

A fiftieth anniversary reflection on the living coelacanth, *Latimeria chalumnae*: some new interpretations of its natural history and conservation status*

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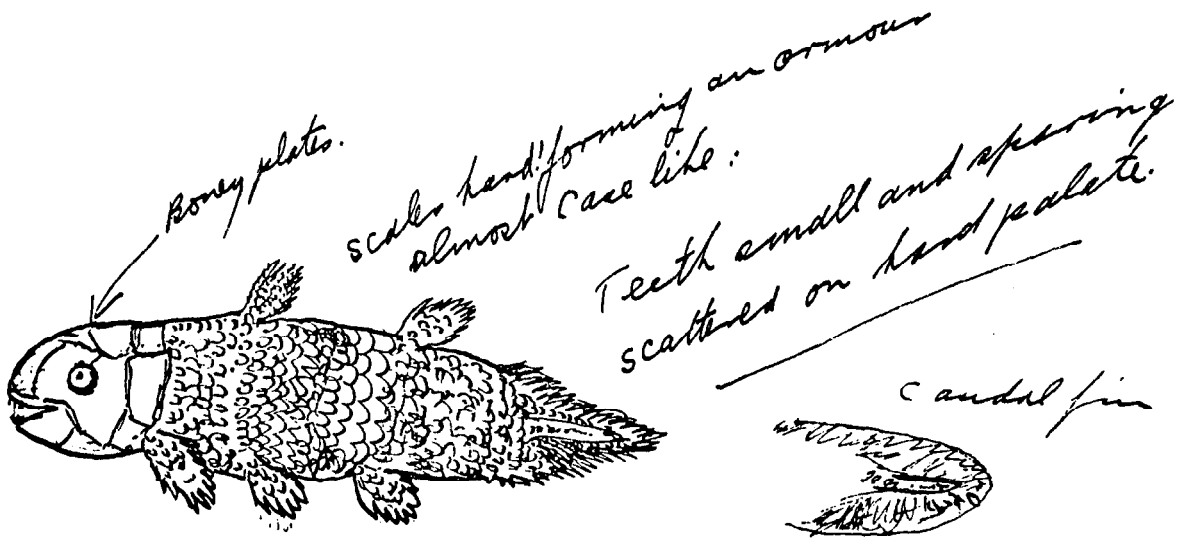
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Synopsis

It all started about 400 million years ago, when representatives of a group of fish-like fleshy-finned creatures appeared in the fossil record (or was it through a childhood dream shared by all of us that we would one day study the coelacanth?). Many of the coelacanth's characters placed them close to the ancestry of terrestrial vertebrates. About 70 million years ago they disappeared from the fossil record. The discovery in 1938 of the first living coelacanth, in 1952 of the second and until now over 200 specimens parallels in excitement an encounter with a live dinosaur on a weekend walk, and in significance even more than that. For this year's 50th anniversary of the famous discovery of the first living coelacanth, we retraced the routes and visited the main actors of this zoological drama. New insights into coelacanth natural history were facilitated by novel interpretation of earlier data and our expeditions to the Comoro Islands, retracing the route of the second specimen, measuring unrecorded specimens, interviewing fishermen and describing their fishing crafts, and taking part in recent events on land and water near the only known habitat of the living coelacanth. Entry into this habitat and observations from the research submersible GEO opened up a new era in coelacanth research. Past studies of preserved specimens, which were caught as an incidental bycatch, were supplemented for the first time by studies of free-living coelacanths in their natural habitat. The first film footage taken from the submersible revealed the entirely unfishlike movements of this creature. Its mode of locomotion is a combination of flying and gliding, interspersed with head stands and belly-up drifts which appear to defy gravity. The narrow range of habitat in which the coelacanth has been encountered has led us to realize how vulnerable this ancient relict is. The members of our expeditions therefore cooperated in establishing an international organisation to coordinate efforts to conserve the coelacanth.

* Editorial



Colour Dark grey black. (uniform)

Length. 4. 1/2 ft.

depth of body 18 inches

depth of tail 12 inches.

length of fins.

Spinous dorsal.	8"
Soft dorsal	9"
Pectoral	12"
Pelvic	8"
ANAL	12"

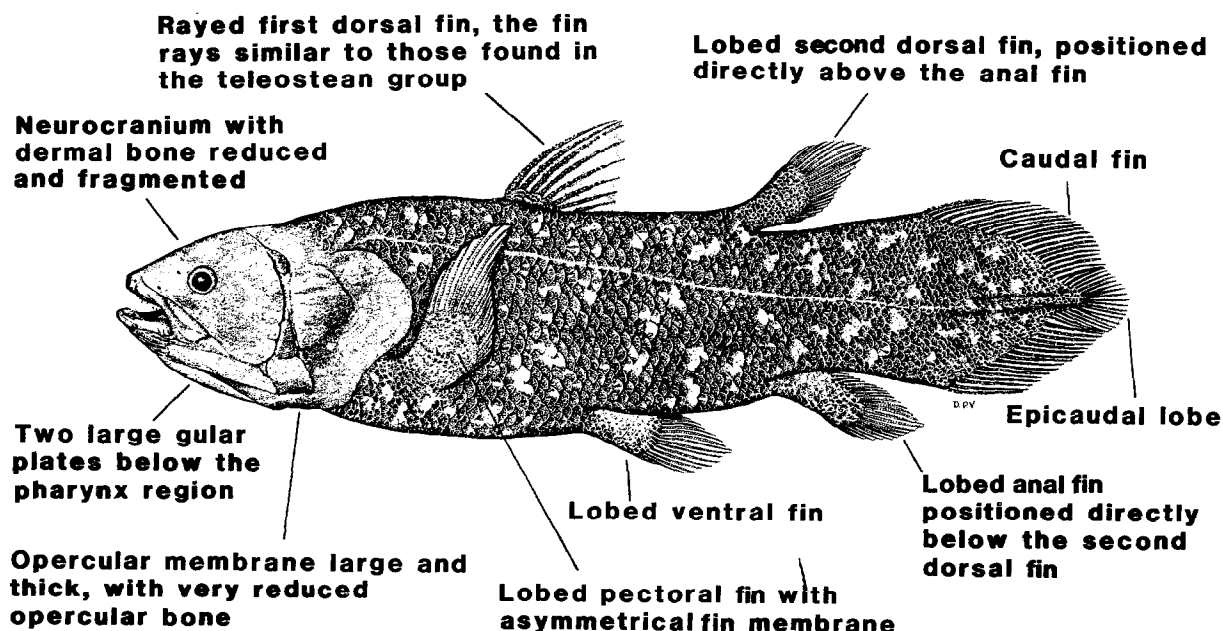
The most important part of the letter Marjorie Courtenay-Latimer wrote to J.L.B. Smith and which started it all.

Introduction

'22 December 1938 dawned a hot, shimmering summers day. At 10:30 my newly installed phone rang to say the trawler Nerine had docked and had a number of specimens for me. I was busy completing the creating of a fossil reptile in a case, and at first thought "what shall I do with fish now? So near Christmas?" Then I considered I should go down and wish the men on the trawler a "Happy Christmas". So I rang for a taxi and went down to the fishing wharf. It was now 11:45 and all the men had left leaving an old Scotsman who said "Lass they have all gone but I will show you the specimens set aside for you by Capt. Goosen." . . .'. With these words Marjorie Courtenay-Latimer (1979, p. 7) recollected the events leading to the great discovery which has, ever since, excited scientific and public consciousness alike (see Smith 1956).

In 1986 and 1987 the three of us began retracing the routes and revisiting and interviewing the main actors in this great biological drama in preparation for this 50th anniversary. At the same time the submersible GEO opened up a new era in coelacanth exploration by facilitating direct observa-

tions of the beast in its natural habitat. Two films which celebrate the jubilee anniversary have been released and broadcast ('The story of the coelacanth' filmed and produced by M. Vincent in South Africa and 'Coelacanth – living fossil in the Indian Ocean' filmed and produced by H. Fricke in West Germany). Recently, a number of papers have been published on the locomotion (Fricke et al. 1987), habitat (Fricke & Plante 1988), taxonomic relationships (Northcutt 1986, Robineau 1986, Fritzsche 1987), morphology (Hensel 1986, Bjerring 1986), palaeontology (Forey 1984), physiology (Kihira et al. 1984, Waehneltd et al. 1986), conservation status (Bruton 1988) and other aspects of the coelacanth story (e.g. Thys 1984, Bell 1984, van der Merwe 1985, Fricke & Schauer 1987, Fricke 1988, Munnion 1988, Globig 1988, Lizmore 1988, and even Isaac Asimov 1987). Most recently, research has been conducted on frozen coelacanth specimens using advanced computerised X-ray tomography and magnetic resonance imaging (see Cloutier et al. 1988) as well as on endocrinology, DNA and RNA, blood proteins, gonadal steroids, parasitology, xenobiotics, and the cytochrome p450 system, to mention a few, by a group of scientists in association with the Virginia Institute of Marine



Science (see University of Washington 'University Week' 5 (15) Jan 28, 1988, Harden 1988, and H.-P. Schultze, personal communication). An anniversary anthology of reviews and new research is in preparation (Bruton, Musick & Greenwood 1989). In this editorial we attempt a brief review and synthesis of old and new findings that are relevant to an understanding of the urgent need to protect this 'living fossil'.

History of early captures

The story of the capture of the first coelacanth is a tale of remarkable coincidences and even more remarkable people. An enlightened trawler skipper, Hendrik Goosen, who made a habit of collecting specimens for the aquarium and museum in East London, was caught in bad weather off the eastern Cape coast (South Africa) and, on heading for home, decided to shoot his trawl once more in water about 70 m deep several kilometers off the Chalumna River mouth (Fig. 1). A cold-water upwelling had occurred and he hoped to catch unusual fishes. His catch consisted of a number of sharks

which he did not usually catch and a large blue fish which he had never seen before. The large fish was still alive when it landed on board and in fact snapped at him when he tried to lift it. It would not fit into the onboard aquarium so it was left on deck where it survived for several hours.

On arriving in East London harbour he ordered an Irvin & Johnson clerk to telephone the young curator of the museum, Miss (later Dr.) Marjorie Courtenay-Latimer (Fig. 2), then 22, who decided to go to the harbour to examine the fishes (Fig. 3). She was intrigued by the large blue fish and was determined that it must be kept. Intuitively suspecting something most unusual (a lungfish perhaps?), she sent a letter to J.L.B. Smith, then a Senior Lecturer in Chemistry and also a recognized ichthyologist at Rhodes University in Grahamstown (and Honorary Curator of Fishes for the East London Museum), with a description of the peculiar fish.

James Leonard Brierley Smith was at the time on Christmas leave at his holiday house on the edge of Knysna Lagoon and the letter only reached him on January 3rd, 1939. In disbelief he realized that the fish was probably a crossopterygian, a group

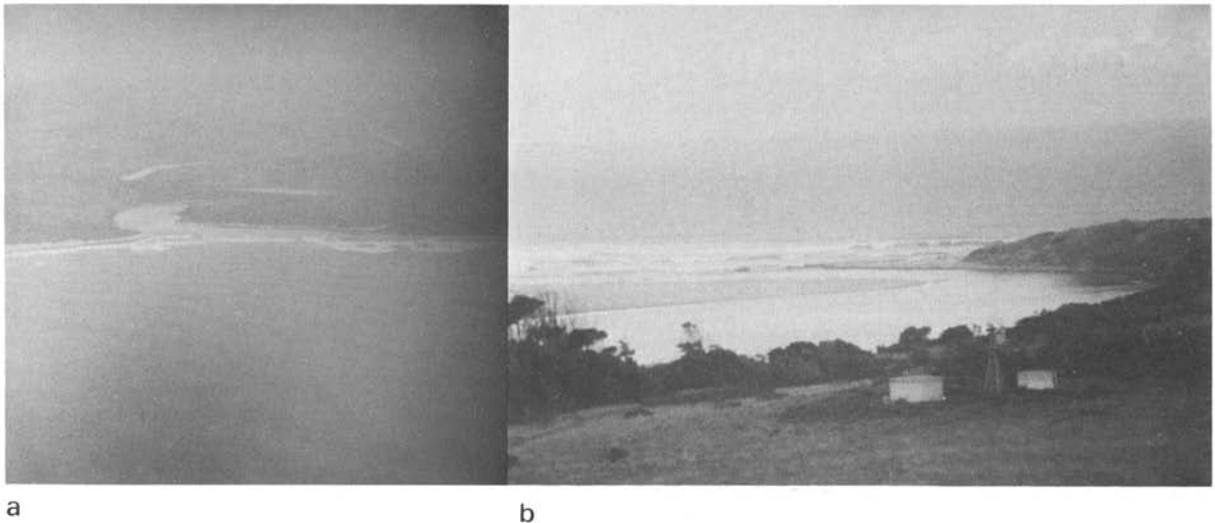


Fig. 1. On the return journey from the Comoro Islands the captain of our aircraft was so intrigued by the saga that upon take-off from East London he kept the large Boeing low and over the assumed coelacanth capture locality in the Indian Ocean of the trawler Nerine and enabled this photograph (a) of the Chalumna River estuary (3 May, 1987). Later we decided to reach the Chalumna River mouth from inland (b), finding no road but dangerously wet paths over grassy hills only (12.5.1987). All photographs in this article by E.K. Balon except when given otherwise.



Fig. 2. Dr. Marjorie Courtenay-Latimer at the entrance to the East London Museum, still charming in her retirement (5 April, 1987).

thought extinct for the last 70 million years. Due to a lack of refrigeration facilities, and despite Miss Courtenay-Latimer's best efforts to preserve the whole fish (cf. Lizmore 1988), the soft inner parts had to be discarded, even before the telegram from Smith alerted her to the importance of the find. (On our visit last year, she was still most unhappy about this.) Heavy rains made some roads impassable, and the Smiths were only able to reach East London six weeks later to confirm that it was truly a member of the 'extinct' group of lobe-finned fishes. Subsequent descriptions of the coelacanth by J.L.B. Smith (1939a-d, 1940) caused an immediate sensation (e.g. Gross 1939, Woodward 1940), and he was heralded (and mocked) by scientists and laymen throughout the world. The loss of the soft

parts had, however, denied him the opportunity to describe the internal organs of an animal of such an ancient origin, and he vowed to find another specimen.

His search took 14 years, and it was only in December 1952 that a second coelacanth was caught, this time at its true home, the Comoro Islands (Fig. 4). His dramatic quest is well described in one of the few 'biological thrillers' ever published ('Old Fourlegs', Smith 1956).

At last he was able to study and describe the internal anatomy (Smith 1953a, b), after which he felt that his task had been completed. Most of the subsequent specimens, all captured off the islands of Grand Comoro and Anjouan in the Comoro archipelago (Fig. 5), went to France, where they



Fig. 3. For the sake of our anniversary film we brought the three main actors of the first coelacanth drama – (from right to left) H. Goosen, M. Courtenay-Latimer and the ‘taximan’, C.D. Harrold, who strongly objected to take the fish – together for the first time in 49 years to the spot where *Nerine* was moored with the fish on board (5 April, 1987).

were subject to detailed anatomical studies by a team of French scientists consisting of J. Millot and J. Anthony and, later, D. Robineau and M. Lemire (e.g. Millot 1954, Millot & Anthony 1958a, b, 1965, Millot et al. 1978). In the past two decades scientists from other nations have also conducted intensive studies on the approximately 130 specimens which are in museum collections (see reviews by Millot et al. 1972, McCosker 1979, Locket 1980, Forey 1980, 1984). Since 1952 a known catch of 2 to 12 individuals per year has been made, with a total catch of about 200 specimens, of which only about 130 can definitely be traced. A more complete list will be published in the forthcoming anniversary volume (Bruton et al. 1989), for which any supplementary data are hereby requested.

Why is the living coelacanth so remarkable?

A complete review of the literature on the living coelacanth will not be attempted, especially since much of it has been summarized by McCosker & Lagios (1979) and Locket (1980), and will again be reviewed in Bruton et al. (1989). We will limit our review to the essential highlights only and to interpretations other than those previously made. Special attention will be given to the newest findings from our recent expeditions and to the significance of these findings to the conservation of the coelacanth.

Evolution

Coelacanths are first known from Upper Devonian fossils about 400 million years old (Fig. 6). They were once widespread in seas and inland waters throughout the world, although they all had basi-

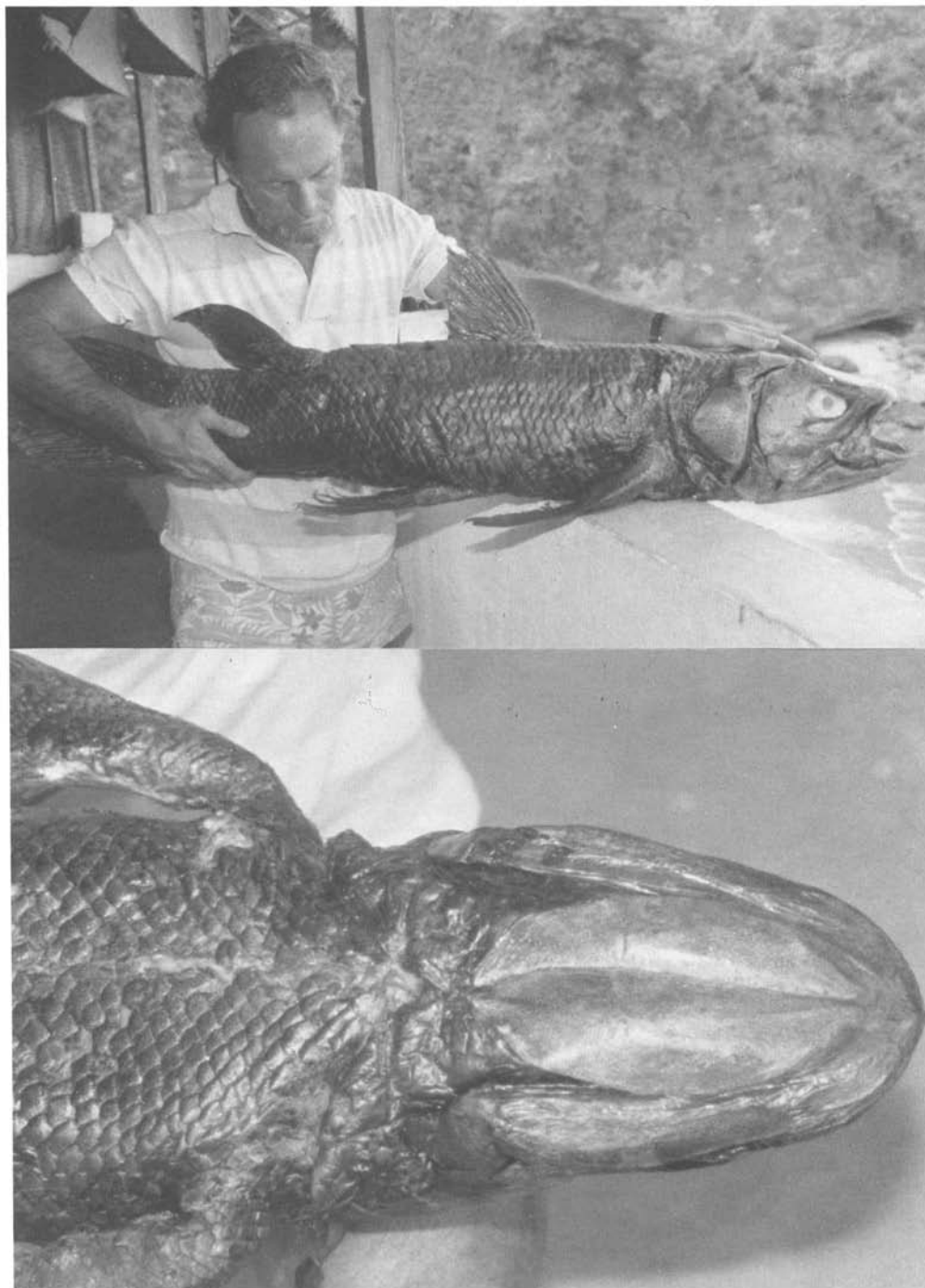


Fig. 4. In Domoni on Anjouan where the second coelacanth was landed 35 years ago, we found an unrecorded and poorly preserved specimen of *L. chalumnae*, which we measured, on display in restaurant Karima. Later we learned that the transport of the 1952 specimen was not as dramatic as reported by J.L.B. Smith (1956); instead of being carried laboriously across the mountains it was driven in the Governor's jeep to Mutsamudu (29 April, 1987).

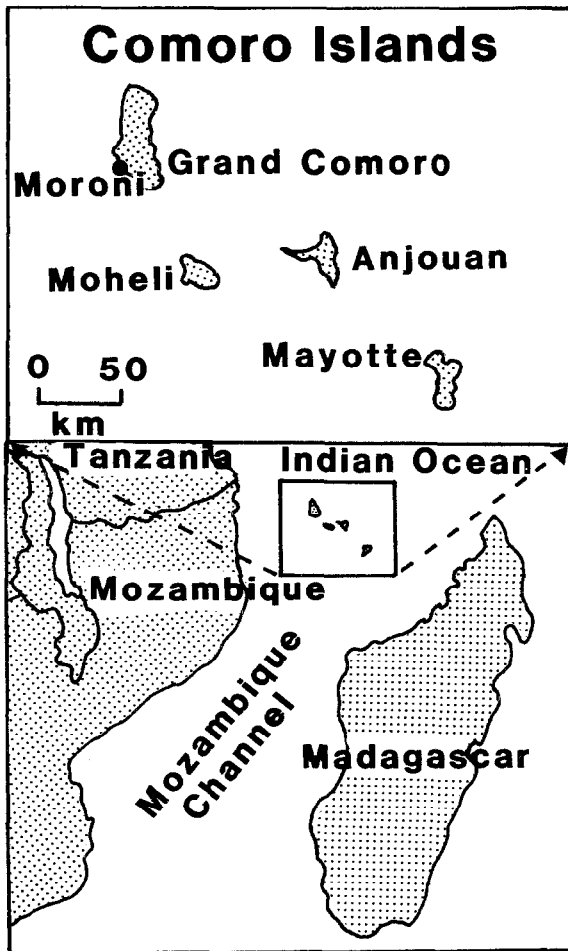


Fig. 5. All the known catches of the living coelacanth, except the first, have been made at Grand Comoro and Anjouan in the Comoro Islands.

cally the same form ('there is relatively little morphological difference between *Latimeria* and the Devonian *Diplocercides*'; Forey 1984). About 70 species of extinct coelacanths in four families and 28 genera are known. About six species (one Permian and five Triassic) were apparently confined to freshwaters, 4 may have been euryhaline (including *Rhabdoderma elegans*, Forey 1981) and 60 were marine. Coelacanths achieved their greatest diversity in the Lower Triassic (200 million years ago) when there were about 30 species (Forey 1984). The longest lived and most widespread coelacanth appears to have been *Rhabdoderma elegans* which persisted for about 30 million years and

is known from the U.S.A. to the U.S.S.R. (Forey 1981, 1984). The coelacanth fossil record ends abruptly at the end of the Cretaceous, about 70 million years ago, with three species of *Macropoma* (the hypothesized sister group of *Latimeria*; Forey 1984), which are known from England and Czechoslovakia. It was universally assumed that the group had played its role in evolution and had become extinct along with the dinosaurs and many other ancient groups. Previous to the description of *Latimeria*, coelacanths were known for 100 years only as fossils following Agassiz's (1839) description of several Permian *Coelacanthus* species. *Latimeria chalumnae* itself has no known fossil record.

Coelacanths are near the origin of bony fish-tetrapod evolution, and are regarded as being close to the mainline of tetrapod ancestry (cf. Rosen et al. 1981, but see Schultze 1986). They belong to the infraclass Actinistia, of which *L. chalumnae* is the sole living representative; their sister groups are the Rhipidistia and Dipnoi – of the rhipidistians including tetrapods there are, of course, many living representatives, the writers of this essay included.

Phylogenetic relationships

The living coelacanth has features that are characteristic of both chondrichthyan and osteichthyan fishes. There are two schools of thought as regards the taxonomic affinities of the coelacanth. Løvtrup (1977), Lagios (1979), Lemire & Lagios (1979) and some others ally *L. chalumnae* with the Chondrichthyes, whereas Compagno (1979), Forey (1980), Lund & Lund (1985), Maisey (1986), Robineau (1986), Smith & Heemstra (1986), Schultze (1986), Trueb & Cloutier (1989) and others regard the coelacanth as a primitive sarcopterygian member of the Osteichthyes (truly fleshy-finned sarcopterygians, Radinsky 1987). The features that *L. chalumnae* shares with the cartilaginous fishes include: a rectal gland, a certain type of pituitary gland, similar means of osmoregulation by retaining urea and trimethylamine oxide in the blood and secretions of the rectal gland, very large eggs, fatty livers, and similarities in the structure of the eye,

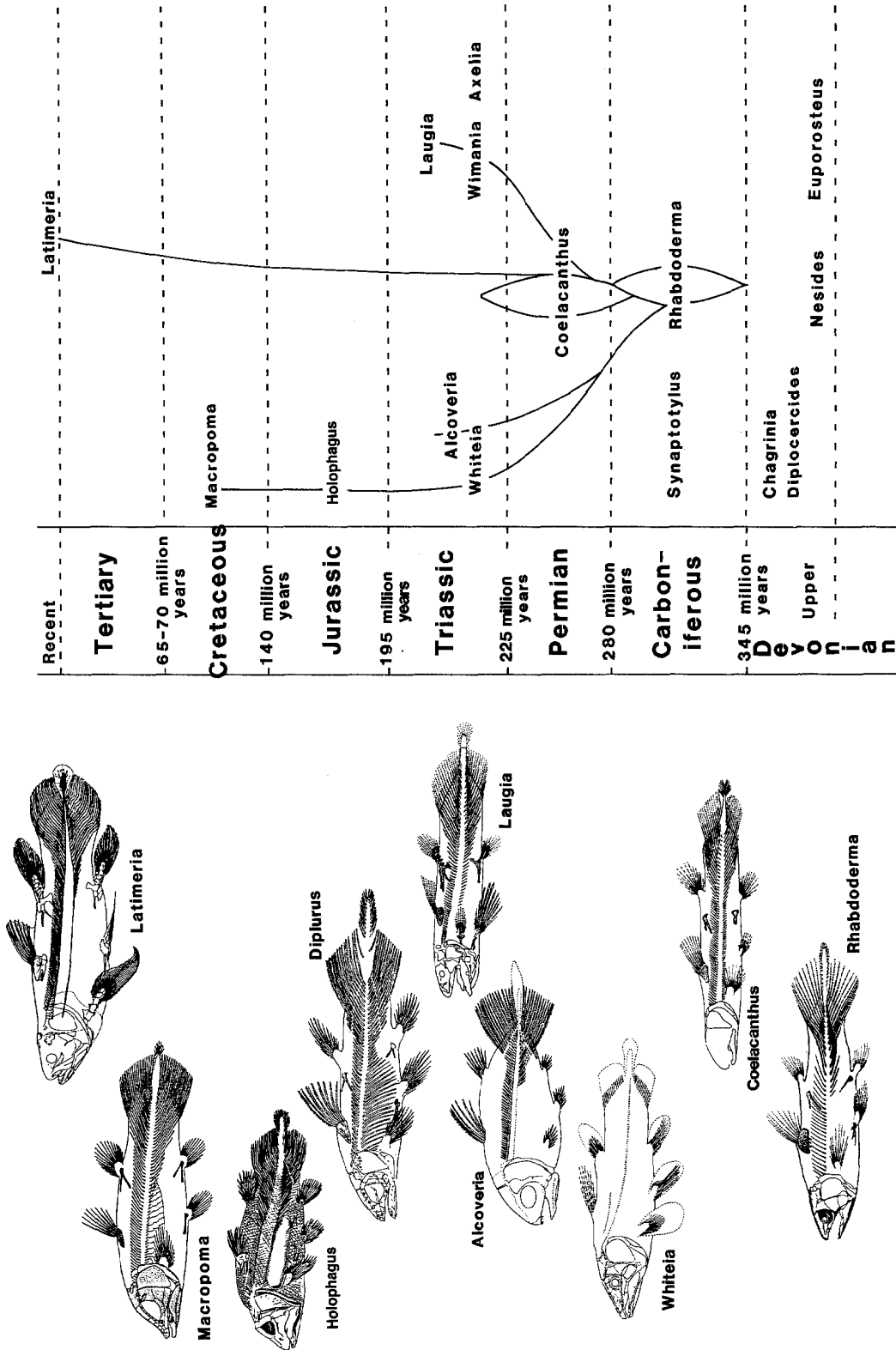


Fig. 6. Coelacanthus in various geological times from Devonian to Cretaceous and the extant *Latimeria chalumnae* (after Thys van den Audenaerde 1984).

pancreas and spinal chord. It has, however, been argued that some of the above features are plesiomorphic or ambiguous and cannot be used to derive phylogenetic relationships. Forey (1980) has proposed that *Latimeria* is the plesiomorphic sister taxon of the choanates, but the problem is by no means resolved.

Structural attributes

The coelacanth has a spiral valve with unique, extremely elongate, nearly parallel spiral cones in its intestine and not a scroll valve as assumed earlier. The valvular intestine is a shared character with ancestral gnathostomata, progressively reduced in actinopterygians and replaced by an elongated intestine in Teleostei and tetrapods (McAllister 1987).

Coelacanths have a form of intracranial kinesis (mid-cranial joint), as have rhipidistians and possibly some early amphibians (e.g. *Ichthyostega*), that allows the mouth to be opened by lowering the lower jaw and simultaneously raising the upper jaw (Lauder 1980).

Adult coelacanths have a minute brain (occupying only 1.5% of the cranial cavity; Locket 1980) in common with many deep-sea sharks and the sixgill stingray *Hexatrygon bickelli* (Heemstra & Smith 1980). This brain reduction may have resulted from the reduced levels of sensory information in the deep-sea environment (cf. Fine et al. 1987), although the coelacanth is not really a deep-sea fish. More likely the cranial cavity is enlarged and filled with low density fluid for buoyancy (J.A. Musick, personal communication).

The structure of the pineal complex, which is known to be concerned with photoreception in many vertebrates (Eakin 1973), is unique in *Latimeria*, having undifferentiated pineal and parapineal vesicles which retain their primitive relations with the ventricle (Hafeez & Merhige 1977).

The fleshy (lobate or pedunculate) fins are the most obvious and unique feature of the coelacanths, approximated by the paired counterparts in fossil lungfishes, rhipidistians and some polypterids. No other fish group has developed seven

fleshy fins (Fig. 7). The paired fins are supported by girdles that resemble the purported precursors of the pectoral and pelvic girdles of tetrapods (Szarski 1961, Schmalhausen 1968, Radinsky 1987). The function of the three fleshy unpaired fins – second dorsal, anal and epicaudal – was revealed only recently (Fricke et al. 1987) and will be returned to later.

The axial skeleton of coelacanths evolved differently from that of other vertebrates, even those with a persistent notochord. Instead of developing vertebrae, the notochord of the living coelacanth develops into a tube over 4 cm in diameter which is stiffened by fluid under pressure. This tube consists of three outer layers: a thin elastica externa, a substantial fibrous or collagenous sheath with circumferentially oriented collagen fibres and aligned fibroblasts, and an elastica interna (Fig. 8). The slightly vacuolated cells of the notochord proper fill this tube entirely only in the extreme tail region, in the other parts they form a one-cell thick lining of the sheath. The remaining lumen may comprise 1.4% of the body volume and is filled with a 'viscous opalescent fluid' (Griffith 1979). The notochord was found to be hollow even in a 30 cm yolksac juvenile (fetus) removed from the oviduct of a female. The axial skeleton of *L. chalumnae* is not primitive but specialized, although in a different direction from that of most vertebrates. Instead of segmental vertebral centra, the coelacanth has found another solution to the problem of axial support, the stiffened rod of the obscure hydraulic principle in evolution advanced by Gutmann (1981, 1988, see Bonik & Gutmann 1977).

Demography

In a sample of over 100 specimens, the average size of *L. chalumnae* males is 130 cm and females 150 cm. The largest individuals seem to be all females. The largest specimen so far recorded is a 183 cm dry-preserved female displayed in the house of the Comoran President in Moroni (Fig. 9). The next largest specimen examined by us was a female 182 cm TL caught in December 1986 and stored (until about September 1987) in a freezer in Moroni

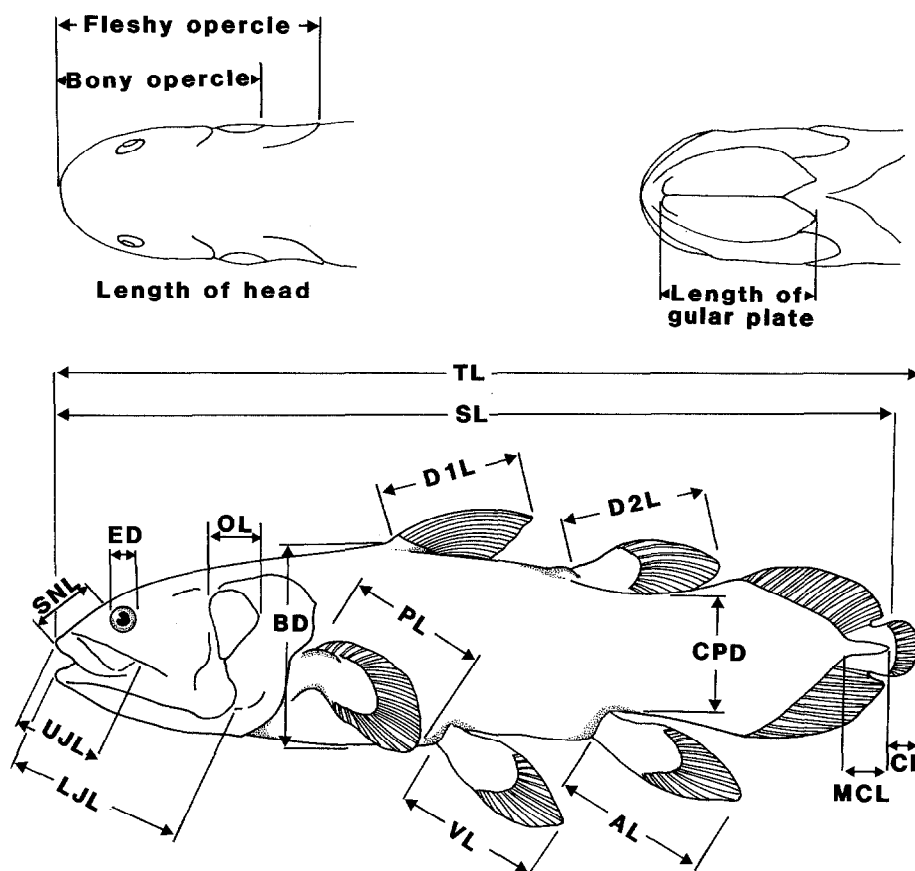


Fig. 7. Body outlines of *L. chalumnae* and the scheme of recorded mensural characters (after McAllister & Smith 1978). AL – length of anal fin, BD – body depth, CL – length of caudal fin, CPD – depth of caudal peduncle, D1L – length of first dorsal fin, ED – eye orbit diameter, LJL – length of lower jaw, MCL – length of epicaudal lobe, OL – operculum width, PL – length of pectoral fin, SL – standard length, SNL – length of snout, TL – total length, UJL – length of upper jaw, VL – length of pelvic fin.

harbour (Fig. 10). Hureau & Ozouf (1977) tried to estimate the age of 12 specimens of *L. chalumnae*, ranging in size from a 31 cm fetus to a 180 cm fe-

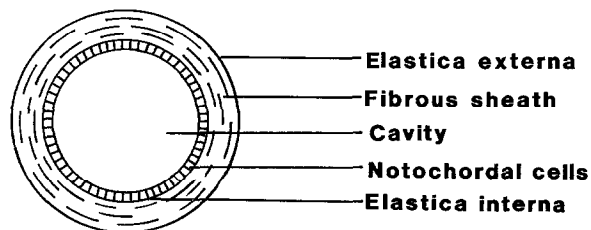


Fig. 8. Schematic section through the axial notochord-tube of *L. chalumnae*. The lumen contains fluid of known chemical composition under pressure and the whole notochord is enveloped by thick perichordal connective tissue (after Lockett 1980).

male, and found 2 to 23 rings on their scales. Their conclusion was that two rings are laid down each year in association with seasonal changes in growth rate during January–February and August–September. This conclusion may, however, be incorrect, as shown in other tropical fishes whose scales record an internal circa-annual rhythm in spite of two distinct rainy seasons (e.g. Balon 1974). Consequently, coelacanth age estimates – which range from a month before parturition to 11 years – may be an underestimate. It is more likely that the rings are formed annually after the yolk-sac juvenile is born with two rings (one marking the transition to exogenous feeding, and the other formed during the 13-month gestation period). The largest fish



Fig. 9. The largest known specimen of the coelacanth is a dry-preserved individual 183 cm TL displayed in a carved cabinet in the entrance hall of the President's house near Moroni (1 May, 1987).

may therefore be at least 22 years old, most likely more, and the age at first maturity correspondingly high.

Reproduction

Sufficient data have gradually accumulated to enable a realistic interpretation of the mode of reproduction of *L. chalumnae* (cf. Locket 1976). The coelacanth seems to be neither oviparous nor ovoviviparous, as assumed in all previous accounts, but a special kind of live-bearer (Atz 1976) with uterine gestation that we call a matrotrophous oophage and (possibly) adelphophage (Wourms 1981, guild C.2.3 of Balon 1981a). This energetically efficient type of viviparity is also known in most mackerel sharks (Lamniformes), for example porbeagle sharks, *Lamna cornubica* and sandtiger shark, *Eugomphodus taurus* (Springer 1948, Stribling et al. 1980); the large and dense yolk facilitates the early creation of a definitive (fully formed) phenotype

within the female's oviduct. Consequently, this allows the large young to begin oral feeding on other less advanced siblings and ova in the same oviduct, causing one or a few large, fully developed, urea retaining, predatory young to be born instead of all the ovulated or fertilized ova coming to term (Balon 1985). For further arguments supporting the above see the recent compilation by Wourms et al. (1988).

A 163 cm long female caught off Anjouan during the 1972 British-French-American expedition contained 19 ripe but seemingly unfertilized eggs, each about 9 cm in diameter and over 325 g in weight (Anthony & Millot 1972, Millot & Anthony 1974). The eggs were all about the size and color of an orange. These eggs were in soft envelopes with no sign of a shell or shark-like case. Griffith & Thomson (1973) pointed out 'that the urea-retaining elasmobranchs either bear live young or lay eggs enclosed in an impermeable egg case, since the embryos do not develop the ability to retain urea until late in their development, needing the protective



Fig. 10. We found the second largest coelacanth specimen 182 cm long in the freezer of Moroni harbour (1 May, 1987).

environment of the egg case or the maternal oviduct for their development' (Locket 1980, p. 283). When another female coelacanth was found to contain five fully formed yolk sac juveniles of 32 cm average length and 550 g weight (Smith et al. 1975), the case for oviparity was finally falsified (e.g. Witkowski & Szymczak 1976).

At the Second European Ichthyological Congress (1976), one of us dared to predict the size of *L. chalumnae* at birth from a comparison of yolk sizes and yolk densities of the above coelacanth young and those of mouthbrooding cichlids (Balon 1976, 1977). The precision of this prediction surprised both the author and Professor Anthony, who revealed that the smallest specimen (C79)¹ of

¹This smallest free-living specimen caught is designated by the French as C79 (cf. Hensel 1986) but as C82 by McCosker (1979).



Fig. 11. The smallest, young female *Latimeria chalumnae* caught on 17.7.1974 at Iconi in 180 m depth. It was probably newly born, but already attracted to a bait.

L. chalumnae, which is 42.5 cm long and to be described soon, is remarkably close to the predicted length (Anthony & Robineau 1976, Hureau & Ozouf 1977). Later, remnants of yolk were found in the body cavity of this 800 g specimen which makes it likely that it is a freshly born young (Fig. 11).

At the same time circumstantial evidence was presented which explained the respiratory oxygen supply to the yolk sac juveniles enclosed in the oviduct (Balon 1977, 1981a, b). The oviduct-ovarian walls and yolk sac young revealed no traces of any specialized placenta-like structures (Wourms et al. 1980), although Amoroso (1981) interpreted the retention of a large yolk sac as placenta. Recently Wourms et al. (1988, p. 53) concluded that indeed 'there is very close contact between yolk sac and oviducal tissue and that there may even be a distinct zone of contact. Retention of a large yolk sac in a late- or near-term embryo is a specialized condition'. Consequently, the living coelacanth may combine the embryonic cannibalism with placentalotrophy – an entirely novel reproductive style. In addition, in *L. chalumnae*, the yolk lipid content is partly replaced by a higher carotenoid pigment content (Devys et al. 1972), e.g. in contrast to mouthbrooding cichlids. The 21% carotenoids in coelacanth yolk colors the yolk a deep orange and provide a supply of molecular oxygen for the long

gestation period (see Karnaukhov 1979, Balon 1981a).

As concluded by Griffith & Thomson (1973) and Locket (1976, 1980), the male external genitalia of *L. chalumnae*, with their specialized folds of erectile tissue, clearly function as an intromittent organ for internal fertilization. The matrotrophic oophagy (vulgo 'fetal cannibalism'), and the associated long gestation period, make the reproduction of the living coelacanth a very specialized and slow affair (Randall 1980). Although the young, when born, are large and capable predators fully able to survive on their own, only a small number can be produced during one generation.

This mode of reproduction may have existed in some coelacanths at least since the Jurassic, 150 million years ago, since Watson (1927) has found *Holophagus (Undina)* from the Jurassic with two young fetuses within the fossilized adult body cavity (cf. Schultze 1980, 1985). *Rhabdoderma exiguum* from the upper Carboniferous, which was so ably observed as a developmental series by Schultze (1972, 1980, 1985), may also be an intermediate type of bearer (sensu Balon 1981a) and not simply oviparous only. Many of its early ontogenic features approximate those found in the mouth-brooding cichlid *Cyphotilapia frontosa* (cf. Balon 1985): large eggs with dense yolk, early hatching and the formation of a yolk sac juvenile by direct development (see next section).

Locomotion

On the few occasions when caught coelacanths were still alive when pulled to shore and biologists were on hand, their movements were described and filmed. In all cases the fish were, however, stressed and dying, and the full extent and potential of their movements were not appreciated (e.g. Milot 1955, Stevens 1966, Locket & Griffith 1972).

The first observations of a free-swimming coelacanth in its natural environment were made from the submersible GEO and revealed a fascinating pattern of locomotion (Fricke et al. 1987). Of the 40 dives performed at 30 different locations around the island of Grand Comoro, six ~120–180 cm long

coelacanths were observed. These fish were all seen at depths of 117 to 198 m along a 2 km stretch of rocky shore which had been covered by lava flows from the volcano Kartala. The coelacanths were relatively undisturbed by the submersible and its lights and were observed for a total of 500 min and recorded on 16 mm film, videotape and on 300 still photographs. One individual was observed for 6 hours.

'All individuals took advantage of up- or downwellings and drifted slowly with the current. Both paired fins stabilized and corrected the "underwater flying" used in a bird wing fashion (. . .). During drifting, all individuals seemed perfectly oriented in that they avoided obstacles in their environment, apparently detecting them well in advance. (. . .) All individuals irregularly performed a curious head-stand, lasting up to 2 minutes, the purpose of which is unknown. Furthermore, the body can be held steadily in any position; two were observed drifting with the belly facing the surface and also swimming backwards' (Fricke et al. 1987, pp. 331–332). When moving, the paired pectoral and pelvic fleshy fins are flapped alternately in the manner of a trotting horse in slow motion, a pattern which is also common to lungfish and a few other bottom-dwelling fishes and, of course, tetrapods. The unpaired second dorsal and anal fleshy fins, as described by Locket (1972), are sculled in unison from one side to the other, which explains their similar shape and exact juxtaposition (Fig. 12). The first non-fleshy dorsal fin appears to be used as a sail and/or as a lateral display when threatened, and is usually folded flush with the dorsal surface in undisturbed fish. The large caudal fin is held rigid during drift-swimming but provides powerful propulsion during a rapid forward burst. The small epicaudal lobe² is bent to and fro while the coelacanth is swimming, drifting or standing on its head, and may be implicated in electroreception together with the rostral organ and lateral line organs (Northcutt 1980). The GEO team was able to induce headstands in the coelacanth by emitting

²Incidentally, this epicaudal lobe was extremely long in small specimens of *Rhabdoderma exiguum*, forming a whip-like trailing structure (Schultze 1972).

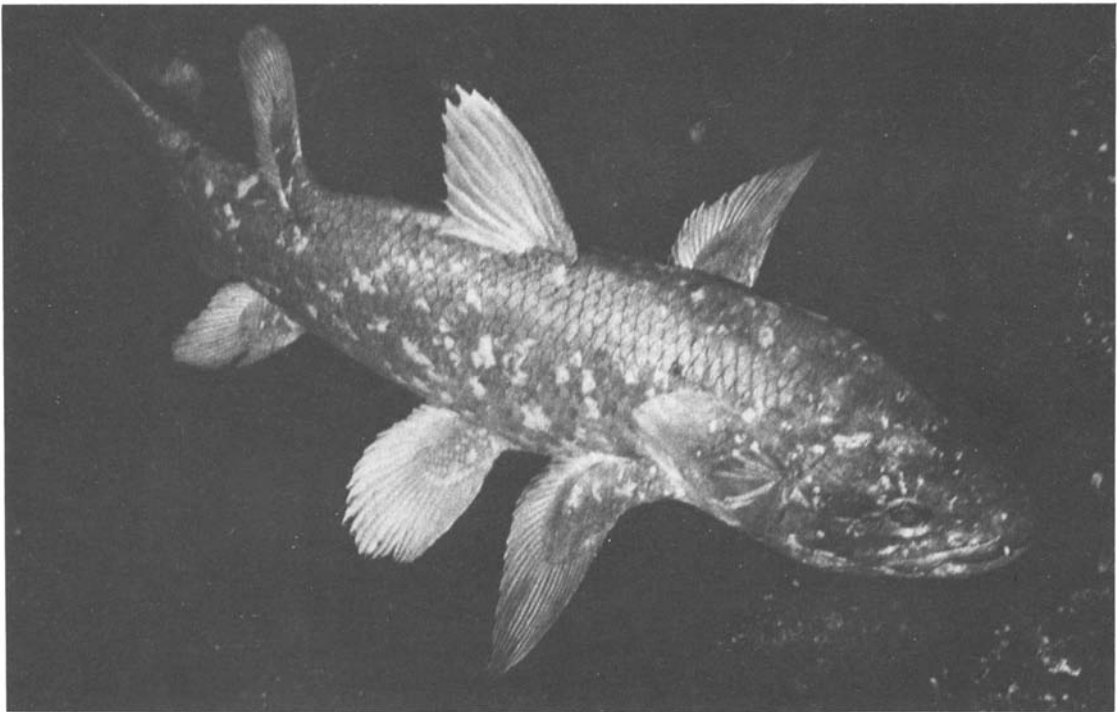


Fig. 12. A frame of *Latimeria chalumnae* taken from the submersible GEO while the fish was drifting in an upwelling current with paired fins functioning as hydrofoils to stabilize and correct the 'underwater flying' (photo. by H. Fricke, 1987).

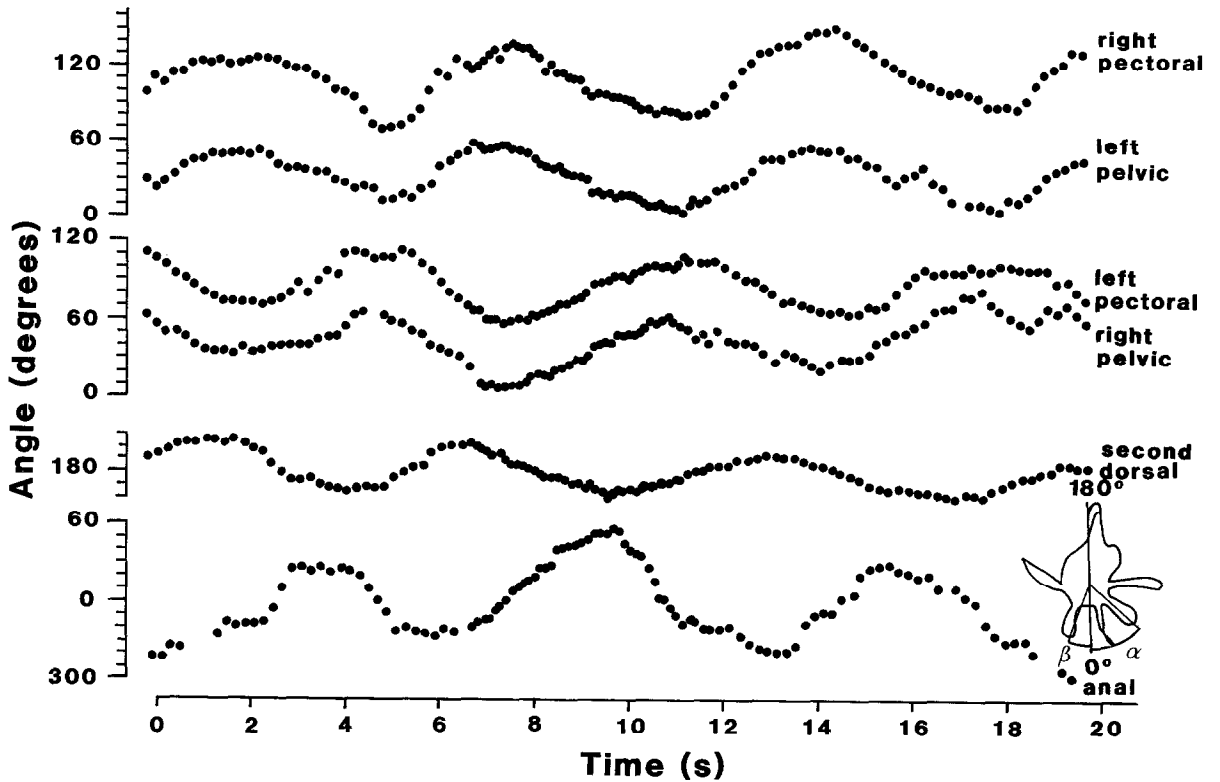


Fig. 13. Coordination of the lobate fins of *L. chalumnae* during slow forward motion (from Fricke et al. 1987).

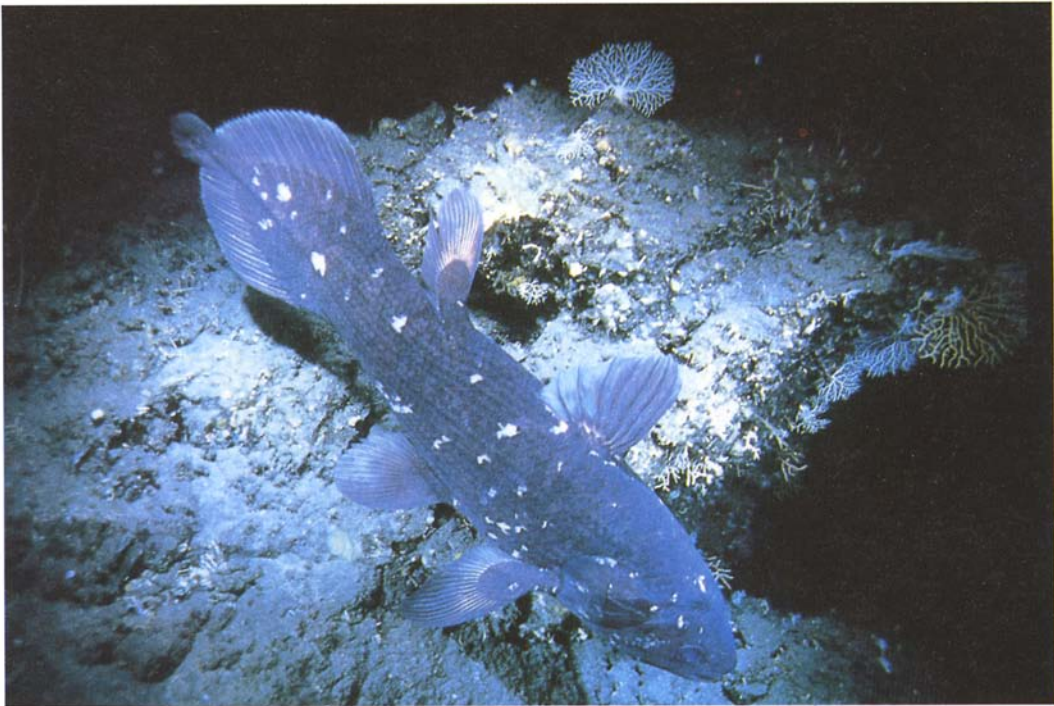


Fig. 14. Followed by the submersible, a specimen of *L. chalumnae* frequently touched the bottom with its belly or tips of paired fins but never used the latter to walk on the bottom. During diagonal or head down postures the fins were all engaged in stabilizing and swim-flying motions (photo. by H. Fricke, 1987).

weak electric currents from electrodes held in the submersible's remote control arms (e.g. Fricke 1988).

Figure 13 illustrates fin coordination during slow forward motion. 'The pectoral fins were synchronized with a phase difference ϕ of approximately half a cycle (180° ; ~ 3.8 s); the same relationship held for the pelvic fins. The left pectoral and right pelvic, and the right pectoral and left pelvic fins were synchronized' (Fricke et al. 1987, p. 333). This fin coordination probably developed to stabilize the bulky body of the coelacanth, but could in its extinct ancestors have facilitated the eventual transition to locomotion on land. When the coelacanth came in contact with the ocean bottom, the paired, fleshy fins were never observed to be used for any form of locomotion. 'Old Fourlegs' therefore probably never walks (Fig. 14).

Habitat

Except for the first specimen, all coelacanths have been caught off the volcanic islands of Grand Comoro and Anjouan in the Comoro archipelago, and only off steep, rocky shores often associated with relatively recent lava flows (Millot et al. 1972, Locket 1980, Fricke & Plante 1988). This limited distribution suggests that some peculiarities of the habitats of these islands may facilitate the coelacanth's survival.

Earlier investigations of coelacanth blood revealed interesting characteristics of the hemoglobin: increasing environmental temperatures sharply reduced the hemoglobin's oxygen affinity (Hughes & Itazawa 1972). This may explain why *L. chalumnae* is normally distributed below the 18°C isotherm (Fricke & Plante 1988). Furthermore, all available catch records indicate that the depth range of the coelacanth is 150 to at least 300 m. The coelacanth is apparently not tolerant of a 10°C

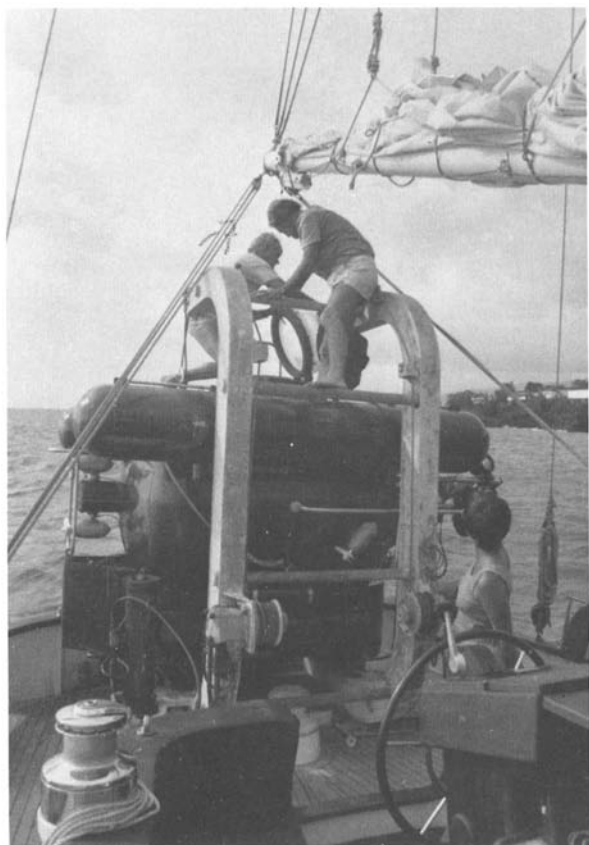


Fig. 15. The submersible GEO on its mothership at Moroni (30 April, 1987).

range in temperature, as suggested by Forey (1984), but migrates vertically with the 18°C isotherm into shallower water at night (Fricke & Plante 1988).

The underwater surveys performed in 1987 by the two-man research submersible GEO (Fig. 15) and mothership 'Metoka' (Fig. 16) have provided additional information on the habitat preferences of the coelacanth (Fricke & Plante 1988). An initial land survey found fishing villages to be distributed evenly along the entire coastline of Grand Comoro with no marked higher concentration along the west coast. In all villages, the traditional deep-water hook and line fishing for the oilfish was active. Interviews with fishermen (Fig. 17) established that no coelacanth catches had been made along the east coast. When all these catch and interview data were correlated with electroacoustic profiles

taken by the 'Metoka' (Fig. 18), two contrasting types of coast became obvious: in the west, extremely steep slopes with no terraces, little sand, and many shelters with abundant prey versus, in the north, east and south, lesser slope angles, terraces covered with sand, lack of shelters and fewer prey. Out of 40 dives with a total duration of 138 hours during December 1986, January 1987 and April/May 1987, coelacanths were found only on the west shore of Grand Comoro. All six coelacanth encounters during the 40 dives were 'between 117 and 198 m depth and a water temperature between 16.9–20.1°C. The animals spend most of their time in water below 18°C (. . .), or at 170 m depth.' The coelacanth is respiratorily stressed in warmer water and cannot survive for prolonged periods in shallower zones. 'We detected no freshwater outlets below 80 m (. . .)' (Fricke & Plante 1988, p. 150). Therefore *L. chalumnae* is not confined in its distribution to colder areas of freshwater flow (as suggested by McCosker 1979) but is restricted to temperatures of less than 20°C, i.e. more than 120 m depth. As the coelacanth lacks a gas-filled swimbladder, it probably suffers less from decompression when hauled to the surface than from respiratory stress as a result of the high temperatures and low oxygen tension of the water.

It was further noticed during the submersible survey that the water temperature off the west coast of Grand Comoro was significantly colder than that along the east coast, the 18°C isotherm being located at 173 m in the west and 193 m on the east coast. On the east coast few prey fish were seen at the depth preferentially occupied by the coelacanth (170–180 m). On the west coast that depth was inhabited by holocentrids, apogonids, anthinines, lutjanids and groupers, all of which are fishes that have been recorded as prey of the coelacanth. The scarcity of suitable prey within the preferred temperature range on the east coast of Grand Comoro is the most likely factor explaining the absence of coelacanths there. The geologically older islands of Moheli and Mayotte as well as the offshore seamount Banc Vailheu have a submarine topography similar to that of the east coast of Grand Comoro and this may explain the absence of coelacanths at these localities. In contrast, An-



Fig. 16. A galawa landing at Moroni, Grand Comoro. In the background the yacht 'Metoka' with the two-person submersible GEO (30 April, 1987).

jouan island, which is of intermediate geological age and has steep submarine slopes deeply eroded into caves and crevices, probably provides sufficient suitable shelters for benthic prey fish in spite of having more sand cover than the west coast of Grand Comoro.

Respiratory restrictions would prevent *L. chalumnae* from reaching abundant prey in water warmer than 20°C. Even on the west coast of Grand Comoro the prey within reach are found at a low density and may not be sufficient to support a large predatory fish. This may explain why the coelacanth conducts vertical migrations at night into shallower water. It moves from colder deep water (13–14°C, 300 m) to warmer feeding grounds (Fricke et al. 1987), thus saving energy during vertical movements. Remaining in colder water during resting periods saves metabolic costs and less food is needed. The energy-conserving life style of the coelacanth makes it less likely that the average

annual growth increment is 16 cm as estimated by Hureau & Ozouf (1977). We predict that a more accurate figure is at most half of it, thus doubling the existing age estimates of the fish.

The six coelacanths seen from GEO were all along a narrow stretch of coast, 2 km long, on the south-western shore of Grand Comoro. None of these individuals was close to a fishing village. Recent lava flows had occurred in the area and it was therefore not easily accessible from land, and there was no native fishing pressure there. The preponderance of coelacanths occurring over lava flows may therefore be due to lack of fishing pressure rather than to a specific habitat preference of the coelacanth.

The limited global distribution of the coelacanth is in stark contrast to the apparent cosmopolitan distribution of many deep-sea animals, including sharks which have similar habits to the coelacanth, such as *Hexanchus griseus*, *Chlamydoselachus*,

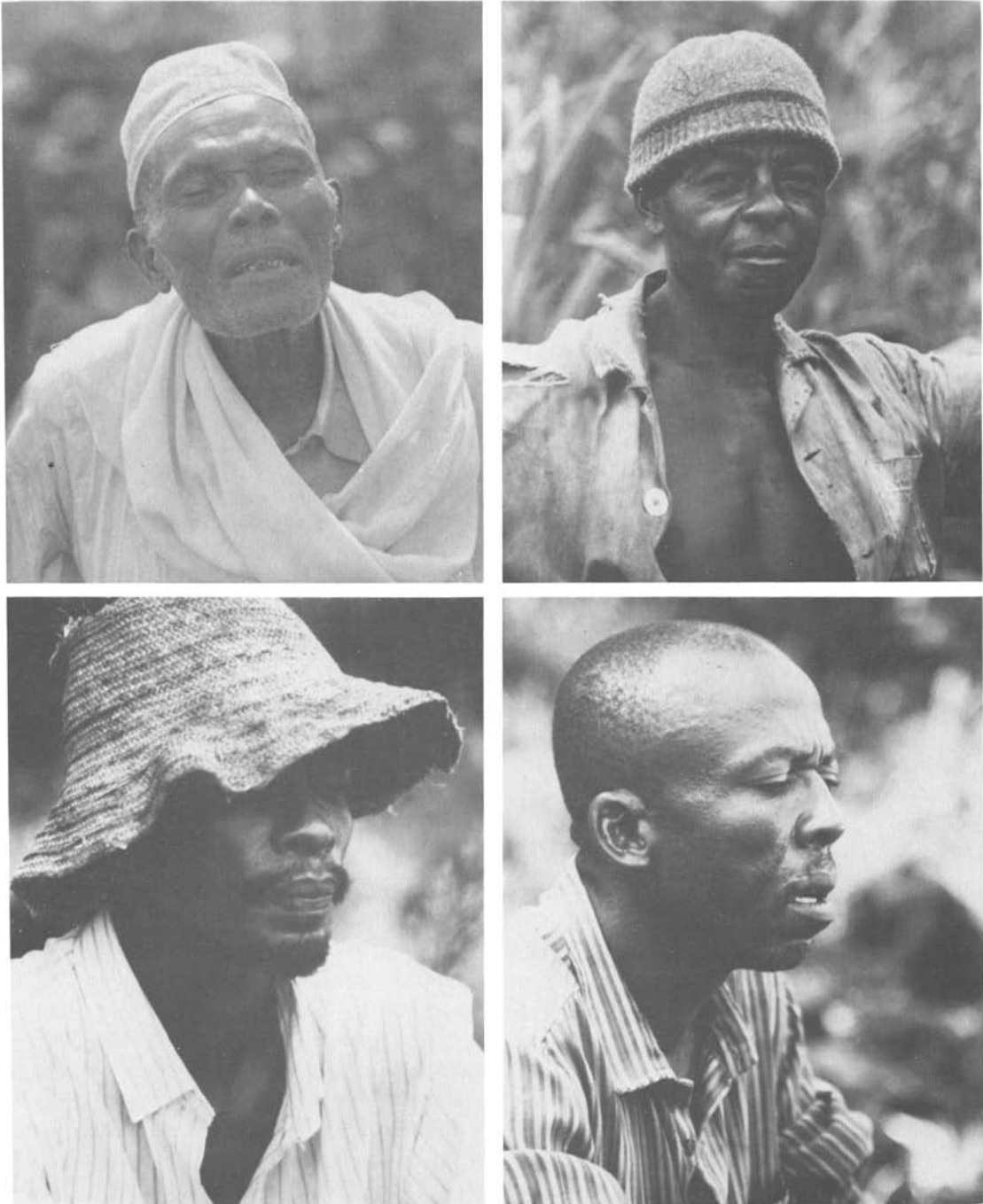


Fig. 17. Fishermen interviewed near Iconi and Dzahadjou on Grand Comoro (20–21 April, 1987), familiar with the coelacanth as a bycatch.

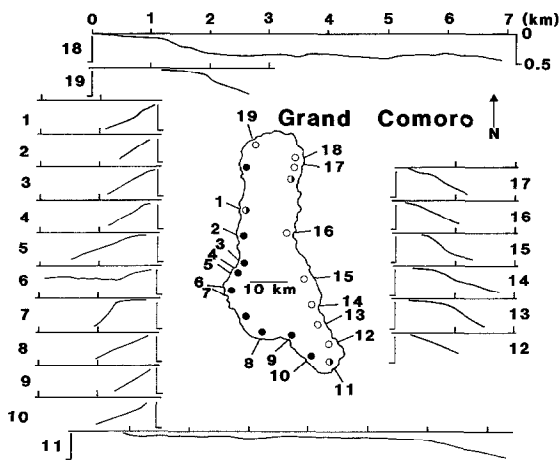


Fig. 18. Locations of *L. chalumnae* catches and electroacoustic profiles around the coast of Grand Comoro. Dots are locations of two or more coelacanth catches from interviews, circles no coelacanth catch confirmed, and numerals mark fishing villages and dive sites, e.g., 3 – Issandra, 4 – Moroni, 6 and 7 – Iconi, 8 – Singani; for more details see the original source (from Fricke & Plante 1988).

Mitsukurina, *Echinorhinus* and *Pseudotriakis* species. The apparent restriction of the coelacanth to the Comoros, and to seemingly impoverished habitats, might be indicative of its more advanced specialization relative to the highly successful deep-water sharks.

The East London coelacanth is now thought to be a stray from the main population in the Comoros. Although the J.L.B. Smith Institute of Ichthyology has received reports over the past 50 years of additional South African coelacanths as well as sightings off the coast of northern Mozambique and even in the Mediterranean Sea, none of these reports has been substantiated. Fricke & Plante (1988) have predicted that further coelacanth populations are unlikely to be found in warmer parts of the western Indian Ocean or along the shallow coasts of East Africa or Madagascar, where fluvial terrigenous sediments cover the continental shelf (e.g. Dingle 1988) and thus restrict the shelters and consequently populations of benthic deep-water prey fishes.

Two silver ornaments found in churches in Spain represent an excellent likeness of a coelacanth, though they differ from *L. chalumnae*, and are

unlikely to have been modelled from a fossil (de Sylva 1966, Anthony 1976, Fricke & Schauer 1987). One discoverer of the ornament, Ladislao Reti, a chemist, 'believes that this fish was made by a silversmith possibly a century before living coelacanths were known to science' (de Sylva 1966). The artisan may either have had access to a specimen from the Comoros or to a specimen from a population of coelacanths closer to Europe, perhaps off the Cape Verde, Canary or Azores archipelagos. The lack of hook and line fishing for deep-water targets, like the oilfish, may have kept coelacanths at these locations from being discovered.

Predators and prey

The coelacanth feeds on small, bottom-living reef fishes (snappers, cardinal fishes) or mesopelagic fishes (lanternfishes) as well as on cuttlefish (McCosker 1979). They have an unusual method of approaching their prey. According to Fricke (1988), the coelacanth is a nocturnal drift-hunter which moves very slowly in up- or downcurrents and uses the paired fins for stabilisation. The paired and unpaired lobed fins provide thrust, and fast starts are made with the powerful caudal fin. The coelacanth has a high burst speed potential [mean acceleration about 2.4 g, vs. 1.1 g for pike (*Esox lucius*) and 4.9 g for trout (*Salmo trutta*); Fricke et al. 1987]. This behavior may be similar to that of some deep-sea sharks, such as the sleeper sharks *Somniosus* species (Squalidae), whereas the method of procuring the prey may be similar to that of the groupers (Serranidae). The jaw structure and short gut length, together with deductions about the jaw mechanism (Lauder 1980), suggest that the coelacanth is a carnivore using a suction-inhalation mechanism.

Although coelacanths have not as yet been recorded as the prey of other predators, they are likely to be taken by large deep-sea sharks such as the cowshark *Hexanchus griseus* (which exceeds 5 m) as well as by oceanic or shallow-water sharks that occasionally hunt in deeper waters. The multi-layered scale covering of coelacanths, which probably provides adequate protection against injuries

caused by scraping against rocks, would not deter these large predators. Several coelacanth specimens have missing fins, including the second one caught in 1952 (which was therefore erroneously considered a different genus and species, *Malania anjouanae*).

Is *Latimeria chalumnae* generalized or specialized?

The coelacanth is both primitive and specialized. From a life history point of view, it is one of the most specialized and precocial of all fishes. A typical generalized fish, such as a sardine, has a life cycle consisting of a sequence of periods – embryo, larva, juvenile, adult and senescent. In more specialized taxa the large endogenous nutrient supply (yolk) enables the embryo to differentiate and develop directly from an embryo into the definitive phenotype (juvenile) without the need for an intermediate food-gathering device (the larva) and its remodelling by metamorphosis (Flegler-Balon 1989). In some cases, an increased duration of endogenous feeding and the acceleration of exogenous feeding causes an extremely long interval of mixed feeding. As a result, a ‘yolksac juvenile’ is produced as in *L. chalumnae* (e.g. Balon 1986).

A sequence of ontogenies (generations) reflects the epigenetic tendency to specialize (Balon 1988); shifts in the boundaries between different ontogenetic periods result in different life-history trajectories ranging from altricial (generalistic) to precocial (specialistic). The altricial forms (e.g. sardine), which have a relatively heterogenous genome, the broadest epigenetic variation and an ability to survive in unpredictably perturbed environments, are usually organisms that mature early, have protracted or annually repeated reproductive activity, delayed somatic differentiation and low parental investment per individual young. Because early ontogenetic features of a highly generalized nature are retained by the numerous offspring, an extremely broad range of variation is possible. Given time, the tendency to specialize will ‘use up’ the sources of variation. Age and size at maturation will eventually be delayed, vitellogenesis will be enhanced and ultimately the high reproductive cost

will be shared only by a few precious zygotes. These processes will reduce variation to such an extent that any environmental perturbations, that may previously have been accommodated, will now become harmful to the species (Bruton 1989). We do not know how close *L. chalumnae* is along its specialization trajectory to natural extinction (Balon 1985, 1988), except that at present it is a highly precocial organism.

The living coelacanth has progressed for a long time along the specialization trajectory, probably more than any other living vertebrate. Besides being of very ancient ancestry, some features which were earlier considered to be primitive can now not be regarded as such. For example, the notochord is a highly specialized axial organ, as explained earlier, although it is specialized in a different way from that of most extant vertebrates. The heart is elongate but is not simple; it is as complex as in other fishes (Millot et al. 1978), and far removed from the superficial earlier interpretation as an S-shaped embryonic tube. Many structures, for instance the fleshy-fin skeletons (Schmalhausen 1968) and the basilar papilla of the inner ear (Fritzsche 1987), have some affinities with those of tetrapods. In summary, many of the claims that *L. chalumnae* has a primitive morphology can be attributed to a common bias of western man to call everything that is different, primitive. Even recent studies of the soft anatomy and body fluids, which revealed various chondrichthyan affinities and are considered to be ‘primitive vertebrate features’ (e.g. Forey 1980), do not conflict with the idea that the coelacanth is specialized but merely indicate that it has retained some ancestral attributes. Likewise, the complex dermal canals known only from fossil jawless and jawed fishes are combined in *L. chalumnae* with the common pit lines of superficial neuromasts of extant fishes (Hensel 1986). Therefore, retention and specialization of ancestral structures, no longer present in other living fishes, is one of the most significant attributes represented, along with their evolutionary persistence, in this true ‘living fossil’ (sensu Forey 1984).

It could be argued that the coelacanth has become overspecialized and is therefore unable to compensate for changes that are occurring in its

environment, such as the increased mortality rates, and reduced abundance of prey, that are likely to have been caused by man's intensive fishing activities. Furthermore, the living coelacanth is further proof that specialization is a result of epigenetic processes rather than 'competition'. In this respect it joins the company of, among many others, the duck-billed platypus *Ornithorhynchus anatinus*, the Everglades kite *Rostrhamus sociabilis*, and the fisherman bat *Noctilio leporinus* (Kikkawa 1987).³

The Federal Islamic Republic of the Comoros

As the only known population of living coelacanths is found off the Comoro Islands, it is clear that their destiny will be decided there. It is therefore important to obtain some understanding of the cultural and natural history of this archipelago and of the attitude of its people to conservation when assessing the future of the coelacanth, which is locally known as 'gombessa'.

The Comoro Islands are situated in the northern entrance to the Mozambique Channel equidistant from the mainland of Africa and the northern tip of Madagascar, about 300 km from each (Fig. 5). Historically, they have been important stepping stones from Africa to Madagascar and from the West (via the Cape sea route) to the East. The history of the Comoro Islands is inextricably bound to that of Madagascar, which was first colonized between 400 and 1000 AD, probably by maritime Malayo-Polynesians (Newitt 1984). Early inhabitants of these western Indian Ocean islands also included

³Incidentally, there may be another interesting zoological find at the Comoro Islands. Much of the seaside birdlife is replaced by the day- and dusk-active flying fox, *Pteropus comorensis* or *P. livingstonei* (Kingdon 1974, Meirte 1984). These large bats are normally nocturnal and fruit-eating, but during our expeditions in 1987 we noticed that, in addition to being diurnal and crepuscular, the bats catch fish in the sea in a similar way to fish-eagles *Haliaeetus vocifer*. The bats then fly onto land with the fish in their claws, hang inverted on a tree, and eat their catch (Fig. 19). Although it has been reported that these bats may scavenge when their natural habitat has been disrupted by agricultural developments, we could not find any mention in the literature of this active fishing habit. Are we witness to evolution in making?



Arab slave traders and slaves from the African mainland. Later Portuguese, French, Dutch, German and other aspiring colonial powers reached the islands. Pirates and buccaneers, including the notorious Edward England and Davy Jones, established bases in the Comoro Islands to take advantage of the easy pickings from the lucrative East Indies trade (Newitt 1984).

Despite the comings and goings of western nations for nearly 500 years, they left no lasting impression on the culture of the Comoro Islands (except the French language), and the Arab influence predominates. There are minorities of Black African, Indian and Persian origin. Today over 95% of the population are Sunni Muslims, with small numbers of Catholics and Protestants (Anon. 1984, 1987). The official languages are French and Arabic, but the lingua franca is Comorian, a loose term that collectively describes the various Swahili patois spoken on the islands. English and African languages are spoken by a few inhabitants. The Bantu element in the Comoran population is predominantly Makua, a tribe from the coastal regions of southern Tanzania and northern Mozambique, which has a strong tradition of artisanal subsistence fishing (Stobbs 1987). The Comoro archipelago is thus a cultural meeting place of Arabs and Arabised negroes as well as Malagasy people of African and Indonesian descent.

The Comoro Islands have had a colorful political history (Newitt 1984, Gould 1985), but what matters in our context is that the most dominant foreign power of late has been France. In 1947 the islands were granted administrative autonomy and became an overseas territory within the Republic of France. In 1973 France announced that it would

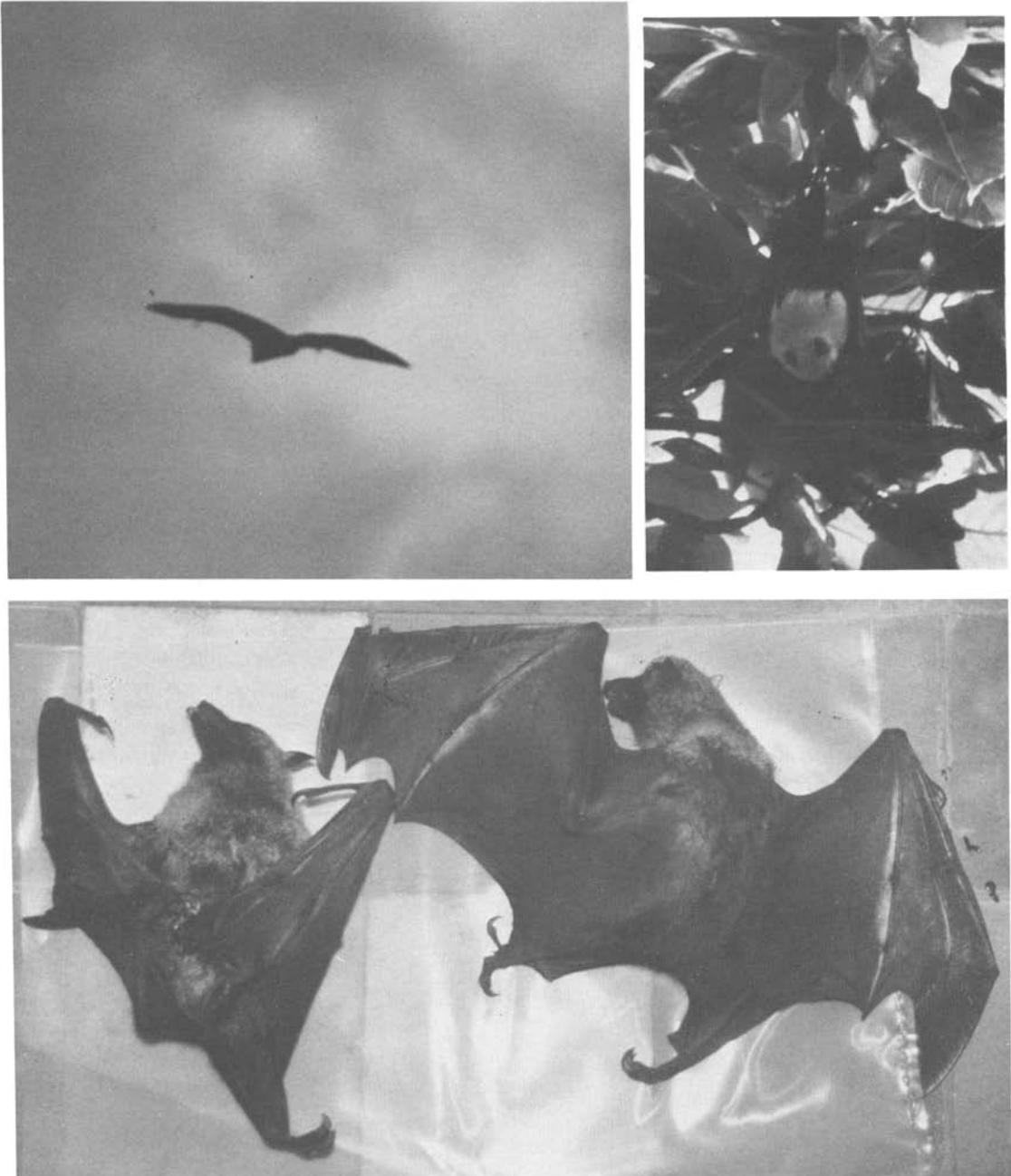


Fig. 19. An airborne, a treeborne and two grounded flying foxes, *Pteropus comorensis*, at Grand Comoro, often seen fishing in the sea (21 April, 1987).

grant independence to the Comoros within five years, but in 1975 the Comoran parliament under Ahmed Abdallah Abderemane declared independence. A month later his government was overthrown in a bloodless coup, but he has since been restored to the Presidency. At present the three islands – Grand Comoro (locally known as Ngazidja), Anjouan (Ndzouani) and Moheli (Moili) – form the Federal Islamic Republic of the Comoros, and Mayotte (Maore) has retained its status as an overseas territory of France.

The Comoro Islands are situated at a latitude of 12°S and have a hot, wet tropical climate. The 'cool' season lasts from May to October with shade temperatures between 20°–22° C and the hot season from November to April (25°–35° C) (Gould 1985). All the islands are scenically spectacular and have lush vegetation, palm-fringed beaches and warm, clear, relatively shark-free waters. The Comoro Islands are subject to seasonal rain-bearing winds during the northerly monsoon, which usually lasts from November to March. The four islands differ markedly in topography. Grand Comoro is dominated by the huge Kartala volcano, which is 2361 m high and has a caldera 4 × 3 km and the largest active crater in the world, Chahale (1300 × 800 m). Kartala erupted in 1857–1862 (5 times), 1872, 1880, 1904, 1918 (a major eruption), 1945, 1952, 1965 and 1977, and the barren, black lava flows are much in evidence. None of the other islands has active volcanoes, but Anjouan is also steep and mountainous whereas Moheli and Mayotte are more eroded islands with less steep profiles.

All the islands have a diverse terrestrial and marine flora and fauna [see 1984 special issue of *Africa-Tervuren* 30 (1–4), 107 pp. on the Royal Museum for Central Africa at Tervuren and its activities on the Comoro Islands, M. Louette (ed.)]. There is, however, considerable pressure on the natural environment from the rapidly increasing human population that is still very dependent on natural resources for food, house- and boat-building materials and medicines. The human demography of the islands is quite frightening. There are about 420 000 people on the three islands of the Islamic Republic, an increase of over 25% in the

last decade, largely due to repatriation from East Africa and Madagascar but also due to the high birth rate [variously reported as 2.2% (1981) (Anon. 1987) to 4.16% (1978–1982) (Newitt 1984)]. About 65% of the population is under 15 years of age (Anon. 1984) and there are, on average over all three islands, more than 180 people per square kilometer (ranging from 56 km⁻² on Moheli to 322 km⁻² on Anjouan, Newitt 1984), despite the fact that much of the islands is uninhabitable because of the steep topography. One-third of the people live in urban areas. Life expectancy is 44 years in males and 47 years in females (Anon. 1984). The diet of the Comorans consists of 95% plant and 5% animal products, and is generally of a high quality, meeting 98% of the FAO minimum requirements (Anon. 1984).

The economy of the Republic is one of the poorest in the world with a large foreign debt. In 1980 the value of imports exceeded that of exports by 295% (Gaspard 1983, Newitt 1984). The Gross National Product (GNP) in 1982 was US \$ 120 million, which is equivalent to about US \$ 285 per capita (137th in the world ranking) (Anon. 1987). The real growth rate (average 1973 to 1982) was 0.0%. Foreign aid from the United Nations, Arab countries and France represents 45% of the GNP; agriculture contributes 45% to the GNP and industry 5%. Only 40% of the population is economically active. The main exports are natural products such as cloves, vanilla, ylang-ylang perfume essence, spices, sisal, copra, cocoa and coffee, mainly to France (up to 50% of exports). Virtually all manufactured goods as well as food, fuel and building materials have to be imported, but there are no well-equipped harbours (Newitt 1984).

The Comoro Islands have a number of unusual, and some usual, conservation problems. Despite the high average annual rainfall (from 1092 to 2896 mm in different places, Gould 1985), there is a lack of surface water on Grand Comoro as there are no permanent streams due to the porous nature of the volcanic rock (Fig. 20). The dramatic human population increases have resulted in the progressive abandonment of traditional, stable, mixed cropping systems that depended on shifting cultivation and the use of long fallow periods for the



Fig. 20. Freshwater delivery system at Iconi, Grand Comoro (21 April, 1987).

maintenance of soil fertility and the control of insect pests. This has culminated in massive soil erosion and forced farmers to cultivate more land, even in steeply sloping areas, in order to feed more people and compensate for declining soil fertility and crop yields (Weightman 1987). On Grand Comoro there is a marked lack of sand with the result that the sandy beaches have been greatly depleted. Live and dead coral heads are also heavily exploited for sand as well as for calcium carbonate to make crude cement. These activities have resulted in severe and expensive ecological imbalances, and have necessitated the building of massive sea walls at some coastal towns, e.g. at Bangoi-Koni on the northern shore of Grand Comoro. The inshore marine life such as turtles, coral reef communities, molluscs, crayfish, shallow water fishes and dugongs have all been heavily exploited and are unlikely to be able to sustain present levels of utilization unless they are better managed (Newitt 1984, Buxton et al. 1988). Inshore reef fishes are currently exploited using spearguns, even by SCU-

BA divers, and tephrosia poison and explosives were used until recently to collect fishes (Stobbs 1987).

Tourism may become an important source of foreign revenue in future as the islands have excellent potential for tourists interested in outdoor activities such as skiboat angling, SCUBA and free-diving, yachting, powerboating and hiking (e.g. Dobie 1987, van der Merwe 1988). Large sums are currently being invested in two new hotels on Grand Comoro and additional hotels are being planned for Moheli and Anjouan. The success of tourism will depend, however, not only on the provision of luxury facilities but also on the integrity of the natural environment (Buxton et al. 1988).

The gombessa fishermen and their fishing canoes

The traditional fishing canoes of the Comoros have been studied by Stobbs (1987). Typically, they are single hull dugouts, with double outrigger floats on Grand Comoro and single outrigger floats on Anjouan and Moheli. The typical canoe hull is double-ended and about 4.5 m long, with twin outrigger booms about 1.9 m long and 5 cm in diameter. The two outrigger floats are on average 1.9 m long planks, 15 × 3 cm thick and tapered at both ends. On Anjouan the hulls range in size from 3 to 4.5 m long. The single outrigger is usually attached on the starboard side and the float is substantially thicker than on the double outriggers. The hull sides are about 3 cm thick and carved of kapok *Ceiba pentandra* or jackfruit *Artocarpus incisa* tree trunks. On occasion, mango *Mangifera indica* and breadfruit *Artocarpus actilis* timber is also used. There is apparently a severe shortage of suitable timber in coastal areas on Grand Comoro and inferior wood is now being used. The canoes are propelled using paddles about 1.4 m long with a lanceolate blade and board-like loom. The size of the dugout canoes, which are called galawas, is determined by their handling efficiency, as they have to be both launched and landed through rough surf on a rocky, boulder-strewn shore (Fig. 21). The rough landing conditions also result in the canoes having a short average life span, from 2 to 5 years on Grand

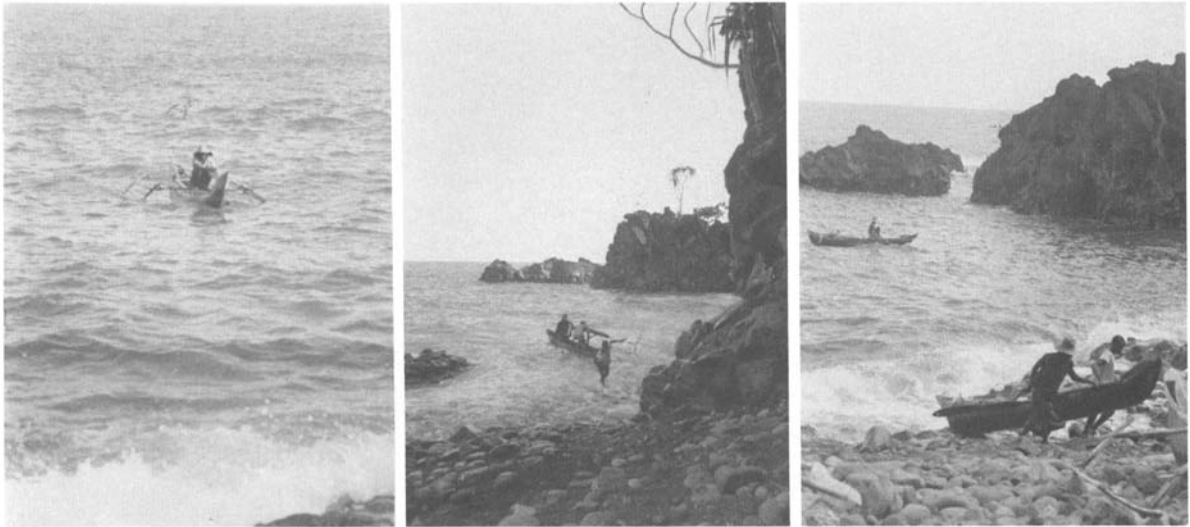


Fig. 21. Landing a galawa at Itsuzu on Grand Comoro (26 April, 1987).

Comoro and 2 to 7 years on Anjouan (Stobbs 1987). de San (1983) estimated that there were 1500 galawas on Grand Comoro, 1200 on Anjouan and 300 on Moheli. Stobbs (1989), after a survey in April 1987, estimates that there are about 4000 galawas on the Comoro Islands: 2000 on Grand Comoro, 1600 on Anjouan and 400 on Moheli.

The fishing methods of the Comorans are becoming more modern and efficient. Hand-twisted cotton fishing lines have been replaced by strong, rotproof nylon monofilament lines of 180 to 200 kg breaking strain, and steel hooks have replaced iron hooks (Stobbs 1987). Furthermore, the traditional wooden dugout canoes with one or two outriggers have been enlarged to 5 m or more and modernized in some ports, especially Mutsamudu on Anjouan, and many now have a transom for an outboard motor. According to our interviews and surveys, 4% of the galawas are now motorized. It is likely that these sophisticated galawas will provide an efficient platform from which to catch coelacanths (Fig. 22). A further innovation is the introduction of 7.5 to 9 m 'Yamaha beachable fibre reinforced plastic fishing boats', or 'japawas'⁴, which are made by the Japanese. These boats are driven by diesel inboard motors and greatly increase the range and

duration of fishing excursions, as well as the load that can be carried in rough seas. In 1987 there were 52 japawas in the Comoro Islands: 25 on Grand Comoro, 22 on Anjouan and 5 on Moheli (Japanese Fishing School, Mutsamudu). Despite assurances from Japanese fishing instructors that these boats would only be used for surface trolling, at least one [sic] coelacanth has already been caught from a japawa (Buxton et al. 1988).

Coelacanths are caught on handlines using fish as bait. The favourite bait is *Promethichthys promethus*, a gempylid fish. All the coelacanths landed in the Comoros (except the one caught from a japawa) have been incidental catches by dugout fishermen while fishing for their main target species, the oilfish *Ruvettus pretiosus*. The coelacanth is therefore not specifically targeted as a catch but is a bycatch of the oilfish fishery. Increased incentives to catch coelacanths, and improved fishing craft and tackle, have, in our opinion, changed the attitude of the fishermen towards the coelacanth. Whereas previously (before 1952) it used to be discarded as a relatively useless catch (they are rarely eaten, Stobbs 1987, 1989), the coelacanth is now worth the equivalent of about three years income to a Comoran fisherman and it is likely that it is being targeted for the first time.

⁴The name 'japawa' was invented by Jean-Louis Geraud.

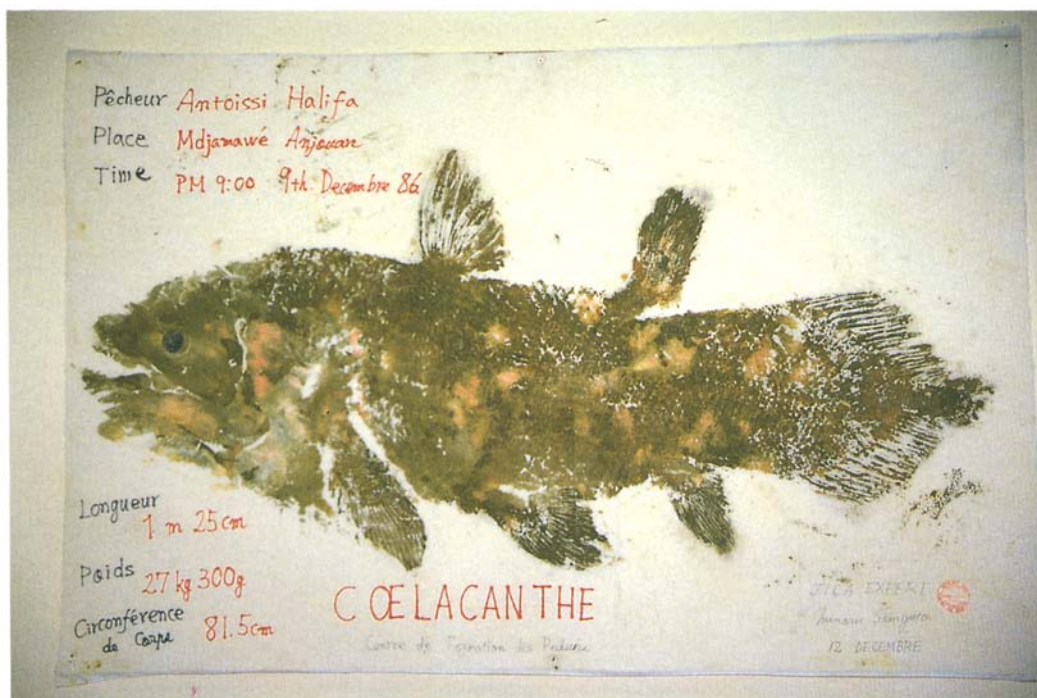


Fig. 22. At the Japanese fishing school near Mutsamudu on Anjouan the instructors showed us their coelacanth gyotaku. Note the 3 days elapsed between capture and the gyotaku production. In November 1987 more coelacanths were spotted in the freezer of this school (25 April, 1987).

During the 'kaskazi' (northerly monsoons) and inter-monsoon calms almost every serviceable canoe is at sea day and night with one or two fishermen, whereas during the 'kuzi' (southerly monsoons) when the sea is very rough, the fishermen do not venture out except from sheltered areas. The result is that more coelacanths are caught when the sea is calm than when it is rough (McCosker 1979, Stobbs 1987). The japawas and motorised dugout canoes are used under rougher sea conditions and venture farther from land than the more primitive paddled canoes. de San (1983) estimates that the average Comoran fisherman has 180 outings per year, which is equivalent to about 720 000 man days per year at sea for all fishermen, a considerable fishing effort on the restricted inshore reefs of the Comoro Islands.

Stobbs (1987) has estimated that the average dugout fisherman does not normally venture more than 2 km from shore. The six coelacanths seen from the submersible GEO (Fricke & Plante 1988)

were all found more than 2 km from any fishing village and were therefore beyond the normal fishing range of fishermen using dugout canoes.

The coelacanth trade

Except for the first specimen, which was caught in a trawl net, all coelacanths have been a bycatch of the oilfish fishery, mainly at night. Prior to 1952 all or most coelacanths were released on capture as they are relatively unpalatable (in contrast to the statement by Smith 1986). Coelacanths were therefore of little use to Comoran fishermen. At least 200 coelacanths have been caught since 1952 (J. Peron, FAO consultant, personal communication) (an average of 5.5 per annum). The reported annual catch rate ranged from 2 to 4 for many years (Fig. 23) but may be increasing as 12 coelacanths were caught in 1987 according to our records. Although coelacanth specimens in museums are rea-



Fig. 23. Aerial photograph of Iconi, the village on Grand Comoro with the highest record of coelacanth landings. Kartala volcano under clouds in the background (2 May, 1987).

sonably well documented (Millot et al. 1972, McCosker 1979), accurate catch statistics on the coelacanth are not being kept in the Comoro Islands. Furthermore, political unrest during the past two decades has reduced the research effort in the islands and during the regime of Ali Soilih (1976 to 1978) all official government records were destroyed, including all recent coelacanth catch data (Lamb 1978, Gould 1985).

There is a ready market for coelacanths worldwide, and the Comoran government has even advertised coelacanths for sale. Coelacanths are used as official gifts by the Comoran government and they are also sold as trophies by tourist agencies. Although *L. chalumnae* is listed in Appendix II of the Convention on International Trade in Endangered Species (CITES 1987a), which means that trade may not be carried out if it threatens the future survival of the species, there is an ongoing trade in the animal. The official records of CITES

(1987b) report that the coelacanth 'has never been recorded in trade since 1975' and that there is 'No evidence' of illegal trade. The potential trade threats are reported to be 'None. The species is merely of scientific interest'. This inaccurate information is not the fault of CITES but the fault of the various nations (U.S.A., Canada, South Africa, Federal Republic of Germany, etc.) that are signatories to CITES (1988) and have not reported trade in coelacanths as they are required to do. The coelacanth was first placed on CITES in 1973 at the request of the U.S.A., with the suggestion that it be granted Appendix I status due to the risk posed by scientific collecting (CITES 1987b). The coelacanth was subsequently placed on Appendix II and its status was not reviewed until the Ottawa meeting of CITES in 1987, where there was an initial request to have the species removed from all CITES listings. Fortunately, representations were made in time by two of the authors (HF and MNB)

and consequently the following recommendation ensued from the CITES secretariat: 'that the species be kept in Appendix II pending further studies and consultation with the Government of the Comores' (CITES 1987c). An application is now being prepared for consideration at the October 1989 meeting of CITES in Djakarta which recommends that the coelacanth should be placed on Appendix I.

The present listing of the coelacanth in Appendix II of CITES imposes the following limitations on its trade, *inter alia*: (a) the export of any specimen requires the granting of an export permit, which should only be granted if the State of export has been advised by a scientific authority that such export will not be detrimental to the survival of that species, (b) a scientific authority may advise the exporting State that the number of export permits should be reduced if there is evidence that the species may be threatened, (c) the import of any specimen shall require the prior presentation of an export permit (CITES 1973). Furthermore, Article VIII of the Convention requires, *inter alia*, that 'Each party shall maintain records of trade in specimens of species included in Appendices I, II and III: (a) the names and addresses of exporters and importers; and (b) the number and type of permits and certificates granted; the States with which such trade occurred; the numbers or quantities and types of specimens, names of species . . .' (CITES 1973).

Although the Comoran government is not a signatory of CITES, the spirit of the Convention is observed by requiring that all coelacanths which are caught must be sold to the Ministry of Production, which is then responsible for further trade, but there is insufficient control. A black market in coelacanths has developed, particularly to the Far East where it is rumored that the notochord fluid promotes longevity. This ridiculous rumor reminds one of the so-called aphrodisiac powers of rhinoceros horn which once threatened the white rhinoceros with extinction. A Japanese medical technical college has recently organised four expeditions to the Comoros to buy coelacanths for 'medical research'.

Recently (late 1986), an Explorers Club/New York Aquarium Coelacanth Research Project led by J. Hamlin mounted expeditions to the Comoros with the objective of catching a live coelacanth as well as obtaining specimens for study. They have also placed an advertisement in the International Game Fish Association newsletter 'The International Angler' calling for volunteers (who have to pay US \$4000 each) to participate in the expeditions. These expeditions are offering a higher reward for a coelacanth than that offered by the Comoran government. One of their rationales is that the coelacanth requires a program of captive propagation in order to ensure its survival, and they aim to transport live coelacanths back to New York with the intention of establishing a 'breeding colony' (Hamlin 1988).

We opposed this initiative as their activities may further threaten the coelacanth by increasing the incentive to catch the fish and we are pleased by the positive reaction from the New York Zoological Society and the New York Aquarium (in litt. 28.3.1988 by William Conway and by Louis E. Garibaldi). The IUCN (1987) has listed the following characteristics which are typical of species at a high risk of extinction, and all of them apply to the coelacanth: restricted distribution, large body size, high economic value, at the top of their food chain, occur only in climax habitats. The capture and translocation of coelacanths can only be justified if there is a reasonable chance that they can be propagated in captivity and then re-stocked in the wild. In our opinion, this is unlikely due to the specialized nature of the coelacanth and its apparent narrow physiological tolerances. Laboratory captive maintenance in order to study many of the unknown aspects of physiology and behavior is, of course, a different issue for which peer reviewed and closely monitored permit may be justified. Even so the effort and funds of scientific granting bodies would in the short term be far better spent improving the management of the Comoran fishery so that coelacanths are not caught as frequently, and by taking actions to enhance their survival, such as creating a Coelacanth National Park (see below). Attempts at captive propagation may lead to competition among aquaria to catch more and

more coelacanths and also undermine the efforts of other conservationists in the Comoros who are attempting to reduce the rate at which coelacanths are caught. Notwithstanding that the Explorers Club expeditions have obtained coelacanth specimens for the valuable research that is being organised by John A. Musick at the Virginia Institute of Marine Science, Gloucester Point (Browne 1988a, b, c, Cloutier et al. 1988) and others, we feel that any such future acquisitions should take care not to provide incentives to catch additional fishes and be approved by an international council.

The coelacanth was included in the International Red List for the first time in 1986 (IUCN 1986) but is listed in category 'K' which means that insufficient is known about the species for it to be properly categorised. Representations are now being made to the IUCN to have the species listed as 'endangered'. The coelacanth is not officially listed in the South African Red Data Book but Skelton (1987) states: 'The status of one notable species, the coelacanth *Latimeria chalumnae* Smith, is, however, being investigated at present (...) and may well be included on the South African Red Data list in future'.

Coelacanth specimens fetch each US \$500 to \$2000 on the open market. Although Comoran fishermen are only paid about US \$150 by the government, this represents a considerable amount in the Comoros (the average annual income is about US \$30, Stobbs 1987) and is therefore a strong incentive for fishermen to catch a coelacanth. We therefore suspect that coelacanths may now be targeted by Comoran fishermen who modify their gear and their fishing techniques in order to increase the likelihood of catching coelacanths (especially when incentives are provided by foreign expeditions), while still relying on the oilfish and other food fish for their normal income.

Some of the coelacanths that are sold to the Comoran government are sent to an enterprising but poorly trained and equipped taxidermist based near Mutsamudu. Working under appalling conditions, he produces an inferior product that is virtually useless for museum display (Fig. 24). Furthermore, valuable material and information is lost by the taxidermist who is not aware of the scientific

significance of the coelacanth. When we last visited this taxidermist in October 1987, he showed us a bottle of rotten eggs which he had taken from a female. Three-quarters of the eggs from this female had been discarded. Coelacanth material, especially the young stages, is so rare that we cannot afford to lose it in this way.

The intense fishing pressure around Grand Comoro (see earlier and Stobbs 1987) combined with the low density of benthic fishes recorded by Fricke & Plante (1988) from the submersible suggest that the inshore rocky reefs of this island are overfished. This observation supports earlier statements that there is overfishing at Grand Comoro in comparison with other Indian Ocean islands (e.g. Foster et al. 1970, Foster 1974).

Even if strict conservation measures are introduced, the coelacanth will continue to be caught as a bycatch of the artisanal fishery. Individuals brought to the surface usually die within a few hours as a result of respiratory stress. The research of Musick and others has already shown that the coelacanth has proportionately more muscle tissue of the type in which lactic acid builds up rapidly, thus causing pain and fatigue (Browne 1988a). When a coelacanth struggles after being hooked, this characteristic of its muscle structure could lead to potentially lethal trauma. A fast recompression could possibly prevent death and the fish may survive if released immediately.

A recompression cage $250 \times 80 \times 80$ cm was therefore built by the members of the GEO expedition in which a caught *L. chalumnae* could be returned by the submersible to the depth at which it was caught, and observed. It was considered that if the coelacanth survived for a week in the cage then this would prove that it is feasible to release coelacanths after their accidental capture; and one would expect them to survive. The experiment was planned for April or May 1987 and the fishermen were requested on Comoran radio to keep any gombessa that were caught alive. Unfortunately, the weather was unfavourable for fishing at the time and no coelacanths were caught. Although a coelacanth could have been caught from the submersible, it was decided that the possible death of such a rare animal could not be justified. In addi-

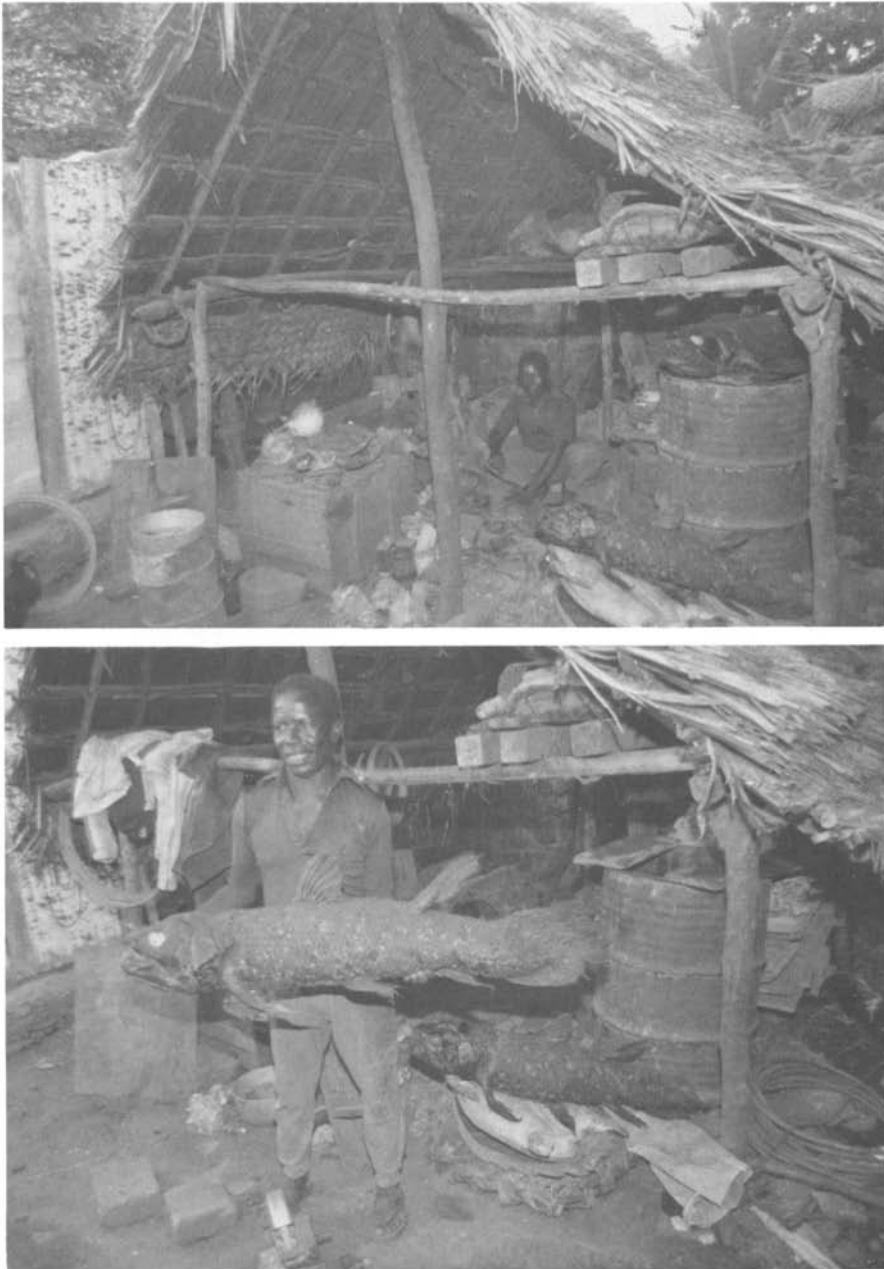


Fig. 24. Stuffed coelacanths in the ‘workshop’ of the local taxidermist Sid Bakari near Mutsamudu on Anjouan (24 April, 1987).

tion, the conditions of capture would be different from those using a hook and line. Upon our departure, the above program and equipment were handed over to Jean-Louis Geraud (Fig. 25), an experienced diver-instructor who runs the ‘Gombessa Plongée’ diving club at the ‘Hotel Coela-

canthe’ in Moroni and who has been a serious and enthusiastic coelacanth conservationist over the past nine years. Geraud is supported by a group of Comoran divers. If a coelacanth is caught they plan to place it in the cage and to lower the cage to 180 m on a rope. The cage will be raised after 5 days to a



Fig. 25. The diver-conservationist Jean-Louis Geraud from Moroni with his daughter and a mummified coelacanth from under his bed (1 May, 1987).

depth of 80 m where divers will check the condition of the fish. If it is still alive, the coelacanth will be released.

The Coelacanth Conservation Council

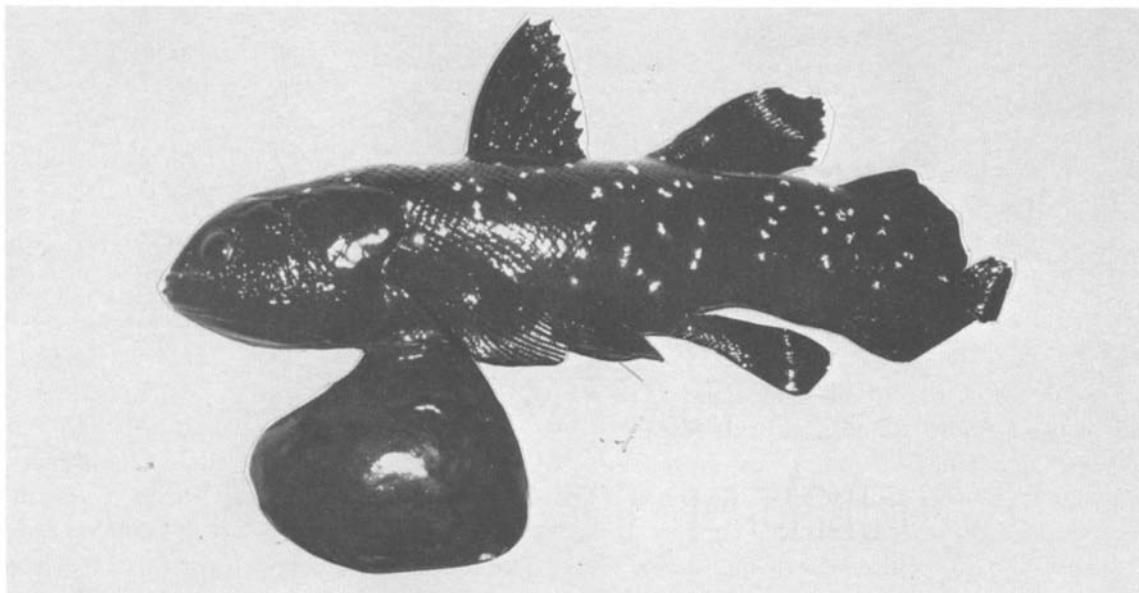
Twenty-five years ago J.L.B. Smith (1963) warned that the unrestricted catching of coelacanths may threaten their future survival and in 1964, while opening an exhibition at the East London Museum, he proposed that an international society should be formed to ensure the survival of the coelacanth. After his death in 1968, a research institute was established in his name in Grahamstown. The staff of the modern institute have retained an interest in the coelacanth (Bruton 1988),

and three expeditions were mounted to the Comoro Islands in 1986 and 1987, partially with the aim of investigating the conservation status of 'old four-legs'. Eugene and Christine Balon, as well as Robin Stobbs and Mike Bruton, were members of the April 1987 expedition from the J.L.B. Smith Institute of Ichthyology. Another expedition led by Hans Fricke and also included Raphael Plante of the Centre d'Océanologie de Marseille, France, coincided with the former expedition and we were able to discuss the conservation status of the coelacanth among ourselves and with the Comoran authorities. A decision was made to form an organisation which would co-ordinate research and conservation activities related to the coelacanth, and it was named the Coelacanth Conservation Council/Conseil pour la Conservation du Coelacanth (CCC). Government officials of the Federal Islamic Republic of the Comoros were consulted and they all expressed interest in and support for the Council.

The formation of the Council was first announced during an evening devoted to coelacanth talks and films at the conference entitled 'Alternative life history styles of fishes and other organisms' held in Grahamstown, South Africa, in June 1987. It was decided that the headquarters of the Council would be in Moroni, capital of the Comoros, and that the secretariat would be based at the J.L.B. Smith Institute of Ichthyology in Grahamstown. The newsletter of the Council would be published as material became available in the journal 'Environmental Biology of Fishes'. Material for the newsletter should be sent to the secretariat at Private Bag 1015, Grahamstown 6140, South Africa, or to the editor of the journal.

The Coelacanth Conservation Council has thus far made the following recommendations to the Comoran authorities, the World Wide Fund for Nature, the International Union for the Conservation of Nature and other relevant organizations:

* A series of marine nature reserves should be established around the Comoro Islands. These reserves should include a Coelacanth National Park along the southwestern shore of Grand Comoro in the area where GEO has found most coelacanths, and a resource area around this national park



where bottom fishing at depths greater than 120 m should be prohibited, at least for part of the year. In addition, a marine park should be established around the northeast peninsula of Anjouan, which is an area of peak coelacanth catches. Other marine reserves have also been proposed on the three islands to conserve biotic diversity, ensure the sustainable utilization of species and ecosystems and to retain essential ecological processes in coral reef and sandy, rocky and muddy coastal environments, especially along the southern shore of Moheli (Buxton et al. 1988). Marine animals that are particularly in need of protection, in addition to the coelacanth, include the green turtle, dugong, various coral species and certain molluscs, especially the triton *Charonia tritonis*, which is one of the main predators of the crown-of-thorns starfish, and cowries (*Cypraea* species).

* Nature conservation legislation that protects marine resources outside the proclaimed reserves without interfering with legitimate food-gathering activities should also be introduced.

* The incentive to catch or trade in coelacanths should be removed. Ironically, it is the very institutions that most appreciate the value and importance of the coelacanth – museums, universities and research institutes – which may now threaten its survival, although there is also an increasing

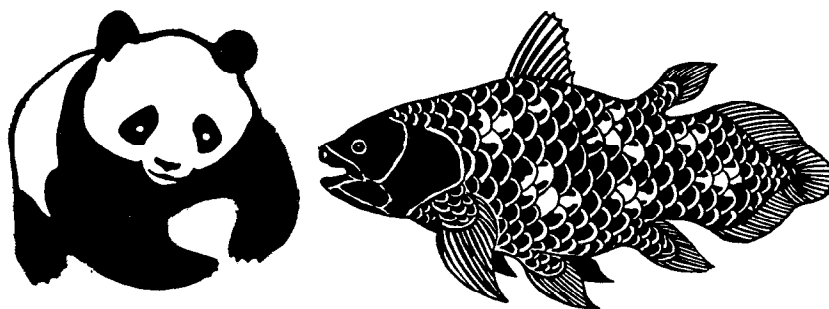
private trade. There should be a moratorium on all trade with museums and other scientific institutions except for approved research, and the coelacanth should have no price. Those specimens that are landed incidentally and do not survive should be properly curated and preserved by professional staff and made available free for study to the laboratories which and scientists who are best able to carry out the necessary research.

* An education campaign should be launched in the Comoros to inform the populace of the importance of the coelacanth, both to their nation as well as to mankind as a whole.

* Good quality fibre reinforced plastic replicas of coelacanth adults and juveniles, like the one reproduced above, should be made available for display in museums as an alternative to real specimens.

* Research should be conducted to determine whether a caught coelacanth can be released and survive recompression to 200 m. If this is the case, incentives should be provided for fishermen to release coelacanths that are caught. A penalty should be imposed if a coelacanth is purposely killed (as was the norm until recently) unless under a specific permit.

* Further research should be conducted from research submersibles (remote operated and manned) on the biology, ecology, demography and



conservation status of juvenile and adult coelacanths in the Comoro Islands, and this research should also be extended to other western Indian Ocean islands in order to determine whether the coelacanth lives elsewhere. Financial support for this research should be provided by international aid agencies and conservation bodies, and fulltime researchers should be placed in the Comoro Islands to monitor the fishery.

* The oilfish fishery should be studied in order to devise ways in which oilfish can be targetted without catching coelacanths when longlining in deep water. The possibility should be investigated of finding a low-priced substitute for the oilfish, as the oilfish seems to be used mainly for its anti-malaria properties rather than for food. Other malarial antidotes should be found.

* Offshore fisheries should be developed to reduce the pressure on the overexploited inshore fish communities of the Comoro Islands. The possibility of increasing protein production by fishfarming should also be investigated. The hot, wet climate of the Comoros combined with the abundance of inexpensive labour and a ready market for aquacultural products would suggest that fishfarming would be a viable undertaking there.

* The conservation status of the coelacanth in the Convention on International Trade in Endangered Species (CITES) should be upgraded and the World Wide Fund for Nature (previously the World Wildlife Fund) should be asked to adopt the coelacanth as its logo for aquatic conservation along with the panda for terrestrial conservation. The coelacanth should be listed in the IUCN International Red List as endangered.

Conclusion

Conservation methods on the coelacanth can be divided into direct actions, such as restricting trade, removing the incentive to catch coelacanths, establishment of protected areas, further studies on the fish, and indirect ones, such as developing offshore fisheries, investigating an alternative to the oilfish, and enhancing fish yields through the development of aquaculture. Both approaches need to be adopted as the information at hand, however sparse, indicates that the coelacanth is threatened. In addition that this last actinist may yet answer how vertebrates made their living in the Paleozoic and Mesozoic, there are many reasons why the coelacanth, among the 26 000 species of living fishes, should be a special case for conservation: its long evolutionary history, its roots close to those of tetrapod origins, its combination of primitive and derived characters, its advanced reproductive style, its remarkable behavior and method of swimming, its success in geological time coupled with the extreme apparent vulnerability of the only extant species. The most important reason, however, is that coelacanths occupy a unique place in the consciousness of man: they represent a level of tenacity and immortality which man will never achieve during his short stay on earth. For the sake of future generations, can man afford to cause the coelacanth, which represents a group that has survived for over 400 million years, to become extinct within 50 years of discovering it?

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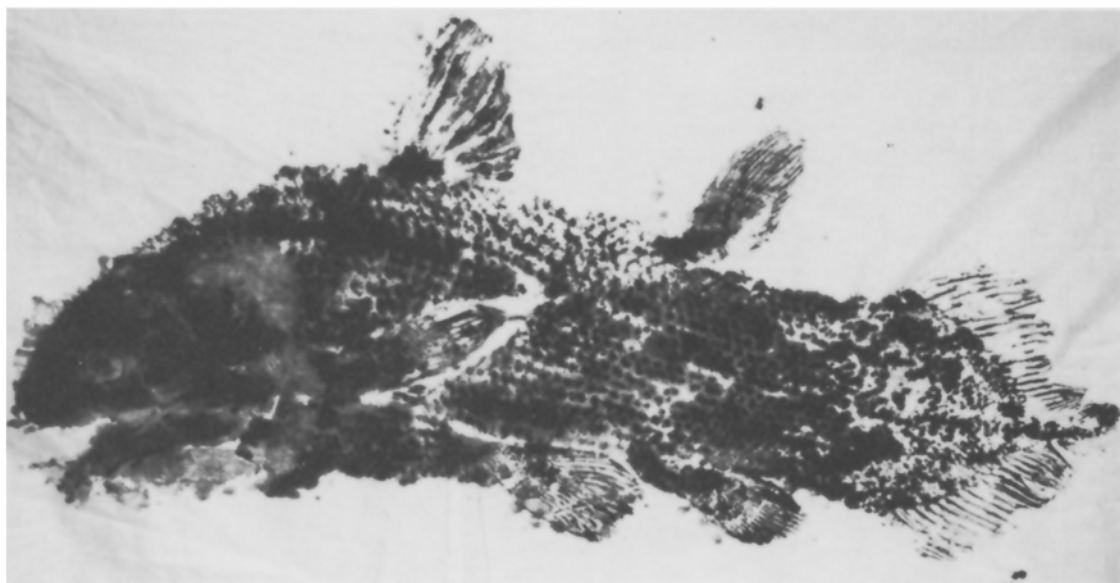
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Dedicated to the memory of

Margaret Mary Smith (1916–1987) OMS(G)

who saw the results of J.L.B. Smith's initial encounters with the coelacanth and of our recent expeditions, but did not live to see the new interpretations.