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Osteological observations on the larger species of the skink *Cyclodina* and the subfossil occurrence of these and the gecko *Hoplodactylus duvaucelii* in the North Island, New Zealand

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Abstract Some osteological characters by which the large *Cyclodina* species can be distinguished are described. Features of the dentary, frontal, parietal, maxilla, quadrate, and the braincase were of most use for specific identification. The subfossil distribution of these and the large gecko, *Hoplodactylus duvaucelii*, is examined and found to indicate a much broader range over the North Island for *C. whitakeri, C. macgregori, C. alani,* and the gecko. Reasons for the recent reduction of the range of these species are discussed.

Keywords Subfossil *Cyclodina; Hoplodactylus;* osteology; former distribution; recent extinctions

INTRODUCTION

Currently 23 species of skink and 17 geckos are recognised in New Zealand, but these numbers may change with further taxonomic revision (Towns 1985a). Of these, the gecko Hoplodactylus duvaucelii and some skinks of the genus Cyclodina (C. whitakeri, C. macgregori, C. oliveri, C. alani) are the largest and amongst the rarest (Towns 1985b). Each have apparently relict distributions, being restricted to islands scattered along the northeast coast of the North Island or around Cook Strait (Towns et al. 1985). The Cyclodina species are chiefly nocturnal and occur primarily in forest habitats whereas H. duvaucelii is presently more common on rocky beach cliffs and other marginal

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habitats. C. whitakeri is the only one of these species occurring on the mainland, inhabiting a boulder bank at Pukerua Bay on the Wellington west coast, in addition to its relict island distribution in northeast New Zealand. The numerous cracks and crevices in such a habitat probably afford this population protection from rat predation (Whitaker 1978; Towns 1985b). Negative correlations between the present distribution of these large lizards and that of kiore, Rattus exulans, provide strong circumstantial evidence that kiore may have reduced populations of this and other species (Whitaker 1973, 1978; Atkinson 1978; Towns et al. 1985). No direct cause and effect between kiore and lizards has been demonstrated. Since these species have geographically relict distributions it is possible that the habitats presently occupied are not entirely representative of those previously exploited.

New Zealand lacks a fossil record of terrestrial lizards and the subfossil record is poorly studied (Fordyce 1982). Subfossil deposits occur in swamps, dunes, and caves throughout New Zealand (Millener 1981; Worthy 1986). Additional material has been recovered from archaeological sites (e.g., Gill 1985; Anderson pers. comm.; Nichols pers. comm.). Most studies merely report the presence of a lizard fauna (e.g., Millener & Templer 1982; Worthy 1984), however, Gill (1985) demonstrated that bones from an archaeological site on Motutapu Island were those of a skink.

I examined the subfossil lizard fauna of New Zealand to determine whether any of these five large species are present and, if so, what were their former distributions. Osteological descriptions of *Cyclodina* species do not exist; thus, diagnostic characters likely to be present in subfossil material were sought by study of reference material. Length data for subfossil *C. alani* were examined to see whether the range of the extant populations are representative of those that occurred in the past. Evidence for the date of retraction of these species from their former range was sought, and this is discussed in relation to the advent of the kiore in the New Zealand fauna.

MATERIALS AND METHODS

Subfossil collections of the following institutions were examined: the Auckland University Geology Department (AU); Waitomo Caves Museum (WO); and the National Museum (NMNZ). In addition, caves in Northland, around Waitomo, in Hawkes Bay, the Wairarapa, northwest Nelson, Punakaiki, and Fiordland were searched for subfossil remains. Collections made were subsequently lodged with the Waitomo Caves Museum or remain in the author's collection. All material ascribed to these species is listed in Appendix 1.

Subfossil material was compared to the following reference skeletal material from the Auckland Institute and Museum (AIM), and the National Museum (NMNZ):

Cyclodina oliveri — NMNZ R920, AIM H885, AIM H882; Cyclodina whitakeri — AIM H839; Cyclodina macgregori — NMNZ R1634, NMNZ Unreg.; Cyclodina alani — NMNZ R1854; Hoplodactylus duvaucelii — NMNZ R1852; and two unregistered skeletons in the National Museum from the South Trios Islands and from Coppermine Island. In addition skeletons of the following Leiolopisma species were compared with those of Cyclodina: L. suteri (NMNZ Unreg., AM H674); L. smithi (NMNZ Unreg.); L. moco (AM H886); L. infrapunctatum (NMNZ R1853, NMNZ Unreg.); L. striatum (NMNZ R1736); L. zelandicum (NMNZ R1683); L. nigriplantare maccani (NMNZ Unreg.

2 ind.); L. acrinasum (NMNZ Unreg.); L. lineocellatum (NMNZ R1740). The bones of Hoplodactylus duvaucelii are easily recognised, being considerably larger than bones of any other endemic gecko in a comparable stage of development, and substantially different from those of skinks, e.g. Gill (1985). Comparisons with reference material were made in all instances verifying the initial identifications. Detailed comparisons of skeletal elements were made to enable specific

identification of subfossil remains of Cyclodina

species. The following elements were chosen

because they are the most frequently occurring bones in subfossil deposits: femur; humerus; dentary; frontal; parietal; maxilla; quadrate; and braincase. Illustrations of these elements were prepared with the aid of a camera lucida. Because teeth are successively replaced, tooth number included counts of tooth sockets, alveoli, which would usually be filled with teeth.

Identification of the three smaller *Cyclodina* species was reliant on diagnostic cranial bones being present. Limb bones were not diagnostic for these species. In contrast, those in the size range of, and of similar shape to, *C. alani* were considered diagnostic if from Waitomo or areas further south, since there is no indication among cranial material that any other large skink existed over this range. However, in Northland the former presence of an equally large or larger, possibly undescribed, species is known from Otangaroa Station Cave and the same or another species from dentaries in dunes at Tokerau Beach. The majority of bones here are femora or humeri and the presence of *C. alani* was only accepted if cranial bones were present.

X-ray studies of several preserved individuals of C. alani (NMNZ S666-669, S670-672, S760) were made to augment the skeletal comparisons. Two reference bones were placed on the plate with the specimens, thus enabling the measurements taken from the plate to be verified. These were only used if the relevant limb element was horizontal to the surface of the X-ray plate.

RESULTS

Osteological comparisons of the large extant *Cyclodina* species

Femora and humeri. The form of these bones is similar and no characters could be defined which reflected interspecific variation. Size and relative robustness of adult bones of C. *alani* is greater than for any of the other three species (Table 1).

 Table 1
 Length data for femora and humeri of the large Cyclodina species.

Species	Ref.	Left femur	Left humerus	Notes
C. alani	NMNZ R1854	15.4	13.2	complete
C. macgregori	NMNZ Unreg.	11.8	10.0	post. epiphyses absent
C. whitakeri	AIM H839	10.3	8.75	post. epiphyses absent
C. oliveri	AIM H885	12.8	10.9	complete
	AIM H882	11.2	10.0	epiphyses absent
	NMNZ R920	13.0		complete

Fig. 1 Length measurements of femora (hollow symbols) and humeri (solid symbols) of *C. alani* derived from X-ray plates of animals from Middle Is. (squares) and Green Is. (triangles) plotted against SVL.



Fig. 2 Medial views of dentaries for C. oliveri (A), C. whitakeri (B), C. macgregori (C), and C. alani (D), Leiolopisma infrapunctatum (E), to illustrate how Leiolopisma differs from Cyclodina. Scale bar in mm.

Measurements from X-ray plates plotted against snout vent length (SVL), (Fig. 1) indicate that the Middle Island population of *C. alani* reaches maximum size at about 115 mm SVL, with femora of 15-16 mm, and humeri of 13-14 mm in length. These data also suggest that the Green Island population consists of less robust individuals, i.e., the bones are relatively shorter for a given SVL. They also allow a reasonable size estimate of individuals represented in the subfossil assemblage.

The mean proportional length of humeri and femora relative to the SVL taken from X-rays of C. alani are 11.71% (SD=0.54) and 12.98% (SD=0.50). These values were used to calculate SVL for individuals of C. alani represented in the subfossil record. Sizes of humeri and femora ascribed to C. alani from Waitomo ranged in length from 13-18.5 mm, with a modal maxima between

17 and 17.5 mm (n=16), and a mean length of 16.3 mm. Eleven femora from Martinborough had a mean length of 16.4 mm and a range which was not significantly different from that for Waitomo. The mean length of humeri from Waitomo is 14.5 mm (n=12), but as four of the specimens were missing distal epiphyses their length would be 0.5-1.0 mm larger. These measurements were then used to calculate SVL, using the above proportions. Values so derived, ranged from 102 mm for the smallest femur (13.2 mm) to 140 mm for the largest (18.2 mm). Similarly, humeri provided values which ranged from 108 mm to 134 mm.

Calculated sizes of *C. alani*, from subfossil material, show that it was of uniform size throughout its previous range and that this is within that observed in extant populations (Gill 1985). The skink bones recorded by Gill (1985) were identified during this study as *C. alani*. Gill's specimen had a humerus length of 15.7 mm suggesting a SVL of 125-144 mm using the above ratios.

Dentary (Fig. 2). Dentaries of Leiolopisma and Cyclodina differ in the form of the two posterior notches. In the former genus the lower notch extends further anteriorly than the upper (Fig. 2E), whereas in *Cyclodina* the upper notch extends the furthest. Within the three smaller Cyclodina there is little variation other than number of teeth: C. oliveri has 29 and 30 teeth (n=3); C. whitakeri 31 (n=1); C. alani 29 (n=1); and C. macgregori 25 and 26 (n=2). Number of teeth varies by between one and three in several skink species (unpubl. data) and with age (Arnold 1980). Since all reference material of the smaller species was of mature individuals with dentaries of similar length, it seems probable that C. macgregori has fewer teeth than other species, but because of the low sample sizes a statistical test of significance for this was not possible. The dentary of C. alani differs from other species by its greater size and in having a proportionally greater change in height along its length.

Frontal (Fig. 3). Frontals are very similar in size and shape in each species except *C. alani* in which they are larger and proportionally longer. Frontals of *C. whitakeri* and *C. macgregori* have wider ventral processes than those in *C. oliveri*. The shape of the anterior margin varies with the degree of ossification exhibited by the specimen. The posterior margin of the frontal, where it articulates with the parietal, also varies. Similarly, the relative widths across the centre and posterior end may vary; however, without a larger sample such variation cannot be quantified and is not yet of diagnostic value.



Fig. 3 Ventral views of frontal bones of *C. oliveri* (A), *C. whitakeri* (B), *C. macgregori* (C), and *C. alani* (D). Scale bar in mm.

Parietal (Fig. 4). This bone shows significant interspecific variation in form, especially on the ventral surface associated with the two posterior processes. *C. macgregori* (Fig. 4C) has a sharply defined ridge crossing the posterior process at its origin. The parietal of *C. oliveri* (Fig. 4A) is relatively narrow across the apices of the ventrally directed lateral ridges. The parietal of *C. alani* (Fig. 4D) is considerably larger than that of other species, but is also distinctively shaped in that the posterior processes are angled on their exterior edge. At their base is a characteristic notch and ridge on the medial side.

Maxilla (Fig. 5). This bone differs between species principally in the form of the pars facialis, but other minor differences are apparent (Fig. 5). The



pars palatina is more domed in *C. macgregori* (Fig. 5C) than in other species. The maxilla of *C. alani* (Fig. 5D) is considerably larger than other species. *C. whitakeri* (Fig. 5A) has the highest maxilla tooth count, 28 (n=1), although the difference from other species is not as marked as for the dentary.

Quadrate (Fig. 6). Quadrates of these species exhibit a structure found to be characteristic of *Cyclodina*. The lateral expansion is sharply angled and often pronounced into a ridge running ventrally from the dorsal edge and the widest part of the lateral expansion is midway between the dorsal and ventral surfaces. This ridge is accentuated by a depression on its medial side. In comparison, quadrates in the *Leiolopisma* species examined had no ridge and the widest part was in the upper third of the bone's height, (Fig. 6E). Quadrates of *C*.

macgregori and *C. whitakeri* are similar to each other, whereas that for *C. oliveri* has a smaller fenestra. The quadrate of *C. alani* has a smaller fenestra and is considerably larger than other species. Accentuation of the ridge is restricted to the dorsal third of the bone whereas in other species it extends over the length of the ridge.

Braincase (Fig. 7). The braincase is a structure formed by fusion of the following elements: supraoccipitals; exoccipitals; opisthotics; basioccipitals; basisphenoid; parasphenoid; and prootic. This complex structure varies between species. All four species have a relatively poorly developed ridge along the zone of fusion between the prootic and the supraoccipital, a feature typical of *Cyclodina*. *C. alani* has a much larger braincase than the other three species, but it has the least expanded supraoc-



Fig. 5 Medial views of maxillae of *C. oliveri* (A), *C. whitakeri* (B), *C. macgregori* (C), and *C. alani* (D). Scale bar in mm; pp — pars palatina; pf — pars facialis.



Fig. 6 Quadrates of C. oliveri (A), C. whitakeri (B), C. macgregori (C), C. alani (D), and Leiolopisma infrapunctatum to illustrate how Leiolopisma differs from Cyclodina. Scale bar in mm.

Fig. 7 The braincase in dorsal (left) and right lateral (right) aspects. (A, B) = C. oliveri (C, D)= C. whitakeri, (E, F) = C. macgregori, (G, H) = C. alani. P = prootic; so = supraoccipital; zp = zygomatic process; bp = basisphenoid process; op = occipital process; pa = parasphenoid process, scale bar in mm.



cipital. A lateral view is largely obstructed by the zygomatic process. In dorsal aspect it is flat in posterior outline, whereas in the other species it is posteriorly expanded (Fig. 7G, H). In addition, the extent of the posterior notch on the supraoccipital just medial to the zygomatic process varies interspecifically. When the braincase is viewed in dorsal aspect as it rests on the occipital process and the basisphenoid processes (Fig. 7A, C, E, G), this notch is almost twice as wide anterio-dorsally in C. macgregori as in C. whitakeri or C. oliveri. The parasphenoid process is relatively larger in C. alani. The basisphenoid processes provide easily recognised variation. Those of C. oliveri are the most robust (Fig. 7A); those of C. macgregori and C. whitakeri are relatively thin (Fig. 7C, E). At the base of the basisphenoid processes is a complex area of spines which surround fenestra for the olfactory nerves. The structure of these spines is diagnostic (Fig. 8). In C. oliveri they are well developed and similar in shape to those of C. alani but extend anterior to the mesial origin of the basisphenoid process. In comparison they are relatively short and widely spaced in C. whitakeri, whereas in C. macgregori they are of similar length to the latter species but much closer together.

There is intraspecific variation in the following features: in the degree of development of the forwardly directed projection on the dorsal side of the supraoccipital; in the shape of the prootic; and the anterior parts of the basisphenoid processes. Hence, these features are of little taxonomic significance.

To summarise, the post cranial skeleton of the larger *Cyclodina* species does not vary significantly between species, except that all elements are larger in *C. alani.* However, a combination of cranial characters allows skeletons of each of these species to be identified with confidence. The maxillae, quadrates, parietals, and braincases may allow specific identification when in isolation. The larger size of the *C. alani* allows bones of this species to be easily separated from bones of the other species.

DISCUSSION

The majority of lizard subfossils are derived from cave deposits. Only one bone, referable to *H. duvaucelii*, is known from swamp deposits. A relatively large fauna is known from dune deposits, but because of the small size of lizard bones and the harsh condition they experience on ablating dune surfaces, only the more robust bones such as humeri and femora commonly survive. Skink bones are present, but very few can be ascribed to the genus *Cyclodina* with any certainty. The most common species appears to be a large *Leiolopisma*, a con-



Fig. 8 The basisphenoid processes showing structure of the basal spines for *C. oliveri* (A), *C. whitakeri* (B), *C. macgregori* (C), and *C. alani* (D). Scale bar in mm.

clusion supported by the occasional associated dentary which have a shape characteristic of *Leiolopisma*. Occasional bones of *H. duvaucelii* are also found. A few bones have recently been excavated from archaeological sites.

The majority of diagnostic material was from large *Cyclodina* species and most could be identified except in the case of a large, possibly undescribed, species from a cave near Kaitaia, in the far north. For Waitomo and areas further south there is no suggestion of any other undescribed species in the size range of *C. alani* or larger.

All subfossil material examined from the South Island lacked Cyclodina although bones of small geckos and Leiolopisma species were present (unpubl. data). The distribution of C. alani, C. macgregori, C. whitakeri, C. oliveri, and H. duvaucelii is tabulated in Appendix 1. C. alani was the most commonly occurring species although a fair comparison is not possible as, unlike other species, post cranial material was used for identifications. Also, since bones of this species are larger they are more likely to be preserved and recovered. C. macgregori and C. whitakeri were both recovered from several sites as far south as Waitomo. In comparison, the only evidence for *C. oliveri* is a single record from the far north. *H. duvaucelii* was widespread but rare.

Subfossil data confirm that C. alani, C. macgregori, C. whitakeri, and H. duvaucelii were once more widespread in the North Island than they are today. No evidence for a former South Island distribution was found. Although caution is needed in using negative evidence, it may be significant that no remains of C. oliveri were found at Waitomo or sites further south. This may imply a northern distribution for this species.

The subfossil distribution of C. alani and H. duvaucelii provides some insight into the preferred habitat of these species in prehuman times. Although the range of *H. duvaucelii* is similar to that for C. alani, there are differences in the frequency of occurrence in different areas. H. duvaucelii is most common in dune deposits and is relatively rare in inland cave sites (Appendix 1). Such dune deposits were laid down in forested habitats, 3000-4000 years ago (Millener 1981); these were certainly guite unlike the rocky cliff habitats frequented by the species today. C. alani was more common in inland sites within forested areas. This suggests that although both species were once widely distributed, H. duvaucelii may have preferred coastal forests and C. alani inland forests. The present distribution of these species does not provide any evidence to support or refute this conclusion as all populations are now restricted to small islands. Both Waitomo and Martinborough are believed to have supported mixed podocarpbroadleaf forests during the Holocene (Millener 1981; Worthy 1984; Yaldwyn 1958). The majority of the subfossils have accumulated over the last 14 000 years (Millener 1981; Worthy 1986). Sites containing herpetofauna which have been dated are few (Worthy 1986) and only two contain remains of the large species under consideration. The layer in which the herpetofaunal material was collected from F1c (a cave at Waitomo) has been dated by C14 methods to 1680 + 50 years BP (Worthy 1984). Herpetofaunal material from 'The Canyon' at Waitomo must be younger than the 2350 + 90 years BP estimated for the age of a moa found beneath the layer containing this material (Worthy 1986).

Thus, these large lizards, other than *C. oliveri*, were present throughout the North Island during the Holocene. The retreat from at least the Waitomo area occurred in the last 2000 years. Most avian extinctions in New Zealand occurred during the last 1000 years (Cassels 1984). The factors causing these extinctions are probably the same as, or linked to, those causing the decline of the lizard populations. Recent research into the subfossil frog

fauna of New Zealand (Worthy 1986) has revealed that three extinctions and the reduction in range of two other species can also be traced to this period.

Other large lizards have had their distributions severely reduced, e.g., Tuatara (Crook 1975). L. homalonotum is presently restricted to Great Barrier Island, but since there have been recent land connections to the mainland and as there is also a lack of other endemics on this island a previous mainland distribution seems probable. There is also the unique specimen of L. gracilicorpus from Hokianga in Northland. Perhaps the unidentified subfossil skinks from Northland deposits represent either of these species. Yet another large unidentified Leiolopisma has been found at Waitomo (unpubl. data). It is apparent therefore, that extinction of lizard populations is not just confined to the large *Cyclodina* species. In the South Island large bodied Leiolopisma have survived, albiet in isolated populations. However, these are diurnal species, that inhabit rock outcrops or screes (Towns 1985b; Towns et al. 1985) unlike the large North Island lizards, that are predominantly nocturnal and inhabitants of forested areas.

New Zealand was devoid of mammalian predators until about 1000 years BP when humans arrived with the dog and the kiore. Prior to this the main predators, birds, (e.g., raptors, kingfishers, rails, owlet-nightjars, and owls) had lived in association with the rest of the fauna for thousands of years. Therefore, the sudden appearance of man, a highly efficient predator, and the kiore, had predictably disastrous results. Cassels (1984) concludes that direct predation by man or kiore, and habitat changes brought about by either immigrant, were responsible for all of the avian extinctions. The small nocturnal ground dwelling frogs, *Leiopelma*, were represented by at least six species during the Holocene. The three largest are extinct, and two of the remaining have relict distributions caused by either predation, competition for a similar food resource, or a combination of both (Bell 1985; Worthy 1986). It is also probable that mainland New Zealand once had a more abundant largeinsect fauna, that is now largely restricted to ratfree islands (Ramsay 1978; Watt 1979). Direct evidence for this was found in a subfossil deposit at Waitomo where Worthy (1984) recovered the remains of about 24 insect species, mainly carabids and weevils. Four large, extinct, species were present in this assemblage dated from 1680 ± 50 years BP. Thus the diversity of the insect fauna has been reduced. Since forest floor invertebrates are the primary food of these lizard species, this reduction in their food supply, subsequent competition, and direct predation may well have been principle factors in the extinction of these species over most of their previous range.

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Appendix 1: A list of subfossil records for each of the large *Cyclodina* species and for *H. duyaucelii*

C. alani

- NORTHLAND REGION. Otangaroa Station Cave — WO332.7 9/2; Henderson Bay — AU4631 A 1 part skeleton (juv.); Tokerau Beach 2/1 + ?4/3 post cranial (author's coll.); Motutapu Is — NZAA N38/24 19/2, 20/1.
- WAITOMO REGION. F1c WO331.2 16/3; Opening Day Cave WO330.2 — 49/6; The Canyon WO341.1 — 2/1; Haggas Hole WO346 — 1 skeleton; Papamaru Cave WO345.1 — 6/1; Gardners Gut Cave WO347 — 1/1; Skyline Cave WO348 — 1 skeleton; Milns Cave WO349 — 1/1; Hilltop Cave WO Unreg. — 1 skeleton; Rorison's Quarry AU4975P 4/2; St.

Benedicts Caverns AU7091I — 12/1; Tapuae Weka Cave AU7092-E — 35/2; Raukuri A/T Cave AU7686-E — 1/1; Ben Stubb's Tunnel AU7689-C — 1/1; Cave of False Hopes AU7698 — 7/1; Little Lost World AU7700 — 7/3.

- COONOOR REGION. Manawatu Museum Site 25 1/1.
- MARTINBOROUGH. (All unregistered in the National Museum) Haurangi 15E 6/2; Haurangi 12 1/1; Haurangi 11 1/1; Haurangi 6 7/1; DM Cave 1 2/1; Fissure 2 47/7.

C. macgregori

- NORTHLAND. Otangaroa Station Cave WO332.3 — 3/3, WO332.6 — 9/3 (post-cranial material probably referrable to this species). Tokerau Beach 1/1 + ?1/1 post cranial (author's coll.).
- WAITOMO REGION. F1c WO331.1 4/2; Papamaru Cave WO345.2 — 1 skeleton; Tapuae Weka Cave AU7092-E — 1/1; Little Lost World AU7700 — 1 crania.

C. whitakeri

- NORTHLAND. Motutapu Is. NZAA N38/24 3/1.
- WAITOMO REGION. Tapuae Weka Cave AU7092-E — 76/8; Opening Day Cave WO330.1 — 7/1; Ruakuri Cave WO343 — 2/1; Footwhistle Cave WO344 — 1 skeleton.

C. oliveri

NORTHLAND REGION. Otangaroa Station Cave WO332.6 — ?1/1.

Hoplodactylus duvaucelii

- NORTHLAND. Tokerau Beach AU4833 2/1; AU6807.C — 3/1; AU6808.A — 1/1; AU7075 — 7/1 juv.; WO337.1 — 1/1.
- WAITOMO REGION. Companionway Cave WO333 — 1 skeleton; Little Lost World AU7700 — 12/1 juv.
- MARTINBOROUGH. Fissure 2 NMNZ Unreg. — 5/1; Haurangi 15E NMNZ Unreg. — 1/1.
- HAWKES BAY. Poukawa Swamp NMNZ S5478 - 1/1.