

LETTERS

Parental investment by skin feeding in a caecilian amphibian

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Although the initial growth and development of most multicellular animals depends on the provision of yolk, there are many varied contrivances by which animals provide additional or alternative investment in their offspring¹. Providing offspring with additional nutrition should be favoured by natural selection when the consequent increased fitness of the young offsets any corresponding reduction in fecundity². Alternative forms of nutrition may allow parents to delay and potentially redirect their investment. Here we report a remarkable form of parental care and mechanism of parent–offspring nutrient transfer in a caecilian amphibian. *Boulengerula taitanus* is a direct-developing, oviparous caecilian³, the skin of which is transformed in brooding females to provide a rich supply of nutrients for the developing offspring. Young animals are equipped with a specialized dentition, which they use to peel and eat the outer layer of their mother's modified skin. This new form of parental care provides a plausible intermediate stage in the evolution of viviparity in caecilians. At independence, offspring of viviparous and of oviparous dermatotrophic caecilians are relatively large despite being provided with relatively little yolk. The specialized dentition of skin-feeding (dermatophagous) caecilians may constitute a pre-adaptation to the fetal feeding on the oviduct lining of viviparous caecilians.

Amphibians are renowned for their diverse forms of parental investment, including hiding, guarding, transporting or feeding their offspring^{4,5}. The reproductive diversity of the tropical caecilian amphibians is more poorly known than that of salamanders and frogs, although it is known to include both oviparity, with an aquatic larva or direct development, and viviparity. Viviparous caecilians are unusual in having a specialized, deciduous, fetal dentition^{6,7} which is thought to be used to scrape lipid-rich secretions and cellular materials from the hypertrophied lining of the maternal oviduct^{6,8–11}. In contrast, it is generally thought that oviparous caecilians provision their offspring only with yolk, with additional investment limited to the attendance of egg clutches¹².

In the 1990s we discovered teeth in hatchlings of the oviparous Neotropical caecilian *Siphonops annulatus* that resemble more the fetal teeth of viviparous caecilians than the teeth of adults of this species¹³. Field observations revealed that hatchlings are altricial and remain with their mothers until they have grown substantially. Mothers also have a paler skin colour than non-attending adults. Speculating on these observations, we proposed that the fetal-like dentition of newborn *S. annulatus* is used to feed on glandular secretions of the mother's skin¹⁴, in a manner analogous to that of mammalian lactation. Here we report detailed observations of *Boulengerula taitanus*, another oviparous³ caecilian species that has

altricial¹⁵ young (see Fig. 1a) equipped with 'fetal-like' teeth, including observations of several bouts of feeding. Rather than scraping up skin secretions, the young of *B. taitanus* use their teeth to peel and eat the specially modified skin of their mothers.

Twenty-one females of the Kenyan caecilian *B. taitanus*, with broods of between two and nine young, were collected from subterranean nest sites and maintained and observed in captivity. Eight episodes of skin feeding by different young from five different broods were observed, and five were filmed (see Fig. 1b, and Supplementary movies 1 and 2). In each episode, the young moved over and around their mother's bodies, vigorously pressing their heads against their mothers while repeatedly opening and closing their mouths, and using their lower jaws in particular to lift and peel the outer layer of the mother's skin.

During one week of maternal care the young increased their total length substantially (about 11%; Fig. 1c) with average individual growth estimated to be about 1 mm per day. No alternative feeding of

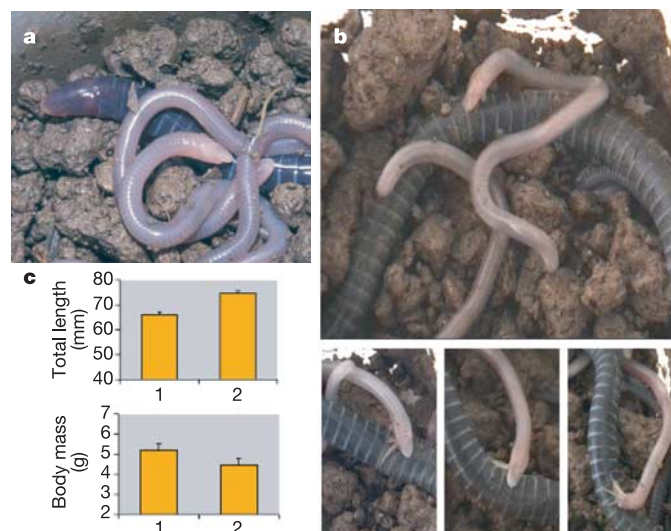


Figure 1 | Skin feeding in *B. taitanus*. **a**, Female with unpigmented young. **b**, Various stills from video footage of a young animal peeling and eating the outermost layer of its mother's skin. **c**, Changes in mean total length ($n = 66$, $P < 0.001$; t -test) of young (top) and mean body mass ($n = 15$, $P < 0.001$; paired t -test) of mothers (bottom) between a first (1) and a second (2) measurement after one week of parental care. Error bars show s.e.m.

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young was observed, and the stomachs of control young preserved in the field immediately on collection contained only monolayers of skin, indicating that ingested skin alone provides sufficient nutrients for the considerable growth observed. Maternal weight loss over the same period (about 14%; Fig. 1c) is consistent with skin feeding imposing a high cost on mothers.

Most attending females of *B. taitanus* were notably paler than non-attending adults, reflecting differences at cellular and tissue levels associated with the skin's role in nutrition (Fig. 2). The outermost layer of the epidermis, the stratum corneum, typically comprises squamous (flattened), keratinized cells (Fig. 2a), whereas in brooding females the cells are far more voluminous and full of vesicles (Fig. 2b). Overall, the epidermis of brooding females is up to twice the thickness of that of non-brooding females, as a result of elongation of the stratified epithelial cells rather than any increase in numbers of cells. Histochemistry reveals that, unlike in non-brooding females, the cytoplasm of modified epidermal cells of brooding females is full of lipid inclusions (staining positive for sudan black B). Tests for carbohydrate (alcian blue and periodic acid–Schiff) were negative. The stratum corneum is also rich in protein (staining positive for bromophenol blue) in both brooding and non-brooding females.

Adult *B. taitanus* are predators and have two rows of pointed teeth in the upper (premaxillary–maxillary and vomeropalatine) and in the lower (dentary and splenial) jaws, with either one (Fig. 3a) or two (a labial and more apical lingual) distinct cusps (Fig. 3b)³. Whereas tooth crowns of larval indirect-developing caecilians resemble those

of adults, those of the dermatophagous young of *B. taitanus* are remarkably divergent and variable (Fig. 3c–f). Bicuspid splenial teeth are present but not yet erupted. The vomeropalatine teeth and the anteriormost three or four teeth of the premaxillary–maxillary and the dentary series are monocuspid. The remaining teeth are multicuspid, combining a pronounced blade-like labial cusp with a lingual cusp that has two or three subsidiary cusps (Fig. 3d), which may be short and blunt (Fig. 3e) or have more elongate and pointed processes resembling a grappling hook (Fig. 3f). Hatchling *B. taitanus* (total length about 28 mm) have several other unusual characteristics, seemingly associated with their altriciality. The skull and axial skeleton are mostly poorly ossified in comparison with hatchlings of direct-developing species¹⁶, and the body musculature and associated external annulation are weakly developed, severely constraining mobility. By the time they become independent of their mothers

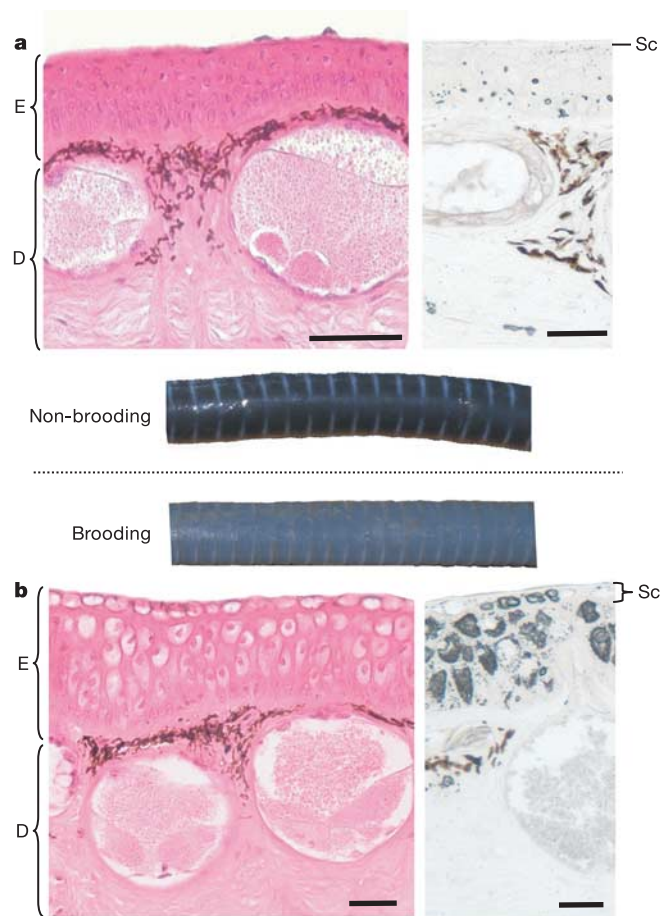


Figure 2 | Comparison of the skin of non-brooding and brooding female *B. taitanus*, showing differences in skin colour, structure and histochemistry. **a**, Non-brooding; **b**, brooding. Sections on the left were stained with haematoxylin and eosin; those on the right were stained (dark) for lipids with sudan black B. E, epidermis; D, dermis; Sc, stratum corneum. Scale bars, 50 μ m.

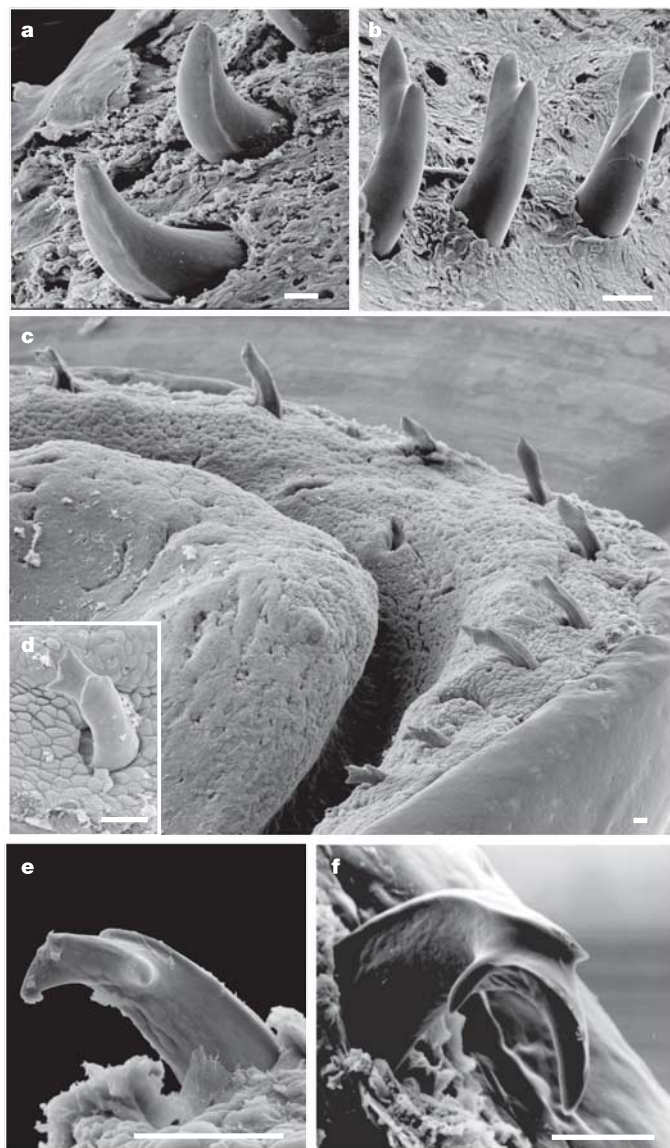


Figure 3 | Dentition of adult and young *B. taitanus*. **a**, Anterior view of two monocuspid, adult premaxillary teeth. **b**, Labial view of three bicuspid, adult vomerine teeth. **c**, Lateral view of a lower jaw of a young specimen (total length 69 mm), showing different dentary tooth crown morphologies. **d**, Labial view of a posterior dentary tooth of this young specimen. **e**, Anterior premaxillary tooth of the same specimen. **f**, Anterior premaxillary tooth of a smaller specimen (total length 57 mm) resembling a grappling hook. Scale bars, 30 μ m.

(total length about 86 mm), young resemble miniature adults in these features.

Dermatophagy, as seen in *B. taitanus*, is a highly unusual mode of parental care previously unknown in tetrapods, in which nutrient provisioning involves remarkable adaptations of both the mothers and the young. Many vertebrates periodically shed their stratum corneum and some, including caecilians, eat and recycle nutrients from their own shed skin (autodermatophagy)¹⁷. In contrast, the altricial young of *B. taitanus* depend for a time entirely on their mother's skin, which is suitably transformed to provide nutrient that, like mammalian milk, is rich in lipids. Amphibian skin is well known for its diverse functions^{18,19}, and its role in *B. taitanus* can be presumed to impose constraints upon other normal functions. For example, dermal granular glands are frequently associated with toxic secretions with a defensive function in amphibians¹⁹, and some downregulation of toxins during skin feeding might be expected. Aggressive dermatophagy could injure the mother, and we might also expect the periodic bouts of feeding to be more or less synchronized with the maternal sloughing cycle, which may itself be modified, and to involve some signalling between parent and offspring. There is clearly scope for both parent-offspring conflict and sibling competition where there is dermatotrophic parental care.

Oviparous caecilians were previously believed only to guard their eggs until hatching and to provide no subsequent parental care^{8,12}, similarly to *Ichthyophis*²⁰. This nutritional investment in offspring only in the form of yolk (lecithotrophy) is seen in all 'primitive' caecilians and is inferred to be the ancestral condition, with viviparity, and fetal feeding on the maternal oviduct lining (matrotrophy), being derived. Maternal dermatotrophy provides a highly plausible intermediate between these different reproductive modes. Current understanding of caecilian phylogeny²¹ indicates that viviparity must have evolved independently several times in caecilians, which implies striking and enigmatic convergent evolution of the associated fetal teeth. The discovery of fetal-like teeth in maternal dermatotrophic caecilians indicates that although viviparity is convergent in caecilians, one of its most distinctive features, fetal teeth, might not be. Fetal-like teeth are known also in some species of the oviparous Neotropical genera *Siphonops* and *Caecilia*^{7,13}, and the distribution of fetal and fetal-like teeth across viviparous and oviparous caecilians is consistent with their having a single origin and thus being homologous (Supplementary Information). This implies that the independently derived lineages of viviparous caecilians evolved from (possibly maternal dermatotrophic) ancestors that already possessed a specialized dentition that was preadapted to feeding in oviducts. This reconstruction and current estimates of divergence times²² indicates that fetal-like teeth evolved in the Mesozoic and that some form of skin feeding might have persisted in caecilians for at least 150 million years.

The use of fetal-like teeth in other oviparous caecilians that possess them, whether in maternal dermatotrophy as exemplified by *B. taitanus* or in some other kind of feeding, has not yet been documented. Newborns of the viviparous west African caecilian genus *Geotrypetes* are altricial and it has been speculated, but not shown, that they might feed on the maternal skin or its secretions^{14,23}. A single reported newborn of the viviparous east African caecilian genus *Scolecomorphus* has a peculiar oral morphology that might be associated with specialized feeding after parturition²⁴. Careful observation of these and other as yet unstudied caecilians may reveal additional forms of parental care that are plausible intermediates between, or might otherwise help to explain, the major evolutionary transitions in caecilian reproduction.

One potential advantage to feeding young rather than providing them with yolk alone, is that investment can be delayed and, if advantageous, redirected. Both maternal dermatotrophic and viviparous caecilians produce fewer, larger independent offspring than lecithotrophic caecilians (A.K., unpublished). Selection for larger

offspring is proposed to have driven the evolution of extended parental care in salamanders⁵ and might have similarly driven the evolution of the peculiar derived life histories in caecilians.

In recent years, the known species diversity of amphibians has been steadily increasing, mainly as a result of biodiversity surveys in the tropics²⁵. At the same time there has been growing concern about apparently declining amphibian populations worldwide. Recently the Global Amphibian Assessment identified many data-deficient species (20%) and the urgent need for more information^{26,27}. Our discovery underscores the need for further studies to improve the documentation of the amazing diversity of amphibian life-history strategies and for greater efforts to conserve it.

METHODS

We studied the caecilian *B. taitanus* in the field in southeastern Kenya (Wundanyi, Taita hills, Taita-Taveta District). Most fieldwork was performed after the short rainy season (Vuli), in January 2004 and 2005 after preliminary fieldwork in January 1996. Field-collected females and their young were housed in small plastic boxes (9 cm × 9 cm × 3.5 cm) containing earth moulded to resemble nests observed in the field. Observations were made daily from 06:00 to 09:00 and from 20:00 to 00:00. Behaviours were recorded with a digital video camera (Sony DCR-HC40E). The total length of young during parental care was measured to the nearest millimetre on plastic-coated graph paper. Female body mass was recorded with a digital balance.

Skin tissue of brooding and non-brooding females was fixed in buffered formalin and/or Bouin's fixative. Samples were embedded in accordance with standard procedures²⁸. Paraffin sections (6–8 µm) were cut with a rotary microtome and stained with either haematoxylin/eosin, sudan black B, bromophenol blue, alcian blue pH 2.5 or periodic acid-Schiff.

Tooth morphology of young and adults was examined with a scanning electron microscope (Hitachi 2500 series). Samples were transferred through an acetone series and critical-point dried with carbon dioxide, mounted on aluminium stubs and sputter-coated with gold-palladium.

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Supplementary Information is linked to the online version of the paper at www.nature.com/nature.

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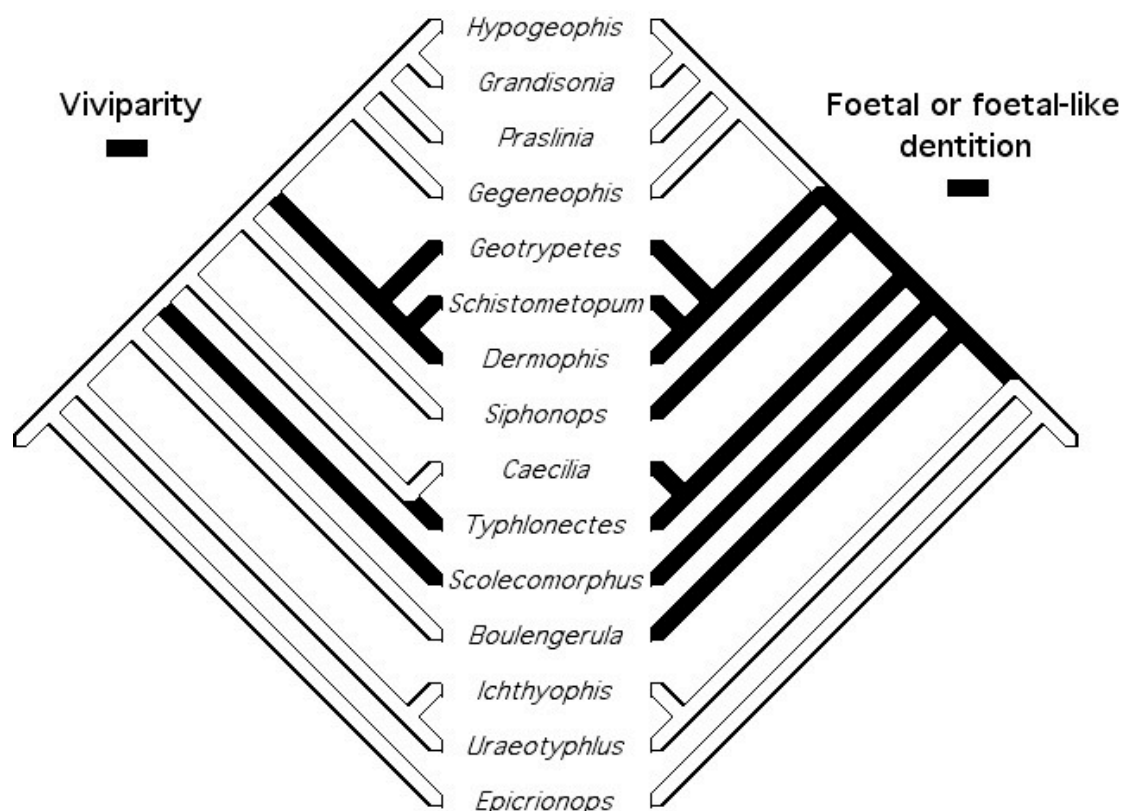
Supplementary data

Supplementary Video 1

Excerpt of a real time video clip of skin feeding in *Boulengerula taitanus* taken on January 21, 2005. Dermatotrophy is otherwise unknown in tetrapods but a form of skin feeding occurs in some cichlid fishes (e.g. *Symphysodon aequifasciatus*) where young feed upon the proliferated multilayered epidermis of both parents (Bremer, 1999), rather than peeling a specialised monolayer of the maternal epidermis.

Supplementary Video 2

Excerpt of a real time video clip of skin feeding in *Boulengerula taitanus* taken on January 21, 2005. Stills (video captures) from this sequence appear in Fig. 1b of the text.



Supplementary Figure 1

Distribution, and parsimonious interpretation of the evolution of, viviparity and of modified foetal or foetal like teeth. Reconstruction uses the maximum likelihood tree

recovered in the most recent broad phylogenetic analysis of caecilian interrelationships using molecular sequence data²¹. At least three independent origins are needed to account for the observed distribution of viviparity (defined here as young hatching before eggs are laid) in caecilians, whereas a single origin accounts for the presence of foetal and foetal like teeth in the viviparous and oviparous caecilians that have them. Indirect developing caecilians

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