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A new fossil provannid gastropod from Miocene hydrocarbon seep deposits, East Coast Basin, North Island, New Zealand

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Provanna marshalli sp. nov. is described from Early to Middle Miocene-age fossil hydrocarbon seep localities in the East Coast Basin, North Island, New Zealand, adding to 18 modern and three fossil species of the genus described. Modern species are well represented at hydrothermal vent sites as well as at hydrocarbon seeps and on other organic substrates in the deep sea, including sunken wood and whale falls. Described fossil *Provanna* species have been almost exclusively reported from hydrocarbon seep deposits, with a few reports of suspected fossil specimens of the genus from other chemosynthetic environments such as sunken wood and large vertebrate (whale and plesiosaurid) carcasses, and the oldest occurrences are dated to the Middle Cenomanian (early Late Cretaceous). The New Zealand fossil species is the most variable species of the genus described to date, and its shell microstructure is reported and found to be comparable to the fossil species *Provanna antiqua* and some modern species of the genus.

Key words: Mollusca, Gastropoda, Provannidae, *Provanna*, hydrocarbon seeps, Miocene, East Coast Basin, New Zealand.

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Introduction

Modern submarine hydrothermal vents and hydrocarbon seeps supporting highly productive chemosynthesis-based faunal communities, quite distinct ecologically from the surrounding sea floor, have become a well known global phenomenon since their discovery in the late 20th century (Lonsdale 1977; Paull et al. 1984; Van Dover 2000; Levin 2005; Suess 2010). These modern "extreme environments" have allowed recognition of vent-seep deposits in the geological record (Campbell 2006) that had previously been enigmatic (e.g., Gilbert and Gulliver 1894; Stanton 1895; Van Winkle 1919; Tanaka 1959; Danner 1966; Moroni 1966; Ager 1986). Establishing the composition and palaeoecological structure of fossil vent-seep communities contributes to better understanding of evolutionary trends in deep-sea faunas, with applications for palaeobiogeographical reconstruction and modelling.

Provanna Dall, 1918 is one of the more widely represented genera associated with hydrothermal vent and hydrocarbon seep environments, with three fossil and 18 extant species described, as well as several undescribed modern species (Anders Warén, personal communication 2009). Modern *Provanna* species are common at vent sites, as well as at hydrocarbon seeps, and it is typical for one or two species to occur in any one chemosynthesis-based community (Warén and Bouchet 1993). Their main mode of nutrition involves grazing on filamentous bacteria, especially amongst mytilid beds, vestimentiferan tube worm bushes, and upon bacterial mats (e.g., Levin and Michener 2002; Sahling et al. 2002; Levin 2005; MacAvoy et al. 2005; Olu et al. 2009). Gut contents including crustacean fragments, polychaete bristles, sponge spicules, and the tests of planktonic organisms such as diatoms and radiolarians have been observed in some species, e.g., *Provanna admetoides* Warén and Ponder, 1991 and *Provanna laevis* Warén and Ponder, 1991, suggesting they also feed on detritus (Warén and Bouchet 1986; Warén and Ponder 1991). At least one species, *Provanna variabilis* Warén and Bouchet, 1986, may harbour symbiotic bacteria (Bergquist et al. 2007). Species of *Provanna* are not thought to have many natural predators within the communities in which they live (Bergquist et al. 2007), but shell remains have been found in the gut contents of opportunistic octopuses that frequent hydro-

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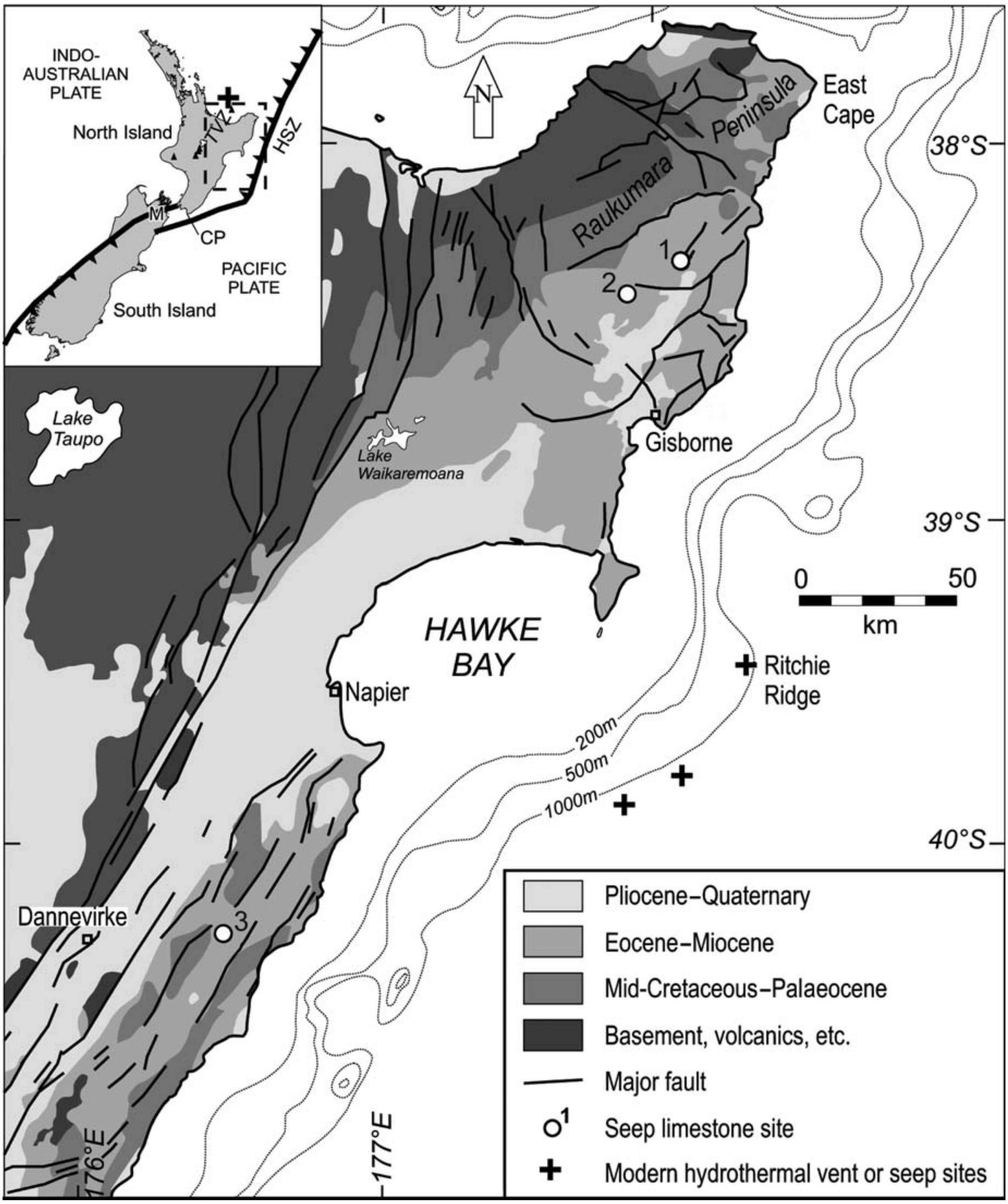

Fig. 1. Overview of relevant geology of the East Coast Basin, North Island, New Zealand, showing locations of the fossil seep deposits from which type specimens and a possible specimen of *Provanna marshalli* sp. nov. were collected. 1. Puketawa. 2. Rocky Knob. 3. Ugly Hill. CP, Cape Palliser; HSZ, Hikurangi subduction zone; M, Marlborough; TVZ, Taupo Volcanic Zone. Also shown are some of the modern offshore seeps on the Hikurangi margin, including Ritchie Ridge, from which several modern *Provanna* specimens have been reported. Inset shows the Hikurangi subduction zone as part of the transpressive boundary between the Indo-Australian and Pacific Plates. Figure modified from Campbell et al. (2008).

thermal vents (Voight 2000, 2008). Kiel (2006) also reported a healed shell injury in a single specimen of *Provanna antiqua* Squires, 1995 from the Oligocene Lincoln Creek Formation, north-western USA, that may have resulted from a predatory crab attack. Species of *Provanna* are often reported as endemic to vent-seep environments (e.g., Hessler and Lonsdale 1991; Warén and Bouchet 1993; Carney 1994; Yamamoto et al. 1999; Fujikura et al. 2002; Cordes et al. 2009), but some species have been reported from other organic substrates such as sunken driftwood (Warén and Bouchet 2001, 2009) and whale falls (Smith et al. 2002; Smith and Baco 2003). These more ephemeral deep-sea habitats may act as stepping stones for dispersal and colonisation between the geographically restricted but more stable and long-lived chemosynthetic environments at vents and seeps (e.g., Distel et al. 2000).

Institutional abbreviations.—GNS, GNS Science, Lower Hutt, New Zealand; GSNZ, Geological Society of New Zealand, Lower Hutt, New Zealand; LEMAS, Leeds Electron Microscopy and Spectroscopy Centre, Institute for Materials Research, University of Leeds, Leeds, United Kingdom; NMNZ, Te Papa Tongarewa, Wellington, New Zealand; UOA, Geology, School of Environment, University of Auckland, Auckland, New Zealand.

Other abbreviations.—AU (preceding five-digit number), collection number for material deposited in the palaeontology collection, UOA; D, shell diameter; d, apertural diameter; G (preceding four-digit number), gastropod specimen number, palaeontology collection, UOA; GS (preceding five-digit number), fossil locality number, GNS; H, shell height; h, apertural height; TM (preceding four-digit number), type specimen number, palaeontology collection, GNS; Y16/f (preceding four-digit number), fossil locality number, registered in archival New Zealand Fossil Record File maintained jointly by GNS and GSNZ.

Materials and methods

29 fossil gastropod specimens were collected during a number of field trips to both the northern and southern Hawke's Bay Miocene seep localities (Fig. 1) over several years (1997–2009), adding to material obtained from the bulk palaeontology collections at GNS. Shell images were obtained via scanning electron microscopy at UOA and LEMAS. Specimens described and figured herein are deposited in the palaeontology collections of UOA. Modern comparative material is housed at NMNZ. Measurements were taken of all of the specimens with vernier callipers to within an error of 0.1 mm.

Geological setting

At least 16 geographically isolated ancient hydrocarbon seep deposits are present along 300 km of the uplifted East Coast Basin forearc, eastern North Island (Campbell et al. 2008). They occur in two distinct regions in the Raukumara Peninsula and near Dannevirke, to the north and south of the Hawke's Bay region, respectively, where they occur as discrete pods or lenses of authigenic carbonate enclosed within thick siliciclastic mudstone deposits (Fig. 2).

The East Coast Basin formed as a result of regional tectonism that has been ongoing since the Early Miocene (Ballance 1976). Extending roughly 650 km north to south, the East Coast Basin varies in width from 60 to 110 km, bounded to the west by NNE–SSW trending axial mountain ranges and extending offshore to its eastern boundary along the similarly trending Hikurangi Trough (Fig. 1). It represents an exhumed forearc, its sediments having been generated during a period of oblique convergence along the Hikurangi subduction zone throughout the Cainozoic (Ballance 1976; Barnes et al. 2002), during the onset of intense deformation, the appearance of andesitic volcanism, and abrupt changes in sedimentation rate and character (Rait et al. 1991). Today, the Hikurangi margin constitutes the southern extremity of the Tonga-Kermadec-Hikurangi system, an east-facing subduction zone oriented roughly parallel to the East Coast of North Island, along which the Pacific Plate is moving north-westward underneath the overriding Australian Plate (e.g., Ansell and Bannister 1996).

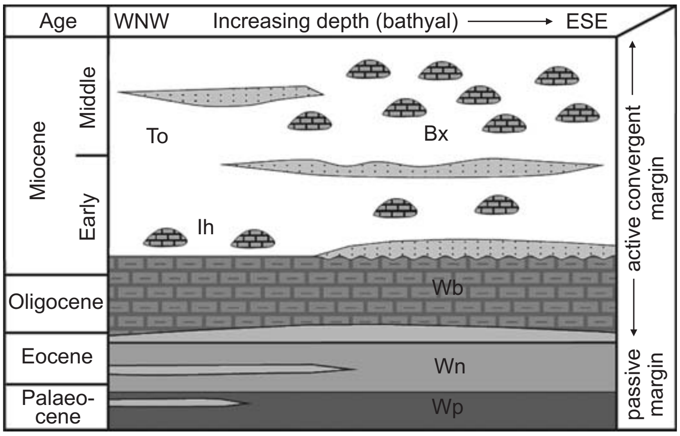

Fig. 2. Generalised stratigraphy of the East Coast Basin, showing the Miocene-age seep carbonates that occur as isolated lenses within the mudstones of the Tolaga Group. The organic-rich, underlying Waipawa Black Shale is thought to be one of the likely source rocks. Abbreviations: Bx, Bexhaven Limestone; Ih, Ihungia Limestone; To, Tolaga Group; Wb, Weber Formation; Wn, Wanstead Formation; Wp, Waipawa Black Shale. Figure modified from Campbell et al. (2008).

We report morphologically highly variable specimens of the genus *Provanna* from two of the northern region New Zealand hydrocarbon seep deposits (Fig. 1): Puketawa and Rocky Knob (late Early to Middle Miocene age). All but a single specimen comes from Rocky Knob, mostly from within a group of closely scattered float boulders originating from the main scarp of the site (Fig. 3A, B), found in association with worm tubes and bathymodioline and large lucinid bivalves (Fig. 3C, D), as well as small, unidentified ?columbellid gastropods and acmaeid limpets. A poorly preserved, possibly juvenile gastropod specimen from the southern region Ugly Hill seep (Early Miocene age) may also belong to the same species, but we have not used it here in the species description. The ages of these deposits are approximate due to stratigraphic correlation limitations of the limestones within the monotonous, voluminous mudstone sequence, which is structurally complex with major, long-active, low-angle normal faults predominating in some areas, especially in the north (Campbell et al. 2008).

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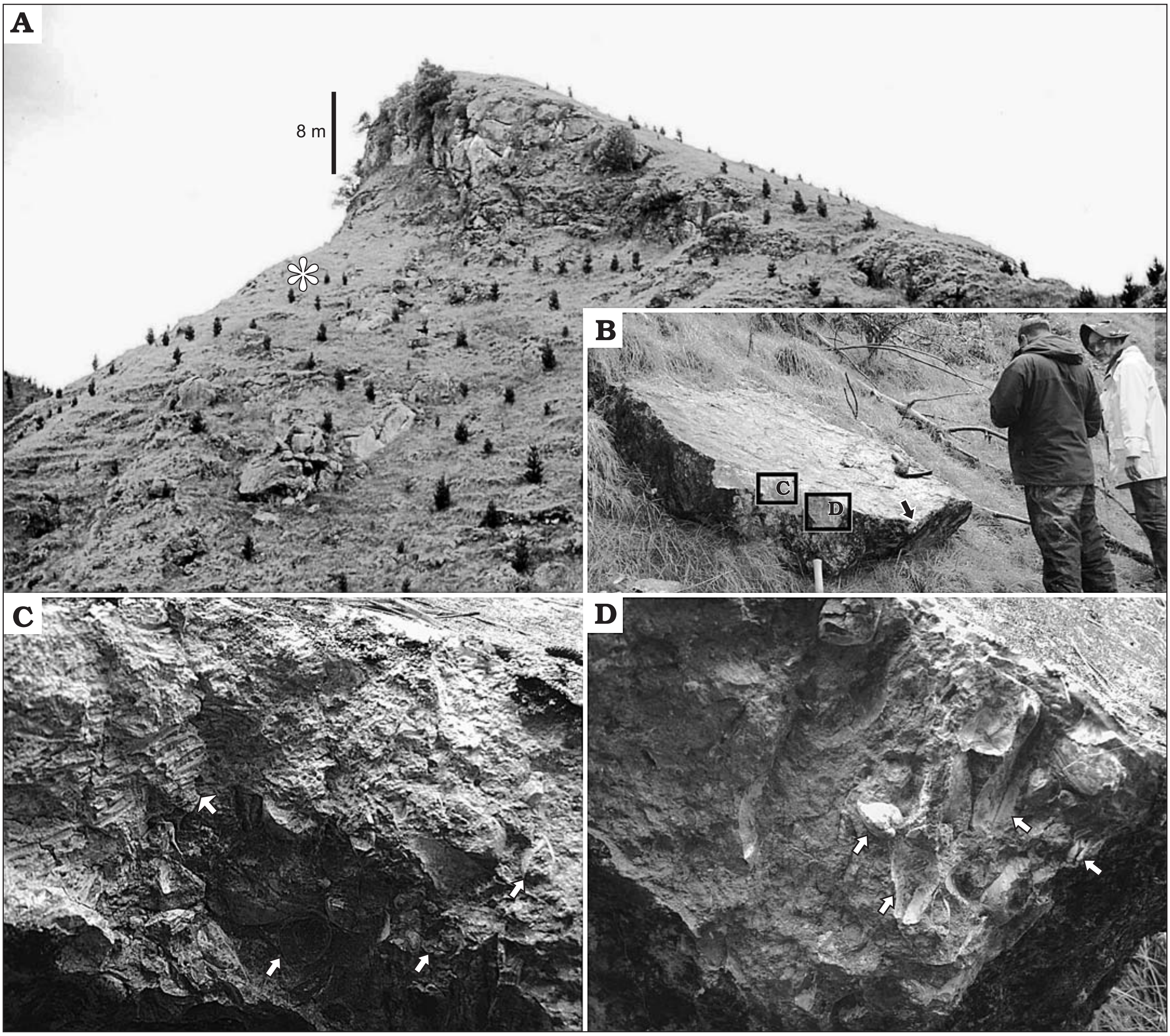

Fig. 3. Field photographs showing the Middle Miocene Rocky Knob type locality and collection location of the assemblages that yielded most of the specimens of *Provanna marshalli* sp. nov. **A**. Main scarp of the deposit, white asterisk marks the collection location. **B**. Slab in which an assemblage (arrowed) was found, located a few metres from a smaller block (not pictured) that yielded the majority of the specimens; locations of photos C and D marked by squares. **C**, **D**. Other taxa (arrowed) found in association with the assemblage within the boulder. **C**. Worm tubes (wide arrow) and lucinid bivalves (thin arrows). **D**. Bathymodioline bivalves. Photographs taken by KAC (1997: fig. 3A) and KPS (2008: fig. 3B–D).

Systematic palaeontology

Phylum Mollusca Linnaeus, 1758

Class Gastropoda Cuvier, 1797

Order Caenogastropoda Cox, 1960

Superfamily Abyssochrysoidea Tomlin, 1927

Discussion.—Placement of the provannids within this superfamily follows Kaim et al. (2008a, 2009). Bouchet et al. (2005) did not recognise this superfamily and placed the provannids alongside the Abyssochrysidae Tomlin, 1927 within the paraphyletic “zygopleuroid group” amongst other caenogastropods of uncertain taxonomic position.

Family Provannidae Warén and Ponder, 1991

Genus *Provanna* Dall, 1918

Type species: ?*Trichotropis (Provanna) lomana* Dall, 1918. Recent; US Pacific coast; by monotypy.

Provanna marshalli sp. nov.

Figs. 4, 5.

Etymology: Named for Bruce A. Marshall, malacologist and collections manager of Mollusca at NMNZ, who has published extensively on New

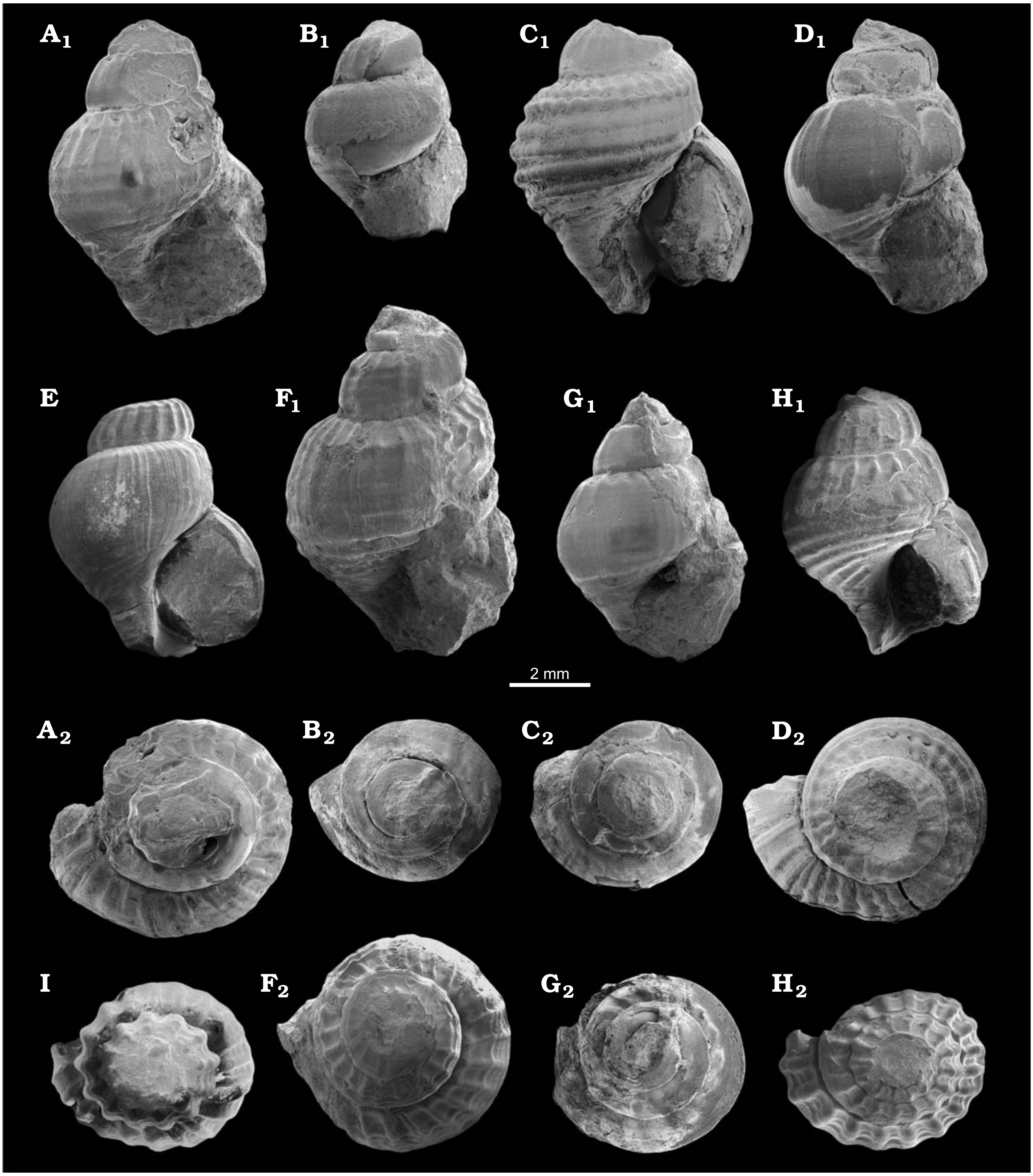

Fig. 4. Variation in provannid gastropod *Provanna marshalli* sp. nov. as seen from the apertural (upper two rows) and apical (lower two rows) views of specimens from the Middle Miocene Rocky Knob type locality. **A**. Paratype G7105. **B**. Paratype G7110. **C**. Paratype G7108. **D**. Paratype G7106. **E**. Paratype G7109. **F**. Paratype G7107. **G**. Paratype G7111. **H**. Holotype G7103. **I**. Paratype G7126.

Zealand molluscan taxonomy, and has been involved in the identification of the modern New Zealand seep faunas since the first official seep collections were made in 1996.

Type material: Holotype: G7103 (Fig. 4H), well preserved shell lacking protoconch and earliest whorls. Paratypes: one moderately preserved specimen, TM8704, from Puketawa (Y16/f0580); nine moderately to

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well preserved specimens from Rocky Knob: Y16/f1027, AU19605, seven specimens (G7105–7109, G7113, G7126); Y16/f1029, AU15834, one specimen (G7110); Y16/f1031, AU19610, one specimen (G7111). All specimens at UOA, TM8704 borrowed from palaeontology collection, GNS.

Type locality and horizon: Rocky Knob (Y16/f1027), northern Hawke's Bay area (38°30.58'S, 177°93.10'E). Fossil hydrocarbon seep deposit of the Bexhaven Limestone Formation, Tolaga Group, Middle Miocene.

Material.—19 poorly to well preserved specimens from Rocky Knob: Y16/f1027, AU19605, 14 specimens (G112, G114–125); Y16/f1028, AU19606, two specimens (G128, one unnumbered specimen); Y16/f1030, AU19609, three specimens (G7104, G7129, one unnumbered specimen). All specimens at UOA.

Dimensions.—See Table 1.

Table 1. Selected measurements of specimens of *Provanna marshalli* sp. nov., this study. Italicised values are approximate. Non-type material is labelled "specimen".

Specimen	Type	D	d	H	h	Site
G7103	holotype	5.1	2.5	*8.3*	4.4	Rocky Knob
TM8704	paratype	4.4	3.1	*6.9*	4.3	Puketawa
G7105	paratype	5.4	3.2	*7.0*	4.3	Rocky Knob
G7106	paratype	5.0	3.4	*8.4*	3.6	Rocky Knob
G7107	paratype	5.7	3.4	*8.5*	5.0	Rocky Knob
G7108	paratype	6.0	2.7	*8.8*	4.4	Rocky Knob
G7109	paratype	5.3	2.9	*8.2*	4.6	Rocky Knob
G7110	paratype	4.0	3.4	*5.5*	3.6	Rocky Knob
G7111	paratype	4.7	2.6	*7.0*	3.9	Rocky Knob
G7113	paratype	5.4	3.4	*7.3*	4.4	Rocky Knob
G7112	specimen	*5.7*	*4.1*	*8.6*	*4.7*	Rocky Knob
G7114	specimen	5.0	2.7	*6.7*	3.6	Rocky Knob
G7115	specimen	5.3	3.7	*8.1*	4.0	Rocky Knob
G7116	specimen	5.4	3.5	*7.2*	4.8	Rocky Knob
G7117	specimen	4.7	3.3	*7.6*	3.6	Rocky Knob
G7118	specimen	5.3	3.2	*7.8*	3.9	Rocky Knob
G7119	specimen	3.4	2.0	*5.6*	3.2	Rocky Knob
G7120	specimen	6.7	*5.0*	*10.8*	*4.9*	Rocky Knob
G7121	specimen	5.1	*3.3*	*7.9*	*4.5*	Rocky Knob
G7122	specimen	5.4	*3.3*	*6.6*	*4.1*	Rocky Knob
G7123	specimen	*5.2*	*3.6*	*7.2*	*4.0*	Rocky Knob
G7124	specimen	*4.2*	*3.2*	*6.2*	*3.6*	Rocky Knob
G7125	specimen	5.2	3.0	*8.0*	4.1	Rocky Knob
G7126	paratype	5.0	*3.0*	*8.1*	4.0	Rocky Knob

Diagnosis.—Shell medium-sized, ovate, fusiform; sculpture highly variable from nearly smooth to strongly cancellate; body whorl with up to 11 spiral ribs and 30 axial riblets, often forming strong nodes at their intersections, especially along tabulate shoulder; suture inclined at roughly 5° from horizontal; at least three teleoconch whorls present.

Description.—Shell medium-sized (D up to 6.7 mm; H up to ca. 10.8 mm), ovate (D/H ≈ 0.60–0.82), fusiform; shell microstructure consists of at least one (outer) simple prismatic layer (ca. 5–10 µm) above thicker crossed lamellar layer (ca. 30–40 µm); periostracum not preserved. Sculpture highly variable, ranging from nearly smooth, with only very weak spiral ribs or very weak axial riblets formed by rugose growth lines, to strongly cancellate with several spiral ribs, widely but evenly spaced. At least three teleoconch whorls present, protoconch and very earliest whorls not preserved (see remarks below); whorls rather convex with tabulate shoulder delineated by spiral rib, often strongly noded; suture distinct, inclined at angle roughly 5° from horizontal (shell axis vertical); last whorl moderately globose with distinct neck having up to three spiral ribs, moderate to weak; 0–5 spiral ribs on penultimate whorl, moderate to weak; on last whorl number of ribs varies from none (or possibly two very weak, one on shoulder, one on neck) to ca. 11, with increased strength towards neck and shoulder; 0–30 axial riblets on last whorl, less on earlier whorls, which often form strong nodes where crossing spiral elements, especially prominent on tabulate shoulders; strong sculpture can be consistent from aperture through to early whorls, or fade out in middle whorls, being expressed only in antepenultimate (possibly earlier) whorl and in latest shell, but usually with some weak sculpture in between. Aperture higher than wide (d/h = 0.61–0.94, probably less variable in life before taphonomic alteration), usually just over half height of shell; basal and outer lips often eroded, where intact forming almost circular continuation; basal lip comprises lowest point of shell from apertural perspective, passing to distinct siphonal canal, visible in a few specimens where not eroded. Operculum unknown.

Remarks.—A single, variable species is herein recognised based upon the following points: (i) the similarity in general shell shape between the specimens, with variations being observed chiefly in ornamentation; (ii) a continuum of ornamental strength, with smooth and strongly cancellate end-member specimens separated by intermediate specimens of incremental ornamental strength that grades from one end to the other; (iii) the frequency of observed morphological variation of a similar nature in other described species of the genus; (iv) the collection of the majority of specimens from a single assemblage within one site. Modern species of this genus are commonly rather simple and variable in shell shape and form, which can make it difficult to compare them across localities, although there is usually some obvious shell morphological difference where two or more species are found at a given site (Warén and Bouchet 1993).

Many of the *Provanna marshalli* specimens are well preserved, shown by the retention of original shell microstructure (Fig. 5), although the protoconchs and very earliest whorls are never present. It is rare to collect the fully intact larval shell of modern species of *Provanna*, because it is thought that the apical whorls of the protoconch are discarded after the veliger phase (Kaim et al. 2008a; Warén and Bouchet 2009). Furthermore, the corrosive condition of their environment often leads to loss of further early whorls in life, and secondary growth of a calcareous plug to replace

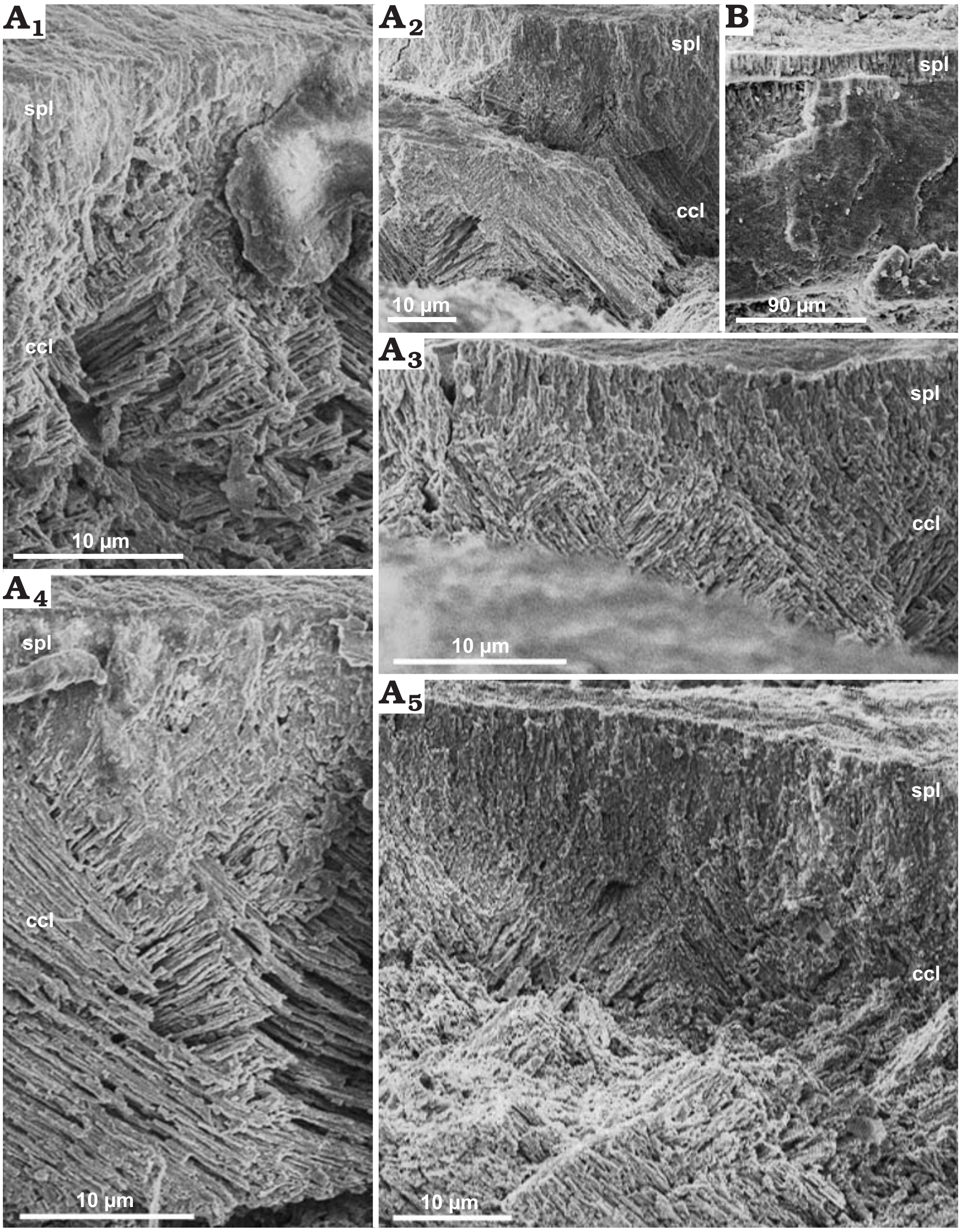

Fig. 5. Microstructure preserved in commarginal exposures of the shell material of two specimens of *Provanna marshalli* sp. nov. from the Middle Miocene Rocky Knob type locality. **A**. Paratype G7106, several sites with clean broken shell from the middle of the last whorl (A_1, A_2, A_4) and the outer lip of the aperture (A_3, A_5). **B**. Paratype G7109, clean broken shell on the outer lip of the aperture. Abbreviations: cl, crossed lamellar; spl, simple prismatic layer.

the protoconch is common (Kaim et al. 2008a; Warén and Bouchet 2009). These environmental factors, along with preservational constraints during fossilisation, make observations of this key taxonomic shell feature in fossil material highly unlikely. Indeed, only once has the protoconch I been reported in fossil material, in two specimens of *Provanna antiqua* (Kiel 2006: fig. 5.1–4). A decollate protoconch II also was reported in a Late Cretaceous-age juvenile *Provanna* specimen by Kaim et al. (2008a), where exquisite preservation occurred by early diagenetic silicification. Moreover, of 18 described modern species, only four species have been figured with an intact protoconch I, and these always from juvenile specimens (Warén and Ponder 1991; Warén and Bouchet 1993, 2009; Gustafson and Lutz 1994; Kaim et al. 2008a).

The smooth specimens of *Provanna marshalli* resemble the species *Provanna chevalieri* Warén and Bouchet, 2009 from off West Africa, *Provanna glabra* Okutani, Tsuchida, and Fujikura, 1992 from Sagami Bay, Japan, and *Provanna laevis* Warén and Ponder, 1991 from the Gulf of California, but none of these species ever develops the strong ornamentation seen in other specimens of *P. marshalli*. Two further species may have smooth-shelled individuals: *Provanna antiqua* and *Provanna variabilis*, and strong morphological variation is seen in both species. However, morphological variation in *P. marshalli* is even greater than that seen in *P. antiqua* and *P. variabilis*, with a similar smooth end-member but ranging up to a far greater number of axial riblets. The suture in *P. marshalli* is different from *P. antiqua* in its greater inclination from the horizontal (where shell axis is vertical).

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Moreover, the shells of *Provanna marshalli* are considerably larger, reaching nearly twice the height of *Provanna antiqua*, are wider but less squat overall, and also with a larger maximum height than *Provanna variabilis*. The new species has similarities to the "Shosanbetsu *Provanna* sp." from a Miocene whale fall community in Japan, which was figured and briefly, but not formally, described by Amano and Little (2005). However, the Japanese species has a maximum measured height of 6.1 mm, which is significantly less than *P. marshalli* (ca. 10.8 mm). It also has weaker sculpture that exhibits less variability (22–26 axial ribs on the last whorl), and a higher maximum number of spiral cords (16) than is seen in any specimen of *P. marshalli*. *Provanna admetoides* is the only species of the genus to possess more axial riblets (35–45 on last whorl) than the maximum observed in specimens of *P. marshalli*. *Provanna admetoides* differs in this character, as well as in its lesser variability, and far stronger and less numerous spiral ribs, which gives it a much more distinctly spirally keeled appearance than *P. marshalli*. Furthermore, the reticulations in the ornament of *P. admetoides*, formed by the intermeshing of axial and spiral elements, are elongated axially, as opposed to more or less equilateral in *P. marshalli*. Specimens of *P. marshalli* with stronger, more cancellate sculpture can resemble *Provanna nassariaeformis* Okutani, 1990, but have a larger maximum number of axial and spiral ribs, a less globose shell, and more variability in ornamentation overall than this species. Specimens of *P. marshalli* with intermediate ornamentation often resemble *Provanna lomana* (Dall, 1918), but the latter does not display the variation in its sculpture, and spiral ornamentation disappears in whorls earlier than the last whorl, unlike in *P. marshalli*, in which it persists, albeit more weakly, in some specimens.

The shell microstructure of *P. marshalli*, where preserved, is shown to be similar to that observed in some modern and fossil specimens of the genus. Kiel (2004) described the microstructure of the shell material of two *P. variabilis* specimens from the Juan de Fuca Ridge, which consists of an outer, organic periostracum slightly separated (probably during preparation) from an outer simple prismatic layer, beneath which is a thicker layer with a complex crossed lamellar structure. Another simple prismatic layer forms the innermost portion of the shell, but this layer is variably present or absent depending upon location on the shell. Kiel (2006) reported a similar shell microstructure in *P. antiqua* and Kaim et al. (2009) also showed this pattern in the shell of a related gastropod, *Hokkaidoconcha hikidai* Kaim, Jenkins, and Warén, 2008a. The periostracum is never preserved in the New Zealand fossil specimens, but there are several places in the shell of one specimen (Fig. 5A) where the outer simple prismatic layer is visible above a thicker crossed lamellar layer. Since the shell microstructure has only been observed in commarginal exposures, it cannot be confirmed whether the nature of the crossed lamellar layer is simple (i.e., two non-vertical dip directions) or complex (i.e., three or more non-vertical dip directions) (cf. Carter 1990). In another specimen from this study (Fig. 5B), a distinct simple prismatic layer is preserved above layers that recrystallised during diagenesis. The boundary is not particularly sharp between the outer simple prismatic and complex crossed lamellar layers in modern specimens (see Kiel 2004: figs. 30–32). In the fossil material, the transition between these layers also is indistinct (Fig. 5A), although there is a rather distinct boundary between the preserved simple prismatic and lower recrystallised layer in one specimen (Fig. 5B). The inner simple prismatic layer, which can form a sharp boundary with the complex crossed lamellar layer in modern specimens (see Kiel 2004: fig. 30) is never preserved in the fossil specimens. This is what might be expected, where the organic periostracum would have protected the outer simple prismatic layer until it naturally decayed after burial, the inner simple prismatic layer afforded no such protection. Weathering of internal shell layers likely occurred on the sea floor or during early burial, leaving the two inner shell layers relatively unscathed where conditions conducive to such preservation prevailed thereafter.

Stratigraphic and geographical range.—Early to Middle Miocene seep carbonates of Hawke's Bay, North Island, New Zealand. Known mostly from the type locality at Rocky Knob (28 specimens), with one confirmed specimen from Puketawa and one possible juvenile specimen from Ugly Hill.

Discussion

***Provanna* in the fossil record**.—*Provanna antiqua* was the first formally described fossil species of the genus, from hydrocarbon seep deposits in Washington, USA (Squires 1995), and it has since been extensively reported from seep deposits of this region (e.g., Squires and Goedert 1995; Rigby and Goedert 1996; Peckmann et al. 2002; Goedert and Benham 2003; Kiel 2006; Table 2). Two more fossil *Provanna* species were recently described from Japan, namely *Provanna tappuensis* Kaim, Jenkins, and Warén, 2008a and *Provanna nakagawaensis* Kaim, Jenkins, and Hikida, 2009. There are other reports of the genus from fossil seep deposits where details have been unavailable for species-level identification (Table 2). The oldest formally described species of the genus is from the Middle Cenomanian (upper Late Cretaceous) "Kanajirisawa" deposit, Yezo Group, northern Japan (Kaim et al. 2008a), although Kiel and Campbell (2005) reported gastropod fossils that may belong to *Provanna* from the Valanginian (Early Cretaceous) Crack Canyon Formation, Great Valley Group, California. Of the reports of provannids in the seep fossil record where it has been possible to identify the genus, all but the recently described *Desbruyeresia kanajirisawensis* Kaim, Jenkins, and Hikida, 2009 belong to *Provanna*. "Provannids" have been reported from Palaeocene seep deposits of California (Schwartz et al. 2003), but these are instead aporrhaids (Kaim et al. 2008a; CTSL, personal observation). There also are several seep

Table 2. Summary of fossil occurrences of the genus *Provanna* Dall, 1918, extended from Kaim et al. (2008a).

Species	Age	Occurrence	Setting	Reference(s)
Provanna? sp.	Upper Miocene	asphalt beds, Leyte Island, Philippines	hydrocarbon seep	Tomoki Kase (personal communication 2008)
Shosanbetsu *Provanna* sp.	Middle Miocene	siltstones, upper Chikubetsu Fm., Japan	whale fall	Amano and Little (2005)
Rekifune *Provanna*? sp.	Middle Miocene	mudstones, Nupinai Fm., Japan	whale fall	Amano et al. (2007)
Provanna marshalli sp. nov.	Lower–Middle Miocene	Bexhaven and Ihungia Limestone Fms., NZ	hydrocarbon seep	present study
Provanna sp.	Lower–Middle Miocene	Lengua Fm., Trinidad; Pozon Fm., Venezuela	hydrocarbon seep	Gill (2005); Gill et al. (2005)
Provanna antiqua Squires, 1995	Lower–Upper Oligocene	Lincoln Creek and Makah Fms., north-western USA	hydrocarbon seep	Goedert and Campbell (1995); Squires (1995); Squires and Goedert (1995); Rigby and Goedert (1996); Peckmann et al. (2002); Kiel (2006)
	Upper Eocene	Lincoln Creek Fm., north-western USA	wood fall	Kiel and Goedert (2006a, b)
Provanna? sp.	Upper Cretaceous	Shirochi and Haborogawa Fms., Yezo Group, Japan	plesiosaurid carcasses	Kaim et al. (2008b)
Provanna nakagawaensis Kaim, Jenkins, and Hikida, 2009	Upper Cretaceous	Omagari and Yasukawa seep deposits, Yezo Group, Japan	hydrocarbon seep	Kaim et al. (2009)
Provanna tappuensis Kaim, Jenkins, and Warén, 2008a	Upper Cretaceous	Kanajirisawa seep deposit, Yezo Group, Japan	hydrocarbon seep	Kaim et al. (2008a)

fossil species described from localities in the Antarctic, France, Japan, and the USA that belong to closely related families of the "zygopleuroid group", the majority of which are now included within Hokkaidoconchidae (see Goedert and Kaler 1996; Kiel and Peckmann 2007; Kiel 2008; Kiel et al. 2008; Kaim et al. 2008a; Kaim and Kelly 2009; Kiel et al. 2010). Of the relatively few reports of *Provanna* from fossil deposits other than hydrocarbon seeps, the only verified species assignment is *Provanna antiqua*, reported from wood fall deposits of the Late Eocene Lincoln Creek Formation by Kiel and Goedert (2006a, b). Undescribed fossils inferred as belonging to *Provanna*, or at least members of the zygopleuroid group, also have been reported from Cretaceous to Miocene-age fossil communities associated with hydrothermal vents (Little et al. 1998, 1999; Little 2002; Little and Vrijenhoek 2003), whale and plesiosaurid carcasses (Amano and Little 2005; Amano et al. 2007; Kaim et al. 2008b), and wood fall deposits (Kiel et al. 2009).

Fossil versus modern New Zealand *Provanna*.—Undescribed *Provanna* species have been reported from modern New Zealand seeps (e.g., Lewis and Marshall 1996; Warén and Bouchet 2001), but not by Baco et al. (2010), who made the largest and most recent attempt to characterise the modern NZ seep faunas. Lewis and Marshall (1996) suggested the presence of two distinct modern species, their spp. A and B, based on four specimens trawled from 1100–1200 m at *Calyptogena* Bank, Ritchie Ridge (between 39°26.4'S, 178°23.6'E and 39°23.6'S, 178°24.7'E; Fig. 1). They also reported a more tentatively assigned "?*Provanna* sp. C" from two specimens collected from 960 m depth off south-eastern South Island at Goomes Hill, Puygesur Bank (46°57.64'S, 165°25.21'E). Each of these specimens is smaller than the specimens of this study. Ongoing studies of the fossil content of New Zealand's East Coast Basin seep deposits suggest that the composition of seep communities from the Hikurangi margin has remained relatively stable over the past ca. 20 Ma, with several fossil groups showing a close relation to those found in analogous modern environments (KPS, unpublished data). Therefore, it is possible that the modern *Provanna* specimens reported by Lewis and Marshall (1996) represent a single variable modern species, perhaps conspecific with, or a descendent of, *Provanna marshalli*. This hypothesis requires confirmation through analysis of a larger amount of modern New Zealand seep material and complete formal characterisation of the New Zealand Miocene seep fauna, which is outside the scope of this study.

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References

Ager, D.V. 1986. Migrating fossils, moving plates and an expanding Earth. *Modern Geology* 10: 377–390.

Amano, K. and Little, C.T.S. 2005. Miocene whale-fall community from Hokkaido, northern Japan. *Palaeogeography, Palaeoclimatology, Palaeoecology* 215: 345–356. http://dx.doi.org/10.1016/j.palaeo.2004.10.003

Amano, K., Little, C.T.S., and Inoue, K. 2007. A new Miocene whale-fall community from Japan. *Palaeogeography, Palaeoclimatology, Palaeoecology* 247: 236–242. http://dx.doi.org/10.1016/j.palaeo.2006.10.017

Ansell, J.H. and Bannister, S.C. 1996. Shallow morphology of the subducted Pacific plate along the Hikurangi margin, New Zealand. *Physics of the Earth and Planetary Interiors* 93: 3–20. http://dx.doi.org/10.1016/0031-9201(95)03085-9

Baco, A., Rowden, A.A., Levin, L.A., Smith, C.R., and Bowden, D. 2010. Initial characterization of cold seep faunal communities on the New Zealand margin. *Marine Geology* (2010), http://dx.doi.org/10.1016/j.margo.2009.06.015.

Ballance, P.F. 1976. Evolution of the Upper Cenozoic magmatic arc and plate boundary in northern New Zealand. *Earth and Planetary Science Letters* 28: 356–370. http://dx.doi.org/10.1016/0012-821X(76)90197-7

Barnes, P.M., Nicol, A., and Harrison, T. 2002. Late Cenozoic evolution and earthquake potential of an active listric thrust complex above the Hikurangi subduction zone, New Zealand. *The Geological Society of America Bulletin* 114: 1379–1405. http://dx.doi.org/10.1130/0016-7606(2002)114%3C1379:LCEAEP%3E2.0.CO;2

Bergquist, D.C., Eckner, J.T., Urcuyo, I.A., Cordes, E.E., Hourdez, S. Macko, S.A., and Fisher, C.R. 2007. Using stable isotopes and quantitative community characteristics to determine a local hydrothermal vent food web. *Marine Ecology Progress Series* 330: 49–65. http://dx.doi.org/10.3354/meps330049

Bouchet, P., Rocroi, J.-P., Frýda, J., Hausdorf, B., Ponder, W.F., Valdés, Á., and Warén, A. 2005. Classification and nomenclator of gastropod families. *Malacologia* 47: 1–397.

Campbell, K.A. 2006. Hydrocarbon seep and hydrothermal vent paleoenvironments and paleontology: past developments and future research directions. *Palaeogeography, Palaeoclimatology, Palaeoecology* 232: 362–407.

Campbell, K.A., Francis, D.A., Collins, M., Gregory, M.R., Greinert, J., and Aharon, P. 2008. Hydrocarbon seep-carbonates of a Miocene forearc (East Coast Basin), North Island, New Zealand. *Sedimentary Geology* 204: 83–105. http://dx.doi.org/10.1016/j.sedgeo.2008.01.002

Carney, R.S. 1994. Consideration of the oasis analogy for chemosynthetic communities at Gulf of Mexico hydrocarbon vents. *Geo-Marine Letters* 14: 149–159. http://dx.doi.org/10.1007/BF01203726

Carter, J.G. 1990. Glossary of skeletal biomineralization. *In*: J.G. Carter (ed.), *Skeletal Biomineralization: Patterns, Processes, and Evolutionary Trends, Volume 1*, 609–671. Van Nostrand Reinhold, New York.

Cordes, E.E., Bergquist, D.C., and Fisher, C.R. 2009. Macro-ecology of Gulf of Mexico cold seeps. *Annual Review of Marine Science* 1: 143–168. http://dx.doi.org/10.1146/annurev.marine.010908.163912

Danner, W.R. 1966. Limestone resources of western Washington. *Washington State Division of Mines Bulletin* 52: 1–424.

Distel, D., Baco, A.R., Chuang, E., Morrill, W., Cavanaugh, C.M., and Smith, C.R. 2000. Do mussels take wooden steps to deep-sea vents? *Nature* 403: 725–726. http://dx.doi.org/10.1038/35001667

Fujikura, K., Fujiwara, Y., Kojima, S., and Okutani, T. 2002. Micro-scale distribution of molluscs occurring in deep-sea chemosynthesis-based communities in the Japan Trench. *Venus* 60: 225–236.

Gilbert, G.K. and Gulliver, F.P. 1894. Tepee Buttes. *Bulletin of the Geological Society of America* 6: 333–342.

Gill, F.L. 2005. *Fossil Cold Seep Communities in the Caribbean Region*. 261 pp. Unpublished Ph.D. thesis. University of Leeds, Leeds.

Gill, F.L., Harding, I.C., Little, C.T.S., and Todd, J.A. 2005. Palaeogene and Neogene cold seep communities in Barbados, Trinidad and Venezuela: an overview. *Palaeogeography, Palaeoclimatology, Palaeoecology* 227: 191–209. http://dx.doi.org/10.1016/j.palaeo.2005.04.024

Goedert, J.L. and Benham, S.R. 2003. Biogeochemical processes at ancient methane seeps: the Bear River site in southwestern Washington. *In*: T.W. Swanson (ed.), Western Cordillera and Adjacent Areas. *Geological Society of America Field Guide* 4: 201–208.

Goedert, J.L. and Campbell, K.A. 1995. An Early Oligocene chemosynthetic community from the Makah Formation, northwestern Olympic Peninsula, Washington. *The Veliger* 38: 22–29.

Goedert, J.L. and Kaler, K.L. 1996. A new species of *Abyssochrysos* (Gastropoda: Loxonematoidea) from a Middle Eocene cold-seep carbonate in the Humptulips Formation, western Washington. *The Veliger* 39: 65–70.

Gustafson, R.G. and Lutz, R.A. 1994. Molluscan life history traits at deep-sea hydrothermal vents and cold methane/sulfide seeps. *In*: C.M. Young and K.J. Eckelbarger (eds.), *Reproduction, Larval Biology, and Recruitment of the Deep-Sea Benthos*, 76–97. Columbia University Press, New York.

Hessler, R.R. and Lonsdale, P.F. 1991. Biogeography of Mariana Trough hydrothermal vent communities. *Deep-Sea Research* 38: 185–199. http://dx.doi.org/10.1016/0198-0149(91)90079-U

Kaim, A. and Kelly, S.R.A. 2009. Mass occurrence of hokkaidoconchid gastropods in the Upper Jurassic methane seep carbonate from Alexander Island, Antarctica. *Antarctic Science* 21: 279–284. http://dx.doi.org/10.1017/S0954102009001813

Kaim, A., Jenkins, R.G., and Hikida, Y. 2009. Gastropods from Late Cretaceous Omagari and Yasukawa hydrocarbon seep deposits in the Nakagawa area, Hokkaido, Japan. *Acta Palaeontologica Polonica* 54: 463–490. http://dx.doi.org/10.4202/app.2009.0042

Kaim, A., Jenkins, R.G., and Warén, A. 2008a. Provannid and provannid-like gastropods from the Late Cretaceous cold seeps of Hokkaido (Japan) and the fossil record of the Provannidae (Gastropoda: Abyssochrysoidea). *Zoological Journal of the Linnean Society* 154: 421–436.

Kaim, A., Kobayashi, Y., Echizenya, H., Jenkins, R.G., and Tanabe, K. 2008b. Chemosynthesis-based associations on Cretaceous plesiosaurid carcasses. *Acta Palaeontologica Polonica* 53: 97–104. http://dx.doi.org/10.4202/app.2008.0106

Kiel, S. 2004. Shell structures of selected gastropods from hydrothermal vents and seeps. *Malacologia* 46: 169–183.

Kiel, S. 2006. New records and species of molluscs from Tertiary cold-seep carbonates in Washington State, USA. *Journal of Paleontology* 80: 121–137. http://dx.doi.org/10.1666/0022-3360(2006)080%5B0121:NRASOM%5D2.0.CO;2

Kiel, S. 2008. An unusual new gastropod from an Eocene hydrocarbon seep in Washington State. *Journal of Paleontology* 82: 188–191. http://dx.doi.org/10.1666/06-029.1

Kiel, S., Amano, K., Hikida, Y., and Jenkins, R.G. 2009. Wood-fall associations from Late Cretaceous deep-water sediments of Hokkaido, Japan. *Lethaia* 42: 74–82. http://dx.doi.org/10.1111/j.1502-3931.2008.00105.x

Kiel, S. and Campbell, K.A. 2005. *Lithomphalus enderlini* gen. et sp. nov. from cold-seep carbonates in California—a Cretaceous neomphalid gastropod? *Palaeogeography, Palaeoclimatology, Palaeoecology* 227: 232–241. http://dx.doi.org/10.1016/j.palaeo.2005.04.022

Kiel, S. and Goedert, J.L. 2006a. A wood-fall association from Late Eocene deep-water sediments of Washington State, USA. *Palaios* 21: 548–556. http://dx.doi.org/10.2110/palo.2005.p05-086r

Kiel, S. and Goedert, J.L. 2006b. Deep-sea food bonanzas: early Cenozoic whale-fall communities resemble wood-fall rather than seep communities. *Proceedings of the Royal Society B* 273: 2625–2631. http://dx.doi.org/10.1098/rspb.2006.3620

Kiel, S. and Peckmann, J. 2007. Chemosymbiotic bivalves and stable carbon isotopes indicate hydrocarbon seepage at four unusual Cenozoic fossil localities. *Lethaia* 40: 345–357. http://dx.doi.org/10.1111/j.1502-3931.2007.00033.x

Kiel, S., Campbell, K.A., and Gaillard, C. 2010. New and little known mollusks from ancient chemosynthetic environments. *Zootaxa* 2390: 26–48.

Kiel, S., Campbell, K.A., Elder, W.P., and Little, C.T.S. 2008. Jurassic and

Cretaceous gastropods from hydrocarbon seeps in forearc basin and accretionary prism settings, California. *Acta Palaeontologica Polonica* 53: 679–703. http://dx.doi.org/10.4202/app.2008.0412

Levin, L.A. 2005. Ecology of cold seep sediments: interactions of fauna with flow, chemistry and microbes. *Oceanography and Marine Biology: An Annual Review* 43: 1–46.

Levin, L.A. and Michener, R.H. 2002. Isotopic evidence for chemosynthesis-based nutrition of macrobenthos: the lightness of being at Pacific methane seeps. *Limnology and Oceanography* 47: 1336–1345.

Lewis, K.B. and Marshall, B.A. 1996. Seep faunas and other indicators of methane-rich dewatering on New Zealand convergent margins. *New Zealand Journal of Geology and Geophysics* 39: 181–200.

Little, C.T.S. 2002. The fossil record of hydrothermal vent communities. *Cahiers de Biologie Marine* 43: 313–316.

Little, C.T.S. and Vrijenhoek, R.C. 2003. Are hydrothermal vent animals living fossils? *Trends in Ecology and Evolution* 18: 582–588. http://dx.doi.org/10.1016/j.tree.2003.08.009

Little, C.T.S, Cann, J.R., Herrington, R.J., and Morriseau, M. 1999. Late Cretacerous hydrothermal vent communities from the Troodos Ophiolite, Cyprus. *Geology* 27: 1027–1030. http://dx.doi.org/10.1130/0091-7613(1999)027%3C1027:LCHVCF%3E2.3.CO;2

Little, C.T.S., Herrington, R.J., Maslennikov, V.V., and Zaykov, V.V. 1998. The fossil record of hydrothermal vent communities. *In*: R. Mills and K. Harrison (eds.), Modern Ocean Floor Processes and the Geological Record. *Geological Society of London, Special Publication* 148: 259–270.

Lonsdale, P.F. 1977. Clustering of suspension-feeding macrobenthos near abyssal hydrothermal vents at oceanic spreading centers. *Deep-Sea Research* 24: 857–863. http://dx.doi.org/10.1016/0146-6291(77)90478-7

MacAvoy, S.E., Fisher, C.R., Carney, R.S., and Macko, S.A. 2005. Nutritional associations among fauna at hydrocarbon seep communities in the Gulf of Mexico. *Marine Ecology Progress Series* 292: 51–60. http://dx.doi.org/10.3354/meps292051

Moroni, M.A. 1966. Malacofauna del "Calcare a Lucine" di S. Sofia, Forli. *Palaeontographia Italica* 60: 69–87.

Olu, K., Caprais, J.C., Galéron, J., Causse, R., Cosel, R. von, Budzinski, H., Ménach, K. Le, Roux, C. Le, Levaché, D., Khripounoff, A., and Sibuet, M. 2009. Influence of seep emission on the non-symbiont-bearing fauna and vagrant species at an active giant pockmark in the Gulf of Guinea (Congo–Angola margin). *Deep-Sea Research Part II: Topical Studies in Oceanography* 56: 2380–2393. http://dx.doi.org/10.1016/j.dsr2.2009.04.017

Paull, C.K., Hecker, B., Commeau, R., Freeman-Lynde, R.P., Neumann, C., Corso, W.P., Golubic, S., Hook, J. E., Sikes, E., and Curray, J. 1984. Biological communities at the Florida Escarpment resemble hydrothermal vent taxa. *Science* 226: 965–967. http://dx.doi.org/10.1126/science.226.4677.965

Peckmann, J., Goedert, J.L., Thiel, V., Michaelis, W., and Reitner, J. 2002. A comprehensive approach to the study of methane-seep deposits from the Lincoln Creek Formation, western Washington State, USA. *Sedimentology* 49: 855–873. http://dx.doi.org/10.1046/j.1365-3091.2002.00474.x

Rait, G., Chanier, F., and Waters, D.W. 1991. Landward and seaward-directed thrusting accompanying the onset of subduction beneath New Zealand. *Geology* 19: 230–233. http://dx.doi.org/10.1130/0091-7613(1991)019%3C0230:LASDTA%3E2.3.CO;2

Rigby, J.K. and Goedert, J.L. 1996. Fossil sponges from a localized cold-seep limestone in Oligocene rocks of the Olympic Peninsula, Washington. *Journal of Paleontology* 70: 900–908.

Sahling, H., Rickert, D., Lee, R.W., Linke, P., and Suess, E. 2002. Macrofaunal community structure and sulphide flux at gas hydrate deposits from the Cascadia convergent margin, NE Pacific. *Marine Ecology Progress Series* 231: 121–138. http://dx.doi.org/10.3354/meps231121

Schwartz, H., Sample, J., Weberling, K.D., Minisini, D., and Moore, J.C. 2003. An ancient linked fluid migration system: cold-seep deposits and sandstone intrusions in the Panoche Hills, California, USA. *Geo-Marine Letters* 23: 340–350. http://dx.doi.org/10.1007/s00367-003-0142-1

Smith, C.R. and Baco, A.R. 2003. Ecology of whale falls at the deep-sea floor. *Oceanography and Marine Biology: An Annual Review* 41: 311–354.

Smith, C.R., Baco, A.R., and Glover, A.G. 2002. Faunal succession on replicate deep-sea whale falls: time scales and vent-seep affinities. *Cahiers de Biologie Marine* 43: 293–297.

Squires, R.L. 1995. First fossil species of the chemosynthetic-community gastropod *Provanna*: localized cold-seep limestones in Upper Eocene and Oligocene rocks, Washington. *The Veliger* 38: 30–36.

Squires, R.L. and Goedert, J.L. 1995. An extant species of *Leptochiton* (Mollusca: Polyplacophora) in Eocene and Oligocene cold-seep limestones, Olympic Peninsula, Washington. *The Veliger* 38: 47–53.

Stanton, T.W. 1895. Contributions to the Cretaceous paleontology of the Pacific Coast: the fauna of the Knoxville beds. *United States Geological Survey Bulletin* 133: 1–132.

Suess, E. 2010. Marine cold seeps. *In*: K.N. Timmis (ed.), *Handbook of Hydrocarbon and Lipid Microbiology, Volume 1, Part 3*, 187–203. Springer-Verlag, Berlin.

Tanaka, K. 1959. Molluscan fossils from central Shinano, Nagano Prefecture, Japan (Part 1). *Journal of the Faculty of Science, Shinshu University* 8: 115–133.

Van Dover, C.L. 2000. *The Ecology of Deep-Sea Hydrothermal Vents*. 424 pp. Princeton University Press, Princeton.

Van Winkle, T. 1919. Remarks on some new species from Trinidad. *Bulletins of American Paleontology* 8: 19–33.

Voight, J.R. 2000. A deep-sea octopus (*Graneledone* cf. *boreopacifica*) as a shell-crushing hydrothermal vent predator. *Journal of the Zoological Society of London* 252: 335–341. http://dx.doi.org/10.1111/j.1469-7998.2000.tb00628.x

Voight, J.R. 2008. Observations of deep-sea octopodid behaviour from undersea vehicles. *American Malacological Bulletin* 24: 43–50. http://dx.doi.org/10.4003/0740-2783-24.1.43

Warén, A. and Bouchet, P. 1986. Four new species of *Provanna* Dall (Prosobranchia, Cerithiacea?) from East Pacific hydrothermal sites. *Zoologica Scripta* 15: 157–164. http://dx.doi.org/10.1111/j.1463-6409.1986.tb00218.x

Warén, A. and Bouchet, P. 1993. New records, species, genera, and a new family of gastropods from hydrothermal vents and hydrocarbon seeps. *Zoologica Scripta* 22: 1–90. http://dx.doi.org/10.1111/j.1463–6409.1993.tb00342.x

Warén, A. and Bouchet, P. 2001. Gastropoda and Monoplacophora from hydrothermal vents and seeps: new taxa and records. *The Veliger* 44: 116–231.

Warén A. and Bouchet, P. 2009. New gastropods from deep-sea hydrocarbon seeps off West Africa. *Deep-Sea Research Part II: Topical Studies in Oceanography* 56: 2326–2349. http://dx.doi.org/10.1016/j.dsr2.2009.04.013

Warén, A. and Ponder, W. F. 1991. New species, anatomy, and systematic position of the hydrothermal vent and hydrocarbon seep gastropod family Provannidae fam.n. (Caenogastropoda). *Zoologica Scripta* 20: 27–56. http://dx.doi.org/10.1111/j.1463-6409.1991.tb00273.x

Yamamoto, T., Kobayashi, T., Nakasone, K., and Nakao, S. 1999. Chemosynthetic community at North Knoll, Iheya Ridge, Okinawa Trough. *JAMSTEC Journal of Deep-Sea Research* 15: 19–24.

doi:10.4202/app.2009.1112