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Female monopolization and paternity assurance in South American crickets (Orthoptera, Grylloidea): mating plugs, extra claspers and forced copulation

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ABSTRACT

*This paper describes the first three cases in which male crickets monopolize females by means of mating plugs. The origin of the plugs vary among the cases (*i.e., *they are not homologous). Female monogamy is assured by the permanent presence of the plug attached to their genitalia after first mating, while males are potentially polygamous. The presence of an additional clasping structure and the occurrence of forced copulation are also described.*

Key-words: Crickets, Grylloidea, Mate monopolization, Mating plug, Mating system Paternity assurance, Rape behavior, Forced copulation, Rape.

INTRODUCTION

A brief account on male insect and arachnid ploys to sexually monopolize females

Male animals of many taxonomical groups show adaptations that avoid or reduce the chances that spermatozoa from rival males succeed in fertilizing the ova of females with whom they copulate. These paternity-directed strategies may have chemical, behavioral, or structural natures.

Male beetles of the genus *Tenebrio* mark females, during copulation, with an anti-aphrodisiacal pheromone which is transferred via genital apparatus; that substance acts by repelling other males (Happ, 1969). Gilbert (1976) describes a parallel case in the butterfly *Heliconius erato* but there special structures have evolved for the transfer and spread of the pheromone. Males of the bee *Centris adani* mark the female body surface with citral from his mandibular glands during copulation. That supposedly makes her smell like a male, since the same substance is used by males to mark the vegetation of their territory (Frankie *et al.,* 1980).

Some female insects become sexually unreceptive for at least a certain period after copulation. That is, for instance, what occurs with the dipterans *Aedes aegypti* (Craig, 1967), *Musca domestica* (Riemann *et al.,* 1967; Riemann & Thorson, 1969), *Drosophila melanogaster* (Burnett *et al.,* 1973), *D. funebris* (Baumann, 1974a, b) and *Hylemya brassicae* (Swailes, 1971). In most of the cases, loss of female sexual receptivity is promoted by stimuli caused by secretions from the male's accessory glands which are transferred to the female during insemination (Leopold, 1976; Gillott & Friedel, 1977), but in *Drosophila,* mating inhibition is thought to be accomplished mainly by the presence of sperm in the spermathe-

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cae (Burnett *et al.,* 1973; Manning, 1967; Merle, 1968).

Behavioral means by which males can reduce the chances for a female to re-mate with a rival include such maneuvers as: concealment of the partner or potential partner from competitors; reduction of the conspicuousness of courtship displays; exhibition of some kind of female guarding (*i.e.,* with or without body contact), among other strategies (Thornhill & Alcock, 1983).

Several species of *Drosophila* exhibit what is called the "insemination reaction". This phenomenon is an enlargement of the vagina produced by the male's ejaculate (Patterson, 1946) which, in intraspecific matings, appears to prevent the female from re-mating for a certain period and thus securing him paternity of offspring (Patterson, 1947). Alonso-Pimentel *et al.* (1994) have argued that, in *Drosophila,* more than one type of phenomena have been considered under the name of insemination reaction and, by judging Patterson's original concept too simplistic, they defined the "true insemination reaction" as "a mass of one amorphous material that greatly distends the vagina of recently mated females".

Some male insects are able to, during sexual contact, displace the sperm of other males which is stored inside the female's spermathecae or bursa copulatrix and, in certain damselflies, the sperm of a precedent male is removed from the female's storage organ by means of the penis (Waage, 1979, 1984). In species where spermatozoa of the last male to copulate are more likely to fertilize a larger amount of eggs, sperm from precedent males may be packed deeper into the female's spermatheca by the penis of subsequent ones. That is the case with the dragonfly *Sympetrum rubicundilum* (Waage, 1984).

Alonso-Pimentel *et al.* (1994) define the term sperm sac as "structures with distinctive materials that stay soft inside the female's vagina and do not cause inordinate distention of the vaginal pouch". According to those authors, sperm sacs contain a great quantity of sperm and become cohesive units in contact with the air; the cohesion of sperm sacs as compact units could be explained by the presence of a gelatin-like substance. This type of structure was reported from *Drosophila mettlery, D. nigrospiracula* and *D. melanogaster;* females of all three species discard the sacs within 24h after mating.

Mating plugs, or copulatory plugs, are male-produced substances or structures which are transferred to the female upon copulation and promote the sealing of her genital opening which will, ultimately, prevent her from copulating with other males for at least a certain period of time. Male hymenopterans like those of the honey bee, *Apis mellifera,* and of harvester ants of the genus *Pogonomyrmex* plug the female genitalia with a portion of their bodies, more specifically with the copulatory apparatus that is lost upon the end of copulation. In these cases the wound causes them to die after having mated (Alcock, 1989; Hölldobler, 1976; Markl *et al.,* 1977; Michener, 1974; Thornhill & Alcock, 1983). The minute male of the ceratopogonid *Johannseniella nitida* blocks the female's genitalia by introducing himself inside of it (Downes, 1978; Goetghebuer, 1914).

Honey bee drones also transfer glandular secretions (mucopolysaccharides) that coagulate within the female and block her genitalia (Blum *et al.,* 1962). Similar cases were reported by Boldyrev (1913) for locusts. Leopold (1976) mentions that secretion-derived plugs are produced by accessory glands, such types of plugs have been found in a number of animals other than insects.

The spermatophore itself may constitute the mating plug once it is inside the female's genital duct, which is the case of the grasshopper *Locusta migratoria.* That species produces a very long and coiled spermatophore which remains inside the female's spermatheca (Gregory, 1965). Landa (1960) reports a similar case in a melolonthid beetle.

Males of certain spiders leave the distal portion of the pedipalpal embolus inside the epigynum after sperm transfer (Abalos & Baez, 1963; Bonnet, 1930; Levi, 1969; Levi, 1975), while others cover the epigynum with membranous scales derived from the palps (Jackson, 1980; Levi, 1972; Robinson, 1982).

Mating plugs in crickets

Female monopolization mediated by mating plugs has never been reported from Grylloidea. In fact, anyone familiar with male and female cricket genital morphology and the way they function during sperm transfer would probably have trouble trying to figure out how a plug system could be possible for this group of insects. Since cricket phallic complexes are not intromittent nor are the spermatophore bodies transferred to the internal tract of the female genitalia during copulation, a mating plug system for crickets can hardly be imagined. In these insects, the spermatophore ampulla is always kept outside the female body during sperm transfer and it will be removed by the male or female, depending on the case, as soon as the transfer is accomplished- for details see Alexander & Otte (1967).

Although male genitalia does have clasping structures that will hold female's copulatory papilla on position for spermatophore attachment, the contact between spermatophore and copulatory papilla is always pinpointed and rather brief. The only contact of the two structures occurs between the neck of the spermatophore and the opening of the papilla and that lasts only the time necessary for sperm transfer, normally a matter of minutes. In some cases, the male will hold the female on position during insemination and afterwards he will remove and eat the empty spermatophore; in other ones he will just attach the spermatophore to her copulatory papilla by means of an specialized structure named "attachment plate" and let her go, carrying the structure on the outside of her body; after completion of sperm transfer she will remove and eat the empty capsule (Alexander & Otte, *op. cit.*).

People interested in the diversity of cricket reproductive strategies should check Zuk & Simmons (1997) and the literature cited therein.

This paper reports the first three cases of mating plugs in crickets, all observed among South American members of the families Eneopteridae and Phalangopsidae.

MATERIALS AND METHODS

The specimens, the way they are preserved, and the methods of observation employed vary among the cases treated in this paper.

The individuals of *Adenophallusia naiguatana* Mello & Camargo e Mello, 1996 belong to the original type-material comprised by two adult males and one female, all dry-preserved and deposited at the Academy of Natural Sciences of Philadelphia. None of them were observed alive.

The individuals of *Aracamby* Mello, 1994 used for observations belong to several species and were the subject of my doctorare thesis which mainly focused on the taxonomy and biogeography of the species of that genus (Mello, 1994). All specimens are now preserved in 80% alcohol and kept at the insect collection of the Zoology Department- São Paulo State University, Botucatu Campus, Brazil. Laboratory observations of courtship and mating behavior were carried out in small terraria (20 cm diameter x 12 cm height) half filled with moist sterilized sand.

The specimens of an undescribed species of *Eidmanacris Chopard,* 1956 were observed, preserved and are deposited as mentioned for those of *Aracamby.*

The terminology for the phallic elements employed here is that of Desutter (1990) with the corrections that author proposed on a subsequent paper (Desutter-Grandcolas, 2003).

Additional information on methodology, when applicable, is given along the text under each case.

RESULTS

The case of *Adenophallusia naiguatana* (Eneopteridae, Tafaliscinae)

Adenophallusia naiguatana is a Venezuelan cricket belonging to a so far monotypic genus (Mello & Camargo e Mello, 1996).

The pseudepiphallus of that species contains a pair of sac-shaped glandular structures, each of them with an external opening located distally, on the inferior face of the pseudepiphallus (Figs. 1 to 3).

Although I have not observed mating behavior itself, I infer that during copulation, as the sperm content of the spermatophore is been transferred to the female through her copulatory papilla (the usual method in crickets), secretion from the pseudepiphallic glands also flows to the surroundings of the papilla. This fluid, after becoming solid, blocks the whole genital opening, preventing the female from projecting the copulatory papilla in order to re-mate. Upon removal of the subgenital plate from a female that has already copulated, one finds the mating plug shaped as a solid plate (Fig. 4).

Pseudepiphallic glands are rare in crickets, but they do occur in certain members of the tropical American subfamily Luzarini (Phalangopsidae) (Desutter-Grandcolas, 1996). Within the eneopterids such glands are only known from *A. naiguatana,* undoubtedly a case of convergence. The relation of these glands to the production of mating plugs has not been established up to now.

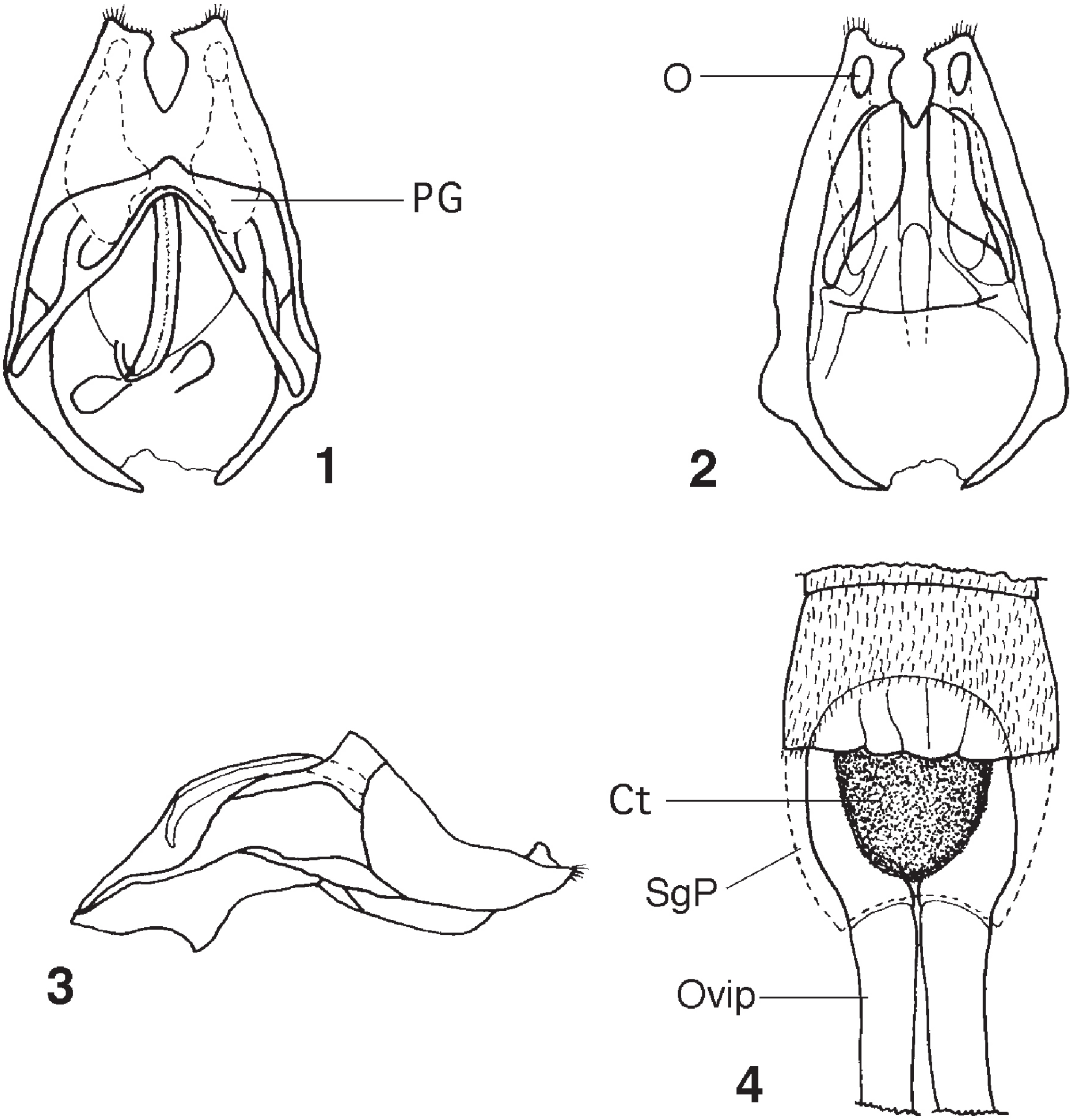
The case of the genus *Aracamby* (Phalangopsidae, Luzarinae) and related genera with pseudepiphallic glands and tubular pseudepiphallic arms

The genus *Aracamby* was the object of a doctorate thesis (Mello, 1994) and comprises, to the present, three species described from the Atlantic Forest of Brazil and eight still undescribed ones (Mello, 1992). It belongs to a cluster of crickets in which the males lack a calling song but do perform a courtship song. In this group of crickets, the presence of metanotal glands is common in males; these glands produce a secretion that is eaten by the female prior to and during copulation. In *Aracamby,* however, such glands are absent and nuptial feeding does not occur.

Another common feature of *Aracamby* and closely-related genera is the possession of a pair of phallic glands (referred to as PG in the figures) located within the main portion of the pseudepiphallus.

The pseudepiphallic arms, normally blade-shaped in related genera not possessing phallic glands, are tubular in *Aracamby* and perform the function of a duct that, during copulation, will deliver glandular secretions to the base of the copulatory papilla. The distal end of the tube is bifurcate and its opening located in the junction of both digits (Figs. 5 to 9).

The base of the copulatory papilla of adult but virgin females is a whitish, long and flexible bellows-shaped membrane that must be distended in order for mating to take place (Figs. 10, 11). That is the region where the digits of the pseudepiphallic arms will hold



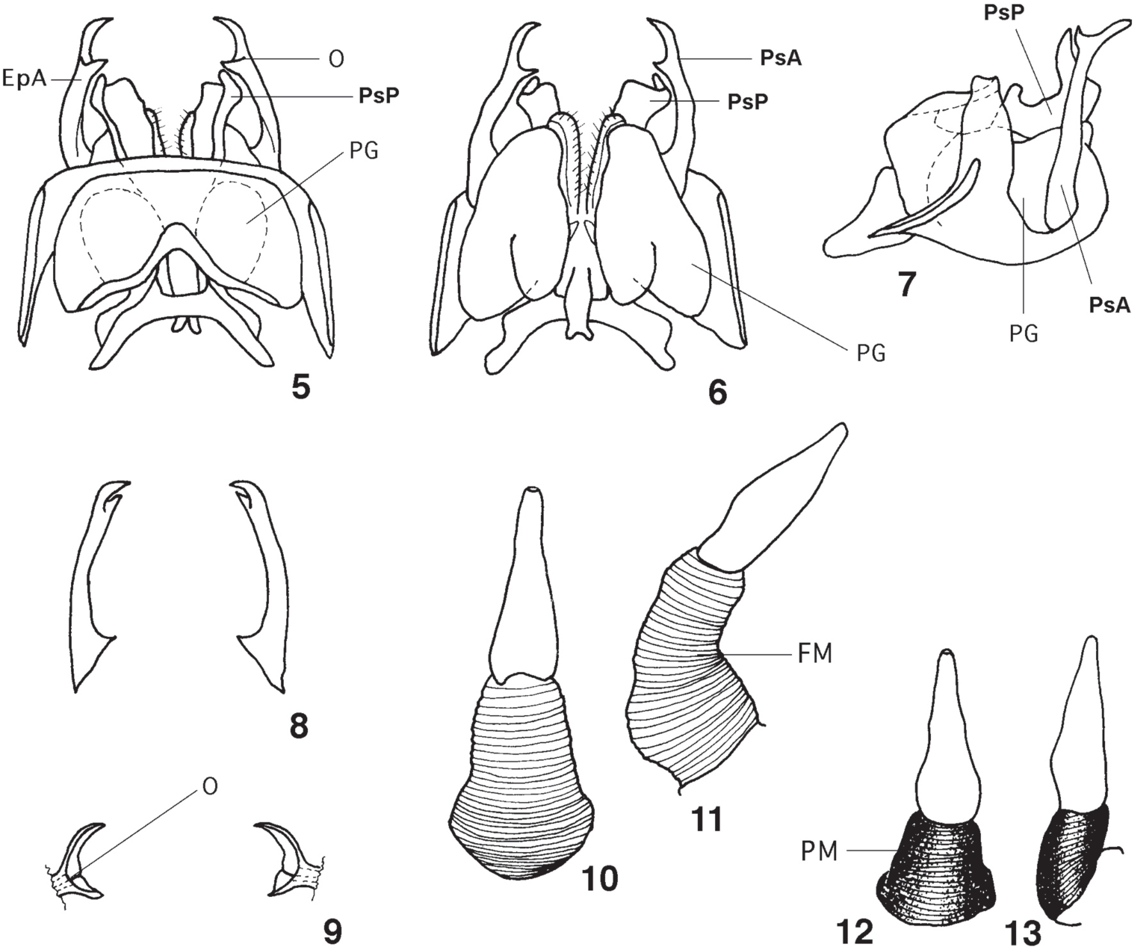
FIGURES 1-4: Phallic complex and female terminalia of *Adenophallusia naiguatana.* **1, 2, 3,** phallic complex in dorsal, ventral and lateral views, respectively; **4,** female distal abdominal sternites. Conventions: PG = phallic gland; Ct = cement; O = outer opening of phallic gland; SgP = dashed line indicating the position of the subgenital plate prior to its removal; OVIP = basal portion of ovipositor. Figures not to scale.

during copulation and where glandular secretion will be discharged. After mating, the secretion causes the flexible membrane to darken, shorten, harden, and lose mobility, that is, it becomes "petrified", rendering the female inability to distend her copulatory papilla and re-mate (Figs. 12, 13).

Sex ratios in species of *Aracamby* appear to be 1:1, but what one really finds in nature is a highly male-biased situation for there are many males wanting to mate and very few virgin (unplugged) females available. Unplugged females are a rare resource to males, which makes the operational sex ratio quite different from the 1:1 condition. It is expected that if assortative mating as a result of female choice does occur in these crickets, certain males will be favored and have chances to re-mate while others will never reproduce.

Low female availability will foster high male competition for mates, which can probably explain the origin of two quite distinct features of *Aracamby* males: the possession of extra clasping devices and forced copulation (or rape behavior, to use an anthropocentrical term).

In addition to pseudepiphallic parameres (Figs. 5 to 9), which are the common clasping devices found in crickets, and pseudepiphallic arms that will hold on the base of female copulatory papilla to deposit "cement" secretion during sperm transfer (Figs. 5 to 9), the paraprocts of *Aracamby* males are furnished with a heavy superior spine, sometimes hook-shaped in certain species, and an inferior bristle (Figs. 45, 46 and 48 to 56). During sperm transfer, the spines of both paraprocts will hold firmly on the female's subgenital plate, keeping her in position and maintain-



FIGURES 5-13: Phallic complex and copulatory papilla of *Aracamby* sp (undescribed species). **5, 6, 7,** phallic complex in dorsal, ventral and lateral views, respectively; **8,** tubular pseudepiphallic arms in rear view; **9,** idem in dorsal view; **10, 11,** copulatory papilla of virgin female in dorsal and lateral views, respectively; **12, 13,** copulatory papilla of a female seven days after copulation. Conventions: PsA = pseudepiphallic arm; PsP = pseudepiphallic paramere; PG = phallic gland; PM = "petrified" membrane; O = outer opening of pseudepiphallic gland; FM = flexible membrane". Figures not to scale.

ing attachment. Female paraprocts have two bristles (Fig. 47), which suggest that the male's paraproctal clasper is also a sexually-selected transformation of the superior bristle originated by competition among males to secure females. At present, similar structures are not known from any other cricket.

I have observed more than sixty matings in species of *Aracamby* and registered thirty copulation durations, which ranged from 23 to 58 minutes. In some instances the females visibly intended to abort the process by trying to remove the male with her hind legs and jumping, but never succeeded. Whenever she jumped the male was also carried with her, so tightly attached they were.

Normally, for copulation to occur in crickets, the female must allow it because she has to protrude her copulatory papilla upon response to male courtship in order to permit genital attachment; without her compliance copulation will not occur. Forced copulation in crickets is thus a hardly conceivable phenomenon; nevertheless, it was observed three times in couples of two different species of *Aracamby* placed in small terraria in the laboratory. Presumably it also occurs in nature.

According to the laboratory observations, this is the scenery in which forced copulations took place: imediately after last moult, when the body wall is still soft, *Aracamby* females remain motionless for tens of minutes with the copulatory papilla distended while the integument dries and hardens. In that moment, an adult male kept in the same terrarium with the respective female started a seconds-brief courting period and, in the absence of a response, backed towards her, slid his terminalia under her body and rapidly attached his genitalia to hers. In all three observed cases, the females, with body wall still very soft, tried to move and free themselves but copulation continued until the males released them. Two of the females started laying eggs few weeks after the forced copulation and did produce offspring; the other one was fixed in 75% alcohol 24 hours after copulation and dissected afterwards: although the ovaries were still undeveloped, the spermatheca was full and the bellows-shaped membrane on the base of her copulatory papilla was already "petrified".

According to my observations, it doesn't seem likely that, in nature, adult males will follow and guard female nymphs that are about to undergo the last moult to copulate with them immediately after ecdysis, but they certainly will try to force copulation with a recently moulted adult female with distended copulatory papilla that they happen to encounter. So, it is impossible to predict how often forced copulation occurs in nature or how often virgin females can practice mate choice.

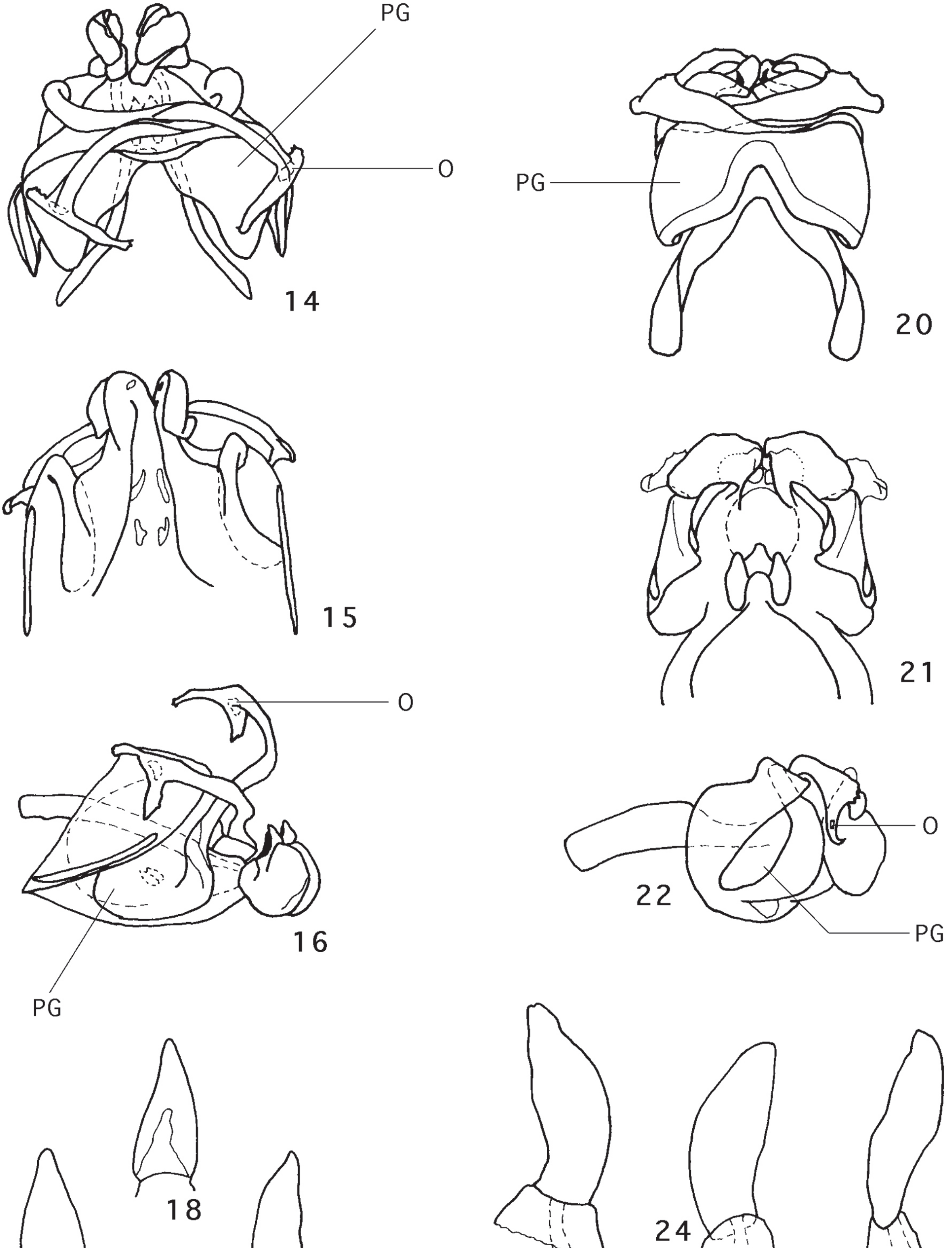
Another evidence that male competition for females is intense, is the fact that *Aracamby* males always carry a spermatophore which is ready to be used in case he does succeed in finding a virgin female to copulate with. Having a ready-to-use spermatophore means that time will not be lost with the elaboration of such a complex structure during courtship, as occur in other crickets. Finding a female in conditions to copulate may indeed be a rare event for *Aracamby* males, so, when it does happen, all his persuasion power must be ready to be employed and the necessary genital weapons must be triggered.

Males of several phalangopsid crickets other than *Aracamby* carry ready-made spermatophores all the time. In these cases the ampulla of the spermatophores is normally hard and darkly pigmented. On the other hand, in crickets that start producing the spermatophore only after a female had been found and courtship has begun, the spermatophore ampulla is generally softer and less pigmented, frequently whitish.

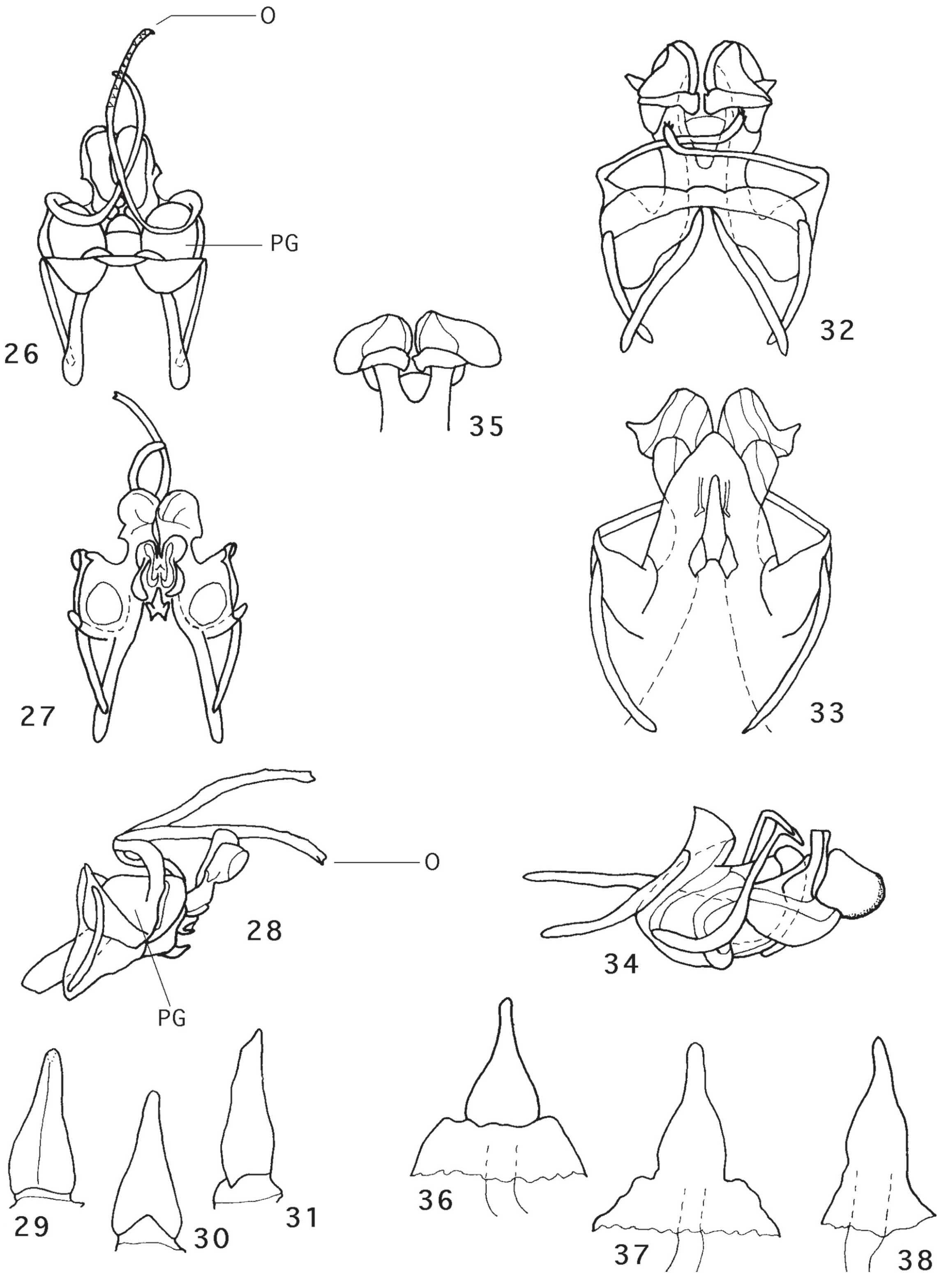
In several occasions I have observed females that had already copulated (*i.e.,* plugged females) responding to courtship. They touched the male body with antenna, palps and fore tarsi; examined the tergal glands on the dorsum of his abdomen with palps and mounted him, assuming copulatory position, but in no case they were able to externalize the copulatory papilla so as to accomplish copulation. Sometimes those females showed an aggressive-like behavior, biting the male on his tegmina, thorax or dorsum of the abdomen. Such behavior was never observed in virgin females.

An obvious outcome of the monogamous mating system of *Aracamby* females is that there is no sperm competition for ova inside their genital tract. In fact, testicle size is very small throughout the genus when compared to those of other phalangopsid genera of similar body size. I have also noticed that, on slide preparations of testicular material for chromosome analysis, the number of cells undergoing divisions per slide is noticeable smaller than in preparations with equivalent amount of material from other phalangopsids.

Aracamby males seem to contribute with few resources, perhaps only with sperm for reproduction; they do not feed females during courtship and copula or show any other type of paternal investment; females also do not guard their eggs once they are laid in soil or take care of brood. But cost of egg production is normally much higher than that of sperm production,



FIGURES 14-25: Dorsal, ventral and lateral views, respectively, of the phallic complex and copulatory papilla of *Vanzoliniella sambophila* and of a species belonging to an undescribed genus. **14, 15, 16,** phallic complex of *V. sambophila;* **17, 18, 19,** copulatory papilla of *V. sambophila;* **20, 21, 22,** phallic complex of "undescribed genus and species"; **23, 24, 25,** copulatory papilla of same. Conventions: PG = phallic gland; O = outer opening of phalic gland. Figures not to scale.



FIGURES 26-38: Dorsal, ventral and lateral views, respectively, of the phallic complex and copulatory papilla of *Izecksohniella aimore* and *Cacruzia bahiana*. **26, 27, 28,** phallic complex of *I. aimore;* **29, 30, 31,** copulatory papilla of *I. aimore;* **32, 33, 34,** phallic complex of *C. bahiana;* **35,** dorso-distal portion of pseudepiphallus of another specimen showing completely swollen pseudepiphallic parameres (compare with Fig. 32); **36, 37, 38,** copulatory papilla of *C. bahiana.* Conventions: PG = phallic gland; O = outer opening of phallic. Figures not to scale.

and since *Aracamby* males produce a small amount of sperm as a result of lack of sperm competition due to female monogamic mating system, there is a disparity regarding relative parental investment, which lead us to the notion of sexual conflict on reproduction (Parker, 1979; Alexander *et al.,* 1997). By being "armed rapists", vaginal blockers, producers of small sperm quantity, and avaricious (investing so little in reproduction), males are noticeably winning the evolutionary battle of sexes. In fact, their ability to permanently plug their mate's genitalia after first copulation is the factor that induces the females' monogamic mating system. Along several years I placed hundreds of pairs composed by one male and one non-virgin female for laboratory observations shortly after returning from collecting trips; although courtship behavior occurred very frequently (and female responses to it somewhat less frequent), copulation never occurred.

Species of other related genera with phallic complexes rather similar to those of *Aracamby* do not secrete mating plugs (personal observations; see below), although agglutinated material from the phallic glands can sometimes be seen protruding from the opening of the pseudepiphallic arms in specimens preserved in alcohol.

Males of *Vanzoliniella sambophila* Mello & Reis, 1994 (Figs. 14 to 19) bear well developed phallic glands but the membranous base of copulatory papilla shows no specialization like a bellows-shaped configuration. The same is true for two species of an undescribed genus (one of them represented in Figs. 20 to 25).

In *Izecksohniella aymore* Mello, 1992 (**Figs. 26 to 31**) phallic glands are well developed, the pseudepiphallic arms are very long and tubular but not bifurcate distally and its orifice is apical; the pseudepiphallic parameres are hollow and swollen, perhaps also glandular or, more likely, functioning as inflatable claspers that operate by means of hydraulic pressure to hold the female's copulatory papilla during sperm transfer.

The phallic glands of *Cacruzia bahiana* Mello, 1992 (Figs. 32 to 38) are vestigial, the pseudepiphallic arms are long and tubular but without an orifice (this entire complex of structures seems to have lost its initial function); the pseudepiphallic parameres are also hollow as in *Izecksohniella aymore* and, in some alcohol-preserved specimens, they appear more inflated than in others.

Several females captured in the field as egg-laying adults belonging to all of the just-mentioned species were dissected and a mating plug was never found on their genitalia. Differently from *Aracamby,* in which the pseudepiphallic arms are lateral, straight and kept hidden in upward position in non-mating males, the pseudepiphallic arms in all those other species are comparatively longer and bent dorsally over the main body of the phallus in a way that that the tip of each structure of the pair protrudes outside the male body, but on the opposite side of the origin of the arm. From all those cases, only in *Vanzoliniella sambophila* the tip of the epiphallic arms is bifid like in *Aracamby* species but, in three copulations which occurred in the laboratory, I observed that there is no contact of the digits or of the opening of the arms with the base of the female's copulatory papilla. No copulation was observed in the other cases.

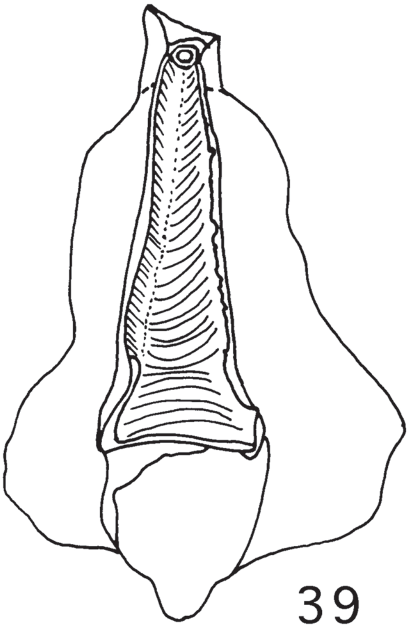
Since phallic glands in those genera do not secrete structural mating plugs, what could be their function(s) ? This question waits an answer, but perhaps some reasonable hypothesis should include: 1- production of antiaphrodisiacs that will act either upon female, by making her unwilling to re-mate, or upon other males, by making copulated female unattractive to them; 2- elaboration of some kind of stimulatory substance that acts during mating [see Eberhard's (1991, 1994) concept of copulatory courtship]; 3- generation of some kind of nutritional benefit that would increase female fecundity or the weight of her eggs; 4- synthesis of chemicals that could physically alter the functionality of female genitalia in a similar way to the insemination reaction exhibited by certain *Drosophila* species; 5- production of pheromones that will attract females from a distance or function during courtship. There is also the possibility that the phallic glands still present in those species lost their original functions but are still present as evolutionary relicts.

Desutter-Grandcolas (1995) mentions the occurrence of genitalic glands in males of several other genera of neotropical phalangopsids; their functions also remain unknown.

The case of *Eimanacris* sp (Phalangopsidae, Luzarinae)

Eidmanacris Chopard, 1956 is currently an assemblage of species known from Brazil, Bolivia and Paraguay (Desutter-Grandcolas, 1995). Males of all but two described species (*E. tridentata* and *E. fusca* Desutter-Grandcolas, 1995) bear metanotal glands, while phallic glands do not occur in the genus.

The spermatophores of several described and undescribed species that I have examined bear a large grayish or white ampulla and a rather thin neck which is occasionally longer than the ampulla. The neck is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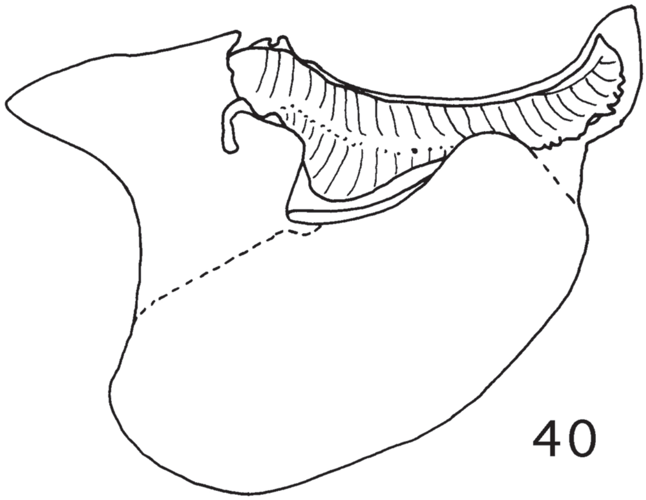
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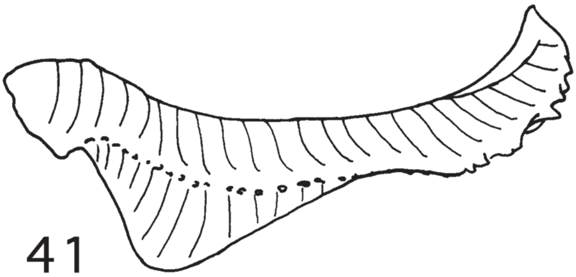
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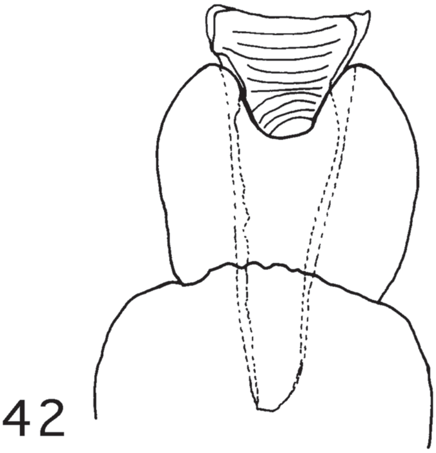
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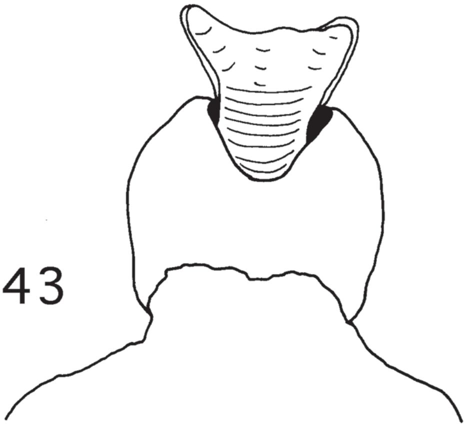
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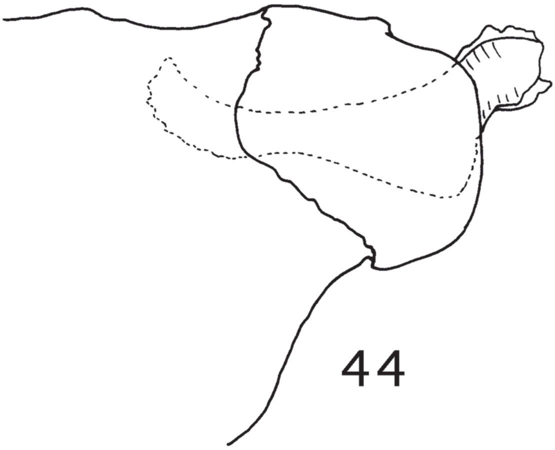
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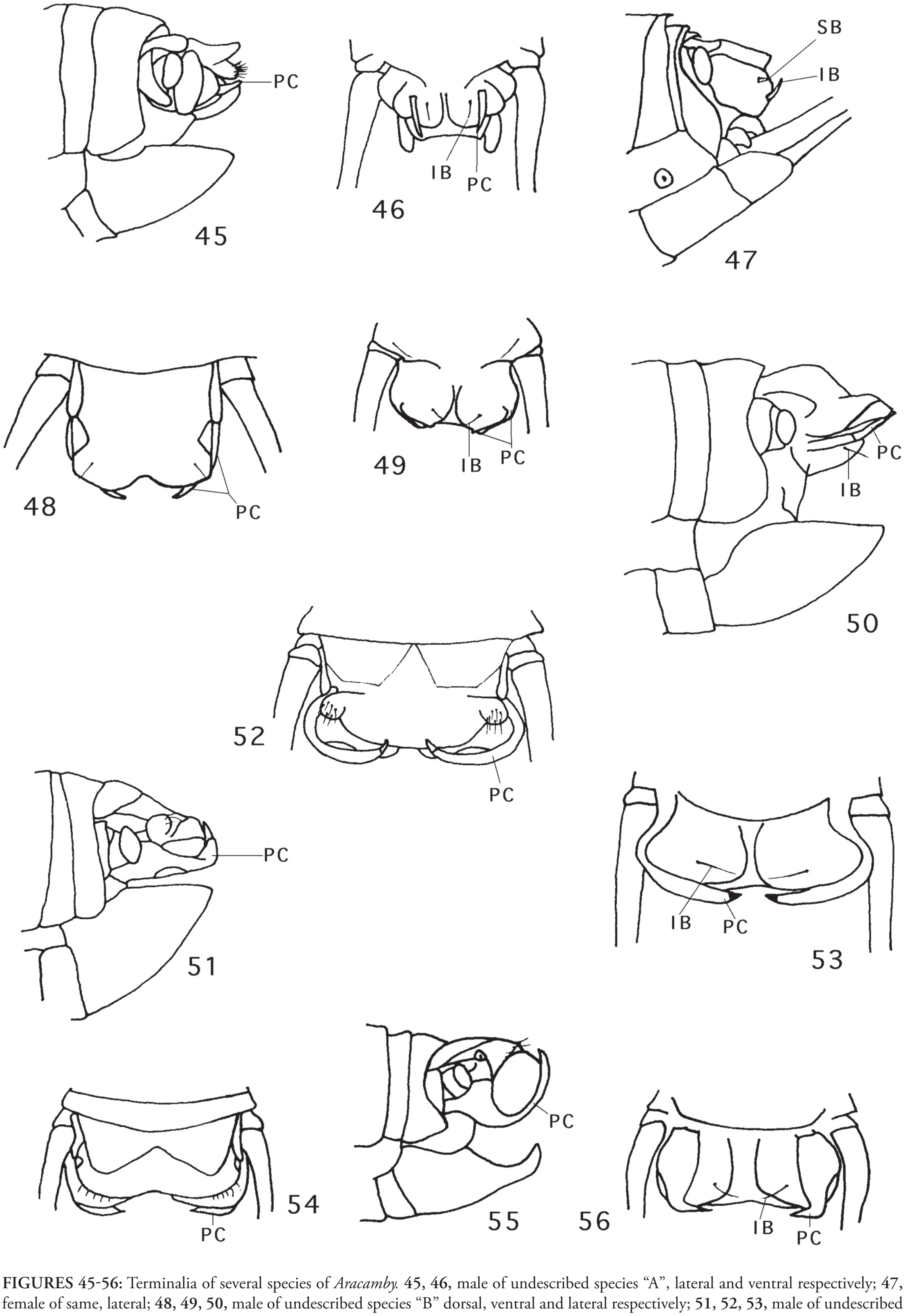
FIGURES 39-44: 39, 40, spermatophore of *Eidmanacris* sp. in dorsal and ventral views, showing the specialized neck which functions as a mating plug; **41,** detailed side view of spermatophore neck; **42, 43, 44,** dorsal, lateral and ventral views of copulatory papilla of same species showing the mating plug inserted in its orifice. Figures not to scale.



FIGURES 45-56: Terminalia of several species of *Aracamby.* **45, 46,** male of undescribed species "A", lateral and ventral respectively; **47,** female of same, lateral; **48, 49, 50,** male of undescribed species "B" dorsal, ventral and lateral respectively; **51, 52, 53,** male of undescribed species "C", lateral, dorsal and ventral respectively; **54, 55, 56,** male of *Aracamby balneatorius* Mello, 1992, dorsal, lateral and ventral respectively. Conventions: IB = inferior bristle of paraproct; SB = superior bristle of paraproct; PC = paraproctal clasper. Figures not to scale.

always devoid of an attachment plate (terminology after Alexander & Otte, 1967).

The copulatory papilla is generally small, with an inconspicuous outer opening, but Desutter-Grandcolas (1995) mentions the occurrence of larger papillas in *E. marmorata* and *E. paramarmorata.* She also refers to the spermatheca duct of those species as being enlarged and atrium-shaped.

A still undescribed species from south Brazil that lacks metanotal glands produces a spermatophore with a strongly modified neck, shaped as a large and highly sclerotized structure (**Figs. 39 to 41**). The copulatory papilla in that species is also very large for the genus, as well as its orifice. In females that have already mated, the papilla remains plugged by the spermatophore`s neck for the rest of their lives (Figs. 42 to 44). Two adult females captured in the field were kept in captivity apart from males until they died, 45 and 76 days after being collected; both had their copulatory papilla blocked by the mating plug upon death. A third female, captured as a pre-adult nymph and kept isolated in a terrarium, was allowed to copulate 15 days after moulting; she died 79 days after copulation and the mating plug was still attached to her. During her adult life she laid eggs and was experimentally placed together with two males several times, one of them being the one she had copulated with. Courtship behavior occurred in all observations and she responded positively to it, climbing on top of the males and trying to copulate without accomplishing it.

In the present case, the copulatory plug is a portion of the spermatophore- its large and specialized neck- that detaches itself from the ampullae to remain blocking the orifice of the female´s copulatory papilla after sperm transfer. In *Adenophallusia* and *Aracamby,* in which mating plugs are derived from male secretions, the glands involved in plug formation are specialized phallic glands, not accessory glands, which, as stated by Leopold (1976), are the most frequent type of glands responsible for plug production in insects and other animals.

RESUMO

*Este trabalho descreve os primeiros três casos em que grilos machos monopolizam suas fêmeas através de plugues de acasalamento. A origem dessas estruturas varia entre os casos (*i.e., *não há homologia entre as mesmas). A monogamia feminina é assegurada pela presença permanente do plugue de acasalamento aderido a sua genitália após a primeira cópula, enquanto que os machos são potencialmente poligâmicos. Descrevem-se ainda a presença de clásper adicional e a ocorrência de cópulas forçadas.*

Palavras-chave: Grilos, Grylloidea, Cópula forçada, Estupro, Garantia de paternidade, Monopolização da fêmea, Plugue de acasalamento, Sistema de acasalamento.

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