

28. Kurzanov, S. M. Braincase structure in the carnosaur *Itemirus* n. gen. and some aspects of the cranial anatomy of dinosaurs. *Paleontol. Zh.* **1976**, 127–137 (1976).
29. Holtz, T. R. Jr Phylogenetic taxonomy of the Coelurosauria (Dinosauria: Theropoda). *J. Paleontol.* **70**, 536–538.
30. Perle, A., Norell, M. & Clark, J. A new maniraptoran theropod *Achillobator giganticus* (Dromaeosauridae) from the Upper Cretaceous of Burkhan, Mongolia. (Dept Geol., Natl Univ. Mongolia, Ulaanbaatar, 1999).

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Chameleon radiation by oceanic dispersal

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Historical biogeography is dominated by vicariance methods that search for a congruent pattern of fragmentation of ancestral distributions produced by shared Earth history^{1–3}. A focus of vicariant studies has been austral area relationships and the break-up of the supercontinent Gondwana^{3–5}. Chameleons are one of the few extant terrestrial vertebrates thought to have biogeographic patterns that are congruent with the Gondwanan break-up of Madagascar and Africa^{6,7}. Here we show, using molecular and morphological evidence for 52 chameleon taxa, support for a phylogeny and area cladogram that does not fit a simple vicariant history. Oceanic dispersal—not Gondwanan break-up—facilitated species radiation, and the most parsimonious biogeographic hypothesis supports a Madagascan origin for chameleons, with multiple ‘out-of-Madagascar’ dispersal events to Africa, the Seychelles, the Comoros archipelago, and possibly Reunion Island. Although dispersal is evident in other Indian Ocean terrestrial animal groups^{8–16}, our study finds substantial out-of-Madagascar species radiation, and further highlights the importance of oceanic dispersal as a potential precursor for speciation.

The break-up of Gondwana provides one of the most obvious test cases for vicariance biogeography, with the separation of Africa, Madagascar, the Seychelles and India providing a well documented geologic history⁴. Magnetic anomaly data and Mesozoic timescales reveal that Madagascar and Greater India first broke away from Africa 165 Myr ago, with movement ending by 121 Myr ago¹⁷; Greater India and Madagascar separated approximately 88 Myr ago based on dating of Marion hot-spot-related volcanism¹⁸, and the

Seychelles granitic archipelago split from India during formation of the Deccan basalt province between 69 and 65 Myr ago¹⁹. The main source of current controversy concerns the sequence and timing of separation of Antarctica with India, South America and Australia between 80–100 Myr ago^{18,20}.

Gondwanan origins have been proposed for extant terrestrial vertebrates in Madagascar⁸; however, no modern systematic evidence congruent with a Gondwanan break-up vicariant pattern has been reported to date. Chameleons (family Chamaeleonidae: subfamily Chamaeleoninae²¹) are claimed to be an ancient Gondwanan group, on the basis of limited immunological distances and a calibrated albumin molecular clock⁷. Previous cladistic studies, using 11–24 morphological characters, supported conflicting biogeographic hypotheses that are partly congruent with Gondwanan break-up^{6,22}, or that suggest a post-Gondwanan, Madagascan origin for chameleons²³.

To test the Gondwanan vicariance hypothesis, we conducted a phylogenetic analysis that included 52 chameleon taxa (approximately 40% of all chameleon species). These taxa represent all Chamaeleoninae genera and subgenera, and include species found in each continental region (including the granitic Seychelles), and the Comoros archipelago and Reunion Island (both of volcanic origin). To test the monophyly of chameleons, the two other Chamaeleonidae subfamilies (Leiolepidinae and Agaminae) were also included. Molecular characters (mitochondrial DNA (mtDNA), NADH subunit 4 and adjacent transfer RNA sequences), morphological characters, and behavioural/life-history characters were used to produce a combined data set of 644 potentially parsimony-informative characters.

Three equally parsimonious trees were found for the combined equally weighted data set. These results (Fig. 1) support the monophyly of chameleons, with the two most basal clades representing dwarf chameleons (*Brookesia*), which are endemic to Madagascar. Basal to the crown clade of ‘typical’ chameleons (*Furcifer*, *Calumma* and *Chamaeleo*) are the endemic African genera, *Rhampholeon* and *Bradypodion*. The resulting area cladogram (Fig. 1) has the following features: (1) The two most basal lineages are distributed in Madagascar; (2) The more derived lineages occur in Madagascar, Africa, the Seychelles and India, with the two most basal lineages of this clade occurring in Africa; (3) the India lineage is sister to an African clade; (4) the Seychelles lineage is sister to a Madagascan clade; and (5) the Comoros lineage is sister to a Madagascan clade.

The corresponding chameleon continental area cladogram (Fig. 2a) cannot be reconciled²⁴ with proposed Gondwanan break-up

Table 1 Chameleon area cladogram reconciled with origin hypotheses

Biogeographic hypothesis	Minimum assumption*		
	Extinction†	Dispersal	Total
Gondwanan origin 1‡			
Vicariance only	38	0	38
Vicariance and dispersal	3	5	8
Gondwanan origin 2§			
Vicariance only	25	0	25
Vicariance and dispersal	1	5	6
Partial Gondwanan origin			
Madagascar + Seychelles + India	0	12	12
Madagascar + Seychelles + India	1	11	12
Seychelles + India	0	14	14
Post-Gondwanan origin			
Madagascar	0	5	5
Africa	0	6	6
Seychelles	0	12	12
India	0	11	11

* Minimum number of assumption events to reconcile area cladogram with biogeographic hypothesis.
 † Minimum number of losses²⁴. Inclusion of all missing nodes (items of error⁷) would add additional extinction events.
 ‡ Conventional hypothesis.
 § Hypothesis of ref. 20.

vicariance models (Fig. 2b, c) or models of post-Gondwanan origin, without invoking assumptions of dispersal or extinction. The most parsimonious biogeographic hypothesis that minimizes dispersal or extinction events supports a post-Gondwanan origin in Madagascar, with subsequent oceanic dispersal from Madagascar. These continental dispersal events include three dispersals to Africa, and

a single dispersal to both India and the Seychelles (Table 1). Other less parsimonious biogeographic hypotheses place chameleon origins in Madagascar, Africa or Gondwana, and also include a minimum of five dispersal events (Table 1). An utter rejection of oceanic dispersal requires a minimum of 25 or 38 independent extinction events, depending on the choice of Gondwanan break-up model (Table 1). Both of these 'no-dispersal' hypotheses reject a role for tectonic vicariance facilitating the origin of the major species radiations, because all generic lineages would have to predate Gondwanan break-up.

Previously proposed alternative phylogenies (and their associated biogeographic patterns) are substantially less parsimonious compared with our hypothesis, requiring greater numbers of character state changes. Forcing a strict Gondwanan break-up topology (Fig. 2b, c) on the chameleon area clades (AF(M(SE,I))); see Fig. 2 legend for definitions) increases tree length by a minimum of 49 steps. The previously proposed Gondwanan vicariance split for Brookesini (*Brookesia/Rhampholeon*) and Chamaeleonini (*Bradypodion* and *Chamaeleo/Calumma* and *Furcifer*)⁶ requires a minimum of 25 additional steps. A Madagascan or African origin hypothesis with a minimum number of three dispersal events (to the Seychelles, India, and either Africa or Madagascar) requires a minimum of 18 and 15 additional steps, respectively.

Evidence corroborating oceanic dispersal for chameleons is provided by the sister species *Furcifer cephalolepis* and *F. polleni*, which are endemic to the volcanic Comoros islands, Moheli and

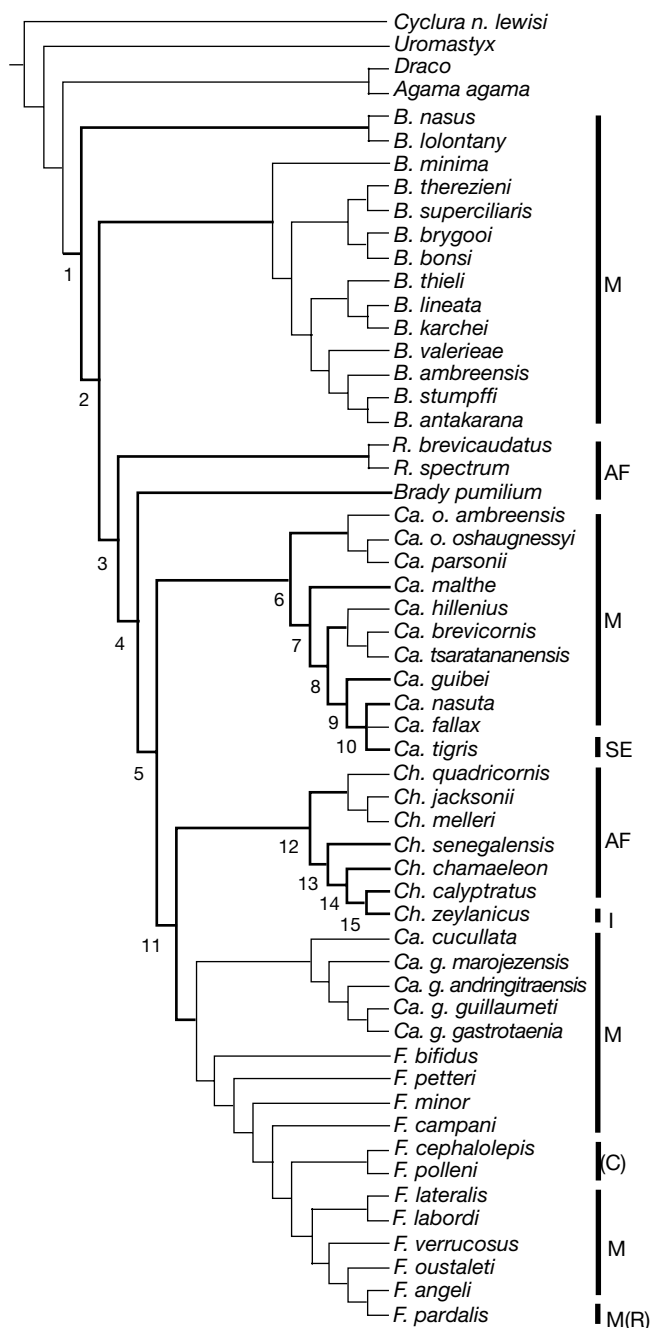


Figure 1 Inter-relationships of chameleons and corresponding area distributions based on equal-weighted molecular and morphological data and maximum parsimony. *B.*, *Brookesia*; *R.*, *Rhampholeon*; *Brady.*, *Bradypodion*; *Ca.*, *Calumma*; *Ch.*, *Chamaeleo*; *F.*, *Furcifer*. Taxon distribution: AF, Africa, Arabian Peninsula and Near-Middle East; M, Madagascar; I, India, Pakistan and Sri Lanka; SE, Seychelles; (C), Comoros; (R), Reunion. Non-continental (volcanic origin) areas are shown in brackets. Continental area cladogram is indicated in bold, with percentage bootstraps (all data/all data except third positions, with successive weighting): 1, 100/100; 2, 73/83; 3, 77/92; 4, 100/100; 5, 76/86; 6, 54/69; 7, 99/100; 8, 81/66; 9, 98/98; 10, 53/32; 11, 78/71; 12, 100/100; 13, 100/100; 14, 100/100; 15, 100/100.

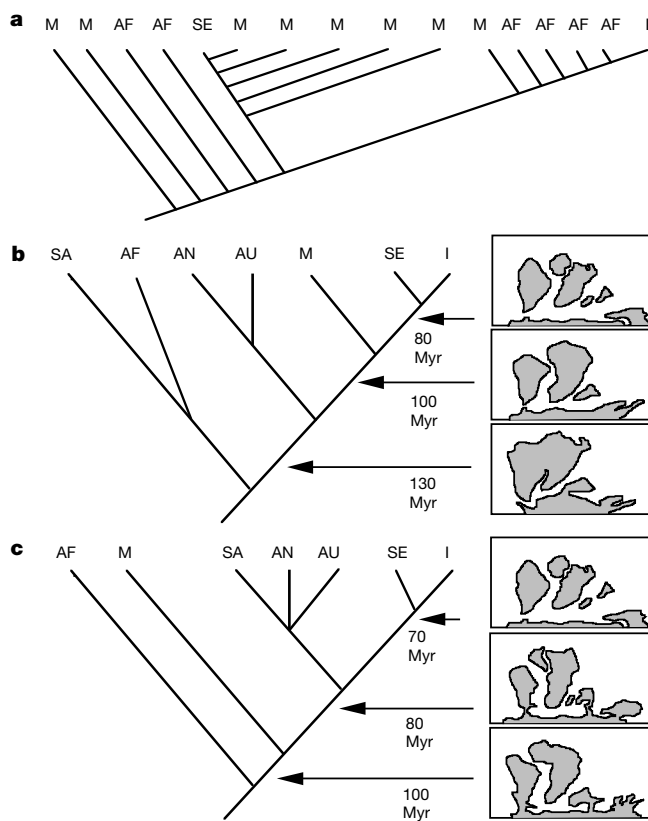


Figure 2 Continental area cladograms for the Indian Ocean region based on chameleon phylogeny and geological break-up models. AF, Africa; AN, Antarctica; AU, Australia; M, Madagascar; SA, South America; SE, the Seychelles; I, India and Sri Lanka. **a**, Chameleon area cladogram based on Fig. 1. **b**, Conventional hypothesis of Gondwanan break-up for the Indian Ocean region¹⁷⁻¹⁹. **c**, Alternative hypothesis of Gondwanan break-up for the Indian Ocean region proposed by ref. 20. The chameleon area cladogram is incongruent with both of the break-up hypotheses.

Grand Comoro, respectively⁸. These islands were formed between 0.13 and 5.4 Myr ago²⁵, and never had contact with other landmasses. The direct ancestor of these endemic chameleons could only have reached the archipelago by means of oceanic dispersal. Our results find these sister species most closely related to the *F. oustaleti* and *F. lateralis* groups in Madagascar, which are separated by 300 km of ocean from the Comoros archipelago. The distribution of the chameleon, *Furcifer pardalis*, in both Madagascar and Reunion Island, may represent another natural oceanic dispersal, as differences in dorsal crest and hemipene morphology found between these island populations do not suggest a modern human introduction, subsequent to human occupation of Reunion Island, in the seventeenth century.

Other evidence is not inconsistent with a post-Gondwanan origin for chameleons. The oldest known chameleon fossils are no older than the Miocene epoch (*Rhampholeon* from Kenya, 18 Myr ago²⁶; *Chamaeleo intermedius* from Kenya, 16–18 Myr ago²⁷; and *Chamaeleo caroliquarti* from Central Europe, 26 Myr ago²⁸). The earliest known fossil acrodont lizard *Mimeosaurus* (Upper Cretaceous period)²¹ is also younger than the Africa–Madagascar separation (extant acrodonts are confined to the Agaminae, Leiolepidinae and Chamaeleoninae). However, all extant lizard groups are poorly represented in the fossil record. Molecular clock mtDNA divergences (assuming a vertebrate ectotherm mtDNA divergence rate of 0.4–0.6% per Myr ago^{11,29}) are also consistent with a post-Gondwanan origin for chameleons. Sequence divergence between chameleons and their sister group (*Agama*, *Draco*) is 28–36%, giving an estimated divergence time of 47–90 Myr, contemporary or younger than the separation of Madagascar and India. Sequence divergence between the basal *Brookesia* clade and all other chameleons is 21–27% (35–68 Myr), *Rhampholeon* and all typical chameleons 20–26% (33–65 Myr), and *Chamaeleo* and *Furcifer* 17–23% (28–58 Myr).

Despite the Gondwanan vicariant history of Madagascar and the Indian Ocean, many regional species radiations (ants, spiders, tortoises, geckos, skinks, rodents, primates) are reported to show transmarine migrations, and have post-Gondwanan origins in Africa or Asia^{8–10}. Our results provide the strongest support for a post-Gondwanan species radiation originating in Madagascar, with subsequent out-of-Madagascar dispersal to Africa, the Seychelles, the Comoros, and possibly Reunion Island. Invasions into Africa from Madagascar are currently not well documented, although dispersal through Madagascar, from Asia to Africa, has been concluded recently for rodents¹⁵. Surprisingly, the absence of biogeographic patterns congruent, or largely congruent with Gondwanan break-up in the Indian Ocean (and other austral regions), has thus far received little attention, although two poorly supported geological hypotheses (Pacifica supercontinent and expanding earth) have been proposed to maintain the plausibility of alternative vicariant patterns^{3,5}. Our analyses provide evidence for considerable oceanic dispersal by chameleons, and support the hypothesis that dispersal, rather than continental break-up, was the precursor for species radiation. □

Methods

For phylogenetic analysis, a total of 85 morphological and behavioural characters, and 972 bases of mtDNA (236 3' terminal codons of ND4, tRNA^{Ser}, tRNA^{His} and tRNA^{Leu}) were used. Sequence alignment was made using CLUSTAL W (see <http://www.mbio.ncsu.edu/BioEdit/bioedit.html>) under a wide variety of gap penalty assignments, and refined by eye. For the list of morphological and behavioural characters see Supplementary Information. The non-Chamaeleonidae specified outgroup taxa was *Cyclura* (Iguanidae). The 55 in-group Chamaeleonidae (from ref. 21) taxa include Leiolepidinae (*Uromastix*), Agaminae (*Agama* and *Draco*) and Chamaeleoninae (14 *Brookesia*, 2 *Rhampholeon*, 1 *Bradypodion*, 16 *Calumma*, 7 *Chamaeleo* and 12 *Furcifer*). Chameleon taxa are shown in Fig. 1. We collected all species from Madagascar and the Seychelles; we obtained other species from tissue and museum collections or commercial sources. Phylogenetic analysis was performed using parsimony with PAUP version 4.0b2. All characters were initially given equal weight and all characters were unordered except eight morphological characters, which were ordered based on intermediacy. Gaps were treated as a fifth base. Searches were heuristic with 10 replicate searches with random stepwise addition of taxa. No upper limit

was imposed on the maximum number of trees saved. Successive weighting was based on maximum rescaled consistency index (RC). Bootstrap branch support was based on 100 bootstrap replicates (each replicate with 10 replicate heuristic searches with random stepwise addition of taxa). MacClade 4.0 was used to determine step costs for alternative phylogenetic hypotheses.

Equal weighting of the combined molecular and morphological characters (644 parsimony informative) recovered three maximum parsimony trees (5,096 steps, consistency index, CI = 0.281, RC = 0.143, strict consensus; Fig. 1). Relaxing parsimony by one step increased the total tree number to 35, with the 50% majority rule consensus congruent with the most parsimonious strict consensus cladogram, but the strict consensus showing basal polytomies. Successive weighting recovered the same strict consensus and area cladogram found with equal weighting (3 trees, 7,016 steps, CI = 0.529, RC = 0.374). Reverse successive weighting, used to explore potential secondary phylogenetic signal³⁰, recovered 262 trees and a strict consensus tree showing: (1) almost no resolution (except within *Brookesia* and *Calumma*); (2) chameleons paraphyletic (with respect to *Draco*); and (3) third position molecular characters representing most of the high reverse-weighted characters. Deletion of third positions, and otherwise using equal weighting, resulted in a strict consensus tree almost identical to the entire data set (incongruence confined to minor polytomies within *Furcifer*) and an area cladogram completely congruent with Fig. 2a. (84 trees, 2,670 steps, CI = 0.336, RC = 0.194). Successive weighting and excluding third positions resulted in a strict consensus area cladogram completely congruent with Fig. 2a (12 trees, 5,141 steps, CI = 0.607, RC = 0.466).

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- Nelson, G. & Platnick, N. I. *Systematics and Biogeography: Cladistics and Vicariance* (Columbia University, New York, 1981).
- Morrone, J. J. & Crisci, J. V. Historical biogeography: introduction to methods. *Annu. Rev. Ecol. Syst.* **26**, 373–401 (1995).
- Humphries, C. J. & Parenti, L. R. *Cladistic Biogeography* 2nd edn (Oxford Univ. Press, Oxford, 1999).
- Brown, J. H. & Lomolino, M. V. *Biogeography* 2nd edn (Sinauer, Sunderland, 1998).
- Crisci, J. V., Cigliano, M. M., Morrone, J. J. & Roig-Juñent, S. Historical biogeography of southern South America. *Syst. Zool.* **40**, 152–171 (1991).
- Klaver, C. J. J. & Böhme, W. Phylogeny and classification of the chamaeleonidae (Suria) with special reference to hemipenis morphology. *Bonn. Zool. Mon.* **22**, 1–64 (1986).
- Hofman, A., Maxson, L. R. & Arntzen, W. Biochemical evidence pertaining to the taxonomic relationships within the family Chamaeleonidae. *Amphibia-Reptilia* **12**, 245–265 (1991).
- Blanc, C. P. in *Biogeography and Ecology in Madagascar* (eds Battistini, R. & Richard-Vindard, G.) 501–614 (Junk, The Hague, 1972).
- Arnold, E. N. Indian Ocean giant tortoises: their systematics and island adaptations. *Phil. Trans. R. Soc. Lond. B.* **286**, 127–145 (1979).
- Kluge, A. G. & Nussbaum, R. A. A review of African–Madagascan gekkonid lizard phylogeny and biogeography (Squamata). *Misc. Publ. Mus. Zool. Univ. Michigan* **183**, 1–20 (1995).
- Coccone, A., Amato, G., Gratry, O. C., Behler, J. & Powell, J. R. A molecular phylogeny of four endangered Madagascar tortoises based on MtDNA sequences. *Mol. Phylog. Evol.* **12**, 1–9 (1999).
- Fisher, B. L. in *Biogeography of Madagascar* (ed. Lourenco, W. R.) 457–466 (Orstom, Paris, 1996).
- Yoder, A. D. in *Biogeography of Madagascar* (ed. Lourenco, W. R.) 245–258 (Orstom, Paris, 1996).
- Mausfeld, P., Vences, M., Schmitz, A. & Veith, M. First data on the molecular phylogeography of scincid lizards of the genus *Mabuya*. *Mol. Phylog. Evol.* **17**, 11–14 (2000).
- Jansa, S. A., Goodman, S. M. & Tucker, P. K. Molecular phylogeny and biogeography of the native rodents of Madagascar (Muridae: Nesomyinae): a test of the single-origin hypothesis. *Cladistics* **15**, 253–270 (1999).
- Griswold, C. E. in *Diversity and Endemism in Madagascar* (eds Lourenco, W. R. & Goodman, S. M.) 345–354 (Société de Biogéographie, Paris, 2000).
- Rabinowitz, P. D., Coffin, M. F. & Falvey, D. The separation of Madagascar and Africa. *Science* **220**, 67–69 (1983).
- Storey, M. *et al.* Timing of hot spot-related volcanism and the breakup of Madagascar and India. *Science* **267**, 852–855 (1995).
- Storey, B. C. The role of mantle plumes in continental breakup: case histories from Gondwanaland. *Nature* **377**, 301–308 (1995).
- Hay, W. W. *et al.* in *Evolution of the Cretaceous Ocean–Climate System* (Spec. Pap. 332) (eds Barrera, E. & Johnson, C.) 1–48 (Geological Society of America, Boulder, 1999).
- Frost, D. R. & Etheridge, R. A phylogenetic analysis and taxonomy of the iguanian lizards (Reptilia: Squamata). *Univ. Kansas Mus. Nat. Hist. Misc. Publ.* **81**, 1–65 (1989).
- Rieppel, O. & Crumley, C. Paedomorphosis and skull structure in Malagasy chameleons (Reptilia: Chamaeleonidae). *J. Zool. Lond.* **243**, 351–380 (1997).
- Rieppel, O. The phylogenetic relationships within the Chamaeleonidae, with comments on some aspects of cladistic analysis. *Zool. J. Linn. Soc.* **89**, 41–62 (1987).
- Page, R. D. M. Maps between trees and cladistic analysis of historical associations among genes, organisms, and areas. *Syst. Biol.* **43**, 58–77 (1994).
- Emerick, C. M. & Duncan, R. A. Age progressive volcanism in the Comores Archipelago, western Indian Ocean and implications for Somali plate tectonics. *Earth Planet. Sci. Lett.* **60**, 415–428 (1982).
- Rieppel, O., Walker, A. & Odhiambo, I. A preliminary report on a fossil Chamaeleonine (Reptilia: Chamaeleonidae) skull from the Miocene of Kenya. *J. Herpetol.* **26**, 77–80 (1992).
- Hillenius, D. A new chameleon from the Miocene of Fort Ternan, Kenya (Chamaeleonidae, Reptilia). *Beaufortia* **28**, 9–15 (1978).
- Moody, S. & Roček, Z. *Chamaeleo caroliquarti* (Chamaeleonidae, Suria): a new species from the Lower Miocene of Central Europe. *Vestník Ústředního ústavu geologického* **55**, 85–92 (1980).
- Rand, D. M. Thermal habit, metabolic rate, and the evolution of mitochondrial DNA. *Trends Ecol. Evol.* **9**, 125–131 (1994).
- Trueman, J. W. H. Reverse successive weighting. *Syst. Biol.* **47**, 733–737 (1998).

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Antagonistic coevolution between the sexes in a group of insects

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In coevolutionary ‘arms races’ between the sexes, the outcome of antagonistic interactions may remain at an evolutionary standstill. The advantage gained by one sex, with any evolutionary exaggeration of arms, is expected to be matched by analogous counteradaptations in the other sex^{1,2}. This fundamental coevolutionary process may thus be hidden from the evolutionist’s eye^{3,4}, and no natural examples are known. We have studied the effects of male and female armament (clasping and anti-clasping morphologies) on the outcome of antagonistic mating interactions in 15 species of water strider, using a combination of experimental and phylogenetic comparative methods. Here we present, by assessing the independent effects of both species-specific level of arms escalation and small imbalances in the amounts of arms between the sexes within species, the consequences of a sexual arms race. Evolutionary change in the balance of armament between males and females, but not in the species-specific level of escalation, has resulted in evolutionary change in the outcome of sexually antagonistic interactions such as mating rate.

Evolutionary conflicts of interests between the sexes are ubiquitous^{1–4}. Such conflict is predicted to fuel sexually antagonistic coevolution^{1,2}, during which adaptations in one sex, which are harmful for individuals of the other sex, select for counteradaptations in the other sex to mitigate costs imposed by such adaptations. The resulting coevolution between the sexes is now recognized to be

a central process of evolution, with the potential to shape various interactions between the sexes^{2,5,6} and their gametes^{7–8}, as well as diversification⁹, speciation and extinction rates^{10–12}. At the core of this coevolutionary interaction is an arms race between the sexes that can include periods of both escalation and de-escalation of arms^{13–15}.

Theory suggests, however, that the outcome of antagonistic male–female interactions should remain relatively unchanged during an arms race because the build-up of arms in one sex may be balanced by a build-up in the other (Fig. 1a, 1–2). The consequences of such arms races on sexual interactions may thus be undetectable, which makes sexually antagonistic coevolution inherently difficult to show^{1–4}. Perhaps for this reason, we have no direct empirical evidence for a primary role of arms races in the evolution of sexual interactions in natural systems.

Despite an expectation of some evolutionary balance in the level of arms between the sexes, one sex may at least temporarily evolve a greater quantity of arms relative to the other (refs 13–15; and Fig. 1a, 3–4). In such cases, the evolutionary consequences of the arms race for interactions between the sexes may be exposed. For example, in an arms race in which it benefits males but not females to mate several times¹³, one may expect relatively high rates of mating in species where the advantage has shifted toward males (Fig. 1a, 4). The converse would be expected for species in which the advantage has shifted toward females (Fig. 1a, 3). Thus, by using tests that are based on phylogeny^{16,17}, one might uncover sexually antagonistic adaptations by analysing the effects on the change in sexual interactions caused by evolutionary change in the relative levels of arms between the sexes.

We have studied the coevolution of relative armament of the sexes and the outcome of sexually antagonistic interactions in 15 congeneric water strider species. Water striders (Heteroptera; Gerridae) are a group of semi-aquatic insects, which have become a model system in which to study sexually antagonistic coevolution. Several experimental in-depth studies, carried out on several different species and using different approaches (reviewed in refs 18, 19), have shown that there is intense and overt sexual conflict over mating rate that results from a strong asymmetry between the sexes in the relative costs and benefits of mating. Matings are preceded typically by a violent pre-mating struggle, in which females try to dislodge harassing males to avoid superfluous and costly mating^{18,19}.

The ability of males to withstand these struggles is related to various morphological grasping adaptations, such as exaggeration of prolonged clasping genitalia and a more flattened abdomen^{20,21}, which allow males to grasp females more firmly. Females’ ability to resist males is related to distinct morphological counteradaptations, such as prolongation of the female abdominal spines and the degree of downward tilting of the abdominal tip^{20,22}, which makes it more difficult for males to grasp females. We have shown elsewhere that the level of these arms in females coevolves closely with those in males within water striders²⁰. Thus, species can be ordinated along a

Table 1 Effects of morphological armament on the outcome of sexually antagonistic interactions

	Duration of pre-mating struggles			Male struggle success			Female mating activity			Female mating rate		
	β	<i>t</i>	<i>P</i>	β	<i>t</i>	<i>P</i>	β	<i>t</i>	<i>P</i>	β	<i>t</i>	<i>P</i>
Male persistence*	12.52	3.20	0.004	0.38	2.59	0.012	0.35	2.50	0.014	0.33	1.93	0.039
Female resistance*	-13.34	3.51	0.002	-0.47	3.28	0.003	-0.38	2.80	0.008	-0.35	2.09	0.029
Absolute level of arms (PC1)	0.83	0.87	0.399	0.06	1.71	0.113	0.02	0.73	0.482	0.02	0.40	0.693
Relative armament of the sexes (PC2)*	-14.83	3.13	0.004	-0.53	3.15	0.004	-0.45	2.83	0.007	-0.41	2.06	0.031

The effects of absolute and relative morphological armament on the outcome of sexually antagonistic interactions are shown. Multiple regression analyses, using behaviour as the dependent variable and either male persistence and female resistance, or PC1 and PC2, as independent variables. Regression models were based on phylogenetically independent contrasts (*n* = 14) and thus were forced through the origin¹⁷. Residuals did not differ significantly from normality (Kolmogorov–Smirnov tests, *P* ≥ 0.107 for the first and *P* ≥ 0.101 for the second group of models). Statistical power analyses of these models showed that our inability to detect any effects of absolute level of arms is not likely to be due to a lack of power. The combined probability of committing four type II errors was β = 0.129, assuming that absolute level of arms accounts for 10% of the variance in the dependent variable.

* *P* values reported test partial regression coefficients under directional null hypotheses (see Methods) and thus are one-tailed.