A New Miocene Herring, Clupea macrocephala, from Sakaki Town, Hanishina County, Nagano, Japan

Authors: Yabumoto, Yoshitaka, and Nazarkin, Mihkail V.

Source: Paleontological Research, 22(4) : 352-363

Published By: The Palaeontological Society of Japan

URL: https://doi.org/10.2517/2018PR002

Paleontological Research, vol. 22, no. 4, pp. 352–363, October 1, 2018

doi:10.2517/2018PR002

A new Miocene herring, *Clupea macrocephala*, from Sakaki Town, Hanishina County, Nagano, Japan

YOSHITAKA YABUMOTO[1] AND MIHKAIL V. NAZARKIN[2]

[1]*Department of Natural History, Kitakyushu Museum of Natural History and Human History, 2–4–1, Higashida, Yahatahigashi-ku, Kitakyushu 805-0071, Japan (e-mail: yabumoto@kmnh.jp)*
[2]*Zoological Institute, Russian Academy of Sciences, 1 Universiteskaya Emb., St Petersburg 199034, Russia*

Received January 15, 2018; Revised manuscript accepted April 4, 2018

Abstract. A fish fossil found from the Miocene Bessho Formation near Amikake, Sakaki Town, Hanishina County in Nagano Prefecture, central Japan is described as a new species of the genus *Clupea*, *C. macrocephala* of the family Clupeidae of Clupeiformes. This new species differs from other species of the genus in having a large head about 3.4 times in the standard length versus more than 4 times in other species. *Clupea macrocephala* sp. nov. is closer to *Clupea pallasii* than *Clupea harengus* in the number of vertebrae. Presence of the fossil herrings of the genus *Clupea* in the deposits of Pacific basin implies that the origin of this genus, probably, was in the Pacific Ocean in the Miocene.

Key words: *Clupea*, fossil, herring, Japan, Miocene, new species

Introduction

The herrings of the Recent genus *Clupea* (Clupeiformes: Clupeidae) are among the most important objects of the commercial fisheries in the Northern Hemisphere (Whitehead, 1985). They are marine pelagic fishes, forming giant schools, and occurring from the surface to a depth of about 200 m, mainly offshore. Two forms, distinguished within this genus, the mostly Atlantic *Clupea harengus* Linnaeus, 1758, and the mostly Pacific *C. pallasii* Valenciennes, 1847, are considered as a distinct species or as a subspecies by different authors (Svetovidov, 1963; Grande, 1985; Whitehead, 1985). These forms differ in some meristic characters, mostly in the number of vertebrae, which is a little greater in the Atlantic form, and, most importantly, in the biological features of their spawning (Svetovidov, 1963).

Several dozen fossil fish species have been described under the generic name "*Clupea*", but later have been recognized as other taxa of clupeids, clupeomorphs or elsewhere (Grande, 1985). The problem with the identification of fossils as belonging to *Clupea* is that this genus lacks the clear and certain morphological characters which would allow fossils to be assigned to it undoubtedly.

In eastern Asia there is only one fossil species assigned to this genus, *Clupea aenemtensis* Sytchewskaya, 1985, from the Miocene of Kamchatka (Sinelnikova *et al*., 1985). This species was described from seven incomplete skeletons, and was not considered in the revision by Grande (1985).

Previous researches reveal only three fossil representatives of the family Clupeidae from the Neogene of Japan. They are *Eosardinella hishinaiensis* Sato, *Sardinella* sp. and *Sardinops* sp. (Sato, 1966; Ohe, 1993; Yabumoto and Uyeno, 1994), all known from Miocene deposits. In the present study, we describe a new clupeid species of the genus *Clupea* on the basis of a single specimen from the Miocene Bessho Formation near Amikake, Sakaki Town, Nagano, Japan.

Earlier, Uyeno (1979) studied fish fossils from Kurumizawa and Koami near Amikake in Sakaki Town, Hanishina County in Nagano Prefecture, central Japan where the Bessho Formation is distributed. He recognized at least eight species belonging to the families Clupeidae and Englaulidae? of Clupeiformes, sternoptychids of Stomiiformes, macrourids of Gadiformes and the sparoids of Perciformes, *Gymnosarda* sp. of Scombridae and scorpaeniforms. Uyeno (1979) mentioned that the fauna somewhat resembles the present fish fauna of Suruga Bay on the Pacific coast of Honshu in Shizuoka Prefecture, Japan, because it contains pelagic (clupeids), mesopelagic (*Gymnosarda*) and bathypelagic (macrourids and sternoptychids) fishes. The new herring specimen

Table 1. Some diagnostic characters of recent and fossil species of *Clupea*. Data from Svetovidov (1963), Grande (1985), Sinelnikova *et al.* (1985), and Mecklenbourg *et al.* (2002). *, in the percent of the body length to the ends of the medial caudal rays, for comparison with data of Svetovidov (1963). **, data from comparative materials of this paper. Abbreviations: pt., pterygiophores; P.r., pleural ribs; P. v., preural vertebrae.

Characters	*Clupea harengus*	*Clupea pallasii*	*Clupea aenemtensis*	*Clupea macrocephala* sp. nov.
Predorsals	18–19	15–16	—	≧10
Pleural ribs	35–37	34–35	—	35
Preural vertebrae	54–59	52–55	~ 50	52
P.r./P.v. ratio	0.64	0.66	—	0.63
Dorsal fin pt	17–18	17–18	17	18
Anal fin pt	16–18	15–16	~ 18	16
Epurals	2	1–2	—	2
Pre-Dorsal distance*	49.1	49.1	—	48.3
Pre-Anal distance*	72.6	72.6	—	75
Pre-Pelvic distance*	53.7	53.7	—	57.2
Head length*	20.2–25.9	19.0–24.6	<25.0	27.4
Prepelvic scutes**	18	16–17	21–22	~ 18
Postpelvic scutes	12–16	10–14	~ 11	8

described here was not mentioned previously, and came from another locality, Amikake of the Bessho Formation.

Material and methods

The sole specimen, holotype, is deposited in the National Museum of Nature and Science, Tsukuba, with the number PV23963-a, b. The specimen was cleaned by preparation needles under a binocular microscope. All measurements were made using vernier calipers to within 0.1 mm, with the standard body length (*SL*) as the main measurement. The so-called "trade length", i.e., the body length to the ends of the medial caudal rays, is used in Table 1 for comparable values with data of Svetovidov (1963). The number of prepelvic scutes was counted between the pectoral and pelvic fin insertions. Osteology of Recent species was studied by radiographs of specimens from the ichthyological collection of the Zoological Institute of the Russain Academy of Science (ZIN): *Clupea pallasii*, ZIN 54831, Bering Sea, *SL* = 180 mm and ZIN 30347, Sea of Okhotsk, 6 specimens, *SL* = 170–185 mm; *C. harengus*, ZIN 39896, North-West Atlantic, 5 specimens, *SL* = 255–280 mm and ZIN 32225, off England, *SL* = 225 mm.

Paleontological description

Order Clupeiformes Bleeker, 1859
Family Clupeidae Cuvier, 1817
Genus ***Clupea*** Linnaeus, 1758

Type species.—Clupea harengus Linnaeus, 1758.

Clupea macrocephala sp. nov.

Figures 1–4

Holotype.—NSM (National Museum of Nature and Science, Tsukuba) PV23963-a, b, almost complete specimen of the part (a) and the counterpart (b).

Locality and horizon.—The locality of the fossil is Amikake, Sakaki Town, along the Chikuma River where the middle Miocene Bessho Formation is distributed (Figure 1). The type locality of the Bessho Formation is the area along the Yukawa River, which is a branch of the Chikuma River near Bessho Onsen (hot spring) (Honma, 1931). The main part of the Bessho Formation is massive black shale with fossils of whales, dolphins, fishes, mollusks and plants (Kato, 1980). The uppermost part of the formation consists of medium- and coarse-grained sandstone, conglomerate and alternation of sandstone and mudstone. The Bessho Formation overlies the Uchimura

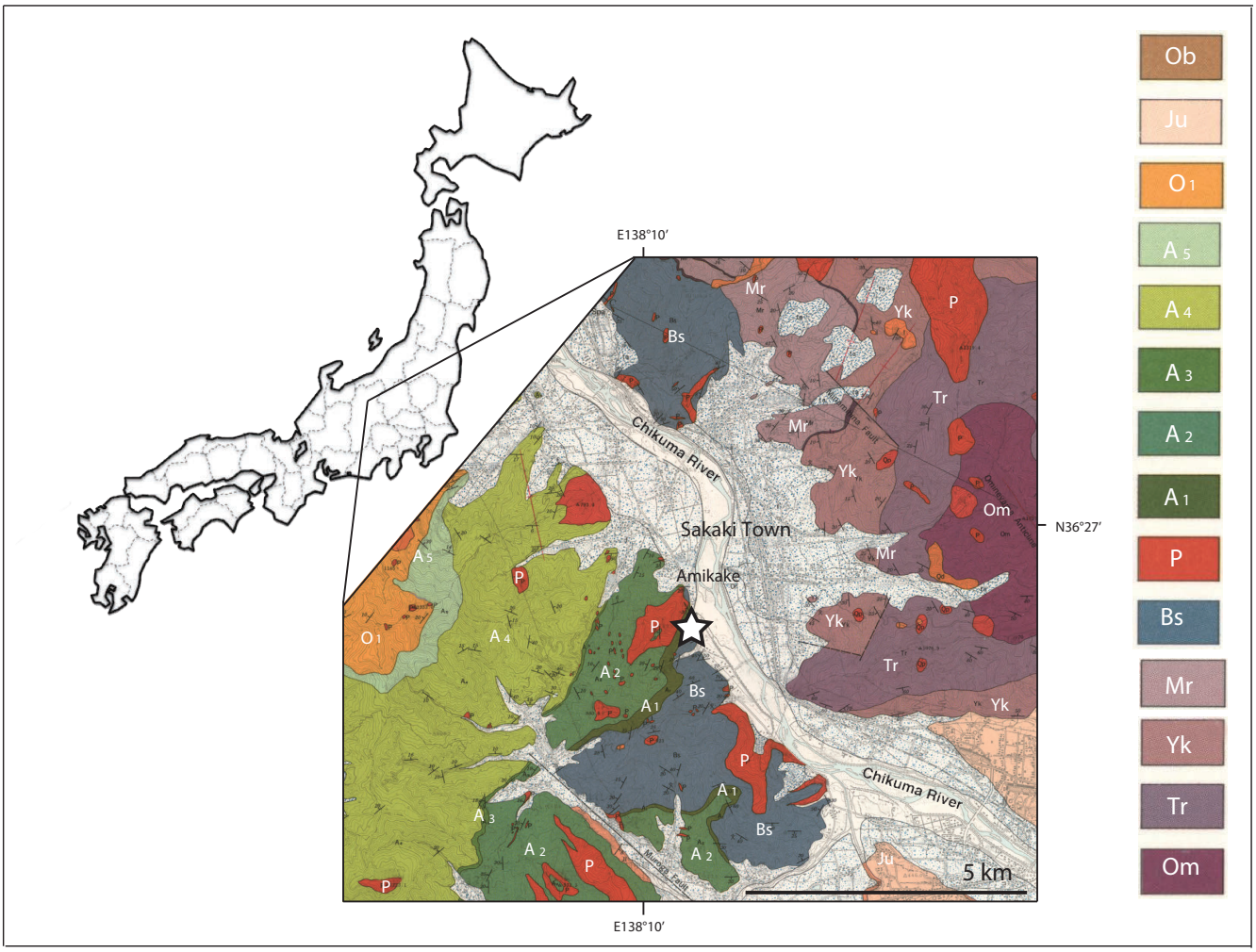

Figure 1. Locality of the holotype, NSMPV23963, *Clupea macrocephala* sp. nov. Abbreviations: A1, lowermost member of Aoki Formation (middle Miocene); A2, lower member of Aoki Formation (middle Miocene); A3, middle member of Aoki Formation (middle Miocene); A4, upper member of Aoki Formation (middle Miocene); A5, uppermost member of Aoki Formation (middle Miocene); Bs, Bessho Formation (middle Miocene); Ju, younger Josho Lake Deposits (Pleistocene); Mr, Mori Member of Uchimura Formation (early Miocene); O1, Sashikiri Member of Ogawa Formation (late Miocene); Ob, Obasute Mudflow (Pleistocene); Om, Omineyama Member of Uchimura Formation (early Miocene); P, Porphyrite of dike and sheet (middle Miocene) (geological map from Kato, 1980).

Formation with conformity and is overlain by the Aoki Formation (Kato, 1980).

Etymology.— *macrocephala* means long head in Greek.

Diagnosis.—The new species is distinguished from other species of the genus *Clupea* by its large head: the standard length about 3.4 times the head length.

Description.—The holotype is an almost complete specimen preserved in the part and counterpart on black shale (Figure 2). The body is compressed because the lateral sides of the specimen are exposed. The estimated total length is 82 mm, the standard length (*SL*) is 71.8 mm. The head is large. The mouth is terminal or somewhat superior, with the mandible slightly protruding. The head is large. The standard length is about 3.4 times the head length and about 3.6 times the body depth. The orbit is large. The head length is 3.9 times the orbit diameter.

The neurocranium is low and wedge-shaped, with its dorsal contour almost straight. The visible portion of the parasphenoid, ahead of the cranial part of the skull, is also straight. The frontal is narrow, triangular, without visible striations of its dorsal surface. The structure of the other cranial bones is not discernible, as well as the condition of the bullae.

The bones of the infraorbital series are not recognizable. The premaxilla is very small. The maxilla is elongated, reaching past the posterior to the front of the orbit,

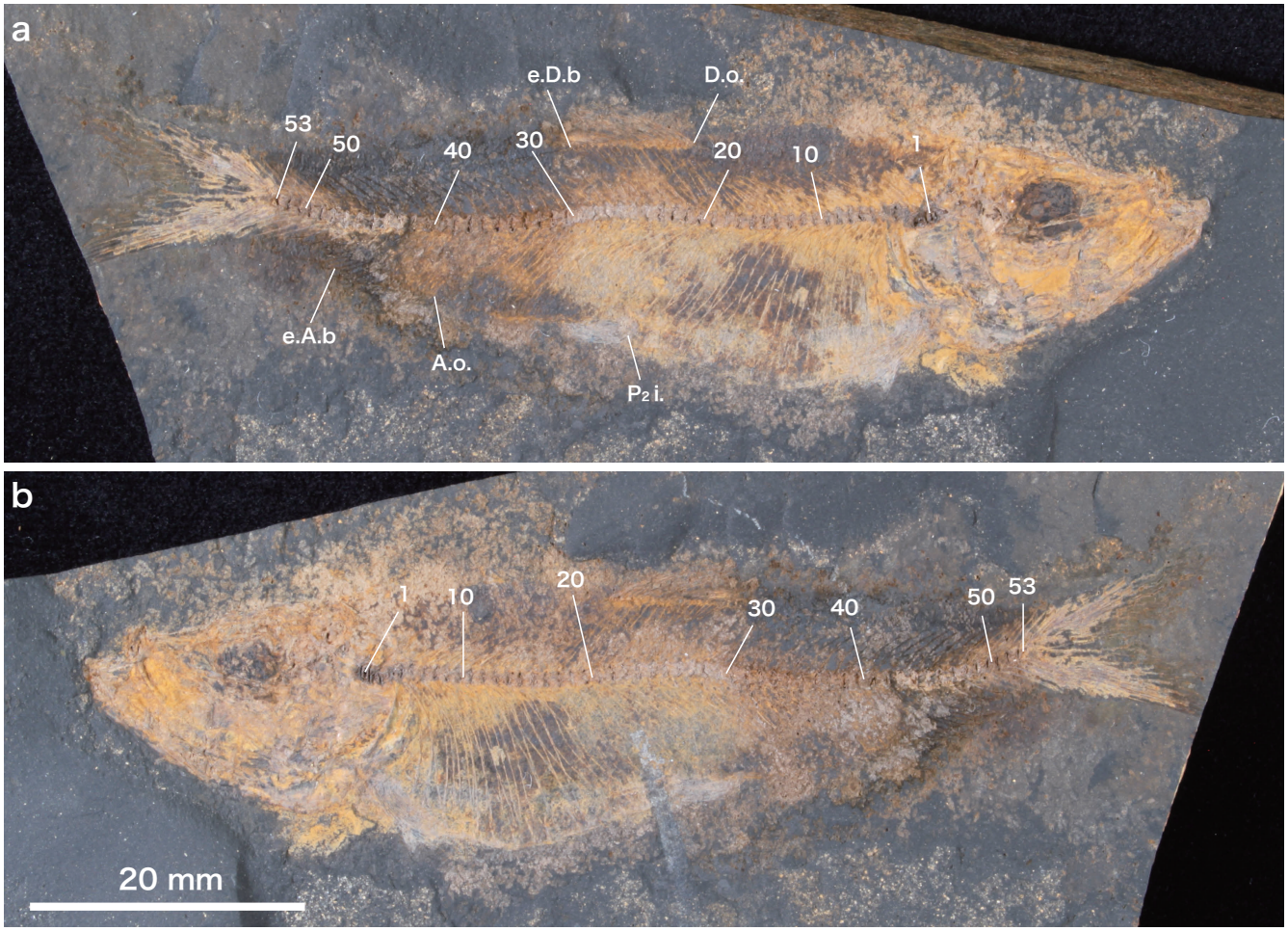

Figure 2. *Clupea macrocephala* sp. nov., holotype. **a,** the part, NSMPV23963-a; **b,** the counterpart, NSMPV23963-b. Arabic numerals show the numbers of centra. Abbreviations: e.A.b., posterior end of the anal fin base; A.o., anal fin origin; D.o., dorsal fin origin; e.D.b., posterior end of dorsal fin base; P_2 i., pelvic insertion.

with a thin anterior arm and strong strut from the anterior tip to the posterior portion (Figure 3). The structure and number of the supramaxillaries are unknown. The mandible is deep and widely triangular. The articulation of the lower jaw is located under and slightly behind the anterior margin of the orbit. There are no traces of the jaw teeth. A part of preopercle and opercle is preserved. The width of the opercle is shorter than its depth. There are no bony radiating striae on its surface. The preopercle is wide, crescentic, with the upper branch slightly longer than the lower one. The quadrate is fan-shaped. Some other bones of the cranium are recognized, however the border of each bone is not clear. The number of branchiostegals is unknown.

There are 54 vertebrae, including the two ural centra, thus the number of preural vertebrae is 52. Of them, 35 are abdominal (Figure 2). The length and the depth of the centra are almost the same, except for two or three anteriormost vertebrae in which the depth exceeds the length. The ribs are slender and long extending almost to the ventral margin of the abdomen. It is difficult to count the ribs, but 33 pairs of pleural ribs are supposed from the number of abdominal vertebrae and the ribs/vertebrae ratio is about 0.63. Epineurals and epipleurals are thin and comparatively short, not longer than 1/8 of the abdominal cavity. These bones can be traced to the 7 or 8 preural vertebrae. There is a series of, at least, 10 supraneurals, which do not reach the dorsal fin base.

The dorsal fin is located slightly behind the middle of the body (Figure 2a). There are 18 slender pterygiophores and at least 19 dorsal fin rays. The height of the longest rays in the anterior part of this fin slightly exceeds the length of the dorsal fin base. The last dorsal fin ray is definitely not elongated (Figure 4a, b). The origin of the dorsal fin is above the 21st centrum and the posterior end of the dorsal fin base is above the 30th centrum. The

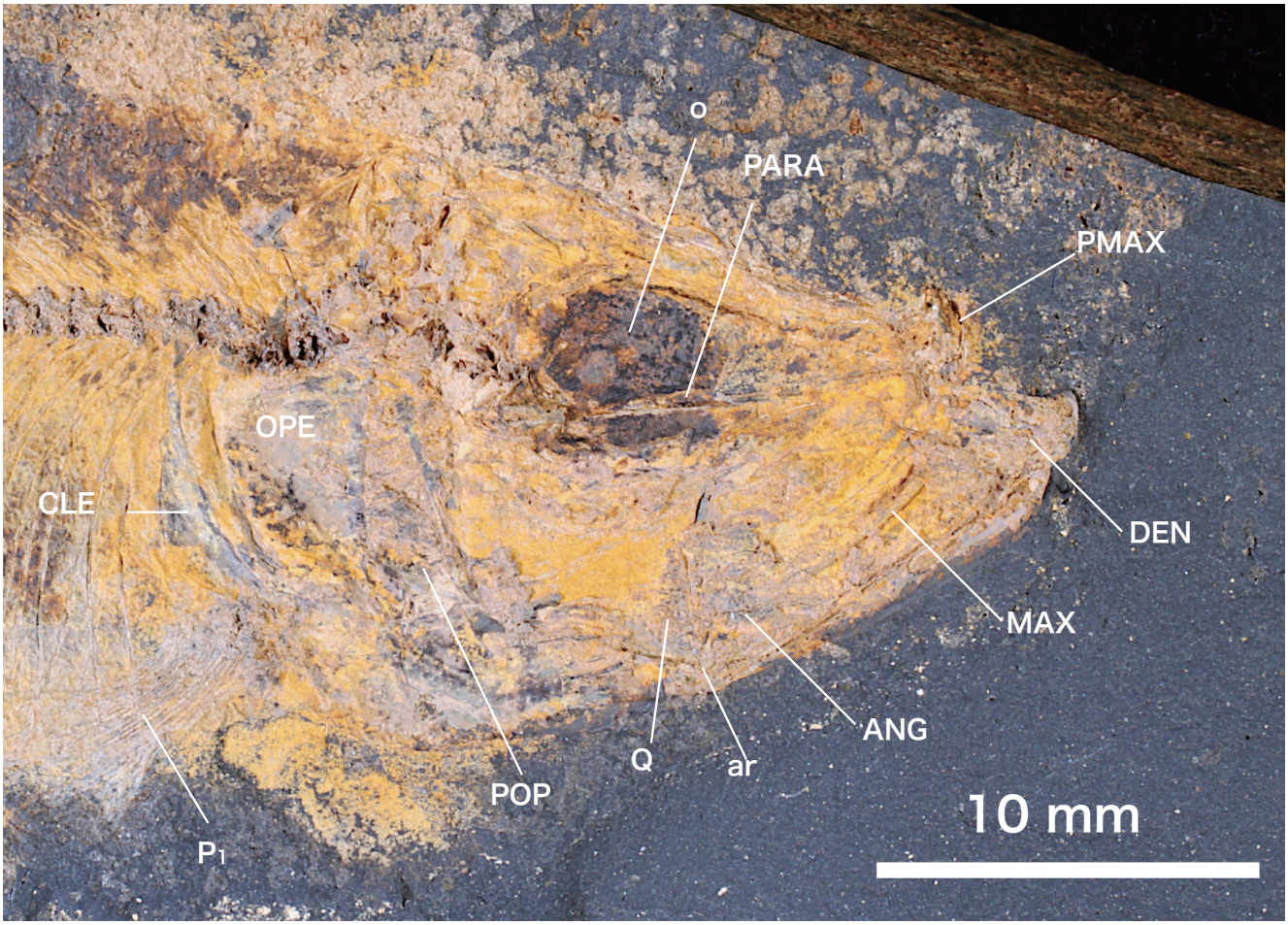

Figure 3. Head of *Clupea macrocephala* sp. nov., holotype, NSMPV23963-a. Abbreviations: ANG, angular-articular; ar, articulation of the lower jaw; CLE, cleithrum; DEN, dentary; MAX, maxilla; o, orbit; OPE, opercle; P_1, pectoral fin; PARA, parasphenoid; POP, preopercle; PREM, premaxilla; Q, quadrate.

insertion of the anterior dorsal pterygiophore is before the neural spine of the 17th vertebra. A long slender stay extending posteriorly is visible behind the last dorsal fin pterygiophore (Figure 4a, b).

The anal fin is located well behind the posterior end of the dorsal fin (Figure 2a). The length of the anal fin base is approximately equal to that of the dorsal fin base. The origin of the anal fin is under the 40th centrum and the posterior end of the anal fin base is under the 47th centrum. Anterior anal fin pterygiophore is positioned before the 36th vertebra. Anal fin pterygiophores number 16; the stay is absent (Figure 4c, d). Seventeen anal fin rays can be counted, at least. The distal parts of the anterior rays are lost and those of other rays are disarticulated, whereas the rays of the last pterygiophore (consisting of two rays) are preserved and not elongated.

The caudal fin is deeply forked, with 9 branched fin rays in the upper, and 8 in the lower lobes (Figure 5). There are 7 unbranched fin rays in the upper and 6 in the lower lobes. The caudal skeleton is typical for clupeoid fishes (see Whitehead, 1985; Grande, 1985). The first hypural is large. The second hypural is slender and fused at the base to the first ural centrum. The third hypural is slightly larger than the first one. The fourth to the sixth hypurals are slender and the fifth one is thinner than the sixth one. The third and fourth hypurals articulate with the second ural centrum. The first uroneural is slender and forms the pleurostyle fused to the first preural centrum. The second and third uroneurals are also slender and located behind the pleurostyle. The third uroneural is short and located above the sixth hypural and behind the second uroneural. Two rod-like epurals are clearly visible ahead of the pleurostyle.

The pectoral base is placed close to the ventral body border, under the vertebrae 2–4. The longest pectoral rays extend to about the anterior one-third of the abdomen

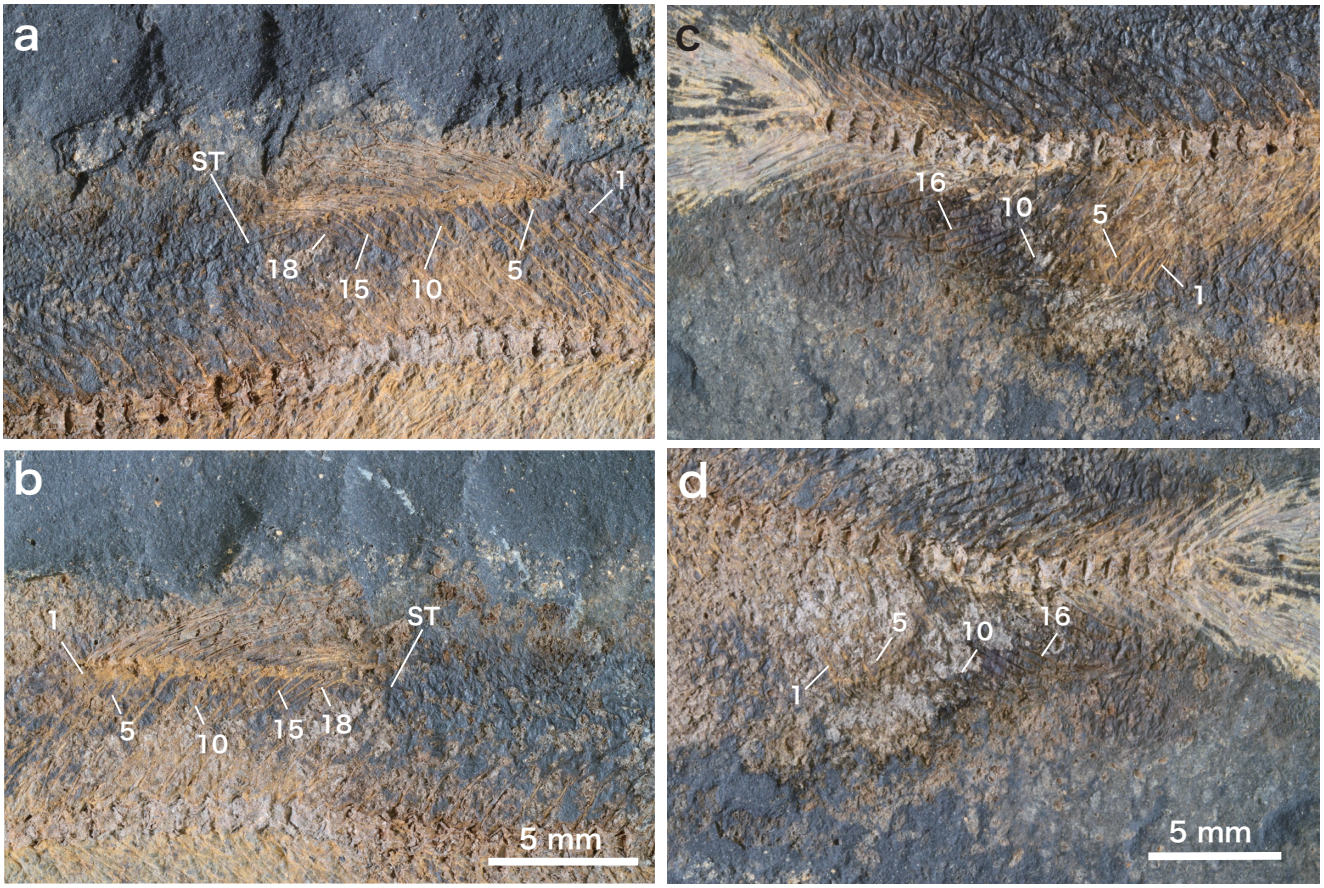

Figure 4. *Clupea macrocephala* sp. nov., holotype. **a,** dorsal fin on NMS 23963-a; **b,** dorsal fin on 23963-b; **c,** anal fin on NMS 23963-a; **d,** anal fin on NMS 23963-b. Arabic numerals indicate the numbers of the pterygiophores. Abbreviation: ST, stay.

(Figure 2). Seventeen or 16 fin rays can be counted. The cleithrum is wide and extends from the vertebral column to the ventral body edge. The postcleithrum is a slender, slightly sigmoidal bone. The other bones of the pectoral girdle are not recognized.

The pelvic fin is abdominal. The distance between the pectoral and pelvic fin insertions is 1.5 time the distance between the pelvic fin insertion and the anal fin origin. The pelvic fin insertion is positioned under the dorsal fin base, slightly ahead of its midpoint, and shows the ventral surface of both sides (Figure 2). There are 6 to 8 rays in each, left and right. The pelvic fin is long and slightly shorter than the pectoral fin. The structure of the pelvic girdle is indiscernible.

The shape and size of body scales are indiscernible. The series of the ventral scutes are well developed and present before (approx. 18 scales) and behind (8 scales) the pelvic fin. The dorsal scutes are absent.

Measurements.—Standard length (*SL*) = 71.8 mm. Percentage with *SL*: body length to the ends of the medial caudal rays, 107.4%; head length, 29.4%; maximum body depth, 27.6%; caudal peduncle depth, 11.6%; predorsal distance, 51.9%; preanal distance, 80.6%; prepectoral distance, 30.0%; prepelvic distance, 61.4%; dorsal fin base, 13.3%; dorsal fin height, 13.9%; anal fin base, 13.5%; caudal fin length, 22.4%; pectoral fin length, 15.2%; pelvic fin length, 9.0%; preorbital length, 10.2%; orbit length, 7.4%.

Comparison.—The new species from Japan is very close to both Recent representatives of the genus, *Clupea harengus* and *C. pallasii* in the body proportions and counts (Figure 6, Table 1). It can be clearly separated from these by its larger head (Figure 7), lower number of abdominal postpelvic scutes, and, probably, by the lower number of supraneurals. The low number of the preural vertebrae makes *C. macrocephala* sp. nov. more similar to the recent Pacific herring *C. pallasii*. It should be noted here that the range in numbers of vertebrae in the two species overlaps more broadly than was shown by Grande (1985) (see Table 1). By the data from Svetovidov (1963),

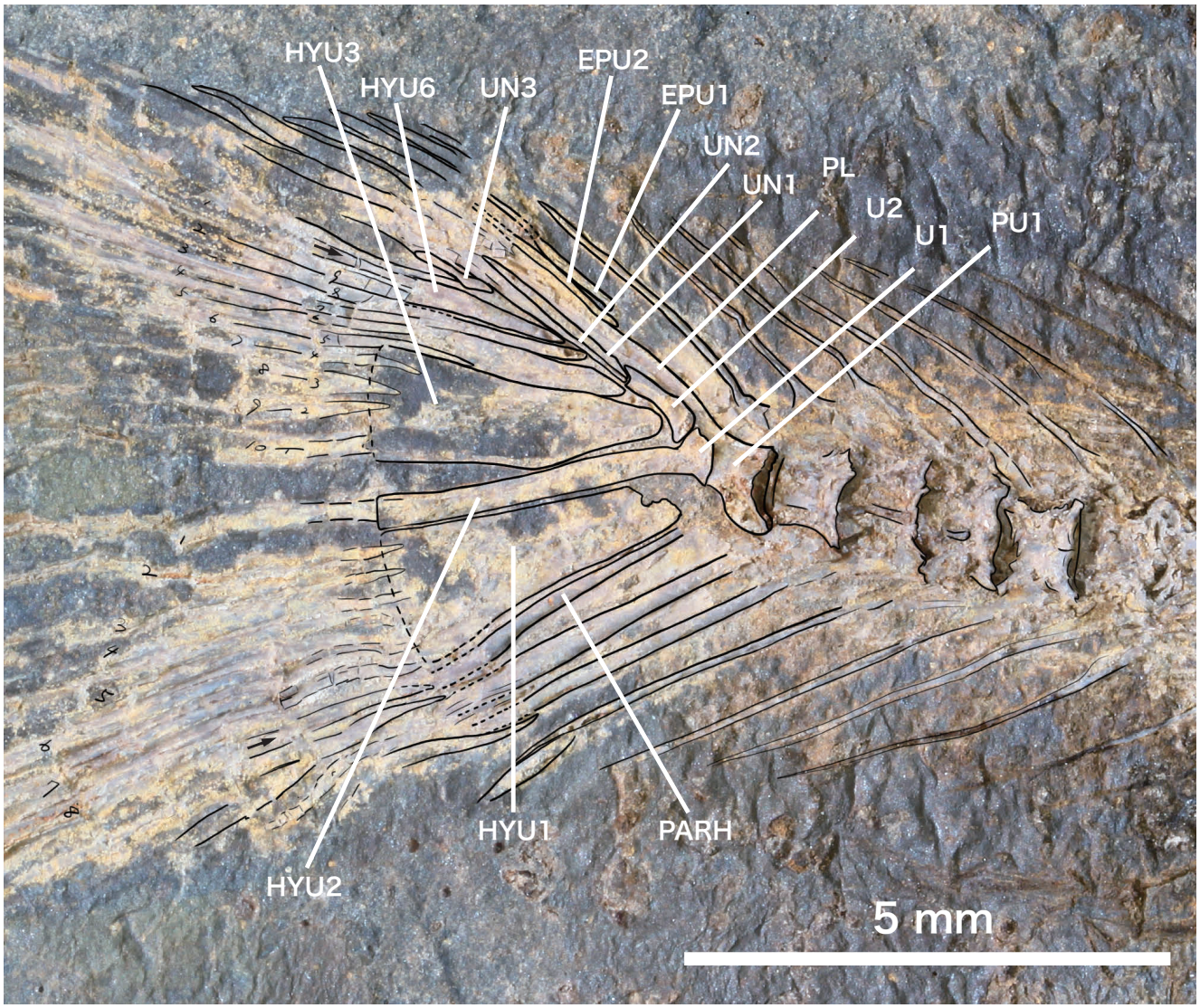

Figure 5. Caudal fin and skeleton of *Clupea macrocephala* sp. nov., holotype, NMS 23963-a. Abbreviations: EPU1, first epural; EPU2, second epural; HYU1, first hypural; HYU2, second hypural; HYU3, third hypural; HYU6, sixth hypural; PARH, parhypural; PL, pleurostyle; PU1, first preuralcentrum; U1, first ural vertebra; U2, second ural vertebra; UN1, first uroneural; UN2, second uroneural; UN3, third uroneural.

the range of this character for the Atlantic species is 51–60, whereas for the Pacific species it is 47–57, if all its populations are considered. At the same time, the prepelvic abdominal scutes of this new species are well developed, as in the Atlantic herring *C. harengus*, whereas they are poorly developed and often are absent in *C. pallasii* (Berg, 1948; Andriashev, 1954). *Clupea macrocephala* sp. nov. well differs from the other fossil eastern Asian species, *C. aenemtensis* from the Miocene of Kamchatka, by the large head, higher number of vertebrae and lower number of prepelvic scutes (Table 1).

Discussion

About 57 genera and 188 Recent species of the family Clupeidae of the order Clupeiformes have been recognized in the world. Clupeidae consists of six subfamilies: Dussumieriinae, Ehiravinae, Pellonulinae, Clupeinae, Alosinae, and Dorosomatinae (Nelson *et al*., 2016). Among them, Dussumieriinae, Clupeinae and Dorosomatinae are distributed in Japan. Furthermore, 34 genera and 118 or more species of fossils have been described from the world (Grande, 1985).

This new species is considered to be a member of Clupeomorpha, as it possesses several abdominal scutes,

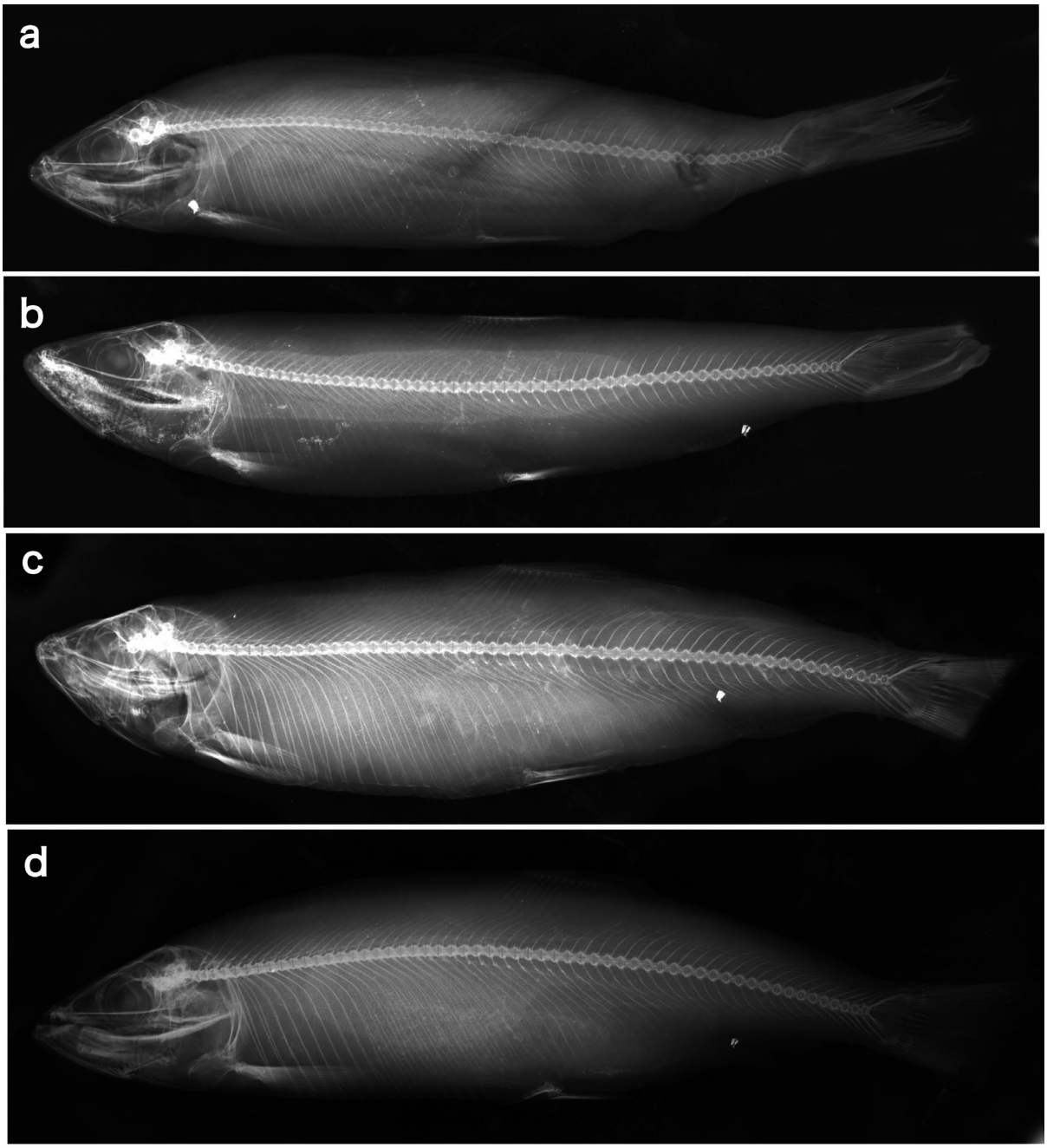

Figure 6. X-ray images of the extant species of the genus *Clupea*. **a,** *Clupea pallasii*, ZIN 54831, Bering Sea, *SL* = 180 mm; **b,** *C. pallasii*, ZIN 30347, Sea of Okhotsk, *SL* = 185 mm; **c,** *C. harengus*, ZIN 32225, England, *SL* = 225 mm; **d,** *C. harengus*, ZIN 39896, Northwest Atlantic, *SL* = 280 mm. Meristic counts and proportional measurements of the specimens are in Appendix 1.

second hypural fused with the first ural centrum, and an autogenous first hypural. Further, the new species is a member of Clupeoidei because of the fusion of the first uroneural with the first preural centrum, and the presence of an autogenous parhypural (see Grande, 1985). The high pleural rib to preural vertebrae ratio (0.63) supports the inclusion of this species within the Clupeoidea. *Clupea macrocephala* sp. nov. should be included to the family Clupeidae because of the absence of the dagger-like teeth inherent for Chirocentridae. This new Miocene species did not possess any characters of the well diagnosed clupeid subfamilies: a peculiar, unkeeled, W-shaped pel-

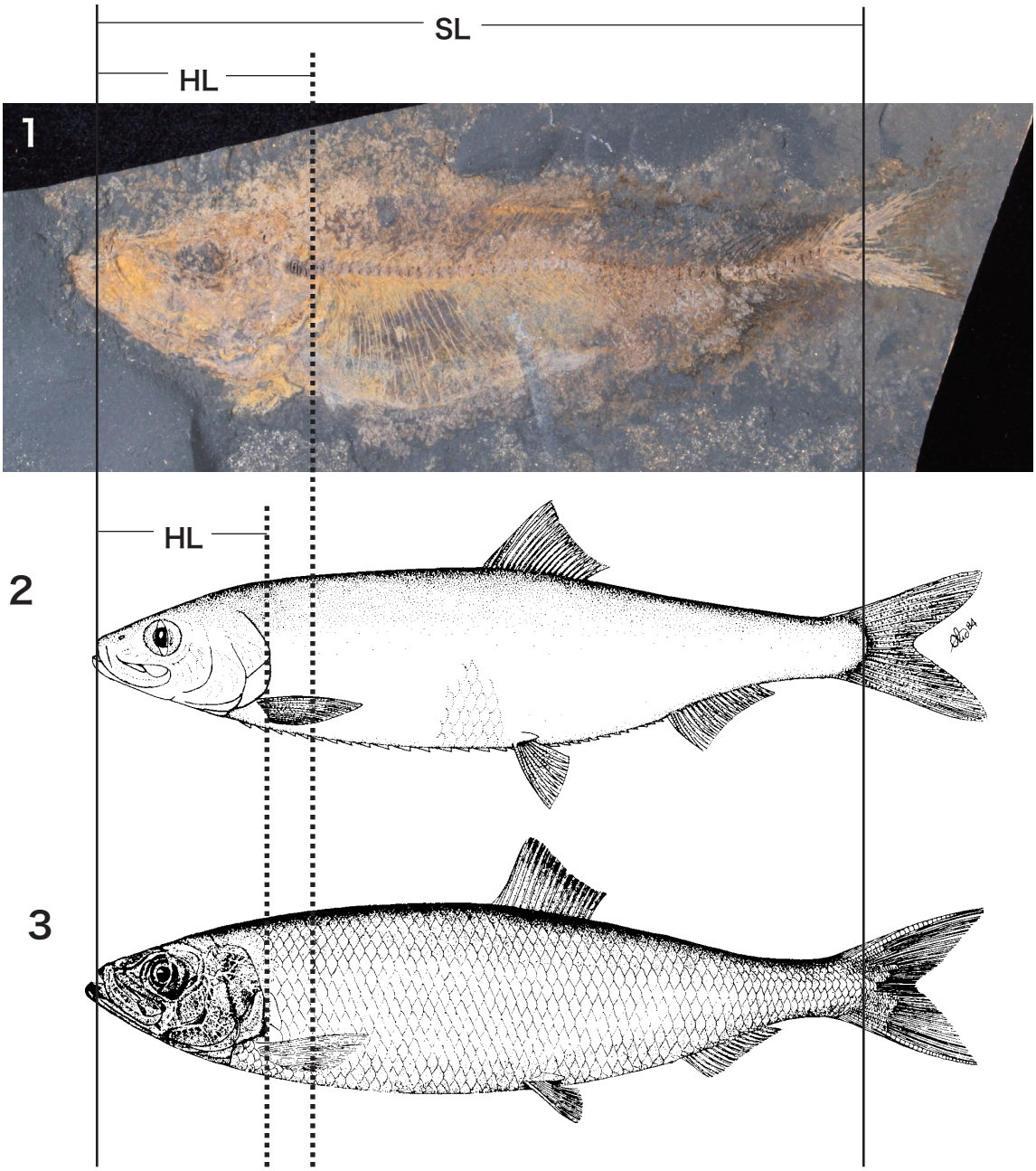

Figure 7. Comparison of head length. **a,** *Clupea macrocephala* sp. nov.; **b,** *C. pallasii* Valenciennes, 1847; **c,** *C. harengus* Linnaeus, 1758 (b and c from Whitehead, 1985). Abbreviations: *HL*, head length; *SL*, standard length.

vic scute (Dussumieriinae), inferior mouth and long filamentous last dorsal-fin ray (Dorosomatinae), complex of paedomorphic features (Ehiravinae), comparatively large body height, enlarged scales (ala) at the base of the caudal fin and well developed scutes on the throat (Alosinae) (Svetovidov, 1963; Grande, 1985; Whitehead, 1985; Nelson *et al*., 2016). This Miocene herring from Japan differs from the genera of Pellonulinae by the absence of well developed pronounced abdominal keel, dorsal scutes and jaw teeth, and by the position of the pelvic fin under the middle of the dorsal base (*vs.* under the beginning of the dorsal base or ahead of it in Pellonulinae). The number of supramaxillaries (diagnostic character of Grande, 1982) is unfortunately unknown. Thus, this new species described here should be treated as a member of the subfamily Clupeinae.

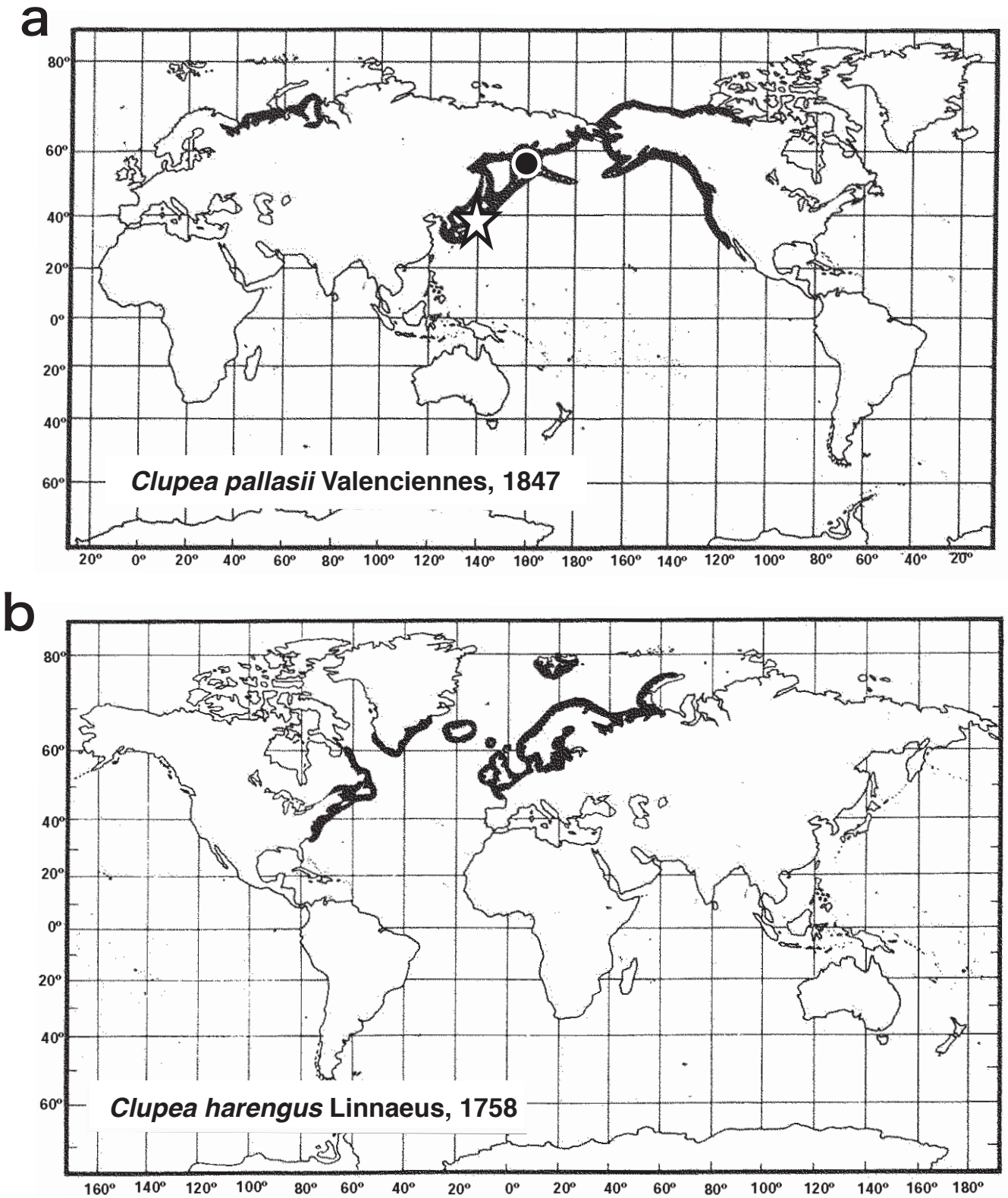

Figure 8. Distribution of Recent species of the genus *Clupea* (bold lines) and localities of *Clupea aenemtensis* (circle) and *C. macrocephala* sp. nov. from Nagano, Japan (star). **a,** *Clupea pallasii* Valenciennes, 1847 and the fossil from Nagano; **b,** *Clupea harengus* Linnaeus, 1758. (maps from Whitehead, 1985).

Within the subfamily Clupeinae the new species is assigned to the genus *Clupea* by the following combination of characters: opercle smooth; fronto-parietal striae on top of head are absent; last dorsal and last two anal fin rays are not enlarged; the abdominal scutes not forming a strong keel and scutes before pectoral fin are absent; the lower jaw joint is placed beneath the anterior portion of the orbit; the dorsal fin origin is immediately behind the middle of body; the pelvic fin base is under the middle of the dorsal base; 18 dorsal fin pterygiophores, 16 anal fin pterygiophores, 52 preural vertebrae and two epurals (see Svetovidov, 1963; Grande, 1985; Whitehead, 1985).

The first opening of the Bering Strait between the Arctic and North Pacific happened about 5 Ma. Since this opening fish faunas from the Atlantic and Pacific could exchange their species through the Arctic. Thus, there was enough time for separation of Atlantic and Pacific populations at the species/subspecies level. The two extant species of the genus *Clupea* are distributed in the northern Pacific Ocean including Japan and the western cost of Russia in the Arctic Sea (*C. pallasii*), and in the northern Atlantic Ocean and the western cost of Russia in the Arctic Sea (*C. harengus*) (Svetovidov, 1963; Whitehead, 1985) (Figure 8). The finding of the second fossil species of the genus *Clupea* in the deposits of the Pacific basin implies that the origin of this genus, probably, was in the Pacific Ocean in the Miocene. The Atlantic herring, then, was derived from that group passed through the Bering Strait into the Arctic Ocean and the Pacific herring was derived from the group that stayed in the Pacific Ocean. Later the Pacific herring migrated through the Bering Strait into the Arctic Ocean and settled in the White, Barents and Kara seas in Russia separated from the population of the Pacific Ocean (Figure 8). However, more extensive paleontological data are required for determining the time and the original basin of these fishes more or less reliably.

Acknowledgements

We are grateful to Makoto Manabe and Gento Shinohara (National Museum of Nature and Science, Tsukuba, Japan) for their kind help with collections. We would like to thank Lance Grande (Field Museum, Chicago, Illinois, USA) for his constructive comments on the manuscript and useful remarks. The study was supported by the Russian Foundation for Basic Research, grant 17-04-00596 a, and JSPS KAKENHI Grant Number JP26400506.

References

Andriashev, A. P., 1954: *Fishes of the Northern Seas of the Soviet Union*, 566 p. Akadiya Nauk SSSR, Moscow. (*in Russian; original title translated*)

Berg, L. S., 1948: *Freshwater Fishes of the USSR and Adjacent Countries*, 504 p. Zoological Institute of the Academy of Sciences of the U.S.S.R., Guide to the Fauna of the USSR, vol. 1. Moskow-Leningrad, Israel Program for Scientific Translations, Jerusalem. (*English translation from 1948 Russian original*)

Bleeker, P., 1859: Enumeratio specierum piscium hucusque in Archipelago indico observatarum, adjectis habitationibus citationibusque, ubi descriptiones earum recentiores reperiuntur, nec non speciebus Musei Bleekeriani Bengalensibus, Japonicis, Capensibus Tasmanicisque. *Acta Societatis Regiae Scientiarum Indo-Neêrlandicae* [= *Verhandelingen der Natuurkundige Vereeniging in Nederlandsch Indië*], vol. 6. p. i–xxxvi + 1–276.

Cuvier, G. L. C. F. G., 1817: *Le Règne Animale Distribué d'après son Organisation, pour Servir de Base à l'Histoire Naturelle des Animaux et d'Introduction à l'Anatomie Comparée*, *Tome 2*, 532 p. Deterville, Paris.

Grande, L., 1982: A revision of the fossil genus *Knightia*, with a description of a new genus from the Green River Formation (Teleostei, Clupeidae). *American Museum Novitates*, no. 2731, p. 1–22.

Grande, L., 1985: Recent and fossil clupeomorph fishes with materials for revision of the subgroups of clupeoids. *Bulletin of the American Museum of Natural History*, vol. 181, p. 231–372.

Honma, F., 1931: *Geology of the Central Part of Shinano, Japan*, 331 p. Kokon Shoin, Tokyo. (*in Japanese; original title translated*)

Kato, H., 1980: *Geology of the Sakaki district. Quadrangle Series, scale 1:50,000*, ii+57 p. Geological Survey of Japan, Tokyo.

Linnaeus, C., 1758: *Systema Naturae per Regna Tria Naturae, Secundum Classis, Ordines, Genera, Species cum Characteribus, Differentiis, Synonymis, Locis, Editio decima, reformata*, 824 p. Laurentius Salvius, Holmiae (Stockholm).

Nelson, J. S., Grande, T. C. and Wilson, M. V. H., 2016: *Fishes of the World. Fifth edition*, xli+702 p. John Wiley and Sons, Inc., Hoboken.

Ohe, F., 1993: Osteichthyes. Deep fish assemblage from the Middle Miocene Morozaki Group, southern part of Chita Peninsula, Aichi Prefecture, central Japan. *In*, Tokai Kaseki Morozakiso Kankokai (Tokai Fossil Morozaki Group Publication Society) *ed.*, *Fossils from the Miocene Morozaki Group*, p. 169–262. Tokai Fossil Society, Nagoya.

Sato, Y., 1966: A new genus and species of sardine from the Miocene Hishinai Formation, northeastern Japan. *Japanese Journal of Ichthyology*, vol. 13, p. 112–126.

Sinelnikova, V. N., Bratzeva, G. M., Dubrovo, I. A. and Sytchewskaya, E. K., 1985: Biostratigraphic characteristic of the Miocene of Kavran outcrop of Kamchatka (molluscs, flora and desmostylids). *In*, Puscharovsky, Yu. M. and Gladenkov, Yu. B. *eds.*, *Correlation of the Cenozoic beds of the Far East, Part 1*, p. 84–156. Geological Institute of the Academy of Sciences of the USSR, Moscow. (*in Russian*)

Svetovidov, A. N., 1963: *Fauna of the USSR. Fishes, 2 (1), Clupeidae*, 428 p. Zoological Institute of the Academy of Sciences of the USSR. New series, vol. 48. Moskow-Leningrad, Israel Program for Scientific Translations, Jerusalem. (*English translation from 1952 Russian original*)

Uyeno, T., 1979: Fish fossils of the Bessho Formation in Sakaki Town, Nagano Prefecture. *In*, Akahane, S., Uyeno, T., Matsuo, H. and Kurumizawa Fossil Excavation Research Group *eds.*, *Report of the Survey of the Kurumizawa Fossil Assemblage from Sakaki Town, Hanishina, Nagano Prefecture, Japan*, p. 5–12. Sakaki-machi Board of Eduction, Sakaki. (*in Japanese; original title translated*)

Valenciennes, A., 1847: *Histoire Naturelle des Poissons, vol. 20*, 472 p. Chez F. G. Levrault, Paris.

Whitehead, P. J. P., 1985: FAO species catalogue, vol. 7. Clupeoid fishes of the world (suborder Clupeoidei). An annotated and illustrated catalogue of the herrings, sardines, pilchards, sprats, shads anchovies and wolf-herrings. Part 1. Chirocentridae, Clupeidae and Pristigasteridae. *FAO Fisheries Synopsis*, no. 125, vol. 7, part 1, p. i–x + 1–303.

Yabumoto, Y. and Uyeno, T., 1994: Late Mesozoic and Cenozoic fish faunas of Japan. *Island Arc*, vol. 3, p. 255–269.

Author contributions

Y. Y. and M. V. N initiated the study and examined the specimen together. Y. Y. was primarily responsible for the taxonomic aspects and made a first draft of this manuscript and M. V. N. added many parts of the description and took x-ray images of extant species of the genus *Clupea* for Figure 6 and made Table 1. All authors contributed to the writing of the paper.

Appendix 1. Meristic counts and proportional measurements of the specimens in Figure 6. Abbreviations: AC, body length from the tip of snout to the ends of medial caudal fin rays; HL, head length; pre-A, pre-anal distance; pre-D, pre-dorsal distance; pre-P_2, pre-plevic distance.

Clupea pallasii, ZIN 54831 (Figure 6a), preural vertebrae = 54 (36+18), pleural ribs from 3 to 35 = 33, ribs/vertebrae ratio = 0.61, supraneurals ≧ 12, intermusculars to the pu7-pu8, epurals = 2, dorsal pterygiophores = 16+stay, anal pterygiophores ÷ 12, pre-pelvic scutes = 23, post-pelvic scutes = 10. Percentage with AC: pre-D = 45.6%; pre-A = 71.6%; pre-P_2 = 52.4%; HL = 18.8%.

Clupea pallasii, ZIN 30347 (Figure 6b), preural vertebrae = 55 (37+18), pleural ribs from 3 to 37 vertebrae = 35, ribs/vertebrae ratio = 0.64, supraneurals ÷ 12, intermusculars to the pu5-pu6, epurals = 2, dorsal pterygiophores = 18+stay, anal pterygiophores = 16, pre-pelvic scutes = 24, post-pelvic scutes = 11. Percentage with AC: pre-D = 48.0%, pre-A = 74.1%, pre- P_2 = 55.5%, HL = 22.0%.

Clupea harengus, ZIN 32225 (Figure 6c), preural vertebrae = 57 (40+17), pleural ribs from 3 to 40 vertebrae = 38, ribs/vertebrae ratio = 0.67, supraneurals = 19, intermusculars to the pu4, epurals = 2, dorsal pterygiophores = 18+stay, anal pterygiophores = 14, pre-pelvic scutes = 24, post-pelvic scutes ÷ 8. Percentage with AC: pre-D = 48.5%, pre-A = 73.7%, pre- P_2 = 53.7%, HL = 18.7%.

Clupea harengus, ZIN 39896 (Figure 6d), preural vertebrae = 56 (38+18), preural ribs from 3 to 37 vertebrae = 35, ribs/vertebrae ratio = 0.63, supraneurals = 17, intermusculars to the pu5-pu6, epurals = 2, dorsal pterygiophores = 18+stay, anal pterygiophores = 15, preventral scutes = 22, postventral scutes = 10. Percentage with AC: pre-D = 52.1%, pre-A = 72.0%, pre-P_2 = 54.0%, HL = 21.1%.