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Evidence for Lecithotrophic Viviparity in the Living Coelacanth

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The live-bearing coelacanth *Latimeria chalumnae* has been considered an embryonic cannibal practicing oophagy (ingestion of mature eggs) with a yolk sac placenta for gas exchange and the limited uptake of maternal nutrients to supplement the embryo's yolk reserves [1 – 6]. In August 1991 a large female coelcanth (98 kg wet weight, and 179 cm total length) was caught for the first time off Moçambique, western Indian Ocean [7]. The female carried 26 fully developed late-term pups which composed 12.2% of the mother weight (Fig. 1). Their dry weight was on average 23% below the dry weight of a maturing egg, indicating that embryos depend solely on their own yolk reserves (lecithotrophy). This observation and anatomical findings favor earlier arguments against embryonic cannibalism and matrotrophy [8].

Although 172 coelacanth catches have been reported [9], only one gravid female was found among them [10,11]. She carried five advanced pups (301 – 327 mm total length) with well-developed yolk sacs (7 – 129 mm in diameter). Thus, the fact that coelacanths are live-bearers was established. Coelacanth eggs (85 – 90 mm diameter, 334 g wet weight, 185 g dry weight [12]) are among the largest in fish; the number of ovulated, unfertilized eggs ranges between 19 to 59, of unovulated eggs to maximally 67 [7,12,14,15]. The disproportion between the small number of late-term pups and high number of ovulated eggs inferred feeding on eggs or egg debris [1,3,6]. Oral ingestion of excess eggs or of their breakdown products was proposed as the main supplementary source of maternal nutrients. The large

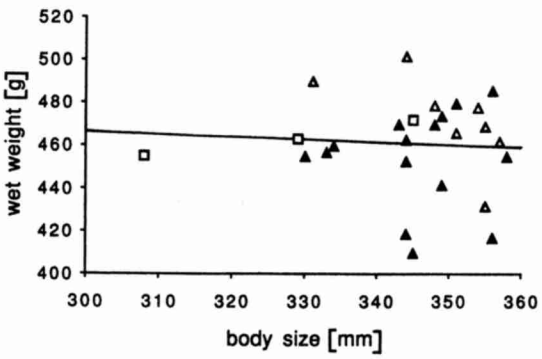

Fig. 1. Relationship between body size (total length from snouth tip to tip of small supplementary fin) and wet body weight (regression line $y = -0.57\,x + 480$, $r^2 = 0.001$). Wet body weight is the weight of the thawed fish taken from the refrigerator; storing temperature 0 to −4 °C. Symbols of data points indicate the state of yolk sac withdrawl shown in Fig. 2 (▲ stage 1 = yolk sac totally withdrawn, △ stage 2 = small slit at ventral site, remnant of external yolk sac with some yolk visible, □ stage 3 = small pouch of an external yolk sac)

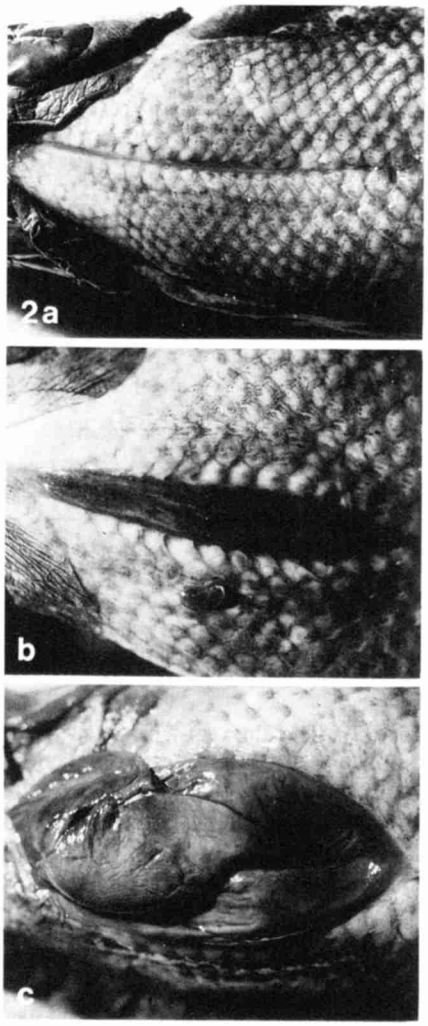

Fig. 2. Stages of yolk sac withdrawl in late-term juveniles; a) stage 1, b) stage 2, c) stage 3. Further explanation see Fig. 1

yolk sacs of the young were not attached to the uterine walls and had a vascularized contact zone between maternal and embryonic tissue [2–4, 6]. The retention of a large yolk sac to term was taken as evidence for a yolk sac placenta supplying embryos with maternal nutrients to supplement their initial yolk supply [2,6]. Such a matrotrophic form of embryonic nutrition during gestation was extrapolated from the dry weight of a mature egg [13] and estimated dry weight of a single pup (preserved in alcohol). The pup's dry weight was maximally 11–30% above the egg's dry weight and this was accepted as evidence of some form of matrotrophy [4,6]. Such approaches have their limitations when, as in coelacanths, only preserved specimens are available.

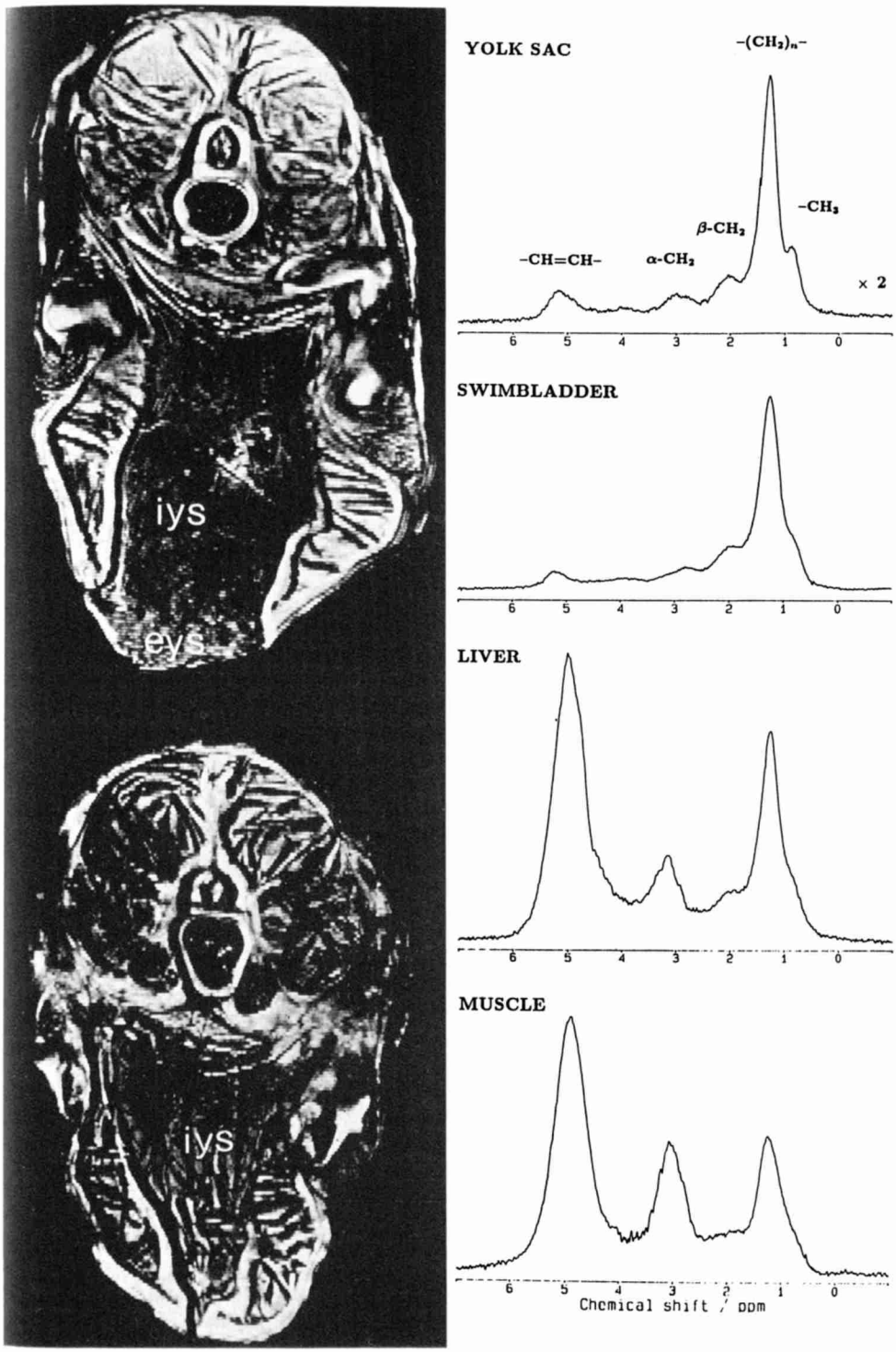

Fig. 3. ^{1}H-NMR images of frozen coelacanths depicting a transverse section through a juvenile with external yolk sac (*eys*) (stage 3, upper left) and a juvenile with internal yolk sac (*iys*) only (stage 1, lower left). The images were obtained at a field strength of 2.35 T (Bruker Biospec, Oxford actively shielded gradients) using a multi-slice FLASH sequence (TR/TE = 150/11 ms, 70° flip angle) yielding a spatial resolution of 0,25 × 0,25 mm² (2 mm section thickness [16]). Localized ^{1}H-NMR spectra in situ (right) of 2–4 ml volumes-of-interest within various tissues were obtained at 2.0 T (Siemens Magnetom) using a STEAM localization sequence (TR/TM/TE = 3000/30/20 ms) [17]. Lipids are a major source of the NMR signal in frozen coelacanths. Yolk sac and swimbladder exhibit a ^{1}H-NMR spectrum typical of saturated fatty acids ($C_{12}-C_{16}$) with negligible contributions from water. Liver and muscle contain similar amounts of lipids, but also strong contributions at about 4.9 ppm chemical shift frequency that are most likely due to tissue water. The resonances at 2.8–3.2 ppm probably reflect a wide range of substances including metabolites such as creatine as well as choline-containing phospholipids

The Moçambique female carried 26 fully developed pups 308 – 358 mm in total length (mean = 345 mm, SD = 11 mm) and had a wet body weight of 410 – 502 g (mean = 461 g, SD = 11 g). There were no additional eggs in the body cavity, and dissection of three specimens revealed no egg fragments in the stomach. Oophagy seems most unlikely at this stage of gestation. The pups resembled small adults except for remnants of an external yolk sac. However, they did not carry the large yolk sacs described for the pups in 1975. Figure 1 presents a size-weight diagram and stages of progressive withdrawl of the external yolk sac (illustrated in Fig. 2). Fifteen pups had lost their external yolk sac. One pup carried only a small oval pouch 50 mm long that still contained yolk. Inasmuch as the external yolk sac withdraws close to term, it cannot function as a yolk sac placenta for additional nutrient transfer during such late stages of gestation. The scatter of the data points relating body size, weight, and stage of yolk sac resorption also suggests that the Moçambique pups were fully grown and very close to term. A size of 340 – 350 mm seems to be the body size at birth. CT- and ^{1}H-NMR images of pups of stages 1 and 3 showed a large cavity of the internal yolk sac filled with yolk (Fig. 3, left) consisting mainly of lipids (probably saturated fatty acids [C_{12} – C_{16}] with a negligible contribution from water; Fig. 3, right). The pups are released with a considerable yolk reserve; a further hint for lecithotrophy even at the end of gestation. All pups were very oily and covered with olive-green fecal matter similar in color to the yolk. Yolk was present in the intestine. Proponents of matrotrophy found yolk in the stomach and gut [6]. Because they could not locate a direct connection (vitelline duct) between the digestive system and the yolk sac, ingestion of eggs was assumed. However, a recent dissection performed at the J. L. B. Smith Institute established a vitelline duct between the internal yolk sac and the intestine [18]. Two further dissections at the Max-Planck-Institute confirmed this finding; the intestine was filled with yolk, while the whitish transparent stomach was in one case empty, in the other partially filled with a gelatinous amorphous substance (possibly histotrophs). The presence of yolk in the intestine cannot be taken as proof of oophagy; the yolk must have originated from the own yolk sac.

In order to estimate whether a particular species is lecithotrophic or matrotrophic, the dry weight of the egg is compared with the dry weight of a full-term pup [3,4,6]. Only lecithotrophic live-bearers undergo an embryonic dry weight loss in the range of 25 – 55 % [4]. The dry freeze weight of one pup (460 g wet weight) was 144 g; the dry weight of an ovulated egg was 185 g [6,13]. Thus, the dry weight of the pup is 22.8 % below the egg's weight. Taking the ratio of the dry/wet weight of 31.3 % into account (a value close to shark pups: 30 % [6]), the dry weight of all pups was calculated. It ranged between 15 – 31 % below the dry weight of the eggs (mean = 23 %, SD = 4 %). The values are far below the data of former studies [4,6], but within a range of lecithotrophic live-bearers.

The body size of the Moçambique pups (mean 345 mm) compared to those found earlier reveals that the five pups of 1975 with their large yolk sacs were at a fairly advanced stage of gestation but not yet at full term. Their otherwise adult-like form led to the conclusion that they were already fully grown and retained their yolk sac to term in order to assist maternal nutrient transfer. Proponents of oophagy and placentotrophy also claimed that it is highly unlikely that 19 ovulated eggs could come to term, as this would necessitate an oviduct length of more than 7 m [6]. Now we have found an even higher number of term pups but meanwhile the number of maturing eggs has also increased. Evidently, it is not the oviduct length that is the critical constraint of litter size but the volume of the mother's visceral cavity in relation to the volume of the term pups [7]. Obviously, the fecundity of coelacanth females can vary considerably, and brood weight reveals high maternal investment. The Moçambique pups indicate an obligate lecithotrophic live-bearing, the most primitive form of viviparity. We have no clear evidence for the most recently proposed advanced matrotrophic reproductive guild of internal bearing combining lecithotrophy and matrotrophy [5].

Nothing is known about the delivery time, depth, and location of parturition. At the Comores we have carried out a total of 199 submersible dives and surveyed at a depth of 400 m [19]: juveniles having the expected birth size have not been found; the smallest coelacanths had an estimated size of 60 – 90 cm [19]. In October 1991, we tagged a pregnant female with a VEMCO pressure pinger (V3-P-4HI). The female had a swollen abdomen and her cloacal region was protruded and pink in color. In contrast to four other tagged adult coelacanths, the female went below the depth range of adults (180 – 480 m) and remained over 1 day at 698 m at least. This indicates that birth could take place beyond the adult's depth range; juveniles may live in deeper waters. We can expect further surprises in coelacanths.

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Letter to the Editors

A Universal Constant in Temporal Segmentation of Human Speech

A reply to Schleidt and Feldhütter (1989)

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Schleidt, Eibl-Eibesfeldt and Pöppel [1] and Schleidt and Feldhütter [2] demonstrated a universal time constant in rhythmically repeated movements and also in working activities and movements with hand-body contact. Corresponding to the observation of Pöppel [3] that human time perception is based on perceptual patterns of short duration with an upper limit of 3 s, they found a 3-s temporal window for the segmentation of short-term movement in different cultures. This result was regarded as indicating a general structure underlying mental activity.

If this is true, a similar constant should be found in speech, as speaking is the behavior where sequencing is a necessary condition. At the level of speech perception, sequential acoustic events have to be integrated yielding the perception of syllables. At a semantic level, syllables are integrated resulting in the perception of the message which is to be transferred. Thus, it was hypothesized that a rhythmic temporal organization underlies the production of speech (for example by Pöppel [3]).

To investigate this notion, 195 talks from 159 subjects were analyzed. The subjects were German students and older people, the talks included provoked and everyday conversations in the free field. These talks were recorded by means of the LOGOPORT, a portable device designed for sampling speaking behavior as a pattern of on (= speaking) and off (= pausing) during the whole day (described in [4]). The duration of speech units was examined at two different time levels: At the vocalization level where phonations (roughly corresponding to vowel-consonant units) are integrated, forming syllables and words (the vocalizations), and at the utterance level, where intonational phrases are combined, resulting in utterances.

As in human short-term movements, two kinds of units can be distinguished: First, those consisting of a single speech event, that is, an utterance which corresponds to one intonational phrase, or a vocalization which contains only one phonation (this is similar to the nonrepetitive behavior of Schleidt and Feldhütter [2]). Second, those consisting of several speech events, that is, an utterance which contains multiple intonational phrases, or a vocalization containing multiple

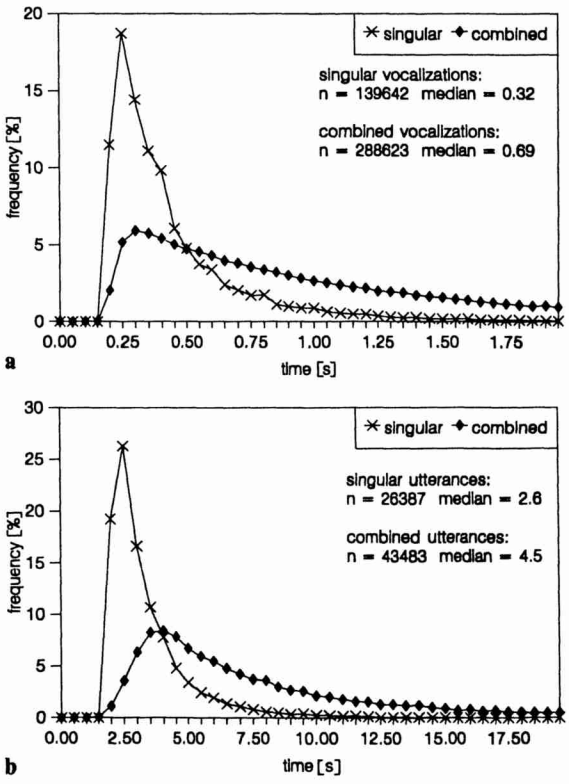

Fig. 1. Histograms for the duration of speech events at the vocalization level (a) and utterance level (b) divided in "repetitive" and "nonrepetitive" events