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A NEW LIGHTFISH, †*VINCIGUERRIA ORIENTALIS*, SP. NOV. (TELEOSTEI, STOMIIFORMES, PHOSICHTHYIDAE), FROM THE MIDDLE MIOCENE OF SOUTH KOREA

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ABSTRACT—A new fossil species of miniature lightfish, †*Vinciguerria orientalis*, sp. nov., is described from the middle Miocene beds of the Duho Formation, South Korea. This is the second extinct species of this genus described from skeletal remains. The new Neogene species is very similar to recent congeners in its general appearance, morphometrics, and body proportions. It is characterized by a combination of the following features: 37–40 vertebrae, 13–16 dorsal fin rays, 13–17 anal fin rays, 13–16 photophores in the ventral series from the pectoral fin base to the pelvic (ventral) fin base, 14 or 15 photophores in the ventral series from the anal fin base to caudal fin base of the ventral series, ca. 26 gill rakers, and a caudal body part length of more than 30% of standard length. The main difference separating †*Vinciguerria orientalis* from all other representatives of the genus is the lack of fusion between hypurals 1 and 2 and hypurals 3 and 4 and the separation of the urostylar centrum from hypural elements. This caudal skeleton structure appears to be a transition link between the Paleogene and Neogene–Recent species of this evolutionary lineage.

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INTRODUCTION

The middle Miocene Duho Formation (DF), located in the vicinity of Pohang City in southeast South Korea, is well known due to the exceptionally preserved fossils of marine and terrestrial organisms, especially plants (Chun, 2004; Kim, 2009; Seong et al., 2009). Fossils from the DF have been studied since the beginning of the 20th century (Tateiwa, 1924). These studies resulted in the descriptions of significant numbers of fossil echinoderms, mollusks, marine arthropods, and terrestrial insects (Seong et al., 2009; Kim and Lee, 2011; Lee, 2014). At the same time, data on fossil fishes from these beds are still very scarce. The presence of fish fossils in DF deposits has been noted in several reports on the stratigraphy or paleontology of South Korea (Um et al., 1964; Yun, 1986; Kim and Paik, 2013; Lee et al., 2014). More recently, a few fossil fishes have been described (Ko, 2016; Ko and Nam, 2016; Nam and Nazarkin, 2018). During joint research on the Neogene fish fauna of South Korea, we concluded that the DF fossil ichthyofauna contains at least 17 fish species belonging to 12 orders (Nam and Nazarkin, 2019). The mesopelagic dwellers, such as lanternfishes Myctophidae and lightfishes Phosichthyidae, are predominant and account for more than 50% of all fish remains collected to date. The goal of this paper is to describe a new species of lightfish of the genus *Vinciguerria*, the second largest group of fish fossils in the DF after the myctophids.

There are five species of *Vinciguerria* (Phosichthyidae) in the modern fauna (Gorbunova, 1972). The recent lightfishes of this

genus are among the most abundant mesopelagic fishes, and they are frequently caught in large numbers by pelagic trawls (Gorbunova, 1972). *Vinciguerria* is probably one of the most abundant in terms of individuals of any vertebrate genus (Parin, 1988; Nelson et al., 2016). The body size of these lightfishes is very small and, apparently, does not exceed 78 mm total length (Fadeev, 2005). Externally, they are characterized by a moderately elongated body with short-based dorsal and anal fins; the beginning of the first of these fins is slightly behind the middle of the body, whereas the beginning of the last one is under the middle or rear part of the dorsal fin base; the small, short-based adipose fin is present; the pectoral fin base is low on the body, just behind the gill cover; the pelvic fin is slightly anterior to the dorsal fin; the scales are cycloid, roundish, and deciduous; the eyes are big and round; the mouth is oblique, large, with the lower jaw articulation behind the eye; and the jaw teeth are of different sizes, but without the regular alteration of large and small teeth (Grey, 1960, 1964; Gorbunova, 1972; Badcock, 1984). Like other members of their family, the species of this genus possess two rows of serial photophores on the body, extending from the isthmus to the caudal fin base, along with several separate photophores on the head (Grey, 1964; Morrow, 1964; Gorbunova, 1972; Ahlstrom et al., 1984). In contrast to other phosichthyans, in the caudal fin skeleton of *Vinciguerria*, the terminal vertebra is fused to the hypural bones and hypurals 1 and 2, and hypurals 3 and 4, are fused together (Weitzman, 1967; Borodulina, 1982; Fujita, 1990; Harold, 1998); this characteristic is considered unique to the genus (Harold and Weitzman, 1996).

Vinciguerria species are widespread in the tropical, subtropical, and temperate zones of all oceans, between approximately the 40th latitudes of both hemispheres (Grey, 1964; Gorbunova, 1972; Badcock, 1984). They are members of a sonic scattering layers community, and like other fishes of this community they

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are involved in vertical daily migrations. Usually, they inhabit the upper water layer to a depth of 600 m, rising to the surface in the dark to follow their small crustacean prey (Gorbunova, 1972). An unusual behavior, with a part of schooling fishes remaining near the surface during daytime, has been observed for some species (Marchal and Lebourges, 1996; Cornejo and Koppelman, 2006). The species of *Vinciguerria* are an important forage item for many larger fishes such as tuna, making up an essential part of their diet (Gorbunova, 1972; Marchal and Lebourges, 1996). They have a relatively short life span, with maximum age of about 2 or 3 years (Gorbunova, 1972; Fadeev, 2005).

Several fossil phosichthyids, known by skeletal remains from the Tertiary of Europe, were initially described under the generic name '*Vinciguerria*' (Daniltshenko, 1946, 1960, 1962, 1980; Bogachev, 1961; Ciobanu, 1977; Bannikov and Parin, 1997). Prokofiev (2001, 2002, 2005) later revised these fossil taxa and synonymized some of them. Furthermore, he proposed two new genera for the Paleogene forms of '*Vinciguerria*': †*Sychevskia* Prokofiev, 2002, with one species, †*S. distincta* (Daniltshenko, 1962), from the middle Eocene of Georgia, and †*Eovinciguerria* Prokofiev, 2002, with one species, †*E. obscura* (Daniltshenko, 1946), from the early Oligocene of the Caucasus and Carpathian Mountains (Prokofiev, 2005). The main differences between these genera and *Vinciguerria* are in the comparatively primitive structure of the caudal fin support: all hypural elements are separated from each other and from the terminal vertebrae, the second ural center is present (although strongly reduced in some specimens), and there are two or three epurals instead of one. The Neogene forms were combined into one species of *Vinciguerria* itself, †*V. merklini* Daniltshenko, 1946, from the Miocene of the Crimea, the Caucasus, and the Carpathian Mountains (Prokofiev, 2005). This is the sole extinct species of *Vinciguerria* known hitherto by its skeletal remains. Fossil *Vinciguerria* sp. was recorded in the Pliocene of Italy (Sorbin, 1988:pl. 6, fig. 1). Some recent species are also known as fossils: skeletons of *V. poweriae* (Cocco, 1838) and *V. attenuata* (Cocco, 1838) were described from the Pliocene and Pleistocene deposits of the Mediterranean Basin (Landini and Menesini, 1978, 1986). Fossil skeletons of the representatives of the genus were also recorded in the Pacific Basin: at least two forms, *Vinciguerria* sp. and *V. cf. lucetia*, came from the middle Miocene Yamami Formation in Japan (Ohe, 1993; Yabumoto and Uyeno, 1994). Unfortunately, these fossils have not been described in detail and thus cannot be fully classified.

Isolated otoliths referred to *Vinciguerria* spp. are known from the late Eocene–Pliocene of central and southern Europe (Prochazka, 1893; Steurbaut, 1984; Nolf and Brzobohaty, 1994, 2002; Brzobohaty and Nolf, 2002; Girone and Nolf, 2009; Agiadi et al., 2013). Among them, at least four otolith-based species were described from the late Eocene–Miocene of Italy, France, and the Czech Republic (Prochazka, 1893; Brzobohaty, 1982; Nolf and Brzobohaty, 2002; Girone and Nolf, 2009). Most of the Miocene and Pliocene otolith records were identified as belonging to the recent species *V. poweria* or to *Vinciguerria* sp. (Nolf and Brzobohaty, 2002; Brzobohaty and Nolf, 2002; Agiadi et al., 2013).

Institutional Abbreviations—GNUE, Gongju National University of Education, Daejeon, South Korea; KIGAM, Korea Institute of Geoscience and Mineral, Daejeon, South Korea; NSMT, National Museum of Nature and Science, Tokyo, Japan; ZIN, Zoological Institute, Russian Academy of Sciences, St. Petersburg, Russia; ZMMU, Zoological Museum of Moscow State University, Moscow, Russia.

Anatomical Abbreviations—**ar**, anguloarticular; **br**, photophores of BR series; **brs**, branchiostegals; **chy**, ceratohyal; **clt**, cleithrum; **cor**, coracoid; **d**, dentary; **ecp**, ectopterygoid; **ehy**, epihyal; **epn**, epineurals; **eu**, epural; **fr**, frontal; **h1–6**, hypurals 1–6; **hh**, hypophyals; **hm**, hyomandibular; **md**, mandible; **mx**, maxilla; **npu2**, neural spine of the second preural vertebra; **op**, opercle;

orb, photophores of ORB series; **phy**, parhypural; **plr**, pleural ribs; **pmx**, premaxilla; **pop**, preopercle; **pp1–3**, proximal pterygiophores 1–3; **prs**, parasphenoid; **ptt**, posttemporal; **q**, quadrate; **scl**, supracleithrum; **smx a**, supramaxilla anterior; **smx p**, supramaxilla posterior; **sn**, supraneural; **sop**, subopercle; **sy**, symplectic; **uh**, urohyal; **un**, uroneural; **ur**, urostylar centrum.

Other Abbreviations—**A**, number of anal fin rays; **aA**, preanal length; **AC**, anal-caudal; **aD**, predorsal length; **Ah**, anal fin height; **Al**, anal fin base length; **aO**, snout length; **aP**, preopercular length; **Cl**, caudal fin length; **D**, number of dorsal fin rays; **DA**, dorsoanal distance; **Dh**, dorsal fin height; **DI**, dorsal fin base length; **Gr**, number of gill rakers; **H**, greatest body depth; **hc**, caudal peduncle depth; **HL**, head length; **Lcd**, caudal body part length; **IP**, pectoral fin length; **IV**, pelvic fin length; **Mdb**, lower jaw length; **Mxl**, upper jaw length; **O**, orbit length; **PI**, number of pectoral fin rays; **P2**, number of pelvic fin rays; **P1P2**, pectoventral distance; **VA**, ventroanal distance; **Vc**, number of caudal vertebrae; **Vp**, number of precaudal vertebrae; **VT**, total number of vertebrae.

MATERIALS AND METHODS

The materials studied include 61 complete, or nearly so, fish skeletons collected by the first author from the middle Miocene Duho Formation and deposited in the collections of the KIGAM and GNUE. The matrix was removed from the fossils by needles under a stereomicroscope. Measurements were made with dial calipers to the nearest 0.1 mm. Standard length (SL) is used throughout. The osteology of recent species was studied by radiographed (x-r) and cleared and stained (c-s) specimens from the collections of ZIN, ZMMU, and NSMT. Extinct taxa are marked with a dagger symbol. The nomenclature of photophores follows Morrow (1964), Ahlstrom et al. (1984), Badcock (1984), and Prokofiev (2005).

Comparative Material Examined—The following specimens of *Vinciguerria* species were studied: *V. lucetia* (Garman, 1899), ZMMU P 13740, 2 specimens, 57.0 and 58.5 mm SL (x-r, c-s); *V. nimbaria* (Jordan and Williams in Jordan and Starks, 1895), ZIN uncataloged, 2 specimens, 48.0 and 51.5 mm SL (x-r, c-s); ZIN 36775, 1 specimen, 25.3 mm SL (x-r); ZIN 49394, 1 specimen, 51.1 mm SL (x-r); NSMT-P 76519, 1 specimen, 36.0 mm SL (x-r); NSMT-P 35397, 2 specimens, 42.0 and 44.0 mm SL (x-r); †*V. merklini* Daniltshenko, ZIN 447p-j, 1 specimen, 33.5 mm SL.

SYSTEMATIC PALEONTOLOGY

Order STOMIIFORMES sensu Harold and Weitzman, 1996
Infraorder PHOTICHTHYA sensu Harold and Weitzman, 1996

Family PHOSICHTHYIDAE Weitzman, 1974

Genus *VINCIGUERRIA* Jordan and Evermann in Goode and Bean, 1896

VINCIGUERRIA ORIENTALIS, sp. nov.
(Figs. 1–6)

Holotype—KIGAM 9A169, complete articulated skeleton, 51.5 mm SL (Fig. 1A).

Paratypes—KIGAM 9A170, 38.3 mm SL (Fig. 1C); KIGAM 9A171, 33.7 mm SL; KIGAM 9A172, 39.2 mm SL; KIGAM 9A173, 29.5 mm SL; KIGAM 9A174, 47.3 mm SL; KIGAM 9A175, 47.0 mm SL (Fig. 1B); KIGAM 9A176, 38.8 mm SL (Fig. 1D); all complete articulated skeletons, most in part and counterpart.

Referred Specimens—Fifty-three complete or partly disarticulated specimens, 13.0–52.1 mm SL, in the collection of GNUE: 32003, 32007, 32009–32013, 32015–32028, 32030, 32034, 32035, 32037, 32039–32045, 32047–32052, and 32054–32068.

Type Locality and Horizon—The materials described herein were collected from three outcrops (industrial pits or road cuts)

in Pohang City, South Korea. The fossiliferous beds belong to the Duho Formation and are composed mainly of dark gray, slightly laminated mudstones, whitening from the surface. They were formed during the gradual subsidence of suspended pelagic sediments, such as fragments of diatom or siliceous silts (Noh, 1994). The microplankton fauna analysis dates the Duho Formation beds to the end of the middle Miocene (Serravallian), ca. 13.4 Ma by foraminifera and 14.0–12.0 Ma by dinoflagellates (Chun, 2004).

Diagnosis—A *Vinciguerria* species with 19–22 + 16–19 = 37–40 vertebrae, 13–16 dorsal fin and 13–17 anal fin rays, 13–16 photophores of PV series, 14 or 15 photophores of AC series, ca. 26 gill rakers, caudal body part length more than 30% of SL, and autogenous hypurals and parhypural in caudal fin skeleton.

Etymology—From the Latin word ‘orientalis,’ eastern.

DESCRIPTION

The main counts and the measurements of the type specimens are given in Tables 1 and 2, respectively. The body is slightly elongated and laterally compressed (Fig. 1). Its greatest depth is in the area of the pectoral fin base and is about a quarter of SL. The body is gradually tapered to the caudal fin base. The caudal peduncle is comparatively deep; its depth is usually more than one-fifth of SL. The pectoventral distance is 1.1–1.8 (average: 1.4) times the ventroanal distance; the caudal body part, measured from the beginning of the anal fin to the end of the hypurals, is 1.4–2.9 (average: 2.0) times the length of the ventroanal distance. The head is large, usually more than the body depth. The mouth is terminal, oblique, and wide; the lower jaw articulation is far behind the orbit. The lower jaw is slightly protruding before the upper one. The orbit is big and round. In most specimens, the snout is slightly longer than the orbit diameter, but this may be a result of a small displacement of the upper jaw forward after death.

The neurocranium is almost triangular in lateral view and sharply pointed anteriorly (Fig. 2). Its orbitorostral part is approximately two times longer than the cranial one. The orbit is large, constituting about one-third of the neurocranium. The frontals are long, triangular, firmly attached to each other

medially, and form small lateral wings above the anterior half of the orbit. The parasphenoid is thin and straight anteriorly and gently curved posteriorly. Other bones of the neurocranium are impossible to determine with certainty due to poor preservation and small sizes.

There are no traces of the circumorbital bones preserved in the studied specimens.

The shape of most head bones is very similar to those of recent representatives of the genus (Figs. 3, 4). The premaxilla is short, tapering posteriorly, with the short ascending process on its anterior end. The premaxilla is ca. one-fifth to one-third the length of the maxilla (Fig. 4A). Up to 18 conical teeth arranged in a single series can be observed along much of its ventral margin; some of them are slightly longer than the others. The maxilla is a long convex bone, with a row of up to 52 sharp, needle-like teeth on its ventral border. Its posterior edge reaches beyond the posterior border of the orbit. The maxillary teeth are of different sizes, basically gradually enlarged posteriorly. There is no alteration of small and large maxillary teeth. Most of the upper jaw teeth are settled perpendicularly to the bone border, whereas six to eight large teeth in the posterior-most part of the maxilla are inclined anteriorly. The anterior supramaxilla has the shape of an elongated rectangle; the posterior one is leaf-like, with a sharp anterior outgrowth (Fig. 4A). The mandible is low and elongate, with a rounded coronoid process of the anguloarticular, and tapering anteriorly dentary (Figs. 3, 4E). The dentary bears, apparently, two rows of needle-like teeth of different sizes, totaling more than 34 teeth.

Some bones of the suspensorium are clearly recognizable. The hyomandibula shaft is slightly inclined posteriorly so that its short opercular process is nearly horizontal (Fig. 2). The dorsal articular head is not divided into anterior and posterior parts. The anterior edge of the hyomandibula has a long and slim process projecting anteroventrally (Fig. 2). The ectopterygoid is elongate, considerably expanded posteriorly, and becomes very thin anteriorly. The mesopterygoid is wide and roughly oval. The palatine is high, trapezoid, and with a slender anterior outgrowth. At least two small conical palatal teeth are seen in the paratype KIGAM

TABLE 1. Selected meristic characters of †*Vinciguerria orientalis*, sp. nov., and related species.

Dimension/ element	<i>Vinciguerria</i>							<i>Eovinciguerria</i> † <i>obscura</i>	<i>Sytchevskia</i> † <i>distincta</i>
	† <i>orientalis</i> , sp. nov.	<i>attenuata</i>	<i>lucetia</i>	<i>mabahiss</i>	<i>nimbaria</i>	<i>poweriae</i>	† <i>merklini</i>		
SL	13.0–52.1 (34.7)/40	up to 45.0	up to 58.5	up to 31.0	up to 53.0	up to 43.0	up to 33.5	up to 70.0	up to 40.0
Vp	19–22 (20.8)/25	—	22–24	—	24–25	—	19–22	23–27	24
Vc	16–19 (17.9)/37	—	17	—	16–17	—	17–19	17–19	21
VT	37–40 (38.5)/19	40–41	39–43	37–38	39–44	38–41	37–40	40–46	45
D	13–16 (13.8)/11	13–15	13–15	12–14	13–15	13–15	11–13	12–14	14
A	13–17 (14.1)/14	13–16	14–16	13–14	13–16	12–15	12–17	15–21	15–20
P1	8–10 (8.8)/4	8–10	8–11	9–10	9–11	9–11	10	10–12	12
P2	7–7 (7.0)/4	6–7	7	7	7	7	7	8–9	~8
Gr	~26–27 /1	18–22	26–35	24–28	17–26	14–16	—	—	—
Photophore series									
BR	8/1	7–8	8	8	7–8	8	—	5–6	—
OV	~12/1	12–13	10–12	10–12	10–15	12–14	10	—	—
VAL	8–10 (8.8)/5	7–10	9–12	8–10	6–12	9–11	7	8–10	—
IP	~7–8/3	7	—	—	7	7	—	—	—
PV	13–16 (14.5)/2	15 – 17	13–15	12	12–17	15–17	11	11–13	—
VAV	7–8 (7.7)/7	7–10	8–11	7–9	7–11	8–10	7	8–10	10
AC	14–15 (14.8)/12	12–14	13–15	10–13	11–15	12–15	15–17	14–17	20–21

Includes new data along with those compiled from Daniltschenko (1946, 1980), Grey (1964), Weitzman (1967), Gorbunova (1972), Badcock (1984), Fujii (1984), Johnson and Feltes (1984), Schaefer et al. (1986), Aizawa (2002), and Prokofiev (2002, 2005). SL in mm. Mean values in parentheses. Number of specimens after slash. Dash indicates data unavailable.

TABLE 2. Selected measurements (as % of SL) of the type specimens of †*Vinciguerria orientalis*, sp. nov., and related species.

Dimension	<i>Vinciguerria</i>									
	† <i>orientalis</i> , sp. nov.		<i>attenuata</i>	<i>lucetia</i>	<i>mabahiss</i>	<i>nimbaria</i>	<i>poweriae</i>	† <i>merklini</i>	<i>Eovinciguerria</i> † <i>obscura</i>	<i>Sytchevskia</i> † <i>distincta</i>
SL	51.5	29.5–47.3 (39.2)	up to 45.0	up to 58.5	up to 31.0	up to 53.0	up to 43.0	up to 33.5	up to 70.0	up to 40.0
HL	26.5	25.4–27.8 (26.6)	25.7–36.1	23.7–30.2	27.9–31.4	23.4–32.4	25.0–32.9	26.1–35.7	25.0–30.2	28.6–29.4
H	26.6	24.6–27.2 (25.9)	19.0–21.0	16.4–18.5	19.5–21.9	14.4–24.7	20.4–22.8	23.8–25.0	15.9–24.4	11.4–14.7
hc	10.9	8.9–12.3 (10.1)	6.7–8.1	5.9–7.4	7.0–8.0	5.9–8.3	7.0–9.1	7.8–11.9	7.0–9.8	5.7–5.9
aD	61.4	51.9–62.3 (58.1)	48.9–60.3	56.0–64.6	60.1–62.8	53.7–63.7	54.3–62.0	53.0–71.4	53.7–61.0	54.4–55.7
aA	72.0	65.5–70.6 (68.7)	57.5–70.9	66.0–73.8	69.1–73.1	66.0–75.8	66.1–75.8	65.9–78.6	70.7–75.6	67.7–68.6
aP	26.7	27.1–31.8 (29.5)	—	17.2–25.0	27.5–30.4	24.7–26.5	—	28.2	—	—
aV	53.9	47.7–54.1 (52.0)	45.5–52.2	47.5–54.4	52.9–55.3	46.6–54.5	47.6–58.8	50.0–59.5	48.7–55.8	44.3–45.6
DA	22.3	18.2–25.6 (20.8)	—	18.2–19.1	—	20.2–22.0	—	19.9	—	—
P ₁ P ₂	27.3	21.3–26.7 (24.2)	—	25.0–28.9	24.1–27.4	26.2–30.1	—	21.9–26.2	—	20.6–21.4
VA	18.4	16.0–19.8 (18.0)	12.6–15.5	17.6–21.7	—	14.3–21.7	13.2–19.0	17.2–19.1	—	20.6–21.4
Lcd	30.2	31.7–39.0 (33.8)	32.5–39.4	26.6–27.6	28.2–31.2	26.0–31.5	29.4–30.9	37.3	—	—
DI	15.8	13.4–15.4 (14.6)	17.5–21.0	—	15.6–18.2	15.3–21.4	16.4–20.6	13.2	—	—
AI	15.9	15.9–20.3 (17.7)	15.8–18.4	—	13.3–16.2	12.4–16.7	11.1–16.4	14.8	—	—
Dh	14.3	13.4–17.0 (14.8)	—	10.7–11.3	—	11.4–12.3	—	16.0	—	—
Ah	9.1	9.6–10.8 (10.0)	—	7.1–7.6	—	5.4–8.3	—	11.7	—	—
CI	21.9	18.6–24.2 (21.8)	—	16.4–19.3	—	15.8–21.3	—	17.3	—	—
IP	16.2	12.0–20.1 (15.5)	15.5–17.5	12.5–14.6	—	14.1–18.5	16.4–20.4	15.5	—	—
IV	10.8	10.2–13.1 (11.6)	10.0–11.1	10.3–10.7	—	8.4–12.9	11.1–15.6	10.3	—	—
aO	9.4	7.6–11.6 (9.1)	5.3–8.5	6.3–9.0	6.8–8.3	6.1–8.9	6.3–9.6	7.1	—	—
O	7.2	6.4–9.0 (7.7)	7.0–10.0	7.8–9.5	8.7–10.7	6.5–9.7	7.5–9.6	9.0	—	—
Mxl	20.8	20.6–22.9 (21.8)	21.0–24.7	17.2–19.3	18.3–21.0	18.7–21.4	20.3–21.8	—	—	—
Mdb	21.5	23.0–28.9 (24.2)	—	18.0–18.4	20.4–23.8	18.1–20.7	—	—	—	—

Includes new data along with those compiled from Grey (1964), Gorbunova (1972), Johnson and Feltes (1984), and Prokofiev (2002, 2005). SL in mm. Mean values in parentheses. Dash indicates data unavailable.

9A172. The quadrate is large and roughly triangular, with an acute angle near the articular head (Figs. 2, 3). The symplectic is small and wedge-shaped.

The long, rod-like ceratohyal and the short and triangular epihyal are articulated synchronally. Eight slender branchiostegals connected with the ceratohyal are preserved in GNUE 32039 (Fig. 3). There are seven posterior branchiostegals in GNUE 32034, three arising from the ceratohyal and four arising from the epihyal; the six anterior ones are slender, whereas the posterior one is broad and flat. Thus, like in recent congeners (Weitzman, 1974), in this fossil species there are apparently one expanded and 11 slender branchiostegals (Fig. 4E–G).

The opercle (Fig. 4C) is subrectangular; its overall shape resembles that of the recent congeners (Fig. 4D). There are several short ridges directed posterodorsally and posteroventrally arising from the opercular joint, as well as the long vertical ridge

along the anterior margin, almost reaching the ventral edge of this bone. The anterior edge of the opercle, just below the opercular facet, is excised for accepting the opercular photophore. The interopercle and the subopercle are flat lamellar bones; the latter has a round incision for the subopercular photophore. The preopercle is crescentic, with almost equal arms and an obtuse angle of about 130° between them (Fig. 3).

In eight specimens, the well-exposed first branchial arches equipped with long gill rakers can be seen (Figs. 1C, 3). The branchial bones are elongate and slender; ceratobranchial 1 is the longest. No less than 19–21 rakers can be observed in most of these specimens, whereas only ca. 10 rakers are discernible in the holotype. At least 26 gill rakers are visible in the most completely preserved first gill arch of specimen GNUE 32039 (Fig. 3): there are about nine rakers associated with hypobranchial 1, about 10 with ceratobranchial 1, and not less than seven with

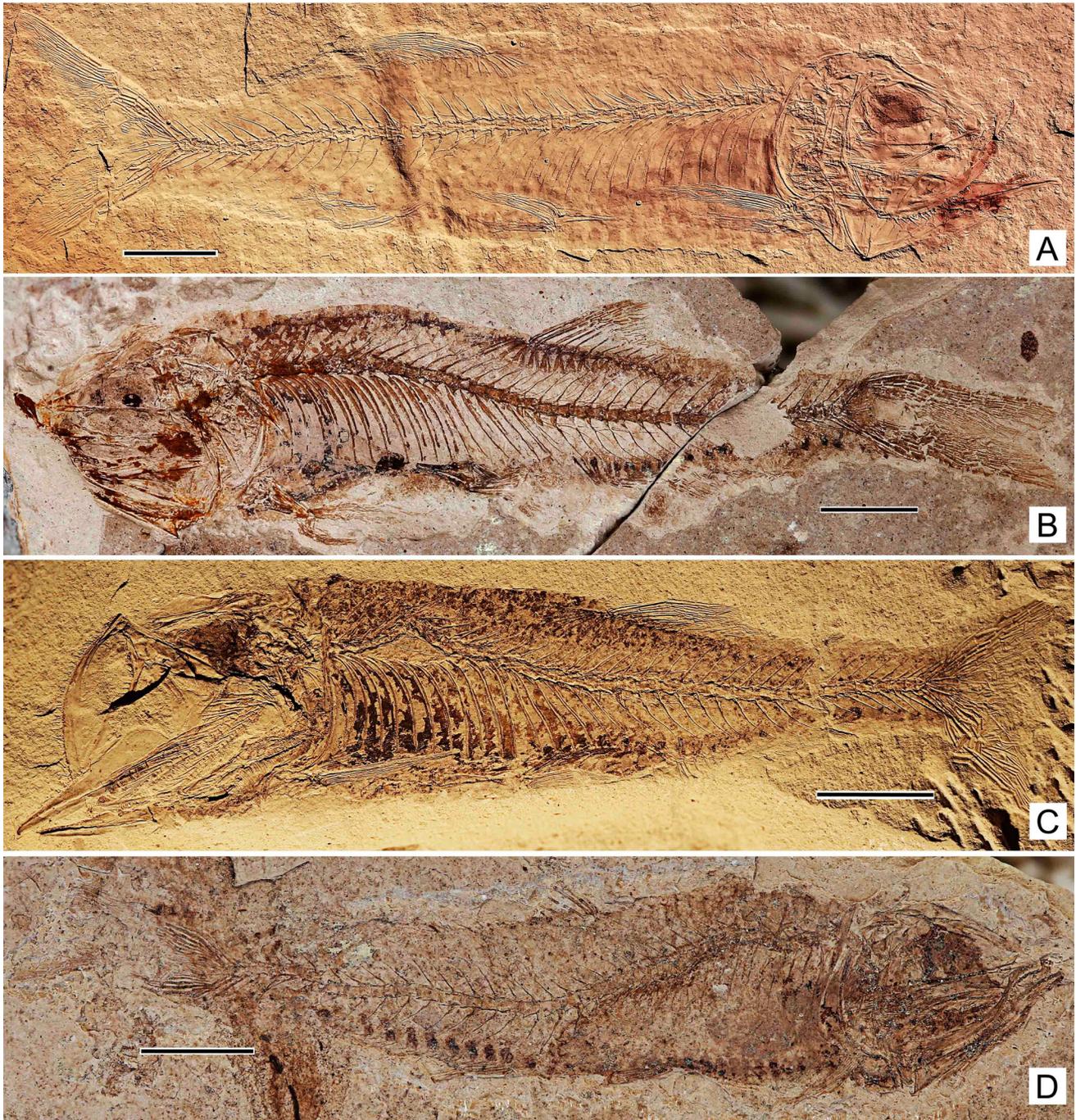


FIGURE 1. †*Vinciguerria orientalis*, sp. nov., from the Miocene of Duho Formation, South Korea. **A**, KIGAM 9A169, holotype, 51.5 mm SL. **B**, KIGAM 9A175, paratype, 47.0 mm SL. **C**, KIGAM 9A170, paratype, 38.3 mm SL. **D**, KIGAM 9A176, paratype, 38.8 mm SL. Scale bars equal 5 mm.

epibranchial 1. In the paratype KIGAM 9A170, up to 27 gill rakers can be counted, but in this case some of the upper rakers may belong to an underlying gill arch. The structure of other branchial bones is unknown.

A total of 37–40 moderately elongated vertebrae are present in †*V. orientalis*; of these 16–19 are caudal (Table 1). The holotype has $21 + 18 = 39$ vertebrae. The exact number of vertebrae in †*V. orientalis* can be directly counted for a few specimens only because, in most cases, several anterior-most vertebrae are hidden under the opercle and the shoulder girdle elements. In

such cases, the number of vertebrae was estimated based on the number of pleural rib pairs. The left and right neural processes of most precaudal centra are not fused to each other medially (Fig. 2); the first neural spine appears under or slightly anterior to the dorsal fin base, on the third to sixth precaudal vertebrae. Most of the precaudal vertebrae bear short parapophyses, which, apparently, are fused with their respective vertebral centra. There are 16–19 pairs of long, saber-like pleural ribs attached to the parapophyses, and they do not reach the ventral edge of the body (Fig. 2). The ribs are spread from the third to

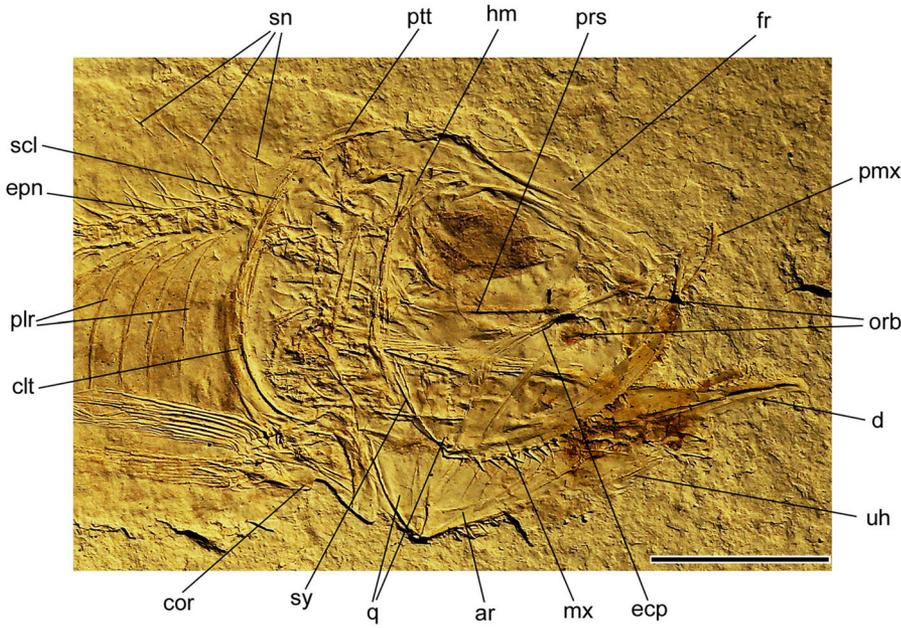


FIGURE 2. †*Vinciguerria orientalis*, sp. nov., KIGAM 9A169, holotype, head. Scale bar equals 5 mm.

the penultimate abdominal vertebra, but in two specimens, to the last abdominal vertebra. The epipleurals are spread from the parapophyses of precaudal vertebrae 1–4 to the hemal arches of caudal vertebrae 3–7. The epineural series apparently begins from the first vertebra and continues to the neural arches of caudal vertebrae 2–7. There is a series of at least 11 short, rod-like supraneurals (Fig. 2) that are placed singly in the interneural

spaces in front of the dorsal fin base; among them, the anterior one is slightly thicker and settled above the first two neural arches. The neural and hemal spines on the caudal vertebrae are elongate, thin, and moderately inclined caudally.

The caudal fin is deeply forked, and its length is about one-fifth of SL. It consists of the 10 + 9 principal rays, of which the uppermost and lowermost are unbranched. There are 3–7 dorsal and 1–

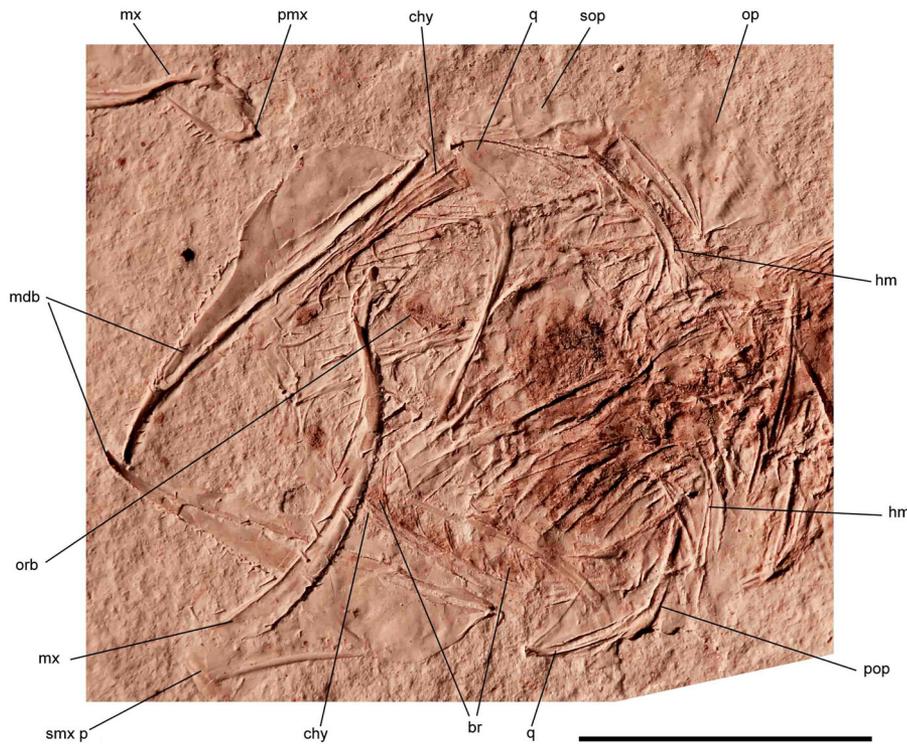


FIGURE 3. †*Vinciguerria orientalis*, sp. nov., GNUE 32039, 32.5 mm SL, head. Scale bar equals 5 mm.

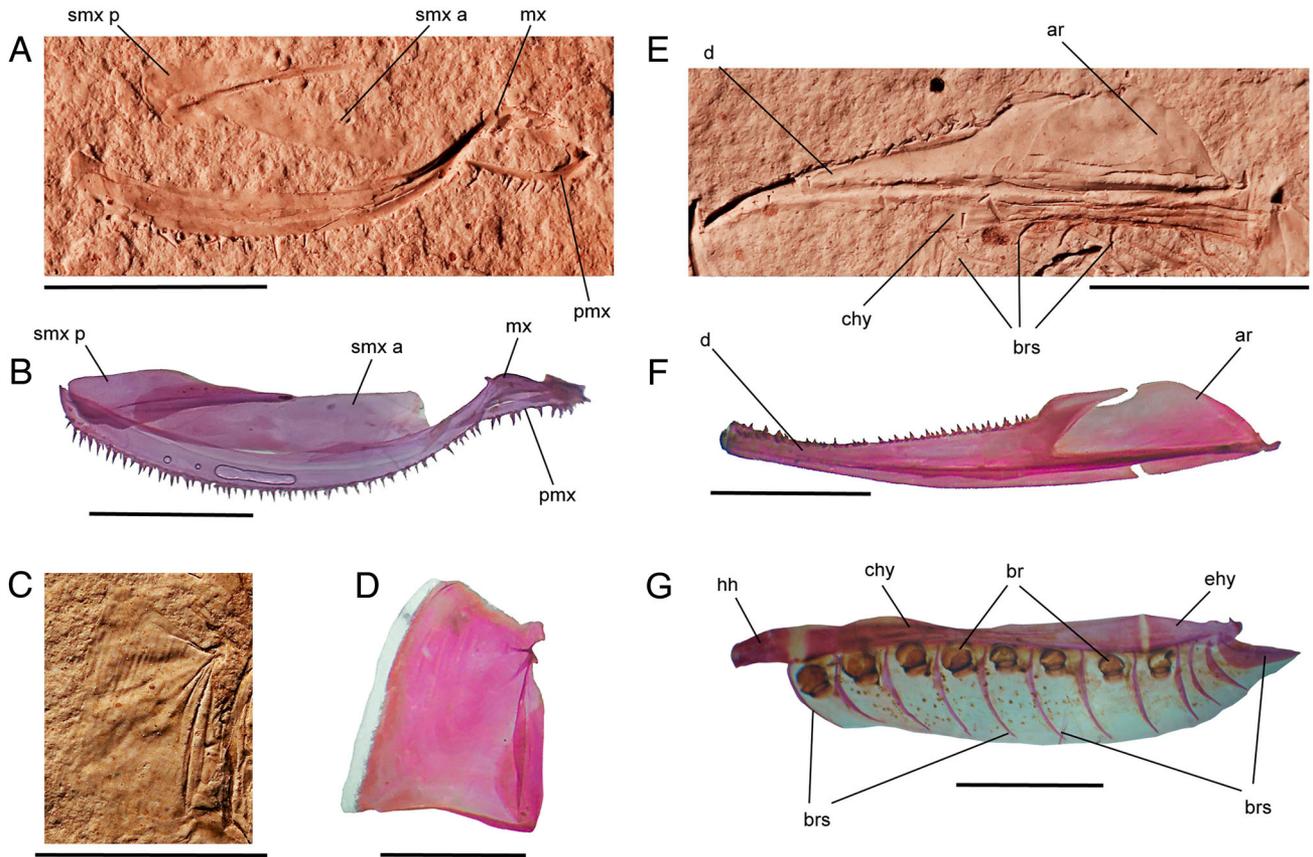


FIGURE 4. Comparison of the visceral bones of †*Vinciguerria orientalis*, sp. nov. (GNUE 32039), and *V. lucetia* (ZMMU P 13740, 57.0 mm SL). Upper jaws of **A**, †*V. orientalis* and **B**, *V. lucetia*. Opercles of **C**, †*V. orientalis* and **D**, *V. lucetia*. Lower jaws and part of hyoid bar of **E**, †*V. orientalis* and **F**, *V. lucetia*. Scale bars equal 3 mm.

4 ventral procurrent rays. The caudal fin support is quite different from that described for all recent and fossil representatives of the genus, in that the parhypural and six hypurals are autonomous, separated from each other and from the terminal vertebral centrum (Fig. 5A). The wide lamellar ventral outgrowth of the third hypural, which fills the gap between the upper and lower lobes of the caudal skeleton (hypural diastema), is also separated from hypural 3 by the prominent groove. This last feature gives the impression of the presence of seven hypural elements. There is a small, round opening for the caudal vein between the parhypural and hypural 1; in some specimens, there is an additional such opening between hypurals 1 and 2. The urostylar vertebra is single; an autonomous second ural centrum is absent. There is a single, wide uroneural, probably fused with the urostylar centrum. The single, well-ossified epural is also present. The neural spine of the second preural centrum is high and well developed. There are no lamellar outgrowths on the neural and hemal spines of the several posterior preural centra.

There are 13–16 (not less than 13 in the holotype) articulated dorsal fin rays, most of which are branched. The dorsal fin origin is slightly behind the middle of the body; its base is shorter than the body depth at this point. The beginning of the dorsal base is located opposite precaudal vertebrae 1–4 (commonly 2–3) from behind and extends to the level of caudal vertebrae 3–8 (commonly 5–6). The second to fifth dorsal fin rays are the longest; their length is more or less equal to the dorsal fin base length. The length of the other rays gradually decreases caudally. The structure of the dorsal proximal pterygiophores is

the same as that of recent species of this genus (Fig. 6). The anterior-most pterygiophore is a complex structure with five to six proximal outgrowths, probably originating from the fusion of several elements. The second proximal radial is rod-like, whereas the following radials are expanded in the sagittal plane and incised ventrally (Weitzman, 1967:fig. 11). The medial radials are seen from the fourth pterygiophore; the distal radials are indiscernible.

The adipose fin is not preserved in any of the examined specimens.

The anal fin consists of 13–17 (not less than 7 in the holotype) articulated and predominantly branched rays. The anal fin origin is beneath the posterior half of the dorsal fin base, opposite to the 7–11 dorsal rays. The anal fin base is slightly longer than the dorsal base; it extends from the level of caudal vertebrae 2–4 to that of caudal vertebrae 9–12. The anterior anal fin pterygiophore is a complex structure, with two long outgrowths proximally, which are followed by the first hemal spine. The following anal fin pterygiophores are slightly expanded in the sagittal plane, but not incised, unlike those in the dorsal fin. The medial and distal radials of the anal fin pterygiophores are usually not recognizable.

The pectoral fin base is positioned low on the body and immediately behind the head (Figs. 1, 2). There are 8–10 pectoral rays (9 in the holotype), most of which are branched. The longest, second to fourth, pectoral rays usually reach far behind the middle of the pelvic girdle. The pectoral fin length corresponds to that of seven to eight precaudal vertebrae. The lowermost,

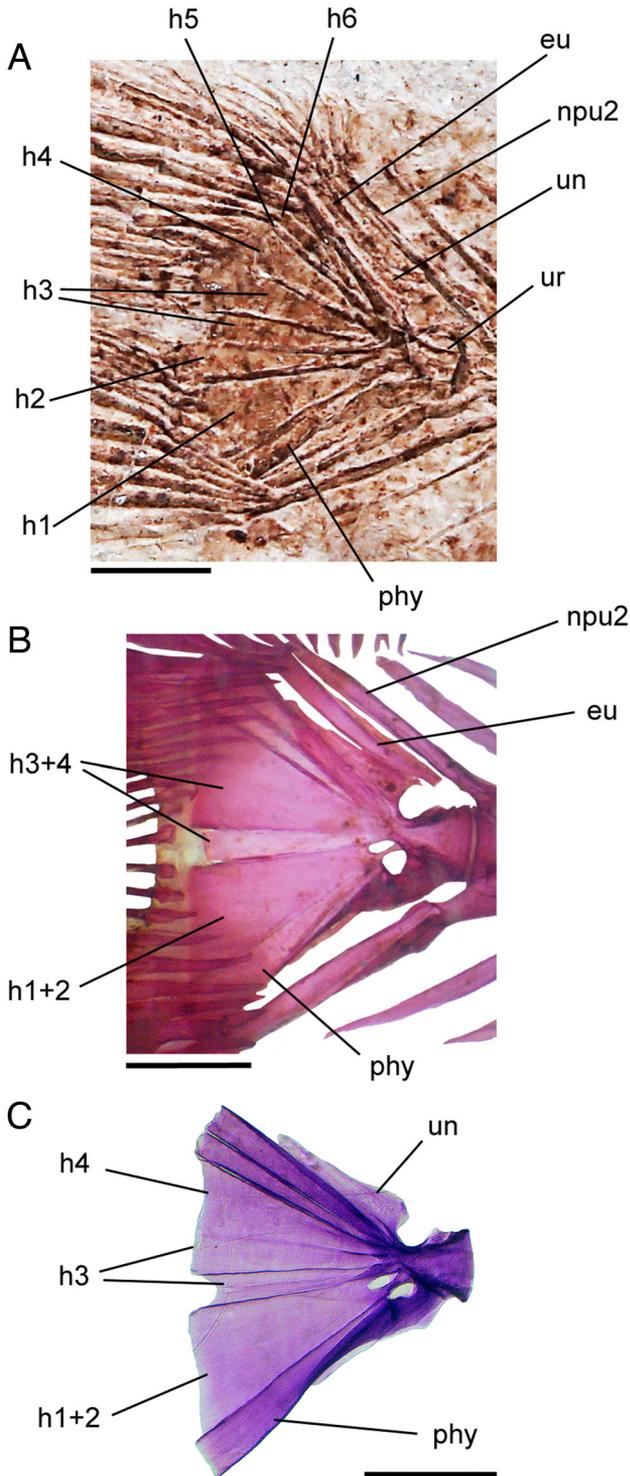


FIGURE 5. *Vinciguerria* caudal skeletons. **A.** †*V. orientalis*, sp. nov., GNUE 32044, ca. 50.0 mm SL. **B.** *V. lucetia*, ZMMU P 13740, 57.0 mm SL. **C.** *V. nimbaria*, ZIN uncataloged, 48.0 mm SL. Scale bars equal 1 mm.

inner pectoral ray is very thin and short. The cleithrum is the largest bone of the pectoral girdle. Its ventral part is strongly hooked downward, which gives an ‘S’ shape to the whole bone. The comparatively wide and long supracleithrum and the forked posttemporal are well exposed in most specimens,

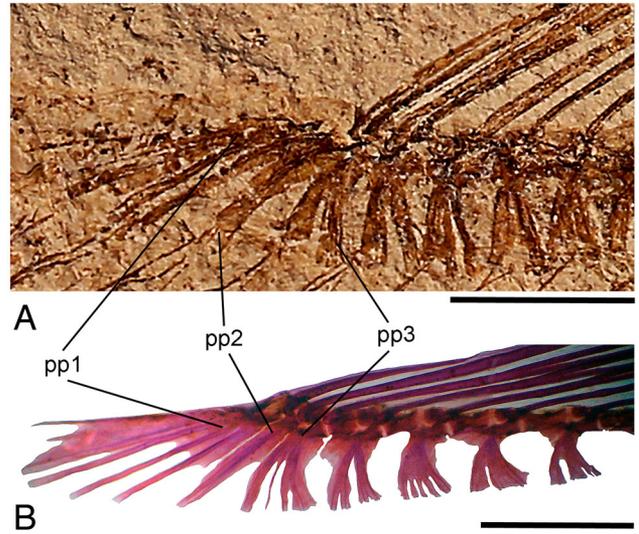


FIGURE 6. *Vinciguerria*, anterior part of the dorsal fin base. **A.** †*V. orientalis*, sp. nov., KIGAM 9A175, paratype, 47.0 mm SL. **B.** *V. lucetia*, ZMMU P 13740, 57.0 mm SL. Scale bars equal 2 mm.

including the holotype (Fig. 2). The postcleithrum is absent. The proximal part of the coracoid is wide, similar to the recent species of this genus. The structure of other bones of the pectoral girdle and the number of pectoral radials are unknown.

The pelvic fin base is slightly anterior to the dorsal fin origin, on the level of precaudal vertebrae 4–7 from behind (Fig. 1). The pelvic fin is comparatively short; its rays do not reach posteriorly to the beginning of the anal fin. In the best-preserved specimens, including the holotype, there are seven pelvic rays; some of which are definitely branched. The pelvic bone is elongate, flattened, and triangular; its length corresponds to that of four to five precaudal vertebrae.

The body is covered by subcircular cycloid scales; their diameter is about 3.5 times that of the orbit.

The numbers of photophores in individual series are as follows (Table 1): BR 8; IP approximately 7–8; PV 13–16 (13 in the holotype); VAV 7–8 (8 in the holotype); AC 14–15 (14 in the holotype); OV approximately 12 (at least 9 in the holotype); VAL 8–10 (8 or 9 in the holotype).

There are 12 specimens in which one or both orbital photophores are preserved; the holotype includes the anterior orbital photophore (Fig. 2). The excised anterior edge of the opercle, as well as the notch in the ventral edge of the subopercle, suggest the existence of upper and posteroventral opercular photophores in the fossil species. The paratype KIGAM 9A170 possesses a light organ in the center of the inner anterior margin of the preopercle, i.e., anteroventral opercular photophore. Thus, the arrangement of light organs on the head of the fossil species is similar to that in recent members of the genus. The suborbital photophore (SO) is not recognized on any specimen.

DISCUSSION

The overall appearance and morphological features of the new Miocene species described above clearly support its assignment to the stomiiform family Phosichthyidae. Among the features are a moderately elongated body; the number of precaudal vertebrae, which is greater than that of the caudal vertebrae; a large mouth with comparatively uniform jaw teeth; well-developed gill rakers; greatly enlarged posterior branchiostegal ray; the position of the pectoral fin low on the body; the presence of

the hook-like curvature of the ventral end of the cleithrum; the long neural process of the second preural vertebra; the absence of spiny fin rays; the presence of two longitudinal rows of body photophores; the presence of photophores on the isthmus; and the presence of a posterior ORB photophore (Fink and Weitzman, 1982; Harold and Weitzman, 1996; Prokofiev, 2005). The presence of an anteroventrally elongated hyomandibular spine in the fossil species supports its inclusion in the clade containing the genera *Vinciguerria* and *Pollichthys* (Harold and Weitzman, 1996), whereas the short-based anal fin and comparatively short premaxilla allow assignment to *Vinciguerria* (Badcock, 1984).

Unlike most Phosichthyidae, including the Paleogene genera mentioned, *Vinciguerria* spp. are characterized by short premaxillae, constituting less than one-third of the maxillary length (Prokofiev, 2005). So, for the specimen of *V. lucetia*, Borodulina (1984) noted the small premaxilla, which is one-seventh the length of the maxilla. The two specimens of *V. lucetia* examined in this paper possess a different ratio: the premaxilla is ca. 27% the length of the maxilla, which coincides with that of the new fossil species (Fig. 4A).

The general appearance and morphology of the new fossil species from South Korea are very similar to those of other representatives of *Vinciguerria*. Most of its main counts and proportions partly overlap with the values for congeners. The high number of gill rakers in the fossil species makes it closer to *V. lucetia* and *V. mabahiss* Johnson and Feltes, 1984, whereas the low numbers of abdominal and total vertebrae suggest that it is closer to *V. mabahiss*, *V. poweria*, and †*V. merklini* (Table 1). The high number of photophores in the PV series separates this new species from †*V. merklini* and *V. mabahiss*, whereas the high number of photophores in AC series separates it from *V. mabahiss* only. Slightly greater body and caudal peduncle depths in the new species (Table 2) probably reflect the post-mortem displacement of the body soft tissues. †*Vinciguerria orientalis* possesses a comparatively long caudal body part, measured from the anal fin beginning to the edge of the hypurals. This character separates it from most of its recent congeners, excluding *V. attenuata*, which can be separated from †*V. orientalis* by the longer dorsal fin base (Table 2).

The main feature that separates †*V. orientalis* from its congeners is the primitive structure of the caudal fin support with free hypurals and parhypural (Fig. 5A, B). In this respect, the new fossil species resembles the Paleogene phosichthyans †*Sytchevskia*, and †*Eovinciguerria*, which are undoubtedly closely related to *Vinciguerria*. On the other hand, unlike in †*V. orientalis*, the caudal skeleton structure of both Paleogene genera is characterized by two more primitive characters: the presence of the separate second ural centrum and the presence of three (†*Sytchevskia*) or two (†*Eovinciguerria*) epurals (Prokofiev, 2002, 2005). The Neogene †*V. merklini* possesses a somewhat intermediate structure of caudal fin support; it has free hypurals 5 and 6, and the suture groove in the proximal part of the plate of hypurals 3 + 4 (Prokofiev, 2002). The last condition is also observed in some recent species: one specimen of *V. nimbaria* studied here has a prominent furrow in the upper hypural plate between hypurals 3 and 4 (Fig. 5C). Thus, in caudal skeleton structure, †*V. orientalis* is a kind of transitional link between the Paleogene and Neogene to recent fishes of this evolutionary lineage and appears to be somewhat more primitive than †*V. merklini*.

A little can be said about the ecological conditions during the deposition of the Duho Formation. The discovery of *Vinciguerria* in this fossil fish complex suggests deep-sea accumulation of these Miocene beds. Most of the collected skeletons are nearly complete, which indicates that long distance transport of dead fishes before fossilization is a low possibility, whereas a high rate of sedimentation is quite probable. Some fossil specimens possess mouths that are wide open (Fig. 1C); this feature suggests

sudden death caused by oxygen deprivation. In the modern fish fauna of the seas surrounding the Korean Peninsula, representatives of *Vinciguerria* are absent, as are most other stomiiforms, with the only exception being the silvery lightfish *Maurolicus muelleri* (Gmelin) (Kim et al., 2005). Apparently, deep-sea conditions, suitable for mesopelagic fishes, were more common in this area in the middle Miocene than today.

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