



General palaeontology, systematics and evolution (Vertebrate palaeontology)

Occurrence of pharyngeal teeth of the carp, *Cyprinus Linnaeus* (Teleostei, Cyprinidae) in the Middle and Upper Miocene of Andalusia (southern Spain): A puzzling disconnected palaeobiogeographical distribution



Présence de dents pharyngiennes de carpe, Cyprinus Linnaeus (Teleostei, Cyprinidae) dans le Miocène moyen et supérieur d'Andalousie (Sud de l'Espagne) : une surprenante répartition paléobiogéographique disjointe

Jean Gaudant^{a,*}, Antonio García-Alix^b, Matthijs Freudenthal^c

^a USM 203 du Muséum national d'histoire naturelle et UMR 7207 du CNRS, 17, rue du Docteur-Magnan, 75013 Paris, France

^b Instituto Andaluz de Ciencias de la Tierra (IAC-CSIC-UGR), Consejo Superior de Investigaciones Científicas, Universidad de Granada, Avenida de las Palmeras nº 4, 18100 Armilla, Granada, Spain

^c Departamento de Estratigrafía y Paleontología, Campus Fuentenueva, Universidad de Granada, 18071 Granada, Spain

ARTICLE INFO

Article history:

Received 27 July 2014

Accepted after revision 9 October 2014

Available online 24 November 2014

Handled by Hans-Dieter Sues and Michel Laurin

Keywords:

Cyprinus

Cyprinidae

Teleost

Middle Miocene

Upper Miocene

South Spain

Palaeobiogeography

ABSTRACT

Three pharyngeal teeth of carp, *Cyprinus Linnaeus*, were found when washing and screening sediment in the Middle and Upper Miocene of Andalusia (Spain). Their examination has shown that they look very similar to those of the recent carp, *Cyprinus carpio Linnaeus*, so that it would not be impossible that they belong to this species. Their presence in southern Spain at that time is surprising because *Cyprinus* remains are unknown before the Pleistocene in the countries westward of Ukraine, as no articulated skeleton or bony fragment of this genus has ever been identified in the many Mio-Pliocene localities investigated throughout central and western Europe.

© 2014 Académie des sciences. Published by Elsevier Masson SAS. All rights reserved.

RÉSUMÉ

Trois dents pharyngiennes de carpe, *Cyprinus Linné*, ont été découvertes en lavant et tamisant du sédiment dans le Miocène moyen et supérieur d'Andalousie (Espagne). Leur examen a montré qu'elles sont très semblables à celles de la carpe actuelle, *Cyprinus carpio Linné*, si bien qu'il ne serait pas impossible qu'elles appartiennent à cette espèce. Leur

Mots clés :

Carpe

Cyprinidae

Téléostéens

* Corresponding author. USM 203 du Muséum national d'histoire naturelle et UMR 7207 du CNRS, 17, rue du Docteur-Magnan, 75013 Paris, France.
E-mail addresses: jean.gaudant@orange.fr (J. Gaudant), agalis@ugr.es (A. García-Alix), mfreuden@ugr.es (M. Freudenthal).

Miocène moyen
Miocene supérieur
Sud de l'Espagne
Paléobiogéographie

présence dans le Sud de l'Espagne à cette période est surprenante, parce que l'existence de restes du genre *Cyprinus* est inconnue avant le Pléistocène dans les pays situés à l'ouest de l'Ukraine, car aucun squelette en connexion, ou aucun reste osseux de carpe n'a jamais été identifié dans les nombreux gisements mio-pliocènes d'Europe centrale et occidentale.

© 2014 Académie des sciences. Publié par Elsevier Masson SAS. Tous droits réservés.

1. Introduction

During field-work in the Miocene of Andalusia, three pharyngeal teeth of carps (genus *Cyprinus* Linnaeus) were found when washing and screening sediments in two different Middle and Upper Miocene outcrops of the Guadix–Baza depression and of the Granada Basin (southern Iberian Peninsula).

2. Geological setting

The fossiliferous levels of the Guadix–Baza Depression are situated in the SW sector. According to Martín Suárez et al. (2012), we use the term “Guadix–Baza Depression” instead of “Guadix–Baza Basin” because the palaeogeographic configuration of the “Guadix–Baza Basin” (sensu stricto) started in the Late Tortonian (Soria et al., 1999; Viseras et al., 2004, and references therein), and earlier deposits correspond to a different palaeogeographic context.

The fossil locality of La Peza-4A (PEZ-4A) is located in a dark lutite level having a thickness of about 60 cm at the base of a formation mainly constituted by lacustrine limestones with lutite levels (Fig. 1). These limestones show fenestral porosity, which can be related with shallow lake level stages. These limestones alternate with continental lutites (with aquatic gastropods) and some lignite levels. Above this limestone unit, a thick lutite deposit can be observed. The transition between this lutite formation and that of the limestones is progressive, with alternation of lutite levels between the limestones. On top of the limestone unit, continental lutites crop out, and these change progressively into marine marls. Although Vera (1968) suggested a Burdigalian age with much doubts, Navarro-Vilá and García Dueñas (1977), using stratigraphic criteria, suggested a Serravallian age for these deposits. The succession clearly shows a shallowing trend (from lutites to porous limestones), and afterwards a deepening trend (from porous limestones to continental lutites and finally marine marls).

The Otura section is situated in the eastern sector of the Granada Basin (Fig. 1). This section has yielded three different fossiliferous levels with a Latest Tortonian-Earliest Messinian age: OTU-4 (Latest Tortonian), OTU-1 and OTU-3 (Earliest Messinian) (García-Alix et al., 2008). The chronology of this section was based on small fossil mammals (García-Alix et al., 2008). The studied specimen appeared in OTU-1 (Earliest Messinian age). The predominant sediments in this section are fine sands and some intercalated lutites, frequently with lignites. These deposits are related with a braided system, and the fossil levels are located in lutites and lignitiferous levels of the floodplain area.

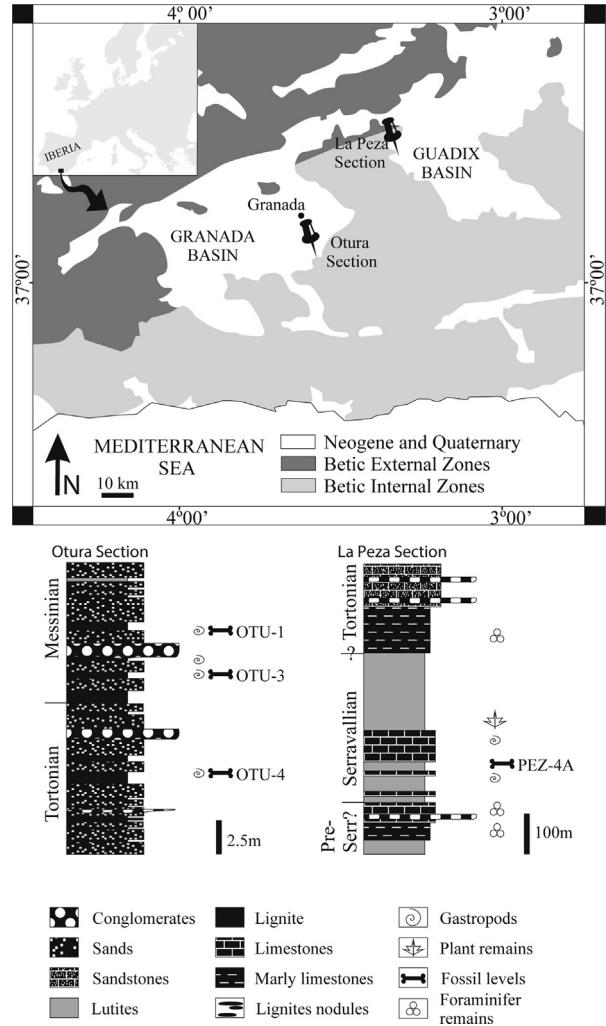


Fig. 1. Geographic situation and geology of the Guadix and Granada basins (modified from García-Alix et al., 2011). Synthetic stratigraphic columns of the studied sections (modified from Vera, 1968, and García-Alix et al., 2008).

Fig. 1. Localisation géographique et géologie des bassins de Guadix et Grenade (modifié d'après García-Alix et al., 2011). Colonnes stratigraphiques synthétiques des coupes étudiées (modifié d'après Vera, 1968 et García-Alix et al., 2008).

3. Material and methods

The studied fossil localities (PEZ-4A and OTU-1) were intensively sampled to collect small mammal remains, and about 200 and 1440 kg of sediment were extracted and processed respectively. Sediment was washed and sieved with different mesh sizes (2.5 mm, 0.7 mm, and 0.5 mm).

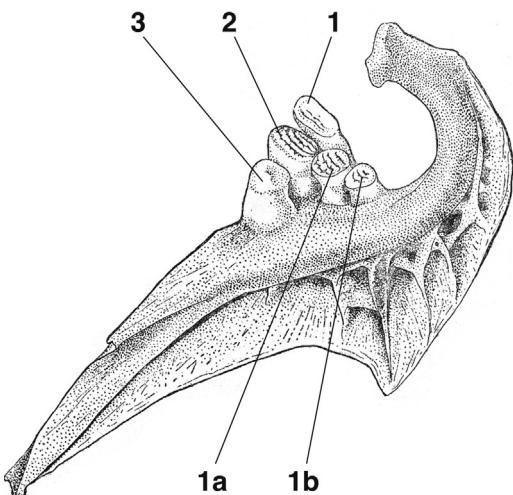


Fig. 2. Left pharyngeal bone of *Cyprinus carpio* Linnaeus. Adapted from C.J. Spillmann (1961: faune de France, 65: poissons d'eau douce, pl. II, fig. D). 1, 2, 3: teeth of the main (inner) row; 1a: tooth of the middle row; 1b: tooth of the lateral row.

Fig. 2. Os pharyngien gauche de *Cyprinus carpio* Linné. Adapté de C.J. Spillmann (1961 : faune de France, 65 : poissons d'eau douce, pl. II, fig. D). 1, 2, 3 : dents de la rangée principale ; 1a : dent de la rangée médiane ; 1b : dent de la rangée latérale.

After that, bone and tooth remains were manually collected under a binocular microscope. The teeth of *Cyprinus* were finally examined and described. A scanning electronic microscope was used for preparing the pictures.

4. Description

In the recent *Cyprinus carpio* (Linnaeus), each pharyngeal bone bears five teeth distributed in three rows (Figs. 2 and 3). The main row, or inner row, is composed of the largest teeth. The anterior one (noted 3 by Rutte, 1962),



Fig. 3. Teeth series borne by the left pharyngeal bone of a recent tench, *Cyprinus carpio* Linnaeus.

Fig. 3. Série dentaire portée par l'os pharyngien gauche d'une tanche actuelle, *Cyprinus carpio* Linné.

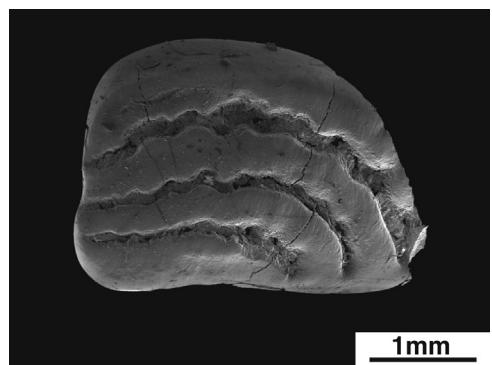


Fig. 4. Isolated pharyngeal tooth of *Cyprinus* sp. found in the level OTU-1 (earliest Messinian) of the Otura section of the Granada basin (South Spain). It was the second tooth of the main row (noted 2).

Fig. 4. Dent pharyngienne isolée de *Cyprinus* sp. provenant du niveau OTU-1 (Messinién inférieur) de la coupe d'Otura du bassin de Grenade (Sud de l'Espagne). Il s'agit de la deuxième dent de la rangée principale (notée 2).

which is cylindrical, ends distally in a hook. The second one (noted 2), which is molariform, is flattened posteriorly. Its grinding surface is typically ornamented by three or four concentric scalloped grooves. The posterior tooth (noted 1) is peg-shaped. The single tooth of the middle row (noted 1a) is quite smaller and shorter than the teeth of the mesial row. Its grinding surface is ornamented by three or four transverse grooves. The single tooth of the lateral row (noted 1b) is still smaller and shorter; when it is not worn, three transverse grooves are present on its grinding surface.

The largest and most significant fossil tooth is that from a left pharyngeal bone, which has been found in the Granada Basin, in the lower lignite level (OTU-1) of the Otura section (Fig. 4). Its crown measures 3.15 mm transversally and 2.2 mm longitudinally. Its more or less oval grinding surface is ornamented by three transversal wavy grooves that are arched backwards. This tooth is very similar to the median tooth of the main (inner) row (noted 2).

The two smaller fossil teeth (PEZ-4A) have somewhat different shapes: one, which has a quadrangular crown, has a length of 1.45 mm and a width of 1.3 mm. Its grinding surface is ornamented by two transversal grooves: one slightly convex forward, and the second almost straight (Fig. 5). The second tooth has a subcircular section. Its grinding section is ornamented with two transverse parallel wavy grooves. These two teeth may be interpreted as being the single tooth of the median row (noted 1a).

The fact that the fossil pharyngeal teeth described above do not significantly differ from those of the common carp suggests that it is not impossible that they may have belonged to the recent species *Cyprinus carpio* Linnaeus. However these remains are too much fragmentary to ascertain this hypothesis.

5. Discussion

The find of three pharyngeal teeth of the genus *Cyprinus* Linnaeus in the Upper Miocene of South Spain has a considerable biogeographical significance if we consider the

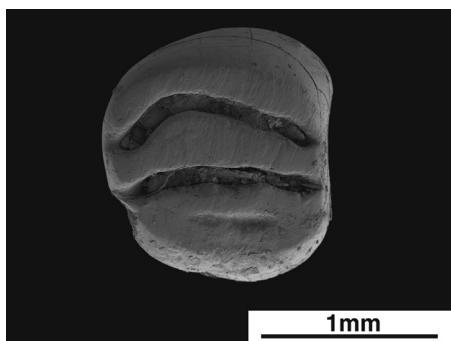


Fig. 5. Isolated tooth of *Cyprinus* sp. found in the La Peza-4A locality (Serravallian) of the Guadix-Baza Depression (South Spain). It was the tooth of the median row (noted 1a).

Fig. 5. Dent isolée de *Cyprinus* sp. provenant du gisement de La Peza-4A (Serravallien) de la dépression de Guadix-Baza (Sud de l'Espagne). Il s'agit de la dent de la rangée médiane (notée 1a).

recent distribution of this genus. In fact, the carp, *Cyprinus carpio* Linnaeus, 1758, is presently a widespread Eurasian teleost species which, in the native state, is present in the “Rivers of the Pacific Ocean basin and in East Asia from the Amur to and Burma” (Myanmar), and also in the “basins of the Black, Caspian and Aral Seas” and, eventually, “partly perhaps western Europe” (Berg, 1949/1964: 835). Additionally, because of domestication, it is also widely distributed in ponds throughout the world for the purpose of aquaculture.

In the fossil record, the genus *Cyprinus* Linnaeus is rather poorly known. Sytchevskaya (1989) described as *C. mediocris* two pharyngeal teeth from the Upper Miocene of central Asia and the subspecies: *Cyprinus carpio altaicus* Sytchevskaya, based on two incomplete pharyngeal bones from the Upper Pliocene of the Altaï territory (Siberia). Remains of *Cyprinus carpio* were also identified by Tarashchuk (1962: 17) in the Late Pliocene of the Kherson oblast (Ukraine), whereas Kovalchuk (2013) extended recently its stratigraphical occurrence to the Upper Miocene of Ukraine.

Although it is unknown in the fossil record before the Pleistocene in central and western Europe, the genus *Cyprinus* Linnaeus was several times wrongly reported from the Oligo-Miocene of Germany. The first quotation was from Brönn (1828), who called *Cyprinus papyraceus* a small cyprinid fish from the Late Oligocene of the Siebengebirge, near Bonn (Germany), which was soon after referred by Agassiz (1839) as belonging to the genus *Leuciscus* Cuvier. Later, von Meyer (1850) created the species *Cyprinus priscus* for fishes from the Lower Miocene of Unterkirchberg (Württemberg, Germany). The same species was later identified by Weitzel (1933) in the Middle Miocene of Beuern (Hessen, Germany). However, Obrhelová (1970) rightly suggested that these teleosts are really directly related to the recent Crucian Carp, *Carassius carassius* (Linnaeus) and belong to the recently created genus *Palaeocarassius* Obrhelová.

Consequently, the genus *Cyprinus* Linnaeus is presently unknown in the European fossil record before the Pleistocene in the countries westward of Ukraine where its distribution in the fossil state has been recently

re-examined by Kovalchuk (2013) who noted the occurrence of *Cyprinus* cf. *carpio* Linnaeus in the Lower Turolian (MN 11 mammal zone) of Lysa Gora-2 (Zaporizhzhia oblast) and that of *C. carpio* Linnaeus, in the Late Pliocene of the Kherson oblast, previously reported by Tarashchuk (1962). All the other Ukrainian occurrences of the genus *Cyprinus* Linnaeus are either Pleistocene (such as Lysa Gora-1: Rekovets et al., 2014) or Holocene in age.

In central and western Europe, the genus *Cyprinus* was only correctly reported from the Pleistocene (undetermined ante-Mindel warm period) of Stuttgart-Bad Cannstadt, Germany (Böttcher, 1994). However, it cannot be totally excluded that *Cyprinus* remains may exist in hitherto unknown Cenozoic localities of central and western Europe.

6. Conclusion: an unexpected palaeobiogeographical distribution

The find of pharyngeal teeth of the genus *Cyprinus* in the Late Miocene of Andalusia raises a quite unexpected palaeobiogeographical problem for explaining their occurrence in South-West Europe. In fact, it can be hardly admitted that this genus was widely distributed in central and western Europe during the Miocene and that its geographical distribution area became subsequently disconnected. The reason is that the Miocene freshwater teleosts of central and western Europe have been intensively studied during the last fifty years, so that many localities of articulated skeletons are known in the Miocene of Bulgaria (Gaudant and Vatsev, 2006 and unpublished data), Serbia (Gaudant, 1998), Hungary (Gaudant, 2005), Austria (Böhme, 2002; Gaudant, 1994, 2000a, 2010), Czech Republic (Obrhelová, 1967, 1969, 1970, 1990), Germany (Böhme, 2010; Gaudant, 1980, 1989, Gaudant and Reichenbacher, 1998; Keller et al., 2002; Reichenbacher, 1988, 2000), Switzerland (Gaudant et al., 2002; Reichenbacher, 1993) and France (Gaudant, 2000b; Mein et al., 1983) but none of them has yielded the slightest remain of the genus *Cyprinus*. Additionally, no pharyngeal tooth of *Cyprinus* has ever been found when washing and screening lacustrine sediments of central and western Europe for collecting vertebrate remains.

An alternative, highly improbable, hypothesis might have been that the carps that have been living in Andalusia during the Late Miocene and had been able to penetrate from North Africa into South-West Europe, like the characiforms and channids that have been identified in the Middle Miocene of Sansan, a well-known mammalian fossiliferous locality of the northern piedmont of the Pyrenees. However, no *Cyprinus* remain, has ever been reported from the Neogene of North Africa. Moreover, the genus *Cyprinus* is presently unknown in the native state in North Africa. Consequently, the palaeobiogeographical significance of the occurrence of this genus in the Late Miocene of Andalusia remains presently unexplained.

Acknowledgements

Philippe Loubry (Paris) is acknowledged for having prepared with a scanning electronic microscope the pictures of the fossil teeth.

References

- Agassiz, L., 1833–1844. *Recherches sur les Poissons fossiles. Imprimerie de Petitpierre, Neuchâtel* (5 volumes).
- Berg, L.S., 1949/1964. Freshwater Fishes of the U.S.S.R. and adjacent countries (in Russian, 4th ed.), vol. 2. Israel Program for scientific Translations, Jerusalem.
- Böhme, M., 2002. Freshwater fishes from the Pannonian of the Vienna Basin with special reference to the locality Sandberg near Götzendorf, Lower Austria. *Cour. Forsch.-Inst. Senckenberg* 23, 151–173.
- Böhme, M., 2010. Ectothermic vertebrates (Actinopterygii, Allocaudata, Urodea, Anura, Crocodylia, Squamata) from the Miocene of Sandelzhausen (Germany, Bavaria) and their implications for environment reconstruction and palaeoclimate. *Palaont. Z.* 84, 3–41.
- Böttcher, R., 1994. Niedere Wirbeltiere (Fische, Amphibien, Reptilien) aus dem Quartär von Stuttgart. Stuttg. Beitr. Naturkd. B 215, 1–75.
- Bronn, H., 1828. Ueber die fossilen Reste der Papierkohle von Geistinger Busch im Siebengebirge. *Zeitschrift für Mineralogie*, 1828 (1) + Taschenbuch für die gesammte Mineralogie 22 (1), 374–384.
- García-Alix, A., Minwer-Barakat, R., Martín, J.M., Martín Suárez, E., Freudenthal, M., 2008. Biostratigraphy and sedimentary evolution of Late Miocene and Pliocene continental deposits of the Granada Basin (southern Spain). *Lethaia* 41, 431–446.
- García-Alix, A., Furió, M., Minwer-Barakat, R., Martín Suárez, E., Freudenthal, M., 2011. Environmental control on the biogeographical distribution of Desmanella (Soricomorpha, Mammalia) in the Miocene of the Iberian Peninsula. *Palaontology* 54, 753–762.
- Gaudant, J., 1980. Mise au point sur l'ichthyofaune miocène d'Öhningen (Baden, Allemagne). *C. R. Acad. Sci. Paris Ser. D* 291, 1033–1036.
- Gaudant, J., 1989. Nouvelles observations sur l'ichthyofaune miocène de Steinheim am Albuch (Wurtemberg, Allemagne). Stuttg. Beitr. Naturkd. B 15, 1–33.
- Gaudant, J., 1994. L'ichthyofaune du Pannonien supérieur de Götzendorf an der Leitha (Basse Autriche). *Ann. Nat. Hist. Mus. Wien* 96A, 117–131.
- Gaudant, J., 1998. L'ichthyofaune des eaux continentales miocènes de Serbie (Yougoslavie). *Neues Jahrb. Geol. P.-A.* 207, 107–123.
- Gaudant, J., 2000a. Nouvelles recherches sur l'ichthyofaune lacustre du Karpatien inférieur d'Eibiswald et observations sur quelques os isolés de poissons découverts aux environs de Wies (Styrie). *Sitzungsberichte der österreichische Akademie der Wissenschaften (Wien), math.-naturwiss. Kl.*, [Abt. I] 207, 15–43.
- Gaudant, J., 2000b. L'ichthyofaune de Sansan (Gers). In: Ginsburg, L. (Ed.), *La faune miocène de Sansan et son environnement. Mémoires du Muséum national d'Histoire naturelle*, 183, pp. 155–175.
- Gaudant, J., 2005. L'ichthyofaune du Badenien supérieur diatomitique de Várpalota (Comté de Veszprém, Hongrie): signification paléocologique. *Földtani Közlöni* 135 (1), 1–30.
- Gaudant, J., 2010. A short account on the Miocene fish fauna from the Fohnsdorf basin (Styria, Austria). *Ann. Naturhist. Mus. Wien* 112A, 471–487.
- Gaudant, J., Reichenbacher, B., 1998. Skelette der Gattung Enoplophthalmus Sauvage, 1880 (Teleostei, Osmeridae) mit Otolithen in situ aus dem Unter-Miozän des Mainzer Beckens. *Neues Jahrb. Geol. P.-A.* 210, 237–266.
- Gaudant, J., Vatsev, M., 2006. Une ichthyofaune lacustre dans le Miocène moyen du graben de Kjustendil (Bulgarie occidentale). *Geodiversitas* 28 (1), 55–70.
- Gaudant, J., Weidmann, M., Berger, J.-P., Bolliger, T., Kälin, D., Reichenbacher, B., 2002. Recherches sur les dents pharyngiennes de la molasse d'eau douce oligo-miocène de Suisse et de Haute-Savoie (France). *Rev. Paleobiol.* 21 (1), 371–389.
- Keller, T., Reichenbacher, B., Gaudant, J., 2002. Erstnachweis von Atheriniden-Skeletten (Pisces Teleostei, Atheriniformes) mit Otolithen in situ aus dem Unteren Hydrobien-Schichten (Wiesbaden-Formation) des Mainzer Beckens, mit einem Beitrag zur Sedimentologie und Paläontologie. *Cour. Forsch.-Inst. Senckenberg* 237, 319–343.
- Kovalchuk, O.M., 2013. History of the fossil carp fishes (Teleostei, Cyprinidae) in Ukraine. *Acta Zool. Cracov.* 56 (1), 41–51.
- Martín-Suárez, E., García-Alix, A., Minwer-Barakat, R., Agustí, J., Freudenthal, M., 2012. Filling the gap: first evidence of Early Tortonian continental deposits in southern Iberia. *J. Vert. Paleontol.* 32, 1421–1428.
- Mein, P., Méon, H., Romaggi, J.-P., Samuel, E., 1983. La vie en Ardèche au Miocène supérieur d'après les documents trouvés dans la carrière de la Montagne d'Andance. *Nouv. Arch. Mus. Hist. Nat. Lyon* 21 suppl., 37–44.
- Navarro-Vilá, F., García-Dueñas, V., 1977. *Mapa Geológico de España 1:50.000. Hoja 1010 (La Peza)*. Instituto Geológico y Minero de España, Madrid.
- Obrhelová, N., 1967. Cyprinoidei (Pisces) aus dem Hangenden des miozänen Braunkohlenflözes Nordböhmens. *Palaontographica* 126 (A), 141–179.
- Obrhelová, N., 1969. Die Karpfenfische im tschechoslowakischen Süßwassertertiär. *Časopis pro mineralogii a geologii* 14, 39–52.
- Obrhelová, N., 1970. Fische aus dem Süßwassertertiär im Süden von Čechy. *Geologie* 19 (8), 967–1001.
- Obrhelová, N., 1990. Fische des nordböhmischen Brankohlenbeckens. *Acta Mus. Nat. Pragae* B 46 (1–2), 1–35.
- Reichenbacher, B., 1988. Die Fischfauna der Kirchberger Schichten (Unter-Miozän) an der Typuslokalität Illerkirchberg bei Ulm. Stutt. Beitr. Naturkd. B 139, 1–53.
- Reichenbacher, B., 1993. Mikrofaunen, Paläogeographie und Biostratigraphie der miozänen Brack- und Süßwassermolasse in der westlichen Paratethys unter besonderer Berücksichtigung der Fisch-Otolithen. *Senckenb. Lethaea* 73 (2), 277–374.
- Reichenbacher, B., 2000. Das brackisch-lakustrine Oligozän und Unter-Miozän im Mainzer Becken und Hanauer Becken: Fischfaunen, Paläökologie, Biostratigraphie, Paläogeographie. *Cour. Forsch.-Inst. Senckenberg* 222, 1–143.
- Rekovets, L., Černák, S., Kovalchuk, O., Prisyazhniuk, V., Nowakovski, D., 2014. Vertebrates from the Middle Pleistocene locality Lysa Gora 1 in Ukraine. *Quatern. Int.* 326–327, 481–491.
- Rutte, E., 1962. Schlundzähne von Süßwasserfischen. *Palaontographica (A)* 120 (4–6), 165–212.
- Soria, J.M., Fernández, J., Viseras, C., 1999. Late Miocene stratigraphy and palaeogeographic evolution of the intramontane Guadix Basin (Central Betic Cordillera, Spain): implications for an Atlantic–Mediterranean connection. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 151, 255–266.
- Sytchevskaya, E.K., 1989. Neogene freshwater fishfauna of Mongolia. *Joint Soviet-Mongolian Paleontol. Expedition Trans.* 39, 1–141.
- Tarashchuk, V.I., 1962. Materiali po vyvchennya prisnovodnykh ryb iz neogenovykh ta antropogenovykh mistseznakhodzen' Ukrayiny. *Zbirnik Prac Zoologichnogo Muzeyu* 31, 3–27 (in ukrainian).
- Vera, J.A., 1968. El Miocene del borde SW de la Depresión de Guadix. *Acta Geol. Hispánica* 5, 124–127.
- Viseras, C., Soria, J.M., Fernández, J., 2004. Cuencas neógenas postorogénicas de la Cordillera Bética. In: Vera, J.A. (Ed.), *Geología de España. Sociedad Geológica de España*. Instituto Geológico y Minero de España, Madrid, 576–581.
- von Meyer, H., 1850. Fossile Fische aus dem Tertiärthron von Unterkirchberg an der Iller. *Palaontographica* 2, 85–113.
- Weitzel, K., 1933. Fische aus der Kieselgur von Beuern (Kreis Gießen) und deren Alter. *Notizblatt des Vereins für Erdkunde und der hessischen geologischen Landes-Anstalt zu Darmstadt* 14 (5), 98–100.