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SEXUAL MALES IN THE PARTHENOGENETIC *Hemidactylus* cf. *garnotii* (SQUAMATA: GEKKONIDAE) IN MIZORAM, INDIA

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Abstract
Most lizard species reproduce sexually, with both males and females contributing genetic material to offspring. However, a subset, including certain gecko species, reproduces via parthenogenesis, wherein females produce offspring without fertilization. *Hemidactylus garnotii* Duméril & Bibron, 1836 *sensu lato*, a parthenogenetic species complex native to parts of Southeast Asia and India, was previously understood to consist solely of females. Despite earlier reports suggesting the possible existence of males, these were attributed to misidentification or incomplete verification. In this study, based on histological and gonadal examination, we report the first confirmed male individuals of *H. garnotii* from Mizoram, India. Specimens collected from Dampa Tiger Reserve and Palak National Wetland were analysed through morphological assessments, histology, and genetic sequencing (ND2 gene). Histological findings revealed spermatogenesis stages in males, establishing the presence of functional testes. Our results thus document a notable exception to the presumed all-female composition of *H. garnotii*, with implications for understanding reproductive strategies in this species.

Keywords: Fertilization, ND2 gene, histology, offspring, reproduction, spermatogenesis

Introduction

The study of reptilian reproduction reveals a predominance of sexual reproduction across most lizard species, involving both males and females contributing genetic material to offspring. This mode, while common, is energetically costly and can be hindered by the need for mates and environmental factors. However, in specific lineages, a unique form of asexual reproduction known as parthenogenesis has evolved, allowing certain species to reproduce without males. Parthenogenesis in lizards, first observed as an absence of males in certain populations, has now been documented in various reptilian taxa, notably in the genera *Lepidodactylus*, *Cnemidophorus*, and *Hemidactylus* (Maslin

1971, Lampert 2008). Parthenogenesis can occur facultatively, where females alternate between sexual and asexual reproduction, or obligately, where females reproduce solely through cloning without male involvement (Lampert 2008). This evolutionary strategy has allowed these lineages to thrive in stable environments, where genetic diversity is less critical for survival.

The species *Hemidactylus garnotii* (Duméril & Bibron 1836) is an example of obligate parthenogenesis in geckos. It has historically been classified as a strictly unisexual, all-female species, with extensive studies across its natural and introduced ranges consistently failing to detect male specimens (Kluge & Eckardt 1969). This has led to its classification as a triploid species, with each female producing clonal offspring without fertilization. The natural distribution of *H. garnotii* spans the Pacific and Southeast Asia, including countries such as India, Myanmar, Thailand, and Indonesia. Over time, this species has been introduced to regions outside its native range, including other islands in the Pacific and parts of the Americas, often associated with human activities such as trade and transport (Kluge & Eckardt 1969, Darevsky *et al*. 1978). Its ability to establish populations without requiring males has contributed to its success as an invasive species in various habitats. While some researchers reported the sporadic discovery of male individuals, these were largely attributed to misidentifications or errors in sex determination, reinforcing the view of *H. garnotii* as an exclusively parthenogenetic species (Darevsky *et al*. 1978).

The reproductive complexities observed in lizards are further exemplified by the *Lepidodactylus lugubris* complex, as described by Ineich (1988). This group, found in French Polynesia, demonstrates a unique unisexual-bisexual dynamic with the presence of diploid and triploid female clones, sexual males and females, and sterile intersex hybrids. These hybrids, originating from crosses between diploid clonal females and sexual males, exhibit abnormal genital tracts and are incapable of reproduction. Further studies revealed that the sexual males and females from French Polynesia were later assigned to a newly described sexual species from Indonesia, *Lepidodactylus pantai* (Karin *et al*. 2024). This intricate reproductive system highlights the coexistence of clonal and sexual lineages within the same geographical area and underscores the evolutionary and ecological significance of such systems. The situation observed in the *Lepidodactylus lugubris* complex provides a comparative framework for understanding *Hemidactylus garnotii*. Unlike the sterile intersex hybrids observed in *L. lugubris*, the females of *H. garnotii* exhibit normal genital tracts, and the males have been confirmed to possess functional testes, suggesting fertility. This distinction emphasizes the need for further research to unravel the evolutionary pathways and reproductive mechanisms within these gecko species (Ineich 1988, Karin *et al*. 2024).

In the present study, we report a novel observation of male individuals of *H. garnotii* sensu lato from Mizoram, India. Through detailed morphological examination and histological analysis, we confirm that these males exhibit normal, functional testes with active spermatogenesis, indicating fertility. Additionally, our DNA sequencing of the ND2 gene demonstrates that both males and females belong to the same genetic lineage, closely related to populations from Myanmar. This finding challenges the longstanding assumption of strict unisexuality in *H. garnotii*, suggesting either an overlooked aspect of reproductive flexibility or the possibility of cryptic sexual populations within what was believed to be a clonal lineage.

Material and Method

Material examined. Adult males MZMU 3074, MZMU 3075 and MZMU 3076, and adult female MZMU 3032 collected from Dampa tiger reserve (DTR), Mamit district, Mizoram, India (23.49964″N, 92.417487″E; alt. 903 m a.s.l) and adult females MZMU 3091, MZMU 3297 and MZMU 3299 collected from DTR and Palak National Wetland, Siaha district (22.202467″N, 92.88891″E; alt. 300 m a.s.l), Mizoram, India respectively.

Sampling and preservation. The collected specimens were catalogued, fixed in 10% buffered formalin, and later transferred in 70% ethanol in the Reptile section, Departmental Museum of Zoology, Mizoram University (MZMU), Aizawl. Species Identification was carried out with the help of relevant literature (Smith 1935, Giri & Baur 2008).

Morphological data. We made the following measurements using Mitutoyo dial vernier caliper to the nearest 0.1 mm under a dissecting microscope following the character definitions by Smith (1935), Giri & Bauer (2008), and Javed *et al*. (2010): snout-vent length (SVL, from tip of snout to vent), trunk length (TRL, distance from

axilla to groin measured from posterior edge of forelimb insertion to anterior edge of hindlimb insertion), body width (BW, maximum width of body), crus length (CL, from base of heel to knee), tail length (TL, from vent to tip of tail), tail width (TW, measured at widest point of tail), head length (HL, distance between retroarticular process of jaw and snout-tip), head width (HW, maximum width of head), head height (HH, maximum height of head, from occiput to underside of jaws), forearm length (FL, from base of palm to elbow), orbital diameter (OD, greatest diameter of orbit), nares to eye distance (NE, distance between anteriormost point of eye and nostril), snout to eye distance (SE, distance between anteriormost point of eye and tip of snout), eye to ear distance (EE, distance from anterior edge of ear opening to posterior corner of eye), internarial distance (IN, distance between nares), interorbital distance (IO, shortest distance between left and right supraciliary scale rows). Scale counts and external observations of morphology were made using a Wild M5 dissecting microscope.

***Histology*.** Histological studies were carried out according to a previously described protocol (Bancroft & Gamble 2002; Jerang *et al.* 2024). Briefly, the Bouin's fixed testis was dehydrated by ascending grades of ethanol (70%, 90%, 100%) and embedded in a paraffin wax block. The tissue block was then sectioned at a thickness of 7 µm using a Leica rotary microtome (model RM2125 RTS). The sections were deparaffinised in xylene, then rehydrated in a series of alcohol and stained with hematoxylin and eosin, followed by dehydration, clearing and lastly mounted with DPX mountant. The histological sections were observed and photographed using a camera-mounted microscope (Model DC.1359 F100, Euromex, Holland, Netherlands).

Molecular data. Genomic DNA of specimen of *H. garnotii* sensu lato (MZMU3075, MZMU1878, MZMU3032) was extracted from ethanol (100%) preserved liver tissue using Tissue Kit (Qiagen) following the manufacturer's instructions. PCR reaction was prepared for 20 µL reaction mixture containing 1× amplification buffer, 2.5 mM MgCl2, 0.25 mM dNTPs, 0.2 pM each forward and reverse primer, 1µL genomic DNA, and 1U Taq DNA polymerase with MetF1 & H5934 (Macey *et al.* 1997) primers. Sequence chromatograms were quality-checked, edited, and assembled into contigs using Sequence Scanner v1.0 (Applied Biosystems). Comparative ND2 sequences comprising *H. garnotii* and other close members of *Hemidactylus* were obtained from GenBank.

Sequence alignment was done using MUSCLE (Edgar 2004) in MEGA7 (Tamura & Nei 1993, Kumar *et al.* 2016) with default parameter settings. The best partitioning schemes for the dataset were searched through PartitionFinder v2 (Lanfear *et al.* 2017). The maximum Likelihood (ML) phylogenetic tree was reconstructed using an unpartitioned dataset in IQ-TREE (Nguyen *et al.* 2015) with the substitution model K3Pu+F+I selected based on the BIC scores by Model Finder (Kalyaanamoorthy *et al.* 2017). The ML analysis was run with an ultrafast bootstrap option (Minh *et al.* 2013) for 1000 iterations to assess clade support. The Uncorrected pairwise *p*-distance was calculated in MEGA7 (Kumar *et al.* 2016) with pairwise deletions of missing data and gaps.

Results

Based on the ND2 gene, the three specimens of *H. garnotii* (MZMU3075, MZMU1878, MZMU3032) are nested with *H. garnotii* from Myanmar, differing by an uncorrected *p*-distance of 0.001–0.004 (Fig 1, Table 1).

Table 1. Uncorrected *p*-distance amongst some members of *Hemidactylus* for ND2 gene

No	Sample	1	2	3	4	5	6	7	8	9	10	11
1	MZMU1878 *H. garnotii* (Mz)											
2	MZMU3032 *H. garnotii* (Mz)	0.000										
3	MZMU3075 *H. garnotii* (Mz)	0.000	0.000									
4	HM559631 *H. garnotii* (My)	0.001	0.001	0.001								
5	EU268364 *H. garnotii* (My)	0.002	0.002	0.002	0.003							
6	EU268363 *H. garnotii* (My)	0.003	0.003	0.003	0.004	0.004						
7	EU268374 *H. bowringii*	0.225	0.225	0.225	0.223	0.189	0.188					
8	EU268373 *H. bowringii*	0.227	0.227	0.227	0.226	0.191	0.190	0.002				
9	EU268362 *H. karenorum*	0.231	0.231	0.231	0.229	0.198	0.199	0.196	0.197			
10	EU268352 *H. platyurus*	0.269	0.269	0.269	0.267	0.233	0.231	0.237	0.238	0.234		
11	EU268371 *H. fasciatus*	0.315	0.315	0.315	0.313	0.287	0.286	0.270	0.272	0.308	0.307	

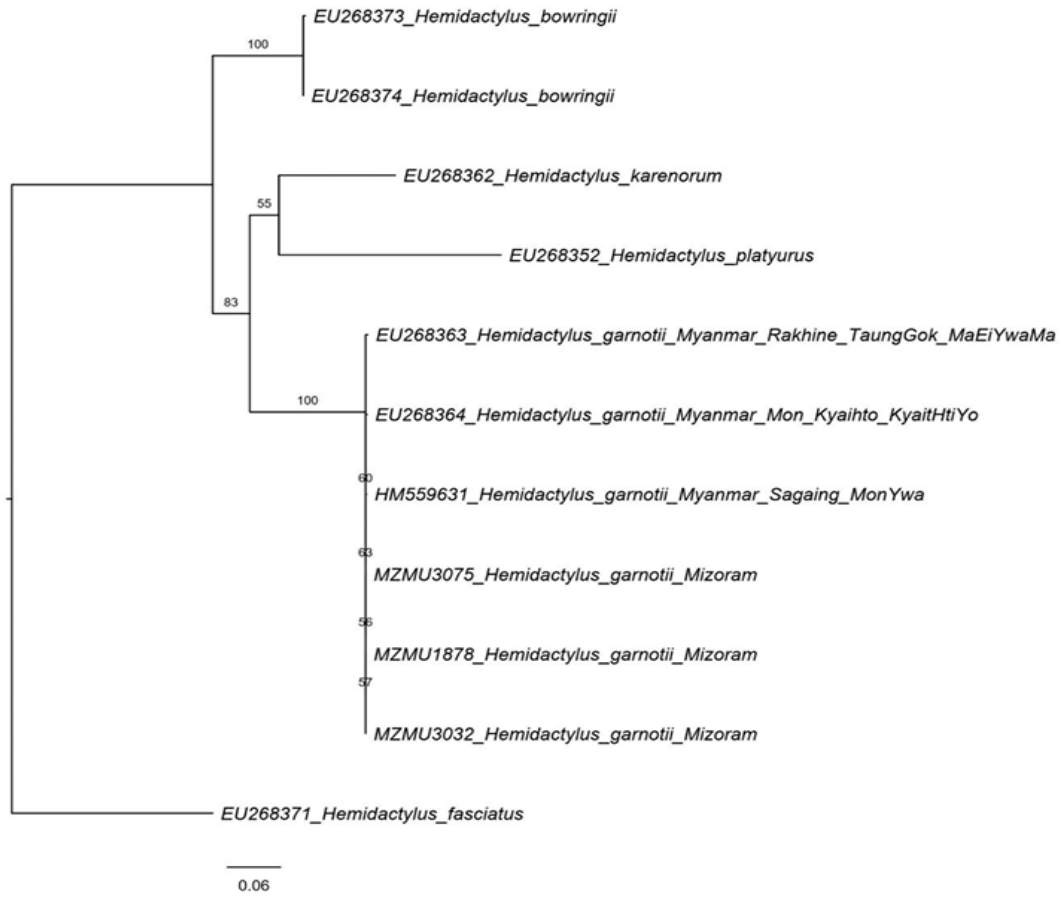

Figure 1. Maximum likelihood phylogeny of *Hemidactulus* cf. *garnotii* and other closely related congeners based on ND2 gene (MZMU3075 = Male, MZMU3032 = female, MZMU1878 = not determined); preceding the species name is NCBI accession number and numbers at nodes represent bootstrap support values.

Morphologically, the specimens from Mizoram have key diagnostic characteristics of *H. garnotii*, which include an outer pair of postmentals separated from infralabials by small scales; the presence of skin fold along the posterior margin of hind limbs; a depressed tail, possessing a sharp, serrated lateral edge; ventral side of the tail having median series of transverse enlarged rows of plates (Fig. 2).

Thus, based on genetic and morphological analyses, we can confirm the population of Mizoram to be *H. garnotii* sensu lato. However, as we do not possess samples from its type locality, Tahiti, French Polynesia, the Mizoram population of *H. garnotii* sensu lato is considered here to be *H.* cf. *garnotii* for the time being.

Mensural and meristic data. An adult *H.* cf. *garnotii* male SVL ranges from 48.42 to 54.06 mm and female ranges from 42.4 to 56.44 mm (Fig. 3, Table 2). Head is distinct from neck with pointed snout, covered with minute homogenous granular scales (HeadL/SVL 15–18%), (HeadW/HeadL 100–120%), and (HeadH/HeadL 49–61%). Eyes round and large, vertical pupil, ear opening distinct and oval (OD/HL 35–50%), (EE/OD 84–122%), (SE/HL 63–75%) and (OD/SE 51–69%). Body is dorsoventrally flattened, and moderately slender (Trunk/SVL 32–51%). Two pairs of pentagonal chin shields, the inner post mental are in contact with the infralabial scales, and the outer post mental is separated from the infralabial scales by a row of smaller gular scales; the anterior chin shield is moderately larger than the posterior chin shield (supralabials 11–13), (infralabial 9–12). Males with distinct femoral and pre-cloacal pores ranging from 35–39 in number interrupted by 1 or 2 poreless scales, and females may have pitted scales in the femoral and pre-cloacal region (20). Dissected males show the presence of distinct testicles which are bean-shaped and are present obliquely in the lower abdominal region.

The dorsal surface of the body is covered with minute uniform granular scales, the ventral surface of the body is distributed with even smooth oval/cuboidal scales from the axilla to the groin region; intermixed with larger cuboidal scales on the central region and smaller cuboid scales along the peripheral region of the ventral surface; no ventrolateral skin fold on the trunk.

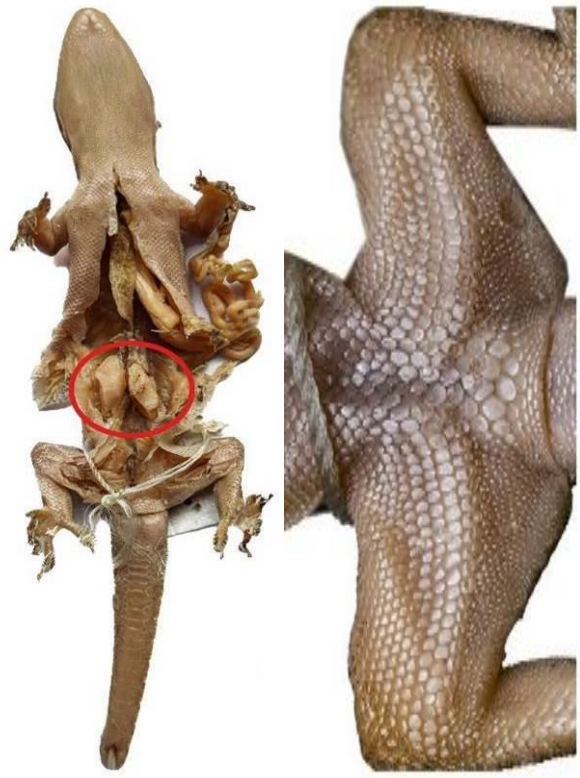

Figure 2. An adult male of *Hemidactylus* cf. *garnotii* (MZMU 3076) from Mizoram, India: **(A)** ventral view of the body with red circle points to the testis; (B) femoral and cloacal region showing distinct pores.

Digits free, strongly clawed, moderately long bearing divided scansors except for the terminal lamellae pad; hindlimbs comparatively longer than forelimbs; limbs are indistinctly webbed at the base of the both pes and manus digits (FL/SVL 8–12%), (CL/SVL 12–16%). The dorsum surface of the limb is also distributed with small granular tubercles; smooth scale underneath. The IV digit of forelimb possesses (10–12) lamellae pads and IV digit of hindlimb possesses (12–13) lamellae pads.

Tail is strongly depressed with serrated margins or with sharp denticulated lateral edge, ventrally flattened and distinctly segmented with uniform subcaudal scales overlapping ventrolaterally from vent to at least mid-length (Tail/SVL 58–124%). Dorsally the tail is covered with small granular tubercles; notably more swollen at the base ventrally in males than females. A pair of pre-cloacal spurs is distinctly present in males but not distinct in females and males have cloacal and femoral pores absent in females. Furthermore, *H.* cf. *garnotii* has an outer pair of postmental separated from infralabials by small scales *versus* outer pair of postmental touches the infralabials in other regional congeners.

Colouration in life. In life, the dorsum colour varies in all individuals from light grey to light brown. Mid dorsal line prominent, continuous with a white spot-bearing lateral strip, usually the dorsal surface with small white spots commonly present, running laterally from head to tail, and also scattered to the limbs. In the light phase, the dorsum is nearly uniform beige or with faded markings on a light background. The ventral surface is whitish-beige underneath.

In preservative, the dorsum colour is lighter in comparison and has turned pale greyish in preservative; the small white spots distributed throughout the dorsal laterally not visible; Yellowish beneath. The tail is regenerated from the mid-length.

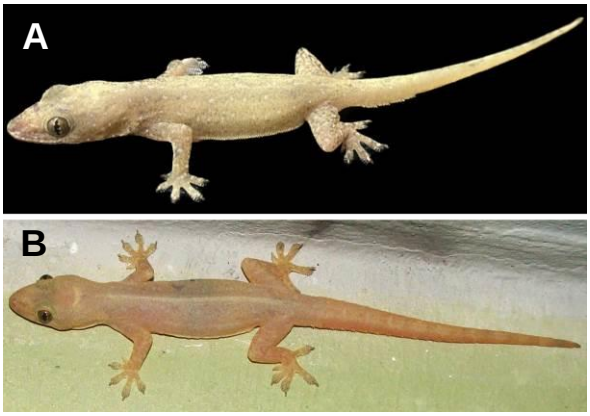

Figure 3. *Hemidactylus* cf. *garnotii* in life from Mizoram, India: **(A)** female (MZMU3032) and **(B)** male (MZMU3074)

***Histology*.** Histological examination of the gonads of *H.* cf. *garnotii* revealed the presence of distinct stages of spermatogenesis (Fig. 4). The testes exhibited well-defined seminiferous tubules containing germ cells at various developmental stages. Spermatogonia, the undifferentiated germ cells, were predominantly located along the basal lamina of the seminiferous tubules. Moving toward the tubular lumen, we observed primary spermatocytes, which were characterized by enlarged nuclei undergoing meiotic division. Secondary spermatocytes, arising from the first meiotic division, were identified closer to the tubular lumen, exhibiting condensed chromosomes indicative of ongoing meiosis. Further progression of spermatogenesis was evident with the presence of round spermatids, characterized by condensed chromatin and prominent acrosomal structures. Finally, mature spermatozoa, displaying characteristic tail structures and compacted nuclei, were observed

within the lumens of the seminiferous tubules. The sequential arrangement of these germ cell populations within the seminiferous epithelium reflects the progression of spermatogenesis from undifferentiated spermatogonia to mature spermatozoa, indicative of active spermatogenic activity in male *H.* cf. *garnotii* individuals.

Discussion

Considering all available data, it is confirmed that males of *H.* cf. *garnotii* exists in Mizoram, which has not been documented. Kluge & Eckardt (1969) reported that this species is exclusively composed of females and considered it a parthenogenetic species and all the previous reports of males were deemed inaccurate. In contrast, we recorded three male specimens found only in Dampa, Mamit District. Among them, a continuous series of femoral pores (35–39 in total) that separated at the pelvic region by 1 or 2 non-pored scales, a hemipenial bulge, and a pair of testes were observed on a dissection from the male species of *H.* cf. *garnotii.* However, no femoral pores and hemipenial bulges were observed in females with less prominent precloacal spurs.

Other noteworthy features include that all of the morphometric and meristic measurements of the male *H.* cf. *garnotii* match the description of the female *H. garnotii* features provided by Smith (1935), which all contribute to sexual dimorphism in this species. According to Cole (1996), some "all-female" species such as *Cnemidophorus* do possess femoral pores but the pores are only exclusive to males in certain species and both (Smith 1935 and Taylor 1922) described female *H. garnotii* with femoral pores, which is quite unusual.

Even though many female species of lacertids have been reported with femoral pores the female species of these genera particularly *Hemidactylus* except *H.* cf. *garnotii* are all reported to have no femoral pores, this character being limited to males to date. Nevertheless, the presence of spermatogonia, primary spermatocyte, secondary spermatocyte, round spermatids, and spermatozoa from the testicular histology of the male *H.* cf. *garnotii* strongly indicates that they are for sure a male and are sexually dimorphic as the other *Hemidactylus* species.

Table 2. Morphometric (in mm) and meristic data of *Hemidactylus* cf. *garnotii* from Mizoram, India

Character	MZMU 3074	MZMU 3075	MZMU 3076	MZMU 3032	MZMU 3091	MZMU 3297	MZMU 3299
Sex	M	M	M	F	F	F	F
snout-vent length (SVL)	54.06	50.46	48.42	42.4	49.3	56.44	56.16
trunk length (TRL)	22.98	21.72	24.89	13.86	20.12	24.84	22.72
body width (BW)	9.32	7.18	7.36	9.18	8.28	13.66	9.62
crus length (CL)	7.98	7	6.94	6.08	7.94	7.06	7.26
tail length (TL)	52	30.5	28.54	47.02	61.62	72.64	61.98
tail width (TW)	5.96	4.28	4.26	4.46	5.92	6.24	5.84
head length (HL)	8.54	8.28	7.7	7.84	8	10.02	9.58
head width (HW)	10.26	8.56	7.32	7.92	8.06	9.24	8.52
head height (HH)	4.24	4.9	3.92	4.82	4.3	5.96	5.12
forearm length (FL)	5.12	4.24	5.92	4.38	5.06	5.18	5.34
orbital diameter (OD)	3.72	3.62	3.58	3.94	3.66	4.32	3.36
nares-eye distance (NE)	4.4	4.26	3.1	3.7	3.78	4.69	4.02
snout-eye distance (SE)	5.76	5.54	5.48	5.92	5.24	6.32	6.52
eye-ear distance (EE)	3.9	4.42	3.08	3.58	3.36	3.65	3.04
internarial distance (IN)	1.56	1.74	1.08	1.4	1.42	1.42	1.54
interorbital distance (IO)	4.7	4.18	3.9	4.48	3.46	3.68	3.86
lamellae (left) manus	6-9-10-11-8	6-10-10-12-9	6-7-10-11-10	6-8-10-11-8	5-10-10-11-9	6-9-10-12-10	6-9-10-11-9
lamellae (right) manus	6-9-10-12-9	6-10-11-11-9	6-8-10-11-10	6-8-10-11-8	5-10-9-10-8	6-9-11-11-9	6-9-11-11-9
lamellae (left) pes	6-10-11-13-10	6-11-11-13-9	6-10-12-13-10	6-9-11-13-10	6-10-11-13-9	6-10-11-13-10	6-10-12-13-10
lamellae (right) pes	6-10-12-13-10	6-9-10-13-10	6-10-12-13-10	6-9-10-12-9	6-10-10-13-10	6-10-12-13-10	6-10-11-13-10
supralabial (left)	12	11	11	13	11	12	13
supralabial (right)	13	11	11	11	11	12	12
infralabial (left)	12	11	10	11	9	10	10
infralabial (right)	12	9	10	10	9	9	10
Femoral + precloacal pores	35	38	39	–	–	–	–

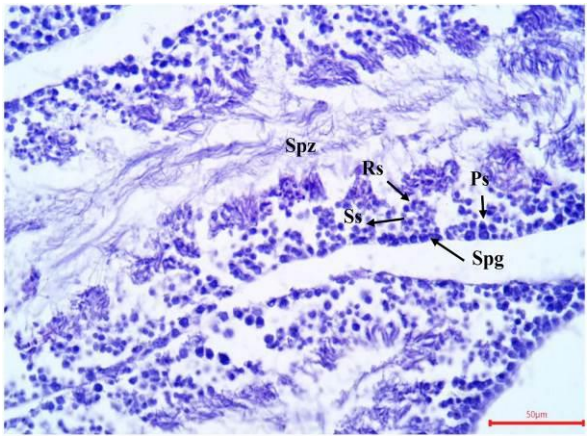

Figure 4. The testis of *Hemidactylus* cf. *garnotii* (MZMU 3075) showed normal testicular morphology and regular spermatogenesis events including the presence of primary spermatocytes (Ps), secondary spermatocytes (Ss), round spermatids (Rs), Sertoli cells in the seminiferous tubules, the presence of Leydig cells in the interstitium and sperms (Spz) in the lumen of the tubules. Magnification 40×, scale bar: 50 µm.

Our study revealed that male *Hemidactylus* cf. *garnotii* specimens from Mizoram exhibit functional testes with active spermatogenesis, strongly indicating fertility. This contrasts with observations in other parthenogenetic geckos, such as the *Lepidodactylus lugubris* complex, where sterile intersex hybrids are commonly documented. Molecular analysis showed that the Indian populations of *H.* cf. *garnotii* share a close genetic relationship with those from Myanmar, as evidenced by the low uncorrected pairwise *p*-distances. However, specimens from the type locality (l'Ile de Taiti [=Tahiti, French Polynesia]) of *H. garnotii* have not been sequenced, leaving uncertainty about whether the populations in Myanmar and India represent the true *H. garnotii* or a cryptic lineage. This finding underscores the importance of future studies, including the sequencing of specimens from the type locality, to clarify the taxonomic and genetic status of these populations.

Our study confirms that the *Hemidactylus* cf. *garnotii* population in Mizoram comprises both males and females of the same taxon, as evidenced by morphological, histological, and genetic analyses. The males are fertile, and the females are normal and reproductively viable, supporting the hypothesis of a stable sexual population within what was previously thought to be an exclusively unisexual species. Molecular data further reveal that these Indian populations are genetically similar to those from Myanmar, though the absence of genetic data from the type locality of *H. garnotii* leaves open the possibility of taxonomic uncertainty.

Future studies should focus on cytogenetic analyses to determine whether the females in this population are triploid, as in *H. garnotii* sensu stricto, or if they are diploid, representing an ancestral sexual lineage. This ancestral lineage may have hybridized with another species to give rise to the triploid clonal populations previously documented. These findings underscore the complexity of *H. garnotii* sensu lato's reproductive biology and highlight the need for further research to unravel its evolutionary history and clarify its taxonomic and genetic relationships.

Author contributions

All the authors contributed equally.

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Research permits

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