

## The Omma-Manganji ostracod fauna (Plio-Pleistocene) of Japan and the zoogeography of circumpolar species

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**ABSTRACT**—The Omma-Manganji fauna of Japan signifies a time during the late Pliocene and Pleistocene when arctic-subarctic species migrated far south of their present geographic range in response to oceanographic changes. Omma-Manganji deposits exposed on Hokkaido, northern Honshu, and Sado Islands yielded about 224 species of marine Ostracoda. At least 26 are circumpolar species known previously from Arctic seas off the British Isles, eastern North America, Scandinavia and Europe, comprising between 14 and 47% of the ostracod assemblage in eight of ten formations studied. The 26 circumpolar species and 21 other western Pacific cryophilic species are illustrated and their distribution in Japanese deposits is discussed.

### INTRODUCTION

The zoogeography and taxonomy of arctic-subarctic sublittoral ostracods from high-latitude seas of the British Isles, northern Europe, Scandinavia, Greenland, and eastern North America have been the subject of considerable study. Among the most important papers on Recent Arctic ostracods are those of Brady (1868, 1878), Brady & Norman (1889), Sars (1865, 1922–1928), Elofson (1941), Neale & Howe (1975, and references therein), and Whatley (1982). Hazel (1970a) provided a detailed study of sublittoral ostracod zoogeography off northeastern North America. Studies of late Pleistocene ostracod faunas along eastern North America (Brady & Crosskey, 1871; Hazel, 1968; Cronin, 1981, in press) and Europe (Brady, Crosskey & Robertson, 1874; Neale & Howe, 1975; Lord, 1980) document southward migration of cryophilic species during glacial periods demonstrating their utility for climatic reconstruction of Pleistocene deposits.

Unlike the North Atlantic, cryophilic ostracods from Neogene and Quaternary deposits of the North Pacific are not so well known, despite their potential in palaeoclimatology and, as pointed out by Hanai (1977), in evolutionary studies. The Japanese Islands, located between 46°N and 24°N latitudes, are characterised by relatively steep water temperature gradients and include cold temperate to subtropical marine climatic zones. The Omma-Manganji fauna, originally applied to cold water molluscan assemblages in the Pliocene of Japan (Otuka, 1939; Chinzei, 1978), represents one or several periods during which high-latitude species migrated southward and offers an excellent opportunity to investigate cryophilic ostracods in Japan. Early studies by Hanai (1957a, b, c, 1959 a, b, 1970) laid the

taxonomic groundwork on Omma-Manganji ostracods, showing that typical high-latitude genera such as *Palmenella*, *Cythere* and *Semicytherura* occurred as fossils in the Sawane and Setana Formations of Japan. Ishizaki (1966, 1971) also described Japanese ostracod species having similarities with arctic forms. Recently, Okada (1979) and Ishizaki & Matoba (1985) illustrated additional ostracods from Plio-Pleistocene deposits of Akita Prefecture having affinities with North Atlantic species. Similarly, Tabuki (1986) found several previously unrecognised cryophilic ostracod genera in the Daishaka Formation of northern Honshu and Hayashi (in press) gave a useful discussion of the stratigraphy and ostracods of the Setana Formation.

In our study of Omma-Manganji ostracods, we recognised at least 26 cryophilic species which either live today in high-latitude seas off the British Isles, northeastern North America, Europe and Scandinavia and/or occur in late Pleistocene deposits of that region. Although the taxonomy of some Omma-Manganji ostracods is in a preliminary state, we felt the discovery of well known cryophilic species merited special attention because of the zoogeographic and evolutionary implications. Consequently, our primary goals are 1) to record the distribution of circumpolar species in Japanese Neogene and Quaternary Omma-Manganji deposits from the Oshima Peninsula of Hokkaido, Sado Island in the Sea of Japan, the Oga Peninsula and the Hokuriku area on the Japan Sea side of Honshu (Fig. 1), 2) to illustrate circumpolar species and other cryophilic species not known from seas off Europe and North America and 3) to briefly discuss some evolutionary patterns in cold water genera.

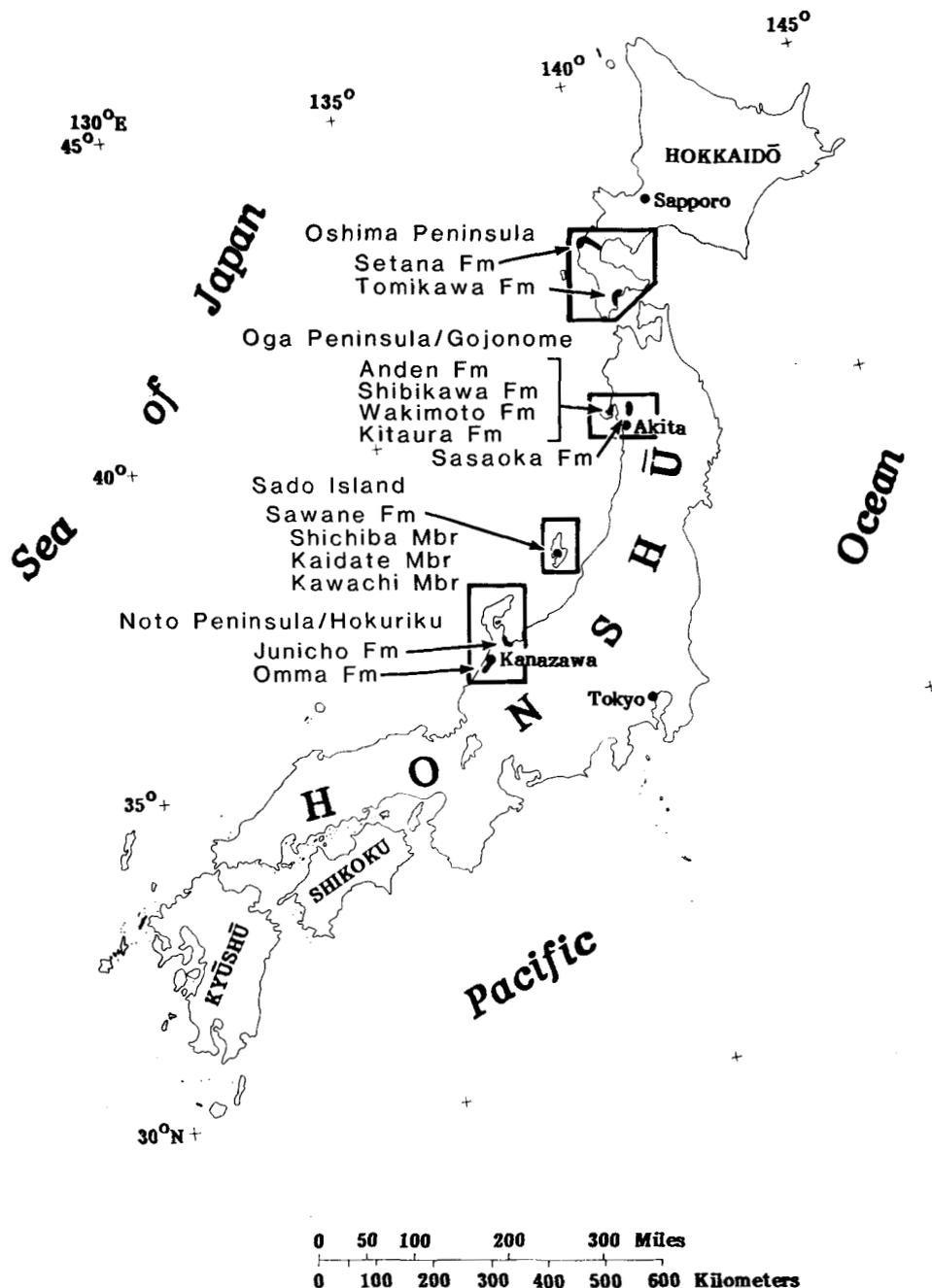


Fig. 1. Map showing regions studied for Omma-Manganji marine ostracods.

#### MATERIAL AND METHODS

A total of 53 ostracod-bearing samples form the basis of this paper. Most were collected by the authors during the summer of 1984 from the Oshima Peninsula, Sado Island, and the Hokuriku province, those from the Oga Peninsula and Gojonome region, Akita Prefecture, collected in 1985 by N. Schmidt and Dr. K. Ishizaki were also examined.

Between 50 and 100g of dried sediment were washed through nested sieves in U.S. Geological Survey (USGS) laboratories in Reston, Virginia. Most sediments were unconsolidated and disaggregated easily. Sodium carbonate ( $\text{NaCO}_3$ ) or varsol, a kerosene product, were used to break down indurated samples. When dry, sediment coarser than  $150\mu\text{m}$  was sieved;

each size fraction was sprinkled on a tray and ostracods were picked and placed on micropaleontologic slides.

Collections in the Smithsonian's Museum of Natural History, the U.S. Geological Survey, the University Museum, Tokyo University, and the Institute of Geosciences, Shizuoka University were examined to identify species. Scanning electron photomicrographs were taken on a JEOL 35-C at the USGS.

**STRATIGRAPHY**

The stratigraphic relationships of the geological formations studied are shown in Fig. 2 as based on biostratigraphic, palaeomagnetic and radiometric data. In some cases, the age of a formation is not precisely known and the correlations are considered approximate. Table 1 gives locality information for stratigraphic sections yielding ostracods. The 18 localities studied are shown on location maps in Figs. 3 and 4; stratigraphic sections for each are shown in Fig. 5.

**Oshima Peninsula, Hokkaido**

The Setana Formation is exposed in the Yakumo, Imagane, and Kuromatsunai areas of the Oshima Peninsula. Samples were collected along the Soibetsu River, a tributary of the Shubuto River in the Kuromatsunai area; and along the Penkerupeshube and Sakkurubetsu Rivers, which are tributaries of the Yurappu River in the Yakumo area, and the Kuroiwa River, a tributary of the Toshihetsu River in the Imagane area (Figs. 3b, c). Ikeya & Uematsu (1968) and Ikeya &

Hayashi (1982) discussed the stratigraphy of these areas in detail. The Setana Formation represents planktonic foraminiferal zone N22 (early Pleistocene) and Chitoku (1983) correlated the Setana in the Imagane and Kuromatsunai areas to coccolith subzone CN14a (0.9–0.3my) based on calcareous nannofossils *Gephyrocapsa* spp. and *Pseudoemiliania lacunosa*.

The Tomikawa Formation, located in southwestern Hokkaido, consists of fossiliferous conglomerate, pebbly sandstone and coarse to medium sandstones. Samples were collected for ostracods from sections exposed on the Muneyama River 6km northwest of Kamiiso and the Hosokomata-zawa River about 3km northwest of Tomikawa (Fig. 3d). Although previously considered Pliocene in age, Akiba (1981) found the diatom *Rhizosolenia curvirostris* in this formation indicating a lower to middle Pleistocene age.

**Oga Peninsula and Gojonome Region, Akita**

The Oga Peninsula in northwestern Honshu exposes a complex series of Pleistocene marine deposits: the Anden, Shibikawa, Wakimoto, and Kitaura Formations. Okada (1979) documented six cycles of sedimentation in the Pleistocene formations of the Oga Peninsula and the distribution of temperature-sensitive ostracods in these formations suggested a general increase in water temperatures upward in the section. The Sasaoka formation in the Gojonome area consists of massive sandy siltstone. Sections 7–9 in the Oga peninsula and sections 10–12 in the Gojonome region

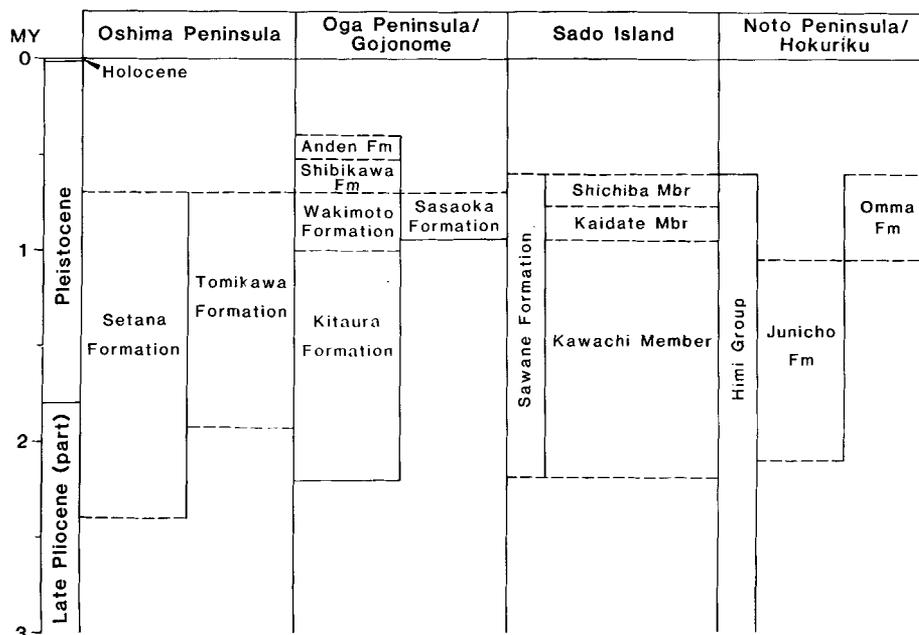


Fig. 2. Stratigraphic correlation chart showing the age relationships of geological formations collected in search of Omma-Manganji ostracods. Absolute ages are considered approximate; relative ages of different formations are based on reliable geological and palaeontological criteria.

**Table 1.** Summary of Stratigraphy and Locality Data of Japanese Neogene and Quaternary Deposits

| Section Number | Section Name       | Formation           | Field Sample Number | Topographic* Map Sheet | Reference                     |
|----------------|--------------------|---------------------|---------------------|------------------------|-------------------------------|
| 1              | Soibetsu R.        | Setana              | 57-59               | Neppu                  | Ikeya & Hayashi, 1982         |
| 2              | Kuroiwa R.         | Setana              | 53, 54              | Pirika                 | Ikeya & Uematsu, 1968         |
| 3              | Sakkurubetso R.    | Setana (Daikan)     | 47, 49              | Kamiyakumo             | Chitoku, 1984                 |
| 4              | Penkerupeshube R.  | Setana              | 44, 46              | Yurappu-Dake           | Ishida, 1981                  |
| 5              | Muneyama River     | Tomikawa            | 29, 30, 32-35       | Jinya                  | Sakagami <i>et al.</i> , 1966 |
| 6              | Hosokomata-zawa R. | Tomikawa            | 36, 37, 40          | Moheji                 | Sakagami <i>et al.</i> , 1966 |
| 7              | Anden              | Waki., Shib., Anden | 85/30-85/35         | Kitaura                | Matsui, 1981                  |
| 8              | Hamamaguchi        | Kitaura             | 85/29               | Kitaura                | Matsui, 1981                  |
| 9              | Oibanazaki         | Kitaura             | 85/28               | Funakawa               | Ishizaki & Matoba, 1985       |
| 10             | Tomita             | Sasaoka             | 85/36               | Gojonome               | Matsui, 1981                  |
| 11             | Monzen             | Sasaoka             | 85/39, 40, 42       | Gojonome               | Matsui, 1981                  |
| 12             | Dai                | Sasaoka             | 85/43, 85/45        | Gojonome               | Matsui, 1981                  |
| 13             | Shichiba R.        | Sawane              | 63, 77, 78          | Sawane                 | Sawane Fm. Res. Grp., 1973    |
| 14             | Mano Bay, NW Coast | Sawane              | 64-67               | Kawaharada             | Sawane Fm. Res. Grp., 1973    |
| 15             | Hanyu R.           | Sawane              | 69, 71-73           | Kawaharada             | Sawane Fm. Res. Grp., 1973    |
| 16             | Mano Bay, W. Coast | Sawane              | 74, 75              | Kawaharada             | Sawane Fm. Res. Grp., 1973    |
| 17             | Asahiyama          | Junicho             | 87, 88              | Himi                   | Hasegawa, 1979                |
| 18             | Okuwa              | Omna                | 91-98               | Kanazawa               | Hasegawa, 1979                |

\* All maps are 1:25000 scale except the Yurappu-Dake which is 1:50,000.

(Figs. 4b-d) correspond to those described by Ishizaki & Matoba (1985). The stratigraphy of these deposits has been described in detail by Kitazato (1975) for the former area and Matsui (1981, 1985) for the latter.

#### Sado Island, Niigata

On Sado Island in the Sea of Japan, the Sawane Formation, including (in ascending order) the Kawachi, Kaidate and Shichiba Members, is exposed in seacliffs on the west coast of Mano Bay. Several sections (numbers 13-16, Table 1) exposing laminated to massive siltstones and shelly pebbly sands were collected from these cliffs and small tributaries nearby (Fig. 4e). The Sawane Research Group (1973) made the following correlations of members of the Sawane Formation with the type sections of the Niigata oil field: Kawachi Member = Nishiyama formation (late Pliocene to early Pleistocene), Kaidate and Shichiba Members = Haizume Formation (middle Pleistocene).

#### Hokuriku Province, Toyama/Ishikawa

The Himi Group includes fossiliferous deposits in the Hokuriku Province on the Japan Sea side of central Honshu, including the namesake of Japanese cold water faunas - the Omna Formation. Ostracods were collected from the Junicho Formation (section 17) exposed near the town of Himi, Toyama Prefecture and the Omna Formation (section 18) along the Sai-gawa River 4km south of Kanazawa, Ishikawa Prefecture (Table 1, Figs. 4f, g). The Junicho and Omna

Formations correspond respectively to sections 28 and 3 of Hasegawa (1979) who demonstrated a late Pliocene to Pleistocene age for the Junicho Formation and a middle Pleistocene age for the Omna Formation.

#### THE OMMA-MANGANJI OSTRACOD FAUNA

A total of 224 ostracod species were identified from the ten formations. Many of these were rare, constituted small percentages of the total assemblages, and were difficult to identify as previously described species. Consequently, from the 224 total species, 135 species occurring in three or more samples were studied in detail and the following analyses refer only to these species. Table 2 summarises the total numbers of samples, specimens, and species for each formation. Almost 9000 specimens of the 135 common species were examined. The average number of specimens per sample was 170 valves and/or carapaces.

We calculated Jaccard similarity coefficients to compare the overall similarities between the ostracod assemblages from the ten formations studied based on the presence or absence of the 135 common species (Table 3). The Jaccard coefficient is calculated as  $C/N_1 + N_2 - C$ , where  $C$  is the number of species common to two formations being compared and  $N_1$  and  $N_2$  are the total numbers of species in the two formations (Hazel, 1970b). The highest Jaccard coefficients are for the Sawane and Setana Formation (.582), which have 64 species in common, and the Setana and Tomikawa Formations (.562), with 59 species in

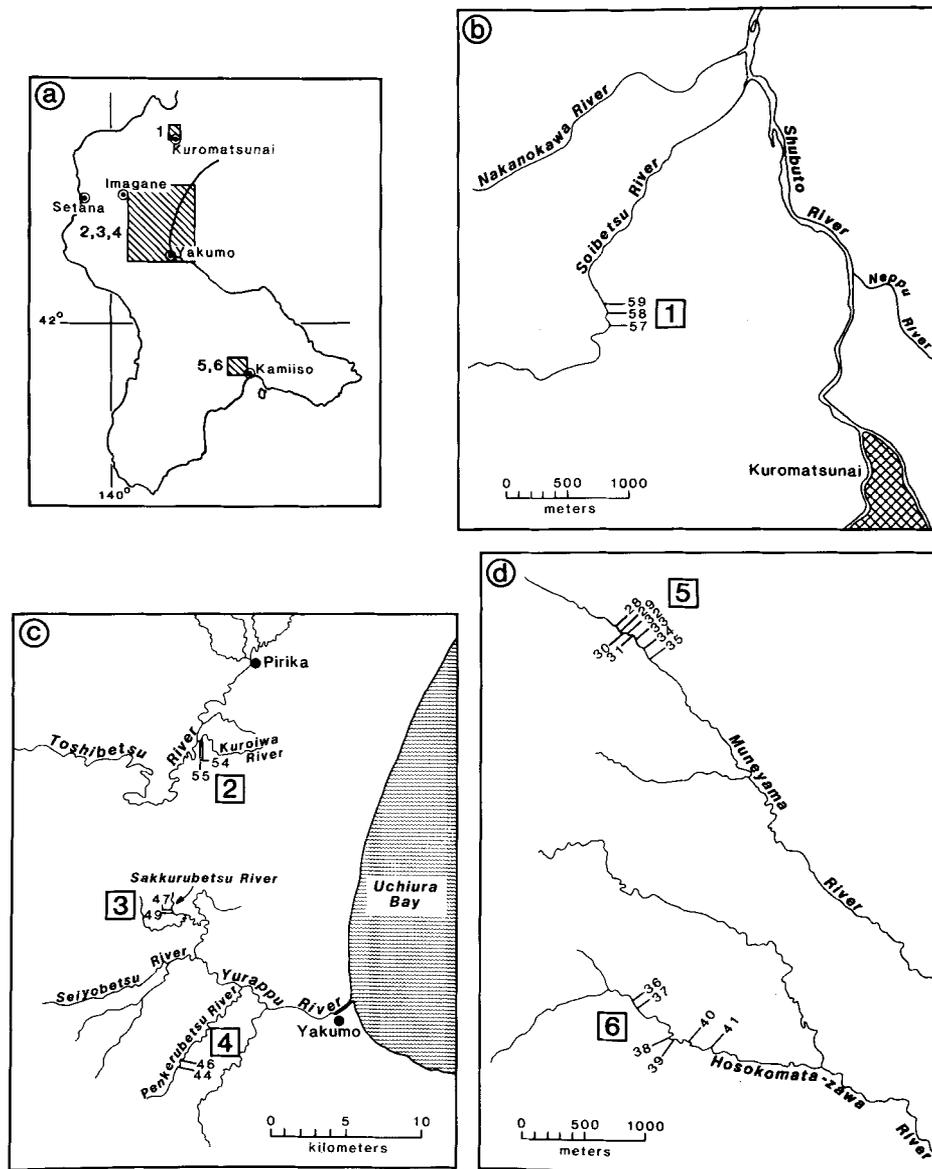


Fig. 3. Locality maps for Oshima Peninsula, Hokkaido samples: a, general locality map for Setana and Tomikawa Formations (sections 1–6); b, location of section 1 (Setana Formation), Soibetsu River; c, location of sections 2, 3 and 4 (Setana formation), Imagane area; d, location of sections 5 and 6 (Tomikawa Formation), Kamiiso area.

common. Relatively high values were also obtained for the following pairs of formations: Setana-Sasaoka, Sawane-Sasaoka and Sasaoka-Junicho.

The lowest Jaccard coefficients were obtained for the Omma and Kitaura Formations (.120) with only 9 species in common, and the Omma and Wakimoto Formations (.130) with only 10 in common. Other low Jaccard values were obtained for the Kitaura-Junicho, the Kitaura-Anden and Wakimoto-Anden Formations.

High similarities are generally interpreted to signify similar palaeoenvironments, in particular, similar water

temperatures and depths. Likewise, the low similarities are believed to signify faunal differences associated with differences in these environmental parameters. For example, the low similarities between the Omma Formation and most other formations may reflect a deeper water environment, probably mid to outer shelf, in contrast to inner shelf or bay for other formations and Ogasawara (1981) has postulated a complex sequence of oceanographic changes for Omma-Manganji deposits.

Because our focus was on cryophilic species, we

**Table 2.** Summary of ostracods from the ten Omma-Manganji Formations studied.

| Formation | Number of Samples | Number of Species | Total | Numbers of specimens                        |  |   |
|-----------|-------------------|-------------------|-------|---|--|---|
|           |                   |                   |       | Circumpolar Species<br>(% total assemblage) | Cryophilic Species<br>(% total assemblage) | Temperate Species<br>(% total assemblage) |
| Setana    | 9                 | 94                | 2198  | 507 (23.1)                                  | 883 (40.2)                                 | 808 (36.7)                                |
| Tomikawa  | 9                 | 70                | 484   | 224 (46.3)                                  | 158 (32.6)                                 | 102 (21.1)                                |
| Anden     | 1                 | 35                | 262   | 4 (1.5)                                     | 15 (5.7)                                   | 243 (92.8)                                |
| Shibikawa | 2                 | 52                | 723   | 162 (22.4)                                  | 339 (46.9)                                 | 222 (30.7)                                |
| Wakimoto  | 2                 | 40                | 333   | 122 (36.6)                                  | 33 (9.9)                                   | 178 (53.5)                                |
| Kitaura   | 2                 | 37                | 356   | 168 (47.2)                                  | 51 (14.3)                                  | 137 (38.5)                                |
| Sasaoka   | 6                 | 77                | 1050  | 185 (17.6)                                  | 314 (29.9)                                 | 551 (52.5)                                |
| Sawane    | 12                | 80                | 2848  | 395 (13.8)                                  | 930 (32.7)                                 | 1523 (53.5)                               |
| Junicho   | 2                 | 56                | 281   | 17 (6.0)                                    | 37 (13.2)                                  | 227 (80.8)                                |
| Omma      | 8                 | 47                | 461   | 85 (18.4)                                   | 179 (38.8)                                 | 197 (42.7)                                |

divided the total ostracod fauna into three categories of species. First, the 26 species we refer to as “circumpolar” (Table 4) are well documented in Recent and/or fossil deposits of the North Atlantic and adjacent Arctic seas. Herein, the term “circumpolar” refers only to the Arctic, not the Antarctic. We do not imply necessarily that these circumpolar species live in the Arctic region today, only that they are known from fossil and/or modern sediments from high-latitude northern hemisphere seas.

Many circumpolar species are reported here for the first time from the Pacific. In some cases, morphological differences between Pacific and other Arctic regions (particularly the North Atlantic) populations may only signify intraspecific variation. For example, *Baffinicythere howei* and *Cytheropteron champlainum* are morphologically distinct from Atlantic forms, but the overall similarities appear to be so strong that we believe they merit subspecies status. Conversely, in other cases, such as *Hemicytherura clathrata*, *Heter-*

*ocyprideis fascis*, *Sarsicytheridea bradii*, *Palmenella limicola*, *Hemicythere emarginata*, *Semicytherura affinis* and others, Pacific specimens are within the range of normal intra-population variability for Atlantic forms. Taxonomic affinities are discussed briefly in the systematic palaeontology section below.

A second group of 21 species, referred to here as “cryophilic”, typically occur with circumpolar species in Japanese deposits and, in most cases, are members of high-latitude genera (Table 4). Many of these cryophilic species were described by Hanai (1957a, 1970), Schornikov (1974), and Tabuki (1986). Hanai & Ikeya (in prep.) describe the species listed as “*Urocythereis*” under two new genera. Their modern distributions are poorly known and none of them are known from the Atlantic region, although William M. Briggs, Jr. has found *Kotoracythere* sp. A and a form similar to *Howeina camptocytheroidea* in the Beaufort Sea off Canada (Briggs, pers. comm., 1986) and others are probably related to Atlantic species.

**Table 3.** Jaccard Similarity Coefficients for Japanese Omma-Manganji deposits

|   |           | Jaccard Coefficient |      |      |      |      |      |      |      |      |      |
|---|-----------|---------------------|------|------|------|------|------|------|------|------|------|
|   |           | Set                 | Tom  | Wak  | Shi  | And  | Kit  | Sas  | Saw  | Jun  | Omm  |
| Number<br>of<br>Species<br>in<br>Common | Setana    | —                   | .562 | .276 | .417 | .240 | .323 | .513 | .582 | .376 | .270 |
|   | Tomikawa  | .59                 | —    | .294 | .386 | .235 | .321 | .427 | .351 | .273 | .286 |
|   | Wakimoto  | .29                 | .25  | —    | .260 | .210 | .400 | .272 | .348 | .215 | .130 |
|   | Shibikawa | .43                 | .34  | .19  | —    | .318 | .271 | .387 | .333 | .350 | .303 |
|   | Anden     | .25                 | .20  | .13  | .21  | —    | .200 | .287 | .237 | .230 | .281 |
|   | Kitaura   | .32                 | .26  | .22  | .19  | .12  | —    | .281 | .300 | .192 | .120 |
|   | Sasaoka   | .58                 | .44  | .25  | .36  | .25  | .25  | —    | .510 | .494 | .442 |
|   | Sawane    | .64                 | .39  | .31  | .33  | .22  | .27  | .53  | —    | .347 | .221 |
|   | Junicho   | .41                 | .27  | .17  | .28  | .17  | .15  | .44  | .35  | —    | .392 |
|   | Omma      | .30                 | .26  | .10  | .23  | .18  | .09  | .38  | .23  | .29  | —    |

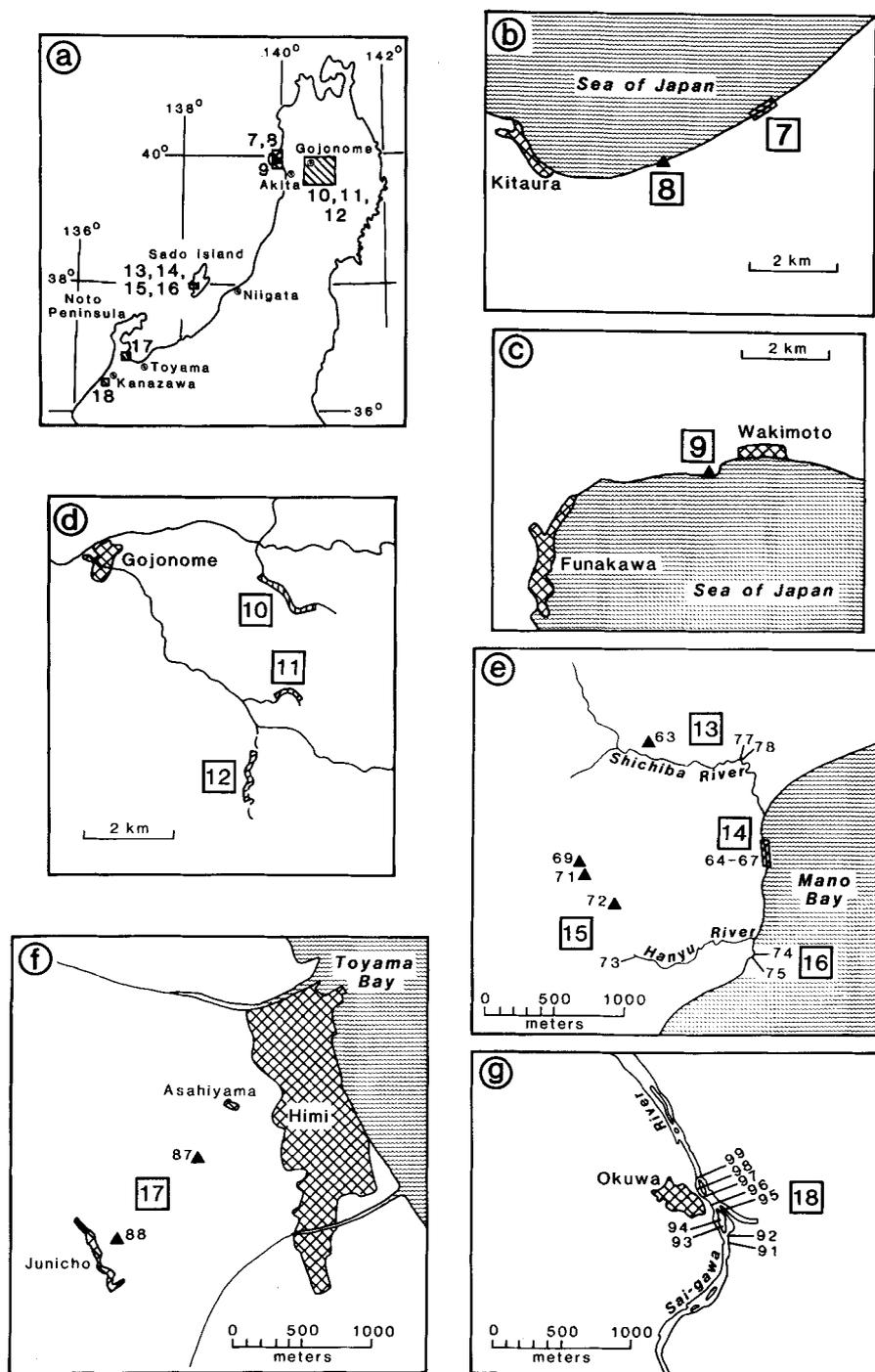


Fig. 4. Locality maps for northern Honshu: a, general localities of sections 7-18; b, location of section 7 (Anden, Shibikawa and Wakimoto Formations), Oga Peninsula; c, location of section 9 (Kitaura Formation), Oga Peninsula; d, location of sections 10, 11, 12 (Sasaoka Formation), Gojonome area; e, location of sections 13-16 (Sawane Formation), Sado Island; f, location of section 18 (Omma Formation), Okuwa area; g, location of section 17 (Junicho Formation), Himi area.

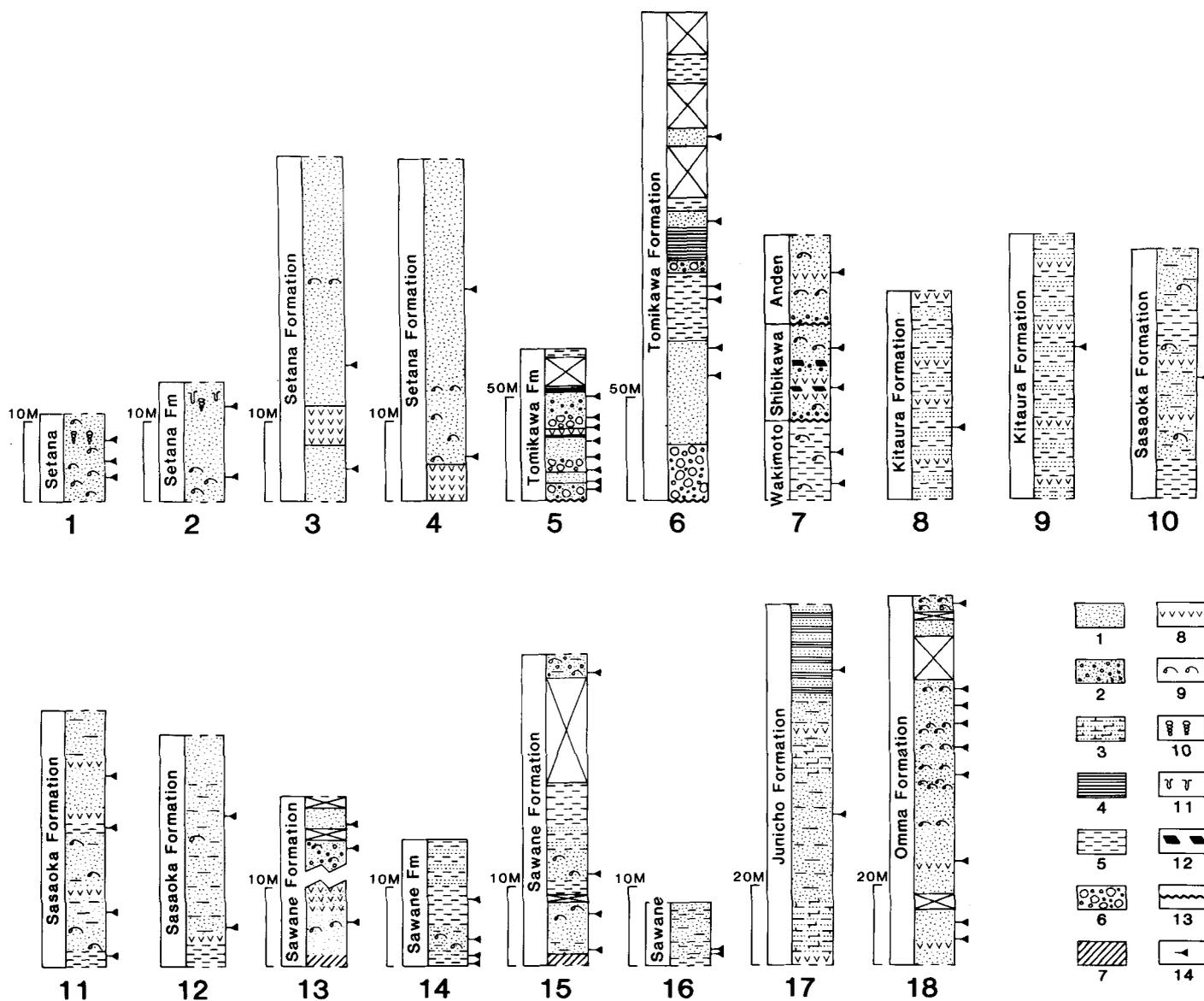


Fig. 5. Columnar sections for Omma-Manganji sections 1-18. Datum is base of section, and sections 7-12 are schematic representations. Lithological symbols: 1-sand, 2-coarse sand, 3-calcareous sand, 4-clay, 5-silt, 6-conglomerate, 7-diatomite, 8-tuff, 9-shell, 10-gastropods, 11-burrows, 12-wood, 13-unconformity, 14-ostracod sample horizon.

The third group includes the remaining 88 species which we refer to as "endemic temperate" to distinguish them as taxa that are typical of the temperate climatic zones in the western Pacific. Many are living along Japanese coasts today; others are probably extinct. Detailed discussion of these species is beyond the scope of this paper. However, it is noteworthy that circumpolar species co-occur with species that are apparently more thermophilic in habitat in species-rich assemblages that contrast with typical low diversity, post-glacial assemblages from the North Atlantic (Neale & Howe, 1975; Cronin, 1981; in press).

These three categories of species are admittedly somewhat arbitrary and, with additional work on modern North Pacific faunas, a better zoogeographic zonation will be available. Nonetheless, they conveniently subdivide the fauna for the purpose of discussion. Table 2 lists and Fig. 6 graphically displays the percentages of circumpolar, cryophilic and temperate species in each formation.

The Tomikawa Formation contains 21 of the 26 circumpolar species, comprising 46.3% of the total Tomikawa assemblage. It is the only formation in Japan to yield *Heterocyprideis fascis* and *Sarsicyther-*

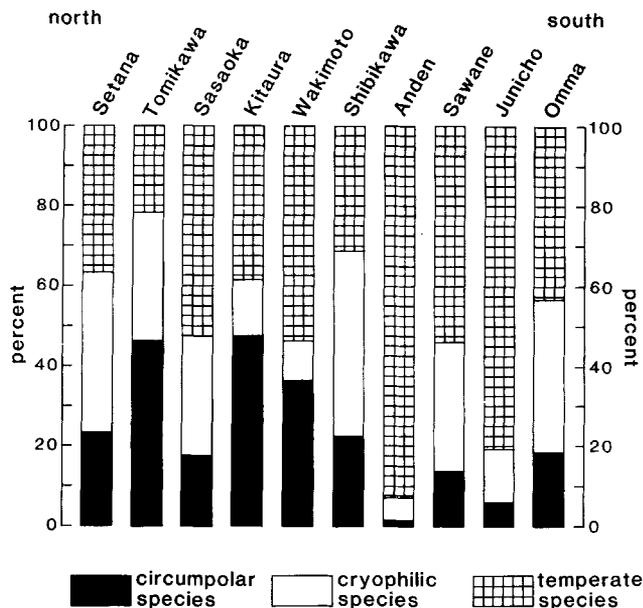


Fig. 6. Percentage of circumpolar, other cryophilic, and endemic temperate species in the total ostracod assemblages from the ten formations studied.

*idea macrolaminata*. *Rabilimis septentrionalis* occurs in the Tomikawa, Wakimoto and Shibikawa Formations, while *Hemicytherura clathrata* occurs in the Tomikawa and Setana Formations. *Sarsicytheridea bradleyi* occurs in the Tomikawa and Shibikawa Formations. The presence of several circumpolar species of *Cytheropteron* and the absence of such temperate genera as *Cornuconcha*, *Loxoconcha*, *Aurila* and *Bythoceratina* also reflects the cold water environment of the Tomikawa.

The Setana Formation contains a more diverse ostracod assemblage including 20 circumpolar species, which comprise 23.1% of the total. *Baffinicythere howei*, *Finmarchinella angulata*, *Acanthocythereis dunelmensis* and circumpolar species of *Semicytherura*, *Cytheropteron*, characterise this unit, which also contains abundant *Finmarchinella*, *Hemicythere*, and *Cythere*.

In Akita Prefecture, the Sasaoka, Wakimoto, Kitaura, and Shibikawa Formations contain moderate amounts of circumpolar species (13, 12, 11 and 9 species respectively, representing 17.6, 36.6, 47.2, and 22.4%, Table 2). The Wakimoto includes the characteristic species *Acanthocythereis dunelmensis*, *Rabilimis septentrionalis*, *Semicytherura undata*, and rare *Jonesia simplex* and *Cluthia japonica*.

The Sawane Formation of Sado Island contains 12 (13.8%) circumpolar species including the large form of *Acanthocythereis dunelmensis*, *Baffinicythere howei*, *Hemicythere emarginata*, *Cytheropteron champlainum*, *Semicytherura subundata* and *S. undata*.

The Junicho, Omma and Anden formations contain

few circumpolar species (7, 6 and 4 species respectively, representing 6.0, 18.4 and 1.5%, Table 2) and, as suggested by the Jaccard coefficients, are faunally quite distinct from other Omma-Manganji assemblages.

Temporal changes in the ostracod assemblages were examined in the Tomikawa (section 5), Sawane (section 14), and Omma (section 18) Formations and in the composite sequence of the Kitaura, Wakimoto, Shibikawa and Anden Formations from the Oga Peninsula (sections 7, 8 and 9) (Figs. 7a–d). The percentage of circumpolar species ranges from moderate in the lower part of the Tomikawa to very high (60–85%) in the middle part and dropping back to moderate in the upper part (Fig. 7a). The four samples in section 14 show little change in ostracod assemblages for this part of the Sawane Formation (Fig. 7c). The Omma Formation sequence (Fig. 7d) shows widely fluctuating percentages but this is partly attributable to small numbers of specimens and also perhaps to the complex oceanography (Ogasawara, 1981). In the Oga sequence (Fig. 7b), the Kitaura and Wakimoto Formations show moderate percentages and the overlying Shibikawa and Anden Formations show significant decreases in circumpolar species (see also Okada, 1979).

Figs. 8a and 8b show the percentages of each category for the nine and six samples respectively from the Setana and Sasaoka formations suggesting little variation within each formation in the contribution of circumpolar, cryophilic and temperate species.

## DISCUSSION

Hanai's early studies on selected genera of Setana and Sawane ostracods clearly showed the cold water affinities of the fauna. Tabuki (1986) convincingly demonstrated that the Daishaka Formation (also part of the Omma-Manganji fauna) ostracods include many genera and species in common with other high-latitude assemblages, especially those from seas off the British Isles, northern Europe, Scandinavia and eastern North America. Our data builds on these studies and three conclusions can be made at the present time.

First, the Omma-Manganji ostracod fauna actually consists of a heterogeneous array of species assemblages signifying different palaeoenvironments and water temperatures. Despite the preliminary nature of ostracod data for several formations, important similarities and differences can already be identified. The Setana and Sawane Formations, for example, show strong similarities in their high species diversity and the overall composition of the faunas. In general, water temperature, depth and substrate were probably the most important factors influencing the particular species occurring in each formation. This conclusion corroborates results derived from Omma-Manganji molluscan assemblages, which include a variety of species associations that have been subdivided by

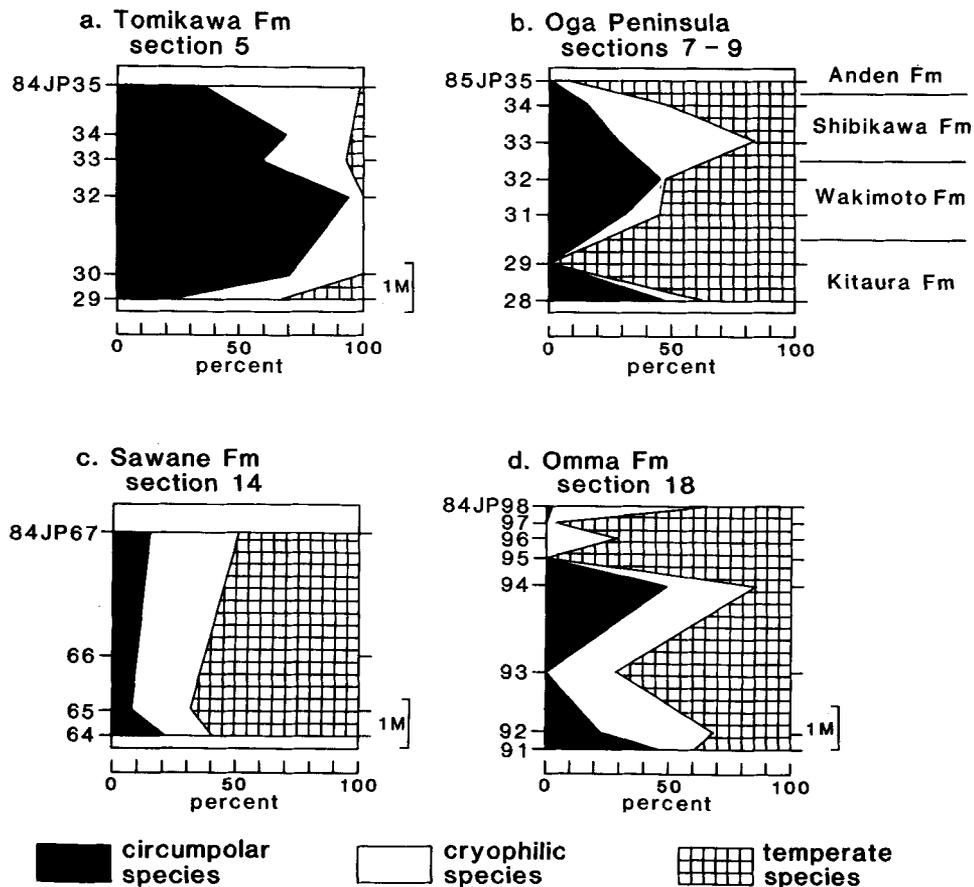


Fig. 7. Temporal variation in percentages of circumpolar, other cryophilic and endemic temperate species: a, Tomikawa Formation, section 5; b, Oga Peninsula, sections 7-9 composite; c, Sawane Formation, section 14; d, Omma Formation, section 18.

Chinzei (1978) into two coastal associations and one offshore muddy bottom association. However, more detailed sampling than we were able to obtain is required to determine short-term oceanographic changes within a single formation.

Second, we expand the growing list of ostracod species common to the North Pacific and North Atlantic Neogene and Quaternary. Of the 26 circumpolar species discussed above, Tabuki (1986) recorded 10 from the Daishaka Formation: *Acanthocythereis dunelmensis*, *Argilloecia conoidea*, *Baffinicythere howei*, *Cytheropteron nodosolatum* (= *C. yajimai* Tabuki, 1986, part, Pl. 17, fig. 13), *Elofsonella concinna*, *Finmarchinella angulata*, *Hemicythere emarginata*, *Munseyella hatatensis*, *Palmenella limicola*, *Semicytherura subundata*, and perhaps *Sclerochilus contortus*. Tabuki (1986) also found *Cluthia japonica* and *Cytheropteron angulatum* (= *C. tsugaruense* Tabuki, 1986). We add 16 species to the list of circumpolar species occurring as fossils in Japan and first occurrences in the Pacific region for three genera, *Heterocyp-*

*rideis*, *Rabilimis*, and *Sarsicytheridea*.

Third, we propose the hypothesis, on the basis of our qualitative assessment of cryophilic genera from different high-latitude seas, that during periods of climatic oscillations, populations of stenotopic species give rise more frequently to new species than do eurytopic species. We also suggest that, for unknown reasons, certain genera diversified to greater degrees in the Pacific compared with the Atlantic despite the fact that both regions were influenced by the same global climatic changes. It is well known that global climatic changes frequently altered North Pacific (Sancetta & Silvestri, 1986) and North Atlantic (Shackleton *et al.*, 1984) palaeoceanography, affecting the zoogeography of temperature-sensitive species. Climatic cooling caused range expansion of cryophilic species into lower latitudes and, climatic warming, range contraction to higher latitudes. For example, southward shifts in species' zoogeographic ranges are known from the occurrence of cryophilic species in post-glacial deposits in the British Isles (Brady, Crosskey & Robertson,

1874), and eastern North America (Brady & Crosskey, 1871; Cronin, 1981, in press). The Omnia-Manganji fauna demonstrates that similar range shifts occurred in the Northern Pacific. Further, the late Pliocene-middle Pleistocene age predates the late Pleistocene (15,000–10,000 years) age of most North Atlantic faunas. By extending the stratigraphic ranges of cryophilic species, we can assume these species were subjected to many climatic cycles and that populations of cryophilic species have repeatedly shifted their ranges during glacial-interglacial cycles. In theory, range expansion and contraction might result in evolutionary divergence and the evolution of new species in the distal-most populations (Hanai, 1977).

Some cryophilic genera contain one or several seemingly ubiquitous species, while the opposite is true of other genera that diversified during the last few million years and include species endemic to different regions. Those in the former category include more eurytopic taxa able to withstand broad temperature and depth ranges. For example, *Palmenella limicola* is common in high-latitude deposits in the Atlantic and Pacific representing many types of palaeoenvironments. Elofson (1941) and Hazel (1970a) found this species tolerant of a wide range of depths and

temperatures. Similarly, *Sarsicytheridea bradii*, *S. macrolaminata* and *Heterocyprideis fascis* are eurytopic species tolerant of a wide range of environmental conditions.

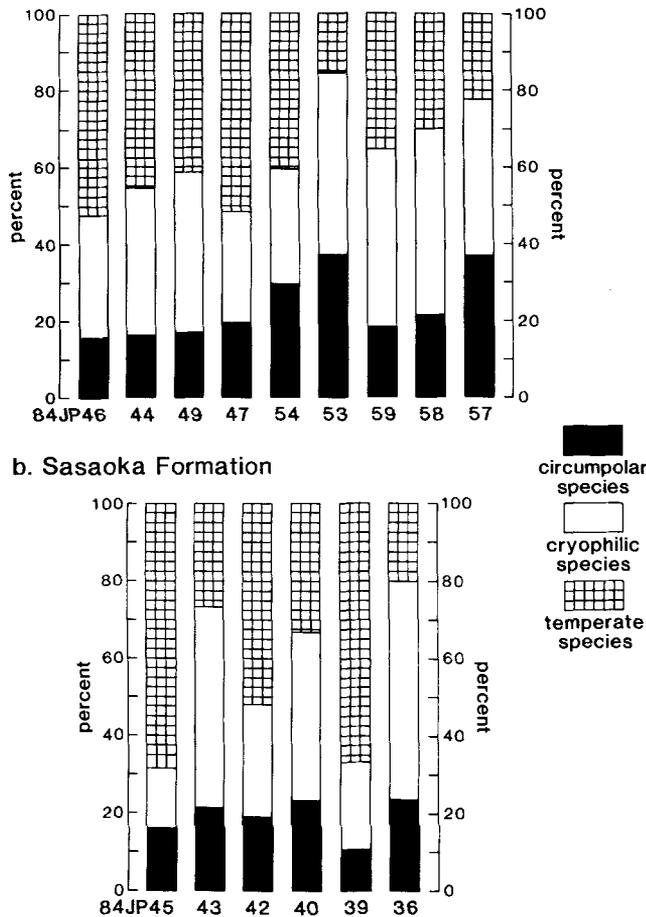
Other cryophilic genera have been undergoing active speciation during the Neogene/Quaternary. Among them, several are more diverse in the Pacific: *Finmarchinella*, *Robertsonites*, *Hemicythere*, and *Cythere*, and include species endemic to the Pacific. Cold water members of the genera *Cytheropteron* and *Semicytherura* also diversified during the last few million years along Asia and North America and Europe, although it is not yet clear how many species in these genera are endemic to the Atlantic, Pacific or both.

These hypotheses require rigorous evaluation. One approach that we advocate is phylogenetic and zoogeographic analysis of monophyletic groups employing detailed morphological analyses of populations from the entire geographic range of the taxon. Studies of *Cythere* (Ikeya & Tsukagoshi, in press) and the thermophilic genus *Puriana* (Cronin, 1987) are examples in which the effects of climate change on ostracods having different ecologies can be assessed. The apparent relationships of Omnia-Manganji ostracods to other high-latitude forms brings out the need for direct

**Table 4.** Circumpolar and other Cryophilic ostracods occurring in the Omnia-Manganji Fauna.

| Circumpolar Species   | Cryophilic Species   |
|---|--|
| <i>Acanthocythereis dunelmensis</i> (Norman, 1865)                            | <i>Baffinicythere</i> sp. A                                |
| <i>Argilloecia</i> cf. <i>A. conoidea</i> Sars, 1923                          | <i>Finmarchinella daishakaensis</i> Tabuki, 1986           |
| <i>Baffinicythere howei</i> Hazel, 1967 subspecies                            | <i>Finmarchinella hanaii</i> Okada, 1979                   |
| <i>Cytheropteron alatum</i> Sars, 1865  | <i>Finmarchinella nealei</i> Okada, 1979                   |
| <i>Cytheropteron</i> cf. <i>C. arcuatum</i> Brady, Crosskey & Robertson, 1874 | <i>Finmarchinella rectangularata</i> Tabuki, 1986          |
| <i>Cytheropteron champlainum</i> Cronin, 1981 subsp.                          | <i>Hemicythere gurjanovae</i> Schornikov, 1974             |
| <i>Cytheropteron</i> cf. <i>C. elaei</i> Cronin, in press                     | <i>Hemicythere? kitanipponica</i> (Tabuki, 1986)           |
| <i>Cytheropteron nodosolatum</i> Neale & Howe, 1973                           | <i>Hemicythere ochotensis</i> Schornikov, 1974             |
| <i>Elofsonella concinna</i> (Jones, 1856)                                     | <i>Hemicythere quadrinodosa</i> Schornikov, 1974           |
| <i>Finmarchinella angulata</i> (Sars, 1865)                                   | <i>Howeina camptocytheroidea</i> Hanai, 1957               |
| <i>Hemicythere emarginata</i> (Sars, 1865)                                    | <i>Kotoracythere</i> sp. A                                 |
| <i>Hemicytherura clathrata</i> (Sars, 1865)                                   | <i>Normanicythere? cf. N. japonica</i> Tabuki, 1986        |
| <i>Heterocyprideis fascis</i> (Brady & Norman, 1889)                          | <i>Normanicythere</i> sp. A                                |
| <i>Jonesia simplex</i> (Norman, 1865)   | <i>Patagonacythere robusta</i> Tabuki, 1986                |
| <i>Munseyella hatatensis</i> (Ishizaki, 1966)                                 | <i>Robertsonites hanaii</i> Tabuki, 1986                   |
| <i>Normanicythere leioderma</i> (Norman, 1869)                                | <i>Robertsonites reticuliforma</i> Tabuki, 1986            |
| <i>Palmenella limicola</i> (Norman, 1865)                                     | <i>Robertsonites tsugaruana</i> Tabuki, 1986               |
| <i>Patagonacythere dubia</i> (Brady, 1868)                                    | <i>Schizocythere okhotskensis</i> Hanai, 1970              |
| <i>Rabilimis septentrionalis</i> (Brady, 1866)                                | " <i>Urocythereis</i> " <i>posterocaudata</i> Tabuki, 1986 |
| <i>Sarsicytheridea bradii</i> (Norman, 1865)                                  | " <i>Urocythereis</i> " sp. A                              |
| <i>Sclerochilus contortus</i> (Norman, 1862)                                  | " <i>Urocythereis</i> " sp. C                              |
| <i>Semicytherura affinis</i> (Sars, 1865)                                     |  |
| <i>Semicytherura complanata</i> (Brady, Crosskey & Robertson, 1874)           |  |
| <i>Semicytherura mainensis</i> (Hazel & Valentine, 1969)                      |  |
| <i>Semicytherura subundata</i> Hanai, 1957                                    |  |
| <i>Semicytherura undata</i> (Sars, 1865)                                      |  |

## a. Setana Formation



## b. Sasaoka Formation

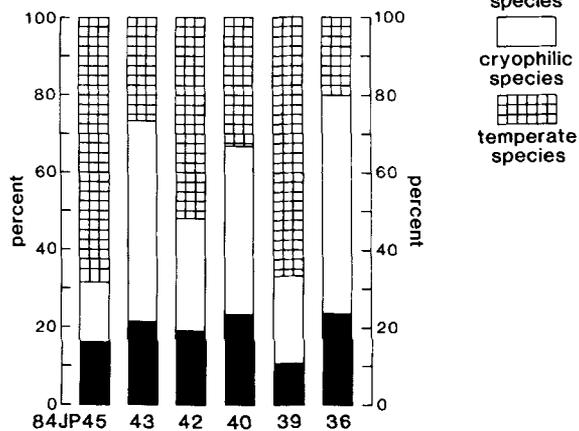


Fig. 8. Percentage of circumpolar, other cryophilic and endemic temperate species in all samples: a, Setana Formation; b, Sasaoka Formation.

comparison of high-latitude species from different regions and the integration of climatic change into our phylogenetic analyses.

## NOTES ON THE SYSTEMATIC PALAEOLOGY

This section provides brief comments about the 26 circumpolar, the 21 cryophilic species and several other species deserving special attention regarding their affinities with North Atlantic species. Illustrated specimens are deposited in the Department of Paleobiology, U.S. Museum of Natural History, Washington, D.C.

Family Pontocyprididae G. W. Müller, 1884

Genus *Argilloecia* Sars, 1865

*Argilloecia conoidea* Sars, 1923

**Remarks.** This species was also reported from the Daishaka Formation by Tabuki (1986).

**Distribution.** Setana, Sawane, and Wakimoto Formations.

**Material.** 22 specimens.

Family Cytherideidae Sars, 1925

*Heterocyprideis* Elofson, 1941

*Heterocyprideis fascis* (Brady & Norman, 1889)

(Pl. 1, fig. 15)

**Remarks.** *H. fascis* is very rare in the Tomikawa Formation. It is known from Pleistocene deposits off the eastern United States (Hazel, 1968), in eastern Canada (Cronin, in press), and in Norway (Lord, 1980) and in Recent sediments off Newfoundland (Benson *et al.*, 1983), where it was recorded as *H. sorbyana*. Masson & Whatley (1977) described a closely related species, *H. macrotuberculata* from the Quaternary of the North Sea, which we think might be conspecific with *H. fascis*.

**Distribution.** Tomikawa Formation.

**Material.** 3 specimens.

Genus *Kotoracythere* Ishizaki, 1966

*Kotoracythere* sp. A

(Pl. 3, fig. 18)

**Remarks.** This species was referred to as *Kotoracythere* sp. by Tabuki (1986) and by Ishizaki & Matoba (1985). W. M. Briggs, Jr. (pers. comm., 1986) reported a related species from the Beaufort Sea off northwestern Canada.

**Distribution.** Tomikawa, Omma, Shibikawa, and Sasaoka Formations.

**Material.** 62 specimens.

Genus *Munseyella* van den Bold, 1957

*Munseyella hatatatensis* Ishizaki, 1966

(Pl. 3, fig. 16)

**Remarks.** We believe *M. hatatatensis* is conspecific with *M. mananensis* Hazel & Valentine, 1969, a North Atlantic species common off northeastern North America and in Pleistocene deposits in eastern Canada (Cronin, in press).

**Distribution.** Tomikawa, Setana, Junicho, Omma, Shibikawa and Sasaoka Formations.

**Material.** 85 specimens.

Genus *Sarsicytheridea* Athersuch, 1982

*Sarsicytheridea bradii* (Norman, 1865)

(Pl. 1, fig. 12)

**Remarks.** *S. bradii* shows no obvious differences with specimens from the North Atlantic.

**Distribution.** Tomikawa, abundant in the Shibikawa Formation.

**Material.** 83 specimens.

*Sarsicytheridea macrolaminata* (Elofson, 1939)

(Pl. 1, fig. 10)

**Remarks.** Only late instars were found in the Tomika-

wa Formation.

**Distribution.** Tomikawa Formation.

**Material.** 3 specimens.

Family Leptocytheridae Hanai, 1957

Genus *Cluthia* Neale, 1973

*Cluthia japonica* Tabuki, 1986

**Remarks.** This species is rare in Japanese deposits. Tabuki (1986) described *C. japonica* from the Daishaka Formation.

**Distribution.** Setana and Wakimoto Formations.

**Material.** 3 juvenile specimens.

Family Hemicytheridae Puri, 1953

Genus *Baffinicythere* Hazel, 1967

*Baffinicythere howei* Hazel, 1967, subspecies  
(Pl. 2, fig. 16)

**Remarks.** This species is represented in Japan by several morphotypes ranging from coarsely reticulate to variably tuberculate. Tubercles are often well developed in the posterior half. Japanese specimens resemble *B. howei* from the North Atlantic in overall shape, size, and ornament and in the strong sexual dimorphism of the carapace, but they have a much stronger ridge along the anterior margin and, in the posterior area, a less conspicuous triangular shaped area formed by ridges. At present we consider the Japanese form a distinct subspecies of *B. howei*.

**Distribution.** Tomikawa, Setana, Sawane, Junicho, Omma, Kitaura, Wakimoto, Shibikawa., and Sasaoka Formations.

**Material.** 347 specimens.

*Baffinicythere?* sp. A  
(Pl. 2, fig. 18)

**Remarks.** This large, thick-shelled species was referred to as *Ambostracon* sp. 1 by Tabuki (1986) and is tentatively placed in *Baffinicythere*.

**Distribution.** Setana, Sawane, and Shibikawa Formations.

**Material.** 46 specimens.

Genus *Elofsonella* Pokorny, 1955

*Elofsonella concinna* (Jones, 1856)  
(Pl. 1, fig. 13)

**Remarks.** Tabuki (1986) reported this species from the Daishaka Formation. Japanese specimens have a less conspicuous anterior marginal rim than North Atlantic specimens. W. M. Briggs (pers. comm., 1986) reports this form as *Elofsonella neoconcinna* Bassiouni, 1965 from Chesterfield Inlet, Hudson Bay, Canada.

**Distribution.** Tomikawa, Setana, and Sasaoka Formations.

**Material.** 72 specimens.

*Finmarchinella* Swain, 1963

*Finmarchinella angulata* (Sars, 1865)  
(Pl. 1, fig. 9)

**Remarks.** Comparison of specimens of *Finmarchinella angulata* from off Greenland, Norton Sound and the Gulf of Alaska with fossil specimens of *F. japonica* (Ishizaki, 1966) indicate the two are conspecific. Okada (1979) also identified *F. angulata* from late Cenozoic deposits of the Oga Peninsula, Akita Prefecture, Japan and Tabuki (1986) lists it from the Daishaka Formation.

**Distribution.** Tomikawa, Setana, Sawane, Kitaura, Wakimoto, Shibikawa, and Sasaoka Formations.

**Material.** 306 specimens.

*Finmarchinella daishakaensis* Tabuki, 1986  
(Pl. 1, fig. 6)

**Remarks.** This species seems most closely related to *F. logani* (Brady & Crosskey, 1871) but is quite distinct in shape and ridge pattern.

**Distribution.** Tomikawa, Setana, Sawane, Kitaura, and Wakimoto Formations.

**Material.** 187 specimens.

*Finmarchinella hanaii* Okada, 1979  
(Pl. 1, fig. 3)

**Distribution.** Tomikawa, Setana, Sawane, Junicho, Kitaura, Wakimoto, Shibikawa, Anden, and Sasaoka Formations.

**Material.** 559 specimens.

*Finmarchinella nealei* Okada, 1979  
(Pl. 1, fig. 5)

**Remarks.** *F. nealei* seems most closely related to *F. finmarchica* (Sars, 1865) from the North Atlantic region (see Neale, 1974).

**Distribution.** Tomikawa, Setana, Sawane, Kitaura, Wakimoto, Shibikawa, Anden, and Sasaoka Formations.

**Material.** 77 specimens.

*Finmarchinella rectangulata* Tabuki, 1986  
(Pl. 1, fig. 2)

**Distribution.** Tomikawa, Setana, Sawane, and Wakimoto Formations.

**Material.** 65 specimens.

Genus *Hemicythere* Sars, 1925

*Hemicythere?* cf. *H. boreokurila* (Schornikov, 1974)  
(Pl. 2, fig. 8)

**Remarks.** This rare species is characterised by a finely pitted, faintly reticulate surface and a very compressed carapace in dorsal view. It resembles the form described as *Cythere boreokurila* by Schornikov (1974).

**Distribution.** Tomikawa and Sawane Formations.

**Material.** 5 specimens.

*Hemicythere emarginata* (Sars, 1865)

(Pl. 2, fig. 3)

**Remarks.** Schornikov (1974) also reported this species from the Kuril Islands. Horne & Whittaker (1983) pointed out that *Cythereis emarginata* Sars, 1865 has two frontal muscle scars and a male copulatory appendage with a conspicuous *ductus ejaculatorius* and therefore should be placed in *Hemicythere*.

**Distribution.** Tomikawa, Setana, Sawane, Kitaura, and Wakimoto Formations.

**Material.** 204 specimens.

*Hemicythere gurjanovae* Schornikov, 1974

(Pl. 2, fig. 9)

**Remarks.** This species is similar to *H. posterovestigulata* Schornikov, 1974 and the two species are not distinguished here.

**Distribution.** Setana, Sawane, Junicho, and Sasaoka Formations.

**Material.** 32 specimens.

*Hemicythere? kitanipponica* (Tabuki, 1986)

(Pl. 2, fig. 6)

**Remarks.** Tabuki (1986) assigned this species to *Ambostracon* Hazel, 1962 but its shape, surface ornament, and two frontal muscle scars suggest it be tentatively placed in *Hemicythere*.

**Distribution.** Setana, Sawane, Junicho, and Sasaoka Formations.

**Material.** 84 specimens.

*Hemicythere ochotensis* Schornikov, 1974

(Pl. 2, fig. 4)

**Remarks.** This species lacks the incurved anterior ridge of *H. gurjanovae* but the two can sometimes be confused.

**Distribution.** Tomikawa, Setana, and Sawane Formations.

**Material.** 11 specimens.

*Hemicythere orientalis* Schornikov, 1974

(Pl. 2, figs. 5, 7)

**Remarks.** This species was placed in the "villosa" group by Schornikov (1974) and is one of the more common *Hemicythere* in the Japanese deposits. The development of surface ornament and thickness of the carapace vary among populations from different formations.

**Distribution.** Tomikawa, Setana, Sawane, Junicho, Wakimoto, Shibikawa, Anden, and Sasaoka Formations.

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**Explanation of Plate 1**

Figs. 1, 4. *Acanthocythereis dunelmensis* (Norman, 1865), 1, LV female, USNM 409243, large form, Sawane Fm. (×45). 4, LV male, USNM 409244, small form, Setana Fm. (×45).

Fig. 2. *Finmarchinella rectangulata* Tabuki, 1986, LV female, USNM 409245, Setana Fm. (×75).

Fig. 3. *Finmarchinella hanaii* Okada, 1979, LV female, USNM 409246, Sawane Fm. (×75).

Fig. 5. *Finmarchinella nealei* Okada, 1979, LV female, USNM 409247, Setana Fm. (×75).

Fig. 6. *Finmarchinella daishakaensis* Tabuki, 1986, LV female, USNM 409248, Setana Fm. (×75).

Fig. 7. *Normanicythere leioderma* (Norman, 1869), LV female, USNM 409249, Tomikawa Fm. (×54).

Fig. 8. *Normanicythere* sp. A, LV female, USNM 409250, Tomikawa Fm. (×54).

Fig. 9. *Finmarchinella angulata* (Sars, 1865), LV female, USNM 409251, Sawane Fm (×75).

Fig. 10. *Sarsicytheridea macrolaminata* (Elofson, 1939), RV, USNM 409252, Tomikawa Fm. (×54).

Fig. 11. *Normanicythere?* cf. *N. japonica* Tabuki, 1986, LV female, USNM 409253, Sawane Fm. (×54).

Fig. 12. *Sarsicytheridea bradii* (Norman, 1865), LV female, USNM 409254, Tomikawa Fm. (×54).

Fig. 13. *Elofsonella concinna* (Jones, 1856), LV female, USNM 409255, Tomikawa Fm. (×54).

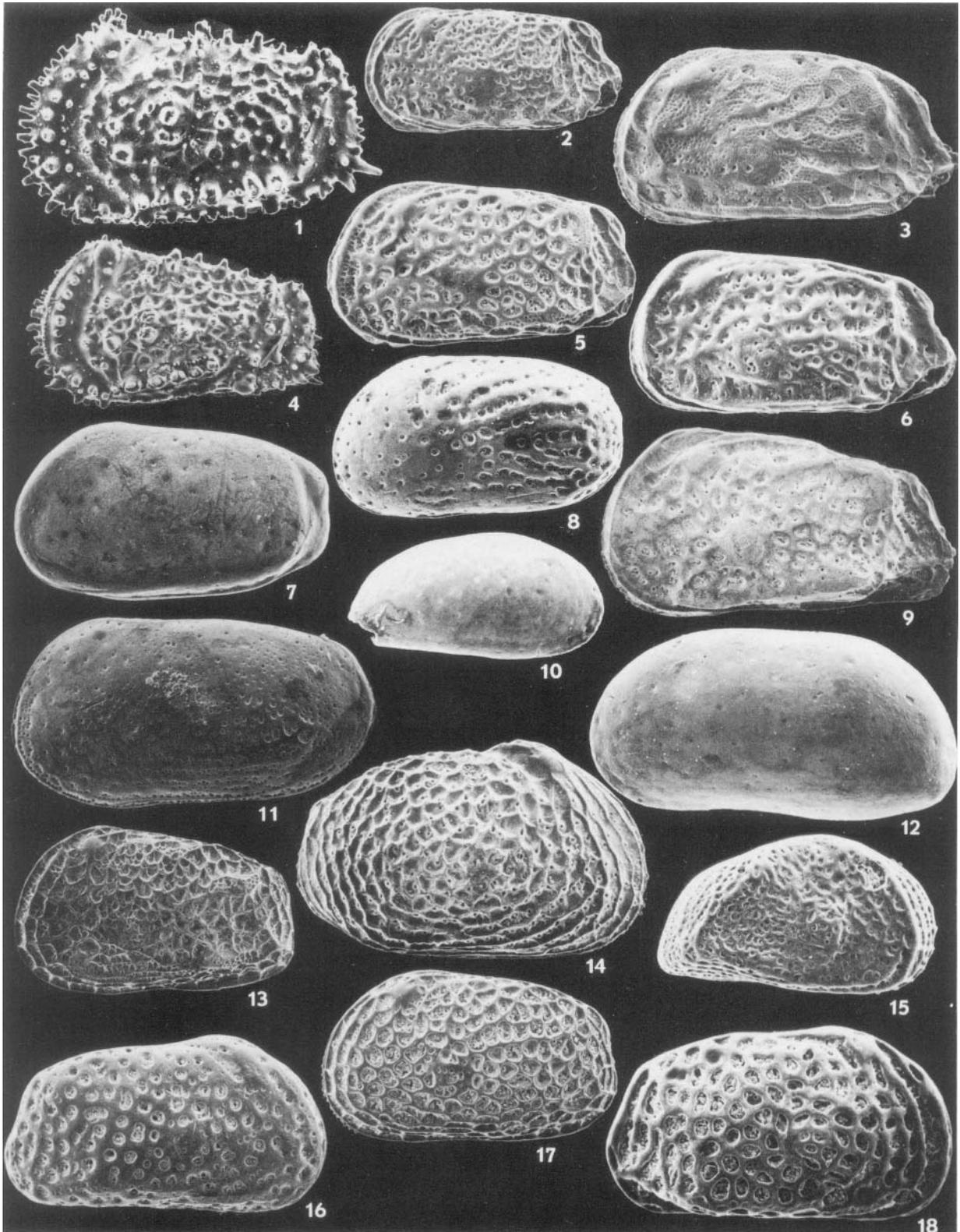
Fig. 14. *Rabilimis septentrionalis* (Brady, 1866), RV female, USNM 409256, Tomikawa Fm. (×45).

Fig. 15. *Heterocyprideis fascis* Brady & Norman, 1889), RV female?, USNM 409257, Tomikawa Fm. (×54).

Fig. 16. "*Urocythereis*" sp. C, RV female, USNM 409258, Setana Fm. (×54).

Fig. 17. "*Urocythereis*" sp. A, RV female, USNM 409259, Setana Fm. (×54).

Fig. 18. "*Urocythereis*" *posteroaudata* Tabuki, 1986, RV female, USNM 409260, Sawane Fm. (×54).



**Material.** 95 specimens.

*Hemicythere quadrinodosa* Schornikov, 1974  
(Pl. 2, fig. 1)

**Remarks.** This species is distinguished from others by its large, thick carapace and the conspicuous nodes in the dorsal and posterior parts of the carapace surface.

**Distribution.** Setana Formation.

**Material.** 12 specimens.

*Hemicythere* sp. C  
(Pl. 2, fig. 2)

**Remarks.** This species bears some resemblance to *H. emarginata* but it is smaller, has a rounded outline and a different ridge pattern.

**Distribution.** Setana and Sawane Formations.

**Material.** 30 specimens.

Genus *Normanicythere* Neale, 1957

*Normanicythere* cf. *N. japonica* Tabuki, 1986  
(Pl. 1, fig. 11)

**Remarks.** The specimens from the present study are more finely pitted than those described by Tabuki (1986) from the Daishaka Formation. In lateral view they bear a superficial resemblance to *Cytheretta*

*teshekpukensis* Swain, 1963 (see Neale, 1975), but they lack the characteristic hinge and the inner margin of *Cytheretta*.

**Distribution.** Tomikawa, Setana, Sawane, Omma, and Sasaoka Formations.

**Material.** 22 specimens.

*Normanicythere leioderma* (Norman, 1869)  
(Pl. 1, fig. 7)

**Remarks.** Tabuki (1986) also found this species in the Daishaka Formation.

**Distribution.** Tomikawa, Setana, Omma, and Sasaoka Formations.

**Material.** 30 specimens.

*Normanicythere* sp. A  
(Pl. 1, fig. 8)

**Remarks.** This species is characterised by a variably reticulated surface. The fossae are arranged in subhorizontal rows in the posterior half of the carapace; the anterior half has a few scattered pits.

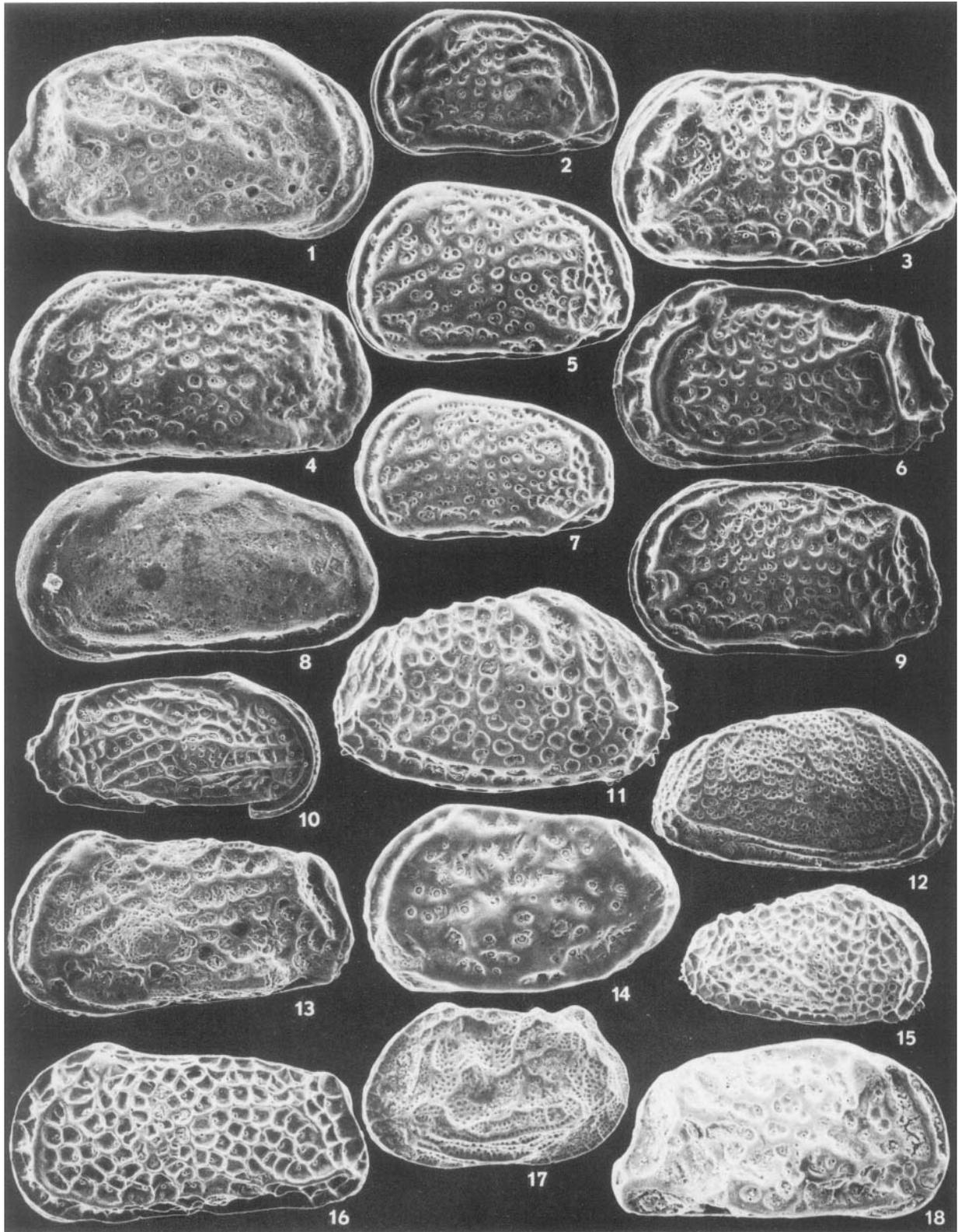
**Distribution.** Tomikawa, common in the Omma Formation.

**Material.** 53 specimens.

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#### Explanation of Plate 2

- Fig. 1. *Hemicythere quadrinodosa* Schornikov, 1974, RV female, USNM 409261, Tomikawa Fm. ( $\times 75$ ).  
 Fig. 2. *Hemicythere* sp. C, LV female, USNM 409262, Sawane Fm ( $\times 54$ ).  
 Fig. 3. *Hemicythere emarginata* (Sars, 1865), LV female, USNM 409263, Setana Fm. ( $\times 81$ ).  
 Fig. 4. *Hemicythere ochotensis* Schornikov, 1974, LV female, USNM 409264, Setana Fm. ( $\times 69$ ).  
 Figs. 5, 7. *Hemicythere orientalis* Schornikov, 1974. 5, LV female, USNM 409265, Kitaura Fm. ( $\times 75$ ). 7, LV male, USNM 409266, Kitaura Fm. ( $\times 75$ ).  
 Fig. 6. *Hemicythere?* *kitanipponica* (Tabuki, 1986), LV female, USNM 409267, Setana Fm. ( $\times 81$ ).  
 Fig. 8. *Hemicythere?* cf. *H. boreokurila* Schornikov, 1974, LV female?, USNM 409268, Sawane Fm. ( $\times 81$ ).  
 Fig. 9. *Hemicythere gurjavnovae* Schornikov, 1974, LV female, USNM 409269, Sawane Fm. ( $\times 63$ ).  
 Fig. 10. *Patagonacythere dubia* (Brady, 1868), RV ?female, USNM 409270, Setana Fm. ( $\times 54$ ).  
 Fig. 11. *Robertsonites hanaii* Tabuki, 1986, RV female, USNM 409271, Tomikawa Fm. ( $\times 54$ ).  
 Fig. 12. *Robertsonites tsugaruana* Tabuki, 1986, RV female, USNM 409272, Tomikawa Fm. ( $\times 54$ ).  
 Fig. 13. *Patagonacythere robusta* Tabuki, 1986, LV female, USNM 409273, Setana Fm. ( $\times 54$ ).  
 Fig. 14. *Schizocythere okhotskensis* Hanai, 1970, LV female, USNM 409274, Tomikawa Fm. ( $\times 81$ ).  
 Fig. 15. *Robertsonites reticuliforma* Tabuki, 1986, Rv male, USNM 409275, Tomikawa Fm. ( $\times 54$ ).  
 Fig. 16. *Baffinicythere howei* Hazel, 1967, subspecies, LV female, USNM 409276, Shibikawa Fm. ( $\times 54$ ).  
 Fig. 17. *Palmenella limicola* (Norman, 1865), LV female, USNM 409277, Tomikawa Fm. ( $\times 81$ ).  
 Fig. 18. *Baffinicythere* sp. A, RV female, USNM 409278, Shibikawa Fm. ( $\times 54$ ).



Genus *Patagonacythere* Hartmann, 1962

*Patagonacythere dubia* (Brady, 1868)

(Pl. 2, fig. 10)

**Remarks.** Japanese specimens are very similar to North Atlantic specimens (Cronin, in press). Two other related, undescribed species of *Patagonacythere* also occur in the Omma-Manganji fauna.

**Distribution.** Setana, Sawane, Junicho, and Omma Formations.

**Material.** 15 specimens.

*Patagonacythere robusta* Tabuki, 1986

(Pl. 2, fig. 13)

**Distribution.** Tomikawa, Setana, Sawane, Junicho, Omma, and Sasaoka Formations.

**Material.** 117 specimens.

Genus *Urocythereis* Ruggieri, 1950

*"Urocythereis" posteroicaudata* Tabuki, 1986

(Pl. 1, fig. 18)

**Remarks.** It was not possible to distinguish this species

from *U. abei* Tabuki, 1986 in our material. Hanai & Ikeya (in prep.) describe this species as a member of a new genus.

**Distribution.** Tomikawa, Setana, Sawane, Junicho, Omma, Kitaura, Shibikawa, and Sasaoka Formations.

**Material.** 393 specimens.

*"Urocythereis" sp. A*

(Pl. 1, fig. 17)

**Remarks.** This species is characterised by its strong sexual dimorphism and strongly and evenly reticulate surface. It is congeneric with "*U.*" *posteroicaudata*.

**Distribution.** Tomikawa, Setana, Junicho, Omma, Shibikawa, and Sasaoka Formations.

**Material.** 344 specimens.

*"Urocythereis" sp. C*

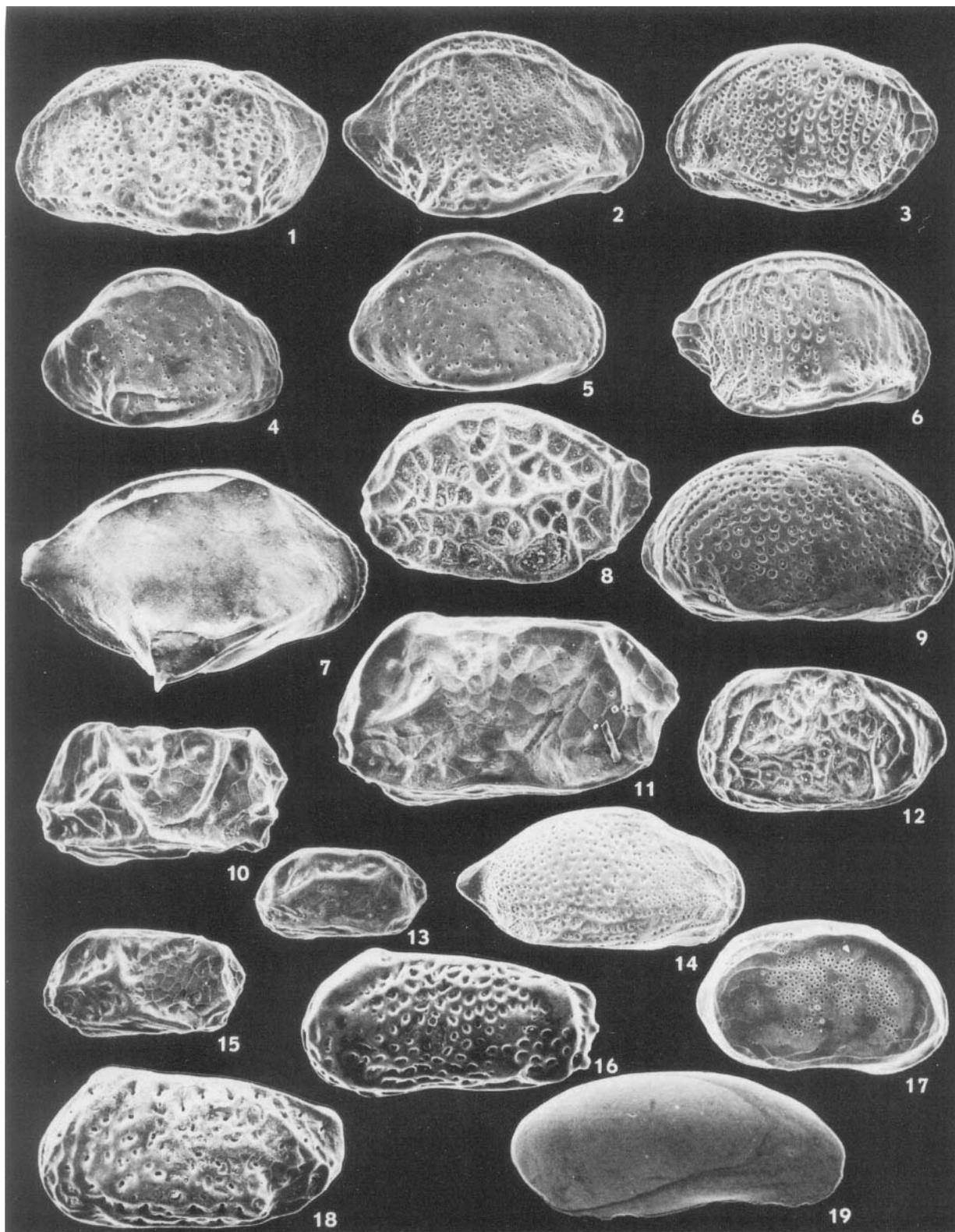
(Pl. 1, fig. 16)

**Remarks.** This species has a very thick heavy carapace and rounded fossae over most of the surface. Hanai & Ikeya (in prep.) describe this species as a member of a new genus.

**Distribution.** Tomikawa, Setana, Junicho, Omma,

### Explanation of Plate 3

- Figs. 1, 2. *Cytheropteron nodosoalatum* Neale & Howe, 1973. 1, LV ?female, USNM 409279, Tomikawa Fm. (×81).  
2, RV female, USNM 409280, Kitaura Fm. (×81).
- Fig. 3. *Cytheropteron champlainum* Cronin, 1981, subspecies, LV female, USNM 409281, Tomikawa Fm. (×81).
- Fig. 4. *Cytheropteron* cf. *C. elaei* Cronin in press a, RV ?female, USNM 409282, Tomikawa Fm. (×81).
- Fig. 5. *Cytheropteron* cf. *C. arcuatum* Brady, Crosskey & Robertson, 1874, RV female, USNM 414 999, Tomikawa Fm. (×81).
- Fig. 6. *Cytheropteron champlainum* Cronin, 1981, subspecies, RV female, USNM 415000, Tomikawa Fm. (×81).
- Fig. 7. *Cytheropteron alatum* Sars, 1865, LV ?female, USNM 415001, Kitaura Fm. (×81).
- Fig. 8. *Hemicytherura clathrata* (Sars, 1865), LV male, USNM 415002, Tomikawa Fm. (×81).
- Fig. 9. *Howeina camptocytheroidea* Hanai, 1957, RV female, USNM 415003, Tomikawa Fm. (×81).
- Fig. 10. *Semicytherura* n. sp. A, LV female, USNM 415004, Setana Fm. (×81).
- Fig. 11. *Semicytherura subundata* Hanai, 1957, LV female, USNM 415005, Setana Fm. (×81).
- Fig. 12. *Semicytherura mainensis* (Hazel & Valentine, 1969), LV female, USNM 415006, Sasaoka Fm. (×81).
- Fig. 13. *Semicytherura* aff. *S. henryhowei* Hanai & Ikeya, 1977, LV female, USNM 415007, Setana Fm. (×81).
- Fig. 14. *Semicytherura affinis* (Sars, 1865), RV female, USNM 415008, Anden Fm. (×81).
- Fig. 15. *Semicytherura undata* (Sars, 1865), LV female, USNM 415009, Setana Fm. (×81).
- Fig. 16. *Munseyella hatatensis* (Ishizaki, 1966), LV female, USNM 415010, Junicho Fm. (×94).
- Fig. 17. *Semicytherura complanata* (Brady, Crosskey & Robertson, 1874), RV female, USNM 415011, Tomikawa Fm. (×100).
- Fig. 18. *Kotoracythere* sp. A, LV female, USNM 415012, Sasaoka Fm. (×81).
- Fig. 19. *Sclerochilus contortus* (Norman, 1862), RV ?male, USNM 415013, Setana Fm. (×81).



Kitaura, Shibikawa, and Sasaoka Formations.

**Material.** 82 specimens.

Family Trachyleberididae Sylvester-Bradley, 1948

Genus *Acanthocythereis* Howe, 1963

*Acanthocythereis dunelmensis* (Norman, 1865)

(Pl. 1, figs. 1, 4)

**Remarks.** Two morphotypes are present, a large and a small form. Both have generally the same pattern of spines and tubercles although the smaller form tapers more posteriorly. It is not yet clear how the Japanese *A. dunelmensis* are related to the large and small forms recognised by Elofson (1941).

**Distribution.** Tomikawa, Setana, Sawane, Omma, Kitaura, Wakimoto, and Sasaoka Formations.

**Material.** 152 specimens.

Genus *Robertsonites* Swain, 1963

*Robertsonites hanaii* Tabuki, 1986

(Pl. 2, fig. 11)

**Distribution.** Tomikawa, Setana, Junicho, and Sasaoka Formations.

**Material.** 85 specimens.

*Robertsonites reticuliforma* (Ishizaki, 1966)

(Pl. 2, fig. 15)

**Distribution.** Sawane, Omma, Wakimoto, and Sasaoka Formations.

**Material.** 47 specimens.

*Robertsonites tsugaruana* Tabuki, 1986

(Pl. 2, fig. 12)

**Distribution.** Tomikawa, Setana, and Sawane Formations.

**Material.** 22 specimens.

Family Cytheruridae Müller, 1894

Genus *Cytheropteron* Sars, 1865

*Cytheropteron alatum* Sars, 1865

(Pl. 3 fig. 7)

**Remarks.** This species belongs to a group of cold water *Cytheropteron* having a smooth surface and large, pointed triangular alae (the *Cytheropteron alatum* Group of Whatley & Masson, 1979). It closely resembles *C. alatum* in its outline and the shape of the ala. Specimens of *C. alatum* illustrated by Whatley & Masson (1979) show posterior-pointing alae whereas the Japanese forms point outward. Both forms have a narrow ridge along part of the dorsal margin.

**Distribution.** Kitaura and Wakimoto Formations.

**Material.** 6 specimens.

*Cytheropteron* cf. *C. arcuatum* Brady, Crosskey &

Roberston, 1874

(Pl. 3, fig. 5)

**Remarks.** This species is generally similar in size and

shape to true *C. arcuatum* but its surface has conspicuous scattered pits. The Japanese form also lacks the evenly rounded dorsal margin that is typical of North Atlantic specimens.

**Distribution.** Tomikawa and Setana Formations.

**Material.** 11 specimens.

*Cytheropteron champlainum* Cronin, 1981 subsp.

(Pl. 3, figs. 3, 6)

**Remarks.** This species appears to belong to a nexus of cold water species of *Cytheropteron* including *C. champlainum*, *C. latissimum* (Norman, 1865), *C. complanatum* Brady & Crosskey, 1871, and *C. dimlingtonensis* Neale & Howe, 1973 all having a generally similar subovate to subrectangular outline in the left valve, small, weakly sulcate alae, vertically-orientated rows of fossae on the posterior half of the carapace, and a pitted anterior half. Two forms are illustrated here, one having a weak, evenly curved ala (Pl. 3, fig. 3), the other having a stronger ala projecting posteriorly (Pl. 3, fig. 6). A thorough comparative study of these forms is necessary to establish the affinities of each.

**Distribution.** Tomikawa, Setana, Sawane, Kitaura, Shibikawa, and Sasaoka Formations.

**Material.** 79 specimens.

*Cytheropteron* cf. *C. elaeni* Cronin, in press

(Pl. 3, fig. 4)

**Remarks.** Cronin (in press) proposed the new name *C. elaeni* for *Cytheropteron nealei* Cronin, 1981, a pre-occupied name. The Japanese form resembles specimens from Pleistocene Champlain Sea deposits of northeastern North America in its size and general shape, although North Atlantic forms are more drawn out posteriorly. Both forms have sulcate alae, postero-dorsal nodes and a ridge along the dorsal margin. The Japanese form is distinguished by scattered surface pits, which are aligned in subvertical rows in the central region of the carapace.

**Distribution.** Tomikawa and Wakimoto Formations.

**Material.** 8 specimens.

*Cytheropteron nodosoalatum* Neale & Howe, 1973

(Pl. 3, figs. 1, 2)

**Remarks.** Japanese specimens differ only slightly from North Atlantic specimens in details of the surface pitting.

**Distribution.** Tomikawa, Setana and Wakimoto Formations.

**Material.** 15 specimens.

Genus *Howeina* Hanai, 1957

*Howeina camptocytheroidea* Hanai, 1957

(Pl. 3, fig. 9)

**Remarks.** McDougall *et al.* (1986) illustrated a similar species they referred to as *Cytherura* sp. C and *Cytherura* sp. B from Pleistocene deposits of Prudhoe

Bay, Alaska. W. M. Briggs, Jr. (pers. comm., 1986) also reports a similar form from the Beaufort Sea of Canada.

**Distribution.** Tomikawa, Setana, Junicho, Shibikawa, and Sasaoka Formations.

**Material.** 48 specimens.

Genus *Semicytherura* Wagner, 1957

**Remarks.** Cold water *Semicytherura* include a complex group of species and subspecies for which we have only limited knowledge as to their phylogenetic relationships. The Japanese forms discovered in this study show a greater taxonomic affinity between North Atlantic and North Pacific *Semicytherura* than had previously been suspected. The diverse array of morphologies suggests the genus has undergone evolutionary divergence in the two regions during the Neogene and Quaternary.

*Semicytherura affinis* (Sars, 1865)  
(Pl. 3, fig. 14)

**Remarks.** Specimens referred to by Ishizaki & Matoba (1985) as *Semicytherura* sp. A are probably conspecific with *S. affinis*.

**Distribution.** Tomikawa, Setana, Junicho, Kitaura, and Anden Formations.

**Material.** 16 specimens.

*Semicytherura complanata* Brady, Crosskey &  
Robertson, 1874  
(Pl. 3, fig. 17)

**Remarks.** Cronin (in press) showed that North Atlantic populations of this species have carapaces that vary from finely ribbed over the entire surface to ribbed near the margins and densely pitted in the central area. The Japanese specimens also have such pitting. Specimens referred to as *Cytherura* sp. D and also as *Cluthia* aff. *C. cluthae* by Brouwers in McDougall *et al.* (1986) from the Pleistocene of Prudhoe Bay are also considered to be *S. complanata*.

**Distribution.** Tomikawa, Setana, Kitaura, and Shibikawa Formations.

**Material.** 8 specimens.

*Semicytherura* aff. *S. henryhowei* Hanai & Ikeya, 1977  
(Pl. 3, fig. 13)

**Remarks.** This species is related to *S. henryhowei* Hanai & Ikeya, 1977.

**Distribution.** Setana, Sawane, Kitaura, and Sasaoka Formations.

**Material.** 36 specimens.

*Semicytherura mainensis* Hazel & Valentine, 1969  
(Pl. 3, fig. 12)

**Remarks.** Most Japanese specimens referred to *S. mainensis* have slightly narrower ridges in the central

and posterior regions, however the pattern of surface ornament is almost identical in Atlantic and Pacific forms. Japanese *S. mainensis* can be confused with *Howeina higashimeyaensis* Ishizaki, 1971 which is distinguished by prominent vertical ridges in the posterior region and a ventral ridge sometimes overlapping the margin. However, the two species appear to be closely related and, as suggested by Van Morkhoven (1963), *Howeina* and *Semicytherura* may be subgenera of a single genus.

**Distribution.** Tomikawa, Setana, Sawane, Omma, Kitaura, Shibikawa, and Sasaoka Formations.

**Material.** 141 specimens.

*Semicytherura subundata* Hanai, 1957  
(Pl. 3, fig. 11)

**Remarks.** The *Semicytherura subundata* – *S. undata* group of species represents a most difficult group for understanding intraspecific variability and taxonomic affinities among Atlantic and Pacific forms. Nonetheless, it appears that at least two species, *S. subundata* and *S. undata* are circumpolar and common to North Atlantic and Pacific regions. Cronin (in press) illustrates forms from the Pleistocene of Canada which he considers to be the first recorded *S. subundata* from the Atlantic. This large, distinctive species occurs in most Japanese formations studied here.

**Distribution.** Tomikawa, Setana, Sawane, Junicho, Kitaura, Wakimoto, and Sasaoka Formations.

**Material.** 94 specimens.

*Semicytherura undata* (Sars, 1865)  
(Pl. 3, fig. 15)

**Remarks.** North Atlantic *S. undata* have been well illustrated from Novaya Zemlya by Neale & Howe (1975) and from the late Pleistocene of Canada by Cronin (in press). Specimens assigned to this species occur in the Setana, Sawane, Kitaura, Shibikawa, and Sasaoka Formations. As is the case with *S. subundata*, a complex group of morphotypes have been found, some of which probably represent distinct subspecies.

**Distribution.** Setana, Sawane, Kitaura, Wakimoto, Shibikawa, and Sasaoka Formations.

**Material.** 59 specimens.

*Semicytherura* sp. A  
(Pl. 3, fig. 10)

**Remarks.** This undescribed species is closely related to the *S. undata* group and is distinguished from other species by its very prominent, sharp ridges which in the anterior region their intersection forms a laterally projecting point.

**Distribution.** Setana and Sawane Formations.

**Material.** 36 specimens.

Family Bythocytheridae Sars, 1865

Genus *Jonesia* Brady, 1866

*Jonesia simplex* (Norman, 1865)

**Remarks.** Rare specimens of this species had carapaces broken at the margins.

**Distribution.** Wakimoto Formation.

**Material.** 4 specimens.

Family Paradoxostomatidae Brady & Norman, 1889

Genus *Paradoxostoma*

*Paradoxostoma* sp. A

**Remarks.** A large, thick-shelled species of *Paradoxostoma* occurring in the Tomikawa, Setana and Kitaura Formations is possibly related to *P. arcticum* Elofson, 1941.

**Distribution.** Tomikawa, Setana, and Kitaura Formations.

**Material.** 23 specimens.

Genus *Sclerochilus contortus* (Norman, 1862)

(Pl. 3, fig. 19)

**Remarks.** This species may be conspecific with *Sclerochilus* sp. 1 of Tabuki (1986) from the Daishaka Formation.

**Distribution.** Tomikawa, Setana, and Sawane Formations.

**Material.** 16 specimens.

Family Schizocytheridae Howe, 1961

Genus *Palmenella* Hirschmann, 1916

*Palmenella limicola* (Norman, 1865)

(Pl. 2, fig. 17)

**Distribution.** Tomikawa, Setana, Sawane, Junicho, Wakimoto, and Sasaoka Formations.

**Material.** 36 specimens.

Genus *Schizocythere* Triebel, 1950

*Schizocythere okhotskensis* Hanai, 1970

(Pl. 2, fig. 14)

**Remarks.** *Schizocythere* has also been reported from the Beaufort Sea of Canada (W. M. Briggs, Jr., pers. comm.).

**Distribution.** Tomikawa, Setana, Sawane, Omma, Kitaura, Wakimoto, Shibikawa, Anden, and Sasaoka Formations.

**Material.** 590 specimens.

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