SYSTEMATICS, MORPHOLOGY AND PHYSIOLOGY

# Allometry and Ontogeny in *Callibia diana* Stål (Mantodea: Acanthopidae)

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**Abstract**

The life-cycle of *Callibia diana* Stål is described and linear and geometric morphometrics are used for studying allometrics and shape changes throughout this neotropical mantid species' life-cycle. Significant changes were expected in the allometry and shape of the raptorial leg and abdomen, given the importance of hunting and reproduction. The allometric slopes were obtained by using total length as the independent variable. Geometric morphometrics of landmarks were used for frontal femur and tibia. Hunting and reproduction-related structures had the steepest slopes and positive allometries. Negative growth of both disc width and head width found in the last moulting event may be a consequence of prothoracic muscle growth which is responsible for predatory strike strength. The tibial claw and femur of the raptorial leg become larger, while their spines become more orthogonal to the longitudinal axes which may facilitate prey retention. These changes in mantid shape throughout ontogeny were consistent and suggested the resource allocation and development programming of the body that improved reaching distance and prey retention.

## Introduction

The size of different parts of an organism can change so that the adult shape is different from that of immature stages, and shape changes in certain body parts are thus related to overall body size changes, which is the concept of allometry simultaneously proposed by Teissier and Huxley in 1936 (Gayon 2000). Allometric differences can be influenced by several factors, such as food availability, temperature, habitat characteristics, ontogeny, sexual selection, evolutionary tradeoffs, and functional requirements (Robinson & Robinson 1978, Alberch *et al* 1979, Arnqvist & Johansson 1998, Nijhout & Emlen 1998, Shingleton *et al* 2007). Despite numerous studies on the allometric changes of sexual selection-related structures such as those related to fiddler crab forceps or scarab horns (Pounds *et al* 1983, Nijhout & Emlen 1998, Emlen

& Nijhout 2000, Kodric-Brown *et al* 2006, Shingleton *et al* 2007), allometric studies on the relationship between body size and structure ontogeny are less frequent (Pounds *et al* 1983, Arnqvist & Johansson 1998, Iglesias *et al* 2008).

Shape changes can be better described with the development of geometric morphometrics (Zelditch *et al* 2004) since landmarks allow for a more complete coverage in bi- or three-dimensional spaces. This approach may allow a better understanding of the ontogenetic changes experienced by a trait and, in several cases, it may shed light on the adaptive process occurring (Frederich *et al* 2008). The relationship between function, environment, and shape has been studied by comparing specimens of different ages sampled in different field conditions (Frederich *et al* 2008).

*Callibia diana* Stål is a rarely-collected praying mantis

found in the Amazon and the eastern savannas between Venezuela and Colombia (Salazar 2002, Agudelo *et al* 2007). Only two of almost 1,500 specimens deposited in Colombian museums belong to this species. This species is morphologically very different from other members of the family, such as *Acanthops falcata* Stål, and very little is known about its biology. Although there are nearly 2,400 species of praying mantids with highly modified forelegs and varied hunting strategies, and several studies have shown a relationship between their behavior and body shape (Terra 1980, Svenson & Whiting 2004, Holwell *et al* 2007), little is known on their biology (Travassos 1945, Travassos & Heitzmann 1960, Robinson & Robinson 1978, Kaltenpoth 2005).

This paper was thus aimed at describing the life-cycle of the praying mantis *C. diana* and the allometric and shape changes of this species' different body parts throughout its ontogeny. The present study is perhaps unique in that it used specimens of different ages reared in almost constant conditions.

## Material and Methods

### Life-cycle description

A colony of *C. diana* was started from two oothecae laid by a single female collected in San Martín, Meta (03°41′40"N, 73°41′37"W, 27°C, 405 masl); 44 nymphs eclosed and were reared at 22.5 ± 6°C in Bogotá, Colombia (2,569 masl) following Travassos (1945) and Travassos & Heitzmann (1960) with some modifications. Groups of 10-12 individuals were kept in separate plastic containers until third instar and were then separated in individual containers. We are aware of the potential difficulties of using a single mother to initiate a colony for analysis, but the species' rareness made it an unavoidable obstacle.

Mantids were fed twice every week. Several *Drosophila melanogaster* Meigen (Diptera: Drosophilidae) adults were provided as the food source per individual until third instar, while older instars were fed with a variety of arthropods collected in surroundings of the rearing site, including larger flies, moths, silverfish and spiders.

### Morphometric analysis

Changes in body proportions were analyzed by linear morphometrics and PCA analysis. Given sample size and mortality, body measurements were taken from preserved specimens up to fourth instar whilst exuviae were used for the fifth through seventh instar. Measurements were restricted to body parts which underwent no deformation by moulting; thus, exuviae were carefully manipulated to avoid deformation. These precautions explain why some instars contained fewer individuals than the following instar. A total of eleven linear measurements were taken

for every specimen as follows: front leg (femur length, tibia length and tarsus length), mid leg (femur length, tibia length and tarsus length), pronotal disc width, prozone length, metazone length, head width and total body length (Fig 1a).

Since males and females could emerge from the oothecae and each sex might have distinct allometric trends, data could have been biased by using all specimens together. However, we had two sources of evidence which suggested that only females were obtained from the oothecae. The first concerned this species showing strong sex dimorphism in colour pattern and general body shape, males being brown and thin, while females were green-white and robust; but no significant differences in colour pattern were observed throughout the immature development. Second, PCA analysis revealed no strong differentiation among individuals and the only two cases which appeared separated were the first instars, which fused general variation in the posterior instars.

Body variables were subjected to principal component analysis (PCA) (Díaz 2007) regarding seven immature instars and the adult to study variations in general body proportions. The first two components explaining most of the variation were used for plotting specimens and finding differentiations. As Jolicoeur (1963) stated, traditional logarithmic regression coefficients cannot properly express changes in dimensions of complex structures, and thus, a correct generalization of the allometric equation should use multivariate approaches. Therefore, the allometric coefficient for each variable was obtained as suggested by Kowalewski *et al* (1997), by dividing the loadings of each variable of the first principal component of a Principal Component Analysis by the average loading for all variables. The confidence intervals for the allometric coefficients were estimated by 100 bootstrap replicates.

Changes in the shape of the raptorial leg were analyzed by using geometric morphometry (Zelditch *et al* 2004). Images of the right raptorial leg were taken with an 8Mp digital camera attached to a stereomicroscope (Leica S8apo). Structures were positioned so that parts appeared in the same plane and the image never reached the very edge of the stereomicroscope visual field where lens distortion is more evident. These procedures maximize image accuracy (Seifert 2002). Several pictures of the structure were taken, changing the focus point to avoid field depth problems due to magnification, and images were then processed with the freeware Combine Z5.3 software which produces a single image with all parts in focus (Haldey 2006). This multiplane final image keeps every part of the structure in focus without deformation and allows accurate definition of landmarks.

The ontogenetic changes in raptorial leg shape were analyzed for individuals from second through last instar. Both the internal and external view of the tibia and femur
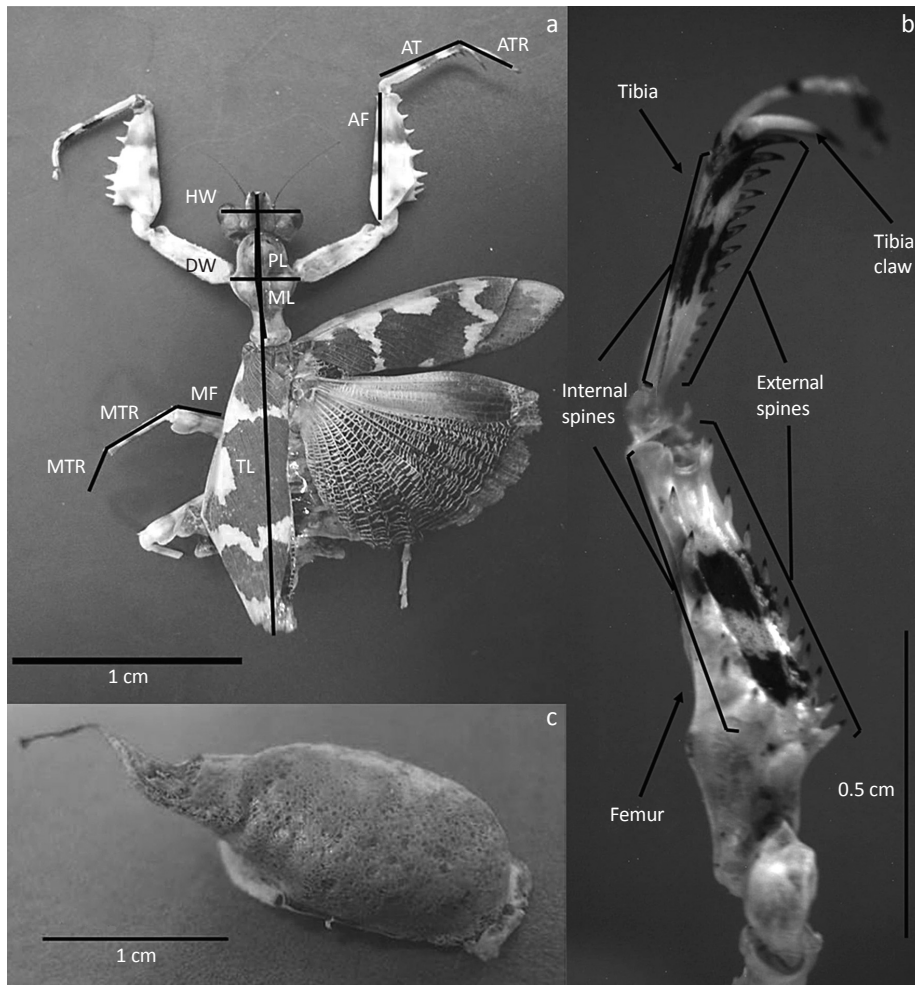
Fig 1 *Callibia diana*. a) Adult female, indicating the structures measured for the morphometric analysis (ATR = anterior tarsus length, AT = anterior tibia length, AF = anterior femur length, HW = head width, DW = disk width, PL = prozone length, ML = metazone length, MTR = mid tarsus length, MT = mid tibia length, MS = mid femur length, TL = total body length); b) Different structures of the raptorial leg; c) Ootheca.

were studied separately since the distribution of the spines was different in each case and no single plane could be established for both areas simultaneously (Fig 1b). Regardless of current tendencies in several morphometric studies, a conservative approach was taken here to define the homology of points and strong preference was thus given to landmarks, while semi-landmarks were selected only in cases where a large portion of the structure was devoid of parts having recognizable homologous features (Zelditch *et al* 2004). Seven landmarks were selected for both the external and internal view of the femur. An additional semi-landmark was included for the internal view to cover the entire shape of the structure. A total of 23 and 24 individuals were studied respectively in each view. Seven landmarks and one semi-landmark were used for the external view of the tibia, while six landmarks and one semi-landmark were selected for the internal view, using 29 and 30 individuals for the analysis of each view. As earlier explained, the number of individuals included in each analysis varied according to the availability of specimens which had not become deformed by moulting.

Multivariate ANOVA of the relative warps was used for studying the statistical difference between instars using the Statistica 6.0 software (Statsoft Inc.). The freeware programs TPSdig 2.05, TPSutil 1.34, TPSrelw 1.42, and TPSsplin 1.20 (Rohlf 2004, 2005, 2006, 2007), were respectively used to digitize the landmarks, prepare files, conduct the procrustes analysis to obtain the relative warps, and observe the thin-plate spline deformation grids. The angle of insertion for the tibial claw was measured using the freeware program MBruler 3.6 on the digital images (Bader 2002-2008)

## Results

### Life-cycle

The field-collected female laid two oothecae 35 days apart. The female stood over the ootheca during oviposition for several hours. Such behaviour is typical of the subfamily. The ootheca matched early descriptions provided for mantids (Fabre 1984), with a few noticeable differences.

The total length was 27 mm, and the pedicel was curved and about 8 mm long. The operculae were orientated toward the surface close to the pedicel (Fig 1c).

Average incubation time was 46 days. A total of 16 individuals eclosed from the first ootheca, while 28 individuals emerged from the second one. A total of seven nymphal stages and the adult were observed. A prenymphal stage was also observed right after eclosion. Average developmental time was 195 ± 20 days. The highest mortality occurred in the first instar (Table 1); only three individuals reached adulthood, all being female.

Prenymphal instars remained attached to the ootheca by the apex of the abdomen and moulting to the next instar took less than five minutes. The prenymphs were almost entirely testaceous, having strongly dark-pigmented eyes. A hood-like structure covering the antennae which has been reported in the literature for other species (Cockerell 1898) was also observed.

The number of antennomeres did not change from the second to the last instar. The dorsal margin of the eyes was lower than that of the vertex in a straight frontal view. The first discoidal spine of the raptorial leg was long and thin in the second instar, but was not present in the older instars. Second instar nymphs were the darkest of all. The prozone was clearly coloured and four abdominal spots were visible; these spots became larger in older instars.

The eyes of third instars became dorsally projected above the vertex, and a frontal projection on the head was observed. Large green areas were visible on the head and metazona which would then expand. Fourth instars presented small morphological changes if compared to the previous instar.

Fifth instars had abdominal lobes that became clearly apparent and the green abdominal spots became larger. Larger green areas were observed on the head and

Table 1 Total body length (mm), development time (d), and survivorship of immature of *Callibia diana*.

| Instar | Length (mm) (avg ± SD) | Duration (days) (avg ± SD) | Mortality percentage | |
|---|---|---|---|---|
| | | | Ootecae 1 (N:16) | Ootecae 2 (N:28) |
| Prenymph | 3.9 ± 0.18 | 0.0035 | 80 | 80 |
| 1 | 5.5 ± 0.52 | 25 ± 3.23 | 44 | 64 |
| 2 | 6.9 ± 0.62 | 24 ± 7.31 | 86 | 12 |
| 3 | 8.3 ± 0.75 | 26 ± 6.54 | 50 | 0 |
| 4 | 9.5 ± 0.35 | 21 ± 4.51 | 33 | 0 |
| 5 | 12.5 ± 1.15 | 24 ± 5.13 | 0 | 0 |
| 6 | 13.7 ± 0.14 | 30 ± 3.61 | 0 | 0 |
| 7 | 20.0 ± 0.08 | 44 ± 12.06 | 0 | 0 |
| Adult | 22.7 ± 1.09 | 24 ± 7.94 | ---- | ---- |

metazone. The wing buds were observed for the first time in sixth instars and the green coloration became more extensive. The development time of the seventh instar was the longest, which might be explained by the cost of generating structures related to flight and reproduction. Spots in the tegminae were very noticeable. Adult females were almost completely green (Fig. 1a). It is interesting to note that while younger instars held their prothorax and abdomen upright when eating or resting, adults lowered their abdomen, only keeping their prothorax upright.

Characteristics of taxonomic importance at the generic level appear at different moments of the development of *C. diana*: the bifid projection of the head is seen as a small bump at the second instar, it becomes bifurcate in the third instar, reaching its final shape in the fourth instar, growing in size in the following instars. The distal lobes in the mid and posterior femorae appear with their shape completely defined at the third instar.

*Body morphometry*

Growth increase was monotonic and close to 10% per instar, although there was a noticeable 23% increase between the sixth and seventh instar. Two decreases in growth were observed during two stages of the mantids' life-cycle. The first occurred between the third and fourth instar and was stronger in two of the eleven structures studied: the front tarsus and the mid tarsus (Fig 2). The second one occurred between the seventh and the last instar due to the negative disc width and head width growth (-8.5% and -1.9%, respectively) (Fig 2).

The allometric coefficients (AC) of every body part throughout the life-cycle revealed that growth was focused in two body regions: the abdomen and the "anterior part of the body" consisting of the prozone length, front femur, front tibia, and mid femur (Fig 3). These allometric trends suggested that individuals focused their resources on the growth of body parts related to reproduction and hunting which are key traits for individual success (Heitzmann 1960, Terra 1980, Dusse & Hurd 1997).

The first PCA component for all linear variables measured throughout the life-cycle explained 98.46% of body size variation, thereby suggesting that all structures follow a similar trend. The second component explained 0.05% of variation. Most individuals from the different instars could be consistently grouped when the first two PCA components were plotted (Fig 4). Two individuals from the first instar exhibited strong differentiation from the others; however, such differences were not observed in the following instars. The differentiation of one third instar individual was attributed to sampling error. The evident differentiation between instars was mostly due to the first component, indicating that major changes were due to body size modification. The second component
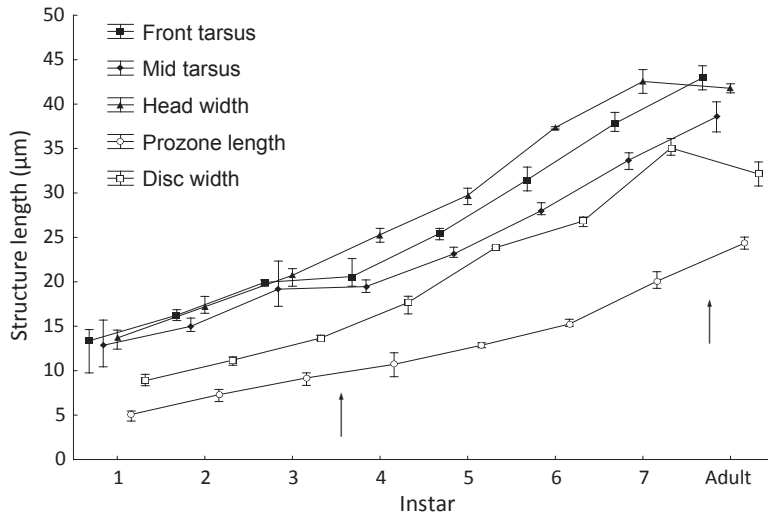
Fig 2 Size increase of six structures per instar of *Callibia diana*. Arrows point out two events where growth was severely reduced in some structures (see Results section for explanation).

showed strong differentiation events, the first between the third and fourth instar and the second between the seventh instar and the adult. These changes were related to the previously-described growth alterations.

*Morphometry of the raptorial leg*

There were differences in the centroid size of the external view of the femur during development stages ($X^2$ = 11.3, df = 6, P = 0.02), while differences regarding the internal view were marginal ($X^2$ = 12.6, df = 6, P = 0.048). The larger variations in femur shape during ontogeny occurred in the apical ventral area and at the second distal spine, while mid dorsal and ventral regions barely changed (Fig 5). Consequently, grid deformation showed that the ventral part of the femur where the spines are located expanded apically; however, the angle of the spines became smaller, resulting in the spines becoming perpendicular to the major axes of the femur.

There were differences in centroid size of both external and internal views of the tibia during development ($X^2$ = 20.32, df = 6, P = 0.02, $X^2$ = 15.29, df = 5, P < 0.05 respectively). The external view of the dorsal area of the articulation of the tibia underwent very little change while the remaining areas showed noticeable variation. The tibial claw underwent a strong change in its insertion angle, with the position in older nymphs being more orthogonal if compared to that of younger individuals (Fig 6). Consequently, the angle of insertion for the tibial claw before the major axis of the tibia for second instars was 126.15 degrees, compared to the 116.15 degrees for adults.

The tibia generally became enlarged during ontogeny, but the dorsal region of the articulation and the tip of the tibial claw were more stable regions if compared to the basal and apical areas where the spines are located. These changes followed a similar trend described for the femur.
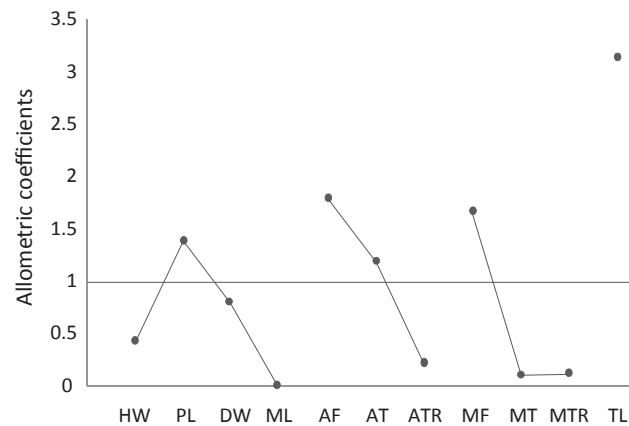


Fig 3 Multivariate allometric plot of different *Callibia diana* body parts. ATR = anterior tarsus length, AT = anterior tibia length, AF = anterior femur length, HW = head width, DW = disk width, PL = prozone length, ML = metazone length, MTR = mid tarsus length, MT = mid tibia length, MS = mid femur length, TL = total body length.
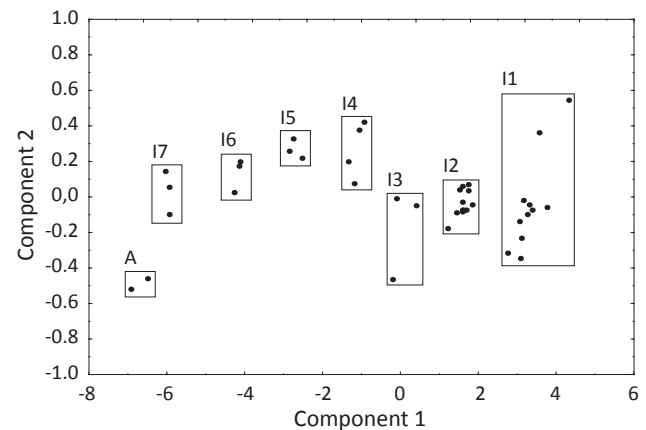


Fig 4 Principal component analysis plot of PC1 vs. PC2 using all data throughout the life-cycle of *Callibia diana*. Variance explained by PC1 = 98.46%, variance explained by PC2 = 0.5%. I1 through I7 indicated the instar, A = adult.
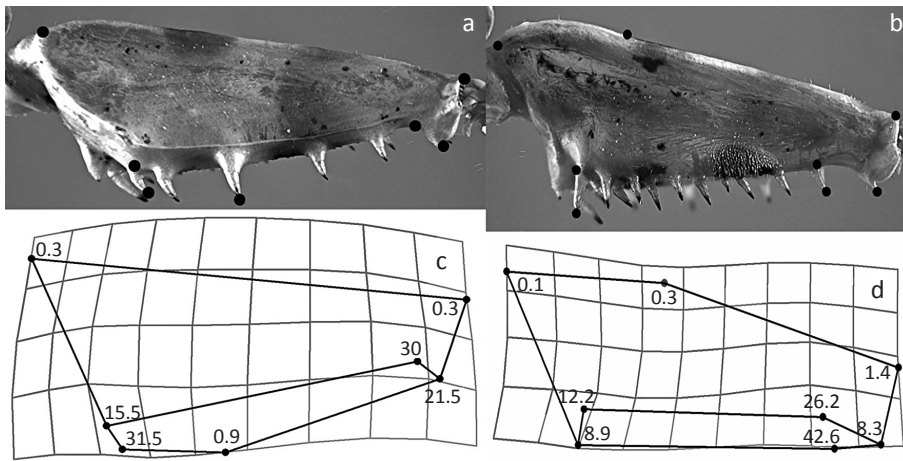
Fig 5 Shape changes of the anterior femur during *Callibia diana* ontogeny. Location of landmarks in external view (a) and internal view (b). Deformation grid for adult femur, external view (c) and internal view (d). Numbers by landmark locations indicate the percentage contribution of each landmark to total grid variation.
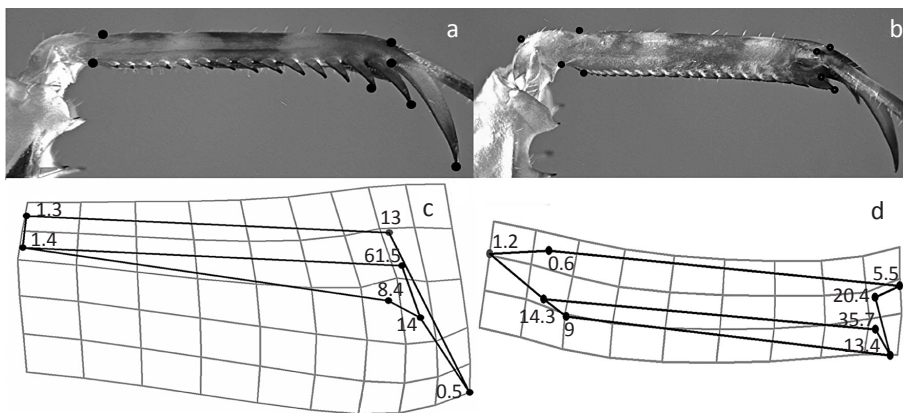


Fig 6 Shape changes of the anterior tibia during *Callibia diana* ontogeny. Location of landmarks in external view (a) and internal view (b). Deformation grid for adult tibia, external view (c) and internal view (d). Numbers by the landmark locations indicate each landmark's percentage contribution to total grid variation.

## Discussion

*Callibia diana* presented the same number of instars and pattern of incremental growth displayed by *A. falcata* (Robinson & Robinson 1978, Suckling 1984).

The two reduction events in overall growth required different explanations. The first event was perhaps an effect of a change in diet, as lab-cultured *D. melanogaster* flies were provided as the only food source up to the third instar, while a diverse array of arthropod preys were offered later on, similarly to the food effect observed on the growth of other mantids (Eisenberg *et al* 1981, Hurd & Eisenberg 1984, Snyder & Hurd 1995, Dusse & Hurd 1997).

The second growth reduction event occurred between the seventh instar and the adult stage, and may have been a consequence of a compensatory growth process (Nijhout & Emlen 1998). The negative expansion of the disc width could have been a result of prothorax lengthening since the prozone steadily lengthened from the sixth instar onwards, as was also evident from the positive AC value (Fig 3).

Many groups of insects possess energy storage mechanisms such as the well-known semi-lunar hind leg process of the Orthoptera (Burrows & Morris 2003). This mechanism allows them to generate more efficient speed movements, thereby optimising muscle requirements. However, this strategy has not been reported in mantids (Gray & Mill 1983) and it is speculated that allocation for muscle development should be very important. Given that the muscles responsible for speed, flexibility, power and precision of the predatory leg strike, such as the coxal promotor and coxal extensor (Gray & Mill 1983, 1985), are located in the frontal part of the prothorax, a lengthening of this region may facilitate muscle growth. These observations concur with Levreault's (1936) morphological study, who concluded that the prothorax lengthening may have increased the raptorial leg mobility in *Stagmomantis carolina* (Johanson). Positive allometry of the raptorial legs was observed in accordance with the pattern described above, thereby indicating the importance of these structures in hunting.

On the other hand, geometric morphometrics of frontal femur and tibia showed shape changes suggesting progressive hunting improvement, since the smaller angle of both the tibial claw and femur spines in later instars may facilitate prey retention. Similar studies in several predatory insect groups having raptorial-like front legs

have found that an increased curvature of the raptorial leg and a reduced angle between spines and the major axis of the segment significantly reduced the energy required for prey retention (Petie & Muller 2007).

Even though compensational growth has been proposed by Nijhout & Emlen (1998) for the developmental events during the closed system of the insect pupal stage, it suggests that an open system, such as the mantid development cycle, exhibits both positive and negative growth in related body parts. Several studies have shown compensational growth by different body parts when positive selection response was exerted on specific regions (Dodson 1984, Marden 1989, Marden & Chai 1991).

Our research has shown allometric and shape changes throughout *C. diana* growth and development which could be explained as an increase in prey capturing ability as observed in other groups (Galis *et al* 1994, Frederich *et al* 2008). For example, Mondor & Roitberg (2002) described that the cornicles of the pea aphid *Acyrthosiphon pisum* (Harris) showed positive allometry in relation to both alarm pheromone production and the high predation pressure.

## Acknowledgments

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