XVI. *Description of the Fœtal Membranes and Placenta of the Elephant* (Elephas Indicus, Cuv.), *with Remarks on the value of placentary characters in the classification of the Mammalia.* *By Professor* Owen, *F.R.S.*

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Seba gives a figure of the fœtus of an Elephant in tab. iii. vol. i. of his great 'Thesaurus'*; but a knowledge of the fœtal membranes of this remarkable quadruped has long been a great desideratum in both physiology and zoology.

From the period of my appointment to the Hunterian Professorship of Physiology at the Royal College of Surgeons, London, in 1836, I lost no opportunity of urging this desideratum upon the attention of correspondents in Ceylon and India; and, after some years, I had the gratification to receive a letter from Dr. Morton, an accomplished Army Medical Officer quartered in Ceylon, stating that he had forwarded to me the membranes of a fœtal Elephant, addressed to the Museum of the Royal College of Surgeons. On the arrival of this specimen in a keg of arrack, I prosecuted as complete an examination as the condition of the parts would permit, and made the preparations (Nos. 3558 c. and 3558 d.), which are now in the Physiological Series of that Museum. The results of this examination were orally communicated in the Theatre of the College, in the 17th Lecture of my Course "On the Generation and Development of the Vertebrate Animals," delivered in 1850†; and were illustrated by diagrammatic views of the chief peculiarities which the parts presented. Circumstances prevented further publication of the facts at that time; but I am now able to submit the following description of the fœtal membranes and placenta of the Elephant to the Royal Society.

The chorion of the Elephant (Plate XVI. fig. 1, *a*, *a'*, *d*), at about the middle of the period of utero-gestation, forms a transversely oblong sac, 2 feet 6 inches in long diameter, and 1 foot 4 inches in short diameter, encompassed at its middle part by an annular placenta (*b*, *b*), 2 feet 6 inches in circumference, varying from 3 to 5 inches in breadth, and from 1 to 2 inches in thickness. This placenta is partially divided by opposite constrictions into two moieties, one measuring 12 inches, the other 10 inches in length, and the extreme breadth being 5 inches in each; the connecting isthmus is 3 inches in breadth. The placenta presents the same spongy texture and vascularity as does the annular placenta of the Hyrax and of the *Carnivora*; but the capillary filaments or villosities enclosing the fœtal vessels enter into its formation in a larger proportion,

* Locupletissimi Rerum naturalium Thesauri accurata Descriptio, &c., 4 vols. fol. Amst. 1734—1765.

† "Fœtal membranes of the Hog- and Horse-tribe: fœtal membranes and placenta of the Hyrax and Elephant." Printed Synopsis, 1850.

and are of a relatively coarser character. The greater part of the outer convex surface of the placenta is smooth; the rough surface, which had been torn from the maternal or uterine placenta, exposed the fœtal capillaries, and occupied chiefly a narrow tract (*c*, *c*) near the middle line of the outer surface. A thin brown deciduous layer is continued from the borders of the placenta, for a distance varying from 1 to 3 inches, upon the outer surface of the chorion. Flattened folds of a similar substance, or false membrane, could be raised from some parts of the surface of the placenta; at other parts the substance formed irregular fibrous bands, the fibres extending in the direction of the circumference of the placental ring. The outer surface of the chorion is for the most part smooth and shining; but at each of the obtuse extremities of the sac there was a villous and vascular subcircular patch (*d*, *d*), between 2 inches and 3 inches in diameter, the villi being short and graniform, $\frac{1}{6}$th of a line in diameter, or less. Thus the chief points of attachment of the chorion to the uterus are, at the equator, by the annular placenta, and at each pole of the elongated sac, by the subcircular villous patch.

The umbilical cord (*f*), formed by one venous and two arterial trunks, and by the slender neck of the allantois, with the connecting cellular tissue and the covering of amnios, is short and somewhat flattened. It measured about 6 inches in length, before the division of the vascular trunk, and about 3 inches in circumference.

The inner surface of the amnios is roughened by brownish hemispherical granules, from one line to $\frac{1}{10}$th of a line in size, commonly about half a line; the outer surface is finely wrinkled, but smooth. The amnios is continued from the base of the umbilical cord upon the allantois, which is of considerable size, and is so interposed between the chorion and amnios, as to prevent any part of the amnios attaining the inner surface of the placenta. The amnios consists of two layers: one is the granular layer, continued upon the inner or fœtal surface of the allantois, and thence upon the umbilical cord; the other is the smooth outer layer, continued upon the outer or chorional surface of the allantois, and thence upon the inner surface of the chorion.

The allantois, into which the urachus (*g*) at the torn fœtal end of the cord rapidly expands, divides, where the amnios begins to be reflected upon it, into three sacculi: one, which is the largest, extends over the inner surface of the annular placenta, and projects a little way into the unruptured sac of the chorion (*a*): a second division or horn of the allantois extends into the opposite or ruptured sac of the chorion (*a'*), whence the fœtus had escaped; it there bends round towards the placenta, and its apex adheres at that part to the first division of the allantois: the third prolongation subdivides into two smaller cavities, each terminating in a cul-de-sac, encompassing, and closely attached to the primary divisions of the umbilical vessels. The line of adhesion of the amnios to the allantois, where it is reflected upon these cul-de-sacs, measures 3 feet 6 inches.

The umbilical vein, at the distance of 6 inches from the torn or fœtal end of the cord, divides; and, 3 inches further, one of the branches subdivides. The first division of the umbilical arteries takes place 9 inches from its torn extremity. The primary branches of the umbilical arteries and vein diverge from the umbilical cord in four divisions.

The allantois, coexpanding with the divergence of these trunks, developes its principal sac through two opposite interspaces, and the two smaller divisions at the intermediate interspaces.

It may, perhaps, aid in the comprehension of this rather complex structure, if I here cite from the rough notes which I penned on the first examination of the connexions of the allantois:—"The urachus expands in an infundibular form into the allantois. About 4 inches from the infundibular commencement of the allantois an umbilical vessel recedes from the amnios towards the chorion, carrying with it a fold of the free and thickened margin; this fold expands to 5 inches in breadth: the layers adhere together, but could be separated. Each of the other two hypogastric vessels carry similar folds of the allantois inwards, from the surface of the amnion to the chorion, and the allantois is again reflected by three broad folds diverging from one centre upon the amnios of the opposite side. The amnios becomes blended with, or closely adherent to, the allantois about 3 inches from the umbilical cord; prior or anterior to this part, the two membranes are connected by loose reticulated tissue."

I now proceed with the description, which was written after a recognition of the nature of the several parts observed in the course of the examination. The primary branches of the umbilical vessels reach, first, the borders of the placenta, and then ramify in the substance of the placenta and upon the inner surface of the chorion, being supported there, and more or less surrounded, by the continuation of the allantois which forms the so-called endochorion.

Upon the endochorionic vessels are developed a number of flattened, oval or subcircular bodies (*e*, *e*), varying in diameter from an inch or more to half a line. On separating the chorion from the allantois, these bodies were found to belong entirely to the latter membrane. To the naked eye they present a compact, structureless tissue, of a grey colour. On dissecting one of the branches of an umbilical vessel, upon which one of these bodies was developed, the vessel was found to pass on the chorionic side of the body without undergoing any apparent change in the passage, the body being developed from the allantois and from that part which forms the allantoic side of the sheath of the vessel. These bodies are most abundant near the placenta, where they are separated from each other by interspaces often less than their own diameter. They are wider apart upon the non-placental part of the chorion, especially as they approach the poles of the chorionic sac. Their number on the unruptured division of the chorionic sac was about 120. They are exclusively an allantoic development. Several small specimens occur on the free duplicatures of the allantois continued from the umbilical trunks near the placenta: in almost every case they are developed on the course of the large vessels, and are restricted, with few exceptions, to that part of the allantois which is in contact with the chorion, and which forms the endochorion of embryologists. The free surface of these peculiar bodies is smooth and polished, not villous like the cotyledons of the *Ruminantia*; from which they likewise differ essentially in projecting inwards towards the cavity of the allantois.

The most important modification in the vascular structures connecting the chorion with the uterus, in the Elephant, is their combination of two forms of the placenta, viz. the 'annular' and the 'diffused,' which forms are restricted in other Mammalia to distinct kinds of quadrupeds.

This fact appears to me to point to the inapplicability of modifications of the placenta to the characterising of primary groups of the Class *Mammalia*.

According to the annular or zonular part of the placental structure in the Elephant, it should be classed with the true *Carnivora*: according to the diffused vascular villosities at the two poles of the chorion, it would rank with the true Pachyderms of the Cuvierian System. The Elephant, however, is not the only hoofed quadruped which has an annular placenta: the Hyrax, which CUVIER so sagaciously discerned to be a kind of miniature Rhinoceros, differs from its great ally by having an annular or zonular placenta.

Professor MILNE-EDWARDS, who has revived Sir EVERARD HOME'S idea* of a system of Mammalogy on placental characters†, consistently included the Hyrax with the Seals, Dogs, Cats and other *Carnivora* having a zonular placenta‡; and a logical application of the same principles of classification would lead to a transference of the Proboscidian *Ungulata* to the same association. Those Naturalists who, with the able Professor of the Jardin des Plantes, may have placed confidence on the value of the temporary fœtal structures, as indications of natural affinity in the mammalian class, will feel surprised, perhaps, since the chorion of the Elephant developes a compact placental body, that it should not have presented either the discoid or the cotyloid form, so common in the *Rodentia*. Perhaps no existing hoofed mammal offers so many similarities of structure to the *Rodentia* as does the Elephant. CUVIER long ago pointed them out, and others have expressed their idea of this affinity, by calling the proboscidian pachyderm a 'gigantic mouse.'

But the placenta does not present the same form in all *Rodentia*: in the Guinea-pig it is more cup-shaped than plate-shaped, more cotyloid than discoid; whilst in the Hare and Rabbit it is a thin oblong mass, divided into from three to five lobes§. In the Rat, the maternal position of the placenta is cotyloid, and is applied to a small convex lobe or button-shaped process on the middle of the uterine surface of the fœtal placenta, which may thus be said to be 'pedunculate.' In the Water-vole (*Arvicola amphibia*) the fœtal placenta is small and circular, convex towards the uterus and flat towards the chorion, which is attached to the centre of the disk.

In most of the *Insectivora* the placenta is proportionally larger than in most of the

* Lectures on Comparative Anatomy, 4to, vol. iii. 1823, p. 501.

† "Considérations sur quelques Principes relatifs à la Classification Naturelle des Animaux: et plus particulièrement sur la distribution méthodique des Mammifères," Annales des Sciences Nat., sér. 3. tom. i. p. 65, 1844.

‡ Ibid. p. 96.

§ Description of Preparation, No. 3472, 'Physiological Catalogue, Museum, Royal College of Surgeons,' vol. v. p. 118, 4to, 1840.

Rodentia. In the Hedgehog, when the embryo is from half an inch to an inch in length, it is enclosed in a cup-shaped placenta, as in a nest: this is subsequently spread out and flattened by the growth of the fœtus, and converted into a thin, shallow discoid plate, with its concavity applied to the back of the embryo, and with the central part of its convex surface attached to the uterus. In the Mole the placenta is a circular disc at the early period of gestation, and subsequently becomes an oblong flat band, with its long axis parallel to that of the fœtus: the linear tract of the uterine surface to which the placenta is attached shows a fine areolar structure, penetrated by the fœtal placentary filaments, which are brought away, distinct from the maternal structure, like the fœtal cotyledon in the Cow. In the Bat (*Vespertilio noctula*), the placenta has the form of an obtuse cone. In all the foregoing insectivorous mammals the umbilical sac is large in proportion to the allantois.

In a female large frugivorous Bat (*Pteropus medius*, TEMMINCK), preserved in spirits, which I found, on dissection, to be pregnant, the vitellicle, or umbilical sac, was a small reniform, compactly folded body, which lay in the concavity of the placenta, between it and the allantois: the placenta was subcircular, discoid, slightly concave towards the fœtus, proportionally more convex towards the uterus. The fœtal villi are long, delicate, and branched, giving a flocculent appearance to the small portion of the centre of the disk by which the fœtal placenta is attached to the womb. In a loose and general way, all the varieties of the placenta in *Rodentia* and *Insectivora*, with those in *Quadrumana*, may be termed 'discoid.' But the structure of the discoid placenta in the *Pteropus* more resembles that of the fœtal portion of the cotyledon in the Cow, than that of the cellulo-vascular spongy placenta of the *Quadrumana*; and this difference, with the more important one of the larger umbilical sac in the Bats and Insectivora, appears to me to greatly outweigh the degree of resemblance, such as it is, in the mere outward form of the placenta, in the above-cited orders of Mammalia.

Any argument in favour of the affinity of the *Cheiroptera* to the *Quadrumana*, based on that degree of resemblance, must be affected by the prevalence of the double discoid placenta in the *Quadrumana*. Since JOHN HUNTER first made known that modification* in a species of *Macacus*, which, from a comparison of the fœtus now preserved in the Museum of the Royal College of Surgeons, I believe to be the 'Wrinkled Baboon' of SHAW (*Macacus rhesus*, DESM.), Professor BRESCHET† has described and figured the two separate discoid placentæ in the small South American Squirrel-monkey (*Callithrix Sciureus*, KUHL), in the Green-monkey (*Cercopithecus sabæus*, DESM.), in the Mitre-monkey (*Semnopithecus mitratus*, Is. GEOFF.), and in the Long-nosed Monkey (*Nasalis larvatus*, GEOFF.). Yet this well-marked modification of the cellulo-vascular placenta is not constant in the *Quadrumana*, nor even in the primary groups of the order. In the Platyrhines, *e. g.* the Howler (*Mycetes seniculus*, KUHL) has a single placenta‡, and, amongst

* Animal Economy, 1786, 4to.

† Mémoires de l'Académie des Sciences, tom. xix. 1845.

‡ BRESCHET, *loc. cit.* p. 57.

the Catarhines, I have ascertained that in the Chimpanzee (*Troglodytes niger*) the placenta is single, as in the Human subject.

The true or horned Ruminants all present the much subdivided cotyledonal type of placenta; but the Camel-tribe are unquestionably much more nearly allied to the true Ruminants than to the Equine-tribe, which they resemble in the diffused vascular villosity of the chorion, which is substituted for a placenta. Thus that organ is not one of the characters which indicate the real affinities, and which guide to the true grouping, of the *Ungulata*, any more than it subserves to the formation of natural groups of the *Quadrumana*. The Hog, which has a diffused chorionic villosity, as in the Camel, but with a modification in the arrangement of the vessels, which Sir EVERARD HOME defines by the term 'stellate structures*,' is, like the Camel, much more nearly related to the true Ruminants than to the odd-toed hoofed animals, such as the Horse, Tapir and Rhinoceros. So, likewise, the Hyrax, with an annular placenta, is more closely related to the Rhinoceros than to the Elephant or the Lion.

I would not be misunderstood as deeming the placenta to present no correlation of form with modifications of mammalian structure: the constancy of the annular type in the *Carnivora*, and that of the cotyledonal type in the true *Ruminantia*, are valid instances of the degree to which that correlation exists. But the modifications of the placenta do not form a true guide to the affinities or classification of the *Mammalia* generally. The primary groups of that class are based upon modifications of a much more important and significant organ—the brain: and of this truth Sir EVERARD HOME himself appears to have been aware†, when he published the placentary system of classification, which has lately been revived, with modifications, by the distinguished Professor in the Jardin des Plantes‡.

The placenta of the phytiphagous Sloth (*Bradypus*), which has a complex subdivided stomach, is almost as much subdivided as in the smaller Ruminants; whilst the placenta of the Armadillo, which has a simple stomach, is a single thin oblong body, as in the Hedgehog. But the true affinities of the Sloth would be as much violated by transferring it to the *Ruminantia*, as those of the Armadillo would be by classing it with the *Insectivora*, or as those of the *Hyrax* are by its transference to the same primary group with *Carnivora*, on the score of mere accordance of placental form.

A very significant evidence of the limited correlation of any particular form of placenta with any of the known modifications of the mammalian type, is afforded by the

* See ESCHRICHT, 'De organis quæ respirationi et nutritioni fœtus mammalium inserviunt,' 4to, 1837, p. 4; and the description of the venous plexules of the chorion, in 'Catalogue of the Physiological Series, Mus. College of Surgeons,' vol. v. p. 134, No. 3543.

† "The truth becomes obvious of there being no organ belonging to an animal, except the brain, that will bear us out in affording characters for a general classification, the structure of the other organs being varied whenever it was necessary to adapt the animal to the climate which it is to inhabit, or the food on which it is to subsist: and the brain we are not sufficiently acquainted with, to take it as our guide."—Lectures on Comparative Anatomy, vol. iii. p. 445.

‡ MILNE-EDWARDS, *loc. cit.* Annales des Sciences Naturelles, sér. 3. vol. v. 1844.

ill-success of guesses as to the nature of the fœtal membranes, from the natural affinities indicated by any such known modification. Thus, as regards the Elephant itself, Sir EVERARD HOME wrote:—"The mare has no placenta, only a chorion; the period" (of gestation) "is eleven months. The Elephant, whose period is twenty-two months, I have no doubt, from the appearance of the inside of the uterus, has no placenta, but a chorion*;" and the Elephant is classed accordingly with the Horse, Whale, Hog, and Camel †.

The convictions as to the limited value of the placenta, in Mammalian Classification, which were expressed and illustrated in the Hunterian Lectures for 1850, and were derived mainly from a study of the series of fœtal structures in the Hunterian Physiological Collection, described in the concluding volume of the 'Catalogue' of that Collection‡, appear to me to be strengthened by the remarkable modifications of the placental structures of the Elephant, which form the chief subject of the present communication.

EXPLANATION OF THE PLATE.

PLATE XVI.

Fig. 1. Chorion and placenta of the Elephant (*Elephas Indicus*), on the scale of 2 inches to a foot.

a, *a'*. The chorion; *a'*, the torn end from which the fœtus had escaped.

b. The annular placenta.

c. The tract along which the fœtal was connected with the maternal portion.

d, *d*. The superficial villosity at the poles of the chorion.

e. The allantoic corpuscles, seen through the exochorion.

f. Umbilical cord.

g. The urachus, before expanding into the allantois.

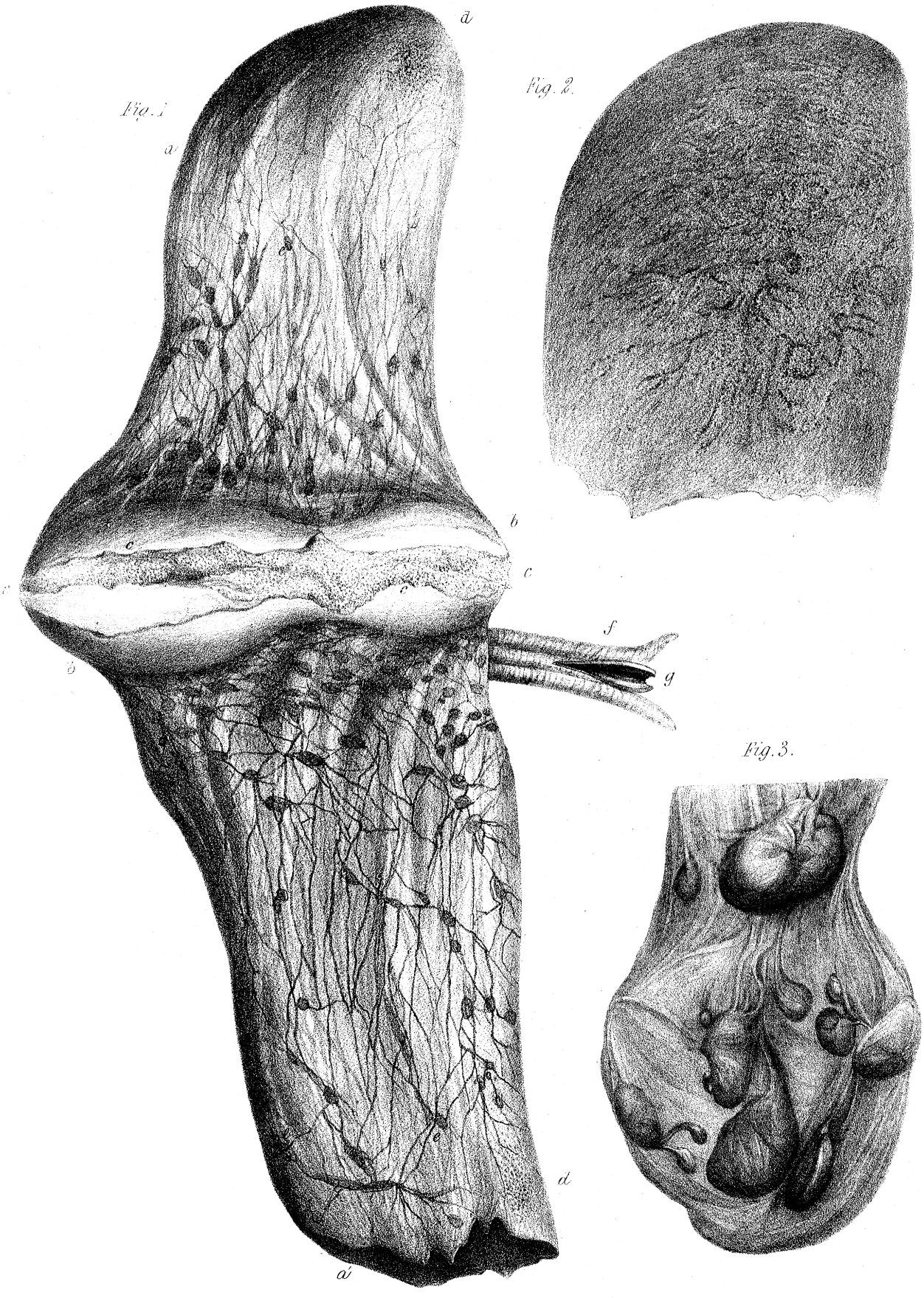
Fig. 2. A portion of the villous surface of the chorion, from the part marked *d* in fig. 1, of the natural size.

Fig. 3. A portion of the allantois, viewed from its amniotic surface, showing the corpuscles of the natural size.

* *Tom. cit.* p. 452.

† 'Order 7,' *tom. cit.* p. 503.

‡ "Physiological Series," vol. v. 4to, 1840, pp. 112—170.



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FETAL MEMBRANES & PLACENTA OF THE ELEPHANT (EL. INDICUS.)