Fossil evidence of wing shape in a stem relative of swifts and hummingbirds (Aves, Pan-Apodiformes)

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A feathered specimen of a new species of Eocypselus from the Early Eocene Green River Formation of Wyoming provides insight into the wing morphology and ecology in an early part of the lineage leading to extant swifts and hummingbirds. Combined phylogenetic analysis of morphological and molecular data supports placement of Eocypselus outside the crown radiation of Apodiformes. The new specimen is the first described fossil of Pan-Apodiformes from the pre-Pleistocene of North America and the only reported stem taxon with informative feather preservation. Wing morphology of Eocypselus rowei sp. nov. is intermediate between the short wings of hummingbirds and the hyper-elongated wings of extant swifts, and shows neither modifications for the continuous gliding used by swifts nor modifications for the hovering flight style used by hummingbirds. Elongate hindlimb elements, particularly the pedal phalanges, also support stronger perching capabilities than are present in Apodiformes. The new species is the smallest bird yet described from the Green River Formation, and supports the hypothesis that a decrease in body size preceded flight specializations in Pan-Apodiformes. The specimen also provides the first instance of melanosome morphology preserved in association with skeletal remains from the Green River Formation.

1. Introduction

An unparalleled fossil assemblage from the Early Eocene Fossil Butte Member of the Green River Formation has shed light on the taxonomic composition and ecological diversity of one of the earliest known Cenozoic avifaunas. Fossil feathers, in particular, have revealed details of wing shape in Eocene birds that cannot be inferred from skeletal specimens alone, and have been recovered from Fossil Butte Member deposits both as isolated specimens and associated with semi-articulated skeletons [1–5]. Feathers occur in the Fossil Butte Member in various states ranging from poorly preserved carbonized traces to finely preserved specimens with identifiable rachises and barbs. Formerly, detailed feather preservation in Green River birds was attributed to fossilized feather-degrading bacteria and associated glycy routinely [6]. More recently, apparent microbes associated with feather preservation at other localities have been reinterpreted as melanosomes [7]. Melanosomes have thus far been described only from one isolated feather from an unidentified Green River bird [8]. Here, we report a representative of Pan-Apodiformes with well-preserved plumage and intact melanosomes.

Pan-Apodiformes comprises the tree swifts (Hemiprocnidae), true swifts (Apodidae) and hummingbirds (Trochilidae), along with their extinct relatives. Despite their small average body size, they have a relatively extensive...
Palaeogene fossil record in some regions. A plethora of ‘swift-like’ fossil birds are known from Eocene–Oligocene deposits throughout Europe [9–16]. Although superficially swift-like in skeletal morphology, only a few of these extinct species are closely related to extant Apodidae. Several of these taxa are members of the hummingbird stem lineage [17], whereas others fall outside the crown clade Apodiformes [16]. Surprisingly, no Pan-Apodiformes have been formally described from contemporary deposits of North America, nor indeed from any pre-Pleistocene North American deposits. This apparent disparity between the European and North American Palaeogene avifaunas may be deceptive, given that several specimens of swift-like birds from the Green River Formation reside in private collections [1,2] and also because such small taxa may potentially suffer from collecting biases.

Extant Apodiformes exhibit some of the most unique flight characteristics among birds, in terms of overall wing shape, feather structure and flight style. Hummingbirds possess a short blade-like wing and use a unique hovering flight style that generates lift on both the upstroke and downstroke [18]. Swifts, by contrast, have greatly elongated wings that allow them to excel at metabolically efficient gliding and also reach the fastest speeds measured for birds in level flight [19]. Both swifts and hummingbirds exhibit a variety of ornamental tail shapes and colour patterns [19–22]. Given the disparity in wing shape observed within extant swifts and hummingbirds, fossil relatives of extant swifts and hummingbirds are key to informing the ancestral wing shape and flight style in Pan-Apodiformes. Proportions and discrete characters of the wing skeleton have provided insights into the flight style of extinct Pan-Apodiformes [16,23,24], but predicting feather length is difficult from skeletal remains alone. Thus, feathered specimens are particularly important in reconstructing the early evolution of these specialized birds.

2. Systematic palaeontology

Strisores Baird 1858
Cypselomorphae Huxley 1867
Pan-Apodiformes Mayr 2010
Eocypselidae Harrison 1984
_Eocypselus_ Harrison 1984
_Eocypselus rowei_ sp. nov.

(a) Holotype
Wyoming Dinosaur Center (WDC, Thermopolis, WY, USA) CRG-109, complete skeleton with intact feathering preserved as slab and counterslab (figure 1). Measurements are presented in table 1.

(b) Etymology
The species name honours John W. Rowe, a generous and knowledgeable supporter of evolutionary research and educational outreach at The Field Museum in Chicago, Illinois, where he is currently serving as chairman of the board.

(c) Locality and horizon
Locality B [25], also known as Lewis Ranch Site 2 or Smith Hollow Quarry, of the Fossil Butte Member of the Green River Formation of Lincoln County, Wyoming, USA. Deposits at this locality are from a mid-lake setting (F-1 facies of Grande & Buchheim [25]) and have previously yielded partial skeletons of the stem frigatebird _Limmnofregata azugosterman_ [4] and the stem roller _Primobucco mcgregori_ [26]. Radiometric 40Ar/39Ar dating of an overlying tuff deposit indicates an age of approximately 51.66 ± 0.09 Ma for the fossil horizon [27].

(d) Diagnosis
_Eocypselus rowei_ differs from _Eocypselus vincenti_ by (i) the stouter humerus (midshaft width equals approx. 20% total length for _E. rowei_ versus 13% for the _E. vincenti_ holotype), (ii) the presence of a rounded tubercle that projects ventrally from the body of metacarpal III near the contact with the troclea carpalis and (iii) a proportionally shorter tarsometatarsus (tarsometatarsus length equals 50% of tibiotarsus length versus 54% for _E. vincenti_). The second character is not present in _E. vincenti_ (fig. 6f of [16]) and other Pan-Apodiformes, and is considered an apomorphy of _E. rowei_. In comparing proportions, we note that the specimen is not badly crushed. Rather, it has been damaged by the splitting of the slab, so that several long bones are broken into two pieces exposing the internal surfaces. An expanded differential diagnosis is included in the electronic supplementary material.

(e) Comment
Pan-Apodiformes is defined here as the clade uniting all taxa more closely related to Apodiformes than to any other extant taxon of Strisores (Aegothelidae, Nyctibiidae, Caprimulgidae, Steatornithidae and Podargidae).

(f) Scanning electron microscope methods
Samples from WDC-CGR-109 were initially coated with gold, but had to be recoated with 15 nm of gold/palladium mixture to prevent charging. Samples were imaged with a Zeiss Supra 40 VP field emission scanning electron microscope (located at University of Texas at Austin, Institute for Cellular and Molecular Biology) using 5 kV accelerating voltage and 15 mm working distance.

(g) Phylogenetic analysis
We expanded a recently published combined phylogenetic matrix [28] (see also [16,17,29–32]) by adding 17 characters and 14 taxa. Taxonomic sampling includes eight extant species and seven fossil species of Pan-Apodiformes. In order to polarize character states, we also included 10 representatives of Strisores, the larger clade uniting the paraphyletic ‘Caprimulgiformes’ [29] and Pan-Apodiformes. Because the placement of Strisores within the context of higher avian phylogeny remains controversial, we rooted trees to the palaognath _Crypturellus undulatus_. Taxa were sampled at the species level to facilitate inclusion of molecular data. Molecular data were obtained from GenBank for the genes _RAG-1_, _myoglobin exon 2_ and _c-myc exon 3_ and aligned using CLUSTALX [33]. A nexus file containing the matrix, along with character descriptions, GenBank accession numbers for molecular sequences and a list of specimens examined, is presented in the electronic supplementary material.

Two analyses, the first one using the combined dataset and the second using only the morphological dataset, were conducted using PAUP*4.0b10 [34], with a branch and bound search strategy. All characters were equally weighted,
multistate codings were used only to represent polymorphism and branches with a minimum length of zero were collapsed. A single most parsimonious tree (tree length, TL = 3744 steps) was recovered in the combined analysis (figure 2). Results of the analysis using only morphological data also yielded a single most parsimonious tree (TL = 235) that is identical to the tree from the combined analysis with the exception that the branch uniting the extant swifts *Aerodramus vanikorensis* and *Apus apus* collapsed.

Our results agree with one previous hypothesis (fig. 8 of [16]) in placing *Eocypselus* basal to the swift–hummingbird split. *Eocypselus* is supported as a member of Pan-Apodiformes by two unambiguous synapomorphies: an abbreviated humerus (character 54: state 1, ratio of length to midshaft width less than 10.0) and an ossified arcus extensorius of the tarsometatarsus (92: 1; see [16]). Monophyly of crown Apodiformes to the exclusion of *Eocypselus* is supported by eight derived characters (see the electronic supplementary material). Another previous study recovered *Eocypselus* within the crown clade Apodiformes [35] (see comments on scoring issues in [36]), but we find no support for this hypothesis, which is 12 steps less parsimonious using our dataset.

*Eocypselus vincenti* and *E. rowei* did not form a clade in our results. We consider this result likely to be related to the incomplete preservation of bone surfaces on the *E. rowei* holotype, which precludes scoring of characters that may potentially unite these fossil taxa (see the electronic supplementary material).

A key finding of the new analysis is that the Eocene *Scaniacypselus wardi* and *Scaniacypselus szarskii* are supported...
as members of the stem lineage leading to Apodidae, more closely related to extant true swifts than to tree swifts. *Scaniacypselus* has previously proved difficult to place, because this taxon retains some primitive character states supporting a stem placement [17], but also other features that have been interpreted as potentially supporting placement within crown Apodidae [9,12]. One previous phylogenetic analysis of a smaller character set with more limited taxonomic coverage interpreted as potentially supporting placement within the stem lineage leading to Apodidae, more closely related to the derived absence of this fossa (61 : 1), a blunt olecranon as opposed to the derived presence of a proximally directed flange extending proximally from the base of the plantar flange of trochlea metatarsi II (97 : 2) and diastataxic feathering (106 : 1). We find no support for a previous morphology-only hypothesis that *Streptoprocne* represents a more basal divergence, sister to Hemiprocniidae + all other Apodidae [40].

Our results differ from previous molecular studies [38] and agree with morphology-based hypotheses [40] in supporting monophyly of the Chaeturini (represented by *Chaetura* and *Hirundapus*). This clade is supported by the presence of a bony canal on the plantar surface of the base of trochlea metatarsi II (98 : 1) and the presence of needle-like rectrices (117 : 1). A clade uniting *Acrocinus* (Collocaliini) and *Apus* (Apodini) was supported in our combined analysis, in agreement with Chubb [38], though we identified no morphological synapomorphies of this clade, which collapses in our morphology-only analysis. The grouping of Collocaliini and Apodini to the exclusion of Chaeturini was also supported by a multi-locus molecular analysis [41], though that study did not include any representatives of Cypseloidini.

Relationships within Trochilidae are congruent with previous hypotheses [16,17,42], but more fully resolved, with the placement of *Argornis* closer to the crown clade than *Pantargornis* supported by the elongation of the carpometacarpus (72 : 2).

### 3. Skeletal anatomy and feathering

*Eocypselus rowei* was a very small bird, with a total body size slightly smaller than that of the extant *Chaetura pelagicus* (chimney swift). Although the holotype is essentially complete, many bones were split along with the slab, so that surface details such as muscle insertions are not observable. It is evident that the impressions of limb bones have been retouched with paint in a few obvious areas. However, microscopic details of preserved feathers indicate these structures are genuine.

A complete but poorly preserved skull preserves a short, rounded beak. Proportions are similar to those in extant swifts, but notably the tip does not show evidence of downturning. The internarial bar is narrow, and the nares extend nearly to the tip of the beak. The mandible is very slender. Although the sclerotic ring is incomplete, it does not appear to show any specializations such as enlargement or tubular morphology. As indicated by the articulated vertebral column, the foramen magnum appears to have faced ventrally. The prominentia cerebellaris appears to have projected caudally far past the margin of the foramen magnum.

Although the sternum is not well preserved, it appears that the sulci for the coracoids are oriented at an angle of less than 45°, so that the coracoids are strongly laterally directed in articulation. It is also clear that the caudal border of the sternum was wide and flat. No evidence of incisurae or fenestrae is visible, but because of poor preservation their presence cannot be ruled out with certainty. In both coracoids, the omal ends are mostly intact, and the sternal portions are preserved as impressions. The processus acrocoracoideus is hooked as in other Pan-Apodiformes and in Aegothelidae. Although

### Table 1. Measurements from WDC-CGR-109.

<table>
<thead>
<tr>
<th>element</th>
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<th>measurement (left/right; mm)</th>
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<tr>
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<td>scapula</td>
<td>length</td>
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</tr>
<tr>
<td>humerus</td>
<td>length</td>
<td>—/12.1</td>
</tr>
<tr>
<td>midshaft width</td>
<td>—/2.3</td>
<td></td>
</tr>
<tr>
<td>radius</td>
<td>length</td>
<td>—/16.5</td>
</tr>
<tr>
<td>carpometacarpus</td>
<td>length</td>
<td>10.8/10.8</td>
</tr>
<tr>
<td>alular phalanx</td>
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<td>2.9/3.0</td>
</tr>
<tr>
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<td>5.4/5.5</td>
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<tr>
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<td>length</td>
<td>5.2/5.3</td>
</tr>
<tr>
<td>phalanx III-1</td>
<td>length</td>
<td>—/3.0</td>
</tr>
<tr>
<td>primary feather</td>
<td>tip of phalanx to tip of feather</td>
<td>55.5</td>
</tr>
<tr>
<td>femur</td>
<td>length</td>
<td>—/11</td>
</tr>
<tr>
<td>tibiotarsus</td>
<td>length</td>
<td>20.0/20.2</td>
</tr>
<tr>
<td>tarsometatarsus</td>
<td>length</td>
<td>10.0/10.0</td>
</tr>
</tbody>
</table>

as members of the stem lineage leading to Apodidae, more closely related to extant true swifts than to tree swifts. *Scaniacypselus* has previously proved difficult to place, because this taxon retains some primitive character states supporting a stem placement [17], but also other features that have been interpreted as potentially supporting placement within crown Apodidae [9,12]. One previous phylogenetic analysis of a smaller character set with more limited taxonomic sampling yielded *S. wardi* in a position basal to the tree swift–true swift (*Apodidae–Hemiprocniidae*) split [35], whereas another recovered composite terminals coded for *Scaniacypselus, Apodinae* and *Cypseloidini* [37] in a polytomy.

Species-level codings and expanded character sampling help resolve the placement of *Scaniacypselus*, which is supported as a basal member of Pan-Apodidae by four synapomorphies: the great abbreviation of the humerus (54 : 2; ratio of length to midshaft width less than 5.0), strong projection of the processus supracondylaris dorsalis (62 : 1), proximal displacement of this process (63 : 1) and elongation of the carpometacarpus (72 : 2). Relationships within Trochilidae are congruent with previous hypotheses [16,17,42], but more fully resolved, with the placement of *Argornis* closer to the crown clade than *Pantargornis* supported by the elongation of the carpometacarpus (72 : 2).
The hindlimbs are proportionally long and slender compared to those of extant Apodiformes. The tarsometatarsus is short and squared, indicating a relatively high aspect ratio. A small feather preserved near the base of the head crest suggests the presence of a feathered head crest, which is characteristic of most extant Apodiformes, including tree swifts (Hemiprocnidae) and some hummingbirds.

Figure 2. Most parsimonious tree from combined analysis (TL = 3744 steps, RC = 0.329, RI = 0.484). The topology of the most parsimonious tree from the morphological analysis (TL = 235 steps, RC = 0.436, RI = 0.794) is identical with the exception that the branch uniting Apus and Aerodramus is collapsed. Extinct taxa are indicated by grey font.

Damaged on its medial edge, the cotyla scapularis of the coracoid is clearly cup-shaped as in extant Apodiformes. The scapular blade is straight over the proximal two-thirds of its length, but prominently deflected at its distal end. The furcula is broken into three segments with slight displacement. A portion from near the symphysis is quite robust in cross-section and bears a small apophysis furculae. Two sections from the osm end of the furcula show a more flattened cross-section.

The humerus is strongly abbreviated. The crista bicipitalis is straight over the proximal two-thirds of its length, but prominently deflected at its distal end. The furcula is broken into three segments with slight displacement. A portion from near the symphysis is quite robust in cross-section and bears a small apophysis furculae. Two sections from the osm end of the furcula show a more flattened cross-section.

Individual feathers can be discerned within the darkened halo surrounding the skull. If the feathers preserved near the base of the beak are not displaced, then a feathered head crest may have been present. Such crests occur in some extant Apodiformes, including tree swifts (Hemiprocnidae) and some hummingbirds (e.g. Orthorhyncus cristatus) [19,21]. Feather preservation along the wing is of high quality, with darkened rachises and individual barbs visible. The primaries are elongate, and the outermost feathers are longer than the entire wing skeleton, accounting for more than 50 per cent of total wing length. As preserved, the outer primaries are much longer than the inner primaries (visible on the right side), indicating a relatively high aspect ratio. A small feather near the leading edge of the left wing is tentatively identified as a covert. On the right side, the rounded distal end of the outermost rectrix appears to be intact, suggesting the very short and squared tail shape reflects the true morphology.

One previously reported specimen of Eocypselus rowei preserves feather impressions, but these are too incomplete to provide information on wing or tail shape [15,43]. Eocypselus rowei provides insights into the variability of melanosome preservation in Green River feathers. Three-dimensionally preserved melanosomes from the dorsal head...
feathers of *E. rowei* are interpreted as well-defined, densely packed and dominantly rod-like eumelanosomes (figure 1g). Such morphologies are most commonly associated with black, glossy black and some forms of iridescent colours in birds [44]. Additional sampling along the wing feathering revealed melanosome morphologies represented primarily as voids rather than as three-dimensional forms. Although melanosome preservation has been reported in fossil feathers from other lacustrine and near-shore depositional environments [45–49], only one account of melanosomes in Green River feathers has been reported. Wogelius et al. [8] sampled three isolated Green River feathers and an isolated wing with feathers. All had regions containing high amounts of copper, a proposed biomarker of melanin [8]. However, only in one of the isolated feathers were three-dimensionally preserved melanosomes, described as rod-like eumelanosomes [8], discernible. In the other three specimens, preserved evidence of melanosome morphology was not reported, despite macrostructural feather preservation.

4. Discussion

Despite sharing distinctive features of the wing skeleton, such as a remarkably stout humerus and elongate carpometacarpus and phalanges, swifts and hummingbirds have markedly different wing shapes. Shortening of the humerus results in a shift in muscle attachments towards the shoulder joint, which in turn reduces moment of inertia [23,50]. Elongation of the primary feathers has been hypothesized to compensate for shortening of the proximal wing skeleton in Apodiformes [23]. In swifts, abbreviation of the proximal wing bones is indeed accompanied by elongation of the distal wing bones as well as the primaries, resulting in overall elongation of the wing (figure 3) and optimization for fast flap-gliding and gliding flight. Hummingbirds also possess a strongly abbreviated humerus and elongated primaries, but have much shorter wings relative to overall body size, resulting in the higher wing loading values used in hovering flight [51,52].

Because the disparate wing shapes of extant swifts and hummingbirds are only truly appreciable when feathering is taken into account, it is difficult to infer the ancestral wing morphology for Apodiformes based solely on data from extant taxa and fossils that preserve only skeletal material. While the brachial index (humerus : ulna ratio) [53] of *Eoecypselus* falls within the range of extant swifts (table 2), the overall wing length in the fossil taxon is much shorter. Likewise, despite the fact that the carpometacarpus and phalanges of *E. rowei* are shorter than those of hummingbirds, the primary feathers are proportionally longer. *Scaniacypselus szarskii* provides the best data on feathering from an early swift [12]. In this taxon, the primaries greatly exceed the combined length of the wing bones and appear to have accounted for about two-thirds of the overall wing length. However, because this species is closely related to Apodidae, it provides little insight into the ancestral wing morphology of Apodiformes. A single specimen of the stem hummingbird *Parrrornis messelensis* with fine feather preservation reveals a different morphology—a short, rounded wing—in a stem member of the hummingbird lineage [13].
Table 2. Comparative ratios of wing bones for Pan-Apodiformes. Ratios for fossil hummingbirds, extant Trochilidae and extant Apodidae from [24], ranges for Eocypselus vincenti from [16]. Ulna length of Eocypselus rowei was estimated from the length of the intact radius.

<table>
<thead>
<tr>
<th>taxon</th>
<th>humerus : ulna</th>
<th>CMC : humerus</th>
<th>phalanx II-1 : CMC</th>
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<tr>
<td>Eocypselus rowei</td>
<td>0.73</td>
<td>0.89</td>
<td>0.50</td>
</tr>
<tr>
<td>Eocypselus vincenti</td>
<td>0.72 – 0.76</td>
<td>0.86 – 0.90</td>
<td>—</td>
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<tr>
<td>Hemiprocne mystacea</td>
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<td>0.67</td>
</tr>
<tr>
<td>Scaniocypterus wardi</td>
<td>0.66</td>
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</tr>
<tr>
<td>extant Apodidae</td>
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<td>1.22 – 1.41</td>
<td>0.76 – 0.85</td>
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<tr>
<td>Parargornis messelensis</td>
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<td>0.93</td>
<td>—</td>
</tr>
<tr>
<td>Argornis caucasicus</td>
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<td>—</td>
</tr>
<tr>
<td>Junornis tesselatus</td>
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<td>—</td>
<td>—</td>
</tr>
<tr>
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<td>—</td>
</tr>
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<td>Eurotrochilus sp.</td>
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<td>1.23 – 1.45</td>
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</table>

Eocypselus rowei provides the first direct evidence of overall wing shape in a stem lineage representative of Pan-Apodiformes. This specimen shows a wing shape intermediate between that of extant swifts and hummingbirds. The outermost primary (55 mm) slightly exceeds the combined length of the wing bones. In the similarly sized stem hummingbird P. messelensis, this primary is less than half as long (approx. 25 mm), whereas the outermost primary is much longer (approx. 74 mm) in the slightly smaller stem true swift S. szarskii. The moderately elongated wing feathering and the phylogenetic position of Eocypselus outside the crown clade Apodiformes together support the inference that the shortened wings of hummingbirds and the elongated wings of swifts were each derived from a less specialized ancestral wing shape.

Extant swifts have very short legs and rarely perch during their foraging intervals. Thus, it is noteworthy that the elongate hindlimbs and toes of Eocypselus appear suited to perching [16]. Because the stem hummingbird Parargornis also possessed elongate legs, it is likely that the shortened hindlimbs of extant swifts arose after the divergence between swifts and hummingbirds, perhaps in order to conserve mass in support of a highly aerial lifestyle [13].

Eocypselus rowei falls within the lower end of the size spectrum for extant swifts. This species represents the smallest reported avian species from the diverse Green River avifauna. With the exception of the elongated carpometacarpaceus, all overlapping skeletal elements are shorter than those of the tiny birds Eozygodactylus americanus [54] and Neantis kistneri [55]. Consistent with a mass reduction strategy, extant Apodiformes are very small birds and include the smallest known avian species Mellisuga helenae (bee hummingbird). Most fossil and extant representatives of Strisores are relatively large birds, though the Aegothelidae (owlet nightjars) fall within the size range of large swifts. Given the small size of E. rowei and support for Aegothelidae as the extant sister clade of Apodiformes [17], a shift to small body size can reliably be inferred to have occurred well prior to the swift–hummingbird split.

Eocypselus rowei offers a glimpse into the early evolution of one of the most diverse and ecologically important clades of birds. Similar stem Pan-Apodiformes survived alongside more derived stem swifts for much of the Eocene, but appear to have died out by near the Eocene–Oligocene boundary in Europe [56]. Owing to the very sparse North America record and complete lack of sampling in South America, the patterns of replacement among Pan-Apodiformes in the New World remain shrouded in uncertainty.

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