
http://dx.doi.org/10.4202/app.2012.0002
Miocene abyssochrysoid gastropod *Provanna* from Japanese seep and whale-fall sites

KAZUTAKA AMANO and CRISPIN T.S. LITTLE


We describe three Miocene species of *Provanna* from Japan, two new and one in open nomenclature, that represent the only known fossil examples from whale-falls and a considerable increase in the Miocene diversity of the genus. *Provanna hirokoae* sp. nov. comes from the latest Middle Miocene Kuroiwa seep site in central Honshu. The shells of this species are mostly recrystallized, but contain relict crossed lamellar microstructures. *Provanna alexi* sp. nov. is from the early Middle Miocene Shosanbetsu whale-fall site in northwestern Hokkaido, and has well preserved shells comprising an outer simple prismatic layer and an inner crossed lamellar layer. The two *Provanna* specimens from the Middle Miocene Rekifune whale-fall site, in eastern Hokkaido, are preserved as external moulds only, so are left in open nomenclature. Based on current knowledge, the presence of an outer prismatic layer and an underlying crossed lamellar layer seems to be a common feature in the shells of *Provanna*, as well as in other genera belonging to the family Provannidae and the superfamly Abyssochrysoidae. Although the oldest occurrence of *Provanna* was in the Late Cretaceous, the genus did not spread geographically and ecologically until the Miocene (with four, or possibly five species), a date concordant with some molecular estimates. However, this could be an artefact of the fossil record because the known pre-Miocene seep and whale-falls are more geographically restricted than those from the Miocene.

**Key words:** Mollusca, Gastropoda, *Provanna*, seep, whale-fall, Miocene, Japan.

Kazutaka Amano [amano@juen.ac.jp], Department of Geoscience, Joetsu University of Education, 1Yamayashiki, Joetsu 943-8512, Japan;
Crispin T.S. Little [earctsl@leeds.ac.uk], School of Earth and Environment, University of Leeds, Leeds LS2 9JT, UK.

Received 6 January 2012, accepted 24 May 2012, available online 5 June 2012.

Copyright © 2014 K. Amano and C.T.S. Little. This is an open-access article distributed under the terms of the Creative Commons Attribution License, which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.

**Introduction**

The small gastropod genus *Provanna* Dall, 1918 is one of the characteristic and species-rich molluscan taxon in modern chemosynthetic faunas (e.g., Warén and Bouchet 1993, 2001, 2009; Sasaki et al. 2010). Most *Provanna* species are grazers on filamentous bacteria, while some are detritus feeders. Although Bergquist et al. (2007) suggested that *Provanna variabilis* Warén and Bouchet, 1986 may also harbor symbiotic bacteria, Sasaki et al. (2010) raised doubts about this interpretation based on the anatomy of the species.

Eighteen Recent species of *Provanna* have so far been described (Table 1), most from hydrothermal vent and hydrocarbon (cold) seep sites, but some also from whale-fall and wood-fall sites (e.g., Smith and Baco 2003; Warén and Bouchet 2001, 2009; Sasaki et al. 2010). In contrast to this diversity, only four fossil *Provanna* species have been formally described: two from Cretaceous seep deposits in Hokkaido, Japan, one from upper Eocene to Oligocene seep deposits and upper Eocene wood-falls in Washington State, USA, and one from Miocene seeps in New Zealand (Table 1). In addition to these, fossil gastropods from four different Miocene localities have been figured, but not formally described, as *Provanna* or other provannids. These include “provannids” from the Freeman’s Bay Limestone (a suspected seep deposit) of the Miocene Lengua Formation, Trinidad (Gill et al. 2005: fig. 7I, J) and three *Provanna* species from two whale-fall sites and one seep site from Japan (Amano and Little 2005; Amano et al. 2007, 2010). Here we formally describe these Japanese species and discuss the shell microstructures and the fossil record of the genus *Provanna*. The Japanese occurrences represent the only known fossil examples of *Provanna* from whale-falls and a significant increase in the Miocene species diversity of the genus.

Institutional abbreviations.—JUE, Joetsu University of Education, Joetsu, Japan.
Material

Twenty-seven Provanna specimens were collected from the Shosanbetsu whale-fall site in northwestern Hokkaido (locality 1 in Fig. 1; Amano and Little 2005). This site is from the lower Middle Miocene (15.9–14.9 Ma) Chikubetsu Formation (Amano et al. 2007). We examined and measured nine of the specimens, all of which have well preserved shells, allowing microstructural details to be studied.

Two Provanna specimens were collected from the Rekifune whale-fall site in eastern Hokkaido (locality 2 in Fig. 1; Amano et al. 2007). This site is from the Middle Miocene Nupinai Formation (ca.13–12 Ma). The specimens are preserved as external moulds only, from which silicone rubber casts were made for examination.

A total of 124 Provanna specimens were collected from a hydrocarbon seep deposit at the Kita-Kuroiwa Quarry in Kakizaki-ku, Joetsu City, Niigata Prefecture, central Honshu, Japan (locality 3 in Fig. 1; Amano et al. 2010). The Kuroiwa seep site is from the uppermost Middle Miocene (11.64±0.65 Ma) Ogaya Formation (Amano et al. 2010). Twenty-eight of the specimens are relatively well preserved and were examined in detail. The shells of these specimens are recrystallized, but relict microstructural details are visible in a few.

To compare shell microstructural details of our fossil Provanna species with modern species we studied the shell of one specimen of P. reticulata Warén and Bouchet, 2009. This was collected with samples of seep carbonate (M56B, GeoB 8212-1 TV grab) from 3100 m water depth at the Hydrate Hole pockmark site, on the Congo deep-sea fan (Sahling et al. 2008) during RV METEOR Cruise M56 (Chief Scientist Gerhard Bohrmann, MARUM, University of Bremen, Germany).

Systematic paleontology

Phylum Mollusca Linnaeus, 1758
Class Gastropoda Cuvier, 1797
Order Caenogastropoda Cox, 1959
Superfamily Abyssochrysoidea Tomlin, 1927
Family Provannidae Warén and Ponder, 1991
Genus Provanna Dall, 1918

Type species: Trichotropis (Provanna) lomana Dall, 1918; Recent, US Pacific Coast.

Provanna hirokoae sp. nov.

Diagnosis.—Medium-sized Provanna with variable sculpture ranging from sigmoidal axial growth lines and many indistinct spiral cords to strong sigmoidal axial ribs crossed by weaker spiral cords. Whorls with broad, smooth sutural ramp and distinct rounded shoulder, tabulated at axial ribs, where present.

Description.—Medium-sized shell, up to 9.8 mm high, ovate fusiform; teleoconch at least three whorls; protoconch not preserved. Sutures weakly impressed. Body whorl with broad, smooth sutural ramp sloping gently to rounded shoulder. From shoulder abapically body whorl sides gently curved. Ornament variable; some specimens, like holotype (Fig. 2A) and paratype JUE 15902-2 (Fig. 2C), having whorls with sigmoidal growth lines and many indistinct spiral cords best developed on the body whorl near the shoulder and at whorl base; other specimens, like paratype JUE 15902-3 (Fig. 2D) having nearly smooth whorls with sigmoidal growth lines only. Strong sigmoidal axial ribs on apical whorls of some specimens, such as paratype, JUE 15902-4, up to eighteen in number on penultimate whorl (Fig. 2E). In some specimens, distinct axial ribs also on body whorl, as in paratype, JUE 15902-4.
Table 1. Distribution, ecology, and shell microstructure of the fossil and modern species of *Provanna*. 1) after Kiel (2010). The fossil occurrence bathymetry estimations are in brackets because they are estimations. 2) The type material for these species was trawled and therefore the original habitats are unknown. The habitats given are from subsequent discoveries. 3) From inner layer (left) to outer layer (right); ccl, complex crossed lamellar structure; cl, crossed lamellar structure; homo, homogeneous structure; spl, simple prismatic structure.

<table>
<thead>
<tr>
<th>Species name</th>
<th>Age</th>
<th>Height (mm)</th>
<th>Geographic distribution</th>
<th>Depth (m)</th>
<th>Habitat</th>
<th>Shell microstructure</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Provanna tappuensis</em></td>
<td>Cenomanian</td>
<td>3.9</td>
<td>Northwestern Hokkaido, Japan</td>
<td>–</td>
<td>seep</td>
<td></td>
</tr>
<tr>
<td><em>Provanna nakagawaensis</em></td>
<td>Coniacian, Campanian</td>
<td>5.4</td>
<td>Northwestern Hokkaido</td>
<td>–</td>
<td>seep and wood-fall</td>
<td></td>
</tr>
<tr>
<td><em>Provanna antiqua</em> Squires, 1995</td>
<td>Eocene to Oligocene</td>
<td>5.8</td>
<td>Washington State, USA (400–800)</td>
<td>seep and wood-fall</td>
<td>spl, ccl, homo (Kiel 2006)</td>
<td></td>
</tr>
<tr>
<td><em>Provanna marshali</em> Saether, Little and Campbell, 2010</td>
<td>Miocene</td>
<td>10.8</td>
<td>North Island, New Zealand</td>
<td>–</td>
<td>seep</td>
<td>spl, cl (Saether et al. 2010)</td>
</tr>
<tr>
<td><em>Provanna hirokoae</em> sp. nov.</td>
<td>Miocene</td>
<td>9.8</td>
<td>Central Honshu, Japan (1000–2000)</td>
<td>seep</td>
<td>cl (this study)</td>
<td></td>
</tr>
<tr>
<td><em>Provanna alexi</em> sp. nov.</td>
<td>Miocene</td>
<td>6.5</td>
<td>Northwestern Hokkaido (1000–2000)</td>
<td>whale-fall</td>
<td>spl, cl (this study)</td>
<td></td>
</tr>
<tr>
<td><em>Provanna</em> sp. (Rekifune Whale-fall)</td>
<td>Miocene</td>
<td>5.0</td>
<td>Eastern Hokkaido</td>
<td>(50–500)</td>
<td>whale-fall</td>
<td></td>
</tr>
<tr>
<td><em>Provanna loiana</em> (Dall, 1918)</td>
<td>Recent</td>
<td>8.5</td>
<td>Oregon to California, USA</td>
<td>450–1200</td>
<td>seep, vent, and whale-fall</td>
<td></td>
</tr>
<tr>
<td><em>Provanna pacifica</em> (Dall, 1908)</td>
<td>Recent</td>
<td>4.9</td>
<td>Gulf of Panama, Oregon Margin</td>
<td>2311</td>
<td>wood-fall</td>
<td></td>
</tr>
<tr>
<td><em>Provanna ios</em> Warén and Bouchet, 1986</td>
<td>Recent</td>
<td>9.5</td>
<td>East Pacific Rise</td>
<td>2450–2600</td>
<td>vent</td>
<td></td>
</tr>
<tr>
<td><em>Provanna muricata</em> Warén and Bouchet, 1986</td>
<td>Recent</td>
<td>5.8</td>
<td>East Pacific Rise, North Fiji, Lau Back-arc Basin,</td>
<td>2451–2457</td>
<td>vent</td>
<td></td>
</tr>
<tr>
<td><em>Provanna goniata</em> Warén and Bouchet, 1986</td>
<td>Recent</td>
<td>12.3</td>
<td>Guaymas Basin</td>
<td>2000–2020</td>
<td>seep</td>
<td></td>
</tr>
<tr>
<td><em>Provanna variabilis</em> Warén and Bouchet, 1986</td>
<td>Recent</td>
<td>8.7</td>
<td>Juan de Fuca Ridge, Oregon Margin, Gorda Ridge</td>
<td>675–2200</td>
<td>vent and seep</td>
<td>spl, ccl, spl (Kiel, 2004)</td>
</tr>
<tr>
<td><em>Provanna macleani</em> Warén and Bouchet, 1989</td>
<td>Recent</td>
<td>7.1</td>
<td>Oregon Margin</td>
<td>2713–2750</td>
<td>wood-fall</td>
<td></td>
</tr>
<tr>
<td><em>Provanna segonzaci</em> Warén and Ponder, 1991</td>
<td>Recent</td>
<td>7.6</td>
<td>Lau Basin</td>
<td>1700–1900</td>
<td>vent</td>
<td></td>
</tr>
<tr>
<td><em>Provanna laevis</em> Warén and Ponder, 1991</td>
<td>Recent</td>
<td>10.0</td>
<td>Guaymas Basin</td>
<td>500–2000</td>
<td>vent and seep</td>
<td></td>
</tr>
<tr>
<td><em>Provanna sculpta</em> Warén and Ponder, 1991</td>
<td>Recent</td>
<td>7.1</td>
<td>Louisiana Slope, USA</td>
<td>550</td>
<td>seep</td>
<td></td>
</tr>
<tr>
<td><em>Provanna admetoides</em> Warén and Ponder, 1991</td>
<td>Recent</td>
<td>7.9</td>
<td>Florida Escarpment, USA</td>
<td>624–631</td>
<td>seep</td>
<td></td>
</tr>
<tr>
<td><em>Provanna glabra</em> Okutani, Tsuchida, and Fujikura, 1992</td>
<td>Recent</td>
<td>10.6</td>
<td>Off Hatsushima, Japan</td>
<td>1110–1200</td>
<td>seep</td>
<td></td>
</tr>
<tr>
<td><em>Provanna buccinoideos</em> Warén and Bouchet, 1993</td>
<td>Recent</td>
<td>9.5</td>
<td>North Fiji Basin and Lau Basin</td>
<td>1900–2765</td>
<td>vent</td>
<td></td>
</tr>
<tr>
<td><em>Provanna abyssalis</em> Okutani and Fujikura, 2002</td>
<td>Recent</td>
<td>7.1</td>
<td>Japan Trench</td>
<td>5343–5379</td>
<td>seep</td>
<td></td>
</tr>
<tr>
<td><em>Provanna shinkaiae</em> Okutani and Fujikura, 2002</td>
<td>Recent</td>
<td>11.0</td>
<td>Japan Trench</td>
<td>5343–5379</td>
<td>seep</td>
<td></td>
</tr>
<tr>
<td><em>Provanna reticulata</em> Warén and Bouchet, 2009</td>
<td>Recent</td>
<td>14.0</td>
<td>Regab, Guiness, MPS 1-Congo and Kouilou sites, West Africa</td>
<td>750–3150</td>
<td>seep</td>
<td>spl, cl, spl (this study)</td>
</tr>
<tr>
<td><em>Provanna chevalieri</em> Warén and Bouchet, 2009</td>
<td>Recent</td>
<td>11.5</td>
<td>Regab site, West Africa</td>
<td>3113–3956</td>
<td>seep</td>
<td></td>
</tr>
</tbody>
</table>
In specimens with axial ribs, spiral cord at shoulder at deflection point in shape of ribs relatively stronger than other spiral cords, forming weak nodes at intersection points with axial ribs. Aperture broad and rounded, with evidence for weak siphonal notch. Shells mostly recrystallized, but relict crossed lamellar structure visible on inner shell surface of one specimen.

Remarks.—Provanna lomana Dall, 1918 from seep, vent, and whale-fall sites off California resembles P. hirokoae in outline, shell size and shape of axial ribs on the apical whorls. However, P. lomana has stronger spiral cords and axial ribs on the body whorl. P. chevalieri Warén and Bouchet, 2009 from seep sites off West Africa is also similar to P. hirokoae in outline and size, but differs in having deeper sutures, a narrower and less sloping sutural ramp, and strong spiral cords on the basal part of the body whorl.

Provanna hirokoae specimens have very variable sculpture, particularly on the early whorls, and share this characteristic with several fossil (P. antiqua Squires, 1995 and P. marshalli Saether, Little, and Campbell, 2010) and modern (P. variabilis) species in the genus.

Stratigraphic and geographic range.—From the type locality only.

Provanna alexi sp. nov.

Fig. 3.

2005 Provanna sp.; Amano and Little 2005: figs. 5H–K.

Etymology: Named for the second author’s son Alex.

Type material: Holotype, JUE 15904 (Fig. 3A); Paratypes, JUE 15905-1 (Fig. 3B), JUE 15905-2 (Fig. 3C), JUE 15905-3 (Fig. 3D).

Type locality: 5.5 km upstream of Shosanbetsu Village on the Setakinai River in northwestern Hokkaido, Japan (see Amano and Little 2005); whale-fall site.

Type horizon: Fossil whale-fall deposits of the Chikubetsu Formation, lower Middle Miocene.

Dimensions.—See Table 3.

Diagnosis.—Small-sized Provanna with strong, tabulated shoulder, 8–16 spiral cords and 22–26 axial ribs on body whorl.

Description.—Shell small, up to 6.5 mm high, with ovate fusiform shape; teleoconch with three whorls; protoconch not preserved. Sutures weakly impressed. Apical whorls sculptured by strong spiral cords, three to six in number on penultimate whorl, and strong, straight axial ribs, six to twenty-one in number on penultimate whorl. Very distinct angular shoulder formed by strong spiral cord with strong nodes at intersection with axial ribs. Narrow sutural ramp adapically of shoulder. Whorl sides ranging in shape from nearly straight to weakly curved. Stronger spiral cords causing distinct angulations in body whorl sides of some specimens. Body whorl large, comprising roughly 60–70% of shell height. Ornamentation on body whorl weaker than on apical whorls, with eight to sixteen spiral cords, best developed near shoulder and whorl base, and twenty-two to twenty-six axial ribs.
Shoulder also weaker on body whorl and sutural ramp having greater slope angle. Aperture ovate with suggestion of weak apertural notch. Shells formed of two distinct microstructural elements: inner crossed lamellar layer (up to 120 μm thick) and outer simple prismatic layer (up to 20 μm thick).

Remarks.—In having a tabulate shoulder, *Provanna alexi* is similar to *P. antiqua* from Eocene wood-falls and Eocene to Oligocene seep deposits in Washington State, USA and *P. marshalli* from Miocene seeps of New Zealand. However, *P. antiqua* differs from *P. alexi* by having less numerous spiral cords on the body whorl (2–7 in *P. antiqua*; 8–16 in *P. alexi*). The number of spiral cords in *P. marshalli* (0–11) is generally less than in *P. alexi*, but there is some overlap. In addition, axial ribs are always present in *P. alexi*, whereas this character is lacking in some specimens of both *P. antiqua* and *P. marshalli*.

**Stratigraphic and geographic range.**—From the type locality only.

---

**Provanna sp.**

2007 *Provanna?* sp.; Amano et al. 2007: fig. 3A, B.

**Material.**—Two specimens from the whale-fall site of the Middle Miocene Ogaya Formation, eastern Hokkaido, Japan.

**Measurements.**—See Table 4.

**Description.**—Shell small, up to 5.0 mm high, ovate fusiform; teleoconch with three whorls; protoconch not preserved. Suture very shallow; whorl side curved without shoulder. Surface ornamented by distinct axial ribs and spiral

---

**Table 4. Measurements of *Provanna* sp. specimens.**

<table>
<thead>
<tr>
<th>Specimens</th>
<th>Number of whorls</th>
<th>Height (mm)</th>
<th>Maximum diameter (mm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>JUE 15846-1</td>
<td>3</td>
<td>5.0+</td>
<td>3.4</td>
</tr>
<tr>
<td>JUE 15846-2</td>
<td>3</td>
<td>4.0+</td>
<td>2.9</td>
</tr>
</tbody>
</table>
cords, forming cancellate sculpture at crossing points. Axial ribs almost straight, numbering 13 on penultimate whorl and 16 on body whorl. Four spiral cords on penultimate whorl and eight on body whorl.

**Remarks.**—There are three *Provanna* species with cancellate ornament that can be compared to the Rekifune species. However, two of these (*P. admetoides* Warén and Ponder, 1991 and *P. marshalli* Saether, Little, and Campbell, 2010) have distinct tabulated shoulders, lacking in the Rekifune species, and one (*P. nassariaeformis* Okutani, 1990) has a wider body whorl than seen in either of the Rekifune specimens.

We do not name this species at present because we have only two specimens, and these are present as external moulds only. Amano et al. (2007) illustrated these specimens as *Provanna*? sp., but small gastropods having such cancellate sculpture recorded from chemosynthetic communities can be also be found amongst the nassariids, cancellariids, and turrids. However, we are confident that the Rekifune specimens do not belong to these families for the following reasons. The lack of a fasciole and folding on the aperture inner lip suggests the Rekifune specimens are not nassariids, and collumellar folds, which are characteristic of the cancellariids, are also lacking in the Rekifune specimens, indicating they do not belong to this family either. Further, species of...
top of aperture where it meets the body whorl wall.  

C. Topotype, JUE 15906-1, fractured apical whorl shell, white arrows indicate relict crossed lamellar structures in the innermost layer.  

D. Paratype, JUE 15905-1, fractured apical whorl shell.  

E. *Provanna hirokoae* sp. nov., paratype, 15902-4, fractured body whorl shell.  

Abbreviations: cl, crossed lamellar layer; ?cl, possible crossed lamellar layer; p, periostracum; spl, simple prismatic layer.
the nassariids and cancellariid are rare in the modern chemo-
synthetic fauna. The Rekifune specimens lack the posteriorly
situated growth lines which characterize the turrids.

Discussion

Shell microstructures in Provanna.—In contrast to the nu-
merous published studies on the anatomy and gross shell
morphology of Provanna species there are few reports detail-
ing shell microstructures, within the genus specifically, and
the provannids more widely (Table 1). Kiel (2004) showed
that the shell of P. variabilis Warén and Bouchet, 1986 has
three layers of microstructure: an outer thin simple prismatic
layer, a thicker central complex crossed lamellar layer and
a thin inner simple prismatic layer (Table 1). He noted that
the innermost part of the complex crossed lamellar layer
sometimes has loosely packed crystals (Kiel 2004: fig. 30)
and the inner prismatic layer is not present in all parts of the
shell (Kiel 2004: fig. 32). Kiel (2004) identified the same
microstructural shell composition in the large provannid Al-
viniconcha hessleri Okutani and Ohta, 1988, but in this spe-
cies the layers are extremely thin compared to the thick outer
periostracum (Kiel 2004: fig. 33).

We found the same layers in the modern species P. reticu-
lata (Fig. 5A, A1). Around the fractured aperture of the stud-
ied specimen the outer prismatic layer stays roughly the same
width (ca. 20 μm), although it slightly thickens (to 25 μm)
where the spiral cords intersect with the shell edge. The inner
prismatic layer is present along the whole aperture margin,
but thickens substantially (to ca. 50 μm) adapically where the
outer lip of the aperture meets the body whorl wall (Fig. 5A1).
Both the outer simple prismatic and crossed lamellar layers
are present in the shells of the fossil species Provanna (as seen in Kiel
1995: fig. 32). This layer also often has vertical
structures running through it, and, in places, relic patches
of crystals with oblique orientation which are parallel to the
crystals in the crossed lamellar layer (Fig. 5C). We suggest
that this layer is the innermost portion of the crossed lamellar
layer that is undergoing dissolution and recrystallization. It
could correspond to the inner zone of loosely packed crystals
in the crossed lamellar layer in P. variabilis (as seen in Kiel
2004: fig. 30). There is no inner prismatic layer in P. alexi,
which is also the case for P. marshalli. Saether et al. (2010)
suggested that the lack of this layer in P. marshalli might have
been due to differential taphonomic and diagenetic processes
affecting the shells, either on the seafloor or during early
burial, where the outer shell microstructural layers were
protected for longer from these processes by the periostracum
in relation to the innermost shell layers. An alternative explana-
tion is that an inner layer of simple prismatic microstructure
was not present in P. alexi and P. marshalli. The shells of P.
hirokoae sp. nov. are largely recrystallized, but relic textures
in the crystals on the inner surface of one specimen (Fig. 5E)
indicates that crossed lamellar microstructures were present
in this species. Kiel (2006) identified three microstructural
layers in the shell of the fossil species P. antiqua Squires,
1995: an outer prismatic layer, a central complex crossed
lamellar layer and an inner homogeneous layer. Given what
we have seen in P. alexi this inner layer of P. antiqua might not
be a primary structure, but could rather represent an innermost
layer of dissolution and recrystallization, as suggested for P.
marshalli by Saether et al. (2010).

Amongst gastropods related to the provannids shell mi-
crostructures have been recorded in the fossil abyssochry-
soidean gastropod Hokkaidoconcha hikidai Kaim, Jenkins,
and Warén, 2008 from the Cretaceous seep sites in Hokkaido.
This species has an outer prismatic layer, a crossed lamellar
central layer and an inner prismatic layer (Kaim et al. 2009:
fig. 11B). So, based on the available data, it seems that the
presence of an outer prismatic microstructural layer and an
underlying crossed lamellar microstructural layer is a com-
mon feature in the shells of all Provanna species, as well as in
other provannid genera and in the superfamilly Abyssochry-
soidea. The structure of the innermost layer, where present,
may be more variable (simple prismatic or homogeneous),
although identification of microstructures is more difficult in
fossil specimens where shell preservation is an issue.

Fossil record of Provanna.—The oldest record of the ge-
nus is P. tappuensis Kaim, Jenkins, and Warén, 2008 from a
Middle Cenomanian (Late Cretaceous, 95–96 Ma) seep
site in Hokkaido, where it co-occurs with another provannid
species, Desbruyeresia kanajirisawensis Kaim, Jenkins,
and Warén, 2008, and a hokkaidoconchid species, Hokkaidocon-
cha tanabei Kaim, Jenkins, and Warén, 2008 (Kaim et al.
2008). The only other Mesozoic record of Provanna is P.
nakagawaensis Kaim, Jenkins, and Hikida, 2009 from two
Lower Campanian (Late Cretaceous, 80–83 Ma) seep sites
and one Coniacian (86–89 Ma) wood-fall site, also in Hok-
kaido (Kaim et al. 2009). This species co-occurs with Hok-
kaidoconcha hikidai at one of these sites (Kaim et al. 2009).

In the Paleogene and Neogene the range of habitats and
geographic areas from which fossil Provanna specimens
have been found increases in relation to the Mesozoic occur-
cences (Table 1). In the Paleogene P. antiqua is found in five
Late Eocene to Late Oligocene (23–37 Ma) seep sites and
also in two Late Eocene (34–37 Ma) wood-fall sites in Wash-
ington State, USA (Goedert and Campbell 1995; Squires
1995; Squires and Goedert 1995; Rigby and Goedert 1996;
Peckmann et al. 2002; Kiel 2006; Kiel and Goedert 2006a,
b). In the Early to Middle Miocene Provanna species are
found in seep sites in New Zealand (P. marshalli), Japan
(P. hirokoae) (Table 1), and possibly also Trinidad (Gill et
al. 2005; Saether et al. 2010). Also in the Miocene two spe-
cies of Provanna (P. alexi and Provanna sp.) occurred at
whale-falls. Today only one Provanna species (P. lomana),
is known from modern whale-fall communities (Smith and Baco 2003), although two species of the provannid genus Rubyspira occur at whale-falls in Monterey Bay, California (Johnson et al. 2010). The modest species diversification of Provanna in the Early to Middle Miocene has some congruence with the upper estimates in Johnson et al. (2010) for the radiation of the genus at 15–35 Ma (vicariance calibration) or 17–45 Ma (fossil calibrations). However, it should be noted that for at least two of the Miocene occurrences of Provanna or provannids (New Zealand and Trinidad) there are presently no known older seep deposits in the same geographic areas, meaning that there could have been a greater pre-Miocene diversity and palaeobiogeographic distribution in Provanna, not currently seen in the fossil record. This alternative would be more consistent with the older molecular divergence estimates in Johnson et al. (2010).

Acknowledgements

We thank Misaki Aikawa (Okawa City Office, Japan) for helping us collect specimens of Provanna hirokoei. We also thank Gerhard Bohrmann and Jörn Peckmann (both, MARUM, University of Bremen, Germany) for specimens of Provanna reticulata from the Congo Fan seeps, and Steffen Kiel (University of Göttingen, Germany) for his information about the shell microstructure of Provanna. Useful comments from Anders Warén (Swedish Museum of Natural History, Sweden) and an anonymous referee are acknowledged. This study was partly supported by a Grant-in-aid for Scientific Research from the Japan Society of Promotion of Science (C, 23540546, 2011–2013) to KA, and a Hanse-Wissenschaftskolleg Fellowship to CTSL.

References


Sasaki, T., Warén, A., Kano, Y., Okutani, T., and Fujikura, K. 2010. Gastro-


