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Original Article

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The world's largest worm lizard: a new giant trogonophid (Squamata: Amphisbaenia) with extreme dental adaptations from the Eocene of Chambi, Tunisia

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ABSTRACT

We here describe *Terastiodontosaurus marcelosanchezi*, a new amphisbaenian genus and species from the Eocene of Chambi, Tunisia. Using micro-computed tomography (μCT), we document the peculiar anatomy of the new taxon, which is characterized by extreme dental morphology, including one massive tooth on the maxilla and dentary, flat cheek teeth, and an array of other diagnostic features that readily differentiate it from all other amphisbaenians. We also redescribe the oldest named African amphisbaenian, *Todrasaurus gheerbranti*, from the late Palaeocene of Morocco, using μCT. Phylogenetic analysis recovers *Terastiodontosaurus* and *Todrasaurus* as sister taxa and provides strong support for a sister-group relationship of those two large-toothed amphisbaenians with extant *Trogonophis*. Accordingly, *Todrasaurus* shows that the divergence of crown Trogonophidae occurred much earlier than currently thought. Our survey of μCT scans reveals that *Terastiodontosaurus*, *Todrasaurus*, and *Trogonophis* are characterized by a great enamel thickness on their teeth, a feature that is absent in other examined amphisbaenians. Size estimates show that *Terastiodontosaurus* was the largest known amphisbaenian ever to have lived, with an estimated skull length of >5 cm. Based on new muscle data of *Trogonophis*, we estimate very high bite forces for *Terastiodontosaurus*, which would allow it to crush a wide variety of snails.

Keywords: new genus and species; Palaeogene; North Africa; phylogenetic analysis; bite force; size; autecology

INTRODUCTION

Amphisbaenians are a charismatic group of fossorial squamates, with bizarre morphological features and extreme anatomical modifications (Zangerl 1944, 1945, Gans 1969, 1978, Montero and Gans 1999, Kearney 2003, Gans and Montero 2008). In particular, their unique skeletal anatomy has attracted and puzzled researchers since the 19th century (e.g. Müller 1831, Wagner 1841, Gervais 1853, Bedriaga 1884). Before the advent and broad acceptance of phylogenetic systematics, amphisbaenians were considered to be the third major group of Squamata, together with Serpentes and the paraphyletic 'Lacertilia' (Zangerl 1944, Hoffstetter 1955, 1962, Kuhn 1960, 1966, Müller 1968,

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Gans 1969, 1978, Estes 1983). Recent phylogenetic analyses, however, have placed them as the sister group of lacertid lizards, a topology that has been supported by both molecular and combined morphological and molecular evidence (Townsend *et al.* 2004, Vidal and Hedges 2009, Müller *et al.* 2011, Jones *et al.* 2013, Pyron *et al.* 2013, Hipsley and Müller 2014, Čerňanský *et al.* 2015a, Zheng and Wiens 2016, Pyron 2017, Streicher and Wiens 2017, Simões *et al.* 2018, Burbrink *et al.* 2020, Singhal *et al.* 2021, Tałanda *et al.* 2022, Brownstein *et al.* 2023); a name, Lacertibaenia Vidal & Hedges, 2009, was even proposed for the clade Amphisbaenia + Lacertidae.

Amphisbaenians have a relatively rich fossil record across the Cenozoic of Europe (Roček 1984, Schleich 1988, Augé and Rage 1995, Delfino 2003, Augé 2005, 2012, Blain *et al.* 2007, Blain 2009, Delfino *et al.* 2011, Folie *et al.* 2013, Bolet *et al.* 2014, Vianey-Liaud *et al.* 2014, Čerňanský *et al.* 2015a, 2015b, 2016a, 2020, Georgalis *et al.* 2016, 2018b, 2024, Ivanov *et al.* 2020, Syromyatnikova *et al.* 2021, Čerňanský 2023) and North America (Loomis 1919, Gilmore 1928, 1942, Taylor 1951, MacDonald 1970, Berman 1973, 1977, Estes 1983, Sullivan 1985, Kearney *et al.* 2005, Smith 2006, 2009, Hembree 2007, Smith and Gauthier 2013, Jiménez-Hidalgo *et al.* 2015, Longrich *et al.* 2015, Stocker and Kirk 2016), coupled with a few Neogene and Quaternary occurrences from South America (Gans and Montero 1998, Scanferla *et al.* 2006, Camolez and Zaher 2010, Brizuela and Albino 2012), a few Palaeogene, Neogene, and Quaternary occurrences from Africa (Rage 1976, Charig and Gans 1990, Bailon 2000, Augé and Rage 2006, Stoetzel *et al.* 2008, Rage *et al.* 2013, 2021, Saidani *et al.* 2016, El-Hares *et al.* 2022), a very few Neogene occurrences from the Arabian Peninsula (Rage 1982, Head and Müller 2022), and a very few occurrences from the Neogene of southwestern Asia (Georgalis *et al.* 2018a, Syromyatnikova *et al.* 2019). In addition, the Late Cretaceous (Campanian) *Slavoia* Sulimski, 1984, from Mongolia has been re-interpreted as a stem amphisbaenian by Tałanda (2016, 2017), and if this identification is correct, it would push back the origin of the group substantially.

Trogonophidae are a rather distinctive group of amphisbaenians that are today distributed in northern and north-central Africa (including Socotra Island, Yemen) and the Middle East (Gans 1960, 2005). Four extant genera are currently recognized, i.e. *Agamodon* Peters, 1882, *Diplometopon* Nikolski, 1907, *Pachycalamus* Günther, 1881, and the type genus, *Trogonophis* Kaup, 1830 (Gans 1960, 2005, Gans and Montero 2008). The most distinctive feature of trogonophids is their acrodont dentition (Gans 1960, El-Assy and Al-Nassar 1976, Maisano *et al.* 2006, Gans and Montero 2008), a feature that, within squamates, is otherwise present solely in the iguanian group Acrodonta (Estes 1983, Smith 2011, 2020, Smith *et al.* 2011, Georgalis *et al.* 2023). Trogonophids also possess other unique features among amphisbaenians, including locomotion and burrowing patterns, shoulder girdle or hemipenial morphology, chromosomes, vertebral arrangement, the absence of caudal autotomy, and a triangular body in cross-section (Lee 1998, Gans and Montero 2008).

Recent fieldwork in Eocene levels of the Natural Park of Djebel Chambi, Tunisia, involving French palaeontologists (Institut des Sciences de Évolution de Montpellier) and geologists (Géosciences Montpellier) and Tunisian geologists (Office National des Mines, Tunis), has led to the discovery of one of the oldest records of Amphisbaenia in Afro-Arabia. Specimens originate from the Chambi-1 (CBI-1) fossil-bearing locality, dating from the late early–early middle Eocene (e.g. Hartenberger *et al.* 2001, Ravel *et al.* 2016). Fossils consist of craniodental and vertebral remains whose morphology is so unusual that it has led us to describe here a new genus and species. Using micro-computed tomography (μCT), we assess microanatomical features of the dentition of the new taxon and compare them with other amphisbaenians. In addition, we conduct phylogenetic analysis in order to highlight the affinities of the new Tunisian taxon and of the oldest amphisbaenian from Africa, *Todrasaurus gheerbranti* Augé & Rage, 2006, from the late Palaeocene of Adrar-Mgorn 1, Morocco, which we also redescribe here using μCT imaging. With proxies such as the maxilla length and comparisons with skeletons of *Trogonophis wiegmanni* Kaup, 1830, we provide size estimates for the new taxon. Also, using new muscle data of the extant *Trogonophis*, we conduct an estimation of bite force for the new Tunisian taxon. Finally, biogeographical implications about the origins and evolution of trogonophids are proposed, in addition to implications for the functional morphology of the new taxon with these unique dental adaptations.

LOCALITY

The Djebel Chambi National Park is situated in the Kasserine area, in the Central Western part of Tunisia (Fig. 1). The material of this study comes from a fossil-bearing site [Chambi locus 1 (CBI-1)], which consists of fluvio-lacustrine deposits situated at the base of the continental sequence of Chambi (e.g. Ravel *et al.* 2016). These localities have yielded a diverse assemblage of aquatic and terrestrial vertebrates, including fishes, amphibians, turtles, crocodiles, squamates, birds (Mourer-Chauviré *et al.* 2013, 2016), and mammals, such as bats, primates, eulipotyphlans, hyaenodonts, hyracoids, an elephant shrew, a marsupial, a rodent, and a sirenian (Crochet 1986, Hartenberger 1986, Sigé 1991, Court and Hartenberger 1992, 1993, Hartenberger and Marandat 1992, Vianey-Liaud *et al.* 1994, Hartenberger *et al.* 1997, 2001, Gheerbrant and Hartenberger 1999, Tabuce *et al.* 2007, 2011, Ravel *et al.* 2011, 2012, 2015, 2016, Benoit *et al.* 2013a, 2013b, 2013c, Marivaux *et al.* 2013, 2015, Solé *et al.* 2016, Tabuce 2017). Although abundant, no remains of amphibians and reptiles from Chambi have been described to date. They were initially being studied by Jean-Claude Rage (MNHN, Paris), but unfortunately, he was unable to complete his study (Rage†, 1943–2018); amphibians were mentioned only briefly by Gardner and Rage (2016). As a first step in the publication of the diversity of the herpetofauna from Chambi and as a continuation of Rage's preliminary work, we report here the identification of a new trogonophid amphisbaenian.

MATERIALS AND METHODS

All fossil specimens of the new taxon described herein originate from recent field campaigns in the fossil bearing locality of CBI-1. The fossil specimens were found after several rounds of acid processing and screen washings of the indurated calcareous matrix of Chambi-1. All fossil material

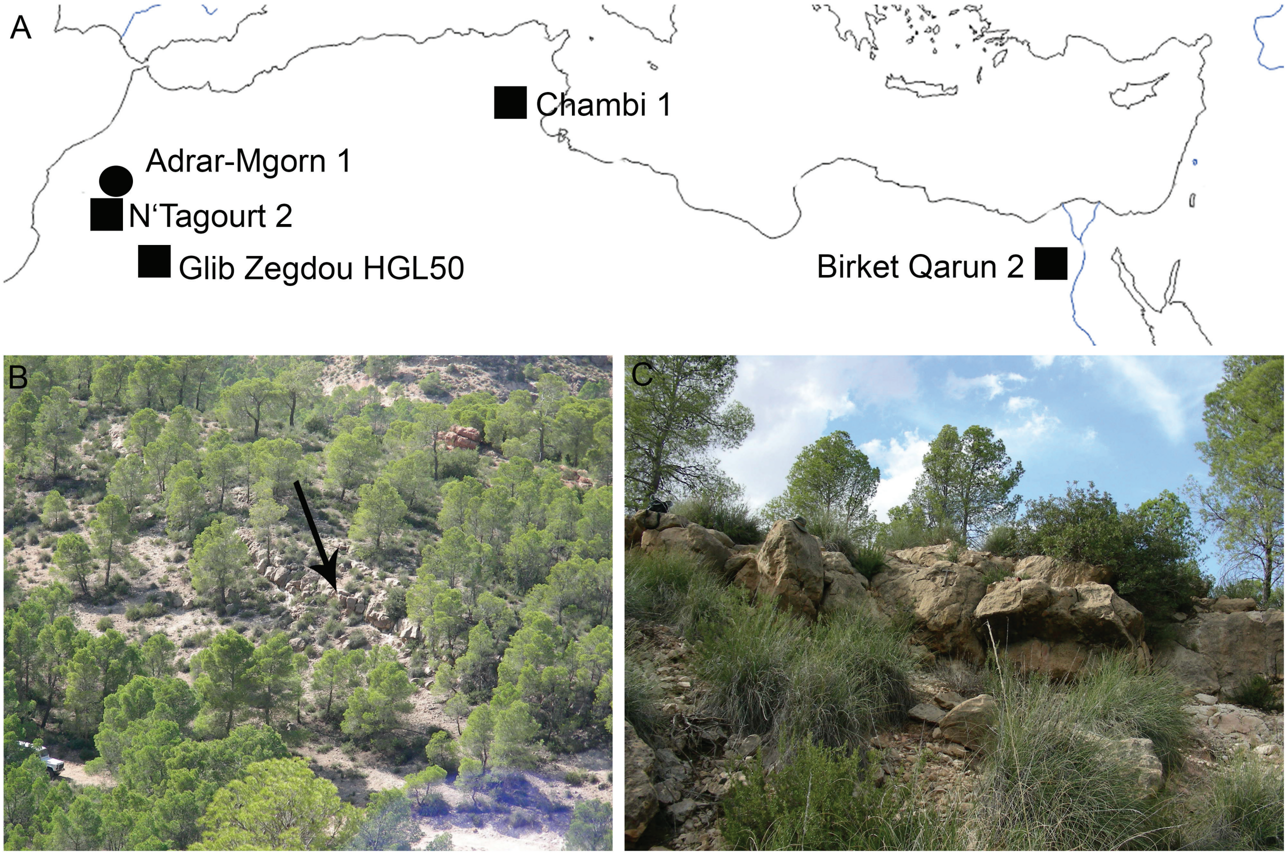

Figure 1. A, map of northern Africa, indicating the position of the late early–early middle Eocene locality of Chambi-1 (CBI-1). Also shown are the sole other few Palaeogene African localities that have yielded fossil amphisbaenians (with the exception of the record from the middle Eocene of Black Crow, Namibia). Circle for Palaeocene, square for Eocene. Map adapted from d-maps (d-maps.com). B, photograph of the CBI-1 fossil-bearing locality; arrow indicates the position of the fossiliferous limestone. C, close-up photograph of the fossiliferous limestone.

described herein from Chambi is curated at the collections of the Office National des Mines (ONM) of Tunis, Tunisia. The holotype (UM THR 407) of *Todrasaurus gheerbranti* from the late Palaeocene (Thanetian) of Adrar-Mgorn 1, Morocco, is curated permanently in the collections of the Université de Montpellier (UM). Abundant comparative material of extant amphisbaenians was studied in the collections of ISEZ, MGPT-MDHC, MNCN, NHMC, and SMF-PH. In addition, we studied μCT scans of the extant amphisbaenians *Geocalamus acutus* Sternfeld, 1912, *Monopeltis capensis* Smith, 1848, and *Zygaspis quadrifrons* (Peters, 1862), all from the collection of one of us (A.H.), plus the following specimens from the online repository of Morphosource (https://www.morphosource.org): *Geocalamus modestus* Günther, 1880 [MCZ:Herp:R-18294 (Media 000472154; ark:/87602/m4/472154)]; *Monopeltis leonhardi* Werner, 1910 [MCZ:Herp:R-150042 (Media 00472731; ark:/87602/m4/472731)]; *Pachycalamus brevis* Günther, 1881 [MVZ:Herp:236445 (Media 000066461; ark:/87602/m4/M66461)]; *Trogonophis wiegmanni* [FMNH 109462 (Media 000098610, ark:/87602/m4/M98610); MVZ:Herp:250710 (Media 000070546, ark:/87602/m4/M70546); YPM HERR 6903 (Media 000073996; ark:/87602/m4/M73996)], and one specimen of *Amphisbaena alba* Linnaeus, 1758 (FMNH 195924), available at Digimorph (Digimorph.org 2002–2024; http://www.digimorph.org/).

Anatomical terminology follows Gans (1960) and Gans and Montero (2008). Taxonomy of extant trogonophids follows Gans and Montero (2008). Authorships and original spellings of taxa were also checked directly in the primary references of Linnaeus (1758), Oppel (1811), Kaup (1830), Bonaparte (1838a), Gray (1844), Smith (1848), Baird (1858), Peters (1862, 1882), Günther (1880, 1881), Boulenger (1890), Peracca (1903), Nikolski (1907), Werner (1910), Sternfeld (1912), Dickerson (1916), Loomis (1919), Gilmore (1942), MacDonald (1970), Berman (1973, 1977), Sulimski (1984), Charig and Gans (1990), Bailon (2000), Augé and Rage (2006), Vidal and Hedges (2009), Müller *et al.* (2011), and Čerňanský *et al.* (2015a).

Micro-computed tomography

Micro-computed tomography (μCT) scanning of several fossil specimens of the new taxon from Chambi and the holotype of *Todrasaurus gheerbranti* was conducted using a μCT-scanning station EasyTom 150/Rx Solutions [Montpellier RIO Imaging (MRI), ISE-M, Montpellier, France]. Specimen ONM CBI-1-648 was damaged during μCT scanning, and the three-dimensional (3D) model of the mesh file therefore appears more incomplete than the photograph.

The 3D virtual restoration was performed with MorphoDig software (v.1.5.3; Lebrun 2018), Avizo.Lite 2019.4 (Visualization Sciences Group) software, 3D Slicer (Fedorov *et al.* 2012), and VG Studio MAX (v.2023.1). The 3D model files of the fossil specimens are deposited in MorphoMuseuM (Georgalis *et al.* in press).

Phylogenetic analysis

In order to assess the phylogenetic relationships of the Chambi taxon, we used the character–taxon matrix of Longrich *et al.* (2015). A revision of this matrix is in development; for the present, our changes were minimal. We deleted their character 308 (geographical distribution) and made some further corrections, as detailed in the list of characters (see Supporting Information, Supplementary Text), which is otherwise taken from Longrich *et al.* (2015). Furthermore, we added three characters that we discovered during our study of Trogonophidae: #308 (hypertrophy of dentary tooth), #309 (thickness of enamel on tooth crowns), and #310 (premaxillary diastema/lateral tooth 'twinning'). We also excluded a substantial number of highly fragmentary taxa in order to focus on the relationships of the better-known taxa. In total, we included 38 taxa and 310 characters.

We analysed the resulting character–taxon matrix (Supporting Information, Supplementary Text) in TNT v.1.5 (Goloboff *et al.* 2003, 2008, Goloboff and Catalano 2016) with a parsimony ratchet and with additive characters ordered, at first without any topological constraints. For our main analysis, we enforced two minimal monophyletic groupings as indicated by molecular phylogenies (e.g. Longrich *et al.* 2015), i.e. Afrobaenia (of Longrich *et al.* 2015) and *Amphisbaena* + *Leposternon*, specifically letting the new Chambi taxon, *Todrasaurus gheerbranti*, *Listromycter leakeyi* Charig & Gans, 1990, and the unnamed 'Adrar-Mgorn 1 amphisbaenian' float. Given that these results differ from recent molecular studies with respect to higher-level relationships within Afrobaenia (Graboski *et al.* 2022), we also conducted a separate analysis with constraints compatible with said studies: (Trogonophidae (*Chirindia* clade (*Monopeltis* clade, South American Amphisbaenidae))). Other fossil amphisbaenians (members of Rhineuridae, Blanidae, and Bipedidae) have not been considered to be part of Afrobaenia, hence their exclusion from that clade is not of consequence. We calculated a strict consensus and assessed the level of Bremer support and of bootstrap support (BS) for clades in it using 100 replications.

Bite force estimation

A specimen of *Trogonophis wiegmanni* from the collections of MNHN (MNHN-RA-1987.1895) was used for dissection. The jaw adductors were removed sequentially, and their 3D coordinates of origin and insertion were recorded. Muscles were subsequently weighed using a precision balance (Mettler AE100; precision, ±0.0001 g), and fibre lengths were measured using nitric acid digestion. In brief, we submerged the muscles in a 30% aqueous nitric acid solution for 24–48 h. After digestion of the connective tissue, fibres were teased apart, and the nitric acid was replaced by a 50% aqueous glycerol solution to stop further digestion. Fibres were photographed and measured using ImageJ (Schneider *et al.* 2012). For each muscle bundle, the physiological cross-sectional area was calculated assuming a muscle density of 1.06 gcm^{-1} (Mendez and Keys 1960, Leonard *et al.* 2021) and used as input for a static bite force model (Herrel *et al.* 1998). Model output was validated with *in vivo* data recorded using a Kistler force transducer (Herrel *et al.* 1999, Baeckens *et al.* 2017). Based on the orientation of the force vectors (which were derived from the anatomical features of the fossil) and assuming isometric scaling of each muscle bundle and muscle force, we then calculated the bite force of the fossil trogonophid from Chambi using the mandible of the paratype (ONM CBI-1-646).

Nomenclatural acts

The electronic edition of this article conforms to the requirements of the amended International Code of Zoological Nomenclature (ICZN), hence the new names contained herein are available under that Code from the electronic edition of this article. This published work and the nomenclatural acts it contains have been registered in ZooBank, the official registry of zoological nomenclature for the ICZN. The ZooBank LSIDs (Life Science Identifiers) can be resolved and the associated information viewed through any standard web browser by appending the LSID to the prefix 'https://zoobank.org/'. The LSID for this publication is: urn:lsid:zoobank.org:pub:6DF599A3-0A7B-4A76-AA28-81147F6733FF. The LSID for the new genus *Terastiodontosaurus* is: urn:lsid:zoobank.org:act:DC23B781-B109-4EFB-9C0B-DA42DC09B838. The LSID for the new species *Terastiodontosaurus marcelosanchezi* is: urn:lsid:zoobank.org:act:881978AE-4954-4D2C-8D6E-12CD56CB4C20.

Institutional abbreviations

FMNH, Herpetology collection, Field Museum of Natural History, Chicago, IL, USA; **ISE-M,** Institut des Sciences de l'Évolution de Montpellier, Montpellier, France; **ISEZ**, Institute of Systematics and Evolution of Animals, Polish Academy of Sciences, Krakow, Poland; **MCZ**, Herpetology collection, Museum of Comparative Zoology, Harvard University, Cambridge, MA, USA; **MGPT-MDHC**, Massimo Delfino Herpetological Collection, University of Torino, Torino, Italy; **MNCN**, Museo Nacional de Ciencias Naturales, Madrid, Spain; **MNHN**, Muséum national d'Histoire naturelle, Paris, France; **MVZ**, Herpetology collection, Museum of Vertebrate Zoology, University of California, Berkeley, CA, USA; **NHMC**, Natural History Museum and University of Crete, Herakleion, Greece; **NHMUK,** Natural History Museum, London, UK; **ONM**, Palaeontological collections of the Museum of the Office National des Mines, Tunis, Tunisia; **SMF-PH**, Palaeoherpetology collection, Senckenberg Forschungsinstitut und Naturmuseum, Frankfurt am Main, Germany; **UM**, Université de Montpellier, Montpellier, France; **YPM**, Herpetology collection, Yale Peabody Museum of Natural History, New Haven, CT, USA.

RESULTS

Systematic palaeontology

Squamata Oppel 1811

Amphisbaenia Gray, 1844

Trogonophidae Bonaparte, 1838a

Terastiodontosaurus Georgalis & Smith **gen. nov.**

Zoobank registration: urn:lsid:zoobank.org:act:DC23B781-B109-4EFB-9C0B-DA42DC09B838

Etymology: The genus name derives from the Greek words 'τεράστιος' ('terastios'), meaning 'huge'/'enormous', 'ὀδούς' [in genitive: 'ὀδόντος' ('odontos')], meaning 'tooth', and 'σαύρα' ('saura'), meaning 'lizard'. The gender of the new genus name is masculine.

Type and only known species: Terastiodontosaurus marcelosanchezi Georgalis & Smith gen. et sp. nov.

Diagnosis: As for the type and only known species.

Note on the proper authorship and spelling of Trogonophidae: Although authorship of Trogonophidae is generally attributed to Gray (1865) (e.g. Estes 1983, Bailon 2000, Kearney 2003), it should be noted that versions of that name had also appeared earlier. These are the Trogonophidina of Bonaparte (1838a), Trogonophina of Bonaparte (1838b, 1839, 1840a, 1840b), Trogonophidæ of Gray (1840), and Trogonophes of Fitzinger (1843). Even within the works of Gray, that author earlier misspelled this group as Trigonophes and Trigonophidae (Gray 1844), with Kuhn (1966, 1967) subsequently assigning authorship to Gray (1844). Vanzolini (1951) supposedly created Trogonophinae as a new subfamily; however, obviously this cannot be the case following the Principle of Coordination of ICZN (1999: Article 36), which dictates that 'A name established for a taxon at any rank in the family group is deemed to have been simultaneously established for nominal taxa at all other ranks in the family group'. This being said, it thus appears that Trogonophidina of Bonaparte (1838a: 392) is the first introduction of the name, although it was not accompanied by a diagnosis or an explicit mention of a type genus. The same applies to the second usage of the name, again by the same author and again in the same year, Trogonophina of Bonaparte (1838b: 124), which also was not accompanied by a diagnosis or a type genus. The following year, Bonaparte (1839: 10) applied, for the first time, a (rather brief) diagnosis for Trogonophina, simply stating 'Dentes cum maxillis concreti', but again still no explicit mention of a type genus was made; this is also exactly the case for his subsequent works (Bonaparte 1840a: 286, 1840b: 99), where he applied the name with the same exactly diagnosis but again with no explicit mention of a type genus. Later on, the same author added the number of species he included in that group (i.e. one) and its geographical distribution as 'Africa' (Bonaparte 1850, 1852). Duméril and Bibron (1839) used the name Trogonophides, also providing a thorough description of *Trogonophis wiegmanni*; however, it is evident in their text that this name was simply an informal plural name for the genus *Trogonophis*, for which they were also using the informal singular term 'Le Trogonophide'. Gray (1840: 42) was the first explicitly to mention a genus ('*Trogonophis*, Kaup') associated with his family group name Trogonophidæ, and Fitzinger (1843) was the first explicitly to mention both a genus ('*Trogonophis*. Kaup') and a species ('*Trogonoph. Wiegmanni*. Kaup') associated with his family group name Trogonophes. Nevertheless, an explicit mention of a type genus is not a formal requirement for family-group names that were established before 1999, but instead it is enough that there is an indirect inference of the genus from the stem of the family-group name (see ICZN 1999: Article 11.7). Accordingly, authorship of Trogonophidae should be attributed to Bonaparte (1838a).

This being said and now that the proper authorship of the family-group name is clarified, a further comment on the proper spelling of the name is also required. Taking into consideration that the proper authorship of the family-group name is Bonaparte (1838a), it follows that his Trogonophidina would be transformed into Trogonophididae, a spelling that has not appeared the literature. It should be noted that some, mostly recent, authors have used the spelling Trogonophiidae (e.g. Pyron *et al.* 2013, Čerňanský *et al.* 2015a, Zheng and Wiens 2016, Burbrink *et al.* 2020). Nevertheless, the spelling that has made the most frequent appearance in the literature is Trogonophidae (e.g. Gray 1840, Cope 1887, Taylor 1951, El-Assy and Al-Nassar 1976, Gans 1978, Estes 1983, Charig and Gans 1990, Bailon 2000, Kearney 2002, 2003, Augé 2005, 2012, Vidal and Hedges 2005, Maisano *et al.* 2006, Gans and Montero 2008, Vidal *et al.* 2008, Wiens *et al.* 2010, 2012, Longrich *et al.* 2015, Baeckens *et al.* 2017, Hawkins *et al.* 2022, Araújo Salvino *et al.* 2024, Bell *et al.* 2024). Following ICZN (1999: Article 29.5), the spelling of a family-group name that is in prevailing usage should be maintained, even if this spelling is not the original spelling and even if its derivation from the name of the type genus is not formed in a grammatically correct manner. Accordingly, the proper spelling of this family-group name is Trogonophidae.

Terastiodontosaurus marcelosanchezi
Georgalis & Smith sp. nov.

(Figs 2–17, 23A; Supporting Information, Figs S1–S6)

Zoobank registration: urn:lsid:zoobank.org:act:881978AE-4954-4D2C-8D6E-12CD56CB4C20

Etymology: The species epithet is named after Professor Marcelo Sánchez-Villagra, director of the Palaeontological Institute of the University of Zurich, as an honour for his major contributions to palaeontology, zoology, and evolutionary biology, in addition to the kind friendship and his great support to the first author (G.L.G.) for many years.

Holotype: A right maxilla (ONM CBI-1-645) (Figs 2, 3).

Paratype: A left dentary (ONM CBI-1-646) (Figs 4, 5, 23A).

Referred specimens: Four premaxillae (ONM CBI-1-658, ONM CBI-1-672, ONM CBI-1-711, and ONM CBI-1-1021), five right maxillae (ONM CBI-1-649, ONM CBI-1-651, ONM CBI-1-654, ONM CBI-1-667, and ONM CBI-1-1017), six left maxillae (ONM CBI-1-648, ONM CBI-1-653, ONM CBI-1-1012, ONM CBI-1-1016, ONM CBI-1-1018, and ONM CBI-1-1022), one right maxilla fragment (ONM CBI-1-650), five right dentaries (ONM CBI-1-656, ONM CBI-1-660, ONM CBI-1-666, ONM CBI-1-1013, and ONM CBI-1-1020), 10 left dentaries (ONM CBI-1-647, ONM CBI-1-655, ONM CBI-1-657, ONM CBI-1-659, ONM CBI-1-661, ONM CBI-1-662, ONM CBI-1-668, ONM CBI-1-670, ONM CBI-1-1014, and ONM CBI-1-1015), a fragment of the coronoid process of a left dentary (ONM CBI-1-664), and 17 tooth-bearing bone fragments (ONM CBI-1-652 and ONM CBI-1-671 [16 elements]). Tentatively also: numerous presacral vertebrae (ONM CBI-1-673, ONM CBI-1-682, ONM CBI-1-685, ONM CBI-1-687,

ONM CBI-1-691 [‘lot / batch’ with numerous vertebrae], ONM CBI-1-706 [‘lot / batch’ with numerous vertebrae], ONM CBI-1-820, ONM CBI-1-833, and ONM CBI-1-860) and two caudal vertebrae (ONM CBI-1-686 and ONM CBI-1-689).

Diagnosis: Terastiodontosaurus marcelosanchezi can be referred to Amphisbaenia based on the prominent and enlarged median premaxillary tooth, the large anterior premaxillary foramina, the low tooth count on the maxilla and dentary, the ventral extension of the mandibular symphysis below Meckel’s groove, the broad insertion fossa for mandibular adductor muscles on the posterolateral surface of the dentary, and the strong and elevated coronoid process of the dentary. *Terastiodontosaurus marcelosanchezi* can be referred to Trogonophidae based on the presence of acrodont dentition, closely appressed (‘fused’) teeth, the interdigitating suture between the frontal and the facial process of the maxilla, and ectopterygoid abutting the posteromedial corner of the maxilla.

Terastiodontosaurus marcelosanchezi is united with *Trogonophis wiegmanni* by: thick enamel on marginal teeth, and ‘twinning’ of paired premaxillary teeth, with median tooth separated by a diastema from paired teeth. *Terastiodontosaurus marcelosanchezi* is united with *Todrasaurus gheerbranti* by: thick enamel on marginal teeth, extremely enlarged (>60% longer than adjacent teeth) dentary tooth 3–4 positions from the rear, and small ‘hills’ on posterior dentary teeth. *Terastiodontosaurus marcelosanchezi* can be differentiated from all other amphisbaenians by the combination of the following features: very large size (with maximum known maxilla length >16 mm and maximum dentary length of 17 mm), the flat apical surface of the cheek teeth, the position of the largest tooth on the maxilla, the number of maxillary teeth (usually three maxillary teeth), the ratio of the largest maxillary tooth length to the total maxillary tooth row length (between 0.5 and 0.7), and the position of the largest tooth on the dentary (fourth from posterior).

Type locality and horizon: Chambi 1 (CBI-1), Djebel Chambi, Kassérine region, western part of Central Tunisia, Tunisia; late early to early middle Eocene (late Ypresian to early Lutetian).

Geographical and stratigraphical range: Taxon known exclusively from its type locality.

Nomenclatural remark on the new taxon: The authorship of this new genus and species should be referred to as *Terastiodontosaurus* Georgalis & Smith gen. nov. (for the new genus) and *Terastiodontosaurus marcelosanchezi* Georgalis & Smith gen. et sp. nov. (for the new species), following Article 50.1 and the ‘recommendation 50A concerning multiple authors’ of the International Code of Zoological Nomenclature (ICZN 1999).

Description

Holotype (Figs 2, 3)

The holotype right maxilla (ONM CBI-1-645) is almost complete (Figs 2, 3). The premaxillary process curves up anterodorsally, forming part of the medial border of the external naris. The sharp rim weakens anteriorly, and the anterior portion of the process as a whole slopes ventrolaterally. The dorsal surface is slightly striated, probably where it was overlapped by the septomaxilla. The ventral surface of the premaxillary process curves upwards and is more coarsely striated where it overlaps the premaxilla. The superior alveolar canal opens anteriorly through two foramina: a dorsally directed foramen on the medial side of the facial process, and an anteriorly directed foramen immediately anterior to the facial process; between them the canal is roofed, but there appears to be a narrow groove, as if two growing folds of perichondral bone met over a channel but did not fuse fully. Anterior to the anterior opening of the superior alveolar canal the dorsal surface of the premaxillary process is coarsely striated; here it was probably overlain by the septomaxilla, into which the neurovascular structure(s) of the superior alveolar nerve continued. It is unclear whether the division of the anterior opening of the superior alveolar canal marks a separation of the course of the subnarial artery and superior alveolar nerve, as in Iguanidae (Oelrich 1956, Smith 2009).

On the medial side of the premaxillary process is a strong, dorsomedially facing facet for the vomer. Behind this the palatal shelf is restricted and its dorsal surface hollows out, where Jacobson’s organ sat; together with the vomer, here the maxilla formed the fenestra vomeronasalis externa. Posterior to the cavity for Jacobson’s organ the maxilla possesses a distinct medial process that contacts the horizontal wing of the vomer. The process continues laterally across the palatal shelf and extends posterodorsally as a weak ridge on the medial surface of the facial process of the maxilla. In other squamates, Smith and Gauthier (2013) identified this as the ‘nasolacrimal ridge’ after ascertaining a relationship with the lacrimal duct.

Behind this process the palatal shelf is medially extensive. A distinct palatine process is absent, but an extensive, striated facet for the palatine articulation is present. The (posterior) superior alveolar foramen opens at the level of the anterior end of the palatine facet. A distinct facet for the ectopterygoid cannot be discerned, but it must have been an abutting one, and it might be confluent with the palatine facet.

The posterior process of the maxilla is broad and flares sharply outwards (or laterad *fide* Gans and Montero 2008). Although striated surfaces of this maxilla commonly show tiny holes, the entire posterior surface of the posterior process is heavily porous and coarsely striated. Dorsally, the posterior process is thick and also coarsely longitudinally striated; there is no evidence that a distinct element articulated on this suborbital part of the maxilla.

The facial process is thick. A rough facet for the nasal bone is found on the anterior margin of the facial process and turns posterodorsally as it ascends the process. There is a distinct change in angulation below the peak of the facial process, and the facet behind it (now more on the medial than the anterior surface of the facial process) is smoother; probably, the change marks the boundary between the nasal and part of the frontal facet. Immediately behind its apex the facial process is deeply notched, almost certainly to receive a tongue-like process of the frontal bone. Additionally, there is a number of rough, anteroventrally trending ridges and grooves posterior to the frontal notch, which possibly indicate a more extensive overlap of the maxilla on the prefrontal (like in lizards) than is observed today in *Trogonophis wiegmanni*.

Figure 2. Holotype right maxilla (ONM CBI-1-645) of ***Terastiodontosaurus marcelosanchezi***. Photographs of the specimen in labial (A), medial (B), dorsal (C), and ventral (D) views.

The lateral surface of the maxilla is porous and weakly rugose in its dorsal part, with some longitudinal grooves and ridges on the posterior process. There are three distinct labial foramina, all of them more or less above the level of the largest tooth. The two anterior ones are more closely spaced, while there is a considerable distance between the middle and posterior one, the latter

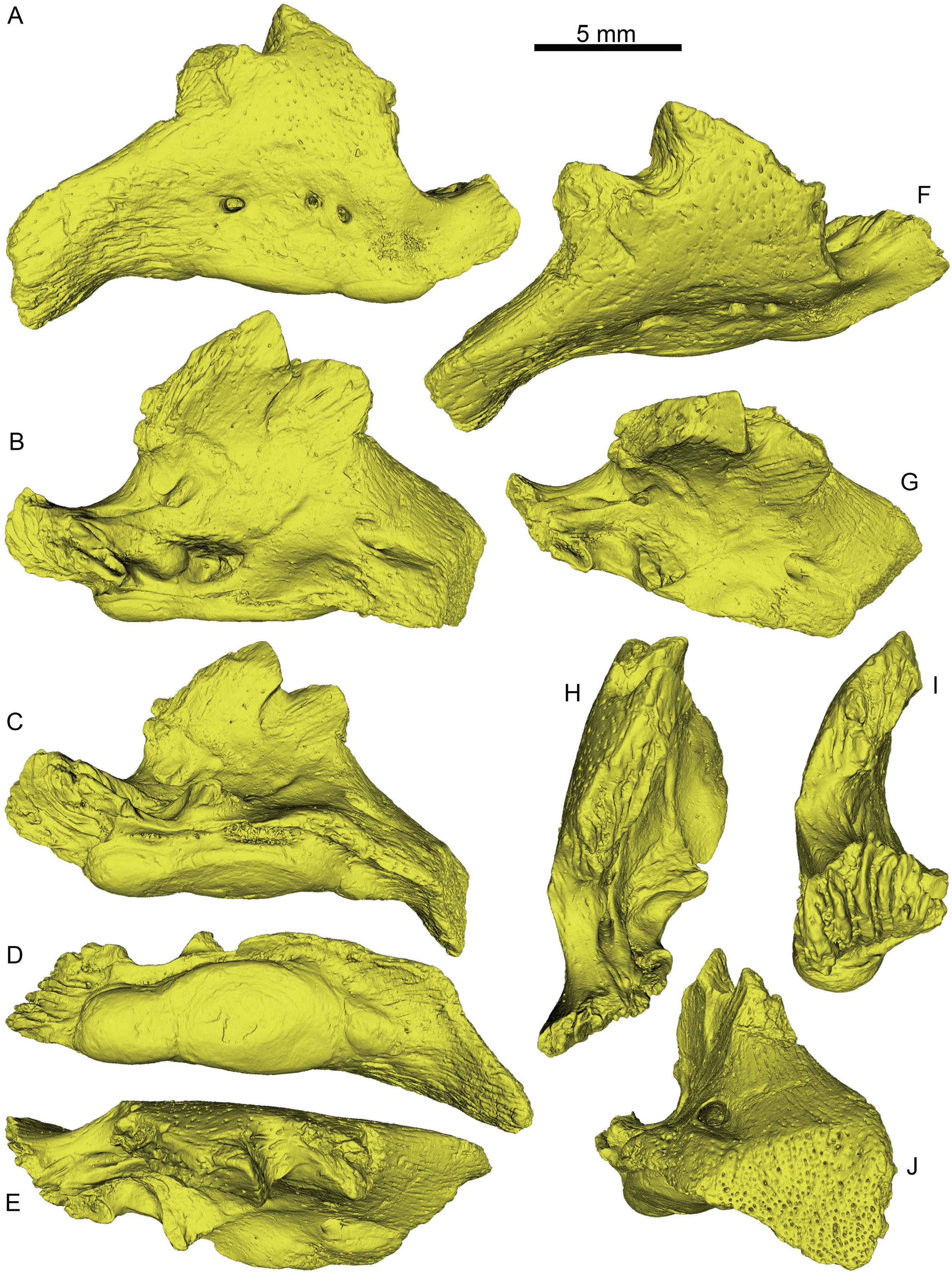

Figure 3. Holotype right maxilla (ONM CBI-1-645) of ***Terastiodontosaurus marcelosanchezi***. μCT 3D reconstructions of the specimen in labial (A), medial (B), ventromedial (C), ventral (D), dorsal (E), dorsolateral (F), dorsomedial (G), anterodorsal (H), anterior (I), and posterior (J) views.

also being the largest. These foramina communicate internally, as expected, with the superior alveolar canal, which runs longitudinally through the maxilla immediately above the tooth row. It conveys the superior alveolar nerve, which passes from the orbit into the maxillary canal through the superior alveolar foramen, in addition to the maxillary artery (Oelrich 1956).

The dentition is acrodont. The maxilla possesses only three teeth, of which the second is by far the largest (some 75% longer than the next-largest tooth) and, in fact, covers much of the ventral portion of the bone; this tooth is followed in size by the anteriormost tooth, while the posteriormost tooth is considerably tiny. The teeth are closely appressed, with no interdental gaps between them. All three teeth are much flattened, particularly the two largest ones: their dorsoventral height is extremely low. Moreover, the µCT scan reveals that the enamel is extremely thick (Supporting Information, Fig. S1A). Several nutritive foramina are present at the base of the teeth.

Paratype (Figs 4, 5)

The paratype left dentary (ONM CBI-1-646) is relatively complete (Figs 4, 5). It is referred to the same species on the basis of co-occurrence and the following derived morphological

Figure 4. Paratype left dentary (ONM CBI-1-646) of ***Terastiodontosaurus marcelosanchezi***. Photographs of the specimen in labial (A), medial (B), and dorsal (C) views.

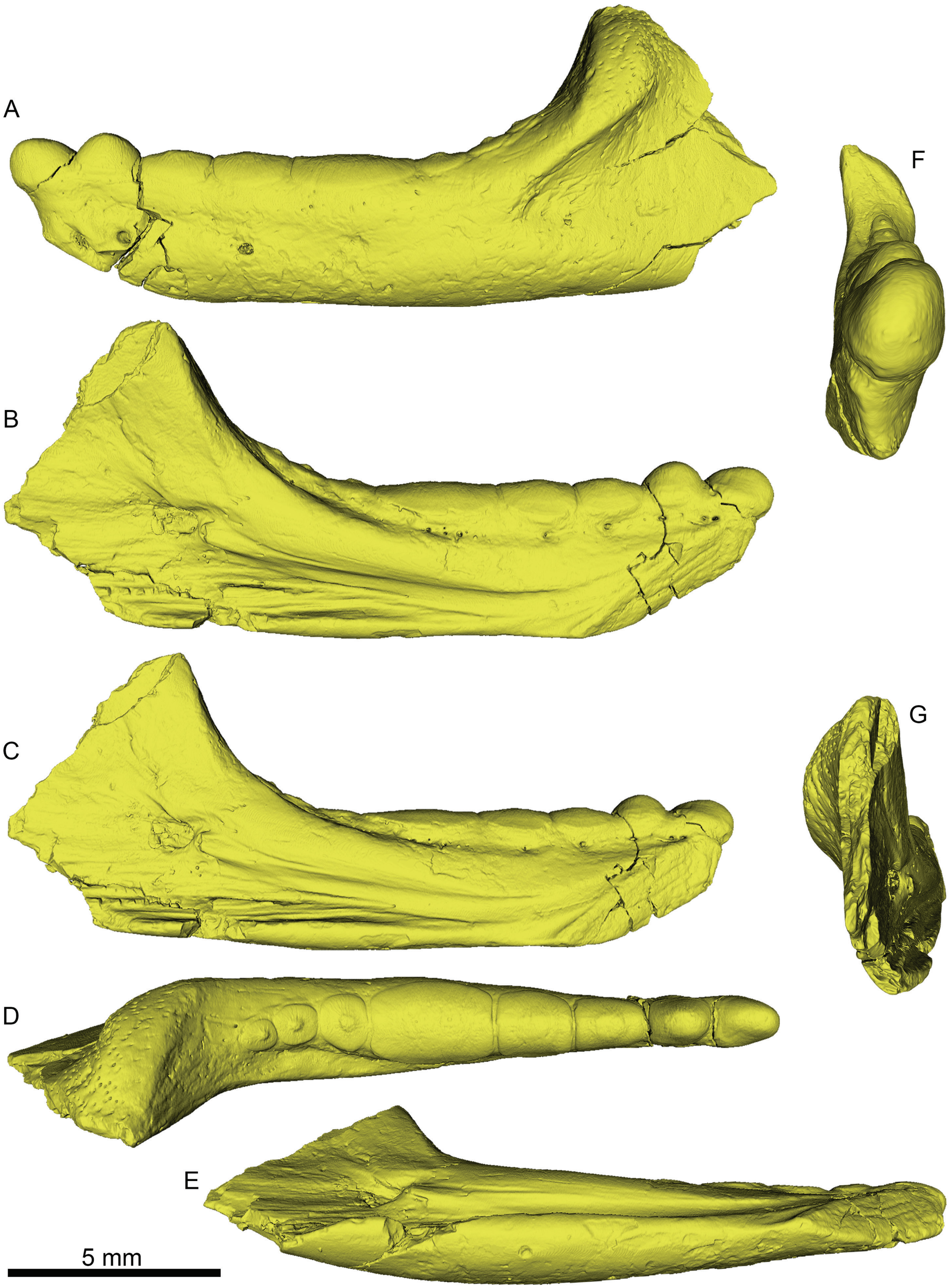

Figure 5. Paratype left dentary (ONM CBI-1-646) of ***Terastiodontosaurus marcelosanchezi***. µCT 3D reconstructions of the specimen in labial (A), medial (B), ventromedial (C), dorsal (D), ventral (E), anterodorsal (F), and posterior (G) views. Note that the specimen was slightly damaged during micro-computed tomography scanning, hence the difference from the photographs in Figure 4.

features: great enamel thickness, reduced tooth row length and tooth count, presence of a greatly enlarged tooth, the 'hill' on the small, posteriormost teeth, and the apically flat teeth in the middle.

The symphysis is broad and anterodorsally inclined. As in other amphisbaenians (Longrich *et al.* 2015), it is not restricted to the area above the Meckelian groove but instead curves anteroventrally around it and terminates posteroventrally in a sharp corner. It appears as though the Meckelian groove is closed and fused immediately behind the symphysis and that the Meckelian cartilage itself might be ossified as an anterodorsally–posteroventrally extensive wedge in the centre of the symphysis, but this interpretation is not entirely clear.

Meckel's groove is open (Figs 4, 5B, C). Above it is the indistinct supra-Meckelian lip (of Bhullar and Smith 2008), above which is the subdental shelf (*sensu* Rage and Augé 2010) that extends medial to the tooth row. The subdental shelf commences below the posterior portion of the first tooth. It is narrow anteriorly and becomes gradually wider in the posterior half of the dentary, and behind the tooth row it grades into the coronoid process. The part of the groove in which Meckel's cartilage was situated is relatively narrow throughout most of its length, but it widens a bit posteriorly, immediately in front of the mandibular foramen. That groove is straight for most of its length but turns up strongly near the symphysis, giving it a hockey-stick shape, as in other amphisbaenians (Longrich *et al.* 2015). Posteriorly in the dentary there are two strong, elongate facets below the groove for Meckel's cartilage, for the angular and the splenial. The presence of two distinct facets strongly suggests that those mandibular elements were discrete, not fused, as in *Trogonophis wiegmanni*, where only one facet is present; of course, without the remainder of the mandible this cannot be taken as certain. The angular facet extends as far anteriorly as the anterior end of the enlarged tooth (fourth from the back), whereas the splenial facet only just passes the posterior end of the enlarged tooth. The ventral margin of the dentary behind the symphysis is straight.

The dentary possesses a posterodorsally ascending coronoid process immediately behind the posteriormost tooth. The dorsal tip of the process is incomplete, but even the preserved portion extends high above the tooth row, as in other amphisbaenians. The process is prominent and thick. There is a strong diagonal ridge on its lateral surface that delineates the adductor fossa dorsally. The ridge is narrower at its base but grows thick and porous as it curves dorsally and then diminishes; it might have served as an attachment site for other jaw adductors, probably via a bodenaponeurosis.

The mandibular canal runs across the length of the dentary, transmitting the inferior alveolar nerve and mandibular artery; it communicates with the labial foramina present in the labial surface of the dentary and with the nutritive foramina at the bases of the teeth. Its entrance is the mandibular foramen, which is located well behind the tooth row at the level of the anterior edge of the coronoid process. In labial view (Figs 4A, 5A), four labial foramina are present in the anterior half of the dentary.

The dentary bears eight acrodont teeth, of which the largest is the fourth from posterior. The posteriormost tooth is the smallest one. The first two teeth are bulbous, and the anteriormost tooth is procumbent, extending beyond the anterior margin of the symphysis. As in the holotype maxilla described above, the teeth are closely appressed, with almost no interdental gaps between them (at maximum, only tiny empty spaces between some but not all teeth). All teeth except for the first two are much flattened (particularly the two largest ones), with the exception of the two anteriormost ones, which are bulbous and tall. The posterior teeth have tiny central cusps. Multiple nutritive foramina are situated above the subdental shelf ventrally to the each of the tooth bases.

Referred specimens

Premaxillae (Figs 6–8)

The most complete premaxillae are ONM CBI-1-672 and ONM CBI-1-711, which include a large portion of the nasal process, whereas this structure is mostly broken in ONM CBI-1-658 and ONM CBI-1-1021 (Figs 6–8; Supporting Information, Fig. S2). The nasal process is large, dorsoventrally elongated and moderately wide; it gradually narrows in width apically. Given its preserved extent, it is likely that the nasal process reached the frontals, a condition unique to Trogonophidae among amphisbaenians (Kearney 2003), but more complete specimens are needed to verify this. A pair of large anterior premaxillary foramina is developed at the base of the nasal process. These are the anterior openings for the ethmoidal nerve that enters the premaxilla through the posterior premaxillary foramina on the posterior side of the nasal process. No rostral process or rostral blade is present. The palatal shelf or alveolar plate is most complete in ONM CBI-1-672 (Figs 7C, D, 8P–R), but it is ONM CBI-1-658 (Figs 6F, G, 8J–L) that most clearly shows it to be bipartite.

The dentition is acrodont. On the alveolar plate, there are five teeth, all of bulbous morphology. The central median tooth is the most robust and prominent (a synapomorphy of amphisbaenians; see Gans 1978, Smith 2009). The μCT scans reveal that the median tooth possesses great apical enamel thickness (Supporting Information, Fig. S1C). There is a diastema between the median tooth and the lateral ones that contrasts strongly with the otherwise close appression of the teeth generally and gives the impression of the lateral two teeth being 'twinned'. In fact, in the two pairs of lateral teeth, the dental gaps between the teeth are almost absent. A slight vertical striation is observable on all teeth, being more distinct in the central tooth.

Maxillae (Figs 9–12)

The available maxillae pertain to different-sized individuals, as can be attested by the drastic size range between the smallest and the largest specimens (see Supporting Information, Figs S3, S4). The most complete maxillae are the holotype (ONM CBI-1-645) and the specimens ONM CBI-1-649 (Figs 9E, F, 11J–Q) and ONM CBI-1-654 (Fig. 11A–I), which are both significantly smaller. In fact, the holotype ONM CBI-1-645 (Figs 2, 3) represents the largest known individual of *Terastiodontosaurus marcelosanchezi*, whereas ONM CBI-1-649 represents one of the smallest among our sample. Nevertheless, the morphology of the maxillae overall is very similar. Here, we focus on comparisons.

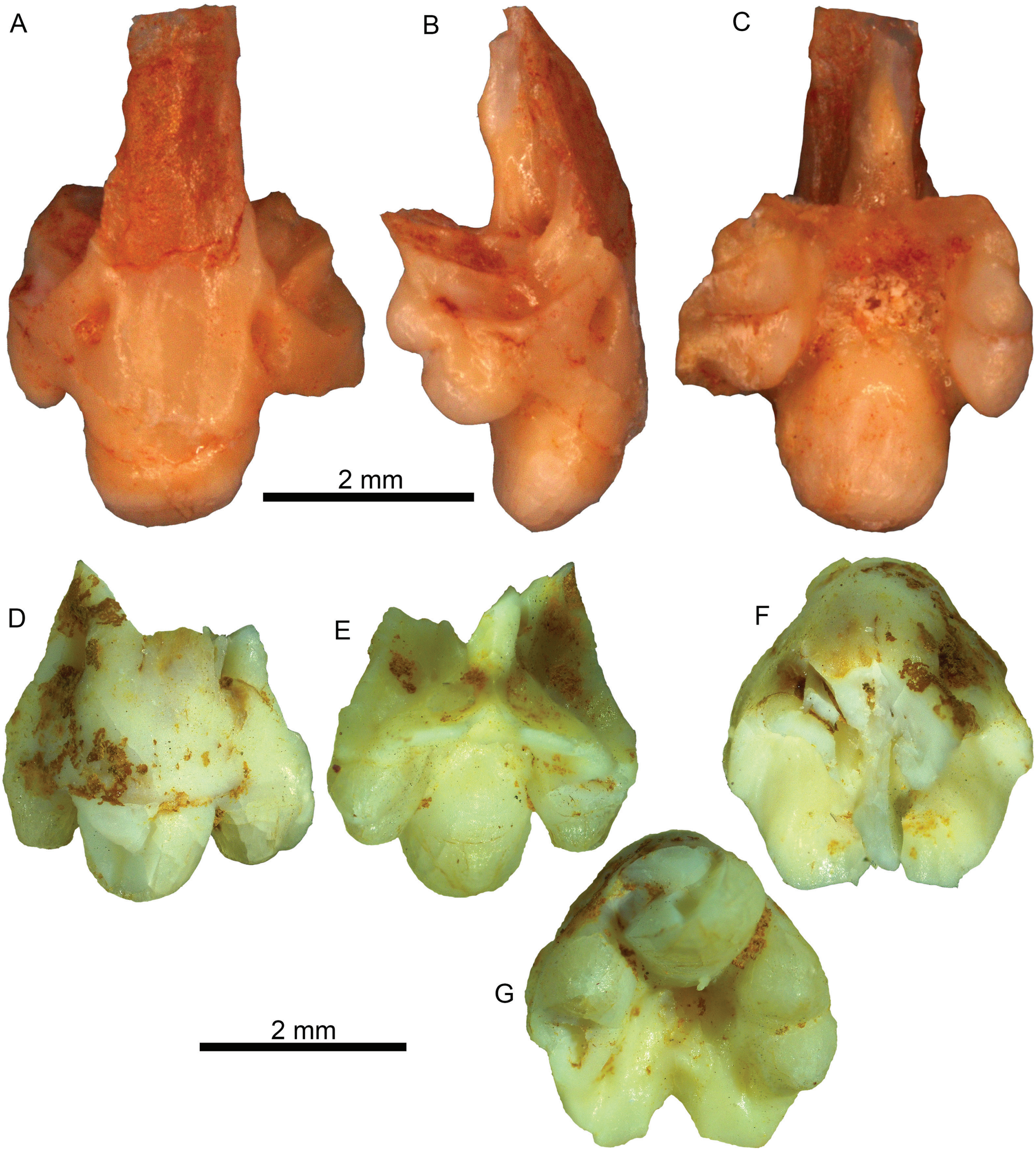

Figure 6. Premaxillae of ***Terastiodontosaurus marcelosanchezi***. Photographs of the larger specimens: A–C, ONM CBI-1-711 in anterior (A), right lateral (B), and posterior (C) views; and D–G, ONM CBI-1-658 in anterior (D), posterior (E), dorsal (F), and ventral (G) views.

The anterodorsally trending premaxillary process is best preserved or complete in ONM CBI-1-654 (Fig. 11A–I), ONM CBI-1-649 (Figs 9E, F, 11J–Q), the holotype ONM CBI-1-645 (Figs 2, 3), and the fragmentary specimens ONM CBI-1-1012 (Fig. 12G–I), ONM CBI-1-1016 (Fig. 12J–L), ONM CBI-1-1018 (Fig. 12M–O), and ONM CBI-1-1022 (Fig. 12P–R). The outwardly flaring posterior process of the maxilla is most complete in ONM CBI-1-654 (Fig. 11A–I), followed in completeness by the holotype ONM CBI-1-645 (Figs 2, 3), ONM CBI-1-649 (Figs 9E, F, 11J–Q), ONM CBI-1-651 (Fig. 10E–J), ONM CBI-1-653 (Fig. 11R–U), ONM CBI-1-667 (Fig. 12A–C), and ONM CBI-1-1017 (Fig. 12D–F). A medial process that contacts the horizontal wing of the vomer is clearest in the holotype (ONM CBI-1-645) and especially in ONM CBI-1-648

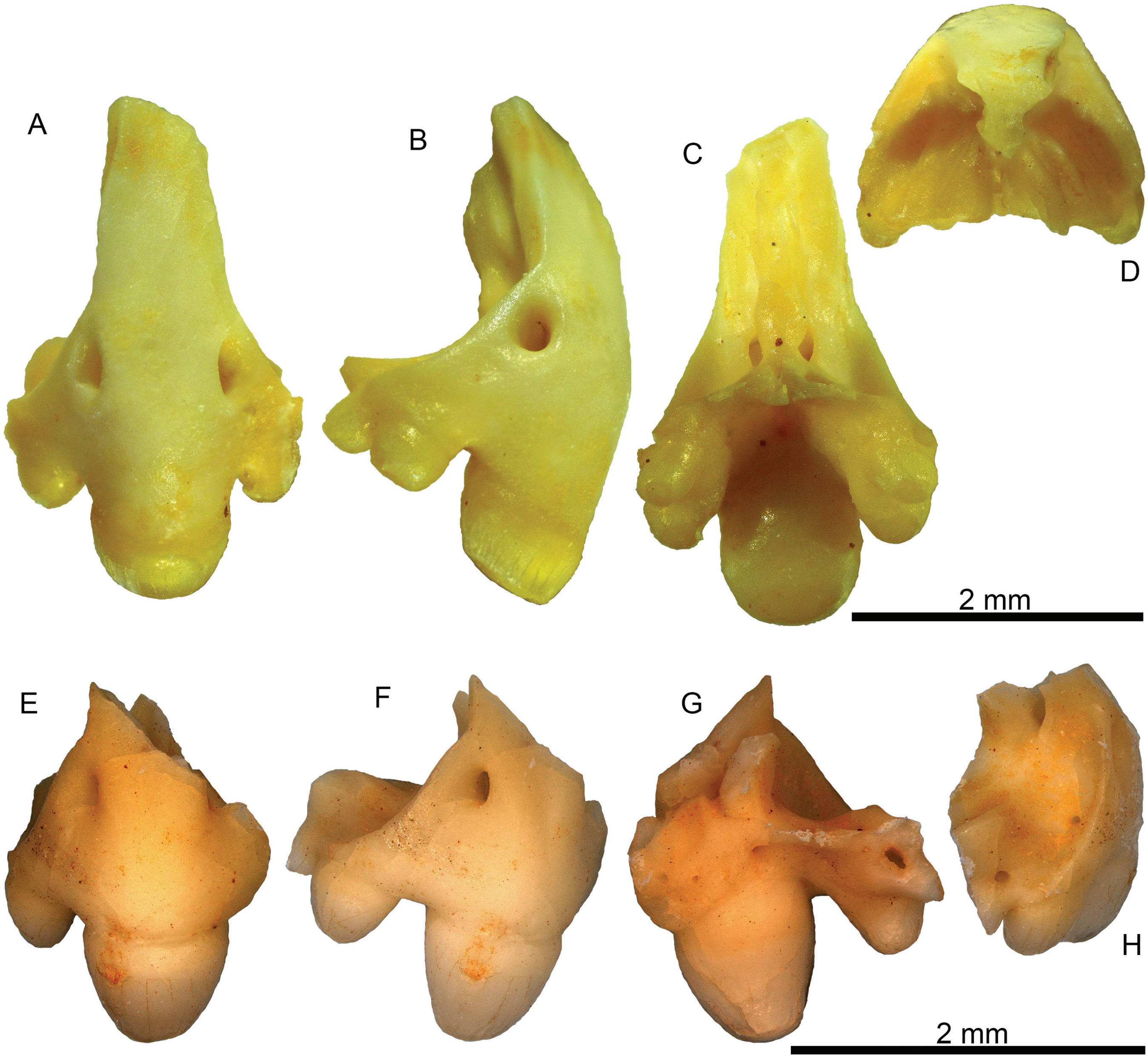

Figure 7. Premaxillae of ***Terastiodontosaurus marcelosanchezi***. Photographs of the smaller specimens: A–D, ONM CBI-1-672 in anterior (A), right lateral (B), posterior (C), and dorsal (D) views; and E–H, ONM CBI-1-1021 in anterior (E), right anterolateral (F), posterior (G), right dorsolateral (H) views.

(Figs 9B, C, 10B, C) and ONM CBI-1-649 (Figs 9E, F, 11K–Q). The porosity and ridge-like form of the labial surface, observed in the holotype ONM CBI-1-645 (Figs 2A, 3A, F), is otherwise evident only in the second largest specimen (ONM CBI-1-651; Fig. 10E) and is absent in all other smaller specimens, in which this surface is almost completely smooth. This suggests that this feature is subject to size/ontogenetic variation.

There are three labial foramina, placed almost in a row, in the holotype ONM CBI-1-645 (Figs 2A, 3A) and in ONM CBI-1-649 (Figs 9G, 11J); in both these specimens, the two anterior foramina are more closely spaced. ONM CBI-1-648 also has three labial foramina (Fig. 9A), but the posterior two foramina are more closely spaced. In ONM CBI-1-649, there is also a further foramen situated dorsal to the row of the three foramina, situated approximately above the first foramen. Even more, in ONM CBI-1-654, there are two small foramina above the two of three foramina (Fig. 11A). The number of foramina cannot be assessed fully in the remaining incomplete maxillae. The superior alveolar foramen is usually relatively large.

Similar to the holotype (ONM CBI-1-645), maxillae almost always bear three teeth, of which the second is by far the largest and, in fact, covers much of the ventral portion of the bone; this tooth is followed in size by the anteriormost tooth, while the posteriormost tooth is tiny. However, there are two notable exceptions, denoting some degree of variability: in ONM CBI-1-651, there is a fourth tiny tooth located posteromedially to the third tooth, not in line with it (Fig. 10F), while in ONM CBI-1-649 the tiniest tooth is absent, meaning that specimen

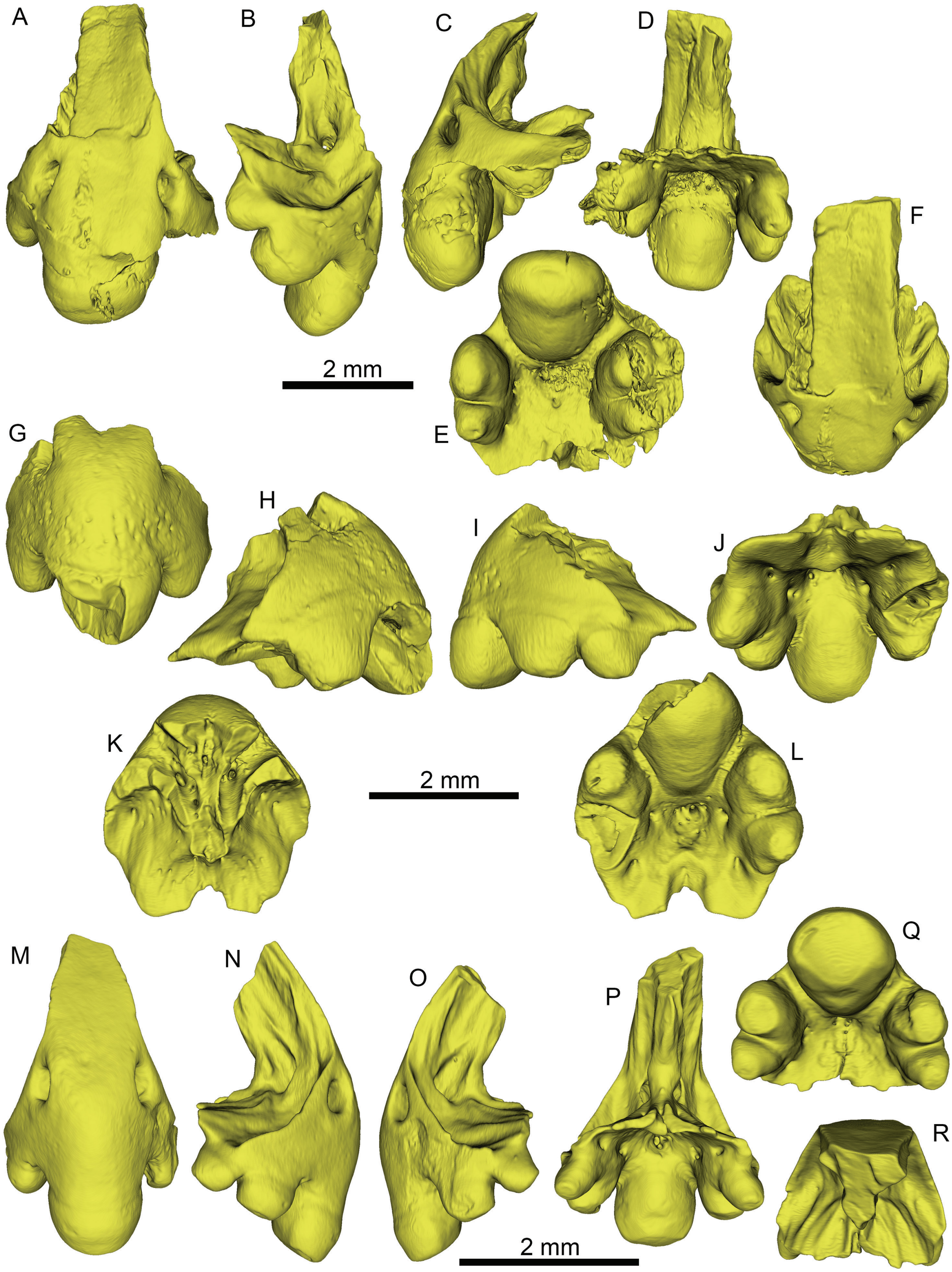

Figure 8. Premaxillae of ***Terastiodontosaurus marcelosanchezi***. μCT 3D reconstructions of: A–F, ONM CBI-1-711 in anterior (A), right lateral (B), left ventrolateral (C), posterior (D), ventral (E), and dorsal (F) views; G–L, ONM CBI-1-658 in anterior (G), right lateral (H), left lateral (I), posterior (J), dorsal (K), and ventral (L) views; and M–R, ONM CBI-1-672 in anterior (M), right lateral (N), left lateral (O), posterior (P), ventral (Q), and dorsal (R) views.

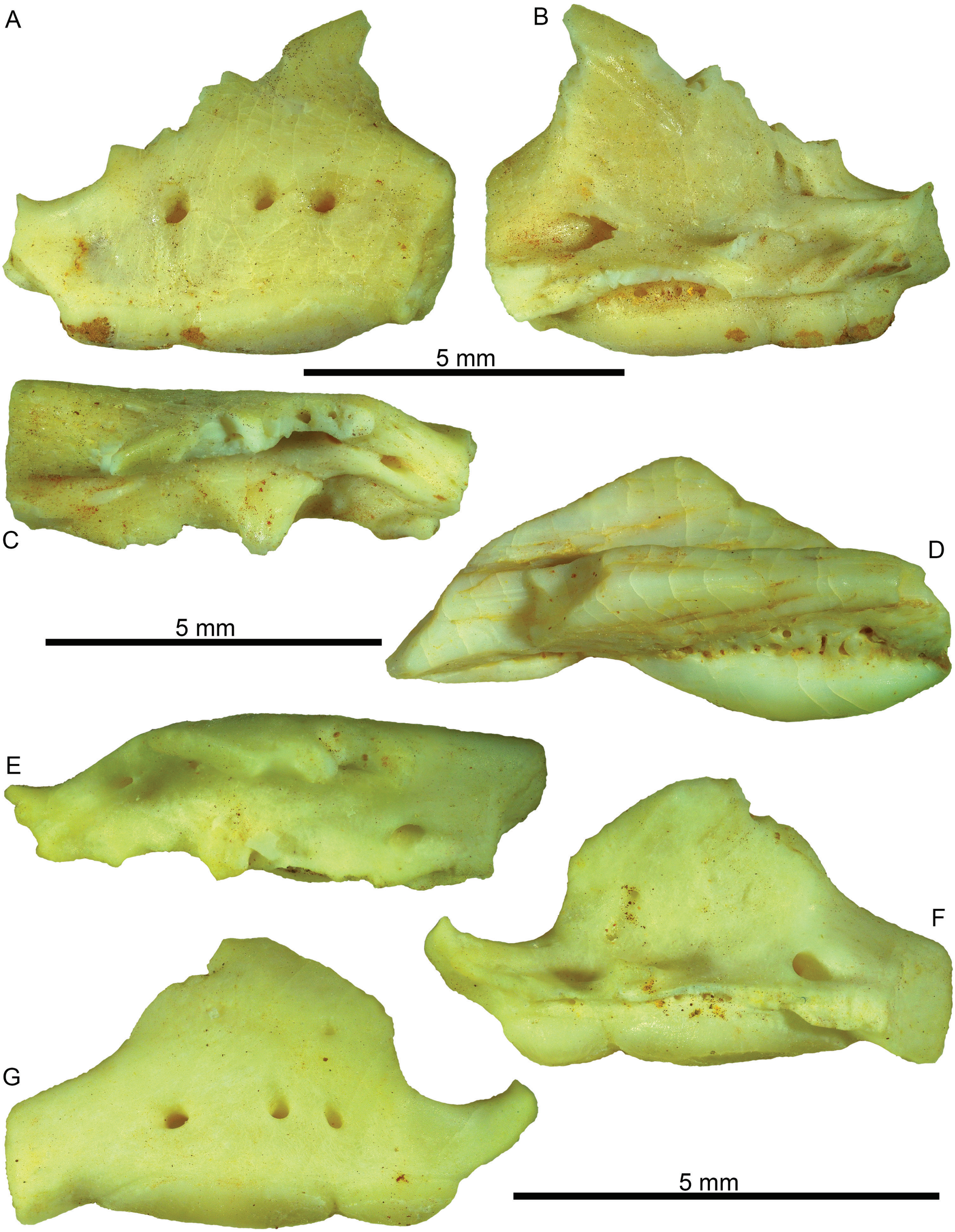

Figure 9. Maxillae of ***Terastiodontosaurus marcelosanchezi***. Photographs of: A–C, left maxilla ONM CBI-1-648 in labial (A), medial (B), and dorsal (C) views; D, fragment of right maxilla ONM CBI-1-650 in medial view; and E–G, right maxilla ONM CBI-1-649 of a small-sized individual in dorsal (E), medial (F), and labial (G) views.

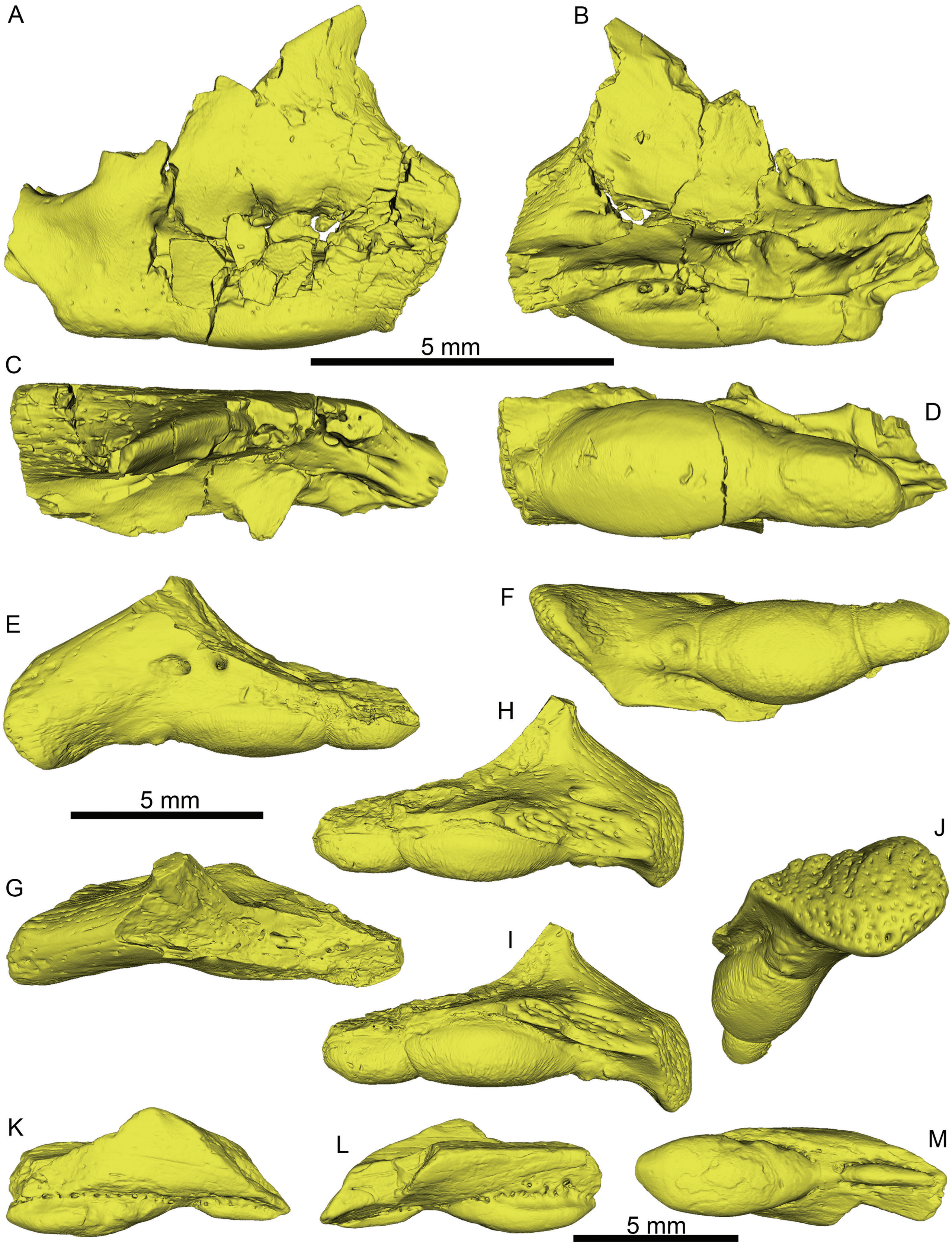

Figure 10. Maxillae of ***Terastiodontosaurus marcelosanchezi***. μCT 3D reconstructions of: A–D, left maxilla ONM CBI-1-648 in labial (A), medial (B), dorsal (C), and ventral (D) views; E–J, right maxilla ONM CBI-1-651 in labial (E), ventral (F), dorsal (G), medial (H), ventromedial (I), and posteroventral (J) views; and K–M, fragment of right maxilla ONM CBI-1-650 in labial (K), medial (L), and ventral (M) views. Note that specimen ONM CBI-1-648 was slightly damaged during micro-computed tomography scanning, hence the difference from the photographs in Figure 9.

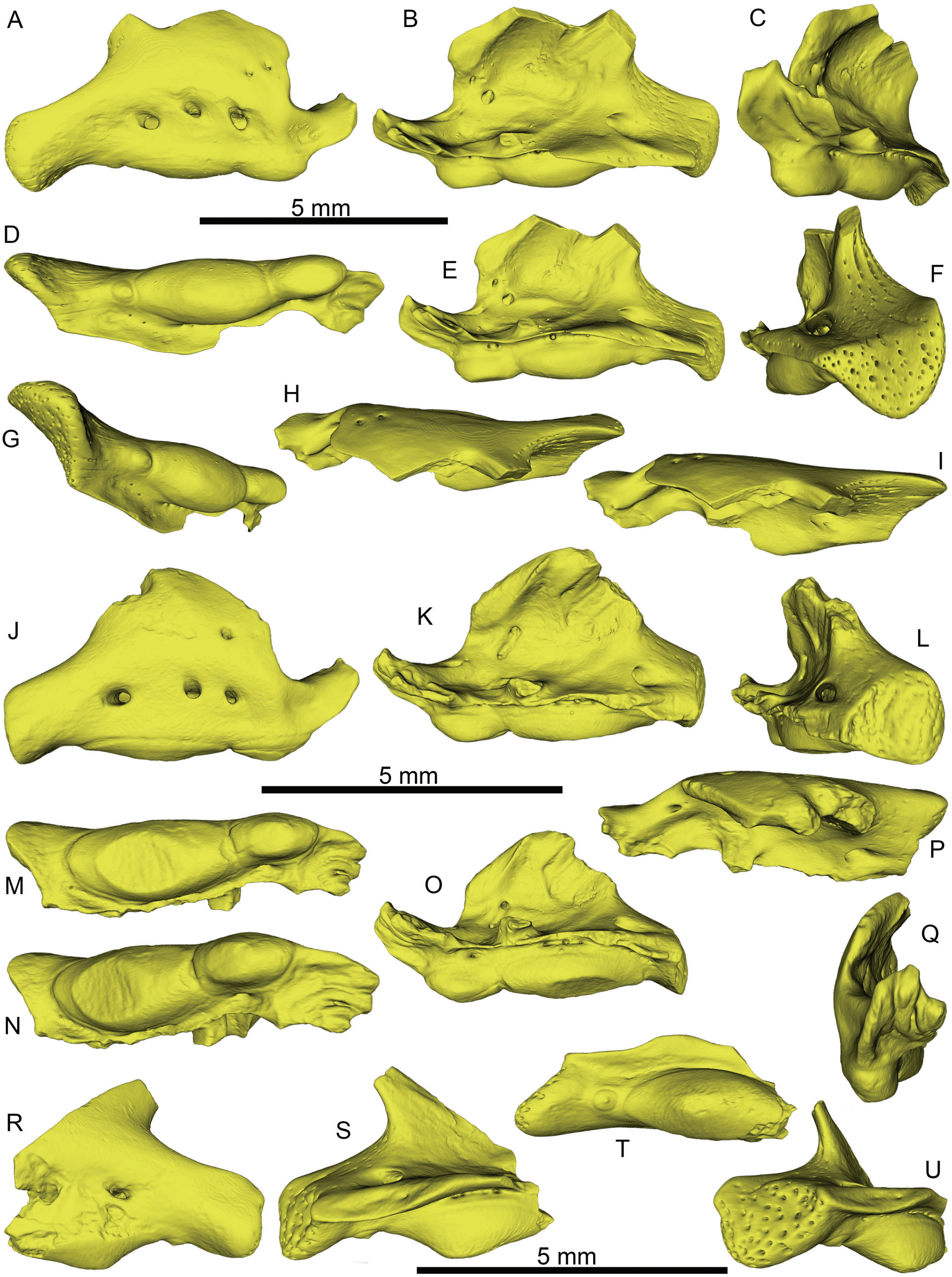

Figure 11. Maxillae of ***Terastiodontosaurus marcelosanchezi***, small-sized individuals. μCT 3D reconstructions of: A–I, right maxilla ONM CBI-1-654 in labial (A), medial (B), anteromedial (C), ventral (D), ventromedial (E), posteromedial (F), posteroventral (G), dorsal (H), and dorsomedial (I) views; J–Q, right maxilla ONM CBI-1-649 in labial (J), medial (K), posteromedial (L), ventral (M), anteroventral (N), ventromedial (O), dorsal (P), and anterior (Q) views; and R–U, posterior portion of left maxilla ONM CBI-1-653 in labial (R), medial (S), ventral (T), and posteromedial (U) views.

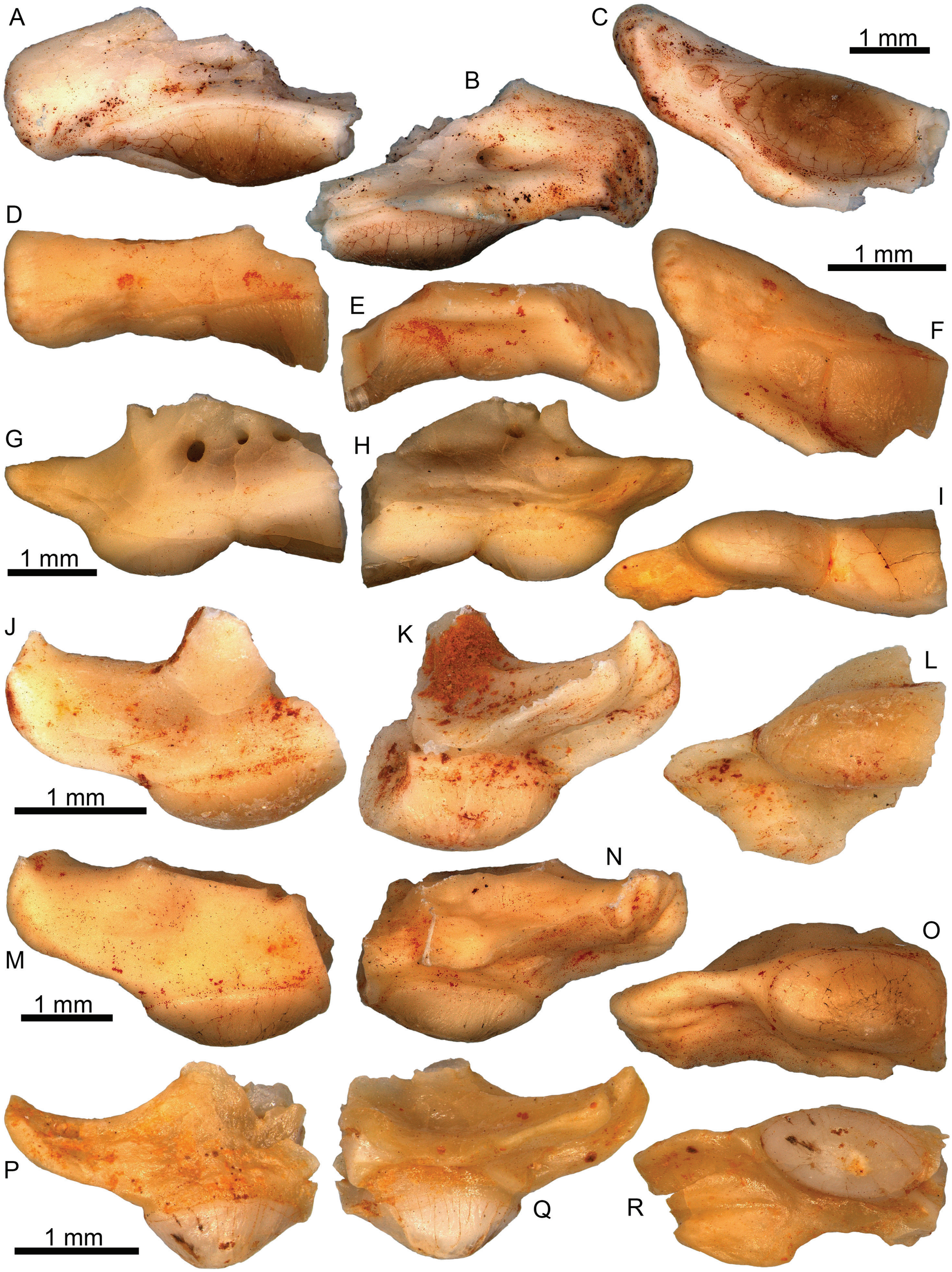

Figure 12. Maxillae of ***Terastiodontosaurus marcelosanchezi***. Photographs of: A–C, posterior fragment of right maxilla ONM CBI-1-667 in labial (A), medial (B), and ventral (C) views; D–F, posterior fragment of right maxilla ONM CBI-1-1017 in labial (D), ventromedial (E), and ventral (E) views; G–I, anterior fragment of left maxilla ONM CBI-1-1012 in labial (G), medial (H), and ventral (I) views; J–L, anterior fragment of left maxilla ONM CBI-1-1016 in labial (J), medial (K), and ventral (L) views; M–O, anterior fragment of left maxilla ONM CBI-1-1018 in labial (M), medial (N), and ventral (O) views; and P–R, anterior fragment of left maxilla ONM CBI-1-1022 in labial (P), medial (Q), and ventral (R) views.

bears only two teeth (Figs 9G, 11M–O). A further, interesting variation occurs also in the right maxilla fragment ONM CBI-1-650, where the anterior (smaller) preserved tooth is different from the same tooth in other specimens, being extremely narrow (Figs 9D, 10K–M). Tentatively, we attribute this variation as being intraspecific (or even ontogenetic). This could indeed be the case, taking into consideration that especially if the more anterior teeth are being 'de-emphasized' in favour of the huge tooth (which serves as the prey 'cracker'), and thus the anterior teeth perhaps become more of a remnant/vestige, then one would expect a greater variation. Moreover, again in the same specimen, there seems to be a considerable gap between the two preserved teeth (Figs 9D, 10K–M); this is unusual, because in most remaining maxillae and dentaries, the teeth are closely appressed, with no interdental gaps between them (but in ONM CBI-1-653 the third tooth is somewhat more widely separated; Fig. 11T).

Notably also, in some cases, there is a distinct 'hill' forming on the smallest tooth or teeth. This is the case with ONM CBI-1-651 (where the 'hill' is prominent in both the small third and fourth teeth; Fig. 10E, I, J) and ONM CBI-1-653 (Fig. 11S–U).

Several nutritive foramina are always present at the base of the teeth in all specimens, in the remnants of the subdental gutter; however, their number and size are variable. Usually, these foramina are mostly at the medial side of the maxilla; however, there is also some variation: in ONM CBI-1-650, they are equally present in both labial and medial aspects of the bone (Figs 9D, 10K, L).

In order to facilitate quantitative investigation, we introduce the ratio of largest tooth length on the maxilla to total tooth row length of the maxilla. This was complete in only four specimens:

- Holotype, ONM CBI-1-645: largest tooth length, 4.9 mm/total tooth row length, 9.5 mm; ratio, 0.52.
- ONM CBI-1-649: largest tooth length, 2.6 mm/total tooth row length, 3.7 mm; ratio, 0.70.
- ONM CBI-1-651: largest tooth length, 3.7 mm/total tooth row length, 7.3 mm; ratio, 0.51.
- ONM CBI-1-654: largest tooth length, 2.3 mm/total tooth row length, 4.1 mm; ratio, 0.56.

Besides, some information on this ratio can also be gleaned tentatively from some incomplete maxillae:

- ONM CBI-1-650: largest tooth length, 4.8 mm/preserved tooth row length (incomplete), 7.8 mm; estimated ratio, <0.62.
- ONM CBI-1-648: largest tooth length, 3.2 mm/preserved tooth row length (incomplete), 5.6 mm; estimated ratio, <0.57.

Dentaries (Figs 13–16)

Apart from the paratype dentary ONM CBI-1-646, all remaining dentaries are rather incomplete. The available sample denotes a range of sizes, but substantially less disparate than the maxillary sample (cf. Supporting Information, Figs S3–S6). The paratype ONM CBI-1-646 represents one of the largest individuals, with the fragmentary dentary ONM CBI-1-659 pertaining to a more or less similar size. All dentaries closely approach in overall morphology the paratype ONM CBI-1-646 described above. Some specimens are nevertheless highly incomplete, sometimes preserving only the anterior portion of the dentary (e.g. ONM CBI-1-1014, ONM CBI-1-1015, and ONM CBI-1-1020), while ONM CBI-1-664 is only a fragment of the coronoid process of a left dentary.

The tooth row is complete only in the paratype ONM CBI-1-646, where it comprises eight acrodont teeth, the largest being the fourth one (counting from posteriorly). Otherwise, the tooth row is almost complete in ONM CBI-1-657 (Figs 14A, 15A–C), which preserves all but the seventh tooth (counting from posteriorly). In that specimen also, the fourth tooth is the largest one and the posteriormost tooth is the tiniest one (both counting from posteriorly). One important difference in ONM CBI-1-657 is that there appears to be a dental gap between the anteriormost tooth and the succeeding tooth position (although we cannot be certain that this is not an artefact). Otherwise, in all specimens, all teeth are almost adjoined, with almost no interdental gaps between them (at maximum only tiny empty spaces between some, but not all teeth, do exist). As in the paratype ONM CBI-1-646, also in ONM CBI-1-647, ONM CBI-1-655, ONM CBI-1-657, ONM CBI-1-662, ONM CBI-1-666, ONM CBI-1-1014, ONM CBI-1-1015, and ONM CBI-1-1020, the anteriormost tooth is more bulbous and dorsoventrally high and projects beyond the anterior surface of the symphysis. This is also the case for the second anteriormost tooth in the paratype ONM CBI-1-646, as in ONM CBI-1-647, ONM CBI-1-655, ONM CBI-1-662, ONM CBI-1-666, ONM CBI-1-1014, ONM CBI-1-1015, and ONM CBI-1-1020, which is also relatively bulbous and dorsoventrally tall. In dentary ONM CBI-1-670, the teeth are not that flattened but apparently represent the anterior teeth [second, third, or fourth (counting from anteriorly)], near the symphysis.

As in the maxillae, there is a distinct 'hill' on the tiny teeth (e.g. ONM CBI-1-646 and ONM CBI-1-657). Great enamel thickness is also found on the dentary teeth.

Nutritive foramina are open at the base of various teeth above the subdental shelf in all dentaries; their number is not consistent, and it can vary between tooth positions and individuals at the same position. In ONM CBI-1-657, these are poorly developed.

Meckel's groove is open in all specimens where this can be studied, most notably ONM CBI-1-660. Owing to their incompleteness, besides the paratype dentary ONM CBI-1-646, which bears four, the exact number of labial foramina cannot be assessed in the remaining dentaries. Interestingly, however, ONM CBI-1-659 is pierced by several (at least nine) tiny foramina in its labial surface, most of which are closely spaced.

As in the case of the maxillae above, in order to facilitate further quantitative investigation, we introduce the ratio of largest dentary tooth length to the total tooth row length of the maxilla. This was complete in only two specimens:

- Paratype ONM CBI-1-646: largest tooth length, 2.8 mm/total tooth row length, 11.9 mm; ratio, 0.24.
- ONM CBI-1-657: largest tooth length, 1.6 mm/total tooth row length, 6.4 mm; ratio, 0.25.

Besides these specimens for which ratios could be calculated, the following dentaries provide data on the length of the largest tooth in further specimens:

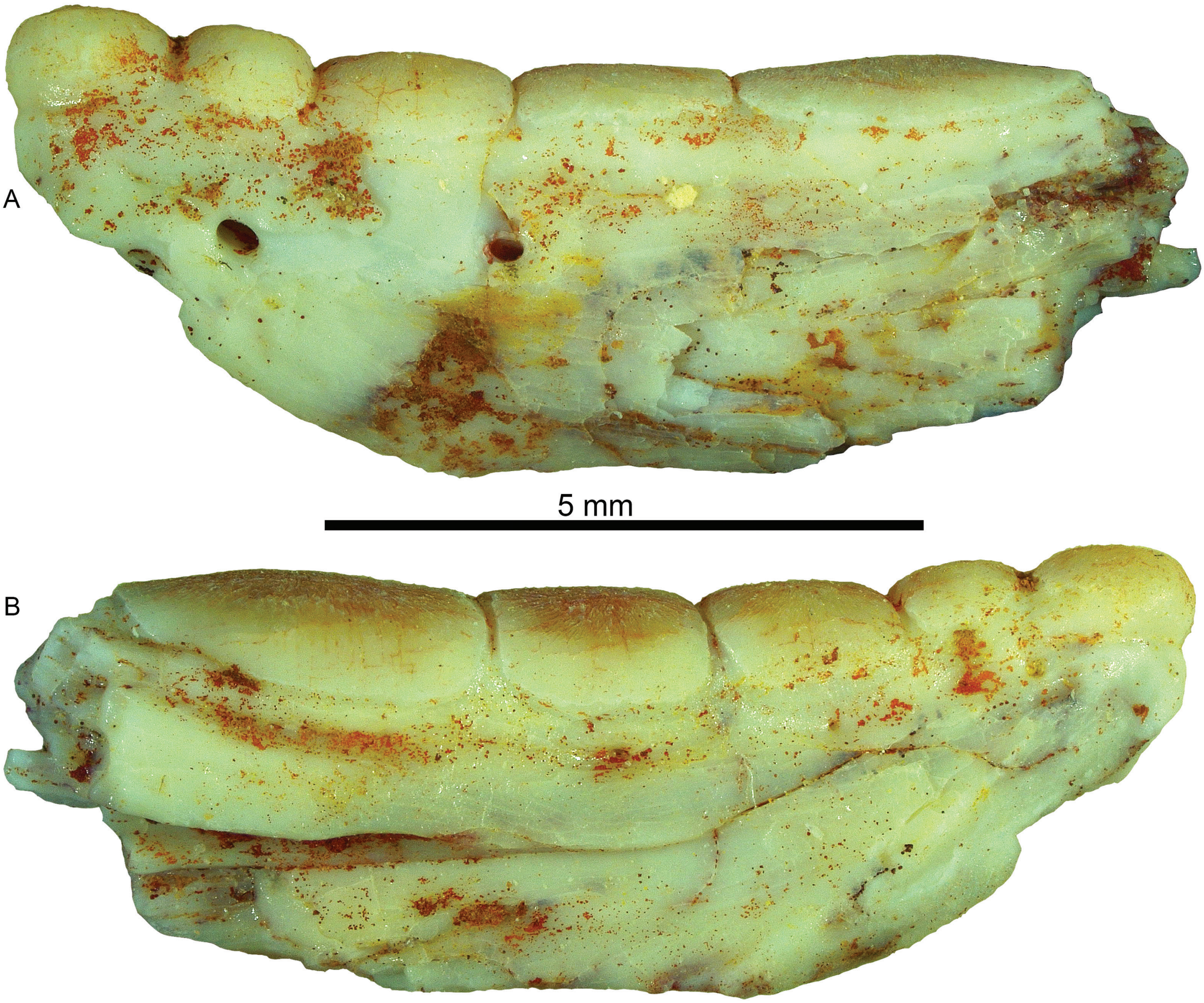

Figure 13. Dentary of ***Terastiodontosaurus marcelosanchezi***. Photographs of left dentary ONM CBI-1-647 in labial (A) and medial (B) views.

ONM CBI-1-647: largest tooth length, 2.9 mm.
ONM CBI-1-659: largest tooth length, 2.3 mm.
ONM CBI-1-655: largest tooth length, 1.9 mm.
ONM CBI-1-656: largest tooth length, 1.5 mm.

Vertebrae (Fig. 17)

Vertebrae are referred tentatively to the same taxon on the basis of co-occurrence and the fact that large numbers of jaws have yielded only a single species of amphisbaenian thus far from the locality.

Presacral vertebrae range in size between ~1 and 5 mm (Fig. 17A–U). They are procoelous and dorsoventrally compressed. In anterior view, the prezygapophyses are strongly inclined, much exceeding in height the anterodorsal edge of the neural canal. There is no zygosphene. The cotyle is elliptical and strongly depressed. In posterior view, the condyle is also elliptical and strongly depressed. The neural arch is depressed. The lateral walls of the neural arch form moderately robust centropostzygapophyseal laminae (*sensu* Georgalis *et al.* 2018b). There is no zygantrum. In dorsal view, the prezygapophyses extend anterolaterally. The prezygapophyseal articular facets are large and broad; in some specimens, there are prominent prezygapophyseal accessory processes. There is no neural spine. The interzygapophyseal constriction is deep. There is practically no posterior median notch of the neural arch. In ventral view, the centrum is flattened, with only slightly concave lateral margins. Two usually large, occasionally asymmetrical subcentral foramina are present, one at each lateral side of the ventral surface of the centrum. The synapophyses are robust and more or less rounded. In lateral view, the neural arch rises distinctly, with a gentle curve towards its posterior end. Each prezygapophysis is connected to the related postzygapophysis by a relatively low interzygapophyseal ridge.

Caudal vertebrae have haemapophyses fused to the centrum. A short anterior caudal vertebra has forked lymphapophyses (Fig. 17V, W), whereas more elongate posterior caudal vertebrae have unitary pleurapophyses (Fig. 17X, Y). If the number of caudal to presacral vertebrae can be determined, the methodology of Smith (2013) might be used to estimate the proportion

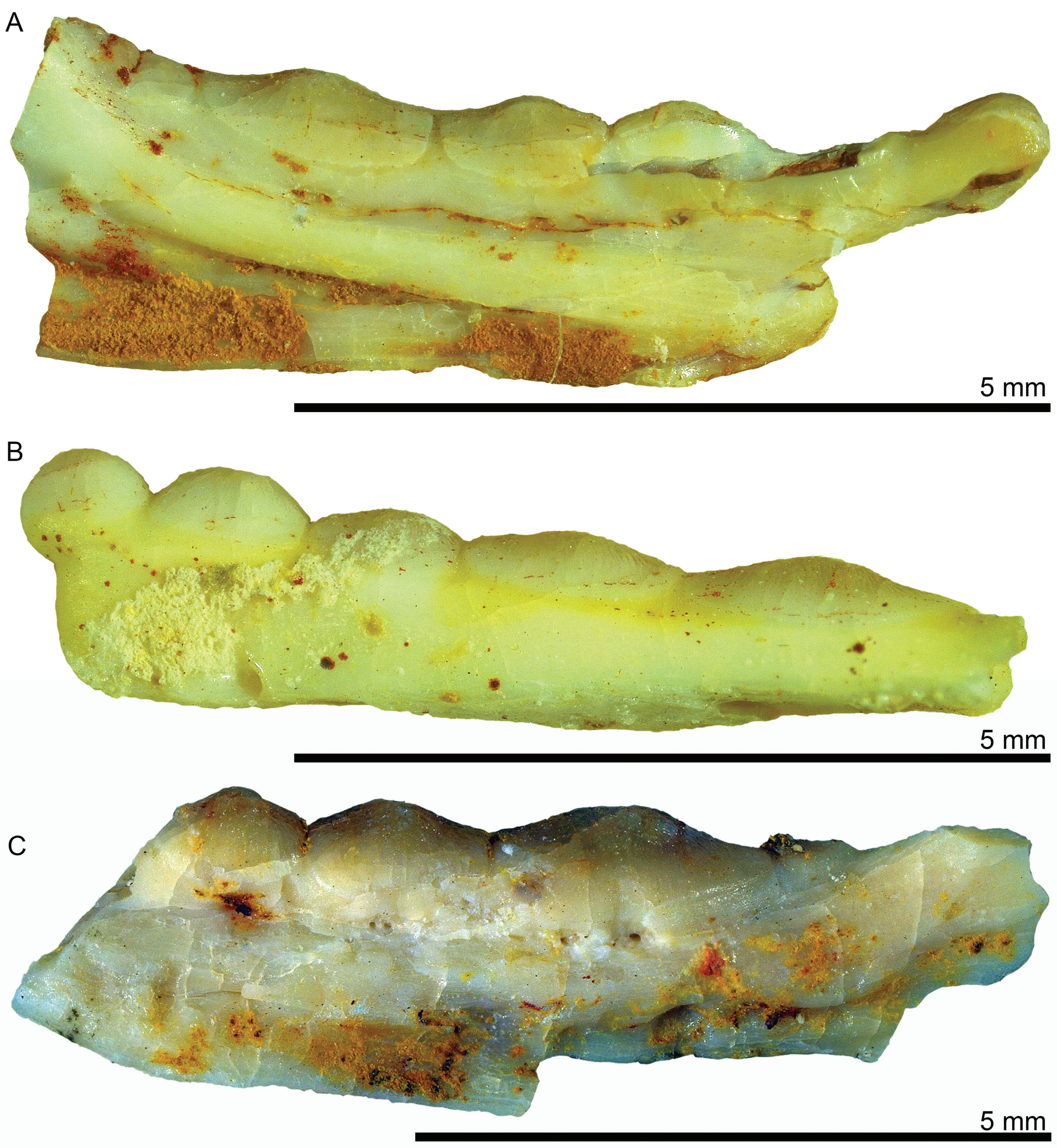

Figure 14. Dentaries of ***Terastiodontosaurus marcelosanchezi***. Photographs of left dentary ONM CBI-1-657 in medial view (A); left dentary ONM CBI-1-655 in labial view (B); and right dentary ONM CBI-1-656 in medial view (C).

of caudal vertebrae and thus to constrain the relative length of the tail.

Results of the phylogenetic analysis

Our main analysis used only two topological constraints: Afrobaenia and South American Amphisbaenidae. Fully consistent with all recent phylogenetic analyses (e.g. Kearney 2003, Müller *et al.* 2011, Gauthier *et al.* 2012, Jones *et al.* 2013, Čerňanský *et al.* 2015a, Longrich *et al.* 2015, Zheng and Wiens 2016, Streicher and Wiens 2017, Simões *et al.* 2018, Burbrink *et al.* 2020, Singhal *et al.* 2021, Tałanda *et al.* 2022, Brownstein *et al.* 2023, Čerňanský and Vasilyan 2024), our analysis finds strong support for amphisbaenian monophyly (Fig. 18). The position of *Cryptolacerta hassiaca* Müller, Hipsley, Head, Kardjilov, Hilger, Wuttke & Reisz, 2011, from the early to middle Eocene of Messel, Germany, originally described as a link between

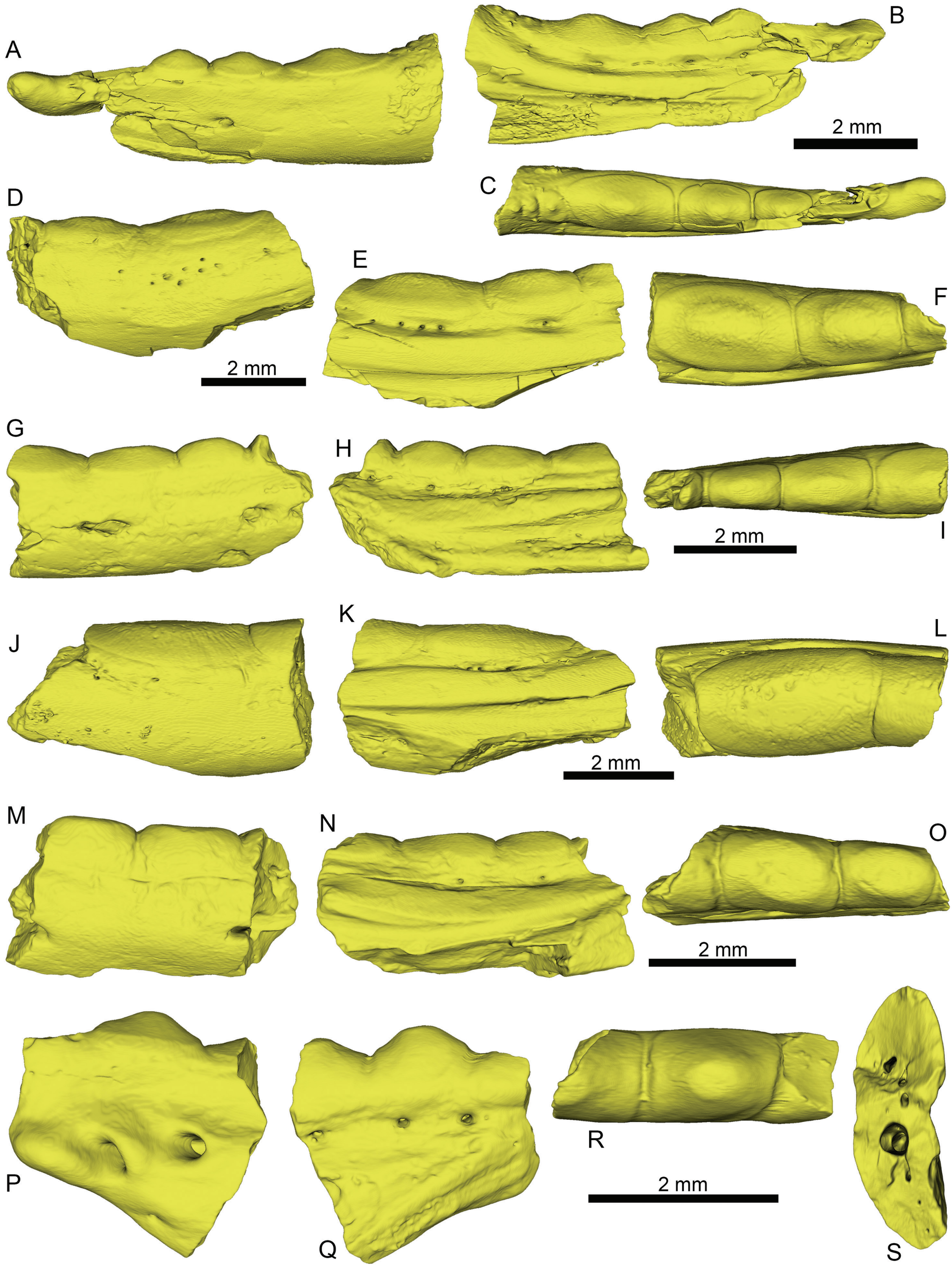

Figure 15. Dentaries of ***Terastiodontosaurus marcelosanchezi***. μCT 3D reconstructions of: A–C, left dentary ONM CBI-1-657 in labial (A), medial (B), and dorsal (C) views; D–F, left dentary ONM CBI-1-659 in labial (D), medial (E), and dorsal (F) views; G–I, right dentary ONM CBI-1-660 in labial (G), medial (H), and dorsal (I) views; J–L, left dentary ONM CBI-1-661 in labial (J), medial (K), and dorsal (L) views; M–O, left dentary ONM CBI-1-668 in labial (M), medial (N), and dorsal (O) views; and P–S, left dentary ONM CBI-1-670 in labial (P), medial (Q), dorsal (R), and posterior (S) views.

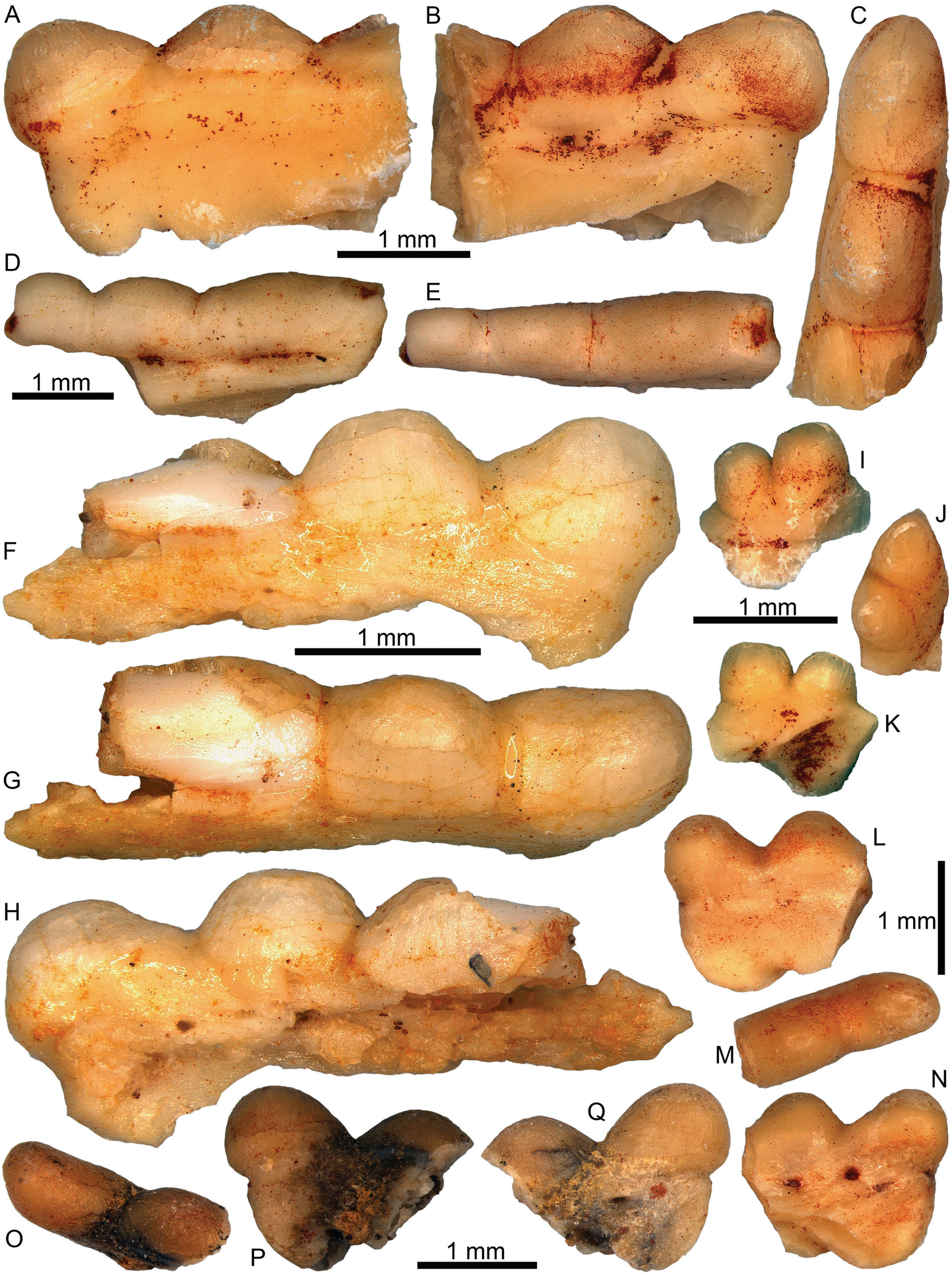

Figure 16. Dentaries of ***Terastiodontosaurus marcelosanchezi***. Photographs of: A–C, left dentary ONM CBI-1-662 in labial (A), medial (B), and dorsal (C) views; D, E, right dentary ONM CBI-1-1013 in labial (D) and dorsal (E) views; F–H, right dentary ONM CBI-1-666 in labial (F), dorsolabial (G), and medial (H) views; I–K, anterior fragment of right dentary ONM CBI-1-1020 in labial (I), dorsal (J), and medial (K) views; L–N, anterior fragment of left dentary ONM CBI-1-1015 in labial (L), dorsal (M), and medial (N) views; and O–Q, anterior fragment of left dentary ONM CBI-1-1014 in dorsal (O), labial (P), and medial (Q) views.

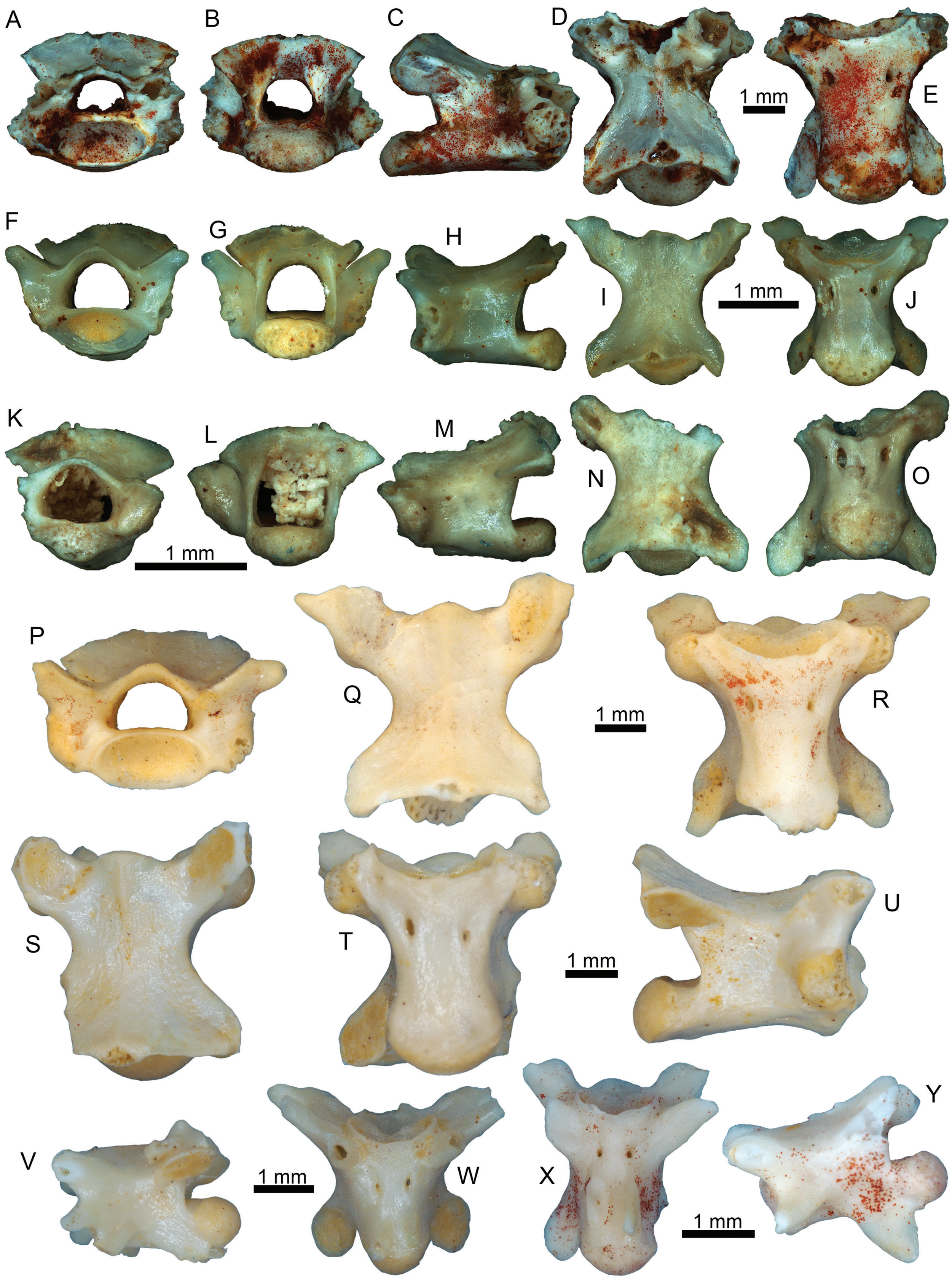

Figure 17. Vertebrae tentatively attributed to ***Terastiodontosaurus marcelosanchezi***. A–E, presacral vertebra ONM CBI-1-833 in anterior (A), posterior (B), right lateral (C), dorsal (D), and ventral (E) views; F–J, presacral vertebra ONM CBI-1-860 in anterior (F), posterior (G), left lateral (H), dorsal (I), and ventral (J) views; K–O, presacral vertebra ONM CBI-1-820 in anterior (K), posterior (L), left lateral (M), dorsal (N), and ventral (O) views; P–R, presacral vertebra ONM CBI-1-682 in anterior (P), dorsal (Q), and ventral (R) views; S–U, presacral vertebra ONM CBI-1-687 in dorsal (S), ventral (T), and right lateral (U) views; V, W, anterior caudal vertebra ONM CBI-1-689 in left lateral (V) and ventral (W) views; X, Y, posterior caudal vertebra ONM CBI-1-686 in ventral (X) and left lateral (Y) views.

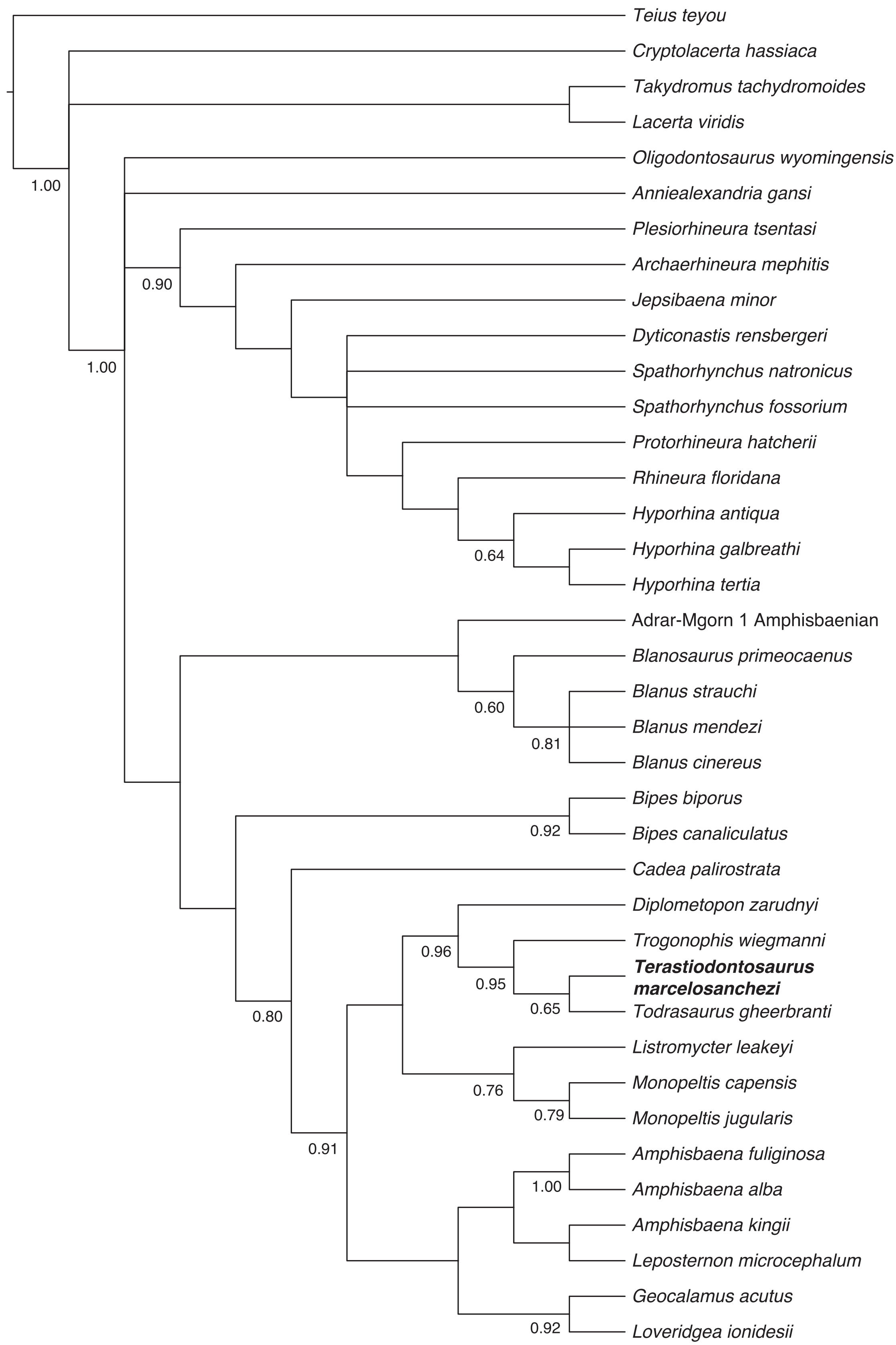

Figure 18. Phylogenetic analysis of Amphisbaenia, strict consensus of maximum parsimony trees, indicating the position of ***Terastiodontosaurus marcelosanchezi***.

lacertids and amphisbaenians by Müller *et al.* (2011), is unresolved (but see also Longrich *et al.* 2015, Brownstein *et al.* 2023, Čerňanský and Vasilyan 2024). In general, higher-level relationships within Amphisbaenia are poorly supported, but our analysis shares the basal position of Rhineuridae with Gauthier *et al.* (2012), which was the first purely morphological analysis

Table 1. Unambiguous morphological synapomorphies (under acctran or deltran) of trogonophid clades inferred based on our phylogenetic analysis.

Clade	Character	Change	Description
Trogonophidae	10	0 → 1	Maxillary process of premaxilla extends lateral to level of palatine–maxilla suture
	17	1 → 0	Nasal descending lamina extends below level of nasal–maxilla suture
	26	1 → 0	Nasals abut or overlap frontals
	28	0 → 1	Frontals deeply notched to clasp a long and narrow caudal process of the nasals
	55	0 → 1	Parietal–supraoccipital opening closed
	59	1 → 2	Premaxillary process of maxilla extremely elongate, forming ventral border and part of medial border of external naris
	66	0 → 2	Maxilla notched to receive a long, narrow process of the frontal
	67	0 → 1	Jugal process of maxilla strongly turned outwards (flared in dorsal view)
	94	0 → 1	Stapedial shaft projects anterolaterally in ventral view
	107	1 → 0	Vomers do not overlap palatal shelf of maxilla behind posterior margin of opening for vomeronasal organ
	114	0 → 1	Vomers contacting for nearly all or all of their length
	117	1 → 0	Palatine contact with braincase weak or absent
	120	0 → 1	Palatines with anterior contact only
	130	4 → 1	Ectopterygoid abuts posteromedial corner of maxilla, rather than interdigitating
	131	1 → 0	Finger-like anterior process of ectopterygoid absent
	132	1 → 0	Maxillary process of ectopterygoid tapers or parallel sided
	141	1 → 0	Posterior margin of supraoccipital straight to weakly incised in dorsal view
	152	3 → 1	Short basipterygoid process develops
	158	1 → 0	Occipital condyle convex and ball shaped or only weakly divided
	174	1 → 0	Posterior margin of dentary lacks broad, U-shaped cut-out extending to back of tooth row
	205	0 → 1	Surangular foramen located along dentary–surangular suture
	219	0 → 1	Marginal teeth fused to each other
	224	1 → 2	Premaxillary tooth count decreases to five
	225	1 → 0	Premaxillary teeth continuous with maxillary tooth row
	230	2 → 1	Length of maxillary tooth row extends to anterior half of orbit
	237	0 → 2	Third tooth from back in dentary enlarged
Trogonophis + (***Terastiodontosaurus*** + *Todrasaurus*)	5	1 → 0	Dorsal foramina of premaxilla absent
	195	1 → 0	Anterior margin of coronoid process delimited by wall of bone anteriorly
	218	1 → 0	Teeth straight, or recurved only anteriorly
	228	1 → 0	Caniniform maxillary tooth absent
	309	0 → 1	Enamel on tooth crowns very thick
Terastiodontosaurus + *Todrasaurus*	308	0 → 1	Hypertrophied dentary tooth ≥50% longer than adjacent teeth

to recover this topology. A surprise was the close relationship between the unnamed amphisbaenian from Adrar-Mgorn 1 of Augé and Rage (2006) to Blanidae, although with poor support (BS < 0.50); furthermore, if all higher-level relationships within Afrobaenia (e.g. Graboski *et al.* 2022) are enforced, its position becomes unresolved. This unnamed pleurodont form represents the second amphisbaenian from the locality of Adrar-Mgorn 1 in Morocco (the other being *Todrasaurus gheerbranti*) and was originally described by Augé and Rage (2006) as bearing some resemblance to both blanids and amphisbaenids, whereas the phylogenetic analysis of Longrich *et al.* (2015) recovered it as an Amphisbaenia *incertae sedis*. The cadeid *Cadea palirostrata* Dickerson, 1916 was assessed with relatively strong support as the sister taxon of Afrobaenia, i.e. the group encompassing Cadeidae, Trogonophidae, and Amphisbaenidae (BS = 0.80). *Terastiodontosaurus marcelosanchezi* was inferred with moderate support (BS = 0.65, one unambiguous character state change, Bremer support 1; Table 1) to be the sister taxon of *Todrasaurus gheerbranti*, and the two together were inferred with strong support to be the sister taxon of *Trogonophis wiegmanni* (BS = 0.95, five unambiguous character state changes, Bremer support 3), a novel result. The herein novel topology of *Todrasaurus* differs from that of Longrich *et al.* (2015), who had tentatively recovered this Moroccan taxon on the stem of Afrobaenia (Longrich *et al.* 2015). Moreover, Trogonophidae (comprising *Trogonophis* and its stem plus *Diplometopon zarudnyi* Nikolskyi, 1907) was inferred to be monophyletic with strong support (BS = 0.96, 26 unambiguous character state changes, Bremer support 5). Enforcing all major topological constraints within Afrobaenia (*fide* Graboski *et al.* 2022) did not affect the relationships within Trogonophidae (including fossil taxa) or their basal position in Afrobaenia.

DISCUSSION

Taxonomic identification and comparisons

The new fossil cranial material from the late early–early middle Eocene of Chambi is characterized by an array of anatomical features (i.e. a heavy premaxilla with prominent facial processes and a median azygous tooth that is most robust and prominent, the presence of large anterior premaxillary foramina, the low tooth count on the maxilla and dentary, the interdigitating maxilla–frontal suture, the broad insertion area for mandibular adductors on the posterolateral surface of the dentary, the strong coronoid process of the dentary, the elongated nasal process of the premaxilla, and the acrodont dentition) that allow referral to Amphisbaenia and, more specifically, suggest an affinity with Trogonophidae (Gans 1960, Charig and Gans 1990, Kearney 2003, Augé and Rage 2006, Gans and Montero 2008). All preserved cranial material from Chambi corresponds to the so-called 'snout segment' of the amphisbaenian skull (*sensu* Gans and Montero 2008) and the mandibles, although the abundance of the material suggests that other elements might be discovered; in any case, such 'snout segment' elements, together with frontals, generally appear to be the most common cranial remains in the amphisbaenian fossil record (Estes 1983, Augé 2012).

Terastiodontosaurus marcelosanchezi bears a certain degree of resemblance to extinct and extant trogonophids, but also possesses also some highly distinctive features that can readily differentiate it from all other amphisbaenians.

More specifically, *Terastiodontosaurus marcelosanchezi* is very distinct from the older *Todrasaurus gheerbranti*, known exclusively from its holotype left dentary (UM THR 407) from the late Palaeocene (Thanetian) of Adrar-Mgorn 1, Morocco. We here provide, for the first time, photographs and μCT 3D images of the holotype of *Todrasaurus* (Figs 19–21), in order to investigate its anatomy further and demonstrate with clarity these differences from *Terastiodontosaurus*. These substantial differences between the Moroccan taxon and the new Tunisian taxon include the shape of teeth in the two taxa (all teeth much taller and amblyodont in *Todrasaurus*), the type of tooth implantation (fully acrodont in *Terastiodontosaurus* vs. more pleurodont in *Todrasaurus*), the number of dentary teeth (eight in *Terastiodontosaurus* vs. probably fewer in *Todrasaurus* [four preserved in its holotype but there might have been more in life]), shape of the subdental shelf (highly concave in *Todrasaurus*), the position of the enlarged tooth on the dentary (the fourth position counting from posteriorly in *Terastiodontosaurus* vs. the third position counting from posteriorly in *Todrasaurus*), and the overall size (with *Terastiodontosaurus* being much larger).

It is further worth noting that in the original establishment and description of *Todrasaurus gheerbranti*, Augé and Rage (2006) claimed that this taxon also possessed a splenial, a feature that they considered as distinctive, stating that this structure is otherwise present in amphisbaenians solely in the North American Rhineuridae (Kearney *et al.* 2005; but see Gans and Montero 2008, who claim that a splenial is also absent in Rhineuridae); in any case, a splenial has also been described in other amphisbaenians, such as the extinct *Cuvieribaena* Čerňanský, Augé & Rage, 2015a from the Eocene of France (Čerňanský *et al.* 2015a) and, occasionally, in the extant *Blanus* Wagler, 1830 (e.g. Blain *et al.* 2007, Villa *et al.* 2019, Čerňanský 2023). However, the splenial is not clearly discernible in the original drawing of the holotype of *Todrasaurus gheerbranti* by Augé and Rage (2006: fig. 2), and the element was not labelled there by the authors. Based on our newest investigation of the holotype of *Todrasaurus* using μCT, we were unable to detect the presence of a splenial in that specimen (Fig. 20). As such, we see no reason to claim that a splenial was indeed present in *Todrasaurus*. Furthermore, Maisano *et al.* (2006) showed that in *Diplometopon*, the compound bone and splenial appear to be co-ossified. This seems also to be the case and, in fact, is even more prominent in *Trogonophis* (Fig. 22; Supporting Information, Fig. S7). Finally, in *Terastiodontosaurus*, the splenial seems to be present, because there are two distinct facets medially on the dentary of the Chambi taxon, although it is unclear whether the splenial was fused to the angular.

Terastiodontosaurus marcelosanchezi shows great similarity to the type genus of Trogonophidae, *Trogonophis*. *Terastiodontosaurus marcelosanchezi* resembles the extant *Trogonophis wiegmanni* (the sole valid extant species of *Trogonophis*) in terms of: the shape of the frontal notches of the facial process of the maxilla; the premaxilla with one enlarged central azygous tooth separated from two 'twinned' lateral teeth by a diastema greater than the interdental spaces of the remainder of the marginal dentition; the presence of eight teeth on the dentary (primitive feature); one highly enlarged tooth in the maxilla; the presence of three maxillary labial foramina, with the two

Figure 19. *Todrasaurus gheerbranti*, holotype left dentary UM THR 407. Photographs of the specimen in labial (A), medial (B), and dorsal (C) views.

ones close to each other (variable); and strongly flared posterior process of the maxilla (Gans and Montero 2008). On the other hand though, there are also important differences between *Terastiodontosaurus marcelosanchezi* and *Trogonophis wiegmanni*, including: the shape of the teeth; the position of the enlarged dentary tooth; the number of maxillary teeth (almost always three in *Terastiodontosaurus*, with the exception of ONM CBI1-651 [three + a tiny one] and ONM CBI1-649 [two] vs. usually four in *Trogonophis wiegmanni*, but can rarely be three [e.g. YPM HERR 6903; Supporting Information, Fig. S7]); the ratio of the largest maxilla tooth length to the maxillary total tooth row length (always >0.5 in *Terastiodontosaurus* vs. almost always <0.5 in *Trogonophis* [the only known exception being 0.51 in YPM HERR 6903, where, notably, there are only

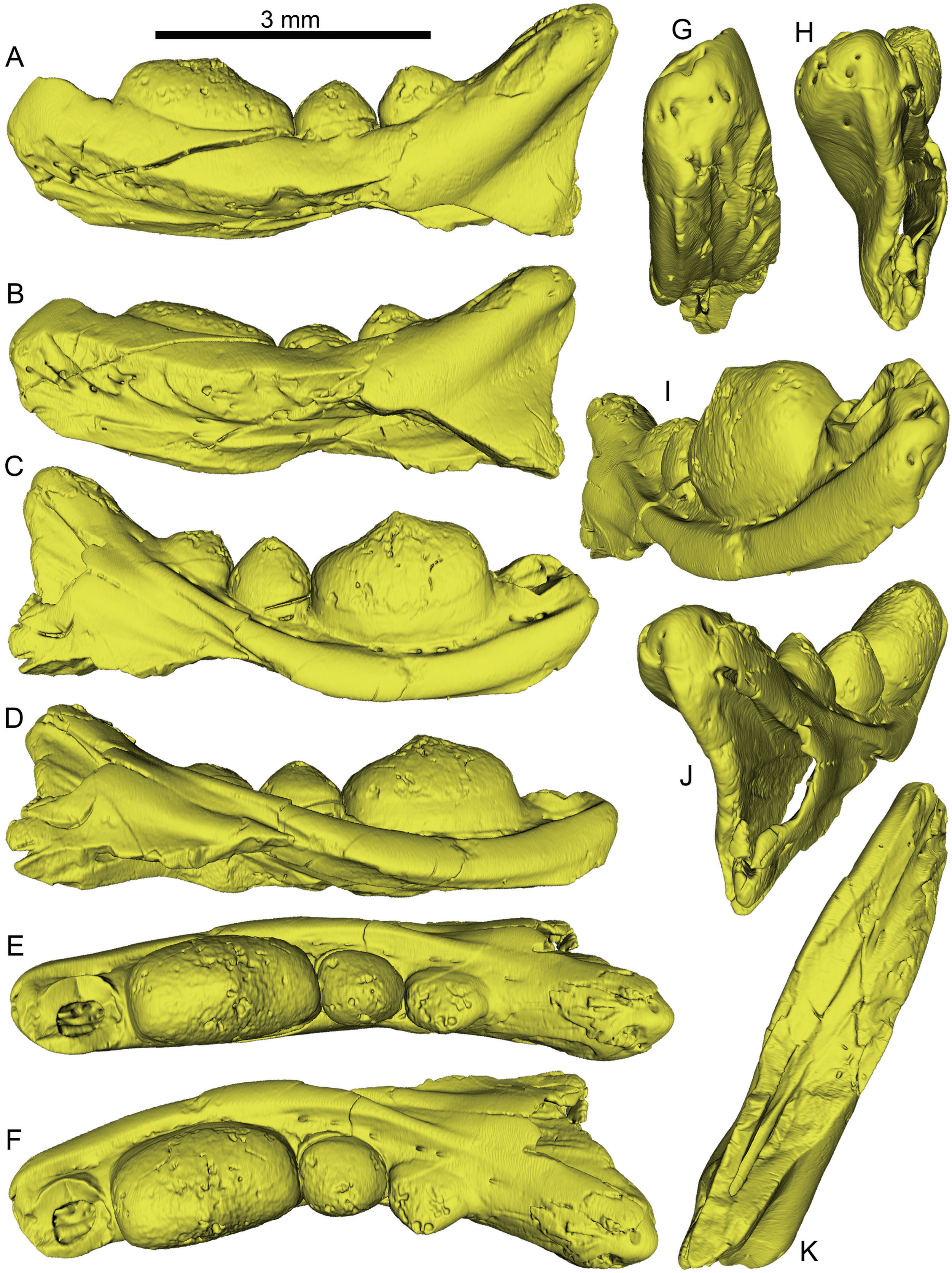

Figure 20. *Todrasaurus gheerbranti*, holotype left dentary UM THR 407. μCT 3D reconstructions of the specimen in labial (A), ventrolabial (B), medial (C), ventromedial (D), dorsal (E), dorsomedial (F), anteroventral (G), posterior (H), anteromedial (I), posteromedial (J), and ventral (K) views.

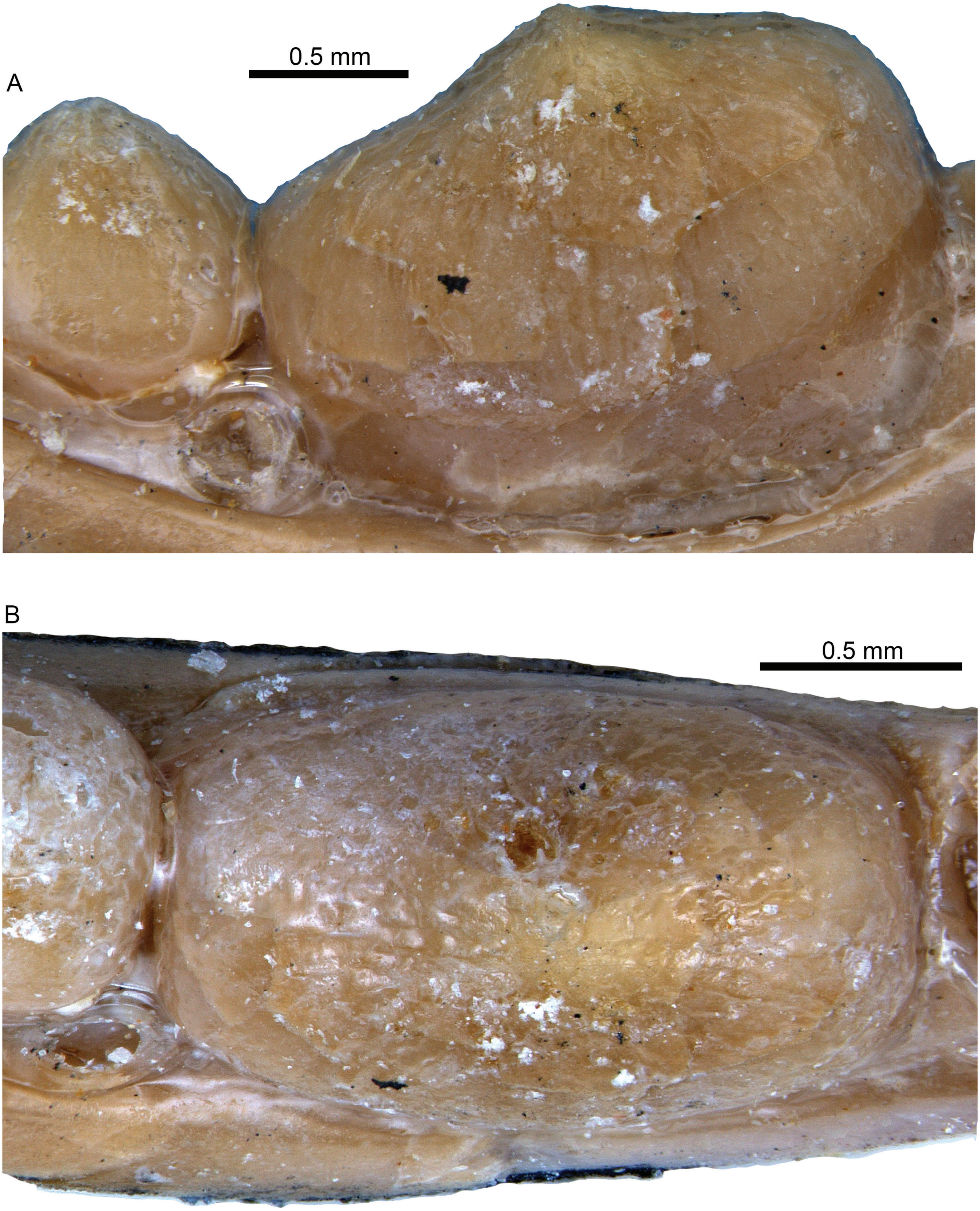

Figure 21. *Todrasaurus gheerbranti*, holotype left dentary UM THR 407. Close-up of the largest tooth in medial (A) and dorsal (B) views.

three teeth, as if the largest tooth 'took over space' for one of the smaller teeth]; see Table 2); the ratio of the largest dentary tooth length to the dentary total tooth row length; and the premaxilla in *Terastiodontosaurus* is taller.

It is worth noting that beyond the extant species, there is also an extinct species assigned to *Trogonophis*, i.e. *Trogonophis darelbeidae* Bailon, 2000, from the Late Pliocene–Early Pleistocene of Ahl al Oughlam, Morocco (Bailon 2000). This

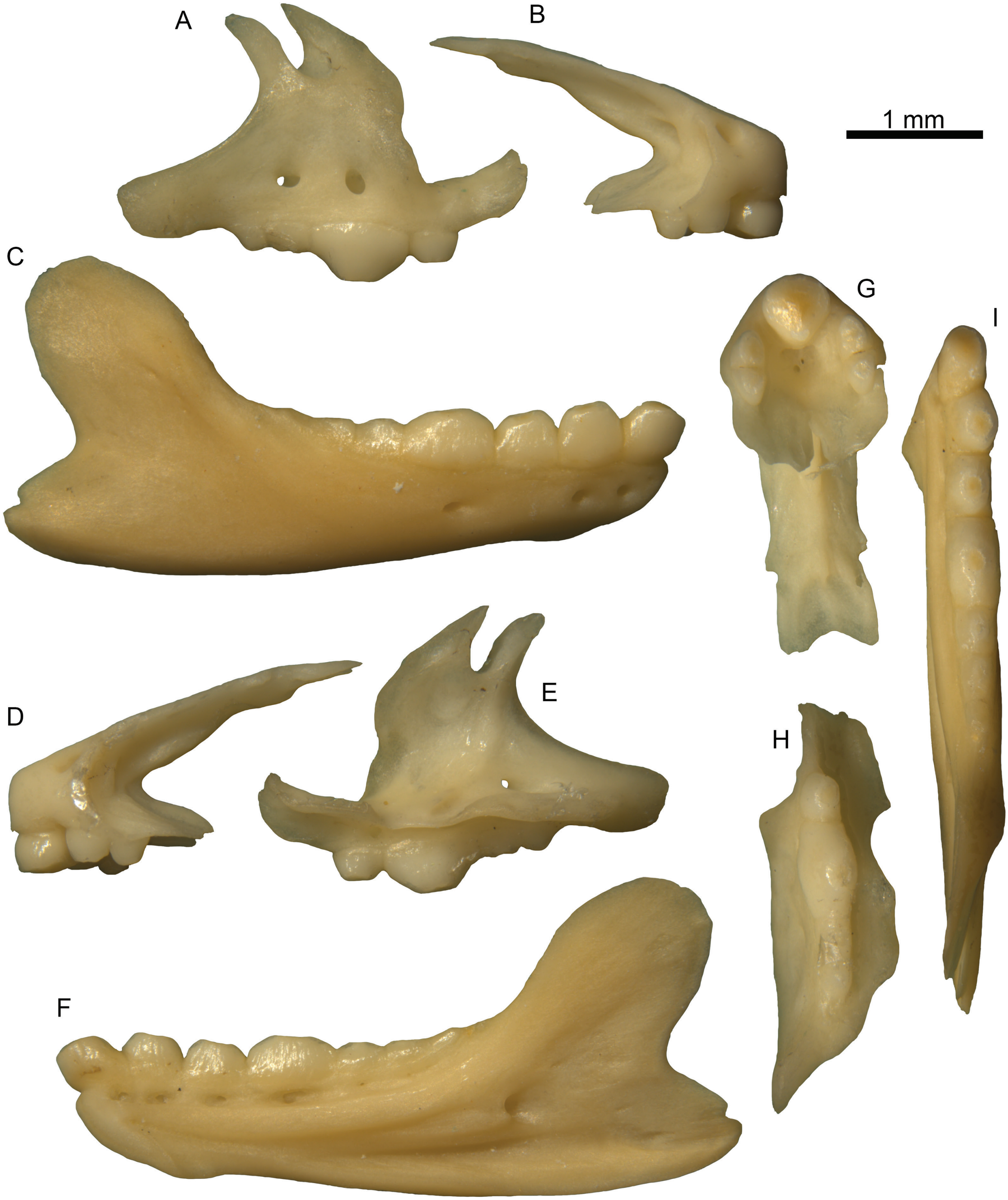

Figure 22. *Trogonophis wiegmanni*, specimen SMF-PH 566. Premaxilla (B, D, G), right maxilla (A, E, H), and right mandible (C, F, I) in right lateral (A), labial (B, C), left lateral (D), medial (E, F), and occlusal (G–I) views.

Plio-Pleistocene taxon bears much resemblance to the extant *Trogonophis wiegmanni*, from which it was differentiated by certain features in the dentary, premaxilla, and quadrate (Bailon 2000). *Trogonophis darelbeidae* possesses three teeth in its maxilla, but nevertheless, *Terastiodontosaurus marcelosanchezi* is much different from the former taxon in terms of: the shape of the dentary teeth; the position of the enlarged dentary tooth; the ratio of the length of the largest dentary tooth to tooth row length; the number of labial foramina on the maxilla (only two in *Trogonophis darelbeidae*); the premaxilla in *Terastiodontosaurus* is taller; and the central azygous tooth of the premaxilla is more robust in *Terastiodontosaurus* (Bailon 2000: see text and figures).

Terastiodontosaurus differs greatly from the remaining three extant trogonophid genera (*Agamodon*, *Diplometopon*, and *Pachycalamus*). Indeed, it can be differentiated from them by: much different shape of teeth (in all extant taxa); number of maxillary teeth (two in *Agamodon*); degree of flaring of the posterior process of the maxilla (weaker in the remaining three genera); position of the largest tooth on the maxilla (in all extant taxa); ratio of the length of the largest maxillary tooth to the total tooth row length; number of dentary teeth (eight in *Terastiodontosaurus* vs. six in *Diplometopon* and *Pachycalamus* and five in *Agamodon*); position of the largest tooth on the dentary; ratio of the length of the largest dentary tooth to the total tooth row length; and the shape and size of the premaxillary teeth (see descriptions and figures in the papers by Gans 1960, El-Assy and Al-Nassar 1976, Maisano *et al.* 2006, Hawkins *et al.* 2022).

One remarkable feature observed in the μCT scans of *Terastiodontosaurus* and *Todrasaurus* is the great apical enamel thickness on their teeth. The enamel appears to be considerably thicker on all tooth tips (Fig. 23; Supporting Information, Fig. S1). This feature is also present in *Trogonophis wiegmanni* but is lacking in *Diplometopon zarudnyi*. Based on our observations on μCT scans of various amphisbaenian taxa, this enamel thickness appears to be absent from rhineurids, bipedids, and amphisbaenids. If indeed unique to *Trogonophis* and its stem, this feature could represent a synapomorphy to that group, as is presently inferred from our phylogenetic results. Interestingly, in the maxilla ONM CBI-1-649 of *Terastiodontosaurus*, there are areas of both the largest and the second largest teeth in which enamel is very thin or almost absent (Supporting Information, Fig. S1B), seemingly the result of apical wear caused by abrasion (i.e. resulting from tooth–food particle contact) or attrition (i.e. resulting from tooth–tooth contact).

The cranial anatomy of trogonophids shows intraspecific variation, with differences concerning the number and position of labial foramina, the interdigitation between the frontals and parietal, and the extent of co-ossification among the occipital complex, fused basioccipital and parabasisphenoid, as has been exemplified recently for *Diplometopon* (Hawkins *et al.* 2022). The shape of the premaxilla and maxilla is also variable, particularly regarding the presence or absence of a rostral blade cleft in the premaxillae and the number, size, and placement of the labial foramina and the point of the frontal processes in the maxillae (Hawkins *et al.* 2022). Moreover, there is a significant degree of sexual dimorphism observed in the extant *Trogonophis wiegmanni*; although males and females have the same total lengths, the former have considerably larger heads and tails than the latter (Martín *et al.* 2012).

The abundance of the preserved material of *Terastiodontosaurus marcelosanchezi*, consisting of several maxillae, dentaries, and premaxillae, pertaining to a variety of different individuals of different sizes (minimum number of individuals for premaxillae, maxillae, and dentaries equal to 4, 6, and 11, respectively), allows some assessment of the intraspecific variation of the new taxon and more precise comparisons with other trogonophid taxa. In any case, as exemplified in the descriptions above, the observed variation in the premaxillae, maxillae, and dentaries of *Terastiodontosaurus marcelosanchezi* seems to be relatively low. Indeed, the most important variation is the deviation of the typical formula of three maxillary teeth that is observed in ONM CBI-1-651 (three teeth plus a tiny one) and ONM CBI-1-649 (two teeth). Notably, ONM CBI-1-649, which has only two teeth, represents the smallest available individual. In contrast, in ONM CBI-1-651, the unique maxilla with four teeth (three plus a tiny one), the extra fourth tiny tooth is situated posteriorly from the posteriormost small tooth; although it is situated not exactly in a row with the other teeth (but rather a bit more medially), this does not represent a replacement tooth, because the teeth are not replaced. The tooth ratios we introduced above also show variation, although together they point to population means that distinguish *Terastiodontosaurus* from other trogonophids (see also Table 2). As for the characteristic 'hill' that is present in some small teeth of maxillae and dentaries, this could be present because these teeth had not been much abraded like the large ones. Finally, the number, spacing, and positions of labial foramina and nutritive foramina in both maxillae and dentaries show also some degree of variation.

Regarding the vertebrae from Chambi, these pertain to Amphisbaenia based on the dorsoventrally compressed centrum with a nearly flat ventral surface and roughly parallel lateral margins, the massive and hemisphaerical synapophyses, the absence of the zygosphene, and a dorsally weakly convex neural arch lacking a neural spine (Estes 1983, Georgalis *et al.* 2018b). Among Amphisbaenia, vertebrae appear to be rather homogeneous and similar among different taxa, usually not allowing distinction at the genus or even family level (Georgalis *et al.* 2018b). A notable exception is Rhineuridae, the vertebrae of which are characterized by longitudinal striae on the vertebrae and a denticulate neural arch (Berman 1973, Estes 1983, Folie *et al.* 2013). Vertebrae of Trogonophidae do not seem to possess adequate diagnostic features, but admittedly only a few studies have dealt with these bones in this group. It seems that only the monumental work by Gans (1960) provided some observations and figures for vertebrae of all trogonophid genera; however, even in that work figuring was confined solely to the anterior vertebrae. Apparently, his focus on anterior vertebrae was attributable to the fact the he had highlighted the fusion of the cervical vertebrae as characteristic of Trogonophidae, being most prominent in *Agamodon* (Gans 1960). Earlier, Zangerl (1945) had noticed that in *Trogonophis*, all transverse processes in caudal vertebrae point forwards; however, this feature should be more widely evaluated before it is used taxonomically. Augé (2012: fig. 4c) also provided a figure of the dorsal view of a presacral vertebra of *Agamodon*. Recently, Araújo Salvino *et al.* (2024) investigated, through μCT scanning, the atlanto-axial complex of various trogonophid species, revealing a feature unique among amphisbaenians and thus a synapomorphy of Trogonophidae, i.e. the pointed (instead of spade-shaped) odontoid process of the axis. It is worth noting that Čerňanský *et al.* (2015a, 2020) mentioned that, similar to the condition observed in rhineurids, vertebrae of trogonophids too possess a denticulate vertebral posterior margin, further stating that this feature was also variably present in some amphisbaenids. There are few published observations that would confirm or refute this assumption. In the African amphisbaenid *Geocalamus acutus* (collection of A.H.,

Table 2. Morphometric data of specimens of *Trogonophis wiegmanni* and ***Terastiodontosaurus marcelosanchezi***.

Taxon	Specimen number	Maxilla length (mm)	Maxilla tooth count	Largest maxilla tooth length/total tooth row length ratio	Skull length (mm)	Snout–vent length (mm)	Tail length (mm)	Skull/ maxilla length ratio	Total length/ maxilla length ratio	Total length (mm)
Trogonophis wiegmanni	SMF-PH 565	3.23	4			134.4	9.9		44.7	144.3
Trogonophis wiegmanni	SMF-PH 566	3.4	4	0.44						
Trogonophis wiegmanni	SMF-PH 567	3.32	4	0.47	11	156.4	13.4	3.31	51.1	169.8
Trogonophis wiegmanni	FMNH 109462	4.2	4	0.46	14.2			3.38		
Trogonophis wiegmanni	YPM HERR 6903	2.16	3	0.51	6.94			3.21		
Terastiodontosaurus marcelosanchezi	ONM CBI-1-645 (holotype)	16.3	3	0.52	**53.8 (estimated)**					**781 (estimated)**

uncatalogued), we find denticulation to be well developed in the anterior one-half of the presacral vertebral column (Supporting Information, Fig. S8), but in multiple specimens of *Trogonophis wiegmanni* (e.g. SMF-PH 566 and SMF PH-567) it is essentially absent throughout. The presacral vertebra of *Agamodon* figured by Augé (2012: fig. 4c) shows some ridges, but still not the prominent denticulation that is otherwise observed in rhineurids. At present, the development of fluting or denticulations of the neural arch in extant Trogonophidae is uncertain.

Vertebrae of fossil (or subfossil) *Trogonophis* have been documented only by Stoetzel *et al.* (2008). Given that *Terastiodontosaurus marcelosanchezi* is the only recognized amphisbaenian taxon among the abundant cranial fossil material from Chambi, it seems reasonable to assume at present that most of the fossil vertebrae from Chambi pertain to the said taxon. However, taking into consideration the overall high diversity of Eocene amphisbaenians in Europe and North America, coupled with the fact that the late Palaeocene of Adrar-Mgorn 1 in Morocco yielded two amphisbaenian forms, we cannot exclude the possibility that a second amphisbaenian taxon was also present in Chambi, for which there is currently no available cranial material. Moreover, there is considerable size disparity among the available amphisbaenian vertebrae from Chambi, and some of them are very small, with centrum lengths only ~1 mm. Accordingly, although the referral of most of the vertebral material from Chambi to *Terastiodontosaurus marcelosanchezi* is probable, we consider the referral in any particular case as tentative.

Diet and bite force

Amblyodonty is characterized by the presence of large and blunt teeth. Blunt teeth can be observed among an array of distantly related squamates and are considered to represent adaptations for crushing hard-shelled prey items (Edmund 1969, Böhme *et al.* 2022). Indeed, these have been described in various lizard taxa that are known to feed on molluscs, including scincids (Edmund 1969), teiids (Peyer 1929, Presch 1974, Dalrymple 1979, Leite *et al.* 2021), extinct lacertids (Roček 1984, Augé 2005, Čerňanský *et al.* 2016b, 2017, Georgalis *et al.* 2021), a few amphisbaenians (see below), anguids (Klembara *et al.* 2010, 2014, 2017, Smith and Gauthier 2013, Loréal *et al.* 2023, 2024), varanids (Mertens 1942, Rieppel and Labhardt 1979, D'Amore 2015), iguanians (Estes and Williams 1984, Herrel and Holanova 2008), and some Cretaceous mosasaurs (Bardet *et al.* 2005), in addition to snakes feeding on hard-bodied arthropods (Rajabizadeh *et al.* 2021, Böhme *et al.* 2022).

Amblyodont dentition is rare among amphisbaenians. Besides the herein documented *Terastiodontosaurus*, amblyodonty is otherwise observed solely in the late Palaeocene African *Todrasaurus*, the late Palaeocene North American *Oligodontosaurus* Gilmore, 1942, the Eocene European *Cuvieribaena*, the extant trogonophid *Trogonophis*, and a single species of the extant *Amphisbaena*, the insular endemic *Amphisbaena ridleyi* Boulenger, 1890 (Gilmore 1942, Gans 1960, Pregill 1984, Augé and Rage 2006, Čerňanský *et al.* 2015a, this paper). Dietary study of one insular population of *Trogonophis wiegmanni* during the springtime showed that it is at least partly durophagous, selecting and feeding on snails, which it crushes and swallows with the shell (Martín *et al.* 2013). It should be noted that this species had previously been considered, based on mainland populations, to feed on ants and termites (e.g. Schleich *et al.* 1996). Martín *et al.* (2013) suggested, on the basis of its dentition, its documented diet, and the flaring of the jugal process of the maxilla (which would provide more space for the jaw adductor musculature), that *Trogonophis wiegmanni* could be a snail specialist. Baeckens *et al.* (2017) further suggested that there are modifications to the musculature of *Trogonophis wiegmanni* that allow it to bite harder than its head size would normally allow.

Based on the dissection of the specimen of *Trogonophis wiegmanni* (MNHN-RA-1987.1895), we attempted to make a bite force estimation for *Terastiodontosaurus marcelosanchezi*. The muscle data for the specimen (MNHN-RA-1987.1895) of *Trogonophis wiegmanni* are provided in Table 3. Our calculations estimated a bite force for the *Trogonophis* MNHN specimen of 9.6 N at the tip of the jaw and 14.2 N at the largest tooth. These results are similar to *in vivo* measurements of two *Trogonophis* specimens of slightly smaller size (lower jaw length: 7.99 ± 0.62 mm vs. 11.74 mm for MNHN-RA-1987.1895),

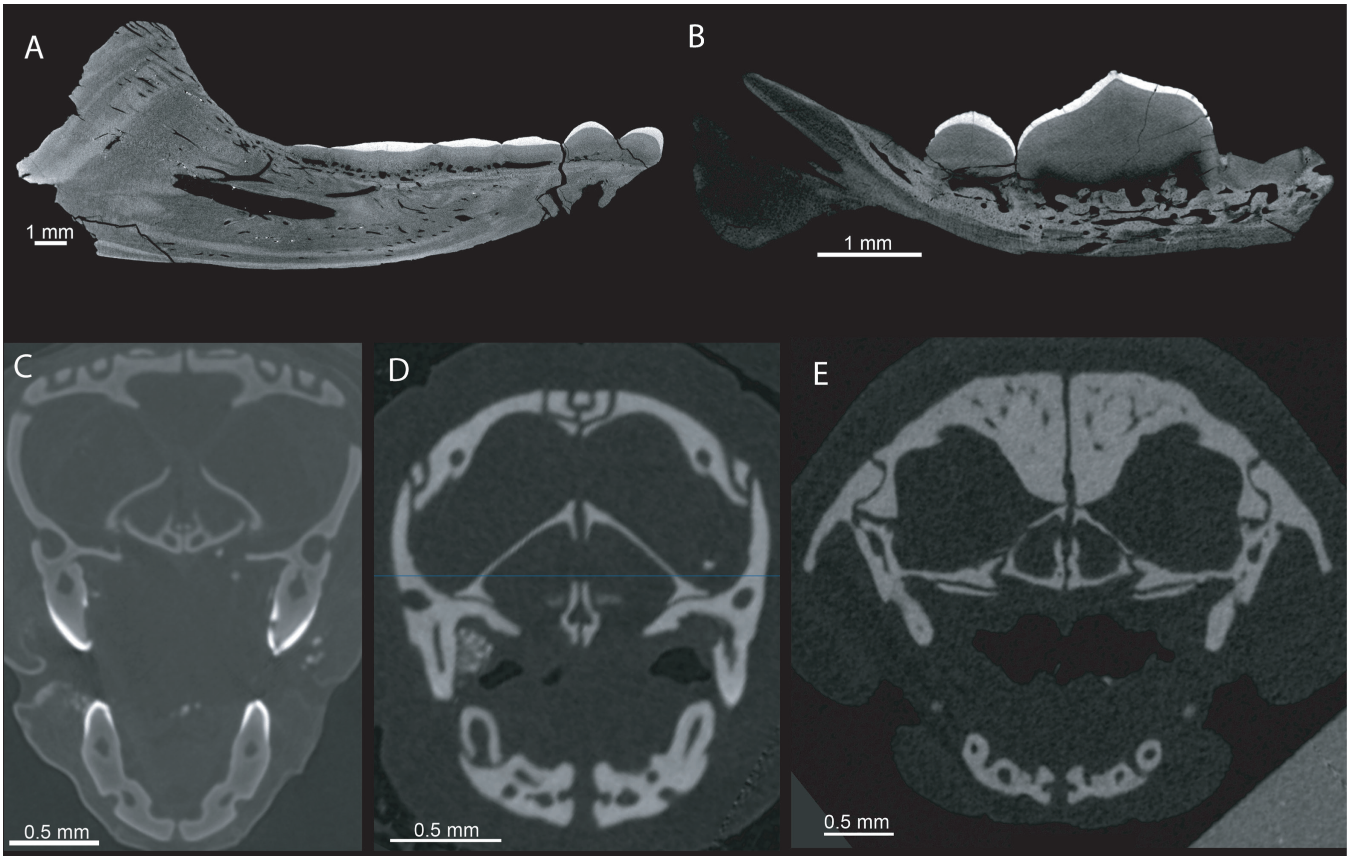

Figure 23. The profound enamel thickness in the teeth of Trogonophidae in comparison to other amphisbaenians. A, paratype dentary (ONM CBI-1-646) of ***Terastiodontosaurus marcelosanchezi***. B, holotype dentary (UM THR 407) of *Todrasaurus gheerbranti*. C, *Trogonophis wiegmanni* (YPM HERR 6903), transverse section of snout. D, *Zygaspis quadrifrons* (collection of A.H., uncatalogued), transverse section of snout. E, *Monopeltis capensis* (collection of A.H., uncatalogued), transverse section of snout.

Table 3. Measurements of the muscles of the dissected specimen of *Trogonophis wiegmanni* (MNHN-RA-1987.1895). Abbreviations: Add., adductor; ext., externus; m., musculus; mand., mandibulae; PCSA, physiological cross-sectional area; sup., superficialis.

Muscle	Mass (g)	Fibre length (cm)	PCSA (cm^2)
m. depressor mandibulae	0.0042	0.15	0.03
m. cervicomandibularis	0.0636	0.36	0.17
m. add. mand. ext. sup. anterior	0.0024	0.27	0.01
m. add. mand. ext. sup. posterior	0.0278	0.27	0.10
m. add. mand. ext. medialis	0.0303	0.26	0.11
m. add. mand. externus profundus	0.0516	0.24	0.20
m. adductor mandibulae posterior	0.0042	0.17	0.02
m. pseudotemporalis superficialis	0.0146	0.27	0.05
m. pseudotemporalis profundus	0.0065	0.27	0.02
m. pterygoideus	0.006	0.11	0.05

which produced 8.31 ± 1.42 N at the middle of the tooth row. Based on these results, we estimated the bite force of the paratype (ONM CBI-1-646) of *Terastiodontosaurus marcelosanchezi* to be 16.71 N at the tip of the jaw and 24.83 N at the largest tooth. This would allow *Terastiodontosaurus* to crush a wide variety of snails (Fig. 24).

Size estimation and locomotion of *Terastiodontosaurus marcelosanchezi*

The holotype maxilla of *Terastiodontosaurus marcelosanchezi* has a length of 16.3 mm. Based on the linear dimensions of the maxilla and skull in *Trogonophis wiegmanni* (Table 2) and assuming isometry of growth and identical skull proportions in the adult, we estimate that the individual from which the holotype of *Terastiodontosaurus marcelosanchezi* derives had a skull length of 53.8 mm. This renders it the largest known amphisbaenian ever to have lived, as judged by skull size.

All other known amphisbaenians, either extinct or extant, appear to be smaller than the new taxon from Chambi. *Listromycter leakeyi*, from the Early Miocene of Kenya, is known only by its holotype (NHMUK PV R 8292), an almost complete skull missing only the lower jaw. Its premaxilla (characterized as 'enormous' by Charig and Gans 1990) is 12.7 mm in length, and these authors estimated a total skull length of 36 mm ('estimated length of whole skull, measured in a straight line from tip of premaxillary rostral process to occipital condyle: about 36 mm'), leading them to suggest this taxon to represent the largest known amphisbaenian (Charig and Gans 1990). Only slightly smaller is *Spathorhynchus fossorium* Berman, 1973, from the Eocene of the USA, with a skull length of 35.4 mm (Berman 1973, Müller *et al.* 2016). Other large species are *Spathorhynchus natronicus* Berman, 1977, from the early Oligocene of the USA (skull length estimated at 28 mm, according to Berman 1977), *Ototriton solidus* Loomis, 1919, from the Eocene of the USA (32 mm according to Estes 1983), and *Macrorhineura skinneri* MacDonald, 1970, from the Early Miocene of the USA (also 32 mm according to Estes 1983).

Extrapolation of skull length for *Terastiodontosaurus marcelosanchezi* is probably fairly accurate, given its strong overall similarity to extant *Trogonophis wiegmanni*, but extrapolation of total length is much less certain. The maximal presacral vertebral count in *Trogonophis wiegmanni* is ~77 (Table 2; Alexander and Gans 1966, Hoffstetter and Gasc 1969), and in *Agamodon* spp. it is no higher, but in *Diplometopon zarudyi* and *Pachycalamus brevis* it reaches nearly 90. The count in *Trogonophis wiegmanni* is lower than in almost any other extant Amphisbaenia except *Agamodon* (Hoffstetter and Gasc 1969). Assuming this value is applicable to *Terastiodontosaurus marcelosanchezi*, we extrapolate for the individual from which the holotype maxilla derives a total length of 781 mm (Table 2). Supposing that this number

Figure 24. Life reconstruction of ***Terastiodontosaurus marcelosanchezi*** ready to prey on a large snail of the family Bulimulidae. Artwork by Jaime Chirinos.

might have been higher (e.g. 90 presacral vertebrae), then a value of >900 mm is likely for the new extinct amphisbaenian taxon.

Amongst extant amphisbaenians, *Amphisbaena alba* is the largest species, reaching a maximum total length of 810 mm (Colli and Zamboni 1999, Feldman *et al.* 2016, Jared *et al.* 2024) and a skull length of >31 mm [31.8 mm in the paper by Montero and Gans 1999; 36.59 mm in specimen FMNH 195924 (Digimorph); but <30 mm in several other published specimens (e.g. Clark and Rene Hernandez 1994, Montero and Gans 1999)], followed by *Dalophia gigantea* (Peracca, 1903), and a few species of *Monopeltis* Smith, 1848, *Leposternon* Wagler, 1824, and *Amphisbaena* Linnaeus, 1758, which also achieve large (but not very large) sizes (Gans and Montero 2008, see Feldman *et al.* 2016).

Practically all extant amphisbaenians represent burrowing animals, which appear only rarely on the surface, outside their subterranean environments (Gans 1969, 1978, Gans and Montero 2008, Vidal *et al.* 2008). Nevertheless, certain features in *Terastiodontosaurus* (e.g. the very large size and the tall premaxilla) seem to contradict this natural history pattern and suggest instead that the new Tunisian taxon was likely to be a surface dweller (Fig. 24). This is further supported by the extreme size of the new taxon, which would render subterranean habits as less likely; as a matter of fact, the largest extant amphisbaenian, *Amphisbaena alba*, only rarely makes burrows in captivity (Jared *et al.* 2024). The preferred habitat of Amphisbaenia is also related to their coloration, with deeply burrowing species, such as *Rhineura floridana* (Baird, 1858) and *Agamodon* spp., almost devoid of pigmentation, hence appearing pinkish, whereas species that spend considerable time much closer to the surface, such as *Amphisbaena alba* and *Trogonophis wiegmanni*, show distinct pigmentation patterns (Gans 1978). Given our inferences concerning its preferred habitat, we can safely assume that *Terastiodontosaurus* had pigmented skin.

Altogether, our study points to remarkable new insights into the biology of Amphisbaenia. With a skull size >5 cm in length, *Terastiodontosaurus* was larger than any previously known amphisbaenian, living or extinct, and accordingly, it was probably more of a surface dweller than a strictly fossorial animal. This broadens our understanding of amphisbaenian evolutionary ecology and the limits of the amphisbaenian body plan. That this animal probably lived during around the Early Eocene Climatic Optimum (Zachos *et al.* 2001) is noteworthy in view of the relationship between ambient temperature and maximum body size within a higher taxonomic group (Makarieva *et al.* 2005, Head *et al.* 2009). Furthermore, the documentation of characteristics associated with molluscivory, such as flared jugal processes of the maxilla and thick tooth enamel, in stem representatives of *Trogonophis* suggest that this lineage has conserved this unusual aspect of its niche for tens of millions of years until the present day.

Trogonophidae origins and biogeography

Terastiodontosaurus marcelosanchezi represents a substantial contribution to the so far poorly known African fossil record of Amphisbaenia, representing only the fifth named extinct species from the continent, adding to *Lophocranion rusingense* Charig & Gans, 1990 and *Listromycter leakeyi*, both from the Early Miocene of Rusinga Island, Kenya, and the aforementioned trogonophids *Todrasaurus gheerbranti* from the late Palaeocene of Morocco and *Trogonophis darelbeidae* from the Plio-Pleistocene of Morocco. Moreover, the abundant Chambi material adds to the extremely scarce Palaeogene Afro-Arabian record of Amphisbaenia, which were so far known exclusively from the holotype of *Todrasaurus gheerbranti* from the late Palaeocene (Thanetian) of Adrar-Mgorn 1, Morocco (Augé and Rage 2006, this paper) and indeterminate remains from the late Palaeocene (Thanetian) of Adrar-Mgorn 1, Morocco (Augé and Rage 2006), the early Eocene (middle Ypresian) of N'Tagourt 2, Morocco (Augé and Rage 2006), the early–middle Eocene (late Ypresian–early Lutetian) of Glib Zegdou HGL50, Algeria (Rage *et al.* 2021), the middle Eocene of Black Crow, Namibia (Rage *et al.* 2013), and the late Eocene (earliest Priabonian) of Birket Qarun 2, Fayum, Egypt (El-Hares *et al.* 2022) (see also Fig. 1). Note that amphisbaenian vertebrae described by Rage *et al.* (2013) from the locality of Silica North in Sperrgebiet, Namibia, were originally considered to be middle Eocene in age, but recent studies have reappraised that site to be much younger, pertaining to the late Oligocene or even the Early Miocene (Coster *et al.* 2012, Marivaux *et al.* 2014, Sallam and Seiffert 2016, 2020, Rage *et al.* 2021, El-Hares *et al.* 2022, Smith and Georgalis 2022). Accordingly, it is evident that the Palaeogene record of Amphisbaenia in the (then isolated) Afro-Arabia seems so far to be known almost exclusively from the northern margins of the continent. This pattern contrasts with the relatively high extant diversity of the group in sub-Saharan Africa, where amphisbaenians represent a principal component of the squamate faunas (e.g. Broadley *et al.* 1976, Broadley and Broadley 1997, Gans 2005). This Palaeogene distribution is apparently collection biased, because Palaeogene northern African fossil localities have been more intensively investigated and sampled.

Moreover, the new material from Chambi adds further to the extremely poor fossil record of Trogonophidae, which was so far confined solely to the holotype of *Todrasaurus gheerbranti* from the late Palaeocene (Thanetian) of Adrar-Mgorn 1, Morocco (Augé and Rage 2006, this paper), the material of *Trogonophis darelbeidae* from the Plio-Pleistocene of Ahl al Oughlam, Morocco (Bailon 2000), and material of the extant species *Trogonophis wiegmanni* from the Holocene (Neolithic) of El Harhoura 2, Morocco (Stoetzel *et al.* 2008) and the Holocene (Neolithic) of Gueldaman Cave, Algeria (Saidani *et al.* 2016), plus a mentioned (but not described) record from the Late Pleistocene of Ifri n'Ammar, Morocco (Mouhsine *et al.* 2022).

Interestingly, most molecular studies have suggested that the split of Trogonophidae from the remaining amphisbaenians took place only at around the Eocene. Graboski *et al.* (2022) placed this estimated divergence date of Trogonophidae at ~44 Mya (i.e. middle Eocene). A similar result is also the case in other recent studies, including Vidal and Hedges (2005), who placed this divergence at ~43–23 Mya, Vidal *et al.* (2008) at ~51 Mya, and Pyron (2017) and Burbrink *et al.* (2020) at around the mid-Palaeogene. In the combined analysis by Longrich *et al.* (2015), Trogonophidae were found to diverge from other Afrobaenia in the early Eocene, and the basal divergence in Trogonophidae (between *Trogonophis* and *Diplometopon* + *Agamodon*) in the late Eocene. An even younger (early Oligocene; 31.5 Mya) age for the divergence of *Trogonophis* from *Amphisbaena* was estimated in the combined phylogeny of Brownstein *et al.* (2023), while the same divergence was estimated as even younger (~20 Mya) by Jones *et al.* (2013). Only the molecular analysis by Zheng and Wiens (2016) placed the split of Trogonophidae from its sister group, Amphisbaenidae, at a much older time, ~80 Mya, with *Trogonophis* splitting from *Diplometopon* at ~41 Mya.

The close relationship between *Todrasaurus gheerbranti* recovered in this study (see above, Fig. 18) indicates that the basal divergence of Trogonophidae took place before the end of the Thanetian, i.e. late Palaeocene. Our study therefore pushes back the known origin of the group substantially. *Todrasaurus gheerbranti* can serve as a critical new fossil calibration for molecular studies of Amphisbaenia.

Amphisbaenia witnessed an astonishing history of long ocean dispersals, as has been implied by both the fossil record (Longrich *et al.* 2015) and molecular data (Vidal *et al.* 2008, Graboski *et al.* 2022). However, it has to be noted that Tałanda (2016) suggested instead that amphisbaenian dispersals occurred mainly through existing land bridges or at least across not-so-distant marine barriers. Nevertheless, transatlantic rafting during the Eocene has been suggested for various amphisbaenian groups (Vidal *et al.* 2008, Longrich *et al.* 2015, Graboski *et al.* 2022). Although amphisbaenians are almost strictly burrowing reptiles, swimming capabilities have been observed even in certain extant taxa, either in order to escape extreme situations or to find new food resources (Quinteros-Muñoz *et al.* 2023); of course, such swimming capabilities fall far short of performance expectations for crossing a long sea barrier. As a matter of fact, such long-distance, overseas dispersals of amphisbaenians would be possible only by using 'floating islands of vegetation' ('floatons', 'flotsams'), aided by some marine currents and wind (Houle 1998, Vidal *et al.* 2008, Bandoni de Oliveira *et al.* 2009, Longrich *et al.* 2015, Marivaux *et al.* 2023). This might explain the long dispersal routes over large marine barriers in their geological past, their current geographical distribution, and their current presence on remote islands (Vidal *et al.* 2008, Longrich *et al.* 2015, Graboski *et al.* 2022). Dispersals are a major key to the evolution of reptile assemblages over time (Longrich *et al.* 2015); this is particularly true for Afro-Arabia, a landmass that was isolated for practically the whole Palaeogene and shows an astonishing diversity of dispersals of non-marine vertebrates from and to other continents, particularly during the Eocene (see Georgalis 2021). Longrich *et al.* (2015) suggested that stem afrobaenians (i.e. in their analysis, the total group encompassing Cadeidae, Trogonophidae, and Amphisbaenidae) dispersed directly from North America to Africa, via marine dispersal, during the Palaeocene or early Eocene; this opinion was criticized by Tałanda (2016), who also noticed that this scenario was incompatible with marine palaeocurrent reconstructions and that no other vertebrate group is known to have dispersed from North America directly to Africa during the Palaeogene. Longrich *et al.* (2015) further suggested that the ancestor of Trogonophidae originated in Africa. The identification of the new trogonophid *Terastiodontosaurus marcelosanchezi* from the late early–early middle Eocene of Tunisia gives some strength to this latter assumption. Nevertheless, more fossil remains are necessary in order to comprehend fully the early evolutionary and biogeographical patterns of Amphisbaenia. We anticipate that rich and diverse African fossil assemblages, such as Chambi, will decipher further valuable clues about the origins and fossil record of these charismatic squamates.

SUPPLEMENTARY DATA

Supplementary data are available at *Zoological Journal of the Linnean Society* online.

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CONFLICT OF INTERESTS

None declared.

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DATA AVAILABILITY

All fossil specimens of *Terastiodontosaurus marcelosanchezi* from Chambi described herein are permanently curated in the collections of ONM. The holotype (UM THR 407) of *Todrasaurus gheerbranti* from the late Palaeocene of Adrar-Mgorn 1, Morocco, is permanently curated in the collections of UM. Three-dimensional model files of several premaxillae, maxillae, and dentaries of *Terastiodontosaurus marcelosanchezi* (including the holotype and paratype specimens) plus the holotype dentary of *Todrasaurus gheerbranti* are deposited in MorphoMuseuM (Georgalis *et al.* in press).

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