Geol. Mag. **155** (*8*), *2018*, *pp. 1742–1760.* © *Cambridge University Press 2017*
doi:10.1017/S0016756817000693

First discovery of Eocene coastal-estuarine ostracods from Japan, with the geological history of the migration of estuarine genera in the Far East

GENGO TANAKA*†, YASUHISA HENMI‡, TOSHIFUMI KOMATSU§, KOJI HIROSE¶, HIROAKI UGAI¶, SHIGEHIRO KAWANO||
& HARUYOSHI MAEDA#

*Institute of Liberal Arts and Science, Kanazawa University, Kakumama-machi, Kanazawa City, Ishikawa 920-1192, Japan
‡Center for Marine Environment Studies, Kumamoto University, 6061 Aitsu, Matushima, Kami-amakusa City, Kumamoto 861-6102, Japan
§Graduate School of Science and Technology, Kumamoto University, 2-39-1, Kurokami, Kumamoto 860-8555, Japan
¶Goshoura Cretaceous Museum, 4310-5, Goshoura, Amakusa City, Kumamoto 866-0313, Japan
||Tochigi Prefectural Museum, 2-2, Mutsu-machi, Utsunomiya City, Tochigi 320-0865, Japan
#Kyushu University Museum, 6-10-1, Hakozaki, Fukuoka 812-8581, Japan

(*Received* 16 September 2016; *accepted* 17 July 2017; *first published online* 6 September 2017)

Abstract – The genus *Neomonoceratina*, which dominated the ostracod assemblage in the uppermost part of the Akasaki Formation (Miroku Group) of the Kyushu Island, Japan, is associated with the benthic foraminifer *Ammonia* cf. *beccarii*, mollusca *Terebralia*? sp. and *Anomia* sp., and the oogonium of Charophyceae, indicating a marine-to-brackish estuarine environment involving inflowing freshwater. This is the first record of Eocene coastal-estuarine ostracods from the eastern margin of the Eurasian continent and demonstrates that different pre-Neogene coastal-estuarine ostracod assemblages flourished in this region. The assemblages comprised five ostracod species (including one novel species) assigned to the genera *Neomonoceratina*, *Paijeiborchella*, *Propontocypris* and *Parakrithella*. These species exhibited genus-level links with the Eocene borehole cores along the continental shelf of the East China Sea and other areas of Kyushu. Fossil data of characteristic Eocene coastal-estuarine genera collected worldwide indicate that different characteristic genera inhabited each region. For example, *Neomonoceratina* originated on the Indian subcontinent by the Early Paleocene period at the latest, along with the northern drift of the Indian subcontinent. These species subsequently diversified west and east with the equatorial current and counter-current via the Tethys and reached the eastern margin of the Eurasian continent among the various eastwards-migrating species, where one genus ultimately adapted to the coastal-estuarine environment. Notably, the coastal-estuarine ostracod assemblage of the eastern margin of the Eurasian continent differs completely from that of the Tethys during the Eocene period. Our results suggest that coastal-estuarine ostracod assemblages are a powerful tool for palaeogeographic reconstruction.

Keywords: Eocene, Ostracoda, Kyushu Island, Japan, palaeoenvironments, palaeobiogeography

1. Introduction

The Japan archipelago is situated at the eastern margin of the Eurasian continent as a result of early–middle Miocene back-arc formation (Baba *et al*. 2007; Sawada *et al*. 2013) by the clockwise and anticlockwise rotations of SW and NE Japan, respectively (Otofuji, Matsuda & Nohda, 1985), or of late Oligocene – middle Miocene spreading axes in the Sea of Japan (Yanai, Aoki & Akahori, 2010). The formation of the Sea of Japan after the (at the latest) late Oligocene regional tectonic events and global sea-level changes (e.g. Zachos, Dickens & Zeebe, 2008) led to the formation of many sedimentary basins in Japan and the preservation of continuous fossil records after the early Miocene period. However, little is known regarding the pre-Oligocene (Palaeogene) fossil assemblages because of the limited sedimentological record. The lifespan of ostracods (Crustacea) does not include a planktonic larval stage (Horne, Cohen & Martens, 2002). The abundantly preserved shells and limited environmental and trans-oceanic distribution capabilities of these organisms have been widely used to reconstruct palaeoenvironments of basins and infer the palaeobiogeography of animals. Previous studies have focused on clarifying ostracod assemblages in Japan from the early–middle Miocene period (Ishizaki, 1963, 1966; Yajima, 1988, 1992; Irizuki & Matsubara, 1994, 1995; Irizuki *et al*. 1998, 2004; Tanaka *et al*. 2002, 2013; Irizuki, 2003; Tanaka, 2003; Tanaka, Tsukawaki & Ooji, 2004; Tanaka & Nomura, 2009; Matsuura, Irizuki & Hayashi, 2013; Tanaka, Nomura & Hasegawa, 2012). However, only seven studies have reported a Palaeogene ostracod assemblage in Japan (Yamaguchi, 2004, 2006; Yamaguchi, Matsubara & Kamiya, 2005; Yamaguchi, Nagao & Kamiya, 2006;

---

†Author for correspondence: gengo@staff.kanazawa-u.ac.jp

Yamaguchi & Kamiya, 2007, 2009; Yamaguchi & Kurita, 2008). Furthermore, no reports have described Palaeogene coastal-estuarine ostracod assemblages in Japan or East Asia. These coastal-estuarine ostracods are very important with respect to the speciation and biogeographic distribution of marine animals because, unlike many other littoral and bathyal ostracods, the true habitats of coastal-estuarine ostracods are restricted to embayments (Abe, 1988).

Palaeogene fossiliferous deposits are widely distributed around northern Kyushu Island, Japan (Nagao, 1926*a*–*e*, 1927, 1928*a*, *b*; Matsushita, 1949; Takai & Satoh, 1982; Takai, Bojo & Harada, 1997); recently compiled chronostratigraphic studies (see fig. 8 of Yamaguchi, Tanaka & Nishi, 2008) have been based on molluscan assemblages (Mizuno, 1962*a*, *b*, 1963, 1964; Matsubara & Ugai, 2006), transgression and regression based on sedimentological studies (Sakai, 1993), planktonic foraminifers (Ibaraki, 1994; Yamaguchi, Tanaka & Nishi, 2008) and calcareous nanofossils (Okada, 1992; Yamaguchi, Tanaka & Nishi, 2008). The Amakusa area (Fig. 1) covers the longest and oldest Palaeogene deposits in Kyushu; these range in age from early Eocene (*c.* 49 Ma) to late Eocene (*c.* 36 Ma) (see fig. 8 of Yamaguchi, Tanaka & Nishi, 2008; Miyake *et al.* 2016). In particular, during early–middle Eocene time (*c.* 49–45 Ma) successive floodplain to deep-sea marine deposits were only distributed on Amakusa Kamishima Island, providing the best exposure for the study of coastal-estuarine assemblages. In the study area, the early–middle Eocene Miroku Group overlaps with the Late Cretaceous Himenoura Group as a result of stratigraphic unconformity or fault contact (Fig. 1c). The Miroku Group can be subdivided into the Akasaki Formation and the Shiratake Formation, and is covered by the Kyoragi Formation. The thicknesses of the Akasaki and Shiratake formations are 120–220 m and *c.* 190 m, respectively (Inoue, 1962).

The study area is located *c.* 700 m NE of Sengan-san Mountain (Fig. 1), with continuous exposure of the uppermost layer of the Akasaki Formation to the lowermost layer of the Shiratake Formation (Fig. 2). Furthermore, this section provides a record from the brackish tidal-flat environment to the shallow-sea environment, according to sedimentary structures and molluscan assemblages (Tanaka, Kondo & Tashiro, 1997).

2. Materials and methods

Six ostracod materials were collected from a study area near the Sengan-san Mountain, Amakusa Kamisima Island, Kyushu, Japan. A total of 233 ostracod specimens were acquired from *c.* 800 g of consolidated muddy-silt via the sodium tetraphenyl borate method (Yasuda, Takayanagi & Hasegawa, 1985). Water was used to wash the residues over a 16-mesh (1 mm) sieve and subsequent attached 120-mesh (125 µm) sieve; the residues were then collected in a beaker and dried in an oven at 80 °C for 2 days, selected under a binocular microscope (SZH-10; Olympus Corp., Tokyo, Japan) at ×30 magnification and stored on faunal slides. Uncoated ostracod specimens were analysed and imaged using a microscope (TM-1000; Hitachi Corp., Tokyo, Japan) under a low vacuum at Aitsu Marine Station, Center for Marine Environment Studies, Kumamoto University, Japan.

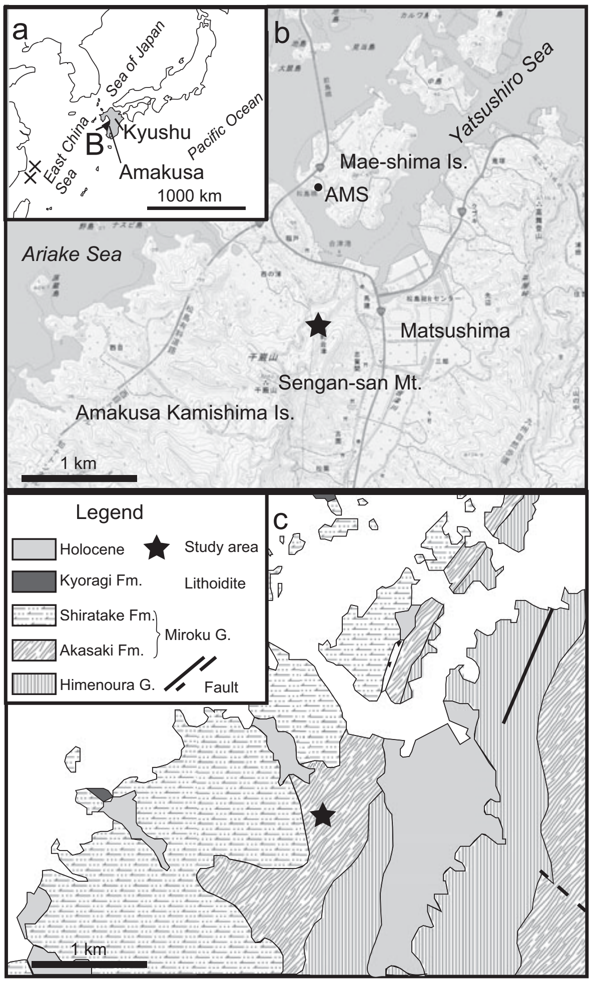

Figure 1. Location of the study area in (a, b) Matsushima town, Amakusa Kamishima Island and Kamiamakusa city, Kyushu Island, Japan. (c) Geological map of (b) based on a Misumi–Kyoragi–Minamata surface geological map (1:50,000) generated by Toyohara & Hase (1991). Two crosses in the East China Sea (a) indicate the borehole locations described by Yang, Chen & Wang (1990). AMS – Aitsu Marine Station of Kumamoto University.

3. Palaeoecology and palaeoenvironment

In terms of numbers, the ostracod assemblage is dominated by *Neomonoceratina iwasakii* sp. nov., the second characteristic species *Paijenborchella amakusensis* sp. nov. and *Parakrithella* sp., as well as the less-abundant *Propontocypris* sp. The ostracod assemblage occurred together with that of the abundant benthic foraminifer *Ammonia* cf. *beccarii* (Fig. 2c; identified by R. Nomura of Shimane University), mollusca *Terebralia*? sp. and Charophyceae oogonium, suggesting

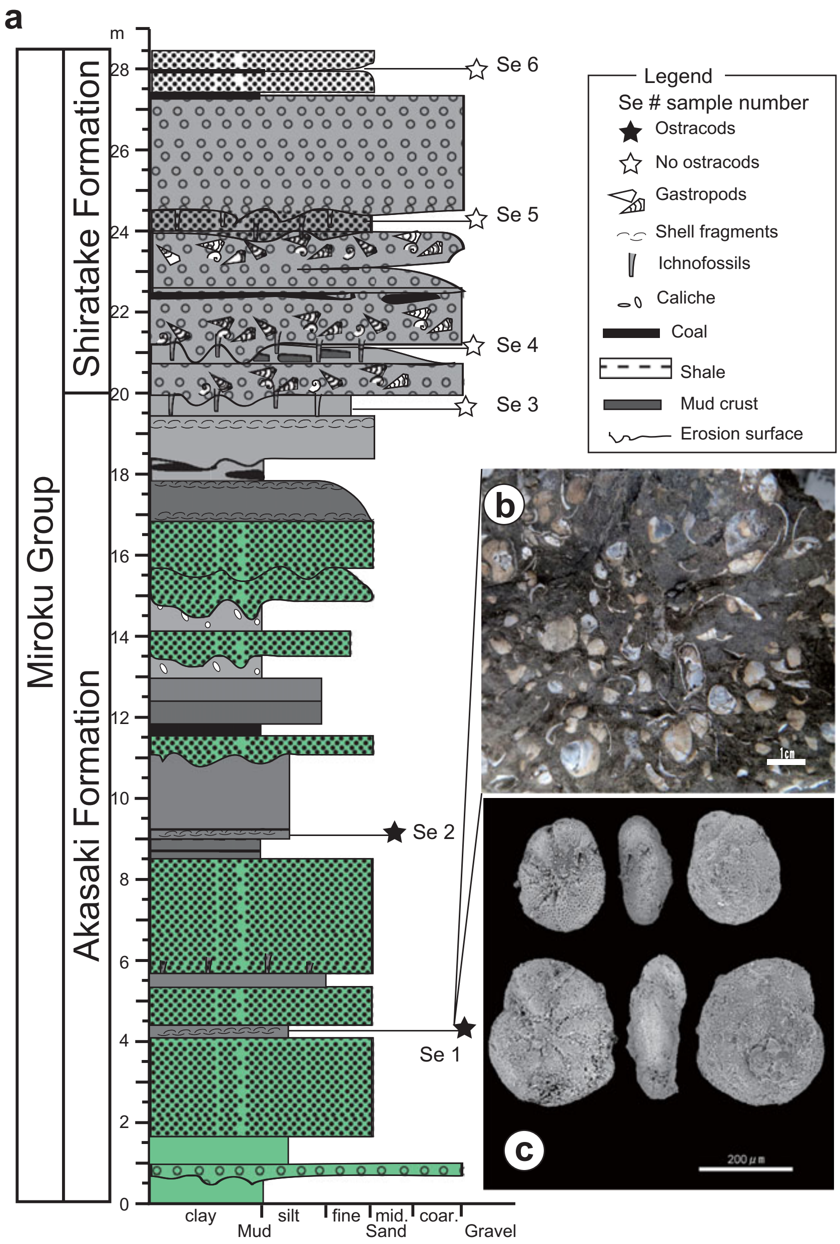

Figure 2. (Colour online) Columnar section of the study area (asterisk in Fig. 1). (a) Detail from columnar section showing ostracod collected horizon (Se-number). (b) Many ostracods were extracted from Se 1 sample which contained many bivalves (mostly *Pitar* and some *Anomia* species) and (c) benthic foraminifer (*Ammonia* cf. *beccarii*).

an coastal-estuarine environment with inflowing freshwater. However, different species of *Paijenborchella* (Liu, 1989) and *Propontocypris* (*Paracypris* spp. described by Liu, 1989; Yamaguchi, 2006; considered to belong to *Propontocypris* from the anterior and dorsal outlines) have been reported from marine depositional facies in other Palaeogene localities. The extant species *Parakritherella pseudadonta* (Hanai, 1959) lives at depths of 0–17.5 m and attaches to algae or burrows in substrate (Tanaka, 2016). Ostracods have also been discovered in muddy siltstone which contains abundant molluscs such as *Pitar* sp. and some *Anomia* sp. (Fig. 2b). Extant genera of *Pitar* and *Anomia* live in marine environments (Tanaka, Kondo & Tashiro, 1997). No planktonic foraminifers were identified on the ostracod-bearing horizon (Se 1) of the Akasaki Formation, suggesting that the depositional environment was not an open-sea environment. Moreover, the ostracod-containing muddy siltstone was sandwiched between massive greenish sandstone layers indicative of river deposits. Furthermore, most ostracod specimens were juvenile with carapaces, indicating rapid burial *in situ* or near their original microhabitats (Whatley, 1983, 1988). Liu (1989) reported *Neomonoceratina donghaiensis* from the Paleocene Lingfeng Formation along with the genera *Cytherella* and *Krithe*, and suggested a littoral to neritic depositional environment with planktonic foraminifers. Carbonel & Hoibian (1988) discussed the relationship between ornamentation development on extant *Neomonoceratina* spp. and the influence of deltaic freshwater, and concluded that poorly ornamented species inhabit brackish inlet areas of the deltaic front, whereas strongly ornamented species flourish in the marine coastal zone of the deltaic front. In summary, the ostracod assemblage of the Akasaki Formation was determined to be unique, with a habitat in the euryhaline environment of a closed coastal estuary.

4. Palaeobiogeography of coastal-estuarine ostracod assemblages during Eocene time

Many papers have described Eocene ostracods worldwide; however, few studies have evaluated coastal-estuarine ostracod assemblages because of the limited number of depositional environments relative to normal marine environments. Including this study, Eocene coastal-estuarine ostracod assemblages in 36 localities worldwide have been reported (Table 1). Of the 36 localities, 13 localities (localities 1–13) were of early Eocene age, 13 localities of middle Eocene age (14 – 26) and 10 localities (27–36) were of late Eocene age (Table 1).

The Eocene ostracod assemblages from coastal-estuarine environments listed in Table 1 are characterized by dominant occurrences of one or more species similar to extant ostracods living in estuary (e.g. Athersuch, Horne & Whittaker, 1989; Ikeya & Shiozaki, 1993; Tanaka, Seto & Takayasu, 1998). Estuarine environments usually have highly varying salinities, pH values and levels of dissolved oxygen over any given year (Tanaka, Seto & Takayasu, 1998). Generally, many ostracods have strong tolerances of environmental change (Williams *et al.* 2015), and estuarine environments receive much organic matter from the land (e.g. Irizuki, Matsubara & Matsumoto, 2005). These combined facts mean that the estuary is one of the most preferable places for ostracods to escape predators and find food. Based on their strong tolerance of environmental change, all taxa seem to have an equal potential of invading the estuarine environments from the sea and/or river. If this hypothesis is true, the characteristic inner-bay ostracods are different from those of (palaeo-) estuaries.

To test this hypothesis, we investigated early, middle and late Eocene ostracod palaeozoogeography (Fig. 3). Five early Eocene ostracod provinces have been recognized (Fig. 3a): (1) North America and Europe, characterized by *Haplocytheridea* and *Brachycythere*; (2) Middle East, dominated by *Neocyprideis* and *Stigmatocythere*; (3) Central Asia, which consists of *Cytheridea*, *Neocyprideis* and *Echinocythereis*; (4) Indian subcontinent, represented by *Cytheridea* and *Alocopocythere*; and (5) East Asia, which consists of *Neomonoceratina* and *Paijenborchella*. The genus *Haplocytheridea* is widely distributed along the eastern coast of the USA and across the Atlantic Ocean in Europe; in contrast, the genus *Neocyprideis* is distributed in the Tethys (the Middle East and the Central Asia provinces). Other genera are observed sporadically in limited regions, such as *Brachycythere*, *Echinocythereis*, *Stigmatocythere*, *Alocopocythere*, *Neomonoceratina* and *Paijenborchella*. Even for widely distributed species such as *Haplocytheridea*, differences in the species are observed between the eastern coast of USA and the Europe, indicating that the genus *Haplocytheridea* migrated independently between America and Europe towards coastal-estuaries until early Eocene time from one common ancestor. On the other hand, the eastern margin of the Eurasian continent was already isolated (along with the Tethys) by the Indochina blocks that connected the Eurasian continent (Fig. 3a). Furthermore, the genus *Neomonoceratina* was reported in lower Paleocene (66.0–61.6 Ma) sediments from the eastern coast of India (Khosla & Nagori, 2002), the middle Paleocene Lingfeng Formation in borehole cores from the East China Sea (Liu, 1989) and the lower Eocene Crescent Formation in SW USA (Yamaguchi & Goedert, 2009), which represent deposits from marine environments. The oldest fossil record of *Neomonoceratina*, discovered in India, is a closely related common ancestor of the *Neomonoceratina*-*Spinileberis* and *Parakrithella* clades according to molecular phylogenetic estimations (Clarke & Boyd, 2015) (52.97 Ma by penalized likelihood in r8s software; 96.71–38.89 Ma, mean: 67.80 Ma by mean path length implemented in PaThd8 software; 106.73–25.83 Ma, mean: 66.28 Ma by Bayesian analysis). Although more data concerning pre-Eocene ostracods are needed, existing data indicate that *Neomonoceratina* spp. originated on the Indian subcontinent during the early Paleocene period, along with the northern drift of the Indian subcontinent; subsequently, these species diversified west and east with the equatorial current and counter-current via the Tethys and reached the eastern margin of the Eurasian continent among the various eastwards-migrating species, where one species ultimately adapted to the coastal-estuarine environment. Notably, the coastal-estuarine ostracod assemblage of the eastern margin of the Eurasian continent differs completely from that of the Tethys during the Eocene period. Furthermore, it is important that the genus *Paijenborchiella* already existed in the normal early Eocene marine environment of the Europe (Keij, 1957). The genus *Paijenborchella* could not be characteristic coastal-estuarine species in Europe, because the coastal-estuarine environments were already occupied by *Haplocytheridea*.

During middle Eocene time, although ostracods are not reported from East Asia, at least six other ostracod provinces are recognized (Fig. 3b): (1) North America, characterized by the early Eocene assemblage *Haplocytheridea*, *Brachycythere* plus *Echinocythereis*; (2) Europe, dominated by the early Eocene characteristic genus *Haplocytheridea* and newcomer *Novocypris*; (3) NE Africa, which consists of newcomers (different genera from early Eocene time in this area) *Costa*, *Paracosta*, *Novocypris*, *Limburgia* and *Ruggieria*; (4) Middle East, represented by the genus *Echinocythereis* and newcomer *Haplocytheridea*; (5) East Africa, comprising two genera of the early Eocene Middle East

Table 1. Characteristic Eocene ostracods from around the world

Locality	Age	Formation or group	Characteristic genus	References
1. South Carolina, USA	Early Eocene	Black Mingo Formation	*Brachycythere*, *Haplocytheridea*	Pooser (1965)
2. Alabama, USA	Early Eocene	Nanafalia Formation	*Brachycythere*, *Haplocytheridea*	Pooser (1965)
2. Alabama, USA	Early Eocene	Sabine Group	*Brachycythere*, *Haplocytheridea*	Pooser (1965)
3. Georgia, USA	Early Eocene	Hatchetigbee Formation	*Brachycythere*, *Haplocytheridea*	Pooser (1965)
4. Louisiana, USA	Early Eocene	Wilcox Gr.	*Brachycythere*	Howe & Garrett (1934)
5. North Carolina, USA	Early Eocene	–	*Brachycythere*	Pooser (1965)
6. Eastern USA	Early Eocene	–	*Haplocytheridea*	Keen (1977*a*)
7. Almelo, Netherlands	Early Eocene	Boring core	*Haplocytheridea*	Keij (1957)
8. Belgium	Early Eocene	–	*Haplocytheridea*	Keij (1957)
9. Muscat, Oman	Early Eocene	Rusayl Shale Formation	*Neocyprideis*, *Stigmatocythere*	Keen & Racey (1991)
10. Tarim Basin, China	Early Eocene	Upper Qimgen Formation	*Neocyprideis*, *Cytheridea*, *Echinocythereis*	Yang, Jiang & Lin (1995); Wan *et al*. (2014)
11. Sulaiman Range, Pakistan	Early Eocene	Ghazij Formation	*Neocyprideis*	Siddiqui (2000)
12. Surat, India	Early Eocene	Cambay Shale Formation	*Neocyprideis*, *Alocopocythere*	Bhandari, Singh & Rana (2005)
13. Kyushu, Japan	Early Eocene	Akasaki Formation	*Neomonoceratina*, *Paijenborchella*	This study
14. South Carolina, USA	Middle Eocene	Warley Hill Formation	*Brachycythere*, *Haplocytheridea*, *Echinocythereis*	Pooser (1965)
14. South Carolina, USA	Middle Eocene	McBean Formation	*Brachycythere*, *Haplocytheridea*, *Echinocythereis*	Pooser (1965)
15. Texas, USA	Middle Eocene	Weches Formation	*Brachycythere*, *Haplocytheridea*	Stephenson (1946)
16. Alabama, USA	Middle Eocene	Gosport Formation	*Brachycythere*, *Haplocytheridea*	Blake (1950)
17. Eastern USA	Middle Eocene	–	*Haplocytheridea*, *Echinocythereis*	Keen (1977*a*)
18. Isle of Wight, UK	Middle Eocene	Barton Clay Formation	*Haplocytheridea*	Keij (1957); Keen (1977*b*); Lord, Whittaker & King (2009)
19. Almelo, Netherlands	Middle Eocene	Boring core	*Haplocytheridea*	Keij (1957)
19. Delden, Netherlands	Middle Eocene	Boring core	*Haplocytheridea*	Keij (1957)
20. Belgium	Middle Eocene	–	*Haplocytheridea*	Keij (1957)
21. Paris Basin, France	Middle Eocene	–	*Haplocytheridea*, *Novocypris*	Keij (1957)
22. Sakarya Region, Turkey	Middle–Late Eocene	Halidiye Formation	*Neocyprideis*, *Cladarocythere*, *Loxoconcha*	Şafak, Ocakoğ Lu & Açikalm (2015)
23. Eastern Desert, Egypt	Middle Eocene	Gehannam Formation	*Costa*, *LimburginaCosta*, *Limburgina*	Elewa, Omar & Dakrory (1998)
24. Qattamiya, Egypt	Middle Eocene	Observatory & Qurn Formations	*Paracosta*, *Ruggieria*, *Novocypris*	Shahin, El Halaby & El Baz (2008)
25. Northern Somalia	Middle Eocene	Karkar Formation	*Neocyprideis*, *Stigmatocythere*, *Cyamocytheridea*	Bassiouni & Luger (1996); Elewa, Luger & Bassiouni (2001)
26. Shimla Hills, India	Middle Eocene	Subathu Formation	*Neocyprideis*, *Alocopocythere*	Bhatia & Bagi (1991)
27. Alabama, USA	Late Eocene	Jackson Group	*Brachycythere*, *Haplocytheridea*, *Echinocythereis*	Krutak (1961)
28. Eastern USA	Late Eocene	–	*Haplocytheridea*, *Echinocythereis*	Keen (1977*a*)
29. Hampshire Basin, UK	Late Eocene	Headon Hill Formation	*Neocyprideis*, *Cytheromorpha*	Keen (1978); Lord, Whittaker & King (2009)
30. Belgium	Late Eocene	–	*Haplocytheridea*	Keij (1957)
31. Germany	Late Eocene	–	*Haplocytheridea*	Keij (1957)
32. Paris Basin, France	Late Eocene	–	*Haplocytheridea*	Keij (1957)
33. Tarim Basin, China	Late Eocene	Bashibulake Formation (II, III)	*Haplocytheridea*, *Ruggieria*	Yang, Jiang & Lin (1995); Wan *et al*. (2014)
34. Sulaiman Range, Pakistan	Late Eocene	Kirthar Formation	*Neocyprideis*	Siddiqui (2000)
35. Garo Hills, India	Late Eocene	Kopili Formation	*Alocopocythere*, *Eopaijenborchella*	Bhandari (1992)
36. Magway, Myanmar	Late Eocene	Yaw Formation	*Bicornucythere*	Yamaguchi *et al*. (2015)

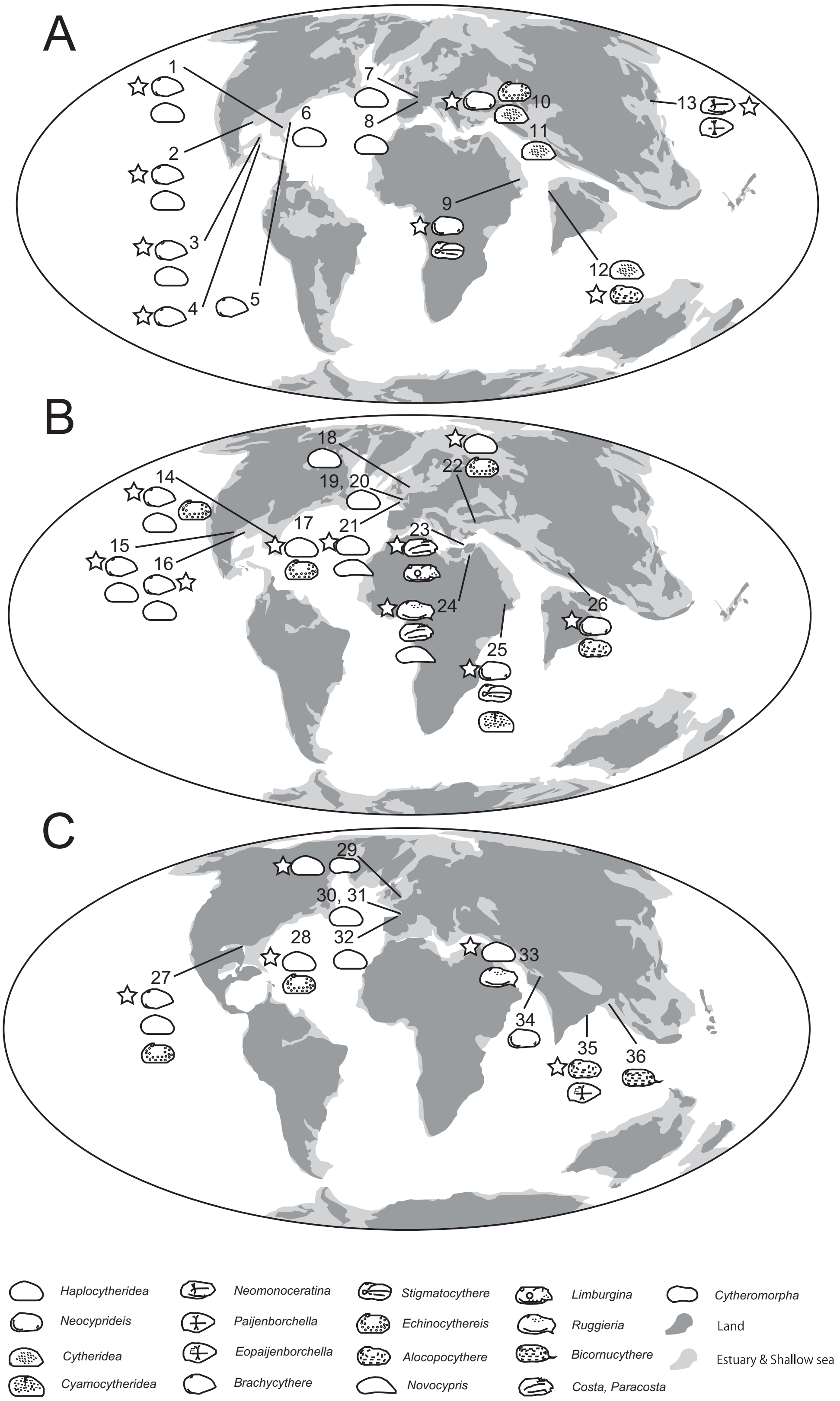

Figure 3. (a–c) Palaeogeographical distribution of the Eocene estuarine ostracods. (a) Early Eocene (Ypresian, 52.2 Ma). (b) Late Middle Eocene (Bartonian, 38.8 Ma). (c) Late Eocene (Priabonian, 35.6 Ma). This palaeogeographical map come from PALEOMAP Project (Scotese, 2013*a*–*c*). Asterisks show main genera in each locality. See Table 1 for details of localities 1–36.

province, namely *Neocyprideis* and *Stigmatocythere* and also newcomer *Cyamocytheridea*; and (6) India, represented by *Alocopocythere* from early Eocene time and newcomer *Neocyprideis*.

During middle Eocene time, different species of genus *Novocypris* appeared in the coastal-estuarine environments of Europe and NE Africa. *Haplocytheridea* had already appeared in the early Eocene coastal-estuarine environments of North America and Europe, indicating that their descendant migrated eastwards (the Middle East province) until middle Eocene time. McKenzie (1967) suggested that, during the early Tertiary period, the Tethys acted as a latitudinal E–W-aligned corridor for marine ostracod genera; the results support this hypothesis. Many genera which appeared in the coastal-estuarine environments of the Tethys region (North Africa, Middle East and East Africa provinces), namely *Costa*, *Paracosta*, *Novocypris*, *Limburgia*, *Ruggieria*, and *Cyamocytheridea*, are especially interesting when considering the 'hotspot' (area of highest number of newly emerging genera) of the middle Eocene coastal-estuarine ostracods.

The late Eocene coastal-estuarine ostracod provinces, excluding East Asia from which ostracods have not been reported, are divided into at least six ostracod provinces (Fig. 3c): (1) North America, from which the same genera as the middle Eocene assemblage (*Haplocytheridea*, *Brachycythere* and *Echinocythereis*) have been reported; (2) Europe, which is also dominated by the middle Eocene characteristic genus *Haplocytheridea* and newcomer *Cytheromorpha*; (3) Middle East, which is represented by the middle Eocene genus *Haplocytheridea* and *Ruggieria*; (4) West India, characterized by the middle Eocene genera *Neocyprideis*; (5) East India, represented by the middle Eocene genus *Alocopocythere* and newcomer *Eopaijenborchella*; and (6) Myanmar, characterized by the newcomer *Bicornucythere*. The genus of *Bicornucythere* of late Eocene age from Myanmar is the oldest fossil record in the world showing adaption to the coastal-estuarine environment (Yamaguchi *et al.* 2015). With the genus *Bicornucythere*, Yamaguchi *et al.* (2015) reported *Cytheromorpha*? sp. from the same material. The genus *Cytheromorpha* appeared in coastal-estuarine environments in Europe (Keen, 1978; Lord, Whittaker & King, 2009) and Myanmar (Yamaguchi *et al.* 2015) in middle Eocene time. The genus *Cytheromorpha* is recorded in marine deposits of pre-Eocene age from Trinidad (Van den Bold, 1957) and Europe (Ozsvart, 1999) and in coastal-estuarine environments of early Paleocene age from India (Khosla & Nagori, 2002), indicating that they independently migrated from normal marine environments in India and migrated east- and westwards via the E-W-aligned corridor of the Tethys (McKenzie, 1967). To summarize, many genera adapted to coastal-estuarine environments in the Tethys and migrated east- and westwards. The Eocene period is characterized by global warming (e.g. Zachos, Dickens & Zeebe, 2008), and many estuarine environments were formed around the world (Fig. 4) during this time.

5. Changes in the post-Oligocene estuarine ostracod assemblage in the Far East

To date, one report of ostracod assemblages has indicated the presence of an estuarine environment in the Far East during Oligocene time. Wang *et al.* (1985) reported on the early–late Oligocene coastal-brackish-water ostracod *Chinocythere* from the coast of China (Fig. 5a), currently the only such report from China.

With the formation of the Sea of Japan after the (at the latest) late Oligocene period in conjunction with regional tectonic events and global sea-level changes (e.g. Zachos, Dickens & Zeebe, 2008) many sedimentary basins were formed in Japan, allowing the preservation of continuous fossil records after the early Miocene period. Early Miocene estuarine ostracod assemblages are composed of completely different genera than those found in both the Eocene (*Neomonoceratina*, *Paijenborchella*) and the Oligocene (*Chinocythere*) assemblage, and contain some endemic genera that are only found in the Far East (Fig. 5b). Among these, *Sinocytheridea* is widely distributed from the northern and southern margins of the Far East; however, other genera are only reported in limited areas (Fig. 5b). Although *Sinocytheridea* is the most ubiquitous genus in brackish-water conditions from the post-Miocene to Recent periods along the coast of China and Taiwan (Fig. 5d–f), species of this genus do not currently inhabit the mainland of Japan (Fig. 5f, Table 2). Compared with other regions, *Sinocytheridea* is also typical of the euryhaline species in this region where *Cyprideis* species flourish under current euryhaline environments (Zhao & Whatley, 1992). The early Miocene period (*c.* 20 Ma) is one of global cooling (Zachos, Dickens & Zeebe, 2008); *Sinocytheridea* widely occupied and adapted under the cool coastal-estuarine environment of the Far East.

Spinileberis first appeared during the middle Miocene period, and was broadly distributed throughout the Far East (Fig. 5c). The geographical distribution and fossil record of the genus *Spinileberis* is limited to the Far East (Tanaka, Kuroda & Ikeya, 2011). The characteristic genus of the Far East estuarine environment therefore shifted from *Sinocytheridea* to *Spinileberis* during the middle Miocene period, and possibly appeared in many (coastal-) estuarine environments due to global warming (Mid-Miocene Climatic Optimum) and the formation of many archipelagos (Japan) in the Far East (Fig. 4).

The oldest fossil record of the genus *Bicornucythere*, which is of late Miocene age, was found in Taiwan (Table 2). This genus originated in South Asia during late Eocene time (Yamaguchi *et al.* 2015) and possibly migrated toward the Far East along the coast of the Indochina Peninsula.

The Pliocene climate experienced a drastic change from warm to cool (Fig. 4) and many new coastal-estuarine ostracods, such as *Hemikrithe*, *Neomonoceratina* and *Cytheromorpha*, appeared in the Far East; *Spinileberis, Bicornucythere* and *Sinocytheridea* already existed there (Fig. 5d). Among these, *Hemikrithe* and *Neomonoceratina* are distributed in the southern part of the Far East and the coast

Table 2. Characteristic estuarine ostracod genera in the Far East after Oligocene time

Locality	Age	Formation or group	Characteristic genus	Reference
1. Beibu Gulf Basin, China	Late Oligocene	Weizhou Formation	*Chinocythere*	Wang *et al.* (1985)
2. Bohai Sea, China	Late Oligocene	Dongying Formation	*Chinocythere*	Wang *et al.* (1985)
3. South China Sea	Early Miocene		*Sinocytheridea*, *Sinocythere*	Wang & Zhao (1991)
4. Beibu Gulf Basin, China	Early Miocene	Xiayang Formation	*Puriana*?, *Psammocythere Puriana*?, *Psammocythere*	Wang *et al.* (1985)
5. Central Japan	Early Miocene	Toyama Formation	*Pectocythere*, *Sinocytheridea*?, Pectocythere, Sinocytheridea?	Irizuki *et al.* (2004)
6. Beibu Gulf Basin, China	Middle Miocene	Jiaowei Formation	*Spinileberis*	Wang *et al.* (1985)
7. East Korea	Middle Miocene	Chunbuk Conglomerate Formation	*Pectocythere*, *Acanthocythereis*, *Spinileberis*	Yun *et al.* (1990)
8. SW Japan	Middle Miocene	Yoshino Formation	*Spinileberis*, *Trachyleberis*	Yajima (1988)
9. NE Japan	Late Miocene	Kubota Formation	*Spinileberis*	Yamaguchi & Hayashi (2001)
10. Beibu Gulf Basin, China	Pliocene	Wanglougang Formation	*Hemikrithe*, *Neomonoceratina*	Wang *et al.* (1985)
11. Taiwan	Late Miocene – Pliocene	Kueichulin Formation	*Neomonoceratina*, *Bicornucythere*, *Sinocytheridea*	Hu & Tao (2008)
11. Taiwan	Pliocene	Chinshui Shale	*Neomonoceratina*, *Bicornucythere*, *Spinileberis*	Hu & Tao (2008)
11. Taiwan	Pliocene	Yunshuichi Formation	*Neomonoceratina*, *Bicornucythere*, *Sinocytheridea*	Hu & Tao (2008)
11. Taiwan	Late Pliocene	Tunghsiao Formation	*Neomonoceratina*, *Bicornucythere*	Hu & Cheng (1977); Hu & Tao (2008)
11. Taiwan	Plio-Pleistocene	Liushuang Formation	*Neomonoceratina*, *Bicornucythere*, *Sinocytheridea*	Hu & Yeh (1978)
11. Taiwan	Plio-Pleistocene	Liushuang Formation	*Neomonoceratina*, *Bicornucythere*, *Sinocytheridea*	Hu & Yeh (1978)
12. Okinawa Island	Plio-Pleistocene	Guga Formation	*Spinileberis*, *Neomonoceratina*	Tabuki (2001)
13. Jiangsu, China	Pliocene	Yancheng Group	*Neomonoceratina*, *Spinileberis*, *Sinocytheridea*	Hou *et al.* (1982)
14. Cheju Is, Korea	Plio-Pleistocene	Sogwipo Formation	*Sinocytheridea*, *Cyrheromorpha*, *Bicornucythere*	Lee & Paik (1992)
15. Central Japan	Late Pliocene	Hijikata Formation	*Bicornucythere*, *Trachyleberis*	Nakao, Tanaka & Yamada (2001)
16. Taiwan	Pleistocene	Chiting Formation	*Neomonoceratina*, *Bicornucythere*, *Sinocytheridea*	Hu & Tao (2008)
16. Taiwan	Pleistocene	Liuchungchi Formation	*Neomonoceratina*, *Bicornucythere*, *Sinocytheridea*, *Cytheromorpha*	Hu & Tao (2008)
17. Kyushu, Japan	Pleistocene	Ogushi Formation	*Bicornucythere*, *Neomonoceratina*	Kawano *et al.* (2011)
18. Central Japan	Pleistocene	Noma Formation	*Spinileberis*, *Bicornucythere*, *Neomonoceratina*, *Cytheromorpha*	Irizuki & Hosoyama (2000)
18. Central Japan	Middle Pleistocene	Hamamatsu Formation	*Spinileberis*, *Bicornucythere*, *Neomonoceratina*	Irizuki & Seto (2004)
18. Central Japan	Late Pleistocene	Furuya Mud	*Spinileberis*, *Bicornucythere*, *Neomonoceratina*, *Cytheromorpha*	Ishizaki & Kato (1978)
18. Central Japan	Late Pleistocene	Kamiiwahashi Formation	*Spinileberis*, *Bicornucythere*, *Neomonoceratina*, *Cytheromorpha*	Yajima (1978, 1982)
19. North Vietnam	Recent		*Neomonoceratina*, *Bicornucythere*, *Sinocytheridea*	Tanaka, Komatsu & Phong (2009)
20. South China Sea	Recent		*Sinocytheridea*, *Stigmatocythere*, *Neomonoceratina*, *Bicornucythere*	Cai & Chen (1987); Zheng *et al.* (1994)
21. Hong Kong, China	Holocene	Borehole core	*Sinocytheridea*, *Pistocythereis*, *Bicornucythere*	Wang & Zhang (1987)
21. Fujian, S China	Holocene	Borehole core	*Bicornucythere*, *Spinileberis*, *Cytheromorpha*, *Sinocythere*	Zheng (1987)
22. Kaoshun, Taiwan	Recent		*Sinocytheridea*, *Paijenborchella*	Hu & Tao (2008)
23. Coast of China	Recent		*Sinocytheridea*, *Spinileberis*, *Neomonoceratina*	Zhao (1987); Zhao & Wang (1988*a*); Wang & Zhao (1991)
24. East China Sea	Recent		*Sinocytheridea*, *Bicornucythere*, *Pistocythereis*, *Neomonoceratina*	Wang *et al.* (1985)
25. Yellow Sea, China	Recent		*Bicornucythere*, *Pistocythereis*, *Sinocytheridea*, *Neomonoceratina*	Zhao (1984); Zhou *et al.* (1996)
26. Bohai Sea, China	Recent		*Sinocytheridea*, *Neomonoceratina*, *Spinileberis*	Wang *et al.* (1985)
27. Kyushu, Japan	Holocene	Ariake Clay	*Spinileberis*, *Sinocytheridea*, *Bicornucythere*	Iwasaki (1992)
28. SW Japan	Holocene	Borehole core	*Spinileberis*, *Bicornucythere*, *Pistocythereis*	Irizuki *et al.* (2001)
28. SW Japan	Recent		*Bicornucythere*, *Spinileberis*, *Cytheromorpha*	Ikeya & Shiozaki (1993)
29. Central Japan	Holocene	Borehole core	*Spinileberis*, *Bicornucythere*, *Cytheromorpha*, *Trachyleberis*	Sasaki *et al.* (2007)
30. NE Japan	Recent		*Bicornucythere*, *Spinileberis*, *Cytheromorpha*	Ikeya & Itoh (1991)

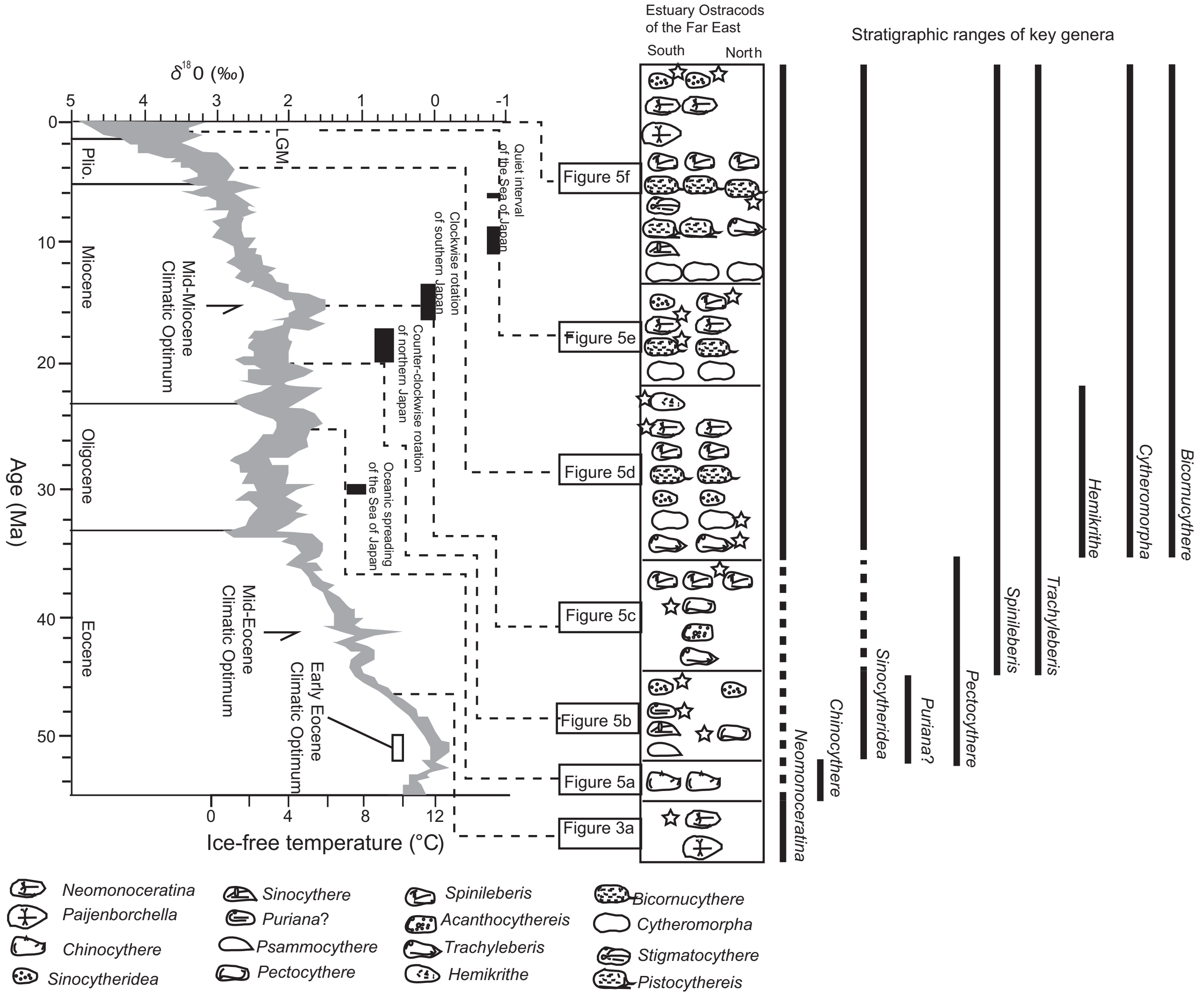

Figure 4. Global climate changes according to deep-sea benthic foraminifars (grey curve) after the Eocene period (Zachos, Dickens & Zeebe, 2008), regional tectonic events in the Far East (Jolivet, Tamaki & Fournier, 1994) and changes in the characteristic estuarine ostracod genera. Asterisks show main genera in each locality.

of China (Fig. 5d); however, the genus *Cytheromorpha* tends to be distributed in the northern area (Fig. 5d). Furthermore, the oldest fossil record of *Cytheromorpha* is reported from the Plio-Pleistocene Sogwipo Formation, which was deposited under cold-water influence (Lee & Paik, 1992).

During the Last Glacial Maximum (LGM, *c.* 1.8 Ma), only five ostracods remained in the coastal-estuarine environment of the Far East (Figs 4, 5e); other Pliocene species disappeared from this region. After the LGM, the diversity of the coastal-estuary ostracods in the Far East increased with the appearance of many coastal-estuary environments as a result of global warming and sea-level rise (Figs 4, 5f). In particular, the number of genera characterizing the Recent coastal-estuary ostracod assemblages tends to increase for lower latitudes (i.e. towards the equator). Two extant ostracods (*Neomonoceratina delicata* and *Sinocytheridea impressa*) are widely distributed throughout the mud to sandy mud areas of SE Asian and south Chinese estuaries (Zhao & Whatley, 1989; Dewi, 1997; Tanaka, Komatsu & Phong, 2009; Zhao & Wang, 1988*b*). However, fresh shell specimens of the two genera have not been reported in the mainland of Japan except for the west coast of Kyushu Island; the population of *Neomonoceratina* and *Sinocytheridea* therefore seemed to disappear from Japan during the Holocene Epoch (Fig. 5, Table 2).

The oldest fossil record of coastal-estuarine ostracods such as *Neomonoceratina*, *Chinocythere*, *Sinocytheridea* and *Spinileberis* were found in the Far East and their Recent distributions are also restricted to the area spanning the Far East to South Asia, indicating that the four genera first invaded the coastal-estuarine environment in the Far East. The genus *Bicornucythere* originated in South Asia and migrated to the Far East during late Miocene time. However, *Cytheromorpha* first appeared in the Plio-Pleistocene under cool environmental conditions. Coastal-estuarine *Cytheromorpha* has a continuous late Eocene – Recent

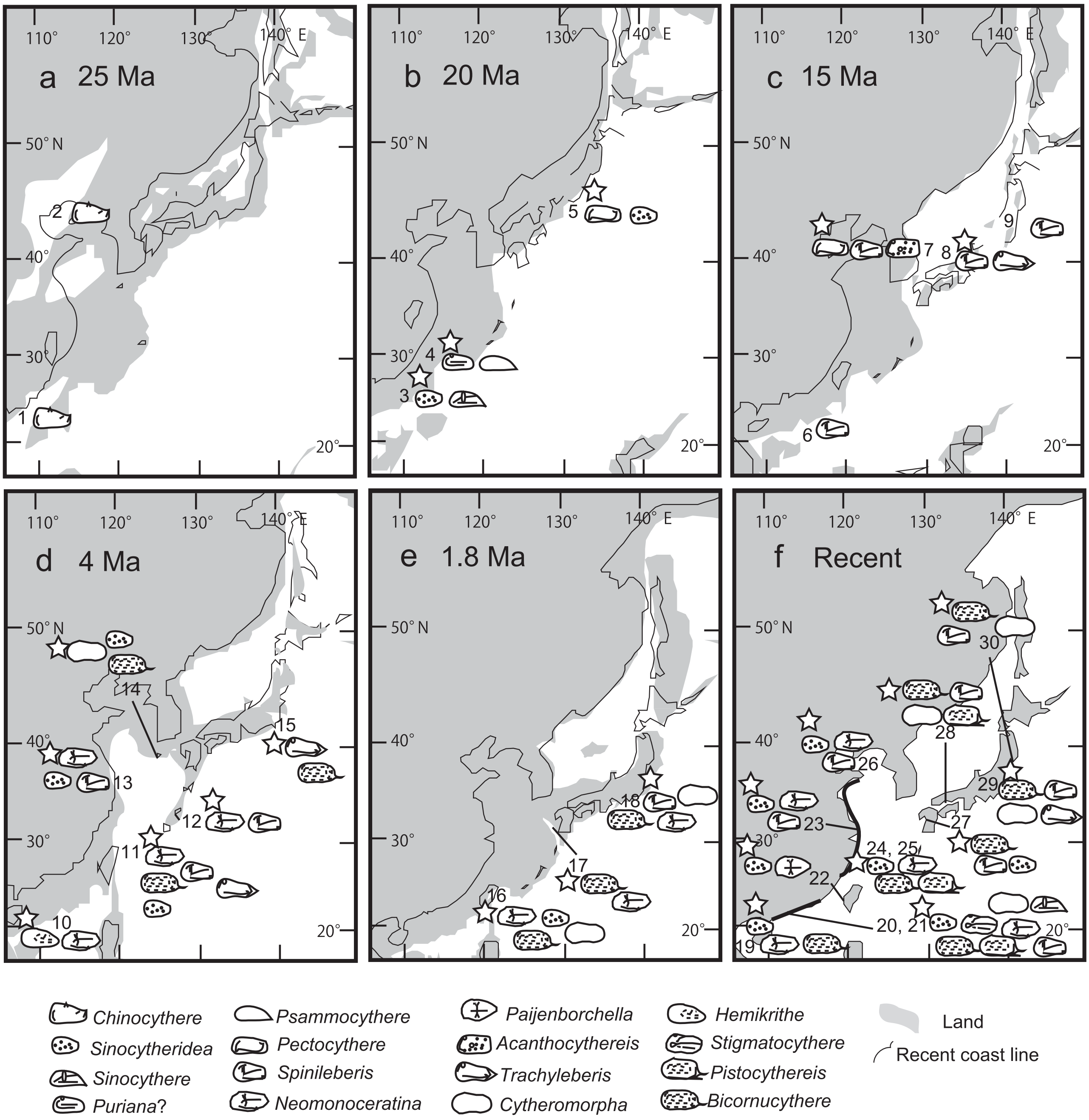

Figure 5. (a–f) Palaeogeographical distribution of estuarine ostracods in the Far East after Oligocene time. Palaeogeographical maps were downloaded from the online service of the Ocean Drilling Stratigraphic Network (http://www.odsn.de) and are also based on the findings of Jolivet, Tamaki & Fournier (1994). Pliocene map (d) is partly based on the data from Iijima & Tada (1990). See Table 2 for details of localities 1–30. Asterisks indicate main genera in each locality.

fossil record in North America and Europe (e.g. Keij, 1957; Swain, 1974; Gemery *et al*. 2017), suggesting that *Cytheromorpha* invaded from North America or Europe via the Arctic region. To summarize, even in cooler environmental conditions, new ostracods invaded and adapted to wider range of temperature such as *Sinocytheridea* and *Cytheromorpha*. Local geological history has also affected the geographical distribution of the coastal-estuarine ostracods.

6. Conclusions

Dark grey silty claystone samples containing *Pitar* and *Anomia* species from the uppermost layer of the Akasaki Formation (Miroku Group, Kyushu Island, Japan) also contained a *Neomonoceratina*-dominated ostracod assemblage. This, the first record of coastal-estuarine ostracods from the Eocene Epoch along the eastern margin of the Eurasian continent, reveals that a different estuarine ostracod assemblage flourished in this region before the Neogene Period.

Neomonoceratina species originated on the Indian subcontinent during early Paleocene time (or earlier) and, with the northern drift of the Indian subcontinent, later diversified west and east via the Tethys along the equatorial current and counter-current; eventually, one of the eastwards-migrating species reached the eastern margin of the Eurasian continent and adapted to the estuarine environment. Accordingly, the estuarine ostracod assemblage along the eastern margin of the Eurasian continent differs completely from that of the Tethys during the Eocene period.

After the Oligocene period, coastal-estuarine ostracod assemblages in the Far East shifted along with global sea-level changes and regional tectonic effects.

7. Systematic palaeontology (by Gengo Tanaka)

The classification and morphological terminology suggested by Horne, Cohen & Martens (2002) were followed here. Classification of the genera *Neomonoceratina* and *Paijenborchella* was conducted according to Benson *et al.* (1961) because of the subsequent detailed morphological analyses of these genera (Hanai, 1970). All specimens described here were collected from the uppermost part of the lower Eocene Ypresian, Akasaki Formation, Miroku Group (49.1 ± 0.4 Ma by Miyake *et al.* 2016).

All illustrated specimens have been deposited in the collections of the Goshoura Cretaceous Museum (GCM IVP number).

Class Ostracoda Latreille, 1802
Order Podocopida Müller, 1894
Family Schizocytheridae Howe, 1961 (in Benson *et al.* 1961)
Genus *Neomonoceratina* Kingma, 1948
Type species *Neomonoceratina columbiformis* Kingma, 1948
Neomonoceratina iwasakii sp. nov. (Fig. 6a–q)

Holotype. Carapace (GCM-IVP3495) Figure 6i–e

Derivation of name. Named after Professor Emeritus Yasuhide Iwasaki (Kumamoto University), a former head of the Aitsu Marine Station who studied ostracods from Kumamoto.

Type locality and horizon. Approximately 700 m NE of Sengan-san Mountain, Matsushima town, Kamiamakusa city, Kumamoto Prefecture, Kyushu, Japan (32° 30′ 51.5″ N; 130° 25′ 26.7″ E). A sample shown at Se 1 of Figure 2 comprised dark grey silty claystone with *Pitar* and *Anomia* spp. in the uppermost region of the Akasaki Formation, Miroku Group.

Material. A total of 196 specimens.

Diagnosis. Straight and posteriorly inclined dorsal margin is observed. Two murus extend from the anterodorsal to posterodorsal area, parallel from the anterior to posterior margins. Primary reticulation is visible at the posterior half. The left valve overlaps the right valve dorsal and ventral margins.

Description. Carapace forms a sub-rectangle from a lateral view. The anterior margin is evenly rounded, the dorsal margin is straight and inclined posteriorly, the posterior margin is obliquely and acutely rounded with a weak caudal process and the middle of the ventral margin is sinuated. A distinct dorsomedial sulcus and weak anterodorsal and posterodorsal tubercles are present. Two parallel murus extend from the anterodorsal to posterodorsal area from the anterior to posterior margins. A short muri slopes from the dorsomedial sulcus to an area just dorsoposterior of the centre. A short ala projects posteroventrally in the posteroventral area. Primary reticulation of the posterior half is visible. The outer carapace surface is entirely covered with pitted fossa. The left valve overlaps the right valve dorsal and ventral margins. In the ventral view the carapace appears arrowhead-shaped, with tapering anterior and posterior ends and prominent posteriorly directed ala. The posterior view reveals a rounded, dorsally pointing pentagonal shape. A Schizodont hinge is observed; the left valve contains an anterior hinge socket and small tooth at the anterior of the median hinge groove, and the right valve features a median bar with crenulations and an elongated posterior tooth. Inner anterior, posteroventral and posterior margins had developed. A selvage had developed along the anterior inner margin. Distribution of several normal pores can be observed. No ocular sinus is present. Adductor muscle scars had developed on the median ridge; these correspond to the dorsomedial sulcus from the outer lateral view. Sexual dimorphism is prominent: in the lateral view, the male appears longer and more slender than the female. In addition, the dorsal margin is more steeply inclined on the male compared to the female. Furthermore, the posterior margin of the male is more acutely rounded than that of the female. In the ventral and posterior views, the male appears to be more slender than the female.

Remarks. The new species, with its short muri slopes on the dorsomedial sulcus and pitted fossa over the entire carapace, is similar to *Neomonoceratina donghaiensis*, which was originally described from the Paleocene Lingfeng Formation among borehole core materials in the East China Sea (Liu, 1989). However, *Neomonoceratina iwasakii* sp. nov. features an evenly rounded anterior margin, a more gently curved posterior margin and a slender lateral outline. *Neomonoceratina iwasakii* sp. nov. is similar to *Neomonoceratina bullata*, described by Yang & Chen, 1982 (in Hou *et al.* 1982) from the Eocene Funing Group, Jiangsu, China, with respect to an evenly rounded anterior margin and sub-rectangular outline in the lateral view; however, the new species is distinguished by the presence of two murus from the anterodorsal to posterodorsal area, primary reticulation of the

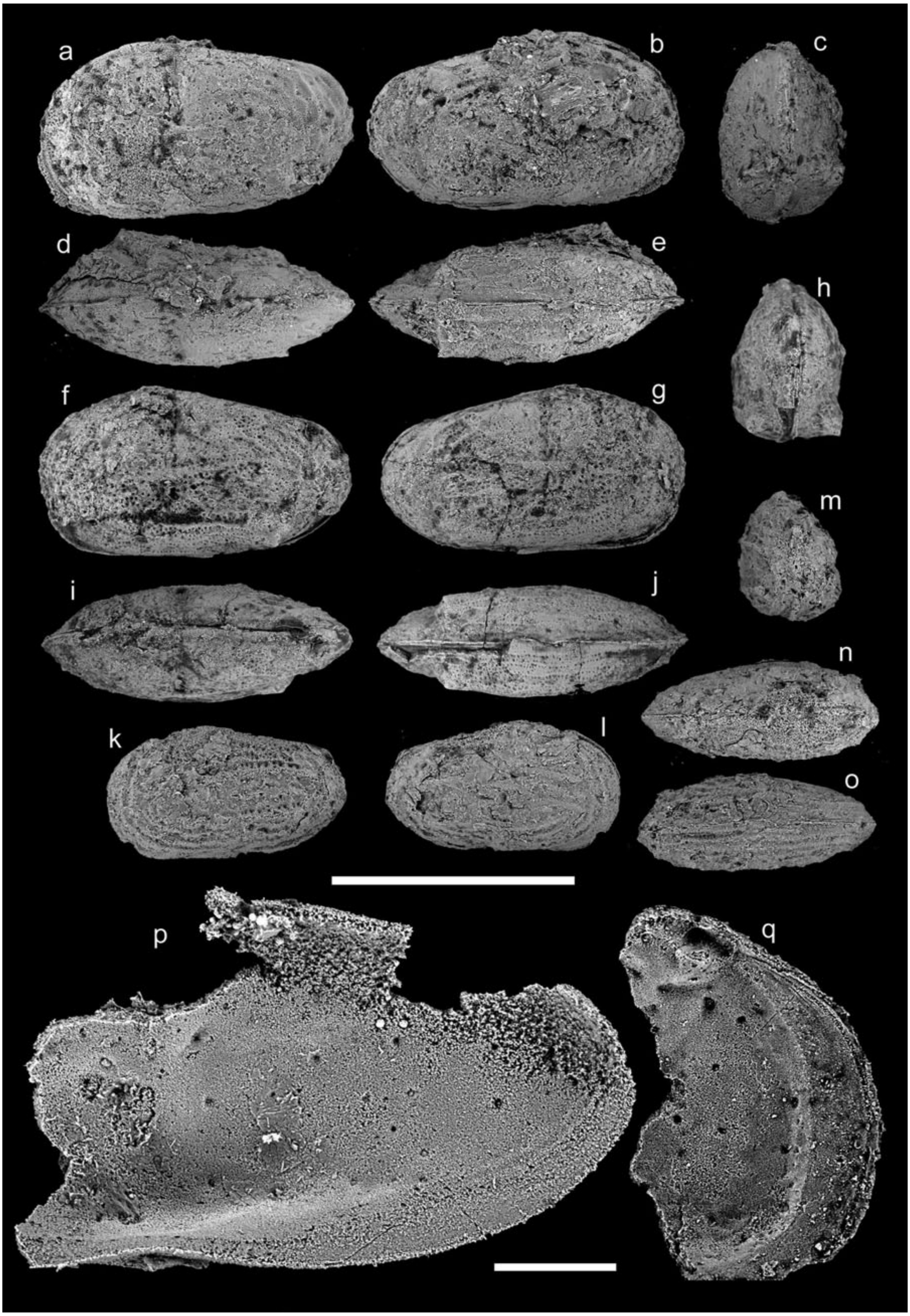

Figure 6. Scanning electron micrographs (SEMs) of *Neomonoceratina iwasakii* sp. nov. from the Akasaki Formation. (a–e) GCM-IVP3495: female carapace from (a) left lateral; (b) right lateral; (c) posterior; (d) dorsal; and (e) ventral views. (f–j) GCM-IVP3496: (f) male carapace from left lateral; (g) right lateral; (h) posterior; (i) dorsal; and (j) ventral views. (k–o) GCM-IVP3497: (k) juvenile carapace from left lateral; (l) right lateral; (m) posterior; (n) dorsal; and (o) ventral views. (p) GCM-IVP3498: internal view of a fragmented female right valve. (q) GCM-IVP3499: internal view of a fragmented female left valve.

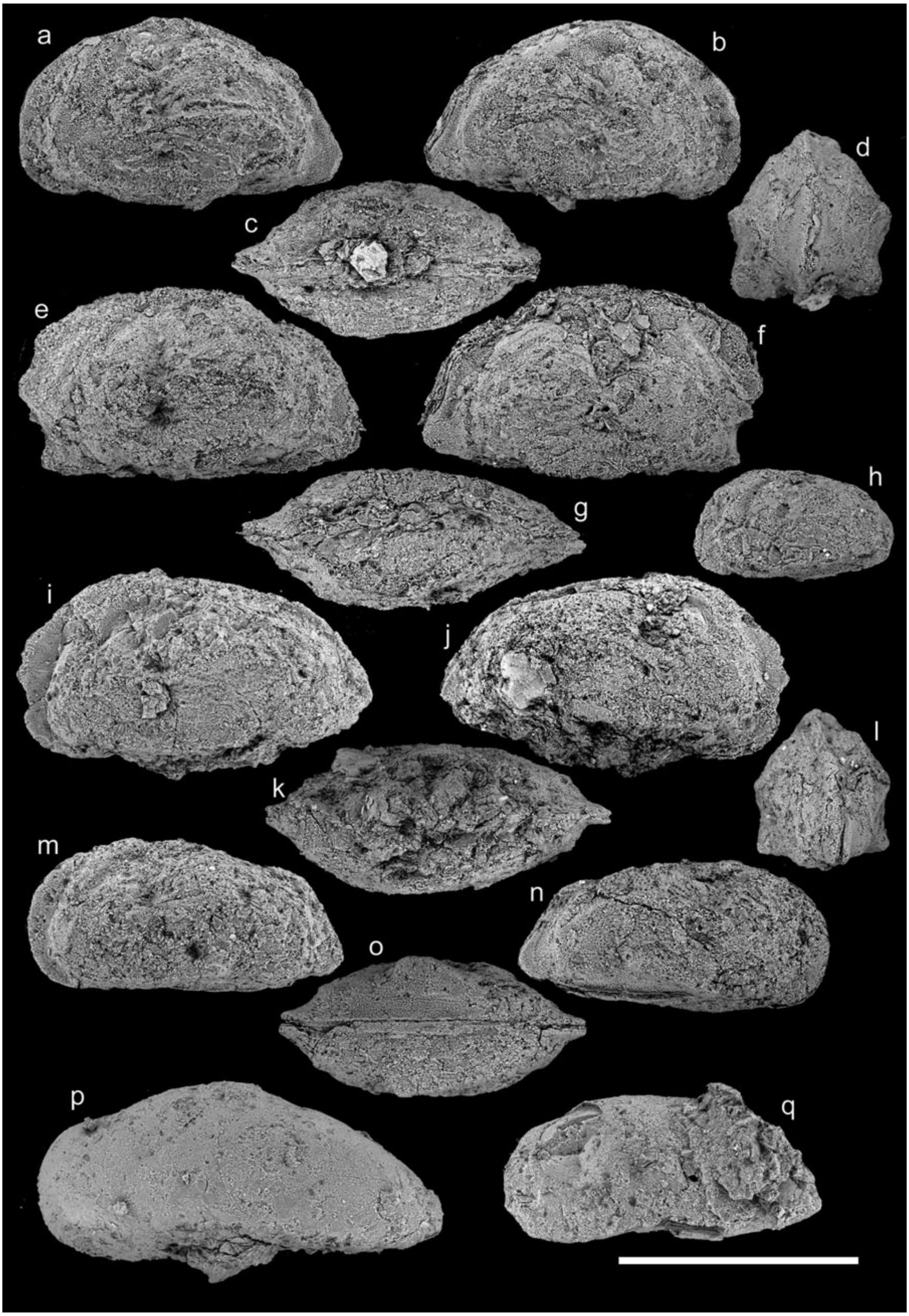

Figure 7. Scanning electron micrographs (SEM) of ostracods from the Akasaki Formation. (a–o) GCM-IVP3500, *Paijenborchella amakusensis* sp. nov.: (a) left lateral, (b) right lateral; (c) ventral; and (d) posterior views of a juvenile carapace. GCM-IVP3501: (e) left lateral; (f) right lateral; and (g) ventral views of a female carapace. (h) GCM-IVP3502: left lateral view of a juvenile carapace. (i–k) GCM-IVP3504: (i) left lateral; (j) right lateral; and (k) ventral views of a male carapace. (l–o) GCM IVP number 05: (l) posterior; (m) left lateral; (n) right lateral; and (o) ventral views of a juvenile carapace. (p) GCM-IVP3505, *Propontocypris* sp.: left lateral view of a carapace. (q) GCM-IVP3506, *Parakrithella* sp.: left lateral view of a carapace.

posterior half and pitted fossa over the outer surface of carapace.

Genus *Paijenborchella* Kingma, 1948
Type species *Paijenborchella iocosa* Kingma, 1948
Paijenborchella amakusensis sp. nov. (Fig. 7a–o)

Holotype. Carapace (GCM-IVP3504) Figure 7i–k

Derivation of name. Named after the province in which the specimens were found.

Type locality and horizon. Approximately 700 m NE of Sengan-san Mountain, Matsushima town, Kamiamakusa city, Kumamoto Prefecture, Kyushu, Japan (32° 30′ 51.5″ N; 130° 25′ 26.7″ E). The sample, from Se 1 of Figure 2, comprises dark grey silty claystone containing *Pitar* sp. and *Anomia* sp. The sample was collected from the uppermost part of the Akasaki Formation, Miroku Group.

Material. A total of 22 specimens.

Diagnosis. The carapace has a sub-trapezoid shape in the lateral view. The dorsal margin is gently arched. Prominent muri, extending from anterodorsal area and widely arched midventral area, terminates at the posteroventral area. The left valve overlaps the right valve dorsal margin.

Description. The carapace has a sub-trapezoid appearance from a lateral view. The anterior margin is obliquely rounded, the dorsal margin is gently arched, the posterior margin slopes to the ventral margin with a prominent caudal process, and the ventral margin is sinuated as a result of midline and slightly posterior muri projections. A distinct dorsomedial sulcus and anterodorsal tubercle are present. Prominent muri extend from the anterodorsal area and widely arched midventral area to terminate at the posteroventral area. Short muri also developed from the dorsomedial sulcus and terminated slightly posterior to the central area. Flattened anterior and posterior marginal areas are visible. The left valve overlaps the right valve dorsal margin. In a ventral view the carapace appears spindle-shaped, with anterior and posterior tapering. Sexual dimorphism is prominent. In the lateral view, the male appears longer and more slender than the female. In addition, the posterior margin of the female exhibits a steeper posteroventral incline compared with that of the male.

Remarks. This species is similar to *Paijenborchella optima* (Liu, 1989) from the Eocene Wenzhou Formation, detected in borehole core samples from the East China Sea, with respect to the widely arched midventral muri and anterodorsal tubercle, but differs with respect to the presence of short muri developed on the dorsomedial sulcus, a more elongated lateral outline and wider, flattened anterior and posterior marginal areas. *Paijenborchella amakusensis* sp. nov. is also similar to *Paijenborchella simplex* Yang, 1995, discovered in the lower Tertiary strata of the western Tarim Basin in China, with respect to the wider, flattened anterior and posterior marginal areas; however, the new species is distinguished by the presence of a left valve that overlaps the dorsal margin of the right valve, a gently arched dorsal margin, pitted fossa on the outer surface of the carapace and prominent muri extending from the anterodorsal to posteroventral areas.

Family Krithidae Mandelstam (in Bubikyan, 1958)
Genus *Parakrithella* Hanai, 1961 (in Benson *et al.* 1961)
Type species *Neocyprideis pseudadonta* Hanai, 1959
Parakrithella sp. (Fig. 7q)

Remarks. Although we recovered 12 specimens from the material, many were fragmented and juvenile and therefore could not be described as novel. This species is similar to *Parakrithella pseudadonta* (Hanai, 1959) from Recent sediments obtained from beach sand in Hayama-cho, Kanagawa Prefecture, Central Japan with respect to the broadly arched dorsal margin, but differs with respect to the strongly protruding caudal process, more sinuated ventral margin and obliquely rounded anterior margin. *Parakrithella* sp. is similar to *Parakrithella* ? *arca* (Yang, 1995) from the lower Tertiary strata of the western Tarim Basin, China, with respect to the broadly arched dorsal margin, but differs with respect to the sinuated anteroposterior margin, obliquely rounded anterior margin and prominent caudal process.

Family Pontocyprididae Müller, 1894
Genus *Propontocypris* Sylvester-Bradley, 1947
Type species *Pontocypris trigonella* Sars, 1866
Propontocypris sp. (Fig. 7p)

Remarks. Only three specimens were recovered from the material and could not be described as novel. This species is similar to *Paracypris donghaiensis* from the borehole core samples of the Eocene Wenzhou Formation in the East China Sea described by Liu in 1989 with respect to the smooth outer surface, but differs with respect to the strongly arched dorsal margin, sinuated anterodorsal margin and short caudal process. *Propontocypris* sp. is also similar to *Paracypris? kuritai* from the late Eocene Funazu Formation (data by Yamaguchi, Nagao & Kamiya, 2006), Nagasaki Prefecture, Japan, with respect to the strongly arched dorsal margin, but differs with respect to the sinuated anteroposterior margin, absence of surface ornamentation and shorter caudal process.

Acknowledgements. We are grateful to staff of the Amakusa Geopark for permitting the geological survey and collection of microfossils. The helpful comments of Professor Ashraf Elewa (Minia University), an anonymous referee and Professor Paul Upchurch (editor of the Geological Magazine) are appreciated. The authors express their gratitude to Crimson Interactive Pvt. Ltd for editing the English. This study was partly supported by a Grant-in-Aid for Science Research from the Ministry of Education and Science of the Government of Japan (No. 16K05592 to GT).

References

ABE, K. 1988. Speciation completed? In *Keijella bisanensis* species group. *In Evolutionary Biology of Ostracoda: Its Fundamentals and Applications* (eds T. Hanai, N. Ikeya & K. I. Shizaki), pp. 919–25. Tokyo: Kodansha.

ATHERSUCH, J., HORNE, D. J. & WHITTAKER, J. E. 1989. Ecology and distribution. In *Marine and Brackish Water Ostracods* (eds J. Athersuch, D. J. Horne & J. E. Whittaker), pp. 28–34. New York: E. J. Brill.

BABA, A. K., MATSUDA, T., ITAYA, T., WADA, Y., HORI, N., YOKOYAMA, M., ETO, N., KAMEI, R., ZAMAN, H., KIDANE, T. & OTOFUJI, Y. I. 2007. New age constraints on counter-clockwise rotation of NE Japan. *Geophysical Journal International* **171**, 1325–41.

BASSIOUNI, M. A. A. & LUGER, P. 1996. Middle Eocene Ostracoda from Northern Somalia. *Courier Forschungsinstitut Senkenberg* **192**, 1–139.

BENSON, R. H., BERDAN, J. M., VAN DEN BOLD, W. A., HANAI, T., HESSLAND, I., HOWE, H. V., KESLING, R. V., LEVINSON, S. A., REYMENT, R. A., MOORE, R., SCOTT, H. W., SHAVER, R. H., SOHN, I. G., STOVER, L. E., SWAIN, F. M., SYLVESTER-BRADLEY, P. C. & WAINWRIGHT, J. 1961. Part Q Arthropoda 3 Crustacea Ostracoda. In *Treatise on Invertebrate Paleontology* (ed. R. C. Moore). Colorado: Geological Society of America and University of Kansas Press, 442 pp.

BHANDARI, A. 1992. Eocene Ostracoda from the subsurface sections of Garo Hills, Meghalaya and Assam, India. *Journal of the Palaeontological Society of India* **37**, 37–83.

BHANDARI, A., SINGH, H. & RANA, R. S. 2005. A note on occurrence of ostracodes from the Vastan Lignite Mine, Gujarat. *Journal of the Palaeontological Society of India* **50**, 141–6.

BHATIA, S. B. & BAGI, H. 1991. Early Lutetian charophyta from the Shimla Hills, Lesser Himalayas. *Bulletin de la Société Botanique de France. Actualités Botaniques* **138**, 7–14.

BLAKE, D. B. 1950. Gosport Eocene Ostracoda from Little Stave Creek, Alabama. *Journal of Paleontology* **24**, 174–84.

BUBIKYAN, S. A. 1958. Ostracods of the Paleogene deposits of the Erivan Basin. *Izvestiya Academii Nuakarmyanskoi, Erevan, SSR (series Geology-Geography)* **11**, 3–16.

CAI, H. & CHEN, M. 1987. An approach to the distribution and environmental characteristics of microfaunas in surface sediments in the South China Sea. *Acta Micropalaeologica Sinica* **4**, 73–85 (in Chinese with English abstract).

CARBONEL, P. & HOIBIAN, T. 1988. The impact of organic matter on ostracods from an equatorial deltaic area, the Mahakam Delta-southeastern Kalimantan. In *Evolutionary Biology of Ostracoda: Its Fundamentals and Applications* (eds T. Hanai, N. Ikeya & K. I Shizaki), pp. 353–66. Tokyo: Kodansha.

CLARKE, J. A. & BOYD, C. A. 2015. Methods for the quantitative comparison of molecular estimates of clade age and the fossil record. *Systematic Biology* **64**, 25–41.

DEWI, K. T. 1997. Ostracoda from the Java Sea, West of Bawean Island, Indonesia. *Marine Geological Institute, Special Publication* **4**, 1–78.

ELEWA, A. M. T., LUGER, P. & BASSIOUNI, M. A. 2001. Middle Eocene Ostracoda from northern Somalia (Paleoenvironmental appraisal). *Revue de Micropaléontologie* **44**, 279–89.

ELEWA, A. M. T., OMAR, A. A. & DAKRORY, A. M. 1998. Biostratigraphical and paleoenvironmental studies on some Eocene ostracodes and Foraminifers from the Fayoum Depression, Western Desert, Egypt. *Egyptian Journal of Geology* **42/2**, 439–69.

GEMERY, L., CRONIN, T. M., BRIGGS JR, W. M., BROUWERS, E. M., SCHORNIKOV, E. I., STEPANOVA, A., WOOD, A. M. & YASUHARA, M. 2017.An Arctic and Subarctic ostracode database: biogeographic and paleoceanographic applications. *Hydrobiologia* **786**, 59–95.

HANAI, T. 1959. Studies on the Ostracoda from Japan. IV. family Cytherideidae Sars 1925. *Journal of the Faculty of Science, University of Tokyo* **11**, 291–308.

HANAI, T. 1961. Parakrithella Hanai, nom. subst. herein. In *Treatise on Invertebrate Paleontology Part Q Arthropoda 3 Crustacea Ostracoda* (ed. R. C. Moore), p. 289. Colorado: Geological Society of America and University of Kansas Press.

HANAI, T. 1970. Studies on the ostracod subfamily Schizocytherinae Mandelstam. *Journal of Paleontology* **44**, 693–729.

HORNE, D. J., COHEN, A. & MARTENS, K. 2002. Taxonomy, morphology and biology of Quaternary and living Ostracoda. In *The Ostracoda: Applications in Quaternary Research* (eds J. A. Holmes & A. Chivas), pp. 5–36. American Geophysical Union, Washington, Geophysical Monograph no. 131.

HOU, Y., CHEN, T., YANG, H., HO, J., ZHOU, Q. & TIAN, M. 1982. *Cretaceous–Quaternary Ostracoda Fauna from Jiangsu*. Peking: Geological Publishing House, 386 pp. (in Chinese with English abstract).

HOWE, H. V. 1961. Family Schizocytheridae Howe, n. fam. In *Treatise on Invertebrate Paleontology Part Q Arthropoda 3 Crustacea Ostracoda* (ed. R. C. Moore), p. 331. Colorado: Geological Society of America and University of Kansas Press.

HOWE, H. V. & GARRETT, J. B. 1934. Louisiana Sabine Eocene Ostracoda. *Geological Bulletin* **4**, 1–64.

HU, C. & CHENG, Y. 1977. Ostracodes from the Late Pleistocene Lungkang Formation near Miaoli, Taiwan. *Memoir of the Geological Society of China* **2**, 191–205.

HU, C. & TAO, H. 2008. Studies on the ostracod fauna of Taiwan and its adjacent seas. *National Taiwan Museum Special Publication Series* **13**, 1–910 (in Chinese).

HU, C. & YEH, K. 1978. Ostracod faunas from the Pleistocene Liushuang Formation in the Tainan area, Taiwan. *Proceedings of the Geological Society of China* **21**, 151–62.

IBARAKI, M. 1994. Age and paleoenvironment of the Tertiary in northwestern Kyushu on the basis of the pkanktonic foraminifers. *Chikyu Monthly* **16**, 150–3 (in Japanese).

IIJIMA, A. & TADA, R. 1990. Evolution of Tertiary sedimentary basins of Japan in reference to opening of the Japan Sea. *Journal of the Faculty of Science, the University of Tokyo, Section 2, Geology, Mineralogy, Geography, Geophysics* **22**, 121–71.

IKEYA, N. & ITOH, H. 1991. Recent Ostracoda from the Sendai Bay region, Pacific coast of northeastern Japan. *Reports of Faculty of Science, Shizuoka University* **25**, 93–145.

IKEYA, N. & SHIOZAKI, M. 1993. Characteristics of the inner bay ostracodes around the Japanese islands – the use of ostracodes to reconstruct paleoenvironments. *Memoirs of the Geological Society of Japan* **39**, 15–32 (in Japanese with English abstract).

INOUE, E. 1962. El Terciario inferior en la region cerca Misumi-machi, la peninsula de Uto, la prefectura de

Kumamoto. *Bulletin of the Geological Survey of Japan* **13**, 61–75 (in Japanese with Spanish abstract).

Irizuki, T. 2003. Miocene stratigraphy and microfossils from the eastern Setouchi Province. *Shimane Prefecture Chigakkaishi* **18**, 1–5 (in Japanese).

Irizuki, T. & Hosoyama, M. 2000. Fossil ostracodes (Crustacea) from the Pleistocene Noma Formation, Aichi Prefecture, central Japan. *The Bulletin of Aichi University of Education* **49**, 9–15 (in Japanese with English abstract).

Irizuki, T., Ishizaki, K., Takahashi, M. & Usami, M. 1998. Ostracode faunal changes after the mid-Neogene climatic optimum elucidated in the Middle Miocene Kobana Formation, Central Japan. *Paleontological Research* **2**, 30–46.

Irizuki, T., Masuda, F., Miyahara, B., Hirotsu, A., Ueda, S. & Yoshikawa, S. 2001. Vertical changes of Holocene ostracodes in bore hole cores from off Kobe, related to the opening of straits and relative sea-level change in western Japan. *Quaternary Research* **40**, 105–20.

Irizuki, T. & Matsubara, T. 1994. Vertical changes of depositional environments of the Lower to Middle Miocene Kadonosawa Formation based on analysis of fossil ostracode faunas. *Journal of the Geological Society of Japan* **100**, 136–49 (in Japanese with English abstract).

Irizuki, T. & Matsubara, T. 1995. Early Middle Miocene ostracodes from the Suenomatsuyama Formation, Ninohe City, Northeast Japan and their paleoenvironmental significance. *Transactions and Proceedings of the Palaeontological Society of Japan, New Series* **177**, 65–78.

Irizuki, T., Matsubara, T. & Matsumoto, H. 2005. Middle Pleistocene Ostracoda from the Takatsukayama Member of the Meimi Formation, Hyogo Prefecture, western Japan: significance of the occurrence of *Sinocytheridea impressa*. *Paleontological Research* **9**, 37–54.

Irizuki, T. & Seto, K. 2004. Temporal and spatial variations of paleoenvironments of Paleo-Hamana Bay, central Japan, during the Middle Pleistocene – Analyses of fossil ostracode assemblages, and total organic carbon, total nitrogen and total sulfur contents. *The Journal of the Geological Society of Japan* **110**, 309–24 (in Japanese with English abstract).

Irizuki, T., Yamada, K., Maruyama, T. & Ito, H. 2004. Paleoecology and taxonomy of Early Miocene Ostracoda and paleoenvironments of the eastern Setouchi Province, central Japan. *Micropaleontology* **50**, 105–47.

Ishizaki, K. 1963. Japanese Miocene ostracodes from the Sunakosaka Member of the Yatsuo Formation, east of Kanazawa City, Ishikawa Prefecture. *Japanese Journal of the Geology and Geography* **34**, 19–34.

Ishizaki, K. 1966. Miocene and Pliocene Ostracodes from the Sendai area, Japan. *Science Reports of the Tohoku University, Second Series (Geology)* **37**, 131–63.

Ishizaki, K. & Kato, M. 1978. The basin development of the Dilvium Furuya Mud Basin, Shizuoka Prefecture, Japan, based on faunal analysis of fossil ostracodes. In *Progress in Micropaleontology* (eds Y. Takayanagi & T. Saito), pp. 118–43. New York: Micropaleontology Press.

Iwasaki, Y. 1992. Ostracod assemblages from the Holocene deposits of Kumamoto, Kyushu. *Bulletin of Faculty of Science, Kumamoto University* **13**, 1–12 (in Japanese with English abstract).

Jolivet, L., Tamaki, K. & Fournier, M. 1994. Japan Sea, opening history and mechanism: a synthesis. *Journal of Geophysical Research* **99**, 22237–9.

Kawano, S., Tsujimoto, A., Ugai, H., Irizuki, T. & Nomura, R. 2011. Paleoenvironment and microfossil assemblages in the Pleistocene Ogushi Formation, Kumamoto Prefecture, Southwest Japan. *Journal of Fossil Research* **44**, 1–10 (in Japanese with English abstract).

Keen, M. C. 1977*a*. Cenozoic Ostracoda – North Atlantic. In *Stratigraphic Micropaleontology of Atlantic Basin and Borderlands* (ed. F. M. Swain), pp. 467–93. Amsterdam: Elsevier, Developments in Palaeontology and Stratigraphy 6.

Keen, M. C. 1977*b*. Ostracod assemblages and the depositional environments of the Headon, Osborne, and Bembridge beds (Upper Eocene) of the Hampshire Basin. *Palaeontology* **20**, 405–45.

Keen, M. C. 1978. The Tertiary – Palaeogene. In *A Stratigraphical Index of British Ostracoda* (eds R. H. Bate & E. Robinson), pp. 384–450. Geological Society of London for the Micropalaeontological Spociety, Geological Journal, Special Issue 8.

Keen, M. C. & Racey, A. 1991. Lower Eocene ostracods from the Rusayl Shale Formation of Oman. *Journal of Micropalaeontology* **10**, 227–33.

Keij, A. J. 1957. Eocene and Oligocene Ostracoda from Belgium. *Institut Royal des Sciences Naturelles de Belgique, Memoires* **136**, 1–210.

Khosla, S. C. & Nagori, M. L. 2002. Ostracodes from the Inter-trappean beds (Early Paleocene) of the east coast of India. *Paleontological Research* **6**, 191–210.

Kingma, J. T. 1948. *Contributions to the Knowledge of the Young-Caenozoic Ostracoda from the Malayan Region*. Utrecht: Kermink Printers, 119 pp.

Krutak, P. R. 1961. Jackson Eocene Ostracoda from the Cocoa Sand of Alabama. *Journal of Paleontology* **35**, 769–88.

Latreille, P. A. 1802. Historie naturelle, générale et particulière des Crustacés et des Insectes. *Histoires des Cypris et des Cytherées* **8**, 232–54.

Lee, E. & Paik, K. 1992. Late Cenozoic ostracod fauna and paleoenvironments of the marine sedimentary strata in the Cheju Island. *Paleontological Society of Korea Special Publications* **1**, 121–60.

Liu, Z. 1989. Ostracoda. In *Cenozoic Paleobiota of the Continental Shelf of the East China Sea (Donghai)* (eds Research Party of Marine Geology, Ministry of Geology & Mineral Resources Institute of Geology Chinese Academy of Geological Science), pp. 136–163. Beijing: Geological Publishing House (in Chinese with English abstract).

Lord, A. R., Whittaker, J. E. & King, C. 2009. Palaeogene. In *Ostracoda in British Stratigraphy* (eds J. E. Whittaker & M. B. Hart), pp. 373–409. London: The Micropalaeontological Society.

Matsubara, T. & Ugai, H. 2006. Paleoecology and taxonomy of Middle Eocene molluscs from the Shiratake Formation on Takeshima Island, Amakusa Islands, southwest Japan. *Bulletin of Goshoura Cretaceous Museum* **7**, 1–17.

Matsushita, H. 1949. Geology of coal fields in northern Kyushu: Stratigraphical study of the Paleogene in the northern part of Kyushu. *Report of Faculty of Science, Kyushu University, Geology* **3**, 1–57 (in Japanese with English abstract).

Matsuura, Y., Irizuki, T. & Hayashi, H. 2013. Microfossil assemblages associated with Argonaut fossils from the Middle Miocene Fujina Formation, Shimane Prefecture, southwestern Honshu, Japan. *Journal of the*

Geological Society of Japan **119**, 312–20 (in Japanese with English abstract).

McKenzie, K. G. 1967. The distribution of Caenozoic marine Ostracoda from the Gulf of Mexico to Australasia. In *Aspects of Tethyan Biogeography* (eds C. G. Adams & D. V. Ager), pp. 219–38. London: Systematics Association.

Miyake, Y., Tsutsumi, Y., Miyata, K. & Komatsu, T. 2016. LA-ICP-MS zircon U-Pb dating of acidic tuff from the Eocene Akasaki Formation, Amakusa, Kumamoto Prefecture, western Kyushu, Japan: implications for the age of the land mammal fauna. *Paleontological Research* **20**, 302–11.

Mizuno, A. 1962*a*. Paleogene and lower Neogene biochronology of western Japan (I. On the Paleogene stratigraphy and molluscan fauna in the vicinity of Nishisonogi Peninsula, northwestern Kyushu). *Journal of the Geological Society of Japan* **68**, 640–8 (in Japanese with English abstract).

Mizuno, A. 1962*b*. Paleogene and lower Neogene biochronology of western Japan (II. On the correlation and biochronologic division of the Paleogene strata in the vicinity of Nishisonogi Peninsula, northwestern Kyushu). *Journal of the Geological Society of Japan* **68**, 687–93 (in Japanese with English abstract).

Mizuno, A. 1963. Paleogene and lower Neogene biochronology of western Japan (III. Stratigraphic and geographic distribution of molluscan faunas in west Japan). *Journal of the Geological Society of Japan* **69**, 38–50 (in Japanese with English abstract).

Mizuno, A. 1964. Paleogene and early Neogene molluscan faunae in west Japan. *Report of Geological Survey of Japan* **204**, 1–72.

Müller, G. W. 1894. Die Ostracoden des Golfes von Neapel und angrenzenden Meeresabschnitte. In *Fauna und Flora des Golfes von Neapel*. R. Friedlaender & Sohn Berlin, Monographie 21, 404 pp.

Nagao, T. 1926*a*. Stratigraphy of the Palaeogene formations of Kyushu (Part 1). *Journal of Geography (Chigaku-Zassi)* **38**, 115–30 (in Japanese).

Nagao, T. 1926*b*. Stratigraphy of the Palaeogene formations of Kyushu (Part 2). *Journal of Geography (Chigaku-Zassi)* **38**, 263–9 (in Japanese).

Nagao, T. 1926*c*. Stratigraphy of the Palaeogene formations of Kyushu (Part 3). *Journal of Geography (Chigaku-Zassi)* **38**, 317–23 (in Japanese).

Nagao, T. 1926*d*. Stratigraphy of the Palaeogene formations of Kyushu (Part 4). *Journal of Geography (Chigaku-Zassi)* **38**, 369–73 (in Japanese).

Nagao, T. 1926*e*. Stratigraphy of the Palaeogene formations of Kyushu (Part 5). *Journal of Geography (Chigaku-Zassi)* **38**, 457–61 (in Japanese).

Nagao, T. 1927. The Paleogene stratigraphy of Kyushu. *Journal of Geography (Chigaku-Zassi)* **39**, 86–90 (in Japanese).

Nagao, T. 1928*a*. The Paleogene stratigraphy of Kyushu. *Journal of Geography (Chigaku-Zassi)* **40**, 193–214 (in Japanese).

Nagao, T. 1928*b*. The Paleogene stratigraphy of Kyushu. *Journal of Geography (Chigaku-Zassi)* **40**, 278–88 (in Japanese).

Nakao, Y., Tanaka, G. & Yamada, S. 2001. Pleistocene and living marine Ostracoda in Shizuoka district, Japan. In *14th International Symposium on Ostracoda Guidebook of Excursions* (ed. N. Ikeya), pp. 127–47. Shizuoka University Press, Shizuoka, Organizing Committee of ISO 2001.

Okada, H. 1992. Calcareous nannofossils and biostratigraphy of the Paleogene sequences of the northern Kyushu, Japan. *Journal of the Geological Society of Japan* **98**, 509–28.

Otofuji, Y., Matsuda, T. & Nohda, S. 1985. Opening mode of the Japan Sea inferred from the paleomagnetism of the Japan Arc. *Nature* **317**, 603–4.

Ozsvart, P. 1999. Middle Eocene foraminifer, mollusk and ostracod fauna from the Csordakut Basin (Gerecse Mountains, Hungary): palaeoenvironments recorded in a transgressive sequence. *Annals Universitatis Scientiarum Budapestinensis, Sectio Geologica* **32**, 73–135.

Pooser, W. K. 1965. *Biostratigraphy of Cenozoic Ostracoda from South Carolina*. Paleontological Institute, University of Kansas, Paleontological Contributions, Arthropoda **8**, 80 pp.

Şafak, Ü., Ocakoğ Lu, F. & Açikalm, S. 2015. Ostracoda assemblage and the environmental characteristics of the Eocene succession of the Central Sakarya Region. *Micropaleontology* **61**, 49–68.

Sakai, H. 1993. Tectonics and sedimentation of the Tertiary sedimentary basins in the northern Kyushu. *Memoir of the Geological Society of Japan* **42**, 183–201 (in Japanese with English abstract).

Sars, G. O. 1866. Oversigt af Norges marine Ostracoder. *Forhandlinger Videnskabs-Selskabet i Christiania*. Oslo: Norske Videnskabs Akademi, 130 pp. (in Norwegian).

Sasaki, Y., Irizuki, T., Abe, K., Uchida, J. & Fujiwara, O. 2007. Fossil ostracode assemblages from Holocene Tsunami and normal bay deposits along the Tomoe River, Tateyama, Boso Peninsula, central Japan. *Quaternary Research* **46**, 517–32 (in Japanese with English abstract).

Sawada, Y., Mishiro, Y., Imaoka, T., Yoshida, K., Inada, R., Hisai, K., Kondo, H. & Hyodo, M. 2013. K-Ar ages and paleomagnetism of the Miocene in the Izumo Basin, Shimane Prefecture. *Journal of the Geological Society of Japan* **119**, 267–84 (in Japanese with English abstract).

Scotese, C. R. 2013*a*. *Map Folio 10, Late Eocene, Priabonian, 35.6 Ma*. PALEOMAP PaleoAtlas for ArcGIS, volume 1, Cenozoic. PALEOMAP Project, Evanston, IL.

Scotese, C. R. 2013*b*. *Map Folio 11, late Middle Eocene, Bartonian, 38.8 Ma*. PALEOMAP PaleoAtlas for ArcGIS, volume 1, Cenozoic. PALEOMAP Project, Evanston, IL.

Scotese, C. R. 2013*c*. *Map Folio 13, Early Eocene, Ypresian, 52.2 Ma*. PALEOMAP PaleoAtlas for ArcGIS, volume 1, Cenozoic. PALEOMAP Project, Evanston, IL.

Shahin, A., El Halaby, O. & El Baz, S. 2008. Middle Eocene ostracodes of the Qattamiya area, northwest Eastern Desert, Egypt: Systematics, biostratigraphy and paleobiogeography. *Revue de Paléobiologie, Genève* **27**, 123–57.

Siddiqui, Q. A. 2000. Some species of the genus *Neocyprideis* in early Tertiary of Pakistan. *Journal of Micropalaeontology* **19**, 1–7.

Stephenson, M. B. 1946. Weches Eocene Ostracoda from Smithville, Texas. *Journal of Paleontology* **20**, 297–344.

Swain, F. M. 1974. *Some Upper Miocene and Pliocene (?) Ostracoda of Atlantic Coastal Region for use in Hydrogeologic Studies*. US Geological Survey, Washington, Professional Paper **821**, 1–50, 13 pls.

Sylvester-Bradley, P. C. 1947. Some ostracod genotypes. *Annals and Magazine of Natural History, Series 11* **13**, 192–9.

Tabuki, R. 2001. Plio-Pleistocene and Recent subtropical Ostracoda in Okinawa. In *14th International Symposium on Ostracoda Guidebook of Excursions* (ed. N. Ikeya), pp. 21–44. Shizuoka: The Organizing Committee of ISO 2001.

Takai, Y., Bojo, T. & Harada, T. 1997. *Explanatory Text of the Geology of the Amakusa Coal Field. Geology and Coal Deposits in the Amakusa Coal Field, Kumamoto Prefecture, Japan*. Tsukuba: Geological Survey of Japan, 77 pp. (in Japanese with English abstract).

Takai, Y. & Satoh, H. 1982. *Geology of the Onikizaki and Ushibuka District (including a part of the Akune District)*. Tsukuba: Geological Survey of Japan, 87 pp. (in Japanese with English abstract).

Tanaka, G. 2003. Middle Miocene ostracods from the Omori Formation, Izumo City, Southwest Japan: Its implications for paleoenvironment of the Proto-Japan Sea. *Earth Science (Chikyu-Kagaku)* **57**, 111–27.

Tanaka, G. 2016. Redescription of two krithid species (Crustacea, Ostracoda) from the Sea of Japan, with a comment on the taxonomic characters of Krithidae. *Paleontological Research* **20**, 31–47.

Tanaka, G., Itami, M., Kurosawa, S., Yoshioka, A., Yokota, M., Arai, R., Idehara, Y. & Hayashi, H. 2013. The depositional environment of the singular Middle Miocene strata from southwestern Tomioka City, Gunma Prefecture, central Japan, from the view point of fossil ostracod assemblage. *Journal of the Geological Society of Japan* **119**, 17–24 (in Japanese with English abstract).

Tanaka, G., Komatsu, T. & Phong, N. D. 2009. Recent ostracod assemblages from the northeastern coast of Vietnam and the biogeographical significance of the euryhaline species. *Micropaleontology* **55**, 365–82.

Tanaka, G., Kuroda, S. & Ikeya, N. 2011. Taxonomy and microhabitats of the genus *Spinileberis* (Ostracoda, Crustacea) from Japan. *Paleontological Research* **15**, 213–32.

Tanaka, G. & Nomura, R. 2009. Middle Miocene ostracods from the Furue Formation, Shimane Prefecture, Southwest Japan. *Journal of the Geological Society of Japan* **115**, 261–5 (in Japanese with English abstract).

Tanaka, G., Nomura, S. & Hasegawa, Y. 2012. Miocene ostracods from the Midorimachi Formation, Ota City, Gunma Prefecture, central Japan. *Bulletin of Gunma Museum of Natural History* **16**, 31–40.

Tanaka, G., Seto, K., Mukuda, T. & Nakano, Y. 2002. Middle Miocene ostracods from the Fujina Formation, Southwest Japan and their paleoenvironmental significance. *Paleontological Research* **6**, 1–22.

Tanaka, G., Seto, K. & Takayasu, K. 1998. The relationship between environments and ostracode assemblages from Miho Bay to Lake Shinji. *LAGUNA* **5**, 81–91 (in Japanese with English abstract).

Tanaka, G., Tsukawaki, S. & Ooji, A. 2004. Preliminary report on Ostracodes from the Miocene Sunagozaka Formation, southern part of Kanazawa City, Ishikawa Prefecture, central Japan. *Bulletin of the Japan Sea Research Institute* **35**, 53–63 (in Japanese with English abstract).

Tanaka, Y., Kondo, Y. & Tashiro, M. 1997. Paleoecology of molluscan associations of Paleogene Senganzan Formations, Miroku Group in Amakusa-kamijima Island, Kumamoto Prefecture. *Abstracts of Annual Meeting of the Geological Society of Japan* **414** (in Japanese), Fukuoka, October 1997.

Toyohara, F. & Hase, Y. 1991. Surface geological map, Misumi-Kyoragi-Minamata. Available at http://nrb-www.mlit.go.jp/kokjo/tochimizu/F3/ZOOMA/4312/index.html (accessed 29 July 2017).

Van den Bold, W. A. 1957. Ostracoda from the Paleocene of Trinidad. *Micropaleontology* **3**, 1–18.

Wan, X., Jiang, T., Zhang, Y., Xi, D. & Li, G. 2014. Palaeogene marine stratigraphy in China. *Lethaia* **47**, 297–308.

Wang, P., et al. 1985. *Marine Micropaleontology of China*. Beijing: China Ocean Press, 370 pp.

Wang, P. & Zhao, Q. 1991. Paleobiogeography of Ostracoda and Foraminifera in the China sea area. *Acta Oceanologica Sinica* **10**, 93–105.

Wang, Q. & Zhang, L. 1987. Holocene ostracod fauna and paleoenvironment in the sea region around Hong Kong. *Acta Oceanologica Sinica* **6**, 281–8 (in Chinese with English abstract).

Whatley, R. 1983. The application of Ostracoda to palaeoenvironmental analysis. In *Applications of Ostracoda* (ed. R. F. Maddocks), pp. 51–77. Houston: University of Houston Geosciences.

Whatley, R. 1988. Population structure of ostracods: some general principles for the recognition of palaeoenvironments. In *Ostracoda in the Earth Sciences* (eds P. De Decker, J. P. Colin & J. P. Peypouquet), pp. 245–56. Amsterdam: Elsevier.

Williams, M., Perrier, V., Bennett, C., Hearing, T., Stocker, C. & Harvey, T. 2015. Ostracods: the ultimate survivors. *Geology Today* **31**, 193–200.

Yajima, M. 1978. Quaternary Ostracoda from Kisarazu near Tokyo. *Transactions and Proceedings of the Palaeontological Society of Japan, New Series* **112**, 371–409.

Yajima, M. 1982. Late Pleistocene Ostracoda from the Boso Peninsula, central Japan. *The University Museum, University of Tokyo Bulletin* **20**, 141–227.

Yajima, M. 1988. Preliminary notes on the Japanese Miocene Ostracoda. In *Evolutionary Biology of Ostracoda: Its Fundamentals and Applications* (eds T. Hanai, N. Ikeya & K. I. Shizaki), pp. 1073–85. Tokyo: Kodansha.

Yajima, M. 1992. Early Miocene Ostracoda from Mizunami, central Japan. *Bulletin of the Mizunami Fossil Museum* **19**, 247–67.

Yamaguchi, T. 2004. Oligocene ostracode assemblages from the Itanoura Formation, Nishisonogi Group, Nagasaki Prefecture, southwest Japan. *Paleontological Research* **8**, 53–70.

Yamaguchi, T. 2006. Eocene ostracodes from the Iojima Group, Nagasaki Prefecture, southwestern Japan. *Journal of Paleontology* **80**, 902–18.

Yamaguchi, T. & Goedert, J. L. 2009. Early Eocene marine ostracods from the Crescent Formation, southwestern Washington State, USA. *Journal of Micropalaeontology* **28**, 117–29.

Yamaguchi, T. & Hayashi, H. 2001. Late Miocene ostracodes from the Kubota Formation, Higashi-Tanagura Group, Northeast Japan, and their implications for bottom environments. *Paleontological Research* **5**, 241–57.

Yamaguchi, T. & Kamiya, T. 2007. Oligocene-Miocene ostracode assemblages with the genus *Palmoconcha* from Japan. *Journal of Paleontology* **81**, 632–42.

Yamaguchi, T. & Kamiya, T. 2009. Eocene ostracodes from Hahajima Islands of the Ogasawara (Bonin) Islands, Northwestern Pacific, and their paleobiogeographic significance in the West Pacific. *Journal of Paleontology* **83**, 219–37.

Yamaguchi, T. & Kurita, H. 2008. Eocene ostracode assemblages with *Robertsonites* from Hokkaido and their implications for the paleobiogeography of Northwestern Pacific. *Bulletin of the Geological Survey of Japan* **59**, 369–84.

Yamaguchi, T., Matsubara, T. & Kamiya, T. 2005. Eocene ostracods from the Iwaya Formation on Awajishima Island, southwestern Japan. *Paleontological Research* **9**, 305–18.

Yamaguchi, T., Nagao, R. & Kamiya, T. 2006. Paleogene ostracodes from the Kishima Formation, Kishima Group, southwestern Japan. *Bulletin of the Mizunami Fossil Museum* **33**, 87–101.

Yamaguchi, T., Suzuki, H., Soe, A.-N., Htike, T., Nomura, R. & Takai, M. 2015. A new late Eocene *Bicornucythere* species (Ostracoda, Crustacea). *Zootaxa* **3919**, 306–26.

Yamaguchi, T., Tanaka, Y. & Nishi, H. 2008. Calcareous nannofossils and planktic foraminiferal biostratigraphy of the Paleogene Iojima Group, Nagasaki Prefecture, southwest Japan. *Paleontological Research* **12**, 223–36.

Yanai, S., Aoki, K. & Akahori, Y. 2010. Opening of Japan Sea and major tectonic lines of Japan: MTL, TTL and Fossa Magna. *Journal of Geography (Chigaku Zasshi)* **119**, 1079–124 (in Japanese with English abstract).

Yang, H. 1995. *Paijenborchella (Eopaijenborchella) simples* Yang sp. nov. In *Late Cretaceous–Early Tertiary Ostracoda Fauna from Western Tarim Basin, S. Xinjiang, China* (eds H. Yang, X. Jiang & S. Lin), pp. 113–4. Beijing: Science Press (in Chinese).

Yang, H. & Chen, T. 1982. *Neomonoceratina bullata* Yang et Chen sp. nov. In *Cretaceous–Quaternary Ostracoda Fauna from Jiangsu* (eds Y. Hou, T. Chen, H. Yang, J. Ho, Q. Zhou & M. Tian), pp. 222–3. Peking: Geological Publishing House (in Chinese).

Yang, H., Chen, D. & Wang, J. 1990. Eocene Ostracoda from the southwestern continental shelf of the East China Sea. *Acta Micropalaeontologica Sinica* **7**, 367–38 (in Chinese with English abstract).

Yang, H., Jiang, X. & Lin, S. 1995. *Late Cretaceous–Early Tertiary Ostracoda Fauna from Western Tarim Basin, S. Xinjiang, China*. Beijing: Science Press, 62 pp.

Yasuda, N., Takayanagi, Y. & Hasegawa, S. 1985. On the tetraphenylborate method for hard-rock maceration. *Fossils (Kaseki)* **39**, 17–27 (in Japanese).

Yun, H., Paik, K., Chang, S. & Yi, S. 1990. Microfossil assemblages from the Bomun area. *Journal of Paleontological Society of Korea* **6**, 1–63.

Zachos, J. C., Dickens, G. D. & Zeebe, R. E. 2008. An early Cenozoic perspective on greenhouse warming and carbon-cycle dynamics. *Nature* **451**, 279–83.

Zhao, Q. 1984. Recent Ostracoda from the coast zone of the East China Sea and the Yellow Sea. *Marine Geology & Quaternary Geology* **4**, 45–57 (in Chinese with English abstract).

Zhao, Q. 1987. A study of the distribution of recent ostracod faunas from coastal areas of the East China and Yellow seas. *Acta Oceanologica Sinica* **6**, 413–20.

Zhao, Q. & Wang, P. 1988*a*. Distribution of modern Ostracoda in the Shelf off China. In *Evolutionary Biology of Ostracoda: Its Fundamentals and Applications* (eds T. Hanai, N. Ikeya & K. I. Shizaki), pp. 805–21. Tokyo: Kodansha.

Zhao, Q. & Wang, P. 1988*b*. Modern Ostracoda in sediments of shelf sea off China: Quantitative and qualitative distributions. *Oceanologia et Limnologia Sinica* **7**, 562–77 (in Chinese with English abstract).

Zhao, Q. & Whatley, R. 1989. Recent podocopid Ostracoda of the Sedili River and Jason Bay, southeastern Malay Peninsula. *Micropaleontology* **35**, 168–87.

Zhao, Q. & Whatley, R. 1992. A revision of the genus *Sanyuania* Zhao and Han, 1980 (Ostracoda, Crustacea) with the description of new species from the late Cainozoic of China. *Journal of Micropalaeontology* **11**, 151–8.

Zheng, S. 1987. Quaternary Ostracoda fauna from coastal deposits along the coast of Fujian. *Memoirs of Nanjing Institute of Geology & Palaeontology, Academia Sinica* **23**, 190–207 (in Chinese with English abstract).

Zheng, Z. et al. 1994. *A Comprehensive Ecological and Paraecological Study on the Sedimentary Organisms in the Northern and Eastern Area of the South China Sea*. Hubei: Hubei Science Technology Press, 175 pp. (in Chinese with English abstract).

Zhou, B., Zhao, Q., Huang, W. & Gao, J. 1996. A restudy of ostracode assemblages in the surface sediments of the Huanghai Sea. *Acta Oceanologica Sinica* **15**, 209–29.