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biology (e.g., Dunn et al. 2001; Van Valkenburgh and Sacco 2002).

Perhaps the taxon most amenable to broadly documenting sexual dimorphism in the geological record is the Ostracoda (Ozawa 2013). Brooding of eggs or juveniles occurs throughout the major groups of ostracodes, and in these taxa females can often be distinguished by their greater lateral width or other modifications to the shell for housing young (van Morkhoven 1962; Horne et al. 1998b; Ozawa 2013). An additional style of sexual dimorphism characterizes the superfamily Cytheroidea. Whether or not they brood, living species of this clade have males that are relatively more elongate than females in lateral view (van Morkhoven 1962; Cohen and Morin 1990), a difference that is thought to result from the need to accommodate the large copulatory apparatus in males. Each hemipenis is com-

after being placed on double-sided tape or,
more often, modeling clay shaped to situate

lateral views but digitized two landmarks that defined the ala's anterior and posterior extent and used an R script to remove the intervening points (Fig. 2).

Body size was measured as the area of the digitized outline. Shape was measured as the length to height ratio (L/H), where length and height were estimated as the major and minor axes of an ellipse fit to the outline (Fig. 1). These lengths and heights are similar to the lengths and heights traditionally employed by ostracode researchers, but we found our approach to be less subjective, because specimens did not need to be oriented by eye. Both area and L/H were natural log transformed prior to analysis.

Sexual dimorphism is often examined in the ostracode literature via plots of length versus height. Here we use plots of area versus L/H, which is similar to rotating the traditional plots by 45° (Fig. 3). We found this approach more useful for several reasons. First, it decomposes male–female differences neatly into size dimorphism and shape dimorphism, which have clear biological interpretations. Because males are relatively more elongate than females in living cytheroids, the cluster with higher L/H ratios was interpreted as male. Second, we have found that using area and L/H as axes sometimes gives better statistical separation between males and females in populations with visually obvious clusters.

the female mean. This bias is usually easy to recognize, because it can muddle clusters in the combined data, even when they are distinct in left and right valves viewed separately. In addition, this bias will cause left and right valves to be offset within sex clusters (Supplementary Fig. S1). In a few such cases (Supplementary Table S1), we used a different

TABLE 2. Dimorphism estimates and information about analyzed populations. Status indicates whether reasonable dimorphism estimates could be obtained ("OK") or why they could not be found. ΔBIC is the difference in support between the best one- and two-group models, with positive values indicating greater support for the two-group model. Shape dimorphism (Shape DM) and size dimorphism (Size DM) are differences between the sexes in natural log-transformed shape (L/H ratio) and size (area), respectively. Table S1 provides additional information for these populations.

Population label	Species	Status	ΔBIC	No. individuals	No. samples	Shape DM	Size DM
ACU_ACUM-1	Acuminobrachycythere acuminata (Hazel & Paulson, 1964)	OK	8.6	19	1	0.058	−0.167
ACU_ACUM-3	Acuminobrachycythere acuminata (Hazel & Paulson, 1964)	OK	2.1	16	1	0.052	−0.090
ACU_BLUF-1	Acuminobrachycythere blufftownensis Puckett, 2002	OK	0.4	26	1	0.013	−0.065
ACU_CUSS-1	Acuminobrachycythere cussetensis Puckett, 2002	OK	5.3	17	1	0.066	−0.078
ACU_DIMI-1	Acuminobrachycythere diminuta Puckett, 2002	OK	0.0	17	1	0.042	−0.069
ACU_FORA-1	Acuminobrachycythere foraminosa (Alexander, 1934[b])	OK	−2.2	60	1	0.054	0.026
ACU_RALE-1	Acuminobrachycythere raleighensis (Brown, 1957)	OK	16.8	46	1	0.083	−0.038
ACU_RALE-2	Acuminobrachycythere raleighensis (Brown, 1957)	OK	−4.0	17	1	0.074	−0.005
ACU_RALE-3	Acuminobrachycythere raleighensis (Brown, 1957)	OK	5.3	17	1	0.086	−0.075
ACU_VENT-1	Acuminobrachycythere ventrolevis Puckett, 2002	OK	38.1	78	1	0.078	−0.093
AMP_COPI-3	Amphicytherura copicosta Crane, 1965	OK	−4.5	43	1	0.022	−0.071
AMP_PAND-1	Amphicytherura pandicosta Crane, 1965	OK	−8.2	26	1	0.096	0.013
AMP_PAND-4	Amphicytherura pandicosta Crane, 1965	OK	0.9	38	1	0.042	−0.050
ANB_CRAS-1	Antibythocypris crassa Brouwers & Hazel, 1978	OK	30.3	27	1	0.123	0.168
ANB_CRAS-2	Antibythocypris crassa Brouwers & Hazel, 1978	OK	27.9	23	1	0.090	0.216
ANB_ELON-1-2	Antibythocypris elongata Brouwers & Hazel, 1978	OK	4.8	32	1	0.095	0.014
ANB_FABA-1	Antibythocypris fabaformis (Berry, 1925)	OK	43.4	100	1	0.083	0.049
ANB_GOOB-1	Antibythocypris gooberi Jennings, 1936	OK	105.1	129	1	0.112	0.142
ANB_GOOB-2	Antibythocypris gooberi Jennings, 1936	OK	26.2	36	1	0.104	0.076
ANB_MACR-1	Antibythocypris macropora (Alexander, 1929)	OK	6.2	46	1	0.117	0.088
ANB_MINU-1	Antibythocypris minuta (Berry, 1925)	OK	26.0	46	1	0.088	0.115
ANB_PATA-1-2-3	Antibythocypris pataulensis (Crane, 1965)	OK	9.4	22	3	0.112	−0.173
ANB_PHAS-1-2-3	Antibythocypris phaseolites (Berry, 1925)	OK	27.1	73	3	0.105	0.054
ANT_CACU-1-2	Anticythereis cacumenata (Brown, 1957)	OK	5.0	35	1	0.074	−0.018
ANT_COPE-1	Anticythereis copelandi Smith, 1978	OK	12.7	40	1	0.064	−0.022
ANT_COPE-2	Anticythereis copelandi Smith, 1978	OK	6.6	53	1	0.069	−0.035
ANT_RETI-1-2	Anticythereis reticulata (Jennings, 1936)	OK	−5.1	52	1	0.044	−0.031
ASC_HAZA-1	Ascetoleberis hazardi (Israelsky, 1929)	OK	21.5	40	1	0.103	0.107
ASC_HAZA-2	Ascetoleberis hazardi (Israelsky, 1929)	OK	6.9	25	1	0.094	0.076
ASC_PLUM-3	Ascetoleberis plummeri (Israelsky, 1929)	OK	25.8	47	1	0.100	0.067
ASC_RUGO-1	Ascetoleberis rugosissima (Alexander, 1929)	OK	15.2	35	1	0.129	0.030
LIM_VERR-1	Aysegulina verricula						

TABLE 2. Continued

Population label	Species	Status	ΔBIC	No. individuals	No. samples	Shape DM	Size DM
BIC_POLI-2	Bicornicythereis polita (Crane, 1965)	OK	4.6	16	1	0.119	0.018
BIC_POLI-4	Bicornicythereis polita (Crane, 1965)	OK	19.0	32	1	0.101	0.073
BIC_VECL-2	Bicornicythereis veclitella (Crane, 1965)	OK	34.7	65	1	0.102	0.161
BRA_ASYM-1-2	Brachycythere asymmetrica Puckett, 1994	OK	28.5	67	1	0.080	0.023
BRA_CREN-2	Brachycythere crenulata Crane, 1965	OK	50.6	92	1	0.090	0.063
BRA_CREN-3	Brachycythere crenulata Crane, 1965	OK	57.8	52	1	0.067	0.083
BRA_DURH-1-2	Brachycythere durhami Hazel & Paulson, 1964	OK	5.2	37	2	0.042	0.133
BRA_NAUS-1	Brachycythere nausiformis Swain, 1952	OK	39.8	77	1	0.066	0.109
BRA_OVAT-2	Brachycythere ovata (Berry, 1925)	OK	34.4	43	1	0.063	0.214
BRA_OVAT-3	Brachycythere ovata (Berry, 1925)	OK	46.3	70	1	0.064	0.161
BRA_PYRI-1-2-3-4	Brachycythere pyriforma Hazel & Paulson, 1964	OK	24.5	51	4	0.099	0.112
BRA_PYRI-5	Brachycythere pyriforma Hazel & Paulson, 1964	OK	11.4	32	1	0.103	0.071
BRA_RHOM-2-3	Brachycythere rhomboidalis (Berry, 1925)	OK	17.8	41	1	0.070	0.114
CUN_PEDA-1-2-3-4-5	Cuneoceratina pedata (Marsson, 1880)	OK	0.7	28	5	0.042	−0.191
CUN_PEDA-6-7	Cuneoceratina pedata (Marsson, 1880)	OK	−3.5	28	2	0.044	−0.100
CUN_PEDA-8-9	Cuneoceratina pedata (Marsson, 1880)	OK	−0.3	44	2	0.044	−0.118
CYS_CAUD-4-5	Cythereis caudata Butler & Jones, 1957	OK	5.8	20	2	0.094	0.048
CYS_DALL-1	Cythereis dallasensis Alexander, 1929	OK	−2.3	32	1	0.067	0.050
CYS_DALL-2	Cythereis dallasensis Alexander, 1929	OK	7.0	25	1	0.075	0.056
CYS_HANN-1	Cythereis hannai Israelsky, 1929	OK	22.8	20	1	0.105	0.267
CYM_ARBE-1	Cytheromorpha arbenzi (Skinner, 1956)	OK	33.4	23	1	0.135	0.167
CYM_UNIF-1-2	Cytheromorpha unifossula Crane, 1965	OK	26.2	33	2	0.112	0.106
CYM_UNIF-3	Cytheromorpha unifossula Crane, 1965	OK	43.6	26	1	0.141	0.151
CYT_CAST-3	Cytheropteron castorensis Butler & Jones, 1957	OK	8.2	40	1	0.124	−0.142
CYT_FURC-3-4	Cytheropteron furcalatum Alexander, 1933	OK	2.3	66	2	0.130	−0.025
CYT_NAVA-1-2-3	Cytheropteron navarroense Alexander, 1929	OK	10.7	25	2	0.112	−0.187
ESC_MAGN-1-3	Escharacytheridea magnamandibulata Brouwers & Hazel, 1978	OK	8.3	25	2	0.095	−0.095
ESC_MICR-2	Escharacytheridea micropunctata (Alexander, 1929)	OK	56.7	50	1	0.122	0.082
ESC_MICR-3	Escharacytheridea micropunctata (Alexander, 1929)	OK	4.3	42	1	0.088	0.096
ESC_PINO-1-2	Escharacytheridea pinochii (Jennings, 1936)	OK	12.3	30	2	0.078	0.085
ESC_PINO-3-4	Escharacytheridea pinochii (Jennings, 1936)	OK	13.9	59	2	0.078	0.047
EUC_SOHL-2	Eucythere sohli Brouwers & Hazel, 1980	OK	17.5	22	1	0.155	−0.164
FIS_GAPE-2	Fissocarinocythere gapensis (Alexander, 1929)	OK	100.0	90	1	0.103	0.195
FIS_HUNT-1-2	Fissocarinocythere huntensis (Alexander, 1929)	OK	3.9	31	1	0.070	0.085
FIS_PIDG-1	Fissocarinocythere pidgeoni (Berry, 1925)	OK	10.4	19	1	0.104	0.199
FIS_PIDG-2	Fissocarinocythere pidgeoni (Berry, 1925)	OK	39.8	32	1	0.104	0.218
FIS_PIDG-3	Fissocarinocythere pidgeoni (Berry, 1925)	OK	34.6	56	1	0.105	0.184
FIS_PITT-1	Fissocarinocythere pittensis (Swain & Brown, 1964)	OK	20.3	28	1	0.090	0.126
FIS_PITT-2	Fissocarinocythere pittensis (Swain & Brown, 1964)	OK	28.8	25	1	0.098	0.176
FLO_LIXU-1	Floricythereis lixula (Crane, 1965)	OK	14.9	31	1	0.090	0.072
FLO_LIXU-2	Floricythereis lixula (Crane, 1965)	OK	18.3	47	1	0.087	0.071
HAP_BRUC-1	Haplocytheridea bruceclarki (Israelsky, 1929)	OK	44.2	30	1	0.118	0.141
HAP_BRUC-2	Haplocytheridea bruceclarki (Israelsky, 1929)	OK	61.9	64	1	0.112	0.191
HAP_BRUC-3	Haplocytheridea bruceclarki (Israelsky, 1929)	OK	27.0	17	1	0.125	0.188
HAP_EUTA-1	Haplocytheridea eutawensis Puckett, 1994	OK	26.0	20	1	0.148	0.275

HAP_EVER-1	Haplocytheridea everetti (Berry, 1925)	OK	28.3	20	1	0.123	0.157
HAP_GRAN-1	Haplocytheridea grangerensis Howe & Laurencich, 1958	OK	41.1	19	1	0.128	0.199
HAP_INSO-1	Haplocytheridea insolita (Alexander & Alexander, 1933)	OK	101.8	59	1	0.157	0.119
HAP_NANI-1	Haplocytheridea nanifaba Crane, 1965	OK	78.5	53	2	0.116	0.254
HAP_PLUM-1	Haplocytheridea plummeri (Alexander, 1929)	OK	33.1	25	1	0.151	0.290
HAP_PLUM-2	Haplocytheridea plummeri (Alexander, 1929)	OK	113.2	53	1	0.149	0.302
HAP_RENF-1	Haplocytheridea renfroensis Crane, 1965	OK	47.7	20	1	0.119	0.263
HAP_RENF-3	Haplocytheridea renfroensis Crane, 1965	OK	26.8	40	1	0.058	0.141
HAP_RENF-4	Haplocytheridea renfroensis Crane, 1965	OK	14.3	78	1	0.061	0.064
HAP_RENF-5	Haplocytheridea renfroensis Crane, 1965	OK	22.9	63	1	0.064	0.059
HAZ_AUST-1-2	Hazelina austinensis (Alexander, 1929)	OK	17.9	25	2	0.117	0.223
MOS_REES-1-2	Hazelina reesidei (Swain, 1948)	OK	39.1	31	2	0.150	0.184
KRI_CUSH-1-2	Krithe cushmani Alexander, 1929	OK	2.3	32	1	0.129	

TABLE 2. Continued

Population label	Species	Status	ΔBIC	No. individuals	No. samples	Shape DM	Size DM
VEE_PARA-2	Veenia parallelopora (Alexander, 1929)	OK	18.1	25	1	0.105	0.178
VEE_POND-2	Veenia ponderosana (Israelsky, 1929)	OK	128.8	59	1	0.124	0.270
VEE_POND-3	Veenia ponderosana (Israelsky, 1929)	OK	45.4	39	1	0.112	0.242
VEE_QUAD-1	Veenia quadrialira (Swain, 1952)	OK	21.3	21	1	0.125	0.219
VEE_SPOO-2	Veenia spoori (Israelsky, 1929)	OK	75.1	45	1	0.136	0.272
XES_OPIN-1	Xestoleberis opina Schmidt, 1948	OK	18.9	16	1	0.137	−0.091
ANB_MULT-1	Antibythocypris multilira (Schmidt, 1948)	No estimates—multiple species		27	1		
CAR_PRID-1	Anticythereis priddyi Smith, 1978	No estimates—multiple species		19	1		
BRA_CREN-1	Brachycythere crenulata Crane, 1965	No estimates—multiple species		96	1		
BRA_OVAT-1	Brachycythere ovata (Berry, 1925)	No estimates—multiple species		17	1		
ESC_MICR-1	Escharacytheridea micropunctata (Alexander, 1929)	No estimates—multiple species		29	1		
PTE_NADE-2	Pterygocythereis nadeauae Hill, 1954	No estimates—multiple species		32	1		
SHU_TRAV-2	Schuleridea travisensis Hazel & Paulson, 1964	No estimates—multiple species		18	1		
ASC_PLUM-1-2	Ascetoleberis plummeri (Israelsky, 1929)	No estimates—female only	−2.1	25	2		
BIC_VECL-1	Bicornicythereis veclitella (Crane, 1965)	No estimates—female only	−3.0	30	1		
CYS_CAUD-1-2-3	Cythereis caudata Butler & Jones, 1957	No estimates—female only	−7.1	15	3		
HAZ_CUPI-2-3-4	Hazelina cupiossata (Crane, 1965)	No estimates—female only	0.8	42	3		
MOS_SAGE-1-2-3-4-5-7-8	Hazelina sagena (Crane, 1965)	No estimates—female only	−3.2	72	7		
PHA_BICO-1-2-5-6	Phacorhabdotus bicostilimus Crane, 1965	No estimates—female only	−7.6	34	4		
PHA_BICO-3-4	Phacorhabdotus bicostilimus Crane, 1965	No estimates—female only	−2.4	33	1		
PHA_VENO-1	Phacorhabdotus venodus Crane, 1965	No estimates—female only	−8.2	30	1		
PTE_POND-1	Pterygocythereis ponderosana (Israelsky, 1929)	No estimates—female only	−2.9	16	1		
ACU_ACUM-2	Acuminobrachycythere acuminata (Hazel & Paulson, 1964)	No estimates	−4.9	16	4		
ACU_RALE-4	Acuminobrachycythere raleighensis (Brown, 1957)	No estimates	−2.3	23	1		
AMP_DUBI-1-2	Amphicytherura dubia (Israelsky, 1929)	No estimates	−5.9	37	2		
AVE_FOSS-1-2	Aversovalva fossata (Skinner, 1956)	No estimates	−7.2	12	1		
CYT_CAST-1-2	Cytheropteron castorensis Butler & Jones, 1957	No estimates	5.5	15	2		
CYT_FURC-1-2	Cytheropteron furcalatum Alexander, 1933	No estimates	−5.7	13	2		
MOS_HYPH-1	Hazelina hypha (Crane, 1965)	No estimates	8.6	12	1		
LOX_CRET-1	Loxoconcha cretacea Alexander, 1936	No estimates	−2.8	17	1		

formally with power analysis implemented using the simulation function in the 'mclust' package. For example, consider the small (n = 13) population from the species Cytheropteron furculatum, CYT_FURC-1-2, for which sexes could not be identified. If we take the sexual dimorphism pattern from the larger sample from this species (CYT_FURC-3-4, n = 66) and simulate 1000 data sets based on these parameter estimates but with the lower sample size of CYT_FURC-1-2, we find that the two-group solution is favored by BIC only 45% of the time. Thus, we should expect that some populations with low sample sizes should not result in clear dimorphism, even when sexes are distinct.

In addition to statistical support and biological plausibility, inferred sex ratios offer another check on our interpretations of sexual dimorphism. Livingpp but with thesP2;5(rat)1sracr

strongly dimorphic populations, but sexes in populations closer to the origin in Figure 7 are difficult to discern without measurement. The shaded region of this plot includes dimorphism magnitudes that are smaller than two units of within-sex standard deviation, where size and shape standard deviations are taken as the average of the benchmark populations from Figure 5. Sex differences within this region are small enough that the underlying probability distribution is no longer bimodal, and thus males and females should be difficult to resolve without very large sample sizes.

The scatter in Figure 7 indicates that size and shape dimorphism can vary independently. There is a noisy but significant relationship between the two variables ($r = 0.348$, $t = 4.396$, $df = 140$, $p \leq 0.0003$). This correlation is moderately strong when size dimorphism is positive ($r = 0.411$, $t = 4.68$, $df = 108$, $p \leq 0.0001$) but absent in populations with males that are smaller than females ($r = -0.136$, $t = -0.754$, $df = 30$, $p = 0.456$).

Sexual shape dimorphism is weakly but significantly correlated with valve size and shape of females, being stronger in populations with small bodies and squat shapes (Table 3, Supplementary Fig. 2). Populations with stronger shape dimorphism also tend to have more strongly skewed (female-dominated) sex
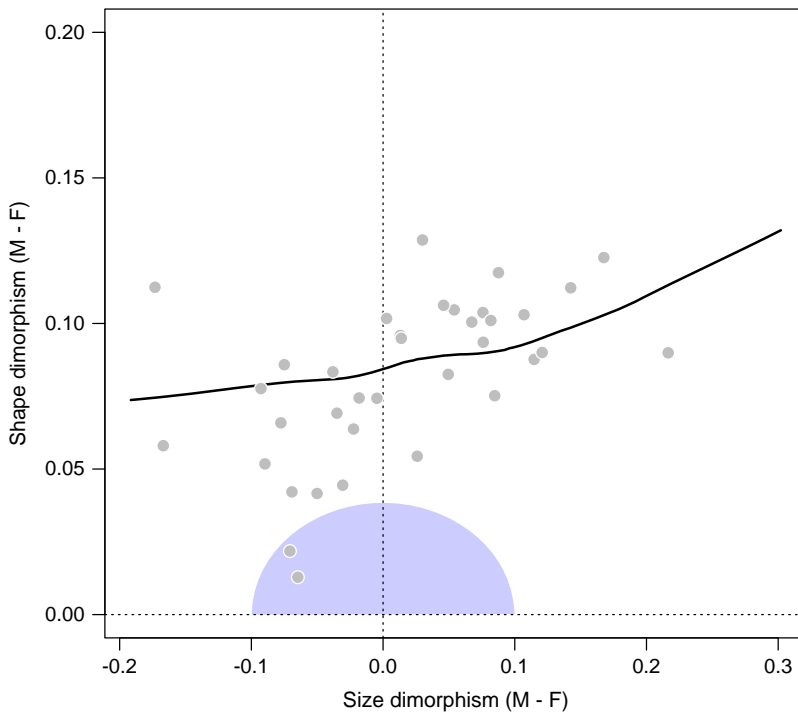
ratios (Fig. 8). Size dimorphism, in contrast, has weaker and mostly l6, has
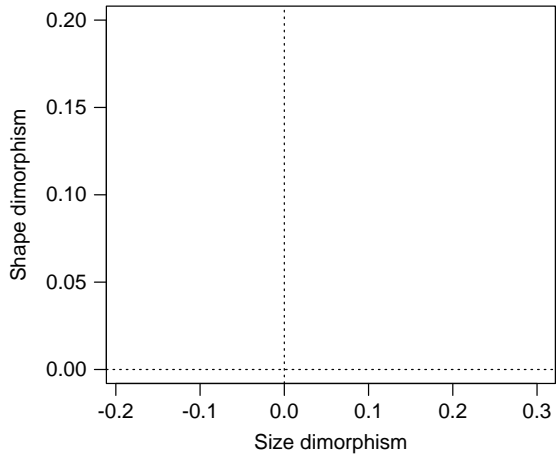
H. renfroensis

males and females: Ascetoleberis plummeri, Bicornicythereis veclitella, and Phacorhabdotus venodus. The lack of males in some but not all well-sampled populations of a species indicates that these species reproduced asexually over parts of their range, a pattern known as geographic parthenogenesis. This condition has been observed in living marine cytheroid ostracodes, though it is rather more common in nonmarine cypridoids (Athersuch et al. 1989; Butlin et al. 1998; Horne et al. 1998a). Puckett (2002) found a similar pattern in two species of Acuminobrachycythere for which males were recovered in nearshore facies but absent in offshore environments.

Three species remain for which we have reasonable sample sizes but for which no males seem to have been encountered: Hazelina cupiossata (n = 42), Hazelina sagena (n = 72), and Phacorhabdotus bicostilimus (two populations, n = 67 total). These relatively high sample sizes, combined with the fact that all other species within these two genera have sex differences that are moderate to strong, suggest that the failure to detect clusters is not due to low statistical power. We have scanned additional samples and reviewed published figures for these taxa, but we have yet to see any specimens that appear to be male. Additional sampling may yet recover males for these species, or, alternatively, they may be truly asexual. Completely parthenogenetic reproduction is present but uncommon in modern marine cytheroids. In the well-known British ostracode fauna, for example, four of 111 living cytheroid species reported by Athersuch and colleagues (1989; see also Horne et al. 1998a) are known only from female specimens around the British Isles, although two of these are known to be sexual in other regions. This amounts to a percentage of asexual species of 2–4%, similar to the 3% we document in this Cretaceous fauna.

An alternative explanation for the putatively female-only populations is that they are sexual but not sexually dimorphic. The very low shape variation of these samples (Fig. 5) would require that dimorphism be extremely low to absent, rather than just somewhat reduced. Moreover, whereas geographic parthenogen-

assessing whether variation in valve dimorphism was correlated with the size of the hemipenis in several species of Cyprideis. (This genus is member of the Cytherideidae, a family well represented in our Cretaceous fauna.) They found that size of male valves was related to hemipenis dimensions, especially of the large and muscular sperm pump, even after controlling for the effects of overall body size. This finding supports shell dimorphism as resulting from male investment in reproduction and thus being a product of sexual selection. The high correlations with the size of the sperm pump suggest a possible relationship to the size, quantity, or transfer efficiency of sperm.

Martins et al. (2017) did not find evidence that valve shape was related to male reproductive investment in Cyprideis. However, because shape varied rather little within the examined species, that study had limited power to detect

3. Dimorphism patterns were quite variable across the fauna, especially for sexual size dimorphism. Males were usually larger than females, by up to 30% in some taxa. However, in other taxa, males were similar in size to females or even up to about 20% smaller. Similarly, sexual shape dimorphism varied from modest to substantial.

4. Replicate samples within species produced dimorphism estimates that were nearly always quite similar over the lifetime of a species, suggesting that dimorphism generally behaves as a consistent species-level trait. Only one species, Haplocytheridea renfroensis, was found to change markedly in sexual dimorphism. Dimorphism patterns were also conserved within genera, albeit less strictly so.

5. Studies on extant ostracodes suggest that sexual size and shape dimorphism in cytheroids is very likely a result of sexual selection operating on male investment, along with other kinds of sexual and natural selection. Thus, this study system is one that potentially allows for tracking of the intensity of sexual selection over geological time.

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