The hitherto unknown pheromone gland of female *Stenophylla lobivertex* Lombardo, 2000, a poorly understood praying mantis distributed in the Neotropics, is described and figured. In contrast to other mantodeans, this species has a protrusible, bifurcated (Y-shaped) gland of 6 mm length. It is protracted by sexually receptive females during nighttime and only when undisturbed. The significance of this morphological and behavioral adaptation is discussed in light of the reproductive strategy of the species and its assumed rarity in the natural habitat.

**Keywords**
Calling behavior, Neotropics, praying mantis, reproductive strategy

**Introduction**
Morphologically and phylogenetically unique taxa often exhibit traits not found in related groups (Pavoine et al. 2005, Redding et al. 2008). Such traits might provide crucial information on the evolution of morphological and behavioral characters that cannot be inferred from the study of their relatives alone. Among insects, notable examples are the stenopelmatoid ensiferan *Coolola* Rentz, 1980 (Rentz 1999), the phasmatodean *Dryococelus* Gurney, 1947 (Buckley et al. 2008), and the mantodean *Metallyticus* Westwood, 1835 (Wieland 2008). This also highlights the importance of including such taxa in phylogenetic analyses.

Mate attraction is facilitated through pheromones in many insect taxa, and praying mantises (Mantodea) are no exception. Behavioral experiments suggesting pheromone emission of praying mantis females were first described by Kelner-Pillault (1957), who observed a caged European mantis female (*Mantis religiosa* Linnaeus, 1758) attracting males from surrounding habitats. Meanwhile, several observations in captivity and in the wild have documented pheromone-emitting behavior in many mantodeans (e.g., Edmunds 1975, Robinson and Robinson 1979; Hurd et al. 2004; Gemoeno et al. 2005; Perez 2005, Holwell et al. 2007, Maxwell et al. 2010, Berg et al. 2011, Schwarz 2018). Hurd et al. (2004) were the first to show that a pheromone is indeed produced by sexually active female mantodeans.

During the attracting behavior, usually named “calling”, the apex of the abdomen is bent ventrad in long-winged species (to an extreme in *Acanthopinae*; Robinson and Robinson 1979), exposing the intersegmental membrane between the sixth and seventh tergite, where the pheromone gland is located. In the groups studied so far, this membrane protrudes, at most, very slightly.

Here, we present a unique sexual attraction mechanism exhibited by the leaf-like mantis *Stenophylla lobivertex* Lombardo, 2000, a member of the exclusively Neotropical family *Acanthopidae* (Schwarz and Roy 2019).

**Materials and methods**
We observed and documented the behavior of four females from November 2017 to June 2018 (N = 1) and from October 2019 to March 2020 (N = 3). The first observations were made by the second author in a female from the Panguana research station (9°37’S, 74°56’W, 260 m a.s.l.) in Amazonian Peru. Three additional females were part of a captive bred stock, likewise from Peru, obtained by the first author from a Mantodea breeder in Germany.

**Results**
As in other species studied so far, the pheromone gland of *Stenophylla lobivertex* is located between the sixth and seventh tergite. It is inflated into a Y-shaped structure during calling and usually sticks out almost vertically from the body (Fig. 1), but each lobe can also be moved in a tentacle-like manner. The fully inflated organ is 6 mm long, about 1 mm thick at both ends and filled with haemolymph, which gives the organ a greenish-blue appearance. Tracheae can be seen shining through the thin membrane.

The captive stock females continued to call after being mated multiple times but produced unfertile oothecae, indicating that the copulations might have been unsuccessful. Our observations so far suggest that calling behavior is reduced in females older than six months.
Fig. 1. Pheromone gland of *Stenophylla lobivertex*. A. Lateral view of calling female; B. Pheromone gland in anterolateral view; C. Pheromone gland in posterolateral view. Photos by C. J. Schwarz.
Calling in *Stenophylla* occurred, like in other mantodeans, over the course of 2–5 hours per night and only in deep darkness and when undisturbed. Temperature during the observational period reached 26 to 29°C by day and 22 to 24°C by night, at 70–90% relative humidity. The protraction of the gland occurred over the course of several minutes, but upon disturbances, such as vibrations or illumination by artificial lights, the pheromone gland was retracted instantly.

**Discussion**

So far, *Stenophylla lobivertex* is the only species of more than 2,500 known mantodean species whose pheromone gland has evolved into a distinct, inflatable morphological structure. While the pheromone glands can attain the shape of a pair of small bulges in some other taxa (e.g., Acanthopinae, *Tarachodes* Burmeister, 1838: Edmunds 1975, Robinson and Robinson 1979), no other known mantodean inflates its pheromone gland into a Y-shaped structure. However, the two congeners of *S. lobivertex* might possess a similar structure.

The significance of this unique structure remains speculative at this point, but we argue that this type of protrusible gland with its increased surface might be able to distribute pheromones more efficiently than the less elaborate glands of other mantodean species. This structure might, therefore, help to assure efficient mate finding in a species apparently characterized by low population density in combination with a short reproductive period.

*Stenophylla* are rarely observed in nature, and only a handful of specimens of the three known species are present in museum collections. The rarity of this taxon might be partly due to its reproductive K strategy (MacArthur and Wilson 1967). Preliminary observations on captive specimens revealed that females produce only 3–5 oothcae during their lifetime, which contain at most 30 eggs (Rönisch and Schwarz 2019). Females guard their egg cases until the young hatch; the hatchlings are 13 mm long (as compared to 40–44 mm in adults). The natural phenology of *Stenophylla* is unknown, but during more than 35 years of regular collections at the Panguana field station in Peru, adult specimens (deposited in the Staatliches Museum für Naturkunde, Karlsruhe [SMNK], the Zoologische Staatssammlung München [ZSM], and in the collection of CJS) were only found in the months of August to October (Schwarz et al. 2020). The specimens of the type series were captured in October and November (Lombardo 2000). Finding a sexual partner when population density is low and adults are not found year-round is challenging. This is especially true in a highly complex rainforest ecosystem and thus may explain the low population density in combination with a short reproductive period.

References

Berg M, Schwarz CJ, Mehl JE (2011) Die Gottesanbeterin, *Mantis religiosa*. Die Neue Brehm-Bücherei Bd. 656, Westarp Wissenschaften, Hohenwarsleben, 521 pp.

Buckley TR, Attanayake D, Bradler S (2008) Extreme convergence in stick insect evolution: phylogenetic placement of the Lord Howe Island tree lobster. Proceedings of the Royal Society B 276: 1055–1062. https://doi.org/10.1098/rspb.2008.1552

Edmunds M (1975) Courtship, mating and possible sex pheromones in three species of Mantodea. Entomologist's Monthly Magazine 111: 53–57.

Gemeno C, Clarambut J, Dasca J (2005) Nocturnal calling behavior in mantids. Journal of Insect Behavior 18: 389–403. https://doi.org/10.1007/s10905-005-3698-y

Holwell GI, Barry KL, Herberstein ME (2007) Mate location, antennal morphology, and ecology in two praying mantids (*Insecta: Mantodea*). Biological Journal of the Linnean Society 91: 307–313. https://doi.org/10.1111/j.1095-8312.2007.00788.x

Hurd LE, Prete FR, Jones TH, Singh TB, Co JE, Portman RT (2004) First identification of a putative sex pheromone in a praying mantid. Journal of Chemical Ecology 30: 155–166. https://doi.org/10.1023/B:JOEC.0000013188.79411.18

Kelner-Pillault S (1957) Attraction sexuelle chez *Mantis religiosa*. Bulletin de la Société entomologique de France 62: 9–11.

Linnaeus C (1758) Systema naturae per regna tria naturae, secundum classes, ordinem, genera, species, cum characteribus, differentiis, synonymis, locis. Tomus 1, editio decima, reformata, Laurentii Salvii, Holmiae, Stockholm, 824 pp. https://doi.org/10.5962/bhl.title.542

Lombardo F (2000) *Stenophylla lobivertex*, a new species of Stenophyllini from Amazonia (*Insecta, Mantodea*). Studies in Neotropical Fauna and Environment 35: 34–37. https://doi.org/10.1076/0165-0521(200004)35:1;1-M;FT034

MacArthur RH, Wilson EO (1967) The Theory of Island Biogeography. Princeton University Press, Princeton (NJ), 224 pp.

Maxwell MR, Barry KL, Johns PM (2010) Examinations of female pheromone use in two praying mantids, *Stagmomantis limbuta* and *Tenodera aridifolia sinensis* (*Mantodea: Mantidae*). Annals of the Entomological Society of America 103: 120–127. https://doi.org/10.1603/008.103.0115

Pavoine S, Ollier S, Dufour A-B (2005) Is the originality of a species measurable? Ecology Letters 8: 579–586. https://doi.org/10.1111/j.1461-0248.2005.00752.x

Perec B (2005) Calling behaviour in the female praying mantis, *Hiero dula patellifera*. Physiological Entomology 30: 42–47. https://doi.org/10.1111/j.0307-6962.2005.00426.x

Redding DW, Hartmann K, Mimoto A, DeVos M, Mooers AØ (2008) Evolutionarily distinctive species often capture more phylogenetic diversity than expected. Journal of Theoretical Biology 251: 606–615. https://doi.org/10.1016/j.jtbi.2007.12.006

Rentz DCF (1999) Pearson’s Monster, a new species of *Cooloola* Rentz from Queensland (*Orthoptera: Cooloolidae*). Journal of Orthoptera Research 8: 25–32. https://doi.org/10.2307/3530421

Robinson MH, Robinson B (1979) By dawn’s early light: Matutinal mating and sex attractants in a Neotropical mantid. Science 205: 825–827. https://doi.org/10.1126/science.205.4408.825

Rönisch T, Schwarz CJ (2019) Die “Drachenmantis” *Stenophylla lobivertex*. Zoologischer Zentral-Anzeiger 2019: 50–52.

Schwarz CJ (2018) Extravagante Schönheiten – die Gattung *Mantodea* revisited: an updated classification incorporating multiple data sources (*Insecta: Dictyoptera*). Annales de la Société entomologique de France (NS) 55: 101–196. https://doi.org/10.1080/00379721.2018.1556567

Schwarz CJ, Ehrmann R, Stiewe MBD, Mörtter R, Falkenberg M (2020) Mantodea of Panguana (*Insecta: Dictyoptera*). Zootaax 4824: 1–66.

Wieland F (2008) The genus *Metallurus* reviewed (*Insecta: Mantodea*). Species, Phylogeny and Evolution 1: 147–170.

Acknowledgments

We thank the Peruvian nature conservation authority and forestry office [Servicio Forestal y de Fauna Silvestre (SERFOR), Ministerio de Agricultura y Riego (MINAGRI)] for contribution and export permits (SERFOR 2014–2019: No. 007–2014–SERFOR-DGGSPFFS + No. 0406–2017–SERFOR-DGGSPFFS; SERFOR 2014–2019: No. 0000326–SERFOR - No. 003492–SERFOR). Thomas Rönisch (Böblingen, Germany) and the members of the Panguana collection team provided *Stenophylla* specimens, in particular Ernst-Gerhard Burmeister (ZSM) and Amelie Höcherl.