

A partly endemic euryhaline fish fauna (otoliths, teeth) from the Early Miocene of the Aix-Basin (Provence, southern France)

With 2 figs, 3 pls, 2 tabs

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Abstract

A fossil fish fauna from the St. Donat locality at Aix-en-Provence (Early Aquitanian, Early Miocene) is described on the basis of otoliths, jaw teeth, and pharyngeal teeth. Other organisms (gastropods, ostracods, charophytes) are briefly mentioned. Otoliths and ostracods are figured by SEM. The fish fauna consists of six taxa including cyprinids, atherinids, cyprinodontids, sciaenids, and moronids. Three fish species are new: *Hemitrichas denisae*, *Prolebias fritzsteineri*, and *Morone maritima*. The palaeoecological analysis reveals that the aquatic organisms from St. Donat present a mixture of marine, brackish, and lacustrine taxa. Due to the dominance of *Hemitrichas*, an occasionally hypersaline water body is suggested, in which a partly endemic fish fauna evolved. The palaeobiogeography of *Morone maritima* suggests an estuarine or brackish connection between the Mediterranean Sea and the western part of the Western Paratethys.

Key words: otoliths, Aix-Basin, Early Miocene, brackish water, palaeoecology, palaeogeography

Zusammenfassung

Von der Fundstelle St. Donat bei Aix-en-Provence (Südfrankreich) wird eine untermiozäne Fischfauna anhand von Otolithen, Kieferzähnen und Schlundzähnen beschrieben, die Otolithen werden abgebildet. Die ebenfalls bearbeitete Begleitflora und -fauna umfasst Charophyten, Gastropoden, Ostracoden, letztere werden ebenfalls abgebildet. Die Fischfauna besteht aus sechs Taxa, die sich auf die Familien der Cyprinidae, Atherinidae, Cyprinodontidae, Sciaenidae und Moronidae verteilen. Drei Arten sind neu: *Hemitrichas denisae*, *Prolebias fritzsteineri*, und *Morone maritima*. Die paläoökologische Auswertung ergab, dass die aquatische Organismen von St. Donat sowohl marine als auch brackische sowie Süßwasserelemente umfassen. Die Dominanz des Ährenfisches *Hemitrichas* weist auf ein zumindest zeitweise hypersalines Gewässer hin. In diesem herrschten wahrscheinlich besondere ökologische Bedingungen, welche zur Evolution speziell angepasster endemischer Fischarten führten. Darüber hinaus wurde aufgrund der Paläobiogeographie von *Morone maritima* eine ästuarine bis brackische Verbindung zwischen dem westlichen Mittelmeer und der westlichen Paratethys postuliert.

Schlüsselwörter: Otolithen, Aix-Becken, Unter-Miozän, Brackwasser, Paläoökologie, Paläogeographie

Introduction

During the Oligocene, continental basins developed in the Provence and Languedoc areas in southern France, among them the basin of Aix-en-Provence (Aix-Basin). The basins resulted from rifting processes within the Ligurian-Provençal Basin and are probably related to the subduction of the African Plate under the European Plate (GUIEU & ROUSSEL 1988, NURY & ROUSSET 1988).

The Basin of Aix-en-Provence (Aix-Basin) and the Durance Basin (fig. 1) are the northernmost of the con-

tinental basins in southern France and originated in the Upper Oligocene. Today a mountain range (Eguilles and Trevaresse) separates the Aix-Basin in the south from the Durance Basin in the north. However, during the Late Oligocene and Early Miocene, both basins contributed to a single coherent basin, in which the approximately 150 m thick "Formation d'Aix-en-Provence" was deposited. This formation, which is divided into seven informal subunits (tab. 1), consists of carbonates and clastic rocks, deposited under terrestrial, lacustrine, brackish and hypersaline conditions (NURY 1988, NURY & RAYNAUD 1986). Previously,

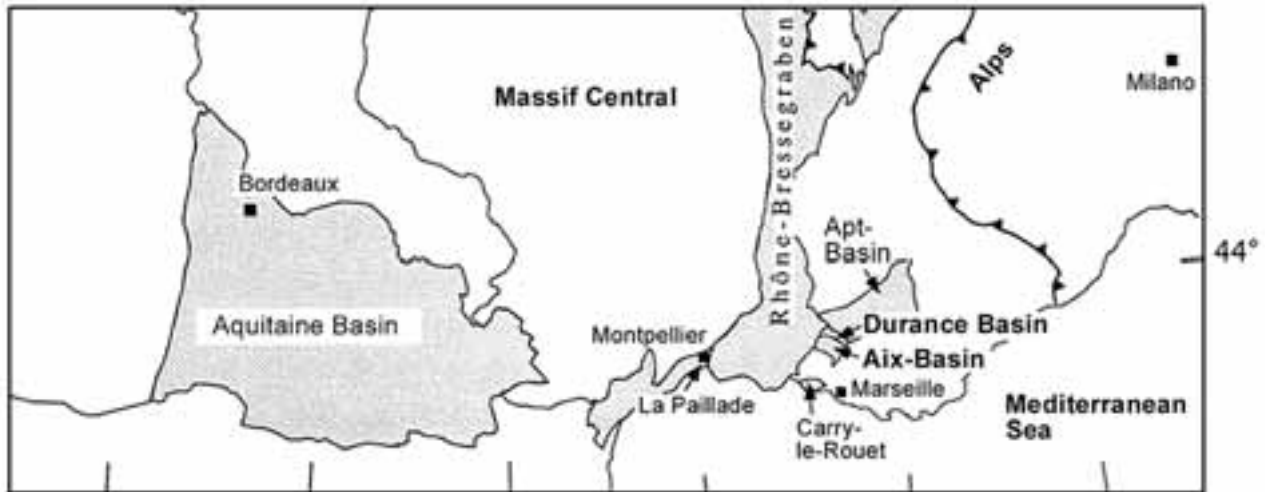


Fig. 1: Location of the Aix-Basin with the fossiliferous locality St. Donat, southern France. Oligo-Miocene depositional areas are marked in grey.

the whole sequence of the “Formation d’Aix-en-Provence” was thought to be Upper Oligocene in age based on mammal and mollusc biostratigraphy (e.g., AGUILAR et al. 1978, NURY 1988). COMTE (2000), however, analysed in detail the Rodent fauna from the locality “Venelles”, which is situated 6 km NNE’ of Aix-en-Provence in the Durance Basin. The sequence of Venelles can be correlated with the “Formation d’Aix-en-Provence”, and, more precisely, with the “Calcaires et Marnes à gypse d’Aix” (table 1). According to COMTE (2000), the Rodent fauna of Venelles is of Early Miocene age. Consequently, the “Calcaires et Marnes à gypse d’Aix” and the overlying subunits of the “Formation d’Aix-en-Provence”, belong to the early Lower Miocene. Additionally, the fish faunas from Venelles (REICHENBACHER 1998) and Aix-en-Provence (GAUDANT 1978, 1981) support

an Early Miocene age. They are dominated by *Prolebias* species and thus can be correlated with the otolith-zone OT-M1 (REICHENBACHER 1999), which is typical for the Early Miocene (Aquitanian).

Location and Material

The locality St. Donat studied herein is a small outcrop at the north of Aix-en-Provence. According to D. NURY (personal communication), the sequence of St. Donat belongs to the subunit “Calcaire d’Eguilles”, which represents the uppermost part of the “Formation d’Aix-en-Provence” (table 1).

Table 1: Chronostratigraphy and lithostratigraphy of the “Formation d’Aix-en-Provence” in the Aix- and Durance-Basins and lithostratigraphic position of the localities St. Donat and Venelles (after COMTE 2000, NURY 1988, REICHENBACHER 1998).

		Aix-Basin	Durance-Basin
Oligocene	Early Miocene (23,8 - 23,0 Ma)	Formation d’Aix-en-Provence	
			Formation de Rougiers (mammal zone MN 1)
		* St. Donat Calcaire d’Eguilles	Calcaire de la Trèvaresse
		Sable des Figons	Sable des Figons
		Marnes-du Puy-du-Roy	
		Calcaires et Laminites des Platrières	Calcaires et Marnes
		Calcaires et Marnes à gypse d’Aix	* Venelles
		Calcaires et Marnes des stations d’essence	de Venelles
	Marnes et Conglomérats de Sainte Anne		

The profile of St. Donat is presented here briefly from top to bottom:

- 12 cm light brownish limestone, many imprints of gastropods (probably Hydrobiidae)
- 25 cm marls with moulds of gastropods (probably Hydrobiidae)
- 40 cm brown marls with tests of Hydrobiidae (sample 7-1)
- 55 cm light brownish and grey marly limestone, rarely with gastropods
- 50 cm light brown marl without macrofossils
- 30 cm light grey limestone with moulds and imprints of gastropods (probably Hydrobiidae)
- 30 cm light brown marl with *Potamides*, *Mesohalina* and Hydrobiidae (sample 7-2)
- 30 cm yellow-brown, dark brown and blue-grey marls with *Potamides*, *Mesohalina* and Hydrobiidae (sample 7-3)

Sample 7-1 (10 kg), 7-2 (30 kg) and 7-3 (30 kg) yielded many gastropods (> 600), a few ostracods and charophytes, and a large number of fish otoliths (391 specimens) and fish teeth. Sample 7-1 yielded only Hydrobiidae, one cyprinid tooth and one juvenile *Morone* otolith. For this reason, more sediment was taken and washed from the layers 7-2 and 7-3.

Most fossils are well preserved, except the charophytes, which are incomplete and deformed. Also a few otoliths and gastropods show signs of corrosion and dissolution, but this is probably caused by Recent weathering of the sediment and not by reworking.

Methods

Samples were processed with a mixture of H₂O and a 35 percent H₂O₂-solution, by washing and sieving (smallest screen 0,2 mm). From the residue > 0,4 mm, all biota was picked under a binocular microscope.

Fossil fish-remains

The samples 7–2 and 7–3 have yielded large numbers of fish remains, among them otoliths (sagittae, lapilli) and teeth. Due to the type of the sediment (marls), no articulated skeletons were preserved.

Saccular otoliths

Teleost fishes have three pairs of aragonitic bodies in the auditory systems of their skulls which are named otoliths. Commonly, palaeontologists use the term otolith for the largest pair, the saccular otoliths or so-called sagittae (exceptions are found, for example, in the Family Cyprinidae). Sizes of sagittae range up to 10 mm and more, but most fossil sagittae are rather small (0,4–4 mm) deriving from fishes of about 5 to 15 cm total length (NOLF 1995: 517). Recent and fossil sagittae of teleost fish species reveal distinct morphological characters (e.g., details of contour, shape of the sulcus) and thus make species identification possible. For fossil otoliths, taxonomical identification is based on comparative studies with the sagittae of the nearest Recent relatives (see NOLF 1985, SMALE et al. 1995).

Fossil otoliths lead to the reconstruction of fossil fish faunas even if no skeletal remains are present. They have contributed greatly to our knowledge of fossil teleost fish faunas: 58 families (24%) of the 244 extant teleost families known as fossils are exclusively recorded from otoliths (PATTERSON 1993). Besides their systematic and phylogenetic importance, otoliths contribute greatly to our knowledge of palaeoecology, biostratigraphy and palaeoclimate, especially during the Cenozoic.

Systematic description of saccular otoliths (sagittae)

General systematic follows NELSON (1994).

Class Actinopterygii KLEIN 1885
 Division Teleostei MÜLLER 1846
 Order Atheriniformes ROSEN 1964
 Family Atherinidae RISSO 1826

Genus *Hemitrichas* PETERS 1877
 (= *Palaeoatherina* GAUDANT 1976)

Hemitrichas denisae n. sp.
 (pl. 1, figs 1–9)

Etymology: This species is dedicated to Denise Nury (Marseille). She greatly supported my field-studies in southern France.

Material: 170 sagittae.

Holotype: Left sagitta, Plate 1, Fig. 1 (SMF PO 64332).

Paratypes: 169 sagittae, eight of them figured.

Type Locality: St. Donat at the north of Aix-en-Provence, southern France.

Type Strata: “Calcaire d’Eguilles”, uppermost part of the “Formation d’Aix-en-Provence”, Lower Miocene (Aquitanian).

Description: The sagittae present a strongly convex inner face and a slightly concave outer face, which is thickened ventrally. The diagnostic characters are the elongate shape and the short, but prominent rostrum. Most sagittae display a straight dorsal rim that is distinctly crenulated. The posterior rim reveals a more or less developed posterodorsal angle, from which it steeply runs to the pronounced posteroventral angle. The ventral rim is rounded and passes into the rostrum, which is short and pointed. At some sagittae, the antirostrum is small and pointed while other sagittae reveal an antirostrum that is thick and truncated. An excisura may be present or not. The long and narrow sulcus is situated slightly suprmedian and running straight or slightly upwards. The division in ostium and cauda is distinct, the small ostium is more deepened than the cauda.

Dimensions: Length: 0,75–1,6 mm; height: 0,6–1,05 mm; thickness: 0,25–0,55 mm; ratio length/height: (1,25) 1,4–1,7.

Variability: Sagittae of *H. denisae* show a rather high variability, especially concerning the morphology of the posterodorsal angle and the antirostrum. This variability is also visible in the L/H-index. Comparable variability is known from the Late Oligocene and Early Miocene *Hemitrichas* species of the Mayence and Hanau Basins (KELLER et al. 2002, REICHENBACHER 2000). It may be related to unstable environments, for example to rapidly changing salinities.

Affinities: The fossil genus *Hemitrichas* was primarily identified based on skeletons (see GAUDANT 1998).

Meanwhile, it is well known by isolated otoliths (e.g., REICHENBACHER 2000) and by skeletons with otoliths *in situ* (KELLER et al. 2002).

A similar morphology of the sulcus is known from Recent sagittae of *Atherina* LINNAEUS 1758, e.g., from the Atlantic species *A. presbyter* CUVIER 1829 (REICHENBACHER 2000: fig. 36), and the Mediterranean species *A. boyeri* RISSO 1810 (pl. 1, figs 10–12). However, sagittae of *Atherina* species are clearly distinct from those of *Hemitrichas* species due to their flat inner face (strongly convex in *Hemitrichas*), and the ovate-shaped ostium with its long upper rim (see pl. 1). The osteological characters of *Hemitrichas* are similar to *Atherinomorus* FOWLER (cf. CHEDHOMME & GAUDANT 1984, KELLER et al. 2002), which is also true for otolith features. *Atherinomorus* does not belong to the native species of the modern Mediterranean Sea, because *A. lacunosus* (FORSTER 1801) has immigrated through the Suez Canal (WHITEHEAD et al. 1986). However, NOLF (unpublished data) has found *Atherinomorus* from the Mediterranean Lower Miocene near Turin. Consequently, *Atherinomorus* was also present during the Early Miocene in the Mediterranean Sea and may be closely related with *Hemitrichas*.

Differential diagnosis: From the skeleton-based species *H. britannica* (GAUDANT 1989) from the Oligocene of northwestern France, only one otolith (sagitta) is known. It displays a sulcus morphology which is very similar to that of *H. denisae*. *H. britannica*, however, as opposed to the new species, possesses a highly rounded dorsal rim, and a long upper ostial rim. Moreover, *H. denisae* resembles several *Hemitrichas* species known from the Western Paratethys and from the Northern Rhinegraben area (REICHENBACHER & WEIDMANN 1992, REICHENBACHER 1993, as “*Atherina*”, REICHENBACHER 2000). *H. denisae* can be distinguished from all these species, due to its more elongate shape. The nearest fossil relative is probably *H. dentifera* (STINTON in STINTON & KISSLING 1968) from the Western Paratethys area (western Switzerland). Compared with this species, which is less elongate (length/height-ratio: 1,3–1,4), *H. denisae* also differs by its straight dorsal rim.

Order Cyprinodontiformes ROSEN 1964
Family Cyprinodontidae GILL 1865

Genus *Prolebias* SAUVAGE 1874

Prolebias fritzsteiningeri n. sp.
(pl. 2, figs 1–11, 14–16 cf.)

Etymology: This species is dedicated to the honour of Prof. Dr. Fritz STEININGER.

Material: 37 sagittae; additionally 25 sagittae of *P.* cf. *fritzsteiningeri*.

Holotype: Right sagitta, pl. 2, fig. 3 (SMF PO 64354).

Paratypes: 36 sagittae, ten of them figured.

Type Locality: St. Donat at the north of Aix-en-Provence, southern France.

Type Strata: “Calcaire d’Eguilles”, uppermost part of the “Formation d’Aix-en-Provence”, Lower Miocene (Aquitanian).

Description: Sagittae display a round shape with a symmetrically curving dorsal rim, which in most specimens reveals a weak median tip. Inner and outer faces are convex; the ventral portion may be strongly thickened in large sagittae. The posterior rim is more or less rounded, the ventral rim straight or slightly rounded. The rostrum is well developed and not (or very slightly) longer than the antirostrum, which is prominent and pointed. A deep excisura is present. The sulcus is situated median and is divided weakly in a very small, round ostium and a cauda that may be straight or slightly curving downwards at its end. A strong crista superior, which anteriorly and posteriorly curves upwards, underlines the deep dorsal area.

Sagittae with a more triangular outline probably also belong to this species (see below) and are determined as cf. *fritzsteiningeri*.

Dimensions: Length: 0,65–1,03 mm; height: 0,69–0,94 mm; thickness: 0,22–0,43 mm; ratio length/height: 1,0–1,1.

Affinities: *Prolebias* is an extinct genus, which was widely distributed in euryhaline environments during Oligo-Miocene times (e.g., GAUDANT & REICHENBACHER 2002). Its nearest living relative may be the Mediterranean cyprinodontid *Aphanius iberus*, whose sagittae display similar outline, dimensions, and shape of the sulcus, but no median tip of the dorsal rim (see REICHENBACHER & SIENKNECHT 2001).

Differential diagnosis: *P. fritzsteiningeri* differs from previously described fossil *Prolebias* species by the combination of the following characters: rounded outline, weak dorsal median tip, and prominent rostrum. It differs from the probably nearest related *P. boudryensis* and *P. cephalotes* by its reduced median tip and stronger rostrum.

Remark: 25 sagittae present the same characters as *P. fritzsteiningeri*, except their outline, which is more triangular. It is possible that this is due to a sexual dimorphism of males and females, which is known from the cyprinodontid species *Aphanius apodus* and *A. iberus*, in which the sagittae of the males are of a more high-triangular shape compared with the females (REICHENBACHER & SIENKNECHT 2001). If this can be transferred to the fossil species, the cf.-determined specimens should be the males.

***Prolebias aff. cephalotes* (AGASSIZ 1839)**
(pl. 2, figs 12–13)

- aff. * 1939 *Lebias cephalotes*. – AGASSIZ, vol. 5.
 aff. 1978 *Prolebias cephalotes* (Ag.). – GAUDANT, p. 394, tab. 1.
 aff. 1981 *Prolebias cephalotes* (Agassiz). – GAUDANT, p. 1109.
 1999 *Prolebias* sp. – REICHENBACHER & CAPPETTA, p. 14,
 figs 13–15.

Material: 32 sagittae.

Preliminary remark: GAUDANT (1978, 1981) mentioned skeletons of *Prolebias cephalotes* from the subunit “Calcaires et Marnes à gypse d’Aix”, which is situated lithostratigraphically in the middle part of the “Formation d’Aix-en-Provence” (table 1). Jean GAUDANT kindly handed me SEM pictures from sagittae found *in situ* in skeletons of *P. cephalotes*. Based on these pictures, it is evident that the cyprinodontid sagittae from the sediments of the fossiliferous site “Venelles” belong to *P. cephalotes* (REICHENBACHER 1998, here pl. 2, figs 17–18).

Description: Sagittae reveal a rounded outline and present a prominent dorsal tip. The inner face is flat, the outer face slightly convex. Generally, the dorsal rim behind the dorsal tip curves steeper than before the tip. The posterior rim is rounded. In most specimens, the posteroventral curve is also rounded. The ventral rim is straight. The prominent rostrum is slightly longer than the antirostrum, its anterior rim is truncated, rarely rounded. An excisura is present. The sulcus morphology is identical with the sulcus of *P. fritzsteingeri*.

Dimensions: Length: 0,65–1,0 mm; height: 0,69–1,0 mm; thickness: 0,15–0,3 mm; ratio length/height: 0,90–1,05.

Differential diagnosis: *Prolebias aff. cephalotes* differs from *P. cephalotes* (AGASSIZ) by the truncated anterior rim of its rostrum, which in *P. cephalotes* is rounded or tapering. *P. boudryensis* REICHENBACHER 1992 has a more triangular shape and its cauda distinctly curves downwards at its end. *P. aff. cephalotes* probably descends from the slightly older *P. cephalotes*. It was described in my unpublished thesis (REICHENBACHER 1998) as new species (*P. boudrylotes*), but due to a better knowledge of Recent cyprinodontid otoliths, I now prefer the open nomenclature.

Further distribution: This species was described by REICHENBACHER & CAPPETTA (1999) as *Prolebias* sp. from the Early Miocene locality La Paillade near Montpellier (see fig. 1), where it occurs in a small number.

Order Perciformes BLEEKER 1859
 Family Moronidae FOWLER 1907

Genus *Morone* MITCHELL 1814

***Morone maritima* n. sp.**
(pl. 1, figs 13–16)

- 1992 *Morone aequalis* – REICHENBACHER & WEIDMANN, p. 36, pl. 6,
 figs 17–19.

Etymology: The name refers to the habitat of this species.

Material: 127 sagittae, among them 47 sagittae of juvenile fishes with a length < 2,5 mm.

Holotype: Right sagitta (pl. 1, fig. 13), SMF PO 64341.

Paratypes: 126 sagittae, 3 of them figured.

Type Locality: St. Donat at the north of Aix-en-Provence, southern France.

Type Strata: “Calcaire d’Eguilles”, uppermost part of the “Formation d’Aix-en-Provence”, Lower Miocene (Aquitanian).

Description: Sagittae of elliptical shape with a long dorsal rim terminating in a posterodorsal angle. The significant character of this species is the ventral rim of the ostium, which is vertically dropping from the collum, forming an angle of 90° with the crista inferior. The inner face of the sagitta is slightly convex, the outer face slightly concave and thickened. The dorsal rim is straight or slightly rounded, the posterior rim short and rounded or pointed. A weak incision may be present at the posteroventral curve. The ventral rim is rounded and runs into the broad and prominent rostrum. The antirostrum is small, pointed or rounded. The sulcus presents the typical shape of moronids with a slightly deepened, large, shovel-shaped ostium and a less deepened straight cauda, which bends downwards at its end.

Dimensions: Length: 1,2–5,4 mm; height: 0,9–3,3 mm; thickness: 0,3–1,1 mm; ratio length/height: (1,3) 1,5–1,7.

Affinities: The nearest living relative of *Morone maritima* may be the Mediterranean moronid *M. labrax* (LINNAEUS), whose sagittae display similar outline, dimensions, and shape of sulcus (cf. REICHENBACHER 1993: pl. 7, fig. 111). But *M. labrax* is also clearly different from the fossil species due to its narrower ostium.

Differential diagnosis: *M. aequalis* (KOKEN) from the Late Oligocene and Early Miocene of the Upper Rhine-graben area reveals similar dimensions and outline (see pl. 1, figs 17–18) and probably was closely related. It can be distinguished from the new species due to its deeper rounded ventral rim and the shape of its cauda, which stronger curves downwards at its end.

Utricular otoliths (lapilli)

The utricular otoliths (pl. 3, figs 1–4) belong to a cyprinid species, perhaps be to the genus *Tarsichthys*. Regarding the pharyngeal teeth (see below), *Tarsichthys* is the single cyprinid taxon in the fish fauna from St. Donat.

Teeth of fishes

Determination of teeth (jaw teeth and pharyngeal teeth) was kindly done by Jean GAUDANT (Paris). The pharyngeal teeth belong to the cyprinid genus *Tarsichthys* and the jaw teeth to a sciaenid taxon. Pharyngeal teeth of the *Tarsichthys* type are widely distributed in freshwater deposits of the Upper Oligocene and Lower Miocene of the Western Paratethys (GAUDANT et al. 2002). Jaw teeth of sciaenids have been described from marine influenced euryhaline environments of Late Oligocene and Early Miocene age in the Mainz and Hanau Basins (e.g., MARTINI 1981, REICHENBACHER 1998, 2000).

From the fossil record it is evident, that sciaenid jaw teeth are always much more frequent than sciaenid otoliths. This could be due to the regular tooth replacement: like many teleost fishes, a sciaenid individuuum produces a large number of teeth during its life; but only two sacular otoliths. Moreover, a sciaenid individuuum can deposit several teeth into the sediment *during its life*; but its two sacular otoliths are only deposited *after its death*. Thus, the absence of sciaenid otoliths in the St. Donat fish fauna may indicate, that sciaenid fishes lived only occasionally in the water body of St. Donat.

Gastropods

The determination of the gastropods was kindly made available by Dietrich KADOLSKY (Aberdeen) and is summarised in table 2.

Ostracods

Determination of ostracods was kindly supported by Peter SCHÄFER (Mainz). Four taxa were identified: *Moenocypris* sp. (pl. 3, figs 5–6), *Hemicyprideis dacica* (HÉJAS 1894) (pl. 3, figs 7–11), *Ilyocypris* sp. (pl. 3, fig. 12), and *Eucypris* sp. (not figured). *H. dacica* is widespread in the Upper Oligocene and Lower Miocene Molasse deposits of Southern Germany (MÜLLER 1985).

Palaeoecology and palaeoclimatic implications

The fish fauna of the lower part of the St. Donat profile (layer 7-3, 7-2) consists of six taxa whose nearest fossil and Recent relatives are typical for lagoonal (*Prolebias*), brackish to hypersaline (*Hemitrichas*), freshwater (*Tarsichthys*) and marin-euryhaline (*Morone*, Sciaenidae) environments. Three species are new: *Hemitrichas denisae*, *Prolebias fritzsteiningeri*, and *Morone maritima*. *H. denisae* and *P. fritzsteiningeri* are so far not known from any other locality and indicate the partly endemic character of the fish fauna of St. Donat.

Regarding the gastropods of the lower part of the St. Donat profile (layer 7-3, 7-2), it is obvious that *Hydrobia* is very dominant. Additionally, *Potamides* and *Mesohalina* are present with many specimens. Recent Potamididae-Hydrobiidae-associations are widespread in estuaries, the landward portion of mudflats, and coastal swamps (BANDEL & KOWALKE 1999, KOWALKE 2001). Fossil assemblages including *Hydrobia*, *Potamides* and *Mesohalina* are well known from lagoonal and estuarine Oligocene and Early Miocene environments, especially from the Rhinegraben area (e.g., KADOLSKY 1988, 1995). *Hydrobia* species obviously could survive in waters of very low salinity, but Potamididae were mainly distributed in brackish to hypersaline environments (see KOWALKE 2003). *Turbonilla* is typical for marine facies. *Gyraulus* is a freshwater snail, which is also known from oligohaline

Table 2: Distribution and numbers of gastropods from the St. Donat locality.

Gastropod species	7/3 (base)	7/2	7/1 (top)
<i>Potamides druenticus</i> FONTANNES 1884	33	88	
<i>Mesohalina margaritacea margaritacea</i> (BROCCHI 1814)	14	25	
<i>Granulolabium concisum</i> (MATHÉRON 1843)	2		
<i>Hydrobia gregaria</i> (SCHLOTHEIM 1820)	49	321	51
<i>Turbonilla</i> sp.	3		
<i>Vitta subangularis matheroni</i> (WENZ 1919)		9	
<i>Vitta subangularis matheroni</i> (WENZ 1919) opercula		27	
<i>Gyraulus</i> sp. aff. <i>dealbatus</i> (BRAUN 1851)		1	
Total number of specimens	101	475	51

environments (e.g., REICHENBACHER 1989, HARZHAUSER & KOWALKE 2002).

Among the ostracods, *Moenocypris* is a freshwater genus (CARBONNEL et al. 1985). *Ilyocypris* is known from freshwater (e.g., SCHÄFER 2002) and also from slightly brackish deposits (REICHENBACHER 1989). *Hemicyprideis* species are widespread in brackish sequences of the Paratethys and the Rhinegraben area (e.g., MÜLLER 1985, SCHÄFER 1984). In this context it is worth mentioning that the charophytes, which are mainly indicative for freshwater environments, are very rare. However, this may not only result from high salinity, but also from a water depth beyond 4 metres (PICOT 2002).

In conclusion, the organisms from the lower part of the St. Donat profile (layer 7-3, 7-2) consist of a mixture of marine, brackish, and lacustrine taxa. This points to an euryhaline environment with occasionally changing salinities. The dominating *Hemitrichas* species lead to the assumption that the water body from time to time was hypersaline. This was probably due to dry climatic conditions and evaporation effects, which prevailed since the Late Oligocene in the western part of the Western Paratethys (e.g., BERGER 1990), in the northern Rhinegraben area (e.g., KADOLSKY 1988, REICHENBACHER 2000) and in southern France (e.g., NURY 1988).

During the upper part of the St. Donat profile (layer 7-1), a water body with more freshwater influx and low salinities (oligohaline) can be assumed, due to the absence of marine-euryhaline or brackish to hypersaline fishes (sciaenids, *Morone*, *Hemitrichas*, *Prolebias*) and gastropods (*Turbonilla*, Potamididae). Consequently, evaporation effects were less prominent and the climate became wet. A similar climatic change was reported from the Early Miocene (mammal-unit MN 1) of the Mainz Basin (FÖRSTERLING & REICHENBACHER 2002, for more discussion see COMTE 2000: 87).

Palaeogeography

Morone maritima is an interesting species considering the palaeogeography of the western part of the Western Paratethys (western Switzerland), the Mediterranean, and the Rhinegraben area. In western Switzerland, this species appears for the first time at the end of the Oligocene (late Chattian, mammal-unit MP 29-30) and is restricted to a small time span until the beginning of the Miocene (early Aquitanian, mammal-unit MN 1) (REICHENBACHER & WEIDMANN 1992, as "*M. aequalis*"). Thus, *M. maritima* hints to an estuarine or brackish connection between the Mediterranean Sea and the Western Paratethys during the latest Oligocene and the earliest Miocene (fig. 2).

On the other hand, *M. maritima* is not present in the Rhinegraben region, where it is replaced in strata of the same age by the very similar and thus probably closely related *M. aequalis*. This supports previous data suggesting distinct faunal provinces in the Rhinegraben area on

the one hand and in the Paratethys region on the other hand during the Late Oligocene and the Early Miocene (e.g., REICHENBACHER & WEIDMANN 1992, REICHENBACHER 2000; see fig. 2).

It is evident that during the Early Miocene, marine influences and transgressive trends occur both in the north and in the south of Central Europe (see fig. 2). This could be related with the so-called "Aquitanian transgression". It is well known, however, that this transgression had already started during the terminal Oligocene.

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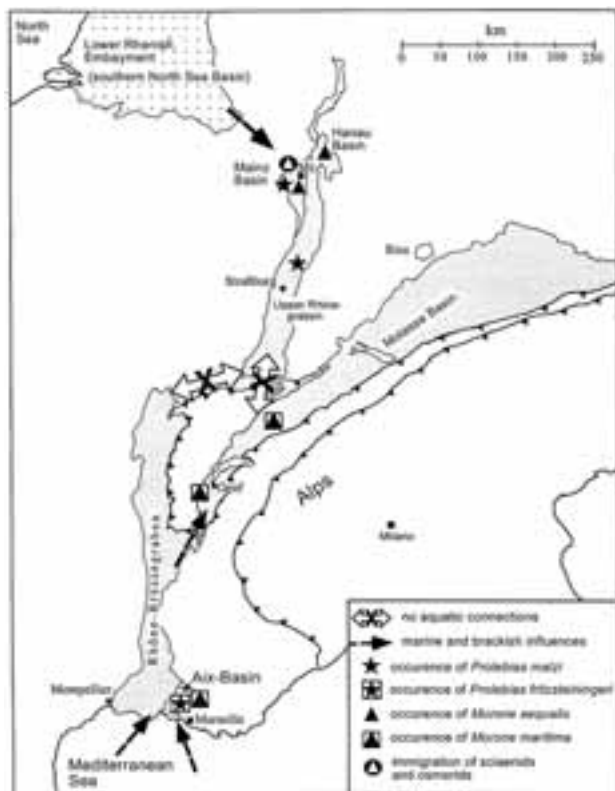


Fig. 2: Palaeobiogeography of *Prolebias* and *Morone* species during the Late Oligocene (late Chattian) and Early Miocene (early Aquitanian) suggest distinct faunal provinces in the north (Upper Rhinegraben area) and in the south (western Molasse Basin, Rhône-Bressegraben, Mediterranean Sea). The presence of *Morone maritima* in the Suisse Molasse Basin indicates marine influences from the Mediterranean region. During the same time, marine influences from the North Sea are visible in the Mainz and Hanau Basins of the northern Rhinegraben area (for more details see REICHENBACHER 2000).

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Plate 1

All otoliths, except figs 10–12 and 17–18, originate from the Early Miocene (Calcaire d’Eguilles, uppermost part of the Formation d’Aix-en-Provence) of St. Donat (Aix-Basin). All figured otoliths are saccular otoliths (sagittae), shown from the inner face. L = left sagitta, R = right sagitta. They are deposited in the Forschungsinstitut Senckenberg (SMF PO), except *Atherina boyeri*.

Figs 1–9: *Hemitrichas denisae* n. sp.

Fig. 1: L, holotype, SMF PO 64332.

Figs 2–4: L, paratypes, SMF PO 64333–35.

Figs 5–9: R, paratypes, SMF PO 64336–40.

Figs 10–12: *Atherina boyeri* (Risso 1810).

Recent, Mediterranean Sea (ex. collection Institut Royal des Sciences naturelles de Belgique).

Figs 13–16: *Morone maritima* n. sp.

Fig. 13: R, holotype, SMF PO 64341.

Fig. 14: R, paratype, SMF PO 64342.

Figs 15–16: L, paratypes of juvenile specimens, SMF PO 64343–44.

Figs 17–18: *Morone aequalis* (KOKEN 1891).

Late Oligocene and Early Miocene, Mainz Basin (see REICHENBACHER 2000 and FÖRSTERLING & REICHENBACHER 2002 for details).

17: R, SMF PO 64345.

18: L, SMF PO 64303 (also figured in FÖRSTERLING & REICHENBACHER 2002, pl. 1, fig. 3).

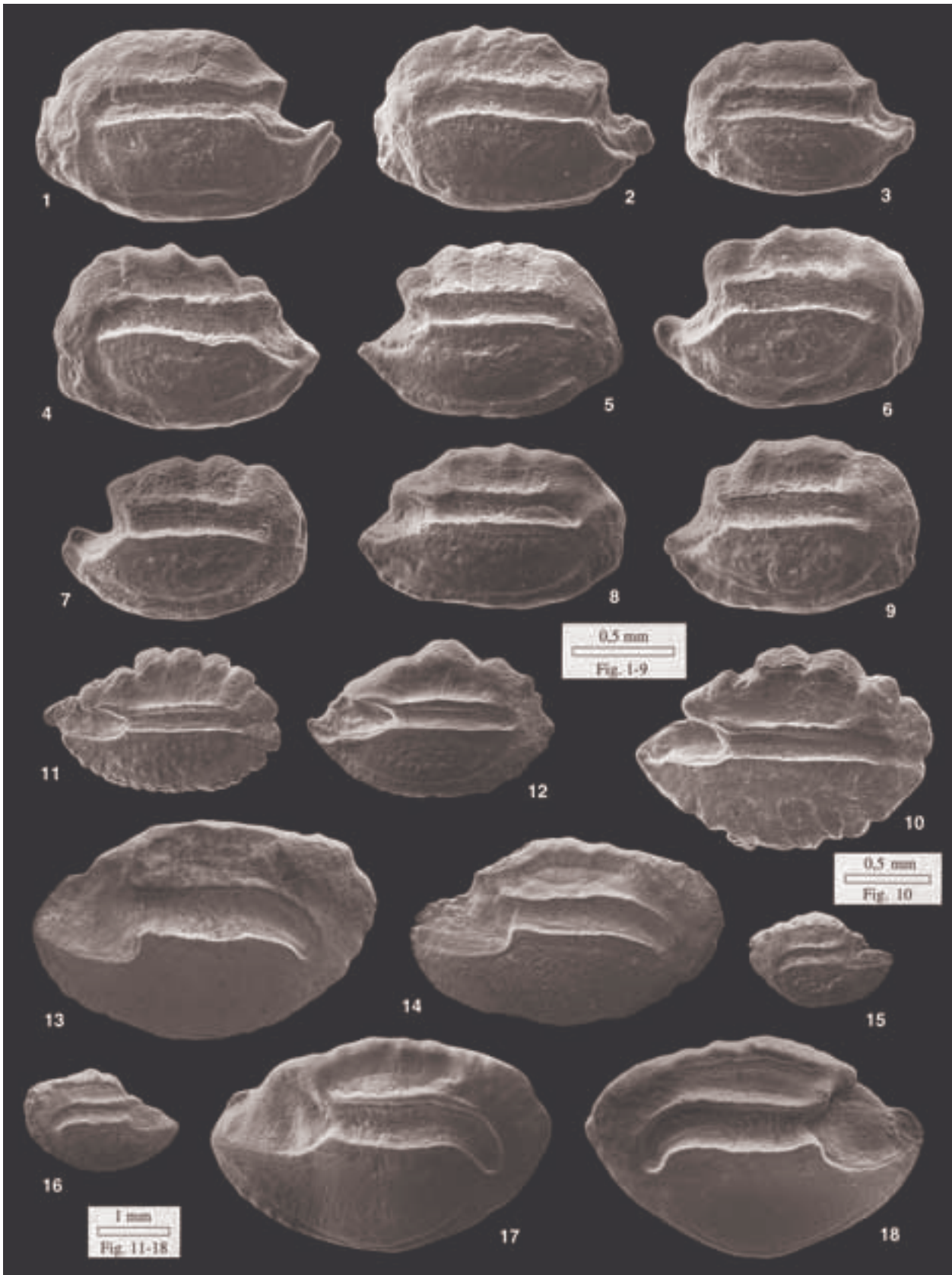


Plate 2

All otoliths, except figs 17–18, originate from the Early Miocene (Calcaire d’Eguilles, uppermost part of the Formation d’Aix-en-Provence) of St. Donat (Aix-Basin). All figured otoliths are saccular otoliths (sagittae), shown from the inner face. L = left sagitta, R = right sagitta. They are deposited in the Forschungsinstitut Senckenberg (SMF PO).

- Figs 1–11: *Prolebias fritzsteiningeri n. sp.*
Figs 1–2, 4–6, 8–10: L, paratypes, SMF PO 64346-47, 64348-50, 64351-53.
Fig. 3: R, holotype, SMF PO 64354.
Fig. 7, 11: R, paratypes, SMF PO 64355, -56.
- Figs 12–13: *Prolebias aff. cephalotes (Agassiz 1839)*.
L, SMF PO 64357-58.
- Figs 14–16: *Prolebias cf. fritzsteiningeri n. sp.*
R, SMF PO 64359-61.
- Figs 17–18: *Prolebias cephalotes (Agassiz 1839)*.
Formation d’Aix-en-Provence of the locality Venelles (material from REICHENBACHER 1998).
L (fig. 17) and R, SMF PO 64362-63.

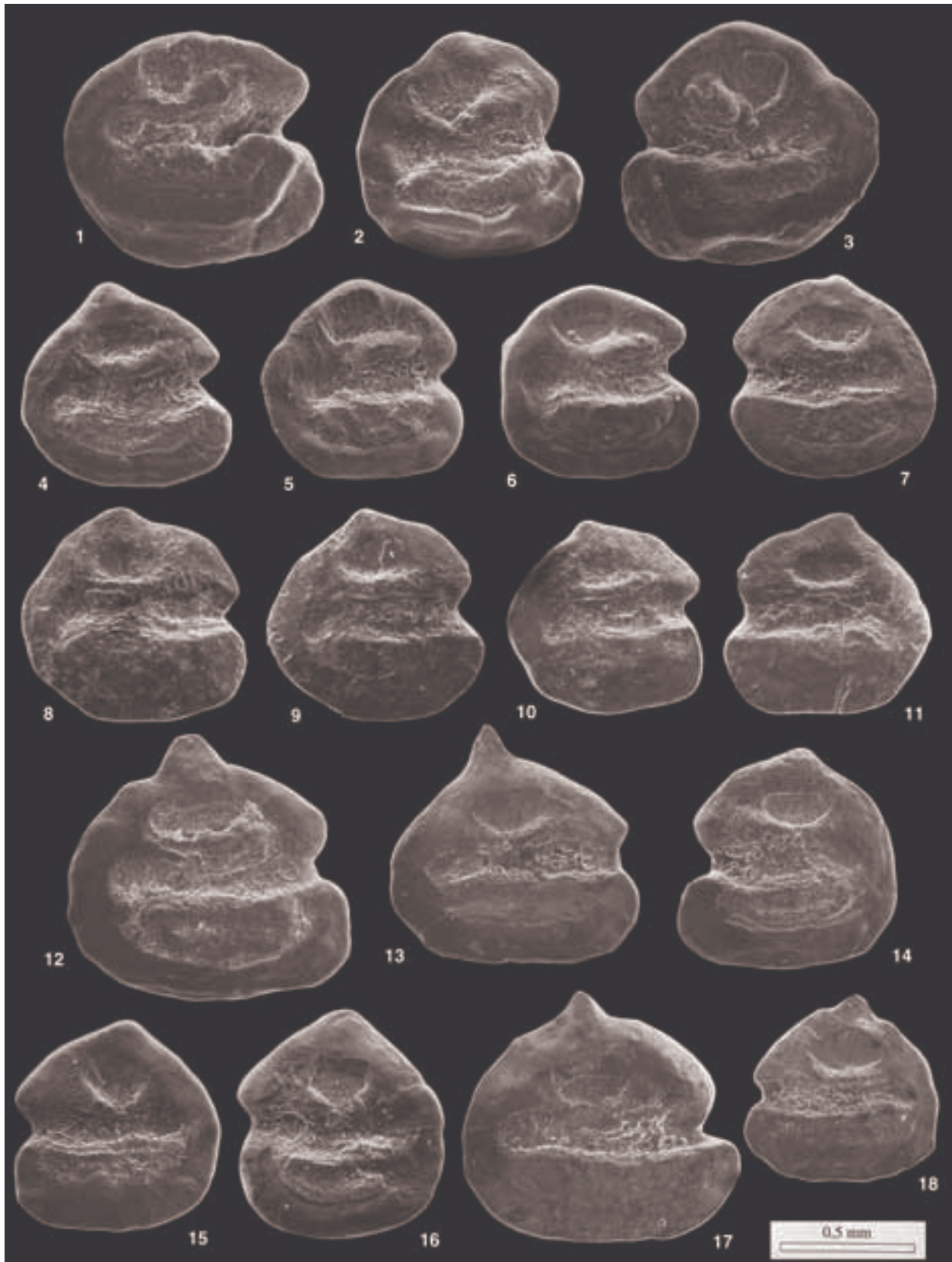


Plate 3

All otoliths and ostracods originate from the Early Miocene (Calcaire d'Eguilles, uppermost part of the Formation d'Aix-en-Provence) of St. Donat (Aix-Basin). The fossil otoliths are utricular otoliths (lapilli).

Figs 1–4: *cf. Tarsichthys sp.*
Lapilli showing the outer face (figs 1–2) and the inner face (figs 3–4).

Figs 5–6: *Moenocypris sp.*
Right valves.

Figs 7–11: *Hemicyprideis dacica* (HÉLIAS 1894).

7: Left valve of female.

8–9: Left valves of males.

10: Right valve of male.

11: Left valve of male, inner view.

Fig. 12: *Ilyocypris sp.*
Left valve.

