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A new genus of lucinid bivalve from hydrocarbon seeps

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We erect a new genus, *Elongatolucina,* for distinctive large, elongate lucinid bivalve specimens from Miocene sediments from Venezuela. We interpret *Elongatolucina* to have had a chemosymbiotic mode of life and it may have been seep-restricted. *Cryptolucina elassodyseides* from Eocene hydrocarbon seep sites in Washington State, USA is incorporated in *Elongatolucina*.

Introduction

A large, elongate bivalve from Miocene sediments in Venezuela was figured by Gill et al. (2005: fig. 9B) and referred to as belonging to the family Vesicomyidae. However, on re-examination of this and other specimens from the same locality, it was apparent that it actually belongs to the family Lucinidae, based on the distinctive anterior adductor muscle scar, which is elongated and detached from the pallial line for much of its length. The Venezuelan specimens are very similar to the lucinid *Cryptolucina elassodyseides* Saul, Squires, and Goedert, 1996. As noted by other authors (e.g., Kase et al. 2007) there are considerable differences between *C. elassodyseides* and the type species of *Cryptolucina*, *C. megadyseides* (see below for details), and because of these differences we erect a new genus, *Elongatolucina,* to accommodate both *C. elassodyseides* and the Venezuelan lucinid specimens.

Institutional abbreviations.—BHNM, Natural History Museum Basel, Basel, Switzerland; CSUN, California State University Northridge, Northridge, USA; LACMIP, Natural History Museum of Los Angeles County Invertebrate Palaeontology Section, Los Angeles, USA; MNHN, Museum national d'Histoire naturelle, Paris, France.

Systematic palaeontology

Class Bivalvia Linné, 1758

Subclass Heterodonta Neuymar, 1884

Order Veneroidea Adams and Adams, 1856

Superfamily Lucinoidea Fleming, 1828

Family Lucinidae Fleming, 1828

?Subfamily Myrteinae Chavan, 1969

Remarks.—The supra-generic level systematic classification of the family Lucinidae has been in a state of flux, with conflicting classification schemes based on modern and fossil shell morphology (e.g., Chavan 1969; Bretsky 1976). However, recent molecular analyses of modern species have shown the previously identified subfamilies of Chavan (1969) and Bretsky (1976) to be paraphyletic (Williams et al. 2004, Taylor and Glover 2006; Taylor et al. 2011). Taylor et al. (2011) identified seven lucinid subfamily divisions, and within one of these, the Myrteinae, Taylor et al. (2011) tentatively placed the deep sea genera *Elliptiolucina*, *Taylorina*, *Rostrilucina*, *Graecina*, and *Jorgenia* (although no suitable material was available for molecular analysis for these). *Elongatolucina* gen. nov. is very similar to *Elliptiolucina* in morphology and may thus also belong to the subfamily Myrteinae.

Genus *Elongatolucina* nov.

Fig. 1.

Type species: *Cryptolucina elassodyseides* Saul, Squires, and Goedert, 1996; see below.

Etymology: The name reflects the elongated shell shape of this genus.

Species included.—*Elongatolucina elassodyseides* and *E.* sp. aff. *E. elassodyseides*.

Diagnosis.—A large (up to 135 mm in length) elongate, elliptical shell with straight ventral margin, virtually straight dorsal margin and evenly rounded anterior and posterior margins. Umbones are low, prosogyrate and situated one third of total shell length from the anterior. An indistinct ridge runs from the umbo to the antero-ventral corner and a more prominent ridge extends from the umbo to the postero-ventral corner with a shallow sulcus inbetween. Valves are compressed. Lunule depressed, elongate and demarked by an angulation. Hinge plate narrow and edentulous. In both valves is a shallow, triangu-

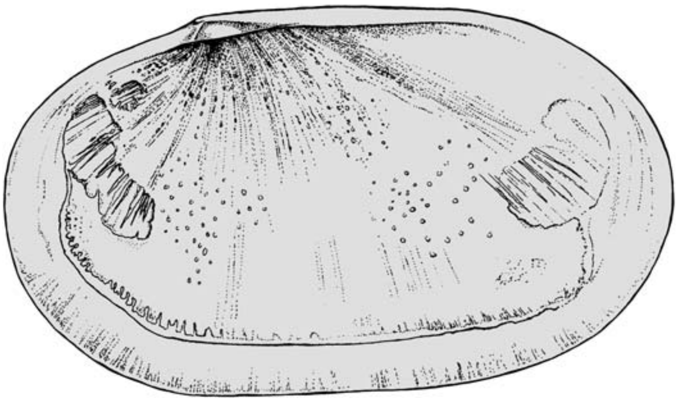

Fig. 1. Composite sketch of *Elongatolucina* showing right valve internal shell features. Image produced by James McKay (University of Leeds, UK).

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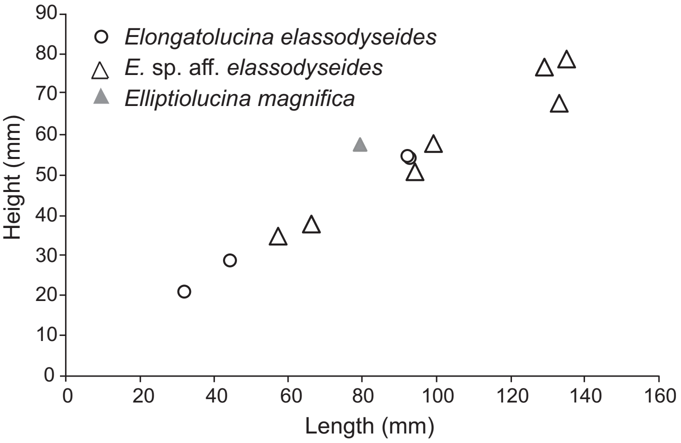

Fig. 2. Plot of length versus height data for *Elongatolucina elassodyseides*, *E.* sp. aff. *Elassodyseides*, and *Elliptiolucina magnifica* holotype.

lar-shaped depression underneath the umbo, which extends further to the posterior than the anterior, and causes a deflection in ventral margin of hinge plate. Anterior margin of depression bounded by sharp ridge. Exterior shell ornament with commarginal growth lines and faint radial striae in anterior portion of well-preserved shells. Anterior adductor muscle scar elongate, diverging from pallial line at an angle of approximately 40°, with divergent part approximately twice as long as non-divergent part. Posterior adductor muscle scar kidney-shaped to rounded with notch in anterior margin visible in some specimens. Both muscle scars crossed by fine, irregular striations.

Remarks.—*Elongatolucina* is characterised by an elongate, elliptical shell shape with umbones positioned one third of the total length from the anterior. It possesses a straight ventral margin, and an elongated anterior adductor muscle scar which diverges from the pallial line at an angle of 40°. The sub-umbonal depression on the hinge plate could be interpreted as a socket but does not correspond to a projecting tooth in the other valve and instead corresponds to a similar depression. Therefore, we consider the hinge to be edentulous. *Elliptiolucina* species have a similar hinge morphology.

Elongatolucina is similar to *Cryptolucina* Saul, Squires, and Goedert, 1996, the genus to which the type species was originally assigned, in that it is a large fossil lucinid with an edentulous hinge. However, *Elongatolucina* is distinguished from *Cryptolucina* (now considered to contain only *C. megadyseides* Saul, Squires, and Goedert, 1996 and *C. kuhnpassetensis* Kelly in Kelly et al., 2000) by its thinner shell, considerably greater degree of elongation (height to length ratio 0.59–0.66 for *Elongatolucina* compared to 0.76 for *Cryptolucina*), elliptical rather than circular to sub-triangular outline, much lower and less prominent umbones, which are situated well anterior of the mid-line rather than centrally, and a straight rather than convex ventral margin. These morphological features are, in our opinion, sufficiently different to the warrant separation of *C. elassodyseides* from the remaining species of *Cryptolucina* at the generic level. The existing genus diagnosis for *Cryptolucina* remains accurate for the remaining species without amendment.

Nipponothracia Kanie and Sakai, 1997 is another large, somewhat elongate, edentulous fossil bivalve genus, which although originally described as a thraciid (Kanie and Sakai 1997), was recognised as a lucinid by Kase et al. (2007). However, *Nipponothracia* differs from *Elongatolucina* in being less elongated and more rounded in shell outline, with more centrally positioned umbones and a conspicuously rounded ventral margin.

Elongatolucina also closely resembles the modern lucinid genus *Elliptiolucina* von Cosel and Bouchet, 2008 in its elongate outline and edentulous hinge. However, *Elongatolucina* differs in being generally more elongate than *Elliptiolucina* (Fig. 2), with evenly rounded anterior and posterior margins and a straight ventral margin, in contrast to the truncated anterior and posterior margins of *Elliptiolucina. Elliptiolucina* also has a convex ventral margin, which results in a somewhat trapezoid shell outline. In addition, the angle of divergence of the anterior adductor muscle scar is consistently greater in *Elongatolucina* (40–43°) than in *Elliptiolucina* (22–30°).

A further modern species that bears a superficial resemblance to *Elongatolucina* is *Jorgenia* Taylor and Glover, 2009, which is an elongate lucinid with a fairly straight dorsal margin. *Elongatolucina* can be easily distinguished from this genus, however, by being more elongate and having a straight ventral margin. *Jorgenia* has truncated posterior and anterior margins and a distinctly rounded ventral margin. In addition, *Elongatolucina* is completely edentulous, whereas *Jorgenia* has one or two small cardinal teeth in each valve.

Geographic and stratigraphic range.—Eocene Humptulips Formation, Washington State, USA (CSUN localities 1582 and 1583), Miocene Huso Formation, Venezuela.

Elongatolucina elassodyseides (Saul, Squires, and Goedert, 1996)

Fig. 3.

Type locality: CSUN locality 1583, East fork of Humptulips River, Grays Harbour County, southwestern Washington, USA.

Type horizon: Humptulips Formation, Eocene.

Material.—Type (five specimens) and non-type (seven specimens) material of *Cryptolucina elassodyseides* stored in LACMIP, including holotype LACMIP 11422 and paratypes LACMIP 11423-6.

Fig. 3. Lucinid bivalve *Elongatolucina elassodyseides* (Saul, Squires, and Goedert, 1996), CSUN localities 1582 and 1583, Humptulips Formation, Middle to Upper Eocene, southwestern Washington, USA. **A**. Paratype (LACMIP 11426), dorsal view (A_1), silicon rubber cast of left valve, internal view (A_2), right valve (A_3), detail of external shell ornament (A_4). **B**. Holotype (LACMIP 11422), dorsal view (B_1), left valve (B_2), right valve (B_3). **C**. Paratype (LACMIP 11424), right valve. **D**. Non-type specimen (LACMIP13728), hinge detail of silicon rubber cast of left valve, internal view, sub-umbonal depression indicated by arrow (anterior to the right).

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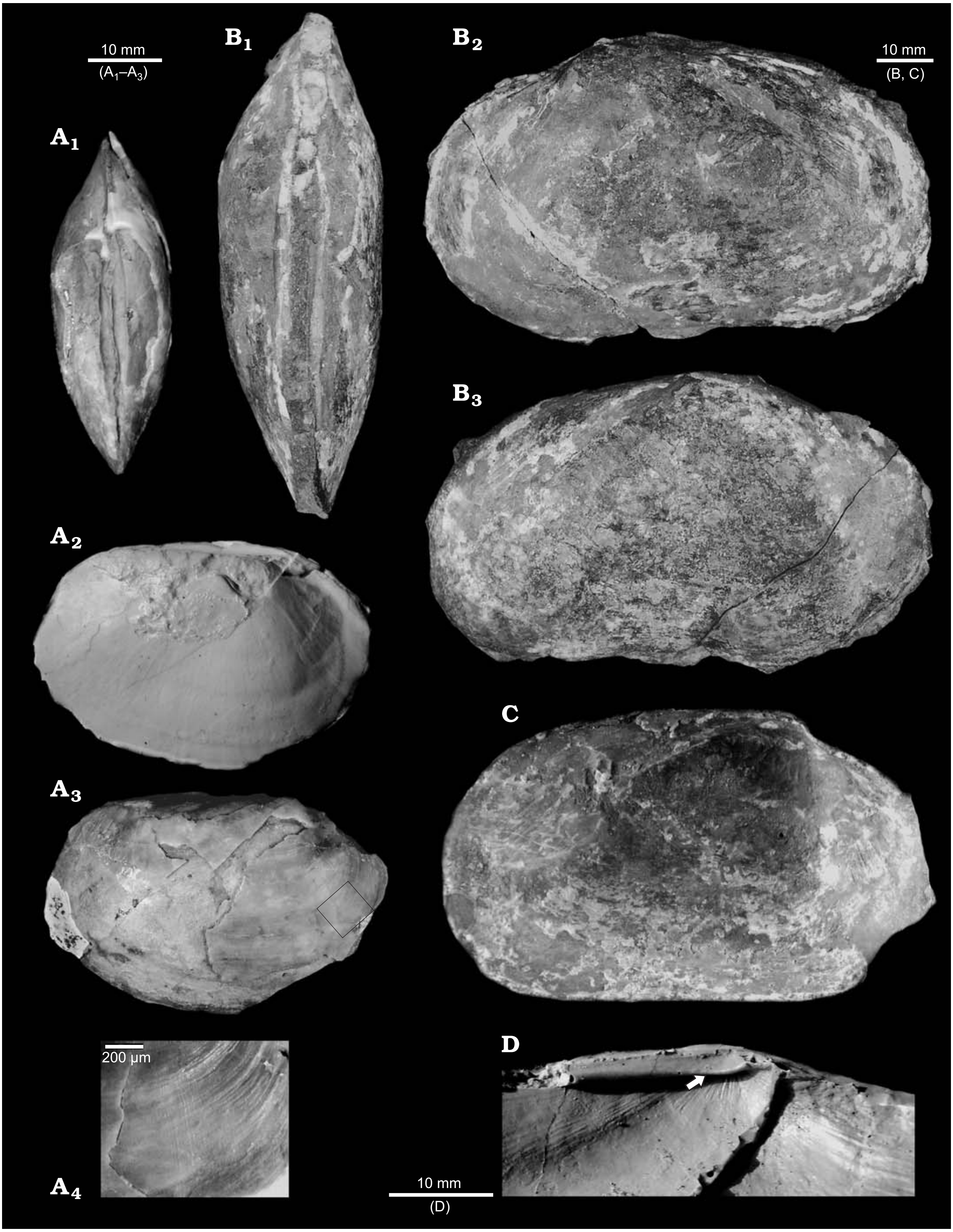
10 mm
(A1–A3)
B1
B2
10 mm
(B, C)
A1
B3
A2
C
A3
A4
200 µm
D
10 mm
(D)

Amended description.—In addition to the original description we note the following features. In the left valve there is a shallow, triangular-shaped depression underneath the umbo, which extends further to the posterior than the anterior, and causes a deflection in the ventral margin of the hinge plate. The anterior margin of this depression is bounded by a sharp ridge. The exterior shell ornament consists of commarginal growth lines, with fine radial striae in the dorso-anterior area of the paratype LACMIP 11426. The anterior adductor muscle scar is elongate (2.5 to 3 times longer than wide) and detached from the pallial line for 2/3 of its length, with an angle of divergence of approximately 40°. The pedal retractor muscle scar is separated from the anterior adductor muscle scar. The posterior portion of the posterior adductor muscle scar cannot be clearly seen on any of the specimens, so its overall shape cannot be discerned, despite being described as elongate and oval by Saul et al. (1996). Radial striations are present in the umbonal region and extend in the anterior and posterior regions across the adductor muscle scars. The area between the pallial line and the shell margin has a faint suggestion of radial striations and immediately dorsal to the pallial line are a series of digitations. These represent sites of pallial muscle attachment (John Taylor, personal communication 2011).

Geographic and stratigraphic range.—Eocene, Humptulips Formation, Washington State, USA (CSUN localities 1582, 1583).

Elongatolucina sp. aff. *E. elassodyseides* Saul, Squires, and Goedert, 1996

Fig. 4.

2005 Vesicomyid sp. B; Gill et al. 2005: fig. 9B.

Material.—Nine specimens from BNHM localities 13968 and 17345, Miocene Huso Member, Pozon Formation, Falcon State, Venezuela.

Description.—The shell is very similar in shape to *E. elassodyseides,* i.e., elongate and elliptical with a straight ventral margin, and has a maximum length of 135 mm. The hinge plate is long and narrow with no teeth or sockets. There is a shallow, triangular-shaped depression underneath the umbo, which extends further to the posterior than the anterior, and causes a deflection in the ventral margin of the hinge plate. The anterior margin of this depression is bounded by a sharp ridge. The anterior adductor muscle scar is elongate and detached from the pallial line with an angle of divergence of approximately 40°. The pedal retractor muscle scar is separate. The pallial line is entire and immediately dorsal to it are a series of digitations. A series of radial striations is clearly visible in the area between the pallial line and the shell margin. The posterior adductor muscle scar is reniform and has a cleft in its anterior margin. Radial striations extend from the umbo to the shell margin and are stronger in the anterior and posterior margins, and weaker in the centre of the shell. Those in the anterior portion, dorsal to the anterior adductor muscle scar have distinct pustules. The radial striations also pass across the adductor muscle scars.

Remarks.—Although they are morphologically very similar, there are a number of differences between the Venezuelan specimens and the type specimens of *E. elassodyseides* that means we do not presently feel confident in stating that they are conspecific. Additional well preserved specimens from Washington State or Venezuela may resolve this issue. The morphological differences are as follows. On average the Venezuelan specimens are larger than those of *E. elassodyseides*, although there is some overlap in size (Fig. 2). The shape of the posterior adductor muscle scar is distinctive in the Venezuelan material but cannot be fully discerned in any of the *E. elassodyseides* specimens examined. Further, none of the Venezuelan specimens has any original shell material preserved, therefore no information is available on features such as shell thickness or external ornament.

Geographic and stratigraphic range.—Miocene, Huso Member, Pozon Formation, Venezuela (BNHM localities 13968 and 17345).

Palaeoecology and palaeogeography of *Elongatolucina*

All modern lucinids whose nutrition has been investigated have been found to contain chemosymbiotic sulphide-oxidising bacteria, housed within bacteriocytes in the modified gill filaments (Taylor and Glover 2000). The symbiosis is thought to be responsible for several of the distinguishing features of lucinid anatomy, notably the elongated adductor muscle detached from the pallial line. The size and orientation of the adductor muscle scar has been interpreted to be of functional significance, separating the site of respiration (the mantle area anterior to the anterior adductor muscle, which may also feature mantle gills) from the site of sulphide oxidation (the gills) (Taylor and Glover 2000, 2006). This is necessary to avoid the symbiont substrate hydrogen sulphide being oxidised before it reaches the bacteriocytes in the gills. Since the adductor muscle leaves a distinctive scar visible in fossil shells, this feature has been interpreted as evidence for a chemosymbiotic mode of life in fossil lucinids (e.g., Taylor and Glover 2000, 2006, 2009). We follow this interpretation and suggest that *Elongatolucina* also possessed sulphide-oxidising chemosymbiotic bacteria.

Modern lucinids occur in a wide range of sulphide-rich habitats including cold seeps (Taylor and Glover 2006). Cold seeps are sites on the seafloor where fluids rich in reduced compounds, typically (but not necessarily) methane or other hydro-

Fig. 4. Articulated internal moulds of the lucinid bivalve *Elongatolucina* sp. aff. *E. elassodyseides* Saul, Squires, and Goedert, 1996, BNHM localities 13968 and 17345, Huso Member, Pozon Formation, Miocene, Falcon State, Venezuela. **A**. BNHM G17488, dorsal view (A_1), right valve (A_2), left valve (A_3), hinge detail of silicon rubber cast of interior of articulated valves (A_5), sub-umbonal depression of right valve indicated by arrow (anterior to the left), ventral view of A_5 (A_4), note deflection of hinge plate corresponding to sub-umbonal depression. **B**. BNHM G17487, dorsal view (B_1), left valve (B_2), right valve (B_3), silicon rubber cast of left valve, internal view (B_4).

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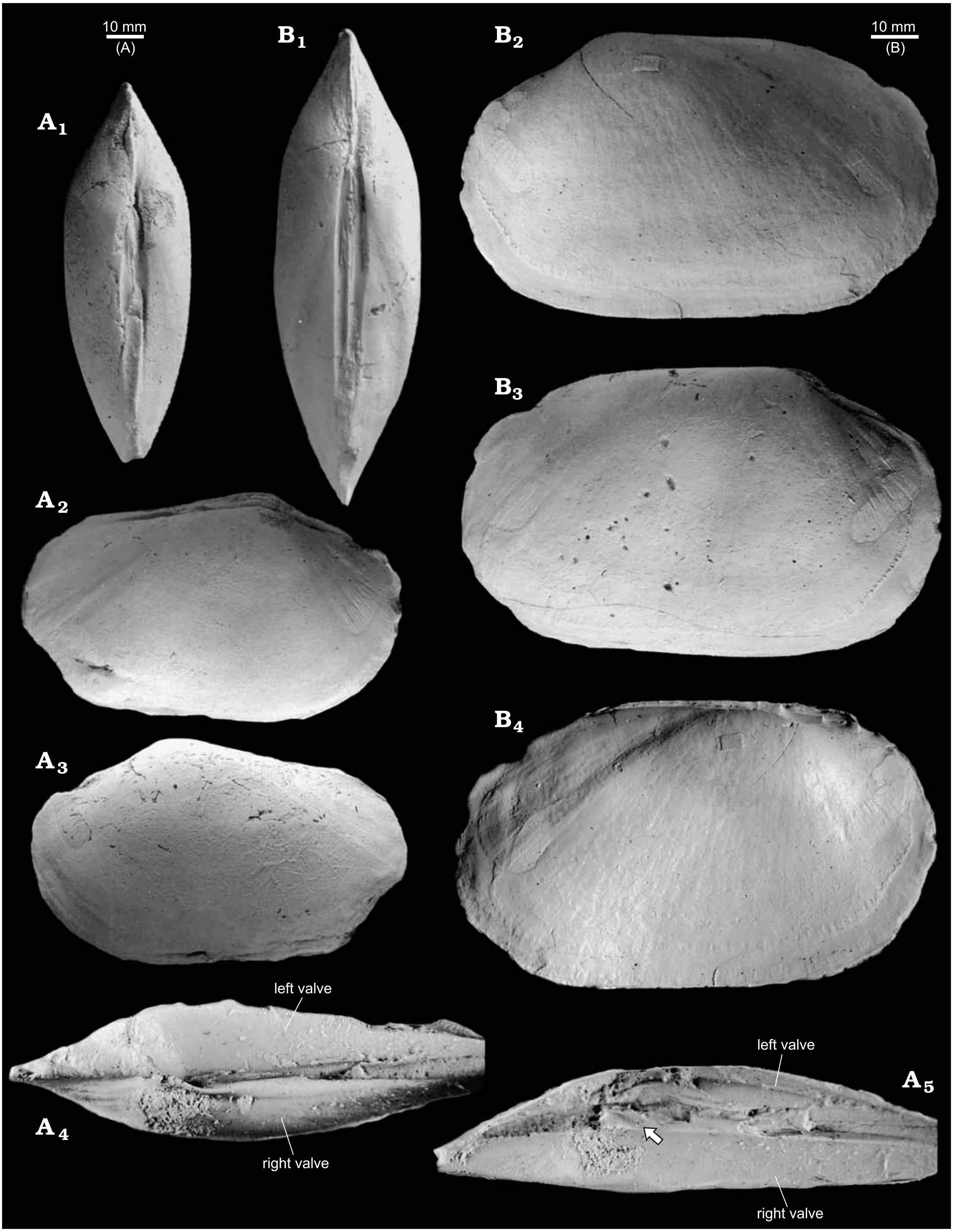
10 mm
(A)
B1
B2
10 mm
(B)
A1
A2
B3
B4
A3
left valve
A4
right valve
left valve
A5
right valve

carbons, are released at around ambient seawater temperature. Since they were first discovered in the Gulf of Mexico (Paull et al. 1984), cold seeps have been found worldwide, and many previously enigmatic fossiliferous carbonate deposits have been identified as ancient seep sites, based on distinctive cement facies and stable isotopic signatures (see Campbell 2006 for review). *E. elassodyseides* was found within the Eocene Humptulips Formation at CSUN localities 1582 and 1583, which have been interpreted to represent ancient seep sites, based on the occurrence of typical seep taxa, such as solemyid, thyasirid and vesicomyid bivalves, within carbonate bodies with characteristic seep cements (Goedert and Kaler 1996). The *Elongatolucina* sp. aff. *E. elassodyseides* specimens were collected during the early part of the twentieth century from the Miocene Huso Member of the Pozon Formation, Agua Salada Group, northern Venezuela. Although no details of the original field relations of the specimens are recorded, the association of lucinid, solemyid, and modioliform bivalves (Gill et al. 2005) suggests a hydrocarbon seep origin for this material. This is consistent with the location of the sampling site within a known hydrocarbon province (e.g., Wavrek and Butler 2000). Therefore, *Elongatolucina* tentatively joins the growing list of seep-restricted lucinids (e.g., Kiel 2010). The occurrence of *Elongatolucina* in both the Pacific and Caribbean regions shows the genus had a fairly widespread distribution during the Paleogene and Neogene, although prior to the formation of the Isthmus of Panama in the Pliocene there was an open ocean connection between these two areas (Duque-Caro 1990).

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