

# Squeaking with a sliding joint: mechanics and motor control of sound production in palinurid lobsters

Sheila N. Patek

*Duke University, Biology Department, Durham, NC 27708, USA*

Address for correspondence: University of California, Department of Integrative Biology, 3060 VLSB 3140, Berkeley, CA 94720-3140, USA  
(e-mail: patek@socrates.berkeley.edu)

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## Summary

The origin of arthropod sound-producing morphology typically involves modification of two translating body surfaces, such as the legs and thorax. In an unusual structural rearrangement, I show that one lineage of palinurid lobsters lost an antennal joint articulation, which transformed this joint from moving with one degree of freedom into a sliding joint with multiple degrees of freedom. With this sliding joint, ‘stick-and-slip’ sounds are produced by rubbing the base of each antenna against the antennular plate. To understand the musculo-skeletal changes that occurred during the origin and evolutionary variation of this sound-producing mechanism, I examined joint morphology and antennal muscle anatomy across sound-producing and non-sound-producing palinurids. Plectrum movement and antennal muscle activity were measured in a sound-producing species, *Panulirus argus*. The promotor muscle pulls the plectrum over the file

during sound-producing and non-sound-producing movements; a higher intensity of muscle activity is associated with sound production. The promotor muscle is larger and attaches more medially in sound-producing palinurids than in non-sound producers. In *Panulirus argus*, each shingle on the file has an additional ridge; in *Palinurus elephas*, the shingle surfaces are smooth. These differences in shingle surface features suggest variation in the stick-and-slip properties of the system. Translational motion permitted by the sliding joint is necessary for sound production; hence, the construction of a sliding joint is a key modification in the origin of this sound-producing mechanism.

Key words: stridulation, Palinuridae, spiny lobster, *Panulirus argus*, *Palinurus elephas*, joint, biomechanics, sound production, bioacoustics, stringed instrument.

## Introduction

Arthropods produce sound using an extraordinary array of body parts. The majority of these acoustic mechanisms are stridulatory, in which two hard surfaces rub against each other (Dumortier, 1963; Ewing, 1989). These systems range from the tuned stridulating of cricket elytra to appendages rubbing across ridges on the cephalothorax of grapsid and portunid crabs (Dumortier, 1963). Most arthropods use modified exoskeletal surfaces to generate pulsed sounds. Typically, one surface has a series of bumps that are rubbed by another hard surface to produce sound pulses in a manner similar to a stick scraped across a washboard. This rubbing motion is most often made by body parts and musculature that existed prior to the origin of the sound-producing mechanism, so major motor and mechanical changes are not usually associated with the construction of stridulatory mechanisms. For example, stridulatory mechanisms are often found between the neighboring rubbing surfaces of the (cephalo)thorax and abdomen of insects and crustaceans (e.g. myrmecid ants, penaeid shrimp; Dumortier, 1963). Even more common are mechanisms in which appendages rub against the body, e.g. in members of such diverse groups as the Coleoptera, Orthoptera

and Heteroptera (Dumortier, 1963). These mechanisms only required modification of the rubbing surfaces and not the development of new muscle anatomy and joint mechanics to generate these translational motions.

Spiny lobsters (Palinuridae) also produce sound (Fig. 1). At first glance, the sound-producing mechanism found in some palinurids appears similar to typical arthropod washboard mechanisms, such as those used by crickets, in which a hard pick (the plectrum) rubs over hard macroscopic ridges (the file). However, a closer look at the spiny lobster’s morphology reveals that the plectrum is made of soft tissue and the file lacks macroscopic ridges (Phillips et al., 1980). The pulsed sound, called the ‘rasp’, is made by rubbing two macroscopically smooth surfaces together, which produces sound through frictional interactions between the surfaces (Patek, 2001b).

These frictional interactions are analogous to the frictional stick-and-slip mechanism in stringed instruments (Patek, 2001b), whereby a bow rubs over a string and elicits vibrations in the string (Benade, 1990). In a model of stick-and-slip sound production in bowed stringed instruments (e.g. violins), a bow sticks and slips over the surface of the string as a result of static

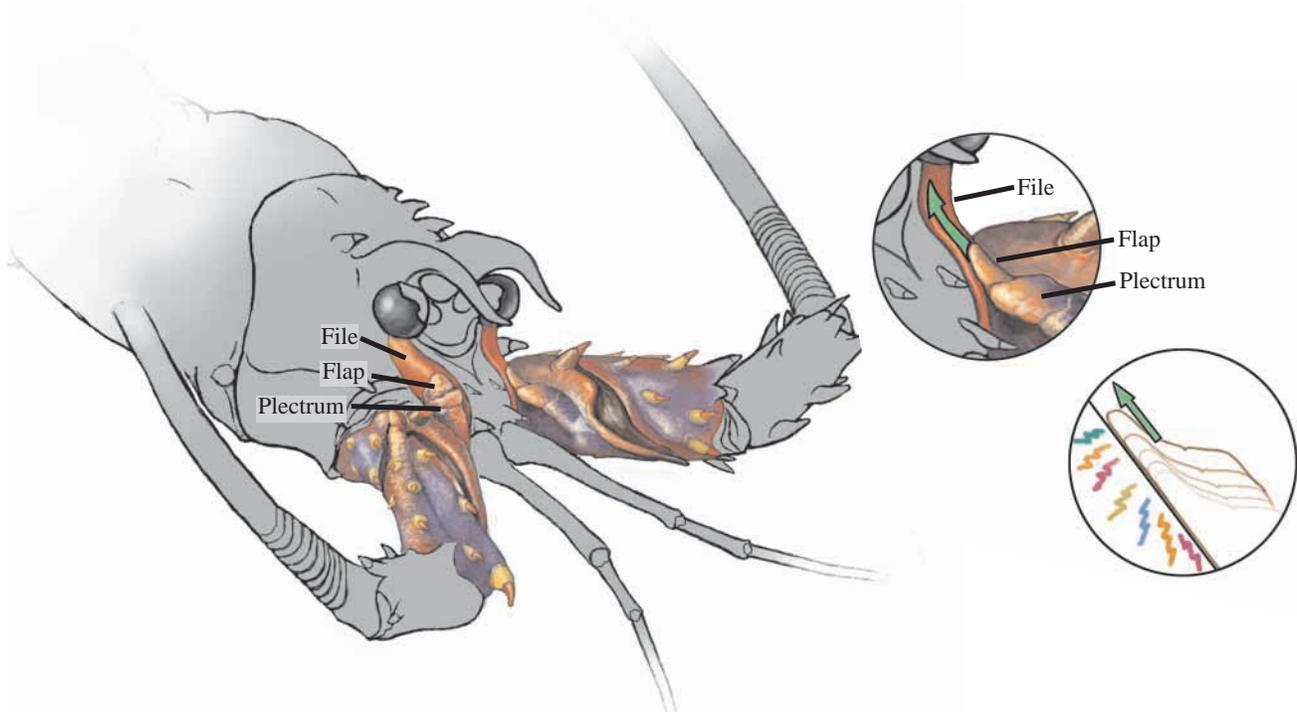


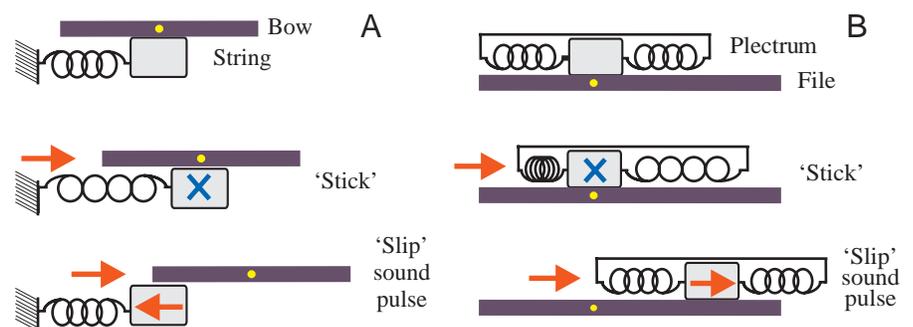
Fig. 1. The sound-producing mechanism found in the Caribbean spiny lobster *Panulirus argus*. The plectrum is a medial extension of the base of each antenna that rubs over a file, located on each side of the antennular plate. The flap extends posteriorly from the edge of the plectrum and is not necessary for sound production (see Discussion). The plectrum ridges, part of the stridulatory membrane, are confined to the ventral surface of the plectrum. Image © Sally J. Bensussen/courtesy Natural History Magazine.

and sliding friction between the surfaces (Benade, 1990) (Fig. 2A). With slight modification, this violin model can be applied to the spiny lobster's apparatus in which the soft tissue plectrum is a mobile mass/spring system that moves over the stationary surface of the file (Fig. 2B) (Patek, 2001b). In this case, the plectrum consists of a mass connected between two springs, and the mass/spring system is pulled over the file. As it is pulled, static friction between the plectrum and file surfaces causes the two surfaces to stick relative to each other. The two plectrum springs eventually extend/compress to a point at which the static friction between the plectrum and file surfaces is exceeded and the two surfaces slide relative to one

another. The soft, elastic tissue of the plectrum resists compression and tension and probably stores energy during the stick phase and releases energy during the slip phase. This type of mechanism has not been reported in any other biological system and may be unique to the sound-producing palinurids (Patek, 2001b).

The stick-and-slip mechanism is found at an intriguing location compared with most arthropod acoustic mechanisms that use adjacent rubbing surfaces, such as those mentioned above. The sound-producing apparatus is located at the proximal antennal joints which, in other taxa, are limited to one degree of freedom and do not permit translational motion

Fig. 2. A comparison of stick-and-slip sound production in stringed instruments and spiny lobsters. (A) In stringed instruments, a bow rubs over a string to generate sound. The string is modeled as a mass attached to a fixed point with a spring (representing the elasticity of the string). As the bow rubs over the string, the bow sticks to the string because of static frictional forces. When the spring extension causes sliding friction to exceed static friction, the bow slips over the surface of the mass, and the spring returns to the resting position. (B) The proposed mechanism of sound production in spiny lobsters in which a plectrum rubs over a file to generate pulsed sounds. The plectrum is modeled as moveable unit consisting of a mass attached to two springs; the file is fixed in place. A series of sound pulses is produced when the static friction between the plectrum and file surfaces is periodically exceeded as the plectrum is pulled over the file. When the plectrum slips over the file, a sound pulse is produced. Adapted from Patek (2001a,b).



The plectrum is modeled as moveable unit consisting of a mass attached to two springs; the file is fixed in place. A series of sound pulses is produced when the static friction between the plectrum and file surfaces is periodically exceeded as the plectrum is pulled over the file. When the plectrum slips over the file, a sound pulse is produced. Adapted from Patek (2001a,b).

between two adjacent surfaces. Arthropod joints are usually hinges with two articulations, one degree of freedom and a simple flexor–extensor muscle arrangement (Alexander, 1983). However, the sound-producing palinurids generate sound by rubbing the plectrums over the files through a translational movement of the proximal antennal joints (Fig. 1).

In this study, I address three questions: (i) what structural modifications permit the translational movement of the proximal antennal joint; (ii) how do muscles control sound production given the unique architecture of the antennal joint; and (iii) how do the acoustic surfaces and antennal muscle anatomy vary across palinurid lobsters? To address these questions, I examined the antennal joint mechanics and associated muscle anatomy in both non-sound-producing and sound-producing lobsters. I measured antennal muscle activity and kinematics in the Caribbean spiny lobster *Panulirus argus* during rasp sound production and other antennal movements. The muscle activity patterns were used to assess the functional implications of evolutionary variation in palinurid antennal muscles. The acoustic surfaces of sound-producing lobsters were compared using scanning electron microscopy.

## Materials and methods

### Experimental animals

*Panulirus argus* Crustacea, Decapoda, Palinuridae (Caribbean spiny lobsters) were collected at the Keys Marine Laboratory (Long Key, FL, USA) under FL DEP permit 99S-428 and housed at Duke University in artificial sea water at 19–22 °C. Carapace lengths ranged from 47 to 97 mm. *Palinurus elephas* (common spiny lobster), 138–148 mm carapace lengths, were collected by Cleggan Lobster Fisheries Ltd (Galway, Ireland) and housed at 10–11 °C in synthetic sea water at Duke University. All experiments were conducted in a 378.51 Rubbermaid farm stock tank (132.1 cm×78.7 cm×63.5 cm) with the interior walls covered with thick foam to reduce acoustic reverberations. Lobsters were hand-held during all experiments included here because rasp sound production was typically accompanied by a tail flip that easily detached the electronic equipment from their exoskeleton. Rasp sounds are produced naturally during interactions with predators and were thus elicited during handling. Non-sound-producing lobsters were examined, including a specimen of *Jasus edwardsii* (red rock lobster) purchased in Shirahama, Japan. Two specimens of *Jasus verreauxi* (green rock lobster) were provided by the Australian Museum. Forty-one preserved palinurid species were studied at the National Museum of Natural History, Smithsonian Institution, Washington, DC, USA.

### Muscle and joint anatomy

Muscles attaching to the base of the antennae control movement of the proximal antennal joint. The muscles attaching to the first segment of the antenna had not previously been described in a sound-producing lobster, although they had been described in a non-sound-producing lobster (*Jasus*

*lalandii*) in the palinurid family (Paterson, 1968). I dissected 15 *Panulirus argus* and examined joint morphology and the anatomy of muscles attaching to the posterior edges of the first segment of the antennae. The muscles were identified using the nomenclature from Paterson (1968). The artist Natalia Rybczynski observed three of these dissections and illustrated the anatomy, as seen in Fig. 4. *Palinurus elephas* and *Jasus verreauxi* specimens were also dissected. Joint morphology was inspected in forty-one preserved palinurid species.

### Acoustics and kinematics

Rasps were recorded to test for correlations between sound, movement and muscle activity. A hydrophone (HTI-94-SSQ, High Tech Inc.) was placed 0.3 m deep and at least 0.15 m from the lobster. Output from the hydrophone was recorded digitally using an analog/digital (A/D) acquisition board (AT-MIO-16E-10, National Instruments).

To measure the timing of plectrum movements over the file, I attached a Hall-effect sensor (0.06 g, A3515LUA, Allegro MicroSystems) just posterior to the file and a samarium/cobalt magnet (0.03 g) to the plectrum. The sensor tracked changes in magnetic flux density as the plectrum moved over the file (Deich et al., 1985). The magnet was glued to the plectrum using a combination of dental repair resin (Hygenic Corp.) and cyanoacrylate glue. I wired the sensor and coated it with aquarium silicone sealant to exclude water. The sensor was attached with a sticky rosin/wax mixture, and the wires were led from the cephalothorax of the lobster to the A/D board. The voltage output was measured using a customized LabVIEW virtual instrument (National Instruments) sampling at 3750 or 5000 samples s<sup>-1</sup>. Several trials were run at 10 000–25 000 samples s<sup>-1</sup> to verify that lower sampling rates collected accurate temporal data. Acoustic and kinematic data were recorded simultaneously to correlate rasp pulses and plectrum movements. I conducted kinematic experiments with 97 rasps produced by six *Panulirus argus*. The onset and offset times of the acoustic pulses and the plectrum movement were measured.

### Electromyography

Electromyography was used to measure muscle activity during sound production and other antennal movements in *Panulirus argus* (techniques described in Basmajian and Luca, 1985; Loeb and Gans, 1986). Recordings were made from the medial (Pm) and lateral (Pl) lobes of the promotor, the lateral levator (LL) and the depressors (Da, Dc, Dd) (see Results and Fig. 4 for a description of muscle anatomy). Small holes were drilled through the exoskeleton using a Xacto hand drill, and five or six electrodes were inserted into the muscles attaching to the first segment of an antenna. Bipolar hook electrodes with 1 mm bared ends were inserted into each muscle using a 23 gauge needle and 74 µm diameter Teflon-coated silver wire (California Fine Wire). The wires were glued to the exoskeleton with a hygenic resin/cyanoacrylate mixture and coated with a sticky violin rosin/beeswax mixture. The wires were gathered as a bundle on the dorsal surface of the

cephalothorax and run from the sea water to an amplifier (A-M Systems differential AC amplifier) and then to an A/D board (National Instruments AT-MIO-16E-10). The electromyographic (EMG) signals were notch- and band-pass filtered (10 Hz and 1000 Hz) at the preamplifier and were sampled at 3750 Hz by the A/D board. The EMG signals were recorded simultaneously with acoustic and kinematic data in a LabVIEW virtual instrument. Experiments were conducted in six lobsters with a range of 30–50 rasps per lobster. Periodic difficulties with electrode recordings resulted in recordings not being made from some muscles in all lobsters. Following each experiment, electrode placement was verified through dissection.

A digital high-pass Blackman –60 dB filter (100 Hz) removed movement artifacts from the EMG signals. Since EMG signals typically range from 20 to 2000 Hz, removing lower-frequency movement artifacts does not appreciably distort the EMG signal. I processed the signals using a wide range of high-pass filter frequencies and filter types and verified that the choice of filters did not affect the timing of EMG traces at a scale relevant to the sound production events.

The timing, duration and intensity of muscle activity were measured. For measurements of muscle onset relative to rasp onset and percentage duration of muscle activity within the rasp, the EMG traces were rectified, and an activity threshold was then applied in which a muscle was considered ‘on’ when the trace was at least two times greater than baseline measures (the baseline was calculated during times of no movement). A muscle was considered ‘off’ if the muscle showed no activity for a minimum of 5 ms. However, when measuring single units of motor activity during the rasp, the onset/offset of the muscle was considered regardless of the time between bursts. Muscle activity was compared in non-sound-producing movements and sound-producing movements to assess the mechanism by which the sound is turned ‘on’ and ‘off’. Muscle intensity ( $\mu\text{V}$ ) was calculated by rectifying the high-pass-filtered signal, measuring the area ( $\mu\text{V s}$ ) under the trace during the event and dividing it by the duration (s) of the event. The non-parametric Kruskal–Wallis test (Sokal and Rohlf, 1981) was used to determine whether the mean intensity of muscle activity differed more than expected by chance across no movement (F), non-sound-producing and posteriorly directed movements (P) and sound-producing movements (R) within each lobster. Significance threshold was set at  $P < 0.05$ .

#### Scanning electron microscopy

The files and plectrums of *Panulirus argus* and *Palinurus elephas* were viewed using scanning electron microscopy. Using freshly dead lobsters, I removed the file and plectrum by cutting the carapace with a dental drill. The tissue was placed immediately in 2% glutaraldehyde in phosphate-buffered saline and fixed for 1.5 h (see Dykstra, 1992). The tissue was rinsed in distilled water and dehydrated in an ethanol series. The specimens were stored in 100% ethanol until critical-point drying and were then sputter-coated (60:40 gold:paladium mixture, Anatech Hummer V) and observed at

up to 6000 $\times$  magnification with a scanning electron microscope (Philips 501 SEM).

## Results

### Antennal joint and muscle anatomy

The proximal antennal joint in all non-sound producers possessed two articulations at the lateral and medial edges of the antennae (Fig. 3A). The medial joint articulation was absent from all sound producers and instead was replaced by the plectrum, which rubbed antero-posteriorly over the file (Fig. 3B). Hence, in non-sound-producing lobsters, the proximal joint of each antenna was limited to rotation about the dorso-ventral axis, whereas in sound-producing lobsters the antennae could move dorso-ventrally as well as postero-anteriorly (Fig. 3B).

The proximal antennal muscles varied in position and size between sound producers and non-sound producers and varied in size within sound producers. I illustrated and compared the muscles of the sound-producing *Panulirus argus* with those described previously for the non-sound-producing palinurid lobster *Jasus lalandii* (Paterson, 1968). I also contrasted the muscles between two sound producers, *Panulirus argus* and *Palinurus elephas*.

In *Panulirus argus*, the promotor muscle attached at the medial edge of the antenna, just lateral to the plectrum, and extended to the dorsal surface of the carapace (Fig. 4A). In

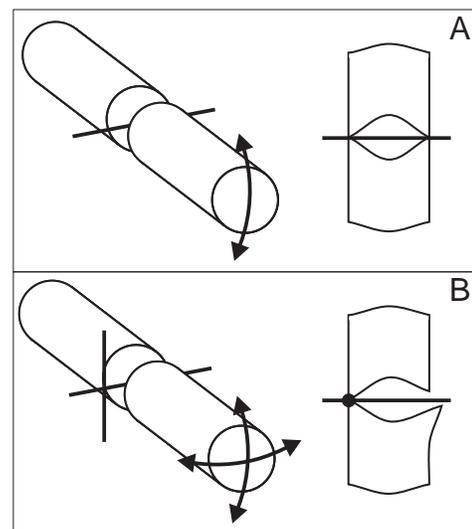


Fig. 3. Models of the antennal joints found in sound-producing and non-sound-producing spiny lobsters. (A) In non-sound-producing palinurids, the joint between the antenna and cephalothorax is limited to one degree of freedom (left, adapted from Wainwright et al., 1976) and has an axis of rotation aligned between the two joint articulations (right). (B) In sound-producing palinurids, the same joint has multiple degrees of freedom (left), which is permitted by the loss of the medial joint articulation. With only one joint articulation, the medial process of the antenna (the plectrum) can generate translational motion over the file.

sagittal view (Fig. 4B), the promotor was pinnate, with two lobes, one attaching to the lateral portion of the carapace and a second attaching medially below the rostral horns, just lateral to the midline of the carapace. The promotor muscle of *Palinurus elephas* also attached at the medial edge of the antenna, lateral to the plectrum; however, it had only one pinnate lobe, attaching on the lateral region of the dorsal carapace. In *Jasus lalandii* and *Jasus verreauxi*, the promotor muscle attached at the midpoint between the two joint articulations and extended dorsally to the carapace (Paterson, 1968).

In all four species, the lateral levator attached to the dorso-lateral edge of the first antennal segment and extended ventrally to attach to the dorsal and posterior surfaces of the infolding of the epistome (the ventral surface of the antennular plate, extending between the antennae) (Fig. 4A,B). The remotor muscle described by Paterson (1968) in *Jasus lalandii* was not apparent in *Panulirus argus* and, in any case, was unlikely to be involved in antennal movement since it attaches to two immovable structures [Paterson (1968) suggested that it might function in bladder control or structure].

The depressor muscles were more difficult to discern as suggested by both Paterson's (1968) and Berkeley's (1928) descriptions in crustaceans. In *P. argus*, three of the four depressor muscles described by Paterson in *Jasus lalandii* were readily identified (Fig. 4B,C). Depressor A attached to the medio-ventral edge of first antennal segment and extended to several areas of epistomal infolding. It was pinnate and stretched both posteriorly and ventrally to the epistome and to the lateral facet of a thin, midline extension of the epistome. Depressor B, described by Paterson (1968) as extending from the 'postero-medial corner of the first segment' to the 'dorso-medial joint of the first segment', was not apparent in *P. argus*. The absence of depressor B may be related to the fact that *P. argus* lacks the dorso-medial joint articulations of the antennae that are present in *J. lalandii*. Depressor C attached to the middle of the postero-ventral edge of each antenna and spread to the floor of the epistome. Depressor D, oriented slightly differently from the description by Paterson (1968), attached the medio-ventral edge of the antenna to the medial floor of the epistome. The depressor muscles of *Palinurus elephas* were generally similar to those of *Panulirus argus*. However, the epistome's median process was larger in *P. elephas* and reached almost completely across the epistome, forming a clear separation between the left and right sections of the epistome.

#### Kinematics and acoustics

Sound pulses and plectrum movements occurred simultaneously in all experiments ( $N=97$  rasps, six *Panulirus argus*). Sound was produced only during posteriorly directed movements when the plectrum rubbed against the anteriorly

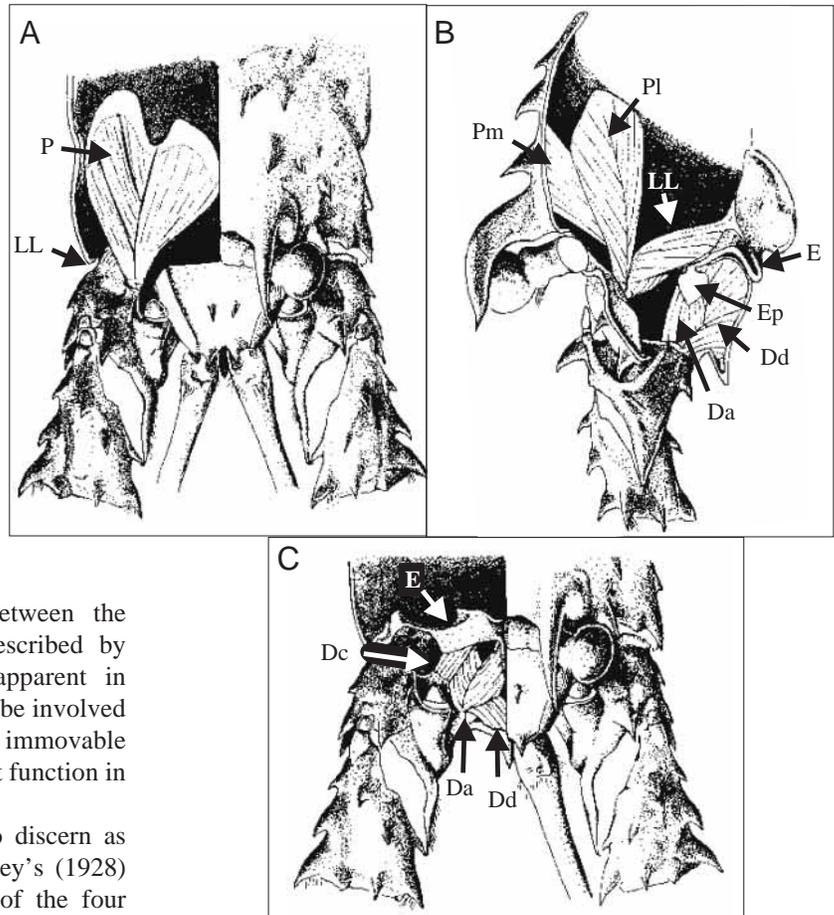


Fig. 4. Muscles attaching to the base of each antenna in *Panulirus argus*. Anterior is towards the bottom of the page. (A) Dorsal view with half the dorsal carapace removed to show the promotor (P) and lateral levator (LL). (B) Sagittal view of the promotor medial lobe (Pm), promotor lateral lobe (Pl), lateral levator, depressor A (Da) and depressor D (Dd). The epistome (E) forms an internal skeleton upon which depressor A attaches. (C) Dorsal view with dorsal carapace, promotor and lateral levator removed to show depressor A (Da), depressor C (Dc) and depressor D (Dd). Drawing based on specimen with 64 mm carapace length.

projecting shingles on the file. The plectrum movement consisted of a series of steps in which there was a still period and a sliding period; sound was emitted only during the sliding movement (Fig. 5). Average signal features are listed in Table 1.

#### Electromyography

Table 1 summarizes results for the activity of different antennal muscles during sound production in *Panulirus argus*. Only the promotor muscle (Pl and Pm, Fig. 4) was active during 100% of rasps; other muscles were active only during a proportion of the rasps measured (LL, Da, Dc and Dd; Fig. 4). The depressor muscles (Da, Dc and Dd; Fig. 4) were active most often during anterior movements of the plectrum over the file. The lateral levator (LL, Fig. 4) was active during

Table 1. *Descriptive statistics for signal features and muscle activation during sound production*

Variable	Mean	Minimum	Maximum	Number of rasps	Number of individuals
Rasp duration (ms)	103.7±5.7	19.20	331.6	140	6
Number of pulses per rasp	6.9±0.4	2	24	139	6
Pulse duration (ms)	1.7±0.03	0.6	13.0	139	6
Pulse rate (Hz)	76.7±3.2	24.1	218.0	139	6
Lateral promotor (active during 100 % of rasps)				118	6
Onset (ms)	-69.3±4.5	-272.0	3.6	118	6
Offset (ms)	27.0±5.5	-87.6	356.8	119	6
Percentage of rasp duration	85.2±2.0	5.5	100.0	120	6
Medial promotor (active during 100 % of rasps)				82	4
Onset (ms)	-134.4±9.5	-518.9	-16.8	78	4
Offset (ms)	92.7±12.2	-36.3	560.3	78	4
Percentage of rasp duration	95.0±1.7	16.0	100.0	82	4
Lateral levator (active during 98.4 % of rasps)				61	3
Onset (ms)	-133.6±22.3	-865.6	23.7	56	3
Offset (ms)	83.6±25.7	-59.2	1006.0	56	3
Percentage of rasp duration	85.4±3.3	0	100.0	61	3
Depressor A (active during 59.2 % of rasps)				98	5
Onset (ms)	18.4±5.0	-79.0	142.8	58	5
Offset (ms)	-10.2±7.4	-169.6	195.5	58	5
Percentage of rasp duration	17.4±2.9	0	100.0	98	5
Depressor C (active during 23.2 % of rasps)				118	6
Onset (ms)	-13.5±5.6	-271.5	95.6	91	6
Offset (ms)	-26.2±6.0	-243.0	254.4	91	6
Percentage of rasp duration	23.3±3.0	0	100.0	118	6
Depressor D (active during 46.3 % of rasps)				108	6
Onset (ms)	9.8±3.0	-40.4	88.0	50	6
Offset (ms)	-41.9±8.0	-261.1	32.8	50	6
Percentage of rasp duration	9.0±1.9	0	100.0	108	6

Negative values of onset/offset indicate that the event occurred before onset/offset of sound production.

Mean values are given ± S.E.M.

many different movements and often during sound production (98.4 % of rasps).

In a typical sound-producing event (Fig. 6), the depressor muscles were activated prior to sound production and pulled the plectrum to an anterior starting position on the file. The promotor muscle lobes were activated just prior to the onset of sound production. The lateral levator (LL, Fig. 4) often was active during sound production, but with substantially higher variability than the promotor muscle as represented by the standard errors of the mean (Table 1).

The promotor invariably generated a single, tonic contraction during the rasp with no evidence of pulsed activity correlating with the ratcheted movements of the plectrum. Single electrical units of activity occurred in some recordings

of the depressor muscles (Fig. 7), with maximum occurrence in depressor C muscle with 25 % of sound pulses occurring simultaneously with electrical units of activity (786 pulses, five lobsters). These are probably products of stretch receptor activation when promotor and levator muscles pull upon the opposing depressor muscles during sound production (Ache and Macmillan, 1980). The occurrence of these electrical units of activity primarily during movements, rather than during the stationary times between pulses, is consistent with this interpretation. If these units of activity functioned to stop plectrum movement during the 'stick' part of the rasp, the electrical activity should have been visible during the stationary periods between pulses of sound. However, the activity occurred during sliding, which suggests an electrical

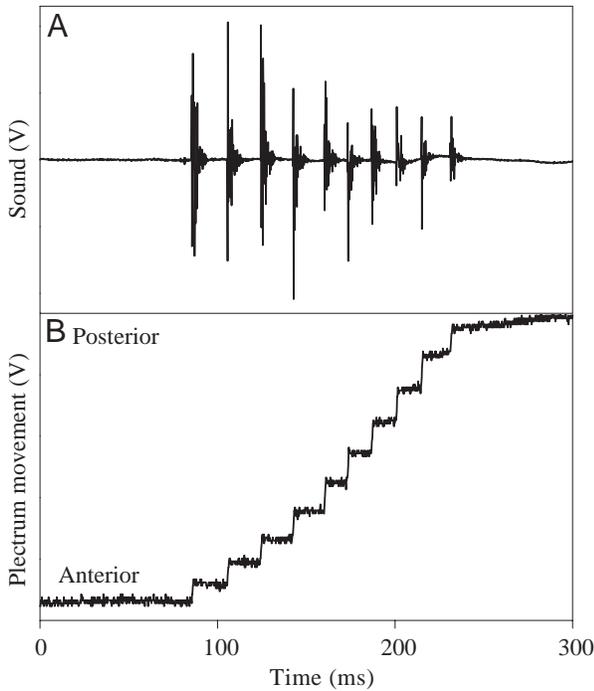


Fig. 5. Sound and movement correlation. Each pulse of sound (A) is correlated with movement of the plectrum (B), illustrated by a stepped-like motion of the plectrum over the file. Sound is produced only during posteriorly directed movements of the plectrum (towards the top of the page).

response due to pulling on the stretch receptors of muscles opposing movement. While it is possible that these spikes are due to movement artifacts, their clear depolarization and hyperpolarization suggest a biological signal, not a mechanical depolarization due to electrode movement.

Electromyographic results suggested that the promotor muscle activates the sound-producing mechanism; however, the promotor was also active during posterior movements of the plectrum that do not produce sound. To determine whether the promotor muscle activated differently during sound-producing movements from during non-sound-producing movements, I simultaneously recorded activity in both the medial and lateral lobes of the muscle (Pm and Pl; Fig. 4). Within each individual, the mean intensities of the medial and lateral lobes were significantly different across no movement (F), non-sound-producing posteriorly directed movements (P) and sound-producing movements (R) of the plectrum, with higher intensities during sound-producing movements (lateral promotor lobe, 228 events, five lobsters;  $\chi^2$  for each individual=24.52, 37.94, 29.65, 31.81, 37.00; d.f.=2; all  $\chi^2$  values indicated a significance of  $P \leq 0.001$ ; medial promotor lobe, 191 events; four lobsters;  $\chi^2=38.31, 29.93, 36.78, 31.71$ ; d.f.=2;  $P \leq 0.001$ ) (Fig. 8A,B). The mean intensity differences between the two lobes (medial lobe intensity minus lateral lobe intensity) were also significantly different across the three categories of plectrum movement, with highest values during sound-producing movements (191 events; four lobsters;

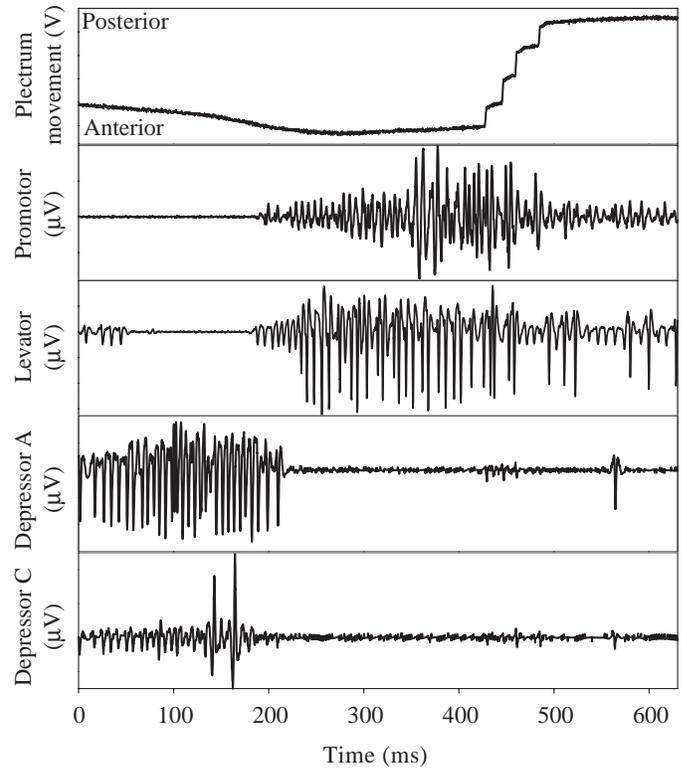


Fig. 6. Overall pattern of muscle activity during a rasp. Depressor muscles are active during anterior movement of the plectrum (0–200 ms on the graph). Promotor and levator muscles are active prior to (approximately 200 ms on the graph) and during (450–500 ms on the graph) sound production. Sound production is indicated by the stepped movement of the plectrum.

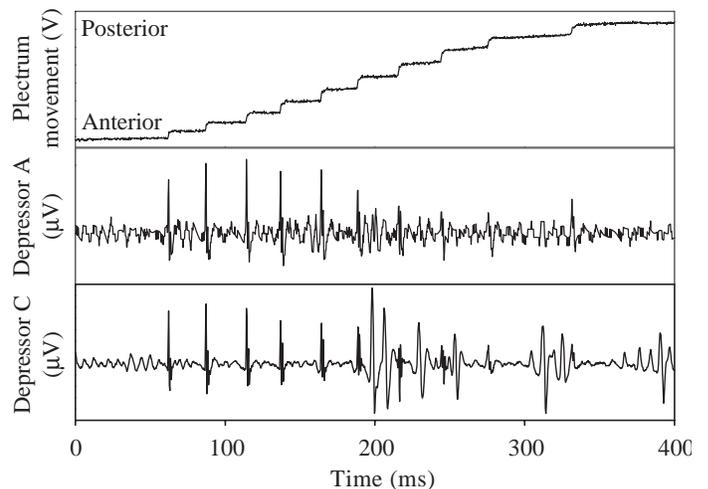


Fig. 7. Single electrical units of activity occurred in some recordings of the antenual muscles. These are probably products of stretch receptor activation when the promotor muscle pulls upon the opposing depressor muscles during sound production.

$\chi^2=36.49, 30.06, 36.59, 7.15$ ; d.f.=2;  $P < 0.05$ ) (Fig. 8C). However, no clear threshold of activity was apparent in lateral, medial or lateral minus medial promotor intensities to

distinguish between sound-producing and non-sound-producing movements (Fig. 8).

#### Scanning electron microscopy

In *Panulirus argus*, file shingles were similar to those observed in previous studies using air-dried preparations, having a mean width of 10  $\mu\text{m}$  (Fig. 9C). However, the plectrum ridges were distinctly different from previously published air-dried preparations and showed smooth surfaces

at magnifications up to 6000 $\times$  with no evidence of the accordion-like wrinkles as seen by Meyer-Rochow and Penrose (1976) and Smale (1974). The plectrum ridges showed no microscopic structures at the scale of the shingles; they have a smooth uniform surface (Fig. 9D). The shingles of *Palinurus elephas* lacked the transverse ridge found on each shingle in *Panulirus argus*, and the plectrums were similar in most respects (Fig. 9A,B).

#### Discussion

The stick-and-slip mechanism in spiny lobsters appears to have originated once in the clade. Palinurids are divided into the 'Silentes', which do not have a sound-producing apparatus, and the 'Stridentes', which produce sound (George and Main, 1967; Parker, 1883). A new species and genus, *Palibythus magnificus*, has a sound-producing apparatus, although the placement of this species in the Palinuridae is unresolved (Davie, 1990). Several phylogenetic studies of the family support a single origin of the sound-producing apparatus; however, further evidence is necessary to define genus relationships consistently among palinurids (Baisre, 1994; Patek, 2001a).

Key structural changes are associated with the origin of the stick-and-slip sound-producing mechanism in palinurid lobsters. The loss of the medial joint articulation at the base of each antenna is a major mechanical transition to sound production (Fig. 3). In non-sound producers, the proximal antennal joint is limited to dorsal and ventral movements. In contrast, sound producers can move the proximal antennal joint antero-posteriorly as well as dorso-ventrally, allowing the plectrum, a medial process extending from the base of each antenna, to produce sound with a translational motion over the file.

In sound producers, the translational plectrum movements are often silent and are used in positioning the antenna. Preliminary data show that the plectrum can be planted at a particular location on the file, and the antenna then rotates as if there were two joint articulations with one degree of freedom, although with less range of motion. This suggests a sliding external joint that can be reoriented as necessary and, through repositioning, retains the stability of a typical arthropod hinge joint with two articulations. Such an external, repositionable articulation in a sliding joint that is also used in sound production has not, to my knowledge, been described previously in biological systems.

The plectrum flap, a fleshy extension from the posterior edge of the plectrum, is found in a subset of sound-producing taxa with especially elongate files (*Panulirus*, *Justitia* and *Palinurus*) (Patek, 2001a) (Figs 1, 9). When this process was removed in specimens of *Panulirus argus*, the plectrum could still be manually manipulated over the file to produce sound (Patek, 2001a). The structure may form a pivot point for the sliding joint articulation when the plectrum is planted in place on the file and the antenna moves dorso-ventrally. The elongate file of some taxa may necessitate more stability when the

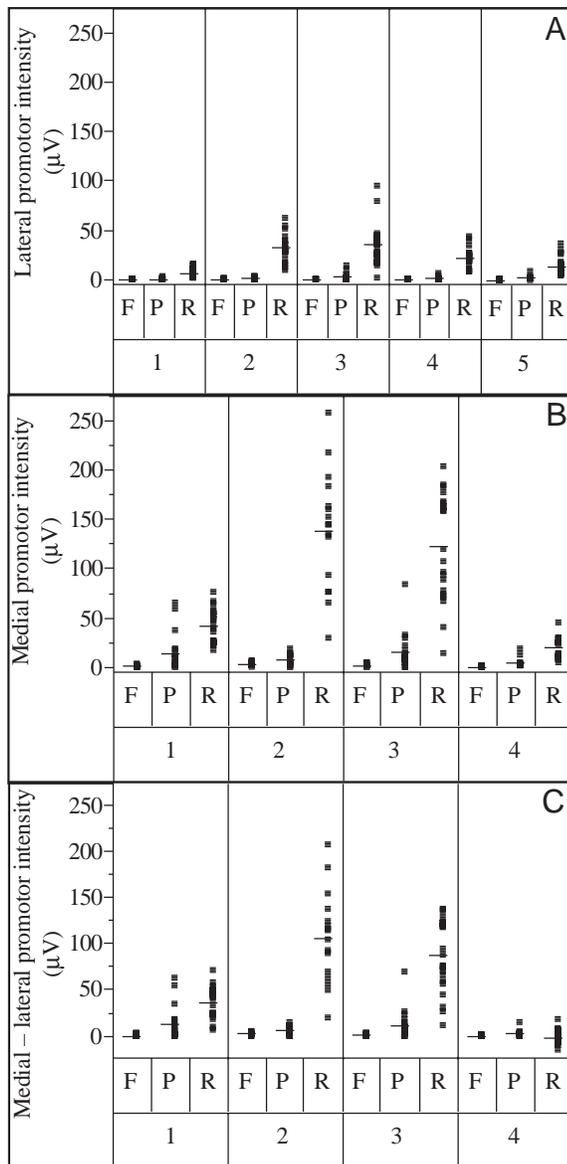
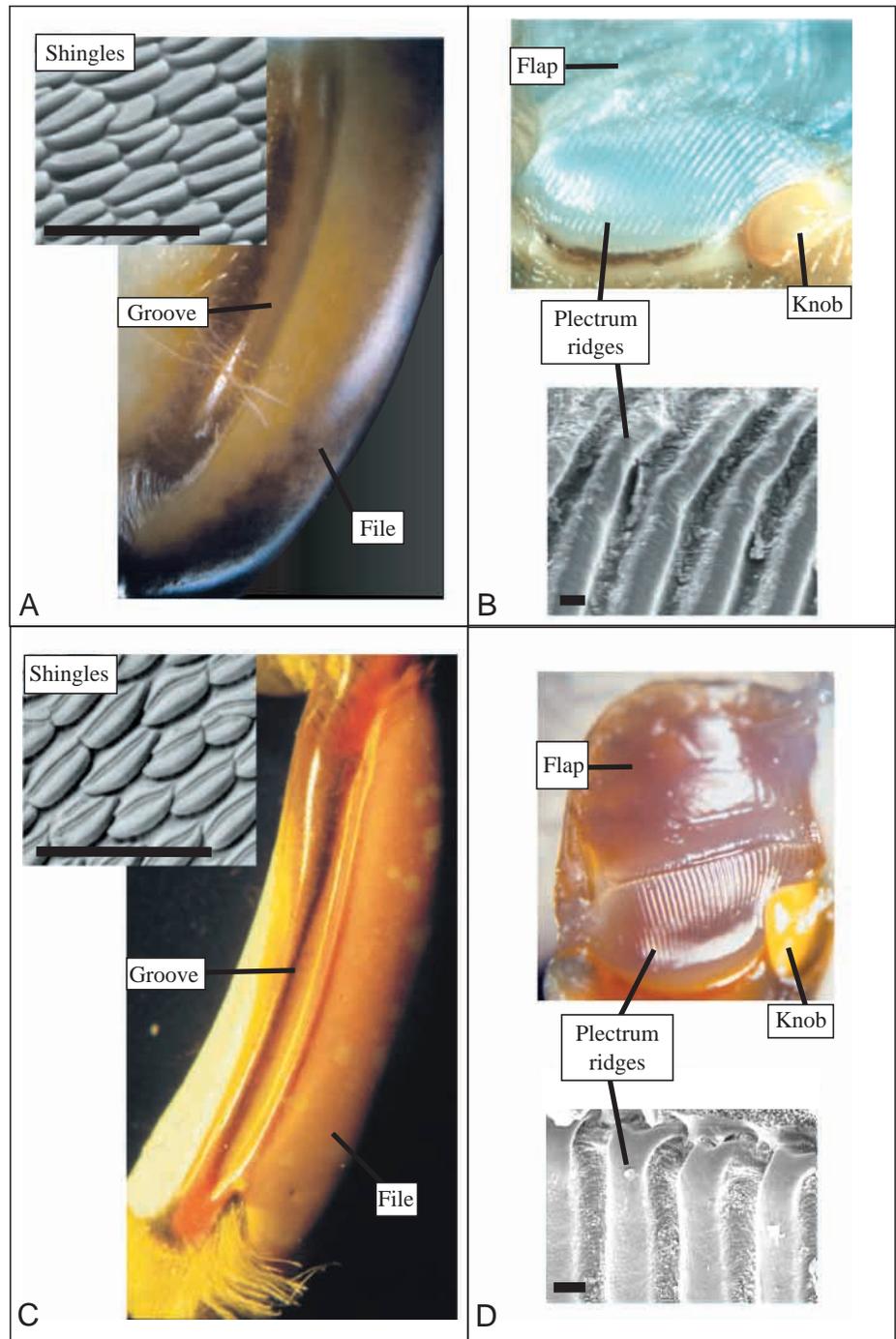


Fig. 8. Promotor muscle intensity during sound-producing and non-sound-producing movements. Mean values are indicated by horizontal bars. Lateral promotor lobe intensity (A), medial promotor lobe intensity (B) and the relative intensity of the two lobes (medial lobe intensity minus lateral lobe intensity) (C) are shown across individual lobsters (1–5) and three movement categories, no movement (F), posterior movement with no sound production (P) and sound production (R). See Materials and methods for the calculation of muscle intensity.

Fig. 9. A comparison of plectrum and file morphology in *Panulirus argus* and *Palinurus elephas*. (A) *Palinurus elephas* (carapace length 145 mm); a dorsal view of the surface the lobster's right file (18 mm long); anterior is towards the bottom of the page, lateral is to the left of the page. Covering the file are microscopic shingles with anteriorly projecting edges (inset). Scale bar, 25  $\mu$ m. On the lateral side of the file is a long groove. (B) *Palinurus elephas*; the ventral surface of the lobster's right plectrum (6 mm wide); lateral is to the right of the page. The plectrum consists of a hemisphere of soft tissue ridges, the stridulatory membrane, and the flap extends from the posterior edge of the stridulatory membrane. These ridges rub against the file; the long axis of the ridges is parallel to the long axis of the file and thus parallel to their motion over the file. A knob, adjacent to these ridges, fits into the groove on the file. The plectrum rubs posteriorly over the shingle edges (towards the top of the page). The scanning electron micrograph (inset) shows the posterior limit of the plectrum ridges on the stridulatory membrane. Scale bar, 50  $\mu$ m. (C) The same view as in A for the file (14 mm long) and shingles of *Panulirus argus* (85 mm carapace length). Scale bar, 25  $\mu$ m. (D) The same view as in B for the plectrum (4 mm wide) and plectrum ridges of *Panulirus argus*. Scale bar, 50  $\mu$ m.

plectrum can move a long distance along the file and thus permits more play in the system.

Associated with these changes in joint mechanics are dramatic changes in the position and size of the promotor muscle. The functional implications of these differences can be inferred by the motor control of sound-producing and non-sound-producing movements in *Panulirus argus*. The electromyographic and kinematic results from *Panulirus argus* show that the promotor functions to pull the plectrum over the file with and without producing sound (Fig. 8). Rasps are produced when the plectrum rubs over the file in a ratcheted movement (Fig. 5). During each sliding period within that ratcheted movement, a pulse of sound is produced. A higher intensity of promotor muscle activity generates sound-producing movements compared with non-sound-producing posterior movements and no movement of the plectrum, but there appears to be no specific threshold of muscle intensity at which sound production occurs (Fig. 8). There are several possible



explanations for this observation. First, there might be localized neural control over parts of the promotor muscle or different muscle fiber types responding to stimulation, such that one muscle region or fiber type is activated only during sound production (Ache and Macmillan, 1980). The recordings of the medial and lateral promotor lobes do not show localized areas of activation, but the type of electrode design used here may not have been localized or sensitive enough to distinguish between activity of these two lobes. More localized recordings of muscle activity or recordings from motor nerves may be necessary to discern any actual threshold or localization of control.

Another explanation is that a second muscle, in addition to the promotor muscle, is activated during sound production and not during simple posterior movements. The lateral levator muscle seems a likely candidate since it was active during 98 % of rasps. However, the levator attaches between the lateral facet of each antenna and an interior process of the epistome – providing a line of action that should rotate the antenna ventro-laterally and counter to the posterior movement of the plectrum. Also, the high variability in the onset/offset times of the levator muscle relative to the rasp suggests irregular patterning of muscle activity, unlike the regularity observed in the promotor muscle (Table 1). The lateral levator is probably active during many kinds of antennal movement and, while it is often active during sound production, it does not serve to turn the production of sound on or off during posterior plectrum movements.

The promotor muscle in non-sound producers attaches to the midline of the posterior edge of each antenna and pulls the antenna dorsally (Paterson, 1968). In contrast, the promotor muscle is located more medially in sound producers and pulls the antenna both dorsally and posteriorly. *Panulirus argus*, with a long file, has a large promotor muscle with two lobes that spread over most of the available surface of the dorsal carapace (Fig. 4). *Palinurus elephas*, with a shorter file, has a relatively small promotor muscle with only one lobe. The shift of the promotor attachment towards the plectrum in sound producers is probably necessary to control the antero-posterior translation of the plectrum over the file. This is in contrast to the simple dorso-ventral movements of non-sound producers with two joint articulations, which can be controlled by simple extensor–flexor muscle attachments. In this latter case, the promotor attachment in the center of the antennal base makes sense: a central attachment point pulls equally on both sides of the antenna.

The increase from one promotor lobe in *Palinurus elephas* to two lobes in *Panulirus argus* probably reflects the need for more motor control of the antennal base over the longer file in *Panulirus argus*. The longer file gives more translational area for the plectrum and, to manipulate the sliding joint at multiple plectrum positions, the promotor probably needs to generate both posteriorly and laterally directed lines of contractions. This issue could be resolved by measuring localized patterns of promotor activity across multiple palinurid species, particularly when the sliding joint produces non-sound-producing motions.

The hemisphere of soft-tissue plectrum ridges is similar across sound producers, but the file's surface varies considerably. The plectrum appears to be derived from arthrodial membrane, and the shingles are modifications of the exoskeletal surface features of the antennular plate. Differences in shingle structure suggest modification in frictional properties: in *Panulirus argus*, each shingle has a prominent ridge, whereas the surfaces of *Palinurus elephas* shingles are smooth (Fig. 9A,C). Meyer-Rochow and Penrose (1976) suggest that, in *Panulirus longipes*, shingles may fuse during development to form the additional ridge on each

shingle. Shingle surface features could affect the amount of sliding and static friction and may have important implications for the 'stick-and-slip' properties and motor control of the system. Greater sliding or static friction may require more muscle force to drag the plectrum over the file. More friction between the plectrum and file could result in higher-amplitude rasps by generating larger displacements of the vibrating surfaces.

The mechanical and muscular changes that occurred with the reconstruction of the proximal antennal joint are significant in explaining both the evolutionary origin of sound production and the subsequent variation of the stick-and-slip mechanism. They also provide an example of how arthropods can modify limiting joint architecture to allow a wider range of movements. These observations raise the question of whether the loss of the joint articulation occurred during the origin of the sound-producing apparatus or whether it preceded sound production for the purposes of increasing the range of antennal motion. Palinurid lobsters use their antennae for mechanical defense, and the subset with a sound-producing apparatus generates rasps when interacting with predators (Lindberg, 1955; Meyer-Rochow and Penrose, 1976; Mulligan and Fischer, 1977; Smale, 1974). The single origin of stick-and-slip sound production and the function of antennae for both mechanical and acoustic defense leaves open the issue of whether the initial mechanical changes in this system were for antennal maneuverability or solely for sound production.

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