

astragalus of artiodactyls) indicates that these similarities represent homoplasies rather than synapomorphies.

The cotylar fossa (and associated enlarged medial malleolus), present in apheniscines and macroscelideans, is shared with hyracoids, proboscideans, tubulidentates, and their possible extinct relatives *Meniscotherium* and *Plesiorcyteropus*^{24–26}. Living members of this assemblage of mammals have been classified in Ungulata by morphological systematists, but in Afrotheria by molecular systematists. Presence of a cotylar fossa does not seem to be associated with any particular mode of locomotion, because it occurs in fossorial (*Tubulidentata*, *Plesiorcyteropus*) and scansorial (Hyracoidea) mammals, as well as in the cursorial/saltatorial macroscelideans. The cotylar fossa is also present in cercopithecoïd primates and macropodid marsupials^{25,27}, and is therefore not unique to potential afrotheres, but it is absent in most mammals, including other cursorial and saltatorial mammals. The broad functional but restricted taxonomic distribution of the cotylar fossa makes it a potentially significant indicator of phylogenetic affinities and argues for a relationship of apheniscines and macroscelideans to hyracoids, proboscideans and tubulidentates. The combination of dental and tarsal characters in apheniscines is most consistent with a relationship to Hyracoidea and Proboscidea, regardless of whether these taxa are classified in Afrotheria or a monophyletic Ungulata.

Identification of North American sister taxa to Macroscelidea suggests a North American origin for the order and a non-African origin for Afrotheria. Present evidence indicates that the restriction of Macroscelidea to Africa from the middle Eocene to the present is either relictual or (more likely) indicative of Palaeocene or Eocene dispersal to Africa. Therefore, the subsequent distribution of Macroscelidea no longer supports an African origin. Because Holarctic Palaeocene apheniscines and *Paschatherium* potentially represent the oldest known afrotheres, a non-African origin or relictual distribution is also implied for Afrotheria, a supposition supported by early non-African records of sirenians²⁸, proboscideans²⁹ and possibly tubulidentates³⁰. Neither possibility supports claims that Placentalia originated in Gondwana, which are based partly on the assumption of an African origin for Afrotheria⁴. This conclusion agrees with that of a recent phylogenetic analysis combining morphologic and molecular data that suggested paenungulate affinities for other North American ‘condylarths’⁷. □

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- Kingdon, J. *East African Mammals. Volume IIA: Insectivores and Bats* (Univ. Chicago Press, Chicago, 1974).
- Rathbun, G. B. The social structure and ecology of elephant-shrews. *Z. Tierpsychol.* **20** (suppl.), 1–77 (1979).
- Stanhope, M. J. *et al.* Molecular evidence for multiple origins of Insectivora and for a new order of endemic African insectivore mammals. *Proc. Natl Acad. Sci. USA* **95**, 9967–9972 (1998).
- Murphy, W. J. *et al.* Resolution of the early placental mammal radiation using Bayesian phylogenetics. *Science* **294**, 2348–2351 (2001).
- Asher, R. J. A morphological basis for assessing the phylogeny of the ‘Tenrecoidea’ (Mammalia, Lipotyphla). *Cladistics* **15**, 231–252 (1999).
- Whidden, H. P. Extrinsic snout musculature in Afrotheria and Lipotyphla. *J. Mammal. Evol.* **9**, 161–184 (2002).
- Asher, R. J., Novacek, M. J. & Geisler, J. H. Relationships of endemic African mammals and their fossil relatives based on morphological and molecular evidence. *J. Mammal. Evol.* **10**, 131–194 (2003).
- Archibald, J. D. Timing and biogeography of the eutherian radiation: fossils and molecules compared. *Mol. Phylogenet. Evol.* **28**, 350–359 (2003).
- Novacek, M. J. The skull of lepidictid insectivores and the higher-level classification of eutherian mammals. *Bull. Am. Mus. Nat. Hist.* **183**, 1–111 (1986).
- Novacek, M. J. & Wyss, A. Higher-level relationships of the recent eutherian orders: morphological evidence. *Cladistics* **2**, 257–287 (1986).
- Meng, J., Hu, Y. & Li, C. The osteology of *Rhombomylus* (Mammalia, Glires): implications for phylogeny and evolution of Glires. *Bull. Am. Mus. Nat. Hist.* **275**, 1–247 (2003).
- Hartenberger, J.-L. Hypothèse paléontologique sur l’origine des Macroscelidea (Mammalia). *C.R. Acad. Sci. II* **302**, 247–249 (1986).
- Simons, E. L., Holroyd, P. A. & Bown, T. M. Early Tertiary elephant-shrews from Egypt and the origin of the Macroscelidea. *Proc. Natl Acad. Sci. USA* **88**, 9734–9737 (1991).
- Butler, P. M. Fossil Macroscelidea. *Mamm. Rev.* **25**, 3–14 (1995).
- Tabuce, R., Coiffait, B., Coiffait, P.-E., Mahboubi, M. & Jaeger, J.-J. A new genus of Macroscelidea (Mammalia) from the Eocene of Algeria: a possible origin for elephant-shrews. *J. Vertebr. Paleontol.* **21**, 535–546 (2001).

- McKenna, M. C. & Bell, S. K. *Classification of Mammals Above the Species Level* (Columbia Univ. Press, New York, 1997).
- Archibald, J. D. in *Evolution of Tertiary Mammals of North America. Volume 1: Terrestrial Carnivores, Ungulates, and Ungulate-like Mammals* (eds Janis, C. M., Scott, K. M. & Jacobs, L. L.) 292–331 (Cambridge Univ. Press, Cambridge, 1998).
- Cifelli, R. L. The origin and affinities of the South American Condylarthra and early Tertiary Litopterna (Mammalia). *Am. Mus. Novit.* **2772**, 1–48 (1983).
- Gazin, C. L. A study of the Eocene condylarthran mammal *Hyopsodus*. *Smithson. Misc. Coll.* **153**, 1–90 (1968).
- Van Valen, L. M. New Paleocene insectivores and insectivore classification. *Bull. Am. Mus. Nat. Hist.* **135**, 217–284 (1967).
- Rose, K. D. The Clarkforkian land-mammal age and mammalian faunal composition across the Paleocene-Eocene boundary. *Univ. Mich. Pap. Paleontol.* **26**, 1–197 (1981).
- Jennings, M. R. & Rathbun, G. B. *Petrodromus tetradactylus*. *Mamm. Species* **682**, 1–6 (2001).
- Rose, K. D. Postcranial skeletal remains and adaptations in early Eocene mammals from the Willwood Formation, Bighorn Basin, Wyoming. *Spec. Pap. Geol. Soc. Am.* **243**, 107–133 (1990).
- Court, N. Limb posture and gait in *Numidotherium koholense*, a primitive proboscidean from the Eocene of Algeria. *Zool. J. Linn. Soc.* **111**, 297–338 (1994).
- MacPhee, R. D. E. Morphology, adaptations, and relationships of *Plesiorcyteropus*, and a diagnosis of a new order of eutherian mammals. *Bull. Am. Mus. Nat. Hist.* **220**, 1–214 (1994).
- Godinot, M., Smith, T. & Smith, R. Mode de vie et affinités de *Paschatherium* (Condylarthra, Hyopsodontidae) d’après ses os du tarse. *Palaeovertebrata* **25**, 225–242, plate 1–2 (1996).
- Szalay, F. S. *Evolutionary History of the Marsupials and an Analysis of Osteological Characters* (Cambridge Univ. Press, Cambridge, 1994).
- Savage, R. J. G., Domning, D. P. & Thewissen, J. G. M. Fossil Sirenia of the West Atlantic and Caribbean region. V. The most primitive known sirenian, *Prorastomus sirenioides* Owen, 1855. *J. Vertebr. Paleontol.* **14**, 427–449 (1994).
- Ginsburg, L., Durrani, K. H., Kassi, A. M. & Welcomme, J.-L. Discovery of a new Anthracobunidae (Tethytheria, Mammalia) from the lower Eocene lignite of the Kach-Harnai area in Baluchistan (Pakistan). *C.R. Acad. Sci. Ila* **328**, 209–213 (1999).
- Thewissen, J. G. M. Cephalic evidence for the affinities of Tubulidentata. *Mammalia* **49**, 257–284 (1985).

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Evidence that sensory traps can evolve into honest signals

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Conventional models^{1–4} explaining extreme sexual ornaments propose that these reflect male genetic quality^{2–4} or are arbitrary results of genetic linkage between female preference and the ornament¹. The chase-away model⁵ emphasizes sexual conflict: male signals attract females because they exploit receiver biases^{6–9}. As males gain control of mating decisions, females may experience fitness costs through suboptimal mating rates or post-copulatory exploitation. Elaboration of male signals is expected if females increase their response threshold to resist such exploitation. If ornaments target otherwise adaptive biases such as feeding responses^{8–10}, selection on females might eventually separate sexual and non-sexual responses to the signal. Here we show that the terminal yellow band (TYB) of several *Goodinae* species evokes both feeding and sexual responses; sexual

responsiveness phylogenetically pre-dates the expression of the TYB in males and is comparable across taxa, yet feeding responsiveness decreases in species with more elaborated TYBs. Displaying a TYB is costly, and thus provides an example where a trait arose as a sensory trap but has evolved into an honest signal.

We tested whether inappropriate female responses and increasing cost of male display ornaments^{11–13} promote the separation of sexual and non-sexual responses to ornaments using a signal found in some species of the Goodeinae, a group of viviparous fish endemic to Central Mexico¹⁴. The males of several species have terminal yellow bands on their tails, which in some species are made conspicuous by the presence of a black sub-terminal band. As the tail fin undulates, the TYB resembles a quivering yellow worm or larva, with a length, movement pattern and size similar to those of damselfly larvae. The TYB occurs in only a few species, but it may have evolved independently at least six times in the group (Fig. 1). The clade containing the most species with TYBs consists of the genera *Allophorus*, *Chapalichthys*, *Ameca* and *Xenotoca* (a polyphyletic genus¹⁴). We used one species of each of the above genera, except for the monospecific *Allophorus*, a large piscivore unsuitable for use in our experiments. We also used two species of the sister group (*Xenophorus captivus*, with a poorly marked TYB, and

Xenotoca eiseni, whose males lack TYB but have somewhat orange fins), and one species of the most basal Goodeinae genus (*Characodon audax*), the males of which have black tail fins and no TYB.

We quantified the conspicuousness of the TYB from its spectral curve. We then evaluated whether females of the different species showed preferences for males with conspicuous TYBs. In experiment 1 we first evaluated whether the TYB is a sexual ornament in the species where males possess a conspicuous TYB (*C. pardalis*, *X. variata* and *A. splendens*). We then evaluated female preference for an artificial (painted) TYB in all the species; this allowed comparisons of female sexual responsiveness to males with TYBs across different species, including those lacking a TYB. In experiment 2 we quantified female and male feeding responsiveness to TYBs. We also evaluated in one species (*X. variata*) whether the lack of feeding responsiveness to the TYB of their own species could be due to resistance, by exposing the fish to increasingly conspicuous TYBs. In experiment 3 we compared the response of *C. audax* to TYBs and to damselfly larvae. In experiment 4 we evaluated whether having a conspicuous TYB is costly by measuring damage to tails of male and female *A. splendens* kept in outdoor ponds, and subsequently assessing weight loss after fin clipping.

In experiment 1 we tested whether the TYB might have evolved

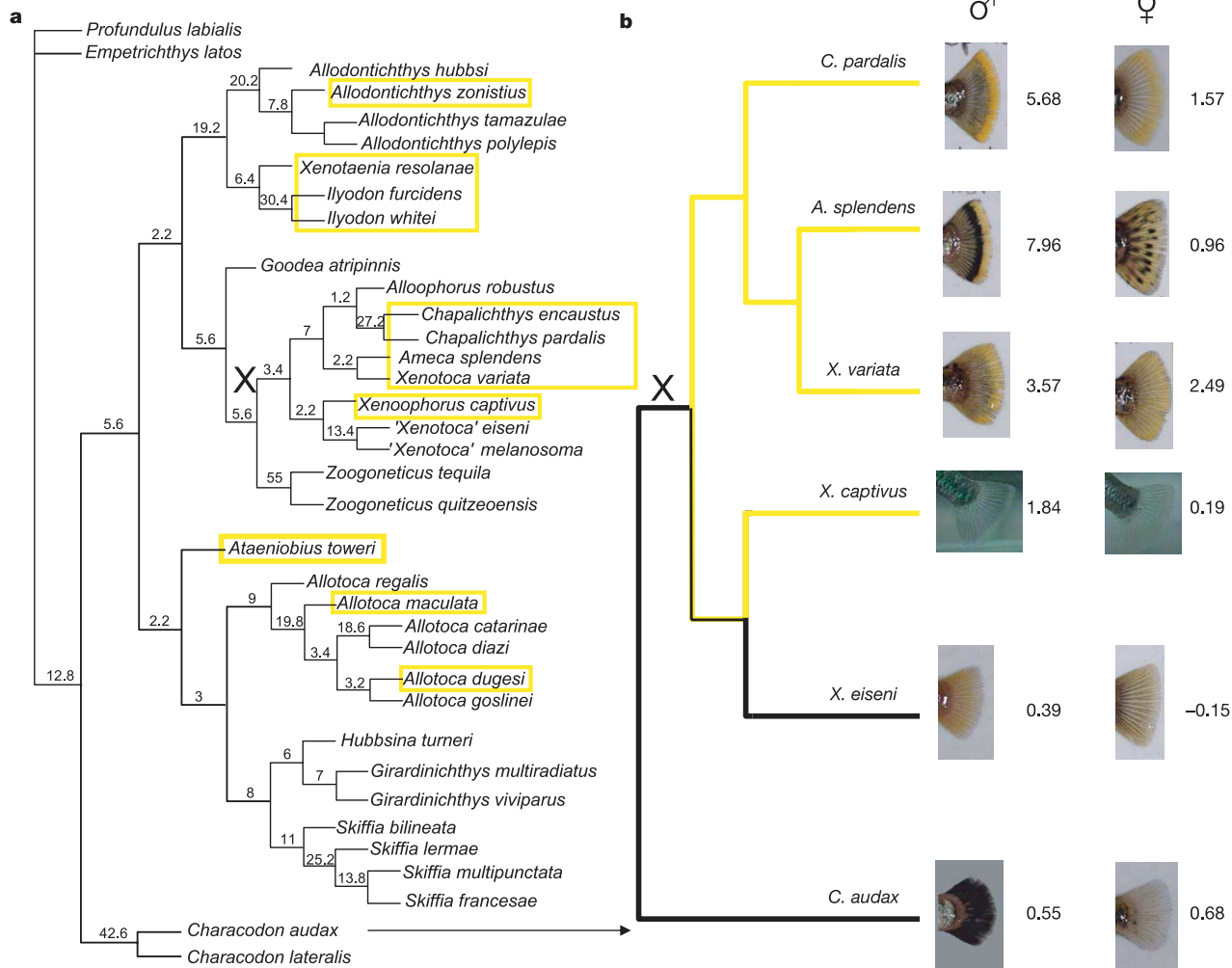


Figure 1 Tail terminal yellow band in Goodeinae. **a**, Occurrence of the TYB (yellow) in the Goodeinae phylogeny¹⁴; node support is indicated by decay indices. **b**, We used one species of each genus from the clade marked 'X' (except *Allophorus*) as well as *C. audax*. Parsimony suggests either seven independent origins of the TYB or six origins and one

loss (bicoloured lines show ambiguous ancestral state). Values next to the images of tails are measures of TYB elaboration derived from calculating the yellow contrast of the TYB in ten males and ten females of each species (see Supplementary Information).

through female choice. Females of all species spent significantly more time visiting the male with a conspicuous TYB than visiting the male with a plainer tail (Fig. 2). In species with a conspicuous TYB, preference for males with an artificial TYB was also significant. Thus, in the species studied, the preference for males with a TYB is universal and pre-dates the expression of the male attribute (Fig. 1). In experiment 2, designed to evaluate whether the TYB evokes foraging behaviour, females and males of species lacking a conspicuous TYB bit tails with conspicuous TYBs (Fig. 3). Fish of all species visited the tail with a conspicuous TYB more often and for longer periods, although this trend was only significant for those species lacking a conspicuous TYB (Fig. 3). Fish of all species except *X. variata* and *C. pardalis* directed bites at the TYB of male *X. variata* (or of conspecific males in the case of *A. splendens*) (Fig. 3). We also found that when confronted with more conspicuous tails from heterospecific males, *X. variata* made longer and more frequent visits, and directed more bites to the tail with the conspicuous TYB ($F_{(3,35)} = 3.03$, $P = 0.04$; see Supplementary Information). In experiment 3 we evaluated whether the tail edge of a species with a conspicuous TYB acts as a stronger feeding stimulus than a damselfly larva. Faced with a choice of a larva and a tail with a TYB, *C. audax* approached and attacked first the tail with the TYB ($\chi^2_1 = 7.2$, where subscript denotes d.f.; $P = 0.0073$), and only afterwards turned to the larva. In experiment 4 we verified that tails of male and female *A. splendens* were of similar size (tail length

given as mean \pm s.d.; male, 7.8 ± 0.4 mm; female, 7.4 ± 1.3 mm; $t_{11} = -0.85$, $P = 0.41$), and that the area of the measured band was also similar (mean \pm s.d.; male, 44.3 ± 5.6 mm²; female, 40.6 ± 14.1 mm²; $t_{13} = -0.80$, $P = 0.44$). Male tails were significantly more damaged than female tails; the damage was largely confined to the area of the TYB (mean damaged area \pm s.d.; male, 5.1 ± 2.5 mm²; female, 1.6 ± 1.2 mm²; $t_{14} = -4.06$, $P = 0.0012$). Males subjected to fin clipping lost weight in proportion to the amount of tissue regenerated, as evidenced by the negative association between the rate of weight change and the proportion of tissue regenerated ($r^2 = 0.34$, $F_{(1,10)} = 5.04$, $P = 0.049$; see Supplementary Information).

The conspicuous terminal yellow band of some Goodeinae evokes feeding responses in both males and females. Regardless of whether they mimic the shape and movement pattern of damselfly larvae or of another prey item, elaborated TYBs are powerful feeding stimuli. They probably evolved through exaggeration of prey attributes in order to retain female interest, given that conspicuous TYBs provide stronger stimuli than readily consumed larvae, and that fish of species with conspicuous yellow bands show reduced feeding responsiveness to TYBs than fish from species with poorly developed or absent TYBs. The decrease in female feeding responsiveness with increasing (conspecific) male ornament elaboration (Fig. 4), whether through an increase in response threshold (that is, resistance⁵) or because females evolve the ability to discriminate between the model (food) and the mimic (TYB), does not lead to a decrease in female responsiveness to males displaying a TYB. Instead, feeding disappears but the TYB still functions to attract females (Fig. 4). We suggest that selection has led females to disentangle the feeding and sexual responses, so that they remain responsive to a frequent prey item that would otherwise provide an insufficient stimulus if females merely increased their resistance to the signal produced by the mimic⁵. This solution may also permit females to incorporate a new criterion for mate choice¹⁵: the expression of an honest ornament in the form of a TYB. We did not quantify indirect fitness benefits for the females, but have shown that displaying a TYB entails costs in terms of damaging bites and regeneration expenditure. Another potential cost stems from the brightness of TYBs^{4,16}, which may require diverting carotenoids from other functions¹⁷.

Both the ornament and the responsiveness to it could, in principle, be present in both sexes^{10,18,19}. In fact, sex-limitation of the TYB is not universal, as both male and female *Chapalichthys* spp. have TYBs. Females in species with rudimentary TYBs and in species with the most conspicuous ornament (Fig. 1) lack a TYB. We suggest that this pattern arises because selection for males with TYBs in species with incipient markings (a condition probably represented by *X. captivus*) leads to conspicuous yellow bands in both sexes (as in *Chapalichthys* spp., Fig. 1). As the cost of displaying the TYB mounts, this promotes mechanisms that limit its expression in the females (such as *A. splendens*). A similar process may have led to the testosterone-determined control of the expression of orange spots in the trinidadian guppy (*Poecilia reticulata*)²⁰, and might be a mechanism of sex-limitation that contributes to the transformation of a sensory trap into a condition-dependent ornament²¹. On the other hand, feeding responsiveness to the TYB, when present, is similar in males and in females (Fig. 3). This may imply that males and females have roughly the same diet¹⁰ (if the visual system and related neural structures are not sexually dimorphic, which need not be the case²²). Female and male feeding responsiveness to TYBs decreased with TYB elaboration (Fig. 3). This may mean that both sexes face similar costs of responding to a food mimic. It is possible that such reduction in responsiveness is due to increased resistance to avoid manipulation (in females)^{23,24} or to avoid a maladaptive response (in males). One alternative is that the means to differentiate between food and the TYB evolved in both males and females. This would permit both

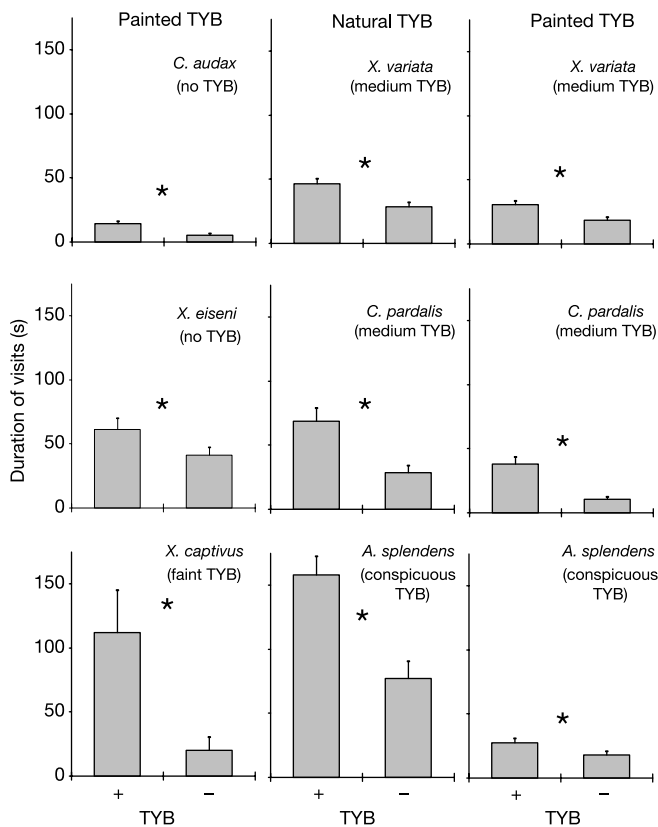


Figure 2 Female preference for males with elaborate TYBs. Preference for conspecific males with conspicuous (+) or inconspicuous (-) TYBs was assessed using either natural variation (central column; *X. variata*, *C. pardalis* and *A. splendens*) or artificial (painted) TYBs. Mean time spent next to each male during the 5-min trials (\pm s.e.m.) was contrasted using a balanced analysis of variance (ANOVA) design with three factors (treatment, pair of males, and female) for each species. Here we show only the results for the first factor (treatment: intensity of TYB; see Supplementary Information). Asterisks denote significant differences ($P < 0.05$).

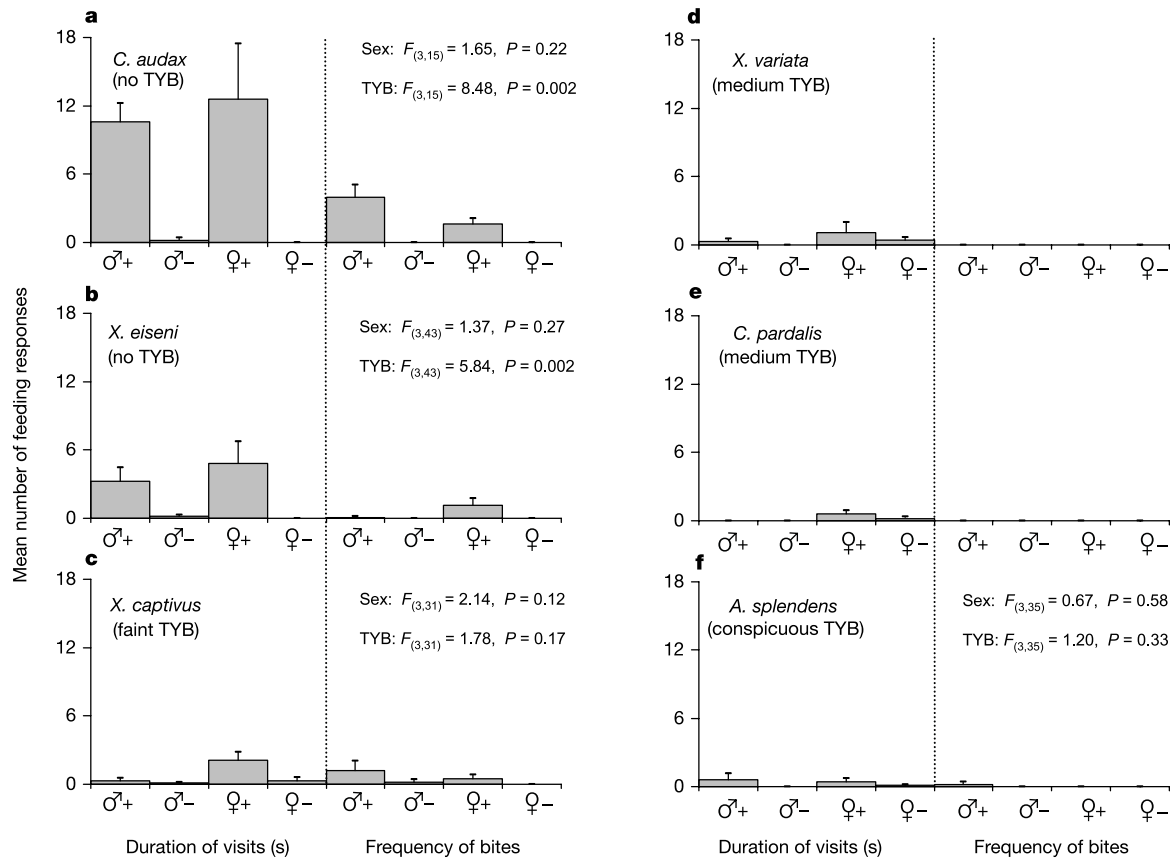


Figure 3 Feeding responsiveness to tails with (+) and without a TYB (-). Different pairs of tail-exhibiting *X. variata* (a-d) or *A. splendens* (e, f) were used in each trial, which involved the simultaneous observation of two focal fish. Differences in responsiveness (mean \pm s.e.m.) between TYB treatments (+ and -) and between sexes were

simultaneously compared using a two-way multiple analysis of variance (MANOVA) for each species. Dependent variables were frequency of bites, frequency of visits (not shown) and duration of visits (see Supplementary Information). Tests were not possible with *X. variata* and *C. pardalis* owing to an excess of 'zero' scores.

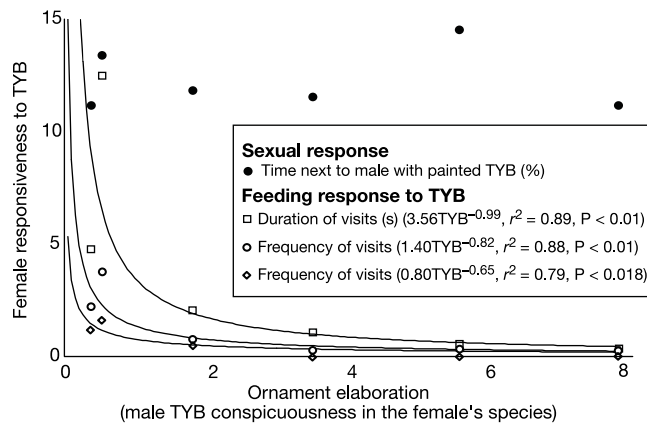


Figure 4 Female responsiveness and male ornament elaboration. Feeding responsiveness (open symbols) decreases significantly as ornament elaboration increases (male TYB conspicuousness in the female's own species; Fig. 1), whereas sexual responsiveness (to standard, artificial TYB; closed circles) remains significant and substantial across species. Instead of using the tails of *X. variata*, the TYB signal presumed to provide the strongest stimulus (*A. splendens*' TYB) was conservatively used to test feeding responses of species with conspicuous TYBs (*C. pardalis* and *A. splendens*). Strong sexual responsiveness across taxa suggests that ornament elaboration in clades with conspicuous TYBs retains a high level of female interest that cannot be explained by feeding responsiveness.

sexes to escape a sensory trap without compromising foraging efficiency. We recorded few feeding responses by male *A. splendens* to a TYB when presented next to a plain tail, but pilot trials showed that this species frequently bite the TYB in the presence of a damselfly larva, suggesting that additional stimuli are required to trigger feeding behaviour in species with conspicuous TYBs. Although we have no evidence for the mechanism involved, it seems that females in some species of this fish clade escaped a sensory trap⁹ while retaining sexual responsiveness to a male attribute that has become a costly signal. □

Methods

TYB conspicuousness

Ten males and ten females of each species were kept in outdoor ponds either on their own (*Ameba splendens*) or with other species (*X. eiseni*, *C. audax*, *X. captivus*, *C. pardalis* and *X. variata*; see Supplementary Information); a further ten male and ten female *C. audax* were collected shortly before trials. Fish were anaesthetized (using 20 ml of a 2% dilution of benzocaine in acetone per 100 ml of water) and laid on a white board. The reflectance spectra of the terminal and sub-terminal bands were measured using a Minolta CM-2600D spectrophotometer with pulsed xenon lamps (360–740 μ m). Spectra were used to calculate an index of TYB elaboration (see Supplementary Information). Recovery was accelerated using aeration and fin conditioner (Stress-Coat, Aquarium Pharmaceuticals).

Female sexual responsiveness

Fish were housed individually between trials. Responsiveness to natural TYB variation was investigated in *C. pardalis* ($n = 9$), *X. variata* and *A. splendens* ($n = 10$ each). These were exposed to 4 (*C. pardalis*) or 5 pairs of males of equal size but with contrasting TYB intensity (+ or -) as judged by two independent observers. Experimental tanks (50 \times 25 \times 25 cm deep aquaria) were divided into one female (25 \times 25 \times 25 cm) and two male compartments (12.5 \times 25 \times 25 cm, separated by mirrors to standardize the male social environment). Males of one pair were placed in their compartments, and each

female was exposed to them in turn. A female was placed in the centre of the female compartment within a plastic bag for 5 min, then released and the number and duration of visits (approaches within one body length) to each male was recorded for 5 min (a common index of mate choice^{25,26}, which correlates with mating probability in the goodeid *Girardinichthys multiradiatus*). She was then transferred to her home tank and a new female was tested until all had been exposed to that male pair. This was repeated on consecutive days until all females had been exposed to all male pairs. Position (left or right) of the TYB + male changed between pairs. Female preference in *X. captivus* (faint TYB) and *X. eiseni* and *C. audax* (no TYB) was assessed by painting an artificial TYB to one male of each pair using nail varnish. We proceeded as above but after completing the trials with a male pair, the treatment was reversed and all females were tested again. We used 10 females and 4 male pairs. This protocol was repeated, painting the tails of different species with conspicuous TYB (*A. splendens*, *C. pardalis* and *X. variata*).

Feeding responsiveness

Fish were kept without food for 24 h in the presentation tank, then exposed to two fish kept in green plastic boxes (4 × 2.5 × 2.5 cm) with adjustable walls that enabled only their tails to protrude. Boxes were hung at opposite sides of the tank, and gently rocked with a motor to stimulate tail movement. Before each trial, a partition hid the presentation boxes from the focal fish. Stimuli fish were one male with a conspicuous TYB and one female *X. variata* lacking a TYB (focal *C. pardalis* and *A. splendens* were exposed to *A. splendens* as stimuli). To minimize stress, stimuli fish were briefly exposed to a weak dilution of benzocaine and placed in the presentation boxes. The motor was then started and the partition was removed. Frequency and duration of approaches and frequency of bites to each tail were recorded for 10 min, then both focal and stimuli fish were replaced by new pairs, and the procedure was repeated until all fish had been tested. We also exposed *X. variata* to stimuli fish of species with more conspicuous TYBs (*A. splendens* and *C. pardalis*). Feeding responsiveness of *C. audax* (10 males and 10 females, tested in groups) to TYBs and damselfly larvae was assessed with a similar procedure, except that the male *X. variata* was presented alongside a damselfly larva (*Argia* sp.) of the same length as the male's TYB. We recorded which stimulus was approached first and which was bitten first.

Cost of the TYB

Digital images of tail fins of 11 male and 11 female *A. splendens* from outdoor ponds were measured using Paint Shop Pro v. 7. We traced TYB area, both bridging the gaps ('intact' band), and following the contour of tissue present (actual band). The difference measured the amount of tissue lost. Females lack a TYB but have a discontinuous black sub-terminal band seemingly homologous to the black sub-terminal band that limits the male TYB (Fig. 1). This was used in tracing the area of the female terminal band. The effect of fin regeneration on weight loss was evaluated by removing sections (23 ± 7.4%) of fin tail in 12 anaesthetized males. These were kept in individual 40-litre aquaria under controlled conditions (including equal feeding opportunity and antibiotics), and were measured, photographed and weighed weekly for two months.

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1. Fisher, R. A. *The Genetical Theory of Natural Selection* 146–156 (Dover Publications, New York, 1958).
2. Anderson, M. Evolution of condition-dependent sex ornaments and mating preferences: sexual selection based on viability differences. *Evolution* **40**, 804–816 (1986).
3. Hamilton, W. D. & Zuk, M. Heritable true fitness and bright birds: a role for parasites? *Science* **218**, 384–387 (1982).
4. Milinski, M. & Bakker, T. C. M. Female sticklebacks use male coloration in mate choice and hence avoid parasitized males. *Nature* **344**, 330–333 (1990).
5. Holland, B. & Rice, W. R. Chase-away sexual selection: antagonistic seduction versus resistance. *Evolution* **52**, 1–7 (1998).
6. Ryan, M. J. Sexual selection, sensory systems and sensory exploitation. *Oxf. Surv. Evol. Biol.* **7**, 157–195 (1990).
7. Ryan, M. J. & Keddy-Hector, A. Directional patterns of female mate choice and the role of sensory biases. *Am. Nat.* **139**, S4–S35 (1992).
8. Dawkins, M. S. & Guilford, T. Sensory bias and the adaptiveness of female choice. *Am. Nat.* **148**, 937–942 (1996).
9. Endler, J. A. & Basolo, A. L. Sensory ecology, receiver biases and sexual selection. *Trends Ecol. Evol.* **13**, 415–420 (1998).
10. Rodd, F. H., Hughes, K. A., Grether, G. F. & Baril, C. T. A possible non-sexual origin of mate preference: are male guppies mimicking fruit? *Proc. R. Soc. Lond. B* **269**, 475–481 (2002).
11. Kokko, H., Brooks, R., McNamara, J. M. & Houston, A. I. The sexual selection continuum. *Proc. R. Soc. Lond. B* **269**, 1331–1340 (2002).
12. Kokko, H., Brooks, R., Jennions, M. D. & Morley, J. The evolution of mate choice and mating biases. *Proc. R. Soc. Lond. B* **270**, 653–664 (2003).
13. Cordero, C. & Eberhard, W. G. Female choice of sexually antagonistic male adaptations: a critical review of some current research. *J. Evol. Biol.* **16**, 1–6 (2003).
14. Webb, S. A. *et al.* Molecular phylogeny of the live-bearing Goodeidae (Cyprinodontiformes). *Mol. Phylogenet. Evol.* **30**, 527–544 (2004).
15. LeBas, N., Hockham, L. R. & Ritchie, M. G. Nonlinear and correlational sexual selection on 'honest' female ornamentation. *Proc. R. Soc. Lond. B* **270**, 2159–2165 (2003).
16. Kodric-Brown, A. Dietary carotenoids and male mating success in the guppy: an environmental component to female choice. *Behav. Ecol. Sociobiol.* **25**, 393–401 (1989).
17. Olson, V. A. & Owens, I. P. F. Costly sexual signals: are carotenoids rare, risky or required? *Trends Ecol. Evol.* **13**, 510–514 (1998).
18. Partridge, L. & Parker, G. A. in *Evolution of Biological Diversity* (eds Magurran, A. E. & May, R. M.) 130–159 (Oxford Univ. Press, Oxford, 1999).
19. Basolo, A. L. Congruence between the sexes in preexisting receiver responses. *Behav. Ecol.* **13**(6), 832–837 (2002).

20. Jayasooriya, A. P., Weisinger, R. S., Weisinger, H. S., Mathai, M. L. & Sinclair, A. J. Attraction to orange: sexiness, not gluttony. *Science* **296**, 847–848 (2002).
21. Grether, G. F., Hughes, K. A. & Rodd, F. H. Response to Jayasooriya *et al.* *Science* **296**, 847–848 (2002).
22. Burton, B. G. & Laughlin, S. B. Neural images of pursuit targets in the photoreceptor arrays of male and female houseflies *Musca domestica*. *J. Exp. Biol.* **206**, 3963–3977 (2003).
23. Córdoba-Aguilar, A. Sensory trap as the mechanism of sexual selection in a damselfly genital trait (insecta: calopterygidae). *Am. Nat.* **160**, 594–601 (2002).
24. Holland, B. & Rice, W. R. Experimental removal of sexual selection reverses intersexual antagonistic coevolution and removes a reproductive load. *Proc. Natl Acad. Sci. USA* **96**, 5083–5088 (1999).
25. Ryan, M. J. & Wagner, E. Asymmetries in mating preferences between species: female swordtails prefer heterospecific males. *Science* **236**, 595–597 (1987).
26. Basolo, A. L. Evolutionary change in a receiver bias: a comparison of female preference functions. *Proc. R. Soc. Lond. B* **265**, 2223–2228 (1998).

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Genome-wide non-mendelian inheritance of extra-genomic information in *Arabidopsis*

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A fundamental tenet of classical mendelian genetics is that allelic information is stably inherited from one generation to the next, resulting in predictable segregation patterns of differing alleles¹. Although several exceptions to this principle are known, all represent specialized cases that are mechanistically restricted to either a limited set of specific genes (for example mating type conversion in yeast²) or specific types of alleles (for example alleles containing transposons³ or repeated sequences⁴). Here we show that *Arabidopsis* plants homozygous for recessive mutant alleles of the organ fusion gene *HOTHEAD*⁵ (*HTH*) can inherit allele-specific DNA sequence information that was not present in the chromosomal genome of their parents but was present in previous generations. This previously undescribed process is shown to occur at all DNA sequence polymorphisms examined and therefore seems to be a general mechanism for extra-genomic inheritance of DNA sequence information. We postulate that these genetic restoration events are the result of a template-directed process that makes use of an ancestral RNA-sequence cache.

We have recovered 11 point mutations at the *hth* locus⁶ that share the unusual property that they segregate phenotypically wild-type plants at a high frequency when homozygous mutant plants are allowed to self-fertilize. The frequency with which these 'revertant' plants are recovered varies, but is generally in the range of 10⁻¹ to 10⁻² revertants per chromosome per generation (Table 1). This is in stark contrast to most point mutations, which are completely stable (for example *erecta* (*er*) in Table 1). Because of the high frequency