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ON THE LAW OF IRREVERSIBLE EVOLUTION

BY

BRANISLAV PETRONIEVICS, PH. D.

FROM THE SMITHSONIAN REPORT FOR 1918, PAGES 429-440

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ON THE LAW OF IRREVERSIBLE EVOLUTION.¹

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Louis Dollo, the great Belgian paleontologist, first publicly formulated in 1893 (Dollo, 4) his famous law of irreversible evolution, one of the most important laws of the evolution of organized beings.² This law has often been debated and applied, but I do not know that anyone has attempted to set it forth, basing his exposition on Dollo's own works. This is what I propose to do here, adding to my account some critical remarks on the value of the law in question.

The law of irreversible evolution was stated by Dollo as follows:

An organism can not return even in part to a previous condition already passed through [déjà réalisé] in the series of its ancestors. (Dollo, 4 p. 165.)³

It is usually supposed that the law thus expressed applies only to parts and organs which are reduced or eliminated; but this is not correct. The law is much wider in its application, covering functional organs as well. In order to understand more clearly the far-reaching nature of Dollo's law we must make certain distinctions in the concept of organic evolution and give some definitions of them.

Organic evolution may be, as we know, progressive, regressive, and mixed.⁴ If, during mixed evolution (which is the most wide-

¹Translated, with permission, by Gerrit S. Miller, jr., from *Science Progress*, January, 1919.

²He previously stated this law in 1892, in his *Cours autographié*, etc. (Dollo, 1), the same year in a note which appeared in the *Bulletin de la soc. belge de Géol.*, etc. (Dollo, 2) and in an article which appeared in A. Giard's *Bulletin scientifique de la France et de la Belgique* (Dollo, 3).

³Later, Dollo expressed his law with greater exactitude:

"An organism never exactly renews a previous condition, even if it finds itself placed in an environment identical with one through which it has passed. But, by virtue of the indestructibility of the past, it always retains some trace of the intermediate stages which it has traversed." Dollo 17, p. 107, and 10, p. 443.) Let us note that Dollo definitely admits the reversibility of conditions of existence: "Evolution is irreversible as regards the structure of organisms. * * *, but reversible as regards environment (Ethology)." (Dollo, 7, p. 15.)

⁴In my course of independent lectures (on universal evolution) given at the Sorbonne this year, which will later be published, I have defined evolution in general as follows: "Evolution is a thing's coming into being by successive stages of change." When each successive stage of the evolutionary process contains something more than the preceding stage, evolution is progressive; it is regressive when each successive stage contains something less than the preceding. Evolution is mixed when in an evolving whole one part evolves progressively and the other regressively.

spread type in the domain of organic evolution) progression predominates, or, to put it in another way, if the final condition reached represents progress in comparison with the initial condition, we then shall call such a mixed evolution "ascending evolution," and of this process the extreme type is represented by pure progressive evolution with or without the addition of new parts. But if, in mixed evolution, regression predominates, or, in other words, if the final condition reached is a regress in comparison with the initial condition, we shall call mixed evolution of this kind "descending evolution," pure regressive evolution evidently representing the extreme type of such a process. The foot of the horse, made of a single digit, which has come from a pentadactyle foot by the atrophy of the lateral digits and the great increase of the median digit, is the best-known example of ascending mixed evolution, while the skull of the living *Ceratodus*, in comparison with that of *Dipterus*, its probable Devonian ancestor, presents an example of descending mixed evolution.

Taking into consideration on the one hand, the definitions which we have just made, and, on the other, the examples cited beyond, which Dollo brought forward in favor of his law, we ought to separate the cases of ascending evolution from those of descending evolution, something which Dollo himself did not do. Clearly, if the structure of an organ or if the parts of an organ are lost through *descending* evolution, and if it is not possible, as is almost unanimously agreed, to replace the lost structure or parts, it does not at all follow—at least *a priori*—that a reversal of evolution would not be possible in the contrary case: that is, when the structure of an organ has been lost by the *ascending* evolution of this organ.

We should therefore replace Dollo's single law by three different laws, one of which, the first and most fundamental, will express the impossibility of a reacquisition of lost parts, the second of which will apply to the cases in which the original structure of an organ has been lost by ascending evolution, and the third to the cases in which the structure has been lost by descending evolution.

These three laws are as follows:

1. Organs and parts of organs reduced or lost through regressive evolution can not be regained by a new progressive evolution.¹
2. If the original structure of an organ has been lost through ascending evolution (with or without the addition of new parts) the original structure can not be regained:
 - (a) By the reacquisition of the lost parts, this reacquisition being impossible according to the first law.

¹For the first law, see Dollo, 7, p. 5 (lost manduclyle of *Dermochelys*), Dollo, 9, p. 139 (the atrophied pharyngeal cone of *Phlebotomus*), and Dollo, 16, remark 2, p. 100.

(b) By the regressive evolution of the new parts, the total disappearance of these parts being impossible.

(c) By the ascending evolution of these new parts in a new direction.

3. If the original structure of an organ has been lost through descending evolution (with or without the loss of parts), this original structure can not be regained:

(i) By the reacquisition and progressive evolution of the lost parts, this reacquisition being impossible according to the first law.

(ii) By the ascending evolution of the nonreduced parts in a new direction.

(iii) By the ascending evolution of altogether new parts.

II.

The various cases falling under these three laws we wish now to explain by examples found in the writings of Dollo.

For the first law examples are very numerous. The birds lost their teeth during the Cretaceous period; no subsequent bird has been able to regain these lost parts. The mandible of mammals consists of a single piece homologous with the dentary part of its reptilian ancestors; no mammal has been able to regain the lost other parts of the reptilian jaw, etc.

But the examples that especially demonstrate the validity of the first law are those in which the return to ancestral conditions would necessitate the reappearance of parts which an organism has lost. As these examples are at the same time illustrations of the two other laws we shall deal with them in connection with these laws.

The best-known example of the first alternative under the second law is the pseudo dentition of *Odontopteryx*, an Eocene fossil bird. Instead of the true teeth that have been lost, *Odontopteryx* has the margin of the beak and of the lower mandible dentate like a saw.

The most striking example of the second alternative under the second law is the pelvis of *Triceratops*. The dinosaurian ancestors of *Triceratops* had become adapted to bipedal life, and therefore were possessed of a very long and very narrow ischium and of a pubis provided with a postpubis which was similarly very long and very narrow (Dollo, 10, p. 444). In its secondary adaptation to quadrupedal life *Triceratops* was not able morphologically to regain the triardiate pelvis of its far-distant quadrupedal ancestors, for it has retained traces of the bipedal phase in the rudimentary postpubis and in the narrow, recurved ischium. That is to say, the postpubis, the new structure acquired during bipedal life, could not totally disappear, and the new form of the ischium could not disappear either (Dollo, 10, p. 446).

The most important and most obvious example of the third alternative under the second law is also found in a dinosaur, nearly related

to the preceding, *Stegosaurus*. This animal had for its immediate ancestors bipeds like the ancestors of *Triceratops*, and, like *Triceratops*, it became readapted to quadrupedal life. But while the tri-radiate pelvis of its far-away quadrupedal ancestors has been physiologically reestablished through regressive evolution (atrophy) of the postpubis and ischium in *Triceratops* (Dollo, l. c. p. 446) these parts have evolved in a new direction in *Stegosaurus*. Here the ischium becomes shortened and flattened; the postpubis does the same and moreover applies itself closely along the ventral margin of the ischium. But morphologically there is here no return to the former tri-radiate condition of the pelvis, since the ischium has kept some trace of the form which it acquired in the biped phase, and the posterior branch of the pelvis is no longer formed by the ischium alone but by the ischio-postpubic complex. While evolving in the new direction the postpubis has thus changed in function (Dollo, l. c. p. 447).

We find an illustration of the first alternative of the third law in the evolution of the arms in the Octopods. These animals in adapting themselves to bottom sea life have lost a pair of arms (the tentacular arms) possessed by their immediate ancestors the heteropod decapods. They have thus become isopods again (excepting the peculiar case of the Argonauts, and the hectocotylisation of one of its arms) like their distant ancestors the Belemnitenthids (isopod decapods) without having been able to regain the same number of arms (see Dollo, 17, pp. 415-416).¹

The best illustration for the second alternative of the third law is the foot of *Dendrolagus*, an arboreal Kangaroo. The structure of the foot in the saltatorial Macropodidae—the predominance of the fourth toe, the syndactylism of the second and third, the reduction of the fifth and the complete disappearance of the great toe—shows us that their immediate ancestors were arboreal. In *Dendrolagus*, a Macropodid which has again become arboreal, the opposable great toe, completely atrophied in its immediate ancestors the terrestrial kangaroos, was not able to reappear. But the unreduced parts of the foot have undergone an ascending evolution in a new direction. While the metatarsals and the phalanges have diminished in length, the phalanges and claws have become lengthened and the claws have at the same time become curved. Thus the foot of *Dendrolagus* has not been able to return to the structure of the foot of its distant

¹A still more convincing history would be the secondary stenogeocephaly of the cheilommia. This stenogeocephaly differs from the primary stenogeocephaly of the ancestral stenogeocephalopodophyllans in that the post-orbital, the septo-temporal, and the epiotic do not reappear in the cranial mould when once lost (see Dollo, 19, p. 59). But the secondary stenogeocephaly of the cheilommia, although very probable (see especially the account given by A. Benoit, "Revue de la place des Cheilommies dans la classification" in *Comptes rendus*, vol. 167, 1918, p. 544), is not yet beyond doubt. See Dr. M. S. Watson, *Limulocarcinus africanus*, in *Proc. Zool. Soc., London*, 1917, p. 1041.

ancestors, which possessed an opposable great toe, syndactyly of the second and third toes, dominant fourth toe, and reduced claws. (See Dollo, 6, pp. 194 and 199.)

Finally, for the third alternative of the third law we have an illustration in the secondary carapace and plastron of the turtle *Dermochelys*. The distant ancestors of this turtle were, like it, sea-turtles; its reduced primary plastron (a ring formed of four pieces) and its still more reduced primary carapace (represented by the nuchal plate alone) bear witness to the fact. When adapting themselves to littoral life the immediate ancestors of *Dermochelys* reacquired a carapace and a plastron, but this carapace and plastron are entirely new structures of superficial dermal origin. Readapting itself to marine life *Dermochelys* has preserved this carapace and plastron of its immediate ancestors, although both are already much reduced. (See Dollo, 7, pp. 9-14.)

III.

The importance of the law of irreversible evolution is multiple. In the first place, this law has a phylogenetic application, that is, it places us in position to reconstruct, with the often insufficient paleontological material which we possess, phylogenetic series which, if they are not true series are at least series which represent indubitable evolutionary stages. Its ethological application is yet more considerable. It is often the only means of determining the conditions of existence and the method of adaptation to life of fossil organisms. But sometimes this law has a morphological importance also, because by using it we can distinguish homologies from mere analogies. Finally Dollo has shown that it can act also as a guide in classification, that it therefore has a systematic application.

The most important phylogenetic application of the law was made by Dollo in the difficult question of the phylogeny of the Dipnoi. Dollo's very ingenious paper on this subject (Dollo, 5) should be considered a model presentation of the philosophic point of view in the new paleontology. Before Dollo this subject was in a truly chaotic state, one of the most eminent paleontologists having declared *Dipterus*, the oldest and most primitive type, to be the most specialized.¹ Nowhere else has the conception of the irreversibility of evolution given such brilliant results. Since this conception expresses the idea that we never fully return to an ancestral structure it can be used to determine whether a particular condition is primary or secondary. Consequently it can be used to decide upon the direction of evolution when we have a series containing a sufficient num-

¹ See A. S. Woodward, *Catalogue of the Fossil Fishes in the British Museum*, pt. 2, 1891, p. XX. But after Dollo published his important memoir Woodward accepted his conclusions. See his presidential address to the Section of Geology, in *Nature*, vol. 81, 1909, p. 292 (and Dollo, 16, rem. 2, p. 387).

ber of terms intermediate between the extremes (Dollo, 5, p. 97¹). Just such a series we possess in the paleontological series of the Dipnoi: *Dipterus valenciennesi*, *Dipterus macropterus*, *Scaumenacia*, *Phaneropleuron*, *Uronemus*, *Ctenodus*, *Ceratodus*, *Protopterus*, *Lepidosiren* (l. c., p. 88). Dollo shows that the structure of the tail as well as that of the top of the head, the squamation, the pugal plates, the opercular apparatus, the ganoin, and the ossification of the mandible, the suborbital band—all this proves that the course of evolution has been in the direction from *Dipterus* to *Ceratodus*. and not the opposite (l. c., p. 89-97). It is especially by the structure of the tail that the concept of irreversibility is illustrated. In a long and thorough treatment of the subject Dollo shows (l. c., pp. 89-97) that the diphyccercal tail of the Dipnoi (and of the other known ancient and modern fishes) is a secondary diphyccercal tail whose morphological value in the Dipnoi (the second dorsal fin, the second anal fin) is not equivalent to the morphological value of the primitive diphyccercal tail (caudal fin). In this secondary diphyccercal condition there is therefore no return to the primitive structure.

The most important other cases of phylogeny which Dollo has considered are the phylogeny of the sirenians (Dollo 3, p. 119), the phylogeny of the Leather-backed turtle (Dollo, 7, p. 9), and the phylogeny of the Holocephali (Dollo, 13, p. 107).

One of the most important cases with regard to the ethological application of the law of irreversibility is found in the memoir on the Dipnoi. If it be assumed that *Dipterus* comes from *Ceratodus*, as the latter is an adaptation to life in turbid water, it would be necessary to suppose either that *Dipterus* represents an adaptation to life in mud (excessively turbid water), or else that it represents a return to life in clear water. The first alternative being that of *Lepidosiren*, the second is the only one which remains open for discussion (Dollo, 5, p. 99). But, putting aside paleontological and purely ethological reasons, the law of irreversibility is sharply opposed to such a view.

"Would the lost ganoin return? Would the cephalic shield resolve itself into its ancestral elements? Would the suborbital band with its ossicles in varying number become once more a solid arch? Would the opercular apparatus resume its original dimensions? Would the vanished jugular plates reappear?" As all of these structures are reduced in *Ceratodus* (l. c., p. 100), *Dipterus* can only represent a primary adaptation to life in clear water, that is to say it is purely a fish ("the most pisciform of Dipnoi," l. c., p. 101).

¹ Discussing the subject of the phylogeny of the Holocephali (Dollo, 13, pp. 107-108), Dollo says: "The idea of the irreversibility of evolution, which has led me to the results that I have just demonstrated, has once more shown its usefulness. Without it one would be led to assert that specialized organisms could become primitive again and then once more specialize themselves in the same or another direction. Such an assumption, unless supported by absolutely complete paleontological series—which we are far from possessing—must destroy all possibility of discovering phylogeny, the main object of morphology."

Another important instance of the ethological application is furnished by the bipedal habits of the immediate ancestors of *Stegosaurus* and *Triceratops*.

If evolution were reversible these two dinosaurs would have exactly regained their former quadrupedal structure, and there would have been no way to distinguish their secondary quadrupedal existence from the first (Dollo, 10, p. 448).

The other most important cases of ethological application are: The secondary adaptation to the swimming sea life of the *Pycnodonts* (Dollo, 17, pp. 108-9), the secondary adaptation to the swimming sea life of the *Trilobites* *Dephon* and *Aeglina* (Dollo 16, pp. 410 and 412), etc.

Among the instances of the morphological application of the law, that of the secondary abdominal ventral fins in the teleosts has a special importance. As is known, the ventrals of teleosts may be either abdominal or thoracic or jugular. But among the abdominal ventrals we have two types—those which have no connection whatever with the pectoral girdle, and those joined to the clavicular symphysis by a ligament. As there is no reason for the presence of this ligament in situ we have to conclude that it is the degenerate remnant of a former direct connection with the pectoral girdle. In conformity with the irreversibility of evolution the ventrals in again becoming abdominal have kept the connection with the clavicular symphysis which they acquired when occupying a thoracic or jugular position (Dollo, 14, p. 139).

The other important instances of the morphological application of the law are: (1) The very anteriorly placed choanae of the sea turtles (Dollo, 8, pp. 817-820), (2) the longirostral and brevirostral condition in *Crocodylians* (Dollo, 12, p. 85), etc.

Finally, we must mention the one instance in which Dollo has used his law in systematic work—the *Ptyctodonts*. Before Dollo these fossil fishes, then known from their dental plates only, had been placed among the *Holocephali*. In his important memoir on this subject (Dollo, 13) Dollo showed that, by virtue of the law of irreversible evolution, the *Ptyctodonts* can not be regarded as *Holocephali* and that they ought to be treated as *Arthroderes*. Since then Dollo's conclusion has been wholly confirmed.

Although the empiric evidence for the validity of his law has been abundant and varied, Dollo was not satisfied with such a wholly empiric demonstration. He has attempted to give a deductive demonstration as well. He says:

The Irreversibility of Evolution is not, as many have believed it to be, merely an empiric law based purely on facts of observation. But it has deep-seated causes which carry it in final analysis to a question of probabilities, as in the case of the other laws of nature. Evolution being a summation of exactly determined individual variations in an exactly determined order, to have it reversible would be to admit the possibility of the intervention of causes exactly the inverse of those which produced and fixed the individual variations from which the first transformation arose, and in an exactly inverse

order—circumstances too complex for it to be imagined that they are ever realized. (Dollo, 19, p. 59, rem.; see also Dollo, 3, p. 127.)

And, when speaking of the impossibility of the descent of *Dipterus* from *Ceratodus* (Dollo, 5, p. 100, the passage referred to above) he says:

And let it be noted that it is here a question not of one isolated character, but of a whole group of characters, something that is much more serious so far as irreversibility is concerned * * * But it is particularly in its action on elements as multiple as these that we can affirm with certainty that evolution is not reversible (l. c. rem. 72, p. 122).

The irreversibility of evolution becomes, therefore, according to Dollo, the more probable as the number of elements increases, and it is practically a necessity when the number of elements is considerable.

IV.

Having explained the law of irreversible evolution, the various cases which it makes clear, also its applications, and its logical basis, we now wish to make some critical remarks on the various aspects of the law.

In the first place, its logical basis. The deductive demonstration of his law, attempted by Dollo, is very doubtful. As to the number of elements on which evolution acts, it is not a question of cells, but of organs and parts of organs (because it is only these last which have their peculiarities determined in the germ), and the number of these organs and parts is not relatively great even in the most complex organism. But, if we consider the much greater number of individuals in which the organs and parts of organs show individual variations, the chance that they will vary in different directions and consequently also in inverse directions becomes possible. It is only if we assert that individual variations are relatively not very numerous—predetermined—that this course of reasoning founded on pure probability becomes weak. In that case, however, the law of irreversible evolution is not the result of numerical probability, but the result of unknown internal causes of organic evolution.

There is, therefore, no logical necessity in the law of irreversible evolution, and this law remains a purely empirical rule. Let us now see how much the three laws of this evolution are confirmed by experience, and to what extent we should expect possible exceptions.

As to the first law,¹ this law appears to be without exceptions so far as it applies to lost organs and parts. For the loss of an organ or of a part having become final by the loss of the corresponding tendency in the germ, it is almost impossible to imagine the reappearance of this tendency, bearing in mind, on the one hand, the

¹ Compare the similar observations of A. Handlirsch, 24, p. 1328 (cited by Dollo, 15 rem. (2), p. 429).

difficulty of producing new tendencies in the germ by the influence of external causes, and on the other the degree of correlation that would be needed among these tendencies. When it is a question of the reduction of an organ or part, two alternatives must be distinguished. If the reduction has gone so far that the corresponding tendency in the germ is verging on complete disappearance, the reduced organ or part will find itself practically in the same condition as if it were already lost. But if their reduction has not reached to such an extreme their evolution in an inverse direction will not be impossible.

For the second law we must distinguish between the case of a single part and that of a complex organ. The regressive evolution of a single part, if during this evolution and the preceding progressive evolution no change of form has taken place, could clearly lead back to the point where the progressive evolution started. And the regressive evolution of a single part, if the corresponding arrangement in the germ is not too much enfeebled, could evidently also be followed by a new progressive evolution. But if a change of form has taken place during the first progressive evolution, and if this change of form has been so great that a change in the corresponding arrangement of the germ has been necessary, then neither the regressive evolution following the original progressive evolution will be able to lead back to the point of departure of the latter, nor will a new progressive evolution have the power to accomplish it, because to do so would necessitate the return to a disappeared condition. If, for instance, a tooth has first increased in size and afterwards diminished without change of form this tooth will be able by diminution to assume the dimensions which it had at the beginning of its increase, and a new increase of the same kind will not be impossible (if the reduction has not gone too far). But if the increase in size has been accompanied by a radical change of form, if, for instance, a conical tooth has become laterally compressed, then a return to the conical form will not be possible either during its diminution¹ or during a new increase in size.

In the case of a complex organ Dollo asserts that its return to the previous condition through the action of regressive evolution is impossible on account of the "indestructibility of the past." But if a single reduced part of an organ is regarded as the supposed reason why reversibility is impossible, we are able to affirm almost with certainty that in such a case the indestructibility of the past does not exist, because it would find itself in contradiction with the well es-

¹ This impossibility is exactly what W. D. Matthew supposes to have happened during the evolution of the *Felidae* when he supposes that the felines come from *Dinictis*, a primitive saber-toothed cat (see W. D. Matthew, "The Phylogeny of the *Felidae*," Bull. Amer. Mus. Nat. Hist., vol. 28, 1910, p. 290 s). Scott has clearly had a glimpse of the fact that this phylogeny contradicts the law of irreversible evolution (see W. B. Scott, 28, p. 540 s).

established law of the necessary regressive evolution of nonfunctional parts and organs. The reversibility of the ascending evolution of a complex organ, when it depends on a reduced part, is therefore not impossible (we can suppose, for instance, that the secondary ventrals of teleosts will return in the future to their original condition through the complete disappearance of the clavicular ligaments).

In the case of a nonreduced part, whose form has, however, changed during ascending evolution, the indestructibility of the past again does not exist in the strict sense, the nonreduced part being able to change its form again by a new progressive evolution, although the original condition of this part, and consequently the original condition of the organ in question can not be reestablished. The pelvis of *Triceratops* may be taken as an example. The postpubis of this pelvis exists in a very rudimentary condition, and as rudimentary parts tend to disappear, the postpubis certainly would have disappeared if *Triceratops* had lived long enough. It is therefore only its recurved ischium, very different in form from the ischium of its distant tetrapod ancestors, which was able to prevent *Triceratops* from recovering its original pelvis.

Finally, if there is an ascending evolution of nonreduced parts (pelvis of *Stegosaurus*) it is the change of function which saves these parts from a regressive evolution; the indestructibility of the past does not exist here either. And it is clear that the same reasoning is also applicable under the third law to the evolution of a complex organ.

To sum up: The irreversibility of the evolution of a complex organ depends entirely on the irreversibility of the evolution of the reduced or nonreduced individual parts which enter into its composition, and the second and third laws are not without exceptions in this respect any more than the first; as we have seen, it is the germinal base of the first law which underlies the entire subject.

As I said at the beginning, most naturalists know Dollo's first law only. This is only a part of his general law, although the most important and most certain part.¹ This general law, in spite of the possible exceptions, has an extraordinary importance for biological philosophy and evolutionary philosophy in general. Dollo will al-

¹ Besides the law of irreversible evolution Dollo has formulated (see Dollo, 4, p. 165) two other laws—that of discontinuous evolution (before H. de Vries) and that of limited evolution. In his subsequent writings Dollo has only rarely touched on these two other laws (on the law of limited evolution see Dollo, 7, p. 9, Dollo, 8, p. 813 and p. 820, Dollo, 9, p. 131; on the law of discontinuous evolution see Dollo, 5, rem. (66), p. 120; Dollo, 7, rem. (11), p. 9; and Dollo, 17, pp. 139-140).

ways be regarded, like Cuvier before him, as the founder of a great law of the organic world.¹

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¹ To the list of Dollo's writings on the law of irreversible evolution I am adding the titles of some other papers (most of them already cited by Dollo) whose authors have discussed or applied this law. Among these treatises the important book by O. Abel, *Grundzüge der Paläobiologie der Wirbeltiere*, 1912, deserves special mention because it contains nearly all the examples cited by Dollo and many others besides. Dollo's law is discussed, pp. 616-618.

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