

Molecular phylogenetics and morphology reveal the Plettkea lineage including several members of Arenaria and Pycnophyllopsis to be a clade of 21 South American species nested within Stellaria (Caryophyllaceae, Alsineae)

Authors: Montesinos-Tubée, Daniel B., and Borsch, Thomas

Source: Willdenowia, 53(3) : 115-148

Published By: Botanic Garden and Botanical Museum Berlin (BGBM)

URL: <https://doi.org/10.3372/wi.53.53301>

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Molecular phylogenetics and morphology reveal the *Plettkea* lineage including several members of *Arenaria* and *Pycnophyllopsis* to be a clade of 21 South American species nested within *Stellaria* (*Caryophyllaceae*, *Alsineae*)

Daniel B. Montesinos-Tubée^{1,2} & Thomas Borsch¹

Version of record first published online on 21 December 2023 ahead of inclusion in December 2023 issue.

Abstract: *Caryophyllaceae* with a cushion-like life form occur with a large number of species at the higher altitudes of the Andes (3500–5000 m) and have evolved convergently in several different lineages. Based on molecular phylogenetic analysis it is shown that members of the former genera *Plettkea* and *Pycnophyllopsis*, but also certain species previously classified as *Arenaria* constitute a subclade nested within the monophyletic genus *Stellaria*. Both plastid (*trnK-matK-psbA* + *trnL-F*) and nuclear (nrITS) trees converged on such a highly supported ‘*Plettkea*’ clade. Morphologically, the members of the ‘*Plettkea*’ subclade of *Stellaria* are further characterized by reduced to completely absent petals and seeds with a more or less conspicuous tuberculate testa. This clade is described as *S. sect. Plettkea* (Mattf.) Montesinos & Borsch. Species-level relationships within *S. sect. Plettkea* are also congruently inferred by plastid and nuclear genomic compartments, with three further sublineages recognized: Altogether, our detailed taxonomic revision showed that the ‘*Plettkea*’ clade in fact constitutes an Andean radiation of 21 species within *Stellaria*, four of which are described as new to science. Earlier treatments indicated just a few species with a putative placement. The results of this investigation underscore the importance of fieldwork and integrated molecular-morphological approaches to assess the species diversity in Andean plant groups. In addition to the phylogenetic analysis, we provide a taxonomic backbone including all names and types, descriptions and information on distribution and ecology and a key for identification. Regarding the next relatives of the *S. sect. Plettkea* clade, our plastid trees depict the ‘*Nitentes*’ clade of *Stellaria* as sister, whereas nrITS instead suggests a sister group relationship of the ‘*Nitentes*’ with the speciose ‘*Larbreae*’ clade. Our inferred relationships of major clades further deviate from published molecular trees by indicating an early branching position of the ‘*Petiolaes*’ clade.

Keywords: Bolivia, molecular phylogeny, new species, Peru, *Plettkea*, *Pycnophyllopsis*, South America, *Stellaria*, taxonomic treatment

Resumen: Las *Caryophyllaceae*, con forma de vida en matas o almohadillas, se encuentran en las mayores altitudes de los Andes (3500–5000 m) con un gran número de especies y han tenido una evolución convergente en diversos linajes. Análisis filogenéticos moleculares, recuperan un subclado anidado dentro del género monofilético *Stellaria*, constituido por los miembros previamente clasificados en *Plettkea* y *Pycnophyllopsis* y especies clasificadas hasta ahora en *Arenaria*. Tanto los árboles de plástidos (*trnK-matK-psbA* + *trnL-F*) como los nucleares (nrITS) convergen en un clado de ‘*Plettkea*’ altamente apoyado estadísticamente. Morfológicamente, los miembros del subclado ‘*Plettkea*’ de *Stellaria* se caracterizan, además, por compartir pétalos reducidos o completamente ausentes y semillas con un tegumento tuberculado más o menos conspicuo. El subclado se valida como *S. sect. Plettkea* (Mattf.) Montesinos & Borsch. Las relaciones a nivel de especie dentro de esta sección también se infieren congruentemente por compartimentos genómicos plástidiales y nucleares, con tres sublinajes. En conjunto, nuestra detallada revisión taxonómica mostró que el clado *Plettkea* constituye una radiación andina de 21 especies dentro de *Stellaria*, cuatro de las cuales se describen como nuevas para la ciencia. Tratamientos anteriores indicaban sólo unas pocas especies con una ubicación putativa. Los resultados de esta investigación destacan la importancia del trabajo de campo y la integración de métodos moleculares y morfológicos para evaluar la diversidad de especies en los grupos de plantas andinas. Además del análisis filogenético, proporcionamos una columna vertebral taxonómica que incluye todos los nombres y datos de los tipos nomenclaturales. Se proporcionan descripciones e información sobre distribución y ecología así como una clave para identificarlas. Con respecto a los parientes próximos del clado de *S. sect. Plettkea*, nuestros árboles de plástidos muestran al clado ‘*Nitentes*’ de *Stellaria* como hermano, mientras que nrITS sugiere más bien una relación de grupo hermano de los ‘*Nitentes*’ con el clado ‘*Larbreae*’. Las relaciones inferidas de los clados principales se desvían aún más de los árboles moleculares publicados previamente, al indicar una posición de ramificación temprana del clado ‘*Petiolaes*’.

Palabras clave: Bolivia, filogenia molecular, nuevas especies, Perú, *Plettkea*, *Pycnophyllopsis*, *Stellaria*, Sudamérica, tratamiento taxonómico

Article history: Received 12 September 2023; peer-review completed 10 November 2023; received in revised form 28 November 2023; accepted for publication 29 November 2023.

Citation: Montesinos-Tubée D. B. & Borsch T. 2023: Molecular phylogenetics and morphology reveal the *Plettkea* lineage including several members of *Arenaria* and *Pycnophyllopsis* to be a clade of 21 South American species nested within *Stellaria* (*Caryophyllaceae*, *Alsineae*). – Willdenowia 53: 115–148. <https://doi.org/10.3372/wi.53.53301>

1 Botanischer Garten und Botanisches Museum Berlin, Freie Universität Berlin, Königin-Luise-Str. 6–8, 14195 Berlin, Germany.

2 Instituto de Ciencia y Gestión Ambiental de la Universidad Nacional de San Agustín de Arequipa, Calle San Agustín 108, Arequipa 04001, Peru.

Author for correspondence: Daniel B. Montesinos-Tubée, d.montesinos@bo.berlin

Introduction

Members of the family *Caryophyllaceae* constitute important elements of the flora in the Andes, mostly at higher altitudes. All together the diversity of *Caryophyllaceae* in the interandean dry valleys, the altiplano, Patagonian plateaus, the paramos, and high mountain peaks may be estimated with c. 280 species and new species continue to be described (e.g. Timaná 2017; Montesinos-Tubée & al. 2018, 2020). Species of different genera show adaptations as cushion plants such as *Arenaria* L., *Pycnophyllopsis* Skottsb. or *Pycnophyllum* J. Rémy, some of which are well known for their large cushions like *Pycnophyllum molle* J. Remy. These cushion plants, especially the exclusively Andean *Pycnophyllum* spp. and *Pycnophyllopsis* spp. grow at altitudes of 4000–5500 m (Catorci & al. 2014; Montesinos-Tubée 2015). They are not easily distinguishable in the field and also comprehensive phylogenetic analyses were so far lacking, limiting insights on the naturalness of these genera. Apart from details in the cushion growth form, the species of *Pycnophyllum* are dioecious, whereas this feature is less consistent in *Pycnophyllopsis* in which most species are dioecious with pistillate and staminate individuals but not all (*P. smithii* Timaná and *P. weberbaueri* Muschler are hermaphroditic; Timaná 2017; Sharples & Tripp 2019). In *Pycnophyllopsis* the leaves bear scarious margins and possess a sparse indumentum, both of which are absent in *Pycnophyllum* which tends to have glabrous leaves. In the case of *Pycnophyllum* the species included (*P. bryoides* (Phil.) Rohrb., *P. molle* J. Remy, *P. spathulatum* Mattf.) in the overall molecular tree of the *Caryophyllaceae* by Greenberg & Donoghue (2011) depicted this genus in the monophyletic tribe *Polycarpeae*, and thus in a major lineage of the family distant from both the *Alsineae* and *Arenarieae* clades.

Even though there are treatments by J. L. Zarucchi and R. E. Gereau in the *Catalogue of the flowering plants and gymnosperms of Peru* (Brako & Zarucchi 1993), and F. O. Zuloaga & C. A. Zanotti in the *Catálogo de las plantas vasculares del Cono Sur* (Zuloaga & al. 2008), no comprehensive taxonomic revisions or monographs have been elaborated for most of the larger genera of the *Caryophyllaceae* in South America like *Arenaria*, *Cerastium* L., *Drymaria* Willd. ex Schult. or *Stellaria* L. since Williams (1898) and Macbride (1937). To some extent *Pycnophyllum* is an exception as it was the focus of more recent studies (Timaná 2005, 2017), although only including a few new ITS sequences analysed with parsimony in a broad context of *Caryophyllaceae* with sequences available at the time (Timaná 2005). The representation of South American *Caryophyllaceae* in molecular phylogenetic analyses is so far rather scarce.

Based on a few species, Greenberg & Donoghue (2011) showed that *Pycnophyllum* and *Drymaria* belong to the ‘*Polycarpeae*’ subclade of the broadly paraphyletic subfamily *Paronychioideae*. To the contrary,

most other genera comprising Andean species are part of the *Alsinoideae*. The circumscription of the subfamily *Alsinoideae* and of its tribes has varied over time, and the first more comprehensive molecular phylogenetic analysis by Harbaugh & al. (2010) revealed that not only the subfamily but also most of the tribes were para- or polyphyletic. This extends to many other genera as evident through the broader taxon sampling in Greenberg & Donoghue (2011). The pre-phylogenetic classification by Bittrich (1993) included 23 genera with an estimated 700 species in the tribe *Alsineae*. The re-definition of the tribe by Harbaugh & al. (2010) to make it monophyletic just contained the genera *Cerastium* L., *Holosteum* L., *Lepyrodiclis* Fenzl, *Moenchia* Ehrh., *Myosoton* Moench, *Odontostemma* Benth. ex G. Don, *Plettkea* Mattf., *Pseudostellaria* Pax, and *Stellaria* but not *Arenaria* and relatives. The latter were classified in the tribe *Arenarieae* along with the genera *Brachystemma* D. Don and *Moehringia* L. Arabi & al. (2022) presented phylogenetic trees inferred from nrITS and from combined nrITS + chloroplast *rps16* sequence data. The authors found two subclades of the monophyletic *Alsineae*, one including the genera *Mesostemma* Vved., *Shivparvatia* Pulsalkar & D. K. Singh, *Odontostemma*, *Pseudostellaria*, *Stellaria* (“*Alsineae* A”), and the other comprising *Nubelaria* M. T. Sharples & E. A. Tripp, *Hartmaniella* M. L. Zhang & Rabeler, *Rabelera* M. T. Sharples & E. A. Tripp, *Dichodon* (Bartl. ex Rchb.) Rchb., *Holosteum*, *Moenchia*, and *Cerastium* (“*Alsineae* B”). The monotypic genus *Pseudocerastium* C. Y. Wu & al., an endemic of the Anhui and Hubei provinces in China, was found to be nested within *Cerastium* (Yao & al. 2021) and consequently merged with that genus. Recently, Xue & al. (2023) described the three further monotypic genera *Hesperostellaria* Gang Yao & al., *Reniostellaria* Gang Yao & al. and *Torreystellaria* Gang Yao & al. of the *Alsineae*. The genus *Plettkea*, which was not sampled by Arabi & al. (2022), is a further Andean taxon of the *Alsineae* that forms small cushions. However, Sharples & Tripp (2019) had already included one of its members, *Plettkea tetrasticha* Mattf., in their RAD analysis of the genus *Stellaria* along with nine South American species of *Stellaria* (from the ‘*Petiolares*’ clade), and depicted it nested within *Stellaria*.

Mattfeld (1934) described *Plettkea* as different from *Pycnophyllopsis* using the single-seeded closed fruit (capsule) and bipartite petals in combination with strongly perigynous flowers as diagnostic characters and, in contrast, considered *Pycnophyllopsis* to differ by having only slightly perigynous flowers with a broadened disk. Although Mattfeld (1934) noted that the 1-seeded capsule would be a difference of both *Pycnophyllopsis* and *Plettkea* from *Stellaria*, he believed that this feature could have originated multiple times in the *Caryophyllaceae* (e.g. in *Pycnophyllum*). In his view, the 1-seeded capsule would not be a “very strong” character to serve as indicator for the overall affinities of the two genera (Mattfeld 1934). Mattfeld considered the two completely

free styles as diagnostic for the *Alsineae* whereas *Pycnophyllum* with the stigmas fused for most of their length was believed to be only distantly related (tribe *Pycnophylleae*). Consequently, Mattfeld (1934) transferred *Pycnophyllum macrophyllum* Muschler and *P. weberbaueri* to *Plettkea*, thus assuming the convergence of both the cushion plant life form and of the 1-seeded capsule fruit. Bittrich (1993) accepted *Plettkea* as different from *Pycnophyllopsis*, considering the flowers being strongly perigynous, pentamerous, or tetramerous, and with episealous stamens. In contrast to this, Timaná (2017) merged *Plettkea* with *Pycnophyllopsis* to then consist of eight species, one of which (*Pycnophyllopsis smithii*) was newly described based on a specimen from Huarochirí (Peru, Dpto. Lima). Timaná (2017) did not analyse the phylogenetic relationships of these two genera.

The genus *Stellaria* consists of herbs, commonly known as chickweeds or starworts that occur in a wide range of ecosystems, from low to high altitudes on nearly all continents (Sharples & Tripp 2019). Pax & Hoffmann (1934) attempted the last worldwide species-level classification and estimated the genus to contain over 100 species. Sharples (2019) and Sharples & Tripp (2019) re-circumscribed *Stellaria* to be monophyletic based on their RAD trees that yielded much better resolution than the tree of Greenberg & Donoghue (2011) for *Stellaria* and relatives. Sharples & Tripp (2019) segregated *S. holostea* L. into the new genus *Rabelera*, morphologically differing from *Stellaria* by the square and ciliate stems, elongated sessile and lanceolate leaves, leafy bracts and by the petals that are only bilobed for one half of their length. Another distant lineage, *S. arisanensis* (Hayata) Hayata and allies was described as the new genus *Nubelaria*. For the monophyletic core of *Stellaria*, Sharples & Tripp (2019) found five major clades that they named informally as ‘Insignes’ (species from North America and Asia), ‘Larbrae’ (being the most diverse clade with species in temperate Asia, Europe and North America), ‘Nitentes’ (three species from Central and North America), ‘Plettkeae’ represented by one species from the central Andes and ‘Petiolares’ (South America, represented by nine species). Although three of the names (‘Insignes’, ‘Larbrae’, ‘Petiolares’) were among the unranked divisions that first appeared in Fenzl’s (1840) treatment of *Stellaria*, Sharples and Tripp (2019) did not equate their clades to a formal infrageneric classification.

Most species of *Stellaria* bear showy petals but approximately one-fourth of the genus is characterized by petal reductions, ranging from absent to partial or reduced petals as shown by Sharples & al. (2021). According to their reconstruction of character evolution, petal loss or reduction evolved independently in multiple lineages, including the branch to *Plettkea* where this is an obvious feature, even when looking at the plants in the field. The evolution of apetaly can be linked to abiotic pollination (Culley & al. 2002) or it could be associated with the evolution of autogamy (Pieper & al. 2016; Klepikova &

al. 2021). Recently, Wei & Ronse De Craene (2019) investigated the development of petals in *Caryophyllaceae*. Although their publication did not specifically present results on *Stellaria*, the most likely explanation seems a reduction and loss of petals is linked with an acceleration of stamen initiation, thus leading to reduced space for the development of petals (Louis Ronse De Craene, pers. comm.). We would therefore assume gradual petal reductions in our study group. The finding of numerous evolutionary transitions between petaly and apetaly, both within and across multiple genera (Sharples & al. 2021), adds to the convergent evolution of life forms in different unrelated lineages of the *Caryophyllaceae*. Interestingly, the presence or absence of petals or their reduction was not used in pre-phylogenetic definitions of genus concepts, while both *Arenaria* and *Stellaria* were said to contain species groups lacking petals (e.g. in Pax & Hoffmann 1934).

Apart from *Stellaria*, several species that show highly reduced petals (sometimes simplified to being apetalous) were previously included within the genus *Arenaria*, such as *A. alpamarcae* A. Gray, *A. andina* Rohrb., *A. aphanantha* Wedd., *A. crassipes* Baehni & J. F. Macbr., *A. engleriana* Muschl., *A. nitida* (Bartl.) Rohrb. and *A. pedunculosa* Wedd.. These South American members of *Arenaria* were placed variously in *A.* subg. *Dicranilla* (Fenzl) Fenzl, *A.* subg. *Leiosperma* (F. N. Williams) McNeill and *A.* subg. *Eremogoneastrum* F. N. Williams. And even more interestingly, several of them such as *A. alpamarcae* were reported to form small cushions and grow at high altitudes in the central Andes. However, no comprehensive phylogeny of *Arenaria* was available. Considering the high level of homoplasy in petal evolution, we could not take the presence or absence of petals as a solid indicator for assigning a species to any of the genera *Arenaria* in tribe *Arenarieae* or *Pycnophyllopsis* and other genera of the tribe *Alsineae*.

In the context of ongoing work aiming at a new species-level taxonomic backbone for the family *Caryophyllaceae* as part of the *Caryophyllales* Taxonomic Expert Network (see Borsch & al. 2015; Arias & al. 2018) sequence data are being generated for speciose genera that lack comprehensive recent revisions such as *Arenaria*. As a first step, phylogenetic work has been directed toward including as many species as possible across *Alsineae*, *Arenarieae* and other tribes, while keeping the sequencing effort per sample at a minimum (Mansion & al. 2012), which then allowed us to formulate specific questions on the hypothesized clades. More specifically, fieldwork was initiated in 2015 with the intention of gathering a significant number of the species of the *Caryophyllaceae* from the central Andes to be included in this phylogenetic approach, considering the high and still insufficiently known species diversity in the area with significant levels of convergent evolution of life forms adapted to high mountain habitats. Based on this first set of *trnL-F* and ITS sequence data, all members of the genera *Plettkea*

and *Pycnophyllopsis* along with a number of taxa currently classified as *Arenaria* and further specimens that could not be identified using the available Floras, were recovered as part of a strongly deviant clade including the members of core *Stellaria* sensu Sharples & Tripp (2019) and Arabi & al. (2022).

The specific objectives of this investigation were to (1) reconstruct phylogenetic relationships within the clade of the *Caryophyllaceae* comprising *Stellaria*, *Plettkea*, *Pycnophyllopsis* and the entities formerly classified as *Arenaria* but belonging here (2) evaluate species-level relationships in *Plettkea* and related taxa and (3) to provide an updated species-level treatment of *Plettkea* and related taxa including morphological descriptions, a consistent classification of all known entities with the correct nomenclature and a first assessment of species distribution using available material.

Material and methods

Sampling strategy and selection of material

Fieldwork was undertaken in the highlands of the central Andes between 2015 and 2022 covering all species of *Caryophyllaceae*. Herbarium specimens were collected with duplicates and corresponding leaf tissue was dried in silica gel. Collecting focused on eight Andean departments of Peru (c. 200 localities), allowing us to cover most of the type localities of previously described species in *Arenaria*, *Pycnophyllopsis* and *Stellaria* as hitherto classified. In addition, herbarium material was evaluated from B and several other herbaria from which material was loaned to B (GOET, L, LPZ, O and PRC) and sampled for molecular analysis in case the respective taxon was not found in the field. The following institutions were visited: CONC, CUZ, F, GOET, HSP, HOXA, HUT, K, LP, LPB, LPZ, MO, MOL, NY, P, PRC, SI, US and USM (herbarium codes according to Thiers continuously updated).

Following a first round of phylogenetic assignment of the material to major clades using short sequences (plastid *trnL-F* and nrITS) that could easily be generated for many samples following the approach of Mansion & al. (2012), a fraction of these samples including species from all three genera mentioned above turned out to belong to a very distinct subclade of a *Stellaria* clade. Further research then focused on these samples. To determine the precise position of this subclade, the sampling was extended to represent all major lineages of *Stellaria*, guided by the trees of Sharples & Tripp (2019).

Compilation of all previously published names / taxa

A list of *Arenaria* names was received from the WFO Data Centre in February 2018 and imported into the EDIT Platform. This import included names accepted in the WFO

backbone and their synonyms therein (WFO 2018). For *Plettkea*, *Pycnophyllopsis* and *Stellaria*, the names were obtained from the World Checklist of Vascular Plants dataset received from the Royal Botanic Gardens, Kew in December 2019 (Kew WCV 2019). In both cases, the import included accepted names and synonyms and each of these taxonomic states was preliminarily assigned to entities that were considered to be part of the *Plettkea* lineage based on molecular data. With the objective of ensuring that we gathered all names published in our study group, the relevant treatments of South American *Caryophyllaceae* were also consulted, especially Williams (1898), Mattfeld (1922), Macbride (1936), Zarucchi & Gereau in Brako & Zarucchi (1993) and Beck & al. (2014) for the central Andes. Furthermore, the *Catálogo de las plantas vasculares del Cono Sur* was considered (Zuloaga & al. 2008) and the recent review by Montesinos-Tubée & Teillier (2022) for Chile. Further names were entered into the TEN's database using the EDIT Platform for Cyber-taxonomy (Berendsohn 2010), if not already present. The EDIT Platform is an open-source software with tools and services covering all parts of the taxonomic workflow. Moreover, we cross-checked this data set with Tropicos.org (2023). We then used JSTOR Global Plants (JSTOR 2023) to search for type material associated with the respective names to verify information in the protologues and discover additional type specimens.

Identification of plant material and elaboration of the taxonomic treatment

In the absence of a modern Flora or identification keys, type and other herbarium specimens cited in the original works were examined for a spectrum of morphological characters including those mentioned in the original descriptions to compare with our recently collected material. This process included further specimens of our Andean study group at the cited herbaria to assess the amount of morphological variation and to group the available specimens into morphologically distinct entities including the type specimens. It must be noted that many of the herbarium specimens had so far remained unidentified to species. In a second step, these entities were compared with the specimens included in lineages recovered by molecular phylogenetic analysis in order to check consistency in the presence of morphological character states. In general, in terms of species delimitation the molecular trees are taken as a hypothesis of what the closest relatives of a species are, and thus the differences in morphology these taxa will be discussed (in the notes of the taxonomic treatment). Also, the geographic location of the type specimens was checked in order to see if these localities were included within a hypothesized range of a respective taxon at species level. Due to the often very small number of specimens available for the respective entities, we did not employ any morphometric approach.

Assessment of morphological characters

Habit characters were mostly examined during fieldwork and recorded for the collected specimens. All other characters were assessed from herbarium specimens with Olympus SZX10 and NSZ-405 1X–4.5X stereo microscopes. For new to be described species, macro photos were taken in addition to the text description. The colour of the distinct organs was assessed with a colour chart. Seed morphology was evaluated under a Hitachi FE-SEM (Field Emission Scanning Electron Microscope) at BGBM. Furthermore, field photographs of the collected and analysed specimens were taken. In Fig. 1 the cushion type habits of species belonging to the *Plettkea* clade is shown. Fig. 2 depicts living specimens of species of the ‘Petiolares’ clade of *Stellaria* from Peru.

DNA extraction, PCR amplification and sequencing

Genomic DNA was isolated from silica-gel dried or herbarium materials using the triple extraction Cetyltrimethylammonium bromide (CTAB) procedure by Borsch & al. (2003).

The chloroplast *trnL-F* region was amplified with universal primers *trnTc* and *trnTf* (Taberlet & al. 1991). Reaction conditions entailed 5.0 µl of 10X Taq Reaction Buffer, 3.0 µl of 25 mM MgCl₂, 5.0 µl of 5 M betaine, 2.0 µl of 10 pmol/µl of the forward and reverse primer, 6.25 µl of dNTP (each 1.25 mM) and 0.25 µl Hot Start Taq polymerase made up to a total of 50 µl with ultrapure water. The following temperature and timing were applied for the PCR amplifications: denaturation at 95 °C for 2 min; 30 cycles consisting of 94 °C for 30 s, 52–54 °C for 30 s, 72 °C for 90 s; and 72 °C for 10 min; 4 °C hold. Due to microsatellites, primers *trnL460F* (Worberg & al. 2007) and *trnTd* (Taberlet & al. 1991) were employed as additional sequencing primers. For *matK* we amplified the whole region spanning the *trnK* 5' exon to the *psbA* gene, thus covering the *trnK* group II intron, the *matK* CDS and the *trnK-psbA* spacer. This region was generally amplified in two halves using primers *trnKF* + *CARYmatK1440R* (upstream) and *CARmatK480F* + *psbA5R* (Steele and Vilgalys 1994). For degraded DNAs from herbarium samples, the region was amplified in quarters using primer pairs *trnKF* + *CARmatK978R* (5'-TTT GGT TAG AAW AAT TAG CCG-3'; designed here), *CARmatK745F* (5'-CTA TCC ACT TAT CTT TCA GG-3'; designed here) + *CARYmatK1440R* (Schäferhoff & al. 2009), *CARmatK480F* (GBOL Project, T. Borsch, pers. comm.) + *CARmatK910R* (5'-AAT GAC TGC AAA TCC TTC TGA-3'; designed here), and *CARmatK1040F* (5'-AGT CAA ATG TTA GAA AAT GC-3'; designed here) + *psbA5R*. Due to several mismatches that prevented amplification the new primer *CARmatK1033F* (5'-GGTACGGAGTCAAATGTTAG-3') was designed for *Stellaria radians* to replace *CARmatK1040F*. Most of these primers were also used for sequencing. *CAR-*

matK537R (5'-TTTAGATTATTCCAATTATG-3') was designed as an additional specific sequencing primer to fill gaps between long microsatellites in some species. The nrITS region was generally amplified with the universal primers ITS4 and ITS5 (White & al. 1990). Since this led to the amplification of fungal DNA in a number of samples, the *Caryophyllaceae*-specific primer *CAR-ITS5* (5'-AGGATCATTGYCGAAACCTG-3') was designed to replace ITS5 in these cases. PCR products were then run over a long gel and excised to remove unspecific fragments and purified over a GenepHlow™ Gel/PCR Kit from geneaid (article no. DFH300). Concentrations were measured using the Nanodrop – Spectrophotometer nd-1000-v3.7. Cycle sequencing was then carried out by MacroGen Europe in Amsterdam (the Netherlands) with the BigDye® Terminator v3.1 Cycle Sequencing Kit (Applied Biosystems) on an ABI 3730xl DNA Analyzer (96-capillary sequencer).

Multiple sequence alignment, indel coding and tree inference

Pherograms were assembled with PhyDE 0.9971 (Müller & al. 2010) and errors in base calling, which occurred as a slippage effect in particular after long microsatellites, were corrected manually. Multiple sequence alignment followed a motif approach to recognize microstructural mutational events including one to several nucleotides at once (Kelchner 2000; Morrison 2009) following the alignment rules as laid out in Löhne & Borsch (2005). Simple indel coding (Simmons & Ochoterena 2000) was done through SeqState (Müller 2005). Maximum parsimony was implemented in PAUP* version 4.0a169 (Swofford 2002) using random addition with 1000 replicates, TBR Branch swapping and MULTREES in effect. PAUP* was also used for Jackknifing with 36.788 % of characters deleted in each of 10,000 replicates. The program jModeltest 2.1.10 (Darriba & al. 2012) was used to determine the best-fitting evolutionary models using the Akaike Information criterion to select them. For the *trnK* intron and *trnK-psbA* spacer as well as the *trnL-F* region TIM1+G were found, for the *matK* CDS the TVM+G model and for ITS (SYM+I+G). Bayesian trees were inferred with MrBayes v. 3.2 (Ronquist & al. 2012), implementing four independent runs with four chains each and 5 million MCMC generations. Convergence and effective sample size (ESS) were checked with Tracer v. 1.7 (Rambaut & al. 2018). The burn-in was set at 2500 and every 1000th generation was sampled to calculate a majority rule consensus tree. The detailed specifications in the MrBayes block can be seen in the matrices provided for the plastid and ITS partitions (see results). Maximum Likelihood calculations were done with RAxML v.8.2.12 on XSEDE in CIPRES using the GTR model for substitutions and the BIN model for indel characters. Tree-Graph 2.15.0-887 beta (Stöver & Müller 2010) was used to visualize and annotate the trees based on the Bayesian



majority rule consensus, and depicting confidence values for nodes from all three tree inference methods. *Scleranthus annuus* L. was selected to root the trees to a relatively distant taxon outside the *Alsineae* and *Arenarieae* tribes as its putative sister (Arabi & al. 2022). This way, the circumscription of *Stellaria* proposed by Sharples & Tripp (2019) could be further tested with sequence data and an extended taxon sampling including many species hitherto not represented in any phylogenetic analysis.

Results

Sequence data sets

The plastid data set contained 51 samples. The *trnL-F* and *trnK-matK* sequences of 49 samples (all 23 from the *Plettkea* clade) were generated in this investigation and two (DB38206 *Rabelera holostea* (L.) M. T. Sharples & E. A. Tripp and DB38311 *Stellaria* cf. *alsine* Grimm) were taken from the German Barcode of Life (GBOL) project. The multiple sequence alignment of the *trnL-F* region contained 1345 positions, from which the first 32 and the last 36 were trimmed (Supplementary appendix S1). Seven short mutational hotspots were excluded because of poly-AT microsatellites (poly GC in pos. 1256–1267 in *Arenaria*) and a part of the *trnL* p8 loop (pos. 364–455) constituted by a long polyA/T satellite and AT-rich elements for which no homology could be assessed between the *Stellaria* clade (including *Plettkea*) and the other lineages. The *trnL-F* region contributed 1105 characters to the final matrix of which 420 (34.9 %) were variable and 220 (18.3 %) were informative, plus 99 indel characters of which 37 were informative. The multiple sequence alignment of the *trnK-matK* partition (Supplementary appendix S1) had a length of 3124 positions, comprising the complete *trnK* intron with the *matK* CDS, the *trnK* 3' exon, the *trnK-psbA* intergenic spacer and 40 nucleotides of the *psbA* gene. Ten short mutational hotspots (mostly microsatellites and regions comprising short AT-rich repetitive elements without clear homology) were excluded from the *trnK* intron partition. The *matK-trnK* region contributed 2935 characters, of which 1086 (37 %) were variable and 535 (18.2 %) informative. The indel partition contributed 117 of these characters from which 38 were informative. The complete combined plastid matrix used for analyses is provided in Supplementary appendix S2.

The ITS dataset included 49 sequences, from which 47 were generated in this study and 2 were obtained from the GBOL project to complement the ITS partition for the same samples. The alignment contained 802 nucleotide positions (Supplementary appendix S3), all of which were used in the matrix for tree inference. Simple indel coding resulted in additional 78 binary characters (Supplementary appendix S4).

Trees inferred from the plastid partition

The Bayesian majority rule consensus tree is shown in Fig. 3 and depicts a well resolved and statistically supported backbone of the *Alsineae*. Three sublineages (A, B, C) are found within a *Plettkea* clade, although these three and sublineages defined by two other species (*Stellaria galianoi* Montesinos & Borsch, *S. macbridei* Montesinos & Borsch) remain in a polytomy. An identical picture is given by the maximum parsimony strict consensus tree summarized from 5780 shortest trees with a score of 2267 (Supplementary appendix S5). The ML tree with the best likelihood score (Supplementary appendix S5) shows these species in inconsistent, unsupported positions as sisters to subclades C and A, respectively. The sample representing the ‘Nitentes’ clade (DB38311) is found with high support as sister to the *Plettkea* clade by all tree inference methods (Fig. 3). A further exploratory tree with the sequences available from GenBank of *S. cryptantha* (Mattf.) M. T. Sharples & E. A. Tripp (*trnL-F* and partial *matK*) and several species of the other major *Stellaria* clades (c. 800 nt fragments of *matK*) can also be found in Supplementary appendix S6 (and matrix in S7).

Trees inferred from nrITS

The ITS Bayesian majority rule tree (Fig. 4) provides slightly more resolution within a well-supported *Plettkea* clade with sublineage B plus *Stellaria utubambensis* Montesinos & Borsch (CAR433) and sublineage C being sisters, although not very well supported. The lineage with the two samples of *S. galianoi* then appears as sister to this clade albeit with significant support (0.98 PP) for the respective node only by Bayesian inference. The respective positions of the representatives of the ‘Larbrae’ (*S. pungens* Brongn., *S. ruscifolia* D. F. K. Schltdl.) and ‘Nitentes’ clades sensu Sharples & Tripp (2019) differ inconsistently between the Bayesian and the ML tree (Supplementary appendix S8) while the first branching posi-

Fig. 1 (p. 120). Habit in natural environment of some species of the *Plettkea* clade of *Stellaria*. – A: *S. alpamarcae*, Huánuco, Huamalies, 4400 m (Montesinos 5487, CAR440); B: *S. congesta*, Huánuco, Huamalies, 4200 m (Montesinos 4900, CAR661); C: *S. galianoi*, Cusco, Urubamba, near Malaga pass, 4240 m, shady rocky slopes in moist grasslands (Montesinos & von Mering 4523, CAR677); D: *S. macbridei*, Huánuco, Lauricocha, 4790 m (Montesinos 4590, CAR630); E: *S. pedunculosa*, Moquegua, near Ticsani volcano, 4818 m, pumice slopes (Montesinos & Chicalla 5395d, CAR777); F: *S. utubambensis*, Amazonas, Chachapoyas, Leymebamba, Tajopampa, 3700 m, rocky summits of recently burnt slopes (Montesinos & Garcia 4979, CAR433); G: *S. weberbaueri*, Arequipa, 4876 m, forming cushions with eventually elongated stems (Montesinos & von Mering 4496, CAR670); H: *S. xanthophylla* Amazonas, S Leymebamba, 3540 m, forming dense mats (Montesinos 6970a, CAR691). – All photographs by Daniel B. Montesinos-Tubée.

tion of the ‘Petiolares’ followed by the ‘Insignes’ clade is congruently found in both, although not very well supported by Bayesian PP or Likelihood BS. An exploratory analysis with available published ITS sequences with a much better sampling of the ‘Larbreae’ and ‘Nitentes’ clades (Supplementary appendix S9 and matrix in S10) shows both in a sister group relationship with high support, contrary to the ITS tree in Fig. 4. Nevertheless, the first branching position of the ‘Petiolares’ clade in *Stellaria* remains unaffected by taxon sampling (Fig. 4, Supplementary appendix S9).

Discussion

Overall relationships in *Stellaria* and position of the *Plettkea* clade

In comparison with previous phylogenetic analyses of *Plettkea* that were only represented by two species, one in the RAD study by Sharples & Tripp (2021), and another in the tree of *Caryophyllaceae* by Greenberg & Donoghue (2011) we could include 14 of the 20 species of the *Plettkea* lineage into a phylogenetic analysis of both plastid and nrITS regions (Fig. 3, 4) which resulted in a maximally supported clade throughout all analyses that was recovered as deeply nested within the monophyletic genus *Stellaria* according to the circumscription of Sharples & Tripp (2019). An additional species of the *Plettkea* clade, *S. laevis* (Bartl.) Rohrb. (AC912) was recovered with ITS (Supplementary appendix S9) within the *Plettkea* clade. The RAD trees of *Stellaria* presented by Sharples & Tripp (2019), depicted five major clades. The only specimen from the *Plettkea* clade represented therein is *S. tetrasticha* (Mattf.) M. T. Sharples & E. A. Tripp, annotated by the authors as “Plettkeae”. It appeared as sister to the ‘Larbreae’ and ‘Nitentes’ clades, whereas the ‘Insignes’ clade (represented by *S. radicans* L., *S. pubera* Michx. and *S. sessiliflora* Y. Yabe) was found sister to the ‘Petiolares’ clade.

The relationships of the species-rich ‘Larbreae’ clade (Sharples & Tripp 2019) to the ‘Nitentes’ clade and the *Plettkea* clade remain unclear. Whereas our plastid topology provides a well-supported hypothesis of the ‘Nitentes’ being sister to the Andean *Plettkea* clade, ITS seems to favour a sister group relationship of the ‘Larbreae’ and ‘Nitentes’, also shown by the best-scoring ML tree of the RAD data in Sharples & Tripp (2019). Future phylogenomic analyses using hybseq data should be employed to test for a possible reticulate event that could have occurred before the divergence of the *Plettkea* crown group in the Andes. The more broadly sampled ITS tree (Supplementary appendix S9) indicates that *Stellaria alsine* as currently accepted contains at least two different evolutionary lineages, while further samples with this annotation in GenBank rather seem to be misidentified (in the ‘Petiolares’ clade). Sharples (2023)

proposed in a short paper that appeared during the revision of this manuscript, that the name *S. undulata* Thunb. (\equiv *S. alsine* var. *undulata* (Thunb.) Ohwi) would apply to the lineage of specimens resolved in the ‘Larbreae’ clade, so that the specimens shown in our Fig. 3 and 4 in the ‘Nitentes’ clade are true *S. alsine*. Nevertheless, a detailed analysis of species limits and distribution of this entity is still lacking. A further question arises regarding the phylogenetic position of the ‘Petiolares’ clade which also contains a significant number of South American species of *Stellaria* (e.g. *S. cuspidata* Willd. ex D. F. K. Schltdl., *S. recurvata* Willd. ex D. F. K. Schltdl., *S. sp.*, *S. weddellii* Pedersen; Fig. 3, 4) and which may constitute another south American radiation within *Stellaria*. Whereas ITS data indicate a first branching position of the ‘Petiolares’ clade, the analyses of RAD data by Sharples & Tripp (2019) yielded different results depending on the selection of loci and the genetic distances covered by the taxon set. Their analysis based on more loci showed a tree incongruent to our ITS phylogenies (Fig. 4, Supplementary appendix S9). Also, our plastid trees are different, providing evidence for a possible paraphyly of the ‘Petiolares’ clade with respect to *S. radicans* (‘Insignes’ clade). However, a detailed plastid phylogenomic analysis needs to be undertaken to recover the true history of the plastid genome as the current plastid sequences may not provide a sufficient character sampling of this genomic compartment to properly recover the respective nodes. The sister group relationship of the ‘Petiolares’ and ‘Insignes’ lineages in the ITS tree (Fig. 3) is supported only through Bayesian posterior probabilities but not by ML-BS and MP-JK and thus depends on the inference method.

Composition and species-level relationships within the *Plettkea* clade

The *Plettkea* clade gains maximum support in all trees (Bayesian Inference, Maximum Parsimony, Maximum Likelihood inferred from plastid and nuclear partitions) and appears as a crown group on a rather long internal branch within *Stellaria*, suggesting that it forms an Andean radiation within this genus. In our trees the clade contains 13 taxa (represented by 23 samples). Considering that this is the first thorough sampling of this Andean plant group, and that so far, no comprehensive taxonomic revision existed, several entities turned out to represent new species, and changes are required in nomenclature. These are presented in the taxonomic treatment section (below). For simplicity and better readability, we already use the correct names here in the discussion and to annotate species in the phylogenetic trees. Fig. 3 and 4 include colour bars for species previously recognized under *Arenaria* and under *Pycnophyllopsis* (*sensu* Timaná 2017). This includes the two former species of *Pycnophyllopsis* that Sharples & Tripp (2019) already merged with *Stellaria* (*S. cryptantha* (Mattf.) M. T. Sharples &



Fig. 2. Representatives of the ‘Petiolares’ clade. – A: *Stellaria cuspidata*, S Peru, Arequipa, Chiguata, 3300 m; B: *Stellaria* sp., central Peru, Huánuco, Huamalies, 3200 m; C: *S. recurvata*, N Peru, Amazonas, 3200 m; D: *S. weddellii*, S Peru, Cusco, Urubamba, 4200 m, forming clumps, growing together with *Aciachne pulvinata* Benth. (*Poaceae*). – All photographs by Daniel B. Montesinos-Tubée.

E. A. Tripp and *S. tetrasticha* (Mattf.) M. T. Sharples & E. A. Tripp) based on RAD data of *S. tetrasticha*.

The trees inferred from plastid and nrITS sequence data are largely congruent and depict three sublineages (A, B, C) in addition to branches representing three more isolated species (*Stellaria galianoi*, *S. utcubambensis*, *S. macbridei*, respectively). According to Timaná (2017) eight species were classified as *Pycnophyllopsis*, all of which belong to the *Plettkea* clade as part of the genus *Stellaria* (Fig. 3, 4). The first is *P. muscosa* Skottsbo., which is the type species of the genus *Pycnophyllopsis* and is considered to stand out by a “stellate calyx rather than the typical oblong, nearly cylindrical oblong calyx that characterizes all the other species in this genus [*Pycnophyllopsis*]” (Timaná 2017). then *P. keraioptala* Mattf., *P. cryptantha* (Mattf.) Molinari, *P. laevis* (Bartl.) Timaná, *P. macrophylla* (Muschl.) Molinari, *P. smithii* Timaná, *P. tetrasticha* (Mattf.) Timaná and *P. weberbaueri* (Muschl.) Timaná. According to our molecular trees, the genus *Pycnophyllopsis* would therefore be polyphyletic within the *Plettkea* clade, considering that *P. keraioptala* and *P. weberbaueri* belong to sublineage C and

P. cryptantha and *S. laevis* to sublineage A (Fig. 3, 4 and Supplementary appendices S6 and S9).

Sublineage A in the plastid tree comprises the two individuals of *Stellaria alpamarcae* (CAR439 and CAR440) in a tritomy together with the only sample of *S. engleriana* (Muschl.) Montesinos & Borsch (CAR632). The plastid sequence of *S. xanthophylla* Montesinos & Borsch represented by the single specimen is depicted as sister with 1.0 BI-PP and 83.3 % MP-JK whereas ITS does not resolve relationships among these individuals [CAR429 = *S. spinulosa* Montesinos & Borsch is inconsistently depicted as part of a polytomy with a general score of 64.3 % to which CAR439 does not belong]. The plastid data set further resolves the two specimens of *S. congesta* Montesinos & Borsch as sisters in the plastid tree that are also just depicted within the broad polytomy of the core of sublineage A with ITS. *Stellaria cryptantha* (CAR431) is congruently resolved as sister to the other members of the sublineage by the plastid and nuclear genomic partition, and with high support (Fig. 3, 4). This sublineage A is characterized for its occurrence in central Peru, the plants form mats, leaves and sepals with

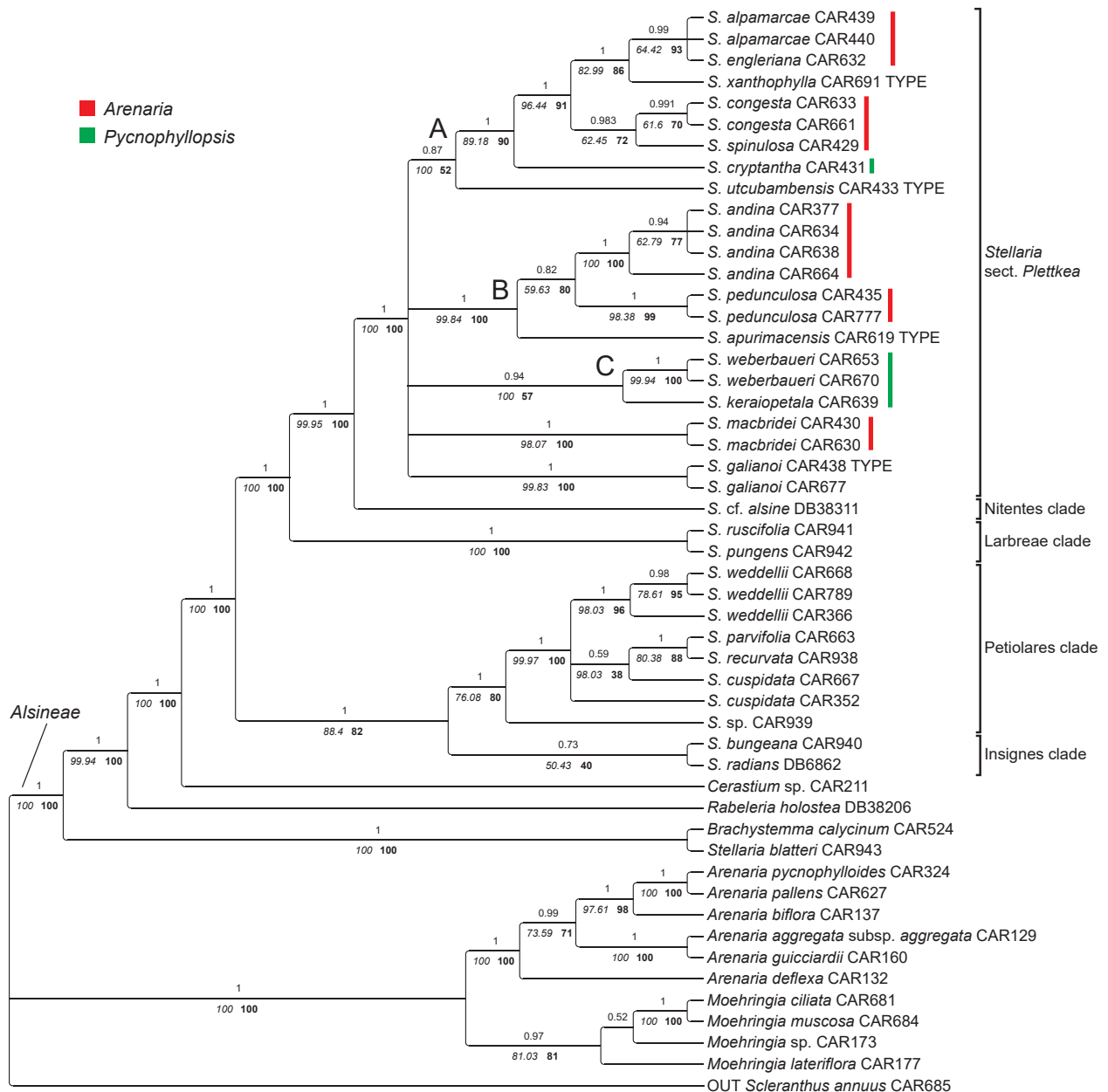


Fig. 3. Bayesian majority rule consensus tree inferred from combined *trnK-matK-psbA* + *trnL-F* sequence matrix including indels. Posterior probabilities are above branches, parsimony jackknife values are below branches left and in *italics*, and maximum likelihood bootstrap percentages right and in **bold**. The monophyletic *Stellaria* sect. *Plettkea* is deeply nested within the genus *Stellaria*. Species previously classified within *Arenaria* and *Pycnophyllopsis* are annotated with a red or green bar, respectively.

true spine-like apical portions rather than the usual compact or sprawling forms found in the sister sublineage B which also occur in S Peru and NW Bolivia.

Sublineage B is found in all trees and comprise *Stellaria andina* (Rohrb.) Montesinos & Borsch and relatives. This species is best represented in our molecular analysis with three samples from Bolivia (CAR377, B101149337; CAR634, B101149331; CAR638, B101149337) and one sample from Peru (CAR664, B100745260). These form a well-supported clade (1.0 BI-PP and 100 % MP-JK) in which a single sequence from Peru appears as sister to the three sequences from Bolivia (0.82 BI-PP and 51.1 %

MP-JK in the plastid tree and this is congruently found in the ITS tree (86.6 % MP-JK and 59.3 MP-JK, respectively). All four specimens share the glabrous, petiolate leaves and the subglobose calyx, and occur in similar habitats, indicating that the molecular differences show a pattern of phylogeographic differentiation within this species. Although node support is not very high, *S. pedunculosa* (Wedd.) Montesinos & Borsch is congruently inferred as sister to the *S. andina* clade with both genomic compartments. *Stellaria apurimacensis* Montesinos & D. Cornejo constitutes the earliest branch of subclade B, consistently in both the plastid and nuclear trees. The species is repre-



Fig. 4. Bayesian majority rule consensus tree inferred from nuclear ribosomal (ITS) sequence matrix including indels. DNA posterior probabilities are above branches, parsimony jackknife values are below branches left and in italics, and maximum likelihood bootstrap percentages right and in bold. The monophyletic *Stellaria* sect. *Plettkea* is deeply nested within the genus *Stellaria*. Species previously classified within *Arenaria* and *Pycnophyllopsis* are annotated with a red or green bar, respectively.

sented here by one specimen (CAR619) that is the type. Whereas our molecular data provide confidence for the position of *S. apurimacensis* in subclade B (1.0 BI-PP and 99.7 MP-JK in *matK-trnK-psbA* + *trnL-F* and 89.2 MP-JK in ITS) the support for the clade comprising *S. andina* and *S. pedunculosa* is rather low and appears to be connected to its short internal branch. Nevertheless, considering that these two other species of subclade B appear to be clearly monophyletic, our phylogenetic results underscore the status of *S. apurimacensis* as a distinct species.

Sublineage C (Fig. 3, 4) is constituted by samples of two species previously classified as *Pycnophyllopsis*. These are *Stellaria keraiopectata* (Mattf.) Montesinos & Borsch (one specimen CAR639, B101149336) sister to the lineage of the two sequenced specimens of *S. weberbaueri* (Muschl.) Montesinos & Borsch (1.0 BI-PP and 99.9 % of MP-JK in the plastid tree and 87.9 in MP-JK with ITS). The ITS tree depicts maximum support for subclade C (100 % MP-JK) whereas the branch leading to the respective node in the plastid tree is rather short (0.54 BI-PP, 52.8 MP-JK). Sublineage C entails two morphologically rather different species. Apart from the deviating dioecious reproductive system in *S. weberbaueri* (Timaná 2017), *S. keraiopectata*

differs by a reduced stamen number. In terms of habit as seen in the field, both species, however, appear to be very similar and resemble cushion-forming species of *Pycnophyllum*. In terms of the taxon concepts at species level we agree with Timaná (2017) who accepted *Pycnophyllopsis keraiopectata* as different from *P. weberbaueri*. The latter of which is sampled by two individuals (CAR653 and CAR670) that appear as sisters.

The plastid tree recovered three entities in an unresolved position within the *Plettkea* clade that do not belong to any of the three subclades (A, B, C); this is corroborated by ITS. *Stellaria macbridei* (a new name for *Arenaria crassipes*) is the first of these and represented by two sequences in our trees [CAR430 (B100766225) and CAR630 (B100761527)] that form a well-supported clade with 1.00 BI-PP and 98.3 % MP-JK (plastid tree) and 99.9 % MP-JK in the ITS tree. Both sequences were obtained from two isolated populations near the boundary of the Huánuco-Áncash departments, in highland slopes. These plants are characterized by having subcoriaceous or membranous leaves with a hirsute midrib, a character not found in the other species of the clade. The second isolated entity is *S. galianoi*. The sequences represent the

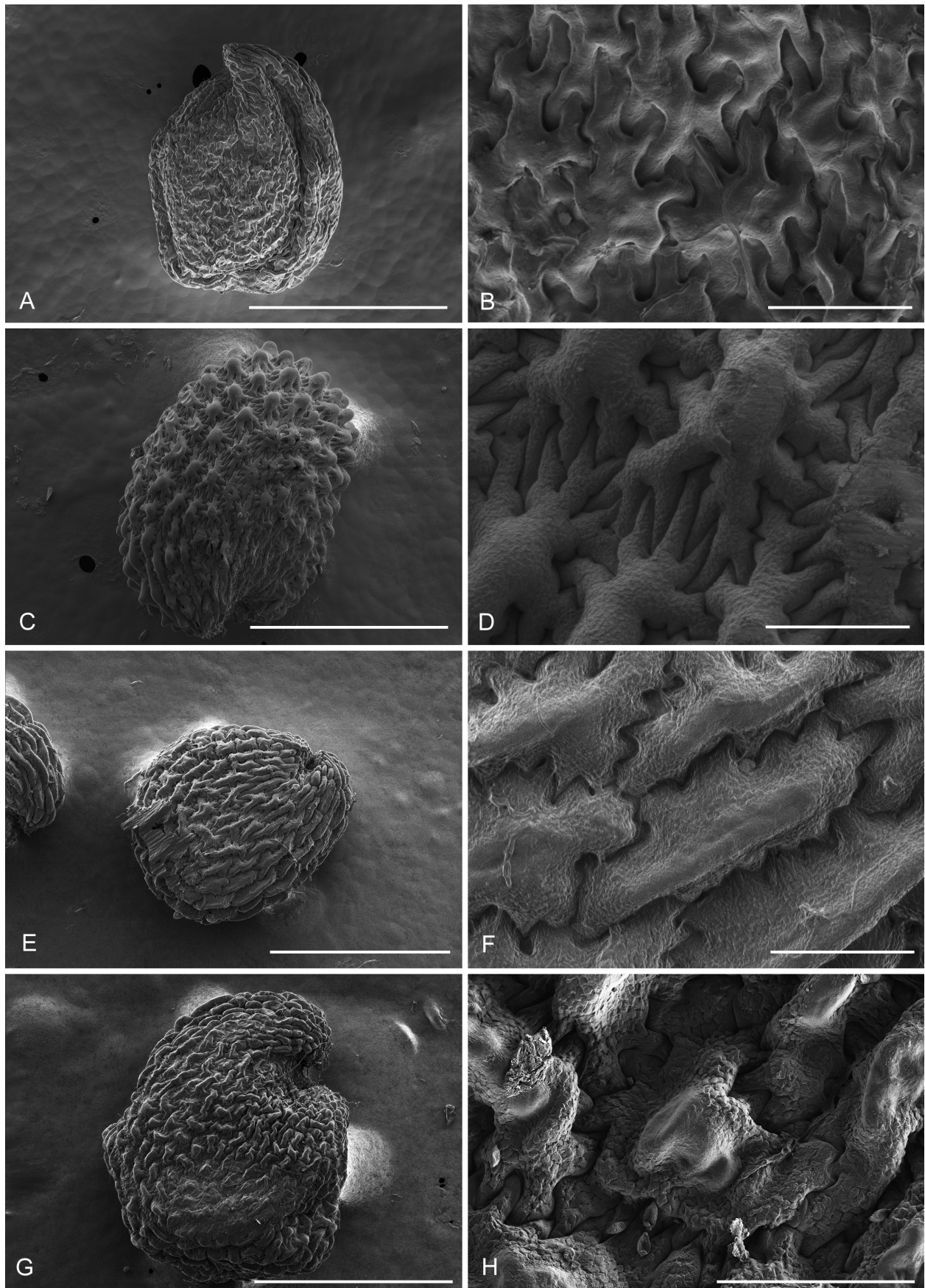


Fig. 5. SEM images of seeds of *Stellaria* species described as new species – A, B: *S. apurimacensis*; C, D: *S. galianoi*; E, F: *S. utcubambensis*; G, H: *S. xanthophylla*. – Scale bars: A, C, E, G = 0.5 mm; B, D, F, H = 50 µm.

species based on two collections, one of which is the type of the species (CAR438), in a lineage supported by 1.0 BI-PP and 99.5 % MP-JK. Whereas the plastid tree does not allow any conclusions on its relationships with the *Plettkea* clade, the ITS tree suggests it is sister to subclades B plus C. *Stellaria galianoi* is characterized by its flexible stems and leaves, long internodes and shady habit, and considered as a unique taxon in the clade for having longer internodes than all other species of the *Plettkea* clade. The third of these more isolated entities is *S. utcubambensis*, newly discovered here and is based on a single specimen from the Amazonas department in N Peru [CAR433 (B100766222)]. The ITS tree indicates a sister-group relationship of *S. utcubambensis* to subclade B. This species is unique in the clade since it is the easternmost distributed in the Andes in an isolated canyon that is formed by the Utcubamba river, which leads to the Amazonas in N Peru.

Biogeography of the *Plettkea* clade

Stellaria sect. *Plettkea* (Mattf.) Montesinos & Borsch represents another radiation of angiosperms at mostly high altitudes in the central Andes. This investigation revealed the existence of a clade of some twenty species that are distributed in the region. Similar examples of central Andean radiations can be found in other genera such as *Lupinus* (*Fabaceae*; Hughes & Eastwood 2006), which more recently were shown to consist of geographically structured sub-radiations along the Andes (Contreras-Ortiz & al. 2018) or *Gomphrena* (*Amaranthaceae*; Ortuño Limarino & Borsch 2020).

All of these radiations are relatively young, starting 1.5–2 mya in *Lupinus* (Hughes & Eastwood 2006) or 3.5–4 mya as in *Gomphrena* (Ortuño Limarino & Borsch 2020). Whereas the Andean clade of *Gomphrena* has two sublineages, one in central Bolivia and S Peru and the other in central to south Bolivia and northern Argentina, species diversification in the *Plettkea* clade to some extent seems to reflect the biogeographic subdivision of the Amotape-Huancabamba zone (Weigend 2004) in Peru. *Stellaria* sect. *Plettkea* subclade A (*Stellaria alpamarcae*, *S. congesta* and relatives) occurs in the northern half of Peru (from the departments of Lima and Junín northward) whereas subclades B and C (Fig. 3, 4) seem to be confined to areas further southeast of the Amotape-Huancabamba zone, reaching into Bolivia. It will be interesting to further test if an early branching position of *S. galianoi* (from department of Cusco in the southwestern part of the distribution of the *Plettkea* clade) in subclade B as suggested by the ITS tree (Fig. 4) will be substantiated by adding further molecular characters. The *Plettkea* clade will therefore be an interesting study group to better understand the biogeographical patterns in the central Andes. It is to be hoped that the key provided in our study will help to discover further specimens of *S.* sect. *Plettkea* for an improved mapping of species distributions.

Taxonomic treatment

Stellaria sect. *Plettkea* (Mattf.) Montesinos & Borsch, **comb. & stat. nov.** = *Plettkea* Mattf. in *Schriften Vereins Naturk. Unterweser*, n.s., 7: reprint p. 13 (11, 17). 1934. – Type: *Stellaria cryptantha* (Mattf.) M. T. Sharples & E. A. Tripp (= *Plettkea cryptantha* Mattf.).

= *Baretia* Timaná in *Adansonia*, ser. 3, 45: 502. 2023, **syn. nov.** – Type: *Baretia lanata* (Phil.) Timaná (= *Pycnophyllum lanatum* Phil.).

Morphological description — Annuals or perennials, mostly prostrate, cushion-forming or mat-like, sometimes in small and dense tufts. *Stems* often decumbent, rarely ascending, 2–60 cm high (*Stellaria galianoi* having greatest height), stems glabrous with few exceptions (*S. apurimacensis*) specially at nodes of leaves where hirsute hairs may occur, often glandular in surface; internodes hirsute or glabrous, short as in most of species and longer in *S. apurimacensis* and *S. galianoi*. *Leaves* mostly ovate, but linear to lanceolate in some species, 2–10 mm long, with acute or mucronate apex, usually hirsute near base, margins glabrous or ciliate, rarely lanuginose. *Flowers* solitary, only terminal, or in some species also axillary on short peduncles, with 5 sepals, free to base, mostly ovate to lanceolate, acute to acuminate in apex, base hirsute and stiff in texture, 1.8–5 mm long; petals mostly 5, rarely 4 or 3, showy and white or cream in colour and then usually bifid at apex, 10–15 mm long, or reduced to various degrees, mostly obtuse at apex, cream to translucent, and only up to 5 mm long and not overtopping sepals; stamens 5, often adherent to petals, filaments filiform and terete throughout (in all species for which descriptions are provided here), rarely thickened at base (*P. keraiopetala*, *P. patagonica*), in dioecious species sometimes a few staminodes present in pistillate flowers; ovary ovoid to globose, with trifid or rarely bifid styles, very rarely style single and unbranched (*S. villasenorii*), in dioecious species often rudimentary pistillodes present in staminate flowers, these not more than 1 mm long and seedless. Capsule 1–12-seeded; seeds more or less conspicuously tuberculate.

Notes — Until now there was no formal infrageneric name for the *Plettkea* clade. Sharples & Tripp (2019) annotated the lineage of *Stellaria tetrasticha*, corresponding to the *Plettkea* clade, in their trees with “Plettkeae” albeit without any reasoning for that name. The first infrageneric classification system by Fenzl (1840) recognized four entities, one of which, “*Eustellaria*”, was further subdivided. However, no specific nomenclatural rank was designated, until Pax & Hoffmann (1934) specified these entities as sections and subsections, respectively. We therefore suggest continuing the use of the sectional rank for the subdivision of *Stellaria*. No entity corresponding to a section *Plettkea* was included by Fenzl (1840) or Pax & Hoffmann (1934), so it is described here as a section of *Stellaria*.

As Sharples (2019) and Sharples & Tripp (2019) already pointed out, more work needs to be done to develop a consistent infrageneric classification for *Stellaria*, which includes testing if existing sectional/subsectional names are validly published. Considering that *S. graminea* was designated as the neotype for the monophyletic genus *Stellaria* (Tikhomirov 2016), and that the name “*Eustellaria*” is not permitted under Art. 21.3 of the *Code* (Turland & al. 2018), the ‘Larbreae’ clade (sensu Sharples & Tripp 2019) would become the typical *S. sect. Stellaria* (Sharples & Tripp 2019; Supplementary appendix S9).

Pax & Hoffmann (1934) validated the rank of *Arenaria* sect. *Dicranilla* (Fenzl) Pax & K. Hoffm. that was originally described by Fenzl (1840) based on *A. dicranoides* Kunth and *A. bryoides*, both described based on material from Mexico. In their treatment, Pax & Hoffmann (1934) also extended the concept of this section to include Andean species like *A. bisulca* (Bartl.) Fenzl & Rohrb., *A. pycnophylloides* Pax, *A. alpamarcae* A. Gray, *A. boliviana* F. N. Williams, *A. pedunculosa* Wedd., and *A. pycnophylla* Rohrb. However, the authors overlooked that these species do not match the original diagnosis by Fenzl (1840), who stated that the species of *Dicranilla* (Fenzl) Rchb. possess smooth, shiny, black seeds. On the contrary, members of the Andean *Plettkea* clade have tuberculate, brown seeds. Molecular phylogenetic data (T. Borsch, unpublished) further show that *A. dicranoides* belongs to the core *Arenaria* clade, underscoring that Pax & Hoffmann (1934) created an extended, morphologically heterogeneous and polyphyletic section. McNeill (1962) typified the genus name *Dicranilla* based on the section with *Arenaria dicranoides*, and commented on the misinterpretation of the seed characters by Pax & Hoffmann (1934). In summary, there was no name available for the ‘*Plettkea*’ clade at the level of section.

The publication by Timaná (2023), describing the new genus *Baretia* based on *Pycnophyllum lanatum* (*Stellaria villasenorii*), was received while correcting the proofs of this paper. We treat *Baretia* as a synonym here because to accept the new genus would make *Stellaria* paraphyletic.

Key to the species of *Stellaria* sect. *Plettkea*

1. Plants annual; leaves thin; roots fibrous 2
 - Plants perennial; leaves thick; roots mostly woody (except *S. utcubambensis* has fibrous roots) 5
2. Petals 2–3 mm long; seeds 10–12 per capsule; internodes of vegetative stems very long, 1–1.5 cm long in upper part *S. galianoi*
 - Petals 0.8–1.8 mm long; seeds 2–6 per capsule; internodes of vegetative stems less than 1 cm long 3
3. Forming large mats 5–8 cm high and up to 30 cm in diam. *S. andina*
 - Forming small cushions 1–2 cm high and 2–10 cm in diam. 4
4. Stamens 5, 0.2–0.4 mm long; seeds orbicular *S. pedunculosa*
 - Stamens 10, 0.3–0.4 mm long; seeds ovate *S. apurimacensis*
5. Flowers hermaphroditic (with pistils and stamens) 6
 - Flowers pistillate or staminate (plants dioecious) .. 17
6. Root fibrous; leaf blade linear, 0.5–1 mm long; calyx lobes mucronate with extending midrib *S. utcubambensis*
 - Root woody and thick; leaf blade lanceolate or with broader outline, > 0.8 mm long; calyx lobes acute .. 7
7. Flowers in leaf nodes (not terminal); sepals 5–7 mm long *S. xanthophylla*
 - Flowers terminal; sepals 1.6–4.9 mm long 8
8. Margins of blades hirsute or ciliate, sometimes only densely ciliate near truncate base (in *S. spinulosa*) . 9
 - Margins of blades glabrous 13
9. Leaf blade triangular; petals 5, deeply bifid 10
 - Leaf blade lanceolate, ovate or oblong; petals 3–5, obtuse or bifid (if bifid then only 3 in number) .. 11
10. Leaf sheath 1.4–1.7 mm long; petals 4; stamens 4; capsule 2–2.2 mm long *S. cryptantha*
 - Leaf sheath 0.8–1 mm long; petals 5 (rarely 4); stamens 5; capsule 1.5 mm long *S. macrophylla*
11. Flowers distinctly pedunculate (peduncle 2–2.9 mm long); plants forming mats with decumbent stems up to 50 cm long *S. spinulosa*
 - Flowers very shortly pedunculate (peduncle 0.1–0.5 mm long); plants forming dense small cushions not more than 12 cm in diam. 12
12. Stamens 3 (rarely 4 or 5 in flowers on same plant), antisepalous *S. keraiopetala*
 - Stamens 5, episepalous *S. engleriana*
13. Shrub with branches woody in lower part; petals deeply bifid *S. laevis*
 - Plants herbaceous; petals obtuse at apex 14
14. Forming small tussock-like cushions up to 2 cm in diam.; root with a thick tuber *S. macbridei*
 - Forming flat cushions 8–15(–20) cm in diam.; root not tuberous 15
15. Margin of leaf blades thickened, densely ciliate at base with 1–3 mm long trichomes .. *S. alpamarcae*
 - Margin of leaf blades not deviant in thickness, completely glabrous or with only very short (c. 0.1 mm long) trichomes 16
16. Internodes of stems almost invisible; leaves rigid with midrib prominent on underside; seeds 0.2–0.3 mm long *S. congesta*
 - Internodes 0.1–0.3 mm long; leaves thick and glossy, midrib not prominent on underside; seeds c. 0.5 mm long *S. standleyi*
17. Plants with densely lanuginose indumentum; leaf blades chartaceous, densely lanuginose at margin leaf sheath weak; style single *S. villasenorii*
 - Plants glabrous; leaf blades scarious, ciliate to denticulate at margin, leaf sheath strongly developed; styles 2- or 3-fid 18

18. Leaf blade 3–5 mm long; petals 0.3–1.5 mm long; capsules 1.5–2.9 mm long **19**
 – Leaf blade 1.5–2.5 mm long; petals 0.3–0.5 mm long; capsules 1–1.5 mm long **20**
 19. Inflorescence terminal, exserted; petals 1–1.5 mm long; capsules 2.5–2.9 mm long *S. patagonica*
 – Inflorescence terminal, included; petals 0.4–0.5 mm long; capsules 1.5–1.8 mm long *S. tetrasticha*
 20. Leaf margin sparsely ciliate, trichomes c. 0.05 mm long, leaf apex mucronate; sepals 1.2–1.5 mm long *S. smithii*
 – Leaf margin distinctly ciliate, trichomes 0.1–0.2 mm long, leaf apex acute to obtuse; sepals 1.6–2 mm long *S. weberbaueri*

Species-level taxonomic backbone and descriptions

1. *Stellaria alpamarcae* (A. Gray) Montesinos & Borsch, **comb. nov.** \equiv *Arenaria alpamarcae* A. Gray, U.S. Expl. Exped., Phan. 15: 116. 1854. – **Lectotype (designated here):** Peru, 1838–1842, Wilkes Expedition s.n. (GH00037630 image!; isolectotype: NY00342438 image!). – Fig. 1A.

Morphological description — Perennial herb, caespitose forming pulvinate dwarf cushions 2–4 cm high and 8–20 cm in diam.; root woody. *Stems* short or elongated erect in young plants becoming decumbent later on, usually covered by old foliage; internodes 1–2 mm long, with a scarce indumentum of trichomes < 0.1 mm. *Leaves* imbricate, lamina ovate-lanceolate, 4–7 mm long and 0.9–1.2 mm wide, longitudinally striate, midrib prominent on underside, margins thick, delicately folded toward adaxial surface, glabrous in distal part and at acuminate apex, turning ciliate toward base, where hairs can be dense (1–3 mm long). *Plants* bisexual-hermaphrodite. *Flowers* on 2–6 mm long, glabrous peduncles, terminal and axillary; perigynous, oblong, c. 4.5 mm long and 1.5–2.5 mm wide; calyx cylindrical-oblong; sepals 5, imbricate, oblong, 3–4 mm long and 1–2 mm wide, smooth, glabrous on surface and margins, apex acute-acuminate, usually folded and forming a cone-like cylinder that covers capsule; petals 5, strongly reduced, translucent, ovate, apex obtuse, c. 0.8 mm long and 0.5 mm wide; stamens 4 or 5, episepalous, 0.8–1.1 mm long; ovary cylindrical-turbinate, 0.6–0.9 mm long and 0.4–0.6 mm wide, style 3-fid, stigma aciculate, terete. *Capsule* ovoid, c. 1.5 mm long, containing 5–8 seeds, these globular in shape, c. 0.2 mm wide and 0.3 mm long; testa pale brown and cells with whitish stellate tubercles.

Distribution and ecology — *Stellaria alpamarcae* is endemic to Peru (Cano & Sánchez 2006), occurring in Áncash, Huancavelica, Huánuco, Junín and Lima departments, at altitudes of 4000–4700 m. The species occurs in Puna grasslands distributed in highland passes, which are relatively humid throughout the year.

Notes — The specimen chosen as the lectotype was likely examined by Asa Gray for the description of the species. Assuming it came from the same gathering, the specimen in NY (NY00342438) with a label indicating the years 1838–1842 and “Peru” would be an isolectotype.

The identity of further historical material annotated as isotypes of *Arenaria alpamarcae* available through JSTOR Global Plants (JSTOR 2023) is less clear. The locality information on a specimen in US (US00103277) given as “Alpamarca above Obrajillo and Banos [possibly Baños]” corresponds to the highlands of the Lima department in central Peru, which is possibly a different place. A second specimen in NY (NY00342437) lacks collector and geographical information and a specimen in P (P00335842) has just a label indicating the years 1838–1842 but lacks any collector or locality data beyond “Peru”.

2. *Stellaria andina* (Rohrb.) Montesinos & Borsch, **comb. nov.** \equiv *Arenaria andina* Rohrb. in Linnaea 37: 255. 1872. – **Lectotype (designated here):** Bolivia, Prov. Larecaja, vicinities Quiabaya via ad Tacacoma, 20 May 1860, G. Mandon 954 (K000471618 image!; isolectotypes: F0053255 image!, P00335843 image!, P00335844 image!, P00335845 image!, P01902983 image!, S-R-351).

Morphological description — Annual herb, sometimes forming large mats or carpets, 5–8 cm high and up to 30 cm in diam.; roots fibrous. *Stems* erect or decumbent, diffuse, usually loose, internodes 4–6 mm long, glabrous. *Leaves* opposite, lamina ovate, 2.5–3.5 mm long and 1–1.5 mm wide, surface glabrous on both sides, bright green to yellowish with age, margins bearing c. 0.1 mm long trichomes, midrib imposed on adaxial side, base petiolate and hirsute, apex acuminate. *Plants* bisexual-hermaphrodite. *Flowers* on short 1–4 mm long glabrous peduncles, terminal; perigynous, campanulate to subglobose, 4–5 mm long and wide, crateriform; sepals 5, imbricate, oblong, slightly involute, apex obtuse-acute, base attenuate, 3–4 mm long and c. 2 mm wide, bright green to green-yellowish with age, glabrous to rarely covered by thin white trichomes (< 0.1 mm long) at margins; petals 5, ovate, translucent to pale yellowish, rarely whitish, 1–1.8 mm long and 0.5–1 mm wide, apex rounded to obtuse; stamens 5, episepalous, 0.7–1 mm long; ovary ovoid, 0.8–1.1 mm long, style 3-fid, stigma terete to aciculate. *Capsule* ovoid, c. 2 mm long, containing 4–6 seeds, these ovate, c. 0.3 mm long; testa maroon, tuberculate.

Distribution and ecology — The species is only known to occur in SW Bolivia and SE Peru, inhabiting highland Puna environments and humid grasslands at altitudes of 4600–5100 m.

Vernacular name — *Wanupi Tika*, given in Quechua language (Zoilita Salazar Patiño, Arequipa, pers. comm.).

Notes — Paul Rohrbach (Berlin) aimed at a taxonomic synthesis of Andean *Caryophyllaceae* but died at an early age, so Garcke arranged to have his manuscript published in *Linnaea*. Rohrbach himself wrote (p. 184) “... so bildet die Mandon’sche Sammlung aus Bolivia den Kern des mir von dort vorliegendem Materials. Ich habe dieselbe in ziemlich gleicher Vollständigkeit in drei Herbarien, dem des k.k. botanischen hofkabinetts zu Wien, dem De’Candolleschen und dem des Grafen Franqueville gesehen; ...” in the protologue, Rohrbach (1872) mentioned “Mandon 954!” but without designating any particular specimen as a type. There is no specimen in W because Mandon material appears to have been lost due to a fire in the Second World War (Heimo Rainer, pers. comm. and as stated in https://www.nhm-wien.ac.at/en/research/botany/collections/lost_families).

3. *Stellaria apurimacensis* Montesinos & D. Cornejo, **sp. nov.** — Fig. 5A, B, 6; Supplementary appendix S11. Holotype: Peru, Apurimac, Cotabambas, Haquira, NW of Haquira, 4525 m, 28 Mar 2017, *D. Montesinos & D. Cornejo 5194* (HSP [HSP-9443!]; isotypes: B [B 10 0761536!], CUZ!, F!, USM!).

Diagnosis — The new species is distinguishable by its rosette or small mat, ovate leaves, apetalous flowers and short internodes.

Morphological description — Annual herb, densely ramified at base, forming cushions c. 2 cm high and 6–10 cm in diam.; roots fibrous. *Stems* decumbent or creeping, 4–6 cm long, often densely branched and covered by older leaves in central and lower parts; internodes 4–10 mm long, glabrous. *Leaves* opposite, petiolate, lamina elliptical-lanceolate, 2–3 mm long and 0.8–1.2 mm wide, sparsely pilose along margin, trichomes 0.1–0.3 mm long, acuminate, plain or curved, thin, slightly involute, glabrous on both sides, midrib protuberant on underside. *Plants* bisexual-hermaphrodite. *Flowers* on rigid or slightly curved 2–5 mm long glabrous peduncles, terminal; perigynous, 2.5–3.5 mm long and 1.5–2.2 mm wide, calyx campanulate, glabrous; sepals 5, imbricate, slightly involute, lanceolate-ovate, cupuliform at base, apex acuminate, glabrous, 2–3 mm long and 1–1.5 mm wide, pale green to yellowish; petals 5, translucent, ovate, 0.8–1.2 mm long and 0.4–0.6 mm wide, apex rounded; stamens usually 10, episepalous, filaments 0.3–0.4 mm long; ovary ovoid, 0.4–0.6 mm long and 0.3–0.5 wide; style 3-fid, curved, glandular, 0.3–0.5 mm long. *Capsule* ovoid, glabrous, c. 2.2 mm long, containing 4–6 seeds, these roundish to ovate, 0.4–0.5 mm long and 0.3–0.4 mm wide; testa pale brown, cells with tuberculate and stellate protuberances of c. 50 µm in diam.

Distribution and ecology — This species occurs in the Apurimac department on the boundary with the Cusco department at altitudes of 3980–4530 m in open grass-

lands with rocky outcrops in which species such as *Stipa ichu* Ruiz & Pav. (*Poaceae*), *Senecio adenophyllus* Meyen & Walp. and *S. algens* Wedd. (*Asteraceae*) occur.

Etymology — The epithet name is allusive to the Apurimac department located in S Peru, the site of the type locality.

Vernacular name — *Hatun Yuraq Tika*, given in Quechua language (Zoilita Salazar Patiño, Arequipa, pers. comm.).

Notes — *Stellaria apurimacensis* is morphologically similar to *S. galianoi* but differs by the internode length (4–10 mm vs. 2–15 mm in *S. galianoi*), smaller leaves (2–3 mm long and 0.8–1.2 mm wide vs. 3–5 mm long and 1.4–1.8 mm wide in *S. galianoi*), shorter peduncles (2–5 mm vs. 7–15 mm in *S. galianoi*), wider sepals (1–1.5 mm vs. 0.8–1 mm in *S. galianoi*) and smaller seeds (0.4–0.5 mm long vs. 0.6–0.8 mm long in *S. galianoi*). *Stellaria apurimacensis* differs from *S. macbridei* by the longer internodes (4–10 mm vs. 3–4 mm in *S. macbridei*), smaller leaves (2–3 mm long and 0.8–1.2 mm wide vs. 5–7 mm long and 2–2.5 mm wide in *S. macbridei*) and from *S. utcubambensis* by the weaker stems and leaves (vs. robust in *S. utcubambensis*).

4. *Stellaria congesta* Montesinos & Borsch, **nom. nov.** ≡ *Cherleria nitida* Bartl. in Presl, Reliq. Haenk. 2: 12. 1831 ≡ *Arenaria nitida* (Bartl.) Rohrb. in *Linnaea* 37: 249. 1872 [non *Stellaria nitida* Hook. in Scoresby, J. Voy. North. Whale-Industry: 411. 1823]. — **Lectotype (designated here):** Peru, Cobradillo [illegible, possibly misspelled as Obrajillo, town located in Canta, Lima], 1821, *Haenke s.n.* (GOET000573!). — Fig. 1B.

Morphological description — Perennial herb, caespitose, forming cushions or small mats, c. 4 cm high and up to 20 cm in diam.; root woody. *Stems* procumbent, numerous, forming a densely congested structure, with 6–10 cm long branches; internodes short, c. 0.1 mm long, glabrous. *Leaves* imbricate dense, rigid, lamina thick, ovate, 4–7 mm long and 1–1.2 mm wide, acute or slightly mucronate at apex, base scarcely attenuated, margins glabrous, also at base, margins involute, midrib prominent on underside. *Plants* bisexual-hermaphrodite. *Flowers* on 2.5–3 mm long, glabrous peduncles, terminal and axillary; perigynous, oblong, 3.5–4.5 mm long and 1–1.5 mm wide; calyx cylindrical-turbinate; sepals 5, imbricate, lanceolate, involute, 2–2.5 mm long and 1–2 mm wide, pale green to yellow, glabrous on surface and margins, apex acute-acuminate, folded and forming a cone-like cylinder that covers capsule; petals 5, strongly reduced, translucent, ovate, apex obtuse, 0.8–1 mm long and 0.5–0.7 mm wide; stamens 4 or 5, episepalous, 0.8–1.1 mm long; ovary cylindrical-turbinate, 0.8–1.2 mm long and 0.8–1.1 mm wide, style 3-fid, stigma aciculate. *Capsule* narrowly ovoid, shorter



Fig. 6. Morphological details of *Stellaria apurimacensis* – A: ramified stem; B: leaves; C: detail of pilose hairs on leaf margins; D: mature flower with capsule; E: sepals; F: tuberculate seeds. – From Montesinos & Cornejo 5194b. – Scale bars: A = 2 mm; B, D, E = 0.5 mm; C = 100 μ m; F = 200 μ m.

than calyx when mature, 1.5–2 mm long, opening with 6 valves, containing 6 seeds, these suborbicular, lenticiform, 0.2–0.3 mm in diam.; testa pale brown, bearing whitish protuberances.

Distribution — The species is endemic to Peru (Cano & Sánchez 2006) and is known to occur in Áncash, Huánuco, La Libertad and Junín departments according to the material revised and at altitudes of 3900–4500 m.

Etymology — The epithet *congesta* refers to the uniform and compact growth of the species.

Notes — The specimen at GOET has the annotation “rel. Haenk. II, 12 (cum descriptione)”, which indicates that the specimen may have been used to make a description.

5. *Stellaria cryptantha* (Mattf.) M. T. Sharples & E. A. Tripp in Syst. Bot. 44: 871. 2019 \equiv *Plettkea cryptantha* Mattf. in Schriften Vereins Naturk. Unterweser, n.s., 7: reprint p. 15 (19). 1934 \equiv *Pycnophyllopsis cryptantha* (Mattf.) Molinari in Polish Bot. J. 61: 276. 2016. – Holotype: Peru, Morococha, A. Raimondi 8392 (B⁺). – Neotype (designated by Timaná 2017: 6): Peru, Lima, Hua-

rochirí, Paso de Anticona, Ticlio, 4850 m, 16 Dec 1998, Timaná & Tate 3767 (USM; isoneotype: MO-1100075!).

Morphological description — See Timaná (2005).

Distribution — The species is found in highland passes in Andean mountainous ranges between the departments of Puno and Lima in Peru at altitudes of 4800–5200 m.

Notes — According to Timaná (2017), this distinctive species, has tetramerous flowers and 2 free styles. The species, originally described by Mattfeld (1934) as *Plettkea cryptantha*, is characterized by decussate sepals with the inner pair shorter and non-ciliate as opposed to the outer pair. Molinari-Novoa (2016) described the new combination *Pycnophyllopsis cryptantha* (Mattf.) Molinari, without studying any type specimen; the holotype was destroyed and no neotype had yet been selected. Timaná (2017) solved this by selecting a new type for the species based on a specimen collected near the type locality by Raimondi in Lima. Later, Sharples & Tripp (2019) stated that Greenberg & Donoghue (2011) recovered a sample of *Pycnophyllopsis cryptantha* (Mattf.) Timaná from Peru as embedded within core *Stellaria*. The *trnL-F* sequence available in GenBank is resolved as sis-

ter to CAR431 (Supplementary appendix S6) that is the representative of *S. cryptantha* in our analysis.

6. *Stellaria engleriana* (Muschl.) Montesinos & Borsch, **comb. nov.** \equiv *Arenaria engleriana* Muschl. in Bot. Jahrb. Syst. 45: 449. 1911. – **Lectotype (designated here):** Peru, Junín, Tarma, La Oroya, encima de Tarma en el camino a La Oroya, 4000 m, A. Weberbauer 2542 (MOL [MOL00000453!]).

Morphological description — Perennial herb, diffuse caespitose, cushions 5–12 cm in diam.; root woody. *Stems* subwoody, lower parts clothed with a greyish-green thick bark, or very minutely ridged-reticulated, prostrate, sometimes rooting at nodes, 3–6 cm long, internodes 0.1–0.5 mm long, glabrous or with sparse slightly yellowish-whitish pubescence, trichomes 1–2 mm long. *Leaves* opposite, sessile; lamina lanceolate or ovate or rarely linear-lanceolate, fleshy or rarely membranous, thick, apex acute or mucronate, 5–10 mm long and 2–5 mm wide, hirsute near base and midvein, margin slightly hairy, midrib prominent on underside. *Plants* bisexual-hermaphrodite. *Flowers* subsessile or on short up to 0.5 mm long, glabrous peduncles, terminal and axillary; perigynous, cylindrical-oblong, 3.5–4.5 mm long and 1–1.8 mm wide; calyx cylindrical-turbinate; sepals 5, imbricate, ovate-oblong, slightly involute, yellow, 3–4 mm long and 1–1.5 mm wide, glabrous on surface but margins densely ciliate, apex acute-attenuate, folded and forming a narrow cylinder that covers capsule; petals 5, strongly reduced, yellowish to translucent, ovate, apex obtuse, 0.8–1.2 mm long and 0.3–0.5 mm wide; stamens 4 or 5, episealous, 1.8–2.1 mm long; ovary ovoid-turbinate, 0.4–0.7 mm long and 0.4–0.6 mm wide, style 3-fid, stigma aciculate. *Capsule* subglobose, dehiscent with six valves, ovate-oblong, 1.3–1.7 mm long and 1.2–1.5 mm wide, containing 2–4 seeds, these lenticular, 0.7–1 mm in diam.; testa dark brown, bearing brown tubercles.

Distribution — Central Peru, in Junín and Huánuco departments, at altitudes of 4000–4400 m.

7. *Stellaria galianoi* Montesinos & Borsch, **sp. nov.** — Fig. 1C, 5C, D, 7; Supplementary appendix S12. Holotype: Peru, Cusco, Urubamba, Urubamba, Puerto Yanamayo, Patacancha, road to Ocobamba, 4440 m, 3 Apr 2016, D. Montesinos 4572 (HSP [HSP-9443!]; isotypes: B [B 10 0766217!], O [O-227237!], USM!).

Diagnosis — This species is easily distinguished by its long internodes (2–15 mm long), leaf laminae bearing white protuberances, absent characters in other species of *Stellaria* sect. *Plettkea*.

Morphological description — Perennial herb, forming diffuse mats, 4–8 cm high and 20–60 cm in diam.; roots fibrous. *Stems* decumbent or creeping 8–25 cm

long, densely ramified at base and along whole length, glabrous, or nearly so (scarcely covered with minute papillae), covered by older leaves in central and lower parts; internodes 2–15 mm long. *Leaves* opposite, sessile; lamina oblanceolate-oblong to gladiate, plain or curved, nearly involute, glabrous on both sides, 3–5 mm long and 1.4–1.8 mm wide, midrib protuberant on underside, margin from base to mid of lamina with 4–7 multicellular pilose hairs (0.3–1 mm long, 6–14 cells) born on protuberances, usually persistent on older leaves; base truncated and apex aristulate; leaves pale green to yellow-brownish with age. *Plants* bisexual-hermaphrodite. *Flowers* perigynous, on rigid 7–15 mm long and glabrous peduncles, terminal, 2.2–3 mm long and 3–5 mm wide; calyx campanulate, glabrous; sepals 5, lanceolate, slightly involute, cupuliform at base, apex apiculate-aristulate, glabrous, 1.8–2.4 mm long and 0.8–1 mm wide, pale green to yellowish; petals 5, white, subglandular, ovate, with revolute obtuse apex, 2–3 mm long and 1–1.5 mm wide; stamens usually 10, episealous, filaments often curved toward centre of flower, 0.3–0.5 mm long; anthers roundish to elliptical, reniform, yellowish and 0.15–0.3 mm long; style 3-fid, curved, glandular, pistil 0.5–0.7 mm long; stigma papillate or glandular; ovary cylindrical-ovoid, 0.7–1.1 mm long and 0.8–1.1 mm wide. *Capsule* ovoid, glabrous, c. 1.8 mm long and 2.5 mm wide, containing 10–12 seeds, these ovate or roundish, 0.6–0.8 mm long and 0.4–0.6 mm wide; testa brown, grooved, cells with bulgy stellate protuberances.

Distribution and ecology — Peru, Cusco, Urubamba. The species inhabits continuously moist environments dominated by tussock grasslands and bryophyte communities located on high passes that divide the inter Andean valleys, between the highland tropical forests and the puna scrublands in the upper basins near the Urubamba River lower slopes. The altitudinal range is 4230–4400 m and is restricted to this region. The exhaustive field collection of *Caryophyllaceae* in most parts of Peru for the past seven years and examination of nearly all available herbarium material did not reveal additional areas where the plant occurs. Nevertheless, further fieldwork in Urubamba is needed better understand the frequency and population structure of the species. Flowering specimens have been collected from March to May; fruiting specimens have been observed between April and June (pers. obs.). Associated taxa are: *Gentianella* sp. (*Gentianaceae*), *Plantago rigida* Kunth (*Plantaginaceae*), *Senecio rhizomatus* Rusby (*Asteraceae*) and *Stellaria weddellii* Pedersen (*Caryophyllaceae*), among others.

Etymology — The specific epithet refers to Prof. Washington Galiano (1950–), for his devoted career on studying the floristic diversity of the Cusco department in S Peru.

Notes — *Stellaria galianoi* is most likely monophyletic and is phylogenetically rather isolated among other mem-

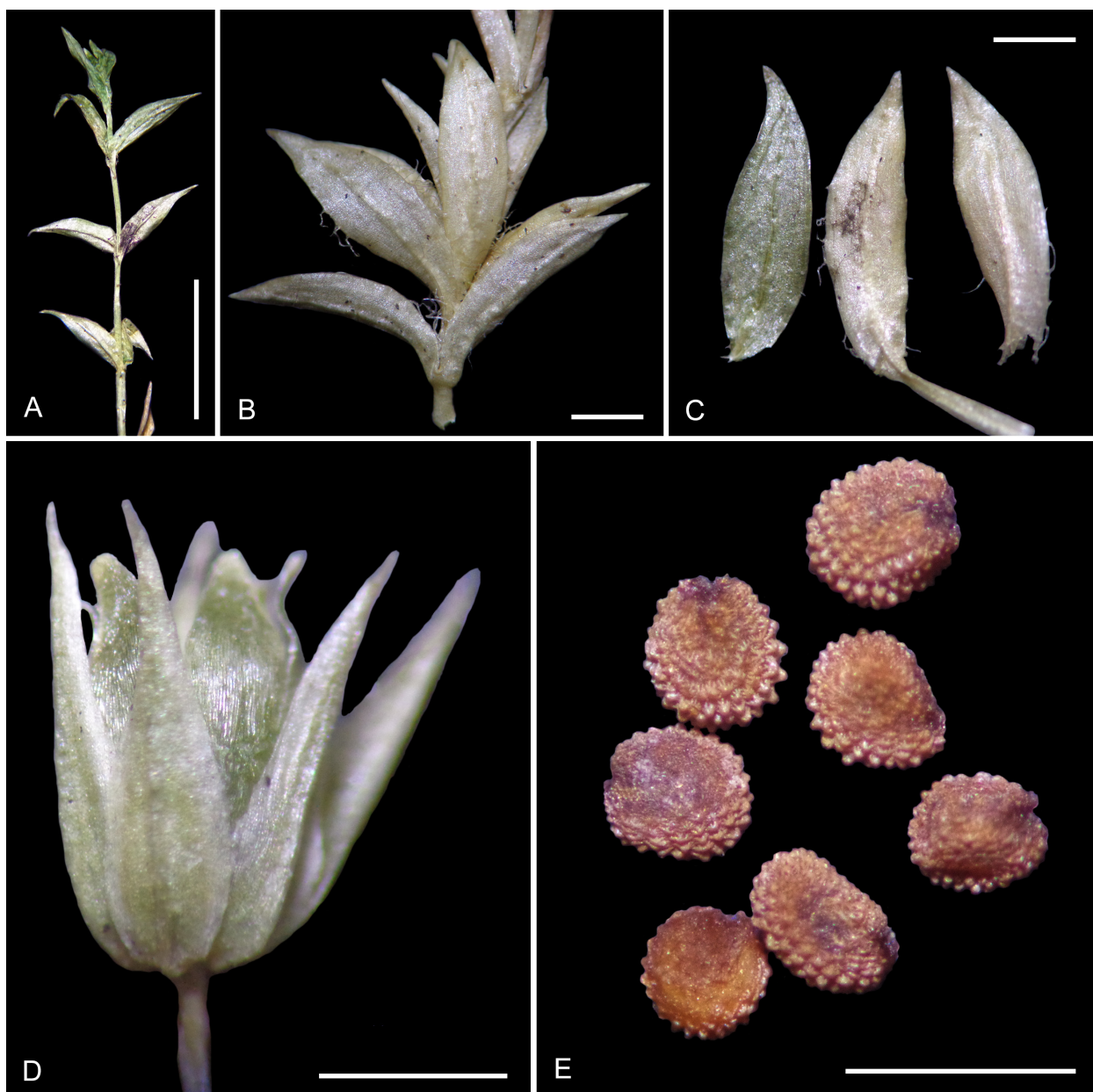


Fig. 7. Morphological details of *Stellaria galianoi* – A: ramified stem; B: detail of pilosity on leaf surface; C: detail of leaves; D: mature flower with capsule; E: tuberculate seeds. – From Montesinos 4572. – Scale bars: A = 5 mm; B–E = 1 mm.

bers of the *Plettkea* clade (Fig. 3, 4). This species has the longest internodes of vegetative stems across the *Plettkea* clade, eventually, in the uppermost the internode is long, sometimes as reaching 1.5 cm. This character makes it easy to recognize among the apetalous taxa of Andean *Stellaria*. The new species differs from the known South American species of *Arenaria* by its leaf form and by the densely tuberculate seeds. Furthermore, *S. galianoi* differs from *S. apurimacensis* by the internode length (2–15 mm vs. 4–10 mm in *S. apurimacensis*), larger leaves (3–5 mm long and 1.4–1.8 mm wide vs. 2–3 mm long and 0.8–1.2 mm wide in *S. apurimacensis*), longer peduncles (7–15 mm vs. 2–5 mm in *S. apurimacensis*), narrower sepals (0.8–1 mm vs. 1–1.5 mm in *S. apurimacensis*) and larger seeds (0.6–0.8 mm long vs. 0.4–0.5 mm long

in *S. apurimacensis*). *Stellaria galianoi* differs from *S. andina* in the leaf form (oblanceolate-oblong to gladiate vs. ovate in *S. andina*) and longer peduncles (7–15 mm vs. 1–4 mm in *S. andina*).

8. *Stellaria keraipetala* (Mattf.) Montesinos & Borsch, comb. nov. \equiv *Pycnophyllopsis keraipetala* Mattf. in *Schriften Vereins Naturk. Unterweser*, n.s., 7: reprint p. 22 (26). 1934. – Holotype: Bolivia, zwischen Palca und La Paz, an Felsen, 4800 m, Apr 1908, *K. Pflanz* 233 (B \dagger). – Neotype (designated by Timaná 2017: 6): Bolivia, La Paz, Murillo, Cordillera Real, road to nevado Chacaltaya, N of Milluni crossing E of Lake Milluni along roadsides, 4600–4900 m, 25 Jan 2000, *Timaná* 3804 (LPB0000524; isoneotypes: BM, K, LL, MCSN, MICH, USM).

Morphological description — See Timaná (2005).

Distribution — The species is endemic to Bolivia and based on two collections and according to Timaná (2017), it is known to occur at altitudes of 4600–5100 m.

Notes — The neotype located at the Herbario Nacional de Bolivia, Universidad Mayor de San Andrés (LPB) was designated by Timaná since the original material collected by K. Pflanz 223 was lost (B†). According to Timaná (2017), *Pycnophyllopsis keraipetala* (now *Stellaria keraipetala*) is the only species with trimerous petals and stamens, although tetramerous and pentamerous forms are also found (sometimes all three forms in the same plant). *Stellaria keraipetala* is the sister to *S. weberbaueri*, and both share the habit of dense small cushions with stems covered by overlapping leaves. *Stellaria keraipetala* and *S. weberbaueri* appear to be geographically vicariant species due to its distribution in the highest parts of the Andes in Bolivia and Peru, respectively.

9. *Stellaria laevis* (Bartl.) Rohrb. in Linnaea 37: 275. 1872 = *Cherleria laevis* Bartl. in Presl, Reliq. Haenk. 2: 12. 1831 = *Pycnophyllopsis laevis* (Bartl.) Timaná in Lundellia 20: 8. 2017. – Lectotype (designated by Timaná 2017: 8): Peru, Quebrada de l'Obrachillo, s.d., Haenke s.n. (PR not seen; isoelectotypes: GOET 000715!, HAL 0117903 image!). = *Cherleria bisulca* Bartl. in Presl, Reliq. Haenk. 2: 12. 1831, **syn. nov.** = *Arenaria bisulca* (Bartl.) Fenzl ex Rohrb in Linnaea 37: 248. 1872. – Type: Peru, Peru, 1791, T. P. X. Haenke s.n. (HAL01178886 [image!]).

Morphological description — See Timaná (2005).

Distribution — The species inhabits highland plateaus of the central Andes in Peru, at altitudes of 4660–4800 m, in the Lima and Junín departments. The environments where the species grows are highland plateau Andean grasslands with rocks, with template and harsh wind conditions.

Notes — Mattfeld (1934) tentatively included the species described by Bartling (1831) under the genus *Cherleria* into *Plettkea*. Mattfeld considered the characters mentioned in the original description as he had no access to specimens. Rohrbach (1872) transferred the species to *Stellaria* without further reference. Timaná (2017) encountered the Haenke specimen at PR and respective duplicates at HAL and GOET and argued that the species belongs to *Pycnophyllopsis*. The examination of the type specimen at GOET showed the presence of hirsute leaf margins, apetalous flowers supporting the position in the *Plettkea* clade. In the ITS tree specimen CAR912 of *S. laevis* is resolved as sister to *S. cryptantha*, albeit with low support (it was not possible to amplify plastid regions in this specimen). The examination of the type

specimen further revealed the similarity with *Arenaria bisulca* (Bartl.) Fenzl & Rohrb. A species also described by Bartling (1831) under *Cherleria*, which is therefore put into synonymy in this study. Also, Zanotti & al. (2022) discussed if *S. laevis* could be closely related to *Arenaria bisulca*, an opinion to which we agree with due to the exact match of morphological characters. Moreover, *S. laevis* appears to be morphologically similar to *S. andina* having several differences such as the habit and growth form (loose mat-forming herb vs. weak herbs *S. andina*), leaf form and stiffness (rigid in *S. laevis* vs. weak in *S. andina*) and minor flower characteristics. Sequence data of ITS resolve *S. laevis* as part of subclade A within the *Plettkea* clade of *Stellaria* (Supplementary appendix S9).

10. *Stellaria macbridei* Montesinos & Borsch, **nom. nov.** = *Arenaria crassipes* Baehni & J. F. Macbr. in Publ. Field Mus. Nat. Hist., Bot. Ser. 13(2): 598. 1937 [non *Stellaria crassipes* Hultén in Bot. Not. 1943: 261. 1943]. – Holotype: Peru, Lima, Río Blanco, 3000 m, prostrate on upland slopes, *Macbride* 812 (F [F0042702F image!]; isotypes: NY [NY00342439 image!], US [US00103284 image!]). – Fig. 1D.

Morphological description — Perennial herb, individual stems visible (not caespitose); root thick, reaching c. 4 cm deep. *Stems* 7–12 per individual, decumbent to ascending, 3–5 cm long; internodes 3–4 mm long, densely hirsute near nodes; trichomes irregularly shaped, multicellular, uniseriate, 0.5–1 mm long. *Leaves*, with broad and hirsute petioles, alternate; lamina oblong, 5–7 mm long and 2–2.5 mm wide, subcoriaceous or membranous, thickened at base, shiny, glabrous on both sides, thin, margins ciliate or hairy-ciliate, apex acuminate and slightly involute, only midrib hirsute. *Plants* bisexual-hermaphrodite. *Flowers* perigynous, on 1–1.8 mm long ciliate peduncles, axial and terminal; cylindrical-oblong, 2.5–3 mm long and 1.2–1.8 mm wide; calyx cylindrical-turbinate, thicker at base, crateriform; sepals 5, imbricate, narrowly lanceolate, 2–2.3 mm long and 0.4–0.6 mm wide, glabrous on surface, light green to bright yellow, apex acute-attenuate, involute, folded and forming a narrow cylinder that covers capsule; petals 5, reduced, translucent-stramineous, ovate, apex obtuse, 1–1.3 mm long and 0.2–0.4 mm wide; stamens 4 or 5, episepalous, 1–1.5 mm long; ovary ovoid-turbinate, 0.4–0.8 mm long and 0.6–0.8 mm wide, style 3-fid, stigma aciculate. *Capsule* ovoid, 0.9–1.2 mm long containing 4 seeds, these orbicular, 0.2–0.3 mm in diam., testa reddish-maroon and shiny, cells bearing light maroon tubercles.

Distribution and ecology — *Stellaria macbridei* is endemic to central Peru (Cano & Sánchez Vega 2006) occurring in puna grasslands ecosystems that receive continuous rainfall throughout the year, it is distributed in Áncash, Huánuco, Junín and Lima departments at altitudes of 4200–4800 m.

Etymology — The specific epithet refers to J. F. Macbride (1892–1976), American botanist who provided the last comprehensive revision for *Stellaria* and *Arenaria* from Peru and also was one of the authors who originally described this species.

Notes — Macbride (1936) mentioned that *Stellaria macbridei* has similarities with *S. congesta* but differs from that species by the tuber-like root and the small erect habit. Other differences include suboblong leaf form (ovate in *S. congesta*) and the narrowly lanceolate sepals (lanceolate in *S. congesta*). The two sequenced specimens are sisters and form a distinct lineage within the *Plettkea* clade in both the plastid and nuclear trees (Fig. 3, 4) underscoring the identity of *S. macbridei* as a distinct and eventually monophyletic species.

11. *Stellaria macrophylla* (Muschl.) Montesinos & Borsch, **comb. nov.** \equiv *Pycnophyllum macrophyllum* Muschl. in Bot. Jahrb. Syst. 45: 458. 1911 \equiv *Plettkea macrophylla* (Muschl.) Mattf. in Schriften Vereins Naturk. Unterweser, n.s., 7: reprint p. 18 (22). 1934 \equiv *Pycnophyllopsis macrophylla* (Muschl.) Molinari in Polish Bot. J. 61: 276. 2016. – Lectotype (designated by Molinari-Novoa 2016: 276): Peru, Áncash, Cordillera Blanca, 4500 m, 14 May 1903, A. Weberbauer 2975 (MOL00000509!).

Morphological description — See Timaná (2005).

Distribution — Huascarán National Park in Áncash department, central Peru, at altitudes of 4500–4800 m (Timaná 2017).

Notes — Muschler (1911: 458) described *Pycnophyllum macrophyllum* based on the leaf shape and few relevant flowers characters. Molinari-Novoa (2016) simply transferred the species to *Pycnophyllopsis* referring to Timaná (2005) who recognized *Pycnophyllopsis* s.l. (including *Plettkea*) as distinct from *Pycnophyllum* without any own analysis of plant material. According to Timaná (2017), *Stellaria macrophylla* differs from *S. cryptantha* in the number of floral parts: *S. macrophylla* is pentamerous with three free styles while *S. cryptantha* a tetramerous species with two free styles. In addition, the leaves of *S. macrophylla* are slightly narrower toward the apex, where in *S. cryptantha* these are more triangular. The only collection known is the type specimen at MOL. This specimen has no seeds which was also confirmed by physical examination (G. Tello, Lima, pers. comm.). Therefore, it is unclear from where Muschler took the information on seeds, which does not even correspond to specimens of the *Plettkea* clade and therefore could be wrong.

12. *Stellaria patagonica* Montesinos & Borsch, **nom. nov.** \equiv *Pycnophyllopsis muscosa* Skottsberg. in Kongl. Svenska Vetensk. Acad. Handl., n.s., 56(5): 216. 1916 [non *Stellaria muscosa* (L.) Jess., Deut. Excurs.-Fl.: 288. 1879

\equiv *Moehringia muscosa* L., Sp. Pl. 1: 359. 1753]. – Lectotype (designated by Timaná 2017: 6): Argentina, Patagonia Andina, territorio Chubut, Meseta Chala, c. 1300 m, 5 Dec 1908, Skottsberg 606 (S [S05-10321 image!]; isolecotypes: LD [LD1418578 image!], SG [SGO000001982 image!]).

Morphological description — See Timaná (2005).

Distribution — Patagonian plateaus in Argentina, at altitudes of 800–1300 m, in open slopes, rocky and very windy.

Etymology — In allusion to the Patagonia region in Argentina where the species grows.

Notes — The species shows morphological affinities to *Stellaria* sect. *Plettkea*, such as short stems bearing short internodes, densely appressed leaves with ciliate margins, apical, solitary flowers, shortly pedunculate, bearing five sepals and an equal number of reduced petals, so to be placed under *Stellaria*. The type specimen has no seeds and the protologue does not mention any seed characters.

13. *Stellaria pedunculosa* (Wedd.) Montesinos & Borsch, **comb. nov.** \equiv *Arenaria pedunculosa* Wedd. in Ann. Sci. Nat., Bot., ser. 5, 1: 294. 1864. – **Lectotype (designated here)**: Bolivia, La Paz, Ravin de Chuquiaguillo, 1851, H. Weddell s.n (P [P 00274242 image!]). – Fig. 1E.

Morphological description — Annual herb, forming small caespitose tufts, 1–2 cm high and 2–3.5 cm in diam.; roots fibrous. *Stems* few, often further ramified at base; internodes 1–4.5 mm long, glabrous. *Leaves* opposite, sessile; lamina oblong-ovate, 4–6 mm long and 1–1.6 mm wide, thin, to some extent curved at tip, rarely involute, scarcely covered by tomentulose hairs on upper- and underside, midrib inconspicuous; base truncated and apex acute, margin tomentulose with multicellular hairs 0.1–0.25 mm long (occasionally mammillate and without distinct trichomes), usually persistent on older foliage; leaves pale green to yellow-brownish with age. *Plants* bisexual-hermaphrodite. *Flowers* perigynous, on rigid 8–11 mm long peduncles covered with minute papillae, terminal, ovoid, 2–2.6 mm long and 1–1.6 mm wide; calyx cylindrical-campanulate, crateriform; sepals 5, ovate, 1.8–2.4 mm long and 0.8–1 mm wide, slightly involute, green to yellowish-translucent with age, cupuliform at base, apex acute, mucronate, pale green to yellowish, surface glabrous, margins with scattered papillae, 0.08–0.1 mm long; petals 5, reduced, light green, ovate, obtuse, equalling sepals or shorter, 1.2–1.5 mm long and 0.6–0.8 mm wide; stamens 5, very short, 0.2–0.4 mm long, episepalous; style 3-fid, glandular, 0.25–0.35 mm long, aciculate; ovary ovoid, 0.2–0.5 mm long and 0.3–0.5 mm wide. *Capsule* ovoid, c. 1 mm long, glabrous,

containing 2–5 seeds, these orbicular, 0.6–0.8 mm in diam., testa brown-yellowish, granulate.

Distribution — Based on two collections (DBMT 5395b, 4565), *Arenaria pedunculosa* is located at the lower slopes SE of Ticsani volcano (Moquegua department), on volcanic pumice soils at altitudes of 4500–4820 m. Flowers and fruits were observed between February and March. In Bolivia the species is known only from the type collection, and a search of material at LPB in 2019 provided no evidence that the species has been collected again.

Vernacular name — *Jiska Volcanqura Panqara*, given in Aymara language (Kent Chicalla, Moquegua, pers. comm.).

Notes — Even though the intense survey done at the herbaria mentioned in the methods, no specimens have been found as additional collections for Bolivia, but two specimens have been found from the Moquegua department in Peru.

14. *Stellaria smithii* (Timaná) Montesinos & Borsch, **comb. nov.** \equiv *Pycnophyllopsis smithii* Timaná in *Lundellia* 20: 10. 2017. – Holotype: Peru, Lima, Huarochirí, Paso de Anticoná, Ticlio, 4850 m, 16 Dec 1998, *Timaná & Tate* 3768 (USM!; isotypes: BM, F, K!, LL, LPB [LPB0000525], MICH).

Morphological description — See Timaná (2005).

Distribution — According to Timaná (2017), the species should be distributed in the boundary between the Peruvian departments of Lima and Junín, at altitudes of 4300–4900 m, but should also be present in the Áncash department (Huascaran National Park) at an altitude of c. 4800 m. However, no further specimens in addition to the type appear to be known.

Notes — The characters such as the imbricate, lanceolate, stiff leaves, with ciliate margin, the short flower peduncles and the staminoid petals are considered to provide evidence for the inclusion of the species in the *Plettkea* clade.

15. *Stellaria spinulosa* Montesinos & Borsch, **nom. nov.** \equiv *Arenaria aphanantha* Wedd. in *Ann. Sci. Nat., Bot.*, ser. 5, 1: 293. 1864 [non *Stellaria aphanantha* Griseb. in *Abh. Königl. Ges. Wiss. Göttingen* 24: 27. 1879]. – **Lectotype (designated here)**: Peru, 1839–1840, *C. Gay* 1818 ([P(P00335797)]; isolectotype: ([MO-840929]).

Morphological description — Perennial herb, varying from few stems up to 50 cm long to forming dense mats 2–4 cm high; root woody. *Stems* decumbent, creeping and with branches distinctly shorter than stems, bear-

ing remains of old foliage along stems; internodes 1–1.5 mm long; sparsely pubescent with erect 0.1–0.3 mm long trichomes. *Leaves* alternate, lamina lanceolate to linear-lanceolate, 4–6 mm long and 1–1.5 mm wide, coriaceous, with acuminate to subaristate apex, densely ciliate near truncate base. *Plants* bisexual-hermaphrodite. *Flowers* perigynous, terminal, on hirsute, thick, 3.5–4 mm long peduncles, but these hidden by uppermost leaves; calyx cylindrical to rarely subcampanulate, 3.5–4 mm long and 1.5–2 mm wide, crateriform, usually thickened at bottom; sepals 5, lanceolate, cupuliform at base, involute, 3–3.5 mm long and c. 0.8 mm wide, apex acute, light green to pale yellowish, glabrous on surface and along margins; petals 5, strongly reduced, translucent, ovate, apex obtuse, 1.2–1.6 mm long and 0.7–0.8 mm wide; stamens 4 or 5, episepalous, 1.1–1.3 mm long; ovary cylindrical-turbinate, 0.5–0.7 mm long and 0.6–0.8 mm wide, style 3-fid, stigma aciculate. *Capsule* ovoid, c. 1 mm long, containing 2 or 3 seeds, orbicular, 0.5–0.6 mm in diam., testa maroon, shiny and distinctly tuberculate, cells bearing whitish asymmetrical protuberances.

Distribution — *Stellaria spinulosa* occurs in a variety of highland ecosystems across Peru and is considered as the most collected species of the clade (as observed in the material from the different herbaria visited) and extends to Ecuador. Jørgensen & León-Yáñez (1999) mentioned the occurrence of the species in Ecuador, which can be confirmed based on an analysis of material stored at MO according to Tropicos.org (2023) and as evaluated by the first author during two visits to MO in 2013 and 2016 and more recently, at PRC, four collections were identified to be *S. spinulosa* located mostly in central Ecuador, between Chimborazo and Cuicocha. The altitudinal range is from 2800–5000 m according to the specimens evaluated.

Etymology — The epithet refers to the spine-like leaves of the plant, which can be felt as tingling by simple touch; *spinulosa* is derived from the Latin *spinula* (small spine) in relation to the thorny and pungent characters of the leaves. The former epithet *aphanantha* is derived from the Greek *aphanes* (invisible obscure) and *anthos* (flower), probably referring to the resemblance of the flower sepals to the leaves.

Notes — The specimen *C. Gay* 1818 (P00335797) is selected as the lectotype for being most representative with a complete set of morphological characters. As evidenced by this specimen, the species is easily distinguishable from the other members of the clade by the intense yellowish colour of the stems and leaves, the stiff ovate leaf lamina and the nearly sessile flowers with long calyx, the presence of staminoid petals reduced to filaments and the tubercle seeds, which is characteristic for this kind of habit.

16. *Stellaria standleyi* (Baehni & J. F. Macbr.) Montesinos & Borsch, **comb. nov.** \equiv *Arenaria standleyi* Baehni & J. F. Macbr. in Publ. Field Mus. Nat. Hist., Bot. Ser. 13(2): 604. 1937. – **Lectotype (designated here):** Peru, Ayacucho department, Mt. Razuhuillca, Prov. Huanta, 4200 m, A. Weberbauer 7489 (F-562398!).

Morphological description — Perennial herb, caespitose, densely branched, cushions 1–4 cm high and 10–15 cm in diam.; roots subwoody. *Stems* numerous, densely covered by stiff foliage; internodes 0.1–0.3 mm long, glabrous; leaves alternate, lamina ovate to linear-lanceolate, 3–4 mm long and 1–1.5 mm wide, thick and glossy, apex acute and base truncate, yellowish in colour and glabrous on both sides, midrib prominent on underside, margins usually folded toward underside, densely covered by a narrow band of trichomes < 0.1 mm long. *Plants* bisexual-hermaphrodite. *Flowers* perigynous, terminal and axillary, on 1–2 mm long glabrous peduncles, oblong, 3–3.5 mm long and 0.8–1.1 mm wide; calyx cylindrical-turbinate, crateriform, thicker at base, 2.7–3.2 mm long and 2.5–3.4 mm wide; sepals 5, imbricate, ovate, 2.5–3 mm long and 0.5–1 mm wide, glabrous on surface, green or pale green to yellowish-translucent with age, involute, apex acuminate; petals 5, reduced, white-translucent, ovate, apex obtuse, 2–2.4 mm long and 0.3–0.4 mm wide; stamens 4, episepalous, anthers orbicular-ovate, yellowish-translucent, 0.3–0.4 mm long; ovary ovoid-turbinate, 0.6–0.9 mm long and 0.6–0.8 mm wide, style 3-fid, stigma aciculate, pale white. *Capsule* ovoid, 1.2–1.5 mm long and 1.1–1.3 mm wide, glabrous, containing 3–5 seeds, these ovoid, c. 0.5 mm long, testa brown, tuberculate.

Distribution — Peru, Ayacucho department at an altitude of c. 4200 m in open grasslands in Puna ecosystems characteristic of the central Andes. No further collections were found, so this is to be considered as a rare species.

Notes — The collection A. Weberbauer 7489 shows the typical characters of *Stellaria* sect. *Plettkea* by sharing the leaf size, texture, and form, as well as the flower and seeds characteristics as described in the morphological description. Because Macbride (1937) did not mention a specific type specimen in the protologue, a lectotypification is made here, using the locality information in the protologue that matches with the Weberbauer specimen that also exhibits the morphological characters described.

17. *Stellaria tetrasticha* (Mattf.) M. T. Sharples & E. A. Tripp. in Syst. Bot. 44: 871. 2019 \equiv *Plettkea tetrasticha* Mattf. in Schriften Vereins Naturk. Unterweser, n.s., 7: reprint p. 21 (25). 1934 \equiv *Pycnophyllum mattfeldii* J. F. Macbr. in Publ. Field Mus. Nat. Hist., Bot. Ser. 13(2): 611. 1937 [non *Pycnophyllum tetrastichum* J. Rémy in Ann. Sci. Nat., Bot., ser. 3, 6: 356. 1846] \equiv *Pycnophyl-*

lopsi tetrasticha (Mattf.) Timaná in Lundellia 20: 8. 2017. – Holotype: Peru, Áncash, Cajatambo, Schwarze Cordillere über Ocros, auf dürrtig bewachsenem, steinigem Boden, 4500–4800 m, A. Weberbauer 2804a (B⁺). – Neotype (designated by Timaná 2017: 8): Peru, Áncash, Yungay Province, Huascarán National Park, Llanganuco sector, Quebrada Demanda, W of Chacrara-ju base camp, 09°01'S, 77°36'W, 4750–4900 m, 13 Apr 1985, D. N. Smith & V. Cautivo 10287 (MO-052068!; isoneotype: F!).

Morphological description — See Timaná (2005).

Distribution — Central Peru, Áncash department inside the Huascarán National Park on highland peaks at altitudes of 4500–4900 m, where considered a narrow endemism.

Notes — *Stellaria tetrasticha* was originally described as a member of the genus *Plettkea* by Mattfeld (1934) and later accepted by Bittrich (1993). The species has a mat form with spreading stems, ovate leaves c. 2 mm long bearing carinate acute apex and sepals with ovate-oblong form. Later, Timaná (2017) named *Pycnophyllopsi tetrasticha* (Mattf.) Timaná based on the morphological affinities found within flower measurements in the neotype he selected. Sharples & Tripp (2019) included a sample of the species in their phylogenetic analysis showing it to be strongly supported as a member of the *Plettkea* clade.

18. *Stellaria utcubambensis* Montesinos & Borsch, **sp. nov.** – Fig. 1F, 5E, F, 8; Supplementary appendix S13. Holotype: Peru, Amazonas, Chachapoyas, Leymebamba, Tajopampa Camino Inca, 3696 m, 14 Aug 2016, D. Montesinos 4979 (HUT [HUT-60181!]; isotypes: B [B 10 0766222!], O [O-227246!], USM!).

Diagnosis — The species can be easily distinguished from the other members of the clade by the stiff linear-lanceolate leaves and the prominent calyx apex that forms a needle-like stiff point, a feature that is not seen in any other species.

Morphological description — Perennial herb, forming mats 2–4 cm high and 10–30 cm in diam.; roots fibrous. *Stems* suberect or decumbent to prostrate, trailing, densely ramified at base, clothed with older leaves down to base; internodes 2–4 mm long, nodes slightly thickened, glabrous, yellowish. *Leaves* opposite, narrowly involute or plane, eventually curved with age, lamina linear-lanceolate, stiff and coriaceous, truncate at base and aristulate-acuminate near apex, 4–6 mm long and < 1 mm wide, glabrous on both sides, midrib prominent on underside, margins glabrous toward apex, basally with 0.1–0.3 mm long trichomes. *Plants* bisexual-hermaphrodite. *Flowers* perigynous, terminal and axillary, always suspended on



Fig. 8. Morphological details of *Stellaria utcubambensis* – A: ramified stems with flower; B: leaves; C: mature flowers; D: flower capsule; E: tuberculate seeds. – Montesinos 4572. – Scale bars: A–C = 1 mm; D = 0.5 mm; E = 200 μ m.

2–5 mm long, erect and glabrous peduncles; calyx cylindrical, 4–6 mm long and 0.8–1.1 mm wide; sepals 5, ovate-lanceolate, 4–6 mm long and c. 1 mm wide, involute, glabrous on both sides except at base of margins, where minute c. 0.1 mm long trichomes are present, truncate at base and cuspidate at apex, midrib excurrent as a thin 0.1–0.25 mm long needle, surface greenish-white turning yellowish with age; petals 5, deeply bifid, bright white, ovate-elliptical, in total 7–10 mm long, lobules ovate-lanceolate 0.3–0.6 mm long and 0.3–0.5 mm wide; filaments c. 0.4 mm long, stamens 5–10, episepalous, c. 0.4 mm long, anthers 0.1–0.2 mm long, styles 3-fid, ovary ovoid, 0.2–0.3 mm long and c. 0.3 mm wide. *Capsule* ovoid or nearly so, 0.6–0.8 mm long and c. 0.5 mm wide, containing 3 seeds, these roundish or nearly so, flattened, 0.4–0.5 mm in diam., testa dark maroon to blackish, covered with rectangular stellate tubercules.

Distribution and ecology — The species inhabits the mountain summits of the tributaries leading to the Utcubamba river in the Amazonas department in N Peru,

with an expected growth at altitudes of 3600–3900 m. The species was found in areas where slope burning is an unfortunate practice applied by the local people; such events and climate change could lead to the gradual disappearance of this species. Flowering has been observed during the months of September and November.

Etymology — The specific epithet refers to the Utcubamba river in N Peru that divides Amazonas department from south to north. The new species was found in its uppermost tributaries, and it is very likely that there are further populations on the mountains draining into this river.

Notes — This species is known so far from only one collection, but further populations might be encountered after searching in the field. *Stellaria utcubambensis* differs from *S. apurimacensis* by having leaves stiff, linear-lanceolate and with margins glabrous toward apex (vs. weak, elliptical-lanceolate and with margins sparsely pilose in *S. apurimacensis*). Moreover, the internodes in *S. utcubambensis* are 2–4 mm long (vs. 4–10 mm long in

S. apurimacensis) and the calyx is cylindrical (vs. campanulate in *S. apurimacensis*).

19. *Stellaria villasenorii* Montesinos & Borsch, **nom. nov.** \equiv *Pycnophyllum lanatum* Phil. in Anales Univ. Chile, I, Mem. Ci. Lit. 81(6a): 774. 1892 [non *Stellaria lanata* Hook. f., Fl. Brit. India 1: 232. 1874] \equiv *Baretia lanata* (Phil.) Timaná in Adansonia, ser. 3, 45: 502. 2023. – Lectotype (designated by Timaná 2023: 502): Chile, Las Mollacas, Cordillera de Illapel, Jan 1888, R. Philippi s.n. (SGO000001980 [image!]).

Morphological description — See Timaná (2005).

Distribution — Mountain plateaus in Coquimbo, Chile, at altitudes of 2600–2800 m, endemic.

Etymology — The species name is chosen to honour Rodrigo A. Villaseñor Castro (1947–, Concepción, Chile), a professor in Biology and Natural Sciences, who extensively contributed to the knowledge of the Chilean flora.

Notes — The species conspicuously deviates from the other members of the *Plettkea* clade by its dense lanuginose indumentum and by its shrubby habit.

Timaná (2005) proposed to classify this species in its own new subgenus, *Pycnophyllopsis* subg. “Coquimbo”, but this name, because it appeared in a thesis, was not effectively (and therefore not validly) published according to Art. 30.9 of the *Code* (Turland & al. 2018). The same applies to the species combination under *Pycnophyllopsis* and the lectotypification, all of which were not included in Timaná’s (2017) paper on the genus. Flower and seed morphology provide evidence for a position in the *Plettkea* clade. In his thesis, Timaná (2005) depicted a representative of this species in an ITS tree in a lineage with *Pycnophyllopsis cryptantha* and *P. weberbaueri*, thus supporting this position. However, these phylogenetic results cannot be reproduced because the sequences are not available and the tree was never properly published.

There are two specimens at SGO (old herbarium number 048875 corresponding to barcode SGO000001980 and old herbarium number 090982 corresponding to barcode SGO000001981) that were apparently collected by Philippi from the same locality, but the latter lacks a date.

20. *Stellaria weberbaueri* (Muschl.) Montesinos & Borsch, **comb. nov.** \equiv *Pycnophyllum weberbaueri* Muschl. in Bot. Jahrb. Syst. 45: 455. 1911 = *Plettkea weberbaueri* (Muschl.) Mattf. in Schriften Vereins Naturk. Unterweser, n.s., 7: reprint p. 19 (23). 1934 \equiv *Pycnophyllopsis weberbaueri* (Muschl.) Timaná in Monogr. Syst. Bot. Missouri Bot. Gard. 127: 1271. 2014. – **Lectotype (designated here)**: Peru, Vincocaya, statio viae ferreae ad Arequipam, 4100 m, 24 Aug 1902, A. Weberbauer 1373 (MOL [MOL 00000507!]). – Fig. 1G.

Morphological description — See Timaná (2005).

Distribution — The species inhabits highland plateaus, also known as subnival puna, at altitudes of 4660–5000 m. It is known to occur in the Arequipa and Moquegua departments of Peru, while its occurrence in the Bolivian Andes is not confirmed.

Notes — The species was first described as *Pycnophyllum weberbaueri* Muschl. by Muschler (1911), presumably based on the cushion growth form, plicate leaves and apical flowers. Later, the species was transferred to the genus *Pycnophyllopsis* by Timaná (2017), as *Pycnophyllopsis weberbaueri* (Muschl.) Timaná, based on the consistently pentamerous flowers with three free styles. Muschler (1911) apparently described characters for *Stellaria weberbaueri* such as true petals, which are actually not present in the specimens examined. Moreover, *S. weberbaueri* has leaves that do not overlap to be completely imbricate, giving the general impression of a loose cushion with longer internode length. Sharples & al. (2021) reported “*Stellaria weberbaueri* (Muschl.) M. T. Sharples & E. A. Tripp” in their Appendix 2, but this name has not been validly published anywhere.

21. *Stellaria xanthophylla* Montesinos & Borsch, **sp. nov.** – Fig. 1H, 5G, H, 9; Supplementary appendix S14. Holotype: Peru, Amazonas, Chachapoyas, Leymebamba, construcciones de piedra, restos arqueológicos La Boveda, 3540 m, 20 Jun 2018, D. Montesinos 6970a (HSP [HSP-20000!]; isotype: B [B 10 1098616!]).

Diagnosis — This species is similar to *Stellaria laevis*, from which it can easily be distinguished by its leaf margin, which is ciliate in the lower-middle part of the leaf, whereas in *S. laevis* the margin is completely covered by thin trichomes.

Morphological description — Perennial herb, forming dense mats, 6–10 cm high and up to 20 cm in diam.; root woody. *Stems* decumbent or more commonly curved, 10–18 cm long, branched; internodes 1–5 mm long, glabrous, sometimes bearing a few trichomes at node base, nodes thickened. *Leaves* involute, opposite, basally fused, lamina ovate-lanceolate to linear-lanceolate, subtruncate at base and mucronate at apex, stiff or spine-like, 6–8 mm long and 1–1.5 mm wide, glabrous, thick, with midrib prominent, densely covered by thin trichomes at base, tending to be glabrous toward apex; trichomes multicellular, straight or curved, 0.2–0.5 mm long, increasing in length toward base of lamina; older foliage usually covering stems, yellowish in colour. *Plants* bisexual-hermaphrodite. *Flowers* perigynous, terminal and axillary, on erect or slightly curved, 5–15 mm long peduncles, bearing tiny protuberances on surface as well as minute trichomes, rarely glabrous, old



Fig. 9. Morphological details of *Stellaria xanthophylla* – A: flowering stem; B: stem with leaves; C: leaves; D: mature flowers. – From Montesinos 6970a. – Scale bars: A–D = 1 mm.

flowers persistent; calyx cylindrical, imbricate, turbinate, slightly wider at base, 8–10 mm long and 1.4–2.2 mm wide; sepals 5, lanceolate to narrowly ovate-lanceolate, involute, pale green to dark yellow with age, 5–7 mm long and 1.5–2 mm wide, midrib prominent, margins entire, truncate at base, acute at apex, surface glabrous or nearly so; petals 5, strongly reduced, 2–3 mm long and 1–1.8 mm wide, translucent, elliptical, apex obtuse; stamens 5, 1.5–2 mm long; style 3-fid, less than 1 mm high; ovary cylindrical, 0.9–1.1 mm long and 0.8–1 mm wide, stigma aciculate and obtuse. *Capsule* ovoid, 0.8–1 mm long, glabrous, containing 4–6 seeds, these ovate, compressed, c. 1 mm in diam., testa maroon, densely tuberculate.

Distribution and ecology — The species is recorded in northern and central Peru, in the mountains adjacent to the Alto Marañón river in Huari province, Áncash department, and in the Utcubamba high mountains river basins in southern Amazonas department, near the boundary with La Libertad and San Martín departments. An additional specimen to the one sequenced comes from the department of Áncash in Peru: Huari, San Pedro de Chaná 4410 m, 5 May 2018, D. Montesinos & G. San-

cho 6147 (B-101249409!, HCSM!, HSP-12974!, HUT-62033!, USM!). The habitat varies in vegetation cover and floristic composition but not in precipitation, as these environments tend to receive over 800 mm/year. The typical ecosystem is humid puna grasslands, with rocky outcrops and highland subhumid forest patches with species of *Hesperomeles* Lindl. (*Rosaceae*) and *Verbesina* L. (*Asteraceae*).

Etymology — The specific epithet derives from the Greek words *xanthos*, yellow, and *phylla*, leaves, referring to the persistent, yellow leaves along the stems of the plant.

Notes — *Stellaria xanthophylla* shows morphological similarities with *S. engleriana* but can be differentiated by the following characters: bearing thin trichomes at the base of the lamina (vs. dense trichomes at the base in *S. engleriana*); sepal form, size and texture (lanceolate to narrowly ovate-lanceolate, 5–7 mm long and 1.5–2 mm wide, surface and margins glabrous or nearly so in *S. xanthophylla* vs. ovate-oblong, 3–4 mm long and 1–1.5 mm wide, with a ciliate lamina surface and margin in *S. engleriana*).

Author contributions

D.B.M.T. and T.B. designed the study and implemented the phylogenetic analyses. Fieldwork and herbarium work as well as the examination of morphological characters was done by D.B.M.T. who also wrote a first draft of the manuscript. Both authors then discussed species delimitation and nomenclatural aspects, re-evaluated certain characters and then together adjusted the final text.

Acknowledgements

This work was done as part of the postdoctoral project of the first author sponsored by the Alexander von Humboldt-Stiftung through a Georg Forster-Forschungsstipendium. The first author is grateful to J. S. Ingham for logistical support during the first phases of fieldwork in central Peru. Thanks are due to Anna Guengerich for fieldwork support in the Amazonas region financed by National Geographic Society grant no. HJ-090R-17. Further field assistance by Kent Chicalla (Moquegua, Peru), Doris Cornejo (Aurimac, Peru), Miquer Cornelio (Huánuco, Peru), Washington Galiano (Cusco, Peru), Luis Garcia (Amazonas, Peru), Néstor Hanco (Aurimac, Peru), Percy Núñez (Cusco, Peru), Ángel Christian Pinto (Arequipa, Peru), Julia Suárez (Aurimac, Peru) and Sabine von Mering (Berlin) is acknowledged. The botanical collections formed part of the permits N° 061-2015-SERFOR-DGGSPFFS, N° 056-2016-SERFOR/DGGSPFFS, N° 045-2017-SERFOR/DGGSPFFS, N° 133-2018-MINAGRI-SERFOR/DGGSPFFS, N° 437-2019-MINAGRI-SERFOR/DGGSPFFS and N° D000081-2020-MINAGRI-SERFOR-DGGSPFFS issued by the Servicio Nacional Forestal y de Fauna Silvestre (SERFOR, Ministerio de Desarrollo Agrario y Riego), Peru. Julia Dietrich, Anna Luisa Raff and Kim Govers helped with the extraction of the DNA as well as PCR and preparing the samples for sequencing. The participants of the 2023 “Introduction into molecular phylogenetics” MSc course at the Freie Universität Berlin taught by the second author helped by providing a few sequences of *Stellaria* through their course project dedicated to the *Caryophyllaceae*. Some *matK-trnK-psbA* sequences were generated in the course of the BSc thesis of Katharine Reinecke focusing on the genus *Arenaria*. Stephan Beck (La Paz, Bolivia) helped with checking some specimens in LPB. Markus S. Dillenberger and Nadja Korotkova (both Berlin) are acknowledged for their discussion on various aspects of *Caryophyllaceae* phylogenetics and the elaboration of a species-level taxonomic backbone of this family in the context of the work of the WFO's *Caryophyllales* TEN. Nicholas Turland provided valuable advice on various questions regarding nomenclature and typification, for which we are grateful. We also thank two anonymous reviewers for their comments on an earlier version of this work.

References

- Ankei T. 1982: Habitat gradient and reproductive habits of the seven *Stellaria* species in Japan. – Bot. Mag. (Tokyo) **94**: 35–48. <https://doi.org/10.1007/BF02493409>
- Arabi Z., Ghahremaninejad F., Rabeler R. K., Sokolova I., Weigend M. & Zarre S. 2022: Intergeneric relationships within the tribe *Alsineae* (*Caryophyllaceae*) as inferred from nrDNA ITS and cpDNA *rps16* sequences: a step toward a phylogenetically based generic system. – Taxon **71**: 608–629. <https://doi.org/10.1002/tax.12688>
- Arias S., Berendsohn W. G., Borsch T., Flores-Olvera H., Ochoterena H., von Mering S. & Zuloaga F. O. 2016: *Caryophyllales* 2015 in Berlin and the Global *Caryophyllales* Initiative. – Taxon **65**: 427–428. <https://doi.org/10.12705/652.60>
- Bartling F. G. 1831: *Alsineae*. – Pp. 11–18 in: Presl C. B. (ed.), *Reliquiae haenkeanae; seu descriptiones et icones plantarum, quas in America meridionali et boreali, in insulis Philippinis et Marianis collegit Thaddeus Haenke, [...] 2*. – Pragae: J. G. Calve. <https://doi.org/10.5962/bhl.title.515>
- Beck S. G., Rojas P., Romero C. & Timaná M. E. 2014: *Caryophyllaceae*. – Pp. 490–497 in: Jørgensen P. M., Nee M. H. & Beck S. G. (ed.), *Catálogo de las plantas vasculares de Bolivia*. – Monogr. Syst. Bot. Missouri Bot. Gard. **127**(2). – St. Louis: Missouri Botanical Garden Press.
- Berendsohn W. G. 2010: Devising the EDIT Platform for Cybertaxonomy. – In: Nimis P. L. & Vignes Lebbe R. (ed.), *Tools for identifying biodiversity: progress and problems*. – Trieste: EUT Edizioni Università di Trieste. <https://www.openstarts.units.it/handle/10077/3690>
- Bittrich V. 1993: *Caryophyllaceae*. – Pp. 206–236 in: Kubitzki K., Rohwer J. G. & Bittrich V. (ed.), *The families and genera of vascular plants II*. – Berlin: Springer. https://doi.org/10.1007/978-3-662-02899-5_21
- Borsch T., Hernandez-Ledesma P., Berendsohn W. G., Flores-Olvera H., Ochoterena H., Zuloaga F. O., von Mering S. & Kilian N. 2015: An integrative and dynamic approach for monographing species-rich plant groups – building the global synthesis of the angiosperm order *Caryophyllales*. – Perspect. Pl. Ecol. Evol. Syst. **17**: 284–300. <https://doi.org/10.1016/j.ppees.2015.05.003>
- Borsch T., Hilu K. W., Quandt D., Wilde V., Neinhuis C. & Barthlott W. 2003: Noncoding plastid *trnT-trnF* sequences reveal a well resolved phylogeny of basal angiosperms. – J. Evol. Biol. **16**: 558–576. <https://doi.org/10.1046/j.1420-9101.2003.00577.x>
- Brako L. & Zarucchi J. L. 1993: Catalogue of the flowering plants and gymnosperms of Peru / Catálogo de las angiospermas y gimnospermas del Perú. – Monogr.

- Syst. Bot. Missouri Bot. Gard. **45**. – St. Louis: Missouri Botanical Garden Press.
- Cano A. & Sánchez I. 2006: *Caryophyllaceae* endémicas del Perú. – Revista Peruana Biol. **13**: 246–252. <https://doi.org/10.15381/rpb.v13i2.1835>
- Catorci A., Piermarteri K. & Tardella F. M. 2014: Distribution of the nurse species *Pycnophyllum molle* J. Rémy and *P. weberbaueri* Muschl. in the Andean dry puna (Arequipa district — southern Peru): role of topographic/soil variability and disturbance regime. – Polish J. Ecol. **62**: 385–390. <https://doi.org/10.3161/104.062.0201>
- Contreras-Ortiz N., Atchison G. W., Hughes C. E. & Madriñán S. 2018: Convergent evolution of high elevation plant growth forms and geographically structured variation in Andean *Lupinus* (*Fabaceae*). – Bot. J. Linn. Soc. **187**: 118–136. <https://doi.org/10.1093/botlinnean/box095>
- Culley T. M., Weller S. G. & Sakai A. K. 2002: The evolution of wind pollination in angiosperms. – Trends Ecol. Evol. **17**: 361–369. [https://doi.org/10.1016/S0169-5347\(02\)02540-5](https://doi.org/10.1016/S0169-5347(02)02540-5)
- Darriba D., Taboada G. L., Doallo R., Posada D. 2012: jModelTest 2: more models, new heuristics and parallel computing. – Nature, Meth. **9**: 772. <https://doi.org/10.1038/nmeth.2109>
- Fenzl S. 1840. Classis XLIX. *Caryophyllinae*. – Pp. 945–978 in: Endlicher S. (ed.), Genera plantarum secundum ordines naturales disposita. – Vindobonae: Fr. Beck. <https://bibdigital.rjb.csic.es/idviewer/10951/1013>
- GBIF 2023: Global Biodiversity Information Facility. GBIF occurrence download. – Published at <https://www.gbif.org/species/7937950> [accessed 14 Jul 2023].
- Greenberg A. K. & Donoghue M. J. 2011: Molecular systematics and character evolution in *Caryophyllaceae*. – Taxon **60**: 1637–1652. <https://doi.org/10.1002/tax.606009>
- Harbaugh D. T., Nepokroeff M., Rabeler R. K., McNeill J., Zimmer E. A. & Wagner W. L. 2010: A new lineage-based tribal classification of the family *Caryophyllaceae*. – Int. J. Pl. Sci. **171**: 185–198. <https://doi.org/10.1086/648993>
- Hernández-Ledesma P., Berendsohn W. G., Borsch T., Von Mering S., Akhani H., Arias S., Castañeda-Noa I., Eggli U., Eriksson R., Flores-Olvera H., Fuentes-Bazán S., Kadereit G., Klak C., Korotkova N., Nyfeler R., Ocampo G., Ochoterena H., Oxelman B., Rabeler R. K., Sanchez A., Schlumberger B. O. & Uotila P. 2015: A taxonomic backbone for the global synthesis of species diversity in the angiosperm order *Caryophyllales*. – Willdenowia **45**: 281–383. <https://doi.org/10.3372/wi.45.45301>
- Holmgren N. H., Holmgren P. K., Reveal J. L. & collaborators 2012: Intermountain Flora; vascular plants of the Intermountain West, U.S.A.: subclasses *Magnoliidae–Caryophyllidae* **2(A)**. – Bronx: New York Botanical Garden Press.
- Hughes C. E. & Eastwood R. 2006: Island radiation on a continental scale: exceptional rates of plant diversification after uplift of the Andes. – Proc. Natl. Acad. Sci. USA **103**: 10334–10339. <https://doi.org/10.1073/pnas.0601928103>
- Iamónico D. 2021: *Engellaria* (*Caryophyllaceae*), a new North American genus segregated from *Stellaria*. – Acta Bot. Mex. **128**(e1846). <https://doi.org/10.21829/abm128.2021.1846>
- IUCN 2016: A global standard for the identification of key biodiversity areas, version 1.0, first edition. – Gland & Cambridge: IUCN (International Union for Conservation of Nature).
- Jørgensen P. M. & León-Yáñez S. 1999: Catalogue of the vascular plants of Ecuador / Catálogo de las plantas vasculares del Ecuador. – St. Louis: Missouri Botanical Garden Press.
- JSTOR 2023: JSTOR Global Plants. – Published at <https://plants.jstor.org/> [accessed 20 Jun 2023].
- Kelchner S. A. 2000: The evolution of non-coding chloroplast DNA and its application in plant systematics. – Ann. Missouri Bot. Gard. **87**: 482–498. <https://doi.org/10.2307/2666142>
- Kew WCV 2019: Dataset export of the Kew World Checklist of Vascular Plants database [dated 14 Jul 2023].
- Klepikova A. V., Shnayder E. D., Kasianov A. S., Remizowa M. V., Sokoloff D. D. & Penin A. A. 2021: *lepidium*-like, a naturally occurring mutant of *Capsella bursa-pastoris*, and its implications on the evolution of petal loss in *Cruciferae*. – Frontiers Pl. Sci. **12**(714711). <https://doi.org/10.3389/fpls.2021.714711>
- Lepší M., Lepší P., Koutecký P., Lučanová M., Koutecká E. & Kaplan Z. 2019: *Stellaria ruderalis*, a new species in the *Stellaria* media group from central Europe. – Preslia **91**: 391–420. <https://doi.org/10.23855/preslia.2019.391>
- Löhne C. & Borsch T. 2005: Molecular evolution and phylogenetic utility of the *petD* group II intron: a case study in basal angiosperms. – Molec. Biol. Evol. **22**: 317–332. <https://doi.org/10.1093/molbev/msi019>
- Mabberley D. J. 2017: The plant book, ed. 4. – Cambridge: Cambridge University Press.
- Macbride J. F. 1937: *Caryophyllaceae*. – In: Flora of Peru. – Publ. Field Mus. Nat. Hist., Bot. Ser. **13**(2): 578–638. <https://www.biodiversitylibrary.org/page/2392506>
- Madhani H., Rabeler R., Pirani A., Oxelman B., Heubl G. & Zarre S. 2018: Untangling phylogenetic patterns and taxonomic confusion in tribe *Caryophylleae* (*Caryophyllaceae*) with special focus on generic boundaries. – Taxon **67**: 83–112. <https://doi.org/10.12705/671.6>
- Mahdavi M., M. Assadi F., Fallahian & Nejdassattari T. 2012: The systematic significance of seed micro-

- morphology in *Stellaria* L. (*Caryophyllaceae*) and its closest relatives in Iran. – *Iranian J. Bot.* **18**: 302–310.
- Mansion G., Parolly G., Crowl A., Mavrodiev E., Cellinese N., Oganessian M., Fraunhofer K., Kamari G., Phitos D., Haberle R., Akaydin G., Ikinici N., Raus T. & Borsch T. 2012: How to handle speciose clades? Mass taxon-sampling as a strategy towards illuminating the natural history of *Campanula* (*Campanuloidae*). – *PloS one* **7**(e50076). <https://doi.org/10.1371/journal.pone.0050076>
- Mattfeld J. 1922: Revision der Gattung *Pycnophyllum* Remy. – *Feddes Repert.* **17**: 167–179. <https://doi.org/10.1002/fedr.19220181003>
- Mattfeld J. 1934: *Plettkea* eine neue Gattung der *Alsinoideae* aus den Hochanden Perus. – *Schriften Vereins Naturk. Unterweser, n.s.*, **7**: 1–22.
- McNeill J. 1962: Taxonomic studies in the *Alsinoideae*. I. Generic and infra-generic groups. – *Notes Roy. Bot. Gard. Edinburgh* **24**: 79–155.
- Molinari-Novoa E. 2016: Further nomenclatural changes regarding Peruvian endemics. – *Polish Bot. J.* **61**: 275–277. <https://doi.org/10.1515/pbj-2016-0021>
- Montesinos-Tubée D. B. 2015: *Pycnophyllum molle* and its tenants in southern Peru. – *J. Alpine Garden Soc.* **82**: 438–443.
- Montesinos-Tubée D. B. 2019a: *Arenaria alpamarcae*. The IUCN Red List of threatened species 2019: e.T133260422A133261100. – Published at <https://doi.org/10.2305/IUCN.UK.2019-3.RLTS.T133260422A133261100.en> [accessed 13 Sep 2022].
- Montesinos-Tubée D. B. 2019b: *Arenaria aphanantha*. The IUCN Red List of threatened species 2019: e.T133260468A133261105. – Published at <https://doi.org/10.2305/IUCN.UK.2019-3.RLTS.T133260468A133261105.en> [accessed 13 Sep 2022].
- Montesinos-Tubée D. B., Cano A., García-Llatas L. F., Ju Y. & Kool A. 2018: *Paronychia sanchez-vegae* (*Caryophyllaceae*), a new woody species of *Paronychia* from north Peru. – *Phytotaxa* **334**: 41–48. <https://doi.org/10.11646/phytotaxa.334.1.6>
- Montesinos-Tubée D. B. & Teillier S. 2022: *Arenaria* L. (*Caryophyllaceae*) en Chile. – *Gayana Bot.* **79**: 124–139. <https://doi.org/10.4067/S0717-66432022000200124>
- Montesinos-Tubée D. B., Tovar C., Ibérico-Vela G., Montoya-Quino J. & Sánchez-Vega I. 2020: *Drymaria veliziae* (*Caryophyllaceae*), a new species from the Andes of Cajamarca (north Peru). – *PhytoKeys* **140**: 47–56. <https://doi.org/10.3897/phytokeys.140.47738>
- Morrison D. A. 2009: A framework for phylogenetic sequence alignment. – *Pl. Syst. Evol.* **282**: 127–149. <https://doi.org/10.1007/s00606-008-0072-5>
- Morton J. K. 2005: *Stellaria*. – Pp. 96–114 in: *Flora of North America* Editorial Committee (ed.), *Flora of North America North of Mexico* **5**. – New York: Oxford University Press.
- Müller K. 2005: SeqState: primer design and sequence statistics for phylogenetic DNA datasets. – *Appl. Bioinformatics* **4**: 65–69. <https://doi.org/10.2165/00822942-200504010-00008>
- Müller K., Müller J., Neinhuis C. & Quandt D. 2010: PhyDE – Phylogenetic Data Editor, version 0.9971. Program distributed by the authors. – Published at <http://www.phyde.de/>
- Muschler R. 1911: *Caryophyllaceae* andinae. – *Bot. Jahrb. Syst.* **45**: 441–461. <https://www.biodiversitylibrary.org/page/217385>
- Ortuño Limarino T. & Borsch T. 2020: *Gomphrena* (*Amaranthaceae*, *Gomphrenoideae*) diversified as a C₄ lineage in the New World tropics with specializations in floral and inflorescence morphology, and an escape to Australia. – *Willdenowia* **50**: 345–381. <https://doi.org/10.3372/wi.50.50301>
- Pax F. & Hoffmann K. 1934: Trib. II. 1. *Alsinoideae-Alsineae*. – Pp. 314–334 in: Engler A. & Harms H. (ed.), *Die natürlichen Pflanzenfamilien*, ed. 2, **16c**. – Leipzig: Wilhelm Engelmann.
- Philippi R. A. 1892: Plantas nuevas chilenas de la familia de las Cariofiláceas. – *Anales Univ. Chile, I, Mem. Ci. Lit.* **81**: 761–775. <https://www.biodiversitylibrary.org/page/49704917>
- Pieper B., Monniaux M. & Hay A. 2016: The genetic architecture of petal number in *Cardamine hirsuta*. – *New Phytol.* **209**: 395–406. <https://doi.org/10.1111/nph.13586>
- Posada D. 2008: jModelTest: phylogenetic model averaging. – *Molec. Biol. Evol.* **25**: 1253–1256. <https://doi.org/10.1093/molbev/msn083>
- Rambaut A., Drummond A. J., Xie D., Baele G. & Suchard M. A. 2018: Posterior summarization in Bayesian phylogenetics using Tracer 1.7. – *Syst. Biol.* **67**: 901–904. <https://doi.org/10.1093/sysbio/syy032>
- Rohrbach P. 1872: Beiträge zur Systematik der Caryophyllinen. – *Linnaea* **37**: 183–312. <https://www.biodiversitylibrary.org/page/133563>
- Ronquist F., Teslenko M., Van Der Mark P., Ayres D. L., Darling A., Höhna S., Larget B., Liang L., Suchard M. A. & Huelsenbeck J. P. 2012: MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. – *Syst. Biol.* **61**: 539–542. <https://doi.org/10.1093/sysbio/sys029>
- Schäferhoff B., Müller K. F. & Borsch T. 2009: *Caryophyllales* phylogenetics: disentangling *Phytolaccaceae* and *Molluginaceae* and the description of *Microteaceae* as a new isolated family. – *Willdenowia* **39**: 209–228. <https://doi.org/10.3372/wi.39.39201>
- Sharples M. T. 2019: Taxonomic observations within *Stellaria* (*Caryophyllaceae*): insights from ecology, geography, morphology, and phylogeny suggest widespread parallelism in starworts and erode previous infrageneric classifications. – *Syst. Bot.* **44**: 877–886. <https://doi.org/10.1600/036364419X15710776741459>

- Sharples M. T. 2023: The paraphyly of *Stellaria alsine* (*Caryophyllaceae*) necessitates taxonomic readjustment. – J. Torrey Bot. Soc. **150**: 516–524. <https://doi.org/10.3159/TORREY-D-22-00033.1>
- Sharples M. T., Bentz P. C. & Manzitto-Tripp E. A. 2021: Evolution of apetaly in the cosmopolitan genus *Stellaria*. – Amer. J. Bot. **108**: 869–882. <https://doi.org/10.1002/ajb2.1650>
- Sharples M. T. & Tripp E. A. 2019: Phylogenetic relationships within and delimitation of the cosmopolitan flowering plant genus *Stellaria* L. (*Caryophyllaceae*): core stars and fallen stars. – Syst. Bot. **44**: 857–876. <https://doi.org/10.1600/036364419X15710776741440>
- Simmons M. P. & Ochoterena H. 2000: Gaps as characters in sequence-based phylogenetic analyses. – Syst. Biol. **49**: 369–381. <https://doi.org/10.1093/sysbio/49.2.369>
- Skottsberg C. J. F. 1916: Botanische Ergebnisse der schwedischen Expedition nach Patagonien und dem Feuerlande 1907–1909. V. Die Vegetationsverhältnisse längs der Cordillera de los Andes S. von 41° S. Br. Ein Beitrag zur Kenntnis der Vegetation in Chiloé, Westpatagonien, dem andinen Patagonien und Feuerland. – Kongl. Svenska Vetensk. Acad. Handl., n.s., **56**(5). <https://www.biodiversitylibrary.org/page/41854120>
- Steele K. P. & Vilgalys R. 1994: Phylogenetic analyses of *Polemoniaceae* using nucleotide sequences of the plastid gene *matK*. – Syst. Bot. **19**: 126–142. <https://doi.org/10.2307/2419717>
- Stöver B. C. & Müller K. F. 2010: TreeGraph 2: combining and visualizing evidence from different phylogenetic analyses. – B. M. C. Bioinf. **11**(7). <https://doi.org/10.1186/1471-2105-11-7>
- Swofford D. L. 2002: PAUP*: phylogenetic analysis using parsimony (*and other methods), version 4.0a, build 167. – Sunderland: Sinauer Associates.
- Taberlet P., Gielly L., Pautou G. & Bouvet J. 1991: Universal primers for amplification of three non-coding regions of chloroplast DNA. – Pl. Molec. Biol. **17**: 1105–1109. <https://doi.org/10.1007/BF00037152>
- Thiers B. continuously updated: Index herbariorum: a global directory of public herbaria and associated staff. New York Botanical Garden's virtual herbarium. – Published at <https://sweetgum.nybg.org/science/ih/> [accessed 20 Jun 2023].
- Tikhomirov V. N. 2016: (2427) Proposal to conserve the name *Stellaria* (*Caryophyllaceae*) with a conserved type. – Taxon **65**: 389–390. <https://doi.org/10.12705/652.21>
- Timaná M. E. 2005: Systematic studies in *Pycnophyllum* and *Pycnophyllopsis* (*Caryophyllaceae*) of the high Andes. – Austin: Ph.D. dissertation, University of Texas, School of Biological Sciences. <https://repositories.lib.utexas.edu/handle/2152/29683>
- Timaná M. E. 2017: Nomenclatural notes on the Andean genera *Pycnophyllopsis* and *Pycnophyllum* (*Caryophyllaceae*). – Lundellia **20**: 4–24. <https://doi.org/10.25224/1097-993X-20.1.4>
- Timaná M. 2019: *Pycnophyllopsis weberbaueri*. The IUCN Red List of threatened species 2019: e.T133302349A133302749. – Published at <https://doi.org/10.2305/IUCN.UK.2019-3.RLTS.T133302349A133302749.en> [accessed 13 Sep 2022].
- Timaná M. E. 2023: Honoring Jeanne Baret: *Baretia lanata* Timaná, comb. nov. (*Caryophyllaceae*), a new endemic genus and species combination for the Flora of Chile. – Adansonia, ser. 3, **45**: 497–505. <https://doi.org/10.5252/adansonia2023v45a27>
- Tropicos.org 2023: Tropicos. Missouri Botanical Garden. – Published at <https://tropicos.org/> [accessed 14 Jul 2023].
- Turland N. J., Wiersema J. H., Barrie F. R., Greuter W., Hawksworth D. L., Herendeen P. S., Knapp S., Kusber W.-H., Li D.-Z., Marhold K., May T. W., McNeill J., Monro A. M., Prado J., Price M. J. & Smith G. F. (ed.) 2018: International Code of Nomenclature for algae, fungi, and plants (Shenzhen Code) adopted by the Nineteenth International Botanical Congress, Shenzhen, China, July 2017. – Glashütten: Koeltz Botanical Books [= Regnum Veg. **159**]. <https://doi.org/10.12705/Code.2018>
- Volponi C. R. 1985: Sinopsis de las especies argentinas de *Arenaria* (*Caryophyllaceae*). – Darwiniana **26**: 331–351.
- Volponi C. R. 1993: *Stellaria cuspidata* (*Caryophyllaceae*) and some related species in the Andes. – Willdenowia **23**: 193–209. <https://www.jstor.org/stable/3996805>
- Weddell H. A. 1864: Plantes inédites des Andes. – Ann. Sci. Nat., Bot., sér. 5, **1**: 283–296. <https://www.biodiversitylibrary.org/page/41640989>
- Wei L. & Ronse de Craene L. 2019: What is the nature of petals in *Caryophyllaceae*? Developmental evidence clarifies their evolutionary origin. – Ann. Bot. **124**: 281–295. <https://doi.org/10.1093/aob/mcz075>
- Weigend M. 2004: Additional observations on the biogeography of the Amotape-Huancabamba zone in northern Peru: defining the south-eastern limits. – Revista Peruana Biol. **11**: 127–134. <https://doi.org/10.15381/rpb.v11i2.2447>
- WFO 2018: World Flora Online taxonomic backbone data export for *Caryophyllales*. received from William Ulate, Missouri Botanical Garden [dated 5 Nov 2018].
- White T. J., Bruns T., Lee S. J. & Taylor J. 1990: Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. – PCR protocols: a guide to methods and applications **18**: 315–322. <https://doi.org/10.1016/B978-0-12-372180-8.50042-1>
- Williams F. N. 1898: A revision of the genus *Arenaria*, Linn. – J. Linn. Soc., Bot. **33**: 326–437. <https://doi.org/10.1111/j.1095-8339.1898.tb00290.x>
- Worberg A., Quandt D., Barniske A. M., Löhne C., Hilu K. W. & Borsch T. 2007: Phylogeny of basal eu-

- dicots: insights from non-coding and rapidly evolving DNA. – *Organisms Diversity Evol.* **7**: 55–77. <https://doi.org/10.1016/j.ode.2006.08.001>
- Wyatt R. 1988: Phylogenetic aspects of the evolution of self-pollination. – Pp. 109–131 in: Gottlieb L. D. & Jain S. K. (ed.), *Plant evolutionary biology*. – Dordrecht: Springer. https://doi.org/10.1007/978-94-009-1207-6_5
- Xue B., Song Z., Cai J., Ma Z., Huang J., Li Y. & Yao G. 2023: Phylogenetic analysis and temporal diversification of the tribe *Alsineae* (*Caryophyllaceae*) with the description of three new genera, *Hesperostellaria*, *Reniostellaria* and *Torreyostellaria*. – *Frontiers Pl. Sci.* **14**(1127443). <https://doi.org/10.3389/fpls.2023.1127443>
- Yao G., Xue B., Liu K., Li Y., Huang J. & Zhai J. 2021: Phylogenetic estimation and morphological evolution of *Alsineae* (*Caryophyllaceae*) shed new insight into the taxonomic status of the genus *Pseudocerastium*. – *Pl. Diversity* **43**: 299–307. <https://doi.org/10.1016/j.pld.2020.11.001>
- Zanotti C. A., Chiarini F. E., Mering S. von & Acosta J. M. 2022: Análisis morfológicos y moleculares respaldan la identidad de *Arenaria pycnophylloides* (*Caryophyllaceae*, *Arenarieae*) y la exclusión del género *Sabulina* para la Flora Argentina. – *Darwiniana*, n.s., **10**: 435–450. <https://doi.org/10.14522/darwiniana.2022.102.1081>
- Zhou Y. & Zheng Z. 2022: Genetic diversity and inter-relationship among *Stellaria* L. (*Caryophyllaceae*) species by ISSR markers. – *Genetika* **54**: 119–130. <https://doi.org/10.2298/GENSR2201119Z>
- Zuloaga F. O., Morrone O., Belgrano M. J., Marticorena C. & Marchesi E. (ed.) 2008: Catálogo de las plantas vasculares del Cono Sur. – *Monogr. Syst. Bot. Missouri Bot. Gard.* **107**(3). – St. Louis: Missouri Botanical Garden Press.
- Supplementary appendix S2. Sequence and indel matrices of combined plastid data set as used for analysis including details of best-fitting models.
- Supplementary appendix S3. alignment of ITS data including hotspots
- Supplementary appendix S4. Sequence and indel matrices of ITS data set as used for analysis including details of best-fitting models.
- Supplementary appendix S5. ML and MP strict consensus trees from combined plastid data set.
- Supplementary appendix S6. Exploratory plastid tree (Bayesian majority rule consensus) with additional sequences from GenBank. Bayesian posterior probabilities are above branches and parsimony jackknife percentages below.
- Supplementary appendix S7. Matrices used for exploratory plastid analysis.
- Supplementary appendix S8. ML and MP strict consensus trees from ITS data set.
- Supplementary appendix S9. Exploratory ITS tree (Bayesian majority rule consensus) with additional sequences from GenBank. Bayesian posterior probabilities are above branches and parsimony jackknife percentages below.
- Supplementary appendix S10. Matrices used for exploratory ITS analysis.
- Supplementary appendix S11. Isotype of *Stellaria apurimacensis* stored at B.
- Supplementary appendix S12. Isotype of *Stellaria gali-anoi* stored at B.

Supplemental content online

See <https://doi.org/10.3372/wi.53.53301>

Supplementary appendix S1. Multiple sequence alignment of combined *trnK-matK-psbA* + *trnL-F* plastid sequence data including hotspots (annotated).

Supplementary appendix S13. Isotype of *Stellaria utcu-bambensis* stored at B.

Supplementary appendix S14. Isotype of *Stellaria xanthophylla* stored at B.

Willdenowia

Open-access online edition bioone.org/journals/willdenowia



Online ISSN 1868-6397 · Print ISSN 0511-9618 · 2022 Journal Impact Factor 1.900

Published by the Botanic Garden and Botanical Museum Berlin, Freie Universität Berlin

© 2023 The Authors · This open-access article is distributed under the CC BY 4.0 licence

Appendix 1

List of sampled species with code, voucher specimen, geographic origin and GenBank accession numbers for *matK-trnK-psbA*, *trnL-F* and ITS sequences. Herbarium codes are according to Thiers (continuously updated).

Species	Code	Voucher	Geographic origin	<i>matK-trnK-psbA</i>	<i>trnL-F</i>	ITS
Outgroup						
<i>Scleranthus annuus</i> L.	CAR685	Schmalz & Hellwig s.n. (MJG 011702)	Germany, Rheinland-Pfalz	OR920948	OR921028	OR914605
Ingroup						
<i>Arenaria aggregata</i> (L.) Loisel.	CAR129	Romo 9004 (B 10 0521582)	Spain	OR920957	OR921037	—
<i>Arenaria biflora</i> L.	CAR137	Görk & al. 23985 (B 10 0520390)	Turkey	OR920950	OR920993	OR914570
<i>Arenaria deflexa</i> Decne.	CAR132	Snogerup & Snogerup 7504 (B 10 0521885)	Greece	OR920989	OR920992	OR914569
<i>Arenaria guicciardii</i> Heldr. ex Boiss.	CAR160	Nielsen 11229 (B 10 0739001)	Greece	OR920958	OR920994	OR914571
<i>Arenaria pallens</i> Muschl.	CAR627	Montesinos 4902 (B 10 0766251, HSP)	Peru, Huánuco	OR920960	OR921011	OR914588
<i>Arenaria pycnophylloides</i> Pax	CAR324	Acosta & von Mering 620 (B 10 1009997, SI)	Argentina, Catamarca	OR920959	OR920998	OR914573
<i>Brachystemna calycinum</i> D. Don	CAR524	Third Darwin Nepal Fieldwork Training Expedition BX299 (E 00289509)	Nepal	OR920961	OR921009	OR914586
<i>Cerastium parvum</i> (Pedersen) M. T. Sharples & E. A. Tripp	CAR359	Acosta & von Mering 651 (B 10 1009987, SI)	Argentina, San Juan	—	—	OR914575
<i>Cerastium</i> sp.	CAR211	Borsch & al. 5798 (B 10 0719152)	Russia	OR920963	OR920997	—
<i>Moeblingia ciliata</i> (Scop.) Dalla Torre	CAR681	Messerschmid & Kadereit 2018-021 (MJG 025418)	Switzerland, Schwyz	OR920955	OR921026	OR914603
<i>Moeblingia lateriflora</i> (L.) Fenzl.	CAR177	Grondin & al. s.n. (B 10 0739324)	Canada, Québec	OR920954	OR920996	OR914572
<i>Moeblingia muscosa</i> L.	CAR684	Kadereit 2007/I6 (MJG 041251)	Switzerland, Schwyz	OR920956	OR921027	OR914604
<i>Moeblingia</i> sp.	CAR173	Scholz & Hiepkö 838 (B 10 0739328)	Spain	OR920949	OR920995	—
<i>Rabelleria holostea</i> (L.) M. T. Sharples & E. A. Tripp	DB38206	Borsch 5475 (B)	Germany, Hesse	OR948792	OR920941	—
<i>Stellaria alpamarcae</i> (A. Gray) Montesinos & Borsch	CAR440	Montesinos 5487 (B 10 0766215, CUZ, HSP, HUT, L, MO, O, USM)	Peru, Huánuco	OR920972	OR921008	OR914585
<i>Stellaria alpamarcae</i>	CAR632	Montesinos 5486 (B 10 0766216)	Peru, Huánuco	OR920986	OR921013	OR914590

<i>Stellaria cf. alsine</i> Grimm	DB38311	<i>Borsch 5706</i> (B)	Germany, Hesse	OR948793	OR920940	—
<i>Stellaria andina</i> (Rohrb.) Montesinos & Borsch	CAR377	<i>von Mering 2016-017</i> (B 10 1149337, LPB)	Bolivia, La Paz	OR920964	OR921001	OR914577
<i>Stellaria andina</i>	CAR634	<i>von Mering 2016-029</i> (B 10 1149005, LPB)	Bolivia, La Paz	OR920976	OR921015	OR914592
<i>Stellaria andina</i>	CAR638	<i>von Mering 2016-017</i> (B 10 1149337, LPB)	Bolivia, La Paz	OR920977	OR921016	OR914593
<i>Stellaria andina</i>	CAR664	<i>Montesinos 5169</i> (B 10 0745260, HSP)	Peru, Arequipa	OR920979	OR921021	OR914598
<i>Stellaria apurimacensis</i> Montesinos & D. Cornejo	CAR619	<i>Montesinos & Cornejo 5194</i> (B 10 0761536, CUZ, F, HSP, USM)	Peru, Apurimac	OR920973	OR921010	OR914587
<i>Stellaria blatteri</i> Mattf.	CAR943	<i>Freitag 15284</i> (B 10 1149456)	Iran	OR920962	OR921036	OR914614
<i>Stellaria bungeana</i> Fenzl	CAR940	<i>Chukhina & al. ERS20010</i> (B 10 0149856)	Russia, Altay	OR920953	OR921034	OR914611
<i>Stellaria congesta</i> Montesinos & Borsch	CAR633	<i>Montesinos 4905</i> (B 10 0766250, HSP, HUT, MO)	Peru, Huánuco	OR920975	OR921014	OR914591
<i>Stellaria congesta</i>	CAR661	<i>Montesinos 4900</i> (B 10 0766252, HSP, HUSA, HUT, L, MOL, O)	Peru, Huánuco	OR920980	OR921019	OR914596
<i>Stellaria cryptantha</i> (Mattf.) M. T. Sharples & E. A. Tripp	CAR431	<i>Montesinos 4592</i> (B 10 0766224, CUZ)	Peru, Huánuco	OR920967	OR921003	OR914580
<i>Stellaria cuspidata</i> Willd. ex D. F. K. Schltdl.	CAR352	<i>Acosta & von Mering 603</i> (B 10 1009982, SI)	Argentina, Salta	OR920990	OR920999	OR914574
<i>Stellaria cuspidata</i>	CAR667	<i>Montesinos 4521</i> (B 10 0761183, CUZ, HSP, HUT, O)	Peru, Cusco	OR920945	OR921022	OR914599
<i>Stellaria engleriana</i> (Muschl.) Montesinos & Borsch	CAR439	<i>Montesinos 5486</i> (B 10 0766216, HSP, HUT, MO)	Peru, Huánuco	OR920971	OR921007	OR914584
<i>Stellaria galianoi</i> Montesinos & Borsch	CAR438	<i>Montesinos 4572</i> (B 10 0766217)	Peru, Cusco	OR920970	OR921006	OR914583
<i>Stellaria galianoi</i>	CAR677	<i>Montesinos 4523</i> (B 10 0761503, HSP, HUT, K, O, USM)	Peru, Cusco	OR920982	OR921025	OR914602
<i>Stellaria keraipetala</i> Mattf.	CAR639	<i>von Mering 2016-050</i> (B 10 1149336, LPB)	Bolivia, La Paz	OR920988	OR921017	OR914594
<i>Stellaria laevis</i> (Bartl.) Rohrb.	CAR912	<i>Kunkel 353</i> (B 10 1226293)	Peru, Junin	—	—	OR941553
<i>Stellaria machbridei</i> Montesinos & Borsch	CAR430	<i>Montesinos 4591</i> (B 10 0766225, HUT)	Peru, Huánuco	OR920966	—	OR914579
<i>Stellaria machbridei</i>	CAR630	<i>Montesinos 4590</i> (B 10 0761527, CUZ, HSP, O)	Peru, Huánuco	OR920974	OR921012	OR914589
<i>Stellaria pedunculosa</i> (Wedd.) Montesinos & Borsch	CAR435	<i>Montesinos 4565</i> (B 10 0766220, HSP, HUT, O)	Peru, Arequipa	OR920969	OR921005	OR914582

Appendix 1 (continued from p. 147)

Species	Code	Voucher	Geographic origin	<i>matK-trnK-psbA</i>	<i>trnL-F</i>	ITS
<i>Stellaria pedunculosa</i>	CAR777	Montesinos & Chicalla 5395b (B 10 1167157, HSP)	Peru, Huánuco	OR920985	OR921030	OR914607
<i>Stellaria pungens</i> Brongn.	CAR942	Greuter 21301 (B 10 1149457)	Australia, New South Wales	OR920987	OR921035	OR914613
<i>Stellaria radicans</i> L.	DB6862	<i>Anonymous s.n.</i> (B 10 0356308)	North Korea	OR920952	—	OR914615
<i>Stellaria recurvata</i> Willd. ex D. F. K. Schltl.	CAR938	<i>Sklenář & Laegaard</i> 7188 (B 10 1097789, PRC)	Ecuador, Chimborazo	OR920942	OR921032	OR914609
<i>Stellaria ruscifolia</i> D. F. K. Schltl.	CAR941	<i>Shvedchikova s.n.</i> (B 10 1149458)	Russia, Kuriles	OR920951	OR920991	OR914612
<i>Stellaria serpyllifolia</i> Willd. ex D. F. K. Schltl.	CAR663	Montesinos 5642 (B 10 0745211, HSP)	Peru, Huánuco	OR920944	OR921020	OR914597
<i>Stellaria spinulosa</i> Montesinos & Borsch	CAR429	Montesinos 4683 (B 10 0766226, HSP, HUT, O)	Peru, Huánuco	OR920965	OR921002	OR914578
<i>Stellaria utubambensis</i> Montesinos & Borsch	CAR433	Montesinos & García 4979 (B 10 0766222, HUT, USM)	Peru, Amazonas	OR920968	OR921004	OR914581
<i>Stellaria weberbaueri</i> (Muschl.) Montesinos & Borsch	CAR653	Montesinos 4498 (B 10 0761150, CUZ, HSP)	Peru, Arequipa	OR920978	OR921018	OR914595
<i>Stellaria weberbaueri</i>	CAR670	Montesinos 4496 (B 10 0761152, CUZ, HSP, HUT, O)	Peru, Arequipa	OR920981	OR921024	OR914601
<i>Stellaria weddellii</i> Pedersen	CAR366	<i>von Mering</i> 2016-05 (B 10 1149327)	Bolivia	OR920943	OR921000	OR914576
<i>Stellaria weddellii</i>	CAR668	Montesinos 4487 (B 10 0761316, HSP, HUT, O)	Peru, Moquegua	OR920946	OR921023	OR914600
<i>Stellaria weddellii</i>	CAR789	Montesinos 4577 (B 10 0761290, HSP, HUT)	Peru, Huánuco	OR920947	OR921031	OR914608
<i>Stellaria xanthophylla</i> Montesinos & Borsch	CAR691	Montesinos 6970a (B 10 1098616, HSP)	Peru, Amazonas	OR920983	OR921029	OR914606
<i>Stellaria</i> sp.	CAR939	Montesinos 9382 (B 10 1228088, HOXA)	Peru, Huánuco	OR920984	OR921033	OR914610