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Stridulation by cosmetid harvestmen (Arachnida: Opiliones)

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Abstract. Stridulatory organs have not been previously investigated for harvestmen in the family Cosmetidae. During a field study, we observed the infrequent production of vibrations by adult *Cynorta marginalis* Banks, 1909. Using SEM, we examined the surfaces of several appendages for potential stridulatory organs. Our observations indicate that *C. marginalis* has denticles on the mesal surfaces of the basichelicerites that when rubbed together may function as an isomorphous stridulatory organ. In addition, there are denticles on the ectal surfaces of the basichelicerites and furrowed ridges on the femora of the pedipalps that may represent heteromorphous stridulatory organs. We did not observe any sexual dimorphism in morphology at either anatomical location. We also examined the appendages of two additional cosmetid harvestmen: *Paecilaema inglei* Goodnight & Goodnight, 1947, a species that also stridulates when held and *Erginulus clavotibialis* (Pickard-Cambridge, 1905), a species that has not been observed to produce vibrations. As in *C. marginalis*, we observed denticles on mesal and ectal surfaces of the basichelicerites and a furrowed ridge on the mesal surfaces of the femora of the pedipalps of adult *P. inglei*. In contrast, the basichelicerites of *E. clavotibialis* had relatively fewer and smaller denticles on the external surfaces of the chelicerae and the mesal surface of the femora of the pedipalps lacked ridges and were relatively smooth. Our comparative morphological data supports the hypothesis that there are cosmetid harvestmen that may use surface features on the chelicerae and pedipalps to produce vibrations which may function as a secondary defense mechanism.

Keywords: Chelicerae, Gonyleptoidea, heteromorphous, isomorphous, pedipalp

In arthropods, stridulation refers to the act of rubbing the external surfaces of appendages or segments of the body together to produce vibrations or sounds (Masters 1980; Schultz & Pinto-da-Rocha 2007). Stridulatory organs are most well studied in terrestrial arthropods, especially insects from the orders Coleoptera (Wood 1961; Mampe & Neunzia 1966; Wilkinson et al. 1967), Hemiptera (Schmidt 1994; Riede & Kroker 1995), Hymenoptera (Masters 1979, 1980; Coelho 1998; Grasso et al. 2000), Lepidoptera (Haskell 1961; Fullard et al. 1994), Mantodea (Chopard 1938; Maldonado 1970), and Orthoptera (Bellwood 1990; Field & Bailey 1997). Stridulatory organs have also been investigated in a variety of arachnids including members of the orders Araneae (Hinton & Wilson 1970; Jocqué 2005), Opiliones (Lawrence 1937; Juberthie 1957, 1968; Gruber 1968, 1978; Šilhavỳ 1978; Pomini et al. 2010; Kury 2014), Scorpiones (Pocock 1896; Alexander 1958; Lourenço & Cloudsley-Thompson 1995; Lourenço et al. 2000; Lourenço et al. 2004) and Solifugae (Hrušková-Martišová et al. 2008)**.** The functional significance of stridulation varies between different lineages of arthropods and, in some groups, its biological role is still not fully understood (Masters 1980; Gnaspini & Hara 2007). Stridulation has been hypothesized to serve as anti-predator defense (Haskell 1964; Hill 2007) or as a mechanism for intraspecific communication, especially during courtship (Alexander 1958; Edwards 1981; Hillyard & Sankey 1989; Hrušková-Martišová et al. 2008).

In arachnids, stridulatory organs have been reported to occur as pairs of structure that may be located on the mesal surfaces of the chelicerae (Lawrence 1937; Gruber 1978; Hrušková-Martišová et al. 2008), the ectal surfaces of the chelicerae and mesal surface of the pedipalps (Šilhavỳ 1978; Huber 1995; Kury 2014), the ventral surfaces of the booklung covers and the podomeres of leg IV (Hinton & Wilson 1970), the coxae of leg I and trochanters of leg II (Hinton & Wilson 1970; Jocqué 2005), the retrolateral surfaces of the trochanter of the pedipalp and the prolateral surface of trochanter I (Marroquín 2014), and the retrolateral surfaces of femora II and the prolateral surfaces of femora III (Šilhavỳ 1978). In the spider *Holocnemus pluchei* (Scopoli, 1763) (Pholcidae), a distinct file and scraper mechanism composed of ridges occurs on the ectal surfaces of the chelicerae and the mesal surfaces of femora of the pedipalps (Huber 1995). In solifuges, there are a series of ridges and bristles on the mesal surfaces of the chelicerae (Hrušková-Martišová et al. 2008). Similar structures are used to produce vibrations in several species of scorpions (Pocock 1896; Alexander 1958; Lourenço et al. 2000, 2004). In a few species of arachnids, stridulation may not be limited to a single site on the body. In the genus *Mallinella* Strand, 1906 (Zodariidae), some species of spiders may have as many as six different locations for stridulatory organs on the body (Jocqué 2005).

In Opiliones, sonograms of vibrations have only been recorded for the stygnopsid harvestman *Hoplobunus mexicanus* Roewer, 1915 (Pomini et al. 2010). However, even with the aid of scanning electron microscopy (SEM), Pomini et al. (2010) were unable to determine the location of any potential structures on the chelicerae, pedipalps or legs that could be used to generate vibrations. Over the years, putative stridulatory organs, based upon morphological observations, have been reported for a number of species of harvestmen in the suborder Dyspnoi including representatives of the families Ischyropsalididae (Gruber 1968, 1978) and Nemastomatidae (Juberthie 1957; Gruber 1976, 1978) and among several families in the Laniatores, including members of the Cryptogeobiidae (Kury 2014), Gonyleptidae (Kury & Pinto-da-

Rocha 2007; Schultz & Pinto-da-Rocha 2007), Guasiniidae (Pinto-da-Rocha 2007), Phalangodidae (Roewer 1949), Samoidae (Roewer 1949), Travuniidae (Juberthie 1968), Triaenonychidae (Lawrence 1937; Juberthie 1957; Schönhofer 2008), and Zalmoxidae (Šilhavỳ 1978). In a review by Šilhavỳ (1978), three common sites for stridulatory organs were noted for Opiliones including 1) the mesal surfaces of the basichelicerites and fixed fingers of the chelicerae; 2) the ectal surfaces of the chelicerae and the mesal surfaces of the femora of the pedipalps that oppose the chelicerae; and 3) the retrolateral surfaces of the proximal segments of leg II and the prolateral surfaces of the proximal podomeres of leg III. Šilhavỳ (1978) also proposed a fourth potential type of stridulatory organ consisting of the lateral side of the ocularium and the prolateral surface of leg II; however, this structure was later determined to be a part of the porous area on the ocularium, a feature observed in several other taxa (Kury & Pérez González 2007).

Šilhavỳ (1978) modified the terminology of Gruber (1968) for referencing stridulatory organs (i.e., symmetrical and asymmetrical) and classified the stridulatory organs of Opiliones as either isomorphous or heteromorphous. In isomorphous organs, there are two symmetrical roughened areas that rub together and occur on the right and left appendages of the harvestman; usually these structures occur on the chelicerae (Šilhavỳ 1978). Isomorphous stridulatory organs have been observed in species of Guasiniidae (Pinto-da-Rocha 2007), Phalangodidae (Roewer 1949) and Triaenonychidae (Lawrence 1937). In heteromorphous organs, the two components that rub together are referred to as the *plectrum* and *pars stridens* and occur on different appendages, i.e., chelicera and pedipalp or leg II and leg III. The plectrum is an area of setae or pegs whereas the pars stridens is composed of raised ridges or denticles (Šilhavỳ 1978). Heteromorphous stridulatory organs have been reported for harvestmen from the families Ischyropsalididae (Gruber 1978), Cryptogeobiidae (Kury 2014), Gonyleptidae (Kury & Pinto-da-Rocha 2007) and Nemastomatidae (Juberthie 1957; Šilhavỳ 1978). In several species, stridulatory organs have been observed on adults (males and females) and nymphs (Gruber 1968).

While conducting a mark-recapture study (Zvonareva et al. 2016) of adult *Cynorta marginalis* Banks, 1909, we noticed that several adults actively stridulated when held between the thumb and forefinger or in the palm of the closed hand. These vibrations consisted of infrequent, short pulses (1–3s) of vibrations that were inaudible. We used SEM to investigate the morphology of three anatomical locations that could be potential sources of vibrations in these harvestmen: (1) mesal surfaces of the basichelicerites and fixed fingers of the chelicerae, (2) ectal surfaces of the chelicerae and mesal surfaces of the pedipalps, and (3) the prolateral and retrolateral surfaces of the coxae, trochanters and femora of legs II and III). In addition, we compared the surface morphology of the chelicerae and pedipalps of *C. marginalis* with those of two additional cosmetid harvestmen, *Paecilaema inglei* Goodnight & Goodnight, 1947 and *Erginulus clavotibialis* (Pickard-Cambridge, 1905). In the past, we have handled over 100 live individuals of each species (Townsend et al. 2008; Schaus et al. 2013). While we have never observed stridulation by *E. clavotibialis*, we have infrequently detected vibrations emanating from adult *P. inglei*.

METHODS

For scanning electron microscopy (SEM), adult *Cynorta marginalis* were captured by hand from perches in the understory in forested habitats at the La Selva Biological Station, Heredia Province, Costa Rica (10°27′20″N, 84°0′20″W, datum: WGS84) from 11–24 August 2015 (Zvonareva et al. 2016) and preserved in 70% ethanol. We also dissected the chelicerae and pedipalps of the cosmetid harvestmen *Paecilaema inglei* and *Erginulus clavotibialis*. Individuals of these species were collected from the northern range in Trinidad, W.I. and Belize, respectively, in previous studies (Rodriguez et al. 2014; Walker & Townsend 2014). Voucher specimens will be deposited into the collections of the Universidad de Costa Rica and the American Museum of Natural History (AMNH).

With the aid of forceps, a dissecting scalpel and a Leica EZ4 stereomicroscope, we carefully removed the chelicerae, pedipalps, femora-patella of legs II–IV and the coxae of legs I–IV from 3–5 adults of each sex. Specimens were cleaned by ultrasonication for 1–2 min and then dehydrated in a graded ethanol series. We used hexamethyldisilazane (Nation 1983) to dry the appendages prior to mounting them on aluminum stubs coated with a carbon adhesive. Specimens were sputter-coated with gold for 2 min to produce a 15–30 nm coat and examined with a Hitachi S-3400N Scanning Electron Microscope on the campus of Virginia Wesleyan University.

RESULTS

In *Cynorta marginalis*, the mesal surfaces of the basichelicerites (Fig. 1) have fields of small, densely packed, denticles with distinct, non-overlapping bases (Figs. 1C–D, 2), whereas the mesal surfaces of the fixed fingers are generally smooth (Figs. 1A, C–D). Sensilla chaetica, trichomes and other setae are generally absent from the mesal surfaces of both segments (Figs. 2A–B), although there are large tubercles on the dorsal (Figs. 1B, D, 2A–B) and ventral surfaces of the basichelicerites. The denticles are pyramidal or subtriangular in shape and project above the surface of the cuticle (Figs. 2C–H). In comparison to the denticles on the dorsal surfaces of the basichelicerite (Figs. 1B–C), those occurring on the mesal surface are larger and more numerous (Figs. 2A–B). The denticles are most densely distributed on the anterior third of the mesal surface of each basichelicerite, between the dorsal and ventral tubercles (Fig. 2B). In several specimens, we found patches of denticles that appeared to be moderately or severely worn (Fig. 2E). We observed denticles on the mesal surfaces of the chelicerae of males (Figs. 2A, F) and females (Figs. 2B, G–H). We also found intraspecific variation with respect to the morphology of the denticles, with some being relatively smooth and broader (Figs. 2D, G) and others possessing small projections along the distal edges and more sharply pointed (Figs. 2F, H).

In adult cosmetid harvestmen, the ectal surfaces of the basichelicerites and fixed fingers of the chelicerae are covered by and in close proximity to the mesal surfaces of the femora and patellae of the pedipalps (Figs. 3A–B). In *Cynorta*

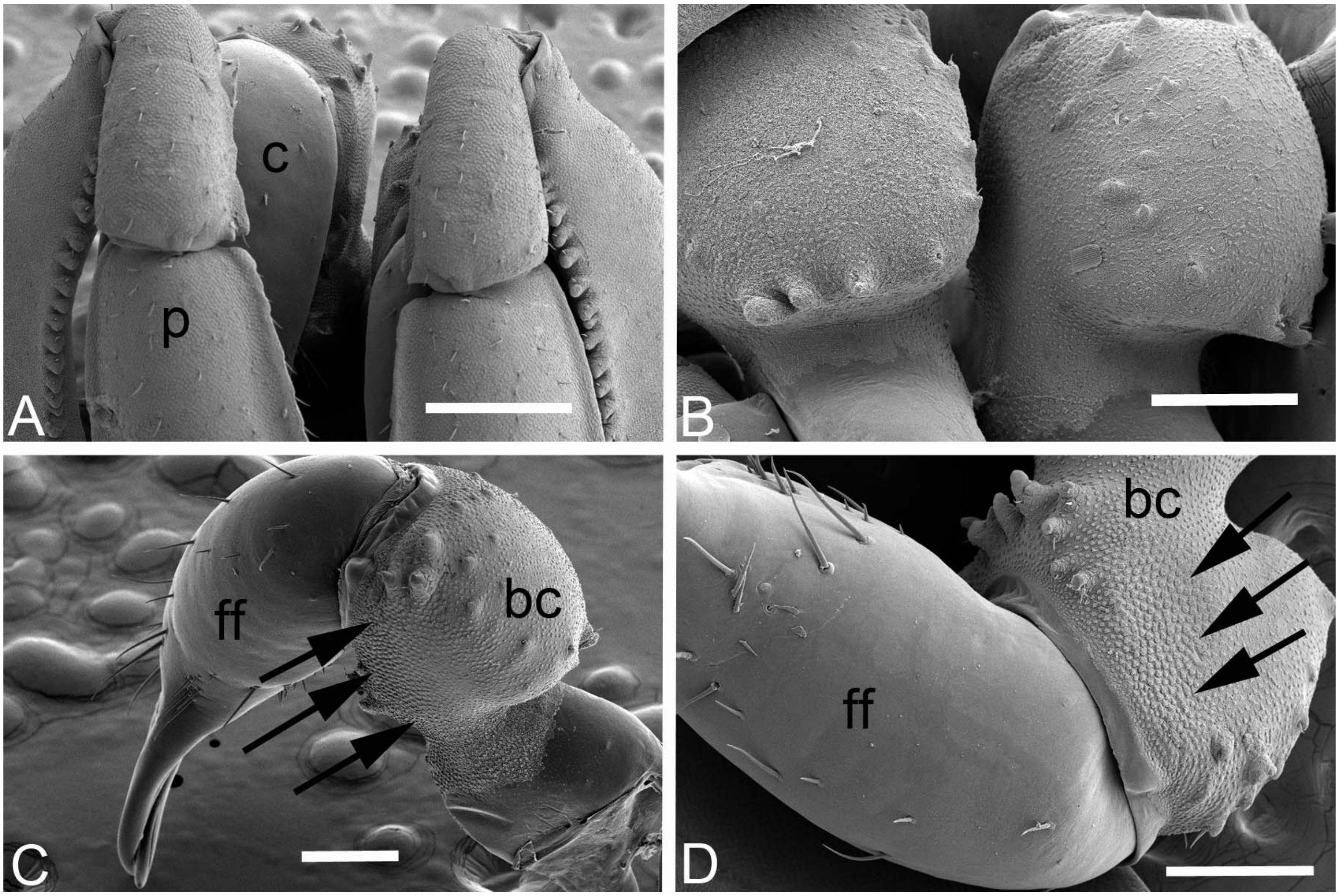

Figure 1.—SEM micrographs of the potential stridulatory organ on the mesal surfaces of the chelicerae of *Cynorta marginalis*. A) Anterior view of the chelicerae (c) and pedipalps (p) of a female, B) Dorsal view of the basichelicerites of a female, C) Mesal view of right chelicera of a female, D) Mesal view of the basichelicerite (bc) with field of small denticles and smooth surface of the fixed finger (ff) of the left chelicera of a female. Arrows indicate fields of small denticles. Scale bars = 250 µm.

marginalis, the ectal surfaces of the basichelicerites feature prominent tubercles on the dorsal and ventral surfaces (Fig. 3C) with fields of conical or pyramidal denticles (Figs. 3C, G–H). The ectal surfaces of the fixed fingers of the chelicerae are smooth (Fig. 3C). With respect to the pedipalp, the mesal surface of the femur is flattened and generally smooth (Fig. 3D), however, there is a raised ridge on the distal femur, near the patella (Figs. 3E–F) that features a series of small, parallel furrows and has a roughened surface morphology (Figs. 3E–F). Sensilla chaetica, trichomes, and other setae are generally absent from this region of the pedipalp. The mesal surface of the patella resembles the surface of the distal femur and has a cuticle with scale-like pattern (Figs. 3E–F). On the ectal surface of the basichelicerite are fields of densely packed, non-overlapping tubercles (Figs. 3G–H) that are similar in size and shape to those that occur on the mesal surface (Fig. 1). We also observed intraspecific variation with respect to the morphology of the denticles, with some being relatively smooth and triangular (Fig. 3G) and others being more conical (Fig. 3H).

The surfaces (prolateral and retrolateral) of the femora of legs II and III of *Cynorta marginalis* have rows of regularly spaced granular tubercles (Fig. 4) and a relatively smooth cuticle that has a scale-like pattern (Fig. 4D), but lacks raised denticles (Fig. 4). There are also many sensilla chaetica occurring at regular intervals along the length of the femora that usually emerge from sockets at the bases of the granular tubercles (Figs. 4B, D).

In *Paecilaema inglei*, the mesal and ectal surfaces of the fixed fingers of the chelicerae are relatively smooth (Figs. 5A, B). The mesal and ectal surfaces of the basichelicerites feature prominent triangular denticles (Figs. 5C, D) and, in some places, show signs of physical wear (Fig. 5D). On the pedipalp, the mesal surfaces of the femora are generally smooth (Fig. 5E), however, there are raised ridges on the distal surfaces, near the patellae (Fig. 5F). As in *Cynorta marginalis* (Figs. 3E, F), these ridges feature series of small, parallel furrows and have a roughened surface morphology (Fig. 5F). The mesal surface of each patella also features an irregular surface with small folds and a scale-like pattern (Fig. 5F). Sensilla chaetica, trichomes and other setae are generally absent from the mesal surface of the femur and patella, but do occur on the anterior and posterior surfaces of these segments. The mesal surface of the patella resembles the roughened surface of the distal femur (Fig. 5F).

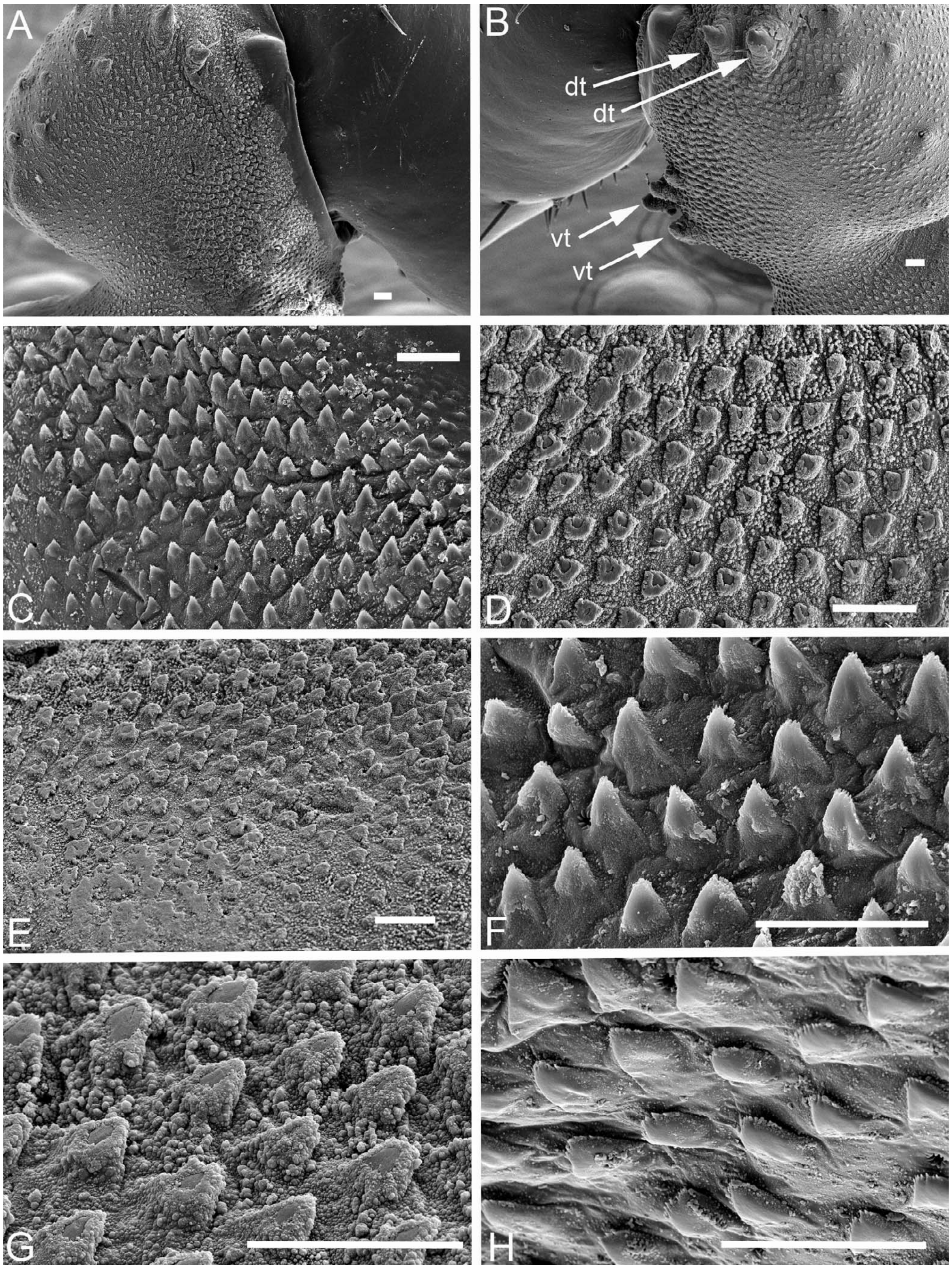

Figure 2.—SEM micrographs of the fields of denticles on the mesal surface of the basichelicerite of *Cynorta marginalis*. A) Dorsal view of the male, B) Dorsal view of the female, C) Field of denticles on a male, D) Field of denticles on a female, E) Field of smooth and worn denticles on a female, F) Morphology of the denticles of a male, G) Morphology of the denticles of a female, H) Morphology of the denticles of a female. Note: intraspecific variation in microanatomy of the denticles. dt = dorsal tubercles, vt = ventral tubercles. Scale bars = 30 μm.

The chelicerae of *Erginulus clavotibialis* have denticles on the mesal and ectal surfaces of the basichelicerites (Figs. 6A–D), but the fixed fingers have smooth external surfaces (Figs. 6A, C). Sensilla chaetica, trichomes, and other setae are absent from basichelicerites and fixed fingers. The denticles are evenly spaced and are only slightly raised from the surface (Figs. 6B, D). The mesal surfaces of the femora and patellae of the pedipalps (Figs. 6E, F), including the distal ridge on the femur (Fig. 6F) are smooth. There are sensilla chaetica present on the mesal surface of the distal ridge of the femur (Fig. 6F).

DISCUSSION

The suborder Laniatores includes at least 29 families and more than 4,200 species (Sharma & Giribet 2011; Pinto-da-Rocha et al. 2012; Giribet & Sharma 2014). In the superfamily Gonyleptoidea, previous studies have reported recordings of

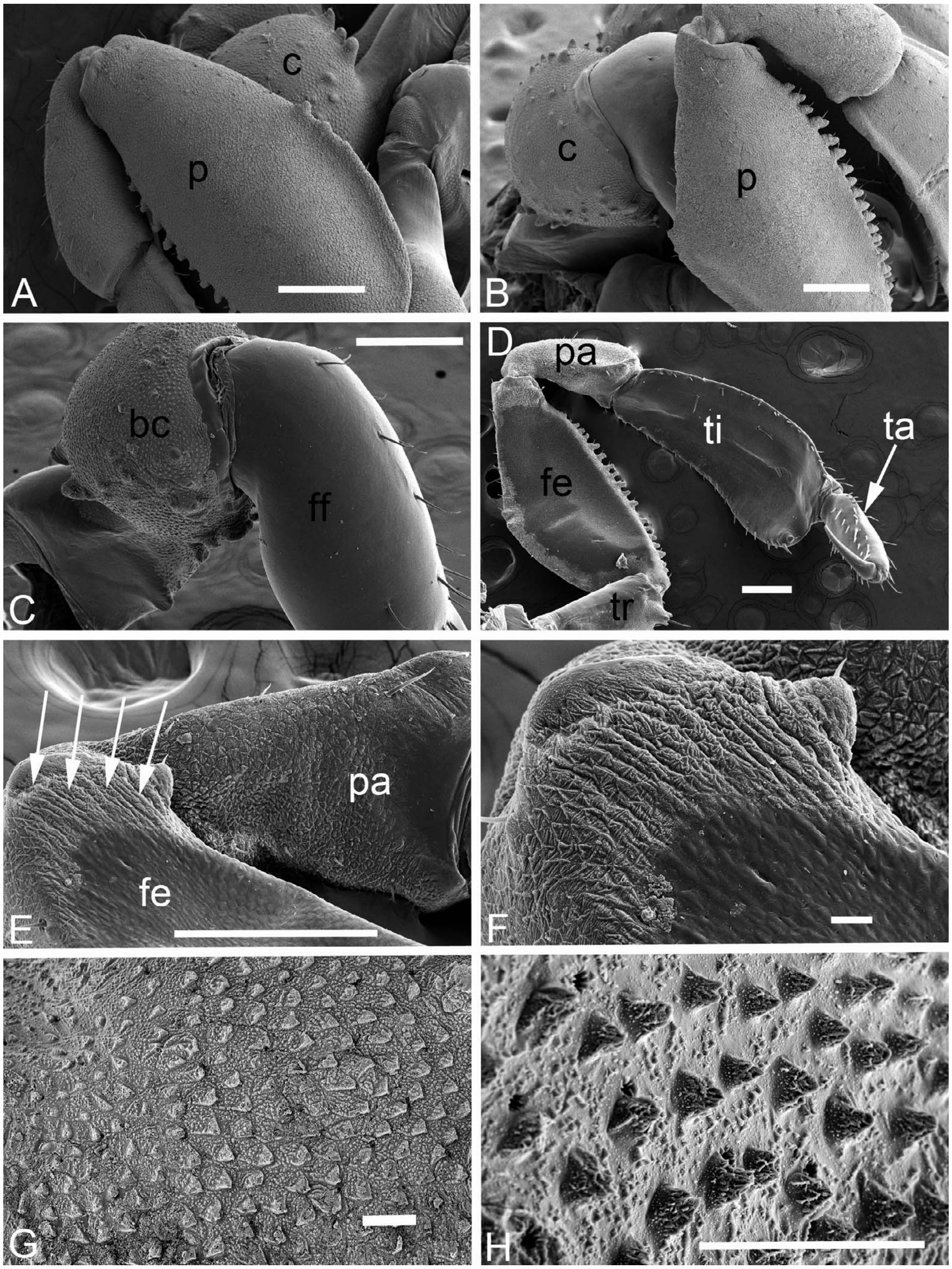

Figure 3.—SEM micrographs of the potential stridulatory organ of the ectal surface of the basichelicerite (bc) and the mesal surface of the distal female of the pedipalp (p) of *Cynorta marginalis*. A) Left pedipalp, basichelicerite, ectal view of female, B) Right pedipalp, basichlicerite and fixed finger of female, ectal view, C) Basichelicerite (bc) and fixed finger (ff) of the right chelicera, ectal view of female, D) Trochanter (tr), femur (fe), patella (pa), tibia (ti) and tarsus (ta) of the left pedipalp, mesal view of male, E) Femur and patella of the left pedipalp, mesal view, of male (note: parallel ridges (arrows) on the distal tip of femur), F) Distal tip of the left femur of the pedipalp, distal mesal view, G) Basichelicerite, ectal surface, female, H) Basichelicerite, ectal surface of female. Scale bars = 300 μm for A–E; 30 μm for F–H.

stridulation (Pomini et al. 2010) or the morphology of stridulatory organs (Kury & Pinto-da-Rocha 2007) for species in primarily three families including the Stygnopsidae (Pomini et al. 2010), Guasiniidae (reviewed by Pinto-da-Rocha 2007) and Cryptogeobiidae (Kury 2014). Our study is the first to identify putative stridulatory organs for the second largest family (700+ species) in this superfamily, the Cosmetidae. We found considerable differences in the morphology of the surface features of the femora of the pedipalps and the distribution and relative sizes of the denticles on mesal and ectal surfaces of the basichelicerites between stridulating and non-stridulating species.

Our SEM study revealed two potential stridulatory organs, an isomorphous apparatus on the mesal surfaces of the

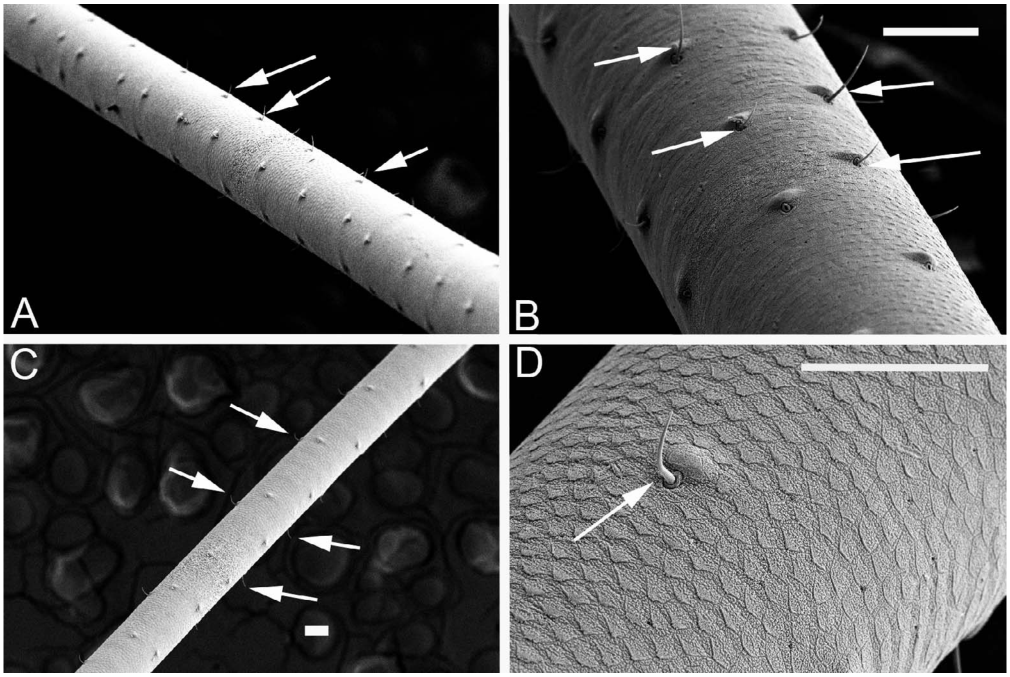

Figure 4.—SEM micrographs of the retrolateral surface of femur II (A–B) and prolateral surface of femur III (C–D) of *Cynorta marginalis*. Note: scale like pattern of cuticle, absence of denticles and regular arrangement of sensilla chaetica (arrows). Scale bars = 100 μm.

basichelicerites and heteromorphous organs on the ectal surfaces of the basichelicerites and mesal surfaces of the femora of the pedipalps. Both types of putative stridulatory organs were observed for adults in two species, *Cynorta marginalis* and *Paecilaema inglei*. In both species, these structures did not exhibit sexual dimorphism. In contrast, these structures were reduced (denticles were smaller and less numerous on mesal surfaces of the basichelicerites) or absent (parallel ridges were absent from distal femur of pedipalp) from the appendages of a third cosmetid species, *Erginulus clavotibialis*. The isomorphous organs featured fields of elevated, closely-packed denticles in which setae (e.g., sensilla chaetica and trichomes) were absent. With respect to comparisons with other putative stridulatory organs among harvestmen (Lawrence 1937; Gruber 1976), the structure that we observed most closely resembles the stridulatory apparatus of *Guasinia persephone* Pinto-da-Rocha & Kury, 2003 (Guasiniidae) with respect to morphology and location (Pinto-da-Rocha & Kury 2003). In multiple specimens of *C. marginalis*, we also observed areas where the denticles appeared to be worn down, possibly as a direct result of the friction produced during prior bouts of stridulation. Additional observations and experiments are needed to test if these putative stridulatory organs actually generate vibrations. Future manipulations could include observation with a stereomicroscope of live animals that have had the mesal and ectal surfaces of the chelicerae sealed with paint or scraped (to remove or damage denticles).

In *Cynorta marginalis* and *Paecilaema inglei*, the plectrum of the heteromorphous organ occurs on the ectal surfaces of the basichelicerites and is very similar in structure to the morphology of the isomorphous organ. The pars stridens that we observed occurred on the mesal surfaces of the femora of the pedipalps. In *Ceratolasma tricantha* Goodnight & Goodnight, 1942 (Ischyropsalididae), the pars stridens consists of a series of ridges on the proximal femur and the plectrum is represented by a series of small denticles on the ectal surface of the basichelicerites (Gruber 1978). Several species of harvestmen in the family Cryptogeobiidae have stridulatory “grates” on the basal, mesal surfaces of the trochanters and femora of the pedipalps (reviewed in Kury 2014). Presumably, there is a field of denticles or series of ridges on the ectal surfaces of the basichelicerites or fixed fingers of the chelicerae of these harvestmen, but the structure of the chelicerae of this subfamily was not discussed in the review. In the stygnopsid *Hoplobunus mexicanus*, Pomini et al. (2010) were unable to identify stridulatory organs, even with the aid of SEM, when examining the surfaces of pedipalps, chelicerae and podomeres of legs I–IV. They did note that males and females both stridulated when seized by one of their fourth legs.

Our discovery of two potential stridulatory organs in cosmetid harvestmen is somewhat atypical as the occurrence of multiple stridulatory organs in an individual has not been previously reported for the order Opiliones. However, the occurrence of multiple locations on the body that produce sounds or vibrations have been observed in spiders (Jocqué 2005) and scorpions (Lourenço et al. 1995). In the field, we captured adult *Cynorta marginalis* and observed that individuals frequently produced sounds or vibrations when physically restrained by human fingers or hands. These field observations appear to support the hypothesis that stridulation in cosmetid harvestmen is a secondary defense mechanism (Gnaspini & Hara 2007; Pomini et al. 2010) rather than a mechanism for intraspecific communication during courtship (Hillyard & Sankey 1989). The lack of sexual dimorphism in the stridulatory organs also supports this hypothesis. Pomini et al. (2010) noted that after stridulation, individuals released defensive compounds but never attempted thanatosis, leading

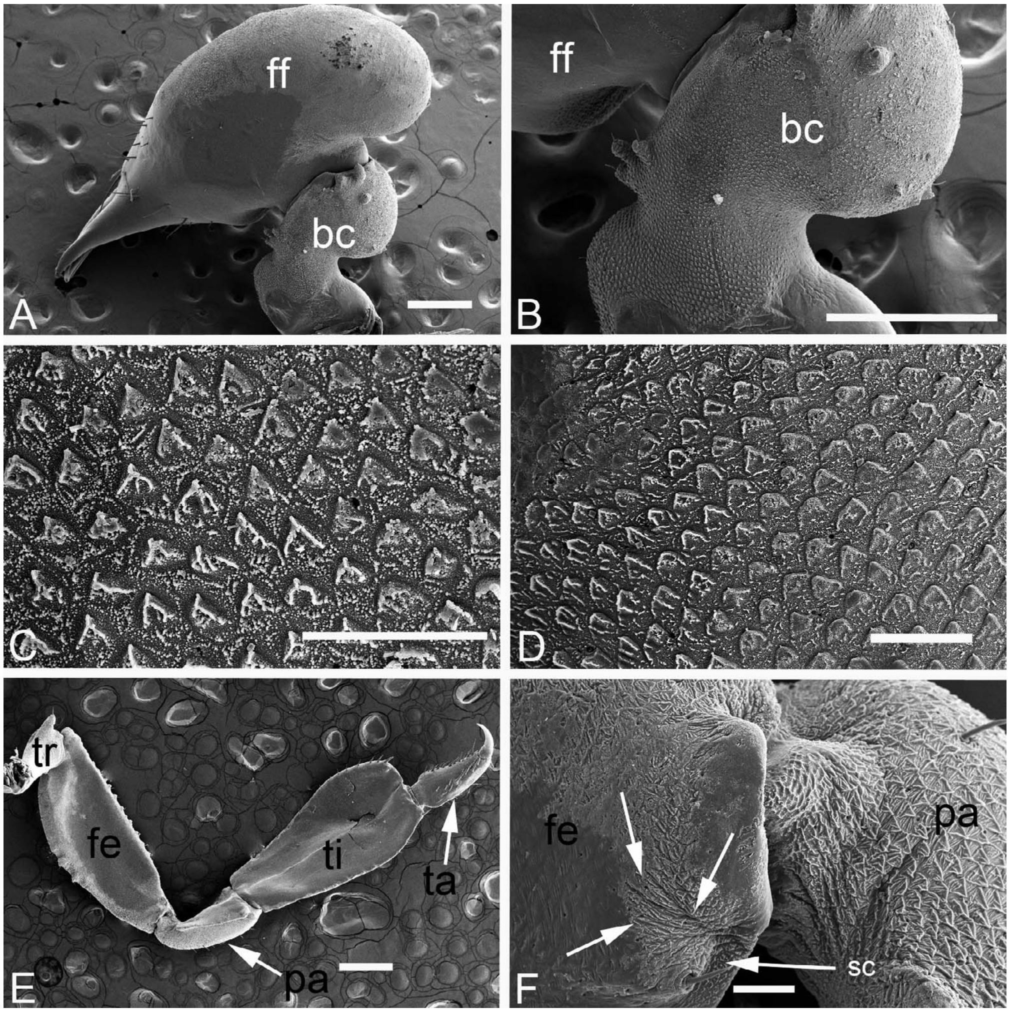

Figure 5.—SEM micrographs of potential stridulatory organs of *Paecilaema inglei*. A) Mesal view of the basichelicerite (bc) and smooth external surface of the fixed finger (ff) of the right chelicera, B) Field of denticles on mesal surface of basichelicerite, C) Surface features of denticles on mesal surface of basichelicerite, D) Field of denticles on the ectal surface of the basichelicerite, E) Mesal view of the trochanter (tr), femur (fe), patella (pa), tibia (ti) and tarsus (ta) of the right pedipalp, F) Mesal surfaces of the distal femur and proximal patella of right pedipalp. Note: parallel ridges (arrows). sc = sensillum chaeticum. Scale bars = 500 µm for A–B and E and 50 µm for C–D and F.

them to hypothesize that stridulation may be employed primarily in interactions with nocturnal, rather than diurnal, predators. Additional behavioral studies of cosmetid harvestmen are needed to test the antipredator defense and the intraspecific communication hypotheses for stridulation.

During the day, adult C. *marginalis* occupy perches on the understory vegetation and are mostly inactive (Wade et al. 2011; Zvonareva et al. 2016). Crypsis probably serves as the primary defense in this species and may enable these harvestmen to avoid potentially lethal encounters with diurnal predators such as birds and lizards. At night, adults move around significantly more, forage, and engage in interactions with conspecifics (Wade et al. 2011; Zvonareva et al. 2016). During this nocturnal activity period, these harvestmen are more likely to encounter generalist predators such as ctenid spiders, scorpions, anurans and mammals that rely upon olfactory or tactile stimuli, rather than strictly visual cues (Cook et al. 2013). In these encounters with nocturnal predators, harvestmen may use one or more secondary defenses, including the relative thickness of the exoskeleton (Souza & Willemart 2011; Dias & Willemart 2013), the release of noxious chemicals from defensive glands (Eisner et al. 1971, 2004; Pomini et al. 2010), or stridulation (Gnaspini & Hara 2007; Pomini et al. 2010). Additional laboratory studies are needed to determine how individuals respond to predators, specifically to assess the frequencies and efficacies of different secondary defenses, such as stridulation.

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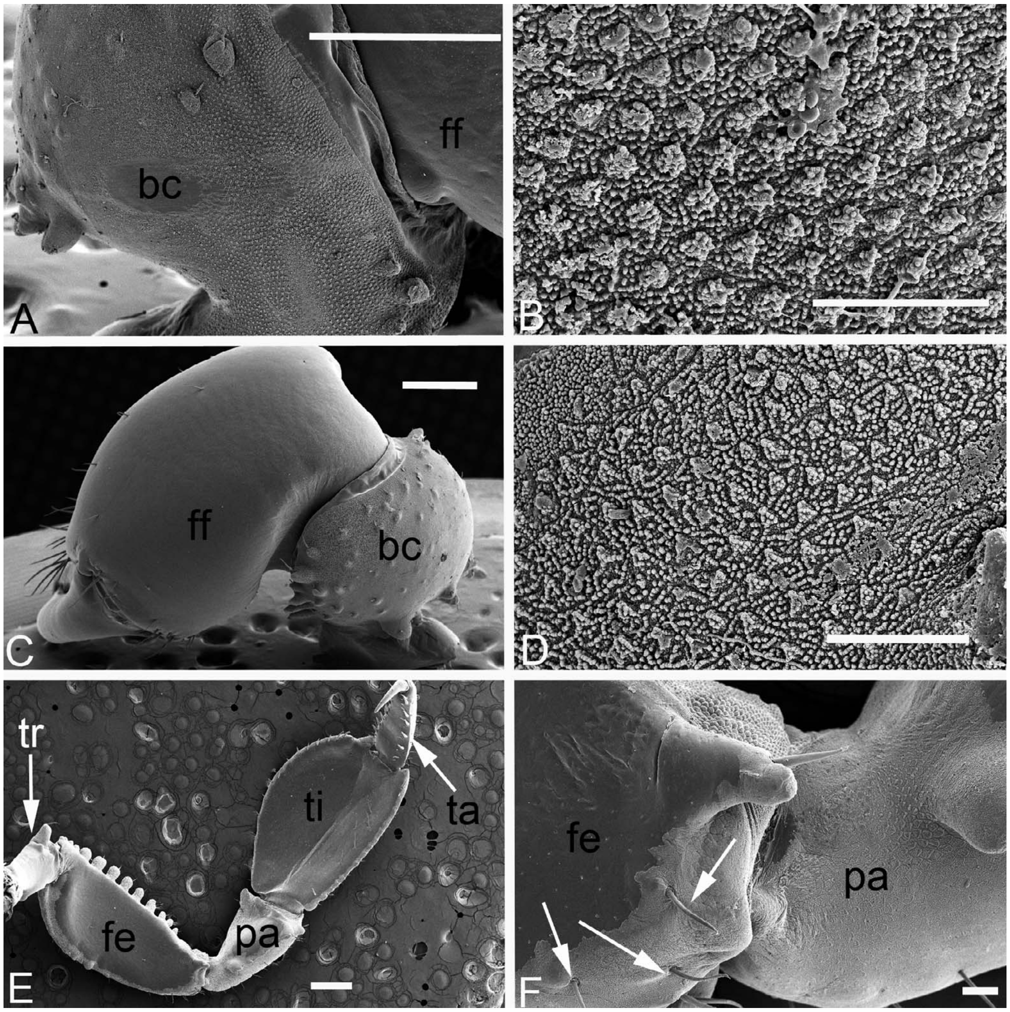

Figure 6.—SEM micrographs of the surfaces of the chelicerae and pedipalps of *Erginulus clavotibialis*. A) Mesal view of the basichelicerite (bc) and fixed finger (ff) of the right chelicera, B) Field of denticles on mesal surface of basichelicerite, C) Ectal view of the basichelicerite (bc) and fixed finger (ff) of the right chelicera, D) Denticles on the ectal surface of the basichelicerite, E) Mesal view of the trochanter (tr), femur (fe), patella (pa), tibia (ti) and tarsus (ta) of the right pedipalp, F) Mesal surface of the distal femur and proximal patella of right pedipalp. Note: smooth surfaces without parallel ridges and the presence of sensilla chaetica (arrows). Scale bars = 500 µm for A, C, and E and 50 µm for B, D and F.

under permit number #CD/60/3/12 (1) from the Belize Ministry of Forestry. The specimens from Trinidad were legally collected and exported under permit numbers 000541 (to VRT in 2005) and 001284 (to Daniel Proud in 2006) from the Forestry Division of the Ministry of Agriculture, Land and Marine Resources of Trinidad and Tobago.

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