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The uppermost Oligocene of Aix-en-Provence (Bouches-du-Rhône, Southern France): A Cenozoic brackish subtropical Konservat-Lagerstätte, with fishes, insects and plants

L'Oligocène supérieur d'Aix-en-Provence (Bouches-du-Rhône) : un Konservat-Lagerstätte *cénozoïque subtropical saumâtre à poissons, insectes et plantes*

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ABSTRACT

Aix-en-Provence is one of the most famous localities for Cenozoic fossils in Europe, known since the end of the 18th century for the exquisitely preserved fishes, insects and plant remains extracted from laminated deposits exposed in the underground quarries developed for the exploitation of the gypsum, and in some sites located inside and around the city. The Aix-en-Provence fossil assemblage includes a considerable variety of organisms that provide a well-documented evidence of the existence of a large subtropical brackish (primarily oligohaline) lagoon temporarily connected to the sea in southern France during the latest Oligocene.

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RÉSUMÉ

Aix-en-Provence est, parmi les localités fossilifères les plus remarquables du Cénozoïque européen, connu depuis la fin du XVIII[e] siècle pour ses poissons, insectes and plantes extraordinairement bien préservés, qui ont été extraits des dépôts laminés présents dans les carrières de gypse souterraines, mais aussi de quelques sites de surface dans et autour de la ville. Cette association de fossiles d'Aix-en-Provence contient une diversité considérable d'organismes, qui apporte de très forts arguments en faveur de l'existence d'un vaste lagon d'eau saumâtre (initialement oligohalin) temporairement connecté à la mer dans le Sud de la France à la fin de l'Oligocène.

1. Foreword

In France, Aix-en-Provence is the most famous locality for Cenozoic fossil fishes and one of the most famous for Oligocene fossil insects, mainly because of the extensive exploitation of the gypsum underground quarries called "Les Plâtrières", where fossils were collected during the 19th century in laminated deposits currently referred to the Aix-en-Provence Formation. Unfortunately, these artisanal quarries are not accessible, the last one having been closed before the Second World War and blasted during the fifties of the last century. For this reason, most of the information related to quarrying activity and collection of fossils can be solely derived from the old descriptions published by several travellers interested in natural history.

In the last decades, however, new productive sites were discovered and explored inside and around the city of Aix-en-Provence, resulting in the discovery of a large amount of fossils that broadly contribute to increase our knowledge of the overall palaeobiodiversity of this Oligocene locality, as well as of its general palaeoenvironmental context and stratigraphic evolution.

2. The subterranean "Plâtrières" of Aix-en-Provence

The earliest description of the "Plâtrières" was provided by Michel Darluc (1717–1783) in his *Histoire naturelle de la Provence* (1782). He visited the main quarry exploited at that time, called Jean's quarry, and observed the occurrence of small fossil fishes characterized by a red coloration and showing a broad head, a pointed snout and a diamond-shaped body. He compared them to small-sized sea breams, or alternatively, probably because of their red colour, to "malarmats", which are commonly called by "armoured searobins" (*Peristedion cataphractum*). Moreover, he also hypothesized that some other fishes possibly represented grey mullets and sea perches.

Five years later, in 1787, Horace-Bénédict de Saussure (1740–1799) visited the Louis's quarry, in which he distinguished seven strata, and noted the presence of fossil fishes in the stratum called "pierre schisteuse". He hypothesized that the deposits of these quarries originated at the bottom of large lakes filled either with fresh water or with salt water, as testified by the co-occurrence of both freshwater and marines fishes (Saussure, 1796).

In September 1805, Barthélemy Faujas de Saint-Fond (1741–1819) visited the Antoine Féraudi's quarry and provided a detailed stratigraphic description, in recognizing 17 strata of different thickness and lithology (Faujas de Saint-Fond, 1806). He reported the occurrence of fossil fishes in two separate levels, the lower of which is represented by a relatively thick stratum (his stratum 7) located about two to three meters above the upper gypsum and including several fish species with an overall length ranging from about 15 cm to one meter. The second productive level, which is located immediately below the second gypsum, contained abundant fishes of small size (his stratum 17).

However, the most comprehensive description of the gypsum quarries was provided by Charles Bertrand-Geslin (1796–1863), who in 1823 documented and figured the sections of two quarries, one of which comprised at least 26 strata and located near the road to Avignon, and the second one located in the nearby of Éguilles (Bertrand-Geslin, 1823, pl. XVIII). The tunnels of these two quarries are still present and their entrances visible.

Finally, in 1828, during their trip to northern Italy, Roderick Impey Murchison (1792–1871) and Charles Lyell (1797–1875) visited a quarry in which they distinguished 16 strata above the upper gypsum (Murchison & Lyell, 1829). Among the others, they observed the "Feuille à poissons", the "Feuille à mouches, or Insect bed", a "very thinly laminated" marl in which they were able to count "more than seventy distinct laminae in the thickness of an inch". However, it should be noted that their description was strongly inspired by that of Charles Bertrand-Geslin as their stratigraphic succession is almost identical to that provided by Bertrand-Geslin (1823) for the interval comprised between the strata 15 to 26.

3. The geology and the age of the Aix-en-Provence Formation

The Aix-en-Provence basin is one of the numerous irregular semi-grabens that originated during the Oligocene in southern France in response to the extensional tectonics that affected the European platform, leading to the formation of West-European rift system and the Liguro-Provençal basin (see Hippolyte et al., 1991, 1993). These Oligocene extensional basins were primarily characterized by shallow water continental sedimentation (Nury, 1988),

even if towards the end of the Oligocene some of them were occasionally connected to the Paleomediterranean.

The Aix-en-Provence Formation is largely exposed in the homonymous basin showing an overall thickness of about 150 meters. It is subdivided into informal subunits that accumulated in terrestrial, lacustrine and brackish palaeoenvironments (Nury, 1988; Nury and Raynaud, 1986). The celebrated fossils of the Aix-en-Provence Formation come from two of these subunits, the "Calcaires et marnes des stations d'essence" and the overlying "Calcaires et marnes à gypse d'Aix" (e.g., Gaudant, 2013a; Gierl et al., 2013; Nury, 1988). In particular, the largest part of the fossil fishes from the "Plâtrières" were collected in the 18th and 19th centuries in the upper part of the "Calcaires et marnes à gypse d'Aix".

The earliest attempt of a stratigraphic estimation of the age of the "terrain à gypse d'Aix" was proposed by Matheron (1839: 89), who correlated the gypsum from Aix-en-Provence with that largely exposed in the Paris area, which is overlaid by the Fontainebleau sandstone, considered at that time as an equivalent of the "molasse coquillière" of Provence (Southern France). Matheron never changed his opinion about the age of the gypsum from Aix-en-Provence and three decades later, he (Matheron, 1862: 21) considered the gypsum and the flora from Aix-en-Provence as the equivalent of the upper part of the gypsiferous sequence of the Paris area. Subsequently, Collot (1880) followed Matheron's stratigraphic interpretation and five years later, Fontannes (1885) referred the gypsum from Aix to the lower Tongrian, corresponding to the lower Rupelian (or, at least, to the Priabonian). At the end of the 19th century, Vasseur (1897) published a stratigraphic table showing that the calcareo-gypsiferous Formation of Aix – including the lower limestones with *Potamides* and the upper sequence of limestones, marls and gypsum – is equivalent to the Stampian (= Rupelian) Fontainebleau sands, whereas the overlying sands of Les Figons were considered to be coeval to the "Horizon d'Ormoy" (uppermost Oligocene).

The late Chattian age of the Aix-en-Provence Formation was debated for a long time up to the discovery of a rich mammal fauna at Venelles, (about 7 km northeast of the centre of Aix-en-Provence), Durance Basin, in deposits apparently coeval to the "Calcaire et Marnes à gypse d'Aix" (Nury, 1988, Reichenbacher, 2004). Together with a typical malacofauna that comprises *Potamides lamarcki*, *Potamides margaritaceus*, *Granulolabium plicatum*, and *Wenzia ramondi*, sixteen species of rodents characterizing the Coderet mammal zone (MP 30) were identified (Aguilar et al., 1978; Aguilar et al., 1997). The attempt of Comte (2000) to consider Venelles as basal Miocene (MN 0) instead of uppermost Oligocene (MP 30) results only from his proposal of lowering the Oligocene-Miocene boundary, with consequent redefinition of the MP 30 mammal zone renamed as MN 0.

The fossiliferous succession exposed westward of the city center of Aix-en-Provence (Figs. 1, 3) was described by Nury (1988) (Fig. 1B) who distinguished, above a marly and conglomeratic subunit called "Marnes et conglomérats de Sainte-Anne", the whitish chalky "Calcaires et marnes des stations d'essence" exposed along the road to Avignon (more precisely in the "Montée d'Avignon") covered by the "Calcaires et marnes à gypse d'Aix", in turn overlain by the "Calcaires et laminites des plâtrières". The "Calcaires et marnes à gypse d'Aix" includes three beds of saccharoid gypsum: the lower one has a thickness of about 0.70 m, the middle one, is about three meters thick, and the upper one is about one meter thick. Unfortunately, her description is essentially lithostratigraphic because her work is based on observations made in an area where the outcrops exhibit subhorizontal or feebly inclined strata. However, Saporta (1872) figured a hypothetic section of the Aix-en-Provence

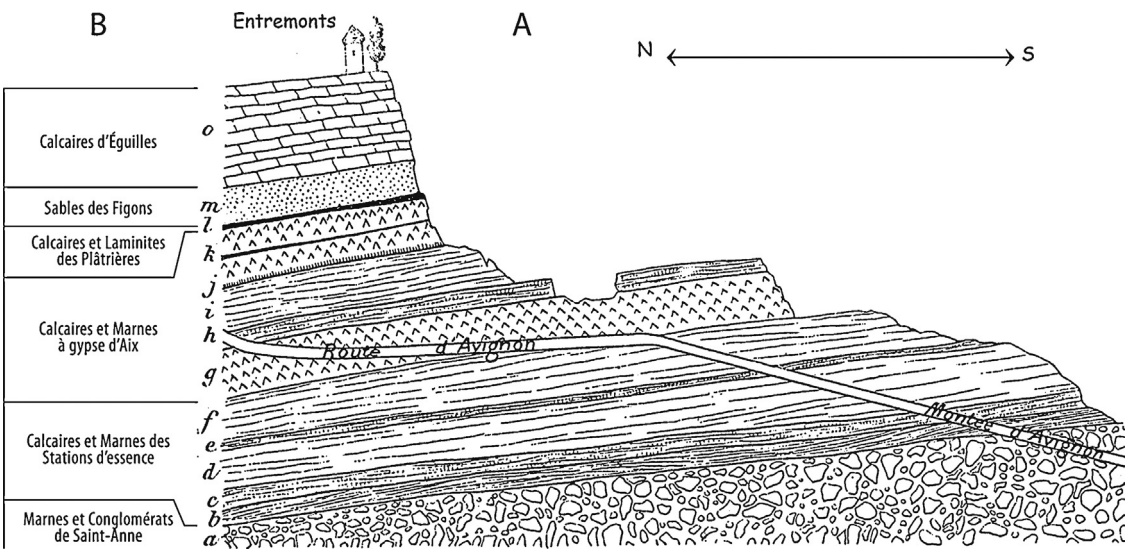

Fig. 1. The Aix-en-Provence Formation. **A**. Interpretative reconstruction of the stratigraphic section of the escarpment of the "Plâtrières" from the Avignon rise to the Entremonts tower (redrawn from Saporta, 1884). **B**. The subdivision into informal units proposed by Nury (1988).
Fig. 1. Formation d'Aix-en-Provence. **A**. Reconstruction hypothétique de la section stratigraphique de l'escarpement des « Plâtrières », montée d'Avignon vers la tour d'Entremonts (d'après Saporta, 1884). **B**. Subdivision en unités informelles proposée par Nury (1988).

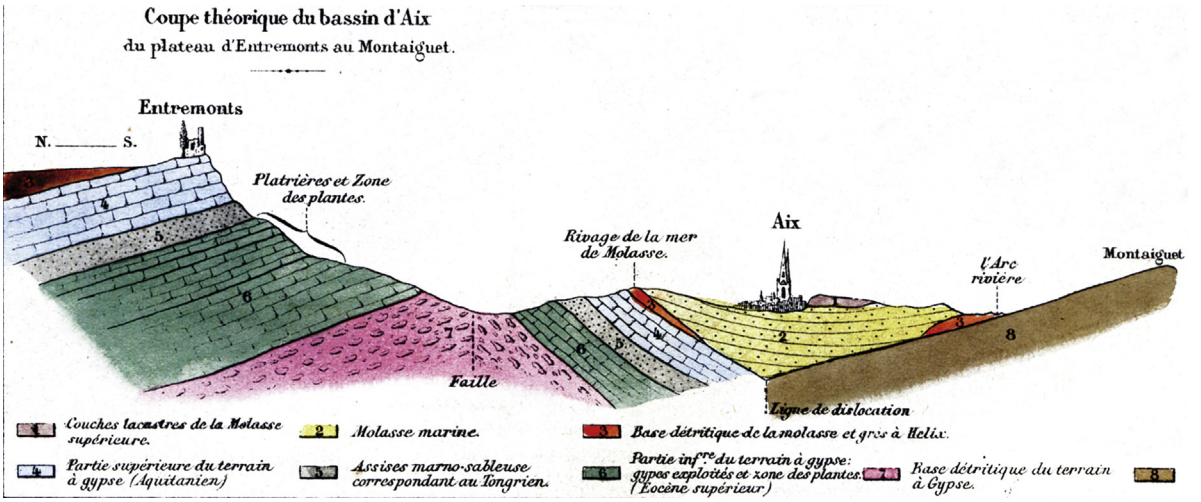

Fig. 2. The hypothetical stratigraphic section of the Aix-en-Provence basin proposed by Saporta (1872).
Fig. 2. Section stratigraphique hypothétique du bassin d'Aix-en-Provence proposée par Saporta (1872).

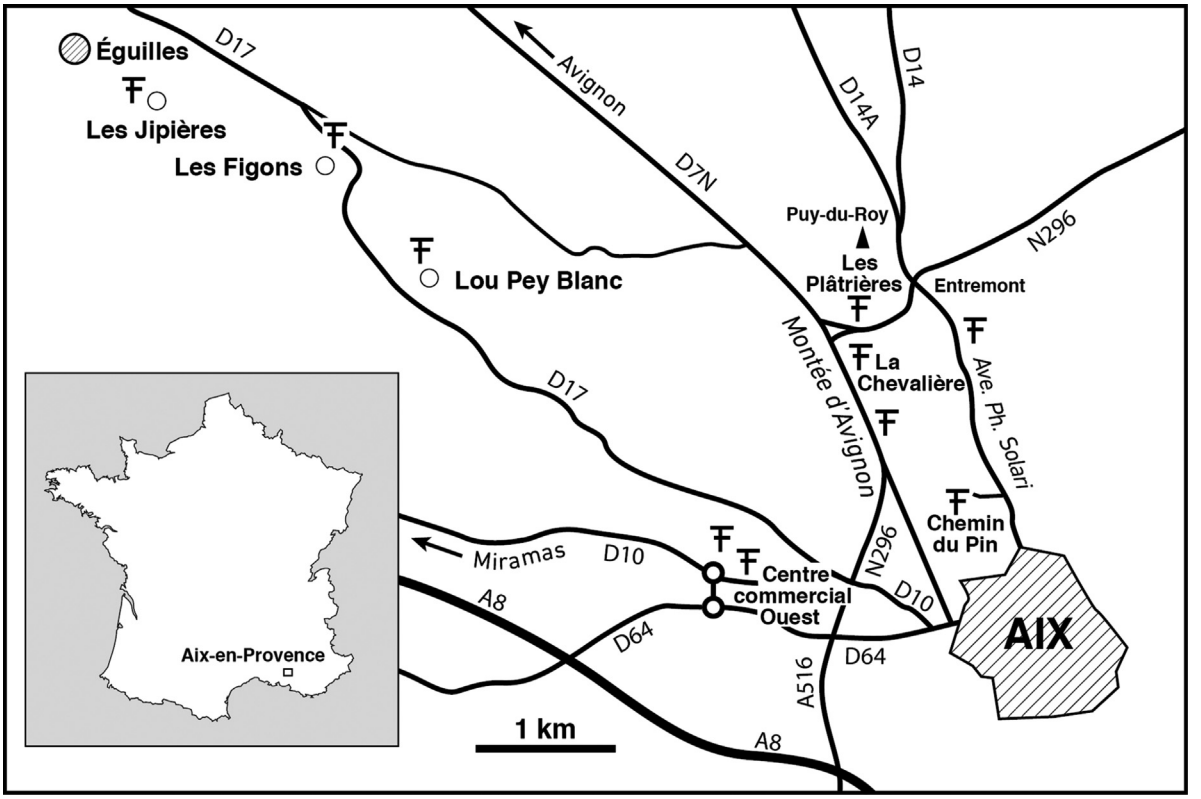

Fig. 3. Location of the fossiliferous sites of the Aix-en-Provence Formation discussed in the present paper.
Fig. 3. Localisation des sites fossilifères de la formation d'Aix-en-Provence discutés dans le présent article.

Basin showing an anticlinal structure and a fault (Fig. 2). According to him, the strata show a northern dip near the Plâtrières and a southern one near the northern limit of the marine Miocene molasse, an interpretation subsequently confirmed by the excavations made at the corner between "chemin du Pin" and "avenue Philippe-Solari", where the dip of the fossiliferous strata is about 45° SE (see Gierl et al., 2013).

The insects of the Aix-en-Provence Formation are restricted in a relatively thin level (ca. 80 cm thick, corresponding to the so-called "Feuille à mouches, or Insect bed". According to Murchison & Lyell (1829) and Saporta

(1889), the "Insect bed" is placed between a compact gypsum layer (the so-called "Le Diablon") exploited during the 18th and 19th centuries and a layer with extremely abundant individuals of '*Prolebias*' (= *Paralebias*) *cephalotes*. The latter corresponds to the "feuille à poissons" mentioned in the stratigraphic section of the "Plâtrières" published by Saporta (1889) (Fig. 3). Nury (1988) considered this mass mortality layer as belonging to the "Calcaires et laminites des Plâtrières" also based on the stratigraphic architecture of a core drilled by the "Bureau de recherches géologiques et minières" in the site of Puy-du-Roy, north of the Plâtrières. Insects are associated with abundant plant remains (leaves, fruits, seeds, flowers, roots), a few shrimps of the family Penaeidae, small *Discalioides* jellyfish possibly related to chondrophorid siphonophores, and fishes (mainly *Paralebias cephalotes*). In the other fossiliferous intervals of the formation, only gastropods, fishes and plants can be found. This insect level is subhorizontal in every site where it can be traced in the surroundings of Aix-en-Provence. This "Insect bed" consists of two members separated by a 50 cm-thick level of hard white limestone. The layers exhibit an extremely fine lamination. Surprisingly, each lamina has a specific thickness and colour, allowing one to determine the vertical position of each fossil in the "Insect bed". The fossiliferous laminae bearing insects are present in outcrops from east to west between Aix and the village of Éguilles (Fig. 3), viz. "avenue Philippe-Solari", "Les Plâtrières", "Les Figons", "Lou Pey Blanc", and "Les Jipières" near Éguilles always showing the same thickness, color and stratal architecture. The lateral development of this fossiliferous interval reaches 6 km from east to west, thereby suggesting that the aquatic palaeobiotope was remarkably large at least during the deposition of the "Insect Bed".

4. The fossil fishes from the "Plâtrières"

The first scientific study of the fossil fishes from Aix-en-Provence was realized by Henry Ducrotay de Blainville (1777–1850), who was in charge of the "*Poissons fossiles*" for the *Nouveau Dictionnaire d'Histoire naturelle appliqué aux Arts* (Blainville, 1818). He distinguished three different species in the private collections of MM. De Drée, Ménard de la Groye and Brongniart.

The first one was named *Mugil cephalus* by Blainville because of its overall similarity to the extant Mediterranean species, exemplified by similar body physiognomy, possession of a reduced number of vertebrae (22), first dorsal fin comprising three strong spines and large scales ornamented with radiating lines. Subsequently, Louis Agassiz (1833–1844) distinguished this Oligocene species from the extant one and renamed it *Mugil princeps* (Fig. 4A), a species name still valid today.

The second species, named by Blainville *Perca minuta*, is the second most common species in the Aix-en-Provence fish assemblage after *Paralebias cephalotes*. Blainville described it as a small perch-like fish, two or three inches (ca. 5 to 7.5 cm) long, with 23 vertebrae, three of which bearing ribs, posteriorly serrated preopercle, smooth opercle, anterior dorsal fin with seven relatively long spines, posterior dorsal fin with seven or eight rays, anal fin originating more posteriorly and comprising two strong spines and seven rays, and deeply furcated caudal fin with eighteen principal rays. Agassiz (1836) described this species as *Smerdis minutus*; however the generic name *Smerdis* was preoccupied, and it is presently known as *Dapalis minutus* (Fig. 4B).

The third species identified by Blainville in the Drée's collection was *Cyprinus squammosseus*. This fish has an elongate body and apparently about forty vertebrae, of which 26 caudal and 14 abdominal. According to Blainville (1818), the size, thickness, shape of the opercle, and presence of three broad branchiostegal rays suggest some relationship with the carps. Blainville (1818) noted that the pectoral fin inserts rather low on the body flanks and contains ten rays, whereas the pelvic fins, which are supported by large basipterygia and originates at midlength of the body, contain seven or eight rays, the first of which is very strong; there is a single dorsal fin, situated just above the pelvic fins and containing 16 or 17 rays supported by a similar number of pterygiophores; the anal fin is poorly developed, situated at midlength between the pelvic fins and the caudal fin and contains ten or eleven rays; the very large caudal fin is preceded by a long caudal peduncle and consists of 18 very long rays; the body is completely covered by rather large, elongate and solid scales forming a sort of delicate armour around the body. This species was re-examined by Agassiz (1844), who renamed it *Sphenolepis squammosseus.* However, also this generic name was preoccupied for a hymenopteran insect, and for this reason Cope (1885) replaced it with *Notogoneus* and assigned it to the family Gonorhynchidae (Fig. 4C).

Between 1833 and 1844, Louis Agassiz (1807–1873) published his outstanding milestone *Recherches sur les Poissons fossiles*, where in the volumes IV and V the first modern description of the Aix-en-Provence fish fauna became available and four new taxa were added. The first of these was the perch-like *Perca beaumonti*, currently referred to as *Beaumontoperca beaumonti* (see Gaudant, 2000) (Fig. 5A), perhaps a member of the family Moronidae, as suggested by the morphology of its saccular otolith (see Gaudant and Carnevale, 2015).

Another species created by Agassiz (1839) was originally called *Cottus aries* and subsequently renamed *Lepidocottus aries* (Fig. 5B) by Sauvage (1873, 1875a). The study of a newly collected material has shown that it is a gobioid apparently belonging to the Butidae (Gierl et al., 2013).

Agassiz (1839) described *Lebias cephalotes*, a small cyprinodontiform that is very abundant in certain fossiliferous horizons which are sometimes referred to as "friture" (fried fish). This species was subsequently assigned to the genus *Prolebias*, created by Sauvage (1874) for Cenozoic cyprinodontiform fishes. Costa (2012) recently demonstrated that this species can be placed within the Poeciliidae as member of the extinct genus *Paralebias* (Gaudant, 2013b) (Fig. 5C).

Finally, Agassiz described the eel *Anguilla multiradiata* based on a fragment that belonged to a private collector. This specimen cannot be found any more and is currently considered to be lost. Additional material has been collected more subsequently, including a single

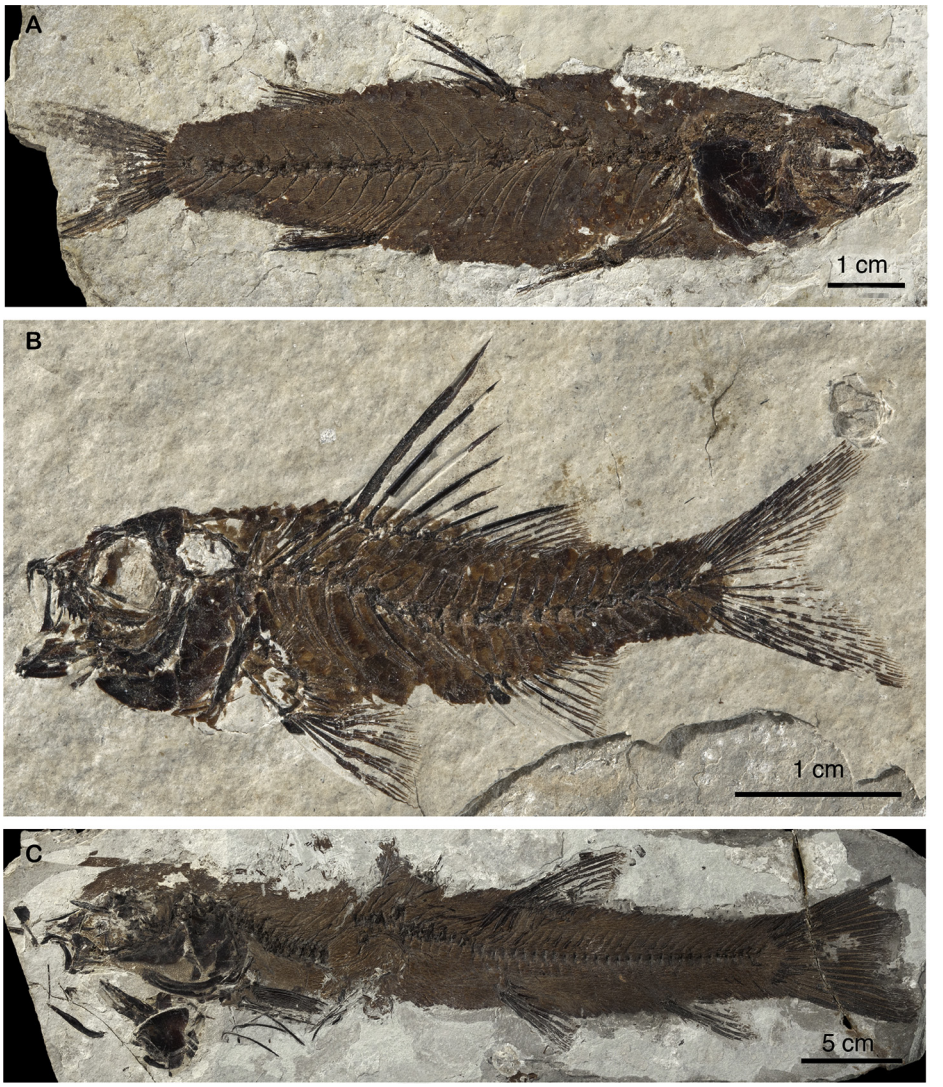

Fig. 4. The latest Oligocene fishes from the Aix-en-Provence Formation formerly described by Blainville (1818). **A**, *Mugil princeps*, MNHN.F.AIX195; **B**, *Dapalis minutus*, MNHN.F.AIX243; **C**, *Notogoneus squammosseus*, MNHN.F.AIX250.
Fig. 4. Poissons de l'Oligocène terminal de la formation d'Aix-en-Provence, anciennement décrits par Blainville (1818). **A**, *Mugil princeps*, MNHN.F.AIX195 ; **B**, *Dapalis minutus*, MNHN.F.AIX243 ; **C**, *Notogoneus squammosseus*, MNHN.F.AIX250.

incomplete specimen currently deposited in the "Muséum national d'histoire naturelle" (MNHN), Paris (Fig. 5D). Even if the generic assignment of this eel species seems to be supported by certain morphological meristic features (Gaudant, 1981), a complete revisionary study would be desirable (Blot, 1978)

Several additions to the faunal list of the fish fauna from the "Plâtrières" were made by Henri-Emile Sauvage (1842–1917). Sauvage considered surprising the presence of *Cottus aries* at Aix-en-Provence because the genus *Cottus* Linnaeus is currently confined to the cold regions of the Atlantic ocean (Sauvage, 1873) and two years later, he (Sauvage, 1875b), created the new genus *Paraperca* and the new species *P. provincialis* to include a specimen currently referred to *Lepidocottus aries*.

An additional new genus, *Desmichthys* was created by Sauvage for a partially complete skeleton from the Bouches-du-Rhône (Sauvage, 1878) possibly belonging to *Beaumontoperca*, which is kept in the geological collection of the "Muséum national d'histoire naturelle", Paris.

Five years later, Sauvage (1883) named *Sparosoma ovalis* a percoid fish housed in the palaeontological collections of the "École nationale supérieure des mines" in Paris and currently considered to be lost.

Moreover, Sauvage (1883) also reported the presence of a flatfish that he described as *Solea provincialis* based on a single specimen in a private collection. However, as suggested by Woodward (1901: 611), this fossil actually represents a cyprinodontiform fish; such hypothesis was subsequently corroborated and discussed by Gaudant (1981), who regarded it as a new species of the genus *Prolebias*.

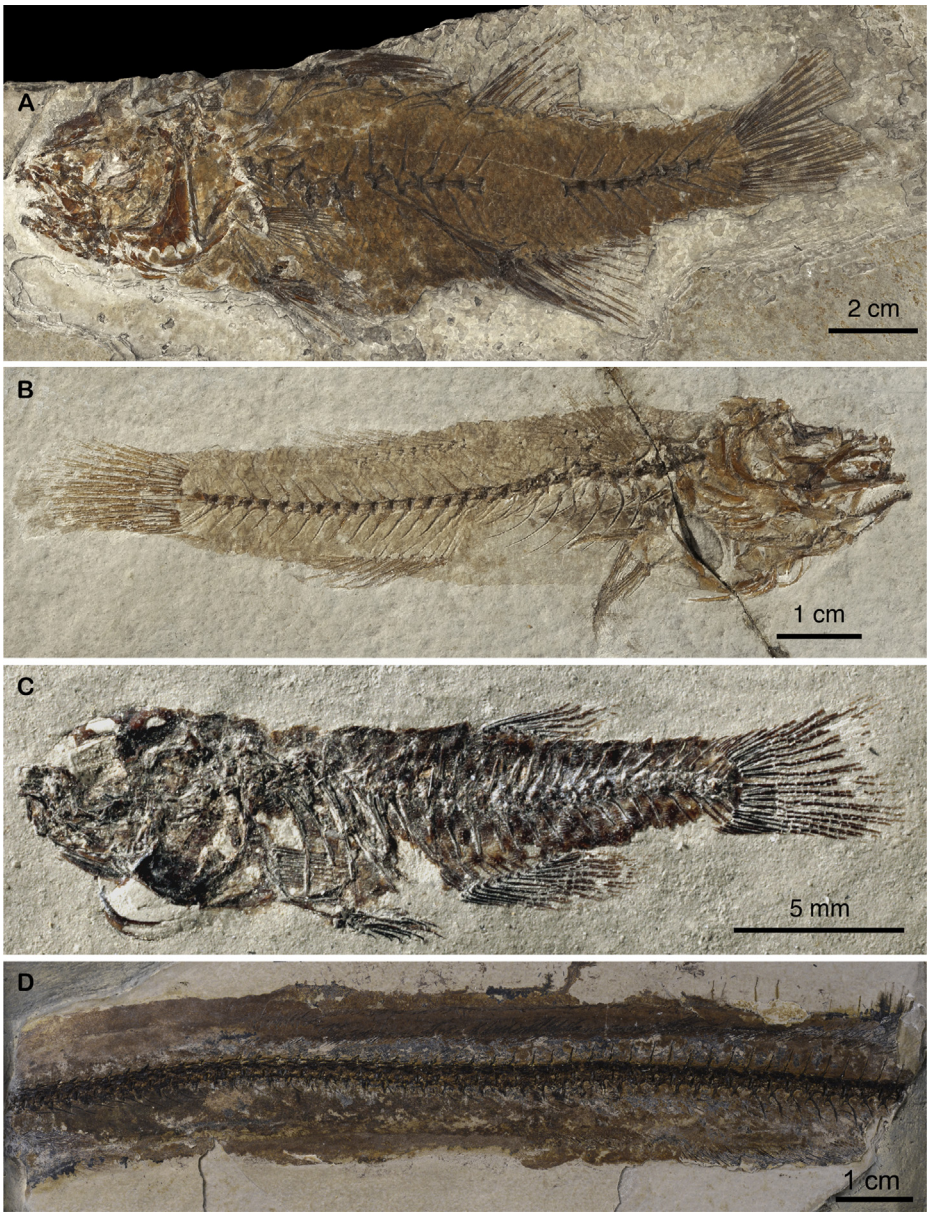

Fig. 5. The latest Oligocene fishes from the Aix-en-Provence Formation formerly described by Agassiz (1833–1844). **A**, *Beaumontoperca beaumonti*, MNHN.F.AIX232; **B**, *Lepidocottus aries*, MHNH.F.AIX237; **C**, *Paralebias cephalotes*, MNHN.F.AIX225, male individual; **D**, *Anguilla multiradiata*, MNHN.F.AIX135.
Fig. 5. Poissons de l'Oligocène terminal de la formation d'Aix-en-Provence, anciennement décrits par Agassiz (1833–1844). **A**, *Beaumontoperca beaumonti*, MNHN.F.AIX232 ; **B**, *Lepidocottus aries*, MHNH.F.AIX237 ; **C**, *Paralebias cephalotes*, MNHN.F.AIX225, individu mâle ; **D**, *Anguilla multiradiata*, MNHN.F.AIX135.

The last addition to the fish fauna from the "Plâtrières" were made in 1977 by Gaudant. Gaudant (1977) identified in the collections of the "École nationale supérieure des mines", currently deposited in the "Muséum national d'histoire naturelle", Paris, what he considered to be a new species of the genus *Lates*, *L. aquensis*, which was subsequently reassigned to the extinct genus *Eolates* (Gaudant, 1981). This specimen is currently deposited in the "Muséum national d'histoire naturelle", Paris (Fig. 6). A more recent comprehensive revision of latid fishes (Otero, 2004) demonstrated the polyphyletic status of the genus *Eolates*, thereby suggesting that a separate generic status would be desirable for the Oligocene fossil species from Aix-en-Provence.

Gaudant (1977) also described an articulated caudal skeleton apparently belonging to an indeterminate species of the genus *Amia* based on a single specimen in the collection of the "Laboratoire de géologie historique et de paléontologie de l'université de Provence", Marseille. According to Grande & Bemis (1998), the specimen does not exhibit substantial morphological evidence that would enable a generic attribution, and for this reason it should be referred to as Amiinae indet.

Fig. 6. The latest Oligocene fishes from the Aix-en-Provence Formation. *Eolates aquensis*, holotype, MNHN.F.AIX240.
Fig. 6. Poissons de l'Oligocène terminal de la formation d'Aix-en-Provence. *Eolates aquensis*, holotype, MNHN.F.AIX240.

Table 1
The latest Oligocene fish taxa from Aix-en-Provence.
Tableau 1
Liste des taxons de poissons de l'Oligocène terminal d'Aix-en-Provence.

Family	Taxon
Amiidae	Amiinae indet.
Anguillidae	*Anguilla multiradiata* Agassiz
Clupeidae	Clupeidae indet.
Gonorynchidae	*Notogoneus squamosseus* (Blainville)
	Notogoneus sp.
Cyprinidae	*Palaeotinca* sp.
	Protothymallus sp. vel *Varhostichthys* sp.
	Tarsichthys macrurus (Agassiz)
	Tarsichthys sp.
Mugilidae	*Mugil princeps* Agassiz
Cyprinodontidae	*Prolebias* n. sp.
Poeciliidae	*Paralebias cephalotes* (Agassiz)
Ambassidae	*Dapalis minutus* (Blainville)
	Dapalis cf. *macrurus* (Agassiz) *Dapalis* n. sp.
Latidae	*Eolates aquensis* (Gaudant)
Moronidae	*Beaumontoperca beaumonti* (Agassiz)
Gerreidae	*Pharisatichthys aquensis* Gaudant and Carnevale
Butidae	*Lepidocottus aries* (Agassiz)

5. New fish finds from other sites located inside and around the city of Aix-en-Provence

In the last four decades, fossil fishes were collected from several new sites located inside or in the surroundings of the city of Aix-en-Provence (Fig. 3), thereby increasing the overall diversity of the assemblage (Table 1). The fossiliferous layers of most of these sites refer to the lower portion of the Aix-en-Provence Formation, which was not explored in the "Plâtrières". Among them, three can be considered especially relevant in terms of abundance and quality of the fossils.

1. The first of these sites was temporarily exposed during the building of a house close to the city center of Aix-en-Provence, at the corner between "chemin du Pin" and "avenue Philippe-Solari" (Gaudant, 1978; Gierl et al., 2013; Pharisat, 1978). According to Gaudant (2013a) and Gierl et al. (2013), the fossiliferous layers of this site pertain to the middle portion of the "Calcaires et Marnes de stations d'essence" (see also Nury, 1988). The detailed excavations carried out at this site allowed for the first time to properly interpret the palaeoenvironmental context and evolution, which was impossible solely based on the collections of fishes from the Plâtrières that had been mixed together. These excavations evidenced the actual nature of what is generally considered as the latest Oligocene ichthyofauna from Aix-en-Provence, which consists of a dense succession of monotypic (most frequently *Paralebias cephalotes*) or oligotypic fish assemblages (i.e. *Lepidocottus aries* and *Paralebias cephalotes*; *Dapalis* sp., and *Lepidocottus aries*; *Dapalis* sp., *Mugil princeps* and *Eolates aquensis*; Gaudant, 1978). Among the fishes, *Dapalis* is extremely abundant and exclusively represented by an indeterminate species, which replaces *D. minutus*, one of the dominant taxa in the "Plâtrières" assemblage (Gaudant, 1978). A second relevant information derived from the stratigraphic excavations was that some horizons may be interpreted as spawning areas, as demonstrated by Chemin du Pin horizon XI, which has only yielded juvenile individuals of three species with standard lengths that never exceeds 22.5 mm, including *Pharisatichthys aquensis*, *Mugil princeps*, and *Eolates aquensis* (Fig. 7). In this horizon, predators apparently were uncommon, represented by isolated large scales of *Notogoneus squammosseus* and partially complete articulated skeletal remains likely belonging to *Beaumontoperca beaumonti*. Moreover, this site also provided cyprinid remains (*Palaeotinca*? sp.; Gaudant, 2013a) and André Pharisat unexpectedly extracted an adult specimen of a mojarra belonging to the family Gerreidae: *Pharisatichthys aquensis* (Gaudant and Carnevale, 2015) (Fig. 8A).
2. A second productive site was located along the road to Avignon between an AGIP gas station and the cloverleaf of La Chevalière, in the portion of the road called "Montée d'Avignon" where the "Calcaires et marnes des stations d'essence" are exposed. There, in a white marl bed also known as "Marne blanches de la Chevalière" articulated skeletons of *Dapalis* are so abundant that a nearby blind alley is presently officially named "Impasse des Dapalis"! The *Dapalis* specimens from this site seem to represent two different taxa, *D. minutus* plus what appears to be a new, previously undescribed species

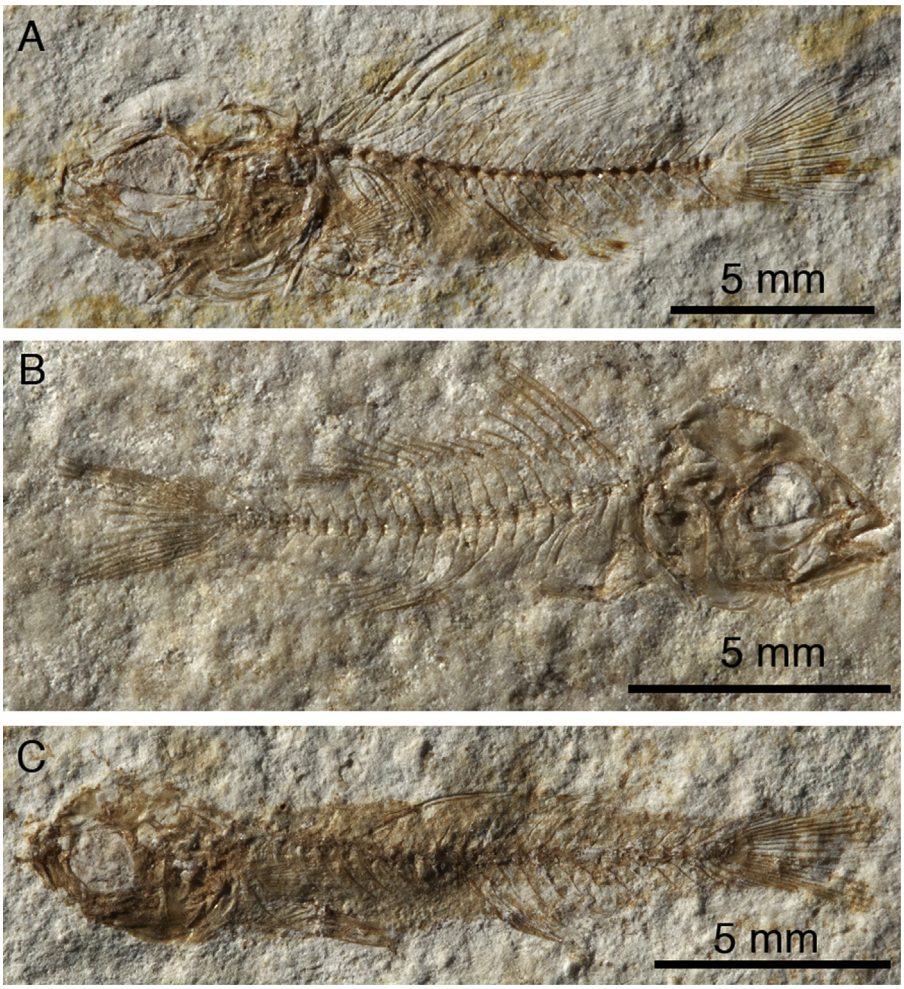

Fig. 7. The latest Oligocene fishes from the Aix-en-Provence Formation. Juvenile individuals from the level XI of the site of "chemin du Pin". **A**, *Eolates aquensis*, MNHN.F.AIX313; **B**, *Pharisatichthys aquensis*, MNHN.F.AIX314; **C**, *Mugil princeps*, MNHN.F.AIX331d.
Fig. 7. Poissons de l'Oligocène terminal de la formation d'Aix-en-Provence. Individus juvéniles du niveau XI du site du chemin du Pin. **A**, *Eolates aquensis*, MNHN.F.AIX313 ; **B**, *Pharisatichthys aquensis*, MNHN.F.AIX314 ; **C**, *Mugil princeps*, MNHN.F.AIX331d.

(Fig. 9A–B). Together with *Dapalis*, remains of the tench-like cyprinid *Tarsichthys* sp. were also found (Gaudant, 2013a).

3. Another interesting site was explored in 1981 when the laminated calcareous and marly strata pertaining to the "Calcaires et Marnes des stations d'essence" (see Nury, 1988) outcropping in the "Centre commercial Ouest", just behind a big store (presently "Géant Casino") provided a dense succession of mono- or oligotypic fish assemblages. In one of them (level IV), the very abundant *Paralebias cephalotes* is associated with a partially complete articulated skeleton of a cyprinid fish of problematic interpretation (*Protothymallus* sp. vel *Varhostichthys* sp.; Gaudant, 2013a), as well as with an indeterminate species of gonorynchid genus *Notogoneus* (Fig. 10B). *Dapalis* and *Lepidocottus* are also present in several strata of this site. Moreover, ten years ago, well-preserved articulated skeletons of clupeiform fishes (Fig. 10A) were collected by the private collector Mr. Daniel Roggero, together with scarce *Dapalis* and *Lepidocottus*, in a clayey level exposed in the nearby of the "Centre commercial Ouest", several metres below the calcareous and marly strata excavated in 1981.
4. Additional sites are located north-west of the city of Aix-en-Provence (Fig. 3) where the upper portion of the "Calcaires et Marnes à gypse d'Aix" are largely exposed. Numerous well-preserved fish remains were collected in the "Insect bed" by one of us (A.N.). In one site located not far from the village of Les Figons a complete articulated skeleton of the cyprinid *Tarsichthys macrurus* was discovered (see Gaudant, 2013a) (Fig. 8B). In the Jipières site, not far from the village of Éguilles, a rich assemblage of exquisitely well-preserved articulated fish skeletons were collected from infra-millimetrically laminated marls, including abundant *Paralebias*, some *Dapalis* and *Lepidocottus*, and a few specimens of what appears to be a new species of the extinct cyprinodontiform genus *Prolebias* (Fig. 10C).

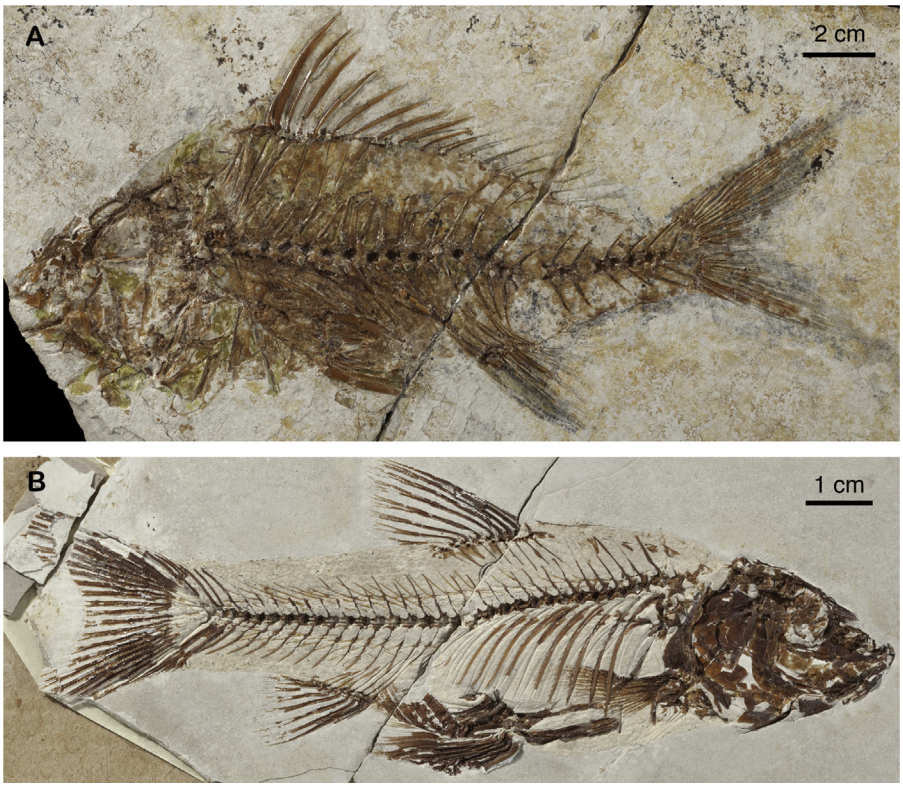

Fig. 8. The latest Oligocene fishes from the Aix-en-Provence Formation. **A**, *Pharisatichthys aquensis*, holotype, MNHN.F.AIX 231d, site of "chemin du Pin", level XI; **B**, *Tarsichthys macrurus*, MNHN.F.AIX 224g, site of Les Figons.
Fig. 8. Poissons de l'Oligocène terminal de la formation d'Aix-en-Provence. **A**, *Pharisatichthys aquensis*, holotype, MNHN.F.AIX 231d, site du chemin du Pin, niveau XI ; **B**, *Tarsichthys macrurus*, MNHN.F.AIX 224g, site des Figons.

6. Biogeographic and palaeoecological significance of the fish fauna from Aix-en-Provence

The latest Oligocene fish fauna of Aix-en-Provence consists of a mixture of freshwater, diadromous and a variety of estuarine taxa, defining a complex and heterogeneous biogeographic and palaeoecological scenario. The freshwater contingent includes the cyprinids, which are remarkable members of the Palaearctic fish fauna (Nelson et al., 2016), *Paralebias*, which appears to be closely related to the extant East African procatopodine poeciliid genus *Pantanodon* Myers (Gaudant, 2013b), and *Notogoneus* Cope, a freshwater gonorynchid that commonly occurred in Europe and North America from the late Cretaceous to the early Miocene (Grande and Grande, 2008; Reichenbacher, 2000). Putative diadromous (possibly catadromous) fishes are represented by the eel *Anguilla multiradiata*, an extinct member of a genus today widely distributed with a geographical range extending from North America to Australia and New Zealand, including Polynesia (e.g., Ege, 1939; Tesch, 1977); adult eels usually inhabit fresh and brackish waters. All the other fishes of the Aix-en-Provence assemblage may be considered as estuarine taxa, which were probably characterized by a migratory behaviour between fresh and brackish and marine waters. Among these, the mugilids are cosmopolite which are widely distributed in tropical and temperate seas (Thomson, 1997). The other fish taxa exhibit a Tethyan distribution. The palaeoecological affinities of the latid *Eolates aquensis* are of problematic interpretation. However, from a palaeobiological point of view, the extinct genus *Eolates* has been traditionally aligned to the extant amphidromous Indo-Pacific barramundi *Lates calcarifer* (see Sorbini, 1973). The genus *Dapalis* seems to be in some ways related to the extant members of the family Ambassidae (Gaudant, 1987), which are widespread in fresh, brackish and coastal marine waters of southern Asia and Australia (Nelson et al., 2016). The mojarra *Pharisatichthys* is one of the few extinct representatives of the family Gerreidae, a group primarily occurring in brackish and shallow marine waters with circumtropical distribution (see Chen et al., 2007) ranging from the Caribbean Sea and Gulf of Mexico to the Indian and the western Pacific oceans to Australia. The Oligocene genus *Lepidocottus* is most likely a member of the gobioid family Butidae (Gierl et al., 2013), a group currently mostly occurring in fresh and brackish waters of West Africa, Madagascar, South Asia and Australia (Thacker, 2011). Other species of the genus *Lepidocottus* have been reported from deposits originated in freshwater or brackish palaeobiotopes (e.g., Pandolfi et al., 2017). Finally, the putative moronid *Beaumontoperca beaumonti* can be also added to this group, although the recent distribution of this family is mostly restricted to the western Tethys, in the subtropical marine and brackish waters of the Gulf of Mexico and

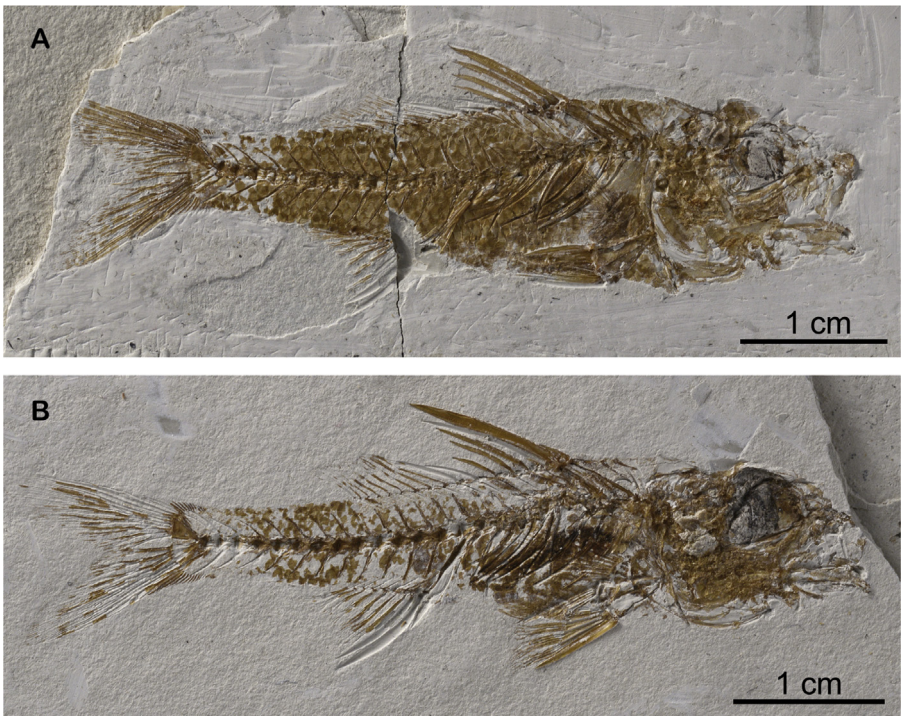

Fig. 9. The latest Oligocene fishes from the Aix-en-Provence Formation. The *Dapalis* from the site of La Chevalière. **A**, *Dapalis* n. sp., MNHN.F.AIX261.B; **B**, *Dapalis minutus*, MNHN.F.AIX259.
Fig. 9. Poissons de l'Oligocène terminal de la formation d'Aix-en-Provence. *Dapalis* du site de La Chevalière. **A**, *Dapalis* n. sp., MNHN.F.AIX261.B ; **B**, *Dapalis minutus*, MNHN.F.AIX259.

the Mediterranean Sea but also along the Atlantic coasts of North America and Europe (Nelson et al., 2016).

The analysis of the possible ecological preferences of the members of the latest Oligocene ichthyofauna of Aix-en-Provence clearly evidenced that most of the taxa were able to live in brackish and/or fresh waters. Therefore, considering that the fossil fish fauna from Aix-en-Provence consists of successive mono- or oligotypic assemblages, and that some of the laminated strata, such as the fish level XI of the Chemin du Pin site have exclusively provided juvenile individuals (Fig. 7) the fossiliferous series may be interpreted as being accumulated in a quiet brackish lagoon temporarily connected to the sea, which was only 25 km far, in the surroundings of the area where Marseilles and Carry-le-Rouet are today (see also Reichenbacher, 2004).

7. Gaston de Saporta and the Aix-en-Provence fossil flora

Saporta (1889) described a diverse assemblage of fossil plants from the fossiliferous deposits of the Aix-en-Provence Formation, which comprises both aquatic and terrestrial taxa (Figs. 11–12). Aquatic plants include typical freshwater taxa, including members of the families Hydrocharitaceae (*Vallisneria*), Nymphaeceae (*Anoectomeria*, *Nymphaea*) and Potamogetonaceae (*Potamogeton*). Moreover, a number of riparian plants were also present, including *Carex*, *Sparganium* and *Typha*.

According to Saporta (1879: pp. 237–239), the Oligocene lagoon/lacustrine palaeobiotope of Aix-en-Provence (Fig. 11) was surrounded by rather small pine trees represented by twigs, pine cones and even buds and catkins. Pine trees were associated with Thujas of African affinities, similar to the African cypress *Widdringtonia*, and with a juniper (*Juniperus ambigua*) showing similarities with an extant species living in Middle East and Greece. Moreover, three main groups of exotic plants were present near the shore line. First of all, there were fan-like palm trees of the genus *Flabellaria*, characterized by a relatively reduced size, like the Recent Chusan palm tree, *Trachycarpus fortunei*, but bearing remarkably developed fronds about 1.5 m long. A second exotic tree was a Dragon tree with sword-like leafs, comparable with the modern *Dracaena draco* living in the Canary islands. Banana trees were also present at Aix-en-Provence, as shown by leaf and petiole fragments apparently similar to those of the extant Abyssinia banana tree, *Ensete ventricosum*, from Ethiopia and tropical Africa.

A complete list of the fossil plant collected by Saporta was published by Gregor and Knobloch (2001).

8. The insect assemblages

The sediments of the Aix-en-Provence Formation are known for their well-preserved fossil insects since the beginning of the 19th century. Some of these latest Oligocene insects are very famous, as for example, *Neorinopis sepulta*, which represents the first fossil butterfly to be described (Nel and Nel, 1986). This entomofauna was extensively studied by various authors during the

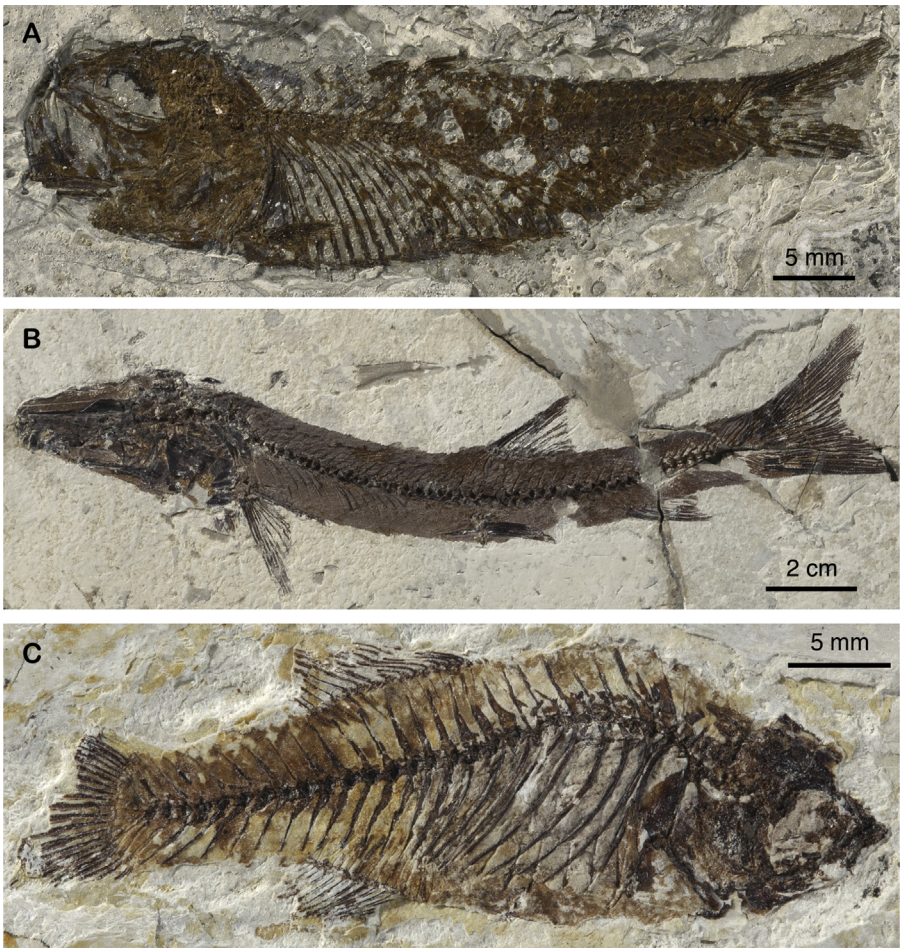

Fig. 10. Previously unknown fishes from the Aix-en-Provence Formation. **A**, Clupeidae indet., MNHN.F.AIX356, "Centre commercial Ouest"; **B**, *Notogoneus* sp., MNHN.F.AIX352, Centre commercial Ouest; **C**, *Prolebias* n. sp., MNHN.F.AIX354, Éguilles.
Fig. 10. Poissons non encore décrits de la formation d'Aix-en-Provence. **A**, Clupeidae indet., MNHN.F.AIX356, Centre commercial Ouest ; **B**, *Notogoneus* sp., MNHN.F.AIX352, Centre commercial Ouest ; **C**, *Prolebias* n. sp., MNHN.F.AIX354, Éguilles.

19th century. The most important works were made by Serres (1828, 1829), Scudder (1875), Oustalet (1874), Meunier (1913a,b,c, 1914, 1915, 1918), and Théobald (1934, 1937a,b). Overall, these authors described hundreds of different species. Unfortunately, they worked on the basis of the knowledge of their time, and therefore, nearly all the taxa they described are badly in need of a complete revision and reinterpretation.

The ancient collections of fossil insects from Aix-en-Provence are in large part housed in the Muséum National d'Histoire Naturelle, Paris, with a few fossils in the Natural History Museum, London, as well as in the museums in Lyon, Aix-en-Provence and Marseilles. One of us (A.N.) made extensive excavations in all the known sites located around the city of Aix-en-Provence since 1980, resulting in a new collection of more than 50,000 specimens.

The type of preservation of the insects is rather infrequent for the Oligocene localities. Except for the fossils discovered in the ancient site of the "Plâtrières" in which some carbon of the original cuticle is preserved, the organic matter is usually completely replaced by calcite. Except for the Odonata that are frequently dislocated, the insects are generally complete and fully articulated.

The insect fauna mainly comprises beetles (in the great majority Curculionoidea), and flies (mainly Bibionidae). Other orders are much less frequent, except for the dragonfly nymphs, extremely abundant in some layers together with numerous chironomid larvae and pupae. Except for these nymphs and one small species of hydrophilid beetle, the aquatic fauna is clearly underrepresented compared to the terrestrial insects. A few Hydrometridae, a single Notonectidae, a single Nepidae, and a single Naucoridae were found. The quality of the water was probably not excellent, considering that no larvae of Ephemeroptera, Plecoptera, or Trichoptera have been found (no caddisfly case).

The following orders are represented (see Fig. 13) in decreasing order of abundance: Coleoptera, Diptera, Hymenoptera, Hemiptera (cicada-like fossils and bugs), Odonata, Lepidoptera, Isoptera. Representatives of some other orders are very uncommon (Trichoptera, Thysanoptera, Psocoptera, Blattodea, etc.), and some are

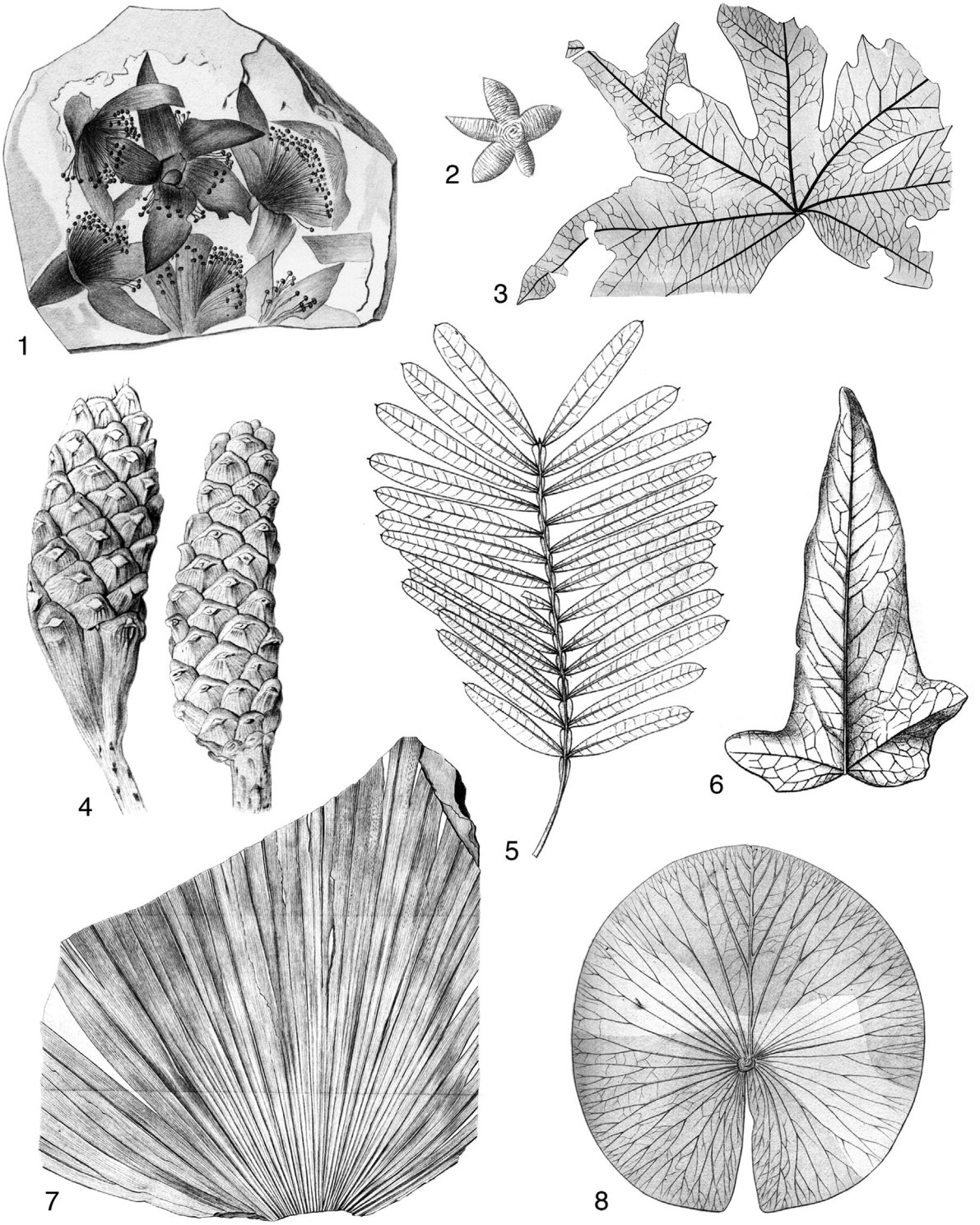

Fig. 11. Fossil plant remains from the "Plâtrières" of Aix-en-Provence described and figured by Gaston de Saporta (Saporta, 1872). **A**: flowers of *Bombax sepultiflorum*; **B**: flower of *Diospyros rugosa*; **C**: leaf of *Aralia aquisextana*; **D**: pine cones of *Pinus robustifolia*; **E**: leafy branch of *Pistacia aquensis*; **F**: leaf of *Hedera philiberti*; **G**: leafy branch of *Flabellaria costata*; **H**: leaf of *Nymphaea gypsorum*.

Fig. 11. Plantes fossiles du site des « Plâtrières », Aix-en-Provence, décrites et figurées par Gaston de Saporta (Saporta, 1872). **A**. Fleurs de *Bombax sepultiflorum* ; **B** : fleur de *Diospyros rugosa* ; **C** : feuille d'*Aralia aquisextana* ; **D** : cônes de *Pinus robustifolia* ; **E** : branche feuillue de *Pistacia aquensis* ; **F**, feuille d'*Hedera philiberti* ; **G** : branche feuillue de *Flabellaria costata* ; **H** : feuille de *Nymphaea gypsorum*.

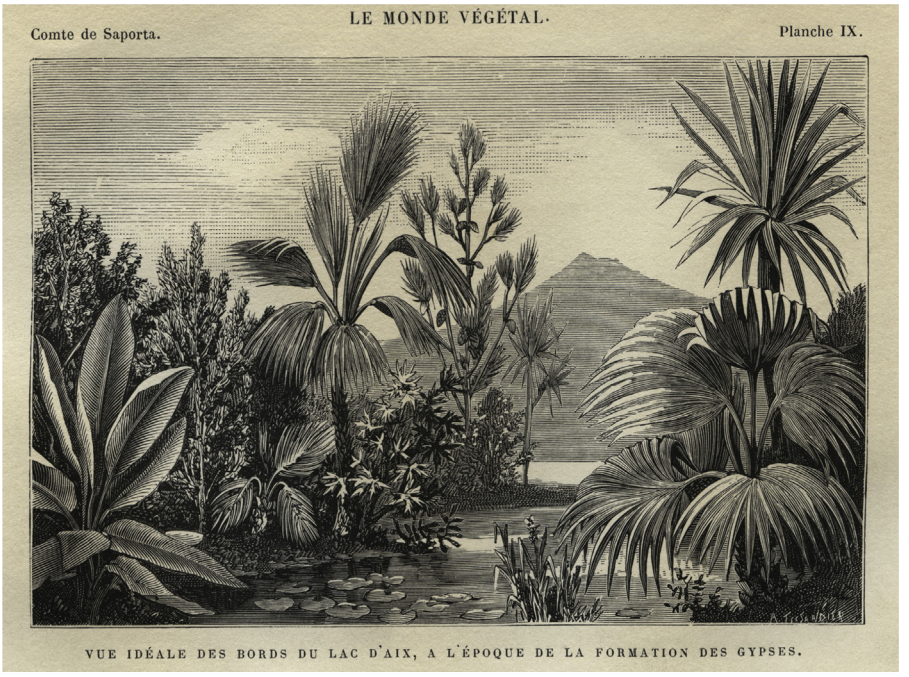

Fig. 12. Hypothetical reconstruction of the vegetation surrounding the depositional environment of the latest Oligocene Aix-en-Provence Formation (Saporta, 1879), showing the palm tree *Flabellaria lamanonis*, dragon tree *Dracaena brongniartii*, water lily *Nymphaea gypsorum*, banana tree (*Musa*), oaks (*Quercus*), spikenard (*Aralia*), and pine *Pinus philiberti*.
Fig. 12. Reconstitution hypothétique de la végétation entourant le milieu de dépôt de l'Oligocène terminal d'Aix-en-Provence (Saporta, 1879), montrant le palmier *Flabellaria lamanonis*, le dragonnier *Dracaena brongniartii*, le nénuphar *Nymphaea gypsorum*, le bananier (*Musa*), des chênes (*Quercus*), un *Aralia* et le pin *Pinus philiberti*.

completely not recorded (Ephemeroptera, Plecoptera, Mantodea).

There are very few traces of insect activities on plants (attacks on leaves) or in the sediment (no bioturbation due to insect larvae).

The overall diversity of the entomofauna from Aix-en-Provence is comparable to those from the Oligocene of Céreste and Bois d'Asson (Lubéron) with an estimation of ca. 1000 different species of insects. Some taxa are extremely rare, known only by a single specimen.

The Oligocene insects belong in their great majority to modern families (and even genera), and only a few can be referred to extinct families (Odonata Sieblosiidae for instance). This distributional pattern is fully confirmed by the assemblages documented for Aix-en-Provence. These insects are highly significant for the palaeobiogeography and the palaeoclimatic reconstructions. Some insects from Aix belong to clades that are now restricted to very distant areas. For instance, a termite of the modern Australian genus *Mastotermes* is known from Aix (Nel and Paicheler, 1993). Some others are indicators of the establishment of the earliest geographic connections between western Europe and Africa during the Oligocene (viz. the damselfly genus *Sapho* now restricted to western Africa) (Nel and Papazian, 1992).

Théobald (1937a) supposed that the main part of this entomofauna had its modern relatives in the Indo-Malaysian region. A comprehensive revision of the entire entomofauna would be necessary to confirm such hypothesis. Anyway, it is evident that these insects clearly document the presence of warm tropical-subtropical conditions, even though a relative cooling trend seems to be indicated by the analysis of the proportions of the different genera of the Bibionidae, compared to the older localities of Céreste and Bois d'Asson (Collomb et al., 2008).

9. The palaeoenvironmental context

The ecological conditions that characterized the Aix-en-Provence basin during the deposition of the homonymous formation have been extensively debated since 1880 when Collot (1880: 111) suggested that the entire sequence "from its base to its top, shows so excellently the imprint of a lacustrine sedimentation implying that it is impossible to believe that the gypsum could be the result of a concentration of sea waters" (translation from the French by J.G.). Such a point of view was in some ways shared by Saporta (1879) and Denizot (1939) who discussed certain features of this latest Oligocene palaeolake.

The presence of several articulated skeletal remains of the frog *Rana aquensis* (Fig. 14A) in the "Plâtrières" and in the "Insect bed", reported for the first time by Coquand (1845) and then confirmed by Piveteau (1927), is a remarkable evidence of the occurrence, at least periodic, of freshwaters in the basin. According to Piveteau (1927), this late Chattian frog species is closely related to the extant *Rana esculenta*. Similar palaeoecological information seems to be also provided by the chelonians, among which fully

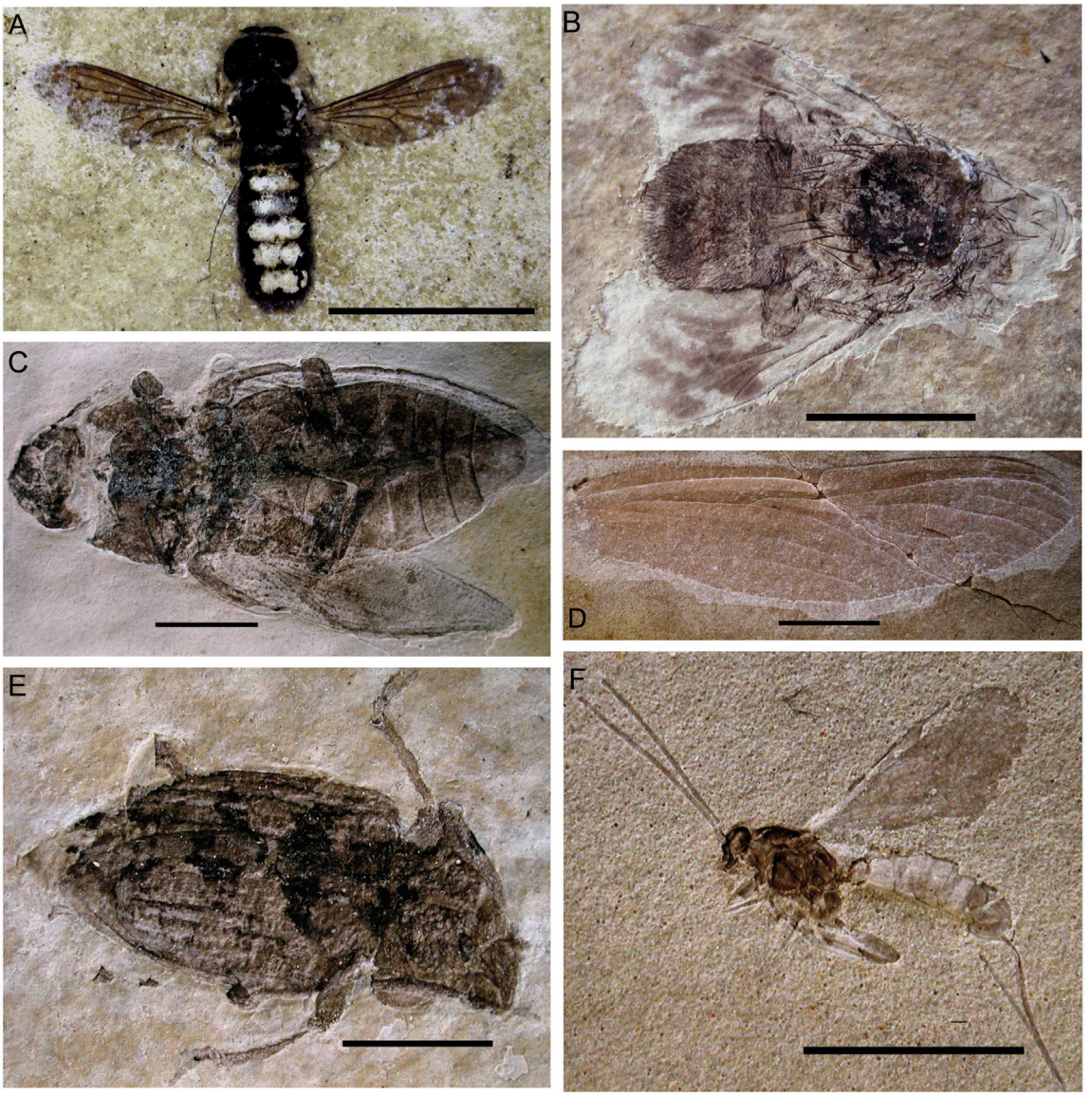

Fig. 13. Fossil insects from the Aix-en-Provence Formation. **A**, Diptera Bombyliidae, MNHN.F.B44306, Les Plâtrières; **B**, Diptera Tephritidae, MNHN.F.A59036, Les Figons; **C**, Coleoptera Buprestidae, MNHN.F.A59037, Les Figons; **D**, Odonata Libellulidae, forewing, MNHN.F.A59038, Les Figons; **E**, Coleoptera Curculionidae, MNHN.F.A59039, Les Figons; **F**, Hymenoptera Ichneumonidae, MNHN.F.A59040, Les Figons. Scale bars 5 mm.
Fig. 13. Insectes fossiles de la formation d'Aix-en-Provence. **A**, Diptera Bombyliidae, MNHN.F.B44306, Les Plâtrières ; **B**, Diptera Tephritidae, MNHN.F.A59036, Les Figons ; **C**, Coleoptera Buprestidae, MNHN.F.A59037, Les Figons ; **D**, Odonata Libellulidae, aile antérieure, MNHN.F.A59038, Les Figons ; **E**, Coleoptera Curculionidae, MNHN.F.A59039, Les Figons ; **F**, Hymenoptera Ichneumonidae, MNHN.F.A59040, Les Figons. Échelles : 5 mm.

terrestrial and lacustrine taxa have been recognized (see Fontes et al., 1980).

In order to explain the presence of the gypsiferous deposits in a continental setting, Corroy and Denizot (1943) suggested that the sedimentary basin was filled with selenitic water derived from the leaching of Triassic evaporitic deposits that were probably exposed in the hinterland.

A different interpretation was proposed by Nury (1968, 1988), who primarily based on an erroneous interpretation of the fossil record hypothesized that a marine influence was responsible of the origin of the evaporitic (gypsiferous) sediments of the Aix-en-Provence Formation. Her main argument was based on the ecological affinities of the certain molluscs that she (erroneously) regarded as remarkable indicators of marine influence. However, genuine freshwater pulmonate gastropods, including planorbids of the genera *Anisus* and *Gyraulus* and lymnaeids, have been recorded in certain fossiliferous levels, in some cases associated with euryhaline taxa (Gaudant, 1978). Nury's second argument was based on the erroneous identification of a flatfish by Sauvage (1883). Such identification, however, was rejected by Woodward (1901: 611), who suggested that this specimen actually represents a

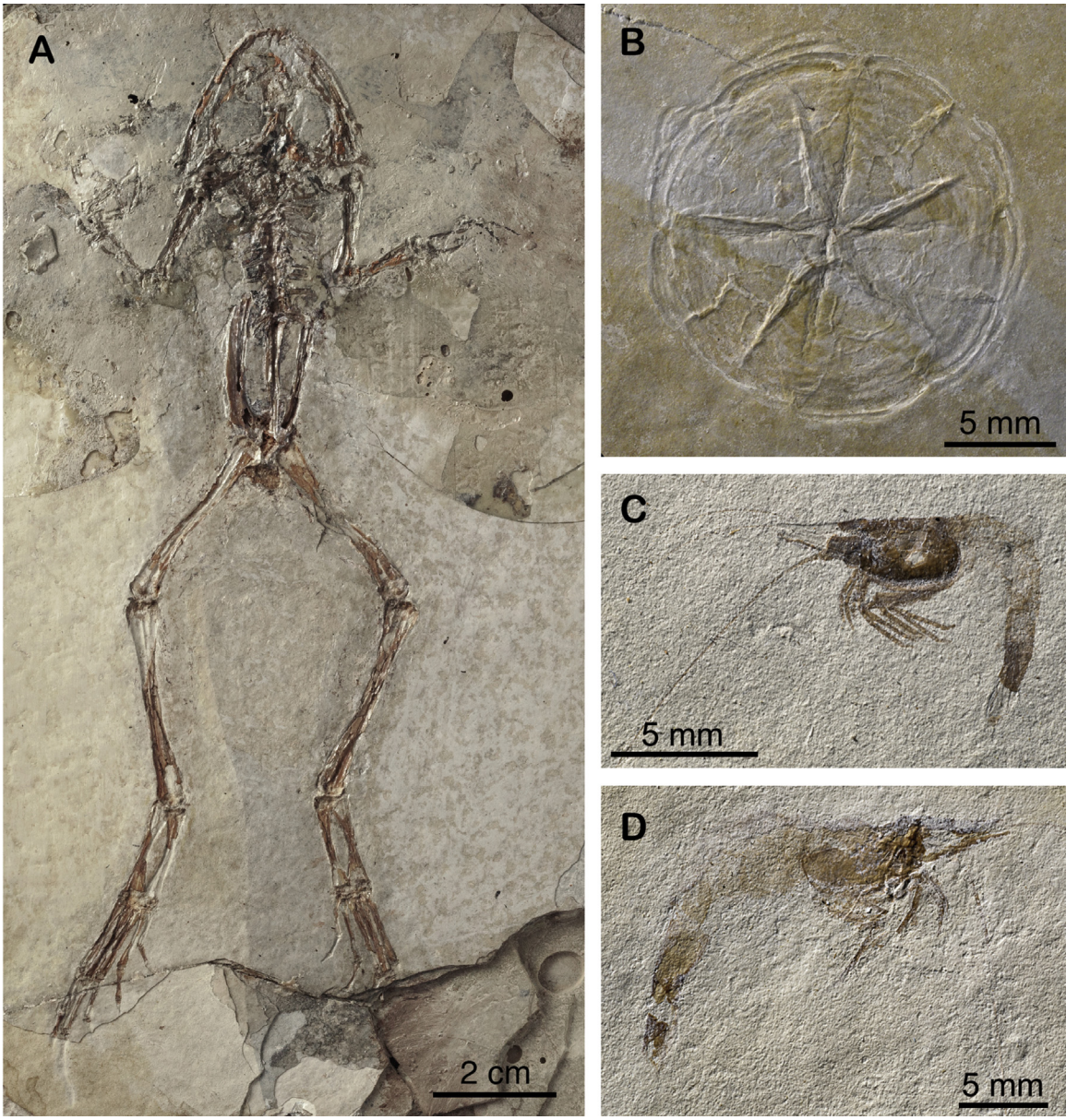

Fig. 14. A: the fossil frog *Rana aquensis*, MNHN.F.AIX355 (specimen collected at les Plâtrières by Gaston de Saporta); **B**: the chondrophoride siphonophore *Discalioides*, MNHN.F.A59035, Éguilles; **C–D**: penaeid shrimps, MNHN.F.A59323 and MNHN.F.A59324, Les Figons.
Fig. 14. A. Grenouille fossile *Rana aquensis*, MNHN.F.AIX355 (spécimen collecté sur le site des Plâtrières par Gaston de Saporta) ; **B** : chondrophoride siphonophore *Discalioides*, MNHN.F.A59035, Éguilles ; **C–D** : crevettes penaeides, MNHN.F.A59323 and MNHN.F.A59324, Les Figons.

cyprinodontiform fish. Her third argument, concerning the presence of charophytes, is also not conclusive since it is based on the possibility that certain taxa of these freshwater algae are also able to live in hypohaline waters.

Nevertheless, it is evident that short-lived connections may have episodically occurred between the Aix-en-Provence Basin and the sea, as suggested by the presence of penaeid shrimps (Fig. 14C–D) as well as by the peculiar composition of the fish assemblage that comprise typical catadromous fish such as the eel *Anguilla multiradiata* and the mullets, which are genuine marine migratory fishes that usually spend part of their juvenile phase in brackish or fresh waters before returning to the sea as adults for spawning. Moreover, the presence of the marine family Gerreidae (*Pharisatichthys aquensis*), whose representatives are able to penetrate into brackish coastal lagoons provides further support to this hypothesis. However, even if these data are in agreement with Nury's statement of the existence of an episodic connection between the lagoon and the open sea, this does not mean that marine waters invaded the depositional environment since no skeleton or otolith of a marine stenohaline fish taxon has never been found in the Aix-en-Provence Basin. The only exception to this palaeoenvironmental scenario may be related

to some very peculiar small discoid imprints that have been observed in the finely laminated sediments of the "Insect bed", especially in the upper section. These enigmatic fossils, called *Discalioides*, have been interpreted to as the remains of the discoid rigid pneumatophore-like structure of small jellyfishes (Fig. 14B) possibly related to the chondrophorid siphonophores (Nel et al., 1987). These structures are much more frequent in the site of "Les Jipières", in the western part of the Formation of Aix-en-Provence, corresponding to the zone that was certainly closer to the sea during the latest Oligocene. These Siphonophores are especially frequent in a set of thin laminae, together with hundreds of dragonfly nymphs that certainly died in mass maybe in relation with the arrival of marine water in the lagoon. This Siphonophore level also contains several specimens of the mullet *Mugil princeps*, a fish that is relatively uncommon in the rest of the succession, and possibly corresponds to a genuine short-lived episode marine transgression in the lagoon.

Finally, another argument proposed by Nury was her rejection of the model proposed by Corroy and Denizot (1943) for explaining the gypsum origin, as she did not accept in any way that it could derive from the leaching of Triassic evaporitic sediments and from a precipitation in an endorheic basin. A geochemical support to the hypothesis proposed by Corroy and Denizot (1943) was provided by Fontes et al. (1980) who, using isotopic analyses of sulphates, demonstrated that the ^{34}S content of the saccharoid gypsum is lower than that of the Tertiary marine waters and rather similar to the values characterizing the Permo-Triassic evaporites. Moreover, the ^{13}C values are indicative of an important contribution of pedogenic carbonates. Finally, it should be emphasized once again that a marine origin of the gypsum would have not been compatible with the presence of frogs (*Rana aquensis*) in the "Plâtrières" and with the cyprinid skeletons in at least four other sites (Gaudant, 2013a), including the "Centre commercial Ouest" (*Protothymallus* sp. vel. *Varhostichthys* sp.), "chemin du Pin" (*Palaeotinca* sp.), La Chevalière (*Tarsichthys* sp.) and Les Figons (*Tarsichthys macrurus*).

The fish assemblage seems to suggest that the fossiliferous sequence of the Aix-en-Provence Formation originated in a quiet brackish lagoon characterized by periodic variations of the salinity. Such variations possibly resulted from the alternated seasonal influence of the marine connections and continental discharges. The mollusc taxa collected in these fossiliferous deposits appear to be consistent with such interpretation. Overall, there is a heterogeneous assemblage of freshwater and oligohaline (*Anisus*, *Cyrena*, *Gyraulus*, *Theodoxus*) taxa associated with euryhaline (*Granulolabium plicatum*, *Potamides margaritaceus*) taxa indicative of oligo-mesohaline coastal lagoons and mudflats (see Esu and Girotti, 2010; Harzhauser, 2004). According to Gaudant (1978), the salinity of the waterbody of this latest Oligocene lagoon generally ranged between 0 and 10‰, with some phases characterized by values not

Fig. 15. Mass mortality layer of *Paralebias cephalotes* from the "Calcaires et laminites des Plâtrières", Aix-en-Provence Formation, MNHN.F.AIX278; core drilled north of the Plâtrières, in the site of Puy-du-Roy, by the "Bureau de recherches géologiques et minières".
Fig. 15. Niveau de mort en masse de *Paralebias cephalotes* des « Calcaires et laminites des Plâtrières », formation d'Aix-en-Provence, MNHN.F.AIX278 ; carotte obtenue au nord du site des Plâtrières, dans le site de Puy-du-Roy, par le Bureau de recherches géologiques et minières.

higher than 5‰, as indicated by the freshwater mollusc and fishes. Moreover, this faintly brackish palaeobiotope also experimented episodes of increased salinity of various extent related to an intensification of the marine influence.

As a final palaeoclimatological note, it is interesting to remark that the fish, insect, mollusc and plant assemblages from Aix-en-Provence Formation include a number of thermophilous stenotherm taxa that are indicative of a warm, at least subtropical climate.

Summarizing all this long discussion, it appears to be evident that the upper Oligocene Aix-en-Provence Formation is a unique example of Cenozoic Konservat-Lagerstätte in Europe documenting a subtropical brackish palaeobiotope. The fossils from this extraordinary Konservat-Lagerstätte are in general exquisitely well-preserved as testified by the remains of skin, muscles, digestive system, eyeballs and original pigmentation patterns in both vertebrates and arthropods. The excellent preservation quality was probably related to the development of a microbial film at the bottom that promoted the rapid fossilization of the soft parts (see Peinado, 2002). Good examples of this exquisite preservation of the soft parts can be easily observed in the mass mortalities of *Paralebias cephalotes* known as "friture" (Fig. 15) as well as in certain frog skeletons (Fig. 14A).

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