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THE MORPHOLOGY OF THE MALE TERMINALIA OF BEETLES BELONGING TO THE GENUS PRIACMA (CUPESIDÆ),

by J. Gordon Edwards (San Jose, California).

The phylogenetic position of family *Cupesidæ* (*Cupedidæ* or *Cupidæ* of some authors) has been the subject of much controversy in recent years. For this reason the author was especially pleased when he collected a series of forty males of the rare species *Priacma serrata* (Leconte) in Glacier National Park, Montana (U. S. A.) in 1950. Nearly all of these specimens have been carefully dissected so that a thorough study of the genital appendages could be made. These appendages, as well as the ninth abdominal segment (genital segment), bear very little resemblance to corresponding parts of members of other species which have been placed in the same family. In *Priacma* these structures are so peculiar and so different from those of any other beetle dissected previously that it is believed that illustrations and descriptions of them will interest many entomologists.

A comparative study of the morphology of male terminalia indicates that the family *Cupesidæ* must be decidedly diphyletic. The phylogenetic position of *Cupes* and *Priacma* in relationship to other Coleoptera is still debatable, although recent work by Jeannel and Paulian (1944) and by Monros and Monros (1952) has offered some ideas concerning their inclusion, with *Micromalthus*, in suborder *Archostemata*. It seems possible that the forbears of this group branched from

the ancestral stock of Coleoptera long before the Adephaga and Polyphaga diverged. The knowledge of the nature of the structure of the abdomen and genitalic appendages of members of *Priacma* may prove valuable to coleopterists interested in phylogenetic relationships.

The abdomen of members of *Priacma serrata* (LECONTE) is nearly identical to that of members of genus *Cupes,* with only five visible abdominal sternites and eight tergites. Careful examination of dissected abdomens reveals a basal sternite which is nearly completely membranous except for a very slender, delicate, transverse anterior margin which is lightly sclerotized. The second sternite is very short and broad and is heavily sclerotized. This sternite bears a strong longitudinal median carina which is high and sharp, and separates the hind coxæ in repose. The third sternite is considerably longer than the second and is composed of a sunken proximal portion for partial reception of the femora in repose, and a less heavily sclerotized distal half. At the rear of the sunken area a prominent, sharp-pointed, median process arises, also separating the hind coxæ in repose. Sternites 4, 5, and 6 are nearly identical in size and shape, although they taper slightly posteriorly. Sternite 7 is elongate and relatively slender, with an acute but rounded apex. Sternite 8 is invaginated into the abdominal tip. It is almost membranous except near the apex and along each side, where it becomes rather heavily sclerotized. The lateral sclerotized portions extend forward and taper into thin, sclerotized bands which serve as pleurites and are firmly fused with the sides of the eighth tergite. The ninth sternite lies embraced within the eighth abdominal segment, invaginated into the abdominal tip and enveloping the phallic structures, in repose. Normally, only sternites 3, 4, 5, 6, and 7 are visible, because the eighth and ninth segments are retracted and the coxæ conceal most of the third sternite. All transverse sutures are distinct and complete.

The eight dorsal abdominal segments are all distinctly visible after the wings are removed or lifted up. The first abdominal tergite bears an extremely long, thin spiracle on each side, extending from the lateral membranous areas to about a third of the distance to the median line. The second tergite is not as broad as the first, and it bears a small, slightly oval spiracle on each side in the membrane near its outer front corner. (This spiracle is just about the same distance back along the

body as is the outer front edge of the second sternite.) Tergites 3, 4, 5, 6, and 7 are nearly equal in length but become increasingly narrow. A spiracle is borne in the membranous pleural area on either side of each tergite, just anterior of the middle of each sclerite. The eighth tergite is more slender than any other and is firmly connected to the eighth sternite by the narrow pleural sclerite, with no movable or visible sutures present. The eighth pair of spiracles are about the same size as those preceding them and are elevated on short stalks arising from the membrane just posterior to the narrow pleural band, an equal distance from the eighth tergite and sternite. Concealed within this eighth abdominal segment is the genital segment (segment 9), which is illustrated at the top of Figure 2 from dorsal, lateral, and ventral aspects. The anal opening vents near the tip of the proctiger, which is the lightly sclerotized dorsal posterior prolongation visible in Figure 2, drawing A.

The phallus in repose is embraced by the tubular genital segment, with only the tips of the parameres visible beyond the ninth sternite. An interesting condition exists here, with the parameres held in position against the concave inner surface of the ninth sternite by the complex armature on each side of that sternite near its tip. The manner in which the parameres are held in place by this armature, at least at times, is illustrated in Figure 1, B. Although it has not yet been positively verified, the author believes that the extrusion of the copulatory organs usually breaks off the circular and distal portions of this armature, which is very frgile and easily broken at the point indicated by the small arrow in Figure 2. One specimen was discovered which had the left armature thus broken, while the right paramere was resting between the convex curved part of the right armature and the blunt median terminal portion of the ninth sternite. Evidently the parameres are extended laterally to extricate them from this armature before being extruded, at least in some cases.

The phallus is on extremely bizarre organ in *Priacma* males. Basically, it consists of a median lobe and two lateral lobes (parameres), but each of these structures is complex and a discussion of their detailed appearance deserves inclusion here. The general appearance of the phallus of *Priacma serrata* (LECONTE) males may be ascertained by examining drawings D, E, and F of Figure 2. For greater clarity, an enlarged drawing has been included (Figure 1) with numbers affixed

to each prominent part. The median lobe (6) bears large, lightly sclerotized membranous lobes (8). This median lobe is attached to the phallobase by membranes which contain muscle fibres that function in extruding the median lobe prior to copulation. The external genital orifice is located about one-third the distance from the base of the median lobe, on the convex surface (visible only in the ventral view of Figure 2, drawing F). A membranous tube (the endophallus)

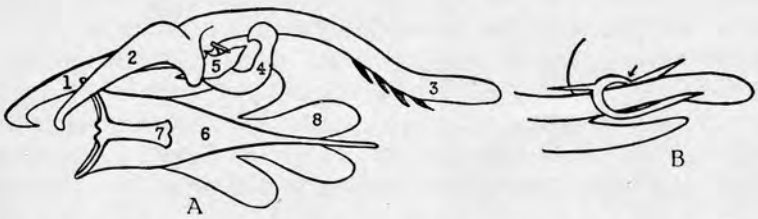

Fig. 1. — *Priacma serrata* (LECONTE): A. Median lobe and right lateral lobe of phallus, from dorsal aspect (left lateral lobe removed) (× 27). 1: volsellar plate; 2: parameral plate; 3: paramere; 4: « digitus volsellaris »; 5: « cuspis volsellaris »; 6: median lobe of ædeagus; 7: reflexed proximal portion of median lobe; 8: membranous lobe arising from median lobe of ædeagus. B. Lateral tip of ninth abdominal sternite, with left paramere in position of repose (× 53).

equipped with a row of slender spines is present within this genital orifice and must function as an eversible penis during coitus. The phallobase mentioned earlier is composed of a pair of dorsal apodemes (2), here called the parameral plates (probably the « pièces principales » of BOULANGÉ), and a pair of ventral apodemes (1), here called the volsellar plates (probably the « pièces complémentaires » of BOULANGÉ). Each of these slender plates extends forward from a broad sclerite best illustrated in drawing E of Figure 2. These broad lateral sclerites, together with the parameral and volsellar plates, are considered by the writer to be the equivalent of the *caulis,* or *phallobase,* discussed by SNODGRASS (1941) in his work on the male genital appendages of Hymenoptera. The long lateral arms (3) are termed the parameres. According to JEANNEL (1941) such structures probably serve as the sensory portion of the phallus. The shorter, sharply-curved structures (4) which arise ventrally, curve inward and

dorsally, then curve outward and anteriorly to terminate in a large, broad hook seem to correspond most closely with the *digitus volsellaris* of some Hymenoptera (the « lacinia » of THOMSON, 1872, and the « pièce en trébuchet » of BOULANGÉ, 1924). A small, movable, sclerotized structure (5) arises near

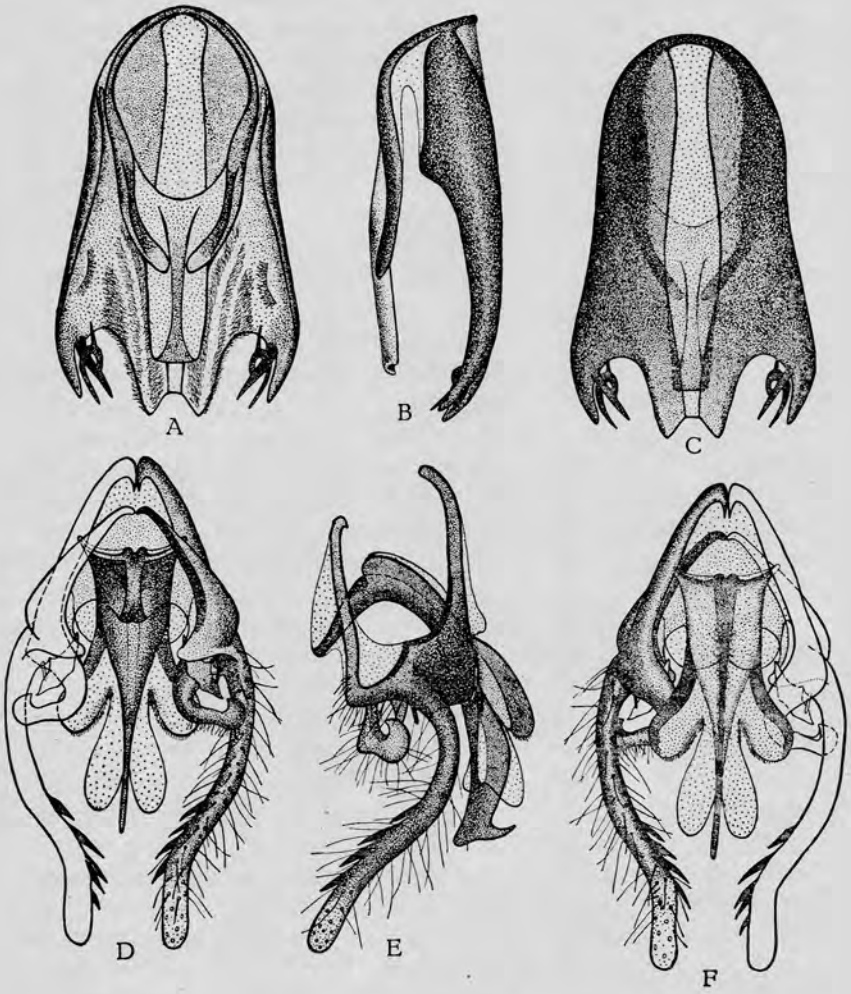

Fig. 2. — *Priacma serrata* (LECONTE): The ninth (genital) segment of a male (× 27). A: dorsal view. — B: lateral view. — C: ventral view. — The phallus, or ædeagus (× 27). D: dorsal view. — E: lateral view. — F: ventral view.

the base of each « digitus volsellaris ». It terminates anteriorly in a slender apophysis and posteriorly in a sharp, slightly-hooked point. This structure might well be homologous to the *cuspis volsellaris* of hymenopterous males (the « distivolsella » of PECK, 1937). Paired processes similar to the *digitus volsellaris* and *cuspis volsellaris* just mentioned were referred to by CRAMPTON (1919) as the « copulatory ossicles » of certain Hymenoptera. The structures discovered on *Priacma* are quite similar to these « ossicles » or « volsellar lobes » of Hymenoptera, in location, appearance, and function, hence are here referred to as « volselli ». Such homologies may be disproved when embryological studies of the development of these parts are made, but rather than coin new terms for these structures of unknown embryological origin the author deems it better to apply current terms wich might be correct, and leave the matter open to future revision based upon more complete information. It should be noted here that the choice of the term « *cuspis volsellaris* » for the movable, muscled structure, and « *digitus volsellaris* » for the larger, heavier, immobile part is based upon morphological position rather than upon relative size or musculature. In hymenopterous males the muscle fibres which sometimes pinch the tips of the volsellar lobes together are inserted upon the sclerotized surface between them. When contraction occurs, the area between the lobes is pulled upon, causing the tips of the lobes to pinch together. As will be mentioned soon, the mechanics of pinching in *Priacma* « volsellari » differs considerably from that method. Muscle fibres which are inserted on the anterior apophysis of each « cuspis volsellaris » of *Priacma* males have their origin within the concave lateral wall of the hollow base of the nearby « digitus volsellaris ». When these muscle fibres contract, the slender apex of each « cuspis volsellaris » is pinched tightly against the thick, sharply-hooked tip of the opposing « digitus volsellaris ». The point of attachment of each « cuspis volsellaris » is laterad, at the base of the corresponding paramere, between the parameral plate and the volsellar plate of that side of the phallus. No distinct suture was visible at that slender point of attachment. When the muscle fibres contract, the delicate, resilient, sclerotized stalk which joins the « cuspis » to the parameral base is bent until the volsellar tips pinch together. When the fibres relax, the natural elasticity of the sclerotized connecting-stalk causes the « cuspis » to spring back to its original position. This action has been convincingly

demonstrated many times while the phallus was submerged in alcohol, by pulling on the muscle fibres with a dissecting needle and then releasing them abruptly. When tension was placed on those fibres, the tip of the « cuspis » touched the tip of the « digitus » quickly, but as soon as the tension was released the « cuspis » sprang back to its former position. No doubt this pinching mechanism is used during the copulatory act, to hold the male genitalic appendages in the correct position in relation to those of the female. The exact feminine structures thus grasped are not known to the author, but it is hoped that specimens in coitus may be collected next summer and further details discovered at that time. The musculature of the « cuspis volsellaris » has been recently illustrated by EDWARDS (1953).

Laterad from the point of attachment of each « cuspis volsellaris » a short, slender, heavily-sclerotized spine arises from the base of each paramere. These spines are quite prominent but are deciduous and break off easily, hence may not be seen during the dissection of *Priacma* male terminalia. No function can be surmised for them, at present.

The forty males used in this study were attracted by the odor of « Super Suds » (a laundry soap sold in the form of flakes). Only a small proportion of the beetles attracted by this odor were collected, and most of them appeared to be copulating. Later, however, it was discovered that a l l of these « copulating » individuals were males !! Consequently, EDWARDS (1951) concluded that the odor of this soap must exert a powerful sexual stimulus upon these males.

It is hoped that future summers in Montana will enable the author to collect females of *Priacma serrata* (LECONTE) as well as additional males, and to make observations on the mating behavior and immature stages of these interesting animals. Such observations will be included in his forthcoming revision of the *Cupesidæ* of the world.

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SAN JOSE STATE COLLEGE, CALIFORNIA.

AD. GOEMAERE, Imprimeur du Roi, 21, rue de la Limite, Bruxelles