

A NEW FROG (ANURA, DICROGLOSSIDAE), RELATED TO *OCCIDOZYGA SEMIPALMATA* SMITH, 1927, FROM THE EASTERN PENINSULA OF SULAWESI, INDONESIA

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ABSTRACT. – *Occidozyga semipalmata* is found to be unique based on the flattened finger and toe tips that lack circum-marginal grooves and in having a tongue with rounded tip. Another form, *O. tompotika* new species, is found at Mount Tompotika, Eastern Peninsula of Sulawesi, appears to be closely related to species from the Wallacean region and the Philippines. This is a medium sized species, toes and fingers with larger flattened tips lacking a circum-marginal groove and more extensive toe webbing compared to *O. semipalmata*. However these two species, together with *O. floresiana*, are retained within the genus and not assigned to *Ingerana* because they have most characters allied to the genus, especially by the lack of external tympanum and having a single bony protuberance at the lower jaw tip.

KEY WORDS. – Amphibia, Dicroglossidae, Systematics, *Occidozyga*, new species, Wallacea.

INTRODUCTION

The genus *Occidozyga* [type species *O. lima* (Gravenhorst, 1829)], comprises 11 species, widely distributed in Southeast Asia, extending to India in the west and China in the north, with endemic species in the Philippines, Sundaland and Wallacea (Frost, 2011; ASW, 2010). This is a genus that has raised many controversies, as the generic assignment of several of its members is a source of disagreement among scientists, aside from various orthographical versions. Günther (1859 “1858”) described *Oxyglossus laevis* based on specimens from the Philippines. Boulenger (1896) described *Oreobatrachus baluensis* from Mt. Kinabalu. Taylor (1922) described *Micrixalus diminutivus* from Mindanao based on the presence of a very small disk on the toes, very different to the wide flattened disks of other *Micrixalus* species, so that its generic allocation was rejected by Smith (1922) and Myers (1942), and was later transferred to the genus *Ooeidozyga* by Inger (1954). Van Kampen (1923) placed all known species in *Oxyglossus*. In 1927, Smith described *Ooeidozyga celebensis* and *O. semipalmatus* from South Sulawesi and in 1931 placed *Oxyglossus laevis* in the genus *Phrynoglossus*. Mertens (1927) described *Oxydozyga floresiana* from West Flores in the Lesser Sunda Island. *Micrixalus magnapustulosus*

Taylor & Ebel (1958) is a species described based on a juvenile specimen and later considered as a valid species (Matsui, 1979). *Phrynoglossus martensi* Peters, 1867, described from Thailand was considered as a subspecies of *Oxyglossus laevis* after the work of Smith (1916) and was only resurrected recently as a valid species (Frost, 1985, 2011; Frost et al., 2006). On the other hand, another species from Vietnam, described as *Oxyglossus laevis* var. *vittatus* Anderson, 1942, is the only form that remains obscured. Dubois (1981, 1982) pointed out the proper orthography for these tiny frogs should be *Occidozyga*, but retained *laevis* in *Phrynoglossus*. The placing of *Occidozyga laevis* in *Phrynoglossus* was opposed by Inger (1993), and Frost et al. (2006), supported by genetic analysis. Iskandar (1998) resurrected *Microdiscopus sumatranus* Peters, 1877, as a valid species of the genus *Occidozyga*, separate from the very large species, *O. laevis*, but creating uncertainty about the exact range of each species. Iskandar & Colijn (2001) noted that *O. semipalmata* might not be a member of the genus but did not make any decision about its generic position or the reason behind it. Dubois (1987), confirmed by Sailo et al. (2009) placed *Micrixalus borealis* Annandale, 1912 from India in *Ingerana* based on phenetical analysis and ecology of the species, despite it also having fingers and toes with tiny

flattened disks devoid of circum-marginal grooves, having a single tooth-like protuberance at the tip of lower jaw and an indistinct tympanum as most *Occidozyga* species.

A recent expedition to the eastern peninsula of Sulawesi resulted in finding a species presumably closely related to *Occidozyga semipalmata*. The generic position of the new species and *O. semipalmata* could not be determined adequately without firm data about nuclear and mitochondrial genetic analysis covering most other members of the genera to which it could belong. In addition, tadpoles for *O. semipalmata* and the new species are not yet known. For this reason, we prefer to leave this problem unresolved and concentrate on the species at hand.

MATERIAL AND METHODS

Specimens used in this study were euthanized via immersion in aqueous solution of chloroform. Liver tissue was removed for subsequent molecular work. Specimens were covered with 10% formaldehyde wet tissue and later soaked in 4% formaldehyde for several days before being transferred to 70% ethanol for permanent storage. At present the whole series is kept in the Institut Teknologi Bandung (ITB) reference collection, Bandung, Indonesia upon acceptance of the manuscript. Unless specified, the holotype and part of the paratypes will be deposited in Museum Zoologicum Bogoriense, Research and Development Center for Biology, Indonesian Institute of Sciences (MZB). Other paratypes will be distributed among a number of other museums as stipulated in the text under a cooperative scheme and for safety. Almost all specimens have been examined in our laboratory. Institutional abbreviations are as listed in Leviton et al. (1985).

Sex was determined by the presence of secondary sex characters such as enlarged thenar tubercle, the presence of velvety nuptial pad on the first finger in adult males, darker gular pigmentation and the presence of tubercles on the gular. The following measurements were made to the nearest 0.1 mm using digital calipers as follows: snout-vent length (SVL) – from cloaca to tip of snout; head width (HW) – widest distance between posterior ends of lower jaws; head length (HL) – from ends of lower jaw to the tip of the snout; femoral length (FE) – between cloaca to end of femur at right angle to body; tibial length (TI) – from knee to end of tibia with foot 90° perpendicular to tibia up to the fold of the upper tibia; foot length (FL) – from tibia-fibula end to tip of 4th toe; inner metatarsal tubercle (IM); upper arm length (UA) – from the base of arm to elbow; lower arm length (LA) – from elbow joint to the base of middle palmar tubercle; hand length (HA) – from lower border of the middle tubercle to tip of third finger; third finger tip width (F3W) – width of first toe disk (T1W); width of fourth toe disk (T4W); snout length (SL) – measured from bony border of eye socket to tip of snout; (EY) – outer diameter, measured from bones bordering the eye; inter-orbital distance (IO) – between borders of bones bordering the eyes; eye-narial distance (EN) – eye socket border to posterior border of the

nostril; internarial distance (IN) – shortest distance between nostrils; nostril to tip of snout (NT); eye mouth distance (EM). Statistical analysis was performed with Kruskal-Wallis and followed with Mann-Whitney U test at $p < 0.01$ level of significance. Institutional abbreviations are as listed in Leviton et al. (1985). For comparative materials, some other species were examined at RMNH, Leiden; FMNH, Chicago; BPBM, Hawaii; LSUMZ, Baton Rouge, MVZ, Berkeley, and RMBR (ZRC), Singapore. BSI, DTI, DL, JAM, MK and KU are referring to field numbers.

RESULTS AND DISCUSSION

Comparison between populations. – We measured specimens from all over Sulawesi, and found that specimens referable to *O. semipalmata* vary among populations from all over Sulawesi as well as around the eastern Peninsula (Fig 1). These specimens are lumped into five geographic populations for comparison and statistical purposes, and therefore potentially biased by inclusion of single individual from a neighbouring area. There are no differences in general body morphology between males and females, so our comparisons are not affected by sexual dimorphism. The result shows that populations from three highland areas are found to differ in many ways (Table 1). The population from Mount Tompotika is composed of larger individuals, similar to those from Mount Karua. The population from Kebun Kopi (Fig. 2) is also slightly larger but does not differ significantly compared to those from Mt Lompobatang and Bogani Nani Wartabone National Park. The population of Mount Karua differs from other populations in size and several aspects of the snout (e.g. IN, EN and NT) and physically, the head and snout appear to be slightly bulging. Specimens from the type locality (Mount Lompobatang) are smaller, but about equal to those of Kebun Kopi and Bogani Nani Wartabone National Park. Those from Mount Tompotika have the smallest head in terms of width and length, but considerable overlapping occurs. The eyes of frogs from Mount Tompotika are distinctly smaller so that IO, EN and EM are wider compared to other populations. The most pronounced feature is seen on the larger toe and finger tips of frogs from Mount Tompotika, as seen in members of the genus *Ingerana*. The toe and finger tips are flattened and devoid of circum-marginal grooves. In populations from other areas, the finger tips are equally flattened and also ornamented with a white bar straddling the tips as observed in *Ingerana baluensis* and *Ingerana* n. sp. (Iskandar et al., 2011a). However in other populations of *O. semipalmata*, the toe and finger tips are very small. Flattened finger disks lacking circum-marginal grooves have also been reported from *Occidozyga floresiana* (Mertens, 1927) and *Occidozyga martensi* (Sailo et al., 2009). Statistical analysis showed that populations from Kebun Kopi and Bogani Nani Wartabone National Park are nearly identical, but the one from Mount Karua is distinct as are those from Balantak Mountains. This distinction does not hold for Mount Karua population when populations from Mount Lompobatang, Kebun Kopi and Bogani Nani Wartabone are lumped together, however. Only the population from Balantak Mountains has very distinctive flattened and wide finger and toe tips. The population from

Table 1. Characters that show statistical differences between the five *Occidozyga* populations of Sulawesi at $p < 0.01$ significance level by Kruskal-Wallis t-test. Upper line, average \pm SD; lower line, range. Abbreviations see Material and Methods.

	Mount Lompobatang, South Sulawesi N=13	Mount Karua, South Central Sulawesi N=9	Kebun Kopi, North Central Sulawesi N=25	Bogani Nani Wartabone, North Sulawesi N=4	Mount Tompotika East Sulawesi N=7
	average \pm SD range	average \pm SD range	average \pm SD range	average \pm SD range	average \pm SD range
HW/SVL	0.39 \pm 0.03 0.36–0.45	0.38 \pm 0.02 0.36–0.42	0.39 \pm 0.01 0.38–0.42	0.40 \pm 0.03 0.38–0.44	0.36 \pm 0.01 0.34–0.38
HW/HL	1.01 \pm 0.06 0.92–1.13	0.97 \pm 0.04 0.94–1.09	1.03 \pm 0.05 0.96–1.17	1.03 \pm 0.02 1.01–1.06	0.95 \pm 0.04 0.89–0.98
IO/SVL	0.07 \pm 0.01 0.06–0.09	0.08 \pm 0.01 0.06–0.09	0.07 \pm 0.01 0.06–0.08	0.06 \pm 0.01 0.05–0.08	0.09 \pm 0.01 0.08–0.09
ED/SVL	0.17 \pm 0.01 0.15–0.19	0.17 \pm 0.01 0.15–0.18	0.16 \pm 0.01 0.15–0.18	0.16 \pm 0.02 0.15–0.19	0.15 \pm 0.01 0.13–0.16
EN/SVL	0.05 \pm 0.01 0.03–0.07	0.05 \pm 0.00 0.04–0.05	0.06 \pm 0.01 0.04–0.06	0.05 \pm 0.02 0.04–0.07	0.07 \pm 0.00 0.06–0.07
NT/SVL	0.08 \pm 0.01 0.06–0.09	0.09 \pm 0.01 0.08–0.10	0.07 \pm 0.01 0.06–0.08	0.08 \pm 0.01 0.07–0.09	0.07 \pm 0.00 0.06–0.08
IN/SVL	0.11 \pm 0.01 0.10–0.12	0.12 \pm 0.01 0.11–0.14	0.11 \pm 0.01 0.10–0.12	0.11 \pm 0.01 0.10–0.12	0.11 \pm 0.01 0.10–0.12
PL/SVL	0.73 \pm 0.03 0.68–0.79	0.72 \pm 0.04 0.66–0.81	0.75 \pm 0.04 0.68–0.83	0.72 \pm 0.08 0.64–0.80	0.55 \pm 0.02 0.50–0.58
T1W/SVL	0.03 \pm 0.00 0.03–0.04	0.03 \pm 0.00 0.02–0.04	0.03 \pm 0.00 0.03–0.04	0.03 \pm 0.01 0.03–0.04	0.04 \pm 0.00 0.03–0.04
F3W/SVL	0.03 \pm 0.00 0.02–0.03	0.03 \pm 0.00 0.02–0.03	0.03 \pm 0.00 0.03–0.03	0.03 \pm 0.00 0.02–0.03	0.04 \pm 0.00 0.04–0.05
T4W/SVL	0.03 \pm 0.00 0.02–0.04	0.03 \pm 0.00 0.03–0.05	0.03 \pm 0.00 0.03–0.04	0.03 \pm 0.01 0.03–0.04	0.04 \pm 0.00 0.04–0.05
EM/SVL	0.06 \pm 0.01 0.05–0.07	0.06 \pm 0.01 0.04–0.07	0.05 \pm 0.00 0.04–0.06	0.05 \pm 0.00 0.05–0.06	0.05 \pm 0.01 0.04–0.06



Fig. 1. Map of Sulawesi showing the distribution of Sulawesi *Occidozyga*. Legend: Circle, *Occidozyga semipalmata*; small circles denote localities with one or two specimens; Circle, Mount Lompobatang (the type locality); Star, *Occidozyga tompotika*; Inverted triangle, *Occidozyga celebensis*. Map modified from Google map.

Mount Karua together with those from Mount Lompobatang, Kebun Kopi and Bogani Nani Wartabone National Park show very little differences in finger and toe tips and are lumped together as *O. semipalmata*. For this reason, only the population from Mount Tompotika, the most distinctive form, is described below as the new species.

SYSTEMATIC SECTION

Occidozyga tompotika, new species (Fig 2A, B)

Holotype. – MZB (Field number DTI 2816), SVL: 34.1 mm, a gravid female from Bantayan, Mount Tompotika, Balantak Mountains (between S 00°39'39.5"; E 123°06'39.1"; 757 m ASL and S 00°39'50.0"; E 123°06'42.2"; 778 m ASL), Desa (=Village) Bualemo, South Sulawesi Province, Indonesia, by Umilaela and A. Rachmansah coll., 21 May 2009.

Paratypes. – MZB (DTI 02767, 02812, 02814, 02815, 02830, 02853) 6 ex., collected at several camps around the same surrounding area as for the holotype, collected between 18 May and 2 Jun.2009. MVZ (DTI 02768) from Longkoga Stream (between 00°39'16.6"S; 123°06'47.2"E; 526 m ASL and 00°39'29.7"S; 123°06'41.0"E; 574 m ASL), Bualemo, South Sulawesi Province, by Umilaela and A. Rachmansah coll., 18 May 2009. FMNH (DTI 02813) from Longkoga Stream (between 00°39'39.5"S; 123°06'39.1"E; 757 m ASL and 00°39'50.0"S; 123°06'42.2"E; 778 m ASL), Bualemo, South Sulawesi Province, by Umilaela and A. Rachmansah coll.,

21 May 2009. RMBR-ZRC (DTI 02888) from Lemon Nipis Stream, Bantayan (between 00°45'05.0"S; 123°06'08.2"E; 462 m ASL and 00°44'55.5"S; 123°06'03.0"E; 505 m ASL), Bualemo, South Sulawesi Province, by Umilaela and A. Rachmansah coll., 2 Jun.2009.

The description is based on 10 specimens: 3 males, 4 females and 3 juveniles.

Diagnosis. – A medium large species with half webbed toes, dorsum uniformly coloured, no light dorsolateral stripe, no dark blotch at midbody around the scapular region, fingers and toes with wide expansions at tips, all toes webbed to base of penultimate phalange except the fourth toe, which is webbed up to the position of second subarticular tubercle; tympanic annulus hidden under skin and completely covered under temporal musculature. Vomerine teeth absent, tongue completely rounded, no median notch behind, and fixed to the floor of mouth for about 70% of its length at the middle so that the margins are still free.

Description. – A medium large species, SVL in adults 34.1 ± 2.12 mm (n=7), body robust and plump. Head slightly longer than wide, eyes about equal to length of snout, pupil ovoid, oriented horizontal; snout rounded, with a straight canthus seen from above and rounded in profile, lores concave; nostrils slightly below canthus rostralis, closer to tip of snout than to eye; distance between eyes narrower than internarial distance, tympanic annulus hidden under skin and covered with muscle, but a rounded soft area could be located after incision of the skin covering the tympanic area; a distinct supratympanic fold, extending from slightly below the middle part of eye, curving straight down to dorsal part of fore limb and not looping above the position of the tympanic annulus as usually seen in most frogs. Vomerine teeth absent and lower jaws with a single protuberance at the tip. Upper arm with small tubercles, longer than lower arm; limbs short, hands with two palmar tubercles; subarticular tubercles distinct. Fingers with narrow fringe of skin and wide, truncated and flattened tips devoid of circum-marginal grooves; a rounded inner and elongated outer metacarpal tubercle, no supernumerary metacarpal tubercles. Fingers in length order 2<1<4<3. Disks of toes about equal to fingers,

also with wide flattened tips bearing circum-marginal grooves with extensive webbings to base of flattened disks, only in the fourth toe, the last phalange is free from webbings, a single inner metatarsal tubercle, flattened, its length slightly greater than its distance to the base of the widened toe tip; tarsal fold present, short and running across the tarsus and ended at about midline of the tarsus. Tibias do not meet when the femurs are placed perpendicular to body axis, slightly shorter than femur. Toes in length order 1<2<5<3<4. Dorsal skin rough but no large tubercles are present on the head, snout or eyelids. Lower part of body, gular surface and ventrum are essentially smooth.

Secondary sex characters. – Males are slightly smaller compared to females, have enlarged thenar tubercle at the dorsal surface of first finger and have paired vocal sac with openings at inner side of mouth corner near end of jaws. The gular skin is darker compared to that of females and the upper jaw of males are covered with small whitish tubercles.

Detailed measurements of the female holotype (in mm): SVL, 34.1; HL, 12.7; HW, 12.3; IO, 2.9; ED, 5.1; SL, 4.5; EN, 2.4; NT, 2.1; IN, 3.7; UA, 8.8; LA, 6.2; HA, 9.7; FE, 17.3; TI, 14.5; PL, 19.2; F3W, 1.3; T1W, 1.5; T4W, 1.7; IM, 2.4; EM, 2.1.

Coloration in life. – All specimens are dark brown or blackish, usually without faint markings, pattern or mottling. Lower parts are heavily marbled with dark brown and gular surfaces more heavily marked. Lips uniform as other parts of head and body, not barred although the region below the eyes is distinctly darker, bearing a single white dot exactly below the eyes. A similar darker area is on the lip below the nostril. A pineal spot is faintly present. Upper arm is essentially uniform, with no bands visible. The femur and tibia have three indistinct dark cross bands. Few white spots are scattered at the sides of body and head and lower parts of sides and on the hands and limbs (Fig. 1). All fingers and toes have a white bar straddling the middle of the truncated, flat disk and a brownish tint in the middle of the white bar. The iris is dark brown with indistinct reticulation. A mid-dorsal light line is present in two specimens including the holotype (DTI 2812), but there is no indication of lighter dorsolateral band.



Fig. 2. *Occidozyga semipalmata* from Lore Lindu, proximity of Kebun Kopi showing the flattened finger disks ornamented with a white bar. Photo by T. C. Wanger.

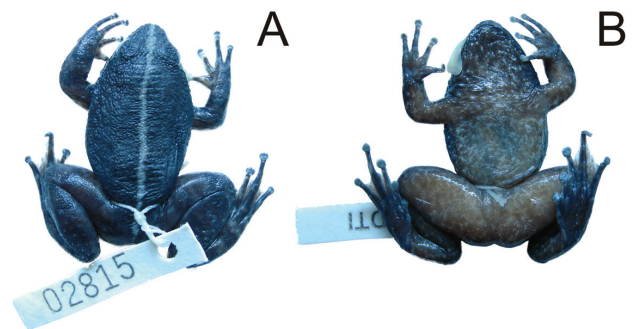


Fig. 3. Dorsal (A) and ventral (B) aspect of the female holotype (SVL 34.1 mm) of *Occidozyga tompotika*. Folds on the dorsum are partially an artifact from paper towel during preservation. Photo by D. T. Iskandar.

Table 2. Detailed comparison between *Occidozyga semipalmata* and *O. tompotika*.

	<i>Occidozyga semipalmata</i> N=51		<i>Occidozyga tompotika</i> N=7	
	average \pm SD	range	average \pm SD	range
SVL	30.66 \pm 3.65	22.8–40.9	33.39 \pm 2.84	28.3–36.5
HL	11.86 \pm 1.35	8.5–15.8	12.63 \pm 0.80	11.0–13.6
HW	12.01 \pm 1.21	8.7–14.9	12.04 \pm 0.74	10.7–13.0
IO	2.18 \pm 0.38	1.5–3.0	2.85 \pm 0.33	2.2–3.3
ED	5.00 \pm 0.57	3.8–6.7	4.92 \pm 0.19	4.6–5.2
SL	3.97 \pm 0.48	3.0–5.0	4.41 \pm 0.23	3.9–4.6
EN	1.61 \pm 0.31	0.9–2.2	2.24 \pm 0.13	2.1–2.4
NT	2.31 \pm 0.33	1.7–3.2	2.21 \pm 0.29	1.8–2.7
IN	3.42 \pm 0.48	2.4–4.7	3.68 \pm 0.23	3.4–4.1
UA	8.28 \pm 0.70	6.5–9.9	8.54 \pm 0.34	7.8–8.9
LA	6.16 \pm 0.74	4.3–8.6	6.39 \pm 0.45	5.6–7.0
HA	8.04 \pm 0.99	5.2–10.2	9.18 \pm 0.52	8.4–9.8
FE	15.47 \pm 1.53	11.5–19.0	17.13 \pm 1.24	14.7–18.4
TI	13.49 \pm 1.36	11.0–17.3	14.4 \pm 0.92	13.1–15.7
PL	22.27 \pm 2.87	13.6–27.5	18.28 \pm 1.64	15.7–20.5
F3W	0.85 \pm 0.14	0.5–1.1	1.3 \pm 0.11	1.1–1.4
T1W	0.97 \pm 0.18	0.6–1.3	1.45 \pm 0.18	1.2–1.7
T4W	1.05 \pm 0.19	0.5–1.4	1.41 \pm 0.17	1.1–1.7
IM	2.00 \pm 0.35	1.2–2.8	2.24 \pm 0.17	1.9–2.4
EM	1.60 \pm 0.20	1.2–2.2	1.79 \pm 0.20	1.5–2.1
HL/SVL	0.39 \pm 0.01	0.36–0.44	0.38 \pm 0.01	0.36–0.40
HW/SVL	0.39 \pm 0.02	0.36–0.45	0.36 \pm 0.01	0.34–0.38
HW/HL	1.02 \pm 0.05	0.92–1.17	0.95 \pm 0.04	0.89–0.98
IO/SVL	0.07 \pm 0.01	0.05–0.09	0.09 \pm 0.01	0.08–0.09
ED/SVL	0.16 \pm 0.01	0.15–0.19	0.15 \pm 0.01	0.13–0.16
SL/SVL	0.13 \pm 0.01	0.12–0.15	0.13 \pm 0.01	0.12–0.14
EN/SVL	0.05 \pm 0.01	0.03–0.07	0.07 \pm 0.00	0.06–0.07
NT/SVL	0.08 \pm 0.01	0.06–0.10	0.07 \pm 0.00	0.06–0.08
IN/SVL	0.11 \pm 0.01	0.10–0.14	0.11 \pm 0.01	0.10–0.12
UA/SVL	0.27 \pm 0.02	0.23–0.32	0.26 \pm 0.02	0.23–0.31
LA/SVL	0.20 \pm 0.01	0.17–0.23	0.19 \pm 0.01	0.18–0.20
HA/SVL	0.26 \pm 0.02	0.23–0.30	0.28 \pm 0.01	0.25–0.30
FE/SVL	0.51 \pm 0.02	0.45–0.57	0.51 \pm 0.01	0.50–0.55
TI/SVL	0.44 \pm 0.03	0.37–0.51	0.43 \pm 0.02	0.41–0.46
PL/SVL	0.73 \pm 0.07	0.47–0.83	0.55 \pm 0.02	0.50–0.58
F3W/SVL	0.03 \pm 0.00	0.02–0.03	0.04 \pm 0.00	0.04–0.05
T1W/SVL	0.03 \pm 0.00	0.02–0.04	0.04 \pm 0.00	0.03–0.04
T4W/SVL	0.03 \pm 0.00	0.02–0.04	0.04 \pm 0.00	0.04–0.05
EM/SVL	0.05 \pm 0.01	0.04–0.07	0.05 \pm 0.01	0.04–0.06
IM/SVL	0.06 \pm 0.01	0.05–0.08	0.07 \pm 0.00	0.06–0.07

Etymology. – Refers to the type locality, Mount Tompotika at the Balantak Mountains, eastern peninsula of Sulawesi.

Ecology. – We have collected a large number of *Occidozyga celebensis* in freshly ploughed rice fields at Cikoro, together with tadpoles in 1992, indicating that this species has the same habitat as *O. lima* and *O. sumatrana*. *Occidozyga tompotika* and *O. semipalmata* were collected in very shallow creeks

with continuous running water, in contrast to at least three *Occidozyga* species usually found submerged in stagnant waters. Different features of the head and laterally situated eyes in *O. tompotika* and *O. semipalmata* set them apart from other members of the genus, fit with their habits of living in ditches or shallow water and rarely stay submerged under water. This is also more or less the same habitat as many small sized *Limnonectes* such as *L. rhacodus* and also in three

Ingerana species (Sailo et al., 2009; Iskandar et al., 2011a). Judging from the nearly fully webbed toes, *O. tompotika* may be more aquatic compared to *O. semipalmata*. The species has been collected together with three undescribed species of *Limnonectes*, one of them is a very large species up to 200 mm. The other two species represent a medium (50–60 mm) and a small species (25–35 mm). The small species lay eggs on land. Otherwise *Rana mocquardii* and *R. celebensis* have been collected in the same habitat.

Up to present, many members of the genus have undergone considerable moving from one genus to another even after the genus *Ingerana* was erected. Many members of *Ingerana* and some *Occidozyga* are uncommon in museum collections, even *O. semipalmata* for which we have examined a good series originating from at least dozen different expeditions beginning 20 years ago.

Comparisons. – When comparing between species and from a literature search, it is evident that aside from *Occidozyga lima* and *O. laevis*, other members have tiny disks on the toes. Judging from the overall physiognomy, *O. semipalmata* and *O. tompotika* are very closely related. These two forms have a robust head with laterally oriented eyes and ovoid pupil. In other *Occidozyga*, the snout is more or less pointed and the eyes are situated at the top of the head directing upwards facilitating viewing the surroundings while still submerged under water. The pupil of *O. sumatrana* is known as diamond shaped, those of *O. martensi* is ovoid. The pupil form varies within the genus, but can be due to the strength of light when observed during daylight or when photographed; stronger light will force the pupil to contract and giving the diamond aspect. *Occidozyga tompotika* is most closely related to *O. semipalmata*, its congener in Sulawesi by the nature of flattened finger and toe disks. Both species also have a rounded tongue, partially adherent to the floor of the mouth. However *O. tompotika* has more extensive webbing on the toes compared to *O. semipalmata*. In *O. semipalmata*, webbing on the first and second toes extend to the base of tips as in *O. tompotika*. On the outer side of the third toe, the webbing is also starting from the base of the tip, but deeply excised so that practically the last phalange is free from extensive webbing and so is the fifth toe. The fourth toe has the last two phalanges free from extensive webbing although the web starts from the last penultimate phalange. In addition, the tongue is adherent to the mouth floor for about 50% of its length in *O. semipalmata* and the dorsum has some dark mottling. *Occidozyga floresiana* is another species to be considered as closely related to *O. semipalmata* and *O. tompotika*. The species was described as having distinctive disks on the fingers and toes and suggest a close relationship with *O. semipalmata* (Mertens, 1927). It is a large species approaching the size of *O. laevis*. In addition this form is also reported in having the same snout form as *O. semipalmata*. *Occidozyga floresiana* differs from *O. tompotika* by being larger and has all toes fully webbed up to the flattened tips and a tiny notch at the tip of tongue. These three species appears to constitute a single clade and are easily distinguished from other members of the genus in the Sundaland by the flattened toe and finger disks as well as

having rounded snout and laterally oriented eyes, as no other members of the genus have all of these characters. *Occidozyga tompotika* appears to be also closely related to *O. diminutiva* based on the reduced toe webbing and having flattened toe disks without circum-marginal groove. However fingers of *O. diminutiva* lacked flattened disks and the tongue has a tiny notch behind (Inger, 1954). In *O. martensi*, only the fingers have flattened disks, contrasting to *O. diminutiva* where disks are evident only on the toes. *Occidozyga baluensis* is similar to *O. tompotika* by having reduced webbing to the same extent, but differs from the new species by being slightly smaller, having a light saddle at the scapular region, ventral, gular and underside the femur is heavily blotched and a weak scapular marking or broken dorsolateral fold behind the eyes to scapular region. The eyes are directing upwards and the head is also much pointed and not highly built as in the Sulawesi species mentioned above. It is important to stress that *O. baluensis* also has toes with tiny flattened disks. *Occidozyga tompotika* differs from *O. sumatrana* and *O. celebensis* by its larger size, laterally oriented eyes, reduced toe webbing, having rounded tongue, and by being black instead of grayish. *O. sumatrana* is described as having a very small toe disks, however this characteristic is not clearly evident compared to *O. laevis* as it is more likely a conical tip. It differs further from *O. tompotika* by having dorsum and lateral sides covered with tubercles and at each sides of cloaca there are a dark brown band and some brown stippling at the ventral surface of the thigh. *Occidozyga tompotika* differs from *O. laevis* of the Philippines by being much smaller and having reduced webbing aside for different dorsum coloration, despite both species having a same rounded tongue without median notch behind. *Occidozyga tompotika* differs from *O. lima* by being larger and from the smooth skin in contrast to the pearly tubercles and the fully webbed toes. In addition, *O. lima* has distinct markings at the ventral side of the femur. *Occidozyga magnapustulosa* is also a species having rounded tongue without median notch similar to the new species (Matsui, 1979). *Occidozyga tompotika* differs from *O. magnapustulosa* by the smooth skin in contrast to the tuberculated area at posterior part of the dorsum and blotched skin of the latter. *Occidozyga tompotika* occupy a similar habitat as *Ingerana borealis*, share the toe and finger tips characteristics as well as having slightly reduced webbing; however it has a rounded tip of the tongue without terminal notch and no lighter dorsolateral band. The same reason is applicable for comparison between *I. tenasserimensis* and *O. tompotika*, which also have reduced toe webbings, small, flattened finger and toe tips and a light dorsolateral region. *Ingerana tenasserimensis* has a tympanic annulus, easily distinguishable from *O. tompotika*. The finding of this small frog species with relatively large finger and toe disks at Mount Tompotika enforced our previous idea that *Occidozyga semipalmata* is distantly related to the other members of the genus (Iskandar & Colijn, 2000) and supported further by the lateral eye orientation and the general head form. Genetic analysis on several mitochondrial and nuclear genes supports our suggestion that *O. semipalmata* is very distinctive compared to other members of *Occidozyga* (Wogan, pers. comm., 2009, data not shown). *Occidozyga tompotika*, *O. semipalmata*, *O. floresiana* and potentially

O. diminutiva might be placed among the *Ingerana* species with at least toe tips with flattened disks devoid of circum-marginal grooves or to *Limnonectes* or even a distinct genus of its own. *Rana charlesdarwini* from Nicobar also has the same type of finger and toe tips (Das, 1998), and without strong arguments is placed in *Ingerana* (Frost, 2006). A recent finding of a large *Ingerana* from Borneo lacking external tympanic annulus has weakened its generic definition and makes the species also closely allied to the genus *Occidozyga* (Iskandar et al., 2011a).

A number of small *Limnonectes* are about the same size as *Occidozyga tompotika*, and could easily be confused in the field. Most *Limnonectes* have smooth skin and none have flattened finger and toe tips, hence can be differentiated easily by those two characteristics. *Limnonectes hascheanus* and *L. limborgi* differ in smaller size and having very reduced toe webbings. *Limnonectes parvus* is also a small species, with smooth skin and having very reduced webbings and a pair of dorsolateral folds, so not easily misidentified. *Limnonectes palawanensis* is easily distinguished from this species by having smooth skin and a pairs of dorsolateral folds and from the inverted V shaped black scapular markings. *Limnonectes nitidus* is a much larger species, has also smooth skin with dorsolateral folds. *Limnonectes tweediei* is another small species with smooth skin and no the dorsolateral folds, but does not have expanded finger and toe disks. *Limnonectes rhacodus* is the most similar species to any *Occidozyga* and easily confounded with *Occidozyga baluensis*, as both have more or less a dorsolateral fold. However, *L. rhacodus* can be excluded from *O. tompotika* by having a pairs of dorsolateral folds and dorsum with lateral oriented wrinkles. An undescribed Sumatran species has flattened toe and finger disks with circummarginal groove and a white bar straddling on the flattened disks, but it will be placed in *Limnonectes* as other characters such as enlarged head in the males, a well developed odontoid processes and smooth skin, suggest that it is inappropriate to place it in *Ingerana* (unpubl.).

Initially the flattened finger and toe tips were thought to be a parallel character and as the tips are rather small, assignment of *O. semipalmata* and *O. floresiana* to another genus was not taken into consideration, despite of its having a relatively higher and rounded snout and laterally oriented eyes compared to other *Occidozyga*. Based on the finding of a distinctive form from Mount Tompotika closely related to *O. semipalmata* or *O. floresiana*, it might be justifiable to assign these species to a different genus. Decision about their generic position will be put forward after the tadpole morphology and vocalization characteristics are available and thorough genetic analysis based on nuclear and mitochondrial genes of all members of the genera *Ingerana* and *Occidozyga*. Marmayou et al. (2000) found that *Ingerana tenasserimensis* is closely related to *Occidozyga* which also enforced our conclusion that a lot more information is needed to serve as the base in placing members of *Ingerana* and *Occidozyga* in a proper generic position.

Biogeography. – Considering examples of other vertebrates such as monkeys, lizards, toad and frogs based on both genetic

and morphological analyses, parts of *Occidozyga semipalmata* populations are potentially distinct and separated from each other and fit with the ancient micro-continent of Sulawesi (Evans et al., 2001, 2003a, 2003b; McGuire et al., 2007). Recent studies show that numerous cryptic species are surging as molecular techniques are very useful and widely used (Evans et al., 2003a; Bickford et al., 2007; Inger et al., 2009). *Occidozyga* can be used as another supporting taxon where Sulawesi and the Philippines are found to be tightly linked as shown in several mammalian genera (i.e. Musser, 1982; Shekelle & Salim, 2009), as well as reptiles and amphibians (de Haas, 1950; Iskandar & Tjan, 1996; Iskandar & Colijn, 2001; de Lang & Vogel, 2005; Evans et al., 2003b). The result of this study reinforces the fact that biogeographically, the southern Philippines, especially Mindanao, has a very strong connection with the Wallacean region. Conversely, much more information is needed to associate Sulawesi with the Lesser Sunda Islands. Up to present it is not clear how effective Salayar and Tanah Jampea Island served as landbridges in the past. These islands have three endemic snakes of the genera *Cylindrophis*, *Trimeresurus*, *Boiga*, and a *Cyrtodactylus* which are not enough to be used to explain the close relationships between Sulawesi and the Lesser Sunda Islands (Hayden et al., 2009; Iskandar et al., 2011b). The presence of endemic species on this Papuan origin micro-continent within Sulawesi supports the urgent need to protect the Balantak Mountains and promote more conservation efforts. At least three reptiles and one amphibian species are now considered endemic to this peninsula (Inger & Marx, 1965; Brown et al., 2000; Iskandar et al., 2011b).

Artificial key to *Occidozyga* species inhabiting Wallacea and the Philippines:

1. Size very large, males 25–40 mm and females 30–62 mm
..... *O. laevis*
- Size smaller 2
2. Toes or fingers or both with flattened disks 3
- Toes and fingers at most with conical tips, ventral immaculate or with few dark spots *O. celebensis*
3. Toes fully webbed to terminal disks *O. floresiana*
- Fourth toe with one or two last phalanges free from extensive webbings 4
4. Only the toes are armed with terminal disks, finger are smooth without enlarged and flattened disks *O. diminutiva*
- Fingers and toes with flattened terminal disks 5
5. Disks of fingers and toes much larger compared to phalange diameter, only terminal phalange of fourth toe free from extensive webbings *O. tompotika*
- Disks of fingers and toes slightly wider than the diameter of penultimate phalange, fourth toe with two phalanges free from extensive webbings *O. semipalmata*

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Comparative material. – *Occidozyga semipalmata*: RMNH 6889 (paratype, MAS 8546) RMNH 6888 (paratype, MAS 8740); FMNH 252490 (paratype); JAM 6062; 6063; 6085; 6088; 6553; 7049; 7050; 7052; 7053; 7080; RMNH 0866, 0667; MZB Amph.8449–8450 (2 ex.) all from Mt Lompobatang at 1200 m asl. (the type locality), South Sulawesi; LSUMZ 81803, 81804, 81805, 81807, 81808, 81860 from Gunung Karua at 1200 m asl., Tanah Toraja South Sulawesi Province; JAM 5957 from Polewali Masawa road at 100 m asl., West Sulawesi Province; LSUMZ 84158, 84161, 84163, 84166, 84168, 84169, 84170, 84171, 84177, 84178, 84179, 84180, 84181, 84182, from Gua Keramat, Kebun Kopi at 50 m asl., Central Sulawesi Province; JAM 8504 from Uwekuli at 50 m asl., Central Sulawesi Province; BSI 2198 from Poso, Central Sulawesi Province; BSI 2231 from Mamuju at 60 m asl., Central Sulawesi Province; RMNH 0866–0867 (2 ex) from Kabila range at 1080 m asl., Bogani Nani Wartabone National Park, North Sulawesi Province. JAM 4817; BSI 0764 from Bogani Nani National Park at 60 m asl., North Sulawesi Province. *Occidozyga celebensis*: MZB 8451 (1 ex.) from Malino, Mt. Lompobatang at 1200 m asl., South Sulawesi Province. DTI unnumbered 85 ex., from Cikoro, Mt Bawakaraeng (type locality) at 1000 m asl., South Sulawesi Province. *Occidozyga sumatrana*: DTI-DP 14–17 from Dempar, Maruwai at 350 m asl, Central Kalimantan Province. DTI-MV1398, 1 ex, from Lalut Birai, Kayan Mentarang National Park at 200 m asl. DTI, 5 ex from Maruwai at 350 m asl., Central Kalimantan Province, DL 1–15, 15 ex., from Kudamis, near Kayan Mentarang National Park at 150m asl., East Kalimantan Province; MK 875–878 (3 ex.) from Kahyong river, Ketapang at near sea level; MK 854–855 (2 ex.) from Sungai Tiga km 33, Ketapang at near sea level, West Kalimantan Province; MK 398–405, 8 ex, from Mentangai, Ketapang, West Kalimantan

at near sea level. MK 910, 936 2 ex., Lamie, at near sea level Nanggroe Aceh Darussalam Province. *Occidozyga baluensis*: DTI-MV., 3 ex from Lalut Birai, Kayan Mentarang National Park, East Kalimantan Province; KU (1 ex.) from Kahoil river (1°35'40"S; 115°30'30"E) at 115 m asl., South Kalimantan Province

Limnonectes hascheanus: FMNH 189959; 1 ex., from Bukit Lanjang, Selangor, Peninsular Malaysia; FMNH 190350, 1 ex., from Kuala Lumpur, Selangor, Peninsular Malaysia, RMBR-ZRC 1. 614–619, 6 ex., from Penang Island, Peninsular Malaysia. *Limnonectes limborgii*: FMNH 186355, –358, –365, –370, –373, –377, –378, –418, –448, –885, 12 ex., from Bukit Lanjan, Peninsular Malaysia; FMNH 172787–90, 4 ex., from Bhetong, Yala Province, Thailand; 216054, 1 ex., from Doi Suthep, Chiang Mai Province, Thailand. *Limnonectes parvus*: FMNH 50269, 50270, 96073, 131315, Mindanao, the Philippines. *Limnonectes microdiscus*: ITB coll, RMBR-ZRC, FMNH, 104 ex, 61 females and 43 males, from Cibodas, West Java province. *Limnonectes nitidus*: RMBR-ZRC 1.849 & 1.850, 2ex, ad and juv. (paratypes) from Cameron highland, Peninsular Malaysia. *Limnonectes palawanensis*: FMNH 245115, 245116, 245121, 245123, 4 ex., from Sabah, Malaysia; ITB coll., 1 ex., from Central Kalimantan Province. *Limnonectes tweediei*: FMNH 141815, 141824, 141831, 141839, 141837, 181845, 181823; BPBM 4873, 3449, 3448, 4570, 4523, 4571, 4530, 4567 15 ex., from Peninsular Malaysia. *Limnonectes rhacodus*: DTI (7 ex., unnumbered). from Betung Kerihun National Park, West Kalimantan Province; MK 854, 875–877, 1200 (5 ex.) from Murung Raya, Upper Barito river, Central Kalimantan Province; RMBR (7 ex.) from Bukit Baka-Bukit Raya National Park, West Kalimantan Province; DTI (13 ex.) from Maruwai, Upper Barito river, near border to East Kalimantan Province. (KU, 23 ex) from Kahoil river (1°35'40"S; 115°30'30"E), South Kalimantan Province.

Ingerana tasanae: RMBR-ZRC. 1.11795. 1 ex, juv. from Khao-Lak, Phang-Nga Province, Thailand, juv. (identified as *I. tenasserimensis*). FMNH 216071 (1 ex.) from Thailand; FMNH 171414–171416 (3 ex.) from Ranong, Thailand. *Ingerana tenasserimensis*: FMNH 21635–21637 (3 ex.) From Trang Province, Thailand. *Ingerana baluensis*: RMBR-ZRC 1.2737 from Lahad Datu, Danum Valley, Sarawak, Malaysia; RMBR-ZRC 1.11069, 1.11070. from Kapit Palagus, Sarawak, Malaysia; RMBR-ZRC 1.3152. from Temburong, Batu Apoi, Brunei Darussalam. MZB Amph. (3 ex.) from Mt, Lawit, Betung Kerihun National Park, West Kalimantan Province. ITB coll. (3 ex.) from Sebuku–Sebakung, Kayan Mentarang National Park; *Ingerana mariae*: FMNH 51359–51360 (2 ex., Types) from Palawan, the Philippines.

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