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A NEW SPECIES OF THE PLEISTOCENE FURNARIID *PSEUDOSEISUROPSIS* (AVES, PASSERIFORMES)

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ABSTRACT—*Pseudoseisuropsis wintu* sp. nov. is described from cranial material that had formerly been designated as a paratype of the extinct *Pseudoseisuropsis nehuen*. Thorough comparisons were made between the cranial specimens ascribed to *Pseudoseisuropsis* and many extant furnariid species. This new species is lower Pleistocene in age and increases the known diversity of *Pseudoseisuropsis* to three species. Cladistic analyses were performed using 43 cranial characters and a backbone constraint based on a well-supported phylogeny from a recent molecular analysis. In the most parsimonious tree, *Pseudoseisuropsis* was retrieved as a sister group of woodcreepers (Dendrocolaptinae) with low support. However, slightly suboptimal hypotheses, which could not be completely ruled out, suggest that this genus may be more closely related to other clades of Furnariidae. Hence, we agree with previous authors in regarding *Pseudoseisuropsis* as Furnariidae Incertae sedis. In addition, two fragmentary fossils ascribed to *Pseudoseisuropsis* were included in taxonomic comparisons: *P. cuelloi*, in order to assess the possibility that *P. wintu* sp. nov. belongs to that species, and another paratype of *P. nehuen*, to reassess its taxonomic identity.

<http://zoobank.org/urn:lsid:zoobank.org:pub:D26FF563-B9DB-48BD-BA9F-8C54CD13F03E>

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

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INTRODUCTION

Ovenbirds and woodcreepers, family Furnariidae (sensu Remsen et al., 2014), are major constituents of the Neotropical avifauna (Marantz et al., 2003; Remsen, 2003). They occur from northern Mexico to southern Argentina, occupying every terrestrial and water-edge habitat (Skutch, 1996; Remsen, 2003), and exhibit tremendous morphological and architectural nest diversity (Zyskowski and Prum, 1999). The family includes 293 extant species in 69 genera (Remsen et al., 2014).

The fossil record of furnariids is scarce and consists of only six species reported from Argentina, Uruguay, and Brazil (Marantz et al., 2003; Remsen, 2003; Claramunt and Rinderknecht, 2005). Two of them belong to the genus *Pseudoseisuropsis* Noriega, 1991. This is the only furnariid genus without extant representatives and it occurred in the Pampean Region at least from the early to the late Pleistocene.

The type species of the genus is *Pseudoseisuropsis nehuen* Noriega, 1991, which is represented by two incomplete skulls (the holotype MLP69-XII-3-1 and the paratype MMP570-M), one fragmentary rostrum (the paratype MMP5667), and several postcranial elements (paratypes under the batch MMP5666). The other species of the genus, *P. cuelloi* Claramunt and Rinderknecht, 2005, is represented by an incomplete rostrum.

Preliminary observations revealed differences among specimens ascribed to *P. nehuen*. Therefore, thorough comparisons

considering qualitative as well as quantitative features were made in order to reappraise their taxonomic status. These comparisons also included *P. cuelloi* and a wide array of extant furnariids. It is noteworthy that the comparison of the paratype MMP5667 with the other cranial materials of *Pseudoseisuropsis* and the comparison between the paratype MMP570-M and *P. cuelloi* had not been made previously.

The evolutionary relationships of *Pseudoseisuropsis* within Furnariidae, although previously investigated, remain unclear (Noriega, 1991; Tonni and Noriega, 2001; Claramunt and Rinderknecht, 2005). In order to clarify these relationships, cladistic analyses were performed here using skull characters of the fossils, as well as many extant furnariids. Because osteological traits are not useful to fully clarify phylogenetic relationships within passerines at lower taxonomic levels in general (Oswald and Steadman, 2011) and among Furnariidae in particular (Claramunt and Rinderknecht, 2005), the analyses were performed using a backbone constraint based on a recent large-scale molecular phylogeny.

Institutional Abbreviations—**AMNH**, American Museum of Natural History, New York, New York; **FCEN**, Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires, Buenos Aires, Argentina; **MACN**, Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia', Buenos Aires, Argentina; **MLP**, Museo de La Plata, Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, La Plata, Argentina; **MLP PV-OR**, Colección Anexa de osteología de aves actuales de la División Paleontología de Vertebrados, Museo de La Plata, Facultad de Ciencias Naturales y Museo, Universidad Nacional

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FIGURE 1. Map showing provenance of the fossil materials in the Pampean Region, Argentina. **Abbreviations:** PH, Punta Hermengo, Miramar, holotype MLP 69-XII-3-1 of *Pseudoseiuropsis nehuen*; SE, near Santa Elena (Camet Norte), north of Mar del Plata, paratypes MMP570-M and MMP5667 of *Pseudoseiuropsis nehuen*; SL, Balneario San Luis, Department of Canelones, holotype MNHN 1634 of *Pseudoseiuropsis cuelloi*.

de La Plata, La Plata, Argentina; **MMP**, Museo Municipal de Mar del Plata “Lorenzo Scaglia”, Mar del Plata, Argentina; **MNHN**, Museo Nacional de Historia Natural y Antropología, Montevideo, Uruguay; **UF**, Florida Museum of Natural History, University of Florida, Gainesville, Florida; **USNM**, National Museum of Natural History, Smithsonian Institution, Washington, D.C.

MATERIALS AND METHODS

Fossil Material—The four known cranial specimens ascribed to *Pseudoseiuropsis* came from the South American Pampas (Fig. 1). MMP570-M and MMP5667 are stored in the Museo Municipal de Mar del Plata; MLP69-XII-3-1 and MNHN 1634 are stored in Museo de La Plata and Museo Nacional de Historia Natural y Antropología, respectively.

Comparative Specimens—Dry skulls of extant species of Furnariidae were examined for the osteological descriptions, phylogenetic analysis, and coefficient of variation (CV) comparisons. In addition, data were taken from published drawn and photographed skulls (in ventral, lateral, and dorsal views) of several species unavailable in the collections we visited. Information about the specimens mentioned above is provided in Table S1

included in Supplementary Data 1. These specimens together represent all the major lineages of Furnariidae, including 34 of the 69 genera recognized by Remsen et al. (2014).

Anatomical Terminology—The osteological nomenclature of Baumel and Witmer (1993) is followed, with Latin names of the osteological features mentioned herein provided in Appendix 1.

Measurements and Osteological Variation—In order to assess whether the variation observed in the population of *P. nehuen* exceeds the range of expected intraspecific variation among extant furnariids, we measured eight continuous traits in the skulls of the three fossil specimens ascribed to *P. nehuen* (Table 1) and 15 specimens of *Furnarius rufus* (Table S2 in Supplementary Data 1). We calculated the CVs for each trait to determine the level of variability and allow meaningful comparisons (Table 2). Due to the small fossil sample size ($n \leq 4$), no statistical test to assess significance could be used. Thus, CVs were compared directly by evaluating the superposition of 95% confidence intervals (CIs) estimated by bootstrapping (simple bootstrap with 9,999 replicates). Those traits that showed marked variation in our intraspecific analysis (i.e., their CIs do not overlap) were also evaluated in an interspecific context. This allowed us to assess whether interspecific variation exceeds the level of variation within a genus. This was done by adding three additional species of *Furnarius* and data on *P. cuelloi* to the evaluation of one of the characters (Table 2).

In the interspecific analysis, MLP69-XII-3-1-M, MMP5667, and MMP570-M (all of them formerly ascribed to *P. nehuen*) were treated as different entities to test their specific identities. Because some measured values of continuous traits did not exactly match those previously reported (Noriega, 1991; Claramunt and Rinderknecht, 2005), a figure was included showing how these measurements were taken (Fig. S1 in Supplementary Data 1). Specimens available only from photos were measured digitally with image software Screen Caliper 4.0 (Iconico Inc., New York, New York). Although no significant differences between measurements taken digitally and those taken with calipers were found, specimens available as dry skulls were photographed in dorsal, lateral, and ventral views and then measured digitally to avoid potential differences between the methods. In the particular case of *P. cuelloi*, measurements were taken on photos obtained from the literature (Claramunt and Rinderknecht, 2005: fig. 1A–C).

Cladistic Analysis—The phylogenetic analyses were performed using maximum parsimony as the optimality criterion. The fossil skull specimens of *Pseudoseiuropsis* (i.e., MMP570-M, MMP5667, MLP69-XII-3-1, and MNHN 1634) were included in a data matrix of 43 cranial osteological characters (Appendix 1) coded for 43 species of extant furnariids and *Thamnophilus ruficapillus* (Thamnophilidae). The latter was used to root the topology (see character-taxon matrix in Appendix 2 and in the Furnariidae.tnt file provided in Supplementary Data 2). Many of these characters are from Claramunt and Rinderknecht (2005) and Kopuchian (2008), but 11 new characters primarily concerning the morphology of the nasal bars, palate, ectethmoid plate, and orbital and temporal regions of the skull were added (Appendix 1).

TABLE 1. Measures (in millimeters) of the morphometric traits of fossil materials ascribed to *Pseudoseiuropsis* used for coefficient of variation comparisons. **Abbreviations:** BL, braincase length; BW, braincase width; DBW, dorsal bar width; EPW, ectethmoid plate width; IAW, interorbital area width; PRL, premaxillary rostrum length; PRW, premaxillary rostrum width; RL, rostrum length.

Species	PRL	DBW	PRW	RL	EPW	IAW	BW	BL	Specimen
<i>Pseudoseiuropsis nehuen</i>	13.45	2.20	5.03	26.70	11.60	4.96	23.60	27.40	MLP69-XII-3-1
<i>Pseudoseiuropsis wintu</i>	12.85	3.01	5.95	25.4	12.04	6.16	22.29	29.30	MMP570-M
Paratype MMP5667 of <i>P. nehuen</i>	—	2.33	5.76	—	—	—	—	—	MMP5667
<i>Pseudoseiuropsis cuelloi</i>	15.40	2.34	5.28	—	—	—	—	—	MNHN 1634

TABLE 2. Intraspecific and interspecific variation in selected skull measurements for specimens formerly attributed to *Pseudoseisuropsis nehuen* and the extant *Furnarius rufus* as assessed by coefficients of variation and confidence intervals. In the interspecific comparisons, *Furnarius* species analyzed include *F. rufus*, *F. l. leucopus*, *F. torridus*, and *F. figulus*. **Abbreviations:** **BL**, braincase length; **BW**, braincase width; **CI**, confidence interval; **CV**, coefficient of variation; **DBW**, dorsal bar width; **EPW**, ectethmoid plate width; **IAW**, interorbital area width; **PRL**, premaxillary rostrum length; **PRW**, premaxillary rostrum width; **RL**, rostrum length. Asterisks mean that the value is the same as reported in the intraspecific variation analysis.

	PRL	DBW	PRW	RL	EPW	IAW	BW	BL
Intraspecific variation								
CV <i>F. rufus</i>	8.68	10.17	8.17	8.05	4.61	5.80	2.60	3.04
CI <i>F. rufus</i>	5.5–14.5	8.04–14.78	6.08–12.51	5.65–14.62	3.54–6.31	4.04–8.23	2.07–3.4	1.99–4.68
n	6	15	14	6	15	15	15	15
CV <i>P. nehuen</i> ⁽¹⁾	3.22	17.30	8.70	3.36	2.63	15.26	4.04	4.74
CI <i>P. nehuen</i>	3.2–6.4	15.88–34.61	7.45–17.4	3.36–7.33	2.63–5.66	15.26–30.52	4.03–8.07	4.73–9.47
n	2	3	3	2	2	2	2	2
Interspecific variation								
CV <i>Furnarius</i> species	—	16.56	—	—	—	15.25	6.12	6.54
CI <i>Furnarius</i>	—	11.9–32.5	—	—	—	9.76–29.45	4.05–12.02	4.89–11.57
n	—	4	—	—	—	4	4	4
CV <i>Pseudoseisuropsis</i> ⁽²⁾	—	14.80	—	—	—	*	*	*
CI <i>Pseudoseisuropsis</i>	—	12.74–29.39	—	—	—	*	*	*
n	—	4	—	—	—	*	*	*

⁽¹⁾Values estimated using the holotype MLP69-XII-3-1 and paratype MMP570-M of *P. nehuen* for the eight traits evaluated plus the addition of MMP5667 measure in DBW and PRW traits.

⁽²⁾Values estimated using the holotype MLP69-XII-3-1 and the paratype MMP570-M of *P. nehuen* for the four traits evaluated plus the addition of *P. cuelloi* and MMP5667 in DBW trait.

Within the data matrix, several characters are morphometric ratios that were discretized by applying a cluster analysis to the data. States of each character were established by well-delimited clusters recovered in the distance trees. Cluster analyses were done in PAST v.3.0 (Hammer et al., 2001) using Euclidean distances. Multistate characters were treated as ordered during optimization when they entail clear morphoclines.

The evolution of cranial osteological characters was reconstructed by constraining relationships with a molecular scaffold tree (e.g., Springer et al., 2001; Gaubert et al., 2005). The latter was obtained by trimming the well-supported topology (>80% of nodes with posterior probability >0.95) of Derryberry et al. (2011) to our taxon sampling in Mesquite v.2.75 (Maddison and Maddison, 2011). This molecular-based phylogeny was then used as a backbone constraint in a morphological phylogenetic reconstruction, including extant species with fixed positions on the scaffold topology. Fossils were left as floating taxa to take any position on the tree. Two separate analyses were carried out: the first included only the holotype MLP69-XII-3-1 and paratype MMP 570-M of *P. nehuen* and the second included all known cranial specimens of *Pseudoseisuropsis*. Due to high levels of homoplasy in the data set, topologies up to two steps longer than in the most parsimonious tree (MPT) were also examined in the first analysis to explore slightly suboptimal alternative positions of *Pseudoseisuropsis*. The analyses were performed in TNT v.1.1 (Goloboff et al., 2008) under equal weights and each consisted of a heuristic search of 500 replicates of Wagner trees with random addition sequence of taxa followed by tree bisection and reconnection (TBR) branch swapping, holding ten trees per replication and collapsing branches of zero length after tree search. Node support was assessed by 1,000 bootstrap replicates in TNT.

SYSTEMATIC PALEONTOLOGY

Order PASSERIFORMES Linnaeus, 1758

Family FURNARIIDAE Gray, 1840 (sensu Remsen et al., 2014)

Genus *PSEUDOSEISUROPSIS* Noriega, 1991

Type Species—*Pseudoseisuropsis nehuen* Noriega, 1991

Included Species—*P. cuelloi* Claramunt and Rinderknecht, 2005

Revised Diagnosis—The ascription of *Pseudoseisuropsis* to Furnariidae is supported by three traits: the caudal extent of the nares is

slightly rostral to the craniofacial hinge; nares narrow caudally; and the culmen and tomia are uniformly decurved in lateral view. *Pseudoseisuropsis* is diagnosed by the following combination of features: temporal fossa with sinusoidal shape; orbital margin of quadrangular shape; parasphenoidal sheet with two conspicuous rostral projections on both sides; rostrum long and robust; premaxillary rostrum medium-sized (more than half but less than two thirds of the total length of the rostrum); nares bounded by thick bars, mainly the pila dorsal bar, which is vaulted and high in lateral view; olfactory sulcus deep, visible in the rostral and dorsal area of the interorbital septum; zygomatic process strongly developed, extending backwards in a conspicuous crest, being accentuated by the deep excavation of the temporal fossa; postorbital process short; temporal crest slightly marked; transverse nuchal crest prominent, dorso-ventrorostrally directed; foramen magnum medio-laterally expanded; mandibular process of quadrate with conspicuous lateral condyle.

PSEUDOSEISUROPSIS WINTU, sp. nov.

(Fig. 2)

Holotype—MMP570-M consists of a fragmentary braincase and rostrum (Fig. 2). The braincase lacks part of the frontal region and almost all of the squamosal, supraoccipital, parietal, and exoccipital regions of the right side. The left side is better preserved but also lacks an important part of the squamosal and exoccipital region (Fig. 2A, B). The rostrum is repaired, mainly in the narial region, and is somewhat rotated leftward with respect to the braincase. Quadrates, pterygoids, palatal elements, and jugal bars are absent (Fig. 2D).

Locality—Near Santa Elena (Camet Norte), north of Mar del Plata, Buenos Aires Province, Argentina.

Stratigraphic Origin—Lower levels of the Miramar Formation. Early Pleistocene.

Etymology—‘Wintu’ is a word of the Mapudungun language spoken by Mapuches, natives of south-central Chile and southwestern Argentina, and it means ‘old’ or ‘ancient’.

Diagnosis—Thick dorsal bar; lateral bars rostrally curved; rostrum length relative to the braincase shorter than in *P. nehuen*; premaxillary rostrum shorter and thicker than those of *P. nehuen* and *P. cuelloi*; tomia straighter in dorsal view; pronounced hump at the base of the culmen; frontal with interorbital area wider than in *P. nehuen*; laterosphenoid with vertical crest; parasphenoidal rostrum conspicuous; subcondylar fossa rostrally excavated.

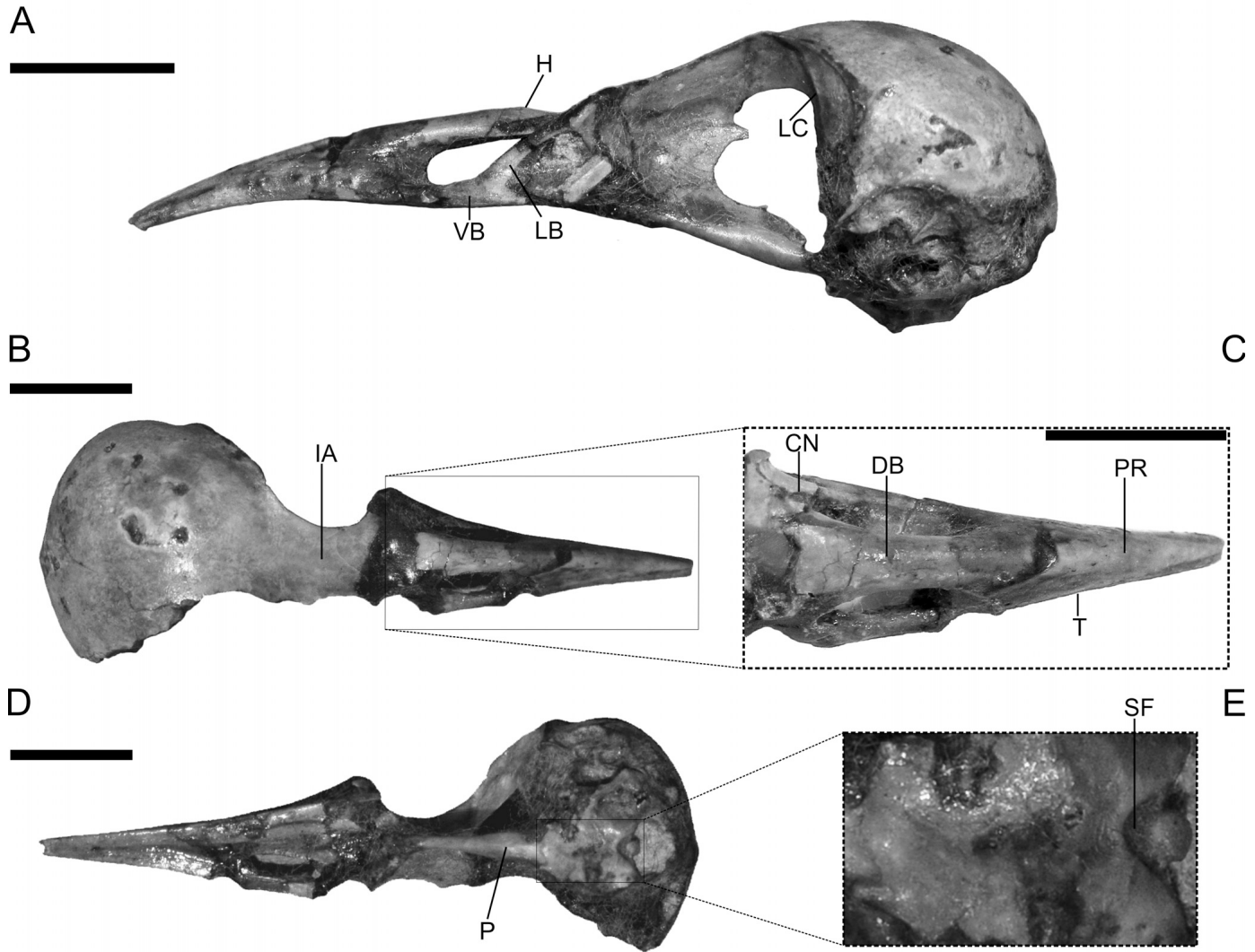


FIGURE 2. Skull of *Pseudoseiuropsis wintu*, sp. nov. (Holotype MMP570-M). **A**, left lateral view; **B**, dorsal view with the rostrum (narial and ectethmoid regions) covered with a dark layer of glue; **C**, close-up of the rostrum after restoration to remove glue; **D**, ventral view; **E**, close-up of basicranium. **Abbreviations:** CN, caudal region of nares; DB, dorsal bar; H, hump of culmen; IA, interorbital area; LB, lateral bar; LC, laterosphenoidal crest; P, parasphenoidal rostrum; PR, premaxillary rostrum; SF, subcondylar fossa; T, tomium; VB, ventral bar. Scale bars equal 1 cm.

Description and Comparisons—The rostrum is robust and long but is shorter than the braincase. The premaxillary rostrum is more robust and longer than in most furnariids (e.g., Furnariinae, Sclerurinae, and Xenopinae), being more than half but less than two thirds of the total length of the rostrum. However, the premaxillary rostrum is shorter than that of *P. nehuen* and even shorter than that of *P. cuelloi* (Table 1). In lateral view, like in the other fossils of *Pseudoseiuropsis*, both the culmen and the tomia are uniformly decurved and the rostrum resembles that of some philydorines (e.g., *Automolus ochrolaemus*, *Thripadectes holostictus*) or dendrocolaptines (e.g., *Xiphorhynchus guttatus*; Fig. 3A–E). Moreover, the base of the culmen bears a hump that is more pronounced than in other species of *Pseudoseiuropsis* (Fig. 2A). In dorsal view, the tomia are slightly concave like in many extant furnariids (e.g., *Thripadectes holostictus*). In *P. nehuen*, *P. cuelloi*, and MMP5667, on the other hand, the tomia are markedly laterally concave and, therefore, their rostra have a clear biconcave shape in dorsal view (Fig. 3F–J). The concavity observed in the tomia of the MMP5667 has a more rounded contour than those of *P. nehuen* or *P. cuelloi*.

In ventral view, the premaxillary rostrum of *P. wintu* has a median sulcus resembling that of *P. cuelloi* because it is caudally well delineated and becomes shallower rostrally, around three quarters of the length of the rostrum (Fig. 3L, O). In contrast, the median sulcus in *P. nehuen* is narrower, seemingly deeper than in *P. wintu*, and well delineated along the entire palatal surface of the premaxillary rostrum (Fig. 3N). Furthermore, in MMP5667, the median sulcus is caudally wider and shallower than in *P. wintu*, but it cannot be compared rostrally because the rostrum tip is lost (Fig. 3M). This sulcus is also present in many of the examined extant furnariids (e.g., *Thripadectes holostictus*; Fig. 3K).

Species of *Pseudoseiuropsis* have thicker narial bars than most furnariids (with the exception of many species of Dendrocolaptinae; Fig. 3B–E). Specifically, *P. wintu* has a dorsal bar that is remarkably thick in relation to those of the other members of the genus (Fig. 2C). The dorsal bar of MMP5667 is narrower than that of *P. wintu* and it is similar to that in *P. cuelloi* and *P. nehuen* (Table 1). The dorsal bar of *P. wintu* is further distinguished by the absence of a slender sulcus in the middle of the dorso-caudal surface that is present in *P. nehuen* (Fig. 3I).

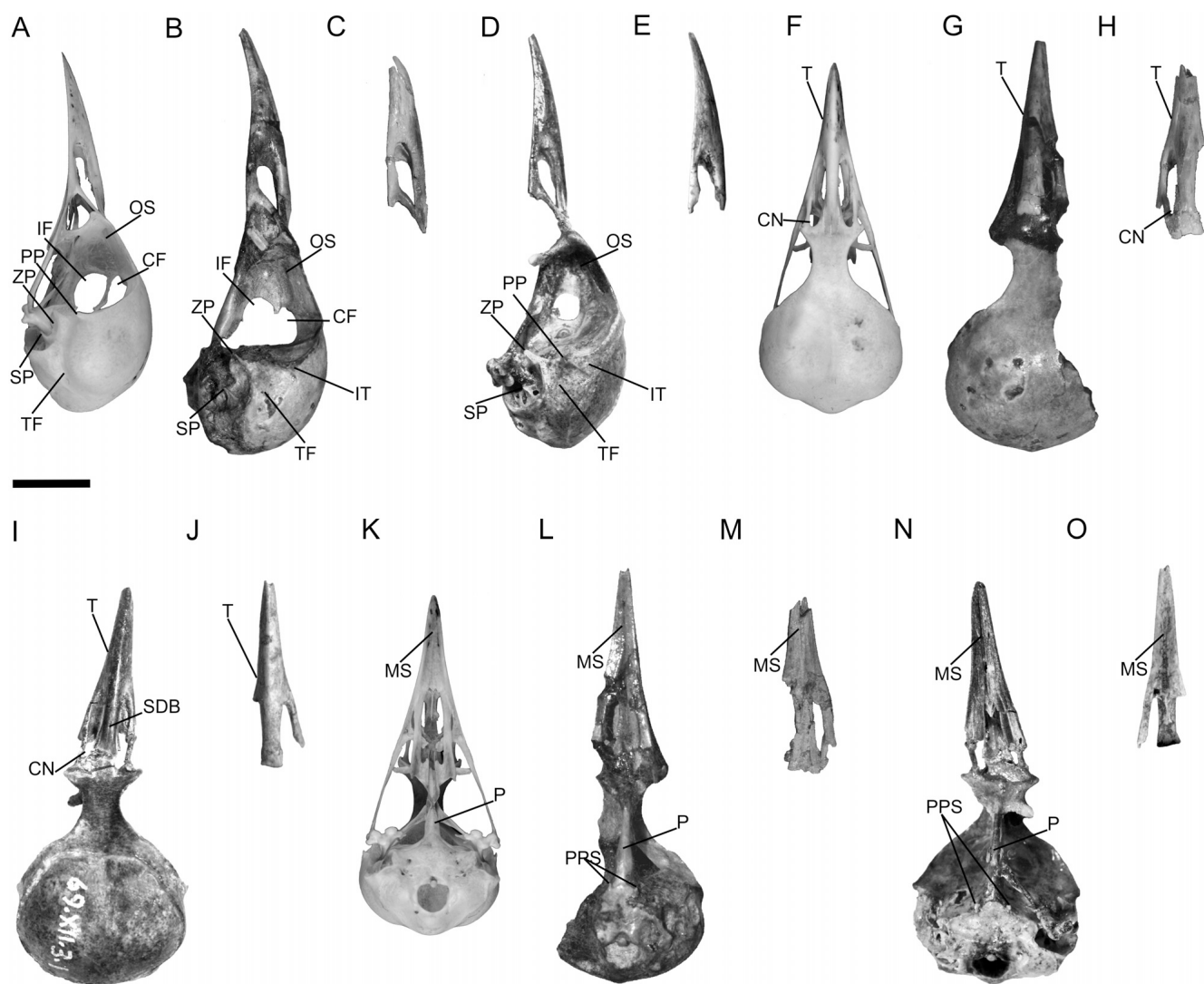


FIGURE 3. Comparisons among fossils of *Pseudoseiuropsis* and extant furnariids: **A**, **F**, and **K**, the extant furnariid *Thripadectes holostictus*; **B**, **G**, and **L**, holotype MMP570-M of *P. wintu*; **C**, **H**, and **M**, paratype MMP5667 of *P. nehuen*; **D**, **I**, and **N**, holotype MLP 69-XII-3-1 of *P. nehuen*; **E**, **J**, and **O**, holotype MNHN 1634 of *P. cuelloi* (modified from Claramunt and Rinderknecht 2005); **A**–**E**, left lateral view; **F**–**J**, dorsal view; **K**–**O**, ventral view. **Abbreviations**: **CF**, cranial fenestra; **CN**, caudal region of nares; **IF**, interorbital fenestra; **IT**, inverted-triangle region; **MS**, median sulcus; **OS**, olfactory sulcus; **P**, parasphenoidal rostrum; **PP**, postorbital process; **PPS**, projections of parasphenoidal sheet; **SDB**, sulcus of dorsal bar; **SP**, suprameatic process; **TF**, temporal fossa; **T**, tomium; **ZP**, zygomatic process. Scale bar equals 1 cm.

Specimen MMP5667 and *P. cuelloi* also lack this sulcus. In *P. wintu* and MMP5667, the lateral bars are curved rostrally, thus differing from the straight bars of the holotype of *P. nehuen* (in *P. cuelloi*, these bars are not preserved; Fig. 3B–E). *Pseudoseiuropsis wintu* and MMP5667 have rostrally thicker ventral bars than those of *P. nehuen* and *P. cuelloi*. Like in *P. nehuen*, the nares of *P. wintu* end caudally slightly rostral to the craniofacial hinge. This feature, together with the absence of thinning in the rostral region of the ventral bar, result in a prokinetic rostrum (Zusi, 1984). In addition, *Pseudoseiuropsis* species lack the slit-like gap between the lateral and ventral bars (Fig. 3B–E) commonly found in rhynchokinetic furnariids and, therefore, they would have prokinetic skulls (Claramunt and Rinderknecht, 2005). Moreover, Zusi (1984) linked this kind of cranial kinesis with holorhiny and these have become virtually synonymous. If we follow this definition, we could consider that *Pseudoseiuropsis* species were furnariids with prokinetic and holorhinal skulls.

However, as already noted and discussed by Claramunt and Rinderknecht (2005), *P. nehuen* has a long and narrow caudal border to the nostrils as found in the pseudoschizorhinal configuration (Fig. 3I). These traits are also present in both *P. wintu* and MMP5667 (Figs. 2C, 3G). Because prokinetic and holorhinal are synonymous, pseudoschizorhinal is virtually synonymous with rhynchokinesis (Zusi, 1984). In this scenario, the combination in *Pseudoseiuropsis* of prokinetic skulls with nares that resemble a pseudoschizorhinal type is a unique feature among furnariids.

The *P. wintu* braincase is slightly longer than that of *P. nehuen* (Table 1) and has an absolute height similar to the average for Philydorini and basal Dendrocolaptinae (*Sittasomus* and *Dendrocincla*) examined. The interorbital area of the frontal region is wider than that in *P. nehuen* (Fig. 3G, I; Table 1) and similar in relation to braincase width to the average for some Philydorini (e.g., *Thripadectes* and *Automolus*) and some Dendrocolaptinae (e.g., *Dendrocincla* and *Dendrocolaptes*; Appendix 1). In

addition, this area is more depressed than in *P. nehuen*, giving a different profile to the orbit, with its upper margin exceeding the height approximately at the boundary between the frontal and parietal regions. The interorbital septum exhibits moderate ossification and has a rounded, medium-sized interorbital fenestra and a small cranial fenestra with a small rostral notch (Fig. 3B). In *P. nehuen*, these traits could not be evaluated with certainty because the interorbital septum, and therefore both fenestrae, are covered with glue. This synthetic layer is interrupted in the center by a smaller circular hole within the real fenestra. The interorbital fenestra under the adhesive layer appears larger and ellipsoidal in shape, although whether this is original cannot be discerned (Fig. 3D); therefore, traits related to the interorbital septum in *P. nehuen* were excluded from comparisons and cladistic analyses. Both *P. wintu* and *P. nehuen* have a deep olfactory sulcus (Fig. 3B, D). The squamosal region of *P. wintu* presents a more robust zygomatic process than that of *P. nehuen* (Fig. 3B, D). In this region, the temporal fossa is longer than broad (extending almost to cerebellar prominence), with sinusoidal shape, and is well excavated (less than in *P. nehuen*; Fig. 3B, D). *Pseudoseisuropsis wintu* and *P. nehuen* differ in the shape of the dorsocaudal region of the postorbital process between its rostral and latero-caudal margins (Genbrugge et al., 2011). This region is less extended rostro-caudally in *P. wintu* than in *P. nehuen* (Fig. 3B, D). In the material of *Pseudoseisuropsis* where the braincases were preserved (i.e., *P. wintu* and *P. nehuen*), the orbital margin has a peculiar quadrangular shape in lateral view that is otherwise only found in the philydorines *Automolus ochrolaemus* and *Thripadectes rufobrunneus* among the examined species. In the caudal region of the orbit of *P. wintu*, the laterosphenoidal wall bears a 'laterosphenoidal crest' that is absent in *P. nehuen* and in all of the examined furnariids (Fig. 2A). The suprarectal process is somewhat longer than that of *P. nehuen* (Fig. 3B, D). The subcondylar fossa is more extended rostrally than in *P. nehuen* (Fig. 2E). The new species shares the presence of a pair of well-developed projections on the rostral margin of the parasphenoidal sheet with *P. nehuen*, though in the former they are narrower and less conspicuous than in the latter (Fig. 3L, N). If present, these projections are less pronounced in other furnariids than in *Pseudoseisuropsis*. The parasphenoidal rostrum of *P. wintu*, located rostral to the parasphenoidal sheet, is conspicuous and notably thicker than in *P. nehuen* (Figs. 2D, 3L, N).

Intraspecific and Interspecific Analyses

The evaluation of intraspecific variation shows that measurements of four continuous traits in the specimens formerly ascribed to *P. nehuen*, namely, dorsal bar width, interorbital area width, braincase width, and braincase length, exceed the expected range of intraspecific variation as indicated by data for *F. rufus*. In these traits, the 95% confidence intervals do not overlap, indicating that the CV values of *F. rufus* and *P. nehuen* as originally defined differ significantly (Table 2). In contrast, the variation in *P. nehuen* as originally defined is similar to that seen across four species of *Furnarius*.

CLADISTIC ANALYSES

The cladistic analysis that included only the holotypes of *P. nehuen* and *P. wintu* n. sp. yielded a single MPT (length = 513 steps) in which *P. nehuen* and *P. wintu* form a clade (bootstrap support of 35%; Fig. 4). This monophyletic group is supported by three unambiguous synapomorphies, namely: (1) temporal fossa of sinusoidal shape (ch. 18:2); (2) orbit of quadrangular shape (ch. 28:2); and (3) parasphenoidal sheet with a pair of well-developed projections (ch. 40:2). The sister-group relationship of *P. nehuen* and *P. wintu* was also recovered in five suboptimal trees two steps longer than the MPT. *Pseudoseisuropsis* is

paraphyletic in the shortest suboptimal tree of 514 steps in which *P. nehuen* and *P. wintu* are successive sister groups of Dendrocolaptinae (Fig. 5A) and in two trees of 515 steps where *P. nehuen* is a sister group of Furnariinae (Fig. 5B, C) and *P. wintu* is depicted alternatively as sister group of Furnariidae (Fig. 5B) and Sclerurinae (Fig. 5C). These results partially reflect some differences between the two fossils, including width (ch. 25) and depression (ch. 26) of the interorbital area, excavation depth in the squamosal region (ch. 19) of the temporal fossa, and height of the rostrum at the level of the intersection among ventral, lateral, and jugal bars (ch. 42).

In the MPT, *Pseudoseisuropsis* was shown as sister group of Dendrocolaptinae (Fig. 4) with low bootstrap support (20%). The relationship is supported by one unambiguous synapomorphy related to a longer premaxillary rostrum than the narial region (ch. 7:2). This is one derived condition exhibited by most dendrocolaptines but not by the basal dendrocolaptine *Sittasomus griseicapillus*, which has a shorter premaxillary rostrum than the narial region (ch. 7:0).

In two trees of 515 steps, *P. wintu* and *P. nehuen* form a clade nested within philydorines, being sister group of *Automolus* (Fig. 5D), or nested within the *Thripadectes* clade (Fig. 5E). The two species of *Pseudoseisuropsis* share an orbit of quadrangular shape (ch. 28:2) and a temporal fossa of sinusoidal shape (ch. 18:2) with *Automolus*. Cladistic analysis conducted by Claramunt and Rinderknecht (2005) purposely included *Automolus ochrolaemus* because of its overall similarity to the rostrum of *P. nehuen*, though their results did not reflect this resemblance. The relationship between the *Pseudoseisuropsis* clade and *Thripadectes* is supported by three synapomorphies involving the relative length of the premaxillary rostrum (ch. 7:2) and features of the interorbital septum (ch. 30:0, 31:2). Moreover, one topology of 515 steps shows *Pseudoseisuropsis* as sister group of the basal Furnariini *Pseudocolaptes lawrencii* (Fig. 5F), sharing the relative length of the premaxillary rostrum (ch. 7:2) as well as a low hump at the base of the culmen (ch. 11:1). In the remaining evaluated suboptimal trees (steps = 515), a *Pseudoseisuropsis* group appears as sister of the clade Dendrocolaptinae + Furnariinae (Fig. 5G) or as sister of Furnariinae (Fig. 5H).

It is noteworthy that in the obtained suboptimal topologies, the bootstrap support for the clade of *Pseudoseisuropsis* species was very low (<20% in seven topologies and more than 20% but less than 50% in one topology).

The cladistic analysis that included not only *P. wintu* and *P. nehuen* but also the fragmentary rostra (i.e., the holotype of *P. cuelloi* and the paratype MMP5667 of *P. nehuen*) yielded 82 MPTs of 513 steps (the strict consensus is shown in Fig. S2 in the Supplementary Data) and only three of them showed the four specimens ascribed to *Pseudoseisuropsis* forming a monophyletic clade. The inclusion of *P. cuelloi* and MMP5667 did not affect the relative position of *P. wintu* and *P. nehuen* in the backbone topology with respect to the MPT of the first analysis because in all of the results, both species were retrieved as more closely related to Dendrocolaptinae than other furnariids. However, the addition of the fragmentary fossils negatively affected the level of support for the relationship between *P. wintu* and *P. nehuen*, decreasing from 35% to 5% in most of the obtained trees. In some topologies, MMP5667 appeared alternatively as sister group of the clade formed by *P. nehuen* and *P. wintu*, of *P. nehuen*, or of *P. wintu*. In other results, MMP5667 adopted many different positions through the backbone topology.

Pseudoseisuropsis cuelloi was recovered across all topologies nested within or related to Dendrocolaptinae in almost all of the possible combinations. In any topology, *P. cuelloi* appeared as sister group of *P. wintu* or *P. nehuen*. Furthermore, *P. cuelloi* was retrieved as sister group of the clade

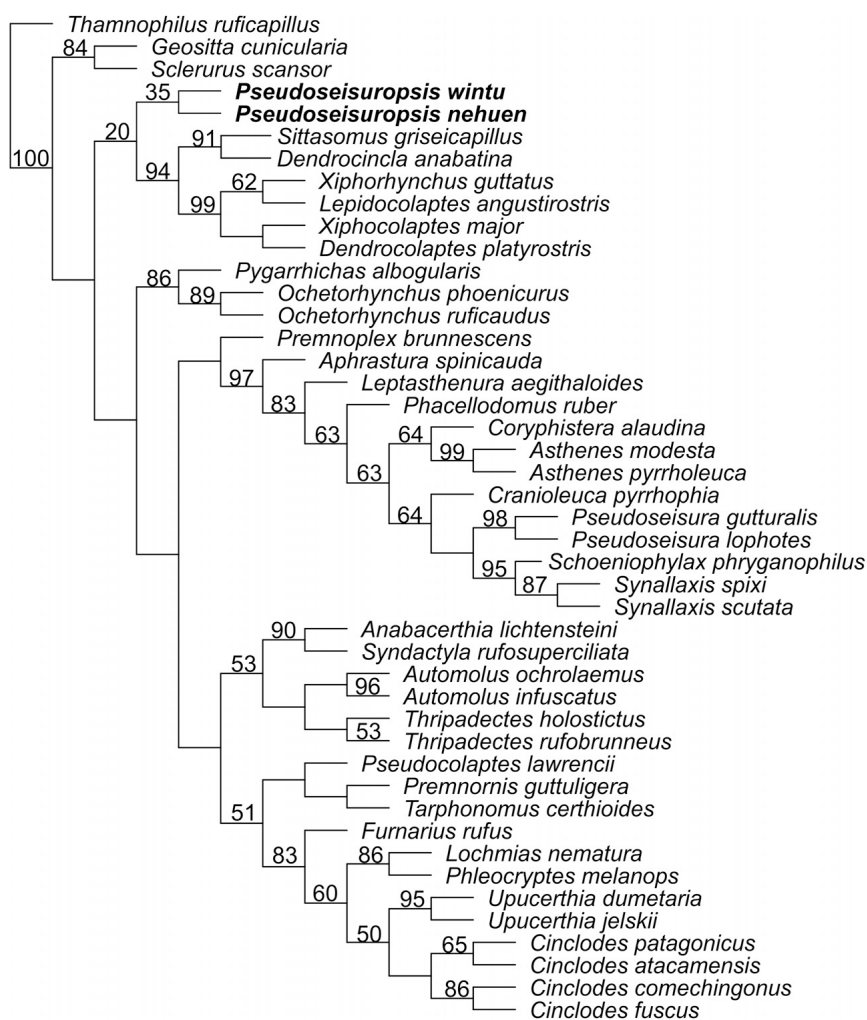


FIGURE 4. The most parsimonious tree (MPT) of 513 steps obtained in the first cladistic analysis, which included only the materials of the holotype of *Pseudoseisuropsis nehuen* (MLP 69-XII-3-1) and *P. wintu* (MMP570-M). Consistency index = 0.152, retention index = 0.453. Numbers above the branches indicate bootstrap support (only values over 50% reported except for the *Pseudoseisuropsis* and *Pseudoseisuropsis* + *Dendrocolaptinae* clades). Lines indicate the Furnariidae subfamilies represented in the cladistic analysis: Grey line indicates Sclerurinae, solid black line indicates Dendrocolaptinae, and dotted black line indicates Furnariinae.

formed by *P. wintu* and *P. nehuen* in only 12 of 82 topologies. These results contrasted with those of Claramunt and Rinderknecht (2005) in which *P. cuelloi* was always grouped with *P. nehuen*.

DISCUSSION

Taxonomy

The paratype MMP570-M of *P. nehuen* is notably different from the holotype of this species in having smaller dorsal bar width, greater interorbital area width, greater braincase width and braincase length, smaller premaxillary rostrum length, and parasphenoidal rostrum size. The first four variables showed a marked difference between the CVs (Table 2). The taxonomic separation of MMP570-M as *P. wintu* sp. nov. is also warranted and validated by the following discrete features: lateral bars rostrally curved, median sulcus shallow and rostrally diffused, presence of laterosphenoidal crest, subcondylar fossa rostrally expanded. These traits differ qualitatively between *P. wintu* and *P. nehuen* and they are almost invariable among the specimens of *F. rufus* analyzed here.

Pseudoseisuropsis wintu has a median sulcus similar to that of *P. cuelloi*. This similarity is relevant because Claramunt and Rinderknecht (2005) assigned taxonomic importance to that trait. However, we found that *P. wintu* differs from *P. cuelloi* in four aspects: the dorsal bar is wider, the premaxillary rostrum is shorter and wider, and the tomia are straighter in dorsal view.

The first two differences were considered by Claramunt and Rinderknecht (2005) to be as important as the morphology of the median sulcus. We consider that these four differences taken together are enough to conclude that MMP570-M is distinct from *P. cuelloi*.

The holotype of *Pseudoseisuropsis wintu* MMP570-M presents some differences from MMP5667, another paratype of *P. nehuen*, such as thicker dorsal bar and a straighter tomia in dorsal view. These traits suggest that these specimens are specifically distinct, because the variation in dorsal bar width significantly exceeds the intraspecific variation quantified in *Furnarius rufus* (Table 2) and the intraspecific variation qualitatively observed in other extant furnariids. However, the two fossils exhibit similarities (e.g., morphology of lateral and ventral bars) and were found close to each other in the same strata of the Miramar Formation, suggesting that they could be conspecific. If so, the observed differences in dorsal bar width and tomium shape would represent an extraordinary intraspecific variation or some kind of undocumented sexual dimorphism for extant furnariids. Specimen MMP5667 also differs from the holotypes of *P. nehuen* and *P. cuelloi* in some aspects (e.g., morphology of ventral and lateral bars) and it therefore cannot belong to either of those two species. Given these observations and the fragmentary nature of MMP5667, we believe that the most prudent decision is to treat it as representing an undetermined species of *Pseudoseisuropsis*.

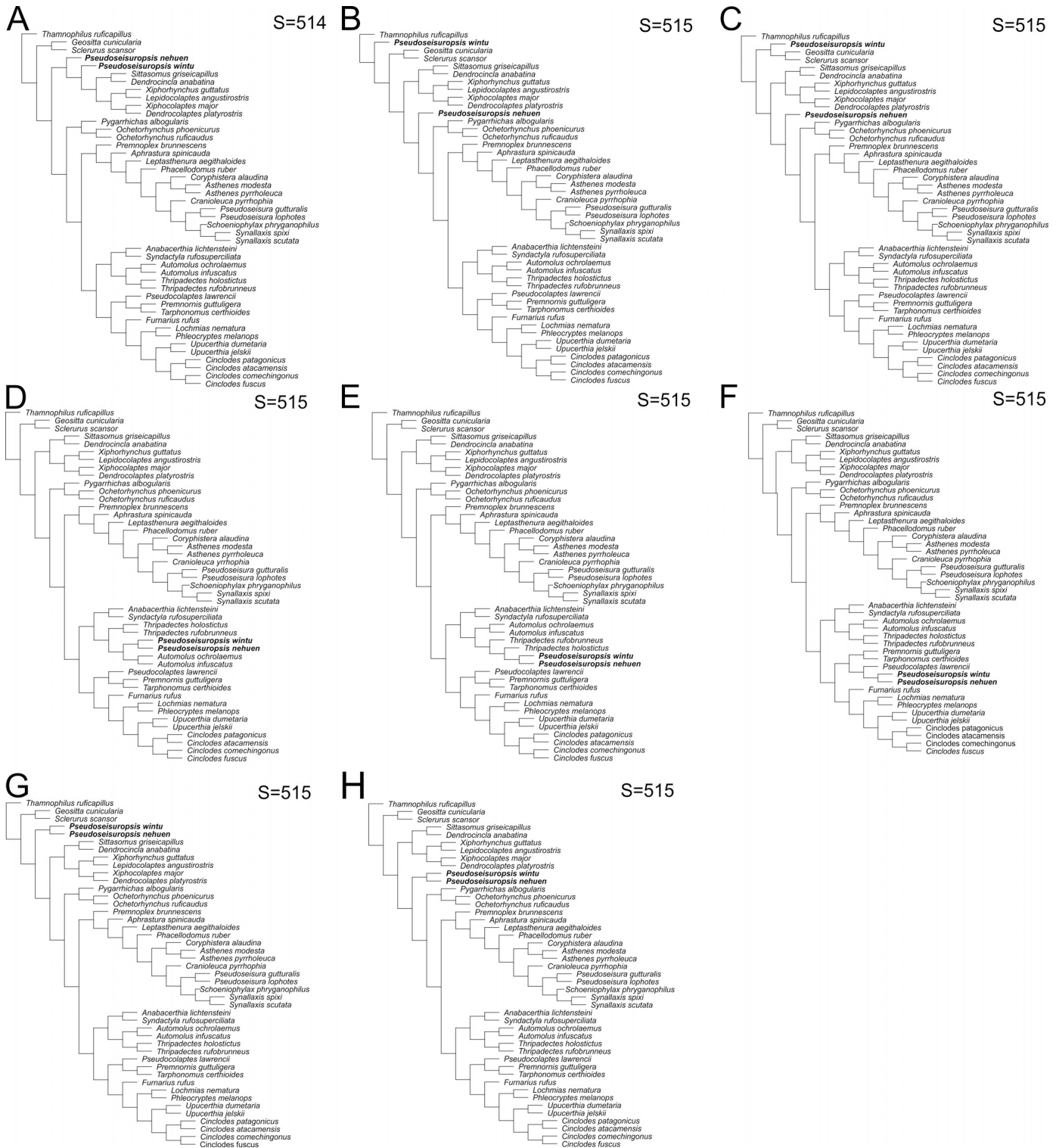


FIGURE 5. Suboptimal topologies, with one and two more steps than the most parsimonious tree (MPT), from the first cladistic analysis, which included only the materials of the holotype of *Pseudoseisurospis nehuen* (MLP 69-XII-3-1) and *P. wintu* (MMP570-M). **A**, shortest suboptimal tree at 514 steps; **B–H**, suboptimal trees of 515 steps. All positions retrieved from the *Pseudoseisurospis* species in the topologies had bootstrap support < 50%. **Abbreviation: S**, number of steps.

Phylogenetic Relationships

Our results show *Pseudoseisurospis* alternatively as related to Dendrocolaptinae (Fig. 4), in a basal position within Furnariidae (Fig. 5A, G), as a derived Furnariinae nested within Philydorini

(Fig. 5D, E), or even as a basal Furnariini (Fig. 5F). However, because these results show low values of support (less than 50% bootstrap), in addition to the fact that the data set shows high levels of homoplasy, we cannot rule out any of these alternative results. Therefore, we agree with Claramunt and Rinderknecht

(2005) in treating species of *Pseudoseisuropsis* as Furnariidae incertae sedis until a better supported consensus is achieved.

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APPENDIX 1. Description of characters used for phylogenetic analyses. When osteological features are mentioned for the first time their names are provided in Latin between parentheses. **Abbreviations:** CR, Claramunt and Rinderknecht, 2005: character number; K, Kopuchian, 2008: character number; *, modified states.

1. Ventral bar rostrally flattened (zona flexoria rostroventralis): absent (0); slightly flattened (1); very flattened (2) (ordered). CR 7*.
2. Slitlike gaps in the lateral bars of the rostrum (zona flexoria nasalis ventralis): absent (0); small (1); large (2). CR 8*.
3. Nares (apertura nasi ossea), caudal extension: clearly rostral to the craniofacial hinge (zona flexoria craniofacialis medialis) (0); slightly rostral to the hinge (1); at the same level as the hinge (2); caudally surpass the craniofacial hinge (3) (ordered). CR 13.
4. Premaxillary process of the nasals (os. nasale: processus premaxillaris), lateral border: concave (0); straight (1); convex (2). CR 14*.
5. Nasal septum (septum nasi osseum): not ossified (0); poorly ossified (1); moderately to fully ossified (2) (ordered). CR 9.
6. Rostrum (rostrum maxillare) length (RL), size relative to the length of the braincase (neurocranium) (BL): shorter ($0 < RL/BL < 0.9$) (0); equal ($0.9 < RL/BL < 1$) (1); longer ($1 < RL/BL$) (2) (ordered). K 59*.
7. Premaxillary rostrum (rostrum maxillae) length, size relative to the length of the narial region (NRL) (from rostral end of nares to craniofacial medial hinge): shorter (0); equal (1); longer (less than two times) (2); much longer (more than two times) (3) (ordered). CR 1.
8. Palatal surface of the premaxillary rostrum, median sulcus (sulcus neurovascularis medianus; sensu James, 2004): absent (0); present (1). CR 2*.
9. Recurrent lamina of the nasal septum, size: short (0); medium-sized (1); long (2) (ordered). CR 10.
10. Culmen (culmen): straight (0), curved (1) (ordered). CR 3*.
11. Hump in the base of the culmen: absent, culmen smooth (0); a slight angle (1); a small hump (2) (ordered). CR 4.
12. Angle between the rostrum and the jugal bar (arcus jugalis) (RJA): $RJA < 161^\circ$ (0); $161^\circ < RJA < 166^\circ$ (1); $166^\circ < RJA$ (2) (ordered).
13. Accessory process (processus accessorius; sensu Zusi and Livezey, 2006) (AP), caudal extension, size relative to the total length of the jugal bar (JBL): short ($0 < AP/JBL < 0.4$) (0); large ($0.4 < AP/JBL$) (1). K 84*.
14. Accessory process, ventral projection (visible in a lateral view of skull): not projecting (0); projecting (1).
15. Pars lateralis (os. palatinum: pars lateralis palatini): wide (0); slightly constricted rostrocaudally (1); very constricted (2). CR 18*.
16. Caudolateral angle (angulus caudolateralis): rounded (0); diagonal (1); square (2). K 85.
17. Temporal fossa (fossa temporalis), caudal extension: poorly developed (0) (less than a half of the braincase length); developed (1) (more than a half of the braincase length); well developed (2) (temporal fossa contacts the cerebellar prominence) (ordered).
18. Temporal fossa, shape: downward curved (0); straight (1); sinusoidal (2) (ordered).
19. Temporal fossa, depth of excavation in squamosal region (os. squamosum): little excavated (0); excavated (1); very excavated (2) (ordered).
20. Temporal fossa, depth of the excavation in caudomedial region of the skull: little excavated (0); excavated (1); very excavated (2) (ordered). K 40*.
21. Cerebellar prominence (prominentia cerebellaris): inconspicuous (0); conspicuous (1). K 28.
22. Jugal projection of ectethmoid (os. ectethmoidale), contact with jugal bar: in contact (0); without contact (1). K 49.
23. Jugal projection of ectethmoid, width: thin (0); medium-sized (1); broad (2) (ordered). K 50.
24. Ectethmoid plate width (EPW), relative to the maximum width of braincase (BW): narrow ($0 < EPW/BW < 0.41$) (0); medium-sized ($0.41 < EPW/BW < 0.51$) (1); broad ($0.51 < EPW/BW$) (2) (ordered).
25. Frontal (os. frontale), width of interorbital area (IAW), relative to the maximum width of braincase (BW): thin ($0 < IAW/BW < 0.25$) (0); medium-sized ($0.25 < IAW/BW < 0.3$) (1); broad ($0.3 < IAW/BW$) (2) (ordered). CR 27.
26. Frontal, depression of the interorbital area (depressio frontalis): little depressed (0); very depressed (1); not depressed (2). CR 28*.
27. Orbital margin (os. frontale: margo supraorbitalis) at the level of the postorbital process (processus postorbitalis): a uniform arch (0); sinusoidal over the postorbital process (1). CR 29.
28. Orbit, shape of margin: rounded (0); triangular (1); square (2).
29. Orbit length (OL), size relative to the length of the braincase (BL): short ($0 < OL/BL < 0.55$) (0); medium-sized ($0.55 < OL/BL < 0.6$) (1); broad ($0.6 < OL/BL$) (2) (ordered).
30. Interorbital septum (septum interorbitale), degree of ossification: poorly (0); moderately (1); highly (2).
31. Relative size between the interorbital fenestra (fonticuli interorbitale) and cranial fenestra (fonticuli orbitocraniales) of the interorbital septum: larger cranial fenestra (0); equal (1); larger interorbital fontanelle (2). K 57*.
32. Interorbital fenestra: big, bigger rostrally (0); medium-sized, square (1); small, circular (2); absent (3) (ordered). CR 25.
33. Cranial fenestra, presence of a notch in the rostral border: absent (0); present (1). CR 26.
34. Orbital process of the quadrate (os. quadratum: processus orbitalis), distal end: acute (0); slightly widened (1); spatulated (2) (ordered). CR 22.
35. Postorbital process, size: short (0), long (1). CR 31*.
36. Postorbital process, shape: acute (0); square (1). CR 32*.
37. Zygomatic process (processus zygomaticus): short (0); long (1). K 35*.
38. Fusion between the zygomatic process and postorbital process: absent (0); present (1). K 33.
39. Suprameatal process (processus suprameaticus): absent (0); short (1); medium-sized (2). K 36*.
40. Parasphenoidal sheet (lamina parasphenoidalis), two small projections in the rostral margin at both sides of the parasphenoidal rostrum (rostrum parasphenoidale): absent (0); very small (1); well developed (2). CR 33.
41. Height of dorsal bar (pila supranasalis) of nares (DBH), size relative to the rostrum height at the same point (RBH): low ($0 < DBH/RBH < 0.15$) (0); medium-sized ($0.15 < DBH/RBH < 0.25$) (1); high ($0.25 < DBH/RBH$) (2) (ordered).
42. Height of rostrum at the level of fusion of the ventral, lateral, and jugal bars (RH), size relative to the maximum height of the braincase (BH): low ($0 < RH/BH < 0.25$) (0); medium-sized ($0.25 < RH/BH < 0.35$) (1); high ($0.35 < RH/BH$) (2) (ordered).
43. Height of braincase (BH), size relative to the length of the braincase (BL): low ($0 < BH/BL < 0.6$) (0); medium-sized ($0.6 < BH/BL < 0.75$) (1); high ($0.75 < BH/BL$) (2) (ordered). K 26*.

APPENDIX 2. Character-taxon matrix used for phylogenetic analyses. Polymorphic states are indicated by letters: **A**, (0, 1); **B**, (0, 2); **C**, (1, 2); **D**, (2, 3); **E**, (3, 4).

Taxon	10	20	30	40	43
<i>Thamnophilus ruficapillus</i>	00000-0101	0211111111	1120001010	2010202110	221
<i>Sclerurus scansor</i>	0011112--1	011111111-	00120-0010	011-01001-	101
<i>Geositta cunicularia</i>	2212100111	1111000102	0101010001	0211000110	111
<i>Dendrocincla anabatina</i>	0011112011	0101201110	1021120011	0200101010	201
<i>Sittasomus griseicapillus</i>	0011100100	1210201111	1021220001	1200111010	211
<i>Dendrocolaptes platyrostris</i>	0001222001	2210102110	1022120012	0202101011	220
<i>Xiphocolaptes major</i>	0001123101	2101002111	1012220002	0202011011	120
<i>Lepidocolaptes angustirostris</i>	0000122111	2210101110	1101221002	0202011010	100
<i>Xiphorhynchus guttatus</i>	0002023101	1211102110	1012221002	0212011001	220
<i>Ochetorhynchus ruficaudus</i>	1211220121	0-1-111021	1100001101	201-110010	201
<i>Ochetorhynchus phoenicurus</i>	1111120101	0000111020	1120000101	21111000A1	201
<i>Pygarrhichas albogularis</i>	2112120110	0110001010	1110000101	211-010011	210
<i>Cinclodes fuscus</i>	2131000001	1010100001	1100000000	2112100100	201
<i>Cinclodes comechingonus</i>	2122101111	0010111001	1111010100	211-101-1A	101
<i>Cinclodes atacamensis</i>	11121----1	111-110001	11100B0100	211A100110	111
<i>Cinclodes patagonicus</i>	1212110121	0011--0001	1111010100	2111000010	201
<i>Upucerthia jelskii</i>	1222222111	1-1-100012	0101000101	201-000011	101
<i>Upucerthia dumetaria</i>	2122222111	1111101120	0111010C00	2110000011	211
<i>Phleocryptes melanops</i>	1222C02111	001001C001	1110000100	201-110010	000
<i>Lochmias nematura</i>	1212101A21	0010102020	1110000100	200-1--1-1	001
<i>Furnarius rufus</i>	2232000111	0001101B01	0011101120	2110001010	010
<i>Tarphononcus certhioides</i>	2112000101	0111021010	0100000100	20110A1010	221
<i>Premnornis guttuligera</i>	1111001-01	0111112020	1000020000	0100010010	-01
<i>Pseudocolaptes lawrencii</i>	11100221-1	1-1110C020	00-1000101	201-010020	210
<i>Syndactyla rufosuperciliata</i>	1121200110	1210112220	1100020101	1110010021	112
<i>Anabacerthia lichtensteini</i>	0112202110	1110122222	1100010101	010?000010	011
<i>Thripadectes rufobrunneus</i>	0011120111	C011112010	1-12100211	010-010012	211
<i>Thripadectes holostictus</i>	0111C12111	2011112020	10111-1100	2000010020	211
<i>Automolus infuscatus</i>	0011102101	C101112120	00121-1211	010101101-	211
<i>Automolus ochrolaemus</i>	0011111101	1101102120	00021?0211	1101011011	211
<i>Premnoplex brunnescens</i>	1211200-10	001-122120	1100010100	201-010010	--1
<i>Aphrastura spinicauda</i>	2C32100121	0010102010	0100010101	0010001111	202
<i>Leptasthenura aegithaloides</i>	2132000121	0010111211	0100021101	010-0A1012	001
<i>Phacellodomus ruber</i>	11D22--121	2111111-11	1000000101	2011101010	110
<i>Coryphistera alaudina</i>	11122--111	2101112011	0011010100	2110000010	100
<i>Asthenes pyrrholeuca</i>	2132000001	0110110001	0100000100	2010101110	001
<i>Asthenes modesta</i>	2232000001	0110110-01	0100000000	2000101110	002
<i>Cranioleuca pyrrhophia</i>	2232200021	011-10C202	011002A100	2100011010	101
<i>Pseudoseisura lophotes</i>	2232200121	1111122220	0111000101	2100001011	111
<i>Pseudoseisura gutturalis</i>	1232000111	1-11111220	0110000121	210-010011	210
<i>Schoeniophylax phryganophilus</i>	1212200011	0011101011	0110020100	201-001010	001
<i>Synallaxis scutata</i>	122C100--1	1010101001	0101001100	201-011010	101
<i>Synallaxis spixi</i>	2122100011	2011120001	1100000000	2010001010	021
<i>Pseudoseisuroopsis nehuen</i> ⁽¹⁾	0012112101	1011101220	1-1100020-	2---011012	211
<i>Pseudoseisuroopsis wintu</i>	00AC1121-1	C-----121A	0-11110200	211---1012	221
Paratype of <i>P. nehuen</i> MMP5667	00121--1-1	-----	-----	-----	2--
<i>Pseudoseisuroopsis cuelloi</i> ⁽²⁾	0---1-2101	0-----	-----	-----	2--

⁽¹⁾The structures of characters 13, 14, 15, and 43 are damaged or absent. Due to that, the states of these characters were scored from photos included in Noriega (1991).

⁽²⁾All characters states were scored from photos included in Claramunt and Rinderknecht (2005).