

A new Early Carboniferous tetrapod with a *mélange* of crown-group characters

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Living (that is, crown-group) tetrapods represent the phylogenetic end-points of two lineages which diverged from each other during the mid/late Palaeozoic era. These two groups of tetrapods are the Amphibia (frogs, salamanders and caecilians), with their roots among temnospondyls^{1,2}, and the Amniota (mammals, turtles, crocodiles, birds, lizards and snakes), with their roots among anthracosaurs^{3,4}. The earliest representatives of both lineages, including a stem amniote, are known from the Viséan of East Kirkton, Scotland⁵. Here I describe a new taxon from this locality that not only combines characters of each lineage, but also represents the basal member of a third Palaeozoic group, the baphetids. The baphetids lie within the base of the crown clade of tetrapods and the morphology of the new taxon, their most primitive member, is a new benchmark for studying the polarity and evolution of crown tetrapod characters.

The specimens derive from Unit 82, the black shale member of the East Kirkton Limestone⁶. This locality has already yielded many important tetrapod fossils, including the earliest temnospondyl⁷, the two earliest anthracosaurs^{8,9}, the stem amniote *Westlothiana*¹⁰ and an aistopod¹¹. It has also yielded early terrestrial invertebrates such as eurypterids¹², scorpions¹³, myriapods¹⁴ and an opilionid¹⁵. The assemblage is considered to be one of the oldest assemblages that is indisputably terrestrial¹⁶, and is thought to have been preserved in association with a shallow lake that was subject to hydrothermal activity. At most times, the chemical-rich waters of the lake were probably inimical to vertebrate life but the shores supported a rich flora and fauna¹⁶.

Osteichthyes

Division: Crown group Tetrapoda Goodrich 1930

Order: undesignated

Family: Baphetidae Cope 1875

Eucritta melanolimnetes gen. et. sp. nov.

Etymology. Eu (Greek) true; critta (American vernacular): creature; *melano* (Greek): black; *limnetes* (Greek): living in a pool or marsh, from the black lagoon (in reference to the locality of East Kirkton).

Holotype. UMZC (University Museum of Zoology, Cambridge) T1347a and b; an almost complete articulated individual of skull length 50 mm.

Referred material. UMZC T1348 a and b, UMZC T1285 a and b and NMS (National Museums of Scotland) 1992.14 part and counterpart.

Locality. East Kirkton Quarry, near Bathgate, West Lothian, Scotland, UK.

Horizon. Unit 82 of the East Kirkton Limestone, Bathgate Hills Volcanic Formation.

Age. Brigantian, Viséan, Lower Carboniferous.

Diagnosis. Derived characters: postorbital broadly crescentic with no ventral process into orbit margin, supratemporal broadly crescentic, short snout with square or hexagonal nasals, temporal notch conspicuous with distance from its apex to the orbit margin less than the diameter of the orbit, skull table approximately square, maxillary dentition about 38–40 tooth positions including a peak at positions 7–14. Characters shared with baphetids: anteroventral embayment to orbit in (at least) larger individuals, supratemporal surrounds majority of temporal notch to the exclusion of the squamosal, narrowly triangular ventral plate to clavicle subtending

an angle of ~30° from lateral to medial. Primitive tetrapod characters: full complement of dermal roofing bones including intertemporal, supratemporal–postparietal contact, large orbits, closed palate with denticulated pterygoids meeting in the midline, broad vomerine region, fang pairs on vomers and palatines, denticulated parasphenoid with elongate triangular body, unsutured basal articulation, lozenge-shaped interclavicle, L-shaped humerus, long cleithra well ossified and expanded distally, scapulocoracoid a single ossification, cervical ribs somewhat expanded, trunk ribs scarcely curved, pentadactyl pes, ilium with both dorsal blade and posterior process, ventral armour of narrow gastralia.

The taxon is represented by four specimens, the skulls of which vary in length from 30 mm to about 90 mm. Two of these skulls preserve postcranial material. The skull roof of this species is superficially similar to that of the contemporary temnospondyl *Balanerpeton*⁷, sharing the short snout, large orbits, conspicuous temporal notch and primitive pattern of skull table bones, which show supratemporal–postparietal contact. Subtle differences distinguish them, such as the shape of the parietal plate, the position of pineal foramen, the shape of the postorbital and the extent of the contribution of the supratemporal to the margin of the temporal notch. The palate, however, does not possess the large interpterygoid vacuities that are characteristic of temnospondyls, but has the primitive closed structure that is found in other early tetrapods, including anthracosaurs and baphetids (Fig. 1). The largest specimen shows that the orbit was slightly excavated into an embayment at the anteroventral corner. A highly exaggerated version of this embayment is one of the characters that unites the other baphetids¹⁷, so *Eucritta* shows what appears to be a more primitive expression of this unusual feature.

The postcranial skeleton includes a lozenge-shaped interclavicle and an ilium bearing both a dorsal blade and a posterior process (Fig. 2), features which are also associated with other early groups including the Devonian genus *Acanthostega*¹⁸, anthracosaurs and lepospondyls¹⁹. Until recently, the postcranial skeleton morphology of baphetids (formerly known as loxomatids²⁰) was unknown, but it is now known that *Baphetes* too possesses a biramous ilium²⁰. There are also similarities in the humerus such as the shape of the entepicondyle, which is found as a quarter circle rather than as the rectangle that is found in many other tetrapods. The elongate gastralia of *Eucritta* more closely resemble those of *Baphetes* than those of *Balanerpeton*. The poorly ossified axial skeleton of *Eucritta* may likewise be characteristic of baphetids as a group, explaining why axial material in particular and postcranial material in general has so rarely been found.

The phylogeny derived from the current data set is not particularly robust (Fig. 3). This instability undoubtedly results from the extreme degree of character conflict that *Eucritta* presents, and the computed phylogeny is to that extent in agreement with initial subjective impressions. One of the more strongly supported nodes is that which places *Eucritta* as a basal baphetid (node 10). A further strong signal is that baphetids as a whole lie within the crown group (node 4) if temnospondyls and anthracosaurs are both taken to be early members of it, as is accepted by the majority of workers^{1–4} (but see ref. 21 for a conflicting view). Baphetids do not appear as a stem tetrapod plesion in any trees suggested by this analysis, but cluster more consistently with anthracosaurs than with temnospondyls.

The morphology and phylogenetic position of *Eucritta* have wide implications for studies of early tetrapods. The anterior orbital extensions of baphetids appear as small embayments in the largest skull of *Eucritta*, indicating that they may have developed by peramorphosis among more derived forms. Baphetids, like temnospondyls^{7,22} and anthracosaurs^{8,9} originated as small to medium-sized terrestrially adapted forms and each lineage convergently radiated into large, aquatic, coal-swamp piscivores. Many terrestrial forms had thus evolved by the late Viséan. The large temporal notch of *Eucritta* is difficult to interpret functionally as the

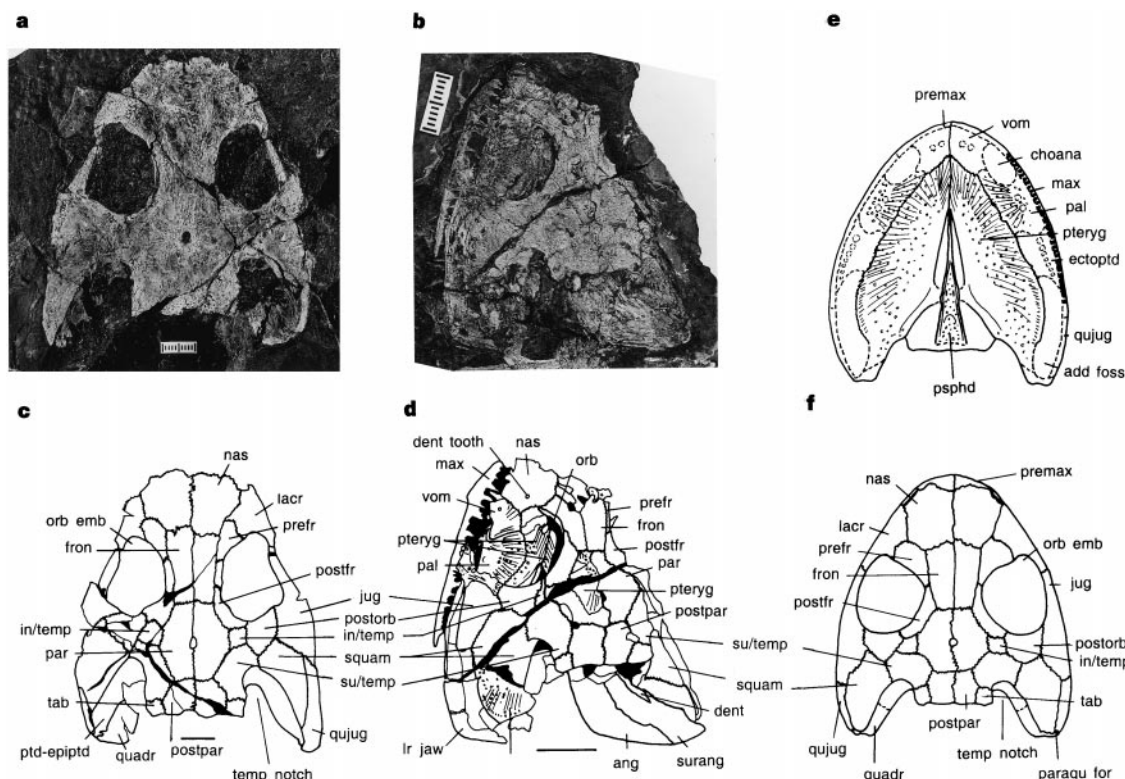


Figure 1 Skull of *Eucritta melanolimnetes*. **a**, Photograph of specimen NMS 1992.14; internal view of skull roof. **b**, Photograph of UMZC T1347b; close-up of skull in dorsal view. **c**, Composite specimen drawing from NMS 1992.14; part and counterpart (reversed from internal view). **d**, Interpretive drawing of UMZC T1347b, showing parts of palate. **e, f**, Reconstruction of palate (top) and skull roof

(bottom) of *Eucritta*; outline is based on UMZC T1347, palate on UMZC T1347 and T1348, orbital embayments from NMS 1992.14, parasphenoid from UMZC T1285. Areas coloured black represent cracks. Scale bars represent 10 mm. For abbreviations, see Methods.

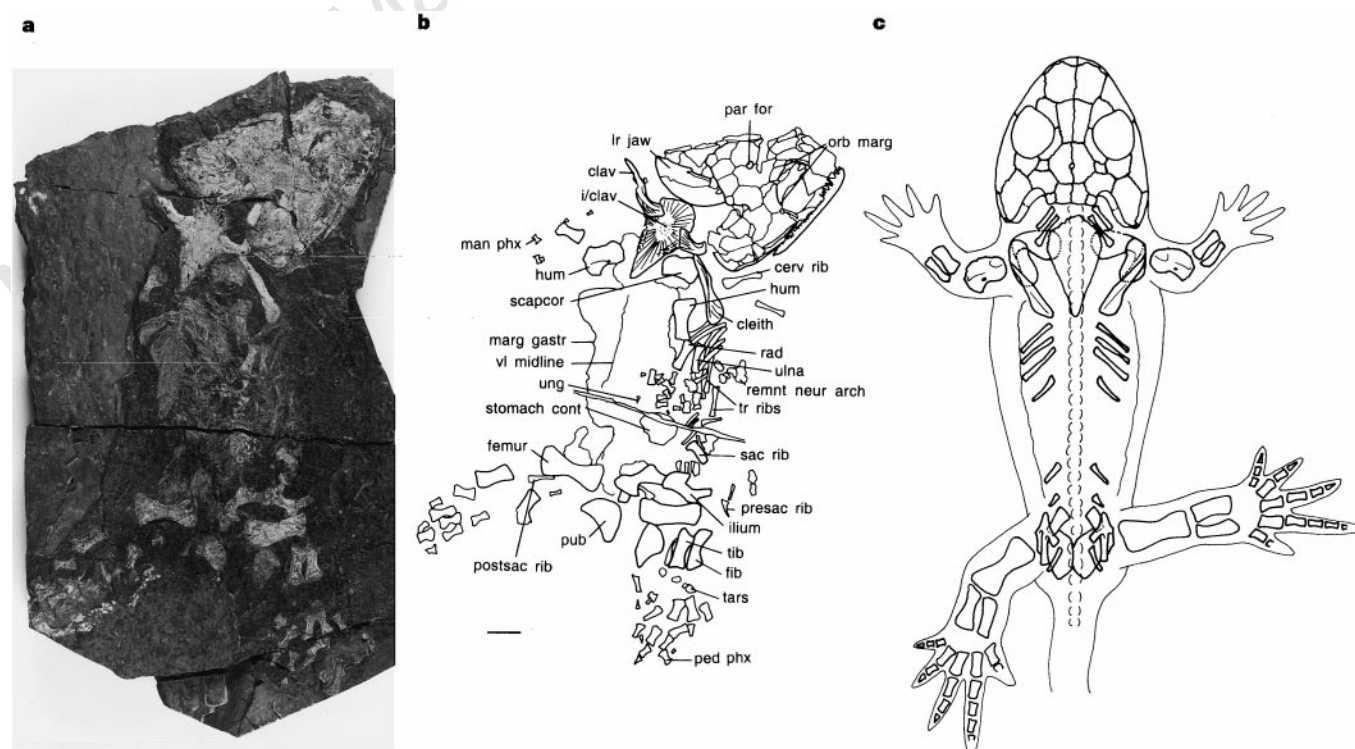


Figure 2 Body of *Eucritta melanolimnetes*. **a**, Photograph of specimen UMZC T1347a, in ventral view. **b**, Interpretive drawings of UMZC T1347a; specimen shown in ventral view. **c**, Reconstruction of postcranial skeleton based on specimen UMZC T1347. Elements from the right and left sides are freely duplicated. The carpus, tarsus and vertebrae are barely ossified; the number of

presacral vertebrae is proposed to be 24. The number of digits on the manus is unknown. *Eucritta* is a short-bodied form, with hind limbs that are conspicuously larger than the forelimbs. The dashed lines show reconstructed margins; the dotted lines show outlines of parts not visible in dorsal view. Scale bars represent 10 mm. For abbreviations, see Methods.

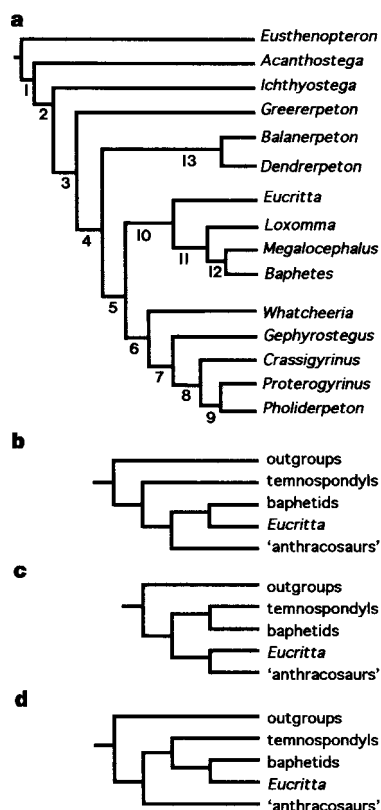


Figure 3 Phylogenetic analysis. **a**, The single most parsimonious tree. **b**, Trees placing *Eucritta* as a basal baphetid, with this clade as the sister group to anthracosaurs plus *Whatcheeria* and *Crassigyrinus* ('anthracosaurs'). **c**, Trees placing *Eucritta* with the anthracosaurs plus *Crassigyrinus* and *Whatcheeria*, and that clade as the sister group to baphetids plus temnospondyls. **d**, Tree placing *Eucritta* with the baphetids as the sister pair to temnospondyls and this clade as the pair to anthracosaurs plus *Whatcheeria* and *Crassigyrinus*. Characters supporting nodes 5, 6 and 10 are: 27, postparietal occipital exposure present; 37, suture of squamosal with supratemporal ventrally placed in embayment; 50, parasphenoid body with single median depression; 61, maxillary tooth number fewer than 30; 67, parasphenoid shagreen field situated both anterior and posterior to basal articulation; 70, premaxillary tooth number fewer than 10; 86, skull table/cheek junction square/abrupt profile; 103, trunk ribs ventrally curved; 104, length of trunk ribs more than twice the height of the neural arch plus centrum; 109, scutes tapered and elongate. (Characters 67 and 109 support their respective nodes only in their plesiomorphic state.)

stapes is unknown, but later baphetids had stapes of primitive form that are like those of the earliest tetrapods²³ and which are not associated with tympanic ears^{24–26}. The large notch in *Eucritta*, even if not part of a tympanic ear, represents a feature from which the notch in temnospondyls may have developed. *Eucritta* has a mixture of characters from three apparently diverse groups, the baphetids, temnospondyls and anthracosaurs, indicating that these three groups, which include the two crown-group lineages, diverged only a little earlier in the Carboniferous, rather than having been separate since the Devonian^{18,27}. Finally, *Eucritta* provides an important new outgroup taxon against which to examine the character polarity, and thus the phylogeny, of early crown-group members. □

Methods

Phylogenetic analysis. I analysed 15 taxa and 111 characters (87 cranial and 24 postcranial; see Supplementary information), using the phylogenetic packages PAUP²⁸ and MacClade²⁹. The taxa were chosen to represent a range of early tetrapods and members of established groups such as temnospondyls, baphetids and anthracosaurs. None of the 'lepospondyl' groups was included.

An heuristic search gave a single most parsimonious tree of length 269, consistency index 0.53 and retention index 0.57; in this tree *Eucritta* was placed as the most basal member of a clade containing three other baphetid species (*Megaloccephalus pachycephalus*, *Baphetes kirkbyi* and *Loxomma acutirhinus*). This clade emerged as the sister group to one containing the anthracosaurs species *Gephyrostegus bohemicus*, *Pholiderpeton scutigerum* and *Proterogyrinus scheeli*, as well as two other early tetrapods, the monospecific genera *Whatcheeria* and *Crassigyrinus*. That grouping proved to be the sister group to the group consisting of temnospondyls *Dendrerpeton acadianum* and *Balanerpeton woodi*. At the base of the tree, three monospecific tetrapod taxa, *Greererpeton*, *Ichthyostega* and *Acanthostega*, appeared as successively more primitive plesions. The tristichopterid fish *Eusthenopteron foordi* was used as the outgroup. A branch and bound analysis produced two equally parsimonious trees of length 269. One of these had an identical topology to that produced by the heuristic search, whereas the second was of the pattern shown in Fig. 3c.

An heuristic search made for all trees of length 270 or less resulted in recovery of a further nine trees. Of all these ten trees, three variants can be identified. Four trees (including the most parsimonious) placed *Eucritta* as a basal baphetid, with this clade as the sister group to the group consisting of the anthracosaurs plus *Whatcheeria* and *Crassigyrinus*. Five trees placed *Eucritta* with the anthracosaurs plus *Crassigyrinus* and *Whatcheeria*, and placed that clade as the sister group to baphetids plus temnospondyls. One tree placed *Eucritta* with the baphetids as the sister pair to temnospondyls, and this clade as the pair to anthracosaurs plus *Whatcheeria* and *Crassigyrinus*. Apart from the position of *Eucritta*, the major clades usually remained intact, the arrangements of genera within each clade being the main source of inconsistency. An analysis of skull characters produced similar groupings but placed *Eucritta*, the baphetids and the temnospondyls together more frequently.

A strict consensus of the ten trees places *Eucritta*, *Whatcheeria*, the temnospondyls, the baphetids and *Crassigyrinus* plus the anthracosaurs in an unresolved polytomy. A 50% majority rule consensus resolves the position of *Whatcheeria* and places it at the base of the anthracosaur/*Crassigyrinus* clade, but makes no difference to the other nodes. Computing a consensus tree is a less informative exercise than analysing the ten trees separately, and disguises the occurrence of three distinct patterns.

In the single most parsimonious tree from the heuristic search, basal nodes 2–4 each have many (more than nine) unambiguous characters supporting them, and these remain stable in the strict consensus tree. Node 5 (*Eucritta* and the baphetids plus the 'anthracosaurs') has only two unambiguous characters supporting it (characters 50 and 103), with a further five equivocal ones. This is the least strongly supported node in the cladogram, and is the one which breaks down most frequently in trees of one step longer. Five unambiguous characters (characters 27, 37, 61, 67 and 109) and a further four equivocal ones support node 10 (*Eucritta* plus remaining baphetids), whereas three unambiguous characters (characters 70, 86 and 104) and a further four equivocal ones support node 6 (the 'anthracosaurs').

Abbreviations used in figures. add foss, adductor fossa; ang, angular; cerv rib, cervical rib; clav, clavicle; cleith, cleithrum; dent, dentary; ectoptd, ectopterygoid; fib, fibula; fron, frontal; hum, humerus; i/clav, interclavicle; in/temp, intertemporal; jug, jugal; lacr, lacrimal; lr jaw, lower jaw; man phx, manual phalanx; marg gastr, margin of gastralia; max, maxilla; nas, nasal; orb, orbit; orb emb, orbital embayment; orb marg, orbit margin; pal, palatine; par, parietal; par for, parietal foramen; paraqu for, paraquadrate foramen; ped phx, pedal phalanx; postfr, postfrontal; postpar, postparietal; postorb, postorbital; postsac rib, postsacral rib; prefri, prefrontal; premax, premaxilla; presac rib, presacral rib; psphd, parasphenoid; pteryg, pterygoid; ptd-epitd, pterygoid-epiterygoid complex; pub, pubis; quadr, quadrate; quijug, quadratojugal; rad, radius; remnt neur arch, remnant of neural arch; sac rib, sacral rib; scapcor, scapulocoracoid; stomach cont, ball of stomach contents; surang, surangular; su/temp, supratemporal; squam, squamosal; tab, tabular; tars, poorly ossified tarsus; tib, tibia; tr ribs, trunk ribs; temp notch, temporal notch; ung, ungual; vl midline, ventral midline; vom, vomer.

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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.

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Adaptive radiation in a heterogeneous environment

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Successive adaptive radiations have played a pivotal role in the evolution of biological diversity^{1–3}. The effects of adaptive radiation are often seen^{4–6}, but the underlying causes are difficult to disentangle and remain unclear^{7–9}. Here we examine directly the role of ecological opportunity and competition in driving genetic diversification. We use the common aerobic bacterium *Pseudomonas fluorescens*¹⁰, which evolves rapidly under novel environmental conditions to generate a large repertoire of mutants^{11–13}. When provided with ecological opportunity (afforded by spatial structure), identical populations diversify morphologically, but when ecological opportunity is restricted

there is no such divergence. In spatially structured environments, the evolution of variant morphs follows a predictable sequence and we show that competition among the newly evolved niche-specialists maintains this variation. These results demonstrate that the elementary processes of mutation and selection alone are sufficient to promote rapid proliferation of new designs and support the theory that trade-offs in competitive ability drive adaptive radiation^{14,15}.

Explanation of macroevolutionary phenomena (for example, adaptive radiation and punctuated evolution) by direct extrapolation from microevolutionary processes (for example, mutation and competition) is contentious^{1,16–18}. Conventional explanations for adaptive radiation frequently invoke no more than vacant niches and stringent competition between niche specialists^{14,19–21}. Experimental studies have lent credence to this view²², but by necessity

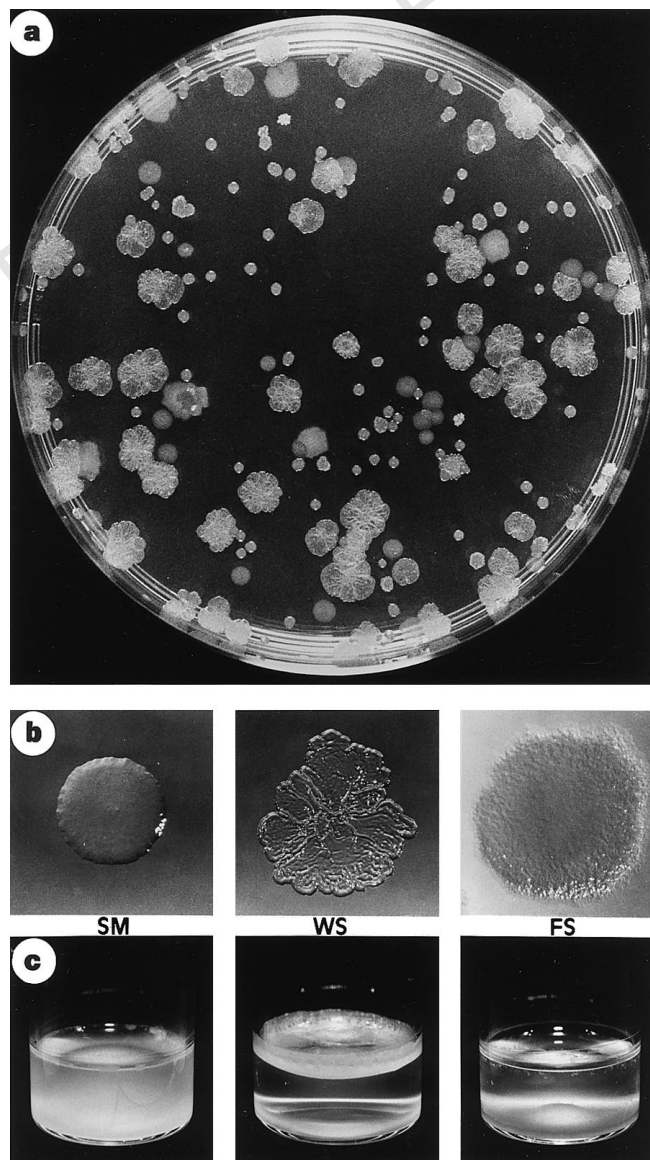


Figure 1 Phenotypic diversity and niche specificity among *P. fluorescens* SBW25 colonies evolved in a spatially heterogeneous environment. Populations were founded from single ancestral 'smooth' (SM morph) cells and propagated in 6-ml King's medium B contained in a 25-ml microcosm at 28°C. Microcosms were incubated without shaking to produce a spatially heterogeneous environment. **a**, After 7 days, populations show substantial phenotypic diversity which is seen after plating. **b**, Most phenotypic variants can be assigned to one of three principle morph classes: (SM), wrinkly spreader (WS) and fuzzy spreader (FS). **c**, Evolved morphs showed marked niche preferences.