Deep-sea benthic ostracodes from multiple core and epibenthic sledge samples in Icelandic waters

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Abstract: Deep-sea benthic Ostracoda (Crustacea) in Icelandic waters are poorly known. Here we report deep-sea ostracode assemblages from the multiple core (MUC) and the epibenthic sledge (EBS) samples collected from Icelandic waters by the first cruise of the IceAGE (Icelandic Marine Animals: Genetics and Ecology) project. Samples from shelf-edge and lower-bathyal working areas are examined. The results show (1) distinct MUC and EBS faunas due to the large difference in mesh size of MUC and EBS; and (2) distinct shelf-edge and lower-bathyal ostracode faunas. Such remarkable faunal turnover from shelf to bathyal depths is similar to the faunal turnovers reported from depth transects in the adjacent regions of the western North Atlantic Ocean, the Greenland Sea, and the North Sea, but, at the same time, there are certain differences in the faunal composition between the Icelandic waters and these adjacent regions. In addition, we illustrate many Icelandic deep-sea ostracode species with high-resolution scanning electron microscopy and composite all-in-focus stereomicroscopic images for the first time. These results provide important basic information on deep-sea ostracode research and biogeography of this important region connecting North Atlantic proper and Nordic Seas.

Key words: Icelandic, Ostracoda, shelf-edge, lower-bathyal, IceAGE, biogeography.
Introduction

Deep-sea Ostracoda (Crustacea) from the North Atlantic Ocean and Nordic Seas are relatively well investigated. After the initial 19th century taxonomic investigation (e.g. Brady 1880), the North Atlantic deep-sea ostracode taxonomy was established largely by Whatley and Coles (1987) and Coles and Whatley (1989) who studied many DSDP (Deep Sea Drilling Project) cores and depicted and described numerous species. Recently, Yasuhara et al. (2009c) conducted an intensive taxonomic study in the western North Atlantic Ocean, where they described 28 new species and revised taxonomy of several common species to reduce taxonomic uncertainty in the literature. There are a few more studies on taxonomy and distribution of North Atlantic deep-sea ostracodes (Rosenfeld and Bein 1978; Benson et al. 1983; Cronin 1983; Dingle and Lord 1990; Coles et al. 1996; Alvarez Zarikian 2009). In the Nordic Seas, Whatley and his colleagues intensively studied Greenland Sea deep-sea ostracods in the late 1990s (Whatley et al. 1996; Whatley and Eynon 1996; Whatley et al. 1998). Apart from taxonomic studies, Quaternary fossil deep-sea ostracodes have been investigated in several deep-sea sediment cores both from the North Atlantic Ocean and Nordic Seas for paleoceanographic and paleoecological reconstructions (Cronin et al. 1999; Didié et al. 1999, 2002; Didié and Bauch 2000; Cronin et al. 2002; Yasuhara and Cronin 2008; Yasuhara et al. 2008; Alvarez Zarikian et al. 2009; Yasuhara et al. 2009b).

Around Iceland, marine ostracode research started in the 19th century (Brady 1868; Brady and Norman 1889). Since then, there have been a few taxonomic and paleontological studies on Icelandic marine ostracodes (Stephensen 1938; Cronin 1991). However, all of them are on shallow-marine species, and deep-sea ostracode faunas are poorly understood in the vicinity of Iceland (van den Bold 1965).

Iceland is an important region to understand the North Atlantic deep-sea biogeography because it connects the North Atlantic proper and Nordic Seas. Furthermore, the vicinity of Iceland is a well-known climatically-sensitive region, where the North Atlantic Deep Water forms. IceAGE (Icelandic Marine Animals: Genetics and Ecology) (http://www.iceage-project.org/home.html) is a multidisciplinary research project aiming to better elucidate the biodiversity and the phylogeography of deep-sea animals in this important region. During the IceAGE1 cruise by R/V Meteor (cruise M85/3) samples were collected from 31 working areas, using a multiple corer (MUC), three types of grab samplers (boxcorer, Van Veen grab and Shipek grab), three types of epibenthic sledges (EBS), an Agassiz trawl, and a plankton net (Brix et al. 2012). Here we show initial results on the deep-sea ostracodes from the IceAGE samples. The main purpose are threefold: (1) to show poorly-known deep-sea ostracod fauna and species in the Icelandic region with high-resolution scanning electron microscopy (SEM) and stereomicroscope images; (2) to compare the faunal composition between MUC and EBS ostracodes; and (3) to compare shelf-edge and lower-bathyal ostracode faunas.
Materials and methods

We used two MUC and two EBS samples from the IceAGE1 working areas 01 and 09 (WA01 and WA09, hereafter) (Fig. 1) that are from lower-bathyal and shelf-edge depths, respectively. The samples 959 MUC and 963 EBS are from the WA01, and the samples 1035 MUC and 1032 EBS are from the WA09.

As mentioned above, three types of EBS were used during the IceAGE1 cruise. The sample 963 EBS was collected by the Brenke sledge (Brenke 2005), and the sample 1032 EBS was collected by CliSAP sledge that is a modified Brenke sledge with camera systems. These sledges are equipped with two nets, an epinet directly above the ground and a supranet, which lies above the epinet. Each net is composed of 500-μm-mesh net with 300-μm-mesh net bucket at cod end. The ostracodes were picked from the wet samples, which were preserved and kept in 96% ethanol. Both “live” (i.e. specimens collected with soft parts) and dead specimens (i.e. empty shells) were picked. For a better comparison with the MUC samples, only the dead assemblages are analyzed herein.

The MUC sediment samples were washed through a 63 μm sieve and dried. The ostracodes were picked from the >150 μm dried residue, and all the specimens present were picked. All specimens were dead, empty shells and there was no living specimen (i.e. specimen with soft parts) found.

Twenty-seven well-preserved specimens were selected for SEM and stereomicroscope imaging. Uncoated specimens from the MUC samples were digitally imaged with Hitachi S-3400N Variable Pressure SEM in low-vacuum mode (at the Electron Microscope Unit, University of Hong Kong), and with Leica M205C stereomicroscope (at M.Y. laboratory) using Leica LAS Multifocus system that produces a composite, all-in-focus, Extended Depth of Focus image. For imaging purpose, specimens from additional five MUC stations were used (see Table 1 and Fig. 1). Specimens from the EBS samples were coated with gold in an evaporation

<table>
<thead>
<tr>
<th>Site</th>
<th>Depth interval (cm)</th>
<th>Working area</th>
<th>Latitude (°N)</th>
<th>Longitude (°E)</th>
<th>Water depth (m)</th>
</tr>
</thead>
<tbody>
<tr>
<td>959 MUC</td>
<td>0–2</td>
<td>1</td>
<td>60.0455</td>
<td>-21.5023</td>
<td>2749.0</td>
</tr>
<tr>
<td>963 EBS</td>
<td>NA</td>
<td>1</td>
<td>60.0455</td>
<td>-21.4677</td>
<td>2749.4</td>
</tr>
<tr>
<td>987 MUC</td>
<td>0.5–1</td>
<td>4</td>
<td>60.9280</td>
<td>-18.6968</td>
<td>2493.3</td>
</tr>
<tr>
<td>1004 MUC</td>
<td>0–1</td>
<td>6</td>
<td>62.5583</td>
<td>-20.3530</td>
<td>1392.2</td>
</tr>
<tr>
<td>1032 EBS</td>
<td>NA</td>
<td>9</td>
<td>63.3085</td>
<td>-23.1577</td>
<td>289.4</td>
</tr>
<tr>
<td>1035 MUC</td>
<td>0–0.5</td>
<td>9</td>
<td>63.3333</td>
<td>-23.1668</td>
<td>306.7</td>
</tr>
<tr>
<td>1115 MUC</td>
<td>0.5–1</td>
<td>19</td>
<td>67.2137</td>
<td>-26.2718</td>
<td>684.3</td>
</tr>
<tr>
<td>1127 MUC</td>
<td>0–1</td>
<td>20</td>
<td>67.6463</td>
<td>-26.7460</td>
<td>320.0</td>
</tr>
<tr>
<td>1175 MUC</td>
<td>0.5–1</td>
<td>25</td>
<td>67.6170</td>
<td>-9.7377</td>
<td>1710.8</td>
</tr>
</tbody>
</table>
unit PD170AZ from Leybold-Heraeus and digitally imaged with a LEO 1525 SEM (Carl Zeiss SMT) at Biozentrum Grindel und Zoologisches Museum, Universität Hamburg. High-resolution figures of ostracod SEM and stereomicroscope images are available at Dryad (http://datadryad.org/; http://doi.org/10.5061/dryad.s3013).

Results and discussion

Ostracode faunal compositions in the two working areas are summarized in Fig. 2. The SEM and stereomicroscope images of selected ostracode species are shown in Figs 3–8. Many of them are well known species either from the North Atlantic Ocean or the Nordic Seas. See Taxonomic Notes below for further details of each species.

**EBS versus MUC ostracode faunas.** — Faunal differences between EBS and MUC samples are substantial (Fig. 2). Dominant species are always different between EBS and MUC samples in one working area. In the EBS sample of the WA01 (~2700 m water depth), *Pennyella rexi* and *Echinocythereis echinata* are the dominant species, and these two species constitute ~50% of the total fauna. In contrast, *Krithe* constitutes ~60% of the total fauna, and *Pennyella rexi* and *Echinocythereis echinata* constitute just 13% and 1%, respectively, in the MUC
sample of the WA01. Within an EBS, epinet and supranet dead-shell assemblages are similar in the present study (Fig. 2). In the WA09 (~300 m water depth), *Muellerina abyssicola* is the dominant species constituting ~70% of the total MUC fauna, while *Pterygocythereis mucronata* constitutes ~99% in the EBS sample.

EBS fauna exclusively includes very large ostracodes, and smaller ostracode specimens pass through the EBS mesh (i.e. 300–500 μm). In this context, MUC samples better represent the entire ostracode assemblages because they include adults and late juveniles of most species. As discussed in Yasuhara *et al.* (2009b), most small species have a >150-μm minor axis (i.e. height) of their adult valves, and therefore will be recovered on a 150-μm sieve. These small species show low diversity and abundances, even when finer size fractions are used (Corrège 1993; Coles *et al.* 1996; Didié and Bauch 2000). Furthermore, species identification of early juveniles is often very difficult. Thus, usage of the widely used sieve size of 150-μm (or slightly finer 125 μm) is preferable in recent and fossil ostracode studies because it is

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**Fig. 2.** Ostracode faunal compositions in the EBS and MUC samples from the WA01 and 09. Relative abundance of each taxa is shown.
important to accumulate standardized data for future meta-analyses. In contrast, the main advantage of the EBS is that much more specimens are usually collected compared to the MUC, because the sampling area of the EBS is much larger than the MUC sampling area (hundreds of square meters and 69.4 cm², respectively).

**Shelf-edge versus lower-bathyal ostracode faunas.** — Because the MUC samples better represent the entire ostracode fauna as discussed above, we discuss faunal composition mainly based on MUC samples below. The ostracode assemblages of the two working areas are distinct (Fig. 2). In the lower-bathyal WA01, typical deep-sea North Atlantic ostracode fauna was found. The WA01 fauna is composed of *Krithe, Pennyella, Henryhowella, Ambocythere, Rugocythereis*, and other typical deep-sea genera. In contrast, the shelf-edge WA09 assemblage is mostly composed of *Muellerina* and *Pterygocythereis*, constituting >90% of the fauna. This faunal difference from shelf to bathyal depths is similar to the faunal distributions reported from the subpolar western North Atlantic Ocean (Benson et al. 1983), the Greenland Sea (Whatley et al. 1998), and the North Sea (Penney 1993). But there are several differences in the faunal composition between the area off Iceland and other areas, for example: the northwestern Atlantic shelf-edge fauna lacks *Pterygocythereis* (Benson et al. 1983); the Greenland Sea shelf-edge fauna shows much higher species diversity (Whatley et al. 1998); the Greenland Sea lower-bathyal fauna includes different species of *Krithe* and has much higher *Cytheropteron* abundance (Whatley et al. 1998); and North Sea shelf-edge fauna is dominated by *Krithe* (Penney 1993). These differences may be due to local water properties or perhaps the isolated nature of Iceland surrounded by >500 m depth areas, that are potential barriers for shelf species, and further investigating all IceAGE samples will enable us to discuss these potential mechanisms causing the faunal differences quantitatively.

**Conclusions**

Our initial results on the IceAGE ostracodes include several important findings. First, we depicted many Icelandic deep-sea ostracode species with high-resolution SEM and composite all-in-focus stereomicroscopic images for the first time. Second, our ostracode data showed distinct MUC and EBS faunas due to the difference in mesh size of MUC and EBS. The MUC >150-μm fauna better represents whole ostracode assemblage. The EBS macrofaunal ostracodes are important for taxonomic studies (Brandão 2010; Brandão and Päplow 2011), because much more living specimens of large species are available from EBS sample than from MUC sample. Third, we found distinct shelf-edge and lower-bathyal ostracode faunas that have both similarities and differences to the ostracode faunas from the adjacent regions. Our preliminary results clearly show the importance of further investigating deep-sea ostracode faunas around Iceland to better understand the
large-scale biogeographic and biodiversity patterns in the North Atlantic Ocean, the Nordic Seas, and the Arctic Ocean.

Taxonomic notes

Class Ostracoda Latreille, 1802
Subclass Podocopa Müller, 1894
Order Platycopida G.O. Sars, 1866
Suborder Platycopina G.O. Sars, 1866
Superfamily Cytherelloidea G.O. Sars, 1866
Family Cytherellidae G.O. Sars, 1866
Genus Cytherella Jones, 1849
Cytherella robusta Colalongo et Pasini, 1980
(Fig. 8.1)

Note: This species has certain intraspecific variation and the details will be discussed in a separate paper (Yasuhara and Okahashi in press).

Order Podocopida G.O. Sars, 1866
Suborder Cypridocopina Jones, 1901
Superfamily Macrocypridoidea Müller, 1912
Family Macrocyprididae Müller, 1912
Genus Macrocypris Brady, 1868
Macrocypris sp.
(Fig. 8.2)

Superfamily Pontocypridoidea Müller, 1894
Family Pontocyprididae Müller, 1894
Genus Argilloecia G.O. Sars, 1866
Argilloecia acuminata Müller, 1894
(Fig. 3.1–2)

Note: See Yasuhara et al. (2009c) and Aiello and Szczechura (2004) for comprehensive synonymy.

Argilloecia cf. conoidea G.O. Sars, 1923
(Fig. 3.3–4)

Note: Argilloecia cf. conoidea is similar to Argilloecia conoidea G.O. Sars, 1923, but the outline of our specimen is slightly different from that of the original sketches in G.O. Sars (1923). Argilloecia cf. conoidea is probably conspecific with the species that Whatley and others reported as female specimens of Argilloecia conoidea (Whatley et al. 1996, pl. 1, figs 3–4). The specimens that Whatley and others reported as males of Argilloecia conoidea (Whatley et al. 1996, pl. 1, figs 1–2) belong to a different species in our opinion.
Suborder Cytherocopina Gründel, 1967
Superfamily Cytheroidea Baird, 1850
Family Bythocytheridae G.O. Sars, 1866
Genus Pseudocythere G.O. Sars, 1866
Pseudocythere caudata G.O. Sars, 1866
(Fig. 5.1–2)

Note: There is a certain degree of morphological variation in this species, and further details will be discussed in Yasuhara et al. (in press).

Family Cytheridae Baird, 1850
Genus Cytheropteron G.O. Sars, 1866
Cytheropteron higashikawai Ishizaki, 1981
(Fig. 6.1–2)

Note: This species is very similar to Cytheropteron alatum G.O. Sars, 1866 (e.g. Penney 1993 for a SEM image of a specimen from the topotypic location, i.e., off Norway), but the former has a slightly different outline, a distinct ridge along the posterodorsal margin, and only one large spine at the base of the posterior edge.
of the ala (Cytheropteron alatum have two large spines there). Cytheropteron alatum has more upturned caudal process and thin carina along posterior edge of ala. Further details will be discussed in a separate paper (Yasuhara et al. in press).

Cytheropteron carolinae s.l. Whatley et Coles, 1987
(Fig. 6.3–4)

carolinae Whatley et Coles, 1987 by having a less punctate carapace and lacking distinct spines on the posterior edge of the ala.

*Cytheropteron perlaria* Hao, 1988 (in Ruan and Hao 1988)  
(Fig. 6.5–6)  
*Note:* Comprehensive synonymy and detailed discussion are found in Swanson and Ayress (1999) and Stepanova (2006) and Yasuhara *et al.* (2009c).

*Cytheropteron* sp.  
(Fig. 6.7–8)  
*Note:* Our specimen is conspecific with *Cytheropteron* gr. *punctatum* Brady, 1868 *sensu* Coles *et al.* (1996, in part, pl. 3, figs 7–8 [non 5–6]) and is not conspecific with *Cytheropteron punctatum* Brady, 1868.

*Cytheropteron inflatum* s.l. Brady, 1868  
(Fig. 6.9–10)  
*Note:* Our specimen is conspecific with *Cytheropteron inflatum* *sensu* Stepanova *et al.* (2004). This species is similar to *Cytheropteron inflatum* Brady 1868, but the former has a much more inflated carapace and lacks surface punctation.

Family Cytheruridae Müller, 1894  
Genus *Eucytherura* Müller, 1894  
*Eucytherura delineata* Whatley *et al.*, 1996  
(Fig. 5.5–6)  
*Note:* This species is known from the Arctic Ocean and Nordic Seas (Cronin *et al.* 1995; Jones *et al.* 1998; Whatley *et al.* 1998).

Family Eucytheridae Puri, 1954  
Genus *Eucythere* Brady, 1868  
*Eucythere* sp.  
(Fig. 5.3–4)  
*Note:* This species is very similar to and may be conspecific with the species reported as *Eucythere argus* (G.O. Sars, 1866) by Whatley *et al.* (1996, 1998). True *Eucythere argus* (G.O. Sars, 1866) has a more elongate outline and a much less angular posterior margin (G.O. Sars 1866; Horne and Rosenfeld 1986).

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Fig. 5. Scanning electron microscopy (1, 3, 5, 7, 9) and composite stereomicroscope (2, 4, 6, 8, 10) images of ostracode species from the MUC samples. 1–2, *Pseudocythere caudata* G.O. Sars, 1866, 1115 MUC, 0.5–1.0 cm depth, adult female? LV. 3–4, *Eucythere* sp., 1035 MUC, 0.0–0.5 cm depth, adult RV. 5–6, *Eucytherura delineata* Whatley *et al.*, 1996 1127 MUC, 0.0–0.5 cm depth, adult male LV. 7–8, *Muellerina abyssicola* (G.O. Sars, 1866), 1127 MUC, 0.0–0.5 cm depth, adult female LV. 9–10, *Thaerocythere crenulata* (G.O. Sars, 1866), 1127 MUC, 0.0–0.5 cm depth, adult male? LV. Scale bars = 1 mm. All lateral views.
Family Hemicytheridae Puri, 1953
Genus Muellerina Bassiouni, 1965
Muellerina abyssicola (G.O. Sars, 1866)
(Fig. 5.7–8)

Note: This species is widely reported from the subpolar North Atlantic regions (Hazel 1967; Benson et al. 1983; Penney 1993; Whatley et al. 1998).

Family Krithidae Mandelstam, 1958 (in Bubikyan 1958)
Genus Krithe Brady, Crosskey et Robertson, 1874

Note: We followed Coles et al. (1994) for the Krithe taxonomy.

Krithe ayressi Coles, Whatley et Moguilevsky, 1994
(Fig. 4.1–4)

Krithe dolichodeira van den Bold, 1946
(Fig. 4.5–6)

Krithe minima Coles, Whatley et Moguilevsky, 1994
(Fig. 4.7–8)

Genus Parakrithe van den Bold, 1958
Parakrithe sp.
(Fig. 3.5–6)

Note: This species is similar to a male specimen of Parakrithe angusta (Brady et Norman, 1889). However, Brady and Norman’s (1889) original sketches of male and female specimens seem not to be conspecific each other in our opinion. Since the type specimens are not designated, the identity of Parakrithe angusta (Brady et Norman, 1889) is not clear.

Family Thaerocytheridae Hazel, 1967
Genus Bradleya Hornibrook, 1952
Bradleya mesembrina Mazzini, 2005
(Fig. 8.3)

Note: See Mazzini (2005) and Yasuhara et al. (2009a) for details. Alvarez Zarikian (2009) reported this species as Bradleya normani.

Fig. 6. Scanning electron microscopy (1, 3, 5, 7, 9) and composite stereomicroscope (2, 4, 6, 8 10) images of ostracode species from the MUC samples. 1–2, Cytheropteron higashikawai Ishizaki, 1981, 1127 MUC, 0.0–0.5 cm depth, adult LV. 3–4, Cytheropteron carolinae s.l. Whatley et Coles, 1987, 1115 MUC, 0.5–1.0 cm depth, adult LV. 5–6, Cytheropteron perlaria Hao, 1988, 1127 MUC, 0.5–1.0 cm depth, adult female? LV. 7–8, Cytheropteron sp., 1127 MUC, 0.0–0.5 cm depth, adult LV. 9–10, Cytheropteron inflatum s.l. Brady, 1868, 1004 MUC, 0.0–0.5 cm depth, adult LV. Scale bars = 1 mm. All lateral views.
Genus *Thaerocythere* Hazel, 1967

*Thaerocythere crenulata* (G.O. Sars, 1866)

(Fig. 5.9–10)

*Note:* See Wood and Whatley (1997) for comprehensive synonymy.

Family Trachyleberididae Sylvester-Bradley, 1948

Genus *Ambocythere* van den Bold, 1957

*Ambocythere* sp.

(Fig. 7.1–2)

*Note:* This species is identical to *Ambocythere ramosa* van den Bold, 1965 sensu Benson *et al.* (1983). *Ambocythere ramosa* van den Bold, 1965 has a more slender outline and lacks a distinct dorsolateral ridge.

Genus *Buntonia* Howe *et al.* Chambers, 1935

*Buntonia textilis* Bonaduce, Ciampo *et al.* Masoli, 1976

(Fig. 7.3–4)

*Note:* See Yasuhara *et al.* (2009c) and Aiello *et al.* (2000) for synonymy.

Genus *Echinocythereis* Puri, 1954

*Echinocythereis echinata* (G.O. Sars, 1866)

(Fig. 7.5–6)

*Note:* See Yasuhara *et al.* (2009c) and the references therein for comprehensive synonymy.

Genus *Henryhowella* Puri, 1957

*Henryhowella asperrima* (Reuss, 1850)

(Fig. 7.7–8)

*Note:* This species has considerable intraspecific variation and taxonomic confusion in our opinion, and detailed discussion will be available in a separate paper.

Genus *Legitimocythere* Coles *et al.* Whatley, 1989

*Legitimocythere acanthoderma* (Brady, 1880)

(Fig. 8.4)

*Note:* See Jellinek and Swanson (2003), Mazzini (2005), Yasuhara *et al.* (2009a) for detailed discussion and comprehensive synonymy.

Fig. 7. Scanning electron microscopy (1, 3, 5, 7, 9–11) and composite stereomicroscope (2, 4, 6, 8, 10, 12) images of ostracode species from the MUC samples. 1–2, *Ambocythere* sp., 959 MUC, 0.0–1.0 cm depth, adult female LV. 3–4, *Buntonia textilis* Bonaduce, Ciampo *et al.* Masoli, 1976, 1004 MUC, 0.0–0.5 cm depth, adult LV. 5–6, *Echinocythereis echinata* (G.O. Sars, 1866), 1004 MUC, 0.5–1.0 cm depth, adult RV. 7–8, *Henryhowella asperrima* (Reuss, 1850), 1175 MUC, 0.5–1.0 cm depth, adult Male LV. 9–10, *Pennyella rex* i, 987 MUC, 0.5–1.0 cm depth, adult RV. 11–12, *Pterygocythereis macronata* (G.O. Sars, 1866), 1035 MUC, 0.0–0.5 cm depth, adult LV. Scale bars = 1 mm. All lateral views.
Genus *Pennyella* Neale, 1974

*Pennyella rexi* Yasuhara, Hunt, Okahashi et Brandão, 2013

(Fig. 7.9–10)

*Note:* This species has been confused with *Pennyella dorsoserrata* (Brady, 1880) and was recently described as a new species by Yasuhara *et al.* (2013).

Genus *Pterygocythereis* Blake, 1933

*Pterygocythereis mucronata* (G.O. Sars, 1866)

(Fig. 7.11–12)

*Note:* Our identification is based on the comparison with a SEM image of a Norwegian (*i.e.* topotypic) specimen shown in Freiwald and Mostafawi (1998).

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