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**Author for correspondence:**
Gene Hunt
e-mail: hunte@si.edu


†Present address: Interdisciplinary Center for Archaeology and Evolution of Human Behaviour, Universidade do Algarve, Faro, Portugal.
‡Present address: Division of Invertebrate Paleontology, Florida Museum of Natural History, Gainesville, FL, USA.

# Shifts in sexual dimorphism across a mass extinction in ostracods: implications for sexual selection as a factor in extinction risk

Maria João Fernandes Martins[1,†], Gene Hunt[1], Carmi Milagros Thompson[1,‡], Rowan Lockwood[2], John P. Swaddle[3] and T. Markham Puckett[4]

[1]Department of Paleobiology, National Museum of Natural History, Smithsonian Institution, Washington, DC, USA
[2]Department of Geology, and [3]Department of Biology, College of William and Mary, Williamsburg, VA, USA
[4]School of Biological, Environmental and Earth Sciences, The University of Southern Mississippi, Hattiesburg, MS, USA

GH, 0000-0001-6430-5020; RL, 0000-0003-3731-8445; JPS, 0000-0002-7930-9187

Sexual selection often favours investment in expensive sexual traits that help individuals compete for mates. In a rapidly changing environment, however, allocation of resources to traits related to reproduction at the expense of those related to survival may elevate extinction risk. Empirical testing of this hypothesis in the fossil record, where extinction can be directly documented, is largely lacking. The rich fossil record of cytheroid ostracods offers a unique study system in this context: the male shell is systematically more elongate than that of females, and thus the sexes can be distinguished, even in fossils. Using mixture models to identify sex clusters from size and shape variables derived from the digitized valve outlines of adult ostracods, we estimated sexual dimorphism in ostracod species before and after the Cretaceous/Palaeogene mass extinction in the United States Coastal Plain. Across this boundary, we document a substantial shift in sexual dimorphism, driven largely by a pronounced decline in the taxa with dimorphism indicating both very high and very low male investment. The shift away from high male investment, which arises largely from evolutionary changes within genera that persist through the extinction, parallels extinction selectivity previously documented during the Late Cretaceous under a background extinction regime. Our results suggest that sexual selection and the allocation of resources towards survival versus reproduction may be an important factor for species extinction during both background and mass extinctions.

## 1. Introduction

Observations from the fossil record demonstrate that extinction risk can be influenced by body size [1,2], physiology [3] and geographical range size [4], among other traits [5,6] and that the nature of such extinction selectivity can differ between time periods, and between background and mass extinction regimes [4,7,8].

Despite broad documentation of extinction selectivity with respect to many kinds of traits, sexually selected traits have received little attention in this context. Sexual selection arises from fitness differences related to competition for mates [9]. A common outcome of sexual selection is an investment, often by males, in traits that increase mating success. These traits can influence pre-copulatory processes, such as competition for access to mates or choice of reproductive partners, and they can influence post-mating processes such as sperm selection and cryptic choice [9,10]. Such sexually selected traits are often sexually dimorphic and usually costly (e.g. [11]), and it has been suggested that species which allocate excessive resources to traits not directly related to survival may elevate their extinction risk when environmental conditions change [12–14].

However, a conflicting body of theory suggests the opposite: for traits that reflect male condition, sexual selection may reinforce natural selection by favouring males that are otherwise healthy, resulting in more effective adaptation and making extinction less likely [15–17]. This hypothesis was supported by a recent meta-analysis of experiments that manipulated sexual selection, which found that sexual selection generally improves population fitness [18].

Although experimental evidence supports the view that sexual selection should promote adaptation and thereby reduce extinction risk, studies of natural populations have more often yielded the opposite result, where indicators of high sexual selection correlate with proxies for elevated extinction risk [19–22]. One significant challenge is that all these studies analyse living populations, but infer extinction without fossil data [23]. Conversely, whereas extinction selectivity can be inferred reliably with fossils, sexual selection is usually undetectable in fossil taxa, in part because males and females cannot be distinguished from each other.

Ostracods are one of the few fossil taxa in which sexual selection and extinction can be simultaneously quantified. These small, bivalved crustaceans have one of the richest known fossil records [24]. Furthermore, in the ostracod superfamily Cytheroidea, male shells are systematically more elongate than those of females, and sexes can thus be identified in fossil specimens [25–27]. This shape difference arises from an expansion of the posterior region in the mineralized shell that accommodates the large sperm pump and copulatory apparatus in males [28]. In living ostracod species, the degree of dimorphism can be taken as an indicator of the intensity of sexual selection, with larger and more elongate males indicating greater male investment in reproduction [29]. In a previous study examining background extinction in the Late Cretaceous, we reported that increased extinction risk was associated with strong size and shape dimorphism that reflect high investment in male sexual traits [30].

The focus of the present work is to examine the role of sexual selection across a mass extinction regime and into the subsequent period of biotic recovery. If costly male traits are an evolutionary risk when environments change, then this risk should be especially pronounced during the environmental upheavals associated with the Cretaceous/Palaeogene (K/Pg) mass extinction [31–33]. Here, we test this prediction by comparing the patterns of sexual dimorphism in cytheroid ostracod faunas before and after the K/Pg boundary. We find a significant shift in sexual dimorphism across this interval, with the most extreme dimorphism styles underrepresented following the mass extinction, in the early Palaeocene. These findings suggest that sexual selection, in addition to being a fundamental agent of microevolution, can play an important role in macroevolutionary dynamics.

## 2. Material and methods

### (a) Fossil material

Late Cretaceous data were presented by Hunt et al. [27] (electronic supplementary material, table S1). These include dimorphism estimates from 142 fossil populations representing 106 species, spanning approximately the last 20 Myr of the Cretaceous (Santonian–Maastrichtian) of the United States Gulf and Atlantic Coastal Plain. Newly analysed Palaeocene populations were sampled from collections at the National Museum of Natural History (Smithsonian Institution), Louisiana State University (primarily Joseph Hazel's collection), the University of Houston (Rosalie Maddock's collection) and new field collections (electronic supplementary material, table S2; the spatial distribution of samples is shown in the electronic supplementary material, figure S1). We focused sampling efforts on the early part of the Palaeocene, from the Midwayan regional stage. This corresponds primarily to the Danian stage (Brightseat, Clayton, Kincaid Formations), although two of the sampled units extend from the Danian into at least the Selandian (Wills Point and Beaufort Formations), and one is restricted to the Selandian (Coal Bluff Member of the Naheola Formation). Two additional populations were drawn from Texas samples for which stratigraphy could not be refined beyond early Palaeocene because of local faulting.

### (b) Measuring specimens and quantifying dimorphism

We followed the protocol developed in Hunt et al. [27] for photographing, digitizing and measuring specimens, and for quantifying sexual dimorphism. Each specimen was oriented in lateral view and digitally photographed through a dissecting microscope. Outlines of valves or carapaces were digitized using the software TPSDig [34]. Ornamentation, such as spines and denticles was digitized as is, except for the species Pterygocythereis lemnicata, which has prominent wing-like alae that can mask shape differences. In this species, we followed the protocol described by Hunt et al. [27, p. 3] to digitally remove the ala before analysis. All specimens from a species recovered in a sample were photographed, and in some cases (20 out of 71), two or more samples from the same formation were combined into a single analytical population to increase the sample size (electronic supplementary material, table S2). We quantified body size using the area of the digitized outline and measured shape as the ratio between major axis (length) and minor axis (height) of the ellipse fitted to the outline. Both size and shape variables were log-transformed prior to analysis.

We fitted mixture models to the scatterplots of size versus shape to infer sex clusters, as implemented by the R package mclust [35,36]. This approach considers data to be drawn from a mixture of bivariate normal distributions. Evidence in favour of sexual dimorphism was assessed by comparing the Bayesian information criterion (BIC) for the two-group solution (one group for each sex) to that of the single-group solution. From the best two-group solution, sexual dimorphism was quantified as the male mean minus the female mean, for both size and shape (figure 1). As noted above, males are more elongate than females among living cytheroid species, and therefore sexual shape dimorphism (shape DM) is always positive. By contrast, sexual size dimorphism (size DM) is positive when males are larger than females and negative when males are the smaller sex.

About 30% of Palaeocene species were represented by more than one dimorphism estimate, which were averaged for species-level analyses. For genus-level analyses, we averaged these species-level averages within genera.

### (c) Statistical methods

To compare changes in average sexual dimorphism before and after the K/Pg mass extinction, we performed an ANOVA with respect to age (Cretaceous, K versus Palaeocene, P, which is the earliest epoch of the Palaeogene), with an additional covariate of taxonomic family to account somewhat for phylogenetic differences in dimorphism. This family covariate included categories Cytherideidae and Trachyleberididae, the two dominant families, with the remaining taxa lumped into other.

In addition to shifts in mean dimorphism, other aspects of the sexual dimorphism space may have changed between the Cretaceous and Palaeocene. We examined temporal changes in the dispersion of sexual dimorphism using Bartlett's test for unequal variances [37], applied to both size and shape
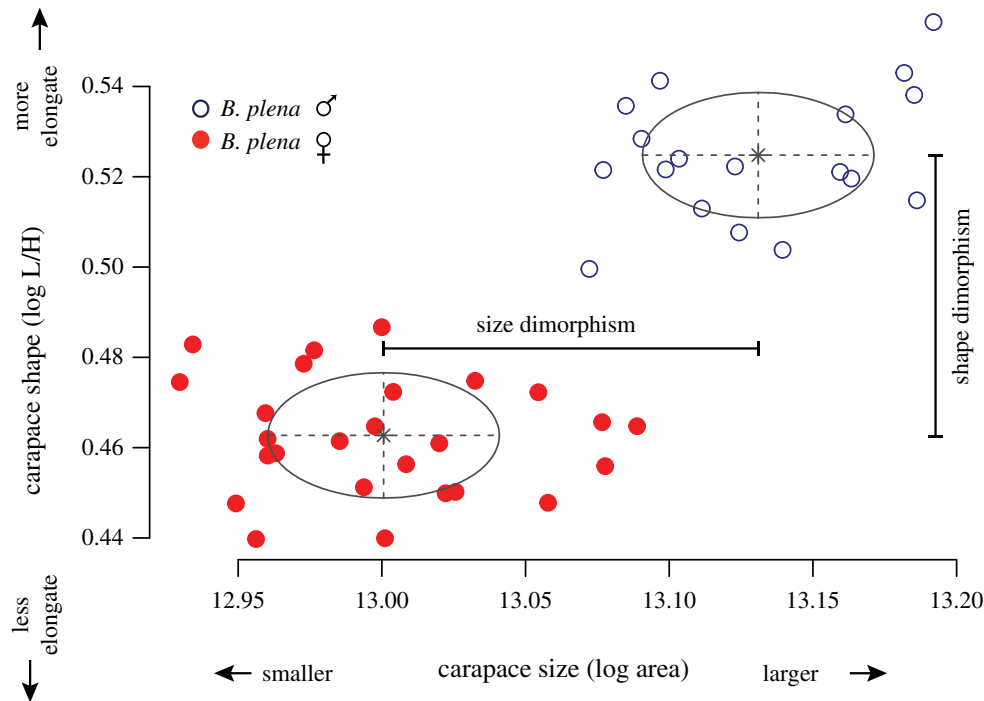
**Figure 1.** A fossil population from *Brachycythere plena*, showing sexual dimorphism in carapace size and shape (open circles, males; filled circles, females). Sexual dimorphism was quantified as the difference between male and female means. This population was sampled from the Clayton Formation from Alabama, USA. (Online version in colour.)

dimorphism. Because variances are unbiased with respect to sample size, this test is unaffected by the deeper sampling of taxa in the Cretaceous, compared to the Palaeocene. We used species as the unit of analysis for all of these tests.

We visualized differences in the distributions of sexual dimorphism using two-dimensional kernel-density estimators. Cretaceous and Palaeocene bivariate distributions of size dimorphism and shape dimorphism were estimated, using a shared smoothing bandwidth taken as the mean of the optimal bandwidths for the two faunas as returned by the R function *bandwidth.nrd* [38]. We subtracted Palaeocene minus Cretaceous densities to yield a contour plot showing differences between the distribution of sexual dimorphism from these two intervals. Positive values indicate regions of the dimorphism space that are disproportionately occupied in the Palaeocene, relative to the Cretaceous, and negative values indicate regions more densely occupied in the Cretaceous.

Species-level turnover is 100%, or nearly so, across the K/Pg, and there are no species for which we have dimorphism estimates on both sides of the boundary. We, therefore, used genera as operational clades to help dissect the causes of change in sexual dimorphism across the K/Pg boundary. We considered differences among three kinds of genera: victims (V) that last appeared in the Cretaceous; survivors (S) that spanned the Cretaceous and Palaeocene; and new genera (N) that first appeared in the Palaeocene (electronic supplementary material, table S3). These categories are defined regionally, based on Coastal Plain occurrences, because phylogenetic continuity within genera is less certain at global scales. We performed a series of *t*-tests on the following genus subsets: (i) Cretaceous dimorphism was compared in victim versus survivor genera ($V_K$ versus $S_K$) to test for selective generic extinction across the boundary; (ii) Palaeocene dimorphism was compared between survivor and new genera ($S_P$ versus $N_P$) to test for selective generic origination after the boundary; and (iii) survivor genera were compared before and after the boundary ($S_K$ versus $S_P$) to test for evolutionary changes within genus-level lineages. Such a shift can arise from anagenetic changes within species, or from differential speciation or extinction among the species that comprise a genus. This last *t*-test was run as a paired test because the same genus is compared on both sides of the boundary.

For the most part, we follow generic assignments as they have been applied in the literature. However, shifts in taxonomic practice across major extinction boundaries can cloud true extinction patterns [39,40]. Specifically, in our study, there are three pairs of genera for which a Cretaceous genus persists into the Palaeocene but with the bulk of its diversities carved off into newly arising Palaeocene genera: *Brachycythere–Opimocythere, Haplocytheridea–Vetusocytheridea* and *Antibythocypris–Clithrocytheridea* [41]. We treat these new genera for the generic subset analyses as separate taxa. However, we also test the robustness of these analyses by rerunning tests while considering the pairs of genera as operationally congeneric (e.g. considering *Opimocythere* species to be members of *Brachycythere* for purposes of analysis).

# 3. Results

## (a) Sexual dimorphism estimates

We analysed 71 Palaeocene populations, assigned to 52 species (electronic supplementary material, table S2). In 60 of these 71 populations (85%), the two-group solution is favoured by BIC, and dimorphism estimates calculated from the two-group solution are consistent with male and female clusters. One such example population is shown in figure 1. In five of the 11 remaining populations, we estimated sexual dimorphism from the two-group solution even though this solution was marginally less supported than the one-group solution because the implied dimorphism was similar to estimates from closely related populations (see discussion in [27, p. 11]). Populations of *Opimocythere verrucosa* and *Phacorhabdotus sculptilis* yielded low sample sizes (n = 9 and 10, respectively), and no viable solution was obtained for them. The four remaining populations were interpreted to represent female-only, putatively asexual populations [27, p. 16], as evidenced by their narrow size and shape variation, similar to that observed within individual sexes in sexual populations, and they were not considered further

in these analyses. For populations with dimorphism estimates, BIC support for the two-group solution was generally moderate to strong ($\Delta$BIC > 4 in 3 out of 4 of populations), indicating that the dimorphism estimates are generally well founded.

## (b) Sexual dimorphism across the Cretaceous/ Palaeogene mass extinction: species-level patterns

The two most striking differences we see across the K/Pg boundary are that sexual dimorphism is overall lower in the Palaeocene than in the Cretaceous, and that early Palaeocene species show much more limited variation in sexual dimorphism. This section treats each of these findings in turn.

Shape dimorphism is significantly lower in the Palaeocene, compared to the Cretaceous (ANOVA: K-Pg mean species difference = −0.015; $F_{1,139} = 6.79$; $p = 0.01$). Size dimorphism also decreases by a similar amount, though this difference is not statistically significant (ANOVA: K-Pg difference = −0.018; $F_{1,139} = 1.86$; $p = 0.175$). In both aspects of dimorphism, family-level taxonomy partly explains the distribution of sexual dimorphism, reflecting the presence of some phylogenetic structure in sexual dimorphism (shape DM: $F_{2,139} = 5.33$; $p = 0.006$; size DM: $F_{2,139} = 7.58$; $p < 0.001$). The reduction in shape dimorphism is particularly evident in the family Cytherideidae (electronic supplementary material, figure S2).

In addition to shifts in location, the spread of sexual dimorphism is markedly less in the Palaeocene (Bartlett's test for equal variance: size DM: $\sigma_K^2 = 0.0134$, $\sigma_P^2 = 0.0068$, $K^2 = 6.43$, $p = 0.01$; shape DM: $\sigma_K^2 = 0.00091$, $\sigma_P^2 = 0.00044$, $K^2 = 7.10$, $p = 0.008$). This contraction occurs independently within the two dominant families (electronic supplementary material, figure S2), and it is caused by the preferential loss of species with extreme sexual dimorphism in the Palaeocene (areas of light shading in the top-left, bottom-left and the top-right of figure 2b). This change is particularly pronounced in the upper-right quadrant of sexual dimorphism space, which represents males that are much bigger, and much more elongate than females. This condition signifies high investment by males in sexual traits. One-third of Cretaceous species (33%, 32 out of 96) plot in the upper-right quadrant of sexual dimorphism space (figure 2a), with dimorphism estimates greater than the Cretaceous medians for both dimorphism dimensions. By contrast, only one (2.1%) Palaeocene species, *Loxoconcha nuda*, falls in this region of the sexual dimorphism space.

The Cretaceous data span almost 20 Myr, compared to the approximately 5 Myr encompassed by the Palaeocene samples. However, there is no indication of substantial changes in sexual dimorphism before the K/Pg boundary. The distributions of size and shape dimorphism for species that are found in the Maastrichtian, the latest stage of the Cretaceous, are extremely similar to those from species that are limited to earlier stages (electronic supplementary material, figure S3; KS test: size dimorphism $D = 0.143$, $p = 0.662$; shape dimorphism $D = 0.103$, $p = 0.936$).

## (c) Survivors, victims and new taxa: genus-level patterns

Next, we compared genera that were victims versus survivors of the K/Pg extinction (figure 3, V versus S panel). Although these two groups did not vary according to size dimorphism ($t$-test: size: $t_{30.67} = 0.33$, $p = 0.75$; figure 3a), surviving genera had significantly higher shape dimorphism than victim genera ($t$-test: shape: $t_{29.91} = 2.96$, $p = 0.005$; figure 3b). This difference in shape dimorphism between victim and surviving genera is evident only among taxa with negative size dimorphism (males smaller than females, those on the left side of figure 4a).

We obtained dimorphism estimates for seven of the genera that newly appear in the early Palaeocene: *Acanthocythereis*, *Clithrocytheridea*, *Opimocythere*, *Vetusocytheridea*, *Hermanites*, *Leguminocythereis* and *Platycythereis*. Dimorphism in these genera is very similar to Palaeocene values for genera that survive the extinction (figure 3, S versus N panel; $t$-test: size: $t_{7.52} = −0.11$, $p = 0.92$; figure 3c; shape: $t_{11.77} = −0.04$, $p = 0.97$; figure 3d). This similarity suggests that selective generic origination does not account for shifts in dimorphism across the boundary.

Sexual dimorphism within surviving genera markedly decreased from the Cretaceous to the Palaeocene (figure 3, K versus P panel). This difference was not quite significant for size dimorphism ($t$-test: size: $t_{11} = 1.78$, $p = 0.10$; figure 3e) but was strongly significant for shape dimorphism ($t_{11} = 4.40$, $p = 0.001$; figure 3f). Of the 12 genera that we sampled in both the Cretaceous and Palaeocene, all 12 show decreases in mean shape dimorphism across the boundary (figure 4b). For the genera *Hazelina*, *Loxoconcha* and perhaps *Antibythocypris*, some or all Palaeocene descendants have size and shape dimorphism well below the range of their Cretaceous relatives (electronic supplementary material, figure S4). In other genera, Palaeocene species are offset to lower dimorphism values, but still fall within the range of Cretaceous values for that genus (electronic supplementary material, figure S4).

Lastly, the above results treated *Clithrocytheridea*, *Opimocythere* and *Vetusocytheridea* as new Palaeocene genera. Classifying them as their probable ancestral genera did not qualitatively change the results for the generic subsets analyses (electronic supplementary material, figure S5).

## 4. Discussion

The Cretaceous/Palaeogene extinction crisis resulted in substantial changes in the sexual dimorphism of the ostracod fauna. Palaeocene sexual dimorphism values are lower than in the Cretaceous, especially for shape dimorphism, and the dispersion of sexual dimorphism becomes strikingly narrower after the extinction. This reduction in a spread is driven mostly by a decrease in the frequency of species in two opposite regions of the sexual dimorphism space (figure 2): (i) the upper-right quadrant with strong sexual dimorphism in both size and shape, and (ii) the lower-left region with very low-shape dimorphism and negative size dimorphism. These two regions are at opposite ends of a continuum between very high (upper right) and very low (lower left) male investment in reproduction. Changes in occupancy of these two regions of the dimorphism space have different underlying bases and, potentially, causal drivers.

In the Late Cretaceous, ostracod species with dimorphism indicating very high male investment were common: 32 out of 96 species had values for both metrics higher than the Cretaceous median. Moreover, this condition was phylogenetically dispersed, with these 32 species being drawn from 14 different genera. And yet, this region of the dimorphism
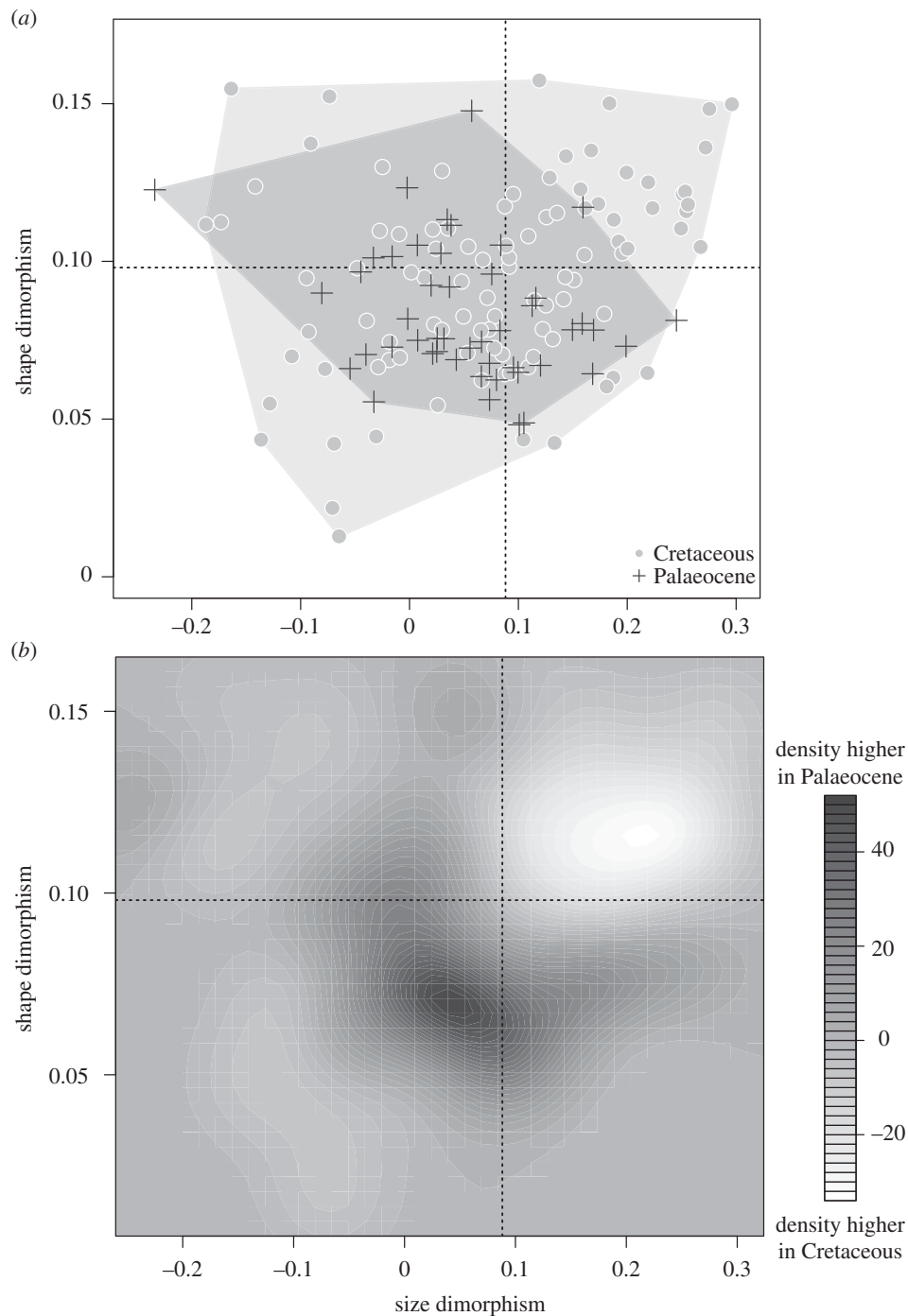
**Figure 2.** Size dimorphism versus shape dimorphism of cytheroid ostracods across the Cretaceous–Palaeocene boundary. (*a*) Scatterplot of 96 Cretaceous (circles) and 52 Palaeocene species (crosses). Light grey shading shows the convex hull outlining the Cretaceous species and darker shading shows the same for the Palaeocene. (*b*) Two-dimensional density plot showing the shift in dimorphism space occupation across the boundary. Light areas (negative densities) indicate regions less occupied in the Palaeocene, compared to the Cretaceous and dark areas (positive densities) indicate the opposite.

space is nearly empty in the early Palaeocene (1 out of 46 species), even though 8 out of the 14 genera occupying this region in the Cretaceous survive the K/Pg extinction. The reduction in species with this high-investment form of dimorphism is consistent with this condition being a liability during the dramatic environmental upheavals associated with the mass extinction. It also parallels the finding of higher extinction risk in species with high dimorphism during intervals of background extinction [30].

However, we cannot directly document the selective extinction of species across the K/Pg boundary because of extremely high turnover; there are no known surviving species to which we can compare the sexual dimorphism of the victims (Palaeocene species may have ancestors among

the Cretaceous fauna, or they may derive from related lineages entering the region after the extinction from more distant areas). Genera, however, can be compared because some survive the K/Pg whereas others do not.

Two highly dimorphic genera, *Veenia* and *Schuleridea*, do not survive into the Palaeocene, but generic extinctions are not, in general, clustered in genera with strong dimorphism (figure 4*a*). Rather, the emptying out of the upper-right quadrant of figure 2 is instead driven by systematic shifts to weaker dimorphism occurring *within* genera (figure 4*b*). These shifts within genera may well be caused by the selective extinction of high-investment species within genera, similar to the selectivity documented during background extinction in the Late Cretaceous [30]. However, these generic
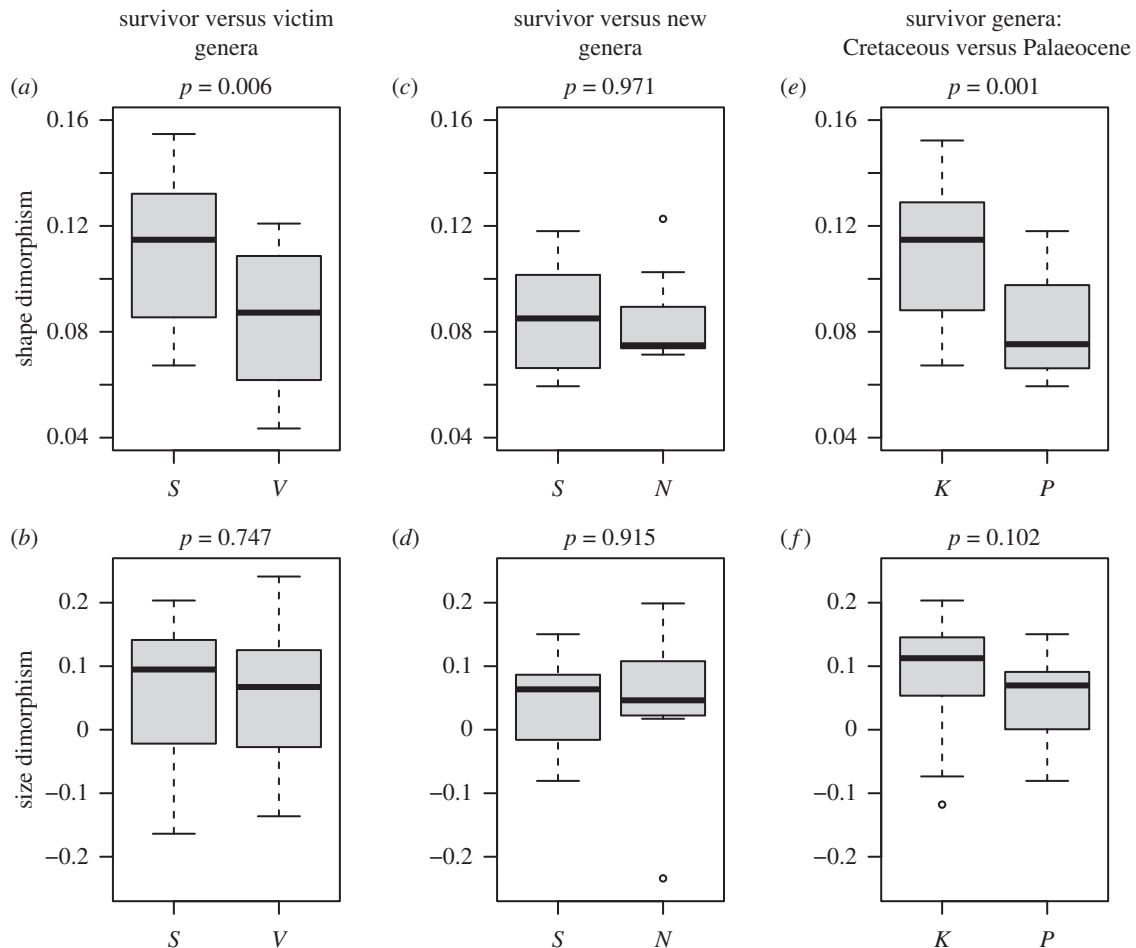
**Figure 3.** Boxplots showing shape dimorphism (*a,c,e*) and size dimorphism (*b,d,f*) in genera of three different categories: victim (*V*) genera, those that terminate in the Cretaceous; survivor (*S*) genera who persist from the Cretaceous into the Palaeocene; new (*N*) genera, who appear first in the early Palaeocene. Left figures (*a,b*) show contrast between Cretaceous dimorphism values for survivors and victims ($V_K$ versus $S_K$); middle figures (*c,d*) show contrast in Palaeocene dimorphism between survivors and newly arising genera ($S_P$ versus $N_P$); right figures (*e,f*) show, for genera that persist through the K/Pg, dimorphism in the Cretaceous versus that in the Palaeocene ($S_K$ versus $S_P$). *p*-value for the relevant *t*-test shown at the top of the plot.

shifts may also be caused by selective origination among species within a genus, by phyletic trends within individual species, or by some combination of these three processes. Although sexual dimorphism is usually stable within species over time, we have previously documented striking reduction in dimorphism within the species *Haplocytheridea renfroensis* [27]. Similar trends within species could account for the within-genus shifts that we document. Indeed, when Palaeocene species have dimorphism values outside the range of that genus in the Cretaceous (electronic supplementary material, figure S3), then the dimorphism shift cannot be caused solely by selective extinction and therefore selective origination or within-lineage evolution must play a role. A resolved phylogeny could help to disentangle these possibilities, but, unfortunately, no phylogenetic hypotheses are available for these taxa.

No matter which processes best explain the patterns we report, the evolutionary shift away from strong male investment in reproduction is consistent with conditions during the extinction interval being unfavourable to this kind of dimorphism. If the cost of diverting resources into mating/reproductive success does not directly translate into the increased numbers of offspring, the selection on traits related to reproduction relaxes [42]. The observed reduction of sexual dimorphism within genera would be consistent with reduced sexual selection across the K/Pg interval. Under conditions of elevated abiotic environmental change, it may be expected that selection

would favour resources to be redirected to other traits more closely associated with survival.

There is a similar, though less marked, absence in the Palaeocene of species with very low-shape dimorphism and negative size dimorphism (females larger than males) which accounts for the significantly higher shape dimorphism in survivor versus victim genera. This change in the lower-left of the dimorphism space (figure 2) is caused by the extinction of five genera that populate this corner of dimorphism space in the Cretaceous: *Acuminobrachycythere*, *Amphicytherura*, *Anticythereis*, *Cuneoceratina* and *Schizoptocythere* (figure 4*a*). The last two of these genera have last appearances that are several million years before the mass extinction, and therefore their extinction is unrelated to the K/Pg crisis. The other three genera do range into the late Maastrichtian with ranges that terminate near the boundary. The preferential demise of these low-investment genera may indicate extinction selectively occurring when sexual selection is low. This is opposite in direction to the finding of a systematic shift to lower dimorphism within surviving genera, and of a significant shift to lower dimorphism overall at the species level.

One way to reconcile these conflicting findings about extinction selectivity and sexual selection is to suggest that sexual selection is detrimental to species survival either when it is very strong or very weak. Elevated extinction risk may be appreciable only when sexual selection is quite strong, either because it takes strong sexual selection to
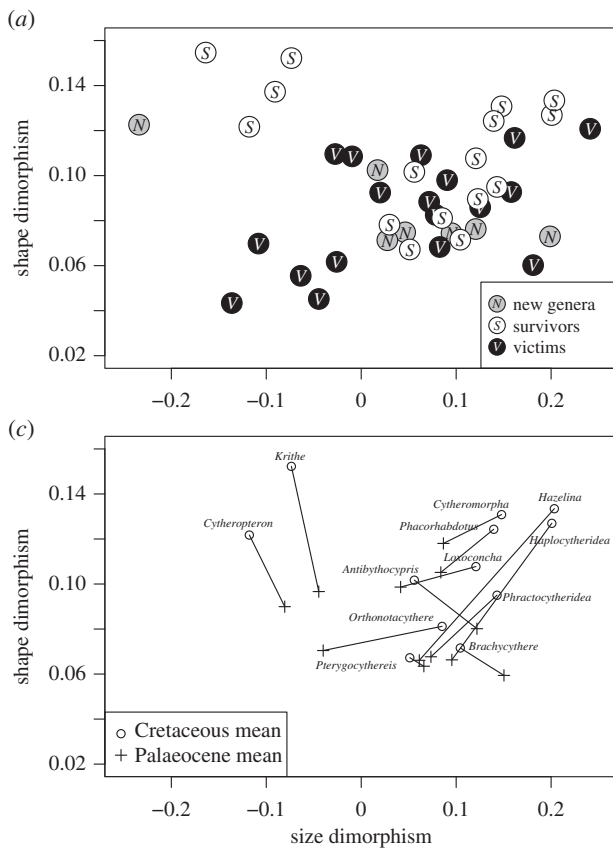
**Figure 4.** Genus-level patterns in size and shape sexual dimorphism. (*a*) Mean dimorphism within genera, shown separately for survivor (*S*), victim (*V*) and genera newly arising (*N*) in the Palaeocene. The position of surviving genera is shown with respect to their Cretaceous mean only, so that dimorphism in survivors and victims at the time of extinction can be compared (*S*$_K$ versus *V*$_K$). Note that the apparent selectivity against genera in the lower left of the plot is not present in species-level comparisons (see main text). (*b*) Shifts in dimorphism within genera that survive the K/Pg extinction. For each genus, its Cretaceous mean (circle) is connected to its Palaeocene mean (cross) by a line segment. Genus labels are placed near to the Cretaceous means. Note that we lack Palaeocene dimorphism for some surviving genera; such genera will be included in part (*a*) but not part (*b*) of this figure.

substantially shift the population from its optimal phenotype for survival [43], or because only mating systems with quite strong sexual selection tend to favour behaviours that foster sexual conflict and, hence, reduce the fitness of females and thus lower population growth [44]. At the other end of the continuum, extinction risk may be elevated when sexual selection is very low because populations experiencing such selection do not benefit from the purging of deleterious alleles and an overall increase in adaptation [18]. Under this hypothesis, the distribution of sexual dimorphism contracted at both corners during the K/Pg crisis as conditions favoured intermediate strengths of sexual selection. The environmental and demographic context of species may also affect whether strong sexual selection reduces or intensifies extinction risk [16,44,45], which might account for some of the complexity of the patterns we document.

From the Cretaceous to the early Palaeocene, we see an emptying out of the high sexual selection region of the sexual dimorphism space, which is not re-filled as of several million years later. This persistent vacancy is a puzzle for which we do not currently have an adequate explanation. It may be that the most extreme sexual dimorphism condition was associated with behavioural or reproductive traits that

changed or disappeared through extinction, and that such traits are not readily re-evolved. However, a large number of high-dimorphism Cretaceous species, drawn from many different genera, suggests that this condition evolved frequently, at least during the Cretaceous. Moreover, although conditions must have been challenging during the immediate crisis interval [33], our Palaeocene data post-date this interval, occurring after environmental conditions had stabilized. Traits should respond readily to changing circumstances, in part because sexual investment is closely linked to fitness, and yet high male-investment forms did not re-evolve over the several million years following the crisis. It is plausible that a relevant aspect of the biotic or abiotic environment changed in a lasting way after the K/Pg. We do not know of obvious candidates for such a persistent change, but some possible factors, such as shifts in mortality, population density, or predation regime, would not be easily recognized in the fossil record. We must also acknowledge that our ability to identify causal factors is limited by how little is known about sexual selection and mating systems in living cytheroids. Although mating and sexual behaviours have been observed in a few species [26,28], the tiny size and marine habitat of these animals have prevented the collection of broad comparative data for mating-related traits.

## 5. Summary

Here, we report changes in sexual dimorphism, probably reflecting changes in sexual selection, across the K/Pg mass extinction. The distribution of sexual dimorphism contracts across the boundary, with losses concentrated in species with dimorphisms indicative of very weak, or very strong, sexual selection. The first of these manifests as the preferential extinction of low-dimorphism genera, and the second is driven by shifts to lower dimorphism occurring independently within genera that survive into the Palaeocene. This systematic shift in dimorphism within genera is consistent with conditions during the extinction interval being unfavourable to behaviours and mating systems that result in strong sexual selection. This result is consistent with theoretical arguments which suggest that high sexual selection can elevate extinction risk during environmental change. Selective extinction of very low-investment genera provides evidence, albeit more limited, that extinction risk may also be elevated under conditions of very low sexual selection.

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