A new, large-bodied omnivorous bat (Noctilionoidea: Mystacinidae) reveals lost morphological and ecological diversity since the Miocene in New Zealand

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A new genus and species of fossil bat is described from New Zealand’s only pre-Pleistocene Cenozoic terrestrial fauna, the early Miocene St Bathans Fauna of Central Otago, South Island. Bayesian total evidence phylogenetic analysis places this new Southern Hemisphere taxon among the burrowing bats (mystacinids) of New Zealand and Australia, although its lower dentition also resembles Africa’s endemic sucker-footed bats (myzopodids). As the first new bat genus to be added to New Zealand’s fauna in more than 150 years, it provides new insight into the original diversity of chiropterans in Australasia. It also underscores the significant decline in morphological diversity that has taken place in the highly distinctive, semi-terrestrial bat family Mystacinidae since the Miocene. This bat was relatively large, with an estimated body mass of ~40 g, and its dentition suggests it had an omnivorous diet. Its striking dental autapomorphies, including development of a large hypocone, signal a shift of diet compared with other mystacinids, and may provide evidence of an adaptive radiation in feeding strategy in this group of noctilionoid bats.

The main islands of New Zealand are the largest emergent part of the continental fragment of Zealandia, other landmasses of which today include New Caledonia, Lord Howe, Chatham and Campbell Islands1,2. Zealandia separated from the Australia-Antarctica part of Gondwana in a split that began 130 Ma (million years ago), with the Tasman Sea opening from south to north in the interval 83–52 Ma3,4 and with ~1600 km of ocean now separating Australia and New Zealand. Australia, Antarctica and South America remained connected until ~40 Ma, as the last vestiges of Gondwana5–7.

Today, New Zealand has a biogeographically highly distinctive fauna that includes many old endemic lineages and recent immigrants, with both vicariance and dispersal implicated in its assembly8,9. Its modern terrestrial mammal fauna comprises three bat species, all other modern mammals having been introduced during the last 800 years10. Chalinolobus tuberculatus, of the cosmopolitan bat family Vespertilionidae, is closely related to its Australian congeners and probably made a trans-Tasman crossing from Australia less than 2 Ma11. The other two Recent bat species, Mystacina tuberculata and M. robusta, are the only living members of the family Mystacinidae. These are morphologically and ecologically very distinctive chiropterans, also known as burrowing bats, which...
spend 30% of their foraging time on the forest floor, under leaf litter and on tree branches\textsuperscript{12}. Mystacina tuberculata is considered vulnerable to extinction and M. robusta critically endangered or extinct\textsuperscript{13,14}.

Mystacinidae is one of the six to seven extant families that make up the bat superfamily Noctilionoidea, along with the Neotropical families Phyllostomidae, Noctilionidae, Mormoopidae, Pteropusidae and Thyropteridae\textsuperscript{15}. Madagascar’s Myzopodidae is also typically included in Noctilionoidea as sister to the remaining families (e.g.\textsuperscript{16,17}), but some analyses of molecular data suggest it has a sister-group relationship with Vespertilionoidea (e.g.\textsuperscript{18,19}), or that it is sister to Emballonuroidea, or (within Emballonuroidea) Nycteridae\textsuperscript{20}.

With or without Myzopodidae included, Noctilionoidea is the only bat superfamily interpreted to have a Gondwanan origin\textsuperscript{16}. The noctilionoid fossil record is poor, especially for the Paleogene\textsuperscript{21,22}, but biogeographic reconstructions suggest that this morphologically and ecologically diverse superfamily probably originated in Africa (e.g.\textsuperscript{18,22,23}), with subsequent dispersal and radiation producing Australasia’s mystacinids and the five modern Neotropical noctilionid families. According to molecular data, the divergence of the Australasian and South American noctilionid clades occurred ~50–37 Ma\textsuperscript{20,24,25}.

Fossils show that mystacinids once occurred in Australia (26–12 Ma; ref.\textsuperscript{26,27}) and were present in New Zealand from at least the early Miocene\textsuperscript{28}. In New Zealand, remains of the two modern Mystacina species have been recovered from numerous Pleistocene and Holocene cave deposits\textsuperscript{29}. The Miocene mystacinid Mystacina miocenalis has been described\textsuperscript{30} and material indicative of two smaller mystacinid species has been reported\textsuperscript{30} from freshwater lake sediments (16–19 Ma) near St Bathans, Central Otago, South Island. The St Bathans fossil assemblage also includes plants, invertebrates, fish, frogs, lizards, kiwi, moa, New Zealand wrens, parrots, waders and many other water birds, a tuatara, crocodilian and turtle, and fragments of a small non-volant archaic mammal (e.g.\textsuperscript{28,31–37}). As Zealandiā’s only known Tertiary terrestrial vertebrate fauna, the St Bathans fossil assemblage offers critical insight into the deep-time history for most of its vertebrate lineages.

Here, we describe a new bat genus and species from St Bathans, and discuss its bearing on hypotheses regarding the radiation of the southern superfamily Noctilionoidea and the family Mystacinidae in the Australian region. This fossil bat indicates that there once was greater ecological diversity in the New Zealand’s bat fauna, and, as only the third bat genus recorded from New Zealand, it signals substantial loss of diversity since the Miocene.

**Systematic palaeontology**

Order Chiroptera Blumenbach, 1779

Suborder Yangochiroptera Van den Bussche & Hoofer, 2004

Superfamily Noctilionoidea Gray, 1821

Family Mystacinidae Dobson, 1875

*Vulcanops jennyworthyae* gen. et sp. nov.

(Figs 1–2)

**Generic diagnosis.** As for the type and only species.

**Stratigraphic and geographic distribution.** Lower Miocene of Central Otago, New Zealand.

**Etymology.** From *Vulcan*, mythological god of fire and volcanoes (Roman), and *ops*, a suffix commonly used for bats; in reference to New Zealand’s tectonically active nature, as well as to the historic Vulcan Hotel, centre of the hamlet of St Bathans, from which the fauna takes its name. The species name honours Jennifer P. Worthy in recognition of her pivotal role in revealing the diversity of the St Bathans Fauna.

**Holotype.** CM 2013.18.790, left dentary fragment with m2-3 (Fig. 1a–c), HH1a, Bannockburn Formation, Manuherikia River, Home Hills Station, Otago, New Zealand (see Locality and age).

**Referred specimens.** NMNZ S.42876, right m1, HH1a; NMNZ S.52078, right m1 (Fig. 1d–f), HH1a; NMNZ S.52076, left m1/2 (fragment), HH1a; CM 2013.18.916, left m1, HH1a (Fig. 2a); NMNZ S.44071, right M1, HH1a (Fig. 2d); NMNZ S.51461, right M1, HH1b Trench; CM 2013.18.1, left M1, Croc Site Layer 1; NMNZ S.51746, left M2, HH1b Trench; NMNZ S.50383, right M2, HH1a (Fig. 2b); NMNZ S.50778, right M1/2 (postero-lingual fragment), HH1a; NMNZ S.52400, left M3, HH1a Trench (Fig. 2c); NMNZ S.52351, right incomplete M3, HH1a; NMNZ S.50384, left M3 incomplete, HH1a. A minimum of four individuals is represented. Measurements of the fossils are given in Table 1.

**Locality and age.** Bed HH1a (New Zealand Fossil Record File number H41/f088), a 5–10 cm thick sandy conglomerate, 6.88–7.0 m above base of Bannockburn Formation, Manuherikia River section, Home Hills Station, St Bathans, Otago, New Zealand; 44.907944°S, 169.858222°E. HH1b Trench (H41/f0103), a 10 cm thick sandy conglomerate, 9.5–9.58 m above the base of the Bannockburn Formation, foot of hill 50 m across terrace from river bank, Manuherikia River section, Home Hills Station, Otago; 44.90780°S, 169.837833°E. Altonian local stage, lower Miocene, 19–16 Ma\textsuperscript{35}.

**Species diagnosis.** A bat with: m1-2 myotodont, with talonid longer and conspicuously wider than trigonid (particularly on m1), and rounded talonid basin; m1-2 paraconid buccally displaced, not aligned with metaconid and entoconid; m1-2 entoconid very tall, with pre-entocristid interrupted such that talonid opens lingually; m1-2 paraconid buccally displaced, not aligned with metaconid and entoconid; m1-2 paraconid buccally displaced, not aligned with metaconid and entoconid; m1-3 cristid obliqua curved, with inflection close to trigonid, contacting trigonid conspicuously buccal to midpoint between protoconid and entoconid; m1-3 with complete anterior, buccal and posterior cingulid; m1-3
with relatively shallow hypoflexid; m3 reduced in length and width, talonid narrower than trigonid, myotodont with small hypoconulid; M1-2 as wide as long, three rooted with anteroposteriorly extended lingual root, paracone reduced in volume but subequal in height with protocone, metacone taller, parastyle conical, non-cuspidate mesostyle on buccal margin of crown, postmetacrista elongated, large posterolinguually directed heel (hypocone shelf) bearing tall, bulbous hypocone, metaconule in postprotocrista with short posterolingual crest not reaching hypocone, protofossa long, deep and open posteriorly, narrow paracingulum present, posterior cingulum indistinct, lacking paraloph, metaloph and anterolingual cingulum; M3 long, metacone with complete premetacrista but no postmetacrista, heel (hypocone shelf) with small hypocone. An expanded description is given in the Supplementary Information online.

**Differential diagnosis.** Differ from other mystacinids (species of *Mystacina* and *Icarops*) in exhibiting the following traits: m1-2 paracristid buccally displaced, not aligned with metaconid and entoconid, with talonid conspicuously wider than trigonid; m1-3 cristid obliqua curved rather than straight, with inflection near trigonid, contacting trigonid buccal rather than at midpoint between protoconid and metaconid; m1-3 with only shallow hypoflexid; m3 more reduced in length and width; M1-2 with hypocone present and conical parastyle; M3 long with broad angles between ectoloph cristae and with hypocone shelf and hypocone present. Differ additionally from *Mystacina* spp. in M1-2 having long, wide heel (hypocone shelf).

Differ from myzopodids in having: m1-3 cristid obliqua curving linguually rather than buccally; all trigonids with equally wide trigonid angle; m3 with small hypoconulid present. Differ additionally from *Myzopoda* spp.

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**Figure 1.** *Vulcanops jennyworthyae* gen. et sp. nov., Bannockburn Formation, St Bathans, Central Otago, New Zealand. Lower dentition. CM 2013.18.790, holotype, left dentary fragment containing m2-3. (a) Buccal view; (b–b’) stereopair, occlusal view; (c) lingual view m2-3. NMNZ S.52078, paratype, right m1. (d–d’) Stereopair, oblique occlusal view; (e) buccal view; (f) occlusal view. Abbreviations: cld, cingulid; co, cristid obliqua; end, entoconid; ecd, entocristid; hyd, hypoconid; hyl, hypoconulid; med, metaconid; pacd, paracristid; pad, paraconid; pcd, postcristid; prcd, protocristid; prd, protoconid; tal, talonid; trig, trigonid. Scale bars = 2 mm.
in having: M1–3 with hypocone shelf and hypocone; M1–2 as wide as long, with broader angles between ectoloph cristae, preparacrista shorter than postparacrista and postmetacrista elongated, ectocingulum variably present but indistinct.

Differs from thyropterids and furipterids in having: m1–2 paraconid buccally displaced, not aligned with metaconid and entoconid; cristid obliqua contacting trigonid conspicuously buccal to midpoint between protoconid and metaconid; m1–3 with only shallow hypoflexid; m3 reduced in length and width; M1–3 lacking paraloph and metaloph; M1–2 with hypocone shelf and hypocone; M1–2 long with broader angles between ectoloph cristae; postmetacrista elongated; presence of ectocingulum; lacking buccally extruded mesostyles (deep

Table 1. Measurements (mm) of lower molars (m) and upper molars (M) of *Vulcanops jennyworthyae* gen. et sp. nov. from the lower Miocene Bannockburn Formation, St Bathans, Central Otago, New Zealand. *Figured, ‡holotype.
Body mass. Using the equations of Gunnell et al.38 and the proxies of upper first molar (M1) area, lower first molar (m1) area, and diameter of mid-shaft humerus, the body mass of eight of the ten known extinct and extant mystacinids are given in Table 2. For the previously known mystacinids, these values range from ~8.5 g (Icarops breviceps) to 39.3 g (Mystacina miocenalis). For Vulcanops jennyworthiae, the estimates are 42.6 g (based on M1 area) and 39.8 g (m1 area). This indicates a relatively large bat, compared with the median value of 13.8 g for 905 extant bat species (refs38,39; see Discussion).

Phylogeny
The 50% majority rule consensus of post-burn-in trees from our Bayesian total evidence analysis is given in Fig. 3. Mystacinidae, Furipteridae + Noctilionidae, Thyropteridae, and Mormoopidae + Phyllostomidae formed clades, all with relatively high support (posterior probabilities shown in Fig. 3). Yangochiroptera had 100% support; Noctilionoidea and Vespertilionoidea were sister groups but with low support (50%). Myzopodidae was the most distantly placed of the remaining clades, all with relatively high support (posterior probabilities shown in Fig. 3). The Bayesian analysis identified eight unequivocal synapomorphies uniting Mystacinidae (i.e. Icarops + Vulcanaops) and Mystacinid indet. 1,27 which are lacking in all other bat clades, all with relatively high support (posterior probabilities shown in Fig. 3). Body mass estimate

| Taxon                  | Location | Age      | Body mass estimate | M1       | m1       | humerus | Live weight |
|------------------------|----------|----------|--------------------|----------|----------|---------|-------------|
| *†Icarops jennyworthiae* | NZ       | E.Miocene| 42.6 (1)           | 39.8 (1) | —        | —       | —          |
| *†Mystacina miocenalis* | NZ       | E.Miocene| 39.3 (1)           | —        | —        | —       | —          |
| *†Mystacinid indet. 1*  | NZ       | E.Miocene| —                  | —        | 114.33 (1) | —       | —          |
| *Mystacina tuberculata* | NZ       | Holocene | 12.77 (20)         | 14.28 (20)| 112.23 (5) | 13.6 (300) | —          |
| *Mystacina robusta*     | NZ       | Holocene | 22.90 (12)         | 22.19 (12)| 117.70 (1) | —       | —          |
| *†Icarops paradox*      | Aus      | E.Miocene| 8.43 (2)           | 10.31 (1) | —        | —       | —          |
| *†Icarops aenea*        | Aus      | L.Oligo-E Mio | 17.74 (2)      | 21.52 (1) | 115.07 (2) | —       | —          |
| *†Mystacinid indet. 5*  | Aus      | L.Oligocene| 11.34 (1)         | —        | —        | —       | —          |

Table 2. Body mass estimates (g) of extinct and extant mystacinids from New Zealand (NZ) and Australia (Aus) based on equations in Gunnell et al.38 and using the proxies of upper first molar (M1) area, lower first molar (m1) area, and humerus mid-shaft diameter. † Indicates extinct taxon; E, Early; L, Late; (#), number of specimens. Humerus mid-shaft measured in this work. Dental and weight data from: 1, this paper (Table 1); 2, 30, 31, 32, 33, 34; 3, 35, 36, 37, 38, 39 (Codfish Is); 4, 40, 41, 42 (Coffin Is); 5, 43, 44, 45 (Stewart Is); 6 & 7, 27, 8, 29. No estimates available for Icarops breviceps (known from m2-326) but tooth size similar to I. aenea27, nor Mystacinid indet. 2 but distal humerus is smaller than in Mystacinid indet. 1.28
Bayesian total evidence analysis (mitochondrial and nuclear genes plus dental characters) places the New Zealand Miocene bat *Vulcanops jennyworthyae* among Australasia’s living and fossil mystacinids. The overall results of our phylogenetic analysis are broadly congruent with recent large-scale molecular studies of bats\(^1\). Like some of these studies (e.g.\(^2\)), our analysis raises questions about the inclusion of Africa’s Myzopodidae within Southern Hemisphere Noctilionoidea, suggesting instead that myzopodids may be more closely related to cosmopolitan emballonurids.

Our analysis finds a sister-group relationship between Madagascar’s extant *Myzopoda* species and North Africa’s *Phasmatonycteris* species, supporting referral of those fossil taxa to the family Myzopodidae\(^2\). These fossil taxa were described by Gunnell *et al.*\(^2\) from the Eocene Birket Qarun (~37 Ma) and Oligocene Upper Jebel Qatrani (~30 Ma) Formations of the Fayum in Egypt and referred to Myzopodidae on the basis of their lower dentitions (upper teeth are unknown). Although there are similarities between *Vulcanops* and myzopodids in the morphology of the lower dentition (e.g. m1-2 paraconid buccally displaced, not aligned with metaconid and entoconid, with talonid conspicuously wider than trigonid; m1-3 cristid obliqua curved rather than straight, with inflection near trigonid, and contacting trigonid buccal to rather than at midpoint between protoconid and metaconid; m1-3 with only shallow hypoflexid; m3 reduced in length and width with respect to m1-2; see Differential diagnosis), our phylogenetic analysis indicates these similarities are likely homoplastic.

Unequivocal noctilionoid families, from the Americas and Australasia, first appear in the fossil record slightly later: mormoopids 32–30 Ma in Florida\(^4\), mystacinids 26 Ma in South Australia\(^2\), phyllostomids 21 Ma in Panama\(^6\), and noctilionids and thyropterids 13–12 Ma in Colombia\(^7\). Furipterids are first recorded from the Pleistocene of Brazil, French Guiana, and Peru\(^8\). Older dates for the divergence of these lineages are estimated from recent molecular clock analyses (which use fossils as calibrations): Mystacinidae at 50.3 to 37.3 Ma\(^2\), and the base of the neotropical noctilionoid radiation (Thyropteridae + Furipteridae + Noctilionidae + Mormop teridae + Phyllostomidae) at 47.0 to 37.3 Ma\(^2\).
With respect to Southern Hemisphere palaeogeography, these divergence times long postdate estimated dates for the separation of India-Madagascar and Africa from Gondwana (>100 Ma), with Madagascar isolated in the Indian Ocean for more than 80 Ma\(^2\). The divergence dates, however, span those estimated for the breakup of the Australia-Antarctica-South America landmass, with Australia and Antarctica separating ~45 Ma and South America and Antarctica ~41 Ma\(^3\). New Zealand has been isolated in the South Pacific from ~52 Ma\(^4\), possibly before the divergence of the mystacinid lineage from other noctilionoids.

Based on phylogenetic inference and tectonic events, a number of biogeographic hypotheses have been proposed to explain the modern distribution of noctilionoids in the Southern Hemisphere. These include: a trans-Atlantic dispersal of stem noctilionoids from Africa to North or South America in the Eocene (e.g.\(^18\),\(^23\)); a North American origin (or transit) of stem noctilionoids, with dispersal to South America via an Eocene proto-Caribbean archipelago (e.g.\(^21\)); or an American origin or transit with subsequent dispersal of ancestral mystacinids to Australasia (e.g.\(^51\)). Gunnell et al.\(^22\) proposed that noctilionoids originated and initially diversified in Africa (giving rise there to myzopodids) with a subsequent dispersal to Australia (producing mystacinids) and then to South America via Antarctica (this lineage leading to the five neotropical noctilionid families).

Even if myzopodids are not noctilionoids, as suggested by some recent molecular data and by our total evidence analysis, one of these scenarios may still be valid. The modern bat crown-clade is thought to have originated in either Africa\(^52\)–\(^55\) or Eurasia\(^56\), with estimates for the age of the base of the extant bat radiation ranging from 62.6 Ma\(^56\) to 50.3 Ma\(^57\). Potential living sister-groups of Noctilioidea (sensu 20, i.e. excluding Myzopodidae) are vespertilionoids and emballonurids. These two speciose groups have cosmopolitan distributions, occurring on all continents except Antarctica today, but molecular data suggest their roots were in Africa (stem and crown) and their oldest fossils are from North Africa\(^48\). These data, and an estimated divergence time of ~50 Ma to 37 Ma for Noctilioidea\(^20\),\(^24\)–\(^25\), are not inconsistent with the many previous biogeographical hypotheses for the distribution of superfamily Noctilioidea outlined above.

The data are also potentially consistent with a vicariant origin of Mystacinidae (e.g.\(^56\)). In the early Paleogene, global temperatures were up to 12 °C higher than today, mainland Antarctica supported a frost-free, paratropical flora until 50 Ma and Nothofagus forests until at least 15 Ma, and intercontinental distances in the Southern Hemisphere were generally less than now\(^57\),\(^58\). The Paleogene remnants of Gondwana may have supported a broadly distributed noctilionoid fauna. If so, final fragmentation of the supercontinent may have led to the extinction of noctilionoids in Neogene Antarctica as ice-sheets grew\(^59\), with Mystacinidae vicariately isolated in the Australian region. However, fossil bats have yet to be found in Antarctica, and a divergence date for mystacinids from other noctilionoids of ~50 to 37 Ma, after isolation of New Zealand in the Pacific ~52 Ma\(^4\), suggests that their presence in at least New Zealand probably reflects one or more post-Gondwanan dispersals.

Other bats were present in the Australian region in the early Paleogene, as demonstrated by the archaic Australonycteris clarkae from the 55 Ma Tingamarra fauna of southeastern Queensland, Australia\(^60\),\(^61\). The likely route taken by the first bats to reach Australia is unknown (the relationship of Australonycteris to other early chiropterans from Northern and Southern Hemispheres is unclear\(^62\)). Between 55 and 26 Ma, there is long gap in the Australian mammal record\(^63\),\(^64\) but when it resumes in the late Oligocene mystacinids were widespread, occurring in deposits in both central and northern Australia\(^7\). In New Zealand's oldest terrestrial mammal-bearing deposit, in 19–16 Ma sediments of the lower Bannockburn Formation near St Bathans, mystacinids are present and there is evidence that long-term ecological associations between Mystacina and its arthropod prey and roost trees and food plants were already established\(^7\).

If Vulcanops is a mystacinid, as we suggest here, it brings the number of representatives of this bat family in the Miocene St Bathans fauna to four\(^27\),\(^30\). In Australia, at least another four mystacinid species, all in the genus Icarops, are recorded from Oligocene to Miocene deposits in South Australia, Queensland and the Northern Territory, with two species co-occurring in some Queensland deposits\(^27\). In our total evidence analysis (Fig. 3), Vulcanops forms a clade with Mystacina species, with Icarops species paraphyletic relative to Vulcanops + Mystacina; this arrangement is congruent with a single origin of New Zealand mystacinids from an Australian source, but the topology receives only weak support.

A striking feature distinguishing the dentition of Vulcanops from previously known mystacinids (Mystacina spp. and Icarops spp.) is the presence of a large hypocone on its upper molars (Fig. 2). This structure is similar to that found in neotropical noctilionoids (phyllostomids and mormoopids). In that speciose group, it appears to have evolved multiple times\(^65\), but it is otherwise uncommon (and particularly rare on M3) in bats with dilambdodont dentition. Outside Noctilioidea, a large bulbous hypocone also occurs in the late Eocene Egyptian bat Aegyptonycteris knightae Simmons, Seiffert & Gunnell, 2016\(^66\). The latter is known only from its dilambdodont M2-3 and is the only member of its family whose relationships to other bats are unknown\(^67\). This large fossil bat differs significantly from Vulcanops in that its M2-3 also have a large conule at the base of the metacone and an ectostyle on the buccal margin, two features unknown in other bat families, living or extinct\(^68\). Among mammals, a hypocone increases occlusal area, effectively doubling the tooth surface devoted to processing food\(^69\). It is strongly correlated with a less strictly carnivorous diet, often involving an increase in plant consumption\(^66\). In Vulcanops, a long, broad, deep talonid on m1-2, low curved postcristid (=posthypocristid), cristid obliqua lacking carnassial notches, and long broad protocone on M1-2 are also horizontal shearing adaptations associated with a relatively more herbivorous diet. At the same time, elongation of the molar crests as also seen in Vulcanops (postmetacrista on M1-2 twice length of preparacrista, shallow ectoloph, open angle of m1-3 trigonids, cristid obliqua meeting trigonid buccal to centre of crown) are adaptations for vertical shearing, possibly indicating relatively more flesh eating.

As body size increases in bats, species with dilambdodont molars often include small vertebrae in their diets\(^65\)–\(^70\). The presence of a well-developed hypocone in the ~40 g Vulcanops, however, argues against a strictly carnivorous diet. A tall, rounded hypocone is absent in flesh-eating bats (e.g. nycterids, megadermatids and phyllostomines Vampyrum and Trachops\(^71\)), although a crestiform hypocone is present in fish-eating noctilionids.
(Noctilio spp.) and is similar to the condition seen in some specimens of *Vulcanops* (e.g. CM 2013.18.916; Fig. 2a). Other aspects of Noctilio teeth that are possibly adaptations for piscivory (e.g. the discontinuous centrocrista of M1-2, in which the central blades reach the buccal margin of the crown, and the cristid obliqua of m1-2, which extends to the lingual margin of the crown) are very different from those of *Vulcanops*. The latter's dentition, and diet, was perhaps most similar to some phyllostomines that consume invertebrates, nectar, fruit, flowers, as well as small vertebrates (e.g. the large-bodied omnivorous *Phyllostomus hastatus*).

New Zealand's Recent * Mystacina* species also have very broad, omnivorous diets consisting of nectar, pollen, fruit, flowers, and flying and terrestrial arthropods, but are not known to hunt small vertebrates. However, *Vulcanops* exhibits several dental apomorphies, such as a large, blunt hypocone and long, broad, deep talonid, that are lacking in *Mystacina* species (as well as in Australia's extinct *Icarops* species) and suggest additional feeding capabilities in this extinct bat. No other extant or extinct bat known from the Australasian region has similar dental features. If a large blunt hypocone is indicative of increased herbivory in bats, as argued above (see also), this may provide evidence for the wider adoption, both geographically and taxonomically, of phytophagy in noctilionoid bats by the early Miocene. It may also have relevance to phylogenetic reconstructions of the ancestral diet in Noctilionoidea and its constituent families.

There is some evidence from dental remains that Australia's extinct *Icarops* species were more insectivorous than New Zealand's omnivorous extant and extinct *Mystacina* species. The derived features present in the dentition of *Vulcanops* that are absent in other mystacinids signal a further shift in diet. This could reflect exploitation of new, abundant and/or underutilized food resources in New Zealand compared with Australia where omnivorous peramelemorphian (bandicoot) and phalangerid (possum and kangaroo) marsupials were morphologically diverse, speciose and abundant in forest ecosystems shared with mystacinids. Baker et al. have argued that the adaptive radiation of feeding strategies seen in the extant and extinct noctilionoids (the most radical derived from a common ancestor for any monophyletic group of mammals – was triggered by the dietary inclusion of a common plant material in addition to insects, in concert with new environmental opportunities in Oligo-Miocene South America.

The large body size (~40 g) estimated for the early Miocene New Zealand mystacinids *Vulcanops jennyworthiae* and *Mystacina miocenalis* Hand, Lee, Worthy & Archer, 2015 is notable compared with other extant and extinct mystacinids (Table 2), and especially given that the ancestral body mass for noctilionoids and the *Mystacina* lineage has been estimated at ~10–14 g. The evolution of relatively large size in certain bat lineages has been associated with ecological release from the biophysical constraints imposed by flight and echolocation during aerial insectivory, and occurs in lineages exhibiting divergent dietary and behavioural specializations such as frugivory (e.g. pteropodids) or gleaner and perch-hunting behaviour in extreme insectivory and animalivory (e.g. megadermatids, noctilionoids). That some mystacinids have reached notably large sizes may be another example of this evolutionary trend. Mystacinids are renowned for their peculiar walking habits which enable them to exploit an exceptionally broad range of plant and animal resources, including ground-flowering plants and large invertebrate prey that they can pursue on foot.

In early Miocene New Zealand, *V. jennyworthiae* was part of a diverse faunal community living in semitropical to warm-temperate Gondwanan rainforest on the shores of the vast 5000 sq km Manuherikia palaeolake. A number of distinctive vertebrate taxa present in the early Miocene St Bathans assemblage, like *Vulcanops*, disappeared sometime before the late Pleistocene. These include crocodilians, terrestrial turtles, flamingo-like palaeloquenidae, swiftlets, several pigeon, parrot and shorebird lineages and non-volant mammals (e.g. *Icarops*). Most of these were probably warm-adapted species. After the middle Miocene, global climate change brought colder and drier conditions to New Zealand, with significant changes to vegetation and palaeoenvironments. It is possible that this general cooling and drying trend also drove extinction of the *Vulcanops* lineage, and overall loss in mystacinid diversity over time. In Australia, the *Icarops* lineage also went extinct, sometime after the late Miocene.
The total evidence matrix was analysed using an undated Bayesian approach in MrBayes 3.2.6.41. First, PartitionFinder 2.1.142 was used to select an appropriate partitioning scheme and set of models for the molecular data, assuming linked branch lengths, and using the "greedy" algorithm and AICc for model selection; only models implemented by MrBayes were tested. The morphological data was assigned the Mk model of Lewis43 assuming that variable characters had been scored, and with a gamma distribution with four rate categories to model rate heterogeneity among the morphological characters. The MrBayes analysis comprised four runs of four chains (three "heated," one "cold"), sampling trees every 5000 generations. The analysis was run for 5 × 106 generations, with the first 25% of sampled trees discarded as burn-in; the post-burn-in trees were summarised using 50% majority rule consensus, with Bayesian posterior probabilities as support values.

To estimate body mass in extinct bats, Gunnell et al.38 developed a set of algorithms based on dental, skeletal and weight measurements in 1,160 extant bats from eight families. We used these equations, and the proxies of upper first molar (M1) area, lower first molar (m1) area, and diameter of mid-shaft humerus, to estimate the body mass of eight of the ten known extinct and extant mystacinid taxa (Table 2).

The morphological datasets generated or analysed during this study are included in this published article's tables or are available in the MorphoBank repository as Project 2737 (http://morphobank.org/permalink/?P2737).

Nomenclatural Act. This published work and the nomenclatural acts it contains have been registered in ZooBank, the proposed online registration system for the International Code of Zoological Nomenclature. The ZooBank life science identifiers can be resolved and the associated information viewed by appending the life science identifiers to the prefix http://zoobank.org/. The life science identifier for this publication is 13BDBA9F-4BC3-4711-A331-4EB83DE52DC2, for Mystacina is 498FA8A8-7DAF-4703-94F3-02931CE7F85F, and for V. jennyworthyae is 3A625804-F490-46F6-BDA0-C93A6523EE6D.

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Author Contributions

S.J.H. & R.M.D.B. drafted the paper; T.H.W., A.J.D.T., R.P.S., M.A., S.W.S., V.D.P., R.M.D.B. carried out fieldwork; N.B.S., G.F.G., S.J.H. coded taxa for phylogenetic analysis; R.M.D.B. performed phylogenetic analyses; S.J.H. & R.M.D.B. drafted the paper; T.H.W., A.J.D.T., R.P.S., M.A., S.W.S., V.D.P., R.M.D.B. carried out fieldwork; N.B.S., G.F.G., S.J.H. coded taxa for phylogenetic analysis; R.M.D.B. performed phylogenetic analyses; S.J.H. produced the figures; all authors wrote parts of the paper, and read and approved the final version.

Additional Information

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