Classification and Morphological Variations of the Japanese Species of Lumbrinerides (Annelida: Lumbrineridae)

Tomoyuki Miura

Faculty of Agriculture, University of Miyazaki, 1-1 Gakuen-Kibanadai-Nishi, Miyazaki 889-2192, Japan
E-mail: miurat@cc.miyazaki-u.ac.jp

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A new classification is proposed for the Japanese species of the genus Lumbrinerides Orensanz, 1973 (Annelida: Lumbrineridae), based on the observation of as many specimens as possible so as to determine the extent of intra-populational variation of each morphological character. Morphological differences apparent in material from ten local sites were compared statistically among 16 tentative, operational taxonomic units, the morphologically recognizable units then being subjected to a taxonomic consideration with other known species. By their morphology, five species were recognized from Japanese waters, three being new to science. Diagnoses and descriptions of each species are given.

Key Words: Lumbrineridae, Annelida, taxonomy, morphological variation, new species.

Introduction

The genus Lumbrinerides Orensanz, 1973 (type species L. gesae Orensanz, 1973) was proposed with five additional species formerly assigned to the genus Lumbrineris Blainville, 1828. Subsequently, it has been treated as valid in several taxonomic works (Gardiner 1976; Perkins 1979; Miura 1980; Uebelacker 1984; Imajima 1985; Frame 1992; Carrera-Parra 2001; Aguirrezabalaga and Carrera-Parra 2006). Because external features are very simple in the family Lumbrineridae compared with other annelid families, only a few morphological characters are diagnostic for the classification of the species. In Lumbrinerides, these include prostomial length and shape, the number of anterior reduced parapodia, the occurrence of two kinds of chaetae and maxillary plate dentition. To date, the genus includes nineteen nominal species, although only five were based on more than ten specimens, most of the remainder being known only from a few type specimens. Morphological variability in characters used for classification is either unknown or poorly known, except for some cases reported by Perkins (1979) and Miura (1980).

Imajima (1985) described four new species, one new subspecies and one previously known species on the basis of thirteen specimens collected from three sites in Japanese waters, each species being described from three or fewer specimens, without any attention to their morphological variability. However, morphological characters are thought to be rarely stable throughout life, particularly when comparing juvenile and adult stages, and the possibility of damage to specimens during field sampling and fixation, which may modify the appearance of worms, is always present. In addition, three of the Japanese species were based on specimens collected from a geographically restricted area, at depths between 50 and 102 m near a biological station in Shimoda. While such diversity is interesting in the point of view of Japanese coastal fauna, a lack of appreciation of morphological variability may result in an elevated view of apparent species diversity richness.

Lumbrinerides species have been noted as dominant annelids on both coastal sandy bottoms and on the continental shelf. Individual numbers of Lumbrinerides acuta (Verrill, 1875) were recorded as >900 per square meter in medium sand at depths of 30–70 m in Delaware Bay (Kinner and Maurer 1978). The same species was also found abundantly in coarse to medium, low organic content sand in the New York Bight Apex (Caracciolo and Steimle 1983). In Japan, a species of Lumbrinerides (reported as Lumbrinieriopsis sp.) was recorded as abundant (65 individuals per square meter) on a sandy bottom in Tosa Bay (Tamai et al. 1989). Such numbers suggest that the classification of Lumbrinerides species to date need not have been restricted to the small sample sizes indicated above.

The purpose of this study was to propose a new classification for Japanese species of Lumbrinerides, based on a wide range of specimens so as to obtain a comprehensive coverage of the intra-populational variation exhibited by each morphological character. Specimens were collected from various locations, tentatively sorted into operational taxonomic units for statistical comparisons of their morphological differences, and then compared with other known species. New diagnoses and descriptions are given for all known Japanese species of the genus, including three new species.
Materials and Methods

The materials used in this study were chiefly sampled from the Pacific coast of the main islands of Japan (Fig. 1).

In the field, sediment grab samplers were used in most cases. Benthic organisms were sieved from the sediment (1.0 or 0.5 mm mesh), sorted, fixed in 10 to 15% formalin-seawater and preserved in 70% ethyl alcohol. Subsequently, each specimen was soaked in 10% ammonium water and carefully brushed under a binocular dissecting microscope so as to remove mucus and dust. The specimen was then transferred to distilled water and the swollen specimen under a microscope was measured the body width excluding parapodia at the largest anterior chaetiger and the proportion of prostomium length to width by drawing with the aid of a camera lucida. The measured specimen was transferred to 70% alcohol for further observations. Sex was determined by the sampling location, date and first occurrence of the penis in females and the presence or absence of the spermatophore in males. For each of the latter, the sampling data, location, collection name (if not the author) were as follows:

(TEN) 29 immature specimens, near Tenryu River, 34°38.1′N 137°47.6′E, 5–10 m, sand, 25 May 1983;
(TOSA N) four gamete-bearing males and 20 immature, 33°27.3′N 133°29.0′E, 15 m, sand, Smith-McIntyre grab, 26 November 1980, collected by K. Tamai;
(TOSA D) one female and four immature, 23 December 1980, other data as for TOSA N;
(TOSA J) 30 immature, 8 June 1981, other data as for TOSA N;
(TOMA) 30 immature, off Tomakomai, Hokkaido, 42°36.7′N 141°37.6′E, 10–20 m, muddy fine sand, June 1986;
(IMA A) one female, off Imabetsu, Aomori Prefecture, 41°12.0′N 140°28.8′E, 21 m, sand, 29 August 1983;
(IMA B) one male and one immature, off Imabetsu, 41°12.0′N 140°28.8′E, 20 m and 19 m, 29 August 1983;
(SOMA) 26 immature, off Soma, Fukushima Prefecture, 37°48.9′N 140°59.4′E, 38–46 m, sand, 31 August 1983;
(EK A) Seisui-maru Cruise 1984 R-07, Enshu-Nada and Kumano-Nada, Station 201 A and B, three immature, off Hamana-Lake, 34°38.2′N 137°35.7′E, 41 m, fine sand, Smith-McIntyre grab, 21 September 1984; Station 301 A and B, six immature, off Tawara, Atsumi Peninsula, 34°33.0′N 137°20.5′E, 41 m, coarse sand, 21 September 1984; Station 302 A, three immature, off Tawara, Atsumi Peninsula, 34°31.9′N 137°21.4′E, 61 m, fine sand, 21 September 1984; Station 402 A and B, three females and nine immature, Irago Strait, 34°20.2′N 136°60.0′E, 59 m, fine sand, 13 September 1984; Station 403 A and B, five immatures, Irago Strait, 34°18.6′N 136°59.9′E, 80 m, fine sand, 13 September 1984; Station 501 B, one male, Ago Inlet, 34°15.4′N 136°43.7′E, 39 m, fine sand, 16 September 1984; Station 502 A and B, two females and three immatures, Irago Strait, 34°14.3′N 136°43.3′E, 60 m, fine sand, 16 September 1984; Station 701 B, one immature, off Kuma-no river, 33°43.0′N 136°02.9′E, 39 m, mud, 16 September 1984;
(EK B) Seisui-maru Cruise 1984 R-07, Enshu-Nada and Kumano-Nada, Station 405 A and B, two females and one immature, Irago Strait, 34°16.1′N 136°59.9′E, 120 m, fine sand, 13 September 1984; Station 406 A and B, one female and two immatures, Irago Strait, 34°15.0′N 136°60.0′E, 150 m, fine sand, 13 September 1984; Station 504 A, one female and four immatures, Ago Inlet, 34°12.0′N 136°41.8′E, 102 m, muddy coarse sand, 16 September 1984; Station 505 A and B, three females, one male and six immatures, Ago Inlet, 34°11.2′N 136°41.5′E, 124 m, muddy coarse sand, 16 September 1984; Station 506 A and B, three immature, Ago Inlet, 34°10.2′N 136°40.7′E, 158 m, silty fine sand, 16 September 1984;
(BUNG) Tansei-maru Cruise KT-84-12, Bungo Strait, Station 31, three immature, off Tsukumi, 33°02.2′N 132°05.5′E–33°02.2′N 132°05.4′E, 72–76 m, coarse sand with pebbles, ORI Dredge, 4 September 1984; Station 33, one immature, off Tsukumi, 33°06.9′N 132°08.0′E–33°06.7′N 132°07.9′E, 89–91 m, muddy coarse sand, 4 September 1984;
(KII A) Tansei-maru Cruise KT-84-12, Kii Channel, Station 11-2, one immature, off Susami, 33°30.3′N 135°31.1′E–33°30.4′N 135°30.9′E, 73–75 m, shell and...
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sandy mud, ORI Dredge, 31 August 1984; Station 12-1, one immature, off Susami, Kii Channel, 33°29.9′N 133°30.9′E–33°30.0′N 133°30.7′E, 100–101 m, shell and sandy mud, 31 August 1984;

(KII B) Tansei–maru Cruise KT-84-12, Kii Channel, Station 12-1, five immature, off Susami, Kii Channel, 33°29.9′N 133°30.9′E–33°30.0′N 133°30.7′E, 100–101 m, shell and sandy mud, 31 August 1984;

(MISA) two immature, off Misaki, 35°07.3′N 139°38.4′E, 110–122 m, sand, dredge, 10 July 1985;

(SADO A) Tansei–maru Cruise KT-85-14, Station F-5 BC-2, two immature, South Sado Strait, Japan Sea, 37°17.4′N 138°16.4′E, 58 m, coarse sand, Box Corer 1/10 square meters, 10 September 1985; Station F-5 SM-1, one immature, 37°13.6′N 138°16.9′E, 52 m, Smith-McIntyre Grab, 10 September 1985; Station F-5 SM-2, one female and one immature, 37°13.6′N 138°16.9′E, 52 m, 10 September 1985;

(SADO B) Tansei–maru Cruise KT-85-14, Sado Strait, Japan Sea, Station D-2 SM-2, one immature, 38°17.8′N 138°54.4′E, 148 m, fine sand, 7 September 1985; Smith-McIntyre Grab; Station F-2 SM-1, two immature, 37°22.4′N 138°10.1′E, 143 m, fine sand, 10 September 1985, Smith-McIntyre Grab; Station F-2 SM-2, one immature, 37°22.4′N 138°10.1′E, 140 m, fine sand, 10 September 1985; Station F-2 SM-3, one immature, 37°22.4′N 138°10.1′E, 139 m, fine sand and gravel, 10 September 1985; Station F-2 SM-4, two immature, 37°22.4′N 138°10.1′E, 139 m, 10 September 1985; Station F-3 BC-1, two immature, 37°18.1′N 138°14.0′E, 91 m, fine sand, 10 September 1985; Station F-3 BC-2, two immature, 37°18.7′N 138°13.9′E, 97 m, fine sand, 10 September 1985; Station F-3 BC-3, one female and one immature, 37°18.7′N 138°13.9′E, 97 m, fine sand, 10 September 1985; Station F-3 SM-1, one female and one immature, 37°18.5′N 138°13.8′E, 93 m, fine sand, 10 September 1985; Station F-3 SM-2, two females and five immature, 37°18.5′N 138°13.8′E, 92 m, fine sand, 10 September 1985; Station F-3 SM-3, one female and 11 immature, 37°18.6′N 138°13.8′E, 93 m, fine sand, 10 September 1985; Station F-4 SM-1, one female and one immature, 37°16.4′N 138°16.4′E, 75 m, fine sand, 10 September 1985; Station F-4 SM-2, two immature, 37°16.8′N 138°16.3′E, 76 m, fine sand, 10 September 1985; Station F-4 SM-3, one immature, 37°16.6′N 138°16.2′E, 77 m, fine sand, 10 September 1985; Station F-4 SM-4, one immature, 37°16.6′N 138°16.1′E, 77 m, fine sand, 10 September 1985.

The type series of species in the genus Lumbrinerides were also reviewed and listed below. Some previously unpublished data for the types of congeneric species revised by Miura (1980) were also utilized.


Lumbrinerides lineatus Imajima, 1985: Holotype NSMT-Pol H-198; Paratype NSMT-Pol P-199, off Shimoda, 70–63 m and 102–92 m, respectively, October 1981.

Lumbrinerides bidentatus Imajima, 1985: Holotype NSMT-Pol H-200; Paratype NSMT-Pol P-201, around Tsushima, 85 and 125 m, respectively, July to August 1968.

Lumbrinerides acutus japonicus Imajima, 1985: Holotype NSMT-Pol H-202; Paratypes NSMT-Pol P-203, off Shimoda, 70–63 m and 60–50 m, respectively, October 1981.


Lumbrineris acutiformis Gallardo, 1967: Holotype AHF Poly 0291 in the Allan Hancock Foundation, Bay of Nha Trang, Station 224, 16 m; Paratypes, Station 223, 15 m, 3 March 1960 and Station 153 II, 43 m, 2 February 1960.

Lumbriconeris acuta Verrill, 1875: USNM 12895 in the United States National Museum, Rhode island, off Block Island, 26 m, summer 1874.

Lumbrinerides dayi Perkins, 1979: Paratype USNM 55598, off Beaufort, 20 m, 19 April 1978; DMLM 2481 in Duke University Marine Laboratory, off Beaufort, 20 m, 19 April 1965, collected by J. H. Day.

For each specimen, the number of anterior reduced parapodia with rounded postchaetal lobes, the position of the first fully developed parapodium, the number of hooks and limbate chaetae on each parapodium, the number of teeth on each maxillary plate, and the number of concentric growing lines on the mandibles were measured, except on badly damaged specimens. In this study, the accessory teeth on maxillae I were recognized as teeth with internal pulp cavity situated just posterior to the main tooth on the central inner margin. Although a projection (without an internal cavity) is recognizable at the posterior end of the central inner margin of maxillae I (Fig. 7), regarded as an accessory tooth in some studies, including Imajima (1985), all species of Lumbrinerides have such a projection, which is considered here as non homologous with the accessory teeth and therefore not considered as such. Only teeth with internal cavities were considered as descriptive for maxillae II, differences between the numbers of tube-like cavities and external teeth being noted. This application was presented in 1989 in a special session of the third International Polychaeta Conference by the author (Miura 1991). In other papers such as by Carrera-Parra and Orensanz (2002), this recognition was established in another genus of the family.

The newly recorded specimens and types have been deposited in the National Museum of Nature and Science, Tokyo (NSMT), Japan.

A statistical analysis using the commercial software Mac Statistical Analysis for MS Excel ver. 2.0 (Esumi Co. Ltd.) was applied for selected operational taxonomic units containing more than 20 specimens and the taxonomic importance of morphological characters evaluated.

Variation of morphological characters

The main morphological characters of the operational taxonomic units containing more than 20 specimens were
summarized as frequency histograms of each character state or measurement value (Fig. 2). These characters were then evaluated on their variability within a unit and distinguishability among units.

**Chaetae.** In the genus *Lumbrinerides*, three kinds of chaetae are known. Limbate chaetae and simple bidentate hooded hooks are common to all species, and multidentate composite hooks are also known. Although a lumbrinerid species with composite hooks has been recognized in the genus by Uebelacker (1984) and was later described as a new species, *L. uebelackerae* Carrera-Parra, 2001, its inclusion in *Lumbrinerides* is questionable due to the presence of multidentate composite hooks, black acicula, well-developed nuchal organs, and the prostomium with a keel-like structure reminiscent of other genera of the family. Although more likely to belong to another lumbrinerid genus, if *L. uebelackerae* is eventually included in *Lumbrinerides*, it is set apart from all other species in the genus and has therefore been excluded here to simplify further considerations on chaetae.

The operational taxonomic units in Japanese waters had limbate chaetae and simple bidentate hooks. Although the
chaetae did not differ significantly in morphology among units, they differed in their occurrence. All units were divided into two main groups by a difference in the first occurrence of simple hooks (Table 1). In TEN, TOSA, SOMA, TOMA, SADO A, EK A, BUNG and KII A, the first hooks always occurred on chaetiger 1. However, in KII B, MISA, and SADO B, the first hooks occurred on chaetiger 2 or 3. Table 1 shows the variation in starting site of simple hooks represented by chaetiger number. The number of specimens varied from 2 to 41 across different samples. 

Fig. 3. Chaetal composition on each parapodium of large, most intact specimens selected for each operational taxonomic unit, plus the holotype (AHF Poly 0291) of *Lumbrinerides acutiformis* (Gallardo, 1967). Open circles, simple hooks; closed circles, limbate chaetae.
SADO B and EK B, the hooks started on chaetiger 7 (or more posteriorly in large specimens). IMA included specimens in which hooks started on either the first (IMA A) or third parapodium (IMA B).

The distribution of both hooks and limbate chaetae was examined by counting chaetae per parapodium for each chaetiger in all specimens, and appeared to be applicable to further grouping within the Japanese species complex. Specimens in which the chaetae had been retained almost intact in their preserved condition were selected for eight operational units and their chaetal distribution (numbers of each kind of chaetae and chaetiger numbers) was compared (Fig. 3). Chaetal distribution was also examined in the holotype of *Lumbrinerides acutiformis* (Gallardo, 1967). In the first group of units (hook occurring on the first chaetiger), each of the first six to twelve parapodia had two hooks and two to four limbate chaetae. Thereafter, the chaetal composition changed to become a single hook and three or four limbate chaetae, with the number of hooks increasing posteriorly to three or four (maximum) and the number of limbate chaetae decreasing to two or one. The total number of chaetae on each parapodium was thus four or rarely five or six on the first twenty parapodia and five on most of the subsequent parapodia. Although the chaetal composition in the far posterior region usually remained unclear due to most specimens lacking a considerable number of posterior chaetigers, observations on some intact specimens suggested that the number of limbate chaetae decreased to one or zero, whereas hooks increased in number to compensate for limbate chaetae; thus each of the far posterior parapodia had four or more hooks.

A chaetiger difference among operational units was apparent wherein chaetal composition changed from two hooks and two limbate chaetae (2H-2L) to one hook and three limbate chaetae (H-3L). Thereafter, changes in chaetal composition occurred from 1H-3L to 2H-2L, and from 2H-2L to 3H-2L or from 1H-3L directly to 3H-2L. Only the first point of change from 2H-2L to 1H-3L was relatively stable within the operational unit, other points moving irregularly. The first changing point occurred between chaetigers 11 to 13 in *Lumbrinerides acutiformis* and unit TEN, chaetigers 9 to 13 in SOMA, chaetigers 10 and 11 in TOSA, and chaetigers 6 to 8 in SADO A and EK A.

In the group of units characterised by the first hooks on chaetiger 7 or later in large specimens, each of several anterior parapodia had four limbate chaetae. The chaetal composition of this group changed from anterior to posterior in each individual specimen as follows: 4L, 1H-3L, 2H-2L and 3H-2L (Fig. 3). The first occurrence of simple hooks, i.e., the first changing point of chaetal composition, was relatively stable within the unit, as shown below in each species description. In this group, the linear relationship between first occurrence of hooks and body width was significant in small specimens, but the hook condition became stable in larger specimens as shown in unit EK B (Fig. 4). In particular, specimens smaller than 0.4 mm in body width had the first hooks on more anterior parapodia in unit EK B (Fig. 4).

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**Fig. 4.** Relationship between each taxonomic character state and body size (width) in an operational taxonomic unit, EK B. The number of accessory teeth on both plates of maxilla I, chaetiger number on which first hooks present, prostomium length to width proportion, number of anterior reduced parapodia and number of concentric lines on mandibles were plotted against body width in 24 specimens.
Each of the two groups showed well defined bathymetric distributions. The operational units with simple hooks on the first chaetiger were recorded only at depths <100 m in mean sampling depth, whereas those with hooks starting on chaetiger 6 or more posteriorly were collected only at depths >100 m (Fig. 5).

**Prostomium.** The proportion of prostomium length to width was estimated for each specimen. The proportional range (1.10–3.55) was not related to body size or sampling depth (Figs 4, 5). Scheffe’s method for multiple comparisons on the proportion values for units including more than four specimens showed TOMA to have significantly higher values compared with the other units (Table 2, see also Fig. 2).

**Parapodium.** The number of anterior reduced parapodia has been described by several authors as an important specific character, but none has mentioned variability within species. Because the number of reduced parapodia may differ among local Japanese populations (Table 3), values were analysed statistically among operational taxonomic units and evaluated as significant in several combinations (Table 4). Shallow water specimens had comparatively larger numbers of reduced parapodia than those from greater depths (Fig. 5).

Posterior to the first several chaetigers with reduced parapodia, the postchaetal lobes became gradually larger on some chaetigers, with the subsequent appearance of fully developed parapodia. The appearance of such parapodia corresponded closely with the changing point of chaetal composition. Each of the first fully developed parapodium was provided with one hook and three or more limbate chaetae in many specimens.

**Maxillae.** The number of accessory teeth on maxillae I showed remarkable variability corresponding with sampling depth (Fig. 5), tending to decrease with increments of depth, possibly depending upon the operational taxonomic unit. Although the number usually varied slightly within the unit (Table 5), it remained constant in SOMA and SADO A, all specimens of those samples having two accessory teeth. Most specimens of unit TEN (shallowest site in this study) had three accessory teeth. On the other hand, the number was one or less in SADO B and EK B specimens, collected from the greatest depth. In general, three teeth were observed on maxillae II. The teeth were sometimes modified for meshing the teeth of the right and left plates, and occasionally showed an externally bidentate appearance. In such a case, the internal cavity became the marker for judging whether or not the plate was truly bidentate. In the specimens examined, only one collected from Bungo Channel (KT-84-12, Station 12-1) was judged as having truly bidentate maxillae II. A pair of large maxillary carriers are situated posterior to maxillae I in *Lumbrinerides*, the difference between the two groups divided by the first occurrence of hooks being found in the outer shape of the maxillary carriers. The posterior ends of the carriers tended to be pointed and close to each other in the group with the first hook on chaetiger 1, but relatively truncated and separated from each other in the other group.

**Mandible.** There were no significant differences in mandible shape between local populations. The number of concentric lines observed on the mandible cutting edge ranged from 2 to 7 (Table 6), the number tending to corre-

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**Fig. 5.** Relationship between each taxonomic character state and mean sampling depth (m) for each operational taxonomic unit. The number of accessory teeth on both plates of maxilla I, chaetiger number on which first hooks present, prostomium length to width proportion, number of anterior reduced parapodia and number of concentric lines on mandibles of each OTU were plotted against the mean sampling depth for each lot of specimens.
spond with body width (Fig. 4) and possibly representing growth lines, but the relationship between their formation and time taken was unknown. In the TOSA sample, the mode of lines was seven in November 1980 and five in June of the following year (Fig. 2). This may have been due to the addition of juveniles with fewer lines and death of aged or large worms with a greater number of lines. The number of concentric lines was thus considered important for estimating the age of each specimen, but not as a taxonomic character.

Body width. Specimens with the first hooks on chaetiger 1 were greater in body width than those with the first hooks on chaetiger 7 or 8 (Table 7; Fig. 2). In some samples, two modes of size distribution were recorded. Samples TOMA, TOSA J and N and SOMA consisted of two size classes for body width (Fig. 2).

Materials for taxonomic description. The descriptions are better based on a particular life stage among comparable taxa, such as mature adult specimens, due to the possible confusion resulting from morphological comparisons of young or juvenile specimens of one species with matured specimens of another. Some means for assessing the age or growth stage of individual specimens would be useful in this regard. In the present study, body width was measured as carefully as possible, but the error caused by body size reduction at the time of fixation could not be eliminated. On the other hand, the concentric lines on the mandibles could be counted easily and were not affected by fixation, being therefore more useful for estimating individual growth.

In this study, specimens less than 0.4 mm in body width and with four or fewer concentric lines on the mandibles were considered to be juveniles and therefore not used.

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**Table 2. Difference in prostomial proportion of length to width among operational taxonomic units under Scheffe’s method test for multiple comparisons on values for all units.**

<table>
<thead>
<tr>
<th>OTU</th>
<th>TOMA</th>
<th>TEN</th>
<th>TOSA N</th>
<th>TOSA D</th>
<th>TOSA J</th>
<th>SOMA</th>
<th>SADO A</th>
<th>EK A</th>
<th>BUNG</th>
<th>KII B</th>
<th>SADO B</th>
<th>EK B</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mean Sampling Depth (m)</td>
<td>15</td>
<td>10</td>
<td>15</td>
<td>15</td>
<td>15</td>
<td>37</td>
<td>55</td>
<td>60</td>
<td>82</td>
<td>101</td>
<td>113</td>
<td>130</td>
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<tr>
<td>Number of Observed Specimens</td>
<td>29</td>
<td>29</td>
<td>24</td>
<td>5</td>
<td>30</td>
<td>24</td>
<td>5</td>
<td>38</td>
<td>4</td>
<td>5</td>
<td>40</td>
<td>24</td>
</tr>
<tr>
<td>Mean Value</td>
<td>2.47</td>
<td>1.71</td>
<td>1.74</td>
<td>1.89</td>
<td>1.64</td>
<td>1.87</td>
<td>1.58</td>
<td>1.77</td>
<td>1.76</td>
<td>1.74</td>
<td>1.67</td>
<td>1.72</td>
</tr>
</tbody>
</table>

TOMA — ** ns ** ** ** ** ns * ** **
TEN ** ns — ns ** ns ** ns ns ns ns ns
TOSA N ns ns ns — ns ns ns ns ns ns ns ns
TOSA D ns ns ns ns — ns ns ns ns ns ns ns
TOSA J ** ns ns ns — ns ns ns ns ns ns ns ns
SOMA ns ns ns ns — ns ns ns ns ns ns ns
SADO B ** ns ns ns ns — ns ns ns ns ns ns
EK A ** ns ns ns ns ns — ns ns ns ns ns
BUNG ns ns ns ns ns ns — ns ns ns ns ns
KII A * ns ns ns ns ns ns ns ns — ns ns
SADO A ** ns ns ns ns ns ns ns ns — ns ns
EK B ** ns ns ns ns ns ns ns ns ns — ns

*: p<0.1; **: p<0.01.

**Table 3. Variation in number of anterior reduced parapodia among operational taxonomic units.**

<table>
<thead>
<tr>
<th>Sample</th>
<th>Depth (m)</th>
<th>Max</th>
<th>Mini</th>
<th>Mean</th>
<th>Variance</th>
<th>Number of Observed Specimens</th>
</tr>
</thead>
<tbody>
<tr>
<td>TEN</td>
<td>10</td>
<td>10</td>
<td>9</td>
<td>9.9</td>
<td>0.10</td>
<td>29</td>
</tr>
<tr>
<td>TOSA N</td>
<td>15</td>
<td>11</td>
<td>9</td>
<td>10.0</td>
<td>0.30</td>
<td>24</td>
</tr>
<tr>
<td>TOSA D</td>
<td>15</td>
<td>9</td>
<td>8</td>
<td>8.8</td>
<td>0.20</td>
<td>5</td>
</tr>
<tr>
<td>TOSA J</td>
<td>15</td>
<td>10</td>
<td>6</td>
<td>8.9</td>
<td>1.24</td>
<td>30</td>
</tr>
<tr>
<td>TOMA</td>
<td>10–20</td>
<td>10</td>
<td>7</td>
<td>8.6</td>
<td>0.73</td>
<td>30</td>
</tr>
<tr>
<td>IMA A</td>
<td>21</td>
<td>—</td>
<td>—</td>
<td>10.0</td>
<td>—</td>
<td>1</td>
</tr>
<tr>
<td>IMA B</td>
<td>18–20</td>
<td>8</td>
<td>7</td>
<td>7.5</td>
<td>—</td>
<td>2</td>
</tr>
<tr>
<td>SOMA</td>
<td>38–46</td>
<td>9</td>
<td>6</td>
<td>7.2</td>
<td>0.80</td>
<td>24</td>
</tr>
<tr>
<td>SADO A</td>
<td>52–58</td>
<td>7</td>
<td>6</td>
<td>6.8</td>
<td>0.20</td>
<td>5</td>
</tr>
<tr>
<td>EK A</td>
<td>40–80</td>
<td>7</td>
<td>3</td>
<td>4.9</td>
<td>0.59</td>
<td>38</td>
</tr>
<tr>
<td>BUNG</td>
<td>72–91</td>
<td>invariant</td>
<td>5.0</td>
<td>0.00</td>
<td>4</td>
<td>4</td>
</tr>
<tr>
<td>KII A</td>
<td>73–101</td>
<td>5</td>
<td>5</td>
<td>5.0</td>
<td>—</td>
<td>2</td>
</tr>
<tr>
<td>KII B</td>
<td>100–101</td>
<td>5</td>
<td>4</td>
<td>4.5</td>
<td>0.30</td>
<td>5</td>
</tr>
<tr>
<td>MISA</td>
<td>110–122</td>
<td>5</td>
<td>4</td>
<td>4.5</td>
<td>—</td>
<td>2</td>
</tr>
<tr>
<td>SADO B</td>
<td>75–150</td>
<td>4</td>
<td>3</td>
<td>3.2</td>
<td>0.15</td>
<td>40</td>
</tr>
<tr>
<td>EK B</td>
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<td>4</td>
<td>3</td>
<td>3.9</td>
<td>0.11</td>
<td>24</td>
</tr>
</tbody>
</table>

---
for morphological comparisons among species. Similarly, TOSA and TEN specimens less than 0.5 mm and with five or fewer lines were considered as juveniles, as were TOMA and SOMA specimens less than 0.7 mm and with four or fewer lines.

**Taxonomy and descriptions of Japanese species**

**Genus Lumbrinerides** Orensanz, 1973


**Diagnosis.** Body cylindrical without color pattern; prostomium acorn-shaped with tapered distal end, pygidium with semicircular profile. Maxillary apparatus comprising four pairs of maxillae; maxilla I furcate with or without accessory teeth on inner edge, maxilla II a semi-circular plate with two or three teeth, maxilla III a rectangular (semi-circular in dorsal view) plate lacking well-formed teeth on cutting edge, maxilla IV a long broad oval plate without obvious teeth; maxillary carriers long, thick, winged posteriorly; lateral supports triangular comprising many thin small plates. All species with limbate chaetae and simple bidentate hooded hooks (after Orensanz 1973).

**Additional characters on staining patterns.** Anteriorly, from prostomium to ca. chaetiger 15, body strongly stained by methyl green, except for parapodia, ventral oral region, antero-dorsum of chaetigers 2–3, and mid-dorsum of chaetigers 3–6; distal tip of prostomium strongly stained; dorsal and postdorsum covered by many dark blue dots stained by methyl green. In each parapodium, distal tip of postchaetal lobe markedly stained by methyl green compared with base. Similar staining patterns noted for all species described here.

**Gender.** Feminine. Although Imajima (1985) treated...
the generic name as masculine, Orensanz (1973) stated that it was feminine when he erected the genus (ICZN 1999: Article 30.1.4.4).

**Lumbrinerides shimodaensis** Imajima, 1985  
(Figs 6–10)

*Lumbrinerides shimodaensis* Imajima, 1985: 174–176, fig. 3a-i.  
*Lumbrinerides lineatus* Imajima, 1985: 176–178, fig. 4a–j.  
Syn. nov.  
*Lumbrinerides bidentatus* Imajima, 1985: 178–180, fig. 5a–l.  
Syn. nov.

**Material examined.** Holotype of *Lumbrinerides shimodaensis*, NSMT-Pol H-197, off Shimoda, 50–59 m, October 1981. Holotype and paratype of *Lumbrinerides lineatus*, NSMT-Pol H-198 and P-199, off Shimoda, 63–70 and 92–102 m, respectively, October 1981. Holotype and paratype of *Lumbrinerides bidentatus*, NSMT-Pol H-200 and P-201, around Tsushima, 85 and 125 m, respectively, July to August 1968.

**Comparative material.** Four syntypes of *Lumbriconereis acuta*, USNM 12895, Rhode Island, off Block Island, 26 m, August 1874. Holotype and two paratypes of *Lumbrinerides acutus japonicus*, NSMT-Pol H-202, off Shimoda, 63–70 m, October 1981 and NSMT-Pol P-203, off Shimoda, 50–60 m, October 1981, respectively.

**Non-type material.** (EK B) Seisui-Maru Cruise 1985-R-07, Stations 405 A: one female; 405B: one female, one immature; 406 A: one juvenile; 406 B: one female, one juvenile; 504 A: one female, four juveniles; 505 A: two males, two immature, one juvenile; 505 B: one female, one immature, one juvenile; 506 A: two juvenile; 506 B: one immature. (KII B) Tansei-Maru Cruise KT-84-12, Kii Channel, Station 12-1: five immature. (SADO B) Cruise Table 6. Variation in number of concentric lines on mandibles.

<table>
<thead>
<tr>
<th>Sample</th>
<th>Depth (m)</th>
<th>Max</th>
<th>Mini</th>
<th>Mean</th>
<th>Number of Observed Specimens</th>
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<tr>
<td>TEN</td>
<td>10</td>
<td>6</td>
<td>3</td>
<td>4.5</td>
<td>29</td>
</tr>
<tr>
<td>TOSA N</td>
<td>15</td>
<td>8</td>
<td>4</td>
<td>6.0</td>
<td>24</td>
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<tr>
<td>TOSA D</td>
<td>15</td>
<td>7</td>
<td>3</td>
<td>5.0</td>
<td>5</td>
</tr>
<tr>
<td>TOSA J</td>
<td>15</td>
<td>8</td>
<td>3</td>
<td>5.0</td>
<td>30</td>
</tr>
<tr>
<td>TOMA</td>
<td>10–20</td>
<td>9</td>
<td>2</td>
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<td>30</td>
</tr>
<tr>
<td>IMA A</td>
<td>21</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>2</td>
</tr>
<tr>
<td>IMA B</td>
<td>18–20</td>
<td>4</td>
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<tr>
<td>SOMA</td>
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<td>2</td>
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<td>26</td>
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<tr>
<td>SADO B</td>
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</tr>
<tr>
<td>EK A</td>
<td>40–80</td>
<td>8</td>
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<td>7</td>
<td>5</td>
<td>5.5</td>
<td>4</td>
</tr>
<tr>
<td>KII A</td>
<td>73–101</td>
<td>9</td>
<td>5</td>
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<td>3</td>
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<tr>
<td>KII B</td>
<td>100–101</td>
<td>7</td>
<td>3</td>
<td>4.5</td>
<td>6</td>
</tr>
<tr>
<td>MISA</td>
<td>110–122</td>
<td>5</td>
<td>4</td>
<td>4.5</td>
<td>2</td>
</tr>
<tr>
<td>SADO A</td>
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<td>9</td>
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</tr>
<tr>
<td>EK B</td>
<td>100–160</td>
<td>5</td>
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<td>3.9</td>
<td>24</td>
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</table>

Table 7. Variation in body width.

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<tr>
<th>Sample</th>
<th>Depth (m)</th>
<th>Max</th>
<th>Mini</th>
<th>Mean</th>
<th>Number of Observed Specimens</th>
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<tr>
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<td>0.606</td>
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</tr>
<tr>
<td>TOSA J</td>
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<tr>
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<td>0.36</td>
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</tr>
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<td>—</td>
<td>—</td>
<td>1</td>
</tr>
<tr>
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<td>0.70</td>
<td>0.850</td>
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</tr>
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<td>0.646</td>
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</tr>
<tr>
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<td>0.506</td>
<td>38</td>
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<tr>
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<td>72–91</td>
<td>0.68</td>
<td>0.51</td>
<td>0.598</td>
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<td>0.720</td>
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<tr>
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<td>0.41</td>
<td>0.615</td>
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<tr>
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<td>110–122</td>
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<td>0.44</td>
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<td>0.438</td>
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</tr>
<tr>
<td>EK B</td>
<td>100–160</td>
<td>0.60</td>
<td>0.27</td>
<td>0.458</td>
<td>24</td>
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</table>
Lumbrinerides from Japan

KT-85-14, Japan Sea, Stations D-2 SM-2: one immature; F2-SM1: two juveniles; F2-SM2: one immature; F2-SM3: one immature; F2-SM4: one immature, one juvenile; F3-BC1: one immature, one juvenile; F3-BC2: one immature, one juvenile; F3-BC3: one female, one immature; F3-SM1: one female, one juvenile; F3-SM2: two females, two immature, three juveniles; F3-SM3: one female, six immature, five juveniles; F4-SM1: one immature, one juvenile; F4-SM2: two immatures; F4-SM3: one immature; F4-SM4: two juveniles. (MISA) two immature.

**Description.** Prostomium acorn-shaped with smooth surface without keel-like or other structure except wrinkles by shrinkage, 1.2–2.4 times longer than wide in larger specimens (Fig. 6A). Peristomium with two apodous rings (Fig. 6A). Three to five anterior parapodia reduced with low conical postchaetal lobe and inconspicuous prechaetal one (Fig. 6B); fully developed parapodia with elongate subconical postchaetal lobe about twice as long as prechaetal one beginning from chaetigers 7–8 (Fig. 6C, D); both lobes well-developed on far posterior parapodia. Four or more broadly limbate chaetae with tapering end occurring on less than ten anterior parapodia, three to one on posterior parapodia, disappearing on far posterior parapodia (Figs 6B–D, 9, 10). A single hooded hook occurring on parapodia 7–20 (Fig. 6C), two or three on posterior parapodia (Figs 6D, 9, 10), up to six on far posterior parapodia. Maxilla I normally with one accessory tooth (Figs 6G, 7), occasionally without tooth (Fig. 6E, right maxilla I). Maxilla II generally with three teeth (Figs 6E, G, 7); each tooth always with a single inner cavity, even if with occasional bidentate outline or completely lacking third tooth in a single exceptional large specimen (Fig. 8). Mandibles slender posteriorly, several concentric lines on anterior flared part (Fig. 6F, H).

**Variations.** Accessory teeth on Maxilla I number zero or one in this species (Fig. 2; EK B). The prostomium is 1.2 to 2.4 times longer than wide. The first simple hooks occur on chaetigers 4–6 in juveniles (Fig. 4). The number of anterior reduced parapodia varies between three and five (Table

Fig. 6. *Lumbrinerides shimodaensis* based on specimens from Kumano Nada. A–F, 505 B, collected from Irago Strait: A, anterior end of specimen; B, parapodium 1; C, parapodium 8; D, parapodium 21; E, maxillae; F, mandibles; G, H, 505 A, collected from Irago Strait: G, maxillae; H, mandibles.
3). In the Japan Sea population, individuals with three reduced parapodia were dominant (Fig. 2; SADO B), whereas those with four reduced parapodia were dominant off the Pacific coast of Japan (Fig. 2; EK B).

Remarks. In the shape of chaetae and parapodia, no significant difference was found in the type specimens of three species listed as synonymies. They were very short including 15–30 chaetigers and I could not find any difference in these characters as in the original description by Imajima (1985).

The basal tooth-like projection on the proximal parts of the inner edge of the maxilla I was not considered as an accessory tooth in this study. Although such projection was illustrated to imply a kind of functional teeth in the original descriptions of *L. shimodaensis*, *L. lineatus* and *L. bidentatus* (Fig. 7A-3, B-3, B-4, C-4, C-5), no second accessory tooth was found in the reexamined type specimens (Fig. 7A-1, B-1, B-2, C-1, C-2). Similarly, the left maxilla I of the paratype (NSMT-Pol P-201) of *L. lineatus* lacks accessory teeth, the dentition of maxillae I in those nominal species varying from zero to one. Maxillae II of the above three nominal species were also identical (Fig. 7A-2, C-3). The modified external dentation observed may have resulted from meshing between the maxillae II, and between the shafts of maxillae I and the plates of maxillae II. The true bidentate state of maxillae II, namely two external teeth and two pulp cavities was observed only on an exceptionally large specimen collected from the Bungo Channel (Fig. 8A-2).

The chaetal composition of all of the type specimens for the three nominal species erected by Imajima (1985) was also examined by counting both kinds of chaetae on each parapodium (Fig. 9). In these specimens, a maximum of four limbate chaetae were found on each of the first five or
six parapodia, becoming fewer thereafter. In compensation, simple bidentate hooded hooks appeared singly on each parapodium after chaetiger 7 or 8, increasing to two or three after chaetiger 20 (Fig. 9). In other more intact specimens, chaetal composition was more clearly evaluated (Fig. 10), specimen 505 A-01, for example, collected from Kumano Nada and measuring 0.51 mm wide, having four limbate chaetae each on the first seven parapodia, three on the following seven parapodia, and finally two on the remaining posterior parapodia. The same specimen had simple hooded hooks starting on parapodium 8, one on the next 12 parapodia, two on the next 11 parapodia and three on the subsequent parapodia (Fig. 10). The change in chaetal composition was almost stable in specimens with a body width of more than 0.4 mm (Fig. 4). As a conclusion of revision, \textit{L. lineatus} and \textit{L. bidentatus} were regarded as synonyms of \textit{L. shimodaensis}.

\textit{Lumbrinerides shimodaensis} differs from all other Japanese species in having a single accessory tooth or none on the maxillae I, a small number of reduced anterior parapodia and simple bidentate hooks starting on ca. chaetiger 7 in adult specimens. \textit{Lumbrinerides amoureuxi} Miura, 1980, \textit{L. crassicephala} (Hartman, 1965) and \textit{L. platypygos} (Fauchald, 1970) are also known to have simple hooks starting on ca. chaetigers 6–9. \textit{Lumbrinerides crassicephala} has one accessory tooth on maxilla I and the remaining species differ from \textit{L. shimodaensis} in having two teeth or none.
Lumbrinerides crassicephala has a long prostomim (length to width ca. 3.0) compared with *L. shimodaensis* in which the proportion is 2.0.

The holotype and two paratypes of *Lumbrinerides acutus japonicus* are all immature and lack a considerable number of posterior chaetigers. In addition, most of the chaetae on the anterior parapodia and the initial position of simple hooks could not be determined. The occurrence of simple hooks mentioned by Imajima (1985) could not be confirmed, only a single hook on parapodium 4 in one paratype, and on parapodium 6 on the other paratypes and on the holotype (Fig. 11) being found. The presence of three to five limbate chaetae on anterior parapodia in one of the paratypes suggests an absence of hooks on those parapodia as the maximal number of chaetae on a single anterior parapodium is thought to be four in most Japanese specimens, as mentioned above. This chaetal composition closely resembles that described for *L. shimodaensis*, in which the first several parapodia lack simple hooks and are provided with only four limbate chaetae, or possibly five (Fig. 10). In these details, the specimens do not differ from *L. shimodaensis*. The presence of an accessory tooth on maxillae I is also consistent with the latter. *Lumbrinerides acutus japonicus* is therefore thought to represent a juvenile phase of *L. shimodaensis*, which was recorded from the same locality. Imajima (1985) remarked that those specimens were similar to *L. acuta*, but differed in the number of anterior reduced parapodia, *L. acuta* having about ten reduced anterior parapodia, compared with four to six in *L. acutus japonicus*. The chaetal distribution of *L. acuta* is not comparable with other species because of damage to the anterior parts of the syntypes and consequent loss of most chaetae. The first occurrence of hooks in *L. acuta* has been termed ‘middle body region’ by many authors (Pettibone 1963; Perkins 1979; Miura 1980; Uebelacker 1984). The types of *L. acutus japonicus* are also problematic for the taxonomic identification, because of the loss of many chaetae on the first several parapodia of the holotype. The exact taxonomic status of *L. acutus japonicus* thus remains unclear, despite the type series including damaged juvenile specimens of *L. shimodaensis* (based on
Lumbrinerides from Japan

Biological notes. Some ovigerous specimens were collected from the Irago Strait, off Ago Bay in September 1984 and south part of the Sado Strait in September 1985. The spawning season of this species is therefore thought to be in late summer.

Distribution. Off Shimoda (50–102 m), Irago Strait (120–150 m), off Ago Bay (102–158 m), off Misaki (110–122 m), off Susami, Bungo Channel (72–101 m), South Sado Strait (75–143 m), North Sado Strait (148 m) and around Tsushima (75–125 m), on sandy substrate, reported only in Japan.

Lumbrinerides dayi Perkins, 1979 (Figs 11, 12)

Lumbrinerides dayi Perkins, 1979: 421–423, fig. 1c–e; Miura 1980: 1025–1026, fig. 3B.

Syn. nov.

Material examined. Holotype and paratype of Lumbrinerides hayashii, NSMT-Pol H-195 and NSMT-Pol P-196, respectively, both Wakasa Bay, 10 m, July 1970; 5 paratypes of Lumbrinerides dayi, USNM 55598, Florida, off Panama City, 47 m, coarse carbonate sand, November 1977.

Fig. 12. Chaetal distribution pattern in type specimens for Lumbrinerides hayashii Imajima, 1985 and Japanese comparative specimens identified as Lumbrinerides dayi Perkins, 1979 from off Soma, in 38–46 m depth. Numbers of hooks (closed circle) and limbate chaetae (open circle) per parapodium were plotted for each parapodium from the first to the last chaetigers of fragmented specimens.

Non-type material. (SOMA) (12 immature, 14 juveniles); (IMA A) (one female) and IMA B (one male, one juvenile); (SADO A) Tansei-maru Cruise KT-85-14, Japan Sea, Station F-5 BC-2, (two immature); Station F-5 SM-1 (one immature); Station F-5 SM-2 (one female, one immature).

Diagnosis. Prostomium up to three times longer than wide (Fig. 11A). Two apodous peristomial rings. Six to ten anterior parapodia reduced (Fig. 11A–C), thereafter fully developed (posteriorly from chaetigers 10–12) (Fig. 11D, E). Maxillae I with two well-defined accessory teeth, maxillae II with three teeth (Fig. 11F). Large specimens with more than 3 concentric lines on mandibles considered as adults (Fig. 11G). Bidentate simple hooded hooks beginning on chaetigers 1–6 (Fig. 11H).

Variations. The prostomium length to width proportion in Japanese specimens varied between 1.14–2.23, slightly less than given in the original description, 1.2–3.0. The types of *L. hayashii* are immature and lack considerable posterior portions of the body. The chaetae were generally well preserved and their distribution in the type specimens and other material could be examined in detail (Fig. 12). Specimens collected off Imabetsu and off Soma and referred to this species had two accessory teeth on maxillae I, ten anterior reduced parapodia and simple hooks on chaetiger 1–3, being more intact in chaetal possession. The limbate chaetae started on the first chaetiger as two per parapodium in most specimens, the number becoming three on ca. parapodia 10 to 30–35, subsequently reducing to two on more posterior parapodia and one on ca. parapodia 80–130 (possibly depending on specimen size), and eventually zero on well posterior parapodia (Fig. 12). Hooks numbered two on parapodia 1–10 or somewhat later, one on ca. parapodia 10 to 30–35, and two or three on more posterior parapodia (Fig. 12).

Remarks. In 26 specimens (12 immature, 13 juvenile and one damaged) collected from off Soma, the number of anterior reduced parapodia varied from seven to nine (Fig. 2), but fully developed parapodia were apparent on chaetiger 10–12, as given in the original description of *L. dayi* by Perkins (1979) and also in the description of *L. hayashii* by Imajima (1985). As no significant morphological differences were apparent in other characters between these two species, they are synonymized here. One of two Shimoda specimens recorded as *L. dayi* by Imajima (1985) was reexamined and its identification confirmed.

Biological notes. The spawning season of *L. dayi* is thought to be in summer, based on the collection of an ovig-

Fig. 13. *Lumbrinerides kristiani* sp. nov., paratype (NSMT-Pol P-612: A, B), and holotype (NSMT-Pol H-610: C–J). A, lateral view of anterior end; B, dorsal view of maxillae; C, ventral view of mandibles; D, anterior view of parapodium 1; E, anterior view of Parapodium 5; F, anterior view of parapodium 7; G, anterior view of parapodium 10; H, anterior view of parapodium 18; I, anterior view of parapodium 20; J, anterior view of parapodium 152.
erous female in August 1983 from off Imabetsu and another in September 1985 from south part of the Sado Strait.

**Distribution.** Wakasa Bay (10 m), off Imabetsu (18–21 m), off Soma (38–46 m), South Sado Strait (52–58 m), on sandy substrates, Japan; off Panama City (47 m), off Beaufort (5–20 m), Atlantic coast of US.

*Lumbrinerides kristiani* sp. nov. (Figs 13, 14)

**Material examined.** Holotype: NSMT-Pol H-610, Seisui-Maru Cruise 1984-R-07, Station 402 B (intact female), Irago Strait, 34°20.2′N, 136°60.0′E, 39.2 m, 13 September 1984; 3 paratypes: NSMT-Pol P-611 (one female, two immature), same site as holotype; seven paratypes: NSMT-Pol P-611 (one female, six immature), Station 402 A, same site as holotype; three paratypes: NSMT-Pol P-612 (two females, one immature), Station 502 A, Ago Inlet, 60.0 m, 16 September 1984.

**Non-type material.** (EK A) Seisui-Maru Cruise 1984-R-07, Stations, 201 A (including two immature); 301 A (one immature, one juvenile) and 301 B (three immature, one juvenile); 302 A (one immature, one juvenile) and 302 B (one immature); 402 A (one juvenile); 403 A (two immature, one juvenile) and 403 B (one juvenile); 501 B (one male); 502 B (two immature); 701 B (one immature). (KII A) Tansei-Maru Cruise KT-84-12, Station 11-2 (one immature); 12-1 (one immature). (BUNG) Tansei-Maru Cruise KT-84-12, Stations 31 (three immature); 33 (one immature). Station 12-1 (one immature), (BUNG) Tansei-Maru Cruise KT-84-12, Stations 31 (three immature); 33 (one immature).

**Description.** The holotype is an intact female measuring 20 mm long by 0.47 mm wide with 175 chaetigers.

Prostomium 1.94 times longer than wide. Peristomium comprising two apodous rings (Fig. 13A). First five parapodia reduced (Fig. 13D, E). Postchaetal lobes rounded with a very short projection on central outer edges between chaetigers 5–8 (Fig. 13E, F). Projection becoming larger, fused with basal parts, being digitiform to conical from chaetiger 9 (Fig. 13G–J). Limbatae chaetae broadly limbate at least on first several parapodia, becoming narrower posteriorly. Limbatae chaeta numbering two per parapodium on chaetigers 1–6, three on chaetigers 7–22, two on chaetigers 23–87 and one on chaetigers 88–126 (Fig. 14). A single limbata chaeta on each parapodium on last chaetiger in holotype (Fig. 14). Simple bidentate hooded hooks beginning on chaetiger 1, two per parapodium on chaetigers 1–6, one on chaetigers 7–22, two on chaetigers 23–26, three (sometimes two or four) on chaetigers 27–174 and none on chaetiger 175 in holotype (Fig. 14). Mandibles with four concentric lines on anterior flared end in holotype, but sometimes eight in larger specimens of 0.66 mm width (Fig. 13C). Maxillae I with a single well-defined accessory tooth (Fig. 13B). Maxillae II with three blunt teeth on both plates. Maxillae III lacks defined teeth. Maxillae IV comprising long oval plates without teeth.

**Biological notes.** The spawning season of this species is thought to be in summer since a collection in September 1984 (EK A) included matured specimens with fully developed gametes.

**Variations.** Accessory teeth on maxillae I usually numbered one (rarely two) on one or both sides. In the case of two accessory teeth on each maxilla I, such were intermeshed with only one being well developed whereas the remaining tooth could be recognized only from their internal cavities found in the medulla of maxillae I. The prostomium length to width proportion varied from 1.3 to 2.6. First simple hooks always occurred at the first parapodium, the number of anterior reduced parapodia varying between four and six. Well developed parapodia with prolonged postchaetal lobes began from chaetigers 7–11 (chiefly 9–10).

**Remarks.** This species differs from other Japanese species in having a combination of character states, such as having only one accessory tooth on maxillae I in general, a small number of anterior reduced parapodia and simple hooks starting on chaetiger 1. *Lumbrinerides dayi* differs from the new species in having ten anterior reduced parapodia instead of four to six. One of the specimens identified as *L. dayi* by Imajima (1985) may in fact be referred to this new species, due to having six anterior reduced parapodia, a single accessory tooth on maxillae I and hooks starting on anterior parapodia (parapodium 4 in an Imajima’s damaged specimen).

**Etymology.** The new species is named for Dr Kristian Fauchald, Research Zoologist at the Smithsonian Institution, who encouraged me at the beginning of my scientific research.
life and passed away 4 April 2015.

**Distribution.** Off Hamana Lake (40–41 m), off Tawara (40–61 m), Irago Strait (39–80 m), Ago Bay (39–60 m), off Kumano River (39 m), off Susami, Kii Channel (73–101 m), off Tsukumi, Bungo Channel (72–76 m), on sandy substrates, Pacific coast of Japan; East China Sea (40 m).

**Lumbrinerides tamaii** sp. nov.
(Figs 15–17)


**Material examined.** Holotype: NSMT-Pol H-613 (immature) and 14 paratypes: NSMT-Pol P-614 (14 immature) Tenryu River mouth, 34°38.1′N 137°47.6′E, 5–10 m, 5 May 1983. 19 paratypes: NSMT-Pol P-615 (four males, 15 immature), Tosa Bay, 15 m, 26 November 1980; four paratypes: NSMT-Pol P-616 (one female, three immature), same site, 23 December 1980; 20 paratypes: NSMT-Pol P-617 (20 immature), same site, 8 June 1981.

**Non-type material.** (Tenryu) 14 juveniles, same site and date as holotype; (Tosa N) five juveniles; (Tosa D) one juvenile; (Tosa J) 10 juveniles.

**Description.** The holotype comprises an anterior body fragment (0.76 mm wide) with 71 chaetigers. One of paratypes NSMT-Pol P-615 from Tosa Bay is an incomplete male (ca. 50 mm long, 0.64 mm wide) with 188 chaetigers with some caudal chaetae missing. Another paratype NSMT-Pol P-616 from Tosa Bay in December 1980 is an intact female with a discoidal pygidium (Fig. 15B).

Prostomium length about 1.2 times width in holotype, 1.1–2.7 in paratypes (Figs 2, 15A). Peristomium comprising two apodous rings. First 11 parapodia reduced. Parapodia fully developed posteriorly on chaetiger 12 in holotype and on chaetigers 11–13 in paratypes (Fig. 15G, H). First 11 parapodia with two broadly limbate chaetae in holotype, thereafter three per parapodium becoming two on chaetigers 32–71. Relatively undamaged and smaller paratypes with a single limbate chaeta on each parapodium on posterior chaetigers, eventually being lost (Fig. 16). Holotype with simple bidentate hooded hooks on chaetiger 1 (Figs 16, 17), two per parapodium on first 11 chaetigers, one on chaetigers 12–21, two or three on subsequent chaetigers. Mandibles with five concentric lines in holotype, five to eight in adult paratypes (Fig. 15D). Maxillae I with three weakly projected accessory teeth with pulp cavities in holotype, two or three in paratypes (Fig. 15C). Maxillae II with three blunt intermeshing teeth on both plates.

**Biological notes.** Specimens from Tosa Bay, reported as *Lumbrineriopsis* sp. by Tamai *et al.* (1989), included speci-

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Fig. 15. *Lumbrinerides tamaii* sp. nov., paratype (NSMT-Pol P-616, female: A, B, H) and paratype (NSMT-Pol P-615: C–G). A, anterior end, lateral view; B, posterior end, dorsal view; C, maxillae, dorsal view; D, mandibles, ventral view; E, parapodium 1, anterior view; F, parapodium 10, anterior view; G, parapodium 20, anterior view; H, parapodium 19, anterior view.
Lumbrinerides from Japan

Material examined. Holotype: NSMT-Pol H-618, off Tomakomai, Hokkaido, 42°36.7′N 141°37.6′E, 10–20 m, fine muddy sand, June 1986; 10 paratypes: NSMT-Pol P-619, 10 immature, same site and date as holotype.

Non-type material. (TOMA) 19 juveniles, same site and date as holotype.

Description. The holotype (29.3 mm long by 0.86 mm wide) has 54 chaetigers (many posterior chaetigers lost). Prostomium length 3.13 times width in holotype, greater than twice width in most adults (Fig. 18A). Peristomium comprising two apodous rings. Nine anterior parapodia reduced, subsequent postchaetal lobes becoming larger, fully developed parapodia with prolonged postchaetal lobes starting from chaetigers 11–13 in adults, but from chaetiger 8 in a small juvenile (0.3 mm wide).

Remarks. This species is unique among its congeners in having three accessory teeth on at least one side of Maxillae I (Tamai et al. 1989: 73, fig. 13). The spawning season of this species is thus thought to be in winter.

Variations. The number of accessory teeth on Maxillae I varied between two and three in the Tosa Bay population, the maxillae occasionally having asymmetrical forceps (Fig. 15C). In such a case, the left side tends to have three teeth and the right two. Tosa Bay specimens with two accessory teeth on one side of Maxillae I were dominant (56%), but those with three teeth on both sides were dominant (79%) in the Tenryu River mouth population (Fig. 2). Well-developed parapodia with prolonged postchaetal lobes started from chaetigers 11–13 in adults, but from chaetiger 8 in a small juvenile (0.3 mm wide).

Etymology. The new species is named for Dr K. Tamai who kindly donated specimens collected from Tosa Bay.

Distribution. Tenryu River mouth (10 m); Tosa Bay (15 m), sandy substrate, Pacific coast of Japan.

Lumbrinerides yoshioi sp. nov. (Figs 18, 19)

Material examined. Holotype: NSMT-Pol H-618, off Tomakomai, Hokkaido, 42°36.7′N 141°37.6′E, 10–20 m, fine muddy sand, June 1986; 10 paratypes: NSMT-Pol P-619, 10 immature, same site and date as holotype.

Non-type material. (TOMA) 19 juveniles, same site and date as holotype.

Description. The holotype (29.3 mm long by 0.86 mm wide) has 54 chaetigers (many posterior chaetigers lost). Prostomium length 3.13 times width in holotype, greater than twice width in most adults (Fig. 18A). Peristomium comprising two apodous rings. Nine anterior parapodia reduced, subsequent postchaetal lobes becoming larger, fully developed parapodia on chaetigers 11–13 in adults, but from chaetiger 8 in a small juvenile (0.3 mm wide).

Remarks. This species is unique among its congeners in having three accessory teeth on at least one side of Maxillae I. It also spawns in Winter, unlike, for example, L. shimodaeensis, L. hayashii, and L. kristiani spawning in Summer.

Etymology. The new species is named for Dr K. Tamai who kindly donated specimens collected from Tosa Bay.

Distribution. Tenryu River mouth (10 m); Tosa Bay (15 m), sandy substrate, Pacific coast of Japan.
Biological notes. All of the specimens from Tomakomai lacked a considerable number of posterior chaetigers. Although maturation details are unknown, the presence of some posterior fragments with oocytes in the collection indicated a spawning season near early summer. The collection comprised two clearly defined size classes of specimens (Fig. 2). Eleven larger specimens (0.83–0.99 mm in body width) were thought to be adults, their mandibles having four to nine concentric lines on the cutting edges. The remaining 19 juvenile specimens (0.36–0.66 mm in body width) had two to four such concentric lines.

Variations. The number of anterior reduced parapodia varied from eight to ten in adult specimens and seven to nine in juveniles. The prostomial length to width proportion was slightly higher in larger specimens (1.99–3.42, average 2.39) compared 1.90–3.55 (average 2.34) in juveniles. The first hooded hooks always began on chaetiger 1. The number of accessory teeth on Maxillae I was two in most specimens except for one with three teeth on both forceps. Maxillae II always had three intermeshing teeth in each plate.

Remarks. This new species has a uniquely long prostomium among Japanese species. Although Lumbrinerides acutiformis from Nha Trang also has a very long prostomium, the proportion of length to width is 3.5–4.0, greater than that of adults of the new species (1.99–3.42).

Etymology. The new species epithet is named for Yoshio Miura, my late father, who had been in Tomakomai city and supported in part my stay in France for the lumbrinerid study.

Distribution. Off Tomakomai, Hokkaido (10–20 m), Pacific coast of Japan, known only from the type locality.

Concluding remarks

The statistical analyses of morphological characters of local Japanese populations of the genus Lumbrinerides resulted in the recognition of five species in Japanese waters. Because of variations in morphological characters in different life history stages, only adult or large immature specimens of non-spawning seasons could be classified with certainty. Each species is restricted to preferred depths within geographical areas around Japan. Two groups of Japanese Lumbrinerides species were apparent, a shallow group living...
Lumbrinerides from Japan

in less than 100 m (L. dayi, L. kristiani, L. tamaii, L. yoshioi) and the deeper occurring L. shimodaensis. The two groups were also clearly divided by the chaetiger on which the first hooks arise. The mean number of accessory teeth on maxillae I and number of anterior reduced parapodia tend to become smaller in the deeper sites, such morphological trends apparently being associated with the evolutionary pathway and habitats occupied by each species. Lumbrinerides tamaii is also distinguished from the other Japanese species of Lumbrinerides by spawning in winter, compared with summer in the others.

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References


