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Another piece in the puzzle: A new species of *Phyllodytes* Wagler, 1830 (Anura, Hylidae) from the Atlantic Forest of southern Bahia, northeastern Brazil

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Abstract. We describe *Phyllodytes gravata* sp. nov., a new species of bromeligenous treefrog from the Atlantic Forest of southern Bahia, Brazil. The new species is characterised by its small body size (males 19.5–22.0 mm snout-vent length; female 23.5 mm), a rounded snout with an apical tubercle, an inconspicuous row of tubercles along the tarsus, with a single prominent tubercle at the tibiotarsal articulation, a dorsolateral brown stripe, and an advertisement call composed of long series of pulsed notes (22–34 notes/call; call duration 5.2–7.3 s; dominant frequency 2.75–3.83 kHz). The species is currently known from only two nearby localities within the Central Corridor of the Atlantic Forest (CCAF), in the municipality of Porto Seguro, district of Trancoso, Bahia, a major tourist destination, where it inhabits bromeliads in sandy-soil ecosystems known as mussunungas. Its apparently microendemic distribution and strict association with bromeliads render it vulnerable to several anthropogenic threats, such as bromeliad harvesting, increasing tourism, urbanisation, and agriculture. This discovery underscores the persistent hidden diversity of the CCAF and reinforces the urgent need to protect its highly special microhabitats.

Keywords. Taxonomy, Amphibia, Bioacoustic, Bromeliad, Conservation.

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Introduction

The Brazilian Atlantic Forest (BAF) is recognised for its high levels of biodiversity and endemism, often attributed to its complex topography and environmental heterogeneity (Martini *et al*. 2007; Peres *et al*. 2020; Paz *et al*. 2021). The BAF comprises several vegetation types, known as phytophysiognomies, such as Dense Ombrophilous Forest (evergreen rainforest), Seasonal Deciduous and Semideciduous Forests, Restingas (coastal sandy plains), and High-Altitude Grasslands (Veloso *et al.* 1991; Fundação SOS Mata Atlântica 2021). Within the Dense Ombrophilous Forests, particularly in the coastal lowlands, the so called Tabuleiro Forests are situated, which contain enclaves of sandy soils known as Mussunungas, distributed across the states of Bahia and Espírito Santo (Peixoto & Simonelli 2007). Mussunungas are open vegetation formations characterised by sandy, oligotrophic soils with high water stress, resulting in low-statured (7 to 10 m) and sparsely distributed vegetation, resembling Restingas but occurring further inland (Simonelli *et al*. 2008; Saporetti-Junior *et al*. 2012). Although they share similar edaphic characteristics, Restingas are directly influenced by marine environments, exhibiting denser vegetation adapted to coastal salinity conditions (Opolski-Neto & Melo-Jr. 2022).

These vegetation types share plant species adapted to sandy soils, particularly members of the Bromeliaceae Juss. family. Many bromeliads have leaf axils that retain water, forming plant-held water bodies that serve as microhabitats for various organisms called phytotelmata (Peixoto & Simonelli 2007; Alarcón-Elbal *et al*. 2024). A diverse array of organisms is associated with these phytotelmata, including invertebrates (Arango *et al*. 2011; Laviski *et al*. 2021), as well as vertebrates such as lizards and amphibians (Gondim-Silva *et al.* 2016; Oliveira *et al*. 2017; Sabagh *et al*. 2017; Martins *et al*. 2019; Rocha *et al*. 2021; Jorge *et al*. 2021). Among amphibians, two ecological categories are recognised: bromelicolous species, which utilize bromeliads primarily for shelter and foraging (e.g., Albertim *et al*. 2010), and bromeligenous species, which complete their entire life cycle within bromeliads, relying on these plants for reproduction and larval development (e.g., Alves-Silva & Silva 2009; Pimenta *et al*. 2009; Faivovich *et al*. 2010; Ferreira *et al*. 2015).

Among bromeligenous anurans, the genus *Phyllodytes* Wagler, 1830 has been the focus of numerous studies in recent years, with an emphasis on taxonomy, phylogenetics, ecology, and behaviour (Ferreira *et al*. 2012; Campos *et al*. 2014; Orrico *et al*. 2018; Tonini *et al*. 2020; Blotto *et al*. 2021; Carilo Filho *et al*. 2021; Marques *et al*. 2024; Sato *et al*. 2025). Blotto *et al*. (2021) conducted a comprehensive phylogenetic analysis of the tribe Lophyohylini Faivovich *et al*., 2005, identifying seven candidate species within *Phyllodytes*. Subsequent studies have formally described two of these lineages (Dias *et al*. 2020; Santos *et al*. 2023), whereas the taxonomic status of the remaining lineages has yet to be clarified (*Phyllodytes* sp. 1, 4–7). Despite recent advances in the taxonomy of *Phyllodytes*, the genus remains incompletely understood and each newly described species represents a key piece of the puzzle for understanding the diversity, evolutionary history, and biogeographic patterns of this bromeligenous genus within the BAF.

Among the 16 recognised species of *Phyllodytes*, at least four – *P. luteolus* (Wied-Neuwied, 1821), *P. melanomystax* Caramaschi, Silva & Britto-Pereira, 1992, *P. praeceptor* Orrico, Dias & Marciano, 2018 and *P. punctatus* Caramaschi & Peixoto, 2004 – are associated with bromeliads in sandy soil environments (Bokermann 1966; Caramaschi *et al*. 1992; Caramaschi & Peixoto 2004; Orrico *et al*. 2018). Field surveys conducted in Mussununga areas of the Environmental Protection Area (APA) of Caraíva, Trancoso, in southern Bahia, Brazil, yielded specimens of *Phyllodytes* identified in the molecular phylogeny by Blotto *et al*. (2021) as the candidate species *Phyllodytes* sp. 6, a sister clade to *P. amadoi* Vörös, Dias & Solé, 2017 plus the candidate species *P.* sp. 7. More recently, we visited Mussununga areas within the Private Natural Heritage Reserve (RPPN) Rio do Brasil, also in Trancoso, where we collected additional specimens and bioacoustic data of *Phyllodytes* sp. 6. Based on the analysis of this material, we describe a new species for *Phyllodytes* from the Atlantic Forest of southern Bahia.

Material and methods

Fieldwork and voucher specimens

Individuals and bioacoustics data for the new species were collected during two field expeditions (March 2007 and January 2024) in the district of Trancoso, Porto Seguro, Bahia, Brazil. Specimens were collected under permit SISBIO/ICMBio #84813-2 and euthanised using 5% lidocaine hydrochloride, fixed with 10% formalin, and preserved in 70% ethanol. Muscle tissue samples were preserved in 100% ethanol. The collected material was deposited in the Museu de Zoologia da Universidade Estadual de Santa Cruz (MZUESC, Ilhéus, Bahia, Brazil), amphibian collection of the Museu de História Natural da Bahia, Universidade Federal da Bahia (UFBA, Salvador, Bahia, Brazil), and the Museu de Zoologia da Universidade de São Paulo (MZUSP, São Paulo, Brazil).

Institutional abbreviations

CHUFPE = Coleção Herpetológica da Universidade Federal de Pernambuco.
MBML = Museu de Biologia Professor Mello Leitão.
MZUESC = Museu de Zoologia da Universidade Estadual de Santa Cruz, Ilhéus, Brazil.
MZUSP = Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil.
UFBA = Museu de História Natural da Bahia, Salvador, Bahia, Brazil.

Morphological data

We compared the new species with all its congeners, including the candidate species *Phyllodytes* sp. 7 sensu Blotto *et al*., (2021). Diagnostic characters were chosen following the characters most frequently used in previous taxonomic descriptions of *Phyllodytes* species. Specimens used for comparison are deposited in MZUESC, MZUSP, CHUFPE and MBML. See Appendix 1 for a complete list of examined specimens. Additionally, we reviewed literature data (Peixoto & Cruz 1988; Caramaschi *et al*. 1992; Peixoto *et al*. 2003; Caramaschi & Peixoto 2004; Cruz *et al.* 2007; Marciano *et al*. 2017; Vörös *et al*. 2017; Orrico *et al*. 2018; Dias *et al*. 2020).

We recorded the following measurements:

DF3 = width of disc on 3rd finger
ED = eye diameter
END = eye-nostril distance (from naris to anterior edge of the eye)
FL = foot length (distance from proximal edge of inner metatarsal tubercle to tip of 4th toe)
HAL = hand length (from base of inner metacarpal tubercle to tip of 3rd finger)
HL = head length (distance from angle of jaws to snout-tip)
HW = head width (measured at posterior angle of jaws)
IND = internarial distance
IOD = interorbital distance
SVL = snout-vent length (distance from the tip of the snout to the back edge of vent)
TAL = tarsus length (distance from heel to proximal edge of inner metatarsal tubercle)
TBL = tibia length (distance from outer edge of flexed knee to tip of hee)
TD = tympanum diameter
THL = thigh length (from vent to outer edge of flexed knee)
4TD = 4th toe disc diameter

SVL, HL, HW, THL, TBL, and FL were measured with digital calipers to the nearest 0.02 mm, while the remaining measurements were taken using a stereo microscope equipped with a millimetre scale. Measurements and definitions followed Kok & Kalamandeen (2008), except for IOD, which was measured between the anterior corners of the eyes to improve repeatability. The shape of the snout in dorsal and lateral views was assessed according to Heyer *et al*. (1990), the description of dorsal skin texture followed Kok & Kalamandeen (2008), and the webbing formula was defined following Savage & Heyer (1967, 1997), with measurements taken from the left hand and foot. Colouration in life was described from digital photographs of living individuals. Sex was determined based on the presence of external secondary sexual characters (nuptial pads, vocal slits, and vocal sac expansion). To investigate the morphological divergence between the new species and *Phyllodytes amadoi*, we performed a Principal Component Analysis (PCA) based on morphometric variables. The analysis included ten males of *P. amadoi* and 14 of the 15 individuals from the type series of the new species. One specimen (MZUSP-A 149540) was excluded due to unreliable data for two of its measurements. The PCA was applied to two datasets: one using untransformed (raw) measurements, and another based on the residuals obtained from regressing all morphometric variables against SVL, aiming to remove the influence of body size. All analyses were carried out using the software PAST, ver. 4.12 (Hammer *et al*. 2001).

Molecular data

The new species is assigned to the genetic lineage previously identified as *Phyllodytes* sp. 6 by Blotto *et al.* (2021). This taxonomic assignment is supported by the direct morphological examination of the voucher specimens sequenced by those authors (MTR13517 = MZUSP-A 149538 and MTR13518 = MZUSP-A 149539), which are included in our type series. Our newly collected specimens, including the holotype, are morphologically indistinguishable from these genetically identified reference specimens and were collected in the same district and within similar habitats, further supporting their conspecific status. The new species (*Phyllodytes* sp. 6) was recovered as the sister taxon to *Phyllodytes amadoi* + *P.* sp. 7 in the phylogenetic analysis by Blotto *et al.* (2021). These authors also reported a 16S rDNA fragment (~570 bp) divergence of 8.5% between *P.* sp. 6 (MTR13518) and *P. amadoi* (MZUESC 14953, 14954), and of 7.4–7.7% between *P.* sp. 6 (MTR13518) and *P.* sp. 7 (MTR 16426, 16428; MZUESC 18949, 18951). Additionally, we analysed two specimens of *Phyllodytes* sp. 7 (MZUESC 18949, 18951), which were also sequenced by Blotto *et al.* (2021).

Bioacoustic data

Advertisement calls were recorded from eight individuals at the RPPN (Private Natural Heritage Reserve) Rio do Brasil, Trancoso, Bahia, Brazil, between January 26 and 27, 2024. Recordings were made using a Tascam DR-40X digital recorder coupled with a Sennheiser ME66/K6 unidirectional microphone. All calls were recorded in uncompressed WAV format with a sampling rate of 44.1 kHz and 16-bit resolution. The holotype was recorded on January 27, 2024, at 25.6°C air temperature and 84.7% relative humidity. Paratypes (MZUESC 23884, 23885, 23887, 23890, 23892, 23915, 23922) were recorded on 26 and 27 January 2024, at air temperatures ranging from 25.2°C to 27.2°C and relative humidity between 84.1% and 84.7%. Five consecutive advertisement calls were selected per individual for analysis.

Acoustic analyses were conducted using Raven Pro 1.6 (Cornell Lab of Ornithology, Ithaca, NY, USA). Temporal parameters were measured from oscillograms, and spectral parameters were obtained from spectrograms. Spectrogram settings were as follows: Hann window with a size of 1024 samples, 3 dB filter bandwidth of 61.9 Hz, 90% time grid overlap, time grid size of 102 samples, Discrete Fourier Transform (DFT) size of 1024 samples, and frequency grid spacing of 43.1 Hz. Call descriptions followed the recommendations and note-centered terminology proposed by Köhler *et al.* (2017).

Advertisement calls were analysed using the following parameters: (1) call structure, (2) call duration (measured from the peak amplitude of the first note to the peak amplitude of the last note), (3) inter-call interval (from the peak amplitude of the last note of a call to the peak amplitude of the first note of the subsequent call), (4) number of notes per call, (5) note duration, (6) inter-note interval, (7) note rate (notes per second), (8) dominant frequency of the call, (9) dominant frequency of individual notes, (10) 90% bandwidth, (11) 5% frequency, (12) 95% frequency, and (13) number of pulses per note. Numerical data are presented as mean ± standard deviation, with minimum and maximum values in parentheses, along with the sample size. Comparative data on advertisement calls of congeners were obtained from the literature (Weygoldt 1981; Simon & Gasparini 2003; Nunes *et al.* 2007; Lima *et al.* 2008; Juncá *et al.* 2012; Roberto & Ávila 2013; Campos *et al.* 2014; Cruz *et al.* 2014; Magalhães *et al.* 2015; Marciano *et al.* 2017; Vörös *et al.* 2017; Orrico *et al.* 2018; Dias *et al.* 2020).

Results

Class Amphibia Linnaeus, 1758
Order Anura Fischer von Waldheim, 1813
Family Hylidae Rafinesque, 1815
Subfamily Hylinae Rafinesque, 1815
Genus *Phyllodytes* Wagler, 1830

Phyllodytes gravata sp. nov.
urn:lsid:zoobank.org:act:FF6D0BDA-3533-4340-BC19-2BFE9069F75E
Figs 1–2; Table 1

Phyllodytes sp. 6 – Blotto *et al*. 2021: 7–9, table 1, fig. 5.

Diagnosis

The new species is assigned to the genus *Phyllodytes* based on the occurrence of odontoids in the lower jaw and molecular data supporting the placement of *Phyllodytes gravata* sp. nov. (as *Phyllodytes* sp. 6) as sister taxon of *P. amadoi* + *Phyllodytes* sp. 7 (Blotto *et al*. 2021). The new species is distinguished from its congeners by a combination of the following characters: small-sized adults, SVL = 19.5–22.0 mm in

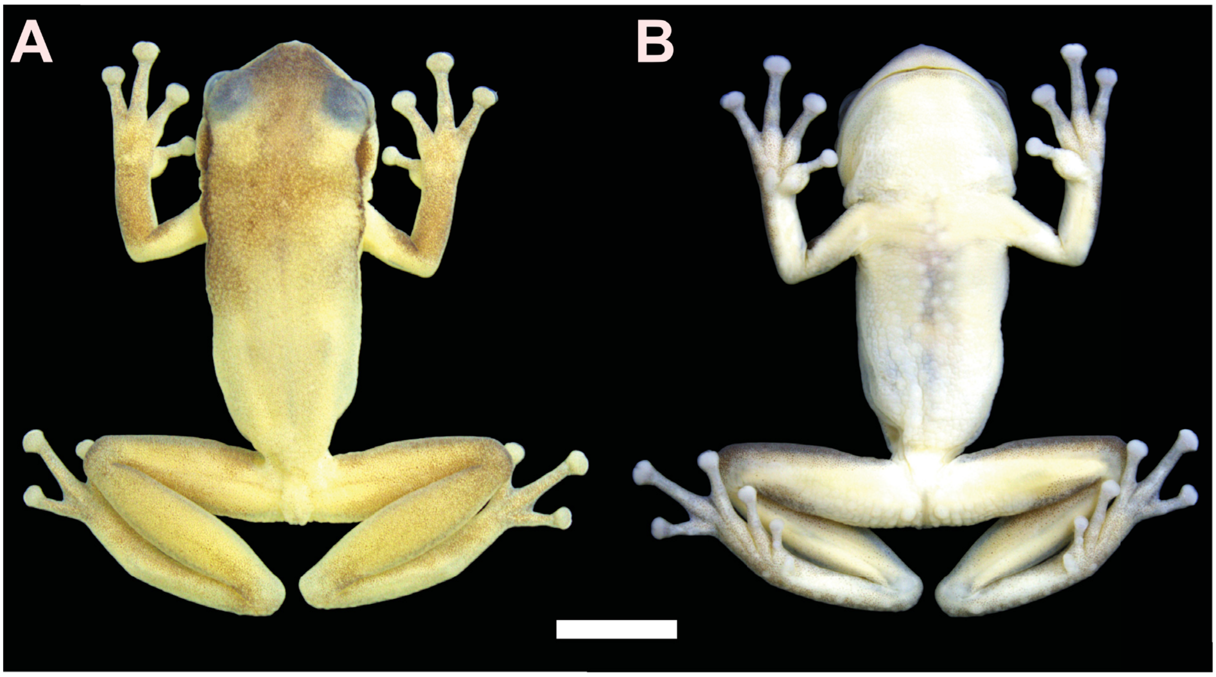

Fig. 1. *Phyllodytes gravata* sp. nov. in preservative, holotype, ♂ (MZUESC 23891). **A**. Dorsal view of body. **B**. Ventral view of body. Scale bar = 5 mm.

males (n = 15) and SVL = 23.5 mm in the female (n = 1); slender body; head slightly wider than long (HL 90.5% of HW); snout rounded in dorsal view and lateral profile with a small apical tubercle; canthus rostralis rounded; loreal region concave; tympanum and tympanic annulus distinct; supratympanic fold extending from the posterior region of the eye to near the arm insertion; single subgular vocal sac; two large anterior odontoids followed by three to six smaller ones on each side of the mandible in adults; lateral margin of the forearms with three to four discrete outer tubercles, with either fused or unfused bases; a discrete row of tubercles along the tarsus, ending with a prominent tubercle near the tibio-tarsal junction; light brown coloration on the snout, gradually becoming lighter along the dorsum until turning cream, usually with small light brown blotches on the dorsum; a brown stripe extending from the snout to slightly beyond the arm or midbody; venter with two to four central rows of tubercles flanked by smaller irregularly arranged tubercles; and advertisement call consisting of a series of 22–34 pulsed notes, with a duration of 5.2–7.3 s and a dominant frequency ranging from 2.75 to 3.83 kHz.

Etymology

The specific epithet *gravata* is a popular name used in Brazil for plants of the family Bromeliaceae. This name is used as an invariable noun in apposition and derived from the Tupi language, Karawatá, largely used by native people before the colonization. As an oxytone, its pronunciation follows [gra-va-TAH], with stress on the final syllable. The first and second ‘a’ sounds resemble the ‘a’ in ‘apple’. This new species name is a reference to the habits of species of *Phyllodytes* that characteristically live and reproduce in tank-bromeliads of the Atlantic Forest.

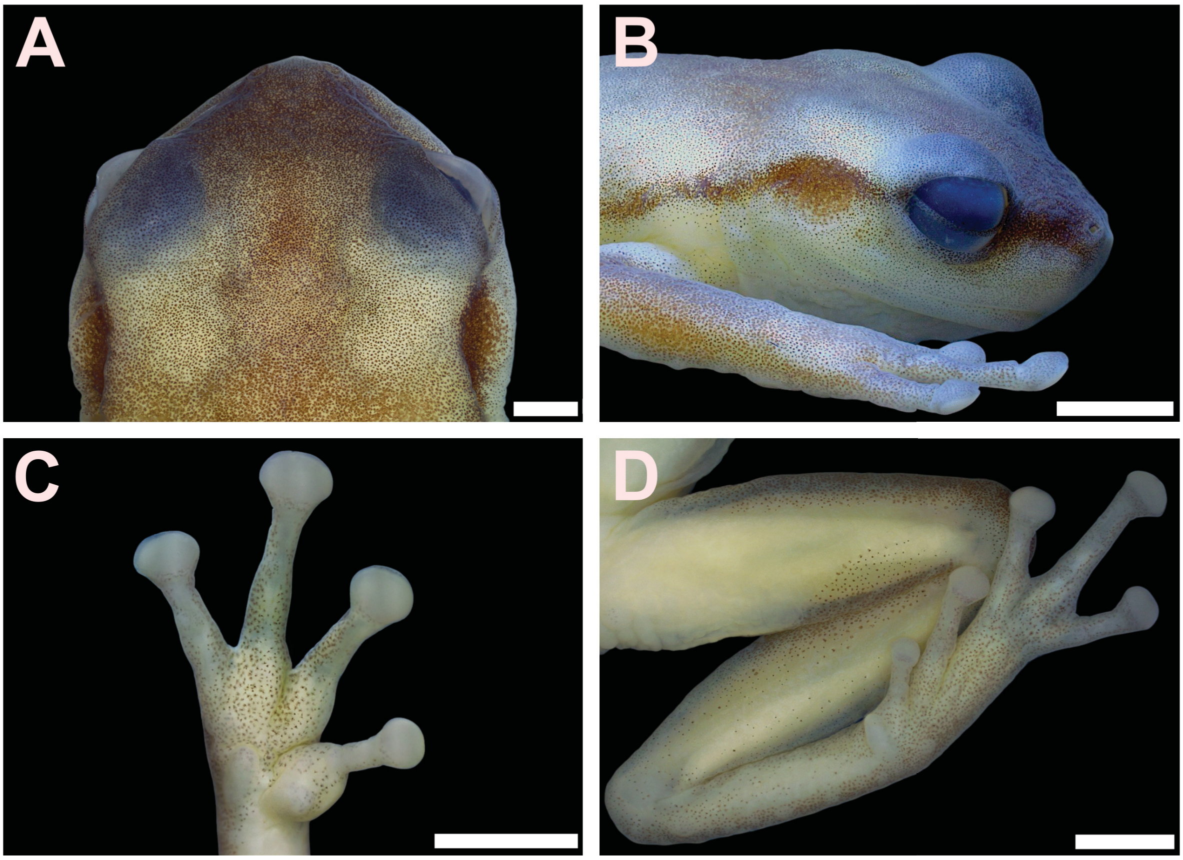

Fig. 2. *Phyllodytes gravata* sp. nov. in preservative. Holotype, ♂ (MZUESC 23891). **A**. Dorsal view of head. **B**. Lateral view of head. **C**. Ventral views of hand. **D**. Ventral view of foot. Scale bars: A = 1 mm; B–D = 2 mm.

Table 1. Measurements (mm) of the holotype and type series of *Phyllodytes gravata* sp. nov. Values are presented as mean ± SD.

	Males (n = 15)		Female (n = 1)
	Holotype MZUESC 23891	**Mean ± SD (Min – Max)**	**MZUESC 23889**
SVL	20.0	20.8 ± 0.6 (19.5–21.7)	23.5
HW	7.1	7.7 ± 0.3 (6.9–8.3)	8.0
HL	6.5	7.0 ± 0.3 (6.2–7.3)	7.8
IND	1.0	1.1 ± 0.2 (0.9–1.6)	1.0
END	1.9	1.8 ±0.1 (1.5–2.0)	2.3
IOD	4.4	4.3 ± 0.4 (3.7–5.0)	4.9
ED	2.2	2.2 ± 0.1 (1.8–2.3)	2.7
TD	1.4	1.2 ± 0.2 (0.9–1.6)	0.9
THL	9.7	9.8 ± 0.5 (8.7–10.6)	10.9
TBL	10.4	10.5 ± 0.3 (9.9–11.0)	11.5
TAL	5.7	5.6 ± 0.2 (5.3–6.0)	6.4
FL	8.1	8.2 ± 0.5 (7.3–9.2)	9.0
HAL	5.9	6.0 ± 0.3 (5.5–6.5)	6.5
DF3	1.2	1.0 ± 0.2 (0.5–1.3)	1.4
4TD	1.3	1.0 ± 0.2 (0.5–1.3)	1.3

Type material

Holotype

BRAZIL – **Bahia State** • ♂; Porto Seguro, Trancoso, RPPN Rio do Brasil; -16.557547, -39.120899; 54 m a.s.l.; I.R. Dias and L. Santos leg.; 27 Jan. 2024; MZUESC 23891.

Paratypes

BRAZIL – **Bahia State** • 1 ♀; same collection data as for holotype; MZUESC 23889 • 5 ♂♂; same collection data as for preceding; MZUESC 23887, 23890, 23892 and 23922; UFBA 17656 (ex-MZUESC 23888) • 4 ♂♂; same collection data as for holotype; 26 Jan. 2024; MZUESC 23884–85, 23915; UFBA 17657 (ex-MZUESC 23886) • 5 ♂♂; Porto Seguro, Trancoso, Fazenda Nova Alegria; -16.606111, -39.144833; 50 m a.s.l.; M.T. Rodrigues, P.M.S. Nunes, M. Teixeira Jr., T. Mott, and J.M. Guellere leg.; 26–27 Mar. 2007; MZUSP-A 149538, 149539, 149540, 149541, 149542.

Description of holotype

Adult male in good state of preservation. Measurements are given in Table 1. Body slender; head wider than long (HL 91.5% of HW; HW 35.5% of SVL; HL 32.5% of SVL); snout rounded in dorsal view, with a small apical tubercle; rounded in profile; nostrils small, round, directed anterolaterally; canthus rostralis rounded; loreal region concave; internarial distance smaller than eye-nostril distance (IND 52.6% of END); eyes large, prominent, and directed anterolaterally (ED 33.8% of HL; 31.0% of HW; 115.8% of END; tympanum medium-sized (TD 19.7% of HW; 7.0% of SVL), distinct, and nearly circular, diameter larger than internarial distance (TD 140.0% of IND), more than half of the eye-to-nostril distance (TD 73.7% of END) and eye diameter (TD 63.6% of ED); tympanic diameter greater than the third finger disc width (TD 116.7% DF3) and the fourth toe disc diameter (TD 107.7% of 4TD); tympanic annulus evident; supratympanic fold evident, extending from the posterior corner of the orbit, covering the dorsal edge of the tympanum, to near the insertion of the arm; vocal sac subgular; vocal slits present; oval, flat tongue; vomerine teeth arranged in two slightly spaced, horizontal rows, positioned between and behind the choanae; each side of the mandible with two large anterior odontoids, followed by three small ones; horizontal pupil.

Forearms slightly wider (in cross-section) than arms, with three or four small tubercles along the lateral edge; one tubercle on the lateral side of the fourth finger; hands large (HAL 90.8% of HL); subarticular tubercles round, largest on the fourth finger; supernumerary tubercles indistinct; palmar tubercle oval, smaller than the thenar tubercle; thenar tubercle elongated; relative finger lengths: I < IV < II < III; light-coloured nuptial pad on the internal base of the finger I, unspotted and lacking dark excrescences, contrasting with the surrounding skin, which bears dark spots; finger webbing formula I 2 ½ – 1- II 1+ – 2+ III 2+ – 1- IV.

Hind limbs long (THL + TBL + TAL + FL equals 169.5% of SVL); thigh length shorter than tibia length (THL 93.3% of TBL; THL 48.5% of SVL; TBL 52.0% of SVL); sum of thigh and tibia lengths equal to SVL (THL + TBL 100.5% of SVL); one prominent tubercle at the insertion of each leg; a discrete row of tubercles on the tarsus, with a single large tubercle on posteroventral internal margin of tarsus, near to tibiotarsal junction; tarsal length smaller than foot length (TAL 70.4% of FL); foot length smaller than thigh and tibia lengths (FL 83.5% of THL; FL 77.9% of TBL); subarticular tubercles rounded; supernumerary tubercles indistinct; inner metatarsal tubercle is large and elongated; outer metatarsal tubercle small and round; toe webbing formula I 1 – 2+ II 2- – 3- III 1 – 3- IV 3+ – 1+ V.

Supracloacal crest absent; skin smooth, except for chest, belly and ventral of thighs that rugose; ventral tubercles arranged in two central rows, bordered by smaller tubercles not arranged in rows.

In preservative, the snout is light brown, with dark brown markings extending to the middle of the body and the tibia region, while the rest of the body is pale yellow. A light brown stripe extends from the snout to just beyond the forelimbs. The ventral surfaces are pale yellow.

Variation

Most specimens of the type series are morphologically consistent with the holotype. Variation in measurements is presented in Table 1. MZUSP-A 149539 has a truncate snout in dorsal view, MZUSP 149538-A has a truncate snout in lateral view, and specimen MZUSP-A 149542 has a protruding snout in lateral view. UFBA 17657 exhibits three tubercles at the tip of the snout, one central and two lateral. MZUESC 23915 presents a distinct crest between the nares. In MZUESC 23889 (female), both the tympanum and the tympanic annulus are poorly defined. MZUESC 23885, MZUESC 23890 and UFBA 17657 display a single tubercle on the lateral margin of finger IV. MZUESC 23887 exhibits a second prominent tubercle at the left tibio-tarsal articulation. MZUESC 23884, MZUESC 23891 and UFBA 17657 lack the light brown speckling typically observed along the dorsum. MZUESC 23922, MZUSP-A 149538 and MZUSP-A 149540 have a stripe that starts at the snout and extends to the middle of the body.

In life (Fig. 3), individuals exhibit a predominantly yellowish dorsal colouration, with dark brown speckling reaching the mid-dorsum in most specimens and extending to the posterior limbs in some. Brown dorsolateral stripes originate at the tip of the snout, pass through the ocular and tympanic regions, and become progressively diffuse, terminating just beyond the forelimbs or near the midbody. Some individuals lack a defined dorsal pattern, while in others the lateral stripes are faint or nearly imperceptible. The ventral surfaces are predominantly yellowish.

Comparison with congeners (character states for the other species are shown in parenthesis)

Phyllodytes gravata sp. nov. is distinguished by its smaller adult size (19.5–23.5 mm SVL) when compared to *P. kautskyi* Peixoto & Cruz, 1988 (36.5–43.5 mm SVL), *P. maculosus* Cruz, Feio & Cardoso, 2007 (39.5–43.5 mm SVL), and *P. magnus* Dias *et al.* 2020 (36.4–41.1 mm SVL); from *P. acuminatus* Bokermann, 1966 and *P. iuna* Santos, Roseno, Solé & Dias, 2023 by its wider-than-long head (head as long as wide); and by its rounded snout in dorsal view, differing from *P. acuminatus*, *P. kautskyi*, *P. megatympanum* Marciano, Lantyer-Silva & Solé, 2017, and *P. wuchereri* (Peters, 1873) (pointed snout). It further differs from *P. melanomystax*, and *P. praeceptor* by usually possessing a small apical tubercle on the snout (absent).

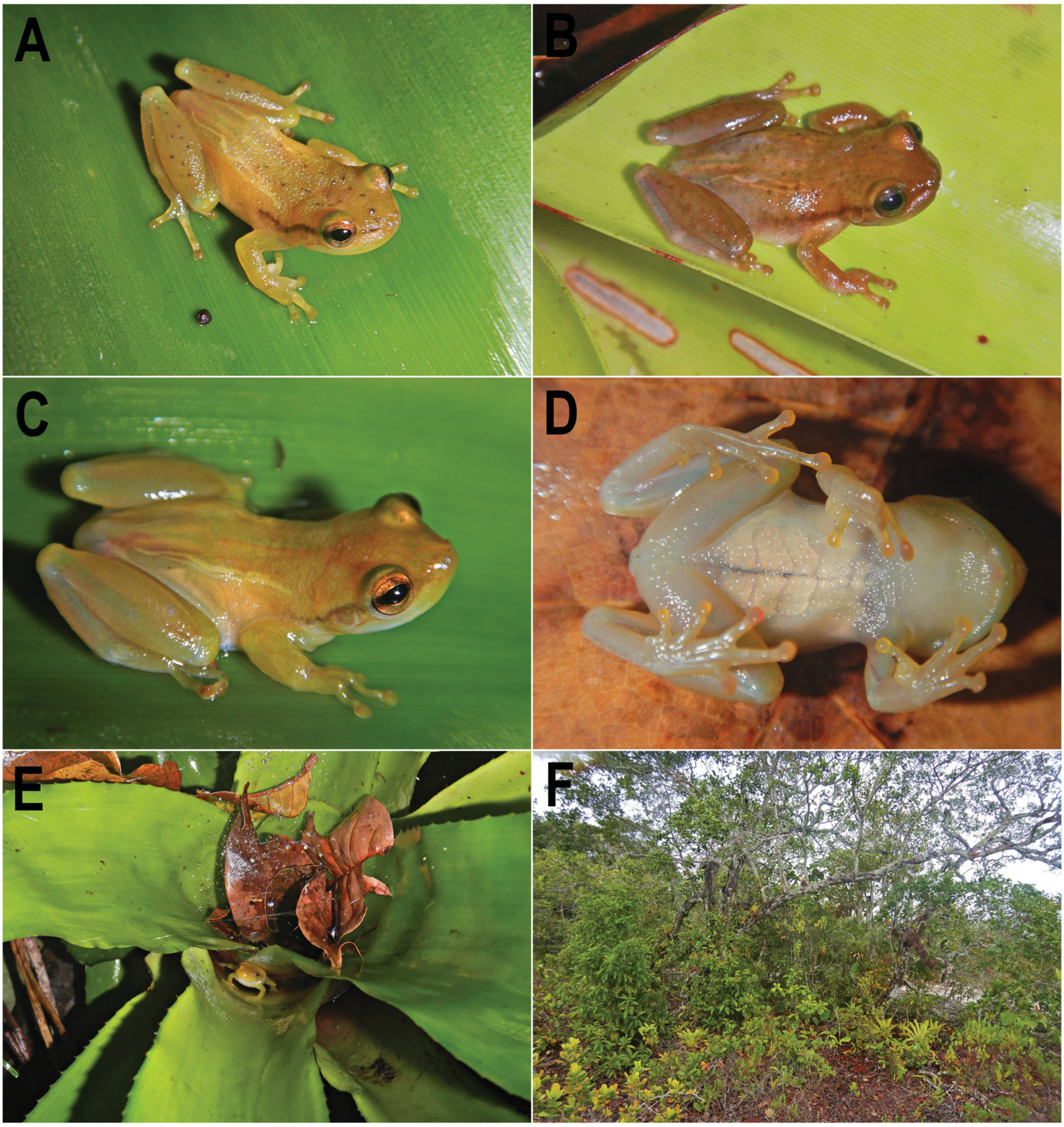

Fig. 3. In-life photographs of *Phyllodytes gravata* sp. nov. **A**. Paratype, ♂ (MZUESC 23915). **B**. Paratype, ♂ (MZUESC 23885). **C**. Paratype, ♂ (MZUESC 23884) Dorsal view. **D**. Paratype, ♂ (MZUESC 23884) ventral view. **E**. *Aechmea lamarchei* Mez; **F**. Mussununga, the natural habitat at the type locality.

Phyllodytes gravata sp. nov. lacks conspicuous groin colouration, a diagnostic feature distinguishing it from *P. gyrinaethes* Peixoto, Caramaschi & Freire, 2003 (red groin) and *P. megatympanum* (yellow groin). Additionally, the tympanum of *P. gravata* is distinct and proportionally smaller (TD 3.8–7.2% of SVL), which contrasts with *P. acuminatus* and *P. megatympanum* (TD 7.73–8.16% of SVL), as well as with *P. gyrinaethes* (tympanum hidden) and *P. melanomystax* (tympanum barely visible). *Phyllodytes gravata* differs from *P. tuberculosus* Bokermann, 1966 by lacking the pair of evident lateral tubercles on the hand (two evident lateral tubercles).

Phyllodytes gravata sp. nov. has an inconspicuous row of tubercles along the tarsus, with a single prominent tubercle at the tibiotarsal articulation, differing from *P. iuna* and *P. praeceptor* (a single prominent tibiotarsal tubercle), and from *P. kautskyi*, *P. luteolus*, *P. maculosus*, *P. magnus*, *P. megatympanum*, *P. melanomystax*, *P. tuberculosus*, and *P. wuchereri* (a row of evident tubercles, which may or may not exhibit a prominent tubercle at the tibiotarsal articulation). Additionally, *P. luteolus*, *P. maculosus* and *P. tuberculosus* may also exhibit a double crenulated row of tubercles along the tarsus. *Phyllodytes gravata* differs from *P. punctatus* by the presence of two large anterior odontoids on each side of the mandible (one large odontoid), and by the absence of supernumerary tubercles on the plantar surface (present) (Caramaschi & Peixoto 2004).

Phyllodytes gravata sp. nov. typically exhibits a dark brown stripe extending from the snout, passing through the eye, and terminating either just posterior to the arm insertion or at midbody (Fig. 4). Between the snout tip and the eye, this stripe is usually paler and may be less distinct or even absent in some individuals (e.g., MZUESC 23922, MZUSP 149538-A, MZUSP 149540-A). Most specimens show dark spots or blotches on the dorsum between the dorsolateral stripes, except for MZUESC 23884, MZUESC 23891 and UFBA 17657. When present, the pale stripe between the snout and the eye distinguishes *P. gravata* from *P. acuminatus*, *P. brevirostris* (Peixoto & Cruz 1988), *P. edelmoi* Peixoto, Caramaschi & Freire, 2003, *P. gyrinaethes*, *P. kautskyi*, *P. maculosus*, and *P. magnus* (absence of an evident stripe between the nostril and the eye) and from *P. melanomystax* (which exhibits a dark stripe). *Phyllodytes gravata* is distinguished from *P. wuchereri* by the presence of a single dorsolateral stripe (two dorsolateral white stripes bordered by dark brown to black lines). Additionally, the new species differs from *P. brevirostris* (Peixoto & Cruz 1988), *P. edelmoi*, *P. kautskyi*, *P. megatympanum*, and *P. magnus* by usually having spots and blotches on the dorsum (immaculate dorsum).

Morphologically, *Phyllodytes gravata* sp. nov. is most similar to *P. amadoi*. However, it differs from *P. amadoi* by having a rounded snout in lateral view (vertical), inconspicuous tubercles along the tarsus with a single prominent tubercle near the tibiotarsal articulation (only one tibiotarsal tubercle in most cases, although some specimens [MZUESC 14941, 14943, 14952, 14959, 24028] present a subtle and barely visible row of tubercles along the tarsus, usually on only one side of the body), and exhibit a dorsal coloration with less contrasting spots and blotches when compared to *P. amadoi* (see Fig. 7). Additionally, *P. gravata* is larger in body size, as evidenced by non-overlapping morphospace in PCA of uncorrected data (PC1+PC2 = 80.75% variance; PC1 driven by SVL, PC2 by FL; Fig. 5, Table 2). This separation disappears when size-adjusted (PC1+PC2 = 54.5% variance; PC1 influenced by FL and THL, PC2 by HW and HL; Fig. 5, Table 2). Under these conditions, individuals of both species showed substantial overlap in morphospace, indicating that the morphological differences observed are largely due to variation in body size. Nevertheless, the new species differs from *P. amadoi* by an divergence of 8.5% in the 16S rRNA gene (Blotto *et al.* 2021), and by differences in the characteristics of the advertisement call (see Bioacustics comparisons with congeners). In addition, *P. gravata* can be distinguished from *P.* sp. 7, a phylogenetically proximate lineage (sensu Blotto *et al.* 2021), by its dorsal colour pattern (see Fig. 7), by a divergence of 7.4–7.7% in the 16S rRNA gene (Blotto *et al.* 2021), and by differences in the advertisement call (see Discussion).

Advertisement call

The advertisement call (Fig. 6) of *Phyllodytes gravata* sp. nov. has a mean duration of 6.1 ± 0.6 s (5.2–7.3 s; n = 40), with inter-call intervals averaging 67.1 ± 18.7 s (range: 42.7–110.9 s; n = 40). Calls consist of 27.0 ± 3.8 notes (22–34; n = 40), each with a duration of 0.02 ± 0.002 s (0.004–0.094 s; n = 1079) and inter-note intervals of 0.19 ± 0.015 s (0.06–0.39 s; n = 1040). The note emission rate is 4.3 ± 0.2 notes/s (4.0–4.9 notes/s), each note has a mean of 15.5 ± 2.4 pulses (range 1–37), which are emitted at a rate of 403.36 ± 69.58 (117.6–952.3) pulses/s. The first five notes typically contain fewer pulses (1–13) than the following ones. The advertisement call of *P. gravata* exhibits an ascending pattern of amplitude modulation, with the initial intensity being low and generally increasing gradually over the first eight notes, after which the amplitude tends to stabilise. However, the individual notes themselves display an inverse structure, each beginning with high intensity and decreasing in amplitude to form a distinct descending pattern (Fig. 6)

The mean dominant frequency of calls is 3.31 ± 0.28 kHz (2.75–3.83 kHz; n = 40), while notes exhibit a mean dominant frequency of 3.2 ± 0.3 kHz (1.33–4.17 kHz; n = 1079). In 37.5% of calls (n = 15), the

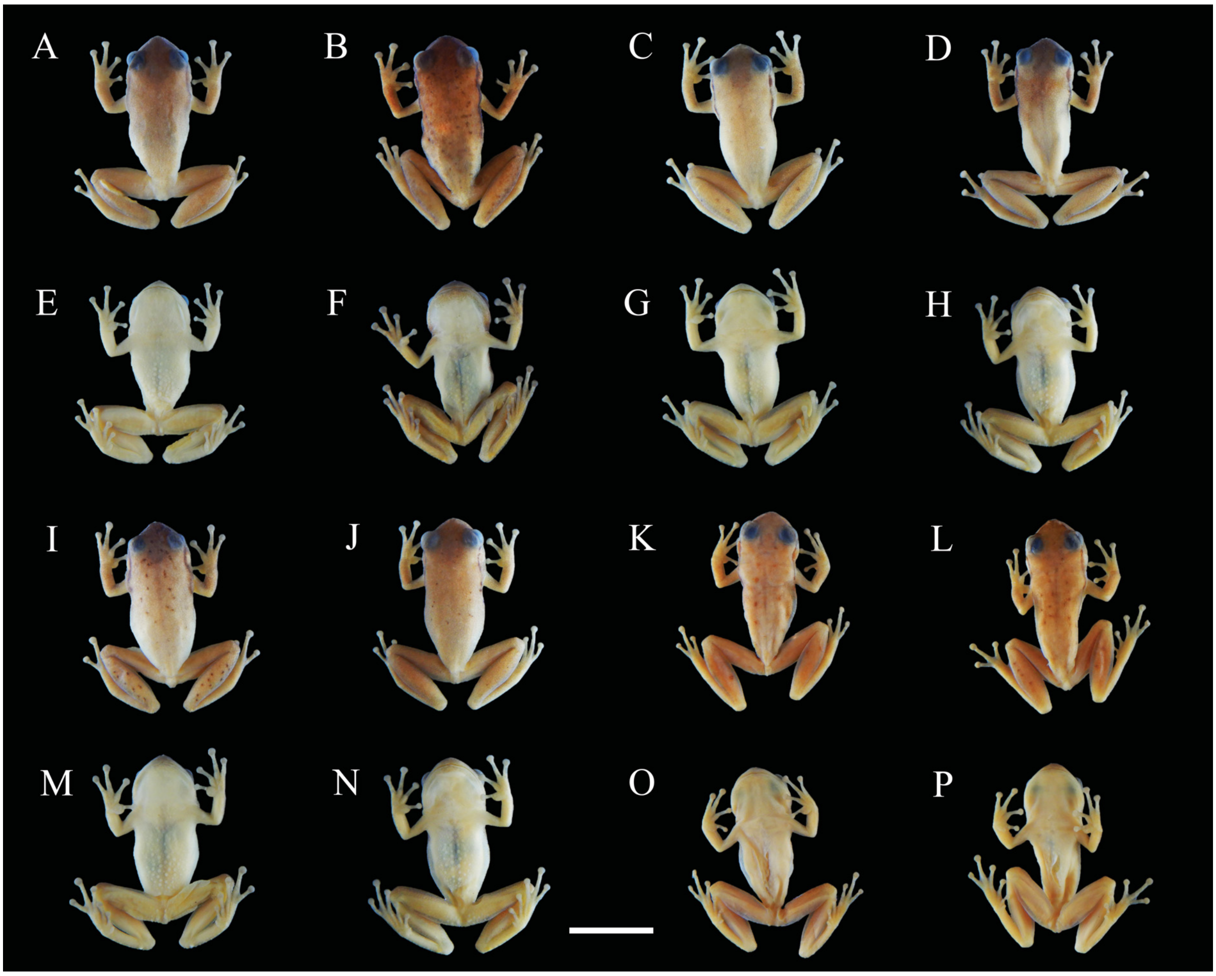

Fig. 4. Dorsal and ventral color pattern variation in preserved specimens of *Phyllodytes gravata* sp. nov. **A, E**. ♂ MZUESC 23884. **B, F**. ♂ MZUESC 23885. **C, G**. ♂ MZUESC 23890 **D, H**. ♂ MZUESC 23891. **I, M**. ♂ MZUESC 23915. **J, N**. ♂ MZUESC 23922. **K, O**. ♂ MZUSP 149538-A. **L, P**. ♂ MZUSP 149539. Scale bar: 10 mm.

Table 2. Loadings of the principal component analysis of male measurements of *Phyllodytes gravata* sp. nov. (n = 14) and *P. amadoi* (n = 10).

Variables	Raw Measurements		Residual SVL	
	Component 1	Component 2	Component 1	Component 2
SVL	0.747	-0.531	-	-
HW	0.280	0.074	0.339	0.630
HL	0.170	-0.138	0.101	0.641
IND	0.079	0.002	0.062	0.105
END	-0.014	0.164	0.110	-0.062
ED	0.064	0.043	0.093	0.083
IOD	0.101	0.160	0.185	0.031
TD	0.086	0.183	0.177	-0.091
THL	0.239	0.362	0.453	-0.057
TBL	0.258	0.239	0.347	-0.079
TAL	0.165	-0.039	0.096	0.160
FL	0.319	0.636	0.639	-0.340
HAL	0.224	0.085	0.193	-0.088
DF3	0.054	0.030	0.049	-0.024
D4TD	0.043	0.042	0.051	-0.044

first two notes displayed dominant frequencies below the mean (1.33–2.5 kHz). The 90% bandwidth averages 1.5 ± 0.1 kHz (1.4–1.7 kHz; n = 40). The 5% and 95% frequency limits are 2.4 ± 0.3 kHz (1.7–2.9 kHz) and 4.0 ± 0.2 kHz (3.4–4.7 kHz), respectively (n = 40 for both).

Bioacoustic comparisons with congeners

The number of notes per call in *Phyllodytes gravata* sp. nov. (27 ± 3.8; 22–34; n = 40) is greater than in *P. amadoi* (14.5 ± 1.0; 13–17; n = 17, Vörös *et al.* 2017), *P. acuminatus* (1–4, Campos *et al.* 2014), *P. gyrinaethes* (4.9 ± 0.6; 4–6, Roberto & Ávila 2013), *P. luteolus* (8–15, Weygoldt 1981), *P. megatympanum* (13.37 ± 2.56; 10–19; n = 19, Marciano *et al.* 2017), *P. melanomystax*

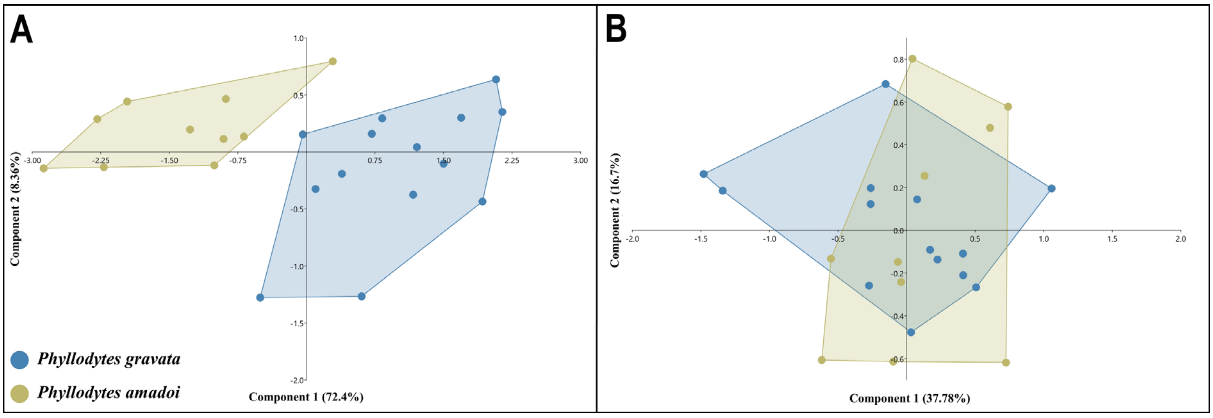

Fig. 5. A. Principal component analysis (PCA) of raw morphological measurements. **B**. PCA of size-corrected residuals (accounting for SVL) in adult specimens of *Phyllodytes gravata* sp. nov. (blue) and *P. amadoi* (green). The variance explained by each axis is indicated in parentheses.

(1, Nunes *et al.* 2007), *P. praeceptor* (8.3 ± 1.5, 6–12; n = 28, Orrico *et al.* 2018), and *P. wuchereri* (10–21, Cruz *et al.* 2014; Magalhães *et al.* 2015). However, there is overlap with the upper range of *P. tuberculosus* (18.6 ± 3.3; 14–23; n = 5, Juncá *et al.* 2012).

The call duration of *P. gravata* sp. nov. (6.1 ± 0.6 s; 5.2–7.3; n = 40) is longer than that of *P. amadoi* (3.41 ± 0.28 s; 2.99–4.11; n = 17, Vörös *et al.* 2017), *P. gyrinaethes* (1.3–2.3 s; n = 13, Roberto & Ávila 2013), and *P. melanomystax* (0.07 ± 0.04 s, Nunes *et al.* 2007). The note duration in *P. gravata* (0.02 ± 0.002 s; 0.004–0.094; n = 1079) is shorter than that of *P. edelmoi* (0.1 ± 0.003 s; 0.044–0.163 , Lima *et al*. 2008), *P. luteolus* (0.125 s, Weygoldt 1981) and *P. praeceptor* (0.295 ± 0.075 s; 0.141–0.538; n = 235, Orrico *et al.* 2018).

Phyllodytes gravata sp. nov. has a lower mean number of pulses (15.5 ± 2.4; 1–37; n = 1079) than *P. praeceptor* (28.7 ± 9.4; n = 89), *P. tuberculosus* (24.55 ± 4.36; n = 40), and *P. wuchereri* (16.18 ± 3.2; n = 11). In contrast, its mean pulse repetition rate is higher (403.3 ± 69.58; 117.6–952. 3; n = 1079) than that of the aforementioned species (*P. praeceptor*: 98.9 ± 15.8 pulses/s; *P. tuberculosus*: 169.1 ± 28.1 pulses/s; *P. wuchereri*: 204.6 ± 41.4 pulses/s). Moreover, *P. gravata* also exhibits a higher mean pulse repetition rate than *P. amadoi* (368.4 ± 86.6 pulses/s).

Additionally, the pulsed call structure of *P. gravata* distinguishes it from species with harmonic calls such as *P. acuminatus*, *P. kautskyi*, *P. megatympanum*, and *P. melanomystax* (Simon & Gasparini 2003; Nunes *et al.* 2007; Campos *et al.* 2014; Marciano *et al.* 2017), and *P. magnus* (pulsed and harmonic, Dias *et al.* 2020).

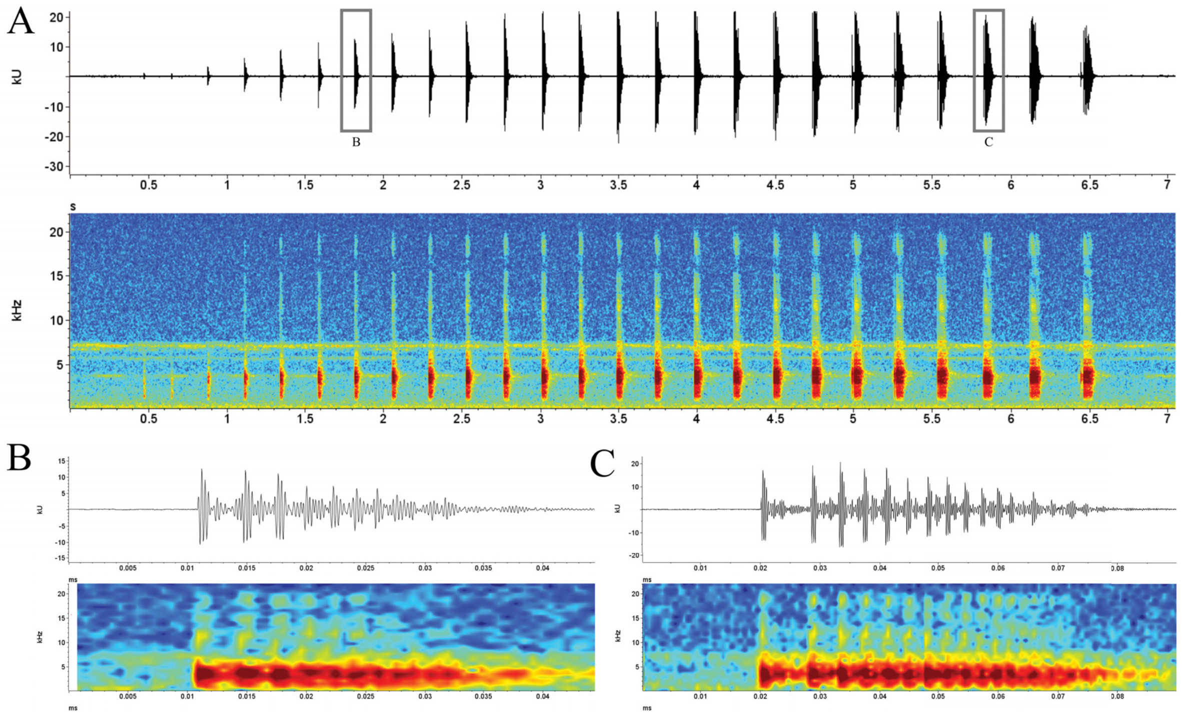

Fig. 6. Advertisement call of *Phyllodytes gravata* sp. nov., holotype, ♂ (MZUESC 23915, 25.6°C). **A**. Oscillogram and audiospectrogram of the advertisement call (Hann window, 512-point FFT**,** 90% overlap). **B**–**C**. Oscillograms and audiospectrograms of the seventh and twenty-third notes, respectively, showing pulse organisation (Hann window, 64-point FFT, 50% overlap).

Natural history and geographic distribution

Specimens of *Phyllodytes gravata* sp. nov. were recorded vocalizing shortly after sunset in mussununga formations in the district of Trancoso, Porto Seguro, southern Bahia, Brazil (Fig. 7). Individuals were observed in both terrestrial (*Aechmea lamarchei* Mez and *Vriesea* sp. Lindl - Bromeliaceae; Fig. 3E–F) and epiphytic bromeliads, the latter located approximately 50 cm above ground level. Some males were observed with the posterior part of their body submerged in water while vocalizing. The species was recorded at two nearby localities: (1) the Private Natural Heritage Reserve (RPPN) Rio do Brasil, encompassing an area of approximately 9 km², and (2) Fazenda Nova Alegria. Both sites are situated within the Central Corridor of the Atlantic Forest (Fig. 7). Mussunungas are often mistaken for restinga formations; however, they occur inland as enclaves of sandy soil within Florestas de Tabuleiro (tableland forests) and are not associated with the shoreline. These ecosystems remain understudied, but existing research indicates that they harbour distinctive assemblages of flora and fauna, including several endemic and understudied species (Simonelli *et al.* 2008; Borges *et al.* 2020; Godoy & Piratelli 2020; Lima *et al.* 2021). Although *P. gravata* has so far only been recorded in mussununga, our field sampling was geographically restricted. Further research is needed to determine whether this species also occurs in adjacent vegetation types.

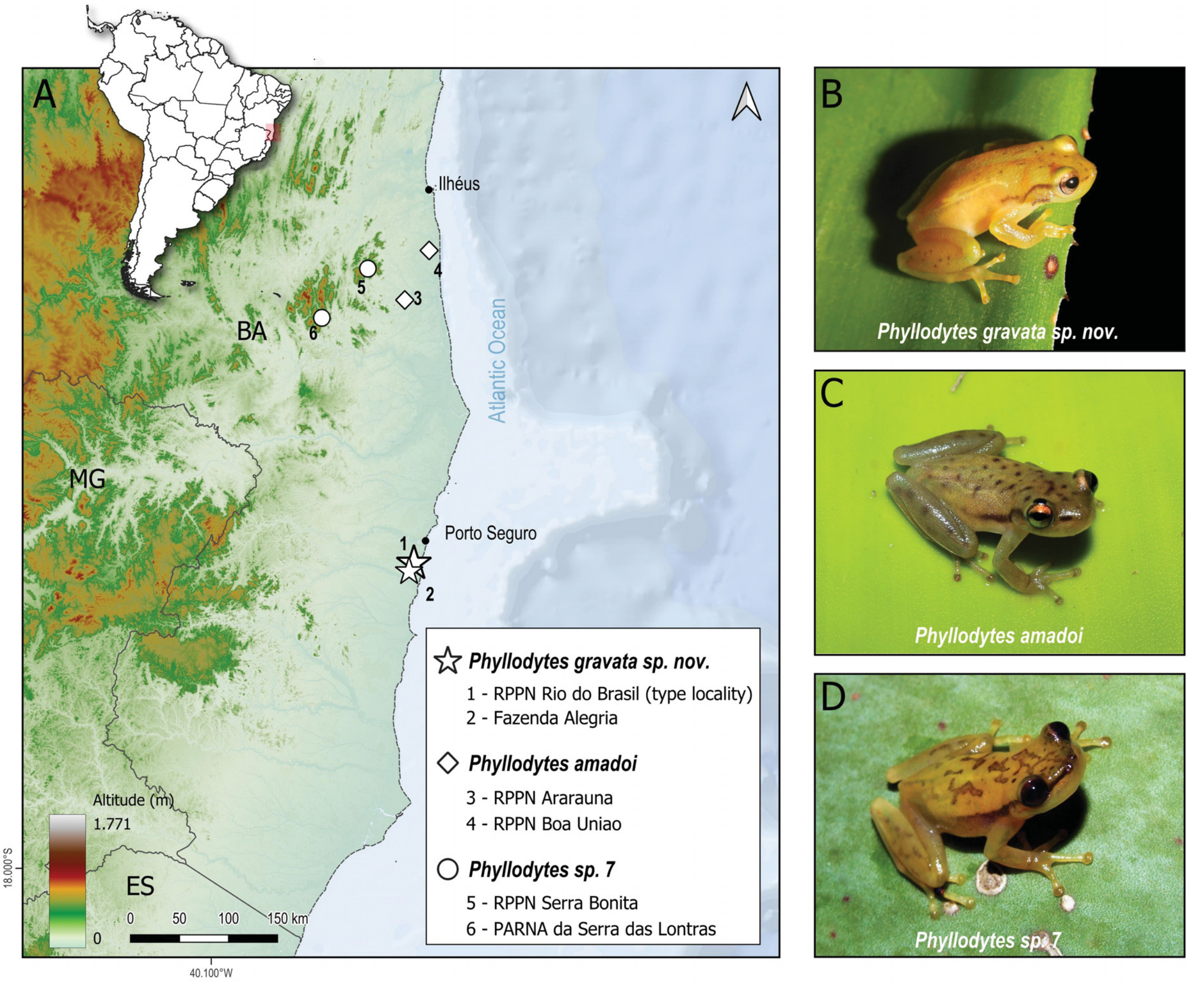

Fig. 7. A. Map showing the distribution of *Phyllodytes gravata* sp. nov. and its sister species, *P. amadoi* and *Phyllodytes* sp. 7. in southern Bahia, northeastern Brazil. **B**. *Phyllodytes gravata* sp. nov., paratype, ♂ (MZUESC 23915). **C**. *Phyllodytes amadoi*, ♂ (MZUESC 24030 – photograph by Tadeu T. Medeiros). **D**. *Phyllodytes* sp. 7, ♂.

Discussion

The knowledge on species diversity within the genus *Phyllodytes* has been gradually increasing in recent years (Marciano *et al*. 2017; Vörös *et al*. 2017; Orrico *et al*. 2018). Advances in molecular studies, combined with acoustic and morphological data, have facilitated species delimitation and enhanced our understanding of the genus richness. Among the seven candidate lineages identified by Blotto *et al*. (2021), two have been formally described in subsequent studies (Dias *et al*. 2020; Santos *et al*. 2023), and with the description provided here, four additional lineages remain to be assessed taxonomically. The actual number of species in the genus is likely even higher, considering the frequent reports of unidentified *Phyllodytes* morphotypes in regional herpetological surveys (Mira-Mendes *et al.* 2018; Rojas-Padilla *et al.* 2020; Bastos & Zina 2022).

Phyllodytes gravata sp. nov. can be morphologically distinguished from its closest relatives (*P. amadoi* and *P*. sp. 7) by subtle differences in dorsal colouration pattern, snout shape, and the arrangement of tarsal tubercles. However, the most pronounced differences are in bioacoustic parameters. A notable feature of *P. gravata* is the high number of notes in its advertisement call (27 ± 3.8; 22–34; n = 40), approximately twice that observed in *P. amadoi* (14.5 ± 1.0; 13–17; n = 17), resulting in a longer call duration (5.5–7.3 s). This duration is about twice as long as the advertisement call of *Phyllodytes* sp. 7 (2.94–3.89 s; n = 13, L. Santos, pers. comm.). The presence of multiple notes in advertisement calls is a common feature in *Phyllodytes*. However, *P. acuminatus* and *P. melanomystax* are exceptions, with calls composed of fewer than five notes and a single note, respectively (Nunes *et al*. 2007; Campos *et al*. 2014).

Of the 17 described species within the genus *Phyllodytes*, 13, including the present study (76.5%), have documented advertisement calls (Dias *et al*. 2020). This is a relatively high proportion compared to other anurans. For instance, among the Lophyohylini, less than 50% of species have described advertisement calls (Forti *et al*. 2018). In genera with more than 10 species, such as *Osteocephalus* Steindachner, 1862 and *Trachycephalus* Tschudi, 1838, only approximately 25% and 50% of the species, respectively, have acoustic descriptions, positioning *Phyllodytes* among the groups with the highest proportion of documented calls. Forti *et al*. (2018) suggest that this discrepancy may be associated with habitat accessibility. Species inhabiting the Atlantic Forest, where access is relatively easier, tend to have more acoustic descriptions than those from remote regions of the Amazon. These areas have been classified by the authors as "bioacoustic coldspots" due to the scarcity of acoustic data. In addition to limited accessibility, factors such as behavioural patterns, reproductive aspects, and habitat preferences contribute to the deficit in bioacoustic data. Among *Phyllodytes* species whose advertisement calls remain undescribed, two (*P. brevirostris* and *P. maculosus*) are typically associated with large bromeliads in the forest canopy, making both the recording of vocalisations and specimen collection particularly challenging.

Phyllodytes gravata sp. nov. is the ninth species within the genus endemic to the Central Corridor of the Atlantic Forest and the fourth recorded in physiognomies characterised by sandy soils and low vegetation, such as restinga and "mussununga" habitats (Bokermann 1966; Caramaschi *et al*. 1992; Caramaschi & Peixoto 2004; Orrico *et al*. 2018). Sandy soils have low water retention capacity, making the family Bromeliaceae important water reservoirs and stable microhabitats due to their ability to maintain moisture and more constant temperatures compared to the external environment (Rocha *et al*. 2004; Oliveira *et al*. 2017). Furthermore, there is evidence that animal species associated with bromeliads contribute to the nutrition of these plants through nitrogen-rich excretions, characterising a mutualistic relationship rather than mere inquilinism (Sabagh *et al*. 2017). Considering species that complete their entire life cycle within bromeliads (bromeligenous), a mutual dependence between the amphibian and the plant is observed (Koh *et al*. 2004; Sabagh *et al*. 2017). In the case of bromeligenous amphibians, there is evidence of selectivity in the choice of bromeliads, seeking specific characteristics such as tank size, number of leaves, and water volume and quality (Oliveira & Navas 2004; Mageski *et al*. 2017; Sato *et al*. 2025). Habitat alterations caused by anthropogenic activities can be particularly detrimental to these species, as the loss or reduction of bromeliads results in decreased availability of suitable habitats (Lopez *et al*. 2009; Sabagh *et al*. 2017).

Phyllodytes gravata sp. nov. is currently known from only two nearby localities (approximately 6 km apart in a straight line), where it exclusively inhabits bromeliads, a very unique microhabitat. These bromeliads are frequently collected for ornamental and landscaping purposes, posing a direct threat to the habitat of the species. Moreover, its known range lies within a region subject to intense tourism pressure and urban expansion, both of which may compromise the availability of suitable habitats. Although further studies are needed to precisely define its geographical distribution, the confirmed localities should be prioritised in conservation planning. Additional research is also recommended to investigate its natural history and assess potential impacts on its populations.

The description of *Phyllodytes gravata* sp. nov. further emphasizes that the diversity of bromeliad-associated anurans in the Atlantic Forest remains underestimated, particularly in poorly sampled environments such as Mussununga formations. Given the close association between species of *Phyllodytes* and tank bromeliads, future biogeographical studies may also help to clarify whether patterns of diversification in the genus are linked to the evolutionary history and diversification of Bromeliaceae in the Atlantic Forest.

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APPENDIX 1.

List of examined specimens.

Phyllodytes acuminatus: Pernambuco, Buíque (CHUFPE A-1434; A-1435; A-1920)
Phyllodytes amadoi Bahia, Una, RPPN Ararauna (MZUESC 14941; 14943; 14950; 14952; 14953; 14954; 14955; 14957; 14958; 14958; 14959; 14960; 24028;24029; 24030)
Phyllodytes edelmoi: Pernambuco, Tamandaré (CHUFPE A-2001; A-2002)
Phyllodytes gyrinaethes: Pernambuco, Caruaru (CHUFPE A-1530; A-1896)
Phyllodytes iuna: Bahia, Wenceslau Guimarães, Estação Ecológica de Wenceslau Guimarães (MZUESC 18950; 18852; 23000; 23002; 23001; 23003)
Phyllodytes kautskyi: Espiríto Santo, Domingos Martins, Reserva Kautsky (MZUESC 17427; 17428)
Phyllodytes luteolus: Espírito Santo, Regência (MZUESC 22628, 22629; 22630; 22634; 22635; 22636; 22637; 22638; 23893; 23894; 23895; 23896; 23897; 23898; 23899; 23900; 23902; 23904; 23905; 23906; 23907; 23908; 23909; 23910; 23911; 23912; 23913; 23914)
***Phyllodytes maculosus*:** Bahia, Porto Seguro, RPPN Estação Veracel (MZUESC 17433; 17827); Itacaré (MZUESC 17828; 17829)
Phyllodytes magnus: Bahia, Santa Terezinha/Elísio Medrado, Serra da Jibóia (MZUESC 18264); Ilhéus (MZUESC 22112, 22113, 22114, 22115, 22116, 22119, 22120, 22121, 22122, 22127, 22128).
Phyllodytes megatympanum: Bahia, Ilhéus (MZUESC 11671, 11672, 16056, 16061)

Phyllodytes melanomystax: Bahia, Ilhéus (MZUESC 7502, 9417, 11671, 11672, 14256, 14247, 14745, 16056, 16061); Itabuna, (MZUESC 9417); Ituberá, Reserva Ecológica Michelin (MZUESC 13015, 15965); Maraú, Península de Maraú (MZUESC 20170, 20176, 20178); Uruçuca (MZUESC 18373).
Phyllodytes praeceptor: Bahia, Ilhéus (MZUESC 7297, 7298, 7299, 10498, 10499, 11584, 11585, 14200, 14207, 14212); Itacaré, Faz. Capitão (MZUESC 9769, 9175); Ituberá, Reserva Ecológica Michelin (MZUESC 13016, 13026, 13027, 17487); Una, REBIO (MZUESC 11610, 11611, 11612, 17481, 17482, 17483, 17485)
Phyllodytes tuberculosus: Bahia, Maracás (MZUESC 23868; 23869; 23870; 23872; 23873; 23874; 23875; 23876; 23877; 23878; 23882; 23883)
Phyllodytes wuchereri: Bahia, Camacan, RPPN Serra Bonita (MZUESC 8319; 9052); Serra da Pedra Lascada, Barro Preto (MZUESC 18946).
***Phyllodytes* sp. 7**: Bahia, Camacan, RPPN Serra Bonita (MZUESC 18949); Arataca, PARNA da Serra das Lontras (MZUESC 18951)