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Preliminary study on the ecomorphological signification of the sound-producing complex in Carapidae

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Abstract

Carapidae can be classified in four ecological groups : pelagic, demersal, commensal and parasitic. Carapidae display otophysic structures associated with the anterior part of the swim bladder and highly modified labyrinths, which suggest particular acoustic performances. The commensal and parasitic species have the best developed sound-producing features and also the thickest sagitta within the largest otic cavity, and surrounded by the thinnest cranial wall. However, these features do not necessarily imply a direct relation between the sound emission and reception in a given species but suggest a selective pressure lying in the habitat use of the species. The structures involved in sound-production and hearing are seemingly adapted to match the loss of energy of the sonic vibrations when travelling through the host tissues.

Key words: ecomorphology, sound apparatus, ear, Carapidae.

Introduction

The aim of ecomorphological studies is to reveal and understand possible relationships between organism morphology and its way of life (Norton et al. 1995).

Ecomorphological studies on fishes often focus on the relation between one morphological trait and one ecological feature : for example, buccal apparatus morphology and diet (Clifton and Motta, 1998; Kotschal, 1989), digestive tract length and diet (Veregina, 1991), body shape and fin position, and habitat (Webb, 1988 ; Belwood and Wainwright, 2001). Ideally, the study of the relations between the ecological characteristics of a species and the particularities of one of its morphological systems requires firstly a complete knowledge of all the biological roles the morphological system fulfills in the natural environment of the studied species. In other words, the mechanical performance of the system interacting with the environment should thus be examined. Secondly, a comparison with related species living in different ecological conditions is essential to allow an evaluation of the potential advantages of the morphological character complex in a given environment. Moreover, an organism does not consist of one single morphological complex, but of many such complexes, interacting to improve the fitness of the individual in given ecological conditions (i.e. adaptation to the many components of the ecological niche; Goldschmid and Kotschal, 1989). The morphology of a species consequently appears as an assembly of functional characters interacting with environmental factors.

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In carapid fishes (Paracanthopterygii: Ophidiiformes), two ecomorphological studies, each focusing on a different functional complex, have been performed. The first one aimed to understand the relations between diet and cephalic morphology in a comparative study (Parmentier et al., 2000 ; Parmentier and Vandewalle, in press). The second one focussed on the links between internal ear (size and shape of sagittae, labyrinths and otic region of the skull) and habitat use in different species (Parmentier et al., 2001).

Carapidae display spectacular specializations of the anterior vertebrae, swim bladder and associated muscles which are generally interpreted as a sound-producing device (Courtenay and Mc Kittrick, 1970 ; Markle and Olney, 1990 ; Parmentier et al., 2000). Additionally, highly modified labyrinths are present which suggest an improved acoustic performance (Parmentier et al., 2001).

The present study is a comparison of the sound-emitting and sound receptor apparatuses in different species of Carapidae, including representatives of the entire spectrum of habitat use in this family. The sound-producing structures in the Carapidae are described in detail, and used to investigate potential ecomorphological relationships between habitat use and the morphology of the sound producing and receiving apparatuses.

Materials and methods

10 specimens of *Carapus boraborensis* (TL: 13 to 30 cm), 5 specimens *Carapus homei* (TL: 8 to 17 cm) and 3 specimens *Encheliophis gracilis* (TL: 16 to 24 cm) were collected by the authors in Opunohu bay, Moorea, French Polynesia. These specimens were found in three holothurians: *Bobadschia argus*, *Thelenota ananas* and *Thelenota anax*. Eight adults of *Onuxodon fowleri* (TL: 57-90 mm) were collected in Hansa Bay (Bismarck sea) in Papua New Guinea. They were found in specimens of *Pinctada margaritifera* (Lamellibranch). Three specimens of *Echiodon drummondi* (TL: 20 cm) were collected from the North Sea. All fishes were fixed in formalin and stored in 70% ethanol for further analyses.

Specimens of other species were gifts or loans: *Snyderidia canina* n°9669 (TL: 17 cm, University of Kyoto), *Pyramodon lindas* I. 25804-018 (TL: 23 cm, Australian Museum), *Pyramodon punctatus*: I.29744001 (TL: 240 mm, Australian Museum), *Echiodon cryomargarites*: NMNZ P25406 (TL: 215 mm, National Museum of New Zealand), *Echiodon excilium* SIO 65-292 (TL: 118 mm, Scripps Institution of Oceanography, California), *Echiodon rendhali*: IB.4353 (TL: 106 mm, Australian Museum).

The fishes were dissected and examined using Wild M10 binocular equipped with a camera lucida and camera (Leica Camera AG).

Results

Ecology

Parmentier and Vandewalle (in press) consider the seven genera of Carapidae as belonging to four ecological categories (EC). The genera *Snyderidia* and *Pyramodon* are pelagic (EC1 -Trott, 1970). *Echiodon* and *Eurypleuron* are demersal (EC2 - Fries et al., 1893 ; Trott, 1970 ; Williams, 1984 ; Nielsen et al., 1999). *Onuxodon* and the members of the tribe Carapini (*Carapus* and *Encheliophis*) are able to penetrate into different invertebrates such as sea cucumbers (Smith, 1964 ; Smith and Tyler, 1969 ; Shen and Yeh, 1987 ; Jangoux, 1990), sea stars (Meyer-Rochow, 1977, 1979), bivalve molluscs (Tyler, 1970 ; Machida, 1989 ; Castro-Aguirre et al., 1996 ; Paredes-Rios and Balart, 1999) and ascidians (Weber, 1913). Species of the genera *Onuxodon* and *Carapus* seem to be commensals (EC3), and those of the genus *Encheliophis* are parasites (EC4 - Parmentier et al., 2000).

Data about the habitat use and lifestyle of *Echiodon drummondi* (demersal; North Sea), *Carapus boraborensis*, *Carapus homei*, *Carapus mourlani* (commensal; Madagascar, Moorea), *Carapus acus* (commensal; Calvi, Corsica) and *Encheliophis gracilis* (parasitic; Madagascar, Moorea) were confirmed by recent personal observations.

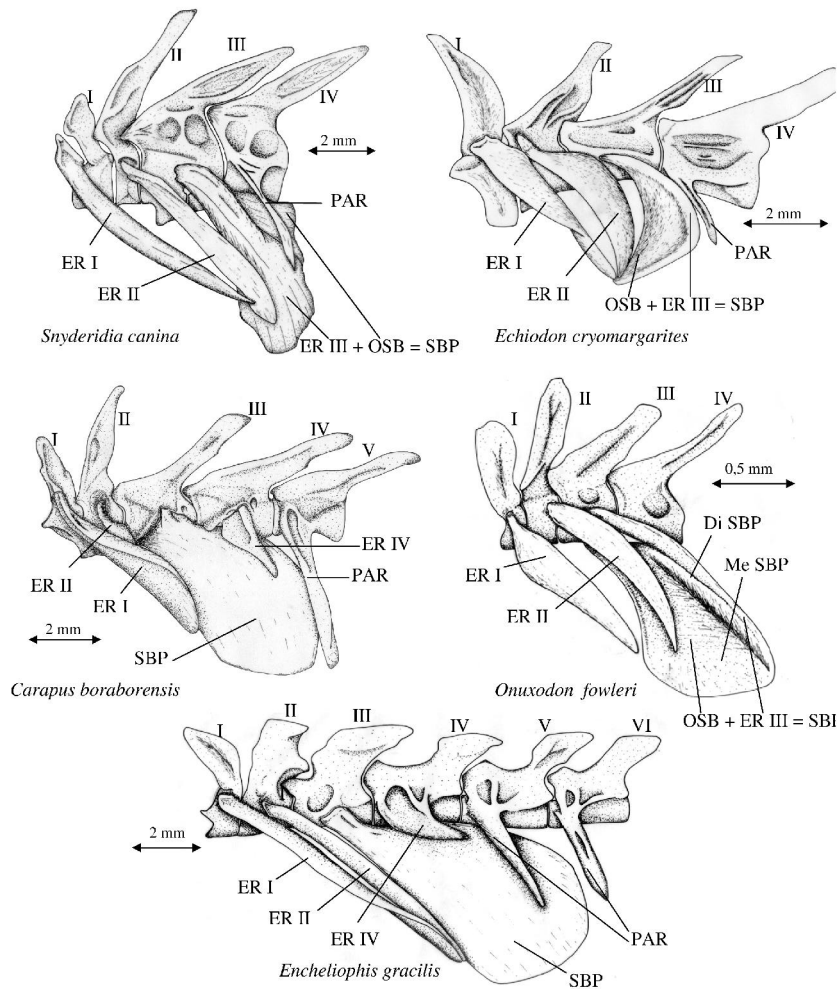


Figure 1. Lateral view of the first vertebrae with the associated epipleural ribs and swim bladder plate in five species of Carapidae.

Sound-production apparatus

In all the Carapidae, the 'bauplan' of the presumed sonic apparatus displays common characteristics. The first two vertebrae display epipleural ribs that are movable in all directions (Fig.1) and linked to the swim bladder by a ligament inserting at their distal end (Fig.2). The third vertebra bears paired, broad, ossified plates resulting from the fusion of the third epipleural rib with an ossified area of the swim bladder wall: the "swim bladder plates" (Fig.1). The parapophyses of the following vertebrae bear no or indistinct epipleural ribs (Markle and Olney, 1990). The almost

cylindrical swim bladder may be divided into three regions (Fig.2); the anterior regions (1 and 2) are dilated anteriorly and the posterior region (3) is strongly compressed against the abdominal vertebrae. The wall of the second region is situated just under the swim bladder plate and is thinner; it is the "swim bladder fenestra" (name coined by Howes, 1992, for ophiidiforms). Paired "primary sonic muscles" (coined by Courtenay and Mc Kittrick, 1970) run from the anterior end of the swim bladder (region 1), in front of the swim bladder fenestra, up to the upper wall of the orbit. Two pairs of secondary sonic muscles join the first two epipleural ribs with the epiotics.

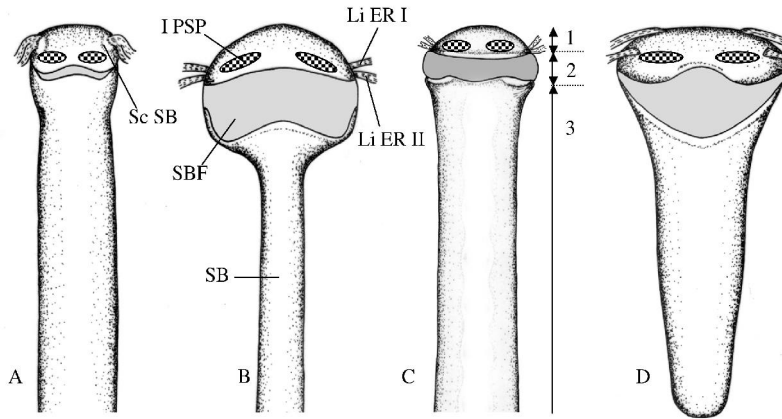


Figure 2. At the same scale, dorsal views of the anterior part of the swim bladder in *Echiodon cryomargarites* (A), *Encheliophis gracilis* (B), *Carapus boraborensis* (C) and *Snyderidia canina* (D). The total lengths of the swim bladder are respectively 35mm, 30mm, 20,5mm and 13,75mm. The swim bladder regions are shown in *Carapus boraborensis*.

Intergeneric specializations concern the shape and size of the epipleural ribs, the swim bladder plate and fenestra, and the lateral elements of the 4th vertebra.

1. In the three studied Pyramodontinae (*Pyramodon lindas*, *Pyramodon punctatus* and *Snyderidia canina*), the 3rd epipleural ribs are the broadest and the thickest ones. In *S. canina*, the dorsal ossification of the swim bladder forms one single plate fused anteriorly to the 3rd epipleural ribs and with the ventral part of the 3rd vertebra. In *Pyramodon lindas* and *Pyramodon punctatus*, the dorsal ossification is also fused to the ventral part of the 4th vertebra. In the latter three species, the 4th centrum bears parapophyses surmounting the swim bladder plate.

2. In the genus *Echiodon*, the swim bladder plate is concave and principally composed of a thin anterior ossification of the swim bladder wall followed by the epipleural ribs of the 3rd vertebra (Fig.1). Specific differences are as follows : *Echiodon cryomargarites* and *Echiodon drummondi* possess epipleural ribs on the first three vertebrae. *Echiodon rendhali* and *Echiodon exsilium* bear 4 and 5 pairs of epipleural rib respectively. In *Echiodon exsilium* and *Echiodon drummondi*, the ligaments of the first two epipleural rib pairs insert laterally onto the swim bladder, in front of the small swim bladder fenestra. In *Echiodon cryomargarites*, the ligaments of the epipleural ribs 1 and 2 fuse with each other at the level of an antero-lateral fibrous area (Fig. 2A) (Markle and Olney, 1990). In *Echiodon rendhali*, the ligaments of the first epipleural ribs are well separated from the ligaments of the second epipleural ribs; the latter ligament inserting laterally on the swim bladder. The ligaments of the two first pairs of epipleural ribs reach the same insertion in the middle of the anterior face of the swim bladder.

3. In Carapini, the swim bladder plate is proportionally the broadest and it is characterized by its continuous convexity. It is very difficult to observe a border between the 3rd epipleural rib and the swim bladder wall ossification. The 4th vertebra bears a pair of short epipleural ribs above the swim bladder plate to which they are attached by connective tissue fibres. In the parasitic species *Encheliophis gracilis*, the swim bladder plate is the most developed and reaches the 6th vertebra (Fig. 1). In all the Carapini, the ligaments of the epipleural ribs 1 and 2 insert on the left and the right in front of the swim bladder fenestra (Fig. 2B).

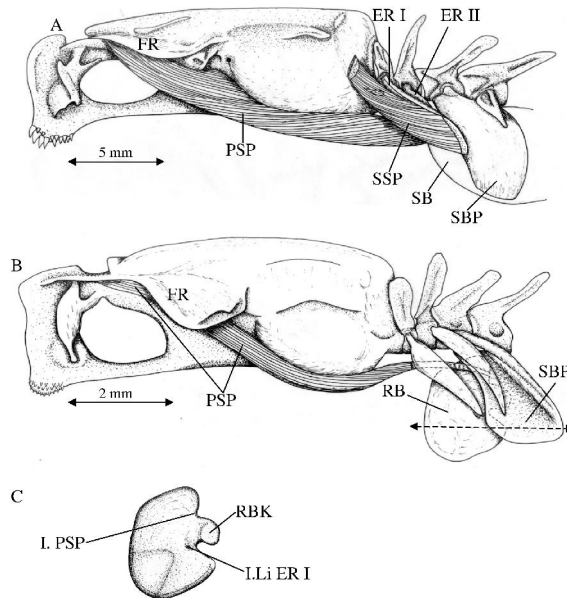


Figure 3. Lateral view of the musculature associated with the swim bladder in *Carapus boraborensis* (A) and in *Onuxodon fowleri* (B). Secondary sound producing muscles are omitted in this second species. (C) Isolated rocker bone.

4. The sonic apparatus of *Onuxodon margaritiferae* and *Onuxodon parvibrachium* was described by Courtenay and Mc Kittrick (1970). It is very similar in *Onuxodon fowleri* as examined in the present study (Fig. 3). The swim bladder is a more or less regular cylinder and the swim bladder fenestra constitutes its anterior face. The swim bladder plate is wedge-shaped. The distal parts of the swim bladder plates lean against the swim bladder fenestra. The anterior part of left and right wings forming the swim bladder plate are bent anteriorly (Fig. 4 : Me SBP) and delimit a longitudinal corridor closed posteriorly by the swim bladder fenestra (Fig. 4A, C). That latter corridor is filled by the so-called "rocker bone" (name coined by Courtenay and Mc Kittrick, 1970), which is probably not a bone, since it does not stain in an alizarin solution; its exact nature remains to be determined. The posterior face of the rocker bone displays a knob imbedded in the tissue of the swim bladder fenestra tunica. The primary sonic muscles insert by means of a long tendon onto the knob, and not on the swim bladder wall. The ligaments of the first epipleural ribs attach on the left and right faces of the rocker bone, under the knob and in front of the primary sonic muscles. The position of the ligaments provides a perpendicular axis of support for the rocker bone. The two ligaments of the second epipleural ribs are thicker than in the other species in the present study and

insert on the lateral faces of the swim bladder plate. The swim bladder wall is generally thinner than in the other Carapidae studied.

In all Carapidae but *Onuxodon*, rhythmic contraction of the sonic muscles seems to result in a forward movement of the part of the swim bladder anterior to the fenestra and hence, tension and vibrations in the thin area. The secondary sonic muscles could modulate the swim bladder volume via the ligaments of the epipleural ribs 1 and 2. In *Onuxodon*, contraction of the sonic muscles moves the rocker bone forward. This causes the latter to swing around the vertical bisector of the ligaments of the first epipleural ribs and moves the knob and the swim bladder fenestra forward. Sound could therefore result from vibration of the swim bladder thin area of the fenestra when the knob moves forward.

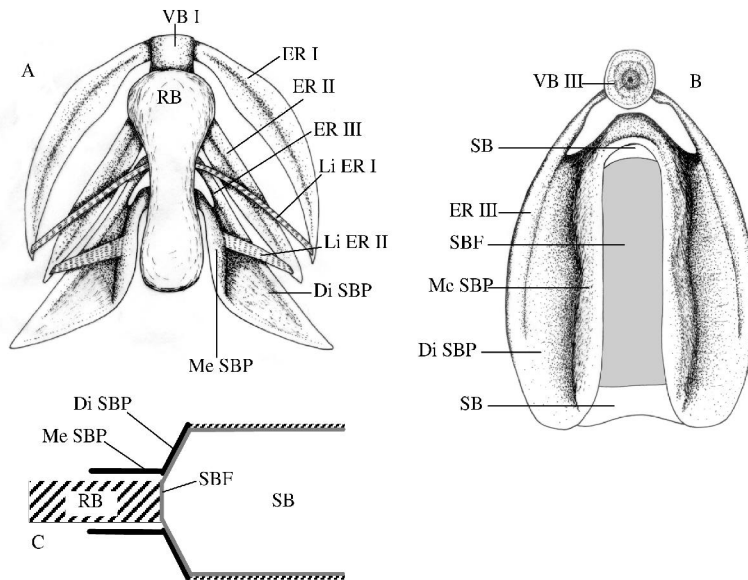


Figure 4. *Onuxodon fowleri*. A. Ventral view of the sound producing complex (without the muscles); B. front view of the swim bladder plate and the swim bladder fenestra; C. Schematic frontal view according to the dotted line in the figure 2.

Sound reception organ

Part of the following results were recently published by Parmentier et al. (2001). The internal ear in Carapidae (Fig.5) is fundamentally organized as in generalized teleosts (e.g. Platt and Popper, 1981; Popper, 1982), but differences in shape and proportions of the parts are considerable.

Viewed internally, the very wide otic cavity is limited posteriorly by the basioccipital and anteriorly by the bridge of the prootic (fig. 5). The membranous labyrinths occupy nearly the entire otic cavity: the metencephalon hardly reaches the back of the prootic bridge. Only the narrow myelencephalon crosses the otic cavity, separating the left and right inner ear at the level of the partes superiores (semi-circular canals and utricles). The left and right partes inferiores (sacculi and lagenae) occupy the ventral volume of the neurocranium: their sacculi are in contact above the basioccipital and their lagenae touch each other at the level of the foramen of the asterisci. In *Snyderidia canina*, *Pyramodon lindas* and *Pyramodon punctatus*, the bones surrounding the otic cavity are thicker than in all other Carapidae species. The otic cavities are proportionately larger in the

commensal species (*Carapus*) and parasitic ones (*Encheliophis gracilis*) than in the benthic (*Echiodon*) and pelagic species (Pyramodontinae). In *O. fowleri*, the otic cavity appears shorter, but deeper than in the Carapini.

In the Carapini, the sagitta is semi-convex. In frontal view, the sagitta looks like a half-sphere, terminated by a particularly long post-rostrum with a pointed end. *Encheliophis gracilis* has a marked protuberance on the distal face, which gives a more compact appearance. In *Echiodon drummondi*, the sagitta is also semi-convex, but regular and less tapered. It differs from that of the Carapini by an undifferentiated post-rostrum. The sagitta of *O. fowleri* is almost biconvex. It appears proportionately shorter but much higher, which might be related to the more rounded shape of the floor of the otic capsule. *Pyramodon punctatus* and *Snyderidia canina* otoliths are characterised by a more or less regular, oval shape without a developed rostrum or post-rostrum. The ratio of the thickness of the sagitta to its length is greatest for *Encheliophis gracilis* (34%). It is between 22 and 25% for the *Carapus* species and *Echiodon drummondi*, and *S. canina* and *P. punctatus* have relatively thin sagittae (16%). The sagittae of *Onuxodon fowleri*, is rounded, with a comparatively high length to thickness ratio (27%), it seems to have deepened at the expense of lengthening.

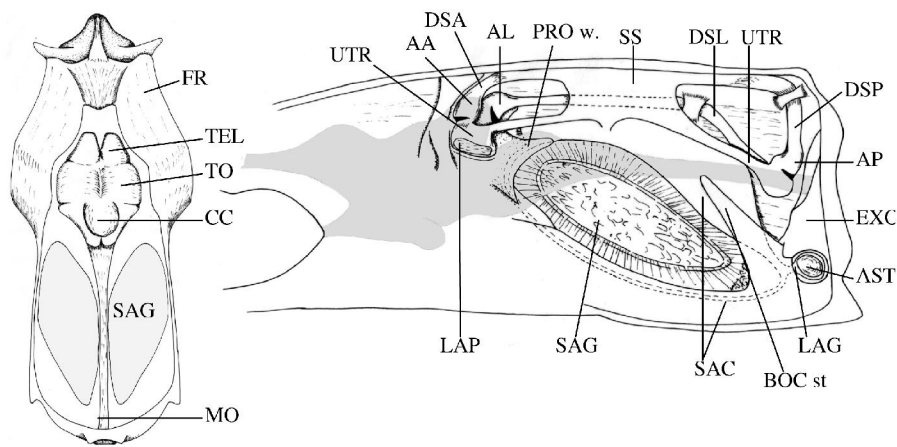


Figure 5. *Carapus boraborensis*. A. Dorsal view of the otic region. Bones of the dome of the skull are removed to see the relative size of the sagitta and the brain B. Internal sagittal view of the right labyrinth with the brain position in grey.

Discussion

Sound production has been identified within several phylogenetically distant groups of fish. Two main types of voluntary sound production are recognized among teleosts (Fine et al., 1977 ; Hawkins and Myrberg, 1983 ; Ladich and Bass, 1998) : (1) stridulation : sounds are emitted by rubbing parts of the body against each other and (2) swim bladder vibrations (Alexander, 1966 ; Popper and Coombs, 1980 ; Hawkins, 1993 ; Ladich, 2000). Species-specific sounds were registered in three different Carapini species, *C. boraborensis*, *C. homei* and *E. gracilis* (Parmentier et al., in press) and, according to the authors, could be produced by swim bladder vibrations. Up to now, nothing is known about the function and/or biological advantage of the production of sounds in these fish. The specificity of the sounds emitted by different species likely results from differences in the swim bladder plate, the other structures being relatively similar among species. The actinopterygian swim

bladder is a resonant but damped structure (Blaxter et al., 1981), thus preventing prolonged resonant vibrations (Fine et al., 2001). Moreover, the size of the swim bladder in Carapidae probably makes it inefficient at the reception of high frequencies, as has been proposed for gadids (Blaxter, 1981). Damping, however, seems to result more from the influence of the surrounding tissues than from the swim bladder wall itself as Demski et al. (1973) demonstrated that resonance was better in isolated swim bladders. The swim bladder plate may decrease the damping by covering the fenestra and thus protecting it from the pressure and movements of the hypaxial musculature. As the swim bladder plate is broader, thinner and more regularly shaped in Carapini, it likely provides a better amplification of the sounds produced at the level of the fenestra.

The large swim bladder plate of the Carapini could be related to two aspects of their way of life: a very noisy environment (the coral reefs and coastal waters), and the fact that they live inside invertebrates. The teguments of the latter most likely disturb sound propagation. In the genus *Echiodon*, the narrower swim bladder plate would be less efficient in its function as a resonance box. The swim bladder plate is broader, but also thicker in Pyramodontinae than in *Echiodon*, moreover, it is tightly connected to the 3rd and 4th vertebral centra, so that part of the vibratory energy could be absorbed by the backbone.

The rocker bone of the *Onuxodon* species is a priori the most sophisticated specialization to improve sound production, which might be linked to life inside the thick shells of bivalves. Although their sonic apparatus is different, a rocker bone in front of the swim bladder exists also in some ophidiids species (Rose, 1961; Stevovidov, 1961; Casadevall et al., 1996). The Ophidiidae with a rocker bone do not live in bivalves, but they are able to burry themselves into sandy soils (Herald, 1953; Greenfield, 1968; Cohen and Nielsen, 1978; Schwarts, 1997) that probably also restrain sound propagation. The improvement of the sonic apparatus could thus be linked to difficulties in sound propagation rather than to life in an invertebrate per se.

Comparing representative species of a family allows a tentative reconstruction of the evolutionary pathway leading from primitive structures to derived ones, such as the specializations of *Onuxodon*. It is hypothesized here that the rocker bone is homologous to the anterior part of the swim bladder (region 1) for the following reasons: in all carapids but *Onuxodon*, the primary sonic muscles and the ligaments of the first epipleural ribs both insert on the swim bladder tunica in front of the fenestra; in the genus *Onuxodon*, the same muscles and ligaments insert on the rocker bone in front of the swim bladder fenestra, while region 1 seems to be absent. Moreover, in both cases, the region 1 and the rocker bone is situated in front of the swim bladder fenestra. The hypothesis receives some support from the observation of region 1 in two species of the sister genus *Echiodon* (Williams, 1984; Markle and Olney, 1990): (1) region 1 has developed more hard and fibrous tissue on the outer part of the swim bladder in *Echiodon cryomargarites*, possibly as a response to the mechanical stress of the traction transmitted by the ligaments of the first and second epipleural ribs; (2) the confluence of the ligaments of the first epipleural ribs on region 1 in *Echiodon rendhali* could be a first evolutionary step toward the formation of a rocker bone and of a ligamentary axis.

The major functions associated with the otoliths are the registration of orientation and accelerations of the head (static and dynamic equilibrium) and sound transduction (Lowenstein, 1971; Tavalga, 1971; Platt and Popper, 1981; Schuijf, 1981; Popper, 1982; Gauldie, 1988). In Carapidae, the large size of the pars inferior of the labyrinths results from the hyper-development of the saccule and sagitta, which are specifically involved in audition (Dijkgraaf, 1960; Popper and Coombs, 1980; Popper, 1982; Fay, 1984). In Carapidae, the species with the most developed sound-producing structures also possess the largest labyrinths and the thickest sagittae. One could indeed envision that the sound receptor is adapted to the reception of the species specific emitted sounds. However, by comparing sonic emission frequencies and auditory capacities of different teleosts, Ladich (2000) concluded that the best bands of the auditory spectrum do not match significantly those of the

emitted sounds. This suggests that the studied fishes can hear the sounds produced by their conspecifics, but that the natural selection acting upon the sonic apparatus is not the only selective pressure. Likely other biological roles of audition are important too, with prey and predator detection being two important ones (Ladich, 2000).

The thickest sagittae, lodged in the thinnest cranial structures and in the proportionally largest otic cavity, are found in the commensal and parasitic species (Parmentier et al., 2001). Just like the sound producing apparatus, the acoustic receptor could be adapted to the habitat. In Carapini and in *Onuxodon* species, the thicker otolith surrounded by thinner bones should produce a greater inertia and a more pronounced shearing effect on the macula hair cells (Parmentier et al., 2001) and hence improve the hearing capabilities. Thicker sagittae could match the loss of energy by the sonic vibrations when travelling through the host tissues or shell.

However, like all functional structures in an animal, the stato-acoustic and sound-producing systems are also governed by other demands which may result in compromises. Pyramidontinae, for example, have thinner sagittae and smaller labyrinths than the other carapids and the shape of these organs resembles that in good swimmers such as Gadidae, Merluccidae and Macrouridae (Dale 1976; Lombarte and Fortunato, 1992 ; Lombarte and Morales-Nin, 1995). In these fishes, thinner otoliths are probably favourable as they result in a decrease of the mean density (Parmentier et al., 2001). In demersal, benthic or parasitic species such as benthic Congridae and Ophidiiformes, swimming is less important, thus resulting in thicker and heavier crests and sagittae and larger labyrinths (Nolf, 1985).

Conclusions

Morphological differences in the presumed sound-producing apparatus and sonograms of three Carapini species suggest that the sounds emitted by the Carapidae are species specific. Similar morphological features of the sound-producing apparatus suggest that all Carapidae are able to produce sounds. Morphological differences are likely related to variations in the amplitude as well as the frequency of the sounds. Some features suggest that those differences are related to the habitat occupied by the different species of Carapidae. It is likely that in commensal and parasitic Carapidae species the increased development of the sonic emitter and receptor apparatuses allows sonic communication through the host tissues or shell. As the present study is a preliminary one, more species should be investigated. Especially the sonic apparatus and the pars inferior of the labyrinth should be described in greater detail and the ecology of the other Carapidae should be studied in order to better understand the ecomorphological relations between morphology, sound production and habitat use.

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List of abbreviations

I, II, III, IV : vertebra I, II, III, IV
AA : ampulla anterior
AL : ampulla lateralis
AP : ampulla posterior
AST : asteriscus
BOC : basioccipital stem
CC : crista cerebellum
Di SBP : distal part of the swim bladder plate
DSA : ductus semicircularis anterior
DSL : ductus semicircularis lateralis
DSP : ductus semicircularis posterior
ER I : epipleural rib 1
ER II : epipleural rib 2
ER III : epipleural rib 3
ER IV : epipleural rib 4
EXO : exoccipital
FR : frontal
I. Li ER I : insertion of epipleural rib 1ligament
I. PSP : insertion of the primary sound producing muscle
Me SBP : mesial part of the swim bladder plate
LAG : lagena
LAP : lapillus
Li ER I : ligament of epipleural rib 1
Li ER II : ligament of epipleural rib 1
MO : medulla oblongata
OSB : osseous part of the swim bladder
PAR : parapophyse
PRO w. : prootic wing
PSP : primary sound producing muscle
RB : rocker bone
RBK : rocker bone knob
SAG : sagitta
SAC : sacculus
SB : swim bladder
SBF : swim bladder fenestra
SBP : swim bladder plate
Sc SB : sclerification of the swim bladder
SS : sinus superior
SSP : secondary sound producing muscle
TEL : telencephalon
TO : tectum opticum
UTR : utriculus
VB I : vertebral body 1
VB III : vertebral body 3