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# New and poorly known species of *Neonesidea* (Bairdiidae, Ostracoda, Crustacea) from French Frigate Shoals, the Hawaiian Islands

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# Abstract

*Neonesidea tenera* and four new species (*N. plumulosa, N. holdeni, N. bacata, N. edentulata*) are described from scrapings of spur and groove habitats on French Frigate Shoals and O'ahu, Hawaiian Islands. Some anatomical details have potential taxonomic significance for the genus *Neonesidea*, including the caudal setae of the carapace, the masticatory apparatus, and the antennal claw.

Key words: Ostracoda, Bairdiidae, Neonesidea, Hawaiian Islands

# Introduction

The marine Ostracoda of the Hawaiian Islands are poorly known, and the Bairdiidae especially so. Although Bairdiidae contribute substantially to the diversity of shallow-marine tropical assemblages, especially on coral reefs, relatively few species have been described from the Hawaiian Islands. All of the existing records are based on empty valves and carapaces, and the taxonomic affinities of many species remain uncertain.

The present study describes five new and poorly known species of the genus *Neonesidea* collected from spur and groove habitats on French Frigate Shoals and O'ahu in the Hawaiian Islands (Fig. 1). These include *N. tenera* (Brady, 1886), which has been identified previously at scattered localities but never as a living population (Brady 1886, Maddocks 1969, Whatley *et al.* 2000).

In spite of the ubiquity and diversity of the Bairdiidae in modern faunas, the biology of the living animals is poorly understood. The schematic explanations of the digestive and reproductive systems by Müller (1894, summarized by Hartmann 1967) are based on only two or three species. Ontogeny has been documented for only a couple species (Müller 1894, Smith & Kamiya 2002). Population variability, age-class structure, and responsiveness to environmental influences remain largely uninvestigated. Potentially useful taxonomic characters are undocumented for many species.

*Neonesidea* is a diverse, cosmopolitan genus in shallow sublittoral and reefal environments with more than 100 named species (living and fossil). Maddocks (1969, 1995, Nosy Be), Titterton & Whatley (1988a, Solomon Islands) and Weissleader *et al.* (1989, Micronesia) each reported 8 co-occurring species of *Neonesidea* (some in open nomenclature). This level of diversity appears to be reasonable for larger atolls and well-sampled lagoons and platforms (contrary to Eagar 1998, 1999). Table 1 lists 38 species of *Neonesidea* for which appendage and genital anatomy has been described (incompletely for most). Although Maddocks (1995) clarified the taxonomic concept of the genus *Neonesidea* and provided additional detail about carapace structures, more comprehensive anatomical documentation is needed. This report is a small step in that direction.



**FIGURE 1.** Map of Midway-Hawaiian Islands chain, showing location and bathymetry of French Frigate Shoals, Kane'ohe Bay, O'ahu, and sample locations.

TABLE 1. Species of Neonesidea (38) for which soft-part characters are known, at least in part.

- *N. aduncicorpulenta* Maddocks, 1969 (Nosy Be)
- *N. anfieldingae* Hartmann, 1984 (Rangiroa, Tuamotus)
- N. antonbruuna Maddocks, 1969 (Mozambique Channel)
- N. arenigena Maddocks, 1969 (Nosy Be)
- N. corpulenta (Müller, 1894) (Mediterranean)
- *N. cracenticlavula* Maddocks, 1969 (Mozambique Channel)
- N. decipiens (Müller, 1894) [? = "Bairdia subrhomboidea" of Sars, 1888] (Mediterranean)
- N. dinochelata (Kornicker, 1961) (Bahamas)
- N. edentulata Maddocks, n. sp. (Hawaiian Islands)
- N. frequens (Müller, 1894) (Mediterranean)
- N. longisetosa (Brady, 1902) [? =N. gerda (Benson and Coleman, 1963) of Maddocks (1969, fide Teeter 1975) (Florida, Bahamas, Belize)
- N. gierloffi (Hartmann, 1959) (El Salvador)
- N. guildertonensis Hartmann, 1978 (SW Australia)
- N. holdeni Maddocks, n. sp. (Hawaiian Islands)
- N. ifalikensis Maddocks, 1969 (Ifalik Atoll, Caroline Islands)
- N. incognita (Lerner-Seggev, 1964) (Mediterranean)
- N. lenitiphila Hartmann, 1984 (Rangiroa, Tuamotus)
- N. longevaginata (Müller, 1894) (Mediterranean)
- N. maddocksae Hartmann, 1974 (Mozambique, Tanzania)
- N. manningi Maddocks, 1975 (Ascension Island)
- N. mediterranea (Müller, 1894) (Mediterranean)
- N. michaelseni Hartmann, 1982 (NW Australia, ?Rangiroa, Tuamotus)
- *N. minor* (Müller, 1894) (Mediterranean)
- N. bacata Maddocks, n. sp. (Hawaiian Islands)
- N. obscura (Müller, 1894) (Mediterranean)
- *N. oligodentata* (Kajiyama, 1913) [*sensu* Okubo 1975. Smith & Kamiya (2002, p. 246) stated that the identity is uncertain, but the largest of three species at the type locality occurs commonly around Japan and "is widely accepted to be *N. oligodentata*."] (Japan)
- N. omnivaga Maddocks in Maddocks & Iliffe (1986) (Bermuda)
- N. parilihamata Maddocks, 1969 (Nosy Be)
- N. pateriformis Maddocks, 1969 (Nosy Be)
- N. phlegeri (McKenzie and Swain, 1967) (Baja California)
- *N. plumulosa* Maddocks, n. sp. (Hawaiian Islands)
- N. rosalieae Hartmann, 1978 (W Australia)
- N. schulzi (Hartmann, 1964) (Red Sea, Nosy Be)
- N. tenera (Brady, 1886) (Gulf of Mannar, Samoa, Easter Island, Hawaiian Islands, ?Gulf of Aqaba, ?St. Peter and St. Paul's Rocks)
- N. thomassini Maddocks, 1991 (Tulear, Madagascar)
- N. sp. of Danielopol, 1972 (Ifalik Atoll, Caroline Islands)
- N. sp. 1 of Hartmann, 1980 (SE Australia)
- N. sp. 1 of Maddocks, 1969 (Mozambique Channel)

#### **Sampling localities**

French Frigate Shoals is an atoll, consisting of a 32-km long, crescent-shaped reef and lagoon on an almost submerged seamount in the Hawaii-Midway chain, 900 km northwest of Honolulu and about the same distance southeast of Midway Island (Fig. 1). La Perouse Pinnacle stands as an erosional remnant of volcanic rock in the center of the lagoon. It is part of the Hawaiian Islands National Refuge and a National Marine Sanctuary within the Papahānaumokuākea Marine National Monument.

Kāne'ohe Bay is a sheltered embayment of about 55 km<sup>2</sup> behind a barrier reef, located on the northeast shore of the island of O'ahu.

Appendix I describes the sampling localities. For more maps of the localities and description of collecting methods see Coles *et al.* (2002a, 2002b), DeFelice *et al.* (2002), and Kornicker *et al.* (2007). The samples are part of the same collection from which Kornicker *et al.* (2007) reported the Myodocopina Ostracoda. Additional species of Podocopida Ostracoda from these samples will be described in future papers.

#### Materials and methods

These live animals were collected by hand scraping from hard surfaces, coralline rubble and macroalgae. The number of individuals is small (Table 2), as is usual for hand collections of such microhabitats.

Unfortunately, most specimens are decalcified by storage in preservative. A few retain sufficient calcite to suggest the curvature and surface texture of the original carapace, although the valves are soft and easily torn during dissection. Most consist only of the chitinous fabric and soft body with appendages. From such shreds, the carapace outlines and setae are discernable, but surface puncta, marginal denticles, hingement, and muscle-scar patterns are subtle or not visible. None of the specimens could be observed dry or by SEM, and dorsal views were mostly not obtainable. Secondary crystalline encrustations obscure many details. It is a challenge to identify such material. Although appendages and genitalia provide diagnostic information, no such comparative data exist for species previously reported from the Hawaiian Islands, nor from most other Pacific localities.

Lengths and heights of carapaces and valves are plotted in the L/H scatter plots. For the Hawaiian populations, decalcification may have introduced a small amount of distortion into these values. For populations elsewhere, dimensions are given as published, or as estimated from published illustrations, or as arbitrary combinations of the minima and maxima of published ranges (which may not be representative of an actual individual). In most cases only carapaces and left valves are plotted, because right valves are predictably smaller and do not provide independent information.

	French Frigate Shoals							Kaneohe		
	FFS-TC- station								Bay	
	6	8	9	10	11	12	15	17	1	
N. tenera		3	14	1	5	6	1	7	1	
N. plumulosa			1							
N. holdeni					1					
N. bacata					1					
N. edentulata	1						1			

TABLE 2. Number of specimens collected at each station.

# Depository

All type and identified specimens are deposited in the Bishop Museum, Honolulu.

# Abbreviations

A-1	last (pre-adult) instar
A-2	previous or penultimate instan
AMSP	adductor muscle scar pattern
F	female
Н	height
J	juvenile (instar unspecified)
L	length
LV	left valve
М	male
N, S, E, W	north, south, east, west
NPC	normal pore canal
RPC	radial pore canal
RV	right valve

## **Previous work**

The first report of Ostracoda from the Hawaiian Islands was by Brady (1880), who described 15 podocopid and platycopid species (including 4 species of Bairdiidae) from a single sample collected by the Challenger Expedition "off Reefs, Honolulu" at a depth of 40 fathoms (73 m).

Holden (1967) described 35 recent and fossil species of podocopid and platycopid Ostracoda (including 7 Bairdiidae) from drowned terraces in the Hawaiian Islands. Ladd *et al.* (1970) and Resig (1969) mentioned the occurrence of Ostracoda (identified by J.E. Hazel) in Cenozoic cores drilled on Midway and Oahu. Holden (1976) described 115 species of late Cenozoic Ostracoda (including 30 Bairdiidae, many in open nomenclature) from drill holes on Midway Island. Malz (1981) described Paleocene Ostracoda from drill-holes of the Deep Sea Drilling Program on the Emperor Seamounts. Izuka & Kaesler (1986) presented a quantitative biostratinomic analysis of Ostracoda from a reef flat in Maunalua Bay, O'ahu, but they did not include a list of the species identified. Hartmann (1991) described 26 living species of marine interstitial Ostracoda from several of the Hawaiian Islands, and Wilkinson &Williams (2004) added one more (none are Bairdiidae). Sharpe (1908) reported one myodocopine species off Honolulu. Kornicker (1976, 1978) described 4 species of benthic myodocopines from south of O'ahu and Kane'ohe Bay, O'ahu. Kornicker *et al.* (2007) described 11 species of Myodocopina from O'ahu and French Frigate Island.

The first checklist for Pacific Ostracoda was compiled by Benson (1965). Hartmann (1984, 1988) evaluated a checklist of 268 benthic marine and freshwater Ostracoda reported from Pacific islands, including the Hawaiian Islands. Titterton & Whatley (1988b) analyzed provinciality, origins, and dispersal routes for marine Ostracoda of the entire Pacific, but they have never published the supporting database of species names and occurrence lists on which the analysis was based. They characterized the North Pacific as species-poor, in which isolated localities show little commonality with each other or with other Pacific and Indo-Pacific provinces. This status also reflects the poor taxonomic knowledge of this part of the world. Meisch *et al.* (2007) published a checklist of 58 nonmarine (freshwater and anchialine) species of Pacific islands, of which 8 species were reported in the Hawaiian Islands. From such sources Eldredge & Miller (1997) tallied a total of 202 published species of Ostracoda in Hawaii (8 freshwater, 194 marine, including fossils).

# Status of species described from Honolulu by Brady (1880)

#### Bairdia amygdaloides Brady, 1866

**History.** Brady (1866) described *Bairdia amygdaloides* from "Australia, 17 fathoms (Prof. Jukes's soundings)." Brady's drawings show a smooth, siliquose LV, a dorsally arched RV of a different species, and a juvenile LV interior. The name is sometimes included in checklists, but the identity and provenance of the species described by Brady have not been clarified. In the absence of type fixation and a topotypic population, the species is not recognizable.

Brady (1880) reported *B. amygdaloides* from six Challenger stations, including Hawaii (Fig. 2). It is likely that these records apply to several species, none of which is the true (unrecognizable) *B. amygdaloides*. Brady figured two morphotypes, one smaller and more tumid, but it is not known whether any of the illustrated specimens were from Hawaii. The high-arched lateral outline, densely punctate surface, and large size are traits found in many genera and species of bairdiids.

Brady (1890) reported *B. amygdaloides* from localities near Fiji, New Caledonia, and Samoa. His description itemized traits that are now known to be common throughout the genus *Neonesidea* and not of specific value. He did not provide illustrations or dimensions, and it is likely that several species and genera were included within his material. Chapman (1902) reported *B. amygdaloides* from Funafuti but did not illustrate it.

Maddocks (1969, pp. 19–20) did not reclassify *B. amygdaloides* into *Neonesidea*, as implied by Kempf (1986, p. 213). She merely suggested that the material erroneously identified under this name by Brady (1890) might include one or more species of *Neonesidea*. This is not a nomenclatural action.

Holden (1967) synonymized Brady's (1880, not 1866) identification of *B. amygdaloides* from Hawaii (only) with his new species *B. kauaiensis*. He illustrated several instars of *B. kauaiensis* and compared them with Brady's

illustrations. As Figure 2 shows, it is unlikely that Brady's (1880) illustrated specimens belong to *N. kauaiensis*. He mentioned finding two specimens at Clipperton Island, but this identification was not confirmed by Allison & Holden (1971).

Holden (1976) reported fossils of *N. kauaiensis* from Midway, emphasized the invisibility of the pitting and reclassified it in *Neonesidea*. As Figure 2 shows, it is likely that the Midway population is not conspecific with either Brady's (1880) or Holden's (1967) Hawaiian material.

**Conclusions:** The true *B. amygdaloides* is unrecognizable at present, and this name (though available) is best treated as a *nomen dubium* until useful type or topotypic material can be examined. The Hawaiian record belongs to another, unidentified species.



FIGURE 2. L-H scatter plot for Hawaiian records of Bairdia amygdaloides of Brady (1880) and similar species.

# Bairdia attenuata Brady, 1880

**History:** Brady (1880) described *B. attenuata* from off Honolulu and from Challenger Station 185 in the Torres Strait (11°35'25"S, 144°02'0"E, 135 fathoms) (Fig. 3). His drawings show a sinuously arched, moderately inflated carapace with a distinctly punctate surface, but the provenance of the illustrated specimen was not mentioned.

Chapman (1902) reported *B. attenuata* from Funafuti but did not illustrate it. Reports by Fyan (1916, in synonymy of *Nesidea molengraaffi* Fyan, late Pliocene, Timor) and Egger (1901, west coast of Africa) probably apply to other species.

Holden (1967) reported *B. attenuata* living and fossil in the Hawaiian Islands. His figures of the LV lateral outline show a more sinuous dorsal margin, with an indistinct anterodorsal concavity and a distinctly concave posterodorsal segment above a narrowly produced, up-swung caudal process. Holden concluded (p. 14) that

Brady's illustrations apply to a specimen with "a more upturned posterior and anterior" from another locality, not from Honolulu. Holden (1976) did not report the species from Midway.



FIGURE 3. L-H scatter plot for Indo-Pacific records of Bairdia attenuata Brady, 1880.

Puri & Hulings (1976) selected the lectotype from the Torres Strait station. Their figures show an abraded, featureless RV, which is high-arched and angulate in lateral outline, with a more broadly rounded, less produced, less caudate posterior end than Holden's or Brady's figures, and an AMSP that is compatible with *Neonesidea*. [Having seen the scar of this specimen in 1967, Maddocks (1969) speculated that the species might be assignable to *Neonesidea*.] It is likely that their selection of this lectotype specimen, which is obviously not the specimen illustrated by Brady, transferred the name to a different species. Study of a topotype population may be required for a diagnosis of this Torres Strait species.

McKenzie and Pickett (1984) listed *Paranesidea* cf. *attenuata* (Brady) in several cores of the late Pleistocene of New South Wales, Australia, without discussion. Their illustrations show a uniformly punctate surface and a symmetrical, less sinuous and less caudate outline. The dimensions (Fig. 3) agree with those of Brady.

Mostafawi (1992) reported "*Bairdia* cf. *attenuata*" from the Sunda Shelf, commenting that the outline was like the Torres Strait species, but that the surface was finely punctate except in the median region. His illustrated specimen is similar to Brady's, but not as high relative to length, and has a less sinuous dorsal outline. The dimensions (Fig. 3) agree with those of Brady but are smaller than those of Puri & Hulings (1976).

Whatley *et al.* (1996, p. 6–7, pl. 1, fig. 1, pl. 7, figs. 1, 2, from Lee Point on Shoal Bay, Northern Australia) reclassified Brady's nominal species into *Bairdoppilata:* 

"A bairdiacean species with a puntate [sic] surface ornament more typical of *Paranesidea* species but possessing 'auxillary [sic] dentition'. The specimens illustrated here are almost identitical [sic] to the

original illustration of *Bairdia attenuata* Brady, 1880. However, the illustration of the lectotype specimen designated for *B. attenuata* by Puri and Hullings [sic], 1976 cannot be confidently equated with Brady's (1880) original illustrations."

Here, Whatley *et al.* apparently intended to suggest that the lectotype designation should be set aside or ignored. Unfortunately, this is not possible under the Rules, even though the lectotype specimen may belong to a different species. The passage concluded:

"A nomina nuda species from Florida, described by Puri, of specimens illustrated by McKenzie and Pickett (1984) as *Paranesidea attenuata* (Brady) were not shown or described, making the synonymy with specimens illustrated here tentative."

No species is described by this name from Florida. Any *nomen nudum* is unavailable under the Rules and must be ignored.

Whatley *et al.* (1996) did not mention Holden or evaluate the record from Hawaii. They illustrated a densely punctate RV with a sinuous dorsal outline and slightly caudate posterior.

**Conclusions:** The lectotype designation by Puri & Hulings (1976) governs the application of this name. It transferred Brady's name to a third, poorly defined species.

The original species, illustrated by Brady (1880) from the Torres Strait and now reclassified in *Bairdoppilata*, requires a new specific name. It lives in Indonesian and North Australian waters, although its variability and geographic range are not well delineated. It includes the records by Mostafawi (1992), Whatley *et al.* (1996), and perhaps also McKenzie & Pickett (1984).

Brady's (1880) Hawaiian record probably applies to a second, similar but slightly larger species, which was redescribed and illustrated under the name *Bairdia attenuata* by Holden (1967). It requires a new name.

The soft parts of all three of these species are unknown. Figure 3 displays their relative size relationships.

#### Bairdia crosskeiana Brady, 1866

**History:** *B. crosskeiana* was originally described by Brady (1866) from the eastern Mediterranean. Brady (1880, 1890) later reported it from several Pacific islands, but the provenance of the illustrated specimens was not documented (Fig. 4). Chapman (1910) listed it at Funafuti but did not illustrate it.

Holden (1967) considered Brady's (1880) report from Hawaii to be a misidentification. He illustrated Hawaiian specimens for comparative purposes and mentioned some distinctive details but did not propose a new name for them. Holden (1976) included *B. crosskeiana* of Brady (1880, not 1866) and of Holden (1967) in the synonymy for his identification of *Neonesidea gierloffi* at Midway and the Hawaiian Islands. This identification was probably erroneous (Fig. 4).

Titterton *et al.* (2001) selected and illustrated a lectotype for *B. crosskeiana*. Their synonymy excluded the subsequent reports by Brady (1880, 1890), and they commented (p. 33) that, "For the moment, it is considered doubtful whether this species occurs in the Pacific Ocean." They mentioned that slides bearing this name in the Brady Collection from Pacific locations include specimens identifiable as *Neonesidea woodwardiana* (Brady, 1880), *N. schulzi sensu lato* (Hartmann, 1974), and perhaps *N. schulzi ifalikensis* Maddocks, 1969. Unfortunately, their synonymy also included *Bairdia crosskeiana* Brady of Holden (1967)—which contradicts Holden's evaluation, their exclusion of Brady (1880), and their stated doubt concerning the validity of Pacific records! Their remarks (p. 33) added to the muddle by stating that the Hawaiian material of *B. crosskeiana* is similar to *N. ritugerda* except "higher and more elongate," although Holden's statements and drawings clearly show the opposite. They did not mention Holden (1976).

**Conclusions:** The true *Neonesidea crosskeiana* (Brady, 1866) lives in the eastern Mediterranean, and reports from the Pacific Ocean are considered dubious. Its soft parts are unknown.

The records from Hawaii (Brady 1880, Holden 1967) and Midway (Holden 1976) belong to three different, unidentified species. Figure 4 shows their size relationships. Other records from the Pacific require re-evaluation.



FIGURE 4. L-H scatter plot for Pacific records of Bairdia crosskeiana of Brady (1880) and similar species.

# Bairdia expansa Brady, 1880

**History:** Brady (1880) described *B. expansa* from off Honolulu. Puri & Hulings (1976) designated and illustrated the lectotype.

The species was reported by Brady (1890) from tide-pools in Samoa and by Chapman (1910) from deep-water dredgings near Funafuti (not illustrated). Holden (1967) identified fossils from drowned terraces of the Hawaiian Islands. It was not reported by Holden (1976) from Midway.

The reclassification in *Neonesidea* by Eagar (1971, without discussion, in a checklist of New Zealand Ostracoda) is unsupported. An updated generic classification must await additional information.

**Conclusions:** *B. expansa* should be easily identifiable but does not occur in the material studied here.

# Status of species described from Hawaii by Holden (1967)

*Bairdia attenuata* **Brady**, **1880**: This is probably a species of *Bairdoppilata*. Holden's drawings (1967, Figs. 7a–d) show sinuous lateral outlines, not closely resembling the lectotype specimen selected by Puri & Hulings (1976) from the Torres Strait. The dimensions reported by Holden are smaller than those reported by Brady (1880), which in turn are smaller than those given by Puri & Hulings (1976) (Fig. 3).

*Bairdia crosskeiana* of Brady, 1880: This is one of several closely allied Indo-Pacific species within the *N. schulzi* species-group, not represented in the present collection (Fig. 4).

*Bairdia expansa* **Brady**, **1880**: This is a distinctive species of uncertain generic affinity, not represented in the present collection.

*Bairdia hanaumaensis* Holden, 1967: The generic affinity of this finely pitted species is uncertain. Holden (1976) reclassified it in *Triebelina* and described fossils of a similar but more elongate species from Midway Island. It is not represented in the collection studied.

*Bairdia kauaiensis* Holden, 1967: This may be a species of *Neonesidea*, probably not conspecific with either *Bairdia amygdaloides* Brady of Brady (1880) or *Neonesidea kauaiensis* (Holden) of Holden (1976) (Fig. 2). It is not represented in the collection studied.

*Bairdia ritugerda* Holden 1967: This may be a species of *Neonesidea*. Holden (1976) reclassified it in *Neonesidea* and reported fossils from Midway Island (Fig. 2). It is not represented in the collection studied.

Bairdia sp. of Holden 1967: The identity and generic affinity of this species are unknown.

#### Taxonomy

# Order PODOCOPIDA Müller, 1894 Superfamily BAIRDIOIDEA Sars, 1888 Family BAIRDIIDAE Sars, 1888

#### Genus Neonesidea Maddocks 1969

1969*Neonesidea* Maddocks: 16. 1995*Neonesidea*, Maddocks: 199.

# Remarks

The taxonomic concept of this genus as clarified by Maddocks (1995) remains generally sound. Species of *Neonesidea* are easily recognized by the thin-walled, nearly symmetrical, smooth or finely punctate carapace with streamlined contours, a central opaque spot, and compact zigzag arrangement of AMSP. The most reliable traits are the bifid antennal claw of the male and the three-segmented, folding hemipenes with elongate median and terminal parts.

Maddocks (1969, p. 20) recognized three species-groups, of which the most populous is the *N. schulzi* group. The usefulness of species-groups is limited, however, because anatomical information is incomplete for many species.

Species of *Neonesidea* occur commonly on marine plants, rubble, washings of marine invertebrates, and sandy muds in inner sublittoral and reefal environments. The genus is circumtropical. In the absence of anatomical evidence, species from deeper habitats and higher latitudes should not be referred to *Neonesidea*.

Details of some morphological characters of *Neonesidea*, which may have potential taxonomic value, are discussed below.

#### **Carapace** setae

All Ostracoda have numerous setae on the carapace (also termed hairs, bristles, sensilla). Those of Bairdiidae are often large, conspicuous and decay-resistant. Because in Bairdiidae they are mostly simple in form, and their sensory function is hypothetical, the straightforward term "setae" is used here. Details of carapace setae are rarely described for Bairdiidae, although they are likely to have taxonomic value. *Neonesidea* often has conspicuous setae on an otherwise featureless carapace, and the hirsute appearance is frequently mentioned in descriptions.

The color of a seta (yellow to brown) reflects the thickness of the chitin wall and probably the ontogenetic age of the seta. Pale setae are more flexible, but dark brown (sclerotized and sometimes pigmented) setae are stiff,

brittle, decay-resistant, and are retained on some subfossil valves and carapaces. The articulation at the base is relatively rigid. Electron micrographs of the cuticular ultrastructure of these setae and the associated pores were provided for *Neonesidea* sp. by Okada (1983, pl. 1, figs. 6, 7, 11, 12).

The corresponding nerve-cell in the underlying epidermis is thought to be responsive to tactile stimuli (Müller 1894, Rome 1947). Collectively, the setae might also serve other functions: as a fence to protect the domicilium from intruders, as guard hairs to minimize carapace abrasion, as an umbrella to keep detritus from settling on the carapace surface, as cat-like whiskers to measure the dimensions of a crevice, as spring-like anchors to hold the animal steady in a crevice, as extensions to occupy and claim a surrounding volume of water, as a deformable outer membrane to minimize turbulence, and perhaps for lift to improve the effective buoyancy of the animal. A streamlining function is plausible for *Neonesidea*, because many species live in high-energy environments.

The setae themselves are usually quite clean, and little sedimentary debris collects on them or on the carapace surface below. Occasional epibionts, such as stalked ciliates, typically attach near the free margins of the valves rather than to the setae. Most boreholes in valves are postmortem.

Old setae are shed with the molted exuvium of each instar. New setae grow as part of the new chitinous integument, which is visible within the interlamellar cavity of the old carapace in a molting animal (Fig. 8A–C, F; see also Okada 1983, pl. 2, fig. 11). Additional setae and NPC are added at each molt. The length and thickness of a particular seta probably increase with each molt. Adults of many species of *Neonesidea* have a shaggy coat of setae of many sizes and colors (Figs. 24E, 35A). It is likely that the longest, thickest, and darkest setae originated earlier in ontogeny.

Most carapace setae are simple, unbranched, and taper smoothly to a sharp point (Figs. 5A–E, 8D, 18J, 25F, I, 28F, G). Occasional barbed setae (having small proximal thorns) and polyfurcate setae (having shorter branches arising near the base) have been documented for *N. anfieldingae*, *N. pateriformis*, *N. arenigena* and *N.* sp. (Hartmann 1984, pl. 3, fig. 5; Maddocks 1995, pl. 9, fig., fig. 4, pl. 10, figs. 3–5; Okada 1983, pl. 2, figs. 5, 6, 11), as well as for some other bairdiid genera. They are suspected to occur on some of the species described here, but were clearly seen on only one species (*N. tenera*, Fig. 7F), because they require SEM observation.

#### Eyelash setae

Eyelash setae [new term] arise at the very edge of the calcified part of each valve (just inside the narrow, uncalcified, epicuticular, chitinous edge-strip). They form a close-spaced array with uniform thickness, length, and curvature, curling outward as a protective screen. Their smaller diameter, shorter and uniform length, parallel curvature, and lighter color easily distinguish eyelash setae from the nearby, more heterogeneous, simple setae (Figs. 8G, 8H, 18H, 24G–H, 25F, 29C, 30C–E). Eyelash setae are more numerous and more closely spaced along the anterior margins, more widely spaced and somewhat larger along the posteroventral margins, but absent on the dorsal edge of the caudal process (dorsal to the terminal spine or angle). They are probably homologous with (modified from) simple setae.

#### **Caudal setae**

About 6 to 8 caudal setae [new term] may be present along the dorsal edge of the caudal process of each valve (Fig. 5). Caudal setae are feathered, having numerous minute barbs or vanes that form a thistle-, leaf- or fan-like structure (Figs. 5A–E, 8D–E, 19A–D, 25F–I, 26H). The shafts are short, wide, thick-walled, and inflexible. The distal plumose fan or lamellar fringe overlaps with that of neighbors to form a tight, protective fence or palisade.

Caudal setae arise from enlarged pores in a short, closely spaced row, which is located almost at the valve edge on the outer surface of the valve, distal to the simple setae that crowd this region (Figs. 25G–H). In the LV this row of caudal setae extends from the posterior end of the posterodorsal overhang (overlap over RV) to just above the terminal angle or terminal spine. In the RV this row extends from a subtle marginal angle (where the selvage joins the valve edge) along the slightly flared or beveled edge of the caudal process to the posterior angle; it is just proximal to (inside of) the thin, ragged flange (edge-strip) of chitin that may wrap around the posterior angle. There are no caudal setae present at the corresponding anterodorsal location (anterior to the anterior end of the LV overhang).



**FIGURE 5.** Caudal setae and simple setae on caudal process. A, C, *Neonesidea tenera* Brady, female specimen **3905F**, LV and RV exteriors. B, D, *Neonesidea tenera* Brady, juvenile female instar A–1 specimen **3957J**, RV and LV exteriors. E, F, *Neonesidea plumulosa* n. sp., male specimen **3960M**, LV and RV exteriors. Scale bar = 10 µm.

Caudal setae represent a discrete morphological trait with potential taxonomic value. They are probably homologous with (modified from) eyelash setae; which they resemble in marginal location, transparency, uniformity of length, and parallel alignment, and which are not present at this location if caudal setae are present. The number of caudal setae is probably fixed, 6 to 8, though they are not easy to count. They are present in late instars as well as adults.

Caudal setae are especially well developed in species of the *N. schulzi* species-group, which have smooth, teardrop-shaped carapaces ending in a posterior spine. The plumose or palmate caudal setae are arrayed in a

cuspate hedge just dorsal to this terminal spine, which may protect the spine or assist in streamlining. In species of the *N. pateriformis* species-group the caudal setae are smaller, thistle-like and more difficult to distinguish. No information is available about caudal setae in the *N. dinochelata* species-group.

Caudal setae were first indicated in drawings by Müller (1894, pl. 15, fig. 8, 10) and Hartmann (1964, pl. 4, figs. 14, 15). SEM photos have been published by Hartmann (1978, pl. 1, figs. 14, 15; 1982, pl. 6, fig. 4; 1984, pl. 2, fig. 4) and Maddocks (1995, pl. 8, figs 2, 3, 8).

Caudal setae are somewhat resistant to decay and may be retained on subfossil specimens after other setae have vanished. On dry valves, these overlapping, close-pressed fans merge as a continuous chitin wall.

The corresponding pores are enlarged, without rim-walls or muri. A row of larger pores in this position in fossils might indicate presence of caudal setae in life. This point requires further investigation, as other enlarged pores may occur in this general region, which correspond to simple carapace setae and eyelash setae (Figs. 5A–E). Local thickening (extra calcification) of the nearby carapace wall makes a slight but distinctive elevation, often described as a "humped caudal process." In fossils this hump should be another indicator of the likely presence of caudal setae in life.



**FIGURE 6.** *Neonesidea tenera* (Brady). A, D, G, female specimen **3892F** with decalcified carapace: A, RV exterior; D, LV exterior; G, right side of entire animal before dissection. B, C, F, I, female specimen **3905F** with partially calcified carapace: B, RV exterior; C, LV exterior; F, I, right side of entire animal before dissection. E, J, male specimen **3906M** with partially calcified carapace: E, RV exterior; J, right side of entire animal before dissection. H, K, female specimen **3962F** with calcified carapace: H, left side of entire animal in reflected light before dissection, showing small secondary crystalline concretions, clear marginal regions, brown carapace lining, light orange food balls; K, same in transmitted light. L, juvenile female instar A-1 specimen **3957J** with decalcified carapace, right side of entire animal. Scale bar = 100 μm.



**FIGURE 7.** *Neonesidea tenera* (Brady). A, B, male specimen **3906M:** RV and LV exteriors with AMSP, NPC, setae. C, F, G, I, female specimen **3892F:** C, left exterior of entire animal, showing masticatory organ, food ball, and female genitalia; F, fragment of carapace cuticle showing several barbed setae (smaller) and simple setae (larger); G, detail of fig. C showing NPC and setae; I, detail of fig. C showing anterior marginal setae, antennules, antennae, mandibles, S-shaped strut of head capsule, esophagus, and masticatory organ. D, E, female specimen **3905F:** RV and LV exteriors with AMSP, NPC, and setae. H, juvenile female instar A-1 specimen **3910J:** right side of entire animal with numerous secondary crystalline concretions. Scale bar = 50 µm.

# Anchor setae

In a few Bairdiidae, one or a few carapace setae, located on the posterolateral and posterior flanks of the carapace, may be much larger than the other simple setae and grow exceptionally long, even longer than the carapace. In dorsal view these anchor setae [new term] project outward and trail posteriorly (Figs. 28A–D). When touched with a dissecting needle, they feel rough or sticky. This friction might be caused by extremely small scales or thorns (not observed).

Anchor setae have been illustrated occasionally (Müller 1894, for *Bairdia raripila, B. reticulata,* and *B. serrata*; Maddocks 1975, for *Triebelina* aff. *T. raripila*). It is speculated here that the function of these setae may be to catch on external surfaces to resist current drag. Observations in living animals will be necessary to establish this function. No modification of the associated NPC has been noticed.



**FIGURE 8**. *Neonesidea tenera* (Brady). A–C, F, juvenile male instar A-1 specimen **3920MJ**, molting animal: A, left exterior view, with old carapace partly flaking off, new cuticle and setae visible within interlamellar cavity; B, C, fragment of unexpanded new cuticle, removed from interlamellar cavity of LV; F, right posterior (caudal) view of same specimen, showing new cuticle within the old. D, E, juvenile female instar A-1 specimen **3957FJ:** RV and LV exteriors of caudal process, with caudal setae, simple setae, RPC and false RPC. G-J, female specimen **3905F:** G, H, LV anterior margin with eyelash setae and simple setae; I, J, LV posterior margin with simple setae and caudal setae. Scale bar = 50 µm.

#### Normal pore canals

Each carapace seta rises from a normal pore canal (NPC). In ontogeny, existing NPC and setae are retained, and new NPC and setae are added with each molt. Smith & Kamiya (2002, for *N. oligodentata*) demonstrated that the number of pores increases through ontogeny, as is the case for other Podocopida. Because of the large number in most species, it is impractical to map their locations (but see Smith & Kamiya 2002, fig. 5).

The diameter of existing (inherited) pores probably increases with each molt, as the adults have a range of pore sizes. Most pores are rimless, but a narrow marginal rim may appear on a few pores late in ontogeny (Figs. 7A–B, D–G, 18J, 30A–B, G–H).



**FIGURE 9.** *Neonesidea tenera* (Brady). A, G, H, female specimen **3962F:** A, genital lobe as seen through carapace before dissection; G, posterior region of body with furcae, ovaries, oviducts, and genital lobes; H, genital lobe. B–F, female specimen **3905F:** B, genital lobe with spermatophore plug; C, D, left side of female body with eggs in uteri; E, dehydrated eggs and food ball; F, posterior region of body with furcae, ovaries, oviducts, and genital lobes. Scale bar =  $10 \mu m$ .

# **Radial pore canals**

Radial pore canals (RPC) house the nerve leading from an eyelash seta to the nerve cell in the epidermis within the vestibule. They are usually short in *Neonesidea*. A row of regularly arranged, slightly enlarged pores just inside the margin of the valve marks the openings of RPC and insertions of eyelash setae.

In adults, numerous false radial pore canals of various lengths may also be observed (Figs. 7D–E). Each accommodates the nerve for a simple seta, and each ends at a pore located near but not quite at the edge of the valve. The number of false RPC increases at the last molt (A-1 to adult), when additional calcite is deposited at the valve edge (infold), shrinking the vestibular cavity and expanding the so-called zone of concrescence.

## Hingement

*Neonesidea* has the usual bairdiid hingement, in which the straight, narrow, dorsal edge of the RV functions as the hinge bar (Fig. 29D–E). This thin bar is slightly thicker (dorsoventrally) at the anterior and posterior ends but lacks laterally-projecting terminal teeth. It fits into a straight median shelf (groove) on the LV, below the overreaching, curved, dorsal (exterior) LV surface (Fig. 18B). The functional hinge encompasses only this median segment, forming an axis around which the valves rotate but remain attached by flexible ligament. Yamada (2007) provided electron transmission micrographs for *N. oligodentata* (Kajiyama, 1913) and classified its hinge structure as "exterior type."

Many species of *Neonesidea* show a delicately grooved or striate texture along the dorsal surface of the median hinge bar (RV) and groove (LV). This texture marks the surface where cuticular fibers of the ligament pass from one valve into the other (Maddocks 1969, 1990, 1995). It does not function for articulation in valve rotation, and the ridges do not fit into the grooves on the other valve. This hinge detail was first reported by Hartmann for *N. schulzi* (1964, pl. 5, figs. 20, 21) and has been especially well illustrated for *N. michaelseni* (Hartmann 1982, pl. 9, figs. 7, 8; 1984, pl. 1, fig. 9). It has been observed also in other genera of Bairdiidae, Macrocyprididae, and Cytheroida, and it probably has no special taxonomic value.

The anterodorsal and posterodorsal segments of the tripartite dorsal margin (as seen in lateral outline) are not part of the hinge proper. Along these segments of the free margin, protected by an overhanging fold of the LV, the RV selvage makes contact only when the valves are closed (Fig. 28E). *Neonesidea* lacks auxiliary, bairdoppilatan dentition (anterior and posterior teeth on the RV selvage, which fit into sockets beneath the LV overhang).

#### Valve outlines

As usual in Bairdiidae, the LV and RV lateral outlines are asymmetrical, because of the pronounced dorsal and ventral overlap (LV>RV) (Figs. 6B–C, 18D, F, 28A–B, 35A–B). The outline of the LV is always more distinctive and more reliable for identification of species and sexual dimorphs.

#### Dimorphism of carapace size and shape

The female carapace of *Neonesidea* is typically somewhat longer and slightly higher in proportion to length than that of the male (Fig. 15). In L/H scatter plots of large populations, the adult cluster is diagonally elongated, with males located in the lower left and middle, and females in the middle and upper right (Maddocks 1995, Graph 1). Because the domains overlap, it is somewhat difficult to sort males and females without soft-part control.

Holden (1967, 1976) erroneously considered the larger specimens to be males, and the stated sex attributions in those papers should be reversed.

# **Dimorphic antennal claw**

The most consistent anatomical character of *Neonesidea* is the bifid hook at the end of the male antennal claw (in contrast to the smoothly tapered or slightly barbed termination in other genera). This dimorphic hook was first illustrated by Sars (1888, pl. 17, figs. 4, 5, for *"Bairdia subdeltoidea"*) and Müller (1894, pl. 15, fig. 31, for *B. frequens*) but was not used in taxonomy until Maddocks (1969).

Details of this hook deserve consideration. Attention should be paid to the length, thickness, and angle of curvature of the tip of the anterior horn, as compared to the posterior horn. In some species, the terminal claw is slightly constricted just before the hook, and then the hook flares distally to a wider breadth and exaggerated curvature. In other species the anterior margin of the hook continues the smooth profile of the claw to the very tip of the anterior horn.

The sigmoid groove or cleft between the two horns of the hook is oriented at an oblique angle to the flat plane of the hook. It is not perpendicular to this plane but slopes posteriorly, and therefore the width of this groove appears to vary as one focuses up and down through it. Along the flared proximal edge of the anterior horn (the convex, inner, posterior edge), a marginal ridge and submarginal channel are incised on the flat surface. These surface corrugations may accomplish a more secure, forceps-like hold.

It is likely that this hook functions to hold the female for copulation. It is postulated here that the sigmoid groove between the two prongs of this hook serves to catch one of the larger setae located on the posterolateral region of the female carapace.

In adult females and juveniles of both sexes, the antennal claw tapers smoothly to a gently curved point, with no indication of a bifid hook.

In juvenile males (A-1 instar) that are preparing to molt, the adult hook can be seen inside, already fully formed and withdrawing from the interior of the juvenile claw. This transition was first illustrated by Maddocks (1975, pl. 1, fig. 6) for *Neonesidea manningi*.

#### Fused antennal claw

The second, shorter antennal claw (incompletely separated from the terminal podomere in most Bairdiidae) appears smooth in unstained specimens of both sexes of *Neonesidea*. Danielopol (1972, p. 42, fig. 2C, from stained specimens) illustrated a double row of minute, pectinate barbs for *Neonesidea* sp.

This is in contrast to the coarsely barbed or serrate condition of this claw in other genera, such as *Paranesidea*, which is usually more strongly developed in the male. It is speculated here that the function of the enlarged barbs is to catch on one of the thicker seta on the posterolateral region of the female carapace, in a fashion analogous to the sigmoid groove of *Neonesidea*.

#### Anterior accessory antennal seta

In *Neonesidea* the anterior accessory seta of the terminal podomere of the antenna is thin (not developed as a claw, as in *Bairdoppilata*) and sexually dimorphic (short in males, long in females). Its function, if any, is unknown.

# Medial accessory antennal seta

Another fairly short accessory seta originates medially and a little proximally, above the base of the terminal claw and near the base of the fused claw. It is thin, often nearly invisible, and sometimes overlooked. It is not known to exhibit sexual dimorphism, and its function (if any) is unknown. Danielopol (1972, fig. 2C) illustrated an additional Y-aesthetasc at this position.

# Segregated setae of the maxillule

The six segregated setae of the maxillule (fourth limb, first maxilla) are the so-called mouthwards-directed or reflexed setae of many Podocopida. In Bairdiidae they are thin, unfeathered, and have flattened, obliquely spatulate, wedge-like terminations. They arise from a lobate plate that is somewhat differentiated from the ventral-proximal edge of the vibratory plate but not separately muscularized. All six setae are of uniform length and form, and there is no sexual dimorphism.

In life position these setae hang down ventrally (not anteriorly or mouthward). They are "reflexed" only in comparison to the pectinate setae of the vibratory plate, which are oriented radially and posteriorly. Müller (1894, p. 59) stated that they have a tactile function because they are innervated, but other functions (cleaning, chemosensory) might also be worth consideration.

#### Plumose setae of the vibratory plate of the maxillule

*Neonesidea tenera, N. plumulosa* and *N. bacata* have 25 plumose setae on the vibratory plate of the maxillule. For *N. holdeni* they could not be counted, and for *N. edentulata* the number is uncertain (at least 23 or 24).

The 6 published illustrations of this limb for *Neonesidea* show 25 setae for *N. manningi*, *N. omnivaga*, *N. schulzi*, and *B. subdeltoidea* of Sars (1888), and 26 setae for *N. oligodentata* and *N. pateriformis*. The range for most other genera of Bairdiidae appears to be 24 to 26 (Smith *et al.* 2005, Appendix A).



**FIGURE 10.** *Neonesidea tenera* (Brady). A, B, E–L, male specimen **3906M:** A, B, posterior of body with hemipenes and furcae; E, spermatophore; F–H, hemipenes; I, spiral vas deferens; J, L, masticatory processes of maxillule; K, terminal claw of palp of maxillule. C, D, female specimen **3905F:** C, head capsule with S-shaped struts, sternum, and mouth; D, masticatory organ. Scale bar =  $10 \mu m$ .

# Segregated setae of the vibratory plate of the fifth limb

The vibratory plate of the fifth limb (first walking leg) of Bairdiidae has four anteroventral, proximal setae, which are thin, smooth, and cylindrical. Each one ends in a flat, slightly widened, obliquely truncated, spatulate or chisel-shaped wedge. These four setae are segregated and distinct from the flattened, tapering, regularly spaced, pinnate setae that line the dorsal (posterior) margin and tip of the vibratory plate. In form they are similar to the six segregated, unfeathered setae of the maxillule.

In females of *Neonesidea*, one of these featherless setae is set apart from the others at the anteroventral edge of the vibratory plate and oriented ventrally. The other three setae, of similar structure but graduated lengths, are spaced widely along the ventral edge of the vibratory plate, and they are oriented more posteriorly.

In males of *Neonesidea* two of these four setae are segregated anteroventrally. The other two are spaced along the ventral margin and have graduated lengths. [The report of four proximally segregated setae plus two more featherless setae in males of *N. maddocksae* is probably an error (Hartmann 1974, p. 248, pl. 15, fig. 118).]

By contrast, in some other genera of Bairdiidae (*Bairdoppilata, Paranesidea*) all four featherless setae are segregated proximally, having the same length and ventral orientation, and there is no sexual dimorphism in this character.

The function of these setae is unknown, although the stiffness, ventral orientation, and spatulate ends suggest either a cleaning or chemosensory role. Müller (1894, p. 66) speculated that they are tactile organs, because they are provided with nerves (an argument that applies to most if not all setae). The reason for their dimorphism in *Neonesidea* is unknown.

# Plumose setae of vibratory plate of fifth limb

The vibratory plate of the fifth limb is elongate-triangular, tapering posteriorly. The dorsal edge and tip are lined with a close-spaced row of about 13 plumose setae, similar to those of the vibratory plate of the maxillule. The setae are flexible, flattened, wide, almost touching at their bases, tapering distally, armed on both sides with minute, close-spaced vanes (too small to draw). They are of graduated lengths, increasing distally. Seta 12 at the tip is longest and thickest); seta 13 below is straight, indented, and not as long.

*N. tenera*, *N. plumosa*, *N. holdeni* and *N. edentulata* have 13 plumose setae. *N. bacata* n. sp. appears to have 12 plumose setae.

In 11 of the 14 species of *Neonesidea* for which this structure has been illustrated, the number of plumose setae is 13. The number of setae was drawn as both 13 and 14 for *N. frequens* (Müller 1894), as 14 for *B. subdeltoidea* of Sars (1888), and as 12 for *N. ifalikensis* (Maddocks 1969).

Among 23 species of 6 other genera of Bairdiidae for which this structure has been illustrated, 13 species have 13 setae, 6 have 12 setae, and 4 have 10 or 11 setae. Perhaps because of evident discrepancies, there is no consistent trend at the generic level.



**FIGURE 11.** *Neonesidea tenera* (Brady). A, B, juvenile male instar A-1 specimen **3920MJ**, molting animal: hook of adult antennal claw is visible within juvenile claw. C–E, male specimen **3906M:** C, D, antennal claw; E, other antennal claw, foreshortened and out of focus, to show how details of shape depend on exact focus and perspective. F, female specimen **3892F:** antennal claw. G, female specimen **3905F:** antennal claw. H, juvenile female instar A-1 specimen **3910FJ:** antennal claw with sharply beveled tip, as usual for bairdiid juveniles. Scale bar = 10 μm.

#### Hemipenes

The hemipenes of *Neonesidea* have a three-segmented, jackknife configuration, well described by Müller (1894). This apparatus hangs at the end of the soft, accordion-pleated, protrusible abdomen, attached to a stout chitinous framework that also supports the post-abdominal bristle and paired setose rami (furcae or uropods). After protrusion from the carapace, muscles within the sturdy basal and median segments contract, causing these overlapping pieces to unfold and extend. The smaller terminal segment rotates by contraction of a set of muscles attached to its base from within the median segment. It is a flat or curved lamellar plate, with or without projections, and may include an incised groove to accommodate the copulatory rod.

In published illustrations these details may vary according to whether the organ is folded or erect and whether the drawing was made in life position (after dissection but before mounting) or after compression by the cover glass. Because of differences in perspective and artistic style, many drawings are hard to interpret. An exception is the meticulously labeled drawings of Danielopol (1972, figs. 3, 4, for *Neonesidea* sp.), who also suggested homologies with the corresponding organ of the Cyprididae. The termination (tapering, coiled, hooked, or discoidal) of the copulatory rod (ejaculatory tube), though frequently damaged, has potential taxonomic as well as functional significance (Danielopol 1972).

#### Eyes

The median eye in Bairdiidae is poorly described and often overlooked, perhaps because the pigmentation fades after specimens are stored in fixative (Danielopol, personal communication). Müller (1894, p. 266, pl. 40, fig. 50) published a sketch for *Bairdia* sp. Like Claus (1891), he pointed out that in many shallow-water Bairdiidae a small anterodorsal region of the carapace is transparent, to allow light to reach the eye below, although the rest of the epidermis or carapace lining may be pigmented or opaque. He said (p. 269) that in species of his group (1) (roughly equivalent to the genus *Neonesidea*) the eye is always present, whereas in other groups it may be poorly developed or absent.

Tanaka (2005, Figs. 1a,b) investigated one bairdiid species (*Neonesidea oligodentata*). From this he generalized that bairdiids have Eye Type 1, the centralized type, with the naupliar eye and lateral ocelli separated from the carapace, no cuticular lens, and no modification of the carapace as a refractive lens.

In the preserved specimens of all five species of *Neonesidea* investigated here, the eye is small and unpigmented. It is located on the anterior midline at the isthmus, just dorsal and posterior to the bases of the antennules.

#### Masticatory organ

All Bairdiidae have this unique chewing structure at the top of the esophagus, which was first illustrated by Brady (1880, pl. 3, fig. 3b) and Sars (1888, p. 301, pl. 18, figs. 1, 2). Müller (1894) described its architecture and named the parts (see also the summary by Hartmann 1967, p. 357). Its function is to break up particles and pass food into the midgut.

The half-cylindrical ring does not show distinctive differences in the species investigated here. Details of the upper plate, or *Kauplatte*, of this structure do vary and may have taxonomic significance, although unfortunately they have not been described for most species.

Neonesidea tenera (Brady, 1886)

(Figs. 5A–D, 6–17)

1886Bairdia tenera Brady: 304, pl. 39, figs. 13–15.
1890Bairdia tenera Brady—Brady: 495, pl. 1, figs. 11–12.
1905Bairdia inornata A. Scott: 372, pl. 1, figs. 11–12.
1969Neonesidea tenera (Brady)—Maddocks: 33, pl. 2, fig. 4.

1999Neonesidea tenera (Brady)—Whatley & Jones: pl. 1, fig. 10.
2000Neonesidea tenera (Brady)—Whatley: Table 1.
2000Neonesidea tenera (Brady)—Whatley, Jones & Wouters: 85, pl. 2, figs. 1, 2, 4 (not fig. 3).
? 1902Bairdia tenera Brady—Chapman: 422.
? 1983Neonesidea n. sp. 1—Bonaduce et al.: 478, fig. 4, figs. 6–9.
? 1983 Neonesidea ? tenera (Brady)—Bonaduce et al.: 481.
? 1995Neonesidea tenera (Brady)—Whatley & Roberts: fig. 1–1.

? 2002 Neonesidea gr. tenera (Brady)—Hoibian et al.: p. 183.

? 2012Neonesidea tenera? (Brady)—Antonietto et al.: 35, fig. 4, figs. 16-22.

Not 1894 Bairdia inornata T. Scott: 136, pl. 14, figs. 40-41 [= senior homonym of B. inornata A. Scott].

**Types and type locality.** The statement by Antonietto *et al.* (2012, p. 35) is incorrect—Maddocks (1969, p. 33) did not designate a neotype.

The Rules (ICZN, 1999, Article 5, p. 84–85) concerning neotypes are strict. A neotype may be designated only if necessary to "define the nominal taxon objectively" and to resolve an existing "zoological problem"—not just because the original type has been lost, and never as a matter of routine. Such a designation must be accompanied by demonstration of "exceptional need," by a statement of purpose, by a differential diagnosis, and by "evidence that the neotype came as nearly as practicable from the original type locality." A type-specimen has only nomenclatural, not taxonomic, significance. It is merely the name-bearer, in case of later dispute concerning the applicability of a species name. In the absence of any dispute, it has no function, because it does not define the taxonomic concept associated with the name or describe the contents of a biological population.

There is no reason to designate a neotype for *N. tenera*. Although the specimen was lost (Brady 1890, p. 493), and the original description is skimpy, *N. tenera* has been identified globally by multiple authors with reasonable confidence.

The type locality remains as originally specified: "dredged in a depth of 2 fathoms off Calpentyn, in the Gulf of Manaar" (Brady 1886, p. 293). Contrary to Antonietto *et al.* (2012, p. 35), the label on the specimen subsequently identified by Maddocks (1969) is not the type locality for the species.

**Material.** 38 specimens in 8 samples (Table 2). This is the most abundant of the five species of *Neonesidea* in this collection. Adults of both sexes and three instars are represented.

The material includes a range of preservation, from partial to total decalcification. One female (3962F) displays the dark brown color of the carapace epidermis and orange eggs. Among the many juveniles, one A-1 male (3920MJ) was molting when captured, and the adult antennal hook is clearly visible within the juvenile claw. The juvenile carapace has split around the free margin and partly flaked off, releasing the unexpanded chitinous template for the adult carapace, including hundreds of close-packed setae.

**Dimensions**. Female specimen 3862F L 811  $\mu$ m, H 471  $\mu$ m; female specimen 3892F L 833  $\mu$ m, H 500  $\mu$ m; female specimen 3905F L 824  $\mu$ m, H 473  $\mu$ m; male specimen 3906M L 797  $\mu$ m, H 453  $\mu$ m. See also Figure 15.

**Description.** Carapace (Figs. 6A–L, 7A–I, 8A–J) moderately compressed, greatest height and greatest thickness located slightly anterior to midlength (0.46–0.49); surface smooth; epidermis or inner chitinous lining dark brown except for small clear region over eye, margins translucent white; bleached specimens with small opaque streak located centrally over AMSP. Lateral outline of left valve oblong; dorsal margin broadly arched, curving smoothly and nearly equally anteriorly and posteriorly, without any anterodorsal and posterodorsal angles; anterior margin broadly and evenly rounded, ventral margin with very weak ventral indentation or nearly straight, posteroventral margin curving smoothly upward; posterior end weakly caudate, with slight posterodorsal concavity above broadly rounded caudal process, center of caudal process located slightly above one-third of height (0.35–0.36). No anteroventral marginal denticles; posteroventral marginal denticles suspected but not clearly visible. Marginal fused zone narrow, vestibules deep and broad; false RPC numerous, of many lengths, each ending in a seta. NPC of several sizes, simple, without distinct marginal walls. AMSP rosette-shaped, with 8 polygonal scars close-packed, two by two; one small frontal scar and two small mandibular scars.

Carapace setae (Figs. 5A–D, 6A–L, 7A–I, 8A–J) numerous, evenly spaced, of various lengths and thicknesses, but all fairly short, stiff, simple, tapering smoothly to sharp point; a few of the smallest setae have 2 or 3 divergent, shorter barbs or branches near base, but larger setae never have barbs. Eyelash setae simple, evenly spaced, all of the same length. Caudal setae about 6 in number, delicately feathered, thistle-like, located along posterodorsal margin of caudal process of each valve, clearly seen only in A-1 instar; caudal setae thought to be present also in adult, but too fine to see clearly.



**FIGURE 12.** *Neonesidea tenera* (Brady). A, B, female specimen **3905:** A, B, first and second segregated setae of vibratory plate of fifth limb, unfeathered and with wedge-shaped terminations. C–H, male specimen **3906M:** C, maxillule; D, antennule (ends of four longest setae are displaced); E, antenna; F, antennal claw with terminal hook; G, masticatory organ; H, mouth.

Antennal claw of male (Figs. 11A–E, 12E–F) relatively short, wide; distal edge of outer horn only slightly curved, continues smooth profile of claw; end of outer horn slightly curved, pointed; inner horn shorter, tapers sinuously, ends in sharply curved point; sigmoid groove between horns.

Hemipenis (Figs. 10A–B, F–H, 14D) with wedge-shaped base, heavily muscularized; median lobe oblongsubovate in outline, consisting of D-shaped outer capsule containing three groups of muscles attached to proximal and medial chitinous ridges, plus broadly flared lamellar flange or brim; terminal segment broad-based, heavily chitinized, with a somewhat blunt, lobose, smooth termination, as well as an incised medial groove to house copulatory tube. Copulatory tube long, tapering, flexible; distal (free) part more than twice as long as proximal (fixed, arched) part. *Kauplatte* (Figs. 10D, 12G) of masticatory organ with 8 wide teeth of nearly equal sizes, with bluntly rounded margins; end teeth slightly larger than others and set apart by small gaps; 2 thin, straight, hairlike spines located at ends, projecting slightly beyond teeth.

**Comparisons.** *N. tenera* is poorly known in the type locality (Gulf of Mannar, Sri Lanka, northern Indian Ocean), and all three descriptions were based on single specimens. Maddocks (1969) considered *B. inornata* Scott to be a subjective synonym of *B. tenera* because of the similar dimensions and provenance. The lack of information concerning population variation, dimorphism and soft anatomy limits assessment of the validity of identifications elsewhere.

The Hawaiian specimens of *N. tenera* are larger than the dimensions given by Brady (1886) and Scott (1905) (Fig. 16). The lateral outline has a more high-arched, symmetrically curving dorsal margin and a less exaggerated caudal process, and there are no conspicuous posteroventral marginal denticles.

The Hawaiian population agrees closely in size and shape with specimens illustrated as *Neonesidea* n. sp. 1 from the Gulf of Aqaba by Bonaduce *et al.* (1983). *N*. n. sp. 1 appears to be slightly larger than *N. tenera* from the type locality but corresponds in many details (slightly caudate lateral outline, nearly straight ventral margin, delicately punctate surface, minutely denticulate posteroventral margin of LV, gently curved contours of the dorsal view). Their mention of *N.? tenera* in the same paper (not illustrated) may support this identification.

The Hawaiian population is about the same size as the specimen illustrated as *N. tenera* by Brady (1890) from Samoa. The Hawaiian specimens have a slightly more arched dorsal margin, without distinct anterodorsal and posterodorsal angles, and lack conspicuous posteroventral marginal denticles.

Chapman (1902, p. 422) reported *B. tenera* from a dredging at 200 fathoms near Funafuti (Tuvalu) but did not illustrate it. Hoibian *et al.* (2002, not illustrated) cited *N.* gr. *tenera* from New Caledonia.

The Hawaiian specimens are larger than those illustrated by Whatley & Jones (1999) and Whatley *et al.* (2000) from Easter Island but similar in LV lateral outline and absence of posteroventral denticles. The illustrated RV (Whatley *et al.* 2000, pl. 2, fig. 3) has a more prolonged, acute-angled caudal process and probably belongs to a different species. The LV from Henderson Island illustrated by Whatley & Roberts (1995, fig. 1-1) has an acute caudal process, and the dimensions indicate that it may be a juvenile of a different species.

Although Whatley *et al.* (2000) had thousands of specimens, they provided dimensions only for the four illustrated specimens and did not analyze variation. Without explanation, they excluded Brady's (1890) identification from Samoa and did not mention Funafuti (Chapman 1902). No description or taxonomic evaluation was provided for the species, only the following enigmatic remarks (p. 85):

"This is the most abundant species at Easter Island. With its laterally compressed carapace and densely hirsute or punctate surface, it not [sic] difficult to recognise. The Easter Island population, despite its isolation, does not materially differ in size or shape from other populations of the species."

These remarks are somewhat misleading: All species of *Neonesidea* are hirsute, several species are punctate, and all species of the *N. pateriformis* species-group are strongly compressed. No populations (multiple adults of both sexes plus juveniles) have been documented for *N. tenera* at any locality before now. We know little about sexual dimorphism, growth stages, individual variability, and regional trends in *N. tenera*.

The Hawaiian specimens are much larger than the supposed juveniles tentatively identified from Saint Peter and Saint Paul Rocks, central Atlantic Ocean (Antonietto *et al.* 2012). The SEM photos of the Saint Peter and Saint Paul specimens (kindly furnished by Dr. Claudia Pinto Machado) show recently dead, closed carapaces with abraded epicuticle, broken shafts of a few setae near the margins, and post-mortem boreholes. The lateral outline is similar to that of *N. tenera* except for the slightly more angulate caudal process.

The Hawaiian population of *N. tenera* has slightly larger carapace size than *N. pateriformis* at Nosy Be (Fig. 17). It is less symmetrical in lateral outline, having a more broadly arched dorsal margin, a smooth (rather than denticulate) posteroventral margin, and a subtly caudate posterior end (rather than the smoothly curving, noncaudate termination of *N. pateriformis*). The Hawaiian specimens are apparently smooth, whereas *N. pateriformis* has numerous, small, shallow, regularly spaced puncta. Posteroventral marginal denticles are suspected but not clearly seen on the Hawaiian specimens of *N. tenera*, perhaps because of decalcification; they are present in *N. pateriformis*, although small and barely visible on some specimens. Polyfurcate or basally barbed carapace setae are present in both species, although more systematic documentation of this feature is needed. The hemipenis of *N. tenera* is distinctive, having a broad, even, lamellar brim on the median segment, a longer copulatory tube, and a lobose, bluntly rounded terminal segment (rather than the sinuously tapering, flame-shaped termination of *N. pateriformis*).

Maddocks (1969) reported other occurrences of *N. pateriformis* (without dimensions or illustrations) in collections from Ifalik Atoll (West Caroline Islands) and Mombasa (Kenya). Because of this apparently broad distribution, she placed Brady's (1890, Samoa) and Chapman's (1902, Funafuti) identifications of *B. tenera* in synonymy. This synonymy now appears unconvincing, and all of these identifications should be re-evaluated.

*N. tenera* resembles *N.* sp. CP of Maddocks (1995, Nosy Be), which has a similarly compressed, faintly punctate to nearly smooth carapace, a weakly caudate lateral outline with nearly straight ventral margin, and no marginal denticles. *N.* sp. CP is much larger, however, and has more elongate proportions than *N. tenera* at any locality. The nearly straight anteroventral and posteroventral margins and acute-angled caudal process of *N.* sp. CP may also be distinctive.

*N. tenera* is substantially smaller and smoother than *N.* sp. 2 aff. *pateriformis* of Cabioch *et al.* (1986, New Caledonia). The latter species corresponds closely to *N.* sp. CP in lateral outline but is much larger, with deeper, better defined surface puncta than *N. pateriformis* or *N. tenera* at any locality.

*N. tenera* differs from *N.* sp. 1 of Gou (1990, South China Sea) by its smaller size and weakly caudate lateral outline. *N.* sp. 1 of Gou closely resembles *N. pateriformis* in lateral outline and proportions but is distinctly larger. The dorsal view (Gou, 1990, fig. 12b) is diamond-shaped, with greater medial thickness and more nearly straight anterior and posterior margins than *N. tenera*, easily distinguishable from the gentle curves shown by Bonaduce *et al.* (1983, fig. 4, fig. 9) and Brady (1890, pl. 1, fig. 12), though resembling the sketches by Brady (1886, pl. 39, fig. 14) and Scott (1905, pl. 1, fig. 12).

*N. tenera* is easily distinguished by size and details of the hemipenis from several other species of the *N. pateriformis* species-group, which share the weakly caudate lateral outline, brown color, and feathered caudal setae. *N. anfieldingae* and *N. lentiphila* (Hartmann, 1984, Rangiroa) are much smaller than *N. tenera*, have more acute caudal angles, and have large posteroventral marginal denticles on both valves. *N. maddocksae* Hartmann (1974, Mozambique) is about the same size but less compressed and has a much thicker, distally widened antennal hook. *N. manningi* Maddocks (1975, Ascension Island) is much smaller than *N. tenera* and smooth, with posteroventral denticles on the RV; the hemipenis has an ovate terminal segment with outer distal horn.

**Geography.** *N. tenera* does not closely resemble any of the species described by Holden (1967, 1976) from Hawaii and Midway. It is a first record for the *N. pateriformis* species-group for the Hawaiian Islands.

The scarcity of *N. tenera* in the type region is noteworthy. The early descriptions were based on single specimens. It is not listed in numerous assemblages described in recent years from the east and west coasts of India, the Gulf of Mannar, and the Andaman Islands. Although Whatley & Jones (1999), Whatley (2000), and Whatley *et al.* (2000) described *N. tenera* as "pandemic" and "widely distributed in the Indian Ocean," in actuality the species is unknown in the Indian Ocean south of the Gulf of Mannar<sup>1</sup>.

*N*. n. sp. 1 of Bonaduce *et al.* (1983) closely resembles *N. tenera* and may be conspecific, extending the range west to the Gulf of Aqaba. The reported occurrence of *N. tenera* in the Java Sea (Whatley & Roberts 1995, Antonietto *et al.* 2012), while plausible, is based on a never-published M.S. thesis (Watson, 1988).

On the basis of the published carapace illustrations, the identifications of *N. tenera* at Samoa (Brady 1890) and Easter Island (Whatley & Jones 1999, Whatley *et al.* 2000) are credible. The record at Henderson Island (Whatley & Roberts 1995) is less certain, and the species was not collected at Pitcairn and Oeno Islands. The occurrence of *N. tenera* in Chile (Antonietto *et al.* 2012, contradicted by Whatley & Jones 1999) is unlikely.

The tentative identification of *N. tenera* in the Atlantic Ocean (Antonietto *et al.* 2012) suggests a circumtropical distribution, although at present no representatives of this species-group are known in West Africa, the Caribbean, and the tropical East Pacific. It is intriguing that *N. manningi*, at another mid-Atlantic island (Ascension), also has small carapace size. Perhaps small size favors survival on isolated, wave-swept rocks.

The Indo-Pacific occurrences of *N. tenera* spread across at least 3 and maybe 5 of the 13 zoogeographical provinces in the classification by Titterton &Whatley (1888b, text-fig. 1). This is a broad and somewhat spotty distribution, as the species has not yet been recognized in numerous assemblages at intervening localities. Perhaps these conspicuous gaps result in part from insufficient sampling of high-energy, hard-bottom habitats. Most faunal collecting for Ostracoda is based on sediment samples collected by dredging or coring. The diversity of Ostracoda on hard substrates is less well surveyed.

<sup>1.</sup> Munef *et al.* (2012, p. 154, Pl. 1, figs. 10–11) identified *N. tenera* from shallow marine sediments along the northern coast of Socotra Island, Yemen (east of the horn of Africa in the northwestern Indian Ocean). This occurrence should be added to the synonymy and geographic distribution described above for *N. tenera*.



**FIGURE 13.** *Neonesidea tenera* (Brady). A, female specimen **3905F:** vibratory plate of fifth limb. B–D, male specimen **3906M:** B, distal part of fifth limb; C, other fifth limb, entire; D, sixth and seventh limbs, brush-shaped organ.

#### Neonesidea ifalikensis Maddocks, 1969

1969Neonesidea schulzi ifalikensis Maddocks: 22, figs. 4e-m.

**Remarks.** As suggested by Maddocks (1995, p. 203), this is not a geographic subspecies of *N. schulzi* but a separate species in the *N. schulzi* species-group. Although this population must be restudied to establish the diagnostic taxonomic characters, it is convenient to elevate the name formally to species rank. Danielopol (1972) re-examined paratype female specimens but did not describe or illustrate them. Titterton *et al.* (2001) suggested that it belongs to a complex of Pacific species including *N. woodwardiana* (Brady, 1880) and *Bairdia crosskeiana* of Brady (1880, 1890, not 1866). It is not closely related to any of the Hawaiian species described here.

Geography. Ifalik Atoll, West Caroline Islands.



**FIGURE 14.** *Neonesidea tenera* (Brady). A, B, E, female specimen **3905F:** A, antenna; B, antennal claw; E, posterior of body with furcae, genital lobes, and post-abdominal bristle. C, D, male specimen **3906M:** C, mandible; D, posterior of body with hemipenis, furca, post-abdominal bristle.

# Neonesidea plumulosa n. sp.

(Figs. 5E–F, 18–23)

**Etymology.** Latin noun *plumula*, diminutive of *pluma*, a soft feather, down; plus adjectival suffix *-osus*, full of, prone to; referring to the caudal setae.

Material. One adult male specimen, holotype male specimen 3960M.

Dimensions. Holotype male specimen 3960M, LVL 1008 µm, LVH 563 µm.

**Type locality.** French Frigate Shoals, FFS–TC–09, 23° 52.9 N, 166° 15.1 W, 12 September 2000. N forereef, N of Tern Island, depth 10–15 m.

Description. Carapace (Figs. 18A-J, 19A-D) elongate-ovoid, streamlined, siliquose, moderately inflated, tapering, greatest thickness and greatest height located a little anterior to midlength (0.42). Surface smooth, not punctate, with fine granular microtexture visible in transmitted light. Lateral outline of left valve elongate-ovate, with smoothly curved, low-arched dorsal margin, no anterodorsal or posterodorsal angles; anteroventral margin obliquely rounded, evenly curved; ventral margin straight to very slightly convex, without ventral indentation; posteroventral margin slightly curved, rising gradually to slightly caudate posterior end; caudal process obliquely truncated, humped, slightly flared and thickened dorsally beneath weak posterodorsal concavity; posterior end narrowly rounded, forming symmetrical obtuse angle, located at about one-third of height (0.35). Anteroventral margin of LV smooth, except for extremely short, triangular granules or minute denticles, regularly spaced with wide gaps, located between RPC, barely visible. Posteroventral margin of LV edged with numerous, easily visible, asymmetrical, triangular denticles, with long axis oriented posteroventrally, increasing in size toward posterior, then decreasing in size dorsally; no terminal spine. Anterior and posterior margins of RV with extremely narrow chitinous flange; short, flaring, ragged chitinous frill at caudal process. Marginal fused zone narrow, vestibules deep and broad; NPC and false RPC numerous but not clearly observed because of preservation. AMSP large, rosette-shaped, not clearly seen; obscured by oval opaque patch located centrally; indistinct somewhat opaque regions located mid-dorsally, anteroventrally and posteroventrally.



**FIGURE 15.** L–H scatter plot for the population of *Neonesidea tenera* (Brady) at French Frigate Shoals, including males, females and three instars.

Carapace setae (Figs. 5E-F, 18E-F, H, J, 19A-D) numerous, easily visible though not conspicuous, yellow, closely spaced; of various sizes, most relatively short, none excessively long; all simple in form, tapering to a

single point. Barbed setae suspected to be present but not clearly observed. Eyelash setae numerous, close-spaced, short, thin-walled, arranged in even row along all free margins, curving out and up. About 6 caudal setae located along posterodorsal edge of humped caudal process in each valve; each with 15–20 close-spaced, fairly short, lateral vanes or barbs alternating along both sides; outline leaf-like but not palmate or fringed.



FIGURE 16. L-H scatter plot for reported occurrences of Neonesidea tenera (Brady).

Male antennal claw (Figs. 20C–D, G, J, 21A–B) relatively short, wide, slightly curved; distal edge of outer horn continues smooth profile of claw; outer horn weakly curved with narrowly rounded termination; inner horn shorter, thinner, tapering, distal edge nearly straight, ending in sharp point; sigmoid groove between horns.

Hemipenis (Figs. 19E–H, 20B, 22F) with large, wedge-shaped, basal segment; shorter, curled, lamellar median segment, which is straight-edged and polygonal as seen in life position but circular in outline as compressed in dissection mount; terminal segment short, with two tapering chitinous ribs or spines supporting a thin, slightly curved wall between, enclosing a cuspate space, distal (outer) spine a little longer and thinner than proximal (inner) spine; copulatory tube short, inflexible, nearly straight, barely reaching terminal segment, ending in short, rigid copulatory rod.

*Kauplatte* (Figs. 20F, 21E) of masticatory organ with 8 broad marginal teeth of unequal sizes, with triangular or irregular terminations, two center teeth broadest and highest; end teeth separated from others by gaps; 2 straight thin spines at ends, longer than teeth.

**Comparisons.** *N. plumulosa* is easily distinguished from species of the *N. schulzi* species-group by its softly rounded, sinuous, subtly caudate lateral outline (rather than elongate-subtriangular or teardrop-shaped) and the absence of a terminal spine in the LV. The caudal setae are leaf-like, not fringed and lamellose as in *N. schulzi*.

*N. plumulosa* is distinct from another complex of species, which includes *N. woodwardiana* (Brady, 1880, off Tongatabu, Fiji Islands; as redescribed by Puri & Hulings 1976, Titterton *et al.* 2001), *N.*? sp. aff. *N. woodwardiana* 

of Titterton & Whatley (1988a, Solomon Islands), and *N*.? sp. aff. *N. woodwardiana* of Gou (1990, Hainan Island, South China Sea), by its more gently curving contours, conspicuous marginal denticles, and absence of a patch pattern, as well as significant size discrepancies.



FIGURE 17. L-H scatter plot for species of the Neonesidea pateriformis species-group.

At first glance, *N. plumulosa* appears to resemble some species of the *N. pateriformis* species-group, but its lateral outline is more elongate and more caudate, and in dorsal view it is less compressed. The caudal setae appear to have more numerous, more closely spaced vanes and do not taper like those of *N. tenera*.

*N. plumulosa* is the same size as *N*. sp. CP of Maddocks (1995, Nosy Be) and is similar in lateral outline, although its lateral outline curves more gracefully, and it has conspicuous marginal denticles. Maddocks (1995, pl. 10, fig. 1) illustrated enlarged pores on the dorsal edge of the caudal process for *N*. sp. CP, which may indicate the presence of caudal setae in life.

*N. plumulosa* is substantially smaller than *B. ritugerda* Holden (1967, Hawaii) and more elongate, with a smoothly arching dorsal margin, a longer, more nearly straight mid-dorsal segment, a curved (rather than straight) anterodorsal segment, indistinct anterodorsal and posterodorsal angles, and a curved rather than straight anteroventral margin. It is more elongate and much smaller than *B. kauaiensis* Holden (1967, Hawaii).

*N. plumulosa* is somewhat similar in lateral outline to *N. lenitiphila* Hartmann (1984, Rangiroa), though less elongate through the midsection, and it lacks many distinctive details, including the unique hemipenis with wartlike terminal tubercles. It is much larger than *N. anfieldingae* Hartmann (1984, Rangiroa), lacks the bushy, many-branched carapace setae, and most details of the hemipenis are different.

*N. plumulosa* is similar in size, lateral outline and marginal denticles to *N. michaelseni* Hartmann (1982, Sharks Bay, Western Australia), except that the posterior end is slightly less acutely extended, and it lacks the terminal spine in the LV. Hartmann's drawing of the hemipenis (1982, fig. 49) is generalized but resembles that of *N. plumulosa* in its compact proportions, oblong terminal part, and short, straight copulatory tube.



**FIGURE 18.** *Neonesidea plumulosa* n. sp., all male specimen **3960M.** A, B, E, I, interior of LV containing entire body, E also shows caudal setae and marginal denticles; C, D, right and left exteriors of intact carapace; F, G, RV exteriors, showing opaque patch and AMSP; H, right anterior margin of carapace, showing eyelash setae and simple setae; J, RV exterior with NPC and setae. Scale bar =  $50 \mu m$ .

*N. plumulosa* has much larger carapace size than the specimens identified as *N. michaelseni* by Hartmann (1984, Rangiroa), and it differs in lateral outline (weakly convex ventral margin, more symmetrically extended caudal process). Hartmann stated that he had about 50 adults of both sexes, and that Polynesian populations often are smaller than the same species in Australian waters. The ranges of adult dimensions reported by Hartmann (1984, p. 123) are excessive for a single cluster, however (Fig. 23). It is likely that his population included juveniles as well as adults, and perhaps more than one species. Hartmann provided excellent SEM illustrations of the Polynesian male and female, displaying evident sexual dimorphism, but unfortunately he did not report the individual dimensions or magnifications. He meticulously illustrated many carapace details, including eyelash setae, caudal setae, simple setae, marginal denticles and the terminal spine. Hartmann's drawings of the hemipenis (1984, figs. 27, 28) show a more elongate central capsule, a tapering terminal part with stepped margin, and a long, flexibly coiled, tapering copulatory rod and tube. This record from Rangiroa cannot be confidently identified with either *N. michaelseni* (Sharks Bay, Australia) or *N. plumulosa*.

Geography. Known at present only from French Frigate Shoals in the Hawaiian Islands.



**FIGURE 19.** *Neonesidea plumulosa* n. sp., all male specimen **3960M.** A, left posterior end of carapace to show caudal setae and simple setae; B–D, right posterior end of carapace to show angulate, slightly humped caudal process, caudal setae, simple setae, and zigzag chitinous frill around terminal angle; E, left and right hemipenes; F, both hemipenes; G, detail of F to show copulatory tube and terminal segment. Scale bar =  $10 \mu m$ .



**FIGURE 20.** *Neonesidea plumulosa* n. sp., all male specimen **3960M.** A, left side of entire body; B, dorsal view of both hemipenes and furcae; C, left antennal hook before dissection with too-slender proportions, because the hook is slightly bent and rotated relative to the plane of the claw and limb, to show how perspective alters shape; D, G, same left antennal hook after dissection, seen straight-on, enlarged to show corrugated surface of anterior horn; J, right antennal hook; E, maxillule; F, masticatory organ; H, I, spermatophore. Scale bar =  $10 \mu m$ .



**FIGURE 21.** *Neonesidea plumulosa* n. sp., all male specimen **3960M.** A, antenna; B, antennal claw with hook; C, vibratory plate of maxillule; D, maxillule with palp, masticatory processes and segregated setae; E, masticatory organ.

# Neonesidea holdeni n. sp.

(Figs. 2, 24–27)

**Etymology.** For John C. Holden, who was the first to undertake comprehensive identifications of Ostracoda from the Hawaiian Islands and Midway.

Material. One adult male.

**Type locality.** French Frigate Shoals, Hawaiian Islands, station FFS–TC–11. 23° 47.7 N, 166° 04.97 W, 13 Sep 2000. E perimeter backreef, 14 km due E of East Island, depth 4–6 m.



**FIGURE 22.** *Neonesidea plumulosa* n. sp., all male specimen **3960M.** A, teeth of mandible; B, fifth limb; C, anterior part of mouth; D, sixth limb; E, seventh limb; F, posterior region of body, with hemipenis, post-abdominal bristle and furca.

Dimensions. Holotype male 3908M, L 786 µm, H 375 µm.

**Description.** Carapace (24A–H, 25F–I) elongate-siliquose, streamlined; greatest height and width located about at midlength (0.49); transparent, lacking any patch pattern, surface smooth. Left valve lateral outline subtriangular, with nearly straight anterodorsal and posterodorsal margins sloping steeply anteriorly and posteriorly from distinct, rounded mid-dorsal angle; no posterodorsal angle; anteroventral margin broadly but obliquely rounded; midventral margin straight, without ventral indentation; posteroventral margin curved, rising gradually to caudal process located a little below one-third height (0.29); posterior end narrowly rounded, obliquely truncated, forming a slightly acute angle; caudal process humped, but no posterodorsal concavity above it. Broad-based, flat, triangular terminal spine projects at posterior end of LV; complementary spine at end of RV smaller, more transparent, may be extension of chitinous flange rather than calcified; no marginal denticles on anteroventral or posteroventral margin of either valve. Fused zone very narrow, vestibules deep and broad, false RPC not

observable. NPC numerous, conspicuous, many with ring-walls. AMSP not clearly observable; adhering muscles form a small, central, wedge-shaped cluster.



FIGURE 23. L-H scatter plot for Neonesidea plumulosa n. sp. and similar Indo-Pacific species.

Carapace armed with a ferocious array of setae of many sizes (Figs. 24A–H, 25F–I, 26H); those of anterior region mostly quite short, those in posterior region longer; all simple in form, tapering to a point; most directed posteriorly in streamlined fashion, with a few diverging posterodorsally and posteroventrally in protective fashion. No barbed or polyfurcate setae observed. Eyelash setae unusually long, conspicuous, evenly spaced in uniform row along all margins, curving outward. About 6–8 fan-shaped, pinnate caudal setae located in row along dorsal edge of caudal process in both valves, just above terminal spine; having thick, cylindrical shafts and flattened, palmate crowns; each with 30 or more thin, close-spaced, featherlike barbs or vanes on each side, producing a stiff, densely fringed fan; these flat fans overlap tightly to form a stiff, brown, protective wall above the terminal spine.

Hook of male antennal claw (Figs. 24I–J, 26C–D) slender, long, with delicate, spine-like anterior and posterior horns, both horns sharply bent near tip; outer horn continues smooth profile of claw; inner horn thinner; sigmoid groove between horns.

Hemipenis (Figs. 25D–E, 26A, G) with narrow basal segment. Median segment longer, broader, lamellar, rounded-oblong in outline; inner-upper edge broadly arched, flared, and reinforced with a chitinous strip, forming a channel to house and support the arched copulatory tube; extending distally beyond terminal segment as a narrow, bluntly truncated, thumb-like plate. Terminal segment elongate-oblong, boomerang-shaped, with a broad base, thickest medially, slightly tapered distally; with slightly concave margins and a square, smooth, right-angled termination; indented at distal-outer edge by broad groove for copulatory tube; it functions as a brace, holding the arched inner edge of the median capsule in place and closing the half-socket through which the copulatory rod exits. Copulatory tube long, thin, tapering, flexibly coiled.



**FIGURE 24.** *Neonesidea holdeni* n. sp., all male specimen **3908M:** A, B, right and left exteriors of entire animal; C–F, RV and LV exteriors; G, H, anterior margins of LV and RV with setae and chitinous edge-strip, eyelash setae are longer and anteriorly directed; simple setae are shorter and ventrally directed; the chain of black dots near the inner margin is a row of gland cells (?) in the underlying epidermis; I, J, left antennal claw with hook. Scale bar = 50 µm.

*Kauplatte* of masticatory organ with about 10–14 small, unevenly terminated teeth, divided by an indistinct cleft into 5–7 teeth on either side, the 2 end teeth set apart by a gap from and not as long as the others, some of the middle teeth small and spine-like or fused at the base with neighbors.

**Comparisons.** In carapace shape *N. holdeni* belongs to a complex of rather elongate species of the *N. schulzi* species-group, which are widely distributed in the Pacific Ocean, and which are not yet easily discriminated. These include, among others, *N. woodwardiana* (Brady 1880, Puri & Hulings 1976, Titterton *et al.* 2001; off Tongatapu, Fiji), *N.*? sp. aff. *N. woodwardiana* of Titterton & Whatley (1988a, Solomon Islands); *Bairdia crosskeiana* of Brady (1880, not 1866) of Holden (1967, Hawaiian Islands), *N. ifalikensis* Maddocks (1969, Ifalik Atoll, Caroline Islands), *N. gierloffi* (Hartmann, 1959) of Holden (1976; Hawaiian Islands, Midway), *N. michaelseni* Hartmann (1982, 1984; Western Australia, Rangiroa), and *N. supercaudata* Whatley, Jones & Wouters (2000, Easter Island). For most of these species the soft anatomy and carapace details (i.e. patch pattern, terminal spine, marginal denticles, setae) are not documented. As Figure 2 shows, populations identified at different localities display significant discrepancies in size.



**FIGURE 25.** *Neonesidea holdeni* n. sp., all male specimen **3908M.** A, right side of body; B, masticatory organ; C, masticatory processes and palp of maxillule; D, E, hemipenes; G–J, posterior ends of LV and RV to show humped caudal process, terminal spine, caudal setae, and simple setae. Scale bar = 50 µm.

*N. holdeni* is significantly smaller than the specimens identified as *B. crosskeiana* Brady (1880, not 1866) by Holden (1967, figs. 6*h*–*l*) from Hawaii. Both of the Hawaiian species are substantially smaller than the dimensions reported by Brady (1880), which may apply to an unknown species from another locality. Holden (1976) identified Cenozoic fossils from Midway as *Neonesidea gierloffi* (Hartmann, 1959), and he included the Hawaiian records of *B. crosskeiana* by Brady (1880) and Holden (1967) in that synonymy. The discrepancies shown in Figure 4 do not support this conclusion.

*N. holdeni* differs from *N. gierloffi* (as described by Hartmann from El Salvador) in many anatomical details, including setation and podomere proportions of the fifth limb and furca. The antennal claw of *N. holdeni* is thinner with sharply pointed, needle-like horns, the inner horn being markedly shorter; whereas the claw of *N. gierloffi* is thicker and more compact, with a flared hook and sinuously curved horns. The hemipenis of *N. gierloffi* has different proportions and construction: the median segment is oval and tapers basally, the terminal segment is broader than high and bluntly terminated, there is no thumblike lamellar projection, and the copulatory tube does not extend beyond the terminal segment.



**FIGURE 26.** *Neonesidea holdeni* n. sp., all male specimen **3908M.** A, G, hemipenes and furca; B, furca; C, D, antenna; E, mouth; F, segregated setae of maxillule with wedge-shaped terminations; H, one caudal seta; I, masticatory organ.

*N. holdeni* is close in size and shape to *N*.? sp. aff. *N. woodwardiana* (Brady) of Titterson & Whatley (1988a, Solomon Islands), but it is smooth rather than finely punctate and lacks the spinose anterior and posteroventral marginal denticles in the LV. The lectotype of *N. woodwardiana* (Brady) is much larger, has a distinctive patch pattern, has a more broadly arched dorsal margin, ends in a bluntly upturned, obtusely beveled caudal process, and lacks the terminal spines (Puri & Hulings 1976; Titterton *et al.* 2001, off Tongatabu).

*N. holdeni* is much smaller than *N. ifalikensis*, with a more streamlined carapace; both horns of the antennal claw are sharply angled and finely pointed (not bluntly rounded), the podomere proportions and claws of the walking legs are more compact; and the terminal segment of the hemipenis is less tapered and lacks the distal setose projection.



**FIGURE 27.** *Neonesidea holdeni* n. sp., all male specimen **3908M.** A, sixth limb; B, seventh limb; C, fifth limb; D, brush-shaped organ; E, mandible; F, palp and masticatory processes of maxillule.

*N. holdeni* is much smaller than *N. michaelseni* (as originally described from Sharks Bay, Western Australia, by Hartmann 1982). It lacks the patch pattern and the numerous, long, anterior and posterior marginal denticles. *N. holdeni* can also be distinguished by the tapering, lamellar shape of the terminal segment of the hemipenis (vs. ovate in *N. michaelseni*) and the long, flexible copulatory rod (not reaching beyond terminal segment in *N. michaelseni*).

Hartmann (1984) had about 50 specimens of both sexes in the population identified as *N. michaelseni* from Rangiroa, Tuamotu Islands. The dimensions (reported only as ranges) suggest two clusters, of which one agrees with the holotype of *N. michaelseni* (from Australia), but the other is much smaller (though significantly larger than *N. holdeni*). If all specimens are adults, as stated, then at least two species may be represented in the Rangiroa

population. From the information provided, it is not possible to determine whether the anatomical structures he illustrated belong to the larger or the smaller species. The long, flexible copulatory rod and the proportions of the hemipenis are similar to *N. holdeni*, except for the distally stepped end of the terminal segment (bluntly rounded in *N. holdeni*). The RV illustrated as *N. michaelseni* by Gou (1990, pl. 1, fig. 7) is similar in lateral outline to *N. michaelseni* from Rangiroa but is minutely punctate rather than smooth.

*N. supercaudata* Whatley, Jones and Wouters (2000) is significantly larger than *N. holdeni* and has angulate, diamond-shaped outlines with an unusually low-set, extended caudal process.



**FIGURE 28.** *Neonesidea bacata* n. sp., all male specimen **3912M.** A, B, RV and LV exteriors, with simple setae and anchor setae; C, dorsal view of LV, focused at ventral edge; D, dorsal view of RV, focused at mid-height; E, left exterior view of entire animal before dissection; F, G, RV and LV exteriors with AMSP, NPC, setae, and numerous small papillae. Scale bar =  $50 \mu m$ .

*Neonesidea bacata* n. sp. (Figs. 28–34)

Etymology. Latin bacatus, set with pearls, referring to the papillate microornament of the carapace.

Material. One adult male.

Types. Holotype male 3912M.

**Type locality.** French Frigate Shoals, Hawaiian Islands, station FFS–TC–11, 23° 47.7 N, 166° 04.97 W, 13 Sep 2000. E perimeter backreef, 14 km due E of East Island, depth 4–6 m.



**FIGURE 29.** *Neonesidea bacata* n. sp., all male specimen **3912M.** A, posteroventral lateral region of LV to show simple setae, anchor seta, small papillae; B, dorsal view of LV, focused at ventral edge, to show anchor setae, striate anterior chitinous edge-strip, papillate texture, eyelash setae; C, tilted dorsal view of RV, focused at ventral edge, to show inset selvage at anterior and posterior ends, neat row of anterior and posterior eyelash setae; D, E, dorsal views of LV and RV, focused below hinge, to show simple hinge, short simple setae, NPC, papillate texture; F, posteroventral region of LV, to show marginal denticles, setae, papillae. Scale bar =  $50 \mu m$ .

Dimensions. Holotype male 3912M, L 605 µm, H 285 µm. See also Figure 34.

**Description.** Carapace (Figs. 28A–G, 29A–F, 30A–H) oblong, inflated; thickness greater than height, greatest height and greatest thickness both located distinctly anterior to midlength (0.38, 0.39). Surface of valves nearly smooth medially, with a velvety, micropapillate texture elsewhere; marginal regions visibly papillate. Micro-ornament of numerous, tiny, hemispherical granules or papillae; 1 to 4 µm in diameter, larger and more densely packed near valve edge. Adductor muscle scars expressed externally as smooth regions outlined by rows of micropapillae. Lateral outline of LV subrhomboidal, tapering posteriorly; dorsal margin distinctly tripartitite, with broadly curving, anterodorsal and posterodorsal angles; nearly straight, sloping anterodorsal segment, gently arched, slightly sloping median segment, and straight, steeply sloping posterodorsal segment; anteroventral margin

slightly convex, obliquely truncated; ventral indentation broad, shallow, distinct; posteroventral margin curving obliquely upward to posterior end; posterior end not caudate, bluntly rounded, located at one-fifth of height (0.20); no caudal process, no posterodorsal concavity. Posteroventral margin of LV with numerous, fairly large, triangular marginal denticles, whose long axis is oriented posteroventrally; narrow flange wraps around posterior angle. Anterior margin of RV with broad chitinous flange and indented selvage; posterior margin with deeply indented selvage and narrow chitinous frill or flange around posterior angle. NPC large, conspicuous, not especially numerous, mostly about the same diameter, some with narrow to fairly broad walls.



**FIGURE 30.** *Neonesidea bacata* n. sp., all male specimen **3912M.** A, B, anterior region of RV at mid-height to show papillate texture, setae, NPC; C, posterior end of RV, to show marginal setae, short chitinous fringe around posterior angle, inset selvage; D, posterior end of LV, to show triangular marginal denticles, chitinous flange, and setae; E, posteroventral margin of LV, to show triangular marginal denticles and setae; F, enlarged view of three marginal denticles from D; G, H, RV and LV exteriors to show AMSP, NPC, setae, and papillae. Scale bar =  $10 \mu m$ .

Carapace setae (Figs. 28A–G, 29A–F, 30A–H) conspicuous, not especially abundant, mostly about the same length; of simple form, smooth, tapering to point, standing erect or oriented posteriorly; with a few longer ones located on posterior lateral surfaces. On each valve, about three exceptionally long, thick anchor setae originate posteromedially and posteroventrally (near but not at posteroventral margin), project outward, and trail posteriorly. Simple setae of uniform size and spacing are aligned along all free margins of both valves, curving outward like eyelash setae, but not differing in size or structure from other simple setae elsewhere. No feathered caudal setae observed.



**FIGURE 31.** *Neonesidea bacata* n. sp., all male specimen **3912M.** A, B. left and right sides of body; C, E– G, I, hemipenes and furcae, before and after dissection; D, mouth; H, testes and spiral vas deferens; J, K, right antennal claw; L–N, left antennal claw in natural position before dissection and after dissection, to show slender anterior horn, V-shaped cleft, and obliquely beveled anterior surface of posterior horn; O, masticatory organ. Scale bar = 10 m.

Male antennal claw (Figs. 31J–N, 32C–D) nearly straight, slightly tapering; anterior horn continues smooth profile of claw; anterior horn slightly shorter and distinctly thinner than posterior horn, nearly straight and rodlike in some views, slightly tapering with pointed termination in other views; posterior edge of anterior horn nearly straight (only weakly sigmoid); cleft between horns tapering (only weakly sigmoid); posterior horn broadly pointed, with obliquely beveled or faceted anterior edge, which may facilitate forced overlap of the two horns in scissors-fashion.

Hemipenis (Figs. 31C–G, 33D) with stout trapezoidal basal segment; median segment oblong to ovate with rounded margins, broadly flared or sinuous lamellar edge, with asymmetrically tapering distal process extending beyond terminal segment; terminal segment a bluntly truncated, hook-shaped lamellar plate, with broad indentation on outer edge. Copulatory tube thin, arched, tapering, barely reaching distal end of terminal segment.

*Kauplatte* (Fig. 31O, 33E) of masticatory organ with smooth, gently curved, toothless perimeter; with central cleft; end teeth broad, offset by wide gap.

**Comparisons.** In anatomical characteristics this species is indisputably allied with *Neonesidea*. No other known species of *Neonesidea* has a papillate carapace.



FIGURE 32. Neonesidea bacata n. sp., all male specimen 3912M. A, maxillule; B, mandible; C, D, antennae.

The tuberculate ornament of *N. bacata* is reminiscent of that in *Mydionobairdia* and *Papillatabairdia*, though on a finer scale and more subtly developed. Species of *Mydionobairdia* have fewer but much larger, flat-topped, volcano-like tubercles, together with conspicuous anterior and posterior marginal spines. In *Papillatabairdia* the tubercles are broader, low-hemispherical in shape, and may be arrayed in uniform rows. Species of *Papillatabairdia* are also distinguished by reniform lateral outlines, with distinctly indented ventral margin and broadly rounded anterior and posterior margins. The relationships among *Mydionobairdia*, *Papillatabairdia*, and *Triebelina* have been evaluated at length by Keij (1974, 1976), Bentley (1881), Warne (1986), Titterton & Whatley (1988a), Maddocks (1991), Maddocks & Wouters (1990), and references cited therein.

Soft parts have been described for only one species of *Mydionobairdia*. The soft anatomy of *Triebelina* appears to be close to that of *Paranesidea*, but no males have been described. The anatomy of *Papillatabairdia* is unknown.

The elongate-subrhomboidal lateral outline of *N. bacata*, with low-set, tapered posteroventral angle and flattened ventral surface, is distinct from the upward-curving, caudate posterior end that is typical for species of *Triebelina* (always visible in the RV if not so much in the LV outline). Species of *Triebelina* have much greater valve asymmetry and pronounced anterodorsal and posterodorsal LV overlap.



**FIGURE 33.** *Neonesidea bacata* n. sp., all male specimen **3912M.** A, fifth limb; B, sixth limb; C, seventh limb; D, hemipenis, furca and post-abdominal bristle; E, masticatory organ; F, mouth.



FIGURE 34. L-H scatter plot for *Neonesidea bacata* n. sp., *Bairdia hanaumaensis* Holden, and Indo-Pacific species of *Papillatabairdia*.

As compared to *Mydionobairdia tulearensis* Maddocks (1991, the only species of that genus for which the soft parts have been described), *N. bacata* is less elongated medially in lateral outline, with a gently curving rather than perfectly straight mid-dorsal segment, and with a more acutely extended (rather than rounded) posteroventral angle. The surface tubercles are smaller, more numerous, lower except near the edge, mostly low granules or papillae rather than the isolated, flat-topped table-mounts of *M. tulearensis*. *N. bacata* also lacks the two sizes of simple setae, the smaller trifurcate setae, the three long anteromarginal tubercles, and the four long posteroventral marginal tubercles of *M. tulearensis*, and there is no record of anchor setae in *M. tulearensis*.

*N. bacata* is similar in L/H proportions to *Bairdia hanaumaensis* Holden (1967) but smaller, with a more extended posteroventral end but a more rounded (less acute) posteroventral angle; other distinctions include the several long anchor setae, the LV posteroventral marginal tubercles, the LV anteroventral marginal fringe, and the RV marginal fringe or flange. Holden described *B. hanamauensis* as finely pitted, evenly covered with short hairs, and uniform brown in color, comparing it to *Bairdia acanthigera* Brady, 1880 and *Bairdia tuberculata* Brady, 1880. [It is unclear whether Holden intended the latter name to refer to the punctate species described from Mauritius by Brady (1868), which was perhaps a species of *Triebelina*, or the spinose species described from New Caledonia by Brady (1890). Holden's drawing shows a species that is distinct from both of these species, being more elongate, with markedly angular contours, and entirely lacking marginal denticles.] Holden (1976) identified *B. hanaumaensis* from Midway (on the basis of a single juvenile RV, unillustrated) and reclassified it in *Triebelina*.

The configuration of the hemipenis and the shape of the *Kauplatte* of the masticatory organ are unique in *Neonesidea*.

#### Neonesidea edentulata n. sp.

(Figs. 2, 35-37)

Etymology. Latin *edentulatus*, toothless; referring to the shape of the *Kauplatte* of the masticatory organ.

Material. Four specimens at two localities, including one adult male and three juveniles.

Types. Holotype male 3958M, and three paratype juveniles.

**Type locality.** French Frigate Shoals, Hawaiian Islands, station FFS–TC–15, 23° 46.107 N, 166° 15.689 W, 14 Sep 2000. Central lagoon, W side of La Perouse Pinnacle, depth 3–7 m.

**Dimensions.** Holotype male 3958M L 690  $\mu$ m, H 373  $\mu$ m. Paratype juvenile L 418  $\mu$ m, H 212  $\mu$ m. See also Figure 2.

**Description.** Carapace (Figs. 35A–H) bairdian in shape, nearly symmetrical, with angular contours and valves of nearly equal size; greatest height located at about one-third length (0.34), greatest thickness located a little anterior to midlength (0.43). Lateral outline of LV with tripartite dorsal margin, anterodorsal segment straight; median segment nearly straight, only very slightly arched, sloping gently from well-marked anterodorsal angle; posterodorsal angle broadly rounded but distinct, posterior segment nearly straight, sloping steeply to distinct, obtuse angle; anterior margin obliquely rounded; ventral margin deeply indented in mouth region; posteroventral margin at first weakly convex, then nearly straight, rising smoothly; posterior end a narrowly rounded, acute angle, subtly caudate, located at one-fourth height (0.26); caudal process flanged but not humped. Fused marginal zone narrow, vestibules deep and broad; false RPC not observable (obscured by setae). LV margins smooth, lacking marginal denticles; RV with narrow chitinous flange along anterior margin and narrow frill along posteroventral margin. Selvage distinctly indented at the posterior end of both valves. NPC simple, most without walls.

Carapace setae (Figs. 35A–H) numerous, conspicuous, both light and dark; of many lengths, somewhat longer posteriorly, but none trailing; all of simple form, with thick shafts, stiff, tapering to point, erect or oriented slightly posteriorly. Eyelash setae regularly arrayed along anterior margins of both valves, recognizable by regular spacing, uniform length and curvature, and light color; crowded by numerous simple setae of many sizes and colors, which are also densely, untidily packed at very edge of valve. Posteroventral and ventral margins of both valves have numerous simple setae of all sizes. Caudal process with only simple setae, caudal setae absent; anchor setae absent.

Male antennal claw (Figs. 35F, 36F–G, H–J, 37A–B) weakly curved, anterior horn continues profile of claw; anterior horn longer than posterior horn, slender, tapering, with sigmoid posterior margin; posterior horn about the same thickness with similar curvature, tapering; thin tips of both horns bent inward (curved) through 90°; cleft between horns weakly sigmoid with broad opening.



**FIGURE 35.** *Neonesidea edentulata* n. sp., all male specimen **3958M.** A, RV exterior; B, left side of entire animal; C, interior of LV with body; D, anterior margin of LV; E, posterior end of LV; F, right antennal claw, as seen through carapace before dissection; G, posterior end of entire animal from right side, showing numerous simple setae but no caudal setae; H, anterior end of entire animal from right side. Scale bar =  $50 \mu m$ .

Hemipenis (Figs. 36A–E, M, 37F) with wedge-shaped, muscular basal segment; large, oval, folded-lamellar median segment, with reinforced inner edge that projects beyond terminal segment; terminal segment an oblong plate, bluntly terminated except for one long, curved, pointed spine located at upper-inner edge; copulatory tube curved, tapering to a thin, looped thread beyond terminal segment.

*Kauplatte* (Figs. 36L, 37G) of chewing organ lacking marginal teeth along most of the perimeter, having only end teeth separated by gaps from a broad, smooth, nearly straight margin, without any median cleft.

**Comparisons.** None of the species described from Midway or the Hawaiian Islands (Holden 1967, 1976) closely resemble this species.

The carapace shape is rather ordinary, but there are no close similarities to any species of *Neonesidea* for which the soft parts have been described.

*N. edentulata* differs from most members of the *N. schulzi* species-group by the more emphatically bairdian carapace shape (rather than streamlined, teardrop-shaped), the rather small size, and the absence of marginal denticles, terminal spine, and caudal setae. In carapace and soft parts the species shows no close affinity to the *N. pateriformis* or *N. dinochelata* species-groups.



**FIGURE 36.** *Neonesidea edentulata* n. sp., all male specimen **3958M**. A–C, dorsal view of right hemipenis, focused from higher to lower; D, E, dorsal view of left hemipenis, focused higher and lower; F, G, right antennal claw; H–J, left antennal claw; K, mouth; L, *Kauplatte* of masticatory organ; M, dorsal view of both hemipenes and furcae; N, wedge-shaped ends of two proximal segregated setae of vibratory plate of fifth limb. Scale bar =  $10 \mu m$ .

The antennal hook is unique, with horns of nearly equal size curved through more than 90°.

The distal spine on the terminal segment of the hemipenis of *N. edentulata* is a configuration that is shared by several species. In *N. edentulata* the single spine is on the inner edge; in *N. obscura* it is also on the inner edge, but much thicker and separated by a deep cleft from the rounded outer lobe; in *N. manningi* and perhaps in *N. maddocksae* the spine is on the outer edge. In *N. decipiens* and *N. frequens* there are two spines, of which the inner spine is the longer one in *N. decipiens* and the shorter one in *N. frequens*. In most of these species the terminal segment is ovate to nearly equant, rather than the more oblong proportions of *N. edentulata*.

The toothless *Kauplatte* of the masticatory organ is unique in *Neonesidea*.



**FIGURE 37.** *Neonesidea edentulata* n. sp., all male specimen **3958M.** A, B, antenna; C, sixth limb; D, seventh limb; E, mouth, F, posterior of body with hemipenis, furca and post-abdominal bristle; G, masticatory organ.

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# APPENDIX I. Descriptions of sampling stations and specimens of species collected.

French Frigate Shoals stations, Northwestern Hawaiian Islands Rapid Assessment Monitoring Program (NOW-RAMP), Sep 2000, specimens collected by R. DeFelice ("FFS-R") and D. Minton ("FFS-TC"). R = Rapture; TC = *Townsend Cromwell*.

# FFS-TC-06

(23°52.5N, 166°17.68W), 11 Sep 2000

N forereef, 1.5 km N of Tern Island, depth 5–12 m

Spur and groove habitat with moderate current and surge. Top of spurs at 5 m depth were scoured carbonate pavement with encrusting *Porites*. Some areas of dead coral matrix on spur top and slopes. Most common macro invertebrate was the boring urchin *Echinostrephus aciculatus*. Grooves at 10–12 m with carbonate sediments and rubble deposits shifting with surge.

N. edentulata: 1 juvenile.

# FFS-TC-08

(23° 52.494 N, 166°15.032 W), 12 Sep 2000

N forereef, N of Trig Island, depth 10-17 m

Spur and groove habitat with weak current and low surge at the time of the dive. Spurs more massive than FFS-TC-02 and with moderate coral cover, mainly encrusting *Porites lobata*. Spur slopes steep and groove floors with shifting carbonate sediments and rubble. Boring urchins, especially *Echinostrephus aciculatus*, were numerous on the upper exposed surface of the spurs.

N. tenera: 3 specimens, including adult female, 2 juveniles.

# FFS-TC-09

(23° 52.9 N, 166° 15.1 W), 12 Sep 2000

N forereef, N of Tern Island, depth 10–15 m

Spur and groove habitat with some surge. Spurs of moderate height (4 m) and width (4 m), with low coral cover (encrusting *Porites lobata*) and considerable bare consolidated reef surfaces, evidence of frequent scour. *Echinostrephus aciculatus* was abundant and patches of *Polythea caecia* (zoanthid) were common. *N. tenera*: 14 specimens, including 2 adult males (3906M), 3 adult females (3905M), 9 juveniles. *N. plumulosa*: 1 adult male (3960M).

# FFS-TC-10

(23° 52.9 N, 166° 15.8 W), 12 Sep 2000

N forereef, W of Tern Island, near Shark Island, depth 3–10 m

Similar spur and groove habitat as FFS-TC-7, but consolidated reef with relatively lower relief and more discontinuous, separated by shallow sand/rubble grooves and patches. Surge was low at the time of dive, but unconsolidated sediments harbored few macroinvertebrates which suggests this area is frequently disturbed by ocean swell. Encrusting *Porites lobata* was the most abundant coral. *N. tenera*: 1 juvenile (3910J).

# FFS-TC-11

(23° 47.7 N, 166° 04.97 W), 13 Sep 2000

E perimeter backreef, 14 km due E of East Island, depth 4–6 m

Shallow backreef habitat with heavy surge at the time of the dive. Reef is level but rugose pavement with pockets of semi-consolidated rubble and sand deposits. Small *Pocillopora meandrina* heads were common. Large echinoderms were abundant, especially *Echinometra mathaei*.

N. tenera: 5 juveniles.

N. holdeni: 1 adult male (3908M).

N. bacata: 1 adult male (3912M).

# FFS-TC-12

(23° 47.326 N, 166° 13.198 W), 13 Sep 2000

Central lagoon patch reef, 1 km W of East Island, depth 5–15 m

Patch reef with base at 15 m, surrounded by coarse sand flats with some rubble fields and isolated deposits. *Porites lobata* was the most abundant coral on some of the upward-facing surfaces. Reef sides heavily eroded by an unusually dense population of *Arca ventricosa* with some *Chama iostoma*, forming a virtual "bivalve reef." *N. tenera:* 6 juveniles (3920J).

# FFS-TC-15

(23° 46.107 N, 166° 15.689 W), 14 Sep 2000

Central lagoon, W side of La Perouse Pinnacle, depth 3-7 m

Caved-pocked vertical slope of basalt pinnacle with adjacent coral mounds and sand/rubble channels and patches. Coral mounds dominated by *Porites lobata* and *Porites* sp. Some large table coral (*Acropora* sp.) were present. *N. tenera:* 1 adult female (3892F).

N. edentulata: 1 adult male (3958M), 2 juveniles.

# FFS-TC-17

(23° 38.894' N, 166° 09.311' W), 15 Sep 2000 *S perimeter backreef, 2 km E of Disappearing Island, depth 3–7 m* Shallow backreef site with heavy surge at the time of the dive. Scoured pavement with shallow depressions with overlying coarse sand and some rubble. Some *Pocillopora* spp. colonies were present. *N. tenera*: 7 juveniles.

# Kane'ohe Bay, O'ahu, Station 1

(21° 30' 22.1" N, 157° 50' 57.1" W), 17 Nov 1999

North Channel, depth 1-6 m.

Wave turbulent area along south side of main channel near Buoy Marker 5, on reef area with abundant live coral extending from 4 to 6 m depth next to dredged channel. Outside of live coral area bottom is consolidated limestone with coarse sand and moderate *Halimeda* algae cover.

N. tenera: 1 adult female (3862F).