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Frogs Hiding in Plain Sight: Phylogenetic Systematics of Myanmar's Occidozyga Species Complex, and the Identification of a Novel Species

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Thesis

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Abstract

Different species can be difficult to distinguish from one another when they are morphologically similar. Such cryptic species are the reason many anuran species go undetected. For this study, the taxonomic identity of the *Occidozyga* complex across Myanmar was investigated. An integrated approach was used combining molecular, morphological and phylogeographic data to better assess its taxonomy. Results indicate the presence of three new candidate species within *Occidozyga,* and three evolutionarily significant unit (ESU) lineages. Two mitochondrial gene fragments (16S, COI) and one nuclear gene fragment (Rhodopsin) were examined from DNA isolated from forty-seven preserved specimens from the California Academy of Science (CAS). Spatial data from collection localities for specimens was integrated into phylogeographic analyses. Additionally, morphological data was analyzed for morphometrics and principal component analysis (PCA) from 259 specimens at the CAS and National Museum of Natural History (NMNH). Significant molecular differentiation was observed, uncovering a novel species from central Tanintharyi. Additional evolutionary significant units were identified. From these findings, we advocate for adequate protection of each of these distinct evolutionary lineages.

I. Introduction

Over the past two decades, the need for conservation measures to protect global amphibian populations has been increasing at a rapid pace. Numerous threats to survival are confronting amphibian populations such as habitat loss, environmental pollution, competition with invasive species or predation by invasive species, diseases and fungal pathogens, and as well as various anthropogenic factors from use and trade (Collins and Storfer, 2003; Mendelson et al., 2006; McLeod, 2010; Grant et al., 2016). Since amphibians are environmental indicators for both overall habitat health and climate change, the focus on research efforts towards their conservation is not a misguided priority. The most recent IUCN Red List report implicates that 40% of all 6,724 recognized amphibian species (32-53% lower and upper estimates respectively) are currently threatened with extinction. In contrast, for anurans specifically, 2,560 species are considered to be of "low risk/least concern" and 1,281 species are "data deficient" (IUCN et al., 2019).

Many of the taxa categorized as "least concern" based on an assumption of widespread distribution, local abundance, and tolerance to anthropogenic disturbance yet they do not actually represent a single species, but instead, are a complex of several cryptic species. Multiple morphologically similar or indistinguishable phenotypes that are actually multiple separate species can often remain 'hidden' in a complex under a single species name, despite absence of inbreeding or gene flow among them (Kotaki et al., 2008). These "cryptic" species by their very nature are often left unaccounted for in field surveys, despite being another species entirely. Cryptic species are neither taxonomically nor biogeographically unique but are instead common

among many taxa and are found across the globe (Pfenninger and Schwenk, 2007). Many recent studies have revealed cryptic diversity among species of Southeast Asian anurans (Evans et al., 2003; Stuart et al., 2006, Inger et al., 2009;). In Stuart et al. (2006) it is even suggested that no single wide-spread species of forest-dwelling anuran Southeast Asia exists, and that cryptic lineages occurring in sympatry is likely the rule rather than the exception.

In the frog genus *Occidozyga*, there are currently twelve described species which have a history of widespread presence across Indonesia, Malaysia, Laos, Thailand south of the Isthmus of Kra, Cambodia, northern Vietnam, and China, but only two species have confirmed presence in Myanmar, *O. lima and O. martensii* (Mulcahy et al., 2018 ; Frost, 2019;). Most commonly known as Javan, puddle, or floating frogs, members of this genus have primarily been found in streamside puddles, seepages, lowland plains, as well as in temporary rain puddles or small pools along edges of areas with human activity. Typically, they reside in forest clearings and edges rather than in actual forest, along foothills on flatter ground with highly seasonal rainfall (Ali and Khan, 2001). *Occidozyga* is a rather enigmatic assemblage of species, with quite a long history of taxonomic turmoil and a multitude of synonymous names for each of the recognized species. The lack of comprehensive phylogenetic and morphological analysis has long prevented a resolution to these controversies.

Conservation Concerns

Frogs historically identified as *O. lima* (colloquially known as the Puddle Frog) are include at least three distinct morphotypes, with taxa varying in size and coloration as well as variance in toe webbing (Smith et al., 1916; Mulcahy et al., 2018). The southern region of the Tanintharyi division, "*O. lima*" is observed to be smaller and possess bold black and white ventral patterns,

lacking in the "*O. lima*" from the more northern Mon State and in the adjacent region of Bago, but it does share the same bold, dark thigh stripe pattern of the northern frogs (Mulcahy et al., 2018). Martin's floating frog is morphologically similar to *O. lima* but smaller and nothing is known about its status in Myanmar yet Mulcahy (et al., 2018) observed a high degree of genetic variation within the group. Current population estimates for *Occidozyga* are likely to be inaccurate given the high probability for the presence of unidentified cryptic species within the genus. At the time of both historical and even more recent biodiversity surveys, these cryptics could not have been taken into consideration due to a lack of appropriate molecular technology, they could be far more critically threatened than the known described species.

Myanmar's relatively recent shift from military rule towards a democratic leaning government has largely ended decades of economic and political isolation. Although Myanmar currently remains heavily forested, increased development over the past decade has been accompanied by exceptionally high rates of forest loss. Myanmar has an ambitious policy target of including 10% of the country's area in its Protected Area System by 2030, with the overarching goals of preserving both biodiversity and unique pattern of mountainous and lowland ecosystems (MOECAF, 2011). However, low land wet evergreen forest is currently underrepresented in the Protected Area System (MOECAF, 2011), and long delays informally designating protected areas have corresponded with an ongoing period of intense deforestation countrywide.

This is potentially problematic because Myanmar is already designated as part of the Indo-Burman biodiversity hotspot with many identified threatened species, however no species within the genus *Occidozyga* has been classified with a conservation status above 'vulnerable' as evidenced by the Conservation International and the International Union for Conservation of

Nature's Red List of Threatened Species (conservation.org; iucnredlist.org). The amount of time and funding invested in monitoring genera of lesser concern is consequently lower, and over time a lack of accurate, present-day data ultimately develops. Currently, eight out of eleven IUCN recognized species of *Occidozyga* have outdated species information, with the last assessment having been conducted in 2004 (IUCN, 2019).

Assessing the state of amphibian genera in ecosystems represents one of the larger challenges conservation biologists face in the age of modern science. Despite the known diversity of anurans, the number of described species is underestimated, particularly in their tropical, semi-aquatic habitats of Southeast Asia which are some of the most threatened biomes in the world (Collins & Storfer, 2003; Mendelson, 2006). Although Myanmar currently retains one of the largest forest areas in Southeast Asia, increased rates of development and trade in recent years have been accompanied by incredibly high rates of deforestation (Connette et al., 2017). Myanmar experienced the third highest rate of forest acreage lost globally from 2010–2015 (FAO, 2015), but recent annual rates of deforestation for primarily closed-canopy 'intact forest' are even higher (Bhagwat et. al, in review). Most of this forest clearing and habitat encroachment is due to logging, but some habitat disruption is due to mining and the ongoing Rohingya refugee crisis. There are 120,000 people settled in camps for Internally Displaced Persons (IDP) centered in the Rakhine capital, near in the outskirts of Sittwe alone (Aung and Lewis, 2018). Mining in primarily the northern regions around and within Kachin was reported at 902,025.300 MMK mn in Mar 2018, an increase from the previous number of 835,279.500 MMK mn for Mar 2017 (CEIC.com) , and residents from over twenty-two villages in the region have submitted formal complaints to the government due to polluted water sources from unregulated mine chemical packing (RFA.org).

The following is a report on the molecular and morphological analyses conducted on *Occidozyga* specimens collected from distinct locations within Myanmar. This project was done to examine the biodiversity within *Occidozyga* and highlight any exisiting lineage divergence within the genus.

Taxonomic Concerns

Assessments of evolutionary history and biodiversity of *Occidozyga* puddle frogs are often challenging due to their relatively conserved morphological evolution and homoplasy (Noble, 1931; Mulcahy et al., 2018). There has long been debate as to whether this genus belongs in either the Ranidae or Dicroglossidae family. The taxonomy of these families has a convoluted history, and still is not fully resolved but there is one monophyletic clade generally recognized as possessing two subfamilies: Occidozyginae and Dicroglossinae (Frost, 2019). The genera of *Occidozyga* and *Phyrnoglossus* were recognized by Dubois (1992) as belonging to the subfamilies Raninae Rafinesque-Schmaltz, (1814) and Dicroglossinae by Anderson (1871) respectively. However, from Marmayou et al. (2000) the two genera- *Occidozyga* Kuhl and Van Hasselt, (1822) and *Phrynoglossus* Peters, (1867)- form an independent well-supported clade and are a sister-group to all other Ranidae. They argued the clade should be excluded from the latter group. The particular characteristics of the tadpoles of these two aforementioned genera had already led Fei et al. (1991) and Ye et al. (1993) to consider both as a subfamily of their own within the Ranidae, the Occidozyginae Fei et al. (1991). Dubois (1987) had further suggested that *Occidozyga* shared several characters: “development passes through a free tadpole stage and whose lateral line persists in general in the adult” with the genus *Euphlyctis.* Fitzinger (1843), and had proposed to place the genera *Euphlyctis*, *Occidozyga* and *Phrynoglossus* in a group

called Dicroglossini of the subfamily Dicroglossinae. The characteristics of *Occidozyga* in this comparison were based on Gravenhorst's (1829) *O. lima* diagnosis and the description given earlier by Dubois (1987). Within Occidozygidae, Fei et al., (2010) recognized two subfamilies: Occidozyginae and Liuraninae. Within Occidozyginae, the authors recognized *Occidozyga* and *Phrynoglossus* (although recognition of *Phrynoglossus* on their terms essentially renders *Occidozyga* paraphyletic. Also noteworthy, is that *Phrynoglossus*, and consequently *Occidozyga*, is paraphyletic with respect to *Ingerana* on the tree of Pyron and Wiens (2011), where *Occidozyga* fall squarely within Dicroglossidae based on molecular analysis of 12 genes (three mitochondrial, nine nuclear). Ranidae have historically been characterized as having upper jaw toothed; diapophyses of sacral vertebra cylindrical, or very slightly dilated, versus Dicroglossidae which are historically characterized as also having upper jaw toothed; diapophyses of sacral vertebra dilated; short ribs articulated to the anterior diapophyses (Boulenger, 1882).

Morphologically, *Occidozyga* tend to most closely reflect the other members of the very diverse Dicroglossidae family, but their species descriptions in the literature are often contradictory and teeth are typically not detectable in specimens. Formalized morphological distinctions between most *Occidozyga* species have been incongruent, with distinctions primarily based upon webbing of the toes, and metatarsal tubercle presence, but these characteristics have historically been dismissed of much value for species delimitation (Smith, 1916). Generally, *Occidozyga* are small (15-55 mm adult SVL), with webbed feet and pointed digits. A lateral-line system is present in adults, and some species exhibit inguinal rather than axillary amplexus (Vitt & Caldwell, 2008). Dorsum color is typically dark gray-brown, with the ventral side of the head being a speckled dark gray, and infrequent pale whiteish yellow tinged venter and undersides of the thighs.

However, some specimens exhibit a thick light or dark stripe down the dorsum (Inger and Stuebing, 2005). Due to their cryptic morphology, species within the genus are difficult to differentiate from each other based on qualitative characteristics alone. Mulcahy et al. (2018) found GenBank specimens identified as *O. lima* (AF215398 and AB488903) were misidentified as they were not closely related to known *O. lima* specimens based upon phylogenetic analysis. A closer reexamination of morphological characters may unveil that suitable diagnostic characters are present. Yet, morphology alone cannot delineate species. Molecular phylogenetic analysis is needed especially for cryptic species (Fouquet et al., 2007; Elmer and Cannatella, 2008; Funk et al., 2012; Ron et al., 2012; Elmer et al., 2013; Jungfer et al., 2013; Caminer and Ron, 2014).

Gravenhorst (1829), first described *O. lima* from a specimen from Java, which serves as the type species of the genus, by subsequent designation of Stejneger (1925). Since that time, numerous additional specimens have been collected and are now available for a more thorough morphological examination. With an increased sample size, even slight deviations in morphological characters could reasonably emerge as reliable and distinctive enough to distinguish among *Occidozyga* species. Furthermore, reports of *Occidozyga* sightings from differing countries would likely result in the identification of additional *Occidozyga* subspecies or cryptics, as distribution maps for the known species are generally poor and ranges are only assumed to be broad (Frost, 2019).

Even if morphological characters are detected, the morphological species concept used to delimitate species has limitations in contrast with a unified and general lineage concepts that are now applied thanks to available tools that exist for genetic analysis. Mulcahy et al. (2018),

uncovered four novel groups of genetically divergent *Occidozyga* using the 16S molecular marker. It was noted as being a species complex, and that each new clade should be treated as separate, unidentified candidate species (Mulcahy et al., 2018).

Molecular Genetics

Recent improvements in molecular-based methods of identification are revealing a large number of new species (Gehara et al., 2014; Dever, 2017; Mulcahy et al., 2018; Grismer et al., 2019; Labisko et al., 2019). The molecular markers with greatest utility for animal species identification are from the mitochondrial DNA (mtDNA), which are maternally inherited, are highly variable, easily amplified, has a relatively low rate of recombination, and are nearly neutral in its evolution, (Avise, 1987; Lin et al., 2010; Chen et al., 2017). For anurans, preference has been shown for the 16S and COI markers to determine interspecific variation (Dever et al., 2015; Vences et al., 2016; Dever 2017; Gao et al., 2019). In fact, many analyses of mtDNA have shown to be effective for not only amphibian phylogenetics at different taxonomic levels but even for prediction of divergence periods of more than three hundred million years ago (Zhang et al., 2008; P. Zhang et al., 2009; Wiens and Morrill, 2011). Nuclear genes (nuDNA) when appropriate sample size of multiple taxa and sufficient phylogenetic analyses in animal systems and are useful to better support observed patterns of mtDNA evolution (Reyes et al., 2003). Phylogenies based on the nuDNA gene rhodopsin provide some additional support for close relationships of anuran genera in combined marker analyses but are less unequivocal when analyzed individually (van der Meijden et al., 2005).

The major issue with DNA barcoding of amphibians- a method of species identification using a short section of DNA from a specific gene or set of genes- is related to high

mitochondrial variability. Intra- and interspecific divergence values sometimes overlap in mitochondrial markers, thereby reducing the inherent value of a barcoding gap to identify candidate species (Vences et al., 2005, Vieites et al., 2009). The accuracy of the method depends on the 'barcoding gap' between intraspecific and interspecific divergences, but previous work on amphibians has shown a wide overlap of these values and absence of a distinct barcoding gap (Vences et al., 2005). Ideally, a barcoding gene should have a definitively observable gap between intra- and interspecific divergence levels and, and perhaps most critically, correctly identify species. In Vences et al. (2005) high intraspecific COI divergence values of 7–14% were observed within the whole set of amphibian sequences analyzed, however the high values were not caused by particularly high substitution rates of the gene but by generally deep mitochondrial divergences within and between species. Despite the high divergences, COI sequences were able to identify the correct species, including geographic variants. Two primary issues with COI barcoding of amphibians are the high variability of priming sites which hinder the application of universal primers to all species and the observed distinct overlap of intraspecific and interspecific divergence values, which implies difficulties in the definition of threshold values to identify candidate species (Collins and Cruickshank, 2012). Common discordances between geographical signatures of mitochondrial and nuclear markers in amphibians indicate that a single-locus approach to phylogeny revision can be problematic when high accuracy DNA barcoding is required, as mitochondrial DNA diverges at a faster rate for vertebrates.

Due to its current limitations, DNA barcoding is best used as a tool for preliminary identification of candidate species, and it is best practice to favor a conservative approach that minimizes the error probability of false positives (Vieites et al., 2009). This approach may miss species of more recent origin, but it will more efficiently help taxonomists to focus on those

genealogical lineages likely to be undescribed species. Others argue that it is better to over-estimate rather than under-estimate species in more rapid molecular focused biodiversity surveys in order to secure sufficient protection of the area, and consequently for its evolving lineages (or Operational Taxonomic Units, OTUs) which acknowledges the genetic diversity contained within a lineage (even if multiple lineages are eventually found to be the same species) (Moritz, 1994; Sanders et al., 2006; Mulcahy et al., 2018; Labisko et al., 2019).

Li et al. (2014) found a novel vertebrate mtDNA gene rearrangement in *Occidozyga martensii*, which serves to further clarify the phylogenetic relations of this genus within anurans. They found that in the WANCY tRNA-gene cluster, the tRNA-Asn gene was located between the tRNA-Tyr and COI genes instead of between the tRNA-Ala and tRNA-Cys genes. Additionally, Li et al. (2014) found that *Occidozyga* have two tandem tRNA-Met genes rather than one, and that the tandem duplication of the tRNA-Met gene can be regarded as a synapomorphic character of Dicroglossidae. Some multiple deletions of redundant genes appear to be incomplete in *O. martensii*, which might be responsible for the non-coding regions occurring around the genes involved in the rearrangements. Their phylogenetic results were also consistent with the latest taxonomic systems, with Dicroglossidae being a sister clade to (Ranidae +(Mantellidae+ Rhacophoridae)), and the monophyly of Ranidae and Dicroglossidae was well supported (BP= 100% and BPP=1.00), which is in accordance with the analysis of mt genome rearrangement (Dicroglossidae retains tandem duplication oftRNA-Met, (Ranidae has only one copy) (Li et al., 2014). Moreover, *O. martensii* was found to occupy the basal phylogenetic position among the dicroglossids studied. This is indicative that Occidozyginae represents the ancient/ancestral lineage in Dicroglossidae, which is consistent with the opinion of Roelants et al. (2004).

As of now, the current dominant choice among most herpetologists conducting systematics research is the use of 16S gene for species delimination (Vences et al., 2005; Fouquet et al., 2007; Garg and Biju, 2019; Labisko et al., 2019). Assessments of specimen identification based on 16S data alone should be done on a case-by-case basis, considering the geographic placement between specimen and whether or not specimens met the morphological description of the species they cluster with (Mulcahy et al., 2018). Alternatively, more than 95% of animal species genetically examined possess a diagnostic COI sequence array, and COI divergences rarely exceed 2% within a named species, while members of different species tend to show higher divergence, making it a useful locus for species delineation in conjunction with 16S (Hebert et al., 2003a; Hebert et al., 2003b). Speciation cases linked to mitochondrial introgression cannot be resolved through mtDNA analysis alone but can be partitioned through the analysis of one or more nuclear genes, suggesting that improvement for species delineation in rarer complex cases should involve tactful incorporation of nuclear gene information from multiple loci (Ratnasingham and Hebert, 2013). Since a comprehensive COI barcode library is still lacking for most southeast Asian anurans, it will be necessary for this study to include 16S sequence data as a supplemental barcode marker to help identify specimens, as well as including a nuclear marker to compare with known sequence materials already published in GenBank. However, it's important to remember that nuDNA and mtDNA have been co-evolving synergistically in ensuring the survival of the organism that carries them, but antagonistically in their race for long term existence. The nucleus is under selective pressure to impose/maintain uniparental inheritance of mtDNA and increase its independence from mtDNA via effectively "borrowing" functional genes from it. Mitochondrial DNA, on the other hand, undergoes constant pressure to avoid uniparental inheritance, mutational meltdowns, while simultaneously

increasing its indispensability for the organism by incorporating novel information that is necessary for the organism's functionality in its ecosystem. Therefore, it's important to consider the importance of both markers when looking at divergence across populations.

Phylogeography and Population Distributions

In Myanmar, one of the most prominent topographical features is its elongate and inverted U-shaped mountainous border that naturally surrounds its centralized basin lowlands to the north, east and west. Ranging from west to east, the Irrawady Basin's borders consists of the Indo Burman Range, eastern Himalayan syntaxis, Sinoburman Range, Shan Highlands, and the Tenasserim Range (Lieberman, 2010; Oh, 2016). All these ranges together create substantial geographic borders between Myanmar and the neighboring countries of India, Tibet, China, Laos, and Thailand. This topographic layout facilitates potential geographic isolation of species due to constrained gene flow from migration limitations in Myanmar. In this region, these huge mountain ranges (e.g. the highest peak believed to be Hkakabo Razi at 5,881 m in Kachin) and deep valleys (e.g. less than 700 m elevation in Rakhine)-as noted in Oh, 2016-were expected to promote diversification, especially in amphibians (Dever et al. 2012; Grismer et al., 2019). In a study of *O. semipalmata,* by Iskandar et al. (2011), populations from three highland areas exhibited congruent body sizes with the population from Mount Tompotika (~1492 m) having been composed of larger individuals, similar to those from Mount Karua (~2700 m) as compared to those from lower elevations. Secular migration may be able to occur, with only certain species or individuals being able to traverse to other gene pools for mixing. Wherever there an overlap in their range exists, one could expect to see phylogenies that follow the respective geographic pattern of isolation. This has already been reflected in the phylogeny of the *Amolops*

marmaoratus species complex (Dever et al., 2012). Indeed, the same phylogeographic patterns of long-term historical isolation within Myanmar with only relatively recent additions of new 'founder genes' to the previously isolated populations, either by the introduction of founder individuals or their genetic material, remains true even for native Asian elephants and Eld's deer (Fleischer et al., 2001; Zhang et al., 2008). Mulcahy et al. (2018), found multiple anuran specimens initially identified as four morphospecies in four genera (including *Occidozyga*). Ultimately, DNA barcoding and comparison with northern Myanmar reference specimens revealed each genus was likely represented by two to three species based on the fact that at least one Tanintharyi clade (within each genus) grouped with specimens from further north, rather than with the other clades (of the respective genus) within Tanintharyi. *Occidozyga* appears to be undergoing a similar evolutionary pattern of geographic isolation as previously seen in *Amolops*, with only the majority of sequenced samples clustering with samples from within the same regional locality in Myanmar.

I. Materials and Methods

Over 250 adult *Occidozyg*a samples were available for morphological analysis, and a smaller subsample of these were utilized for DNA sequencing through the California Academy of Sciences (CAS). Additionally, 72 specimens from the Smithson Museum of Natural History (USNM) were provided to better determine the taxonomy and evolutionary relationships of species within *Occidozyga*.

Morphology. — Comparative morphological data was recorded from 259 specimens collected from across Myanmar, fixed in 10% formalin and then stored in 70% ethanol. Specimens were analyzed from the CAS and the USNM collections. Morphometric data were

taken from the right side of the body (to the nearest 0.1 mm) with digital calipers. Measurements include snout-vent length (SVL, from tip of snout to vent); head length (HL, from tip of snout to rear of jaws); head width (HW, width of head at the commissure of the jaws); internarial distance (IND, distance between nares); interorbital distance (IOD, minimum distance between upper eyelids); tympanum diameter (TD, horizontal diameter of tympanum); distance from nostril to eye (DNE, from center of a naris to anterior corner of eye on same side); eye width (EW, distance from posterior to anterior corners of eye); forelimb length (FLL, from elbow to tip of third finger); thigh length (THL, from vent to knee); tibia length (TIL, from knee to ankle); foot length (FL, from proximal end of the tarsus to tip of fourth toe). Descriptions of any foot webbing were made according to the foot webbing formula by Myers and Duellman (1982) as modified by Savage (1997). Any variations in skin texture, dorsal or ventral coloration, presence of any supratympanic folds, circummarginal grooves, transverse grooves, dorsolateral folds, vomerine teeth, hind limb banding, forelimb banding, ventrolateral margins, metacarpal or metatarsal tubercles were also noted for each specimen. While some specimens had been sexed as determined by direct observation of mating during life at time of collection, permission was received to attempt to determine sex of additional specimens- this entailed some minor dissection to locate gonads, since they do not portray any of the common visible secondary sexual characters (presence of nuptial pads or vocal sac openings). BioVinci v1.1.5 was used to perform principal component analysis (PCA) and summary statistics of the morphological data and to visualize the PCA analysis (2017 BioTuring Inc.).

Molecular taxon sampling. —Total genomic DNA was extracted from liver tissue samples collected from forty-seven Myanmar *Occidozyga* specimens prior to preservation, that represented four described species and potentially multiple undescribed species (Table 1).

Additional homologous sequences were retrieved from GenBank to expand the number of specimens and localities. Tissue of sequenced specimens are from the CAS tissue collection and were initially collected into 95% EtOH and subsequently stored at -80 °C. Specimens were selected in order to have multiple tissue representatives from ten of the fourteen provinces within Myanmar (Ayeyarwade, Shan, Kachin, Yangon, Magway, Rakhine, Bago, Tanintharyi, Mandalay, Mon) [See Appendix I]. Using the DNeasy Tissue Kit and protocol (Qiagen, Inc., Valencia, California, USA), genomic DNA was eluted in 100 µl of re-suspension buffer. Polymerase chain reactions (PCR) were conducted for the mtDNA 16S rRNA (16S), cytochrome oxidase subunit I (COI), and nuDNA from the rhodopsin subunit (RHOD) using the primers as indicated from Table 1.

Table 1: Primer pairs for PCR of *Occidozyga* puddle frogs.

Locus	Sequences (5'-3')
16S (Fwd)	CGCCTGTTTACCAAAAACAT
16S (Rev)	CCGGTCTGAACTCAGATCACGT
COI (Fwd)	CTACAAYCCRCCRCCTRCTCGGCCAC
COI (Rev)	TADACYTCDGGRTGDCCAAARAATCA
RHOD (Fwd)	AACGCAACAGAAGGYCC
RHOD (Rev)	GTAGCGAAGAARCCTTC

For the sequencing region in each sample, one forward and one reverse primer were used, 0.5 µl each at 5uM, for amplification. The master mix for each singular reaction contained both primers, along with 12.5 µl of MyTaq Red, 9.5 µl of ultra-pure water, and 2 µl of the template DNA to be amplified. Amplified DNA was produced in 25 µL reactions after 33 cycles of

denaturation for 45 s at 95 ºC, annealing for 45 s at 58ºC, and extension for 1.5 min at 72 ºC for 16S; for COI there were 6 cycles of 30 s at 94 ºC, 90 s at 45 ºC and 1 min at 72 ºC followed by 35 cycles of 30 s at 94 ºC, 90 s at 53 ºC, and 1 min at 72 ºC; for Rho after 35 cycles of denaturation for 45 s at 95 ºC, annealing for 45 s at 57 ºC and extension for 1.5 min at 72 ºC. PCR products were held at 12 ºC and then purified using Promega Wizard SV Gel and cleaned using Exosap-It. Purified PCR products were then sent off in 10 ul aliquots for sequencing using an Automated ABI 3730 sequencer at MCLAB in South San Francisco, CA (2011 Life Technologies). Returned forward and reverse sequences were verified as representing the correct target marker using a BLAST search against GenBank; raw chromatograms were then edited in Sequencher v5.1 (2012 Gene Codes Corp.), complementary strands were aligned and inspected for proper translation with Geneious Pro 11.1.4. Alignments were conducted using the MUSCLE and ClustalW options in Sequencher and Geneious. Ends of reads were trimmed with an error probability limit of 0.05, prior to allowing reads to overlap and assemble.

Genetic variation and phylogenetic analysis. —After aligning sequences in Sequencher, the MAFFT v7.222 100 (Katoh et al. 2002) algorithm in Geneious Pro 9.02 was used using the E-INS-I mode and standard 101 parameters. Phylogenetic trees were inferred via Bayesian analyses (BI) in Geneious Pro using the MrBayes plugin v3.2.6 (Ronquist and Huelsenbeck, 2003) with the four chains run option at temperature of 0.2 for a chain length of 100,000, a sub-sampling frequency of 200, burn-in length of 10,000 and random number seed with gamma rate variation. Scale bars at the bottom of each tree represent uncorrected genetic distances (*p*). MEGA 7 was used to calculate nucleotide diversity, and to obtain inter- and intraspecific genetic *p*-distances for mtDNA, with pairwise deletion of missing sites. The MEGA 7 software was also used to conduct Maximum Likelihood (ML) alignment analyses, and to construct ML trees. Using the

program jModelTest (v2.1.7; Posada, 2008), the TPM evolutionary model worked best, however given the programs and software available for use, jModel testing indicated that the HKY85 model was still a suitable nucleotide substitution model and was more readily available in current software. The least appropriate model was determined to be the JCI evolutionary model. Therefore, the HKY85 model of evolution was utilized, and the –ln L per generation was plotted in Geneious. Because *O. lima* is the most ancestral lineage (Frost, 2018), it was set as the outgroup taxon within the genus in the absence of available GenBank sequences from their closest Dicroglossidae and Hyperoliidae cousins (*Ingerana, Sylvirana,* and *Phlyctimantis*).

Phylogeography. — Specimens' decimal degree latitudes and longitudes [see Appendix II] were then mapped onto both topographical and terrain maps of Myanmar. Molecular clades were color-coded using Esri Online's ArcGis mapping software. Ecoregions of specimens were mapped using Data Basin software and base maps from the Conservation Biology Institute.

II. Results

Morphology. —Quantitative Morphological Analysis via PCA

Principle component analysis of the quantitative morphological comparisons showed strong contrast between *O. lima* and *O. martensii* specimens (Fig. 1), but there was no statistically significant variance from the analysis for differences in components within individuals initially identified as *O. martensii* (Fig. 2). PC1- snout-vent length- was found to be responsible for the largest proportion of observed variance, accounting for about 62% of the variation in the data set (Table 2). Snout-vent length also had the highest standard deviation (STDV) of about 2.74, with PC2, head length coming in second with a STDV of ~1.26 while only accounting for an additional 13% of the variation between the species types based on the resulting molecular clades

(Table 2). PC1 is the only component that was more than two standard deviations away from the mean, with the assumption of a normal distribution and a 95% confidence interval. Sexual dimorphism checks of specimens resulted in males (n=10) having an average SVL of 26.71 mm with a range of 23.46-35.22 mm in length, and females (n=24) with an average SVL of 29.62 mm with a range of 24.91-39.94 mm. All morphometric variables aside from SVL had relatively little variance and insignificant deviation across both *O. lima* and *O. martensii* (Table 3 and Table 4). [See Appendix III for full list of all specimens used for morphological analysis and their respective morphological measurements.]

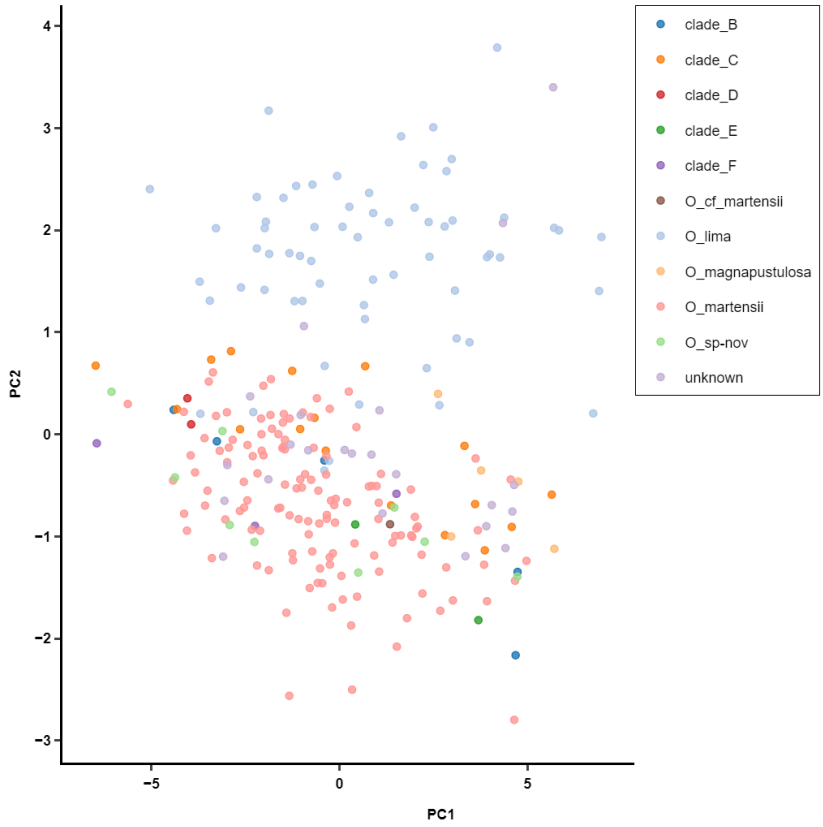

Figure 1: Principal component analysis of twelve morphological measurements. N = 259 *Occidozyga* specimens. PC1 on the x-axis is snout-vent length and PC2 on the y-axis is head length.

Table 2: Principal component analysis scores for *Occidozyga* species. Components correspond to the same measurements as in Fig.6. Values rounded to four decimal places.

Component	Standard Deviation	Proportion of Variance
PC1	2.7352	0.6235
PC2	1.2567	0.1316
PC3	0.8303	0.0574
PC4	0.7398	0.0456
PC5	0.6757	0.0380
PC6	0.6083	0.0308
PC7	0.5133	0.0211
PC8	0.4456	0.0166
PC9	0.4181	0.0146
PC10	0.3232	0.0087
PC11	0.2794	0.0065
PC12	0.2368	0.0047

Table 3: Summary statistics for Myanmar *Occidozyga lima* specimens. Measurement units are in millimeters (mm). All decimal values rounded to two decimal places. (N= 64).

	SVL	HL	HW	IND	IOD	TD	DNE	EW	FLL	THL	TIL	FL
Mean	28.08	7.77	9.72	1.82	1.42	2.67	2.03	3.41	12.01	13.46	12.89	14.87
Standard deviation	3.93	1.10	1.34	0.25	0.35	0.51	0.32	0.43	1.74	2.12	1.70	2.02
Variance	15.46	1.20	1.79	0.06	0.12	0.26	0.11	0.18	3.03	4.49	2.88	4.06
Min	17.60	5.83	6.88	1.35	0.71	1.84	1.36	2.36	9.00	9.59	9.13	10.98
1st quantile	25.85	6.95	8.86	1.67	1.19	2.37	1.82	3.11	10.49	12.00	11.62	13.43
Median	27.73	7.57	9.41	1.80	1.41	2.61	2.02	3.39	11.88	13.38	12.95	14.75
3rd quantile	30.20	8.43	10.60	1.93	1.64	2.93	2.25	3.72	13.12	14.79	14.10	16.14
Max	39.94	10.52	13.21	2.64	2.46	4.02	2.90	4.21	16.27	17.76	16.35	19.41

Table 4: Summary statistics for Mynamar *Occidozyga martensii* complex specimens. Measurement units are in millimeters (mm). All decimal values rounded to two decimal places. (N=158).

	SVL	HL	HW	IND	IOD	TD	DNE	EW	FLL	THL	TIL	FL
Mean	27.39	6.86	9.00	2.50	1.72	2.22	1.95	3.36	10.20	12.80	12.38	13.07
Standard deviation	3.93	0.74	1.18	0.29	0.33	0.46	0.25	0.45	1.53	1.87	1.66	1.56
Variance	15.45	0.55	1.39	0.08	0.11	0.21	0.06	0.20	2.34	3.51	2.74	2.44
Min	17.80	4.48	6.37	1.80	1.06	1.41	1.09	1.76	6.96	8.05	8.33	8.93
1st quantile	24.89	6.41	8.16	2.30	1.47	1.88	1.78	3.06	9.02	11.56	11.25	11.93
Median	26.86	6.78	8.93	2.49	1.70	2.14	1.94	2.30	10.13	12.69	12.15	12.91
3rd quantile	29.92	7.26	9.70	2.72	1.90	2.49	2.10	3.66	11.17	13.90	13.58	14.26
Max	36.93	9.39	12.59	3.13	2.75	4.18	2.90	4.43	13.95	17.44	16.95	16.77

Species Descriptions based on Morphology. —

O. lima

Image Credit: Frank Schafer (2007).

O. lima is characterized by the following combination of characteristics: narrow mouth, indistinct tympanum, lack of vocal sacs, fully webbed feet, pointed digits. Skin covered with small, noticeable pearl-colored tubercles. Dorsum color is typically dark gray-brown, with the ventral side of the head being a speckled dark gray, and infrequent pale whiteish yellow tinged venter and undersides of the thighs. Gular with distinct V-shaped lines. The distribution for O. lima is significantly broader than of any member of Occidozyga, being recorded from India through Myanmar to southern China, Vietnam to Malaysia and Indonesia (Frost, 2019). There is a clear presence of metacarpal tubercles; bold black horizontal stripe on rear of thighs beneath vent; strongly patterned pelvic venters with angled paired stripes; and pairs of dark chin

stripes. To a lesser degree, but only seen in the *O. lima* specimens analyzed, were dark short stripes present across both axillary regions.

O. martensii

Image credit: Myint Kyaw Thura and Daniel G. Mulcahy (2018).

Dubois (1982) noted that *O. martensii* exhibited variation in coloration, from solid dark gray dorsum to having a solitary medial stripe on the dorsum. Herein variation was also observed with several specimens possessing a dorso-medial line yet not all. A dorso-medial line was absent in all *O. lima* specimens; however all possess an inner metatarsal tubercle that is weakly projecting and partially attached.

Despite mention of nuptial pads being present in male members of *O. laevis* specimens from the Philippines by Inger (1954), morphological examination of specimens catalogued in the CAS collection as male did not indicate any sexually dimorphic traits. Neither nuptial pads on the forelimbs nor internal paired vocal sac openings were observed. Sexing of these specimens could only be achieved if the specimen was visibly gravid/with eggs, or if minor dissection was done to look for mature gonads (as presence of seminiferous tubules and testes would confirm a sexually mature male specimen). Overall body size dimorphism was also excluded as a diagnosable trait, even given that 90% of female anurans are larger on average than male counterparts of their species (Shine, 1979). The average SVL length of confirmed male Occidozyga was 26.71 mm (n=10) ranging from 23.46 mm-35.52 mm, versus the average confirmed female *Occidozyga* SVL was 29.62 mm (n=24) ranging from 24.91 mm-39.94 mm in length.

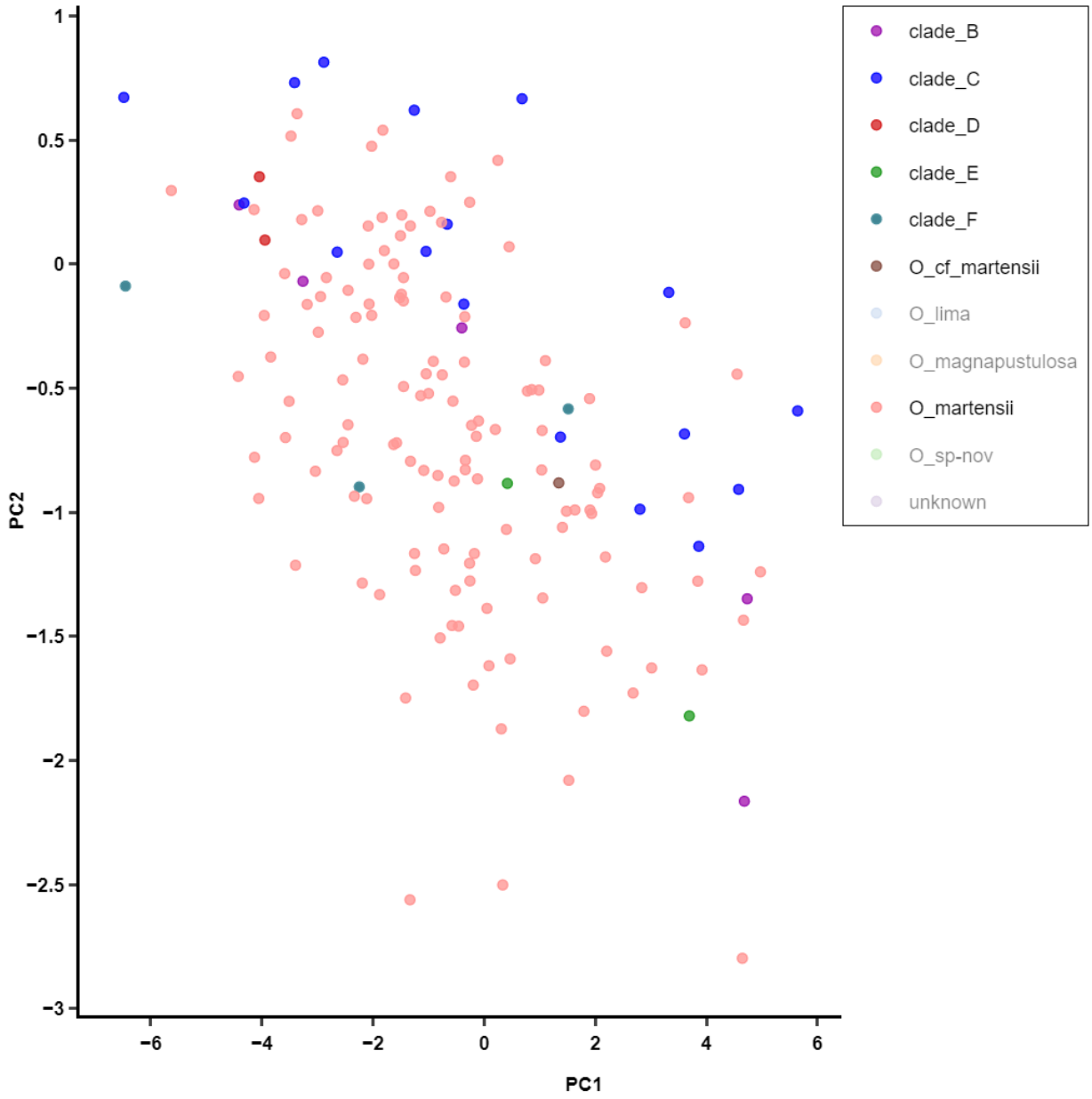

Figure 2: Principal component analysis of twelve morphological measurements for specimens within the *O. martensii* complex. N = 128 *Occidozyga* specimens. PC1 on the x-axis is snout-vent length and PC2 on the y-axis is head length

Even in a PCA analysis where solely the *O. martensii* complex specimens are on display (Fig. 2), there is not strong enough correlation for any of the clades within the complex for any morphological measurement to be an accurate indicator of species. The present morphological diversity within *O. martensii* makes this an impractical method of species identification.

Molecular. —Genetic variation and phylogenetic analyses.

Here we report consensus sequences of forward and reverse reads for 16S, and forward reads for COI and RHOD, as reverse sequencing was not successful for all 47 tissue specimens at both of those two latter loci. This is likely because the primer binding sites for those specimens had been mutated, and not the quality of the DNA liver sample, since some samples sequenced fine for COI but not RHOD and vice versa. After removing gaps, the aligned 16S fragments produced a 669 base pair region; the COI fragments produced a 760 bp region; the concatenated mtDNA fragments produced a 1,332 bp region and the nuDNA RHOD fragments produced a 327 base pair region. The HKY85 model of sequence evolution was selected with jModelTest for all regions. Within *Occidozyga*, the overall average genetic distance was 11.9%-however between *O. lima* and other groups. The among genetic distance showed large net average distances (16%-17%, Table 5). The differentiation between the other clades and candidate clade B was much smaller, only (3.8%-6.9%, Table 5). The unresolved and geographically broad clade that resulted was grouped together to represent the large *O. martensii* complex consisting of clades C, D, and E (Table 5). The Bayesian analyses for both mtDNA regions show the genetic distinction of the Myanmar specimens from confirmed *Occidozyga* species, with moderate (0.75-0.94) to high (0.95-1.00) Bayesian Posterior Probability (bpp) support values at all terminal clades (Figs. 3,Fig. 5, and Fig. 7). The central Tanintharyi clade of specimens are distinct enough to be considered a separate, distinct species from *O. lima*. Maximum Likelihood analyses for mtDNA regions support the Bayesian analyses with less strong support values at the intermediary nodes, but maintained the high support values at terminal nodes (Fig. 4 and Fig. 6)

Overall average genetic distance of COI between species groups analyzed were higher than those for 16S (Table 6 and Table 5 respectively), with *O. lima* being slightly more divergent than *Sylvirana* for the new species from central Tanintharyi. Phylogenetic analyses of the COI region within the *Occidozyga* complex revealed slightly more significant diversity, (p=0.09). Four distinct lineages emerged, with one clade forming three more strongly supported subgroups from the regions of Rakhine, Kachin, and Ayeyarwade (Fig. 5). The nodal probability values are higher for COI than for 16S, and is consistent with the higher genetic distances observed between groups versus in 16S (Table 5); the smallest observed genetic difference for COI results between unconfirmed species (UCS) clade A (9.3%). The new species clade from central Tanintharyi was consistently supported across all three trees (16S, COI and RHO). The *O. lima* clade, indicated in red (Fig. 3,Fig. 5, and Fig. 7), remains persistent across 16S and COI trees and is still present in the RHO tree, although at a far lower (0.51) Bayesian probability (Fig.8). Based on relatedness to *O. martensii* GenBank outgroups, all the new putative species groups appear to be most closely related to *O. martensii* than *O. lima*, which is the most ancestral *Occidozyga* lineage. Within *Occidozyga* the overall average genetic distance for rhodopsin (RHOD) is the lowest of all markers, at 3.8%. Between *Occidozyga* groups the average genetic distances for the RHOD loci only range from 1.7%-7.2% (Table 7). Interestingly, the largest average genetic distance is observed between the new central Tanintharyi species and *O. lima* rather than with the sister *Phlyctimantis* outgroup, which is very similar to *O. baluensis* and clade B. Bayesian analysis of the rhodopsin nucNDA shows far less support for the genetic distinction that clade out consistently for both mtDNA regions, with weak (0.50-0.074 bpp) values separating the clades (Fig. 8).

Table 5: Estimates of Evolutionary 16S Divergence over Sequence Pairs between Groups. The number of base differences per site from averaging over all sequence pairs between groups are shown. The analysis involved 53 nucleotide sequences. All ambiguous positions were removed for each sequence pair. Evolutionary analyses were conducted in MEGA7 (Kumar et al., 2016).

	Ing.	*O. lima*	*O.* sp nov	C	D	E	F	B	*O.marte.*
Ingerana									
O. lima	0.289								
O. sp nov	0.284	0.176							
Clade C	0.280	0.186	0.181						
Clade D	0.274	0.198	0.183	0.058					
Clade E	0.273	0.173	0.159	0.062	0.051				
Clade F	0.277	0.185	0.173	0.057	0.051	0.039			
Clade B	0.279	0.195	0.164	0.074	0.064	0.065	0.068		
O. martensii	0.284	0.183	0.174	0.067	0.070	0.063	0.069	0.055	

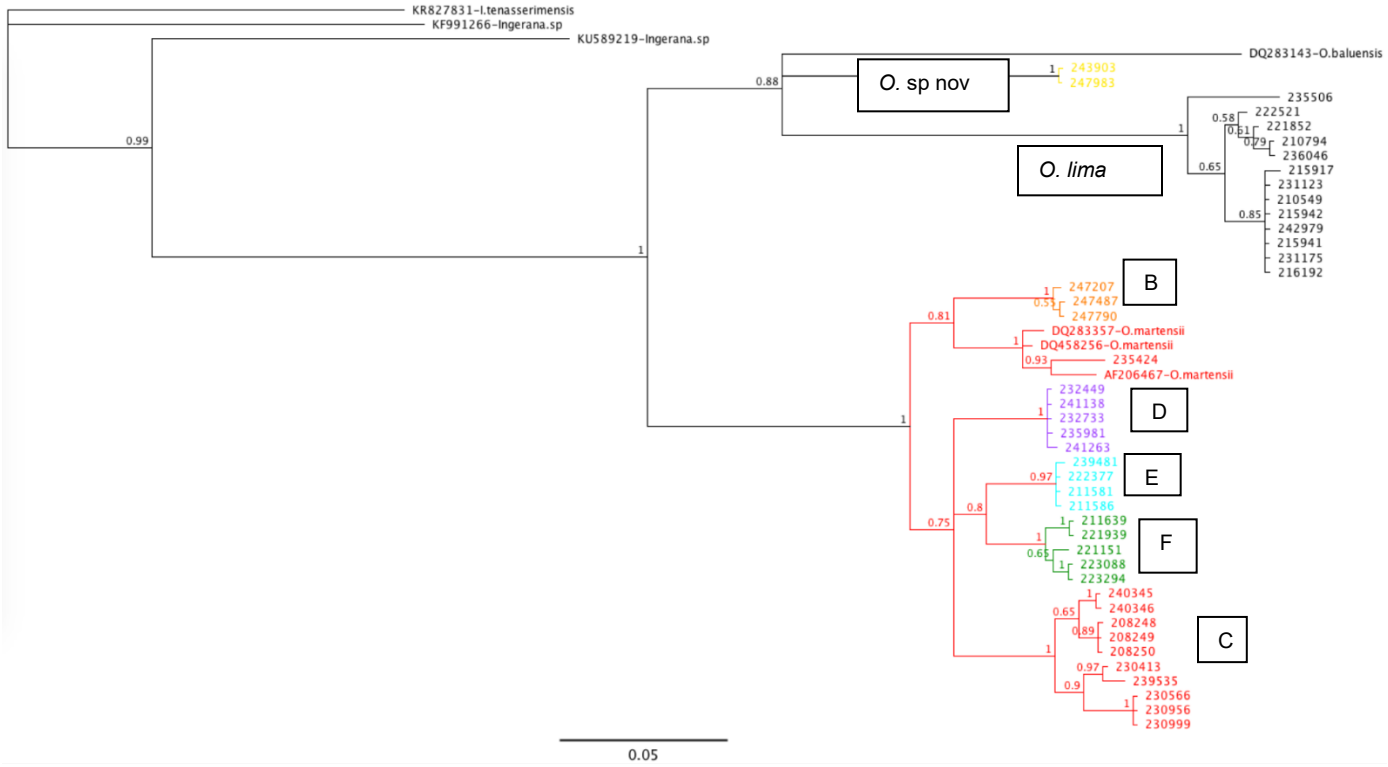

Figure 3: Phylogram of 16S sequenced *Occidozyga* specimens from Myanmar. Compared to GenBank data from known *O. martensii*, *O. baluensis*, and *Ingerana* sp. individuals. Individuals are identified by their sample ID number or by their sourced GenBank ID. Four unique lineages which largely cluster based on geographical region are highly supported, with one lineage comprised of three unconfirmed putative species. The clade of specimens from central Tanintharyi is distinct from the *O. lima* clade and represents a separate species.

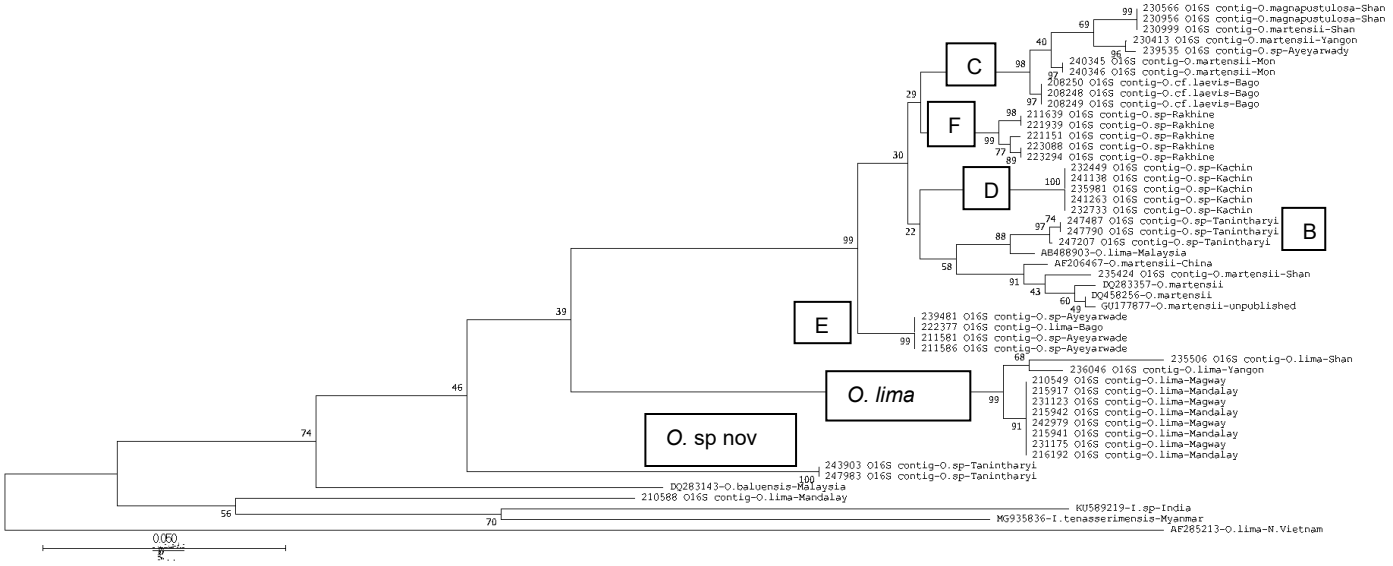

Figure 4: Molecular Phylogenetic analysis of 16S locus by Maximum Likelihood method. The evolutionary history was inferred by using the Maximum Likelihood method based on the Tamura-Nei model. The tree with the highest log liklihood is shown. The percentage of trees in which the associated taxa clustered together is show next to the branches. Initial tree(s) for the heuristic search were obtained automatically by applying Neighbor-Join and BioNJ algorithms to a matrix of pairwise distances estimated using the Maximum Composite Likelihood (MCL) approach, and then selecting the topology with superior log likelihood value. The tree is drawn to scale, with branch lengths measured in the number of substitutions per site. The analysis involved 51 nucleotide sequences. All positions containing gaps and missing data were eliminated. Evolutionary analyses were conducted in MEGA 7.

Table 6: Estimates of Evolutionary COI Divergence over Sequence Pairs between Groups. The number of base differences per site from averaging over all sequence pairs between groups are shown. The analysis involved 53 nucleotide sequences. All ambiguous positions were removed for each sequence pair. There were a total of 727 positions in the final dataset. Evolutionary analyses were conducted in MEGA7 (Kumar et al., 2016).

	O. lima	*Sylvirana*	*O.* sp nov	B	E	F	D	*C/ O. martensii*
O. lima								
Sylvirana sp.	0.275							
O. sp nov	0.265	0.257						
Clade B	0.282	0.296	0.245					
Clade E	0.285	0.275	0.220	0.207				
Clade F	0.288	0.280	0.223	0.209	0.094			
Clade D	0.269	0.290	0.233	0.181	0.166	0.151		
Clade C/ *O. ma*	0.302	0.297	0.274	0.206	0.191	0.185	0.150	

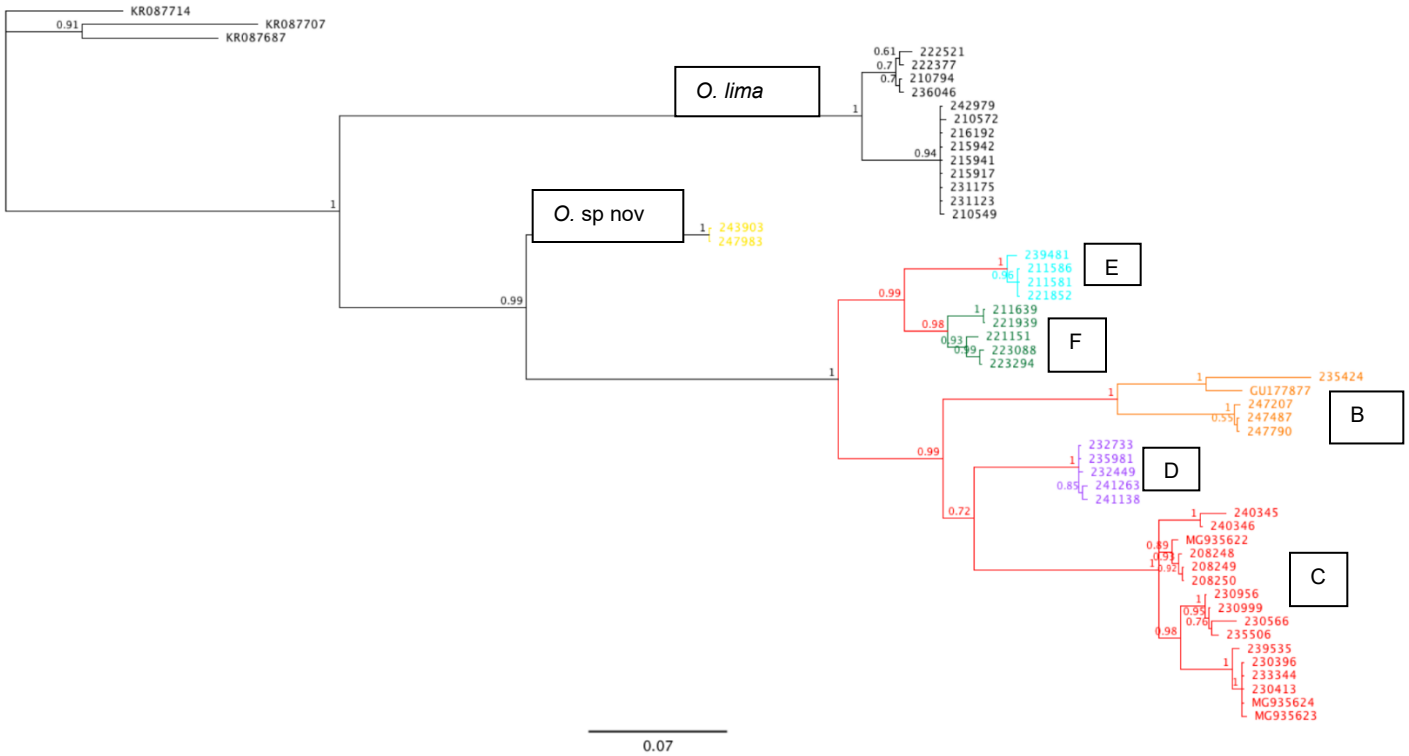

Figure 5: Phylogram of *Occidozyga* COI sequenced specimens from Myanmar. Compared with GenBank data from known *O. martensii*, *O. sp.*, and *Sylvirana sp*. individuals. Four unique lineages which largely cluster based on geographical region are highly supported and are supported by the clading of 16S (Fig. 3). The clade of specimens from central Tanintharyi is distinct from the *O. lima* clade and represents a separate species.

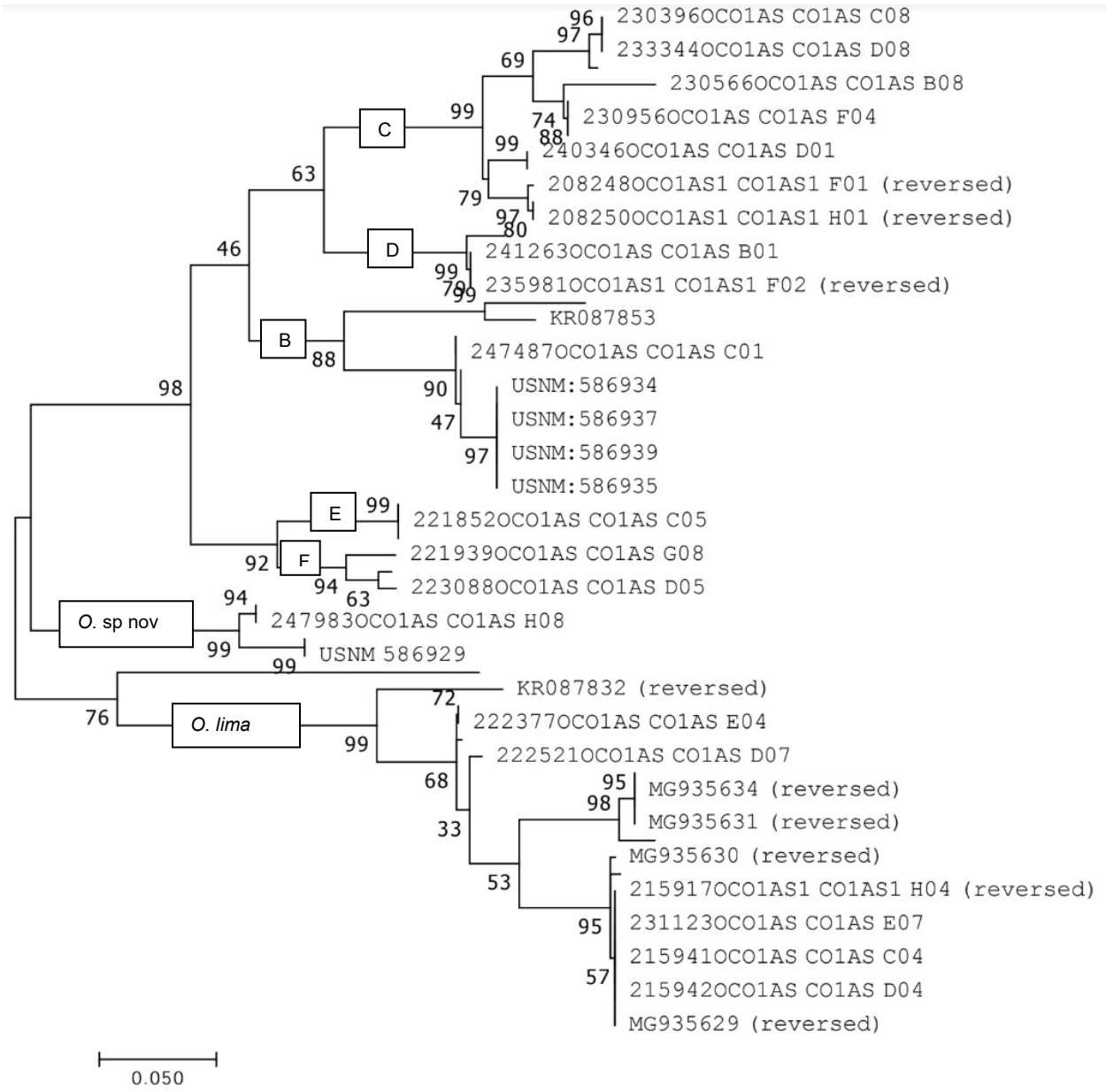

Figure 6: Molecular Phylogenetic analysis of COI locus by Maximum Likelihood method.
The evolutionary history was inferred by using the Maximum Likelihood method based on the Tamura-Nei model. The tree with the highest log likelihood is shown. The percentage of trees in which the associated taxa clustered together is shown next to the branches. Initial tree(s) for the heuristic search were obtained automatically by applying Neighbor-Join and BioNJ algorithms to a matrix of pairwise distances estimated using the Maximum Composite Likelihood (MCL) approach, and then selecting the topology with superior log likelihood value. The tree is drawn to scale, with branch lengths measured in the number of substitutions per site. The analysis involved 53 nucleotide sequences. All positions containing gaps and missing data were eliminated. Evolutionary analyses were conducted in MEGA7

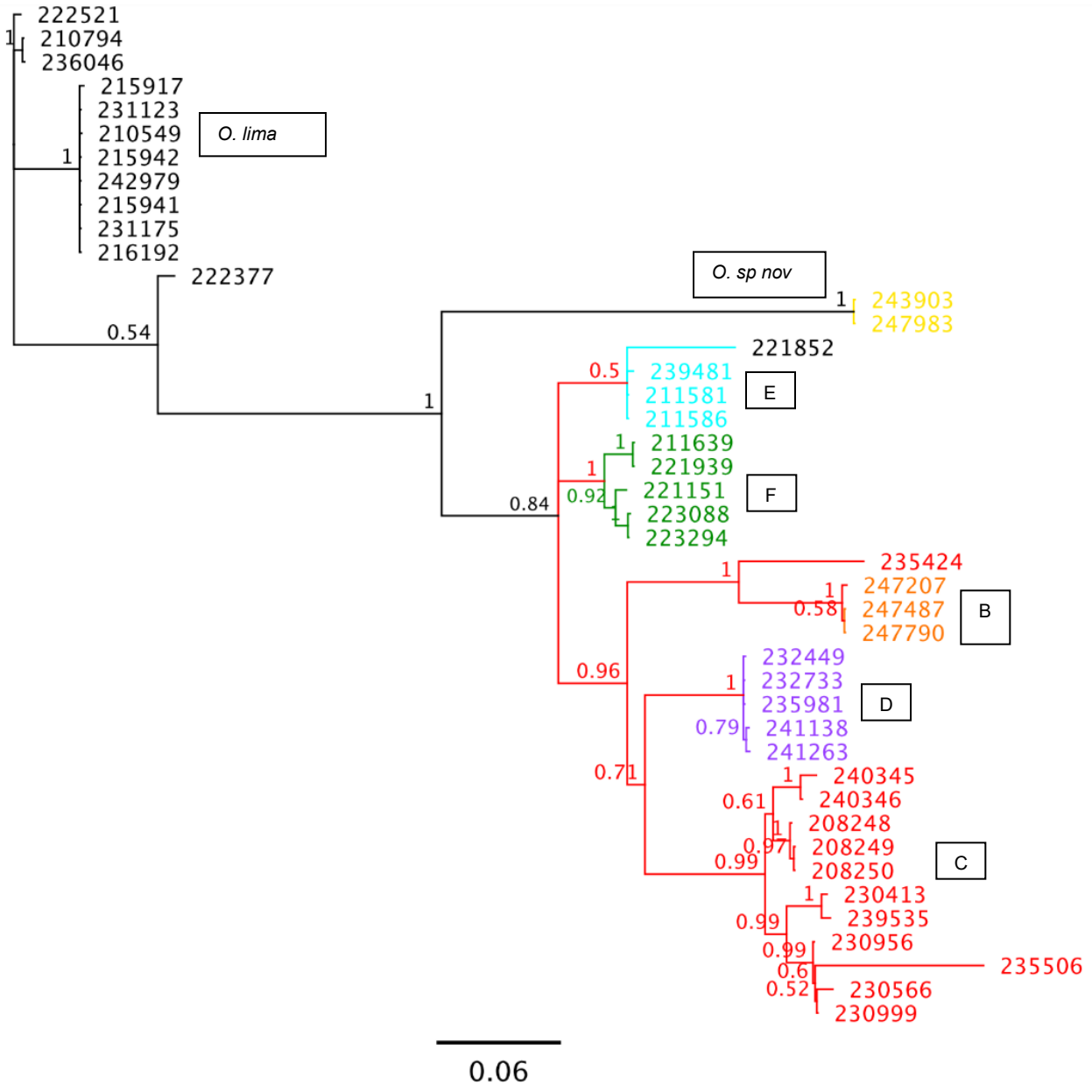

Figure 7: Phylogram of *Occidozyga* sp. resulting from Bayesian inference of the concatenated mitochondrial data (COI, 16SrRNA). Nodal support values are Bayesian posterior probabilities. Numbers at terminals correspond to Sample IDs in Table 1. The capital letters (B-F) above branch nodes correspond to putative Clade IDs in Fig. 3, and Fig. 4.

Table 7. Estimates of Evolutionary RHOD Divergence over Sequence Pairs between Groups. The number of base differences per site from averaging over all sequence pairs between groups are shown. The analysis involved 52 nucleotide sequences. All ambiguous positions were removed for each sequence pair. There were a total of 491 positions in the final dataset. Evolutionary analyses were conducted in MEGA7 (Kumar et al., 2016).

	O. martensii	*O. lima*	*P.boulengeri*	*O.* sp nov
O. martensii				
O. lima	0.072			
P. boulengeri	0.049	0.055		
O. sp nov	0.039	0.045	0.029	0.017

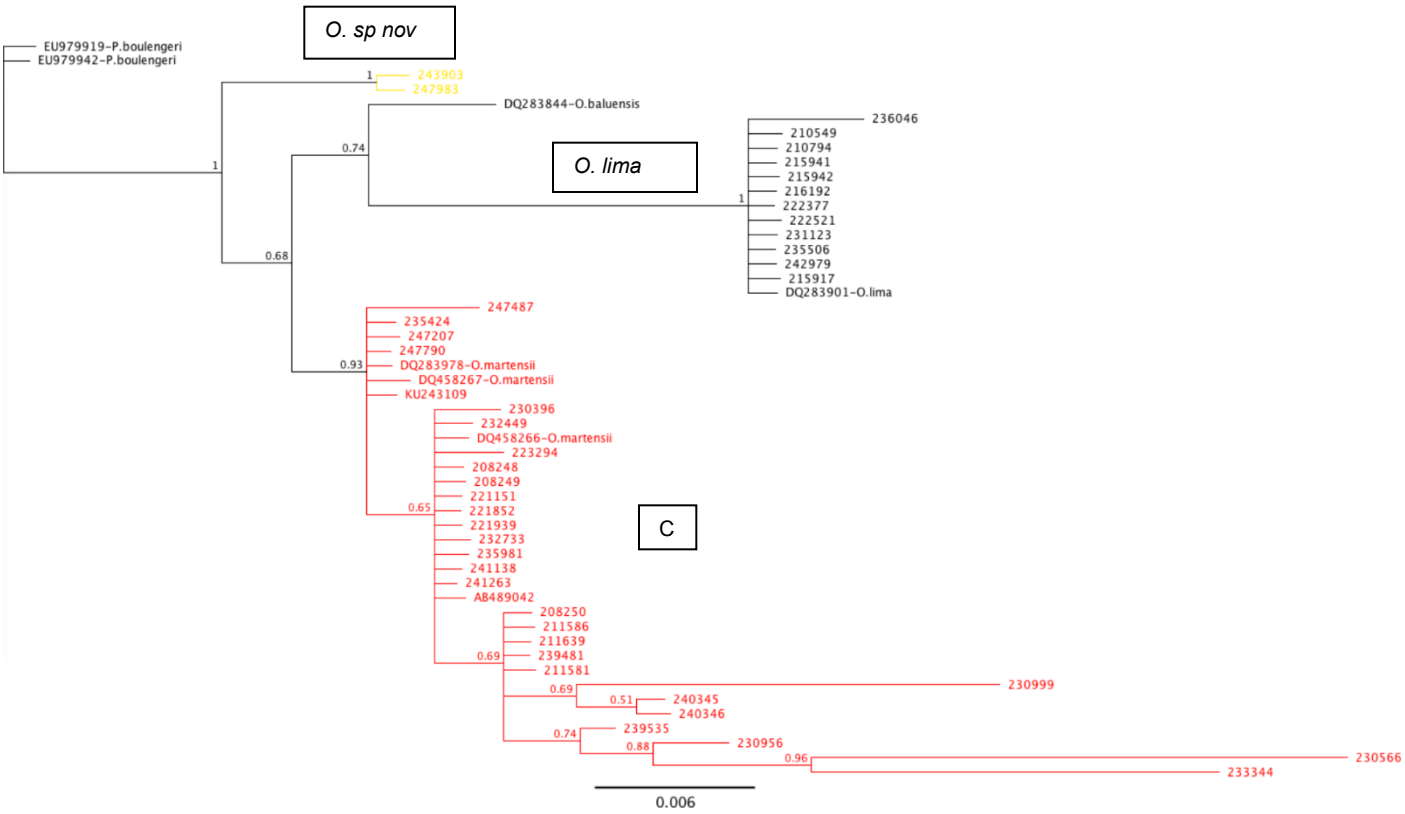

Figure 8: Phylogram of *Occidozyga* sp. resulting from Bayesian inference of the nuclear gene data (RHOD). Outgroup is composed of *Phlyctimantis boulengeri* GenBank specimens. Nodal support values are Bayesian posterior probabilities. Numbers at terminals correspond to Sample IDs in Table 1. The high mutation rate, fast coalescence time owing to a small effective size and matrilineal inheritance make mtDNA more likely to track lineage divergence than any single nuclear gene such as RHOD could and is thus a relatively leading molecular indicator of population differentiation. This RHOD phylogram does indicate that in terms of deep-level phylogeny there has not been much divergence versus the divergence seen given the mitochondrial populations in each region of Myanmar. The clade for new species from central Tanintharyi is still present and consistent with their position in both mitochondrial trees and confirms it as a candidate species.

The individuals from central Tanintharyi represent a novel species based upon the congruency among all three molecular markers. When analyzed with additional taxa from the region provided by Mulcahy (pers. Comm.) the support values increased significantly. The new species is morphologically identical to *O. martensii* having a small body (SVL 17.77-31.11mm); lacking small spiculate tubercles covering the entirety of the dorsum; incomplete webbing of the

hindtoes; vent stripe absent; distinct dorsal spots absent; dorsum sparsely covered with granular but not spiculate tubercles; dark, wide dorsal midline stripe present; v-mark on ventral jaw absent but patchy color on edges; pelvic v-mark absent; banding pattern on hindlimbs present but indistinct; short dark brown patches in axillary region absent; stripe across the ventral lateral edge of both hindfeet present but less distinct; pale ventral belly with weakly speckled ventrolateral margins (Fig. 9 and Fig. 10).

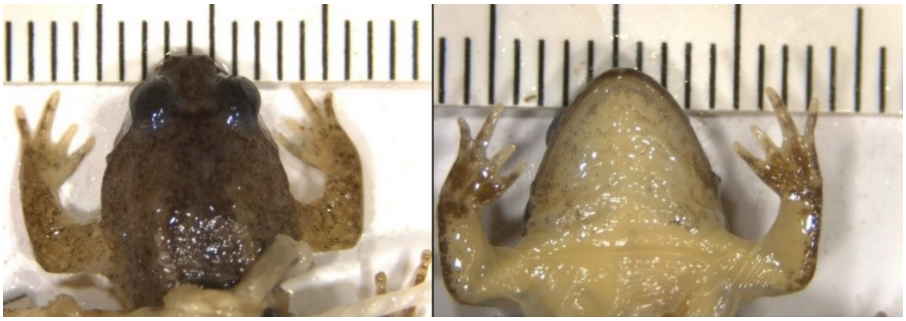

Figure. 9: Specimen CAS 247983 ventral (left) and dorsal (right) views of cranial and axillary regions. Images of novel species from central Tanintharyi.

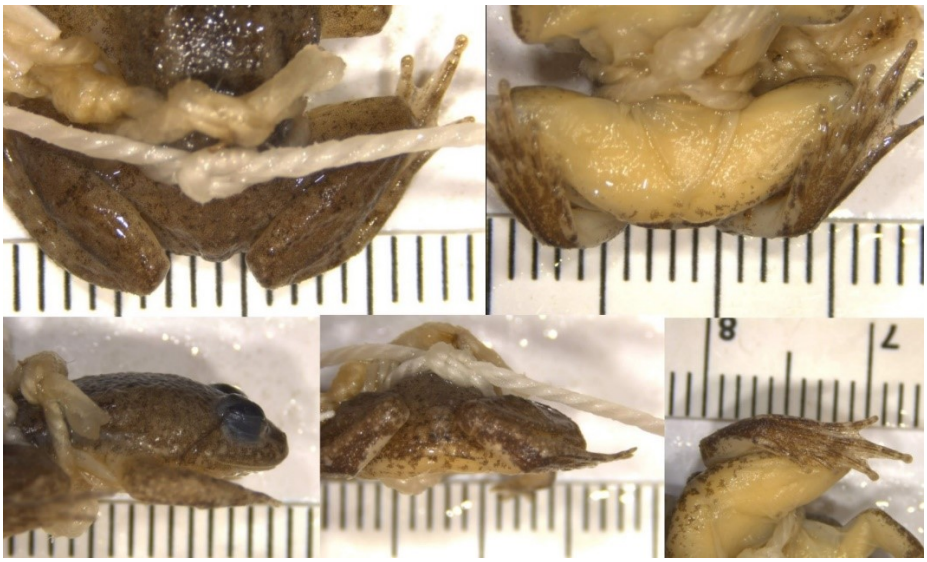

Figure 10**:** Specimen CAS 247983 dorsal and ventral views. Clockwise from top left image; Dorsal view of caudal region, ventral view of caudal region, ventral right hindfoot, posterior vent region, sagittal view of right side. Images of novel species from central Tanintharyi.

Geographic Distribution*:* This novel species is known from two localities in Tanintharyi Division, Myanmar ~11 km apart, with elevations ranging from 82 m to 162 m. The holotype collection locality was in the H3 [Eithe] stream, Tanintharyi Nature Reserve, Yebyu Township, Tanintharyi Division, Myanmar at an elevation of 162 m.

Phylogeography. —

The pattern of distribution observed in the phylogeographic analysis of the 16S tree is shows the *Occidozyga* evolutionary differentiation throughout Myanmar has been directly impacted by the geographic history of Myanmar (Fig. 11 and Fig. 12). The Ayeyarwady Basin is a wide, massive, elongate floodplain of approximately 404,200 square km that extends nearly the entire length of non-peninsular Myanmar and separates the vast, mountainous Shan Plateau in the east from the rugged Chin Hills in the west (Fig. 12). A complex series of foothills associated with these upland areas delimit the eastern and western fringes of the Ayeyarwady Basin and the relatively featureless floodplain itself is punctuated by a series of isolated, north-south tending, mountainous ridges and low hills (Grismer et al., 2019). Populations representative of *O.martensii* clade C show lineages that are concentrated in Rakhine, showing isolation on the western side of the Kachin Hills in northern collection sites but have been able to extend their range into the Ayeyarwady Basin beneath the southernmost point of the Chin hills. While individuals of *O. lima* (blue)*,* and clade E Ayeyarwade were observed to extend throughout the lower confines of the Ayeyarwady Basin floodplain, the individuals of clade D of Kachin all cluster tightly in the uppermost region of the basin without extension areas where the aforementioned populations were interspersed. While the novel species from central Tanintharyi

is observed to be limited to a small region in Tanintharyi, specimens of clade B appears to have been able to extend its evolutionary lineage to the southernmost tip of Myanmar in Tanintharyi. Within clade B the elevation barely ranges from CAS 247790 for the holotype at 21 m down to just 8 m of elevation. From the ecoregion mapping in Fig. 12, we see that the *O. martensii* complex clades observed in Fig . 11 are each constrained to generally one to two ecoregions respectively and are different from the other clades. The novel central Tanintharyi *Occidozyga* species sits squarely in the Tenasserim semi-evergreen tropical rainforests, while *O. lima*- its most closely related ancestor- is primarily dispersed throughout the Irrawady Basin's moist or dry deciduous forests with an outlier in the east and two specimens extending from the southern border of the Irrawady Basin. Clade B in orange resides in either the Tenasserim rainforest or the N. IndoChina subtropical forests. Clade C, representative of voucher *O. martensii* specimens, have a broader range of ecoregions it can occupy and tends to occupy intermediary ecoregion zones to the south and east of the Irrawady Basin. Clade D of the Rakhine region in green is restricted to Myanmar's coastal rainforests, while Clade E in light blue (partially obscured by *O. lima* and *O.martensii* specimens) occupies the Irrawady freshwater swamps and coastal mangrove regions. The most northern, Clade F specimens are all tightly clustered in the Mizoram-Manipur rain forests of Kachin.

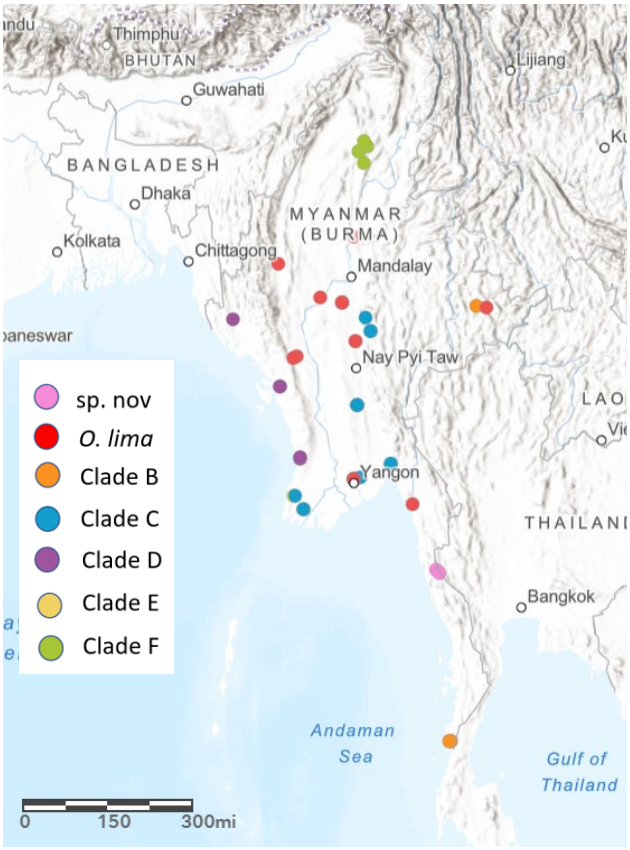

Figure 11: Topographical map of *Occidozyga* within Myanmar. Distribution of the species of the Occidozyga group specimens 1-47 sequenced for this study with respect to the mountain ranges and lowlands. Three major clades in the legend (A-C) and *O. lima* correspond to those identified in mtDNA phylogenies (Fig. 1; Fig. 2; Fig. 3). Locality coordinates in latitude and longitude form at time of collection can be found in Appendix II.

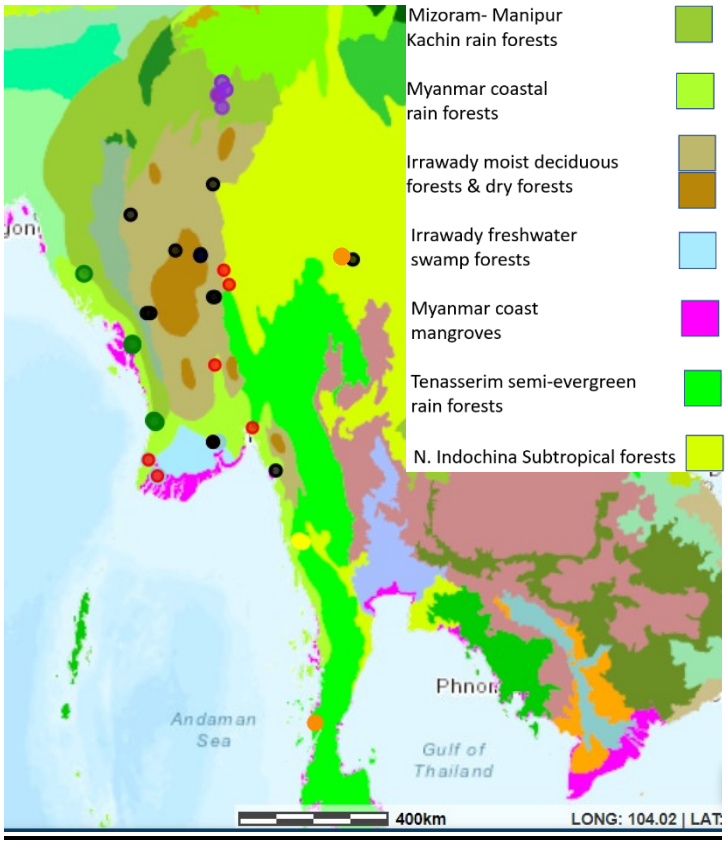

Figure 12: Ecoregion map of *Occidozyga* within Myanmar. Distribution of the species of the Occidozyga group specimens 1-47 sequenced for this study. Note here, the novel Occidozyga species is in yellow, *O. lima* in black, Clade B in orange, Clade C in red, Clade D in green, Clade E in light blue (obscured by an *O. lima*) , Clade F in purple.

III. Discussion

Most cryptic congeners in the genus *Occidozyga* are difficult to distinguish from each other due to the superficial similarities in morphology. To solve this problem, extensive sampling with careful and robust diagnoses are required to uncover the cryptic diversity of the genus. Specifically *O. martensii* harbors great diversity and each of the distinct lines of evidence provided herein (morphological, molecular, and phylogeographic) supports the recognition of a putative cryptic species from central Tanintharyi that is most closely related to *O. lima* and a high amount of genetic diversity within the *O. martensii* complex with phylogeographic patterning that match likely pathways of evolutionary radiation around the mountains of the region. The genetic distance data and constructed phylogenetic trees (with sequenced NCBI DNA included from known *Occidozyga* species) strongly suggest the existence of at least six unidentified candidate species within this group that are highly divergent in both 16S and COI. The results from this study illustrate the ambiguity of parsing taxonomy and distributions based on distinctive morphological differences present in *Occidozyga*.

While there is strong support for the variance in snout-vent length being a reliable morphological indicator of whether a specimen is of *O. lima* or *O. martensii* lineage via PCA, no other morphological measurements tested were features that were statistically strong enough for distinguishing the novel putative species and lineages, nor distinguishing between established species. The lack of sufficient clustering and similarity between traits is indicative of and reaffirms that this species complex is indeed cryptic, where quantitative morphology alone is not sufficient for proper identification of these specimens. This is especially true considering there are multiple *O. martensii* related lineages as well as sp. A being more closely related to *O. lima.*

There are no clear distinguishing factors between *O. martensii* complex candidate types using morphology as the defining characteristic.

Based on the present information, it is likely that even more additional undescribed species within this group exist and may be uncovered with increased sampling frequency from additional regions of Myanmar. Mulcahy et al. (2018), observed similar patterns of tri-clustering within the genus- which also were distinct from *O. martensii* and *O. lima*- which they suggest are significantly different sub-species. These cryptic species are morphologically indistinguishable, yet credible molecular, and phylogeographic evidence exists which suggests that they represent evolutionarily distinct lineages. Due to this morphological crypsis, it will likely be necessary that additional species complexes, such as those already seen in Myanmar, need to be discovered and diagnosed using a multitude of data formats such as DNA sequences, evidence of reproductive isolation (e.g. whether ecological or bioacoustic), and morphological comparison (Castroviejo-Fisher, et al., 2017) in other neighboring countries. Recent work by Cryer et al. (2019) has successfully advocated for the status of just one species, *Lithobates warszewitschii,* as a candidate cryptic species complex, based primarily on sequence data from mitochondrial genes COI and 16S. Using concatenated phylogenies, nucleotide diversity (K2P-π), net between group mean distance (NBGMD) (πnet) and species delimitation methods, they were able to further reveal cryptic diversity within this species. Cryer et al. also found that patterns of phylogeographic structure did not appear to be explained by geographic barriers or isolation by distance, suggesting that *L. warszewitschii* is a wide-ranging species complex. This could help to support the divergence that is occurring within Myanmar in the Irrawady basin or in the regions where the species niches overlap or where hybrid zones may be occuring. Conversely, research by Gao et al. (2019) on Dicroglossidae *Quasipaa shini*, which is distributed across southcentral

China, utilized mitochondrial COI gene sequences, haplotype network, AMOVA and genetic distance estimations to establish support for separations into six phylogroups. *Q. shini* is commonly found in the mountain streams at 510–1500 m elevation in south-central China, ranging all the way from the northern Guangxi, Guizhou, extreme southern Hunan, to southern Chongong provinces (Fei et al. 2012). Across this region, tall mountains (e.g. Nanling Mountains and Dayao Mountains) and deep valleys (e.g. major distributaries of Zhujiang River) were expected to promote genetic diversification, especially in amphibians (Che et al. 2010). Based on their results, they proposed that at least the one clade out of their six phylogroups should represent a cryptic species. The very similar topography of Myanmar and the way in which the phylogroup clades/subclades conform to location for another Dicroglossidae family species is strikingly similar to that of *Occidozyga* despite the difference in species and the precise region of study, and could possibly explain the mitochondrial divergence observed between clades that had strong correlations to the ecoregion they inhabit and explain why the complex has evolved to occupy many ecoregions.

The combination of low levels of nuclear genetic diversity but extensive mitochondrial and phylogeographic structure within *O. martensii*- with unsubstantial morphological variation- is perhaps best explained by more localized adaptations to variance in environmental settings, ecophenotypic plasticity, previous genetic bottlenecks and/or continuing small population sizes (Nussbaum and Wu, 1995). If the phylogeography and molecular clock for the genus is further explored, it would be possible to further determine how relatively recently they have diverged from each other. If the most recent divergences are within the *O. martensii* complex, it could be further evidence to support a genetic framework that is influenced by recent anthropogenic induced ecosystem and ecoregion modification (see Fig. 12). Currently, *Occidozyga* is thought

to have originated on the Indian subcontinent and then dispersed to and diversified within Southeast Asia, subsequent to the Indian subcontinent's collision with Eurasia about 35 mya (Duellman & Trueb 1994; Bossuyt & Milinkovitch 2001; Bocxlaer et al. 2006). *Occidozyga* would have then evolved further from an ancestor that arrived on the mainland, later spreading to Sundaland in the south (Duellman & Trueb 1994). Bossuyt et al. (2006) later estimated the divergence time of the Ranoidea superfamily, finding that the genus *Occidozyga* (O. lima and O. laevis being established as earliest lineages) diverged sometime in the late Oliocene period, c. 23 mya. This period was when mainland Asia was undergoing the pressing out of the Indochina block while the Burmese block was forced northward and there met with the Indian plate (Hall 2002). Myanmar was far more near to Southern Indochina at the estimated time *Occidozyga* would have begun to diverge than its current geographical orientation. These hypotheses may explain the results of this study which found that all *O. martensii* complex clades (B- F) formed sister lineages despite being largely separated geographically. Furthermore, the physical geography and geologic history strongly indicates that Southern Indochina and Myanmar originally belonged to the same biome, the Southeast Asian Lowlands (Inger 1999).

For the *Occidozyga* species complex, this study was limited to analysis of morphological and molecular traits which can be observed and tested from pre-collected museum collection specimens. More recently observed and collected specimens in life will still be necessary to further investigate the populations within these geographic ranges that appear to be endemic, while remaining amendable to reconciling the lineages of the present with more historical data sets and descriptions. These three resulting phylogenies could naturally and logically be further supported by extensions of field work in Myanmar to better establish true species ranges for sufficient habitat protection with increased sampling for each region that *Occidozyga* occupy

within the Ayeyarwady Basin. Recent discussions of conservation efforts in Myanmar have primarily been focused on hills, caves, and tower formations (Grismer et al, 2019). This study and many other pending studies, however, add to a growing foundation of data suggesting that the Ayeyarwady Basin should be incorporated into more ongoing discussions of conservation as it accounts for almost one-half of the total area of the country and is currently serving as a hospitable refuge for an ever-increasing number of endemic species of reptiles and amphibians (Wilkinson et al. 2014; Connette et al. 2017; Mulcahy et al. 2017; Lee et al. 2018).

National Biodiversity Strategies and Action Plans (NBSAPs) are developed by the IUCN based on information of known and documented species and their associated standing on the IUCN's red list of threatened species (IUCN, 2015). While the criterion and accuracy of IUCN's listings are already problematic, the issue is further exacerbated by inaccurate or incomplete species surveys (Webb, 2008). Application of biodiversity hotspots occurs via discrete measurements of biodiversity, as opposed to evaluation of candidate regions over time (Myers et al., 2000; Wallington et al., 2005; Willis et al., 2007; Piacenza et al., 2015), has resulted in biases towards potential 'hotspot' areas that exhibit higher biodiversity during those most critical initial periods of assessment. Unfortunately, this creates designations of hotspots without a true reflection of preexisting conditions (i.e. cyclical or periodic perturbances that temporarily deflated or inflated the appearance of biodiversity), nor considers the effects of continued anthropogenic change in the area. Additionally, the thresholds of biodiversity used to designate biodiversity hotspots are quite frequently user-constructed or set arbitrarily and rarely based on ecological data collected long-term within the candidate region (Kareiva and Marvier, 2003).

The ongoing development of phylogenetic approaches has led to a proliferation of metrics for measuring phylogenetic diversity (Tucker et al., 2017). The use of many separate and

ununified metrics over time across the discipline has dampened the statistical power of potential meta-analyses, syntheses, and generalizations of existing results that are critical for conservation management efforts. Reconciling phylogenetic relationships established from the past into accurate and reliable trees and divergence timescales for use in the future has become the new challenge for conservationists, especially since anurans are often used as model organisms to address fundamental issues of morphological, developmental, and biogeographical evolution (Bryne et al., 2003; Evans et al., 2004; Liu et al., 2016; Chan and Brown, 2017). Thus, accurate taxonomic recognition is a prerequisite for preserving amphibian biodiversity, given the context of amphibian declines and extinctions occurring worldwide due to anthropogenic induced perturbations (Stuart et al., 2004).

Reliance on variations in phenotype and morphology alone for species delimitation has shifted from being the only evidence required, to being only a supportive piece of evidence in combination with genetic, geographic and bioacoustic analysis. Phylogenetic analysis conducted by Tarvin et al. (2017) of Dendrobatid poison frogs found low levels of genetic divergence (2.6% in the 16S gene) despite substantial differences in coloration, suggesting that historical claims of species diversity may be artificially inflated for aposematic amphibian species (Tarvin et al., 2017). The *Occidozyga* specimens sequenced have a relatively higher level of 16S genetic divergence at 17.8%, while conversely possessing very little substantial differences in coloration and morphology- indicating that the complex will likely not be well resolved or well conserved if traditional morphospecies concepts are relied upon. Without combination of delimination methods for species identification and use of a consolidated-species concept to guide the process, there is an enormous potential for a vast number of *Occidozyga* species or subspecies which may currently be ‘cryptic’ to remain unnoticed and unaccounted for. Not only could they be omitted

from the taxonomic and phylogenetic records, but cryptics would then be overlooked when efforts towards conservation of amphibian biodiversity in their native region occur (Angulo and Icochea, 2010; Vieties et al., 2009; Bell et al., 1998). As records stand now, *O. martensii* and *O. lima* are thought to be quite numerous and are not under any form of protection (IUCN, 2017). However, severe issues in systematics and conservation efforts can occur when morphological characters either do not reflect genetic diversity or are grossly misleading. Misidentifications not only inflate range estimates, but also lead to inaccurate niche models (Aubry et al., 2017). The exponential radiation of rhacophorine frogs in Sri Lanka provides a prime example, as an integrative taxonomic study using morphological, ecological, bio acoustical, and genetic data increased the number of species from a mere 18 to over 100 (Meegaskumbura et al., 2002). Since these species counts and population estimates depend on the species concepts applied and/or chosen molecular markers, biodiversity surveys are likely yielding extremely divergent results for the biodiversity actually present in that same habitat. Surveys using the morphospecies concept for instance can result in lower species counts than surveys based solely on environmental DNA. Biological species concepts effectively cannot be assigned at all in most biodiversity surveys, since this would require DNA extraction, processing, and sequencing in the field.

Future directions for research of this genera would require more "boots on the ground" in order to sample more specimens- especially to garner tissue- more intensively from the unsampled states and divisions within Myanmar, and even still from within some of the regions in this analysis to further bolster a specimen count for the novel species. Sample sizes are still moderately low per region and many were taken from sites within the respective division that were not very far away from each other. Ideally, each division/state should be given a proper

biodiversity analysis in order to most accurately conduct a taxonomic revision of the genus and would involve a multi-year field study whereupon a more detailed natural history for these specimens and information on population density could be assessed, including collecting bioacoustic call data and observation of mating of specimens or tadpole development. Capturing images of these different emerging clades in life could only benefit further recognize and conserve the diversity within this genus.

However, this study is the first of its kind for *Occidozyga* with respect to conducting a broad country-wide genetic analysis with a relatively large sample size for morphological analysis of the 'cryptic-ness' of the genus. Field work in Myanmar would allow for bioacoustic analysis which could be revealing of any reproductive isolation that might be occurring between species, as well as monitoring during mating season for any possible hybridization between species or candidate species in contact zones. Additionally, more molecular work would be beneficial to test more mitochondrial and nuclear loci within their genome to see if they further support the phylogenies resulting from our analysis.

V. Concluding Remarks

In conclusion, allocations of funding and resources that are based on numbers of threatened species may be inaccurately distributed elsewhere if taxonomic records are not a true reflection of the diversity of anurans that are currently extant. Morphological systematics in tandem with molecular genetics has a great advantage in its suitability to the large-scale museum collections of preserved specimens (Hillis, 1987), especially since a sizable percentage of anuran species are on the verge of going extinct and can only be studied through preserved collections (Ponder, 2001). Today, many species are protected through rare species conservation acts that

prohibit DNA sample collections to take place, or the DNA samples are too difficult or costly to collect. The study of comparative anatomy has been the foundation for essentially all species identifications up until the modern era, and the addition of molecular findings may provoke greater conservation implications for the 'common puddle frogs' of *Occidozyga* since each newly discovered, genetically distinct group's distribution is more reduced than once conceived and, hence, all the more perilous to maintain. This is especially true given that the populations' natural ranges appear to be constrained due to geographic isolation- whereas many original cryptic frog species complexes initially had broad geographical ranges- the actual biological species in those complexes have far more limited ecological distributions, making each more prone to extinction. Therefore, we support the recognition and protection of these distinct evolutionary lineages as evolutionary significant units (ESUs) in order to best preserve the genetic diversity within each clade and the diverging evolutionary trajectories upon which they are on, as well as suggesting further in the field study of this genus to determine if interbreeding may be taking place between them *in situ*. Genetic diversity serves as a critical way for populations to adapt to changing environments, whether it be an anthropogenic change (deforestation or climate change), novel diseases, or change based on a purely abiotic factor. By maintaining and preserving more variation, it becomes far more likely that some individuals within any given population will possess some variations of alleles that are better suited for the changing environment and landscape. Those individuals are more likely to survive to produce offspring bearing that beneficial allele or set of genes and the population will have a better chance of continuing for more generations because of the success of these individuals within their lineage. An important consideration in species conservation efforts is to avoid having to manually create and maintain high genetic diversity in a given genus or population, in order to

not have to rely on species rescue efforts to ensure the longevity of a species contributing to its ecosystem. Although much of the rainforest has already vanished from most of Southeast Asia, Myanmar can still take crucial action to preserve one of the most biodiverse places on Earth as a whole by preserving each of the members of its ecosystems as individuals.

Increasing global disturbance and destruction of natural ecosystems are accelerating catastrophic-level extinctions of species (Brook et al., 2006). Given that many species remain undescribed, efforts being made to both catalogue and explain the necessity of biodiversity need to be prioritized; investigating novel speciation mechanisms, planning conservation given new data on novel cryptic species, and updating taxonomic, regional and global diversity indices are worthwhile avenues for future research.

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Appendices:

Appendix I: Samples of *Occidozyga sp.* and outgroups used in molecular analysis.
Sequences generated for the present study are samples indicated by the ID 1-47, with the other sequences downloaded from GenBank; N/A indicates that data is lacking for that gene of the taxon. The museum abbreviations for the sequenced samples are CAS, California Academy of Sciences; USNM, Smithsonian Natural History Museum; FMNH is Field Museum of Natural History; AMNH, American Museum of Natural History; SCUM, Zoological Museum of Sichuan University; YNU, Yunnan University.

Sample ID	Clade Original	Voucher Tissue ID	Locality	GenBank No.		
				16S rRNA	COI	RHOD
1	*O. cf. laevis*	CAS 208248	Bago, Myanmar	N/A	N/A	N/A
2	*O. cf. laevis*	CAS 208249	Bago, Myanmar	N/A	N/A	N/A
3	*O. cf. laevis*	CAS 208250	Bago, Myanmar	N/A	N/A	N/A
4	*O. lima*	CAS 210794	Yangon, Myanmar	N/A	N/A	N/A
5	*O. sp.*	CAS 211581	Ayeyarwade, Myanmar	N/A	N/A	N/A
6	*O. sp.*	CAS 211639	Rakhine, Myanmar	N/A	N/A	N/A
7	*O. lima*	CAS 215917	Mandalay, Myanmar	N/A	N/A	N/A
8	*O. lima*	CAS 216192	Mandalay, Myanmar	N/A	N/A	N/A
9	*O. sp.*	CAS 221939	Rakhine, Myanmar	N/A	N/A	N/A
10	*O. lima*	CAS 222521	Mon, Myanmar	N/A	N/A	N/A

11	*O. sp.*	CAS 223294	Rakhine, Myanmar	N/A	N/A	N/A
12	*O. martensii*	CAS 230396	Yangon, Myanmar	N/A	N/A	N/A
13	*O. magnapustulosa*	CAS 230566	Shan, Myanmar	N/A	N/A	N/A
14	*O. lima*	CAS 231123	Magway, Myanmar	N/A	N/A	N/A
15	*O. lima*	CAS 231175	Magway, Myanmar	N/A	N/A	N/A
16	*O. sp.*	CAS 232449	Kachin, Myanmar	N/A	N/A	N/A
Sample ID	Species	Voucher Tissue ID	Locality	GenBank No.		
				16S rRNA	COI	RHOD
17	*O. sp.*	CAS 232733	Kachin, Myanmar	N/A	N/A	N/A
18	*O. martensii*	CAS 233344	Yangon, Myanmar	N/A	N/A	N/A
19	*O. martensii*	CAS 235424	Shan, Myanmar	N/A	N/A	N/A
20	*O. lima*	CAS 235506	Shan, Myanmar	N/A	N/A	N/A
21	*O. sp.*	CAS 235981	Kachin, Myanmar	N/A	N/A	N/A
22	*O. lima*	CAS 236046	Yangon, Myanmar	N/A	N/A	N/A
23	*O. sp.*	CAS 239481	Ayeyarwade, Myanmar	N/A	N/A	N/A
24	*O. sp.*	CAS 239535	Ayeyarwade, Myanmar	N/A	N/A	N/A
25	*O. martensii*	CAS 240345	Mon, Myanmar	N/A	N/A	N/A
26	*O. martensii*	CAS 240346	Mon, Myanmar	N/A	N/A	N/A
27	*O. sp.*	CAS 241138	Kachin, Myanmar	N/A	N/A	N/A

28	*O. sp.*	CAS 241263	Kachin, Myanmar	N/A	N/A	N/A
29	*O. lima*	CAS 242979	Magway, Myanmar	N/A	N/A	N/A
30	*O. sp.*	CAS 243903	Tanintharyi, Myanmar	N/A	N/A	N/A
31	*O. sp.*	CAS 247207	Tanintharyi, Myanmar	N/A	N/A	N/A
32	*O. sp.*	CAS 247487	Tanintharyi, Myanmar	N/A	N/A	N/A
33	*O. sp.*	CAS 247790	Tanintharyi, Myanmar	N/A	N/A	N/A
34	*O. sp.*	CAS 247983	Tanintharyi, Myanmar	N/A	N/A	N/A
Sample ID	*Species*	Voucher Tissue ID	Locality	GenBank No.		
				16S rRNA	COI	RHOD
35	*O. lima*	CAS 210572	Mandalay, Myanmar	N/A	N/A	N/A
36	*O. lima*	CAS 210549	Magway, Myanmar	N/A	N/A	N/A
37	*O. lima*	CAS 210588	Mandalay, Myanmar	N/A	N/A	N/A
38	*O. sp.*	CAS 211586	Ayeyarwade, Myanmar	N/A	N/A	N/A

39	*O. lima*	CAS 215941	Mandalay, Myanmar	N/A	N/A	N/A
40	*O. lima*	CAS 215942	Mandalay, Myanmar	N/A	N/A	N/A
41	*O. sp.*	CAS 221151	Rakhine, Myanmar	N/A	N/A	N/A
42	*O. sp.*	CAS 221852	Ayeyarwade, Myanmar	N/A	N/A	N/A
43	*O. lima*	CAS 222377	Bago, Myanmar	N/A	N/A	N/A
44	*O. sp.*	CAS 223088	Rakhine, Myanmar	N/A	N/A	N/A
45	*O. martensii*	CAS 230413	Yangon, Myanmar	N/A	N/A	N/A
46	*O. magnapustulosa*	CAS 230956	Shan, Myanmar	N/A	N/A	N/A
47	*O. martensii*	CAS 230999	Shan, Myanmar	N/A	N/A	N/A
48	*O. baluensis*	DQ283143	Sabah, Malaysia	DQ283143	N/A	N/A
49	*O. martensii*	DQ458256	China	DQ458256	N/A	N/A
50	*O. martensii*	GU177877	China	GU177877	GU177877	N/A
51	*O. martensii*	DQ283357	Ha Tinh, Vietnam	DQ283357	N/A	N/A
52	*O. martensii*	AF206467	Yok Don, Vietnam	AF206467	N/A	N/A
53	*Ingerana sp.*	CAS-246787	Tanintharyi, Myanmar	KF991266	N/A	N/A

Sample ID	Species	Voucher Tissue ID	Locality	GenBank No.		
				16S rRNA	COI	RHOD
54	*Ingerana sp.*	TAD_P918	Phangnga, Thailand	KR827831	N/A	N/A
55	*I. tenasserimensis*	IASST AR83	Assam, India	KU589219	N/A	N/A
56	*O. sp.*	USNM 587105	Bago, Myanmar	N/A	MG935622	N/A
57	*O. sp.*	USNM 587402	Yangon, Myanmar	N/A	MG935623	N/A
58	*O. sp.*	USNM 587395	Yangon, Myanmar	N/A	MG935624	N/A
59	*S. cubitalis*	2005.0224	Phongsali, Laos	N/A	KR087687	N/A
60	*S. faber*	0289Y2	Chanthaburi, Thailand	N/A	KR087707	N/A
61	*S. maosonensis*	K742	Vinh Phuc, Vietnam	N/A	KR087714	N/A
62	*O. lima*	AB489042	Kuala Lumpur, Malaysia	N/A	N/A	AB489042
63	*O. baluensis*	FMNH242747	Sabah, Malaysia	N/A	N/A	DQ283844
64	*O. martensii*	CAS 213254	Yangon, Myanmar	N/A	N/A	DQ283901
65	*O. martensii*	AMNH A161171	Ha Tinh, Vietnam	N/A	N/A	DQ283978

66	*O. martensii*	SCUMH020	Hainan, China	N/A	N/A	DQ458266
67	*O. martensii*	SCUM0437980	Yunnan, China	N/A	N/A	DQ458267
68	*P. boulengeri*	YNU-HU20024060	Yunnan, China	N/A	N/A	EU979919
69	*P. boulengeri*	KIZ-HUB293	Yichang, China	N/A	N/A	EU979942
70	*O. martensii*	FMNH268805	Xizang, China	N/A	N/A	KU243109

Appendix II: CAS *Occidozyga* Tissue Geo-Index for GIS Mapping

CAS ID	Clade	Lat DD,N,19,11	Long DD,N,19,11	Year Collected	Country	Region State
208248	C	18.85601	96.17259	1998	Myanmar	Bago
208249	C	18.85601	96.17259	1998	Myanmar	Bago
208250	C	18.85601	96.17259	1998	Myanmar	Bago
210572	lima	20.442333	96.121333	1999	Myanmar	Mandalay
210549	lima	21.50672222	95.19472222	1999	Myanmar	Magway
210588	lima	20.43658333	96.13722222	1999	Myanmar	Mandalay
210794	lima	17.046694	96.115417	1999	Myanmar	Yangon
211581	E	16.280056	94.770611	1998	Myanmar	Ayeyarwady
211586	E	16.28005556	94.77055556	1998	Myanmar	Ayeyarwady
211639	F	17.51925	94.688556	1998	Myanmar	Rakhine
215917	lima	21.399278	95.796917	2000	Myanmar	Mandalay
215941	lima	21.3945	95.80416667	2000	Myanmar	Mandalay
215942	lima	21.3945	95.80416667	2000	Myanmar	Mandalay
216192	lima	22.982222	96.108444	2000	Myanmar	Mandalay
221151	F	20.97822222	92.93861111	2001	Myanmar	Rakhine
221852	C	16.28005556	94.77055556	1998	Myanmar	Ayeyarwady
221939	F	17.584222	94.677778	2001	Myanmar	Rakhine
222377	C	17.06302778	96.25194444	1997	Myanmar	Bago
222521	lima	16.402917	97.649222	2002	Myanmar	Mon
223088	F	19.33744444	94.13555556	2002	Myanmar	Rakhine
223294	F	19.313833	94.150194	2002	Myanmar	Rakhine
230396	C	17.045639	96.092667	2002	Myanmar	Yangon
230413	C	17.04880556	96.09472222	2002	Myanmar	Yangon
230566	C	21.036083	96.395528	2002	Myanmar	Shan
230956	C	20.70586111	96.51277778	2002	Myanmar	Shan
230999	C	20.70586111	96.51277778	2002	Myanmar	Shan
231123	lima	20.068278	94.597306	2002	Myanmar	Magway
231175	lima	20.047444	94.493333	2002	Myanmar	Magway
232449	D	24.749417	96.348528	2003	Myanmar	Kachin
232733	D	25.016472	96.236556	2003	Myanmar	Kachin
233344	C	17.048417	96.094028	2003	Myanmar	Yangon
235424	B	21.320417	99.295028	2003	Myanmar	Shan
235506	lima	21.273389	99.548722	2003	Myanmar	Shan
235981	C	25.017333	96.235694	2003	Myanmar	Kachin
236046	lima	17.0465	96.108972	2003	Myanmar	Yangon
239481	D	16.626972	94.517889	2007	Myanmar	Ayeyarwady
239535	C	16.626389	94.534694	2007	Myanmar	Ayeyarwady
240345	C	17.406	97.078056	2008	Myanmar	Mon

240346	C	17.406	97.078056	2008	Myanmar	Mon
241138	D	25.135833	96.422444	2008	Myanmar	Kachin
241263	D	25.271472	96.340917	2008	Myanmar	Kachin
242979	lima	22.321639	94.10475	2008	Myanmar	Magway
243903	Sp. Nov.	14.736944	98.240361	2009	Myanmar	Tanintharyi
247207	B	10.375639	98.604111	2010	Myanmar	Tanintharyi
247487	B	10.361361	98.629194	2010	Myanmar	Tanintharyi
247790	B	10.366306	98.603972	2010	Myanmar	Tanintharyi
247983	Sp. Nov.	14.6825	98.322917	2010	Myanmar	Tanintharyi

Appendix III: Specimens of *Occidozyga sp.* from Myanmar used for morphological analysis.

Species	Museum ID	Voucher ID	SVL	HL	HW	IND	IOD	TD	DNE	EW	FLL	THL	TIL	FL	SEX	Location State	District Providence Township
O. lima	CAS	15249	23.56	6.42	8.7	1.58	1.11	2.61	1.85	3.2	10.9	9.85	10.79	13.47	NA	Rangoon	8 mi N of Rangoon
O. lima	CAS	15250	25.11	6.88	8.88	1.79	1.06	2.38	1.88	2.99	10.48	9.96	11.04	13.98	NA	Rangoon	8 mi N of Rangoon
O. martensii	USNM	58059	24.39	6.59	8.3	1.96	1.66	2.01	2.32	3.13	7.67	11.27	11.36	14.42	NA	Bago	Palon
O. cf. laevis	CAS	208248	17.8	5.45	6.37	1.89	1.16	1.58	1.54	2.81	7.99	8.05	8.33	8.98	NA	Bago	Bago Yoma
O. cf. laevis	CAS	208249	22.15	6.35	8.11	2.07	1.28	1.9	1.76	2.95	6.97	9.57	9.89	10.05	NA	Bago	Bago Yoma
O. lima	CAS	208489	27.66	7.46	9.23	1.69	1.37	2.79	1.88	3.68	11.99	12.66	13.56	14.25	NA	Mandalay	Mandalay
O. lima	CAS	208490	22.65	6.29	6.88	1.47	1.19	2.57	1.53	3.2	9.35	10.95	11.21	12.15	NA	Mandalay	Mandalay
O. lima	CAS	210572	26.58	7.11	9.39	1.83	1.69	2.71	2.24	3.09	12.92	12.81	13.21	14.9	NA	Mandalay	W of Yamethin
O. martensii	CAS	210780	30.45	7.6	9.53	2.76	1.37	2.07	2.16	3.81	9.85	14.05	13.03	13.65	NA	Yangon	Hlawga
O. martensii	CAS	210780	30.17	7.54	9.26	2.57	1.69	2.7	2.23	3.61	10.11	13.42	12.98	13.23	NA	Yangon	Hlawga Wildlife Park
O. sp	CAS	211581	27.32	5.67	10.18	2.55	1.71	1.96	2.07	3.35	10.93	14.77	13.79	14.75	NA	Ayeyarwady	vicinity Mwe Hauk Village
O. sp	CAS	211639	18.65	4.48	6.61	2.13	1.22	1.68	1.46	2.54	7.81	9.36	8.77	8.93	NA	Rakhine	Yoma Mountain Range
O. lima	CAS	213325	23.54	7.17	8.26	1.35	1.48	1.9	1.7	3.78	9.78	10.63	11.13	13.12	NA	Yangon	Mingalardon
O. lima	CAS	213437	28.69	7.42	9.6	1.76	1.02	2.37	2.13	3.33	11.58	12.71	13.04	14.85	NA	Yangon	Mingalardon
O. lima	CAS	213548	25.69	7.56	8.77	1.81	0.84	2.12	1.8	3.17	11.43	13.06	11.58	13.83	NA	Yangon	Mingalardon
O. lima	CAS	213548	26.25	7.79	9.16	1.71	0.95	2.46	1.75	3.44	11.34	13.38	11.86	12.72	NA	Yangon	Mingalardon
O. lima	CAS	215294	26.64	7.05	8.38	1.89	1.84	2.15	1.58	2.92	9.58	11.11	10.85	12.27	NA	Mandalay	Thazi
O. lima	CAS	215942	23.86	6.51	9.33	1.93	1.34	2.42	2.27	2.36	11.29	13.38	12.03	14.15	NA	Mandalay	Na Htoe Gyi Township
O. lima	CAS	216301	29.76	6.84	9.1	2.02	1.37	1.87	1.85	3.3	10.31	13.89	12.89	14.25	NA	Shan	Moe-Maik
O. lima	CAS	219876	24.51	7.74	9.26	1.59	1.3	2.38	1.49	2.89	11.32	11.84	11.21	14.44	NA	Ayeyarwady	Pya-bon

O. martensii	CAS	220460	26.41	6.64	8.26	2.47	1.42	2.18	1.57	3.65	9.81	11.34	12.31	12.96	NA	Rakhine	Gwa
O. martensii	CAS	220517	31.92	6.9	10.2	2.49	2.01	2.39	2.21	3.84	12.22	14.5	14.11	14.05	NA	Yangon	Mingalardon
O. martensii	CAS	220518	35.17	7.99	10.82	2.78	1.74	3.83	2.14	3.9	12.32	14.92	14.02	14.7	NA	Yangon	Mingalardon
O. martensii	CAS	220519	29.35	7.66	9.05	2.51	2.23	2.18	1.83	3.91	11.37	13.76	12.91	14	NA	Yangon	Mingalardon
O. martensii	CAS	220520	27.09	6.77	8.72	2.33	1.35	2	2.16	3.33	9.62	12.25	11.67	10.96	NA	Yangon	Mingalardon
O. martensii	CAS	220521	26.14	6.46	7.36	2.31	1.52	1.88	1.74	3.17	10.43	11.1	10.88	12.23	NA	Yangon	Mingalardon
O. martensii	CAS	220523	28.15	7.02	8.58	2.35	1.82	2.22	1.89	3.18	10.82	12.43	12.03	12.8	NA	Yangon	Mingalardon
O. martensii	CAS	220524	24.08	6.05	7.65	2.01	1.82	2.14	1.87	3.25	8.9	10.23	10.42	11.44	NA	Yangon	Mingalardon
O. lima	CAS	220531	24.01	7.19	8.42	1.58	1.64	2.02	1.48	3.07	11.7	12.73	10.76	12.67	M-catalog	Yangon	Mingalardon
O. martensii	CAS	220534	28.25	7.03	9.19	2.45	1.57	2.26	1.9	3.4	10.51	13.09	12.22	13.14	NA	Yangon	Mingalardon
O. martensii	CAS	220535	28.77	7.38	8.61	2.45	1.83	2.53	2.07	3.72	10.39	13.26	11.26	11.39	NA	Yangon	Mingalardon
O. martensii	CAS	220536	24.75	5.55	7.97	2.13	1.09	1.94	1.75	3.16	9.01	11.01	10.18	10.99	NA	Yangon	Mingalardon
O. martensii	CAS	220537	29.64	6.69	9.2	2.22	1.34	2.13	2.11	3.89	10.31	13.24	12.14	12.07	NA	Yangon	Mingalardon
O. martensii	CAS	220538	30.92	7.65	9.9	2.66	1.97	2.76	2.04	3.73	11.74	14.19	13.94	14.55	NA	Yangon	Mingalardon
O. martensii	CAS	220539	24.66	7.18	7.99	2.21	1.3	1.98	1.96	3.47	9.85	12.09	11.05	12.03	NA	Yangon	Mingalardon
O. martensii	CAS	220545	28.82	7.04	9.07	2.3	1.41	2.49	2.03	3.56	10.88	14.07	12.48	13.58	NA	Yangon	Mingalardon
O. martensii	CAS	221126	26.53	6.93	8.76	2.76	1.74	1.91	1.94	3.8	10.63	13.33	12.97	12.95	NA	Rakhine	Sittawe
O. lima	CAS	221607	25.69	6.76	8.49	1.68	1.6	2.49	1.86	3.02	11.67	12.26	11.87	13.12	NA	Sagaing	Pale
O. lima	CAS	221607	26.44	6.45	8.02	1.7	1.32	2.86	2.05	3.18	11.67	12.11	11.77	13.05	NA	Sagaing	Pale
O. lima	CAS	221664	26.34	6.97	9.33	1.65	1.38	2.75	1.6	3.36	11.87	12.04	11.7	14.65	NA	Sagaing	Mon Ywa
O. lima	CAS	221665	33.34	8.11	10.72	1.89	1.64	3.6	2.34	3.72	13.35	15.89	14.39	17.06	NA	Sagaing	Mon Ywa
O. lima	CAS	221666	32.12	7.98	11.01	2.04	1.9	3.27	2.36	3.49	13.56	14.61	14.68	16.15	NA	Sagaing	Mon Ywa
O. sp	CAS	221938	22.15	5.98	8.05	2.25	1.78	1.86	1.77	3.03	8.88	11.02	10.98	11.87	NA	Rakhine	Gwa Township
O. sp	CAS	221939	24.04	6.29	8.44	2.51	1.69	1.96	1.58	3.38	8.76	11.97	11.6	12.3	NA	Rakhine	Gwa Township
O. sp	CAS	221940	24.25	5.75	7.96	2.22	2.02	1.64	1.85	2.8	9.05	10.53	11.31	11.57	NA	Rakhine	Gwa Township
O. martensii	CAS	222062	28.58	7.43	8.63	2.75	2.62	3.22	2.04	4.43	11.35	12.85	12.95	12.38	NA	Rakhine	Sittawe
O. martensii	CAS	222063	28.13	7.74	8.78	2.94	1.8	2.27	2.08	3.62	10.34	12.29	12.6	12.21	NA	Rakhine	Sittawe
O. lima	CAS	222096	29.01	7.59	9.1	1.53	1.15	3.06	1.71	4.04	10.49	11.86	12.06	14.16	NA	Bago	Kyauk Taga

O. lima	CAS	222521	26	7.22	9.92	1.53	1.52	2.73	2.22	2.98	10.17	11.66	11.63	13.15	NA	Mon	Mawlamyine
O. lima	CAS	222867	23.88	8.67	8.38	1.5	0.71	2.15	2.34	3.31	10.32	10.56	10.35	11.44	NA	Ayeyarwady	Myaungmya
O. lima	CAS	222900	31.17	8.36	11.42	1.97	2.19	2.47	2.26	2.83	11.72	15.63	13.96	17.16	NA	Ayeyarwady	Myaungmya
O. cf. martensii	CAS	223207	27.69	7.5	9.35	2.69	1.88	2.42	2.12	4.03	11.63	13.75	13.82	13.57	NA	Rakhine	Taung-Gok
O. sp	CAS	223293	24.14	6.12	8.14	2.42	1.37	1.98	1.68	2.97	8.8	11.38	11.19	11.4	NA	Rakhine	Taung Gok Township
O. sp	CAS	223294	30.16	7.14	9.74	2.69	1.59	2.29	2.12	3.31	10.93	15.9	14.41	15.02	NA	Rakhine	Taung Gok Township
O. martensii	CAS	229596	25.15	7.35	8.82	2.4	1.45	2.58	2.02	3.13	10.9	12.99	12.1	12.72	NA	Tanintharyi	Kawthaung
O. martensii	CAS	230312	30.07	7.62	9.73	2.99	2.16	2.32	2.29	4.22	12.16	14.9	13.89	15.4	NA	Kachin	Myitkyina
O. martensii	CAS	230335	26.62	7.32	9	2.16	1.75	2.14	2.09	3.72	9.3	12.34	11.68	12.66	NA	Kachin	Myitkyina
O. martensii	CAS	230396	32.2	8.37	10.53	2.91	2.15	2.94	2.27	4.43	13.15	15.35	13.71	15.29	NA	Yangon	Insein
O. martensii	CAS	230405	30.93	6.46	9.57	2.46	2.04	2.48	2.01	3.98	11.58	15.39	13.64	14.48	NA	Yangon	Insein
O. martensii	CAS	230405	30.45	6.53	8.98	2.38	1.74	2.58	1.96	1.76	11.27	14.74	13.79	13.16	NA	Yangon	Insein
O. martensii	CAS	230406	26.29	6.9	8.57	2.34	1.48	2.56	1.74	4.17	10.22	12.72	11.19	12.26	NA	Yangon	Insein
O. martensii	CAS	230406	26.18	6.67	8.46	2.17	1.19	1.49	1.86	3.38	10.05	12.69	11.19	11.89	NA	Yangon	Insein
O. martensii	CAS	230407	25.34	6.62	9.06	2.38	1.75	2.61	1.88	3.26	10.34	13.44	11.61	11.88	NA	Yangon	Insein
O. martensii	CAS	230407	25.15	6.37	7.96	2.41	1.39	1.86	1.86	3.22	10.19	13.07	11.37	11.48	NA	Yangon	Insein
O. martensii	CAS	230413	32.12	7.98	11.11	2.71	1.59	2.72	2.18	4.12	12.96	15.73	14.4	14.79	NA	Yangon	Insein
O. martensii	CAS	230424	30.01	6.73	9.87	2.48	2.04	2.79	1.96	3.43	11.12	14.34	12.8	14.34	NA	Yangon	Insein
O. martensii	CAS	230434	31.38	6.99	10.19	2.48	2.05	2.78	2.41	3.53	11.82	15.16	13.69	13.44	NA	Yangon	Insein
O. martensii	CAS	230434	31.63	7.93	11.13	2.6	2.34	2.33	2.21	3.43	11.52	14.81	13.88	13.33	NA	Yangon	Insein
O. magnapustulosa	CAS	230566	27.1	6.59	7.96	2.3	1.61	2.93	1.94	3.3	10.68	12.68	12.09	13.17	NA	Shan	Taunggyi
O. magnapustulosa	CAS	230585	33.49	7.78	9	2.54	2.27	3.04	2.27	3.8	11.97	15.65	14.14	15.42	NA	Shan	Taunggyi
O. magnapustulosa	CAS	230585	33.35	9.06	9.41	2.5	2.1	2.89	2.71	3.86	12.62	15.07	14.28	15.45	NA	Shan	Taunggyi
O. magnapustulosa	CAS	230608	34.98	10.61	10.99	2.94	2.38	2.9	2.48	4.15	13.34	16.78	15.2	16.35	NA	Shan	Taunggyi
O. magnapustulosa	CAS	230608	35.69	9.62	10.38	2.76	2.06	2.94	2.12	4.1	13.51	16.84	14.75	16.3	NA	Shan	Taunggyi
O. magnapustulosa	CAS	230955	32.52	7.84	9.29	2.58	1.35	2.6	2.03	4.02	12.68	16.52	14.43	15.14	M-catalog	Shan	Taunggyi

O. magnapustulosa	CAS	230956	23.47	6.99	7.57	1.95	1.26	1.83	1.75	3.48	9.29	11.86	10.63	10.57	M-catalog	Shan	Taunggyi
O. martensii	CAS	230999	24.09	6.65	8.27	2	1.64	1.78	2.07	3.04	8.74	10.97	10.64	11.86	NA	Shan	Taunggyi
O. martensii	CAS	231000	25.85	6.48	8.41	2.25	1.7	1.86	2.06	3.04	8.88	11.54	10.73	10.53	NA	Shan	Taunggyi
O. martensii	CAS	231001	25.38	5.84	7.81	2.11	1.32	1.95	2.05	2.94	9.16	11.38	10.43	11.09	NA	Shan	Taunggyi
O. martensii	CAS	231002	26.19	6.7	8.59	2.28	1.83	1.66	1.97	2.96	9.91	12.62	11.9	12.09	NA	Shan	Taunggyi
O. martensii	CAS	231003	26.5	5.39	7.32	2.24	1.65	1.68	1.93	2.95	9.23	11.47	11.42	10.79	NA	Shan	Taunggyi
O. martensii	CAS	231004	24.92	6.41	8.58	2.28	1.52	1.63	2.14	2.94	9.01	12.34	11.41	11.74	NA	Shan	Taunggyi
O. lima	CAS	231121	39.94	9.27	12.49	2.11	1.78	3.46	2.52	4.04	14.61	17.76	16.18	19.18	F-catalog-eggs	Magway	Minbu
O. lima	CAS	231122	28.68	8.44	9.83	1.9	1.29	2.88	2.05	4.03	12.15	15.23	14.1	16.48	NA	Magway	Minbu
O. lima	CAS	231123	29.18	7.58	11.39	1.95	0.99	3.5	2.03	3.98	11.89	15.4	14.11	17.51	NA	Magway	Minbu
O. lima	CAS	231124	31.75	7.82	10.59	1.75	1.5	2.46	2.39	3.9	13.12	13.64	13.39	16.11	NA	Magway	Minbu
O. lima	CAS	231125	25.9	7.44	9.36	1.73	1.5	2.37	1.87	3.26	10.77	12.74	12.14	14.35	NA	Magway	Minbu
O. lima	CAS	231153	27.91	8.06	9.56	1.96	1.07	2.47	1.77	3.68	13.12	14.13	13.15	14.62	NA	Magway	Minbu
O. lima	CAS	231154	32.66	9.87	11.75	2.18	1.53	3.45	2.25	4.21	15.41	17.2	15.5	17.47	NA	Magway	Minbu
O. lima	CAS	231155	30	9.99	9.86	1.77	0.97	3.42	2.49	3.63	15.04	15.42	14.91	18.28	NA	Magway	Minbu
O. lima	CAS	231156	27.81	9.55	10.75	1.75	1.36	3.25	2.19	3.72	13.26	14.69	14.29	15.73	NA	Magway	Minbu
O. lima	CAS	231166	29.77	7.94	10.25	1.59	1.78	2.37	1.98	3.36	12.52	13.86	13.4	16.14	NA	Magway	Minbu
O. lima	CAS	231167	32.55	9.03	11.57	1.93	1.54	2.87	2.15	3.94	14.24	16.47	14.78	15.4	NA	Magway	Minbu
O. lima	CAS	231168	32.44	8.4	11.14	1.77	1.66	2.5	2.26	3.42	12.61	16	15.11	15.9	NA	Magway	Minbu
O. lima	CAS	231171	27.53	6.9	10.51	1.59	2.22	2.72	2.17	3.26	9.58	13.39	13	14.5	M-testes	Magway	Minbu
O. lima	CAS	231172	36.64	9.03	12.15	2.24	2.46	4.02	2.84	3.37	14.83	17.28	16.33	18.01	NA	Magway	Minbu
O. lima	CAS	231173	31.09	7.83	10.61	1.89	1.4	3.56	2.26	3.59	13.79	14.7	14.2	15.82	NA	Magway	Minbu
O. lima	CAS	231174	30.19	8.89	10.42	1.87	1.57	3.5	2.48	3.41	12.95	12.93	13.73	16.02	NA	Magway	Minbu
O. lima	CAS	231175	36	10.52	13.21	2.14	1.51	2.07	2.9	4.16	16.27	17.38	15.9	19.41	F-eggs-present	Magway	Minbu
O. lima	CAS	231192	30.13	8.79	10.45	1.84	1.29	2.67	1.91	3.72	12.61	13.8	13.71	16.01	NA	Magway	Minbu
O. lima	CAS	231193	33.97	9.8	11.96	1.91	1.79	3.75	2.69	3.27	14.85	16.73	16.35	17.45	NA	Magway	Minbu
O. lima	CAS	231429	31.3	8.87	11.6	1.76	1.53	2.82	2.37	3.66	14.05	17.31	15.76	17.12	NA	Mandalay	Myingyan

O. lima	CAS	232436	26.47	8.38	9.36	1.8	1.45	2.92	1.83	4.18	12.7	13.75	12.58	15.09	F-catalog	Kachin	Myitkyina
O. lima	CAS	232436	27.26	7.55	9.42	1.85	1.66	3.12	1.67	3.56	12.61	14.2	12.58	15.09	NA	Kachin	Myitkyina
O. lima	CAS	232448	27.3	8.23	10.02	1.89	0.94	2.45	2.02	3.88	11.81	14.25	12.19	14.14	NA	Kachin	Myitkyina
O. sp	CAS	232449	21.12	6.47	8.16	2.09	1.21	1.99	1.93	3.18	9.13	10.51	9.69	10.86	NA	Kachin	Myitkyina
O. sp	CAS	232450	23.48	6.67	8.67	1.92	1.55	1.56	2.09	3.33	9.59	11.26	10.61	11.81	NA	Kachin	Myitkyina
O. lima	CAS	232498	30.21	8.38	10.54	2.23	1.78	2.66	2.26	3.12	12.93	14.7	13.65	15.73	NA	Kachin	Myitkyina
O. lima	CAS	232507	28.21	9.36	9.55	1.91	1.17	2.94	2.07	3.57	13.58	14.41	13.94	15.77	NA	Kachin	Myitkyina
O. lima	CAS	232507	28.31	7.48	8.8	1.84	0.86	3.32	2.07	3.73	13.12	15.05	13.7	15.9	NA	Kachin	Myitkyina
O. sp	CAS	232560	26.31	7.44	9.33	2.07	1.16	1.94	2.2	3.48	10.3	11.99	11.65	12.27	NA	Kachin	Myitkyina
O. sp	CAS	232561	21.25	7.68	8.8	2.27	1.91	2.08	2.45	3.25	9.21	10.64	9.88	11.09	NA	Kachin	Myitkyina
O. sp	CAS	232732	26.03	7.44	8.83	2.11	1.65	2.14	2.42	3.08	9.51	11.78	11.36	12.53	NA	Kachin	Myitkyina
O. sp	CAS	232733	28.26	9.24	9.96	2.24	1.61	2.33	2.31	3.06	11.12	12.79	12.15	13.12	NA	Kachin	Myitkyina
O. martensii	CAS	233344	26.62	7.09	8.86	2.49	1.06	2.92	1.9	2.96	8.67	12.25	12	12.76	M-catalog	Yangon	Yangon Northern
O. martensii	CAS	233345	30.4	7.25	9.28	2.46	1.35	1.63	1.84	3.51	11.75	14.34	13.79	14.14	NA	Yangon	Yangon-Northern
O. lima	CAS	235444	33.56	8.84	11.16	2.13	1.5	3.04	2.25	3.62	14.43	16.51	14.34	17.8	NA	Shan	Maisatt
O. martensii	CAS	235446	25.7	6.5	8.29	2.46	1.46	1.95	1.71	2.99	9.99	11.6	10.64	12.6	NA	Shan	Maisatt
O. lima	CAS	235506	17.6	5.83	7.54	1.41	0.94	1.95	1.74	2.61	9.33	9.59	9.13	11.4	NA	Shan	Kyaitone
O. sp	CAS	235981	25.78	6.61	9.46	2.43	1.28	1.77	2.19	3.28	10.27	13.18	11.44	12.65	NA	Kachin	Myitkyina
O. lima	CAS	236047	32.9	8.43	11.71	1.93	1.88	2.49	2.06	3.95	12.9	13.86	14.1	16.58	F-catalog-eggs	Yangon	Yangon-Northern
O. martensii	CAS	236054	24.51	6.57	8.9	2.6	1.3	1.96	1.6	3.1	8.46	11.49	11.75	11.34	M-catalog	Yangon	Mingalardon
O. martensii	CAS	236055	25.99	6.71	8.39	2.29	1.32	1.95	1.78	3.29	9.55	12.84	12.4	11.11	M-catalog	Yangon	Mingalardon
O. martensii	CAS	236056	24.49	6.29	7.88	1.88	2.11	1.71	1.8	2.9	8.7	13.62	11.11	11.51	M-catalog	Yangon	Mingalardon
O. martensii	CAS	236059	27.11	7.1	8.05	2.44	1.66	1.53	2.04	3.18	9.64	12.63	11.46	12.2	NA	Yangon	Mingalardon
O. martensii	CAS	236065	27.01	6.8	8.9	2.26	1.53	3.05	1.86	3.68	8.85	12.02	11.08	12.38	NA	Yangon	Mingalardon
O. sp	CAS	239216	32.69	8.69	10.66	2.79	2.37	3.07	2.44	3.46	13.04	15.84	15.5	17.03	NA	Sagaing	Khandi
O. sp	CAS	239217	25.86	8.19	9	2.47	1.66	2.35	2.28	2.93	9.3	11.12	11.52	12.99	NA	Sagaing	Khandi

O. sp	CAS	239218	26.77	7.52	9.34	2.4	1.69	2.57	2.44	3.32	9.88	12.41	12.25	13.31	NA	Sagaing	Khandi
O. lima	CAS	239267	26.23	7.17	8.97	2.55	1.64	2.74	1.82	3.47	9.92	12.7	12.51	13.8	NA	Ayeyarwady	Pathein
O. lima	CAS	239267	25.99	6.98	8.52	2.64	1.51	2.62	1.98	3.49	9.87	12.84	12.77	13.29	NA	Ayeyarwady	Pathein
O. lima	CAS	239304	23.76	6.09	7.79	2.27	1.28	2.07	1.51	3.01	9	9.96	10.32	11.15	NA	Ayeyarwady	Pathein
O. martensii	CAS	239363	30.09	6.79	9.29	2.84	1.69	2.26	2.29	4.02	12.19	14.32	14.69	14.67	NA	Ayeyarwady	Pathein
O. martensii	CAS	239363	29.76	6.91	8.95	2.74	1.78	2	2.16	3.52	11.84	14.46	15.34	14.85	NA	Ayeyarwady	Pathein
O. martensii	CAS	239376	31.52	7.13	8.05	2.78	1.69	3.07	2.35	3.55	12.32	13.95	14.48	14.77	NA	Ayeyarwady	Pathein
O. martensii	CAS	239378	35.41	8.07	10.66	3.12	2.75	2.79	2.14	4.02	12.71	16.2	16.42	15.87	NA	Ayeyarwady	Pathein
O. martensii	CAS	239379	33.55	7.93	10.64	3.06	1.62	2.75	2.17	4.14	11.14	16.1	15.65	16.34	NA	Ayeyarwady	Pathein
O. martensii	CAS	239382	35.86	7.46	10.27	2.93	1.38	2.53	2.52	4.15	12.95	17.44	16.95	16.41	NA	Ayeyarwady	Pathein
O. martensii	CAS	239384	35.92	8.02	12.08	3.02	2.04	3.05	1.83	3.97	12.84	17.26	16.69	15.04	NA	Ayeyarwady	Pathein
O. martensii	CAS	239436	23.28	7.23	8.08	2.52	1.5	2.39	1.79	3.75	9.98	11.95	11.57	11.73	NA	Ayeyarwady	Pathein
O. martensii	CAS	239438	26.6	6.33	7.07	2.4	1.88	2.39	1.84	3.05	12.53	13.02	12.41	12.64	NA	Ayeyarwady	Pathein
O. lima	CAS	239446	29.13	9.45	10.14	1.9	0.85	2.05	2.02	4.03	13.94	15.16	13.86	16.88	NA	Ayeyarwady	Pathein
O. sp	CAS	239468	34.17	9.05	11.27	2.01	1.44	2.42	2.21	3.29	13.1	16.65	14.76	22.09	NA	Ayeyarwady	Pathein
O. sp	CAS	239477	36.72	8.11	13.26	2.98	1.54	2.48	2.35	3.84	13.2	15.7	15.07	16.47	NA	Ayeyarwady	Pathein
O. sp	CAS	239481	36.59	7.16	11.5	2.99	2.05	2.59	2.04	3.52	11.18	16.56	16.08	16.47	NA	Ayeyarwady	Pathein
O. martensii	CAS	239488	28.03	6.13	9.1	2.57	1.78	2.59	2	3.63	12.22	14.05	14.88	14.23	NA	Ayeyarwady	Pathein
O. martensii	CAS	239491	24.64	7.57	8.14	2.32	1.53	2.17	1.71	3.42	8.75	11.95	12.26	12.42	M-catalog	Ayeyarwady	Pathein
O. martensii	CAS	239501	29.09	5.51	7.9	2.51	1.94	1.94	1.85	3.32	10.78	13.38	13.68	14.53	NA	Ayeyarwady	Pathein
O. martensii	CAS	239503	24.92	6.27	7.87	2.42	1.37	2.5	1.75	3.29	10.24	12.68	12.69	13.42	NA	Ayeyarwady	Pathein
O. martensii	CAS	239505	35.41	8.49	10.67	2.98	2.15	2.36	2.2	3.46	12.34	16.34	16.15	16.01	NA	Ayeyarwady	Pathein
O. martensii	CAS	239506	25.13	5.32	7.27	2.25	1.32	1.71	1.83	2.93	9.89	12.43	11.53	12.42	NA	Ayeyarwady	Pathein
O. martensii	CAS	239507	36.46	7.21	10.25	3.12	1.87	4.18	2.12	3.73	12.23	15.86	15.37	13.82	NA	Ayeyarwady	Pathein
O. sp	CAS	239528	32.68	8.85	11.55	1.91	1.1	3.87	2.05	4.85	13.49	16.19	14.71	22.85	NA	Ayeyarwady	Pathein
O. sp	CAS	239535	35.17	8.04	12.59	2.72	1.94	2.65	2.9	3.72	12.04	16.33	14.73	15.42	NA	Ayeyarwady	Pathein
O. sp	CAS	239536	35.15	8.09	11.95	2.73	1.83	2.72	2.78	3.8	12.08	15.1	14.36	15.16	NA	Ayeyarwady	Pathein
O. martensii	CAS	239556	34.13	8.48	10.27	3.06	2.21	3.33	2.13	4.19	13.95	16.49	15.78	16.77	NA	Ayeyarwady	Pathein
O. martensii	CAS	239560	33.39	7.04	9.95	3.13	1.7	2.53	1.97	4	13.16	15.41	15.16	14.93	NA	Ayeyarwady	Pathein
O. martensii	CAS	239564	28.34	6.75	8.47	2.7	2.18	2.73	2.05	4.3	9.69	12.92	12.87	11.39	NA	Ayeyarwady	Pathein

O. martensii	CAS	239565	33.6	7.23	9.96	2.78	2.3	2.97	1.9	4.24	11.87	15.17	14.67	15.21	NA	Ayeyarwady	Pathein
O. martensii	CAS	239568	32.77	6.81	9.21	3.08	1.86	1.68	2.01	3.84	12.69	14.6	14.45	15.31	NA	Ayeyarwady	Pathein
O. martensii	CAS	239569	29.18	6.56	9.1	2.53	1.57	2.14	2	3.55	10.56	13.55	13.19	12.48	NA	Ayeyarwady	Pathein
O. martensii	CAS	239756	23.92	6.85	7.67	2.47	1.85	2.91	1.67	3.54	10.14	11.34	11.69	12.18	NA	Rakhine	Kyaukpyu
O. martensii	CAS	239757	24.88	6.17	7.36	2.4	1.38	2.72	1.55	3.47	10.48	11.77	11.52	11.6	NA	Rakhine	Kyaukpyu
O. martensii	CAS	239786	27.01	6.64	9.33	2.47	1.93	2.38	1.74	3.47	10.81	13.05	12.07	12.3	NA	Rakhine	Kyaukpyu
O. martensii	CAS	239810	29.97	6.47	9.95	2.64	1.6	2.93	2.15	3.31	11.35	13.82	13.5	14.27	NA	Rakhine	Kyaukpyu
O. martensii	CAS	239810	29.77	6.39	8.66	2.83	1.94	2.43	1.93	3.13	11.08	13.58	13.61	12.82	NA	Rakhine	Kyaukpyu
O. martensii	CAS	239811	30.53	6.79	10.42	2.93	1.81	2.37	2.22	3.79	12.65	14.55	14	15.01	NA	Rakhine	Kyaukpyu
O. martensii	CAS	239811	30.39	7.26	10.25	3.01	1.65	2.42	1.94	3.66	12.49	14.75	14.53	14.37	NA	Rakhine	Kyaukpyu
O. martensii	CAS	239817	26.59	6.52	7.42	2.58	1.2	2.47	1.86	3.24	10.04	12.29	12.03	12.93	NA	Rakhine	Kyaukpyu
O. martensii	CAS	239834	29.07	6.39	8.81	2.76	2.14	2.11	1.59	3.62	11.87	12.42	12.64	13.48	NA	Rakhine	Kyaukpyu
O. martensii	CAS	240070	23.83	5.54	7.09	2.31	1.55	1.85	1.68	3.31	9.32	10.32	10.79	10.88	NA	Rakhine	Kyaukpyu
O. martensii	CAS	240070	23.75	6.32	7.16	2.34	1.21	1.98	1.78	3.05	9.1	10.92	10.78	11.24	NA	Rakhine	Kyaukpyu
O. martensii	CAS	240085	23.92	5.96	7.6	2.44	1.43	2.35	1.66	3.71	9.88	11.28	11.85	12.42	NA	Rakhine	Kyaukpyu
O. martensii	CAS	240345	35.96	9.39	11.45	2.89	1.93	2.82	2.49	4.39	13.7	17.39	15.22	16.32	NA	Mon	Thaton
O. martensii	CAS	240346	21.94	6.83	7.7	1.8	1.57	2.04	1.8	3.22	8.03	10.26	10.35	11.53	NA	Mon	Thaton
O. sp	CAS	241037	29.44	8.42	10.82	2.57	1.31	2.28	2.24	3.37	11.48	14.13	12.96	11.63	NA	Kachin	Myitkyina
O. sp	CAS	241052	33.42	8.61	11.03	2.75	2.04	2.69	2.72	3.67	12.43	15.51	14.46	15.04	F-eggs	Kachin	Myitkyina
O. sp	CAS	241053	29.59	7.86	9.81	2.43	1.85	2.17	2.69	3.5	11.32	13.27	12.92	14.4	F-eggs	Kachin	Myitkyina
O. sp	CAS	241059	29.8	7.55	10.63	2.43	1.99	2.12	2.4	3.21	10.44	13.88	12.66	14.5	F-eggs	Kachin	Myitkyina
O. sp	CAS	241138	29.5	7.55	10.02	2.6	1.87	2.32	2.29	3.66	11.38	13.13	13.15	14.45	NA	Kachin	Myitkyina
O. sp	CAS	241140	30.35	7.24	10.3	2.44	1.59	1.78	2.29	3.23	11.77	13.45	13.19	14.31	M-sem-tubules-testes	Kachin	Myitkyina
O. sp	CAS	241263	32.38	8.05	10.92	2.54	2.09	2.21	2.69	3.96	11.75	13.78	13.66	14.33	F-eggs	Kachin	Myitkyina
O. lima	CAS	242979	19.92	6.77	7.81	1.76	1.23	2.27	1.7	2.77	9.35	10.89	10.07	10.98	NA	Magway	Pakhokku
O. sp	CAS	243903	31.11	9.3	11.72	2.89	2.42	2.34	2.6	3.66	13.64	16.27	15.15	16.64	NA	Tanintharyi	Dewei
O. sp	CAS	247207	24.26	7.22	9.05	2.23	1.64	1.85	2.19	3.24	9.18	11.81	11.8	12.98	NA	Tanintharyi	Kawthaung
O. sp	CAS	247487	22.65	6.11	7.93	2.07	1.65	2.13	1.82	2.89	8.42	10.43	10.75	11.81	NA	Tanintharyi	Kawthaung
O. sp	CAS	247790	20.89	7.42	7.44	2.05	1.54	1.66	1.45	2.71	7.97	10.34	9.51	10.59	NA	Tanintharyi	Kawthaung

O. sp	CAS	247983	17.77	5.69	6.76	1.96	1.26	1.34	1.61	2.61	7.58	8.93	8.7	10.4	NA	Tanintharyi	Dewei
O. sp	CAS	248169	38.46	8.72	11.78	2.79	1.99	3.09	2.46	3.44	12.77	16.27	14.35	15.5	F-catalog	Yangon	Yangon Northern
O. lima	USNM	520378	27.25	6.79	8.04	1.52	1.17	2	1.96	2.83	10.19	11.32	11.19	14.78	NA	Sagaing	Chatthin
O. lima	USNM	537457	25.94	6.29	9.34	1.58	1.42	2.64	1.88	2.74	11.79	12.11	11.49	13.29	NA	Sagaing	Kanbalur
O. lima	USNM	537458	28.69	6.74	9.49	1.79	1.68	2.35	1.99	3.48	12.24	13.22	13.03	16.22	NA	Sagaing	Kanbalur
O. lima	USNM	537459	23.47	6.19	7.5	1.6	1.41	2.36	1.94	2.78	9.53	9.8	10.23	11.32	NA	Sagaing	Kanbalur
O. lima	USNM	537460	24.67	6.12	9.04	1.57	1.36	2.35	1.78	2.72	11.33	11.85	11.65	13.67	NA	Sagaing	Kanbalur
O. lima	USNM	537461	27.8	7.31	9.33	1.7	1.29	2.61	2.11	3.22	12	12.21	12.57	14.71	NA	Sagaing	Kanbalur
O. sp	USNM	586928	22.36	6.22	7.56	2	1.37	1.58	1.89	2.71	8.8	9.07	10.84	11.13	NA	Tanintharyi	TaninNP
O. sp	USNM	586929	20.76	6.03	7.64	2.12	1.36	1.73	2.09	3.02	8.23	9.81	10.14	10.58	NA	Tanintharyi	TaninNP
O. martensii	USNM	586930	28.81	6.29	9.58	2.63	2.23	2.46	2.18	3.02	11.04	12.93	13.2	14.33	NA	Tanintharyi	Yeybu
O. martensii	USNM	586931	26.42	6.53	9.25	2.58	1.78	1.91	1.92	3.44	10.77	12.56	12.66	14.79	NA	Tanintharyi	Yeybu
O. martensii	USNM	586932	27.32	6.99	9.36	2.45	1.69	2.09	1.91	2.87	9.83	10.6	12.86	13.89	NA	Tanintharyi	Yeybu
O. martensii	USNM	586933	22.48	6.38	8.36	2.44	1.96	1.72	1.84	2.85	8.83	9.07	10.15	11.5	NA	Tanintharyi	Yeybu
O. martensii	USNM	586934	23.81	6.61	8.31	2.43	2.16	1.96	1.74	3.08	9.58	10.54	11.17	12.77	NA	Tanintharyi	Yeybu
O. martensii	USNM	586935	23.32	5.85	7.79	2.26	1.67	1.59	1.82	3.11	7.85	10.35	10.07	12.22	NA	Tanintharyi	Yeybu
O. martensii	USNM	586936	30.18	6.72	10.88	2.57	1.53	1.63	2.01	3.17	10.58	12.99	12.72	11.53	F-eggs	Tanintharyi	Yeybu
O. martensii	USNM	586937	22.3	5.87	7.78	2.27	1.57	1.41	1.57	2.64	9.04	10.76	10.46	12.78	NA	Tanintharyi	Yeybu
O. martensii	USNM	586938	29.08	6.47	9.48	2.57	1.99	1.86	1.92	3.25	10.94	12.6	12.57	13.9	F-eggs	Tanintharyi	Yeybu
O. martensii	USNM	586939	28.3	6.97	9.88	2.6	2.08	2.32	1.85	3.22	11.14	13.03	12.68	14.89	F-eggs	Tanintharyi	Yeybu
O. martensii	USNM	586940	20.91	5.87	7.65	2.19	1.99	1.56	1.68	2.71	8.85	10.14	9.9	11.69	NA	Tanintharyi	Yeybu
O. martensii	USNM	586941	25.78	6.16	8.38	2.07	1.62	1.63	1.65	3.08	9.38	10.89	10.56	11.9	NA	Tanintharyi	Yeybu
O. martensii	USNM	586942	27.48	6.6	10	2.66	1.88	1.88	1.86	3.16	10.25	12.93	12.86	14.43	F-eggs	Tanintharyi	Yeybu
O. martensii	USNM	586943	23.56	6.69	8.36	2.32	1.87	1.69	1.64	2.77	8.9	11.13	11.49	13.05	NA	Tanintharyi	Yeybu
O. sp	USNM	587104	33.77	8.32	11.52	2.72	2.14	2.5	2.47	3.54	11.68	15.18	14.09	15.12	NA	Bago	Dawe
O. sp	USNM	587105	29.98	6.56	9.31	2.46	1.3	2.12	2.01	3.51	9.6	13.93	12.39	12.74	NA	Bago	Dawe
O. sp	USNM	587106	28.55	6.7	10.15	2.48	1.48	1.66	2.01	3.31	11.6	14	13.26	14.57	NA	Bago	Dawe
O. sp	USNM	587107	32.93	8.08	11.69	2.73	1.88	2.36	2.21	4.06	12.96	15.45	14.6	15.52	NA	Bago	Dawe

O. martensii	USNM	587295	23.39	6.23	8.33	2.2	1.37	1.86	1.64	2.87	7.77	10.68	10.86	11.2	NA	Tanintharyi	Ywahilu
O. sp	USNM	587383	22.06	5.35	6.68	2.33	1.39	1.62	1.52	2.78	8.74	11.33	10.59	11.19	NA	Yangon	Mingalardon
O. sp	USNM	587384	30.6	6.96	9.68	2.64	1.83	2.74	1.92	3.79	11.49	14.4	13.48	14.44	F-eggs	Yangon	Mingalardon
O. sp	USNM	587385	23.46	6.08	7.49	2.22	1.56	2.34	1.44	2.69	9.52	11.69	11.13	12.19	M-testes	Yangon	Mingalardon
O. sp	USNM	587386	29.8	6.37	8.82	2.7	1.93	2.61	2.2	3.45	10.24	14	12.85	13.64	NA	Yangon	Mingalardon
O. sp	USNM	587387	30.57	7.28	9.72	2.74	2.09	3.56	2.23	3.57	10.84	14.83	13.66	14.63	NA	Yangon	Mingalardon
O. sp	USNM	587388	24.54	5.5	7.93	2.35	1.91	2.86	1.8	3.08	7.6	12.56	11.39	12	NA	Yangon	Mingalardon
O. sp	USNM	587389	22.27	5.57	7.73	2.35	1.82	2.53	1.89	2.98	8.87	11.68	10.85	10.53	NA	Yangon	Mingalardon
O. lima	USNM	587392	24.56	7.3	9.07	1.78	1.19	1.84	1.36	3.26	9.73	11.22	11.32	11.59	NA	Yangon	NA
O. sp	USNM	587394	36.93	7.57	11.73	2.77	2.66	3.1	2.59	3.83	13.2	16.4	14.74	13.99	NA	Yangon	NA
O. sp	USNM	587395	36.55	8.1	12.15	2.78	2.18	2.73	2.7	3.91	12.77	15.73	15.08	15.07	NA	Yangon	NA
O. sp	USNM	587402	25.98	7.4	9.46	2.27	1.88	2.4	2.08	3.26	10.57	13.08	11.47	12.43	NA	Yangon	NA
O. martensii	USNM	587677	21.8	6.38	7.47	2.3	1.54	1.62	1.65	2.78	9.85	11.62	11.13	12.39	NA	Tanintharyi	LenyaNP6
O. martensii	USNM	587685	25.32	6.99	9.02	2.51	1.69	2.24	1.86	3.44	8.82	11.48	11.75	14.02	NA	Tanintharyi	LenyaNP2
O. martensii	USNM	587686	26.23	7.22	8.91	2.68	1.68	2.22	2	3.21	10.7	13.72	12.92	13.38	F-eggs	Tanintharyi	LenyaNP2
O. martensii	USNM	587687	24.91	6.72	8.56	2.54	1.8	2.27	1.75	3.4	8.16	10.23	10.97	12.75	F-eggs	Tanintharyi	LenyaNP2
O. martensii	USNM	587688	27.12	6.85	9.51	2.65	2.14	1.96	1.76	3.01	8.56	11.65	11.25	13.28	F-eggs	Tanintharyi	LenyaNP2
O. martensii	USNM	587689	27.47	6.92	9.18	2.73	2.42	1.86	1.82	3.1	7.45	12.49	11.32	13.01	NA	Tanintharyi	LenyaNP2
O. martensii	USNM	587690	25.22	6.77	8.37	2.79	1.73	1.84	2	2.83	9.09	11.76	11.45	12.73	NA	Tanintharyi	LenyaNP2
O. martensii	USNM	587691	26.31	7.46	9.24	2.73	1.99	1.73	2	3.26	9.24	12.36	12.13	14.24	F-eggs	Tanintharyi	LenyaNP2
O. martensii	USNM	587692	27.63	6.69	9.84	2.77	1.88	2.02	1.78	3.28	8.58	12.44	11.84	14.18	NA	Tanintharyi	LenyaNP2
O. martensii	USNM	587693	21.61	5.94	7.42	2.37	1.37	1.44	1.6	2.86	7.79	10.54	10.06	11.24	NA	Tanintharyi	LenyaNP2
O. martensii	USNM	587694	27.05	6.47	8.82	2.45	1.77	1.84	2.11	3.01	9.28	12.39	12.09	14.16	F-eggs	Tanintharyi	LenyaNP2
O. martensii	USNM	587695	26.14	6.84	8.93	2.61	1.81	1.82	2.11	3.07	9.11	12.36	11.56	13.05	F-eggs	Tanintharyi	LenyaNP2
O. martensii	USNM	587696	28.11	7.36	9.48	2.79	1.88	2.1	1.95	3.11	8.38	13.19	12.06	13.88	NA	Tanintharyi	LenyaNP2
O. martensii	USNM	587697	26.79	7.45	9.58	2.7	1.69	2.12	2.01	3.14	9.93	13.28	13.21	15.23	F-eggs	Tanintharyi	LenyaNP3
O. martensii	USNM	587698	26.78	7.23	9.19	2.79	1.49	2.02	1.71	2.83	8.74	12.91	11.95	13.49	NA	Tanintharyi	LenyaNP4
O. martensii	USNM	587699	26.3	6.87	8.84	2.39	1.32	1.88	1.74	3.14	9.91	12.37	11.87	13.6	F-eggs	Tanintharyi	LenyaNP5
O. martensii	USNM	587922	29.36	7.05	9.98	2.89	2.45	2.8	2.16	3.16	9.28	12.02	12.76	12.16	F-eggs	Tanintharyi	Ywahilu

O. martensii	USNM	587923	27.01	6.9	9.29	2.57	1.94	2.46	1.74	3.06	10.27	12.55	11.85	12.67	NA	Tanintharyi	Ywahilu
O. martensii	USNM	587924	26.92	6.99	9.36	2.7	1.78	2.19	1.77	3.54	9.84	12.21	12.47	12.06	NA	Tanintharyi	Ywahilu
O. martensii	USNM	587926	22.02	6.32	8.24	2.3	1.78	1.87	1.53	2.55	8.07	10.05	9.93	10.61	NA	Tanintharyi	Ywahilu
O. martensii	USNM	587927	26.33	6.68	8.93	2.69	1.68	2.54	2.05	3.14	9.9	11.85	12.36	12.53	F-eggs	Tanintharyi	Ywahilu
O. martensii	USNM	587928	29.33	7.36	10.36	2.72	2.09	2.67	1.99	3.6	9.96	13.59	12.68	14.13	NA	Tanintharyi	Ywahilu
O. martensii	USNM	587929	21.62	6.07	8.16	2.24	1.39	1.75	1.64	3.17	7.04	10.13	10.37	11.5	NA	Tanintharyi	Ywahilu
O. martensii	USNM	587930	19.91	5.44	7.15	2.09	1.19	1.78	1.58	2.5	6.96	8.71	9.51	10.91	NA	Tanintharyi	Nint Tenku
O. martensii	USNM	587931	26.72	6.26	9.09	2.76	1.82	2.36	1.09	3.22	10.17	13.36	12.62	13.27	NA	Tanintharyi	Nint Tenku
O. martensii	USNM	587932	25.56	6.38	8.94	2.53	1.28	2.26	1.9	2.85	9.57	13.26	12.34	12.33	NA	Tanintharyi	Nint Tenku
O. martensii	USNM	587933	23.61	6.41	8.53	2.32	1.4	1.99	1.98	3	8.88	12.37	11.57	12.89	NA	Tanintharyi	Nint Tenku
O. martensii	USNM	587934	20.87	6.56	7.05	2.21	1.36	2.12	1.81	2.58	7.81	9.57	10.58	11.31	NA	Tanintharyi	Nint Tenku
O. martensii	USNM	587936	26.5	7.22	9.29	2.43	1.81	2.03	2.1	3.14	10.15	12.03	12.3	13.67	NA	Tanintharyi	Nint Tenku
O. martensii	USNM	587938	30.4	7.72	10.87	2.83	1.68	2.25	2.09	3.48	9.01	14.23	13.98	15.54	NA	Tanintharyi	Nint Tenku
O. martensii	USNM	587939	28.04	8.41	9.84	2.57	1.86	2.06	1.93	3.74	10.72	13.43	12.93	14.81	NA	Tanintharyi	Nint Tenku
O. martensii	USNM	587947	26.59	7.32	9.41	2.64	1.9	2.27	1.83	3.46	10.6	12.18	12.53	14.03	NA	Tanintharyi	Nint Tenku
O. martensii	USNM	587948	24.15	6.44	8.33	2.44	1.8	2.02	1.96	3.08	8.26	11.14	10.98	12.51	NA	Tanintharyi	Nint Tenku