

Observation of the first juvenile Indonesian coelacanth, *Latimeria menadoensis* from Indonesian waters with a comparison to embryos of *Latimeria chalumnae*

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ABSTRACT — The juvenile of Indonesian coelacanth, *Latimeria menadoensis* is here described for the first time in detail with comparison to embryos of *Latimeria chalumnae*. The juvenile was found in free swimming at 164.6 m depth off Manado, Indonesia on the 6th October in 2009. Because the total length of the juvenile is 31.5 cm, which is smaller than the embryos of *L. chalumnae*, it is speculated that not much time has passed from its birth. The depth at which the juvenile was found is within the range of the depth where adult *L. menadoensis* were observed, hidden in a narrow and long overhang where large predators could not enter. The juvenile has a more slender body, smaller orbit, shorter and deeper posterior part of the body (caudal peduncle) between the second dorsal and the anal fins and anterior ends of the dorsal and ventral lobes of the caudal fin (the third dorsal and second anal fins), longer dorsal and ventral lobes of the caudal fin (the third dorsal and second anal fins), broader peduncles of broader lobed fins, larger first dorsal fin and longer supplementary lobe of the caudal fin (caudal fin) than embryos of *L. chalumnae*. This indicates clear differences in the first ontogenetic stages of the two species, although adults have almost the same morphological features. *Latimeria menadoensis* appears to reproduce in a rather confined area, because both the juvenile and adults have been found within the same area inside of Manado Bay.

KEY WORDS: habitat, heterochrony, Indonesian coelacanth, juvenile, *Latimeria menadoensis*

INTRODUCTION

The first individual of the extant coelacanth, *Latimeria chalumnae*, was discovered in South Africa in 1938 (SMITH, 1939). The first observation of the living coelacanth habitats using submersible was reported in Comoros (FRICKE *et al.*, 1987). Juveniles or small individuals of *Latimeria* are rarely observed or caught, and the growth and reproductive biology of extant species of *Latimeria* remain mostly unknown. The only knowledge of its reproduction is that *Latimeria* is

ovoviviparous because captured female specimens carried developing embryos (SMITH *et al.*, 1975, WOURMS *et al.*, 1991).

Aquamarine Fukushima has conducted field surveys for Indonesian coelacanth, *Latimeria menadoensis* from 2005 to 2015 (IWATA *et al.*, 2019). During the surveys a small coelacanth was observed in 2009. This discovery was simply reported as a scientific news (HOLDEN, 2009). Heterochrony of recent coelacanths was discussed based on this discovery. However, the detail of findings was not described. In the present paper, this finding will be described in detail and the probable habitat

of juveniles of coelacanth is discussed. In addition, the detail measurements and counts of the juvenile based on video footages are made and compared to embryos of *L. chalumnae*, which are from a large female (CCC no. 162) caught off Mozambique water in 1991 (BRUTON *et al.*, 1992). This morphological data, based on extant coelacanths, should provide invaluable information to the study of fossil and extant coelacanths.

MATERIALS AND METHODS

Materials are the video footage of the juvenile of Indonesian coelacanth *L. menadoensis* (Fig. 1) and photos of the embryos of the African coelacanth *L. chalumnae*, which are CCC no. 162.16 housed in the J. L. B SMITH Institution, South Africa (Fig. 2A) (SECRETARIAT AT THE J. L. B. SMITH INSTITUTE OF ICHTHYOLOGY, 1993, fig. 3), CCC no. 162.12 (Fig. 2B) and CCC no. 162.22 (Fig. 2C) housed in University of Guelph (HENSEL and BALON, 2001, fig. 2a, b). CCC stands for the Coelacanth Conservation Council. The video footages including this finding were taken by a remotely operated vehicle (ROV) (Kowa; HDTV VEGA-300) in the north of Sulawesi Island and Biak Island in Indonesia from 2005 to 2015 (IWATA *et al.*, 2019). The video was recorded with two-line lasers placed 20 cm apart. These lines were applied by two laser beam irradiators attached to the ROV. The measurements of the juvenile were calculated based on the beams (Fig. 3; Table 1) and the fin ray counts are made from the video footages (Fig. 1). Among the embryos, the total length of CCC no. 162.12, 162.16 and 162.22 are 33.3 cm, 34.8 cm and 34.4 cm respectively (SECRETARIAT AT THE J. L. B. SMITH INSTITUTE OF ICHTHYOLOGY, 1993). The body part lengths and proportion to the total length of the three embryos are calculated by measuring the figures (Table 1). In the present study, names of fins follow that of FOREY (1998) which differ from UYENO (1991). Dorsal lobe of caudal fin, ventral lobe of caudal fin and supplementary lobe of caudal fin in FOREY (1998) are 3rd dorsal fin, 2nd anal fin and caudal fin of UYENO (1991), respectively. The terminology of fins by UYENO (1991) is given in parentheses to avoid confusion of names. Fin names are abbreviated in the tables as follows. A₁: Anal fin. A₂: Ventral lobe of caudal fin. C: Supplementary lobe of caudal fin. D₁: First dorsal fin. D₂: Second dorsal fin. D₃: Dorsal lobe of caudal fin. P₁: Pectoral fin. P₂: Pelvic fin. Measurements are abbreviated as follows. HL: Head length. SL: Standard length. TL: Total length.

RESULTS

ROV observations

The juvenile of *Latimeria menadoensis* (ID 15 in IWATA

et al., 2019) was found on the southern coast of Manado Bay of Sulawesi, Indonesia, on the 6th October in 2009 (Fig. 1). The individual stayed in a narrow overhang at 164.6 m depth (Fig. 4A). The overhang was long and progressively became deeper (Fig. 4B). The height of the overhang seemed narrower than the observed juvenile standard length (Fig. 3). The juvenile was observed for 17 minutes from 11:34. It stayed below the overhang and moved slowly, between the depth of 164.6 and 170.9 m. The water current was gentle and the water temperature during the observation was stable, from 14.5 °C to 15.0 °C, the average temperature was 14.8 °C.

Coelacanth has six lobed fins (two pectoral, two pelvic, one dorsal, and one anal fins). It exhibited a unique swimming style by paddling and twisting the lobed fins (FRICKE and HISSMANN, 1992). The swimming of the juvenile was similar to those of adults. During the observation of the juvenile, one cycle of paddling was five seconds and the juvenile swam forward and backward. The paddling pattern and the cycle were the same both the forward and backward swimming.

The dorso-posterior edge of the first dorsal fin, the dorsal edge of the dorsal lobe of the caudal fin (the third dorsal fin), and the ventral edge of the ventral lobe of the caudal fin (the second anal fin) are white. The dorsal margin of the head is convex and angular, where seems to be the intracranial joint (Fig. 1B). Scales have many minute spines, which reflect the light of the ROV.

Comparative description of the juvenile of *L. menadoensis* and embryos of *L. chalumnae*

The total length of the juvenile is 31.5 cm. The standard length is 26.1 cm. It is smaller than the embryos of *L. chalumnae* used here for comparison, which are 30.8–35.8 cm (BRUTON *et al.*, 1992) and it is smaller than the smallest specimen (CCC no. 94) of *L. chalumnae* that has been collected is 42.5 cm TL.. Drawings of the *L. menadoensis* juvenile and *L. chalumnae* embryos (CCC no. 162.16) are shown in Fig. 5. The body of the Indonesian coelacanth juvenile is slender than that of the *L. chalumnae* embryos (Table 1). The body depth is 6.8 cm, 26 % of the standard length in the *L. menadoensis* juvenile and 8.7 cm and 28 % in *L. chalumnae* (Table 1). The head is slightly shorter than that of *L. chalumnae*. It is 5.5 cm and 22 % of the standard length in *L. menadoensis* and 8.0 cm and 26 % in *L. chalumnae*. The depth of the head is slightly smaller than that of *L. chalumnae*. The mouth is slightly smaller than that of *L. chalumnae*. The gape of the mouth is probably smaller than that of *L. chalumnae*. The eye is smaller than that of *L. chalumnae*. The orbit diameter of the *L. menadoensis* juvenile is almost half that of *L. chalumnae*. The part (caudal peduncle) between the second dorsal and the anal fins and the anterior ends of the dorsal lobe of the caudal fin (the third dorsal fin) and the ventral lobe of the caudal fin (the second anal fin) is shorter and deeper than that of *L. chalumnae*. The distance between the posterior end of the base of the second dorsal fin peduncle and the anterior end of the

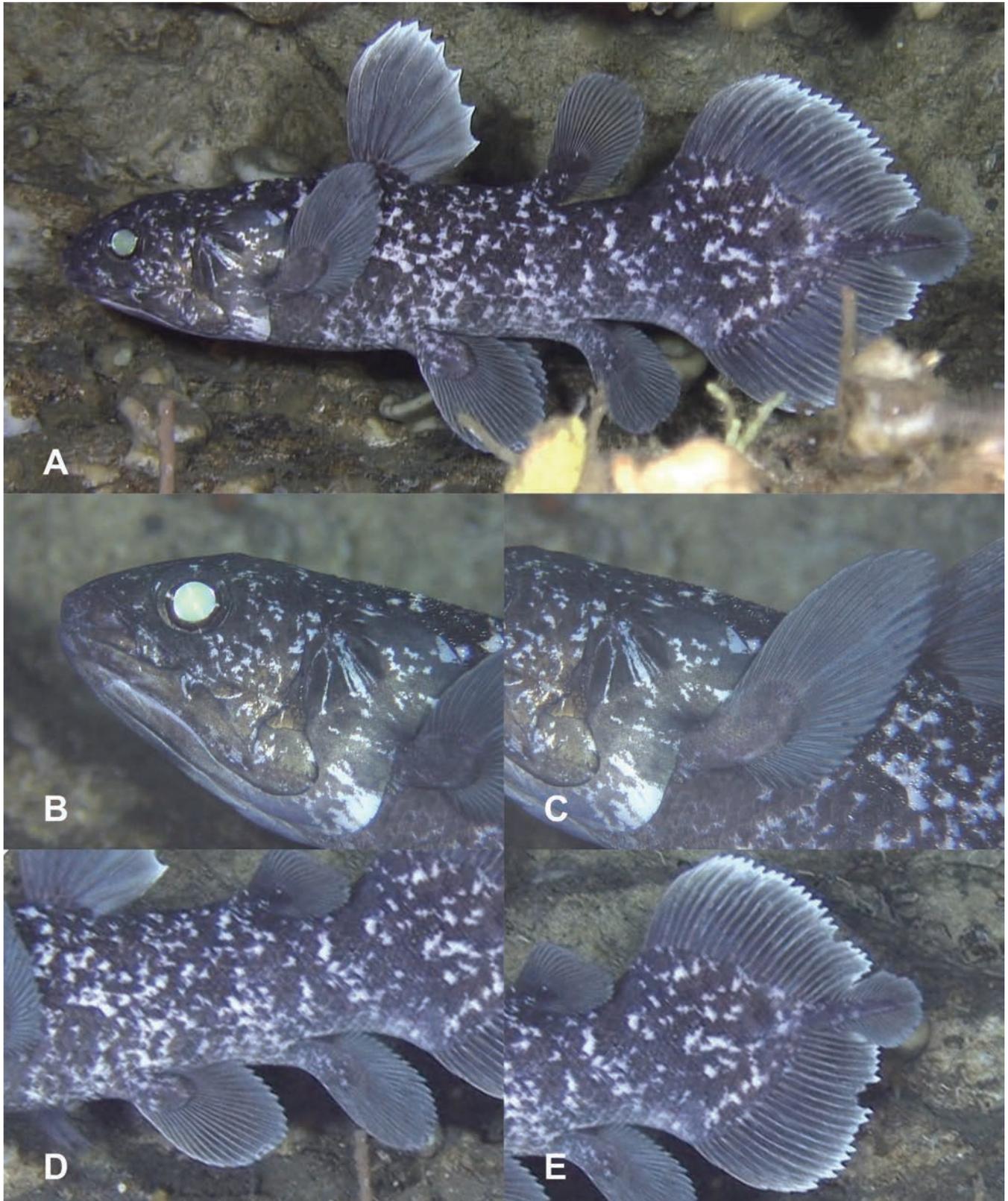


Fig. 1. Juvenile of *Latimeria menadoensis*. A. whole body, B. head, C. pectoral fin, D. pelvic and anal fins, E. caudal region.

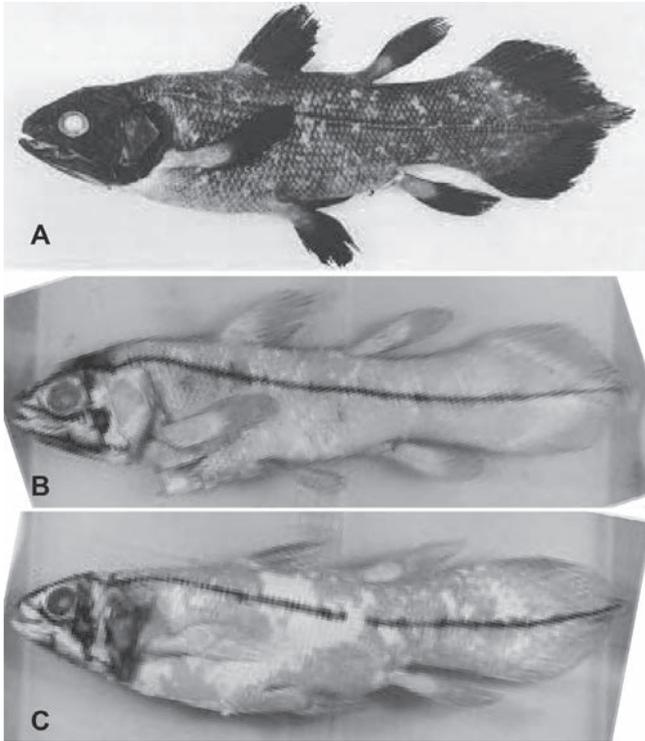


Fig. 2. Embryos of *Latimeria chalumnae*. A. CCC no. 162.16 34.8 cm TL, from SECRETARIAT OF J. L. B. SMITH INSTITUTE OF ICHTHYOLOGY (1993), B. CCC no. 162.22 34.4 cm TL, from HENSEL and BALON (2001), C. CCC no. 162.12 33.3 cm TL, from HENSEL and BALON (2001). All specimens were found in a large female CCC no. 162 from Mozambique, 179 cm TL.

dorsal lobe of the caudal fin (the third dorsal fin) is shorter than that of *L. chalumnae* (Fig. 5). Positions of fins are almost the same in both species, except for the dorsal lobe of the caudal fin (the third dorsal fin). The anterior end of the dorsal lobe of the caudal fin base is located more anteriorly than that of *L. chalumnae* (Fig. 5). The bases of the dorsal lobe of the caudal fin (the third dorsal fin) and the ventral lobe of the caudal fin (the second anal fin) are longer than those of *L. chalumnae* (Table 1). The base of the dorsal lobe of the caudal fin (the third dorsal fin) is longer than that of the ventral lobe of the caudal fin (the second anal fin) in both species. The supplementary lobe of the caudal fin (caudal fin) is longer than that of *L. chalumnae*. All fins are larger and broader than those of *L. chalumnae*. Peduncles of all lobed fins are also broader than those of *L. chalumnae*. The juvenile of *L. menadoensis* has 8 spines of the first dorsal fin; 26 rays of the second dorsal fin; 23 rays of the anal fin; 25 rays of the dorsal lobe of the caudal fin (the third dorsal fin); 23 rays of the ventral lobe of the caudal fin (the second anal fin); 26 rays of the supplementary lobe of the caudal fin (caudal fin); 29 rays of

the pectoral fin and 26 rays of the pelvic fin.

DISCUSSION

Latimeria chalumnae is known to be ovoviviparous (SMITH *et al.*, 1975). To date, no females of *L. menadoensis* with matured eggs or embryos has been captured. Reproductive organs of *L. chalumnae* and *L. menadoensis* are almost the same anatomically (our observation) and, consequently, *L. menadoensis* is here considered to be ovoviviparous as well. A large female of *L. chalumnae* that held juveniles from 30.8 cm to 35.8 cm inside its body was caught off Mozambique water in 1991 (BRUTON *et al.*, 1992). *Latimeria chalumnae* embryo CCC no. 29.5 found inside CCC no. 29 is 32.3 cm TL with a yolk sac, and CCC no. 162.21 is a late embryo without a yolk sac of 35.6 cm TL found inside CCC no. 126 captured in 1991 (CUPELLO *et al.*, 2015). CCC no. 29.5 is housed in Muséum national d'Histoire naturelle, Paris (France) and CCC no. 162.21 is housed in Zoologisches Staatsammlung, München (Germany). These specimens suggest that *L. chalumnae* delivers juveniles of around 30 cm in total length. Since the smaller individuals of *L. chalumnae* observed in their habitat were from 50 to 60 cm long, the ecology of juveniles remain poorly known (FRICKE *et al.*, 2011). According to CCC records, the size of captured small coelacanths are: 50 cm for CCC no. 84 caught in Comoros in 1973; 42.5 cm TL for CCC no. 94 caught in Comoros in 1974; 60 cm TL for CCC no. 116 caught in Comoros in 1979; and 62 cm for CCC no. 160 caught in Comoros in 1989 (NULENS *et al.*, 2011).

The underwater observation at 164.6 m depth off Manado, Indonesia on the 6th October in 2009 is the first account of a live juvenile of *L. menadoensis* in its natural habitat. The juvenile is 31.5 cm in total length. The estimated size at newborn of *L. chalumnae* is around 30 cm as mention earlier. This suggests that not much time has passed since the observed juvenile *L. menadoensis* was born. About 30 adult coelacanths of about 1 m long were found at the depth between 115.6 m and 218.9 m in Indonesia (IWATA *et al.* 2019). The depth of 164.6 m at which the juvenile was recorded is well within the range of adult habitat. The individual of 113 cm total length (ID 16 in Iwata *et al.*, 2019), was observed at 115.6 m depth in the same area three days after the juvenile was found. Presence of both the juvenile and adults of *L. menadoensis* within the same area inside of Manado Bay, suggests that the species reproduce in a rather confined area.

Comparisons of the juvenile *L. menadoensis* and the embryos of *L. chalumnae* show some interesting facts about ontogeny of the congeneric species. The embryos of *L. chalumnae* are larger than the juvenile *L. menadoensis* and have almost completely absorbed their yolk reserves according to CCC newsletter (SECRETARIAT AT J. L. B. SMITH INSTITUTE OF ICHTHYOLOGY, 1993), just before delivery. The juvenile of *L. menadoensis* has a smaller eye, larger peduncles of lobed

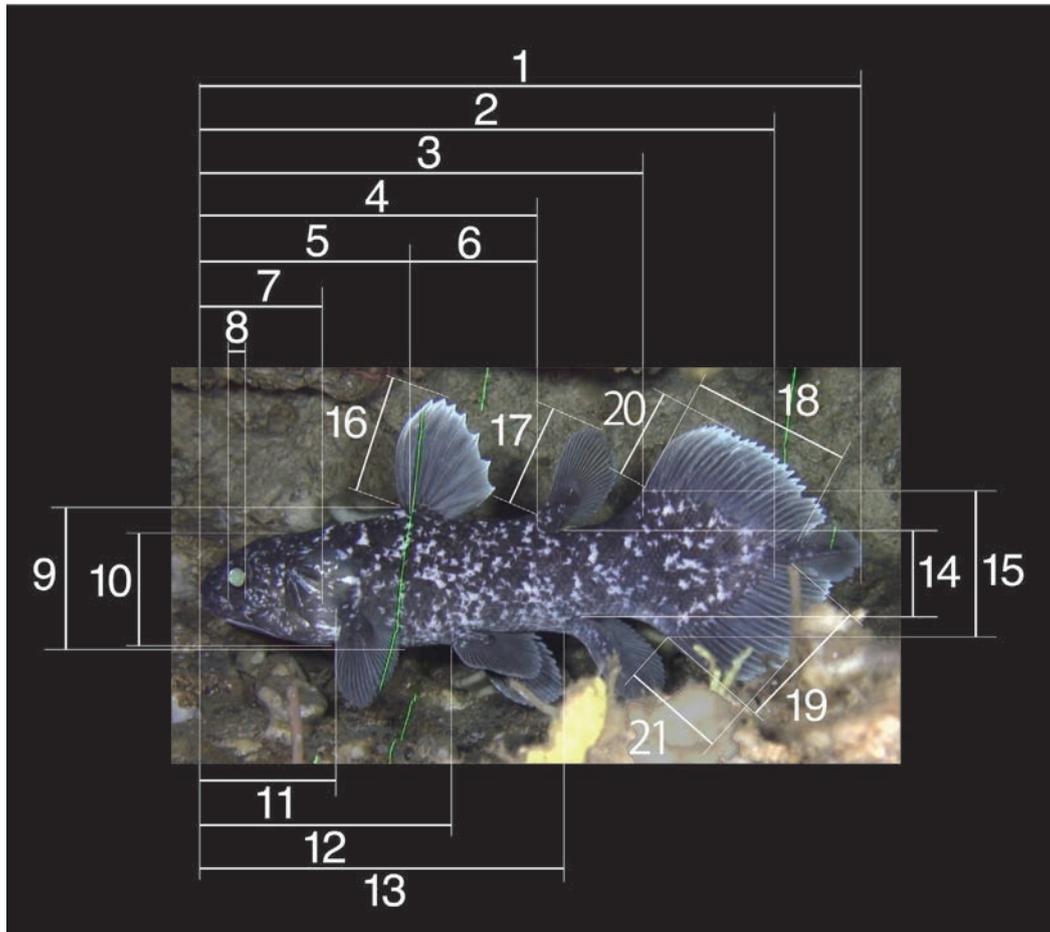


Fig. 3. Measurements made on the juvenile *L. menadoensis* for the comparison of proportion. 1, Total length. 2, Standard length. 3, Snout to D_3 origin. 4, Snout to D_2 origin. 5, Snout to D_1 origin. 6, Distance between origins of D_1 and D_2 . 7, Head length*. 8, Eye diameter. 9, Body depth at D_1 origin. 10, Head depth. 11, Snout to P_1 origin. 12, Snout to P_2 origin. 13, Snout to A_1 . 14, Body depth behind D_2 and A_1 . 15, Distance between D_3 and A_2 . 16, Height of D_1 . 17, Height of D_2 . 18, Length of base of D_3 . 19, Length of base of A_2 . 20, D_3 height. 21, A_2 height. For abbreviations of fins, see materials and methods.

fins, longer fins, larger principal caudal fin (the third dorsal and second anal fins), and longer supplementary lobe of the caudal fin (caudal fin) than those of the embryos of African coelacanth.

One individual of *L. menadoensis*, 90 cm of total length and the second smallest one among the coelacanths observed in Indonesian water from 2005 to 2015 (IWATA *et al.*, 2019), was observed at 187.4 m depth on the 6th December 2012 (Fig. 6: ID 23 in IWATA *et al.*, 2019). Although ID 23 is the second smallest individual among the coelacanths observed in Indonesian water, it is considered to be an adult because its morphological feature is almost identical to other adults. Also, juvenile characters, observed in the juvenile here described, are not observed in ID 23. The body proportion of the juvenile is very different from that of the adult in *L. menadoensis* (Figs. 1 and 6). The morphological differences between *L.*

menadoensis and *L. chalumnae* are scarce when compared between adults. However, there are several differences between juveniles and embryos of these species (Fig. 5). This indicates possibility of the ontogenetic difference of the two species.

The juvenile of *L. menadoensis* has a long supplemental lobe of the caudal fin, which is seen in adult and often young specimens of some fossil species and early stages of embryos of *L. chalumnae* (BENNO *et al.*, 2006, fig. 2; CUPELLO *et al.*, 2015, fig. 1a; FOREY, 1998; YABUMOTO, 2008), indicating *L. menadoensis* retained more juvenile characters during its development than *L. chalumnae*. This indicates presence of heterochrony in the development of *Latimeria*, with *L. menadoensis* being paedomorphic during its juvenile stage.

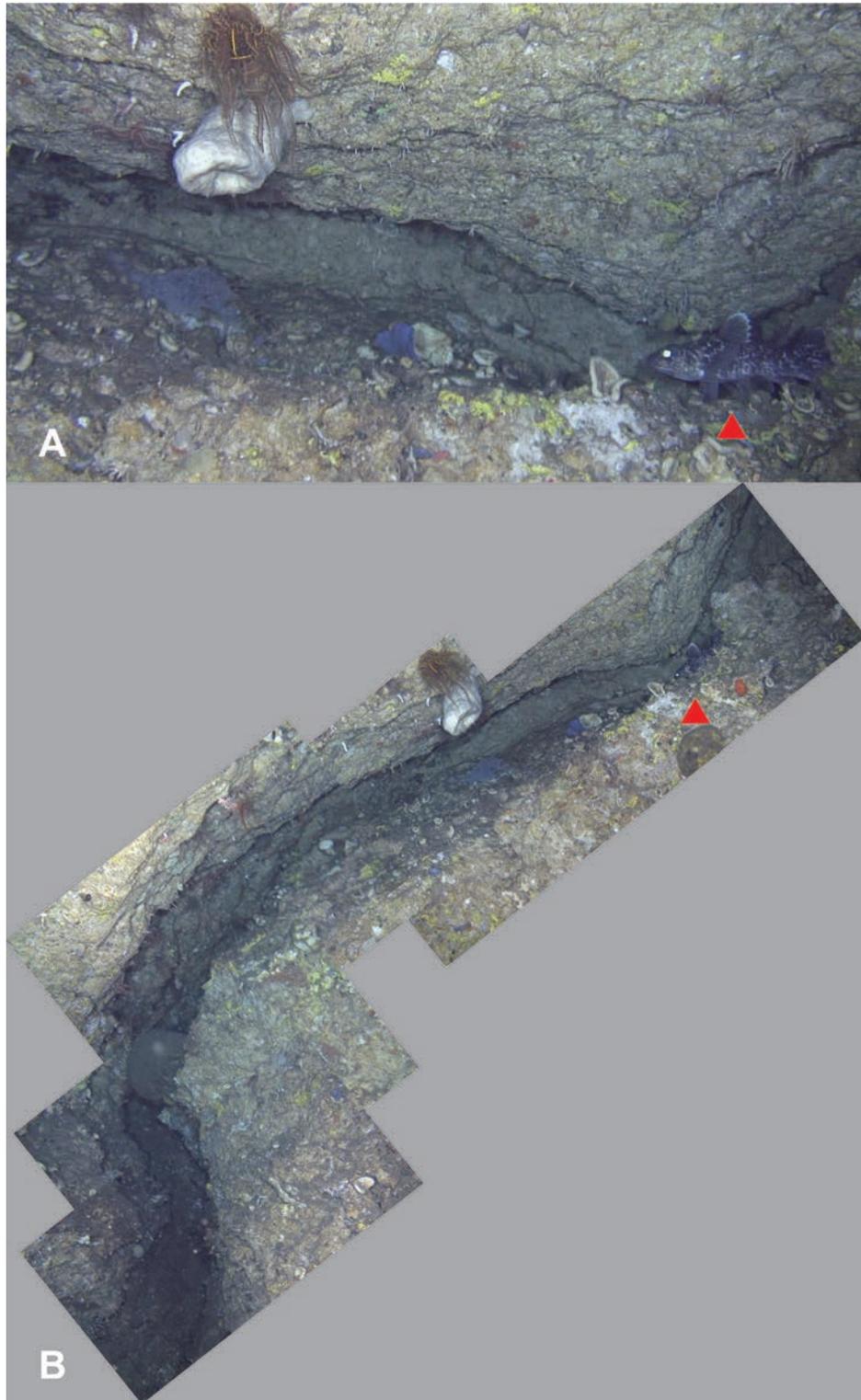


Fig. 4. Habitat of the juvenile coelacanth, *Latimeria menadoensis*. Red triangles indicate the juvenile. A. The individual was encountered under a narrow and long overhang at 164.6 m depth on the 6th September 2009, B. The overhang became deeper to the left of figure. Angle of orientation of the photos is adjusted to actual angle of the terrain.

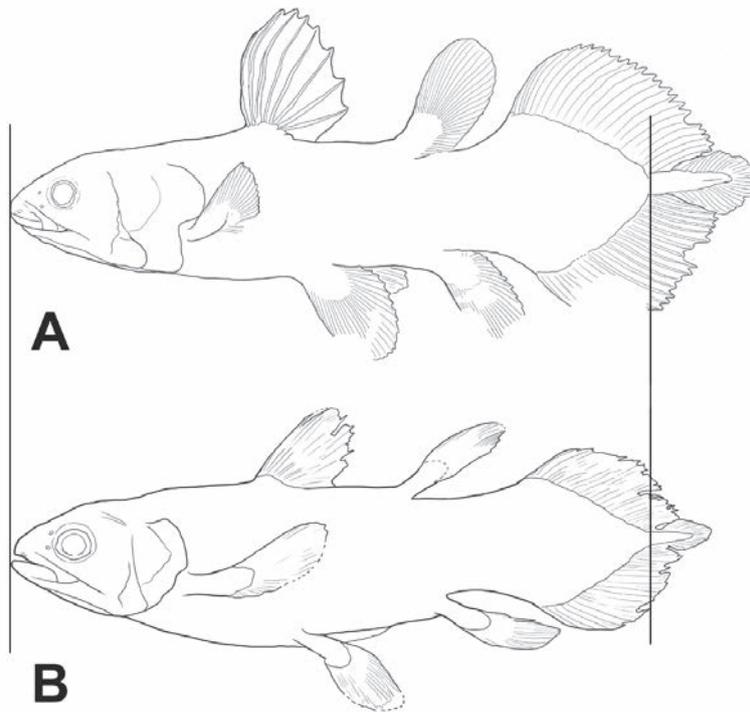


Fig. 5. Comparison of coelacanth juvenile and embryos. A. *Latimeria menadoensis* drawn from Fig. 1A, 31.5 cm TL, B. *Latimeria chalumnae* drawn from the photo of Fig. 2A, 34.8 cm TL.

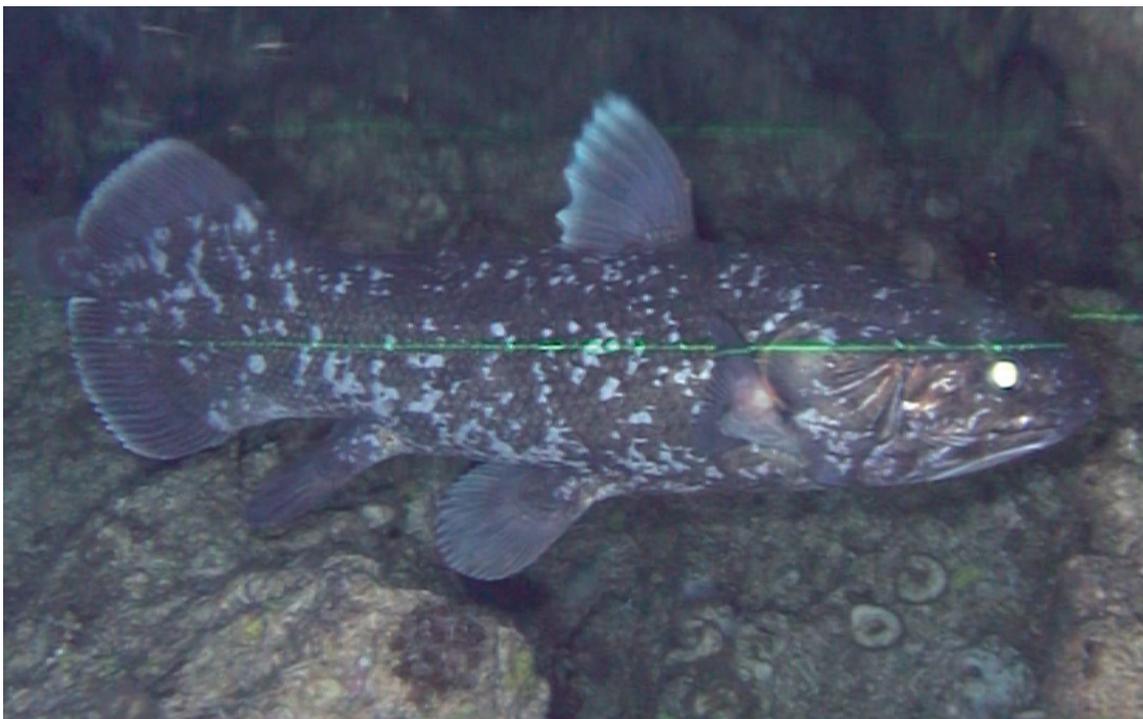


Fig. 6. *Latimeria menadoensis* (ID 23 in IWATA *et al.*, 2019) 90 cm TL recorded at 187.4 m depth off Manado on the 16th December 2012, the smallest adult encountered during the field survey in Indonesian water from 2005 to 2015 by Aquamarine Fukushima (IWATA *et al.*, 2019).

Table 1. Comparison of proportional measurements of the juvenile and embryos of extant coelacanths. The juvenile of *Latimeria menadoensis* is measured from the video footage (ID15 in IWATA *et al.*, 2019). Embryos of *L. chalumnae* are measured from figures of CCC no. 162.16 from Coelacanth Conservation Council newsletter (SECRETARIAT AT THE J. L. B. SMITH INSTITUTE OF ICHTHYOLOGY, 1993), CCC no, 162.12 and 22 from HENSEL and BALON (2001). For abbreviations of fins, see materials and methods.

Body part	<i>L. menadoensis</i>		<i>L. chalumnae</i> CCC.162.16		<i>L. chalumnae</i> CCC162.12		<i>L. chalumnae</i> CCC162.22	
	length (cm)	proportion (%)	length (cm)	proportion (%)	length (cm)	proportion (%)	length (cm)	proportion (%)
Total length	31.5	121	34.8	113	33.3	109.90	34.4	107.725
Standard length	26.1	100	30.9	100	30.3	100.00	31.9	100
Snout to D ₃ origin	21.5	82	25.5	83	25.5	83.36	26.3	82
Snout to D ₂ origin	16.1	62	19.4	63	18.4	60.26	20.2	63
Snout to D ₁ origin	10	38	12.0	39	12.4	40.46	11.2	35
Distance between origins of D ₁ and D ₂	6.1	23	7.3	24	6.1	19.80	7.1	22
Head length	5.8	22	8.0	26	6.9	22.67	7.1	22
Eye diameter	0.8	3	1.7	6	1.8	5.74	2.7	9
Body depth at D ₁ origin	6.8	26	8.7	28	8.6	27.98	8.3	26
Head depth	5.4	21	6.1	20	7.8	25.39	6.5	20
Snout to P ₁ insertion	6.5	25	7.8	25	7.1	23.10	7.1	22
Snout to P ₂ insertion	12	46	14.2	46	13.3	43.47	13.5	42
Snout to A ₁	17.3	66	21.5	70	20.2	66.00	18.9	59
Body depth at A ₁	4.2	16	4.6	15	4.7	15.35	4.3	14
Distance between D ₃ and A ₂	7	27	6.6	21	6.2	20.37	6.5	20
Height of D ₁	5.7	22	5.9	19	4.4	14.35	5.3	16
Height of D ₂	5	19	5.1	17	6.2	20.23	6.2	19
Length of base of D ₃	7.6	29	6.6	21	5.2	17.07	6.1	19
Length of base of A ₂	6.5	25	5.6	18	5.6	18.36	5.4	17
D ₃ height	4.3	16	3.8	12	2.8	9.18	3.5	11
A ₂ height	5	19	3.8	12	2.6	8.46	3.2	10

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