RESEARCH ARTICLE

Correlation between investment in sexual traits and valve sexual dimorphism in Cyprideis species (Ostracoda)

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Abstract

Assessing the

3rd thoracic or walking leg (1A, 2A, Md and 3WL respectively; see Table 1 for landmark positioning, as illustrated in Fig 1). These dimensions were log-transformed and then averaged to compute an overall measure of body size from soft

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Combining data from left and right sides and imputing missing data

We measured all variables on left and right sides of the body whenever possible, though in some cases poor preservation or damage during dissection resulted in data from just the left or

with just one or two missing values, we imputed missing data using the R package *Amelia* [36], which models observations as drawn from a multivariate normal distribution, an assumption that is consistent with the original data set according to Royston's test only slight the primary sexual charact

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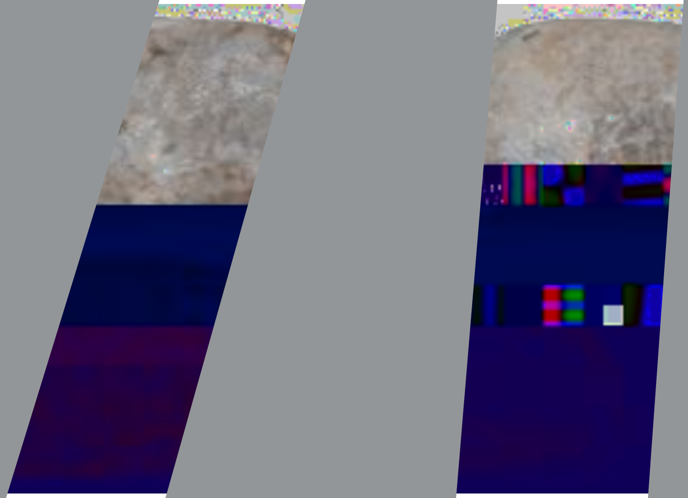
zes (Table trend evident in the species

the lowest sample sizes, *C. mexicana*. Among hemipenis characters, the size of the basal capsule is moderately correlated with body size but its allometric relation with respect to valve size varies across all three species (Table 5). Measurements of the terminal extension



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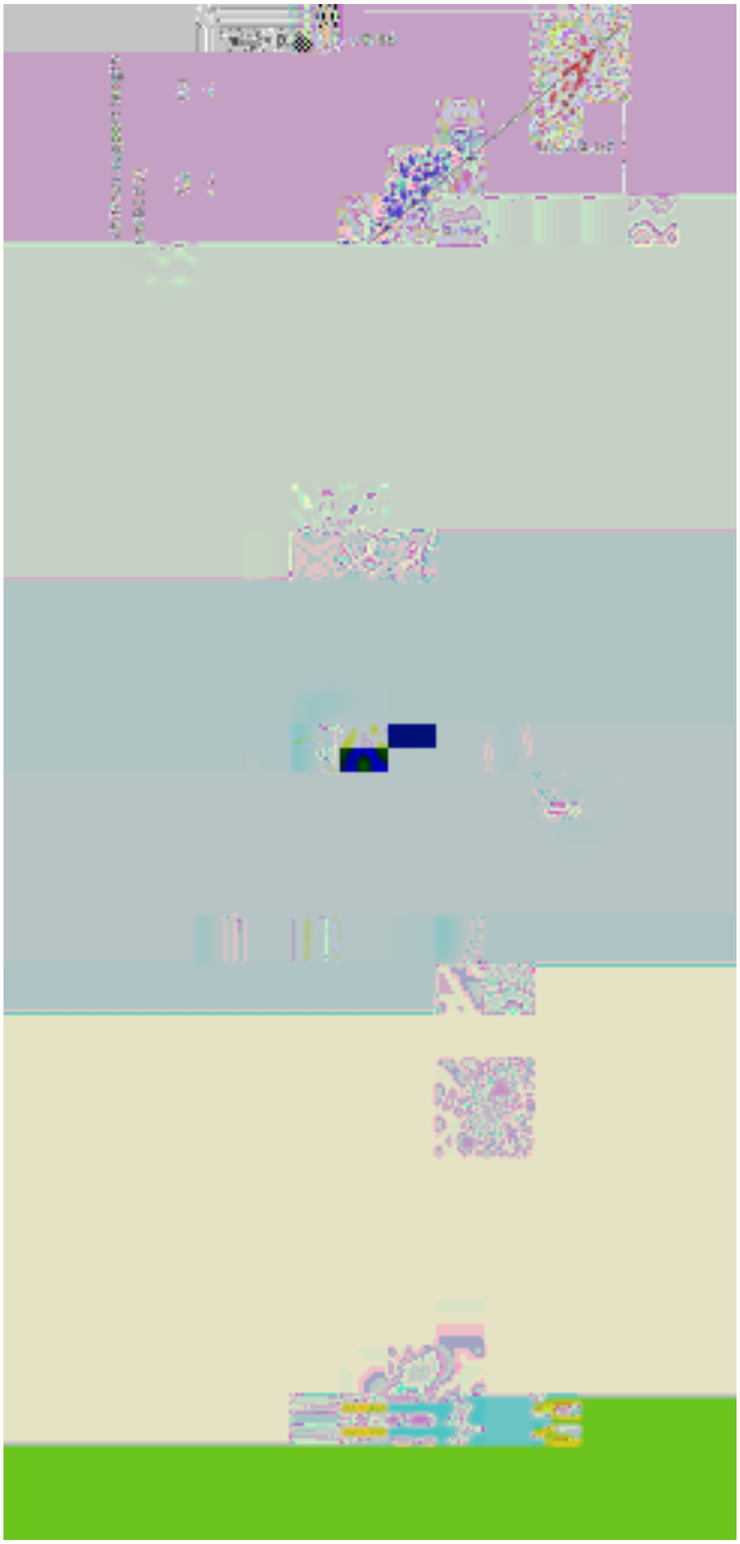

Fig 5. Evolutionary (evol) and static (sta) allometry of the variables representing size in the hemipenis and valve area, used as a proxy for body size. The basal capsule is represented by the Basal Capsule dorsal chitinous support length (HemiBCd L, upper panel); the terminal extension is represented by the Copulatory process length (Hemi TE L, middle panel), and the Terminal extension area (HemiTE A, lower panel). Abbreviations follow Table 1.

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(~20%). We were not able to measure sperm size in the present study, but a significant positive correlation was detected among sperm length, sperm pump size, and valve length within candonid ostracodes (though note that the sperm pump in candonids is a structure separate from the copulatory apparatus, and not homologous with the basal capsule) [19]. Although not consistent across all Ostracoda, this finding does suggest that the size of the sperm pump may be related to sperm size in at least some groups. In other taxa such as *Drosophila*, longer sperm can have higher fertilization success compared to smaller sperm [25, 38, 39].

Like the basal capsule, the area of the terminal extension of the hemipenis also shows significant partial correlations with male valve size for *C*. *torosa* and *C*. *salebrosa*; the same finding for the length of the intromittent organ on the terminal extension holds for *C*. *salebrosa* only. As these are the parts of the male genitalia in contact with females during mating, these structures are more likely to be influenced by sexual selection factors related to mate recognition or sexual conflict with females. Martens [40] proposed that variation in sexual traits across lineages in *Limnocythere*, particularly parts of the copulatory complex that show clear species-specific shape, plays a key role in species recognition, supporting a scenario as envisioned in our study system. The different patterns of static allometry between the basal capsule and the terminal extension suggests that these structures may indeed experience distinct evolutionary dynamics, as does the observation that the basal capsule is conserved across members of the genus whereas the terminal extension is highly divergent in size and shape [30]. Similar dynamics of genital evolution are known in *Drosophila* (e.g., [41]) and in the beetle *Onthophagus* (e.g., [42, 43]). Further investigation of the shape of the copulatory process in *Cyprideis*, and not just its size, has the potential to offer more insight. It is challenging to assess sexual conflict in ostracodes because there have been few attempts to study female genitalia and consequently the coevolution of male and female genitalia [20]. Unlike the male genitalia, female reproductive structures are membranous (see [32]) and their size and shape are not easily characterized.

Although we have shown here that the degree of valve sexual size dimorphism in *Cyprideis* is partly related to the size of the male genitalia, genital size is only one of many factors that may influence male body size. In addition to ecological and environmental factors shape was related to carapace shape in interstitial candonine ostracodes. We are unable to pursue this angle in the present study because it turned out that all three species we examined had very similar magnitudes of shape dimorphism (Fig 3). Broader sampling within the genus *Cyprideis* may help to resolve the relationship between shape dimorphism and male investment in reproductive structures.

In *C*. *torosa*, males with more dimorphic secondary sexual trait (first walking leg) tend to have more elongate valves. Because the right first walking leg is hypothesized to be a clasping structure, this may suggest that valve shape may affect the mechanics of male-female copulation. Little information on species-specific mating position is available in ostracodes [16, 27] although species-specific differences may occur [16]. Within the genus *Cyprideis* no information is available on courting and mating position and species-specific differences are unknown. However, and while the specific mechanisms leading to a chosen mating position are difficult to ascertain [26],

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