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REVIEW

Sexual ornamentation and weapons of sexual conflict in cartilaginous fishes

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Abstract Sexual selection and sexual conflict often result in the evolution of morphological traits that function to improve reproductive success, often termed sexual weapons and ornaments. Sexual weapons serve to increase the reproductive success of the ardent sex (typically males in dioecious taxa) by force, whereas sexual ornaments are considered 'desirable' by the opposite sex, or may exploit pre-existing sensory bias. Cartilaginous fishes (Chondrichthyes: sharks, skates, rays, and chimaeras) exhibit a complex spectrum of reproductive modes and marked variation in the prevalence of genetic polyandry and multiple mating. For these reasons, Chondrichthyes represent an ideal group to study sexual selection, sexual conflict, and their evolutionary consequences. In this review, we summarise existing knowledge regarding the function of several putative 'weapons of sexual conflict' (sexual weaponry used to coerce or force females to mate) and ornaments possessed by cartilaginous fishes. Subsequently, we discuss what chondrichthyans and these traits can tell us about sexual selection more broadly, and we highlight major knowledge gaps in the field. A lack of observational data impedes our ability to make robust claims about the function of several traits. However, there is reason to suggest that weaponry resulting from sexually antagonistic selection is abundant in chondrichthyan taxa, whilst only one potential case of sexual ornamentation is known.

Keywords Chondrichthyes · Sharks · Elasmobranchii · Evolution · Sexual selection · Sexually antagonistic coevolution

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Introduction

The central tenet of natural selection states that individuals act to maximise their 'fitness' or lifetime reproductive success (Haldane 1990; Wade and Kalisz 1990), however, differences in the maximum theoretical reproductive output between males and females result in an evolutionary conflict between the sexes (Lessells 2006; Queller and Strassmann 2018). In other words, sexual selection in females has historically been thought to optimise for mate 'quality', whereas sexual selection in males optimises for

mate quantity; with this dichotomy often referred to as male ardency and female prudence (Baguette et al. 1996; Chapman et al. 2003). One consequence of sexual reproduction and the evolutionary conflict that ensues is the evolution of sexual ornaments and weapons (Doorn and Weissing 2006; McCullough et al. 2016). Ornaments refer to traits, typically in the ardent sex (which in dioecious taxa tends to be male), which increase the probability of successful mating events as they are considered 'desirable' by members of the other sex (Doorn and Weissing 2006; Kekäläinen et al. 2010). Famous examples include the elaborate coloured plumage of birds of paradise and peacocks (Moller and Pomiankowski 1993). Weapons on the other hand, refer to traits in the ardent sex that increase the probability of successful mating events by force; either by improving the outcomes of competitive interactions with other males or by facilitating coercive mating attempts (Moldowan et al. 2020; Rico-Guevara and Hurme 2019). Weapons differ fundamentally from ornaments in that their evolution is not directly driven by mate choice (McCullough et al. 2016). Sexual weapons include a variety of horns and spines observed across a wide array of taxa. Most frequently associated with male-male competition, some sexual weapons are also used by males to force or coerce females into unwanted mating events, potentially resulting in sexually antagonistic coevolution and the acquisition of female defense traits (Crumière et al. 2019; Eberhard 2004). Herein we focus on this form of sexual weaponry (instead of traits used in male-male competition), and use the term 'weapons of sexual conflict' in the interest of clarity. Whilst taxa may exhibit both sexual weaponry and ornamentation (particularly where weapons are used for male-male competition), ornamentation is likely more common where strong female mate choice is present (Candolin 2019; Freed 2000).

The clade Chondrichthyes consists of sharks, rays, skates, and chimaeras, and exhibits unparalleled variation in reproductive biology among vertebrates (Carrier et al. 2004; Conrath and Musick 2012). Reproductive mode in Chondrichthyes represents a complex spectrum from true placental matrotrophy to oviparity, with many intermediates (Katona et al. 2023; Parsons et al. 2008). The prevalence of multiple paternity also appears to vary dramatically between species (Gayford and Flores-Flores 2024; Lamarca et al. 2020), theoretically resulting in highly variable and taxon-specific levels of sexual conflict between males and females. For these reasons, Chondrichthyes are an ideal clade within which to study sexual selection and its phenotypic and genotypic consequences. Unfortunately, until recently, most references to sexual selection in chondrichthyans consisted of speculative hypotheses alone (Gayford 2023; Gayford and Sternes 2024; Rowley et al. 2019). Many sexually dimorphic traits are known in chondrichthyan taxa (Cappetta 1986; Gayford 2023); however, they are rarely discussed in the context of sexual selection or conflict. Thus, despite being a clade of particular interest in terms of their reproductive biology, our understanding of sexual selection and conflict in Chondrichthyes lags far behind that of most other vertebrate clades, particularly regarding mate choice, sexual ornamentation, and weaponry.

In this review, we highlight prominent sexual dimorphisms observed in chondrichthyan taxa that may represent cases of sexual ornamentation or weapons of sexual conflict. We discuss the likely functions of these traits in terms of the three primary stages of mating in Chondrichthyes: courtship, grasping of the female by the male, and clasper intromission followed by sperm transfer. We examine the empirical evidence (or lack thereof) supporting these functions and how comparisons with similar traits in other vertebrate groups may provide novel insight into sexual selection and conflict in Chondrichthyes, and across vertebrate diversity more broadly. Finally, we synthesise major knowledge gaps in our understanding of sexual weaponry, ornamentation, and their underlying drivers in chondrichthyans, and propose novel avenues for research that may facilitate future comparative studies across diverse vertebrate clades. Data paucity is a recurring theme throughout, with information regarding a majority of traits discussed being limited to a minute fraction of total chondrichthyan diversity. For this reason, we take an explicitly qualitative approach to reviewing the evidence for sexual ornamentation and weapons of sexual conflict. Alongside our extensive suggestions for avenues of future research, this approach provides a foundation for quantitative assessments and numerous, testable hypotheses regarding the functional role of the traits discussed.

Pelvic spines and armaments

Clasper spines

One of the most apparent possible weapons of sexual conflict that cartilaginous fishes possess is the array of spines and armaments on the external surface of the male reproductive organs of some taxa (Table 1). Males of all chondrichthyan species possess paired copulatory organs, also known as claspers, which consist of modifications of the pelvic fin skeleton and musculature (Ebert et al. 2021). The proximal part of the clasper connects with the pelvic fin through intermediate cartilaginous segments that vary in number, shape, and relative position (Soares 2020). The clasper shaft is anteriorly composed of three marginal cartilages fused together and attached to a variable number of terminal cartilages (Soares 2020). All these skeletal components together form a path through which sperm travels to the female's reproductive tract (Jungersen 1899; Leigh-Sharpe 1920). Terminal cartilages are the most variable clasper structures in shape, size, and ornaments and also play a crucial role in anchoring the clasper during copulation.

In some elasmobranchs, males possess spiny or spur-like modifications to the accessory terminal cartilages (Fig. 1; Applegate 1967; Compagno 1988; Hulley 1972; Jungersen 1899; Soares 2020; Stehmann 1970). The 'sharp edges' of skate (rajiform) claspers exhibit particularly high levels of complexity and morphological diversity (Hulley 1972; Leigh-Sharpe 1922; Ishiyama 1958). These derivatives can be flexed together with other terminal cartilages when the clasper is inserted into the female reproductive tract, helping to anchor the clasper firmly within the distal end of the oviduct and to spread spermatozoa together with

Table 1 Morphological traits hypothesized to represent either sexual ornaments or weapons of sexual conflict, the taxa in which they occur, and the level of evidence for their hypothesized function

Morphological trait	Taxa	Evidence type	References
Tenaculum	Chimaeriformes (Obruchev 1953)	1	Raikow and Swierczewski (1975), Wourms (1977)
Gynandric heterodonty	Carcharhiniformes (Compagno 1977)	1,2	Compagno (1988), Soares and Zanini (2023), Crooks et al. (2013), Soares and de Carvalho (2019)
	Lamniformes (Berg 1958) (*Alopias* only)	1	Cappetta (2012)
	Hexanchiformes (de Buen 1926)	1	Cappetta (2012)
	Myliobatiformes (Compagno 1973)	1	Herman et al. (1998, 1999)
	Rajiformes (Berg 1940)	1	Herman et al. (1994, 1995, 1996)
	Rhinopristiformes (Naylor et al. 2012)	1,2,3	Gutteridge and Bennett (2014)
	Squaliformes (Goodrich 1909)	1	Cappetta (2012)
Pelvic/clasper spines	Squaliformes (Goodrich 1909)	1	Ishiyama (1958), Hulley (1972)
	Carcharhiniformes (Compagno 1977)	1	Soares (2020), Soares and Carvalho (2019)
	Chimaeriformes (Obruchev 1953)	1	Didier (1995)
Pectoral spines	Rajiformes (Berg 1940)	1	Colonello et al., (2007), Gravendeel et al. (2002)
	Squatiniformes (Duméril 1806)	1	McEachran and Konstantinou (1996)
Bioluminescence and biofluorescence	Carcharhiniformes (Compagno 1977)	1	Gruber et al. (2016)
	Squaliformes (Goodrich 1909)	1	Claes and Mallefet (2009, 2010)
	Orectolobiformes (Applegate 1972)	1, 3	Gruber et al. (2016)
	Myliobatiformes (Compagno 1973)	1	Gruber et al. (2016)

Evidence is categorized as follows: 0, none (a total absence of non-anecdotal data); 1, comparative or anatomical studies (trait functionality can be implied on the basis of interspecific and intraspecific anatomical differences); 2, direct behavioural observations (trait functionality has been observed visually); 3, experimental or analytical evidence (quantitative data drawn from empirical analyses support trait functionality). Whilst we briefly discuss the potential for dorsal fin spines to represent a weapon of sexual conflict, they are omitted from this table due to the lack of any supporting evidence

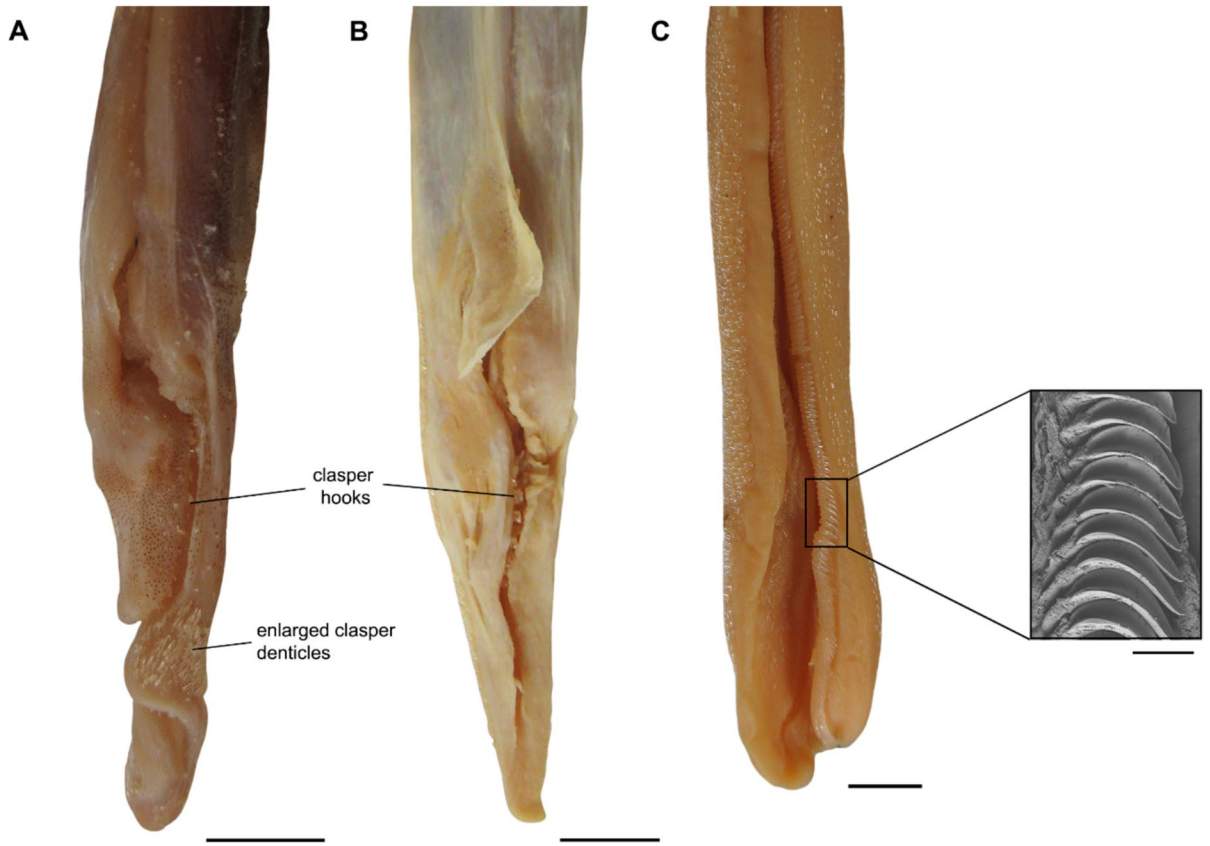

Fig. 1 Clasper denticles and hooks in catsharks. A, *Galeus antillensis* (Springer 1979), UF 148245, 385 mm total length (TL); B, *Halaelurus natalensis* (Regan 1904), SAIAB 26951, 400 mm TL. Scale bars = 2 cm. C, *Scyliorhinus torazame* (Tanaka 1908), NSMT 50632, 427.9 mm TL. Scale bar = 5 mm. SEM image (showing clasper hooks in greater detail), scale bar = 200 µm. Modified from Soares (2020) and Soares & de Carvalho (2019)

the pseudorhipidion (Gilbert and Heath 1972; Leigh-Sharpe 1920; Hulley 1972). In some cases, the external surface of these modified cartilages exhibits modified clasper spines or hooks (Fig. 1). These spiny armaments are observed in an array of catsharks (Scyliorhinidae; Gill 1862) and lanternsharks (Etmopteridae; Fowler 1934) and are also thought to play a role in clasper anchoring (Soares and de Carvalho 2019; Soares 2020). Data on clasper morphology is scarce for many elasmobranch taxa and further investigation is needed to improve our understanding of the diversity and probable function of clasper spines in each clade from which they are known.

Prepelvic clasper denticles

Whilst Holocephali (chimaeras; Bonaparte 1832) do not possess clasper spines, modified dermal denticles also cover the paired prepelvic claspers that are unique to Holocephali (Didier 1995; López-Jofré et al. 2023). Prepelvic claspers are connected to the anterior edge of the pelvic girdle and are housed in pouches right before the pelvic region, with a terminal mass of fleshy tissue covered in dermal denticles (Didier 1995; López-Jofré et al. 2023). When they emerge from their pouches, prepelvic claspers flex anteriorly and the dermal denticles situated

along their medial edge are anchored to the ventral side of the female (Didier 1995).

Synthesis

The fact that clasper spines (and likely prepelvic claspers) are used to secure the position of the claspers during copulation (Didier 1995; Gilbert and Heath 1972; Leigh-Sharpe 1920; Hulley 1972) does not intrinsically make them weapons of sexual conflict. However, clasper spines are likely not essential for copulation since the majority of shark and ray species do not possess them. There is presently no reason to suggest that copulation in clasper spine-bearing species differs from that of other taxa, nor that these structures convey increased reproductive success or efficiency, although the hypothesis has not been tested explicitly. Moreover, these spiny armaments are at least superficially similar to morphological elaborations of the male intromittent organs used to inflict unwanted mating events in other (non-chondrichthyan) taxa (Lane 2018; Reinhardt et al. 2015). For these reasons, we hypothesise that clasper spines can be used as weapons of sexual conflict that are capable of inflicting damage and enabling coercive mating events without any clear adaptive benefit to the female. This is not necessarily the case with the prepelvic claspers of chimaeras. As these structures are present in all chimaera species, and Holocephali exhibit numerous morphological differences from elasmobranchs (Berio et al. 2023; Didier and Rosenberger 2002), it is plausible that the prepelvic claspers are necessary to ensure efficient copulation.

Body spines and armaments

Dorsal fin spines

Spines and body armaments in Chondrichthyes are not confined to the genitalia but are present on several different parts of the external body surface in different taxa (Colonello et al. 2007; Ebert et al. 2021; Gravendeel et al. 2002; McEachran and Konstantinou 1996). It is important to note that as in other clades, some of these structures may function to maximise survival or performance as opposed to playing a role in sexual reproduction (Emlen 2008; Stankowich 2012). Several chondrichthyan groups, including chimaera, batoid groups (stingrays), and squaliform and heterodontiform sharks possess one or more dorsal fin spines, emanating from the anterior origin of each dorsal fin respectively (Jerve et al. 2014; Smith et al. 2016). Dorsal fin spines have also been found in various placoderm and acanthodian remains (e.g., Maisey 2009). However, the homology of these structures is yet to be established (Ferrón et al. 2021; Maisey 2009). Some of these spines secrete venom and are thought to be defensive adaptations (Smith et al. 2016), but there is no evidence that they play any role in copulation, mate choice, or male-male competition.

Alar and malar thorns

The same cannot be said of other body armaments, however. Alar and malar thorns (Fig. 2) are enlarged placoid scales with particular shapes that occur over the dorsal surface of the pectoral fins and lateral to the orbits, respectively, and are known from a wide array of skates (Rajiformes) (Fig. 2) and angel sharks (Squatiniformes) (Colonello et al. 2007; Gravendeel et al. 2002; McEachran and Konstantinou 1996). These spines only develop in males immediately before reaching sexual maturity and may facilitate holding the female during copulation, much like the pelvic armaments discussed earlier (McEachran and Konstantinou 1996). Observations have also been made of the alar spines piercing the skin of the female (Libby and Gilbert 1960; Luer and Gilbert 1985). Again, it could be argued that these armaments are necessary to ensure efficient mating. However, even in the absence of direct observational or experimental evidence (Table 1), a role in coercive or forceful mating cannot be ruled out. Subcutaneous wounds inflicted using the alar or malar spines could result in significant loss of fitness in females due to subsequent infection (Whitehead et al. 2022). Even if these spines form a part of 'typical' copulation events (an assumption that has not been validated beyond isolated behavioural observations in unnatural settings), they could be utilised to ensure mating against the will of the female and thus should be classed minimally as facultative weapons of sexual conflict.

Cephalic claspers

A further male armament that could potentially be used as a weapon of sexual conflict is the cephalic

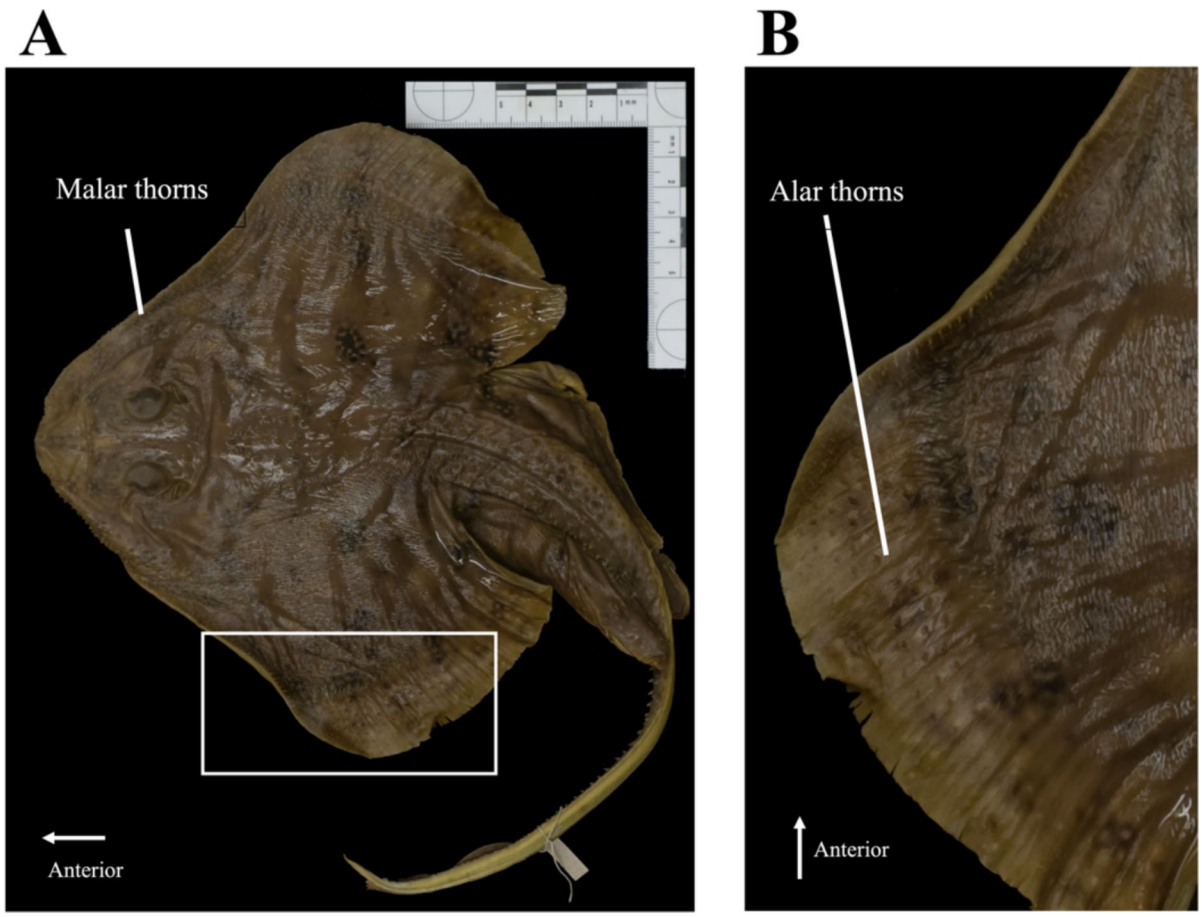

Fig. 2 A male specimen (MCZ ICH176738) of the rosette skate *Leucoraja garmani* (Whitley 1939) exhibiting both alar and malar thorns (**A**), with an enlarged view of the alar thorns (**B**)

clasper, also named tenaculum, of chimaera (Fig. 3). The tenaculum is an unpaired median rod of curved cartilage present on the dorsal surface of the rostrum (Raikow and Swierczewski 1975; Wourms 1977). The structure is only observed in males and used at maturity to grasp the female's pectoral fin to facilitate intromission of the pelvic clasper during copulation (Berio et al. 2023; Klimley et al. 2023; Raikow and Swierczewski 1975). Similarly to all of the armaments discussed here, this means that it could potentially be used to coerce females into unwanted mating events. Unfortunately, very little is known about the reproductive behaviour of chimaeras, and the tenaculum has rarely been observed in use, particularly in a natural setting (Klimley et al. 2023). Whilst the denticles located on the cephalic tenaculum are smaller and likely not capable of inflicting the same degree of damage as clasper spines and alar and malar spines (Cohen et al. 2025), their clear reproductive function (Berio et al. 2023; Klimley et al. 2023; Raikow and Swierczewski 1975), combined with a paucity of behavioural observations means that a role in coercive mating (as a weapon of sexual conflict), cannot be ruled out. Even if the tenaculum is not capable of inflicting significant damage on females, it could still be used to hold females against their will to facilitate copulation, incurring negative fitness costs for the female. However, whereas not all elasmobranchs possess clasper spines or alar/malar spines (Ebert et al. 2021), males of all chimaera possess a cephalic tenaculum (Cohen et al. 2025). This further complicates the interpretation of the tenaculum as a weapon of sexual conflict, as it may instead be necessary to ensure synchronised swimming between males

Fig. 3 Cephalic clasper of the plownose chimaera *Callorhinchus callorynchus* (Linnaeus 1758), MNRJ 619, 547 mm TL

and females during copulation, especially given the absence of individualized teeth in chimaeras. This is not the case for clasper spines or alar/malar spines, as morphologically similar taxa are capable of reproducing successfully without these structures (Ebert et al. 2021). Therefore, whilst it is possible that the tenaculum is used as a weapon of sexual conflict, we caution that more data are required before this hypothesis can be assessed robustly.

Tooth morphology (gynandric heterodonty)

Despite the clear multifunctional role of dentition in chondrichthyans (Berio et al. 2020, 2022; Kajiura and Tricas 1996; Gutteridge and Bennett 2014), there is evidence to suggest that some aspects of dental morphology are sexually dimorphic and may represent weapons of sexual conflict. Among chondrichthyans, chimaeras have three pairs of ever-growing dental plates that may be sexually dimorphic (Dean 1906; Chávez-Hoffmeister and Villafaña 2023), although no study has addressed this possibility explicitly. Furthermore, the only known function of chimaera dental plates is food processing (Didier 1995), and any direct role in copulation or reproduction has yet to be observed. As opposed to chimaeras, the teeth of elasmobranch species are replaced continuously, facilitating ontogenetic changes in dentition (Berio et al. 2020, 2022; Tomita et al. 2016; Türtscher et al. 2022). One example of this is the number of tooth rows, which increases through ontogeny in some species with increasing jaw size (Geniz et al. 2007).

In some elasmobranch species, tooth morphology differs between sexually mature males and females, a sexual dimorphism called gynandric heterodonty (Taniuchi and Shimizu 1993; Powter et al. 2010; Gutteridge and Bennett 2014; Soares & de Carvalho 2019; Berio et al. 2020, 2022). In mature male batoids, a homodont dentition composed of molariform teeth is gradually replaced by a heterodont dentition consisting of cuspidate teeth, with more prominent morphological changes when located in the anterior tooth rows (Cappetta 1986; Nordell 1994; Kajiura and Tricas 1996; Gutteridge and Bennett 2014; Underwood et al. 2015; Rangel et al. 2016). Interestingly, certain species retain this dimorphism permanently following sexual maturation (Nordell 1994) while others develop cuspidate teeth during the mating season and revert to a female-like dentition at the end of it, fuelling hypotheses on the functional role of specific tooth shapes for copulation (Kajiura and Tricas 1996). Gynandric heterodonty in selachians differs from batoids as seasonal modifications are uncommon (Ebersole et al. 2023). Moreover, morphological changes include a wider variety of changes in mature males including more cuspidate, unserrated, needle-like, and larger teeth with fewer cusps relative to juveniles and females (Cappetta 1986, 2012; Soares & de Carvalho 2019; Berio et al. 2020; 2022).

Gynandric heterodonty is perhaps the best documented example of a weapon of sexual conflict in elasmobranchs, and it has long been recognised that in several species, male-specific dentition is used for coercive mating to improve the chances of successful copulation (McEachran 1977; Whitehead et al. 2022). It has also been hypothesised that gynandric heterodonty could be associated with sex-specific trophic ecology (Feduccia and Slaughter 1974), however, the former explanation is generally favoured because the emergence of gynandric heterodonty is concomitant with sexual maturation and because similar diets are reported among mature specimens of species exhibiting such dimorphism (McEachran 1977; Powter

et al. 2010). In the eastern shovelnose ray *Aptychotrema rostrata* (Shaw 1794), Gutteridge and Bennett (2014) have evidenced that bite-grip tenacity of larger and cuspidate mature male teeth was higher than in immature males and mature females, strengthening the hypothesis of elasmobranch teeth functioning as weapons of sexual conflict. As a consequence of biting events, the skin of females during the mating season can bear superficial 'mating scars' (Pratt and Carrier 2001; Ritter and Amin 2019; Whitehead et al. 2022). The deep wounds reported on some females have likely been caused by coercive copulation attempts from males (Ritter and Amin 2019; Whitehead et al. 2022). Interestingly, studies have described thicker skin in females as compared to males of similar size (Nordell 1994; Pratt 1979; Kajiura et al. 2000; Crooks and Waring 2013; Hagood et al. 2023), and the sampled areas co-locate with male's preferred bite zones (Pratt 1979; Kajiura et al. 2000). Similarly, longer, wider, and denser dermal denticles in mature females of small-spotted catsharks *Scyliorhinus canicula* (Linneaus 1758) coincide with body locations where pre-copulatory biting and wrapping occur, supposedly protecting from male bites, but also enhancing mate gripping during copulation (Crooks et al. 2013). Together with skin thickness, sexual dimorphism in dermal denticles could be the result of sexually antagonistic coevolution in elasmobranchs. Whilst we lack the empirical data to formally test this hypothesis further, it is probable that the sexually dimorphic dentition of several elasmobranch species functions to facilitate coercive mating attempts and may be an example of a weapon of sexual conflict.

Bioluminescence and biofluorescence

All of the sexually dimorphic traits discussed until this point likely represent weapons of sexual conflict, however, emerging evidence also suggests the existence of at least one sexual ornament in selachians. Bioluminescence has been detected in three shark families to date: lanternsharks (Etmopteridae), kitefin sharks (Dalatiidae; Gray 1851), and sleeper sharks (Somniosidae; Jordan 1888) (Duchatelet et al. 2021; Ferrón 2023). These are typically deepwater sharks that inhabit low-light environments and may spend substantial proportions of their life below the photic zone (Ebert et al. 2021). In these sharks, bioluminescence manifests as permanent flank markings or spontaneous luminescence, both of which resulting from the presence of photophores and secretory glands (Duchatelet et al. 2021). Importantly, bioluminescent markings are highly species-specific in their distribution across the body surface (Duchatelet et al. 2021).

Bioluminescence in sharks was initially assumed to perform a role in camouflage through counterillumination to improve foraging success (Claes et al. 2010), as commonly observed in other taxa (Ellis and Oakley 2016). Indeed, there is some experimental evidence supporting this hypothesised function, as the velvet belly *Etmopterus spinax* (Linneaus 1758) appears capable of obscuring its silhouette using bioluminescence (Claes et al. 2010). Anti-predator functions have also been posed, including the aposematic use of bioluminescence to advertise the venomous nature of the dorsal fin spines (Duchatelet et al. 2019).

However, recent studies reviewed by Duchatelet et al. (2021) also suggest that bioluminescence in sharks (specifically the lateral flank photophores) is important for intraspecific communication. Visual modelling experiments showed that sharks are capable not only of detecting bioluminescence at distances of up to 10 body lengths but can discern specific luminescent body parts (Claes et al. 2014b). Lateral flank photophores, which were exapted from the ventral photophores that serve a counterillumination function (Claes et al. 2014a), also correlate with speciation rate (Claes et al. 2015). Furthermore, the claspers of all bioluminescent species are covered in photophores and appear to produce more light than the rest of the body (Duchatelet et al. 2021). These lines of evidence suggest that lateral flank bioluminescence in sharks may act as a sexual ornament that mediates female mate choice, similar to the lateral markings of African lake cichlids (Ding et al. 2014; Seehausen et al. 1998), or the bioluminescent courtship displays of other animals [e.g., ponyfish (Gazzinae; Uvarov 1926), octopus (Bolitaeninae; Chun 1911), and beetle (Pyrophorinae; Candèze 1863)] (Ellis and Oakley 2016). There is no direct experimental evidence of bioluminescence-mediated mate choice in Chondrichthyes besides sex-differentiated hormonal regulation of the lateral flank photophores (Claes and Mallefet 2010). However, the enhanced bioluminescence of the male reproductive organs, relative to other parts of the body (even those that also

contain photophores), and elevated speciation rates suggest that bioluminescence acts as a sexual ornament as both are typical of species in which bioluminescence contributes to courtship displays rather than foraging or predator evasion (Claes et al. 2015; Ellis and Oakley 2016).

Whilst it is possible, and indeed likely that bioluminescence performs multiple functions in sharks (and therefore that the overall form and optical properties of photophores are subject to context-dependent trade-offs), it possibly represents the first and only known case of sexual ornamentation in Chondrichthyes.

Biofluorescence has also been described in several chondrichthyan species and may have evolved independently on at least three occasions (Gruber et al. 2016). Biofluorescence differs from bioluminescence in that it requires some external light source to trigger photoreceptor excitation, rather than light being generated through an internal biochemical reaction (Gruber et al. 2016). Similarly to bioluminescence, there is evidence to suggest that biofluorescence, at least in catsharks (Scyliorhinidae), may enhance intraspecific communication by increasing contrast with the background environment (Gruber et al. 2016). However, no data exist regarding speciation rates in biofluorescent versus non-biofluorescent taxa, or concentration of photoreceptors around the genital region, and thus additional studies would be required to determine whether or not biofluorescence performs any role in copulation or courtship behaviours. Additionally, even if biofluorescence is used for intraspecific communication, the physiological and hormonal regulation of these luminous displays differs fundamentally from those observed in bioluminescent taxa.

What does this tell us about sexual selection and conflict in Chondrichthyes?

Non-chondrichthyan analogs

Each of the sexually dimorphic traits discussed in this review is also known from non-chondrichthyan taxa (e.g., Ellis and Oakley 2016; Leigh et al. 2008). Gynandric heterodonty is particularly common in mammals, with examples of the mandibular, protruding tusks that erupt at the onset of sexual maturity in deep-diving beaked whales, long and spiralled left tusks of male narwhals (*Monodon monoceros*; Linneaus 1758), and mandrill (*Mandrillus sphinx*; Linneaus 1758) canines that are 4.5 times longer in males than females (Leigh et al. 2008; Loch et al. 2023). Sexually dimorphic teeth in mammals can constitute sexual weapons for male-male sexual competition and/or coercive mating (i.e., weapons of sexual conflict), as well as sexual ornaments (Gittleman and Van Valkenburgh 1997; Kelley et al. 2015; Loch et al. 2023). Male body spines and armaments too are common in a variety of taxa (Arnqvist and Rowe 2002; Morrow and Arnqvist 2003; Perry and Rowe 2012). In some species, famously water striders (Gerridae; Leach 1815), behavioural observations and experimental evolution have shown that these structures are used for coercive mating and have evolved through sexually antagonistic coevolution (discussed in detail below) in conjunction with female defence traits (Arnqvist and Rowe 2002; Morrow and Arnqvist 2003; Perry and Rowe 2012). Sexual ornamentation and courtship displays featuring bioluminescence are also known in many species (Ellis and Oakley 2016). Given that each of these traits functions as a sexual weapon and/or ornament in other animals, it is not surprising that they appear to fulfil these roles in chondrichthyans. However, far less is understood about the evolutionary basis of these traits in cartilaginous fishes than in the other groups in which they occur. As mentioned previously, research into sexual selection, conflict, and mate choice in Chondrichthyes lags far behind these other major vertebrate groups (Lyons et al. 2021). Historically, it has been assumed that males determine if and when copulation will occur (Lyons et al. 2021), and vague terminology relating to male-male competition such as 'territoriality' or 'agression' is often used with little or no empirical evidence. This is driven at least in part by the difficulty in maintaining experimental populations of chondrichthyan species, and possibly by unconscious bias in a historically male-dominated field (Lyons et al. 2021).

Female counteradaptations and sexually antagonistic coevolution

Weapons of sexual conflict inflict damage on females, and may result in unwanted mating events (Wigby and Chapman 2004). Whilst the latter of these factors may increase the evolutionary fitness of ardent males,

both factors should actively decrease female fitness (Chapman et al. 2003). In other taxa, this discordance in optimal fitness outcomes between the sexes results in a form of evolutionary arms race known as sexually antagonistic coevolution (Parker 1979). The genetic and genomic consequences of sexually antagonistic coevolution are complex (Rowe and Day 2006), but at the phenotypic level this form of selection results in the continuous, cyclical evolution of male weapons, and female defence traits that act to nullify said weapons (Perry and Rowe 2012; Rönn et al. 2007; Rowe and Arnqvist 2002). The textbook example of this evolutionary dynamic is the water strider (*Gerris* ssp; Fabricius 1794), in which females have evolved anti-grasping structures to reduce the risk of superfluous mating events, perpetuated through use of male weapons (Rowe and Arnqvist 2002).

Whilst it is challenging to empirically confirm sexually antagonistic coevolution in wild populations (Rowe and Day 2006), there is some evidence of similar dynamics in chondrichthyans. Throughout the previous sections we have provided multiple lines of evidence to suggest the presence of male weapons of sexual conflict in various chondrichthyan groups. But crucially, there is also evidence of female morphological defence traits that may be co-evolving with sexual weapons. The best-described of these putative defence traits is the thickened dermis of mature female sharks relative to male conspecifics (Pratt 1979; Hagood et al. 2023), which is typically thought to reduce the negative fitness consequences of mating wounds inflicted by males with gynandric heterodonty (Hagood et al. 2023; Ritter and Amin 2019; Whitehead et al. 2022). Specifically, the dermis is known to be thicker in females of several carcharhiniform species (Crooks and Waring 2013; Hagood et al. 2023; Pratt 1979), and the Atlantic stingray (*Hypanus sabinus*; Lesueur 1824) (Kajiura et al. 2000). Whilst assumed (in the absence of direct experimental evidence) to relate to gynandric heterodonty, dermal thickening could theoretically have evolved to protect females from any of the weapons of sexual conflict discussed in here.

Besides dermal thickening, sexually antagonistic coevolution could also result in female chondrichthyans evolving modifications to the dermal denticles. Denticle morphology is extremely variable among species, across ontogeny, and across the body surface of chondrichthyans (Rubin et al. 2025). Principally, this variation is thought to relate to the hydrodynamic function of denticles (Ankhelyi et al. 2018), but it is also plausible that females could evolve larger, thicker, harder, or otherwise more protective denticles in body regions more likely to be targeted by males. Sexual dimorphism in denticle morphology in the lesser-spotted catshark *S. canicula* is consistent with this hypothesis, as the width and length of denticles is greater in females than in males, specifically in regions of the body where males have been observed gripping and biting females (Crooks et al. 2013). However, additional data from a greater range of species would provide more compelling evidence for the hypothesis that denticle dimorphism results from sexually antagonistic coevolution.

Although there is a compelling case for sexually antagonistic coevolution in chondrichthyans, we lack conclusive proof, and it is important to recognise that each of the female defence traits discussed above may also be influenced by other selective pressures (Gayford 2023). For instance, both dermal thickness (Schuitema et al. 2025) and denticle morphology (Ankhelyi et al. 2018) vary substantially among different shark ecomorphotypes. Further studies are required comparing denticle and dermis morphology between the sexes in species with and without gynandric heterodonty to determine the extent to which sexual dimorphism in these traits may result from antagonistic coevolution.

Female mate choice

Whilst male mate choice, often mediated by weapons of sexual conflict, is observed in some taxa, it is by no means ubiquitous (Janetos 1980). The presence of male sexual ornamentation in at least some elasmobranchs is important as it suggests that direct female mate choice may be common in this clade, by which females determine the outcome of potential copulation events. Female perspectives have previously been ignored in studies of chondrichthyan reproductive biology and evolutionary ecology (Lyons et al. 2021). It is typically assumed that males determine the outcome of potential mating events; the threat of sexual aggression by males results in females accepting undesirable males to avoid the infliction of costly mating wounds (Lyons et al. 2021; Pratt Jr. and Carrier 2001; Whitehead et al. 2022). This assumption is largely unfounded, however, and it ignores multiple

lines of evidence that female choice may be prevalent in chondrichthyans.

Firstly, sperm storage and multiple paternity have been reported in a range of elasmobranchs (Lamarca et al. 2020; Gayford and Flores-Flores 2024; Jordan et al. 2021), through which females may selectively fertilise their eggs with the sperm of only the highest 'quality' males (Orr and Zuk 2012). Sperm storage is a widely adopted and well-described mechanism of female choice across mammals, birds, and reptiles, in which fertilisation can be delayed until the highest quality males become available (Birkhead and Møller 1993; Orr and Zuk 2012). Given the prevalence of sperm storage in elasmobranchs (Jordan et al. 2021), it is reasonable to suggest that this form of female choice may also be commonplace in cartilaginous fishes. Similarly, observations of multiple paternity across most major chondrichthyan radiations (Gayford and Flores-Flores 2024) indicate that females of many species may be able to select sperm from specific mating events, avoiding indirect fitness costs associated with producing offspring born of poor-quality males.

Secondly, female elasmobranchs have been observed using a range of behavioural strategies to avoid mating events, including avoidance behaviours such as burial in the substrate and jumping out of the water, and resistance behaviours such as use of spines as a defensive weapon, shielding with the pelvic fins, and altering body pitch (Pratt Jr. and Carrier 2001). This indicates that females may be more than capable of escaping unwanted mating events, despite the sexual weapons possessed by males. Whether or not behaviourally-mediated avoidance of (and resistance to) males strictly classifies as female mate choice has long been the subject of debate (Carbone and Taborsky 1996), but ultimately it represents another mechanism by which females may dictate the outcome of potential copulation events.

Thirdly, and most pertinent to this review, bioluminescence in squaliform sharks may be an example of sexual ornamentation, meaning that female choice could be the predominant mating system in this clade. Comparative morphological studies and behavioural observations are not sufficient to prove complex evolutionary phenomena such as sexually antagonistic coevolution or female mate choice. However, in a clade where life history traits (e.g., late sexual maturation, rare mating events, and long-term sperm storage) and logistical issues effectively prohibit the necessary experimental studies, they represent important circumstantial evidence, indicating the presence of evolutionary dynamics similar to those observed in other taxa more amenable to experimental study.

Future directions

Perhaps the greatest limitation affecting our understanding of weapons of sexual conflict in Chondrichthyes is a lack of behavioural data. Whilst the simple fact that not all chondrichthyan taxa possess clasper spines, alar/malar spines, bioluminescence or gynandric heterodonty (Ebert et al. 2021) suggests that these structures altogether are not essential for successful copulation, direct evidence of coercive mating is scarce. Moreover, the potential for differences in reproductive success of efficiency between taxa with and without these structures remains to be examined. Indeed, behavioural observations of mating in chondrichthyans are rare (for examples, see Pratt and Carrier 2001; Berio et al. 2023), and all evidence of coercive mating is circumstantial (Ritter and Amin 2019; Whitehead et al. 2022). Observational studies of mating behaviour across a wide taxonomic range of chondrichthyan species are needed to conclusively prove that the armaments described in this review are weapons of sexual conflict.

Similarly, despite substantial morphological and physiological evidence that bioluminescence in sharks can act as a sexual ornament, a total absence of behavioural data heavily constrains our understanding of its usage in natural settings. Sexual ornaments in other taxa vary considerably in their usage from static coloration to multi-modal ornaments used in complex courtship rituals (Stafstrom and Heberts 2013; Zuk 1991). Ornaments also vary in their honesty, with some representing genuine signals of male quality (Gilbert and Uetz 2016; Tibbetts 2014) and others using sensory exploitation to increase the probability of mating (Amcoff and Kolm 2014; Arnqvist 2006). Where on these spectra each of the bioluminescent and biofluorescent chondrichthyan species lie cannot be determined without future study, both observational and experimental. Given the previous success of behavioural ecology experiments in *E. spinax* (Claes et al. 2010), this may be an ideal study

system with which to test these hypotheses regarding bioluminescence and biofluorescence.

More broadly, chondrichthyans present a major opportunity to study the impact of variation in reproductive mode and biology on mate choice and sexual selection. The reproductive biology of many species is well characterised (Carrier et al. 2004; Ebert et al. 2021). If sufficient quantitative data can be acquired, this would then provide the potential for comparative phylogenetic studies of sexual selection and mate choice. The taxonomic expansion of existing studies in the coming years should provide large-scale datasets of comparative morphology of putative sexual weapons and ornaments. In turn, these databases may enable quantification of the strength of post-copulatory sexual selection (e.g., Fitzpatrick et al. 2012; Leigh-Sharpe 1926; Moreira et al. 2017; Rowley et al. 2019). We are not aware of any existing empirical literature regarding mate choice in Chondrichthyes besides a single study, failing to find evidence of male mate choice (Almojil 2020). However, at least in the case of bioluminescent shark species, it should be possible to perform classic mate choice experiments using a similar protocol to studies focussing on teleost fishes (e.g., Bisazza et al. 2001; Kaneko et al. 2021).

Conclusions

There is a great scarcity of data regarding sexual selection and sexual conflict in cartilaginous fishes, which severely hampers our ability to fully examine the extent to which the traits outlined in this review represent true sexual ornaments or weapons of sexual conflict. However, several of these structures do not appear to be essential for successful copulation. In the case of putative sexual weapons, all are capable of inflicting substantial damage to females and closely resemble similar traits in other animals, where the dynamics underlying sexual conflict and sexual selection are better understood. Experimental and comparative studies are increasingly providing empirical evidence that bioluminescence in sharks may play a role in mate selection (Claes et al. 2015; Ellis and Oakley 2016), making it the best functionally trait covered in this review. Nevertheless, additional studies will be required to better resolve the functions of these traits, and the extent to which they may be morphological manifestations of coevolutionary arms races, as observed in other taxa (Arnqvist 2006; Arnqvist and Rowe 2002).

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