The sensory canal systems of the living coelacanth, *Latimeria chalumnae*: a new instalment

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Synopsis

Entire sensory canal systems of the coelacanth, *Latimeria chalumnae*, are described: not only the course of principal canals with their primary and secondary collaterals, but also the course and branches of the pit-line and reticular canals. The number of pores on the left side of the head were found to be 296 in an early (yolksac) embryo, 321 in a late term fetus, 485 in a juvenile, and 2974 in adults. This means that in latimeria most of the lateral-line canal system develop after parturition. Pit lines of the living coelacanth are not rows of superficial neuromasts but canals covered by a thin epidermis like in other sensory canals of the lateral line. These pit-line canals, however, have a very specific structure and branching pattern: the medial dorsal pit-line canal is connected by fine branches on top of the head. The infra-dentary pit-line canal connects via these branches with canals deep inside the bones. Several fine and richly branched canaliculi of unknown function radiate from each quadratojugal pit-line canal. The gular plate pit-line canal has superficially branching arms as well as connections to numerous deeper canals inside the bone. These canals consist of fine branches that in turn lead to and open on the ventral surface of the gular plates as small pores. The system is reminiscent of the reticular (pore) canal system known only from some fossil agnathans and fishes. Thus latimeria combines the reticular system of ancient vertebrates with the lateral-line system of modern fishes. The significance of this gular (possibly electro-sensory) system for feeding by the coelacanth will be discussed.

Introduction

The course of the principal sensory canal systems with their primary and secondary collaterals, as well as the branches of the pit-line and the reticular canals of *Latimeria chalumnae* Smith, 1939 of various sizes and ontogenetic states are described in this paper. The lateral-line sensory canal systems and some of its innervations were described earlier by Smith (1939a,b, 1940), Millot & Anthony (1958, 1959, 1965), Hensel (1986) and Bemis & Northcutt (1992) but the precision varied.

Latimeria chalumnae lives on steep slopes of volcanic origin with caves used as daytime shelters. It occurs at depths of 170 to 230 m below sea level which, in its range, is also below the 18°C isotherm, but occasionally it may enter water as warm as 23°C (Fricke et al. 1991). It favors slopes with abundant cavities not covered with coral sand as hideouts for its prey (Balon et al. 1988). Consequently, tactile and electro-sensory systems are probably more important than vision for orientation and acquisition of food (e.g., Thompson 1970, Northcutt 1980, Fricke & Plante 1988, Fricke et al. 1991, Hissmann & Fricke 1996).

The slow swimming and rolling motions seemingly in defiance of gravity, and the intermittent headstands, observed from the submersibles GEO and JAGO (e.g., Fricke et al. 1987, 1991, Fricke & Hissmann 1992, Fricke 1993), are still begging an explanation, although 'it is suspected', writes Forey (1998, pp. 25–26), 'that it may have something to do with electroreception by bringing the rostral organ (p. 21) close to the substrate to detect minute potential differences created by the activity of prey.' Obviously McCosker's (1979) vision of the coelacanth's feeding mode applies no more. Do the new findings concerning the sensory systems support the interpretation of feeding presented by Balon (1990, 1991a, 1999) and Uyeno & Tsutsumi (1991)?

Material and methods

The four late-term fetuses (CCC no. 162. 12, 18, 22, and 25) we studied were from a litter of 26 (Figure 1) found in a large female of 179 cm TL and 98 kg. This female was captured offshore the small port of Pebane northeast of Quelimane, central Mozambique, about 15 km from the adjacent continental slope on 11 August 1991 (Bruton et al. 1992). In addition, we had a female of 168 cm TL (CCC no. 154), two yolksac embryos (CCC no. 29.2 and 29.3), the skeletons of 125.5 cm long male (CCC no. 153) and a 164 cm long female (CCC no. 159). Furthermore, we used photographs and drawings
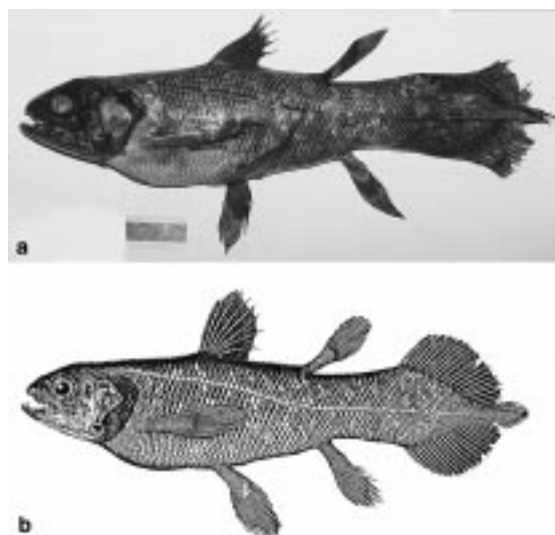

Figure 1. a – Late-term fetus CCC no. 162.18 from the litter of 26 after receipt in Guelph, and b – drawing of the same preserved specimen (orig. by Paul Vecsei).

of sensory canals of the entire lateral-line system of specimens CCC no. 5, 14, 29.5 and 94. More detailed data on each of these specimens can be found in Millot et al. (1972), Bruton & Coutouvidis (1991), and Bruton (1992, 1993).

The canal systems of the fetuses was made visible following the method of Jakubowski (1967): the formaldehyde-preserved specimens were bleached in 2% hydrogen peroxide and a solution of Delafield's
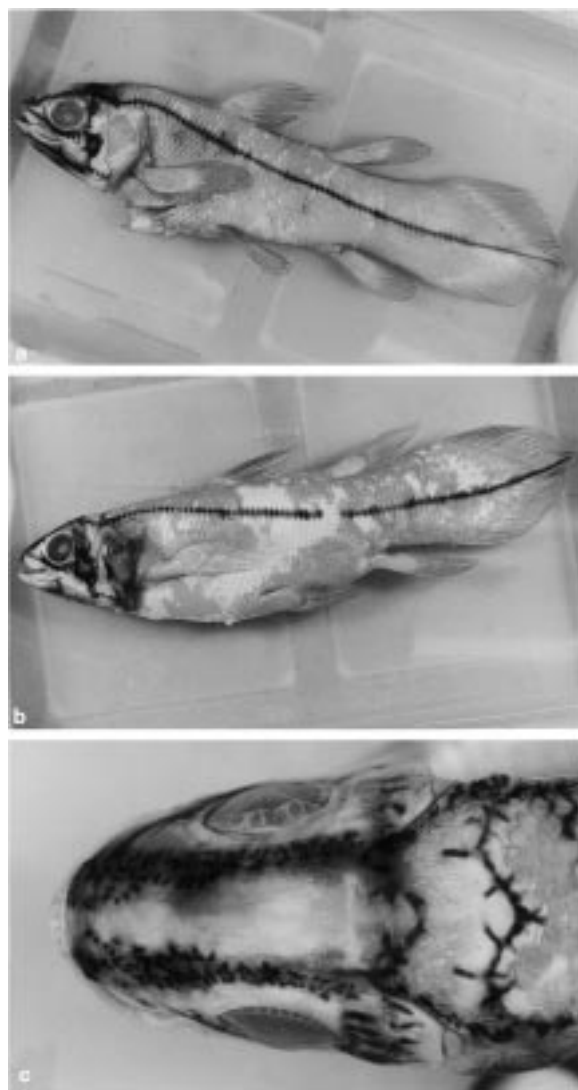

Figure 2. a – Late-term fetus CCC no. 162.22, side view after bleaching and hematoxylin injection into the lateral-line system. b – Lateral view of the fetus CCC no. 162.12 after similar treatment. c – Dorsal view of the head of the same specimen 162.12.
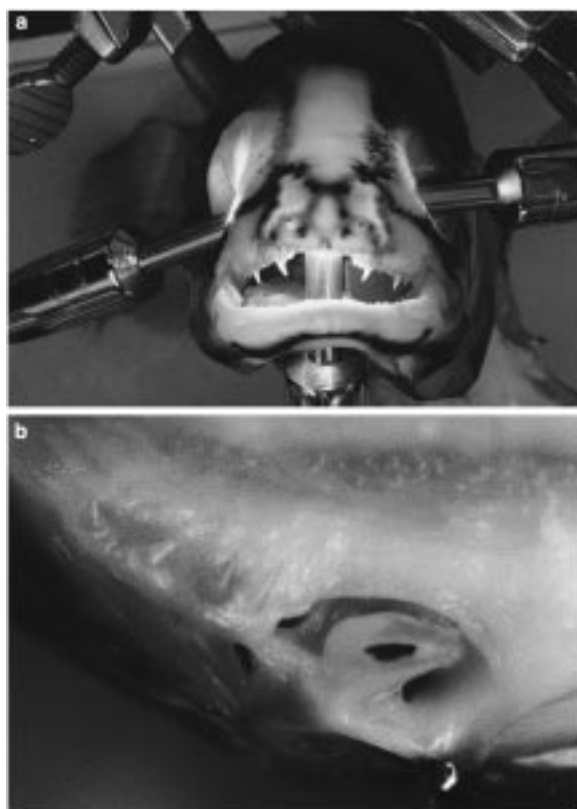
Figure 3. a – Frontal view of fetus CCC no. 162.22 illuminated with fiber optics from the inside for better demonstration of the hematoxylin injected lateral-line canals. b – Ventral view of the infraorbital canal in the area of the tube-like anterior nare of the late term fetus CCC no. 162.12.

hematoxyline diluted in distilled water 1:1 was injected (Figures 2a and b). To enhance the visibility of the injected canals we illuminated the specimens from the inside with fiberoptics (Figure 3a). Photographs and photomicrographs were taken on 35 mm films with macro lens or through dissecting microscope, respectively (Figures 2c, 6a and b). Subsequently on large prints, the canals, pores and canaliculi were further outlined in ink to show their proper proportions and correct sizes.

We use the terminology suggested by Hensel (1986) but not the later introduced modifications by Northcutt & Bemis (1993). There were several methods previously used to name the lateral-line canals (see Hensel 1978). Most often these names were based on the type and structure of bones in which the canals are located, or on the inervation of their neuromasts. This method, however, often caused confusion, because the names for cranial bones are not standardized, and the neuromast-nerve connections in most fishes are not known. We believe that it is best to follow ideation of Allis (1889) who named the canals simply according to the body part over which they are formed. Hence canals that run above or below the orbit are named supra- or infraorbital, canals on the gill cover and lower jaws are operculo-mandibular, canals on the temples are temporal or supratemporal, and canals running along the body sides are simply lateral. Weitzman (1962) stated with respect to the names of bones: '. . . some writers forget that a name is merely a name, not a description'. The same applies to the names of canals as long as they are clear to everybody.

When there is a need, for whatever reason, to stress that a part of a lateral-line canal runs in a specific bone or that its neuromasts are linked to a particular nerve, then it suffices to expand the name, for example, the preopercular part of the operculo-mandibular canal, or the otic part of the temporal canal. When there is a need to highlight other properties of a canal, the addition of an adjective like 'sensory' or 'commissural' solves the problem. In such cases, however, naming should be applied consistently and not like in Northcutt & Bemis (1993) loosely, once 'supraorbital sensory canal' and also 'mandibular canal', or once 'supratemporal sensory canal' and another time 'posterior ethmoid commissure'.

Results and discussion

Lateral-line sensory canals

The course of the main canals of the lateral-line system in the late-term fetuses of *Latimeria chalumnae* (Figures 2a,b and 4) is similar to that described earlier by Hensel (1986). The number of primary and secondary collaterals (canaliculi) and pores through which the canals open to the exterior are, for example, 81 in the infraorbital canal of the yolksac embryo (CCC no. 29.5), 89 in the now studied late-term fetus (CCC no. 162.12) and 135 in the smallest free-swimming juvenile (CCC no. 94) after parturition. Similar conditions are in the other canal systems. The total number of pores on the left side of the head were found to be 296 in an early (yolksac) embryo, 321 in a late- term fetus, 485 in a juvenile, and 2974 in the adult (CCC no. 5). This means that the ramification of the lateral-line canal system is a process which accelerates clearly after parturition, i.e., during life in the external environment.
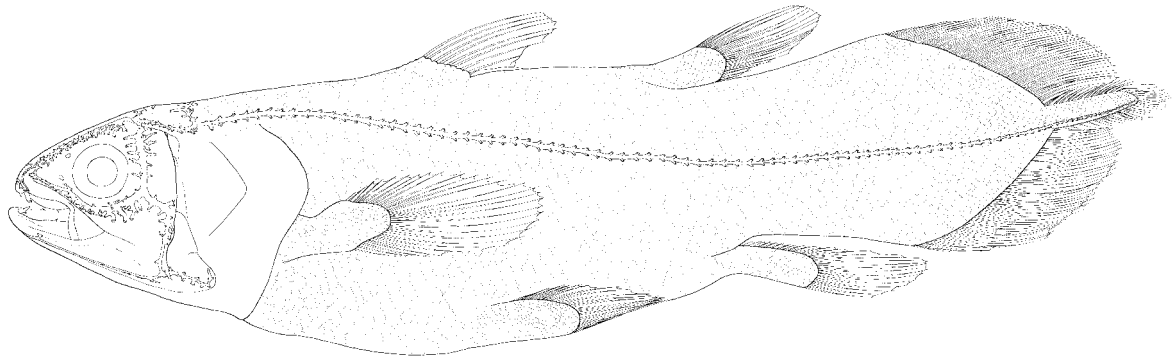
Figure 4. Entire lateral-line canal system on the left side of fetus CCC no. 162.12.
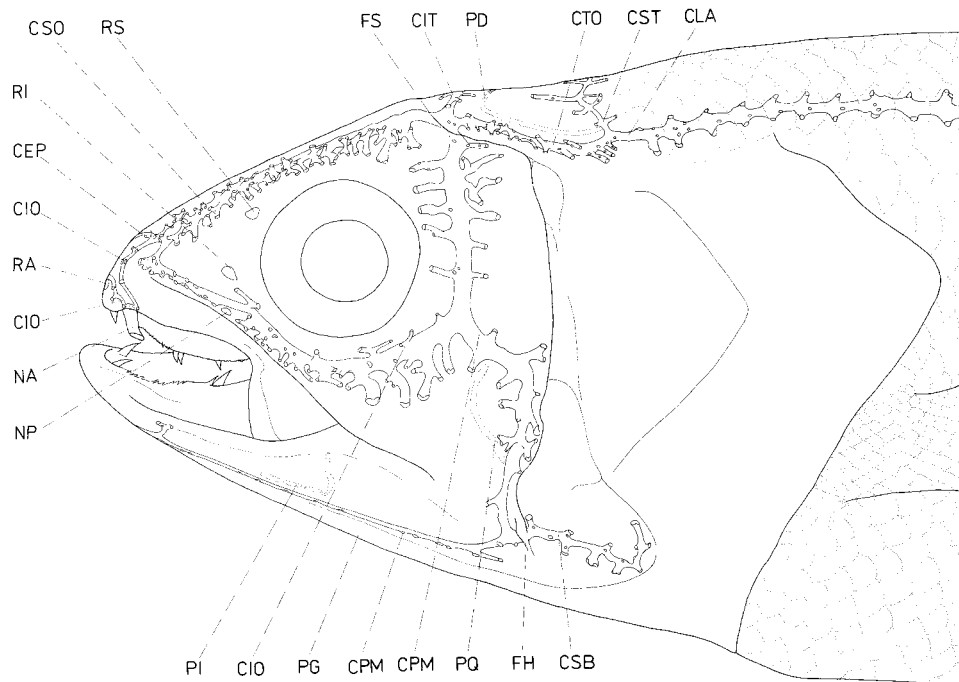

Figure 5. Side view of the head lateral-line canal system of fetus CCC no. 162.12 [abbreviations: CEP = ethmoid (commissural) sensory canal, CIO = infraorbital sensory canal, CIT = intertemporal sensory canal, CPM = preoperculomandibular sensory canal, CLA = lateral (trunk) sensory canal, CSB = subopercular sensory canal, CSO = supraorbital sensory canal, CST = supratemporal (commissural) sensory canal, CTO = temporal sensory canal, FH = hyoid fossa, FS = subtemporal fossa, NA = anteriol nasal opening, NP = posterior nasal opening, PG = gular pit-line canal, PI = infradentary pit line-canal, PD = dorsal pit-line canal, PQ = quadratojugal pit-line canal, RA = anterior opening of rostral organ, RI = inferior opening of rostral organ, and RS = superior opening of rostral organ].

We now observed in more detail the structure of the infraorbital canal under the tube-like anterior nasal opening. In the two fetuses studied (CCC no. 12 and 22), the dorsal and medial walls of the canal are not interrupted and the lateral wall is formed by the tube-like elongated anterior nare. When the tube-like nare is shifted to the side, we can see that the canal beneath is ventrally open (Figures 5 and 3b). It means that it is unnecessary to specify an anterior ethmoid (commissural) canal because it is merely a continuation

of the infraorbital canal. Therefore, even the posterior ethmoid canal may be labeled as the ethmoid (commissural) canal only.

In late-term fetuses the lateral canal runs in a slightly curvaceous manner along the body sides (Figures 1 and 4) to the tip of the epicaudal lobe (= caudal fin according to Uyeno 1991). It runs inside the scales and opens externally in each scale via two branches. One branch aims dorsally, the other ventrally. Only close to the head are several scales that have on their surface fine pores through which this sensory canal connects directly to the external environment.

Pit-line canals

The pit-line canals in both late-term fetuses are basically similar to these of the yolksac embryo and of the juvenile described earlier by Hensel (1986). Nonetheless, we found some other details not known before. It is now certain that the pit lines in the living coelacanth are not lines of superficial neuromasts but pit-line canals covered by a thin epidermis. These canals can be injected with stain like other sensory canals of the lateral line. They have, however, quite a different structure and branching pattern compared to the lateral-line sensory canals of other modern fishes (Hensel 1978).

Both medially oriented branches of the dorsal pit-line canals of the late-term fetus CCC no. 162.12 connect on the head dorsum and clearly branches (Figures 2c and 6a). In addition, within the left medial branch of this dorsal pit-line canal we discovered a section that looks in form and size like the lateral-line sensory canal. While injecting the quadratojugal pit-line canal, we have found several plexuses of fine canaliculi (Figures 6a and b) of unknown function. The infradental pit-line canal runs in a grove of the bone and its branches connect with canaliculi within the bone.

There are two gular pit-line canals, one on each gular plate (see figure 4 in Balon et al. 1988 and figure on the bottom of page 226 in Balon 1999). Each canal is located in a slight depression approximately in the center of the bone; it is covered by a thin epidermis that can be easily pierced with a fine glass cannula (Figure 7a). Through this opening the entire pit-line canal can be injected with stain. After the injection of stain the surface branches of the canal become clearly visible (Figure 7b) as are their connections with the numerous deeper canals within the gular bone. Blowing with more
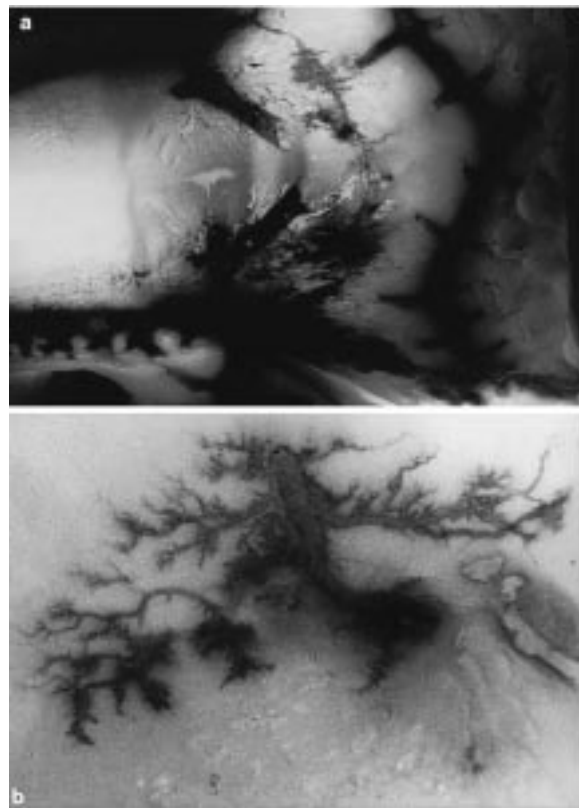

Figure 6. a – Dorsal view of the medial branches of the pit-line canals conjoined by thin canaliculi (CCC no. 162.22). b – Fine, richly branched canaliculi radiating from the quadratojugal pit-line canal of the same specimen.

pressure, it was possible to drive the stain even to the most remote canals of the gular bone. These canals and canaliculi all have fine branches that lead to the ventral surface of the gular bones where they exit to the outside through delicate pores (Figure 7c). As already stated earlier (Hensel 1986), this entire systems of canals in the gular plates is reminiscent of the reticular canal system described in some fossil agnathans and fishes (cf. Thomson 1975, 1977). In order to learn more about this system it would be necessary to find and survey the nerve endings within the gular bones.

Conclusion

Latimeria chalumnae inhabits steep slopes with preferably fresh lava rocks, cavities and caves not filled by coral sand (Balon et al. 1988, Fricke et al. 1991, Fricke & Hissmann 1994). It is a sluggish swimmer
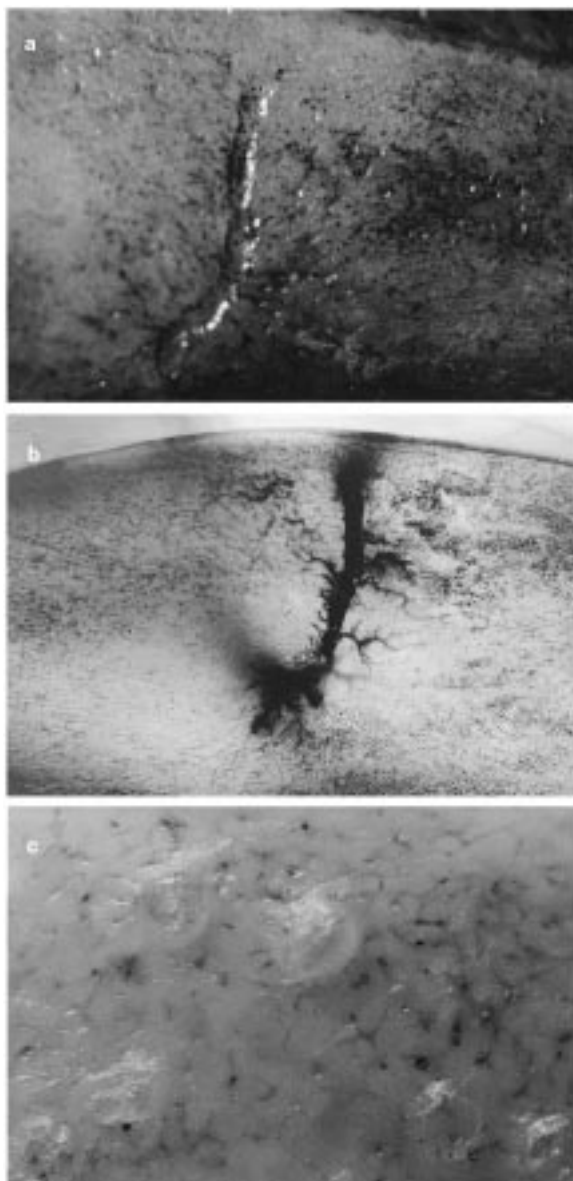
Figure 7. a – Depression on the ventral side of the gular bone at the site of the gular pit-line canals (CCC no. 162.22). b – The gular pit-line reticular canal system after hematoxyline injection of the same specimen. c – Openings of the pore canals at the ventral surface of the gular bone (CCC no. 162.12).

with a low metabolic rate (Hughes 1976) and, during its nocturnal (foraging) drifts along the bottom, regularly performs intermittent head stands (Fricke et al. 1987) which were initially interpreted as a position that 'enables the coelacanth to detect prey with greater ease' (Weinberg 1999, p. 178). The prey found in latime-

ria's digestive system (Uyeno & Tsutsumi 1991, Bruton & Stobbs 1991, Forey 1998) is known to use cavities in the bottom substrate for hiding.

Latimeria is able not only to move its lower jaw but, thanks to an intracranial joint also to lift its upper jaw (Thompson 1966, 1967, 1970, Forey 1990). This feature, unique among extant vertebrates, allows for a considerable increase in the oral gape, as Forey (1998, p. 22) puts it: '. . . the presence of the intracranial joint, together with the unusual hyoid arch and tandem jaw articulation, would allow the jaws to be opened very rapidly to a wide gape in which the lower jaw is thrust forward'. In addition to the rostral organ (Northcutt 1980, 1986, Bemis & Hetherington 1982) it has distinct reticular system in the gular bones that probably also function as an electro-sensory system.

The capture of prey by latimeria was never directly seen or recorded (except for one anecdotal mention by Bruton & Stobbs 1991, p. 320) in its natural habitats, but the scenario of prey capture described earlier by Balon (1990, 1991a) and partly by Uyeno & Tsutsumi (1991) is now further supported by the existence of the downward oriented gular electro-sensory system described in this paper (Figure 7). As tested by Fricke[1], electric fields induce the headstands in latimeria (Fricke & Plante 1988).

'Imagine a coelacanth drifting with the current close to the bottom that suddenly senses with its rostral and especially reticular electro-sensory systems in its gular bones bioelectric field produced by a small fish or cephalopod hiding in a lava cavity. Instead of wasting energy by chasing a free-swimming prey, latimeria makes a head stand, opens both jaws and, with the suction so created, slurps the prey from its hiding. This explains not only its preferred habitat over lava substrate with cavities free of sand, but also its behavior (headstands) and its rare and accidental captures. Bait of fishers is mostly floating above the bottom and only exceptionally drifts into a cavity. Moreover, the bait is dead and does not create an electric emission' (Balon 1999, p. 226, our translation). This interpretation of coelacanth feeding now requires only confirmation by direct observation.

Lack of observation of natural feeding from submersibles can be explained that only disturbed individuals were seen, to which the always erected first dorsal fin attests. Natural feeding may be observed using remote recording from ROV's, or directly in aquaria

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[1] Pp. 30–31. Newton Graphic Science Magazine 8(12): 10–31, 1988 (in Japanese).

if their bottom is accordingly arranged. Until then our interpretation remains only a best scenario that some selfrighteous 'taxonomists' will probably 'attack' with gusto, similarly to their 'expertise' revealed in case of latimeria reproduction (Wourms et al. 1991, Balon 1991b vs. Heemstra 1998).

Acknowledgements

References cited

Allis, E.P. 1889. The anatomy and development of the lateral line system in *Amia calva*. J. Morphol. 2: 463–540.

Balon, E.K. 1990. The living coelacanth endangered: a personalized tale. Tropical Fish Hobbyist 38 (February): 117–129.

Balon, E.K. 1991a. Prelude: the mystery of a persistent life form. Env. Biol. Fish. 32: 9–13.

Balon, E.K. 1991b. Probable evolution of the coelacanth's reproductive style: lecithotrophy and orally feeding embryos in cichlid fishes and in *Latimeria chalumnae*. Env. Biol. Fish. 32: 249–265.

Balon, E.K. 1999. Svědectví o vztahu s živou fosilií (1–3) [A testimony to the relationship with a living fossil] (1–3). Živa (Prague) 47: 176–179; idem (2–3), ibidem 224–227; idem (3–3), ibidem 270–271 + inside front cover.

Balon, E.K., M.N. Bruton & H. Fricke. 1988. A fiftieth anniversary reflection on the living coelacanth, *Latimeria chalumnae*: some new interpretations of its natural history and conservation status. Env. Biol. Fish. 23: 241–280.

Bemis, W.E. & T.E. Hetherington. 1982. The rost[r]al organ of *Latimeria chalumnae:* morphological evidence of an electroreceptive function. Copeia 1982: 467–471.

Bemis, W.E. & R.G. Northcutt. 1992. Skin and blood vessels of the snout of the Australian lungfish, *Neoceratodus forsteri*, and their significance for interpreting the cosmine of Devonian lungfishes. Acta Zoologica (Stockholm) 73: 115–139.

Bruton, M.N. 1992. Addition to the coelacanth inventory. Env. Biol. Fish. 33: 415.

Bruton, M.N. 1993. Additions and corrections to the inventory of *Latimeria chalumnae*: II. Env. Biol. Fish. 36: 398–405.

Bruton, M.N., A.J.P. Cabral & H. Fricke. 1992. First capture of a coelacanth, *Latimeria chalumnae* (Pisces, Latimeriidae), off Mozambique. S. Afr. J. Sci. 88: 225–227.

Bruton, M.N. & S.E. Coutouvidis. 1991. An inventory of all known specimens of the coelacanth *Latimeria chalumnae*, with comments on trends in the catches. Env. Biol. Fish. 32: 371–390.

Bruton, M.N. & R.E. Stobbs. 1991. The ecology and conservation of the coelacanth *Latimeria chalumnae*. Env. Biol. Fish. 32: 313–339.

Forey, P.L. 1990. The coelacanth fish: progress and prospects. Sci. Progress (Oxford) 74: 53–67.

Forey, P.L. 1998. History of the coelacanth fishes. Chapman & Hall, London. 419 pp.

Fricke, H. 1993. Der Quastenflosser. Biologie eines legendären Fisches. Biologie in unserer Zeit 23: 229–237.

Fricke, H. & K. Hissmann. 1992. Locomotion, fin coordination and body form of the living coelacanth *Latimeria chalumnae*. Env. Biol. Fish. 34: 329–356.

Fricke, H. & K. Hissmann. 1994. Home range and migration of the living coelacanth *Latimeria chalumnae*. Mar. Biol. 120: 171–180.

Fricke, H., K. Hissmann, J. Schauer, O. Reinicke, L. Kasang & R. Plante. 1991. Habitat and population size of the coelacanth *Latimeria chalumnae* at Grand Comoro. Env. Biol. Fish. 32: 287–300.

Fricke, H. & R. Plante. 1988. Habitat requirements of the living coelacanth *Latimeria chalumnae* at Grande Comore, Indian Ocean. Naturwissenschaften 75: 149–151.

Fricke, H., O. Reinicke, H. Hofer & W. Nachtigall. 1987. Locomotion of the coelacanth *Latimeria chalumnae* in its natural environment. Nature 329: 331–333.

Fricke, H., J. Schauer, K. Hissmann, L. Kasang & R. Plante. 1991. Coelacanth *Latimeria chalumnae* aggregates in caves: first observations on their resting habitat and social behavior. Env. Biol. Fish. 30: 281–285.

Heemstra, P.C. 1998. Reproduction of the coelacanth (a synopsis and analysis of the oophagy controversy). Ichthos 59: 16–20.

Hensel, K. 1978. Morphology of lateral-line canal system of the genera *Abramis, Blicca* and *Vimba* with regard to their ecology and systematic position. Acta Univ. Carolinae, Biologica 12: 105–153.

Hensel, K. 1986. Morphologie et interprétation des canaux et canalicules sensorieles céphaliques de *Latimeria chalumnae* Smith, 1939 (Osteichthyes, Crossopterygii, Celacanthiformes). Bull. Mus. nat. Hist. nat. Paris 4e sér. 8 A 2: 379–407.

Hissmann, K. & H. Fricke. 1996. Movements of the epicaudal fin in coelacanths. Copeia 1996: 606–615.

Hughes, G.M. 1976. On the respiration of *Latimeria chalumnae*. Zool. J. Linn. Soc. 59: 195–208.

Jakubowski, M. 1967. A method for the manifestation of the lateral-line canals and their neuromasts in fishes. Copeia 1967: 234–235.

McCosker, J.E. 1979. Inferred natural history of the living coelacanth *Latimeria chalumnae*. Occ. Pap. Calif. Acad. Sci. 134: 17–24.

Millot, J. & J. Anthony. 1958. Anatomie de *Latimeria chalumnae*. Tome 1. Squelette, muscles at formation de soutien. Éd. CNRS, Paris. 122 pp.

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Millot, J. & J. Anthony. 1959. Les neuromastes du système latéral de *Latimeria chalumnae*. Ann. Sci. Nat., Zool. 12: 317–328.

Millot, J. & J. Anthony. 1965. Anatomie de *Latimeria chalumnae*. Tome 2. Système nerveux et organes de sens. Éd. CNRS, Paris. 131 pp.

Millot, J., J. Anthony & D. Robineau. 1972. État commenté des captures de *Latimeria chalumnae* Smith (Poissons, Crossoptérygien, Coelacanthidé) effectuées jusqu'au mois d'octobre 1971. Bull. Mus. nat. Hist. nat., Paris, 3ᵉ ser. no. 53, Zoologie 39: 533–548.

Northcutt, R.G. 1980. Anatomical evidence of electroreception in the coelacanth (*Latimeria chalumnae*). Z. Vet. Med. Comp. Anat. Histol. Emryol. 9: 289–295.

Northcutt, R.G. 1986. Electroreception in nonteleost bony fishes. pp. 257–285. *In:* T.H. Bullock & W. Heiligenberg (ed.) Electroreception, John Wiley & Sons, New York.

Northcutt, R.G. & W.E. Bemis. 1993. Cranial nerves of the coelacanth *Latimeria chalumnae* [Osteichthyes: Sarcopterygii: Actinistia], and comparisons with other Craniata. Brain, Behaviour and Evolution 42 Suppl. 1: 1–76.

Smith, J.L.B. 1939a. A living fish of mesozoic type. Nature 143: 455–456.

Smith, J.L.B. 1939b. The living coelacanthid fish from South Africa. Nature 143: 748–750.

Smith, J.L.B. 1940. A living coelacanthid fish from South Africa. Trans. Roy. Soc. S. Afr. 28: 1–106.

Thomson, K.S. 1966. Intracranial mobility in the coelacanth. Science 153: 999–1000.

Thomson, K.S. 1967. Mechanisms of intracranial kinetics in fossil rhipidistian fishes (Crossopterygii) and their relatives. J. Linn. Soc. Zool. 46: 223–253.

Thomson, K.S. 1970. Intracranial movement in the coelacanth *Latimeria chalumnae* Smith (Osteichthyes, Crossopterygii). Postilla 149: 1–12.

Thomson, K.S. 1975. The biology of cosmine. Peabody Mus. Nat. Hist. 40: 1–59.

Thomson, K.S. 1977. On the individual history of cosmine and possible electroreceptive function of the pore-canal system in fossil fishes. pp. 247–270. *In*: S.M. Andrews, R.S. Miles & A.D. Walker (ed.) Problems in Vertebrate Evolution, Academic Press, London.

Uyeno, T. 1991. Observations on locomotion and feeding of released coelacanths, *Latimeria chalumnae*. Env. Biol. Fish. 32: 267–273.

Uyeno, T. & T. Tsutsumi. 1991. Stomach contents of *Latimeria chalumnae* and further notes on its feeding habits. Env. Biol. Fish. 32: 275–279.

Weinberg, S. 1999. A fish caught in time. The search for the coelacanth. Fourth Estate, London. 239 pp. (also 2000, idem, Harper Collins Publishers, New York. 220 pp.)

Weitzman, S. H. 1962. The osteology of *Brycon meeki*, a generalized characid fish, with an osteological definition of the family. Stanford Ichthyological Bulletin 8: 1–77.

Wourms, J.P., J.W. Atz & M.D. Stribling. 1991. Viviparity and maternal-embryonic relationship in the coelacanth *Latimeria chalumnae*. Env. Biol. Fish. 32: 225–248.