A new Eocene anagalid (Mammalia: Euarchontoglires) from Mongolia and its implications for the group’s phylogeny and dispersal

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Anagalidae are extinct primitive Euarchontoglires from Asia, regarded as relatively closely related to basal Glires. So far, the group has been reported only from China and stratigraphically spans from the early Paleocene to the latest Eocene/earliest Oligocene. Anagalids are characterized by a relatively full dental formula featuring slightly enlarged semi-procumbent incisors, prominent canines, and tall cheek teeth with usually heavily worn crowns, indicative of an abrasive diet. Here we report a new genus and species from the late Eocene Ergilin Dzo Formation in southern Mongolia. The first non-Chinese anagalid is also the northernmost record of the family. Zofraigale ergilinensis gen. and sp. nov. is remarkable for its relatively small size (comparable only to the Paleocene genera Huaiyangale and Stenanagale), lack of P1, and molariform teeth showing almost no wear, suggesting a different diet than most Anagalidae. Furthermore, its molars display a strong buccal cingulum, a character in anagalids shared only with Wanogale. Our phylogenetic analysis of representatives of all anagalid genera based on 82 dental characters places Anagale and Anaptogale as the most basal lineages and clusters Zofraigale gen. nov. together with Oipania and Hsiuannania. These results suggest three independent northward dispersal events within the family in the late Eocene.

Anagalidae is an enigmatic and poorly studied group of primitive members of Euarchontoglires known from the Paleogene of Asia, with its geographic distribution so far restricted to China. The only genus ever considered to be an anagalid from outside of China, namely Khashanagale from the Gashato Formation in Mongolia, was reassigned later by McKenna and Bell to Oxyclaenidae, a condylarth-related group of poorly recognized relationships.

The taxonomic status of anagalid genera is contested and different sources consider true anagalids a different number of genera. The first and only phylogenetic analysis of anagalids was done by Hu, who considered just seven of the 14 genera to be unquestionable anagalids. The seven genera were Anagale, Anagalopsis, Limnania, Huaiyangale, Hsiuannania, Eosigale, and Qipania. Hu classified Stenanagale, Anaptogale, and Diacromus tentatively within Anagalidae, but excluded Khashanagale, Chianshania, and Wanogale from the family.

In a recent work, Li considered the three genera that Hu removed from the family as tentative anagalids, and also included Interogale (described by Huang and Zheng) within? Angalidae, a genus that Hu did not discuss.

Anagalids were never common, but their fossil record drops substantially after the middle Paleocene (Nongshanian Asian Land Mammal Age), with the only presence of Anagale from the late Eocene (Ulangochuan ALMA) and Anagalopsis, estimated generally in a broader frame of the earliest Oligocene, but see Zhang and Wang for an earlier estimate. No anagalids have been reported from the early Eocene (Bumbanian and early Arshatan ALMAs) and most of the middle Eocene (recently Li et al. described unidentified anagalid remains from Irdinmahan deposits of Wulanhuza in Nei Mongol). Because of the aforementioned uncertain date of Shanmacheng (Shih-e-ch'eng as reported in Bohlin), the type locality of Anagalopsis kansuensis, it can be

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hard to determine the more precise date of extinction of this group of early Euarchontoglires. However, anagalids were certainly present in Asia for nearly 30 million years.

Here we describe a new anagalid from the late Eocene of the Ergilin Dzo Formation in Mongolia (Fig. 1), the first member of Anagalidae found outside of China, and the northernmost representative of the group. It is characterized by a unique dental morphology and relatively small size. We assign this specimen to a new genus and species. Furthermore, we aim at reconstructing the phylogenetic relationships within Anagalidae in only the second cladistic analysis after Hu’s4, using an extended character-data matrix.

Results

Systematic Paleontology. Superorder EUARCHONTOGLIRES Murphy et al. 2001
Order ANAGALIDA Szalay & McKenna, 1971
Family ANAGALIDAE Simpson, 1931
Genus Zofiagale gen. n.

urn:lsid:zoobank.org:act:51CCC038-A454-4217-B849-6242FEE6F84C

Type species: Zofiagale ergilinensis sp. n., monotypic.

Etymology: Named after Professor Zofia Kielan-Jaworowska (1925–2015), for her exceptional contributions to the understanding of early mammalian fauna from Mongolia; and -gale, γαλή (feminine), Greek, meaning “weasel”, a common suffix used for the names of anagalids.

Distribution: As for the type and only species.

Diagnosis: As for the type and only species.
Zofiagale ergilinensis sp. n.

urn:lsid:zoobank.org:act:1CB04445-F10A-40F5-809A-A6F4EE741C95 Fig. 2.

Holotype: ZPAL MgM-II/100 fragmentary right dentary with the canine alveolus, P₂ roots, and P₃–M₃ in situ; housed at the Roman Kozlowski Institute of Paleobiology, Polish Academy of Sciences, Warsaw, Poland (ZPAL).

Type locality and age: Ergilin Dzo locality, Ergilin Dzo Formation, Dornogovi Province, Mongolia (Fig. 1); Ergilian ALMA, late Eocene.

Diagnosis: Smaller than Anagale, Anagalopsis, Hsiuannania, and Qipania; comparable size to Linnania, Huaiyangale, Eosigale, and Interogale; and larger than Stenanagale; based on area of M₁. Further differs from Anagalopsis, Qipania, and Interogale in having a smaller canine alveolus. Further differs from all anagalids, except for Interogale, in lacking a P₁. From Anagale, Anagalopsis, and Linnania in lacking a diastema between P₂ and P₃. Further differs from Linnania and Eosigale in lacking a diastema between P₃ and P₄. Moreover, it differs from all anagalids, except for Eosigale, in lacking a paraconid on P₄. From Qipania and Interogale it differs in lacking a cristid obliqua on P₄. Further differs from L. lofoensis in lacking a paraconid on M₂, and differs from L. lofoensis, Interogale, and Wanogale in lacking a paraconid on M₃. Further differs from all anagalids, except for L. lofoensis, L. qinglingensis, Interogale, and Wanogale in having a hypoconulid on M₃–M₄. Further differs from L. lofoensis and Interogale in lacking a paraconid on M₃, and differs from all anagalids, except for Wanogale, in having a buccal cingulum on the lower molars. Additionally it differs from Anagalopsis, Linnania, Hsiuannania, and Qipania in having the enamel not extending into the alveolus.

Description and comparisons: The right body of the mandible is broken at the level of the canine alveolus, P₂ roots, and P₃–M₃, in situ; housed at the Roman Kozlowski Institute of Paleobiology, Polish Academy of Sciences, Warsaw, Poland (ZPAL).

Figure 2. Left mandible body of Zofiagale ergilinensis gen. et sp. nov. The holotype and only specimen (ZPAL MgM-II/100) with complete P₄–M₃, fragment of P₃, and roots of P₃ (A–F). Lingual (A), buccal (B,C), anterolingual (D), and occlusal (E,F) views, respectively. Magnification of the buccal sides of P₁–M₁, showing well-developed cingula (C). Note depth and inclined course of alveolus for semi-procumbent canine (D). Explanatory SEM image for dental loci and morphology (F). Abbreviations: c, canine; co, cristid obliqua; ec, ectoconid; hy, hypoconid; hyd, hypoconulid; mc, mesoconid; me, metaconid; pro, protoconid. (Figure created in Photoshop CS5 and Corel Draw X4 (v. 14.0) by Łucja Fostowicz-Frelik).
Li is known to lack a P₁ as well. Another rare characteristic for an anagalid seen in Zofiagale is the presence of a buccal cingulid on M₁–M₃, whereas most anagalids have a completely smooth buccal surface. There is only one other instance of an anagalid with a buccal cingulid: Wanogale. Wanogale is known from only an M₂ and also has another feature more typical of eutherians, which is the presence of a precingulid.

The dentition anterior to P₁ is lost, and only two roots and a large alveolus remain. The large alveolus is here considered to have hosted a moderately large, semiprocumbent canine. All the other anagalids for which information about the canines is known (Anagale, Anagalopsis, Eosigale, Qipania, and Interogale) show that they had relatively larger and stronger canines than those of, e.g., zalambdalestids, a group of Cretaceous Eutheria proposed as primitive members of Anagalida sensu lato. The semiprocumbent canines are known for Anagale and Qipania. No anagalid has a P₁ that is significantly larger than the rest of premolars, therefore it is more likely that the large alveolus hosted a canine rather than a P₁. The two roots between the canine and the P₂ could be interpreted either as a double-rooted P₁ with loss of P₁, or as a single-rooted P₁ and a single-rooted P₂. We favor the first interpretation, even taking into account that the loss of P₁ is rare in anagalids, and only Interogale seems to have lost this tooth position, as some morphological traits strongly imply a two-rooted condition on P₂. The first of the two roots is shifted buccally with respect to the second root, a pattern that coincides with the root positions in P₁ (indeed, the anterior root of P₁ is displaced more buccally than the posterior root, see Fig. 2E,F). This pattern is also seen in other mammals in which there is crowding of the premolars and no lower diastema, such as in the scandentian Pithecopus lowi (e.g., USNM 488054). Therefore, we interpret the buccal torsion of the P₂ and the lack of diastema as a clue that the two roots belong to one double-rooted P₂, the P₁ has been lost, and that there is a fairly high degree of crowding of the premolars in Zofiagale.

The P₃ is broken, with most of the trigonid missing, but the two roots are preserved. Because of the crowding of the anterior dentition, there is no diastema distal to P₁ in Zofiagale, whereas it is observed in Limnania, Eosigale, and Stenanagale. The remains of P₁ indicate presence of a large, tall and presumably single-cusped (protoconid?) trigonid and a small saddle-like talonid (Fig. 2A,B,E,F). The talonid is not basined and its buccal and lingual margins are much lower than the distal one, indicating presence of a mesio-cuspid hypoconulid. Also, the lingual margin of the talonid bears a well pronounced cingulid-like edge.

The P₁ has no metaconid, usually present in other anagalids. The only other anagalid known to lack a metaconid is Eosigale. The paraconid is also absent, although a paracristid is clearly visible. The lack of paraconid is more common in anagalids, and only Anagale and Limnania retain one. The protocristid directed linguodistally is strong and slopes lingually to the lingual side of the tooth, in fact somehow replacing functionally the missing metaconid (see Fig. 2F). The talonid is not basined and is similarly saddle-like as in P₁, but the distal margin bears a more pronounced eminence, which is probably a nascent hypoconulid, developed fully in molars.

The mesiodistal length of P₁ is smaller compared to that of M₁. This feature is shared by most anagalids, except for Eosigale and Qipania, which have similar mesiodistal lengths of the two tooth positions. The P₁ does not have a cristid obliqua, which is rarely present in anagalids (only found in Qipania and Interogale). The P₁ has a buccal cingulid, not seen in any other anagalid.

The M₁ does not have a paraconid, although the paracristid is present, and the trigonid basin is deep (Fig. 2F). Many characters of the dental crown, such as small cusps are sometimes difficult to observe in anagalids, as the crowns in most species are worn down very quickly in ontogeny. In any case, the presence of paraconid on M₁ has only been found in Limnania. The trigonid and the talonid of M₁ have approximately the same area, and the trigonid is less than double of the height of the talonid. The metaconid is higher than the protoconid, and the hypoconid and the entoconid have approximately the same height. The talonid is deeply basined, but the basin area is not very extended. There is a distinct cristid obliqua and small mesoconid at M₁. The entoconid is higher than hypoconid but its area is slightly smaller than the latter; it is also placed slightly more mesially than the hypoconid. A cusp-like, rounded hypoconulid is placed centrally at the distal margin of the tooth. The tooth bears a strong buccal cingulid, which causes some extension of the buccal side of the tooth.

The M₁ is larger than M₂ (Table 1) and more extended buccally. It also does not have a paraconid, but the paracristid is strong and the trigonid basin larger. This contrasts with the expression of the paraconid in Limnania, Interogale, and Wanogale (although there are generic differences in that respect). The metaconid is higher than the protoconid, and the hypoconid and the entoconid are approximately the same height. Both M₁ and M₂ have similarly developed hypoconulids, only present in a few other anagalids (Limnania, Interogale, and Wanogale). The talonid basin has a greater area than in M₁. A weak metaconid and cristid obliqua are present.

The M₂ is smaller than M₁ and also has no paraconid, although the paracristid is present. This contrasts with Limnania and Interogale, which have a paraconid in this locus. The trigonid and talonid are similar in breadth.

| Measurement                  | P₁     | P₂     | M₁      | M₂      | M₃      |
|------------------------------|--------|--------|---------|---------|---------|
| Total length                 | nd     | 3.02   | 3.38    | 3.41    | 4.69    |
| Trigonid width               | 1.47   | 2.14   | 2.74    | 3.28    | 2.69    |
| Trigonid lingual height      | nd     | 2.68   | 2.64    | 2.62    | 2.39    |
| Trigonid buccal height       | nd     | 2.48   | 1.88    | 2.17    | 1.94    |
| Trigonid lingual height      | 1.51   | 2.01   | 2.40    | 2.32    | 2.69    |
| Trigonid lingual height      | 1.30   | 1.76   | 1.42    | 1.62    | 2.09    |

Table 1. Dental measurements of Zofiagale ergilimensis gen. and sp. nov. (in mm). Abbreviations: nd = no data.
This is a rare feature in anagalids, since all other anagalids, except for *Anagalopsis*, have narrower talonids than trigonids. The talonid is taller than the trigonid, which is due to the upward curvature of the M₃ around the area of the hypoconulid lobe. This feature also occurs in *Huaiyangale*, *Eosigale*, and *Qipania*. The hypoconid and the entoconid are approximately the same height, but they are not quite aligned, the entoconid being marginally more distal. The talonid basin is extended and shallower having a relatively flat bottom; it forms a small extension towards a large and distally elongated hypoconulid and invades its surface to some extent (Fig. 2F).

All molars have a distinct hypoflexid. The enamel does not extend into the alveolus, in contrast to a few anagalids (*Anagalopsis*, *Linnania*, *Hsiuannania*, and *Qipania*; Hu 4); furthermore, the molar crowns are relatively wear resistant, a rare trait for anagalids.

**Phylogenetic analysis.** In order to assess the phylogenetic relationships of *Zofiagale* with other anagalid genera, we conducted a cladistic analysis. A list of anagalid-specific characters was created based on character diagnoses from Chow et al. 10, Xu 11, 12, Ting and Tong 13, Ting and Zhang 14, and Li 5, in addition to some of Hu’s 4 characters from his original phylogenetic analysis of the family. These characters have been complemented by characters taken from phylogenies of other groups of Euarchontoglires 1, 18, 19 (see Supplementary Material, Table S1). The primitive eutherian *Zalambdalestes lechei* was chosen as the outgroup for Anagalidae following some broader analyses on Glires 1, 2, 20, 21.

To correctly place *Zofiagale* in a phylogenetic context, a representative for each of the 14 anagalid genera were included. A total of 82 dental characters were scored for 15 taxa (see Supplementary Information 1). The analysis

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**Figure 3.** Hypothesis of relationship of known anagalid genera, with listed synapomorphies. The figured tree is the most parsimonious and only resulting tree of the analysis. For further details of the phylogenetic analysis see text and Supplementary Information (Table S1, and Dataset S1). Color code for character states: yellow (0), red (1), blue (2), green (3), and purple (4). (Figure created by Sergi López-Torres with Corel Draw X4 (v. 14.0)).

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yielded a single most parsimonious tree (Fig. 3). Anaptogale and Anagale are the most basal anagalids in this tree, and constitute two separate primitive lineages (Fig. 3). The rest of anagalid taxa are evenly distributed between two distinct clades. Zofiagale is a sister taxon to Hsiuannania and Qipania, and, in turn, this clade is the sister group to a clade composed of Chianshania and Eosigale, and Huaiyangale at a more basal position. The second major clade contains a clade grouping most genera presumed tentative anagalids (as per Hu4), such as Stenanagale, Wanogale, and Interogale, with Limnania being the most basally nested, and Anagalopsis clustered with Diacronus.

Discussion
Anagalidae are a poorly known group of placental mammals with no extant representatives. The type and best known genus is Anagale gobiensis. By virtue of its almost complete skull and some postcranial remains8, Anagale has been often used in phylogenetic analyses of Eutheria where it has appeared well nested within Euarchontoglires1,22. Our results challenge the general topology of Hu’s hypothesis of relationships among anagalids, relegating Anagale to a basal position on our tree, and separating Limnania and Anagalopsis from Eosigale, Huaiyangale, and Hsiuannania–Qipania cluster. Our tree, however, agrees with Hu’s on the close relationship between Hsiuannania and Qipania, and Huaiyangale and Eosigale. Our tree shows a split between two major groups of anagalids. One of these clades includes Hsiuannania, Qipania, Zofiagale, Huaiyangale, Chianshania, and Eosigale. This clade appears well supported by a few synapomorphies: a P3 smaller than P4, presence of a paracingulum on M1, absence of a paraconule and a metaconule on M1–2, absence of a diastema distal to P2, a talonid taller than the trigonid on M1, and a smaller area of M1 compared to M2. The clade includes four out of seven taxa of Hu’s unambiguous anagalids. The other major group of anagalids is composed of Interogale, Wanogale, Stenanagale, Limnania, Anagalopsis, and Diacronus. This clade is well supported by the following synapomorphies: presence of a minute parastyle on M2, a distinctive paraconule and metaconule on M1–2, an erect rather than semi-procumbent lower canine, a large root of the lower canine, and a trigonid taller than the talonid on M1.

A new genus Zofiagale is well nested within the anagalid tree; in fact, it represents one of the most derived taxa, closely related to Hsiuannania and Qipania. It shows some unique dental characters which stress its independent phylogenetic heritage and imply a long evolutionary history. Interestingly, Zofiagale shares its two most characteristic features with species which do not show the most typical anagalid dental morphology and whose anagalid status has been questioned. With Wanogale it shares a strong buccal cingulum on lower molars and crowns that do not heavily wear down, and with Interogale, a lack of P1. Although Hu did not consider Wanogale to be an anagalid, Li placed it as a tentative member of the family. On the other hand, Interogale, also of questionable status, was considered as belonging to Tilodontia by Wang and Jin26. The taxon sample for our tree does not allow us to decide on what is and what is not an anagalid. In order to do so, other non-anagalid euarchontogliar representatives (i.e., primates, scandentians, lagomorphs, rodents, etc.) should be included in a broader phylogenetic analysis; of course, this raises the question if anagalids are paraphyletic, especially because many tentative anagalids according to Hu and Li are well nested within our sample. Such phylogenetic analysis including representatives of euarchontan and Glires lineages is necessary also to properly assess the position of anagalids within the broader framework of Euarchontoglires. However, an analysis of this magnitude is beyond the scope of this study.

The time bracket for the anagalid evolution spans from the early Paleocene to late Eocene/earliest Oligocene, with the timing of Anagalopsis occurrence still a matter of debate5,26. Nevertheless, it is one of the last occurring anagalids, together with Anagale and Zofiagale (Fig. 4). The fact that all three northern anagalids belong to three
distinct lineages within the family suggests that dispersal events between southern and northern China (including the Mongolian Plateau) were probably common sometime between the late Paleocene and late Eocene, and these happened at least three times within Anagalidae.

Most anagalids have significantly worn-down cheek teeth, which has led McKenna\(^24\) to suggest that they may have obtained fairly abrasive food below the surface of the ground. This view endorsed Bohlin’s\(^8\) idea that anagalids were potentially fossorial. However, back in 1963, the only anagalids known were Anagale and Anagalopsis, and the variety of dental shape and body masses reported in anagalids have increased greatly (Fig. 5). The present record of anagalids shows taxa with non-worn or lightly worn cheek teeth, such as Zofiaagale and Wanagale. This suggests that their diet could not be primarily composed of abrasive foods, and most probably would differ from that suggested for Anagale and Anagalopsis. It is, however, worth noting that this inference derives from a sample size of a single specimen and should therefore be taken with caution. Alternatively, ZPAL MgM-II/100 could belong to a very young adult (the M3 is erupted) who has not started wearing down the crowns. However, if that was the case and this animal had an abrasive diet, it would be expected to find differential wear between M1 and M3 (\(i.e., M_3\) erupts later), and there is not.

Zofiaagale is one of the smallest anagalids, with an estimated body mass of 516 g, Kay’s\(^25\) threshold sets a minimum of 500 g for primates to acquire their protein mainly from leaves based on observations of modern primates, with species below that mass being mostly insectivorous. Besides Eocene euprimates, this threshold has been used in Paleocene and Eocene plesiadapiforms and non-primate euarchontans as well\(^26–29\) and could be tentatively informative in other early Paleogene mammals of generalized morphotypes similar to those of plesiadapiforms. The estimated body mass for Zofiaagale sits closely to the 500 g threshold, suggesting that an animal this size could easily acquire protein from both insects and leaves, without relying solely on any of the two. Given the blunt cusps, it is likely that the diet of Zofiaagale might have been largely enriched with fruits. Whereas the presence of a buccal cingulid (rare in anagalids) helps providing gingival protection from the opposing upper tooth and/or food\(^30–32\), it also effectively broadens the tooth, generating more surface for pressing a bolus of fruit.

Methods

The specimen was photographed with a scanning microscope Hitachi S–3400 N without coating, in a natural mode (low vacuum) at the Museum and Institute of Zoology, Polish Academy of Sciences, Warsaw, Poland. Furthermore, we documented the specimen using a Keyence digital microscope VHX 5000, and a Nikon (SMZ-800) stereo-microscope at the Institute of Paleobiology (IPAL), Polish Academy of Sciences, Warsaw. The measurements (Table 1) were taken using SYLVAC digital caliper and Keyence digital microscope software with an accuracy to the nearest 0.01 mm. Dental terminology generally follows Meng and Wyss\(^22\).

Geological settings. The specimen described here comes from the Ergilin Dzo ridge (“Promontory Bluff”), the locality discovered in 1922 by one of the Central Asiatic Expeditions of the AMNH\(^33,34\), in the Dornogovi Province, southeastern Mongolia. The specimen was collected in 1963 by a Polish field party during the first Polish-Mongolian Paleontological Expedition\(^35\). The Polish team prospected only the southeastern part of the ridge of Ergilin Dzo, in the vicinity of Ergil Obo (=Ardyin Obo as reported in Andrews\(^43\)) and Ergil Ula\(^35\). The Ergilin Dzo ridge is an eminient promontory, ca. 50 km in length, stretching in the EW direction (at ca. 43° 29’ N latitude and 109° 1’ E longitude\(^36\)), composed of late Eocene sediment beds, which comprise the Ergilin Dzo Formation\(^36–38\). The faunal list of fossil vertebrates recovered from Ergilin Dzo currently includes approximately 60 taxa\(^39\) (see also Supplementary Information), with more than 40 mammals assigned to Eulipotyphla, Lagomorpha, Rodentia, Carnivora, ‘Condylarthra’, Artiodactyla, and Perissodactyla\(^37,39–41\) (see Supplementary Information for a detailed list and additional references), the last two groups being the most diverse.

The age of the Ergilin Dzo Formation was originally established as pertaining to the Oligocene\(^36,37\), and the Ergilian ALMA was proposed as an early Oligocene ALMA\(^36\); it was further correlated with the Chadronian NAOM (North American Land Mammal Age). Because the Chadronian, considered equivalent to early Oligocene is now placed in the late Eocene as a result of the revised Eocene-Oligocene Boundary\(^46\), consequently the Ergilin Dzo Fm. also moved into the latest Eocene in age (most probably the middle to late Chadronian; 35.7–33.7 Ma approximate). At present, Ergilin Dzo is a reference section for the Ergilian ALMA, which precedes

Figure 5. Body mass estimates for representatives of Anagalidae. Based on M₃ area, following Conroy’s (1987) equation. Light gray, Eocene species; black, Paleocene species. (Drawing made by both authors with Corel Draw X4 (v. 14.0)).
the earliest Oligocene Shandongian ALMA. The Ergilin Dzo area during the late Eocene witnessed an increasing aridification towards forest-steppe, which agrees with paleoenvironmental conditions at the Eocene-Oligocene transition in central Asia.

**Cladistic analysis.** A parsimony analysis was performed using TNT 1.5 with all characters equally weighted. Multiple character states were set to be interpreted as polymorphisms, instead of uncertainties. Forty-one of the 82 characters (1, 7, 12–13, 20–23, 26–31, 33–34, 37–38, 40, 43, 46, 48, 53, 57, 59–63, 65–72, 75, 79–82) were ordered based on a morphological criterion, and the rest were unordered. A traditional search was implemented with 1000 repetitions. The tree-bisection-reconnection (TBR) algorithm was used for branch swapping, with 1000 trees to save per replication.

**Size estimation.** We estimated the body mass of Zofigale and comparative anagalid taxa using Conroy’s equation for prosimians. Although Zofigale is not a primate, Conroy’s equations have been used to estimate body mass for plesiadapiforms and anagalids have a more similar generalized morphotype to plesiadapiforms than to modern Glires. Therefore, an equation based on a prosimian subset would be preferable for anagalids, rather than equations based on living rodents or lagomorphs.

**Nomenclatural acts.** This published work and the nomenclatural acts it contains have been registered in ZooBank, the Official Register of for the International Code of Zoological Nomenclature (ICZN), mandatory for electronic-only publications. The ZooBank LSIDs (Life Science Identifiers) can be resolved by appending the LSID to the prefix “http://zoobank.org.” The LSID for this publication is urn:lsid:zoobank.org:pub:65C21FB2-3E88-4A00-8900-6380A4661E81. The identifiers for taxa appear following each new name (see Systematic Paleontology).

**Data Availability**

All data generated or analyzed during this study are included in this published article (and its Supplementary Information files).

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Author Contributions
Ł.F.-F. designed the project. Both authors performed the research, analyzed data, discussed results, and wrote the manuscript.

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