

Early Pleistocene freshwater fishes of Copăceni (Dacian Basin, southern Romania)

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ABSTRACT

This paper describes the first early Pleistocene freshwater fish assemblage from the Dacian Basin, Romania. The fossil sample, consisting mainly of isolated teeth, supports the presence of a rich and taxonomically diverse fish assemblage: 17 taxa were identified, belonging to 10 genera of the families Cyprinidae, Salmonidae, Siluridae, Esocidae, and Percidae. The ecological affinities of the identified taxa suggest the early Pleistocene fishes from Copăceni lived in a large lowland mesophitic river. The faunal composition is comparable to that of other southeast European assemblages, however, it includes more thermophilic taxa, suggesting the Dacian Basin represented an early Pleistocene refugium in a cooling post-Pliocene environment. The taxonomical composition of the fossil assemblage suggests a pre-Pleistocene dispersion of freshwater taxa took place in the areas surrounding the Euxinian Basin.

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INTRODUCTION

The Dacian Basin is represented by a sedimentary unit resulted from the fragmenting of the Paratethys during the Middle Miocene. It is bordered by the Carpathians to the north and west, by the Balkans to the south, and by the folded units of Northern Dobrogea to the east (e.g., Jipa and Olariu, 2009; Andreescu et al., 2013). Although some connections to the neighbouring Pannonian and Euxinian basins still existed, since its separation as an individual basin, the water salinity in the Dacian Basin gradually changed from normal marine to brackish, and it became freshwater during the late Pliocene (Jipa and Olariu, 2009; Andreescu et al., 2013). The late Pliocene and early Pleistocene sedimentary units (Andreescu et al., 2013) consist of alluvial and fluvial rudites and arenites, except for a silty unit, the “Copăceni beds”, that will be discussed in detail below.

The Plio-Pleistocene freshwater deposits of the Dacian Basin yielded mammalian fossil remains that were reported from many localities (Athanasiu, 1915; Apostol, 1965, 1968, 1972, 1976, 1981; Apostol and Stancu, 1968; Apostol and Vicoveanu, 1970; Feru et al., 1978, 1979, 1983; Terzea and Boroneanț, 1979; Apostol and Cacoveanu, 1980; Terzea, 1981, 2005; Rădulescu and Samson, 1986, 1990, 2001; Rădulescu et al., 1989, 1993, 1999, 2003; Lister and van Essen, 2003; Markov and Spassov, 2003; Popescu, 2004; Croitor and Popescu, 2011; Vasile et al., 2012, 2013a). Non-mammalian vertebrate fossils described from the Dacian Basin are exceedingly rare. The only two assemblages with reptile and amphibian remains are Tetoiu (Voicu et al., 2015) and Copăceni (Vasile et al., 2013b, 2015, 2016, 2018), both of early Pleistocene age. However, the taxa reported from these sites are still to be described in detail. The Plio-Pleistocene fish assemblages of the Dacian Basin are poorly known, as are other freshwater fossil fish assemblages of Romania, irrespective of age (for a review, see Trif and Codrea, 2018).

The early Pliocene fishes (local Dacian age) of the Dacian Basin are known by otoliths (rare gobiid teeth are also present) belonging to Gobiidae and Sciaenidae. These families include brackish and freshwater species, in agreement with the palaeoenvironment supported by the brackish invertebrates known from successions in western Dobrogea (at Oltina, in south-eastern part of the basin) and Oltenia (several sites in the west of the basin including Corabia, Scoarța, and Ișalnița)

(Pană, 1977, 1982, 1995; see also Bannikov et al., 2018 for a revision of otoliths).

A few isolated pharyngeal teeth, assigned to cyprinid fishes, such as *Tinca* and *Leuciscus* (Pană, 1982), document a transition from brackish to freshwater environments, towards the end of the early Pliocene (the late Dacian local age). Additional fish material was recently described from the late Pliocene (the Romanian local stage) of Podari, consisting of isolated teeth, cranial bones, vertebrae, and fin rays, identified as belonging to *Esox* sp., *Silurus* sp., *Scardinius* sp., and *Tinca* sp. (Trif et al., 2016), suggesting a typical freshwater environment was already present in the Dacian Basin at the end of the Pliocene.

GEOLOGICAL SETTING

The fossil material described in this paper was collected from the sediments cropping out at the left bank of Argeș River, at Copăceni (Ilfov County), a village located about 20 km southwards of Bucharest (Figure 1). In a couple of recent and comprehensive reviews of the Plio-Pleistocene stratigraphic units of the Dacian Basin (Andreescu et al., 2011, 2013), the sedimentary succession from Copăceni is provisionally left unformalized, being referred to as the “Copăceni beds”, a unit that, due to its silty-clayey lithology, stands out from the lower Pleistocene Frătești Formation represented by sands and pebbles. The same authors suggest that the “Copăceni beds” might represent a distinct formation, or the basal sub-unit of the lithologically similar Coconi Formation (a unit known from boreholes in the area surrounding Bucharest, informally known as “the Marly Complex”, term proposed by Liteanu, 1952).

There are, however, some contradictions regarding the age of the Coconi Formation. Andreescu et al. (2013: figure 2, figure 6) considered it to be a middle Pleistocene unit, accumulated during the Netindavian, the early Dinogetian local age, without offering any arguments for this assignment, whereas Andreescu et al. (2011) pointed out that the mollusk assemblage is irrelevant for dating this unit, but the presence of *Prolagurus pannonicus* and *Allophaiomys pliocaenicus* in a borehole sample from Fierbinți (Rădulescu et al., 1997) supports the late early Pleistocene age of the Coconi Formation. In spite of agreeing to this conclusion, Andreescu et al. (2011: figure 2) depicted the Coconi Formation as largely Dinogetian (i.e., middle Pleistocene).

The “Copăceni beds” are considered to have accumulated during the late early Pleistocene (late

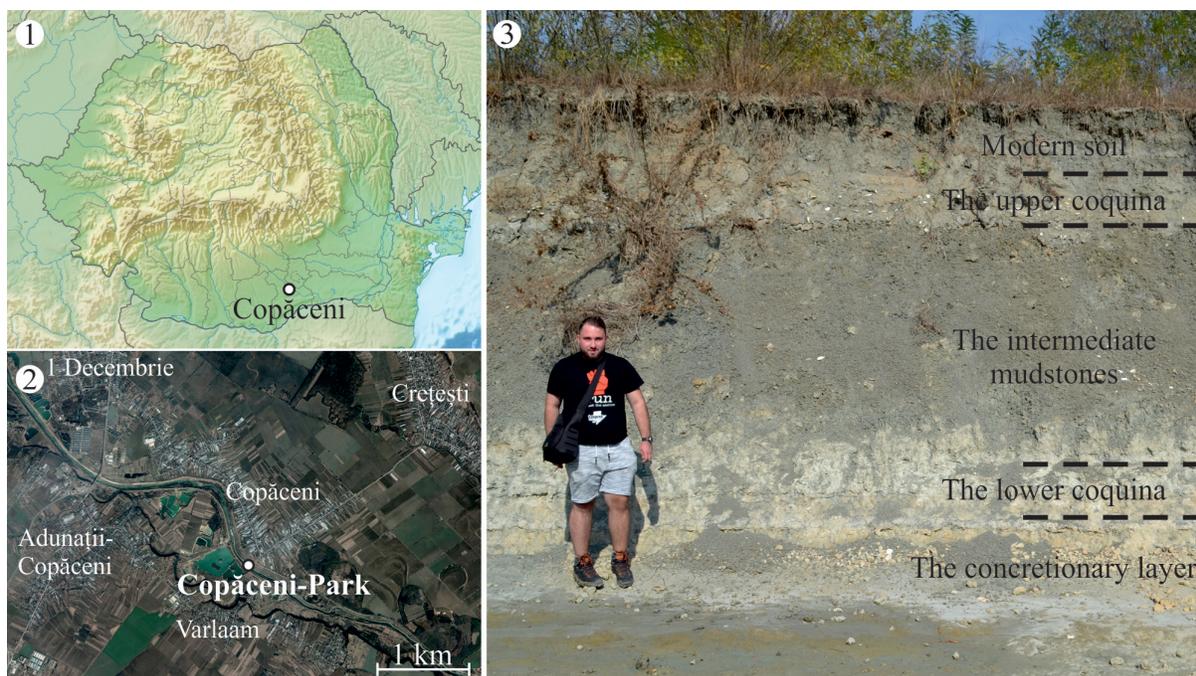


FIGURE 1. 1, location of Copăceni in Romania; 2, location of the fossil site on the left bank of Argeș River; 3, outcrop at the Copăceni-Park fossil site. Human scale equals 1.75 m.

Argedavian local age = Uzunian sub-age), based on the mollusk assemblage (Andreescu et al., 2011), and due to the presence of *Mimomys savini*, *Allophaiomys pliocaenicus*, and *Lagurodon aranka* (Andreescu et al., 2011; Știucă et al., 2012; Vasile et al., 2015). Taking this information into account, and pending research on the small mammalian assemblage of the Coconi Formation, we consider the “Copăceni beds” (1.1–1.0 Ma) as representing the basal member of a lower Pleistocene Coconi Fm., in which only the upper part might be of middle Pleistocene age.

The sedimentary succession near Copăceni (Figure 1.3), in the area of the Children’s Park, appears to be continuous, but several distinct beds can be identified. The base of the succession is not accessible, being covered by the Argeș River. Only the uppermost 20–30 cm of a silty mudstone layer, rich in carbonate concretions (hence referred herein as the concretionary layer) is accessible when the river level is low, during late summer and early autumn. This layer is not very rich in large vertebrate fossils, but it yielded several proboscidean and cervid bones. The concretionary layer is covered by fine sands, 15–20 cm thick, rich in unionid bivalve and microgastropod shells (referred herein as the lower coquina). The lower coquina is covered by silty mudstones (referred herein as the intermediate mudstones), which are

150–180 cm thick, and rich in large mammalian remains including proboscideans, rhinocerotids, and bovids. The uppermost layer, covered by modern soil, consists of 15–30 cm of fine sands with gastropod shells and a few rhinocerotid and bovid remains (referred herein as the upper coquina).

Mollusk fossil remains are very common in the lower and upper coquinas. Andreescu et al. (2011) listed bivalves *Pseudosturia caudata*, *Bogatschevia* cf. *scutum*, *B. sturi*, *B. cf. tamanica*, *Wenziella* ex gr. *wilhelmi*, *Potomida ovata*, *Margaritifera* cf. *arca*, *Crassiana pseudodavilai*, *Unio* cf. *chasaricus*, and *U. kujalnicensis*, but these taxa have not been described in detail so far.

Large mammalian remains can be found in situ or scattered along the river banks, after intense bank erosion occurs during autumn and spring, when the waters of the Argeș River are the highest. These large mammalian remains drew attention on the fossiliferous potential of the site. Proboscidean molar and postcranial bone fragments are the most common findings at the site, and were described in detail. Most of the proboscidean material was assigned to *Mammuthus meridionalis*, but some specimens were suspected as belonging to *Elephas antiquus* (Vasile et al., 2013a). Incipient study of the rhinocerotid material suggests that they belong to *Stephanorhinus etruscus* (Flintașu, 2016; Flintașu et al., 2019), whereas other large speci-

mens were assigned to the cervid *Praemegaceros pliotarandoides*, and to the bovid *Leptobos vallisarni*. A single coprolite suggests the presence of a hyaenid carnivore (Știucă et al., 2012; Vasile et al., 2015).

Following the discovery of large mammalian remains, screen-washing of sediments was used in order to identify biostratigraphically-relevant small mammals. Isolated molars were assigned to *Miomys savini*, *Allophaiomys pliocaenicus*, and *Lagurodon arankae*, but some specimens similar in morphology to *Desmana* cf. *radulescui*, *Allactaga* sp., and a castorid (*Trogotherium* cf. *dacicum*) were also mentioned (Știucă et al., 2012; Vasile et al., 2015).

Ectothermic vertebrates were also found during screen-washing, and preliminarily assigned to fishes (*Squalius* sp., *Rutilus* sp., *Scardinius* sp., *Carassius* sp., *Tinca* sp., and *Silurus* sp.), amphibians (*Rana* sp., *Bufo* sp., *Pelobates* sp., *Pelophylax* sp., *Triturus* sp., and *Lissotriton* sp.), lizards (*Lacerta* sp.), ophidians (*Natrix tessellata*, and *Coronella* sp.), but, except for the fish taxa, described in this paper, none of the groups mentioned above were so far described in detail (Vasile et al., 2013a, b, 2015, 2016, 2018).

MATERIAL AND METHODS

Approximately 1500 kg of sediment were processed in order to obtain small vertebrate remains, being evenly collected from the three main lithological horizons described above: the lower coquina, the intermediate mudstone, and the upper coquina (Figure 1.3).

The sediment collected from the strata cropping out along the Argeș River was dried to remove water contributing to the rock's cohesion. The sediment was subsequently soaked into water containing a small amount (ca. 5 %) of acetic acid, in order to dissolve the carbonate matrix of the mudstone. The soaked sediment was screen-washed, using a battery of two sieves, with 2 mm and 0.75 mm mesh sizes. The concentrate resulted by removal of the silty and clayey fractions was sorted under the binocular, and fossil remains were extracted.

The total number of processed fish remains is 130 specimens. Of these, 17 (13.1 %) are determined to species, 94 (72.3 %) to the genus, and 19 (14.6 %) up to the family level. Isolated pharyngeal teeth and their fragments numerically predominate among the fish remains in the collection, while jaw teeth, pharyngeal bone fragments, fin rays, and vertebrae centra are less numerous. Cranial elements (premaxilla, dentary, opercle) are repre-

sented by a single bone each. Specimens that could be identified taxonomically at least to family level were inventoried and stored in the collection of the "Emil Racoviță" Institute of Speleology, Bucharest.

The systematic affiliation was determined under the generally accepted methodology using the comparative osteological collection of the Department of Paleontology, National Museum of Natural History of the National Academy of Sciences of Ukraine (Kyiv). Ichthyological taxonomy used in the paper follows Nelson et al. (2016), and Froese and Pauly (2019). The names of skeletal elements are consistent with the nomenclature of Lepiksaar (1994) and Radu (2005). Terminology for pharyngeal teeth follows Rutte (1962) and Sytchevskaya (1989). Palaeoecological analysis was conducted using the actualistic approach.

Abbreviations. Co-P, Copăceni-Park Site; ISER, "Emil Racoviță" Institute of Speleology, Bucharest; NISP, number of identified specimens.

RESULTS OF THE STUDY

Following screen-washing procedures, the fossil specimens belonging to actinopterygian fishes proved to be among the most abundant. Most of the specimens consist of isolated teeth, making taxonomical assignment difficult at the species level. Following thorough morphological and morphodimensional comparison to extant fishes and to fossil material, most specimens were determined to generic level, whereas some material was only identified to family level.

Leuciscus sp. is represented by eight isolated pharyngeal teeth (ISER Co-P 32, 50, 55a-b, 73, 80a-c), both complete and fragmented. Slender pharyngeal teeth have elongated and high crowns, cylindrical pedicle, arched or almost straight back, and small blunt hook at the tip. The grinding surface is narrow, with an elevated wrinkled edge (Figure 2.1–2.2).

Ten isolated molariform pharyngeal teeth (ISER Co-P 4, 28a-d, 65a-e) in the material from Copăceni were assigned as belonging to *Rutilus* cf. *frisii* (Nordmann, 1840). They are quite large (up to 4.4 mm in height), with fungiform, laterally compressed crown and straight tooth back. The hook at the tip is absent, and the convex grinding surface is eroded. The tooth belly is rounded, hanging above the neck, while the pedicle is oval in cross-section (Figure 2.3–2.4).

Rutilus sp. is represented by one dentary fragment with rounded symphyseal edge (ISER Co-P 7), one pharyngeal bone fragment (ISER Co-P 6),



FIGURE 2. Cyprinid fossil remains from Copăceni: 1-2, *Leuciscus* sp., pharyngeal tooth in lateral (1) and medial (2) views; 3-4, *Rutilus* cf. *frisii*, pharyngeal tooth in occlusal (3), and side (4) views; 5-12, *Rutilus* sp.: 5-6, pharyngeal bone in medial (5) and ventral (6) views, 7-12, pharyngeal teeth in lateral (7, 10, 12), and occlusal (8, 9, 11) views; 13-15, *Scardinius* cf. *ponticus*, pharyngeal tooth in medial (13), occlusal (14), and lateral (15) views; 16-18, *Scardinius* sp. Copăceni, pharyngeal tooth in medial (16), occlusal (17), and lateral (18) views; 19-20, *Scardinius* sp., pharyngeal tooth in medial (19) and lateral (20) views; 21-22, *Chondrostoma* sp., pharyngeal tooth in occlusal (21) and lateral (22) views; 23-24, *Barbus* sp., pharyngeal tooth in occlusal (23) and lateral (24) views; 25-26, Barbinae gen et sp. indet., dorsal fin ray fragment in left (25) and right (26) lateral views; 27-28, *Carassius* sp., pharyngeal tooth in occlusal (27) and lateral (28) views; 29-30, *Tinca* sp., pharyngeal tooth in occlusal (29) and lateral (30) views; 31, *Abramis* sp., pharyngeal tooth in lateral view; 32, *Squalius* sp., pharyngeal tooth in lateral view; 33, Cyprinidae gen et sp. indet., pharyngeal bone fragment in ventral view. All scale bars equal 1 mm.

and 10 isolated pharyngeal teeth (ISER Co-P 30, 34, 37, 40, 44, 59, 81a-d). The dorsal edge of the dentary is narrow and forms a sharp ridge. The high pharyngeal bone is represented by a small fragment. There was two-line dentition (three teeth in the main row, and two pharyngeal teeth in the second row), but only compressed pedicles are preserved on the bone surface. The cavernous surface is narrow, with three subtriangular caverns having rounded edges (Figure 2.5–2.6). Isolated pharyngeal teeth have laterally compressed, wide and low molariform crowns without the hook at their tips. The pedicle is suboval in cross-section. The wide grinding surface is slightly concave and obliquely cut towards the rounded and narrow belly. There is a clearly defined tooth neck (Figure 2.7–2.12).

Seven isolated pharyngeal teeth (ISER Co-P 26a-g) are similar in morphology to those of *Scardinius ponticus* Kovalchuk, 2014, described from the late Miocene and Pliocene of Ukraine (Kovalchuk, 2014, 2017). These teeth have high and laterally compressed crowns. The narrow and curved tooth back rises upwards, expanding in the rounded hook, which is separated by the distinct furrow from the grinding edge. The grinding surface is long and flattened, being almost parallel to the tooth back. The anterior grinding edge is sculpted by eight convex cogs, separated from each other by protruding ridges. The small belly is laterally compressed. Tooth pedicle is cylindrical in cross-section and narrowed at the base (Figure 2.13–2.15).

There are three other pharyngeal tooth fragments representing the genus *Scardinius* in the processed material (ISER Co-P 70a-b, 79). These specimens differ from other known species of this genus in the presence of an enormous number of cogs (9 and 13) at the anterior grinding edge. Tooth back is straight, with a small hook at the tip (Figure 2.16–2.18). Pending more complete material, that might present additional features to support the description of a distinct species, we provisionally assign these specimens as belonging to *Scardinius* sp. Copăceni. In addition, there are nine pharyngeal teeth of *Scardinius* sp. (ISER Co-P 54a-c, 62, 71a-d, 78) with a blunt hook at the tip, six cogs at the grinding surface, straight or slightly curved back, rounded belly, and clearly pronounced neck (morphology exemplified by specimen ISER Co-P 54b, Figure 2.19–2.20).

Chondrostoma sp. is represented by nine isolated pharyngeal teeth (ISER Co-P 35, 36, 48, 72a-d, 82a-b). The cultriform teeth have elongated,

compressed, and oblique crowns, while the hook at the tip is absent. The grinding surface is narrow and smooth. The cylindrical pedicle is short, tooth back is almost straight, with a distinct neck and rounded belly (Figure 2.21–2.22).

Remains belonging to *Barbus* sp. are quite numerous in the material from Copăceni. There are three small pharyngeal bone fragments with one or two preserved teeth (ISER Co-P 53a-b, 66), as well as seven isolated pharyngeal teeth (ISER Co-P 31, 38, 47, 51, 61, 75a-b). The latter have a cylindrical pedicle, straight back, high spatulate crowns with a small blunt hook at the tip, and wide grinding surface. The tooth belly is small and convex, and the neck is absent or weakly expressed (Figure 2.23–2.24). A small fragment of ceratotrichium (ISER Co-P 69) with a distinct external edge was identified as belonging to *Barbinae* gen. et sp. indet. (Figure 2.25–2.26).

Carassius sp. is represented by two pharyngeal teeth (ISER Co-P 5, 43) having a laterally compressed crown, arcuate back, and rounded belly. The medial surface is concave. The slightly curved and narrow grinding surface is surrounded by low edges (Figure 2.27–2.28).

Nine isolated pharyngeal teeth, both complete and fragmented, in the Copăceni sample were assigned to *Tinca* sp. (ISER Co-P 29, 42, 57, 58, 64, 74a-c, 77). Their crowns are low (up to 2.0 mm in height) and flattened (3.6–4.0 mm in width). The tooth neck is not clearly expressed, with an arched back and a weak widened hook at the tip. The tooth belly is slightly convex, with narrow, laterally compressed grinding surface. The grinding edge is obliquely bevelled towards the tooth belly. A groove at the anterior edge of the grinding surface is indented by transverse wrinkles and forms a keel-form curl at the crown surface. The pedicle is oval (Figure 2.29–2.30).

Two pharyngeal teeth (ISER Co-P 49, 60) with a narrow gracile crowns, small thin hook at the tip, widened middle part of the grinding surface and rounded pedicle (Figure 2.31), resemble those in representatives of the genus *Abramis*, and therefore were assigned to *Abramis* sp.

Squalius sp. is represented by two isolated pharyngeal teeth (ISER Co-P 33, 46) with high elongated crowns, cylindrical pedicle and almost straight back (Figure 2.32).

It is not possible to clearly identify the systematic affiliation of some fish remains from Copăceni closer than to family level due to their poor preservation. Those are one small opercular fragment (ISER Co-P 2) with lenticular-shaped articular facet

located near the upper edge of the bone, well-developed striae, smooth external surface and concave internal one; a pharyngeal bone fragment (ISER Co-P 16, Figure 2.33), as well as two pharyngeal tooth fragments (ISER Co-P 55a-b). These specimens were left here as Cyprinidae gen. et sp. indet.

Silurus sp. is represented by three complete and fragmented pectoral spines (ISER Co-P 10, 15, 23) and one cleithrum fragment (ISER Co-P 24). All these bones belonged to young individuals. The small pectoral spine is gracile, oval in cross-section, with longitudinal striations along its shaft. The articular head of the spine is compact and flattened, with a finely porous surface. The medial and lateral margins of the shaft have numerous small and smoothed weak denticles starting almost from the articular head. The denticles on the medial margin are smaller and located more densely, whereas those on the lateral margin are larger and irregular, their tips are directed proximally. There is a deep and elongated articular facet for attaching the pectoral spine to the medial part of the cleithrum (Figure 3.1–3.4). Other catfish remains (e.g. cranial bone fragment ISER Co-P 14 (Figure 3.5), three isolated trunk vertebrae ISER Co-P 12a-b, 17) are partially broken. The centra are compressed anteroposteriorly and dorsoventrally, with almost flattened surface. We assign these fossils as belonging to Siluridae gen. et sp. indet.

Remains of salmonid fishes (Salmonidae gen. et sp. indet.) are represented by eight complete and partially broken vertebrae (ISER Co-P 1, 3, 11a-d, 13a, 26a). Their centra are small (0.5–5.0 mm in diameter, mean 2.8 mm), with deeply concave, subrectangular anterior surface and diamond-shaped posterior one. One centrum is hexagonal in shape. The aperture of the notochord is displaced dorsally. There is a network of narrow interlaced cords at the ventral surface of the centra, as well as open lattice-shaped structure (longitudinal flattened bone strips and rounded pores) at their lateral surface (Figure 3.6–3.17).

There are numerous isolated teeth of pikes in the Copăceni sample. Most of them (ISER Co-P 25, 41, 45a-b, 52, 63a-g, 76a-d) are elongated and slender jaw teeth of different size (up to 10 mm) having two sharp edges. Their cross-section is interiorly smooth and exteriorly convex (morphology exemplified by specimens ISER Co-P 25 and 52, illustrated in Figure 3.18–3.19, and 3.20–3.21, respectively). Another six pike teeth (ISER Co-P 27, 42, 45c, 63h, 68, 76e) are smaller and significantly differ in morphology. Their base is circular,

and the crown is slightly or moderately curved (Figure 3.22–3.26). These teeth most probably come from the palatine. In addition, there are three small vertebrae (3–4 mm in diameter; ISER Co-P 18, 19, 39) with deeply concave and circular anterior and posterior surfaces, as well as clearly expressed annual rings. Lateral surface of these vertebrae is perforated by the large rectangular pores with rounded edges (Figure 3.27–3.30). All these specimens were assigned as belonging to *Esox* sp. A clearer identification is not possible due to their poor preservation (see Kovalchuk et al., 2017).

Perca sp. is represented in the Copăceni sample by one complete spiny ray of the first dorsal fin (ISER Co-P 9). The fin ray (Figure 3.31–3.33) is narrow and long (16.2 mm), pointed at the tip. Its base is widened, there are small lateral pits from both sides, the anterior surface is sculpted by flattened ridges, while the posterior one has sharp edges. The proximal part of the anal fin ray (ISER Co-P 13) with a wide base and two circular articulation surfaces was also assigned to *Perca* sp. We identified a small fragment of premaxilla (ISER Co-P 67, Figure 3.34–3.35) and one broken vertebra centrum (ISER Co-P 22) as belonging to Percidae gen. et sp. indet.

DISCUSSION

The early Pleistocene freshwater fish assemblage of Copăceni consists of 17 species within 12 genera belonging to the families Cyprinidae, Siluridae, Salmonidae, Esocidae, and Percidae. Cyprinids predominate in the number of identified species over all other families represented by individual taxa. It should be noted that isolated pharyngeal teeth are difficult or even impossible to identify to lower taxonomic levels because of the high morphological variability depending on their position on the pharyngobranchial bone, ontogeny, wear, and fishes' diet (Tadajewska, 1998; van den Hoek Ostende et al., 2015). Therefore, our identifications of the cyprinid remains from Copăceni up to the generic level should be considered as tentative.

All processed skeletal elements are morphologically identical to those in living genera and almost all of them – to those in extant species. The majority of the remains were those of pike *Esox* sp. (NISP = 24; 18.3 %). The roach *Rutilus* sp., barbel *Barbus* sp., Pontic roach *Rutilus* cf. *frisii*, and rudd *Scardinius* sp. were of minor importance numerically (NISP = 12, 11, 10, 9, respectively). Other species are recorded by a fewer number of identified specimens. The minimum number of remains in the Copăceni sample belong to the bream *Abra-*



FIGURE 3. Carnivorous fish remains from Copăceni: **1-4**, *Silurus* sp., first pectoral fin ray in ventral (1), dorsal (2), medial (3), and proximal (4) views; **5**, *Silurus* sp., cranial bone fragment in dorsal view; **6-17**, Salmonidae gen. et sp. indet., isolated vertebrae in anterior (6, 10, 14), lateral (7, 8, 13, 16, 17), ventral (9, 12, 15), and dorsal (11) views; **18-26**, *Esox* sp., isolated maxillary (18-21) and palatal teeth (22-26) in anterior (18, 20, 26), lateral (19, 21, 23, 25), and posterior (22, 24) views; **27-30**, *Esox* sp., isolated vertebra centrum in anterior (27), lateral (28), dorsal (29), and ventral (30) views; **31-33**, *Perca* sp., dorsal fin ray in posterior (31), lateral (32), and anterior (33) views; **34-35**, Percidae gen. et sp. indet., premaxilla fragment in antero-medial (34) and ventral (35) views. All scale bars equal 1 mm. See text for inventory numbers.

mis sp., crucian carp *Carassius* sp., and perch *Perca* sp. (namely, two bones for each species).

Certain fish taxa listed in the faunal assemblage of Copăceni are also known from other Pleistocene localities in Europe. For example, remains of the roach, bream, pike and perch were identified among the osteological material from Greenlands Pit (Schreve et al., 2002) and West Runton (Böhme, 2010), both Middle Pleistocene in age. The ichthyofauna similar in species composition is known from the Stuttgart Wilhelma Bärengehege (Böttcher, 1994) and Rabutz (Böhme and Ilg, 2003) in Germany. Pawłowska (1963) noted the presence of *Rutilus*, *Abramis*, *Carassius*, *Esox*, and *Perca* in the interglacial deposits of Barkowice near Sulejów in Poland. All fish species identified in Copăceni are common in Pleistocene-aged assemblages of Ukraine – Lysa Gora 1 (Rekovets et al., 2014) and Medzhybizh (Kovalchuk, 2017). The fish species list of Copăceni is similar to those for the early Pleistocene Yayladag Site in Turkey (Vasilyan et al., 2014), and the middle Pleistocene Bobovek locality in Slovenia (Gaudant, 1978).

With so few occurrences of freshwater fish assemblages, spread across the entire timespan of the Pleistocene, palaeobiogeographic reconstructions remain difficult to obtain. Nonetheless, each new occurrence adds some information to the existing data. The early Pleistocene deposits from Copăceni were tentatively correlated, based on mollusk and rodent assemblages, to the 8th terraces of the Prut and Dniester rivers (Andreescu et al., 2011, 2013). Although the composition of the mollusk assemblage from Copăceni is only tentative, the correlation between mammalian assemblages from Copăceni and those from the early Pleistocene fluvial deposits of Ukraine and the Republic of Moldova (e.g., Matoshko et al., 2004) support this conclusion. The composition of the fish assemblage from Copăceni is quite similar to those of the Nogaiskian ichthyofaunal assemblage of southeastern Europe (Kovalchuk, 2017). The sedimentology of the deposits from the Dacian Basin (Andreescu et al., 2011, 2013) and that of the coeval units from of Southern Moldova and Ukraine (Matoshko et al., 2004; Nadachowski et al., 2006) suggests, however, that during the early Pleistocene most of the basins were filled with fluvial sediments, and no continuous lake that would ensure dispersion throughout the region existed. A probable isolation of the fish faunas from the Dacian Basin is also supported by a higher diversity of cyprinids, as opposite to the case recorded from Nogaisk, where cyprinid diversity decrease

was linked to a general decrease of temperature compared to the late Pliocene (Kovalchuk, 2017). The Dacian Basin may have thus represented a refugium for thermophilous taxa during the early Pleistocene.

A transfer of taxa between the Dacian Basin and the Moldo-Ukrainian area north of the Black Sea seems more probable to have occurred during the late Pliocene. The presence of a large freshwater lake in the Dacian Basin, continuous from west to east, is supported by the mollusk faunas and otolith assemblage (Pană, 1982). Evidence of connectivity to other freshwater basins to the east is not very well documented, but the study of mollusk faunas (Pană and Müntz, 2003: figure 3) suggest a corridor existed during the late Pliocene between the area north-east of the Dacian Basin and the area of southern Republic of Moldova and southern Ukraine (i.e., using the terms of Pană and Müntz, 2005, a connection across the Bârlad Depression between the Pericarpathian Depression and the Predobrogean Depression). The freshwater fish assemblage reported from the late Pliocene of Podari (Trif et al., 2016), albeit not very diverse, includes similar taxa to the late Shirokinian ichthyofaunal assemblages of southeastern Europe (Kovalchuk, 2017), supporting the idea that some connectivity between the two areas existed prior to the end of the Pliocene. More evidence in this respect could be provided by further research in eastern Romania, where rich mammalian faunas of early Pliocene age were described from Berești and Mălușteni, with freshwater fishes mentioned from the same deposits (Simionescu, 1932a, b). A revision of the material mentioned from these sites is needed.

Blanck et al. (2007) postulated that freshwater fishes can use a large diversity of habitats. It is difficult to provide a clear palaeoecological interpretation of the Copăceni assemblage based on such a poor material due to a wide ecological diversity within genera (Vasilyan et al., 2014).

Dace (*Leuciscus*), roach (for instance, *Rutilus frisii*), nase (*Chondrostoma*), and salmonids (e.g., trout *Salmo trutta*) prefer moderate to fast-flowing streams and rivers with and rock or gravel bottom (Kottelat and Freyhof, 2007). Barbel (*Barbus*) is also a rheophylic and lithophilous fish (Kotlik et al., 2004; Britton and Pegg, 2011). It inhabits moderately flowing waters with a sandy or gravel bottom. The occurrence of the rudd (*Scardinius*), crucian carp (*Carassius*), and tench (*Tinca*) indicates the presence of well-developed underwater vegetation. These fish tend to feed in areas with a large supply

of macrophytes (Nordstrom, 2011) and prefer standing to slowly flowing waters and muddy bottom (Moreno Rendón et al., 2003).

The catfish (*Silurus*) inhabits large and medium-sized lowland rivers and backwaters. This fish is an impressive predator with a wide range of food items (Copp et al., 2009). The pike (*Esox*) is a cool water fish with a wide environmental tolerance (Casselman and Lewis, 1996). It inhabits shallow and moderately productive waters (Craig, 2008; Harvey, 2009). The perch (*Perca*) also prefers the areas with slowly flowing water and thickets of vegetation (Eklöv, 1997).

Summing up the palaeoecological evidence, it can be assumed that the Copăceni fish assemblage lived in a large lowland mesotrophic river. There were rapids with fast-flowing, well-aerated water over sandy or pebbly riverbeds, areas with slowly flowing water, muddy or fine-sandy bottom and thickets of underwater vegetation, as well as backwaters. The Copăceni fish assemblage was adapted to temperate or warm climate. This is indicated by the predominance of thermophilic elements in its composition and a relatively small portion of cryophilic forms.

CONCLUSIONS

The freshwater fish fauna from the early Pleistocene of Copăceni is the first Pleistocene ichthyofaunal assemblage described from the Dacian Basin, southern Romania. It shows high taxonomic diversity, including 17 taxa comprised in 10 genera belonging to the families Cyprinidae (the best represented), Siluridae, Salmonidae, Esocidae, and

Percidae. The faunal composition is comparable to that of other southeast European assemblages, but it includes more thermophilic taxa, suggesting the Dacian Basin represented an early Pleistocene refugium in a cooling post-Pliocene environment. Comparison between the late Pliocene and early Pleistocene fish assemblages of the Dacian Basin and other ichthyofaunas of southeastern Europe, north of the Euxinian Basin, suggests a connection between the two areas existed during the late Pliocene, allowing for freshwater fish taxa interchange. The ecological affinities of the identified taxa show that fishes from Copăceni lived in a large lowland mesotrophic river, with parts of rapid waters flowing over pebbly or sandy riverbeds, but also areas of muddy waters, rich in vegetation.

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