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Inverted Copulation

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Without Abstract

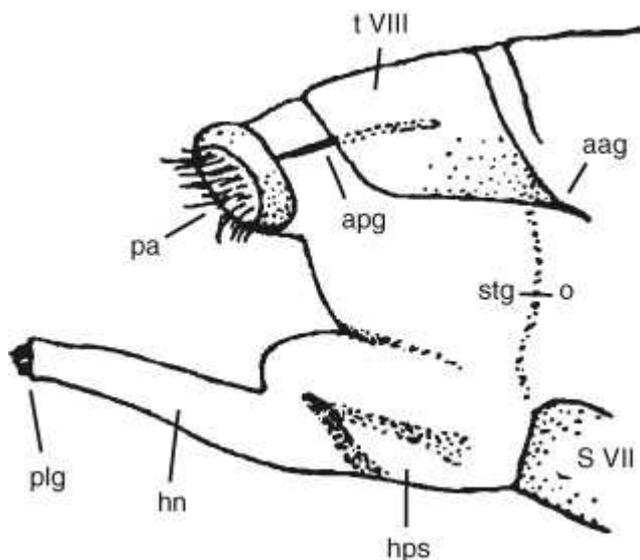
There are extremely rare cases among insects, and possibly among some mites, where females possess a specialized extensible intromittent organ, that collects the male's spermatophore or the male sperm. The cases are known among certain Lepidoptera: Nymphalidae (*Argynnis*) and Lycaenidae (*Plebejus*) and Coleoptera: Scirtidae or Helodidae (*Cyphon*). It could exist among certain Acari: Canestriniidae, but the fact has to be confirmed. However, the whole concept needs further investigation, and in certain cases (Lycaenidae) other interpretations are to be considered. In all cases, anyhow, the female lightly penetrates the male. In some cases, the female seems to capture and aspirate the spermatophore or the semen and actively collect it from the male genitalia. The extensive organs of certain Lepidoptera families seem to have evolved independently and convergently and are divergent in shape if not in function. It is evident that a reevaluation of the structure and of its functioning is necessary.

Lepidoptera

Female erection exists only among two families of Lepidoptera, Nymphalidae and Lycaenidae, and only among some genera and species. The only problem is, what is the function of those erections? The structures seem convergent, but completely different anatomically. It is also evident that those organs are extremely fragile and have escaped the attention of most of the authors. The organs are almost transparent. We can see this strange "inverted copulation" only if we capture a male and a female in copula, if the couple does not separate in the net or in the cyanide killing jar, and if we can clear the preparation for the microscope.

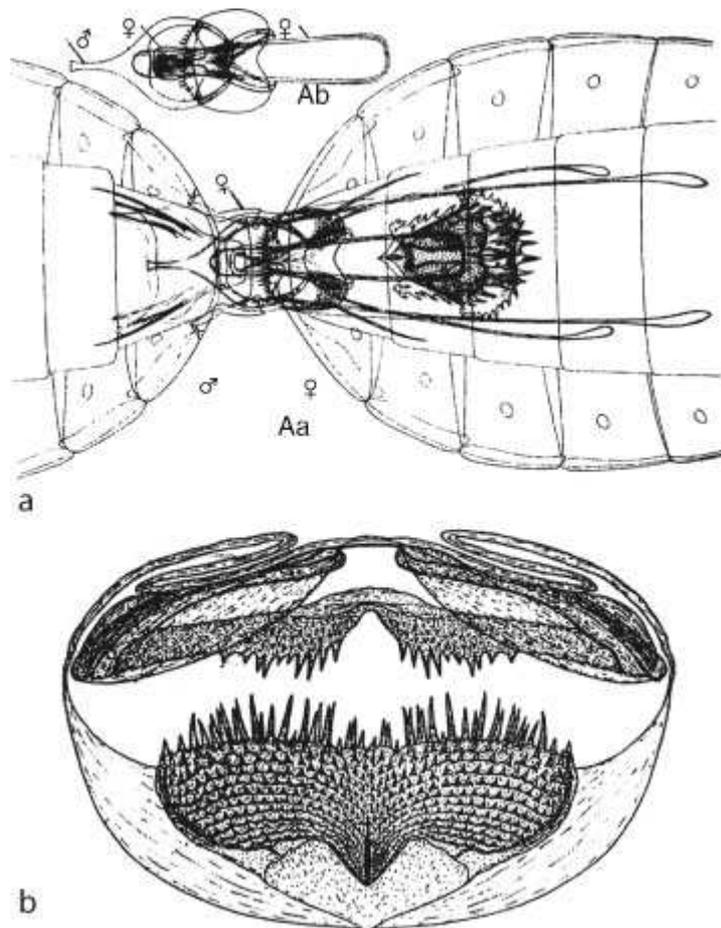
In *Argynnis paphia* (L.) (Nymphalidae), André Bayard was lucky enough to obtain a slide with both individuals, male and female, remaining in copula. This coupling, so easy to obtain in rearing cages with Heterocera, was once believed to be impossible to get in captivity for Rhopalocera. Actually, we can get it easily in mosquitoes, bees, and butterflies by manipulating the male and bringing the male abdomen into contact with the female extremity. Among many insects, artificial mating is currently used, and cutting the male head facilitates the operation.

After removal of the left valve in an *Argynnis paphia* male, Bayard showed the strange mating procedures of that butterfly. In the male, the penis seems somewhat modified. The penis here is a massive asymmetric organ, laterally compressed and partly covered with strong spines set sideways. In the female, there exists an enigmatic organ, partly membranous, partly sclerotized, looking when at rest like an accordion in a rosette. It has been called a “clitoris,” a “horn of plenty,” and a “cornucopia.” Mating among these insects seems to be a reversing of the normal relationships between male and female parts. The female enters in erection. In prolongation of the ostium bursae, this cornucopia is transformed into vulvar prolapsus. The inferior grooves of that organ give it a certain rigidity which transforms it into an accordion. This organ pumps the liquid semen from the spermatophore. This prolapsus, when resting, is folded upon itself but enters into erection when acting. In the male, the penis does not seem to move, but the male uncus folds down at its basal part and its terminal hook and crest catch the female prolapsus to direct the opening towards the ductus ejaculatorius. The adjustment of this female organ, extending toward the male during mating, is done through the hooks which grab the cornucopia. Thus, the female penetrates the male in a system which can look extravagant but works perfectly. The origin of the system is difficult to understand due to the fact that the evolution of the structure is not known among the genus *Argynnis* and relatives (Fig. 35).



Inverted Copulation, Figure 35 Evaginated terminalia of a plebejine (Lepidoptera: Lycaenidae). t VIII, eighth tergite; aag, left anterior apophyse; apg, left posterior apophyse; pa, anal papilla; stg, stigmate; s VII, seventh sternite; hps, hypostema; hn, henia; plg, genital plate (after Séguy, 1967.).

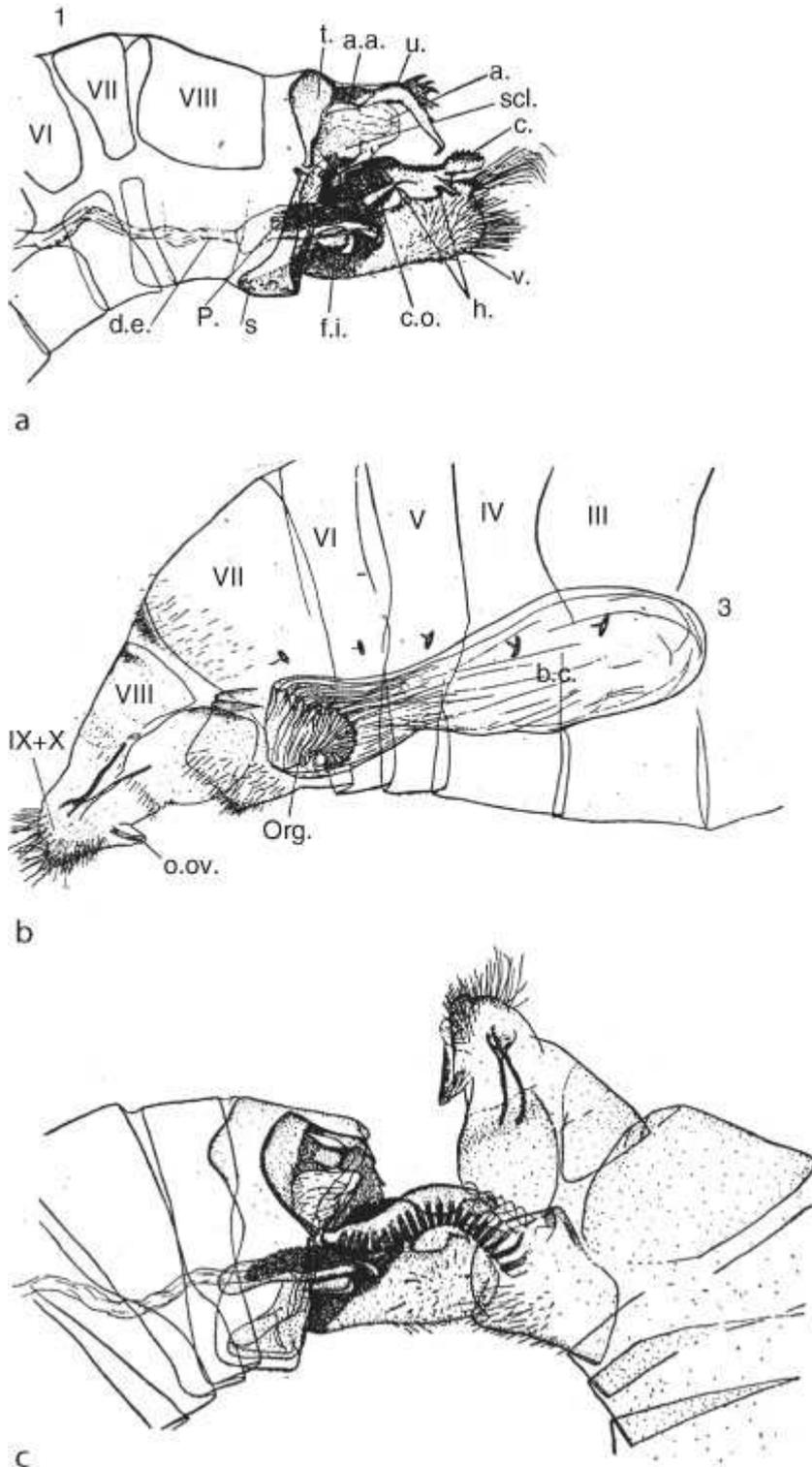
Bayard describes analogous structures among other species of European *Argynnis*, including *A. pandora* (Denis and Schiffermüller) and possibly similar facts exist among many or all (including Asian) species of the genus *Argynnis*. The interpretation of the bursa copulatrix remains to be restudied. Artificial mating must be conducted among other species of the genus to study the evolution of this strange morphology (Fig. 36).



Inverted Copulation, Figure 36 (a) Mating in *Cyphon kongsbergensis* (Scirtidae or Helodidae). The prehensor is in part inside the male abdomen (Ab). Diagram of the male-female interrelationships during mating. (b) Prehensor acting like a trap in *Cyphon coarctatus* Paykull (female) (after Nyholm, 1969.).

Chapman described what seems to be a similar female erection among the *Plebejus* Klug (Lycaenidae, Polyommataini, Plebejini). According to the author, this phenomenon seems limited to the Plebejini. It is really an erection made with organs different from that of *Argynnis*. The female prolapsus is made of two parts: hypostema and henia. A henia is a distal, membranous, tubular part of an erectile everting apparatus by means of which ostium bursae can be extruded to contact the male in copula. An hypostema is the proximal sclerotized part of an erectile everting apparatus. Chapman gives his explanation without showing an illustration of the mating between the sexes. Several hooks maintain a contact of both female and male organs during the mating. Another interpretation of the evaginated henia would be that of a titillator organ and not a sperm pumping organ. The only way to settle this matter is to see a slide showing the sexes in copula. What is surprising is that in *A. artaxerces*, as in other species, the henia seems terminated by an enigmatic sclerotized genital plate. However, certainly this organ penetrates the male parts and it is difficult to see a titillator in this structure.

Probably, female erection exists elsewhere and has not yet be found. So complex and diverse are these structures that slides are necessary to visualize correctly the matching of the sexes in nature (Fig. 37).



Inverted Copulation, Figure 37 (a) Genital armature of *Argynnis paphia* (Linné), VI, VII, VIII, sixth, seventh and eighth abdominal segment; t, tegumen; a.a., angular appendix; u, uncus; a, anus; scl, sclerotized rackets; C, cercina; v, right valve, the left valve being removed; h, harpe; c.o., crista obliqua; f.i., inferior fultura; s, saccus; p, penis; d.e., ductus ejaculatorius. (b) Genital armature of *Argynnis paphia* (Linné) +o, III to VIII, third to eighth abdominal segment; IX + X, last visible segment of the abdomen with its external apophyses; o.ov., oostrium oviductus; org., cornucopia; b.c., bursa copulatrix. (c) Diagram of the mating of *A. paphia* (Linné), according to a slide (after Bayard, 1945.).

Coleoptera

Among Scirtidae (Helodidae or Cyphonidae) with aquatic larvae, females possess a complex mating apparatus with a kind of forceps at the extremity, which acts as a jaw to receive the spermatophore from the male. This odd organ is found among certain species of the genera *Cyphon*, *Hydrocyphon* and related. However, it remains an exception.

Among Helodidae (Scirtidae), the male genital parts do not seem to penetrate much into the female parts. There exists, at the extremity of the female genitalia, an apparatus, the prehensor, made of two multidentate jaws, evoking a shark mouth. Nyholm distinguishes at the base of the female genital chamber two kinds of prehensors: the bimellater and the konfuser. This prehensor seems to seize the extremity of the spermatophore and to pull it into the vagina, then softening it and liberating the spermatozoa. Does the female organ really penetrate the male? It remains strongly probable. Although Nyholm's drawings are really difficult to interpret, others also have noted that because of the undifferentiated structure of the internal sac, mating was abnormal in the genus *Cyphon*, and that it remained possible that the female ovipositor was penetrating the male in the large median orifice.

Conclusion

More research is needed to clarify the previous examples where the female seems to penetrate the male during the mating to pump the spermatozoa. Other interpretations are possible, but this is the explanation suggested by most entomologists. Moths are easy to mate in the laboratory, but for butterflies artificial copulation is needed. Such observations are necessary among *Argynnis* and *Plebejini* and probably among other butterflies to interpret correctly this aberrant behavior and the exact mechanism used. At least, there are very peculiar anatomical designs. Mite behavior has also to be reexamined to see if such interpretations are sometimes possible.

References

- Bayard A (1944) Observations sur l' accouplement de *Dryas paphia* (L.). Bulletin Société Entomologique de France 49:92–94
- Chapman Th (1916) On the pairing of the plebeid blue butterflies. Trans Entomol Soc Lond 64:156–179
- Jolivet P (1999) "Women's Lib." chez les insectes ou quand le sexe faible devient le sexe fort (Col. Scirtidae, Lep. Nymphalidae & Lycaenidae). L' Entomologiste, Paris 55:1037–1122
- Klausnitzer B (1983) Beetles. Exeter Books, New York, NY, 214 pp
- Nyholm T (1972) Zur Morphologie und Funktion des Helodiden-Aedaeagus (Col.) Entomologia Scandanavica 3:81–119