



THE ROLE OF ANDRODIOECY AND GYNODIOECY IN MEDIATING EVOLUTIONARY TRANSITIONS BETWEEN DIOECY AND HERMAPHRODITISM IN THE ANIMALIA

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Dioecy (gonochorism) is dominant within the Animalia, although a recent review suggests hermaphroditism is also common. Evolutionary transitions from dioecy to hermaphroditism (or vice versa) have occurred frequently in animals, but few studies suggest the advantage of such transitions. In particular, few studies assess how hermaphroditism evolves from dioecy or whether androdioecy or gynodioecy should be an “intermediate” stage, as noted in plants. Herein, these transitions are assessed by documenting the numbers of androdioecious and gynodioecious animals and inferring their ancestral reproductive mode. Both systems are rare, but androdioecy was an order of magnitude more common than gynodioecy. Transitions from dioecious ancestors were commonly to androdioecy rather than gynodioecy. Hermaphrodites evolving from sexually dimorphic dioecious ancestors appear to be constrained to those with female-biased sex allocation; such hermaphrodites replace females to coexist with males. Hermaphrodites evolving from sexually monomorphic dioecious ancestors were not similarly constrained. Species transitioning from hermaphroditic ancestors were more commonly androdioecious than gynodioecious, contrasting with similar transitions in plants. In animals, such transitions were associated with size specialization between the sexes, whereas in plants these transitions were to avoid inbreeding depression. Further research should frame these reproductive transitions in a theoretical context, similar to botanical studies.

KEY WORDS: Gonochorism, protandrous simultaneous hermaphroditism, reproductive assurance, sexual dimorphism.

A comprehensive understanding of animal biology requires knowledge of the forces selecting for the vast array of reproductive systems found in this group (Williams 1975). Although the majority of animals are dioecious (i.e., gonochoristic), animals display a diversity of breeding systems (Bell 1982; Leonard 2010), including asexuality, cyclic parthenogenesis, simultaneous hermaphroditism, sequential hermaphroditism, and environmental sex determination, to name a few. Most attention on reproductive issues within the zoological community has centered on topics such as asexual versus sexual reproduction (Williams

1975; Bell 1982; Simon et al. 2002; Agrawal 2006; de Visser and Elena 2007; Lively 2010), sexual selection (Emlen and Oring 1977; West-Eberhard 1983; Kirkpatrick 1987; Hosken and Stockley 2004; Ritchie 2007; Klug et al. 2010; Schuett et al. 2010), environmental sex determination (Adams et al. 1987; Korpelainen 1990; Janzen and Paukstis 1991; Sarre et al. 2004; Janzen and Phillips 2006), sequential hermaphroditism (Warner 1975; Avise and Mank 2009; Kazancioglu and Alonzo 2009), and simultaneous hermaphroditism (Ghiselin 1969; Charnov 1979; Bauer and Holt 1998; Schärer and Janicke 2009; Anthes 2010).

Less attention has been given to the latter reproductive system in animals than in the botanical literature (Schemske and Lande 1985; Barrett 1998, 2002; Charlesworth 2006), which is understandable given the widespread nature of simultaneous hermaphroditism in plants (Barrett 2010). However, the fact that nearly 65,000 animal species are hermaphroditic (Jarne and Auld 2006) warrants a greater level of attention devoted to the evolution of hermaphroditism than this breeding system currently enjoys among zoologists.

Even less attention in the zoological community has been devoted to evolutionary transitions between breeding systems. Two recent papers suggest that transitions between hermaphroditism and dioecy (or vice versa) have occurred in animals at least 10–20 times when considering the class to phylum taxonomic levels (Eppley and Jesson 2008; Iyer and Roughgarden 2008). Unfortunately, very little work has been done to understand what promotes these evolutionary transitions (Charnov 1982) or to predict how such transitions should progress (see Leonard 2010 for a review).

Within the botanical literature, transitions from hermaphroditism to dioecy have been considered in depth. Such transitions have occurred dozens of times in flowering plants (Bawa 1980; Ashman 2002; Barrett 2010). Theoretical work suggests that dioecy does not evolve directly from hermaphroditism but rather that a single sex mutant invades a hermaphroditic population and then coexists with hermaphrodites to form either gynodioecy (females + hermaphrodites) or androdioecy (males + hermaphrodites). The single sex mutant is thought to most easily spread in populations that have some level of self-fertilization among the hermaphrodites that results in moderate to high levels of inbreeding depression (Charlesworth and Charlesworth 1978). It is predicted that a female rather than a male mutant would more easily invade a hermaphroditic population because males would have limited outcrossing opportunities if a large proportion of seeds were the product of selfing. On the other hand, a female would not be similarly limited because pollen would be available in abundance, even if selfing was substantial. Thus, the intermediate breeding system of gynodioecy is predicted to be much more common than androdioecy in plants (Lloyd 1975; Charlesworth and Charlesworth 1978), which is indeed observed (Pannell 2002). Botanists have progressed as far as to predict the underlying genetic changes that might be expected for the evolution of dioecy from hermaphroditism, predicting that a recessive male-sterility mutation would be selected first (creating gynodioecy) followed later by a dominant female-sterility mutation in the remaining hermaphrodites (creating dioecy; Charlesworth and Charlesworth 1978). This transition would be facilitated if the female- and male-sterility mutations were tightly linked (Charlesworth and Charlesworth 1978). The above ideas have been thoroughly tested and have been found to be generally correct (Charlesworth 2006).

No comparable level of attention has been afforded to these transitions in the animal literature. Most transitions between hermaphroditism and dioecy in animals have been from dioecy to hermaphroditism (Ghiselin 1969; Eppley and Jesson 2008; but see Iyer and Roughgarden 2008 for an alternate view). Should we expect that hermaphrodites evolving from a dioecious species have an intermediate step, such as gynodioecy or androdioecy, as has been noted in flowering plants? If so, should gynodioecy be more likely than androdioecy as an intermediate system? What would be the selective force(s) favoring a hermaphroditic mutant? It is unlikely to be the avoidance of inbreeding because hermaphroditism allows the possibility of self-fertilization whereas dioecy does not (Leonard 2010); so is it a response to conditions in which finding a mate is difficult (e.g., low density environments) leading to selection for “reproductive assurance,” as some authors have suggested (Baker 1955; Tomlinson 1966; Pannell 2002; Wolf and Takebayashi 2004)? What would be the underlying genetics of such a transition? The coexpression of both sexes within one individual mutating from a single-sexed progenitor certainly must be more complicated than a “knock-out” of one of the two sexes in a hermaphrodite (as suggested for flowering plants; Charlesworth and Charlesworth 1978); so does this increased complexity imply a constraint on the evolution of hermaphroditism from dioecy that is not evident for the reverse transition? Very few of these questions have been adequately addressed within the zoological literature (Ghiselin 1969; Charnov 1982; Leonard 2010), and none of those have been generally accepted within the animal reproductive community.

In this review, I hope to establish an empirical background for consideration of the topic of transitions between hermaphroditism and dioecy in animals, concentrating on the “intermediate” breeding systems of gynodioecy and androdioecy as pathways from hermaphroditism to dioecy, and vice versa. I start this discussion by assessing the breeding systems from which gynodioecious and androdioecious animals likely derived to note whether evolutionary transitions are equally likely from both “stable” reproductive systems (i.e., hermaphroditism or dioecy). I then assess the hypothesis (Weeks et al. 2006a; 2009) that evolving hermaphroditism from sexually dimorphic, dioecious progenitors constrains hermaphrodites to be “female biased” (i.e., a hermaphrodite that only allocates a small amount of energy to male function) that can only use male function for self-fertilization. Weeks et al. (2006a; 2009) propose that substantial sexual dimorphism limits the likelihood of developing a hermaphrodite fully functional in both sexual roles, and thus argue that a female-biased strategy is most likely to evolve under such a constraint. I end by forwarding ideas on why the patterns observed in animals may have evolved and suggest areas of research that would greatly benefit our understanding of these important breeding system transitions.

Methods

The literature for androdioecious and gynodioecious species was searched using the following procedures. First, ISI's Web of Science was searched using the terms "androdioecy(ious)" and "gynodioecy(ious)." Additionally, ISI was also searched for papers having both "hermaphrodite" and "male" or "female" among the keywords or in the abstract. Second, breeding system information was included from several review articles (Ghiselin 1969; Jarne and Charlesworth 1993; Pannell 2002; Weeks et al. 2006a; Avise and Mank 2009) and two books (Ghiselin 1974; Bell 1982).

The categories of "androdioecy" and "gynodioecy" were broadly defined to be any species in which males or females, respectively, coexist with simultaneous hermaphrodites. Such species were deemed gynodioecious or androdioecious if the frequency of the minority sex (either single-sexed or hermaphroditic individuals) comprised >5% of the total population sampled. This broad definition was used for two reasons. First, the exact nature of what drives the mixtures of the sexes has not been determined in a number of the reported species. The genetics of sex determination has only been determined in two of these animal groups: nematodes (Hodgkin 1988; Carmi and Meyer 1999) and branchiopod crustaceans (Sassaman and Weeks 1993; Weeks et al. 2001; 2006b). In a few others, andro- and gynodioecy are known to be due to differential sex allocation strategies at differing sizes (e.g., all-male when small than male + female when larger). However, in many other species (e.g., the Porifera, barnacles, and Cnidaria), mixtures of single and combined sexes could be due to genetically fixed differences or differential expression of sexuality over age/size. Thus, a broader definition was needed to include all species in this review. Second, it is not clear whether the underlying factors that select for mixes of single and combined sexes substantially depends on whether these mixes are genetically fixed versus plastically expressed (for alternate views on this topic in plants, see Delph and Wolf 2005; Pannell 2005). For both of these reasons, I have used the broader definition of andro- and gynodioecy in this review.

Mixtures of three sexual morphs—male, female, and hermaphrodite, termed trioecy—were found, but in all cases, the hermaphrodites were found to be exceedingly rare (Greve 1996; Labruna et al. 2002; Campos-Ramos et al. 2006; Howard et al. 2007; Narita et al. 2007). Additionally, such trioecious reports often noted that the hermaphrodites appeared to be developmentally abnormal rather than a functional reproductive morph (Maeno and Tanaka 2007; Yoshizawa et al. 2009). Therefore, this trioecy is not considered in this review.

In the determination of breeding system type, sequential hermaphrodites can be problematic. Thus, the classification schemes of Eppley and Jesson (2008) and Iyer and Roughgarden (2008) were followed in that only individuals that express some

level of simultaneous hermaphroditism during their lifetime were considered true hermaphroditic morphs. Following these authors' definition, a group of sequential hermaphrodites were considered "functionally dioecious" because only male and female morphs are present in the population at any given time. Nonetheless, it is clear that the underlying genetics of a sequential hermaphrodite are likely not the same as a strictly single-sexed individual, and thus equating sequential hermaphrodites with dioecy is recognized as a controversial decision. There was only one genus (*Lyssmata*) in which a sequentially hermaphroditic ancestor was termed "functionally dioecious" (see Tables 1 and 2), so this controversial decision did not significantly affect the overall patterns outlined in this review.

Two additional pieces of information were sought for all gynodioecious and androdioecious species: (1) reproductive mode of the most-recent ancestor and (2) level of sexual dimorphism of the most-recent ancestor for species derived from dioecy. For the latter, sexual dimorphism was categorized as low (differences between the sexes limited to differential gamete production), moderate (differential gamete production plus a few secondary sexual differences between the sexes), or high (differential gamete production plus many secondary sexual differences between the sexes). Only five genera of nematodes and one genus of barnacles were categorized as being derived from "moderately dimorphic" ancestors based on the presence of a few morphological secondary sexual characters (e.g., position of the gonopore, presence/absence of bursa, presence/absence of intromittent organ) in addition to the production of sperm versus eggs. All other ancestors with secondary sexual characteristics were categorized as "highly dimorphic." In a few instances, these determinations were made using published phylogenetic analyses to determine the reproductive mode and sexual dimorphism of the nearest relative(s) to the target species: annelids (Rouse and Fitzhugh 1994), nematodes (Kiontke et al. 2007), barnacles (Hoeg 1995; Perez-Losada et al. 2008; Yusa et al. 2012), and clam shrimp (Weeks et al. 2006c). In several taxa (e.g., sponges and cnidarians), appropriate, species-level phylogenetic analyses were unavailable. In these instances, sexual dimorphism and ancestral reproductive mode were inferred from the state of these two characters within the genus. When all other species in the genus had a similar character state, that character was deemed representative of the ancestor to the focal species. If either character state was variable within the genus, the ancestral character state was deemed "inconclusive" and is not reported.

To reduce the potential for over-representation of related taxa (e.g., *Eulimnadia*, *Pristionchus*, etc.; Table 1), transitions to the intermediate sexual systems were compared at the genus level (Table 2). It should be noted, however, that these comparisons do not allow for phylogenetically independent contrasts sensu Felsenstein (1985). Given the uncertain phylogenetic

Table 1. Androdioecious and gynodioecious animals.

Phylum	Class	Order	Family	Genus	Species	Reference	ARM	Reference					
<i>Gynodioecy</i>													
Porifera	Demospongiae	Homosclerophorida	Plakinidae	<i>Oscarella</i>	<i>tuberculata</i>	1	D	2					
	Calcarea	Sycettida	Grantiidae	<i>Grantia</i>	<i>compressa</i> ¹	3							
Cnidaria	Anthozoa	Actiniaria	Sagartiidae	<i>Cereus</i>	<i>pedunculatus</i> ¹	4							
			Actiniidae	<i>Epiactis</i>	<i>prolifera</i> ¹	5	D	6					
			Aiptasiidae	<i>Bartholomea</i>	<i>annulata</i> ¹	7							
			Poritidae	<i>Porites</i>	<i>astreoides</i>	8	D	9					
Sipunculida	Sipunculida	Golfingiaformes	Golfingiidae	<i>Golfingia</i>	<i>minuta</i>	10	D	11					
Annelida	Polychaeta	Canalipalpata	Sabellidae	<i>Demonax</i>	<i>microphthalmus</i>	12	H	13					
Chordata	Myxini	Myxiniformes	Myxinidae	<i>Myxine</i>	<i>glutinosa</i>	14							
<i>Androdioecy</i>													
Cnidaria	Anthozoa	Sceleractinia	Faviidae	<i>Goniastrea</i>	<i>australensis</i>	15	H	16					
			Pocilloporidae	<i>Stylophora</i>	<i>pistillata</i>	17	H	18					
Nematoda	Secernentea	Rhabditida	Rhabditidae	<i>Caenorhabditis</i>	<i>elegans</i>	19	D	20,21					
				<i>Caenorhabditis</i>	<i>briggsae</i>	22	D	21					
				<i>Caenorhabditis</i>	sp. 11	23							
				<i>Oscheius</i>	<i>myriophila</i>	21	D	21					
				<i>Oscheius</i>	<i>dolchura</i>	23	D	23					
				<i>Oscheius</i>	<i>tipulae</i>	24							
				<i>Oscheius</i>	<i>guentheri</i>	25	D	26					
				<i>Rhabditis</i>	<i>rainai</i>	27	D	26					
				<i>Rhabditis</i>	sp. (AF5)	28							
				<i>Rhabdias</i>	<i>nigrovenosum</i>	29							
				<i>Rhabdias</i>	<i>rubrovenosa</i>	29							
				<i>Rhabdias</i>	<i>ranae</i>	29							
				<i>Entomelas</i>	<i>entomelas</i>	29							
						Diplogastridae	<i>Diplogasteroides</i>	<i>magnus</i>	30				
							<i>Koerneria</i>	<i>sudhausi</i>	31				
							<i>Pristionchus</i>	<i>maupasi</i>	32	D	33		
							<i>Pristionchus</i>	<i>pacificus</i>	32	D	33		
							<i>Pristionchus</i>	<i>entomophagus</i>	32	D	33		
							<i>Pristionchus</i>	sp. 6	32	D	32		
							<i>Pristionchus</i>	sp. 10	30	D	32		
			Genus1	sp. 1	34	D	34						
			Genus1	sp. 2	34	D	34						
			Genus2	sp. 1	34	D	34						
			Steinernematidae	<i>Steinernema</i>	<i>hermaphroditum</i>	35	D	23					
		Tylenchida	Allantonematidae	<i>Allantonema</i>	<i>mirabile</i>	29							
				<i>Bradynema</i>	<i>rigidum</i>	36							
	Adenophorea	Dorylaimida	Dorylaimidae	<i>Dorylaimus</i>	<i>liratus</i>	30							
Nemertea	Enopla	Hoploneurtea	Tetrastematidae	<i>Prostoma</i>	<i>eilhardi</i> ²	36							
Arthropoda	Branchiopoda	Notostraca	Triopsidae	<i>Triops</i>	<i>newberryi</i>	37	D	38,39					
				<i>Triops</i>	<i>longicaudatus</i>	37	D	38,39					
				<i>Triops</i>	<i>cancriformis</i>	40	D	40					
							Spinicaudata	Limnadiidae	<i>Eulimnadia</i>	<i>texana</i>	41	D	42
							<i>Eulimnadia</i>	<i>africana</i>	37	D	42		
							<i>Eulimnadia</i>	<i>agassizii</i>	43	D	42		
							<i>Eulimnadia</i>	<i>antlei</i>	44	D	42		
							<i>Eulimnadia</i>	<i>braueriana</i>	40	D	42		
							<i>Eulimnadia</i>	<i>brasiliensis</i>	42	D	42		
							<i>Eulimnadia</i>	<i>colombiensis</i>	42	D	42		
							<i>Eulimnadia</i>	<i>cylindrova</i>	42	D	42		
							<i>Eulimnadia</i>	<i>dahli</i>	42	D	42		
							<i>Eulimnadia</i>	<i>diversa</i>	42	D	42		
							<i>Eulimnadia</i>	<i>feriensis</i>	42	D	42		

Continued.

Table 1. Continued

Phylum	Class	Order	Family	Genus	Species	Reference	ARM	Reference
				<i>Eulimnadia</i>	<i>follisimilis</i>	42	D	42
				<i>Eulimnadia</i>	<i>thompsoni</i>	42	D	42
				<i>Eulimnadia</i>	sp. A	42	D	42
				<i>Eulimnadia</i>	sp. B	42	D	42
				<i>Eulimnadia</i>	sp. C	42	D	42
	Maxillopoda	Lepadiformes	Heteralepadidae	<i>Paralepas</i>	<i>klepalae</i>	45	H	46
				<i>Paralepas</i>	<i>xenophorae</i>	47	H	47
				<i>Heteralepas</i>	<i>vetula</i>	45	H	46
			Koleolepadidae	<i>Koleolepas</i>	<i>tinkeri</i>	48		
				<i>Koleolepas</i>	<i>avis</i>	49	H	47,50
		Ibliformes	Iblidae	<i>Ibla</i>	<i>quadri-valvis</i>	51	D	46
				<i>Ibla</i>	<i>cumingii</i>	52	D	46
				<i>Ibla</i>	<i>idiotica</i>	53	D	46
				<i>Ibla</i>	<i>segmentata</i>	54	D	46
		Scalpelliformes	Calanticidae	<i>Calantica</i>	<i>studerii</i>	55		
				<i>Calantica</i>	<i>siemensii</i>	55		
				<i>Calantica</i>	<i>spinosa</i>	47	H	47
				<i>Calantica</i>	<i>villosa</i>	47	H	47
			Scalpellidae	<i>Arcoscalpellum</i>	sp.	47	H	47
				<i>Euscalpellum</i>	<i>squamuliferum</i>	55		
				<i>Scalpellum</i>	<i>peronii</i>	52	H	46
				<i>Scalpellum</i>	<i>scalpellum</i>	52	H	46
				<i>Scalpellum</i>	<i>vulgare</i>	51	H	46
				<i>Scillaelepas</i>	<i>arnaudi</i> ²	56	H	46
				<i>Scillaelepas</i>	<i>bocquetiae</i> ²	57	H	50
				<i>Scillaelepas</i>	<i>calyculacilla</i>	58	H	50
				<i>Scillaelepas</i>	<i>falcate</i> ²	57	H	50
				<i>Scillaelepas</i>	<i>fosteri</i> ²	57	H	50
				<i>Smilium</i>	<i>hastatum</i>	55		
				<i>Smilium</i>	<i>peronii</i>	47	H	47
		Sessilia	Chelonibiidae	<i>Chelonibia</i>	<i>patula</i> ²	58	H	46
				<i>Chelonibia</i>	<i>testudinaria</i> ²	58	H	46
			Bathylasmatidae	<i>Bathylasma</i>	<i>alearum</i>	59	H	46
				<i>Bathylasma</i>	<i>corolliforme</i>	60		
			Balanidae	<i>Balanus</i>	<i>galeatus</i>	61	H	46
				<i>Balanus</i>	<i>calceolus</i>	62	H	63
				<i>Balanus</i>	<i>merrilli</i>	62	H	63
				<i>Balanus</i>	<i>masignotus</i>	62	H	63
			Pachylasmatidae	<i>Tetrapachylasma</i>	<i>trigonum</i>	64		
				<i>Megalasma</i>	<i>striatum</i>	47	H	47
				<i>Octolasmis</i>	<i>warwickii</i> ²	47	H	47
	Malacostraca	Decapoda	Hippolytidae	<i>Lysmata</i>	<i>wurdemanni</i> ²	65	D ³	66
				<i>Lysmata</i>	<i>amboinensis</i> ²	67	D ³	66
				<i>Lysmata</i>	<i>californica</i> ²	68	D ³	66
				<i>Lysmata</i>	<i>bahia</i> ²	69	D ³	66,70
				<i>Lysmata</i>	<i>intermedia</i> ²	69	D ³	66,70
				<i>Lysmata</i>	<i>grabhami</i> ²	69	D ³	66,70
				<i>Lysmata</i>	<i>seticaudata</i> ²	69	D ³	66,70
				<i>Lysmata</i>	<i>nilita</i> ²	69	D ³	66,70
				<i>Lysmata</i>	<i>hochi</i> ²	69	D ³	66,70
				<i>Lysmata</i>	<i>nayaritensis</i> ²	71	D ³	66,70
				<i>Lysmata</i>	<i>rafa</i> ²	69	D ³	66,70
				<i>Lysmata</i>	<i>boggesi</i> ²	69	D ³	66,70
				<i>Lysmata</i>	<i>ankeri</i> ²	69	D ³	66,70

Continued.

Table 1. Continued

Phylum	Class	Order	Family	Genus	Species	Reference	ARM	Reference
				<i>Lysmata</i>	<i>pedersenii</i> ²	69	D ³	66,70
				<i>Lysmata</i>	<i>debelius</i> ²	69	D ³	66,70
				<i>Lysmata</i>	<i>galapaguensis</i> ²	69	D ³	66,70
				<i>Lysmata</i>	<i>cf. trisetacea</i> ²	69	D ³	66,70
	Insecta	Hemiptera	Monophlebidae	<i>Icerya</i>	<i>bimaculata</i>	72	D	73
				<i>Icerya</i>	<i>purchasi</i>	74	D	73
				<i>Crypticerya</i>	<i>zeteki</i>	73	D	73
Annelida	Polychaeta	Phyllodocida	Syllidae	<i>Salvatoria</i>	<i>clavata</i>	75	D	76
		Aciculata	Dorvilleidae	<i>Ophryotrocha</i>	<i>gracilis</i> ²	77		
				<i>Ophryotrocha</i>	<i>hartmanni</i> ²	77		
				<i>Ophryotrocha</i>	<i>diadema</i> ²	77		
				<i>Ophryotrocha</i>	<i>bacci</i> ²	77		
				<i>Ophryotrocha</i>	<i>maculata</i> ²	77		
				<i>Ophryotrocha</i>	<i>socialis</i> ²	77		
Chordata	Actinopterygii	Cyprinodontiformes	Aplocheilidae	<i>Kryptolebias</i>	<i>marmoratus</i>	78	D	79
		Perciformes	Serranidae	<i>Serranus</i>	<i>fasciatus</i>	80	H	81
				<i>Serranus</i>	<i>baldwini</i>	82	H	81

(1) Meewis (1938) as referenced in Fell (1975); (2) Ereskovsky (pers. comm.); (3) Gatenby (1920); (4) Rossi and Calenda (1974); Rossi (1975); (5) Dunn (1975b); (6) Edmands (1996); (7) Jennison (1981); (8) Chomesky and Peters (1987); (9) Fadlallah (1983); (10) Gibbs (1975); (11) Hyman (1959); Gibbs (1976); (12) Gregory (1905); (13) Rouse and Fitzhugh (1994); (14) Powell et al. (2004); (15) Kojis and Quinn (1981); (16) Richmond and Hunter (1990); (17) Rinkevich and Loya (1979); (18) Kerr et al. (2011); (19) Ward and Carrel (1979); (20) Fitch and Thomas (1997); (21) Kiontke et al. (2004); (22) McCulloch and Gems (2003); (23) Denver et al. (2011); (24) Sudhaus (1993); (25) Sudhaus and Hooper (1994); (26) Kiontke et al. (2007); (27) Carta and Osbrink (2005); (28) LaMunyon and Ward (1999); (29) Maupas (1900); (30) Kiontke et al. (2001); (31) von Lieven (2008); (32) Mayer et al. (2007); (33) Herrmann et al. (2006); (34) Herrmann (pers. comm.); (35) Griffin et al. (2001); (36) Montgomery (1895); (37) Sassaman (1991); (38) Sassaman et al. (1997); (39) Mantovani et al. (2004); (40) Zierold et al. (2007); (41) Sassaman and Weeks (1993); (42) Weeks et al. (2006c; 2009); (43) Weeks et al. (2005); (44) Sassaman (1988); (45) Kolbasov and Zevina (1999); (46) Hoeg (1995); (47) Yusa et al. (2012); (48) Newman, 1996 as noted in Yusa et al. (2001); (49) Yusa et al. (2001); (50) Kelly and Sanford (2010); (51) Darwin (1851); (52) Callan (1941); (53) Batham (1945); (54) Foster (1978); (55) Young (2003); (56) Jones and Lander (1995); (57) Newman (1980); (58) Crisp (1983); (59) Foster (1983); (60) Dayton et al. (1982); (61) Gomez (1975); (62) McLaughlin and Henry (1972); (63) Perez-Losada et al. (2008); (64) Foster (1988); (65) Lin and Zhang (2001); (66) Bauer (2006); (67) Fiedler (1998); (68) Bauer and Newman (2004); (69) Baeza (2008); (70) Baeza et al. (2009); (71) Baeza et al. (2007); (72) Hughes-Schrader (1963); (73) Hughes-Schrader and Monahan (1966); (74) Hughes-Schrader (1925); (75) Hauenschild, 1953, 1959 as referenced in Ghiselin (1969); (76) San Martin (2005); (77) Premoli and Sella (1995); (78) Turner et al. (1992a); (79) Taylor et al. (2001); (80) Hastings and Petersen (1986); (81) Smith (1965); (82) Petersen and Fischer (1986).

¹Reported to be protogynous (female first) simultaneous hermaphrodites.

²Reported to be protandrous (male first) simultaneous hermaphrodites. Note that the hermaphroditic nematodes technically develop as males first, but because they cannot outcross through male function, they are effectively always hermaphroditic.

³Derived from sequential hermaphrodites, which for this review is equated to dioecy, because no individual is simultaneously of both the sexes. See text for further explanation.

ARM, Ancestral reproductive mode (H, hermaphrodite; D, Dioecious).

relationships among the various animal phyla (Dunn et al. 2008; Schierwater et al. 2009; Telford 2009; Edgecombe et al. 2011; Telford and Copley 2011), controlling for phylogeny at the higher taxonomic levels compared herein is impractical at this time.

Results

GYNODIOECY

Although androdioecy is rare in animals, gynodioecy is even rarer. Only nine gynodioecious animals were found in the literature, all but two in the “primitive” invertebrate phyla (Table 1): two sponges (Porifera), three anemones (Cnidaria), one coral (Cnidaria), one sipunculid worm (Sipuncula), one polychaete worm (Annelida), and one vertebrate (a hagfish). All species either broadcast spawn both sperm and eggs

(*Bartholomeaannulata annulata* and *Demonax microphthalmus*) or broadcast sperm only (*Oscarellatuberculata tuberculata*, *Grantiacompressa compressa*, *Cereuspedunculatus pedunculatus*, *Epiactis prolifera*, *Poritesastreoides astreoides*, and *Golfingiaminuta minuta*). Very little is known about the reproductive behavior of hagfish, but no hagfish have copulatory organs (Patzner 1998) and thus fertilization is presumably external.

Of these nine species, only one has been thoroughly studied: *E. prolifera* (Dunn 1975a,b; Edmands 1995, 1996); this species has smaller females and larger hermaphrodites and it appears that the anemones will switch from females to hermaphrodites as they grow larger (Dunn 1975a). However, some individuals appear to never switch, being either all-female or all-hermaphrodite (Dunn 1975b). The one vertebrate (hagfish) is a deep-sea dwelling

Table 2. Reproductive transitions within animals. (A) Numbers of genera transitioning from dioecious or hermaphroditic ancestors to androdioecious and gynodioecious species. "Sexual dimorphism" is the inferred level of sexual dimorphism of the dioecious ancestor to the gynodioecious or androdioecious species. ¹Diplogastridae Nematodes; ²Exact binomial test. See text for an explanation of the level of sexual dimorphism (i.e., Low, Moderate, or High). (B) Statistical tests of equal probability of transitions.

(A) Transition data				
Transition	Genus	No. of spp	Sexual dimorphism	Animal type
Dioecy → Gynodioecy	<i>Epiactis</i>	1	Low	Anemone
	<i>Porites</i>	1	Low	Coral
	<i>Oscarella</i>	1	Low	Sponge
	<i>Golfingia</i>	1	Low	Sipunculid
	Total	4		
Dioecy → Androdioecy	<i>Caenorhabditis</i>	2	High	Nematode
	<i>Pristionchus</i>	5	Moderate	Nematode
	Genus 1 ¹	2	Moderate	Nematode
	Genus 2 ¹	1	Moderate	Nematode
	<i>Oscheius</i>	3	Moderate	Nematode
	<i>Rhabditis</i>	1	Moderate	Nematode
	<i>Steinernema</i>	1	Moderate	Nematode
	<i>Triops</i>	3	High	Branchiopod
	<i>Eulimnadia</i>	16	High	Branchiopod
	<i>Ibla</i>	4	Moderate	Barnacle
	<i>Lysmata</i>	17	High	Shrimp
	<i>Icerya</i>	2	High	Insect
	<i>Crypticerya</i>	1	High	Insect
	<i>Kryptoledias</i>	1	High	Fish
	<i>Salvatoria</i>	1	High	Polychaete
	Total	60		
Hermaphroditism → Gynodioecy	<i>Demonax</i>	1	—	Polychaete
	Total	1		
Hermaphroditism → Androdioecy	<i>Goniastrea</i>	1	—	Coral
	<i>Stylophora</i>	1		Coral
	<i>Paralepas</i>	2	—	Barnacle
	<i>Heteralepas</i>	1	—	Barnacle
	<i>Koleolepas</i>	2	—	Barnacle
	<i>Calantica</i>	2	—	Barnacle
	<i>Arcoscalpellum</i>	1	—	Barnacle
	<i>Scalpellum</i>	3	—	Barnacle
	<i>Scillaelepas</i>	5	—	Barnacle
	<i>Smilium</i>	1	—	Barnacle
	<i>Chelonibia</i>	2	—	Barnacle
	<i>Bathylasma</i>	1	—	Barnacle
	<i>Balanus</i>	4	—	Barnacle
	<i>Megalasma</i>	1	—	Barnacle
	<i>Octolasmis</i>	1	—	Barnacle
	<i>Serranus</i>	2	—	Fish
Total	30			
(B) Statistical tests				
Transitions from Hermaphroditism to:		Total genera	<i>P</i> -value ²	
Gynodioecy		1	0.0001	
Androdioecy		16		
Transitions from Dioecy to:		Total genera	<i>P</i> -value ²	
Gynodioecy		4	0.007	

Continued.

Table 2. Continued

(B) Statistical tests		
Androdioecy	15	
Transitions from Sexually Dimorphic Dioecy to:	Total genera	<i>P</i> -value ²
Gynodioecy	0	<0.0001
Androdioecy	15	
Transitions from Sexually Monomorphic Dioecy to:	Total genera	<i>P</i> -value ²
Gynodioecy	4	0.0625
Androdioecy	0	

species and thus gathering reproductive data has been problematic for this entire group (Powell et al. 2005). Nonetheless, in one comprehensive study of 1080 hagfish (*Myxine glutinosa*), 58% were found to be female and 41% were hermaphroditic; females were of the largest size classes (Powell et al. 2004). The remaining gynodioecious species are from reports of population surveys in which many female-only individuals were collected along with simultaneous hermaphrodites, but no consistent studies have been done to document whether these single-sexed individuals are always females or may switch later in life to hermaphrodites, or vice versa. Additionally, there was some speculation that the single-sexed, broadcast-spawning individuals were actually simultaneous hermaphrodites that had released their sperm earlier than their eggs rather than being truly female-only (Gibbs 1975; Jennison 1981). Further, detailed studies of these species may find that the number of gynodioecious animals may be even smaller than the nine noted here.

Sex is not strictly genetically determined in four of the nine gynodioecious animal species in Table 1: the co-occurrence of females and hermaphrodites reflects a mixture of age states rather than distinct genetic morphs. These four species (*G. compressa*, *C. pedunculatus*, *E. prolifera*, and *B. annulata*) are all protogynous, simultaneous hermaphrodites; in other words, they are female when they are younger and then develop into simultaneous hermaphrodites as they age. There is no report of such sexual plasticity in the other sponge (*O. tuberculata*), the one coral (*P. astreoides*) and the two worms (*G. minuta* and *D. microphthalmus*); all appear to be distinctly female or hermaphroditic morphs. As noted above, very little is known about the deep-sea hagfish (Patzner 1998; Powell et al. 2004), and thus it is unknown whether individual *M. glutinosa* switch sex from hermaphrodites to females as they age. In both *G. minuta* and *M. glutinosa*, there have been reports of male-only individuals, but these are quite rare (Gibbs 1975; Powell et al. 2004).

An additional finding regarding gynodioecy is that there is no evidence, to date, of cytoplasmic male sterility (i.e., genes in cytoplasmic elements, such as mitochondria, that knockout male function in hermaphrodites; for a recent review in plants see

McCauley and Olson 2008) in any animal taxon. Those few species that appear to be gynodioecious are in taxa that have not been intensively studied, reproductively, and thus they could have cytoplasmic elements reducing or eliminating male gamete production in hermaphrodites that have not yet been discovered (Schärer 2009). However, there are no reports of this in any of these species. Additionally, there was no evidence of any form of gynodioecy in the predominately hermaphroditic animals (e.g., pulmonate snails, annelids, platyhelminthes, etc.), which is in stark contrast to the predominately hermaphroditic flowering plants (Barrett 2002; Shykoff et al. 2003). Thus, for some reason, predominately hermaphroditic animals appear to have escaped this form of cytoplasmic manipulation of sexual expression.

Unfortunately, phylogenetic analyses of these “primitive” animal taxa were uncommon. In fact, no reports could be found on the reproductive modes of the congeners for four of the nine species (i.e., one sponge, two cnidarian, and one vertebrate species). For the five remaining species, the closest ancestors were dioecious in four species (one sponge, two cnidarians, and the sipunculid species) whereas the remaining species (the annelid *D. microphthalmus*) had a hermaphroditic closest ancestor (Tables 1 and 2A).

Aside from gamete production, none of the putative gynodioecious animals derived from dioecious ancestors had sexually dimorphic, dioecious ancestors (Table 2A). In fact, the complete lack of sexual dimorphism is one of the problematic issues for sexing individuals of the Porifera and Cnidaria. Because these species can only be sexed during gamete production and release (Edmands 1995; D. G. Fautin, pers. comm.), one needs to be physically present during their reproductive period to determine sex, which can be challenging in marine environments. Thus, all four of the gynodioecious animals derived from dioecious ancestors evolved from ancestors with minimal sexual dimorphism (Table 2A).

ANDRODIOECY

Although androdioecy is rare among animals, it is over an order of magnitude more common than gynodioecy: 115 animal species were found to be androdioecious (Table 1), including

two cnidarians, 27 nematodes, one nemertean, 72 crustaceans, three insects, seven annelids, and three vertebrates. Interestingly, unlike the gynodioecious species, the androdioecious animal taxa are primarily among the “advanced” animal phyla: arthropods, annelids, and chordates. The one important exception is androdioecy in the pseudocoelomate nematodes, which have 27 described androdioecious species in 14 genera and five families. Three of the 115 androdioecious animals have broadcast spawning: the coral *Goniastrea australensis* spawns both sperm and eggs (Richmond and Hunter 1990) whereas the coral *Stylophora pistillata* and the polychaete worm, *Salvatoria clavata*, spawn their sperm but the eggs are fertilized and brooded in pouches on the hermaphrodites (Rinkevich and Loya 1979; Franke 1999). In the remaining androdioecious species, pairing occurs with either sperm fertilizing eggs in a brood pouch (branchiopod and decapods crustaceans), pairing for external fertilization of localized clutches of eggs (*Ophryotrocha* polychaetes and *Serranus* fish), or eggs are fertilized inside the hermaphrodite’s body cavity (remaining species).

The ancestral status was verifiable in 94 of these 115 androdioecious species. Their closest relatives were split between dioecy and hermaphroditism: 64 had dioecious ancestors and 30 had hermaphroditic ancestors. The ancestral states for these 94 species were not randomly distributed across taxa (Table 2A). All of the nematodes were derived from dioecious ancestors. All of the “primitive crustaceans” (Branchiopoda) were derived from dioecious ancestors whereas the “advanced crustaceans” (Maxillopoda and Malacostraca) were primarily derived from hermaphroditic ancestors, with the exception of barnacles in the genus *Ibla* and shrimp in the genus *Lysmata*. The latter are a special case in that they were derived from sequential hermaphroditic ancestors, which although are technically hermaphrodites, they function as dioecious species because they are never simultaneously male and female (see discussion above). The polychaete species, *S. clavata*, was derived from a dioecious ancestor whereas the three fish species were derived from either dioecious or hermaphroditic ancestors (Tables 1 and 2A).

The three insect hermaphrodites are unique, and thus deserve special attention. *Icerya purchasi* is thought to have “transmissible spermatogenic stem cells” that are produced by polyspermy in the fertilized embryo (Royer 1975). One of the sperm actually fertilizes the egg whereas others develop into pronuclei that eventually develop into the sperm-producing tissue within the “hermaphroditic” gonad (Royer 1975; Normark 2009). A recent model of this phenomenon (Gardner and Ross 2011) notes that in the earliest portions of this association, the spermatogenic stem cells are not genetically identical to the “infected” female. However, over time, “the endpoint of the evolutionary process is an integrated individual organism comprising genetically identical ($r = 1$) male and female reproductive tissues” (Gardner and

Ross 2011, p. 198). The remaining two hermaphroditic species (*Iceryabimaculata bimaculata* and *Crypticerya zeteki*) in this family (Monophlebidae) have yet to be examined to note whether their gonads develop similarly (Normark 2009).

All of the androdioecious species derived from dioecious ancestors had medium to high levels of sexual dimorphism among the ancestral forms (Table 2A), in that the males were definitively distinct from the females/hermaphrodites in anatomy (e.g., intro-mittent organ, grasping structures for pairing, brood chambers for storing eggs), behavior (e.g., mate guarding, male mate searching, egg laying), and in the production of pheromones and commonly differed in size (males smaller than hermaphrodites).

Discussion

GENERAL PATTERNS

The most obvious pattern of these data is the rarity of gynodioecious animals. A maximum of nine animal species may be gynodioecious, and likely fewer, given that most of these species have been poorly studied, as noted above. There is good evidence (Dunn 1975b) that only one animal species, *E. prolifera*, has been truly documented to be gynodioecious. This is in stark contrast to the situation in plants wherein approximately 8% of species are gynodioecious (Richards 1997).

The paucity of gynodioecious animals has been noted previously, in passing (Ghiselin 1974; Jarne and Charlesworth 1996; Schärer 2009), but few explanations for why gynodioecy should be almost unheard of in animals have been offered. Schärer (2009) suggests that animals may be less prone to mitochondrial manipulation (i.e., “cytoplasmic male sterility”) than plants because of the small size of animal relative to plant mtDNA. In barnacles, Yusa et al. (2012) suggest “outcrossing and female-biased sex allocation in hermaphrodites probably prevent gynodioecy from evolving.” Given that hermaphroditic animals comprise approximately 65,000 species (~5% of all animals) and are present in approximately 70% of animal phyla (Jarne and Auld 2006), it is amazing that only a single verified case of gynodioecy has been found. In-depth surveys should be undertaken within the primarily hermaphroditic animals groups (e.g., pulmonate snails, annelids, platyhelminthes, etc.) to seek out species with gynodioecy, and a theoretical framework outlining why the evolution of hermaphroditism from dioecy should not include a gynodioecious intermediate (as in plants; Charlesworth and Charlesworth 1978) should be explored (but see below for a possible explanation).

The second obvious pattern is that androdioecy is derived from both hermaphroditism and dioecy in approximately equal numbers, even although dioecy is much more common in animals. Interestingly, androdioecious species derived from hermaphroditic ancestors (e.g., barnacles) do not likely reflect genetic sex determination. For example in many of the barnacles,

androdioecy has been derived from protrandrous, simultaneous hermaphroditism (see Table 1) by the reduction of growth during the initial male phase to produce small, “complemental” males, and in the one fish genus, *Serranus*, androdioecy was derived from simultaneous hermaphroditism in that the largest fish eliminate female investment and become male-only (Petersen and Fischer 1986).

TRANSITIONS FROM HERMAPHRODITISM

As noted above, predictions about the evolution of separate sexes from hermaphroditism stemming from the flowering plants suggest a strong bias for a gynodioecious intermediate rather than an androdioecious one (Charlesworth and Charlesworth 1978; Charlesworth 2006). This pattern was not observed among animals (Table 2A). Animals show only one transition from hermaphroditism to gynodioecy and 16 transitions from hermaphroditism to androdioecy (Table 2A), which is a significant deviation from an equal split between these two “intermediate” reproductive systems (Table 2B). However, Weeks et al. (2006a) point out that the evolution of androdioecy from hermaphroditism in animals is quite different from that proposed for flowering plants. The transition from hermaphroditism to androdioecy in flowering plants has been discussed in terms of the avoidance of inbreeding (Lloyd 1975; Charlesworth and Charlesworth 1978). However, in the hermaphroditic progenitors to these androdioecious animals, selfing is not likely a selective factor due to anatomical considerations that make self-fertilization extremely unlikely (Charnov 1982; Petersen and Fischer 1986; but see Carlon 1999 for a discussion of selfing in corals). Thus, in these species, the avoidance of inbreeding is not likely to explain the evolution of androdioecy.

Instead, it appears that these androdioecious species are expressing sexual differences based on differences in body size. In barnacles, small (i.e., “dwarf” or “complemental”) males are specifically serving a different purpose than the hermaphrodites, being a ready source of sperm to nearby and larger hermaphrodites (Yusa et al. 2012). There are some who argue that these smaller males are essentially following the same sequential reproductive maturity as the *Lysmata* shrimp noted above (i.e., maturing as males when small and then growing to simultaneous hermaphrodites; Callan 1941; Crisp 1983). If so, then this switch may indicate that individuals can gain higher relative fitness as males when they are small because sperm are cheaper to produce than eggs, but then would do better to switch to hermaphrodites when larger and can afford to produce eggs (Charnov 1982). Others argue that the smaller males are a distinct morph to the larger hermaphrodites (Gomez 1975). In either case, the expression of the sexes is based on different roles of the hermaphrodites and males that correspond to different sizes and population densities (Ghiselin 1969; Charnov 1982). Similarly, in the one fish genus,

Serranus, individuals are hermaphroditic when small to intermediate in size but then switch to all-male allocation when they are at the largest sizes (Smith 1965; Hastings and Petersen 1986; Petersen and Fischer 1986). Additionally, in the one coral species (*G. australensis*), the pattern is reversed, with small corals being male and larger ones are hermaphrodite (Kojis and Quinn 1981). Again, these patterns indicate that differential selective pressures on differently sized individuals drive sexual expression (i.e., differential sex allocation strategies with size; see Ghiselin 1969; Charnov 1982) rather than any benefit being derived from the avoidance of inbreeding in the single-sexed (i.e., male) individuals. Therefore, in these animals the processes selecting androdioecy would be distinct from those argued by Charlesworth and others (Lloyd 1975; Charlesworth and Charlesworth 1978; Charlesworth 1984). However, these species should not be seen as evidence that the hypothesis proposed for the evolution of androdioecy from hermaphroditism in flowering plants is incorrect. Rather, this body of theory is specific to flowering plant species that regularly self-fertilize and not to species in which sexual expression is affected by body size (Ghiselin 1969; Charnov 1982).

TRANSITIONS FROM DIOECY

The evolution of hermaphroditism from separate sexes has not been widely debated, but in the few works that have considered this transition, no one has suggested that such a transition is a mere reversal of the predictions for a hermaphroditism to dioecy transition (i.e., that an intermediate stage is likely to evolve first and that this stage would be gynodioecy). Pannell (1997, 2002) has suggested that androdioecy might be a likely intermediate strategy when evolving hermaphroditism from dioecy in a structured metapopulation in which reproductive assurance is strongly advantageous (e.g., early colonizing species) but in which outcrossing is still advantageous when population size is adequately large to allow an appreciable probability of locating a suitable mate. Similarly, Wolf and Takebayashi (2004) predict androdioecy to be likely to evolve from dioecy when there is pollen limitation (similar to the notion of reproductive assurance noted above) and the hermaphrodites are significantly female biased (i.e., allocating most of their reproductive energy to egg/ovule production). Indeed, there were significantly more cases of the evolution of androdioecy than gynodioecy from dioecious progenitors (Table 2B), which generally fit the expectations of these two models, although we cannot say that these data directly support a “reproductive assurance” cause for these observed transitions.

Weeks et al. (2006a; 2009) make a more specific “constraint” argument for why androdioecy rather than gynodioecy should be more commonly derived from dioecy. If hermaphroditism is selectively favored in any dioecious species (e.g., for reproductive assurance in an early-colonizing species), Weeks et al. argue that the most likely hermaphrodite to evolve from a dioecious female

progenitor with strong sexual dimorphism would be a female-biased hermaphrodite that allocates limited resources to male function and lacks the ability to outcross with other hermaphrodites. Their argument is that in dioecious species with many sex-specific phenotypes (and presumably a similarly high level of sex-limited genes), one might expect that a transition to effective expression of both sexes would be highly improbable. The argument relies on the assumption that the minimum amount of mutational “gains” needed to become a functional hermaphrodite would likely be in a female genetic background wherein a “gain” mutation would allow the production of viable sperm in the gonad that would place the sperm into contact with the eggs. In a sexually dimorphic species, the notion that such a hermaphroditic mutant could also simultaneously “gain” the myriad secondary sexual characteristics allowing the hermaphrodite to also fully function as a male would be highly improbable.

An example of the number of gains required to evolve a hermaphrodite from a female progenitor has been elucidated in the nematode *Caenorhabditis* (Ellis and Guo 2011). In *Caenorhabditis*, only two mutations appear to be needed to produce a viable hermaphrodite from a female. Reduced activity of the *tra-2* gene produces “females” that produce a small amount of sperm when young but then switch to egg production when older (Baldi et al. 2009). These modified females had female phenotypes in every other respect but this small amount of sperm production. However, the sperm was not functional, and thus these mutants were termed “pseudohermaphrodites” (Baldi et al. 2009). A second mutation that affects expression of the *swm-1* gene was necessary to “activate” the sperm and allow the mutant hermaphrodites to self-fertilize (Baldi et al. 2009; Ellis and Guo 2011). These authors make a convincing argument that the “sperm activation” mutation would be effectively neutral and could have drifted to such a level as to allow the second (*tra-2*) mutation to be favored in these nematodes in which reproductive assurance was advantageous for early colonization (Ellis and Guo 2011). These studies show that a female-biased hermaphrodite with limited male gamete production and an inability to outcross through male function can evolve in a straightforward, two-step pathway.

In the above example, a more complete hermaphrodite (i.e., a hermaphrodite that combined all aspects of both males and females into an outcrossing hermaphrodite that functioned equally well in both male and female function) would require many more mutations, and thus be much less likely to evolve. Indeed, no such “fully functional” hermaphrodite has evolved within the nematodes even although there have been several transitions to hermaphroditism from dioecy in this group (Kiontke et al. 2004; Mayer et al. 2007; Yusa et al. 2012), which underscores the difficulty of such a “complete” transition. Therefore, androdioecy should be more likely to evolve from sexually dimorphic, dioecious ancestors than gynodioecy because the number of gains

needed to produce a functional hermaphrodite from a male genetic background would be much higher due to the mechanical needs to produce a more complex gamete (e.g., yolking, shell production, storage, etc.) as well as the behavioral requirements of successful offspring production (e.g., egg laying, maternal care, etc.).

For example in dioecious clam shrimp (the ancestral state at the family level; Weeks et al. 2009), males produce ameoboid sperm that fertilize the females’ eggs externally in a “brood chamber” on the dorsal surface of the female (Weeks et al. 2004). A hermaphrodite developed from a female genetic background would need to produce sperm within the tubular gonad typifying clam shrimp (Scanabissi and Mondini 2000) to be capable of self-fertilization in the absence of males. On the other hand, a hermaphroditic clam shrimp developed from a male genetic background would need to gain the ability to produce, yolk, and shell the eggs, develop a brood chamber, gain the ability to store eggs in the brood chamber (i.e., by attaching them to extensions of the phyllopod appendages), and develop the digging behavior needed to bury the eggs in the pond bottom (Zucker et al. 2002). Unless all of these phenotypes are regulated by the same regulatory pathway, it is highly unlikely that all of these gains could occur simultaneously within an otherwise male genetic background. Thus one should expect the evolution of hermaphrodites that are essentially female with a small amount of sperm production, which is what is observed in these shrimp (Zucker et al. 1997; Weeks et al. 2005, 2006a, 2009).

Using this argument, the relative likelihood of transitioning to androdioecy versus gynodioecy from a dioecious progenitor is directly related to the level of sexual dimorphism in that progenitor: a high level of sexual dimorphism should bias transitions toward androdioecy whereas limited (or no) sexual dimorphism should produce no bias for one intermediate reproductive mode over the other. Transitions from monomorphic dioecious ancestors, then, should be equally likely in a female or male genetic background resulting in no transitional bias to either androdioecy or gynodioecy.

These constraint arguments were largely upheld in these data. Fifteen total animal genera transitioned from sexually dimorphic dioecious ancestors (Table 2A). In all 15 cases, this transition was from dioecy to androdioecy and none were to gynodioecy, which is highly significantly different from random expectation of an equal number of transitions (Table 2B). These data perfectly fit the constraint hypothesis outlined above. The transitions from sexually monomorphic dioecious ancestors were not as clear: only four genera transitioned from sexually monomorphic dioecious progenitors, and all four transitioned to gynodioecy (Table 2A) which is not significantly different from an equal transition probability, but is close to significant (Table 2B). The small number of gynodioecious transitions does not allow much power to make a conclusion,

but we can say that gynodioecy is not constrained from evolving from dioecy among sexually monomorphic dioecious ancestors whereas it does appear to be so from sexually dimorphic dioecious ancestors.

Weeks et al. (2006a) also predicted that hermaphrodites derived from a sexually dimorphic ancestor should be “female biased” (i.e., show primarily female secondary sexual characteristics with only a small amount of sperm production). Indeed, in all the androdioecious species derived from dioecious ancestors in which relative allocation patterns between male and female gametes have been reported, the hermaphrodites closely resemble females with only minor amounts of reproductive effort devoted to male gamete production (Weeks et al. 2006a; Chasnov 2010). This observation was clearly stated by Maupas (1900, p. 133), when comparing hermaphrodites to dioecious females in nematodes: “We are thus entitled to state that parthenogenesis and hermaphroditism, when they developed in these nematodes, only exerted a modifying influence on the products of the genital apparatus. The rest of the organism remained absolutely invariable.” In nematodes, the hermaphrodites generate a small amount of sperm during the last larval stage (Wood 1988) that they store for later use before irreversibly switching to egg production in the adult stage (Ward and Carrel 1979; Hodgkin 1988; Kimble and Ward 1988). Similarly, androdioecious branchiopods produce a small amount of sperm in an otherwise female gonad (Zucker et al. 1997; Scanabissi and Mondini 2002; Weeks et al. 2005) and in most other respects resemble the females of closely related dioecious species (Weeks et al. 2008). The fish (Harrington 1963) and decapod shrimp (Bauer 2006) species also show female-biased allocation. The three hermaphroditic insects (Hughes-Schrader 1928) also show a female-biased allocation, but this unique breeding system, in which the male tissue is provided by the polyspermic fertilization of the egg (Royer 1975), may not fit within the constraint arguments of Weeks et al. (2006a). As suggested above, these overall patterns can be explained by assuming a constraint on the development of a hermaphrodite that can competently perform as a male whereas simultaneously being competent as a female when there are numerous traits required to be competent in both male and female roles.

Although the optimal scenario for reproductive assurance is likely the development of self-compatible hermaphrodites that are competent in outcrossing via both male and female function, it is likely that a second level of constraint will disallow the development of such a hermaphrodite when evolving from a sexually dimorphic, dioecious ancestor. Consider a hermaphrodite that evolved from a female, as outlined above. Such a hermaphrodite should bias allocation toward female gamete production, producing only the minimal amount of sperm required to “assure” fertilization when outcrossing opportunities are low. If outcrossing through male function requires the development of many

secondary sexual phenotypes (e.g., an intromittent organ, male mating behaviors, clasping structures for pairing, etc.), it is unlikely that such a female-biased hermaphrodite can simultaneously develop all of these structures to be competent to outcross through male function. Thus, it is likely that the initial hermaphrodite would be minimally competent in the male role, as noted above. The problem that such a “partially male competent” hermaphrodite has is that the further development of a male role would require competing with fully competent, male-only individuals for outcrossings. In this scenario, a hermaphrodite that might develop one (or at most a few) secondary sexual traits would not be likely to compete effectively with fully functional males for outcrossing opportunities. Thus, one might expect that such piecemeal development of a suite of secondary sexual characters would not be advantageous enough to allow the spread of such a “partially male” hermaphrodite that is competing with males with the full suite of secondary sexual traits. Therefore, female-biased hermaphrodites may be constrained to either coexist with males (i.e., androdioecy) or completely replace both males and females to form fully selfing, hermaphroditic populations that cannot outcross. The former alternative should be in species which populate a range of habitats, some of which require reproductive assurance and some of which do not (Pannell 1997, 2002), whereas the latter alternative would be for species in which reproductive assurance is of the utmost importance, or in which outcrossing, per se, is no longer beneficial. Indeed, in the better studied animal androdioecious systems (i.e., nematodes, clam shrimp, tadpole shrimp, and *Kryptolebias* fish), populations have been documented to be either a mixture of males and self-compatible hermaphrodites that cannot outcross through male function or all-hermaphroditic self-fertilizing populations (Sassaman 1991; Turner et al. 1992a,b; Weibel et al. 1999; Zierold et al. 2007; Weeks et al. 2008; Chasnov 2010).

CONCLUSIONS AND FUTURE DIRECTIONS

The overall patterns are clear. Animals are estimated to have an order of magnitude fewer gynodioecious than androdioecious species likely due to a bias of transitions from dioecy and hermaphroditism to androdioecy. Animals evolving single sexes from hermaphroditism are not avoiding inbreeding; rather these single-sexed individuals have a different ecological role to play than their hermaphroditic counterparts. Animals developing hermaphroditism from single-sexed, sexually dimorphic progenitors appear to be constrained to develop a female-biased hermaphrodite that cannot outcross through male function. Animals developing hermaphroditism from single-sexed, sexually monomorphic progenitors do not experience this same constraint.

A possible explanation for the few observed androdioecious or gynodioecious intermediates deriving from the “primitive” animal phyla (i.e., Cnidaria or Porifera) may be that these

sexually monomorphic species may easily be able to develop a fully functional hermaphrodite directly from a dioecious progenitor because such a hermaphrodite does not require many “gains” to be fully functional in both sex roles. Such a hermaphroditic mutant may then quickly sweep through the population/species eliminating both single-sexed competitors if a combined sexual type is advantageous. This could explain the fairly high levels of both dioecy and hermaphroditism in both groups without many intermediate types (Kerr et al. 2011), and also why determining which reproductive system is ancestral to either phylum has proven problematic (Eppley and Jesson 2008; Iyer and Roughgarden 2008; Kerr et al. 2011).

Further understanding of these reproductive transitions would greatly benefit by a series of studies. First, gynodioecy should be extensively examined within the Animalia. A start would be to assess the validity of the reports of the nine instances of apparent gynodioecy noted in Table 1. Several of the gynodioecious Cnidaria and Porifera noted in Table 1 have vertically transmitted, unicellular symbionts, and it would be interesting to assess if these symbionts may be able to manipulate sex expression in these gynodioecious animals in a similar fashion to that noted for mitochondria in gynodioecious plants (Schärer 2009). Additionally, gynodioecy should be sought in the primarily hermaphroditic animals (e.g., pulmonate gastropods, flatworms, gastrotrichs, etc.) because it is quite likely that gynodioecy has evolved at least once (if not repeatedly) among these diverse species.

Second, further phylogenetic assessments of the primitive animals (e.g., sponges and cnidarians) would greatly improve our understanding of reproductive transitions in both groups (e.g., Kerr et al. 2011). Such studies would then allow the mapping of breeding system transitions in these interesting groups. In particular, it would be useful to note how many transitions between hermaphroditism and dioecy have occurred in these groups and whether there is a bias for one transition over another. Of course one additional benefit to such studies would be the potential to resolve the ancestral reproductive state of the Animalia (Eppley and Jesson 2008; Iyer and Roughgarden 2008).

Third, this field needs to develop a solid theoretical foundation predicting the transitions between dioecy and hermaphroditism in animal taxa. At the moment, the most plausible selective agent driving the evolution of hermaphroditism from dioecy is reproductive assurance (Pannell 1997; Wolf and Takebayashi 2004). However, we have no competing hypotheses nor do we have a single study that reveals a benefit of reproductive assurance for hermaphroditic mutants deriving from single-sexed progenitors in animals.

Finally, to assess the constraint hypothesis, the genetic underpinning of male gamete production in androdioecious species derived from dioecious progenitors needs to be undertaken,

similar to that conducted in nematodes (Baldi et al. 2009; Ellis and Guo 2011). This argument relies on the constraint of simultaneously “gaining” many primary and secondary sexual traits of the alternate sex to become a fully functional hermaphrodite (Weeks et al. 2006a; 2009). Thus, the female-biased androdioecious species (e.g., *Triops*, *Eulimnadia*, and *Kryptolebias*) should have relatively simple mutational changes to produce the sperm needed to be a functioning hermaphrodite, as noted in *Caenorhabditis* (Baldi et al. 2009). Assessments of the genetic changes allowing sperm production in species from these genera would allow a thorough examination of this constraint hypothesis.

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