Quaternary deep-sea ostracods from the north-western Pacific Ocean: global biogeography and Drake-Passage, Tethyan, Central American and Arctic pathways

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Twelve genera and 19 species of deep-sea ostracods from the Shatsky Rise, north-western Pacific, were examined and illustrated for taxonomy. Three new species, Cytheropteron nasutum sp. nov., Poseidonamicus shatskyensis sp. nov. and Legitimocythere stellae sp. nov., are described. Based on these Shatsky Rise ostracods and a comprehensive literature survey of synonyms, we discuss global biogeography and possible migration pathways of deep-sea species. The four possible deep-water pathways connecting the Atlantic and Pacific Oceans are: the Drake Passage (Southern Ocean), established by 30 Ma; the Tethys Seaway, which had closed by 19–14 Ma; the Central American Seaway, which had closed by 3 Ma; and the Arctic Ocean Seaway via the Bering Strait, which opened about 4.8–7.4 Ma, and via the Fram Strait, which opened between 10 and 20 Ma. The Drake Passage is likely the major pathway. We argue that the Arctic was an important pathway for some deep-sea species before the mid-Pleistocene. Most deep-sea organisms have poor fossil records, and thus the rich fossil record of deep-sea ostracods is an ideal model system for the study of deep-time biogeography of deep-sea organisms. It may well be that other deep-sea organisms had similar palaeobiogeographical histories and patterns.

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Keywords: Ostracoda; Shatsky Rise; Central American Seaway; Tethys; Panama; Southern Ocean; migration

Introduction

Robin Whatley’s research group conducted comprehensive deep-sea ostracod research in the 1980s and 1990s, which established our baseline understanding of the global distribution of deep-sea ostracod species (Whatley & Ayress 1988; Coles et al. 1990). However, their studies focused mostly on the North Atlantic (Whatley & Coles 1987; Coles & Whatley 1989) and south-western Pacific (Whatley 1983, 1992) where deep-sea sediment core samples were available for their research. Furthermore, detailed information on occurrences and abundances and scanning electron microscope (SEM) images for these sites remain largely unpublished, especially in the south-western Pacific (as they cited many unpublished theses of Whatley’s students). Since then, there have been no synthetic studies on the global biogeographical distributions of deep-sea ostracod species, but many regional studies have added considerable information about species occurrences, not only in the North Atlantic (Yasuhara et al. 2009a; Yasuhara & Okahashi 2014, 2015) and south-western Pacific (Ayress et al. 1995, 1999; Alvarez Zarikian 2015), but also in other areas such as the Southern Ocean (Jellinek & Swanson 2003; Mazzini 2005; Yasuhara et al. 2009b), Arctic (Poirier et al. 2012; Cronin et al. 2014; Yasuhara et al. 2014a; DeNinno et al. 2015; Gemery et al. 2017) and North Pacific (Zhao 2005; Yasuhara et al. 2012; Alvarez Zarikian 2016).

In the North Pacific Ocean, deep-sea ostracod studies have been concentrated in the north-western Pacific continental margin (Ruan & Hao 1988; Zhao 2005; Hou & Gou 2007; Zhao et al. 2011; Alvarez Zarikian 2016), and other regions remain understudied (Boomer 1999; Stepanova & Lyle 2014). The Shatsky Rise is one of a few large carbonate mounds in the North Pacific open ocean that yields abundant calcareous microfossils (Ohkushi et al. 2000; Yasuhara et al. 2012), but its Quaternary ostracods have never been studied comprehensively. We here conduct a detailed taxonomic study of Quaternary deep-sea ostracods from Core NGC
104 taken from the Shatsky Rise, and examine and discuss global biogeographical distributions and migration pathways of selected species, integrating published data comprehensively evaluated for synonymy and misidentification. Previous researchers have suggested the Drake Passage (Southern Ocean) (Whatley & Ayress 1988; Coles et al. 1990) and the Tethys Seaway [Steineck et al. 1988; Coles et al. 1990] as possible migration pathways for deep-sea ostracod species between the Atlantic and Pacific oceans. We argue that the Arctic Ocean is potentially another important pathway and that the global biogeography and migration history of deep-sea organisms may be more complicated than previously thought. Deep-sea Ostracoda (meiobenthic crustaceans) are one of the few deep-sea taxa whose fossil record allows us to track their geographical distributions in the geological past; most deep-sea organisms have virtually no fossil record and poor species-level taxonomy, with many species left in open nomenclature. Thus, it is reasonable and necessary to use Ostracoda as a model system to understand deep-time biogeography of deep-sea organisms.

**Material and methods**

Gravity core NGC 104 (32°10.04′N, 157°59.9′E; 2665 m water depth) was obtained at Shatsky Rise, north-western Pacific (Fig. 1). A total of 39 samples from this core covering the past 250,000 years and Marine Isotope Stages 1–7 were examined for ostracods. Further details of the core, samples, methods, chronology and ostracod faunal patterns can be found in Yasuhara et al. (2012). Full information for the samples and specimens used for the present study is shown in Supplemental Table 1.

Uncoated specimens were digitally imaged with a Philips XL-30 environmental SEM. For the higher classification scheme, we mainly refer to the World Ostracoda Database (Brandão et al. 2017), Whatley et al. (1993) and Horne et al. (2002).

**Repository.** Figured specimens are deposited in the National Museum of Natural History, Washington DC (USNM), under catalogue numbers USNM 698149 – USNM 698227). MY’s personal catalogue numbers are also shown.

**Abbreviations.** LV, left valve; RV, right valve; L, length (in mm); H, height (in mm).

**Systematic palaeontology**

Class Ostracoda Latreille, 1802
Subclass Podocopa G. O. Sars, 1866
Order Podocopida G. O. Sars, 1866
Suborder Cypridocopina Jones, 1901
Superfamily Pontocypridoidea G. W. Müller, 1894
Family Pontocyprididae G. W. Müller, 1894
Genus Argilloecia G. O. Sars, 1866

**Type species.** Argilloecia cylindrica Sars, 1866.

Argilloecia sp. (Fig. 2A)

2016 Argilloecia toyamaensis Ishizaki & Irizuki; Alvarez Zarikian: 102, pl. 1, fig. 11a, b.
Remarks. This species is similar to *Argilloecia robin-whatleyi* Yasuhara, Okahashi & Cronin, 2009a, *Argilloecia* sp. of Zhao *et al.* (2011) and *Australoecia* cf. *A. microa* (Bonaduce, Ciampo & Masoli, 1976) of Boomer (1999), but the posterior margin is more acuminate in the present species. It is also similar to *Argilloecia parallelia* Zhao (in Wang *et al.*, 1988), but the posterior margin is less acuminate and the posterodorsal corner is less angular in the present species. This species may be conspecific with the species identified as *Argilloecia toyamaensis* Ishizaki & Irizuki, 1990 by Alvarez Zarikian (2016), although the dorsal margin is slightly more rounded in that species. The *Argilloecia toyamaensis* specimens in the original description (Ishizaki & Irizuki 1990) have slightly less acuminate posterior margins compared to Alvarez Zarikian’s specimens (Alvarez Zarikian 2016).

Genus *Propontocypris* Sylvester-Bradley, 1947

Type species. *Pontocypris trigonella* Sars, 1866.

*Propontocypris* sp. (Fig. 2B)

Remarks. This species is very similar to and may be conspecific with *Propontocypris* sp. cf. *P. trigonella* (Sars, 1866) *sensu* Whatley & Coles (1987). Both have partial punctuation on the posterior end of the shell, but detailed comparison is difficult as we found only one juvenile specimen. *Propontocypris* species with such partial punctuation are not otherwise known from the Pacific Ocean.

Suborder *Cytherocopina* Baird, 1850

Superfamily *Cytheroidea* Baird, 1850

Family *Cytheruridae* G. W. Müller, 1894

Genus *Cytheropteron* G. O. Sars, 1866

Type species. *Cythere latissima* Norman, 1865, designated by Brady & Norman (1889); see Horne & Whittaker (1988) for details and lectotype.

*Cytheropteron demenocali* Yasuhara, Okahashi & Cronin, 2009a (Fig. 2E–H)

1999 *Cytheropteron* sp. A Boomer: pl. 3, figs 18, 19.

2000 *Cytheropteron porterae* Whatley & Coles; Didié & Bauch: 113, pl. 2, fig. 20 (non figs 19 and 21).


2009a *Cytheropteron demenocali* Yasuhara, Okahashi & Cronin: 900, pl. 9, figs 1–10.

2014 *Cytheropteron demenocali* Yasuhara, Okahashi & Cronin; Yasuhara & Okahashi: 776, fig. 3.3, 3.4.

2015 *Cytheropteron demenocali* Yasuhara, Okahashi & Cronin; Yasuhara & Okahashi: 36, fig. 9C, D.


2016 *Cytheropteron* sp. C Alvarez Zarikian: 103, pl. 1, fig. 4.

Remarks. *Cytheropteron* sp. C of Alvarez Zarikian (2016) and *Cytheropteron* sp. D of Alvarez Zarikian (2015) are conspecific with this species. As seen in the synonym list above, this species is known from the North Atlantic, South Pacific and North Pacific oceans. The oldest record is from the Oligocene (Boomer 1999; Alvarez Zarikian 2015).

*Cytheropteron cf. demenocali* Yasuhara, Okahashi & Cronin, 2009a (Fig. 2I, J)

Remarks. This species is very similar to *Cytheropteron demenocali* Yasuhara, Okahashi & Cronin, 2009a, except for its smaller size and finer reticulation. These specimens may be A-1 juveniles of *Cytheropteron demenocali*, but their poor internal preservation prevents further discussion.

*Cytheropteron nasutum* sp. nov. (Fig. 2K–N)

Derivation of name. From the Latin *nasutum* (adjective, nominative singular, neuter), referring to the well-developed caudal process that looks like a long nose.

Material. Holotype: RV, USNM 698160 (NGC104-49) (Fig. 2L). Paratypes: LV, USNM 698159 (NGC104-48) (Fig. 2K); LV, USNM 698161 (NGC104-63) (Fig. 2M); RV, USNM 698162 (PACNGC40) (Fig. 2N).

Type locality and horizon. Shatsky Rise, north-western Pacific. NGC 104, 40–44 cm depth. Late Quaternary.

Dimensions. USNM 698160 (NGC104-49) (holotype), L = 0.454 mm, H = 0.272 mm; USNM 698161 (NGC104-63) (paratype), L = 0.455 mm, H = 0.287 mm.

Diagnosis. A moderately calcified *Cytheropteron* species with a very well-developed caudal process, semi-vertical ridges intersecting with a horizontal ridge below the posterodorsal corner, and regularly rounded fossae in the central part.

Description. Carapace moderately calcified, moderate in size, highest at mid-length. Outline subrhomboidal in lateral view; anterior margin rounded; caudal process well developed, prominent, upturned especially in RV, pointed at mid-height in LV and above mid-height in RV; dorsal margin sinuous in posterior half with a concavity immediately anterior to the posterior cardinal angle, rounded in anterior half; ala extending below ventral margin, long, almost straight, and having two distinct spines at its apex. Anterodorsal corner rounded; posterodorsal corner weakly angular. Surface reticulation well developed especially in the central part; secondary reticulation developed in the
posteroventral area. Semi-vertical ridges well developed in the posterior third which intersect with a distinct, arched horizontal ridge along the posterodorsal margin just anterior to the posterodorsal corner. Dorsal margin outlined by weak rim in LV. Internal features as for genus.

**Remarks.** This species is similar to *Cytheropteron postornatum* Zhao, 1988 (in Wang et al. 1988), but distinguished by having a better developed caudal process and a distinct ridge along the posterodorsal margin.

*Cytheropteron pherozigzag* Whatley, Ayress & Downing, 1986
(Fig. 2C, D)


1988 *Cytheropteron pherozigzag* Whatley, Ayress & Downing; Whatley & Ayress; pl. 2, fig. 3a, b.

1996 *Cytheropteron pherozigzag* Whatley, Ayress & Downing; Zhao & Zheng; 72, pl. 2, fig. 3.

2000 *Cytheropteron pherozigzag* Whatley, Ayress & Downing; Zhao, Whatley & Zhou; 263, pl. 1, fig. 20.

2005 *Cytheropteron pherozigzag* Whatley, Ayress & Downing; Zhao: 39, pl. 2, fig. 15.

2005 *Cytheropteron pherozigzag* Whatley, Ayress & Downing; Hou & Gou: 309, pl. 125, fig. 17.

2007 *Lobosocytheropteron pherozigzag* (Whatley, Ayress & Downing); Hou & Gou: 309, pl. 125, fig. 17.

2007 *Lobosocytheropteron pherozigzag* (Whatley, Ayress & Downing); Hou & Gou: 309, pl. 125, fig. 17.

2009a *Cytheropteron pherozigzag* Whatley, Ayress & Downing; Yasuhara, Okahashi & Cronin: 906, pl. 5, figs 6–8, 10.

2014 *Cytheropteron pherozigzag* Whatley, Ayress & Downing; Yasuhara & Okahashi: 778, fig. 4.1.

2015 *Cytheropteron pherozigzag* Whatley, Ayress & Downing; Yasuhara & Okahashi: 36, fig. 10C, D.

**Remarks.** There is a slight difference in the surface ornamentation on the posterodorsal part of the shell between our specimens and the type specimens. Three nail-mark-like carinae near the postero-dorsal corner are distinct in some (but not all) of the Pacific specimens (Fig. 2C, D) but are absent in the Atlantic specimens (Whatley et al. 1986). The oldest record of this species is from the Oligocene (Coles et al. 1990).

Family **Eucytheridae** Puri, 1954
Genus **Eucythere** Brady, 1866

**Type species.** *Cythere declivis* Norman, 1867, designated by Brady & Norman (1889); see Horne & Whittaker (1985) for details and lectotype.

**Eucythere multipunctata** Whatley & Coles, 1987
(Fig. 2O–R)

1987 *Eucythere multipunctata* Whatley & Coles: 73, pl. 4, figs 12–14.

2000 *Eucythere multipunctata* Whatley & Coles; Didié & Bauch: 110, p. 3, fig. 22.

2005 *Eucythere multipunctata* Whatley & Coles; Zhao: p. 3, fig. 9.

2009 *Eucythere multipunctata* Whatley & Coles; Alvarez Zarikian: 4, pl. P6, fig. 1.

?2011 *Eucythere serrata* Zhao; Zhao et al.: 27, pl. 1, fig. 6.

**Remarks.** The Atlantic specimens of *Eucythere multipunctata* Whatley & Coles, 1987 have slightly stronger punctation and a slightly straighter dorsal margin along the hingement (Whatley & Coles 1987) compared with our Pacific specimens (Fig. 2O, P). We tentatively consider this to be intraspecific variation. Our Pacific specimens are also similar to the species identified as *Eucythere serrata* Zhao in Wang et al., 1988 by Zhao et al. (2011) and may be conspecific, although punctation is much stronger in our specimens. The oldest record of this species is from the Paleocene (Coles et al. 1990).

**Eucythere pubera** Bonaduce, Ciampo & Masoli, 1976
(Fig. 2S)

1976 *Eucythere pubera* Bonaduce, Ciampo & Masoli: 64, pl. 37, figs 1–8, text-fig. 28.

1980 *Eucythere pubera* Bonaduce, Ciampo & Masoli; Colalongo & Pasini: pl. 21, figs 7, 8.


1987 *Eucythere pubera* Bonaduce, Ciampo & Masoli; Whatley & Coles: 93, pl. 4, fig. 15.

1988 *Eucythere parapubera* Whatley & Downing; Whatley & Ayress: 740, pl. 1, fig. 4a, b.

1988 *Eucythere serrata* Zhao in Wang, Zhang, Zhao, Min, Bian, Zheng, Cheng, & Chen: 238, fig. 5.75, pl. 39, figs 11–16.

1995 *Eucythere cf. parapubera* Whatley & Downing; Ayress: fig. 5.11.

1993 *Pseudoeucythere parapubera* (Whatley & Downing); McKenzie, Reyment, & Reyment: 88, pl. 2, figs 23, 24.

2000 *Eucythere pubera* Bonaduce, Ciampo & Masoli; Aiello, Barra, & Bonaduce: 97, pl. 3, fig. 12.

2000 *Eucythere pubera* Bonaduce, Ciampo & Masoli; Didié & Bauch: 116, pl. 3, fig. 23.

2005 *Eucythere pubera* Bonaduce, Ciampo & Masoli; Zhao: 41, pl. 3, fig. 8.

2007 *Eucythere serrata* Zhao; Hou & Gou: 252, pl. 94, figs 5–7.

2009 *Eucythere pubera* Bonaduce, Ciampo & Masoli; Alvarez Zarikian: 4, pl. P6, fig. 3.

2014 *Eucythere pubera* Bonaduce, Ciampo & Masoli; Yasuhara and Okahashi: 780, fig. 6.1.
Remarks. Following Yasuhara & Okahashi (2014), we consider *Eucythere parapubera* Whatley & Downing, 1983 to be a junior synonym of *Eucythere pubera* Bonaduce, Ciamo & Masoli, 1976. We also consider *Eucythere serrata* Zhao, 1988 a junior synonym of this species. The oldest record of this species is from the Upper Cretaceous (Coles et al. 1990).

Family *Krithidae* Mandelstam in Bubikyan, 1958
Genus *Kritha* Brady, Crosskey & Robertson, 1874

Type species. *Ilyobates praetexta* Sars, 1866.

*Kritha reversa* van den Bold, 1958
(Fig. 3A–F)

1958 *Kritha reversa* van den Bold: 399, pl. 1, fig. 4a–g.
1981 *Kritha reversa* van den Bold; van den Bold: 69, pl. 1, fig. 13a–d.
?1981 *Kritha reversa* van den Bold; Steineck: pl. 2, fig. 12.
?1983 *Kritha* cf. sp. C Cronin: pl. 10, fig. D.
1990 *Kritha* sp. 4 Dingle, Lord & Boomer: 282, figs 17D, 18F, 22E.
1994 *Kritha reversa* van den Bold; Coles, Whatley & Moguilevsky: 77, pl. 1, figs 1–6, text-fig. 3A–D.
1995 *Kritha* sp. 4 do Carmo & Sanguinetti: fig. 2E.
?1997 *Kritha reversa* van den Bold; Zhao & Whatley: fig. 5.1.
1999 *Kritha reversa* van den Bold; Ayress, Barrows, Passlow & Whatley: 8, figs 2F, 3O, 8M.
1999 *Kritha reversa* van den Bold; Rodriguez-Lazaro & Cronin: fig. 3B7–8, pl. 1, figs 16–17.
2004 *Kritha reversa* van den Bold; Ayress, De Dekker & Coles: 31.
on 2006 *Kritha reversa* van den Bold; Bergue, Costa, Dwyer & Moura: fig. 7 C.
on 2008 *Kritha reversa* van den Bold; Bergue & Coimbra: 125, pl. 5, figs 6, 7.
2014 *Kritha* sp. 2 Stepanova & Lyle: pl. 1, fig. 2.
2014 *Kritha* sp. 4 Stepanova & Lyle: pl. 1, fig. 4.

Remarks. We agree with Mazzini (2005) that *Kritha sawanensis* Hanai, 1959 is not conspecific with *Kritha reversa* van den Bold, 1958. The ventral half of the posterior margin in *Kritha reversa* is distinctively convex with a nearly flat extremity, especially in right valves. Male valves of *Kritha reversa* are highest at the anterior cardinal angle. *Kritha sawanensis* does not share these characters (Hanai 1959). We also consider *Kritha reversa* sensu Bergue et al. (2006) and Bergue & Coimbra (2008) (= *Kritha* sp. C of Cronin (1983)) not conspecific with *Kritha reversa*. True *Kritha reversa* has a straight dorsal margin in the right valves, but it is arched in *Kritha reversa* sensu Bergue et al. (2006) and Bergue & Coimbra (2008). This species is a well-known cosmopolitan species (but not known from the Arctic), and its oldest fossil record is from the Miocene (Coles et al. 1994; Ayress et al. 2004).

*Kritha sp.* 1
(Fig. 3I–K)

*Kritha cf. sp.* 1
(Fig. 3G, H)

*Kritha sp.* 2
(Fig. 3L, M)

Family *Rockalliiidae* Whatley, Uffenorde, Harlow, Downing & Kesler, 1982
Genus *Arcacythere* Hornibrook, 1952

Type species. *Arcacythere chapmani* Hornibrook, 1952.

*Arcacythere enigmatica* (Whatley, Frame & Whittaker, 1978)
(Fig. 4A–G)

1978 *Rockallia enigmatica* Whatley, Frame & Whittaker: 137, pls 5-138, 5-140, 5-142, 5-144, text-fig. 1.
1979 Indet. Gen. 3 Ducasse & Peypouquet: pl. 5, fig. 9.
1982 *Rockallia enigmatica* Whatley, Frame & Whittaker; Whatley, Uffenorde, Harlow, Downing & Kesler: 3, pl. 1, figs 1, 4.
1987 *Rockallia* enigmatica Whatley, Frame & Whittaker; Whatley & Coles: 80, pl. 2, figs 3, 4.
1987 *Rockallia* sp. Whatley & Coles: 89, pl. 2, fig. 5.
1988 *Rockallia enigmatica* Whatley, Frame & Whittaker; Ruan & Hao: 377, pl. 70, figs 2–4.
1990 *Rockallia enigmatica* Whatley, Frame & Whittaker; Malz: 143, fig. 4.2.
1996 *Arcacythere enigmatica* (Whatley, Frame & Whittaker); Zhao & Zheng: pl. 1, fig. 16.
2003 *Rockallia enigmatica* Whatley, Frame & Whittaker; Cronin & Dwyer: 263, pl. 2, fig. n.
2005 *Rockallia enigmatica* Whatley, Frame & Whittaker; Mazzini: 86, figs 50P, 51B.
2005 *Arcacythere enigmatica* (Whatley, Frame & Whittaker); Zhao: pl. 4, fig. 21.
Figure 3. Scanning electron microscope (SEM) images of *Krithe* species. A–F, *Krithe reversa* van den Bold, 1958; A, USNM 698168 (PACNGC09), adult female? LV; B, USNM 698169 (NGC104-43), adult female RV; C, USNM 698170 (PACNGC16), adult male RV; D, USNM 698171 (PACNGC32), adult male? LV; E, USNM 698172 (PACNGC03), adult female RV; F, USNM 698173 (PACNGC08), adult male RV. G, H, *Krithe* cf. sp. 1; G, USNM 698174 (NGC104-44), adult female? LV; H, USNM 698175 (NGC104-45), adult female? RV. I–K, *Krithe* sp. 1; I, USNM 698176 (PACNGC33), adult male? LV; J, USNM 698177 (PACNGC29), adult female? LV; K, USNM 698178 (PACNGC30), adult female? RV. L, M, *Krithe* sp. 2; L, USNM 698179 (PACNGC34), adult male LV; M, USNM 698180 (PACNGC35), adult male RV. All lateral views, except E (internal view). Scale bar = 1 mm.
Figure 4. Scanning electron microscope (SEM) images of *Arcacythere* and *Ambocythere*? species. A–G, *Arcacythere enigmatica* (Whatley, Frame & Whittaker, 1978); A, USNM 698181 (NGC104-62), adult LV; B, USNM 698182 (PACNGC47), adult RV; C, USNM 698183 (PACNGC46), adult LV; D, USNM 698184 (NGC104-61), adult RV; E, USNM 698185 (PACNGC06), adult RV; F, USNM 698186 (PACNGC05), adult LV; G, USNM 698187 (PACNGC04), adult RV. H–J, *Ambocythere*? sp.; H, USNM 698188 (PACNGC42), adult? RV; I, USNM 698189 (PACNGC41), adult? LV; J, USNM 698190 (PACNGC01), adult? RV. A–D, I–J, lateral views; E–H, internal views. Scale bars = 1 mm.
2007 Rockallia enigmatica Whately, Frame & Whittaker; 
Hou & Gou: 509, pl. 198, figs 1–4.
2007 Rockallia inceptiocelata Whately, Uffenorde, 
Harlow, Downing & Kesler; Hou & Gou: 509, pl. 198, 
figs 5, 8 (76, 7).
2009 Rockallia enigmatica (Whately, Frame & 
Whittaker); Alvarez Zarikian: 5, pl. P9, fig. 5.
2014 Arcacythere enigmatica (Whatley, Frame & 
Whittaker); Yasuhara & Okahashi: 781, fig. 7.4.
2015 Arcacythere enigmatica (Whatley, Frame & 
Whittaker); Yasuhara & Okahashi: 45, fig. 5D–I.

Remarks. This species has been widely reported from 
the eastern North Atlantic and north-western Pacific, 
as indicated by Yasuhara & Okahashi (2014, 2015) 
and the synonymy list above. The oldest record is from the Oligo-
cene (Zhao 2005).

Family Thaerocytheridae Hazel, 1967
Genus Bradleya Hornibrook, 1952

Type species. Cythere arata Brady, 1880.

Bradleya mesembrina Mazzini, 2005
(Fig. 5A)

2004 Bradleya normani (Brady); Ayress, De Dekker & 
Coles: 31, pl. 2, figs 12, 13, pl. 4, fig. 6.
2005 Bradleya mesembrina Mazzini: 81, figs 47A–K, 48B.
2009 Bradleya normani (Brady); Alvarez Zarikian: 6, pl. 
P9, fig. 2.
2009b Bradleya mesembrina Mazzini; Yasuhara, Cronin, 
Hunt & Hodell: 918, fig. 4.8, 4.9.
2011 Bradleya mesembrina Mazzini; Brandão & Páplow: 
147, pl. 1, figs A–G.
2014 Bradleya mesembrina Mazzini; Brandão, Vital & 
Brandt: 45, fig. 9A.
2014 Bradleya mesembrina Mazzini; Stepanova & Lyle: 
pl. 1, figs 8, 9.
2014b Bradleya mesembrina Mazzini; Yasuhara, Grimm, 
Brandão, Jöst, Okahashi, Iwatani, Ostman & Martínez 
Arbizu 352, fig. 8.3.
2015 Bradleya cf. mesembrina Mazzini; Yasuhara, Hunt, 
Okahashi & Brandão: 167, fig. 94O.
2016 Bradleya mesembrina Mazzini; Alvarez Zarikian: 
104, pl. 2, fig. 2.

Remarks. This species is known from the Quaternary of the North Atlantic, North and South Pacific, and Southern 
oceans.

Genus Poseidonamicus Benson, 1972

Type species. Poseidonamicus major Benson, 1972.

Poseidonamicus shatskyensis sp. nov.
(Figs 5B–M, 6)

Derivation of name. From the type locality.

Material. Holotype: LV, USNM 698202 (PACNGC11) 
(Figs 5L, 6). Paratypes: LV, USNM 698192 (NGC104- 
59) (Fig. 5B); RV, USNM 698193 (NGC104-60) 
(Fig. 5C); LV, USNM 698194 (NGC104-56) (Fig. 5D); 
RV, USNM 698195 (NGC104-57) (Fig. 5E); RV, USNM 
698196 (PACNGC26) (Fig. 5F); LV, USNM 698197 
(NGC104-58) (Fig. 5G); LV, USNM 698198 
(PACNGC21) (Fig. 5H); RV, USNM 698199 
(PACNGC22) (Fig. 5I); LV, USNM 698200 
(PACNGC02) (Fig. 5J); RV, USNM 698201 
(PACNGC17) (Fig. 5K); LV, USNM 698203 
(PACNGC25) (Fig. 5M).

Type locality and horizon. Shatsky Rise, north-western 
Pacific. NGC 104, 137–141 cm depth. Late Quaternary.

Dimensions. USNM 698202 (PACNGC11) (holotype), 
L = 0.979 mm, H = 0.553 mm; USNM 698199 
(PACNGC22) (paratype), L = 1.011 mm, H = 0.547 mm; 
USNM 698194 (NGC104-56) (paratype), L = 0.923 mm, 
H = 0.489 mm; USNM 698195 (NGC104-57) (paratype), 
L = 0.898 mm, H = 0.462 mm.

Diagnosis. A moderately calcified species of Poseidonam-
icus with evenly emphasized vertical muri. It shares sev-
eral features with derived members of this genus, 
including the presence of a pore at the intersection of the 
M7 and M8 fossae, but, like basal members of the genus, 
its A6 fossa is in a relatively anterior position (see 
Remarks). No other species of this genus has this combi-
nation of features.

Description. Carapace moderately calcified, medium-
sized for the genus. Subsquare in lateral view with highest 
point near the anterior cardinal angle in LV and 
just posterior to it in RV. Anterior margin evenly 
rounded, becoming broader near the dorsal margin; pos-
terior margin rounded and somewhat blunt. Dorsal 
marg
in mostly straight, sloping downward from anterior 
to posterior; ventral margin straight in the middle, curling 
smoothly at the anterior and posterior. Anterodorsal 
corner angled in LV but smoothly curved in RV; 
posterodorsal corner often bearing a low, broad spine. 
Entire surface reticulate, with polygonal fossae posterior 
to the adductor scars and rounded fossae and a lower, 
more even reticulum in the anterior. In the posterior 
field, vertical muri are of similar robustness, and some-
what more emphasized than horizontal ones. Dorsal 
ridge continuous, widening towards its posterior termi-
nus; ventral ridge gently curved and well developed. 
Holamphidont hinge and adductor/frontal scars typical 
for the genus.

Remarks. Phylogenetic characters scored by Hunt 
(2007) suggest that Poseidonamicus shatskyensis sp. nov. 
is most similar to derived members of this genus,
Figure 5. Scanning electron microscope (SEM) images of Bradleya and Poseidonamicus species. A, Bradleya mesembrina Mazzini, 2005, USNM 698191 (PACNGC12), adult RV. B–M, Poseidonamicus shatskyensis sp. nov.; B, USNM 698192 (NGC104-59), A-1 juvenile LV; C, USNM 698193 (NGC104-60), A-1 juvenile RV; D, USNM 698194 (NGC104-56), adult male LV; E, USNM 698195 (NGC104-57), adult male RV; F, USNM 698196 (PACNGC26), adult female RV; G, USNM 698197 (NGC104-58), adult female LV; H, USNM 698198 (PACNGC21), adult female LV; I, USNM 698199 (PACNGC22), adult female RV; J, USNM 698200 (PACNGC02), adult female? LV; K, USNM 698201 (PACNGC17), adult female? RV; L, USNM 698202 (PACNGC11), adult female LV; M, USNM 698203 (PACNGC25), adult female LV. All lateral views, except J–K (internal views). Scale bar = 1 mm.
especially Poseidonamicus pintoi Benson, 1972. These features include the arrangement of pores on the anterior margin (characters 3 and 4 of Hunt (2007)) and elsewhere (characters 6 and 10), and the positions of fossae along the anterior margin and in the region posterior to the muscle scars (characters 16 and 19). One noteworthy exception to this is the position of fossa A6 in the scheme of Hunt (2007, character 14; Fig. 6). In Poseidonamicus shatskyensis, this fossa is in a relatively anterior position, a condition found in more basal members of the genus and its outgroups. This combination of characters is not known in any other described species of this genus.

Figure 6. Scanning electron microscope (SEM) image of Poseidonamicus shatskyensis sp. nov., USNM 698202 (PACNGC11). Close-up of the posterior area with fossae labelled according to the coding scheme described in Hunt (2007).

Family Trachyleberididae Sylvester-Bradley, 1948
Genus Ambocythere van den Bold, 1957

Type species. Ambocythere keiji van den Bold, 1957.

Ambocythere? sp.
(Fig. 4H–J)


Remarks. Ambocythere? sp. is similar to Falsobuntonia? sp. 1 of Hou & Gou (2007) but is distinguished by its lack of horizontally arranged parallel ridges. This species is also similar to Phacorhabdotus? sp. of Zhao (2005) but is distinguished by its distinct pore conuli and different ridge arrangement. It may be conspecific with the species identified as Cytheretta? iwasakii Nohara, 1987 by Zhao et al. (2011). Ambocythere? sp. is distinguished from true Cytheretta? iwasakii by its lack of horizontally arranged parallel ridges. We provisionally assign this species to Ambocythere because of its well-developed pore conuli, weakly developed primary reticulation, generally horizontal arrangement of ridges in the central part of carapace and rather flat anterior margin, and the overall shape of its outline.

Genus Henryhowella Puri, 1957

Type species. Cythere evax Ulrich & Bassler, 1904.

Henryhowella sol (Jellinek & Swanson, 2003) (Fig. 7)

2003 Apatihowellia (Fallacihowella) sol Jellinek & Swanson, 2003: 44, pl. 34, figs 1–10, pl. 35, figs 1–6.
2003 Apatihowellia (Fallacihowella) caligo Jellinek & Swanson, 2003: 45, pl. 36, figs 1–6.
2005 Fallacihowella caligo (Jellinek & Swanson, 2003); Mazzini: 54, figs 27A, 30A–N.
2005 Fallacihowella sp. A Mazzini: 54, fig. 31A–M.
2005 Fallacihowella sp. B Mazzini: 57, fig. 32A–Q.

Remarks. Our specimens are very similar to Henryhowella sol (Jellinek & Swanson, 2003) and Henryhowella caligo (Jellinek & Swanson, 2003) in outline and surface ornamentation. We consider the minor differences in size, development of primary and secondary reticulation, and the development and number of spines to be intraspecific variation, and thus interpret Henryhowella caligo as a junior synonym of Henryhowella sol which has page priority in Jellinek & Swanson (2003). Following Yasuhara et al. (2015), we consider Fallacihowella a junior synonym of Henryhowella. This species is known from the Quaternary of the Pacific and Southern oceans.

Genus Legitimocythere Coles & Whatley, 1989

Type species. Cythere acanthoderma Brady, 1880.

Legitimocythere stellae sp. nov.
(Fig. 8A–F)

Derivation of name. From the Latin stellae (a noun in the genitive case), meaning ‘star’, with reference to its star-shaped spines.

Material. Holotype: RV, USNM 698224 (PACNGC44) (Fig. 8D). Paratypes: LV, USNM 698221 (NGC104-66) (Fig. 8A); RV, USNM 698222 (NGC104-50) (Fig. 8B); LV, USNM 698223 (PACNGC45) (Fig. 8C); RV, USNM 698225 (NGC104-67) (Fig. 8E); LV, USNM 698226 (NGC104-69) (Fig. 8F).
Figure 7. Scanning electron microscope (SEM) images of *Henryhowella sol* (Jellinek & Swanson, 2003). A, USNM 698204 (PACNGC18), adult male LV. B, USNM 698205 (NGC104-47), adult male RV. C, USNM 698206 (NGC104-46), adult male LV. D, USNM 698207 (PACNGC36), adult male RV. E, USNM 698208 (PACNGC15), adult male LV. F, USNM 698209 (NGC104-53), adult male RV. G, USNM 698210 (PACNGC28), adult male RV. H, USNM 698211 (PACNGC19), adult male RV. I, USNM 698212 (PACNGC20), adult male RV. J, USNM 698213 (PACNGC27), adult male LV. K, USNM 698214 (NGC104-51), adult female LV. L, USNM 698215 (NGC104-52), adult female RV. M, USNM 698216 (PACNGC23), adult female LV. N, USNM 698217 (PACNGC10), adult female RV. O, USNM 698218 (PACNGC14), adult female LV. P, USNM 698219 (NGC104-54), A-1 juvenile LV. Q, USNM 698220 (NGC104-55), A-1 juvenile RV. A–H, K–M, P–Q, lateral views; I–J, N–O, internal views. Scale bar = 1 mm.
Type locality and horizon. Shatsky Rise, north-western Pacific. NGC 104, 331–335 cm depth. Late Quaternary.

Dimensions. USNM 698224 (PACNGC44) (holotype), L = 1.410 mm, H = 0.858 mm; USNM 698221 (NGC104-66) (paratype), L = 1.434 mm, H = 0.857 mm; USNM 698222 (NGC104-50) (paratype), L = 1.353 mm, H = 0.747 mm; USNM 698223 (PACNGC45) (paratype), L = 1.470 mm, H = 0.844 mm.

Diagnosis. *Legitimocythere* species characterized by its oval and elongated outline, evenly well developed and star-shaped spines, and comparatively subdued ventrolateral ridge.

Description. Carapace moderately calcified, highest at the anterodorsal corner. Outline ovate-subrectangular and elongated in lateral view; anterior margin evenly rounded and spinose; posterior margin rounded and spinose; dorsal

Figure 8. Scanning electron microscope (SEM) images of *Legitimocythere* and *Croninocythereis* species. A–F, *Legitimocythere stellae* sp. nov.; A, USNM 698221 (NGC104-66), adult LV; B, USNM 698222 (NGC104-50), adult male? RV; C, USNM 698223 (PACNGC45), adult male? LV; D, USNM 698224 (PACNGC44), adult female? RV; E, USNM 698225 (NGC104-67), adult RV; F, USNM 698226 (NGC104-69), adult LV. G, *Croninocythereis cronini* Yasuhara, Hunt, Okahashi & Brandão, 2015, USNM 698227 (PACNGC31), adult RV. All lateral views, except E, F (internal views). Scale bar = 1 mm.
margin straight or slightly concave, bearing star-shaped spines; ventral margin convex and densely spinose; ventrolateral ridge subduted and spinose. Anterodorsal corner weakly angular, bearing a long spine in RV. Posterodorsal corner angular, bearing a long spine in LV. Lateral surface ornamented evenly with well-developed spines that terminate in flattened, star-shaped apices. Hingement holamphidont. Frontal muscle scar small and ovate. Adductor muscle scars consist of a vertical row of four elongate scars; dorsomedical scar long and deflected.

Remarks. *Legitimocythere stellae* sp. nov. is similar to *Legitimocythere tomi* Yasuhara, Hunt, Okahashi & Brandão, 2015 but is distinguished by having a comparatively slender outline and regular, star-shaped spines. *Legitimocythere stellae* sp. nov. is distinguished from *Legitimocythere acanthoderma* (Brady, 1880) by its more ovate and slender outline, well developed and evenly distributed star-shaped spines, and comparatively subdued ventrolateral ridge and primary reticulation.

Genus *Croninocythereis* Yasuhara, Hunt, Okahashi & Brandão, 2015

Type species. *Croninocythereis cronini* Yasuhara, Hunt, Okahashi & Brandão, 2015

*Croninocythereis cronini* Yasuhara, Hunt, Okahashi & Brandão, 2015

1976 ‘Hyphalocythere’ sp. Berggren, Benson, Haq, Riedel, Sanfilippo, Schrader & Tjalsma: pl. 6, figs 7, 8.
1988 *Trachyleberis acanthoderma* (Brady); Ruan & Hao: 356, pl. 64, figs 22–25.
1989 *Trachyleberis acanthoderma* (Brady); Ruan: 126, pl. 23, fig. 18.

2004 *Legitimocythere presequenta* (Benson); Ayress, De Dekker & Coles: 36, pl. 1, figs 11, 12, 14–16.
2004 *Legitimocythere acanthoderma* (Brady); Zhao, Jian, & Chen: fig. 2.18.

Remarks. The oldest fossil record of this species is from the Miocene (Yasuhara et al. 2015).

Discussion

A comprehensive taxonomic survey of the species found in Core NGC 104 suggests that many of them have broad geographical distributions (Table 1). However, misidentifications have been common, especially in the early literature, and some deep-sea species that were previously believed to be cosmopolitan have been found on closer analysis to have much narrower geographical distributions (Maddocks 1990; Schornikov 2005; Jellinek et al. 2006; Brandão 2013; Brandão & Yasuhara 2013). To reduce this source of error, we carefully checked images and illustrations of each paper during our taxonomic survey. Moreover, even if some of the nominal species we identify here are actually broader than biological species, they are still useful for tracking biogeographical connections. As long as these taxa are not polyphyletic, their presence in more than one ocean basin implies at least one dispersal event between basins.

Most of the species listed in Table 1 are known from both the Atlantic and Pacific oceans and so there must be at least one migration pathway between these oceans. The deep-water seaway of the Drake Passage (Southern Ocean) was established by 30 Ma (Lawver & Gahagan 2003; Livermore et al. 2005; Scher & Martin 2006), and previous researchers have suggested it as a likely candidate (Whatley & Ayress 1988; Coles et al. 1990). Indeed,

Table 1. Biogeographical distribution of selected species. Oldest age based on the synonym list of this paper, supplemented by Coles et al. (1990). N, north; S, south; Southern O, Southern Ocean; Oldest A, oldest occurrence record in the Atlantic; Oldest P, oldest occurrence record in the Pacific; X, occurrence; Quat, Quaternary; Olig, Oligocene; Plio, Pliocene; Pal, Paleocene; Eoc, Eocene; Cret, Cretaceous; Mio, Miocene; Mod, Modern; No, no occurrence.

<table>
<thead>
<tr>
<th>Species</th>
<th>N. Atlantic</th>
<th>S. Atlantic</th>
<th>N. Pacific</th>
<th>S. Pacific</th>
<th>Southern O</th>
<th>Arctic</th>
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<th>Oldest P</th>
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<td>X</td>
<td></td>
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<td>Olig</td>
<td>Plio</td>
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<td><em>Eucythere multipunctata</em></td>
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<td>X</td>
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<td>X</td>
<td>X</td>
<td>X</td>
<td>Eoc</td>
<td>Cret</td>
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<td>X</td>
<td>X</td>
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<td>Mio Quat</td>
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<td>X</td>
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<td></td>
<td>Mod Mio</td>
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</tr>
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</table>
amongst the nine species found in both the North Atlantic and North Pacific, five have also been recovered from the Southern Ocean (Table 1), which is consistent with the Drake Passage as a migration pathway.

The Central American Seaway, which had closed by 3 Ma (Schmidt 2007; O’Dea et al. 2016; Schmidt et al. 2016), is also a possible deep-water route between the Atlantic and Pacific because this seaway was deep during parts of the Miocene (Schmidt 2007). Indeed, Stepanova & Lyle (2014) reported from the eastern equatorial Pacific the occurrence of Ambocythere cf. sturgio Yasuhara et al., 2009a, which is very similar to Ambocythere sturgio Yasuhara et al., 2009a, a species known only from the north-western Atlantic Ocean (Yasuhara et al. 2009a). In addition, Stepanova & Lyle (2014) recorded from the eastern equatorial Pacific the presence of Bradleya sp. 1 (very similar to Bradleya dicyton (Brady, 1880)), Krithe reversa van den Bold, 1958 (as Krithe sp. 2 and 4) and Agrenocythere hazelae (van den Bold, 1946). Bradleya dicyton is mainly known from the Atlantic Ocean, and Krithe reversa and Agrenocythere hazelae were originally described from the Caribbean region, although these species are known to be distributed globally (Whately et al. 1984 for Bradleya dicyton; Table 1 for Krithe reversa; Yasuhara et al. 2015 for Agrenocythere hazelae). These facts are consistent with the Central American Seaway as a deep-water connection between the Atlantic and Pacific oceans, but the paucity of deep-sea ostracod research in the eastern Pacific Ocean prevents further discussion at this time.

Before it had closed by 19–14 Ma (Harzhauser et al. 2002, 2007; Renema et al. 2008), the Tethys Seaway might have been an important pathway for long-lived ‘old’ species, as suggested by Coles et al. (1990) (see also Steineck et al. 1984, 1988 and McKenzie 1982, 1986, 1991b) for genus-level connections). Cosmopolitan distributions of some deep-sea ostracod species might have been established in the Tethys during the Palaeogene or by the middle Miocene (Coles et al. 1990). For example, Eucythere multipunctata Whatley & Coles, 1987 is known from the Palaeogene from both the North Atlantic and North Pacific oceans, but it is not known from the Southern Ocean (Table 1). It is likely that the Tethys was deep enough to be a corridor for the dispersal of both shallow and deep taxa during the Palaeogene (McKenzie 1991a, b; Leprieur et al. 2016). So, some long-lived ‘old’ species like Eucythere multipunctata may have migrated through the Tethyan pathway. Eucythere pubera Bonaduce, Ciampo & Masoli, 1976 is also an ‘old’ species distributed in both the North Atlantic and North Pacific oceans (Table 1; but note that this species is also known from the Southern Ocean, another possible pathway). Eucythere pubera is known from the modern Mediterranean (Bonaduce et al. 1976). But the modern Mediterranean fauna is usually considered ‘young’ and unrelated to that of the Tethys (McKenzie 1991a). Indeed, both Eucythere multipunctata and E. pubera have no pre-Quaternary fossil occurrences in the Mediterranean region (see synonym list in the Systematic palaeontology section above). So, while a Tethyan connection between the Atlantic and Pacific remains feasible, at present the evidence for this migration pathway is not strong. Re-investigation of Palaeogene Tethyan ostracods using scanning electron microscopy will be needed to further evaluate this possibility.

A final possible pathway between the Atlantic and Pacific is via the Arctic Ocean Seaway, through the Bering Strait, which opened about 4.8–7.4 Ma (Marinovich & Gladenkov 2001; Hu et al. 2015), and the Fram Strait, which opened between 10 and 20 Ma (Engen et al. 2008; Ehlers & Jokat 2013). The deep-sea ostracod fauna from the Arctic is distinct and lacks genera and species that are dominant elsewhere (Yasuhara et al. 2014a). For example, the modern Arctic Ocean lacks deep-sea trachyleberids, except for Henryhowella, and Krithe species other than Krithe hanti Yasuhara, Stepanova, Ohkashi, Cronin & Brouwers, 2014a and K. minima Coles, Whatley & Moguilevsky, 1994. Probably for this reason, the Arctic Ocean has not been considered a migration pathway for deep-sea ostracods between the Atlantic and Pacific oceans. However, Thomas Cronin’s research group has recently discovered (Cronin et al. 2014; DeNinno et al. 2015) that typical deep-sea taxa from the North Atlantic Ocean were also present in the Arctic Ocean before the mid-Pleistocene transition (a major climatic transition during which the dominant periodicity of the Earth’s climate cycles changed). This discovery raises the possibility of an Arctic Ocean pathway for deep-sea taxa. Although the Bering Strait is shallow, its cold temperatures might have allowed migration of deep-sea organisms. Indeed, normally deep-water taxa have been reported at shallow depths in very cold regions at high latitudes (Whatley et al. 1997). Such ‘poleward-emergent’ distributions were also shown by Brouwers et al. (2000) and likely reflect the fact that depth per se is probably not an important controlling factor on the distribution of marine organisms. Rather, depth-related factors such as temperature are much more likely to limit where species occur. An Arctic pathway is especially plausible for Arcacythere enigmatica (Whatley, Frame & Whittaker, 1978), because this species is known only from the northern hemisphere of the Atlantic and Pacific oceans (Table 1), and Cronin et al. (2014) and DeNinno et al. (2015) discovered fossil specimens of this species (or a very similar species) in samples from an Arctic sediment core dated to be older than the mid-Pleistocene. The existence of a few cosmopolitan deep-sea species in the Arctic Ocean, such as Henryhowella asperrima (Reuss, 1850) and Cytheropteron perlaria Hao in Ruan & Hao, 1988 (Yasuhara et al. 2014a), also supports the plausibility of migration into the
Arctic from elsewhere. The distribution of several other species is further consistent with an Arctic corridor between the Atlantic and Pacific oceans. *Cytheropteron higashikawai* Ishizaki, 1981 is known only from the Pacific and Arctic oceans and the Nordic seas (Yasuhara et al. 2014a), and *Cytheropteron demenocali* Yasuhara, Okahashi & Cronin, 2009a and *C. pherozigzag* Whatley, Ayress & Downing, 1986 have been recovered from only the northern hemisphere and are not known from the Southern Ocean (Table 1). In addition, some genera (especially *Polycope* and *Cytheropteron*) have high species diversity in the Arctic Ocean (Gemery et al. 2017; Yasuhara et al. 2014a) and low species diversity in the Southern Ocean (Ayress et al. 2004; Mazzini 2005; Yasuhara et al. 2009b). The Arctic Ocean (rather than the Southern Ocean) might have been an important migration route for at least some species of such genera.

Conclusions

1. Four possible migration pathways between the Atlantic and Pacific Oceans for deep-sea organisms are evaluated using the rich fossil record of deep-sea ostracods as a model.

2. The Drake Passage was established by 30 Ma (Lawver & Gahagan 2003; Livermore et al. 2005; Scher & Martin 2006) and it is likely to be a major pathway for deep-sea organisms between the Atlantic and Pacific oceans over geological time scales.

3. The Central American Seaway, which closed by 3 Ma (Schmidt 2007; O’Dea et al. 2016; Schmidt et al. 2016), is a possible migration pathway for deep-sea organisms, but more data are needed in the eastern Pacific Ocean to further evaluate this possibility.

4. Before its closure by 19–14 Ma (Harzhauser et al. 2002, 2007; Renema et al. 2008), the Tethys Seaway might have been an important pathway for cosmopolitan deep-sea elements that were established during the Palaeogene when the Tethys was deep.

5. As a fourth possible deep-water pathway between the Atlantic and Pacific oceans, we propose the Arctic Ocean Seaway via the Bering Strait, which opened ~4.8–7.4 Ma (Marincovich & Gladenkov 2001; Hu et al. 2015), and the Fram Strait, which opened between 10 and 20 Ma (Engen et al. 2008; Ehlers & Jokat 2013). This Arctic pathway possibility is supported by recent Arctic fossil ostracod studies (Cronin et al. 2014; DeNinno et al. 2015) and the global distribution data of several species compiled in our comprehensive taxonomic survey.

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Supplemental material

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### Supplemental Table 1. Detailed information of the specimens used for the present study.

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<th>Age</th>
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All specimens are from Core NGC 104 (32°10.04’N, 157°59.9’E, 2665 m water depth). Samples are specified by composite core depth (cm). USNM, catalog number; No., M.Y.’s personal catalog number. T, type (P, paratype; H, holotype); V, valve (L, left; R, right); A, adult; J, juvenile; F, female; M, male. Age in ka.