

FOOD HABITS, REPRODUCTIVE BIOLOGY, AND SEASONAL ACTIVITY OF THE DIPSADID SNAKE, *ECHINANATHERA UNdulata* (WIED, 1824), FROM THE ATLANTIC FOREST IN SOUTHEASTERN BRAZIL

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ABSTRACT. *Echinanthera undulata* is an endemic dipsadid snake from the Atlantic forest in southeastern Brazil. We gathered data on body size, food habits, reproductive cycles, and seasonal abundance of 240 preserved specimens. Adult females are larger in snout-vent length and have shorter tails than males. Males and females do not differ in relative head and eye size. *Echinanthera undulata* feed mainly on small leptodactylid frogs on the leaf litter. Apparently, its long tail is used to facilitate the capture of prey in this substrate (using poking behavior, leading the anuran to flee in the leaf litter). Reproductive cycle is seasonal in both females and males. Females showed vitellogenic follicles and oviductal eggs mainly at the onset of the rainy season, and births may occur mainly at the onset of the dry season. Fecundity ranged from one to 19 eggs. Testes volume was significantly larger at the end of the rainy season, but the deferent ducts diameter did not differ significantly throughout the year. Variation in seasonal abundance may be related mainly to reproductive events in females and males.

KEY-WORDS. Snakes; Dipsadidae; Echinantherini; natural history; diet; reproduction.

INTRODUCTION

Natural history data on snakes can provide important information for evolutionary studies, as well as for conservation biology (Greene and Losos, 1988; Hillis, 1995). In the past 20 years, a marked increase in studies on feeding and reproductive biology of South American snakes was observed (e.g., Marques *et al.*, 2001, 2006; Almeida-Santos and Orsi, 2002; Martins *et al.*, 2002; Almeida-Santos *et al.*, 2004; Hartmann and Marques, 2005; Pizzatto *et al.*, 2008a). However, with the high species richness, lineage diversity, and ecological complexity found in the region, there is still a lack of basic information on reproduction and diet for many species.

Echinanthera undulata is endemic to the Brazilian Atlantic Forest (Di-Bernardo, 1991) and belongs to the tribe Echinantherini, that also includes the genus *Taeniophallus* (Grazziotin *et al.*, 2012). Data on natural history are available for only a few members of the tribe (e.g., *Echinanthera cyanopleura*: Di-Bernardo, 1991; Marques and Sazima, 2004; *E. undulata*: Marques, 1998; Marques *et al.*, 2004; Barbo *et al.*, 2011; *Taeniophallus affinis*: Sousa and Cruz, 2000; Marques *et al.*, 2001; Barbo and Marques, 2003; Zacariotti and Gomes, 2010; *T. bilineatus*: Sazima *et al.*, 1992; *Taeniophallus occipitalis*, Sawaya *et al.*, 2008). Limited information is available for *E. undulata* despite its relative commonness in herpetological collections. Published

information on *E. undulata* reveals that it is diurnal and feed mostly on anurans, but further details on natural history are unavailable. The present study provides information on sexual size dimorphism, seasonal activity, reproductive cycles of males and females, and food habits of *E. undulata* (Fig. 1) from southeastern Brazil.

MATERIAL AND METHODS

We examined 240 preserved specimens of *Echinanthera undulata* from the collections of Instituto Butantan (IB), Museu de Zoologia da USP (MZUSP), Museu Nacional do Rio de Janeiro (MNRJ), Museu de História Natural Capão da Imbuia (MHN-CI), Museu de Ciências e Tecnologia da PUC-RS (MCT) and Museu de Ciências Naturais da Fundação de Zoobotânica do Rio Grande do Sul (NOPA). The specimens analyzed in collections come from southeastern Brazil (21°12'S, 26°26'S and 41°41'W, 51°23'W; see Appendix). This area is inserted in the Atlantic forest domain, and has a relatively homogeneous climate characterized by a large amount of rainfall throughout the year (Nimer, 1989). Nonetheless, two broadly defined seasons occur in the region: a rainy season (October-May) with high rainfall and temperature, and a dry season (June-September) with less rainfall and lower temperatures (see Marques *et al.*, 2000).



FIGURE 1. *Echinanthera undulata* (IB 57337), from Tapiraí, SP, Brazil.

We recorded the following data for each individual: head length (HL); eye diameter (ED; to the nearest 0.1 mm); snout-vent length (SVL); tail length (TL); trunk length (TRL = SVL – HL; to the nearest 1.0 mm); condition of tail (mutilated or not); diameter of largest ovarian follicle or oviductal egg; number of vitellogenic follicles (> 10 mm) or oviductal eggs (to estimate fecundity; Shine, 1977a); deferent duct diameter close to the cloaca (cf. Almeida-Santos *et al.*, 2006); testicle length, width, and diameter (to the nearest 0.1 mm); food items in the gut. Female body size at sexual maturity was based on the smallest female (SVL) with vitellogenic follicles or oviductal eggs (Shine, 1977a). Males were considered mature if they had enlarged and turgid testicles and thickened convoluted deferent ducts (Shine, 1977b; Almeida-Santos *et al.*, 2006). Sexual size dimorphism (SSD) was calculated according to the formulae proposed by Gibbons and Lovich (1991) and Shine (1994): $1 - \text{mean adult SVL of the larger sex} / \text{mean adult SVL of the smaller sex}$. Negative values correspond to males larger than females (Shine, 1994). To describe the spermatogenesis period, we estimated the testicular volume as the volume of the ellipsoid ($4/3\pi abc$; which a = length, b = width, and c = diameter) (Almeida-Santos *et al.*, 2006). Gut contents were removed, weighed, and identified to the lowest possible taxonomic level. Eggs found in nature and brought to Instituto Butantan were incubated in moist vermiculite, under temperatures varying from

22 to 26°C. The date of collection was used to estimate seasonal abundance (see Marques *et al.*, 2000). To avoid confounding overlap in seasonal activity, males, females, and juveniles were analyzed separately.

Mean SVL of both sexes was compared with a t-test (Zar, 1999). We used one-way analyses of covariance (ANCOVA) to test for differences in TL, HL, and ED between sexes (factors), with SVL, TRL, and HL as covariates, respectively, to eliminate allometric effects (Zar, 1999). Volume of testicles was also tested using ANCOVA (Zar, 1999), treating months as factors, and SVL as the covariate. We tested for differences in deferent duct diameter with an ANOVA (Zar, 1999), using months as factors. For better graphic visualization, the formula: $TV/SVL \times 100$ was used, where TV = testicle volume and SVL = snout-vent length. Female reproductive cycle was examined throughout the year in terms of length of the largest ovarian follicle or oviductal egg. All statistical analyses were done using Statistica 8. All variables were tested for normality prior to analysis.

RESULTS

Mature females averaged 422 mm SVL (range = 320–570 mm; SD = 56; $n = 95$), and mature males averaged 345 mm (range = 276–440 mm; SD = 51; $n = 73$). This difference was highly significant

($t = -8.90$; $P < 0.001$). The degree of sexual size dimorphism (SSD) was 0.22. Adult males had relatively longer tails than females (ANCOVA = 34.21; $P < 0.001$; Fig. 2). The tail of males represented 47% of body length, and that of females 43%. Fifty-four specimens (22%, $n = 240$) had mutilated tails. Males and females had no significant differences neither in relative head length (ANCOVA = 0.47; $P = 0.5$) nor in eye diameter (ED) (ANCOVA = 0.42; $P = 0.51$).

We found 12 individuals of *E. undulata* (5%, $n = 240$) with gut contents. All items were frogs, mainly leptodactylids (see Table 1 for details). Prey mass ranged from 2 to 12% of the snake mass. All snakes swallowed the frogs head first.

Preserved females of *E. undulata* had vitellogenic follicles (> 10 mm) and oviductal eggs mainly in the rainy season (Fig. 3). Fecundity (number of vitellogenic follicles or oviductal eggs) ranged from one to 19 (mean = 6 ± 3.4 ; $n = 50$).

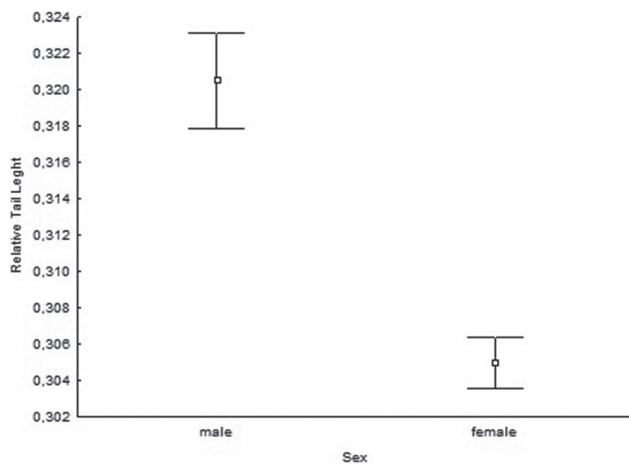


FIGURE 2. Relative tail length in males and females of *Echinanthera undulata*.

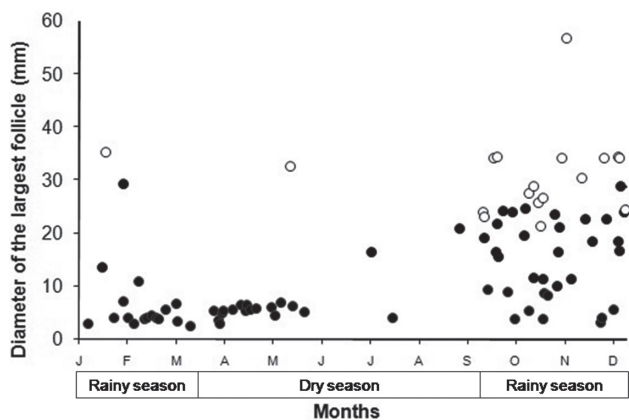


FIGURE 3. Seasonal variation in diameter of the largest follicles or eggs in *Echinanthera undulata*. Solid circles = ovarian follicles; open circles = eggs.

Testes volume was significantly larger from December to March at the end of the rainy season (ANCOVA = 27.92; $P = 0.003$; $n = 67$; Fig. 4). The diameter of the deferent duct did not vary during the year ($F_{(66,1)} = 1.8$; $P = 0.06$; $n = 67$). Large ducts were found throughout the year (Fig. 5).

Newborns were collected mainly from February to May, at the end of the rainy season (Fig. 6). We obtained six eggs in 13 March 2008, and five neonates born after three days of incubation (one egg contained a dead embryo). The SVL of neonates averaged 154 ± 3.3 mm (range 150–158 mm).

Seasonal abundance data indicates that males are more active from January to March, whereas females are more active from September to December (Fig. 6).

In summary, the reproductive cycle of *E. undulata* can be described as spermatogenesis occurring from November to March, pregnant females from September to February, and recruitment from February to May (Fig. 7).

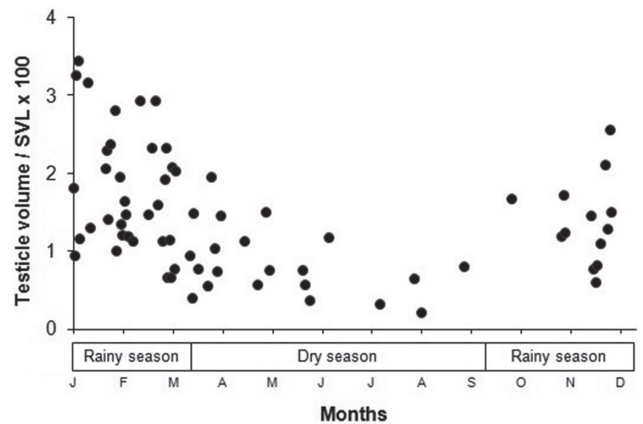


FIGURE 4. Seasonal variation of testicular volume in *Echinanthera undulata*.

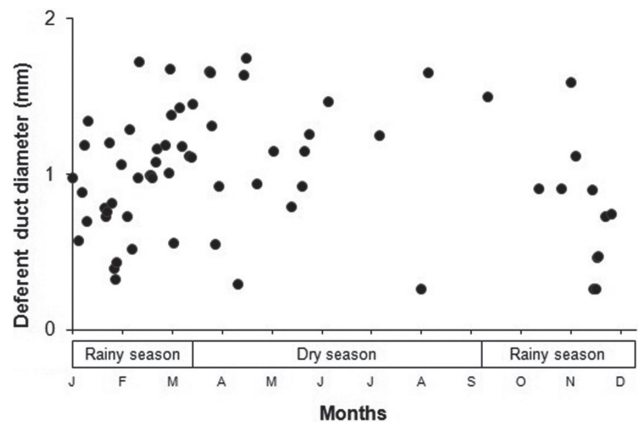


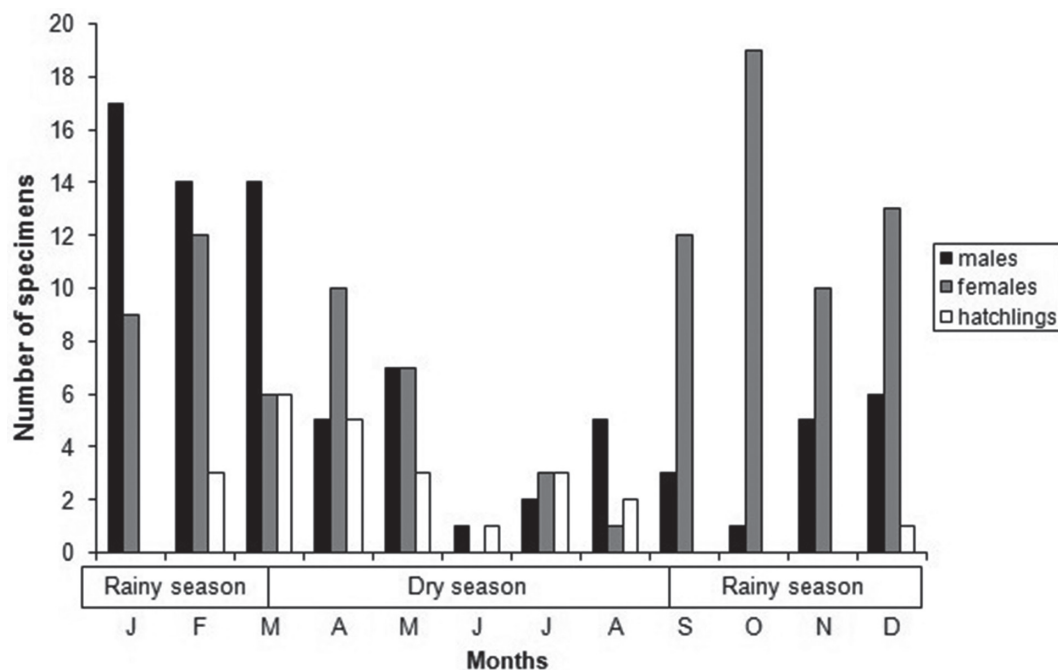
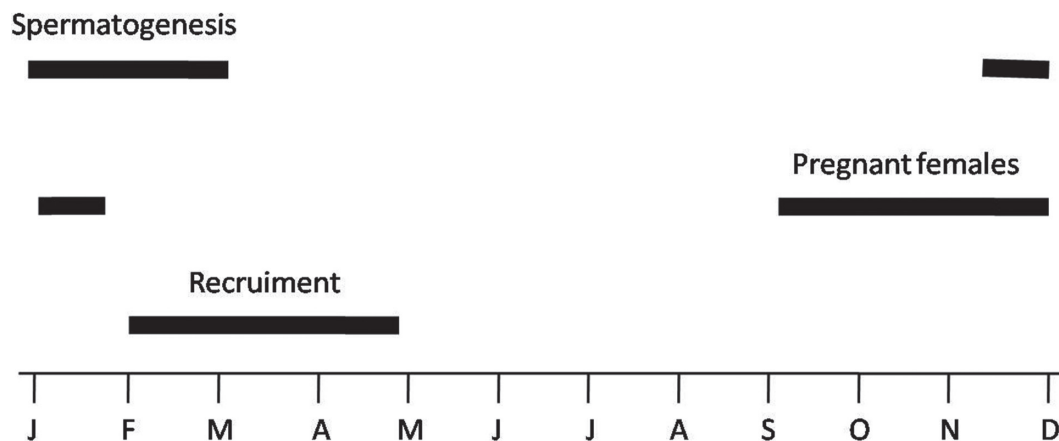
FIGURE 5. Seasonal variation of deferent duct diameter in *Echinanthera undulata*.

TABLE 1. Prey found in the gut of *Echinanthera undulata*.

Prey	Number of records
ANURA	
Hylidae	1
<i>Dendropsophus</i> sp.	
Leptodactylidae	1
<i>Ischnocnema</i> sp.	1
<i>Leptodactylus</i> sp.	6
<i>Physalaemus</i> sp.	2
Unidentified anuran	2

DISCUSSION

The larger body size in female *E. undulata* and the high value of SSD (0.22) suggests that there is no male-male combat in this species (*cf.* Shine, 1993, 1994). Other xenodontine species of the Philodryadini, Pseudoboini, and Xenodontini tribes have also high SSD (> 0.15 ; Hartmann *et al.*, 2004; Pizzatto *et al.*, 2007; Pizzatto *et al.*, 2008a; Zanella and Cechin, 2010). Combat behavior remains unrecorded for the Neotropical Xenodontinae and apparently do not occur in this lineage. Female snakes may be under stronger selective pressure than males to increase

FIGURE 6. Seasonal activity of *Echinanthera undulata*.FIGURE 7. Summary of the reproductive cycle of *Echinanthera undulata*.

body size (Shine, 1994) due to the high correlation between clutch size and body size (Parker and Plummer, 1987; Shine, 1994). On the other hand smaller body size in males could allow a faster movement while searching for females in the breeding season (Pearson *et al.*, 2002). These selective agents may be responsible for the sexual dimorphism in SVL found in xenodontines.

Head and eye size dimorphism in snakes may be related to intersexual dietary divergence (Houston and Shine, 1993). The absence of dimorphism on these characters in *E. undulata* as well as other Xenodontinae snakes (*e.g.*, *Tropidodryas* spp., *Philodryas agassizii*, *Ptychophis* and *Gomesophis* see Marques *et al.*, 2006; Stender-Oliveira, 2008; Oliveira *et al.*, 2003; Scartozzoni and Marques, 2004) indicates that males and females in this lineage usually feed upon the same kind and size of prey. Similar results were found in some Neotropical colubrids (*e.g.*, *Mastigodryas* and *Oxybelis*; see Leite *et al.*, 2009; Mesquita *et al.*, 2010). Males of *E. undulata* have larger tails than females, which is the most common condition for snakes in general (see King, 1989).

The relatively long tail and the high frequency of mutilated tails in *E. undulata* were also observed in other snakes, such as *Scaphiodontophis* and *Dendrophidion* and can be related to tail autotomy or direct effect of predation (*cf.* Lillywhite and Henderson, 1993; Martins, 1993; Hoogmoed and Avila-Pires, 2011). However, a long tail in the genus *Echinanthera* can also reflect tail poking behavior to facilitate the prey capture, according to previous observation on captive snakes (see Di-Bernardo, 1991). The poking behavior of *E. undulata* may cause anurans to flee when the snake moves its tail on the leaf litter, as observed in *Hydrodynastes gigas* (Strüssmann and Sazima, 1990).

The data obtained here confirm the specialization of *E. undulata* on anurans, as reported in previous works (*e.g.*, Amaral, 1977; Di-Bernardo, 1991; Marques *et al.*, 2001; Marques and Sazima, 2004). Another related species, *E. cyanopleura*, also feeds mainly on small leptodactylids (Di-Bernardo, 1991; Marques and Sazima, 2004). *Echinanthera* is mainly diurnal (Marques and Sazima, 2004) and may actively search for anurans in the leaf litter. The poking behavior may facilitate finding leaf-litter frogs. *Echinanthera undulata* has larger eyes than other species with similar body size (*e.g.*, *Crotaphopeltis hotamboeia*, *Enhydrys chinensis*, *Hypsiglena torquata tiburonensis*, *Mehelya nyassae* and *Sibynophis chinensis miyiensis*; *cf.* Liu *et al.*, 2012), what may help in prey location (*cf.* Rooijen and Vogel, 2008) in a low light environment.

Reproductive female cycle of *E. undulata* is seasonal, since vitellogenic follicles and eggs occur predominantly in the rainy season. A similar pattern was found in a southern population of *E. cyanopleura* (Zanella and Cechin, 2010). However, females of *E. undulata* with oviductal eggs in May suggest a continuous cycle. Continuous and seasonal reproductive pattern has been reported in other species in southeastern Brazil (see Marques, 1996; Marques and Muriel, 2007; Pizzatto *et al.*, 2007; Mathies, 2011). Even though *Echinanthera* could reproduce continually, its cycle is seasonal, since there are a larger number of reproductive females in the rainy season. Thus, oviposition occurs mainly in the rainy season. This may be advantageous since egg laying occurs in this season, and eggs are incubated during a warmer and wetter period, which is optimum for embryonic development (Vinegar, 1977; Shine 1977a). Another advantage could be the recruitment of small anurans that occurs in this period (Heyer *et al.*, 1990; Bertoluci, 1998) and represents an increase in the availability of food for the newborn snakes.

Testes volume in snakes may reflect spermatogenic activity (Volsøe, 1944; Almeida-Santos *et al.*, 2006). Male reproductive cycle of *E. undulata* is seasonal, with spermatogenesis occurring during the rainy season, when testicle volume is larger. As in *E. undulata*, other dipsadid snakes (*e.g.*, *Leptodeira* and *Sibynomorphus*; Pizzatto *et al.*, 2008b; Scartozzoni *et al.*, 2009) show no monthly variation in deferent duct diameter, suggesting that they do not store sperm.

Seasonal activity in snakes may be influenced by several factors including humidity, temperature, food availability, and reproductive cycle (Lillywhite, 1987; Gibbons and Semmlitsch, 1987; Shine, 1977a; Marques *et al.*, 2000). The reproductive cycle in *E. undulata* may be a determinant factor for seasonal activity since males are more active from January to March, when they are actively searching for females to mate with (Gibbons and Semmlitsch, 1987). Besides, females are more active from September to December, when they have vitellogenic follicles or oviductal eggs. The more intense activity of females in this period may be due to their thermoregulatory needs during egg development or search for oviposition sites (Shine, 1977a).

RESUMO

Echinanthera undulata é um dipsadídeo endêmico da Floresta Atlântica no sudeste do Brasil.

Coletamos dados sobre tamanho do corpo, ciclo reprodutivo, hábito alimentar e abundância sazonal de 240 espécimes preservados em coleções científicas. Fêmeas adultas apresentam comprimento rostro-cloacal maior e têm caudas mais curtas em relação aos machos. Machos e fêmeas não diferem entre si no tamanho relativo da cabeça e no tamanho do olho. *Echinanthera undulata* se alimenta de pequenos anfíbios anuros, principalmente leptodactídeos, que vivem em meio à serapilheira. Aparentemente, a cauda longa dessa serpente é usada para facilitar a captura da presa nesse substrato (por meio do comportamento de esquadrihar, que causa a movimentação dos anuros em meio a serapilheira). O ciclo reprodutivo é sazonal nas fêmeas e machos. Fêmeas apresentam folículos vitelogênicos e ovos principalmente no início da estação chuvosa e a maior parte dos nascimentos parece ocorrer no início da estação seca. A fecundidade variou de um a 19 ovos. Nos machos o volume do testículo é significativamente maior no final da estação chuvosa, mas o diâmetro dos ductos deferentes não diferiu significativamente ao longo do ano. A variação na abundância sazonal parece ser influenciada principalmente por eventos reprodutivos de fêmeas e machos.

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APPENDIX

Specimens of *Echinanthera undulata* examined (Instituto Butantan – IB; Museu de Zoologia da USP – MZUSP; Museu Nacional do Rio de Janeiro – MNRJ; Museu de História Natural Capão da Imbuia – MHNCI; Museu de Ciências e Tecnologia – MCT; Museu de Ciências Naturais da Fundação de Zoobotânica do Rio Grande do Sul – NOPA).

Brazil: Minas Gerais (MZUSP 14055-58); Paraná (MHNCI 3362, 9980, 8325, 6026; NOPA 7742); Rio de Janeiro (MHNCI 3670); Santa Catarina (MCT 8369, 16751; MHNCI 3189, 7233, 11891; MN 7762); São Paulo (IB 187, 333, 357, 523, 528, 739, 788, 1101, 1188, 1628, 2168, 2644, 2649, 3249, 3367, 4449, 4596, 5037, 5421-22, 5531, 5661, 5804, 5872, 6036, 6566, 6903, 7019, 7253, 7545, 7658, 8149, 8246, 9338, 9374, 9575, 9582, 9610, 9630, 9686, 9891, 9910, 9933, 9970, 10026, 10190, 10238, 10433, 10434, 10518, 10528, 10529, 11412-13, 12467, 12976, 13018, 13021-22, 14613, 15455, 16086, 16305-06, 16730, 18086, 18174-76, 18352-55, 19161, 19708, 21183, 21258, 21501, 22656, 23390, 23638, 23715, 24966-67, 25014, 26569, 26635, 26744, 26748-52, 27131, 27134, 27418, 28237, 28421, 28561-62, 29453, 29470, 30313, 32723, 34356, 52204, 54206, 55652, 55655, 55754, 55757, 57376, 57536, 57589, 57663, 57712, 57746, 57872, 58100, 58142, 58250, 58292, 58405, 58477, 58576, 58478, 59470, 59979, 60159, 60178, 60234, 60241, 62236, 62331, 62393, 62458, 62557, 62670, 62727, 62779, 62934, 63037, 63466, 63992, 64232, 64777, 65083, 65533-35, 67165, 67790, 67940-42, 68100, 68129, 68247, 68711, 68820, 69888, 69995, 70092, 70159, 70427, 71013, 71052, 71264, 71778, 71821, 72093, 72427, 74074, 74271-72, 74279, 74282, 74990, 75321, 75373, 75387, 76331, 76382, 76406, 76426, 76446, 76477-78, 76550, 76721, 76780, 76807, 77172, 77194-95, 77211, 77294; MZUSP 6458-59, 10251, 10666, 11568, 12734, 12900, 13153, 15855, 17942).