

Sexual selection in prehistoric animals: detection and implications

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Many fossil animals bear traits such as crests or horns that probably functioned as sexually selected signals or weapons. Interpretations of these structures as functioning in mate choice or intrasexual contests are often controversial, with interpretations based on biomechanics or physiology being favoured by many. Although testing hypotheses based on sexual selection can be difficult, especially given that there is no single, reliable means of recognising sexual selection, we argue that it is not impossible; indeed, there are now several cases where sexual selection is strongly supported. In other cases, a careful study of features such as sexual dimorphism, ontogeny, and allometry, coupled with testing of alternative hypotheses, will be necessary to distinguish between possible explanations for exaggerated features.

Introducing the problem: why is it difficult to recognise sexually selected traits in extinct animals?

Sexual selection, the process whereby traits are selected because they enhance mating or fertilisation success [1], is not a new phenomenon: ever since gametes diverged into eggs and sperm, their asymmetry in size has provided an opportunity for the operation of sexual selection. Sexual selection is not only responsible for much of the diversity in animal morphology and behaviour that we see today [2,3], but it is also a plausible explanation for many of the best known extravagant features found in extinct animals. Possible sexually selected traits are present across diverse fossil animal taxa (Figures 1 and 2): in some cases, such as the extinct giant deer *Megaloceros* [4], these have modern homologues, but many do not. This latter class includes traits such as the ‘spine-brush complex’ of the Palaeozoic stethacanthid sharks (Figure 1d) [5], the horns and frills of ceratopsian dinosaurs (Figure 1a) [6], the crests of many pterosaurs (Box 3, Figure 1b) and theropod dinosaurs [7,8], the long necks of sauropod dinosaurs [9], the long horns, sabre-teeth and other facial structures of palaeomerycid artiodactyls (Figure 1c) [10] and other fossil hoofed mammals, the lappets extending from the shell aperture in certain ammonite species (Figure 2b) [11], and the anterior spines and other structures found on a variety of trilobite

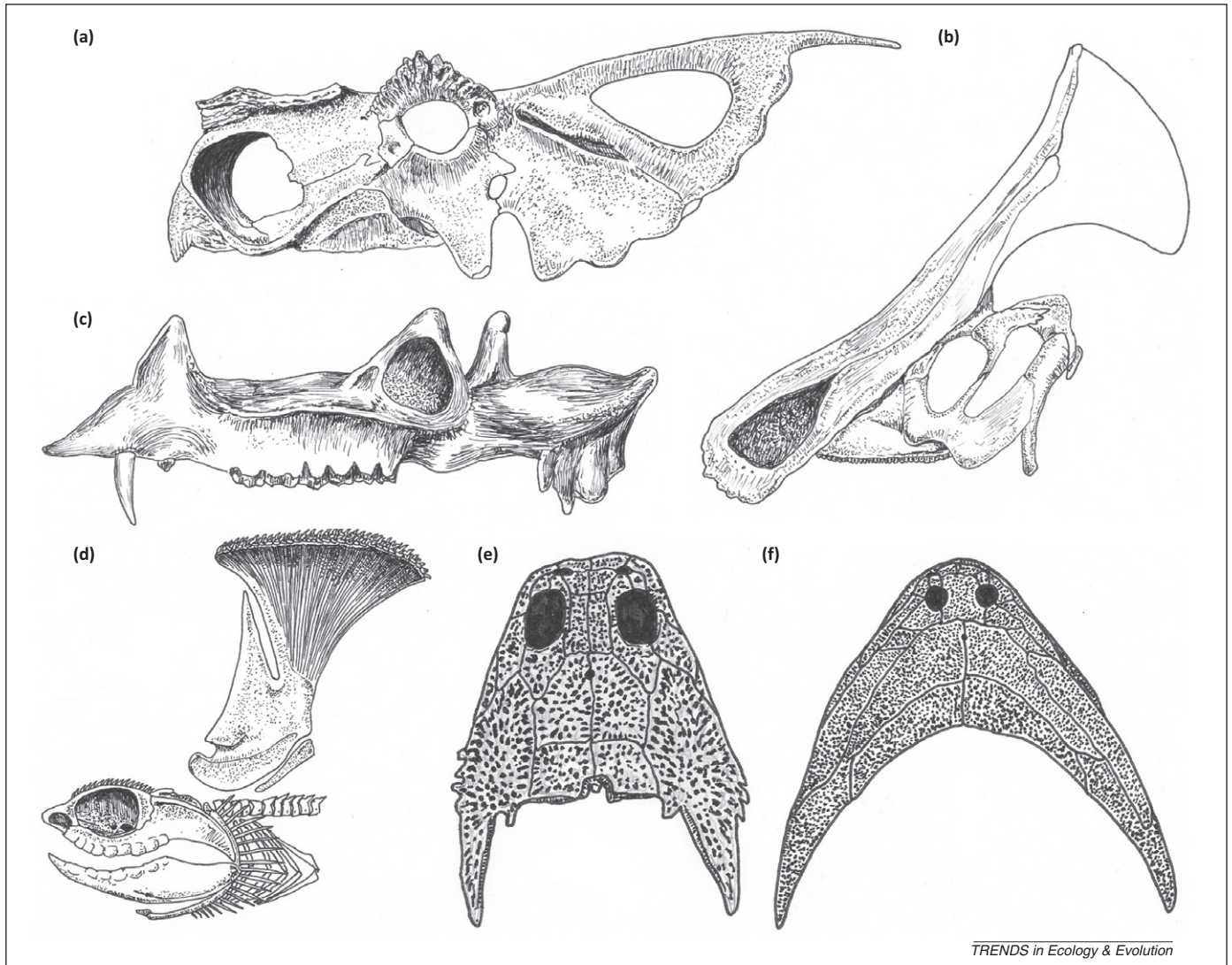
species (Figure 2a) [12]. In addition to these skeletal traits, recently discovered Mesozoic birds and bird-like dinosaurs have revealed a rich variety of feathered structures, some of which have been interpreted as having a possible function in sexual display (Box 1) [13].

Distinguishing sexually selected traits in extinct species from those that have arisen through other types of selection (i.e., viability and survival) is an important aim for two reasons: first, it will give insight into the evolution, reproductive biology, and behaviour of these extinct animals and second, it will allow us to test hypotheses concerning the importance of sexual selection in evolutionary processes such as speciation and extinction (Box 2). However, although there are some cases where a sexual selection role for a particular trait is well supported (Box 3), palaeontologists have historically been reluctant to use sexual selection as an explanation for the evolution of fossil traits. Indeed, substantial controversy remains over the role of sexual selection in generating exaggerated morphologies in palaeontological contexts: see, for example, recent discussions of the commonly held idea that the thickened skulls of pachycephalosaurian dinosaurs were used in head-butting contests analogous to those found in modern wild sheep [14–16], and the suggestion that the long necks of sauropods arose through sexual selection [9,17]. It has even been argued that the majority of extravagant traits in dinosaurs were not sexually selected at all, but had alternative functions, such as species recognition [18]. These controversies have their roots in the simple fact that convincingly demonstrating the role of sexual selection in the function of a fossil trait is normally extremely difficult, for several reasons.

Even in extant animals it is often difficult to assign a function to traits that might have arisen via sexual selection, even when the animal in question is common and well known. The so-called ‘necks for sex’ hypothesis, which proposes that the long neck of the giraffe arose through sexual selection [19], for example, remains controversial (see [20] for a summary of the arguments). Nonetheless, the function of traits in extant animals can ultimately be determined by behavioural observations and experiment, something that is clearly not possible for taxa known only from fossils. Assigning a sexual selection explanation to a trait simply because it appears unusual or lacks an obvious function is unwise: some extant animals exhibit traits

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Figure 1. Exaggerated morphologies in prehistoric vertebrates. (a) Skull of the Cretaceous ceratopsian dinosaur *Achelousaurus horneri* showing a rugose nasal boss, supraorbital horn, cheek flange, and ornamented frill; (b) the fan-shaped cranial crest of the Cretaceous hadrosaurid dinosaur *Olorotitan arharensis*; (c) skull of the Oligocene artiodactyl *Protoceras celer* with maxillary and supraorbital protuberances, a knob-like parietal protuberance, and enlarged upper canines; (d) head and anterior part of the body of the Carboniferous stethacanthid shark *Akmonistion zangerli* showing the 'spine-brush complex', a heavily modified dorsal fin; (e,f) skulls of two Palaeozoic amphibians from the order Nectridea: (e) the Carboniferous *Diceratosaurus brevirostris* showing tabular 'horns'; (f) enormous, back-swept 'horns' in the Permian species *Diplocaulus magnicornis*. Images not to scale.

Box 1. Sexual selection and the evolution of feathers

Extravagant feathers used in display are widespread in modern birds, and similar feathers present in some fossil birds have been interpreted on the basis of analogy as having probably evolved through sexual selection [84,90]. Probably the best example is provided by the elongate, paired tail plumes of the Cretaceous bird *Confuciusornis* [83]. These recall similar plumes in modern birds-of-paradise. Whether the tail plumes of *Confuciusornis* were unique to one sex is currently disputed [83,91–93]; however, as discussed in the main text, a lack of detectable sexual dimorphism does not itself constitute good evidence for a lack of sexual selection and, even if the species was sexually monomorphic, a sexual or sociosexual role remains the favoured interpretation.

In addition to fossil birds, feathers are now known from a variety of non-avian maniraptoran dinosaurs. Some of these are long, complex, and often arranged on the limbs and tail in a manner suggestive of a role in display. The Cretaceous oviraptorosaur *Caudipteryx*, for example, bore long, symmetrical feathers on its arms and the end of its tail [94]. Going further back in time, the

Jurassic scansoriopterygid *Epidexipteryx* bore two pairs of strikingly long tail plumes [13]. Neither of these species could fly, and display seems by far the most likely explanation for the function of these feathers. The putative sexual display role for such ornaments has been strengthened by recent finds of fossils of juvenile *Similicaudipteryx*, a close relative of *Caudipteryx*, which demonstrate that some of the plumage, especially on the arms, only developed in mature animals [95]. Analysis of melanosomes from some of these fossils has even revealed their in-life colours for some taxa: the reddish head crest in the small maniraptoran *Anchiornis* [96] and glossy black feathers in the long-feathered *Microraptor* [74] both imply a display function. The presence of putative sexually selected feathers in animals that did not themselves fly and that were (arguably) not descended from flying ancestors has implications for understanding the evolution of feathers generally: it is conceivable that feather size and complexity in maniraptorans was driven at least in part by a sexual display role, and that large feathers were an exaptation later modified for use in flight.

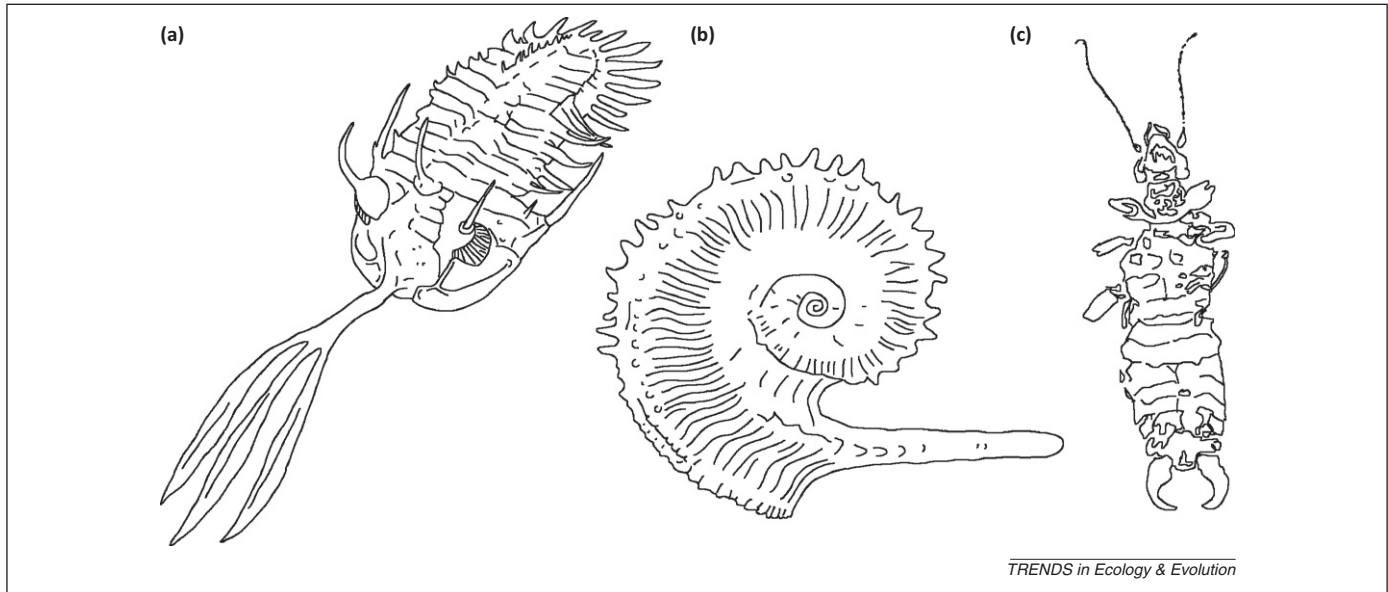


Figure 2. Exaggerated morphologies in prehistoric invertebrates. **(a)** The Devonian trilobite *Walliserops trifurcatus* with horns and ‘trident’; **(b)** the Jurassic ammonite *Kosmoceras* sp. with anteriorly directed lappet; and **(c)** the early Cretaceous fossil earwig *Cratoborellia gorbi* with enlarged caudal appendages. Images not to scale.

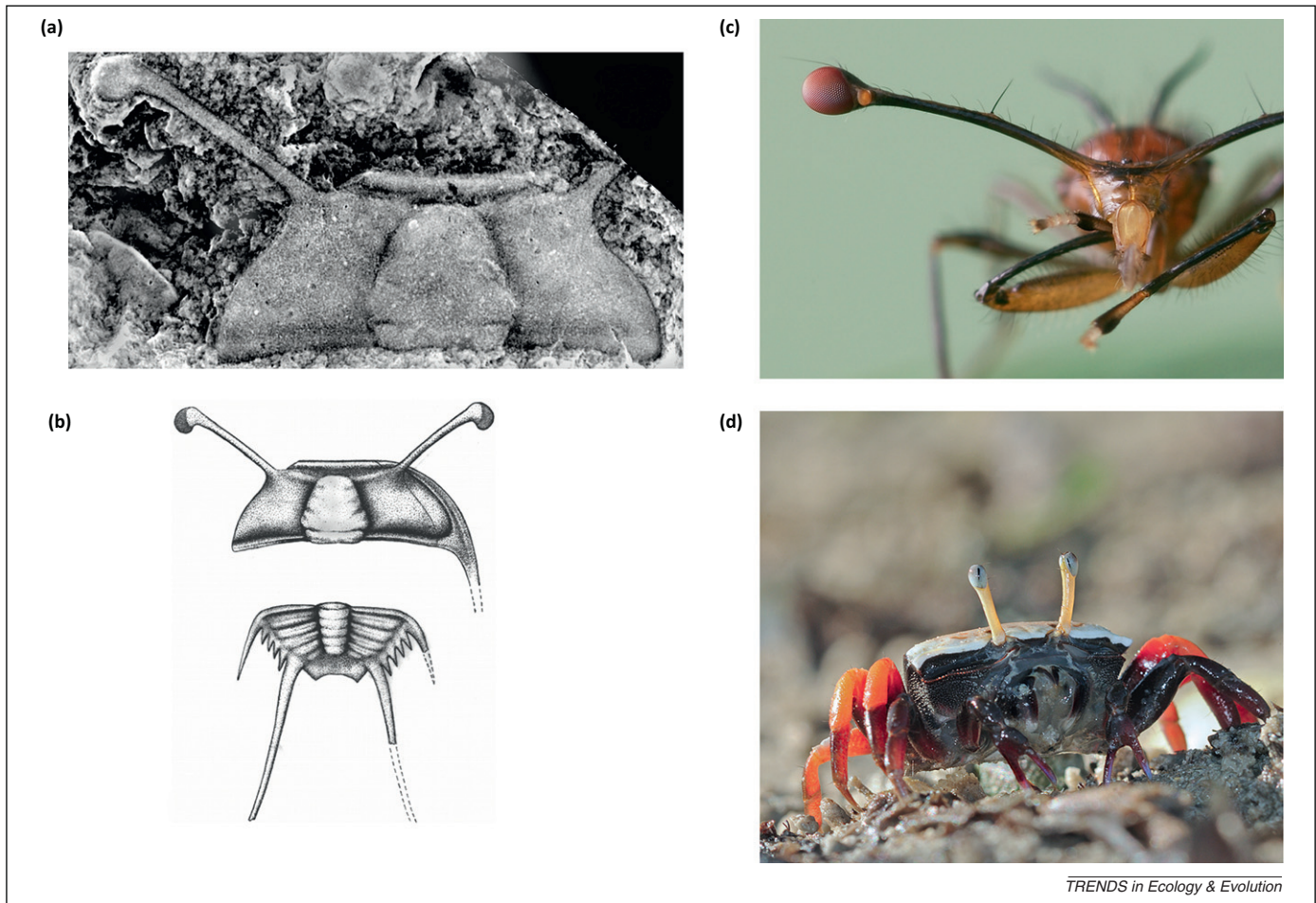


Figure 3. The problem with analogy: were trilobite eyestalks sexual signals or periscopes? Fossil cephalon **(a)** and reconstruction **(b)** of the Cambrian trilobite *Parablackwelderia luensis*, [97]. A variety of fossil trilobites carried their eyes on the ends of stalks that projected upwards, slightly forwards, and to the sides from an origin on the cephalon. These have usually been interpreted as adaptations enabling the animals to see, even while the rest of the body was buried in soft sediments [97,98]. Analogous structures are found in some decapod crustaceans that live in similar habitats: **(c)** a female fiddler crab, *Uca annulipes*, showing analogous structures. The function of these eyestalks in crabs is usually taken to be visual, but it is notable that there is a possible link between eyestalk length and mate search behaviour in these animals [99]. **(d)** Head and one eyestalk of the diopsid fly *Teleopsis dalmanni*. Some trilobite eyestalks are remarkably long, and it can be argued that the closest analogous structures in extant organisms are the eye-stalks of diopsid flies [97], which are widely recognised as being sexually selected structures [56]. It is possible that the eyestalks of trilobites such as *Asaphus kowalewskii* and *Parablackwelderia luensis* also functioned as sexual signals in the same way. The eyestalks of the latter species showed positive allometry during ontogeny, with young animals having relatively short, thick eyestalks and older animals carrying much longer and thinner ones [97], which is consistent with sexual selection being important in their evolution. Reproduced, with permission, from the Paleontological Society (a,b), Yan Leong (d) and R. Knell (c).

Box 2. Why should evolutionary biologists study sexual selection in extinct animals?

Sexual selection is one of the fundamental forces driving evolution: it is the primary mechanism behind some of the most remarkable features seen in animals alive today, is thought to be instrumental in determining rates of diversification [65], speciation [66], adaptation [67], and extinction [68], and has been proposed as a possible mediator of coexistence in similar species [69]. Much is controversial about its potential effects. As an example, it can be argued that sexual selection should lower extinction rates for two reasons: species with strong female choice for 'high-quality' males should adapt quickly to changing environments [68,70], and sexual selection should strengthen selection against deleterious mutations, therefore reducing inbreeding depression and protecting small populations [71]. Conversely, it can also be argued that growing and bearing costly signal traits will make a species increasingly prone to extinction [72]. Data are available to support both arguments [67,71–73].

These various phenomena have all been studied in extant animals, but the predictions involved can all be applied to

palaeontological data. Constructing phylogenies of taxa that vary in their expression of sexually selected traits might allow rates of speciation and extinction to be compared across phylogenetic nodes, and comparisons between taxa where all express sexually selected traits with ones that do not will allow tests of hypotheses about diversification. If sexual selection does indeed promote adaptation to changing environments [67], we can predict that sexually selected organisms should show lower extinction rates during times of rapid environmental change and at times of mass extinction.

Studying sexual selection in extinct organisms could also help understand the evolution of some important morphological features of modern animals. As discussed elsewhere (Box 1), long feathers or feather-like structures are known from Jurassic and Cretaceous birds and other dinosaurs, and it has been suggested that sexual selection played an important role in the evolution of feathers (see Box 1) [74], possibly paving the (run)way for the evolution of flight.

whose function would not be obvious from examination of dead or fossil specimens alone. These include the pectoral fins of flying fish, the rostra of sawfish and paddlefish, the narrow finger of the aye-aye, and the melon-supporting cranial crests of some dolphins. In order to determine the function of putative sexually selected traits, palaeontologists are left with homology and analogy (Box 4), comparing the extravagant structures of fossil animals with those of extant ones; and logic, assessing the presence and possible role of the extravagant structures in terms of what else is known about the organism, coupled with the testing of possible mechanical roles. This approach must be made carefully: the multifunctional nature of some sexually selected traits (for example, both bovid horns and fiddler crab claws are believed to play a role in thermoregulation [21,22]) means that even when a role that is not associated with competition for mates can be established, this is not necessarily sufficient to exclude sexual selection as an alternative.

Even when it is generally agreed that traits evolved under selection for display, which kind of display drove the selection process will often be unclear. In addition to sexual display to potential mates or rivals, signalling traits can also function in social selection of the sort discussed by West-Eberhard [23] and it is hard to distinguish between these when dealing with fossils. Others argue that species recognition [18] might explain extravagant trait evolution in fossil dinosaurs: see [6] and [24] for discussion of this argument, and [25] for a general criticism of the utility of the concept of species recognition as a discrete process that is qualitatively different from other aspects of mate choice.

Clearly, the role that sexual selection might have played in determining the form of exaggerated morphologies in fossil taxa remains controversial. Indeed, it will sometimes be impossible to ever determine with certainty whether a trait functioned in sexual selection (Figure 3). In general, the hypothesis that a trait in a fossil organism was driven to exaggeration through sexual selection raises a prediction that cannot be falsified: that increased expression of this trait led to greater fitness. Where does this leave scientists looking for testable hypotheses and looking to avoid just-so stories about sexual selection in extinct taxa? What are the characteristic features of traits that have

evolved under sexual selection, and which might be used to support hypotheses about sexual signalling traits in fossil organisms?

Characteristics of traits that have evolved under sexual selection

Sexually selected traits are a diverse group of morphological, physiological, and behavioural adaptations [3], ranging in extant taxa from massive weapons such as the horns of bovids and the mandibles of stag beetles, through extravagant and showy display features such as the feathers of birds-of-paradise, behavioural traits such as song, display, and the construction of nests or bowers (that themselves function as signals to members of the opposite sex) to internal adaptations such as enlarged testes, which give selective benefits via sperm competitiveness [26] or the complex genitalia of many insects [27]. Behavioural traits will obviously rarely leave evidence in the fossil record and internal structures such as genitalia will only be preserved in exceptional cases. However, weaponry and display traits are likely to be preserved, especially when there is a skeletal component. There is no single characteristic of such traits that gives a definitive diagnosis of a sexual display or combat function, but there are several features of these traits in modern taxa that can be used to support the sexual selection hypothesis in extinct forms. These include sexual dimorphism, changes during ontogeny, allometry, phylogenetic diversity, and costliness.

Sexual dimorphism

Sexual dimorphism is perhaps the most obvious phenomenon to look for when trying to assess whether a trait was sexually selected. Many taxa are profoundly sexually dimorphic and, in the majority of cases, this is associated with sexual selection. There are some exceptions: sexual dimorphism can also evolve through intersexual niche partitioning [28], as in the case of the sexually dimorphic bills of the recently extinct huia (*Heteralocha acutirostris*) of New Zealand [29], green woodhoopoes (*Phoeniculus purpureus*) [30], and in the body size dimorphism present in certain *Anolis* lizards [31]. Competition between females for resources can also lead to sexual dimorphism with females being ornamented, as in *Eclactus* parrots [32], or

Box 3. Pterosaur crests

Pterosaurs are an extinct group of flying reptiles closely related to dinosaurs. Pterosaur taxa, distributed right across the long Mesozoic history of the group, possess cranial crests. Some are composed entirely of bone, others entirely of soft tissues, and yet others involve soft-tissue components that grew on top of a bony core. Various functions have been proposed for pterosaur crests, including thermoregulation [75], as ‘rudders’ or ‘sails’ used in flight [76], and as a display feature. Two taxa (*Darwinopterus modularis* and *Pteranodon longiceps*) are of special interest in the context of sexual selection.

Darwinopterus is a small pterosaur from the Middle Jurassic of China, known from numerous specimens. Some individuals are crestless, whereas others possess bony crest located along the midline of the skull, which was probably associated with soft tissues that enlarged crest size substantially in life [77]. Crested specimens have a proportionally smaller pelvis and ventrally fused pelvic elements, whereas crestless specimens have an unfused, wider pelvis [78]. Furthermore, one crestless specimen has a pterosaurian egg preserved in close association with its pelvis and so is clearly a female [78]. Sexual dimorphism is clearly present: males have smaller

pelves and cranial crests, and females have wider pelves but crestless heads (Figure 1).

Similar dimorphism has also been documented in *Pteranodon*, a large, Late Cretaceous pterosaur from North America. Again, putative males are larger with a narrower pelvis; although both sexes have cranial crests, those of the males are considerably larger than those of the females [38,79]. Wind tunnel tests on model heads have shown no significant mechanical benefit to such structures [80]. Furthermore, crests were positively allometric, such that larger specimens had relatively much larger crests [7].

Therefore, evidence from two taxa strongly suggests that sexual selection was influencing cranial crest form in at least some pterosaur lineages. In *Darwinopterus*, clear evidence allows one specimen to be identified as female. The crests are sexually dimorphic, other features of the animals are sexually dimorphic, and, in *Pteranodon*, the male is larger overall. In *Pteranodon* at least there is evidence for positive allometry and no support for tested mechanical hypotheses. In the absence of any obvious modern analogues to explain cranial crest form in these animals, the traits are best explained as signalling structures, chiefly selected for by sexual selection operating on males.



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Figure 1. Sexual dimorphism in pterosaurs. (a) Female specimen of the pterosaur *Darwinopterus* preserved with an egg (arrowed) immediately outside the cloaca and (b) life reconstruction of the sexually dimorphic adult *Darwinopterus* showing the crested male and uncrested female (right). Photograph reproduced, with permission, from Lü Junchang and reconstruction reproduced, with permission, from Mark Witton.

carrying weapons, as is the case in the dung beetle *Onthophagus sagittarius* [33]. The extreme sexual dimorphism (manifested as male dwarfism) present in some clades, such as spiders and echiuran worms, has yet to be convincingly explained and ecological factors might play a more important role than sexual selection [34]. Dimorphic structures can also be indicative of different functions, as is the case in some extant bovids, where male horns are specialised for intraspecific dominance contests whereas female horns are better suited for antipredator defence [35].

Nonetheless, in the great majority of cases, sexual dimorphism in terms of either size or the exaggeration of one or more physical traits is likely to indicate a role in

sexual selection. In those cases where sexual dimorphism can be identified in palaeontological material, sexual selection is best regarded as the default hypothesis. While evidence for sexual dimorphism can cautiously be regarded as *prima facie* evidence for sexual selection, however, a failure to detect it does not rule out the presence of sexual selection. Identifying sexual dimorphism in animals known only as fossils is often difficult: specimens of a particular species are sometimes rare, unique, or unavailable, and reliably identifying sex in fossils is often difficult or impossible. In some cases, sexual dimorphism is subtle and requires large sample sizes of definitively sexed individuals to detect: although the long eye-stalks of diopside

Box 4. Homology and analogy

Homology

In fossil taxa with close extant relatives, it can often be inferred that the extravagant structures present in the fossil forms had the same role in sexual display as they do in the extant ones. The antlers of fossil deer and horns of fossil bovids, for example, were almost certainly used in courtship and advertising fitness [4]. Some insect taxa have retained traits for long periods that today function in sexual signalling or intrasexual contests: Cretaceous fossil earwigs (Dermaptera), for example, carry the enlarged abdominal forceps that are typical of their contemporary relatives [81] and the late Eocene diopsid fly *Prospyracephala succini* had sexually dimorphic eyestalks [82]. In such cases, sexual selection must be the primary explanation for the function of the trait.

Analogy

Even in those taxa without close extant relatives, analogy can suggest the function of some extravagant structures. The streamer-like tail feathers of some fossil birds (e.g., the Cretaceous form of *Confuciusornis*) have been interpreted as having a display function on the basis of their similarity to the ornamental feathers of modern birds [83,84], and the horns of ceratopsian dinosaurs invite comparison with the horns of bovids, chameleons, and other lizards [85,86]. Ceratopsian frills also recall the cranial frills present in chameleons. The horns and frills of chameleons and other iguanians function almost exclusively in sexual display and combat [87,88] and the horns of male bovids, similarly, are mostly used for this purpose [89].

Therefore, analogy with features of extant animals can be used to generate hypotheses about function, but it must be used with caution. Judging whether two structures are sufficiently similar to have probably had similar functions is obviously subjective, and a morphological similarity between two traits does not necessarily mean that they shared the same function. Figure 3 (main text) gives details of one difficult example: in the case of stalk-eyed trilobites, there are analogous structures that have both a 'natural selection' and a 'sexual selection' function; with current knowledge, we have no reliable way to distinguish between these potential explanations. Ultimately, a pluralistic explanation might be best: there are many cases of sexually selected traits that are also used for other purposes, and the proposed functions of trilobite eyestalks are not mutually exclusive.

flies have been known for centuries these animals were believed to be sexually monomorphic until the late 1920s because females also carry eyestalks, meaning that sexual dimorphism in this case is a matter of the size of the trait rather than its presence or absence [36]. Similarly, the sexes of the American alligator *Alligator mississippiensis* can be distinguished on the basis of pelvic morphology, but because there is substantial overlap between the sexes, this dimorphism required a large sample size to detect, and individuals cannot be sexed with certainty on this basis [37]. Alternatively, when dimorphism is strong, there is a risk that different sexes will be described as different species: this appears to have happened in *Pteranodon* [38] and most strikingly in the extinct moa *Dinornis*. Originally described from fossil remains as three separate species by Owen in the 19th century, extracted DNA sequences revealed in 2003 that the three species were in fact one, with the two larger 'species' being females and the smaller one males [39].

Even when there is genuinely no morphological difference between the sexes, sexual selection might still be in operation via the phenomenon of mutual sexual selection. This occurs when members of both sexes show mate choice and both exhibit sexually selected structures [40,41].

Mutual sexual selection has only recently been proposed as a mechanism to explain the exaggeration of non-dimorphic traits in extinct organisms [7,8,17] and has previously been largely overlooked by palaeontologists. This has led to the false conclusion that an absence of dimorphism means that sexual selection can be eliminated from consideration.

Changes in growth rate during ontogeny

Sexually selected traits are directly linked to reproduction and, as such, might not appear, or at least not be fully developed, prior to sexual maturity (note that sexual maturity is not necessarily coincident with skeletal maturity in vertebrates [42]). Rapid growth of extravagant structures late in ontogeny is predicted because, prior to sexual maturity, they would be unused and potentially costly to develop and maintain. This is seen in many sexually selected traits in extant animals (e.g., peacock feathers, deer antlers, and the enlarged claws of fiddler crabs). In fossil taxa, some extravagant structures do seem to have increased in relative size and/or changed form during ontogeny. Examples include the bony cranial crests of azhdarchoid pterosaurs [43] and hadrosaurian dinosaurs [44,45], and the horns and other structures of ceratopsian dinosaurs [46,47]. As with sexual dimorphism it must be remembered that changes in allometric slope during, or even late in, ontogeny are not necessarily exclusive to sexually selected traits, so such a change cannot be taken as definitive proof of sexual selection. Nonetheless, we have been unable to find an example of such a change in allometry from a non-sexually selected trait with the exception of the rostrum of the paddlefish, which is reported to change from positive to negative allometry as the animal reaches sexual maturity [48], the opposite direction that would be expected for a trait that evolved under sexual selection.

Positive allometry

It has been recognised for some time that many sexually selected traits exhibit positive allometry [49,50]; that is, where the trait increases in relative size as overall body size increases. Small sample sizes can sometimes generate relatively accurate estimates of the allometric slope, making this an attractive option for palaeontologists working with limited material [12]. However, positive allometry is not present across all sexually selected traits, and some non-sexually selected traits exhibit positive allometry [51]. Demonstration of positive allometry in a fossil trait does not, therefore, conclusively demonstrate that sexual selection acted on the trait in question, although it might be taken as supporting evidence when combined with other arguments.

However, many other hypotheses for the adaptive significance of a trait will generate specific predictions about allometry. Such predictions arise for biomechanical reasons, such as the weight-bearing capacity of bones [52], and the capacity of teeth to process certain types and volumes of food [53]. A different suite of predictions arise more purely from the laws of physics, and these can be used to generate predictions about aerodynamic and hydrodynamic performance and heat exchange [7]. These biomechanical and biophysical predictions are important because they

can provide a null hypothesis against which to test for departures in allometry that might be indicative of a history of sexual selection [7].

Therefore, to test the hypothesis that a particular trait is sexually selected, the best approach is not to simply estimate and report the allometric slope, but to construct a series of hypotheses about the function of the trait in question and to model the allometry expected under each hypothesis. These alternative hypotheses can then be tested, and the possible functions of the trait can then be matched to those that predict an allometric slope consistent with data. As an example, Tomkins *et al.* [7] were able to exclude both thermoregulation and use as a rudder as possible functions for the crest of *Pteranodon longiceps*; the allometric slope predicted for either of these functions was significantly less than the observed slope, leaving sexual selection as the best explanation for the crest (Box 3).

Morphological disparity

Some sexually selected traits show very high phylogenetic lability, being highly diverse between species and with the diversity in the sexually selected traits correlating only weakly with the phylogeny of the taxon in question. Examples from extant groups include the horns of *Onthophagus* dung beetles [54] and the plumage of manakins [55]. By contrast, some sexually selected traits show low diversity and are similar between all species in a taxon, as in diopsid flies [56]. In the case of insect genitalia, highly divergent morphologies are believed to arise from antagonistic co-evolutionary arms races between males and females [27]. When sexually selected traits are used in conflict between males for access to females, a similar process might well operate: Emlen [54] suggested that, if morphological novelty *per se* gave an advantage during contests, it could explain at least part of the morphological diversity present in beetle horns. When traits are selected by female choice, it has been proposed that highly divergent signalling traits within a clade are more likely to arise through Fisherian 'runaway' processes. Conversely, low diversity in signalling traits might be a consequence of their having evolved as 'handicap' traits [55].

Some putative sexually selected traits in extinct taxa, such as ceratopsian horns [18], also show highly divergent morphologies between species. In this case, the similarity with the morphological variation of beetle horns is striking, and antagonistic coevolution between individuals competing with conspecifics seems a probable explanation for the observed diversity. Thus, high morphological disparity of candidate sexually selected traits in fossil taxa can be taken to support a hypothesis of sexual selection. However, although a high degree of variation can be consistent with and indicative of a sexual signalling function for a trait, other hypotheses for such disparity must be considered and, conversely, low interspecific variability does not necessarily mean that a trait did not arise through sexual selection.

Costliness

Many traits used in sexual display or contests impose a considerable cost on the bearer. This costliness is an essential component of the 'handicap principle', which

maintains the honesty of sexual signals [57,58]. Costs can be manifested as resources required to grow and maintain sexual traits being unavailable for other fitness-enhancing traits [59], as well as locomotory and other costs arising from them [60]. Apparent costliness of traits in fossil animals does not necessarily mean that the trait in question arose through sexual selection [17], but it can be useful in rejecting other hypotheses for trait function when these do not predict that the traits should impose a cost on the bearer. As an example, both signaller and receiver benefit from species recognition signals and, in most cases, it is unlikely that there will be a benefit to deceiving the receiver of the signal. Such signals are not predicted to impose a cost on the bearer because there is no requirement to maintain honesty. On this basis, species recognition can be discounted as the prime function of many extravagant fossil traits [6].

Interpreting exaggerated traits

Some palaeontologists have preferred to interpret exaggerated morphologies as having had mechanical or physiological functions rather than as having arisen by sexual selection, probably because of the difficulty in convincingly demonstrating a role in sexual signalling or intrasexual contests for many such traits, as exemplified by this comment by Regal [61]:

However, sexual selection as a general evolutionary force, used to explain miscellaneous conditions that are difficult to account for, is unsatisfying. It can sometimes place the matter at hand beyond critical scientific tests, in as much as the hypothetical selection factors involve 'taste' and are virtually as limitless as imagination.

To an extent, we agree with this: sexual selection should not be used as a blanket explanation for any morphological anomaly that is hard to explain. The strong counter-argument to this point of view is that sexual selection is the most common selective force leading to the evolution of exaggerated traits in contemporary organisms and there is every reason to think that this was also the case in fossil organisms. When we look at prehistoric animals, the sheer extravagance and diversity of exaggerated structures, the general failure of 'functional' or mechanical explanations in many cases, and the similarity of fossil structures to those that function in sexual selection in extant animals, encourage ideas that they evolved primarily under sexual selection. Given the tremendous abundance of sexually selected traits in extant organisms, in fact, it seems obvious that sexual selection is the most parsimonious explanation for much of the diversity of exaggerated traits in fossil organisms. Discounting sexual selection as an explanation because it is difficult to test is likely to lead to many errors in understanding the biology of prehistoric animals.

Hypothesis testing

If we suppose that a given trait evolved under sexual selection pressure, it is important to note the constraints that pertain to hypothesis testing regarding the function of that trait. When a trait is hypothesised to have functioned as a weapon used in intrasexual combat, it is relatively

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easy to make specific predictions that allow the hypothesis to be tested. The potential role of the thickened skulls of pachycephalosaurian dinosaurs in head-butting contests, for example, leads to specific predictions about histology and anatomy [14,15], and the location of damage [16]. Similarly, a comparison of cranial lesions attributable to mechanical damage in the ceratopsian dinosaurs *Triceratops* and *Centrosaurus* found that *Triceratops* had a high frequency of lesions on the squamosal bone of the frill, with ten out of 58 specimens showing damage. This is the region of the frill where the two large supraorbital horns of *Triceratops* would be expected to engage with a conspecific during a contest: by contrast, *Centrosaurus* had very small supraorbital horns and only one of 62 specimens had a lesion on the squamosal bone [62].

However, when the proposed function of the trait is display, whether to rivals of the same sex or to potential mates, the lack of a specific mechanical or physiological function makes tests of specific hypotheses based on function difficult. In such cases, it is necessary to consider the possible alternative functions for the trait and to test them: the hypothesis of sexual selection will gain support if the trait shows some of the characteristics often found in such traits, including steep allometry, ontogenetic change, and sexual dimorphism, but will lose support if there are plausible alternatives. The logic for supporting sexual selection in this case is based on the rejection of probable alternatives, rather than testing hypotheses about the secondary sexual traits per se; something that can be challenging for researchers.

Multifunctionality

What of cases where a trait bears many of the hallmarks of a sexual signalling function, but where there are also other possible functions that cannot be discounted? In these cases it must be remembered that, as mentioned in the introduction, many structures in extant organisms are multifunctional, and there is no reason to think sexually selected traits in prehistoric organisms were different. As one example, the enormous, backswept cranial 'horns' of the extinct amphibian *Diplocaulus* (Figure 1f) might have functioned in mate choice or intrasexual signalling: a change in the allometric relationship for head width indicates a change in growth trajectory in adult animals, with the allometric slope for large adults being approximately two [63], a trajectory similar to that seen in condition-dependent signalling traits in extant taxa. Hydrodynamic studies of the head have indicated that it could have acted as a 'control surface' in moving water, enabling the animal to swim upwards at very steep angles and possibly allowing it to act as a mid-water ambush predator [64]. These two possible functions for the head of *Diplocaulus* are by no means mutually exclusive and, in the absence of further evidence, both must be considered when trying to explain its evolution.

Concluding remarks

Biologists seeking to explain the diversity of exaggerated morphologies and potential display traits found in prehistoric animals face a difficult task. Although some features are suggestive of a role in intrasexual contests or intersex-

ual signalling, there is no single definitive test to ascertain whether a trait was sexually selected: It is necessary to consider both evidence supporting a sexual selection role and evidence in favour of other functions. It is important to face the fact that, in many cases, researchers are limited by small sample sizes, and have little information on the biology of the organisms in question. Conclusive answers about behavioural and reproductive biology will be difficult to achieve. This means that in many, even most, cases from prehistory, understanding of the function of a particular trait will be probabilistic rather than definitive. Nevertheless, as documented here, there are strong lines of evidence that can be brought to bear on fossil taxa and the ability of biologists and palaeontologists to make strong inferences about sexually selected characteristics: this is neither a forlorn nor impossible task.

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