

contrasting geochemical pattern in lavas from the SVZ and the AVZ, reflecting clear differences in petrogenesis to the north and south of the Chile triple junction. In the SVZ, variable enrichment of ^{238}U , but uniform La/Yb, are attributed to slab-derived fluids and mantle melting (Fig. 3), whereas in the AVZ, the uniform ^{238}U deficiency but high and variable La/Yb could result from ~20% partial melting of the young and heterogeneous, subducted, Antarctica plate.

The compositional similarities of adakites and Archaean trondhjemites suggest that the early continental crust is likely to have been generated, at least in part, by partial melting of young and hot subducting oceanic lithospheres^{4,6,16,20}. Progressive cooling of the Earth has led to the subduction of older and cooler slabs which, on dehydration, produce fluids that provoke partial melting of the mantle wedge. This generally results in basaltic addition to the continental crust. However, the results from the AVZ suggest that adakites may have been added to the continental crust throughout Earth's history wherever a sufficiently young and hot oceanic crust was subducted. □

Received 8 May 1997; accepted 11 May 1998.

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Acknowledgements. We thank C. Stern and R. Kilian for the samples, M. Condomines, J. Gill, A. Hochstaedter, M. Schmidt and D. Vielzeuf for discussions, and J. Morris and S. Turner for reviews.

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A complete primitive rhizodont from Australia

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Studies of the origin^{1–3} and developmental genetics^{4–7} of tetrapod limbs have focused attention on the need to identify the precise type of sarcopterygian (lobe-finned fish) fin from which limbs evolved. This can only be achieved through a phylogenetic analysis of sarcopterygians. Sarcopterygian fin skeletons vary in structure^{8,9}; use of an inappropriate fin skeleton as a model limb precursor will lead to erroneous inferences about the evolution of morphology and the developmental pathways at the fish–tetrapod transition. The pectoral fin of the rhizodont sarcopterygian *Sauripteris* is strikingly limb-like and features prominently in discussions about the origin of limbs^{3,7,10–14}. It is thus important to establish the phylogenetic position of rhizodonts. However, their anatomy is incompletely known^{15,16}. Published phylogenetic analyses are based on poorly substantiated characters, such as the alleged presence of two external nostrils in the Australian genus *Barameda*^{17,18}. Here we present, from the Upper Devonian period of Canowindra, Australia, the most primitive and by far the most complete rhizodont discovered so far. It has a single external nostril but possesses no other derived tetrapod-like features. Our new evidence shows that rhizodonts are more remote from tetrapods than are osteolepiform¹⁸ and elpistostegid¹⁹ lobe-finned fishes. Similarities between rhizodont fins and tetrapod limbs are thus probably convergent, and the pectoral fin of *Sauripteris* should not be used as a model limb precursor.

Sarcopterygii Romer 1955

Rhizodontida Andrews and Westoll 1970

Gooloogongia gen. nov.

Type species. *Gooloogongia loomesi* sp. nov.

Diagnosis. Recognizable as a rhizodont by the possession of posteriorly pointed postparietals^{15,17}, short dorsal blade of the cleithrum¹⁵, long basal lepidotrichial segments in the pectoral fin¹⁵, doubled dorsal lateral line canal¹⁵, supratemporal–extratemporal contact¹⁷, and a very short anterior margin of the median extrascapular¹⁷. However, it lacks several derived features of other rhizodonts (premaxillary fang, posterior depressed lamina of cleithrum, long basal lepidotrichial segments in posterior fins^{15–17}), indicating that it represents the sister group of previously known Rhizodontida. The body length is roughly 80 cm. The very slender recumbent mandibular fangs seem to be autapomorphic.

Gooloogongia loomesi sp. nov.

Etymology. *Gooloogongia*: after the town of Gooloogong; *loomesi*: in honour of Bruce Loomes, an enthusiastic supporter of the Canowindra 'Age of Fishes' project.

Holotype. AMF 96860A and B, a skull and partial lower jaw, incomplete cleithrum, incomplete pectoral fin and body scales, exposed in dorsal view. All the material consists of natural moulds in sandstone; specimen numbers refer to permanent resin casts taken from these moulds, housed at the Australian Museum, Sydney.

Referred material. AMF 99900A–D, 99901, 99902, 100073A and B, 100074, 100075 and 101453.

Locality. On the road between Canowindra and Gooloogong, New South Wales, Australia. The site is known as Canowindra.

Horizon. Mandagery Sandstone, Upper Devonian, Famennian²⁰.

Diagnosis. As for genus.

The skull roof of *Gooloogongia* (Figs 1a, b and 2f) is similar to that of *Barameda* (Fig. 2d), the only other rhizodont where it is preserved in articulation¹⁷. However, it appears less derived than *Barameda* in having several bones in the nasal series. The shared characters of the two genera are probably primitive for the Rhizodontida.

Two nostrils have been reconstructed in *Barameda* (Fig. 2e)¹⁷. *Gooloogongia* has only one nostril (Figs 1a, b and 2f, g), with the same relationship to surrounding bones as in osteolepiforms¹⁹ and elpistostegids (panderichthyids)^{21,22}, which are members of the tetrapod stem group (Fig. 3). Re-examination of the *Barameda* material indicates that it too conforms to this pattern. In osteolepi-

forms, elpistostegids and tetrapods, the single external nostril is associated with a palatal nostril or choana. Unfortunately the palate is not preserved in *Gooloogongia*.

The cheek, previously largely unknown in rhizodonts^{15,17} (Fig. 2e), is osteolepiform-like in *Gooloogongia* (Figs 1a, b and 2g). However, it has a broad preopercular (Pop), which is an apparently primitive feature that is shared with porolepiforms and onychodonts^{16,18}, but is absent in osteolepiforms and tetrapods^{16,18} where this bone is narrow.

The preserved elements of the pectoral fin endoskeleton (Figs 1d, 4b) resemble those of *Sauripteris*^{8,14} and other rhizodonts^{8,17} (Fig. 4a), indicating that it was probably of the same elaborate

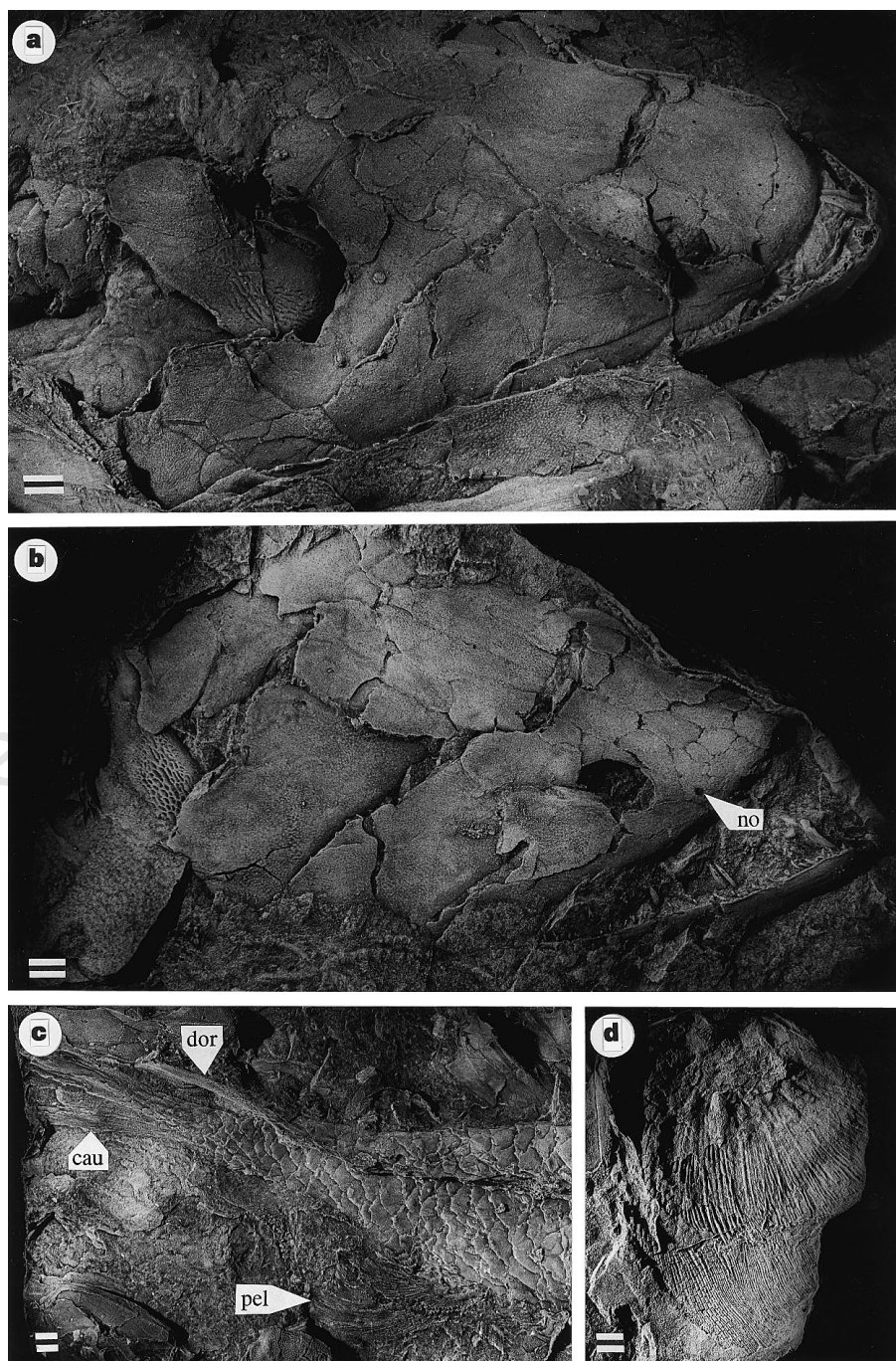


Figure 1 Specimens AMF 9680, 100073 and 99900 of *Gooloogongia loomesi*. **a**, AMF 96860, holotype of *Gooloogongia loomesi*, a skull in dorsolateral view. The large notch in the posterior margin of the opercular is an artefact. **b**, AMF 100073, flattened skull in dorsolateral view, showing the single external nostril (no). Both of these skulls have protruding lower jaws with slender recumbent fangs. **c**, AMF

99900, posterior part of body showing caudal (cau), second dorsal (dor) and pelvic (pel) fins. The basal portions of the lepidotrichia are short, as in most other osteichthyans. **d**, AMF 99900, pectoral fin in ventral view, showing long basal portions of lepidotrichia and traces of a complex endoskeleton. Scale bars, 1 cm.

pattern. The pectoral fin skeletons of osteolepiforms and elpistostegids are much simpler (Fig. 3).

The pectoral fin lepidotrichia of *Gooloogongia* have basal segments that are equal in length to the jointed distal portions (Figs 1d and 4b). In other rhizodonts the basal segments are much longer than the jointed parts¹⁵, whereas the generalized osteichthyan condition (see in, for example, actinopterygians and osteolepiforms) is to have very short basal segments¹⁵. The posterior fins of *Gooloogongia* show this primitive condition (Fig. 1c), whereas other rhizodonts have long basal lepidotrichial segments in all fins¹⁵.

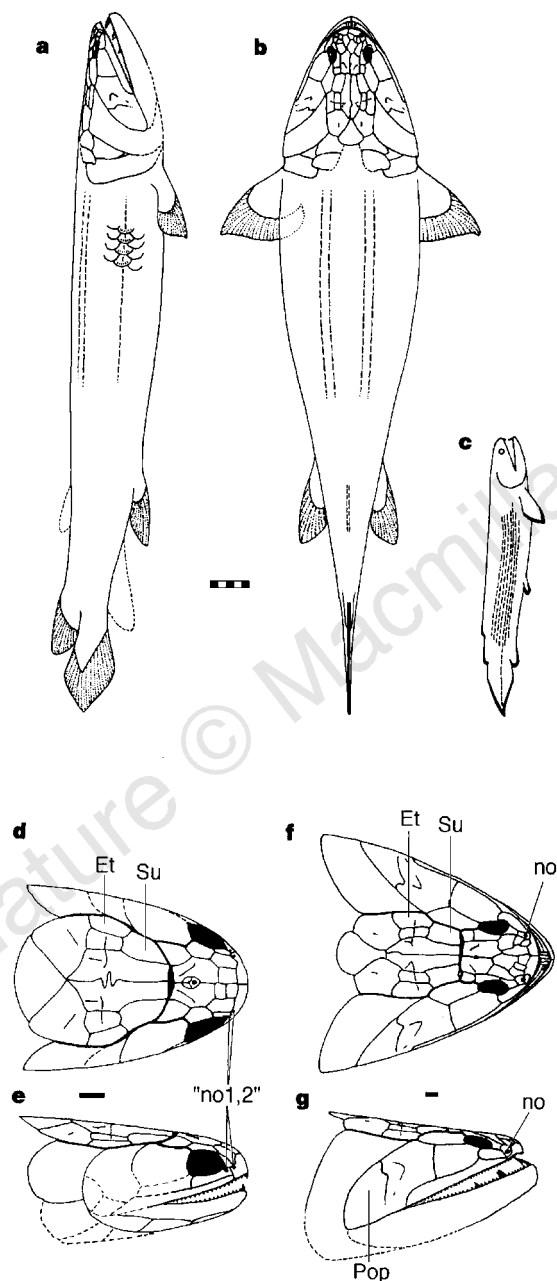


Figure 2 Reconstructions of *Gooloogongia loomesi*, *Strepsodus ancunamensis* and *Barameda decipiens*. **a, b**, Lateral and dorsal reconstructions of *Gooloogongia loomesi*. A sample area of squamation is shown on the flank, with preserved parts of the lateral line canals (dashed lines). Scale bar, 5 cm. **c**, *Strepsodus ancunamensis*, lateral view (modified from ref. 15). A probable juvenile, drawn to scale with **a, b**. Note multiple lateral line canals. **d, e**, Skull of *Barameda decipiens* in dorsal and lateral views (from ref. 17), showing two reconstructed nostrils ("no 1, 2"). Dashed lines are hypothetical. Scale bar, 1 cm. **f, g**, Skull of *Gooloogongia loomesi* in dorsal and lateral views. Pop, preopercular; Et, extratemporal; Su, supratemporal.

The body form of *Gooloogongia*, with its broad head, dorsally facing eyes and small caudal fin (Fig. 2a, b) indicates that it may have been a benthic sit-and-wait predator. It differs considerably from the only other known rhizodont body, of the Carboniferous genus *Strepsodus*¹⁵ (Fig. 2c), which has a symmetrical tail and reduced

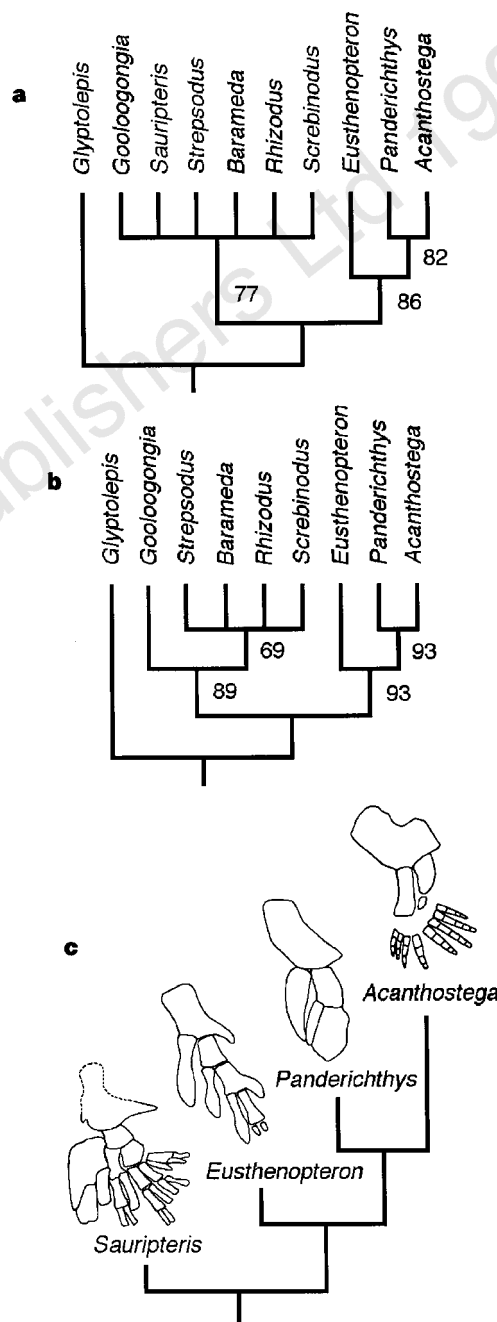


Figure 3 Relationships between rhizodonts, *Eusthenopteron*, *Panderichthys* and tetrapods. **a, b**, Cladograms generated by PAUP3.1 (exhaustive search) from 29 morphological characters, showing relationships of rhizodonts, *Eusthenopteron*, *Panderichthys* and tetrapods. The outgroup is the porolepiform *Glyptolepis*. Figures at internodes are bootstrap support values (heuristic, 100 replicates). **a**, Includes *Sauripteris*, which can only be scored for pectoral fin characters and thus lowers the phylogenetic resolution. Strict consensus of 135 trees, with length 40; consistency index, 0.825; homoplasy index, 0.175; retention index, 0.848, and rescaled consistency index, 0.699. **b**, Excludes *Sauripteris*, and resolves *Gooloogongia* as the sister group of other Rhizodontida. Strict consensus of 15 trees; length, 39; consistency index, 0.846; homoplasy index, 0.154; retention index, 0.864; and rescaled consistency index, 0.731. **c**, Pectoral appendages mapped onto phylogeny.

median fins. Superficially *Strepsodus* resembles an elpistostegid or basal tetrapod, whereas *Gooloogongia* is closer to the generalized sarcopterygian condition exemplified by *Osteolepis*¹⁹. *Strepsodus* has multiple lateral lines¹⁵; *Gooloogongia* shows a simpler pattern with a double dorsolateral line as its only elaboration.

A cladistic analysis (Fig. 3) places the Rhizodontida as the most basal member of the tetrapod stem group, with high bootstrap support. *Gooloogongia* seems to be the most primitive rhizodont (Fig. 3b), although this resolution is lost when *Sauripteris* (which

can only be scored for pectoral fin characters) is included (Fig. 3a).

The main puzzle of rhizodont relationships to date has been the apparent contradiction between an elaborate limb-like pectoral fin skeleton^{3,7,8,10–14} and the supposed presence of two external nostrils^{15,17}. Elpistostegids and osteolepiforms (represented here by *Panderichthys* and *Eusthenopteron*) have the opposite character complement: a tetrapod-like nasal region with a single external nostril and a choana, but a simple pectoral fin skeleton (Fig. 3) that contains no elements resembling digits^{16–18,21,23}. *Gooloogongia* shows that rhizodonts have a single external nostril, thus resolving this spurious character conflict. However, it exhibits no other tetrapod-like characters.

The rhizodont skull morphology illustrated by *Gooloogongia* and *Barameda* differ from the elpistostegid and tetrapod pattern in lacking frontal bones and having a short snout, widely separated eyes, a well developed intracranial joint between parietals and postparietals, and extratemporals (Fig. 4c–e). These characteristics of rhizodont skulls are shared with porolepiforms¹⁹, which are basal stem-group lungfishes^{16,18}; these characteristics are therefore probably shared primitive characters of the lungfish and tetrapod stem groups. They also occur in osteolepidid (but not tristichopterid) osteolepiforms¹⁹, which may indicate that osteolepiforms are paraphyletic relative to elpistostegids and tetrapods.

The description of *Gooloogongia* improves our understanding of rhizodont anatomy, and shows conclusively that rhizodonts are less closely related to tetrapods than are osteolepiforms and elpistostegids. We conclude that the similarities between the pectoral appendage skeletons of rhizodonts and tetrapods^{7,14} are convergent (Fig. 3), and urge that rhizodont pectoral fins not be used as model ancestors for tetrapod limbs. □

Methods

Phylogenetic analysis. The analysis was performed using the software package PAUP with a data matrix (see Supplementary Information) of 10 taxa (the porolepiform *Glyptolepis*^{9,18,19}, the rhizodonts *Gooloogongia*, *Barameda*¹⁷, *Sauripteris*^{8,14}, *Strepsodus*^{8,15}, *Rhizodus*^{8,15} and *Screbiodus*^{8,15}, the tristichopterid osteolepiform *Eusthenopteron*¹⁹, the elpistostegid *Panderichthys*²¹ and the tetrapod *Acanthostega*^{2,24}) scored for 29 morphological characters (see Supplementary information). Most parsimonious trees were identified using the exhaustive search algorithm. All characters were unordered and weighted equally. Bootstrap values were determined from 100 replicates using the heuristic algorithm.

Received 3 December 1997; accepted 24 April 1998.

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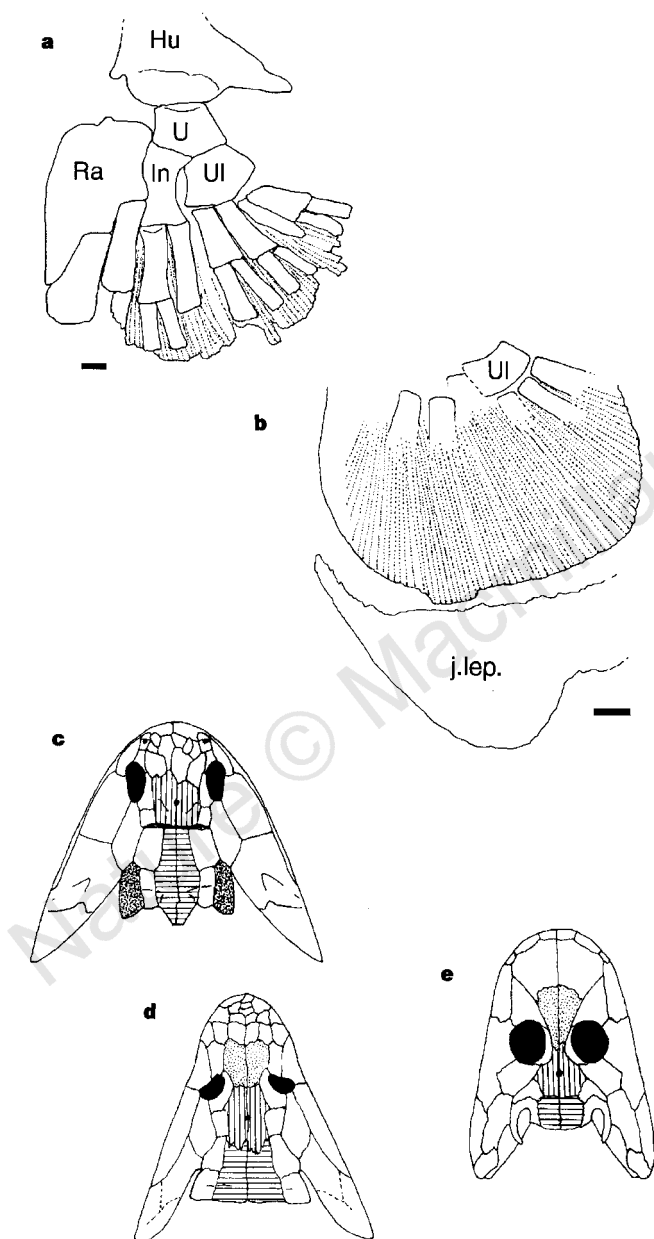


Figure 4 Morphology of ?*Sauripteris*, *Gooloogongia*, *Panderichthys* and *Acanthostega*. **a**, Pectoral fin skeleton of ?*Sauripteris* (from ref. 14), showing humerus (Hu), radius (Ra), ulna (U), intermedium (In), ulnare (Ul), branching distal radials and long unjointed basal segments of lepidotrichia (dotted lines). Left is anterior. Scale bar, 1 cm. **b**, Pectoral fin skeleton of *Gooloogongia*, AMF 99900, same orientation, showing large jointed lepidotrichial web (j.lep.). Scale bar, 1 cm. **c–e**, Heads of the rhizodont *Gooloogongia* (**c**), elpistostegid *Panderichthys* (**d**) (modified from ref. 21) and tetrapod *Acanthostega* (from ref. 24) (**e**), showing frontals (light shading), extratemporals (dark shading), parietals (vertical hatching) and postparietals (horizontal hatching). In *Gooloogongia* and *Panderichthys*, operculars and extrascapulars have been omitted.

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Supplementary information is available on Nature's World-Wide Web site (<http://www.nature.com>) or as paper copy from the London editorial office of Nature.

Acknowledgements. We thank the Australian Museum for their award of a Visiting Fellowship to P.E.A. A. Ritchie for inviting us to work on the Canowindra material and J. Long and J. Jeffery for discussions and access to rhizodont material. Z.J. thanks J. Fairfax for financial support. This Letter is dedicated to the memory of S. M. Andrews.

Selfish genes: a green beard in the red fire ant

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A 'green-beard' gene is defined as a gene that causes a phenotypic effect (such as the presence of a green beard or any other conspicuous feature), allows the bearer of this feature to recognize it in other individuals, and causes the bearer to behave differently towards other individuals depending on whether or not they possess the feature^{1–3}. Such genes have been proposed on theoretical grounds to be agents mediating both altruism and intragenomic conflicts^{1,2}, but until now few, if any, of these genes have been identified^{4,5}. Here we provide evidence of a green-beard gene in the red imported fire ant, *Solenopsis invicta*. In polygyne (multiple-queen) colonies, all egg-laying queens are *Bb* heterozygotes at the locus *Gp-9* (ref. 6). Previous studies suggested that *bb* females die prematurely from intrinsic causes⁶; we now show that *BB* queens initiating reproduction are killed by workers, and that it is primarily *Bb* rather than *BB* workers that are responsible for these executions. This implies that allele *Gp-9^b* is linked to a green-beard allele that preferentially induces workers bearing the allele to kill all queens that do not bear it. Workers appear to distinguish *BB* from *Bb* queens on the basis of a transferable odour cue.

We mimicked the natural recruitment of new reproductive queens into polygyne nests by reintroducing young queens into their parental colonies after they had been kept in small colony fragments with workers but not other queens for three days. (The absence of mature reproductive queens induces reproductive development of young queens⁷.) There was a strong association between queen genotype at *Gp-9* and the probability of being attacked: all attacked queens were homozygous for the *B* allele, whereas none of the queens with a copy of allele *b* faced significant worker aggression (Table 1). A separate experiment in which worker attacks were not interrupted showed that such attacks invariably led to the death of a queen within 15 minutes ($n = 50$).

We next compared the genotypes of workers attacking *BB* queens with those of workers sampled randomly from the same population and discovered that attackers were much more likely to carry the *b* allele (82.5 versus 59.3% of genotypes; $P < 0.01$). To confirm this, we did a second experiment in which we compared the genotypes of workers attacking *BB* queens with those of workers in the vicinity of non-attacked (*Bb*) queens in the same colonies. The proportion of *Bb* and *bb* workers surrounding attacked (*BB*) queens was significantly higher than the proportion surrounding non-attacked (*Bb*)

queens (Table 2). Our assay may considerably underestimate the true extent of genotypic bias among workers attacking *BB* queens because these attacks elicited the formation of compact worker groups around the queens, making it impossible to collect only attacking workers. Thus, although our experiments demonstrate that such attacks are undertaken primarily by workers with at least one copy of allele *Gp-9^b*, they do not allow us to determine whether the attacks are carried out only by these workers. The possibility that these results are due to workers with the *b* allele generally having a lower threshold for aggression can be excluded, because such individuals were not overrepresented among the workers attacking foreign heterospecific ant workers (*Aphaenogaster* sp.) introduced into nests ($n = 788$; $G = 2.42$; d.f. = 1; $P = 0.12$; workers with the *b* allele actually were underrepresented among these attackers).

Some of the workers involved in attacks on *BB* queens subsequently were attacked by nestmates, suggesting that they might have acquired a distinctive odour from the attacked queens. To test this hypothesis, we rubbed randomly chosen workers against the cuticle of *BB* or *Bb* queens and then placed them in groups of nestmate

Table 1 Proportion of young queens of each *Gp-9* genotype attacked by workers

Age	Proportion of queens attacked		
	<i>Gp-9</i> genotype		
	<i>BB</i>	<i>Bb</i>	<i>bb</i>
7–10 days	0.61	0.00	0.00
($n = 19$ colonies)	($n = 90$)	($n = 275$)	($n = 5$)
11–14 days	0.91	0.00	0.00
($n = 18$ colonies)	($n = 11$)	($n = 327$)	($n = 11$)

The frequencies of attacks on 7–10-day-old queens varied significantly according to genotype ($G = 190.78$; d.f. = 2; $P < 0.0001$). The proportion of *BB* queens attacked was significantly greater than the proportion of either *Bb* queens ($G = 189.16$; d.f. = 1; $P < 0.0001$) or *bb* queens ($G = 9.04$; d.f. = 1; $P = 0.003$) attacked (the few *bb* queens found presumably had not yet succumbed to the age-dependent lethal effects of this genotype⁶). The same pattern was revealed within individual colonies: in each of the 16 colonies in which *BB* queens were present, the proportion of such queens attacked was significantly greater than the proportion of attacked queens with the other two genotypes (binomial probability, $P < 0.001$). A similar association between queen genotype and aggression occurred for 11–14-day-old queens ($G = 84.06$; d.f. = 2; $P < 0.0001$), with the proportion of *BB* queens attacked again being significantly greater than the proportion of either *Bb* queens ($G = 83.41$; d.f. = 1; $P < 0.0001$) or *bb* queens ($G = 23.61$; d.f. = 1; $P < 0.001$) attacked. At the colony level, the proportion of attacked *BB* queens of this older class again was greater than the proportion of attacked queens with the other two genotypes in each of the three colonies in which *BB* queens were present. Two lines of evidence suggest that *BB* queens are killed as they approach sexual maturity and become potential egg layers (about 10 d after adult emergence^{8,20}). First, the proportion of attacked *BB* queens was higher for 11–14-day-old queens than for 7–10 day old queens ($G = 4.58$; d.f. = 1; $P = 0.03$). Second, among queens in the younger age class, the non-attacked queens with genotype *BB* were significantly lighter (12.8 ± 1.3 mg; $n = 35$) than the attacked queens with this genotype (14.1 ± 1.1 mg; $n = 55$; two-way ANOVA, weight difference: $F = 23.55$; $P < 0.0001$; colony effect: $F = 1.95$; $P < 0.05$; interaction: $F = 0.831$, NS). Because weight is a good indicator of the age of maturing queens²⁰, these data suggest that younger and lighter *BB* queens were attacked relatively less frequently. Such age-associated attacks on *BB* queens may explain the decrease in the proportion of *BB* genotypes among queens as they age: this proportion was 0.24 in the 7–10-day-old queens, and 0.03 in the 11–14-day-old queens ($G = 77.69$; d.f. = 1; $P < 0.001$).

Table 2 Number of workers of each *Gp-9* genotype surrounding attacked, *Gp-9^{BB}* queens and non-attacked, *Gp-9^{Bb}* queens

Worker <i>Gp-9</i> genotype	Queen <i>Gp-9</i> genotype	
	<i>BB</i> (attacked)	<i>Bb</i> (non-attacked)
<i>BB</i>	50 (0.213)	81 (0.344)
<i>Bb</i>	184 (0.783)	147 (0.626)
<i>bb</i>	1 (0.004)	7 (0.030)
Total	235	235

Proportions of attacking and non-attacking workers with each genotype are shown in parentheses. There was a significant association between queen and worker genotypes ($G = 16.61$; d.f. = 2; $P = 0.0002$), with attacks on *BB* queens being made preferentially by workers having the *b* allele. The difference remains highly significant, both when *bb* workers are eliminated from the analysis ($G = 11.47$; d.f. = 1; $P < 0.001$) and when they are pooled with *Bb* workers ($G = 10.24$; d.f. = 1; $P = 0.001$). The same pattern was found within individual colonies. Of the nine colonies that contained three or more queens of each genotype, eight had a relative overrepresentation of workers with allele *b* attacking queens, an outcome that departs significantly from the null expectation that 50% of nests should have such overrepresentations (binomial test, $P < 0.02$). Furthermore, the overrepresentation of allele *b* in attacking workers was significant in two of these colonies ($G = 6.89$; d.f. = 1; $P < 0.01$ and $G = 5.07$; d.f. = 1; $P = 0.02$). The few *bb* workers found presumably were very young workers that had not yet succumbed to the age-dependent lethal effects of this genotype⁶.