Article

Observations of the sound producing organs in achelate lobster larvae

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Abstract
The Achelata, lobsters lacking claws and having a phyllosoma larva, are divided into two families, the Palinuridae or spiny lobsters and the Scyllaridae or slipper lobsters. Within the Palinuridae adults of two groups were identified by Parker (1884), the Stridentesthat are capable of producing sounds, and the Silentesthat are not known to produce sounds. The Stridentes employ a file-like structure on the dorsal surface of the cephalon and a plectrum consisting of a series of ridges on the proximal segment of the second antenna to produce their sounds. All species of Achelata hatch as an unpigmented thin phyllosoma larva. The phyllosoma larva of the Stridentes have a presumptive file-like structure on the dorsal cephalon. A similar file-like structure is found on the cephalon of one species of Silentes, *Palinurellus wienckki,* and some but not all of the phyllosoma larvae of the Scyllaridae. No presumptive plectrum is found on the second antenna of any of the phyllosoma larvae. Presence of a presumptive file-like structure on phyllosoma larvae of Silentes and Scyllaridae suggests that the ability to produce sounds may have been lost secondarily in the Silentes and Scyllaridae.

Key words Spiny lobster larva; bio-acoustics; slip-stick mechanism; Phyllosoma.

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1 Introduction

The Achelata are Reptantian decapod lobsters lacking claws. Two families comprise the Achelata, the Palinuridae or spiny lobsters and the Scyllaridae or slipper lobsters. Within the Palinuridae are two groups identified by Parker (1884), the Stridentes which produce soundsand the Silentes which are not known to produce sounds. The Stridentesproduce sounds by a “Slip–stick mechanism. Moulton (1957) described the sound producing organs of the Stridentes as being composed of a stridulating apparatus composed of a raised ribbed pad on the first segment of the antennae, which he named the plectrum, and a file like structure on the carapace extending anteriorly from the base of the eye stalk to the base of the antennae. The file – like structure is composed of many small raised structures termed shingles. Patek and Oakley (2003) have shown that the carapace structure and morphology of the Stridentes is significantly different from that of the Silentes with the antennal plate taking up a much larger fraction of the carapace in the Stridentes. These morphological differences are an indication of the evolutionary changes which resulted in the loss of the ability to produce sounds in some members of the Achelata. Smale (1974) produced scanning electron micrographs of these structures and observed the presence of a "resonating box" under the plectrum which amplified the sound produced. These structures are lacking in the adults of the Silentes (George and Main, 1967). The number of ridges on the plectrum increases with size of the individual. Also the duration of the sound produced increases with the size of the individual (Meyer–Rochow, 1974).

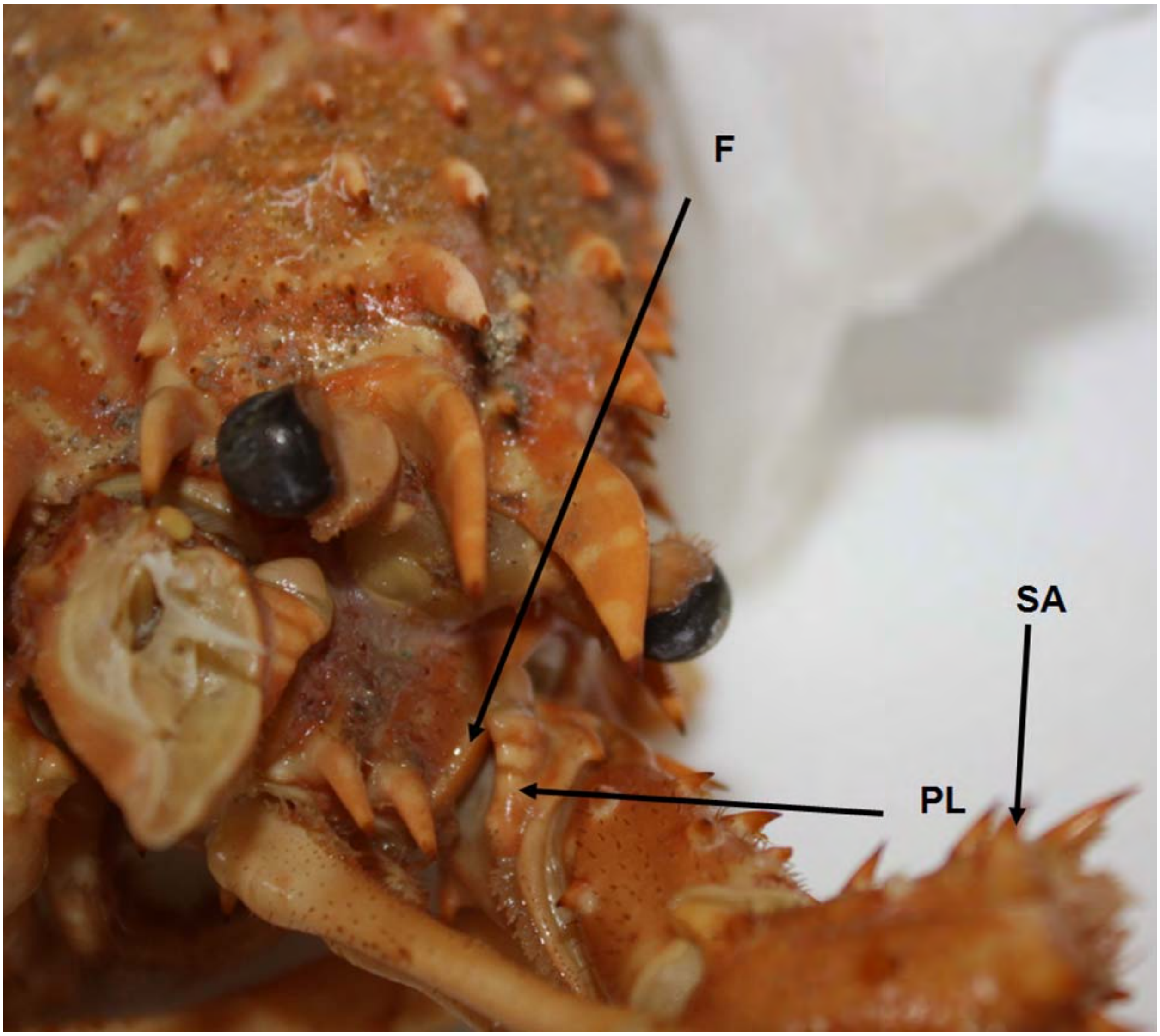

Fig. 1 This figure represents and adult *Panulirus guttatus* (Latreille, 1804) showing the base of the antenna and the plectrum, which appears as a striped fleshy mass of tissue adjacent to the file on the carapace below the eye. The following labels are used: FA= Antennule; SA= Antenna; ES=Eye Stalk; F=file; Sh = Shingle; PL = Plectrum; AP = Antennal plate.

More recently the experimental work of Patek (2001, 2002) has shed much light on the actual physical mechanism of sound production. Patek (2001) introduced the term “Slip-stick mechanism” to describe the action of the plectrum, a mass of soft tissue on the second antenna and file on the carapace. Her experiments showed that the plectrum sticks momentarily to the file and then releases it causing the vibrations (Patek, 2001, 2002). In this work it was also demonstrated that the sound producing mechanism of the Stridentes is functional during the molting process, unlike the sound producing stridulations found on other decapods.

Species of the super family Palinuroidea, to which the Achelata belong hatch as a phyllosoma larva (Holthuis, 1991). This larva is thin and except for the eyes is typically unpigmented. The larval phase may last anywhere from a few weeks to two years as the organisms drift with the current in the surface waters (Palero, 2014). The morphology of the phyllosoma larva is indicative of adaptation for a prolonged pelagic life (Jägersten, 1972). The phyllosoma larva eventually metamorphoses into a second larval type called a puerulus larva in the case of the palinurids and a nisto larva in the case of the scyllarids. These also are typically unpigmented and have the morphological form of the adult. In addition to assuming the adult lobster form, the pleopods become functional in swimming. Both the nisto and the puerulus continue to swim in the water column using their pleonal appendages while seeking a suitable habitat on which to settle. Puerulus larvae of the Stridentes members of the Palinuridae have the file **-** like structure and plectrum, although the latter has a significantly reduced number of ridges compared to juvenile and adult individuals. Experimental studies of the puerulus larva indicated that these structures are not yet functional (Meyer–Rochow and Penrose, 1976).

The primary focus of our research here is on the presence of a presumptive file-like structure on phyllosoma larvae.

2 Materials and Methods

The Stridentes contain seven extant genera, listed by George (1967) and George and Main (1967), *Justitia, Linuparaus, Palibythus, Palinurus, Palinustus, Panulirus* and *Puerulus*. Thirteen specimens of Stridentes were examined for this study including four genera and nine species. The Silentes are represented by four extant genera, *Jasus, Palinurellus, Projasus,*and *Sagmariasus* (George 1967). In addition to these is added the genus *Palinurellus*. The genus *Palinurellus*was originally placed in the Synaxidae, but that family subsequently has been synonymized Palinuridae. One specimen of this genus, *P. wieneckii* DeMan (1881) was also included in our study as an example of the Silentes. Also one species of the Silentes genus *Jasus* was included in this study. The larvae of six genera and seven species of the family Scyllaridae, were also examined: The specimens used in this study are listed in Table I.

The phyllosoma larvae studied here are from the Johnson Slide Collection maintained in the collections of the United States National Museum of Natural History. This slide collection was made by Dr. Marten Wiggo Johnson while he was working at the Scrips Institute of Oceanography over a period of several decades. Specimens were stained with Fast Green and imbedded in Canada balsam before mounting on glass slides. All of the species determinations were made by Marten Wiggo Johnson while at the Scripps Institute of Oceanography. The specimens in the Johnson slide collection are mid to late larval stages. This collection was transferred to the National Museum of Natural History where the present study was made using the collection as a data base. The size of the phyllosoma larva was measured directly from the slides.

A single archived specimen of an adult *Panulirus guttatus* (Latreille, 1804) (NMNH 126193) (Identified by Raymond B. Manning) was used to illustrate the position of the sound producing organs in the adult (Fig. 1). The images of phyllosoma larva used in this study were made using an Olympus DSX100 digital microscope camera in the Natural History Museum Imaging laboratory.

Eight archived specimens of Phyllosoma larva of the genus *Panulirus* (National Museum of Natural History accession number 59586) collected by the Fisheries research Vessel Albatross near the Galapagos Islands, 20^{o} 34'N 92^{o} 06'W were used to make scanning electron micrographs of the presumptive sound producing and sensing organs. At the time of collection the specimens were fixed in a formaldehyde solution and stored in a 70% ethyl alcohol solution at the Natural History Museum. All larvae were transferred to fresh 70% alcohol before processing for electron microscopy. The larvae were dehydrated in progressively more concentrated ethanol solutions and critical point dried and coated with gold alloy for the scanning electron micrographs using a Philips XL30 ESEM LaB6 Electron Microscope. Each image contained 5.7 megapixels. A scale bar is produced by the imaging system for each image.

Table I The specimens used in this study and the United States National Museum of Natural History catalog numbers are given here. The genera *Panulirus, Justitia, Linuparus* and *Puerulus* are Stridentes; *Palinurellus* and *Jassus* are Silentes and *Scyllarides, Arctides, Scyllarus, Evibacus, Thenus* and *Ibacus* are Scyllarids.

Genus and Species names	Museum catalog number
Panulirus penicillatus (Oliver, 1971)	(NMNH 320093and NMNH 140868)
P. inflatus (Bouvier)	(NMNH 140870, NMNH 210163, NMNH 210167 and NMNH 210167)
P. interruptus (Randall)	(NMNH 140889 and NMNH 210038)
P. gracilis Streets	(NMNH 140862)
P. longipes (Milne – Edwards)	(NMNH 210049)
P. longipes (Milne – Edwards)	(NMNH 210049)
Justitia longimana (Milne – Edwards)	(NMNH210006)
Linuparus sp.	(NMNH 137892)
Puerulus angulate (Bate, 1888)	(USNM 210268).
Palinurellus wieneckii DeMan (1881)	(NMNH (140883)
Jassus verreauxi (Milne-Edwards H.)	(NMNH 240252)
Scyllaridessquammosus (Milne – Edwards)	(NMNH 140880)
S. astori Holthuis	(NMNH 140871)
S. nodifer(Stimpson)	(NMNH 232784)
Arctides regsalis Holthuis	(NMNH140879)
Scyllarus timidus Holthuis	(NMNH 140875)
Evibacus princeps Smith	(NMNH 140867)
Thenus orientalis Holthuis	(USNM 210239 and USNM 210242)
Ibacus novemdentatus Gibbes	(USNM 294748)

3 Results

Thirteen phyllosoma larvae representing four genera and nine species of Stridentes, *Linuparus sp., Justitia longimana, Panulirus penicillatus, P. inflatus, P. interruptus, P. penicillatus, P. gracilis, P. longipes* and *Puerulus angulatus* were found to have a structure on the dorsal surface of the cephalon just behind the base of the second antenna (Figs 2 and 3).This position is similar to the location of the sound producing organ in the adults of the same species of lobsters. The structure is more or less in an oval shape the edges are irregular in form with lengths ranging from 0.292 mm to 1.593 mm and widths ranging from 0.176 mm to 1.062 mm. The size of these file primordia and shingle spacing in them is summarized in Table II.

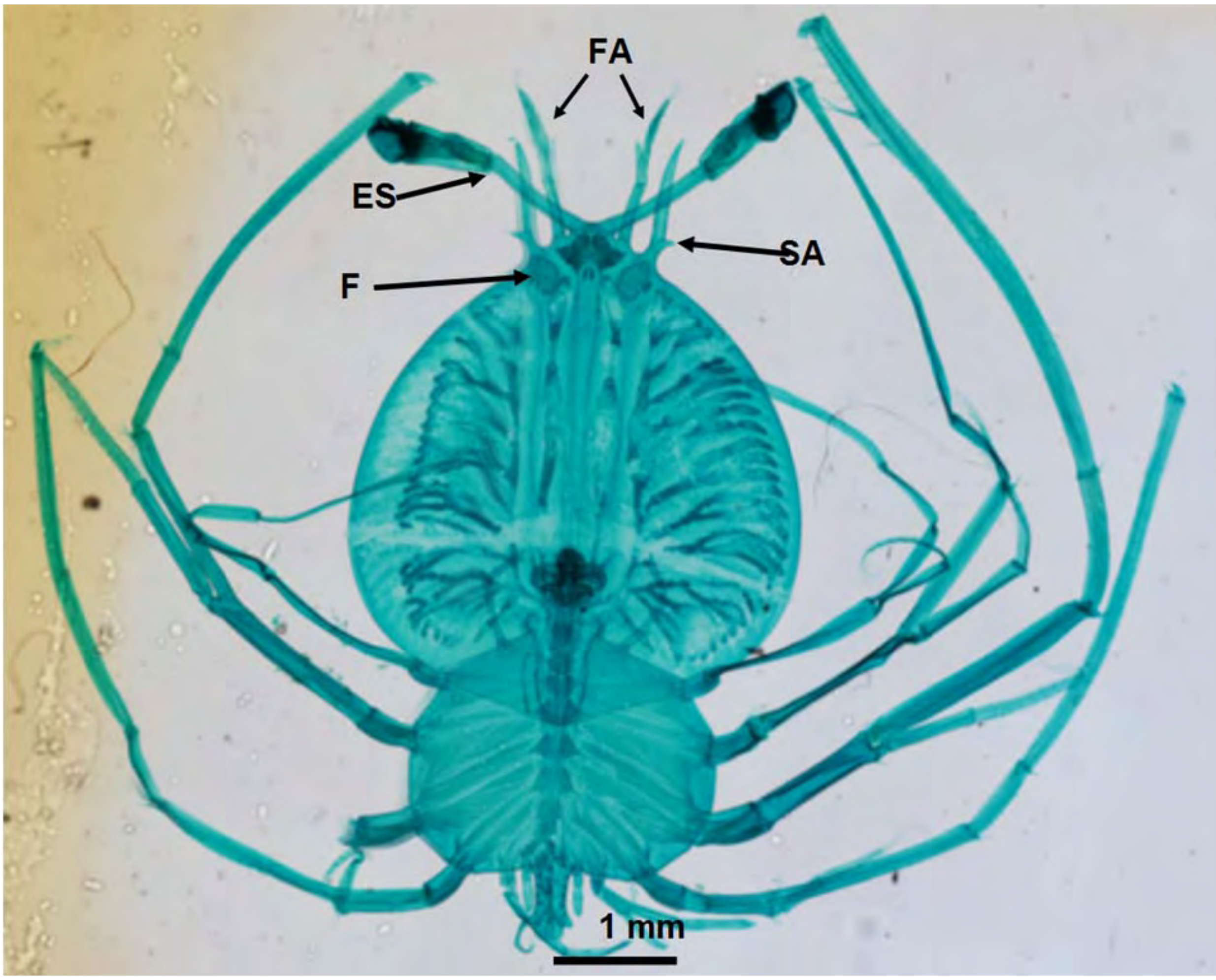

Fig. 2 A composite image of phyllosoma larva of the Stridentes *Linuparus sp.* showing the entire Phyllosoma larva. The following labels are used: FA= Antennule; SA= Antenna; ES=Eye Stalk; F=file.

The file primordia when present are elevated structures on the surface of the carapace (Figs 2 – 5). The larger file sizes were found in the larger larvae. The shingles are in the form of irregular polygons raised slightly above the surface of the file. In the case of *Panulirus penicillatus* the shingles took up more stain around their margins (See Fig. 3). There was no indication of the development of a plectrum on the larval antennae. Based on the location, the structure is interpreted as the presumptive file–like structure in the adult lobster.

The electron micrographs of *Panulirus* phyllosoma larva show a raised structure on the carapace at the base of the second antennae. The presence of shingles is not apparent in the images. The small size of the *Panulirus* phyllosoma larva compared to those in the Johnson Slide Collection would indicate that they were early instars.

One archived specimen of *Palinurellus wieneckii* assumed to belong to Silentes also had the primordia of the file structure.

Five archived specimens representing four genera and five species of slipper lobsters were found to have a similar structure on the dorsal surface of the larva just behind the base of the second antenna: *Arctides regalis, Scyllarus timidus, Scyllarides astori, S. squammosus* and *Evibacus princeps.* This structure is also oval in shape as those found on the larva of the Stridentes, but the shingles are somewhat more raised and pointed. The size of this structure and the shingle spacing is summarized in Table III and are comparable to those of the Stridentes. In the case of *Scyllarus timidus* (See Fig. 4) the central portion of the raised shingle tended to be more darkly stained than the Stridentes. This structure is interpreted as a presumptive file – like structure even though none of the slipper lobsters have a file - like structure as an adult. Three specimens from two genera of the Scyllaridae, *Thenus orientalis* and *Ibacus novemdentaus* did not have the primordia of the file structure.

4 Discussion

4.1 General background

The ability of adult lobsters to produce sounds has been studied from the late nineteenth century to the present (Parker, 1884; Moulton, 1957; George, 1967; George and Main, 1967; Meyer–Rochow, 1974; Meyer-Rochow and Penrose, 1976; Mulligan and Fisher, 1977; Phillips and Penrose, 1985; Popper et al., 2001; Patek, 2001; Patek, 2002; Lathra et al., 2005; Senter, 2008; Patek, 2010). From these studies, it is known that members of the Stridentes can produce a rasping sound and do so when in the presence of predators. Other uses of sound by the adults are not known at this time. The ability to produce and or detect sounds is far more difficult to study in larva and as a result has received less attention and only in more recent research. The Puerulus larvae have both the file and the plectrum, but do not produce detectable sounds (Ishay et al., 1974; Montgomery et al., 1974; Phillips and Penrose, 1985). The larvae of decapods, in particular those inhabiting reefs, appear to use sound to locate their preferred habitat for settling (Montgomery et al., 1974).

Table II Phyllosoma of Stridentes: Specimen length; file length; width and shingle spacing.

Species	Specimen Length	File Width	File Length	Shingle spacing
1. *Linuparus sp.*	5 mm	0.176 mm	0.292 mm	0.016 mm
2. *Justitia longimana*	30 mm	0.796 mm	1.159 mm	0.057 mm
3. *Panulirus penicillatus*	31 mm	0.589 mm	1.233 mm	0.083 mm
4. *Panulirus inflatus*	8.7 mm	0.247 mm	0.530 mm	0.035 mm
5. *P. inflatus* (mid-stage)	15.9 mm	0.433 mm	0.655 mm	0.044 mm
6. *P. inflatus* (IX)	22 mm	0.389 mm	0.664 mm	0.051 mm
7. *P. inflatus* (X)	22.7 mm	0.619 mm	0.796 mm	0.053 mm
8. *P. interruptus* (III)	3.85 mm	0.265 mm	0.442 mm	0.055 mm
9. *P. interruptus* (XI)	27 mm	0.487 mm	1.239 mm	0.088 mm
10. *P. penicillatus*	29.5 mm	0.575 mm	1.150 mm	0.071 mm
11. *P. gracilis*	31 mm	0.487 mm	0.885 mm	0.059 mm
12. *P. longipes*	34.4 mm	0.336 mm	0.752 mm	0.069 mm
13. *Puerulus angulatus*	19.9mm	0.222 mm	0.333 mm	0.028 mm

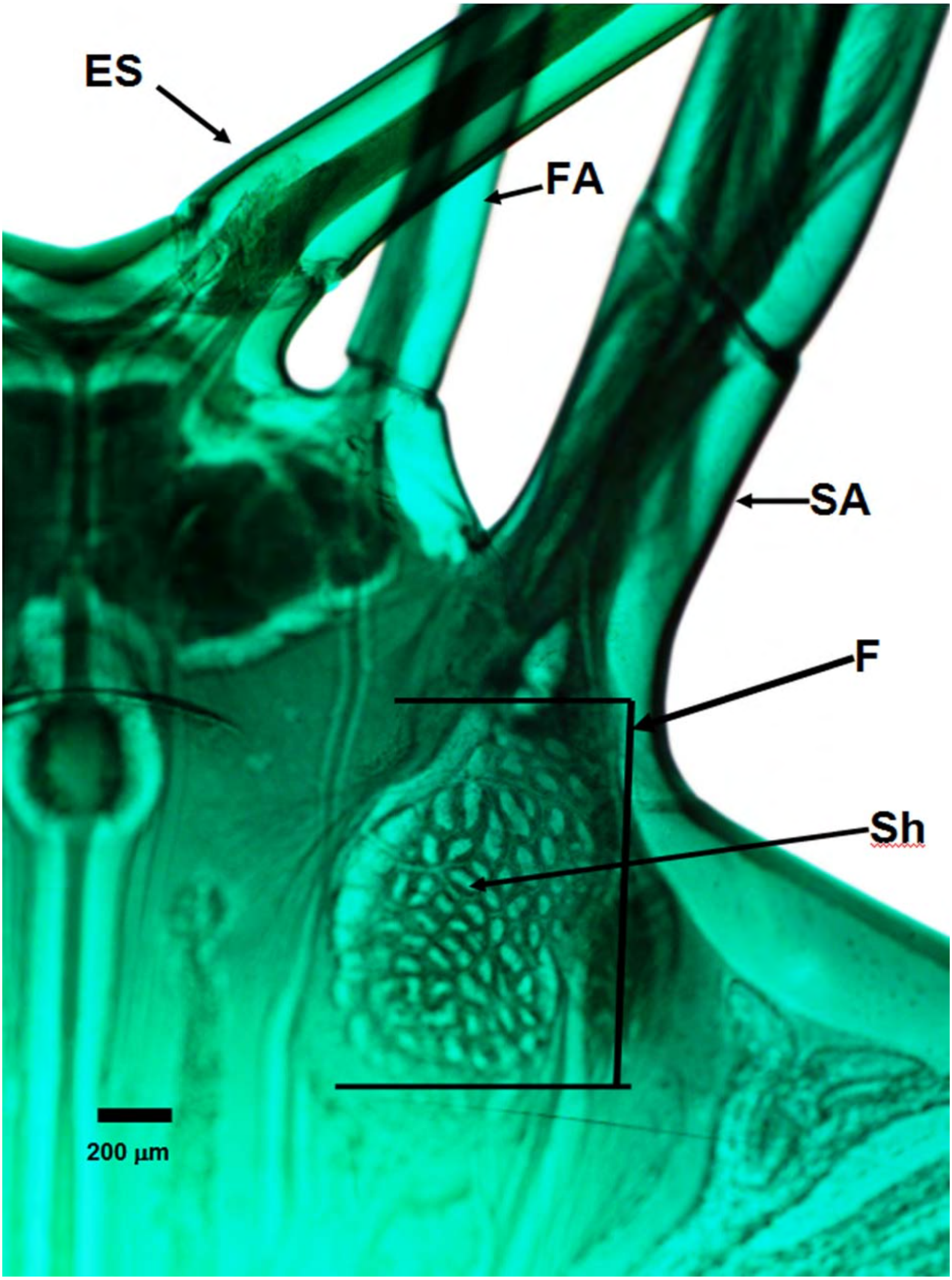

Fig. 3 Dorsal view of the anterior portion of the cephalic shield of the phyllosoma larva of Stridentes *Panulirus penicillatus* showing of showing the position of the file structure. The following labels are used: FA= Antennule; SA= Antenna; ES=Eye Stalk; F=file; Sh = Shingle.

Table III Phyllosoma of slipper lobsters: Specimen size; file length; width and shingle spacing.

Species	length	File Width	File Length	Shingle Spacing
1. *Arctides regalis*	31 mm	0.487 mm	1.000 mm	0.056 mm
2. *Scyllarus timidus*	25.4 mm	1.062 mm	1.593 mm	0.076 mm
3. *Scyllarides astori*	15.3 mm	0.531 mm	0.752 mm	0.062 mm
4. *S. squammosus*	33 mm	0.972 mm	1.416 mm	0.059 mm
5. *Evibacus princeps*	25.7 mm	1.000 mm	1.416 mm	0.067 mm

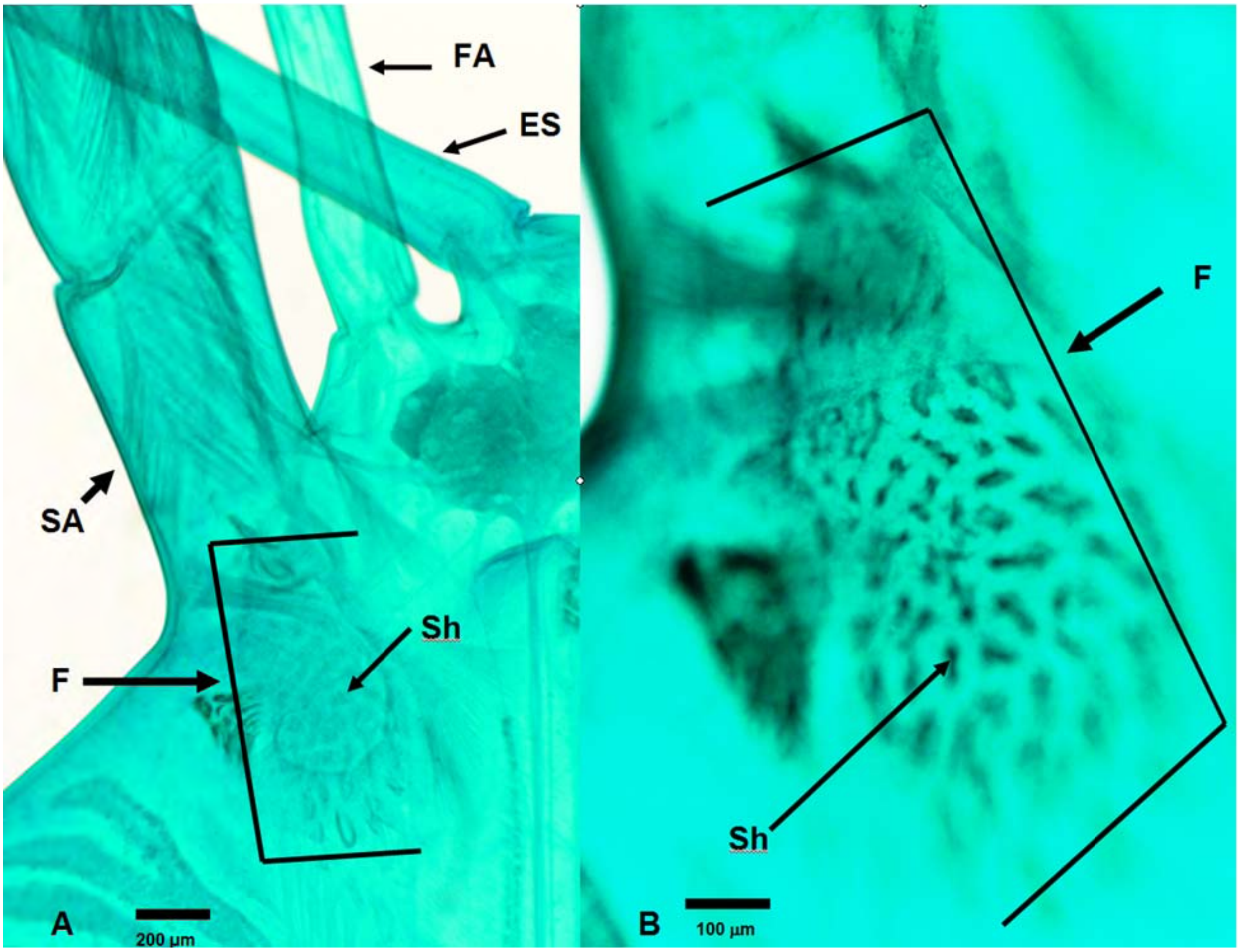

Fig. 4 Dorsal views of the file primordium on the cephalic shield of the phyllosoma larva of the slipper lobster, *Scyllarus timidus* showing the position of the file structure and shingle relative to the eye stalk, antennules and antenna. The following labels are used: FA= Antennule; SA= Antenna; ES=Eye Stalk; F=file; Sh = Shingle.

4.2 Acoustic organ evolution

Senter (2008) working from the fossil record opined that the ability to produce sounds evolved several times in the Euarthropoda. This same source gives the origin of the slip-stick mechanism as occurring in the late Jurassic in the Palinuroidea. Using molecular data Palero et al. (2009) however, reached the conclusion that the ability to produce sounds evolved only once in the Palinuroidea and that the absence in the Silentes and slipper lobsters is the result of the trait being lost in later evolutionary events. The differences in the morphology of the carapace between *Silentes* and *Stridentes* and the changes in the morphology of the antennae of the Slipper

Lobsters would indicate the mechanism(s) by which the ability to produce sounds was lost. In the case of the slipper lobsters, the antennae have become very broad and flattened with the loss of the fleshy structure termed the plectrum by Moulton (1957), Patek (2001 and 2002) and Patek and Baio (2010). In the case of the Silentes, the reduction in the area of the carapace where the file – like structure is found would have necessitated the reduction and loss of the ability to produce sounds with this mechanism. In this study, a presumptive file – like structure was observed in the file structure was observed in all phyllosoma larvae of Palinurid Stridentes. The single Silentes specimen of *Palinurellus wieneckii* also displayed this morphological trait in the phyllosome, but not in the adult. The phyllosoma larva of species in four of six genera of the some members of the Scyllaridae also exhibited a presumptive file – like structure. They did not in any case show the presence of the plectrum found in adult spiny lobsters.

Fig. 5 (4a and 4b) The presumptive file structures of early Stridentes *Panulirus* phyllosoma larva. The scale bars are 25 μm. (4c) A dorsal view of the cephalic shield of a Stridentes phyllosoma larva. FA= Antennule; SA= Antenna; ES=Eye Stalk; F=file; Sh = Shingle. The scale bar is 125 μm.

The presence of sound producing organs in the puerulus larva of Stridentes is reported by earlier workers, but efforts to measure sounds produced by the puerulus larva and post puerulus stage**s** indicated that the organs were not functional in the puerulus larval stage. There is no evidence that they do become functional until the adult form is achieved (Meyer–Rochow, 1974). The file – like structure is much smaller in the phyllosoma but the shingles are on the order of 10s of microns as compared to being on the order of 1 micron in the puerulus as shown in Meyer–Rochow (1974) Figures 1a, 1b, 2a and 2b. Patek (2001, 2002) shows the Shingles as being on the order of 1 micron in the adult.

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