Size-specific defensive structures in a horned weevil confirm a classic battle plan: avoid fights with larger opponents

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A rigid sheath that extends deep into the prothorax of male *Parisoschoenus expositus* serves to receive the horns of opponents in battles over females. The male cannot use his own horn unless he receives his opponent's horn in his sheath. The length of a male's sheath is always approximately equal to the length of his own horns, so his body design is appropriate only for horn-locking battles with males whose horns are equal to or shorter than his own. Horn length and sheath length are dimorphic with respect to each other and to an indicator of body size. The switch points between morphs are very nearly the same for several relationships, so the different aspects of fighting morphology are tightly coordinated.

Keywords: allometry; weapons; beetle horns; weevils

1. INTRODUCTION

Behavioural observations of many animals indicate that when males battle for females, smaller individuals usually avoid or quickly break off direct confrontations with larger opponents (e.g. Andersson 1994). The data in this paper constitute an unusual morphological confirmation of this battle plan in the horned weevil *Parisoschoenus expositus* (Champion 1908)(Curculionidae: Baridinae). Males of *P. expositus* use their paired prothoracic horns (figure 1*a*) to fight each other for sexual access to a female that is drilling a hole into which she will lay an egg (Eberhard & Garcia-C. 2000). Male horn designs are dimorphic, with larger individuals having more elaborate horns (Eberhard & Garcia-C. 2000). The morphs probably result from expression of different sets of genes (Eberhard 1980). Most males have a pit between the bases of their horns that extends internally as a rigid, forked tube or sheath (figure 1*b*). In a large male this sheath projects deep inside his thorax. During intense battles each male inserts one of his horns into the sheath of his opponent, and then each male attempts to twist his opponent and render him helpless by lifting his nearside legs from the substrate (Eberhard & Garcia-C. 2000). The horn enables a male to exert a twisting force on his opponent in a mechanically more effective manner.

Horns and sheaths are stiff, so precise positioning of both beetles is needed for horn insertion to succeed. It is mechanically impossible for a male to insert one of his own horns into an opponent unless he simultaneously receives one of his opponent's horns in his own sheath. The male's sheath thus represents an unusual type of structure: for the proper functioning of his horns as weapons, a male's sheath must receive the horn of his opponent. By examining the static allometric relations between body size, horn length, sheath length and other design features, one can deduce the sizes of the opponents against which a beetle is designed to fight.

2. METHODS

Beetles were collected in plantations of the African oil palm (*Elaeis guianensis*) near Parrita, Puntarenas, Costa Rica (elevation 20 m asl) between 25 January and 10 February 1998. Isolated prothoraces of 145 male beetles were measured to the nearest 0.025 mm using an ocular micrometer. The dimensions of the sheath and several aspects of horn design were then measured after digesting away internal tissues with weak HCl and removing the dorsal and lateral walls. For lateral views of horn and sheath (figures 2 and 3), the longitudinal axis of the prothorax was carefully orientated perpendicularly to the optical axis of the ocular micrometer by aligning the tips of the horns and sheaths and by orientating the ventral surface vertically. The prothorax was then turned to measure the sheath in dorsal view (figure 4*b*), with the axis of the sheath perpendicular to the optical axis. The beetle was also measured in ventral view with the anterior borders of the prothorax aligned; distances between the horns at the base (*H*), midway along the horn (*G*) and at the tips (*F*) were measured (figure 4*d*). By subtracting the calculated distance (*F'* in figure 4*d*) that would have separated the tips if the distal halves of the horns were straight from the measured distance, and correcting for horn length, an indicator of the lateral curvature of the distal halves of the horns, $(F - F')/B$, was obtained. The horn and prothorax were also measured in lateral view in an additional sample of 394 intact males.

Measurement precision was determined by repeated measurements of the same specimens. Absolute differences between first and second measurements, when divided by the mean value of the trait, averaged $2.7 \pm 0.9\%$ (range 1.4–4.4%).

Statistical tests for dimorphisms involved tests for switch points and different regression slopes and intercepts, as in Eberhard & Gutierrez (1991). A test of deviation from simple allometry ($y = ax^b$, $b = 1$) was performed on log-transformed values by attempting to fit

$$y^* = \alpha_0 + \alpha_1 x + \alpha_2 x^{*2} + e, \qquad (1)$$

in which y^* is the log to base e of a measure (e.g. length) of the horn or sheath, x^* is the log to base e of another trait (e.g. an
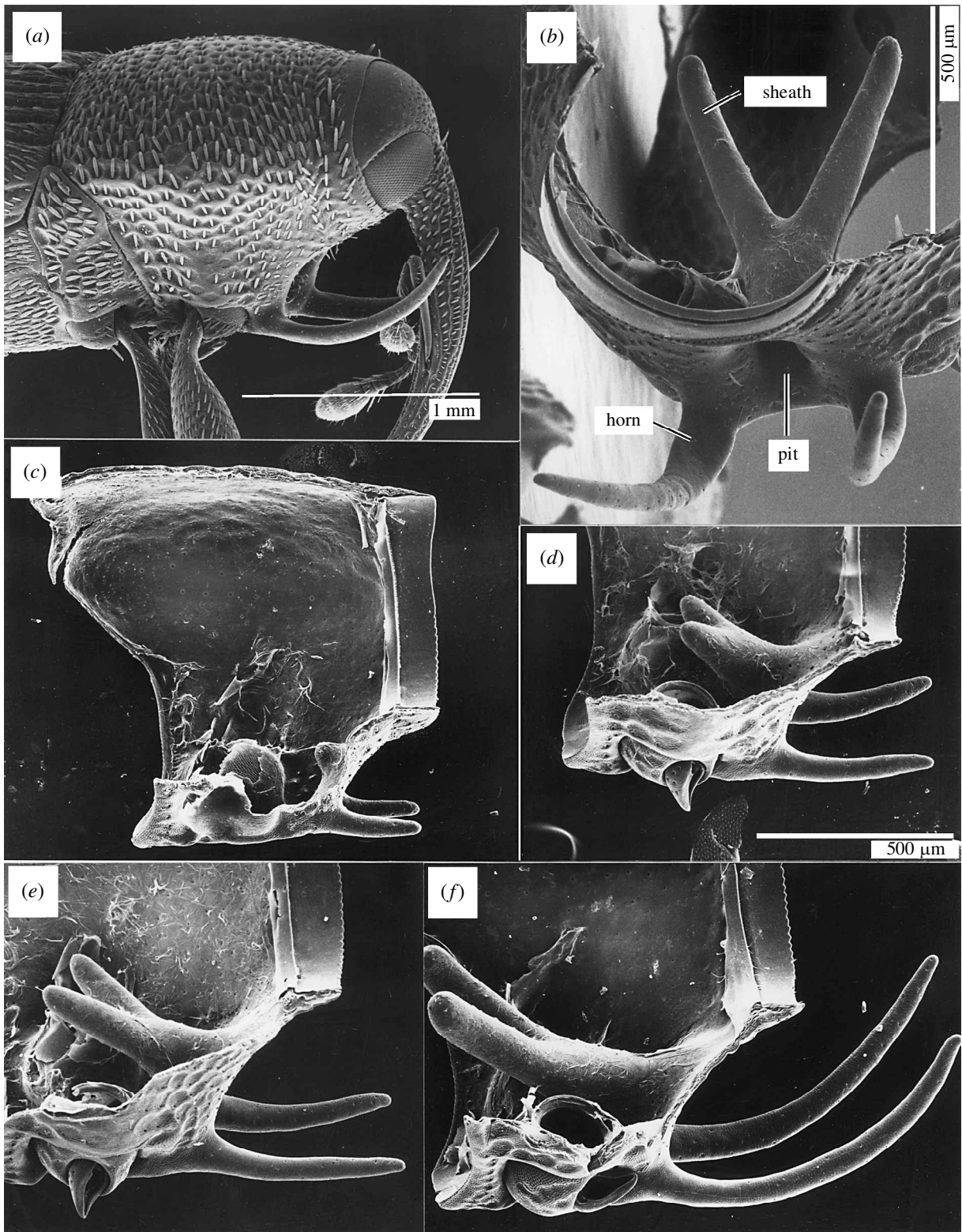
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Figure 1. (*a*) Portrait of an intact male with large horns. (*b*) Anterior view of a male's pit and sheath (head and soft parts of prothorax removed). (*c*)–(*f*) Cutaway views of the horns and sheaths of males of four different sizes shown at the same magnification.

indicator of body size such as prothorax length), α_i are the regression coefficients and e is the random component with assumed normal variation, zero mean and common variance. If coefficient α_2 was significantly different from zero, the existence of a dimorphism was taken to be likely and a hypothesis regarding possible switching mechanisms was tested.

Analysis of dimorphisms was performed by a least-squares piecewise linear regression of the model

$$y = a_1 + b_1 x + M[a_2 + a_1 + (b_1 + b_2)x], \qquad (2)$$

in which y and x are actual measurements, M is 0 if x (or y) is less than the switch point and 1 otherwise, and a_i and b_i are the
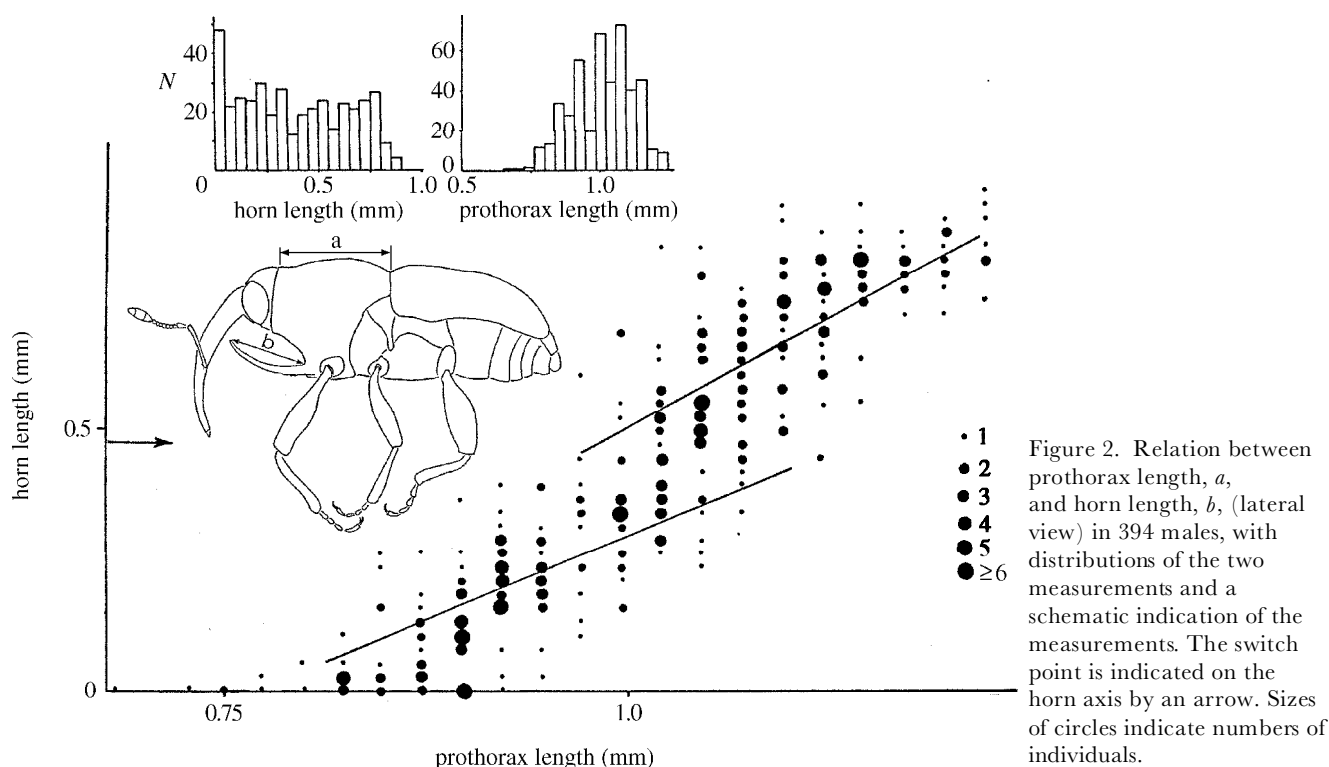
Figure 2. Relation between prothorax length, *a*, and horn length, *b*, (lateral view) in 394 males, with distributions of the two measurements and a schematic indication of the measurements. The switch point is indicated on the horn axis by an arrow. Sizes of circles indicate numbers of individuals.

regression coefficients. The possible significance of both a second intercept (a_2) and a second slope (b_2) were tested against the null hypothesis that $a_2 = b_2 = 0$. The axis with the probable break point (*x* or *y*) was chosen according to the fit with the data on the basis of R^2-values. This permitted tests for possible break points on both axes, instead of only on the *x*-axis, a weakness of the previous technique (Eberhard & Gutierrez 1991). Finally, tests for further switch points in each subset of the data (above and below the switch point) were performed as just described.

3. RESULTS

Sheath length was, in general, approximately equal to horn length. Males were dimorphic for both horn and sheath length when compared with prothorax length; the intercepts were significantly higher for males that had horns and sheaths above the switch points (the slopes did not differ significantly) (table 1, figures 2 and 3). Horn and sheath morphs were highly coincident. All males with horn lengths longer than the switch point value also had sheaths whose lengths were above the switch point value for sheaths; only ten males with sheaths longer than the switch point had horns shorter than the switch point (figure 3). The switch point for horn length (0.48 mm) was nearly identical to that for sheath length (0.49 mm).

It is possible that this coincidence of switch points for horn and sheath lengths is an incidental consequence of their sizes, both resulting from a single developmental switch mechanism. Several additional relations argue, however, that horn length and sheath length are to some extent independent. The relation between horn length and sheath length was not simple: males with shorter horns had sheaths that were shorter proportionally (figure 4*a*—compare with line of equality), with a switch point nearly equal to that just mentioned (horn length = 0.49 mm). The allometry of different portions of

the sheath and horn also suggests a more complex set of developmental switches. The total length of the sheath was determined by the sum of the length of the lateral arms and the central trunk. These two parts did not increase in step. Small males completely lacked lateral arms, and the relations of sheath length with arm length and with distance between the tips were both triphasic (figure 4*b,c*, table 1). Both switch points in males with longer sheath arms corresponded to sheath lengths close to those in other relations. Horn allometry was also complex. The lateral curve of the distal half of the horn (($F - F'$)/B, figure 4*d*) showed a negative relation with prothorax length in smaller but not in larger males, and thus did not fit the dimorphic patterns of other measurements.

The diameters of both the base and the arms of the sheath were substantially greater than the diameters of the same male's horns, especially near their tips (figure 1*b*). The branches of the sheath were straight, even in large males in which the horns had substantial lateral and dorsal curves (figure 1*b*).

4. DISCUSSION

(a) *How long should a male's sheath be?*

A male's ability to fight opponents of different sizes will be affected both by the lengths of his own sheath and horns, and by the lengths of his opponent's sheath and horns. A reasonable lower limit for a male's sheath length can be deduced from arguments based on horn function. A male's sheath should allow him to insert the entire length of his own horn into his opponent. A sheath shorter than his own horn would not make adaptive sense, because a short sheath would hold some opponents at a distance, preventing the male from using the full length of his own horn. In such a case the male's horns
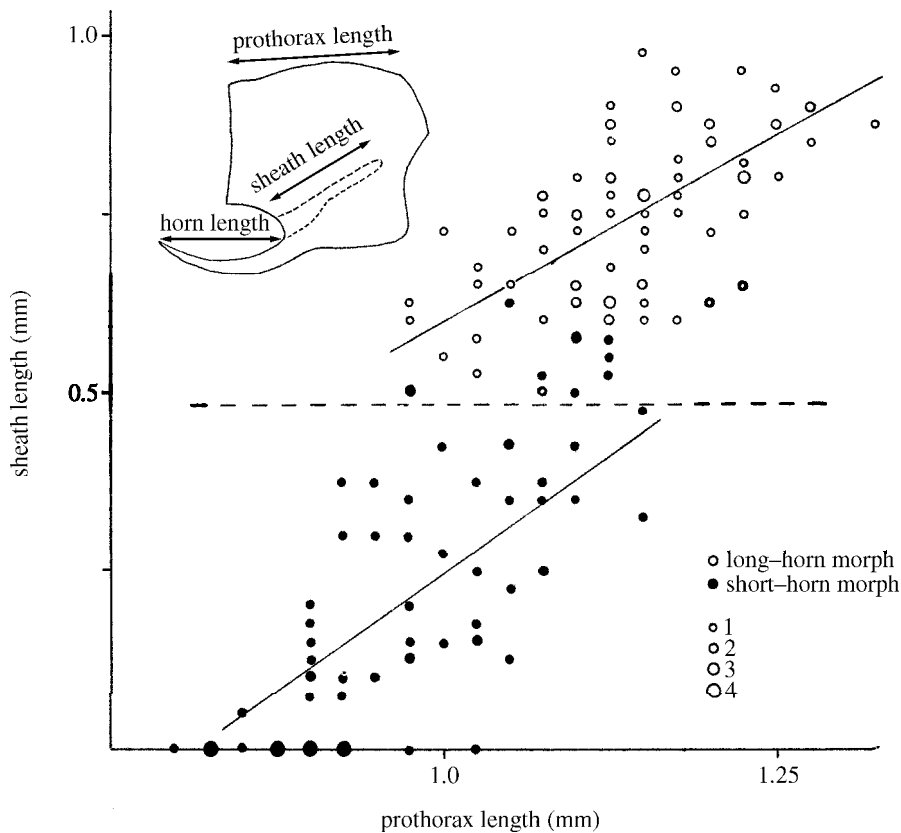
Figure 3. Relation between sheath length (lateral view) and prothorax length; each male with a horn shorter than the switch point value is indicated with a solid circle, while those with horns longer than this value are indicated with open circles. Sizes of circles indicate numbers of individuals.

would have an extra length that could not be used in contests with similarly sized males.

This argument implies that a male can reasonably expect that his opponents will all have sheaths that are at least as long as their own horns. This prediction was confirmed by our data. All males, except for very small individuals, had sheaths that were at least approximately as long as their own horns. In addition, the ten exceptional individuals that were not of the same horn and sheath morph all belonged to the long-sheath morph and short-horn morph (figure 3).

This argument sets an expected minimum for sheath length, but not a maximum. It is possible, for instance, that a male could have a sheath longer than his own horns, and thus be able to accommodate the horns of larger males. This design would only make adaptive sense if the male had a reasonable chance of winning battles with males whose horns are longer than his own. The observed pattern suggests that this is not the case, as sheaths were only about as long as the male's own horns.

The distance that remains between the bases of the horns of males when they lock horns is not known. In dead males manipulated to simulate horn-locking, it was of the order of 5–10% of the length of the horn of a large male. This distance must be added to the length of the sheath to determine the length of an opponent's horn that a male's sheath enables him to receive. The near equality of horn and sheath lengths (figure 4a) thus implies a design that enables males to fully employ their horns in fights with opponents with horn sizes of a length that may be slightly longer than that of their own horns.

The horn length at which the sheath structure first appears is *ca.* 0.12–0.14 mm (figure 4a). This might be

taken to represent the distance separating the two males' horn bases when the males battle. This interpretation would only be logical, however, if horns less than 0.12 mm do not contact the opponent, a proposition unlikely to be true since it implies that such horns are functionless. A seemingly more reasonable hypothesis is that the site engaged by very short horns on the opponent's body is more variable, often allowing a male to contact his opponent with his horns without having to receive his opponent's horns within his own body. Direct behavioural observations are needed to test this idea.

(b) *Allometric patterns*

Several different aspects of horns and sheaths had two distinct designs, and the various dimorphisms were tightly coordinated by having very similar switch points. For instance, nearly all males of the long-horn form were also of the long-sheath form (figure 3). The horn and sheath morphs associated with smaller body size both represented relatively smaller weapons for smaller males, as is common in other horned beetles (Eberhard & Gutierrez 1991). The lower emphasis on fighting ability in smaller males of *P. expositus* is presumably related to their inferior fighting ability, and their frequent use of an alternative aggressive tactic (harassment) that sometimes prevents a larger male from copulating before the contested female oviposits (Eberhard & Garcia-C. 2000). Otherwise, very small males flee from large males or avoid interactions. Similar associations between lack of horn development in smaller males, inferior fighting ability and alternative male tactics occur in horned beetles in other families (Eberhard 1982; Goldsmith 1987; Rasmussen 1994; Emlen 1997).
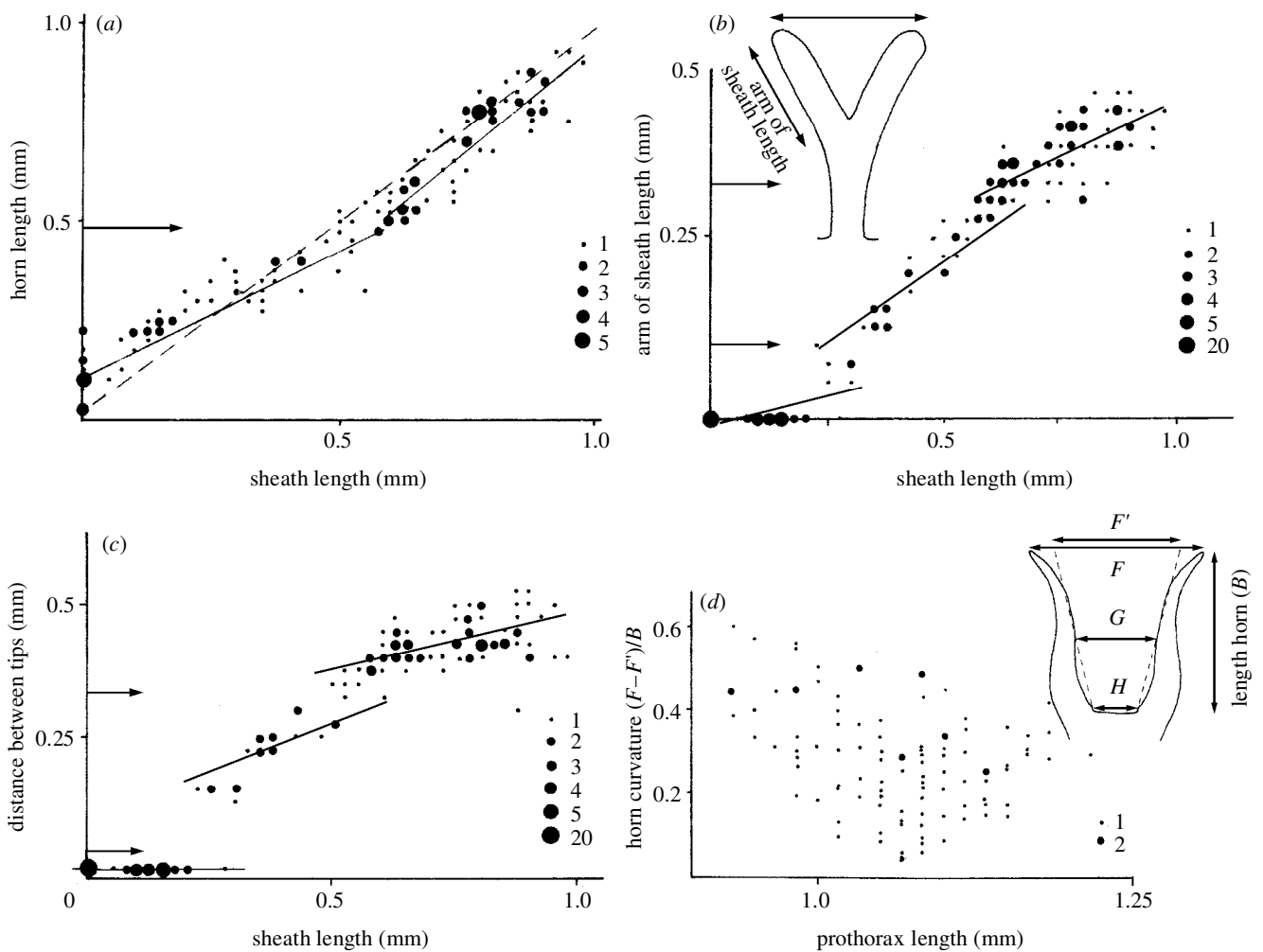
Figure 4. (*a*) Relation between sheath length and horn length (both in lateral view). The switch points (arrows) calculated in analyses against prothorax length are indicated for each (in (*a*)–(*c*)); the dashed line indicates equal lengths of sheath and horn. (*b*) Relation between length of sheath arm and sheath length in lateral view. The switch points (arrows) are indicated on the vertical axis. (*c*) Relation between distance between the tips of the sheath arms and sheath length (lateral view). The switch points (arrows) are indicated on the vertical axis by arrows. (*d*) Relation between an indicator of the degree of curvature of the distal half of the horn (($F - F'$)/B) and prothorax length.

Several other details of horn and sheath design showed allometries of possible functional significance. Males with shorter horns had relatively shorter sheaths (more consistently above the line of equal lengths in figure 4*a*). Possibly this is because short horns are more often used to deliver simple pushes rather than in twisting horn-locking battles. Very small males were never observed in horn-locking battles (Eberhard & Garcia-C. 2000). A second dimorphic design feature, the greater lateral horn curvature in larger males (figure 1*b*), could be explained by mechanical considerations. A greater lateral horn curvature will position the tips of a male's horns further from his opponent's midline, and thus increase the mechanical advantage of any twisting force he applies to his opponent. Accentuation of this feature in larger males may be associated with more frequent use of their horns in horn-locking battles in which twisting occurs, or greater ability to deliver powerful twists. The relatively smaller distance between the tips of the arms of the sheath in larger males (figure 4*c*) and their straight rather than curved arms may represent a counter-adaptation. A shorter distance between sheath tips would mean that the tip of the opponent's horn would be kept closer to the male's central

axis, and thus have less mechanical advantage in attempted twists.

It must be kept in mind, however, that the shape of a male's horns and sheath must at least approximately match the shapes of both the horns and sheaths of similarly sized opponents. For instance, in a population such as that of *P. expositus*, in which large males have curved horns and branched, narrow sheaths, a large male with either straight horns or an unbranched straight sheath would be unable to lock horns with his opponents, and would thus lose the advantage of using his own horn in battles.

Have defensive adaptations in sheath design driven horn evolution in these beetles? Or have offensive adaptations in horns driven sheath evolution? Why are sheaths relatively narrow, thus offering the opponent's horn purchase, when a large, open sheath cavity would seem to provide a better defence against being twisted and pushed? A useful first step to answering these questions would be to determine the probable sequence of evolutionary transitions in horn and sheath design in this group of beetles, taking into account the fact that non-fighting morphs in horned beetles are probably secondarily derived from fighting morphs (Eberhard 1980).

Table 1. *Values and significance levels of final models (equation (2))*

((*a*) and (*b*) are, respectively, prior to and after separation of samples at the first switch point.)

	horn length vs prothorax length	sheath length vs prothorax length	sheath length vs horn length
N	145	145	145
p for α_2	0.000013	0.00003	0.000013
switch point	0.48 mm (horn)	0.49 mm (sheath)	0.49 mm (sheath)
a_1	-0.888 ± 0.122***	-1.110 ± 0.148***	-0.080 ± 0.015***
b_1	1.16 ± 0.13***	1.33 ± 0.15***	1.09 ± 0.06***
a_2	0.402 ± 0.202*	0.642 ± 0.220**	0.262 ± 0.034***
b_2	-0.14 ± 0.19	-0.28 ± 0.21	-0.28 ± 0.07***
	(figure 2)	(figure 3)	(figure 4a)

	(*a*) length of arm of sheath vs sheath length	(*b*) length of arm of sheath (> 0.1 mm) vs sheath length	(*a*) distance between sheath tips vs sheath length	(*b*) distance between sheath tips (> 0.08 mm) vs sheath length
N	145	103	145	105
p for α_2	0.00000	0.0000	0.0000	0.0000
switch point	0.10 mm (arm)	0.321 mm (arm)	0.025 mm (tips)	0.338 mm (tips)
a_1	-0.0057 ± 0.0061***	-0.0085 ± 0.0182	0.00 ± 0.00	0.102 ± 0.023***
b_1	0.138 ± 0.045**	0.465 ± 0.035***	0.00 ± 0.00	0.328 ± 0.053***
a_2	0.0080 ± 0.0136	0.188 ± 0.032***	0.100 ± 0.015***	0.190 ± 0.035***
b_2	0.336 ± 0.049***	-0.210 ± 0.049***	0.429 ± 0.022***	-0.143 ± 0.063*
	(figure 4b)	(figure 4b)	(figure 4c)	(figure 4c)

*$p < 0.05$; **$p < 0.01$; ***$p < 0.001$;

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