

magnetic separation. A cpx-rich fraction was produced using a Frantz isodynamic separator; this fraction was hand-picked under a binocular microscope to obtain a 'pure' cpx fraction. Nd concentrations in cpx are as low as 50 p.p.b., and in general 100 mg of cpx was hand-picked. But this hand-picked fraction still contains some alteration products (distributed in a pattern similar to the crystal structure). Leaching experiments on the cpx separates found that hydrochloric acid at 100 °C removes this alteration to the point that the Nd isotopic composition is reproducible after only few hours of leaching. See also Snow *et al.*¹⁹. The Nd concentration in sea water and hydrothermal waters is low compared to those in cpx, and the effect of alteration on ¹⁴³Nd/¹⁴⁴Nd ratio is limited. However, the Sr content of sea water and hydrothermal fluids is much higher, and effects of alteration on the ⁸⁷Sr/⁸⁶Sr ratio are harder to remove. Cpxs from abyssal peridotites dissolve even if leaching is done with hydrochloric acid only, and only a limited amount of leaching can be done to attempt to obtain a pristine Sr isotopic composition. The cpx fractions were leached with sub-boiling double distilled 6 M hydrochloric acid at 100 °C for 24 h. This sometimes resulted in the removal of most secondary Sr. In almost all cases, leached cpxs have lower ⁸⁷Sr/⁸⁶Sr ratios than the leachates, and the reported values are upper limits for these samples. Dissolution and separation chemistry was performed using standard techniques.

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An early tetrapod from 'Romer's Gap'

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The fossil record of early tetrapods has been increased recently by new finds from the Devonian period¹ and mid-late Early Carboniferous period². Despite this, understanding of tetrapod evolution has been hampered by a 20-million-year gap ('Romer's Gap'³) that covers the crucial, early period when many key features of terrestrial tetrapods were acquired. Here I describe the only articulated skeleton of a tetrapod, *Pederpes*, yet found from the Tournaisian epoch (354–344 million years ago (Myr)). The new taxon includes a pes with five robust digits, but a very small, possibly supernumerary digit preserved on the manus suggests the presence of polydactyly. Polydactylous early tetrapods may have survived beyond the end of the Devonian and pentadactyly cannot be assumed for the pes. However, the pes has characteristics that distinguish it from the paddle-like feet of the Devonian forms and resembles the feet of later, more terrestrially adapted Carboniferous forms. *Pederpes* is the earliest-known tetrapod to show the beginnings of terrestrial locomotion and was at least functionally pentadactyl. With its later American sister-genus, *Whatcheeria*^{4,5}, it represents the next most primitive tetrapod clade after those of the Late Devonian, bridging the temporal, morphological and phylogenetic gaps that have hitherto separated Late Devonian and mid-Carboniferous tetrapod faunas.

Misidentified as a rhizodont fish on its discovery in 1971, recent preparation has revealed the specimen to be a tetrapod of about 650 mm in presacral length, lacking only a few parts of the skull, the tail, and some limb elements (Fig. 1a, b).

Spore analysis shows that the specimen dates from the late Tournaisian. Isolated limb and girdle elements from Horton Bluff in Canada are the only other tetrapod fossils known from this part of the Early Carboniferous²; this time period is otherwise remarkable for its lack of fossils from continental deposits. The recently described *Lacineria kiddi*² and the tetrapods from East Kirkton (for example, ref. 2) are Viséan, about 10 and 15 million years younger, respectively. *Pederpes* is the only Early Carboniferous tetrapod from western Scotland, extending the known geographical range of Early Carboniferous forms, but more importantly, it raises the possibility of further finds in this relatively unexplored area.

The specimen derives from the Ballagan Formation, which was laid down in a shallow-water environment, probably a lagoon or coastal flat that was subject to marked fluctuations in salinity and periodic desiccation⁶. The formation consists of pale grey, fine-grained nodular cementstones with calcareous mudstones and limestones⁷. The specimen is preserved in a clayey limestone nodule typical of a cementstone facies. Except for a few isolated rhizodont and actinopterygian scales, no other vertebrate fossils have been found in the area, so this tetrapod specimen appears to be an erratic. Fish and plant debris as well as *Spirorbis* shells are preserved in the nodule, the latter suggesting at least a marginal marine influence in the preservation of the animal.

Tetrapodomorpha Ahlberg, 1991
Whatcheeriiidae fam. nov.
Pederpes finneyae gen. et sp. nov.

Etymology. *Pederpes*, Peder after Peder Aspen, its discoverer (Peder is the Norwegian form of Peter, which is Greek for rock), and *erpes* (Greek for crawler), that is, 'rock crawler' (*Pederpes* can also be split into Peder and *pes* (foot), that is, 'rock foot'). *finneyae*, after S. M. Finney, who prepared the specimen.

Holotype. Hunterian Museum, Glasgow, GLAHMS 100815, an almost complete articulated skeleton in a clayey limestone nodule.

Locality. Auchenreoch Glen, near Maryland Farm, 2–3 km north of Dumbarton, Scotland.

Horizon and stratigraphy. Ballagan Formation, Inverclyde Group (formerly Cementstone Group, Calcareous Sandstone Series)^{6,7}; *claviger-macra* (CM) palynozone (possibly from the lower part of this zone); Tournaisian Tn3c, Courceyan, Dinantian, Lower Carboniferous.

Age. Ivorian, Early Carboniferous (348–344 Myr).

Diagnosis of family. Derived features include: narrow, steep-sided skull with orbit deeper than its width; massive tooth on maxilla about position 5 or 6; light dermal skull ornament; dorsal branch of mandibular lateral line running along surangular; very broad interclavicle with acutely angled lateral corners.

Primitive features include: grooved, denticulated parasphenoid; closed palate with denticulated surface; supratemporal-postparietal contact, fang pairs on vomers, palatines and ectopterygoids with a row of some smaller accessory teeth on each; row of coronoid teeth nearly continuous; at least some lateral lines in tubes through bone; rhachitinous vertebrae; no differentiated sacral neural arch, ilium with posterodorsal process and dorsal iliac blade.

Features of uncertain polarity include: supratemporal with deeply interdigitated suture to squamosal; small tabular with 'button' terminating in ornamented surface; steeply angled suspensorium with deeply excavated temporal notch, pronounced angle between skull table and cheek in transverse section; scapulocoracoid ossified in two portions; about 28 presacral vertebrae; trunk ribs with expanded distal flanges.

Diagnosis of genus and only known species. Whatcheeriid with the following apomorphies: trunk ribs with at least vertebrae

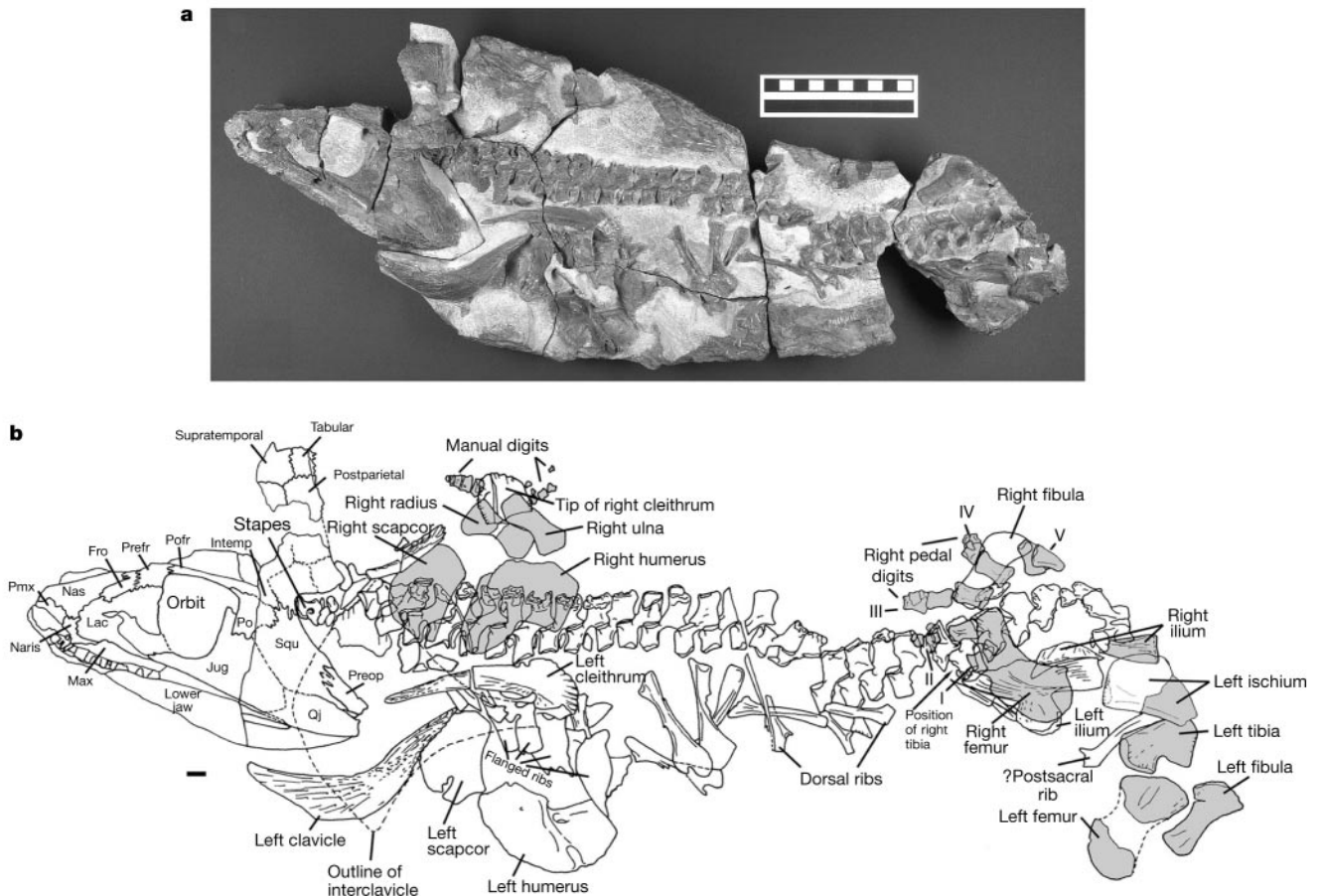


Figure 1 Holotype specimen of *Pederpes finneyae*. **a**, GLAHMS 100815 *Pederpes finneyae*, photograph of holotype and only specimen. Scale bar, 100 mm; **b**, Map of the holotype, showing elements preserved on the reverse in grey. Scale bar, 10 mm. Fro,

frontal; intemp, intertemporal; jug, jugal; lac, lacrimal; max, maxilla; nas, nasal; pmx, premaxilla; po, postorbital; pofr, postfrontal; prefr, prefrontal; preop, preopercular; qj, quadratojugal; scapcor, scapulocoracoid.

numbers 4–9 bearing accessory processes and/or foramina at dorsal edge of acutely triangular terminal expansions and about numbers 10–12 with flared ends; short presacral ribs with accessory processes; minute lateral-most digit on manus; deep striations on anterior edge and anterior region of external surface of stem of clavicle and cleithrum; ovoid dorsal blade of cleithrum with fimbriated edge.

The specimen is distinguished from *Whatcheeria deltae* by many details of the cranial and postcranial skeleton listed under Appendix 1 of the Supplementary Information.

Notable anatomical features of *Pederpes* include a primitive stapes most closely resembling that of the Devonian *Acanthostega*^{8,9} in a narrow skull with a deep wide temporal notch. It unequivocally dissociates such a notch from possession of a slender sound-conducting element (Fig. 2). The humerus has a spike-like latissimus dorsi process more like that of *Baphetes*¹⁰ than *Whatcheeria* or any other tetrapod, presumably convergently derived. The ribs bear expanded triangular flanges, a feature now found in a range of the earliest tetrapods. Those of *Pederpes* most closely resemble

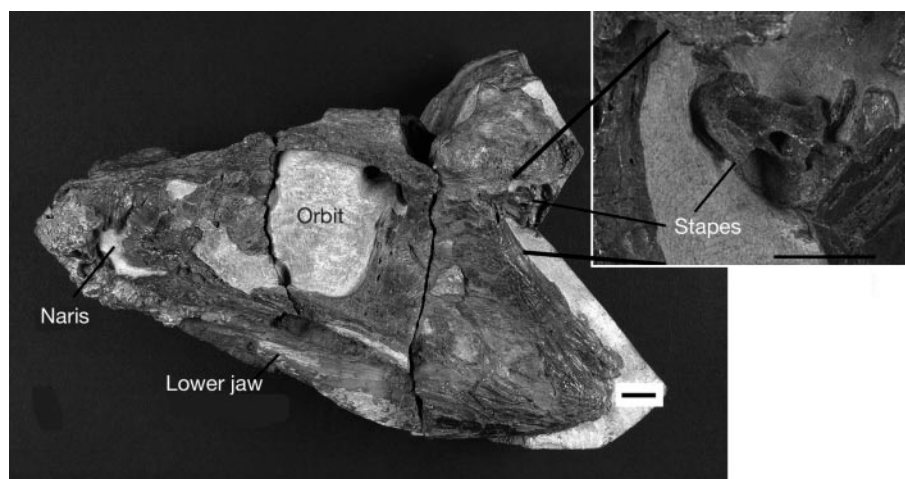


Figure 2 Close-up of the skull of *Pederpes* showing the stapes. Inset, stapes. Scale bars, 10 mm.

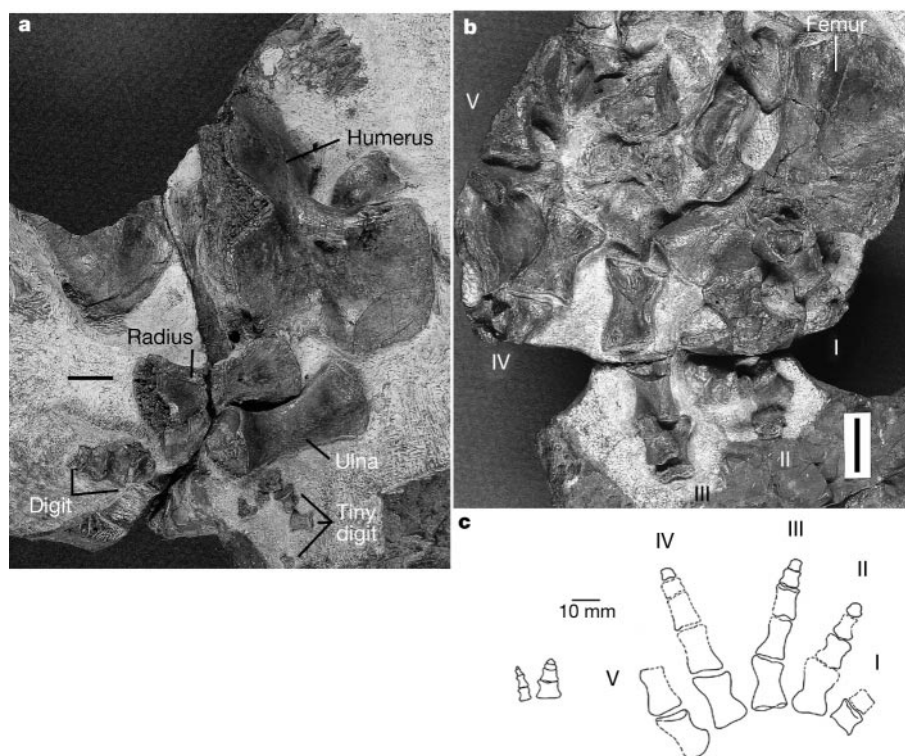


Figure 3 Manus and pes of *Pederpes*. **a**, Humerus, radius, ulna and manual digits from the right forelimb. The minute irregular elements at the base of the tiny digit might be remains of metacarpals. **b**, Pedal digits and femur from the right hindlimb, shown reversed. **c**, Reconstructions of manual (left) and pedal digits (right) of *Pederpes* to the same scale, showing tiny manual digit and asymmetrical metatarsals respectively. Scale

bar, 10 mm. In *Pederpes*, the phalanges of the tiny manual digits are about one-third the length of the pedal phalanges, whereas in *Acanthostega* and the Carboniferous forms such as *Greererpeton* and *Proterogyrinus*, manual phalanges are about one-half the length of the pedal phalanges.

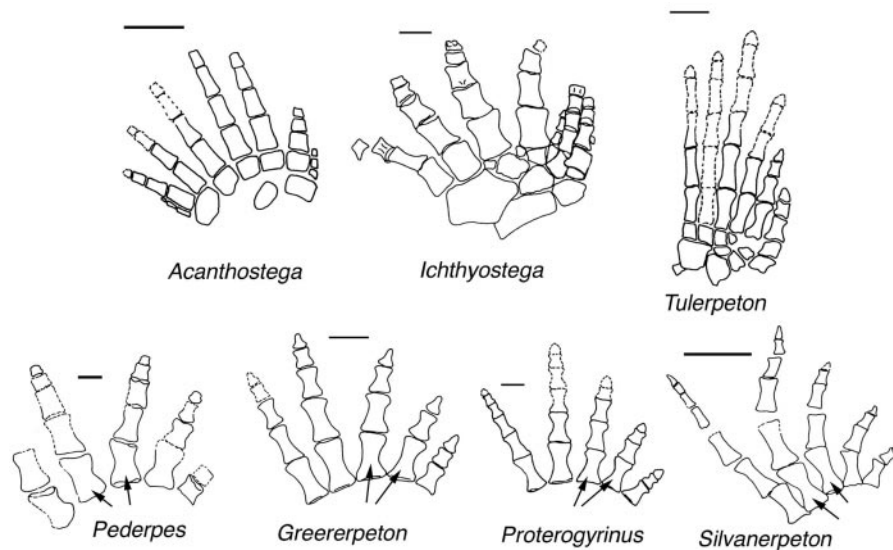


Figure 4 Reconstruction of peds of various taxa. *Pederpes*, *Greererpeton*, *Silvanerpeton* and *Proterogyrinus* show asymmetrical metatarsals (see arrows) compared with those of the Devonian forms *Acanthostega*, *Ichthyostega* and *Tulerpeton*. In *Acanthostega* and

Ichthyostega, the metatarsals are not clearly differentiated, and in *Tulerpeton*, if correctly interpreted, they are cylindrical but include some interarticulations. Scale bars, 10 mm.

those of *Ichthyostega*.

Two digits (only) are preserved on the right manus. One is short, broad and tapered, but the more remarkable is a tiny digit with three phalanges including an ungual, that presumably lay lateral-most on the manus. In its relative size, it most closely resembles the super-

numerary digits found on the limbs (especially the hindlimbs) of the polydactylous Devonian tetrapods^{11,12} (Figs 3 and 4). *Pederpes* conceivably retained a polydactylous manus, suggesting that polydactylous early tetrapods survived into the Carboniferous.

The pes of *Pederpes* preserves a complement of five digits, three of which are complete. Although there is no evidence for more than five digits (Fig. 3b, c), recent understanding of early limb evolution and the existence of the tiny manual digit preclude firm assumptions of pentadactyly in this early tetrapod. No complete manus or pes is known for *Whatcheeria*, and that animal also cannot be assumed to have been pentadactylous. However, the pes of *Pederpes* is closely comparable with those of later Carboniferous tetrapods, especially *Greererpeton*, in its proportions and numbers of phalanges (Fig. 4). It shares a feature otherwise seen only in the pentadactylous forms such as *Greererpeton*¹³, *Silvanerpeton*¹⁴ and *Proterogyrinus*¹⁵, which are assumed to be at least partially terrestrial: they have clearly distinguishable metatarsals that are bilaterally and proximodistally asymmetrical (Fig. 4). This feature may be associated with realignment of the foot from a lateral orientation as in the paddle-like limbs of Devonian forms, into an anteriorly directed stance associated with walking. Thus the pes of *Pederpes* shows an adaptation otherwise known only in pentadactylous forms, and is the earliest form to show what later becomes an established pattern of foot construction.

A phylogenetic analysis shows the whatcheeriids to be the next most primitive clade of tetrapods after those of the Devonian, a position congruent with both the stratigraphic position and the morphology of the animals. As well as showing the beginnings of terrestrial locomotion, *Pederpes*, with its sister taxon *Whatcheeria*, provides a view of the preconditions leading to the tetrapod crown group, whose origins are unclear. □

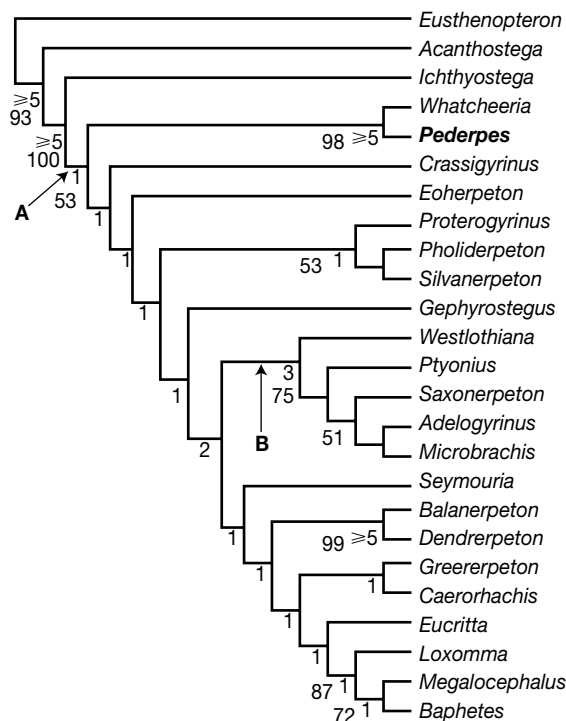


Figure 5 Single most parsimonious tree showing the whatcheeriids to be the next most crownward stem tetrapod clade after the Devonian forms. Nodes A and B show possible origins of the crown group. Bremer support indices are shown for most nodes, and bootstrap values are given for each node supported by more than 50%.

Methods

A phylogenetic analysis using 25 taxa and 141 characters was carried out using PAUP 4.0b (ref. 16) and MacClade 3.04 (ref. 17). A range of early tetrapods was analysed including several 'lepospondyl' taxa and the possible stem amniote *Westlothiana*. The analysis recovered a single most parsimonious tree (MPT) with length 484, consistency index 0.393, retention index 0.561, and rescaled consistency index 0.220. Bremer support values for most nodes and bootstrap values for the best-supported nodes are shown (Fig. 5). Despite the low consistency index, a permutation tail-probability test (PTP) using the PAUP program (10,000 replicates) showed that the data matrix contains a signal

statistically significant (P -value of 0.0001) relative to randomized data, and is thus phylogenetically informative.

The single most parsimonious tree shows the whatcheeriids to be the next most primitive clade after the Devonian forms, with this node supported better than many others in the tree. This analysis produces an unexpected crown topology in some respects, although the data set was designed to explore the relationships of the basal taxa rather than of those more crownward. The three most basal nodes of the tree are robust, but many of the more crownward nodes are only weakly supported, reflecting the radically different views of early tetrapod relationships that have recently been published (compare refs 12, 18–23). According to different analyses, the crown group node could originate as deep as node A (for example, ref. 19) or as crownward as node B (for example, ref. 20); thus the whatcheeriids lie at the base of the most inclusive definition of the crown group clade. Deletion of the taxa above node B does not significantly affect the topology of the rest of the tree, but deletion of the whatcheeriids or the enigmatic genus *Caerorhachis* recovers a grouping including embolomeres plus *Gephyrostegus* and *Eoherpeton*, the traditional ‘anthracosaurs’. A reverse constraint analysis was undertaken to test how strongly the basal position of whatcheeriids is in relation to ‘other tetrapods’ apart from Devonian forms. In this test, all other tetrapods above the whatcheeriids were defined as being monophyletic. PAUP was then asked to find the shortest trees under the reverse constraint, in which ‘other tetrapods’ was not monophyletic. Nine trees four steps longer than the MPT (length 488) were recovered, with the common property of placing *Crassigyrinus* as the next most primitive taxon after the Devonian forms. Eight of these recovered a monophyletic grouping of the traditional ‘anthracosaurs’. A Templeton test reveals no statistically significant difference between the MPT and those recovered in the reverse constraint analysis. *Whatcheeria* and *Crassigyrinus* were originally described as ‘protoanthracosaurs’²⁴, but this may result from the presence of many primitive characters in the traditional ‘anthracosaurs’, whose relationships are in need of review.

See Appendices 1–4 of the Supplementary Information for further diagnosis of *Pederpes* (Appendix 1), source data (Appendix 2), the data matrix (Appendix 3) and the character list (Appendix 4).

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A host–parasite interaction rescues *Drosophila* oogenesis defects

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The cytoplasmically inherited bacterium *Wolbachia pipientis* is a widespread parasite of arthropods that manipulates the reproductive biology of its hosts, often to their detriment, in order to foster its own transmission through egg cytoplasm^{1,2}. Here we report that infection by *Wolbachia* restores fertility to *Drosophila melanogaster* mutant females prevented from making eggs by protein-coding lesions in *Sex-lethal* (*Sxl*), the master regulator of sex determination. Suppression of sterility by *Wolbachia* discriminates markedly among similar germline-specific *Sxl* alleles, and is not observed for mutations in other genes that produce similar ‘tumorous ovary’ phenotypes, including one that blocks *Sxl* germline expression. This allele and gene specificity indicates that suppression probably results from a specific interaction with *Sxl* protein, rather than from a bypass of the normal germline requirement for this developmental regulator or from an effect on *Sxl* expression. The *Sxl*–*Wolbachia* interaction provides a rare opportunity to explore host–parasite relationships at the molecular level in a model insect. Furthermore, demonstration that a parasite infection can counteract the deleterious effects of mutations in host genes illustrates how hosts might become dependent on parasites.

Because *Wolbachia* depends on obligate maternal transmission, it manipulates the reproduction of its host to increase the number of infected females³. Reproductive phenotypes caused by *Wolbachia* infection include parthenogenesis⁴, feminization⁵, male killing⁶, and cytoplasmic incompatibility (inviability of offspring from a mating of infected males with uninfected females)⁷. These effects can skew sex ratios and may even promote speciation⁸. Although *Wolbachia* infection generally has no obvious benefit to the host, the parasitic wasp *Asobara tabida* can be considered an exception. In a remarkable natural parallel to the laboratory phenomenon described here, *Asobara* requires *Wolbachia* infection for oogenesis⁹. Little is known about the mechanisms *Wolbachia* uses to affect reproduction, in part because the host species that display strong phenotypes have not been readily amenable to genetic analysis. Although infection in *D. melanogaster* has been reported to cause low levels of cytoplasmic incompatibility¹⁰ and a shortening of adult life span¹¹, suppression of mutant *Sex-lethal* alleles that we report here represents a robust phenotype for *Wolbachia* infection in this model organism.

Sex-lethal (*Sxl*) is an X-linked, female-specific master switch gene that controls somatic sex determination and the vital process of