Encyclopedia of Entomology
Springer Science+Business Media B.V. 2008
10.1007/978-1-4020-6359-6_1455
John L. Capinera

## Hypertely

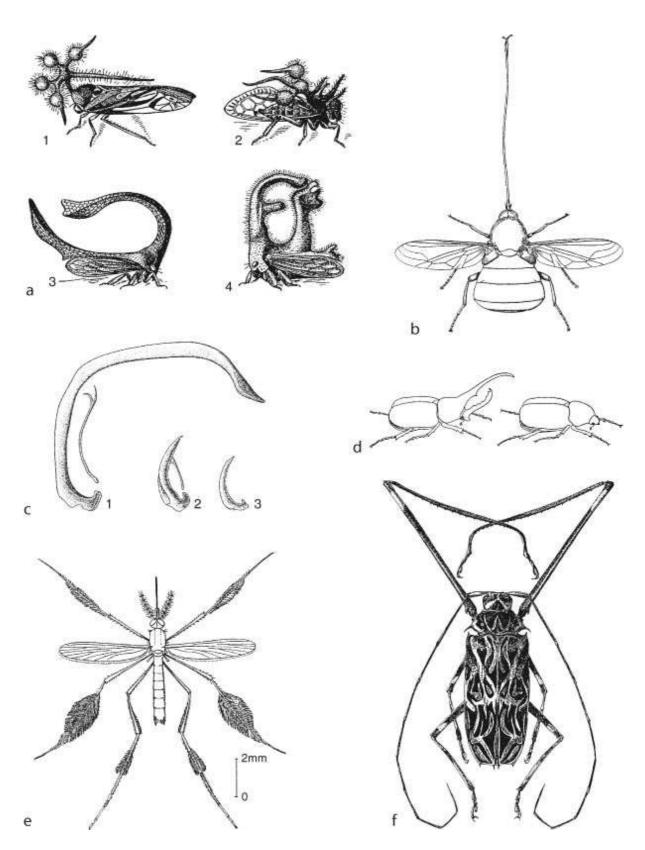
## Pierre Jolivet<sup>2</sup>

(2) Paris, France

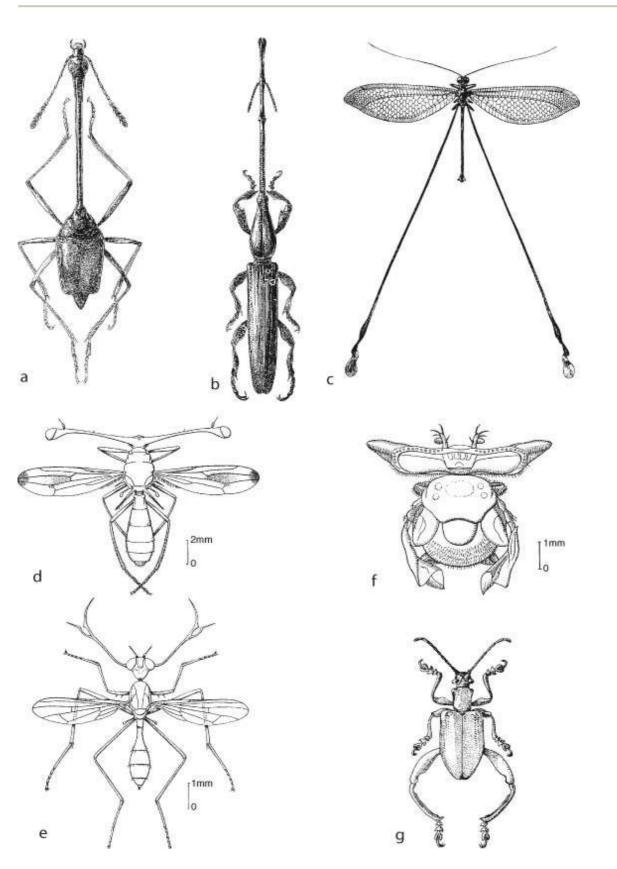
## Without Abstract

The concept of hypertely, a non-Darwinian concept, has been mainly developed by Lucien Cuénot and René Jeannel in France, though originally advanced by certain stubborn lamarckists of the middle of the last century. It can be defined as an excessive development of certain organs, in size and complexity, mostly among males, and was attributed to orthogenesis. The theory of orthogenesis was an alternative to Darwinian natural selection, and at one time found support in the USA and Germany, especially among palaeontologists and developmental biologists. Orthogenesis can be defined as evolutionary change proceeding consistently in one direction, resulting from a tendency to accumulate similar mutations in successive generations rather than by natural selection. Thus, the purported result of hypertely was the development of certain organs (horns, tusks, legs, antlers, etc.) up to the extent of a certain monstrosity.

Such a concept is very much debatable and may be explained as the result of a normal Darwinian selection and just part of natural biodiversity. Such organs are often useful or at least harmless, and the best proof of it is that the animals endowed with them survive, multiply and do not seem to be ill at ease with them. Beetle horns help the males when fighting over access to females, long legs of Sagrines help them, when mating, and also to clutch on the stems, thoracic extensions among the Membracidae or certain Curculionidae can help in camouflage and, in all cases, the insects survive well and reproduce. The extreme flattening of the Mormolyce (Carabidae) in Indonesia allow them to hide under loose pieces of bark during the day, and similarly the aberrant tenebrionid Cossyphus can easily slide under the bark of Acacia trees in the Sudan. Hololepta plana (Histeridae) lives under the loose bark of felled trees; it is so flattened that its height is only a small fraction of its width. Of course many beetles are flattened, but this is an adaptation to their habitat. Mimicry and camouflage are not hypertely, and may provide protection for the animal against his predators. It has been demonstrated recently that pronotal horns help some beetles during ecdysis, at least among Onthophagus (Scarabaeidae), which means that allometry or differential growing is not just a meaningless developmental process. An apparently non-adaptive organ is often an organ not functionally well understood, or at least an organ that was adaptive before some change occurred in the environment (Figs.  $\underline{61}$  and  $\underline{62}$ ).



**Hypertely, Figure 61** Some cases of hypertely (**a**) Hemiptera: Membracidae. 1: *Bocydium*; 2: *Cyphonia;* 3 and 4: *Spongophorus*. Tropical America; (**b**) *Lasia nigritarsis* Blanchard (Diptera: Oncididae). Male. Tropical America; (**c**) Aedeagus of various Monoxia (Coleoptera: Chrysomelidae: Galerucinae). USA. 1: *Monoxia puncticollis* Say; 2: *Monoxia debilis* LeConte; 3: *Monoxia sordida* LeConte; (**d**) *Dynastes hercules* (L.) (Coleoptera: Scarabeidae: Dynastinae). Male and female. Tropical America; (**e**) *Sebethes longipes* Fabricius (Diptera: Culicidae). Male. Tropical America; (**f**) *Acrocinus longimanus* L. (Coleoptera: Cerambycidae). French Guyana (c, after Jolivet, 1957–59; f,



after Grassé, 1949; a, b, e, after Grassé, 1951; d, after Paulian, 1935).

Hypertely, Figure 62 Some additional cases of hypertely (a) *Diatelium* sp. (Coleoptera: Scaphididae).

Male; (b) *Rhyticephalus brevicornis* Chevrolat (Coleoptera: Brentidae); (c) *Nemopistha imperatrix* Westwood (Planipennes). Equatorial Africa; (d) *Diopsis tenuipes* Westwood (Diptera: Diopsidae). Tropical Africa; (e) *Phytalmia cervicornis* Gerstacker (Diptera:Phytalmiidae). Male. New Guinea; (f) *Asyntona tetyroides* Walker (Diptera: Platystomidae). Malaysia; (g) *Sagra femorata* Drury (Coleoptera: Chrysomelidae: Sagrinae). Thailand (figs. a and b, after Paulian, 1988; c, after Cuénot and Tétry, 1951; d, e, f, after Grassé, 1951; g, after Jolivet and Verma, 2002).

Hypertely can be defined as "beyond the bounds of the useful." Some dictionaries give the following definition: "excessive development of certain organs, in size and complexity, among certain species, mostly among males." The horns of the Scarabaeidae and the mandibles of the Lucanidae might sometimes appear excessive, but they help in defense, and during the fight among males the winner is often the most well equipped with such a horn. The thoracic prolongations of the Membracidae can seem a bit odd, but they serve as camouflage. The long thoracic horn of the Cranopoeus (Curculionidae) mimics the seeds of the host tree. The excessive development of certain organs (antennae, legs) of cavernicolous (cave-dwelling) insects compensate for the loss of eyes. The pseudophysogastry (artificial swelling of the abdomen, not connected with ovary development) of some cavernicolous insects is more difficult to interpret, but it increases the isolation of the abdomen against cold or humidity. Pseudophysogastry is known also among termiticolous (living in association with termites) insects, also living in a close and isolated world. The long rostrum of the Brentidae help in digging their tunnels. The enormous legs of certain weevils such as neotropical Cerambycidae (Acrocinus), Malagasy eumolpines (Arsoa; Chrysomelidae) and the big femora of the sagrines (Chrysomelidae), are used for holding on to the stems or mating. The sternal horn of certain Doryphora (Chrysomelidae) is used as a weapon in fighting between males. It is also evident that sensorial dimples on the abdomen of many beetles have their usefulness in detection of humidity or mates. Examples are many of those organs which appear excessively developed, but they are not functionally meaningless.

For Darwinists, the concept of hypertely is a mistake of interpretation, because although the character may look functionless, it is not without its functional significance. The phenomenon seems coherent and related to some function such as sexual selection, mimicry, self defense, clutching, lodging, etc. Some French zoologists such as Jeannel, Cuénot, and Grassé could, in the past, see hypertely as the result of extreme orthogenesis. Cases of hypertely were suggested to include the bent tusks of the mammoths, the bent canines of the babirussa, the teeth of the *Machairodus* or *Smilodon*, the antlers of the Irish deer, the horns of the Tithanotherians, the sword of the saw fish (*Pristis*) and the swordfish (*Xiphias*), the long spines of certain urchins (Cidarids), the dermic armor of the Stegosaurians, the complex septa of certain Ammonites, the thoracic expansions of the Membracidae, the horns of the Scarabeids, the mandibles of the Lucanids, the foliaceous expansions of the legs of certain Hemiptera or Diptera, the reduced hind wings of the Nemopteridae, and even the long legs of the Tipulidae. However, these seemingly unusual structures can be explained. For example, the long legs of those Diptera prevent them from getting captured on spider webs when they dance rhythmically, and the mandibles of the Lucanidae and the horns of the Scarabeidae help them when fighting (and those organs have some other functions too, recently decrypted). Some beetles have a very elongated body, but this form is useful for digging and living in tunnels. Others, as the Cychrus (Carabidae) have the head and pronotum elongated and narrow, but this is an adaptation used to penetrate snail shells. The long proboscis of certain Diptera or moths are needed to penetrate some deep flowers. All those modifications of the morphology seem to be functional specializations, not meaningless exaggerations.

All modern authors see in the so-called hypertely of the carabeid horns a case of allometry,

sometimes under the influence of hormones or food. Individuals are able to express different morphologies in response to environmental conditions during their development. Recently, it was suggested that pronotal horns among *Onthophagus* are crucial during ecdysis of the larval head capsule during the larval-to-pupal molt. This function in molting seem unrelated with fighting and defense, but all criteria are positive and useful for the insect.

Additional examples of exaggeration include organs used in reproduction; often, the male genitalia of certain beetles are very big, while other species of the same genus have a normal aedeagus. That is the case among the galerucines of the genus *Monoxia* (Chrysomelidae), where only one species, *Monoxia puncticollis*, has an enormous intromittent organ, but its body size is not much bigger than the body of other species with a normal aedeagus. The mating is done and successful with the female of *M. puncticollis*, which probably has some kind of adaptation. There is also the case of *Hydrochus interruptus* (Hydrophylidae), an aquatic beetle, which is provided with so complex an aedeagus that some entomologists have doubted its real sexual function. Very often, the beetles or other insects are gifted with so complicated aedeagi that one wonders how they work. But such aedeagi function, and the insect reproduces normally. Also, sometimes the spermatozoa are enormous. This is the case of many Alticinae (Chrysomelidae) or the *Drosophila* flies (Drosophilidae), for instance. However, it appears that, in the case of *Drosophila* which have developed those long spermatozoa have an increased chance to fertilize the eggs successfully.

As far as we can see, the concept of hypertely is obsolete. All those so-called exaggerated morphologies have a function and the animals survive, multiply and they do not seem to suffer from those "monstrosities." As a rule, handicapped specimens are eliminated and only the fit ones survive. A non-adaptative organ is an organ not understood. So-called hypertelic insects are just part of the biodiversity, having evolved through selection.

## References

Carayon J (1977) Insémination extra-génitale traumatique. Traité de Zoologie, Masson publ., Paris 8 (5A):351–390

Cuénot L, Tétry A (1951) L'Evolution Biologique. Masson, Paris, 592 pp

Eberhard DJ (1985) Sexual selection and animal genitalia. Harvard University Press, Cambridge, MA, 244 pp

Emlen DJ, Nijhout HF (2000) The development and evolution of exaggerated morphologies in insects. Ann Rev Entomol 45:661–708

ChemPort

Gould SJ (1977) Ever since Darwin. Reflexions in Natural History. Penguin Books, Harmondsworth, England, 285 pp

Grassé PP (1949) (1951) Traité de Zoologie. Anatomie, Systématique, Biologie. Insectes. IX & X (1 & 1). Masson, Paris, 1117 + 1949 pp

Jolivet P (2004) Inverted copulation. In: Capinera J (ed) Encyclopedia of entomology, vol 2. Kluwer Academic Publishers, Dordrecht, The Netherlands, pp 1208–1212

Moczek AP, Cruickshank TE, Shelby A (2006) When ontogeny reveals what phylogeny hides: gain and loss of horns during development and evolution of horned beetles. Evolution 60:2329–2341 PubMed

Moczek AP, Emlen DJ (2000) Male horn dimorphism in the scarab beetle, *Onthophagus taurus*: do alternative reproductive tactics favour alternative phenotypes? Anim Behav 59:459–466 **PubMed** 

Paulian R (1935) Le polymorphisme des mâles de Coléoptères. Hermann, Paris, 35 pp

Virkki N, Bruck T (1994) Unusually large sperm cells in Alticinae: their formation and transportation in male genitalia system and their evolution. In: Jolivet P, Cox ML, Petitpierre E (eds) Novel aspects of the biology of Chrysomelidae, Kluwer Academic Publishers, Dordrecht, The Netherlands, pp 371–381