spielmann et al. (2007, 2008, 2009) regard T. dornorum as conspecific with T. jacobi, citing similarities of the teeth of the former to large teeth of the latter, but we follow the most recent analysis of Kligman et al. (2020) who consider the two as separate species.

In Europe, two possible trilophosaurids, Tricuspisaurus thomasi and Variodens inopinatus, have been reported from Rhaetian, Upper Triassic fissure infill deposits of the southwestern United Kingdom (Robinson, 1957a; Skinner et al., 2020; pp. 549–551), based on their transversely broadened multi-cuspid dentition and, as in T. thomasi, likely possession of a keratinous rhamphotheca (or beak). This makes them the youngest trilophosaurids, but their phylogenetic identity has been disputed (Robinson, 1957a; Fraser, 1986; Sues and Olsen, 1993; Skinner et al., 2020). The fissure fill rock containing Variodens inopinatus Robinson, 1957a was collected from Emborough Quarry in southwest England and the two specimens were prepared at University College London (UCL; Robinson, 1957a). The specimens that were later named T. thomasi were collected in 1947 or 1948 and recognized as probably trilophosaurid by Walter G. Kühne (1911–1991) in a note of sale to the NHMUK (Skinner et al., 2020). T. thomasi was first described by Robinson (1957a) from jaw fragments and teeth from the Ruthin quarries, east of Bridgend, south Wales (Skinner et al., 2020), the material of which has been stored at the NHMUK ever since. The holotype of T. thomasi, and some additional material from the NHMUK and NMW, was then redescribed by Skinner et al. (2020), whose CT scans we use here.

The Ruthin Tricuspisaurus thomasi and Emborough Variodens inopinatus were located on two different palaeoislands in the Bristol archipelago (U.K. grid references SS 975795 and ST 623505 respectively; Fig. S1), a series of islands formed of uplifted Carboniferous limestone in shallow, tropical seas that existed from the Rhaetian to Sinemurian. The fissure infill deposits contain the fossils of many animals besides these two trilophosaurids, including procolophonids, rhychocephalians, etc.
kuehniosaurids, crocodylomorphs, dinosauromorphs, and cyno-
donts (Robinson, 1971; Evans and Kermack, 1994; Whiteside
et al., 2016; Skinner et al., 2020). These vertebrate faunas docu-
ment the transition through the Late Triassic mass extinction
events, during which several key clades, including trilophosaurids
and procolophonids became extinct.

In this paper we examine the external and internal mor-
phology of the holotype specimen of *Tricuspisaurus thomasi*
using CT scanning and re-evaluate the holotype and paratype
specimens of *Variodens inopinatus*. For the first time we run a cla-
dastic analysis for both European trilophosaurids to evaluate
their relationships among other archosauromorphs.

**Institutional Abbreviations—** NHMUK, Natural History
Museum, London, United Kingdom; NMMNH, New Mexico
Museum of Natural History and Science, Albuquerque, New
Mexico, U.S.A.; NMW, National Museum of Wales, Cardiff,
U.K.; TMM, Vertebrate Paleontology Collections, the University
of Texas at Austin, Austin, Texas, U.S.A.; UMMP, University of
Michigan Museum of Paleontology, Ann Arbor, Michigan,
U.S.A.

**MATERIALS AND METHODS**

The key specimens of *Tricuspisaurus thomasi*, collected by
Kühne, are shown in Fig. 1. The holotype left dentary of *T.
thomasi* (NHMUK PV R6106, Figs. 1, 2) was scanned by
Skinner et al. (2020), using a Nikon XTH 225ST X-ray computed
tomography (CT) scanner at the University of Bristol, and we
use these scans here. We digitally segmented the scans from
scratch as the original surface files were not available, using
Avizo Life 9.0 (Visualization Sciences Group) to examine the
internal and external morphology of the dentary. The two speci-
mens of *Variodens inopinatus* described by Robinson (1957a)
are shown in Figure 3 (NHMUK PV R36850 and NHMUK PV
R36849).

Our phylogenetic analysis is based on the recent archosauro-
morph dataset containing Allokotosauria matrix last modified by
Kligman et al. (2020), and prior to that by Nesbitt et al. (2015),
from Pritchard et al. (2015). We further modified this matrix by
adding nine characters, and the two operational taxonomic units
(OTUs) *Tricuspisaurus thomasi* and *Variodens inopinatus*. We
also identified 25 parsimony-uninformative characters that we
also removed. The new matrix (see Supplemental Material) con-
ists of 33 OTUs and 231 characters and was rooted using the
Late Carboniferous diapsid *Petrolacosaurus kansensis*. We ran a
parsimony analysis in PAUP* 4.0a (Swofford, 2002) using a heur-
istic search and tree-bisection-reconnection (TBR) branch swapping,
in addition to calculating Bremer values, and consistency,
retention, and rescaled consistency indices (CI, RI, RC, respect-
ively). Ten of the characters were ordered (Chs. 1, 4, 9, 10, 19,
31, 47, 62, 181, 189) following the steps of previous authors (e.g.,
Nesbitt et al., 2015; Kligman et al., 2020). All recovered MPTs
were then summarized in a strict consensus tree. We also sought
out rogue taxa using the iterPCR protocol in TNT V1.5 (Goloboff
and Catalano, 2016), but the analysis did not identify any. In
addition, we ran a Bayesian analysis, using MrBayes v. 3.2 (Huelsenbeck
and Ronquist, 2001; Ronquist et al., 2012) for 10^7 genera-
tions, sampling parameters every 1000 generations, and the first
25% of sampled trees were discarded as burn-in.

**SYSTEMATIC PALEONTOLOGY**

**ARCHOSAUROMORPHA** Huene, 1946

**TRILOPHOSAURIDAE** Gregory, 1945

**TRICUSPISaurus** Robinson, 1957a

**TRICUSPISaurus thomasi** Robinson, 1957a

**Holotype**—A near complete dentary, NHMUK PV R6106.

**Referenced Specimens**—A left maxilla, NHMUK PL.R. 500; a
probable right maxilla, NHMUK PV R6107; a probable
maxilla, NHMUK PV R6108; an isolated tricuspid tooth,
NMW 88.12 G.73; left dentary fragment with teeth, NMW
88.12 G.36.

**Locality and Horizon**—Upper Triassic, Rhaetian locality
of Ruthin, South Wales, United Kingdom (Robinson, 1957a;
Skinner et al., 2020). All definite material for *Tricuspisaurus
thomasi* is known from the Ruthin quarries (Robinson, 1957a;
Skinner et al., 2020). The high abundance of reptilian remains in
this deposit was first reported by Thomas (1952), but much of
the material was collected earlier by Kühne including the holotype
*T. thomasi* dentary examined in this paper. This infill accumu-
late in a network of fissures within the uplifted Carboniferous
limestone islands. The infill is dominated by red marl and calcitic
sandstone rich in vertebrate fossils, but also contains a mixture of
non-fossiliferous yellow-gray limestone and brown shale
(Thomas, 1952; Skinner et al., 2020). The quarries at Ruthin
are believed to contain the oldest fissure infill in the Triassic–Jur-
assic Bristol Archipelago (Skinner et al., 2020), and the terres-
trial fauna is dominated by procolophonids, but also includes
archosauromorphs and early diverging rhynchocephalians such as
*Diphylodontosaurus* sp. and *Planocephalosaurus* sp.

**DESCRIPTION**

The holotype, NHMUK PV R6106 (Fig. 1A–D), is a near-
complete left dentary with some damage to its anterodorsal tip,
though part of the symphysis is preserved. Several of the teeth
are missing, the sockets of which are partially obscured anteriorly
beneath lacræ. The rest of the teeth have varying levels of
damage but are, for the most part, complete. Although Skinner
et al. (2020) suggested there were nine teeth and alveoli, there
is evidence for 10 or 11 recognizable tooth implantations, but
there could have been more in the anteriormost area (Fig. 1D)
that is generally regarded as edentulous (e.g., Robinson,
1957a). Skinner et al. (2020) reported about five cusps and possi-
ble alveoli in the anterior region, but this area is substantially
obscured by the lacræ and not visible in the current resolution
of the CT scan. The teeth sit in shallow sockets and are protothec-
dont (Skinner et al., 2020), = ankylothecodont of Heckert et al.,
2006 (Fig. 2L). Protothecodonty describes shallow-rooted,
ankylosed, socketed teeth and ankylothecodonty a more deep-
rooted dentition (see discussions in Small, 1997; Cabreira
and Cisneros, 2009); the teeth of *T. thomasi* are shallow rooted and
of the protothecodont type. The teeth are ankylosed to the
dental alveoli by outer fibrous bone of attachment (Robinson,
1957a), which is prominent on the larger teeth and the distalmost
alveolus (Fig. 1A, B). The most distinctive feature of the teeth is
the three cusps that are positioned labiolingually, with the dis-
tances between the labial to mid cusp and mid to lingual cusp
approximately equidistant (Fig. 1C). The labial and lingual
cusps have slightly larger bases than the mid cusp and they
tend to be higher, but this is not always the case. The tricuspid
teeth are remarkable as they have well developed distal and
mesial cingula on the crown (see Fig. S2). It is clear from the
surface model (Fig. 2C) that a sharp transverse ridge runs
between the labial and mid cusp and another between the mid
and lingual cusp. The mid and distal teeth sit on a laterally and
medially expanded dorsal region of the dentary (Fig. 2L).
There is a gap in the tooth row that we consider to be a pathologi-
ical abnormality that we discuss later.

The ventral part of the dentary is mediolaterally narrow and
dorsoventrally tall and bears a huge facet for the splenial (Fig.
2C, D), similar to the condition in *Trilophosaurus buettneri*
FIGURE 1. Specimens of *Tricuspisaurus thomasi* from Ruthin Quarry. The holotype left dentary of *Tricuspisaurus thomasi* (NHMUK PV R6106) in A, lateral; B, occlusal; C, surface model of the occlusal views; and D, close up of the anterior occlusal region. E, NHMUK PV R6108, a probable maxilla in lateral view. A fragment of a probable right? maxilla (NHMUK PV R6107) in F, occlusal; G, lateral; and H, magnified occlusal (and slightly anterior) views. New character 230-1, bone of attachment above dorsal dentary margin, shown in A. Specimens digitally removed from matrix in A, B and D.
FIGURE 2. The holotype left dentary of *Tricuspisaurus thomasi* (NHMUK PV R6106); A, C, E, G, H, I, segmented in lateral, medial, occlusal, anterior, posterior, and ventral views, respectively; B, D, F, line diagrams in lateral, lingual, and occlusal views, respectively; J, sagittal cross-section of the anterior region of the dentary. K, coronal cross-section of the anterior region of the dentary. L, coronal cross-section of the penultimate tooth. M, sagittal cross-section of the mid-region of the dentary. New character 229-1, pits, foramina and rugosity suggestive of a beak, shown in A, B, and J. Abbreviations: bk, beak; br, broken; cap, pulp cavity; cpr, coronoid process; dent, dentine; fac, facet; por, porosity; ppr, posterior process; reg, region; rid, ridge; soc, socket; spl, splenial; sur, surangular; td, thickened bone; th, tooth.
FIGURE 3. Specimens of Variodens inopinatus. The holotype left dentary of Variodens inopinatus (NHMUK PV R36850), in A, lateral (and slightly occlusal); B, occlusal (and slightly lateral); and C, medial views. The numbers above the teeth in A and G are a guide to the tooth positions (using Robinson’s [1957a] nomenclature), mentioned in the text. The paratype specimen (NHMUK PV R36849), an anterior fragment of a left dentary, in D, medial; E, lateral; and F, occlusal views. Reconstruction of the dentary by PL. Robinson (1957a) in G, occlusal; and H, lateral views. New character 229-0, pits, foramina but no suggestion of a beak, shown in E. New character 230-1, bone of attachment above dorsal dentary margin, shown in A, C and D.
(Spielmann et al., 2008:fig. 28C), indicating the jaw would have been more robust in life. Other bone facets are less defined but one for the surangular appears to be visible on the dorsal postero-lateral surface of the coronoid process (Fig. 2C, D, H). The anterior part of the dentary, either edentulous or bearing very tiny teeth, has porous, highly vascularized bone visible both externally on the lateral surface of the dentary (Fig. 2A, B) and internally in the CT scan (Fig. 2J, K), evidence further supporting the former presence of a trilophosaurid-like beak (Gregory, 1945; Robinson, 1957a; Spielmann et al., 2008; Skinner et al., 2020:549–551). As here, the presence of a keratinous rhamphotheca is inferred in other Triassic groups (e.g., actosaurs, dicynodonts, ornithischians, shuvosaurusids, silesaurids) from an edentulous anterior portion of the dentary and numerous neurovascular foramina (Wynd et al., 2020), all of which are present in *T. thomasi*. The coronoid process has been described as human ‘ear-shaped’ by Robinson (1957a) (Figs. 1A, 2A–D, H) and is more prominent, with a greater dorsal extent, than in *Trilophosaurus buettneri* (see e.g., Gregory, 1945:fig. 4).

The symphyal region of *Tricuspisaurus thomasi* is mediolaterally narrower than in *Trilophosaurus buettneri* (Robinson, 1957a) but is also formed by an interdigitation of the left and right bones (see the dentary of *Trilophosaurus buettneri*, Fig. S3A; Spielmann et al., 2008:fig. 27e), which we infer in *Tricuspisaurus thomasi* (Fig. S2J; Skinner et al., 2020:fig. 10N) and *Trilophosaurus jacobi* (Fig. S3B) and is likely present in *Variodens inopinatus* (see the medial view of the symphysial region, Fig. 3D).

*Tricuspisaurus thomasi* and *Trilophosaurus* species including *T. buettneri* and *T. jacobi* are distinguished further by the large distal dentary teeth lying in variable positions from 3rd–6th most distal in the *Trilophosaurus* dentition (see Spielmann et al., 2008:figs. 27a, 93k; Gregory, 1945:fig. 6) but in the penultimate distal position in *Tricuspisaurus* (Fig. 1C).

Two other *Tricuspisaurus thomasi* specimens collected by Kühne are NHMUK PV R6107 and NHMUK PV R6108 which we identify tentatively as posterior portions of a maxilla. The slightly convex shape of the base of the dentition of NHMUK PV R6108 (Fig. 1E) indicates that this specimen is a very poorly preserved fragment of maxilla. Skinner et al. (2020) regarded NHMUK PV R6107 (Fig. 1F–H) as a possible partial maxilla. The teeth on the specimen have a slightly elongated ‘neck’ near the base of the crown that resemble the distal maxillary teeth of *Trilophosaurus buettneri* in Spielmann et al. (2008: fig. 20A). The penultimate tooth is a curious L-shape blade with a sharp ridge running transversely across the apex of the cusp (Fig. 1H). One interpretation (suggested independently by Edwards [2001] and Skinner et al. [2020]) is that the tooth is fractured, possibly has an exposed pulp cavity, is worn and would have been tricuspid in life, whereas Robinson (1957a) argued that the tooth is complete. Robinson cited similar isolated teeth in the NMW as support for her suggestion and it is clear from Figure 1H that there is no indication of a possible mid cusp, so we cannot resolve this debate. The close-up of the two largest teeth in Figure 1H also indicates a second slight vertical ridge placed to one side of the central cusp. There are also smaller teeth distally on the right and left maxilla of *Trilophosaurus buettneri* TMM 31025-140 (Spielmann et al., 2008:figs. 18d, 19d) and anteriorly on the maxillae of specimens TMM 31025-207 and TMM 31025-143 (Spielmann et al., 2008: figs. 20c, 21d). Of these examples the largest tooth of the right maxilla of TMM 31025-207 bears most similarity to the bladed tooth of *Tricuspisaurus thomasi* NHMUK PV R6108.

Robinson (1957a) referred to a specimen ‘PLR 500’ from her own collection as a maxilla, but this could not be located in the NHMUK. The specimen is shown in Robinson (1957a:fig. 3 and Skinner et al. (2020:fig. 10a) but its appearance is akin to the holotype dentary NHMUK PV R6106 and bears little similarity to the *Trilophosaurus buettneri* maxilla depicted by Spielmann et al. (2008:fig. 20a, b). The bone below the tooth row of ‘PLR 500’ appears to have the ridge developed in the holotype dentary (Fig. 1A) and the base of the dentition follows the dentigerous surface of the bone in the concave manner of NHMUK PV R6106, rather than the straight or slightly convex line of the maxilla of *T. buettneri*. Unless ‘PLR 500’ is rediscovered it is not possible to confirm its identification.

**Pathology of Tricuspisaurus thomasi**

On the dentary of NHMUK PV R6106, there appears to be a small gap between the 3rd and 4th tooth (Fig. 2G–I), and similar gaps in *Trilophosaurus buettneri* have been explained as an artifact of preparation or as tooth replacement (Gregory, 1945; Demar and Bolt, 1981; Spielmann et al., 2008). There has been some debate whether this triangular gap in *Tricuspisaurus thomasi* is an autapomorphy or the result of injury (Robinson, 1957a; Skinner et al., 2020). Our scans provide further evidence to suggest that the latter is the case. In sagittal cross-section (Fig. 2M) the dentine of the teeth on either side of the gap is asymmetrically thickened, and the pulp cavity of these teeth is distorted in shape. The teeth either side of the gap also appear to be growing at an angle rather than vertically, which differs from the rest of the teeth in the tooth row.

There is a bony callus (Fig. 1A) on the upper part of the lateral side of the dentary just below and slightly anterior to the gap. This probably represents a healed fracture, and it was this damage, experienced some time before death, that might have generated the edentulous gap and the deformed teeth. Alternatively, the callus might have been caused by an abscess representing infection, and the bone and dentition has become re-modelled. Overall, the evidence supports the view that the gap is likely pathological and is the reason for the empty tooth alveolus.

We have considered the dentary carefully in our phylogenetic analysis and have left out the triangular gap as a character but assess the main features of the mesial and distal teeth (implantation, relative width, cusps, cingula, and arêtes) as sufficiently characteristic to be scored.

**Variodens inopinatus** Robinson, 1957a

**Holotype**—Mostly complete left dentary, NHMUK PV R36850.

**Referred Specimens**—Paratype, NHMUK PV R36849.

**Locality and Horizon**—Upper Triassic, Rhaetian fissure locality in Emborough Quarry, southwest England, United Kingdom (Robinson, 1957a, b; Whiteside et al., 2016). The type specimens are from a fissure (UK grid reference ST 623505; see Fig. S1) figured by Robinson (1957b:pl. 2–4) and described by Savage (1977:89–90). In addition, there is also a fragment of a probable *Variodens* sp. from a Rhaetian fissure in Holwell ‘Microlestes’ Quarry, collected by Charles Moore in the 1850s and described by Whiteside and Duffin (2017).

The Emborough Quarry Triassic fissure fossil is best known as the type locality for the gliding lepidosauromorph *Kuehneosaurus latus* (Robinson, 1962), found in huge numbers of mostly disarticulated but associated bones in a red conglomeratic matrix, the main fossiliferous lithology in the fissure. We were unable to determine who discovered the *Variodens inopinatus* specimens. However, reptile-bearing Emborough rocks were first collected by Kühne in 1946 (then of UCL; Robinson, 1957b) but Pamela L. Robinson of UCL and Tom Fry, a collector employed by the University of Bristol, also made substantial collections from the site. In addition to *K. latus* and *V. inopinatus*, the fauna collected includes small archosauromorphs and lepidosaurs.
The dating of the Emborough Quarry fissure deposit is debated. Robinson (1957b) considered it to be older than the Rhaetian transgression and, therefore, Norian, whereas White-side et al. (2016) argued that the entrance to the fissure was not inundated by the sea until after the deposition of the base of the Westbury Formation in the early Rhaetian. This early Rhaetian age has been confirmed by detailed mapping studies reported by Lovegrove et al. (2021).

DESCRIPTION

The holotype specimen, NHMUK PV R36850 (Fig. 3A–C), is a mostly complete left dentary, nearly 20 mm long, but lacking the most anterior region and the posterior part of the coronoid process. Although broken, the coronoid process appears to be more similar to that in the reconstruction of *Trilophosaurus buettneri* (Spieelman et al., 2008:fig. 22b, c) than to the much higher feature in *Tricuspisaurus thomasi*. A splenial is probably present on the medial side (Fig. 3C) but the bone is too fractured to discern its contacts with the dentary. The paratype specimen NHMUK PV R36849 (Fig. 3D–F) is a much smaller fragment of the anterior region of a left dentary, including a part of the symphys, but the combination of the two specimens enabled Robinson (1957a) to provide a thorough description and reconstruction (Fig. 3G, H) of the dentary. Her account is paraphrased here together with new information. Robinson (1957a:284) combined the evidence from the two dentaries to demonstrate that there would have been 18–19 teeth on a complete dentary with a length of about 22 mm. From the mesialmost position, the smaller dentary has tooth positions 1–9 and the large dentary alveol from position 5–18 (using Robinson’s 1957a nomenclature). The clearest comparative positions are 8–9 in the paratype and 3–4 in the holotype; in both cases the teeth are readily recognized as tricuspid (compare Fig. 3B with 3F). Considering a composite dentary composed of the two specimens, the holotype would have tooth positions 5–18.

The teeth are protothecodont and sit in shallow alveoli (Fig. 3A, C, D, F); this includes the mesial conical teeth of NHMUK PV R36849 deemed pleurodont by Robinson (1957a). There is prominent fibrous or spongy (Robinson, 1957a) bone of attachment (Fig. 3A, C, D) that ankyloses the base of each tooth crown to the rim of the dental alveoli; this bone of attachment extends up the ‘neck’ region reaching the base of the upper crown. There is a probable resorption pit (Fig. 3C), recognized by Robinson (1957a) as evidence that the teeth were actively replaced. The 14 teeth of NHMUK PV R36850 are all multi-cusped except the most mesial and distal. However even in the most mesial tooth there is evidence of raised areas positioned labially and lingually of the conspicuous central cusp; the tooth lying immediately distal has a rudimentary development of two minor cusps flanking the central apex (tooth 2, Fig. 3A, B). Distal to these two teeth, the characteristic transversely wide tricuspid morphology is present in all but the distalmost erupting tooth, which has a simple small conical shape with its apex directed mesially. The most mesial tooth position of NHMUK PV R36849 consists of a remnant base and partial alveolus but the following four mesial teeth are all simple conical forms. Distally to these teeth, the next two have rudimentary very small, raised cusps which Robinson (1957a:table, p. 284) regarded as ‘transitional to the 3-cusped type,’ and the final two teeth (numbers 8 and 9) are tricuspid. The three cusps on *Vairiodens inopinatus* dentary teeth are all similar in height except on the largest teeth 12 and 13 of NHMUK PV R36850 (Figs. 3A, B, S2D) where the central cusp is noticeably highest. Although mesial and distal cingula are present on teeth 7–13, they are less defined than those of *Tricuspisaurus thomasi* (Robinson 1957a; cf. Fig. 3C, F).

In occlusal view, teeth 6–12 are cassinoid-shaped (Fig. S2B), meaning possessing two rounded ends and a central constriction; this is a unique feature of *Vairiodens inopinatus* among the trilophosaurids. In contrast, the large tooth 13 is sub-circular in occlusal view. Teeth 12 and 13 have the most complex crown surface morphology, with accessory cusps and additional cingula (Robinson, 1957a; Fig. S2D). The most prominent accessory cusps are on the distal sides of the lingual and labial cusps of tooth 12 and behind the labial cusp of tooth 13 (Figs. 3A, B, S2D). However, both teeth also have raised areas or ‘shoulders’ on the distal side of the labial cusp. In lingual view, a ‘shoulder’ is present on the distal side of the apex of the lingual cusp on teeth 12 and 13 (Fig. 3C). As a result of the cusps and accessory cusps, basins (Fig. S2D) are developed between the labial and central cusp and the lingual and central cusp on both these large teeth. In addition to mesial and distal cingula more cingula are present between cusps particularly on tooth 13 (Fig. S2D).

The lateral sides of both dentaries have a profusion of large foramina that are especially numerous at the anterior end of NHMUK PV R36849 (Fig. 3E), indicating that this was a highly vascularized region. The number of foramina is much greater than observed in *Tricuspisaurus thomasi* but unlike that taxon there is no evidence of a rugose anterior region that could indicate the presence of a keratinous rhamphotheca. In common with *T. thomasi*, there is a prominent, laterally projecting, longitudinal ridge of bone on the lateral side of the large dentary below the tooth row (Fig. 3A).

**Remarks**

There are many features, particularly in the dentition, common to both *Tricuspisaurus thomasi* and *Vairiodens inopinatus*. Most notably the transversely wide tricuspid nature of the larger teeth and type of implantation, protothecodont, is similar with the teeth ankylosed in shallow alveoli by fibrous bone of attachment (compare Fig. 1A–C with Fig. 3A, C) which originates from the rim of the alveolus. This bone of attachment reaches the base of the expanded upper crown region in both taxa. There are, however, significant differences, with *T. thomasi* teeth displaying more prominent cingula and a more typical trilophosaurid sub-ovoid shape in occlusal view (cf., Heckert et al., 2006:figs. 3A, 7D, F; Spielmann et al., 2008:figs. 8, 9) with relatively straight mesial and distal sides. This shape is depicted best in the mid tooth region (teeth 4 and 5) of the *T. thomasi* holotype in front of the gap in Fig. 1B, C and two of the teeth in Fig. 1F; H; also see Skinner et al. (2020:fig. 10G, I, M). By contrast, the cassinoid outline of the *Vairiodens inopinatus* tricuspid teeth (Figs. 3B, S2B) differs from all other trilophosaurids. Further, and unlike any other trilophosaurid, *V. inopinatus* has many accessory cusps on the largest distal teeth and the penultimate tooth is a unique sub-circular shape in occlusal view (Fig. S2B, D).

The similar size and relatively equal spacing of the three cusps on *T. thomasi* tricuspid teeth are reminiscent of *Trilophosaurus buettneri* teeth (e.g., Heckert et al., 2006:fig. 7B, D) rather than the larger central cusp and slight asymmetrical placement of cusps in *Trilophosaurus jacobis* (e.g., Heckert et al., 2006:fig. 7A, C). The pronounced cingula of *Tricuspisaurus thomasi* teeth are more similar to those of *Trilophosaurus jacobis* but also resemble the teeth of juvenile *T. buettneri* (see Demar and Bolt 1981:fig. 6). *V. inopinatus* has similarly sized cusps in most tricuspid teeth but, of the three major cusps, the central one of each of the two largest distal teeth is noticeably highest. *V. inopinatus* (Fig. S2D) therefore differs from *T. thomasi* and *Trilophosaurus* species in the unique cassinoid shape (in occlusal view) of most of its tricuspid teeth, but also in the circular shape of the penultimate tooth and the greater complexity of the crown surface in the largest distal teeth (see Fig. S2D).
The occlusal wear on the cusps of the multispid teeth is similar in *T. thomasi* and *V. inopinatus*, forming blunted apices (Figs. 1F, S2C) that suggests an orthal motion of the jaws with the upper and lower cusps meeting. Cusp wear of this type is common in *Trilophosaurus buettneri* (Demar and Bolt, 1981). However, there is additionally mesial wear on the central cusp of tooth 12 of *V. inopinatus* (Fig. S2D) indicating that the upper and lower cusps are slightly offset in that region; Robinson (1957b:284) noted this wear facet and two further concave wear facets on the same tooth. Demar and Bolt (1981:fig. 5) reported six regions of mesial and distal wear facets in some *T. buettneri* teeth. The *V. inopinatus* dentary is dorsoventrally more gracile compared with *T. thomasi* and *Trilophosaurus* species. Further, the anterior region on the dentary of *V. inopinatus* is toothed, rather than edentulous, and lacks any evidence of a beak. *Variodens inopinatus* is the smallest trilophosaurid known from a toothed bone with an estimated length, based on *T. buettneri* of Spielmann et al. (2008) of a body length of about 0.45 m.

*Tricuspisaurus thomasi* is therefore a more ‘typical’ trilophosaurid, albeit with a noticeably greater prominence of the mesial and distal cingula on the dentary teeth compared with adult *Trilophosaurus butti*neri (e.g., the holotype UMPM 2338 in Spielman et al., 2008:fig. 9i) but with a similar eminence to those of *Trilophosaurus jacobsi* and skeletally immature *T. buettneri*. The similarity to *Trilophosaurus* was recognized by Kühne in his sale of the specimens to the NHMUK in 1948 (Skinner et al., 2020). A major problem with the description of *T. thomasi* is that it is based on a holotype dentary with a pathological abnormality. However other specimens, particularly with the characteristic trilophosaurid teeth clearly demonstrate its affinities.

Cladistic Analysis

The maximum parsimony analysis (Fig. 4A) retained 68 trees of length 616 steps (consistency index, CI = 0.409; retention index, RI = 0.644; rescaled consistency index, RC = 0.263), in total there were 616,458 rearrangements tried. The Bayesian analysis result (Fig. 4B) closely resembles the parsimony analysis but with lower resolution within Trilophosauridae. Both analyses retrieve Allokotosauria as monophyletic, with *Pamela* *aria dolichotach*ela* and the azendohsaurids being the earliest diverging groups. In the maximum parsimony analysis *Pamela* *aria dolichotach*ela* is the earliest diverging member of Allokotosauria, whereas in the Bayesian analysis *P. dolichotach*ela* is the sister group to the genus Azendohsaurus (see also Ezcurra, 2016). The earliest diverging member of Trilophosauridae is *Tera*peton *hrwyn*ewichorum, which agrees with previous analyses (Nesbitt et al., 2015; Kligman et al., 2020). The relationships within *Trilophosaurus* are poorly supported with many collapsing to form a polytomy, as in previous analyses (Kligman et al., 2020), but the majority consensus tree for the Bayesian analysis suggests that *T. dornorum* and *T. jacobsi* are sister taxa, with the same relationship suggested by the 50% majority-consensus tree maximum parsimony analysis (Fig. S4). The 50% majority-consensus maximum parsimony tree also tentatively suggests a group comprising *T. phasmalophus*, *Spinus* *achus caseus*, *T. dornorum*, and *T. jacobsi*.

**DISCUSSION**

**Phylogenetic Identity of the European Trilophosaurids**

Our phylogenetic analysis suggests that *Tricuspisaurus thomasi* and *Variodens inopinatus* are both trilophosaurids. In previous discussions, some authors suggested *Tricuspisaurus thomasi* was a procolophonid (Fraser, 1986; Sues and Olsen, 1993; Edwards, 1998; Spielmann et al., 2008), or a trilophosaurid (Robinson, 1957a; Edwards and Evans, 2006; Skinner et al., 2020). We demonstrate that both *T. thomasi* and *Variodens inopinatus* are indeed trilophosaurids based on the following evidence:

1. The teeth of *Tricuspisaurus thomasi* and *Variodens inopinatus* are attached by fibrous bone to the alveolar rim in a protoste- cordont (ankylosteodont of Heckert et al. [2006] and Spiel- mann et al. [2008]) implantation rather than the acrodonty of procolophonids (Cabreira and Cisneros, 2009), and the transversely positioned tricuspid nature of the teeth is in common with *Trilophosaurus* species. Similar tooth implantation is recorded in other allikotosaurians such as *Tera*peton *hrwyn*ewichorum, *Pamela* *aria dolichotach*ela, *Shringasaurus indicus*, and *Azendohsaurus madagaskarenensis* (Sues, 2003; Nesbitt et al., 2015; Ezcurra, 2016; Sengupta et al., 2017).

2. There is evidence that *Tricuspisaurus thomasi* had a kerati- nous rhamphotheca, including highly vascularized bone in the anterior part of the dentary, as in trilophosaurids but not procolophonids. *Variodens inopinatus* also had highly vascular- ized bone on the anterior part of the dentary although there is no evidence of a beak.

3. The tricuspid tooth-bearing region of *Trilophosaurus buettneri*, *Trilophosaurus jacobsi*, *Tricuspisaurus thomasi*, and *Variodens inopinatus* dentaries consist of many emplace- ments or sockets for a battery of teeth. The number of these teeth is similar in the four taxa: about 13 (or 14 if the ultimate tooth is included) in *Variodens inopinatus*, 12–15 in *Trilophosaurus buettneri* (Demar and Bolt, 1981; mean about 12–13, Gregory, 1945), 11 in *T. jacobsi* (Spielman et al., 2008), but fewer, eight (perhaps as many as ten), in *Tricuspisaurus thomasi*. Therefore, despite having consider- ably smaller dentaries, *Tricuspisaurus thomasi* and *Variodens inopinatus* fall within or close to the tooth number range of *Trilophosaurus* species. In comparison, the multispid teeth in the dentary of contemporaneous Late Triassic procolophon- nids are far fewer, *Leptopleuron lacertinum* has 5–6 (Siállí, 2010) whereas *Hypsgnathus fenneri*, has five (Colbert, 1946).

4. The shape of the multispid tooth row in *Trilophosaurus* species and *Variodens inopinatus*, in occlusal view of the dentary, is an elongated ellipse and the largest teeth are in the distal half. In comparison, large teeth of the contempor- neous procolophonid dentaries are positioned mesially (such as the ‘massive’ incisiform of *Hypsgnathus*, Sues et al., 2008:fig. 282), as well as distally (Siállí, 2010). The tooth row of the procolophonid *Leptopleuron lacertinum* is more rec- tangular in occlusal view (Siállí, 2010:fig. 8h); an occlusal view of the *Hypsgnathus fenneri* dentary is not reported. The multispid tooth row of *Tricuspisaurus thomasi* is more triangular and much wider towards the posterior than ellipsoidal in occlusal view (Fig. 1B, C), which is likely due to the pathological damage, but as in *Variodens inopinatus*, the largest teeth are in the penultimate and antepenultimate (3rd from the most distal) positions. The largest teeth vary in position in *Trilophosaurus* species and can be 3rd to 5th from the ultimate distal position (see e.g., *T. buettneri* specimen TMM 31025-125 in Spielman et al. [2008:fig. 27a] and *T. jacobsi* specimen NMMNH P-41400 in Spielman et al. [2008:fig. 93k, l]). Gregory (1945:fig. 6) reconstructs the dentary of *T. buettneri* with the largest teeth in the 5th or 6th position from the most distal.

5. There is a longitudinal bony ridge on the posterior lateral side of the dentary just below the dentigerous region in *T. thomasi* and *V. inopinatus*, as in *Trilophosaurus buettneri* (Spielmann et al., 2008:fig. 27f, h, specimen TMM 31025-125). No such dentary ridge is reported or figured in the Late Triassic procolophonids, e.g., *Acadillia psalidodon*, *Haligonia bolodon*, or *Scoloparia glyphanodon* by Sues.
and Baird (1998). The dentary bony ridge is absent in Libognathus sheddi (Small, 1997), Hypsognathus fenneri (Colbert, 1946), Leptopleuron lacertinum (Säilä, 2010), or the leptopleuronine from Ruthin Quarry described by Skinner et al. (2020: fig. 6).

6. The tricuspid teeth of Tricuspisaurus thomasi and Variodens inopinatus (excepting the penultimate tooth of that species) are labiollygually wider than mesiodistally long at the crown base. This is a feature common to all Trilophosaurus species. Tricuspid teeth are found in some procolophonids such as the unnamed taxon from Cromhall Fraser (1986: fig. 6). However, in that specimen and another from Tytherington mistakenly assigned to Tricuspisaurus by Whiteside and Marshall (2008: fig. 5oo, pp), the middle cusp is distinctively mesially positioned, not in a transverse row, and the acrodont teeth lack the cingula and arêtes of the trilophosaurids. It was these unnamed procolophonid multicusp teeth that led Fraser (1986), Sues and Olsen (1993), Heckert et al. (2006) and Spielmann et al. (2008) to consider that Tricuspisaurus thomasi and/or Variodens inopinatus might be procolophonids rather than trilophosaurs. In comparison, Skinner et al. (2020) and earlier, Edwards (2001), recognized that the procolophonids of the U.K. fissure deposits were quite different to Tricuspusaurus thomasi and Variodens inopinatus and correctly identified those taxa as trilophosaurids.

7. Both Trilophosaurus jacobi and Trilophosaurus buettneri as well as Tricuspisaurus thomasi and Variodens inopinatus (Fig. 1F, H) possess sharp edges (arêtes) between the cusps of their teeth (Heckert et al., 2006: fig. 3; Spielmann et al., 2008: figs. 4, 8, 9; Skinner et al., 2020: fig. 10). Transverse cutting ridges form between the cusps of leptopleuronine procolophonids but where recorded they are curved towards the anterior end of the jaw, e.g., Libognathus sheddi (Small, 1997) and the leptopleuronine teeth figured by Skinner et al. (2020: fig. 6e–h).
contrast the cutting edges between cusps in *Trilophosaurus* species (Spieelman et al., 2008:fig. 9i) and in *Tricuspisaurus thomasi* (Fig. 1H) are straight.

8. In *Trilophosaurus* species, where jawbones are complete or near complete (from figures in Spieelman et al., 2008), there is a digitated anterior in medial view (Fig. S3). In *Trilophosaurus buettneri* the anteriormost region of the dentary is digitated so that an interlocked symphysis is formed between the left and right lower jawbones (Fig. S3A). This digitation is present in *Trilophosaurus jacobi* (Fig. S3B) and a CT sagittal slice of the anterior dentary of *Tricuspisaurus thomasi* (Fig. S2J) indicates that it also has a similar digitation. In fact, the digitation is formed from a sequence of sub-longitudinal ridges and troughs so that in a CT slice a gap between ‘digits’ is observed (see Fig. S2J). *Variodens inopinatus* also displays the features of an interdigitating dentary symphysis in medial view (Fig. 3D); it probably had an interlocking symphysis but as the anteriormost end is damaged we cannot be certain. The symphysis is known to have interdigitated in *Tanystrus* (Spiekan et al., 2020) and rugose areas and small ridges are formed in the lower part of the symphysis in the rhynchosaur *Rhynchosaurus* (Benton 1990:fig. 7b) and *Teyymbaita sulcogonatus* (Montefeltro et al., 2010:fig. 8). In other taxa we researched, the symphysis appears straight in anterior view indicating smooth opposing surfaces such as in early taxa, e.g., *Prolacerta* (Evans, 1975), in the lepidosaur *Gephyrosaurus* (Evans, 1980), and in dinosauers such as *Plateosaurus* (Lallensack et al., 2021:fig. 9g2). In some of these cases the surfaces might be rugose, but in any event, there is no suggestion that they are deeply interlocking as in the trilophosaurids. However, we have not been able to extensively study all taxa in the cladistic matrix for this character and without CT scanning images such as that for *Tanystrus* (Spiekan et al., 2020) we cannot be certain, so it was not included in our phylogenetic analysis. However, a digitated anterior dentary and therefore an interdigitating symphysis is lacking in all the descriptions and figures of procolophonids we researched in the Triassic. These include the Late Triassic *Acadilepsis psalidodon*, *Halogonia bolodon*, or *Scopolaria glyphanodon* in Sues and Baird (1998) and a digitated symphysis is absent in *Libognathus sheddi* (Small, 1997), *Hypsognathus fenneri* (Colbert, 1946), and *Leptopleuron lacertinum* (Sáëlà, 2010). It is also lacking in procolophonids from the Early and Middle Triassic such as *Procolina teresa* (Borsuk–Bialynicka and Lubka, 2009:fig. 9), *Kapes bentoni* (Zaher et al., 2019:fig. 5), and *Eomurrana yurrgenssin* (Hamley et al., 2021:fig. 7b).

From our phylogenetic analysis (Fig. 4) and supplementary characters and matrix we assign *Tricuspisaurus thomasi* and *Variodens inopinatus* to the Trilophosauridae as they have the following synapomorphies in common with the genus *Trilophosaurus*: non-serrated marginal dentition (Nesbitt et al., 2015:Character and state 90-0; here 80-0); morphology of crown base of the marginal teeth a flattened platform with mesiodistally arranged cusps (93-2; here 83-2); tooth shape at crown base of the marginal teeth fabiolingually wider than mesiodistally long (98-2; here 87-2).

From our nine new characters, *Tricuspisaurus thomasi* and *Variodens inopinatus* have seven synapomorphies with *Trilophosaurus*. There are two distal and/or mesial cingula only on the mid dentary teeth, i.e., not multi-cingulate on those teeth, (Ch. 223-2; shared only with *Trilophosaurus*). There is one mesial and one distal cingulum on all dentary teeth (224-2; shared only with *T. buettneri*) excepting that *Variodens inopinatus* has more cingula on the antepenultimate and penultimate teeth. The three cusps are equally or sub-equally spaced (Ch. 225-2; shared with *T. buettneri* and *T. buettneri*). The relative cusps are of equal or sub-equal size in a multiple transversely cusped taxon (226-1; shared with *T. buettneri* and *T. phasmalophos*) except the antipenultimate and penultimate teeth of *Variodens inopinatus* where the middle cusp is the highest; the middle cusp is also highest in *T. jacobi* teeth and one flanking cusp is noticeably lower in *T. dornorum* (Mueller and Parker, 2006:fig. 4). The dentary is mediolaterally thin but dorsally is abruptly greatly expanded (greater than 2× mid dentary) forming a ridge both laterally and medially behind the mid-region (227-1; known in *T. buettneri* and *Teraterpeton hrynewichorum* only, data are lacking in other trilophosaurids). On the dentary teeth, the bone of attachment reaches a pronounced height above the dentary dorsal margin (230-1, known in *T. buettneri* and *T. hrynewichorum*; data are lacking in other trilophosaurids), but also present in *Azednshaurus madagaskarensis*.

Additionally, *Tricuspisaurus thomasi*, but not *Variodens inopinatus*, shares one apomorphy with all *Trilophosaurus* species: a lengthly transverse cutting ridge (arête) between all cusps on at least some dentary teeth. *Tricuspisaurus thomasi* also shares the apomorphy (229-1) with *Trilophosaurus buettneri* and *Trilophosaurus jacobi*: there is prominent anterior vascularization of the dentary marked by many pits and foramina with a rugosity suggesting a keratinous rhamphotheca, but *V. inopinatus* shows no indication of such a beak. *Rhynchosaurus*, *Tricuspisaurus thomasi*, and *V. inopinatus* are the only taxa to share the synapomorphy (231-1); the largest dentary tooth is in the penultimate or antepenultimate position.

**Insular Dwarfism**

Compared with other trilophosaurids, *Tricuspisaurus thomasi* and *Variodens inopinatus* are small animals, their dentaries measuring ∼2–3 cm in length. *Trilophosaurus buettneri* dentaries exceed more than twice this length; the dentary of *T. jacobi* is about 60% longer. Skinner et al. (2020:559) suggested that *T. thomasi* was much smaller than its close relative *Trilophosaurus*, ∼0.6–1 m, compared with 2–2.5 m for the latter, based on relative jaw sizes. *Variodens inopinatus* is smaller still, with an estimated body length of about 0.45 m. Our findings therefore agree with the hypothesis that insular dwarism was a common feature of many tetrapods from the Bristol paleoislands (Klein et al., 2015; Whiteside et al., 2016; Skinner et al., 2020).

**CONCLUSIONS**

We provide evidence that *Tricuspisaurus thomasi* and *Variodens inopinatus* are trilophosaurids and are the youngest currently known members of Trilophosauridae, being the only examples with a probable Rhaetian age. There is an unconfirmed report of a worn trilophosaurid tooth from the Rhaetian Owl Rock Member of the Chinle Formation (U.S.A.) by Kirby (1991) but this identification is generally queried (e.g., Klugman et al., 2020). We confirm that the gap in the tooth row in the holotype of *T. thomasi* is pathological and not an autapomorphy. The two European taxa are relatively small compared with other described trilophosaurids, in accord with the notion that they are insular dwarfs.

**ACKNOWLEDGMENTS**

We thank T. Davies for having created and processed the original CT-scan dataset of NHMUK PV R6106, used here. The CT-
scan dataset is the property of the NHMUK and permission to use it should be sought from that institution. We also acknowledge the Tractman Scholarship for funding SAVC-T’s PhD, and NERC grant NE/I027630/1 to MJB. We thank M. Day and S. Chapman for their great help and permission to study the collections of the NHMUK. We are grateful to F. Ferusen for guidance in the use of the macro photography equipment at the Angela Marmont Centre for UK Biodiversity (NHMUK). We also thank Martin Ezcurra, Adam Marsh and an anonymous referee, as well as the JVP editors, for their very thorough and helpful comments.

ORCID
Sofia A. V. Chambri-Trowell Ω https://orcid.org/0000-0003-1455-7347
David I. Whiteside Ω https://orcid.org/0000-0003-1619-747X
Michael J. Benton Ω https://orcid.org/0000-0002-4323-1824
Emily J. Rayfield Ω https://orcid.org/0000-0002-2618-750X

LITERATURE CITED


Submitted January 06, 2021; revisions received October 05, 2021; accepted October 17, 2021.

Handling Editor: Tyler Lyson.