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***Colemanus keeleyorum* (Braconidae, Ichneutinae s. l.): a new genus and species of Eocene wasp from the Green River Formation of western North America**

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Abstract

A new genus and species of Ichneutinae s. l., *Colemanus keeleyorum* Fisher, is described from the Eocene Green River Formation in Colorado, USA. *Colemanus* was placed on a phylogenetic hypothesis using morphological data. Using a parsimony criterion, *Colemanus* is placed within Proteropini (Ichneutinae s. l.). Reconstructions of well-preserved regions (mesosomal dorsum and wings) are included. A previously described species from lower Oligocene Baltic amber is transferred to *Colemanus*, resulting in the new combination *C. contortus* (Brues, 1933).

Keywords

Microgastriinae, Microgastroidea, Proteropini, Proteropinae, fossil placement

Introduction

Herein we describe *Colemanus keeleyorum* gen. n. et sp. n. (Braconidae: Ichneutinae s. l.) from the Eocene Green River Formation in the western United States. The Green River Formation represents one of the best documented ancient lake systems and has offered a particularly well preserved window into Eocene fauna. The formation is best known for fossil fish (Conrad et al. 2007), but other key discoveries include the oldest known bats: *Icaronycteris index* Jepsen, 1966 and *Onychonycteris finneyi* Simmons et al., 2008.

Recent collecting efforts by David Kohls (Colorado Mountain College) and colleagues have accumulated more than 120,000 specimens, including more than 2,000 insects. One specimen, a wasp collected in 2005 in the Parachute Member of the Piceance Creek Basin (northwestern Colorado), caught the attention of Jim Whitfield (University of Illinois) due to its resemblance to members of a large braconid assemblage called the microgastroid complex.

The microgastroid complex is a well-supported rapid radiation (e.g., Whitfield and Lockhart 2007, Whitfield and Kjer 2008, Murphy et al. 2008, Sharanowski et al. 2011) well-known for its association with host-immunosuppressing polydnviruses (e.g., Whitfield 2000). Overall, the relationships of subfamilies within the complex are poorly understood due to the rapid nature of their diversification (Whitfield and Lockhart 2007, Whitfield and Kjer 2008), but two relationships are clear. First, Cheloninae is sister to all other subfamilies (Whitfield 1997, Dowton and Austin 1998, Dowton et al. 1998, Belshaw et al. 2000, Banks and Whitfield 2006, Murphy et al. 2008, Sharanowski et al. 2011). Second, Ichneutinae s. l., usually excluded from the microgastroid complex because members are not known to contain polydnviruses, is sister to the microgastroid complex (Quicke and van Achterberg 1990, Belshaw et al. 2000, Belshaw and Quicke 2002, Dowton et al. 2002, Murphy et al. 2008, Sharanowski et al. 2011).

Ichneutinae has received considerable attention and endured a chaotic taxonomic history, despite its relatively small size of approximately 100 species (Sharkey 1994, Yu et al. 2005). Three lineages are recognized and traditionally assigned to the tribal level (Proteropini, Ichneutini, and Muesebeckiini); however, tribal designation has been disputed (Sharkey 1994, 1996). Although normally treated as a single subfamily, phylogenetic analysis often renders Ichneutinae paraphyletic (e.g., Quicke and van Achterberg 1990, Belshaw et al. 2000, Dowton et al. 2002, Sharanowski et al. 2011). The most rigorous of these analyses, which investigated multiple ribosomal and nuclear genes, recovered Proteropini as sister to microgastroids and Ichneutini as sister to that complex (Sharanowski et al. 2011). The affinities of the highly-derived muesebeckiines remain unknown as they were excluded from that analysis.

Placing the fossil within the Ichneutinae s. l. + microgastroid complex is difficult due to its resemblance to several lineages. Specifically, the fossil resembles Cardiochilinae because the last abscissa of the fore wing radial sector (3RSb) is recurved, although unlike many cardiochilines this vein remains tubular as it reaches the wing margin; and it resembles Proteropini (Ichneutinae s. l.) because the first abscissa of the fore wing media (1M) is evenly curved. Some Cheloninae also share these characters, but are readily differentiated by the presence of a metasomal carapace.

To determine the fossil's affinity, we placed it on a phylogenetic hypothesis for Braconidae (Sharanowski et al. 2011) using a parsimony criterion (tree length) of morphological characters. The dataset was expanded by adding taxa superficially resembling the fossil (*Bohayella* and *Schoenlandella* (Cardiochilinae); *Helconichia* (Proteropini)). The method implemented herein has the benefit over a standard analysis of easily comparing alternative placements of the fossil.

Materials and methods

The photographs of *Colemanus* gen. n. (Fig. 1) were taken with a JVC KY-F75 3CCD digital camera and prepared with Archimed™ by Microvision Instruments. Reconstructions (Fig. 2) were created by tracing these photographs in Adobe Illustrator CS4, and by editing in Adobe Photoshop CS4. Unfortunately, the metasoma and legs did not preserve during fossilization (or are obscured by the rock matrix), and the head is crushed, offering no codable characters for these regions. The wings are remarkably preserved, complete with wing setae, whereas the dorsal mesosoma and antennae are moderately well preserved.

Thirteen characters (Table 1) were selected from Sharkey and Wharton (1994, with corrections in Sharkey 1996), Sharkey (1997), and Dangerfield et al. (1999), and were modified to reflect characters discernible in the fossil.

Table 1. Description of characters and character states. Sources: 1) Sharkey and Wharton (1994, with corrections in Sharkey 1996); 2) Sharkey (1997); 3) Dangerfield et al. (1999).

Characters	States	Code	Source
1. Fore wing 3RSb	recurved	0	2, 3
	straight	1	
2. Fore wing 3RSb	reaching wing margin as tubular vein	0	2, 3
	not reaching wing margin as tubular vein	1	
3. Fore wing 2RS	strongly curved	0	2
	straight	1	
4. Fore wing (RS+M)b	longer than its width	0	2
	equal to, or shorter than its width	1	
5. Fore wing 1cu-a origin	nearly in line with M	0	2
	not in line with and often far distal to M	1	
6. Fore wing 1cu-a angle	toward apex	0	1
	not toward apex	1	
7. Fore wing 1M	straight or slightly curved	0	2
	evenly curved or bent at mid-length	1	
	apically bent toward wing tip	2	
8. Fore wing 1a	present	0	2
	absent	1	
9. Hind wing M+Cu length	≥ 1st abscissa of M	0	2
	< 1st abscissa of M	1	
10. Hind wing crossvein r	present	0	2
	absent	1	
11. Hind wing M+Cu position	posterior half of wing	0	1, 3
	anterior half of wing	1	
12. Notauli	deep, wide, meeting posteromedially	0	1
	relatively reduced	1	
13. Propodeum	with areolate sculpture	0	2
	without areolate sculpture	1	

Table 2. Character matrix.

Taxa	Characters: 1234567890123
Meteoroidea (<i>Meteoroidea</i>)	1010100101111
Agathidinae (<i>Earinus</i>)	1010000101111
Ichneutini (<i>Ichneutes</i>)	1010012001110
Proteropini (<i>Proterops</i>)	1000111001111
Proteropini (<i>Muesonia</i>)	1011011001100
Proteropini (<i>Helconichia</i>)	1001011001100
Cheloninae (<i>Phanerotoma</i>)	1010100101110
Mendesellinae (<i>Epsilogaster</i>)	1100100101110
Khoikhoiinae (<i>Khoikhoia</i>)	0110100000111
Cardiochilinae (<i>Heteropteron</i>)	0110110110111
Cardiochilinae (<i>Bohayella</i>)	0110100010100
Cardiochilinae (<i>Cardiochiles</i>)	0110110110110
Cardiochilinae (<i>Schoenlandella</i>)	0110110111100
Microgastrinae (<i>Snellenius</i>)	1110100100100
Microgastrinae (<i>Microplitis</i>)	1110100101101
<i>Colemanus</i> gen. n.	0001101001000

Taxa included (Table 2) were based upon the molecular analysis of Braconidae presented by Sharanowski et al. (2011) with the following modifications: 1) highly derived groups were excluded (e.g., Miracinae); 2) sampling of Cardiochilinae was increased given the superficial resemblance of certain genera to *Colemanus* (*Bohayella* and *Schoenlandella*); 3) *Heteropteron* was added due to its basal placement within Cardiochilinae (Dangerfield et al. 1999); 4) although Sharanowski et al. (2011) included only two of the five proteropine genera (*Proterops* and *Muesonia*), we added *Helconichia* due to its resemblance to the fossil.

Fossil placement was investigated with Mesquite 3.01, which allows for quick repositioning of branches while calculating the number of character substitutions (tree length) (Madison and Madison 2014). Tree topology was constrained to the relationships elucidated in previous studies (Sharanowski et al. 2011, Dangerfield et al. 1999). To analyze the matrix on the constrained topology, the fossil was placed at every node and tree lengths were compared to assess the most parsimonious placement. Given the uncertain relationships among Proteropini, our analyses were carried out with each possible relationship of the three included genera (Fig. 3A–C). Figures were created with Adobe Illustrator CS6.

Results

Morphology: Reconstruction of the whole body was not possible, given the poorly preserved head, legs, and metasoma (Fig. 1). Additionally, although the mesosoma contained sections preserved in excellent detail, the overall quality prevented complete reconstruction. Nevertheless, a nearly complete reconstruction of the dorsal mesosoma was possible (Fig. 2A). Some interpretations should be considered “best guesses”, as

they were poorly preserved. These characters are as follows: the degree of notauli sculpturing posteriorly, the medial carina on the lateral scutellum, and the carinae on the lateral metanotum.

The remarkably preserved wings provided most detail and were the principle units used in morphology. Both wings showed some bending, so both wings were used to create a composite hypothesis for wing veins (Fig. 2B). Areas of the wing where unbiased reconstruction were impossible include the apparently non-tubular region surrounding (RS+M) b (Fig. 1C), the apical non-tubular limits of the fore wing media and cubitus, and the apical non-tubular limits of the hind wing radial sector and media. Noteworthy is that (RS+M) b appears to be vertical, which is a rare character for all braconids, although this region is difficult to interpret. Also, the last abscissa of the radial sector (3RSb) is recurved, lending the resemblance to Cardiochilinae and some Cheloninae, although 3RSb in cardiochilines is not tubular as it reaches the wing margin and chelonines have a metasomal carapace.

Despite the great condition of the antennae, no characters could be extracted except flagellomere number (33–34), which itself is inconclusive due to the indiscernible basal antennomeres. Regardless, there are more antennomeres than in other described proteropines (24–31). However, given the variability of this character across Ichneutinae s. l. (12–38), this difference is not considered informative at the level of our analyses and is not included in the matrix.

Morphological phylogenetics: Tree lengths representing placement of *Colemanus* at each possible node can be viewed in Figure 3, across the three possible relationships of Proteropini (A–C). Without the addition of *Colemanus*, total tree lengths varied (33–35) depending on the arrangement of Proteropini (boxed values in Fig. 3). Adding *Colemanus* raises total tree lengths to a minimum of 36 (when placed sister to *Helconichia*+*Muesonia*, given the topology in Fig. 3A) and a maximum of 44 (when placed sister to *Cardiochiles*, given the topology in Fig. 3C). For each topology, the most parsimonious placement of *Colemanus* is within Proteropini.

We conclude from these findings that *Colemanus* should be placed within Proteropini, although given the uncertainty of proteropine relationships, exact placement within this group is not yet feasible. The fossil contains character states that do not fit within any current genus. Therefore, we suggest placement within a new genus, *Colemanus*.

Taxonomy

Braconidae Stephens, 1829

Ichneutinae Förster, 1862

Colemanus Fisher, gen. n.

<http://zoobank.org/DBB8F27A-3FB4-4740-8719-FF760BC6E150>

Figs 1–3

Type species. *Colemanus keeleyorum* Fisher, sp. n.

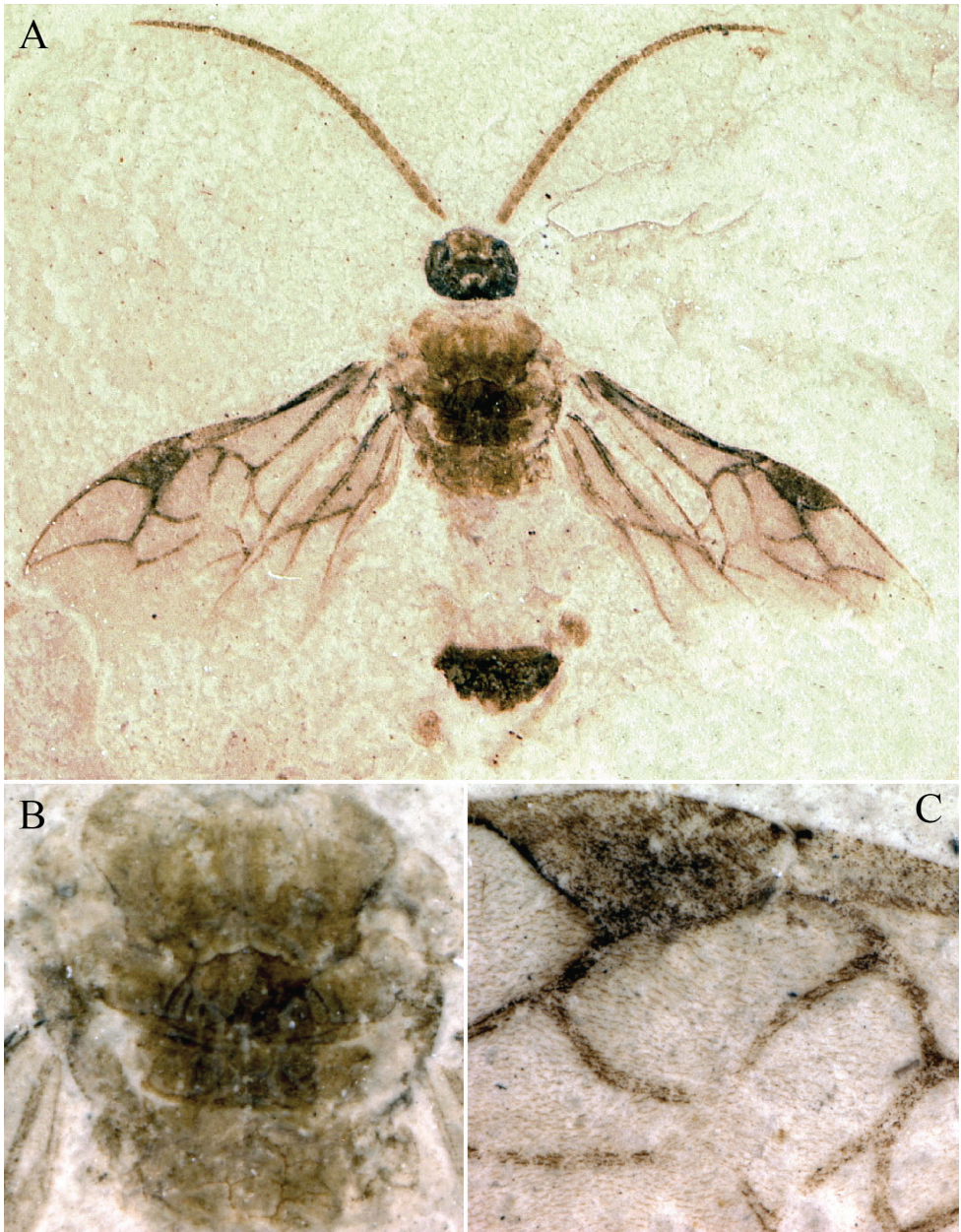


Figure 1. Fossil of *Colemanus keeleyorum* sp. n.: **A** whole fossil **B** close-up of mesosoma **C** close-up of left pterostigma, note preserved microtrichia.

Diagnosis. There are several similarities between *Colemanus* and other braconids, specifically Cardiochilinae and Cheloninae. Like *Colemanus*, some Cheloninae have a recurved 3RSb and an evenly curved 1M. However, chelonines possess a metasomal

carapace. *Colemanus contortus* comb. n. lacks a carapace (Brues 1933) and although the metasoma of *C. keeleyorum* sp. n. is not completely visible, it seems apparent that it also lacks a metasomal carapace (Fig. 1A). Thus, the lack of a metasomal carapace distinguishes *Colemanus* from Cheloninae. *Colemanus* also resembles many Cardiochilinae in having a recurved 3RSb and heavily sculptured mesosoma, but can be readily distinguished by 3RSb remaining tubular as it reaches the wing margin.

Colemanus can be distinguished from other Ichneutinae s. l. by the presence of a curved 3RSb; fore wing 1cu-a curved downward, not angled toward wing margin; hind wing M+Cu positioned in the posterior half of the wing; and a heavily sculptured mesosoma.

Etymology. Named for bodybuilder Ronnie Coleman, who was famous for his back; referring to the robust and sculptured nature of the mesosomal dorsum.

Colemanus keeleyorum Fisher, sp. n.

<http://zoobank.org/AC0F5EA3-4526-43FD-85F3-4544FFC0EF5E>

Figs 1–2

Diagnosis. *Colemanus keeleyorum* can be distinguished from *C. contortus* (Brues, 1933) (new combination; see below) by having curved (RS+M)a and 2RS veins in the fore wing (straight in *C. contortus*). Also, *C. keeleyorum* is only known from the western United States (Eocene) and *C. contortus* is only known from the Baltic region (lower Oligocene).

Description. Holotype (n = 1): body length 9 mm (estimated due to incomplete metasoma); sex unknown. **Head** (Fig. 1A) 1.4 mm long and 1.7 mm wide. Antenna 7.2 mm long with 33–34 flagellomeres. **Mesosoma** (Figs 1B, 2A) 3.8 mm long and 3.3 mm wide; robust and heavily sculptured; notauli deeply crenulate; scutellum with crenulate depression medio-posteriorly; side of scutellum deeply hollowed with crenulate carinae and bordered by prominent carinae; metanotum with median, raised, rectangular tubercle having radiating carinae; scutellar sulcus with carinae; propodeum with areolate sculpturing. **Wings** (Figs 1A,C, 2B) with last abscissa of fore wing radial sector (3RSb) recurved and tubular as it reaches the wing margin; (RS+M)b short, nearly vertical; 1cu-a originating far distal to M and curving downward, thus not angling toward wing apex; fore wing M curved; tubular portion of 1a long; C+SC and R closely fused; second abscissa of RS strongly curved; parastigma well-developed; hind wing M+Cu longer than first abscissa of M; hind wing r-crossvein absent; hind wing M+Cu in posterior half of wing; 1A strongly developed.

Biology. Unknown. However, placement within Proteropini is suggestive of shared biology, koinobiont endoparasitoids of sawflies.

Remarks. Wings, antennae, and dorsal mesosoma are overall well-preserved; metasoma and legs either did not completely fossilize or are obscured by the rock matrix; head is crushed.

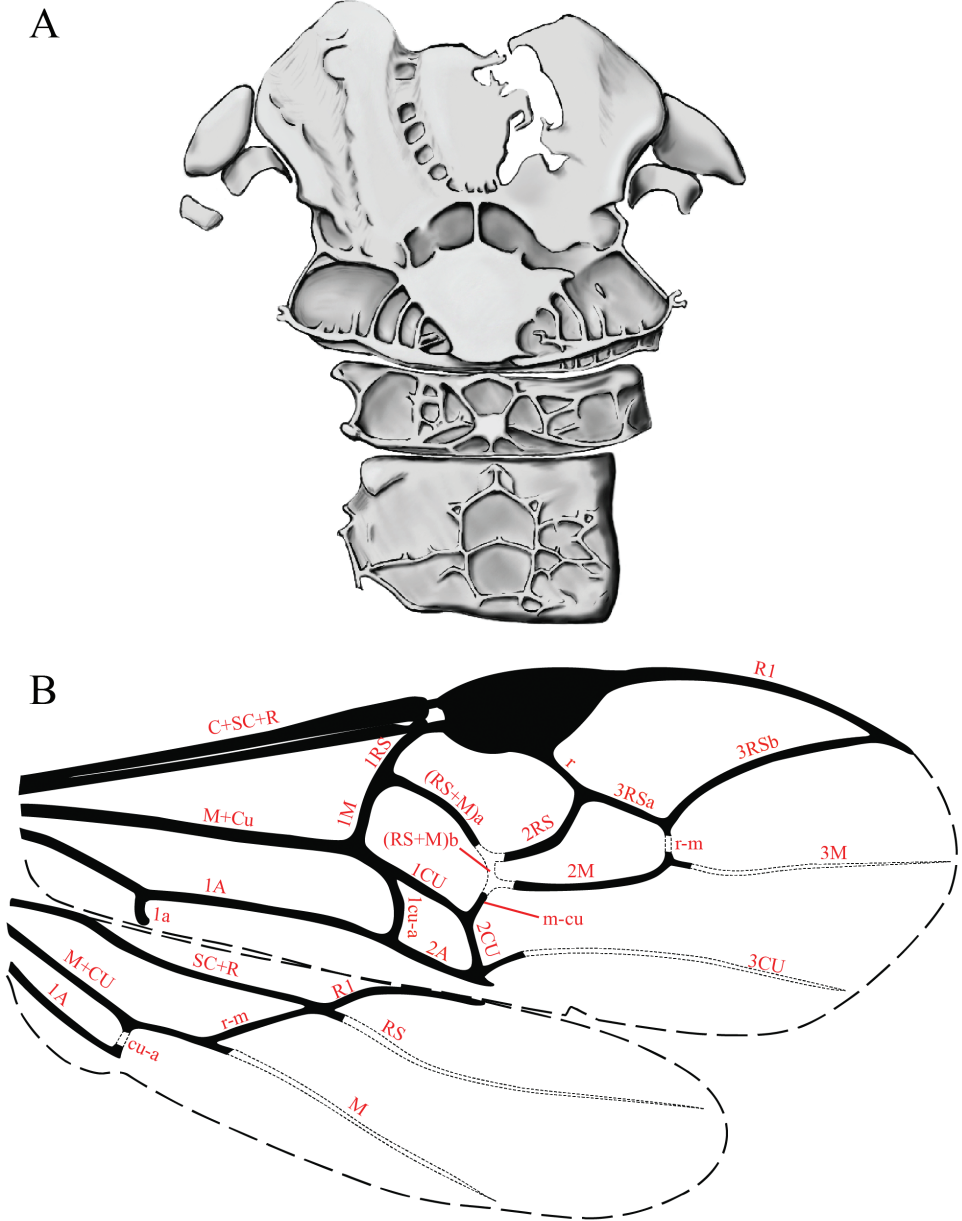


Figure 2. Reconstructions of *Colemanus keeleyorum* sp. n.: **A** dorsal mesosoma, note heavy sculpturing **B** wings, note last abscissa of forewing radial sector (3RSb) is recurved.

Etymology. Named for Dr. Jack and Flo Keeley, who, together with their daughter and her husband (first author’s mother & father), were largely responsible for the first author’s pursuit of the natural sciences.

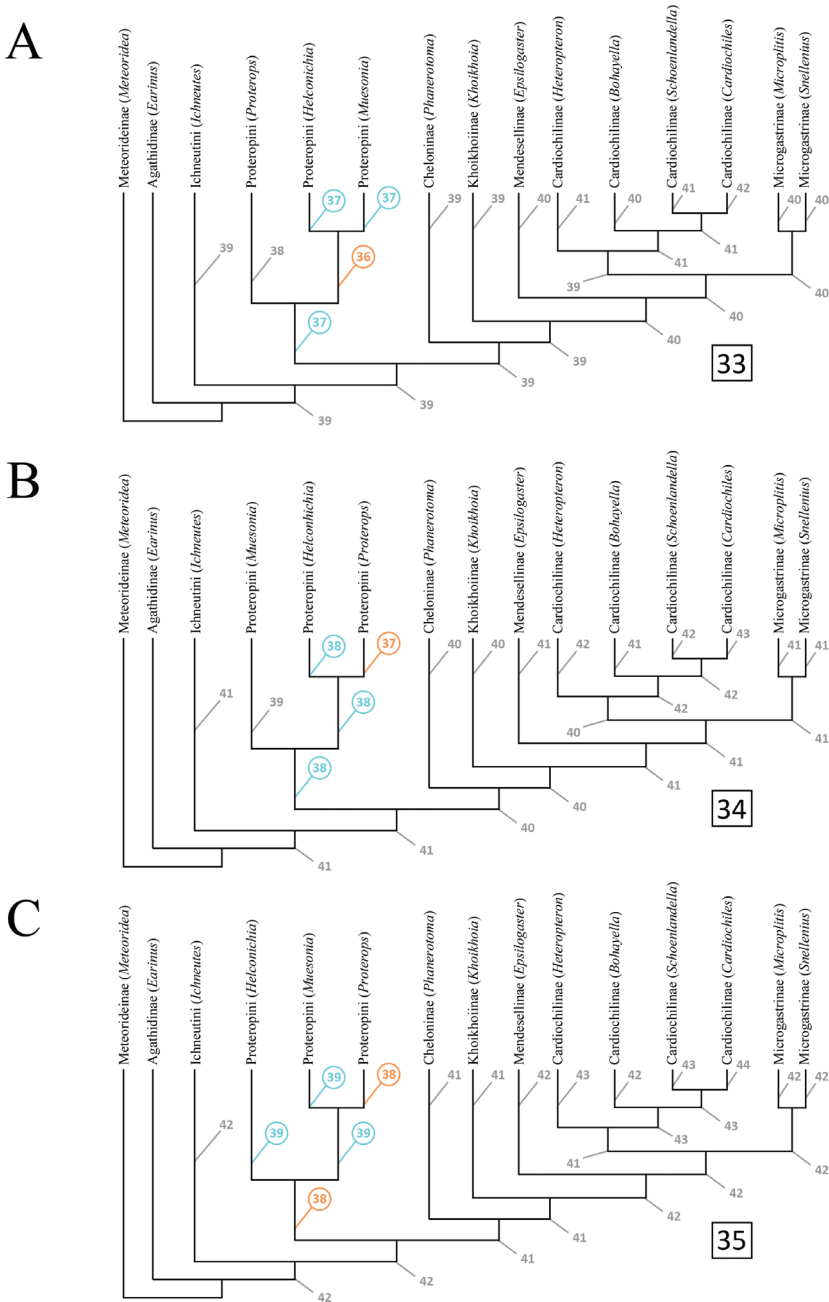


Figure 3. Placement of *Colemanus* gen. n. with known relationships of extant taxa: **A–C** represent the three possible relationships between included Proteropini. Numbers on branches represent total tree length when *Colemanus* is placed at that location. Circled numbers are most parsimonious placements (most parsimonious in orange; second-most in blue). Number boxes are total tree lengths of that topology when *Colemanus* is excluded. Note that lowest tree lengths are always achieved when *Colemanus* is placed within Proteropini.

Material examined. HOLOTYPE: USA, Colorado, Piceance Creek Basin, Parachute Member, 2005. Deposited with the David Kohls collection in the Smithsonian Institution, Museum of Natural History, Washington D.C.

***Colemanus contortus* (Brues, 1933), comb. n.**

Remarks. Two other fossil ichneutines have been described, both from Baltic amber of the lower Oligocene (Brues 1933): *Ichneutes stigmaticus* and *I. contortus*. The illustration of *I. stigmaticus* (Brues 1933: pl. 10 fig. 58) is not similar to *Colemanus*. However, the description for *I. contortus* (Brues 1933: pg. 89–90; pl. 10 fig. 50) is consistent with *Colemanus* in having "coarsely crenulated" notauli (pg. 90) and a fore wing (pl. 10 fig. 50) with recurved 3RSb and nearly vertical (RS+M)b. Further, fore wing 3RSb appears to be tubular as it reaches the wing margin (unlike Cardiochilinae); a carapace is absent (unlike Cheloninae); and 1M is evenly curved (consistent with Proteropini). Therefore, we suggest the new combination *Colemanus contortus* (Brues, 1933).

The material Brues (1933) examined is part of the Königsberg collection. Most of this collection was rescued and is housed at the Geowissenschaftliches Museum (Göttingen, Germany), though some of Brues's collection, which included some of the Königsberg collection, remains at Harvard University, his old institution. However, neither the Museum of Comparative Anatomy (Harvard), nor the Geowissenschaftliches Museum could locate Brues's 1933 material, including *Ichneutes contortus*. The problem is exacerbated by the fact that Brues did not include catalog numbers in his description or any other information regarding deposition. Therefore, the holotype of *I. contortus* should be considered lost.

Key to *Colemanus* gen. n.

- 1 Fore wing (RS+M)a and 2RS straight; Palaearctic..... ***C. contortus* comb. n.**
- Fore wing (RS+M)a and 2RS curved; Nearctic ***C. keeleyorum* sp. n.**

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