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The Sun, the Earth and the Platypus ~ *Dr James Macgregor*

Beguiled by Galls ~ *Rod McQueen*

The Sun, the Earth and the platypus
Dr James Macgregor

[Editor: Between 2011 and 2015, Dr James Macgregor undertook a PhD in platypus health in northwest Tasmania which resulted in a paper published in the *Journal of Wildlife Diseases* (Macgregor et al., 2017) The paper received the 2017 Linda Munson Award, which is an international award for the best zoo or wildlife pathological manuscript published each year by a graduate student or resident in either the *Journal of Wildlife Diseases* or the *Journal of Zoo and Wildlife Medicine*. CNFN has supported James's work and we sincerely congratulate him on this prestigious award. This following article is based on his research.]

When I was crunching the numbers for one of the more mathematical parts of my platypus research, I noticed something that I hadn't expected to see. There was a pattern in the data, and one that I couldn't recall being described previously in platypuses, or in any other species. I was working on haematology and serum biochemistry reference intervals. These are the things that doctors use to interpret blood test results when you have a health screen. A result for a particular test would not be considered abnormal if it lies between the upper and lower limits of the reference interval. Vets will do the same for your dog, cat or farm animal. Blood tests are also an important part of a health examination for wild animals, but reference intervals have to be worked out for each species.

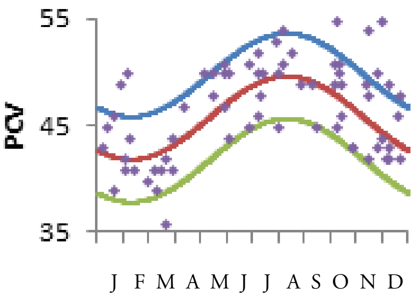
To determine the upper and lower limits of a reference interval the idea is to take the results from a large number of healthy individuals and exclude the (say 2.5%) highest and lowest values. This leaves the middle (say 95% of the) values. The upper and lower of these values are used as the upper and lower limits of the reference interval. So, although reference intervals are often (wrongly) referred to as normal ranges, 5% of healthy individuals can be expected to have results outside of the limits.

As with all statistical methods, when producing reference intervals you want to be sure that there aren't any biases skewing your results. One example of this is to look for outlier results that might arise in a range of ways such as a sick individual being included in the study, an issue with the laboratory testing, or from a simple typing error. When I noticed the pattern in our data, I was checking for any seasonal changes in Packed Cell Volume (PCV – the proportion of the blood that is made of cells; a low value indicating anaemia) using a graph with PCV value plotted against date of sampling. The results seemed to approximate to a sine wave (a smooth repetitive oscillation), repeating twice over the course of the study. Sine waves are common in the world. The oscillating string of a musical instrument takes the form of a sine wave. Waves on the open sea closely approximate to a sine wave. Sinusoidal variations can be seen with natural phenomena created by the rotation of the earth around the sun, such as variation in day length and maximum solar elevation angle.

Other studies in a range of wildlife species have shown difference reference intervals for different times of year, but none have shown such a regular pattern. So I had to come up with a new technique to assess whether these results could adequately be described by a sine wave, and to create a way of expressing these results that would be of use for assessing the health of an individual in the same way as a doctor can do for each of us.

I started by creating a series of 365 artificial parameters, each with a value for each day from Jan 1st to Dec 31st, which when plotted against date had the appearance of a sine wave. The first such parameter had a maximum value of 1 on Jan 1st. The second had a maximum value of 1 on Jan 2nd. We continued through the year until the 365th of the artificial parameters had a maximum value of 1 on Dec 31st.

We then used a statistical method called regression analysis to compare our results to each of these artificial sine wave parameters. Taking PCV in male platypuses as an example, the first thing to do was to determine if at least one of the sine waves showed a statistical correlation to our blood test results - there were several. The second thing to do was determine which sine wave showed the greatest similarity to our results (for PCV in males the maximum was in August). Without knowing the cause of this variation, we could then use the best fit artificial sine wave parameter and our knowledge of its effect to remove the variation from our results. We then used standard methods outlined above to find a reference interval for the adjusted results. We then added back the sine wave variation to our reference interval limits to create a reference interval which varies with day of the year. When plotted against time these limits describe sine waves (as shown below; blue line – upper reference interval limit, green line – lower reference interval limit), and we referred to them as reference curves.



We repeated this process for all the haematology and serum biochemistry parameters that we had tested. We found sine wave variation in five parameters (PCV, Haemoglobin, Red blood cell count, Albumin and Magnesium).

The reference curves we developed are two dimensional, being based on observed values and day of year. Reference intervals are one dimensional and based only on observed hematology/serum biochemistry values. However, reference curves and reference intervals are alike in that a specified proportion (in this case 95%) of observed values lie between the upper and lower reference limits of each (Friedrichs et al. 2012). As such, my co-authors and I proposed that the reference curve is a new concept that fits within the scope of existing theory on reference values. We suggested that reference curves, possibly based on functions other than the sine wave, may be more appropriate than fixed reference intervals for representing variation associated with a range of other continuous factors such as age, stage of pregnancy/ lactation, or altitude.

The variation we found was similar to variation in a range of platypus and environmental temperature data that we gathered. All of these are ultimately influenced by seasonal changes in environmental temperatures due to sinusoidal variation in the amount of energy reaching the earth from the sun.

Statistical testing suggested that the variation was not related to body temperature at or shortly before sampling and is unlikely to be an artifact of capture, holding, or handling. The seasonally varying parameters varied with ambient temperature in recent hours, days, or longer, likely due to variations in metabolic demands.

Parameters such as PCV are complex physiological values that depend of a range of factors such as nutritional status, reproductive status, disease status and body temperature. I find it fascinating that in the results for something so complex, it is possible to see the influence of things as fundamental as the rotation of the earth around the sun.

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Beguiled by Galls

Rod McQueen

Children are often asked, "What do you want to be when you grow up?" Has a single child ever responded, "I want to be a cecidologist"? Yet it is hard to imagine a biological phenomenon more worthy of study, more sure to delight those who poke their noses into its marvels and mysteries, than cecidology—the study of plant galls.

What is a gall?

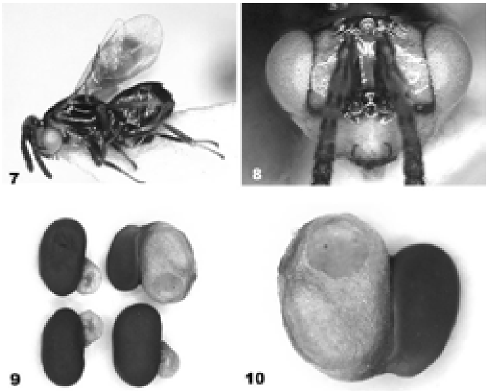
A keen observer of nature on a bushwalk cannot help but notice weird growths on some plants—bizarre lumps, bumps, balls, knobs or swellings on leaves, stems, buds, flowers, or fruits. These are galls, swellings induced by an organism living in a chamber inside living tissue and receiving protection and nourishment from the plant. Some galls, such as those found on the inside of figs or on plant roots, are hidden from prying eyes.

One cecidologist defines galls as "any enlargement of plant cell, tissue or organ induced by the stimulus of a parasitic organism" (Mani 1964, p. 2). Blanche defines them even more parsimoniously as "any abnormal swelling of plant tissue" (2012, p. 2). This definition brings under one roof diverse phenomena; on the one hand the highly differentiated structures of some galls with elaborate morphology and tissue-level of organization as exemplified by most insect-induced galls, and on the other the undifferentiated, tumour-like growths such as the fungus-induced woody galls on silver wattles or the root nodules of leguminous plants containing nitrogen-fixing bacteria.

Wool sower gall *Callirhytis seminator* on oak sapling. Photo: Anita Gould, permission granted

Plant galls are induced by a variety of organisms: bacteria, fungi, nematodes, mites, even rotifers and protozoa. This article is restricted to insect-induced galls ("galls" hereafter). Over the centuries, the diversity of galls has spawned its own colourful vocabulary: oak-apple, gall-nut, bedeguar, gouty gall, roly-poly gall, kammergall and silk button spangle gall. Gall

This oak leaf has 5 different cynipid oak galls.
Photo: Alan Russ (permission sought, no response)



Elaiosomes—*Tanaostigmodes shrek* and galls
Australian Journal of entomology

experts use terminology that reflects shape, such as bladder-, crystalline tube-, ambrosia-, rosette-, pouch-gall and so on.

In about 90% of cases, insect galling species are very particular about where they lay their eggs, restricting their affections to just one host species and just one location on the plant, be it leaf, stem, flower bud, fruit or roots. In other instances, one insect species can infect numerous congeneric plant species. The wasp *Leptocybe invasa* seems equally at home on over twenty eucalypt species and morphological differences between the galls are minimal. A few species can infect plants found in closely-related genera. Gall midges or gnats (order Diptera, family Cedidomyiidae) are a special case, with a few species from a handful of genera displaying a host range cutting across different plant families.

By contrast, one plant species can play host to numerous insect gallers from many genera, in theory allowing one specimen to harbour a kaleidoscope of different forms. Oak trees (*Quercus* spp.) in the northern hemisphere and eucalypts in Australia host a staggering menagerie of gall types. The Indian mango tree hosts up to 250 species of gall midges.

A few years ago a group of primary school children in Canberra, with some help from scientists, discovered a unique gall on a small shrub called *Bossiaea grayi* whose seeds are dispersed by ants. To attract the ants each seed has a specialised oil-rich structure called an elaiosome that ants like to eat. The children found that a previously undescribed chalcidoid wasp induced galls in *B. grayi* elaiosomes. This is the first time a gall had ever been discovered on an elaiosome (Blanche 2012, p. 58)

Galls on a eucalypt leaf, Gog Track.
Photo: Rod McQueen

Gall insects are often characterised as "parasites" or "pathogens", and a heavily infected plant may look unsightly, yet galls cause little permanent injury and seldom result in the death of the plant in their natural environment. (The story can be very different for commercial plantations and for invasive gallers on invasive plants.) It takes a very heavy infestation to affect photosynthesis. However, some gallers, such as *Asphondylia* midges which infest flower buds and fruit of several *Acacia* species, reduce seed set and seriously disrupting the plant's reproductive success. On the other side of the coin, river red gums (*Eucalyptus camalduensis*) "parasitised" by the wasp *Leptocybe invasa*, are less susceptible to frost damage and contain higher levels of chlorophyll than ungalled trees! Fig wasps live in obligatory mutualistic association with fig species around the world; without them, we wouldn't have figs.

Plants are not totally helpless against gall attack and have numerous physical and chemical tricks up their stalks to defend themselves. In certain cases attacked plant tissues, instead of growing into a gall, die in the immediate vicinity of the attacker thus effectively rejecting it. Like parasites, galling insects themselves would suffer if their activities seriously undermined the health of their host species.

Gall diversity

Although the scientific study of gall taxonomy and ecology is considered to be in its infancy, naturalists have long been aware of their stunning array of shapes, sizes, textures and colours. But the shape and other properties of galls produced by individuals of the same insect species are so consistent that the insect can often be identified from the gall they induce. The major challenge for cecidologists is determining *how* each lodger can direct the differentiation and growth processes to produce the predestined form.

Galls can be described as simple or complex. Simple galls consist of rolls, pits, a discoloured spot or a pimple on leaves where the insect is only partly surrounded by gall tissue. They are mostly formed by adult invertebrates with piercing mouthparts, such as aphids and psyllids which do not lay their eggs inside plant tissue. Complex galls can resemble rosettes, horns, thorns, sea urchins, pimples, spines, fuzz, hair or eyes. They are enclosed, often woody and either lack an exit hole or it is small or blocked. Galls induced by wasps, flies, beetles, moths and some thrips that oviposit into actively growing tissue usually develop into complex structures. Galls can have a single chamber in which the larva resides or numerous chambers. Each chamber may contain a single insect or numerous individuals. Most galls house the larvae or nymphs—not the adults—but in the case of thrips, both nymphs and adults can occupy the same domicile.

Gall induction

The process of gall development has three distinct phases: initiation (or induction) and growth—called "cecidogenesis"—and maturation. Galling *usually* occurs during accelerated plant growth when undifferentiated **parenchyma** cells in **meristem** tissue become active and through the process of cell **differentiation** start the process of producing the different tissue needed to form the stems, leaves and flower parts, a process known as **morphogenesis.** (Note: words in bold are defined in the Glossary.)

Gall formation is a special form of morphogenesis initiated by a galling insect irritating active plant tissue. The hatchling not only evades the host's immune system, it also hijacks the host's genetic regulatory mechanism so that it responds with "spectacular and complex tissue reorganization" to produce a swelling that encloses the larva/nymph. ***Voila!*** Instead of growing normally, the host plant lovingly crafts the perfect crib in which the grub, or grubs, can live a cloistered life of

Asphondylia pupa in gall
Photo: Polinizador, CC BY-SA 4.0

Gall on *Allocasuarina* sp. Photo: S. Lloyd

luxury. A new multi-cellular organ has been formed. Strange goings-on can go on. Some galls differ little from the normal plant structure and appear as a slight swelling; in others, leaf buds might fail completely to develop into leaves, or soft hairs on the bud might grow into stiff, woody spines.

Cecidologists generally agree that the alien insect invader, not its host, calls the morphogenetic shots. However, since the gall is formed entirely of plant tissue and not of insect tissue, the development must obey some constraints imposed by the plant's growth. One could say that the insect "manipulates the potentialities" of the host's tissues. This tightly-choreographed waltz of the insect-plant pair is the heart and core of the wonder of galls.

Let's elaborate. During cecidogenesis, "The insect stresses the host organ, the host counters it with newly differentiated tissues and new physiological activities." (Raman 2011, p. 521). One could characterize the whole interaction as a scam by the insect. Stressed plants direct metabolites and nutrients to the area of attack to try to repair any damage. The galler

Gall, probably *Cylindrococcus spiniferus,* on *Casuarina* sp. Photo: Glenda Walter, BowerBird

exploits the plant's repair efforts by feeding on the nutrients and manipulating plant growth and biochemical processes to benefit itself.

The entire galling phenomenon displays considerable variation on the theme. For instance, in some cases gall formation begins before the insect egg even hatches while in others nothing happens until the larva or nymph begins to feed.

The offensive and defensive moves made by each party during cecidogenesis varies considerably. Even the nature of the weapons of gall induction seems to vary. In some cases it's a bit like a cudgel—the chomping and crunching of some asymmetrical insect mouthparts causes physical damage that elicits a response. Bugs use a rapier-like stylet to pierce host tissue intercellularly, inflicting minimal physical damage yet sufficient to cause a reaction. By and large researchers agree that the chief weapons used by gallers to send the host into a rage are chemical in nature, i.e. chemicals secreted in the saliva of hatchlings or, in the case of wasps, injected during oviposition. Plant hormones (auxins, cytokinins), amino acids and other chemicals you and I have probably never heard of are variously targetted. Perhaps hormones produced by insects interact with and stimulate plant hormones in some way. The removal of oxygen from the plant tissues may also play a part in inducing a host response.

Whatever the cause may be, the plant parries against this thrust, sometimes within hours of initial stimulus, sometimes a week or two later. Tissues in the vicinity of attack enter a state of shock and set up osmotic changes that disturb the peace with a cascade of effects. Electrical properties of cell membranes can change and ion transport systems may be disrupted. Under the control of insect secretions, one to three cells nearest the site of attack start dividing and differentiating in abnormal ways. Subtle alterations in cells produced by these divisions at critical moments in time create new tissues composed of novel cell types, such as abnormally thick-walled dead cells or thin-walled living cells. Three new tissue types are created: nutritive, protective and reserve tissues.

At the same time, other surrounding cells increase in mass through **hypertrophy**, **hyperplasia** or both; these changes are not products of differentiation through cell division but of the chemical action of insect saliva upon cell walls and their contents. While this is happening, the epidermis layer surrounding the swelling gall, which is incapable of mechanical stretching, undergoes an increase in cell division in order to accommodate the increasing volume. New, perfectly normal vascular bundles for conducting nutrients into the gall may form and hook up seamlessly with the plant's transport network. Finally, you have a gall.

Gall on coast wattle *Acacia longifolia* subsp. *sophorae.* Photo: S. Lloyd

Eriphyid mite galls on a willow leaf *Salix phylicifolia* http://www.jmeg.fi/IOWgallinducers.htm

The growth phase coincides with the active feeding and all the developmental phases of the lodger, barring its last **instar**. With the last instar, the maturation phase is entered. In this phase the insect is at its most gluttonous;

Gall on dollybush *Cassinia aculeata*. Photo: S. Lloyd

Gall on eucalypt twig. Photo: S. Lloyd

Cecidomyid gall *Daphnephila machilicola* on Machilus leaf. Source: tokyoinsects2.blog

the nutritive layer is consumed and the outer cortex drained of resources. After that, the larva either leaves the gall to pupate or, more normally, undergoes pupation in the chamber, triggering the gall to dry out.

As one would expect, the time involved in cecidogenesis, maturation and insect pupation varies considerably. The subtropical plant louse, *Trioza fletcheri*, takes 20-22 days to develop and another 12-14 days to complete its life cycle. The wasp has been observed to take over 70 days from egg laying to emergence of adult wasp. In these cases, the adult insect lives for a long time outside the natal chamber. Gall-midge larvae with only one generation per year remain in the larval stage for nearly a year as all the other stages are of very short duration. Some thrips galls remain inhabited and active for two or three years.

Developing galls can change the rate of growth in different axes over time. In some instances, the gall initially grows faster in length than in breadth and height, but as it comes to maturation, it flips, with growth slowing in length and speeding up in breadth and height (Raman 2011, p. 522). Generally speaking, the rate of growth decreases until it stops completely. It enters the maturation phase while the insect is feeding, then it slips gracefully into wizening old age and lignification. During maturation, tissue differentiation ceases while the larvae continue to feed, mature and pupate. Important changes can occur, such as the widening of ostioles to enable prisoners incapable of tunnelling through the gall to make good their escape. Numerous insects—either pupae or adults—actively cut or chew their way out. Pupae of some gall midges have “horns” which they use to corkscrew their way to freedom. Almost immediately the gall goes into its final death throes, it accumulates starches, phenols and minerals not found during the active phases, then it dries out.

Unidentified galls on dusty daisy-bush *Olearia phlogopappa*. Photo: Tamara Leitch

Gall structure and function

Describing the gross organization of the mature gall seems straightforward enough, though it varies with the species. In general, there is an inner zone rich in nutrients (e.g. nitrogenous compounds and soluble sugars) in which enzyme activity is elevated. In some instances, the nutritive cells completely line the natal chamber while in others they occur in isolated patches. This inner layer is usually surrounded by a thin layer of thick-walled cells beyond which lies a tough supportive cortex enclosed in turn by the plant's normal epidermis. (The form of this outer cortex is responsible for the final shape of the gall.) Studies show that this cortex serves as a reserve tissue, with high levels of starch, the energy storage substance. An enzyme gradient between it and the inner nutritive layer enables starch breakdown products to be shunted to the larva. Furthermore, levels of tannin and other deterrent and toxic chemicals accumulate in the outer cortex, affording some protection to the squatters.

There may also be a layer where plant components that are difficult for insects to digest are secreted away from where the insect is feeding (Blanche, p. 4). The exact configuration of tissues and distribution of chemicals varies with the structures of the insects' mouthpart and grazing behaviour—bespoke designs to enable the lazy grubs to enjoy life on the gravy train with the least expenditure of effort. Modifications of the lining to facilitate feeding include thinning and increased permeability of cell walls, enlarged plasmodesmata and high turgor pressure. Bliss! Some gall midges cultivate fungi on the lining of the gall and dine on mycelia instead of plant tissues.

Further, surrounding vascular tissues also respond, facilitating "nutrient translocation towards the insect's feeding site", as well as ramifying and anastomosing within the gall tissues. In short, gall insects cause massive changes in the plant's growth and metabolism, all of which result in gall tissues becoming a resource sink for the products of photosynthesis. One study revealed that 38% of a galled leaf's resources are gobbled up by the artful lodger; more nutrients are mobilised from further away.

But all good things must come to an end. Eventually, all galls dehisce—they dry and crack open. And the host plant waits for the cycle to begin again some months later.

Glossary

Differentiation: the process of development during which less specialized cells specialize during mitosis to produce diverse tissue structures. After mitosis, the daughter cells are slightly different from the mother cell, distinguishing differentiation from simple cell division. The mechanism of morphogenesis.
Eclosion: The emergence of an adult insect from a pupa or an insect larva from an egg.
Hyperplasia: an abnormal increase in the number of cells of an organ, or tissue, causing it to increase in size.
Hypertrophy: the enlargement of an organ, or tissue, from an increase in the size of its cells.
Instar: the stages of insects between moults.

Meristem: the growth tissue of plants containing undifferentiated parenchyma cells that can create new tissues through differentiation. Meristem is found in growth zones.
Morphogenesis: the origin and development of morphological characteristics. The result of differentiation.
Parenchyma: undifferentiated, thin-walled cells that are the least specialised of plant tissues, often described as "filler" tissue. It makes up the bulk of the soft parts of plants as well as being the cell type found in meristem.
Plasmodesmata: microscopic channels penetrating the walls of adjacent plant cells, enabling transport and communication between them.
Vascular tissue: conducting tissue, especially the xylem and phloem that transport fluid and nutrients internally.

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Dasineura pteris on bracken fern *Pteridium aquilinum* found in the Palearctic. Photo: S. Rae, Creative Commons Licence

Unidentified galls on abaxial surface of native tamarind *Dipoglottis australis*. Photo: Glenda Walker

Front Cover: An Artichoke Gall bud on English Oak caused by a gall wasp (*Andricus foecundatrix*). The grub lives in a hard, egg-shaped inner gall until it matures in the Autumn. This gall bud was found on a young oak growing in Chambersbury wood Leverstock Green, Hemel Hempstead. Photo: Nigel Coomber, with permission.

Walks and other events

Bring food, water, clothes for all weather, hand lens, binoculars, note book and curiosity.

Sunday September 1 Redwater Creek Falls Approximately 2 km moderate walk. Meet at the car park behind the IGA/Chemist in Sheffield at 10a.m. and we will drive in a convoy. Time permitting, we will also visit the Dasher Falls. Leader Basil Kleinendorst 0400875717

Sunday October 6 Sue Gebicki's property and neighbouring conservation reserve. Meet at 10 a.m. at 369 Priestleys Lane, Birralee. Priestleys Lane (C714) joins both the Frankford Road (B71) to the north and Birralee Road (B72) to the east. We will explore different forest types, lunch at the creek followed by a walk along the creek. There is a choice of shorter, easier walks. There will be numerous birds, fungi, frogs, reptiles and orchids, and possibly Wedge-tailed Eagles and Yellow-tailed Black-Cockatoos. Leader Sue Gebicki 0400860651

Sunday November 3 Henry Somerset Orchid Reserve Meet at 10 a.m. at the reserve which is 5 km south of Railton on the Railton Road (B13). The reserve has 43-45 orchid species, many of which are rare or endangered. It is a 10 minute easy walk in dry sclerophyll forest; there are no facilities. Leader Philip Milner 0364923201

Sunday December 1 Habitat Nursery, Liffey. Meet 10 a.m. at the nursery. From the west take Bogan Road (C504) or from the east Liffey Road (C513). The nursery is well signposted at the Jones Road intersection. We will walk in wet sclerophyll forest looking for *Thismia rodwayi*, fungi, ferns and birds. Herbert and Sally will give us a tour of the nursery and a talk about their attempts to work with and against nature. Check http://www.habitatplants.com.au/ 0408503602

Thismia rodwayi is a small (< 2 cm tall) saprotrophic plant that occurs in the litter layer in wet eucalypt forests in Tasmania, Victoria and New South Wales. In Tasmania it usually occurs in areas with *Bedfordia salicina*, *Coprosma quadrifida*, *Olearia argophylla* and *Pomaderris apetala*. Its 'fairy lantern' flowers, although bright red, are often hidden beneath the leaf litter and much searching is needed to find them. Photo: S. Lloyd

Sunday January 5 Lake Explorer Track, Lake Mackenzie (total length of the track is 4.5 km). Take the Mersey Forest Road (C171) and turn off at the Lake Mackenzie Road. Meet in the parking area near the end of the road at 10 a.m. Alpine experience along the edge of Lake Mackenzie, over the Fisher River to Lake Explorer. Crossing the river involves rock hopping so people may prefer to stop there as they will already have covered a reasonable distance. There is a fascinating range of alpine plants near Lake Mackenzie and at Devils Gullet. Leader will be announced in the e-news.

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