Horn polyphenism and related head shape variation in a single-horned dung beetle: Onthophagus (Palaeonthophagus) fracticornis (Coleoptera: Scarabaeidae)

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Title
Horn polyphenism and related head shape variation in a single-horned dung beetle: *Onthophagus (Palaeonthophagus) fracticornis* (Preyssler, 1790) (Coleoptera: Scarabaeidae).

Short title
Horn and head shape polyphenism in *Onthophagus fracticornis*.

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Abstract

Horns of *Onthophagus* beetles are typical examples of phenotypically plastic traits: they are expressed as a function of environmental (nutritional) stimuli, and their reaction norm (i.e. the full set of horn lengths expressed as a response to different degrees of nutritional states) can be either linear or threshold-dependent.

Horned males of *Onthophagus* (*Palaeonthophagus*) *fracticornis* (Preyssler, 1790) bear a single triangular cephalic protrusion of vertex carina, which has received phylogenetic support as the most primitive horn shape in the genus. Inter- and intra-sexual patterns of horn expression were studied in *O. fracticornis* by means of static allometries while associated variations in head shape were assessed using geometric morphometric techniques. The relation between log-transformed measurements of body size and vertex carina supported an isometric scaling in females. On the contrary, a sigmoidal model described better the horn length-body size allometry in males, with a switch point between alternative morphs at a pronotum width of 3.88 mm. Sigmoidal static allometries of horns in *Onthophagus* populations arise from a threshold-dependent developmental process of horn growth. This process underlies the expression of both plesiomorphic and apomorphic horn shapes in the genus. Given that the single-horn model has been identified as primitive, we propose that such a developmental process giving rise to it may be evolutionarily ancient as well. Horn expression was accompanied by a deformation of the head which makes minor and major morphs appear even more different. Therefore, in this species both horn and head shape expression contribute to male dimorphism.

Key words

Developmental switch, geometric morphometrics, phenotypic plasticity, polyphenism, static allometry.
Introduction

Among horned beetles, *Onthophagus* are emerging as model systems for the study of the origin and differentiation of exaggerated sexually selected structures. This highly diversified and species-rich genus is one of the focal taxa for studies on the evolution and development of morphological diversity (Emlen 2000). Whenever expressed, horns differ greatly among species with regard to shape, size, and physical location; they may extend from the base, centre, or front of the head and from several locations on the thorax (Emlen et al. 2005). The genus *Onthophagus* includes a large number of species whose males develop large and conspicuous horns, while females display very reduced ornaments or none at all.

Males are commonly dimorphic with respect to horn expression, with large males expressing disproportionately long horns whereas smaller males remain hornless or express greatly reduced horns (Balthasar 1963; Simmons et al. 1999).

Although the contemporary presence of a wide range of horn lengths partly depends on genetic differences among males (West-Eberhard 2003), horn size is mainly controlled by environmental (nutritional) stimuli, being mostly determined by differential proliferation of imaginal discs that respond to hormonal signals depending on feeding conditions (Emlen and Nijhout 1999, 2001). On the whole, this process is a typical case of phenotypic plasticity, defined as the ability of a single genotype to give rise to a range of different phenotypes in response to environmental factors (West-Eberhard 2003).

When an individual phenotype varies as a continuous function of some environmental variable, its reaction norm is the full set of phenotypic responses to that variable (West-Eberhard 2003). In *Onthophagus* beetles, horn expression is related to body growth, which is influenced in turn by environmental conditions. Hence, the horn length-body size scaling relationship depicts the horn reaction norm (Emlen and Nijhout 2000), which can be represented by means of a static allometry based on measurements of conspecific individuals at the same life stage (Shingleton
et al. 2007). Three major types of such horn static allometries have been highlighted:

- a positive one, arising from differential (but continuous) horn vs. body size growth rates (Moczek et al. 2004; Emlen et al. 2007);
- a broken one (Nijhout and Wheeler 1996, Emlen and Nijhout 2000, Moczek and Nijhout 2002, Moczek 2008) and a sigmoidal one, both characterized by a discontinuity and derived from a size dependent re-programming of horn growth during development (Nijhout and Wheeler 1996). More specifically, the sigmoidal allometry is underlain by a re-programming model of growth operating through a nutrition-dependent developmental switch whereby males smaller than a certain critical body size develop small or no horns and males larger than the threshold size express fully developed horns (Emlen and Nijhout 2000). The expression of linear vs. sigmoid scaling relationships is thought to require fundamentally different genetic and developmental control mechanisms (Emlen and Nijhout 2000; Nijhout and Grunert 2002). Recent studies have shown that in species where males develop a pair of cephalic horns, the latter type of allometry is the most frequent (Emlen 1994, 1996; Moczek and Emlen 1999; Moczek and Nijhout 2002; Emlen et al. 2007) and the underlying ontogenetic processes begin being investigated (Emlen and Nijhout 1999, 2001; Moczek 2006).

Emlen and colleagues (2005) conducted the most comprehensive analysis of *Onthophagus* horn radiation so far, although a mere 2% of species in the genus were included. They highlighted multiple horn gains and losses as well as morphological modifications along the tree branches, suggesting that relatively little genetic distance is needed to develop strikingly different horn shapes. In spite of a likely underestimation of the evolutionary events responsible for their current stunning diversification, the study of Emlen and colleagues (2005) revealed that a single triangular horn extending from the vertex carina was likely ancestral to this genus and resulted from a single initial evolutionary gain. Subsequent modifications involved the splitting of this original head horn into a pair of horns or, less frequently, into a row of three horns. Sexual dimorphism in horn development, with females dispensing
with horn production, is also believed to be ancestral to horn expression (Emlen et al. 2005).

Horned males of Onthophagus (Palaeonthophagus) fracticornis (Preyssler, 1790) bear a single triangular cephalic horn that protrudes from the centre of the vertex carina and largely reflects the ancestral shape from which horn diversification started (Emlen et al. 2005). In this species, individuals with long to very short horns coexist in the same populations. Medium sized horns protrude straight from the vertex carina, while long horns become S-shaped distally. Females never express horns. Instead, they bear a conspicuous vertex carina. In the present study, we provide a detailed description in terms of allometric relationships of male horn and its female homologue, the vertex carina, to determine inter-sexual differences in type and magnitude of responses to nutritional stimuli. Horn expression results from irreducible interactions between genetic, developmental and environmental factors, each of them possibly having multiple and eventually significant effects over other morphological traits. Recent studies show that costs associated with weapon development can influence the neighbouring morphological structures and that this trade-off is of evolutionary importance (Emlen 2001). In this framework, we tested whether horn development was associated with head shape variation. An integrated analytical approach, combining traditional and geometric morphometrics, was used to characterize O. fracticornis horn static allometry and morphological modifications in head shape.

Materials and Methods

Fieldwork

Between July and August 2006, about one hundred individuals (54 males, 48 females) were collected from two pastures located in Ferret Valley (Aosta Valley region), North-West Italian Alps (Montitaz Desot, 1559 m a.s.l., ED50 UTM E 343119 N 5077148; Praz-Sec, 1652 m a.s.l., ED50 UTM E 345793 N 5079235). Cow
dung pads with typical colonization signs (tunnel entrances on the top, excavated
material all around) and 20 cm of soil below dung pads were carefully inspected for
beetles.

**Morphological measurements and statistical analyses**

In the laboratory, individuals were cleaned in boiling distilled water for
10 min and dissected; heads and pronotums were then separately fixed on plasticine
supports, taking care to align the edges of each structure on the same horizontal plane
by completely plunging their convex ventral portion in horizontally-levelled
plasticine. All morphological measurements were taken using a two-dimensional
image analysis equipment, including a Leica Z16Apo stereoscope, a Leica DFC320
digital camera (Leica Microsystems AG, Wetzler, Germany), and the software LAS v
2.5.0 (Leica Application Suite).

After photographing the lateral profile of the head, measurements were taken
following its outer edge from the frontal carina (i.e., the most clearly identifiable
homologous point between females and males of different morphs) up to the top of
the vertex carina (or the protruding horn). Pronotum width was measured as a proxy
for body size (Emen 1994; Moczek 1998). Kolmogorov-Smirnoff tests were used to
test for normality of natural variation in pronotum width and horn length (Sugiura et
al. 2007).

Horned beetle morphology is commonly described in terms of static
allometries, i.e. through scaling relationships where the horn length of individuals of
different body size is graphed as a function of body size (Eberhard and Gutiérrez
1991; Emen and Nijhout 2000; Moczek and Nijhout 2003). In *O. fracticornis*, such
scaling relationships were determined by fitting to the data a simple linear (\( y = y_0 + b \cdot x \)) and a four-parameter non-linear regression in the form

\[
y = y_o + \frac{a \cdot x^b}{c^b + x^b}
\]

(Moczek et al. 2004)
where $x$ is body size, $y$ is horn length, $y_0$ specifies minimum horn length, $a$ defines the horn length range in the sample, $b$ is a slope coefficient and $c$ is body size at the point of inflection of the sigmoid curve. The residuals from the two regressions were compared by means of an Extra Sum of Squares $F$-test to find out what regression better fitted the data set (Moczek et al. 2004).

Geometric Morphometric techniques (Bookstein 1991; Rohlf and Marcus 1993; Marcus et al. 1996; Adams et al. 2004) are a powerful means to describe shape variation, providing a useful tool for addressing a variety of biological problems. Here, a landmark-based approach was adopted to quantify intraspecific modifications of head morphology and their association with horn development. Eight landmarks on the frontal side of the head (Fig. 1) were digitized by using TpsDig 2.10 (Rohlf 2006): they were all positioned on the left hand side to prevent bias possibly caused by asymmetry (Pizzo et al. 2006a, 2006b, 2008) and chosen for their relative ease of identification, homology between the two sexes and the morphs, and ability to capture the general head shape, excluding the portion from which the horn originates.

To evaluate the confidence of the landmark configuration, a repeatability test was conducted by digitalizing the same set of landmarks on the same specimen 10 times: the landmark configuration was accepted only if the ratio between variance on the same specimen and variance of the total sample [variance = $\Sigma$ (Procrustes distances)$^2/(N-1)$, where N is the number of objects considered in each set of measures] was less than or equal to 0.05 (Pizzo et al. 2006a, 2006b, 2008). The landmarks of each specimen were optimally aligned using a Generalized Procrustes Analysis (GPA) to remove the non-shape effects of translation, rotation, and scale (Rohlf 1990; Rohlf and Slice 1990). The thin-plane spline (TPS) method (Bookstein 1989) was used to allow a multivariate description of shape variables in an Euclidean space tangential to the reference point (the mean shape) in Kendall’s shape space (Kendall 1981, 1984). The effect of horn expression on head shape was evaluated in two ways.
1) To reveal differences between major and minor males, individuals which could not be unambiguously assigned to one of the two morphs (±S.E.) were excluded from analyses and the remaining males were contrasted to a comparable number of randomly chosen females. Generalized procrustean superimposition (Rohlf 1990; Rohlf and Slice 1990), partial warps, relative warps and visualization of deformation grids, which allowed a description of shape variation, were performed using tpsRelw 1.45 (Rohlf 2007). Discriminant analysis was carried out on relative warp scores to obtain a classification matrix based on head shape variation. We used the percentages of correct classification to evaluate whether major and minor morphs could be described as two distinct groups on the basis of head shape variation.

2) To assess the effect of horn expression on male head morphology, the entire sample of males was considered and a multivariate test for a general linear model predicting male head shape variation (captured by partial warps and uniform shape component: Bookstein 1991) as a function of horn length was computed. A series of bivariate regressions of each partial warp and uniform component (as dependent variables) onto horn length (as independent variable) were carried out and the overall significance of multivariate regression was assessed by Wilks’ Lambda and Goodall F-test (Goodall 1991). All tests as well as the visualization of the deformation grid predicting head shape as a function of horn length were performed in tpsRegr 1.28 (Rohlf 2003).

Results

Horn allometry

Male pronotum width was normally distributed (Kolmogorov-Smirnoff test: $d=0.05$, $P>0.20$), whereas horn length was not (Kolmogorov-Smirnoff test: $d=0.21$, $P<0.01$), the plot suggesting a bimodal distribution instead (Fig. 2).

Both a linear and a sigmoidal regression fitted male horn length-body size data. After removing 2 outliers (studentized residual values: $>3.00$ and $<-3.00$), a
simple linear regression model explained over 98% of horn length variation

\[(r^2=0.9783, \ y = -3.1 + 1.17x)\]; a sigmoid regression model led to a moderate, but

nonetheless significantly better fit \[(r^2=0.9897, \ y = 0.73 + \frac{1.41 \cdot x^{25.57}}{3.88^{25.57} + x^{25.57}});\] Extra

Sum of squares F-test: \(F=26.89, \ P<0.001\), suggesting a model of growth where

males smaller than a certain critical body size develop small or no horns and males

larger than the threshold size express fully developed horns was more appropriate to

describe horn development than a linear reaction norm (Fig. 2). The same analyses

performed on log-transformed data gave comparable results (linear regression:

\[r^2=0.8754, \ y = -4.31 + 3.41x;\] sigmoid regression: \[r^2=0.9254,\]

Extra Sum of squares F-test: \(F=16.10, \ P<0.001\).

Female vertex carina scaled largely isometrically with respect to pronotum

width (linear regression, untransformed data: \[r^2=0.9985, \ y = 0.10 + 0.20x;\] Fig. 2;

linear regression, log-transformed data: \[r^2=0.9323, \ y = -1.36 + 0.91x\].

**Geometric Morphometrics**

Given the point of inflection of the sigmoid curve ± its S.E. (3.88±0.03 mm),

males with pronotum width higher than 3.91 mm and lower than 3.85 mm were

respectively classified as *major* (N=19) and *minor* (N=23) and compared with 22

randomly chosen females. Values of the first two relative warp scores obtained from

TPS analysis of the head shape were plotted on an axis system. On the whole, relative

warp 1 and 2 described more than 50% of total head shape variation. In the

morphospace, *major* males were grouped in a distinct cluster along the relative warp

1, thus being clearly differentiated from both *minor* males and females, which were in

turn only partially differentiated along relative warp 2 (Fig. 3). Discriminant analysis

performed on male head relative warp scores showed that the two-class grouping fits

the data adequately (Wilks’ Lambda=0.22, \(\chi^2=52.17, \ P<0.001\)) and that 100% of

*major* and 91.3% of *minor* males were correctly classified.
When all males were considered, regression between horn length and head shape as described by partial warps gave statistically significant results (Wilks' Lambda=0.21, $F_{12,39}=12.461$, $P<0.001$; Generalized Goodall F-test: $F_{12,600}=16.16$, $P<0.001$). It is noteworthy that the deformation predicting head shape as a function of horn length followed closely the one described by relative warp 1 in Fig. 3. The increase in horn length matches with a stretching of clypeus and a convergence of landmarks defining genae and eyes towards the medial axis of the head: as a result, the heads of males developing long horns are more elongated in the fore-hind direction, less enlarged at the genal level and, on the whole, more pointed at the level of the clypeus than those of males expressing short to no horns. Conversely, no correlation was found between female vertex carina height and head shape (Wilks' Lambda=0.62, $F_{12,35}=1.77$, N.S.; Generalized Goodall F-test: $F_{12,552}=1.43$, N.S.).

**Discussion**

The sigmoidal shape of the outlined horn length-body size allometry reflects a bimodale male frequency distribution which results in the separation between small hornless (*minor*) and big horned (*major*) male morphs. Therefore, in *Onthophagus fracticornis*, male horn expression is likely to occur through a size-specific reprogramming model of growth whereby a nutrition-dependent developmental switch causes horn growth to be suppressed in small males and exponential growth to occur only in large males (Nijhout and Wheeler 1996). The ontogenetic mechanisms of this polyphenic development have been extensively studied in the congeneric *O. taurus*, for which both horn length and body size have been shown not to be genetically inherited, but rather expressed under environmental controls, primarily depending on larval feeding conditions (Moczek and Emlen 1999). The sigmoid scaling relation is the macroscopic effect of developmental processes that regulate horn growth in response to circulating titres of Juvenile Hormone (JH). Horns originate from imaginal discs that explosively proliferate during a brief sensitive
period within the prepupal stage (Moczek and Nijhout 2004); under the assumption that JH is secreted as a function of body size, only large males expressing JH titres above a threshold during this sensitive period will moult into horned adults; smaller males will develop rudimental horns or remain hornless (Emlen and Nijhout 1999). In the static allometry, the switch point between the two morphs is identified by the point of inflection of the sigmoid curve; in its proximity, horn length varies conspicuously within a relative narrow range of body sizes. Morph determination occurs relatively late in larval development: the developmental switch determining the fate of a male larva occurs approximately three days before pupation and thus when larval growth is almost completed (Moczek and Nijhout 2002). As a consequence, although the scaling relationship between horn length and body size is highly non-linear due to a switch in developmental trajectories, male morphologies remain typically continuous and with broad overlap between alternative morphs (Moczek 2008). Contrary to males, in females the relation between log-transformed measurements of body size and vertex carina supported an isometric scaling.

The sexual dimorphism exhibited by this species has been proposed to be plesiomorphic in the genus *Onthophagus*, with females never developing horns (Emlen et al. 2005). The presence of a single horn has been proposed as ancestral in the genus *Onthophagus* (Emlen et al. 2005). We therefore suggest that horn polyphenism operating through the described reprogramming model of growth might be evolutionarily ancient as well. Even though *O. fracticornis* was not included in the phylogeny reconstructed by Emlen et al. (2005), the same primitive horn shape was represented, among others, by *O. nuchicornis*. This species belongs to the same subgenus as *O. fracticornis* (i.e., *Palaeonthophagus*) and bears a single laminar polyphenic head horn, with major and minor males coexisting in the same populations as well (Martin-Piera and López-Colón, 2000). On the basis of Zunino’s (1979) considerations on the monophyly of the subgenus *Palaeonthophagus*, the position of *O. fracticornis* in the phylogeny proposed by Emlen et al. (2005) can be equated to that of *O. nuchicornis*. Nonetheless, since some reversals are assumed to
have occurred in the evolution of *Onthophagus* horn shape, it cannot be excluded that
the horn shape observed in *Palaeonthophagus* could be derived from other types,
even though it resembles the putative plesiomorphic shape in the genus. This scenario
is further complicated by the fact that there are four principal trajectories of
*Onthophagus* horn evolution, related to changes in horn location, shape, allometry
and sexual dimorphism (Emlen et al. 2007). While the evolutionary patterns of
*Onthophagus* horn location, shape and dimorphism have been extensively analysed
(Emlen et al. 2005), the evolution of horn length / body size allometry deserves more
detailed phylogenetic analyses. However, although static allometries have been
described only in a few subgenera of *Onthophagus*, in *Onthophagus sensu stricto* the
sigmoidal trend seems to be widespread (Eberhard and Gutiérrez 1991, Emlen 1996,
Moczek and Nijhout 2003, Simmons et al. 2007, Emlen et al. 2007). The presence of
a threshold-dependent male horn polyphenism in both *O. (Palaeonthophagus) nuchicornis* (Simmons et al. 2007) and *O. (Palaeonthophagus) fracticornis* (this
paper) suggests that this process is widespread across subgenera and might indicate
an ancient origin of its underlying developmental patterns, at least within the genus
*Onthophagus*.

The contemporary inspection of the relative warp plot and deformation grids
describing head shape variations provided a detailed characterization of differences
between sexes and morphs. *Major* males formed a distinct group along the relative
warp representing the stretching of clypeus and a convergence of landmarks defining
genae and eyes towards the medial axis of the head. As a result, *major* males have
heads which are more elongated in the fore-hind direction, less enlarged at the level
of the genae and, on the whole, more pointed at the level of the clypeus than those of
*minor* males and females. Furthermore, an explicit correlation emerged between horn
length and head shape. Horn growth matched with a pattern of head shape variation
which followed closely the one described by relative warp 1 within the shift from
*major* to *minor* morphs. It is therefore assumed that horn development and head
morphology are associated. Although landmarks were not placed in the
morphological region from which the horn protrudes, the correlation between horn
expression and head shape was nonetheless apparent. Our results thus revealed that in
*Onthophagus fracticornis*, the horn allometry mediated by a developmental switch
causes large males not just to be enlarged versions of their smaller conspecifics
(Emlen and Nijhout 2000), but to also develop a fundamentally different morphology.
In particular, since horn expression is accompanied by a modification of head shape,
male dimorphism is delineated by both horn presence and head morphology. Such a
head modification (in particular, clypeus stretching in response to horn development)
might have evolved as a balancing static system compensating barycentre backing
due to horn protrusion in *major* males. Similar patterns of head shape modification in
response to horn expression are likely operating in other *Onthophagus* species: a
morph dependent variation of head shape was also highlighted in *Onthophagus
taurus* and *Onthophagus illyricus* (Pizzo et al. 2006a), where *major* males develop a
pair of cephalic horns. The developmental mechanisms underlying this morphological
rearrangement have never been investigated. However, it is possible to hypothesize
that, in males developing horns, other areas of the head such as the clypeus may
respond to nutrition-mediated chemical stimuli. As a matter of fact, recent studies
have shown that there must be some interaction between developmental pathways of
different morphological structures: the production of some horn types can influence
the size of neighbouring (Emlen 2001) or even distant (Moczek and Nijhout 2004;
Simmons and Emlen 2006) structures due to the costs associated with enlarged
weapon development.

Environment-mediated polyphenic development is the highest degree of
phenotypic plasticity, which is thought to be a major enhancer of differentiation,
responsible for the origin of evolutionary novelties (West-Eberhard 2003; Moczek
2008). In *Onthophagus* beetles allometries are particularly prone to rapid evolution:
even slight evolutionary changes in the mechanics of developmental switches, in
particular changes in the body size threshold which defines the transition between
*minor* and *major* morphs, can have significant consequences on phenotypic
expression. It has been demonstrated that polyphenic thresholds and consequently the underlying developmental mechanisms can diverge in closely related species or even in geographically isolated populations of the same species (Moczek 2003, Moczek and Nijhout 2003). The present study represents the first necessary step towards the analysis of differentiation patterns within the three species of the so-called ‘fracticornis-opacicollis’ complex [viz. O. opacicollis Reitter, 1892; O. similis (Scriba 1790); O. fracticornis (Preyssler 1790)]. A controversy regarding the taxonomic status of this complex has been going on for more than a century because species divergence appears to be a function of geography (different divergence patterns have been highlighted in allopatric and sympatric populations). It has been suggested that reproductive isolation is not complete across the geographic range of these species and speciation processes are still ongoing in some areas (Martín-Piera and Boto 1999). The analysis of static allometries will provide an invaluable opportunity for studying divergence patterns in this species complex from an Evo-Devo perspective.

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**Riassunto**

Espressione polifenica del corno cefalico e conseguenti variazioni nella morfologia del capo in *Onthophagus (Palaeonthophagus) fracticornis* (Preyssler, 1790) (Coleoptera: Scarabaeidae).

Le strutture cefaliche degli Scarabeidi sono tipici esempi di tratti soggetti a plasticità fenotipica: vengono espresse in funzione di stimoli ambientali e le norme di reazione sottese al loro sviluppo, ovvero l’intero range di lunghezze delle corna
espresso in risposta a differenti condizioni nutrizionali della larva, può avere
andamento lineare o essere caratterizzate da un effetto soglia. In Onthophagus
(Palaeonthophagus) fracticornis (Preyssler, 1790) i maschi possono esprimere una
singola protrusione cefalica triangolare, emergente dalla carena del vertice ed estesa
in forma di lamina, un carattere considerato plesiomorfo all’interno del genere,
mentre le femmine esibiscono una carena del vertex pronunciata, senza tuttavia
sviluppare corna. I pattern inter- e intrasessuali di espressione del corno di O.
fracticornis sono stati analizzati in termini di relazioni di allometria statica; le
modificazioni della forma complessiva del capo che si evidenziano in concomitanza
con lo sviluppo del corno sono state indagate attraverso l’uso di tecniche di
morfometria geometrica. Nelle femmine, la regressione tra le misure,
logaritmicamente trasformate, della larghezza del pronoto e dell’altezza della carena
cefalica indica una relazione isometrica tra queste due variabili; al contrario, nei
maschi questa relazione risulta meglio descritta da un modello sigmoidale. La
transizione tra maschi minor e major avviene ad una larghezza del pronoto di 3.88
mm. Le allometrie statiche sigmoidali già descritte nelle popolazioni di Onthophagus
risultano da specifici processi di sviluppo che coinvolgono soglie di sensibilità alla
neotenina nei singoli individui. Si può ritenere che tali processi siano relativamente
antichi, in considerazione del fatto che sono alla base dello sviluppo polifenico in
specie che esprimono strutture sessuali secondarie plesiomorfe. Nella specie
analizzata, l’espressione del corno è accompagnata da una deformazione cefalica che
differenzia le morfe anche sulla base della morfologia generale del capo: di
conseguenza, sia il grado di espressione del corno sia la forma del capo concorrono a
determinare il dimorfismo maschile.

References
Adams D. C.; Slice D. E.; Rohlf F. J., 2004: Geometric morphometrics: Ten years of
progress following the ‘revolution’. It. J. Zool. 71, 5–16.


Figure 1. Landmark configuration chosen to describe head shape. All landmarks were set taking care to avoid positioning on the anatomical region from which the horn originates.
Figure 2. Static allometries describing the scaling relations between body size (measured as pronotum width) and horn length (or the corresponding trait in small males and females). Histograms of pronotum width and horn length frequencies are also shown. The described pattern results in the co-existence in the species of large horned (major) males and small (minor) ones bearing reduced horns or no horn. The switch point between alternative morphs is set at a pronotum width of 3.88 ± 0.03
mm. By comparison, female vertex carina scales largely linearly with respect to body size.
Figure 3. Head shape differentiation between sexes and morphs. Scatterplots of the two first relative warp scores obtained from the relative warp analyses are reported. The amount of variation explained by each relative warp (axis) is expressed in percentage terms. Thin-plate spline (TPS) transformation grids on each side of the scatterplot refer to specimens plotted on the left (major males) and right (minor males, females) extremity of the first relative warp axis; only the deformation along the first relative warp (which best allows discrimination) is shown.
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