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Asymmetrical male mandibular horns and mating behavior in *Agathidium* Panzer (Coleoptera: Leiodidae)

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Abstract

Males of some species of *Agathidium* Panzer have a prominent horn on the dorsal surface of the left mandible. The horn is unique in that it is highly asymmetrical. One species, *A. marae* Miller and Wheeler, has an additional horn on the right side of the frons. The horns are categorized into four general morphological types. Scaling relationships are investigated for two species, *A. angulare* Mannerheim and *A. pulchrum* LeConte. These species exhibit a scaling relationship that is strongly discontinuous (sigmoid) with a prominent “switch point”. Measurement data (pronotal width versus mandible height) are fit to a nonlinear regression model to determine the switch points and slopes at the switch points for the populations of each species. Behaviors associated with mating and other behaviors are described for *A. pulchrum*. Males use a head-thrusting behavior to dislodge rival males from the substrate. Horned males appear better able to dislodge opponents. Head thrusting is also used less vigorously on females before and after mating.

Keywords: *Agathidium*, *Coleoptera*, *mandibular horns*, *mating behavior*

Introduction

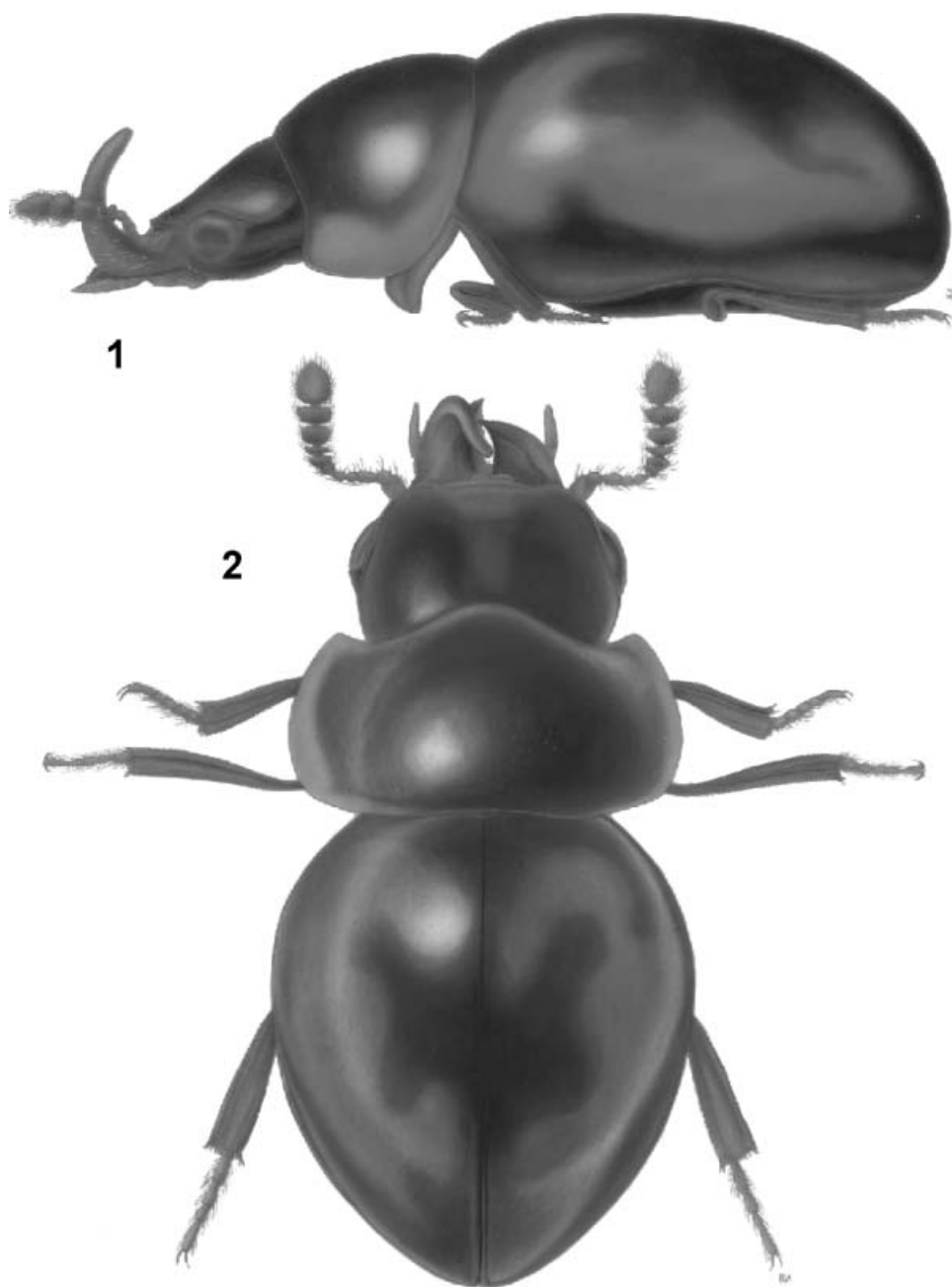
Exaggerated morphology in male beetles such as horns, enlarged mandibles and prolonged appendages have been investigated in a wide variety of correlated contexts including behavior, development, phylogeny, and genetics (for a review of some of these issues, see Eberhard and Gutiérrez 1991; Emlen and Nijhout 2000). Unusual male ornamentations, especially horns and enlarged mandibles, are often associated with intraspecific combat behavior between males. These types of allometric features have arisen throughout the Coleoptera including members of Cerambycidae (Goldsmith 1987), Chrysomelidae (Eberhard 1981), Curculionidae, (Eberhard 1983; Franz 2003), Lucanidae (Otte and Stayman 1979), Tenebrionidae (Brown and Bartalon 1986), and Staphylinidae (Forsyth and Alcock 1990; Hanley 2001). Horns are perhaps best known in the rhinoceros beetles of the family Scarabaeidae (Eberhard 1979; Kawano 1991, 1995). In many cases these features are allometric with larger males exhibiting disproportionately larger ornaments. In some cases these features display distinctive allometric patterns such as sigmoid or

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discontinuous scaling relationships in which small individuals do not express the unusual feature, whereas larger individuals do. This general phenomenon is explained by a complex model of development, behavior and evolution that allows the decoupling of phenotypes of large and small male individuals and phenotypes of males and females, permitting each of these to evolve independently (Emlen and Nijhout 2000).

The unusual horns in species of the beetle genus *Agathidium* Panzer have been known to the few students of leiodid taxonomy for many years. However, they have been overlooked by investigators of beetle horns and other exaggerated insect morphologies in general. The horns of these obscure beetles are unusual in that they are asymmetrical, arising from the dorsal surface or the apex of the left mandible and extending up and over the mandibles or over the front of the head. The horn comes in a variety of forms and its shape is often diagnostic for a given species. In the vast majority of cases in which male insects exhibit horns or other exaggerated morphologies the features are bilaterally symmetrical. Asymmetry in male ornamentation is rarely reported, though examples do exist such as in several groups of crustaceans which have males bearing an enlarged cheliped on one side (Mariappan et al. 2000). In beetles, the staphylinid subgenus *Oxyporus* (*Pseudoxyporus*) Nakane and Sawada includes males with the right mandible longer and more strongly curved than the left (Hanley 2001). Also, some members of the geotrupine genus *Lethrus* Scopoli have prominent horns on the ventral surface of the mandible. In some cases, *Lethrus* horns are asymmetrical with a long, spinous horn on the left mandible and a shorter horn on the right (M. A. Ivie, Montana State University, personal communication), but this appears to be secondarily derived from species with a horn on both sides since the majority of the *Lethrus* species have symmetrical horns, and symmetrical horns are pervasive in the Scarabaeoidea. Interestingly, asymmetry (fluctuating asymmetry) in sexually selected features has often been regarded as a possible indicator of environmental stress in an individual or population (e.g. Palmer and Strobeck 1986; Leary and Allendorf 1989; Parsons 1990, 1992) and as a possible indicator of poor male fitness to females which may tend to choose bilaterally symmetrical males (e.g. Moller 1992, 1993a, 1993b). In *Agathidium*, male horns are very conspicuously asymmetrical clearly implying that, at least in these taxa, asymmetry in these features is not an important indicator of environmental stress or poor male fitness.

Members of *Agathidium* (Figures 1, 2) are small to extremely small beetles in the family Leiodidae and are primarily Holarctic in distribution. They are among the few groups of Coleoptera that regularly occur on slime molds (Myxomycetes) (Lawrence and Newton 1980; Wheeler 1984a, 1984b; Stephenson et al 1994). The group is taxonomically diverse with about 800 described species and probably a great many undescribed members, though the group itself may not be monophyletic (Miller and Wheeler forthcoming; Wheeler and Miller forthcoming). Some of the species are exceptionally common, whereas others are cryptic and uncommonly collected since they occur in leaf litter and other inconspicuous places. The group has been divided into a number of subgenera (see Angelini 1995), also of dubious monophyletic status (Miller and Wheeler forthcoming; Wheeler and Miller forthcoming). Horned species occur mainly in the subgenus *A. (Neoceble)* des Gozis, though a few members of *A. (Cyphoceble)* Thomson and *A. (Macroceble)* Angelini are horned as well. Horned species of *Agathidium* are often relatively commonly collected, and are generally not among the more cryptic in habits. Instead they often occur on the surfaces of myxomycetes, the fruiting bodies of which occur conspicuously on the surfaces of logs and other decaying wood. Extremely little has been published about *Agathidium* behavior in general or their mating biology, and nothing has been written about behavioral correlates of the unusual male horn morphology.



Figures 1, 2. *Agathidium pulchrum*, habitus: (1) lateral; (2) dorsal.

Here for the first time we call attention to the unusual horns of male *Agathidium* by presenting an account of some of the variation in horn morphology, an examination of the scaling relationships of horns in two species, *A. angulare* and *A. pulchrum*, description of mating behavior and other behaviors in *A. pulchrum*, and a discussion of the possible evolution of these features.

Material and methods

Measurements

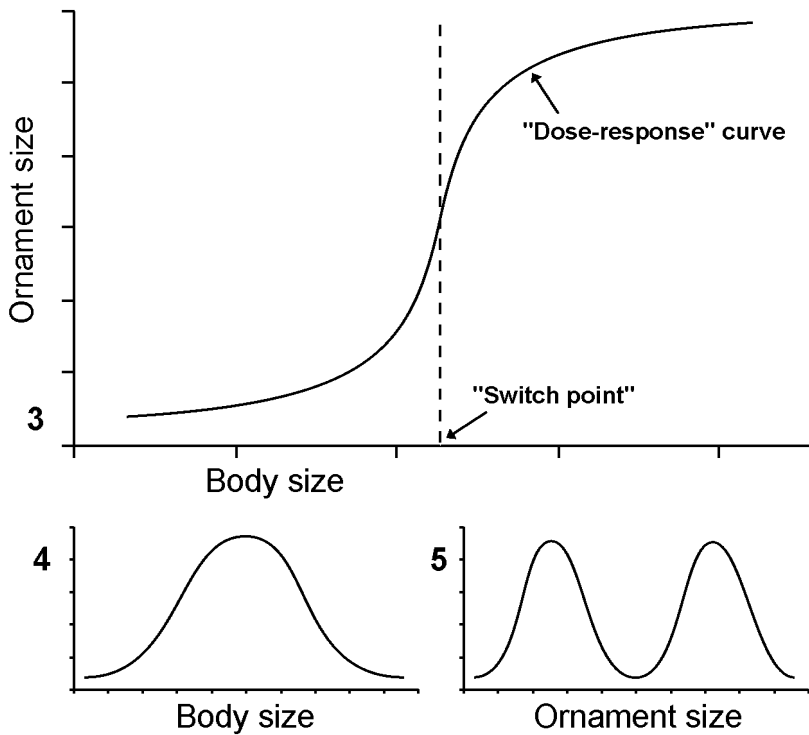
All measurements were made using a Lasico ocular digital micrometer on a Wild M3C dissecting microscope to the nearest 0.01 mm. Large series of male specimens for measurement were available for two species, *A. angulare* and *A. pulchrum*. These series were specimens collected in Alaska, USA and the Yukon and British Columbia, Canada and are deposited in the Canadian Museum of Nature, Ottawa. The specimens were collected from flight intercept traps and sifting of litter and Berlese extraction devices, and probably represent a relatively random sampling of the local populations of beetles. One hundred and eighteen males of *A. angulare* and 64 males of *A. pulchrum* were measured. The greatest width of the pronotum was measured as an indication of overall body size. Mandible height was measured from the ventral margin of the mandible to the apex of the horn, when present, or a point near where the horn originates on the mandible of specimens that lack a long horn (Figures 27, 28).

Statistics

Eberhard and Gutiérrez (1991) established a method of fitting measurement data to particular models to characterize the relationship between male ornament and body sizes. Their procedure involved fitting the data to linear regression models to test for linearity and examine for possible abrupt changes in slope which would indicate a “switch point” in the allometric relationship between body size and ornament size (Eberhard and Gutiérrez 1991). To empirically test for linearity, they fit their data to a quadratic regression model and used results from an *F* test to examine whether this model fit the data significantly better than a linear one. This method is straightforward, but may not always indicate nonlinearity when data are highly sigmoid, as they could be when the switch point is very discontinuous. In some cases, the data may be highly S-shaped (Figure 3). Under these circumstances, body size in a given population may be normally distributed (Figure 4) whereas male ornament size may be bimodal in distribution (Figure 5). In this case, a cubic model may fit the data better than either a linear or a quadratic model, and a quadratic model may not fit the data well at all. Other researchers (e.g. Hanley 2001) found circumstances in which fitting data to a quadratic model failed to indicate nonlinearity despite a nonlinear data pattern apparent from inspection of a scatter plot. Under circumstances where the data are highly sigmoid (i.e. the switch point is highly discontinuous), it may be more appropriate to fit data to a nonlinear regression model. Nonlinear regression is appealing in this and similar cases because the models often have relatively intuitive biological interpretations. In our case it appeared from a scatter-plot graph that in each species the data were clearly sigmoid with a distribution that resembled a dose–response curve. This type of data may be appropriately modeled with the following four-parameter logistic equation:

$$Y = (A - B) / (1 + 10^{(X - P)^{-S}}) + \varepsilon \quad (1)$$

where *Y* is the male ornament length (e.g. mandible height); *X* is an indicator of body size (e.g. pronotum width); *A* is the maximum value of the upper part of the curve; *B* is the minimum value of the lower part of the curve; *P* is the inflexion point; *S* is the slope of the inflection point; and ε is random error. Of these values, *P* and *S* are particularly interesting for this project because *P* can indicate the point in body size below which males tend to lack



Figures 3–5. (3) Expected distribution of body size versus ornament length under nonlinear regression model (dose–response curve) with switch point indicated by dashed line. (4) Expected frequency distribution of body size data in species of *Agathidium*. (5) Expected frequency distribution of ornament length data in species of *Agathidium*.

a horn and above which they tend to possess one and S can indicate how steep or abrupt this “switch point” is. Although this model is certainly not appropriate for all studies of allometry in male ornaments, for apparently sigmoid data it may be more appropriate than the series of linear models used by Eberhard and Gutiérrez (1991).

Data were analysed using SAS (SAS Institute, Cary, NC) using the NLIN procedure and estimating initial parameter values from inspection of graphs of mandible height versus pronotal width for each species.

Behavior

Observations of mating behavior were made of *A. pulchrum* collected during 21–26 June 2002 in several areas of Lincoln, Lake, Flathead, and Ravalli Counties in north-west Montana, USA. Some features of behavior were observed in the field on slime molds, but mating and male–male combat behavior was not. Approximately 15 specimens were taken alive into the laboratory and placed in a small, clear plastic container with wood containing fruiting bodies of the slime molds *Ceratiomyxa fruticulosa* (Müller) and *Stemonitis fusca* Roth, species on which *A. pulchrum* specimens were regularly collected in the field. A single horned male and numerous unhorned males were observed during interactions with each other and several females over several hours. Observations were made under relatively low light conditions through a Wild M3C dissecting microscope. The specimens were observed

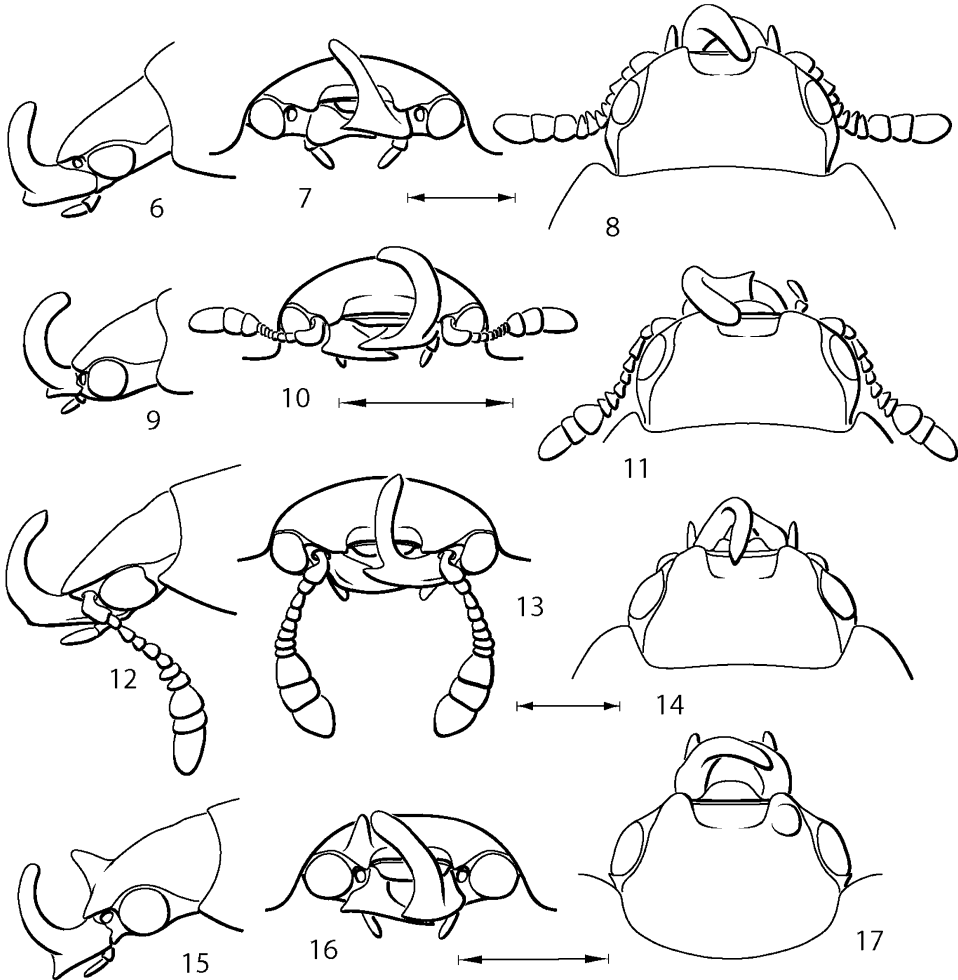
feeding, in combat between males and mating, suggesting that the laboratory conditions, though somewhat artificial, did not strongly inhibit behaviors of the subjects.

Results

Horn morphology

Nearctic *Agathidium* male mandibular horns occur in several forms which are organized here into four general types based on observed similarity in structure and orientation.

Type I (Figures 1, 2, 6–17). This type of horn, when fully developed, is long and roughly circular in cross-section. It is curved and generally extends upward and posteriorly over the

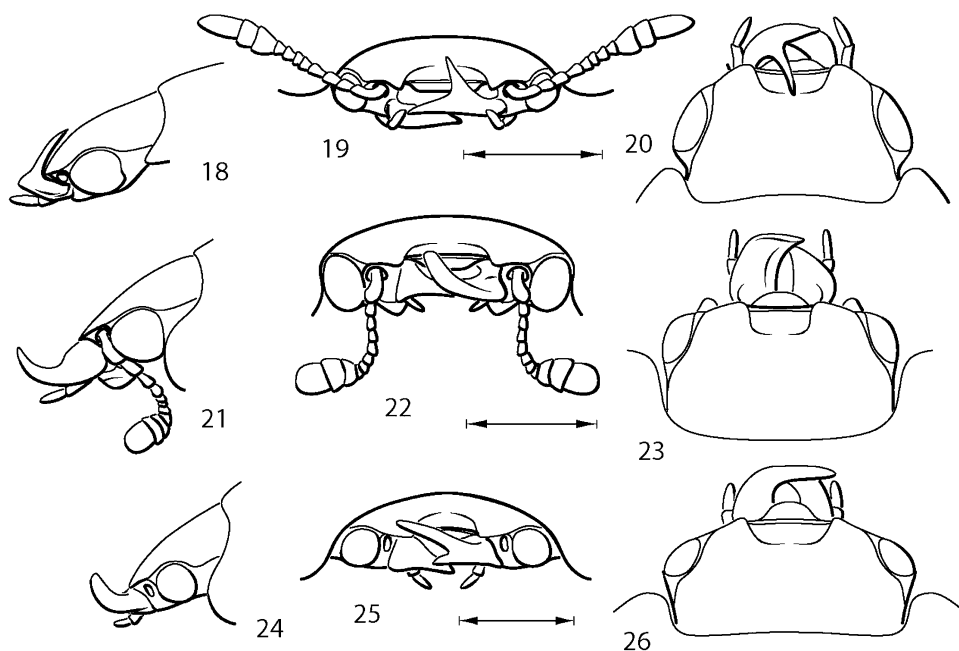


Figures 6–17. *Agathidium* species showing variation in horn morphology. (6–8) *A. angulare*: (6) left lateral; (7) anterior; (8) dorsal. (9–11) *A. mollinum*: (9) left lateral; (10) anterior; (11) dorsal. (12–14) *A. pulchrum*: (12) left lateral; (13) anterior; (14) dorsal. (15–17) *A. marae*: (15) left lateral; (16) anterior; (17) dorsal. Scale bars: 0.5 mm.

clypeus. The horn is setose with a semicircular, subapical line of longer, denser setae. Nearctic species in which this horn occurs include the Nearctic *A. akallebregma* Miller and Wheeler, *A. amae* Miller and Wheeler, *A. angulare* Mannerheim (Figures 6–8), *A. brevisternum* Fall, *A. difforme* (LeConte), *A. hamata* Miller and Wheeler, *A. maculosum* Brown, *A. marae* Miller and Wheeler (Figures 15–17), *A. mollinum* Fall (Figures 9–11), *A. politum* LeConte, and *A. pulchrum* LeConte (Figures 1, 2, 12–14), and the Palearctic *A. mandibulare* Sturm, *A. plagiatum* (Gyllenhal), *A. rhinoceros* Sharp, and probably many more that we have not had the opportunity to examine. There is some variation in the form of the horn. In *A. maculosum* it is longer, straighter and somewhat more dorsoventrally flattened than in other more typical species. In *A. mollinum* the horn extends in a long, sweeping curve to the left rather than up and over the clypeus (Figures 9–11). *Agathidium marae* is particularly unique in having not only this type of mandibular horn, but some specimens also have an additional horn extending from the right side of the frons just to the right of the lateral clypeal margin (Figures 15–17).

Type II (Figures 18–20). This type of horn is relatively short, flattened, spinous and extends very close over the anterior surface of the head. The sharply pointed horn is glabrous and lacks a curved line of dense setae subapically that is present in many other species. Members of the Nearctic *A. picipes* (Figures 18–20) and *A. repentinum* Horn have this type of horn.

Type III (Figures 21–23). In this type of horn the apex of the mandible extends in a sweeping, upward curve. The apex of the horn is truncate and glabrous. Members of *A. aristerium* Wheeler have this horn type (Figures 21–23).



Figures 18–26. *Agathidium* species showing variation in horn morphology. (18–20) *A. picipes*: (18) left lateral; (19) anterior; (20) dorsal. (21–23) *A. aristerium*: (21) left lateral; (22) anterior; (23) dorsal. (24–26) *A. atronitens*: (24) left lateral; (25) anterior; (26) dorsal. Scale bars: 0.5 mm.

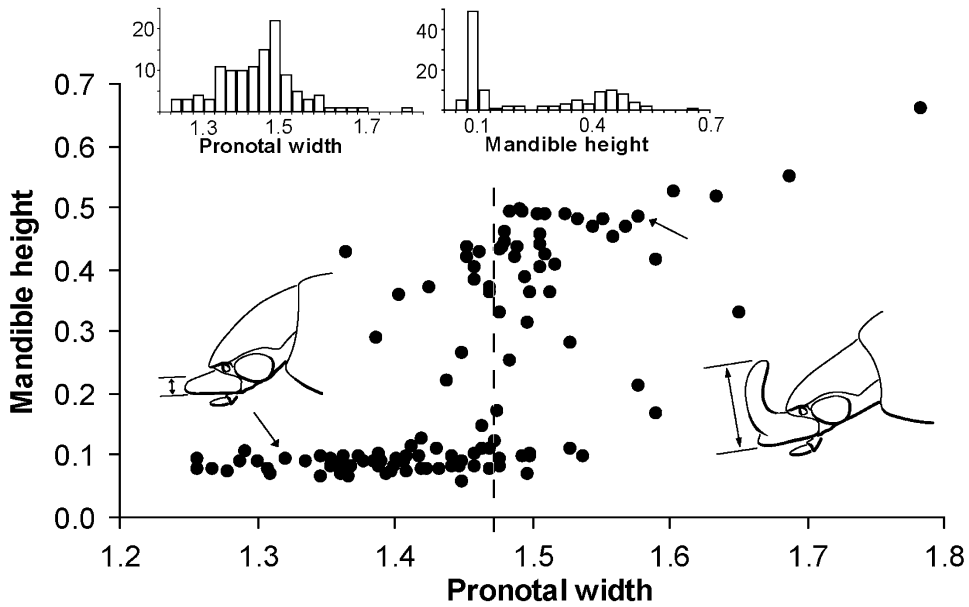


Figure 27. Frequency histograms of greatest pronotal width and mandible height (measured as indicated on illustrations), and relationship between greatest pronotal width and left mandible height for *Agathidium angulare* ($n=118$). Arrows indicate individuals illustrated. Dashed line on X-axis indicates optimal inflexion (switch) point (P in Model 1).

Type IV (Figures 24–26). This type of horn is a moderately short, straight, spinous process extending from the dorsal surface of the mandible at an oblique angle to the right over the right mandible. The horn may be the same as the Type I horn, but its unusual shape and angle suggest it may not be homologous with horns of that type. The Nearctic *A. atronitens* has this horn (Figures 24–26), and the Palearctic *A. discoideum* Erichson and *A. marginatum* Sturm appear to have similar horns, but we have not seen specimens of these species with well-developed horns.

Scaling relationships

Both *A. angulare* and *A. pulchrum* exhibit a distinctly sigmoid, or discontinuous, scaling relationship between pronotal width and mandible height (Figures 27, 28). Pronotal width exhibits a near normal distribution, whereas mandible height is bimodal (Figures 27, 28). An F test indicated very high significance when data were fit to the four-parameter logistic regression model (Model 1 above) in each case (Table I). Parameter estimates are presented in Table I. Switch points estimated from the model are indicated in Figures 27, 28. In each case the slope is positive and extremely steep, indicating a very abrupt switch point in body sizes that either lead to or fail to lead to development of a horn (Table I).

Behavior

Specimens of *A. pulchrum* were observed engaging in several types of behavior. In the field, specimens were found to be sensitive to large-scale movements by the collector. When

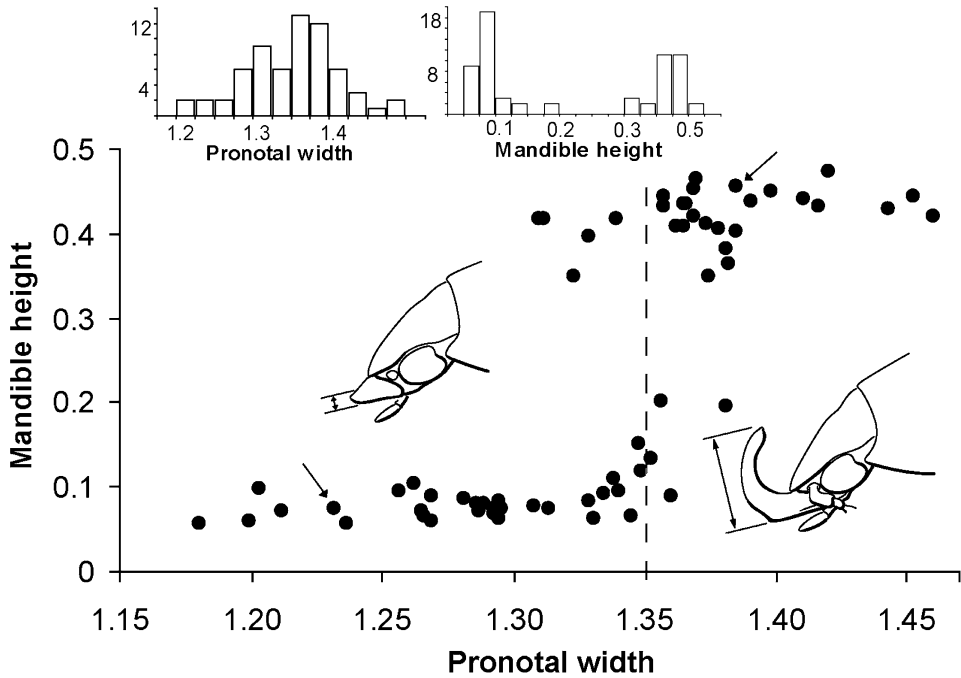


Figure 28. Frequency histograms of greatest pronotal width and mandible height (measured as indicated on illustrations), and relationship between greatest pronotal width and left mandible height for *Agathidium pulchrum* ($n=64$). Arrows indicate individuals illustrated. Dashed line on X -axis indicates optimal inflexion (switch) point (P in Model 1).

approached by a collector individuals that are conspicuously exposed on the surface of a slime mold or nearby on the surface of the wood either begin to move rapidly and do so until concealed or, less commonly, contract the body and drop from the surface to the substrate below where they then move rapidly until concealed. Specimens observed in the laboratory were also found to be negatively phototactic. When strong lights are shone on the specimens they move very rapidly until entering an area of lower light conditions where they move more slowly and/or stop entirely. Members of *Agathidium* are morphologically

Table I. Results of four-parameter logistic regression for two species of *Agathidium*.

Species	Parameter ^a	Estimate	SE	Approximate 95% confidence limits
<i>A. angulare</i> (P value from F test <0.0001)	A	0.43	0.04	0.35–0.51
	B	0.09	0.03	0.03–0.14
	P	1.47	0.01	1.45–1.49
	S	33.49	12.42	8.88–58.09
<i>A. pulchrum</i> (P value from F test <0.0001)	A	0.46	0.05	0.37–0.56
	B	0.08	0.03	0.023–0.14
	P	1.35	0.01	1.33–1.36
	S	50.00	18.81	12.38–87.62

^aParameters are those included in Model 1: A , maximum value of the upper part of the curve; B , minimum value of the lower part of the curve; P , inflexion point; S , slope of the inflection point.

contractile, and when probed by an investigator or another beetle, individuals often contract, directing the head ventrally and tucking the legs and antennae under the body.

Males and females were observed feeding on *Stemonitis fusca* sporangia. Feeding occurred frequently and apparently whenever suitable food was encountered. In most cases an individual feeds on a single cluster of sporangia moving up and down the structure very actively while masticating spores and, apparently, other portions of the structure. Male mandibular horns do not appear to significantly interfere with feeding, but observations of this were limited.

Both males and females were observed to move around on the surface of the slime mold and nearby substrate, stopping to feed, clean themselves with their front legs or simply stopping for no apparent reason. In this last case, individuals often stopped with their heads strongly deflexed in a contracted position. The antennae were typically oriented under the head and were not visible during the time when the individual was not moving. During movement, individuals regularly encountered each other. Upon doing so, they used their antennae to touch and probe each other. When two males encountered each other, the individuals usually (but not always) immediately engaged in fighting behavior. A male rapidly moved his head forward and upward in a rapid, thrusting motion consisting of two to five thrusts. At the same time the male moved forward on the substrate toward his opponent. Angle of attack varied, but was usually not head-to-head, so typically only one of the males made the head-thrusting movements. In many of the observed encounters, the attacking male succeeded in dislodging his opponent from the substrate after the other attempted to evade and orient himself head-first toward the advancing male. Both horned and unhorned males engaged in the head-thrusting behavior upon encountering another male, and each type of male was able to displace his opponent, but a horned male was apparently more successful in dislodging his opponent. In these cases the long horn was hooked under the body of the opposing male and the head-thrusting movements lifted the opponent from the substrate, knocking him off.

When a male and female encountered each other, the male stopped probing and typically very rapidly moved to mount the female to mate. The male genitalia were extruded while the male oriented himself on top of the female in a manner typical of many beetles. Females did not appear to resist male mating advances. Numerous matings were observed and these were all short in duration, on the order of 5–10 s, after which each individual moved away from each other. In many instances a male was observed using the head-thrusting behavior against the female prior to and after mating. In these instances the thrusting behavior was not as vigorous as between two males, and was apparently not as persistent, consisting in most cases of only one or two relatively light thrusts.

Discussion

We have not had the opportunity to examine many Palearctic members of the genus, but several have horns similar to horn Type I (Angelini 1995) and Type IV (see above). Others have rather dramatically different horns such as *A. temporale* Sahlberg which possesses two long horns on the left mandible (Angelini 1995). Many species of *Agathidium* apparently lack horns entirely, even some that appear to be relatively closely related to horned species. The four types of horn presented here represent primary homology assessments, and mandibular horns certainly have potential as phylogenetically informative characters. However, conclusions about relationships based on these primary homologies (and whether the horns or horn types are, in fact, homologous) are not warranted at this time given

the lack of a comprehensive cladistic analysis of all characters. An understanding of the evolution of horns in *Agathidium* would be much improved by a cladistic analysis. This could provide evidence for a single or multiple origins or losses of horns or horn types or for the order of evolution of features related to mating behavior or horn morphology.

The scaling relationships of the two species studied in detail here exhibit a characteristic allometric pattern in which larger males possess horns and smaller males do not. In both of these species there is significant evidence of a distinctive "switch point" in the relationship at which there is a narrow range of body sizes below which males essentially lack a horn and above which males have a horn. This type of scaling relationship is less common in male ornamentalations than other relationships, but it does occur in certain species of beetle (Eberhard and Gutiérrez 1991; Emlen and Nijhout 2000). *Agathidium* males are unique, however, in having these horns dramatically asymmetrical and occurring only on the left mandible or, in the single example of *A. marae*, on the left mandible and the right surface of the frons (Figures 15–17). In the case of these *Agathidium* the test of linearity performed by Eberhard and Gutiérrez (1991), wherein the data are fit to a quadratic model, was shown to be inadequate. The quadratic model did not have a significantly better fit than a linear one with each species which, using the methods of Eberhard and Gutiérrez (1991), would have led us to accept that the data were linear. Fitting the data to a higher-order polynomial and testing the relative fit of the models revealed that the cubic regression model fit the data significantly better than either the linear or quadratic with each species. This suggests that future researchers should take care not to simply accept linearity in a scaling relationship when the data fail to fit a quadratic model, especially when data exhibit a strongly sigmoid shape. The nonlinear four-parameter logistic model we used to fit the data has a biologically intuitive interpretation and indicated clear, extremely abrupt (steep) switch points (Figures 27, 28; Table I).

Prior to this study there were no published observations of possible behavioral correlates of the male mandibular horns in *Agathidium* species. Many beetle species with horns that display discontinuous or sigmoid scaling relationships exhibit combat behavior between those males with horns. In members of *A. pulchrum* both horned and unhorned males appear to engage in combat behavior in the form of rapid head-thrusting and forward movement against an opponent. Since the slime molds on which these beetles live generally occur on the sides of logs or other rotting wood, these head-thrusting behaviors apparently succeed in essentially removing the opposing male from the immediate area. Presumably this would give the remaining male an advantage in accessing available females. The horn appears to be an improved means for competing with rival males by providing greater leverage for removing them from the substrate surface. Based on the relatively limited observations made of *A. pulchrum*, it would appear that the horned males are, in fact, very good at dislodging rival males whereas unhorned males are somewhat less capable of doing so.

The occurrence of head-thrusting behavior of a male against a female prior to and after mating was unexpected given that the behavior is used to displace a rival male. That a male does the activity prior to mating and that the head thrusts appear to be less vigorous against a female than against a male would seem to suggest that it is not an attempt to displace a female or remove her from the substrate since doing so would remove his opportunity to mate with her. It seems more likely that this represents a courtship behavior as it is applied to females, perhaps giving a female the opportunity to assess the relative strength or other fitness cues of the male. A female might presumably be more interested in mating with a

male with the ability to engage in head-thrusting behavior since males that do so may have greater fitness. Thus, the head-thrusting behavior performed on females may be simply signaling a male's ability to do so. This is certainly speculative, and we are not able to offer a well-supported explanation based on the currently limited evidence.

There are several additional things that are not known within this scenario of *Agathidium* horns and mating behavior. To begin with, as previously mentioned, it is not clear whether the various types of horn are homologous or, if they are, which type is derived from which other type. If the evolution of the head-thrusting behavior preceded the evolution of horns, then the independent derivation of several types of horn, which presumably provide greater leverage to dislodge a rival male in each case, would make intuitive sense. However, it is not known whether horns of other types function in a manner similar to the type in *A. pulchrum*. Also, simply based on observation of the morphology there are clearly large differences between the various types of horn such that even regarding them initially as homologous seems equivocal. If the mandibular horns are not homologous, and even if the various species use a head-thrusting behavior, there is no obvious reason for non-homologous horn-like projections to be confined to the left male mandible. It is possible that there are some developmental features of the left mandible that predispose their modification into horns. Asymmetry in beetle mandibles is common (perhaps even pervasive), suggesting that each mandible is already subjected to different independent developmental influences. Mating and combat behavior have not been investigated in other non-horned *Agathidium*, so it is not known how widespread the head-thrusting behavior actually is.

Often in other species of beetles with bimodal (nonlinear) scaling relationships with male horns each of the two male forms exhibits different behaviors and different strategies for acquiring mates (e.g. Eberhard 1982). In *A. pulchrum* both horned and unhorned males engage in head-thrusting combat behavior (and head-thrusting courtship behavior with females), and it is not clear what alternative strategies the two forms might be employing. Larger, horned males may be better competitors during combat, though they may be less mobile or agile. Smaller males, though not horned, may be better at evading aggressive, larger males and may still succeed in dislodging similar-sized or even larger males with head thrusts at least some of the time. There may also be seasonal differences in emergence of unhorned versus horned males, differences in mortality rates, differences in ability to feed, etc.

Agathidium behavior has been rarely reported previously. Several features of non-mating behavior in *A. pulchrum* are noteworthy. Specimens of this species are strongly negatively phototactic. In addition, specimens are sensitive to large-scale movement nearby such as by a collector, even to the point of dropping from the surface of the substrate. These features suggest that individuals seek to evade larger predators that orient visually. There have been no specific accounts of predation on *Agathidium* adults, and the habitats in which they occur, slime mold sporangia on the sides or undersurfaces of logs in dense forests, seem to be areas where predation by large predators, such as vertebrates, would be relatively unlikely. Of possible predators, birds appear to be the most likely candidates for preying on *Agathidium* adults. Contractile behavior, facilitated by contractile morphology, appears to be a defense against small predators, perhaps predatory beetles such as members of Staphylinidae and Carabidae.

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