# Natural History Appendix (Appendix S1)

"This covering of the plant by the particles of soil held by the hairs and glands may also save the plant from destruction by animals." William James Beal, (1878) *American Naturalist* 12: 271-282

Several excellent natural history papers exist on sand-entrapping plants, especially Jurgens (1996), Neinhuis et al (1996) and Danin (1996). Our goal is not to rehash that information. This section focuses on two aspects (1) our observations of sand entrapment in *Abronia*, *Navarretia* and other plants in Northern California and (2) references and notes on the psammophorous taxa in Table 1.

## Methods of substrate entrapment

Glandularity

The presence of glandular trichomes may be most common substrate-entrapping strategy in plants (described with illustrative SEM micrographs in Neinhuis et al. [1996]). Of the plants in Table 1 which we have personally observed, this is by far the most common reason for substrate entrapment.

Non-glandular trichomes

Many non-glandular plants entrap sand and other substrate within their trichomes. This may be due to the substrate being entrapped in complex trichomes (e.g. *Lomatium* sp., *Mentzelia leucophylla*, *Croton setigerus*).

Salt excretion

A variety of plants excrete salt either through salt glands or salt bladders. The salt, unless in a particularly rainy environment, remains on the plant surface, where it may itself be defensive (Newbery et al 1980; LoPresti 2014). Jim Richards, who studies plants in hypersaline environments, hypothesizes that the adhesion of substrate to these plants (for instance saltgrass, *Distichalis spicata*: Poaceae) may be due to the absorption of moisture by the precipitated salt and subsequent stickiness (pers. comm.).

Cavities/depressions/infoldings

Plant structure is extremely complex and many pockets or infoldings occur. Extreme examples include the pitchers of pitcher plants (e.g. Sarraceniaceae, Nepenthaceae) and the fused bracts of *Dipsacus* (Caprifoliaceae), which collect both water and "dirt". Less extreme include the *Navarretia mellita* in this study. While some substrate is entrapped fast in the glandular trichomes, others appears to be settled into the depressions in the inflorescence. Inverting the inflorescence releases some – though not all, and likely not even a majority – of the entrapped substrate.

Mucilage

Root produced mucilage may entrap sand or other substrate fast to the roots of a plant. This is likely common and may protect the plant for the same reasons listed in the manuscript, though this hypothesis needs experimental testing. This feature is particularly well-developed in several desert grasses, including *Lyginia barbata* in Australia (Groom and Lamont 2015) and *Distichlis spicata* in North America (pers. obs.). See also *Dicoria canescens* below.

## Plant family references and observations

The list in Table 1 is obviously vastly incomplete; however it builds significantly on the only major list thus far – Jurgens's (1996) list of 57 species in 14 families. Criteria for inclusion in this list was fairly conservative. Under a microscope, nearly all plants we've examined have some grains of dust on them. The criteria we used were simply that it had to obviously show substrate entrapment in some quantity – a very loose definition and we accepted all records from botanists personally and in the literature (though some we could not confirm).

As we are not suggesting that all these plants gain a defensive benefit from substrate entrapment (especially given Jurgens [1996] set of other hypotheses), this list is simply a starting point for future physiological, ecological, and evolutionary investigations into substrate entrapment in other systems.

A number of these references here are photographs showing substrate entrapment. Many of these come from UC-Berkeley's CalPhoto database (an invaluable museum collection of plant images). These are referenced simply by their 16-digit identification numbers here.

**Acanthaceae**

Jurgens (1996) lists four psammophorous species in this family from the Namib region. These are all perennial shrubs.

**Aizoaceae**

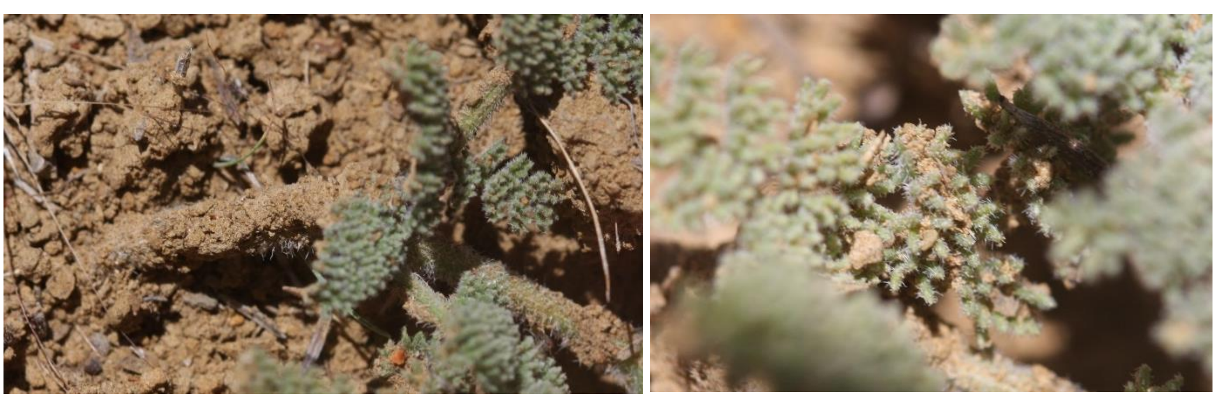
The "type" genus for psammophory, the genus *Psammophora*, is in this family and highlighted in Jurgens (1996) and Danin (1996), with *Arenifera*, a very similar genus.

**Amartyllidaceae**

Jurgens (1996) and Neinhuis et al. (1996) list representatives of four genera of this monocotyledonous family, all from the Namib region. Like better-known members of the family (e.g. *Allium*), these are likely herbaceous perennials.

**Apiaceae**

An unidentified *Lomiatum* sp. (likely *dasycarpum*, but without reproductive structures for a positive identification) at McLaughlin reserve showed much entrapment of substrate on its extremely nonglandular hairy stem and leaflets (EFL).



**Asparagaceae**

Like many of the *Chlorophytum* commonly in cultivation, *C. viscosum* is a perennial. Both Jurgens (1996) and Neinhuis et al. (1996) list it.

**Asteraceae**

*Centaurea*

Lev-Yadun (2006) lists the perennial *C. pumilio* (as *Aegialophila*) as psammophorous and many photographs readily available online confirm this observation. Neal Williams mentioned that the annual yellow star-thistle (*C. solstitialis*) entraps small particles in fine hairs on the bracts surrounding the inflorescence.

*Chaenactis*

*Chaenactis* species are often called "dusty maidens" (Baldwin et al 2012). The annual *C. stevioides* entraps substrate on its bracts and on stems, an illustrative photo is CalPhotos # 0000 0000 0914 0887.

*Dicoria*

This may be a good example of ontogenic shifts in sand entrapment and one of subterranean (though possibly exposed at some times) entrapment. Danin (1996) writes of the southwestern United States annual *D. canescens* "the hypocotyl is covered by viscid material and adhered sand grains".

*Diphormotheca*

Several photographs online show small amounts of sand on *D. fruticosa* growing in sand dunes. An unknown species (http://www.pbase.com/dorff/image/46514661 accessed 9-Sept-2015) demonstrates this quite nicely.

*Helichrysum*

This large genus includes several members classified by Jurgens (1996) as psammophorous. All hail from the Namib region, though hundreds of species occur across Africa and more than these three species may entrap substrate.

*Hemizonia*

*Hemizonia congesta* entraps windblown substrate as well as small arthropods and other material (after a wildfire in the summer of 2015, *Hemizonia, Madia, Holocarpha*, and *Calycedinia* spp. at McLaughlin reserve had entrapped much ash). This occurs primarily on the lower portions of the peduncle, as the basal rosette is nonglandular (but can be abundantly hairy – there is much individual variation in this trait).

*Heterotheca*

Telegraphweed, *Heterotheca grandiflora* entraps substrate on its sticky foliage (Ellen Dean, pers. comm.).

*Holocarpha*

As in *Hemizonia*.

*Ifloga*

Two species are mentioned by Jurgens (1996), one from the Namib and another from the Mediterranean. Nick Helme's excellent photograph (included in Figure 1) adds a third species to the list.

*Lasiopogon*

Jurgens (1996) lists *L. glomerulatus*. Photos online of *L. muscoides* (http://www.wildflowers.co.il/english/picture.asp?ID=6295 accessed 9-Sept-2015) show a small amount of entrapped sand.

*Lessingia*

While not tarweeds in the subfamily Madiniae, *Lessingia* spp. in California have similar ecology. See *Hemizonia*.

*Leysera*

Jurgens (1996) lists this perennial. An illustrative photo is available at http://africanbulbs.com/Leysera%20tenella_07-09-11_1.jpg (accessed 9-Sept-2015).

*Madia*

As in *Hemizonia*. The *Madia elegans* below was growing alongside a busy dirt road and collected much road dust. These covered plants were no longer sticky to the touch (usually they are quite sticky).

*Podotheca*

An Australian plant, *P. angustifolia* entraps much sand on its glandular herbage (https://www.anbg.gov.au/photo/apii/id/dig/35199 accessed 4-Jan-2016).

*Rigiopappus*

In this monotypic genus, wireweed, *R. leptocladus* (an annual) entraps substrate when in suitable conditions. A photo is CalPhotos # 0000 0000 0914 0887

**Boraginaceae**

*Eucrypta*

These small annual borages are glandular-hairy, often sticky, and entrap some amount of substrate (E. Dean, pers. comm.).

*Phacelia*

This large genus includes many species which are glandular or especially hirsute and entrap some amount of substrate (Ellen Dean, Tim Miller, pers. comm.). This is illustrated nicely in *inyoensis* in CalPhotos #0000 0000 0801 0438, *ivesiana* in #0000 0000 0109 2191 & 0000 0000 0413 1777, pulchella in #0000 0000 , and *stellaris* in #0000 0000 1210 1294 *P. parishii* (left) and *pulchella* var. *goodiingii* (right) are shown below (photos: Jim Andre):

*Pholisma*

Two species of chlorophyll-lacking, parasitic plants of Southern California are known as sand food. They entrap sand in glandular trichomes on the inflorescence, stem and leaves, lending the plant the feel of "a squishy gummy bear covered in fuzzy sand covered hairs" (Anna Bennett, pers. comm.). Photos of *P. sonorae* (photos: Anna Bennett) is shown below:

*Tiquilia*

This genus of desert-growing borages includes several psammophorous species. *T. plicata* pictured in Figure 1 has a peculiar habit of entrapping sand grains on the leaf margins. *T. litoralis* entraps much sand, though not in as neat an order; several excellent photos are at http://www.chileflora.com/Florachilena/FloraSpanish/HighResPages/SH1232.htm (accessed 9-Sept-2015).

**Brassicaceae**

*Eremobium*

Lev-Yadun (2006) lists this Middle Eastern annual mustard, though provides no other details.

*Savignia*

Danin (1996) shows a photograph of a seedling of this annual Middle Eastern mustard completely coated with sand.

**Cactaceae**

These species are all listed in Wiens (1978). *Ariocarpus kotschoubeyanus* appears to collect substrate particles between the leaves and stalk, a possible example of collection in cavities (e.g. https://www.flickr.com/photos/aztekium/279363512 - accessed 9-Sept-2015).

**Caryophyllaceae**

*Gypsophila*

*Gypsophila viscosa* is an annual Middle Eastern pink, noted by Lev-Yadun (2006) and Danin (1996). Both both spell it "Gypsophylla" but this is erroneous (it is spelled correctly on Danin's Flora of Israel webpage: http://flora.org.il/en/plants/).

*Silene*

Various *Silene* species, known as catchflies or campions, catch more than flies – they sometimes accumulate significant amounts of substrate on their sticky calyxes (Jurgens 1996; Danin 1996; Anurag Agrawal, Kyle Christie & Tim Miller, pers. comm.).

*Spergularia*

*Spergularia* species worldwide entrap substrate. Jurgens (1996) notes it in purpurea in the Mediterranean, S. villosa (CalPhotos # 0000 0000 1012 2195) and *S. macrotheca* in California does the same (CalPhotos #0000 0000 0412 1240 and below).

*Spergularia macrotheca* is pictured below (photo: Charles Webber © California Academy of Sciences)

**Chenopodiaceae**

Certain members of the Chenopodiaceae have a specialized bladder system (LoPresti 2014) for secretion/excretion of salts and other compounds, as mentioned above this may be the reason that *Atriplex* and *Chenopodium* catch some substrate material (Jim Richards, Ellen Dean, pers. comm.; pers. obs.).

**Colchicaceae**

Jurgens (1996) lists *Hexacyrtis dickiana*, a monocot of the Namib region.

**Crassulaceae**

The South African National Biodiversity Institute suggests “sand-coated crassula” as a common name for *Crassula alpestris*, listed as sand-coated by Weins (1978). Photos

**Euphorbiaceae**

*Croton setigerus* entraps substrate (mostly small particles) in its complex branched trichomes. Jurgens (1996) lists *Euphorbia gummifera*, though I can find no good pictures showing sand entrapment in this species.

**Fabaceae**

Farmer (2014), Lev-Yadun (2006), and Danin (1996) all note *Ononis* spp. entrap sand. Farmer also mentions *Indigofera argentea*, which he notes “Most of the pinnate leaves of these small plants were found to have five to seven leaflets about 3-mm wide and 4-mm long and each covered in white, hair-like trichomes with irregular surfaces. The trichomes on the stems and leaflets trapped sand grains of various sizes. Counting only the sand grains with diameters that exceeded those of the trichomes from ten leaflets from this plant gave the following distribution: an average of seven grains on the upper (adaxial) leaflet surface and 31 grains on the lower (abaxial) leaflet surface. Additionally, grains were found around the leaf edges and, interestingly, they tended to be evenly spaced along these borders”. *I. colutea*, native to Australia, also entraps sand (FloraBase Western Australian Flora). *Stylosanthes* spp. (e.g. *S. viscosa*) Are sticky and entrap insects, as well as substrate (LoPresti et al 2015, pers. obs.)

**Geraniaceae**

Many geraniums (*Geranium* and *Pelargonium* spp.) are sticky, *G. viscosissimum* entraps substrate (Tim Miller, pers. comm. Glandular *Erodium*, including *cicutarium* (CalPhotos #0000 0000 1006 0523) does as well.

**Hyancinthaceae**

This family is the focus of most of Jurgens (1996) and Neinhaus et al. (1996), all of their 21 species in 3 genera hail from the Namib region, though the distribution of the family is far larger and should be examined for more psammophorous species.

**Iridaceae**

Jurgens (1996) and Neinhuis et al (1996) each contribute a genus, without species-level identity, with sand-entrapment from the Namib region.

**Loasaceae**

Kara Moore notes that *M. leucophylla* in the Mojave entraps sand on leaves (pers. comm.), as does *tricuspis* (CalPhotos #0000 0000 1212 0301). *M. albicaulis* traps sand in deeply inset veins on basal leaves (CalPhotos #0000 0000 0314 1279). *Mentzelia* species are known to entrap insects with their complex nonglandular trichomes (Eisner et al 1998).

**Molluginaceae/Limeaceae**

Jurgens (1996) lists two species in the genus *Limeum*; a third, *arabicum*, has many photos showing its sand coating (e.g. http://farm6.staticflickr.com/5467/7176329354_ca3b72e742.jpg accessed 9-Sept-2015). Farmer (2014) also notes the presence of sand coatings in the family, but does not mention any genera or species.

**Nyctaginaceae**

Most genera in the Nyctaginaceae are sticky; many entrap sand. Nearly all species of *Abronia* entrap sand, particularly good examples include the latifolia in Figure 1, *turbinata* (CalPhotos #0000 0000 0610 2526), maritima (CalPhotos #0000 0000 0507 1257) and *fragrans* (below, photo: EFL). *Allionia, Boerhavia, Mirabilis, and Tripterocalyx* species all do as well (pers. obs., Kyle Christie, pers. comm.).

**Orobanchaceae**

Many members of this family of hemiparasites are glandular. Several *Chloropyron/Cordelanthes* species entrap sand (pers. obs., K. Moore, pers. comm.). Many *Castilleja* species entrap substrate including *applegatei* (Tim Miller, pers. comm.). *Orobanche californica* (CalPhotos #0000 0000 0711 1509), *cooperi* (#0000 0000 1213 1668; 0000 0000 1008 0202), *parishii* (# 0000 0000 1113 1358) and *valida* (#0000 0000 0611 1380) also entrap substrate.

**Onagraceae**

*Camissonopsis cheiranthifolia* grows alongside *Abronia latifolia* in dunes at Bodega Bay, California, and entraps a small amount of sand (CalPhoto # 6666 6666 0707 5469). *C. pallida* does as well (#0000 0000 0210 1761). Photo below, *C. cheiranthifolia* - Jean Pawek (CalPhotos #0000 0000 0313 1190)

**Phyrmaceae**

Many glandular *Mimulus* species growing in dusty or sandy areas accumulate dirt or sand (pers. obs.; K. Toll, pers. comm.). *M. breweri* growing in an eroding dirt patch near a small stream in Lassen National Park, California, are pictured in Figure 1. Other quite striking examples include *bigelovii* (CalPhotos #0000 0000 1213 1186), *fremontii* (#0000 0000 0606 0617 & 0000 0000 0605 0536), *mohavensis* (#0000 0000 1110 1567), *pillosus* (#0000 0000 0608 0321), *rattanii* (#0177 3303 3315 0033 & 0000 0000 0412 0268) and *torreyi* (0000 0000 0110 1136).

**Plantaginaceae**

Tim Miller noticed this phenomenon on *Collinsia tinctoria*; *C. corymobosa* has sticky calyxes which catch sand (#0000 0000 0512 0776). *Stemodia viscosa* also exhibits a low level of substrate entrapment in many photos available online.

**Poaceae**

Saltgrass, *Distichlis spicata*, a very widespread grass, catches dust, dirt and other small particles (J. Richards, pers. comm.; pers. obs.) and *Stipagrotis* spp. have sand-covered roots (Farmer 2014).

**Polemoniaceae**

Many Polemoniaceae are glandular-sticky, hairy and have complex structures, therefore it is unsurprising that many entrap substrate.

*Alliciella*

Aliciella species are perhaps the best-developed psammophorous plants of the Polemoniaceae, *leptomeri*a is pictured in Figure 1; *latifolia* (#0000 0000 0210 1718), *lottiae* (#0000 0000 0414 1609), *micromeria, monoensis* (#0000 0000 0109 2488) and *triodon* (#0000 0000 0411 2416) are quite psammophorous as well.

*Collomia*

Low-growing species we have seen in barren areas of California (*diversifolia*) and Chile (*biflora*) entrapped sand on glandular stems, leaves and inflorescences, as does *tinctoria* (CalPhotos #0000 0000 0108 1982). *C. diversifolia* is pictured below (Photo:EFL).

*Eriastrum*

The only woolystar we know of that entraps carrion is *filifolium* (CalPhotos #0000 0000 0413 1447), though others in this small genus may.

*Gilia*

Many *Gilia* species are sticky, many occur in dry areas, thus it is no surprise that at least six entrap substrate: *austro-occidentalis* (#0000 0000 0409 0528), *brecciarum* (#0000 0000 0512 2266), *cana* (#0000 0000 0613 1149), *latiflora* (below left, photo: Michael Charters), *malior* (below right, photo: Jim Andre) and *tenuiflora* (#0000 0000 1101 0278).

*Ipomopsis*

We know of three sand-entrapping species in this genus: *depressa* (#0000 0000 0406 0455), *gunnisonii* (pers. obs.) and *polycladon* (#0000 0000 0607 0821).

*Navarretia*

Likely most species in this large genus collect some substrate as they are usually glandular, hairy and complex. Three we have worked with are especially pronounced – *mellita* (natural inflorescence left below), *pubescens* and *sinistra* (the basal leaves and stem). Below right, a substrate-added *N. mellita* inflorescence. Far below, a grazed *N. mellita* missing three inflorescences (EFL).


*Polemonium*

Tim Miller has noticed this on *viscosum* and it also occurs on *micranthum* (CalPhotos #0000 0000 0509 1129).

**Polygonaceae**

*Eriogononum viscidulum* entraps sand on in its leaf trichomes.

**Scrophulariaceae**

Jurgens listed members of the African genera *Nemesia*, *Peliostomum* and *Sutera*. *Anticharis glandulosa* also entraps sand (e.g. https://www.flickr.com/photos/54915149@N06/8425229481/in/photostream/ accessed 10-Sept-2015)

**Solanaceae**

Many sticky Solanaceae entrap small amounts of substrate on them (see list of insect-entrapping genera in LoPresti et al 2015). All listed species were from my own observations in California and Chile.

*Nicotiana* sp., Chile (Photo: EFL)

**Turneraceae**

*Piriqueta* spp. living in sandy places (including *morongii*) occasionally entrap substrate (Heather Machado, pers. comm., http://www.kew.org/science/tropamerica/neotropikey/families/images/Turneraceae/piriqueta_morongii_1.jpg accessed 10-Sept-2015).

**Xanthorrhoeaceae**

*Trachyandra* species are monocotyledonous perennials; both species listed by Jurgens (1996) and Neinhuis et al (1996) are from the Namib region.

**Zygophyllaceae**

Jurgens (1996) and Lev-Yadun (2006) list species of *Fagonia* from the Mediterranean region.

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