

Towards a revision of *Trianthema*, the Cinderella of Aizoaceae

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Background and aims – The genus *Trianthema* (Aizoaceae – Sesuvioideae) is poorly known. Identification of two well circumscribed subgenera is followed by a revision of *T.* subg. *Papularia*, presenting for the first time a list of all species identified as members of the subgenus.

Methods – Normal practices of herbarium taxonomy have been applied to study all herbarium material available, mainly from AD, B, BRI, C, DNA, E, HBG, K, L, MO, UTB, WAG, and Z.

Key results – Based on an extensive investigation into as many characters as possible, results permitted the identification of new character states, supporting the division of the genus *Trianthema* into the two subgenera, *Trianthema* and *Papularia*. In consequence, species limits can be reliably re-circumscribed, resulting in the recognition of 17 species in the latter subgenus, of which five are described as new here: *T. corallicola*, *T. mozambiquensis*, *T. pakistanensis*, *T. ufoensis*, and *T. vleiensis*. Raised to species rank are *T. clavata* and *T. corymbosa*, and emended and re-circumscribed are *T. crystallina*, *T. hereroensis*, *T. parvifolia*, *T. salsoloides*, *T. sanguinea*, *T. sedifolia*, *T. sheilae*, *T. transvaalensis*, and *T. triquetra*. Unaltered is the description of *T. argentina*, for which, however, the critical features are also described and figured in order to permit a sound identification of each species in *T.* subg. *Papularia*. Distribution patterns are discussed and possible evolutionary pathways are suggested on a morphological base.

Key words – Aizoaceae, comparative morphology, *Cypselea*, distribution of species, *Papularia*, *Sesuvium*, Sesuvioideae, taxonomy, *Trianthema*, *Tribulocarpus*, *Zaleya*.

INTRODUCTION

Within the family Aizoaceae, members of the subfamily Sesuvioideae, including the genus *Trianthema*, deviate most obviously from the other subfamilies Aizooideae, Mesembryanthemoideae, and Ruschioideae in having indehiscent fruits, most of them characterized by circumscissile capsules (= pyxidial), lifting a lid (= operculum) to expose the seeds when dry and developing stipule-like appendages along the petiole, called also pseudostipules. Species in the other three subfamilies lack such stipule-like appendages and are primarily equipped with expanding tissues in the fruit, resulting in most elaborate mechanisms for seed dispersal by rain; dry fruits occur secondarily only in some samples (e.g. *Tetragonia* L.).

None of the five genera in the Sesuvioideae (*Cypselea*, *Sesuvium*, *Trianthema*, *Tribulocarpus*, *Zaleya*, after Klak et al. 2003 and Thiede 2004) has been revised on a worldwide base, although members occur on all continents and have been treated in numerous regional floras. *Trianthema* L. (von Linnaeus 1753), in addition, has received several partial taxonomic and nomenclatural treatments resulting in most

confusing applications of names, especially in the cases of *T. portulacastrum*, *T. triquetra*, and *T. crystallina*.

The identity of the genus has been determined by Jeffrey (1960), who not only distinguished *Trianthema* from the genus *Zaleya* but discussed the history of Linnaeus' naming in detail as well, choosing the drawing of Herman (1698) as the lectotype, based on the fact that the younger name *T. monogyna* (von Linnaeus 1767) definitely indicates that a plant with a single stigma was understood to be this species.

The gender of *Trianthema* has been considered to be feminine by Linnaeus (1767) when describing *T. monogyna*, although the first used name was *Trianthema portulacastrum*; this latter epithet, however, was copied from the older name *Trianthema Portulacastrum* Sauvages (Sauvages 1751: 127), hence the name has to be kept as such (art. 23.5 in ICBN, example 6; McNeill et al. 2006), independent from the gender (for discussion see Tjaden 1995 with the note of Nicolson). Note that Hartmann (2001) did not follow this rule.

A first subdivision of the genus *Trianthema* into two subgenera was undertaken by Jeffrey (1960), and *T.* subg. *Papularia* was validly described, in contrast to notes by Bittrich (1990) and Hartmann (2001), who both erroneously assumed

that nomenclatural requirements had not been fulfilled. The two subgenera have been keyed out as follows (Jeffrey 1960: 237):

- Ovules 4; flowers usually solitary
.....*Trianthema* subg. *Trianthema*
- Ovules 2, superposed; flowers usually clustered.....
.....*Trianthema* subg. *Papularia*

An arrangement of species into subgenera was not undertaken on a worldwide scale until this date, neither for Australia (Prescott 1984) nor for the African tropics (Jeffrey 1961); Adamson (1962) used the subgeneric names formally but did not discuss the matter of distinction since no member of *Trianthema* subg. *Trianthema* is reported to occur in southern Africa. Bittrich (1990) referred to *T.* subg. *Trianthema*, with which he placed the new species *T. kimberleyi* from Australia, but pointed out that a decision on the taxonomy has to rely on more extensive studies on a broader base.

Support for such a subdivision was presented based on a molecular study of the Internal Transcribed Spacer (ITS) by Hassan et al. (2005b) and is supported by additional molecular markers (Liede-Schumann et al., unpubl. data). The investigated species of *Trianthema* fell into two different groups in the former paper, but these were separated by two samples taken from the genus *Zaleya* (Hassan et al. 2005b: 131, 132). A first morphological survey revealed that one group of *Trianthema* (subclade IV in Hassan et al. 2005b) with only two ovules and flowers in clusters keyed out as containing plants that agree with members of subg. *Papularia* (after Jeffrey 1960: 237). The other group of *Trianthema* (Hassan et al. 2005b subclade VI) agreed indeed in morphological character states with subg. *Trianthema* sensu Jeffrey (1960) in having single flowers with principally four seeds. The great majority of species treated for the Flora of Australia (Prescott 1984) and also *T. portulacastrum*, the type species of the genus, fall into this group. Branch support for this group was only moderate in general, but the tree suggests a differentiation into species and species groups in Australia (Hassan et al. 2005b).

Against this background, the present studies concentrate on *Trianthema* subg. *Papularia*, in which group the confusion and lack of clarity regarding the identity of *T. triquetra* and *T. crystallina* resulted in the perception that the assumed species had a very wide geographical distribution area from Australia through southern Asia and Saudi Arabia into northern and even southern Africa.

The conflict started with the fact that the name *T. triquetra* for an Indian species of Rottler had not been published validly by Willdenow (1803) as assumed by Sprengel (1825) but had been considered by the former author to represent a ‘sport’ (‘eine Spielart’) of *T. crystallina*, a species described by Forsskål (1775) as *Papularia crystallina* from Dahi, Yemen. The correct naming and authorship of *T. triquetra* have only been clarified by Daniel & Umamaheswari (1999). In the meantime, both names have been used alternatively for identical material suggesting occurrence of either species in places where none of them has ever been found. An additional cause of irritation was, however, that members of the assumed species *T. triquetra* were identified by different critical character states: *T. triquetra* in Australia keys out as being smooth (Prescott 1984), the ‘same’ species in Pakistan

as slightly papillate (Nasir 1973), and, under the same name, ‘hirsute’ plants are identified in southern Africa (Adamson 1962, Gonçalves 1965, Friedrich 1970).

In this confusing situation, work towards getting order into the chaos and raising *Trianthema* into a usable taxonomic state concentrated on two topics:

1. Disentangle and sort the complex known until now under the names of *T. triquetra* and *T. crystallina* alternatively. With the types of *T. triquetra* (B) and *T. crystallina* (C) having been made available for examination, these species can at last be circumscribed.

2. Distinguish and circumscribe all species that can reliably be placed in subg. *Papularia*.

In this process, a number of species is re-established, two varieties are raised to species rank, and five new species are described, and a workable key to the now recognized species is developed.

MATERIAL AND METHODS

Four hundred and fifty collections of *Trianthema* form the base of the investigations, 83 of these made by H.E.K.H. in Kenya, Namibia, South Africa, Sudan, Tanzania, United Arab Emirates, and Zimbabwe, the bulk having been made available by loan from the herbaria AD, B, BRI, C, DNA, E, HBG, K, L, MO, UTB, WAG, and Z, including type sheets. All specimens cited were seen, unless otherwise indicated (‘n.v.’).

Morphological studies were expanded to cover almost all characters from dry herbarium material and more preserved in liquid, from observations made in habitat, freshly sent plants from South America, and from numerous images. Beside investigations with a binocular microscope, SEM graphs of surfaces were prepared and studied in a Philips/FEI XL 30 ESEM at Bayreuth.

RESULTS OF MORPHOLOGICAL STUDIES

Life span and related features

A distinction between annual and perennial growth is in many cases very difficult: information on herbarium sheets is scarce, and sometimes not correct; and at the same time, most species can flower in their first year already, appearing to be annuals, but they can continue to grow on later, developing a substantial woody shrub (observed in habitat in *T. sheilae*). The type specimen of *T. crystallina* possesses woody white stems, hence has been perennial, too. Even if not shrubby, it has been observed that branches can turn woody, surviving an elongated dry period, e.g. in *T. parvifolia* with strictly procumbent branches living over several to even many years.

Remarkable in this aspect is *T. corymbosa* (described as a variety of *T. crystallina* by Sonder 1862) with persisting mostly obliquely ascending branches that shed their leaves completely during the dry season, the only deciduous member of the genus, as known until now.

The species that grow strictly as annuals are *T. argentina*, *T. clavata*, *T. pakistanensis*, probably *T. sanguinea*, *T. sedifolia*, *T. triquetra*, and *T. ufoensis*, as far as information

is available at this date. Species that already flower in their first year include *T. corallicola*, *T. parvifolia*, *T. salsoloides*, *T. sheilae*, and *T. transvaalensis*, but in favourable conditions they will continue to grow over few (*T. transvaalensis*) to many years (*T. sheilae*). Unknown is whether *T. corymbosa*, *T. hereroensis*, and *T. mozambiquensis* can also flower in their first year.

Independent from the life span, plants can form obliquely ascending branches or/and procumbent ones. Truly procumbent growth is known from *T. mozambiquensis* and *T. parvifolia* in the southern part of its distribution area; in the north, plants with more erect branches have been collected. Procumbent growth predominates also in *T. clavata* and *T. ufoensis* in Australia, *T. corallicola* in Somalia and Kenya, and in young plants of *T. crystallina* and *T. sheilae*.

These two latter develop into rich shrubs with heights up to 35 cm later. In contrast, the young plants of *T. argentina*, *T. sanguinea*, *T. transvaalensis*, and *T. salsoloides* form obliquely erect branches turning decumbent with age. Taking these differences into account, the type material of several synonyms can be identified and placed with the correct species.

Internodes

When young, all internodes are equipped with more or less globose bladder cells, their sizes and numbers differing between species. Smooth internodes have only been documented in *T. corymbosa* (fig. 4A) and *T. hereroensis* (fig. 10A), and *T. parvifolia*; small globose bladder cells (size at most up to 100 µm) have been found in *T. clavata* (fig. 5A), *T. mozambiquensis* (fig. 11A), *T. pakistanensis* (fig. 3A), *T. salsoloides* (fig. 6A), *T. sanguinea* (fig. 7A), *T. triquetra*, *T. ufoensis*, and *T. vleiensis* (fig. 9F), all in loose arrangement on the surface. Bigger (about 150–170 µm) and more densely placed bladder cells on internodes have been documented for *T. argentina*, *T. crystallina* (fig. 2B), *T. sedifolia* (fig. 7E), and *T. sheilae* (fig. 1E). Also densely placed but of an elongate ovoid shape are the bladder cells on internodes in *T. transvaalensis* (fig. 6E). Prominent elongated bladder cells to 500 µm long adorn the internodes of *T. corallicola* (fig. 8A) in a rather dense arrangement, a unique feature in the genus.

A caveat must be raised regarding the assessment of the cover of bladder cells on internodes: their number is fixed during their early ontogeny, and as a consequence, the distances between the single bladder cells increase with growth of the normal epidermal cells on the internodes during their development. Furthermore, the epidermis is rubbed off with aging, and the whole epidermal layer is pushed away once the stem develops secondary xylem inside. All these processes result in smooth old internodes that appear alike in all species.

Internode length depends largely on growing conditions and on the state the individual is in when assessed; measurements of internodes are, therefore, not of value in distinguishing species.

Leaves

General features – Like all members of the subfamily Sesu-

vioideae, leaves of *Trianthea* consist of three parts: the leaf blade, a petiole, and two flaps at each side of the petiole, called often stipules, although they are not formed early in ontogeny, as would be the case in true stipules; instead, these flaps are called pseudostipules here.

Shapes of leaf blades – Although the dried leaves of *Trianthea* appear flat in herbarium specimens, they start off as vigorous succulent three dimensional organs. A species pair showing differences in succulence are the two species in Australia, *T. clavata* and *T. ufoensis*. The former species is characterized by its clavate, i.e. club-shaped, leaves, whereas for *T. ufoensis* leaves are usually described as being wider than thick (Kapitany 2007: 106–107, as *T. triquetra*). Fresh leaves are rarely present for assessment, but it seems that most species form succulent leaves often a little wider than thick, and in some cases the margins are even rolled in the dry state, e.g. in *T. mozambiquensis* (fig. 11B), *T. pakistanensis* (fig. 3B), and *T. sanguinea* (fig. 7B).

Constant are, however, differences in the formation of the leaf tip:

– Rounded leaf tips are found in *T. argentina* (fig. 1A), *T. clavata* (fig. 5B), *T. corymbosa* (fig. 4A), *T. crystallina* (fig. 2C), *T. pakistanensis* (fig. 3C), *T. parvifolia* (fig. 4E), *T. sedifolia* (fig. 7F), and *T. sheilae*.

– Pointed leaf tips occur in their extreme form in members of *T. ufoensis* (fig. 5E), in which species the tips form mucros that break off with age, hence the feature can only be found on young leaves. Also prominent are the sharp tips of *T. corallicola* (fig. 8E), in which species the tips are adorned with prominent papillae resulting in a fuzzy look of the tip. Acute leaf tips are also found in *T. hereroensis* (fig. 10C), distinguishing it at first sight from *T. parvifolia*, with which it has been united in the past.

– Also equipped with apical papillae are the leaves of *T. transvaalensis* in their young state, but less prominent and not as long as those of *T. corallicola*.

– More acuminate than acute the leaf tips of *T. salsoloides*, *T. sanguinea*, *T. triquetra* (fig. 2F), and *T. vleiensis* (fig. 9C & E) present themselves.

– Leaves on the only collection of *T. mozambiquensis* are rolled up so narrowly that they appear acuminate pointed, but fresh material will be needed to assess the leaf shape definitely.

– Since the leaf tips are the first parts of a leaf to develop in ontogeny, their shape and sculpture can be understood to represent old genetically determined lines, less variable under changing environmental conditions, as has been checked in larger samples in detail.

Leaf blade surfaces – Like internodes, leaf blades differ in their equipment with bladder cells. Almost smooth blades with only slightly raised bladder cells are known from *T. corymbosa*, *T. hereroensis* and *T. parvifolia* (fig. 4E), all three also without bladder cells on their internodes, and in the series of *T. clavata* (fig. 5B), *T. pakistanensis*, *T. triquetra* (fig. 2F), *T. ufoensis* (fig. 5E), and *T. vleiensis* (fig. 9C), all sparsely equipped with small bladder cells of about 100 µm on their internodes. Covered by big yet very low bladder cells are the leaf blades of *T. mozambiquensis* (fig. 11B), here in combination with prominent bladder cells on the internodes (fig. 11A). Few to some large globose bladder cells of about

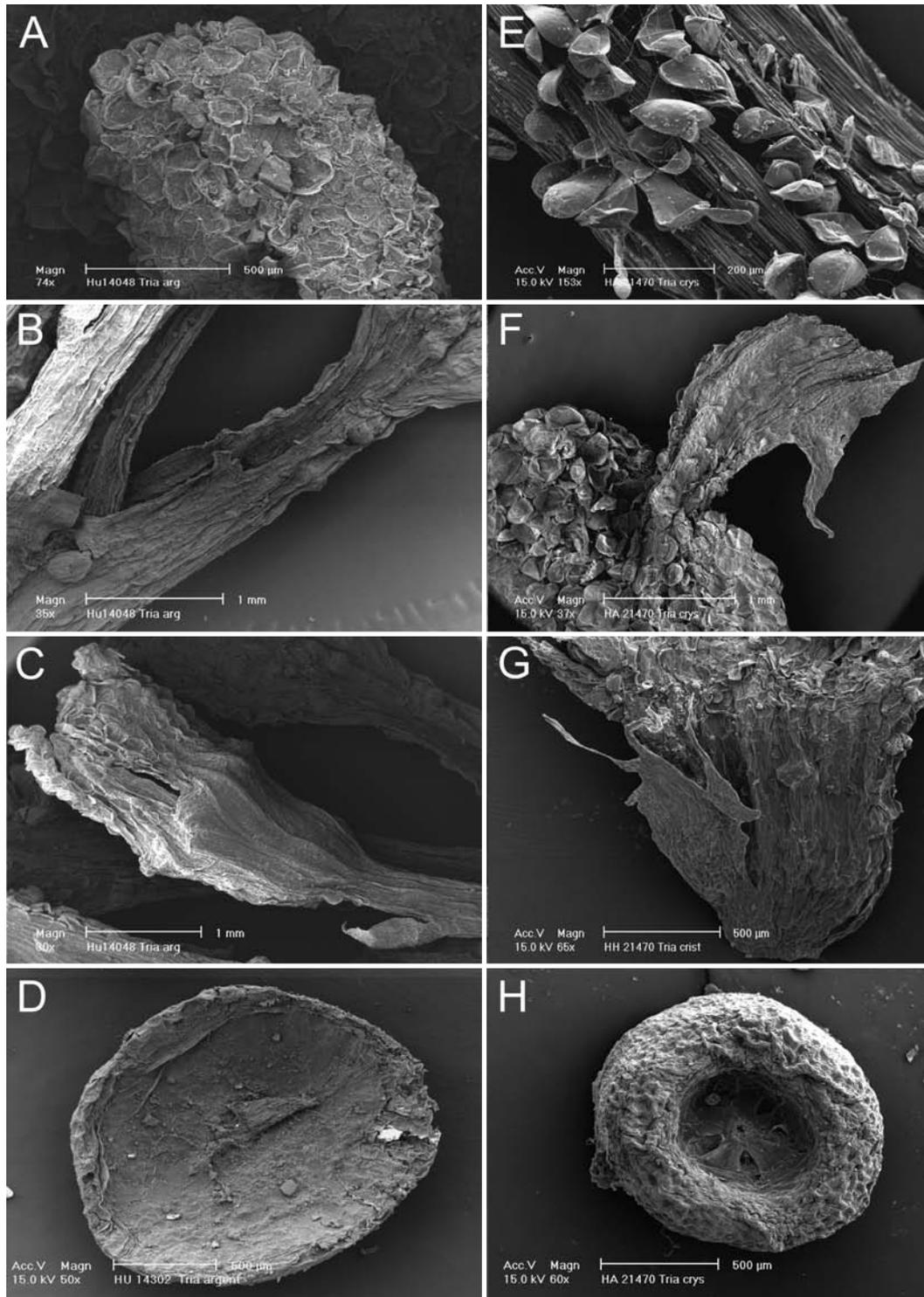


Figure 1 – Comparison of *Trianthena argentina* (A–D) and *T. sheilae* (E–H): A, upper leaf surface and rounded leaf tip, covered completely by big globose bladder cells of almost 200 μm , hiding the normal epidermis; B, petiole with rather narrow yet rectangular flaps (pseudostipules) on either side; C, flower with prominent big bladder cells on the tips of the tepals, showing the same pattern as the leaves; note the very small bracteole on the very short pedicel, a rare combination in the subgenus; D, view of an older operculum as seen from above, the rim pressed in the process of drying; note the central stigma; E, globose bladder cells on an internode, the cells collapsed in the drying process, as it also occurs in *T. argentina*; F, the petiole pointing to the right hand side upper corner, exposing the very broad pseudostipule equipped with a long, pointed tooth; the leaf blade lying in the left hand side corner, note the almost heart-shaped base of the blade base, in contrast to *T. argentina*, fig B; G, flower with fimbriate bracteole at its left hand side; note the smooth base; H, operculum seen from above; note the thick outer rim and the shrunken and partially torn interior surface. A–C from Hunziker *et al.* 14048; D from Hunziker 14302, E–H from Hartmann 21470.

200 µm can be seen distributed all over the blade in *T. sedi-folia* (fig. 7F); pointed bladder cells of c. 160 µm sit mainly along the margins in *T. transvaalensis*; very prominent bladder cells almost forming hairs adorn the tip of the blade in *T. corallicola* (fig. 8E), often visible to the naked eye. The most striking cover of big bladder cells occurs in blades of *T. argentina* (fig. 1A), *T. crystallina* (fig. 2C), and *T. sheilae* (fig. 1F), in which three species a complete secondary cover over the normal epidermis cells is formed by densely placed globose bladder cells of 150–230 µm diam.

Colour patterns on the upper leaf surface – Bittrich (1990) pointed out already that a dark or green line can be seen in fresh leaves of some members of the genus *Trianthema*. Field observations in southern Africa permit the description of three different types of colour patterns:

1. A longitudinal line above the mid vein of the leaf is conspicuous on the upper leaf surface in *T. transvaalensis* and *T. vleiensis* (fig. 9E), visible as a glassy stripe in translucent light, appearing dark green in reflecting light. In this area, the parenchymatic tissue reaches below the epidermis, no intermitting chlorenchymatous tissue being present. When drying, the leaf shrinks along this streak, which can be as long as or shorter than the upper leaf surface, sometimes recognizable as an inward fold on the dry leaf, difficult to distinguish under the binocular microscope (fig. 9C).
2. Local green dots can be seen in *T. parvifolia* (fig. 4D) and *T. corymbosa* (fig. 4A), very rarely aggregating in short sections along the upper surface above the mid vein, joining into something resembling short stripes, but always formed by more or less clearly separated dots. A similar arrangement has been figured by Kapitany (2007) for *T. clavata*, but no further information is available.
3. Until now, no colour pattern has been found in all other species. This is certainly true for *T. crystallina*, *T. sheilae*, and *T. argentina*, in which latter, however, a slight deepening can be seen running along the middle of the upper leaf surface. Without any sign of a different colour are leaves of *T. ufoensis* (figured as *T. triquetra* by Kapitany 2007).

An assessment of the Indian and northern African populations and of *T. mozambiquensis* is not possible at this date since no fresh material is available.

Petioles and lateral flaps – In most cases, the basal lateral flaps along the petiole reach high up, often leaving no discernable petiole visible. The shapes of the pseudostipules or lateral basal flaps appear rather constant, however, per species, and can be used to distinguish species.

The most inconspicuous flaps have been found in *T. triquetra* and *T. pakistanensis* (fig. 3B), in which species often no flaps can be detected because they roll around the axis they clasp, hardly reaching a width of 0.5 mm. There is always a very short petiole present, but the blade tends to break easily above the flaps.

Narrow flaps are also present in *T. corymbosa* (fig. 4B), but in this species they merge into the petiole so gradually that they seem to join the blade itself before the petiole could possibly separate from them. Petioles are also visible in *T.*

clavata, *T. vleiensis* (fig. 9B), and in *T. ufoensis* (fig. 5F), but in these species the attached flaps are distinctly wider, appearing like flags to both sides and often ending in sharp little tips. *T. salsoloides* (fig. 6B) shows this type of pseudostipule as well, but in the otherwise very similar *T. transvaalensis*, the flaps are often less conspicuous (fig. 6E). Broad basal pseudostipules are also found in *T. mozambiquensis*, their shapes almost rectangular, ending in a short broad tooth of 90°, resulting in an almost flag-shaped appendage on either side of the petiole (fig. 11C).

Most prominent are flaps in *T. crystallina* (fig. 2B) and *T. sheilae* (fig. 1F), in both cases very broad and ending in long-drawn acute points, 1–3 per pseudostipule, thus often appearing lacinate. Nevertheless, these flaps merge into the petiole, which in turn is sharply separated from the blade.

Very broad and more or less rectangular lateral flaps catch the eye in *T. parvifolia* (fig. 4E) and *T. corallicola* (fig. 8B). Especially in *T. parvifolia*, the flaps remain regularly on the plant after the blades have withered and decayed, forming an eye-catching white papery envelope around the stem. Populations in the north tend to develop more narrow flaps, hence these have been named '*T. triquetra*' in the past.

T. hereroensis differs from all other species in the subgenus in having semi-elliptic pseudostipules (fig. 10C), the pair on a petiole forming a broadly elliptic shape.

Inflorescences – Rich axillary inflorescences arranged in close bundles are given as typical of the whole subgenus, and indeed can this feature be confirmed for most species. In young plants, the number of flowers can be only one, but usually other nodes will then show at least two flowers (e.g. the type specimen of *T. triquetra*).

The flowers do not develop a pedicel, with the exception of *T. corymbosa*: in this species, the young flowers sit in close arrangement, elongating their pedicel while ripening, resulting in a long-drawn fruiting inflorescence by exposing the smooth pedicel surface.

A peduncle has not been found in members of the subgenus.

Differences exist, however, in the position of the flowers: usually they sit in a close bundle and are free. In *T. salsoloides* (fig. 6C) and *T. transvaalensis* (fig. 6F), however, tissue from the flower base surrounds the bases of the flowers resulting in a compact solid body that breaks out of the axil when old. This common feature has resulted in both species being considered to be one (e.g. Adamson 1962: 248: *T. salsoloides* var. *transvaalensis*), an arrangement not followed here (see also below under seeds).

Bracts and bracteoles – Each flower is subtended by a bract and, in most cases, by two bracteoles, differing in shape and size distinctly from the vegetative leaves.

Most common are lanceolate shapes in bracts and bracteoles, all usually placed at the bottom of the flower and free: *T. triquetra* (fig. 2D), *T. pakistanensis* (fig. 3B), *T. clavata* (fig. 5C), *T. sanguinea* (fig. 7C), *T. sedi-folia* (fig. 7G), *T. corallicola* (fig. 8A), *T. vleiensis* (fig. 9G), *T. hereroensis* (fig. 10B); at a distance to the flower, in *T. argentina* (fig. 1C) a small bract is found as a slight deviation from the normal case. Exceptions are found in *T. salsoloides* (fig. 6C) and

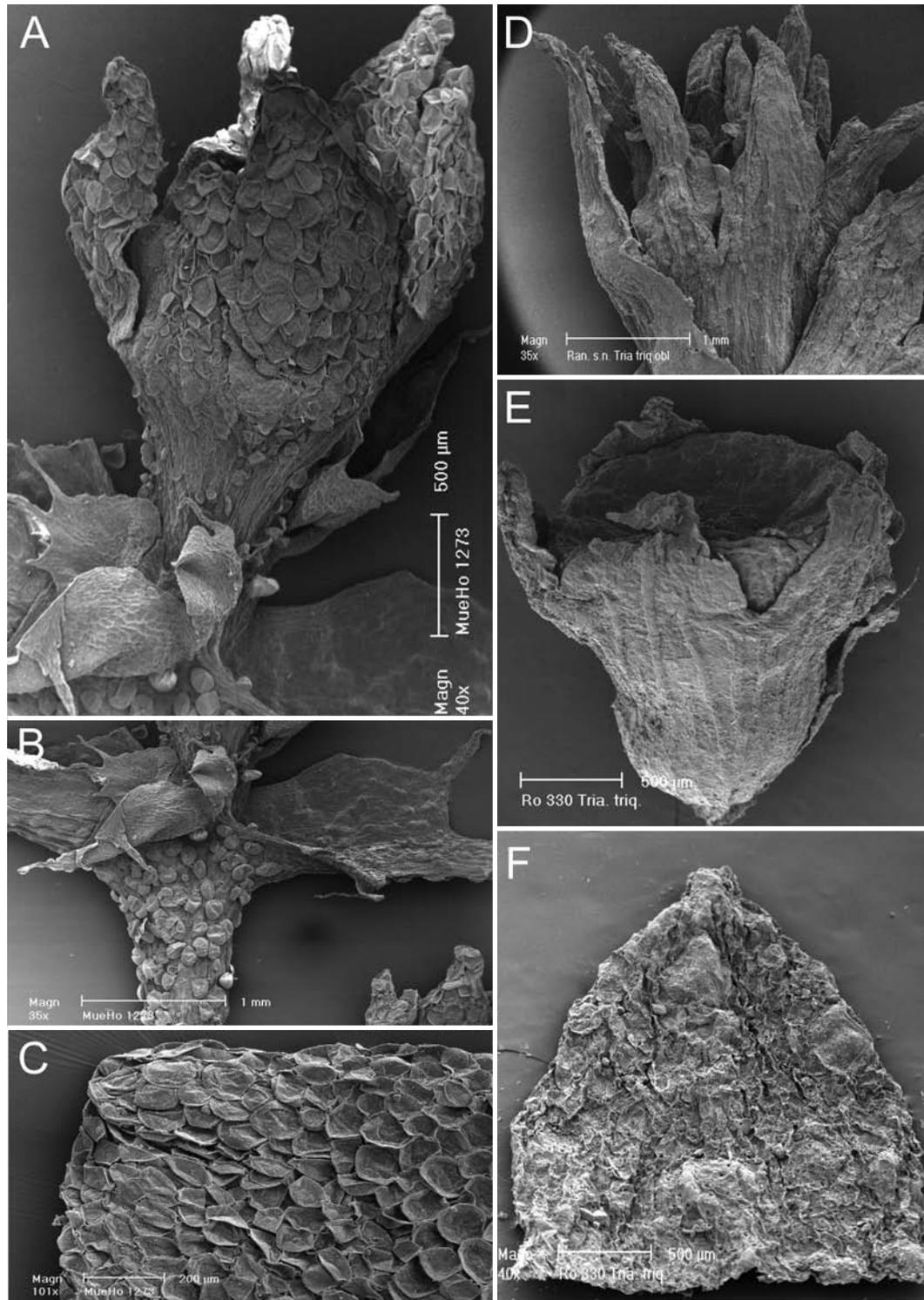


Figure 2 – Comparison of *Trianthema crystallina* (A–C) and *T. triquetra* (D–F): A, flower and subtending laciniated bract and bracteoles, the tepal base almost smooth, the teeth with densely placed big bladder cells; B, node with bract and bracteoles above, to the right, a petiole base with a broad pseudostipule ending in a long tooth, like the condition found in *T. sheilae*; the internode with bladder cells almost 200 µm big; C, close-up of a young leaf tip, covered completely by big bladder cells, not yet in their final size that can reach 200 µm; D, flower in side view with a subtending bract on the left hand side; all surfaces smooth, only the tips of the tepal teeth with low bladder cells; E, tepal tube in side view, showing the three veins continuing into the tepal teeth on top and the shorter vein splitting below the incision of the tepal teeth, bending over the pyxidium top in the middle; F, moderately acuminate tip of smooth upper leaf surface, in contrast to the papillate surface of fig. 2. C. A–C from Müller-Hohenstein 1273, D–F from Rottler 330.

T. transvaalensis (fig. 6F), both with flowers firmly enveloped by the base of the inflorescence forming a solid base on the outside of which the bracts and bracteoles appear as outgrowths.

Also deviating in shape from the majority are *T. crystallina* (fig. 2A) and *T. sheilae* (fig. 1G), both with wide prominent lacinate bracts and bracteoles, easily visible to the naked eye.

Tepals – As in all members of the genus *Trianthea*, the tepals form a basal tube on which veins can be seen. In most cases, three veins extend over the free tepal teeth, and a basal vein splits at the incision of the tepals, sending a lateral vein into the base of the free tooth on either side (*T. triquetra*, fig. 2E). More veins seem to be present in *T. clavata*, *T. parvifolia*, *T. sanguinea* (fig. 7C), *T. sedifolia*, and *T. vleiensis*, but variation and resultant overlap in values is too high to permit clear reliable distinctions between species. An assessment is also made difficult by the different lengths of the veins: the central one reaches to the tip of the tepal, the lateral ones are decreasing in length towards the sides, and often it is impossible to determine how far up the most lateral veins reach.

Tepal tubes lack bladder cells completely in most species, but the surfaces of the free tepal teeth differ distinctly and constantly between species or groups of species.

Most prominent and big are the bladder cells found on tepal teeth of *T. argentina* (fig. 1C), *T. crystallina* (fig. 2A), and *T. sheilae* (fig. 1G), the surfaces resembling those of the leaves in all three species.

Also prominent but more elongate bladder cells occur at the tips of the tepals in *T. corallicola* (fig. 8C), resembling also conditions found on the leaves.

The remaining species show in young flowers some bladder cells, in several cases noticeably long, but these can disintegrate with age and also be rubbed off. In old flowers of this type, the tepals can appear smooth.

In *T. clavata* (fig. 5C) and *T. triquetra* (fig. 2E), however, the tepal tips appear smooth all the time, but no extensive studies have been possible to prove a difference to the aforementioned state.

Further than differences in surfaces, the tepals of different species differ in their relative length and, correlated with this, in the position the tepal teeth take, including also the form of the base of the teeth, i.e. whether they lie smoothly around the tepal tube top or develop bulges at their basal joining points.

All tepal teeth are free by definition, and their tips are formed by pointed protrusions developing from a subapical point, i.e. the tip consists of upper tepal tooth surface tissue only (as is usual in members of the subfamily Sesuvioideae). The five tepal teeth of a flower differ in the length of the subapical protrusion, but overall their tips reach more or less the same level above the flower or fruit.

Low protrusions in the shape of bumps or swellings appear prominently in tepal teeth of *T. parvifolia* and *T. corymbosa*, visible as raised thick green dots in fresh leaves. In dry herbarium material, it is impossible to recognize the swelling which is mainly caused by highly turgescient cells inside the leaf.

Especially long prominent tepal teeth tips are found in *T. salsoloides* (fig. 6C), and *T. transvaalensis* (fig. 6F), the erect tips reaching up to 1 mm regularly, hence being visible to the naked eye. Erect tepal teeth of c. 1 mm are also typical of *T. hereroensis* (fig. 10B). In contrast, the moderately long tepal teeth tips in *T. vleiensis* lean over towards the centre (fig. 9G). In addition, the bases of these longish teeth overlap forming prominent bulges at each incision at the top of the tepal tube. Furthermore, the subapical protrusions are equipped with elongate bladder cells, resulting in a rough aspect.

Tepal teeth less than 1 mm long but also with elongate bladder cells have been found in samples from *T. corallicola* (fig. 8C) and *T. sanguinea* (fig. 7C); in these samples, the bulges at the tepal teeth bases are visible in the scanning electron microscope, yet much less prominent than in the first group.

In a third group of species, the young flowers show erect tepal teeth, but with the ripening of the fruit, the diameter of the operculum increases noticeably. In consequence, the tepal teeth appear relatively shorter and their bases expand the tissue that once formed a bulge in the flower. This ontogenetic change has been observed in *T. corymbosa* and *T. parvifolia*,

Table 1 – Characters of *T. triquetra* and *T. crystallina* in the relevant sources.

| Source | Description: <i>T. triquetra</i> | Type sheet: <i>T. triquetra</i> | Description: <i>T. (Papularia)</i> <i>crystallina</i> | Description: <i>T. (Papularia)</i> <i>crystallina</i> | Type sheet: <i>T. (Papularia)</i> <i>crystallina</i> |
|---------------|-------------------------------------|---|---|---|--|
| | Sprengel (1825) | Rottler 330 (B) | Sprengel (1825) | Forsskål (1775) | Forsskål C III.14 (C) |
| growth form | herbaceous | - | fruticose | - | - |
| leaf shape | subspathulate | elongate oval | oval | - | circular |
| branches | subcompressed-triquetrous | - | ? | round | - |
| Plant surface | ? | bladder cells inconspicuous, mainly visible along margins | papulate | crystalline on both sides | - |
| stamens | 10 | - | 5 | - | - |

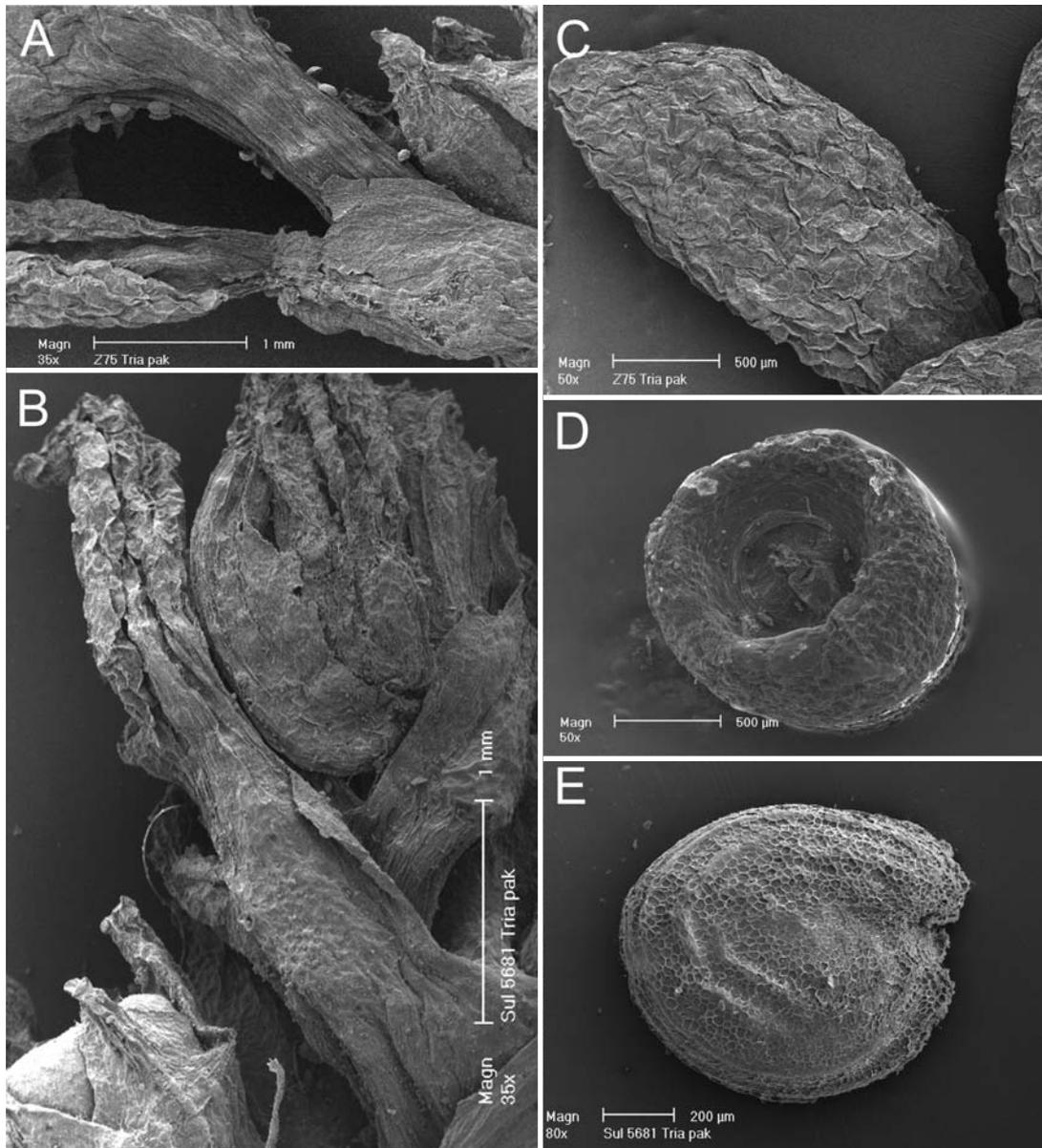


Figure 3 – *Trianthena pakistanensis*: A, the petiole with its narrow pseudostipule envelopes the internode adorned with some small bladder cells of c. 100 µm diam., exposing a short free portion and changing into the base of the leaf blade to the left, which shows incurved margins but no prominent bladder cells; B, side view from the inflorescence: a ripe flower exposing the pyxidium in the lower left hand side corner; the leaf extending over the entire image, showing some elevation of the big but low bladder cells and folded inwards margins; the flowers on top with distinct bladder cells on their tepal teeth; C, old leaf with a smooth surface, resembling that of *T. triquetra*, fig. 2F; D, fully developed operculum with a broad, firm rim; E, side view of a seed as typical of *T.* subg. *Papularia*: beside distinct ridges over the top of the seed, the sides show more or less semi-circular ridges, here partially covered by remains of the formally complete thin aril. A, C from *Zaibanmsia* 75; B, E from *Sultanul Abadin* 5681; D from *Stewart* 15062.

but the samples of *T. pakistanensis* may also belong here (fig. 3B).

A similar development has been traced in the three species with big bladder cells on the tepal teeth: *T. argentina* (fig. 1C), *T. crystallina* (fig. 2A), and *T. sheilae* (fig. 1G). At present, the more erect tepal teeth with basal bulges are understood to represent a typical feature of *T. sheilae*, in contrast to the incurving tepal teeth with smooth bases in *T. crystallina*. Observations on the ontogeny are needed to decide

whether indeed the described and observed differences are constant or represent developmental states.

Tepal teeth at most 0.5 mm long in most cases form a smooth basal area around the top of the tepal tube, there being no bulges, and this is always correlated with the fact that the teeth lie as a cover overarching the operculum surface. It has been said that such teeth can open in moist conditions, but no experiments have been undertaken to check this. Once the fruit is ripe, however, the teeth can spread widely after the operculum has grown conspicuously in diameter: *T. cla-*

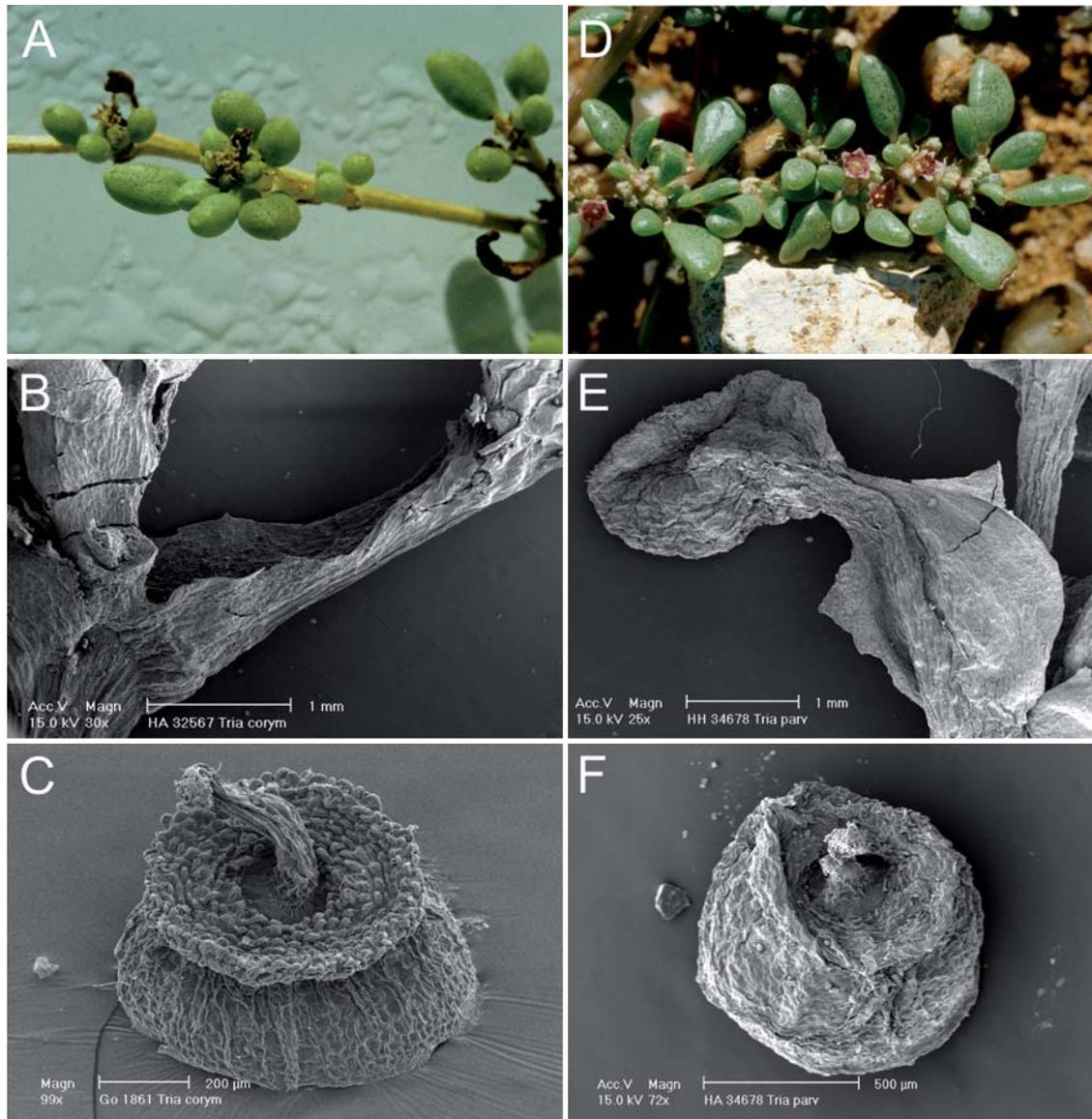


Figure 4 – Comparison of *Trianthema corymbosa* (A–C) and *T. parvifolia* (D–E), both from south western Africa: A, fresh leaves in habitat are ovoid to globose, their surface with dark green dots. Internodes are smooth; B, smooth internode to the left and a petiole with a narrow pseudostipule pointing to the right; C, typical operculum with a prominent rough rim pulled together on top, supported by a base pulled in at its top, forming a puffed sleeve shape; D, ovoid to club-shaped or globose leaves with dark green dots characterize the species; the small flowers attract possible pollinators by forming attractive patterns, including here purple anther walls and yellow pollen forming a ring of dots in the open flower; E, In contrast to *T. corymbosa*, the leaves possess broad and conspicuous pseudostipules, ending in a sharp tooth here; F, The rim of the operculum is less prominent and the sides are somewhat straight, perhaps due to early drying. A & B from Hartmann & Potgieter 32657; C from Goldblatt 1861; D from Hartmann 32889; E & F from Hartmann 34678.

vata (fig. 5C), *T. mozambiquensis*, *T. parvifolia*, *T. sedifolia* (fig. 7G), *T. triquetra* (fig. 2E), and *T. ufoensis* develop such tepals.

In summary, it must be remembered that assessing the tepal teeth needs examination of many, preferably fresh flowers and fruits in detail of several samples, requiring ample material at different ontogenetic states.

Flower colour patterns – As in all members of the subfamilies Sesuvioideae and Aizoioideae, the flower has only one series of tepals, lacking petals entirely. Flowers are small in members of *Trianthema* subg. *Papularia*, rarely exceeding 6

mm in diam., and all elements contribute to forming an optical attraction to possible pollinators. Since not for all species detailed information is available, only some typical combinations of character states can be described at the moment.

In the most widespread species in southern Africa, *T. parvifolia* and *T. vleiensis*, a characteristic model can be demonstrated. The tepals in fresh flowers possess a succulent thick subapical protrusion on the outside that shows when the open flower is looked at, presenting a ring of five dark green dots visible to the approaching visitor through the more or less translucent tepal teeth. The background colour of the inner

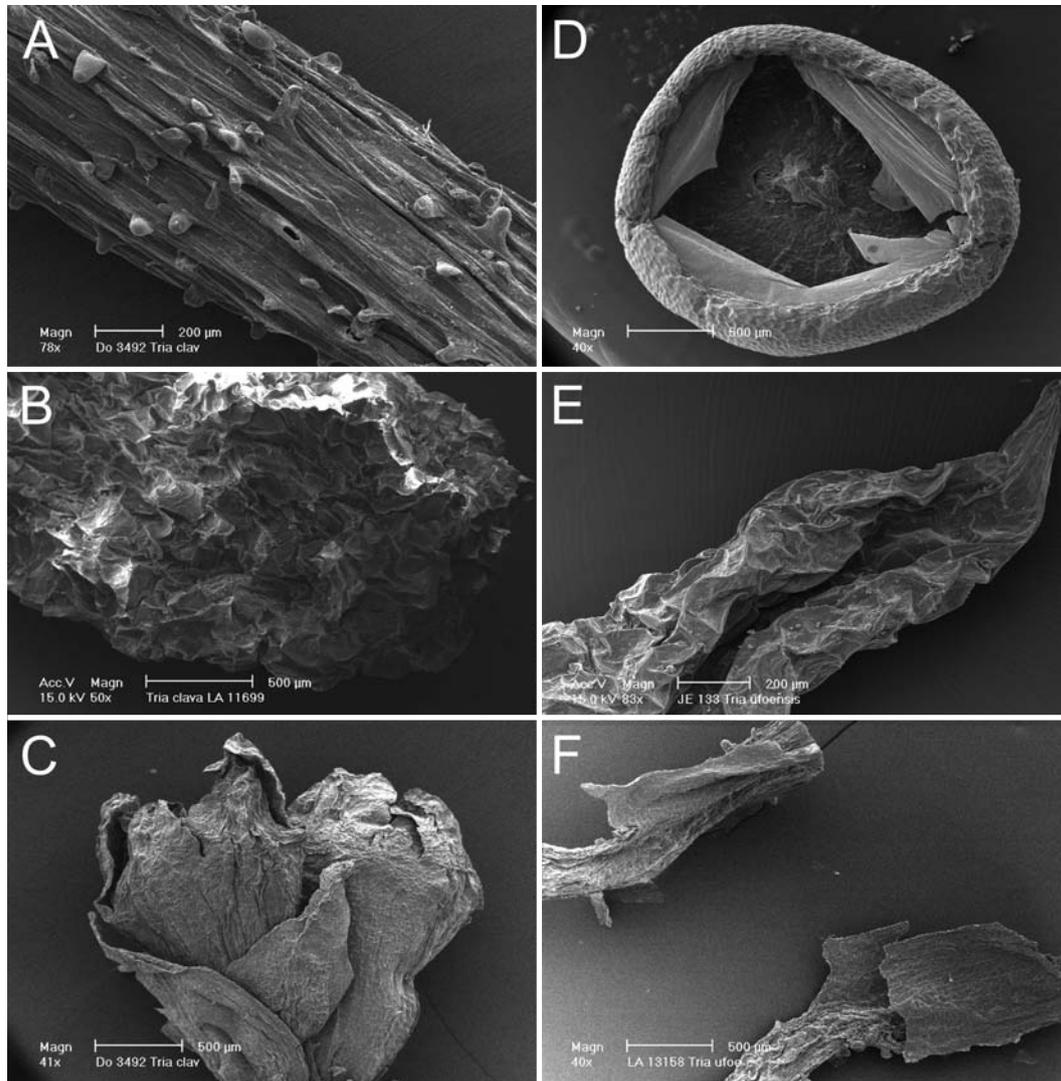


Figure 5 – Comparison of *Trianthea clavata* (A–C) and *T. ufoensis* (D–F), both from Australia: A, small sparsely distributed bladder cells are typical of the internodes, also in *T. ufoensis*; B, the thick leaf blades end in a rounded tip area, the epidermis appears smooth and shiny; C, side view of the inflorescence with an acuminate bract on the left and a similar acuminate bracteole in the middle; the short tepal teeth overarch the hidden operculum; D, view of a typical ripe operculum, the veil has split during the expanding process while ripening; found like this also in *T. clavata*, although only 1–1.5 mm in diam. there; E, leaf ending in a mucro, typical of *T. ufoensis*, showing also the almost smooth leaf surface; F, pseudostipules at the bases of petioles. A, C from *Donner* 3492; B from *Latz* 11699; D from *Short & Dunlop* 4932; E from *Jessop* 133; F from *Latz* 13158.

tepals surface is white or colourless, i.e. a fading green due to the chlorophyll below the epidermis of the inner tepal surface (fig. 4D). The tepal tips can also show some light to darker pink, often more pronounced as a ring around the bases of the tepal teeth or around the tepal tube. The optical ring of attraction is deepened in colour in numerous populations by the formation of purple anthers (fig. 4D), but pink anthers have been found as well. The filaments can be pink, purple, or, in most cases, light yellow, but more conspicuous is the fact that in numerous populations bright orange anthers stand against a paler background colour. Once the anthers open, the pollen is exposed prominently in light yellow, darker yellow, or even in orange. The centre of the flower is marked by a light yellowish-green top of the flower, the later outer rim of the operculum contributing to the pattern of attraction at this state

already (fig. 4D), sometimes changing into dark purple or a light brown (common in *T. ufoensis*, Kapitany 2007).

In the complicated and varying combination of flower colour pattern, no single mode of flower presentation can be seen, but the combination clearly works as an attraction in order to achieve pollination, suggesting strongly that constancy in flower colour pattern is not a means of securing success.

Only in one pair of species have differences in the colour of the inner tepals been used to distinguish species: *T. crystallina* is understood to have small green flowers with diameters about 4 mm whereas *T. sheilae* from the same area possesses bright yellow flowers of 6 mm diameter. It is worth mentioning that *T. sheilae* with usually deep yellow or orange anthers has also been found with scarlet anthers (*Collenette* 5026 E).

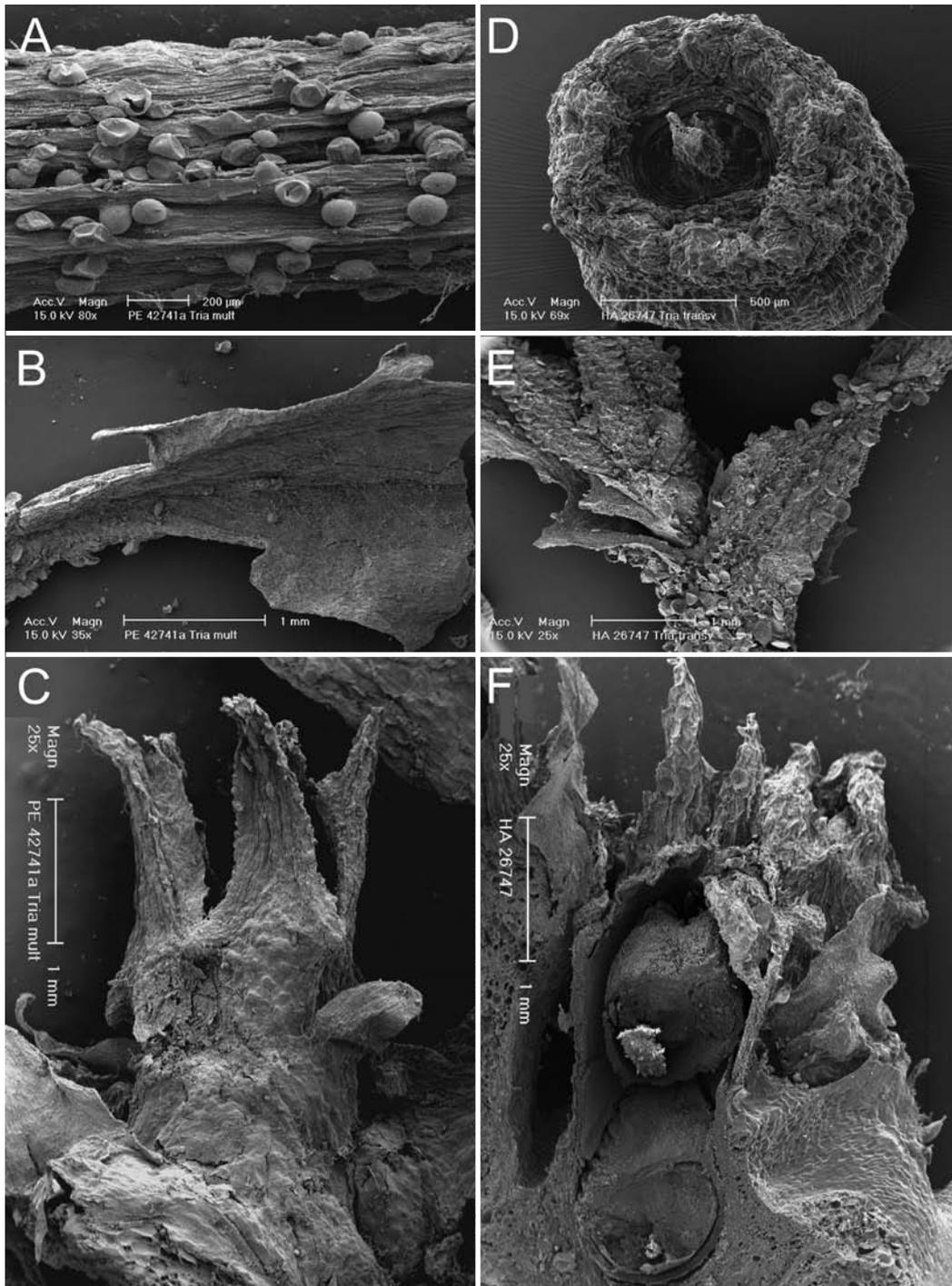


Figure 6 – Comparison of *Trianthema salsoloides* (A–C) and *T. transvaalensis* (D–F): A, small loosely placed bladder cells are found on the internodes of both species; B, the narrow pseudostipules end in a tooth each; C, side view of the flower embedded in the base of the inflorescence, on the left the bract has broken off, on the right the bracteole splits away from the solid base; note the erect very long free tepal tips with many small bladder cells on them; D, operculum with a broad rim on top of almost straight sides; E, node with petiole and its pseudostipule, more narrow than that of *T. salsoloides* and equipped with bladder cells, like the leaves to the upper left; F, section through a flower embedded in the base of the inflorescence, showing two seeds on top of each other, note the erect very long free tepal tips with many small bladder cells on them. A, C from Peter 42741b; B from Hartmann & Newton 21344; D–F from Hartmann 26747.

Overall, it seems that populations follow the same pattern of flower colouring, but it seems at the same time that no strict colour patterns can be related to species as such.

Number of stamens – No more than five stamens have been

found in any of the flowers examined, but in some species a reduction can be observed: *T. sedifolia* and *T. corallicola* possess only 2–3 stamens whereas *T. argentina* has a single stamen mostly, two being rare. Variable appears the situation

in *T. salsoloides*: a single stamen has been found in Kenyan material, two in Tanzanian, but “five or fewer?” in Sudan (*Kotschy* 137, only two found in the isolectotype material, B).

Operculum – As in most members of the subfamily Sesuvioideae, the fruit of *Trianthema* is a pyxidium, forming an operculum as a lid for the ripe dry capsule, lifting the lid when dry enough, exposing the seeds. In the ontogeny, the surface of the gynoeceium in members of *Trianthema* subg. *Papularia* appears flat at first, but early on, the centre seems to be sinking because the rim grows into a broad roll or bulge, like in a certain type of clay bowl. Rarely, the surface resembles a crater with a sharper outer edge with age, as described for *T. argentina* (Hunziker & Cocucci 1959).

In most species, the inner bowl of the operculum is visible, but in young fruits of *T. clavata* and *T. ufoensis*, both from Australia, a layer like a sail is spread over the bowl-shaped inner part of the operculum, hiding the actual surface at first, the stigma protruding through that layer. The veil or velum splits open with growth and expansion of the outer rim, exposing the remaining deeper surface (fig. 5D).

The feature has not been found in other species, but in *T. pakistanensis* (fig. 3D) and *T. triquetra* from India and Pakistan as well as in *T. sedifolia* and *T. sheilae* from northern Africa, a layer at the bottom of the bowl can be seen, suggesting a similar yet less expansive shrinking of the top layer, resembling in structure linen material creased in a circular arrangement. Rarely, some small splits can be seen (*T. sheilae*, fig. 1H).

Four different ontogenetic developments of the fruit including the operculum can be distinguished.

In type 1, a broad rounded outer rim is formed in the opercula of most species, about 400 µm in thickness in young fruits and about 200 µm in old ones, covered by more or less smooth cells and leaving the centre always free. This type of operculum widens conspicuously during the ontogeny, reaching up to 2 mm in diam. and always pushing the rather short tepal teeth outwards while they envelop the rim, the teeth forming a partial cover over the dry ripe fruit (fig. 7G). The centre of the operculum starts off with a small hollow space, resembling the imprint of a thumb with soft slopes. In most cases, these rims are broad and prominent, rough and distinct from the bottom part in *T. crystallina* and *T. sheilae* (fig. 1H). In *T. mozambiquensis* (figs 11D–E), *T. pakistanensis* (fig. 3D), *T. triquetra* (fig. 2E) and *T. sedifolia* (fig. 7G), the rim remains smooth or turns only slightly rough. Independent from the width of the operculum, the base of the pyxidium itself often tapers somewhat towards the base, leaving the fully grown operculum as the widest portion of the whole fruit.

In *T. argentina* (fig. 1D), the slopes become steeper and the central basin wider, resulting in a broad crater- or bowl-shaped central deepening with a smooth surface, the base of the pyxidium also tapering towards the base (Hunziker & Cocucci 1959).

In type 2, the operculum does not widen conspicuously, as is visible in *T. salsoloides*, *T. sanguinea* (fig. 7C), and *T. transvaalensis* (fig. 6D), i.e. the rough rim sits on top of more or less straight sides of the operculum, the tissues of the rim and the sides are uneven and similar to each other. Such opercula are usually equipped with rather long and almost erect

pyxidium bases (fig. 7C), equalling the diameter of the operculum or exceeding it only a little.

In type 3, the rim of the operculum remains narrow while the base of the operculum widens conspicuously, the whole top piece resembling a puffed sleeve; similar to type 2, the tissue of the rim differs clearly from the bottom part, visible in *T. corallicola* (fig. 8G) and *T. vleiensis* (fig. 9D). This type of operculum is correlated with a medium long base of the pyxidium (figs 8C & 9G), as opposed to the wide pyxidium in type 1 (fig. 5D).

In type 4, the operculum exposes a smooth basal portion with straight or concave sides overtopped apically by a rim formed by a broad band of much rougher cells as if crocheted with thicker material and a bigger needle. This top can remain sleeve-like or become flat resembling a ruff as worn by Hanseatic ministers and senators in shape, but not pleated. The opercula of *T. parvifolia* (fig. 4F), *T. corymbosa* (fig. 4C), and *T. hereroensis* (fig. 10D) show this type; the difference in the rough upper rims is similar to that found in type 3.

The opercula fall roughly into three size classes: diameters of 1.5–2 mm have until now only been reported for *T. argentina* and *T. ufoensis*, diameters above 1 mm but below 1.5 mm in *T. clavata* and in *T. mozambiquensis*, and diameters of about 1 mm in all other species. The differences in height can be great since, in lateral view, most opercula appear oblique, due to the fact that they differ in height depending on the position in the inflorescence. Pressure from one side can reduce the height distinctly, but in all cases a horizontal position of the operculum top is achieved.

Seeds – Two seeds are usually found in a pyxidium of *Trianthema* subg. *Papularia*, placed on top of each other (fig. 6F), the top one in some species enclosed almost completely by the operculum and hence carried away with it (e.g. *T. ufoensis*). In many species, however, the two seeds are dispersed as a double package (e.g. *T. sedifolia*, fig. 7H), sticking together at their flat contact zones for some time. This contact area can be flat or even smooth, but the opposite outer side can bear some ornamentation in the shape of ridges or crests. As long as the aril covers the seed, the crests are smooth-edged and soft (figs 7D & H, 8D), later they appear more sharp-edged and more distinct, especially in the upper region in side view (figs 3E & 11F). The ridges on the side of the seed lie vaguely semi-circular, but they can also stop short or deviate from the regularly bending shape. Differences and variation are much less than in the species of *Trianthema* subg. *Trianthema* (Hasan et al. 2005a, Prescott 1984).

A single seed per pyxidium is reported for *T. salsoloides* from NE Africa, a species very similar to *T. tranvaalensis* from NE South Africa, in which latter often an abortive second seed is found.

Smooth seeds have been found in samples of *T. sedifolia* (fig. 7H), *T. hereroensis*, and *T. corallicola* (fig. 8D & H), but some seeds with low ridges have also been met with in these species.

Ripe seeds are usually dark brown to black, the shape in side view is oval to almost circular, the edges appear rough in *T. clavata* and *T. ufoensis*. The maximum length of seeds lies between 0.8 and 1.4 mm, permitting some groupings of species: smallest seeds of 0.8–0.9 mm have been found in *T.*

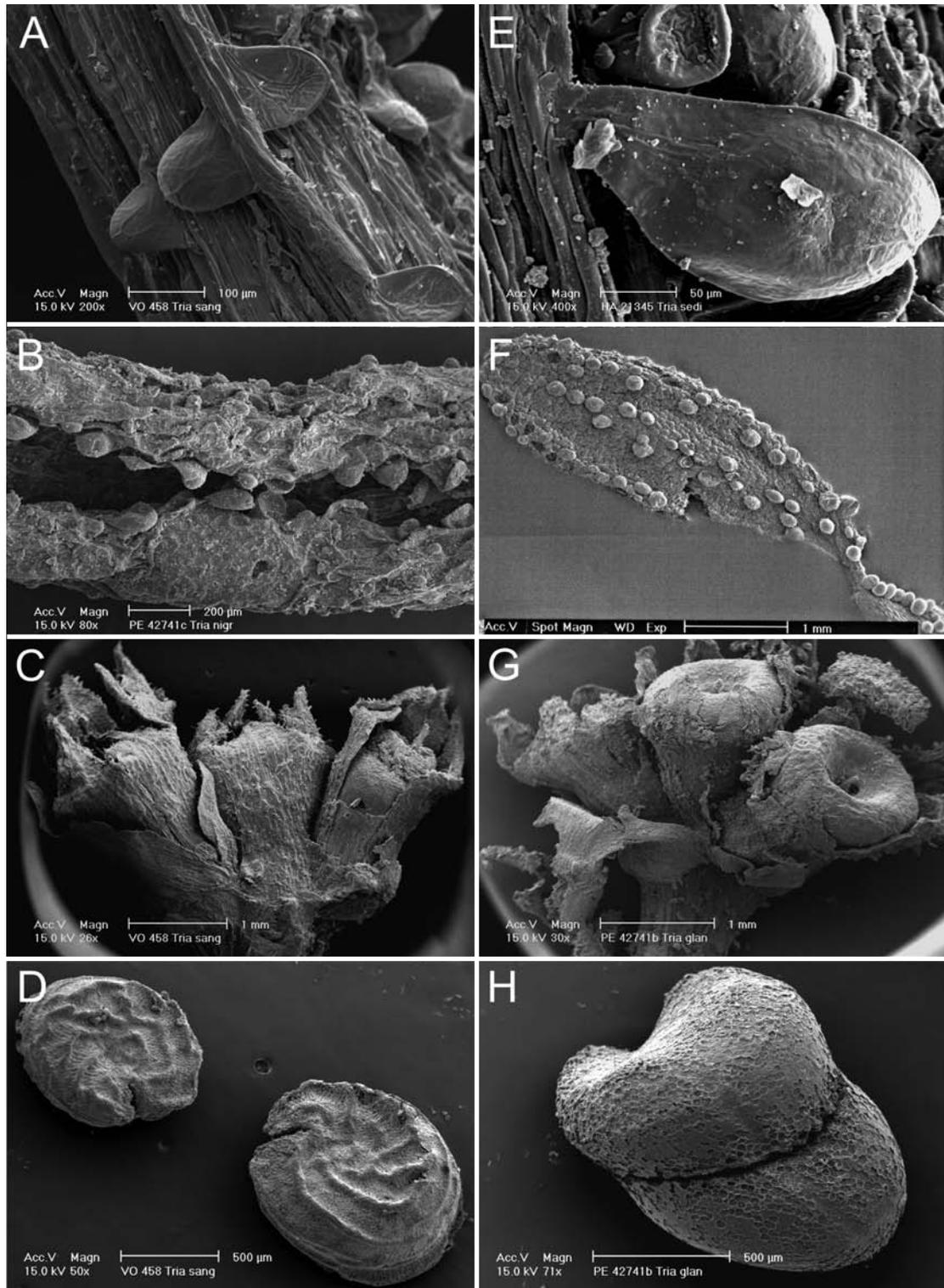


Figure 7 – Comparison of *Trianthema sanguinea* (A–D) and *T. sedifolia* (E–H): A, sparsely distributed bladder cells of about 100 µm sit with a broad base in the epidermis; B, bladder cells on leaves are restricted to the margins of the blade; C, flowers are free in the inflorescence, each with an acuminate bract and usually two bracteoles, one visible near the middle; note the well developed elongate papillae on the more or less erect tepal tips; D, most seeds show meandering ridges on their sides; E, the ovoid bladder cells of the internodes reach almost 200 µm in length and sit with a small area only in the epidermis; F, few big bladder cells of up to 200 µm are found on the leaf blade; G, the almost ripe pyxidia are enclosed by the overarching tepal teeth, here still a little papillate, smooth later; H, in unripe pyxidia, twin packs of seeds can be seen sticking together over their contact zone; they separate with the disintegrating aril, a feature typical of most members of *T.* subg. *Papularia* (exception: *T. salsoloides*). A, C & D from *Volkens* 458; B from *Peter* 42741c; E from *Hartmann & Newton* 21345; F from *Hartmann* 21532; G, H from *Peter* 42741b.

parvifolia and *T. corymbosa*. Medium sized seeds of 1–1.2 mm length predominate in *T. corallicola*, *T. mozambiquensis*, *T. pakistanensis*, *T. sanguinea*, *T. sedifolia*, *T. sheilae*, and *T. vleiensis*. Big seeds of 1.3 mm minimum length, reaching up to 1.5 mm, have been found in *T. argentina*, *T. clavata*, *T. triquetra*, *T. transvaalensis*, and *T. ufoensis*. There are overlaps between the size classes, and seeds alone cannot be used to identify a species.

DISCUSSION

Considerations on possible morphological evolutionary trends and groupings

The results of this morphological analysis confirm the circumscription of the genus *Trianthema* sensu Jeffrey (1960) as the material is distinct in having a single stigma on top of a complete and undivided operculum. This synapomorphy separates the genus clearly from the genus *Zaleya* sensu Jeffrey (1960) with the possession of two stigmas and an operculum breaking longitudinally into two halves. Both genera share the basic character state of developing only four seeds per fruit, placing the two genera as a sister group to the many-seeded genera *Sesuvium* and *Cypselea*. Morphologically, these four genera can be grouped together based on the feature “pyxidium” as the principle fruit construction.

The subdivision of *Trianthema* into two subgenera as introduced by Jeffrey (1960) finds its foundation in the basic formation of single-flowered inflorescences for *T. subg. Trianthema* as opposed to members of *T. subg. Papularia* with richer inflorescences and a reduction in seed number to two, and even below. Seeds can be more numerous in *T. portulacastrum* (*T. subg. Trianthema*, 3–12, Prescott 1984), a state that may be secondary in view of the fact that both, *Zaleya* and *Trianthema*, are thought to have started with only four ovules per fruit. In *T. subg. Trianthema*, a reduction to two or even one seed (Prescott 1984) is reported for some species, especially in a distinct group of species characterized by hairy surfaces, hence understood to represent secondary reduction within *T. subg. Trianthema*. This does, however, not invalidate the fact that members of *T. subg. Papularia* never form more than two seeds, this being a fundamental synapomorphy for the subgenus.

Whereas the opercula and the seeds show a wide variation in the Australian species of *T. subg. Trianthema* (Prescott 1984), also being distinctive and obvious per species, the members of *T. subg. Papularia* have been summarized until now under few species names since, in comparison, the shapes of the opercula and the seeds are much more homomorphous. The present morphological results, however, demonstrate that the bowl-shaped opercula are a synapomorphy for the entire subgenus: the shape of the young gynaecium shows a very broad and rounded rim with only a small central deepening holding the single stigma at the apparently sunken base. While the pyxidium ripens, the solid rim grows into a broad apically rounded wall resembling old earthen fortifications; the bottom spreads below, sometimes ending in the shape of a volcano or even a dining plate (e.g. *T. argentina*), in any case remaining solid and never wing-shaped, a version found in *T. portulacastrum*, appearing irritating at first sight

in *T. subg. Trianthema*. It may be mentioned that a circular thin flap-like wing is also found in *T. megasperma* in the latter subgenus, generally spreading sideways from the globular pyxidium (Prescott 1984).

Within *T. subg. Papularia*, seventeen species can be distinguished and described, based on unique combinations of character expressions. Furthermore, groups of species can be recognized in some cases in which distinctive character states are shared.

Group 1 stands out in having big globose bladder cells of about 160 µm in dense or looser arrangement on the internodes and of about 200 µm diam. in a dense layer on leaves and tepal teeth, forming a secondary surface on the two latter organs, both apically rounded. *T. argentina* (fig. 1A–C), *T. crystallina* (fig. 2A–C) and *T. sheilae* (fig. 1E–G) belong in this group, the first differing from the other two by being annual, developing rather narrow flaps along the petiole, and by forming opercula of 1.5 mm diam. with rather low sharp rims when ripe.

T. crystallina and *T. sheilae*, in contrast, share a finally shrubby growth, although they can also flower in their first year, the possession of lacinate broad and conspicuous flaps along the petioles, and in the formation of opercula with broad rims with rough surface cells equipped with low almost straight sides exposing a central deepening of about half the diameter of about 1 mm; in the hole, a wrinkled layer can be seen (fig. 1H), like in *T. sedifolia*. Since the two former species differ only in their flower colour and diameter, it seems possible that the rank of species may be inadequate for the two taxa. To assess this, more and especially living material will be needed.

Group 2 is characterized by the development of very rough rims of the operculum, consisting of big elevated cells, resembling a short crocheted sleeve made up of thicker material knitted with a thicker needle. In some cases, the rim lies flat towards the sides, possibly a feature developed later during the ripening.

T. corymbosa (fig. 4C), *T. hereroensis* (fig. 10D) and *T. parvifolia* (fig. 4F) belong here, each with a distinct apomorphy. *T. corymbosa* (fig. 4C) is the only deciduous taxon known until now in *T. subg. Papularia*. *T. parvifolia*, on the other hand, is unique in keeping the prominent broad flaps along the petioles longer than the blades on the persisting stems (fig. 4E). In this species, however, the northern populations are of uncertain taxonomic rank. The occurrence of bladder cells in such samples might indicate that another taxon at species rank may possibly be found, but the amount of available material and data from northern Namibia and southern Angola is too little to permit a decision at this state. *T. hereroensis* (fig. 10D) can be distinguished by its acuminate leaf tips

Group 3 comprises plants with a distinct clear longitudinal green line along the entire upper leaf surface, white in translucent light and dark green in incident light. In contrast to groups 1 and 2, the leaf tips are acuminate and hence pointed and the tepal teeth possess prominent bulges at the base of the incisions between them. *T. transvaalensis* and the new species *T. vleiensis* (fig. 9E) can be placed in this group, sharing also the possession of tepal tips up to 1 mm in length adorned

with elongate papillae. *T. vleiensis* forms most striking opercula shaped like short puffed sleeves with a rather narrow rim on top of a basally widening base of the operculum, clearly a synapomorphy of the species (fig. 9G). The species has shiny smooth leaf surfaces and only few bladder cells on the internodes and rather wide flaps along the petioles. *T. transvaalensis* differs distinctly in forming compact solid bases of the inflorescences into which the bases of the flowers appear to be sunken (fig. 6F), with bracts and bracteoles on the solid tissue of the compact bases. The operculum has straight sides ending in a somewhat broader rim on top, the cells inconspicuously rough and not as distinct as in *T. vleiensis*; of the two seeds per pyxidium, one is often abortive and reduced in size in *T. transvaalensis*, which also is remarkable in having elongate papillae on leaves and internodes.

T. salsoloides may also belong in this group, showing all features described above for *T. transvaalensis* except for the fact that a single seed is found in the former species. A final decision cannot be taken yet because no fresh material allowing an assessment of the upper leaf surface is available.

Group 4 deviates from all others in the formation of a veil over the operculum, covering the interior completely until it splits when the width of the operculum has reached its final size of about 1.5–2 mm, the largest known in *T.* subg. *Papularia*. This unique feature has only been found in *T. clavata* and *T. ufoensis* (fig. 5D), both from Australia, and it is correlated with a purple colouring of the ripening operculum. The two species differ in their leaf shapes: *T. clavata* being clavate with a rounded tip, *T. ufoensis* with a pointed tip ending in a distinct mucro that will break off when old. Upper leaf surfaces of *T. clavata* can show shorter or longer dark green lines resembling those of group 3, but the lines never cross the entire leaf lengthwise and samples can be seen with short dark green lines made up of rows of dark dots, resembling rare conditions in *T. parvifolia* and *T. corymbosa*.

Group 5 comprises those species that develop only short tepal teeth overarching the operculum for most of the time but not covering it completely while lacking a veil as described for group 4: the broad rim always remains visible under a lens. *T. triquetra* and *T. pakistanensis* share this feature with *T. sedifolia*, which latter, however, shows a sparse distribution of bladder cells as big as those of group 1, 200 µm wide on the round-tipped leaves and the internodes. All three species exhibit the deep-lying inner surface of the operculum wrinkled in a ring as a common feature as well. The bladder cells on internodes of *T. triquetra* and *T. pakistanensis* (fig. 3D) are very loosely distributed and much smaller than those of *T. sedifolia*, reaching only 100–120 µm. The newly described species *T. mozambiquensis* can best be placed in this group, too, because at first sight, it resembles *T. sedifolia* like an identical twin in pyxidium shape and internode ornamentation with bladder cells, the two species differing prominently in the shapes of the pseudostipules.

The new species *T. corallicola*, on the other hand, cannot be placed in any of the groups, deviating from all other known species in having a more or less dense cover of bladder cells growing as long as 500 µm on the internodes, covering it like fur, the longest ever found in *T.* subg. *Papularia*. The leaves and the tepal teeth are also hairy, especially the

tips, but these bladder cells reach only 200 µm in length (fig. 8). The opercula shaped like puffed sleeves resemble those of *T. vleiensis* most closely, which, however, lack prominent bladder cells completely on the leaves and show only a very sparse occurrence of small globose bladder cells on the internodes.

In summary, the presently accepted species can be distinguished and described reliably, but groups are not necessarily clear-cut since too many similarities exist that could be interpreted as apomorphies as well as parallel evolutionary lines. For the first time, emended descriptions on a worldwide base are presented, for which a reliable key can be offered.

Considerations on phylogeography

The great majority of populations of the whole genus *Trianthema* has been found in a broad belt around the globe between 35°N and 35°S, the subgenera showing a wide overlap for most areas. The greatest variety of species and of character states is documented for *T.* subg. *Trianthema* in Australia (Prescott 1984). Only two very distinct species occur isolated outside this region: *T. hecatandra* in northern Venezuela, South America (Wingfield & Newman 1994) and *T. ceratosepala* in Tanzania, Africa (Volkens & Irmischer 1913). In addition, *T. portulacastrum*, for which synonyms from Ethiopia, Ghana, and India are known (Hartmann 2001), has a very wide distribution area, coinciding for its greater part with the distribution area of the whole genus.

When the investigation in *T.* subg. *Papularia* was started, the species *T. triquetra* was understood to be almost as widely distributed as *T. portulacastrum*, occurring in Australia, SE Asia, Arabia, northern Africa and southern Africa (fig. 12). In this circumscription, however, the species contained highly different plants in each region, as discussed in the introduction. At the end of the investigation, it can be documented that species boundaries had to be re-assessed to comprise identifiable units with similar members, these having in general a much smaller distribution area, and none of the newly circumscribed nor any of the re-established species can be found on different continents (fig. 13).

The high species diversity in *T.* subg. *Papularia* found in NE Africa and the adjacent SW part of the Arabian Peninsula is remarkable: *T. corallicola*, *T. sanguinea*, *T. salsoloides*, *T. sheilae*, and *T. crystallina* occur only in this region whereas *T. sedifolia* has also been reported from western north Africa (fig. 13). These six species do, however, not share common characters at a higher level within the subgenus but exhibit some striking similarities with species found only outside this region.

Most striking is probably the agreement in the possession of rounded leaves with big bladder cells forming a secondary cover over the leaf, the same arrangement on the tepal teeth, and the occurrence of such big bladder cells also on the internodes between *T. argentina*, the only American species of the subgenus, growing in a restricted area in the district of La Rioja, Argentina, at about 530 m altitude, and *T. crystallina* and *T. sheilae* from NE Africa and the SW of the Arabian Peninsula at altitudes ranging from 0 to 1,500 m (group 1 above).

On the other hand, the same big bladder cells of about 200 mm diameter are also known from *T. sedifolia* occurring on the internodes and the leaves, yet very sparsely distributed on the latter (fig. 7F). Notable is the wide distribution area of *T. sedifolia*, suggesting that conditions in NW Africa have been less favourable for speciation than those in NE Africa. But the actual geographic pattern can also be a result of an invasion from west to east in northern Africa or vice versa.

Since a new species similar to *T. sedifolia* was identified as far as away as Mozambique, namely *T. mozambiquensis*, the geographical relations have to be studied in more detail once fresh material is available.

Another line of thought can be developed from the fact that group 1 members share the rounded leaf tips with two members of group 2 in southern Africa: *T. parvifolia* and *T. corymbosa*. These two species with smooth internodes and orbicular to globose leaves showing dark green dots on their surfaces differ not only in their morphology but also in their distribution: *T. corymbosa* is only found in the very dry rocky mountains along the lower Gariep River where it is exposed to winter rainfall, a region in which the very widespread *T. parvifolia* does not grow. This pattern seems to reflect a single adaptive trait in a highly specialized surrounding determined by high geological diversity. *T. parvifolia*, however, settles in highly disturbed and often temporarily open places, e.g. yards of farms or river banks, where it can live over many years if not covered by other vegetation. A taxonomic problem lies in the fact that northern populations tend to develop bladder cells and elongate oval to ovoid blade shapes. Yet, such deviations are not correlated beyond population level, and material is too little to reach well-founded conclusions.

A species with a very restricted area of distribution is represented by *T. hereroensis*, found near the coast in the Namib, separated from populations placed in *T. parvifolia* but widely surrounded by that latter species. Material known until now is reported to grow in river sand, suggesting that soil conditions may restrict the suitable region in which the species can settle.

Beside the similarities in the groups discussed above, more species are found in southern Africa that can be related to other species in NE Africa: *T. salsoloides* in Kenya and Tanzania and *T. tranvaalensis* in Zimbabwe and north-eastern South Africa share the shapes of the tepal teeth with basal bulges and bladder cells on the tips as well as the position of the flowers inside tissue formed by the base of the inflorescence plus an elongate pyxidium taller than wide. Since the two species differ (e.g. in one respectively two seeds per capsule) and are separated by a gap in distribution well over the equator, it can be suggested that they may represent the result of a splitting of an originally compound area, including migration towards the ends of the range with an incidental establishment of different character states.

Notable is the fact that another species agrees in its dark green line over the upper leaf surface with *T. transvaalensis*: *T. vleiensis*, differing from the former mainly in the smooth leaves and the distinctly puffed sleeve-shaped operculum. The two species grow in adjacent areas, but never sympatrically, *T. vleiensis* being restricted to saline pans with pH values of 7–8 in the northern central area of the Great Karoo, a high-

lying plateau in southern Africa (fig. 9A). *T. transvaalensis* grows in much disturbed open places with sparse vegetation. It can be imagined that such a habitat was originally inhabited, the migration to more specialized habitats having been a later step in evolution.

The detection of a new species in NE Africa, *T. corallicola*, brings to mind the possibility of a parallel evolutionary step at the other side of the range of the *T. salsoloides-transvaalensis* bridge. With the formation of long bladder cells like hairs half a millimetre long on the internodes, it stands out in *T.* subg. *Papularia* and does with this feature undoubtedly present the synapomorphy of the species. Yet, the possession of an operculum of short puffed sleeve shape resembles a character state found in *T. vleiensis* occurring southwest of *T. transvaalensis* in South Africa. *T. corallicola* grows coastal and can be understood to represent an adaptation to its habitat of coral deposits along the coasts of Somalia and northern Kenya, also in saline places like *T. vleiensis* growing inland.

Mention must also be made of *T. sanguinea*, a species overlapping in area with *T. salsoloides* in Kenya and Tanzania. *T. sanguinea* differs from the latter in having free flowers and shorter tepal teeth bearing elongate bladder cells. Both species share the opercula with straight sides and a clear distinction between the rougher rim and smoother lateral tissue (fig. 7C). Both species share also the possession of small bladder cells dispersed loosely over the internode surfaces and the leaves, preferably along the margins, but no geographical or environmental factors have been identified to explain reasons for a possible evolutionary separation.

None of these African species can in any way be closely related to material from southern Asia and Australia, based on morphological evidence. All four species from this wide area share the possession of only small bladder cells sparsely distributed over the internodes and smooth leaves, and of short tepal teeth overarched the more or less widely expanding operculum during the ripening process, pushing the tips of the tepal teeth aside. The Australian species *T. clavata* and *T. ufoensis* share a unique character expression: a sail-like cover or veil, hiding the sunken interior of the operculum from view in the young fruit, splitting later while expanding in dimension up to 2 mm, the widest diameter measured in *T.* subg. *Papularia*. This is certainly a synapomorphy of the group, suggesting a common origin by settlement of the ancestor in an outlier of the original wider distribution area. The distribution areas of the two Australian species lie closely together, apparently even overlapping, and some populations are confusing in showing mixed character expressions, indicating that speciation may not be complete at this stage.

The two south Asian species share the possession of opercula smaller than those of the Australian material and a strict adherence to only three veins supplying the tepal teeth; further, they lack the veil over the interior of the operculum and form acuminate leaf tips, neither rounded like in *T. clavata* nor mucronate like *T. ufoensis*. It is at present impossible to suggest a synapomorphy for the group, partly due to severe lack of material for comparison. Populations from around the Gulf of Bengal are placed here, but reservations are expressed as to the reliability of the positions since most of the material is old and incomplete. It can, however, be pointed out that

 Artificial key to the species of *Trianthema* subg. *Papularia*

1. Operculum with a horizontal veil held by the outer rim of the wide central deepening; plants only found in Australia.....2
 - 1'. Operculum without a veil, the concave base openly visible; plants found outside Australia.....3
 2. Leaf blades ovoid with a rounded tip, operculum 1–1.5 mm wide.....2 *T. clavata*
 - 2'. Leaf blade with a hyaline mucro, breaking off with age, operculum about 2 mm wide, resembling a UFO in shape.....16 *T. ufoensis*
 3. Leaf blades and tepal teeth covered completely by big globose bladder cells.....4
 - 3'. Leaf blades and tepal teeth smooth from inconspicuous bladder cells or acuminate bladder cells as short hairs in loose arrangement6
 4. Inflorescence with a fimbriate bract and bracteoles, stamens five.....5
 - 4'. Inflorescence with a tiny acute bract and similar bracteoles, a single stamen, rarely two; only in Argentina1 *T. argentina*
 5. Tepals yellow inside, flowers 6 mm wide; reported from NE Africa, SW Arabia and Yemen13 *T. sheilae*
 - 5'. Tepals green inside, about 4 mm wide; recorded only from SW Arabia and Yemen.....5 *T. crystallina*
 6. Plants deciduous in the dry season, pedicels elongating during fruit ripening; only near the mouth of the Gariep River in South Africa and Namibia.....4 *T. corymbosa*
 - 6'. Plants with leaves during the dry season.....7
 7. Flowers basally embedded in the bottom of the inflorescence, the inflorescence breaking off as a whole; bases of tepal teeth forming prominent bulges on the otherwise straight erect long sides of the flower.....8
 - 7'. Flowers basally free, breaking off individually; without or with inconspicuous bulges at the bases of the tepal teeth.....9
 8. Two seeds per pyxidium, sometimes the basal one not fully developed; from S Zimbabwe through the old Transvaal Province and into KwaZulu/Natal, South Africa.....14 *T. transvaalensis*
 - 8'. Only one seed inside the pyxidium; in a N–S band through the west of Kenya and Tanzania.....10 *T. salsoloides*
 9. Internodes and leaf blades with elongate acuminate bladder cells like hairs visible to the naked eye; only along the southern coast of Somalia and the northern coast of Kenya.....3 *T. corallicola*
 - 9'. Internodes with low and inconspicuous bladder cells, never eye-catching.....10
 10. Pseudostipules along petioles narrowing gradually from the base to the blade.....11
 - 10'. Pseudostipules along petioles broad and wide, separated distinctly and ending well below the blade.....12
 11. Tepal teeth more or less smooth, connivent over the operculum; around the Gulf of Bengal.....15 *T. triquetra*
 - 11'. Tepal teeth always with bladder cells; in Pakistan and adjacent parts of India.....8 *T. pakistanensis*
 12. Pseudostipules to both sides of the petiole rounded, the pair forming a broad ellipse; tepal teeth as long as the basal tepal tube, erect; only known from sandy riverbeds in Namibia near the coast.....6 *T. hereroensis*
 - 12'. Pseudostipules more or less angular, broad and spreading, usually ending in a short broad tooth.....13
 13. Tepal teeth straight with distinct small finger-shape bladder cells.....14
 - 13'. Tepal teeth curving over the pyxidium top to various degrees.....15
 14. Operculum with a smooth broad rounded rim; only in SE Kenya and adjacent parts of Tanzania.....11 *T. sanguinea*
 - 14'. Operculum shaped like a puffed-sleeve; only in the central plateau of South Africa.....17 *T. vleiensis*
 15. Base of leaf persisting as a white sheath with several layers of pseudostipules along the stem; from Namibia to the Great Karoo in South Africa.....9 *T. parvifolia*
 - 15'. The pseudostipules at the base of the leaves short-lived and brittle, decaying soon.....16
 16. Pseudostipules ending in a rectangle pointing outwards; only known from coastal southern Mozambique.....7 *T. mozambiquensis*
 - 16'. Pseudostipules with an oblique edge adorned with a short tooth more or less in its middle; from Morocco to SW Arabia and Yemen.....12 *T. sedifolia*
-

seed sizes of 1.4 mm in *T. triquetra* reach the range of the two Australian species, and it must be mentioned that it cannot be excluded that this species may indeed have reached the western coast of Australia, based on a collection not clearly identifiable as either *T. ufoensis* or *T. clavata* from that region (Western Australia, Warambie Sta., Roebourne, 31 Mar. 1931, Meares 21, K). *T. pakistanensis* grows in an area well separated from *T. triquetra* and can be distinguished by its short bladder cells on the petiole as well as on tepal tips; seeds are 1 mm long, i.e. smaller than those of *T. triquetra*. If the gap in distribution between the two species can be filled by new material, it may be found that the two units are only minor taxa rather than species. Again, lack of material hinders an assessment at the moment.

The two species share features of the operculum and the tepal teeth with *T. sedifolia* from northern Africa; it must remain open at this date whether a common ancestor can be considered to have existed, and it is hoped that material will become available in order to undertake molecular studies.

While for *T. subg. Trianthema*, Australia can be identified as a centre of diversity in species and in character states, such a centre for *T. subg. Papularia* cannot be detected in Africa, based on morphological data. Six species have been identified in NE Africa until now, and with six species found in southern Africa, the two regions keep a balance. None of these twelve species has been found in both African subregions, nor can morphological features be named that would suggest a common origin of either geographical species group. Instead, the widespread species *T. sedifolia* in the north appears most similar to SE Asian species and those in Australia, plus *T. mozambiquensis* in SE Africa. This group shares broad-rimmed opercula and short tepal teeth overarching the ripe operculum. If indeed these species had a common ancestor, the wide distribution area and the fact that the included species are distinctly separated and overlap only partially might point towards a long evolutionary history combined with wide migrations routes.

A long time for the evolution of new species could also be speculated for those species that share opercula widening below a prominent rim, forming puffed-sleeve shapes in various formations. *T. corallicola* in NE Africa shares this feature with *T. vleiensis* in the south of the continent in very distinct expression. In addition, *T. salsoloides* in the north and *T. transvaalensis* in the south probably belong with the same morphological type, yet with straight bases of the collected rough rims; to this latter form, *T. parvifolia* appears most similar, close to which *T. corymbosa* and *T. hereroensis* can be grouped as well.

A third evolutionary line with *T. sheilae* / *T. crystallina* in northern Africa and *T. argentina* in South America appears to be separated from the other two, based on the extensive cover of big bladder cells on all green surfaces.

At present, it seems impossible to relate morphological features directly with geographical distribution patterns of species groups, hence further speculations are deferred until molecular work (in progress by the authors) might indicate relationships that cannot be established on morphological grounds alone.

In summary, these expanded morphological studies reveal that almost all species needed a new circumscription, resulting in completely different distribution patterns in comparison to older approaches. The vast extension of characters analysed permitted a balanced assessment allowing also first speculations regarding the possible evolution within the subgenus and leads to a taxonomic treatment that forms a blueprint for further studies in the much neglected genus *Trianthema*.

TAXONOMIC TREATMENT

Trianthema L. subg. *Papularia* (Forssk.) Jeffrey (Jeffrey 1960: 237). – Type: *T. crystallina* (Forssk.) Vahl.

Annual to perennial plants, perennial plants also flowering as annuals in several species, rarely deciduous, branches erect, decumbent, procumbent, but never with adventitious roots, internodes densely to sparsely papillate from bladder cells, smooth and woody with age, white over yellow to brown and black. Leaves with more or less prominent and elaborate pseudostipules along the petiole, blades always wider than thick, epidermis with prominent to inconspicuous bladder cells. Inflorescences rather dense appearing axillary and almost compact, with five and more flowers, only in young plants also at first single-flowered. Flowers with subapical thickenings or subapically placed enations overtopping the actual tepal tip in shape of acuminate protrusions on the free tepal teeth, the tepal bases forming a tube connate with the base of the unilocular ovary, containing 2 ovules, rarely only one. Stamens 1–5 in alternitetalous positions, never more stamens, anthers and pollen often in contrasting bright colours; gynoecium with a single stigma in the centre which is surrounded by a broad solid rim around its outer edge. Fruit developing into a pyxidium, the operculum always with a prominent persisting rim, the base either with vertical sides or oblique after the rim has been pulled together like a puffed sleeve. Seeds mostly two on top of each other, rarely only one.

1. *Trianthema argentina* Hunziker & Cocucci (Hunziker & Cocucci 1959: 17). – Type: Argentina, La Rioja, Gral. Ocampo, Ambil, sobre la ruta 79, 18 Feb. 1959, Hunziker, Cocucci & di Fulvo 13865 (holo-: CORD).

Annual herbs with obliquely erect to decumbent branches, internodes with sparsely distributed globose or ovoid bladder cells. Leaf blades obovate to spatulate as seen from above, obtuse, covered densely with globose bladder cells, 11–13 × 6–8.5 mm, petioles with narrow rectangular papery wings ending in a short tooth. Inflorescences in rather dense cymes, the bract and bracteoles narrowly acuminate Tepal teeth erect, equipped with globose bladder cells like those on the leaf blades, about as long as the tube. Stamens one, rarely 2–3. Pyxidium obconical, with a very low and flat operculum developing a wing-like margin surrounding the periphery, only a short ring of tissue below this ornamentation, about 2 mm in diam. Seeds two, ovoid, superposed, the lower one sometimes flatter, with some low almost circular ridges, black, 1.2–1.4 mm long. Fig. 1A–D.

Habitat and distribution – In fine loam in disturbed places, e.g. along roads, in the provinces Córdoba and La Rioja of Argentina. Alt. c. 400–550 m.

Additional specimens studied – **Argentina. Córdoba:** cerca de Serrezuela, rumbo a Salinas Grandes (ruta 38: km 931 a 932), 21 May 1959, *Hunziker et al.* 14383 (CORD). **La Rioja:** Gral. Ocampo, Sobre la Ruta 79, 1 km antes de Ambil, 4 Mar. 1959, *Hunziker et al.* 14048 (B, CORD, HBG); Inmediaciones de Patquía rumbo a Talamuyuna, 7 Apr. 1959, *Hunziker* 14302 (B, CORD); Ruta Nacional 38: entre Patquía y la ciudad de La Rioja, a 5 km de la primera, 430 m; 2 Mar. 1979, *Biurrún & Pagliari* 1608 (CORD); Independencia, Mar. 2010, *Kiesling* 10340 (HBG, MERL).

Notes – Similarities with other species include the reduction of stamens, as in *T. sedifolia* and *T. corallicola*, both in NE Africa; the possession of flat opercula with a width of up to 2 mm, as in *T. ufoensis* from Australia; and the dense cover of globose bladder cells on the leaf blades as well as on the free tepal tips, as in *T. crystallina* and *T. sheilae*, both in NE Africa and SW Arabia. The bracts and bracteoles are smaller than those of most other species in the subgenus.

2. *Trianthema clavata* (J.M.Black) H.E.K.Hartmann & Liede, comb. & stat. nov.

– *T. crystallina* (Forssk.) Vahl var. *clavata* J.M.Black, Transactions and Proceedings of the Royal Society of South Australia 47: 369. 1923 (Black 1923). – *T. triquetra* Willd. ex Spreng. var. *clavata* (J.M.Black) H.Eichler (Eichler 1965: 136). – Type: Australia, Lake Eyre Basin, North-East, between Herrgott and Innamincka, Jun. 1916, *Cockburn* s.n. (lecto-: AD; designated by Prescott 1984: 319; seen as scan).

Annual herbs with prostrate branches, up to 40 cm in diam. Internodes purple. **Leaves** clavate with a rounded tip, petiole basally with two translucent pseudostipules, each ending in a short broad tooth pointing outwards, leaf blades exhibiting translucent cells, a number of them arranged in a short longitudinal line on the upper surface, 4–7 × 2–3 mm, epidermis with low bladder cells, some bigger ones along the rounded edges; petioles 2–4 mm long, the lateral pseudostipules about as broad as the petiole. **Inflorescences** with numerous flowers, bract and bracteoles acuminate. **Flowers:** **tepal teeth** subapically thickened, only the outer ones with very short protrusions, all connivent over the capsule surface, often with visible bladder cells, especially at the apex. **Fruits:** **operculum** 1–1.5 mm in diam., with a narrow smooth, later rugose ring around the outer edge, holding a translucent hyaline layer level with the top of the ring, hiding the sunken interior from sight, splitting and disintegrating with age or sinking into the cavity, covering the concave inside of the ring wall, the whole operculum therefore more similar to a pastry crust than to the more common bowl or crater shape, with red-purple dots or coloured reddish purple all over during the ripening process. **Seeds** two, black, appressed to and on top of each other, sides with curved ridges, mostly 1–1.5 mm long. Fig. 5A–C.

Habitat and distribution – In heavy or shallow stony soil, also in damp places like flood plains or at the edge of gravelly watercourses in central parts of Australia, extending towards the SE.

Additional specimens studied – **Australia. Northern Territory:** Rainbow Valley Conservation Reserve, 5 May 1995, *Albrecht* 6661 (DNA); Alice Springs, 6 miles SE of Mt. Allan Homestead, 24 Feb. 1961, *Chippendale* s.n. (K); Andado Station, MacClarke Reserve, 10 Sep. 1992, *Latz* 12713 (DNA); 4 km north of Lake Surprise, 21 Oct. 1988, *Latz* 10956 (MO); Central Tanami Desert, 24 Jul. 1990, *Latz* 11699 (DNA); Uluru (Ayers Rock-Mt Olga) National Park, 19 May 1988, *Lazarides & Palmer* 247 (K); 5 miles E of Alice Springs township, 5 Mar. 1953, *Perry* 3238 (K); 8 mls NE of Tennant Creek, 24 Apr. 1948, *Perry* 554 (K); 4 mls S of Aileron, 1 Aug. 1962, *Swinbourne* 369 (K); Eastside, Alice Springs, 19 Oct. 1962, *Swinbourne* 505 (K). **South Australia:** Wirraminna Station, W shore of Lake Hart, 17 Aug. 1973, *Chinnock* 389 (K); Lake Frome East, c. 40 km ENE of Frome Downs homestead, 23 Jul. 1971, *Donner* 3492 (AD); Mt. Lyndhurst, 1 Mar. 1899, *Koch* 81 (HBG, K); c. 40 km NE of Emu, on Emu-Dingo Claypan Road, 1 Jun. 1967, *Lothian* 3952 (AD); near Betty's Well, Everard river and park Sta. Everard Ranges, 16 Feb. 1965, *Symon* 3338 (K); Northern Flinders Ranges, Lake Torrens Basin, c. 150 km NE of Port Augusta, on road to Marree, 24 Oct. 1968, *Weber* 695 (AD). **West Australia:** Along the domestic drain at Giles, Rawlinson Ruge, 3 Aug. 1962, *Symon* 2530 (K).

Notes – The changes in naming this species in the Australian Floras reflect the application of the names *T. crystallina* (Black 1923), used in earlier publications in agreement with Willdenow (1803), and *T. triquetra* (Eichler 1965), replacing the name *T. crystallina* in later years without changing the taxonomy of the lower taxa involved. Like *T. ufoensis*, the new species described in this paper, the taxon in question was not recognized as being different from *T. triquetra* from India, the type area. The herbarium collections investigated show, however, that *T. clavata* can be distinguished from *T. triquetra* by its club-shaped succulent leaves with a rounded tip, the high number of flowers per node (12–18), the possession of low yet distinct papillae on the erect tepal teeth, and in the development of reddish-purple opercula with a hyaline cover over the concave interior (the last two features shared with *T. ufoensis*) of about 1.5 mm diam. Furthermore, translucent epidermal cells arranged partially in a short line on the upper leaf surface distinguish this taxon from *T. ufoensis*. Based on all these differences, it is therefore decided to place the taxon at species rank instead of a variety only, especially since an inclusion in *T. triquetra* cannot be founded on morphological grounds.

3. *Trianthema corallicola* H.E.K.Hartmann & Liede, sp. nov.

Differt ab omnibus aliis speciebus in Africa septentrionali internodiis hirsutis, foliis fere cylindricis apicibus marginibusque papillatis, epidermide cellularum foliorum plicibus cuticularibus ornata et quod littora corallina habitat, inde epitheton electa; aequat *T. sedifoliae* in 2 staminas habere. – Type: Somalia, Shabellaha Hoose, 2–3 km S of Marka [Merka] along the road to Shalaanbood [Shalambod], 14 Jun. 1987, *Friis, Vollesen & Hassan* 5029 (holo-: C; iso-: B, K).

Prostrate annual to perennial **plants**. Internodes usually longer than the leaves, equipped with reflexed hairs to 0.5 mm long, thinning out towards the bases of the internodes and rubbed off with age. **Leaves** to 18 mm long and to about 4 mm wide, leaf blades ovoid to almost cylindrical, apically ending in a group of elongate papillae sitting on a broad base, the epidermal cells adorned with cuticular folds, petioles ba-

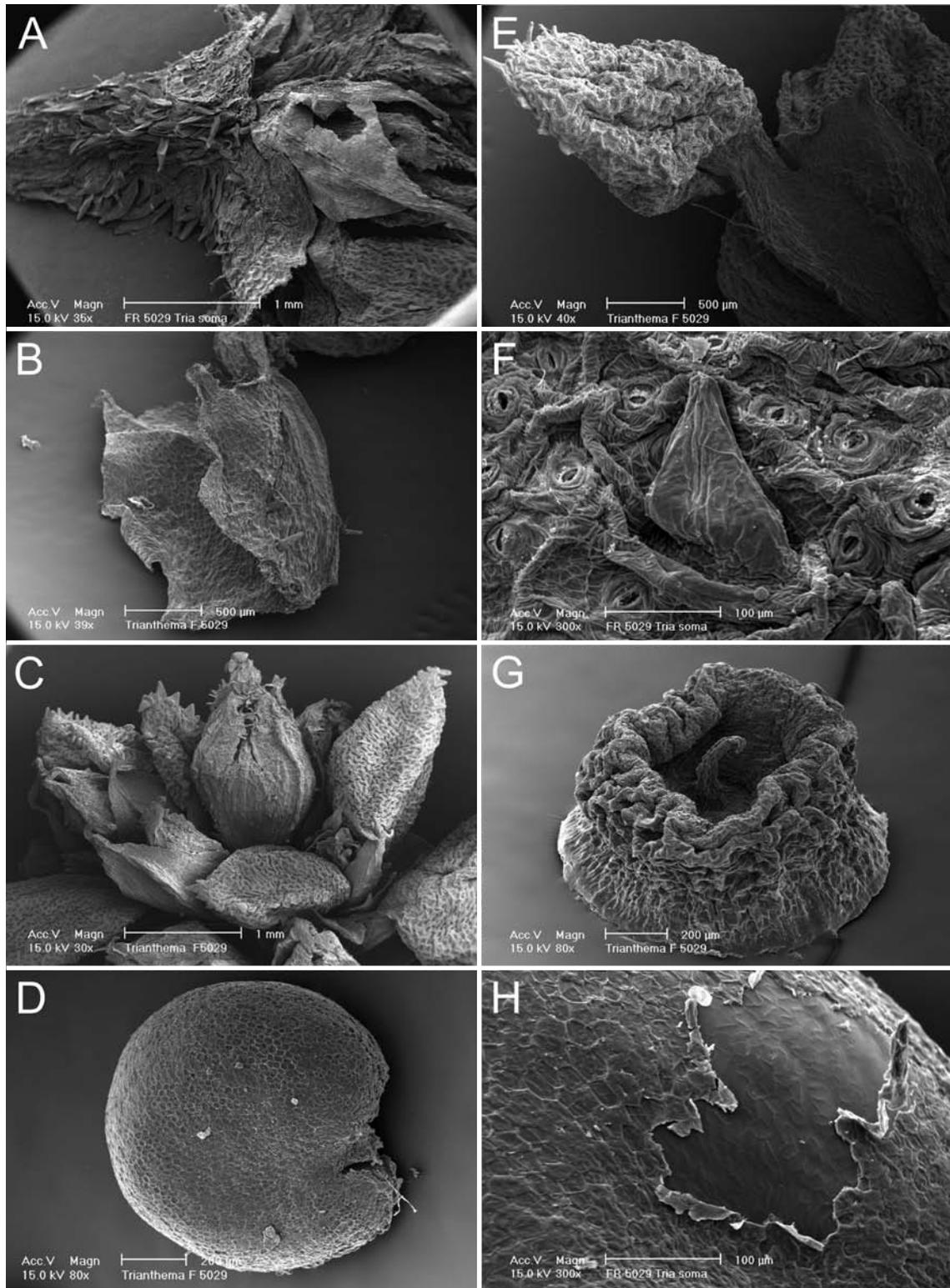


Figure 8 – *Trianthema corallicola*: A, side view of a node with internode to the left, showing the hairs 5 mm long. In the centre, two leaves with hairs are visible; the acuminate bract above them is free of bladder cells; B, pseudostipules a little broader than the petiole embracing the leaf stalk end in acuminate tips; C, the inflorescence is surrounded by leaves, only the erect tepal tips have long bladder cells, the bases of the incisions are not bulgy; D, smooth round seeds are found on the type material, but other collections have some ornamentation; E, the ovoid leaves end usually in long hairs at the tips; F, on the blade, shorter conical hairs are visible dispersed among the normal epidermal cells with a plicate surface, a rare phenomenon in the genus *Trianthema*; G, the operculum shows a typical puffed sleeve shape, note the difference in surface sculpture between the smaller rim and the wider base; H, the aril has been scratched off to demonstrate the absolutely smooth seed surface, bare of ridges. A–H from Friis et al. 5029.

sally with two big translucent flaps, each ending in an acuminate tooth and sometimes with two additional short teeth, the margins and keel also with elongate bladder cells broadest at their bases, more prominent in young leaves. Inflorescences dense in the axils of leaves, the bract broadly acuminate with a row of hairs along its middle, the two bracteoles more slender, prominently pointed; Flowers free to the base, narrowing to tip and base, tepals teeth free, erect to overarching the ripe fruit, with prominent bladder cells increasing in length towards the tooth tip where they can form thin finger-shaped hairs up to 0.1 mm long, just visible to the naked eye, bases of the tepal teeth smooth. Stamens two. Operculum with a narrow later much shrivelled rough rugose ring around the deeply sunken centre, resembling a puffed sleeve and hence more narrow than the well developed base below, about 1.1 mm in diam. and up to 1 mm high. Seeds two, black, appressed to and on top of one another, sides completely smooth, enveloped completely by a thin aril, c. 1.0 mm long and broad. Fig. 8.

Habitat and distribution – In sandy patches on coral reefs along the coast of S Somalia and N Kenya; found also further inland on gypsum in S Somalia.

Additional specimens studied – **Kenya. Lamu:** Takwa, SE side of Manda Island, 3 Oct. 1957, *Greenway* 9270 (K); Takwa Strand, 31 Aug. 1956, *Rawlins* 54 (K); Oxford Univ. Kiunga Islands Expedition 1951 Kenya Coast (K).

Somalia: Galguduud, Ceelbuur (El Bur), the compound of the National Range Agency and its surroundings, gypsum soil, 25 May 1989, *Thulin & Dahir* 6502 (K, UPS).

Note – The species presents a sample for a small distribution area obviously restricted by soil conditions, here along the coast of Somalia and Kenya, but morphologically distinct and unique in the subgenus.

4. *Trianthema corymbosa* (Sond.) H.E.K.Hartmann & Liede, comb. & stat. nov. – *T. crystallina* (Forssk.) Vahl var. *corymbosa* E.Mey. ex Sond., in Harvey & Sonder Flora Capensis: 598. 1862 (Sonder 1862). – *T. parvifolia* Sond. var. *corymbosa* Adamson (Adamson 1962: 251). – Type: South Africa, Northern Cape, Gariiep, Verleptpram, unter 1000 Fuss, Sep., *Drège* s.n. 04-457 (lecto-: S; designated by Adamson 1962: 251).

Trianthema crystallina (Forssk.) Vahl var. *rubens* E.Mey. ex Sond. (Sonder 1862: 598). – *T. parvifolia* Sond. var. *rubens* Adamson (Adamson 1962: 251). – Type: South Africa, Northern Cape, Gariiep, Verleptpram, unter 500 Fuss, Sep., *Drège* s.n. S 04-455 (lecto-: S; designated by Adamson 1962: 251).

Perennial plants of up to 1 m diam., branches decumbent, hence at most 20 cm tall. Taproots to 10 cm long, apically to 5 mm diam. Internodes woody when dry, young ones purple, medium ones ochre to orange, oldest ones in the centre straw-coloured to white, smooth or finely pleated; leaves falling off in the dry season, the bare stems bearing the ripe fruits. Leaves with an ovoid blade, wider than thick, with sparsely dispersed dark spots (white in translucent light) all over, no elevated bladder cells discernable, the blades drying into a wrinkled disc-shape about 5 mm across, about 1.2 mm thick, petioles 6–7 mm long, the two pseudostipules broadening to-

wards the base almost as long as the petiole, sometimes with a broad blunt tooth, their extension at most as broad as the blade but mostly more narrow and less conspicuous. Inflorescences dense when young; later, especially when in fruit, all internodes elongated, developing a very loose inflorescence with mostly 6–9 flowers per group, the tiny pedicel with an acuminate bract from a broad base, sometimes with 1–2 lateral short teeth, and two narrow pointed bracteoles. Tepals completely smooth, their free teeth as green as the tube outside; these teeth connivent in the young flower, erect and even spreading in the ripe fruit later, a green subapical thickening present, but no subapical horn overtopping the actual tepal tip. Stamens five, purple or golden-orange (coccineis fide Drège). Operculum with a broad apical ring of rough surface cells around a tiny central deepening, about 1.2 mm in diam. and 0.6 mm high. Seeds mostly one, black, appressed to and on top of a smaller and sometimes abortive one, the bigger with prominent crests along the edge and the sides, almost round in side view, c. 0.9 mm in diam., c. 0.6 mm thick. Fig. 4.

Habitat and distribution – In open, sandy, stony, gravelly soils mainly below quartz or granite slopes and in disturbed places in the lower ranges near the mouth of the Gariiep River, Northern Cape Province, South Africa. Alt. 240–930 m.

Selection of additional specimens studied – **Namibia. Lüderitz-Süd:** Staatsgebiet, Huobrivier, Hunsberge, südlich der Farm Uitsig, LU 82, 9 Jun. 1976, *Giess & Müller* 14322 (WAG); Warmbad, hills between Aussenkjer und Chamgab, 1 Sep. 1931, *Pillans* 6393 (K).

South Africa. Northern Cape. Namaqualand: Gariiep, s.d., *Drège* 3017, 3018 (B, PRE); *ibid.*, *Drège* 2× s.n. (HBG); Goodhouse nach Pofadder, alt. 350 m, 14 Mar. 1995, *Hartmann & Potgieter* 32698, 32699 (HBG); Vioolsdrif, 21 May 1974, *Goldblatt* 1861 (MO); N foot of Rosyntjiesberg, 30 Aug. 1977, *Thompson & le Roux* 205 (MO); high plateau on western side of Jettle, 27 Dec. 1910, *Pearson* 5989 (K); NNE of spot height 562, alt. 420 m, 10 Mar. 1979, *Van Berkel* 84 (MO); just S of Vyfmylsepoort, 2 Jul. 1986, *Fellingham* 1096 (MO, WAG); Numees, 9 Mar. 1977, *Hartmann* 8255 (HBG); *ibid.*, alt. 390 m, 11 Mar. 1995, *Hartmann & Potgieter* 32657 (HBG); Cornellskop nach Numees, 4 km vom Abzweig nach Wallekraal, alt. 240 m, 31 Mar. 1988, *Hartmann et al.* 26135 (HBG); Kenhardt, 10 km E of Pofadder, alt. 910 m, 8 Mar. 1988, *Hartmann et al.* 25620 (HBG); N of Burgers Farm, im Tal, alt. 870 m, 26 Mar. 1994, *Hartmann et al.* 31630 (HBG). **Richtersveld:** Jenkins Kop, s.d., *Pienaar* 1182 (WAG).

Notes – When Sonder (1862) described the varieties *rubens* and *corymbosa* in *T. crystallina*, he contrasted them formally with *T. parvifolia*, for which he gave no leaf shape nor information on the bracteoles. Comparisons of the lectotypes (S) and *Drège* 3017, 3018 kept at B and PRE plus fresh material from the type area near the mouth of the Gariiep River reveal that the density of cymes changes during ripening and that the colour of the internodes and leaves can vary, both character expressions being considered as specifically distinctive by Sonder (1862). Since also all other features like leaf shapes, fruits, flowers, growth forms and seeds are very similar in both varieties, they are understood to represent members of one species.

Features distinguishing *T. corymbosa* from *T. parvifolia*, under which latter name the former taxon was kept as a variety by Adamson (1962), are the deciduous leaves, the loose arrangement of the flowers in the ripe fruit state, and the erect

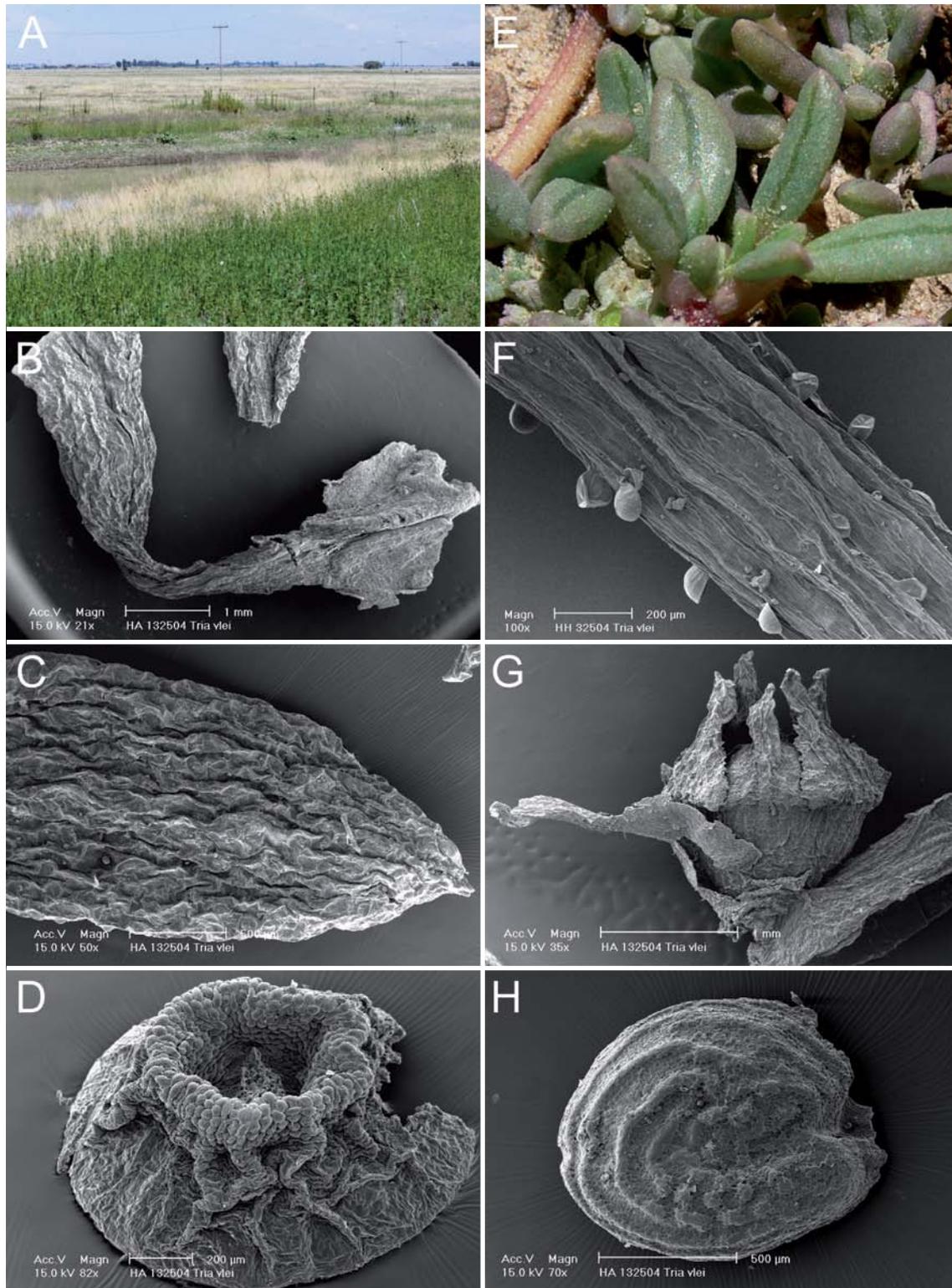


Figure 9 – *Trianthema vleiensis*: A, typical habitat of *T. vleiensis* after rain: a shallow salt pan surrounded by low vegetation; the plants grow at the upper edges, flooded only exceptionally; B, between the broad short pseudostipules, ending in a short tooth, and the blade, a lengthy petiole is visible; C, pointed almost smooth dry leaf tip in which the dark green middle line cannot be recognized; D, the puffed sleeve type of operculum is well developed in this species, showing a distinctly sculptured rim; E, plant in habitat showing the typical dark green line along the middle of the upper leaf surface, leaf tips acuminate; note the smooth internode surface at the left top; F, very few small bladder cells of about 100 μm on an internode; G, side view of a flower, free to the base; to the right, a petiole, to the left an acuminate bract; the incisions between the tepal teeth basally with a bulge; H, a seed inside view showing the almost semi-circular ridges. A from Hartmann 31315; B–E from Hartmann 34781; F–H from Hartmann 32504.

tepal teeth when the fruit is ripe. All these character states support a distinction of the taxon at species level, and the name *T. corymbosa* is chosen here.

5. *Trianthema crystallina* (Forssk.) Vahl (Vahl 1790: 32). – *Papularia crystallina* Forssk. 1775 (Forsskål 1775: 69). – Type: Saudi Arabia, s.l., s.d., *Forsskål* C III.14 (holo-: C).

T. crystallina (Forssk.) Vahl var. *suberosa* Terracciano (Terracciano 1894: 108). – Type: Eritrea, I Midir, 22 Mar. 1892, *Terracciano* 187 (lecto-: FT; **designated here**; seen in Aluka).

T. crystallina (Forssk.) Vahl var. *obscura* Armari (Armari 1904: 146). – Type: Eritrea, Baia de Anfilah, 23 Mar. 1892, *Terracciano* 51 bis (lecto-: FT; designated by Hartmann 2001: 332; seen in Aluka).

Herbs or low perennial shrubs with decumbent to procumbent branches with older woody internodes up to 3 mm diam. Young **internodes** with a dense cover of big erect globose to ovoid bladder cells emerging with their small end from the epidermis and breaking off with age, at first green turning towards straw colour and later coloured white by a smooth layer of secondary bark. Internodes usually longer than the leaves. **Leaves** with an almost circular or oval blade covered very densely with big globose bladder cells drying into flat discs overlapping each other along the edges, sometimes longer than broad, about 7–9 mm across (4–5 when dry), the petiole with only few of such bladder cells, basally with two broad translucent flaps like stipules, each ending in a long sharp tooth. **Inflorescences** with densely placed flowers, rather compact in the axils of leaves. **Flowers** mostly five per axil, 3 mm diam., green inside, basal tepal tube with big bladder cells in some young flowers only, later smooth, while the free lobes of the tepals are coated densely with bladder cells like the leaves; these lobes not exceeding 1 mm in length, erect and only a little connivent in the open flower, also bending over the top of the fruit later, hiding the top of the fruit mostly; the subapical protrusions of the calyx lobes about as long as the translucent rim around the calyx lobe, the outer longer one not exceeding 0.4 mm in length, the tepal lobes themselves smooth where joining at their bases, not bulgy; each flower with a broad translucent bract with mostly 1–2 teeth followed by two fimbriate bracteoles, disintegrating with age. **Stamens** five, in alternitetalous position. **Operculum** with a broad rugose ring around the sunken centre, the inner wall almost straight, about 2 mm in diam. and 0.4 mm high in the old state, young capsules almost globose with a rounded rim descending into the centre in which a short stigma of up to 0.25 mm length is placed. **Seeds** two per capsule, black, appressed to and on top of each other, these seeds with prominent crests around the outer edge fitted with c. 8 straight bulges, the sides smoother, rarely one thick seed only, showing c. 9 crests or bulges also on the sides, the entire surface covered by a thin arillus disintegrating with age, c. 1–1.1 × 0.9 × 0.6 mm. Fig. 2A–C.

Habitat and distribution – In open, sandy, stony, gravelly, and disturbed places, mostly at or near the sea along the West Coast of Yemen and SW coastal areas of Saudi Arabia. Alt. 0–560 m.

Additional specimens studied – **Saudi Arabia**: Jebel Mershed, about 40 km E of Qunfudah, alt. 17 m, 4 Mar. 1980, *Collenette* 1940 (K); Al Moraira, 44 km N of Mahayl on the Dsheddah-Gizan Road, alt. 170 m, 14 May 1981, *Collenette* 2713 (E, K); ENE of Qunfudah, S foot of Jebel Shadha, alt. 100 m, 5 Mar. 1981, *Lavranos & Collenette* 18220 (E).

Yemen: Abydh, Lower Wadi Asurie, 17 Mar. 2002, *Al-Gifri* 1823 (B); Hodeida, N of Az Zuhra, Tihama, 24 Oct. 1982, *Müller-Hohenstein & Deil* 992 (UBT); 5 km N of Sochra, 22 Nov. 1982, *Müller-Hohenstein & Deil* 1273 (UBT); 2 km N of Bab Nishamah / Al Hujaylah, alt. 560 m, 13 Sep. 1986, *Rappenhöner* 331 (UBT).

Notes – Forsskål (1775) described the plant he found in Yemen as *Papularia crystallina*, giving no information on possible differences to the genus *Trianthema*, described by Linnaeus in 1753. Both genera share the possession of a single style and an operculum that never splits into halves but is loosened from the basal portion forming a container for 1–2 seeds and dispersed as such, the seeds falling out when the lid is removed.

Willdenow (1809) wrote that he thought the material sent to him by Rottler from India, named *T. triquetra* by the latter, was only a ‘Spielform’, i.e. a sport, of *T. crystallina*. *T. triquetra*, however, has a smooth blade surface, no prominent bladder cells at all, slender leaf blades with narrow pseudo-stipules along the petiole widening gradually towards the base, mostly one flower per axil with a smooth surface, and a rather narrow ring around the top of the operculum, sloping into the deep centre and not covered completely by the short tepal teeth.

Attention must further be drawn to the fact that northern African material of *T. sedifolia* has often been named *T. crystallina* in error. The former species has, however, a tendency to expose the operculum in ripe state while the tepal teeth spread at the same time; yet, it can easily be distinguished from *T. crystallina* by its slender darker leaves with only moderately elevated semi-orbicular bladder cells not overlapping each other when dry. On the other hand, *T. sedifolia* shares with *T. crystallina* the prominent and numerous bladder cells on the internodes.

Following Willdenow (1803), material from Australia has been named *T. crystallina* in the past (Bentham & von Mueller 1866) and been re-named *T. triquetra* more recently (Prescott 1984). Floras of other countries follow either naming, and care must be taken to check the material before a name is used, especially in southern Asia, but also in Africa, e.g. Sonder (1862) who described two new varieties of *T. crystallina* and delimited the species from his newly described species *T. parvifolia*, into which the two varieties have been transferred by Adamson (1962) later.

The present investigations permit the conclusion that *T. crystallina* in the sense of the type of Forsskål (C) has a restricted distribution on the SW Arabian peninsula and has not been documented reliably from other areas. The species is most similar to *T. sheilae*, both taxa sharing several character states:

- internodes white and woody with age, with prominent yet distant big bladder cells in the young state
- leaves flattish, nearly circular as seen from above, 4–7 mm long, 3–6 mm wide
- leaf epidermis with a dense layer of big globose bladder

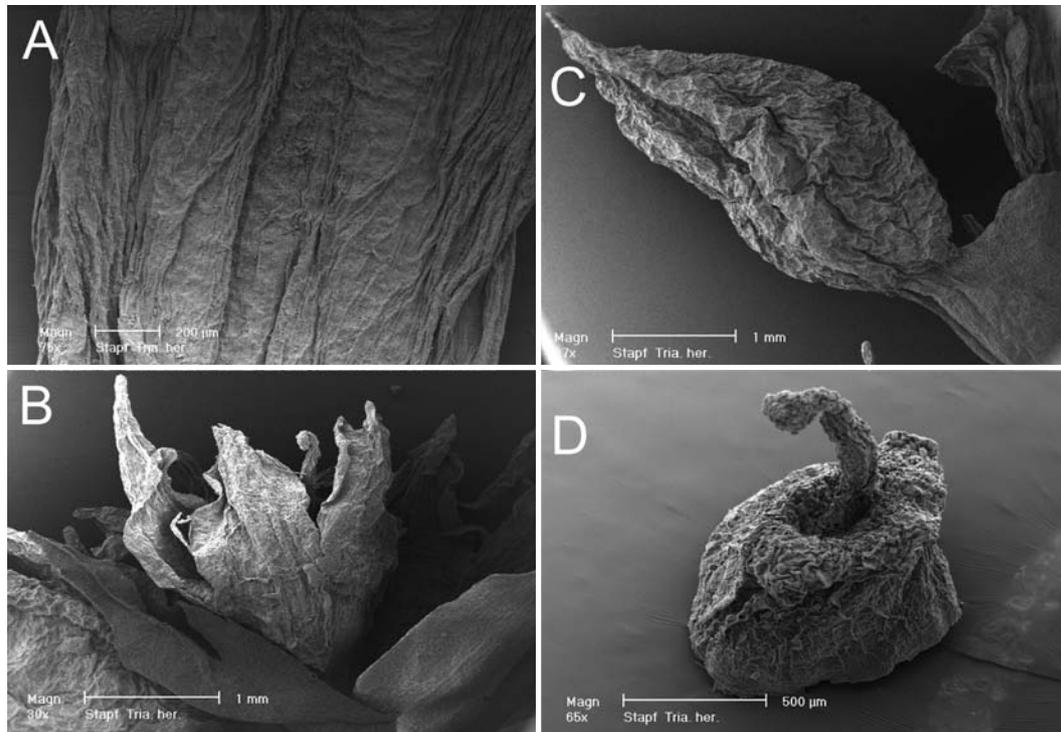


Figure 10 – *Trianthena hereroensis*. A, smooth surface of an internode, pleated from drying; B, side view of a leaf with an acute tip to the left top and the rounded semi-elliptic pseudostipule at the right; C, a flower subtended by an acuminate bract, torn lengthwise in preparation, and with smooth acuminate tepal tips; note the long subapical protrusion on the left hand side and the smooth bases of the tepals at their bases; D, an operculum with a broad apical rim, resembling that of *T. corymbosa*, shaped like a puffed sleeve. A–D from *Stapf* s.n. (Z).

cells, collapsing when drying, the white sharp rims visible as a white network pattern above the mostly blackish lower surface

– the same type of bladder cells prominent on the tepal teeth, absent on the tepal tube

– flowers with a bract and two bracteoles each, these three tiny leaves papery-translucent, broad and more or less clasping the flower, apically ending in thread-like protrusions, looking fimbriate to different degrees

– pseudostipules with a long prominent terminal tooth, pointing upwards or sideways, widening laterally and often developing another tooth at the widest point, narrowing to the base of the petiole

– the young fruit giving the impression of a berry since the operculum of the capsule is round, resembling the top of a balloon, with a small deepening in the centre, shrinking and wrinkling with age, resulting in a rough operculum surface with a distinct elevated rim on the outer top, but differing in precise shape from fruit to fruit, even in one inflorescence

– the black seeds lie in pairs obliquely in the capsule, their contact zone flattened to different degrees, covered in a thin aril, below which many crests or bulges can be distinguished: the 6–8 crests along the back of the seed with straight elongated walls running parallel to each other, those on the sides crescent-shaped, all finely granulate under the lens, and not always filling a complete semicircle, their number around nine on each side.

T. crystallina forma *suberosa* Terracciano (1894) and *T. crystallina* forma *obscura* Armari (1904) from Eritrea are included here, based on evidence from images available in

Aluka; the original material at FT was not made available for examination. Evidence, however, is insufficient from the electronic images, hence the occurrence of *T. crystallina* in Eritrea remains uncertain.

6. *Trianthena hereroensis* Schinz (Schinz 1897: 76). – Type: Namibia, !Kuisseb, 1886, *Stapf* s.n. (lecto-: Z, **designated here**).

Perennial prostrate plants forming semiglobose “dune cushions” (Friedrich 1970). Internodes orange-brownish yellow, smooth, and woody when dry, much longer than the leaves. Leaves ovoid but conspicuously pointed at the tip, which sometimes bend over in dry material, bladder cells inconspicuous, sometimes discernibly near the tips, the blades drying usually into flat shapes, the petioles laterally equipped with broad semi-oval pseudostipules reaching up to the base of the blade but distinctly cut against the blade, about as broad as the blade, turning papery with age, never with a tooth. Inflorescences very dense in the axils of leaves, mostly with 4–6 flowers per group. Flowers with a broadly lanceolate bract and more slender bracteoles. Tepals completely smooth, their free somewhat thickened teeth with conspicuous long protrusions from below the tepal tips, standing erect and about as long as the connate base of the flower. Stamens five. Operculum basally coriaceous and thin, resembling a puffed sleeve in shape, the top portion rough from big cells in contrast to the smooth base. Seeds two, black, appressed to and on top of each other, the entire surface smooth and shiny from a thin aril, almost round, c. 0.9 mm diam., c. 0.6 mm thick. Fig. 10A–D.

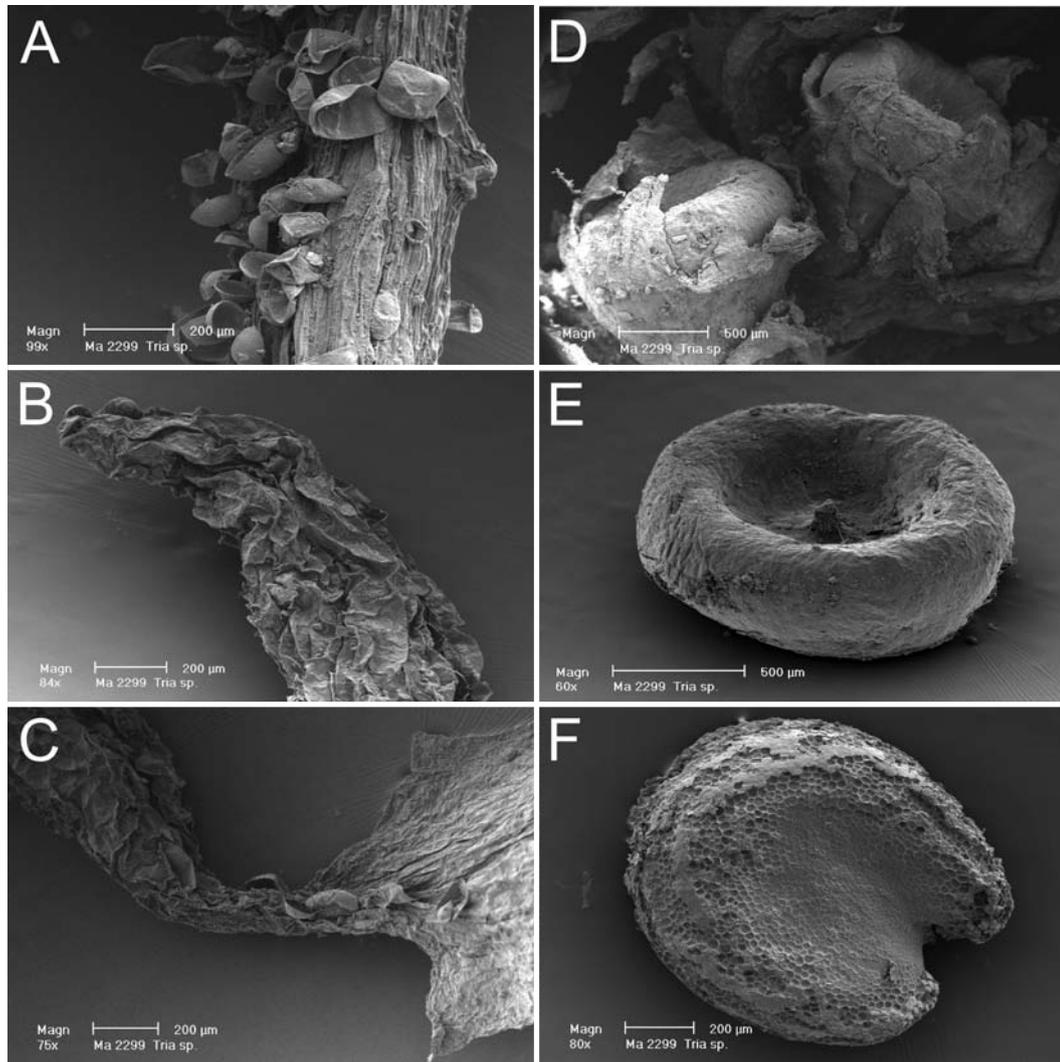


Figure 11 – *Trianthema mozambiquensis*: A, Typical internode surface with almost globose bladder cells fixed in the epidermis at the small end of a papilla, partially removed by age from the surface; B, leaf tip exposing the big yet low bladder cells of the epidermis, the margins are rolled back, the upper leaf surface is exposed; C, a short petiole visible between the blade on the upper left and the broad pseudostipules ending in a broad tooth at each side; D, the two flowers of a typical inflorescence possess an acuminate bract and acuminate bracteoles, shorter than the ripe pyxidium, the tepal tips overarch the operculum partially; E, the ripe operculum shows a smooth surface with a very broad rounded rim around a wide central deepening; F, a seed in side view has lost part of the previously complete layer of the aril, permitting the recognition of bulges around the back and bottom of the seed. A–F from *Marques 2299*.

Habitat and distribution – In river sand in the coastal plains of Namibia. Alt. 30m.

Additional specimens studied – **Namibia**: Tsoachaubsand, Salem, 27 Jul. 1898, *Dinter* 108 (Z, 2 sheets).

Notes – In contrast to Adamson (1962), who included *T. hereroensis* as a synonym under *T. parvifolia*, Friedrich (1970) kept the former species up, based on the observation of the growth form developing into “dune cushions” by growing through the covering sand. This view is supported here with new data from material kept at Z.

The location of the type, given as “HER: Sandwüste zwischen Swartbank und Sandfischhafen, Stapff!” remained unclear since no such sheet can be found at Z. When, however, three sheets kept under *T. hereroensis* were made avail-

able by loan to HBG, it was possible to confirm that one sheet agrees in all details with the description of *T. hereroensis*. The only difference is the locality given as !Kuisib. After the place called Sandfischhafen was identified as lying just south of the mouth of the Kuisib River, it is now possible to relate both informations on the locality as referring to one spot. In consequence, the sheet at Z is chosen here as the lectotype, since it was collected in 1886 and was seen by Schinz, as indicated by the handwritten change of the printed name “Hans Schinz” to “Dr. Stapff”.

Two sheets of another collection kept as *T. hereroensis* at Z, namely *Dinter* 108, belong with that species as well. They were collected in 1898, hence a year after the name had been published, and can, therefore, not be considered for the choice



Figure 12 – Worldwide distribution of all collections of *Trianthema* subg. *Papularia* used in this study. Marked in yellow are those collections that have at one time been named *T. triquetra*, implying an almost worldwide range. Map produced in Taxo 2 Map.

of a lectotype, although the material seems to have been seen by the author, who appears to have named both collections as visible by the handwriting. Since one of these sheets bears in Dinter’s hand the information “Tsoachaubsand. Salem”, the locality can be determined as being along the Swakop River, for which Tsoachaub was the old name.

No further collections can at this date be identified as *T. hereroensis*, and the distribution must at the moment be understood to be restricted to the lower sandy river beds of the Namib desert.

The species differs clearly from *T. parvifolia*, with which it has been united by Adamson (1962), in having pointed acuminate leaf tips and pseudostipules along both sides of the petiole forming almost an oval shape, apically truncate and almost touching the base of the blade there; in having erect long tepal teeth formed mainly by the very long subapical protrusions of the tepals, never arching over the flower or the fruit; and finally, in having very smooth and shiny black seeds.

Curtis (1985) listed *T. hereroensis* as one of the major hosts of honeydew producing scale insects (Hemiptera: Coccoidea), the main food source for the desert ant *Camponotus detritus* Emery.

7. *Trianthema mozambiquensis* H.E.K.Hartmann & Liede, sp. nov.

Differt ab omnibus speciebus in Africa australi inventis operculo circumdato ora elevata lata et circulari, forma muro terreno arcis, superficiebus laevibus, externis quasi perpendicularibus, internis declivis; simillime *T. sedifoliae* Africae septentrionalis in internodiis distincte papillatis et in formis operculorum sed differt in pseudostipulis latioribus et distincte dentatibus. – Type: Mozambique, Lourenço Marques, Matola, km 28,3 de Boane para Porto Henrique, picada a esquerda (links) para a propriedade de Augusto Fonseca ao km. 6,2 (Cq), 28 May 1971, Marques 2299 (holo-: WAG).

Prostrate herbs with more or less globose bladder cells on the internodes, dense on young parts and distant on older ones, rubbing off slowly with age; pseudostipules shorter than the petioles, as wide as or wider than the blade, ending in a short acuminate tooth. Leaf blades about 3.5 mm long, oblong-lanceolate, marginally incurved, hiding the lower leaf surface mostly completely; the entire leaves covered with low yet distinct big bladder cells. Inflorescences usually with two flowers in dense arrangement; the bract and bracteoles acuminate. Flowers smooth with short tepal teeth pushed aside by the growing pyxidium. Operculum with a prominent broad smooth ring wall around its outer edge, the inner sloping wall

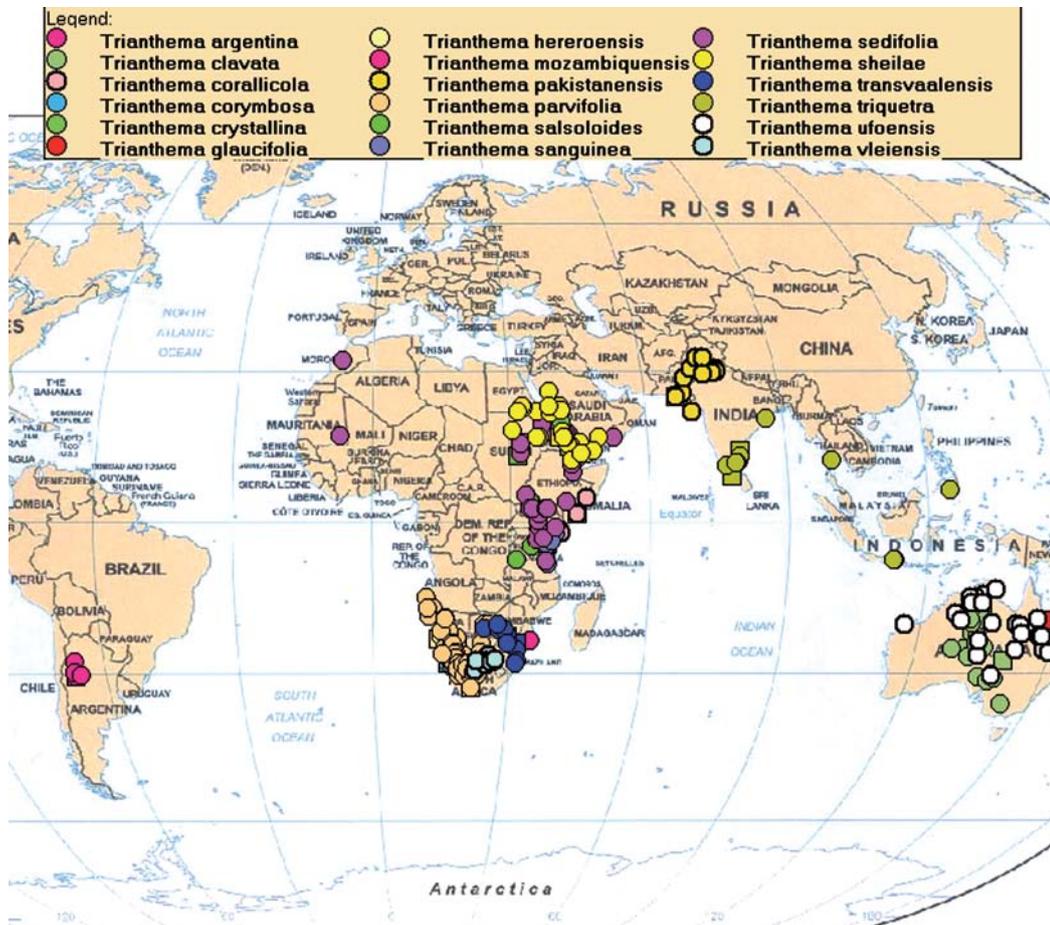


Figure 13 – The same collections plotted as in fig. 12, but the presently recognized species marked in different colours. *T. triquetra* as here circumscribed (marked in olive green) is restricted to southern India and the area around the Gulf of Bengal, perhaps also in Indonesia and on the Philippines. Dots represent vouchers, squares mark the geographical position of the type localities. Map produced in Taxo 2 Map.

also smooth, the outer walls convex to straight, never broadening to their base, about 1.1 mm wide. **Seeds** two, black, lying on top of each other, exposing prominent, mostly sharp ridges in semi-circular around the outer edge, about 0.9 mm long and wide. Fig. 11.

Habitat and distribution – Unknown, Mozambique, Lourenço Marques. Only known from the type collection.

Notes – Differs from all other species in southern Africa in having opercula with broad smooth rims like ring-walls perpendicular on the outside, not widening there; most similar to *T. sedifolia* from northern Africa in having distinctly papillate internodes and in operculum shape, but differing from the latter in possessing broader, strictly rectangular pseudostipules with a prominent tooth.

8. *Trianthea pakistanensis* H.E.K.Hartmann & Liede, sp. nov.

Differt a *T. triquetra* cellulis vesicariis parvis omnes partes assimilantes tegentibus, dentibus tepalorum brevibus sed erectis, foliisque siccis marginibus incurvatis apicaliter acuminatis. – Type: Pakistan, Sindh, Paradise point, Karachi, 24 Dec. 1970, *Sultanul-Abedin* 5681 (holo-: B).

Prostrate annual herbs with short finger-shaped bladder cells on internodes, dense on young parts and distant on older ones, rubbing off slowly with age; pseudostipules almost as long as the petioles, widening gradually from the base of the blade, but not exceeding the width of the flat petiole, yet sometimes with a short acuminate tooth. **Leaf blades** obovate, marginally incurved, hiding the lower leaf surface mostly completely; the entire leaves covered with low yet distinct bladder cells, drying into light coloured pointed shapes, never flat. **Inflorescences** usually with five or more flowers in dense arrangement; the bract and bracteoles acuminate. **Flowers** covered with small bladder cells, especially on their short yet erect teeth. **Operculum** with a rather broad rugose ring wall around its outer edge, the inner sloping wall with finely folded material in circular arrangement, 1.1–1.4 mm wide. **Seeds** two, black, lying on top of each other, exposing prominent, mostly sharp ridges in semi-circular arrangement all over, sometimes the ridges not sharp-edged and formed like a dyke or earthen wall, about 1 mm long. Fig. 3.

Habitat and distribution – On saline soils, from near sea level to about 1,000 m altitude in central and southern parts of Pakistan and adjacent eastern parts of India.

Additional specimens studied – **India. Gujarat:** Saurashtra Bhal, 1 Jan. 1966, *Grontmij* 25 (L). **Haryana:** near Ambala, 1 Jan. 1884,

Edgeworth 95 (K). **Punjab:** Indri, s.d., *Drummond* 24207 (K); Tohana, 18 Oct. 1962, *Nair* 24986 (L). **Rajasthan:** Suratgarh, 25 Oct. 1959, *Jain* 42889 (B).

Pakistan. Punjab: Jhelam, Kheora, alt. 1,000 m, 9 Oct. 1902, *Drummond* 14647 (K); Lahore, Shalimar, 8 Nov. 1936, *Parker* 3374 (K); Sialkot, 1 Sep. 1935, *Stewart* 15062 (MO). **Sindh:** Tando Jam Agricultural Univ., 15 Oct. 1977, *Akhter & Nazimuddin* 749 (B); 6–8 mls from Kashmor on way to Roghar, 26 May 1972, *Sultanul-Abedin & Hussain* 4524 (B); Qasim Garden, Bela. 23 Jun. 1971, *Sultanul-Abedin & Qaisar* 7445 (B, MO); near Stadium Road Karachi, 14 Apr. 1969, *Zaibanmsia* 75 (MO).

Notes – The material has in the past been included in *T. triquetra*, a species found to be restricted to the coastal regions around the Gulf of Bengal and perhaps also on Java. The differences between the two species appear slight in dried material: the dominance of bladder cells on *T. pakistanensis* is as obvious, however, as are the possession of erect short tepal teeth and the bigger inflorescences.

An extensive description in English of the material under the name *T. triquetra* is available in the Flora of West Pakistan (Nasir 1973: Aizoaceae: 6), illustrated by a figure in agreement with the present observations. The distribution data extend a little wider into the Thar desert than the records seen for this study, and the information that the plants grow on saline soil confirms presently seen information on sheets. Further, Nasir (1973) says that it “can be used as a fodder for goats and cattle” and adds the vernacular name “alettie”.

9. *Trianthema parvifolia* E. Mey. ex Sond. (Sonder 1862: 598). – *T. triquetra* Willd. ex Spreng. subsp. *parvifolia* (E. Mey. ex Sond.) Jeffrey (Jeffrey 1960: 237). – *T. parvifolia* E. Mey. ex Sond. var. *parvifolia* (Adamson 1962: 250). – Type: South Africa, Western Cape, Gamka River, Zwartbulletjie, 1837, *Drège* s.n. as S 03-525 (lecto-: S, designated by Adamson 1962: 250).

Trianthema parvifolia E. Mey. ex Sond. var. *annulata* Adamson (Adamson 1962: 251). – Type: Namibia, Achterfontein, on sanddunes, 11 Dec. 1915, *Pearson* 9231 (holo-: K).

Perennial plants of up to 1 m in diam. with strictly procumbent branches. Taproots to 10 cm long, apically to 5 mm diam. Internodes woody when dry, young ones purple, medium ones ochre to orange, oldest ones in the centre of the plant straw-coloured to white, smooth or finely pleated, much longer than the leaves. **Leaves** with an almost globose to ovoid blade with dispersed dark spots all over, elevated bladder cells discernable as papillae only in young leaves, the blades drying into a wrinkled disc-shape about 5 mm across, about 1.2 mm thick, petioles 6–7 mm long, most of their length adorned with two broad more or less rectangular lateral flaps, their extension about as broad as the blade, turning papery with age and clasping the stems, producing white sheaths on the stems, more rarely without a tooth and inconspicuous. **Inflorescences** dense, almost compact in the axils of leaves, mostly with 5–6 flowers per group, but often many more. **Flowers** each with a broad and acuminate bract and more slender bracteoles, sometimes with 1–2 lateral short teeth. **Tepals** completely smooth, their free teeth connivent in the open flower at night, bending also over the top of the fruit later, a green subapical thickening present, but not overtopping the actual tepal tip, green outside and inside.

Stamens five, purple or coccineous, orange-red and almost white. **Operculum** with more or less straight sides, the apical ring with rough cells in- and outside, sloping gradually into the deeper centre and distinctly different in structure from the smoother basal portion, about 1.2×0.6 mm. **Seeds** two, black, appressed to and on top of each other, with prominent crests along the edge and the sides, the entire surface covered by a thin aril with a fine reticulation below, representing the anticlinal epidermal walls, almost round, c. 0.9 mm diam., c. 0.6 mm thick. Fig. 4D–F.

Habitat and distribution – In open, sandy, stony, gravelly, and disturbed places in Angola, Botswana, Namibia, western parts of the Northern Cape Province and Western Cape Province, South Africa. Alt. 500–1600 m.

Selection of additional specimens studied – **Angola:** Between Mossamedes and R. Coroca, 23 Apr. 1909, *Pearson* 2151, 2192 (K); Namibe (Mossamedes), Vimpongos, 20 May 1937, *Gossweiler* s.n. (K).

Botswana: 8 mls SE of Nate River bridge near Makarikari Pan, 23 Apr. 1957, *Drummond & Seagrief* 5197 (B, K); Western Kalahari, Lone Tree Pan, 15 Mar. 1976, *Vahrmeijer* 3107 (K); Kweneng, Takatshwane (Tokotswane), 23 Dec. 1968, *Maguire* 784527 (B).

Namibia: Vogelstruisskluff on road from Seeheim to Rosh Pinah, 6 May 1976, *Oliver et al.* 6358 (WAG); Gabis, 31 Jan. 1909, *Pearson* 4330 (K); Damaraland, Farm Black Range 72, alt. 1,090 m, 2 Apr. 1990, *Ward* 10814 (K); Farm Lekkerwater 32 mls E. of Aranos, 26 Apr. 1960, *Vuuren & Giess* 1101 (K); 12 km W of Sandverhaar, 13 Feb. 1909, *Pearson* 4270 (K); between Achterfontein Gelwater, 11 Dec. 1915, *H.H.W Pearson* 9231 (K); between Gellap and Great Fish River, 8 Dec. 1915, *Pearson* 9287 (K); 70 km NW. of Upington on road to Karasburg, 4 May 1976, *Oliver & Steenkamp* 6246 (MO); Etosha Pan National Park, 10 km südlich Okaukuejo, 6 Mar. 1976, *Giess & Loutit* 14136 (K, MO, WAG); Windhuk Bergland, Avis, alt. 1,600 m, 27 Mar. 1963, *Seydel* 3473, B (MO); Aus, s.d., *Dinter* 6145 (B); Omuramba, s.d., *Dinter* 7192 (B); Nonikam, s.d., *Nemo* 6 (HBG); Okahandja, alt. 1,300 m, 1 Jul. 1906, *Dinter* s.n. (HBG); Gibeon, Marienthal nach Kalkrand, alt. 1,000 m, 29 Feb. 1988, *Hartmann et al.* 25473 (HBG); Gibeon, Farm Haribes, 5 Apr. 1956, *Volk* 12187 (MO); Gobabis, Farm Breitenberg, am Ufer des Weissen Nossob, 7 Feb. 1961, *Seydel* 2561 (B, MO); Kaokoveld, 24 m W. of Otjihua on rd to Orupembe, 3 May 1957, *De Winter & Leistner* 5690 (K); Klein Karas nach Keetmanshoop, 10.8 km S vom Löwenfluß, alt. 860 m, 28 Feb. 1988, *Hartmann et al.* 25465, 25467 (HBG); Lüderitz-Süd, Fish River Canyon, Aussichtspunkt, alt. 870 m, 28 Feb. 1988, *Hartmann et al.* 25447 (HBG); Lüderitz-Süd, 14 Sep. 1972, *Merxmüller & Giess* 28450 (WAG); Maltahöhe, Nub West, W of Maltahöhe, 9 May 1976, *Oliver et al.* 6509 (MO, WAG); Okahandja, Okahandja, 1 Dec. 1906, *Dinter* 318 (B, HBG, K, WAG); Otjiwarongo, 40 km from Kalkfeld on road to Okahandja, 4 Mar. 1983, *Germishuizen* 2545 (WAG); Rehoboth, 4.8 km N Kalkrand, alt. 1,200 m, 1 Mar. 1988, *Hartmann et al.* 25483 (HBG); Warmbad, Vellorsdrif nach Karasberg, 18 km, alt. 910 m, 5 Mar. 1988, *Hartmann et al.* 25547 (HBG).

South Africa. Northern Cape: Gordononia, Massaklous pan, 0.2 mls S of Kuruman River, 19 Mar. 1963, *Leistner* 3132 (K); Britstown, Farm Agterplaas, 15 Jan. 1986, *Retief & Germishuizen* 120 (K, MO, WAG); Calvinia, 8.4 km von Kaus, alt. 950 m, 2 Mar. 1994, *Hartmann et al.* 31711 (HBG); Carnarvon, Nieuwedam, N Vanwyksvlei, alt. 990 m, 18 Feb. 1997, *Hartmann* 33101 (HBG); Kalahari Gemsbok National Park: 2 miles N of Twee Rivieren, alt. 640 m, 18 Apr. 1960, *Leistner* 1852 (K); Lutzputs nach Keimoes, 6 km vom Abzweig nach Keimoes, alt. 780 m, 6 Mar. 1988, *Hartmann et al.* 25562 (HBG); Ariamsvlei nach Upington, 10.4 km vom Abzweig nach Lutzputs, alt. 730 m, 6 Mar. 1988, *Hartmann et al.*

25550 (HBG); Rooipan, alt. 1,050 m, 7 Mar. 1996, *Hartmann* 32896 (HBG); Vrede nach Upington, Christiania Einfahrt, alt. 940 m, 13 Feb. 1998, *Hartmann et al.* 33303 (HBG). **Hay:** Daskop, alt. 1,000 m, 6 Mar. 1966, *Hartmann* 32889 (HBG); Roodemanskloof, Ostzaun, alt. 1,000 m, 11 Feb. 1997, *Hartmann* 33045 (HBG); Kenhardt, 14.2 mls W of Bladgrond on Pofadder road, 22 Apr. 1954, *Gomins* 657 (K); Louisvale nach Kenhardt, 13 km von Teerstraße Keimoes-Kenhardt, alt. 920 m, 7 Mar. 1988, *Hartmann et al.* 25573 (HBG); Klein Vanwykspan, alt. 980 m, 15 Feb. 1994, *Hartmann et al.* 31407 (HBG). **Namaqualand.** Rozybosch, 9 Jan. 1909, *Pearson* 3826 (K); Ghaams Berg S Aggeneyns, alt. 980 m, 18 Feb. 1991, *Hartmann* 30097 (HBG); Springbokkeel, s.d., *Zeyher* 633 (B, S); Postmasburg, Hospital Hill, alt. 1,300 m, 14 Feb. 1997, *Hartmann* 33072 (HBG); Prieska, Boesmansberg, alt. 1,140 m, 4 Mar. 1996, *Hartmann* 32866 (HBG); Upington, Kakamas nach Pofadder, eben W von Kakamas, alt. 670 m, 7 Mar. 1988, *Hartmann et al.* 25601 (HBG). **Western-Cape:** Prince Albert, Abrahamskraal, alt. 515 m, 13 Feb. 2006, *Hartmann & Milton* 34678 (HBG).

Notes – When Sonder (1862) described the species, he contrasted it formally with *T. crystallina*, in which latter he described two new varieties from southern Africa with spatulate leaves, both now united under the name *T. corymbosa*. This latter species lacks the characteristic crystalline leaves and tepal teeth as well as the fimbriate bracts of *T. crystallina*, however. In contrast to Sonder's information, the "roundish leaves" cannot be seen as distinctive for *T. parvifolia* (because *T. crystallina* has more or less round to broadly ovate leaves, too) nor can the number of "3-flowered, not many flowered glomerules" be confirmed (up to 12 flowers per inflorescence have been counted).

The lectotype *Drège* s.n. S 03-525 (S) stems from near the Gamka River, a marginal locality within the wide distribution area. The rediscovery of a rich population in the relevant area permitted a recent assessment of the entire complex, in which different subforms can be recognized based on their distinctive morphological features usually constant per population but not beyond. Note, however, that *T. corymbosa* can be separated as a species of its own.

Examination of the type material of *T. parvifolia* var. *annulata*, *Pearson* 9231, reveals that the material was collected at a particular state during the seasonal circle: the leaf blades are broken off while the basal portions of petiole and the very broad pseudostipules clasping the stem remain visible, described as "white rings". Depending on weather conditions, this phase can last for some time in habitat and can hence be observed in many populations of *T. parvifolia*.

In contrast to Adamson (1962), who included *T. hereroensis* as a synonym under *T. parvifolia*, Friedrich (1970) kept the former species up, based on the observation of the growth form developing into "dune cushions" by growing through the covering sand. Since the present studies show major differences between *T. parvifolia* and *T. hereroensis*, the latter species is restored again here. Nevertheless, a number of herbarium sheets from northern Namibia and southern Angola differ from typical plants of *T. parvifolia* in possessing noticeable bladder cells on their leaves and internodes. In those cases, in which this feature is correlated with more ovoid or flatter more elongate oval blade shapes, the name *T. triquetra* has been applied (e.g. Friedrich 1970). As is shown in this paper, *T. triquetra* is characterized by almost flat leaves and smooth internodes, and also by smaller cymes and narrow

pseudostipules. The populations in question in the northern part of the distribution area differ from both, *T. triquetra* and *T. parvifolia* in their typical forms, in longer, more papillate leaf blades, internodes with globose bladder cells, a rather thin undulating rim of the operculum and, in some cases, longish seeds in contrast to the roundish seeds found in both named species. It appears, however, that the changes occur in steps and gradually, perhaps representing a cline. With only little and old herbarium material available, no conclusions can be drawn at this stage, but the northern and north-eastern populations need further attention and more extensive study based on fresh material.

10. *Trianthena salsoloides* Fenzl ex Oliver (Oliver 1871: 588). – Type: Sudan, "Ad pagum Cordofanum Arasch Cool inter gramina locis siccis. U.i.1841. glareosis d.", 7 Oct. 1839, *Kotschy* 137 (lecto: K, **designated here**; electronic image K000075434; iso: B, BM, BR, M, WAG).

Trianthena multiflora Peter (Peter 1932: 29; as "*T. multiflorum*"). **synon. nov.** – Type: Tanzania, Masai District, Emugur Belekj, alt. 870 m, 15 Jul. 1926, *Peter* 42741a (lecto: B, **designated here**).

Annual to biennial herbaceous plants to 15 cm tall, with erect to decumbent and prostrate branches to 30 cm long; the thin, woody taproot to 14 cm long. Internodes often orange to reddish coloured, sparsely adorned with semiglobose bladder cells, broadest at their bases, in young plants internodes shorter than leaves, in old plants distinctly longer than leaves. **Leaves** linear, petioles basally with two translucent pseudostipules, each ending in an acuminate to acute tooth, margins and keel with hemispheric bladder cells, i.e. broadest at their bases, rather dense and prominent in young leaves, distant and lower in old leaves, margins recurved, leaves 15–30 mm long, up to 3 mm broad. **Inflorescences** compact, composed of the connate flowers embedded into stem tissue in the axils of leaves, described as "consolidated below" by Kotschy, falling off as a whole body when older. **Flowers** 10–15 per axil on older branches, with reduced bracts and bracteoles on the compound base, only parts of the nearly smooth tepal tube visible, the free, erect, acute tepal teeth forming prominent bulges at their bases and developing a subapical long tip overtopping the actual leaf tip in an erect position, teeth about as long as the entire tepal tube; tepals greenish inside with white lateral flaps. **Stamens** one (in Kenyan material), or two (in Tanzanian material), "five or fewer (?)" in Sudanese material (*Kotschy* 137, only two found in the type material), yellow or magenta; **operculum** resembling a puffed sleeve in so far as the rim appears "collected", with more or less straight sides, containing one seed, the lid < 1 mm wide and up to 1.2 mm high, often skewed, apically surrounded by a thick rounded rim, the inner wall of which is almost straight in a ripe fruit but can resemble the slopes of a crater in unripe fruits or collapse flatly when dried too fast, developing almost a ridge. **Seeds** only one per pyxidium, 1.6 × 1.2 mm in side view, 0.9 mm thick, covered completely by a thin aril disintegrating with age, the sides with up to six low bulges in semi-circular arrangement. Fig. 6D–F.

Habitat and distribution – In ruderal, open places with grass to scrub cover, mostly in alluvial loamy or black cotton soil

on which sometimes pebbles can be found from Kordofan in Sudan (only the type of *Kotschy* known from there) through Kenya into Tanzania. Alt. 320–1700 m.

Additional specimens studied – Kenya. Eastern Province: 12 km von Kargi nach Marsabit, alt. 360 m, 11 Mar. 1987, *Hartmann & Newton* 21344 (HBG). **Rift Valley Province:** Ologesailie, Prehistoric Site, 19 Mar. 1987, *Hartmann & Newton* 21426 (HBG); 32 km vom Tarach River, W side of Kakuma, alt. 660 m, 16 Feb. 1989, *Hartmann & Newton* 28427 (HBG); 2.6 km E of Lokichoggia, alt. 660 m, 16 Feb. 1989, *Hartmann & Newton* 28430 (HBG).

Tanzania. Arusha Region: About 1.5 km N of Kwakuchinja, alt. 1,050 m, 21 Jul. 1956, *Milne-Redhead & Taylor* 11188 (B). **Kilimanjaro Region:** Zwischen dem Uguenogebirge (N Pare Mtns) und dem Papyrus, s.d., *Volkens* 451 (B); am Mangasee bei Mkomasi, alt. 400 m, 6 Jun. 1915, *Peter* 10873 (B, syntype of *T. multiflora*). **Rukwa Region:** Nr Tumba, alt. 1,000 m, 29 Jan. 1951, *Bullock* 3639 (B). **Singida Region:** Singida Lake, alt. 1,670 m, 24 Apr. 1962, *Polhill & Paulo* 2209 (B). **Tanga Region:** Betw. Mombo and Same, Tanga to Moshi road, near Mkumbara, alt. 325 m, 2 Jun. 1970, *Mwasumbi et al.* 10742 (WAG).

Notes – The material of both syntypes chosen by Peter when publishing the name *T. multiflora* agrees in the critical features with the type material of *T. salsoloides* in having a connate base of all flowers in the compact lateral inflorescences, in the possession of pronounced basal bulges on the erect tepal teeth, and in containing one seed in the ripe fruit. *T. multiflora* is therefore understood here as a synonym of *T. salsoloides*.

Fenzl distributed material of *Kotschy* 137 with the inscription “*Trianthema salsoloides* Fenzl”, but never published a description. Oliver (1871: 588) gave “Fenzl in Herb. *Kotschy*. Nub. 137” behind the name “*T. salsoloides*”, yet he did not annotate the relevant sheet at K as a type. Nevertheless, Oliver must have seen the sheet kept now at K, where he worked, and this particular sheet is chosen here as the lectotype. All other sheets of *Kotschy* 137 in other herbaria are isolectotypes.

11. *Trianthema sanguinea* Volkens & Irmsch. (Volkens & Irmscher 1913: 498). – *T. triquetra* Willd. ex Spreng. subsp. *triquetra* var. *sanguinea* (Volkens & Irmsch.) Jeffrey (Jeffrey 1960: 237). – Type: Tanzania, Moshi District, Steppe zwischen Pangani- und Himofluß, alt. 700 m, 5 Jul. 1893, *Volkens* 458 (holo-: B; iso-: BR, K).

Trianthema nigricans Peter (Peter 1932: 30). – Type: Tanzania, Masai District, Emugur Belekj, alt. 870 m, 15 Jul. 1926, *Peter* 42741c (holo-: B).

Herbaceous plants with erect or ascending straight branches to 25 cm tall; internodes usually much longer than the leaves, ochre, moderately papillate from almost semiglobose bladder cells broadest at their base. **Leaves** 10–18 × 2 mm, linear, petioles basally with two big translucent flaps, each ending in 1(–3) broad rounded teeth, rarely without a tooth, margins and keel with bladder cells broadest at their bases and only a little longer than thick, more prominent in young leaves, inconspicuous and almost flat all over in old leaves, margins recurved. **Inflorescences** dense, in the axils of leaves, yet each **flower** free to the base, somewhat conical, bracts broadly acuminate, bracteoles slender, small, and acuminate, the free teeth of the tepals erect to overarching

the ripe fruit, outside with numerous elongate bladder cells shaped like tiny fingers and just visible with the naked eye, their length increasing towards the tooth tip, the bases of the tepal teeth forming protrusions or loops at their joining points. **Stamens** five. **Operculum** about 1.2 mm in diam. and 0.6–1 mm high, often skewed and hence with one side longer than the other, with a broad rugose ring around the small sunken centre, the ring visible in the old flower already. **Seeds** two, black, appressed to and on top of one another, about six irregular crests on each side, visible in the SEM below the thin aril, c. 1.2 × 0.8 × 0.6 mm. Fig. 7A–D.

Habitat and distribution – In open, disturbed places among pebbles in SE Kenya and NE Tanzania. Alt. 15–350 m.

Additional specimens studied – Kenya. Rift Valley Province: Btw. Samburu and MacKinnon Road, alt. 350 m, 1 Sep. 1953, *Drummond & Hemsley* 4090 p.p. (B); Within a short distance of the gate at Magadi. Enkarmalasiai–Nanyokie, 30 Jun. 1962, *Glover & Samuel* 2979 (K); ‘Ol Orgesalik’, 19 Aug. 1953, *Verdcourt & Robyns* 1009 (K); Ologesailie Nat. Monument, 13 Jun. 1980, *Gilbert* 6272 (K); *ibid.*, 19 Aug. 1944, *Bally* 3546 (K).

Notes – Jeffrey (1960) cited already *T. nigrescens* as a synonym of *T. sanguinea*, although he named the species wrongly *T. triquetra* and reported that the type of Peter had been destroyed, which is not the case.

Remarkable is the rather small distribution area along the border between Kenya and Tanzania and rather close to the coast.

12. *Trianthema sedifolia* Vis. (de Visiani 1836: 19, t. 3, f1). – *T. crystallina* (Forssk.) Vahl var. *sedifolia* (Vis.) Hiern (Hiern 1898: 415). – Type: Sudan, Khartoum, s.d., *Brocchi* s.n. (holo-: BASSA, n.v.).

Trianthema sedifolia Vis. var. *microphylla* Courbon (Courbon 1862: 156). – Type: Eritrea, Dahlak Island, Dessie (Dissée), lieux argilleux de la plaine du village, s.d., *Courbon* s.n. (holo-: P, n.v.).

Trianthema glandulosa Peter (Peter 1932: 30). – Type: Tanzania, Masai District, Emugur Belekj, alt. 870 m, 15 Jul. 1926, *Peter* 42741b (holo-: B).

Annual herbaceous plants with decumbent to ascending branches to 25 cm long; stringy taproots to 12 cm long, apically to 5 mm in diam.; internodes ochre, densely papillate from egg-shaped prominent bladder cells up to 200 µm long, rising from a narrow base as if glued at one end to the epidermis, internodes usually longer than the leaves. **Leaves** up to 12 mm long, up to 2 mm broad, narrowly ovate, petiole widening into translucent pseudostipules, each ending in a short broad tooth or without one, margins and keel with bladder cells broadest at their bases and longer than thick, more prominent in young leaves, inconspicuous and almost flat all over in old leaves, margins recurved, even in fresh material. **Inflorescences** dense and almost compact in the axils of leaves, few flowers in younger and 8–10 on older branches, the bract and the two smaller bracteoles acuminate to pointed. **Flowers** with free basal tepal tubes, conical, the free teeth of the tepals shortly triangular, not reaching the centre of the ripe fruit and just less than half as long as the tepal tube, over-arching the ripe fruit, sparsely papillate outside, smooth with age. **Stamens** three. **Fruit** in the young state with the **opercu-**

lum forming a broad smooth ring around the sunken centre, the wall usually sloping down gradually, the rim later shrivelling to form an irregular bulge around the edge, about 1.6 mm in diam. and 0.6 mm high, pushing the short tepal teeth outwards during the ripening process, leaving the tips of the tepal teeth visible from above. Seeds two, black, appressed to and on top of each other, c. $1 \times 0.8 \times 0.6$ mm, depending on the position in the capsule, crests on sides absent, often a sharp one at the outer rims of the contact zones and sometimes inconspicuous bulges along the back region of the seed, surface covered by a thin aril. Fig. 7E–H.

Habitat and distribution – In open, disturbed places among pebbles in Saudi Arabia, Yemen, Morocco, Mauritania, Eritrea, Somalia, Sudan, Kenya, northern Tanzania, Uganda. Alt. 5–1,000 m.

Additional specimens studied – Eritrea: Wadi Assarai area, alt. 86 m, 27 Mar. 1949, Bally 12 (K).

Kenya. Coast Province: Tana River, K7 Garissa–Garsen road, 8.3 km towards Garsen from turnoff to Bura, alt. 100 m, 7 Jul. 1974, *Faden & Faden* 741004 (WAG); Kurawa, 30 mls S of Garsen, alt. 15 m, 20 Sep. 1961, *Polhill & Paulo* 504 (B, K). **Eastern Province:** 12 km von Kargi nach Marsabit, alt. 360 m, 11 Mar. 1987, *Hartmann & Newton* 21345 (HBG); 18 km NW of Marsabit, 11 Mar. 1987, *Hartmann & Newton* 21347 (HBG). **Rift Valley Province:** Btw. Samburu and MacKinnon Road, alt. 350 m, 1 Sep. 1953, *Drummond & Hemsley* 4090 p.p. (K); Lake Hannington, 16 Jul. 1945, *Bally* 4547 (K); Southern shores of Lake Baringo, 21 Aug. 1956, *Bogdan* 4226 (K); Turkana, Lorengipe, 1 Oct. 1963, *Bogdan* 5643 (K); *ibid.*, 30 Jan. 1965, *Newbould* 6875 (K); South Turkana, Epesepes, Turkana Suguta Valley, 29 May 1970, *Mathew* 6468 (K).

Morocco: s.l., 1 Jan. 1908, *Müller* s.n. (B).

Mauritania: Flora of French Oualata Region, s.d., *Yamelle* s.n. (K).

Saudi Arabia: Ad GemFadam, s.d., *Ehrenberg* s.n. (B); Bani Malek on the NW side of the mountain, near Jabal Fayfa, 100 km NE of Jizan, alt. 830 m, 30 Sep. 1982, *Collette* 3905 (E, K); Jizan Airport, 23 Mar. 1983, *Collette* 4180 (E, K); 10 km S of Jizan, Abu Arish road, 28 Nov. 1988, *Collette* 6896 (K); nr Usfan, 60 km NE of Jiddah, alt. 27 m, 23 Mar. 1983, *Collette* 7349 (E, K).

Somalia: 20 km on road between Luuq and Beled Xaawo, 7 Jun. 1989, *Thulin & Mohamed* 6962 (K); 1 km E of Tokshi on road going east to Zeila, 26 Jan. 1973, *Bally & Melville* 16134, (MO); Buthar (Butar), 14 Oct. 1912, *Drake-Brockmann* 912 (K).

Sudan: Kassala nach Erkowitz, mls 10763 = 121 km N Aroma, 17 Nov. 1987, *Hartmann* 21465, 21468 (HBG); 42 mls NE of Kapoeta on Boma Rd., 30 Aug. 1953, *Peers* s.n. (K); Ad pagum Cordofanum Abu Gerad, 25 Sep. 1839, *Kotschy* 67 (B, WAG); c. 8 km S of Khartoum, 1 Aug. 1961, *Jackson* 4307 (K); nr Soba Station, c. 12 km S of Khartoum, alt. 390 m, 1 Jul. 1961, *Jackson* 4289 (K); Suakin nach Tokar, c. 10 mls S of Suakin, alt. 20 m, 21 Nov. 1987, *Hartmann* 21532 (HBG); Weisser Nil, Getena, 7 Jan. 1896, *Schweinfurth* 904 (B).

Tanzania. Iringa Region: Iringa, T7, Ruaha National Park, near Ruaha river, about 5 mls NE of park headquarters at Msembe, 14 May 1968, *Renvoize & Abdallah* 2134 (K). **Coast Region:** T8 Kingupira, alkaline flats, 27 Feb. 1976, *Vollesen* 3292 (K); **Kilimanjaro Region:** Mwanga, T3, Kileo Village, 15 Sep. 1981, *Mhoro* 4075 (MO), T3, Lake Manka, 28 Mar. 1975, *Wingfield* 2917 (K).

Uganda: Busoka Province, Karamoja, Kautaku enclosure, 9 Jan. 1959, *Wilson* 625 (K).

Yemen: Große Mahra, coastal Mountains between Al Fay Dam und Hawf Bay with sandy beach and boulders, 10 km E of the village Dam Gawt, alt. 5 m, 12 Nov. 2000, *Hein et al.* 8087 (B); Sheik Othman-Aden, 29 Nov. 1988, *Gifri* 1099 (UBT).

Notes – The placement of the species as a variety of *T. crystallina* by Hiern (1898) was based on material from Angola, where neither *T. crystallina* nor *T. sedifolia* occurs. *T. sedifolia* shares with *T. crystallina* and *T. sheilae*, however, the big prominent and numerous bladder cells on the internodes but lacks the big globose bladder cells on the leaves of the two latter species completely. *T. sedifolia* differs also in its annual growth, the possession of more narrow and acute bracts and bracteoles, and in the formation of almost smooth seed surfaces from the two other species in the area.

No material of Brocchi referable to this species has been found in BASSA in 2007–2008.

The obvious gap in distribution between the southern and the northern parts of the NE African area can, on one hand, be explained by the existence of the Ethiopian Highlands, probably unsuitable for the genus to grow, and also by the fact that no collections from southern Sudan are available, neither recent nor older. A record from Morocco (*Müller* s.n., B) cannot be located precisely, but it suggests that the species is much more widespread in northern Africa than hitherto reported reliably. Nevertheless, the presently known data show a wide distribution area for this species.

13. *Trianthena sheilae* A.G.Mill. & J.A.Nyberg (Miller & Nyberg 1994: 33). – Type: Saudi Arabia, 12 km N of Mukayl road junction Jizan–Qunfudhah road, 4 Feb. 1984, *Collette* 4718 (holo-: E).

Annual herbs to perennial fruticose plants with decumbent to ascending branches forming shrubs to 35 cm tall and up to 75 cm in diam.; internodes terete, young ones with a touch of straw colour and with distant rather small bladder cells, bigger and denser near the uppermost nodes, turning woody and smooth with age, drying almost white. Leaves ovate to almost circular, $4\text{--}8 \times 3\text{--}6$ mm, thickish, covered completely by big bladder cells touching each other, the white dry rims overlapping in herbarium material, contrasting against the sometimes blackish background, tip of leaf usually rounded, rarely somewhat acuminate, petiole mostly below 5 mm long, adorned with two broad flaps on each side resembling stipules, each with a terminal tooth, pointing upwards or sideways, the flaps widening regularly towards the base of the blade, the widest point often adorned with a short broad tooth, the flap narrowing again at the base at the stem, teeth sometimes fimbriate, but not regularly so. Inflorescences of 1–5 flowers, each flower with a fimbriate bract and two fimbriate bracteoles, all papery in consistence and broad, clasping the interior and conspicuous as whitish sheaths with the naked eye. Flowers 5–6 mm in diam. when fresh, 3.5–4.5 mm wide when dry in the herbarium, up to 2 mm long, the free tepal teeth erect, sometimes apically recurved and drawn out acutely, usually 1.25 mm long, subapically with a protrusion overtopping the papery margin of the tooth of c. 0.8–1 mm length; the bases of the tepal teeth at the points of joining the calyx tube with pronounced bulges (“sinuses” of the original description), epidermis covered densely with big bladder cells like those on the leaves; the tepal tube with erect but small bladder cells, smoothing with age because the bladder cells are rubbed off. Stamens five, alternitapalous, with yellow, scarlet, or orange anthers, pollen usually yellow.

Fruit almost globular when young, the operculum blown up like the upper half of a balloon with an indistinct upper rim reaching far into the centre where it leaves a small deepening from which the long stigma protrudes well between the stamens; the operculum surface smooth when young, unevenly shrinking with age, resulting in a wrinkling rim distinct from the wrinkled remaining operculum surface below, in which a seed is held. Seeds two per capsule, the contact side flattened, but all sides equipped with narrow rows of bulges, c. nine more or less crescent-shaped ones per side, and 6–8 straight ones along the back of each seed; seeds almost orbicular, 1.1–1.2 × 0.9–1 × c. 0.7 mm. Fig. 1E–H.

Habitat and distribution – Most often in sand near the sea, amongst lava rocks or coral remains, more rarely inland and in loam near the western coast of Saudi Arabia and along the southern coast of Yemen, in southern Egypt, eastern Sudan, and southern Eritrea. Alt. 10–2,100 m.

Additional specimens studied – **Egypt**: nr Ararib, Umm Qareiyat Mine, 23 Feb. 1963, *Abdallah et al.* 1186 (WAG); nr Ararib, W. Al-laqi, opposite G. Filat Da mer, 1 Mar. 1963, *Abdallah et al.* 1220 (MO, WAG).

Eritrea: About 150 km. SW of Assab (Asabot), along main-road, 11 Jan. 1966, *De Wilde & De Wilde-Duyffes* 9740 (WAG).

Saudi Arabia: Al Wahbah crater, alt. 1,500 m, 13 Apr. 1983, *Collenette* 4297 (E, K); nr Farasan village, S of village, alt. 7 m, 4 Feb. 1985, *Collenette* 5026 (E); 55 km N of Madinah, Khaybar Road, alt. 2,100 m, 30 Oct. 1989, *Collenette* 7286 (E, K); Mahazat Assaid Reserve, 2 km SE of the Khumah-Riyadh road, alt. 1,000 m, 15 Jul. 1991, *Collenette* 7852 (E, K); Wadi Murr, 30 km E of Rabigh, alt. 97 m, 25 Feb. 1992, *Collenette* 7913 (K); Jizan, Sarso Island, Farasan, alt. 20 m, 19 Feb. 1995, *Collenette* 9284 (E, K); In montibus vallis Fatme Arabiae felicis, 27 Feb. 1836, *Schimper* 885 (HBG); circa Geddam (Dschedda?), s.d., *Spitzel* 1690 (B).

Sudan: Dongola, s.d., *Ehrenberg* s.n. (B); Tokodele, s.d., *Ehrenberg* s.n. (B); Kassala nach Erkowit, mls 10763, 17 Nov. 1987, *Hartmann* 21464 (HBG); 81 mls N of Aroma, 17 Nov. 1987, *Hartmann* 21470 (HBG); Ssoturba Gebirge, 22°N, alt. 2,100 m, an der Nubischen Küste. Jebel Choturba, Apr. 1864, *Schweinfurth* 792 (B).

Yemen. Abiyan Governorate: Wadi, 15–20 km E Shuqra, along the coastal road to Ahwar, alt. 10 m, 14 Mar. 1988, *Boulos et al.* 17210 (MO); Shabwa, ruins of Qana, SW Bir Ali, 2 Apr. 2003, *Kilian et al.* 4626 (B); 10, Shabwa, sandy coast between Arga and Ahwar, 26 Mar. 2003, *Kilian et al.* 4342 (B); Kurz vor Al Kanauis, 20 Feb. 1979, *Mueller-Hohenstein* 51 (UBT); Hodeida, alt. 20 m, Küstentihama bei Al-Kawbah, 21 Mar. 1983, *Müller-Hohenstein & Deil* 1467 (UBT); Unteres Wadi Siham (bei Nishamah), alt. 600 m, 13 Sep. 1986, *Rappenhöner* 332 (UBT); Hadramaut, Küstengebiet von Bol Haf, 27 Nov. 1898, *Simony* s.n. (HBG); Hadramaut, Mefa-Makalla, 15 Jun. 1931, *Wissmann* 1631 (HBG).

Notes – *T. sheilae* was described as differing from *T. crystallina* in being a much-branched, ascending bushy annual or perennial herb, having yellowish-green leaves and yellow flowers. Since Forsskål (1775) described the habit of *T. crystallina* as “fruticosa”, he obviously saw a shrubby plant from which he picked a branch, which looks woody and whitish on the type, suggesting perennial growth. Fresh material from Sudan combines decumbent branches with yellow flowers, as reported also for Eritrean material. Furthermore, all plants with appropriate records mention yellowish-green leaves, independent from habit. In the discussion of *T. sheilae*, it is reported that the tepal teeth spread in *T. crystallina*, a character state not visible on the type sheet of the latter species.

Here, the tepal teeth stand erect and only a little connivent in flowers pressed sideways, but they cover the operculum completely in those flowers that were pressed from the top.

T. sheilae is very similar to *T. crystallina*, as is obvious from the list of shared character states under *T. crystallina*. Differences lie in the bigger fresh flowers with yellow inner tepal surfaces (6 mm diam. in *T. sheilae* as opposed to 3 mm in the fresh flower of *T. crystallina*), the fact that the outer tepal lobes exceed the tepal tips distinctly, the formation of “sinuses” at the bases of the tepal lobes, actually representing thickened loops in the closed flower – not visible in the open flower, and the possession of a long stigma reaching up well between the stamens (all described character states for *T. sheilae*).

The most prominent features, the bigger and yellow flowers in *T. sheilae*, lose their size and special colour when being dried, and hence an assessment of herbarium material is extremely difficult, leading to misidentifications. Since the differences are indeed small, it may be worth considering whether the two taxa should not better be ranked as two subspecies in one species, *T. crystallina*.

14. *Trianthea transvaalensis* Schinz (Schinz 1915: 396). – *T. salsoloides* var. *transvaalensis* (Schinz) Adamson (Adamson 1962: 248). – Type: South Africa, Transvaal, in arenos prope Matsaba, alt. 730 m, 4 Mar. 1897, *Schlechter* 4876 (holo-: Z; iso-: K).

Trianthea salsoloides Fenzl ex Oliver var. *stenophylla* Adamson (Adamson 1962: 249). – Type: South Africa, Transvaal, Kruger National Park, Gudjane Rd on turn, 20 Apr. 1954, *van der Schijff & Marais* 3734 (holo-: K; iso-: PRE).

Annual to shortly perennial herbaceous plants with decumbent to ascending branches to 30 cm long, most of them in dichasial branching; woody taproots to 12 cm long, apically to 5 mm in diam. Internodes often orange to reddish or purple coloured, rather densely covered with globose bladder cells, in young plants shorter than leaves, in old plants distinctly longer than leaves. Leaves 15 mm long, up to 3 mm broad, narrowly spatulate, petioles basally with two translucent flaps, each ending in an acuminate tooth or rounded, margins and keel with finger-tip shaped bladder cells, i.e. broadest at their bases and longer than thick, more prominent in young leaves, inconspicuous in old leaves, margins recurved; the upper leaf surface with a translucent line of tissue, due to the absence of chlorenchyma below the epidermis. Inflorescences dense and rather compact in the axils of leaves, 10–15 flowers on older branches, subtended by a broad-based acuminate bract with 0–1 teeth and two more slender bracteoles with a long tip and often a tooth. Flowers with free bases or sunken with their lower parts into a solid basal tissue, the tepal tube visible for half to most of its length, the free, erect, acute tepal teeth forming prominent bulges at their bases and very long subapical tips overtopping the actual leaf tip widely, teeth about as long as the entire tepal tube, covered rather densely with bladder cells, longer ones erect on the teeth, which are smooth and white or greenish inside, with white lateral flaps. Stamens five. Fruit with straight sides in the basal part, the operculum forming a rounded lid with a central deepening on top, surrounded by the rim resembling a short puffed sleeve,

the lid up to 1.2 mm in diam. and c. 0.5 mm high. Seeds in most cases two, but sometimes the second one visible as an abortive small body at the base of the capsule only, 1.3 mm long and 1 mm broad and thick, covered completely by a thin aril disintegrating with age, the sides with irregular rounded crests in curved to semi-circular arrangement, the back with three prominent crests, black. Fig. 6D–F.

Habitat and distribution – In open places with grass to scrub cover, mostly in alluvial loamy or black cotton soil from Botswana, the southern parts of Zimbabwe and through Limpopo Province, Mpumalanga, and KwaZulu/Natal, South Africa into Mozambique. Alt. 100–200 m.

Additional specimens studied – **Botswana:** Overlooking western end of Chenkwanana pan, in block, 18 Feb. 1980, *Smith* 3097 (MO).

Mozambique: Lourenço Marques. Sabie, ao km 31, de Lourenço Marques para Ressano Garcia (Cp), 22 Apr. 1971, *Marques* 2254 (MO).

South Africa. Limpopo: Dongola, 2 Jan. 1949, *Codd* 4862 (PRE); Pietersburg, Magoebaskloof, 1 Nov. 1913, *Pott-Leendertz* 4785 (PRE). **Lydenburg:** Groenlands, 10 Jan. 1939, *Barnard & Mogg* 1044 (PRE). **Pilgrims Rest:** Leeuwpan, 18 Jan. 1953, *Acocks* 16749 (PRE). **KwaZulu/Natal. Ubombo:** Mkuze Park, alt. 100 m, 9 Feb. 1988, *Hartmann & Dehn* 25119 (HBG). **Lower Umfolozi:** Umfolozi, alt. 170 m, 4 Mar. 1999, *Hartmann & Kremling* 33775 (HBG); Mahlabatini, Umfolozi, alt. 176 m, 6 Mar. 1999, *Hartmann & Kremling* 33778 (HBG).

Zimbabwe: Gwanda, near Hwali River crossing near Hwali Store, 22 Mar. 1959, *Drummond* 5887 (B); 2 km N Plumtree, 29 Jul. 1988, *Hartmann* 26747 (HBG); Bulalima Mungwe, Ramaquabane River, 7 May 1962, *Wild* 5856 (K, MO).

Notes – Adamson (1962: 248–249) placed *T. transvaalensis* as a variety in *T. salsoloides*, describing the former as being 50 cm tall, a feature that cannot be confirmed with fresh material; but branches may be 50 cm long, yet these are decumbent to prostrate. Both species share three character states: (1) the possession of prominent bulges at the bases of the tepal teeth, (2) the formation of long bladder cells at the tips of the long, erect subapical horns, and (3) the deeply placed bases of the ovaries at least partially connate.

Conspicuous features present in *T. transvaalensis* and absent in *T. salsoloides* are: (1) the existence of a prominent translucent line along the upper leaf surface combined with a shorter one along the lower leaf surface, (2) the only basally connate flowers and fruits in the lateral densely glomerulate inflorescences, (3) the more densely papillate leaves and internodes, and (4) the operculum resembling a short puffed sleeve when ripe.

The type of *T. salsoloides* var. *stenophylla* shows all features critical for *T. transvaalensis*. It must be noted in this respect that older internodes of *T. transvaalensis* turn smooth with age and that the tepal tips or horns exceed the length of the tepal teeth only in very newly opened flowers, hence no differences remain to justify the upholding of a separate species.

Little material is available for investigation, as is obvious from the list of material studied. It is remarkable that the three collections from lowlands in KwaZulu/Natal agree with the critical features, albeit they occur in a hotter and more tropical climate than those from the highlands of Zimbabwe and the Limpopo Province of South Africa.

15. *Trianthea triquetra* Willd. ex Spreng. (Sprengel 1825: 381). – Type: India, Tiruvallur, s.d., *Rottler* 330 (holo-: B; B 10 0108541).

Trianthea triquetra Willd. ex Spreng. var. *oblongifolia* Gamble (Gamble 1919: 550). – Type: India, Tamil Nadu, Tuticorin (Thoothukudi), Sep. 1900, *Ranjachari* s.n. (holo-: K)

Trianthea gisekioides Fenzl, nomen in schedis [India: Pondichery. ded. 1829, *Reynaud* s.n. (B)], **nom. inval. et synonym. nov.**

Herbaceous plants with smooth internodes adorned with few inconspicuous bladder cells; pseudostipules almost as long as the petioles, widening gradually from the base of the blade, but not exceeding the width of the leaves. Leaves flat, obovate, not incurved in the type material and ending in an acuminate tip; neither the blade nor the margins show any prominent bladder cells; inflorescences of 2–3 flowers, dense, the bract and the bracteoles acuminate. Flowers lacking papillae completely on their entire surfaces, the short tepal teeth lie incurved over the operculum. Operculum c. 1.5 mm diam., hiding the concave surface with a rather broad ring wall around its out edge. Seeds two, black, lying on top of each other exposing prominent ridges in semi-circular arrangement, mainly around the outer edge of the seed. Fig. 2D–F.

Habitat and distribution – Probably in disturbed places along the Coromandel Coast in India and the west coast of Thailand, extending to Indonesia (Java) and the Philippines. i.e. around the Gulf of Bengal. Alt. 0–650 m.

Additional specimens studied – **India. Orissa:** Cuttack, Bank of Kendrapara canal at Tanki Belari, 9 Jun. 1949, *Mooney* 3419 (K). **Tamil Nadu:** South Pichavarm, Chidambaram taluk, South Arcot, alt. 0 m, 15 Apr. 1977, *Matthew* 7349 (L); Ulundurpet, South Arcot, Pulloorkkadu, alt. 30 m, 13 Dec. 1979, *Matthew* 25095 (K); Madras, Forest College Estate, Coimbatore, 22 Nov. 1963, *Subramanian* 908 (L); Coimbatore, on the rd to Varappalayam, alt. 633 m, 25 Jul. 1956, *Subramanyam* 386 (B).

Indonesia. Java: Jawa Timur. Ganung Semonkrong, Pasoeroean, 5 Jun. 1920, *Bolle* 2395 (L); Semonkrong, alt. 10 m, 19 Oct. 1920, *Clon* 42 (L); *ibid.*, alt. 20 m, 6 May 1925, *Jeswiet* 1944 (WAG); *ibid.*, 3 Jun. 1927, *Backer* 36736 (L).

Philippines. Mindanao: Cotabato, General Santos, 1 Aug. 1961, *Barrera* 41680 (L).

Thailand: Prachuap Kiri Khan, Sam Roy Yot., 6 May 1974, *Larsen & Larsen* 33659 (K).

Notes – The material to which this name had been given originally was collected by missionary Rottler on a trip from Trankenbar to Madras and back, described in 1803 and annotated by Willdenow; herbarium material at B. Willdenow (1803) noted on page 181:

“Diese Pflanze ändert sehr in der Form der Blätter ab, die fleischig, bald sehr schmal- und dreikantig, bald aber fast flach und länglich sind. Ich halte sie für eine Spielart der *Trianthea crystallina*”. Two points in this treatment by Willdenow make the name an invalid one: the annotation is not a description, as required for the name to be validly published, and Willdenow had not intended to pick up the name used by Rottler but understood the new plant as being a variety of the old *T. crystallina* Forsskål (from near Dahi, Yemen). Sprengel (1825) picked up Rottler’s name, however, attribut-

ing it to Willdenow, and as a consequence the authorship is *T. triquetra* Willd. ex Spreng. for the Indian material agreeing with the collection of Rottler (as shown by Daniel & Umamaheswari 1999).

In order to demonstrate the differences between the two species, *T. triquetra* and *T. crystallina*, the features are listed in table 1, referring to the original descriptions and the relevant type sheets.

The stamen number of ten in Sprengel (1825) is an error as it cannot be confirmed on the type sheet.

In spite of the obvious differences, the names have been used as synonyms, from Australia over Asia to Africa.

Australian usage: Bentham & von Mueller (1866) applied *T. crystallina* to material that was later called *T. triquetra* (e.g. Eichler 1965), without changing the taxonomy. This practice was followed by Prescott (1984), who distinguished two varieties, one raised to species rank here (*T. clavata*).

African usage: In preparation of his treatment of Aizoaceae for the Flora of Eastern Africa, Jeffrey (1960) gave a survey of the genera *Sesuvium*, *Zaleya*, and *Trianthema*, deciding to combine most African species under the name *T. triquetra*. Consequently, he distinguished only one other species in his subgenus *Papularia*, *T. salsoloides* (Jeffrey 1961). Adamson (1962), however, in his treatment of the Sesuvioideae of South Africa, treated the material under three species names by restoring species rank to *T. parvifolia*, following Sonder (1862).

Comparing keys and descriptions in flora treatments in the assumed enormous distribution area of *T. triquetra* from Australia over southern Asia and as far south in Africa as the Great Karoo and Namibia, it is not surprising that, for example, *T. triquetra* is characterized as being “finely papillose to almost glabrous” in Australia (Prescott 1984: 58), whereas it is described as being “covered all over with prominent papillae becoming hard and hispid in older age” (Adamson 1962: 252). Such contradictions raised suspicion much earlier, and care must be taken when flora treatments are relied upon.

A thorough study of available material from Asia reveals that two different units can be distinguished and that only the material from southern India as well as few collections from the eastern coast of the Gulf of Bengal can be placed in. All other records must bear different names. Several collections have been made in Indonesia, all from the same area in East Java, and a single collection is known from the island of Mindanao (Philippines). These collections agree in most features with *T. triquetra* from India. It is remarkable, however, that the shrivelled outer ring around the operculum is very thin, erect, and distinctly undulate; further, all leafy parts possess papillae when young, turning smooth with age. Although found closer to Australia than to India, the operculum lacks the veil characteristic of the two Australian species. Thus, *T. triquetra* appears to be rather widespread, but it is certainly not frequent.

16. *Trianthema ufoensis* H.E.K.Hartmann & Liede, **sp. nov.**

Herba annua ramis procumbentibus vel ascendentibus diametro ad 60 cm, internodiis ochraceis vel rubicundis, epidermis cellulis vesicariis fere globosis approximatis tecta; foliis li-

nearibus hyalinis mucronibus ornatis, mucro aetate disrumpens, epidermis cellulis vesicariis semiglobosis dense tecta, petioli basaliter late alati, alae dente uno quasi acuminatae, marginibus laminarum incurvatis, laminis ad 14 mm longis ad 2 mm latisque, petiolis 4 mm longis; inflorescentia floribus 1–2 juvenalibus papillatis, laevibus cum aetate; operculum fructus 2–2.5 mm latum, annulum rugosum externe circumdatum, quod stratum hyalinum vel velum expandentem super interiorem depressum tenet, purpureo maculatum vel omnino conspicue suffusum; 2 seminibus atris appressis. – Type: Australia, Northern Territory, 2.9 km from Daly Waters, N along Stuart Highway, 25 Feb. 1999, *Short & Dunlop* 4932 (holo-: DNA)

Annual herbs with procumbent to ascending branches, up to 60 cm in diam.; internodes ochre to reddish, young ones with nearly globose bladder cells rather densely placed. **Leaves** linear, with a hyaline mucro of 2–4 mm length at the tip, breaking off with age, blade covered densely by semi-globose bladder cells, petiole basally with two translucent pseudostipules, each ending in an short broad tooth pointing outwards, margins prominently recurved, blades 10–14 × 1–2 mm in herbarium specimens, petioles c. 4 mm long. **Inflorescences** with 1–3 flowers, very rarely more; the bract and the two bracteoles broadly acuminate. **Flowers** with bladder cells higher than wide when young, older smooth; tepal teeth short and erect in the ripe capsule, surrounding the operculum as a ring and not incurved over it, equipped with subapical teeth overtopping the tepal tip and adorned with bladder cells. **Operculum** very broad (2–2.5 mm in diam.) with a narrow rugose ring around the edge holding a translucent hyaline layer level with the top of the ring, hiding the sunken interior from sight, splitting and disintegrating with age, the inside of the ring wall concave, the whole operculum therefore more similar to a pastry crust than to the more common bowl or crater shape, with red-purple dots or completely suffused reddish-purple during the ripening process. **Seeds** two, black, appressed to and on top of each other, their margins mostly with four crests, sides with very low irregular crests, surface covered by a thin aril, about 1.5 × 0.8 × 0.6 mm. Fig. 5D–F.

Habitat and distribution – In clayey soil, also in sand or in heavy dark brown soil in northern and central parts of Australia.

Additional specimens studied – **Australia. Northern Territory:** Willeroo, 18 May 1971, *Byrnes* 2200 (K); Talbot Well, 38.3 mls NE Tanami, 11 Apr. 1959 *Chippendale* 5652 (K); VRD Station, 17 May 1994, *Egan* 3679 (DNA); Northern Wakaya Desert, 18 May 1993, *Latz* 13158 (DNA); Walker River, Blue Mud Bay, 5 May 1993, *Leach & Dunlop* 3669 (DNA); Elsey Stn., 27 Apr. 1993, *Menkhorst* 1216 (DNA); Buchanan Highway, 18 Mar. 1998, *Michell* 1261 (DNA); Bradshaw Station, 17 Feb. 1999, *Michell & Russell-Smith* 2223 (DNA). **Queensland:** Burke Distr., Julia Creek, Jan. 1962, *Nelson* s.n. (K); Leichhardt Distr. Dawson River at Baralaba, 21 Oct. 1963, *Speck* 1903 (K); Mitchell Distr., Springvale, Jericho and vicinity, Apr. 1946, *Clemens* s.n. (K); North Kennedy Distr., Fletcher View Research Station, near Charters Towers, 14 May 1997, *Corfield* 3145 (BRI); 2 mls from Clermont on Clermont–Emerald rd., 3 Apr. 1974 *Carolin* 8236, (K); Bladensburg National Park, S of Winton, near Mistake Hut, 20 Mar. 1998, *Forster & Booth* 22244 (BRI); Wandoan, 16 Nov. 1930, *Hubbard* 5013 (K); Bundoran, near Nonda, betw. Hughenden & Cloncurry, 6 Feb. 1931, *Hubbard & Winders* 7266, 7308 (K); 30 miles of Windorah on Betoota rd., 12 Jun. 1963, *Macdonald* 536 (K); Port Curtis, 23 Oct. 1947, *Smith* 3488 (K).

South Australia: Todmorden HDL Yard. Region 2: Lake Eyre, 3 Apr. 1992, *Jessop* 133 (AD); Mt. Lyndhurst, 1 May 1898, *Koch* s.n. (K). **West Australia:** Kimberley Region, Duncan Highway, 12 km SE of Halls Creek Old Town, 8 Apr. 1997, *Dürbye* 432 (B).

Notes – Together with *T. clavata*, this species has been named *T. crystallina* or *T. triquetra* until now, irrespective of the fact that *T. triquetra* lacks the translucent layer covering the ripe operculum, which is, in addition, overarched by smooth tepal teeth in *T. triquetra*. *T. ufoensis* differs from *T. clavata* in having flat longer leaf blades of 10–14 mm length, a translucent mucro up to 4 mm long, usually not more than three flowers per inflorescence, a subapical horn on the tepal teeth 0.5–1 mm long, and opercula of diameters between 1.5 and 2 mm. The epithet refers to the ufo-like appearance of the operculum, conspicuously purple even in the dry state and eye-catching in most populations.

17. *Trianthema vleiensis* H.E.K.Hartmann & Liede, sp. nov.

Differt a *Trianthema parvifolia* foliis fusiformibus acuminatis quasi vittatis: linea distincta stricta supra venam centram hyalina in luce translucida, atrovirens in luce repercussa, tepalis longis erectis et summo operculo constricto posito supra basem multo latiore, in qua semina continentur; differt a *Trianthema transvaalensi* ramis prostratis, pseudostipulis latoribus, floribus separatis (nullo modo connexis) et tepalis brevioribus; differt ab duabus speciebus in protuberationibus basalibus dentium tepalorum parce formati. – Type: South Africa, North West Province, Bloemhof, S.A.Lombard Nature Reserve, alt. 1,240 m, 9 Mar. 1993, *Hartmann* 31323 (holo-: HBG).

Annual to perennial herbaceous plants with prostrate branches to 50 cm long from a hypocotyl that can broaden to a diameter of 8 cm, remaining flat on top; in young plants, short branches predominate, forming an almost compact habit; woody taproots to 12 cm long, apically to 3 mm in diam.; internodes ochre, young ones purplish suffused, in young plants shorter than leaves, on the procumbent branches distinctly longer than leaves, bladder cells finger-shaped and sparse. **Leaves** 15 mm long, up to 3 mm broad, spindle-shaped, turning elongate-oval in the drying process, petiole basally with two broad and almost rectangular translucent flaps or pseudostipules, each ending in a short acuminate tooth often pointing sideways, usually half as long as the petiole, bladder cells inconspicuous, tip pointed and often with some short papillae; the upper leaf surface with a distinct straight translucent line of tissue, due to the absence of chlorenchyma below the epidermis. **Inflorescences** dense, comprised of 2–3 flowers in the axils of leaves, appearing more numerous in more compact young plants, due to the proximity of the nodes at which the inflorescences sit. **Flowers** always with completely free bases, the tepal tube completely visible, the bract broadly acuminate with a small tooth or without one, the bracteoles slender and of the same shape, the acute tepal teeth erect at first and bending over the operculum while ripening, inconspicuous bulges at their bases and with only short subapical protrusions overtopping the actual tepal tip, tepals green all over and sometimes purplish at their tips, but not thickened, the inside a light yellowish green, teeth about as long as the entire tepal tube, each about 1 mm long, leaf tips

with some longish bladder cells. **Stamens** five, anthers light yellow or pink, the pollen purple or bright yellow, usually in contrast to the colour of the anther wall, in either case dominating the view in the open flower. **Fruit** basally like a narrow cone, cut at the bottom, the **operculum** forming a rounded lid with a small central deepening on top, surrounded by a narrow shrivelled rim of more or less regularly arranged cells, forming a short puffed sleeve, the lid c. 0.5 mm high and up to 1 mm in diam. **Seeds** two, black, 1.4 × 1 × 1 mm, the sides with irregular crests in almost circular arrangement. Fig. 9.

Habitat and distribution – Always at the upper edges of salt pans ('vleis' in Afrikaans) in grassland or open scrub, very often with some limestones on top of the fine soil in SE North West Province, NW Free State, and NE Northern Cape Province, South Africa. Alt. 1,200–1,400 m.

Additional specimens studied – **South Africa. Free State:** Boshof. Boshof nach Bultfontein, Prinspan, alt. 1,200 m, 9 Mar. 1996, *Hartmann* 32909 (HBG); Kroonstad. Bylskop, 2.8 km vom alten Farmhaus, alt. 1,363 m, 14 Feb. 2007, *Hartmann* 34781 (HBG); Wesselsbron. Eendvogelkuil, bei Windpumpe, alt. 1,330 m, 2 Mar. 1998, *Hartmann et al.* 33532 (HBG); Mahemspan, alt. 1,230 m, 22 Feb. 1995, *Hartmann* 32504 (HBG). **North West Province:** Bloemhof, S.A.Lombard Nature Reserve, alt. 1,240 m, 9 Mar. 1993, *Hartmann* 31322, 31323 (HBG); Delareyville, 3 km N Sannieshof, alt. 1,380 m, 8 Mar. 1993, *Hartmann* 31315, 31316 (HBG). **Northern Cape:** Prieska, 1 Nov. 1939, *Bryants* 203 (K); Kuruman, Kreuzung 14 km ö Kathu, alt. 1,240 m, 11 Feb. 1998, *Hartmann et al.* 33292 (HBG); Warrenton, Ideaal, alt. 1,260 m, 12 Feb. 1994, *Hartmann et al.* 31371 (HBG).

Notes – At first sight, the plants resemble *T. transvaalensis* in having elongate acuminate leaves with a distinct dark longitudinal line along the upper leaf surface, a feature distinguishing the group of populations clearly from *T. parvifolia* with only dotted leaves that are rounded at their tips. Unique to this species are the rather narrow pseudostipules and the moderate bulges at the bases of the tepal teeth – *T. parvifolia* lacks any protrusions at the bases of the tepal teeth, and *T. transvaalensis* has prominent ones, resembling *T. salsoloides* from northern Africa. The populations of *T. vleiensis* settle in an area between the regions in which *T. transvaalensis* and *T. parvifolia* grow, clearly separated and typically at the upper edges of vleis, i.e. salt pans with varying water table. The epithet is chosen after this typical habitat.

Incompletely known taxon

Trianthema glaucifolia F.Muell. (von Mueller 1859: 172). – Type: Australia, Foot of Newcastle, s.d., von Mueller s.n. (K).

Although *Trianthema glaucifolia* can be identified as a member of *T.* subg. *Papularia*, the species cannot be keyed out since the little available material lacks critical features. The taxon is only known from the type collection, which is highly unusual in having long, slender, almost curled, leaves.

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