

LIPARIS INAUDITA (ORCHIDACEAE, MALAXIDINAE), A NEW SPECIES FROM THE BOSQUE DE PROTECCIÓN ALTO MAYO, SAN MARTÍN, PERU

LIPARIS INAUDITA (ORCHIDACEAE, MALAXIDINAE), UNA NUEVA ESPECIE DEL BOSQUE DE PROTECCIÓN ALTO MAYO, SAN MARTÍN, PERÚ

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Abstract

Background: During an ongoing inventory of the orchids of the Bosque de Protección Alto Mayo, northern Peru, a population morphologically assignable to *Liparis* section *Decumbentes* was found. This is a little-known group restricted to wet montane Andean forests and consists of four species, from which the BPAM populations differs in leaf and labellum morphology.

Hypotheses: The features of the plants led us to hypothesize that it represents an unknown species, which can be distinguished morphologically from its congeners.

Taxon: *Liparis* section *Decumbentes*, *Liparis* sp. nov.

Study site and dates: Peru, department of San Martín, Rioja province, Pardo Miguel Naranjos district, Bosque de Protección Alto Mayo, sector Venceremos.

Methods: The unknown entity was studied in detail using fresh, pressed, and alcohol-preserved specimens. We also compared it to type specimens, other specimens of *Liparis* section *Decumbentes* housed in herbaria in Peru and abroad, and with descriptions from specialized literature.

Results: A leaf feature and the unique labellum morphology of the unknown entity permit it to be distinguished clearly from all other species of *Liparis* section *Decumbentes*.

Conclusions: The new species shares with *L. sessilis* the sessile leaf blades and the convex labellum, but differs from it and all other species of the section in its saddle-shaped labellum, which when spread out is narrowly obtrapezoid, with minute basal auricles, lacinate distal margins, and the apex projected into a narrowly triangular lobe.

Key words: Andes, leaf blade, labellum morphology, *Liparis* section *Decumbentes*, wet montane forest.

Resumen

Antecedentes: Durante un inventario, en proceso, de las orquídeas del Bosque de Protección Alto Mayo, en el norte de Perú, se descubrió una población asignable por sus características morfológicas a *Liparis* sección *Decumbentes*. Este es un grupo pobremente conocido restringido a bosques montanos andinos muy húmedos y consistente en cuatro especies, de las que la población descubierta difiere en la morfología foliar y la del labelo.

Hipótesis: Las características de las plantas llevaron a hipotetizar que representa una especie desconocida, distinguible morfológicamente de sus congéneres.

Taxón: *Liparis* sección *Decumbentes*, *Liparis* sp. nov.

Sitio de estudio: Perú, departamento de San Martín, provincia Rioja, distrito Pardo Miguel Naranjos, Bosque de Protección Alto Mayo, sector Venceremos.

Método: La entidad desconocida se estudió detalladamente mediante ejemplares en fresco, herborizados y preservados en alcohol. También se revisaron los ejemplares tipo, otros especímenes de *Liparis* sección *Decumbentes* en herbarios de Perú y otros países, y literatura especializada.

Resultados: Una característica foliar y la morfología del labelo de la entidad desconocida permiten distinguirla claramente de las otras especies de *Liparis* sección *Decumbentes*.

Conclusiones: La nueva especie comparte con *L. sessilis* las láminas foliares sésiles y el labelo convexo, pero difiere de ella y las demás especies de la sección en el labelo en forma de silla de montar, que al ser extendido es angostamente obtrapezoide, con aurículas basales diminutas, márgenes distales laciniados y el ápice proyectado en un lóbulo angostamente triangular.

Palabras clave: Andes, bosque montano muy húmedo, lámina foliar, *Liparis* sección *Decumbentes*, morfología del labelo.

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Liparis Rich. is a cosmopolitan genus encompassing ca. 320 species, distinguished from other Malaxidinae by an elongate, arcuate column with incumbent anther (Ridley 1886, Cribb *et al.* 2005). Although *Liparis* in the broad sense is polyphyletic (Cameron 2005), only a fraction of its species diversity has been included in molecular phylogenetic analyses, with a bias towards Old World groups (*e.g.*, Tang *et al.* 2015, Li *et al.* 2020). Much work remains to be done to achieve a thorough systematic revision of the genus and its limits, but in the meantime the morphology-based sectional classification of *Liparis* by Garay & Romero-González (1999) provides a useful framework for comparison and taxonomic discussion of morphologically discrete groups within the genus. One of the most distinctive groups of *Liparis* in the Neotropics is *L.* sect. *Decumbentes* Garay & G.A. Romero, which consists of four species characterized by their decumbent, creeping long stems with distichously arranged leaves (Garay & Romero-González 1999, Damián *et al.* 2020; [Figure 1](#)). All known species of sect. *Decumbentes* are restricted to wet Andean montane forests and have quite localized populations; they are only rarely collected and remain as one of the lesser-known Neotropical orchids.

Schweinfurth (1959) recorded two species attributable to sect. *Decumbentes* in his inventory of the orchid flora of Peru, namely *L. crispifolia* Rchb.f. and *L. laticuneata* C. Schweinf., and subsequent lists of Peruvian orchids by Brako & Zarucchi (1993) and Zelenko & Bermúdez (2009) followed suit. Recently, Goicochea *et al.* (2019) added *L. brachystalix* Rchb.f. based on specimens listed in the Tropicos.org page of the Missouri Botanical Garden (www.tropicos.org; A. Goicochea pers. comm. 2019). Damián *et al.* (2020) described a new Peruvian species belonging to this section, *L. sessilis* Damián, Salazar & Rimarachín, arguing for the exclusion of *L. crispifolia* from the Peruvian flora in the absence of specimens supporting its presence in the country, and provided an identification key to the four species they accepted in the section.

During a field trip conducted as part of our ongoing inventory of the orchid flora of the Bosque de Protección Alto Mayo, in northern Peru (J.D. Edquén *et al.*, unpubl. data), an additional, unknown species of *L.* sect. *Decumbentes* was discovered. Its comparison with previously known species revealed similarities to *L. sessilis* in the sessile leaf blades and convex labellum, but the new entity differs from it, and all other members of this section, in its unique labellum morphology ([Figures 2, 3](#)). We provide a description and photographic documentation of its vegetative and floral features, highlight the characters that distinguish it from its relatives, and provide an updated identification key for *L.* sect. *Decumbentes*.

The Bosque de Protección Alto Mayo (BPAM) encompasses 182,000 ha of rugged mountainous terrain on the eastern (Amazonian) slope of the Andes in the northwestern portion of the Department of San Martín and adjacent areas of the Departments of Amazonas and Loreto (approximate coordinates: 5.4° - 6.2° S, 77.2° - 77.8° W), in an elevational range from ~ 900 to 3,700 m asl. According to the eco-regionalization of Peru by Britto (2017), the vegetation consists of wet lower montane forest (“bosque muy húmedo montano bajo”) in the foothills, montane rain forest (“bosque pluvial montano”) from ~ 2,500 m asl, and high-elevation grassland (“jalca”) above ~ 3,200 m asl. The BPAM was established in 1987 by the Peruvian government to protect the water sources for agriculture, industrial use, and human consumption in the valley of the Upper Mayo River, as well as to conserve the fauna and flora (SERNANP continuously updated). The area has not been fully inventoried floristically, but a preliminary survey revealed high plant diversity (Dillon & Sánchez Vega 2001), and subsequent studies have found new species of trees (Dillon & Sánchez Vega 2009) and orchids (Acuña-Tarazona *et al.* 2019, Hågsater *et al.* 2019, 2020).

Materials and methods

Plants were photographed *in situ* with a digital camera (Nikon 850, Nikon Corporation, Tokyo, Japan) provided with a 60 mm AF Micro Nikkor lens (Nikon). Image processing and plate preparation was carried out with Adobe Photoshop v.22.4.2. Specimens were pressed to serve as the holotype, deposited in the herbarium of the Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, Lima, Peru (USM), and two isotypes to be distributed to HOXA and KUELAP. Flowers preserved in 70 % ethanol were examined and photographed



Figure 1. *Liparis inaudita* (from Edquén 1937). A. Plant *in situ*. B. Plant removed from the ground showing the branching stems. C. Portion of stem with leaves, top view. D. Portion of stem with three branches arising from a leaf axil, top view. E. Portion of stem with clumps of white trichomes. F. Underside of leaves showing the decurved, crispate margins. G. Stem apex and base of the peduncle of the inflorescence showing the irregularly dentate-crenate keels of the peduncle. Bars: A, B = 10 cm, C = 5 cm, D-G = 2.5 cm. Photographs by José D. Edquén.

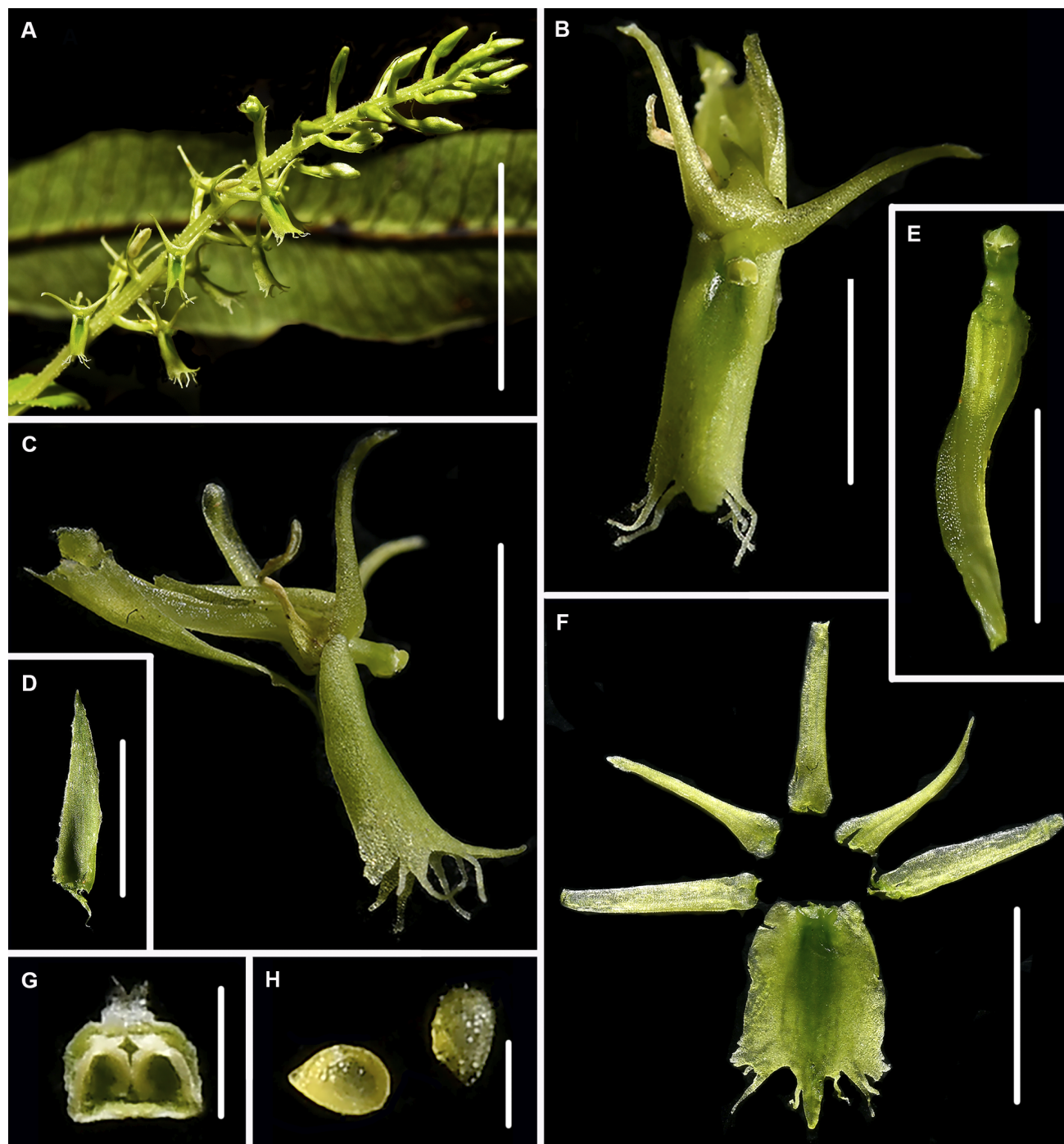


Figure 2. *Liparis inaudita* (from Edquén 1937). A. Inflorescence. B. Flower, front view. C. Flower, side view. D. Floral bract. E. Ovary and column, bottom view. F. Dissection of the perianth with sepals and petals partially spread out. G. Anther, bottom view. H. Pollinaria, side view. Bars: A = 3 cm, B, C = 4 mm, D, F = 5 mm, E = 3 mm, G = 0.5 mm, H = 0.3 mm. Photographs by José D. Edquén.

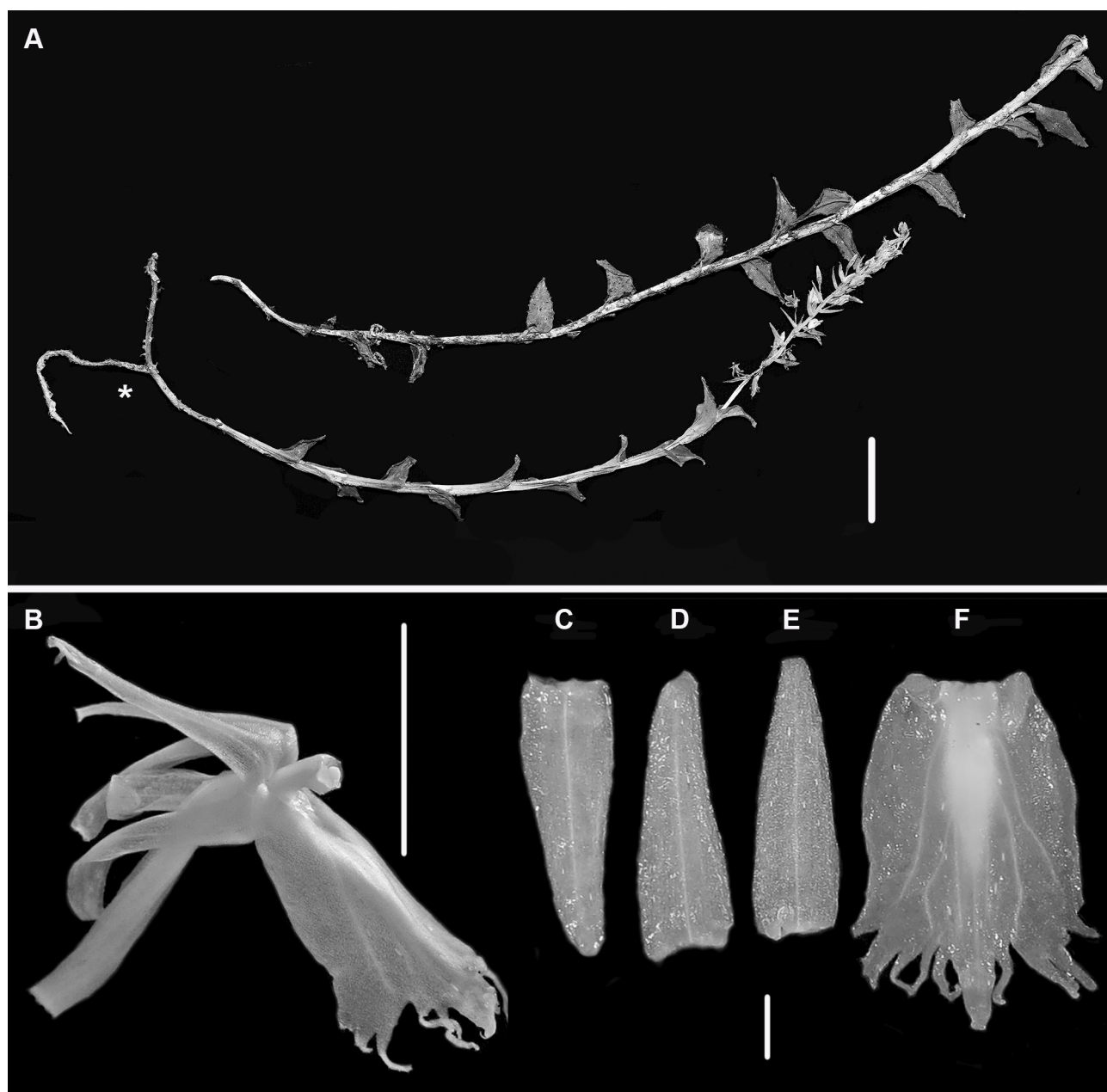


Figure 3. *Liparis inaudita* (from Edquén 1937). A. Pressed specimen showing a single root near the stem base (marked by a *). B. Alcohol-preserved flower, side view. C-F. Spread out floral segments of an alcohol-preserved flower. C. Lateral sepal. D. Petal. E. Dorsal sepal. F. Labellum. Bars: A = 2.5 cm; B = 4 mm, C-F = 1 mm. Photographs by José D. Edquén (A) and Delsy Trujillo (B-F).

under a stereomicroscope. Measurements were made on the pressed specimens and the alcohol-preserved flowers. The pertinent literature was revised, including the protologues of all previously described species of *Liparis* sect. *Decumbentes*, floristic treatments, and other works that include descriptions or illustrations of this group (e.g., Foldats 1969, Vázquez & Dodson 1982, Dodson & Dodson 1984, Dodson 2002, Zelenko & Bermúdez 2009, Damián *et al.* 2020). Type specimens were examined and additional specimens of Neotropical *Liparis* were studied in the herbaria AMES, AMO, GH, HOXA, K, KUELAP, MEXU, MO, MOL, NY, QCE, QCNE, UFV, US, and USM.

Results

Liparis inaudita Salazar, Edquén et D.Trujillo, sp. nov.

Type: Peru. Departamento San Martín, provincia Rioja, distrito Pardo Miguel Naranjos, Bosque de Protección Alto Mayo, sector Venceremos, 1828 m, bosque montano bajo, hierba terrestre postrada de 40 a 60 cm de largo, flores verde claro, 1 Mar 2020, *J. D. Edquén 1937* (holotype: USM!, isotypes HOXA, KUELAP).

Diagnosis. Similar to *Liparis sessilis* Damián, Salazar & Rimarachín in the sessile leaf blades but differing from that and all other species of the sect. *Decumbentes* in the saddle-shaped, narrowly obtrapezoid labellum with minute basal auricles, lacinate distal margins, and prominent, narrowly triangular apical lobule.

Morphological description. Terrestrial, decumbent, creeping herb 40-120 cm long (Figures 1A, B). **Roots** to 5 cm long, 1-1.5 mm in diameter, scarce, produced singly from nodes of the stem in the part of the plant in contact with the ground, terete, dull white (Figure 3A). **Stems** 15-70 cm long, 2-2.5 mm wide, slightly compressed, sparingly branching, with sparse clumps 1-3 mm in diameter of white, short trichomes of unknown function (Figure 1D, E). **Leaves** distichously arranged along the stems, base conduplicate, sheathing the stem, 3-5 × ca. 2 mm, blade 9-15 × 8-15 mm, sessile, ovate-elliptic, its upper surface medium dark green with prominent, reticulate veins, underside pale grayish-green, margins deflexed, crispate, apex acute (Figures 1C, F, G). **Inflorescence** 6.5-8 cm long, terminal, racemose, ascending; peduncle 1.5-2 cm long, 2 mm in diameter, subterete, with several longitudinal, sparsely and irregularly denticulate-crenate keels (Figure 1G); raceme at least 5-6 cm long (not seen with all flowers open), with 25-40 flowers opening in succession, rachis ornamented as the peduncle (Figure 2A). **Floral bracts** 6.5-7.5 mm long, 2-2.5 mm wide near the base, green, conspicuously longer than the ovary, narrowly triangular to triangular-lanceolate, acuminate, margins sparsely and irregularly denticulate (Figure 2D). **Flowers** resupinate, pale green with the column and the central part of the labellum darker green (Figures 2B, C). **Ovary** ca. 5 × 0.8 mm, terete, 3-costate, slightly twisted, incurved above the middle (Figures 2E, 3B). **Dorsal sepal** 4.5-5 × 1.4 mm, strongly reflexed from the base, slightly convex, lanceolate, obtuse-rounded, 1-veined (Figure 3E). **Lateral sepals** 4.5-5 × 1.5 mm, strongly reflexed from the base, slightly convex, obliquely lanceolate, rounded, 1-veined (Figure 3C). **Petals** 4.5-5 × 1.2-1.5 mm, spreading, slightly incurved, convex, obliquely triangular-lanceolate, rounded, 1-veined (Figure 3D). **Labellum** 5.8 mm total length, 3.5 mm wide near the middle, in natural position spreading at an acute angle from the column, saddle-shaped because of its downcurved margins, when spread out narrowly obtrapezoid, obscurely auriculate at each side of the base (auricles retrorse, broadly triangular, obtuse-rounded, ca. 0.25 mm long), lateral margins gently curved outwards, distal margins irregularly lacinate, apex extended into a narrowly triangular, rounded lobule, apical lobule ca. 1.2 × 0.7 mm; 5-veined, the veins next to the central one bifurcating below the middle (Figures 2F, 3F). **Column** ca. 1 × 0.5 mm, clavate, slightly incurved; stigma ventral, slightly concave, subrectangular (Figure 2E). **Anther** ca. 0.5 × 0.6 mm, terminal, incumbent, semiglobose, two-celled (Figure 2G). **Pollinaria** 2, ca. 0.3 × 0.2 mm, semiovoid, translucent yellow, each united at apex to a drop-like viscidium (Figure 2H). **Capsule** not seen.

Distribution and ecology. Known from a single population located in the Sector Venceremos, northwestern part of the BPAM. Creeping terrestrial, in leaf mold and on fallen, rotting tree trunks on a steep slope with lower montane cloud forest dominated by low trees of *Weinmannia* sp. and *Polylepis* sp., with *Chusquea* sp. in the understory, at around 1,830 m elevation.

Phenology. Flowering in February and March, but the numerous flower buds observed suggest that flowering might continue at least into April. Fruits were not observed.

Conservation status. Despite having trekked more than 40 km over several days in that portion of the BPAM, only a single population of this species was found, and it had not been recorded during our several previous collecting trips to other parts of the protected area. The single population of *L. inaudita* consists of about 70 individual stems or

clumps of stems on a few square meters. The creeping, branching nature of the stems did not permit us to ascertain whether such clumps may represent clones resulting from vegetative expansion and fragmentation, or different genetic individuals. Thus, *L. inaudita* seems to be a rare plant, but vast expanses of potentially suitable habitat remain to be explored and it is probable that further field work will result in the discovery of additional populations, as has occurred with other rare BPAM species such as *Magnolia bankardiorum* M.O.Dillon & Sánchez Vega, originally known only from two collections of the BPAM (Dillon & Sánchez Vega 2009), but subsequently recorded elsewhere in Peru and Ecuador (www.tropicos.org; accessed 13 July 2021). The plants of *L. inaudita* occur along a trail and trampling is a potential threat, but otherwise there is no information that permits us to carry out an objective assessment of its risk status. We suggest considering it as “Data Deficient”.

Etymology. From Latin *inauditus*, unheard of, new, in reference to the peculiar morphology of the labellum, which sharply differs from that of all previously known members of *Liparis* sect. *Decumbentes*.

Discussion

Liparis inaudita is unique among the Neotropical species of the genus, including all members of sect. *Decumbentes*, in the saddle-shaped, narrowly obtrapezoid labellum with lacinate distal margins, and prominent, narrowly triangular apical lobule (Figures 2E, 3F). The most similar species is *L. sessilis*, with which *L. inaudita* shares the sessile leaf blades, but in *L. sessilis* the labellum is only slightly convex and, when spread out, ovate-elliptic with irregularly erose distal margins, lacking basal auricles and an apical lobule (see Damián *et al.* 2020: Figures 1A, 2D).

Key to the species of *Liparis* sect. *Decumbentes*.

1. Labellum saddle-shaped, i.e., strongly convex with the lateral margins downcurved, distal margin lacinate, apex projected into a narrowly triangular lobule *L. inaudita*
1. Labellum not saddle-shaped, at most slightly convex without downcurved margins, slightly concave or strongly recurved, distal margins entire or erose, apex rounded to shallowly emarginate, minutely apiculate or mucronate 2
2. Labellum strongly recurved, when spread out abruptly expanded from a short cuneate base, about two times wider than long, transversely oblong-flabellate, apex apiculate *L. laticuneata*
2. Labellum flat, slightly convex or slightly concave, when spread not abruptly expanded from a short cuneate base, longer than wide, oblong-cuneate, ovate-elliptic, ovate-rhombic, or pandurate, apex obtuse, rounded, or shallowly emarginate and apiculate in the sinus 3
3. Leaf blades sessile; labellum slightly convex in natural position, when spread out ovate-elliptic, apex and base rounded *L. sessilis*
3. Leaf blades petiolate; labellum flat or slightly concave in natural position, when spread out obovate, pandurate, or ovate-rhombic, apex obtuse or shallowly emarginate, mucronate, base cordate 4
4. Flowers with pale green sepals and petals, and red purple labellum; labellum ovate-rhombic, obtuse; column slender above a thick base, strongly arcuate, about four times as long as wide or longer *L. crispifolia*
3. Flowers entirely green with a darker green central stripe on the labellum; labellum obovate or pandurate, shallowly emarginate, the sinus apiculate; column thick throughout, slightly arcuate, about 2.5 times longer than wide *L. brachystalix*

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Literature cited

- Acuña-Tarazona M, Hágsater E, Santiago Ayala E. 2019. *Epidendrum choccei* (Orchidaceae), a new species from northern Peru. *Phytotaxa* **394**: 98-104. DOI: <https://doi.org/10.11646/phytotaxa.394.1.7>
- Brako L, Zarucchi J. 1993. *Catálogo de las Angiospermas y Gimnospermas del Perú*. Monographs in Systematic Botany of the Missouri Botanical Garden Vol 45. Saint Luis: Missouri Botanical Garden Press. ISBN: 9780915279197
- Britto B. 2017. Actualización de las ecorregiones terrestres de Perú propuestas en el Libro Rojo de Plantas Endémicas del Perú. *Gayana, Botánica* **74**: 15-29. DOI: <http://dx.doi.org/10.4067/S0717-66432017005000318>
- Cameron KM. 2005. Leave it to the leaves: A molecular phylogenetic study of Malaxideae (Epidendroideae, Orchidaceae). *American Journal of Botany* **92**: 1025-1032. DOI: <https://doi.org/10.3732/ajb.92.6.1025>
- Cribb PJ, Pridgeon AM, Veitch NC, Grayer NJ, Rassmusen FR. 2005. *Liparis*. In: Pridgeon AM, Cribb PJ, Chase MW, Rasmussen FN, eds. *Genera Orchidacearum Vol. 4. Epidendroideae Part 1*. Oxford: Oxford University Press, pp. 465, 467-471. ISBN: 0-19-850712-7
- Damián A, Salazar GA, Rimarachín L. 2020. A new species and a new record of *Liparis* sect. *Decumbentes* (Malaxidinae; Orchidaceae) from Peru. *Phytokeys* **146**: 37-46. DOI: <https://doi.org/10.3897/phytokeys.146.47229>
- Dillon MO, Sánchez Vega I. 2001. *Floristic Inventory of the Bosque de Protección del Río Alto Mayo (San Martín, Peru)*. Project report. http://www.sacha.org/envir/eastlow/intro_sp.html (accessed June 28, 2021).
- Dillon MO, Sánchez Vega I. 2009. A new species of *Magnolia* (Magnoliaceae) from the Alto Mayo, San Martín, Perú. *Arnaldoa* **16**: 7-12.
- Dodson CH. 2002. *Native Ecuadorian Orchids*. Vol. 3. Sarasota: Dodson Trust. ISBN: 9978-42-268-4
- Dodson CH, Dodson PM. 1984. *Icones Plantarum Tropicarum, Vol. 10, Orchids of Ecuador, Part 6*. Sarasota: The Marie Selby Botanical Gardens.
- Foldats E. 1969. *Flora de Venezuela. Orchideaceae. Tomo XV. 1ª parte*. Caracas: Instituto Botánico.
- Garay LA, Romero-González GA. 1999. Schedulae orchidum II. *Harvard Papers in Botany* **4**: 475-488.
- Goicochea A, Gutiérrez AD, Ruiz A, Salas M. 2019. *Orquídeas de Perú: Relación de Especies y sus Sinónimos*. Lima: Corporación G & G. ISBN: 978-612-47895-1-9
- Hágsater E, Edquén JD, Santiago E. 2019. *Epidendrum labrychilum* Hágsater, Edquén et E.Santiago, sp. nov. *Icones Orchidacearum* **17**: Pl. 1730.
- Hágsater E, Santiago E, Cisneros A. 2020. *Epidendrum gygorum* Hágsater, E.Santiago et Cisneros, sp. nov. *Icones Orchidacearum* **18**: Pl. 1813.
- Li L, Chung SW, Li B, Zeng SJ, Yan HF, Li SJ. 2020. New insight into the molecular phylogeny of the genus *Liparis* s.l. (Orchidaceae: Malaxideae) with a new generic segregate: *Blepharoglossum*. *Plant Systematics and Evolution* **306**: 54. DOI: <https://doi.org/10.1007/s00606-020-01679-3>
- Schweinfurth C. 1959. Orchids of Peru. *Fieldiana, Botany* **30**: 261-531. <https://www.biodiversitylibrary.org/page/2452630#page/15/mode/1up> (accessed September 10, 2021).
- SERNANP [Servicio Nacional de Áreas Naturales Protegidas por el Estado]. Continuously updated. *Alto Mayo*. <https://www.sernanp.gob.pe/alto-mayo> (accessed June 28, 2021).
- Ridley HN. 1886. A monograph of the genus *Liparis*. *Journal of the Linnean Society of London, Botany* **22**: 244-297. DOI: <https://doi.org/10.1111/j.1095-8339.1886.tb00468.x>
- Tang G-D, Zhang G-Q, Hong W-J, Liu Z-J, Zhuang X-Y. 2015. Phylogenetic analysis of Malaxideae (Orchidaceae):

- Epidendroideae): Two new species based on the combined nrDNA ITS and chloroplast *matK* sequences. *Guihaia* **35**: 447-463. DOI: <https://doi.org/10.11931/guihaia.gxzw201506015>
- Vázquez R, Dodson CH. 1982. *Icones Plantarum Tropicarum, Vol. 6, Orchids of Bolivia, Part 1*. Sarasota: The Marie Selby Botanical Gardens.
- Zelenko H, Bermúdez P. 2009. *Orchid Species of Peru*. Quito: ZAI Publications. ISBN: 0-9661344-6-X

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