Current Research in Environmental & Applied Mycology (Journal of Fungal Biology)
15(1): 10–21 (2025) ISSN 2229-2225
www.creamjournal.org **Article**
Doi 10.5943/cream/15/1/2

Three new records of Arbuscular Mycorrhizal Fungi (Glomeromycota) from Mexico: *Acaulospora tuberculata*, *Glomus crenatum*, and *Racocetra crispa*

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Polo-Marcial MH, Lara-Pérez LA, Pavón-Reyes PD, Goto BT 2025 – Three new records of Arbuscular Mycorrhizal Fungi (Glomeromycota) from Mexico: *Acaulospora tuberculata*, *Glomus crenatum*, and *Racocetra crispa*. Current Research in Environmental & Applied Mycology (Journal of Fungal Biology) 15(1), 10–21, Doi 10.5943/cream/15/1/2

Abstract

During diversity studies of arbuscular mycorrhizal fungi (AMF) in the coastal sand dunes of southern Veracruz and tropical semi-evergreen forests of Quintana Roo and Campeche, we detected new geographic records of three ornamented species in Mexico. *Acaulospora tuberculata* and *Racocetra crispa* were recorded in coastal sand dunes, an underexplored ecosystem from southern Veracruz. *Glomus crenatum* was isolated from the tropical semi-evergreen forests of Campeche and Quintana Roo. Both *G. crenatum* and *R. crispa* represent their second global records. The three ornamented species are described and illustrated, and we generated an emendation to the original description of *G. crenatum* to present an accurate spore wall morphology. The new records increase the known richness in Mexico to 167 spp., representing 46.5% of that reported worldwide.

Keywords – Diversisporales – ectocarpic species – emendation – Gigasporales – Glomerales – rare species

Introduction

Arbuscular mycorrhiza is the predominant symbiosis in most terrestrial and aquatic ecosystems, formed by arbuscular mycorrhizal fungi (AMF, Glomeromycota) (Brundrett & Tedersoo 2018, Queiroz et al. 2022, Wijayawardene et al. 2022). Symbiosis with AMF allows vascular plants to enhance plant mineral nutrition through extensive hyphal networks, increasing abiotic and biotic stress tolerance and soil carbon storage (Smith & Read 2008, Soudzilovskaia et al. 2019). The distribution patterns of fungi (biogeography) are generally broader than those of other taxonomic groups (Niskanen et al. 2023). However, the distribution of families, genera, and species in Glomeromycota is regionally different, due to the intrinsic characteristics of vegetation type (Bever et al. 2001, Davison et al. 2015, Větrovský et al. 2023, Pontes et al. 2024). The tropical ecosystems of America exhibit a high diversity of AMF, particularly in tropical forests (Maia et al. 2020, Stürmer & Kemmelmeier 2021). However, one of the least inventoried ecosystems, yet responsible for the description of several AMF species are coastal sand dunes, where Diversisporales, Gigasporales, and Glomerales are dominant (Jobim et al. 2016, Stürmer et al.

Submitted 05 September 2024, Accepted 06 December 2024, Published 21 January 2025
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2018, 2022, Goto et al. 2009, 2010, 2012a, b, Błaszkowski et al. 2014, 2015). Despite being an ecosystem with highly diverse AMF communities, most inventories in South America have been concentrated in Brazil, leading to limited understanding of AMF diversity in countries with high biodiversity (Jobim et al. 2016).

In Mexico, the highest number of Glomeromycota species has been reported in agricultural systems (135 spp.) with 110 species distributed in the Neotropical bioregion (Polo-Marcial et al. 2021, 2025). However, the tropical forests and coastal sand dunes of southeastern Mexico have been underexplored with only 57 species and 28 species recorded, respectively (Álvarez-Sánchez et al. 2017, Lara-Pérez et al. 2020, Baleón-Sepúlveda et al. 2022). As part of the research focused on the AMF diversity in the coastal sand dunes of southern Veracruz and tropical forests of Quintana Roo and Campeche, we provided new geographic records in Mexico for three ornamented AMF species. Consequently, our objectives were (i) to describe and illustrate the three species, and (ii) to emend the description of *G. crenatum* with three layers in the spore wall, a rare species recorded only to its original location in Cuba with only two layers.

Materials & Methods

Study area and sampling

During the dry season (2021) we located a coastal sand dune site in Alvarado, Veracruz (18°50'41"N, 95°53'00"W) at an altitude of 8 m. The plant community was dominated by *Ipomoea* sp., *Canavalia* sp., and *Cyperus* sp. 24 – 28°C average, with 1400 – 2100 mm average annual rainfall and soil type Arenosol (INEGI 2010, Espejel et al. 2017). Along a 200 m gradient, 15 soil samples were collected (30 cm deep) at a distance of 20 m from each other. Additionally, during the rainy season of 2020, we collected soil samples from conserved tropical semi-evergreen forests in Nuevo Becal, Campeche (250 masl, 18°48′00"N, 89°20′05"W), and Quintana Roo (5 masl, 18°20'11.99"N, 88°47'48.62"W). The conserved forest is classified as tropical semi-evergreen forests and common tree species include: *Aspidosperma spruceanum* Benth. ex Müll. Arg, *Bursera simaruba* (L.) Sarg, *Metopium brownei* (Jacq.) Urb., and *Swietenia macrophylla* King. These sites have an average temperature of 24.6°C and receive an average rainfall of 1076 mm, with karst soil as the primary soil type (Martínez & Galindo-Leal 2002).

Isolation and identification of glomerospores

The glomerospores were isolated from dry soil by wet sieving and decantation combined with a sucrose gradient (60%) (Błaszkowski 2012). Glomerospores of three species were mounted on PVLG (polyvinyl-alcohol-lacto-glycerin) and a mixture of PVLG and Melzer's (1:1 v/v) (Błaszkowski 2012), observed and identified with specialized literature (Schenck & Pérez 1990, Błaszkowski 2012) and classified according to Wijayawardene et al. (2022). We adopt the term glomerospore proposed by Goto & Maia (2006) and recommendations to access voucher from type material as suggested by Goto et al. (2024). Photographs were taken with a Leica DM3000 LED microscope (Leica, Wetzlar, Germany) and the permanent preparations were stored in the collection of Laboratorio de Estudios Avanzados en Agroecosistemas (LEAA), Tecnológico Nacional de Mexico campus Instituto de Zona Maya (LEAA) and a duplicate deposited in the Herbarium of the Federal University of Rio Grande do Norte (UFRN-Fungos), Brazil.

Results

We provide new records in Mexico for three ornamented species belonging to three different orders Diversisporales (*Acaulospora tuberculata*), Gigasporales (*Racocetra crispa*) and Glomerales (*Glomus crenatum*). *Acaulospora tuberculata* and *R. crispa* were isolated from coastal sand dunes in Veracruz and *G. crenatum* was found in tropical semi-evergreen forests from Campeche and Quinta Roo. Both, *G. crenatum* and *R. crispa* represent second world records.

Morphological analysis indicates that *A. tuberculata* and *R. crispa* are consistent with original descriptions (Janos & Trappe 1982, Souza et al. 2018). However, spores of *G. crenatum* obtained from Mexico present an inner, thin, flexible, hyaline layer that is not reported in the original description (Furrazola et al. 2011). Based on morphological analysis of the spore wall of three ornamented species obtained in Mexico and a review of the type collection of *G. crenatum*, we present descriptions, and illustrations, improving taxonomic notes.

Taxonomy

Glomus crenatum Furrazola, R.L. Ferrer, R.A. Herrera & B.T. Goto. emend. H. Polo-Macial, Lara-Pérez & B.T. Goto Mycotaxon 116: 143 (2011). Figs 2 & 3

Description – glomerospores formed singly in soil, yellow-brown to orange-brown, globose to subglobose (110 – 190 µm diam., Fig. 2a) to elliptic (90 – 105 × 150 – 180 µm diam., Fig. 3a). Spore wall with three layers (SWL1 – 3), 7 – 18 µm thick in total. The first (SWL1), short-lived, hyaline to subhyaline, thin (0.5 – 2.0 µm), smooth in young and not present in mature spores (Fig. 2b, c & d, Fig. 3a & c). SWL2 yellowish-brown to dark orange, laminated, 8 – 17 µm thick, ornamented with hemispherical dome-shaped ornamentation, 5 – 25 µm in diam., 7 – 15 µm high and 9 – 30 µm distance between projections, in planar view the projections are circular to ellipsoid (Fig. 2b, Fig. 3b). SWL3 hyaline, flexible, adherent to SWL2, 1 – 1.5 µm thick, and difficult to detect even in broken spores (Fig. 2e & f, Fig. 3a & c). None of the wall layers react to Melzer's reagent. Subtending hyphal concolorous with the spore wall; one or rarely two straights (Fig. 2c, Fig. 3d), strongly curved or sinuous hyphae; 11 – 19 µm width at the base of the glomerospore and 1 – 1.5 µm in the distal part of the hyphae (Fig. 2c & d, Fig. 3d). Subtending hyphal formed with three wall layers (SHWL1 – 3) continuous with the spore wall layers (SWL). Pore open or occluded by an introverted septum formed by the innermost layers of SWL3 (Fig. 2d, Fig. 3d). Hyphae not straight, generally curved, and difficult to observe SHWL3 even in crushed spores.

Habitat and distribution – arbuscular mycorrhizal fungi, hypogeum, up to 30 – 40 cm deep in soil. *Glomus crenatum* was originally described from the rhizosphere plant communities of secondary forests dominated by *Syzygium jambos* (L.) Alston in eastern Cuba between 400 – 425 masl (Furrazola et al. 2011). In Mexico, *G. crenatum* was isolated only from conserved semi-evergreen rainforests in Quintana Roo and Campeche, at 5 – 6 masl and 250 – 300 masl, respectively.

Material examined – Mexico, Quintana Roo, La Juventud, Rojo Gómez, Othón P. Blanco, soil, at 18°20'11.99"N, 88°47'48.62"W, at 5 – 6 masl, 5 Jul 2020, coll. Hassan Polo (LEAA 041 – 045). Mexico, Campeche, Nuevo Becal, at 18°48′00"N, 89°20′05"W, at 250 – 300 masl, 20 November 2020, coll. Hassan Polo, (LEAA 041–045). Cuba, Holguin province, Moa-Sagua-Baracoa, at 22°45′ to 23°00′N, 82°50′ to 83°10′W, at 400 – 425 masl, (URM82278).

Notes – *Glomus crenatum* is easily distinguishable from other *Glomus* spp. of the family Glomeraceae by its glomerospores adorned with dome-shaped projections in SWL2 (Furrazola et al. 2011). However, the Mexican material, it presented an inner layer (SWL3) strongly attached to SWL2 (Fig. 2) and not reported in the original description (Furrazola et al. 2011). Analysis of the type material showed that *G. crenatum* presents all three wall layers (Fig. 3a & c).

Racocetra crispa F.A. de Souza, I. R. Silva, M.B. Barros-Barreto, B.T. Goto & Oehl, Mycological Progress 17: 1004 (2018). Fig. 4

Description – Sporocarps unknown. Glomerospores are terminally formed in bulbous sporogenous cells, globose to subglobose, 330 – 500 × 340 – 510 µm in diam., pale brown to dark brown (Fig. 4a). Spore with two walls, outer wall with three layers (OWL 1 – 3) and inner wall with three layers (IWL 1 – 3). OWL1 persistent, subhyaline to light yellow, 1 – 2.5 µm thick, randomly ornamented with multiple cloud-like projections, 5 – 30 µm diameter and 5 – 15 µm high (Fig. 4b, c & d). Laterally, the ornamentation is subhyaline to light yellow the distance between projections varies widely (3 –50 µm), in planar view a flower shape is usually observed due to the

grouping of projections (Fig. 4b & d). OWL2 pale brown to dark brown, permanent, laminated, 7 – 15 µm thick. OWL3 light brown, permanent, 1.5 – 15 µm thick, strongly adhered to OWL2 (Fig. 4e). OWL2 and OWL3 in Melzer's reagent are darker, difficult to observe because of the pigmentation of the layers. IWL 1–3: hyaline, flexible and adherent. IWL1 0.5 – 1 µm thick, IWL2 semi-flexible 1 – 2.5 µm thick and IWL3 0.5 – 1 µm thick, semi-flexible, forming folds (Fig. 4f). None of the inner layers react to Melzer's reagent. Germination shield formed on the inner wall (IW) surface, subhyaline to pale yellow, globose to rarely ovoid 210 – 220 × 200 – 215 µm diam., multilobed (6 – 10 lobes) each lobe with germ tube initiation points.

Habitat and distribution – arbuscular mycorrhizal fungi hypogeum, up to 20 cm deep in soil. The species was originally described from agroecosystems within the Cerrado biome in Minas Gerais, Brazil at an altitude between 746 – 778 masl (Souza et al. 2018). The Global Biodiversity Information Facility (GBIF, http://www.gbif.org), only has a record of *R. crispa* from the type locality in Brazil. In Mexico, the species was isolated from the rhizosphere of *Ipomoea* sp. in the coastal sand dunes of Veracruz, at an altitude of 8 – 11 masl. Environmental sequences with 100% of identity indicated the previous presence of *R. crispa* in maize crops in Minas Gerais, Brazil (L3HS244 OTU33) (Gomez et al. 2015) and in coastal dunes in New Zealand (VTX00041) (Johansen et al. 2015).

Material examined – Mexico. Veracruz, Alvarado, soil, at 18°50'41"N, 95°53'00"W, at 8 – 11 masl, 20 May 2021, coll. Hassan Polo, (LEAA 012–013).

Notes – The species *R. crispa* differed from the 14 *Racocetra* spp. by the random and scattered cloud-like ornamentation (Souza et al. 2018). Lately, a new species *Racocetra cromosomica* was described from Mexico, presenting dark spores and ornamented outer wall like *R. crispa* (Chimal-Sánchez et al. 2021). However, the new species differs by chromosome-like ornamentation in the outer wall layer. The Mexican isolates of *R. crispa* show no significant differences in number and phenotypes of wall layers when compared with the original description (Souza et al. 2018). However, the cloud-like ornamentation is slightly smaller in diameter and height (up to 30 µm in diam., and 15 µm in height, respectively), compared to the ornamentation of the original description up to 41 µm in diameter and 18 µm in height.

Acaulospora tuberculata Janos & Trappe, Mycotaxon 15: 519 (1982). Fig. 5

Description – acaulosporoid glomerospores, globose to sub-globose, 250 – 340 µm diam., light brown to reddish, laterally formed from an extension of the neck of the saccule (pedicel). Generally, with saccule and neck collapse, the pedicel remains attached to the glomerospore (Fig. 5a & b). Sporiferous saccule hyaline to light yellow, formed by two continuous layers with the neck of the spore wall, 90 – 150 µm diam. (Fig. 5c). The wall structure consists of three walls: outer wall (OW), middle wall (MW) and inner wall (IW). Outer wall consists of three layers (OWL1 – OWL3). OWL1: hyaline to light yellow, evanescent, up to 3.5 µm thick commonly shed in mature spores, OWL2: thick layer (5 – 12 µm thick), laminated, ornamented with small tubercles up to 3 µm high (Fig. 5d & f). OWL3: hyaline to light yellow, flexible, ~1 µm thick, closely adherent to OWL2 (Fig. 5d). The middle wall is bi-layer (MWL1 and MWL2) both layers hyaline, flexible to semi-flexible, ~ 0.5 – 1.5 µm thick when attached, both independent of the innermost (Fig. 5d & f). The inner wall consists of two layers (IWL1 – IWL2). IWL1: hyaline, flexible ~ 1.5 µm thick, adorned with beaded granules IWL2: hyaline, 1 – 2 µm thick, with some plasticity, which when observed gives a wrinkled appearance (Fig. 5d & f). Only IWL2 stains purplish in Melzer's reagent (Fig. 5b, d & f). Cicatrix: ovoid, 9 – 15 µm in diam., formed in OWL2.

Habitat and distribution – arbuscular mycorrhizal fungi hypogeum, up to 30 cm deep in soil. Originally described from tropical forests and secondary vegetation of Panama and Costa Rica. The Global Biodiversity Information Facility (GBIF, http://www.gbif.org), provides five additional records from Brazil, Portugal, Venezuela, and Argentina. In Mexico, the species was isolated from the rhizosphere of *Ipomoea* sp., and *Canavalia* sp. in coastal sand dunes of Veracruz, at an altitude of 8 – 11 masl. According to environmental sequences, *A. tuberculata* is distributed in Central and South America, as well as in China, India and Egypt (Silva et al. 2022).

Material examined – Mexico. Veracruz, Alvarado, soil, at 18°50'41"N, 95°53'00"W, at 8 – 11 masl, 20 May 2021, coll. Hassan Polo, (LEAA 018–023).

Notes – Mexican isolates of *Acaulospora tuberculata* showed no significant differences in size (250 – 340 µm diam.), ornamentation, number of walls and phenotypes of each layer compared to the original description (Janos & Trappe 1982, Błaszkowski 2012). *Acaulospora tuberculata* is the only species light brown to reddish with spine-like projections, the presence of pedicel, and a second outer wall layer (OWL2) adorned with tubercles up to 3 µm high (Janos & Trappe 1982, Błaszkowski 2012, Oehl et al. 2014).

Discussion

We report three new geographic records of arbuscular mycorrhizal fungi from Mexico, *Acaulospora tuberculata* and *Racocetra crispa* isolated from coastal dunes of Veracruz and *Glomus crenatum* from tropical semi-evergreen forests of Campeche and Quintana Roo. In addition, an emendation for *G. crenatum* is proposed, increasing the known richness in the country to 167 spp. (Polo-Marcial et al. 2021, 2022, Hipólito-Piedras et al. 2024). *Glomus crenatum* had only been reported from its type locality (Cuba) (Furrazola et al. 2011), while *Racocetra crispa* had been reported from Brazil and New Zealand (Gomez et al. 2015, Johansen et al. 2015, Souza et al. 2018). However, the isolation of both species in Mexico suggests that both fungi present a wider geographic distribution concerning the type locality but only *G. crenatum* is restricted to the Neotropical bioregion (Polo-Marcial et al. 2021). In this study, *G. crenatum* was only recorded in conserved semi-evergreen forests of Campeche and Quintana Roo, despite the effort to isolate AMF in nearby vegetation types in the Yucatan Peninsula (Lara-Pérez et al. 2020, Solís-Rodríguez et al. 2020, Gómez-Falcón et al. 2023). Thus, its distribution is restricted to semi-evergreen forests in Mexico and Cuba (Furrazola et al. 2011). *Racocetra crispa* had only been reported in South America from the type region (Minas Gerais), *i.e*. agricultural fields in southeastern Brazil (Gomez et al. 2015, Souza et al. 2018) and in coastal dunes in New Zealand (Johansen et al. 2015). In contrast, *A. tuberculata* is widely distributed in several biomes of South America (Maia et al. 2020, Stürmer & Kemmelmeier 2021, Gomes et al. 2022). Environmental sequence reports indicated that the species is distributed in China, India and Egypt (Silva et al. 2022). In Costa Rica (type locality), *A. tuberculata* is commonly reported in secondary forests and agroforestry systems (Janos & Trappe 1982, Polo-Marcial et al. 2023, Solís-Ramos et al. 2023).

Only two wall layers were reported in *Glomus crenatum*: a semi-persistent and smooth layer (SWL1) and a laminated ornamented layer (SWL2) (Furrazola et al. 2011). However, we detected a third hyaline, semi-flexible layer, adherent to SWL2. Analyzing the type material deposited in URM herbarium (Brazil) the third inner hyaline layers not originally described was detected. Thus, we prepared an emendation to the original description to present an accurate morphology of spore wall of a rare species in the world. However, *G. crenatum* remains as an *insertae sedis* fungus, without phylogenetic information available. Its peculiar morphology, mainly their irregular and ramified subtending hyphae suggest that *G. crenatum* may not be a member of the genus *Glomus*. Identifying members of Glomeromycota with glomoid spores based on spore morphology is difficult and uncertain whereas several new genera described lack a synapomorphy (Goto et al. 2024). This study expanded the natural distribution range of three ornamented species with projections and increased the richness of arbuscular mycorrhizal fungi for Mexico from 164 species to 167, representing 46.5% of the species reported in the world. In addition, we emend with a concise description the wall of *Glomus crenatum*.

Acknowledgements

We are grateful to the Consejo Nacional de Humanidades, Ciencias y Tecnologías (Conahcyt) for the postdoctoral grant awarded to MHPM (757045) and to the TecNM project (19552.24-P) awarded to LALP. We thank the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) for the research grant awarded to BTG (proc. 306632/2022-5).

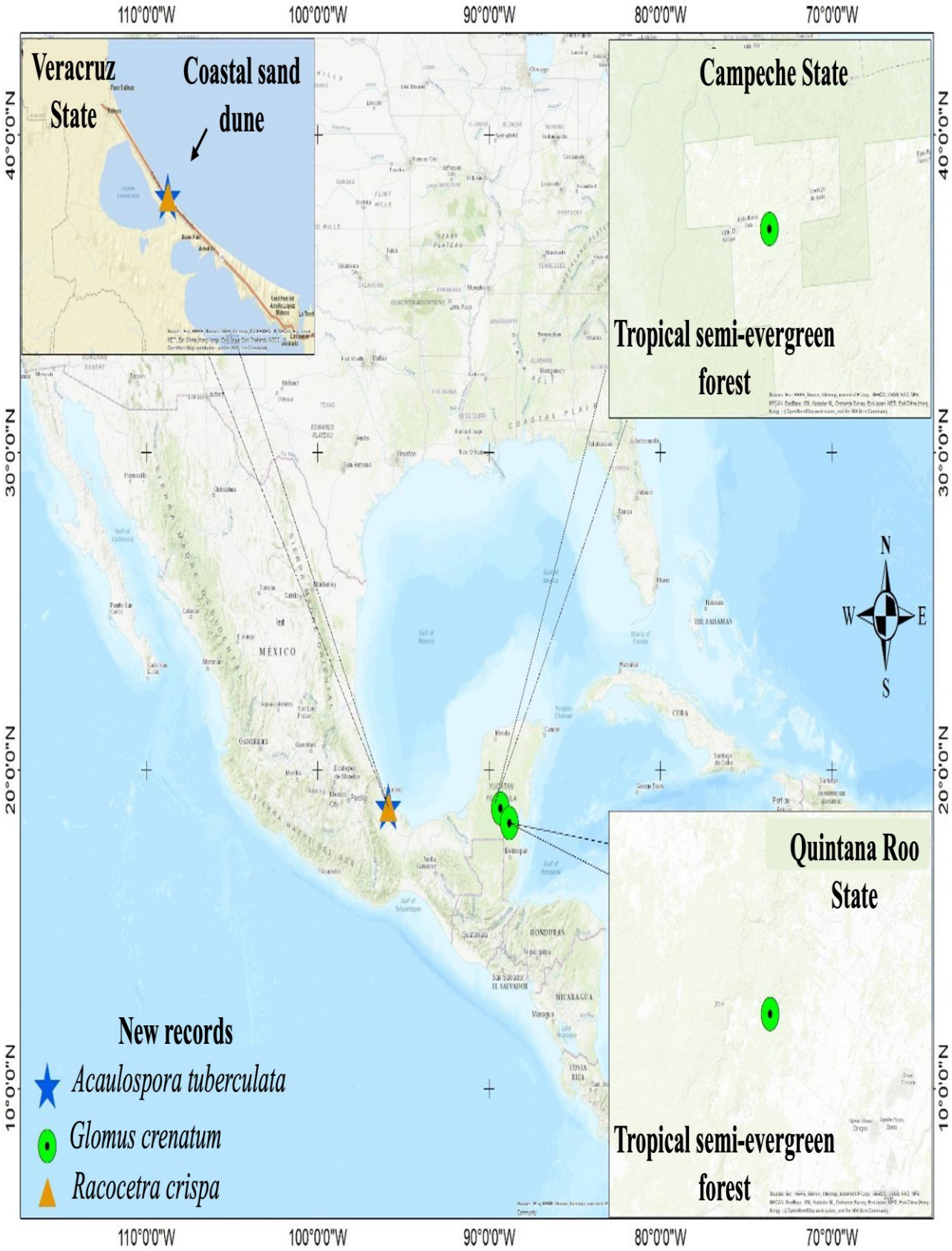

Fig. 1– Geographical location of sampling sites in Veracruz, Campeche, and Quintana Roo, Mexico (left), upper right: coastal sand dune vegetation in Alvarado, Veracruz. Downright: conserved tropical semi-evergreen forests in Nuevo Becal, Campeche and Othón P. Blanco, Quintana Roo.

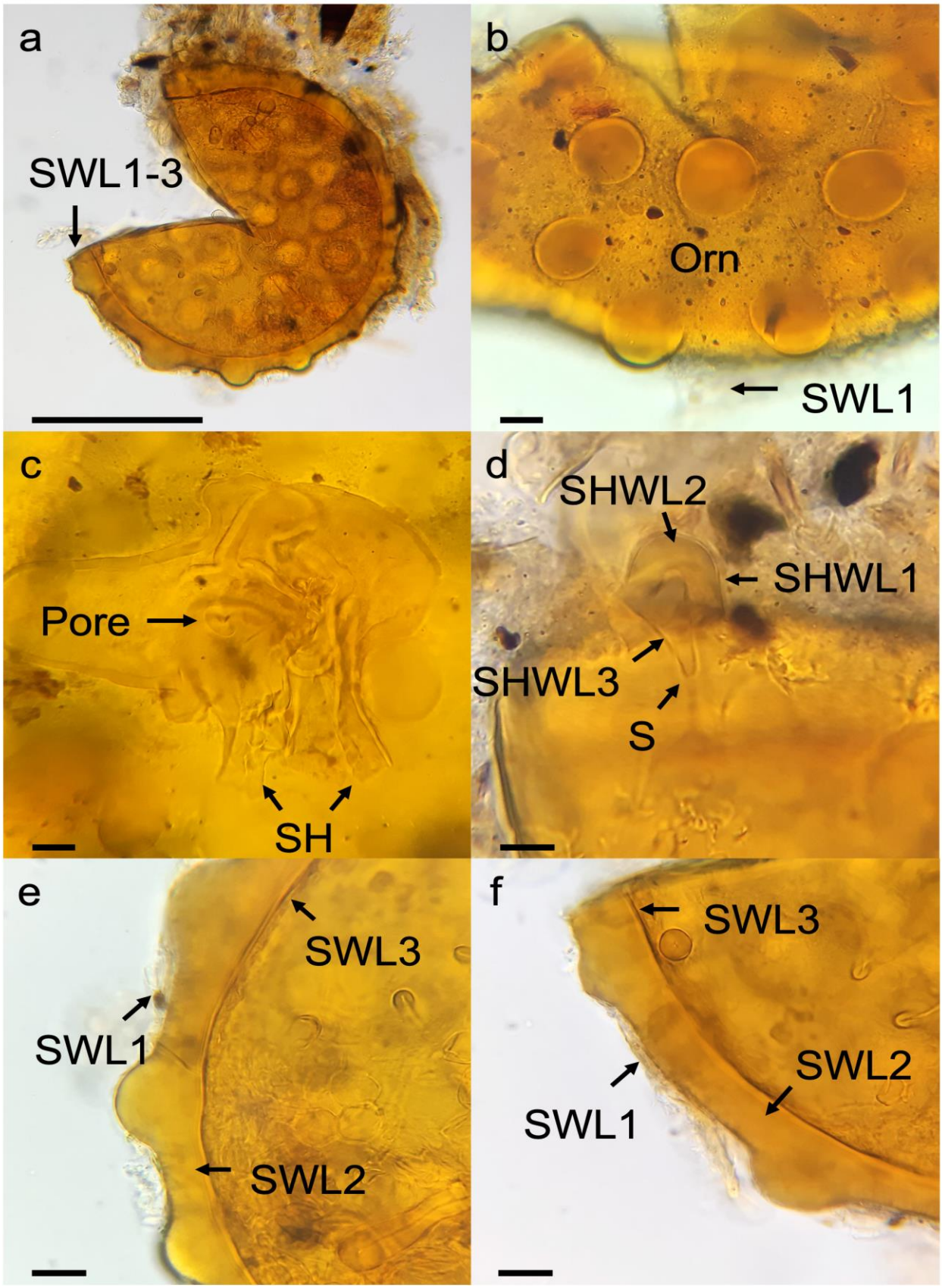

Fig. 2 – Morphological characteristics of *Glomus crenatum* isolated from Mexico. a Glomerospore and structural wall layer (SWL1–3). b dome-shaped ornamentation (Orn). c detail of the subtending hypha and pore. d septum and subtending hyphal wall layers (SHWL1–3). e and f detail of SWL1, SWL2 and SWL3. Scale bars: a = 100 µm, b–f = 10 µm.

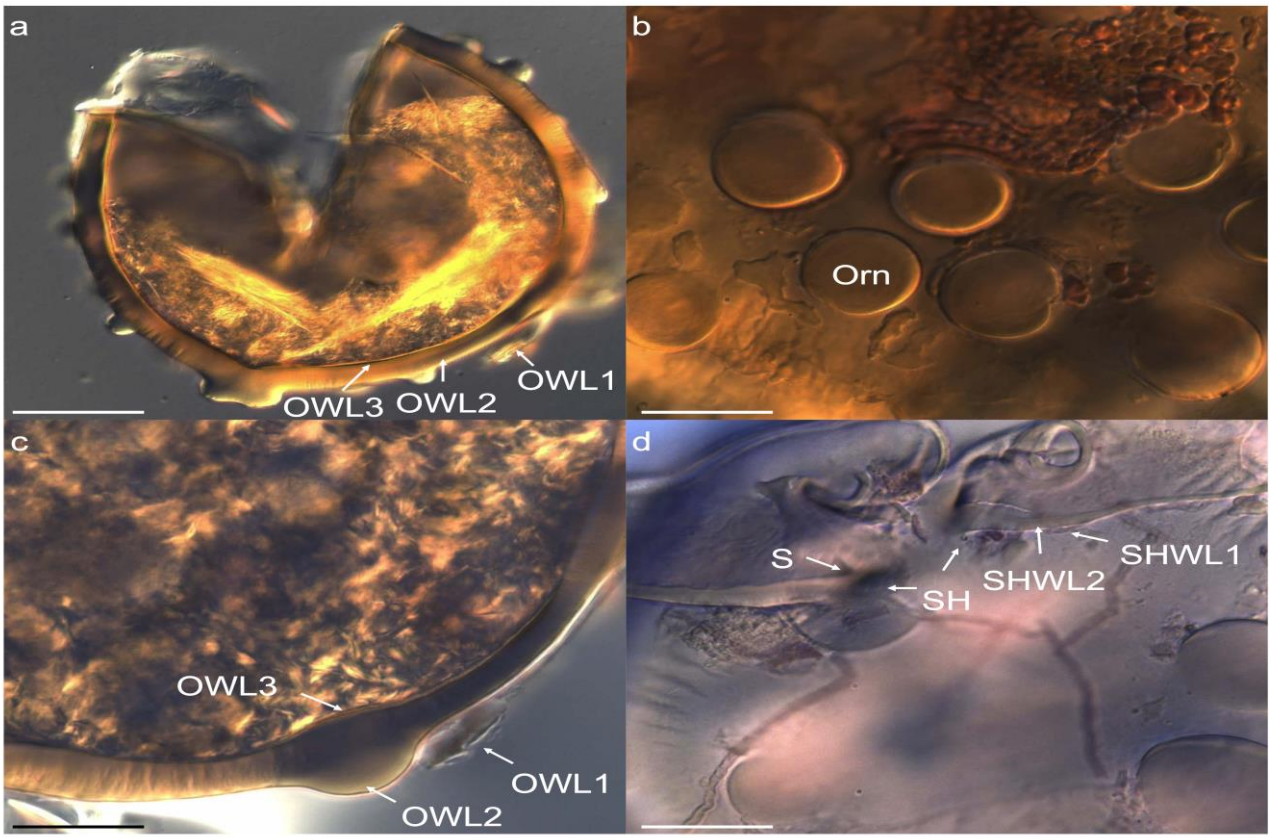

Fig. 3 – Morphological characteristics of *Glomus crenatum* isolated from Cuba locality (URM82278). a Glomerospore and structural wall layer (SWL1–3). b dome-shaped ornamentation (Orn). c detail of SWL1, SWL2 and SWL3. d detail of two subtending hyphae and wall layers (SHWL1–3). Scale bars: a = 50 µm, b – d = 20 µm.

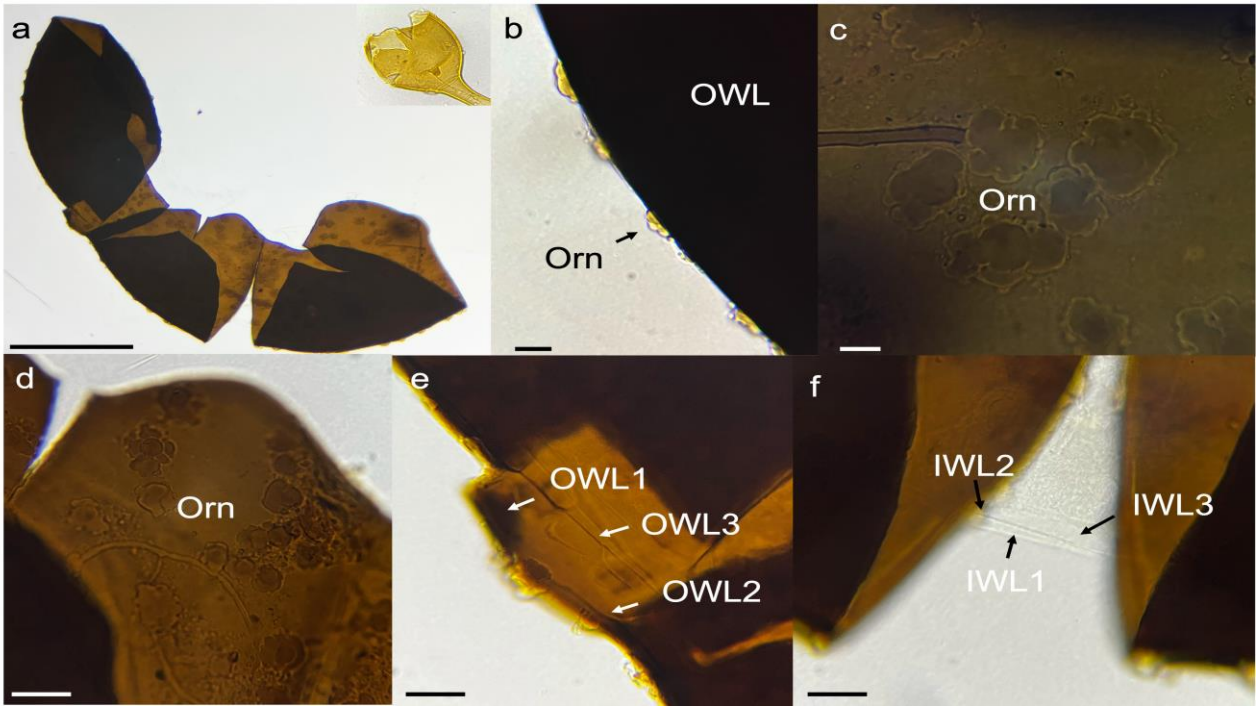

Fig. 4 – Morphological characteristics of *Racocetra crispa*. a Glomerospore and sporogenous cell. b lateral view of the ornamentation. c and d ornamentation (Orn). e outer wall layers (OWL 1–3). f inner walls layers (IWL 1–3). Scale bars: a = 100 µm, b, c, e and f = 20 µm, d = 40 µm.

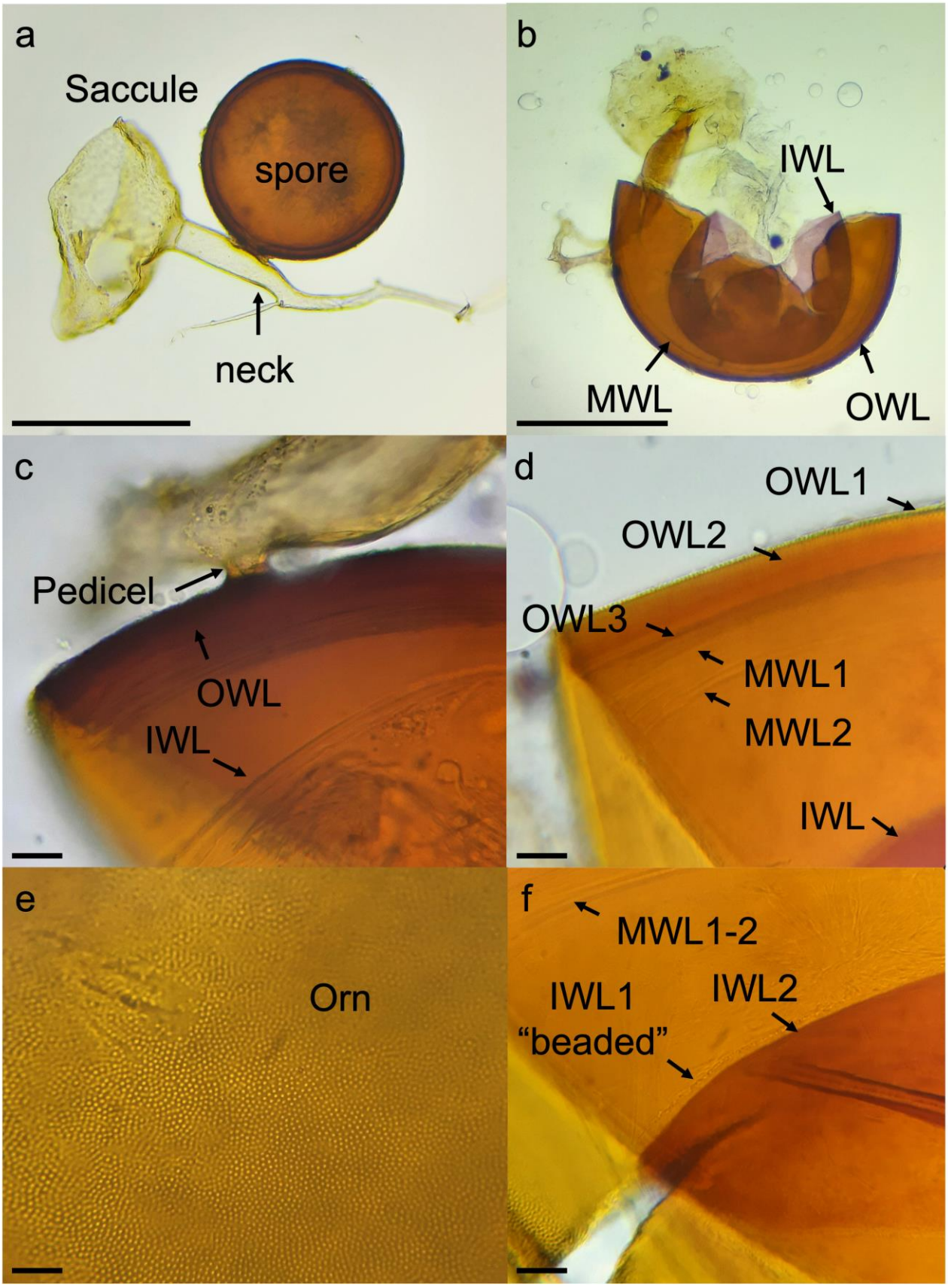

Fig. 5 – Morphological characteristics of *Acaulospora tuberculata*. a) Glomerospore and sporiferous saccule. b detail of outer wall layer (OWL), middle wall layer (MWL) and inner wall layer (IWL). c detail of pedicel, OWL and IWL. d detail of OWL1–3 and MWL1–2. e ornamentation (Orn). f detail of MWL1–2 and IWL1“beaded”. Scale bars: a = 200 µm, b = 100 µm, c, d, e and f = 10 µm.

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