

Systematic revision of the early Miocene fossil *Pseudoepicrates* (Serpentes: Boidae): implications for the evolution and historical biogeography of the West Indian boid snakes (*Chilabothrus*)

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The taxonomy of the early Miocene genus *Pseudoepicrates* is controversial. Originally interpreted as the viperid *Neurodromicus*, subsequent work deemed the material to represent an extinct boid, *Pseudoepicrates stanolseni*. However, more recent work considered *Pseudoepicrates* to be a synonym of the extant *Boa constrictor*. Due to these conflicting interpretations, we provide a revision of the systematic affinities of *P. stanolseni*. This redescription was based on the first-hand analysis of all material of *Pseudoepicrates*, together with the comparison of extant boids. Our findings suggest that, in addition to being an invalid taxon, '*Pseudoepicrates*' cannot be referred to *B. constrictor*. Instead, the extant *Chilabothrus* is here regarded as the most cogent generic assignment, with ***Chilabothrus stanolseni* comb. nov.** proposed for the extinct species. The referral of this material to *Chilabothrus* suggests that the genus originated as early as ~18.5 Mya. The revised history of this record has interesting implications for our understanding of the early divergence of the group. The presence of *Chilabothrus* in the early Miocene of Florida supports biogeographical hypotheses, which suggest that the genus reached the West Indian island complex around 22 Mya, dispersing into the North American territory by at least 18.5 Mya.

ADDITIONAL KEYWORDS: Antilles – *Boa constrictor* – *Epicrates* – fossil snake – Greater Antilles – Hemingfordian – Lesser Antilles – Miocene.

INTRODUCTION

The early Miocene North American snake species *Pseudoepicrates stanolseni* Vanzolini, 1952 has a controversial taxonomic history. Based on isolated preloacal vertebrae recovered from Gilchrist County, Florida, Vanzolini (1952) originally described the fossils as two new species of *Neurodromicus* Cope, 1873: *N. stanolseni* and *N. barbouri*. However, in subsequent years several authors have questioned the validity of this assignment (Auffenberg, 1963; Kluge, 1988a; Albino, 2011).

Auffenberg (1963) was the first to question Vanzolini's (1952) allocation, arguing that a referral to *Neurodromicus* was inconsistent with the boid affinities of the fossil material, especially given the former's

marked similarities with the extant colubroid species *Sistrurus catenatus* (Crotaline: Viperidae). In order to resolve this conflict, Auffenberg (1963) united both '*N. stanolseni*' and '*N. barbouri*' within the new taxon *Pseudoepicrates stanolseni*, arguing that differences between the two represented only superficial intracolumnar variation of the vertebrae. This taxon was subsequently placed in the subfamily Boinae due to features like the developed zygosphenes morphology and the absence of hypapophyses in the mid-preloacal vertebrae (Auffenberg, 1963).

However, in a short communication, Kluge (1988a) reiterated differences between *P. stanolseni* and the original '*barbouri*' material, arguing that the vertebrae of '*barbouri*' were indistinguishable from the extant snake *Boa constrictor* Linnaeus, 1758 and thus the latter should be considered a junior synonym of *Boa*. More recently, Albino (2011) synonymized all associated material of *P. stanolseni*

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with *B. constrictor*, suggesting that the differences addressed by Kluge (1988a) were primarily explicable via intraspecific and intracolumnar variation. This reappraisal had the added corollary of expanding the observed geographic range of *B. constrictor*, with extant representatives of this taxon restricted to an area encompassing South Argentina to northern Central America.

Despite several works evaluating the systematic status of *Pseudoepicrates*, none has provided a detailed anatomical account of the specimens themselves, together with osteological comparison with extant species of Boinae. Here we provide a systematic revision and redescription of the genus *Pseudoepicrates*, utilizing all the materials referred to the taxon (e.g. holotype, paratypes and referred materials). The detailed morphological assessment given within is followed by an exploration of the systematic and biogeographical implications of the taxon within Boinae.

GEOLOGICAL SETTING AND AGE CORRELATION

The material was recovered from the Thomas Farm deposit (NAD 27; 29.86°N, 82.83°W), located in Gilchrist County, Florida. The site was discovered in 1931 (Simpson, 1932) and currently represents one of the richest Miocene deposits of terrestrial vertebrates in North America (Ray, 1957; Olsen, 1962; Pratt, 1990; Beatty, 2010). The two depositional systems are interpreted as sinkholes within a nearshore marine environment, usually associated with cave systems (Pratt, 1990; Beatty, 2010). The fossil remains are found in alternating layers of clay and calcareous sand, occasionally associated with limestones. The age of the deposit is estimated to be early Hemingfordian (early Miocene), at least 18.5 Mya, based on biostratigraphic correlations with the rich mammalian fauna present at the site. Specifically, the presence of the ursid *Phoberocyon johnenryi* (Carnivora: Ursidae) and the amphicyonid *Cynelos caroniavorus* (Carnivora: Amphicyonidae), which are correlated with the same genera from Burdigalian of Western Europe, supports an estimated early Hemingfordian age (LMA, Land Mammal Age) for the deposit (Beatty, 2010).

MATERIAL AND METHODS

MATERIAL

In order to establish the degree of intracolumnar, intraspecific and taphonomic variation present within *Pseudoepicrates*, all available specimens from the American Museum of Natural History (AMNH) and

the Museum of Comparative Zoology (MCZ), which were assigned to the taxon. The redescription was based on the holotype of *N. stanolseni* (MCZ 1977) and the material of *N. barbouri* (MCZ 1978), together with the associated paratypes and additional materials attributed to *N. barbouri* (MCZ 2417) and *N. stanolseni* (AMNH 7627) from the same locality. The fossils were also compared with the axial skeleton of extant snakes (especially boines) (Table 1) and, when comparable material was not readily available, the description was augmented with reference to previously published works.

The anatomical description follows the terminology of Auffenberg (1963), Hoffstetter & Gasc (1969), Rage (1984), Hsiou & Albino (2009) and Albino (2011) (Fig. 1A). The qualitative data for vertebral index and proportions follows LaDuke (1991a, b) (Fig. 1B). The measurements were performed with an analogic caliper (0.02 mm) and expressed in millimetres.

Institutional abbreviations: AMNH: American Museum of Natural History, New York, New York; MCN. D: Coleção Didática de Herpetologia, Museu de Ciências Naturais da Fundação Zoobotânica do Rio Grande do Sul, Porto Alegre, Brazil; MCN-PV DR: Seção de Paleontologia do Museu de Ciências Naturais da Fundação Zoobotânica do Rio Grande do Sul, Coleção de Paleontologia de Vertebrados, Coleção Didática de Répteis, Porto Alegre, Brazil; MCZ: Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts; UFMT: Coleção da Universidade Federal do Mato Grosso, Mato Grosso, Brazil.

Anatomical abbreviations: cl, centrum length; cn, condyle; coh, condyle height; cow, condyle width; ct, cotyle; cth, cotyle height; ctw, cotyle width; ctw > cth, cotyle width greater than cotyle height; ep, epizygapophyseal process (*sensu* Albino, 2011); fpa, foramina in the parazygantral area; h, total height of vertebra; hk, haemal keel; hy, hypapophysis; naw, neural arch width at interzygapophyseal ridge; nc, neural canal; nch, neural canal height; ncw, neural canal width; nf, neural foramina; ns, neural spine; lc, laminar crest; lf, lateral foramina; Ll, lateral lobe; pf, paracotylar foramina; pn, posterodorsal notch; pnl, posterodorsal notch length; po–po, distance between postzygapophyses; ppz, prezygapophyseal process; pr, parasagittal ridges (= laminar crest *sensu* Albino, 2011); pr–po, distance between prezygapophyses and postzygapophyses of the same side; pr–pr, distance between prezygapophyses; pr > po, prezygapophyses width greater than postzygapophyses width; prdp, paradiapophyses; prl, prezygapophyses length; prw, prezygapophyses width; ptz, postzygapophysis; pz,

Table 1. Specimens of snakes compared for the redescription

Taxon	Specimens' catalogue number
<i>Boa constrictor</i>	AMNH R 57467; AMNH R 57476; AMNH R 131475; AMNH R 141144; AMNH R 7204; AMNH R 75267; AMNH R 7118; MCN.D 333; MCN.D 335; MCN.D 343; MCN.D 344; MCN.D 347; MCN.D 351
<i>Boa constrictor imperator</i>	AMNH R 155261; AMNH R 155257; AMNH R 77590; AMNH R 74737; AMNH R 57472
<i>Chilabothrus angulifer</i> (sensu Reynolds <i>et al.</i> , 2013) <i>Epicrates angulifer</i> (tagged at museum)	AMNH R 77596; AMNH R 114497; MCZ 2118
<i>Chilabothrus inornatus</i> (sensu Reynolds <i>et al.</i> , 2013)	AMNH 70023; MCZ 2341
<i>Epicrates inornatus</i> (tagged at museum)	
<i>Chilabothrus striatus</i> (sensu Reynolds <i>et al.</i> , 2013) <i>Epicrates striatus</i> (tagged at museum)	AMNH R 140542
<i>Chilabothrus striatus</i> (sensu Reynolds <i>et al.</i> , 2013) <i>Epicrates striatus striatus</i> (tagged at museum)	AMNH R 155262
<i>Chilabothrus strigilatus</i> (sensu Reynolds <i>et al.</i> , 2013)	AMNH 155259; AMNH R 70263; AMNH R 155259
<i>Epicrates striatus strigilatus</i> (tagged at museum)	
<i>Chilabothrus strigilatus</i> (sensu Reynolds <i>et al.</i> , 2013)	AMNH R 77633; AMNH R 77057
<i>Epicrates striatus fosteri</i> (tagged at museum)	
<i>Corallus annulatus</i>	AMNH R 114496
<i>Corallus batesi</i>	UFMT R 05362
<i>Corallus caninus</i>	AMNH R 57788; AMNH R 73347; AMNH R 57816; AMNH R 155265; AMNH R 169154; AMNH R 155260; AMNH R 73347; AMNH R 155264; AMNH R 139338; AMNH R 155263; AMNH R 57816
<i>Corallus cf. C. caninus</i>	AMNH R 57804
<i>Corallus cropanii</i>	AMNH R 92997
<i>Corallus hortulanus</i>	AMNH R 57786; AMNH 104528; MCN-PV DR 0001; UFTM 02389
<i>Corallus hortulanus cookii</i>	AMNH R 141098; AMNH R 74832; AMNH R 7812; AMNH R 75740; AMNH R 57809
<i>Epicrates cenchria</i>	AMNH R 114716; AMNH R 57473; AMNH R 71153; AMNH R 75796; AMNH R 75795; MCN-PV DR 0002
<i>Epicrates crassus</i>	MCN-PV DR 0003
<i>Eunectes murinus</i>	AMNH 57474; MCN.D 306; MCN.D 316; MCN.D 319; MCN.D 342

prezygapophysis; sb, spinal blade; sf, subcentral foramina; zf, zygantral foramina; zg, zygantrum; zgf, zygantral articular facet; zh, zygosphene height; zs, zygosphene; zsf, zygosphene articular facet; zw, zygosphene width; zw > ctw, zygosphene width greater than cotyle width.

Nomenclatural remarks: In order to clarify the systematic revision of *Pseudoepicrates*, this work employs the following nomenclatural terminology when referring to the identified groups and named specimens: holotype of MCZ 1977 – the valid holotype

of the material assigned to *Pseudoepicrates stanolseni*; MCZ 1978 or 'barbouri material' – the specimens assigned to the species *Neurodromicus barbouri* (= *Pseudoepicrates stanolseni sensu Auffenberg, 1963*); *Chilabothrus* clade – the clade containing all the species of the genus *Chilabothrus*, including the new combination proposed herein; South American mainland clade – the clade referring to the genus *Epicrates* as sister group to the genus *Eunectes*; Total clade – the clade comprising *Chilabothrus* as sister group to the South American mainland clade (*Eunectes* + *Epicrates*).

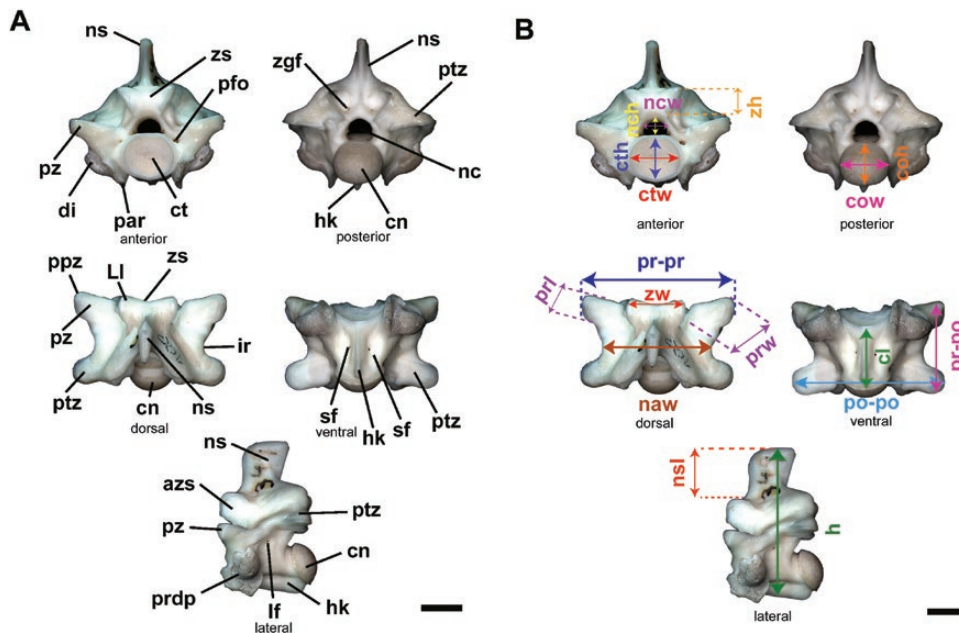


Figure 1. Mid-preloacal vertebra of *Boa constrictor* (MCN.D. 344). A, showing the anatomical features and terminology adopted in the work. Abbreviations are given in the relevant section. B, quantitative proportions and measurements employed in the present work. Anatomical views of the vertebra is present below each image. Scale bar: 10 mm.

RESULTS

SYSTEMATIC PALAEOLOGY

SERPENTES LINNAEUS, 1758

ALETHINOPHIDIA NOPCSA, 1923

MACROSTOMATA MÜLLER, 1831

BOIDAE GRAY, 1825

BOINAE GRAY, 1825

CHILABOTHRUS DUMÉRIL AND BIBRON, 1844 (*SENSU*
REYNOLDS *ET AL.*, 2013)

Remarks: The genus *Chilabothrus* comprises a clade of endemic extant insular boa snakes from Central America, and is supported by both morphological characters and molecular data (Sheplan & Schwartz, 1974; Tolson, 1987; Kluge, 1988b, 1989; Burbrink, 2005; Noonan & Chippindale, 2006; Reynolds *et al.*, 2013; Pyron *et al.*, 2014). It is represented by 12 species and 14 subspecies distributed throughout the Bahamas, Turk and Caicos Islands, and the Greater Antilles (Cuba, Porto Rico, Hispaniola and Jamaica) (Reynolds *et al.*, 2013; Pyron *et al.*, 2014; Reynolds *et al.*, 2016).

CHILABOTHRUS STANOLSENI COMB. NOV.

(FIG. 2; TABLE 2)

Diagnosis: An extinct species of *Chilabothrus* from the early Miocene of North America, characterized

by the following unique vertebral features shared among the referred material: thick zygosphenon with a slight prominence on its mid-portion in anterior view; zygosphenon roof with a crenate anterior edge, with its median lobe weakly developed and bounded by rounded lateral lobes of the zygosphenon articular facets; irregular presence of paracotyloforamina, neural foramina occurring in format of small pits, and variable presence of several foramina distributed in the parazygantral area; neural spine perpendicular to the vertebral centrum, with an elliptical shape in cross-section; articular facet of the zygosphenon oval in shape and strongly oriented anterolaterally; vaulted neural arch slightly depressed dorsoventrally in its median portion; deep interzygapophyseal ridges forming a ‘U’ shape; and a shallow posterodorsal notch length that does not exceed more than the half the distance between the pre- and postzygapophyses.

Holotype: MCZ 1977 *partum*, an anterior preloacal vertebra.

Referred specimens: Six preloacal vertebrae representing the previous paratypes of MCZ 1977 (identified by the same catalogue number), comprising five mid-preloacal vertebrae and one anterior preloacal vertebra. MCZ 1978, four preloacal vertebrae (same catalogue number), including one mid-preloacal vertebra (previously the holotype of *N. barbouri*) and

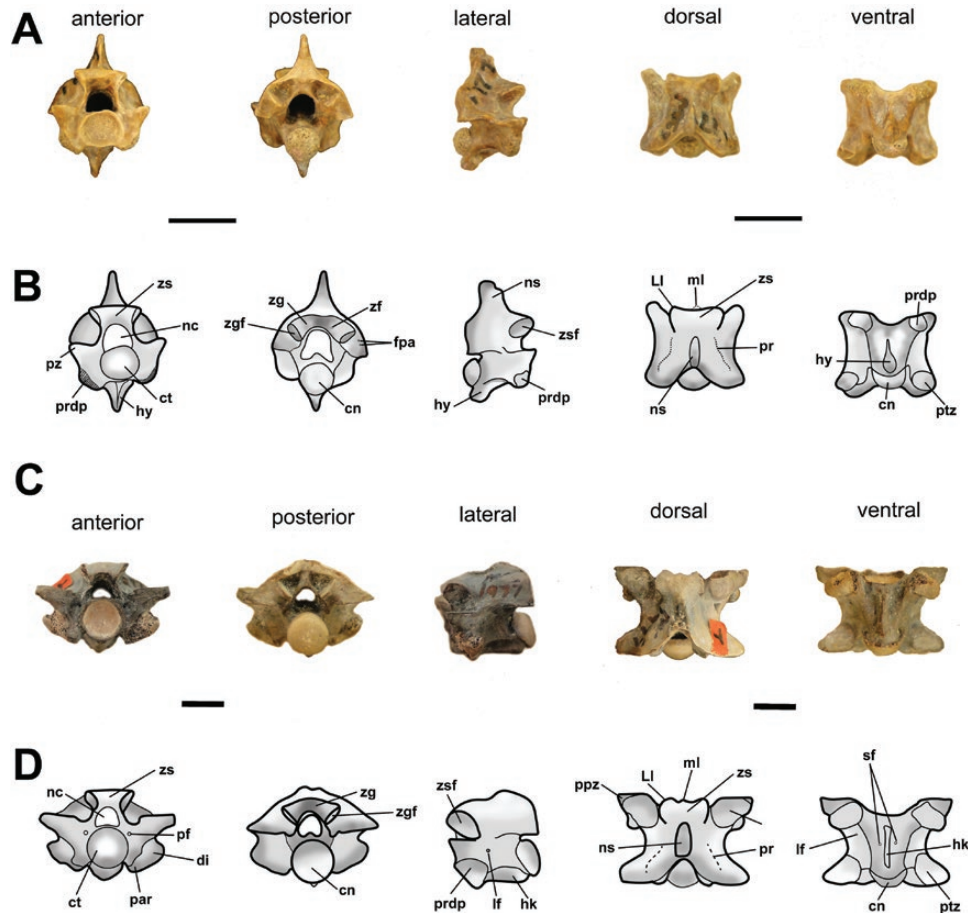


Figure 2. Isolated preloacal vertebrae attributed to *Pseudoepicrates stanolseni*. A, anterior preloacal vertebra MCZ 1977; B, schematic drawing outline of MCZ 1977 (holotype) evidencing its morphological structures; C, mid-preloacal vertebra of MCZ 1978 'barbouri' material; D, schematic drawing outline of MCZ 1978 evidencing its morphological structures. Anatomical views of the vertebrae are sorted in each column. Scale bar: 5 mm. Abbreviations in the anatomical abbreviations' section.

three partial mid-preloacal vertebrae. MCZ 2417, three mid-preloacal vertebrae. AMNH FARB 7627, two-mid-preloacal vertebrae.

Type locality and age: Thomas Farm deposit, Gilchrist County, Florida. Hawthorne Formation. Early Miocene, corresponding to the Early Heminfordian Land Mammal Age (LMA), c. 18.5 Mya. (Hulbert, 2001; MacFadden, 2001; Steadman, 2008; Beatty, 2010).

Description: All vertebrae of MCZ 1977, MCZ 1978, MCZ 2417 and AMNH FARB 7627 are well preserved and assignable to the same taxon. In anterior view, the zygosphene is thick and wider than the cotyle ($zw > ctw$). The mid-ventral region of the zygosphene exhibits a convexly projecting border, being more marked in the mid-preloacal vertebrae. The prezygapophyses are slightly inclined above the horizontal axis ($\sim 10^\circ$), showing a higher inclination in the mid-preloacal vertebrae ($\sim 13^\circ$),

whereas they are angled lower in the anterior elements ($\sim 10^\circ$). A small prezygapophyseal process is observed in some of the vertebrae, extending a little beyond the edge of the articular facet of the prezygapophyses. In the anterior preloacal vertebrae, the dorsoventral height of the neural canal is greater than the transverse width ($nch > ncw$), whereas the opposite condition is observed in the mid-preloacal elements ($ncw > nch$). The cotyle is oval in general shape, being slightly flattened dorsoventrally ($ctw > cth$) in all specimens with the exception of MCZ 1978, in which the cotyle is subrounded ($ctw \sim cth$). Lateral to the cotyle, there is a paracotylar fossa that in some specimens is associated with paired foramina (i.e. MCZ 1978 and some paratypes of MCZ 1977). The paradiapophyses are strongly oriented lateroventrally with both articular facets clearly differentiated: the diapophyseal articular facet has a strongly projecting convex edge, whereas the parapophyseal articular facet is concave (see the paratypes B, C of MCZ 1977).

Table 2. Obtained measurements from the specimens of the genus *Pseudoepicrates*

	MCZ 1978 Hol.	MCZ 2417 (A)	MCZ 2417 (B)	MCZ 1977 Hol.	MCZ 1977 (A)	MCZ 1977 (B)	MCZ 1977 (C)	MCZ 1977 (D)	AMNH FARB (A) 7627	AMNH FARB (B) 7627
cl	7.2	8.1	7.0	4.0	3.9	4.1	3.1	2.9	7.9	3.1
coh	4.7	5.0	4.3	1.9	3.0	2.1	2.0	2.1	4.6	2.0
cow	5.0	5.0	4.5	2.5	3.8	3.7	2.1	2.5	5.8	2.9
cth	4.5	4.5	4.5	2.2	3.0	2.8	2.0	1.7	5.2	2.0
ctw	4.5	4.7	14.1	2.7	3.4	3.5	2.3	2.1	4.9	2.3
h	-	15.0	10.0	-	-	-	7.2	-	-	6.9
naw	9.7	10.9	2.3	6.0	7.6	7.2	4.9	4.9	-	5.0
nch	2.3	2.4	3.2	2.1	2.0	1.9	2.0	1.5	2.7	1.1
ncw	2.7	3.9	3.2	2.0	2.9	2.3	1.7	1.9	3.1	1.7
nsl	-	5.0	4.6	2.4	-	X	2.2	2.0	4.9	2.0
nsh	-	2.4	3.5	2.8	-	X	2.1	1.2	-	2.0
po-po	15.5	-	14.6	7.4	10.1	9.5	7.3	6.3	-	7.2
pr-pr	16.1	-	-	7.5	-	10.0	7.9	6.8	-	7.8
pr-po	10.2	-	10.6	6.0	6.8	6.6	5.3	4.5	-	4.9
prl	4.2	-	4.7	2.0	-	3.0	2.2	1.4	-	2.1
prw	3.5	-	3.4	1.6	-	2.1	1.6	1.5	-	1.7
zh	2.1	2.2	2.0	1.0	1.5	1.7	0.8	0.9	2.3	0.6
zw	5.9	6.5	6.0	4.1	4.7	4.8	3.0	3.3	7.3	3.1

Hol. denotes the specimens previously attributed to the holotype material of *Neurodromicus*; letters denote an individual vertebra specimen; and dash denotes structure not measured due to the preservation of the specimen. Morphological structures abbreviated in the Anatomical abbreviations' section.

In posterior view, the neural arch is vaulted in all vertebrae. The neural spine of the holotype of MCZ 1977 is broken at its dorsal tip, whereas a neural spine is not preserved on MCZ 1978. In the paratypes C and D of MCZ 1977 (Fig. 3) and one specimen of MCZ 2417 (Fig. 4F), on which the neural spines are entirely preserved, this process is thick and rises from the mid-portion of the neural arch. The zygantrum is wide, deep and internally bears a set of paired zygantral foramina on each side of the vertebra. External to the zygantrum, several small foramina are present in the form of small pits distributed along the parazygantral area (see holotype of MCZ 1977 Fig. 2A, B and paratypes B, D of MCZ 1977 Fig. 3B, D). The postzygapophyses are slightly inclined above the horizontal axis ($\sim 10^\circ$) in the anterior preloacal vertebrae, whereas they are nearly horizontally oriented in the mid-preloacal specimens. The condyles of all specimens are wider than high ($cow > coh$), except for one specimen of MCZ 1978, which is rounded in shape ($cow \sim coh$).

In lateral view, the neural spine is high, anteroposteriorly short and bears a straight dorsal edge. The articular facet of the zygosphene is elliptical in shape and anterolaterally orientated. Lateral foramina are present on the mid-portion of all preserved vertebrae. The posterior region of all centrum is characterized by a marked precondylar constriction. A well-defined haemal keel is present on the ventral surface of the mid-preloacal vertebrae, rising from the ventral margin

of the cotyle and extending anteroposteriorly to reach the precondylar constriction, not extending beyond the condyle. The ventral surfaces of the centrum of the preloacal anterior vertebrae do not possess a haemal keel, having instead a hypapophysis. Although broken in the holotype of MCZ 1977 (Fig. 2A, B) and the paratypes B, D of MCZ 1977 (Fig. 3B, D), this structure was clearly developed beyond the posterior margin of the condyle.

In dorsal view, the fossils are wider than long ($pr-pr > pr-po$). The prezygapophyses of the anterior vertebrae are oriented anterolaterally, whereas the mid-preloacal specimens display a nearly transverse orientation. The articular facets of the prezygapophyses are oval-shaped in morphology and longer anteroposteriorly than mediolaterally wide ($prl > prw$). The anterior edge of the zygosphene displays a crenate morphology, whereby its convex lateral lobes are separated by a smaller median projection (= median lobe *sensu* Auffenberg, 1963), which does not extend beyond the anterior margin of the laterals lobes. A set of paired parasagittal ridges (*sensu* Hsiou *et al.*, 2014) extend anteroposteriorly along the roof of the neural arch, beginning on the lateral surfaces of the zygosphene and disappearing just short of the posteriormost edge of the neural arch (Fig. 2B, D). The parasagittal ridges are more pronounced on the mid-preloacal vertebrae than the anterior elements. The neural spine is thick with an ellipsoidal

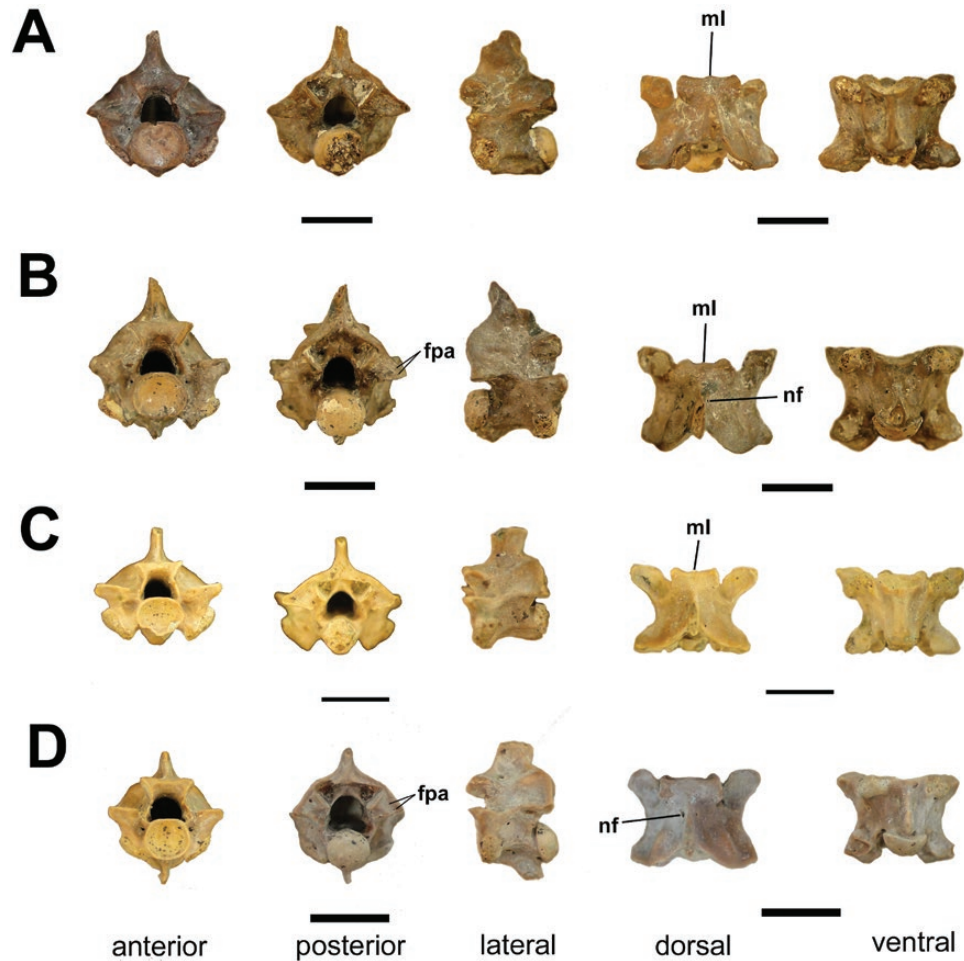


Figure 3. Paratypes attributed to *P. stanolseni* (MCZ 1977). Letters A–D denote the specimens. Anatomical views of the vertebrae are sorted in each column. Abbreviations are given in the relevant section. Scale bar: 5 mm.

shape in cross-section, although the neural spine of the anterior vertebrae is comparatively thin relative to the mid-preloacal elements. Some specimens possess small neural foramina (= paraespinal foramina *sensu* Teixeira, 2013) just lateral to the neural spine. These features (similar to the several foramina in the parazygantral area) occur as either small singleton pits or as paired intrusions located on either side of the longitudinal axis of the neural arch, (e.g. the paratype D of MCZ 1977 (Fig. 3D) and paratypes of MCZ 1978 (Fig. 5). The interzygapophyseal constriction extends from the prezygapophysis toward the postzygapophysis. In the anterior vertebrae, this constriction is relatively anteroposteriorly short, whereas the mid-preloacal vertebrae exhibit a deeper constriction. The posterodorsal notch is relatively shallow in all vertebrae, and does not reach half of the length of the distance between the pre- to postzygapophyses ($pnl < 50\% pr-po$).

In ventral view, the length of the vertebral centrum of all specimens is less than the width of the neural arch ($cl < naw$). In the anterior vertebrae, the hypapophyses rise from the median portion of the centrum, developing anteroposteriorly toward the condyle, extending beyond its ventral rim. In the mid-preloacal vertebrae, the haemal keel originates on the ventral margin of the cotyle, developing longitudinally to reach the prezygapophyseal constriction. The ventral face of the centrum of all specimens has a shallow depression that is more concave in the mid-preloacal vertebrae. The subcentral fossae are delimited laterally by the subcentral margin, being relatively shallow on both the anterior and mid-preloacal vertebrae. The articular facets of the postzygapophyses of the anterior vertebrae are broad and elliptical in outline, whereas they are more subtriangular in shape on the mid-preloacal specimens. In all specimens, the major part of the cotyle is exposed.

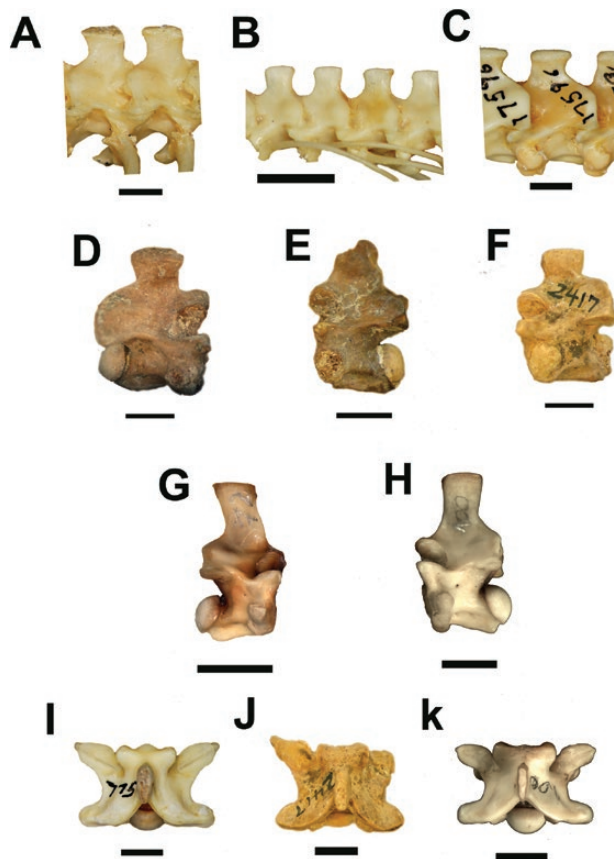


Figure 4. Comparison of the neural spine morphology between *Chilabothrus*, *Epicrates* and the fossils from Thomas Farm. Only mid-preloacal vertebrae are figured here. A, articulated vertebrae of *Chilabothrus inornatus* (AMNH 70023); B, articulated vertebrae of *Chilabothrus striatus strigilatus* (AMNH 70263); C, articulated vertebrae of *Chilabothrus angulifer* (AMNH 77596); D, paratype of *N. barbouri* (MCZ 1978) (= *Pseudoepicrates*); E, paratype of *P. stanolseni* (MCZ 1977); F, *P. stanolseni* (MCZ 2417); G, *Epicrates crassus* (MCN PV DR 003); H, *Epicrates cenchria* (MCN PV DR 002); I, *Chilabothrus angulifer* (AMNH 77596); J, *P. stanolseni* (MCZ 2417); and K, *Epicrates cenchria* (MCN PV DR 002). In (A–H) lateral and (I–K) dorsal views. Scale bar: 5 mm.

Identification and comparisons: All specimens analysed here share with Boinae the following vertebral features: dorsoventrally high, mediolaterally wide and anteroposteriorly short vertebral built; a vaulted neural arch that is wider than the length of the vertebral centrum ($naw > cl$); well-developed neural spine; thick zygosphene; short prezygapophyseal process; presence of a posterodorsal notch; inclination of the prezygapophyseal articular facets lower than 15° ; presence of paracotylar foramina; well-developed precondylar constriction; presence of hypapophyses on preloacal anterior vertebrae; and a haemal keel on mid-preloacal vertebrae (Rage, 1984, 2001; Lee & Scanlon, 2002; Szyndlar & Rage, 2003; Hsiou & Albino, 2009).

Among the boinae, the Thomas Farm fossils specimens strongly differ from the following genera: (a) *Eunectes*, which presents vertebrae that are markedly larger, wider and more robust; possesses a deeper

posterodorsal notch; higher projected parasagittal ridges; and a median tubercle between the neural canal and the zygosphene roof; (b) *Corallus*, which presents a lower neural spine; higher degree of vaulting of the neural arch; and completely horizontally orientated prezygapophyses; and (c) *Boa*, which is discussed in greater detail below (see Discussion).

The specimens described herein share with the genus *Epicrates* the following vertebral features: a thick zygosphene with a protuberance on its mid-portion in anterior view; zygosphene roof with an anterior edge characteristically crenate or entirely straight in dorsal view; irregular presence of paired paracotylar foramina, neural foramina and several foramina occurring in the form of small pits in the parazygantral area; neural spine in elliptical shape in cross-section; articular facet of the zygosphene oval in shape and oriented anterolaterally; vaulted neural arch depressed dorsoventrally in its median portion; interzygapophyseal

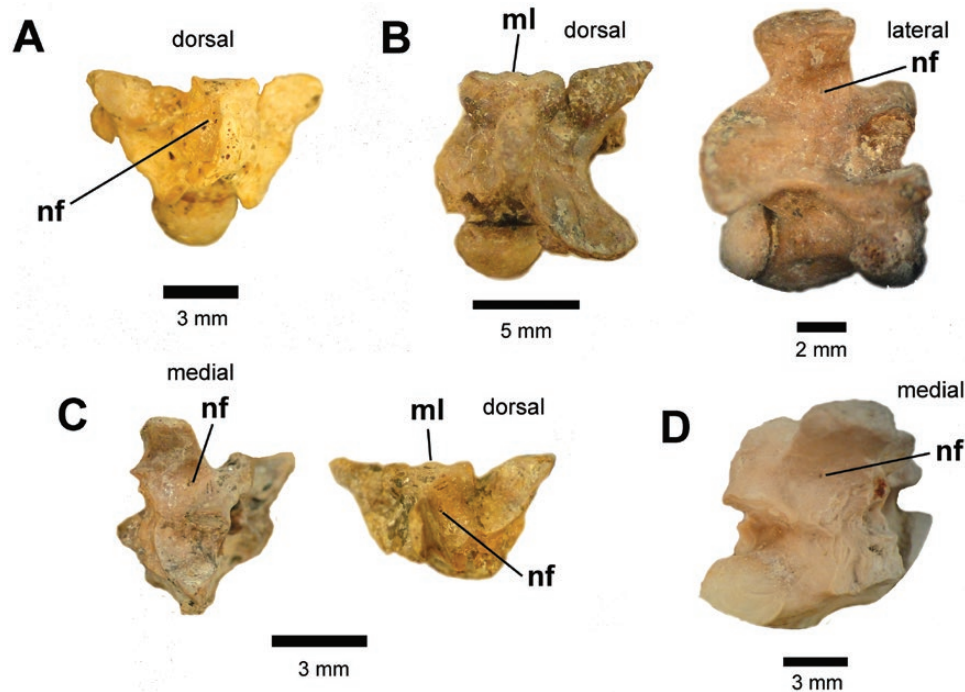


Figure 5. Paratypes previously attributed to *N. barbouri* (= *Pseudoepicrates*). Letters A–D denotes the specimens. Anatomical views of the vertebrae are sorted above each image. Abbreviations are given in the relevant section.

ridges forming a ‘U’ shape; and shallow posterodorsal notch length that does not exceed more than half of the distance between the pre- and postzygapophyses (pnl < 50% pr–po) (Hsiou & Albino, 2009; Camolez & Zaher, 2010; Hsiou & Albino, 2010; Teixeira, 2013).

Historically, *Epicrates* was considered a monophyletic genus that shared a sister-group relationship with *Eunectes*. However, subsequent investigations into the evolutionary relationships of *Epicrates* have suggested potential paraphyly (based on both molecular and morphological data) with respect to the insular forms from the West Indian island complex (*Epicrates sensu lato*) (Sheplan & Shwartz, 1974; Kluge, 1988b, 1989; Burbrink, 2005; Noonan & Chippindale, 2006). Recently, Reynolds *et al.* (2013) undertook the most comprehensive study of the relationships of *Epicrates*, proposing the monophyly of the insular West Indian boid forms and formalizing the clade *Chilabothrus*, which split the insular forms of ‘*Epicrates sensu lato*’ from the mainland (*Epicrates sensu stricto* + *Eunectes*) and suggested divergent biogeographical and evolutionary histories for these groups.

Despite repeated suggestions of paraphyly, none of the previous works demonstrated explicit morphological differences between the axial skeletons of *Epicrates* and *Chilabothrus*. Although at a generic level these genera share a similar combination of vertebral features, there are nonetheless subtle differences that allow for confident referral of the Thomas

Farm material to *Chilabothrus*. These traits can be identified via direct comparison with extant osteological material (Fig. 6).

The main differences between these genera can be recognized via the neural spine morphology, the zygosphene and in the consistently greater mean-average sizes of the vertebral measurements of *Chilabothrus* (Table 2 cf. Teixeira, 2013). *Epicrates* is typified by a high and slender neural spine (Fig. 4G, H), whereas in *Chilabothrus* the neural spine is low, nearly perpendicular in relation to the vertebral centrum and is more robust (Fig. 4A–C). In dorsal view, both genera display an elliptical-shaped neural spine in cross-section; however, in *Chilabothrus* the neural spine is proportionally wider than that observed in *Epicrates* (Fig. 4I–K).

Although the Thomas Farm fossils vary in preservational quality, the completely preserved neural spines of the paratypes of MCZ 1978 (Fig. 5), MCZ 1977 (Fig. 3), as well as one of the vertebrae of AMNH FARB 7627, suggests that these fossils share a unique neural spine morphology with extant members of *Chilabothrus* (compare Fig. 4A–C with D and F). The neural spines of both groups are nearly perpendicular in relation to the vertebral centrum, shortened anteroposteriorly and appear transversely thickened in dorsal view. These combined neural spine characters differ from the observable morphology of *Epicrates* (Fig. 4G, H, K).

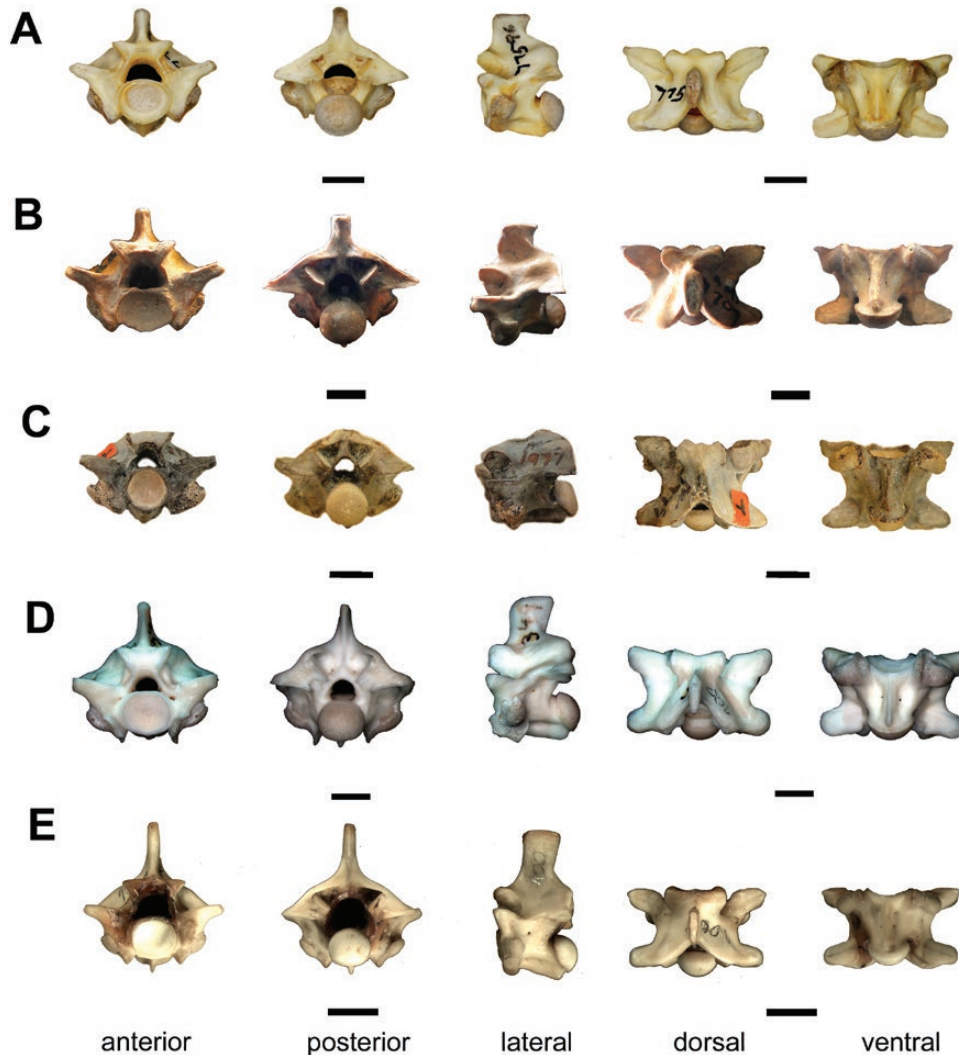


Figure 6. Selected examples of the extant comparative material used in the study. A, midtrunk vertebra of *Chilabothrus angulifer* (AMNH R 77596); B, midtrunk vertebra of *Chilabothrus* cf. *C. inornatus* from the Pleistocene of Cuba (AMNH 7709); C, midtrunk vertebra of ‘*barbouri*’ (previous holotype MCZ 1978); D, midtrunk vertebra of *Boa constrictor* (MCN.D. 344); and E, midtrunk vertebra of *Epicrates cenchria* (MCN PV DR 002). Anatomical views of the vertebrae are sorted in column at the lower portion of the image. Scale bar: 5 mm.

We also note differences in zygosphene shape variation that are potentially useful for the taxonomic differentiation between *Epicrates* and *Chilabothrus*: In dorsal view, the zygosphene of *Chilabothrus* shows the typical crenate morphology; however, it is worth noting that the median lobe is prominent, broad and characteristically convex (Fig. 7).

In contrast, the vertebrae of *Epicrates* show marked variation regarding the development of the median lobe of the zygosphene in dorsal view, ranging from a straight border in which the lobe itself is absent, to the moderately crenate condition and, even, the condition in which the median lobe exceeds the height of the lateral lobes of the articular facets of the zygosphene (Fig. 7)

(Teixeira, 2013). The morphology of the lateral lobes of the zygosphene articular facets also differs among these two genera, with *Epicrates* having triangular-shaped lateral lobes in dorsal view (Fig. 7), whereas those of *Chilabothrus* are rounded (Fig. 7). There are also some differences in the zygosphene median lobe: in *Chilabothrus* the morphology of the lobe is characteristically broad and convex, whereas in *Epicrates* this same process, while also convex, is more ‘triangular’ in shape with a compressed anterior apex (compare the two morphologies in Fig. 7). The Thomas Farm material differs distinctly from these two genera, with the median lobe weakly developed and neither reaching nor exceeding the lateral lobes of the zygosphene articular

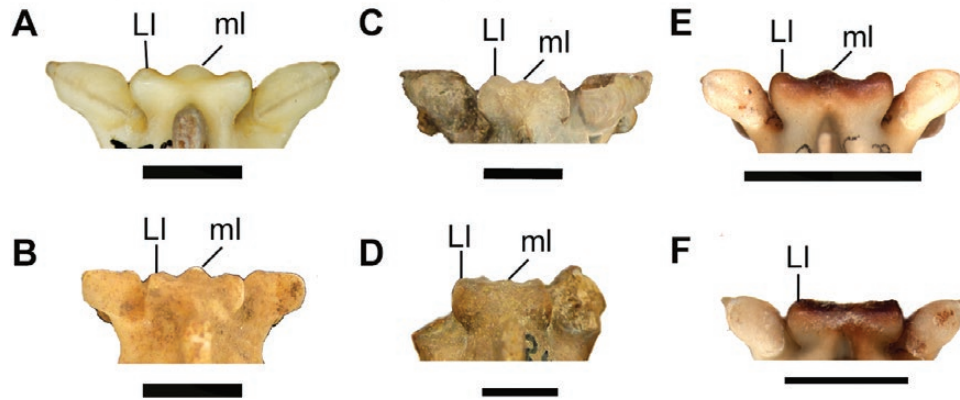


Figure 7. Close up of the zygosphene of different bovine vertebrae. Note the differences between the median lobe and lateral lobe of the specimens. A, mid-preloacal vertebra of *Chilabothrus angulifer* (AMNH 77596); B, *Chilabothrus inornatus* (MCZ 2341); C, mid-preloacal vertebra of ‘barbouri’ (= *P. stanolseni*) material (MCZ 1978); D, mid-preloacal vertebra of *P. stanolseni* (MCZ 2417); E, mid-preloacal vertebra of *Epicrates cenchria* (MCN PV DR 002); and F, mid-preloacal vertebra of *Epicrates crassus* (MCN PV DR 003). Abbreviations are given in the relevant section. Scale bar: 2 mm.

facets (compare the figures with the extant species: Fig. 6A–C; Fig. 4B, C; Fig. 7; Fig. 8A, C, D, F, G).

In summary, the material from Thomas Farm is assignable to the genus *Chilabothrus* with respect to the following exclusive combination of vertebral characters: (1) zygosphene with the anterior border crenate in dorsal view with a projection of the median lobe between the rounded lateral lobes of the articular facets of the zygosphene; and (2) neural spine shortened anteroposteriorly, nearly perpendicular in relation to the vertebral centrum, being ellipsoidal shaped and thick. Moreover, here

we erect the new combination *Chilabothrus stanolseni comb. nov.*, which represents a hypothetical radiation of extinct species of *Chilabothrus* into the early Miocene of North America. Additionally, *Chilabothrus stanolseni comb. nov.* can be identified as a distinct species via a single autapomorphic character: the presence of a weakly developed median lobe, distinct from all conditions observed in the extant genus (see Figs 4, 7, 8). In this respect, all material previously assigned to the species *Pseudoepicrates stanolseni* is synonymized with *Chilabothrus stanolseni comb. nov.*

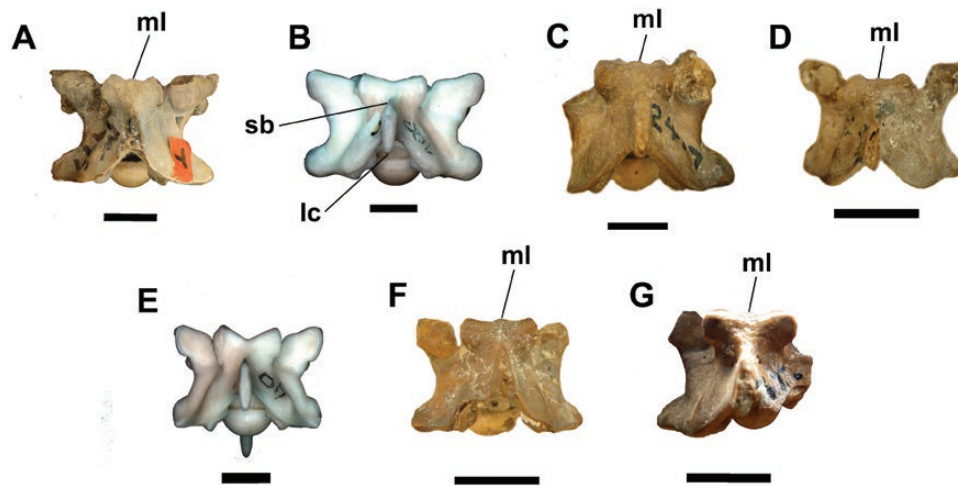


Figure 8. Specimens of Thomas Farm compared with the extant *Boa constrictor*. Note differences concerning the zygosphene roof and the neural spine morphology. All vertebrae are in dorsal view. A, midtrunk vertebra of ‘barbouri’ MCZ 1978; B, midtrunk vertebra of *B. constrictor* MCN. D. 344; C, midtrunk vertebra of *P. stanolseni* MCZ 2417; D, anterior vertebra paratype of *P. stanolseni* MCZ 1977; E, anterior vertebra of *B. constrictor*; F, midtrunk paratype vertebra of *P. stanolseni* MCZ 1977; G, midtrunk vertebra of *P. stanolseni* AMNH 7627. Abbreviations are given in the relevant section. Scale bar: 5 mm.

DISCUSSION

PREVIOUS ANATOMICAL INTERPRETATIONS

Historically, the material attributed *Pseudoepicrates* were a controversial subject of numerous taxonomical interpretations. However, all previous works concerning this question are in some manner problematic due to: (a) not considering intracolumnar and interspecific variation present amongst the specimens; (b) a lack of detailed analysis of all referred material, including the holotype, paratype and attributed specimens; and (c) a lack of detailed anatomical description and comparison with closely related boids.

(a) *Neurodromicus stanolseni* Vanzolini, 1952 and *Neurodromicus barbouri* Vanzolini, 1952 Vanzolini's (1952) original description, which recognized two distinct extinct species, was conducted without any comparison with material from extant boid specimens. Moreover, at that time the evolutionary history of the group was very poorly understood and several important boid fossils still awaited discovery. Some boid species, such as the indeterminate Boidae from the late Cretaceous of Argentina (Albino, 1996) and *Titanoboa cerrejonensis* Head *et al.*, 2009 from the Paleocene of Bolivia, indicate that the group has an old fossil record. Nonetheless, it is worth noting that certain modern genera, such as *Corallus*, were also known from deposits dating back to the Paleocene of Brazil (Rage, 1998). Since it is evident that modern genera have a deep geological history, comparison of fossil specimens with extant osteological material should form a necessary component of any taxonomic hypothesis. The characters employed in Vanzolini's (1952) differential diagnosis of *N. stanolseni* and *N. barbouri* suffer from a variety of issues pertaining to intracolumnar, intraspecific and even taphonomic variation and/or deformation. For example, the zygosphene of the holotype MCZ 1977 is distinguishable from other specimens with respect to its slightly concave anterior edge. However, as mentioned above, the specimen as a whole presents a suite of features consistent with post-depositional alteration (e.g. abrasions, rounded marks and a highly polished surface) (Boyde *et al.*, 1978; Denys, 2002; Fernández-Jalvo *et al.*, 2002).

Despite this, Vanzolini (1952) also listed the following features as diagnostic of *N. stanolseni*: gracile vertebrae; divergent orientation of the prezygapophyses; the thickness of the zygosphene; and the degree of vaulting of the neural arch. However, as has been demonstrated in modern boid genera like *Epicrates* and *Corallus* (Teixeira, 2013), all of these characters are highly subject to both intraspecific and intracolumnar variation. In general, the anterior preloacal vertebrae tend to have a higher degree of inclination of the prezygapophyses in *Epicrates*, *Corallus* and even

Chilabothrus (comparative material consulted here), and a generally more gracile build, when compared with the mid-preloacal vertebrae.

(b) *Pseudoepicrates stanolseni* (Vanzolini, 1952) Auffenberg (1963), while undertaking the revision of the fossil snake material from Florida, addressed the issue of intracolumnar variation amongst the specimens from Thomas Farm. Deeming the '*stanolseni*' and '*barbouri*' specimens as representing anterior and mid-preloacal vertebrae of the same taxon, respectively, Auffenberg proposed the new combination *Pseudoepicrates stanolseni*. Although this interpretation took into account the possibility of interspecific variation between the fossil specimens, it did not consider extant boid species, in turn underestimating the deep evolutionary history of some taxa (e.g. *Corallus*, *Chilabothrus* and *Eunectes*) (Hoffstetter & Rage, 1977; Rage, 1988).

Kluge (1988a) reassessed the fossil specimens, proposing that part of the material of *P. stanolseni* was in fact a distinct extinct taxon closely related to the old and artificial group 'Boini' (*Boa* + *Corallus cropanii*) and considering the '*barbouri*' material as a junior synonym of the extant snake *Boa constrictor*. The characteristics used to justify the position of *Pseudoepicrates* as 'Boini' were the presence of a weak median projection on the zygosphene roof (crenate morphology) and the presence of paracotylar foramina (Kluge, 1988a). However, this interpretation is problematic as the set of features identified by Kluge (1988a) do not represent reliably delimited synapomorphies of a specific clade. Moreover, the phylogenetic arrangement of 'Boini' is clearly paraphyletic with respect to current morphological and molecular hypotheses (Palci, Nydam & Caldwell, 2013; Caldwell *et al.*, 2015; Reeder *et al.*, 2015; Zheng & Wiens, 2016; Harrington & Reeder, 2017). *Pseudoepicrates* differs substantially from *Corallus*, which comparatively possess a lower neural spine; a nearly horizontal orientation of the prezygapophyses in anterior and mid-preloacal vertebrae; a strong degree of neural arch vaulting; and a zygosphene roof, either convex or with a strongly developed crenate morphology. A noteworthy distinction between *Pseudoepicrates* and *C. cropanii* is the presence of a median tubercle between the neural canal and the zygosphene roof of the latter, resembling the condition of *Eunectes* (Hsiou & Albino, 2009).

(c) *Boa constrictor* Linnaeus, 1758 (after Albino, 2011)

Albino (2011) performed the most recent taxonomic revision of *Pseudoepicrates* and, following Kluge (1988a), argued that the Florida fossils share similarities with *Boa constrictor*. However, Albino (2011) went a step further in synonymizing all the referred

material of *Pseudoepicrates* to *B. constrictor*, providing the northernmost record of the latter. Although MCZ 1977 (specimen illustrated in Fig. 2A) shares with *Boa* a slightly concave morphology of the zygosphene roof (a feature that is potentially exaggerated in the former due to taphonomic factors), a host of other features distinguish the axial morphology of *Pseudoepicrates* from *B. constrictor*. The zygosphene of MCZ 1977 and the 'barbouri' material MCZ 1978 is mediolaterally wider and dorsoventrally shorter than in *Boa*, the latter being short and massively robust. The zygosphene articular facets in *Boa* are sharply inclined dorsolaterally, whereas this inclination is much reduced in *Pseudoepicrates*. Likewise, the prezygapophyses of *Pseudoepicrates*, despite being severely eroded in MCZ 1977, are only minimally inclined above the horizontal plane, differing from the more highly inclined condition of *Boa* ($\sim 14^\circ$).

The neural spine of *Boa* bears a well-developed laminar crest and spinal blade (*sensu* Albino, 2011; Figs 8B, 9). In contrast, the neural spine of *Pseudoepicrates* is nearly perpendicular relative to the vertebral centrum. In dorsal view, the neural spine of *Pseudoepicrates* is transversely thick and wide and is elliptical in cross-section (Figs 4J, 8C). In contrast, the cross-section of the neural spine in *Boa* is lacrimiform-shaped in dorsal view (Onary-Alves, Hsiou & Rincón, 2016), with a comparatively thin anterior portion that thickens posteriorly forming, respectively, the spinal blade and spinal crest (Albino, 2011). Additionally, although the neural

spine is slightly broken in MCZ 1978 and absent on the barbouri material (MCZ 1978), both the paratypes and referred material demonstrate that the neural spine is lower in *Pseudoepicrates* compared with *Boa*, this process being especially well-developed in the anterior vertebrae of the latter (Fig. 9).

The neural arches of the MCZ 1978, in addition to being somewhat depressed when compared with *Boa*, do not possess the epizygapophyseal process above the articular facets of the postzygapophyses, a reliable diagnostic character of *Boa*. In dorsal view, the vertebrae of *Boa* tend to possess marked parasagittal ridges (*sensu* Hsiou *et al.*, 2014) on the neural arch roof, whereas in *Chilabothrus stanolseni* **comb. nov.** this morphology is only weak-to-moderately marked. Other features also observable in dorsal view in *Boa* are the larger vertebral width (pr–pr) and the deeper interzygapophyseal constrictions and posterodorsal notches, features that are comparatively shallow in the Thomas Farm material.

Lastly, the anterior edge of the zygosphene roof of *Chilabothrus stanolseni* **comb. nov.** is crenate in morphology, occurring via the weakly developed condition of the median lobe (Fig. 8A, C, D, F, G). This is distinct from the morphology of *Boa*, which shows a characteristic V-shape notch or a well-defined concave border of the zygosphene roof (Fig. 8B, E). All the differences listed above between the fossils specimens and the studied material of *Boa* provides robust grounds

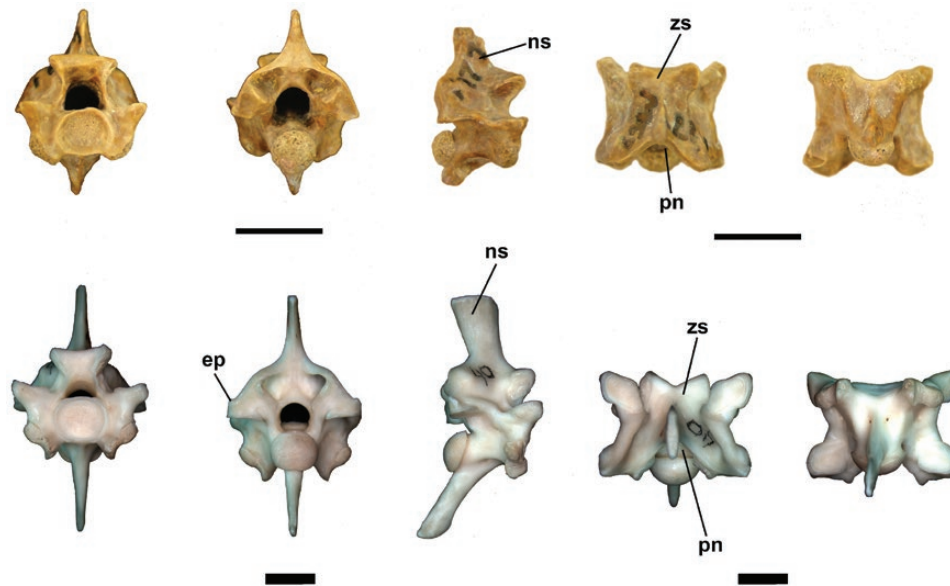


Figure 9. Comparison between the holotype of *P. stanolseni* MCZ 1977 and an anterior vertebra of *B. constrictor* MCN. D. 333. Note differences such as the neural spine orientation; the presence of epizygapophyseal process in *B. constrictor*; the zygosphene roof morphology; and the shallow posterodorsal notch of *P. stanolseni*. Abbreviations are given in the relevant section. Scale bar: 5 mm.

on which to reject the allocation of *Pseudoepicrates stanolseni* to *Boa constrictor*.

EVOLUTIONARY AND PALAEOBIOGEOGRAPHICAL IMPLICATIONS

The boids are a subject of great interest, especially with respect to their patterns of distribution and speciation, which may have been strongly shaped by tectonic events of the old supercontinent Gondwana (Laurent, 1979; Bauer, 1993; Rage, 1988, 2003; Noonan & Chippindale, 2006). The global distribution of some species is conspicuously wide-ranging, extending from the Neotropics (*Epicrates*, *Corallus*, *Eunectes*, *Boa* and *Chilabothrus*), to Madagascar (*Acrantophis* and *Sanzinia*) and the Pacific Islands (*Candoia*) (Noonan & Chippindale, 2006; Reynolds *et al.*, 2013; Pyron *et al.*, 2014). This distribution supports the hypothesis that the fragmentation of Gondwana was the main cause of several vicariant events within Boidae, followed by episodes of over-water oceanic dispersion (Underwood, 1976; Austin, 2000; Vences *et al.*, 2001; Noonan & Chippindale, 2006). The latter phenomenon potentially explains the phylogenetic signal recovered by Kluge (1991), which suggested that the monophyly of certain clades was not constrained by geographic region. Nonetheless, this phylogenetic hypothesis did not include several boid species that are well known today, and a reappraisal of both the character data, as well as the incorporation fossil data, is warranted to further test this pattern (e.g. Palci *et al.*, 2013; Caldwell *et al.*, 2015).

Of particular relevance is the boid *Chilabothrus*, which, due to its recent proposition as a formal clade (Reynolds *et al.*, 2013), raises interesting questions pertaining to its evolutionary and biogeographical history. The current phylogenetic hypothesis suggests that *Chilabothrus* is the sister-taxon of the American mainland clade (*Epicrates* + *Eunectes*) (Reynolds *et al.*, 2013). This hypothesis, when analysed under a divergence time approach, produces two differing interpretations: (1) that the divergence of species within the genus *Chilabothrus* occurred prior to divergence of the constituent clades of its mainland sister-group (*Eunectes* + *Epicrates*) (Noonan & Chippindale, 2006); or (2) that the divergence within the American mainland clade occurred before the diversification of species within *Chilabothrus* clade (Fig. 10A) (Reynolds *et al.*, 2013). The fossil record of the total clade (see Nomenclatural remarks) is very poorly known, limited to the occurrence of vertebral fragments attributed to aff. *Epicrates* sp. from the late Miocene of the Solimões Formation, Brazil (Hsiou & Albino, 2010) and the putative extinct taxon *Eunectes*

stirtoni Hoffstetter & Rage, 1977 from the Miocene of Colombia (~12.37 Mya) (Head, 2015). However, our revision of *Chilabothrus stanolseni* **comb. nov.** places this genus in the early Hemingfordian of Florida (~18.5 Mya), suggesting that the initial diversification of *Chilabothrus* occurred prior to the divergence of the mainland clade (*Epicrates* + *Eunectes*). Thus, the Thomas Farm assemblage represents the oldest record within the total clade, an interpretation further bolstered by the fact that the insular fossil record provides for a more reliable (i.e. better preserved and more fossil specimens) taxonomic assessment than the previous putatively assigned fossils of the American mainland clade.

A common issue regarding the historical biogeography of *Chilabothrus* is the centre of origin of the clade. Previous studies inferred that the divergence of the genus was coincident with a single dispersion episode from South America into the West Indies (Sheplan & Schwartz, 1974; Rosen, 1975). Recent studies of boid phylogeny corroborate this hypothesis (Burbrink, 2005; Noonan & Chippindale, 2006; Reynolds *et al.*, 2013), supported by the close phylogenetic relationship between *Chilabothrus* (West Indies) and the South American clade (*Epicrates* + *Eunectes*). Moreover, the application of ancestral area reconstruction returned high statistical support for the centre of origin of *Chilabothrus* as South America, with a dispersion into the West Indian insular complex followed by speciation within the genus throughout the island banks (Fig. 10B, red arrow) (Reynolds *et al.*, 2013). Another hypothesis, albeit one we consider less likely, is the origin of *Chilabothrus* within the central region of Central America (Reynolds *et al.*, 2013); however, there is currently no strong evidence in favour of a dispersal route for any vertebrate lineage directly from Central America to the Great or Lesser Antilles (Fig. 10B, green arrow) (Hedges, 2001). Alternatively, based on the distribution of fossils of *Pseudoepicrates* and *Paraepicrates*, Tolson (1987) suggested a North American origin for *Chilabothrus* (Fig. 10B, pink arrow). However, this hypothesis is not favoured here due to the lack of evidence for a reliable route of dispersion from North America to the Antilles. The synonymization of *Pseudoepicrates* with *Chilabothrus stanolseni* **comb. nov.** does not give direct insight into the origin of the clade; however, it is consistent with patterns of speciation based on studies of extant vertebrate assemblages within the Antilles (Hedges, 2001; Crawford & Smith, 2005), which suggest a South or Central American origin, and are geologically concordant with biogeographical analyses (Reynolds *et al.*, 2013).

The biogeographical scenario outlined by Reynolds *et al.* (2013) suggests that the divergence

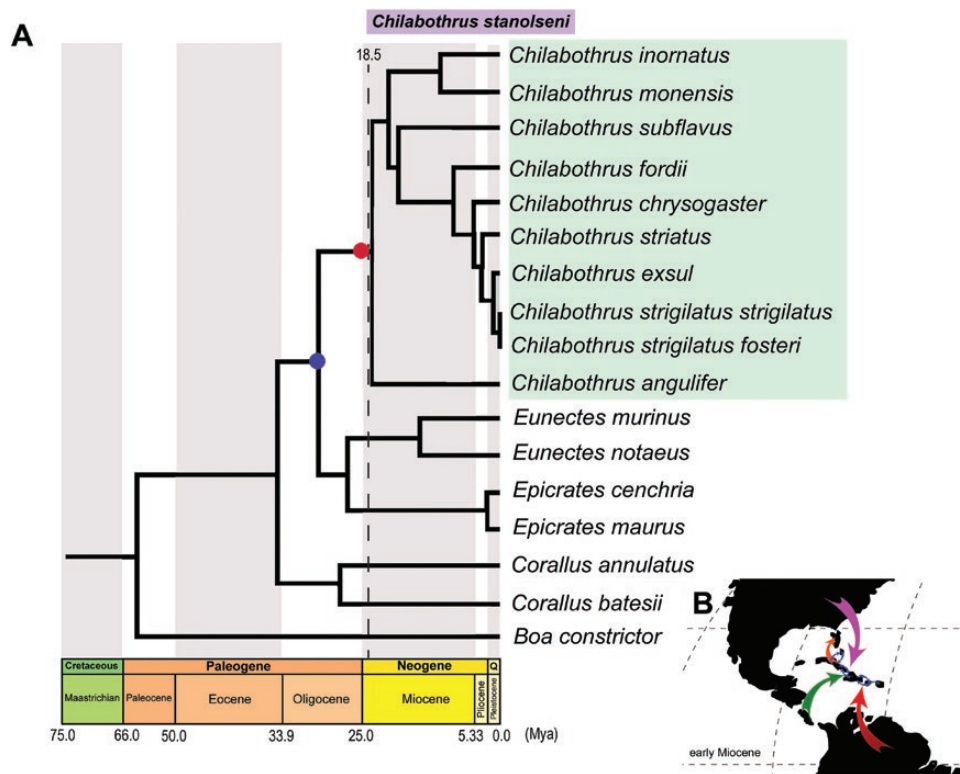


Figure 10. A, calibrated phylogenetic hypothesis of Reynolds *et al.* (2013). Blue dot: the estimated age of divergence of the group [(*Chilabothrus*) + (*Epicrates* + *Eunectes*)] at ~30.0 Mya. Red dot: the estimate age for origin of the genus *Chilabothrus* at ~22 Mya. The dashed line shows the age of the site of *Chilabothrus stanolseni* comb. nov. ~18.5 Mya, marking the oldest record of the genus. B, schematic map of the early Miocene showing the biogeographical dispersion and diversification of the genus *Chilabothrus*. Red arrow: probable route of dispersion via Northern South America, which is here considered the most likely based on multiple lines of evidence, including genetic divergence, oceanic current patterns, incidence of vertebrates taxa and estimated dispersal time of initial dispersion ~22 Mya (Hedges, 1996, 2001; Reynolds *et al.*, 2013). Green arrow: alternative route of dispersion to the West Indian Island complex from the Central America, estimate dispersal time of ~22 Mya (Hedges, 1996). Pink arrow: route of dispersion from North America, hypothesis based on Tolson (1987) due to the presence of *Pseudoepicrates*, considered unlikely here. Orange arrow: second dispersal event of *Chilabothrus stanolseni* comb. nov. to the North American Territory from the West Indies (estimated age of at least ~18.5 Mya). Blue arrow: dispersion throughout the West Indies' island complex, prefacing the diversification of the current extant species of the insular complex (estimated age since ~22 Mya to the Holocene). Hypothesis adapted from Reynolds *et al.* (2013). Paleomap reconstruction based on Scotese (2010).

of *Chilabothrus* from its sister-group (*Epicrates* + *Eunectes*) stemmed from a single dispersion event (from South or Central America to Cuba) dating to around ~30.0 Mya, during the Oligocene (Fig. 10B, red and green arrows). The crown-clade *Chilabothrus* is estimated to have arisen about ±22.0 Mya during the early Miocene, followed by subsequent speciation events throughout the Neogene/Quaternary (Fig. 10 B, blue arrow). The age of the estimated divergence of the genus (±22.0 Mya) is also temporally underscored by potential geological markers, such as the uplifting of the protoantilles (Hedges, 2001; Pindell & Kennan, 2009), which created a suitable overland route for the establishment and further diversification of the genus (Reynolds *et al.*, 2013).

The material reassessed here and assigned to *Chilabothrus stanolseni* comb. nov. is geologically and geographically consistent with the biogeographical hypothesis of Reynolds *et al.* (2013). Following the dispersal of the genus to Cuba about ~22.0 Mya, individuals (or a population thereof) of *C. stanolseni* comb. nov. ultimately reached Florida via suitable routes associated with the protoantilles (Fig. 10B, orange arrow) (Pindell & Kennan, 2009), a possibility that is supported by the geochronological age of the site (~18.5 Mya) and by the recognized ability of overwater dispersion reported among boids (Hedges, 1996; Noonan & Chippindale, 2006; Head *et al.*, 2012). Despite its establishment within North America, the genus nonetheless ultimately disappeared from this landmass.

This is possibly due to intense fluctuations in temperature associated with the Neogene/Quaternary boundary (Peizhen, Molnar & Downs, 2001), with no record of West Indian boids in North America from this period onwards. The modern genus is currently restricted to the Bahamas and Greater Antilles.

CONCLUSIONS

A systematic revision and redescription of the representative material of *Pseudoepicrates* highlights a particularly confusing and problematic interpretive history. The erection of two species of *Neurodromicus* ignored the intracolumnar variation amongst the specimens. Subsequent work proposed the synonymy of *Pseudoepicrates* with *Boa constrictor* (Kluge, 1988a; Albino, 2011). However, as demonstrated here, a series of anatomical differences between modern *Boa* and the fossil specimens argues against this relationship, as well as the attendant palaeobiogeographical inference of *B. constrictor* inhabiting the North American continent during the early Miocene. All of the *Pseudoepicrates* material analysed within, including the holotype, paratype and referred specimens, shares traits with the extant snake *Chilabothrus*, leading us to recognize the presence of an extinct species, *Chilabothrus stanolseni* **comb. nov.** within North America.

The presence of *Chilabothrus* in the early Miocene of Florida has implications for the historical biogeography of the taxon, and is consistent with previous studies based on molecular divergences. Based on our analysis, the genus probably originated in South America prior to its dispersal to Cuba. Once on the island complex, it reached the North American mainland during the early Miocene, becoming later extinct, possibly due to being maladapted for the cooler temperatures (Henderson *et al.*, 1995) that resulted from climatic oscillations at the Neogene/Quaternary boundary (Peizhen *et al.*, 2001). The remaining populations on the island complex diversified throughout the Quaternary, with increased rates of dispersion between islands facilitated by abiotic events, such as a decrease in ocean level and the regular advent of hurricanes, leading to the current diversity of species found on the West Indian complex. The presence of *Chilabothrus stanolseni* **comb. nov.** within the Thomas Farm deposit represents the oldest (and currently only) fossil record of the genus and, in addition to establishing a minimum age for dispersal from South America, could be used to infer a minimum age for the clade and contribute to further combined (molecular and morphological) phylogenetic analyses of boid relationships.

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