DINOSAURS ADAPTED SECONDARILY FOR QUADRUPEDALISM

by

Louis DOLLO[1]
Conservator with the Royal Museum of Natural History, Brussels.

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Boards XI and XII

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I.

Introduction.

1. - In an adaptation it is necessary to carefully distinguish if one is in the presence of a primary adaptation, or if one is dealing with a secondary adaptation.

In other words, if the organism changes primarily for the first time in order to satisfy certain conditions of a determined existence, - or if, having left these conditions of existence, it returns there, after having adopted, during a more-or-less long time, another manner of living.

2. – Thus nobody today believes that, as Gegenbaur[2] thought it, *Ichthyosaurus* was derived directly from fish.

[1] Memoir presented at the meeting of October 17, 1905.
[2] C. Gegenbauer. *Über das Gliedmassenskelet der Enaliosaurier*. Jenaischer Zeitschrift. 1870. Vol. V. p. 332.
- C. Gegenbauer. *Vergleichende Anatomie der Wirbelthiere*. Leipzig, 1898. Vol. I. p. 531.

But everyone understands that one has:

Ichthyosaurs	Secondarily Aquatic Life
Terrestrial Reptiles	Primary Terrestrial Life
Fish	Primary Aquatic Life

Just as, for *Zosterae*, a marine Anthophyte:

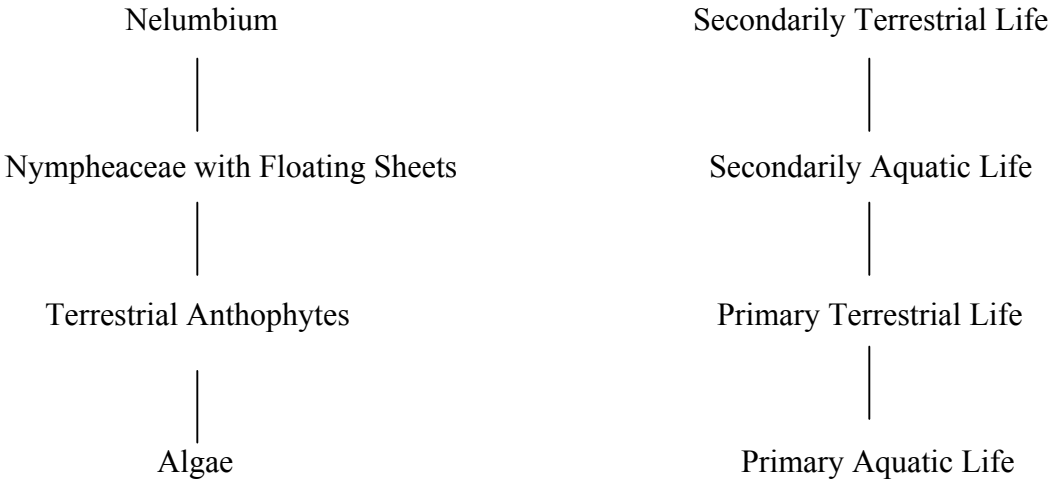
Zosterae	Secondarily Aquatic Life
Terrestrial Anthophytes	Primary Terrestrial Life
Algae	Primary Aquatic Life

3. Sometimes, one still encounters cases more complicated, like that of *Dendrolagus*, the arboreal Kangaroo[1]:

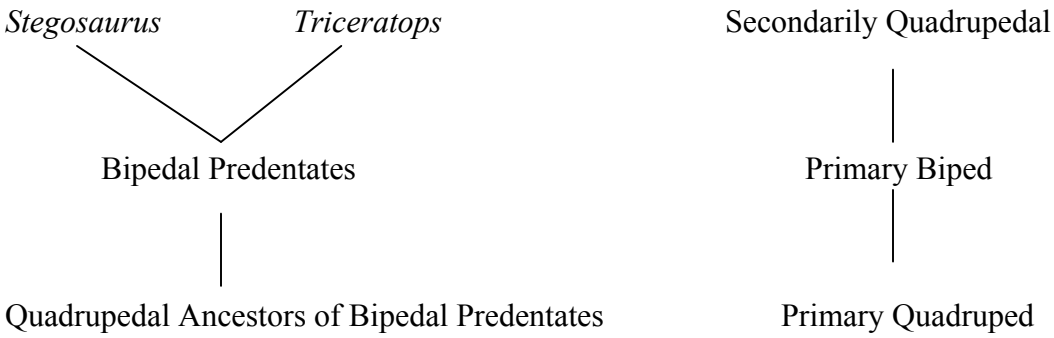
Arboreal Kangaroo	Secondarily Arboreal Life
Terrestrial Kangaroo	Secondarily Terrestrial Life
Arboreal Ancestors of Terrestrial Kangaroo	Primary Arboreal Life
Terrestrial Marsupial Ancestors	Primary Terrestrial Life

[1] L. Dollo. *Les Ancêtres des Marsupiaux étaient-ils arboricoles*?. Miscellanées Biologiques Dédiées au Professeur Alfred Giard l'Occasion du XXV[e] Anniversaire de la Fondation de la Station Zoologique de Wimereux (1874-1899). Paris, 1899.
- L. Dollo. *Le pied du Diprotodon et l'origine arboricole des Marsupiaux*. Bull. Scient. Giard. 1900. Vol. XXXIII. p.278.

Or that of the *Lotus*, Nympheaceae with air sheets, in the process of return to the terrestrial life:



4. Under these conditions one can wonder why we would not have, in particular amongst dinosaurs, primary quadrupedalism and secondary quadrupedalism. However, I will try to show that one has[1]:



5. How to arrive there? By the irreversibility of evolution[2]. An organization never exactly takes a former state again, even if it is placed under conditions of existence identical to those which it has crossed.
But, - under the terms of indestructibility of the past, - as known so well by my

[1] I stated, for the first time, this view, in 1892, in one of my lessons at the Solvay Institute (University of Brussels): L. Dollo. *Cours autographie sur l'Évolution du Squelette des Vertébrés*. Lessons presented at the Solvay Institute (University of Brussels) in 1891-1892.
- M.H.F. Osborn, a professor of the University of New York, has since given a broader publicity to:
- H.F. Osborn. *Reconsideration for the Evidence for a Common Dinosaur-Avian Stem in the Permian*. American Naturalist. 1900. Vol. XXXIV. p.796.
- H.F. Osborn. *Dinosauria*. K.A. von Zittel. *Text-Book of Paleontology*. Vol. II. London, 1902. p.241.
[2] L. Dollo. *Les lois de l'Évolution*. Bull. Soc. Belg. Géol. 1893. Vol. VII. p. 164

eminent Master, A. Giard, member and professor of the Sorbonne Institute[1], - it always keeps some trace of the intermediate stages which it has traversed.

Ichthyosaurus, its lungs, - seaweed, its flowers, - kangaroo, prevalence of the fourth toe and syndactyly, - the *Lotus*, stomata with the higher face of the sheets. *Stegosaurus* and *Triceratops*, transformed functional postpubis or rudimentary postpubis.

II.

Adaptive characters of Bipedal Predentate Dinosaurs

1. - In order to avoid any discussion on the bipedal nature of the selected dinosaurs, let us take a case studied thoroughly: that of *Iguanodon*[2].

2. - The evidence of an *upright station* for the famous dinosaur of Bernissart is double:

1. - *Anatomical*, i.e. being contingent on the structure of the famous reptile;

2. - *Ichnological*, i.e. being based on the prints discovered in the ground.

3. - As the ichnological evidence is sufficient, alone, to establish the bipedal nature of *Iguanodon*, we can determine the *adaptive characters* of *bipedal predentate dinosaurs*.

These characters are multiple. Most prominent are:

1. - Strong preacetabular process of *ilium*;
2. - Very long and slender *ischium*;
3. - The *pubis* is equipped with a very long and slender *postpubis*.

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[1] A. Giard. *L'Évolution des Sciences biologiques*. Revue Scientifique. 1905. Vol. IV. p. 205.
[2] L. Dollo. *Troisième note sur les Dinosauriens de Bernissart*. Bull. Mus. Roy. Hist. Nat. Belg. 1883. Vo. II. p. 85.
- L. Dollo. *Les Allures des Iguanodons, d'après les Empreintes des Pieds et de la Queue*. Bull. Scient. Giard. 1905. XL. p. 1.

4. – Does one find the characters in question in the reptiles where it is possible to observe quadrupedalism, i.e. with the rhynchocephalians, lacertilians, the crocodiles and chelonians?

In no way.

Not more than with the sauropod dinosaurs, moreover.

5. – Where, therefore meets one among the living amniotes? In the birds, i.e. in animals adapted to bipedalism. These characters are agreeably, by consequence, the adaptive characters of bipedal predentate dinosaurs.

6. – But *Stegosaurus*[1] and *Triceratops*[2], whose quadrupedal paces are allowed by all the qualified naturalists, have a postpubis.

Yes, but the postpubis of *Stegosaurus* is transformed.

Yes, but the postpubis of *Triceratops* is atrophied.

7. - And *theropods*, which, however, are *bipeds*, *do not have a postpubis*.

There are various means to carry out an adaptation.

The birds fly in a certain manner; chiropterids, otherwise; pterosaurs, still differently.

Theropods represent to us, consequently, *another adaptation* to bipedalism than that of the predentate dinosaurs.

III.

Stegosaurus and *Triceratops*

1. - As we have just pointed it out, there is *unanimity*, in the qualified mediums, on the *quadrupedal pace* of *Stegosaurus* and *Triceratops*.

2. - In addition, there is also *unanimity* on the *predentate* nature of these two dinosaurs, nature to which testifies, in particular, the predentary bone and the postpubis.

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[1] O.C. Marsh. *The Dinosaurs of North America*. Sixteenth Ann. Rep. U.S. Geol. Surv. (1894-1895). Washington, 1896. p. 186.

[2] O.C. Marsh. *The Dinosaurs of North America*, etc. p. 208.

3. - That posed, that would have us wait, theoretically, for a *predentate biped* who would *turn over* to *quadrupedalism*?

Obviously, the loss of the adaptive characters to bipedalism.

However, this loss can be done in two manners:

1. - By atrophy;
2. - By change of function.

4. - In case *atrophy*, for example, it is necessary to envisage:

1. - A major regression of the postpubis;
2. - A strong shortening of ischium. I.e. one would return from there, *physiologically*, with the triradiate pelvis particular to the quadrupedal life.

SECONDARY QUADRUPEDALISM

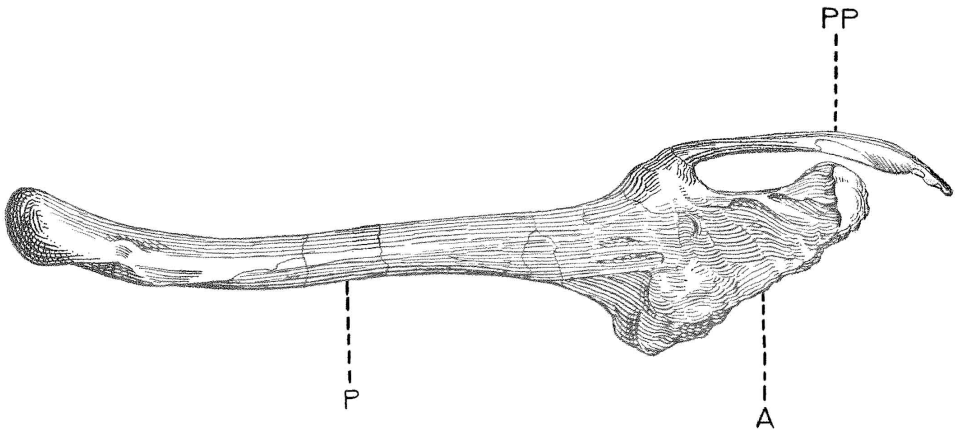

Fig. 1 – Pubis of *Triceratops*

Ventral View. – Scale: 1/8
According to O.C. Marsh (Dinosaurs of North America. Washington, 1896. Pl. LXVII, fig. 3).
Dinosauria. – Predentata. – Ceratopsidae.
Rudimentary Postpubis Shown.
A. - Acetabulum
P. - Pubis
PP. - Postpubis

But not *morphologically*, because of the irreversibility of evolution, and because there will remain indestructible traces of that in:

1. - The rudimentary postpubis;
2. - Narrow and bent ischium.

- Now this case is not a theoretical case: it is that of *Triceratops*.

5. - In the case of a *change of function*, it is reasonable to imagine:

1. - That the ischium is shortened and flattened;

2. - That the postpubis is in the same way and, more, applies closely along the ventral edge of ischium.

I.e. one still returns from there, *physiologically*, with the triradiate pelvis particular to quadrupedalism.

But *not morphologically*, because of the irreversibility of evolution, because there lastly remain indestructible traces in:

1. - The shape of the ischium;

2. - The posterior branch of the pelvis, which is not currently made up any more by ischium alone, but by the ischio-postpubic complex.

And where is the change of function? In the circumstance that the transformed functional postpubis plays, here, the role of the ventral edge of ischium.

- But, this case is not a theoretical case either: it is that of *Stegosaurus*.

6. - Thus, *Stegosaurus* and *Triceratops* show us, precisely, what one should expect from predentate bipeds that would evolve quadrupedalism.

And they carry traces of their past bipedalism, in particular in their postpubis, either functionally transformed, or rudimentary.

7. - Apart from this interpretation, it appears impossible to me to account for the presence of the postpubis in *Stegosaurus* and *Triceratops*.

Indeed, as we saw previously, this character is one of the adaptive characters of bipedalism in the predentates.

How would *Stegosaurus* and *Triceratops* be if they had never ceased being quadrupedal?

IV.

Conclusion.

1. - There are dinosaurs adapted to primary quadrupedalism. They are the sauropods. Examples: *Brontosaurus* and *Diplodocus*.

2. - There are dinosaurs adapted to primary bipedalism. They are the predentate bipeds. Example: *Iguanodon*.

3. - There are dinosaurs adapted to secondary quadrupedalism. They are the predentate quadrupeds. Examples: *Stegosaurus* and *Triceratops*.

4. - Moreover, these reversions to quadrupedalism were independent because they have different adaptations, since one rests on the atrophy of the postpubis (*Triceratops*), while the other depends on its change of function (*Stegosaurus*).
- Moreover, they are not contemporary: one is Upper Jurassic; one Upper Cretaceous.

5. - Thanks to the irreversibility of evolution it was possible to find the bipedalism inserted between the two quadrupeds *Stegosaurus* and *Triceratops*. If evolution were reversible these two dinosaurs would have regained their former quadrupedal shape exactly, and one could not have distinguished secondary from primary quadrupedalism in them.*

* Original citation: Dollo, L. 1905. Les dinosauriens adaptés à la vie quadrupède secondaire. Mémoires de la Société Belge du Géologie 19:441-448. Translated by Kelda Olson, 2008.