Transitions in Sexual and Reproductive Strategies Among the Caenogastropoda

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Abstract

Caenogastropods, members of the largest clade of shelled snails including most familiar marine taxa, are abundant and diverse and yet surprisingly little is known about their reproduction. In many families, even the basic anatomy has been described for fewer than a handful of species. The literature implies that the general sexual anatomy and sexual behavior do not vary much within a family but for many families this hypothesis remains un-tested. Available data suggest that aphally, sexual dimorphism, maternal care, and different systems of sex determination have all evolved multiple times in parallel in caenogastropods. Most evolutionary transitions in these features have occurred in non-neogastropods (the taxa formerly included in the mesogastropoda). Multiple origins of these features provide the ideal system for comparative analyses of the required preconditions for and correlates of evolutionary transitions in sexual strategies. Detailed study of representatives from the numerous families for which scant information is available, and more completely resolved phylogenies are necessary to significantly improve our understanding of the evolution of sexual systems in the Caenogastropoda. In addition to basic data on sexual anatomy, behavioral observations are lacking for many groups. What data are available indicate that mate choice and sexual selection are complicated in gastropods and that the costs of reproduction may not be negligible.

Introduction

The difficulty in understanding evolutionary transitions between sexual systems is not due to a lack of theories or potential selective pressures that could be responsible. Instead the difficulty lies in finding common causes for the diversity of evolutionary patterns observed among divergent groups, when the relevant questions for each group may differ. For example, in heterobranch gastropods, which are simultaneous hermaphrodites (see Table 1 for definitions), the question may be why dioecy has not evolved more often, while in their primarily dioecious sister group, the caenogastropods, the question may be why protandry has evolved so often and simultaneous hermaphroditism so seldom. To answer such question about real organisms rather that theoretical constructs it is important not only to know the phylogenetic distribution of sexual systems and to have a firm basis in evolutionary theory, but also to understand the comparative biology of the organisms. With such understanding it is possible to tackle questions like: Do developmental constraints limit the evolutionary transitions between sexual systems or make

certain transitions more likely than others? Do ecological factors like habitat type or diet impact population density thus influencing the relative importance of sexual selection versus reproductive assurance? Do costly taxon specific behaviors like competition for mates or parental care unduly influence the male or female reproductive gain curves, shifting the pattern of optimal sex allocation? There are few non-model invertebrate taxa for which we have sufficient knowledge to begin to address these questions.

Instead this chapter reviews the diversity of sexual systems and reproductive biology among caenogastropods. I highlight the evidence from phylogenetic distributions that sexual dimorphism, aphally, maternal care, and various systems of sex determination have all experienced evolutionary transitions in caenogastropods. I also review the scattered literature on caenogastropod mating behavior, sexual selection and costs of reproduction. The limited information is insufficient to draw detailed conclusions, but it is vitally important to recognize the diverse behavioral context in which sexual systems evolve and to recognize that snails may incur significant costs of courtship and reproduction.

Caenogastropda

Gastropoda, the most diverse class within the Mollusca, with an estimated 120,000 or more species (Appeltans et al. 2012), is often broken into 3 major groups for discussions of evolutionary patterns (basal gastropods, caenogastropods and heterobranchs). The basal grade of snails including patellogastropods and vetigastropods generally have simple reproductive anatomy, are free spawners, show little evidence of complicated mate choice mechanisms, and are seldom sexual dimorphic (Beesley, et al. 1998 but see Lindberg and Dobberteen, 1981). The monophyletic Heterobranchia includes sea slugs and pulmonate slugs and snails, as well as some basal shelled marine forms. Heterobranchs have complex reproductive anatomies, are almost always simultaneous hermaphrodites and show a wide array of complicated mating behaviors, which are relatively well-studied (Davison and Mordan 2007; Chase, 2007; Valdés et al. 2010; Jarne et al. 2010; Baur 2010).

The subclass Caenogastropoda, the monophyletic sister clade to the Heterobranchia, includes approximately 60% of described gastropod species and more than 100 families. Ceanogastropods are mostly sea snails, but the group includes some terrestrial and freshwater families. They include herbivores, and carnivores of varying levels of specialization, as well as

filter feeders, kleptoparasites, blood sucking parasites, internal parasites and numerous families of deep sea and infaunal micro-snails whose ways of life are poorly known (Fretter and Graham 1962; Beesley et al. 1998). Caenogastropods occur in the sea from the deep ocean to the intertidal and on land from lush rainforests to dry desertic habitats. They display a wider range of reproductive anatomies and systems of sex determination than do heterobranchs, but little is known about sexual selection, mate choice and parental care behaviors in most caenogastropods.

The diversity of sexual systems in the Caenogastropoda make them ideal for the application of comparative methods to understand the factors associated with evolutionary transitions between sexual systems and reproductive strategies. Unfortunately, data available from only one or a few "representative" species, uncertain phylogenetic relationships, and dynamic taxonomy of some families and superfamilies make generalizing difficult. Generalizations (including those made here) should be viewed critically in light of the number of species that have been examined and the systematic stability of the group.

The higher-level taxonomy of caenogastropods is still being refined, but the group is broken into 3 orders: Architaenioglossa (3 superfamilies; 11 families), Littorinimorpha (16 superfamilies; 66 families) Neogastropoda (7 superfamilies; 44 families), and 6 as yet unassigned superfamilies containing 34 families (WoRMS Editorial Board 2016). The best available phylogenies include fewer than half the caenogastropod families, but the most complete analysis to date concludes that (1) the 3 architaenioglossan superfamilies are basal to all other caenogastropods but may not be monophyletic, (2) neogastropods are monophyletic within the Sorbeoconcha (i.e., the non-architaenioglossan caenogastropods), and (3) the relationships among the non-neogastropod Sorbeoconcha remain unclear (Ponder et al. 2008) (see Figure 1).

Evolutionary Patterns of Dioecy, Protandry and Parthenogenesis

Dioecy is inferred to be ancestral in the Gastropoda and the Caenogastropoda (Heller 1993; Ponder and Lindberg 1997; Kay et al. 1998; Fretter et al. 1998; Ponder et al. 2008). Evolutionary transitions to protandry are common among the caenogastropods (Figure 1), while transitions to simultaneous hermaphroditism and parthenogenesis are uncommon. Protogyny is unknown. Protandry occurs in scattered species or genera within primarily dioecious families, suggesting a recent evolutionary origin in these taxa. Other families are entirely protandrous

suggesting that this strategy is ancient and evolutionary stable either because it is advantageous or because ontogenetic canalization makes it difficult to revert to the ancestral state. It is likely that protandry is under-reported, as protandry is more difficult to detect than simultaneous hermaphroditism (Calvo and Templado 2005; Collin 2013).

The Architaenioglossa, including freshwater ampullariids (apple-snails) and viviparids as well as the terrestrial Cyclophoroidea are dioecious. Hermaphroditism is not known to occur, but parthenogenesis has arisen via hybridization in the viviparid *Campeloma* sp. (Johnson and Bragg 1999).

Neogastropods are generally dioecious with the exception of some coralliophilid species which are protandrous (Chen and Soong 2002; Richter and Luque 2004; Johnston and Miller 2007). Protandrous sex change in coralliophilids is similar to sex change in patellogastropods and calyptraeids in that it is socially mediated and closely related to individual size (Chen and Soong 2002; Richter and Luque 2004; Johnston and Miller 2007; Collin 2013). Circumstantial evidence suggests that some species of *Vitularia* (Muricidae) and *Iphinopsis alba* (Cancellariidae) might be protandrous (Warén 1984; Bouchet and Warén 1985; Herbert et al. 2009). One turrid *Propebeta* (=*Oenopota) turricula* has been reported as protandrous with a simultaneous hermaphroditic phase (Smith 1967). However the lack of relationship between sex and size is unusual and imposex, masculinization of females by endocrine disruptors, cannot be ruled out in this case. Imposex is particularly well documented for neogastropods (Oehlmann et al. 1996), but also occurs in ampullariids (Takeda 2000) and some littorinimorphs (Li and Collin 2009). Neither simultaneous hermaphroditism nor parthenogenesis have been reported in the Neogastropoda.

The non-neogastropod Sobreoconcha ("mesogastropods") contain the most diverse assortment of sexual systems and sexual morphologies in the Caenogastropoda (Figure 1). The majority of the families including the well known Naticidae, Strombidae, Buccinidae, and Nassariidae appear to be exclusively dioecious. A number of other families, including Calyptraeidae, Capulidae, Epitoniidae, Hipponicidae, and possibly Janthinidae are probably exclusively protandrous (Calvo and Templado 2005; Churchill et al. 2011; Collin 2013).

Two other families contain a mix of diocious and protandrous species. Eulimids are notable for the diversity of their sexual systems, which includes protandry, dioecy, and simultaneous hermaphroditism. Species of *Melanella, Peasistilifer*, and *Vitreolina* are dioecious

and species of *Eulima*, *Stilifer* and *Haliella* are sequential hermaphrodites (Warén 1980; 1984; Bouchet and Warén 1986). Since many of these specialized parasites show extreme sexual dimorphism and appear to have environmental sex determination it is difficult to fully confirm protandry without either detailed histological analysis or longitudinal observations of individuals (Elder 1979; Matsuda et al. 2013). Triviids can also be dioecious or protandrous, with 4 South African species reported as protandrous and 10 as dioecious (Gosliner and Liltved 1982; 1987).

Other families are primarily dioecious but include one or a few protandrous species. For example littorinids are exclusively dioecious except for the 2 species of *Mainwaringia* (Reid 1986). Likewise, only a single species each of the tiny marine assimineids (*Rugapedia androgyna)* and tornids (*Cyclostremiscus beauii)* have been reported as protandrous (Bieler and Mikkelsen 1988; Fukuda and Ponder 2004). More species need to be examined to determine if protandry is unusual for these groups. Three species of the vermetid genus *Serpulorbis* change sex, one of which, S. *arenarius,* has consecutive hermaphroditism, where animals change from male to female and back again (Calvo and Templado 2005). This is the only known case of consecutive hermaphroditism in a caenogastropod. Sex change may also occur in one species of *Ceraesignum* (as *Dendropoma*) as evidenced by the increased frequency in females in the large size classes (Phillips and Shima 2010). The turritellids *Vermicularia spirata* (Bieler and Hadfield 1990) and *Gazameda gunni* (Carrick 1980), and the planaxid *Fossarus ambiguus* (Houbrick 1990) are also protandrous. The suggestion that *Pedicularia* (Ovulidae) species are protandrous was contested by Goud (2001) but needs to be investigated further. Finally the deep-sea family Laubierinidae may be protandrous based on limited data from one species of these deep-sea tonnoideans (Warén and Bouchet 1989).

Protandry in caenogastropods has often been inferred from size distributions of the sexes, and few details on the natural history of sex change are available for groups other than calyptraeids (reviewed in Collin 2013). In calyptraeids sex change depends on the size of the animal and its social circumstances (Collin et al. 2005; Mérot and Collin 2012a,b). The impact of nearby conspecifics is mediated via touch not waterborne chemicals (Carrillo-Baltodano and Collin 2015). In *Crepidula* cf. *marginalis* large individuals suppress growth and sex change in smaller animals while small animals increase the growth rate of larger animals (Carrillo-Baltodano and Collin 2015). It would be interesting to know if similar interactions occur in other protandrous groups.

Simultaneous hermaphroditism is rare in the Caenogastropoda. The "living fossil" *Plesiotrochus crinitus* (Plesiotrochidae) is a simultaneous hermaphrodite (Houbrick 1990; Healy 1993), as are species in the eulimid genera *Pelseneeria*, *Pisolamia*, *Goodingia* and *Ophioarachnicola*. The eulimids, which generally live in pairs, have a very small testis thought to produce the minimal sperm necessary to fertilize their partner in the absence of sperm competition (Warén 1984). Velutinids also include simultaneous hermaphroditic genera (*Velutina* and *Marsenina*) and dioecious genera (*Lamellaria*, *Coriocella* and *Marseniopsis*) (Fretter and Graham 1962; Wilson 1998).

Parthenogenesis occurs in a number of estuarine and freshwater caenogastropods, especially thiarids and tateids. Parthenogenesis in these groups has been linked to their large geographic ranges and success as invaders (Facon et al. 2003; Alonso and Castro-Diez 2008; Miranda et al. 2011). In the tateid *Potamopyrgus antipodarum* diploid sexual populations have numerous males, while parthenogenic populations are polyploid and males are rare (Wallace 1992). The cochliophid *Heleobia* may also be parthenogenic (Martín 2002).

Sexual anatomy of caenogastropods and aphally

The sexual anatomy of gastropods has been described and reviewed in detail (Fretter and Graham 1962; Hyman 1967; Fretter et al. 1998; Kay et al. 1998; Voltzow 1994; Strong 2003; Hodgson 2010). In male caenogastropods a gonoduct connects the gonad to the prostate gland and then extends as a pallial gonoduct or vas deferens to a penis or a simple gonopore. The gonoduct and prostate can be open over part or all of their lengths. In females the oviduct runs past accessory structures for sperm storage and egg packaging as it connects the single ovary to the female genital opening. The bursa copulatrix, where the sperm are deposited, is usually distal to the seminal receptacle or receptaculum seminalis, where the sperm are stored. The albumin or gel gland and, most distally, the capsule gland make secretions associated with packaging eggs. The morphology and arrangement of these structures can vary between species, genera and families, and the structures may not be homologous across families. During sex change in protandrous caenogastropods the pallial gonoduct usually transforms from the vas deferens to the albumin and capsule glands, and the penis (if present) is absorbed. In simultaneous hermaphrodites there may be a separate testis and ovary, each with its own duct, but in *Velutina*

eggs and sperm are produced in acini in the same gonad (Fretter and Graham 1962; Fretter 1998).

One particularly variable character among caenogastropods is the presence or absence of a penis. Most basal gastropods lack an intromittent organ, but a penis similar to those found in caenogastropods has evolved independently several times in the Neritimorpha and other basal gastropods (Hickman 1992; Kano 2008). Basal caenogastropods either lack a penis (e.g., cerithioidans) or it appears to have evolved independently (e.g., Architaenioglossa). Therefore the ancestral state for caenogastropods is ambiguous. Comparative analyses of the diversity of penis morphologies, assessment of homologies, and close examination of ecological and morphological correlates of aphally could be a fruitful area for future research.

Male architaenioglossans all posses an intromittent organ. However the homology of this organ is unlikely as the organ is a modified right tentacle in the viviparids, derived from the mantle edge and innervated by the right pleural ganglion in ampullariids (Berthold, 1989) and derived from cephalic tissue in cyclophoroids (Kretzschmar 1919). During development of ampullariids both sexes begin to develop a penis, but in females its growth is arrested as the ovary develops (Andrews 1964). This mechanism explains why female ampullariids often have a small "pseudopenis" (Takeda 2000), and may also explain pseudopenes in some other groups (e.g., Kuwamura et al. 1983; Avise et al. 2004). The functional morphology of the penis has been described using snap frozen mating pairs in the ampullariid *Pomacea canaliculata* (Giraud-Billoud et al. 2013). This study is unique in demonstrating that the tip of the penis penetrates to the seminal receptacle, rather than inferring the depth of penetration from the location of sperm in the female reproductive system. Little information is available on the function of the intromittent organs in other architaenioglossan taxa.

Many sorbeconchans have a solid muscular penis behind the right cephalic tentacle. The penis is usually derived from pedal tissue with pedal innevation (Voltzow 1994; Hodgson 2010). Sperm are transferred in an open groove or closed duct that runs along the ventral surface of the penis. The penis may range from long and tapered to broad and paddle-shaped and diverse morphologies are present in many groups. For example, in rissooideans the penis can be tapered with an open groove, bifid with the vas deference in one branch and a flagellum in the other, or can have seven or more circular suckers (Szarowska 2006). When not in use the penis is usually folded back over the head in the mantle cavity. In collumbellids the penis is often held in a

special pouch in the mantle roof under the hypobranchial gland (Marcus and Marcus 1962; deMaintenon 1999).

Penis morphology sometimes correlates with female genital morphology. In calyptraeids genera in which a long tapering penis is tipped with a long terminal papilla are those in which the females have a distinct genital papilla (Collin 2003). Similarly, the presence of simple lobes on the left edge of the rissooidean penis is correlated with the presence of two female receptacles (Szarowska 2006). Penis morphology is relatively stable within genera in some groups (Szarowska 2006; Georgiev 2012). In others it differs among closely related species (Reid 1989; Reed 1995) suggesting that penis morphology may be one of the first characters to diverge during or after speciation.

A number of superfamilies (including cerithioideans, cingulopsoideans, vermetoideans, triphoroideans, and epitonioideans) lack a penis (Ponder et al. 2008). Hodgson (2010, p. 127) included capulids and hipponicids in this group, but their penes are similar to other caenogastropods (e.g., Graham 1954; Poulicek et al. 1997; Collin 2003). The overall similarity of caenogastropod penes suggests that aphally may represent parallel losses of the penis. However the penis of anabathrids and emblandids is innervated by the cerebral ganglion and may have evolved in parallel to other caenogastropods (Ponder 1988), and it is possible that other groups have evolved a penis independently. Aphally is not closely related to characteristics of the female system. For example the female pallial gonoduct can be open in both phallate and aphallate families suggesting that evolutionary transitions to and from aphally are not tightly constrained by female morphology (Fretter et. al. 1998; Hodgson 2010; Figure 1).

The female reproductive system is also evolutionarily dynamic, including mesodermal and ectodermal structures that vary in number and form across taxa (Fretter 1984; Fretter and Graham 1994; Ponder and Lindberg 1997). Comparative analyses could contribute significantly to our understanding of the evolutionary transitions in the arrangement of these structures. One major impediment to such an analysis is the lack of clear homologies, as parts of the female reproductive system are named based on their function rather than on homologies. These may represent convergent morphologies that have evolved to solve the problems of copulation, sperm storage, and embryo packaging (Fretter et al. 1998). Ontogenetic information could be useful in untangling these homologies. For example, comparative development shows that the posterior gonoduct develops from a gonadial and a renal primordia in *Viviparus* and *Littorina* and from a

single primordium in *Nassarius* and *Crepidula* (Drummond 1903; Mortiz 1939; deMaintenon 2001). Ontogenetic information like this could be particularly important in understanding the evolutionary transition from dioecy to simultaneous hermaphroditism.

Sperm, Parasperm and Post-Copulatory Selection

Studies of insects show that the contents of ejaculates (seminal fluids as well as sperm cells) in polyandrous animals are often active in altering fertilization success or female reproductive output (Simmons and Fitzpatrick, 2012). Sperm cells from the same male might work together to ensure fertilization by one of their cohort, sperm may actively hinder sperm from other males and chemicals in seminal fluids may also be active in competition between ejaculates (Holman and Snook 2008; Holman, et al. 2008; Higginson and Pitnick 2011). Little is known about the role of these mechanisms in caenogastropods.

Sperm competition is likely to play an important role in caenogastropod reproduction. Parasperm, sperm that are not used to fertilize eggs, may have been present ancestrally in caenogastropods, as very simple parasperm are present in nerites and some vetigastropods (Buckland-Nicks 1998). Within caenogastropods they have diversified in form and function, although they have been reduced or eliminated in some neogastropods and atlantids (Buckland-Nicks and Hodgson 2005; Jamieson and Newman 1989; Buckland-Nicks 1998; Hodgson 2010). Most kinds of parasperm contain glycoproteins which may be released into the seminal fluid (Buckland-Nicks 1998). In many aphallic species and some other groups (*Littorina* and *Fusitriton*) large parasperm (spermatozeugmata) play a role in transporting eusperm (Buckland-Nicks et al. 1999; Buckland-Nicks and Tompkins 2005). In aphallic species spermatozeugmata enter the female, in other species secretions from the prostate gland cause the eusperm to detach from the parasperm before it leaves the male reproductive tract making their role unclear (Buckland-Nicks et al. 1998). Another kind of parasperm, lancet parasperm, are present in many neogastropods and some caenogastropods. These long cells make a plug in the bursa copulatrix that may inhibit penetration by later males (Buckland Nicks 1998). Experiments confirm the role of parasperm in sperm competition. When male *Viviparus ater* are exposed to rival males or to a male biased population sex ratio they produce a lower ratio of eusperm to parasperm (Oppliger et al. 1998) and produce larger parasperm (Oppliger et al. 2003). When males from male-biased or female-biased environments were mated with virgin females, parasperm length accounted for

15% of male success in siring offspring (Oppliger et al. 2003).

Spermatophores also occur in a number of caenogastropod families (Robertson 1989; 2007). These are comprised of encapsulated packages of eusperm and are distinct from spermatozeugmata (Hadfield and Hopper 1980; Glaubrecht and Strong 2004). Like spermatozeugmata, spermatophores appear to have evolved independently a number of times among caenogastropods (Glaubrecht and Strong 2004; Robertson 2007), and are not obviously correlated with other transitions in the sexual systems of caenogastropods (Figure 1).

Female anatomy sets the stage for sperm competition. Most caenogastropods can store sperm, using the seminal receptacle, the ovary, or the spermatophore bursa (Buckland-Nicks and Darling 1993; Whelan and Strong 2014). Many species can store sperm for several months or more. Calyptraeids can store sperm for 6 months or a year (Brante et al. 2011; pers. obs.) and *Viviparus* can store sperm for up to 2 years (Trüb 1990). The muricid *Dicathais orbita* and the littorinid *Littorina saxatilis* store sperm for more than a year (Westley et al. 2010; Panova, et al. 2010; Johannesson et al. 2016). However, in some temperate species the pallial oviduct atrophies during the non-reproductive season and sperm are not stored between seasons (e.g., Whelan and Strong 2014).

Stored sperm from multiple males result in multiple paternity in many caenogastropods. Genotyping of offspring demonstrates that single broods can have 15-23 sires (*Littorina saxatilis:* Panova, et al. 2010; Johannesson et al. 2016), 10-15 sires (*Solenosteira macrospira*: Kamel and Grosberg 2012), 1-7 sires (*Rapana venosa*: Xue et al. 2014), 2-8 sires (*Busycon carica*: Walker et al. 2007) and 1-5 sires (*Crepidula* spp.: Le Cam et al. 2015; Brante et al. 2011). In some species the proportions of paternity vary among males, but are roughly equal across capsules in a single brood (Walker et al. 2007; Xue et al. 2014). In *Neptunea arthritiga* the last male to mate achieves greater paternity than previous males by removing sperm they deposited inside the female (Lombardo et al. 2012). In *Rapana venosa* the last males to mate also sires the largest proportion of offspring but the mechanism behind this is not known (Xue et al. 2016). In contrast, earlier mates sire a greater proportion of the offspring in *Littorina obtusata* (Paterson et al. 2001) and larger males sire more offspring in *L. saxatilis* (Johannesson et al. 2016).

Copulatory courtship, activities that may impact post-copulatory cryptic female choice may also occur in caneogastropods. For example mating in *Pomacea canaliculata* may take 10-

20 hours. Approximately 2 hours are necessary for final courting and genital connection (Burela and Martín 2011) and dissection of snap frozen animals shows that it takes 2 - 4 hours for the penis to reach maximal penetration (Giraud-Billoud et al. 2013). The remaining time is used for sperm transfer and those snails where copula were limited to 4-6 hours had reduced fecundity after 10 days if they were not allowed to copulate again. A behavior that has been interpreted as nuptial feeding where the female licks a secretion produced by the outer gland of the muscular penis sheath may occur during copulation (Burela and Martín 2007; 2014). The function of such feeding is not clear. The increased incidence of this behavior in high-density populations suggests that it may function to encourage females to continue mating in the presence of other potential mates (Burela and Martín 2014) but it could also act as copulatory courtship which may influence post-copulatory female choice. Models of sperm storage (e.g. Manier et al. 2013), a better understanding of the role played by parasperm, and application of methods developed to track sperm in the reproductive tract of terrestrial gastropods (e.g., Kupfernagel et al. 2013) could help interpret results from mating experiments and paternity analyses.

Sex Determination

The mechanism of sex determination is currently unknown for most caenogastropods. In protandrous groups sex is labile and sex change is environmentally mediated. Genetic effects on sex change have so far not been examined. In dioecious groups, sex is thought to be genetically controlled, and the impact of environmental conditions has not been examined. Cytoplasmic sex factors have not been detected in any caenogastropod (Yusa 2006).

A 50-50 sex ratio, which is commonly reported for dioecious marine gastropods, is consistent with the expectation of heterogametic genetic sex determination. There is karyotype evidence to support sex chromosomes in a few of the 291 gastropod karyotypes reviewed by Thiriot-Quiévreux (2003) and subsequent work. Among the outgroups of caenogastropods, no sex chromosomes are reported for vetigastropods or simultaneously hermaphroditic opisthobranchs, but a XO system has been detected in several nerites Thiriot-Quiévreux (2003). Among architaenioglossans, XY and ZW sex determination systems both occur in the freshwater snail genus *Viviparus* (Barsiene et al. 2000) and ZW has been reported in cyclophorid species (Kongim et al. 2006). Among non- architaenioglossans an XO system has been reported in the pomatiopsid *Neotricula aperta*, the rissoid *Rissoa ventricosa,* and littorinid *Melarhaphe*

neritoides. *Littorina saxatilis* has an XY system (Rolan-Alvarez et al. 1996), as do three species

of neogastropods (*Fasciolaria lignaria, Pisania striata* and *Pisania maculosa*), one carinariid

(*Pterosoma planum*), and one hydroibiid (*Benedictia baiacalensis*) (Thiriot-Quiévreux 2003;

Odierna et al. 2007). Another carinariid and four pterotracheids have a system in which males

are determined by XY_1Y_2 (Thiriot-Quiévreux 2003). In each of these groups there are also

species for which sex chromosomes were not evident in karyotypes (Figure 1).

Breeding experiments with the apple snail *Pomacea canaliculata* have shed light on the

genetics of sex determination. The population sex ratio at hatching is not biased, but the sex ratio

of individual broods is highly variable both in field-collected broods and in the lab (Yusa and

Suzuki 2003). Food availability, temperature, and age do not affect sex ratio, but broods with

heavier eggs tended to include more female offspring (Yusa 2004; Yusa and Suzuki 2003). The

brood sex ratio is determined by genetic contributions from both parents, but with a larger

contribution from the mother (Yusa 2006; 2007). Sex is multi-genic, and probably involves at

least 4 genes are involved (Yusa 2007).

A heritible, sex-linked, microsatellite polymorphism has been demonstrated in *Busycon

carica* and *B. canaliculatus* (Avise et al. 2004). This locus is heterozygous in females and

hemizygous in males. Alleles are transmitted from mothers to both sons and daughters, but

fathers only transmit alleles to their daughters. Using this genetic marker Avise et al. (2004)

demonstrated that embryonic sex ratios do not deviate from 50:50 despite the fact that adult sex

ratios are often highly biased.

Overall theses studies suggest that sex determining systems in caenogastropods are

evolutionarily flexible. This view is supported by the presence of different systems of sex

choromosomes in species from the same genus (V*iviparus*) or the same family (Carinariidea), as

well as the apparent multiple evolutionary origins of sex chromosomes in groups that generally

lack them. In addition multi-gene sex determination, like that observed in *Pomacea canaliculata*

is hypothesizes to occur during evolutionary transitions between different genetic systems of sex

determination (Yusa 2007a). New data, covering a more taxonomically diverse set of species,

would contribute significantly to a more complete picture of the evolution of sex determining

systems in gastropods.

Sexual Dimorphism

Sexual dimorphism is common in many dioecious animals and has been used to infer characteristics of mating systems in organisms for which direct observations are not feasible. As such it could be a useful tool for inferring evolutionary transitions in sex allocation or mating behavior in taxa for which we lack direct observations. Sexual size dimorphism can result from competition for mates (males are larger) or from fecundity advantage (females are larger). Other secondary sexual characteristics may be related directly to offspring production (for example hip morphology in human females), male-male conflicts (weapons) or female mate choice (male ornaments). When viewed in this context sexual dimorphisms in caenogastropod shells appear to be primarily related to female fecundity or egg mass production, while radula dimorphisms are suggestive of weaponry.

Sexual size dimorphism in shell length is relatively straightforward to discover using preserved specimens and is widely documented in caenogastropods. In size dimorphic caenogastropods the female is almost invariably larger than the male. For example, in 14 out of 19 species of littorinids studied by Reid (1986) females were larger than males. In freshwater families like viviparids, hydrobiids and ampullariids larger female size is also common (Estebenet and Cazzaniga 1998; Jakubic 2006), as it is in cypraeids (Irie and Morimoto 2008; Katoh 1989), strombids (Ueno 1997), muricids (Son and Hughes 2000), nassariids (Avaca et al. 2013), and eulimids (Matsuda et al. 2013) as well as in the volutid *Voluta ebraea* (Matthews-Cascon et al. 2010), and the melongenid *Pugilina morio* (Matthews-Cascon et al. 1990b). In *Assiminea japonica* females are larger than males, but in the sympatric *Angustassiminea castanea* the males are larger (Kurata and Kikuchi 2000). Males are also larger than females in the cypraeid *Umbilia hesitata* (Griffiths 1961). Detailed study of these species that do not fit the general pattern could be informative.

Dimorphism in shell shape has been detected using geometric morphometrics (Avaca et al. 2013; Minton and Wang 2011). In most cases the female shape produces a larger volume and therefore a larger space for increased female reproduction. For example, in *Viviparus subpurpureus, Littoraria variegata, Nucella lapillus* and *Buccinanops globulosus* females are more globose or stouter and have larger apertures than males (Son and Hughes 2000; Riascos and Guzman 2010; Minton and Wang 2011; Avaca et al. 2013). In the terrestrial *C. septemspirale* females are taller and have wider whorls than males, resulting in 50% more volume in the shell (Reichenbach et al. 2012). In *B. globulosus* and *C. septemspirale* the sex of

>80% of the snails can be distinguished using multivariate analysis of morphometric data, which could be useful for determining sex ratios of shells in museum collections (Reichenbach et al. 2012; Avaca et al. 2013). Female body size usually correlates with fecundity suggesting these dimorphism may be the result of fecundity selection (Erlandsson and Johannesson 1994; Collin 2000). However in some species, large females are also preferred by males (Erlandsson and Johannesson 1994; Zahradnik et al. 2008), suggesting that sexual selection could also play a role.

Sexual size dimorphism can develop in a variety of ways. Female littorinids grow more quickly than males (Johannesson et al. 1997; Riascos and Guzman 2010). In an apple snail and a eulimid, females grow more rapidly than males only after maturation (Estebenet and Cazzaniga 1998; Matsuda et al. 2013), and females of a cowrie grow for longer than males before adding the terminal shell lips (Irie and Morimoto 2008). Independent of growth, females may also allocate more energy to reproduction. For example, females of dimorphic *Strombus canarium* allocate more energy to body tissue and gonads compared to males, which allocate more energy to shell deposition (Cob et al. 2008). Reproduction can also cost more for females than for males. Compared to males and pre-spawning females, post-spawning *Buccinum undatum* females have lower digestive gland index, lower carbohydrate and protein content of the foot, decreased activity of glycolytic enzymes in the foot, a decrease in foot contortions associated with escape response and a decreased ability to recover from escape exercise (Brokdort et al. 2003). This suggests that the significant metabolic demands of reproduction as a female may select for larger female size.

Sexual dimorphism in shell sculpture, when present, seems to be related to female egg deposition or capsule formation. In the *Olivella plata* (Olividae) the females have a wide, vertical groove adjacent to the parietal callus, which is not present in males or juveniles. This may be related to attaching egg capsules to the parietal callus (Borzone 1995; Pastorino 2007). Mature females of the turrids *Aforia circinata* and *Gemmula lordhoweensis* have a tertiary apertural notch that is not present in juveniles or males (Shimek 1984; Kantor and Sysoev 1991). The notch of *G. lordhoweensis* appears and disappears during the life of each female and could reflect distinct reproductive seasons or events (Kantor and Sysoev 1991). In reproductive female bursids in the genera *Crossata* and *Tutufa* the normally digitate aperture margin is flared and circular (Beu 1998). This may be associated with the way brooding females hold the egg mass over the aperture (Beu 1998). In the nassariid *Buccinanops globulosus* the shell callus is slender

in males and immature females. In large females it is inflated, generating increased space for the attachment of egg capsules to the callus (Márquez and Averbuj 2016). In the vermetid *Serpulorbis arenarius*, the presence of a pallial slit, a feature though to be related to the presence of brooded egg capsules is significantly but not exclusively linked to females (Calvo and Templado 2005). In some cases the possible function of shell dimorphism is not clear. In a species of *Lambis* female shells have a single high knob which is longer than the paired knobs of males. The spines of males are also shorter and flatter than those of females (Ueno 1997). It is temping to imagine that these differences are related to male-male competition.

Radula teeth are sexually dimorphic in a number of groups. Male *Rapana venosa,* have a wider tooth base and wider and taller central cusps on the rachidian that do females (Harding et al. 2008). A similar pattern in rachidian morphology has been reported for other muricids (Fujioka 1982; 1984). In the collumbellids *Euplica varians* and *E. versicolor* the radula is dimorphic in adults (deMaintenon 2004). Females and juveniles of both species have a flat-tipped outer secondary lateral cusp while adult males have a long pointed cusp. Adult males also have more tooth rows (deMaintenon 2004). In some cowries the radula is smaller but has more rows in females than in males (Schilder and Schilder 1961). In the strombid *Conomurex persicus* the outer and inner marginal teeth of females have more cusps than do males (Mutlu 2004). In the buccinid *Pisania pusio* the inner cusp of the lateral tooth is longer and thinner in males than the females (Matthews-Cascon et al. 2005). The function of these radula dimorphisms are unknown but those where males differ from juveniles and adult females could be related to aggressive interactions during reproduction and courtship.

Sexual dimorphism has ocassionally been reported in the color and the soft anatomy of caenogastropods. The dimorphic lateral projections on the propodium are sexually dimorphic in the tonnoidean *Ficus subintermedia* (Arakawa and Hayashi 1972; Fretter 1984). In cowries *Cypraea gracilis* females are red and males are brown (Griffiths 1961) and in *Monetaria annulus* the golden ring on the shell is paler in females than in males (Schilder and Schilder 1961). Some species of the terrestrial *Cochlostoma* show differences in pigmentation between males and females (Gofas 2001). Despite reports of sexual dimorphism from many families of gastropods, no comprehensive studies have been undertaken to determine how sexual dimorphism varies among closely related species and how this relates to mating system.

Mating behavior, mate choice, and sexual selection

      Sexual selection may play an important role in evolutionary transitions between sexual systems as well as maintaining the stability any system (reviewed in Leonard 2005, 2006; 2010). Aspects of sexual selection including pre-copulatory mate choice, sexual conflict over mating decisions, and post-copulatory choice have all been incorporated into theories in this field, but they have been poorly studied in caenogastropods. In many groups mating is difficult to observe under natural conditions and observations are sorely lacking. However data from easily observed intertidal species, and experiments with a few model species have shown that snails show male-male aggression, female choosiness and sexual conflict over mating.

      A number of caenogastropods form mating aggregations and deposit egg communally. This is especially common in muricids (D'Asaro 1986). The black murex *Hexaplex nigritus* makes especially impressive aggregations, extending up to 900m^2, weighing approximately 3 metric tons and including 5000 animals (Cudney-Bueno et al. 2008). The pink-mouthed murex *Phylonotus erythrostomus* aggregate into mountains of animals, as high as 2.5 meters, all contributing to a common egg mass (Cudney-Bueno et al. 2008). Other caenogastropods, most notably strombids also aggregate to mate, with densities of *Strombus luhuanus* reaching 20/m^2 in a mating aggregation of 200 animals (Catterall et al. 1983). Mating aggregations set the stage for sexual selection and mate choice.

      Aggression and male-male conflicts have been reported in both aggregating and non-aggregating species. In *Echinolittorina malaccana* and *E. radiata* males compete to occupy the copulation position. Larger contenders are more likely to succeed in ousting another male from this position on the female's shell (Ng et al. 2016). In *Strombus luhuanus* males also compete for copulations. Males approach a female, then fall behind and approach again until they finally copulate (Kuwamura et a. 1983). When another male approaches a mating pair, the original male moves the operculum up and down and waves the proboscis at the intruder. In *Strombus pugilus* males guard their mates, sparing with approaching males and using their proboscis to jab at each other (Bradshaw-Hawkins and Sander 1981). The winner copulates with the female and takes up the guarding position, touching the outside of the female's shell lip (Bradshaw-Hawkins and Sander 1981). Males of the ovulid *Cyphoma gibbosum* fight by biting at each other repeatedly and rearing up on the foot and lunging at each other (Ghiselin and Wilson 1966).

Copulation may be risky or costly. Costs of copulation include increased likelihood of dislodgement by waves and increased predation risk in copulating pairs compared to individual littorinids (Koch et al. 2007; Johannesson et al. 2010). Mating snails may also risk damage by their partner. For example, copulating female *Strombus* species sometimes pull the male along by their penis, which may be torn or broken (Reed 1995). However, the most ubiquitous cost of copulation might be in terms of time. Copulation generally takes several hours in caenogastropods (e.g., 3-6 hours in *Buccinum isaotakii* [Ilano et al. 2004], up to 20 hours in *Pomacea canaliculata* [Burela and Martín 2011]).

Significant costs of mating may lead to sexual conflict. Sexual conflict appears likely in a number of caenogastropods, where females avoid or reject mating attempts. For example, female *Littorina* species generally produce mucus trails that can be distinguished from males' trails. Males follow these trails to find females (Erlandsson and Johannesson 1994; Ng and Williams 2015). In dense populations *L. saxatilis* females may avoid encounters with males by making trails that cannot be distinguished from those of males (Johannesson et al. 2010). Females of *L. melanostoma* actively reject mating attempts by bending their heads and extruding their snouts to push away the penis of male suitors (Ng and Williams 2015). Female apple snails rotate their shells and shake off 60% of courtship attempts before copulation, and another 30% of males attempting copulation are dislodged in this way (Burela and Martin 2009). *Neptunea arthritica* shows the most extreme sexual conflict over mating reported for any caenogastropod (Lombardo and Goshima 2011). Females routinely try to avoid mating by running away and resist males by biting the penis and foot (Miranda et al. 2008). In one study more than 80% of copulations were terminated by female aggression (Lombardo and Goshima 2010). Female resistance increases with the number of males she has previous copulated with, suggesting that the cost of multiple matings outweigh the benefits for females (Lombardo and Goshima 2011). After copulation males guard the female and may bite or flip her when she tries to resume normal activity (Lombardo and Goshima 2011). In a related species, *Buccinum undutum* receptive females lie on their backs with their foot extended. This behavior has been observed in the lab where the male touches or strokes the female foot with his proboscis during their 2-6 hour copulation (Martel et al. 1986).

Further evidence of active mate choice is provided by patterns of size preference. Male preference for larger females have been reported in *Viviparous ater* (Staub and Ribi 1995),

Buccinanops globulosus (Avaca et al. 2012), and a number of littorinid spp. (e.g., Hollander et al. 2005; Erlandsson and Johannesson, 1994; Johnson 1999), but have not been detected in golden ring cowries (Katoh, 1989) or *Cerithidea rhizophorarum* (Ohtaki et al. 2001). In *Littoraria ardouiniana* male snails prefer larger females at two stages in the mating process; they prefer to follow the trails of larger females and they copulate for longer with larger females (Ng and Williams 2014). A surprising male preference not related to female size in *Neptunea arthritica*, is that males prefer previously mated females to virgins (Miranda et al. 2008).

Parental Care

Parental care is relevant to discussions of sexual systems, as it can significantly alter the relative investment in reproduction made by males and females. Protection of offspring is energetically expensive and the costs are almost always incurred by females. Caenogastropods generally make elaborate capsules and often protect their broods. Among outgroup taxa vetigastropds generally protect eggs with only a simple membrane and jelly coat, opisthobranchs produce gel masses with embedded eggs. Nerites produce blister-shaped egg capsules that are well-defended by calcospherites embedded in the dorsal wall (Kano and Fukumori 2010). Brood protection or brooding is very rare in all of these groups. In caenogastropods, material incorporated into capsule walls and other protective structures can represent up to 50% of the investment in a brood (Perron and Corpuz 1982). The process of egg laying and molding the capsules is also expensive, sometimes taking several days during which the females do not feed and during which they may be vulnerable to predation (Brokordt et al. 2003). In many caenogastropod species parental care extends past this initial investment and ranges from egg guarding and external brooding to eu-vivipary. It is noteworthy that parental care occurs infrequently in basal gastropods (Lindberg and Dobberteen 1981) and is also limited among opisthobranchs and pulmonates (reviewed by Baur 1994).

Caenogastropods from soft-bottom habitats have evolved the strategy of attaching eggs to adult shells (Figure 2). Female nassarids *Bullia melanoides* and *Buccinanops* spp. (Averbuj et al. 2014; Averbuj and Penchaszadeh, 2010; 2016), collumbellids *Bifurcium bicanaliferum* and other species in the *Strombina*-group (Fortunato et al. 1998; Fortunato 2002) and the olivid *Olivella plata* (Pastorino 2007) deposit egg capsules on their own shells. The muricid *Hexaplex nigritus* and the hydroibid *Peringia ulvae* also carry egg capsules, but if they are their own is unclear

(Thorson 1946; Cudney-Bueno et al. 2008). Female *Solenosteira macrospira* (Buccinidae) deposit capsules on their male partners (Kemal and Grosberg 2012). Such parental care has a significant cost. Experiments attaching capsules to both male and female *S. macrospira* demonstrate reduced growth in both sexes compared to controls without capsules (Kemal and Grosberg 2012).

In some families, females guard their benthic egg masses until they hatch (Figure 2). In aquaria females of *Buccinum isaotakii* guard their eggs until another female deposits on the mass (Ilano et al. 2004). *Fusitrition* spp. and other ranellids guard their eggs by sitting on or adjacent to the capsules (Gallardo et al. 2012; Beu 1998; Ramón 1991), as do female cowries (Ostergaard 1950; Wilson 1985; Osorio et al. 1999). Mother cowries may try to deter threats by pushing them away, by lifting the shell up and suddenly bringing it down to the substrate, by biting with the radula, or in one species flashing eyespots on the mantle (Ostergaard 1950). Female snails probably do not feed while guarding their eggs (Wilson 1985). Many mothers only leave the mass when the eggs have hatched, and one species of cowrie has been observed to assist hatching by chewing off the tops of the capsules (Katoh 1989).

In caenogastropods egg capsules can be brooded external to the body under the foot (e.g., calyptraeids; hipponicids) and in the mantle cavity (e.g., coralliophilids; vermetids). Eggs can also be brooded internally within the female reproductive ducts (littorinids; cerithioideans), in the gonad (*Janthina janthina*), or in subhaemocoelic pouches (cerithioideans, planaxids) and novel pouches in the pedal gland (a provannid; Reynolds et al. 2010), or in dorsal pouches behind the head which open via a pore in the sole of the foot (Ovulids in the genus *Pedicularia*; Simone 2005). In general internally brooded embryos are lecithotrophic and are often encapsulated inside the brood pouch. Matrotrophic vivipary, where nutrients secreted from maternal epithelium are provided directly to the embryos, is uncommon and has been demonstrated unambiguously only in some thiarids (Glaubrecht, 2005). However, the size difference between the 40-45 μm eggs and the 250 μm hatchling Warén's larvae suggest that the hydrothermal vent gastropod *Ifremeria nautilei* my also be matrotrophic (Reynolds et al. 2010).

Brooding is phygenetically conserved in some groups (for example all calyptraeids brood), but it is evolutionarily labile in others. In cerithioideans brooding has evolved multiple times, involving different morphological modifications in association with transitions to freshwater (Strong et al. 2011; Köhler et al. 2004; Strong and Glaubrecht 2002; 2007; Glaubrecht

and Strong, 2007; Glaubrecht, et al. 2009). An increase in egg size, subsequent to the invasion of freshwater habitats, may be a preadaptation for the evolution of brooding in pachychilid (Köhler et al. 2004). *Potamopyrgus* (Tateiidae) species have evolved ovovivipary at least twice in parallel, both times preceded by a transition from marine to freshwater habitats (Haase 2005). It is interesting to note that the evolution of parthenogenesis is also associated with transitions to freshwater (Auld and Jarne 2016). In littorinids, another primarily oviparous group, ovovivipary has evolved in at least 3 genera (*Littorina*, *Littoraria*, and *Tectarius*), but is not associated with any obvious shifts in habitat or life-style (Reid and Geller 1997).

Future Directions

It is customary to conclude by highlighting major un-answered questions that current circumstances suggest could be fruitfully addressed. The situation for caeongastropods defies this kind of summary. In no group is there such a broad diversity of sexual strategies spread across such a large number of families, studied by so few researchers. The rich diversity of caenogastropods and the large number of independent evolutionary transitions between different reproductive strategies mean that caenogastropods provide unique opportunities to study the complex interplay of sexual selection, reproductive anatomy, habitat, behavior and sex allocation in the evolution of sexual systems. More basic data must be accumulated before caenogastropods can provide powerful tests of important evolutionary theories. Some areas ripe for study are:

- Many anatomical studies of caenogastropods are old and oft cited. Comparative morphology using modern methods, strategic taxon sampling, and phylogenetic interpretation could provide valuable new insights into homologies among structures and the changes in sexual anatomy that accompany transitions in sexual systems.
- Systems of sex determination are variable among caenogastropods. Strategic taxonomic sampling, inheritance studies, and next generation sequencing could transform the way we view the evolution of sex determination and the mechanisms behind evolutionary transitions from genetic dioecy to environmental sex determination.
- Caenogastropods exhibit diverse mating behaviors with unexplored impacts on sex allocation and reproductive success. Behavioral studies are needed to obtain even a

preliminary understanding of the prevalence and importance of sexual selection, cryptic female choice, and copulatory courtship in gastropod reproduction.

- Reproduction is costly yet fewer than a handful of studies have examined the costs of reproduction over and above the direct investment in gonads or gametes. Comparisons of the costs of egg guarding, brooding, and the production of protective structures will provide important insights into sex allocation.

Switches among diverse strategies occur in caenogastropods at population, species, genus or family levels. Therefore sampling must be dense and phylogenies resolved at the relevant taxonomic scales. If this can be done, caenogastropods offer an unparalleled opportunity to understand evolutionary transitions between dioecy and hermaphroditism, the origins of maternal care, and the molecular evolution of sex determination.

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Table 1: Definition of Terms as Used in This Chapter

Term	Definition
Aphallic	Lacking a penis
Protandry	A sequential hermaphrodite where the male phase precedes the female stage and the two sex do not occur simultaneously.
Consecutive Hermaphrodite	A sequential hermaphrodite where sex can changes more than once.
Dioecy	Separate sexes
Environmental Sex Determination	When sex is determine by environmental conditions like temperature or social interactions and is not set by sex chromosomes.
Parthenogenesis	A sexual reproduction which proceeds from an egg without fertilization with a sperm
Protogyny	A sequential hermaphrodite where the female phase precedes the male stage and the two sex do not occur simultaneously.
Sexual Dimorphic	Males and females show differences in characteristics other than primary sexual characters.
Simultaneous Hermaphrodite	Any individual that has functional male and female structures at the same time. In many species maturity of one sex may develop prior to maturity in the second sex, but during most of the adult life both sexes occur simultaneously.

Figure Legends

Figure 1: Aspects of the sexual systems and reproductive biology mapped onto phylogenetic trees of select caenogastropods generated by Ponder et al. (2008). **A.** Strict consensus tree based on morphological characters, with bootstrap values shown on branches and **B.** Strict-consensus tree from a Bayesian analysis of morphological characters and molecular data with clade credibility values shown on branches. The states of seven characters in each family are indicated in color. Sexual system: Dioecious, protandrous, simultaneous hermaphrodite as indicated by sexual anatomy. Penis: Present/absent in males. Sperm type: Spermatophore present, Spermatozeumata present, normal = eusperm and usually parasperm are present, no data = sperm have not been examined in detail. Female Ducts: open/cosed. Sex Chormosomes: No chromosome = sex chromosomes have not been detected in karyotypes, N/A = not applicable to protandrous or simultaneous hermaphrodites, no data = published studies are not available. Parental Care: External brooding = brooding on the outside of the shell, Internal = under the shell, including under or along side the foot, in the mantle cavity and inside the body, Guarding = adults remain near or on egg capsules but can move around independent of the capsules. Sexual Dimorphism: Includes the characters for which dimorphism has been reported if present in any species in the group, solid squares do not indicate that all species display dimorphism. Diagonal stripes indicate multiple states present in the group. A central spot indicates that this state appears to be an unusual derived state in only one or a few species. See text for relevant citations.

Figure 2: Examples of maternal care in gastropods. **A.** *Margarites vorticiferus*, a vetigastropod broods in the umbilicus of the shell (after Lindberg and Dobberteen 1981). **B.** *Crepidula* species brood their transparent capsules between the propodium, the neck, and the substrate. **C.** Cowries, *Cypraea* species, deposit compact masses of capsules that they guard by sitting on or near. **D.** *Buccinanops* species lay their eggs on their own shells (after Averbuj and Penchaszadeh 2010).