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DR. CASTLE AND THE DZIERZON THEORY.

IN a recent number of *SCIENCE* (March 4, 1904), Dr. W. E. Castle offers some criticism of my paper entitled 'The Origin of Female and Worker Ants from the Eggs of Parthenogenetic Workers,' published in the same journal December 25, 1903. My paper was written for the purpose of calling attention to certain observations which go to show that worker ants can produce worker offspring, probably from unfertilized eggs. I indicated the possible bearings of such observations on current theories of sex, instinct and natural selection. Incidentally, I protested against the wording of the Dzierzon theory in such terms as to preclude further investigation of certain phenomena covered by it, against a premature extension of the theory to groups of social insects less perfectly known than the bees, and against its use in bolstering up other hypotheses.

Castle pleads guilty to having used terms like 'invariably' in formulating the Dzierzon theory, but tries to evade the point by remarking that 'it scarcely requires explicit statement here that *all* conclusions of inductive science must be so qualified,' that is, by using such expressions as 'so far as observed' instead of 'invariably,' 'always,' etc. It is difficult to see what Castle gains by this statement unless he wishes to imply that all the conclusions of inductive science are on the same dead level of probability—Dzierzon's theory, the circulation of the blood, the etiology of cancer, the rotation of the earth and what not.

After virtually admitting that I was justified in objecting to his formulation of the Dzierzon theory, Castle feels called upon to present the arguments in favor of that theory, all of which are well known to every tyro in zoology. The remarks prefacing Castle's disquisition show that he regards the Dzierzon theory as sufficiently and satisfactorily established, and any expression of doubt concerning some of its implications as certainly useless and possibly heretical or even malicious. He desires to 'join issue' with me 'sharply.' Although I am by no means opposed to the Dzierzon theory, I accept the challenge, both because I do not wish to disappoint Castle and because his presentation of my views amounts almost to misrepresentation.

Since its promulgation more than half a century ago, there has never been a time when the Dzierzon theory lacked opponents, both among the bee-keepers and among zoologists and physiologists. That this is still the case is shown by von Buttel-Reepen's renewed defense of the theory within the past two months, that is, since my paper was published.\* Of course, such opposition by no means proves that the theory is false, but it shows very clearly, nevertheless, that the phenomena to be explained must be extremely complicated and difficult of observation. And no one who has studied bees or other social insects can doubt the truth of this statement for a moment. Our knowledge of many of the honey-bee's habits, so unique among animals, is based on inferences often very remote and derived from conditions difficult to control; and hence, from a strictly scientific standpoint, more or less insecure. It is impossible to observe these or any other social insects without a sense of powerlessness to ascertain

\* "Entstehen die Drohnen aus befruchteten Eiern?" *Bienenwirthschaft: Centralbl.*, No. 3, ff., 1904, 28 pp.

just what is taking place in the life of the colony. We see the insects feeding and rearing their broods and regulating the number and character of the personnel of their colonies with a sure instinct analogous to the regenerative and regulatory phenomena manifested by the tissues of the individual organism, but all this takes place as if it were behind a veil. When we are still so profoundly ignorant of the exact way in which these wonderful creatures bring about the differences between the queen and the worker, that is, between two forms of the same sex, is it at all likely that we can pose as knowing how the sexes themselves are differentiated? And even if we accept the Dzierzon theory for the bees, are we justified in transferring it to other insects of which our knowledge is still less satisfactory? Even so confirmed an advocate of the Dzierzon theory as von Buttel-Reepen regards such an extension as inadmissible at the present time.\*

Leuckart long ago stated that complete proof of the Dzierzon theory would be forthcoming only when we should have an accurate knowledge of the bee's egg. There are some, like Castle and von Buttel-Reepen, who believe that this knowledge has been supplied by the recent Freiburg researches carried out by Petrunkevitch.† Knowing from experience the extreme difficulty of interpretation and the possibilities of error involved in a study of the polar bodies of the insect egg, I venture to dissent from this view and to re-

\* 'Die stammesgeschichtliche Entstehung des Bienenstaates,' etc., Leipzig, Georg Thieme, 1903, pp. xii, 1-138, 20 figs.

† 'Die Richtungskörper und ihr Schicksal im befruchteten und unbefruchteten Bienen- und Drohnenei,' Inauguraldissertation, *Zool. Jahrb. Abth. f. Anat. u. Ont.*, 14. Bd., 4. Heft, 1901; 'Das Schicksal der Richtungskörper im Drohnenei,' Habilitationsschrift., *Zool. Jahrb. Abth. f. Anat. u. Ont.*, 17. Bd., 3. Heft, 1902.

gard the knowledge to which Leuckart referred as still in the lap of the gods. In support of this statement, I may briefly discuss one aspect of Petrunkevitch's work, his contention that the reproductive organs of the drone develop from the second polar body of the egg. This fantastical conception, for which not a particle of evidence had ever been furnished by any animal, was suggested as a laboratory hypothesis by Weismann 'mit aller Reserve' to Petrunkevitch while the latter was still working on his dissertation. The suggestion bore fruit in the 'Habilitationsschrift' as a truly miraculous example of Weismann's powers of prophesy. But to any one who is at all familiar with the developmental stages under discussion, Petrunkevitch's figures suggest anything but what he attempts to prove. Even in his first paper there is no satisfactory evidence to show that the cells regarded as derivatives of the polar bodies in the figures on plate 4 are really such, and not dividing cleavage cells or possibly vitellophags. These stages are all separated by a great gap from those represented on plate 3. When we take up the second paper we wonder how anybody could regard the figures there presented as even an adumbration of proof that the testes of the drone are developed from the polar bodies. There is, in fact, every reason to suppose that what Petrunkevitch calls 'Zellen, aus dem Richtungsopulationskern entstanden' in his Figs. 1, 2 and 3, are vitellophags with altered nuclei, such as are often seen in the yolk of fertilized insect eggs (*Doryphora*, e. g.) coexisting with healthier vitellophags provided with more rotund nuclei. When we come to the polar body derivatives in his Figs. 3, 5, 6, 7 and 8, we recognize the well-known 'dorsal organ,' or remains of the serosa aggregating and preparing to pass into the yolk. Between these stages and that of his Fig. 10 with nearly completed mesenteron (which he

derives from the mesoderm [*sic!*]) there is another big gap, and so far as the figures go, no demonstrable connection to show that the testes are really derived from such an absurdly improbable source as the 'dorsal organ,' to say nothing of the polar bodies. The only figures in Petrunkevitch's paper showing unquestionable rudiments of the reproductive organs are Figs. 14, 15, 17, 18, 19 and 20, and in all of these the organs are depicted in the relatively late stages of development that have been figured repeatedly by other authors. Then note the startling migrations described for the drone's testes and their antecedent cells! The second polar body is at first on the anterior cephalic surface of the egg. The cell derivatives leave this surface and divide into two groups which migrate to the dorsocephalic region and there reunite. The mass thus formed then proceeds caudally along the mid-dorsal line just beneath the blastoderm till it enters the abdominal region, where it breaks up into cells, which migrate ventrally on either side as far as the mesoblastic somites, become entangled with these and are again carried dorsally to the position of the definitive testes. Was ever organ more bedeviled in its development? And what shall we say of the 'critical caution' not only of taking work of this kind seriously, but of using it for propping up at one of its weakest points a complicated theory of sex?\* And

\* I allude to that salmagundi (*Bull. Mus. Comp. Zool.*, Vol. XL, No. 4) in which the *dissecta membra* of certain Darwinian, Weismannian and Mendelian theories concerning three such intricate subjects as heredity, sex and parthenogenesis, are stirred to the point of turbidity, garnished with a few accessory hypotheses, and served up in a pamphlet of thirty pages. As if such messes could be either palatable or digestible! Morgan has presented an excellent criticism of this theory ('Recent Theories in Regard to the Determina-

if such work on the origin of the drone's testes can be made the basis of a 'Habilitationsschrift,' how implicit should be our faith in the same author's 'Inauguraldissertation'?

Having, as he supposes, established the Dzierzon theory beyond cavil, so far as it deals with the honey-bee, Castle next proceeds to consider the ants, after the fashion of the typical laboratory zoologist whose motto is 'all species look alike to me.' He finds it necessary to admonish me for deeming it 'even a probability' that workers may develop from the unfertilized eggs of workers. Had he taken the pains to read the observations of Reichenbach and Mrs. Comstock with care, or better still, had he acquired a first-hand acquaintance with the two insects mentioned by those authors, namely *Anergates atratulus* and *Lasius niger*, he would have seen that his criticism is really as feeble as it is captious. A more careful writer would have observed that Reichenbach is not a myrmecologist and that his remarks on *Anergates*, etc., were cited mainly on account of their psychological interest as showing the flurry into which a man is thrown on discovering a fact that conflicts with some formidable theory. *Anergates atratulus* is a rare, monotypic, parasitic ant, which has lost its worker caste and has wingless, pupa-like males. Obviously, in such a species there can be no nuptial flight, and mating would naturally take place in the nest. Since the worker caste is non-existent, Reichenbach's, and hence also Castle's, reference to this species, is really irrelevant. In regard to *Lasius niger* Castle asks: "Is there tion of Sex,' *Pop. Sci. Month.*, December, 1903). It turns out to be merely another case of the old fallacy of juggling the phenomenon to be explained—in this case, sex—back into the germ-cells and then pulling it out again à la Little Jack Horner, with the naïve assurance of having contributed something 'new' to science.

any reason for supposing that the ants captured [by Mrs. Comstock] had not previously been with males? \* \* \* May we not reasonably exercise some 'critical caution' before with Wheeler we conclude it probable 'that worker ants can really produce other workers or even queens parthenogenetically'?" It is clear, in the first place, that Castle is himself not only lacking in 'critical caution,' but in consistency, when he asks such questions. Since he accepts the Dzierzon theory and proceeds to extend it to ants, he has no right to change the theory during the transfer. All adherents of this theory would agree in pronouncing fertilization of worker bees by drones an impossibility. They would contend that this had never been seen. Hence if the Dzierzon theory is to be extended to ants we should consistently make the same assumption. Nor would this be merely an assumption. All observations—in this case far more easily controlled than in the bees—go to show that worker ants do not mate with males. The case for *Lasius niger* is even stronger than in the bees on other grounds also. In this ant the differences in size and structure, both in the reproductive organs and in the soma, are vastly greater between the female and worker than they are between the queen and worker bee. No one, to my knowledge, has ever seen even a receptaculum seminis in a worker *Lasius*, though a very distinct vestige of this structure is present in the worker bee.\* But

\* Castle's familiarity with the conditions in the bee is well illustrated by his remark that 'dissections of egg-laying workers, which were made by Leuckart, revealed no seminal receptacle, hence the eggs of such animals can not have been fertilized.' The existence in worker bees both of a vestigial receptaculum and of accessory glands was pointed out by von Siebold more than sixty years ago. Moreover, Leuckart, as he later admitted, overlooked the receptacle in the dissections al-

even if the receptaculum were present, there is no reason to suppose that it would function any more than it does in the worker bee. This would have to be admitted, however, if we are to interpret Reichenbach's and Mrs. Comstock's observations in accordance with Castle's preconceived notions, for it is clear that in the case of the Reichenbach colony months must have elapsed between the death of the males each year and the laying of the eggs, and Mrs. Comstock mentions the rearing of 'at least three complete broods' of workers in the absence of males. From what we know of other ants we could hardly suppose a *Lasius* worker to function as Castle imagines possible unless it were either a true or an ergatoid queen. But no one has ever seen an ergatoid female *Lasius niger* though this insect is not only the most abundant of ants but the most abundant of animals over a large portion of Europe and North America. In this country it occurs in innumerable colonies from an altitude of 10,000 feet in the Rocky Mountains to the sands of the Atlantic seashore. I have myself collected and examined thousands of these ants without ever seeing anything that even approached an ergatoid female. Is it probable then that two lots of ants collected at random, like those of Reichenbach and Mrs. Comstock, should both contain fertilized ergatoid females indistinguishable externally from normal workers, especially when we consider the remarkable propensity of the workers of this and many other Formicidæ for laying unfertilized eggs? Which, then, is the more probable interpretation of Reichenbach's and Mrs. Comstock's observa-

luded to by Castle. A glance at the well-known Leuckart and Nitsche chart of the honey-bee, which can hardly be lacking in the Harvard laboratory, would have shown Castle a by no means insignificant receptacle in both the sterile and the egg-laying worker.



tions? Assuredly that which I advanced in my former paper.

Since the publication of my paper Professor Forel has sent me a short article,\* from which I take the following paragraph:

Zur Erklärung des Polymorphismus der Ameisen hat man zunächst die Analogie der Bienen herbeigezogen, welche im Stande sind, in den ersten Larvaltagen, durch veränderte Ernährung und Vergrösserung der Zelle eine Arbeiterlarve in eine Weibchenlarve umzuwandeln. Ferner hat man nach Siebold stets angenommen, dass die Männchen aus unbefruchteten Eiern, die Weibchen und Arbeiter dagegen aus befruchteten Eiern stammen. Letzere Thatsache schien auch bei den Ameisen zu stimmen, indem ich selbst and dann auch Andere stets Männchen aus unbefruchteten Arbeiteriern erzogen hatten. *Doch haben die neuesten Untersuchungen Reichenbach's klipp und klar den Nachweis geliefert, dass aus unbefruchteten Arbeiteriern von Lasius niger Fabr. wiederum Arbeiter entstehen. Also wieder ein Dogma verfrühter Verallgemeinerung, dass in Nichts zerfliesst!* †

Surely I may be permitted to express as a probability what the most eminent myrmecologist states in such emphatic language. That I was well aware of the remote possibilities mentioned by Castle, and of others which he does not seem to have surmised, is clear from my express statement that the observations of Tanner, Reichenbach and Mrs. Comstock are 'by no means final.' It would have been natural for a less captious critic to suppose that the views advanced in my paper were not determined solely by the observations cited from other authors, but to some extent by my own experiences, which though less tangible and less readily formulated at the present

\* Ueber Polymorphismus und Variation bei den Ameisen, *Zool. Jahrb. Suppl. (Weismann's Festschrift)*, VII., 1904.

† The italics are mine.

time, are not less suggestive to me of the trend of future investigation.

Academic convictions like those advanced by Castle can be of service only in prejudging a field of inquiry; they can be of no imaginable use in stimulating or furthering research except indirectly through the spirit of contradiction aroused by their dogmatic character. If Castle had any new facts, or original interpretations of old facts, for that matter, to bring to bear on the problems under discussion, I should be the first to welcome them. We need something more, however, than mere discussions of possibility and probability, if we are ever to dispel the mystery that envelops many of the instincts and reproductive processes in the social hymenoptera.

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