First discovery of the genus *Auxis* (Actinopterygii: Scombridae) in the Neogene of South Korea

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*ABSTRACT - A new species of frigate tunas (Scombridae), †*Auxis koreanus *n. sp., is described based on two fragmentary, mostly disarticulated specimens found in the middle Miocene Duho Formation of the Pohang City locality, South Korea (36°03'N; 129°23'E). Such characters of the fossil scombrid as the dorso-ventral outlines of the neurocranium, diamond-shaped mesethmoid, very small teeth, shape of the hyomandibula, huge posttemporal and stout parapophyses lacking the haemal arch at their base indicate its attribution to the genus* Auxis. *However, some osteological details of the Miocene frigate mackerel justify its recognition as a new species. This is the first fossil find in Korea of both the genus* Auxis *and the family Scombridae, as well as the first reliable discovery of* Auxis *in the fossil record known to date. A review of the fossil record of scombrids in the western Pacific is given.*

INTRODUCTION

Marine fossil fishes are currently poorly known from the Cenozoic of the Korean Peninsula. Up to date, only a few finds have been described: elasmobranchs (Kim et al., 2018) and teleosteans (unidentified pleuronectiform: Ko, 2016 and *Pleuronichthys* sp.: Ko & Nam, 2016; zaprorid †*Zaprora koreana*: Nam & Nazarkin, 2018; phosichthyid †*Vinciguerria orientalis*: Nam et al., 2019). They all come from the middle Miocene deposits of the Duho Formation, therefore making this geological body the most important source of information on the Neogene stage of the Korean marine ichthyofauna development.

Recent excavations in the fossiliferous layers of the Miocene Duho Formation (Pohang City locality) resulted in the discovery of two fragments of the scombrid fish described below as †*Auxis koreanus* n. sp. This is the first fossil find in Korea of both the genus *Auxis* and the family Scombridae.

The family Scombridae includes mostly fast-swimming epipelagic marine fishes; it is traditionally placed in the suborder Scombroidei of the order Perciformes (e.g., Nelson, 2006). Recently, however, the traditional classification of fishes has often been replaced by formal cladistic taxonomy based on computer processing of molecular data which often conflicts with the morphological evidence. In cladistic systematics, an ordinal rank is given to the scombroids (Wiley & Johnson, 2010; Near et al., 2012, 2013; Betancur-R. et al., 2013, 2017; Nelson et al., 2016, etc.), within the "division Percomorphacea" (Wiley & Johnson, 2010), "clade Pelagia" (Miya et al., 2013) or "series Pelagiaria" (Betancur-R. et al., 2017).

Fossil scombrids are relatively well-known from the early Eocene to middle Miocene of the Tethys and Paratethys basins (see Bannikov, 1985, 2010, 2020; Monsch & Bannikov, 2012), whereas in the western Pacific their occurrences are restricted to the Miocene. *Scomber* sp. was described based on the articulated caudal part of a skeleton from the middle-upper Miocene Kurasi Formation of south-western Sakhalin Island, Russian Far East (Nazarkin & Bannikov, 2014). Several Miocene records of scombrids in Japan (Yabumoto & Uyeno, 1994) were also based on highly incomplete, disarticulated materials - *Scomberomorus* sp. (Ohe et al., 1986; Ohe & Koike, 1998), †*Scomberomorus chichibu* Uyeno, K. Sakamoto & O. Sakamoto (Uyeno & Sakamoto, 1985; Uyeno et al., 1994), *Grammatorcynus* sp. (Uyeno & Fujii, 1975), "*Acanthocybium*" sp. (Ohe et al., 1981), *Scomber* sp. (Kobayashi, 1938; Ohe & Koike, 1998), *Thunnus* sp. (Uyeno, 1992; Ohe & Koike, 1998, 2012) and gen. et sp. indet. (Uyeno, 1992); only †*S. nomurai* Niino from Gunma Prefecture (Niino, 1951) and *Scomber* sp. from Aichi Prefecture (Ohe, 1993) are known based on complete skeletons. Additionally, an unidentified scombrid figured by Hirao et al. (2005: pl. 1, fig. 7) represents an imprint of an almost complete skeleton of the juvenile fish.

MATERIAL AND LOCALITY

The most common Neogene deposits in the area of Pohang City belong to the Duho Formation, which is dated back to the middle Miocene, with an age of about 15 Ma, as concluded from microfossil faunal analysis (You et al., 1986; Lee et al., 1992; Bak et al., 1996). It consists of siltstones, sandstones, mudstones, and conglomerates (Yun, 1986; Yoon, 1992). These beds are famous due to the rich association of fossils, which include both terrestrial (plants and insects), and marine (echinoderms, crustaceans, mollusks) organisms. The diverse community of marine fishes, comprising demersal, mesopelagic, and

epipelagic fishes discovered from these beds is a source of important information on the Neogene fish fauna of the southern part of the Eastern Sea (Sea of Japan) and on the Miocene stage of the fish fauna development. Two fragmentary, mostly disarticulated specimens described here were collected in the temporary outcrop in a construction site of the building within the borders of Pohang City. The studied specimens are deposited in the collection of Gongju National University of Education (GNUE), Gongju City (South Korea).

METHODS

The specimens were examined using a Leica M80 stereomicroscope equipped with a camera lucida drawing arm. Some details of the specimens examined were best seen when the specimens were moistened with alcohol. All extinct taxa are marked with daggers (†) preceding their names.

SYSTEMATICS

Order PERCIFORMES sensu Nelson, 2006
Suborder SCOMBROIDEI sensu Nelson, 2006
Family SCOMBRIDAE Rafinesque, 1815

Genus *Auxis* Cuvier, 1829
Type species *Scomber rochei* Risso, 1810

†*Auxis koreanus* n. sp.
(Figs 1-2)

Etymology - After Korean Peninsula.

Holotype - Specimen GNUE 32173, slab with the imprints of a neurocranium, several disarticulated bones of the viscerocranium and pectoral girdle, and 14 disarticulated vertebrae.

Paratype - Specimen GNUE 32174, slab with the imprints of 14 articulated abdominal vertebrae, articulated lower jaw (both two branches) and gill cover.

Occurrence - Type locality: Pohang City, South Korea (GPS coordinates 36°03'N; 129°23'E); type horizon: Duho Formation, middle Miocene.

Diagnosis - Neurocranium relatively wide, subtriangular in dorsal view. Each pterotic produced posteriorly into short blunt spine. Dentition minute. Metapterygoid relatively wide ventrally. Opercular apparatus very wide. Preopercle moderately wide and concave anteriorly. Posttemporal large and with a slight lateral lobe at the base of its median process. Cleithrum moderately curved in C-shape and not especially narrow ventrally. Parapophyses lack a haemal arch at their base.

Description - The studied material provides information about the neurocranium, part of the viscerocranium (suspensorium, gill cover, and lower jaw), part of the

pectoral girdle and abdominal vertebrae. The maximum width of the neurocranium measured between the posterior projections of the pterotics is 26 mm.

CRANIAL SKELETON - The neurocranium mostly represents the articulated cranial roof preserved from below, in ventral view; therefore, the medial and temporal ridges are not recognisable. In dorso-ventral view, the neurocranium outline is more or less triangular in shape. Measured from the anterior border of the frontals to the posterior end of the basioccipital, the length of the cranial roof is 1.32 times greater than its width between the pterotic spines. In the ethmoid region, only a small portion of the lateral ethmoid is preserved, whereas the mesethmoid is almost fully preserved; it is slightly displaced laterally from its original position. The mesethmoid is broader than long; it is somewhat diamond-shaped and convex anteriorly. The frontals form the largest portion of the cranial roof; anteriorly they seem to be roundly pointed, and posteriorly they become expanded. There are some traces of the laterosensory canals on the frontals, and the anterior portions of the bones bear wrinklings. The lateral border of the frontal is almost straight, not concave above the orbits. The frontals definitely do not form the medial dorsal ridge characteristic for *Scomberomorus* (e.g., Devaraj, 1977; Collette & Russo, 1984), and there are no data on the orbital lamella or paired fronto-parietal fenestra characteristic for most of Thunnini (Collette & Aadland, 1996). There are some indications of the presence of a pineal opening between the posterior ends of the frontals and a mesial depression anterior to this fenestra (indicated for *Grammatorcynus* by Collette & Russo, 1984). The posterior limits of the frontals are poorly recognisable, as well as the limits of the otic region bones. The pterotics form the lateral posterior corners of the neurocranium. Posteriorly, each pterotic is produced into the short blunt spine. The pterotic ridge is traceable as a groove in the imprint; it diverges anterior to the pterotic spine. Anteriorly, the pterotic ridge terminates in the sphenotic crest, which is oriented obliquely postero-mesially. The sphenotics somewhat project laterally in the neurocranium contour, when viewed dorsally. Neither the parietals and epiotics nor supraoccipital are clearly recognisable. The opisthotic (intercalar) forms a slight rounded projection on the posterior contour of the neurocranium. The basioccipital and exoccipitals project posteriorly as a short and robust truncated condyle. The parasphenoid is detached from the neurocranium and only partially preserved in holotype. It is evident that the anterior portion of the parasphenoid is relatively narrow and robust, and the lateral wing is short and triangular. Posteriorly, the parasphenoid bifurcates into two pointed lateral flanges.

The lower jaw is preserved as an imprint in the matrix in the paratype and is represented by both right and left branches. The dentary is a large laterally flattened forked bone which forms a major part of the lower jaw; there is a slight notch on the anteroventral margin of the dentary just behind the subvertical symphysis. Posteriorly, the dentary forms two arms. The ventral arm seems to be narrower than the dorsal arm and almost as long as the latter. The preoperculomandibular pores (Allis, 1903) are not recognisable ventrally in the dentary. The dorsal arm of the dentary is rounded posteriorly; only a few minute
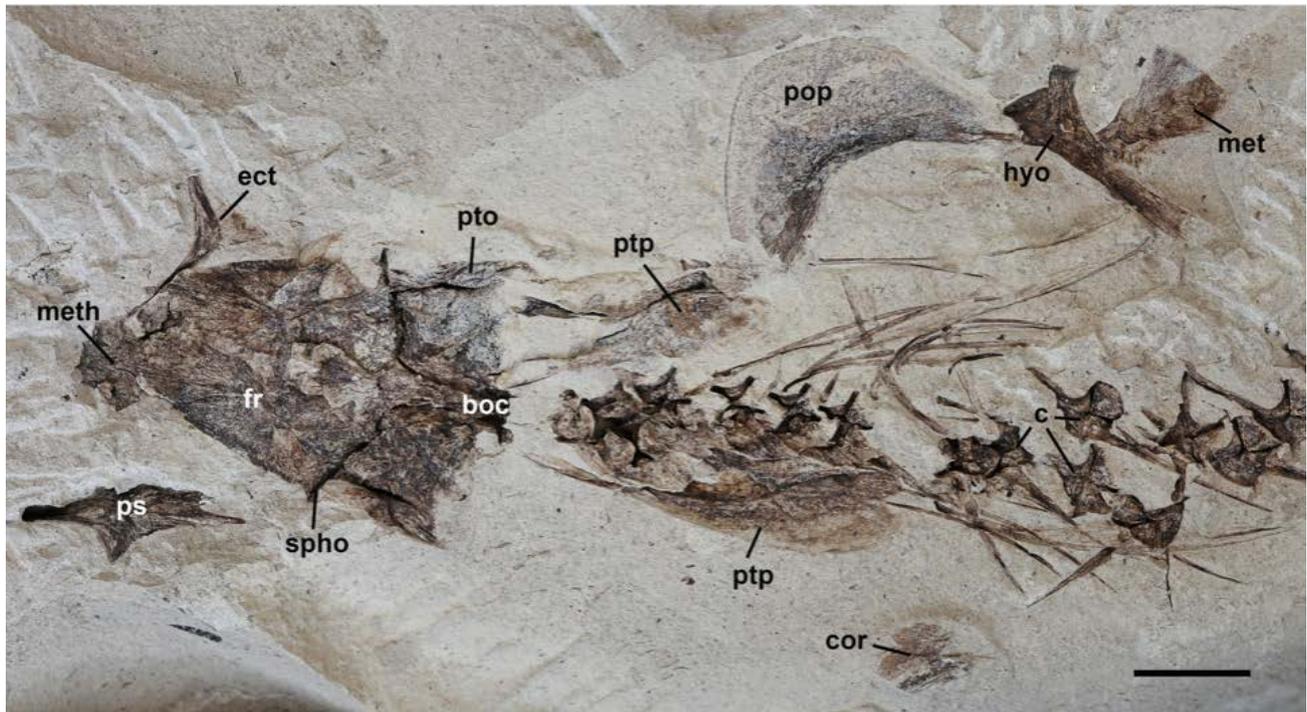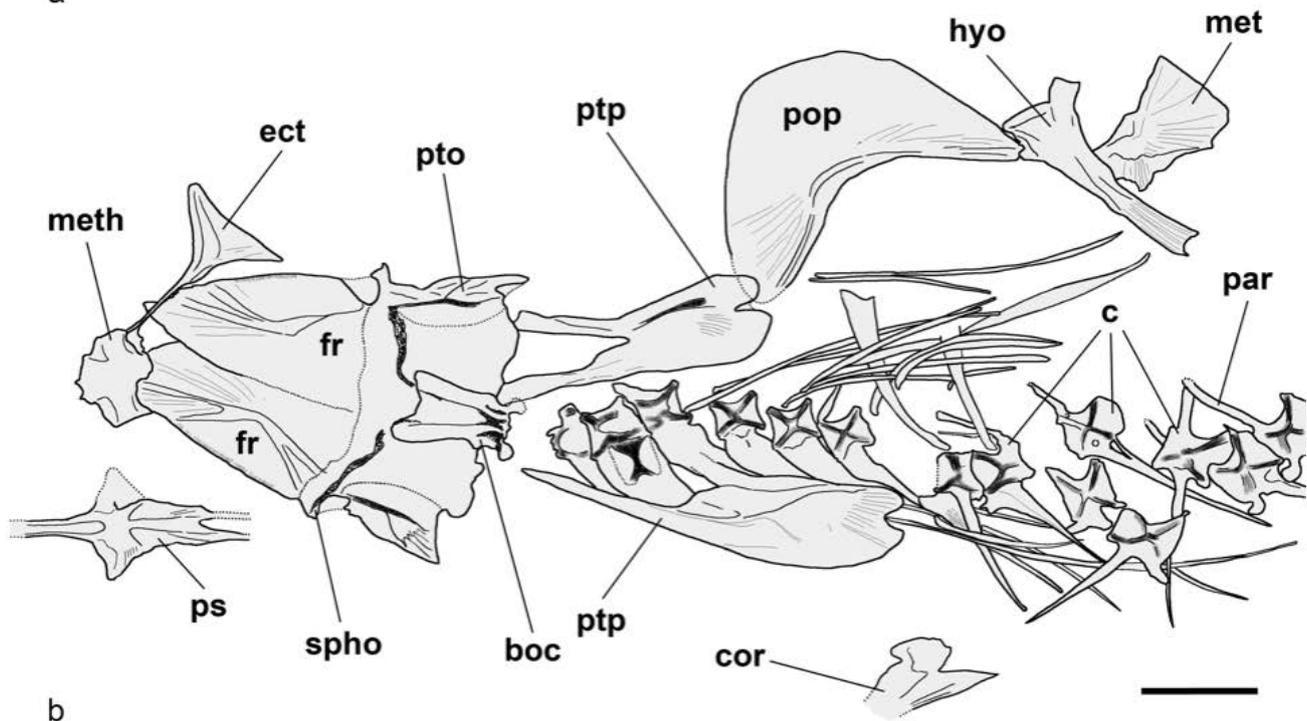
Fig. 1 - †*Auxis koreanus* n. sp. from the Miocene of South Korea, holotype GNUE 32173. a) Photograph. b) Interpretative drawing; boc: basioccipital, c: centrum, cor: coracoid, ect: ectopterygoid, fr: frontal, hyo: hyomandibula, met: metapterygoid, meth: mesethmoid, par: parapophysis, pop: preopercle, ps: parasphenoid, pto: pterotic, ptp: posttemporal, spho: sphenotic. Scale bars correspond to 10 mm.

teeth are recognisable in its alveolar margin due to poor preservation. The triangular anterior end of the angulo-articular fits into the dentary anteriorly. There is a small interosseous space between the posterior end of the dorsal arm of the dentary and the short dorsal process of the angulo-articular. The posteriorly directed retroarticular process of the angulo-articular is moderately strong and hooked. The retroarticular bone is scarcely recognisable. The length of the lower jaw corresponds to the length of the 6.5 middle abdominal vertebrae.

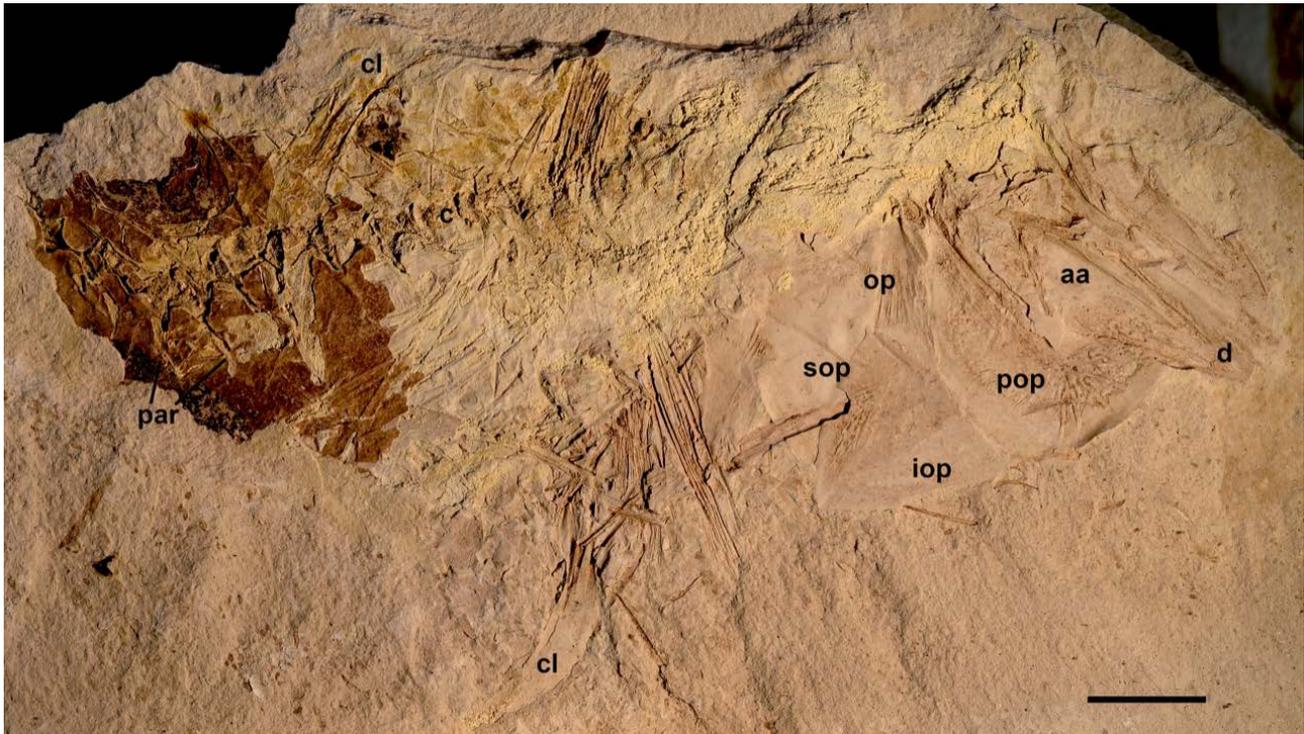The suspensorium bones are disarticulated in the holotype and represented by a single poorly preserved

Fig. 2 - †*Auxis koreanus* n. sp. from the Miocene of South Korea, paratype GNUE 32174. aa: angulo-articular, c: centrum, cl: cleithrum, d: dentary, iop: interopercle, op: opercle, par: parapophysis, pop: preopercle, sop: subopercle. Scale bar corresponds to 10 mm.

hyomandibula in the paratype. The hyomandibula is an elongate, inverted L-shaped bone. There are three condyles on the dorsal end of the hyomandibula. The long dorsal condyle (for the articulation with the pterotic and sphenotic bones) forms the base of the L; its surface is oriented obliquely and forms an angle of about 63° with the longitudinal axis of the hyomandibula. The anterior condyle (for the articulation with the sphenotic) is located on a short stalk oriented anterodorsally. The third condyle (for the articulation with the opercle) lies below the dorsal condyle on the posterior surface of the hyomandibula; evidently, it is faced into the matrix in the specimen. A lamellar region below the anterior condyle is almost not developed. The ventral portion of the hyomandibula becomes poorly ossified towards its tip. The total length of the hyomandibula (ventral tip to the dorsal margin of dorsal condyle) is 2.45 times greater than its maximum width (tip of the anterior condyle to outer margin of posterior condyle). The metapterygoid is a flat, quadrangular bone, which is broader ventrally than dorsally; the maximum width of the metapterygoid is 0.7 of its length. Both the anterior free border of the metapterygoid and the ventral border are nearly straight. The ventroposterior margin (for articulation with the symplectic) forms a strong angle with the ventral margin of the metapterygoid. Of the flat entopterygoid, only its anterior portion is preserved in the holotype as an imprint on the matrix, without bony substance. The ectopterygoid of the holotype is distantly displaced from the other suspensorium bones described above. The ectopterygoid is a T-shaped bone, representing a flat triangular plate, which ends in two pointed posterior arms (dorsal and ventral) and the longer anterior shank. A curved ridge passes through the ventral arm and the shank of the ectopterygoid, thus strengthening the bone.

Of the gill cover, the preopercle is preserved in the holotype. The preopercle is a large crescent-shaped flat bone, with the lower branch broader than the upper branch. The lower anterior margin of the bone forms an angle of about 117° with the upper anterior margin. The anterior portion of the bone is thickened along the margin. The lateral line system pores are scarcely recognisable. The posterior margin of the preopercle is convex and even, with a nearly straight portion in the middle. The maximum width from the anterior margin of the preopercle to its posterior end is 45% of the height of the bone measured from the ventral margin to the dorsal tip of the preopercle. The complete articulated gill cover is preserved in the paratype; however, the limits of its bones are not perfectly visible. The opercular apparatus is very wide, with its width in the middle being almost equal to its height. The preopercle corresponds to that described above, but with better visible lateral line system canals. The opercle is broad and flat; its precise shape is poorly recognisable. The anterior portion of the opercle bears striations in parallel to the anterior margin of the bone. The subopercle forms the slightly convex posterior border of the gill cover; the bone seems to be triangular, and its anterior projection is not recognisable. The interopercle is very broad, triangular, and flat, with most of its anterior surface being covered by the preopercle. The interopercle forms the posterior portion of the ventral border of the gill cover; no fimbriations on the posterior margin of the interopercle are evident (indicated by Collette & Chao, 1975 for the bonitos and *Thunnus*).

POSTCRANIAL SKELETON - The pelvic girdle is missing, and the pectoral girdle is highly incomplete in the holotype. The posttemporals are very large, elongate, and placed

posterior to the occipital portion of the neurocranium, being slightly displaced from their original position. The posttemporal is flat and notched at the middle of its posterior edge. The flat main body of the posttemporal continues anteriorly into the long median (dorsal) process (for articulation with the epiotic). The lateral (ventral) process of the posttemporal is shorter and rodlike; it is directed anteriorly (for articulation with the intercalar). The main body of the posttemporal seems to be produced as a slight lateral lobe at the base of the median process. The whole length of the posttemporal measured from the anterior end of the median process to the posterior edge of the main bone equals the length of the neurocranium (anterior edge of the frontals to the posterior edge of the basioccipital condyle). A single detached coracoid is represented only by its dorsal portion.

In the paratype, two poorly preserved disarticulated cleithra are preserved; one is represented by its pointed lower end only, whereas another one is more complete and moderately curved and C-shaped. At the lower end, the cleithrum is not especially narrow. Soft paired-fin rays are detached and arranged into three groups in the paratype; it seems that the pectoral fin was only moderately long.

There are 14 disarticulated vertebrae in the holotype located posterior to the occipital portion of the neurocranium and arranged into the elongate group. All of them most probably belong to the abdominal (precaudal) vertebral series, because none of them bears both a notably elongated haemal spine and a neural spine. The neural arches and spines are stout and mesially thickened at the base on several (up to six) anterior vertebrae; these vertebrae lack parapophyses. Some of the more posterior vertebrae reveal both relatively slender pointed neural spines and stout parapophyses that are variable in length. It is evident that the parapophyses lack a haemal arch at their base and thus represent the "pedicels or epihaemal processes" (Godsil, 1954; Collette & Aadland, 1996). The vertebral centra are sub-rectangular and constricted in the middle. Few centra reveal neural prezygapophyses. Several long and narrow bones located below and above the vertebrae and oriented mostly along their group evidently represent the pleural ribs (although the most slender of them may belong to epineurals). The ribs are pointed distally. In the paratype, 14 abdominal vertebrae are articulated, and seven posterior of them bear stout anteriorly inclined parapophyses which increase in length posteriorly in the series.

No scales are preserved except for few vague remnants.

DISCUSSION

Available characters of the fragmentary specimens studied, such as the dorso-ventral outlines of the neurocranium, broad crescent preopercle with even posterior border, as well as the shape of the bones of the suspensorium indicate that this fossil fish is a representative of the Scombridae (see osteology of different extant scombrids in Allis, 1903; Godsil, 1954; Gibbs & Collette, 1967; Gnanamuttu, 1971; Collette & Chao, 1975; Devaraj, 1977; Collette & Russo, 1984; etc.). Such characters of the fossil scombrid as the dorso-ventral outlines of the neurocranium, diamond-shaped mesethmoid, very small

teeth, the shape of hyomandibula, huge posttemporal and stout parapophyses lacking haemal arches at their base indicate its attribution to the genus *Auxis*.

The genus *Auxis* Cuvier was considered by many scientists (e.g., Fraser-Brunner, 1950) to be represented by a single extant worldwide species *A. thazard* (Lacepède, 1800). Later it was shown (Fitch & Roedel, 1963; Collette & Nauen, 1983; etc.) that there are two sympatric species of frigate tunas - the narrow-corseleted *A. thazard* and the wide-corseleted *A. rochei* (Risso, 1810). Collette & Aadland (1996) showed that for both species, eastern Pacific populations differ from Atlantic and Indo-West Pacific populations, and described two new eastern Pacific subspecies, *A. thazard brachydorax* and *A. rochei eudorax*. FishBase (Froese & Pauly, 2019) regards all four subspecies as valid species, which is not supported in Eschmeyer's Catalog of Fishes (Fricke et al., 2020). Extant species and subspecies of the genus *Auxis* do not differ osteologically; their differences are limited to the relative body depth, the width of the corselet, the number of gill rakers, and coloration (Collette & Aadland, 1996). These characters are not applicable for comparison with the Korean fossil. However, several osteological differences of the latter justify its attribution to a new species of the genus *Auxis*. The ventral portion of the metapterygoid is wider in relation to the bone height than in extant *Auxis* (width/height relation is 0.7 vs. about 0.5 in extant species). Characteristic for *Auxis* "a narrow tapered projection of the basioccipital on each side, which extends posteriorly at least one-half … of the first vertebra" (Godsil, 1954, p. 90), is not recognisable on the fossil, although the parasphenoid bifurcates posteriorly into two pointed lateral flanges, as in extant *Auxis*. If it is not an artifact of preservation, the pterotic of the Korean fossil lacks a sharp and long posterior process (as in *Auxis* and *Euthynnus*; see Godsil, 1954, figs 53 and 79), but, rather, each pterotic is produced into a short blunt spine (as in *Gymnosarda*; see Collette & Chao, 1975, fig. 10). The preopercle of the fossil is somewhat narrower and less crescent than in extant frigate tunas (an angle between the lower and upper anterior margins of the bone is about 117° vs. not more than 105°), and the cleithrum is less curved in a C-shape and wider ventrally. The main body of the posttemporal seems to be produced at the base of the median process much weaker than in extant *Auxis* which have a strong lateral lobe.

Although several fossil scombrid species were originally described from Europe as belonging to the genus *Auxis*, all of them were subsequently attributed to other genera. Kramberger-Gorjanović (1882) described four species from three Miocene Croatian localities: †*A. croaticus* Kramb. and †*A. minor* Kramb. from Radoboj, †*A. thynnoides* Kramb. from Podsused and †*A. vrabceensis* Kramb. from Vrabče. Later, Gorjanović- Kramberger (1895) added one more species, †*A. stiriacus* Kramb., from the Badenian of Sv. Jurij (Celje, Slovenia). Although Anđelković (1989) confirmed these attributions, it is clear that the Miocene scombrids of the former Yugoslavia cannot belong to the genus *Auxis*, because these fishes lack the evident characters of frigate tunas, e.g., vertebral formula (20+19 = 39), characteristic structure of parapophyses lacking a haemal arch at their base, wide gill cover, minute dentition, etc. The same is true

for †*Auxis caucasica* Bogatshov, 1933 described based on a single specimen from the middle to upper Miocene of the North Caucasus, SW Russia (Bogatshov, 1933). Bannikov (1985) argued that the Miocene scombrids mentioned above with their low vertebral count (31) should be attributed to the genus *Scomber* rather than to *Auxis*. One more fossil scombrid described originally from the lower Eocene of Bolca, northern Italy, as †*Thynnnus propterygius* (Agassiz, 1833-1844), was later tentatively attributed by Woodward (1901) to *Auxis*. Subsequently, the Italian species was transferred (Bannikov, 1985) to the extinct genus †*Scombrosarda* Daniltshenko, 1962. However, Monsch (2006) showed that the generic name †*Auxides* Jordan, 1919 has priority over †*Scombrosarda*.

Thus, †*Auxis koreanus* n. sp. is not only the first fossil *Auxis* from the Korean Peninsula but the first reliable discovery of *Auxis* in the fossil record known to date.

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