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(with a few slight additions on the following days and a postscript on *plant galls and the fossil record* a week later, update 2 November 2017)

Plant Galls and Evolution (I)

How More than Twelve Thousand[1] Ugly Facts are Slaying a Beautiful Hypothesis: Darwinism[2]

[T]he great tragedy of Science – the slaying of a beautiful hypothesis by an ugly fact. …[But] Science commits suicide …when it adopts a creed.

Thomas Henry Huxley

If it could be proved that any part of the structure of any one species had been formed for the exclusive good of another species, it would annihilate my theory, for such could not have been produced through natural selection

Charles Darwin

Even those strongly skeptical about teleological interpretations cannot contest the fact that plant galls are constructions promoting a parasite thus benefiting a foreign organism, devices which already by this support are detrimental to the host plant."

Ernst Küster[3]

The problem which plant galls present for the selection theory has often been neglected. ... [The dilemma] is not slight, since the expediency of galls throws up very serious difficulties for the selection principle.

Erich Becher[4]

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[1] This is a very conservative number. In their paper *How Many Species of Gall-Inducing Insects Are There on Earth, and Where Are They?* M. M. Espirito-Santo and G. Wilson Fernandes state (2007, p. 95) that "Estimates of the global richness of gall-inducing insects ranged from 21,000 to 211,000 species, with **an average of 132,930 species**" - see the details in Ann. Entomol. Soc. Am. **100**:95-99 (2007): http://labs.icb.ufmg.br/leeb/publicacoes/2007_EspiritoSanto_&_Fernandes.pdf

[2] "Darwinism" is an abbreviation used here (and by many further authors) synonymously with "neo-Darwinism", or "The Modern Synthesis" and the "Synthetic Theory of Evolution" with its main focus on "omnipotent" natural selection. For some reasons regarding terms, see please http://www.weloennig.de/BegriffNeodarwinismus.html and "omnipotence": http://www.weloennig.de/NaturalSelection.html

[3] Cecidologist (plant gall scientist) critical of teleology, laying the groundwork for further research in the 20th century especially in Germany by his many own investigations and the first excellent textbook on the topic.

[4] who first discussed systematically all the known problems for Darwinism in connection with plant galls in his book *Die Fremddienliche Zweckmäßigkeit der Pflanzengallen.*

Contents

Abstract

For more than 330 years now it has been known that the service provided by the plants for gall formation "results in their own disfigurement" (Malpighi 1679). Massive infestations can induce stunting, chlorosis, wilting, and even death in certain plant species. Diameter of stem and the total height can be distinctly reduced. We even speak of "gall disease" (cecidiosis) in the case of heavy infestations adversely affecting the plants in culture and/or in the wild. However, in almost all the cases of what may be called 'slight infections', the effects are not so strongly deleterious and the plants seem to control and survive the parasitic load without major damage.

For the gallers the plants usually provide optimal nutrition (feed and house the larvae), administer excellent microenvironments, enemy escape, produce safe and comfortable homes protecting their hosts (*inter alia* by phenolic compounds as tannic and gallic acid, displaying antioxidant, anti-bacterial, anti-inflammatory, and anti-fungal properties). In some cases, the plants even form "a closure similar to that of the ground-glass cap of a liqueur bottle" – to open exactly at the right time and in the optimal form – so that the parasite can easily press it out when ready for pupation. Also, some investigations have shown that proteins of inner-gall and plant tissue were "characteristic only for gall tissues". Moreover, "the chlorenchyma cells within the nutritive tissue are generally homogenous and usually include a large nucleus, conspicuous nucleolus, high enzymatic activity, RNA richness, fragmented vacuole, numerous mitochondria, a dense/abundant cytoplasm, and the accumulation of carbohydrates (and lipids in some systems)" (Richardson et al. 2017); for additional special features, see text. As to a synopsis of the present state of the molecular investigations, *cf*. footnote 171 on p. 59. To sum up: For insects, for example, the plants provide an unsurpassed five-star luxury hotel for free for the entire larval development (and often even more; see please below).

In short, entirely new organs (complex, refined, sophisticated, "high tech" galls), consisting of up to seven differentiated layers with diverse positive functions for the guests, are formed at the exclusive expense of the plant host, i. e. without any useful return by the animals ("fremddienliche Zweckmäßigkeit" (Erich Becher) – not easy to translate, but something like 'extrinsic usefulness', 'disinterested suitability', 'well-directed extraneous utility', closely akin to altruism; *cf*. p. 16).

Now, Darwin formulated the following falsification criterium, among others, for his theory of natural selection – fully applicable to the modern neo-Darwinian versions of the theory as well, because: "Natural selection cannot possibly produce any modification in any one species exclusively for the good of another species; "… ***If it could be proved that any part of the structure of any one species had been formed for the exclusive good of another species, it would annihilate my theory***, for such could not have been produced through natural selection." Also: "Natural selection can produce nothing in one species for the exclusive good or injury of another; though it may well produce parts, organs, and excretions highly useful or even indispensable, or again highly injurious to another species***, but in all cases at the same time useful to the possessor.***"

Inference reached on the basis of the evidence: Because in the case of the galls, in thousands of plant species often entirely new organs have been formed ***for the exclusive good of more than 132,930 other species***, these 'ugly facts' have annihilated Darwin's theory *as well as the modern versions of it*. The galls are not 'useful to the possessor', the plants. There is no space for these phenomena in the world of "the selfish gene" (Dawkins). Moreover, the same conclusion appears to be true for thousands of angiosperm species producing deceptive flowers (in contrast to gall formations, now for the exclusive good of the plant species) – a topic which should be carefully treated in another paper.

Plant galls – a definition

What are plant galls? An answer (first focusing on galls induced by insects, but the principle is also applicable to other taxa):

> "An insect-induced gall is a highly specialized structure resulting from atypical development of plant tissue induced by a reaction to the presence and activity of an insect. The insect induces a differentiation of tissues with features and functions of an ectopic organ, providing nutrition and protection to the galling insect from natural enemies and environmental stresses" (Richardon et al. 2017, p. 254)[5].

Until now systematists have desribed about 1400[6] (1600[7]) species of gall wasps (Cynipidae) – one of the most frequent and well known example, the common oak gall wasp and its gall, is directly shown below:

Left: Common oak gall wasp (*Cynips quercusfolii*), right: Its corresponding oak gall of *Cynips quercusfolii*[8]

Also, there are some 6000 species of gall midges or gall gnats (Cecidomyiidae)[9]:

Left: Gall midge *Mayetiola destructor*[10]. Middle: Gall with larva of *Mikiola fagi*[11]. Right: Galls of *Mikiola fagi*[12]

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5 Ryan A. Richardson, Mélanie Body, Michele R. Warmund, Jack C. Schultz, Heidi M. Appel (2017): Morphometric analysis of young petiole galls on the narrow-leaf cottonwood, *Populus angustifolia*, by the sugarbeet root aphid, *Pemphigus betae*.Protoplasma **254**:203-216.

[6] http://bugguide.net/node/view/14878 (retrieved on 7 August 2017): https://link.springer.com/article/10.1007/s00709-015-0937-8

[7] According to Lexikon der Biologie Vol. 3, Spectrum Akademischer Verlag (1994, p 416)

[8] Both photographs from https://de.wikipedia.org/wiki/Gallwespen (retrieved on 7 August 2017)

[9] According to https://de.wikipedia.org/wiki/Gallm%C3%BCcken with reference to "Forschungsprojekte Diptera, Senckenberg Deutsches Entomologisches Institut Müncheberg (SDEI), abgerufen am 13. Februar 2016"; retrieved on 7 August 2017
https://en.wikipedia.org/wiki/Eriophyidae retrieved on 7 August 2017 including the comment about the 3,600 species that "this is probably less than 10% of the actual number existing in this poorly researched family".

[10] https://nl.wikipedia.org/wiki/Galmuggen; retrieved on 7 August 2017

[11] https://de.wikipedia.org/wiki/Gallm%C3%BCcken; retrieved on 7 August 2017

[12] https://pl.wikipedia.org/wiki/Pryszczarkowate; retrieved on 7 August 2017

Additionally, "10–20% of the 4,700 aphid species [Hemiptera] known worldwide can induce galls on their host plants" (Chen and Qiao 2012, p. 1).[13]

Moreover, about 3600 species of gall mites (Eriophyidae) have been counted[14] – Mites belong to the class Arachnida, subclass Acari (also known as Acarina).[15]

Left: *Aceria anthocoptes*. Right: Galls of *Eriophyes tiliae*[16]

"However, ***insects*** make galls that are more structurally consistent and diverse than those made by all other gall-inducing organisms (Imms 1947; Price et al. 1987). Galling has evolved repeatedly [independently] among and within insects orders: Hymenoptery, Diptera, Hemiptera, Lepidoptera, Coleoptera, and Thysanoptera (Stone and Schönrogge 2003)" – Richardson et al. 2017, p. 254).[17]

(*Emphasis here and in the following quotations added; also words in square brackets*).
(a) So what are the plants doing for their guests? (b) Are the animals doing anything good for their plant hosts? c) What is the problem for natural selection?

What the plants are doing for their guests

Answer for (a): The plants provide "optimal nutrition, modified or buffered microenvironments and enemy escape" (Nabity, 2016, p. 979)[18], so they "feed and house the larvae of specialized insect species" (Weis and Abrahamson 1986, p. 693).[19] Or – in the words of Connie Barlow following the interpretation of Richard Dawkins – "***The insect genes*** somehow induce plant tissues to swell in the spot where the egg has been laid. The plant thereby supplies the growing grup not only with food but also with a safe and comfortable home."[20]

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[13] Chen, J. and Qiao, G. X. (2012): Galling Aphids (Hemiptera: Aphidoidea) in China: Diversity and Host Specificity. Volume 2012, Article ID 621934, 11 pages; https://www.hindawi.com/journals/psyche/2012/621934/ (with reference and link to S. Chakrabarti 2007).

[15] Besides these four (for our topic perhaps most important) taxa, there are further galling organisms like many rust fungi and nematodes. Most authors add various viruses, algae, bacteria and the mistletoe. However, several biologists do not include symbiotic structures like the well known root nodules triggered by *Agrobacterium tumefaciens* within the category of plant galls proper anymore. See, for example, Sitte et al. (2002) Strasburger Lehrbuch der Botanik 200, p. 491, as well as Kadereit et al. (2014, p. 474) Strasburger Lehrbuch der Pflanzenwissenschaften. Springer Spektrum; Heidelberg.

[16] Both from https://de.wikipedia.org/wiki/Gallmilben; retrieved on 7 August 2017

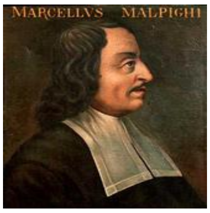
[17] See reference above.

[18] Nabity, P. D. (2016): Insect-induced plant phenotypes: Revealing mechanisms through comparative genomics of galling insects and their hosts. American Journal of Botany 103: 979-989.

[19] Weis, A. M. and W. G. Abrahamson (1986): Evolution of host-plant manipulation by gall makers: Ecological and genetic factors in the *Solidago-Eurosta* sytem. The American Naturalist **127**: 681-695.

[20] Connie Barlow (Ed.) (1991; sixth printing 1998, pp. 223/224): From Gaia to Selfish Genes. Selected Writings in Life Sciences. The MIT Press, Cambridge, Massachusetts. Quotation of Malpighi p. 224.

The plants perform all of these services essentially ***at their own expenses***. And the costs can be alarmingly high – as has already been observed by the famous



physician and naturalist Marcello Malpighi (1628-1694)[21], who, after carefully studying plant galls, stated in his book *De Gallis* (1679) that "nature has endowed them [the insects] with such ingenuity that they force the plants to provide the uterus and, so to speak, the nourishing breasts for the eggs they lay on them. This service provided by the plants results ***in their own disfigurement*** in that they often develop a disease in the form of a swelling to which we give the name "galls" (emphasis added; for the reference see Barlow in the footnote below).

As for the enormous costs the plants sometimes have to pay, let's have a look at the following examples:

Pretorius et al. (2016, p. 1)[22] sum up the damage inflicted by the gall aphid *Pemphigus betae* as follows:

> "Heavy infestations of this aphid can induce significant reductions in yield, sugar content, and recoverable sugar. Under conditions of extreme stress and heavy infestations, the alienicolae[23] ***can induce stunting, chlorosis, wilting, and even death of sugar beet plants***.

Richardson et al. (2017, p. 205):

> *"P. betae* causes significant reductions in sugarbeet yield and reduces sucrose quality. For example, in 1989, a *Pemphigus* infestation ***reduced the sugar content and recoverable sugar by 64 and 73 %, respectively, resulting in a $3,000,000 loss or about $925 per infested hectare*** (Hutchinson and Campbell 1994).

For the gall forming invasive wasp *Leptocybe invasa* Fisher & La Salle (Hymenoptera: Eulophidae), which probably originated from Australia, the following effects on the commercial *Eucalyptus* species in Tanzania have been reported (Petro and Iddi (2017, p. 23):

> "Diameter at breast height (Dbh) and total height for each sampled tree were measured. Results showed that the mean ***Dbh of infested trees were reduced by 2.1%, 7.8% and 13.6% while heights were reduced by 9.5%, 6.6% and 3.8%*** compared to uninfested *E. tereticornis, E. camaldulensis* and *E. saligna* respectively. The mean ***basal area of infested trees was reduced by 17.1%, 16.4% and 24.5% and mean volume were reduced by 16.1%, 17.8% and 23.1%*** compared to uninfested *E. tereticornis, E. camaldulensis* and *E. saligna* respectively."[24]

Similar infestations can also happen in natural environments virtually unaffected by human influence. Check, please, the data provided at picture gallery in http://www.britishplantgallsociety.org/ and/or http://www.pflanzengallen.de/ and/or google "plant galls of the world": images. The ensuing general rule is valid for cultivated plants as well as for plants in the wild:

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[21] Photograph by http://persona.rin.ru/eng/view/f//27857/marcello-malpighi-malpighi-marcello (retrieved 15 August 2017)

[22] Rudolph J. Pretorius Gary L. Hein Jeffrey D. (2016): Ecology and Management of Pemphigus betae (Hemiptera: Aphididae) in Sugar Beet Bradshaw: https://academic.oup.com/jipm/article/doi/10.1093/jipm/pmw008/2658142/Ecology-and-Management-of-Pemphigus-betae

[23] Alienicolae: "a foreign inhabitant; *specifically*: an aphid of a seasonally migrating species" – Merriam-Webster]

[24] Petro, R. and Iddi, S. (2017): *Leptocybe invasa* and Its Effects on Young Plantations of Commercial *Eucalyptus* Species in Tanzania. International Journal of Agriculture and Forestry 2017, 7(1): 23-27. http://article.sapub.org/10.5923.j.ijaf.20170701.04.html

"**In the case of massive infestations, gall formation can adversely affect the plant; then we can speak of a gall disease (cecidiosis).**" – A Textbook of Botany.[25]

Salix alba L. var. *alba* (Salicaceae) – the white willow of Europe and western and central Asia – is "under attack by various pests". "Based on the type of damage imposed, ***insects include S. alba gall-inducing insects***, sap-sucking insects, insects feeding on leaves, wood-boring insects, and non-gall-inducing mites" (Yasaman et al. 2017, p. 1027).[26]

Although not all plants of a species are affected as strongly as shown in the following figures (in fact, often only a minority is thus infested in the wild) – yet can there be any doubt that a heavy infestation of *Quercus robur* by *Cynips quercusfolii* (as shown on the left hand side in the photograph by Alexandra Kehl[27]) or on the right of *Acer pseudoplatanus* by the gall mite *Aceria cephalonea*[28] will cause considerable costs for the host plants?

Left: Gall of *Cynips quercusfolii* on *Quercus robur* (Photo A. Kehl). Right: Gall of *Aceria cephalonea* on *Acer pseudoplatanus.* (See links for the photos in the footnotes).

And the gall-inducing insects are often also protected from others pests by the physical and histochemical constitution of their galls – in fact, the plants are supplying everything for them: optimal nutrition, controlled microenvironments, and, as just mentioned, protection from natural enemies.

Karbasizade et al. (2017, p. 585) have this to report on some key points about these protection mechanisms:

> "Galls not only serve as food reservoirs for their hosts, but also protect their hosts (Cornell 1983). Galls produced by the asexual activity of *Andricus strenlichti* [wasps] (from the family Cynipidae) on the lateral and terminal buds of *Quercus infectoria* ***contain phenolic compounds, such as tannic acid and gallic acid, which possess physiological effects and antioxidant, anti-bacterial, anti-inflammatory, and anti-fungal properties*** (Basri 2005). Acetone, methanol, and ethanol extracts of these galls are also known to have ***high antibacterial activity*** (Karbasizade *et al.*, 2014).[29]

[25] Wilhelm Troll (1973, p. 684). Allgemeine Botanik. Ferdinand Enke Verlag, Stuttgart. (Well-known German Textbook of Botany by the greatest plant morphologist of the 20th century).

[26] Yasaman, S. H., Reza, V. Mohammed, R. Z. Bahman, H. (2017): Patterns of species richness and diversity of willow Salix alba pests in the West Azerbaijan Province of Iran. APPLIED ECOLOGY AND ENVIRONMENTAL RESEARCH **15** (3): 1227-124. http://www.aloki.hu/pdf/1503_12271242.pdf

[27] https://species-id.net/openmedia/File:Cynips_quercusfolii_01_AKehl.JPG

[28] http://www.cecidologie.de/cpg15x/displayimage.php?pid=1721

[29] Karbasizade, V, Dehghan, D., Sichani MM, Shahanipoor, K., Sepahvand, S., Jafari, R., Yousefian, R. (2017): Evaluation of three plant extracts against biofilm formation and expression of quorum sensing regulated virulence factors in *Pseudomonas aeruginosa.* Pakistan Journal of Pharmaceutical Sciences **30**: 585-589. https://www.researchgate.net/publication/315803928_Evaluation_of_three_plant_extracts_against_biofilm_formation_and_expression_of_quorum_sensing_regulated_virulence_factors_in_Pseudomonas_aeruginosa

Some further relevant details on plant galls as new organs (text next page):

Above: Gall of galls wasp *Pediastris aceris* on *Acer pseudoplatanus.* Photo 25 June 2017. Below left: Heavily infested leaf of *Acer* (both: same species as above). 28 August 2017. Right: Silk Button Galls by gall wasp *Neuroterus numismalis* on *Quercus* (probably:) *robur* (27 August 2017). Photos W.-E. L.

There is a consensus among gall researchers that virtually ***entirely new organs*** ("new organs" and "a whole new organ" – Isais et al. 2014, pp. 22/23[30]) are formed in the insect galls. Richardson et al. have – among many other relevant things – this to say regarding organ formation (2017, pp. 203, 204).[31]

> "Insect galls are distinguished from other insect-generated shelters (such as rolled leaves or leave mines by the active differentiation and growth of plant tissues with ***features of a novel organ***" (references).
> … Gall formation is a complex and close interaction between the insect and the host plant resulting from molecular cross-talk between two independent genomes.
> … In some lineages, especially gall wasps (Hymenoptera, Cynipidae) and gall midges (Diptera: Cecidomyiidae), ***gall formation involves elaborate complex external structures, including extrafloral nectaries, hair, spines, and sticky resins*** (Stone and Schönrogge 2003). Thus, the insect gall phenotype is a product of a chemical communication between the host plant and the gall-inducer and is under the influence of **both the insect and the plant genotypes**."

Proteins [of the protein analyses of inner-gall and plant tissue], were "**characteristic only for gall tissues**". "A gall insect can restrain plant growth, reprogram plant gene transcription, and stimulate nutritive tissues ([references])." – Pawlowski et al. 2017, pp. 113, 120.[32]

In their histological study of galls Guzicka et al. (2017, p. 7) reported the following observations on the "Structural modification of *Quercus petraea* leaf caused by *Cynips quercusfolii*":

> "In the structure of galls, we distinguished the following: (1) the protective 'first contact zone' created by epidermal and sub-epidermal sclerenchyma rings, (2) the wide parenchymatous ring, (3) the internal protective zone created by the sclerenchyma ring, and (4) the nutritional zone consisting of cells filled with amyloplasts containing starch. A characteristic for galls in the development stage is the centripetal starch gradient in which starch accumulates in a 'ring of amyloplasts' in the larval chamber."[33]

Correctly Darwin commented on the complexity of plant galls (1875, p. 272):

> "In some galls the internal structure is simple, but in others it is highly complex; thus M. Lacaze-Duthiers has figured in ***the common ink-gall no less than seven concentric layers***, composed of distinct tissue, namely, the epidermic, sub-epidermic, spongy, intermediate, and the hard protective layer formed of curiously thickened woody cells, and, lastly, the central mass, abounding with starch-granules on which the larvæ feed."[34]

Focusing on the "central mass", composed of nutritive cells, Richardson et al. have provided the following excellent summary (2017, p. 204):

> "Galls, especially those induced by Cecidomyiidae and Cynipidae, usually contain a highly differentiated nutritive layer that lines the central chamber and is consumed by the larva during its development (Rohfritsch 1977; Bronner 1992).
> .... The nutritive cells usually display a common set of cytological features, even though other aspects of gall morphology and organization can vary widely (Muñoz-Viveros et al. 2014). The ***chlorenchyma cells within the nutritive tissue are generally homogenous and usually includes a large nucleus, conspicuous nucleolus, high enzymatic activity, RNA richness, fragmented vacuole, numerous mitochondria, a dense/abundant cytoplasm, and the accumulation of carbohydrates*** (and lipids in some systems) (Bronner 1992). These cells also have ***thin walls and reduced intercellular spaces*** that are characteristic of young,

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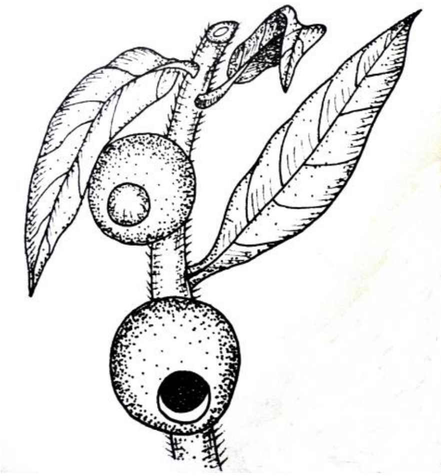
[30] Rosy Mary dos Santos Isaias, Denis Coelho de Oliveira, Renê Gonçalves da Silva Carneiro, Jane Elizabeth Kraus (2014): Developmental Anatomy of Galls in the Neotropics: Arthropods Stimuli Versus Host Plant Constraints. https://link.springer.com/chapter/10.1007%2F978-94-017-8783-3_2 (Chapter 2 in: Neotropical Insect Galls. Editors: G. W. Wilson and J. C. Santos; Springer.) And again for "new organs": Uncounted other authors. Google "plant galls" "new organ" (some **233 hits**) or "plant gall" "novel organ" (about **30 hits**); 21 August 2017.
[31] See reference in footnote above and full article here: https://link.springer.com/article/10.1007/s00709-015-0937-8
[32] Tomasz A. Pawłowski, T. A., Staszak, A. M., Karolewski, P. Marian J. Giertych (2017): Plant development reprogramming by cynipid gall wasp: proteomic analysis. Acta Physiologiae Plantarum **39**: 114-125.
[33] Marzenna Guzicka, Piotr Karolewski & Marian J. Giertych
Structural modification of *Quercus petraea* leaf caused by *Cynips quercusfolii* – histological study of galls. Journal of Plant Interactions Vol. 12 , Iss. 1,2017 . http://www.tandfonline.com/doi/full/10.1080/17429145.2016.1269214
[34] http://darwin-online.org.uk/content/frameset?itemID=F880.2&viewtype=text&pageseq=1

fast-growing tissues (Castro et al. 2012; Vecchi et al. 2013; Carneiro and Isaias 2015a). The lack of intercellular spaces indicates the occurrence of little gas exchange and consequent reduced photosynthetic metabolism (Carneiro and Isaias 2015a). Chloroplasts and mitochondria are numerous and poorly differentiated, often leading to photosynthesis-deficient cells within the galls (Bronner 1992; Huang et al. 2014; Carneiro and Isaias 2015a).“

Some infested plant species built additional ***extremely useful anatomical structures*** for their ungrateful guests (‘as if designed’, some Darwinians might perhaps say) – instead of doing everything possible for them by the “two great constructors of evolution” (Lorenz), mutation and omnipotent selection, to become resistant against these often costly parasites (which appears to be much more likely from a strict selectionist viewpoint).

Just have a look at the “lidgall” (“Stöpselgalle”/“Deckelgalle”) of *Duvalia longifolia*:



Left: “Lid gall” (“Stöpselgalle”/”Deckelgalle”) of *Duvalia longifolia* of the moth *Cecidoses eremita* according to W. Kuhn commenting: ““Lid galls” on the bark of *Duvalia longifolia*. The upper one is still closed, in the lower one the cap was pressed out from the inside when hatching the parasite. It fits like a ground glass cap of a liqueur bottle into the opening.” [35]Middle: Detail from Figure 1a of the paper by V. Loetti, A. Valverde and D.N. Rubel (2016) on galls of *Cecidoses* and *Eucecidoses*.[36]
Right: “Agallas, probablemente de *Cecidoses eremita*, en *Schinus longifolius”*(Syn.*Duvalia*(?), *Duvaua*). Foto Gastó Rodrigues Tourón.[37]

Wolfgang Kuhn – the author of the drawing on the left above – comments:

"The ball-shaped "gall-apples" form ***a closure similar to that of the ground-glass cap of a liqueur bottle***: it is wider on the outside than inside, and can never slip into the interior of the gall, that is onto parasite. Due to the cap’s sophisticated form, the parasite can easily press it out when it has to leave the housing for pupation. Let us imagine, in all peace and contemplation**,** ***the incomprehensible precision of the cells, which are separated from each other along precisely the lines and planes, at exactly the right moment***, so as to form a smooth-walled "stopper" cap, which can effortless be removed only from inside.”[38]

Erich Becher mentions a similar case from Europe, saying:

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[35] According to Professor Wolfgang Kuhn (1984): Stolpersteine des Darwinismus. Band 1, p. 50, Factum Taschenbuch. Schwengeler-Verlag, CH-9442 Berneck.

[31]Veronica Loetti, Alejandra Valverde, Diana Nora Rubel (2016): Galls of *Cecidoses eremita* Curtis and *Eucecidoses minutanus* Brèthes (Lepidoptera: Cecidosidae) in Magdalena, Buenos Aires Province: preliminary study and associated fauna http://www.scielo.br/scielo.php?script=sci_arttext&pid=S1676-06032016000400502 (retrieved 16 August 2017).

[37]http://grtouron.com.ar/GaleriaDeFotos.php?pag=2&Galeria=9 (retrieved 16 August 2017).

[38]The Gerrman original texts reads: “Die kugelrunden “Galläpfel” bilden nämlich einen Verschluss aus, der dem eingeschliffenen Glasstöpsel einer Likörflache gleicht: er ist außen breiter als innen und kann daher niemals in den Innerraum der Galle, also auf den Schmarotzer rutschen, jedoch dank seiner raffinierten Form von diesem leicht herausgedrückt werden, wenn er zur Verpuppung sein Gehäuse verlassen muss. Man möge sich einmal in aller Ruhe und Besinnlichkeit vor Augen stellen, mit welch unbegreiflicher Präzision sich hier die Zellen entlang vorgezeichneter Linien und Flächen genau im rechten Augenblick voneinander lösen, so dass ein glattwandiger “Stöpsel“ entsteht, der sich nur von innen fast mühelos entfernen lässt.“

> ”Something very similar could be explicated for the lidgall of *Cecidomyia* on the Austrian oak, the circular lid of which is peeled off as sharply as if cut with a knife.”[39]

What are the animals doing for their hosts?

(b) In more than 99% of all galling species, the animals are not only doing absolutely nothing for their hosts, but – as we have seen above – rather damage, harm and hurt them – the animals and other guests are indubitably real, perfect and true parasites (ecto- and endoparasites). For the dwindling minority of apparent exceptions, see please below (comments by Becher, Felt, Illies).

So what is the problem for natural selection?

(c) In contrast to most of his modern disciples, Charles Darwin formulated some clear and unmistakable falsification criteria for his theory of natural selection. His following statement is highly relevant for our topic (Origin 1859/1872[40]):

> “Natural selection cannot possibly produce any modification in a [1859: any one] species exclusively for the good of another species; … ***If it could be proved that any part of the structure of any one species had been formed for the exclusive good of another species, it would annihilate my theory***, for such could not have been produced through natural selection.”

However, Darwin continues (1859/1872):

> “Although many statements may be found in works on natural history to this effect, I cannot find even one which seems to me of any weight.” …

He also added in all six editions of the Origin of Species (with very slight variations between 1859 and 1872) the ensuing qualification[41]:

> “Natural selection can produce nothing in one species for the exclusive good or injury of another; though it may well produce parts, organs, and excretions highly useful or even indispensable, or again highly injurious to another species***, but in all cases at the same time useful to the possessor.***”

The test criteria given in (a) the first sentence and (b) “***in all cases at the same time useful to the possessor***” are definitely not true for the plant hosts.

Intriguingly Darwin mentioned plant galls four times in his *Origin of Species* (6th edition 1872), also several times in *Variation of Plants and Animals under Domestication*, (both volumes, both editions 1868, 1875, including a longer paragraph in volume 2), *The Descent of Man*, also both editions 1871, 1874, as well as in his letters to Mr. B. D. Walsh (21 October to 1864 and 27 March 1865) and to Mr. T. Weehan on 9 October 1874.

However, he produced – at least from our present state of knowledge gained by further research during the last more than 150 years – the ensuing extraordinarily doubtful hypothesis of gall induction and formation (*cf.* http://darwin-online.org.uk/):

> “Such facts as the complex and extraordinary out-growths which invariably follow from the insertion of a minute drop of ***poison*** by a gall-producing insect, show us what singular modifications might result in the case of plants from a chemical change in the nature of the sap.”
>
> (1868/1875) “It is impossible to read M. Lacaze-Duthiers' discussion and doubt that the ***poisonous*** secretion of the insect causes the growth of the gall; and every one knows how virulent is the poison secreted by wasps and bees, which belong to the same group with Cynips.”[42]

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[39] Professor Erich Becher (1917, p.77): Die fremddienliche Zweckmäßigkeit der Pflanzengallen und die Hypothese einer überindividuellen Seelischen. Verlag von Veit & Comp., Leipzig. German: “Ein gleiches könnte wohl für die Deckelgalle von Cecidomyia auf der österreichischen Eiche ausgeführt werden, deren kreisförmiger Deckel sich in so scharfer Umgrenzung ablöst, als sei sie mit einem Messer ausgeschnitten.“

[40] http://darwin-online.org.uk/Variorum/1866/1866-241-c-1859.html

[41] Compare http://darwin-online.org.uk/Variorum/1859/1859-205-c-1872.html

> (1872) "…if we bear in mind the power of a minute drop of ***poison*** in producing complex galls, we ought not to feel too sure that, the above variations are not the effect of some local change in the nature of the sap, due to some change in the conditions.

Incessantly he refers to gall insects as producing different "poisons" or "poisonous secretions" injecting them into plant tissues to form different plant galls (4 times in the 6th edition of the *Origin*, altogether some 20 times in his books[43], the places also being repeated in the different editions), speaking even of the "***fittest poisons*** being developed by insects so as to produce galls adapted for them"[44], starting to publish his poison hypothesis in 1859 in the *Origin*.

In fact, Darwin was even convinced that the phenomenon of plant galls clearly supported his theory of evolution, expounding in the final chapter of the *Origin* (just a few pages before the end of the book[45]):

> "Nevertheless all living things have much in common, in their chemical composition, their cellular structure, their laws of growth, and their liability to injurious influences. We see this even in so trifling a fact as that the same poison often similarly affects plants and animals; or ***that the poison secreted by the gall-fly produces monstrous growths on the wild rose or oak-tree***[46]. With all organic beings, excepting perhaps some of the very lowest, sexual reproduction seems to be essentially similar. With all, as far as is at present known, the germinal vesicle is the same; so that ***all organisms start from a common origin***.

Darwin's interest in plant galls continued until the end of his life. His son Francis reports (1887, p. 346)[47]:

> "Shortly before his death, my father began to experimentise on the possibility of producing galls artificially. A letter to Sir J. D. Hooker (Nov. 3, 1880) shows the interest which he felt in the question: "I was delighted with Paget's Essay; I hear that he has occasionally attended to this subject from his youth . . . I am very glad he has called attention to galls: this has always seemed to me a profoundly interesting subject; and if I had been younger would take it up.""

And Francis Darwin subsequently comments on his father's concern, perhaps even enthusiasm, for the topic:

> "His interest in this subject was connected with his ever present wish to learn something of the causes of variation. He imagined to himself wonderful galls caused to appear on the ovaries of plants, and by these means he thought it possible that the seed might be influenced, and thus new varieties arise. He made a considerable number of experiments by injecting various reagents into the tissues of leaves, and with some slight indications of success."

So, concerning natural selection, Darwin appears[48] ***to have been absolutely unaware of any problems plant galls could raise for his theory***, so that he never referred to these phenomena in a direct selectionist context.

The first author who, seven years after Darwin's death, touched on the deep problems plant galls really constitute for the theory of natural selection, was Professor St. George Jackson Mivart[49] – "Darwin's most nettlesome critique"[50] ("famous for starting as an ardent believer in natural selection who later became one of its fiercest critics"). However, after a flare of arguments of the *pros* and *cons* in *Nature* in 1889 and 1890, in a what may be called an intensive discussion of the topic, involving Mivart, Romanes, Hollis, McLachlan, Wetterhan, and Cockerell[51], the controversy on plant galls as a problem for natural selection virtually ceased to be a topic of any larger importance in the English speaking scientific world until now.

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[42] There are several reasons to assume that there is a great genetic distance between *Cynips* of the family of Cynipidae (Superfamily Cynipoidea) and the wasps (Superfamily Vespoidea. Family Vespidae) and even not a small distance between the wasps and bees Darwin referred here to (Superfamily Apoidea, Family Apidae). https://en.wikipedia.org/wiki/Apocrita (retrieved 14 August 2017). Moreover: "Chemically, the venoms [of bees and wasps] are quite different, though the effects are similar" – see details for example in http://archive.boston.com/business/articles/2010/05/17/how_do_bee_and_wasp_stings_differ / (14 Auhust 2017). As far as I could find out, the chemical composition of the poisons of wasps and bees in turn are almost totally different from the "poisons" of, for example, gall wasps.

[43] Compare please http://darwin-online.org.uk/

[44] Letter to James Paget, 14 November 1880, see http://darwin-online.org.uk/content/frameset?pageseq=1&itemID=F1548.2&viewtype=text

[45] http://darwin-online.org.uk/content/frameset?pageseq=1&itemID=F391&viewtype=text

[46] Concerning "the gall-fly": in actual fact, these flies belong to very different species – each one of them parasitizing on only one and the same plant species or on the species of the same plant genus (exception *Pemphigus betae* (sugar beet aphid): primary host is *Populus* and secondary is sugarbeet; for the life cycle see please https://en.wikipedia.org/wiki/Pemphigus_betae#Description. "A **gall-inducing insect** is any insect that can cause the growth of galls within plants. The term **gall fly** is also used to cover these species, although most are not true flies." https://en.wikipedia.org/wiki/Gall-inducing_insect, for a special example of a gall fly see: https://en.wikipedia.org/wiki/Goldenrod_gall_fly (all articles just referred to retrieved 20 August 2017)

[47] http://darwin-online.org.uk/content/frameset?itemID=F1452.3&viewtype=text&pageseq=1

[48] I have chosen "appears" because of his unusually strong interest in plant galls so that, as Francis Darwin wrote (see also above), "shortly before his death, my father began to experimentise on the possibility of producing galls artificially…" – well, perhaps he had a slight suspicion that there was something in that topic that would not only be supporting his theory.

[49] https://en.wikipedia.org/wiki/St._George_Jackson_Mivart; see also the strongly positive review in *The Catholic Encyclopedia* http://www.newadvent.org/cathen/10407b.htm

[50] Abrahamson and Weis 1997, p. 173.

[51] Mivart, St. George (1889): Prof. Weismann's Essays. Nature 41: 38-41, 174-175. Romanes, George J. (1889): Galls. Letter to the Editor. Nature 41: 174 – further references in the supplement of the present paper.

In 1987 Peter W. Price, G. Wilson Fernandes, and Gwendolyn L. Waring tried to "revive the old debate on the adaptive significance of galls (e.g. Hollis 1889, 1890, McLachlan 1889, Mivart 1889, Romanes 1889, 1890, Wetterhan 1889)"[52] – however, without much success. This is their answer concerning the most important question for our topic "fremddienliche Zweckmäßigkeit" (see English term below) on "The 'Adaptive for Plant' or Plant Protection Hypothesis":

> "This hypothesis could be supported if advantages to the plant exceed those to the insect. This imbalance is not generally observed. ***Plants with galls suffer severe decrements in growth and sexual reproduction, whereas insects reproduce effectively in galls and multiply rapidly***. *Rhabdophaga strobíloides* selects relatively large shoots for gall formation, and the gall, and the shoot it is on, act as a sink for photosynthate and nutrients (Weis & Kapelinski 1984). This is a commonly described phenomenon (Fourcroy & Braun 1967, Jankiewicz et al. 1970, Hartnett & Abrahamson 1979, Harris 1980, Col1ins et al. 1983, Abrahamson & McCrea 1985). ***Gal1s may even cause death of shoots and branches and gallers may show preference for the most vigorous shoots*** (Craig et al. 1986). As Weis & Kapelinski (1984, 458) say, "The relationship is strictly parasitic as ***the plant receives no benefit, and may even suffer a loss in reproductive output***" (see also Stinner & Abrahamson 1979, Abrahamson & McCrea 1985). Gallers have been used for biological control of weeds, indicating the strong negative impact that some have on plant fitness (Hol1oway & Huffaker 1957, Harris 1977, Shorthouse 1977a, b).
>
> If plants had the selective advantage we could not explain such conditions as the common development of a nutritive layer in the gall; reductions in plant fitness; widely divergent gall morphology on the same plant species and even when derived from the same plant part; and copious nectar production from galls, when its attractiveness to ants protects the gal1er from enemies."
>
> … "The galler clearly has the potential adaptive advantage in the plant/herbivore relationship (see also Weis & Abrahamson 1986) and we know of no compel1ing arguments to the contrary."

And regarding "The Mutual Benefit Hypothesis" the authors add:

> "There is no evidence in the literature that galls improve the fitness of the plant. ***All the data show negative impact of gallers on plant growth and/or fitness***, as discussed, ***and positive reproductive rates in the gallers: they are parasites***, except for the galling fig wasps (Agaonidae), which are mutualistic pollinators of figs (e.g., Janzen 1979, Wiebes 1979). Thus a hypothesis arguing that gallers and plants are mutualists is untenable."

However, Price et al. – in their otherwise highly informative article – do not address the question of why the plants are so 'altruistic' in view of Darwin's falsification criterion for natural selection (see above). Darwin is not mentioned in their article.

Yet, Darwin and Mivart are referred to in the book of Abrahamson and Weis (1997)[53] ("Thus, in concurrence with Price, Waring, and Fernandes (1987), we conclude that the adaptive benefits go the insect and not to the plant" (p. 173), but again no conclusion concerning Darwin's 'annihilation criterion'.

Also, Mark C. Mescher (2012,) in his chapter 5 *Manipulation of Plant Phenotypes by Insects and Insect-borne pathogens* (pp. 76-78 on galls) ***not only corroborates systematically all the conclusions so far reported here, but also presents even many further relevant details on what the plants are doing for***

[52] 1987 Peter W. Price, G. Wilson Fernandes, and Gwendolyn L. Waring (1987): Adaptive Nature of Plant Galls. FORUM: Environmental Entomology 16: 15-24): http://labs.icb.ufmg.br/leeb/publicacoes/1987.Price.Fernandes.Waring.pdf

[53] Warren G. Abrahamson and Arthus E. Weis (1997): Evolutionary Ecology across Three Trophic Levels. Goldenrods, Gallmakers, and Natural Enemies. Princeton University Press, Princeton (Chapter 6: The Gall as Eurosta's Extende Phenotype: 173-195).

their parasite guests (just to jot down some of the most important key points – his abundant references not included):

> "…there is now considerable evidence that gall development is largely controlled by genes of the galling insects and that ***galling indeed constitutes an adaptive manipulation of the host phenotype*** …there is ample evidence that **galls harm their host plants**. …Gallers can alter plant biomass allocations, elevate photosynthesis rates in affected tissues, and mobilize resources from neighboring tissues. …Consequently **galls are typically energy and nutrient sinks**, which deprive the host plant of recources that it could otherwise employ for growth and reproduction. …many galls exibit differentiated nutritive tissues that appear to be more nourishing and less well defended than ungalled tissues on the same plants. These tissues can exhibit characteristic cytological features including cell wall modifications, cytoplasm enrichment, hypertrophied nuclei, and abundant organelles. …Other potential benefits include **protection from UV radiation, flooding, or physical detachment** from the host plant (*e.g.* by wind, precipitation, or other types of physical disturbances). ….galls provide adaptive benefits to their residents by **providing controlled microenvironments** … larvae…were able to consistently maintain the interior humidity of their galls near saturation over the course of development. … gall tissues are frequently enriched in secondary metabolites (e.g. **phenolics and tannins**) relative to non-galled tissues… "

For many additional points, check, please, the well written original article. Hence, starting systematically with Malpighi 1679, **for more than 330 years now, the basic results on plant gall formation "*for the exclusive good of another species*", i. e. in favour of the parasites, have been strengthened, solidified and further expanded**. Nevertheles, again I could not find an unambiguous, explicit decision concerning the basic problem first addressed by Mivart 1889 (Mescher mentions Darwin, Mivart, and Cockerell).[54]

Intriguingly, Conrad Cloutier (2013)[55] in his book review on *Host Manipulation by Parasites*, edited by Hughes et al. (2012), interprets the paper by Mescher regarding Darwin and natural selection as follows:

> "**Galls as plant structures produced 'for the good of another species' is an observation Darwin wrote he could not explain by Natural Selection**. Galler insects can even induce extra floral nectaries, thus recruiting ants as bodyguards. Phylogenies show that related insect gallers induce similar galls on different plants, and gallers produce specific galls on the same plant. Gall induction is known to be under control of galler genes, which remains to be seen in host behaviour manipulation by parasites."

Although this is not what Darwin wrote, Coutier appears to have touched the sore spot: natural selection cannot explain structures produced for the exclusive good of another species.

Yet, the problem has been addressed directly (if rather briefly) and assumed to have been solved by Ernst Mayr and Richard Dawkins 1963/1982/2016 (see below). Margaret Redfern seems to concur (2011, p. 498) quoting Hermann Adler (1894)[56]: "So far as galls are concerned, Darwin's theory is perfectly safe" – see, please, full quotation in the footnote[57]). So, it appears that none of these

[54] Mark C. Mescher (2012): Chapter 5: Manipulation of Plant Phenotypes by Insects and Insect-borne Pathogens (pp. 73-93). In: David P. Hughes, Jacques Brodeur & Frédéric Thomas (Eds.) (2012): Host Manipulation by Parasites. Forword by Richard Dawkins. Oxford University Press, Oxford.

[55] http://onlinelibrary.wiley.com/doi/10.1111/eva.12062/full

[56] Adler, H. (1894): Alternating generations. A Biological Study of Oak Galls and Gall flies. Translated and edited by C. R. Straton. The Clarendon Press, Oxford. See: https://archive.org/stream/alternatinggene00stragoog/alternatinggene00stragoog_djvu.txt

[57] "It is next of interest to inquire how the various structures of the gall came to be evolved. It may be taken as perfectly certain that the tree does not form them in a disinterested manner for the sake of the Cynips. Darwin says:' If it could be proved that any part of the structure of any one species had been formed I for the exclusive good of another species, it would annihilate my theory, for such could not have been' produced through natural selection' ***So far as galls are concerned, Darwin's theory is perfectly safe***. The 'excitatory emanations,' as Professor Romanes' aptly calls them, which lead to gall-growth, ***can only have arisen by gradual and increasing improvements in the initial stages of their***

authors, except perhaps Coutier, have discerned and fully recognized the immense problem for natural selection inherent in the origin of plant galls (unfortunately, none of the authors refers to the book and papers by Erich Becher).

Nevertheless – although not at the forefront of present biology – research on plant galls has gone on, especially in anatomy, physiology, morphology and systematics, and has even been accelerated in recent years.

In contrast to the near absence in the English scientific literature, in the German speaking countries the controversy about plant galls and natural selection was thoroughly and (one may even say) heavily launched in 1917 by professor Erich Becher of the University of Munich[58], and the topic has been considered to be important ever since until almost the present day by some philosophers and many biologists – zoologists and botanists alike, for example:

Becher 1917, 1918, 1925[59], Klein 1917[60], Frickhinger 1918[61], Heikertinger 1918[62], Küster 1918, 1919[63], Schultz 1918[64], Matouschek 1919[65], Buchner 1921[66], Driesch 1922[67], Miller 1923[68], Hering 1926[69], Ungerer 1926[70], Wolff 1927[71], Demoll 1933[72], Sedlag 1959, 2007[73], Strugger 1962[74], Mayr 1963[75], Zimmermann 1968[76], Schremmer 1973[77], Troll 1937/43, 1973[78], Illies 1982, 1983[79]; Kuhn 1984[80], Heilmann 2000[81], Junker 2001, 2003[82], Probst 2011[83]).

Becher's concept focusing on the main objection to natural selection was condensed in his key concept termed "fremddienliche Zweckmäßigkeit" (not

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formation, acting through natural selection, over an unlimited period of time, and through numerous consecutive species." M. Redfern (2011): Plant Galls. HarperCollins, New York.

58 See https://de.wikipedia.org/wiki/Erich_Becher

59 Becher, E. (1917): Die fremddienliche Zweckmäßigkeit der Pflanzengallen und die Hypothese eines überindividuellen Seelischen. Verlag von Veit & Comp., Leipzig. https://books.google.de/books/about/Fremddienliche_Zweckm%C3%A4%C3%9Figkeit.html?id=f92rPgAACAAJ&redir_esc=y
Becher, E. (1918): Über Ausnutzungsprinzip, Zweckmäßigkeit und fremddeinliche Zweckmäßigkeit. Naturwissenschaften 6: 185-189.
Becher, E. (1925): Fremddienliche Zweckmäßigkeit. Verlag Heise (8Seiten): Philosophische Monatshefte der Kant-Studien. Herausgegeben von V. Engelhardt und J. Lochne: https://archive.org/stream/philosophischemo00kantuoft/philosophischemo00kantuoft_djvu.txt

60 https://archive.org/stream/botanischeszentr40141bota/botanischeszentr40141bota_djvu.txt

61 http://www.archive.org/stream/zeitschriftfrp28stut/zeitschriftfrp28stut_djvu.txt

62 Heikertinger, F. (1918): Das Scheinproblem von der "fremddienlichen Zweckmäßigkeit". Die Naturwissenschaften 6:181-185.

63 http://www.archive.org/stream/zeitschriftfri21berl/zeitschriftfri21berl_djvu.txt

64 https://philpapers.org/rec/SCHBED-4

65 Also https://archive.org/stream/botanischeszentr40141bota/botanischeszentr40141bota_djvu.txt

66 https://archive.org/stream/tierundpflanzein00buch/tierundpflanzein00buch_djvu.txt

67 https://www.amazon.de/Geschichte-Vitalismus-Hans-Driesch/dp/1246459132#reader_1246459132 Paperback 2011.

68 https://www.researchgate.net/publication/246079308_Die_sogen_fremddienliche_Zweckmassigkeit_und_die_menschliche_Pathologie

69 Hering, M. (1923): Biologie der Schmetterlinge. Verlag Julius Springer. Berlin.

70 Ungerer, E. (1926): Die Regulation der Pflanzen. Springer Verlag,Berlin

71 https://www.tib.eu/de/suchen/id/springer%3Adoi~10.1007%252FBF02080955/Zur-Frage-der-fremddienlichen-Zweckm%C3%A4ssigkeit-/?tx_tibsearch_search%5Bsearchspace%5D=tn

72 Demoll, R. (1933): Instinkt und Entwicklung. J. F. LehmennsVerlag, München.

73 Sedlag, U. (1959): Hautflügler III. Schlupf- und Gallwespen. Verlag Geest & Portig (?); Quoted according to J. Illies 1983. 2. Auflage (Nachdruck) 2004. And 2007: https://www.nabu.de/imperia/md/content/nabude/insekten/insecta_10.pdf

74 Strugger, S. (1962): Biologie 1 (Botanik). Fischer Bücherei KG, Frankfurt am Main.

75 Mayr, E. (1963): Animal Species and Evolution.. The Belknap Press of Harvard University Press, Cambridge, Massachusetts.

76 Zimmermann, W. (1968): Evolution und Naturphilosophie. Duncker & Humblot. Berlin.

77 Schremmer, F. (1973): Wechselbeziehungen zwischen Tieren und Pflanzen. In: Grzimeks Buch der Ökologie (Ergänzungsband zu Grzimeks Tierleben. Zitiert nach J. Illies (1983, p. 134): Der Jahrhunderirrtum. Umschau Verlag, Frankfurt am Main.

78 Troll, W. (1937/43): Vergleichende Morphologie der höheren Pflanzen. Berlin, Gebr. Bornträger (but galls not found). (1973): Allgemeine Botanik. Ein Lehrbuch auf vergleichend-biologischer Grundlage. Ferdiand Enke Verlag, Stuttgart.

79 Illies, J. (1982): Das Geheimnis der Grünen Planeten. Umschau Verlag, Frankfurt am Main.
J. Illies (1983, p. 134): Der Jahrhunderirrtum. Umschau Verlag, Frankfurt am Main.

80 Kuhn, W. (1984): Stolpersteine des Darwinismus. Band 1, p. 50, Factum Taschenbuch. Schwengeler-Verlag, CH-9442 Berneck.

81 Heilmann, H. (2000): Proceedings of the 6th International Congress of Organic Viticulture. Edited by H. Willer and U. Meier. CH 5070 Frick

82 Junker, R. (2001): Modell für einen Umbruch in der Schöpfung. http://www.genesisnet.info/schoepfung_evolution/
(2003): Faszination Pflanzengallen. Studium Integrale **10**: http://www.si-journal.de/index2.php?artikel=jg10/heft1/sij101.html

83 http://www.wilfried-probst.de/site/die-fremddienliche-zweckmasigkeit-des-gallapfels/

easy to translate, but perhaps "expediency serving foreign organisms", or "extrinsic usefulness", "disinterested suitability"; German biologist Hartmut Heilmann translated "well-directed extraneous utility"[84] for the *Proceedings of the 6th International Congress of Organic Viticulture*[85]; also something closely akin to "altruism" was suggested by three mindful readers of the present article). The term "fremddienliche Zweckmäßigkeit" has also become positive lexicon and textbook knowledge in Germany: Siegfried Strugger: *Biologie 1 (Botanik)*: 51.-75. Tausend 1963; Wilhelm Troll: *Allgemeine Botanik* [*Textbook of Botany*] in four editions, the last one 1973. Czihak et al. 1996: *Biology* [Textbook][86].

Considering the facts presented above – the immense problem for the theory of natural selection presented by the thousands of examples of complex, refined, sophisticated, "high tech" gall formations, often very energy expensive and thus disadvantageous for the plant hosts (to repeat: "***In the case of massive infestations,…we may speak of a gall disease (cecidiosis)***", but with no reward from the animals – it should be crystal clear for any thoughtful reader that Darwin's falsification criterion has been fulfilled, to recapitulate: "*If it could be proved that any part of the structure of any one species had been formed for the exclusive good of another species, it would annihilate my theory, for such could not have been produced through natural selection.*"

In other words, **it has been proved that thousands of different kinds of elaborate plant galls are formed for the exclusive good of the gall insects and mites**[87], which facts have – according to Darwin's own assessment – annihilated his theory, "for such could not have been produced through natural selection".

And, as we have already noted above, the test criteria given by Darwin in (a) the first sentence and (b) "***in all cases at the same time useful to the possessor***" are definitely not true for the plant hosts in his statement, as cited:

> "Natural selection can produce nothing in one species for the exclusive good or injury of another; though it may well produce parts, organs, and excretions highly useful or even indispensable, or again highly injurious to another species***, but in all cases at the same time useful to the possessor.***"

Darwin also:

> "***Natural selection will never produce in a being anything injurious to itself,*** for natural selection acts solely by and for the good of each."[88]

At this point of our discussion I am going to make a shortcut and go directly to the proposed (and evidently generally accepted) solution of the problem by Mayr and Dawkins.

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[84] This is the only source detected so far for corresponding terms in the English language.
[85] https://studylib.net/doc/18604220/proceedings-6th-international-congress-on-organic-viticul...
[86] C. Czihak, H. Langer, H. Ziegler (Eds.) (1996, p. 553): Biologie. Ein Lehrbuch. Sechste Aufl. Springer-Verlag, Berlin.
[87] Just by the way: "About 98 percent of known gallers affect flowering plants (angiosperms), with most (90 per cent) on dicotyledons (Meyer 1987). Galling often affects the commonest and largest plant species more than others. In Europe and North America, about 50 per cent of galls occur on oaks and beeches (Fagaceae), 20 per cent on the daisy family (Asteraceae), and 15 per cent on roses, brambles, and cherries *etc*. In South America, Africa and India, galls on legumes (Fabaceae) and acacias (Mimosaceae) predominate. In Australia, more than 50 per cent occur on eucalypts (Myrtaceae)." M. Redfern (2011, p.4): Plant Galls. HarperCollins. (Note added 13 September 2017.)
[88] For all editions of the Origin see also http://darwin-online.org.uk/EditorialIntroductions/Freeman_OntheOriginofSpecies.html

Why the solution proposed by Ernst Mayr and Richard Dawkins has failed

In his book *The Extended Phenotype*, Dawkins (1982, p. 219 and 2016, p. 334[89]) refers to Mayr's solution to the problem of galling as follows:

> "Mayr (1963, pp. 196-197) discusses the phenomenon of plants making galls to house insects, in terms so favourable to my thesis that I can quote him verbatim almost without comment:
>
> > "Why ... should a plant make the gall such a perfect domicile for an insect that is its enemy? Actually we are dealing here with two selection pressures. On the one hand, selection works on a population of gall insects and favors those whose gall-inducing chemicals stimulate the production of galls giving maximum protection to the young larva. This, obviously, is a matter of life or death for the gall insect and thus constitutes a very high selection pressure. The opposing selection pressure on the plant is in most cases quite small because having a few galls will depress viability of the plant host only very slightly. The 'compromise' in this case is all in favor of the gall insect. Too high a density of the gall insect is usually prevented by density-dependent factors not related to the plant host."[90]

Dawkins adds:

> "Mayr is here invoking the equivalent of the life/dinner principle to explain why the plant does not fight back against the remarkable manipulation by the insect."

No experimental investigation was suggested by the authors. However, a scientific hypothesis or theory should – in principle – be testable. One may ask a Darwinian how such ideas could be ever proved or disproved: my experience in many discussions over decades so far is that either one does not get any qualified answer or no answer at all. As pointed out by W. R. Thompson in his *Introduction* to the *Origin*, the main reason appears to be the following:

> "The Darwinian doctrine has thus been used, not as a working hypothesis, in the strict sense of the word, but rather as an explanatory principle, which it is sufficient to illustrate by examples, rather than to verify. The role of the Darwinian theory in biology is therefore essentially that of a philosophical doctrine." – W. R. Thompson.[91]

And, as Tom Bethell reported on an interview with Philipp Johnson (2017, pp. 211/212):

> Darwinism "claimed that complex adaptive organs came into existence through the accumulation of micro-mutations by natural selection. And … it assumed "that stories of adaptive evolution require no confirmation from genetics, or paleontology, or anything else ***except the adaptationist community's prevailing sense of plausibility***.""[92]

Nevertheless, the "adaptationist community's prevailing sense of plausibility" has often been found to be nothing but subjective story telling and proved to be false for many biological hypotheses. Thus, this plausibility criterion is

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[89]Dawkins, R. The Extended Phenotype. The Long Reach of the Genes. Oxford Landmark Science. According to Amazon: 2016-11-1.

[90] And Dawkins comments (same page): "Mayr is here invoking the equivalent of the life/dinner principle' to explain why the plant does not fight back against the remarkable manipulation by the insect. It is necessary for me to add only this. If Mayr is right that the gall is an adaptation for the benefit of the insect and not the plant, it can have evolved only through the natural selection of genes in the insect genepool. Logically, we have to regard these as genes with phenotypic expression in plant tissue, in the same sense as some other gene of the insect, say one for eye colour, can be said to have phenotypic expression in insect tissue."

[91] William RobinThompson (1967): *Introduction* to Charles Darwin: The Origin of Species. Everyman's Library No. 811, reprint of the sixth edition of 1872.

[92] Tom Bethell (2017): Darwin's House of Cards. Discovery Institute Press, Seattle.

incomplete, weak and insufficient to establish a solid scientific theory. Much more is necessary for a valid theory – notably falsifiability:

> "Statements, hypotheses, or theories have falsifiability or refutability if there is the inherent possibility that they can be proven false. They are falsifiable if it is possible to conceive of an observation or an argument which could negate them. In this sense, *falsify* is synonymous with *nullify*, meaning to invalidate or "show to be false".
> …. Scientific theories can always be defended by the addition of *ad hoc* hypotheses. As Popper put it, a *decision* is required on the part of the scientist to accept or reject the statements that go to make up a theory or that might falsify it. At some point, the weight of the *ad hoc* hypotheses and disregarded falsifying observations will become so great that it becomes unreasonable to support the base theory any longer, and a decision will be made to reject it." [93]

First inference: ***The statements of Mayr and Dawkins on the different selection regimes on the origin of plant galls (life dinner race of insect parasites vs. plants) are – in the formulation of the authors – untestable, i. e. neither falsifiable nor verifiable and hence nonscientific.*** However, they are just complying very well with the just mentioned subjective and often scientifically baseless "adaptationist community's prevailing sense of plausibility" – gratuitously presupposing the unproven and unprovable "two great constructors of [macro-] evolution", random micro-mutations and omnipotent selection for the origin of new complex organs and novel body plans.

Now, let's analyze Mayr's line of argumentation in detail:

> A "Why ... should a plant make the gall such a perfect domicile for an insect that is its enemy? Actually we are dealing here with **two selection pressures**.

Are there really "…two selection pressures" involved, which are in competition with each other running at different speeds? The doubtful basis for this statement is the imaginary conviction of many evolutionary biologists that "natural selection comes **close to omnipotence**" (John C. Avise 1998, p. 208[94]). Professor Christopher Exley (2009, p. 589) from Keele University is even convinced that "both the beauty and the brilliance of natural selection are reflected in its **omnipotence** to explain the myriad observations of life"[95].

According to Charles Darwin, natural selection displays, in fact, **limitless power and virtually godlike abilities** for the origin of life's "endless forms most beautiful", saying (1859, p. 84):

> "It may be said that natural selection is ***daily and hourly scrutinising, throughout the world, every variation, even the slightest; rejecting that which is bad, preserving and adding up all that is good***; silently and insensibly working, whenever and wherever opportunity offers, at the improvement of each organic being in relation to its organic and inorganic conditions of life. We see nothing of these slow changes in progress, until the hand of time has marked the long lapse of ages, and then so imperfect is our view into long past geological ages, that we only see that the forms of life are now different from what they formerly were."[96]
> (1859, p. 469, 1872, p 412) What limit can be put to this power, ***acting during long ages and rigidly scrutinising the whole constitution, structure, and habits of each creature***,—favouring the good and rejecting the bad? ***I can see no limit to this power***, in slowly and beautifully adapting each form to the most complex relations of life.

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[93] https://en.wikipedia.org/wiki/Falsifiability Retrieved on 11 August 2017

[94] John C. Avise (1998): The Genetic Gods. Evolution and Belief in Human Affairs. Harvard University Press. Cambridge, Massachusetts and London.

[95] Christopher Exley (2009): Darwin. Natural selection and the biological essentiality of aluminium and silicon. Trends in Biochemical Sciences **34**: 589-593.

[96] Beginning 1860, Darwin added "metaphorically" in all following editions. See http://darwin-online.org.uk/content/frameset?pageseq=1&itemID=F391&viewtype=text (1872, p. 65/66) "It may metaphorically be said that natural selection is daily and hourly scrutinising, throughout the world, the slightest variations; rejecting those that are bad, preserving and adding up all that are good; silently and insensibly working, whenever and wherever opportunity offers, at the improvement of each organic being in relation to its organic and inorganic conditions of life. We see nothing of these slow changes in progress, until the hand of time has marked the lapse of ages, and then so imperfect is our view into long-past geological ages, that we see only that the forms of life are now different from what they formerly were."

(1872, p. 85) ***[I] can see no limit to the amount of change***, to the beauty and complexity of the coadaptations between all organic beings, one with another and with their physical conditions of life, which may have been affected in the long course of time through nature's power of selection, that is by the survival of the fittest.[97]

Let's now contrast this somehow deceptively beautiful and alluring language of the delusion of the omnipotence of natural selection with the sobering facts nature.

For an encyclopedia article on natural selection, I stated, among other things[98]:

The Reproductive Powers of Living Beings and the Survival of the Fittest

Dobzhansky's 1937 work Genetics and the Origin of Species is generally viewed as the crystallization point for the origin and growth of the modern synthesis or neo-Darwinian theory of evolution (Lönnig, 1999a). There is hardly a better example to illustrate the key message (and, at the same time, the weaknesses) of the modern theory of natural selection than the following quotation from this pioneering work of Dobzhansky (p. 149):

> With consummate mastery Darwin shows natural selection to be a direct consequence of the appallingly great reproductive powers of living beings. A single individual of the fungus Lycoperdon bovista produces 7 x 1011 spores; Sisymbrium sophia and Nicotiana tabacum, respectively, 730,000 and 360,000 seed; salmon, 28,000,000 eggs per season; and the American oyster up to 114,000,000 eggs in a single spawning. Even the slowest breeding forms produce more offspring than can survive if the population is to remain numerically stationary. Death and destruction of a majority of the individuals produced undoubtedly takes place. If, then, the population is composed of a mixture of hereditary types, some of which are more and others less well adapted to the environment, a greater proportion of the former than of the latter would be expected to survive. In modern language this means that, among the survivors, a greater frequency of carriers of certain genes or chromosome structures would be present than among the ancestors...

For agreement on and further documentation of the principle of natural selection, see the group of authors cited above, beginning with Bell (1997). However, in the 1950s, French biologists, such as Cuénot, Tétry, and Chauvin, who did not follow the modern synthesis, raised the following objection to this kind of reasoning (according to Litynski, 1961, p. 63):

> Out of 120,000 fertilized eggs of the green frog only two individuals survive. Are we to conclude that these two frogs out of 120,000 were selected by nature because they were the fittest ones; or rather - as Cuenot said - that natural selection is nothing but blind mortality which selects nothing at all?

Similar questions may be raised for the 700 billion spores of Lycoperdon, the 114 million eggs multiplied with the number of spawning seasons of the American oyster, for the 28 million eggs of salmon and so on. King Solomon wrote around 1000 BC: "I returned, and saw under the sun, that the race is not to the swift, nor the battle to the strong,...but time and chance happeneth to all of them" (KJV 1611).

If only a few out of millions and even billions of individuals are to survive and reproduce, then there is some difficulty believing that it should really be the fittest who would do so. Strongly different abilities and varying environmental conditions can turn up during different phases of ontogenesis. Hiding places of predator and prey, the distances between them, local differences of biotopes and geographical circumstances, weather conditions and microclimates all belong to the repertoire of infinitely varying parameters. Coincidences, accidents, and chance occurrences are strongly significant in the lives of all individuals and species. Moreover, the effects of modifications, which are nonheritable by definition, may be much more powerful than the effects of mutations which have only "slight or even invisible effects on the phenotype" (Mayr 1970, p. 169, similarly 1976/1997; see also Dawkins, 1995, 1998), specifying that kind of mutational effects most strongly favored for natural selection and evolution by the neo-Darwinian school. Confronting the enormous numbers of descendants and the neverending changes of various environmental parameters, it seems to be much more probable that instead of the very rare "fittest" of the mutants or recombinants, the average ones will survive and reproduce.

Of course, much more is to be said on the weaknesses and failure of natural selection to explain the essential phenomena of life. See, please, for example, the link given above *On the Limits of Natural Selection* (Lönnig 2016).

Applied to the topic of plant galls and evolution, we can conclude that:

Natural selection – which was thought to be "daily and hourly scrutinising, throughout the world, every variation, even the slightest; rejecting that which is bad, preserving and adding up all that is good" – ***not only failed miserably and totally in all the thousands of affected plant host species, but also – against all expectations and predictions – would have been entirely efficacious, successful and victorious exclusively in the ca. 132,930 different galling insect species***.

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[97] Similarly (1859, p. 109): "I can see no limit to the amount of change, to the beauty and infinite complexity of the coadaptations between all organic beings, one with another and with their physical conditions of life, which may be effected in the long course of time by nature's power of selection."

[98] See all the details and subsequent discussion in http://www.weloennig.de/jfterrorchipmunks.pdf
http://www.weloennig.de/NaturalSelection.html

Thus, natural selection does definitely not come "close to omnipotence". Instead of selection reflecting "both the beauty and the brilliance in its omnipotence to explain the myriad observations of life", it has shown its total inefficiency and utter impotence to explain the myriad research results pertaining not only to plant galls but also innumerable further biological phenomena (see, for instance, Behe 1996/2006, 2007; Lönnig 2005, 2012, 2014, 2015, 2016; Meyer 2014; Axe 2017; Bethell 2017; Wells 2017[99], and very many further qualified authors).

There are ***limits*** ***"to this power [of natural selection]***, in slowly and beautifully adapting each form to the most complex relations of life."

Reflecting on the generally accepted mode of evolution – first in the words of Darwin's modern followers and on the next page of Darwin himself:

> **Uncountable successive small microevolutionary steps** have led to large changes in the body forms of organisms in the course of millions of years (**macroevolution, concept of additive typogenesis**)" – Kutschera 2006, p. 204 and 2015, p. 256).[100]

Similar statements have been made by Dawkins (2017) and many other contemporary authors.[101] Textbook author and leading evolutionary biologist Futuyma comments on the present state of evolutionary theories (2017):

> "Newly discovered molecular phenomena have been **easily accommodated in the past by elaborating orthodox evolutionary theory**, and it appears that the same holds today for phenomena such as epigenetic inheritance. In several of these areas, empirical evidence is needed to evaluate enthusiastic speculation. Evolutionary theory will continue to be extended, but **there is no sign that it requires emendation**."[102]

And Carl Zimmer reported (2016) that Futuyman emphasized at the Royal Society Meeting on *New trends in evolutionary biology: biological, philosophical and social science perspectives*[103] concerning the strength and Modern Synthesis:

> ""**We must recognize that the core principles of the Modern Synthesis are strong and well-supported**," Futuyma declared. Not only that, he added, but the kinds of biology being discussed at the Royal Society weren't actually all that new. The architects of the Modern Synthesis were already talking about them over 50 years ago. And there's been a lot of research guided by the Modern Synthesis to make sense of them."[104]

The population geneticists Deborah Charlesworth, Nicholas H. Barton, Brian Charlesworth (and many other biologists) obviously agree (2017):

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[99] Behe MJ (1996/2006) Darwin's Black Box. The Biochemical Challenge toEvolution (2nd Edition with Answers to Critics). New York: The Free Press. Behe (2007) The Edge of Evolution. Testing the Limits of Darwinism. New York: The Free Press.
Lönnig W-E Lönnig W-E (2005) Mutation breeding, evolution, and the law of recurrent variation. Recent Developments in Genetics and Breeding **2**: 45–70. Lönnig W-E (2006) Mutations: the law of recurrent variation. In: Teixeira da Silva JA (ed) Floriculture, Ornamental and Plant Biotechnology, vol. **I**, pp. 601–607. (2012) Die Evolution der karnivoren Pflanzen: Was dieSelektion nicht leisten kann - das Beispiel Utricularia (Wasserschlauch) 3. Auflage. Münster: Verlagshaus Monsenstein und Vannerdat OHG. Lönnig W-E (2014) Unser Haushund: Eine Spitzmaus im Wolfspelz? Oder beweisen die Hunderassen, dass der Mernsch von Bakterien abstammt? Münster: Verlagshaus Monsenstein und Vannerdat OHG. Lönnig W-E (2016): Carnivorous Plants: http://www.els.net/WileyCDA/ElsArticle/refId-a0003818.html
Meyer S C (2014): Darwin's Doubt. The Explosive Origin of Animal Life and the Case for Intelligent Design. HarperOne, San Francisco.
D. Axe (2017): Undeniable. How Biology Confirms Our Intuition That Life is designed. HarperOne, San Francisco. Tom Bethell (2017): Darwin's House of Cards. Discovery Institute Press, Seattle.
Wells, J. (2017): Zombie Science. More Icons of Evolution. Discovery Institute Press, Seattle.
[100] Kutschera, U. (2006/2015): Evolutionsbiologie. Eine allgemeine Einführung. Eugen Ulmer Verlag, Stuttgart (2. und 4. Auflage).
[101] Dawkins, R. (2017): Science in the Soul: Selected Writings of a Passionate Rationalist. Bantam Press, New York. As to an elaborate documentation of the role of micro-mutations for the present synthetic theory (neo-Darwinism), see, for instance, also my book of 2011 on: The Evolution of the Long-Necked Giraffe (Giraffa camelopardalis L.): What do we really know?: Testing the Theories of Gradualism, Macromutation, and Intelligent Design. Monsenstein und Vannerdat OHG, Münster. Lönnig (2014): Unser Haushund: Eine Spitzmaus im Wolfspelz: http://www.weloennig.de/Hunderassen.Bilder.Word97.pdf; Lönnig (2017): http://www.weloennig.de/jfterrorchipmunks.pdf; Bethell (2017): Darwin's House of Cards. Discovery Institute Press, Seattle.
[102] Futuyma, D. J. (2017): Evolutionary biology today and the call for an extended synthesis. Interface Focus http://rsfs.royalsocietypublishing.org/content/7/5/20160145.
[103] https://royalsociety.org/science-events-and-lectures/2016/11/evolutionary-biology/
[104] Zimmer, C. (2016): Scientists Seek to Update Evolution. https://www.quantamagazine.org/scientists-seek-to-update-evolution-20161122/
See also the angry comment by Laurance A. Moran: http://sandwalk.blogspot.de/2017/08/the-extended-evolutionary-synthesis.html

> "We illustrate how careful genetic studies have repeatedly shown that ***apparently puzzling results in a wide diversity of organisms involve processes that are consistent with neo-Darwinism***. They do not support important roles in adaptation for processes such as directed mutation or the inheritance of acquired characters, and therefore no radical revision of our understanding of the mechanism of adaptive evolution is needed."[105]

See also the following concise characterization of today's main evolutionay theory – the Modern Synthesis or neo-Darwinian theory of evolution with its focus on gradualism – by Gerd B. Müller (2017):

> "Even though claims have been made that classical evolutionary biology has continuously incorporated aspects from new conceptual domains, **the majority of tenets and explanations that appear in characterizations of the current theory are still derived from the MS** [Modern Synthesis] **account and its population genetic principles**. In a condensed form, these tenets are as follows: (i) all evolutionary explanation requires the study of populations of organisms; (ii) populations contain genetic variation that arises randomly from mutation and recombination; (iii) populations evolve by changes in gene frequency brought about by natural selection, gene flow and drift; (iv) genetic variants generate slight phenotypic effects and the ***resulting phenotypic variation is gradual and continuous***; (v) genetic inheritance alone accounts for the transmission of selectable variation; (vi) new species arise by a prevention of gene flow between populations that evolve differently; (vii) ***the phenotypic differences that distinguish higher taxa result from the incremental accumulation of genetic variation***; (viii) natural selection represents the only directional factor in evolution."
> ….Criticisms of the shortcomings of the MS framework have a long history. One of them concerns ***the profoundly gradualist conception the MS has inherited from the Darwinian account of evolution***.
> …Connected with the gradualist requirement of the MS theory is the deeply entrenched notion of adaptation."[106]

Darwin had provided the basic idea of continuous evolution more than 150 years ago by postulating:

> "*innumerable* slight variations", "*extremely* slight variations" and "*infinitesimally* small inherited variations" (he also spoke of "infinitesimally small changes", "infinitesimally slight variations" and "slow degrees") and hence imagined "steps not greater than those separating fine varieties","insensibly fine steps" and "insensibly fine gradations", "for natural selection can act only by taking advantage of slight successive variations; **she can never take a leap**, but must advance by the shortest and slowest steps" or "the transition [between species] could, according to my theory, be effected only by ***numberless small gradations***" (emphasis added, see http://darwin-online.org.uk/).

However, for each of these postulated "insensibly fine steps", each of the "numberless small gradations" etc. the following rule has unanimously been established by population genetics:

> "Even a new mutation that is slightly favorable will usually be lost in the first few generations after it appears in the population, a victim of genetic drift. If a new mutation has a selective advantage of S in the heterozygote in which it appears, then the chance is only $2S$ that the mutation will ever succeed in taking over the population. So a mutation that is 1 percent better in fitness than the standard allele in the population will be lost 98 percent of the time by genetic drift."[107]

So, let's keep in mind that for each of the "*extremely slight variations*", each of the "*steps not greater than those separating fine varieties*" a mutation 1 percent better in fitness than the standard allele has to occur at least 50 times (in many cases even much more often[108]) to have a chance to succeed in taking over a population. As for the additional remote possibility of the origin of new genes and protein folds, see, for example, Axe (2017)[109].

Hence, in each and every case of all the different some 132,930 independently arisen galling insects species, correspondingly literally thousands of supposed long evolutionary gall histories must be postulated, all by "*uncountable successive small microevolutionary steps*", "*infinitesimally small inherited variations*" etc. – and each of the necessary mutations had to occur separately of each other at least some 50 times on average to have a chance to succeed in a

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[105] Deborah Charlesworth, Nicholas H. Barton, Brian Charlesworth (2017): The sources of adaptive variation. http://rspb.royalsocietypublishing.org/content/284/1855/20162864
[106] Müller, G. B. (2017): Why an extended evolutionary synthesis is necessary. Interface Focus: http://rsfs.royalsocietypublishing.org/content/7/5/20170015
[107] For a discussion including the references, see Lönnig (2016) http://www.weloennig.de/jfterrorchipmunks.pdf
[108] For this important qualification compare the discussion given in the Link just quoted.
[109] D. Axe (2017): Undeniable. How Biology Confirms Our Intuition That Life is designed. HarperOne, San Francisco.

given population (the regular occurrence of such specific additive gall building mutations simply taken for granted, but so far without any testable evidence).

In other words: for the evolution of complex galls over innumerable intermediary links by the supposed micro-mutations "*with slight or even invisible effects on the phenotype*" (Mayr) in the genomes of the insects, it has to be assumed that these steps must have been successful not just once, but in each case of the individually evolving galling insect species and corresponding gall phenomena even tens of thousands of times, i.e. for each further infinitesimally small step in millions of years, eventually resulting in the present phenomena of elaborate plant galls.

The situation becomes even more difficult considering the many examples of alternations of generations:

> "The reproduction of the gall wasp is partly pure two-sex propagation, and partly pure parthenogenesis, in which a male is completely unnecessary. *With most species, however, an alternation of generations occurs, with one two-sex generation and one parthenogenic generation annually*. This process differentiates the various generations primarily ***in their appearance and the form of the plant galls they induce***."[110]

Thus, in all these cases the improbabilities of the sheer endless processes of the selection of mutations with often invisible effects on the phenotype of the insects and the gall devices must at least be doubled, considering the fact that the insects make two usually very distinctive plant galls from one and the same genome – the one two-sex generation and the one parthenogenic generation. So, in spite of all the dissimilarities, the entire superordinate process must also involve tight interconnections on the genetic level but differential gene expression for the two generations that produce the distinct morphology of the respective insect species[111] and especially their different plant galls.

It must be further assumed that, in contrast to the animals, in the plant hosts natural selection not only failed continually and totally to do anything against the parasites – so far no clear signs of resistance – during all the eons of time, but that the plants, in clear opposition and full defiance to natural selection, must *increasingly* have invested much of their energy and substance to help the parasites flourish, improve and strongly multiply in preparation for the next rounds of infestations.

Additionally all this must be assumed again to be true for all the often strongly different insect (and other) species, ***which share one and the same plant host***. In the case of the oak (*Quercus robur*) 132 (one hundred thirty-two)[112] different galling animals have so far been counted.

And, last not least, imagine for a moment that the host plants are not only "providing nutrition and protection to the galling insect from natural enemies

[110] https://en.wikipedia.org/wiki/Gall_wasp (retrieved 3 September 2017.)
[111] In some cases the different phenotypes of the alternating generations of gall wasps were originally described not only as different species, but even as different genera, for example *Cynisps quercusfolii/SpathegasterTaschenbergi*
[112] Kuhn, W. (1984, p. 46): For the full reverence see footnote above.

and environmental stresses", generally supposed to be exclusively due to the action of the insect, but actively participate – as a consequence of correspondingly 'altruistic' information in its DNA – in constructing and building the houses for the insect parasites (there are some hints at present that they are, indeed, involved, if perhaps only slightly – a testable hypothesis), then it would have additionally been *proved that parts of the structure of any one species had been formed for the exclusive good of another species.* For *natural selection will never produce in a being anything injurious to itself.*

All the cases of deceptive flowers, not only imitating the form of insects (like that of bumble bees and other insects) but also the chemically very special, individual scents of their guests, show that this would, in principle, be possible. According to Kara Rogers (2011):

> "An estimated 1,000 orchid species resort to sexual deception, in which flowers attract pollinators by producing scents that mimic sex pheromones. A striking example of this form of deception is seen in the orchid *Chiloglottis trapeziformis*, which lures males of its pollinator, the thynnine wasp (*Neozeleboria cryptoides*), ***when it releases a compound identical to a sex pheromone normally produced by female thynnine wasps***. The males are enticed to mate with the flower, and in the process of attempting to do so, they pick up pollen from the flower and transfer it to a second plant when again lured by the pheromone-mimicking odor."

See also Peacall 2007, Johnson and Schiestl 2016, Luna and Wester 2017[113]. So, this seems to be an additional category of examples *for structures of one species, which had been formed for the exclusive good of another species* (however, in contrast with the gall formations, now for the exclusive good of the plant species). Gerd B. Müller has recently (2017) correctly pointed out that the Synthetic Theory:

> "…largely avoids the question of ***how the complex organizations of organismal structure***, physiology, development or behaviour—whose variation it describes—**actually** arise in evolution, and it also provides no adequate means for including factors that are not part of the population genetic framework, such as developmental, systems theoretical, ecological or cultural influences."[114]

To reformulate Mayr's point A:

> A "Why ... should a plant make the gall such a perfect domicile for an insect that is its enemy? Actually we are dealing here with a phenomenon, in which not only any selection pressures fail, but also natural selection itself. The idea of two selection pressures in competition with each other has no scientific basis. It is nothing but a pure thought speculation or imaginary thought construction to save the theory of evolution by natural selection from falsification."

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[113] (All references retrieved 24 and 25 August 2017) http://blogs.britannica.com/2011/03/deceptive-flowers-orchids/ For Professor Rod Peacall, see http://biology-assets.anu.edu.au/hosted_sites/orchid_pollination/ ("…**as many as one third of the 30,000 or so species achieve pollination by deception**. That is, they lure animal pollinators to the flower by false promises of food, ***but do not provide any***."). Book by S. D. Johnson and F. S. Schiestl (2016): Floral Mimicry. Oxford University Press. K. Lunau and P. Wester (2017): Mimicry and Deception in Pollination. Advances in Botanical Research **82**: 259-279. P. 259: "Floral mimicry is always beneficial for the mimic, ***but may impose costs for the deceived pollinators***." http://www.sciencedirect.com/science/article/pii/S0065229616301136. My comment: It clearly does impose costs – energy – for he deceived pollinators. And the following sentence of the authors is an example of pure evolutionary speculation in disaccord with natural selection: "Then the deceived pollinators likely evolve mechanisms not being deceived and the flowering plants to continue deception, and deception becomes trickier over evolutionary times." In such cases, the plants would have been repeatedly and finally successful in their evolution for the "exclusive good or injury of another" species and "*If it could be proved that any part of the structure of any one species had been formed for the exclusive good of another species, it would annihilate my theory, for such could not have been produced through natural selection.*" (See Darwin as quoted above)

[114] Müller, G. B. (2017): Why an extended evolutionary synthesis is necessary. Interface Focus: http://rsfs.royalsocietypublishing.org/content/7/5/20170015

To briefly analyze the evolutionary explanatory method here applied: To account for the relationship between two objects: either invent, devise and fabricate a system[115], or better observe real systems in nature, and postulate (almost) omnipotent identical factors, one for each of the two objects, thought to be in competition with each other, running at different speeds and you can imaginarily explain almost everything (note the inherent contradiction in the postulate).

See the many examples for the life/dinner principle of Richard Dawkins[116].

Perhaps an example from the human sphere (although humans psychologically far transcent the animal kingdom): A family overexerts itself for foreigners who consume and even use up all its supplies and provisions so that the latter are flourishing and becoming prosperous and rich at the expense and to the detriment of the former. Would competition – two selection pressures running at different speeds explain the real situation?

Nonetheless a word of caution: I do not deny, for example, that there is some evidence for stabilizing natural selection discarding larger disadvantageous mutations ("defect-mutations", not explaining, of course, the facts presented in this paper), **but I do emphatically deny that selection is omnipotent and implicitly explains the origin of all the life forms on earth** by the assistance of random micro-mutations. In contrast to Darwin's verdict ("*I can see no limit to the amount of change,...*") there are definitely limits to natural selection and the amount of change it can achieve: It systematically fails to explain "the beauty and complexity of the coadaptations between all organic beings".

Mayr continued:

> B "On the one hand, selection works on a population of gall insects and favors those whose gall-inducing chemicals stimulate the production of galls giving maximum protection to the young larva."

But why then, did selection not work on a population of host plants and favored those whose gall resistant chemicals stimulated the production of "poisons" and other safeguard mechanisms against the insects thus providing maximus protection to the young and older plant species sometimes heavily infested over millions of years? Where was ***omnipotent*** natural selection, which Darwin thought to be "daily and hourly scrutinising, throughout the world, ***every variation, even the slightest***; rejecting that which is bad, preserving and adding

[115] Example in the context of falsifiability: Professor Murray Eden stated, after an example of falsifiability and a successful falsification of a hypothesis in physics, that: "This cannot be done in evolution, taking it in its broad case, and this is really all I meant when I called it tautologous in the first place. **It can, indeed, explain anything**. You may be ingenious or not in proposing a mechanism which looks plausible to human beings and mechanisms which are consistent with other mechanisms which you have discovered. But it still is an **unfalsifiable theory**." Comment by Dr. John C. Fentress (Brain Research Center, University of Rochester, Rochester, New York, later Professor in Biology and Psychology, Dalhousie University): "…When I was in Cambridge, we were working with two species of British vole. We had a little test in which an object moved overhead; one species would run away and the other species would freeze. Also, one species happened to live in the woods and the other happened to live in the field. This was rather fun, and, not really being a zoologist, I went up to see some of my zoologist friends and **I reversed the data**. I asked them simply, why a species which lived in the field should freeze and why one that lived in the woods should run away (when the converse was the case). I wish I had recorded **their explanations**, because **they were very impressive indeed**." M. Eden and J. C. Fentress, in the discussion of the chapter, "The problems of Vicarious Selection," George Wald, in Mathematical Challenges to the neo-Darwinian Interpretation of Evolution, P. S. Moorhead and M. M. Kaplan, Eds., Wister Institute Press, Philadelphia, 1967, p. 71. See also comment in the German magazine *Die Zeit*: http://www.zeit.de/1967/50/zweifel-an-darwins-theorie

[116] https://en.wikipedia.org/wiki/Evolutionary_arms_race#Examples

up all that is good"? Where was it ***"scrutinising the whole constitution, structure, and habits of each creature, favouring the good and rejecting the bad"?***

> C "This, obviously, is a matter of life or death for the gall insect and thus constitutes a very high selection pressure."

This, obviously, is just another imaginary thought construction to safe the selection theory. Already in 1917, p. 567, cecidologist Ernst Küster noted the ensuing facts, undeniably falsifying Mayr's statement:

> "For the evaluation of the benefits which the galling animals achieve from the cecidium, and the damage to the host plants arising from the production of the galls, it should also be noted that in the "**facultative galls**" cecidioses are at work, whose cecidiose strength – for still unknown reasons – frequently fails. **Then the formation of the galls does not occur. However, the animal is still developing** – a fact which clearly demonstrates that the supposed indispensability of the gall for the benefit of the parasite now appears in a particular light to us." [117]

Mayr goes on to say:

> D "The opposing selection pressure on the plant is in most cases quite small because having a few galls will depress viability of the plant host only very slightly."

"The opposing selection pressures" in the sense of Darwin, Avise, Kutschera, Exley and many other authors do not exist. And, as we have seen above, many galls can depress viability of the plant host very strongly.

Mayr proceeds:

> E "The 'compromise' in this case is all in favor of the gall insect."

This verdict does not consider heavy infestations. The compromise does not exist. Rather, the facts have called natural selection itself into question, for "*natural selection can produce nothing in one species for the exclusive good or injury of another…*" (see Darwin above).

And finally Dawkins has quoted Mayr as follows:

> F "Too high a density of the gall insect is usually prevented by density-dependent factors not related to the plant host."

The "density-dependent factors" should be speciefied. The important topic of the hyperparasitism may be relevant for this question.

As we have seen, Dawkins adds:

> "Mayr is here invoking the equivalent of the life/dinner principle to explain why the plant does not fight back against the remarkable manipulation by the insect."[118]

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[117] E. Küster (1917) Besprechung von Becher, Erich: Die fremddienliche Zweckmäßigkeit der Pflanzengallen und die Hypothes eines überindividuellen Seelischen. https://www.digizeitschriften.de/dms/img/?PID=PPN34557155X_0005%7Clog442
Original German text: "Für die Beurteilung des Nutzens, den die Gallentiere von dem Zezidium haben, und des Schadens, der den Wirtspflanzem aus der Produktion der Gallen erwächst, sei noch nachgetragen, dass bei den „fakultativen Gallen" Zezidiosen am Werke sind, deren zezidiose Kraft nicht selten – aus noch unbekannten Gründen – versagen kann; dann unterbleibt die Gallenbildung. Das Tier aber entwickelt sich dennoch – ein Umstand, der uns die Bedeutung, die vermeintliche Unentbehrlichkeit des mit der Galle für den Parasiten Gebotenen in besonderem Licht erscheinen lässt."

[118] [S]election will be stronger on the prey [the host plant] than on the predator [the parasites: the galling insects and mites] because a prey individual [the host plant] that loses the race loses its life, whereas the unsuccessful predator [he parasites: the galling insects and mites] loses only a meal."Dr. Michael Kingston, Elon University: https://www.flashcardmachine.com/general-ecology-exam3.html (so definition already for cards seems to be valid not only for u ndergraduates.)

There is an enormous difference between this life/dinner principle and galling insects in relation to their host plants. Dawkins's example of the cuckoo can illustrate this very well (1976/2006, p. 250):

> "In the evolutionary 'armsrace' between cuckoos and any host species, there is a sort of built-in unfairness, resulting from unequal costs of failure. Each individual cuckoo nestling is descended from a long line of ancestral cuckoo nestlings, every single one of whom must have succeeded in manipulating its foster-parent. Any cuckoo nestling that lost its hold, even momentarily, over its host would have died as a result!

Since natural selection "*can never take a leap*" – how could this have been effected by "*innumerable* slight variations", "*extremely* slight variations" and "*infinitesimally* small inherited variations", "*uncountable successive small microevolutionary steps*" etc. (see quotations above)?[119]

Dawkins continues:

> "But each individual foster-parent is descended from a long line of ancestors many of whom never encountered a cuckoo in their lives. And those that did have a cuckoo in their nest could have succumbed to it and still lived to rear another brood next season. The point is that there is an asymmetry in the cost of failure. Genes for failure to resist enslavement by cuckoos can easily be passed down the generations of robins or dunnocks. Genes for failure to enslave foster-parents cannot be passed down the generations of cuckoos."

All things considered, let's put the question again now for the gene level: how could these genes necessary to enslave foster-parents have arisen in a stepwise process by large numbers of "mutations with slight or even invisible effects on the phenotype"?

> "This is what I meant by'built-in unfairness', and by 'asymmetry in the cost of failure'. The point is summed up in one of Aesop's fables: 'The rabbit runs faster than the fox, because the rabbit is running for his life while the fox is only running for his dinner.'[120] My colleague John Krebs and I have dubbed this the 'life/ dinner principle'.
>
> Because of the life/dinner principle, animals might at times behave in ways that are not in their own best interests, manipulated by some other animal. Actually, ***in a sense they are acting in their own best interests***: the whole point of the life/dinner principle is that they theoretically could resist manipulation ***but it would be too costly to do so***. Perhaps to resist manipulation by a cuckoo you need bigger eyes or a bigger brain, which would have overhead costs [W.-E.L.: good example of 'just so story telling']. Rivals with a genetic tendency to resist manipulation would actually be less successful in passing on genes, because of the economic costs of resisting. [121]

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[119] Darwin invented the following story for the behavior of the cuckoo (1872, p. 214): "I can see no special difficulty in its having gradually acquired, during successive generations, the blind desire, the strength, and structure necessary for the work of ejection; for those young cuckoos which had such habits and structure best developed would be the most securely reared. The first step towards the acquisition of the proper instinct might have been mere unintentional restlessness on the part of the young bird, when somewhat advanced in age and strength; the habit having been afterwards improved, and transmitted to an earlier age." How does this agree with the statement of Dawkins?: "Any cuckoo nestling that lost its hold, even momentarily, over its host would have died as a result!" Neverthess, one can easily sympasize with Darwin's formulation calling that behavior of the cuckoo as "this strange and odious instinct".

[120] However, in the example of the plant galls, the roles seem to have been swapped [comments in brackets added]:
"An asymmetrical arms race involves contrasting selection pressures, such as the case of cheetahs [in galls: predator/the parasites: the galling insects and mites] and gazelles [prey: the host plant], where cheetahs evolve to be better [predator: the parasites: the galling insects and mites] at hunting and killing while gazelles [prey: the host plant] evolve not to hunt and kill, but rather to evade capture. This asymmetric example could be more generally seen as the life-dinner principle. The life-dinner principle is the idea that in a situation with the predator [the parasites: galling insects and mites] and prey [the host plant], the prey [the host plant] gets the short end of the stick with either injury or death while the predator predator [the parasites: the galling insects and mites] just has the inconvenience of having to find another meal." https://en.wikipedia.org/wiki/Evolutionary_arms_race (retrieved 1 September 2017)

[121] Richard Dawkins (2006): The Selfish Gene. Oxford University Press, Oxford. 30th Anniversity Edition. http://s-f-walker.org.uk/pubsebooks/pdfs/Richard_Dawkins_The_Selfish_Gene.pdf

Well, the important difference is that the plants are doing ***much more*** than just "not to fight back" (see, please, the details above).

Let's tranfer the multiple devices and actions the infested plants are providing for their parasites to the example of the cuckoo:

In such a case, the foster-parents of the cuckoo themselves would throw out of their nests all their own descendents[122], construct exceptionally appropriate houses for their parasites – distinguished by wall constructions consisting of several fuctionally different layers (to safeguard the cuckoo from possible enemies[123] and provide shelter against cold, winds and rain), would built exclusive devices for particular provisions of food and beverages rich in vitamins, proteins, fats, carbohydrates etc. and would, among many futher protective devices[124], also care for correctly formed and right-sized exits/doors which open automatically only in the right direction exactly at the precise time when the young cuckoo becomes fully-fledged and thus able to fly.

Assume additionally that – similar to plants – in the event of heavy 'infestations' the foster-parents would invest so much of their time and energy that a large part of their population would prematurely die and thus have no further offspring.

And, of course, there would be no reward for the foster-parents.

So, is statement of Dawkins really true that the plants 'actually, ***in a sense are acting in their own best interests:***'? Continuing: "…the whole point of the life/dinner principle is that they [the hosts] theoretically could resist manipulation ***but it would be too costly to do so***."

Well, resistance to the sugar beet aphid, for example, was ascribed to both antibiosis and antixenosis "with more recent **evidence that this resistance is conferred *by a single gene***" ("Resistance in some of the varieties tested may be so pronounced that no aphids are able to survive on them") – Pretorius et al. 2016.[125] ***Why have the plants*** – apart from some exceptions usually achieved by human breeding strategies stopping gall formation at the very beginning of its development – ***been able to produce the most astonishing and intricate devices and means to help their parasites grow and flourish but usually nothing to resist them*** (which latter often seems to have been much easier genetically)?[126]

Would all this have nothing to do with Darwin's falsification criterion for his selection theory as cited above?: "If it could be proved that any part of the structure of any one species had been formed for the exclusive good of another

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122 It was important for Darwin that the act of ejection was **not** performed by the foster-parents themselves. http://darwin-online.org.uk/Variorum/1872/1872-214-c-1869.html.

123 There are often also additional defense systems on the outer wall layer: glues, hairs and thorns. As for "honeydew" by insect galls. Ephraim Porter Felt commented in his book *Plant Galls and Gall Makers*. London, Constable and Company ltd (1940, p. 12) "It would appear from the above that the production of honeydew by certain insect galls, particularly bud galls, is somewhat common and may be rather general. The liquid may be/simply an excessive, possibly modified plant excretion, such as is produced by the opening buds and to some extent by other tissues of various plants. There have been attempts to explain this phenomenon as a result of natural selection, and as possibly affording some protection to the plant, though such an interpretation is open to serious doubt." But perhaps aggressive insects attacked those plants all the more.

124 See text of Becher below.

125 See reference and link above.

126 As for the further idea of Dawkins: "Perhaps to resist manipulation by a cuckoo you need bigger eyes or a bigger brain, which would have overhead costs" I would like to point out that it could be much easier – perhaps similar to the following case in plants. See Helms et al 2017: Identification of an insect-produced olfactory cue that primes plant defences. https://www.nature.com/articles/s41467-017-00335-8

species, it would annihilate my theory, for such could not have been produced through natural selection."

Almost the entire explanation of Mayr and Dawkins is not only theoretically unfounded, baseless and to a certain extent even deceptive (mostly 'plausible' fiction widely accepted as factual explanation), but also internally contradictory and far beyond the limits of the testable realm of science.

To sum up: The biological facts ***have proved that complex parts of the structure of thousands of plant species have been formed for the exclusive good of galling insects (i. e. other species), and this phenomenon has – in his own words – annihilated Darwin's theory***, as well as that of his modern followers, for "natural selection cannot possibly produce any modification in a species exclusively for the good of another species".

The quest for a scientific alternative – to what extent is intelligent design an option?

In the following paragraphs I'm going to reproduce the text of my encyclopedia article on *natural selection*[127] (see also discussion 2016[128]):

»Although in this article alternatives for the origin of species cannot be discussed at length, a few points should be mentioned. As a first step into the direction of a realistic alternative to the doubtful hypothesis of the nearly omnipotent natural selection, let us shortly turn our attention to Behe's arguments again. He writes, "Closely matched, irreducibly complex systems not only are tall problems for Darwinism but also are the hallmarks of intelligent design. What is design? In my definition, design is simply the purposeful arrangement of parts" (1998, p. 179). However, does this inference to intelligent design not lead us directly back into the realm of metaphysics in Popper's sense? Not necessarily. A thoroughly epistemological study to clearly distinguish between the three basic parameters for any explanation in science and other areas of life in terms of either law, chance, or design (and in special cases to discover the proportions in a combination of two or even all three of them), has recently been performed and published by Dembski (1998a, 1998b). In his "explanatory filter" the object of explanation is an event called E. The first question is whether E is a highly probable event. If it is certain that E occurs under a set of standard conditions, E is probably due to deterministic or nondeterministic natural laws. If this first prerequisite is denied, it must be determined whether E is an event of intermediate probability, that is, an event, which one can commonly anticipate to happen by chance in normal situations of life. If an event has the probability of 1 in 10 million, it will happen a 100 times in 1 billion corresponding situations. Concerning intelligent design, Dembski further explains (1998b, pp. 101-102):

> But suppose that E is neither a high probability (HP) nor an intermediate (IP) event. By a process of elimination E will therefore make it all the way to the third and final decision node. In this case E is an

[127] http://www.weloennig.de/NaturalSelection.html
[128] http://www.weloennig.de/jfterrorchipmunks.pdf

> event of small probability, or what I am calling an SP event. Our naive intuition is that SP events are so unlikely as not to occur by chance. To take an example, consider the possibility of a thermodynamic accident whereby a loaded gun (say a perfect replica of a .357 Magnum, complete with bullets) materializes in your hand, gets aimed at your favorite enemy, fires and kills him. Strictly speaking the laws of physics do not preclude such an event from happening by chance. Nevertheless, a court will surely convict you of willful homicide. Why does a court refuse to exonerate you by attributing such an event to chance? How would a jury respond to a defense that argues the gun simply materialized?
>
> ...Yet we cannot deny that exceedingly improbable events (i.e., SP events) happen by chance all the time. To resolve the paradox we need to introduce an extraprobabilistic notion, a notion I referred to as specification. If a probabilistic set-up, like tossing a coin 1,000 times, entails that an SP event will occur, then necessarily some extremely improbable event will occur. If, however, independently of the event we are able to specify it, then we are justified in eliminating chance as the proper mode of explanation. It is the specified SP events (abbreviated sp/SP) that cannot properly be attributed to chance.

For the details and a mathematical treatment of these insights see Dembski, 1998a, 1998b; for further information on a testable (that is, 'non-metaphysical') theory of intelligent design, see also ReMine, 1993 and Lönnig, 1998. In contrast, the modern synthesis with its main pillars of natural selection and random mutations has scientifically failed to explain the origin and history of the living world.**«**

So far the text from the encyclopedia. The mindful, alert and attentive reader is invited to apply this information to the origin of the thousands of examples of what we have called 'complex, refined, sophisticated, "high tech" gall formations' in connection with the phenomenon of "*fremddienliche Zweckmäßigkeit*" ("expediency serving foreign organisms", "extrinsic usefulness", "disinterested suitability", "well-directed extraneous utility", "altruism").

But what can be done experimentally to check and further investigate the possibilities and limits of mutations[129] and selection for plant galls and microevolution? The two ensuing publications of 1997 and 2016 (already referred to above) exemplify, demonstrate and provide a wealth of further approaches and tasks for additional investigations and extended scientific research:

> Warren G. Abrahamson and Arthus E. Weis (1997): Evolutionary Ecology across Three Trophic Levels. Goldenrods, Gallmakers, and Natural Enemies. Princeton University Press, Princeton (Chapter 6: The Gall as Eurosta's Extende Phenotype: 173-195).
>
> Rudolph J. Pretorius Gary L. Hein Jeffrey D. Bradshaw (2016): Ecology and Management of Pemphigus betae (Hemiptera: Aphididae) in Sugar Beet https://academic.oup.com/jipm/article/doi/10.1093/jipm/pmw008/2658142/Ecology-and-Management-of-Pemphigus-betae

As for testability and falsifiability of the intelligent design theory, see please http://www.weloennig.de/NeoC.html and (to be applied on the scientific level for ID) http://www.weloennig.de/Popper.html[130]. See, moreover, Michael Behe (2016).[131]

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[129] See again: http://www.weloennig.de/Loennig-Long-Version-of-Law-of-Recurrent-Variation.pdf http://www.weloennig.de/ShortVersionofMutationsLawof_2006.pdf

[131] Michael Behe (2016): https://evolutionnews.org/2016/10/philosophical_o/
Check also Discovery Institute (2005): http://www.discovery.org/scripts/viewDB/filesDB-download.php?id=494; Jonathan Witt (2016) https://evolutionnews.org/2016/11/intelligent_des_31/

Supplement

I. Original discussion on plant galls in *Nature* 1889/1890[132] (with some annotations 2017)

The paragraph referring to plant galls by St. George Mivart (1889, September 2): *Prof. Weismann's Essays*; Nature 41: 38-41 (Paragraph with footnote from page 41)[133]

St. George Mivart:

"Certainly the influence of the environment is sometimes very surprising; but these surprising results hardly, at least at first sight, seem to harmonize with Prof. Weismann's views. Thus the effect of the movements of the young of *Cynips*, newly hatched from an egg deposited in the tissues of a plant (p. 302), is to cause it to produce a gall — a result " advantageous to the larva but not to the plant." It causes "an active growth of cells" around the larva, much to that larva's advantage. Now surely it is too much to ask us to believe that the germplasm of the plant, in the first instance, before even, say, a single *Cynips* had visited it, had in the complex collocation of its molecules, an arrangement such as would compel the plant which was to grow from it, to grow these cells and form a gall as just mentioned.* However this may be, the production of the gall is certainly a curious effect of the action of the environment on an outgrowth from germ-plasm, conceived of as Prof. Weismann conceived of it."

*[Footnote:] "It would be very interesting to know how "natural selection" (to the action of which, as everybody knows, Prof. Weismann constantly appeals) could have caused this plant to perform actions which, if not self-sacrificing (and there must be some expenditure of energy), are at least so disinterested. No doubt the Professor has an hypothesis to produce, though he only says (p. 302) here that "it would be out of place to discuss here the question".

St. George Mivart, Hurstcote, Chilworth, (2 September 1889)

Comment by George J. Romanes:

Galls.

In his suggestive paper on Prof. Weismann's theory, Mr. Mivart says, while alluding to the formation of galls, "It would be interesting to learn how natural selection could have caused this plant to perform actions which, if not self-sacrificing (and there must be some expenditure of energy), are at least so disinterested.*

Mr. Mivart here strikes what has always appeared to me one of the most important facts in organic nature with reference to the theory of natural selection. I have always so considered it, because it seems to me the one and only case[134] in the whole range of organic nature where it can be truly said that we have unequivocal evidence of a structure occurring in one species for the exclusive benefit of another.

Moreover, the structure is here a highly elaborate one, entailing not only a drain on the physiological resources of the plant (as Mr. Mivart observes), but also an astonishing amount of morphological specialization. Indeed, the latter point is so astonishing, that when we study

[132] https://archive.org/stream/in.ernet.dli.2015.228314/2015.228314.Nature-1889-1890_djvu.txt

[133] See again: https://archive.org/stream/in.ernet.dli.2015.228314/2015.228314.Nature-1889-1890_djvu.txt

[134] Comment by W.-E. L. (13 September 2013): So he first tries to marginize the problem as "the one and only case…" (although there are thousands of them in that category and – as mentioned above – there may also be (at least) 1,000 orchid species likewise relevant for "fremddienliche Zweckmäßigkeit").

the number and variety of gall formations in different species of plants— all severally adapted to the needs of as many different species of insects, and all presenting a more or less elaborate provisions for ministering to such needs — it becomes idle to doubt that, if such cases had occurred elsewhere and with any frequency in organic nature, the theory of natural selection would have been untenable, at all events as a general theory of adaptations and a consequent theory of species. But seeing that the case of galls is unique in the relation which is now before us, it becomes reasonable to attribute the formation of galls to the agency of natural selection, if there be any conceivable manner in which such agency can here he brought to bear.

Now, although it is obvious that natural selection cannot operate upon the plants directly so as to cause them to grow galls for the benefit of insects, I think it is quite possible to suppose that natural selection may operate to this end on the plants indirectly through the insects viz. by always selecting those individual lanre the character of whose excitatory emanations is such as will best cause the plant to grow the kind of morphological abnormality that is required. |

This explanation encounters difficulties in some special cases of gall-formation, which I will not here occupy space by detailing; but as it is the explanation given in a course of lectures which I am at present delivering to the students here, I should like to take the opportunity, which Mr. Mivart's paper affords, of asking whether anybody else has a better explanation to offer.

George J. Romanes, Edinburgh 18 November 1889.

In reaction to Mivart's and Romane's comments on galls, the following letters by **R. McLachlan, D. Wetterhan, W. Ainslie Hollis** were published in *Nature* 41, 12 December 1889.

Galls.

R. McLachlin:

Before rushing into arguments on this subject, it appears tome that more good might be done by entering into investigations of the physiological and morphological problems involved.

A gall-fly of a particular species inserts an egg in a certain position on a certain plant (oak, for instance), Another gall-fly of a different species inserts its egg almost in the same position on the same plant. But the results are totally dissimilar. An abnormal growth is set up, from irritation, in either case; but the nature of this growth is quite different. The initial irritation is setup by the presence of the egg, and in most gall-insects the *egg grows* - that is to say, it increases vastly in size before the larva is hatched. The irritation is continued by the larva, and the gall is produced, varying in form in accordance with the species of gall-fly that deposited the egg. But I want to know in what consists the difference in the active irritation that causes so great e divergence in the results? I am not aware that this has ever been answered. But I am quite sure it could be answered on purely physiological grounds if carefully studied. The answer would not in the least detract from the importance of the point as regards natural selection; but it might very materially modify speculative theories based on results only, without a precise knowledge of the agencies that produced those
results.

R. McLachlan, Lewisham, 29 November 1889

D. Wetterhan:

Although I see no need of a better explanation than Prof. Romanes's (*Nature*, November 28, p. 80) of the difficulty which galls seem at first sight to present for natural selection, yet I beg leave to say some words of further elucidation.

When it was said by Darwin ("Origin of Species," chap.vi): "If it could be proved that any part of the structure of any one species had been formed for the exclusive good of another species, it would annihilate my theory, for such could not have been produced through natural selection," he evidently meant only species living without organic connection with each other[135], viz. his own example of the rattlesnake. The argument does by no means apply to organisms living in a relation of *symbiosis*, as is the case with gall-bearing plants and the larvae inhabiting the galls. Such associations form, as it were, one compound organism. Natural selection evidently may act in favour of each symbiont separately, provided only that the effect will not damage the other symbiont in such a degree as seriously to impair its existence, Some "disinterested" expenditure of energy and of organic substance is not excluded by natural selection, but may be promoted, if of advantage to the other partner. Thus the production of galls will scarcely do any serious injury to an oak, and even if such were sometimes the case, there would be no comparison to the damage worked, for instance, by Trichine, on the organism of man and animals, which hosts, nevertheless, in consequence of the stimulus caused by the parasite, afford the substance for capsules protecting the worms, just as plants produce manifold structures beneficial to the gall-insects. If Trichine would attack a species of mammals as frequently as, for instance, leaf cutting ants attack some tropical plants, then those hosts would be forced either to develop, by survival of the fittest, some protection against their invasion, or they would succumb to the enemy and die out.

Analogous examples might be multiplied of both plants and animals, and it is especially to be remembered, as alluded to by Prof. Romanes, that the chemical activities of parasites, including the elaboration of ferments affecting the saps and tissues of the host, are as much under the guidance of natural selection as are their morphological variations.

Footnote: Darwin's thorough acquaintance with these important structures is shown by his elaborate discussion in "Animals and Plants under Domestication." chap, xxiii. (and ed. vol. ii. p. 272). It is particularly to be noted that Darwin insists on the accordance of galls, for instance, on roses, with structures arising through bud-variation.

D. Wetterhan, Freiburg, Badenia, 30 November 1889.

Answer by **W. Ainslie Hollis**:

With all due deference to your able correspondents Dr. St. George Mivart and Prof. G. J. Romanes, I cannot for the life of me understand how the theory of natural selection can be seriously assailed by investigations into the formation of galls by insects. Gall-formation has always appeared to me to be a pathological, that is a perverted physiological process, and to be due to the action of some animal irritant upon normal vegetable tissues during their period of active growth. These formations are therefore, to my mind, fairly on par with the globular nests produced by the larvae of the OEstrus, or bot-fly, in the hides of oxen; or to the inflammatory foci in the tissues of the kidneys, due to the translation of Bacilli, in the case of ulcerative endocarditis. Other examples bearing on the subject will doubtless occur to your readers. In all such instances we have certain changes in the cellular or protoplasmic tissue-elements of the host, brought about by the growth and development of a foreigner in their

[135] Note by W.-E. L.: This statement: "….he evidently meant only species living without organic connection with each other" is not correctly applied to the plant galls and its insects – as Wetterhan's further example of symbiosis shows. See also comment by Mivart.

midst; and natural selection, in so far as it operates in such cases, seems to have sided mostly with the stranger, and to be to his advantage alone. That the host under these circumstances performs actions "which, if not self-sacrificing", are at least "disinterested" must be admitted; but it is the self-sacrifice of coercion and disinterestedness under compulsion.

W. Ainslie Hollis, Brighton, 1 December 1889

Galls

The answer of **George J. Romanes**:

In answer to Mr. Ainslie Hollis, I should like to observe that, in my opinion, the theory of natural selection is not “seriously assailed by investigations into the formation of galls by insects.” On the contrary, in reply to what appeared to be a challenge from Mr. Mivart, I pointed out the manner in which natural selection might here be fairly supposed to have operated. But, while doing this, it appeared desirable to add that the case is a highly peculiar one. If galls were merely amorphous tumours, or even if they presented but as small an amount of specialization for the benefit of the larvae as is presented by animal tissues for the benefit of their parasites, the case would not be so peculiar. But the degree of morphological specialization which the “pathological process” presents in the case of some galls — and this, of course, for the exclusive benefit of the contained parasites, is very remarkable. And although I doubt not that it is but a higher exhibition of the same principles as obtain in the case of animal tissues and their parasites, it is a case of much greater interest from the Darwinian point of view. For, if the explanation in my last letter be accepted, the facts show how enormous must m the power of natural selection in **building up structures**, seeing that it can do this in so high a degree when working, as it were, at the end of a long lever of the wrong kind — i.e. acting indirectly on the vegetable tissues through the benefits thereby conferred on their animal parasites. I am not aware that there is any other instance of “symbiosis” where so high a degree of adaptive specialization is presented by one of the “partners” for the exclusive benefit of the other.

George J. Romanes, London, 13 December 1889.

The answer of **St. George Mivart**:

Mr. W. Ainslie Hollis has involuntarily misrepresented me as saying that the theory of natural selection can be “seriously assailed” by investigations respecting galls[136]. I said, indeed (Nature, November 14, p. 41), that it would be “very interesting to learn how” natural selection could have caused them ; but I was careful to add that doubtless an explanatory hypothesis was ready to hand. **I do not myself believe they were so caused**; but if they were not, they would none the less, like almost all biological phenomena, be explicable by an **unlimited use of gratuitous hypotheses concerning physiological correlations and imaginary ancesstors**.

I confess I do not see that calling them “pathological” (an epithet I certainly would not deny them), and comparing them with inflammatory renal foci due to Bacilli, will explain them, unless it be affirmed that pathological conditions favourable to parasites are always due to the action of “natural selection ” on the parasites themselves — an affirmation which appears to ask too much.

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[136] Note by W.-E.L.: This could be viewed as something like a half-retraction. However, Abrahamson and Weis comment (1997, p. 173): “…Mivart was sure that the Darwinians would concoct some sort of adaptive explanation for gall formation.” (See full reference for the book *Evolutionary Ecology across Three Trophic Levels above*.) Well, indeed, see the explanation by Mayr and Dawkins also above.

Herr Wetterhan's argument from symbiosis sins against natural selection itself. For that theory requires that, in the arduous and incessant struggle for life it supposes, any prejudicial growth should, in time, be eliminated unless carrying with it some preponderating advantage. The insect and the plant are not partners for the latter does not participate in the gain of the former. How, then, on symbiotic principles; can "natural selection" have been the means of producing a growth which, though important, if not necessary, to the animal symbiont, is more or less prejudicial to the symbiont vegetable organism ?

There can, of course, be no doubt, as Mr. McLachlan says, that the various peculiarities of gall-structure could be "explained" on purely physiological grounds if carefully studied; but **that "natural selection" will suffice to explain them, seems to me by no means equally free from uncertainty**.

St. George Mivart, Hurstcote, Chilworth, December 13.

Galls.

W. Ainslie Hollis:

I AM sorry if I unintentionally misrepresented the opinions of Prof. Romanes and Dr. St. George Mivart in suggesting that they wished to assail the theory of natural selection in their recent communications to Nature on this subject. They must, however, pardon me for saying that I still think the extract to which I alluded in my note admits this interpretation. As my views of the relations of gall-formation to the theory of natural selection are clearly at variance with those of your correspondents, perhaps yon will allow me space to give briefly the grounds upon which I base my conclusions.

There are in England about ninety well-known varieties of galls, and of this number fully a third are found in the oak. About half the oak-galls are formed on growing leaves. In nearly one-third of the total number the grub is hatched, and the gall is fashioned in a developing bud. We can readily imagine, in the case of a tree with deciduous leaves, that the presence of a few galls upon its foliage would not greatly affect its chances of survival, if its fitness was in other respects complete. It is otherwise when a gall occupies the position of a developing bud, especially when the bud is a terminal one. In this case there occurs coincidently with, and as a result probably of, the adventitious formation, an arrest of normal development and growth. Indeed, I believe "the gnarled and twisted oak" owes many of its gnarls and most of the twists to the common oak-apple and other bud-galls. If a tree endowed with less developmental vigour and with fewer supplementary buds than the oak had been exposed to the repeated attacks of the insects for many generations in a struggle for existence, it would doubtless have long ago succumbed, and it would have done so by a process of natural selection operating in the ordinary manner, and not "at the end of a long lever of the wrong kind," what ever that may mean. This selective process in the case of gall-bearing trees has left possible traces of its action to-day, for I am unaware that any other English tree than the oak is attacked by terminal bud-galls. The terminal leaf-galls of certain Salices and Conifers can scarcely affect their growth and development to the same extent as the bud-palls.

When we compare pathological tumours in the higher animals with these vegetable excrescences, we must make due allowances for the different conditions under which each lives. I cannot then see that the "morphological specialization" of galls, which, for the most part, are composed of hypertrophied reproductions of the simpler vegetable tissues, is greater than that exhibited by man himself, when, for instance, he becomes the involunlary host of Dr. Lewis's *Filaria*, and his leg the seat of *Elephantiasis lymphangiectodes*, accompanied by hypertrophy of many integumentary structures of the limb. Oak-spangles, on the other hand, are to my mind comparable to the circular nests of ringworm, or to the sprouting epithelium of a *Verruca necrogenetica*. Such comparisons may be of little scientific value [W.-E..: Indeed, see the strong contrast to "the thousands of examples of complex, refined, sophisticated, "high tech" gall formations"as described above] yet I take it they are as useful in their place as attempts to gauge the amount of "disinterestedness" shown by a cabbage when it becomes the unwilling host of the gall-producing *Ceuthorhynchus sulcicollis*.

W. Ainslie Hollis.
Brighton, December 30, 1889 (Nature **41**, 23 January 1890, p. 272)

Galls

T. D. A. Cockerell:

In Nature of November 28, 1889 (p. 80), Prof. G. J. Romanes speaks of galls as "unequivocal evidence of a structure occurring in one species for the exclusive benefit of another," and states that "it is obvious that natural selection cannot operate upon the plants directly." Nevertheless, there is one way in which galls may be supposed to have been evolved as beneficial — or rather, less harmful — to the plants. Every farmer is aware of the great loss to vegetation caused annually by larvse of insects boring within the branches and twigs of trees. Now suppose that all internal plant feeders were originally borers or leaf-miners — and this is highly probable, — but that some had a tendency to cause swellings in which they fed. These latter would be less injurious to the plants, and the greater the vitality of the plants the more nourishment for them; and so by degrees the globular and other highly specialized and least harmful galls would be developed, by natural selection, for the benefit not only of the insect, but also of the plant. And known galls, which I need not here enumerate, furnish us with all the steps of this evolution.

T. D. A. Cockerell, West Cliff, Colorado, U.S. A., 23 January 1890

Galls.

George J. Romanes:

I HAD not intended to take any further part in this correspondence; but the interesting suggestion which has now been made upon the subject by Mr. T. D. A. Cockerell (Nature, Feb. 13, p. 344) induces me to withdraw the sentences that he quotes from my previous letters, to the effect that it seems impossible to imagine any way in which galls can be attributed to natural selection acting on the plants directly. In my own consideration of the matter this seemed "obvious," and therefore my motive in taking up the difficulty as presented by Mr. Mivart was that of "asking whether anybody else had a better explanation to offer" than the one which my letter suggested — viz. "that natural selection may operate on the plants indirectly through the insects," by always selecting those insects the character of whose secretions is such as will best cause the plants to grow the particular kind of morphological abnormality which the larvae require. Mr. Cockerell, however, has now furnished what seems to me an extremely plausible hypothesis, showing that there is a way in which it is quite conceivable that the growth of galls may be an actual benefit to the plants, and therefore that natural selection may act directly on the plants themselves in evolving these sometimes highly specialized structures for the use of their parasites[137]. Mr. Cockerell informs me in a private communication that he has been verifying this hypothesis by observations in detail; but whether or not he will be able to establish it, I think at any rate he has done good service in thus suggesting another possibility.

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[137] **See full refutation of that doubtful hypothesis by the authors cited above and in the texts of Becher and Illies below.** (Note by W.-E.L. 13 September 2017.)

On the other hand, I cannot see that Mr. Ainslie Hollis has helped us at all (Nature, January 23, p. 272). For he merely enunciates the truism that trees which were not endowed with sufficient "developmental vigour" adequately to resist the attacks of gall-making insects "would doubtless have long ago succumbed in a struggle for existence." And this truism he appears to suppose furnishes an explanation of how "natural selection, operating in the ordinary manner," has produced galls for the exclusive benefit of the insects. But it is obvious that the more detrimental the growth of galls has proved to twigs, the less reason there must have been for natural selection, "operating in the ordinary manner," to have developed these often highly specialized structures for the benefit of parasites.

London, February 13. George J. Romanes.

Galls

D. Wetterhan:

ADMITTING, with Prof. Romanes (NATURE, February 20, p. 369), the plausibility of Mr. Cockerell's view that galls may be attributed to natural selection acting on the plants directly, I beg leave to point out a very obvious difficulty — viz. the much greater facility afforded to the indirect action through insects, by the enormously more rapid succession of generations with the latter than with many of their vegetable hosts — oaks, above all.[138]

D. Wetterhan
Nature **41**, 394-394 (27 February 1890)

Galls. Nature 41, 17 April 1890, pp. 559-560

T. D. A. Cockerell:

The difficulty raised by Mr. Wetterhan (Nature, February 27, p. 394) appears at first sight a serious one, but I think it vanishes on examination. Supposing the attacks of the insects to be constant, trees in their evolution would have to adapt themselves to these circumstances, just as they have adapted themselves to the environment of soil, air, light, wind, and so forth. But the fallacy (as it seems to me) of Mr. Wetterhan's argument lies in the supposition that the life of an oak-tree as such, and the life of an insect, may rightly be compared. A tree is really a sort of socialistic community of plants, which continually die and are supplanted by fresh. Bud-variation is a well-known thing, and in oaks A. de Candolle found many variations on the same tree. Now is it unreasonable to suppose that internal-feeding insects might take advantage of such variation — or rather, be obliged to take advantage of it, if it were in adirection to benefit the tree? I will give two purely hypothetical instances, to illustrate the points involved. Imagine two oak-trees, each with three branches, and each attacked by three internal-feeding insects. The insects infesting one tree are borers; those on the other tree are gall-makers. The borers bore into the branches, which they kill while undergoing their transformations: the tree possibly does not die that year, but next year the progeny of the three, being more numerous while the tree is weaker, effect its destruction, and finally the insects perish for want of food. On the other tree, the gall-makers do no appreciable damage, and the tree is able to support them and their progeny without great difficulty. Now a little consideration will show that the longer the life and the slower the reproduction of the trees the greater will be the contrast. If the plant infested by the borers had been an annual herb, it

[138]http://www.nature.com/nature/journal/v41/n1061/abs/041394b0.html?foxtrotcallback=true

might have contrived to perfect its seeds, and the death of the old stem would be but a natural and inevitable process, and fresh plants might have been produced in sufficient numbers to continue the species in spite of all insect-attacks. But in the case of trees — oak-trees especially, the rate of growth and reproduction is such that, unless the insect-borers can live in galls, they will destroy the plants entirely, and themselves in consequence. Indeed, I have no doubt, that if all the gall-makers now existing could suddenly be transformed into stem-borers, the genera *Quercus*, *Rosa*, and *Salix*, now so dominant, would shortly disappear from off the face of the earth. The other hypothesis — here assuming that the production of galls is due more to the tree than the insect — is this. Suppose an oak-tree with four branches, all attacked by internal-feeding insects. Two of the branches produce swellings in which the insects live, while the other two produce none, and the insects have to devour the vital parts. Now the two branches which produced no swellings would quickly be killed by the insects, but those which produced galls would live, and the more perfect the galls, the greater the insect-population they would be able to support. Hence the tree would finally, by the survival of its gall-producing branches, become purely gall-producing, and we may assume that its progeny would inherit the peculiarity.

I am aware that the above arguments will sound a little like those of the Irishman, who said he ought not to be hanged, because, "in the first place, he did not kill the man; in the second place, he killed him by accident; and thirdly, he killed him in self-defence," — but I do not represent either of the above hypotheses as the precise truth of the matter, and I think they sufficiently illustrate the principles involved.

T. D. A. Cockerell, West Cliff, Colorado, U.S. A., 16 March 1890

II: Erich Becher's[139] original texts (1917 and 1925) as well as excerpts from the comments by Joachim Illies (1983) on plant galls and natural selection

Erich Becher (1917) : Die fremddienliche Zweckmäßigkeit der Pflanzengallen und die Hypothese einer überindividuellen Seelischen, pp. 90-102): Zuchtwahlprinzip[140]

[U]nter den Hypothesen zur Erklärung des Zustandekommens biologischer Zweckmäßigkeit spielt immer noch die Darwinsche Selektionslehre die erste Rolle, obwohl zu den alten gegen sie gerichteten Einwänden inzwischen schwerwiegende neue gekommen sind, die insbesondere aus der Vererbungswissenschaft, aus Johannsens Lehre von den reinen Linien erwachsen[141]. Wir können uns hier nicht der umfangreichen Aufgabe unterziehen, zu prüfen, inwieweit jene Bedenken berechtigt sind. Eines der bekanntesten Bedenken würde jedenfalls durch Heranziehen des Ausnutzungsprinzips erheblich abgeschwächt werden können: Man pflegt wohl gegen Darwin einzuwenden, die ersten Ansätze zu Anpassungen seien vielfach

[139] Anmerkung W.-E. L.: Zu Professor Erich Becher, siehe wieder: https://de.wikipedia.org/wiki/Erich_Becher. .

[140] Text from his book: Die fremddienliche Zweckmäßigkeit der Pflanzengallen und die Hypothese einer überindividuellen Seelischen. Verlag von Veit & Comp., Leipzig.

[141] W. Johannsen, Elemente der exakten Erblichkeitslehre, einschließlich der biologischen Variationsstatistik. Jena 1913; ders., Experimentelle Grundlagen der Deszendenzlehre, Variabilität, Vererbung, Kreuzung, Mutation, in Allgemeine Biologie, Kult. D. Gegenw. III, IV, 1., hrsg. V. Chun u. Johannsen, Leipzig und Berlin 1915 („Zunächst ist es völlig evident, dass die Genetik die Grundlage der Darwinschen Selektionslehre ganz beseitigt hat", S. 659). Umfassende Darstellung und Kritik der Einwände gegen den Darwinismus bei Plate, a.a.O. Vgl. ferner z.B. E.Becher, Naturphilosophie, S. 397 f.

nicht durch Selektion zu erklären, weil sie noch nicht oder nur zu geringem Maße zweckmäßig seien. Hier könnte das Ausnutzungsprinzip häufig, insbesondere bei der Gallenzweckmäßigkeit, Hilfe leisten. Die ersten Stufen in der phylogenetischen Entwicklung der Gallenzweckmäßigkeit wäre durch dies Prinzip zu erklären, wären auf Ausnutzung verwertbarer Wucherungsfähigkeiten und anderer brauchbarer Potenzen der Pflanzen zurückzuführen.

Wir lassen also im Übrigen die allgemeinen Bedenken gegen die Selektionslehre hier beiseite, ohne ihnen ihre Bedeutung absprechen zu wollen, und fragen speziell, ob das Darwinsche Zuchtwahlprinzip uns die fremddienliche Gallenzweckmäßigkeit verständlich machen kann, wobei wir etwa die durch das Ausnutzungsprinzip gebotene Erklärungsgrundlage voraussetzen. Kann das Selektionsprinzip uns da weiterführen, wo das Ausnutzungsprinzip versagt? Konnte natürliche Zuchtwahl die Anfänge fremddienliche Zweckmäßigkeit, die durch Ausnutzung irgendwie entstandener verwertbarer Potenzen sich ergeben hatten, weiterführen bis zu der Fülle zweckmäßiger Erscheinungen, die uns die Pflanzengallen zeigen?

Das Problem, welches die Gallen der Selektionstheorie darbieten, ist vielfach vernachlässigt worden. Darwin selbst, der doch seine Hypothese so vielfältig und gründlich ausbaut, schneidet unseres Wissens jenes Problem nicht an, obwohl er zuweilen[142] den Gallen von anderen Gesichtspunkten aus seine Aufmerksamkeit zuwendet. Und auch das zusammenfassende Handbuch des Darwinismus, welches fast erschöpfend über alle Teilprobleme, Schwierigkeiten, Einwände und über deren Abwehr bis in die neueste Zeit Rechenschaft gibt, Plates Werk über das „Selektionsprinzip und Probleme der Artbildung“, läßt die Frage der Gallenzweckmäßigkeit beiseite, führt auch in seinem reichen Literaturverzeichnis Arbeiten, in denen inzwischen die Bedeutung der Gallen für die Zuchtwahllehre erkannt und geprüft worden war[143], nicht an.

Diese Bedeutung ist nicht gering, da die Gallenzweckmäßigkeit dem Selektionsprinzip sehr ernste Schwierigkeiten bietet. Wir haben bereits eingangs darauf hingewiesen, dass die Zuchtwahlhypothese durchaus auf die Erklärung der selbst- bzw. artdienlichen Zweckmäßigkeit abzielt, der fremddienlichen gegenüber versagt. Wenn durch Variation (oder auch Mutation) der Wirtspflanze und ihrer Potenzen etwas für die Gallparasiten Nützliches ergibt, so haben dadurch die Wirtspflanze und ihre Nachkommenschaft keine Vorteile im Daseinskampf, sondern eher aus der Begünstigung der schädlichen Parasiten fließenden Nachteile. Der Kampf ums Dasein wirkt also nicht auf überdurchschnittliche häufige Erhaltung und Summierung solcher für die Gallgäste nützlicher Wirtspflanzen-Variationen (oder - Mutationen), züchtet nicht fremddienlich- zweckmäßige Eigenschaften.

Man kann nun versuchen, die Gallenzweckmäßigkeit doch noch selektionistischer Erklärung zugänglich zu machen, indem man die Fremddienlichkeit auf Selbst- und Artdienlichkeit zurückführt. Dafür bieten sich zwei Wege an, die durch unsere früheren Betrachtungen bereits angedeutet sind.

Wir haben am Anfang unserer Untersuchung schon darauf hingewiesen, dass zunächst fremddienlich-zweckdienlich erscheinende Einrichtungen, wie die Nahrung-bietenden Gewebe von Früchten und der Nektar der Blüten, bei genauerer Betrachtung sich manchmal doch als selbst- oder nachkommendienlich erweisen. Man hat nun vermutet, auch die Pflanzengallen seien in letzter Linie selbstdienliche Gebilde. Man hat etwa wiederholt gemeint, die Gallbildung bedeute einen Versuch der Wirtspflanze, den Parasiten einzukapseln und aus dem eigenen Leibe zu entfernen; Einkapselung von Fremdkörpern und Parasiten finden wir als Schutzmaßnahme bei Pflanze, Tier und Mensch (z.B. bei der Tuberkulose).

[142] Vgl. z.B. Ch. Darwin, Die Entstehung der Arten usw. Deutsch v. Haek, Leipzig (Reclam) o.J. S. 32.
[143] Einschlägige Literatur (vor allem Beiträge in Nature 41, 1890), bei Küster, a.a.O. S. 368.

Doch lehnt Küster die Ansicht wohl mit Recht ab, da Wundkork – das Gewebe das bei „höheren Pflanzen jene Ausgabe übernimmt und löst – bei der Gallenbildung nicht die geringste Rolle spielt und höchstens erst n a c h der Entwicklung des Gallenerzeugers auftritt, um die Galle abzustoßen“[144] . Jedenfalls würde der Einkapselungsversuch kaum als selbstdienlich-zweckdienlich erscheinen, da er dem Feind Nahrung, Obdach und Schutz gewährt, um ihn dann freizulassen, wenn sein Wohl dies erfordert, diese Einkapselung läuft durchaus auf Förderung des Schädlings und somit auf Selbst- und Artschädigung hinaus. Wenn die Galle ihren Bewohner zur Vernichtung, etwa zum Verhungern, einkerkerte oder ihn frühzeitig durch Wundkorkbildung aus der Pflanze entfernte, so läge die Sache für die selektionistische Erklärung ganz anders.

Oder sollte die Gallbildung für die Wirtspflanze wenigstens relativ zweckmäßig sein, indem sie das kleinere von zwei Übeln darstellte? Indem die Pflanze die Gallparasite an eine bestimmte Stelle fesselt und ihn dort versorgt, verhindert sie ausgebreitete Zerstörungen durch den vagierenden Schädling.

Es ist kaum zu entscheiden, ob die durch die Gallbildung erzielte Lokalisation des Parasiten der Wirtspflanze mehr Nutzen als Schaden bringt. Das Substanzopfer zur Ernährung des Schädlings muß doch gebracht werden, und man könnte vielleicht meinen, die Pflanze könne den Substanzverlust leichter durch Nachbildung von Blättern usw. decken als durch Ausbildung und Regeneration von besonderen Nährgeweben in oder an den Gallen, zumal die Fähigkeit zur Neubildung verlorener Blätter usw. in der Pflanzenwelt allgemein verbreitet ist. Außerdem stände dem etwaigen Nutzen durch Lokalisation des Schädlings der Nachteil gegenüber, der aus der Förderung des Feindes durch die Gallbildung erwächst. Man sollt glauben, die Pflanze habe sehr viel mehr Aussicht, von einer auf den Blättern umherkriechenden Larve durch Vögel u. dgl. oder auch durch Sturm und Regen befreit zu werden, als von einer in der Galle geborgenen.

Nun kommt aber hinzu, dass die Wirtspflanze den Gallengast nicht nur durch Umhüllung und lokale Nährstoffversorgung an eine bestimmt Stelle fesselt, sondern darüber hinaus ihrem Feinde noch mancherlei Wohltaten erweist. Soll es etwa für die Wirtspflanze von Nutzen sein, wenn sie durch Hartschichtbildung, Gerbstoffproduktion, Stachelentwicklung u. dgl. Ihren Feind in der Galle beschirmt? Es erscheint eher vorteilhaft für sie, wenn sie durch auffällige, fruchtähnliche Färbung usw. Tiere anlockt, die Galle zu verzehren und so den undankbaren Gast zu vernichten.[145] Aber gerade gegen den Angriff durch hungrige Tiere erscheinen die Gallen mit ihren Insassen vielfach geschützt. Und warum schaffen manche Gallen ihren Gästen zur rechten Zeit durch selbsttätige Öffnung einen bequemen Ausweg? Geschieht es etwa, um die Verletzung durch das sich andernfalls mit seinen Fresswerkzeugen einen Weg bahnende Tier zu vermeiden? Indessen auch bei der selbsttätigen Öffnung von Beutelgallen und anderen, ihre Cecidozoen völlig einschließenden Gallen erfolgenden Gewebszerreißungen[146], und bei der Betrachtung der von Gallenbewohnern hervorgebrachten Öffnungen hat man nicht den Eindruck, dass die Öffnungsprozedur den Wirtspflanzen schade. Wenn ich das vom Parasiten geschaffene Loch der mir gerade vorliegenden kugelförmigen Eichengalle der Gallwespe Cynips Kollari[147] mit dem Stöpselloch der kugeligen Galle vergleiche, die durch Cecidoses Eremita an den Zweigen von Duvalia longifolia hervorgebracht wird[148], so gewinne ich nicht die Überzeugung, dass die selbsttätige Gallöffnung merklichen Schaden vermeide. Gegenüber dem Übrigen, durch Substanzverlust

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[144] Küster, a.a.O. S. 371.

[145] Anmerkung W.-E.L.: Einige stark gefärbte, auffallende Gallbildungen sind als Mimikry gedeutet worden (auch Form). However, not only all the difficulties described pp. 21-23 above, would also be relevant for this hypothesis, but also additional problems would have to be solved: mimicry of form, for example, could ***not*** have functioned during all the thousands of evolutionary steps until the mimetic form was finally achieved after millions of years (13 September 2017).

[146] Küster, a.a.O. S.356

[147] Abbildung bei Roß, a.a.O. Taf. VI, Fig. 123, 124

[148] Abbildung bei Kerner, a.a.O. S. 526, Fig. 5, u. Küster, S. 359, Fig. 151.

verursachten Schaden kommt der durch die Öffnungsprozedur entstandene (Schaden) wohl gar nicht in Betracht. Fassen wir schließlich nochmals die durch Hormomyia Réaumuriana auf dem Blatt der großblättrigen Linde hervorgebrachte Galle (oder die ihr ähnliche Galle auf dem Blatte einer brasilianischen Celastrus-Art) ins Auge! Welchen Nutzen sollte die Linde von der Abtrennung und Ausstoßung der stöpselartigen Innengalle haben? Es geht doch nicht an, lediglich dem Selektionsprinzip zuliebe bei den Galleneinrichtungen selbst- oder artdienliche Zweckmäßigkeit einfach zu postulieren, wo nur fremddienliche Zweckmäßigkeit zu erblicken ist.

Man könnte auf den Gedanken kommen, die Wirtspflanze beschränke sich nicht auf Umhüllung und Nahrungsversorgung des Parasiten und biete ihm noch weitere Vorteile bei der Gallbildung an, um ihn desto sicherer in der Galle festzuhalten und am Umherschweifen zu verhindern. Doch dürfte dazu die Umschließung und günstige lokale Nahrungsversorgung durchaus genügen; und die Schutzmittel gegen allerhand Feinde oder die Öffnungs- und Ausstoßungseinrichtungen werden die Parasiten, die nichts von ihnen wissen, schwerlich stärker an die Galle fesseln. Man könnte wohl annehmen, dass durch entsprechende Instinktentwicklung die Galltiere um so mehr an die Gallen gebunden würden, je mehr Vorteile diese ihnen böten. Aber die Vorteile müssten zunächst einmal da sein, um die wohl ziemlich langwierige Entwicklung solcher Instinkte veranlassen zu können, welche die Galltiere an die Gallen fesseln; die vorteilhaften Einrichtungen müssten also zustandekommen, lange bevor sie zur Verhinderung des Umherschweifens der Larven beitragen könnten; jene Einrichtungen können daher nicht aus dieser etwaigen Verhinderungswirkung erklärt werden. Auch ist zu bedenken, dass eine Pflanzenart sich selbst empfindlich schadet, indem sie durch Darbietung von Vorteilen einen Parasiten immer mehr an sich fesselt und ihn von anderen, etwa verwandten Pflanzenarten abzieht.

Wie man auch die Sache drehen und wenden mag, es bleibt dabei, dass die Gallenzweckmäßigkeit zahllosen Pflanzenfeinden das Leben ermöglicht und so den Wirtspflanzen gewaltigen Schaden bringt. Wenn Naturzüchtung so komplizierte Bildungen, wie sie manche Gallen darstellen, wegen der äußerst fragwürdigen selbstdienlichen Nützlichkeit derselben entwickeln konnten, warum hat sie dann nicht die einfachere und für die Wirtspflanze viel wertvollere Leistung vollbracht, Vorrichtungen zur Vernichtung oder Ausstoßung der Schädlinge hervorzubringen? Warum umwuchern die Wirtspflanzen die Eier und Larven nicht mit festen, nährstoffarmen, für Luft undurchlässigen Geweben, in denen die eingekerkerten Schädlinge verhungern und ersticken müssten. Wenn Naturzüchtung die komplizierten gastlichen Gallwohnungen produzieren konnte, warum dann nicht solche einfacheren, für die Wirtspflanzen sehr zweckmäßigen Kerker? Wenn natürliche Zuchtwahl in der mehrfach erwähnten Lindengalle eine Einrichtung schaffen konnte, welche die stöpselförmige Innengalle mitsamt der in ihr eingeschlossenen Larve zu einer für diese günstigen Zeit ausstößt, konnte sie dann nicht ein Gebilde hervorbringen, das Ei oder Larve früher hinaufwirft und sie dadurch zugrunde richtet, oder doch von der Wirtspflanze entfernt? Warum wird die Innengalle nicht, zum Schaden des Parasiten, früher ausgestoßen? Eine entsprechende Frage kann man bei anderen Gallen aufwerfen, die sich zu für die Parasiten günstiger Zeit von den Wirtspflanzen ablösen; frühere Ablösung könnte für die Parasiten verderblich und für die Wirtspflanzen sehr nützlich sein.

Man mag gegen solche Fragen einwenden, sie stellten unbillige Anforderungen an den Selektionstheoretiker. Sie zeigen aber, wie wenig das Darwinsche Prinzip auf dem eingeschlagenen Wege für das Verständnis der Gallenzweckmäßigkeit leistet. Wenn natürliche Zuchtwahl in ihrem Einfluss auf die Wirtspflanzen die Entwicklung der Gallen bewirkt hätte, so müssten diese, müsste man meinen, nicht auf die Förderung der schädlichen Parasiten kommen, sondern auf ihre Entfernung oder Vernichtung angelegt sein; die Gallenzweckmäßigkeit ist eine ganz anders gerichtete, als man dann erwarten sollte. Demnach führt unser erster Weg nicht zu dem erstrebten Ziele, die Gallenzweckmäßigkeit selektionistischem Verständnis zugänglich zu machen.

Wenden wir uns nunmehr dem zweiten Wege zu, der eine Zurückführung der fremddienlichen auf selbst- oder nachkommendienliche Zweckmäßigkeit verheißt, womit eine Voraussetzung für eine Anwendung des Selektionsprinzips gegeben wäre. Auch dieser Weg ist durch unsere früheren Erwägungen schon nahegelegt.

Die Gallen sind Produkte von zweierlei Faktoren, der Wirtspflanzen und ihrer Potenzen einerseits und der Parasiten und ihrer Einwirkungen anderseits. Man kann nun versuchen, die Gallenzweckmäßigkeit auf das Konto der Parasiten zu setzen: die Wirtspflanzen produzieren parasitendienliche Gebilde, weil sie von den Parasiten in äußerst zweckmäßiger Weise beeinflusst werden. Die fremddienliche Zweckmäßigkeit der Pflanzengallen geht also auf selbst- und nachkommendienliche Zweckmäßigkeit der Parasiten, der von ihnen ausgeübten Reizkombination, zurück. Das Wesentliche in der Phylogenese der Gallen vollzieht sich nicht an den Wirtspflanzen, sondern auf der Seite der Parasiten; in ihnen züchtet der Daseinskampf Instinkte, diejenigen Wirtspflanzen und Pflanzenteile aufzusuchen, die von vornherein und aus Gründen, welche mit Gallbildung nichts zu tun haben, für diese gut ausnutzbare Fähigkeiten besitzen; ferner entwickelt Naturzüchtung in den Parasiten zusammengesetzte Reizmittel, deren Verwendung die Wirtspflanzen zwingt, parasitendienlich-zweckmäßige Gebilde hervorzubringen.

Nach unseren früheren Betrachtungen ergibt sich leicht unsere Stellungnahme zu diesem Versuch, die fremddienliche Gallenzweckmäßigkeit auf selbst- und artdienliche Parasitenzweckmäßigkeit zurückzuführen. Es liegt ein Teil Wahrheit darin: dass fremddienlich-zweckmäßige Gallen zustande kommen, beruht in der Tat z u m T e i l auf den selbst- und nachkommendienlich zweckmäßigen Instinkten und Reizfähigkeiten, welche die Parasiten betätigen. Aber nachdem, was oben ausgeführt wurde, doch wohl nur z u m T e i l; wir wurden zu der Hypothese gedrängt, dass manche Wirtspflanzen besondere Potenzen eigens für die Gallbildung besitzen müssen, um etwa die zweckmäßige Einrichtung jener merkwürdigen Lindengalle oder der Deckelgallen hervorbringen zu können. Die Instinkte und Reizfähigkeiten der gallenerzeugenden Parasiten kann man mit dem Selektionsprinzip so gut oder so schlecht erklären, wie andere selbst- oder artdienliche Instinkte oder Fähigkeiten; jene besonderen Gallbildungspotenzen der Wirtspflanze widerstreben als fremddienliche selektionistische Erklärung.

Hier zeigt sich die Bedeutung der Annahme, dass manche Wirtspflanzen besondere Potenzen eigens für die Gallbildung besitzen. Wie auch immer man im übrigen über das Darwinsche Prinzip denken mag, es kann schwerlich die Gallenzweckmäßigkeit erschöpfend erklären, wenn jene Annahme zurecht besteht. Sie ist nun freilich hypothetisch, wurde uns aber durch die Tatsachen aufgedrängt.

Die Bedenken gegen die selektionistische Erklärung der Gallenzweckmäßigkeit würden sich sehr vermehren, wenn wir alle jene allgemeinen Einwände gegen die Zuchtwahllehre hier anführen wollten, die auch beim Gallproblem in Betracht kommen. Geben wir etwa einmal zu, dass die Gallbildung auch für die Wirtspflanze einen relativen Vorteil habe, indem sie Schlimmeres vermeiden helfe! Werden nun die zumeist kleinen Fortschritte in der Gallbildung, die Variationen oder Mutationen der Wirtspflanze mit sich bringen mögen, Selektionswert haben, d.h. im Daseinskampfe einen entscheidenden Vorsprung verleihen? Das ist um so fraglicher, als ja gar nicht jede Pflanze, die so ihre Gallenbildungsfähigkeit verändert, von gallenerregenden Parasiten befallen wird; die nichtbefallenen aber haben gar keinen Vorteil von der Veränderung. Die befallenen Pflanzen hinwiederum, welche die Verbesserung der Gallbildungspotenz anwenden, stehen im Daseinskampfe immer noch erheblich ungünstiger da als die nicht befallenen Artgenossen, denen die Verbesserungsvariation fehlt, zumal Galleninfektion vielfach die Reproduktionsfähigkeit hemmt[149]. Unter diesen Umständen ist die Aussicht auf eine züchtende Bevorzugung solcher Variationen und Mutationen durch den Daseinskampf gar zu gering.

Indessen wollen wir solche allgemeineren, jedoch auch beim Gallenproblem in Betracht kommenden Einwände gegen die Zuchtwahlhypothese hier nicht weiter verfolgen. Es genüge der Hinweis darauf, dass bei manchen Gallen auch das sogenannte Koadaptationsproblem[150] Schwierigkeiten machen dürfte.

Inwieweit Roux‘ Lehre vom züchtenden Kampfe der Teile im Organismus[151] auf die Gallen Anwendung finden kann, braucht hier gleichfalls nicht untersucht zu werden, da offensichtlich die fremddienliche Zweckmäßigkeit, wie sie sich in den Öffnungseinrichtungen der Deckel- und Stöpselgallen offenbart, einer Erklärung durch Roux‘ unzugänglich ist.[152]

Erich Becher pp. 85-90: Ausnutzungsprinzip

Ich beginne mit dem „Ausnutzungsprinzip“[153], weil dieses möglicherweise ein Fundament abgibt, auf dem andere Hypothesen weiterbauen können.

Die Lebewesen nutzen das, was sie an sich selbst vorfinden und was die Umwelt ihnen bietet, so gut es geht aus. Bildet es sich z.B. am Körper eines Tieres irgendwo aus irgendwelchen Gründen eine harte, scharfe oder spitze Stelle, so wird sie unter Umständen als Wehr oder Waffe Verwendung finden; durch diese Ausnutzung erscheint dann jenes Gebilde als zweckmäßig, obwohl seine Entstehung mit Wehrzwecken nichts zu tun hatte. Ebenso wird ausgenutzt, was die Umwelt bietet; so sucht etwa der Organismus die Verhältnisse auf, unter denen er seine Eigenschaften am besten verwerten kann, und erscheint dann an jene angepasst, zweckmäßig für sie eingerichtet. Der Verfasser bezeichnet diese Erklärung von Anpassungen als Ausnutzungsprinzip[154].

Unser Prinzip kann nach meiner Meinung freilich nur einen Teil der Anpassungen, und zwar meist nur verhältnismäßig einfache Zweckmäßigkeitserscheinungen erklären. Aber diese beschränkte Leistungsfähigkeit ist vielleicht nicht belanglos für unser spezielles Problem. Wir haben gesehen, wie bei der Gallbildung vielfach eine anomale Auslösung von Potenzen ins Spiel kommt, die normalerweise irgendeinen Teil der Wirtspflanze, Frucht oder Sprossachse z.B., hervorbringen. Diese Potenzen werden also nicht von den Gallparasiten oder für sie geschaffen, sondern sie werden als bereits vorliegende Eigenschaften der Pflanzen von jenen nur ausgenutzt. Dass dabei aber für die Parasiten Zweckmäßiges entsteht, kann man wenigstens z.T. daraus erklären, dass die Galltiere allmählich unter Entwicklung eines auswählenden Instinktes dazu gelangt sind, nur solche Potenzen solcher Pflanzen durch ihre Reize zu aktivieren, die für sie Nützliches hervorbringen. So sind Erzeuger von Markgallen dazu gelangt, speziell die Achsenbildungspotenzen zu aktivieren, weil dadurch die für sie zweckmäßige Folge der Schichten um die Larvenkammer entsteht. So mag es sich erklären, warum Gallen, die den Früchten der Wirtspflanze gleichen, für ihre Gäste zweckmäßig sind: die Parasiten haben es „gelernt“, nur solche Pflanzen und Planzenteile zur Aktivierung von Fruchtbildungspotenzen anzuregen, bei denen die entstehenden fruchtähnlichen Gebilde für sie zweckmäßig gebaut sind. Und in entsprechender Weise mag vielfach geeignete Auswahl von Pflanzen und Pflanzenteilen und Ausnutzung bereits vorhandener Fähigkeiten beim

149 Küster a.a.O. S, 380.
150 Plate, a.a.O. S.209 f., 487 f.; E. Becher, Naturphilosophie, S.401
151 W. Roux, Der Kampf der Teile im Organismus. Leipzig 1881
152 Bechers in späteren Teil seines Buches vorgetragene These zur Erklärung der des überindividuell Seelischen, dass sich „Lust und Unlust des Parasiten irgenwie aud die Wirtspflanze übertragen“ müßten, war Gegenstand des Spottes seiner Kriiker. Er hat sie dann auch 1925 nicht wiederholt
153 E .Becher, Theoretische Beiträge zum Darwinismus. Arch. F. Rass.- u. Gesellsch.-Biol. 7, 1910, S.270 f.
154 Vgl. auch E. Becher, Naturphilosophie, a.a.O. S. 393

Zustandekommen fremddienlicher Gallenzweckmäßigkeit eine Rolle spielen. So wird die Dünnwandigkeit wasserreicher Zellen, die an sich Gallenzweckmäßigkeit nichts zu tun hat, durch Ausnutzung dünnwandiger Zellen als Nährzellen von seiten der Gallparasiten zu einer für sie zweckmäßigen Eigenschaft gestempelt.

Die Fähigkeit, auf gewisse Reize mit Wucherungen zu reagieren, dürfte im Pflanzenreich weit verbreitet und unabhängig von ihrem Nutzen für Gallparasiten entstanden sein. Es gibt nämlich Fälle, in denen durch Eiablage deutliche Geschwülste erzeugt werden, eine fremddienliche Zweckmäßigkeit der Neubildungen aber fraglich erscheint, weil die Larven sogleich nach de Ausschlüpfen aus dem Ei die Wucherungen oder „Procecidien" verlassen. So entstehen Procecidien nach Ablage der Eier der Libelle Lestes viridis auf Alnus, Betula, Cerasus, Cornus, Crataegus, Fagus, Fraxinus, Ligustrum, Nyssa, Pirus, Populus, Prunus, Quercus, Rhamnus, Rubus, Salix, Ulmus und Viburnum; die Wucherungen können bis 2 mm lang und bis 1 mm breit werden[155]. Es liegt nun nahe, anzunehmen, dass bei einigen Pflanzenarten unter dem Einfluss parasitärer Reizung Geschwülste entstanden, die für die Parasiten besser verwertbar waren, durch Ausnutzung dieser verwertbaren Wucherungsfähigkeit ergab sich dann das teleologische Verhältnis. So mag man insbesondere die ersten Anfänge in der Phylogenese der fremddienlichen Zweckmäßigkeit zu erklären versuchen.

Die Ansicht, dass in solcher Weise das Ausnutzungsprinzip zur Erklärung des Zustandekommens der fremddienlichen Zweckmäßigkeit herangezogen werden könne, wird bestärkt durch die Spezialisation, welche die Gallparasiten bei der Wahl der Wirtspflanzen bekunden. Die weitaus meisten Gallenerzeuger sind auf einen engen Kreis von Wirtspflanzen angewiesen, und sehr viele rufen nur auf den Arten einer Gattung oder auf einer einzigen Art Gallen hervor[156]. Wir werden dies mit unserer Berufung auf das Ausnutzungsprinzip in Zusammenhang bringen, indem wir annehmen, dass eben nur bei einigen oder einzelnen Pflanzenarten die bestimmten Gallparasiten gut brauchbare Fähigkeiten vorfanden; um gerade diese auszunutzen, beschränken sie sich auf diese wenigen oder einzelnen Arten.

Natürlich wird man nun weiter fragen, wie denn jener Auswahlinstinkt entstanden sei, und wie die Fähigkeit die betreffenden verwertbaren Potenzen der Pflanzen durch geeignete Reize zu aktivieren. Gewiss sind das wichtige Fragen, zumal die Instinkte, die die Gallentiere zur rechten Zeit die geeignete Pflanze und den richtigen Pflanzenteil finden lassen, höchst staunenswert erscheinen. Aber wir können diese Fragen hier beiseite lassen, da es sich dabei nicht mehr eigentlich um fremddienliche, sondern um art-(nachkommen-)dienliche Zweckmäßigkeit handelt: indem die Gallparasiten geeignete Reize produzieren und Instinkte zur Auswahl der ausnutzbaren Pflanzen und Pflanzenteile entwickeln, fördern sie ihre eigene Nachkommenschaft und Art. Hier kommen also die üblichen Hypothesen zur Zweckmäßigkeitserklärung und speziell die Instinktentstehungshypothese in Betracht: Selektionismus, Lamarckismus, Psycholamarckismus, andere Formen des Vitalismus und sonstige metaphysische Anschauungen. Eine Entscheidung zwischen ihnen kann an dieser Stelle nicht begründet werden. Wir dürfen uns hier auf unsere spezielle Frage beschränken, wie die fremddienliche Zweckmäßigkeit zustande gekommen sei, und wir dürfen uns zufrieden geben, wenn wir dies Problem so weit gefördert haben, dass nur noch selbst- oder artdienliche, also sozusagen „gewöhnliche" Zweckmäßigkeit zu erklären bleibt.

Wenn nun auch das Ausnutzungsprinzip in dieser Richtung einiges leisten mag, so führt es doch nicht durchweg zum Ziele. Man könnte gegen eine weitgehende Verwendung unseres Prinzips zur Erklärung der Gallenzweckmäßigkeit vielleicht schon das Vorkommen von

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[155] Küster, a.a.O. S.6; vgl. Roß, a.a.O. S. 3
[156] Küster, a.a.O. S. 329 f.

Gallen an Vertretern aller Pflanzenordnungen[157] anführen wollen; man könnte meinen, es sei doch unwahrscheinlich, dass bei Pflanzen aller Ordnungen ausnutzbare Fähigkeiten sich finden. Daraus ließe sich immerhin antworten, dass der eine Gallparasit diese, der andere jene Fähigkeit ausnützen mag, je nach den Reizen, über die er verfügt, und je nach seinen Lebensbedürfnissen. Man könnte ferner darauf hinweisen, dass manche Fähigkeiten im Pflanzenreich sehr verbreitet und darum in den verschiedensten Pflanzenordnungen ausnutzbar sind, so etwa die Haarbildungspotenz und wohl auch die Fähigkeit zur Bildung dünnwandiger Zellen bei bestimmten Wasserverhältnissen. Endlich aber wäre zu betonen, dass das Vorkommen von Gallen sich doch nicht gleichmäßig auf das ganze Pflanzenreich verteilt; sie finden sich zahlreicher und vielgestaltiger bei den Samenpflanzen als bei den Sporenpflanzen. Die meisten Gallen treten an Dikothylen auf, unter denen wiederum die Holzgewächse am gallenreichsten sind[158]. Dies mag uns an die oben betrachtete Ähnlichkeit der Schichtenbildung in Markgallen und dikothylen, verholzte Zellwände aufweisenden Achsen erinnern; die große Häufigkeit der Gallen an Dikothylen, insbesondere an Holzgewächsen, ließe sich mit der Ausnutzbarkeit der Achsen- (und Holz-)bildungspotenz für die Gallbildung in Zusammenhang bringen.

Trotz der Abwehr dieses Einwandes bleibt es aber dabei, dass höchstens ein Teil der fremddienlichen Zweckmäßigkeitserscheinungen bei Gallen durch das Ausnutzungsprinzip erklärt werden kann. ***Wir finden, wie oben dargelegt wurde, an Gallen vielfach Bildungen, Gewebe und Zellen, die an den normalen Wirtspflanzen nicht vorkommen. Solche neuartigen Bildungen, die den normalen Wirtspflanzen durchaus fehlen, die außer bei Gallen nicht vorkommen, können aber im allgemeinen nicht durch das Ausnutzungsprinzip erklärt werden; denn damit etwas ausnutzbar sei, muss es zunächst erst einmal vorhanden sein, oder es muss wenigstens die Fähigkeit, die aktivierbare Potenz dazu vorliegen***.

[Anmerkung von W.-E. L. 2017: Zur Veranschaulichung von Bechers Argument seien die folgenden beiden Fotos wiedergegeben:]

Links: Galls of cynipid wasp *Antron douglasii* on oak leaves. Jack Wilburn
https://www.britannica.com/science/gall-plant-disease
Rechts: Hedgehog Gall, posted by Eileen Nelson:
https://fyi.uwex.edu/wihortupdate/2017/07/24/july-21-2017-plant-galls/

[Weiter im Text von Erich Becher:]

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[157] Roß, a.a.O. S. 36.
[158] Roß, a.a.O. S. 36.

Richten wir noch einmal unsere Aufmerksamkeit auf die wiederholt herangezogene, ihre Innengalle ausstoßende Lindengalle, auf die sich selbsttätig öffnenden Deckel- und Stöpselgallen, die besondere Potenzen der Wirtspflanze eigens für die Gallbildung vorauszusetzen scheinen! Hier kann das Ausnutzungsprinzip das Zustandekommen der fremddienlichen Zweckmäßigkeit nicht erklären; denn die Ausstoßungs- und Öffnungseinrichtungen dieser Gallen oder doch die entsprechenden Bildungspotenzen der Wirtspflanzen müssen erst da sein, ehe sie ausgenutzt werden können. Hier gilt es gerade zu erklären, wie die Pflanzen zu Potenzen gekommen sind, die nicht der Bildung ihrer normalen Teile zu dienen scheinen, sondern eigens für die Parasiten geschaffen scheinen. Dieser Frage steht das Ausnutzungsprinzip ratlos gegenüber. Wir müssen uns also nach anderen Erklärungsprinzipien umsehen.

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Porsch zählt „als den Schmarotzer unbedingt vorteilhaft“ folgende Einrichtungen an Pflanzengallen auf:

1. Abschluss des Schmarotzers von der Außenwelt.
2. Verschluss des Eingangs in die Gallenhöhlung durch Verzahnung der Oberhautzellen.
3. Schutz der Galle durch reiche Entwicklung mechanischen Gewebes.
4. Schaffung innerer Lufträume durch Entwicklung einer bestimmten Gewebeart („Sternparenchym“).
5. Häufige Ausbildung eines eigenen Assimilationsgewebes.
6. Entwicklung eines sich stetig ergänzenden Nährgewebes.
7. Lage des Nährgewebes.
8. Förderung der vorhandenen Stoffleitungsbahnen in der Richtung der Stoffleitung zur Galle.
9. Nachträgliche Bildung neuer Stoffleitungsbahnen zur Galle.
10. Gerbstoffreichtum des Gallengewebes.
11. Schaffung anatomisch vorgebildeter Ausgangspforten mit Öffnungsmechanismus für den Austritt des entwickelten Tieres[159]

Aus unseren Betrachtungen ergibt sich, dass diese Zusammenfassung noch erweitert werden könnte; es sei nur an die Dornen und Stacheln mancher Gallen erinnert. –

Das Dargelegte mag genügen, um die Zweckmäßigkeit der Pflanzengallen zu zeigen. Wir haben uns bei unserer Darstellung auf die Werke hervorragender Gallenkenner gestützt, haben diese selbst sehr häufig zu Wort kommen lassen, um die Objektivität unserer Tatsachenberichte sicher zu stellen. Was die teleologische Ausdeutung der Tatsachen angeht, so kommt es hier nicht darauf an, ob sie in a l l e n angeführten Fällen einwandfrei ist. Man mag in einzelnen Fällen die beigebrachten Zweckmäßigkeitsdeutungen für unsicher, ja für verfehlt halten; angesichts des g a n z e n Materials wird man einen oftmals weitgehende Zweckmäßigkeit der Pflanzengallen nicht bestreiten können. […]

Trotzdem werden wir mit dem in teleologischen Betrachtungen äußerst zurückhaltenden Küster nunmehr sagen dürfen: „Dass die Gallen zweckmäßig für den Gallenerzeuger und Gallenbewohner sind, unterliegt keinem Zweifel[160], wir werden mit ihm diese Zweckmäßigkeit in manchen Fällen staunenswert finden[161].”

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[159] Porsch, a.a.O. S.553.
[160] Küster, a.a.O. S.395; vgl. Porsch, a.a.O. S. 553.
[161] Küster, a.a.O. S.397; vgl. de Vries, a.a.O. S. 290.

Erich Becher (1925): Fremddienliche Zweckmäßigkeit[162]

Die zweckmäßigen Gebilde und Vorgänge in der lebenden Natur, wie z. B. das menschliche Auge und die instinktive Arbeit der Bienen beim Bau ihrer Waben, machen den Eindruck, mit mehr oder weniger, Intelligenz zum Erreichen eines vorausgesehenen Zieles erdacht zu sein. Darum haben sie von alters her das Staunen der Beobachter erregt, und immer wieder die Frage nach ihrer Entstehung wachgerufen.

Seit Jahrtausenden bemühen sich Naturphilosophen und Biologen um dieses für Natur- und Weltauffassung hoch bedeutsame Problem. Die theistische und die deistische Lehre vom Naturzweckmäßigen betrachten dieses als das Werk des göttlichen Geistes. Der Vitalismus nimmt an, dass besondere Lebensfaktoren oder -kräfte, die in der toten Natur nicht vorkommen, die organische Zweckmäßigkeit zustande bringen. Der Psychovitalismus lehrt, dass diese besonderen Zweckmäßiges hervorbringenden Lebensfaktoren seelischen Wesens oder dem uns bekannten Seelischen nahe verwandt sind. Der biologische Mechanismus, der besondere Lebensfaktoren leugnet und glaubt, dass die Organismen nichts sind als komplizierte Maschinen, in denen nur physikalische und chemische Kräfte wirken, erklärt die Entstehung des Zweckmäßigen vielfach mit Hilfe der DARWINschen Zuchtwahllehre: Durch kleine Abweichungen der Nachkommen von den Eltern entsteht zufällig Zweckmäßiges und Unzweckmäßiges; das Unzweckmäßige wird im Daseinskampfe ausgemerzt, während das Zweckmäßige erhalten bleibt und durch Vererbung auf die Nachkommen übertragen wird; es wird so im Laufe der Generationen immer mehr gehäuft. Nicht wenige Mechanisten verzichten überhaupt auf eine Erklärung des Zustandekommens der Zweckmäßigkeit in der Meinung, diese sei nichts Objektives, sondern nur durch die menschliche Auffassungsweise in die Natur hineingelegt. Doch ist die Zweckmäßigkeit, das Geeignetsein unseres Auges für das Sehen, des Gänsefußes für das Schwimmen, des Schwalbenflügels für das Fliegen ein objektiv feststellbarer Sachverhalt, dessen Zustandekommen gewiß erklärungsbedürftig ist.
Im folgenden soll nun auf eine äußerst merkwürdige Artorganischer Zweckmäßigkeit hingewiesen werden, die in den allgemeinen Bearbeitungen des biologisch-philosophischen Zweckmäßigkeitsproblems ganz vernachlässigt worden ist, der jedoch große Bedeutung für dieses Problem zukommen dürfte.

Zahlreiche Pflanzengallen zeigen eine auffallende Zweckmäßigkeit, die nicht den gallentragenden Pflanzen selbst, sondern den diese oft schädigenden gallenhervorrufenden Parasiten dienlich ist. Die Pflanzen dienen also durch die Bildung der Gallen fremden Lebewesen, den ,,Gallengästen", in zweckmäßiger Weise. Diese Art von Zweckmäßigkeit, die nur fremden Organismen zugute kommt und geradezu für sie eingerichtet und bestimmt erscheint, bezeichne ich als fremddienlich.

Selbstdienlich nenne ich eine Zweckmäßigkeit, die im Dienste des Organismus steht, der sie aufweist; so ist z. B. die Zweckmäßigkeit unseres Auges und des Raubtiergebisses selbstdienlich. Artdienlich heiße eine Zweckmäßigkeit, die nicht dem sie aufweisenden Individuum, wohl aber seiner Art zugute kommt. Artdienlich sind z. B. die Milchdrüsen der Säugetiere und die Brutpflegeinstinkte. Die artdienliche Zweckmäßigkeit ist meist nachkommendienlich, d. h. sie steht meist im Dienst der Nachkommen der Individuen, die diese Zweckmäßigkeit zeigen. Doch gilt dies nicht immer; es gibt ja auch artdienliche Brutpflegeinstinkte bei Insektenindividuen, die keine eigenen Nachkommen hervorbringen, z. B. bei Arbeiterbienen.

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[162]Aus: Philosophische Monatshefte der Kant=Studien, 1. Jahrgang, 2. Heft, pp. 65- 72. Berlin. R. Heise. https://archive.org/stream/philosophischemo00kantuoft/philosophischemo00kantuoft_djvu.txt

In der älteren theistischen und deistischen Naturauffassung spielte die Annahme fremddienlicher Zweckmäßigkeit eine große Rolle. *Gottes Güte hat zahlreiche Pflanzen geschaffen, die in zweckmäßiger Weise für Mensch und Tier, also für fremde Organismen, nahrhafte Früchte, Heilmittel, Herz und Sinn erfreuende farbenprächtige, duftende, honigspendende Blüten darbieten*.

Die Wissenschaft der neuesten Zeit hat diese Annahme fremddienlicher, insbesondere menschendienlicher Zweckmäßigkeit abgelehnt und nur die selbst-, die nachkommen- und die artdienliche Zweckmäßigkeit anerkannt. Die Früchte bieten sich Mensch und Tier zum Genuß an, damit diese die Samen der fruchttragenden Pflanzen verbreiten; die leuchtenden, duftenden, honigspendenden Blüten locken Insekten und Vögel an, damit dieselben durch Übertragung des Pollens die Befruchtung einleiten. So stehen diese zunächst fremddienlich erscheinenden Gebilde im Dienste der Fortpflanzung der eigenen Art; sie sind artdienlich zweckmäßig.

Die DARWINsche Zuchtwahlhypothese zielt nur auf die Erklärung selbst-, nachkommen- und artdienlicher, nicht aber fremddienlicher Zweckmäßigkeit. Wenn an einem Lebewesen eine **Veränderung auftritt, die nicht für dieses selbst oder seine Nachkommen, sondern für irgendeinen fremden Organismus zweckmäßig ist, so werden jenes Lebewesen und seine Nachkommenschaft dadurch nicht im Daseinskampf begünstigt**; ***fremddienlich Zweckmäßiges wird daher auch nicht durch den Daseinskampf gezüchtet; sein Zustandekommen ist durch natürliche Zuchtwahl nicht verständlich zu machen***.

Auch die vitalistischen und psycho-vitalistischen Lehren, welche das Zweckmäßige an den Lebewesen durch den Individuen innewohnende und zugehörige Lebenskräfte bzw. seelische Lebensfaktoren erklären, zielen auf die Erklärung der selbstdienlichen, nicht aber der fremddienlichen Zweckmäßigkeit. Wie sollten die einem Individuum zugehörigen Lebenskräfte oder seelischen Faktoren dazu kommen, etwas hervorzubringen, was für dieses Individuum schädlich oder unnütz, für einen ganz fremden Organismus aber zweckmäßig ist!

So ist die fremddienliche Zweckmäßigkeit in den neueren allgemeinen Untersuchungen des Problems der Naturzweckmäßigkeit vernachlässigt worden. Und doch ist die Zweckmäßigkeitsart, die wir als fremddienliche bezeichnet haben, an zahlreichen Pflanzengallen in mannigfacher Ausprägung einwandfrei feststellbar und den Gallenforschern längst bekannt; bereits Marcello Malpighi, der in der zweiten Hälfte des 17. Jahrhunderts die wissenschaftliche Gallenkunde begründet hat, spricht sich klar über die den Gallengästen dienende Zweckmäßigkeit der Pflanzengallen aus.

Als Gallen bezeichnet man an Pflanzen auftretende anormale Gebilde, die von fremden, meist tierischen, seltener pflanzlichen Lebewesen hervorgerufen werden und diesen fremden Lebewesen, den „ Gallengästen", Nahrung geben. Die Pflanzen versorgen ihre Gäste in den Gallen oft in erstaunlich zweckmäßiger, reichlicher und bequemer Weise mit Eiweißstoffen, Fetten und Stärke. Vielfach werden besondere Nährgewebe in den Gallen gerade dort gebildet, wo der Gallengast haust. Manchmal erzeugen eigene Assimilationsgewebe der Gallen die Nährstoffe ; oft werden diese durch ein wohl entwickeltes Leitungssystem dem Gallenbewohner zugeführt. Die Feinheit und Weichheit der Häute der nährstoffgefüllten Zellen, welche die Wand der „Larvenkammer", der Behausung des Gastes, auskleiden, erleichtern seine Ernährung. Die Nährgewebe bilden sich bei der Entstehung der Galle so schnell, dass die aus dem Ei schlüpfende Larve sofort ihr Futter findet; die verspeisten Nährzellen werden schnell durch neue ersetzt. In gewissen Milbengallen finden sich dünnwandige, zu futtergefüllten Säcken umgewandelte Haare.

Der Luftversorgung der Gallentiere dienen wohl die großen, lufthaltigen Interzellularräume vieler Gallengewebe.

Die Pflanzen bieten in den Gallen ihren Gästen Wohnungen dar, die nach ganz verschiedenen Bauplänen geschaffen sind. Sicherlich ist es für die Gallenbewohner recht zweckmäßig, von den Pflanzen durch Blattrollungen oder in falten-, beutel-, hörnchen-, köpfchen- oder eiförmigen Blattausstülpungen oder durch umwallende Wucherung oder in irgendwelchen anderen Neubildungen eingehüllt oder gänzlich eingeschlossen und so geschützt zu werden. Selbst unter beengenden Raumverhältnissen, die der Galle eine anormale Gestalt aufnötigen, kann die Larvenhöhle noch die geeignete, normale Form erhalten.

Dem Schutz der Gallengäste, der Abwehr ihrer Feinde, dienen mannigfache weitere Vorkehrungen, wie Gerbstoffgehalt der Gallen, der vor Tierfraß bewahrt, spitze Haare, Stacheln und Dornen an der Außenseite oder an der Öftnung: von Gallen, Steinzelleneinlagerungen und Hartschichten, welche die Gäste umhüllen. usw. Auch dicke, schwammige Gewebeschichten, leere Hohlräume und eine exzentrische Lage der Larvenkammer können verhindern, dass Feinde der Gallengäste mit ihrer Legeröhre bis in die Larvenkammer vordringen und dort Eier ablegen, aus denen sich fatale Hausgenossen entwickeln.

Schöne Beispiele fremddienlicher Zweckmäßigkeit bietet die rechtzeitige spontane Öffnung vieler Gallen, durch welche die Gäste aus ihrem Heim freigelassen werden, wenn ihr Lebenslauf dies verlangt. Durch Welken und Schrumpfung werden enge Öffnungen und Spalte so erweitert, dass die Gallengäste hindurchkönnen; oder es wird durch Zerreißung der Gallenwand oder durch Abtrennung eines Teiles der Galle eine Öffnung geschaffen. Der abgetrennte Teil der Gallenwand bildet bei gewissen Gallenarten einen kreisrunden Stöpsel oder Deckel, der noch mit einem übergreifenden Rande versehen ist.

In anderen Fällen lösen sich die ganzen Gallen oder größere Teile derselben, die den Gast einschließen, von den Pflanzen ab und fallen zu Boden; dort überwintert dann das Gallentier in seiner schützenden Behausung, etwa noch bedeckt vom im Herbst herabgefallenen Laub. Fremddienlich zweckmäßig erscheint es auch, dass manche Gallen das Pflanzenorgan, an dem sie gebildet wurden, um mehrere Monate überleben und so ihren Gast bis zu seiner fertigen Ausbildung beherbergen. —

Bei einigen wenigen Gallenarten leistet der Gallengast der Pflanze nützliche Gegendienste. Im übrigen aber haben die gallenbildenden Pflanzen von ihren Gästen keinen Nutzen, sondern sie werden durch diese oft mehr oder weniger geschädigt; es werden ihnen ja wertvolle Stoffe entzogen, Blätter werden beschädigt, die Fortpflanzungsfähigkeit wird herabgesetzt, usw. Die gallenbildenden Pflanzen zeigen also nicht nur „Altruismus", sondern sogar „ Feindesliebe".

Es gibt sehr zahlreiche Arten von Pflanzengallen und an ihnen eine große Fülle und Mannigfaltigkeit des Fremddienlich-Zweckmäßigen. Auch bei Tieren kommen den Gallen analoge, fremddienlich zweckmäßige Neubildungen vor. Ameisen zeigen fremddienlich-zweckmäßige Gastpflege-Instinkte, indem sie aufopferungsvoll fremde, der eigenen Brut verderbliche Insekten und deren Larven pflegen. Doch können wir darauf und auf andere Beispiele fremddienlicher Zweckmäßigkeithiernicht eingehen.—

Wir stehen nun vor der schwierigen Aufgabe, das Zustandekommen der vielgestaltigen fremddienlichen Zweckmäßigkeit zu erklären. Oben wurde schon angedeutet, dass die Darwinsche Zuchtwahlhypothese, das klassische Zweckmäßigkeits-Erklärungsprinzip der mechanistischen Lebenslehre, hier versagt. Auch die in diesem kurzen Aufsatz nicht zu erörternden Versuche, auf einem Umwege doch noch die Gallenzweckmäßigkeit durch das Zuchtwahlprinzip zu erklären, führen nicht zum Ziele. Sind die Pflanzen rein materielle, ohne Mitwirkung von Intelligenz entstandene Gebilde, in denen nur physikalische und chemische Kräfte wirken, so ist nicht einzusehen, wie sie dazu kommen sollten, für fremde Lebewesen zweckmäßig zu sorgen.

Weiterhin wären der Vitalismus und der Psychovitalismus in Betracht zu ziehen, welche die Entstehung des Zweckmäßigen auf besondere, nicht-physikochemische Lebenskräfte bzw. auf seelische Lebensfaktoren zurückführen. Wenn wir aber annehmen, dass diese Lebensfaktoren den einzelnen lebenden Individuen innewohnen und zugehören, dann wird, wie oben schon betont, wiederum nicht verständlich, wie sie dazu kommen sollten, etwas hervorzubringen, was für das eigene Individuum unnütz oder schädlich, für ein fremdes Individuum aber zweckmäßig ist.

Vermag die Annahme von Lebensfaktoren, die den Individuen innewohnen und auf sie beschränkt sind, die fremddienliche Zweckmäßigkeit nicht zu erklären, bei der ein Individuum für ein ganz anderes, artfremdes Individuum sorgt, so werden wir zu der Vermutung geführt, dass ein über diesen ganz verschiedenen Individuen stehender, ein überindividueller Lebensfaktor sie in Verbindung bringe. Ein solcher Faktor, der sowohl in den dienenden, wie in den bedienten Organismus, in die Pflanze wie in den Gallengast, hineinreichte und verbindend über beiden stände, könnte den Dienst des einen Organismus für den anderen veranlassen.

Die Annahme eines überindividuellen Lebensfaktors mag zunächst sehr kühn erscheinen; doch sprechen auch andere Tatsachen für sie. Manche Pflanzenarten bilden Gallen, die auffällig an Früchte fremder Pflanzenarten erinnern. Man gewinnt den Eindruck, dass derselbe Bauplan bei der Galle der einen Pflanzenart und bei der Frucht der anderen, fremden Pflanzenart zugrunde liegt. Wenn aber hier und dort derselbe Bauplan vorliegt, so wird auch wohl an beiden Stellen derselbe Baumeister, derselbe Lebensfaktor im Spiele sein. Dieser müßte also in Pflanzenindividuen hineinwirken, die verschiedenen Pflanzenarten angehören, müßte mithin über Individuen und Arten hinreichen, müßte ein überindividuelles Wesen sein.

Nicht nur bei fruchtähnlichen Gallen kann man den Eindruck gewinnen, dass dieselben Baupläne oder -ideen im Organismenreich an sehr verschiedenen Stellen Verwendung finden. So treffen wir z. B. Augen von recht ähnlichem Bau bei Wirbeltieren und Tintenfischen, worauf auch Bergson und Driesch hingewiesen haben. Derartige „Analogien" des Bau- und Funktionsplanes begegnen uns oft bei einander sehr fernstehenden Lebewesen.

Wenn aber ein überindividueller Lebensfaktor in so verschiedene Organismenarten, in Wirbeltiere und Tintenfische, ja sogar in Gallentiere und Pflanzen hineinreicht, dann drängt sich die Vermutung auf, dass sich über das ganze Organismenreich hin ein großer überindividueller Lebensfaktor erstreckt.

Da dieser überindividuelle Lebensfaktor Baupläne oder -ideen in sich birgt, wird er wohl seelischer Art sein müssen. Diese Pläne liegen zweckmäßigen Gebilden, wie Gallen, Früchten und Augen zugrunde; sie werden also wohl selbst zweckmäßig sein und also auf Intelligenz oder etwas Ähnliches im überindividuellen Lebensfaktor hinweisen. Der-selbe wird also von seelischem oder dem Seelischen verwandtem Wesen sein und Intelligenz oder etwas Intelligenzartiges besitzen.

Überall, wo ein Organismus für einen anderen sorgt, also nicht nur bei der fremddienlichen, sondern auch bei der nachkommen- und artdienlichen Zweckmäßigkeit, liegt die Vermutung nahe, dass ein überindividuelles Wesen die Individuen verbindet und die Fürsorge des einen für das andere veranlaßt.

Endlich drängt sich der Gedanke auf, dass das überindividuelle Seelische sich wohl auch im menschlichen Bewußtsein geltend macht, in dem Trieb zur Fürsorge für die Kinder, in der Liebe zu Mitmenschen, Tieren und Pflanzen, in Mitfreude, Mitleid, sozialem Pflichtgefühl undGewissen, vielleicht auch im religiösen Bewußtsein und im mystischen Erlebnis des Eins-Seins der Seele mit dem Urquell alles Lebens.

In allen Sphären des Lebensreiches, im Pflanzen-, Tier- und menschlichen Geistesleben, im großen Entwicklungsgang des Lebens von den primitivsten Anfängen bis zu den höchsten

Blüten der Kultur würde also ein überindividuelles seelisch-geistiges Wesen sich auswirken.[163]

Wie aber verträgt sich mit dieser Hypothese der grausame Kampf in der lebenden Welt, die Unvollkommenheit der Organismen, das Unzweckmäßige an ihnen, das oft den Eindruck des „Dummen" macht? Man könnte vermuten, dass sich darin eine innere Unausgeglichenheit, ein ungeheurer innerer Widerstreit oder sonst eine Unvollkommenheit des überindividuellen Seelischen und seiner Intelligenz offenbare.

Näher liegt eine andere Annahme. Ein Blick auf das Bewußtseinsleben zeigt, dass es dem Individuum angehörige seelische Lebensfaktoren: Intelligenz, Gefühle, Triebe usw. gibt, die unvollkommen[164] sind und viel Unvollkommen-Zweckmäßiges und Dummes hervorbringen. Dem Individuum angehörige Gefühle und Triebe, wie Hunger, Neid, Grausamkeit usw. führen zu Kampf und Streit. Darum liegt es nahe, Unvollkommen-Zweckmäßiges und Dummes, Kampf und Streit im Organismenreich auf unvollkommene individuelle seelische Lebensfaktoren zurückzuführen.

Die Hypothese eines umfassenden überindividuellen Seelischen und die Annahme individueller seelischer Lebensfaktoren erscheinen nun wohl vereinbar. Die letzteren bringen Selbstdienlich-Zweckmäßiges hervor; ihre individuelle Beschränktheit läßt das Unzweckmäßige und Dumme und den Kampf in der lebenden Natur wie in der menschlichen Welt begreiflich erscheinen. Das überindividuelle Seelische aber reicht in das Individuum hinein und veranlaßt in ihm Leistungen, die dieses selbst oder andere Individuen fördern; vieles Nachkommen-, Art- und Fremddienliche, auch menschliche Handlungen aus selbstloser Liebe und Pflichtgefühl, mögen der Einwirkung des überindividuellen Seelischen zu verdanken sein, das führend und verbindend über den irrenden und hadernden Individuen waltet.

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H. Driesch, Philosophie des Organischen. 2. Aufl. Leipzig 1921. S. 281.
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F. Heikertinger, Das Scheinproblem von der „fremddienlichen Zweckmäßigkeit". Die Naturwissenschaften. 6. 1918. S. 184ff.

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[163] Anmerkung W.-E.L.: Diese Aussage erinnerte mich an Psalm 104 über Jehova (Verse 29 und 30): „Wenn du dein Angesicht verbirgst, geraten sie in Bestürzung. Wenn du ihren Geist wegnimmst, verscheiden sie, Und zu ihrem Staub kehren sie zurück. **Wenn du deinen Geist aussendest, werden sie erschaffen**; Und du erneuerst die Fläche des Erdbodens. Die Herrlichkeit Jehovas wird auf unabsehbare Zeit währen. Jehova wird sich freuen an seinen Werken

[164] Weitere Anm.W.-E.L.: Bleibt natürlich die Frage zu klären, woher diese Unvollkommenheit kommt. Vgl. dazu **Ein paar offene Fragen der Evolutionstheorie sowie theologische Einwände von Evolutionstheoretikern zum Thema *Intelligent Design*** http://www.weloennig.de/OffeneFragenEvol.html

Edm. J. Klein, Die fremddienliche Zweckmäßigkeit. Institut Grand Ducal de Luxembourg. Arch. trimestrielles. Nouvelle S^rie. 1912 — 1917. Tome VII. Luxembourg 1917. S. 61 ff.
A. KOELSCH, Das Erleben. Berlin 1919. S. 367ff.
H. Kranichfeld, Gemeinschaftsdienliche Zweckmäßigkeit, die Lösung des Problems der Dysteleologien. Naturwiss. Wochenschr. N. F. 20. 1921. S. 513ff.
H. Kranichfeld, Eine neue Untersuchung über die fremddienliche Zweck-
mäßigkeit. Naturwiss. Wochenschr. N. F. 20. 1921. S. 617 ff.
H. MiEHE, Besprechung von E. Becher: Die fremddienliche Zweckmäßigkeit
usw. in Naturwiss. Wochenschr. N. F. XVI. 1917. S. 350.
A. Müller, Die sogenannte fremddienliche Zweckmäßigkeit und die menschliche Pathologie. Virchow's Archiv. 244. 1923. S. 308ff.
E. Wasmann, Die Gastpflege der Ameisen, ihre biologischen und philosophischen
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Über die Pflanzengallen orientieren:

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E. Küster, Die Gallen der Pflanzen. Ein Lehrbuch für Botaniker und Entomologen. Leipzig 1911. Philosophische Monatshefte, Heft II. 2 72
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E. KÜSTER, Galisn, im Handwörterb. d. Naturwiss., hrsg. v. Korschelt u.
Teichmann, 4. Jena 1913. S. 440—462.
E. Küster, Pathologische Pflanzenanatonne. 2. Aufl. Jena 1916.
O. Porsch, Wechselbeziehungen zwischen Pflanze und Tier, in Allgemeine
Biologie, hrsg. v. C. Chun u. W. Johannsen unter Mitwirk. v. A.
GÜNTHART. Kult. d. Gegenw. 111, IV, 1. Leipzig u. Berlin 1915. S. 535—586.
H. Ross, Die Pflanzengallen (Cecidien) Mittel- n. Nordeuropas, ihre Erreger u. Biologie u. Bestimnmngstabellen. Jena 1911.

Joachim Illies[165]
Der Jahrhundert Irrtum[166]

Seite 133: In der Sicht des Darwinismus konnte es nur eine einzige akzeptable Erklärung für Gestaltmerkmale und Verhalten bei Tier und Pflanze geben: die durch positiven Auslesewert bewiesene Zweckmäßigkeit, derzufolge eine zunächst als rein zufällig zu denkende Mutation sich als „Betriebsverbesserungsvorschlag“ durchsetzt. Die „Welträtsel“ – so meinte Ernst Haeckel 1899 – sind auf diese nüchterne Weise zu lösen, jedenfalls so weit es die Entstehung der Arten und ihre Lebensweise betrifft: In kleinen, fast unmerklichen Zufallsabweichungen der Variationen habe sich alles zu stets besserer Anpassung entwickelt, und wo man in einer ungewöhnlichen Erscheinung solchen Anpassungswert nicht erkennen kann, da muss weiter gesucht werden, bis er gefunden ist! […]

Windige Spekulationen

Seite 134: Für die Pflanze ist der ganze Aufwand der Gallenbildung ohne erkennbaren Nutzen, er ist eher ein Schaden, denn er erfordert Nährstoffe, reduziert die assimilierende Blattfläche und stört den normalen Wachstumsverlauf, manchmal sogar die kostbarsten Teile der Pflanzen: Knospen und Samen. Folglich müssten nach Darwin die Pflanzen ohne Gallen gegenüber denen mit Gallen im Vorteil sein, und so hätten sich eigentlich im

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[166] J. Illies (1983): Der Jahrhunderirrtum. Umschau Verlag, Frankfurt am Main.

Laufe der Evolution sehr bald und überall die gallenfreien Varianten unter den Pflanzen als die Tüchtigeren auslesen müssen.

Da sie es offenbar nicht getan haben, bleibt nur eine recht windige Spekulation übrig: ziehen die Pflanzen vielleicht doch einen geheimen Nutzen aus der Galle, die sie so mühsam und so einladend für ihre Parasiten bereitstellen?

Der Greifswalder Zoologie-Professor U. Sedlag, der sich als Insektenforscher mit Gallwespen beschäftigt, denkt als strammer Darwinist in dieser Richtung: „Man sieht es als vorteilhaft an, dass der Gallenerreger auf die Galle beschränkt bleibt. Er erhält damit sozusagen seinen Platz und seine Nahrung zugewiesen und richtet bei seinem Fraß (im allgemeinen) keine Zerstörungen an lebenswichtigen Teilen der Pflanze an." Auch der Heidelberger Zoologe Fr. Schremmer stimmt in diesen Chor ein: „Die Pflanze zieht es vor, den Schädling einzukapseln und ihn besonders zu ernähren, weil sie so weniger Schaden erleidet, als wenn er frei umherklettert und die Pflanze an beliebigen Stellen befällt. Durch die Gallenbildung wird der Angriff des Schädlings nicht nur räumlich auf ein Blatt oder eine Knospe, sondern auch zeitlich beschränkt. Nur so lässt sich die Gallenbildung als Schutzmaßnahme oder Feindabwehr erklären und verstehen."

Solche gedanklichen Salti mortali sind grotesk und zeigen das schwere Dilemma des darwinistischen Erklärungszwanges. Man verallgemeinere einmal diese Logik. Wir Menschen haben Schnupfen (und bereiten dem Virus in unserer Nasenschleimhaut eine gemütliche Unterkunft), weil wir den Erreger dadurch daran hindern, sich bei uns in anderen Organen festzusetzen. Wir beherbergen die Bandwürmer in unserem Darm, damit sie uns nicht an die Leber gehen, und wir stellen den Kopfläusen unsere Haupthaare zur Verfügung, damit sie uns nicht am ganzen Körper plagen – das tun stattdessen die Kleiderläuse, für die wir unseren Körper bereithalten, damit sie uns auf dem Kopf in Ruhe lassen!

Nein, so geht es offensichtlich nicht. Also müssen wir es andersherum versuchen. Nicht die Pflanzen „machen" irgendetwas Sinnvolles, sondern die Gallenerreger sind die eigentlichen Täter: für sie ist es ohne jeden Zweifel zweckmäßig, dass es für ihr Larvenleben pflanzliche Gallenbildung gibt. Durch den Einstich mit der Legeröhre setzt daher das Gallenwespenweibchen das Ei ins Innere der Pflanze (der richtigen Pflanzenart und dort an die richtige Stelle!), die aus dem Ei schlüpfende Larve schafft sich dort einen Hohlraum, und durch Absonderung bestimmter (nämlich genau der richtigen) Wuchsstoffe und anderer hormoneller Reize zwingt sie dann die Wirtspflanze dazu, die komplizierte Gallenbildung in Gang zu setzen. In der Tat zeigen Experimente, dass nur bei Anwesenheit einer lebenden Larve die betreffende Gallenbildung einsetzt und weitergeht, und es lässt sich auch nachweisen, dass die Larve jeder einzelnen Gallenerreger-Art nur an ganz bestimmten Pflanzen (zum Beispiel an Blättern bestimmter Laubbäume) diese spezifische Gallenbildung erzeugen kann. Ein einzelnes Eichenblatt kann auf diese Weise nebeneinander für verschiedene Gallinsekten-Arten viele jeweils ganz verschiedene Gallen bereitstellen.

Hier könnte und müsste nun das Darwin-Modell eine Erklärung einsetzen: Bei gewöhnlichen blattminierenden Insektenlarven bildete sich (zufällig) ein Wirkstoff, der in der Pflanze (zufällig) eine Änderung des Normalwachstums in Richtung auf eine für die Larve günstigere Form bewirkte – eine Schwellung, Eiweißreichtum der Zelle, Öltröpfcheneinlagerung und Wasserzufuhr – und damit lag ein Auslesevorteil für diese Larven vor, die sich in der Selektion durchsetzte. Schrittweise ging es dann (zufällig) immer weiter, die Gallen wurden immer luxuriöser, die Larven immer fetter und schließlich überlebten nur die Arten von Gallinsekten, die als wahre physiologische Wundertäter durch raffinierte Hormonbehandlung das Optimum an Wohnlichkeit und Nahrhaftigkeit aus den Pflanzen herauszuholen verstanden.

Gelernte Zauberkünstler

Seite 136: Denn wie gelernte Zauberkünstler, denen alle Geheimnisse der magischen Beeinflussung offenstehen, bringen die Gallenerreger die erstaunlichsten Wirkungen zustande. Da bilden sich unter ihrem Einfluss nicht nur die bequemen und geschützten Wohnkammern, sondern die Pflanze lässt sich „vorsorglich" besondere Leitbündel wachsen, um sie auch zusätzlich mit Wasser und Nährstoffen versorgen zu können.

Da sprießen Wurzeln in dicken Büscheln hoch oben aus dem Stengel eines Grases (Älchengallen), da setzen die Fichtentriebe gleich die Wachstumsschritte von fünf bis sechs Jahren im voraus auf einmal an (Hexenbesen), da wachsen Gallen selbst auf verwelkten Blättern noch weiter der sogar (bei der Linsengalle der Eiche), nachdem sie sich vom Blatt abgelöst haben und zu Boden gefallen sind. Und – größte aller Zumutungen an den kritischen Verstand! – da bilden die runden Gallenkapseln der südamerikanischen Anakardie Duvaua[167] für ihren Untermieter (die Larve der Motte Cecidosis eremita) schließlich sogar die Schlupflöcher aus, deren Deckel sich rechtzeitig lösen und so maßgerecht der Larve den Weg freigeben, den sie sich aus eigener Kraft nicht bahnen könnte! … Denn sie (die Wirtspflanze) bildet manchmal wie bei der erwähnten Form mit

[167] http://sdei.senckenberg.de/~openaccess/01296.pdf
http://sdei.senckenberg.de/~openaccess/01295.pdf
https://link.springer.com/article/10.1007/BF00540718
Karl Frank (1913, p. 232): The Theory of Evolution in the Light of Facts. London, Kegan Paul.
"Let us, however, go into details and ask, for instance, how it comes about that the lark rises singing into the air, many flat fish lie on their sides, some plants become carnivorous, why the plant *Duvaua dependens* produces for the moth, *Cecidosis eremita*, a gall with a circular cover which renews itself on the inner side and is precisely large enough to let the moth escape, etc. If it be assumed that all this was not always so but has been evolved, then does the question again, as always, recur: Why and wherefore has it been evolved ? What need is there for the plant to keep and cherish a moth since it only does so by constant expenditure of nutrition and to shape a cover at the right time, not earlier and not later, so that when the moth creeps out of the gall the chrysalis skin and that alone is torn off ? We can only say that it must and should happen just so."

dem Deckelstöpsel Organe aus, die sonst bei ihr überhaupt nicht vorkommen. Fr. Schremmer beschreibt diesen Sachverhalt so: „…lassen sich in der Pflanze schlummernde, gewöhnlich nicht in Erscheinung tretende gestaltbildende Fähigkeiten wecken."

Das aber wäre – obwohl der Tatbestand selbst kaum zu bezweifeln ist – eine Vorstellung, die dem landläufigen Darwinismus frontal entgegensteht. Sollte es im genetischen Code der Lebewesen „schlummernde" Fähigkeiten geben, die sich niemals im Ausleseprozess bewähren könnten, sondern einfach nur so und für alle Fälle vorsorglich durch Tausende von Generationen mitgeschleppt werden, bis eben einmal einer kommt wie ein Dornröschen-Prinz und sie wachküsst? Und welcher Zufall sollte alle solche Fähigkeiten auf Vorrat bereitgestellt haben?

Mutiger Schritt in die andere Richtung

Seite 137: Es bleibt dabei, dass die Gallen ein bitteres Ärgernis für den Darwinismus sind. Denn selbst wenn man heute verstehen kann, wie es zu ihrer Bildung kommt – durch eine Hormoncocktail, den der Gallenerreger listig und kenntnisreich verabreicht – so ist man doch völlig außerstande, die Evolution, also die Herausbildung solcher Fähigkeiten bei Pflanze und bei Insekt, nach dem Modell von Mutation und Selektion zu begreifen. Eine Erklärung müsste ganz anders ansetzen, sich vom darwinistischen Eigennutz-Denken der Selektion des Zweckmäßigen ganz freimachen und einen mutigen Schritt in die andere Richtung wagen.

Das tat als erster der Münchner Philosoph Erich Becher, der diesem Problem ein eigenes Buch widmete, dessen Titel bereits sein ganzes Programm verrät: „Die fremddienliche Zweckmäßigkeit der Pflanzengallen und die Hypothese eines überindividuellen Seelischen" (1917).

Im gleichen Sinne argumentierte auch der Biologe und Philosoph Hans Driesch in seiner „Philosophie des Organischen". Zwischen Pflanze und Insekt – so schrieb er – gäbe es in wechselseitiges Angepasstsein, in dem man „Anzeichen für überpersonale Ganzheit" erblicken müsse.

Darwinismus kontra Vitalismus

So eindeutig damit das Konzept des darwinistischen Zufalls abgelehnt und überwunden wird – einer Erklärung im naturwissenschaftlichen Sinn liefert das vitalistische Modell leider auch nicht, sondern allenfalls eine Beschreibung, die von einer anderen Seite her Wesentliches der Erscheinung in den Blick nimmt. Daher gab es aus dem Lager der Darwinisten sofort erbitterten Widerstand gegen jeden Vitalismus. So spricht der Zoologe Fr. Schremmer (in Heidelberg ein später Nachfolger auf Drieschs Lehrstuhl) in erfrischender Ehrlichkeit sein Unbehagen gegenüber der „fremddienlichen Zweckmäßigkeit" aus, „…die zwar von den Naturphilosophen gern aufgegriffen, aber von jeder Kausalforschung abgelehnt wird. Viel aufschlussreicher und klärender ist die unserem menschlichen Werturteil und Nützlichkeitsdenken entsprechende Ansicht, dass sich die Pflanze durch die Gallenbildung vor größerem Schaden schütze.“ Mag sein – „aufschlussreicher“ ist das darwinistische Modell zweifellos, eben weil es unserem Nützlichkeitsdenken entgegenkommt, aber wo bleibt die Objektivität der Wissenschaft, wenn wir ein Modell danach beurteilen, ob es unseren Lieblingsgedanken entspricht? Es kommt doch wohl nach unbestritten allgemeiner Auffassung allein darauf an, dass ein Erklärungsmodell (ob es uns passt oder nicht) die Klärung der Kausal-Zusammenhänge bewirkt, und eben da versagt im Falle der Gallen das darwinistische Modell völlig, und mit ihm offenbar unser eigenes „Nützlichkeitsdenken“.

Gallenbitteres Ärgernis für Darwinisten

So ist es also nur konsequent, wenn die meisten neodarwinistischen Biologen von den Pflanzengallen lieber überhaupt nicht reden oder aber die spezielle Problematik herunterspielen. Dies tat der Tübinger Evolutionsbiologe Walter Zimmermann in seinem Standardwerk von 1968, wo er forsch und bündig die ganze Erscheinung weg-erklärt: „Experimentell ist gezeigt worden, dass vom Insekt Wuchsstoffe produziert werden, die diese für das Insekt eigendienliche Anordnung der Gewebe bedingen. Das spricht dafür, dass der Neuerwerb der Erbvoraussetzungen für die Gallenbildung beim Insekt liegt. Das Gallinsekt parasitiert also in komplizierter Weise auf der Wirtspflanze. Man kann diesen Erwerb der Fähigkeit einer Gallenbildung ebenso wenig „fremddienlich“ nennen wie den Besitz von Laubblättern bei der Buche und der Eiche, weil diese Blätter von einem Maikäfer gefressen werden.

Das ist wirklich stark – es bringt uns aber nicht weiter, sondern wirft die Diskussion zurück hinter den bereits erkannten Stand der Fakten. Dass die Eichen die Blätter extra für den Maikäfer wachsen ließen, hat niemals irgendwer behauptet, und dass sie für die Eichen selbst ohne Nutzen wären, kann selbst der blutigste biologische Laie nicht meinen.

Gallenbildung aber ist – so unbestritten ihr enormer Nutzen für die Gallinsekten ist – nun einmal für die Eiche selbst völlig nutzlos (eher schon lästig), was wiederum kaum jemand bestreiten wird. Zimmermann hat also das eigentliche Problem, das ja gerade in diesem tierischen „Neuerwerb“ von Erbvoraussetzungen liegt, und dazu in der pflanzlichen Fähigkeit zur Gallenbildung, keineswegs erklärt und offensichtlich nicht einmal nicht richtig erkannt. Das aber ist das Schlimmste, was in der Kausalforschung gegenüber der Erscheinung, zu deren Erklärung sie aufgerufen ist, geschehen kann.[168]

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[168] W.-E. L.: Darauf folgen noch einige Hinweise auf das Phänomen des „Überparasitismus“ und ein Statemenent, dass diese Besonderheit weder mit dem Darwinismus noch mit dem Vitalismus zu erklären sei.

Above: Galls of gall wasp *Pediastris aceris* on *Acer pseudoplatanus* on the lower sides of the leaves (28 August 2017). Below: Leaves of *Acer pseudoplatanus*: Every single dot on the upper side of the leaves shows a scar due to the actions of a gall growing, or which had grown, on the underside of the blades (4 September 2017). Photos W.-E-L.

To illustrate the point mentioned on the previous page that every single dot on the upper side of the leaves shows a scar due to the actions of a gall growing, or which had grown, on the underside of the blades. Again: Galls of gall wasp *Pediastris aceris* on *Acer pseudoplatanus*. 28 August 2017. Photos by W.-E.L.

Lower side of leaf with galls.

Just a few new and some older books on plant galls and their insects

Bellmann, H. (2017): Geheinmisvolle Pflanzengallen. 2. Auflage. Quelle & Meyer Verlag Wiebelsheim.

Blanche, R. (2012): Life in a Gall. The Biology and Ecology of Insects that Live in Plant Galls. Csiro Publishing. 150 Oxford Street, Collingwood, VIC 3066, Australia.

Chinery, M. (2011): Britain's Plant Galls: A Photographic Guide. Princeton University Press, Princeton.

Darlington, A. (1968): The Pocket Encyclopedia of Plant Galls. Blandeford Press, London.

Fernandes, G. W. and Santos, J. C. (Eds.) (2014): Neotropical Insect Galls. Springer. Dordrecht, Heidelberg, New York, London.

Gagne, R. J. (1989): The Plant-Feeding Gall Midges of North America. Comstock Pub Assoc. Cornell University Press. Ithaca, New York.

Grosscurt, A. (2017): Plantengallen (in Dutch). KNNV Publishing. Zeist, The Netherlands.

Küster, E. (1911): Die Gallen der Pflanzen. Ein Lehrbuch für Botaniker und Entomologen. Hirzel, Leipzig.

Porter, E. (1940): Plant Galls and Gall Makers. Constable and Co Limited, London.

Randolph, S. (2005): The Natural History of The Natural History of the Rose Bedeguar Gall and Its Insect Community. British Plant Gall Society. http://www.britishplantgallsociety.org/

Redfern, M. (2011): Plant Galls. Collins Publishers, London.

Roß (Ross), H. (1932). Praktikum der Gallenkunde “Cecidologie”. Springer, Berlin.

Russo, R. A.: Field Guide to Plant Galls of California and Other Western States (California Natural History Guides). University of California Press. Berkeley.

Swanton, E. W. (2013): British Plant Galls. Nobel Press. (Originally published before 1912). United Kingdom (no city mentioned).

Several photos of gall insects: http://aramel.free.fr/INSECTES40bis.shtml

For some articles in French, see https://fr.wikipedia.org/wiki/Galle_(botanique)

Left: W.-E.L.at work on the article about plant galls (29 August 2017). In the background in red box: twigs of *Acer pseudoplatanus* infested by galls of *Pediastris aceris* (photo [not retouched]: S. Lönnig). Right: Gall of *Cynips longiventris* on *Quercus robur* (photo W.-E.L.: 28 August 2017).

Postscript

(a) Plant galls and the fossil record[169]

As pointed out above (p. 10), in contrast to the plants often providing complex housing/accommodation including protection (against natural enemies and environmental stresses) and copious nutrition by the formation of galls (often constituting entirely new organs), *in more than 99% of all galling species, the animals are not only doing absolutely nothing for their hosts, but – as was documented above – rather damage, harm and hurt them*.

Now, these features/characteristics have also been established for past ages by many careful studies of the fossil record.

This postscript consists of only a few quotations for the reader – who is invited to check the data himself – to take a glimse on galling insects and plant galls during earth history:

D. V. Vasilenko (2005): *Damages on Mesozoic Plants from the Transbaikalian Locality Chernovskie Ko* [see link to full paper below][170]

Brief explanatory note by W.-E.L.: When speaking of "the explosive nature of coevolutionary processes" (referring, for instance, to Cretaceous deposits), this means that the unexpectedly abrupt appearance of the angiosperms (Darwin's often cited "abominable mystery") in Cretaceous formations may often also be accompanied by an equally abrupt appearance of new plant galls.

> (P. 628) "Wilf and Labandeira suggested a **classification of plant damages** that incorporates four main types of damages, i.e., traces of external feeding, **galls**, mines, and traces of piercing and sucking."
>
> (P. 631) "In a paper on fossil mangrove assemblages from Cretaceous deposits of Israel, Krassilov et al., 2004 provide data on the significance of cecidogenesis as a factor in plant morphogenesis, reaching conclusions on the **explosive nature of coevolutionary processes** with regard to the creation of new biotic communities (Krassilov et al. 2004). It is already clear at this stage of studying **phytopathological processes** that **cecidogenesis** involves mechanisms that are not restricted to simple growth of tissues to isolate a parasite, **but acts at a deeper, probably genetic, level**.[171]
> Fossil galls are known from Carboniferous, Triassic and, to a lesser degree, from Jurassic and Cretaceous deposits; however, they reached their maximum diversity in the Cenozoic."

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[169] 14 September 2017

[170] https://www.researchgate.net/profile/Dmitry_Vassilenko/publication/238795502_Damages_on_Mesozoic_Plants_from_the_Transbaikalian_Locality_Chernovskie_Kopi/links/00463526e6859398a7000000.pdf

[171] The present state oft he art has been summed up by Richardson et al. (2017, p. 204): "Gall formation is a complex and close interaction between the insect and the host plant resulting from molecular cross-talk between two independent genomes. The inducer manipulates the host plant signaling by injecting effectors (small molecules that alter host cell structure and function and modulate plant response) into the wound while initiating interaction with the host (during feeding and/or oviposition depending on insect species) to redirect normal plant development (Chen et al. 2010; Hogenhout and Bos 2011; Giron et al. 2015). The chemical identity and mode of action of the inducing compounds in these secretions, and the plant developmental pathways that they affect, remain unclear (Giron et al. 2015). Unlike the host genetic transformation used by *Agrobacterium tumefaciens* to cause crown gall on plants, insect galls are not thought to involve host genetic transformation because insect gall development stops if the insect is removed. Diverse chemical signals have been proposed in insect gall systems, including phytohormones (especially plant growth factors: auxins and/or cytokinins) (Cornell 1983; Shorthouse and Rohfritsch 1992; Suzuki et al. 2014; Tooker and Helms 2014), amino acids (Stone and Schönrogge 2003), proteins (Higton and Mabberly 1994), mutualistic viruses (Cornell 1983), or bacterial symbionts (Yamaguchi et al. 2012). Whatever their nature, these chemical signals generate galls with morphological phenotypes characteristic of each inducing species (Rohfritsch 1992; Williams 1994; Crespi and Worobey 1998; Stone and Schönrogge 2003). See the entire article here: https://link.springer.com/article/10.1007/s00709-015-0937-8

V. A. Krassilov (2008): *Mines and galls on fossil leaves from the Late Cretaceous of southern Negev, Israel* [see full article in the link below][172]

(P. 13) "The recently described Late Cretaceous (Turonian) flora of Israel contains 46 species of angiosperms. Traces of galling and mining activity are exceptionally abundant and well-preserved. In a collection of more than 1000 specimens of terrestrial and aquatic angiosperms, almost all the leaves were affected. The mines consist of several morphological types, showing varying degrees of specialisation with respect to leaf histology. Some are readily identified with modern mine types; others may represent extinct types. Characters potentially useful for morphological classification of fossil mines are discussed and illustrated. ***Exuvial remains attributable to cecidomyiian dipterans suggest pupation in the gall, an advanced feature of this group***. These findings are evidence of rapid evolution of mining and galling habits during the rise of early angiosperm-dominated communities."

(P. 13) "Traces of mining and galling activity are exceptionally abundant and well preserved. In the collection of more than 1000 specimens of terrestrial and aquatic angiosperms, **almost all the leaves are affected**. The material is preserved as subcrustations or mineral films deposited beneath the cuticle, especially for epidermal mines, which are therefore even more conspicuous than in fresh leaves."

(Pp. 17/19) "Galls are often found on the same leaves as mines. For example, Dewalquea gerofitica is **infested with conical acuminate galls** about 3 mm long, rather evenly spaced along the thickened margin and scattered between the lateral veins. These galls are sometimes so dense that the leaf blade is scarcely exposed at all (Figs 3A, 3B). The galls protrude from the upper leaf surface, opening on to the lower surface, with a disk of thickened epidermal tissue around a circular hole. An imprint of a larva preserved among the galls (arrow in Fig. 6A) shows the posterior end with five abdominal segments, while the anterior part is immersed in the growing gall."

(P. 21) "Galls are known since the Late Carboniferous (Van Amerom 1973; Labandeira & Phillips 2002), but advanced galling habits are commonly held to appear through gradual co-evolution of gall-inducing arthropods and angiosperms during the Tertiary (Ananthakrishnan 1984). **Fossil evidence is inconsistent with this latter hypothesis**."

P. Wilf (2008): *Insect-damaged fossil leaves record food web response to ancient climate change and extinction* [see again full article in the link below][173]

(P. 486) "Uniquely in the fossil record, foliage with well-preserved insect damage offers abundant and diverse information both about producers and about ecological and sometimes taxonomic groups of consumers."

(P. 487) "…The paleobotanical record offers a bright spot in this challenging landscape because bulk assemblages of fossil plant organs frequently bear diverse and well-preserved tissue damage that is diagnostic of insect herbivores."

(P. 491) "….Faced with the need to quantify insect-damage diversity in fossils, Wilf & Labandeira (1999) inspected a set of > 10^4 compressed plant fossils from the late Paleocene and early Eocene of southwestern Wyoming (Wilf, 2000) and delineated 41 reproducible, countable, discrete morphologies of insect damage, termed damage types (DTs; Fig. 1). The DTs were assigned to functional feeding group categories and also assigned to a crude index of host specificity, as known from the extant insects that generally make the DT, with values of 1 for polyphagous, 3 for monophagous or oligophagous, and 2 for intermediate. As many more fossil floras were studied, the number of DTs recognized, still only a small fraction of those present in nature today, rose rapidly to more than 150 to date. The DTs have been illustrated in a series of publications, most notably Labandeira (2002) and Labandeira *et al.* (2002a), and recently exemplary voucher specimens of each DT, along with descriptions, have been compiled in an illustrated guide that is available and continuously updated on the Web (Labandeira *et al.*, 2007b). **An earlier damage type system restricted to fossil galls** was presented by Scott *et al.* (1995). Reliable criteria for distinguishing insect damage from mechanical abrasion and other types of degradation are summarized elsewhere (Labandeira, 2006)."

(P. 496) "….The fact that **nearly all insect families present in the Late Cretaceous are still with us today** (Labandeira & Sepkoski, 1993) is used to argue that insects did not suffer a significant K-T extinction (Grimaldi & Engel, 2005)." [But the situation is more complicated.]

[172] https://www.researchgate.net/publication/228495524_Mines_and_galls_on_fossil_leaves_from_the_Late_Cretaceous_of_southern_Negev_Israel
[173] http://onlinelibrary.wiley.com/doi/10.1111/j.1469-8137.2008.02395.x/full

Labandeira (2006): *The Four Phases of Plant-Arthropod Associations in Deep Time* [see link below][174]

(P. 423) "The Dakota Formation probably has in excess of 300 species of vascular plants (Wang 2002) and many remain undescribed. Plant-insect associations from this important deposit have only recently been investigated (Stephenson, 1991; Scott et al., 1994; Labandeira et al., 1994; Labandeira, 1998b), ***but contain the earliest occurrences of*** leaf mines and among ***the earliest galls and external foliage feeding of any early angiosperm flora.*** There are virtually no insect body fossils."

Sidney Ash (1996): *Evidence of arthropod-plant interactions in the Upper Triassic of the southwestern United States*[175]

(P. 237) "Gall-like swellings are found on the leaves of *Dechellyia gormanii* Ash, another gymnosperm fossil of uncertain relationships. The swellings are well defined, round to deltoid in outline, and bulbous. Typically, only one such swelling occurs on a leaf. **Leaves that have these swellings are often distorted or terminate abruptly at the disturbance, particularly if the structure extends over the edge of the leaf**. ***The swellings resemble galls induced on leaves of certain modern plants*** by eriophyid mites and apparently are either prosoplasmatic histioid pit galls or pouch galls."

Diéguez et al: (1996): Fossil galls (zoocecids) from the Upper Miocene of La Cerdaña (Lérida, Spain)[176]

(P. 329) "Upper Miocene strata of the La Cerdaña basin, Spain, have provided diverse flora of leaf remains assignable to the Magnoliidae, Hamamelididae, Dilleniidae, Rosidae and the Asteridae. Thirteen different types of fossil galls were identified on representatives of all these subclasses except for the Asteridae. The galls are two-dimensional impressions on the leaves and can be attributed to the following gall-inducing arthropods based on their similarity with modern galls: Acari, Eriophyoidea—*Aceria nervisequa* on *Fagus gussonii*, *Eriophyies vilarrubiae* on *Quercus drymeja*, *Artacris macrorhynchus* on *Acer pyrenaicum*, an undetermined species on *Persea*, *Zelkova zelkovaefolia* and *Acer pyrenaicum*; Diptera, Cecidomyiidae—*Mikiola pontensis* on *Fagus pristina*, *Contarinia*? on *Quercus drymeja*; Hymenoptera, Cynipidae—*Neuroterus* sp. on *Quercus hispanica*.

The fossil gall collection studied here from La Cerdaña, Spain, confirms that an arthropod gall-inducing fauna was already well established in the Miocene. Gall-inducer interaction is reported for the first time for all the fossil plants mentioned. The host plant record for two cecidogenous taxa is expanded, and two taxa of parasitized plants as well as two new plant/animal associations are mentioned for the first time.

Schmidt et al. (2012): *Arthropods in amber from the Triassic Period* [177]

(P. 14796) "The occurrence of arthropods in amber exclusively from the Cretaceous and Cenozoic is widely regarded to be a result of the production and preservation of large amounts of tree resin beginning ca. 130 million years (Ma) ago. Abundant 230 million-year-old amber from the Late Triassic (Carnian) of northeastern Italy has previously yielded myriad microorganisms, but we report here that it also preserves arthropods some 100 Ma older than the earliest prior records in amber. The Triassic specimens are a nematoceran fly (Diptera) and two disparate species of mites, Triasacarus fedelei gen. et sp. nov., and Ampezzoa triassica gen. et sp. nov. These mites are the oldest definitive fossils of a group, the Eriophyoidea, which includes the gall mites and comprises at least 3,500 Recent species, 97% of which feed on angiosperms and represents one of the most specialized lineages of phytophagous arthropods. **Antiquity of the gall mites in much their extant form was unexpected, particularly with the Triassic species already having many of their present-day features** (such as only two pairs of legs); further, it establishes conifer feeding as an ancestral trait."

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[174] http://www.redalyc.org/html/505/50540401/
[175] http://onlinelibrary.wiley.com/doi/10.1111/j.1502-3931.1996.tb01657.x/full
[176] http://www.sciencedirect.com/science/article/pii/S0034666796000048
[177] http://www.pnas.org/content/109/37/14796

How is such an enormous morphological stasis (constancy) generally displayed by living fossils (and also be found in and thus ascertained for many galling insects and their plant galls) possible?

John C. Sanford (2014, pp. 140/141) may have pointed out to one important key to answer that question, speaking of poly-functional and poly-constrained DNA as follows (italics by J. C. S.):[178]

> "Most DNA sequences are *poly-functional* and so must also be *poly-constrained*. This means that DNA sequences have meaning on several different levels (poly-functional) and each level of meaning limits possible future change (poly-constrained). For example, imagine a sentence which has a very specific message in its normal form but with an equally coherent message when read backwards. Now let's suppose that it also has a third message when reading every other letter, and a forth message when a simple encryption program is used to translate it. Such a message would be poly-functional and poly-constrained. We know that misspellings in normal sentence will not normally improve the message, but at least this would be *possible*. However, a poly-constrained message is fascinating, in that it cannot realistically be improved. It can really *only* degenerate. Any misspellings which might possibly improve the normal sentence form will be disruptive to the other levels of information. *Any change at all* will diminish total information with nearly absolute certainty. My colleagues and I have demonstrated this mathematically in a recent paper (Montanez et al., 2013).
>
> There is abundant evidence that most DNA sequences are poly-functional, and are therefore poly-constrained."

(b) Explanatory note on the term "parasite"[179]

In the present article most authors (including my humble self) have spoken of the galling insects, and further animals involved in the production of plant galls, as "parasites" in the sense of "*An organism that lives and feeds on or in an organism of a different species and causes harm to its host*." Or, transferring the meaning from the human sphere to these animals "*One who habitually takes advantage of the generosity of others without making any useful return*"[180] – thus, as mentioned above, the gallers "are indubitably real, perfect and true parasites (ecto- and endoparasites)."

However, the ensuing text, transcending the current possibilities and limits of science, which was nevertheless accepted by many of the greatest scientific minds who ever lived on earth ***including most of the brilliant and ingenious founders of modern science***, like Galileo Galilei (1564-1641), Johannes Kepler (1571-1630), Isaac Newton (1642-1726), Carl von Linné 1707-1778), Georges Cuvier (1769-1832), Michael Faraday (1791-1867), Karl Ernst von Baer (1792-1876), Louis Agassiz (1807-1873), Gregor Mendel (1822-1884), Louis Pasteur (1822-1895), James Clark Maxwell (1831-1879), and many others, may add a **new dimension** to this definition concerning the meaning and purpose of plants:

> "Then God said: "Here I have given to you every seed-bearing plant that is on the entire earth and every tree with seed-bearing fruit. Let them serve as food for you. And to every wild animal of the earth and to every flying creature of the heavens and to everything moving on the earth in which there is life,

[178] Genetic Entropy (Forth Edition 2014, pp. 140/141)
[179] Addition 9 September 2017
[180] http://www.thefreedictionary.com/parasite

> I have given all green vegetation for food." And it was so. After that God saw everything he had made, and look! it was very good. And there was evening and there was morning, a sixth day" (Genesis 1:29-31).[181]

"Food: Everything we [and the animals] eat comes directly or indirectly from plants. Throughout human history, approximately 7,000 different plant species have been used as food by people."[182] – The different plant species used by animals not counted.

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[181] NWT 2013
[182] http://www.bgci.org/plantconservationday/whyplantsimportant/