# Mollusca, Bivalvia

The Solemyidae are represented at hydrothermal vent or cold seep biotopes by the genus *Acharax*. Eight named species as well as several still unnamed species are known, but only a single species has been collected at hydrothermal vents (Lau Back-Arc Basin). Representatives of this genus can grow to relatively large sizes between 10 and 22 cm. They live deeply buried in soft sediment. At least some species are characterized by the absence of a digestive tract, and their nourishment relies exclusively on their chemosynthetic symbiotic bacteria.

Of the large mussels living at hydrothermal vents or cold seeps, 20 species have been currently described, 18 of them in the genus *Bathymodiolus*. Of these, 10 are known from hydrothermal vents and are covered herein. Several other large mussels are still awaiting description. All known *Bathymodiolus* have a larval shell of about 0.5 mm or smaller with set-off protoconch 1; in general, the protoconch has a distinct rose color.

The Vesicomyidae are a rather diverse family in size, shape and species number: at the moment 84 recently named species are known, but there are still numerous undescribed species currently under study by several authors. The family comprises on one hand small species (genus *Vesicomya* sensu stricto), which occur in the deep sea but are not necessarily associated with cold seep and/or hot vent habitats and on the other hand, most of the numerous medium-sized or large to very large species are confined to reducing sediments, cold seeps, hydrocarbon seeps or hydrothermal vents. In the past, species of Vesicomyidae have been assigned to different genera or subgenera and many of the large species are now commonly placed in the genus Calyptogena (sensu lato). Recently however, some authors have revised tentatively all Vesicomyidae in the sole genus Vesicomya (in a broad sense) pending future supra-specific revisions based mainly on molecular research. Anyway, shell and soft part morphology remain important and key characters are among others hinge dentition, shell size and shape and presence or absence of a well-developed pallial sinus. Herein, the genus Calyptogena is maintained. The assignment of a vesicomyid species to Calyptogena differs with authors, and the supra-specific systematics of the Vesicomyidae is still far from settled. Most of the larger species have been described from cold seep biotopes, but of the 28 named species currently treated as Calyptogena, seven were found inhabiting also (or exclusively) hydrothermal vents. Not very much is known of the larval development of vesicomyid clams, but many are known to have lecithotrophic development.

The Pectinidae are represented by two species, *Bathypecten vulcani*, present at the Galapagos Spreading Center, the northern East Pacific Rise 13°N and the southern East Pacific Rise 38°S and *Sinepecten segonzaci*, from the Manus Back-arc Basin. More sampling need of these small bivalves, difficult to see in situ, to understand the processes of their distribution.



1: Bathymodiolus azoricus from Rainbow, Mid-Atlantic Ridge, Atos cruise © Ifremer.

# Calyptogena edisonensis Okutani, Kojima & Kim, 2003

### Size: Shell length up to 100 mm.

**Morphology**: Shell rather large, moderately thick, elongateoval, dorsal and ventral margin almost parallel in their middle part. Umbones not prominent, prosogyrous, situated anteriorly at 1/4 to 1/5 of shell length. Surface with irregular commarginal growth lines, periostracum thin, yellowish-straw-coloured, on earlier parts of the valves more or less eroded. Hinge plate strong but not very broad, typical for *Calyptogena*, with three cardinals in each valve. Biology: At hydrothermal vents.

Distribution: Western Pacific: Edison Seamount.



1: Several specimens; by R. von Cosel.

#### Reference:

OKUTANI T.K., KOJIMA S. & D. KIM (2004) Venus 63: 29-32.

# Calyptogena extenta Krylova & Moskalev, 1996

### Size: Shell length up to 246 mm.

Morphology: Shell very large and very elongate, thick, slightly inequivalve, somewhat irregular, bean-shaped, curved with markedly concave ventral margin and somewhat convex dorsal margin, gaping anteriorly and posteriorly. Umbones not prominent, prosogyrous, situated anteriorly at 1/6 of shell length. Surface with low growth ridges, periostracum brownish-olive, persistent only posteriorly and near margins. Hinge plate rather narrow but strong, with three cardinals in the left valve and two cardinals in the right valve.

Biology: At cold seeps and hot vents. The specimens live buried in the sediment but with the posterior part (2/3 of shell)length) free, they are inclined at about 50° to the sediment surface and are capable of moving around by means of their large muscular foot, leaving short tracks in the sediment.

Distribution: Gorda Ridge (hydrothermal vents); Monterey Canyon: 36°35'N, 122°30'5"W, 3041 m (cold seeps).



#### 1: Habitus; by R. von Cosel.

#### **References:**

COAN E.V., SCOTT P.V. & F.R. BERNARD (2000) in COAN E.V., SCOTT P.V. & F.R. BERNARD (Eds.) Bivalve Seashells of Western North America: 336-343. KOJIMA S., FUJIKURA K. & T. OKUTANI (2004) Mol. Phylogen. Evol. 32: 396-406 [400]. KRYLOVA E. & L.I. MOSKALEV (1996) Ruthenica 6: 1-10.

# Calyptogena gigas DALL, 1896

### Size: Shell length up to 125 mm.

**Morphology**: Shell large, regularly oval-oblong, rather thinshelled, very inflated, with broadly rounded anterior and posterior margin. Ventral margin almost straight, dorsal margin slightly convex. Umbones not prominent, prosogyrous. Surface with fine irregular growth lines, sometimes more or less eroded in the umbonal region. Periostracum pale olive to dark brown, often eroded on the earlier parts of the valves. Inside with very short and broad pallial sinus. Hinge plate short and rather strong, with three cardinals in the left valve and three cardinals in the right valve.  ${\bf Biology:}$  At hot vents and cold seeps, collected between 550 and 2610 m.

**Distribution**: Gulf of California, 1567 m (type locality); Guaymas Basin; Juan de Fuca Ridge.



2: In situ; by courtesy of K. Juniper.

#### **References:**

COAN E.V., SCOTT P.V. & F.R. BERNARD (2000) IN COAN E.V., SCOTT P.V. & F.R. BERNARD (Eds.) Bivalve Seashells of Western North America: 336-343. DALL W.H. (1896) Proc. U.S. Natl. Mus. **18**(1034): 7-20 [18-19].

KOJIMA S., FUJIKURA K. & T. OKUTANI (2004) Mol. Phylogen. Evol. 32: 396-406 [400].

# Calyptogena magnifica Boss & Turner, 1980

### Size: Shell length up to 263 mm.

**Morphology**: Shell very large, variable, oval to elongate-oval in outline, inequilateral and equivalve, usually without gape; valves white, entirely aragonitic; periostracum present, but frequently eroded away on older portions of shell; umbos prosogyrous, sometimes partially enrolled; lunule and escutcheon variable, present or absent; ligament external, opisthodetic, and parivincular; foot strong and rugose, with byssal gland.

**Biology**: At hot vents only. The life habit of the adult is semiepibiotic on bare basalt, living in cracks and crevices from which hydrothermal fluids emanate; early life history stages are often encountered living within basaltic rubble associated with such warm cracks and crevices. The presence of this species is correlated with elevated levels of hydrogen sulphide. The soft tissue is coloured dark red when retrieved living due to the presence of intracellular hemoglobin. The thick and large gills contain sulfur oxidizing chemoautotrophic symbionts. The large rugose foot is often seen protruding when the clams are viewed in life position.

**Distribution**: Entire Northern East Pacific Rise and Southern East Pacific Rise: 21°N to 22°S; Galapagos Spreading Center.



1: In situ, among barnacle bed of *Vulcanolepas* n. sp. and chiridotid holothurian; southern East Pacific Rise: 17°S, Biospeedo cruise © Ifremer.



2: In situ; by courtesy of K. Smith Jr.



3: Exterior, interior and dorsal view of left valve, specimen from 21°N; by R. von Cosel & P. Lozouet.

#### **References**:

ARP A. J., CHILDRESS J.J. & C.J. FISHER (1984) Physiol. I Zool. **57**: 648-662. Boss K. & R. TURNER (1980) Malacologia **20**: 161-194.

CHILDRESS J.J., FISHER C.R., FAVUZZI J.A. & N.K. SANDERS (1991) Physiol. Zool. 64: 1444-1470.

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KENNISH M. & R. LUTZ (1992) Rev. Aquat. Sci. 6: 29-66.

Колма S., Fujikura K. & T. Okutani (2004) Mol. Phylogen. Evol. **32**: 396-406 [400].

LUTZ R.A., FRITZ L.W. & R.M. CERRATO (1988) Deep-Sea Res. I **35**: 1793-1810. RIO M. & M. ROUX (1984) C. R.Acad Sci. Paris, Série II **299**: 167-172. VRIJENHOEK R. et al. (1994) Deep-Sea Res. **41**: 1171-1189.

# Calyptogena nankaiensis Okutani, Kojima & Ashi, 1996

### Size: Shell length up to 191 mm.

**Morphology**: Shell very large, solid, elongate-oval, with slightly concave middle part of ventral margin and with posterior part slightly higher than anterior part. Anterior margin narrowly rounded, posterior margin broadly rounded. Umbones prosogyrous, almost subterminal, situated anteriorly at about 1/7 of shell length. Surface with fine, irregular, close-set growth lines. Periostracum thick, straw-coloured, sometimes more or less eroded. Hinge plate strong, with three cardinals in right and left valve. **Biology**: At cold seeps and hot vents, on seep sites sometimes co-occurring with C. *soyoae* OKUTANI, 1957.

**Distribution**: Nankai Trough (cold seeps); Okinawa Trough, North Iheya Knoll (hot vents).



1: Habitus of a specimen; by R. von Cosel.

#### **References**:

Коліма S., Fujikura K. & T. Okutani (2004) Mol. Phylogen. Evol. **32**: 396-406 [400]. Окиталі Т., Коліма S. & J. Азні (1996) Venus **55**: 257-263.

# Calyptogena okutanii Kojima & Ohta, 1997

### Size: Shell length up to 120 mm.

**Morphology**: Shell large, thick and solid, elongate-oval in outline, with slightly concave middle part of ventral margin. Umbones low, prosogyrous. Surface with irregular, close-set commarginal growth ridges and lines. Periostracum thin and brownish, but often more or less erodedon the earlier parts of the valves. Hinge plate strong and rather broad with two strong cardinals in both valves. **Remarks**: Calyptogena okutanii and C. soyoae are sibling species with slight but constant morphological and molecular differences

**Biology**: At cold seeps and hot vents, at some seep sites co-occurring with C. *soyoae* OKUTANI, 1957.

**Distribution**: Sagami Bay and Nankai Trough (cold seeps); Okinawa Trough, Iheya Ridge (hydrothermal vents).



1: Habitus; by R. von Cosel.

#### **References**:

Коліма S. & S. Онта (1997) Venus **56**: 189-195. Коліма S., Fujikura K. & T. Okutani (2004) Mol. Phylogen. Evol. **32**: 396-406 [400].

# Calyptogena solidissima Okutani, Hashimoto & Fujikura, 1992

### Size: Shell length up to 128.5 mm.

**Morphology**: Shell large, thick and robust, oblong-oval in outline; with ventral margin slightly concave in its middle part. Umbones prosogyrous, not prominent. Surface with irregular growth lines and very fine and densely spaced radial threads, visible under a lens only. Periostracum extremely thin and dull yellowish, but generally eroded and persistent only near the margins. Hinge plate strong, with three cardinals in each valve, sub-umbonal pit present. **Biology**: At hot vents and cold seeps. Living clams bury themselves about one half to two-thirds of the shell length into the sediment. A temperature anomaly of 0.3°C was recorded 30 cm below the white-stained bottom surface. The thick and large gills contain sulphur oxidizing chemoautotrophic endosymbionts.

Distribution: Mid-Okinawa Trough: Minami-Ensei Knoll.



1: Habitus of two specimens; by R. von Cosel.

#### **References**:

HASHIMOTO J., OTHA J., FUJIKURA K. & T. MIURA (1995) Deep-Sea Res. **42**(4): 577-598. KOJIMA S., FUJIKURA K. & T. OKUTANI (2004) Mol. Phylogen. Evol. **32**: 396-406 [400]. OKUTANI T., HASHIMOTO J. & K. FUJIKURA (1992) Venus **51**(4): 225-233.

J. HASHIMOTO & R. VON COSEL

# Mollusca, Bivalvia, Protobranchia, Solemyoida, Solemyidae

# Acharax alinae Métivier & Cosel, 1993

### Size: Shell length up to 135 mm (including periostracum).

**Morphology**: Shell elongate-oval. Dorsal margin straight. Anterior and posterior margin rounded. Ventral margin nearly straight or somewhat concave. Umbos at posterior third, broad and flattened, beaks eroded. Periostracum very strong, dark brown, extending far beyond the calcified part of the valve. Animal with very large gills and a voluminous, roughly cylindrical foot which distally ends in a pedal disk. Digestive tract absent. **Biology**: In reducing sediments; found buried 20-30 cm deep in pale-coloured coarse sediment at the base of an isolated large siboglinid tube in a seep area at the edge of a hydrothermal vent. Known from vents only. Gills very likely harbouring chemosynthetic symbiosis. Lecitrotrophic development, most probably no, or extremely short, free swimming larval phase. Larval shell (no separate protoconch I & II) 1.35 mm long and 0.68 mm high.

Distribution: Lau Basin: Valu Fa Ridge, Hine Hina.



1: Holotype, exterior and interior of both valves; by P. Maestrati © MNHN; bottom: Another specimen with soft parts; by P. Briand © Ifremer.

#### Reference:

MÉTIVIER B. & R. VON COSEL (1993) C. R. Acad. Sci. Paris, Sér. III 316: 229-237.

# Bathymodiolus aduloides Hashimoto & Okutani, 1994

### Size: Shell length up to 96 mm.

**Morphology**: Shell large, rather thick and solid. Umbones subterminal, at about one-tenth of the shell length. Ligament strong. Extremely thick and large ctenidia with long demibranchs. No extreme mantle fusion, valvular siphonal membrane short. Anterior adductor muscle scar located in front of the umbo. Posterior adductor muscle scar rounded trapezoid. Gut with a single clockwise loop. **Biology**: This species is found at both hydrothermal vent and cold seeps. The specimens are found with their anterior end thrust into diffused vents and attached with byssus to outcrops close to the vent openings. Periostracum colour is variable according to habitat. Development with planktotrophic larvae.

**Distribution**: Central Japan: Sagami Bay; Okinawa Trough: Minami-Ensei Knoll and Iheya Ridge, 710 m to 1389 m.



1: Paratype MNHN Paris, interior of right valve, exterior of both valves; by R. von Cosel & P. Lozouet © MNHN.



2: In situ © JAMSTEC.

#### **References**:

HASHIMOTO J. & T. OKUTANI (1994) Venus **53** (2): 61-83. HASHIMOTO J., OHTA S., FUJIKURA K. & T. MIURA (1995) Deep-Sea Res. I **42**(4): 577-598.

# Bathymodiolus azoricus Cosel & Comtet, 1998

### Size: Shell length up to 121 mm.

Morphology: Shell variable, more or less elongate-modioliform, beaks subterminal but close to the anterior margin. Ventral margin straight to more or less concave. Postero-dorsal margin slightly to markedly convex, occasionally straight. Ligament plate slightly arched. Exterior with dense irregular growth lines and growth waves. Periostracum dull, warm chestnut brown, in umbonal region and often also postero-dorsally lighter brown. Anterior byssus retractor scar in the umbonal cavity, under the beaks. Anterior part of posterior byssus retractor muscle scar under ligament's end or slightly forward. Animal with large gills. Mantle lobes on anterior half of ventral side separate. Valvular siphonal membrane short, narrow and rather strong. **Biology**: In dense clusters byssally attached to hard substrate around the hydrothermal vent, mostly on the walls and flanges of active edifices, at temperatures from 6° to up to 30°C. Endemic to vents. Development with long planktonic larval phase; protoconch is 0.5 mm long.

**Distribution**: Mid-Atlantic Ridge: Menez Gwen, Lucky Strike, Rainbow (hybrids between *B. azoricus* and *B. puteoserpentis* were observed at Broken Spur vent field).



1: Holotype MNHN, exterior and interior of both valves; by R. von Cosel & P. Lozouet © MNHN.



2: Post-larvae fixed on gastropod probably *Protolyra thorvaldssoni* (det. A. Warén); by P. Briand © Ifremer.



3: In situ at Menez-Gwen vent field, with limpets *Lepetodrilus atlanticus* on the shells; Atos cruise © Ifremer.



4: In situ at Rainbow vent field with strong sulphide deposit; Atos cruise © Ifremer.

#### **References:**

Comtet T., Le Pennec M. & D. Desbruyères (1999) J. Mar. Biol. Ass. U.K. **79**: 1149-1150. Comtet T., Jollivet D., Khripounoff A., Segonzac M. & D.R. Dixon (2000) Limnol. Oceanogr. **45**: 1655-1661. Cosel R. von, Métivier B. & J. Hashimoto (1994) Veliger **42**(3): 218-248 [220-231]. Fiala-Médioni A., McKiness Z., Dando P., Boulegue J., Mariotti A., Alayse-Danet J., Robinson J. & C. Cavanaugh (2002) Mar. Biol. **141**: 1035-1043. O'Mullan G.D., Maas P.A.Y., Lutz R.A. & R.C. Vrijenhoek (2001) Mol. Ecol. **10**: 2819-2831.

# Bathymodiolus brevior Cosel, Métivier & Hashimoto, 1994

### Size: Shell length up to 143 mm.

**Morphology**: Shell oval-wedge shaped, stout, beaks subterminal. Ventral margin straight to more or less concave. Posterodorsal margin slightly convex to almost straight. Ligament plate slightly arched. Exterior smooth, with irregular growth lines. Periostracum dull, dark brown, in umbonal region lighter brown. Anterior retractor scar at the anterior part of the umbonal cavity. Anterior part of posterior byssus retractor muscle scar at 2/3 of the ligament. Animal with large gills. Mantle lobes on anterior half of ventral side separate. Valvular siphonal membrane short, narrow and rather strong. **Biology**: In dense clusters byssally attached to hard bottom around the hydrothermal vents at temperatures up to 18°C. Endemic to vents. Development with long planktonic larval phase; protoconch is 0.4 mm long.

Distribution: North Fiji and Lau Back-Arc Basins.



2: Other specimen, left valve; by P. Briand.

3: In situ view of mussel bed, Lau Back-Arc Basin; Biolau cruise © Ifremer.

#### Reference:

COSEL R. VON, METIVIER B. & J. HASHIMOTO (1994) Veliger 37(4): 374-392 [375-380].

Bathymodiolus elongatus Cosel, Métivier & Hashimoto, 1994

### Size: Shell length up to 155 mm.

**Morphology**: Shell elongate-wedge shaped, slender, beaks well subterminal. Ventral margin straight or slightly convex. Ligament plate somewhat arched to straight. Exterior with irregular growth lines and narrow to broad irregular, concentric grooves, mostly on the ventral part. Periostracum glossy, light chestnut brown, in umbonal region lighter brown. Anterior retractor scar at the anterior part of the umbonal cavity. Anterior part of posterior byssus retractor muscle scar at 2/3 of the ligament. Animal with large gills. Mantle lobes on anterior half of ventral side separate. Valvular siphonal membrane short. **Biology**: Byssally attached to lava around diffuse vents, with absence of massive hydrothermal deposits and vent fluid temperature not exceeding 8.5°C. Endemic to vents. Development not known but most probably with planktonic larval phase.

Distribution: North Fiji Back-Arc Basin.



1: Several specimens, exterior, interior, dorsal view; bottom: Juveniles, exterior and interior of right valve; from North Fiji Back-Arc Basin, Mussel Valley site; cruise Starmer 2; by P. Maestrati © MNHN & P. Briand © Ifremer.

#### **Reference**:

COSEL R. VON, METIVIER B. & J. HASHIMOTO (1994) Veliger 37(4): 374-392 [380-386].

# Bathymodiolus japonicus Hashimoto & Okutani, 1994

### Size: Shell length up to 107 mm.

**Morphology**: Shell rather thick, stout, moderately tumid. Umbones subterminal, at about 5% anterior of the shell length. Posterior end of ligament abrupt. Extremely thick and large ctenidia with long demibranchs. No extreme mantle fusion, valvular siphonal membrane short. Anterior byssus retractor muscle scar located in the anterior part of the umbonal cavity. Pallial line smooth, concave in adult, but slightly concave in juvenile and sub-adult.

**Biology:** This species is found at both hydrothermal vents and cold seeps. It is the most abundant and conspicuous organism of the hydrothermal vent community on the Minami-Ensei Knoll. Development not known but most probably with planktonic larval phase.

**Distribution**: Off Hatsushima site and Sagami Bay, central Honshu, 1170 m. Mid-Okinawa Trough: Minami-Ensei Knoll and Iheya Ridge.



1: Paratype MNHN Paris, exterior of both valves, interior of right valve; by R. von Cosel & P. Lozouet © MNHN.

2: In situ view of a mussel bed © JAMSTEC.

#### **References**:

Назнімото Ј. & Т. Окиталі (1994) Venus **53**(2): 61-83. Назнімото Ј. Назнімото Ј., Онта S., Гилікика К. & Т. Міика (1995) Deep-Sea Res. **42**(4): 577-598.

# Bathymodiolus marisindicus HASHIMOTO, 2001

### Size: Shell length up to 86 mm.

Morphology: Shell oval-modioliform, stout, beaks subterminal. Ventral margin almost straight to slightly concave. Postero-dorsal margin somewhat convex. Ligament plate slightly arched. Exterior with dense fine commarginal lines. Periostracum smooth and glossy, strong, dark brown to blackish brown, in young specimens chestnut brown. Anterior retractor scar at anterior extremity of the umbonal cavity. Anterior part of posterior byssus retractor muscle scar at 2/3 the ligament length. Animal with large gills. Inner mantle folds separate along the whole ventral margin. Valvular siphonal membrane short, narrow and rather strong.

Biology: In dense beds byssally attached to hard bottom along shimmering crevices near black smokers. Endemic to vents. Development with long planktonic larval phase.

Distribution: Indian Ocean: Rodriguez Triple Junction, Kairei hydrothermal field.



1: Some specimens, exterior and interior of valves; by R. von Cosel & P. Lozouet © MNHN.

### mussel bed, among numerous sea anemones Mariactis cf. bythios, alvinocaridid shrimps Rimicaris kairei and gastropod Phymorhynchus sp.

#### **References:**

Назнімото J. (2001) Venus 60(3): 141-149.

HASHIMOTO J., OTHA S., GAMO T., CHIBA H., YAMAGUCHI T., TSUCHIDA S., OKUDAIRA T., WATABE H., YAMANAKA T. & M. KITAZAWA (2001) ZOOI. SCI. 18(5): 717-721.

# Bathymodiolus platifrons Hashimoto & Okutani, 1994

### Size: Shell length up to 115.6 mm.

**Morphology**: Shell rather thick and solid. Umbones often nearly subterminal, but mostly on the same plane with anterior end of the shell. No extreme mantle fusion, valvular siphonal membrane short. Extremely thick and large ctenidia with long demibranchs.

**Biology**: This species is found at both hydrothermal vents and cold seeps. In Sagami Bay, *B. japonicus* is occasionally sympatric in the same habitat. Periostracum colour variable according to habitat. Development not known but most probably with planktonic larval phase.

**Distribution**: Okinawa Bank and off Hatsushima site in Sagami Bay, central Honshu, 1180 m; Mid-Okinawa Trough: Iheya Ridge and Izena Caldron.





2: In situ view of a mussel bed © JAMSTEC.

#### Reference:

HASHIMOTO J. & T. OKUTANI (1994) Venus 53(2): 61-83.

# Bathymodiolus puteoserpentis Cosel, Métivier & Hashimoto, 1994

### Size: Shell length up to 141 mm.

Morphology: Shell oval-wedge shaped, rather stout, beaks subterminal. Ventral margin straight to very weakly convex. Postero-dorsal margin markedly convex. Ligament plate slightly arched in anterior part, straighter in posterior part. Exterior smooth, with pronounced irregular growth lines. Periostracum dark brown and rather glossy. Anterior byssus retractor scar on anterior part of the umbonal cavity, in front of the beaks. Anterior part of posterior byssus retractor muscle scar under the posterior third of the ligament, near the end. Animal with large gills. Mantle lobes on anterior half of ventral side separate. Valvular siphonal membrane short.

**Biology**: Bysally attached to sulfur blocks immediately around diffuse venting of water. Endemic to vents. Development unknown, most probably with long planktonic larval phase.

Distribution: Mid-Atlantic Ridge: TAG, Snake Pit and Logatchev.



1 top: Holotype MNHN, exterior of both valves; middle: Other specimen, interior and exterior of left valve; bottom: Interior of left valve of holotype; by R. von Cosel & P. Lozouet © MNHN.

2: In situ view of a mussel bed, with sea anemones *Maractis* cf. *rimicarivora* and zoarcid fish *Pachycara* cf. *thermophilum*; cruise Microsmoke © Ifremer.

#### References:

Cavanaugh C. M., Wirsen C.O. & H.W. Jannasch (1992) Appl. Environ. Microbiol. **58**: 3799-3803. Cosel R. von, Metivier B. & J. Hashimoto (1994) Veliger **37**(4): 374-392 [387-389]. O'Mullan G.D., Maas P.A.Y., Lutz R.A. & R.C. Vrijenhoek (2001) Mol. Ecol. **10**: 2819-2831.

# Bathymodiolus septemdierum Hashimoto & Okutani, 1994

### Size: Shell length up to 124 mm.

**Morphology**: Shell large, rather thin but solid, inflated, elliptical, more or less compressed. Umbones subterminal, less than one-eighth anterior of the shell length. Ligament weak. Extremely thick and large ctenidia with long demibranchs. No extreme mantle fusion, valvular siphonal membrane short. Anterior adductor muscle scar located below the umbo. Anterior part of the posterior byssus retractor muscle scar under posterior end of ligament, at about four-fifths of ligament length. **Biology**: At hydrothermal vents emitting fluids over 310°C around the living beds. Endemic to vents. The shell surfaces are covered with numerous filamentous bacteria. Periostracum color changes according to growth stages. Development not known but most probably with planktonic larval phase.

Distribution: Izu Ogasawara Arc: Suiyo Seamount and Mokuyo Seamount.



1: Paratype MNHN, interior and exterior of right valve; by R. von Cosel & P. Lozouet © MNHN.



2: In situ © JAMSTEC.

#### Reference:

HASHIMOTO J. & T. OKUTANI (1994) Venus 53(2): 61-83.

# Bathymodiolus thermophilus KENK & WILSON, 1985

### Size: Shell length up to 18.4 cm.

**Morphology**: Shell smooth, modioliform, with subterminal umbones; periostracum present and straw-yellow to brown in colour; external surface lacks sculpture and is dull white beneath periostracum; hinge edentulous; ligament opisthodetic, paricincular, strong, extending most of the length of the dorsal margin; well developed byssus. Valvular siphonal membrane long and stretching towards ventrally; on anterior part fusion of inner mantle fold reaching ventrally to 1/3 shell length, together with siphonal membrane leaving rather short byssus opening in the middle.

**Biology**: The life habit of the adult is epibiotic on bare basalt and other hard substrates (e.g. tubes of vestimentiferans) associated with deep-sea hydrothermal vents. The presence of this species is correlated with elevated levels of hydrogen sulfide. Endemic to vents. Protoconch 0.4 mm in length, indicative of a planktotrophic larval stage with a high dispersal capability. Paired ctenidia consist of inner and outer demibranchs, each with descending and ascending lamellae. The gills contain sulphur-oxidizing chemoautotrophic symbionts. A commensal polychaete (*Branchipolynoe symmytilida*) is frequently found within the mantle cavity of the mussel.

**Distribution**: Galapagos Spreading Center, East Pacific Rise: 13°N to 22°S. At the Pacific-Antarctic Ridge (31°S and 38°S) another species of *Bathymodiolus* was collected in 2005 (R. von Cosel & R. Vrijenhoek, unpublished data).



1: In situ views; cruise Hope © Ifremer; top right, by P. Briand © Ifremer.

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2 top: Interior of right valve and exterior of left valve of specimen 1; bottom: Exterior of left valve and ventral view of specimen 2 to show restricted byssal opening; all from East Pacific Rise: 17°S; by R. von Cosel.

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# Mollusca, Bivalvia, Pteriomorphia, Mytiloida, Mytilidae

# Gigantidas gladius Cosel & Marshall, 2003

### Size: Shell length up to 31.6 cm.

Morphology: Shells large to very large, aduliform, extremely long, elongate and sword-shaped, rather thin for the size but solid, with flattened and very broad umbones situated well subterminally in the anterior half of the valves. Ventral margin well concave. Periostracum strong and dark brown; valves dull white beneath the periostracum. Inner mantle folds separate along whole length of the ventral margin their edges frilled along the posterior fifth of the shell length or less. Valvular siphonal membrane almost absent, but a deep cleft between inner mantle fold of right and left valve. Attachment point of the anterior foot-byssus retractor muscle directly above the anterior adductor scar and united with it; posterior byssus retractor complex multibundle with two principle diverging muscle bundles and two additional thin bundles. **Biology**: Protoconch II about 0.4 mm in length, which indicates a long planktonic larval stage with a high dispersal capability. The extremely enlarged gills contain sulphide oxidizing chemoautotrophic symbiotic bacteria. A commensal polychaete of the genus *Branchipolynoe* was encountered within the mantle cavity of most specimens. Mussels of the genus *Gigantidas* are found on warm seeps near active submarine volcanoes and therefore are included herein. The species lives in dense populations at sulphur-rich hydrothermal seepings, they are partly buried in sediment.

**Distribution**: Southwestern Pacific: Rumble III and Rumble V submarine volcanoes, S-Kermadec Ridge, New Zealand; Western Pacific: Kaikata Seamount, SW of Ogasawara (Bonin) Island.



1: Two paratypes (MNHN), exterior and interior of right valve, exterior of left valve, dorsal view; by D. Brabant © MNHN.

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# Mollusca, Bivalvia, Pteriomorphia, Mytiloida, Mytilidae

# Gigantidas horikoshii Hashimoto & Yamane, 2005

### Size: Shell length up to 19.5 cm.

**Morphology**: Shells large, aduliform, long and slender, rather thick, solid. Ventral margin markedly concave in adults, giving the shell a curved appearance. Umbonal cavity large and swollen. Periostracum strong chocolate or dark brown, umbonal region light brown; valves dull white beneath the periostracum. Inner mantle folds entirely separate, terminating anteriorly on anterior adductor. No valvular siphonal membrane. Anterior retractor scar situated in front of umbonal cavity; posterior byssus retractor complex with two principle diverging muscle bundles.

**Biology**: The mussels were observed on sandy bottom with warm water seepage (18°C). The species live in dense populations, partly buried in the sediment.

Distribution: Kaikata Seamount, SW of Ogasawara.



1: Muscular system; after HASHIMOTO & YAMANE (2005).



2 top: Dorsal view; bottom: Lateral view; after HASHIMOTO & YAMANE (2005).



3: Specimens in situ, from Kaikata Seamount; by J. Hashimoto © JAMSTEC.

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# Mollusca, Bivalvia, Pteriomorphia, Eupteriomorphia, Pectinidae

# Bathypecten vulcani Schein-Fatton, 1985

### Size: Up to 17 mm.

**Morphology:** Small, thin, flattened, left (upper) valve more convex than right (lower); smooth, but early stage with concentric undulations, more developed and regular on upper valve; hinge line straight, posterior auricle not delimited, anterior auricle above a distinct byssal notch in lower valve. **Biology:** Can be abundant at the periphery of vents (30-50 individuals  $m^{-2}$ ) with mussels and gastropods. Byssally attached in diffuse venting areas with a low temperature anomaly. Usual bivalve filter-feeding status. Non planktotrophic larval development.

**Distribution**: Galapagos Spreading Center; East Pacific Rise: 9°N and 13°N; Pacific-Antarctic Ridge: 32°S, observed at 38°S.

1-4: Specimens from East Pacific Rise: 13°N, cruise HOT 96.



1: Specimen viewed from the right (lower) side; by P. Briand.



3: Lower (right) side of the antero-dorsal region showing the anterior auricle above the byssal notch; by P. Briand.



2: Same specimen viewed from the left (upper) side; by P. Briand.



4: In situ view of a population of *B. vulcani* on basalt, among polychaete serpulid tubeworms (*Laminatubus alvini*), and small sea anemones, probably *Chondrophellia* cf. *coronata*; by courtesy of R. Vrijenhoek.

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# Mollusca, Bivalvia, Pteriomorphia, Eupteriomorphia, Pectinidae

# Sinepecten segonzaci SCHEIN, in press

### Size: Up to 28 mm.

**Morphology**: Shell thin, lower (right) valve flat; upper (left) valve convex. Commarginal ridges or lamellae covering the whole of the upper valve, and the lower valve only after the juvenile stage. Posterior auricle poorly delimited. Anterior auricle of the lower valve above a byssal notch which is widely open in the juvenile, but gradually closing and finally overlapped by its lower edge in the adult.

**Biology**: Byssally attached on glassy basalt near vents where the temperature ranged between 2.8°C and about 40°C.

**Distribution**: Manus Back-Arc Basin. A juvenile specimen of the same genus was collected at North-Fiji Back-Arc Basin, close to the vent field White Lady in June 2005 (cruise TU-IM06MV, R. Vrijenhoek © MBARI).

1-3: Specimens collected by J. Hashimoto, cruise Bioaccess 98; from SCHEIN (in press).



1: Outer view of a juvenile left valve (SEM).

2: Lower side of a juvenile specimen.



3: Upper side (left) and lower side (right) of large adult holotype.

Reference:				

# Mollusca, Cephalopoda

The living cephalopods, commonly the finned and finless octopuses, squid and cuttlefishes with the vampire squid and Nautilus, comprise a well-defined class of Mollusca. Although these marine predators have undergone an extensive evolutionary radiation, only benthic incirrate octopuses of Graneledone and Benthoctopus and benthopelagic cirrate octopus species of Cirroteuthis and Grimpoteuthis have been reported near vents, and only one octopod genus is recognized as endemic to hydrothermal vents, Vulcanoctopus on the East Pacific Rise. Octopods may form an ecologically important component of the vent ecosystem as opportunistic rather than endemic predators, but they remain under-collected in the vent habitat. The largest single cause is the difficulty in capturing these animals. Manipulators can grab large individuals of some species, especially cirrate and incirrate octopuses of Graneledone, and suction samplers and traps effectively collect Vulcanoctopus specimens, but individuals of Benthoctopus tend to be much more wary. Even when secured, specimens can be severely damaged.

A second problem limiting our knowledge of these animals is that, even with the specimen in the hand, species-level differences in these little-known groups are often subtle at best and rely heavily on internal characters of sexually mature males. As gravid females of some species are suggested to congregate in rocky areas, such as mid-ocean ridges, collections tend to be female-biased, although in *Vulcanoctopus hydrothermalis* almost all known specimens are male. Based on isolated deep-sea specimens, current species boundaries may be found to be artificial, but only after careful reassessment of type specimens and newly collected specimens.

Videotape from research submarines and remotely operated vehicles have documented a wide repertoire of cirrate octopus behaviours in response to submersible-linked disturbances. They also suggest that incirrate octopus may nearly continually feed as they move slowly across sediment. Despite these advances, we remain largely unable to address questions as basic as whether the animals can change colour, a notable character of shallow-water octopods. Bioluminescence has been observed in some cirrate species and may be a more widespread phenomenon than suspected. Careful collection of live specimens and their maintenance under suitable aquaria conditions can answer this and other intriguing questions on the behaviour of these deep-sea cephalopods.

After specimen collection, a tissue sample from arm musculature should be taken by slitting the skin on the dorsal side of the arm to expose the muscle. Opening the skin avoids perturbing the ventral suckers and minimizes contamination from the skin. The tissue sample should be frozen or preserved in 95% ethanol for subsequent analysis. The specimen should be then placed in a 6% solution of buffered formalin in seawater, if possible with the arms extended. The specimen can be kept in the formalin for several days before being shifted to ethanol. The specimens should be examined for any parasites and their locations should be noted. The presence of adaptations to hydrothermal vent habitat, such as high concentrations of heavy metals in the tissues or presence of amoebocytes clots in the venous system and in the renal sacs, should be carefully examined.



1, 2: Two in situ views of an unknown cephalopod taken at the Mid-Atlantic Ridge, north of Rainbow; cruise Flores © Ifremer.

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# Mollusca, Cephalopoda, Octopoda, Cirroteuthidae

# Cirrothauma murrayi CHUN, 1911

Size: Total length up to 940 mm; mantle length 220 mm, from sampled specimens; may be longer from observations at the East Pacific Rise: 13°N.

**Color:** In situ photographs show cirroteuthids with purple, red and/or brown color on both oral and dorsal surfaces.

**Morphology:** External features: body relatively elongate (i.e., not compressed) and gelatinous. Eyes degenerate, cup-like, without lenses or iris, embedded within the jelly of the skin, look like small black balls. Fins large, wide, longer that head width. Mantle aperture closed around a long, slender funnel. Each arm bears a single longitudinal row of suckers alternating with paired, very long cirri. Suckers strongly modified in barrel-like form. Intermediate web present, linking arms to primary web. Internal features: butterfly-shaped shell.

**Biology**: The spermatophores of the males are small, rounded, simple in structure, and stored in the oviducal gland of the female, indicating an internal fertilization. In gravid females, the ovarian oocytes reach 200 in number and are present in different sizes and stages of development, from 0.4-9 mm long. One or two eggs are stored in the distal oviduct, nearly to be released, measuring to 14 x 8.9 mm. This indicates that once sexual maturity it is attained, eggs are probably released one or two at a time, following a continuous spawning strategy of reproduction. No data exist about the feeding habits of this species and no predators are reported. Despite their small size, the eyes of *C. murrayi* are probably sufficient to detect the bioluminescence produced by other animals and the wide aperture of the cornea allows for detection of flashes over wide angles and for greater sensitivity. Locomotion it is basically by the fins and the animal becomes streamlined during fin swimming.

**Distribution**: Specimens of this species have been collected in Atlantic, Pacific and Arctic Oceans. The animals were seen at great depths (1500-5000 m), often near the bottom, but sometimes 300-450 m above it. In the NE Atlantic COLLINS et al. (2001) collected 27 specimens, most of them below 3000 m depth. Always one or two specimens observed at the East Pacific Rise: 13°N-17°S, around the vents. Probably the same species observed near other vents along the East Pacific Rise.



2: Specimen in situ, East Pacific Rise: 17°S; cruise Biospeedo © Ifremer.

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### Mollusca, Cephalopoda, Octopoda, Cirroteuthidae

# Cirroteuthis magna HOYLE, 1885

Size: Up to 1300 mm total length. The largest known cirrate octopod.

**Morphology**: Deep-sea animals of very great size (up to 1300 mm TL). Butterfly-like shell. Shell Width Index: 26-31. Very voluminous eyes (Eye-ball Diameter Index: 39-43), with large lenses (Lens Diameter Index: 12-18). Arm length up to 940 mm. Primary web inserting at different levels on the oral and aboral ends of the dorso-lateral and ventro-lateral arms on both sides, and at the same levels on both ends of the dorsal and ventral arms. Very long non-retractile cirri (Cirrus Length Index: 96-71); the first cirri commences between the fourth and fifth suckers. Three types of suckers on all arms: cylindro-conical form and those with the acetabulum highly deformable on the first 2/3 and barrel-shaped on the rest of the arm; no enlarged suckers in male or female.

**Biology:** C. *magna* is, as other cirrate octopods, a cephalopod, typically adapted to the deep-sea environment in the abyssal ecosystem. These gelatinous animals are neutrally buoyant.

They can be considered as abyssopelagic animals, although they can also rest on the bottom, where they probably feed. Its voluminous and operative eyes indicate that these animals are able to detect light produced by themselves, other animals of the same species, or by potential predators and prey. This species, and other related ones, have been observed to swim at 2.2 km/h and 0.46 km/h. It occurs near hydrothermal vents, but was rarely observed at the Mid-Atlantic Ridge.

**Distribution:** South Indian (2557 m) and Pacific (1500 m) to subtropical North Atlantic (1350 m). One specimen (1300 mm length) was caught at the Mid-Atlantic Ridge, near Logatchev, 3351 m. Another specimen was captured near a vent site in the southern East Pacific Rise: 17°S, 2574 m (M. Lilley & K. Van Damm, chief Scientists; J. Voight, det.).



1: Ventral view of mature male (220 mm). Reconstruction based on the specimen captured and video images; from GUERRA et al. (1998).



2, 3: In situ views of the specimen caught north of Logatchev; cruise Faranaut © Ifremer. The specimen swans by moving its fins a few meters of the bottom, a locomotion mode named fin-swimming; from VILLANUEVA et al. (1997).

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# Mollusca, Cephalopoda, Octopoda, Grimpoteuthidae

# Grimpoteuthis Robson, 1932

Size: Up to 115 mm mantle length.

**Color:** Skin of red brown, orange or purple color in fresh specimens. Usually oral side more pigmented that dorsal side.

**Morphology**: External features: body gelatinous and bellshaped. Fins medium to large, with distinct lobe near the anterior fin insertion. Thick primary web. Intermediate web absent. Each arm bears a single longitudinal row of suckers alternating with paired, medium-sized cirri. Internal features: optic lobe spherical, optic nerves pass though white body as a single boundle of fibres. Shell U-shaped with other edges of lateral walls parallel, not tapered to single fine points. The genus comprises 14 species. **Biology**: Stomach contents in *G. wuelkeri* and *G. boylei* showed polychaetes, copepods, amphipods and isopods. Mature females have few and large eggs in oviducts, measuring from 10-18 mm in length, suggesting a continuous spawning mode as observed in other cirrate octopods. Individuals of *Grimpoteuthis* sp. have been observed resting and crawling on the sea bottom, swimming basically by the use of fins and also by arm-web contractions. As a response to disturbance, individuals have been observed in web inversion, with arms and web upturned, oral surface facing outward, completely covering mantle, head and fins.

**Distribution**: Specimens of this genus has been collected in the Atlantic and Pacific Oceans. In the NE Atlantic, abundances of *Grimpoteuthis* sp. ranged from 1.3-25 individuals  $km^{-2}$  at depths from 1500-4850 m (COLLINS et al. 2001).



1: In situ specimen taken at East Pacific Rise: 13°N, site Elsa; cruise HOPE 99 © Ifremer.

2: In situ specimen taken at Mid-Atlantic Ridge, north of Rainbow; cruise MARVEL © Ifremer.

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# Mollusca, Cephalopoda, Octopoda, Octopodidae

# Vulcanoctopus hydrothermalis González, Guerra, Pascual & Briand, 1998

Size: Up to 56 mm mantle length, 235 mm total length and 45 g body weight.

Color: In situ, white, eyes black.

Morphology: Body semi-translucent with a muscular consistency; mantle pear-shaped and posteriorly mitre-like; presence of a large white body (which covers the eye, the optic nerves and the optic lobe), an inflated black bulb (dark swelling), in proximal third of the intestine, a crop, and a multilobulate digestive gland; absence of an ink sac. Arms 1.5-4.3 times mantle length. Two rows of suckers on each arm. Arm formula typically 1.2.4.3 or 2.1.4.3. No enlarged suckers. Maximum depth of the largest sector of the web about 22% of the longest arm. Gills with 7-8 lamellae per demibranch. Right arm III hectocotylized (HA 1.5-2.1 times mantle length) in males. Ligula short (8-10% of HA), lance-shaped and without transverse ridges. Calamus represents 30-50% of the ligula length in fully mature specimens. Spermatophore length 70-125% of mantle length. Only one female of 35 mm mantle length was collected; external morphology similar to male. Finger-like oocytes (80) ranging from 0.15-4 mm maximum length.

**Biology**: This benthic species has characters that represent either adaptations to the deep-sea (absence of ink sac, loss of the anal flaps, eye without iris and optic chiasma) or to a hydrothermal vent habitat (eyes are covered by a thin semitranslucent skin, high concentrations of metals and presence of amoebocytes clots in the venous system and in the renal sacs). It inhabits an isolated extreme environment among aggregations of tubeworms *Riftia pachyptila*, Alvinellidae polychaetes or mussels, very close to the chimneys (2-10°C); also observed on the pillow lava at several meters from the active areas. No predation over these species was observed. Octopuses forage on bathypelagic amphipods, apparently targeting their attacks based on contact with the swarming amphipods (e.g. *Halice hesmonectes*). Some male specimens were parasitised by *Genesis vulcanoctopusi*, a species of cholidynid harpacticoid (copepod).

**Distribution**: East Pacific Rise: collected at 13°N (Fig. 2) and 21°S (Fig. 1); observed at 23°S (Fig. 3).



1: Specimen female (scale bar 5 cm) collected at East Pacific Rise: 21°S, hydrothermal vent site Grommit (Biospeedo, 17.04.2004); by P. Briand © Ifremer.



2: Specimen observed on tubes of *Riftia* at East Pacific Rise: 13°N; cruise HOPE'99 © Ifremer.

3: Specimen observed at East Pacific Rise: 23°S in April 2005; cruise PAR 5 © MBARI.

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A. GONZÁLEZ, A. GUERRA & M. SEGONZAC

# Mollusca, Cephalopoda, Octopoda, Octopodidae

# Benthoctopus GRIMPE, 1921

Size: Total lengths can approach one meter, but typically 50 cm or less.

**Color**: Variable, from light to red to violet or deep purple. Reverse counter-shading (the dorsal surface lighter than ventral surface) is pronounced in some species, absent in others.

**Morphology**: The genus is poorly delineated and is likely not monophyletic; it includes octopuses without an ink sac with two rows of arm suckers. Field identification of members of this genus relies on their smooth skin, double rows of suckers (which are distinct from zig-zag sucker rows of octopus of *Graneledone*), the comparatively narrow heads and mantles and, in some species, the mantle being lighter in dorsally than ventrally. Although internal examination of specimens is required to identify species, external characters such as coloration, eye size and, in a few species, dramatically enlarged suckers contribute to species identification. **Biology**: Members of *Benthoctopus* are typically more active and more apt to jet away from submersibles and ROVs than are other deep-sea octopus, making submersible-collected specimens rare. These octopuses sometimes extend their dorsal arms vertically into the water column, perhaps to enhance chemoreception. Egg-brooding females may aggregate on hard substrate where they often sit with the suckered surfaces of their arms facing away from the rock.

**Distribution**: Octopuses of the genus *Benthoctopus* occur worldwide, typically between about 400 m rarely to as deep as 2000 m. Octopuses of *Benthoctopus* have been seen near vents at Juan de Fuca Ridge including Endeavour segment, and Gorda Ridge (where they brood eggs), and cold seeps off South America.





2: Individual on the bottom.

1: Brooding females; with numerous ophiuroids, probably Ophiuridae © MBARI.

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### Mollusca, Cephalopoda, Octopoda, Octopodidae

# Graneledone Joubin, 1918

Size: Adults from shallow in the depth range of the genus (800-1000 m) can exceed 1 m in length; those from in deepest part of the range (2800 m) are only about half as long.

Morphology: Large octopuses with a very broad head and mantle, suckers arranged in a single or at times zig-zag row on each arm; skin texture warty (warts more prominent in specimens from the greater depths), with conspicuous papillae over the eyes which can make the eyes appear larger. Individuals tend to be uniformly colored, but individuals vary in color from violet to orange to blue. These octopuses tend to move with their arms curled dorsally in what appears to be a semi-protective position.

**Remark**: Identifying species of *Graneledone* is difficult, but eggs collected in the Northeast Pacific at near 2660 m depth were shorter than those from near 1500 m depth indicating two distinct species are present.

**Biology**: Hydrothermal vent polychaetes and gastropods were found in the gut of an octopus from Axial Volcano. Egg-brooding females sit with their ventral (suckered) surface toward the hard substrate to which their eggs are attached; groups of eggbrooding females can form locally dense aggregations. On open, sedimented seafloor the octopuses may probe the sediment with their arms to locate infaunal prey.

**Distribution**: Specimens of the genus *Graneledone* have been collected from Juan de Fuca and Explorer Ridges. Photos document an individual of the genus near clams at the Galapagos Spreading Center, near cold seeps off Oregon and California and on the Kermadec Arc at Monowai Caldera (http://ocean-explorer.noaa.gov/explorations/05fire/logs/april12/april12.html). Members of the genus, also known from near Antarctica and South Africa, may associate with chemosynthetic areas.



1: *Graneledone* sp. with tubeworms *Ridgeia*; by courtesy of V. Tunnicliffe, HiRise Expedition.

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