A taxonomic and phylogenetic review of the anhanguerid pterosaur group Coloborhynchinae and the new clade Tropeognathinae

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Anhanguerids are a particular group of pterodactyloid pterosaurs, characterized mainly by their rostral sagittal crests, well laterally expanded jaw tips and enlarged anterior teeth. Due to the fragmentary nature of most known specimens, including holotypes, the taxonomy of the group has proved particularly difficult and controversial. Coloborhynchinae is a recently proposed clade within the Anhangueridae, and was defined as the most inclusive clade containing *Coloborhynchus clavirostris* but not *Anhanguera* or *Ludodactylus*. Coloborhynchinae was originally thought to include *Coloborhynchus*, *Uktenadactylus*, and *Siroccopteryx*. Here we present a reassessment of the taxonomy and phylogeny of all proposed members of the Coloborhynchinae and *Coloborhynchus* complex, with new anatomical comparisons and a novel phylogenetic analysis. Several features allow us to establish that coloborhynchines were much more diverse than previously thought, englobing four genera and seven species: *Aerodraco sedgwickii* gen. et comb. nov., *Coloborhynchus clavirostris*, *Nicorhynchus capito* gen. et comb. nov., *Nicorhynchus fluviferox* gen. et comb. nov., *Uktenadactylus rodriguesae* sp. nov., and *Uktenadactylus wadleighi*. *Nicorhynchus* and *Uktenadactylus* are considered sister taxa, being distinct on the basis of several rostral characters. Although with a homoplastic flat rostrum surface, *Siroccopteryx* was recovered out of the Coloborhynchinae, as sister taxon of *Tropeognathus*, due to similarities on the palatal ridge (which is broad and deep, and starting at the same level) and the relatively stout teeth compared to other anhanguerids. *Tropeognathus* and *Siroccopteryx* are further related to the Australian taxa *Ferrodraco* and *Mythunga*, which are all grouped in a new clade: the Tropeognathinae. Our analysis suggests that morphological evolution within anhanguerids was quite more complex than previously thought, with coloborhynchines representing the oldest recorded lineage of Anhangueridae, which achieved a worldwide distribution at least from the Aptian to the Cenomanian.

Key words: Pterosauria, Pterodactyloidea, morphology, taxonomy, phylogeny, Cretaceous, USA, United Kingdom.

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Introduction

Back in 1874, Richard Owen described *Coloborhynchus clavirostris* from a fragment of a pterosaur rostrum coming from the Berriasian–Valanginian Hastings Beds, in the locality of St. Leonards-on-Sea (East Sussex, England). He then proposed a new genus for the new species due to its particular morphology, not previously recognised in any other known pterosaur at that time: “...the foremost pair of teeth projecting forward in the upper jaw from the truncate surface at a higher level than the alveolar border” (Owen 1874: 6). Albeit Owen (1874) referred other two species from the Cambridge Greensand to the genus *Coloborhynchus*, *C. cuvieri*, and *C. sedgwickii*, none of the three was designated as type species.

Forty years later, however, Hooley (1914) proposed that the uncommon placement of the first dental alveoli in *Coloborhynchus* was a consequence of a full abrasion of the rostral tip. Hooley (1914) then considered *Coloborhynchus*...
Coloborhynchus clavirostris to be a junior synonym of “Criorhynchus” simus (= Ornithocheirus simus) from the Cambridge Greensand. Later, Kuhn (1967) agreed with this view, and finally designated Coloborhynchus clavirostris as the type species of the genus Coloborhynchus.

Although later works accepted such synonymy (e.g., Wellnhofer 1978), Lee (1994) re-validated the genus Coloborhynchus (with the type species C. clavirostris) by describing a new species, Coloborhynchus waddleighi, from the Albion Paw Paw Formation (Texas, USA) on the basis of the following characters: a flattened and triangular anterior margin of the premaxilla; one pair of teeth projecting anteriorly and located above the subsequent teeth; an anterior median depression; and a premaxillary crest beginning near the tip of the skull (Lee 1994; Rodrigues and Kellner 2008). From then on, other authors accepted the re-validation of Coloborhynchus (e.g., Kellner and Tomida 2000; Fastnacht 2001; Unwin 2001; Veldmeijer 2003).

On the basis of the description of a new specimen from the Albion Romualdo Formation (Northeast Brazil), Fastnacht (2001) reconsidered the genus Coloborhynchus and relocated Tropeognathus robustus Wellnhofer 1987 to this genus. Fastnacht (2001) modified the diagnosis after Lee (1994) adding the following characters: upper jaw laterally expanded in a spoon-shape in dorsal view from the second to the fourth pair of alveoli; first pair of teeth projecting anteriorly from the blunt anterior margin of the upper jaw at a significant elevation above the palate relative to subsequent teeth; second and third pair of alveoli of the upper and lower jaw enlarged relative to other alveoli; lower jaw with medial crest rising from its anterior end; and lower jaw laterally expanded in a spoon-shape from the first to the third pair of alveoli (Fastnacht 2001). This new diagnosis was considered in the subsequent literature by some authors (e.g., Unwin 2001, 2002, 2003; Frey et al. 2003; Veldmeijer 2003, 2006; Lü et al. 2006; Martill and Naish 2006; Fastnacht 2008; Martill and Unwin 2012; Witton 2013; Martill 2015; Martín-Silverstone et al. 2018).

Unwin (2001), accepting the re-validation of Coloborhynchus, followed the works of Lee (1994) and Fastnacht (2001) and further added other species to this genus. Among those, there was one of the species from Cambridge Greensand originally referred to the genus Coloborhynchus by Owen (1874): C. sedgwickii. Unwin (2001) also referred “Ornithocheirus” capito to the genus Coloborhynchus, and several other species from Cambridge Greensand were synonymised to this species (see Supplementary material for further details). Furthermore, Unwin (2001) even suggested the presence of Coloborhynchus out of England and the Americas, referring to this genus Siroccopteryx moroccan sis Mader and Kellner, 1999 from the Kem Kem Group (Morocco), as well as a specimen from the Dzun-Bayin Formation, Mongolia (Bakhurina and Unwin 1995; Unwin and Bakhurina 2000). A year later, Unwin (2002) considered Anhanguera piscator as a synonym of Coloborhynchus robustus, what was then followed in subsequent works by some authors (see list above).


However, a few years later, Rodrigues and Kellner (2008) reviewed the genus Coloborhynchus and restricted it to the type species, Coloborhynchus clavirostris, with the following revised diagnosis: an oval depression beneath the first pair of dental alveoli, second to fourth pairs of premaxillary alveoli located laterally, fifth and sixth premaxillary alveoli located more medially than the preceding alveoli on the base of the palatal ridge, and anterior part of the palatal ridge bordered by two shallow longitudinally elongated depressions. They relocated the North-American species, Coloborhynchus waddleighi, to a new genus: Ukenadactylus. Concerning the purported records from the Romualdo Formation, Rodrigues and Kellner (2008) referred them to the genus Anhanguera, as A. piscator, A. robustus (following Kellner and Tomida 2000) and A. spielbergi. Furthermore, they accepted the validity of Siroccopteryx as distinct from Coloborhynchus, and excluded “Ornithocheirus” capito and “Coloborhynchus” sedgwickii from the genus Coloborhynchus; thus, raising the need of new generic names for these latter two.


Later, as a reassessment of the wastebasket genus Ornithocheirus, Rodrigues and Kellner (2013) revised those species once considered within the genus Coloborhynchus in previous works. Following their previous diagnosis (Rodrigues and Kellner 2008), they considered again the genus Coloborhynchus as restricted to the type species, Coloborhynchus clavirostris. Other species were relocated in new genera, as Camposipterus (?) sedgwickii and Cimolopterus cuvieri, or assigned as nomina dubia (Rodrigues and Kellner 2013: 5–7). “Ornithocheirus” capito, despite having been considered as a valid species and potentially representing a new genus, was referred by the name given in its original description “…until better material comes to light”.

In addition, in the last two decades, other specimens were assigned to the genus Coloborhynchus. On the basis of a highly damaged and large fragment of anterior rostrum
from the Cambridge Greensand previously referred to as *Coloborhynchus capito* (see Unwin 2001) or *Coloborhynchus* sp. (Martill 2010), Martill and Unwin (2012) described it as a new specimen of *Coloborhynchus capito* based on the purported presence of a markedly concave anterior margin of the premaxillary crest. Afterwards, Martill (2015) described a specimen attributed to *Coloborhynchus* sp. from the Wessex Formation (Lower Cretaceous) of the Isle of Wight, which is represented by a fragment of an anterior rostrum. Finally, Jacobs et al. (2019) contributed with the description of a new species, named *Coloborhynchus fluviiferox*, on the basis of a well-preserved anterior rostrum fragment. These authors also discussed on the morphology of several species previously referred to the genus *Coloborhynchus*, including *C. capito*, *C. clavirostris*, and the new *C. fluviiferox*, but also *Uktenaadactylus wadleighi* and *Siroccopteryx moroccensis*, and included all of them in a phylogenetic analysis. On the same year, Holgado et al. (2019) reassessed the clade Anhangueria and established a new clade within Anhangueriidae, which contains *Coloborhynchus clavirostris* and relatives: the Coloborhynchinae. Following Holgado et al. (2019), coloborhynchines were characterised by the following synapomorphies (based on Rodrigues and Kellner 2008): a quadrangular expansion of the premaxillary tip and a flat anterior surface of the rostrum.

In this work, we focus on the reassessment of the taxonomy and phylogeny of the proposed members of the Coloborhynchinae/ *Coloborhynchus* complex (see SOM: tables S1 and S2 for further details in taxonomical history of this genus, Supplementary Online Material available at http://app.pan.pl/SOM/app65-Holgado_Pegas_SOM.pdf), with new anatomical comparisons and a novel phylogenetic analysis.

**Institutional abbreviations.**—AODF, Age Of Dinosaurs Fossil, Winton, Queensland, Australia; BSPG, Bayerische Staatssammlung für Paläontologie und Geologie, Munich, Germany; CAMSM, Sedgwick Museum of Earth Sciences, Cambridge, England, UK; FSAC, Faculté des Sciences Ain-Chock, Université Hassan II, Casablanca, Morocco; IWCMS, Isle of Wight County Museum Service, Isle of Wight, England, UK; NHMUK, Natural History Museum, London, UK; QM, Queensland Museum, Brisbane, Australia; SMU, Shuler Museum of Paleontology, Southern Methodist University, Dallas, USA.

**Nomenclatural acts.**—This published work and the nomenclatural acts it contains, have been registered in ZooBank: urn:lsid:zoobank.org:pub:84FCB40E-8207-4EDF-BA46-5455101EE488

**Material and methods**

Here we re-examine all pterosaur specimens associated to the aforementioned *Coloborhynchus* complex, including several rostra housed in different institutions worldwide (see below for further details). For anatomical nomenclature and orientations, we follow Bennett (2001) as well as Rodrigues and Kellner (2013). We further make use of the term deltoid facet, introduced by Jacobs et al. (2019) in reference to the roughly triangular, upturned anterior palatal surface.

The phylogenetic analysis we present here is based on a data matrix modified from Pégas et al. (2019), with the inclusion of characters by Jacobs et al. (2019) and several new rostral characters (see the SOM), as well as of the following taxa: *Nicorhynchus capito* comb. nov. (CAMSM B54265), *Nicorhynchus fluviiferox* comb. nov. (FSAC–KK 10701), *Aerodraco sedgwickii* gen. et comb. nov. (CAMSM B54422), *Uktenaadactylus Rodrigues* sp. nov. (IWCMS 2014.82), *Mythunga camara* (QM F18896), and *Ferrodrac lentoni* (AODF 876).

The modifications on the matrix pointed out above were performed using the software Mesquite 3.6 (Maddison and Maddison 2018). The phylogenetic analysis was performed using the software TNT 1.5 (Goloboff and Catalano 2016). Search for the most parsimonious trees (MPTs) was conducted via Traditional Search (TBR swapping algorithm), 10 000 replicates, random seed, and collapsing trees after search. We also conducted an analysis via New Technology in order to recover the island with the minimum length trees (MLTs). The parameters used in this analysis were Sectorial Search, ratchet (parameters: 20 substitutions made, or 99% swapping completed, six up-weighting prob., six down-weighting prob., and a total number of iterations of 10), tree fusing, Driven search (15 initial addseqs., 15 times of min. length), random seed, and without collapsing trees after search. Subsequently, the results of the New Technology were analysed via Traditional Search (TBR swapping algorithm), starting trees from RAM, and without collapsing trees after search. The latter search aimed for recovering the maximum trees of the island recovered from the first analysis.

**Systematic palaeontology**

**Pterosauria Kaup, 1834**

**Pterodactyloidea Plieninger, 1901**

**Ornithocheiroidea Seeley, 1870 sensu Bennett (1994)**

**Pteranodontoidea Marsh, 1876 sensu Kellner (2003)**

**Lanceodontia Andres, Clark, and Xu, 2014**

**Anhangueria Rodrigues and Kellner, 2013**

**Anhangueridae Campos and Kellner, 1985**

**Coloborhynchinae Holgado, Pégas, Canudo, Fortuny, Rodrigues, Company, and Kellner, 2019**

**Stem-based definition:** The most inclusive clade containing *Coloborhynchus clavirostris* but not *Anhanguera blittersdorffii* or *Ludodactylus sibbicki* (Holgado et al. 2019).

Diagnosis.—Anhanguerids with the anterior end of the rostrum forming a flat surface; a deltoid facet taller than wide; anterior expansion of the premaxilla quadrangular (in occlusal view); a perpendicular angle, in lateral view, between the deflected palatal surface and the rest of the palate; and the third pair of alveoli of the upper jaw double the size of the fourth pair.

Stratigraphic and geographic range.—Late Berriasian–Valanginian, Hastings Beds, St. Leonards-on-Sea, East Sussex, England, UK; Barremian, Wessex Formation, Sudmoor Point, Isle of Wight, England, UK; late Albian, Paw Paw Formation, Fort Worth, Texas, USA; late Albian, Cambridge Point, Isle of Wight, England, UK; Cenomanian, Ifezouane Formation, Kem Kem Group, south-eastern Morocco.

Genus Coloborhynchus Owen, 1874

Type and only species: Coloborhynchus clavirostris Owen, 1874. St. Leonards-on-Sea, East Sussex; late Berriasian–Valanginian.

Coloborhynchus clavirostris Owen, 1874

Holotype: NHMUK PV R1822, an anterior portion of the rostrum displaying the alveoli from the 1st to the 6th pair of teeth (Fig. 1).

Type locality: St. Leonards-on-Sea, East Sussex, England.

Type horizon: Hastings Group (late Berriasian/Valanginian).

Material.—Holotype only.

Diagnosis.—Coloborhynchine distinguished by the following autapomorphies: oval depression on the anterior palatal surface beneath the first pair of alveoli; second, third and fourth pairs of alveoli located laterally; fifth and sixth pairs of alveoli located more medially than the preceding alveoli on the base of the palatal ridge; anterior part of the palatal ridge bordered by two shallow longitudinally elongated depressions (from Rodrigues and Kellner 2008).

Remarks.—Following Rodrigues and Kellner (2008, 2013), who reviewed the taxonomy of the genus Coloborhynchus, we consider Coloborhynchus as restricted to the type species, Coloborhynchus clavirostris. For further details on the taxonomic history of the genus Coloborhynchus and the species Coloborhynchus clavirostris see the Introduction section above.

Genus Nicorhynchus nov.

ZooBank LSID: urn:lsid:zoobank.org:act:36FDC3A2-EA09-4AA3-B738-E79CA3EB6E06

Type species: Ornithocheirus capito Seeley, 1870; see below.

Included species: Nicorhynchus capito (Seeley, 1870), and Nicorhynchus fluviferox (Jacobs, Martill, Ibrahim, and Longrich, 2019).

Etymology: A combination of the Old English nicor, knucker (a kind of water dragon), and Ancient Greek πύργος (rhíghkos, Latinised as rhynchos), snout; in reference to the fact that the new taxon represents a piscivorous flying reptile from marine and fluvial deposits, represented by fragmentary snouts.
Nicorhynchus capito (Seeley, 1870) comb. nov.

Holotype: CAMSM B54625, a fragmented anterior portion of the rostrum displaying the alveoli from the 1st to the 4th pair of the right teeth (Fig. 2).

Type locality: Chesterton, Cambridgeshire, England.

Type horizon: Cambridge Greensand (Campanian, fossils Albian in age).

Material:—Holotype of Ornithocheirus reedi (Cambridge Greensand), described by Seeley (1870) and currently lost; and CAMSM B54434 (SOM: fig. S1) from the type locality and horizon.

Emended diagnosis.—Coloborhynchine characterised by the following autapomorphies: anterior margin of the rostrum slightly concave in lateral view; a roughly rhomboidal depression on the deltoid facet above the first pair of upper teeth; angular dorsal margin of the anteroventral depression beneath the first pair of upper teeth.

Remarks.—Rodrigues and Kellner (2008, 2013) considered “Ornithocheirus” capito to be a valid species, but excluded it from the genus Coloborhynchus. Here, we note several similarities between “Ornithocheirus” capito and other coloborhynchines, attesting its placement within the Coloborhynchinae. Firstly, it can be seen from the holotype and referred specimen that, although incomplete, the lateral margins of the lateral expansion of the premaxilla in ventral view are straight and parallel to each other, indicating the presence of a square-shaped expansion as characteristic of the Coloborhynchinae. It further exhibits an abrupt, perpendicular angle between the ventral and anterior faces of the rostral tip, again as in coloborhynchines. Rodrigues and Kellner (2013) did note some similarities between “Ornithocheirus” capito and Uktenadactylus wadleighi, regarding the concave dorsal margin of the premaxillary crest in lateral view and the presence of a sulcus on the anterodorsal surface of the premaxillary crest.

The holotype of “Ornithocheirus reedi” is herein regarded as conspecific with Nicorhynchus capito, following previous suggestions (Unwin 2001; Rodrigues and Kellner 2013). It shares with the holotype of N. capito a concave anterodorsal margin of the premaxillary crest, a slightly concave anterior margin of the rostrum in lateral view; and a deltoid facet higher than wide, though not extending as far dorsally as in N. fluviferex or N. cf. capito (NHMUK PV R481). Furthermore, this specimen bears a palatal depression (as in N. fluviferex); a roughly rhomboidal depression on the deltoid facet above the first pair of upper teeth; and
an angular dorsal margin of the anteroventral depression beneath the first pair of upper teeth. CAMSM B54434 is also regarded as most likely belonging to *N. capito*. This specimen exhibits a sulcus on the dorsal surface of the rostrum, a slightly higher than wide deltoid facet though not extending as far dorsally as in *N. fluviferox* or *N. cf. capito* (NHMUK PV R481); and a faint depression posterior to the second pair of alveoli; thus conforming to *Nicrohynchus capito*. Its dorsal surface is keeled, though not high, suggesting the presence of an ontogenetically incipient crest.

**Stratigraphic and geographic range.**—Type locality and horizon only.

*Nicrohynchus* cf. *capito* (Seeley, 1870)

**Material.**—NHMUK PV R481, a highly worn portion of the rostrum displaying the alveoli of, presumably, the 1st and 2nd pairs of teeth (SOM: fig. S2), from Albian fossils in Cenomanian Cambridge Greensand, Cambridgeshire, UK.

**Remarks.**—NHMUK PV R481 was originally referred to the species “*Coloborhynchus* capito” based on the purported presence of a markedly concave anterior margin of the premaxillary crest (Unwin 2001; Martill and Unwin 2012), which is a diagnostic feature of the species (Unwin 2001; Rodrigues and Kellner 2008, 2013). Subsequently, such assignment of NHMUK PV R481 to “*Coloborhynchus* capito” was questioned for the first time by Kellner et al. (2013), who mentioned that a markedly concave anterior margin of the premaxillary crest cannot be confidently seen in NHMUK PV R481. In any case, a markedly concave anterior margin of the premaxillary crest is not exclusive of *Nicrohynchus capito*, being also present in FSACK-KK 5024 and *Uktendaractylus wadleighi*. Apart from that, we further note that NHMUK PV R481 displays a remarkably high deltoid facet, which extends dorsally more than twice the level of the first pair of alveoli. This feature cannot be seen in any other coloborhynchine, but is close to *Nicrohynchus fluviferox*, both specimens (Jacobs et al. 2019, 2020), in which the height of the deltoid facet is roughly twice the level of the first pair of alveoli (but not over as in *Nicrohynchus cf. capito*). However, such relationship could indicate a continuous variation rather than a discrete character. Considering that the anhanguerid premaxillary crest grows ontogenetically (Pinheiro and Rodrigues 2017), and that NHMUK PV R481 is a much larger specimen than the other coloborhynchines, then this feature could be linked to the ontogenetic growth of the premaxillary crest. In addition, as the rostral surface is highly worn off, it is possible that what is preserved of the presumable first tooth in NHMUK PV R481 would actually be a root cross section. In that case, the root would taper posteriorly and it would be postero-dorsally directed. This could be a plausible explanation for its comparatively higher position, as well as its distinctively small first tooth. On the other hand, Jacobs et al. (2019, 2020) have presented a phylogenetic analysis in which NHMUK PV R481 was coded separately from the holotype specimen of “*Coloborhynchus* capito”, and a sister-group relationship between NHMUK PV R481 and “*C*. fluviferox” was recovered by their analysis. In any case, they did not present a discussion about this relationship, as a review of the genus *Coloborhynchus* was beyond their scope (Jacobs et al. 2019). Taking all of the above into account, there is not enough evidence to establish NHMUK PV R481 as a new taxon different from *Nicrohynchus capito* due to its poor preservation, and consequently we assign it to *Nicrohynchus cf. capito*.

*Nicrohynchus fluviferox* (Jacobs, Martill, Ibrahim, and Longrich, 2019) comb. nov.

**Holotype.**—FSACK-KK 10701, an anterior portion of the rostrum displaying the alveoli from the 1st to the 3rd pair of teeth (Fig. 3).

**Type locality:** South-eastern Morocco, possibly Aferdou N’Chaft, Hassi El Begaa, Er Rachidia Province (see Ibrahim et al. 2010; Martill et al. 2018; Jacobs et al. 2019).

**Type horizon:** ?Albian–Lower Cenomanian Kem Kem Group, Ifezouane Formation.

**Material.**—FSACK-KK 5024/SMNK PAL 45833 (cast of a private specimen) from the type locality and horizon.

**Diagnosis.**—Coloborhynchine distinguished by the following autapomorphies: deltoid facet defining a high isosceles triangle with concave dorsolateral margins in anterior view; deltoid facet with two shallow, sub-circular depressions located dorsal to first upper tooth pair; deltoid facet dorsal region with a shallow sagittal groove defined by low ridges that transitions into a broad rugose anterodorsal margin of the premaxilla; and central point of first upper alveoli level with dorsal border of second tooth pair (modified from Jacobs et al. 2019).

**Remarks.**—The FSACK-KK 5024 was originally described as a potential second coloborhynchine species from the Kem Kem Group (Jacobs et al. 2020). This specimen shares with the holotype of *N. fluviferox* the following features: high deltoid facet, over twice the level of the first tooth pair; anteroventral depression below first tooth pair (also shared with *N. capito*); ridges on the lateral margin (in anterior) extending dorsally onto the crest base (also shared with *N. capito*); first tooth alveolus ventral border slightly ventral to dorsal border of the second tooth alveolus (unique of *N. fluviferox* among coloborhynchines); and paired depression dorsal to firth tooth pair (unique of *N. fluviferox*).

Jacobs et al. (2019) reported on a paired depression for *N. fluviferox* dorsal to the first tooth pair; and a ventrally bifurcated, single depression for FSACK-KK 5024 (Jacobs et al. 2020). However, in both specimens, the deltoid facet surface is abraded (Jacobs et al. 2019). The division between left and right depressions in the holotype of *N. fluviferox* is very discrete and low, and thus may have been lost to abrasion in FSACK-KK 5024. The well-preserved ventral outline of the depression in FSACK-KK 5024 is strongly bifurcated and matches well the condition seen in the holotype of *N. fluviferox*, in both shape and position. This suggests that the holotype of *N. fluviferox* and FSACK-KK 5024 bore the same feature.
According to Jacobs et al. (2020), FSACK-KK 5024 differed from the holotype of *N. fluviferox* based on the following features: the slight medial depression on the pre­maxillary crest dorsal surface (thought of as unique to the specimen) and the lateral margins in anterior view slightly convex, with no narrowing into the premaxillary crest; while the holotype specimen of *N. fluviferox* exhibits a prominent narrowing and concave margins. The slight medial depression on the dorsal surface of the premaxillary crest (which forms a groove similar to the ones seen in *N. capito* and *Uktenadactylus wadleighi*) cannot be assessed in the holotype of *N. fluviferox* due to incompleteness. The prominent narrowing and concave margins (in anterior view) in the holotype of *N. fluviferox* are the anterior margins of the pre­maxillary crest, located dorsal to the deltoid facet. Therefore, the shape of the lateral margins in anterior view (dorsal to the deltoid facet) are intrinsically related to the development of the premaxillary crest, and the reported variation can thus be easily explained by ontogenetic development and/or sexual dimorphism. In fact, if premaxillary crests are unconsidered, then the anterior outline of the holotype of *N. fluviferox* becomes a match for FSACK-KK 5024, with slightly convex lateral margins without a dorsal narrowing. This feature therefore does not exclude FSACK-KK 5024 from *N. fluviferox* and we regard the two as most likely conspecific, due to the above mentioned features that they share. The referred specimen adds to the known morphology of *N. fluviferox* by showing the presence of a groove on the anterodorsal margin of the premaxillary crest, similar to that seen in *N. capito* and *U. wadleighi*.

Stratigraphic and geographic range.—Type locality and horizon only.

**Genus *Uktenadactylus* Rodrigues and Kellner, 2008**

*Type species:* *Uktenadactylus wadleighi* (Lee, 1994); Albian, Texas, USA.

*Included species:* *Uktenadactylus wadleighi* (Lee, 1994) and *Uktenadactylus rodriquesae* sp. nov.

**Diagnosis.**—Coloborhynchines with a roughly subcircular single depression on the deltoid facet above the first pair of upper teeth; and a palatal bulbous projection between the second pair of upper teeth.

**Remarks.**—In the present work, we regard the genus *Uktenadactylus* to contain two species: *U. wadleighi* and *U. rodriquesae* sp. nov., based on IWCMS 2014.82, originally described by Martill (2015) and attributed to *Coloborhynchus* sp. based on the first pair of upper teeth being of anteriorly directed, and a 90° upturn of the palate. These features are herein regarded as general for the Coloborhynchinae (see Discussion). Martill (2015) mentioned the existence of a palatal bulbous projection between the second pair of upper teeth in IWCMS 2014.82, but did not comment on it further. We note here that it is a shared trait with *Uktenadactylus wadleighi*. We further note that these two taxa share a round depression on the deltoid facet, located above the first pair of upper teeth; which was already reported as present in *U. wadleighi* (Lee 1994; Rodrigues and Kellner 2008). The surface of the dorsal region of the deltoid facet is flat in *Coloborhynchus clavirostris*, whereas it bears a pair of lateral ridges in *Nicorhynchus*.

Jacobs et al. (2019) considered that *Nicorhynchus fluviferox* shared with *Uktenadactylus wadleighi* the following feature: a palatal depression posterior to the second pair of upper teeth. However, upon first-hand analysis of the holotype of *U. wadleighi*, we report here that the condition present in *U. wadleighi* is not the same that was described for *Nicorhynchus fluviferox*. In *Nicorhynchus fluviferox*, a true depression excavates the palatal surface posterior to the second pair of upper teeth, as reported by Jacobs et al. (2019). However, in *Uktenadactylus wadleighi*, this feature is not present. The palatal surface posterior to the second pair of upper alveoli is not level with the surface between the second pair of upper alveoli, indeed; but this does not happen due to a depression posterior to the second pair of upper alveoli. Instead, it happens due to a bulbous projection between the second pair of upper alveoli, protruding...
beyond the palatal plane. This feature can only be seen in *U. wadleighi* and IWCMS 2014.82.

**Stratigraphic and geographic range.**—Barremian–Albian; Wessex Formation, England; Paw Paw Formation, USA.

**Uktenadactylus wadleighi** (Lee, 1994)

*Holotype:* SMU 73058, an anterior portion of the rostrum displaying the alveoli from the 1st to the 8th pair of teeth (Fig. 4).

*Type locality:* Tarrant County, Texas, USA.

*Type horizon:* Paw Paw Formation (Albian).

*Material.*—Holotype only.

*Emended diagnosis.*—*Uktenadactylus* species with slightly convex anterodorsal margins of the deltoid facet; a deep and oval (higher than wide) depression above the first tooth pair; a sharp palatal bulbous projection; and second pair of upper alveoli not as lateralised as in *U. rodriguesae*.

*Remarks.*—As noted above, Lee (1994) considered this specimen as representing a new species of the genus *Coloborhynchus*. "*Coloborhynchys*" *wadleighi* was reassigned to the newly erected genus *Uktenadactylus* by Rodrigues and Kellner (2008), whose updated generic attribution was also recently considered by other workers (Witton 2013; Bantim et al. 2014; Jacobs et al. 2019, 2020). For further details see the diagnosis and remarks for the genus.

**Stratigraphic and geographic range.**—Type locality and horizon only.

**Uktenadactylus rodriguesae** sp. nov.

*ZooBank LSID:* urn:lsid:zoobank.org:act:229644AA-6FA5-4C4B-988D-863C20197C14

*Etymology:* In honour of palaeontologist Taissa Rodrigues, in recognition of her herculean work on the taxonomy of anhanguerians and related forms (e.g., Rodrigues and Kellner 2008, 2013; Rodrigues et al. 2015; Pinheiro and Rodrigues 2017).

*Holotype:* IWCMS 2014.82, rostrum fragment including tooth positions 1–2 from both sides (Fig. 5).

*Type locality:* Sudmoor Point, south west coast of the Isle of Wight, England, UK.

*Type horizon:* Wessex Formation (Barremian), Wealden Group.

*Material.*—Holotype only.

*Diagnosis.*—*Uktenadactylus* species with strongly concave anterodorsal margins of the deltoid facet; a shallow and subcircular (about as high as wide) depression above the first tooth pair; a smooth palatal bulbous projection; and well lateralised second pair of upper alveoli.

*Remarks.*—This specimen was originally reported as *Coloborhynchus* sp. by (Martill 2015), as mentioned above. Such attribution was repeated in subsequent works (Jacobs et al. 2019, 2020). In the present contribution, we note that IWCMS 2014.82 shares with the holotype of *Uktenadactylus wadleighi* two features: a round depression on the deltoid
facet above the first pair of upper teeth, and a palatal bulbous projection between the second pair of upper teeth. These two features are unique within the Anhangueridae as a whole, and are herein regarded as diagnostic for a genus *Uktenadactylus* comprising *U. wadleighi* and *U. rodrigue-sae* sp. nov.

Even though the specimen is broken, it is three-dimensional and its anterior and lateral surfaces exhibit well-preserved bone compacta. The new species differs from *U. wadleighi* in that the dorsolateral margins of the deltoid facet are particularly concave (they are straight in *U. wadleighi*), the second pair of upper alveoli is well lateralised (on both sides, despite some distortion), and that the subcircular depression above the first tooth pair is shallower.

**Stratigraphic and geographic range.**—Type locality and horizon only.

**Genus Aerodraco nov.**


*Type species:* *Aerodraco sedgwickii* gen. et comb. nov.; see below.

*Etymology:* From Ancient Greek *aero*, wind and *draco*, dragon; in reference to the book *Dragons of the Air* (Seeley 1901).

*Holotype:* CAMSM B54422, an anterior portion of the rostrum displaying the alveoli from the 1st to the 7th pair of teeth (Fig. 6).

*Type locality:* Cambridge, Cambridgeshire, England, Albian.

*Type horizon:* Cambridge Greensand (Cenomanian; fossils Albian in age).

*Material:*—Holotype only.

**Emended diagnosis.**—Coloborhynchine with the following autapomorphies: anterior expansion of the rostrum ends abruptly behind the third pair of alveoli; paired row of neurovascular foramina flanking the palatal ridge; third pair of alveoli larger than in any other coloborhynchine relative to the fourth pair (updated from Rodrigues and Kellner 2013).

*Remarks.*—Owen (1859) assigned eight rostra to the species *Pterodactylus sedgwickii*, including the holotype CAMSM B54422, and years later he relocated this species to the genus *Coloborhynchus* Owen, 1874 due to the first pair of premaxillary teeth projecting forward from the truncate surface at a higher level than the alveolar border. After several decades considered as another species within the *Ornithocheirus* complex (Hooley 1914; Wellnhofer 1978; Lee 1994), Unwin (2001) assigned this species to the genus *Coloborhynchus*, due to the shape of the rostrum as well as the arrangement and size of the teeth being similar to "*Coloborhynchus* capito", differing exclusively from the latter on the basis of the purported lack of a premaxillary crest. This lead Unwin (2001) to suggest that this difference could represent sexual dimorphism (Unwin 2001: 208), but did not synonymise the two species waiting for “…a better understanding of the remaining cranial and postcranial anatomy of these taxa and other coloborhynchids” [sic!] (Unwin 2001). Rodrigues and Kellner (2008: 226) excluded *A. sedgwickii* from the genus *Coloborhynchus*, arguing that the anterior end of the rostrum “is round rather than flat” [sic!] as well as a larger spacing between the first and second pairs of alveoli. Posteriorly, Rodrigues and Kellner (2013) tentatively referred it to the genus *Camposipterus* due to the following combination of features: presence of an expansion of the rostrum, absence of a premaxillary crest, and round rostrum in lateral view. However, none of these features is unique to *Camposipterus*, and this is why their referral was only tentative (Rodrigues and Kellner 2013). Although the anterior end of the rostrum is round in lateral view (Rodrigues and Kellner 2008, 2013), the anterior and lateral margins in occlusal view are straight, similarly to other coloborhynchines and differently from any other an­hanguerians. Concerning the premaxillary crest, its absence may remain unclear since the posterodorsal portion of the rostrum is not preserved (Fig. 6A3). The dorsal surface of the preserved fragment is quite tall and keeled, and thus we regard that an incipient crest was most likely present.

Here, we notice that the CAMSM B54422 bears a distinctive paired row of neurovascular foramina flanking the palatal ridge. This feature is absent in anhanguerids for which the palatal bone surface is well-preserved, such as *Uktenadactylus wadleighi*, *Coloborhynchus clavirostris*, *Tropeognathus mesembrinus*, *Maaradactylus kellneri*, and *Anhanguera* sp. AMNH 22555 (Wellnhofer 1987, 1991; Rod­rigues and Kellner 2008, 2013; Bantim et al. 2014; Pinheiro and Rodrigues 2017).

**Stratigraphic and geographic range.**—Type locality and horizon only.
Subfamily Tropeognathinae nov.

Zoobank LSID: urn:lsid:zoobank.org:act:0722EB2F-8A40-40E4-9896-E548202E54FE

Stem-based definition: The most inclusive clade containing *Tropeognathus mesembrinus* but not *Coloborhynchus clavirostris* or *Anhanguera blittersdorffi*.


Diagnosis.—Anhanguerids with reduced premaxillary/den- tary lateral expansions (under 130% the width of the postrosette width); relatively short teeth (crown height under 3 times diameter); and premaxillary crests reaching the rostral tip.

Remarks.—*Tropeognathus mesembrinus* is, alongside *Anhanguera blittersdorffi*, an internal specifier of a node-based Anhangueridae sensu Kellner (2003). In the present work, we recognize the Tropeognathinae as a clade joining *Tropeognathus mesembrinus* (Albian, Romualdo Formation, Brazil), *Siroccopteryx moroccensis* (Albian–Cenomanian, Kem Kem Group, Morocco), *Ferrodraco lentoni* (Winton Formation, Cenomanian–Turonian, Australia), and *Mythunga camara* (Albian, Toolebuc Formation, Australia). The relationships of *Siroccopteryx moroccensis* have been controversial (see Rodrigues and Kellner 2008; Holgado et al. 2019; Jacobs et al. 2019). *Siroccopteryx* has been previously regarded as a close relative of *Coloborhynchus* by several works (Rodrigues and Kellner 2008, 2013; Andres et al. 2013, 2014; Holgado et al. 2019). Recently, anatomical comparisons between *Siroccopteryx*, *Coloborhynchus*, and *Tropeognathus* led Jacobs et al. (2019) to, very eloquently, reinterpret for the first time *Siroccopteryx* as a close rel-
ative of *Tropeognathus* instead of *Coloborhynchus*. The evidence presented by Jacobs et al. (2019) is taken into account here, leading us to support their conclusions (see further below on Phylogenetic Analysis and Discussion). The close relationship between *Ferrodraco* + *Mythunga* and *Tropeognathus mesembrinus* (see Pentland et al. 2019) is also corroborated here.

Concerning the phylogenetic relationships of *Tropeognathus mesembrinus* and previous analyses, under the works of Holgado et al. (2019) and Pégas et al. (2019) *Tropeognathus* was recovered as a monotypic branch within the Anhangueridae, alongside the clades Coloborhynchinae and Anhanguerinae. Jacobsetal.(2019)recovered *Tropeognathus mesembrinus* as closely related to *Ornithocheirus simus* and *Siroccopteryx moroccensis*. Under the analyses of Andres et al. (2014) and Longrich et al. (2018), *Tropeognathus mesembrinus* was recovered as closely related to *Ornithocheirus simus* and *Coloborhynchus clavirostris*.

In the present work, we support a close relationship between *Tropeognathus mesembrinus*, *Siroccopteryx moroccensis*, *Ferrodraco lentoni*, and *Mythunga camara*, composing the Tropeognathinae (comprised within Anhangueridae). However, this clade does not include *Coloborhynchus clavirostris* (or any other coloborhynchine) nor *Ornithocheirus mesembrinus* (regarded as a basal ornithocheiraeae). Our systematic proposal and the synapomorphies behind it are further elaborated below.

**Stratigraphic and geographic range.**—Albian–Cenomanian–Turonian (probably Turonian); Romualdo Formation, Brazil; Toolebuc Formation, Australia; Kem Kem Group, Morocco; Winton Formation, Australia.

**Phylogenetic analysis**

Our phylogenetic analysis resulted in nine most parsimonious trees, with 417 steps, a consistency index of 0.638 and a retention index of 0.871 (SOM: fig. S3). The strict consensus tree recovers a clade Anhangueridae divided into three main lineages: Tropeognathinae, Coloborhynchinae and Anhanguerinae; comprising a total of 20 species (Fig. 10). The clade Tropeognathinae is supported by three synapomorphies: teeth relatively short (crown height under 3× diameter); premaxillary crest reaching rostrum tip; and premaxillary expansion width reduced (under 130% post-rosette width). The relationship *Tropeognathus + Siroccopteryx* is based on two synapomorphies: palatal ridge robust forming a strong keel; and palatal ridge restricted posterior to...
the fifth tooth position. The clade containing *Mythunga* and *Ferrodraco* is supported by one synapomorphy: alveoli margins strongly raised.

The node joining Coloborhynchinae and Anhanguerinae, to the exclusion of Tropeognathinae, is supported by the following synapomorphy: fifth pair of upper teeth medially displaced.

The Coloborhynchinae share the following five synapomorphies: premaxilla, anterior expansion, lateral margins straight and subparallel; dorsal deflection of the palate forming 90º angle; teeth, upper jaw, 3rd pair of teeth double size than 4th pair; teeth, upper jaw, first pair of slender elongated teeth, cross-section, elliptical.

The node containing *Coloborhynchus*, *Uktenadactylus*, and *Nicorhynchus* is supported by one synapomorphy: teeth, upper jaw, second pair, position in horizontal plane; aligned with third pair.

The relationship *Uktenadactylus* + *Nicorhynchus* is based on the following synapomorphy: anterodorsal surface of premaxillary crest grooved. The *Nicorhynchus* is supported by four synapomorphies: deltoid facet higher than wide; deltoid facet dorsolateral edges bearing anteriorly-facing ridges; anteroverentral depression between the first and second pairs of upper teeth; palatal depression posterior to the second pair of upper teeth.

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**Fig. 10.** Phylogenetic relationships of the Coloborhynchinae and Tropeognathinae clade nov. within Lanceodontia. Outgroup relationships are not shown (see SOM: fig. S3 for further details). Gray bar shows uncertain temporal range. Stratigraphic chart modified from Cohen et al. (2013). Drawing by BH. New taxa combinations and species proposed in this paper marked in bold. Abbreviations: Al, Albian; Ap, Aptian; Ba, Barrenian Be, Berriasian; Ca, Campanian; Ce, Cenomanian; Co, Coniacian; Ha, Haueriavian; Ki, Kimmeridgian; Ma, Maastrichtian; Ox, Oxfordian; Sa, Santonian; Ti, Tithonian; Tu, Turonian; Va, Valangian.
Discussion

The composition of the Coloborhynchinae.—The close relationship between *Coloborhynchus clavirostris* and *Uktenadactylus wadleighi* has been well-supported by several distinct authors (Lee 1994; Rodrigues and Kellner 2008; Martill and Unwin 2012; Andres et al. 2014; Jacobs et al. 2019), some of which have even kept *U. wadleighi* under the genus *Coloborhynchus* (Martill and Unwin 2012; Andres et al. 2014). In our analysis, *Coloborhynchus, Uktenadactylus, Nicorhynchus* gen. nov., and *Aerodraco* gen. nov. share the following 5 synapomorphies: rostrum, anterior end, flat surface; premaxilla, anterior expansion, lateral margins straight and subparallel; dorsal deflection of the palate forming 90° angle; teeth, upper jaw, 3rd pair of teeth double size than 4th pair; teeth, upper jaw, first pair of slender elongated teeth, cross-section, elliptical.

As mentioned above, *Coloborhynchus* has been regarded as closely related to *Tropeognathus mesembrinus* and *Ornithocheirus simus* by Andres et al. (2014) and Longrich et al. (2018). However, the purported placement of *Ornithocheirus simus* as closely related to *Tropeognathus mesembrinus* is here considered as inadequate, as explored in depth by Rodrigues and Kellner (2013). *Ornithocheirus simus* lacks a series of anhanguerian and anhanguerid features (Rodrigues and Kellner 2013; Holgado et al. 2019). According to the coding of Longrich et al. (2018), the genera *Tropeognathus, Ornithocheirus, Siroccopteryx*, and *Coloborhynchus* would be joined by a premaxillary crest reaching the rostral tip. However, the presence of a premaxillary crest is not confirmed for *Ornithocheirus simus* (Rodrigues and Kellner 2013; BH personal observations). Under the data matrix of Longrich et al. (2018), *Ornithocheirus simus* would further share with *Coloborhynchus* and *Siroccopteryx* a “strong keel” as a state for the palatal ridge, and also a flat surface for the rostral tip. However, no known specimen of *Ornithocheirus simus* exhibits a preserved palatal ridge (Rodrigues and Kellner 2013; BH personal observations), and therefore this character is coded here as “?” for this taxon. Furthermore, the rostral tip of *Ornithocheirus simus* is blunt and not a flat surface (Rodrigues and Kellner 2013; Jacobs et al. 2019; BH personal observations). The flat rostral surface seen in *Coloborhynchus* is formed by the dorsally deflected palatal surface, or deltoid facet, which is entirely absent in *Ornithocheirus simus* (see Rodrigues and Kellner 2013) and is a synapomorphy of the clade Anhangueria + Targaryendraconia (Pégas et al. 2019). This feature was also not taken into account in the data matrices of Andres et al. (2014) and Longrich et al. (2018). *Ornithocheirus* further lacks a premaxillary expansion (Rodrigues and Kellner 2013; BH personal observations), which is present in all anhanguerians (see Rodrigues and Kellner 2013; Pégas et al. 2019), but this character was miscoded as present for *Ornithocheirus simus* in the matrices of Andres et al. (2014) and Longrich et al. (2018). It has been coded as absent in our analysis, as has been done by Rodrigues and Kellner (2013) as well as Jacobs et al. (2019, 2020).

In our analysis, the Coloborhynchinae is regarded as the sister-group of the Anhanguerinae, with which they share the following synapomorphy: upper fifth tooth position medially displaced. The Tropeognathinae lack this feature, as well as hamipterids and targaryendraconians (see Holgado et al. 2019; Pégas et al. 2019); and tropeognathines are thus set aside from coloborhynchines and anhanguerines, at the base of the Anhangueridae. As such, *Tropeognathus mesembrinus* is not recovered as closer to *Coloborhynchus clavirostris* than to *Anhanguera blittersdorfi* (contra Longrich et al. 2018). Instead, these three species are herein utilised as internal specifiers for three stem-based subgroups for the Anhangueridae: Tropeognathinae, Coloborhynchinae, and Anhanguerinae.

Other species previously referred to the genus *Coloborhynchus* are also regarded as non-members of the Coloborhynchinae here: *Siroccopteryx moroccensis, Amblydectes crassidens, Amblydectes(?) eurygnathus, Anhanguera robustus, Anhanguera araripensis, Anhanguera piscator, Anhaguera spielbergi, and Cimoliopterus cuvieri* (see SOM: table S2). The taxonomic status of *Anhanguera* and *Cimoliopterus* have already been explored in scrutiny and will not be further addressed here (see Rodrigues and Kellner 2008, 2013; Pinheiro and Rodrigues 2017). The phylogenetic position of *Siroccopteryx* as a member of the Tropeognathinae is explored further below.

As for the two species formerly attributed to the genus *Amblydectes*, we consider them here as potentially valid species of non-coloborhynchine anhanguerid. Both species lack a flat surface in the anterior end of the rostrum; a perpendicular angle between the deflected palatal surface and the rest of the palate; and straight anterior and lateral margins of the premaxillary expansion in occlusal view; which are coloborhynchine features. Nevertheless, some features show that the two species are different and most probably not closely related. *Amblydectes crassidens* is not only a non-coloborhynchine anhanguerid, but also a non-anhanguerine anhanguerid since they lack an enlarged 4th pair of upper teeth, which is characteristic of the Anhanguerinae (Holgado et al. 2019). Since the only 4th preserved alveolus (the right one) is incomplete, it is not possible to determine if the 3rd pair of teeth is double the size of the 4th pair, which is a synapomorphy of the Coloborhynchinae (see above). In any case, *Amblydectes crassidens* could be tentatively referred to the Tropeognathinae due to its reduced width of the premaxillary expansion. Still, there is no unambiguous evidence to attribute this anhanguerid species to this clade with much confidence. On the other hand, *Amblydectes(?) eurygnathus* strongly resembles *Anhanguera*, with relatively large alveoli and an oval depression between the 1st pair of teeth as well as the presence of a high crest. However, the incompleteness of the specimen, which only preserves the first two pairs of alveoli, does not reveal if *Amblydectes(?) eurygnathus* is actually an Anhanguerinae or not. Another species involved
in the Coloborhynchus complex is *Pterodactylus woodwardi* (SOM: fig. S4). Originally described by Owen (1861), CAMSM B54433 was referred to as *Ornithocheirus woodwardi* by Seeley (1870), and later, Hooley (1914) referred the species to the genus “Criorhynchus”. Other authors (Lydekker 1888; Wellnhofer 1978) even considered this species as a synonym of *Ornithocheirus (= “Criorhynchus”) simus*. Later, Unwin (2001) synonymised “Criorhynchus” woodwardi to *Coloborhynchus sedgwickii* due to the shape of the rostrum and arrangement of the teeth. Rodrigues and Kellner (2013: 55–57) considered CAMSM B54433 as a nomem dubium since “…several important characters cannot be observed on it”. As observed by Unwin (2001), the anterior and lateral margins of CAMSM B54434 in occlusal view are also roughly straight, which is characteristic of coloborhynchines. Despite the extreme fragmentary nature of CAMSM B54433, it can be confidently assigned to the Coloborhynchinae on the basis of their palatal tip deflection of 90°. However, due to their badly eroded surfaces, they cannot be confidently assigned to, nor excluded from, either *Aerodraco* or *Nicorhynchus*. The same rationale can be extended to specimens CAMSM B54435 and B54436 (SOM: fig. S4).

**The intrarelationships of the Coloborhynchinae.**—According to our phylogenetic analysis, *Aerodraco sedgwickii* is placed at the base of the Coloborhynchinae. It lacks a sec-

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**Fig. 11.** Coloborhynchinae comparative plate. A. *Coloborhynchus clavirostris* in anterior (A1), right lateral (A2), and palatal (A3) views. B. *Aerodraco sedgwickii* in anterior (B1), right lateral (B2), and palatal (B3) views. C. *Uktenadactylus wadleighi* in anterior (C1), right lateral (C2), and palatal (C3) views. D. *Uktenadactylus rodriguesae*, in anterior (D1), left lateral (mirrored, D2), and palatal (D3) views. E. *Nicorhynchus capito* (holotype) in anterior (E1), right lateral (E2), and palatal (E3) views. F. *Nicorhynchus capito* (referred specimen, originally designated as the holotype of *Ornithocheirus reedi*, now presumed lost from CAMSM collections) in anterior (F1) and right lateral (F2) views. G. *Nicorhynchus cf. capito* in anterior (G1) and left lateral (mirrored, G2). H. *Nicorhynchus fluviferox* (holotype) in anterior (H1), right lateral (H2), and palatal (H3) views. Dark grey represents depressions, lighter gray with lines represents bulbous projections, white represents alveoli. Scale bars 50 mm. Drawings by RVP.
ond upper tooth pair aligned with the third pair (in palatal view), which is a synapomorphy of the clade comprising Coloborhynchus, Uktenadactylus, and Nicorhynchus. Coloborhynchus, in turn, lacks an anterodorsal surface of premaxillary crest flat/grooved and a premaxillary crest anterior margin strongly concave. These features unite Uktenadactylus and Nicorhynchus.

We recognize that the Coloborhynchinae as herein defined is partially compatible with Coloborhynchus sensu Martill and Unwin (2012), with the exclusion of Sirocapteryx and Anhanguera spp. However, as observed by Jacobs et al. (2019), the clade formed by Coloborhynchus sensu Martill and Unwin (2012) is too diverse. The high level of morphological disparity (Fig. 11), as well as their wide distribution in time and space, led Jacobs et al. (2019) to regard that more than one genus was possibly present; still, they prevented from reviewing the Coloborhynchus complex. As herein defined, the Coloborhynchinae encompass at least seven species, from five different deposits. In summary, in this work, we follow Rodrigues and Kellner (2008; 2013) in restricting the Coloborhynchinae to encompass at least seven species, from five different deposits. In summary, in this work, we follow Rodrigues and Kellner (2008; 2013) in restricting the genus Coloborhynchus to its type-species, recognizing Uktenadactylus as a distinct genus, and “C.” capito as a third genus. To the genus Uktenadactylus we add the new species U. rodriguesae. We refer “C.” capito to the new genus Nicorhynchus, which also englobes N. fluviferus. For “O.” sedgwickii, located at the base of the Coloborhynchinae, we erect the new genus Aerodraco.

The new clade Tropeognathinae.—The newly named clade Tropeognathinae comprises Tropeognathus mesembrinus, Sirocapteryx moroccensis, Ferrodracon bentoni, and Mystunga camara. The relationships of Tropeognathus mesembrinus and Sirocapteryx moroccensis have not been consensual in the literature and are worthy of note. Tropeognathus mesembrinus has been regarded several times as closely related to Ornithocheirus simus (Unwin 2003; Longrich et al. 2018; Jacobs et al. 2019), but this is based on some misinterpretations as already explored above and demonstrated by Rodrigues and Kellner (2013).

Sirocapteryx moroccensis was originally described as an anhanguerid, though its closer relationships were not investigated (Mader and Kellner 1999). It has been regarded as possibly closely related to Coloborhynchus clavirostris and Uktenadactylus wadleighi by Rodrigues and Kellner (2008), who noted the following similarities: “thickness of the premaxillary crest, the anteriorly-flattened rostrum and the quadrangular anterior expansion of the premaxillae” (Rodrigues and Kellner 2008: 224). However, the relatively broad anterior base of the premaxillary crest can also be found in Tropeognathus mesembrinus and Ferrodracon bentoni (Wellnhofer 1987; Pentland et al. 2019), being herein recovered as synapomorphic for anhanguerids. The deltoid facet perpendicular to the remaining palate is herein recovered as a homoplasy between Sirocapteryx moroccensis and the Coloborhynchinae. A quadrangular anterior expansion of the premaxillae is not coded as such for Sirocapteryx moroccensis in our analysis. The premaxillary expansion of Sirocapteryx is superficially similar to those of coloborhynchines because the anterior margin is straight, due to the anteriorly-flattened rostrum. However, the lateral margins of the premaxillary expansion of Sirocapteryx differ from those of coloborhynchines. In Sirocapteryx, the lateral margins gently curve continuously to meet the post-rotsette constriction, similarly to Tropeognathus mesembrinus and Ferrodracon bentoni (Fig. 12); while in coloborhynchines the lateral margins are somewhat straight and parallel. In our previous analysis by Holgado et al. (2019), we have coded the premaxillary expansion of Sirocapteryx moroccensis as quadrangular in shape, but this has been rectified in the present analysis. The analysis of Longrich et al. (2018) recovered Sirocapteryx moroccensis as the sister-group of Coloborhynchus clavirostris + Uktenadactylus wadleighi. Later, however, Jacobs et al. (2019) offered for the first time a different proposal for the phylogenetic placement of Sirocapteryx, as more closely related to Tropeognathus mesembrinus and Ornithocheirus simus than to Coloborhynchus clavirostris. Jacobs et al. (2019) noted the following similarities between Tropeognathus mesembrinus and Sirocapteryx moroccensis: a blunt, rounded profile of the rostrum in lateral view; a robust palatal keel, restricted posteriorly; and relatively short teeth.

In the present analysis, we have taken into account the similarities noted by Jacobs et al. (2019) and have recovered, accordingly, Tropeognathus mesembrinus and Sirocapteryx moroccensis as sister-taxa. They share as
synapomorphies the following features: palatal ridge broad and deep; and palatal ridge posteriorly restricted, posterior to the fifth tooth position (Fig. 12). A deltoid facet abruptly angled at 90° has been recovered as a homoplasy between *Siroccopteryx moroccensis* and the Coloborhynchinae.

*Ferrodraco lentoni*, in turn, was originally regarded as the sister-group of *Mythunga camara*, with *Ornithocheirus simus*, *Coloborhynchnus clavirostris*, and *Tropeognathus mesembrinus* as their successive sister-taxa (Pentland et al. 2019) according to an analysis based on the dataset of Longrich et al. (2018). The purported placement of *Ornithocheirus simus* and *Coloborhynchnus clavirostris* as close to *Tropeognathus mesembrinus* has already been critically discussed above.

Still, *Ferrodraco lentoni* shares with *Tropeognathus mesembrinus* and *Siroccopteryx moroccensis* the following three features: reduced premaxillary/dentary lateral expansions (under 130% of the post-rosette width), relatively short teeth (crown height under 3x diameter), and premaxillary crests reaching the rostral tip; which are herein recovered as synapomorphies of the Tropeognathinae. In this way, *Ferrodraco lentoni* is herein recovered as a member of this group. We do express some caution regarding the latter feature (premaxillary crest reaching the rostral tip), since it is also present in the anhanguerine *Maaradactylus kellneri* (as a homoplasy in our analysis) and an expressive ontogenetic variation can be found in the premaxillary crest of *Anhanguera* (Pinheiro and Rodrigues, 2017).

Within the Tropeognathinae, *Ferrodraco lentoni* was recovered in a sister-group relationship with *Mythunga camara*, corroborating the proposition by Pentland et al. (2019). These two Australian anhanguerids share as a synapomorphy an alveoli border strongly raised (or laterally prominent, with deeply sulcate interalveolar constrictions), a feature that is absent in other anhanguerids such as *Tropeognathus*, whose jaws are scalloped but are not as deeply sulcate between adjacent alveoli. As such, even though the synapomorphies of the Tropeognathinae cannot be assessed in *Mythunga camara* (since the rostrum is missing from the holotype and only known specimen), it is still recovered as

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The diversity of the clade Anhangueridae through space and time.—Anhanguerids are a diverse clade with a host of recognisable forms and taxa (Fig. 13). As noted by Holgado et al. (2019), the clade Anhangueria could have important ancestral ties in the European archipelago and eastern Asian province. Constricting to the clade Anhangueridae, which is the largest and most diverse clade within anhanguerians, these forms span from the late Berriasian–Valanginian (with the coloborhynchine *Coloborhynchus clavirostris*) to the early Turonian (with the tropeognathine *Ferrodraco lentoni*) comprising more than 40 million of years (Fig. 14).

From the late Berriasian–Valanginian to the Barremian, the only known anhanguerid records come from the European archipelago (Fig. 13A), noting especially the nominal species from England. During the Aptian (Fig. 13B), anhanguerids radiated in several forms and lineages, as well as spread over the eastern boundaries of Laurasia and large parts of Gondwana. But it is during the Albian that anhanguerids reached their peak (Fig. 13C): in this stage they spread severely, with taxa having been found over remote places such as Australia and North America (Barrett et al. 2008; Holgado et al. 2011, 2019). In addition, two of the most anhanguerid species-rich faunas, the ones from the Romualdo Formation (NE Brazil) and Cambridge Greensand (England), occurred during the Albian (Fig. 14)—it should be recalled that even though the Cambridge Greensand is regarded as a Cenomanian deposit, its tetrapod fauna is probably reworked from underlying Albian formations (Unwin 2001; Rodrigues and Kellner 2013). During the Late Cretaceous, the recent discoveries from the Kem Kem Group (Morocco) in the early–middle Cenomanian (Fig. 13D) must be emphasised, as they shed light on the high diversity of anhanguerids during this time. As pointed above, the youngest record of an anhanguerid comes from the Winton Formation, in the Cenomanian–Turonian boundary (most likely early Turonian strata) of Queensland, Australia (Figs. 13D, 14). We must remark that, even though the pterosaur fossil record exhibits a strong taphonomic bias (Kellner 1994; Upchurch et al. 2015), the diversity and distribution of the Anhangueridae is clearly greater than previously thought.

We show here that the clade Coloborhynchinae has a prevailing distribution in Laurasia, being *Nicorhynchus fluviferox* the only known record from northern Gondwana (and from the Late Cretaceous). On the other hand, the clade Tropeognathinae seems to be exclusively distributed in Gondwana, being *Siroccopteryx moroccensis* the northernmost record (Fig. 13D).

**Conclusions**

Our anatomical comparisons and phylogenetic analysis lead us to regard that the Coloborhynchinae were more diverse than previously thought. Supporting previous suggestions, we argue that “*Ornithocheirus* capito” represents a new genus, hereby named *Nicorhynchus*; that *Nicorhynchus capito* is closely related to *Coloborhynchus fluviferox*, which is hereby renamed *N. fluviferox*; and that *Siroccopteryx* is more closely related to *Tropeognathus* than to *Coloborhynchus*. We also corroborate the view that *Ornithocheirus simus* is not closely related to *Coloborhynchus, Tropeognathus or Anhanguera*. We further demonstrate, for the first time, that “*Ornithocheirus sedgwickii*” represents a new genus, named *Aerodraco*; that *Aerodraco sedgwickii* represents a basal coloborhynchine; that IWCMS 2014.82 represents a new species for the genus *Uktenadactylus*, hereby named *U. rodriguesae*; and that *Uktenadactylus* and *Nicorhynchus* are sister-taxa. Finally, we propose the new clade Tropeognathinae, englobing *Tropeognathus, Siroccopteryx, Myrthunga*, and *Ferrodraco*. 

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**Fig. 14.** Histogram showing the distribution of the species and specimens attributed to Anhangueridae during the Cretaceous. Each bar of the histogram represents the number of diverse species found in each labelled site, whilst the geometric figures identified the species within the three anhanguerid clades: Coloborhynchinae, Anhanguerinae, and Tropeognathinae. Drawing by BH. Abbreviations: Al, Albian; Ap, Aptian; Ba, Barrenian Be, Berriasian; Ca, Campanian; Ce, Cenomanian; Co, Coniacian; Ha, Hauterivian; Ma, Maastrichtian; Sa, Santonian; Tu, Turonian; Va, Valangian.
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