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RESEARCH ARTICLE

Hearing and morphological specializations of the mojarra (*Eucinostomus argenteus*)

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SUMMARY

The air-filled swimbladder acts as an acoustic amplifier for some fish by converting sound pressure into particle motion, which is transmitted to the inner ear. Here, we describe in detail the specialized connection between the swimbladder and ear in the mojarra, as well as a modified cone on the anal fin in which the posterior end of the swimbladder sits. Hearing tests show the mojarra has better hearing sensitivity than other species of fish without a connection. However, mojarras do not seem to use this adaptation for communication. Furthermore, the inclined position of the swimbladder may help the fish to catch their prey more easily, as the swimbladder will be horizontal when they are picking up benthic prey.

Key words: acoustic, audition, swimbladder.

INTRODUCTION

Measures of hearing sensitivity have demonstrated that most fish hear over a relatively narrow range of frequencies (Popper and Schilt, 2008). Within fishes there is a great diversity in hearing sensitivity and bandwidth. At one extreme are fish such as flatfishes, which are only able to detect the particle motion component of low frequency sounds (<1 kHz) at relatively high sound levels (Fay, 1988). Other species (e.g. carp, catfishes, mormyrids) detect the pressure component of sounds over a broader frequency range (up to 4–5 kHz) at much lower sound intensities (Amoser and Ladich, 2005). Most known hearing specializations involve modification of the swim bladder (Braun and Grande, 2008). In fish, this air-filled organ acts as an amplifier by converting sound pressure into displacement, which is transmitted to the inner ear (Yan et al., 2000). The simplest hearing enhancement is a forward extension or translation of the swim bladder towards the otic capsule; the closer the swim bladder to the ear, the more sensitive the audition (e.g. Ramcharitar et al., 2001; Ramcharitar et al., 2006). Rostral extensions of the swim bladder are present in some species of different taxa (Braun and Grande, 2008) such as Holocentridae (Neslon, 1955; Coombs and Popper, 1979), Gadidae (Chapman and Hawkins, 1973; Sand and Enger, 1973) or Cichlidae (Stiassny et al., 2001). In Clupeomorpha, the swim bladder extensions can penetrate inside the braincase and expand in two bullae intimately associated with the inner ear (Grande and de Pinna, 2004). Otophysines are characterized by having Weberian ossicles, a mechanical linkage that facilitates sound transmission from the swimbladder to the inner ear (von Frish, 1938; Chardon, 1968; Fay, 1988; Ladich, 2000). In the Holocentridae, *Myripristis* have an intimate connection between the swimbladder and the inner ear and are more sensitive to sound than are *Sargocentron*, which do not have a connection (Coombs and Popper, 1979).

Gerreids or mojarras are strongly compressed fish characterized by a pointed snout and a highly protrusible mouth. They occur over muddy and sandy bottoms in estuaries, hypersaline lagoons and occasionally in fresh water in tropical and subtropical shallow coastal habitats (Matheson and McEachran, 1984; Chen et al., 2007). Fish in the family Gerreidae are also known for two swim bladder specializations. Anteriorly, the swim bladder of *Eucinostomus argenteus* is divided into two horns intimately connected to the auditory bulla through a fenestra. Posteriorly, the swim bladder projects into a cone-shaped structure. This cone (the interhemal bone) is an integral part of the anal fin (Green, 1971). We hypothesized that these swim bladder and bone specializations would allow improved hearing in these fish. In this study we characterized these structures in greater detail than previous examinations using high resolution computed tomography (CT) scanning and histology. We also measured the hearing sensitivity and bandwidth of mojarra using auditory evoked potentials (AEPs).

MATERIALS AND METHODS

Fish acquisition and maintenance

Fifteen *Eucinostomus argenteus*, Baird and Girard 1855 (76.6±6.4 mm total length), were caught using a cast net in Bayboro Harbor, Tampa Bay, FL, USA (27°45′44″N, 82°38′37″W) during May 2007. Fish were kept in the same communal tank (60×30×30 cm, salinity S=35, temperature T=26°C) with an aerator at the University of South Florida (USF). All fish were held for 1–3 days before testing. They were fed a few pinches of Tropical Fish Flakes (Blackburg, VA, USA) twice a day. All procedures were approved by the Institutional Animal Care and Use Committee of the University of South Florida.

Experimental setup

Hearing thresholds were measured using the AEP technique (e.g. Kenyon et al., 1998). The experimental setup was similar to that used for the study of hearing in *Amphiprion* (Parmentier et al., 2009). Each fish was immobilized in a custom-made harness, restricting body and tail movements while allowing normal respiration. Subdermal stainless steel needle electrodes (Rochester Electro-

Medical, Lutz, FL, USA) were used for recording the AEP signal. An electrode was inserted about 1 mm into the head, over the otic region. The reference electrode was placed within the fish's epaxial musculature and a ground electrode was placed directly in the water in close proximity to the fish. Fish were suspended 10 cm below the surface in a steel tube (1.2 m high, 20.3 cm diameter, 0.95 cm thickness), closed at the bottom with a square steel plate (60.96×60.96 cm), and oriented vertically. Four anti-vibration floor mounts (51700 Series, Tech Products Corp., Philadelphia, PA, USA) were placed under each corner of the base of the steel tube. The tube was filled with saltwater of approximately 26°C up to a height of 1.12 m and a loudspeaker was placed at the bottom of the steel pipe.

Sound generation and AEP acquisition

A Tucker-Davis Technologies (TDT, Alachua, FL, USA) AEP workstation was use to generate sound stimuli and record AEP waveforms (see Egner and Mann, 2005). TDT SigGen and BioSig software were used to generate sound stimuli with an RP2.1 enhanced realtime processor, a PA5 programmable attenuator to control sound level, and a power amplifier (Hafler Trans.Ana P1000 110 W professional power amplifier; Tempe, AZ, USA) before being sent to a UW-30 underwater speaker (Lubell Labs Inc., Columbus, OH, USA) where sound was emitted. Stimuli consisted of 50 ms pulsed tones gated with a Hanning window. The phase of the tone was alternated between presentations to minimize electrical artefacts from the recordings. Acoustic stimuli were calibrated with a Reson hydrophone (sensitivity 212 dBV/1 µPa; bandwidth 1 Hz to 170 kHz; Goleta, CA, USA) connected to the RP2. During calibration, the hydrophone was positioned near the fish in the experimental setup, and the sound levels were measured with BioSig, without phase alternation. During each trial, 11 different frequencies were presented: 75, 150, 300, 600, 900, 1200, 1500, 1800 and 3600 Hz. Sound levels at each frequency were presented at up to 164 dB re 1 µPa and were decreased in 6 dB steps until a threshold level was determined. Evoked potentials recorded by the electrode were fed through a TDT HS4-DB4 amplifier (10,000× gain) connected to an RP2.1, routed into the computer and averaged by BioSig software. Up to a total of 2000 signal presentations were averaged to measure the evoked response at each level of each frequency.

Data analysis

Power spectra were calculated using an 8192-point FFT (fast Fourier transform) for all AEP waveforms and were analysed for the presence of peaks at twice the frequency of the stimulus that were at least 3 dB above background levels. AEP thresholds were defined as the lowest sound level at which significant FFT peaks for the dominant frequency were apparent.

Morphology

Seven fish were fixed in 7% formaldehyde for serial histological sections and for dissection. Five specimens were stained with Alizarin Red S according to a previous method (Taylor and Van Dyke, 1985). The general morphology of the auditory apparatus was examined with a Wild M10 (Leica) binocular microscope equipped with a camera lucida and a digital camera (Canon Power Shot S50).

Two *E. argenteus* specimens were dehydrated in butanol, decalcified, embedded in paraffin and serially sectioned using a Reichert microtome (10 µm thickness). Two stains were used (Gabe, 1976): Gallego's ferric fushin stain for elastic fibres and Masson's trichrome stain for collagen. Sections were observed using a polarizing Olympus microscope (Leica DM 100) coupled with a digital camera (Canon Power Shot S50).

One fish was scanned at 30 µm isotropic resolution using a micro-CT scanner (Scanco µCT 40, Scanco Medical AG, Bruttisellen, Switzerland). A smaller segment of the anal spine–cone complex was scanned at 12 µm resolution to provide further details of joint articulations. Scan settings for both scan sets were 55 kV peak, 145 µA, with image durations of 200 ms. Transaxial reconstructions were performed using the standard Scanco software. The 3D reconstructions were performed using MIMICS software (Materialise Medical Software, Leuven, Belgium).

Behavioural observations

A layer of 5 cm of sand and living polychaetes were added in the fish community tank. Fish behaviour was filmed with a Sony HDD video camera over three periods of 15 min. The main aim was mainly to observe fish movement during feeding or searching for food.

RESULTS

Hearing

Eucinostomus argenteus specimens were able to detect frequencies over the range 100 to 1800 Hz (Fig. 1, Table 1). Mean thresholds showed that they were most sensitive at the lower frequencies tested (150–600 Hz). Auditory sensitivity decreased from 600 Hz to 1200 Hz. No artefacts were detected at the high sound levels when a dead fish control was run.

Morphology

The swim bladder was a closed single-chambered vesicle extending the length of the body cavity. The swim bladder anteriorly contacts the cranium by two anterior horns and projects posteriorly into a cone-shaped interhemal bone.

The anal fin of *E. argenteus* is composed of two anal spines and eight anal fin rays (Fig. 2). Both anal spines are suspended by ring-like articulations on the inner cone-shaped interhemal structure (Fig. 2B). This kind of articulation allows back and forth pendulum movements of the spines. However, the ring also forces the spines to be close to the cone. Histological sections and scanning electron microscope (SEM) pictures revealed the cone is not complete but is ventrally split. The cone is firmly attached to the tunica externa of the swimbladder.

The rostral swimbladder extensions end in a rounded otic foramen at the level of the otic capsule (Figs 2 and 3). This fenestra is

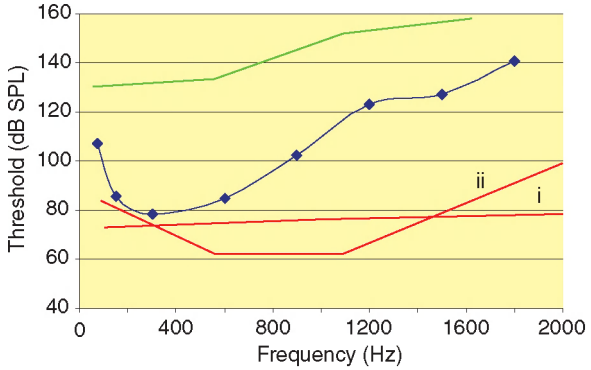

Fig. 1. Audiogram of *Eucinostomus argenteus* (blue), *Abudefduf saxatilis*, representing generalists (green) (Egner and Mann, 2005), and *Cyprinus carpio* (red, i) (Ladich, 2000) and *Pimelodus blochii* (red, ii) (Wysocki et al., 2006), representing specialists. SPL, sound pressure level.

Table 1. Mean hearing threshold values in eight specimens of *Eucinostomus argenteus*

Frequency (Hz)	Mean ± s.e. (dB re. 1 µPa)
75	107±4
150	85±2
300	78±4
600	85±2
900	102±2
1200	123±2
1500	127±2
1800	140±2

delimited by the basioccipital, epiotic and prootic bones, where the swimbladder tissues anchor to the bone edges (Fig. 3). The foramen faces the asteriscus and the posterior part of the sagitta. The asteriscus is closer to the foramen than to the sagitta and its macula is situated more dorsally in comparison to the macula of the sagitta. The sagitta is, however, longer and is not limited to the foramen diameter. The cross-sections show that the two otoliths are not separated by a membrane. Moreover, the posterior part of the right and left pars ventralis of the inner ear are behind the brain and close to each other, being separated only by a very thin bone lamella. At the level of the fenestra, the blind tunica externa swimbladder is thinner than in the horns (Fig. 3). As a result, the swimbladder tissues press against the squamous epithelium of the otosac. So, vibration of the swimbladder is conducted to the saccular endolymph across the swimbladder walls.

Behavioural observations

Specimens were swimming a few centimetres above the sand. Before searching in the substrate, fish stopped swimming and were able to remain immobile for several seconds. They then suddenly rotated their body (35±7 deg, N=17) head first to explore it. The amplitude of the rotation corresponded to the angle between the swimbladder and the vertebral column (±30 deg). Note that fish were able to localize dead and living polychaetes in the sand that we could not see with our camera.

DISCUSSION

Coupling the inner ear to a gas-filled cavity helps fish to sense pressure. Fluctuations in ambient pressure cause the swimbladder to oscillate in volume and the wall of the swimbladder to pulsate. The forward extension of the swimbladder allows the transmission of this motion to the inner ear, enhancing hearing (Braun and Grande, 2008). Although the hearing capabilities of *E. argenteus* cover a broad frequency range and have greater sensitivity than most fish with a swimbladder that is not connected to the ear (Fig. 1B), they do not show the hearing sensitivity and frequency range found in otophysan fishes, which have Weberian ossicles connecting the

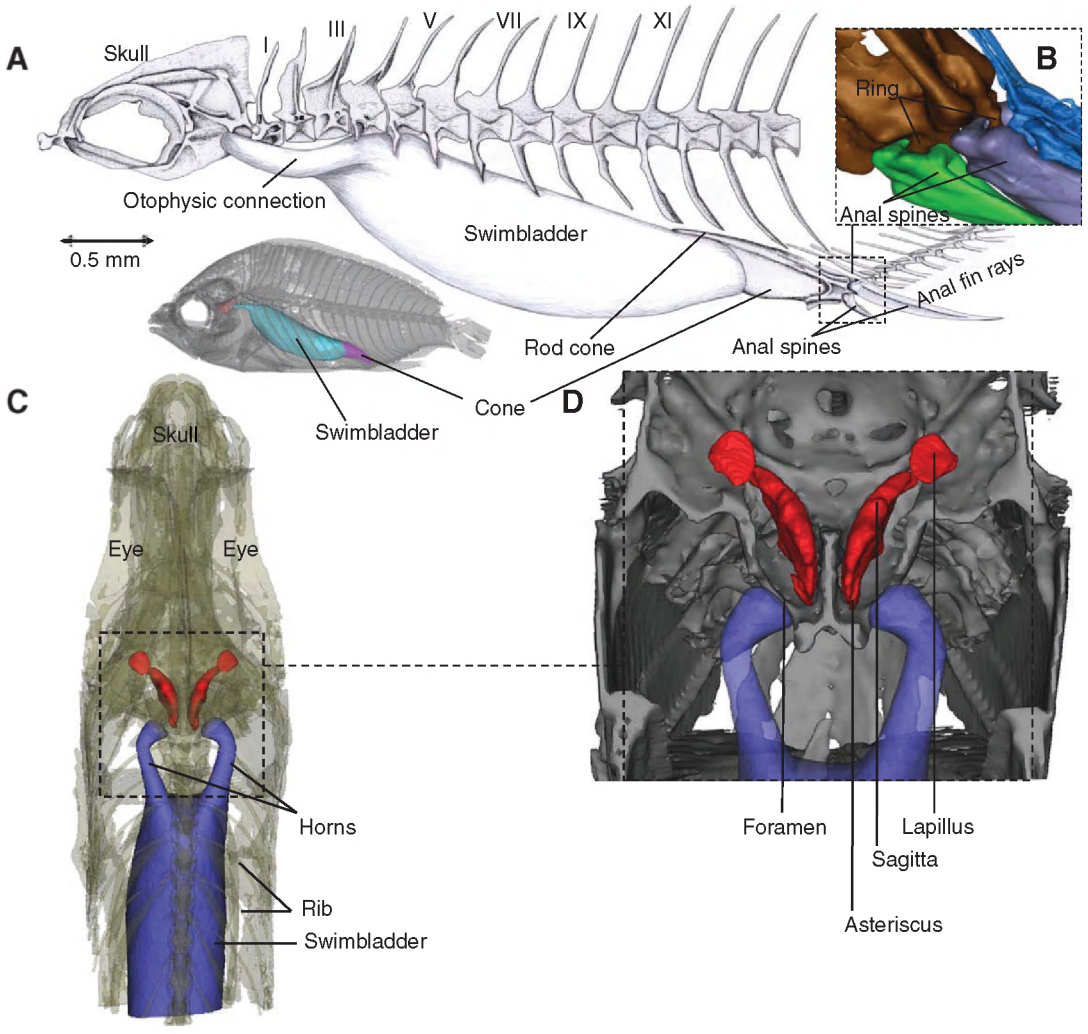

Fig. 2. Left lateral view of the swim bladder in *E. argenteus* (A) and enlargement of the dotted square (B) showing the ring-like articulations of the spines (3D reconstruction from computed tomography, CT). (C,D) Dorsal view of the skull, the connections of the swimbladder and the otic cavity (3D reconstruction from CT). Distal extremities of anal fin rays are not shown.

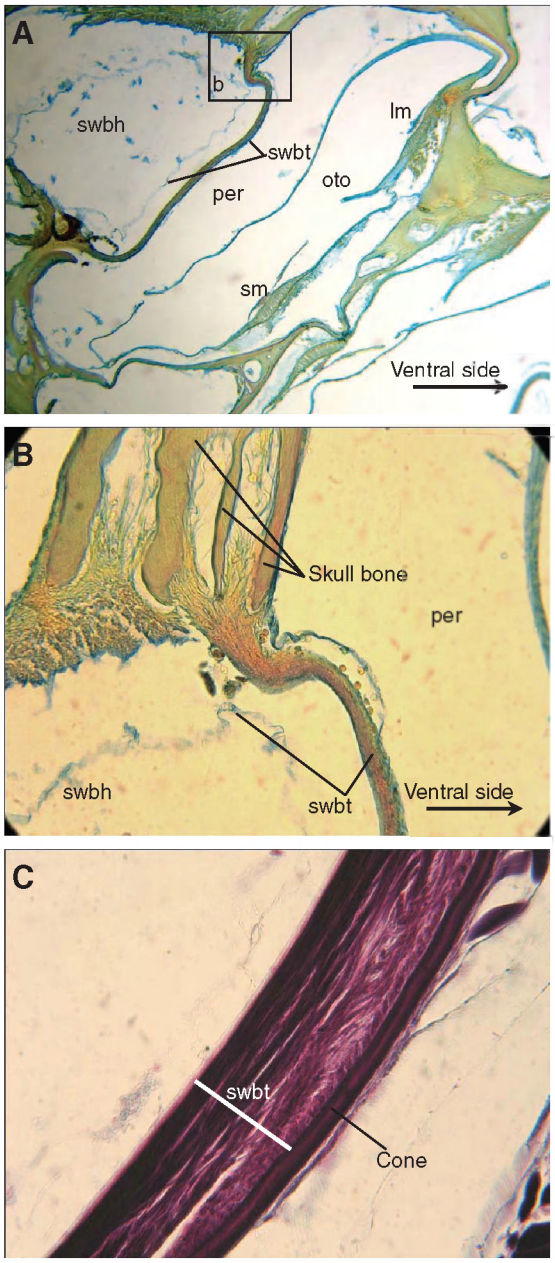

Fig. 3. Cross-section at the level of the otic foramen (A; area b enlarged in B) and at the level of the cone (C) in *E. argenteus*. lm, lagenar macula; oto, otosac; per, perilymph; sm, saccular macula; swbh, swimbladder horn; swbt, swimbladder tissues.

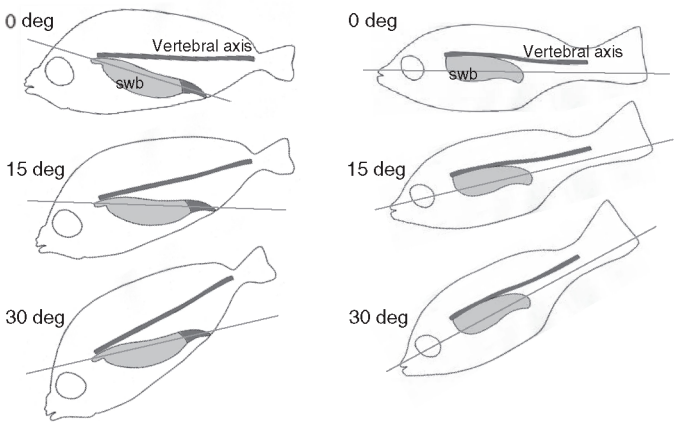

Fig. 4. Comparison of the swimbladder position between *E. argenteus* and a 'classical' teleost (*Oreochromis niloticus*) at different inclinations. Both drawings were made on the basis of X-ray pictures. The darker zone in the swimbladder of *E. argenteus* corresponds to the terminal cone. The angles are those between the vertebral axis and the horizontal plane.

swimbladder to the inner ear (Ladich, 2000; Egner and Mann, 2005; Wysocki et al., 2006; Popper and Schilt, 2008). Coombs and Popper noted relatively high thresholds and limited frequency ranges in *Notopterus* despite a close coupling between the swimbladder and the inner ear (Coombs and Popper, 1982). Clupeiforme fishes that have air-filled auditory bullae in the skull, likewise, have increased bandwidth but not very high sensitivity (Mann et al., 1997; Mann et al., 2001). In the gadid *Gadus morhua*, swimbladder horns, which do not contact the skull, probably lead to a better overall sensitivity and enhancement of directional hearing. However, the cod does not present the same hearing abilities as the squirrelfish *Myripristis* (Chapman and Hawkins, 1973; Coombs and Popper, 1979; Coombs, 1981; Hawkins, 1986; Braun and Grande, 2008). In the family Holocentridae, there is indeed a trend of increasingly specialized swimbladders. Fish with an intimate connection between the swimbladder and the auditory capsule respond to higher frequencies and are more sensitive to sound. In the mojarra, the swimbladder horns should also improve hearing sensitivity because of the contact between the swimbladder and the perilymph. However, their hearing does not appear to be as sensitive as that in *Myripristis* species (Coombs and Popper, 1979). Morphological differences could explain in part the difference in hearing ability compared with the Myripristinae. According to the description given by Nelson, the tunica externa forms an intimate contact with the epithelium of the otosac, although this was not illustrated in a figure (Nelson, 1955). In *Myripristis kuntee*, it appears that connective fibres connect the swimbladder and otosac epithelia (E.P., personal observation). In *Eucinostomus*, we did not see connective fibres between the swimbladder and otosac epithelia. This loose contact could lead to a less efficient transfer of energy between the swimbladder and the inner ear. Moreover, the horn section is proportionally larger and covers almost all of the sagitta area in *M. kuntee* (E.P., personal observation). In *E. argenteus*, the horns are relatively small and face only the third posterior part of the sagittae, meaning the signal from the swimbladder will not stimulate the sagittae in the same way.

Eucinostomus argenteus do not have specialized sound-producing structures (Green, 1971) and are not known to produce sounds. It has been proposed that mojarra drive their anal fin into the sand to detect annelid prey (Green, 1971). According to our behavioural experiments, the fish were able to localize their prey under sediment. It did not appear that vision was used to find prey. Additional experiments are, however, required to determine whether their enhanced auditory abilities are linked to their predatory activity, because the worms were in the sand. We observed that *E. argenteus* remained immobile a few centimetres above the substrate and suddenly rotated their body headfirst to explore it. When rotated, the swimbladder lies approximately horizontally in the body (Fig. 4). Blaxter proposed that an upwardly slanted swimbladder allows the location of gas as near to the ear as possible (Blaxter, 1981). During a dive or feeding, the air remains in the swimbladder horns,

preventing collapse of the tube with increasing pressure, so maintaining auditory function. Moreover, the weight of the bony anal cone could help the fish to revert to the resting position, enabling it to rotate.

The mojarra have a unique swimbladder and ear connection, in that the swimbladder extends from the skull down the body, ending inside a cone at the anal fin. It has been shown that the swimbladder is sensitive to pressure fluctuations because its low density and high compressibility drive the walls to move at high amplitude (Popper and Fay, 1999). We hypothesize that the bony cone that surrounds the caudal part of the swimbladder should prevent posterior swimbladder movements and thus amplify the response on the anterior portion of the swimbladder.

Contractions of ventral muscles of the anal fin inserting on the spines and on the ventral part of the cone (E.P., K.M. and D.M., personal observation) could also modify the cone position and raise the cone rod, modulating the stiffness of the swim bladder. It is not clear how mojarra use their enhanced hearing sensitivity, as mojarra do not appear to produce communication sounds. This would not be surprising as a review of otophysines showed that the selective pressures involved in the evolution of accessory hearing structures are not necessarily linked to the optimization of acoustic communication (Ladich, 2000). Fish living in the shallows may gain an advantage if they can extend the frequency range they use for prey or predator detection (Braun and Grande, 2008).

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