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# Taxonomic Revision of the New Zealand Copper Skink (*Cyclodina aenea*: Squamata: Scincidae) Species Complex, with Descriptions of Two New Species

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ABSTRACT.—**We completed a taxonomic revision for the New Zealand Copper Skink (*Cyclodina aenea*) species complex using morphological and molecular data. Two new species are described on the basis of several morphological characteristics, with the specific status of each species supported by mitochondrial sequence data (ND2). We also redescribe *C. aenea*. One of the new species is restricted to the Poor Knights Islands, whereas the distribution of the other new species is limited to northernmost region of Northland. Both new species exhibit significant genetic divergence from *C. aenea* (~13.5% sequence divergence), indicating that each species has evolved in isolation from *C. aenea* for a substantial period of time.**

New Zealand contains a diverse endemic skink fauna, with 29 described species in two genera, *Oligosoma* (23 species) and *Cyclodina* (six species; Hickson et al., 2000; Gill and Whitaker, 2001; Chapple and Patterson, 2007). *Oligosoma* species are distributed throughout New Zealand (North Island, South Island, Stewart Island, numerous outlying islands), whereas *Cyclodina* is restricted entirely to the North Island and outlying islands (Gill and Whitaker, 2001). The New Zealand skink fauna has experienced a complex taxonomic history caused by the conserved morphology evident in this group, concealing the species diversity that is present (Hardy, 1977; Patterson and Daugherty, 1990, 1995). Molecular studies have provided substantial insight into the taxonomy of New Zealand skinks, revealing a high incidence of cryptic species and providing an additional source of evidence for the description of new species (e.g., Daugherty et al., 1990). Here we use morphological and molecular data to complete a taxonomic revision of the Copper Skink (*Cyclodina aenea*) species complex.

The *C. aenea* species complex has a complex taxonomic history, with Hardy (1977) listing 23 synonyms for the species. *Cyclodina aenea* was first described by Girard (1857) from the Bay of Islands, although Hardy (1977) recognized that one of the syntypes of *Mocoa smithii* (Gray 1845) was in fact typical of *C. aenea*. Girard (1857) caused an additional complication by describing the species twice from specimens from the Bay of Islands, the second time as *Hombronia undosa* (Hardy, 1977). McCann (1955) created further confusion by restricting the name *C. aenea* to populations south of the 38° latitude, which lies approximately 300 km south of the Bay of Islands, and placing populations north of the 38° latitude in the new species *Sphenomorphus pseudornatus*. Hardy (1977) subsequently synonymized *S. pseudornatus* under *C. aenea* and resurrected *Cyclodina ornata* from synonymy. In addition, Hardy (1977) nominated a neotype for *C. aenea* (Te Papa, National Museum of New Zealand, RE1816 [S193], Blue Mountains, Hutt Valley, Wellington), because the holotype was listed as missing.

Hardy (1977) believed that the Poor Knights Islands population (Aorangi Island) was the only *C. aenea* population to exhibit any taxonomically significant variation. The Poor Knights Islands are located 24 km off the northeast coast of the Northland region (Fig. 1) and are believed to have been isolated from the North Island for 1–2 My (Hayward, 1986, 1991). Hardy (1977) demonstrated that *C. aenea* from the Poor Knights Islands were morphologically distinct (high scale counts, subocular series interrupted by the supralabial under the eye, third supraocular often meeting the frontal, and distinctive color pattern) and could be distinguished from most other *C. aenea* populations by allozyme electrophoresis. However, Hardy (1977) refrained from describing the Poor Knights Islands population as a distinct species because of hemoglobin electrophoresis evidence

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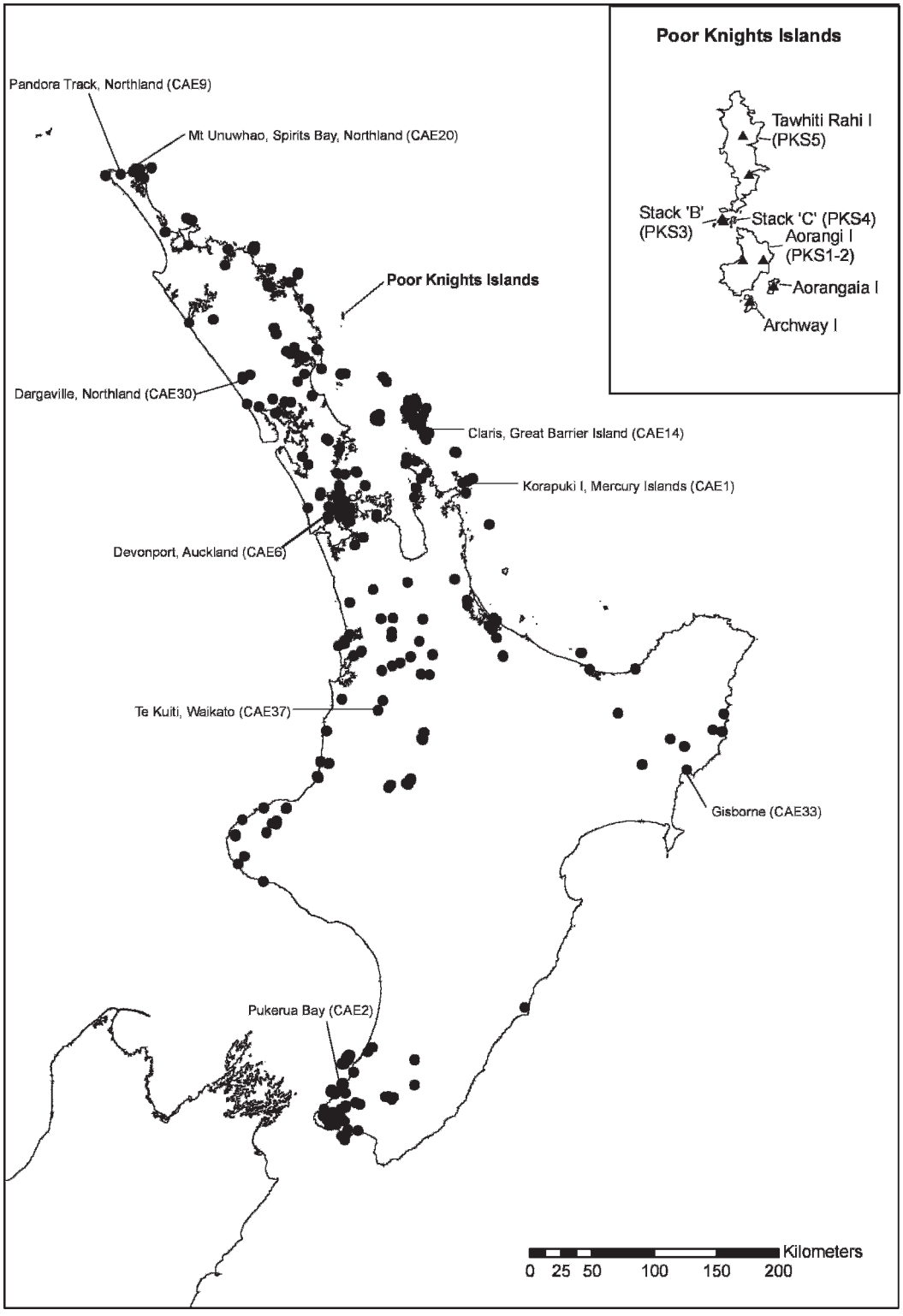
Poor Knights Islands
Tawhiti Rahi I (PKS5)
Stack 'B' (PKS3)
Stack 'C' (PKS4)
Aorangi I (PKS1-2)
Aorangaia I
Archway I
Pandora Track, Northland (CAE9)
Mt Unuwhao, Spirits Bay, Northland (CAE20)
Poor Knights Islands
Dargaville, Northland (CAE30)
Claris, Great Barrier Island (CAE14)
Korapuki I, Mercury Islands (CAE1)
Devonport, Auckland (CAE6)
Te Kuiti, Waikato (CAE37)
Gisborne (CAE33)
Pukerua Bay (CAE2)
Kilometers
0 25 50 100 150 200

indicating that it was similar to the Great Barrier Island population, which displayed typical *C. aenea* morphological characteristics.

Subsequent morphological (Vos, 1988), allozyme (Vos, 1988), and mitochondrial DNA (12S rRNA, Hickson et al., 2000) evidence have provided strong support for the specific status of the Poor Knights Islands ''*C. aenea*'' and indicated that this taxon is closely related to *C. aenea* (Daugherty et al., 1994). However, despite growing evidence since 1977 for its distinct taxonomic status, the Poor Knights Islands ''*C. aenea*'' have yet to be formally described. Here we complete a taxonomic revision of the *C. aenea* species complex using morphological data and mitochondrial DNA (ND2) sequence data. We describe the Poor Knights Islands ''*C. aenea*,'' a taxon that has been managed as a separate species by the New Zealand Department of Conservation for two decades (Towns, 1999), and redescribe the Copper Skink, *C. aenea*. In addition, our data reveal an additional new species within the *C. aenea* species complex from the northern extreme of Northland (*C. aenea* ''Te Paki''). This taxonomic revision of the *C. aenea* species group was listed as a research priority in the *Cyclodina* recovery plan (Towns, 1999) and, therefore, will enhance the conservation management of these species.

## Materials and Methods

*Morphological Analyses*.—We examined specimens from across the entire range of the *C. aenea* species complex. These specimens were obtained from Te Papa (National Museum of New Zealand, Wellington: RE codes; includes the specimen collection from the former Ecology Division, Department of Scientific and Industrial Research: S codes; the collection of Charles H. Daugherty, Victoria University of Wellington, is now housed at Te Papa: FT and CD codes). Descriptions of morphology, including color patterns, are based on preserved and live material.

Descriptions of morphology follow the techniques described in Patterson and Daugherty (1990, 1994, 1995). Midbody scale rows were counted at the midpoint between the fore- and hind legs. Ventral scales were counted in a line from the mental scale to the vent (including the mental and one preanal scale). The subdigital lamellae were counted on the fourth hind toe. Diagnostic head scales were counted (Patterson and Daugherty, 1990). The following nine measurements (in millimeters) were made on all specimens: axilla to groin (AG), snout to axilla (SF), snout to ear (S–E), ear to axilla (EF), head length (HL) from the posterior part of the interparietal to the tip of the snout, head width (HW) between the lateral edges of the left and right parietals, intact tail length (TL), snout–vent length (SVL), and hind-limb length (HLL; measured from the groin to tip of the fourth toe, including claw) (Patterson and Daugherty, 1990, 1994).

### *Mitochondrial DNA Analyses*

*Taxonomic Sampling*.—Tissue samples of the Copper Skink (*C. aenea*) species complex, including the Poor Knights Islands population, were obtained from the National Frozen Tissue Collection (NFTC; Victoria University of Wellington, New Zealand) and ethanol-preserved specimens housed at Te Papa (National Museum of New Zealand, Wellington; Table 1, Fig. 1). The tissue samples used were not always the same as those used for the morphological description (see morphological analyses section; Table 1). Representative samples from across the range of *C. aenea* were selected for inclusion in this study based on the results of a detailed phylogeographic study of *C. aenea* (Chapple, Daugherty, and Ritchie, unpubl. data). Based on the results of a broader phylogenetic study of the relationships among all members of the New Zealand skink radiation (Chapple et al., in press), we included samples from the Ornate Skink (*C. ornata*), the Marbled Skink (*Cyclodina oliveri*), the Common Skink (*Oligosoma nigriplantare polychroma*) and the Shore Skink (*O. smithi*) as outgroups (Table 1). Molecular evidence indicates that the genus *Cyclodina* is not monophyletic (Hickson et al., 2000), with the *C. aenea* species complex representing a separate lineage from the other *Cyclodina* species (Chapple, Daugherty, and Ritchie, unpubl. data).

*DNA Extraction, Amplification and Sequencing*.—Total genomic DNA was extracted from liver, toe, or tail samples using a modified

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FIG. 1. Distribution of the members of the Copper Skink (*Cyclodina aenea*) species complex in the North Island of New Zealand. The known localities for *C. aenea* are shown with black dots, while the distribution of Hardy's Skink (*Cyclodina hardyi*) on the Poor Knights Islands (see inset) is indicated with black triangles (Distributional information adapted from the BioWeb Herpetofauna database, New Zealand Department of Conservation, Wellington, 2006). The locality of tissue samples included in this study is indicated. The precise distribution of the Slight Skink (*Cyclodina levidensa*) is unknown, but it is believed to be restricted to the Te Paki region of Northland (e.g., Pandora Track, CAE9; Unuwhao, CAE20).

TABLE 1. Locality information and GenBank accession numbers for samples used in this study. Samples with CD or FT codes were obtained from the National Frozen Tissue Collection (NFTC) housed at Victoria University of Wellington, New Zealand. Samples with RE codes were obtained from ethanol preserved specimens housed at Te Papa, National Museum of New Zealand, Wellington (S codes refer to specimens from the former Ecology Division collection, now housed at Te Papa).

| Species | Tissue code | Museum code | Locality | GenBank accession no. |
|---|---|---|---|---|
| *Cyclodina aenea* | CAE1 | FT171 | Korapuki Island, Mercury Islands | EF567130 |
| *Cyclodina aenea* | CAE2 | FT5253 | Pukerua Bay | EF567127 |
| *Cyclodina aenea* | CAE6 | FT189 | Devonport, Auckland | EF567131 |
| *Cyclodina aenea* | CAE14 | RE4953 (S1316) | 1 mile south of Claris, Great Barrier Island | EF567132 |
| *Cyclodina aenea* | CAE30 | RE4298 (S656) | Dargaville, Northland | EF567133 |
| *Cyclodina aenea* | CAE33 | RE4131 (S489) | Gisborne | EF567129 |
| *Cyclodina aenea* | CAE37 | RE3995 (S353) | 2 miles north Te Kuiti, Waikato | EF567128 |
| *Cyclodina levidensa* | CAE9 | FT3729 | Kauri Bush, Pandora Track, Northland | EF567121 |
| *Cyclodina levidensa* | CAE20 | RE4749 (S1111) | Mt Unuwhao, Spirits Bay, Northland | EF567120 |
| *Cyclodina hardyi* | PKS1 | CD1036 | Aorangi Island, Poor Knights Island | EF567122 |
| *Cyclodina hardyi* | PKS2 | CD1037 | Aorangi Island, Poor Knights Island | EF567125 |
| *Cyclodina hardyi* | PKS3 | RE4902 (S1265) | Stack ''B,'' Poor Knights Islands | EF567124 |
| *Cyclodina hardyi* | PKS4 | RE4903 (S1266) | Stack ''C,'' Poor Knights Islands | EF567126 |
| *Cyclodina hardyi* | PKS5 | RE4905 (S1268) | Tawhiti Rahi Island, Poor Knights Islands | EF567123 |
| *Cyclodina ornata* | COR1 | FT188 | Devonport, Auckland | EF103954 |
| *Cyclodina oliveri* | COL1 | CD1034 | Aorangi Island, Poor Knights Island | EF033045 |
| *Oligosoma nigriplantare polychroma* | ONP1 | FT5252 | Pukerua Bay | EF033052 |
| *Oligosoma smithi* | OSM1 | FT166 | Middle Island, Mercury Islands | EF033055 |

phenol-chloroform extraction protocol (Sambrook et al., 1989). For each sample we targeted a portion of the mitochondrial gene ND2 (~600 bp). This region was targeted because work at comparable taxonomic levels in other squamate reptile groups has indicated useful levels of variability (e.g., Keogh et al., 2005; Greaves et al., 2008; Hare et al., 2008).

The primers used to amplify and sequence ND2 were L4437 (Macey et al., 1997) and ND2r102 (Sadlier et al., 2004). However, two internal primers were also used to amplify ND2 for some samples (ND2F-infrapunctatum, 5′-GCATGATTYACCGGAAYATGAGACAT-3′; ND2R-infrapunctatum, 5′-GGGGCAAGKCCTAGTTTTATGG-3′; Greaves et al., 2007). PCR and sequencing was conducted as outlined in Greaves et al. (2007).

Sequence data were edited using ContigExpress v9.1.0 (Invitrogen) and aligned using the default parameters of Clustal X (Thompson et al., 1997). The aligned sequences were translated into amino acid sequences using the vertebrate mitochondrial code to check whether the sequences were truly mitochondrial in origin. Because no premature stop codons were observed, we conclude that all sequences obtained are true mitochondrial copies. GenBank accession numbers for all sequences are provided in Table 1.

### *Phylogenetic Analyses*

A maximum parsimony (MP) tree was generated in PAUP* v4.0b10 (D. L. Swofford, Sinauer Associates, Sunderland, MA, 2002) using the heuristic search option. ModelTest 3.7 (Posada and Crandall, 1998) was used to determine the most appropriate model of evolution for our dataset, generating log-likelihood scores for the dataset in PAUP* and conducting a hierarchical likelihood ratio test (hRLT). Base frequencies, substitution rates, the proportion of invariant sites (I) and the among-site substitution rate variation were estimated in ModelTest, with

these values implemented in PAUP* to generate a maximum likelihood (ML) tree.

Bayesian analyses were completed using the computer program MrBayes 3.1.2 (Huelsenbeck and Ronquist, 2001). We used the default value of four Markov chains per run, and ran the analysis for one million generations. The chain was sampled every 100 generations to obtain 10,000 sampled trees. The first 2,500 sampled trees were discarded as the burn-in phase, with the last 7,500 trees used to estimate the Bayesian posterior probabilities. We used both bootstrap values and Bayesian posterior probabilities to assess branch support. Maximum-likelihood bootstraps (1,000 replicates) were generated in PAUP*. We consider branches supported by bootstraps values greater than or equal to 70% (Hillis and Bull, 1993) and posterior probability values greater than or equal to 95% (Wilcox et al., 2002) to be significantly supported by our data. Pairwise K81 corrected genetic distances were calculated in PAUP*.

## Results

### *Morphological Analyses*

### Genus *Cyclodina* Girard, 1857

### *Cyclodina hardyi* sp. nov.

Figure 2A

*Cyclodina aenea*: Girard, 1857 (in part). Hardy, 1977 (in part).

*Holotype.*—Stack ''C,'' Poor Knights Islands (35°31′S, 174°44′E), RE4903 (S1266) (collected by J. C. Smuts-Kennedy, November 1973). Adult male.

*Paratypes.*—Aorangi Island, Poor Knights Islands (35°29′S, 174°44′E), CD1036 (female), CD1037 (female) (collected by A. H. Whitaker and R. Morris, November 1984); Aorangi Island, Poor Knights Islands (35°29′S, 174°44′E), RE1617 (×8 specimens; 61: male, 62: female, 64: male, 66: female, 67: male, 68: female, 69: male, 70: female) (collected by G. S. Hardy, November 1973); Aorangi Island, Poor Knights Islands (35°29′S, 174°44′E), RE3724 (S79) (female), RE3725 (S80) (female), RE3726 (S81) (female) (collected by A. H. Whitaker, December 1964); Stack ''B,'' Poor Knights Islands (35°28′S, 174°44′E), RE4902 (S1265) (male) (collected by J. C. Smuts-Kennedy, November 1973); Tawhiti Rahi Island, Poor Knights Islands (35°27′S, 174°44′E), RE4905 (S1268) (male) (collected by J. C. Smuts-Kennedy, November 1973); Aorangaia Island, Poor Knights Islands (35°31′S, 174°44′E), RE4904 (S1267) (male) (collected by L. R. Moran, November 1973).

*Diagnosis.*—*Cyclodina hardyi* can be distinguished from all other *Cyclodina* species, including the other members of the *C. aenea* species complex, by having suboculars three and four separated by the fifth supralabial under the eye (Fig. 3). In addition, the midbody scale count is greater than that of the new species from the Te Paki region.

*Description of Holotype.*—Adult male, SVL 50.2 mm, tail not intact. Body elongate, squarish in cross-section; limbs moderately well developed, pentadactyl. Lower eyelid with a large, divided opaque central scale margined anteriorly and posteriorly by relatively large scales. Snout blunt. Nostril centered just below middle of nasal, pointing up and back. Supranasals absent. Rostral broader than deep. Frontonasal broader than long, not separated from frontal by prefrontals meeting in midline. Frontal longer than broad, shorter than frontoparietal and interparietal together, in contact with two anteriormost supraoculars. Supraoculars four, the second largest. Frontoparietals distinct, larger than interparietal. A pair of parietals meeting behind interparietal and bordered posteriorly by a pair each of nuchals and temporals, also in contact with interparietal, frontoparietal, fourth supraocular, and two postoculars. One primary temporal. Loreals two, either one the larger; anterior loreal in contact with first and second supralabial, posterior loreal, prefrontal, frontonasal and nasal; posterior loreal in contact with second and third supralabial, first subocular, upper and lower preocular, prefrontal and anterior loreal. Supralabials seven, the sixth largest. Infralabials six, several of them equal in size; fifth supralabial below center of eye. Suboculars three and four separated by fifth supralabial. Postmental similar to mental. Chinshields three pairs. Ear opening round, small, with no projecting granules on anterior margin. Forelimbs shorter than hind limbs. Adpressed limbs not meeting in adult. Digits short, subcylindrical. Third front digit as long as the fourth. Dorsal scales largest, weakly striate. Ventral scales smooth. Subdigital lamellae smooth.

*Coloration (in Preservative).*—Dorsal surface brown. Median dorsal stripe indistinct, broken when present. Dorsal color pattern an irregular arrangement of light and dark speckling. Dorsolateral line pale, broken, runs above eye toward base of tail, becoming indistinct as it proceeds posteriorly. Lateral stripe dark brown extending almost from tip of snout, through eye above limb insertions to base of tail, becoming indistinct thereafter. No striping on limbs. Soles of feet brown/grey. Underside cream, unmarked.

*Measurements.*—Measurements in millimeters. Holotype with the variation shown in the type series in parentheses. SVL 50.2 (37.9–55.5, mean 47.9); HL 7.8 (5.3–7.4, mean 6.9); HW 5.5 (4.1–5.5, mean 5.0); AG 25.8 (19.4–30.2, mean

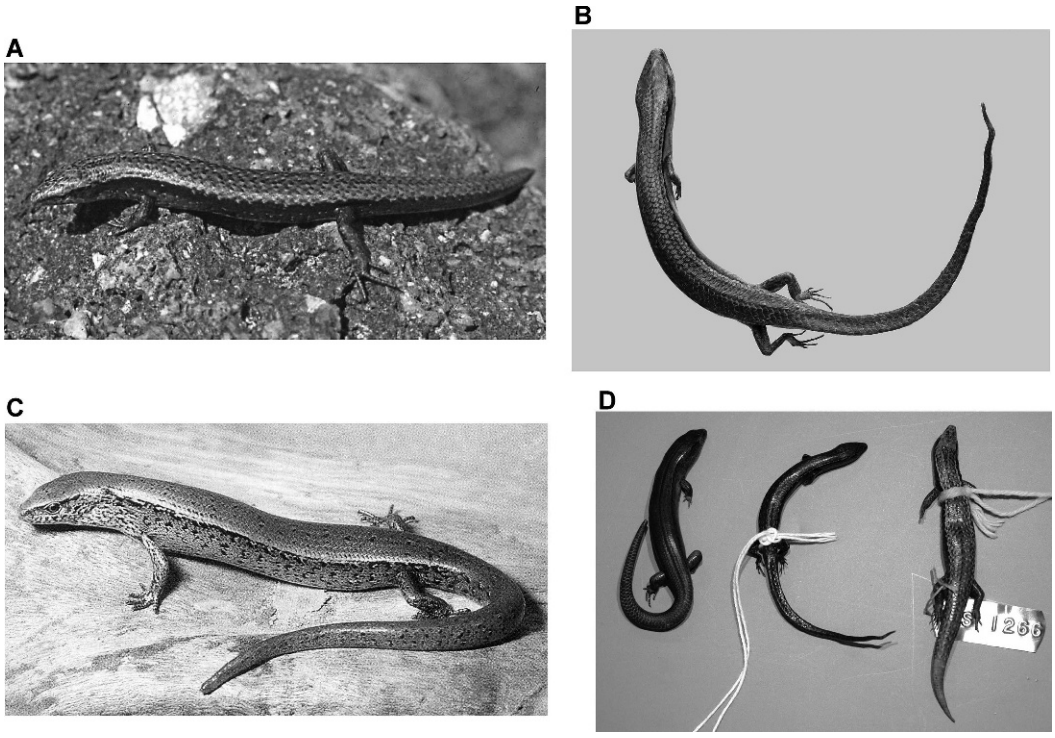


FIG. 2. Photos of species in the *Cyclodina aenea* species complex. (A) Hardy's Skink, *Cyclodina hardyi*; (B) the Slight Skink, *Cyclodina levidensa* (holotype, RE5768); (C) the Copper Skink *C. aenea*; (D) comparison of *C. aenea* (left; RE1932, Great Barrier Island), *C. levidensa* (middle; holotype, RE5768) and *Cyclodina hardyi* (right; holotype, RE4903 [S1266]).

24.5); SF 19.8 (14.5–21.7, mean 18.6); S–E 9.6 (7.7–10.2, mean 9.1); EF 12.4 (7.8–12.5, mean 10.5); HLL 19.0 (14.5–19.0, mean 16.6); TL unknown (39.2–49.8, mean 46.7, $N = 4$).

*Variation*.—Holotype with the variation shown in the type series in parentheses. Upper ciliaries 7 (7–9, mean 8); lower ciliaries 11 (9–12, mean 11); nuchals 1 (1–3 pairs, mean 2); mid-body scale rows 32 (28–32, mean 31); ventral scale rows 70 (67–82, mean 75); subdigital lamellae 22 (19–23, mean 22); supraciliaries 7 (6–7, mean 6); suboculars 7 (5–9, mean 7). Maximum SVL 55.5 mm. Ratios for morphological measurements ($\pm$ SD, $N = 17$): AG/SF 1.30 $\pm$ 0.12; S–E/EF 0.88 $\pm$ 0.10; HL/HW 1.37 $\pm$ 0.10; HLL/SVL 0.35 $\pm$ 0.03. Four specimens had intact tails (tail length/SVL = 1.05). Some of the paratypes displayed light speckling on the chin and belly. Color pattern does not appear to be sexually dimorphic. Juvenile coloration unknown.

*Etymology*.—Named after Graham Hardy who completed the last comprehensive taxonomic revision of the New Zealand skink fauna and first noted that the Poor Knights Islands populations of *C. aenea* were distinctive (Hardy, 1977). The common name is Hardy's Skink.

*Distribution, Ecology, and Life History*.—*Cyclodina hardyi* is restricted to the Poor Knights Islands, occurring on Tawhiti Rahi Island, Aorangi Island, Aorangaia Island, Archway Island, and two rock stacks (Stack ''B,'' Stack ''C'') (Whitaker, 1968, 1978; Towns and Daugherty, 1994; BioWeb Herpetofauna database, New Zealand Department of Conservation, Wellington, 2006; R. Parrish, pers. comm.; Fig. 1). Although *C. hardyi* appears to occupy most available habitat in the Poor Knights Islands and is regularly encountered during surveys (Whitaker, 1978; Towns, 1999), population densities may be low (Whitaker, 1968; R. Parrish, pers. comm.). It is most commonly found in areas where there is ground cover near flax and scrub habitat (Whitaker, 1968). *Cyclodina hardyi* is crepuscular, seeking refuge during the day under stones or thick vegetation (Whitaker, 1968). It is rarely observed basking and is an active forager, searching through the leaf litter for invertebrate prey (Whitaker, 1968). *Cyclodina hardyi* is viviparous, with a mean adult SVL of 51.6 mm (range 44–62 mm, $N = 21$; Whitaker, 1968). *Cyclodina hardyi* is not currently listed by the IUCN but is ranked by the New Zealand Department of Conservation as Range Restricted (Stable) (Hitchmough et al., 2007).

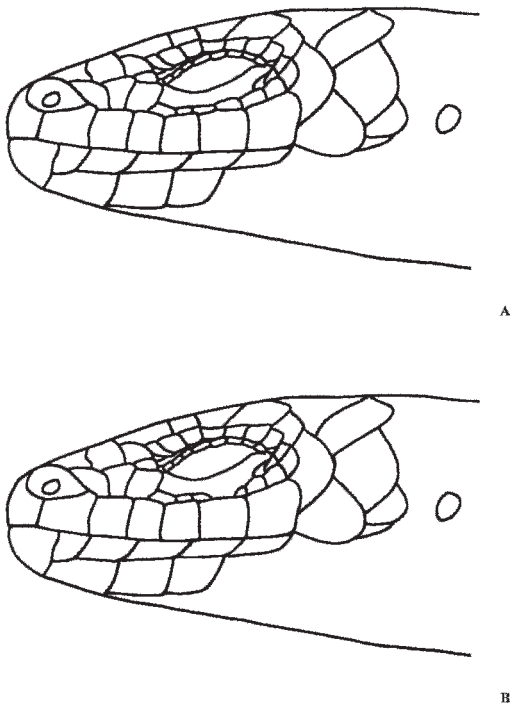


FIG. 3. Diagnostic head scales for the *Cyclodina aenea* species group. (A) *Cyclodina aenea* and *Cyclodina levidensa* have a continuous row of subocular scales, whereas (B) *Cyclodina hardyi* has suboculars three and four separated by the fifth supralabial under the eye.

*Cyclodina levidensa* sp. nov.
Figure 2B

*Holotype.*—Radar Bush, Te Paki, Northland (34°28′S, 172°45′E), RE5768 (collected by O. Ball, November 2006). Adult female.

*Paratypes.*—Kauri Bush, Pandora Track, Northland (34°29′S, 172°45′E), FT3729 (female) (collected by S. Trewick, September 1997); Unuwhao Bush, Northland (34°26′S, 172°53′E), RE2032 (female) (collected by P. Anderson, December 1978); Mt Unuwhao, Spirits Bay, Northland (34°26′S, 172°53′E), RE4749 (S1111) (female) (collected by B. D. Bell, February 1974); Darkies Ridge, Te Paki, Northland (34°28′S, 172°45′E), RE5771 (female) (collected by O. Ball, October 2006); Radar Bush, Te Paki, Northland (34°28′S, 172°45′E), RE5769 (female), RE5770 (male) (collected by O. Ball, December 2006); Kohurunaki, Northland (34°29′S, 172°50′E), RE5772 (male) (collected by O. Ball, February 2007); Darkies Ridge, Te Paki, Northland (34°28′S, 172°45′E), RE5773 (female) (collected by O. Ball, February 2007).

*Diagnosis.*—The scale count ranges are generally lower for *C. levidensa* than for *C. aenea*, although the nuchal count is higher. In particular, the midbody scale count range (24–26) is lower than for all other *Cyclodina* species, except *C. aenea* (26–32). *Cyclodina levidensa* is difficult to distinguish morphologically from *C. aenea*, which is probably why it had not been recognized until now. The main distinguishing feature is the slighter overall body form of *C. levidensa* compared to *C. aenea* (Fig. 2D). The limbs of *C. levidensa* are reduced compared to *C. aenea* and *C. hardyi* (Fig. 2D).

*Description of Holotype.*—Adult female, SVL 48.6 mm, TL 54.3 mm. Body elongate, slender, squarish in cross-section; limbs small, pentadactyl. Lower eyelid with a large divided opaque central scale margined anteriorly and posteriorly by relatively large scales. Snout moderately sharp. Nostril centered just below middle of nasal, pointing up and back. Supranasals absent. Rostral broader than deep. Frontonasal broader than long, not separated from frontal by prefrontals meeting in midline. Frontal longer than broad, shorter than frontoparietal and interparietal together, in contact with two anteriormost supraoculars. Supraoculars four, the second largest. Frontoparietals distinct, larger than interparietal. A pair of parietals meeting behind interparietal and bordered posteriorly by a pair each of nuchals and temporals, also in contact with interparietal, frontoparietal, fourth supraocular and two postoculars. Loreals two, either one the larger; anterior loreal in contact with first and second supralabial, posterior loreal, prefrontal, frontonasal and nasal; posterior loreal in contact with second, supralabial, first subocular, upper and lower preocular, prefrontal and anterior loreal. Supralabials six, the fifth largest. Infralabials six, several of them equal in size; fourth supralabial below center of eye. One primary temporal. Postmental similar to mental. Chinshields three pairs. Ear opening round, small, with no projecting granules on anterior maring. Forelimbs shorter than hind limbs. Adpressed limbs not meeting in adult. Digits short, subcylindrical. Third front digit as long as the fourth. Dorsal scales largest, weakly striate. Ventral scales smooth. Subdigital lamellae smooth.

*Coloration (in Preservative).*—Dorsal surface medium brown. Lacking median dorsal stripe. Dorsal color pattern an irregular arrangement of light and dark speckling. Dorsolateral line pale, broken, runs from behind eye to base of tail, becoming indistinct as it proceeds posteriorly. Bordered below by dark brown stripe. Wider, lighter lateral stripe runs below this to tip of tail. Ventral surface white. Light speckling on throat and chin. Light and dark alternating scales on upper and/or lower margins of jaw. Outer surface of limbs speckled with light and dark blotches.

*Measurements.*—Measurements in millimeters. Holotype with the variation shown in the type series in parentheses. SVL 48.6 (36.2–50.8, mean 46.2); HL 6.3 (5.2–6.5, mean 5.9); HW 4.7 (3.8–4.8, mean 4.4); AG 26.8 (19–28.6, mean 24.8); SF 17.9 (14.1–18.2, mean 16.9); S–E 8.6 (6.9–8.6, mean 7.9); EF 9.2 (7–9.9, mean 9.0); HLL 14.5 (11.5–16.0, mean 13.4); TL 54.3 (38.5–61.0, mean 49.9, $N = 6$).

*Variation.*—Holotype with the variation shown in the type series in parentheses. Upper ciliaries 7 (6–8, mean 7); lower ciliaries 10 (8–11, mean 9); nuchals 3 pairs (1–3 pairs, mean 3); midbody scale rows 24 (24–26, mean 25); ventral scale rows 62 (59–68, mean 64); subdigital lamellae 17 (16–18, mean 17); supraciliaries 5 (5–6, mean 6); suboculars 7 (7–9, mean 7). Maximum SVL 50.8 mm. Ratios for morphological measurements ($\pm$ SD, $N = 9$): AG/SF 1.49 $\pm$ 0.14; S–E/EF 0.88 $\pm$ 0.07; HL/HW 1.35 $\pm$ 0.09; HLL/SVL 0.29 $\pm$ 0.03. Seven specimens had intact tails (TL/SVL = 1.09). Some of the paratypes had a ventral surface that was pale straw yellow, cream on throat and chin, with the underside of the tail flushed with orange. Color pattern does not appear to be sexually dimorphic. Juvenile coloration unknown.

*Etymology.*—The specific name (*levidensa*, Latin: thin, slight) refers to the thin, elongated body and reduced limbs of this skink. *Cyclodina* is assumed to be feminine because *aenea* is the feminine form of the Latin word for copper. The common name is the Slight Skink.

*Distribution, Ecology, and Life History.*—The precise distribution of *C. levidensa* is unknown, but it appears to be restricted to several localities (Radar Bush, Pandora Track, Unuwhao Bush, Mt Unuwhao, Darkies Ridge, Kohurunaki) in the Te Paki region of Northland (Fig. 1). The biology, ecology, and life history of *C. levidensa* are unknown but are presumably similar to those of *C. aenea*. The maximum SVL of *C. levidensa* is less than that of *C. aenea*, which together with its slighter overall body shape makes *C. levidensa* the smallest known native skink in New Zealand. *Cyclodina levidensa* has been found within native forest where it appears to live on the forest floor (O. Ball, pers. comm.). Given the apparent restricted distribution of *C. levidensa* and the lack of information on its biology, surveys and research will be required to assess the conservation status of this species.

### *Cyclodina aenea* Girard, 1857
Figure 2C

The following list of synonyms is adapted from Hardy (1977).

*Mocoa smithi*: Gray, 1845:82 (in part). Gray, 1867:4 (in part). Buller, 1871:6 (in part). Hutton, 1872:168 (in part). McCann, 1955:97 (in part). Fawcett and Smith, 1971:135 (in part).

*Cyclodina aenea*: Girard, 1857:196. Girard, 1858:236–237, 239, pl. xxvi, fig. 9–16 (in part). Troschel, 1859:61. Gunther, 1875:13. Robb, 1973:297.

*Hombronia undosa*: Girard, 1857:196. Girard, 1858:240–242. Gunther, 1875:13. Boulenger, 1887:209.

*Lampropholis smithii* (Gray): Fitzinger, 1861:403. Jouan, 1869:294 (in part).

*Lampropholis (Mocoa) smithi* (Gray): Hochstetter, 1863:429 (in part). Hochstetter, 1867:163 (in part).

*Euprepes smithii* (Gray): Steindachner, 1869:47 (in part).

*Mocoa zealandica* (Gray): Gunther, 1875:13, pl. 7, fig. 4 (in part).

*Lygosoma smithii* (Gray): Boulenger, 1887:274 (in part). Werner, 1895:21 (in part). Hutton, 1904:39 (in part). Hutton and Drummond, 1904:351, 354, 381 (in part). Boulenger, 1906:370 (in part). McCann, 1955:75–76, 97 (in part).

*Lygosoma aeneum* (Girard): Boulenger, 1887:275. Werner, 1895:21. Werner, 1901:387. Hutton, 1904:39 (in part). Hutton and Drummond, 1904:351, 354, 381. Boulenger, 1906:371. Martin, 1929:164.

*Lygosoma (Liolepisma) micans*: Werner, 1895:21.

*Liolepisma aeneum* (Girard): Lucas and Frost, 1897:265, 278–280.

*Liolepisma smithii* (Gray): Lucas and Frost, 1897:265, 277 (in part).

*Liolepisma micans* (Werner): Lucas and Frost, 1897:279.

*Lygosoma (Leiolopisma) aeneum* (Girard): Smith, 1937:223.

*Lygosoma (Leiolopisma) smithi* (Gray): Smith, 1937:223 (in part).

*Leiolopisma aenea* (Girard): Mittleman, 1952:21.

*Leiolopisma smithii* (Gray): Mittleman, 1952:30 (in part).

*Lygosoma moco* Duméril and Bibron: Hard, 1954:145–146.

*Leiolopisma aeneum* (Girard): McCann, 1955:76–77, 79, 102, pl. xiv, figs. 6–9. McCann, 1956:50. Barwick, 1959:331–332, 340, 346–348, 365–348, 346–348, 365–367, 376, 378. Sharell, 1966:77. Fitch, 1970:83. Porter, 1972:403. Schipper, 1972:57. Towns, 1972:95–99, 102–103. Robb, 1973:297. Greer, 1974:16. Morrison et al., 1974:22. Rawlinson, 1974:94. Robb, 1974:687. Bull and Whitaker, 1975:241. Hicks et al., 1975:211. Gill, 1976:143–144. Whitaker, 1976:9.

*Sphenomorphus pseudornatus*: McCann, 1955:76–77, 110–111, 125, fig. 14 (in part). Natusch, 1967:246 (in part). Whitaker, 1968:623, 628–631, 634–635, 644–646, 648–650 (in part). Whitaker, 1970:99. Forster and Forster, 1971:132 (in part).

Towns, 1971:62, fig. 2. Towns, 1972:95–99, 102–104, figs. 2, 3a–c (in part). Towns and Hayward, 1973:94–95, 97. Whitaker, 1973:122–130 (in part). Robb, 1974:683, 689 (in part). Towns, 1974a:156 (in part). Towns, 1974b:217, 219, 223 (in part). Robb, 1975:447 (in part). Hicks et al., 1975:210–212.

*Sphenomorphus pseudornatum*: McCann, 1955:79 (in part). McCann, 1956:50 (in part). Schipper, 1972:58 (in part).

*Sphenomorphus pseudornata*: McCann, 1955:97 (in part).

*Leiolopisma pseudornatus* (McCann): Robb, 1975:483 (in part).

*Cyclodina aenea*: Hardy, 1977:264–266, fig. 2b, c, 18, 19, 39 (in part).

*Leiolopisma ornatum*: Robb, 1977:304–306 (in part).

*Cyclodina aenea*: Wells and Wellington, 1985:63.

*Neotype*.—Blue Mountains, Hutt Valley (41°10′S, 175°01′E) RE1816 (collected by B. L. Enting, January 1968). Adult female.

*Specimens Examined*.—Claris, Great Barrier Island (36°15′S, 175°28′E), RE4953 (S1316) (male); Devonport, Auckland (36°51′S, 174°46′E), FT189 (male), FT190 (female). FT191 (female); Little Barrier Island (36°12′S, 175°05′E), CD1076 (male), CD1077 (male), RE1614 (× 3 specimens; 36: male, 37: male, 41: female); Katherine Bay, Great Barrier Island (36°07′S, 175°22′E), RE1938 (female), RE1940 (male); Motairehe Track, Great Barrier Island (36° 07′S, 175°22′E), RE1932 (male), RE1934 (male), RE2440 (female); Otorohonga, Waikato (38°11′S, 175°13′E), RE3994 (S352) (female); Te Kuiti, Waikato (38°20′S, 175°10′E), RE3995 (S353) (female); Pukerua Bay (41°02′S, 174°54′E), FT183 (female), FT184 (male); Mercury Islands (36°38′S, 175°52′E), FT170 (female); Hukatere, Matakohe, Northland (36°11′S, 174°10′E), RE3829 (S187) (male); Monavale, Hamilton (37°55′S, 175°25′E), RE3992 (S350) (female); Otata Island, Hauraki Gulf (36°41′S, 174°58′E), RE2031 (female); Ohinau Island, Coromandel Peninsula (36°44′S, 175°53′E), RE4711 (S1072) (female); near Waitara, Taranaki (39°13′S, 174°02′E), RE4060 (S418) (female), RE4059 (S417) (male); Gisborne (38°40′S, 178°01′E), RE4131 (S489) (male).

*Diagnosis*.—*Cyclodina aenea* can be distinguished from most other *Cyclodina* by its small body size and low midbody scale count of 26–32 rows, compared with *Cyclodina macgregori* (37–45; Hardy, 1977), *Cyclodina alani* (36–44; Hardy, 1977), *Cyclodina whitakeri* (34–38; Hardy, 1977), *C. townsi* (38–44; Chapple et al., 2008) and *C. oliveri* (34–42; Chapple et al., in press). It can be distinguished from *C. ornata* by body size and color pattern, in particular the lack of a ''teardrop'' under the eye. Unlike *C. hardyi*, it has a continuous row of subocular scales (Fig. 3). It can be separated from *C. levidensa* by a combination of higher scale counts and more heavily built body and limbs (Fig. 2D).

*Description of Neotype*.—Adult female, SVL 55.4 mm, TL 67.2 mm. Body elongate, squarish in cross-section; limbs moderately well developed, pentadactyl. Lower eyelid with a large, divided opaque central scale margined anteriorly and posteriorly by relatively large scales. Snout blunt. Nostril centered just below middle of nasal, pointing up and back. Supranasals absent. Rostral broader than deep. Frontonasal broader than long, not separated from frontal by prefrontals meeting in midline. Frontal longer than broad, shorter than frontoparietal and interparietal together, in contact with two anteriormost supraoculars. Supraoculars four, the second largest. Frontoparietals distinct, larger than interparietal. A pair of parietals meeting behind interparietal and bordered posteriorly by a pair each of nuchals and temporals, also in contact with interparietal, frontoparietal, fourth supraocular, and two postoculars. Loreals two, either one the larger; anterior loreal in contact with first and second supralabial, posterior loreal, prefrontal, frontonasal and nasal; posterior loreal in contact with second, first subocular, upper and lower preocular, prefrontal and anterior loreal. Supralabials seven, the sixth largest. Infralabials seven, several of them equal in size; fifth supralabial below centre of eye. Suboculars in continuous row below eye. Postmental similar to mental. Chinshields three pairs. Ear opening round, small, with no projecting granules on anterior margin. Forelimbs shorter than hind limbs. Adpressed limbs not meeting in adult. Digits short, subcylindrical. Third front digit as long as the fourth. Dorsal scales largest, weakly striate. Ventral scales smooth. Subdigital lamellae smooth.

*Coloration (in Preservative)*.—Dorsal surface copper-brown or grey-brown. Median dorsal stripe indistinct. A series of light and dark flecks running along upper and lower jaws. Dorsal color pattern an irregular arrangement of light and dark speckling. Dorsolateral line pale brown, broken, runs from behind eye toward base of tail, becoming indistinct thereafter. Lateral surface irregularly marked with light and dark flecks. No striping on limbs. Soles of feet grey. Underside yellow. Belly unmarked, with speckling on chin and throat.

*Measurements*.—Measurements in millimeters. Neotype with the variation shown in the specimens examined in parentheses. SVL 55.4 (38.9–59.9, mean 50.5); HL 7.8 (5.4–8.1, mean 7.1); HW 5.5 (4.1–5.8, mean 5.1); AG 30.1 (19.0–33.5, mean 26.6); SF 20.8 (14.8–21.4, mean 18.9); S–E 9.0 (7.3–10.3, mean 8.9); EF 10.1 (7.5–11.8,

mean 10.0); HLL 16.5 (12.0–19.5, mean 15.7); TL 67.2 (42.0–67.2, mean 54.5).

*Variation*.—Neotype with the variation shown in the specimens examined in parentheses. Upper ciliaries 8 (7–10, mean 8); lower ciliaries 10 (8–13, mean 11); nuchals 1 pair (1–2 pairs, mean 1); midbody scale rows 30 (26–32, mean 29); ventral scale rows 71 (66–84, mean 71); subdigital lamellae 16 (14–19, mean 16); supraciliaries 7 (6–8, mean 7); suboculars 9 (7–10, mean 8). Maximum SVL 59.9 mm. Ratios for morphological measurements (± SD, $N = 21$): AG/SF 1.40 ± 0.12; S–E/EF 0.90 ± 0.07; HL/HW 1.38 ± 0.11, HLL/SVL 0.31 ± 0.03. Eight specimens had intact tails (TL/SVL 1.12). In a few specimens both loreals are fused. Some of the specimens examined have a greenish tinge on the ventral surface. Some have a belly marked with speckling, others are completely unmarked on the ventral surface. In living specimens there is frequently distinctive coppery-red coloration on the nape and tail, and the venter region and underside of the base of the tail is often reddish-orange. This is possibly a secondary sexual color in males (A. H. Whitaker, pers. comm.). Juvenile coloration same as adult.

*Etymology*.—The specific name means copper (or bronze) colored (Gill and Whitaker, 2001). The common name is the Copper Skink.

*Distribution, Ecology, and Life History*.—*Cyclodina aenea* is widespread throughout the North Island and is one of the most common skink species in New Zealand (Towns, 1999; Gill and Whitaker, 2001). In the south of the North Island, *C. aenea* occurs in the Wellington, Kapiti Coast, and Wairarapa regions, but there are relatively few reports of it between this area and the central North Island (Towns, 1999; BioWeb Herpetofauna database, New Zealand Department of Conservation, Wellington 2006; Fig. 1). *Cyclodina aenea* occurs across the central North Island (Taranaki, Waikato, East Cape, Bay of Plenty), through the Auckland and Coromandel regions to the north of Northland (Towns, 1999; BioWeb Herpetofauna database, New Zealand Department of Conservation, Wellington, 2006; Fig. 1). It also occurs on several island groups off the northeast coast of the North Island (Towns, 1999; BioWeb Herpetofauna database, 2006; Fig. 1). *Cyclodina aenea* does not appear to be present on the high altitude areas of the central North Island, possibly because the climate in these areas is beyond the physiological tolerances of this species (Towns, 1999). However, the apparent gap in the distribution of *C. aenea* between the southern and central regions of the North Island (Fig. 1) is believed to be a reflection of relative survey effort rather than an actual absence (Towns, 1999). Alternatively, this distribution gap might be the result of repeated volcanic activity in the Central Plateau region over the past 2 My (Worthy and Holdaway, 2002).

*Cyclodina aenea* occurs in forested habitats, preferring open or shaded microhabitats with ground cover such as logs, rocks, and long grass (Gill and Whitaker, 2001). In coastal areas, *C. aenea* can be found close to the high tide line (Gill and Whitaker, 2001). It is the most common garden skink in Auckland and some suburbs of Wellington, occurring in artificial habitats such as compost heaps and rock gardens (Porter, 1987; Gill and Whitaker, 2001). *Cyclodina aenea* is crepuscular to diurnal (Porter, 1987; Towns and Elliott, 1996; Towns, 1999; Hare et al., 2006). It can occur in high densities, with reported densities within populations ranging between 40 and 2,494 per ha (Whitaker, 1968, 1973; Porter, 1987; Towns and Elliott, 1996). *Cyclodina aenea* rarely basks and tends to be thigmothermic (Porter, 1987; Towns and Elliott, 1996). It is an insectivorous forager, with Acari, Araneae, and Coleoptera the most common invertebrate prey items (Porter, 1987).

*Cyclodina aenea* is viviparous, with mating occurring in September through November and parturition in late January and February (Meads, 1971; Porter, 1987; Gill and Whitaker, 2001). Although it appears to be an annual reproducer, not all females manage to reproduce each year (Barwick, 1959; Cree, 1994). Litter size ranges between one and four, and two studies have reported that mean litter size is around 2.2 (Barwick, 1959; Habgood, 2003). The maximum body size of *C. aenea* is 62 mm SVL (Hardy, 1977; Gill and Whitaker, 2001), with sexual maturity reached in 2–3 years at approximately 46–50 mm SVL (Barwick, 1959; Towns, 1991; Habgood, 2003). Sexual dimorphism appears to be evident in both head width and length (Habgood, 2003). Although *C. aenea* is not currently ranked on any current conservation priority lists, it appears to be sensitive to predation by introduced rodents (Towns, 1999). Capture frequencies have been reported to decrease during population eruptions of mice (Newman, 1994; Towns and Elliott, 1996), with substantial increases (up to 10-fold) in population densities following the eradication of rats (Towns, 1994; Towns and Daugherty, 1994).

*Remarks*.—Robb (1977) considered the types of *Tiliqua ornata* (Gray, 1843) to be conspecific with the species we describe as *C. aenea*, rather than *C. ornata*. There has been much confusion relating to the identity of the *T. ornata* type specimens, with the opinions of New Zealand herpetologists varying as to which species they relate (McCann, 1955; Hardy, 1977; Robb, 1977; R. Hitchmough, pers. comm.). The type speci-

mens are completely bleached, removing the color and pattern differences that can usually be used to distinguish *C. aenea* and *C. ornata* (R. Hitchmough, pers. comm.). A previous attempt to resolve this issue using ancient DNA techniques failed (R. Hitchmough, pers. comm.). Given that the identity of the *T. ornata* types remains unresolved, we have chosen to retain the current taxonomic designation that the *T. ornata* type specimens refer to *C. ornata*.

### Taxonomic Key for *Cyclodina*

This diagnostic key for *Cyclodina* has been adapted from Gill and Whitaker (2001):

1. Body oval in cross-section; limbs and toes relatively long; head relatively shallow and pointed; lower eyelid has one transparent disc . . . . . *Oligosoma*
   Body squarish in cross-section; limbs and toes relatively short; head relatively deep and blunt; lower eyelid scaly, or covered by one or two opaque scales . . . . 2
2. Lower margin of eye without dark-edged pale ''teardrop''; midbody scale rows less than 34; ear opening small (scarcely larger than pinprick) . . . . . 10
   Lower margin of eye with distinct dark-edged pale ''teardrop''; midbody scale rows greater than 32; ear opening moderate/large. . . . . 3
3. Eyes large relative to head size; snout short, rounded; body very thickset and particularly squarish in cross-section. . . . . *C. alani*
   Eyes relatively small; snout elongate; body less thickset and squarish . . . . . 4
4. Dorsum with irregularly broken darker stripes from neck to base of tail; venter grey, cream, or light pink . . . . *C. macgregori*
   Dorsum without stripes . . . . . 5
5. Dorsum with numerous black and yellowish flecks; lateral surface dark brown to black from ear to hind limbs, interrupted with small yellowish blotches; venter yellowish-orange. . . . *C. whitakeri*
   Dorsal and lateral surfaces without yellowish flecks or blotches . . . . . 6
6. Throat creamy to reddish, variously flecked with dark grey to black; dorsolateral surface with narrow, continuous dark brown to black stripe from above ear to forelimb insertion; dorsum often with small pale patches . . . . . *C. ornata*
   Throat white, heavily marked with black; dorsolateral surface with broad dark brown band interrupted with paler blotches from above ear to forelimb insertion or further; dorsum light to dark brown, sometimes flecked with black. . . . . 7
7. Midbody scales 38–44. . . . . 8
   Midbody scales < 38 . . . . . *C. oliveri*
8. One primary temporal scale . . . . . *C. townsi*
   Two primary temporal scales . . . . . 9
9. Speckled on venter and throat . . . *C. oliveri*
   Throat heavily speckled; venter not speckled . . . . . *C. townsi*
10. Subocular row discontinuous under eye . . . . . *C. hardyi*
    Subocular row continuous under eye . . . 11
11. Midbody scales 24–26; body and limbs slender; dorsolateral lines prominent. . . . . *C. levidensa*
    Midbody scales usually greater than 26; dorsolateral lines indistinct or absent; body and limbs bulkier. . . . . *C. aenea*

*Mitochondrial DNA Analyses.*—The edited alignment comprised 550 characters, of which 178 (32%) were variable and 126 (23%) were parsimony-informative. For the ingroup only, the alignment contained 115 (21%) variable characters, of which 100 (18%) were parsimony-informative. Base frequencies were unequal (A = 0.328, T = 0.198, C = 0.333, G = 0.141), but a $\chi^2$-test confirmed the homogeneity of base frequencies among sequences (df = 51, $P = 0.228$).

The hRLT from ModelTest supported the K81uf+I substitution model as the most appropriate for our dataset ($-\ln L = 2148.0627$). Parameters estimated under this model were as follows: relative substitution rates (A ↔ C = 1.00, A ↔ G = 10.15, A ↔ T = 0.43, C ↔ G = 0.43, C ↔ T = 10.15, G ↔ T = 1.00), and proportion of invariable sites (0.6028). The topology of the MP, ML, and Bayesian trees was identical. The optimal ML tree ($-\ln L = 2252.6626$) is shown in Figure 4, with bootstrap values and posterior probabilities indicating branch support. There was extremely strong support (100 bootstrap and 1.0 posterior probabilities in all cases) for the presence of three distinct species within the *C. aenea* species complex: *C. aenea*, *C. aenea* ''Poor Knights Islands'' (which we describe as *C. hardyi*); and *C. aenea* from the extreme tip of Northland (which we describe as *C. levidensa*; Fig. 4). There is some support for *C. levidensa* being more closely related to *C. hardyi* (70 bootstrap, 0.86 posterior probabilities) than it is to *C. aenea*. The mean corrected genetic distance within the widespread *C. aenea* (0.034 ± 0.002) is substantially higher than in *C. hardyi* (0.006 ± 0.005) and *C. levidensa* (0.006 ± 0.003), which both have restricted distributions. There is a substantial amount of genetic differentiation between the members of the *C. aenea* species complex (*C.*

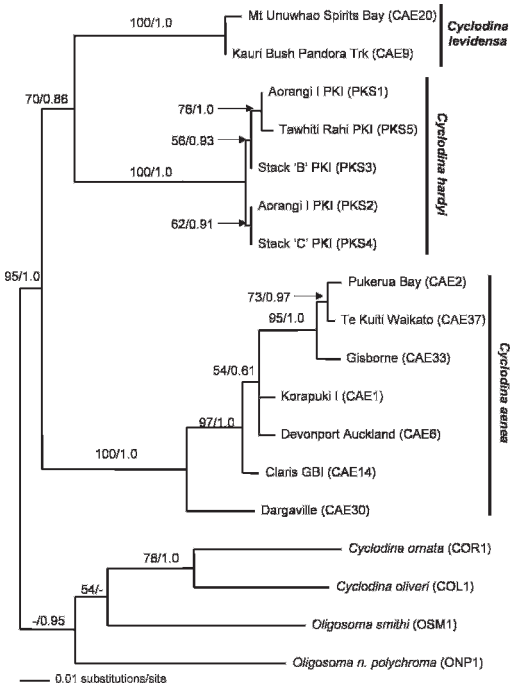


FIG. 4. Maximum-likelihood (ML) tree for the Copper Skink (*Cyclodina aenea*) species complex based on 550 bp of the ND2 mitochondrial gene. The topology of the maximum parsimony and Bayesian trees were identical to the ML tree shown. Two measures of branch support are indicated with parsimony bootstraps (or ML bootstraps) shown on the left and Bayesian posterior probabilities on the right (only values over 50 and 0.7, respectively, are shown).

*aenea* vs. *C. hardyi*: 0.138 ± 0.016; *C. aenea* vs. *C. levidensa*: 0.135 ± 0.016; *C. hardyi* vs. *C. levidensa*: 0.116 ± 0.016). Because the level of genetic differentiation between each member of the *C. aenea* species complex approaches that of the outgroups (*C. aenea* vs. outgroups: 0.163 ± 0.015; *C. hardyi* vs. outgroups: 0.152 ± 0.015; *C. levidensa* vs. outgroups: 0.145 ± 0.014), it suggests that each species has been evolving in isolation for a considerable amount of time.

## DISCUSSION

Our analysis of morphological and genetic variation in the Copper Skink (*C. aenea*) species complex resulted in the description of two new species (*C. hardyi* and *C. levidensa*) and the redescription of *C. aenea*. The description of the Poor Knights Island population as *C. hardyi* is in agreement with previous morphological (Hardy, 1977; Vos, 1988), allozyme (Vos, 1988), and mtDNA studies (Hickson et al., 2000) that have supported the recognition of this population as a distinct taxon. However, contrary to the suggestion of Hardy (1977), our molecular data indicated that the Great Barrier Island *C. aenea* population (CAE14) was not closely related to *C. hardyi* (~13.8% sequence divergence; Fig. 4).

The considerable morphological and molecular divergence of *C. hardyi* from *C. aenea* suggests that these two species have been evolving in isolation for a substantial period of time (Hardy, 1977). This level of divergence is presumably the result of the Poor Knights Islands being isolated from the mainland North Island for 1–2 My, even during the repeated sea level fluctuations associated with Pleistocene glacial cycles (Hayward, 1986, 1991). The high levels of species diversity and endemism present on the Poor Knights Islands are believed to be a consequence of the biota evolving in isolation for a prolonged period (e.g., flora, de Lange and Cameron, 1999; reptiles, Whitaker, 1968; Daugherty et al., 1994).

Although the precise distribution of *C. levidensa* is unknown, it appears to be restricted to the northernmost region of Northland. Relatively few current biogeographic barriers are present in the Northland region; however, this area repeatedly existed as an archipelago of low-lying islands during Pleistocene glacial cycles (Fleming, 1979; Hayward, 1986, 1991). Biota in the Northland region have been found to display the genetic imprint of recent speciation and deep phylogeographic structure (plants, *Metrosideros*, Gardner et al., 2004; weta, *Hemideina thoracica*, Morgan-Richards, 1997; Morgan-Richards and Wallis, 2003; Black Mudfish, *Neochanna diversus*, Gleeson et al., 1999; *Oligosoma* skinks, Hare et al., 2008), which has been assumed to be a consequence of the repeated connection and separation of islands in this region during Pleistocene glacial cycles. In particular, Spencer et al. (2006) provide molecular evidence for recent speciation in Kauri snails in the northernmost region of Northland, suggesting past isolation and allopatric speciation of fauna in this region. The high level of genetic divergence between *C. levidensa* and *C. aenea* (~13.5% sequence divergence) might, therefore, be the result of prolonged evolution in isolation within the Northland region.

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