

THE FUNCTION OF HORNS IN *PODISCHNUS AGENOR* (DYNASTINAE)
AND OTHER BEETLES

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If we could imagine a male *Chalcosoma* . . . , with its polished bronzed coat of mail, and its vast complex horns, magnified to the size of a horse, or even of a dog, it would be one of the most imposing animals in the world (Darwin, 1871).

The bizarre, beautiful, and astonishingly varied shapes of beetle horns have long intrigued zoologists. The horns, usually restricted to males, are found in a number of unrelated families (e.g., Arrow, 1951). Perhaps because many of the horned species are tropical, surprisingly few studies of the beetles have been made in their natural habitats. Consequently, most of the discussions of horn function have been speculations based on the study of dead specimens.

The most prominent hypotheses are these:

1. horns serve as male adornments used by females to choose between potential mates (classical sexual selection: Darwin, 1871);
2. horns function to protect the beetles against predators (Wallace in Arrow, 1951);
3. horns, while originally developed to carry refuse from burrows, have subsequently become adapted for fighting (Lameere, 1904, in Arrow, 1951; Beebe, 1944, 1947);
4. horns serve to dig, perforate, or lacerate plants, permitting the beetle to feed on the plant or its sap (e.g., Smyth, 1920, for *Strategus barbigerus*; Walcott, 1948, for *S. quadrifoveatus*; and Doane, 1913, for *Oryctes rhinoceros*);
5. horns are in general functionless, selectively neutral characters; since their increased development is linked with increased body size, they are an incidental result of selection for larger size (Arrow, 1951).

Some of these hypotheses seem untenable on logical grounds. Females are unlikely to be able to sense males' adornment in many natural situations where there is no light (Arrow, 1951); females would seem to need predator defense as well as males (Arrow, 1951); and the dedication of such relatively large amounts of body material to horns seems unlikely to be a selectively neutral character. But they cannot be definitively rejected or accepted without observations of the behavior of live beetles. This chapter describes such observations made on eight different species in and near Cali, Colombia. In at least seven of the eight, it appears that the horns function as weapons in battles with conspecifics.

The objective of the observations was to see if the beetles behaved in ways which suggested specific functions for their horns. The criteria used to decide on a particular function were these:

1. the behavior which involved use of the horns was performed in more or less natural conditions;
2. the behavior was relatively stereotyped and was seen repeatedly;
3. the successful execution of the behavior was biologically important;
4. the horns' form matched the hypothesized function, so that their mechanical properties were particularly suitable for the effective realization of the function.

If other behaviors observed in the same context were consistent with the apparent purpose of the horns, this was taken as a confirmation of the biological significance of the horn function.

The descriptions below are summaries of more extensive observations which will be presented elsewhere. In several species, small individuals have reduced horns, and unless otherwise noted, all descriptions refer to the behavior of large individuals with well-developed horns.

Podischnus agenor (Oliv.) (Dynastinae)

Large males of this species have a long, thin, slightly curved head horn which projects dorsally and a thick prothoracic horn with a crescent-shaped tip projecting anteriorly (Fig. 1). Small males have reduced horns and females do not have horns. This species ranges through Central America and northern South America (Blackwelder, 1944), where it is locally common in sugar cane and corn fields (Ritcher, 1958; Guagliumi, 1962; T. Jaramillo and D. Rizo, pers. comm.).

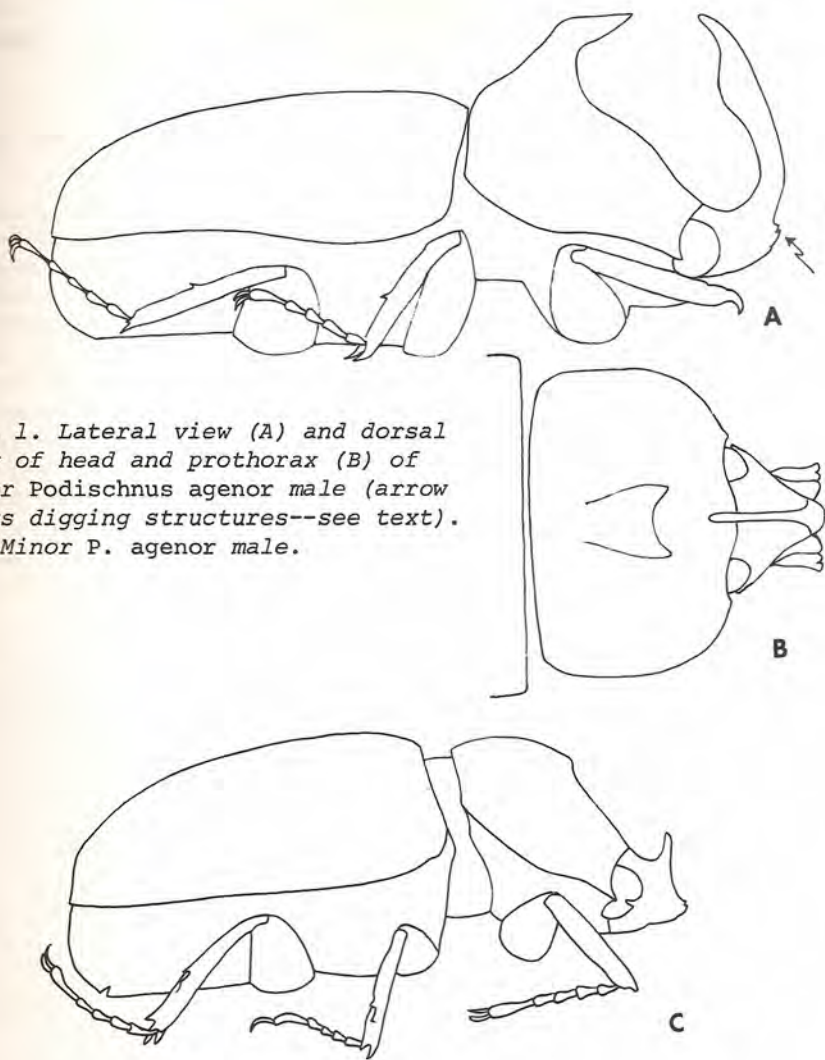


Fig. 1. Lateral view (A) and dorsal view of head and prothorax (B) of Major *Podischnus agenor* male (arrow marks digging structures--see text). (C) Minor *P. agenor* male.

Eggs are laid in the ground where the larvae feed on humus and develop to maturity. The adults are relatively seasonal, emerging in the Cauca Valley near Cali principally during the rainy season. The adults dig burrows in sugar cane stalks (Fig. 2), the tunnel being just wide enough to permit the passage of the beetle's body. Solitary individuals of both sexes as well as pairs (almost always a male and a female) occur in the tunnels. When with a male, the female is almost always facing upward and is above the male, farthest from the mouth of the burrow.

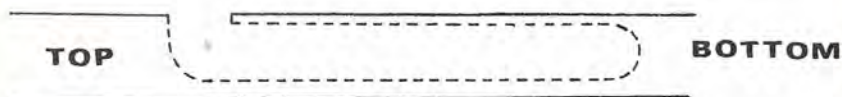


Fig. 2. Typical form of *P. agenor* burrow in a sugar cane stalk.

The beetles' burrowing technique in sugar cane was closely observed, and it was clear that the horns did not function in this process. Instead, the small prominences on the head near the mandibles (arrow in Fig. 1A) and the anterior and lateral surfaces of the mandibles were used (as shown in Fig. 3) to rasp small pieces of cane free. The prominences and the anterior part of the closed mandibles engaged the cane first, and then both the head and the prothorax were flexed upward while the entire body was thrust forward. As the head moved upward, the mandibles were opened, and the cane was thus simultaneously cut and shredded. A small piece of cane came loose with a snap, and the beetle jerked slightly forward as his head and prothorax snapped upward. He then lowered his head again to repeat the process. Females dug in an identical manner.

Both sexes also burrowed readily in the ground, and their digging technique was observed in cages formed by glass plates with earth between. Again the horns played no part. Most of the work was performed by the front legs. Using the tibiae,

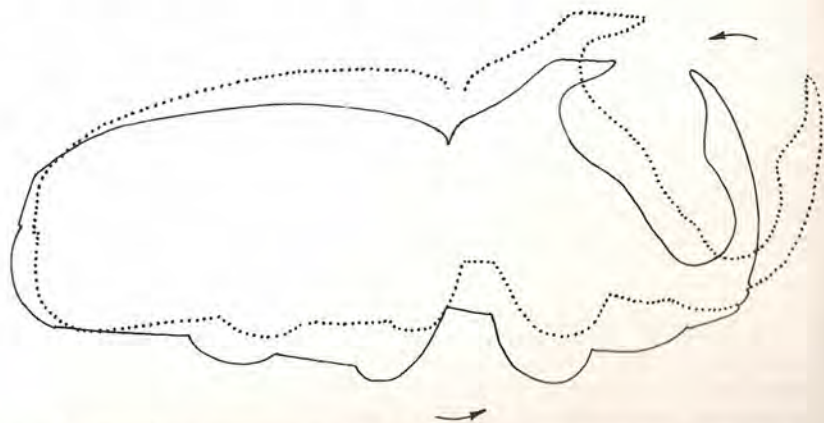


Fig. 3. Digging movement of *P. agenor* in sugar cane stalk. The beetle first lowers his head and arches at his prothoracic-mesothoracic junction (dotted lines), then faces the head up and the prothorax down (solid lines and arrows). The slight forward movement imparted by the legs and the straightening of the body are not shown.

several scoops of earth from just in front and below the animal were scraped back under the prothoracic-mesothoracic joint, and then the accumulated loose earth was passed back by the middle and hind legs to be deposited behind the beetle. The beetle then moved forward, flexed its head and prothorax dorsally so they pressed tightly against the roof of the cavity, and began scooping earth again with the front legs. There was no difference in the behavior of males and females.

Males brought into captivity in their burrows often emerged partway from the entrance at night and produced a pungent odor similar to that of musty apples (Fig. 4). On the basis of studies of the movements of marked beetles to and from burrows in the field, the sequence of activities in Fig. 5 seems typical for the species. The male initiates the burrow and then probably uses his odor to attract a female. She sometimes mates upon arrival, and sometimes she is later allowed to enter the burrow to feed at the upper end. On numerous occasions, a male which had been found and marked in a given burrow had been replaced by another male when the burrow was revisited, suggesting that males may also be attracted to and fight for the possession of burrows.

The possibility of fighting was tested by placing pairs of males in burrows carved in cane stalks and covered with



Fig. 4. Male *P. agenor* releasing odor at the entrance to an artificial burrow.

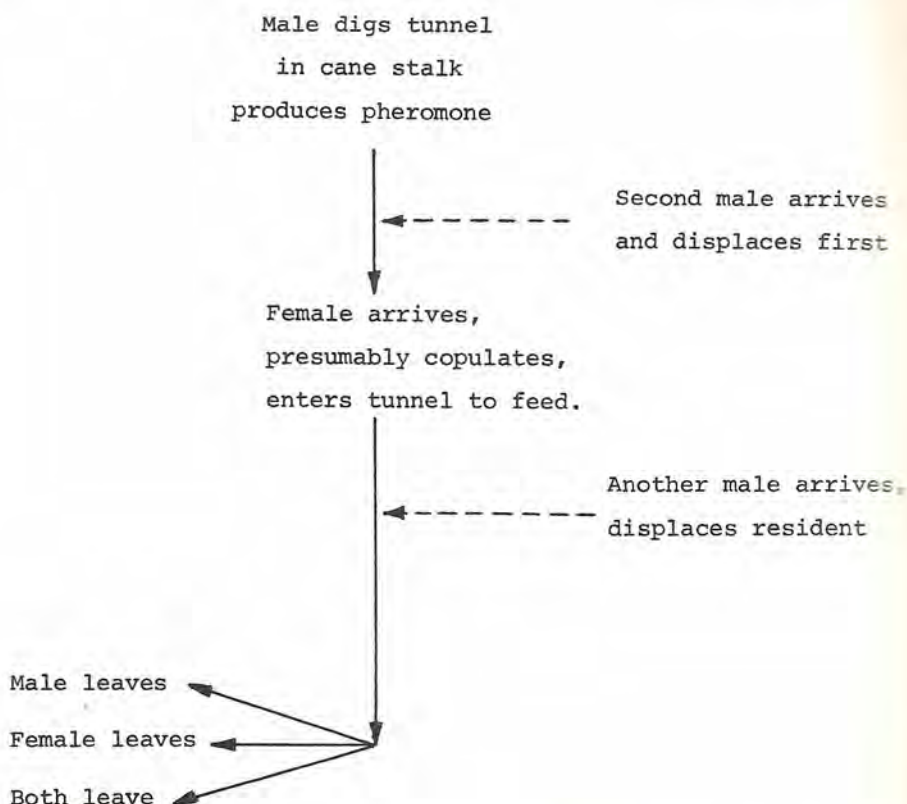


Fig. 5. Common sequence of activities associated with burrows in sugar cane by *P. agenor*.

clear plastic to permit observation of activities inside (Fig. 6). One male (the resident) was allowed to stay at least 12 hr. undisturbed in the burrow, where he usually fed at the upper end, or, at night, emitted an odor at the entrance. Then the other male (the invader), which had been kept alone in a small jar with a piece of sugar cane to feed on, was placed at the entrance. As expected, the beetles did fight, using complex and somewhat stereotyped behavior in attempts to dislodge each other from the cane stalk. Fighting sequences were variable, but two basic patterns were apparent.

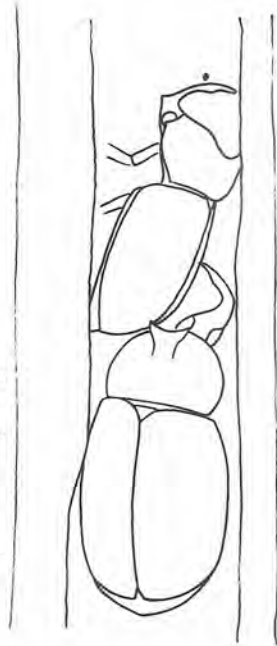
Head-to-Head Combat

My introduction of the intruder into the entrance usually caused the resident to climb part way up the tunnel, and the



Fig. 6. (left)
Artificial burrow
used to observe
fights of *P. agenor*.

Fig. 7. (right)
Males of *P. agenor*
pushing each other
inside an artificial
burrow (drawn from
a photograph). The
upper beetle (resident)
braces his body across
the tunnel to block it;
the invader lowers his
head, but not enough
to get the horn under
the resident's abdomen.



intruder moved on into the tunnel until he was completely inside. When the beetles came into contact, they both began to push each other and/or to brace themselves tightly against the tunnel wall. The head horn and often the prothoracic horn of the intruder were against the rear of the resident (Fig. 7). This pushing stage lasted from 2 to more than 15 min., with the beetles moving up and down inside the tunnel and periodically resting. The position of the invader with respect to the resident was variable, and both his head and thoracic horns made contact and failed to make contact with the elytra and abdomen of the resident in a variety of ways. Since conditions #2 and #4 for establishing an evolved function were not fulfilled (#2 there was no stereotyped use of the horns during pushing, and #4 their forms did not appear especially effective), it was concluded that they are not adaptations for fighting inside burrows.

When the beetles were of about equal size, it appeared that the intruder consistently pushed harder than the resident. This difference is probably due to the beetles being built to develop more power moving forward than backward, as is clear, for example, from the positioning of their legs and spines (Fig. 1A).

After a variable length of time, the beetles finally moved

down the tunnel to the entrance. Usually I could not tell whether the resident forced the invader downward or whether it was the invader who allowed the resident to descend, but, in a few cases in which the resident was old and sluggish, it was evident that it was the invader who initiated the final descent. By the time they arrived at the mouth of the burrow, the beetles had almost always assumed standard positions--the resident with his ventral surface toward the open side of the burrow entrance and the invader with his dorsum toward the same side (Fig. 8A). The only exceptions occurred when the resident was much smaller than the intruder and, probably as a result of having sensed the latter's superior strength during the pushing inside the tunnel, simply left without attempting to defend the burrow.

When they reached the entrance, the invader backed part way out of the burrow, allowing the resident to swing his abdomen upward and turn himself part way around (Fig. 8B). While in this position, the resident male kept his head flexed

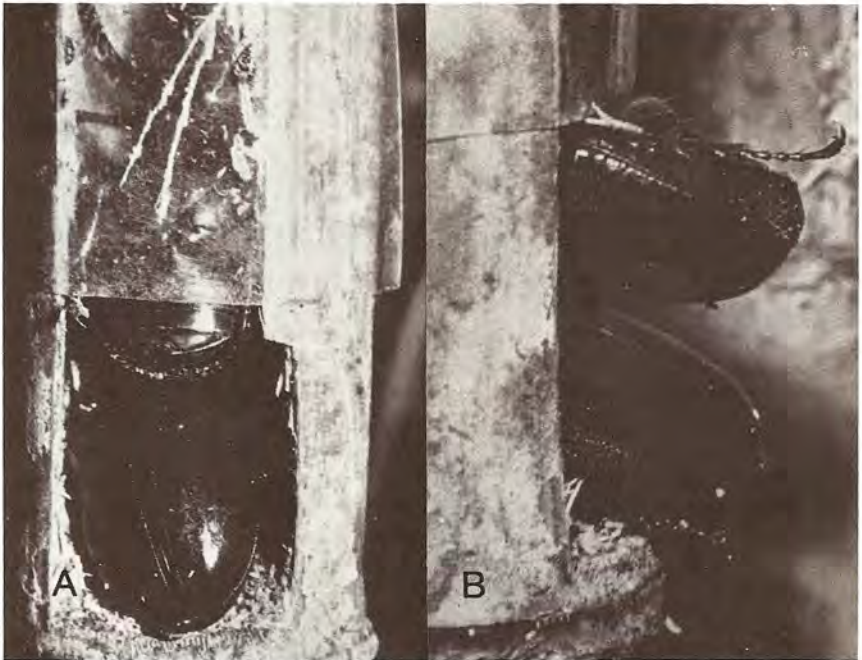


Fig. 8. Behavior associated with the resident's turn in the entrance. (A) Positions of the males as they back down the tunnel just prior to the turn by the resident. (B) Resident male (above) halfway through his turn. At this stage the invader can repeatedly "punish" the resident.

ventrally so that the horn blocked the tunnel, but he had very little purchase on the walls of the burrow with his legs. The invader, meanwhile, remained firmly ensconced in the entrance, and he frequently "punished" the resident by repeatedly driving upward into the tunnel. The curved tip of his prothoracic horn fit snugly against the resident's dorsal surface and often caught in the prothoracic-mesothoracic joint as he pushed upward, forcing the resident's anterior end part way back into the tunnel.

Gradually, after administering a variable amount of punishment, the intruder backed farther and farther out of the entrance, allowing the resident to complete his turn, assume a downward-facing stance, and begin the final fight. This was a critical time since the invader had to retreat enough to allow the resident to turn. The footing outside the entrance was much more difficult, and to retreat too far meant having poor purchase in the test of strength which was to follow.

The definitive fight, which was usually much shorter than the preliminaries, began when the resident had completed his turn (Fig. 9). Each beetle attempted to "clamp" the other by getting his head horn under the other's head and prothorax

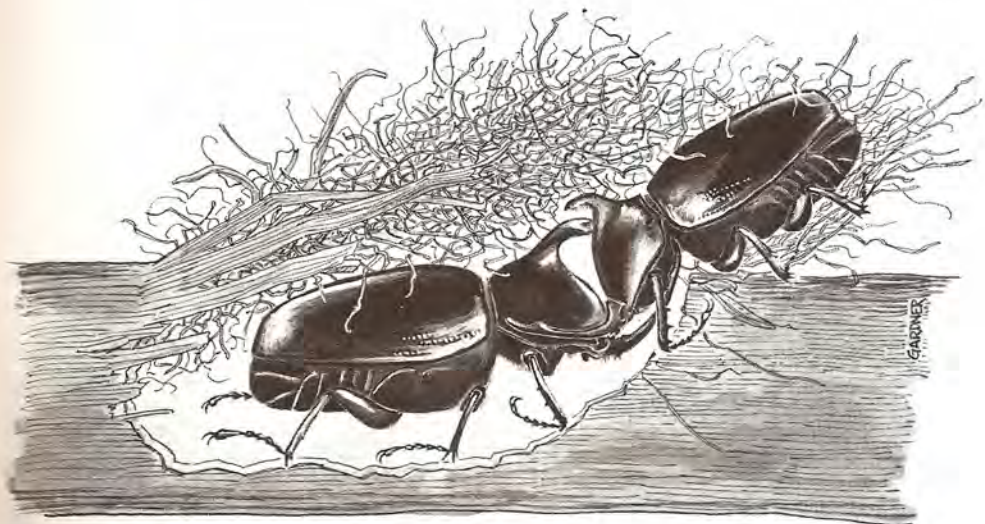


Fig. 9. A head-to-head fight in cutaway view. The resident beetle (above) has clamped the invader and is beginning to lift him. The invader clutches at the shredded cane to avoid being dropped free.

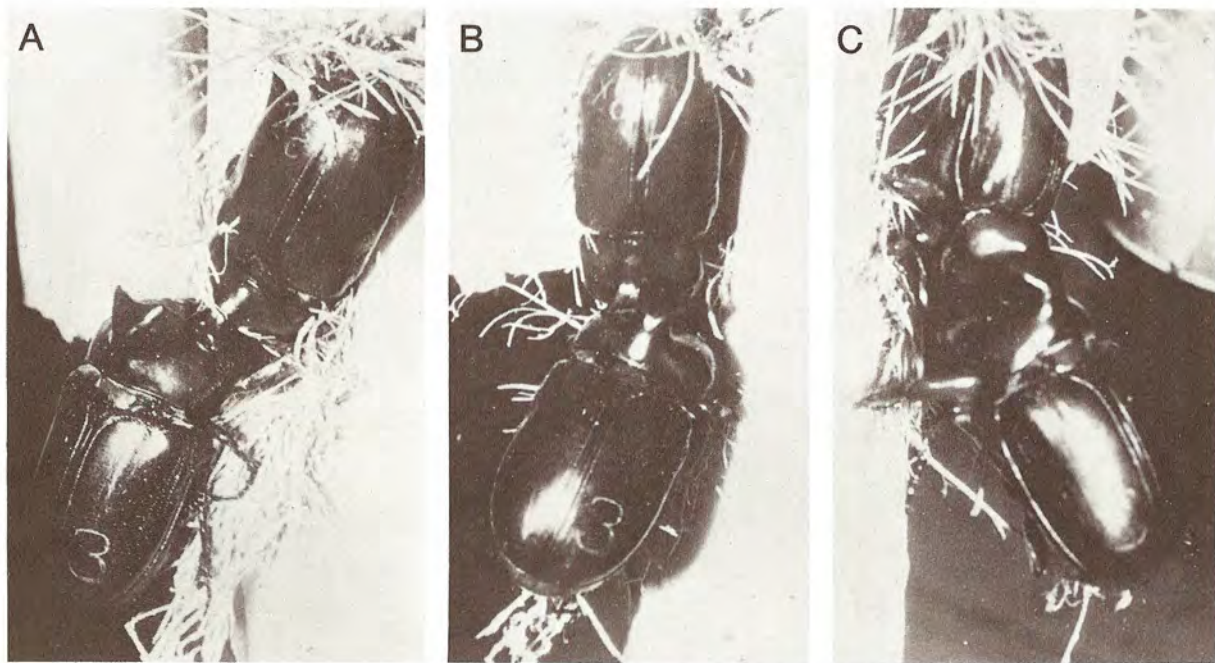


Fig. 10. A head-to-head fight just outside the entrance to a burrow. The invader (#3) shifts from side to side (A and B), attempting to get his head horn under the resident's lowered prothorax, but fails and is clamped and lifted (C). Shortly after photograph C was taken, the resident dropped the invader.

and then, by flexing his head dorsally, to clamp his opponent with his head and prothoracic horns. Sometimes the beetles engaged each other tentatively several times before achieving a clamp hold. Often both succeeded in clamping simultaneously, but soon one predominated (perhaps by squeezing harder or having better footing on the cane) and the other released his hold (Figs. 9 and 10). The beetle with the clamp hold then lifted his opponent away from the cane stalk by extending his legs (Fig. 10C), and, after holding him there for a moment, released his hold. Usually the result of the lifting was that the losing beetle lost his foothold, and he thus fell to the ground when released. Typically the winner then stridulated vigorously by scraping the tips of his elytra with the dorsal surface of his abdomen. On a few occasions the lifted beetle kept his foothold and did not fall free when released, but returned to do battle with his opponent (and occasionally won the rematch). In fights observed in natural burrows, which had accumulations of frayed cane around the burrow entrance (Fig. 9), beetles which had been lifted and dropped were more often able to retain a foothold and avoid falling. Another less common variant was for the intruder to back down below the entrance after the resident made his turn, and when the resident followed him down to attempt a clamp, to try to scramble around the resident and into the vacated entrance.

Neither residents nor invaders were consistent winners, and the results were variable even in rematches between the same individuals in the same situation. The only clear tendency was for beetles substantially larger than their opponents to win.

Blocking the Entrance

Sometimes the resident did not move up into the tunnel when the intruder was introduced but, instead, remained in the entrance facing upward and blocking the hole with his dorsum. The invader's response to this was to attempt to insert his head horn at the resident's side, get it under him, clamp him and lift him from the hole (the resident seemed to be able to offer little resistance), and drop him to the ground. When the invader could not get his horn in under one side of the resident, he sometimes moved across the resident's back to attempt to insert it under the other side. The resident had two responses to these attacks. As the invader climbed across his back, the resident extended his legs and held his body away from the cane, a movement which more or less broke the invader's contact with the cane stalk and which in several cases caused him to fall. When the invader did attempt to introduce his horn at the side, the resident leaned toward that side, reducing the space between his body

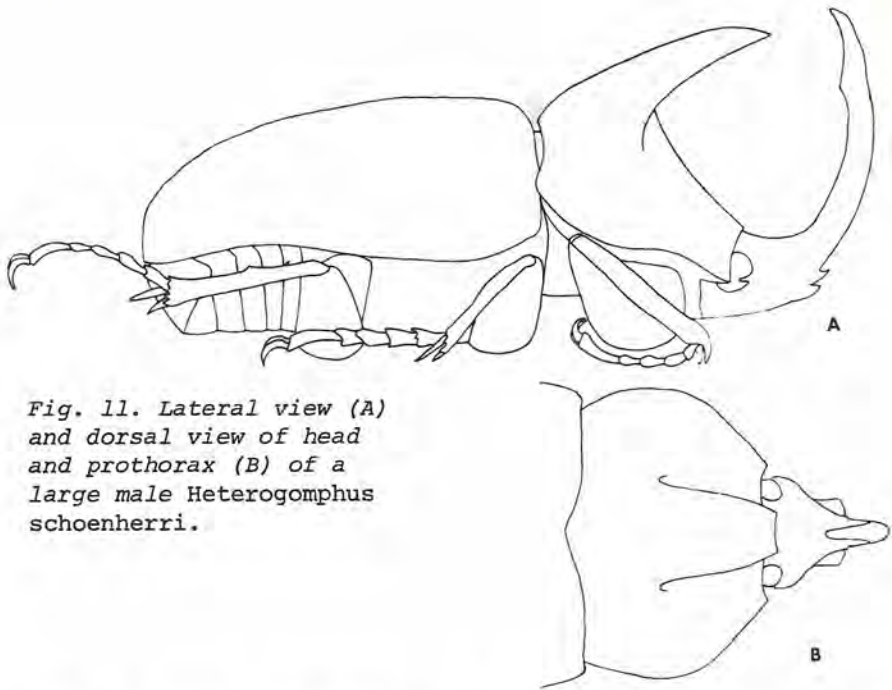


Fig. 11. Lateral view (A) and dorsal view of head and prothorax (B) of a large male *Heterogomphus schoenherri*.

and the side of the tunnel. He also tilted his body so that his dorsum was toward the intruder.

Heterogomphus schoenherri Burm. (Dynastinae)

Fighting between large males of *H. schoenherri* (Fig. 11) placed in grooves carved in sugar cane stalks (the natural habitat of this species is unknown) was similar to that of *P. agenor* males. If the males were not head to head, they turned, leaving the head in the groove and swinging the abdomen out and around 180° so as to face each other. Then they clamped, lifted, and dropped one another just as described for *P. agenor* (Fig. 12). They also used their head horns to pry opponents (especially their posterior ends) out of the groove. They used their heads and mandibles to dig in the cane with a rasping action similar to that of *P. agenor*. The major difference between the two species is that *H. schoenherri* has longer horns which can be strongly clamped together and inflict real mechanical damage. A male *Golofa porteri* (a species with much weaker elytra), after being kept in the same container with several *H. schoenherri* males, had damaged areas which were exactly the same size and shape as the *H.*



Fig. 12. A head-to-head fight between large males of *Heterogomphus schoenherri* in a groove cut in a sugar cane stalk. The upper male has his head horn under the other's prothorax and front leg, and is clamping him and lifting him out of the groove.

schoenherri prothoracic horns. A similarly shaped hole, this time an apparently mortal wound to the ventral surface of another *H. schoenherri* male, was inflicted by a male which had pinned his victim at the end of a tunnel in a sugar cane stalk.

Ceracis cucullatus (Mellie) (Ciidae)

This species, like the three other ciids that follow, is very small (1 mm long or less) and lives in complex galleries in sporophores of bracket fungi. All species were observed by placing the beetles on small pieces of sporophore in cages formed between two plates of glass and then placing the plates under a microscope. The beetles could thus be observed under relatively natural conditions. Beetles were also observed in narrow tunnels formed by cutting tiny grooves in strips of polypore which were then covered with microscope slides. Both sexes of all four species dug--using only their mandibles--in the polypore and sporophore.

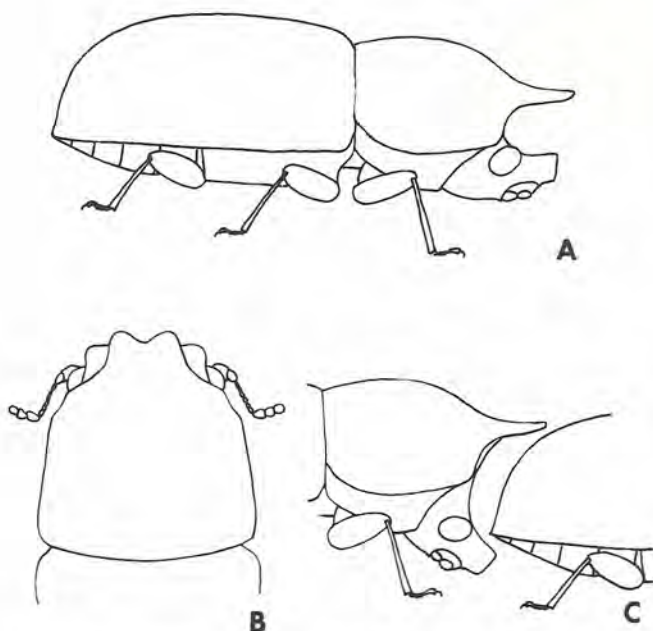


Fig. 13. Lateral view (A) and dorsal view of head and prothorax (B) of a large male of *Ceracis cucullatus* (Ciidae) (C) Curved head and prothoracic plates of a male being used to push against a conspecific male's abdomen.

Males of *C. cucullatus* have a plate-like forward extension of the prothorax (Fig. 13A) and plate-like lateral extensions of the anterior surface of the head (Fig. 13B). When males interacted aggressively, they usually lowered their heads, and the combination of the head and prothoracic plates plus the curved front of the head formed a smooth surface closely approximating the shape of a conspecific's body (Fig. 13C). Fights generally involved one animal lowering his head and pushing the other, engaging his opponent's abdomen more or less as shown in the drawing. In some cases the head was not lowered this far and only the upper and lower plates made contact with the opponent. Head-to-head interactions were variable, rare, and of low intensity; sometimes the head was lowered, and sometimes it was kept up so that the two plates were close together. The pushes were usually "jerky" rather than steady, and sometimes a male flexed his head upward briskly several times during a push. Winning individuals sometimes pinned their adversaries against a tunnel wall for hours at a time.

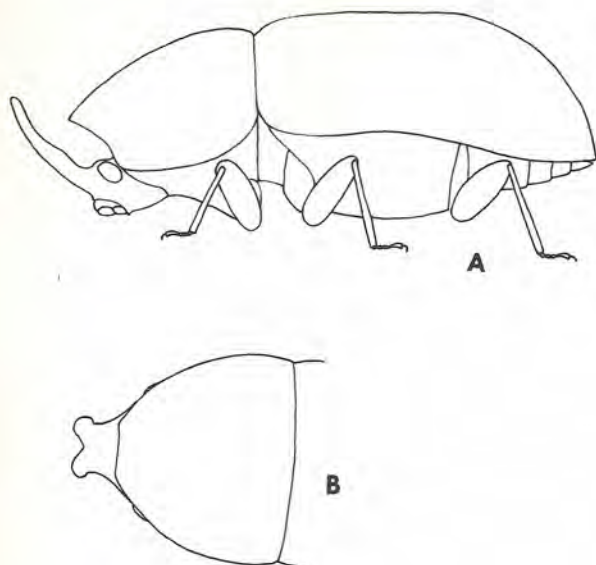


Fig. 14. Lateral view (A) and dorsal view of head and prothorax (B) of a large male *Ceracis* sp. near *furcifer* (Ciidae).

Ceracis sp. near *furcifer* (Ciidae)

Males of this species have a single bifurcated head horn (Fig. 14A) but no projections from the prothorax (Fig. 14B). Again in this species, a male's first reaction to the presence of a beetle in front of him was generally to lower his head so that the horn was directed more or less forward. The fights which developed differed from those of *C. cucullatus* in that there was little sustained pushing, but rather, repeated series of short, quick thrusts or jabs. Both front and back surfaces of the horn as well as the tip and sometimes the mandibles made contact with opponents. Victors sometimes pursued retreating foes for short distances, prodding them repeatedly under the abdomen with their head horns. During attacks on the side or rear of another beetle, the horn was sometimes inserted under the opponent, and in this case the front edge of the prothorax sometimes made contact during brief pushes, but otherwise most contact with opponents was with the head horn.

Head-to-head encounters occasionally resulted in relatively intense fighting. The males moved back and forth along the

sporophore, thrusting with their head horns like fencers, pausing occasionally in mutual attempts to insert their horns under each other. The majority of the contacts seemed to be with the tips and anterior surfaces of the horns, but the beetles' movements were very quick and difficult to follow. On two occasions I saw a male, which seemed to be getting the worst of an exchange, lean slightly to one side and then flex his head dorsally so that the fork in the tip of his head horn engaged the horn of his opponent and pushed it to the side.

Cis sp. near *tricornis* (Ciidae)

Males of this species have one long head horn projecting dorsally (Fig. 15A) and a pair of forward-directed thoracic horns (Fig. 15B). Males attacking other beetles from the side or rear usually lowered their heads, often inserting their head horns below their opponents' bodies and moving forward to bring their thoracic horns into contact. Usually they performed a series of short thrusts and shoves without shifting their feet, in contrast to the sustained pushes of *Ceracis cucullatus*. In at least some cases, it was possible to see that the thrusts had an upward component produced by moving the entire anterior portion of the body upward (rather than by flexing the head upward as in the dynastines). At other times they did not lower their heads and used the front surface of the head horn to push, rub, and hit opponents.

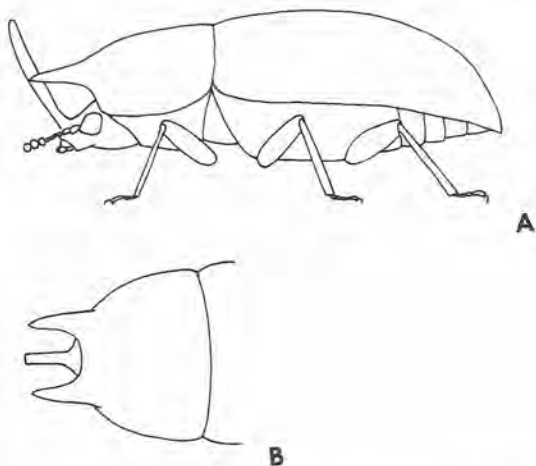


Fig. 15. Lateral view (A) and dorsal view of head and prothorax (B) of a large male *Cis* sp. near *tricornis* (Ciidae).

Head-to-head battles between aggressive males resembled those of *Ceracis* sp. near *furcifer*, with rapid forward and backward lunges combined with side-to-side movements. At times both males thrust repeatedly, their heads lowered and their prothoracic horns engaging each other's prothoraces.

Cis sp. near *taurus* (Ciidae)

Males of this species have a pair of large, forward-directed head horns, but lack prothoracic projections (Fig. 16). The most common type of aggressive movement was for a male to lower his head, insert his horns under the body of another, and give a series of quick lifting thrusts. The beetles did not engage in sustained pushing and seldom shifted their footing as they fought, simply rocking forward and back in one spot. Both head-to-head and head-to-abdomen interactions involved similar lifting thrusts. Only very seldom did I observe contact between an attacking male's prothorax and his adversary.

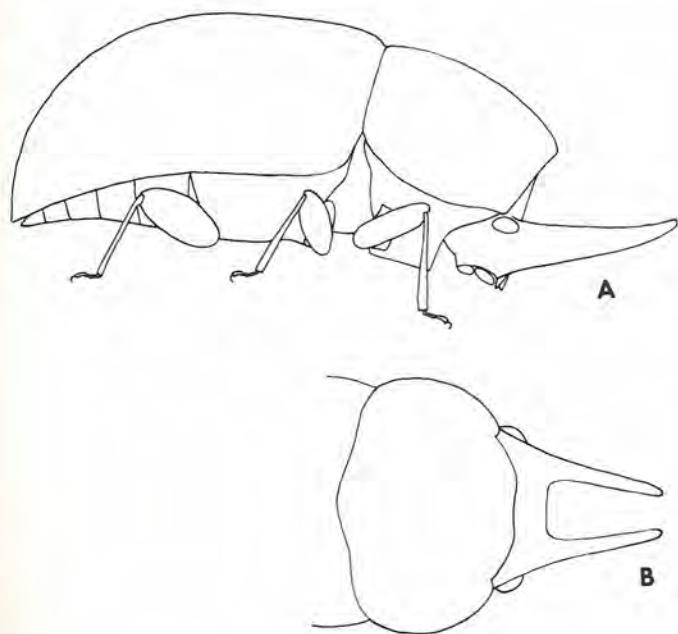


Fig. 16. Lateral view (A) and dorsal view of head and prothorax (B) of a large male *Cis* sp. near *taurus* (Ciidae).

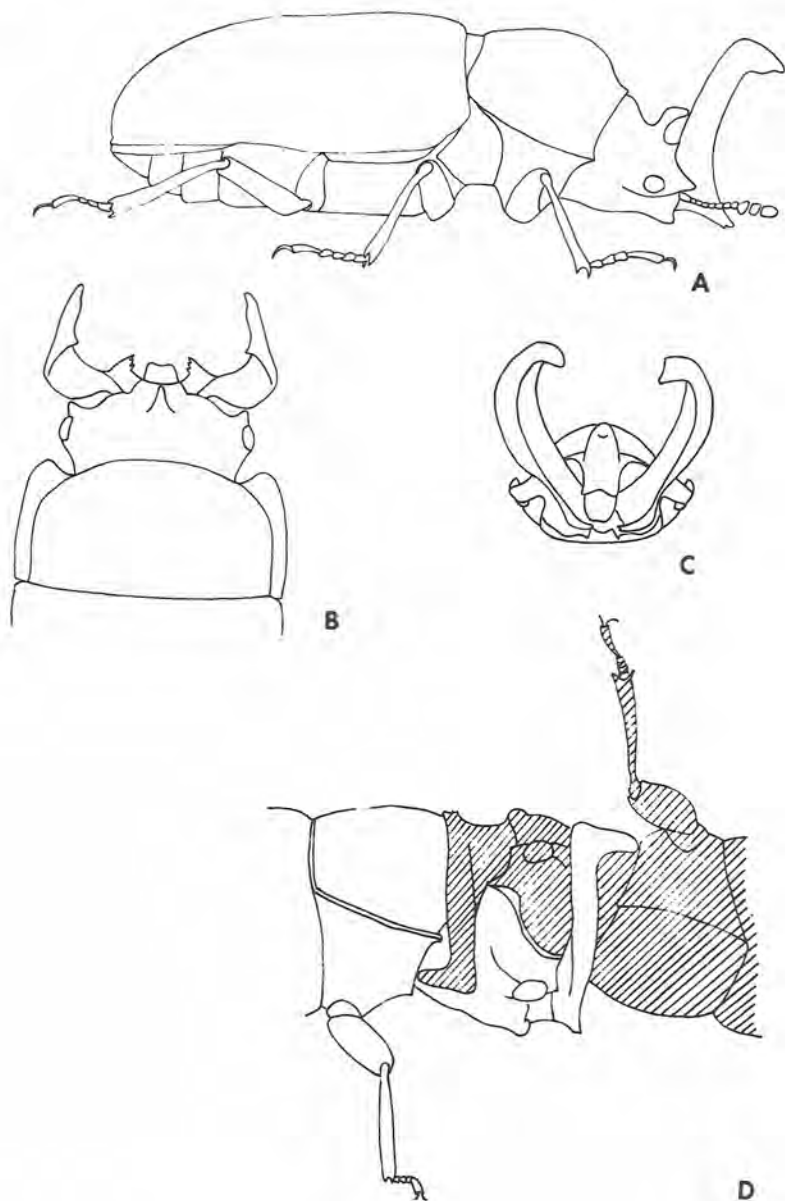


Fig. 17. Lateral view (A), dorsal view of head and prothorax (B), and frontal view of head horns (C) of a *Molion* sp. near *muelleri* (Tenebrionidae). (D) Pair of males mutually locked during an aggressive encounter.

Molion sp. near *muelleri* Kirsch (Tenebrionidae)

This species, found in rotting logs at high altitudes, was observed in cages made by carving horizontal grooves in a flat piece of wood and covering them with a glass plate. The beetles dug the partially rotten wood of their cages by biting free small pieces with the lower, toothed portion of their mandibles. There was no suggestion of the horns being used for this task.

Both males and females have identical horns, consisting of long dorsal extensions of the mandibles (Fig. 17B), and in one population, a short, forward curving horn on the head (Fig. 17C). The sexes could not be differentiated by visual inspection. Subsequent dissections suggested that nearly all the beetles were relatively young and that they had probably grown up as larvae in the logs in which they were collected.

Pairs of beetles were placed in short tunnels facing each other but separated by a cardboard partition until the observations began. Aggressive encounters began when one of the pair of beetles contacted the other. The one being contacted usually lowered its head to the substrate, while the other, if aggressive, slowly spun 180° on its longitudinal axis so that its dorsal surface was against the dorsal surface of its opponent (Fig. 17D). It then moved forward with its mandibles open, pushing when its horns came into contact with the other. As it did so, it opened and closed its mandibles repeatedly. When pushing forward, its head horn sometimes made contact with the opponent, hooking its prothoracic-mesothoracic joint, which apparently aided in the push. In several cases, one beetle grabbed the other with its mandible horns, and one drew blood from a pierced intersegmental membrane. One pair of males collected in nature (by L. Gonzalez) was mutually locked (Fig. 17D).

Peneta sp. near *muchicornis* Gebien (Tenebrionidae)

Both males and females of this species have a plate extending posteriorly from the head to cover the anterior part of the prothorax (Fig. 18). Again in this species I could not distinguish males from females without dissecting them. The beetles were collected in rotting logs and observed in the same type of cage as *Molion*. They showed only low levels of aggression, although they did push or nudge at almost every encounter. They swung their abdomens to place them in the paths of passing beetles, and leaned so as to present their dorsal surfaces to beetles which touched them (both behavior patterns were also seen in *M. muelleri*). They

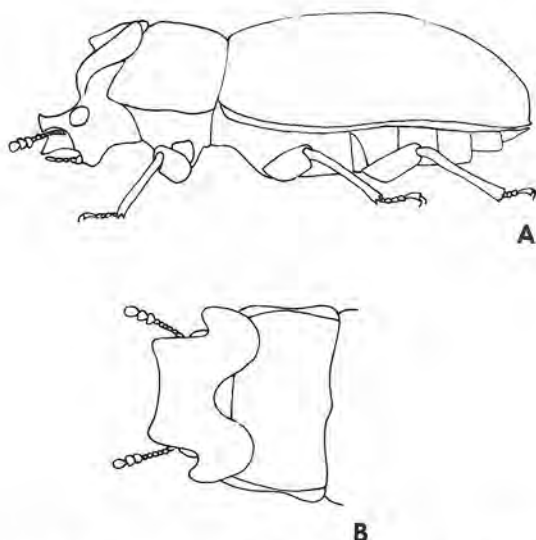


Fig. 18. Lateral view (A) and dorsal view of head and prothorax (B) of a *Peneta* sp. near *muchicornis* (*Tenebrionidae*).

also frequently wedged their anterior ends between other beetles and the sides of the tunnels, and then "pried" dorsally, lifting by raising the entire anterior portion of the body and usually keeping the head more or less immobile. In a few cases the head flexed dorsally somewhat during a pry, but in general it had very little mobility.

DISCUSSION

Table 1 summarizes the evidence with regard to the functions of male horns in *P. agenor*, showing that the criteria of functionality are met with respect to there being more than one function for both head and prothoracic horns. The multiplicity of functions is perhaps not surprising, since once a structure has evolved in one selective context, behavior may evolve to make use of it in additional contexts. The functions are all associated with aggression, thus supporting the "weapon" hypothesis (#3) presented in the Introduction. The existence of these functions invalidates the selective neutrality hypothesis (#5). It was also clear that the horns did not function in digging behavior (#4). No observations were made relative to the predator defense hypothesis (#2), but as noted in the Introduction, it seems unlikely on other grounds. The sexual selection hypothesis

TABLE 1

Functions of the horns of P. agenor which fulfill the conditions for functionality (see text)

Structure	Function	Comments
Prothoracic horn	Push resident during his turn at burrow entrance (Fig. 10).	Crescent tip fits curve of resident's dorsum.
	Form one side of clamp used in head-to-head fights to hold opponent while lifting and dropping him (Figs. 11-13).	Crescent tip results in usually two points of prothoracic horn rather than one holding opponent, making for a more secure grip.
Head horn	Block tunnel against invader as resident executes turn at entrance (Fig. 10).	The slight curve and thinness of horn do not seem particularly designed for this use.
	Form one side of clamp used in head-to-head fights to hold opponent while lifting and dropping him (Figs. 11-13).	The curve could help hold the opponent in the clamp, and the thinness could ease insertion of the horn under the opponent.
	Pry under a resident which blocks the entrance with his body in order to raise him so he can be clamped, lifted, and dropped.	(same)

[#1] was not tested, although females arriving at males' burrows in the field showed no obvious signs of attempting to judge the size of the resident male's horn before entering, and readily entered burrows inhabited by minor males. On balance, it seems likely that horns have evolved in this species for use in intraspecific combat.

The present environment of *P. agenor*, with huge fields of host plants like sugar cane and corn, is certainly different

from the environment in which the species evolved. Although relatives of both corn and sugar cane are native to the neotropics, suitable host plants (presumably thick-stemmed monocots) must have been less common. The resource over which the males fight--a burrow in a suitable host--may thus have been less common formerly, and it is possible that the competition over burrows in the present day is a non-adaptive "anachronism" remaining from previous evolutionary history.

It may seem puzzling that in fights in burrows invading males do not simply try to lift out resident males instead of allowing them to make their 180° turns and thus bring their potentially dangerous horns into play, and also that the residents consent to come down to the entrance to do battle at all when they are in an essentially impregnable position inside the tunnel. The answers are probably these: If the resident were to stay inside the tunnel, he would continue to have access to the feeding end of the tunnel, but would be vulnerable to punishment from the intruder and would not have access to arriving females. The fact that he invariably chooses to come down emphasizes the sexual rather than feeding importance of the burrow for the males. As for the invader's allowing the resident to turn, he has no other alternative if he is to remove the resident (apparently important), since he can only clamp and lift him clear and drop him when the resident is exposed at the entrance. In backing out enough to allow the resident to become exposed, the invader necessarily leaves enough room for him to execute his turn. The readiness of most residents to turn confirms that they usually fight more effectively when facing their opponents, although the size relations of the opponents, the position of the invader (clinging to the shredded cane below the entrance, or firmly ensconced on top of it after backing out of the entrance), and the details of the burrow entrance (footing just outside, size of entrance hole) may also influence the results.

The behavior of the other seven species, although studied in less detail, also suggests that their horns function as weapons in intraspecific combat. The only exception is *Peneta* sp., in which this is possible but was not established, perhaps due to the generally low intensity of the interactions observed. One might object that the observations of *Heterogomphus schoenherrii* were made in unnatural situations, but, as will be argued elsewhere, their natural habitat may well be similar to grooves in sugar cane.

It is interesting that six of the eight species used their head horns and/or heads to lift their opponents away from the substrate in one way or another. The reason why this should be common (and thus a reason why forward-projecting head horns

could often be favored) seems simple. If two otherwise equal individuals are pushing each other, the one which can position his center of gravity lower (closer to the substrate) than that of his opponent will have an advantage, since he will be better able to brace his thrust against the substrate.

Several other observations of beetle horns being used as weapons in natural situations can be added to those reported here. Detailed studies of *Chiasognathus grantii* (Lucanidae) (Joseph, 1928; Ureta, 1934; Hamilton, in this volume), *Diloboderus abderus* (Dynastinae) (Daguerre, 1931), and *Dynastes hercules* (Dynastinae) (Beebe, 1947) in natural or nearly natural conditions, show that the male horns of all three function as weapons in male-male combat. Although the *Dynastes* battles were artificially staged, it is likely that they occur naturally in similar open situations (see below). (Probably the most unnatural aspect of the encounters was their being carried out on a flat surface rather than on something like tree branches where the victor's dropping his opponent would be an effective way of ending the interaction.) Other less complete studies of horned species also suggest that horns serve as weapons. Beebe (1944) observed male *Megasoma elephas* and *Strategus alaeus* (both Dynastinae) using their anterior horns (but not their lateral horns) to turn conspecific males on their backs in battles staged in the open. Smyth's observations (1920) of *Strategus titanus* and *S. quadrifoveatus* in the wild indicate that these species live in burrows rather than in the open; Smyth also notes in passing that *S. titanus* males fight, using their horns "to best advantage" to send their adversaries rolling. Pace (1967 and pers. comm.) saw males of *Bolitotherus cornutus* (Tenebrionidae) fight in nature, using their horns to pry rival males off the backs of females (Fig. 19). Several observers (Davis, 1833; Kirby and Spence, 1818; Westwood, 1840--all cited in Darwin, 1871) have seen *Lucanus cervus* (Lucanidae) males fight using their enlarged mandibles. Ohaus (1900)

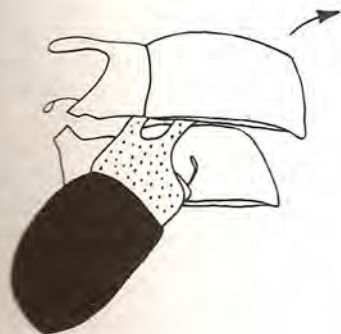


Fig. 19. Fighting behavior of *Bolitotherus cornutus* (Tenebrionidae) drawn from the notes of Ann E. Pace. One male, mounted on the back of a female, is pried off by a second male.

observed that in captivity the dynastines *Enema pan*, *Heterogomphus achilles*, and *Megasoma typhon* all flexed their heads dorsally so that their head horns tightly pinched offending objects such as fingers or pencils. Howden and Campbell (1974) saw males of *Golofa porteri* in nature using their elongated front legs and their head horns to dislodge conspecific males from apparent feeding sites (but they did not note any use of the long prothoracic horns). Wallace (1869, in Darwin, 1871) saw two males of *Leptorhynchus angustatus* pushing at each other with their elongated rostra near a female, and M. Cooper (pers. comm.) also saw unidentified brentheids hit each other with their heads. E. Sleeper (pers. comm.) observed what appeared to be an aggressive interaction between two male brentheids which had pairs of long horn-like structures projecting posteriorly from their elytra. The males approached each other backward along a tree trunk, and as they closed on one another, made rapid tentative "probing" motions backwards. One then succeeded in using his horns to flip the other off the tree with a quick twist.

Thus, although there are few observations and some are only fragmentary or are from unnatural situations, it is striking that all of the reasonably careful studies of living beetles suggest that horns are used as weapons rather than anything else. In sum, the data suggest that usually beetle horns function in fighting.

Continuing this line of thought, it seems permissible to make one general statement about the ways in which different horn types are probably used. There are two general kinds of situations in which fights may occur--in the open (on the ground, on tree trunks, etc.) or in restricted spaces such as burrows. Very long horns (e.g., *Chiasognathus grantii*, some *Golofa*, *Dynastes hercules*, some lucanids, some brentheids) are probably used in interactions which occur in the open, since long structures would be very difficult to maneuver in closed spaces. The observations in nature of *Chiasognathus*, *Golofa*, and the horned brentheid are in accord with this idea. Shorter horns do not necessarily indicate battles in closed spaces, however, since they are sometimes used in the open (e.g., *Diloboderus*, *Bolitotherus*) and sometimes in tunnels (e.g., the ciids and tenebrionids of this study).

An important problem for the weapon hypothesis, and one which troubled Darwin (1871), still remains. Beetle horns often vary widely between large and small individuals of the same species in both degree of development and shape, and two at least partially distinct morphs ("majors" and "minors") exist in some species (see Otte in this volume). How can one explain with a single function structures which vary so drastically within a single species? There are several possible answers: it is possible that the situation is more

complex, and that the structures are designed so that in minor males they have one function and in majors another (Darwin, 1871; Otte, in this volume); a structure may have multiple functions in majors (as in *Podischnus*) and lose some or all of these functions in minors (Gadgil, 1972, and Hamilton, in this volume, discuss how selection could maintain such dimorphisms in a single species); or, as is apparently the case of the ciids of this study, smaller horns may perform essentially the same functions as large ones, albeit less effectively. In this last case, continuous gradations rather than distinct dimorphisms in horn size might be more likely to evolve. These are speculations, however, and detailed observations of the behavior of both major and minor males are needed.

Further, as yet incomplete data for *P. agenor* suggest that the essentially hornless minor males differ from majors in more than just body and horn size. Small individuals were relatively more common in some parts of the breeding season than others, and were less often recaptured after leaving the burrows where they were first observed. The second difference suggests greater mobility in the "nonfighting" form, and accords with observations of other dimorphic species discussed by Hamilton in this volume.

For some beetle species, the question of why they are so highly evolved to fight is also not yet clearly resolved. *Podischnus*, *Diloboderus*, *Bolitotherus*, *Chiasognathus*, *Golofa*, and *Lucanus* apparently fight over highly localized resources whose use is limited to one or a few individuals. *Lucanus cervus* has been seen fighting near sap flows, just like *Chiasognathus* (M. Idar, pers. comm.), and would thus also be expected to evolve effective fighting mechanisms. But other species, such as the ciids and tenebrionids of this study, utilize resources which, although very localized, are so large with respect to the beetles' size that it is difficult to accept the idea that their use is limited to one or a small number of individuals. It is possible that the burrows rather than the substrate are for some reason particularly valuable (attract females, difficult to dig, etc.), but I could distinguish neither consistent associations between males and females nor obviously delimited tunnels occupied by given individuals in either the ciids or the tenebrionids. At least in the densely populated substrates I inspected, the tunnel systems were very complex and interconnected. Males never showed sustained persecution of other males over long distances such as would be required for monopolization of the entire substrate. On the contrary, vanquished individuals were pursued at most only a few body lengths. Another possibility is that the offspring of the first colonizers remain in the substrate for several generations. This would increase

the substrate's value for the colonist. If the subsequent generations maturing there tended to inbreed, the relatedness of the eventual dispersers to the colonist would be increased, raising the apparent value of the substrate to the colonist even more. If one or both of these conditions obtain, small differences in the reproductive contribution of the colonists could be multiplied into large differences in their genetic contribution to the next dispersing generation. There appear to be no data on this point for either the ciids or the tenebrionids.

The reason for the presence of horns in both sexes of the tenebrionids rather than just in the males is also unclear, although Hamilton (this volume) has suggested a possible cause. For all of these points, detailed studies of the behavior and ecology of these beetles, especially during the colonization of new substrates, are needed.

One final question arises with regard to the aggressive function of horns in beetles. If horns are generally effective weapons, why are they so seldom found in other insects? Selection in other groups should be equally strong in favoring individuals able to defeat conspecifics in battles over limited resources. Two factors suggest that in general beetles are preadapted to develop horns:

1. Compared to many other insects, adult beetles tend to live in relatively enclosed spaces. Physical contests in such spaces are less likely to be decided by the contestants' speed or agility than by their brute strength in pushing matches. In many other insects, agility is possible and has already evolved in other contexts (e.g., escape from predators, prey capture), and selection favoring winners of intraspecific contests will often have the effect of perfecting already existing systems that increase agility. Even beetles such as coccinellids, which do not live in enclosed spaces, but which conserve the relative slowness and clumsiness of beetles, have been observed to fight by pushing with their heads (M. Rodriguez, pers. comm.: males of *Hypodamia convergens* fighting over a female).

2. Many beetles dig in some sort of substrate, and morphological characteristics associated with digging--short legs and a thick cuticle--make alternative ways of fighting such as biting and kicking less effective. At the same time, the mechanisms evolved for digging are in some cases easily applied in intraspecific contests of force in which horns are advantageous. This is well illustrated in the cases of *Podischnus* and *Heterogomphus* where the forces used to dig--forward thrust with the legs plus dorsal flexion of head and prothorax--are the same as those

applied in battles. It is equally true, however, that this idea does not apply in other cases such as the ciids of this study, whose digging power, concentrated in the mouthparts, is little employed in fights.

SUMMARY

The only function for beetle horns which has been confirmed by detailed observations is that of weapons for use in intra-specific fights. Many horn designs remain to be studied, but it seems likely that many of these will also be found to function as weapons. More data are needed to answer outstanding questions about the significance of multiple horn designs and the selective pressures favoring fighting in some species. Several factors may have predisposed beetles to evolve horns more readily than other insects.

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