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THE COURSE OF THE BLOOD THROUGH THE HEART OF THE FETAL MAMMAL, WITH A NOTE ON THE REPTILIAN AND AMPHIBIAN CIRCULATIONS.

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The problem of the course of the blood through the heart of the fetal mammal has been taken up because there are three distinct theories regarding the fate of the blood entering the heart through the superior and inferior caval veins. Each of these theories is based upon anatomical findings—a correlation of function to structure, and while injection experiments have been carried out which seem to substantiate each theory, experimental evidence derived from a study of the fetal circulation in the living embryo is entirely lacking. It is our purpose, therefore, to review the important literature; to state the position of the various theories together with their modifications; to analyze critically the evidence produced by the observers; to present the results of personal findings in the living mammalian embryo; and to offer a general summary of the physical, anatomical, and pathological evidence in favor of the one as opposed to all other theories. Finally to give a preliminary account of our observations on the circulation of the reptile and amphibian.

The literature up to the time of Harvey (1628) is drawn from Dalton's excellent work. Extremely comprehensive reviews are to be found in Knabbe's dissertation in Latin, and also in Kilian's article in German. With the exception of the first six references, where direct control is offered by comparison with the original text, and of Wolff's treatise, the articles have been read personally. The reader is referred to literature reviews mentioned for more exhaustive study.

The first definite information on the structure of the fetal heart is found in Galen's work: "In this matter, we have reason to admire the provisions of nature. For so long as the lung has only to be nourished and grow, it is supplied simply with blood; but, when it is ready to take on an active motion, its tissue becomes lighter and capable of expansion and compression by the movements of the chest. On that account the vena cava (right auricle), in the foetus, communicates by an opening with the arteria venalis (left auricle). As this latter vessel thus performs for the lung the office of a vein (that is, supplies it with blood for its nourishment), its companion (the pulmonary artery) must need at this time serve the purpose of an artery, and it is consequently made to communicate with the aorta. As these two vessels (pulmonary artery and aorta) are situated a little distance apart, their communication is effected by means of a third smaller one (ductus arteriosus), which forms a junction with each. In the case of the other two (auricles), which lie in contact with each other, there is a kind of orifice or fenestra (foramen ovale) common to both. At this orifice there is attached a membrane, like a lid or cover, opening toward the pulmonary vessel (left auricle), so that it will yield to the influx of blood from the vena cava (right auricle), but will prevent its regurgitation into that vessel."

Galen furthermore mentions the fate of the foramen ovale and the ductus arteriosus after birth. It must be remembered that at this time (third century) practically all of the work on the heart had been done hundreds of years before by Aristotle, Herophilus and Erasistratus, and despite the investigations of the latter two men on the character of the veins and arteries and the valves in the heart, the doctrine of circulation was shrouded in mystery. Galen assumed that the blood passed from the right into the left ventricle through the ventricular septum, and this may in part account for the curious notion that the ductus arteriosus transmitted blood from the aorta into the pulmonary artery—the passage is ambiguous and this is one interpretation of it. His description, however, of the foramen ovale, its valve and the method of its obliteration, together with the atrophic changes in the ductus arteriosus, are quite accurate.

Some thirteen centuries later Vesalius questioned the teachings of Galen regarding the passage of blood through the ventricular septum. "And accordingly, notwithstanding what I have said about the pits in this situation, and at the same time not forgetting the absorption by the portal vein from the stomach and intestines, I still do not see how even the smallest quantity of blood can be transfused, through the substance of the septum, from the right ventricle to the left." While this questioning the infallibility of Galen's work was little more than rank heresy at the time, Vesalius paved the way for others, and doubt was again raised in Servetus' discovery of the pulmonary circulation in 1553.¹ Servetus says, "This communication, however, does not take place through the median wall of the heart, as commonly believed; but by a grand device the refined blood is driven from the right ventricle of the heart, in a long course through the lungs. By the lungs it is prepared, assuming a bright color, and from the vena arteriosa is transferred into the arteria venosa" (pulmonary vein). Servetus also recognized the foramen ovale, and but for his unitarian views, which resulted in his untimely death at the stake, might have contributed more than a mere description of the pulmonary circulation.

The contemporaries of Vesalius and Servetus, Columbus and Cæsalpinus are also to be mentioned in this connection. We fail to see, however, wherein Columbus bettered the description given by Servetus, and Cæsalpinus did not add materially to what was already known on the subject. It must not be thought that the newer teachings were eagerly accepted, for Fallopius held to the Galenic views to the time of his death (1563). In 1565 Botallus reported the persistence of the foramen ovale and re-described the ductus arteriosus. We agree with many other writers that the use of Botallus' name in connection with these structures is questionable since Galen first mentioned them.

The gradual relief from religious persecution and the works of Vesalius and others stimulated investigation. Comparative anatomy,

¹We do not care to enter into a discussion of who actually did discover the pulmonary circulation and favor Servetus for the reason that his work appeared six years before that of Columbus.

particularly the investigations of Harvey, threw new light on the question. In Harvey's classical work (1628) we note the first scientific description of the course of the blood through the fetal heart. Unfortunately, the terminology is rather vague and the translation leaves much to be desired. For example, Harvey uses the term 'vena cava' as Galen used it—to denote the right auricle, while the left auricle is termed arteria venosa or pulmonary vein; the translator supplied plurals to these structures 'venæ cavæ' and 'pulmonary veins' at discretion, and the meaning is far from being the same. We present a corrected excerpt from Harvey's work, which reads as follows: "The first contact and union of the vena cava (right auricle) with the pulmonary vein (left auricle) which occurs before the vena cava opens into the right ventricle, or gives off the coronary sinus, a little above its escape from the liver, exhibits a lateral anastomosis that is a wide open passage-way from the cava (right auricle) into the vessel already mentioned (left auricle); in such a manner, that (as if by a single vessel) the blood can flow very freely and copiously through that opening from the vena cava into the left auricle and through the left auricle all the way into the left ventricle."

Note the similarity of this passage to the description given by Galen. We must give Harvey credit that he knew of the two caval veins and of the multiple pulmonary veins, otherwise the passage would mean nothing. It is generally accepted that the interpretation is as follows—the blood contained in the right auricle passes through the foramen ovale into the left auricle. He continues: "Further, in this foramen ovale, from the part which regards the pulmonary vein, there is a thin tough membrane, larger than the opening, extended like an operculum or cover; this membrane in the adult blocking up the foramen, and adhering on all sides, finally closes it up, and almost obliterates every trace of it. In the foetus, however, the membrane is so contrived that falling loosely upon itself, it permits a ready access to the lungs and the heart, yielding a passage to the blood which is streaming from the cava (right auricle), and hindering the tide at the same time from flowing back into that vein. All things, in short, permit us to believe that in the

embryo the blood must constantly pass by this foramen from the vena cava into the pulmonary vein, and from thence into the left auricle of the heart; and having once entered there, it can never regurgitate."

It was many years before Harvey's doctrine of the circulation in the adult was generally accepted, while his views concerning the course of the blood through the fetal heart were greatly obscured through the work of Méry, who claimed to demonstrate the passage of blood from left to right. Méry says, "*L'hypothèse du passage du sang de l'oreillette gauche par le trou ovale dans le ventricule droit du cœur du fœtus humain que j'y propose comme une simple conjecture, n'y appuyée que sur le seul rapport que j'ay trouvé entre le trou ovale et le canal de communication du cœur de la Tortue, et les mêmes conduits du fœtus.*"

This position was championed successfully by Méry throughout his life and despite the objections raised by Duverney and others, it was approved by Winslow, Littre and practically the entire French Academy. Winslow speaks of the anomaly reported by Vieussens where no foramen ovale was present (heart incompletely described—probably ventricular defect), and Steno's case of defect in the ductus (probably incomplete separation of the ventral aortic stem).

Some years after Méry's death, the injection experiments of Trew and Roederer proved the scheme a faulty one and in the work of von Haller we find no mention of it whatever. Here again are found vague descriptions; the wording is suggestive of Galen and Harvey, while the context appears to be a forerunner of the Sabatier theory. "But yet the septum betwixt the right and left auricle, conjoining them together, is perforated by a broad oval foramen, through which the blood coming from the abdomen, and a little directed or repelled by the valvular sides of the auricle, flows in a full stream into the pulmonary sinus." In 1773 Sénac repeated Méry's injection experiments and found that blood passed from the right into the left auricle but not the reverse.

About this time Wolff found that the relation of the opening of the inferior cava to the foramen ovale was somewhat different than hitherto described. He placed the orifice of the inferior cava dorsally at the border between the two auricles and considered the auricular

septum to be defective in this situation (foramen ovale). The orifice of the cava inferior was, therefore, split on the limbus Vieussens in such a manner that the left part of the opening transmitted blood directly into the left auricle through the foramen ovale, while the right part of the opening connected with the right auricle. The foramen ovale, in other words, did not afford a communication between the two auricles. This theory differs from the following one in that it was based on anatomical findings rather than inferred physiological necessity.

Some years later Sabatier presented his famous theory on the course of the blood through the fetal part. In his article, he deals with the formation of the inferior cava, devotes a few lines to the passage of blood through the liver, and says of the blood entering the heart through the inferior cava, "Le trou ovale le transmet a l'oreillette gauche." Practically v. Haller's statement. The theory was accepted by Bichat and incorporated in his text book on descriptive anatomy: "All the blood that the trunk of the inferior cava receives, . . . , instead of stopping in the right auricle, as in the adult, passes entire into the left through the foramen ovale, the superior edge of which is so arranged that nothing can mix with the blood of the superior cava; so that it is really with the left auricle that the inferior cava is continued." As we read the literature, it appears that this was really the scheme proposed by von Haller a few years before, but it was probably suggested independently by Sabatier. This theory, the prevalent one to-day, was confirmed by Horner, Murray, and Reid.

Wolff's anatomical findings were substantiated by Kilian: "Die Vena cava inferior öffnet sich nicht allein in den rechten Vorhof, sondern sie ergiesst ihr Blut durch zwei vollkommen isolierte Mündungen durch eine rechte und eine linke, sowohl in das rechte, als wie in das linke Atrium." Kilian, however, went still farther and his monumental work probably came into disrepute because of the curious view he held regarding the distribution of the blood from the right and left ventricles. "Es giebt im Fötus noch keine Arteria pulmonalis, sondern die fälschlich mit diesem Namen belegte Arterie, sammt dem sogenannten Ductus arteriosus Botalli, sind

ein und dasselbe fortlaufende Gebilde und der Ursprung eines sich in die untere Körperhälfte fortsetzenden Gefäßes, welches den Namen Aorta abdominalis zu tragen verdient, im Gegensatze der Aorta cerebralis, welche aus dem linken Ventrikel entspringt." Kilian believed that all of the blood of the left ventricle went to the head and upper extremities, while the blood from the right side was distributed to the lungs and Aorta descendens. An Aorta cerebralis, therefore, in contradistinction to an Aorta abdominalis.

Meckel's case occlusion of the descending aorta at the fourth thoracic vertebra seemed to conform with this scheme, but a careful examination of the drawing shows the constricted area to be well marked above, as well as below, the remains of the ductus. Even granting Kilian's scheme, the case could not represent a persistence of fetal conditions.

Injection experiments were carried on by Reid (1835) in three specimens. He injected a red mass into the cava inferior and a yellow mass into the cava superior, equal quantities under equal pressure; and found in one, that some of the red passed into the right auricle, none into the ventricle, while it filled the left ventricle. In this case a mistake was made of injecting the superior cava the wrong way. In the second attempt, the two masses mixed in the right auricle, with the comment that the injection was not well managed. The third case showed no mixing of the two masses; all the red went to the head, while all the yellow into the Aorta descendens. In his second article, commenting on the first, Reid mentions that he agrees with Sabatier but also states that Magendie's Physiology considers the scheme impossible, while Bostock's Physiology alludes to it as fanciful.

The chief objections to the von Haller-Sabatier theory were taken by Williams and by Peaslee. Williams's article, lamentably hidden, is worthy of no little consideration, because it represents the first critical analysis of the scheme. "From a careful examination of the anatomical character and dependence of the Eustachian valve, notwithstanding the opposing experiments of Dr. John Reid, I have recently convinced myself that it is mechanically inefficient as a means of preserving the individuality of the two caval currents

as they traverse the chamber of the right auricle; at the period of its diastole, when the auricle has attained a moderate limit of distension, it may be readily demonstrated, that the two streams must freely intermingle. It is not true, therefore, that the difference in quality is so considerable as that generally taught by the anatomists between the blood distributed to the anterior segment and that circulating the posterior segment of the body of the fœtus." Peaslee, who by the way believed in a marked aspirating action of the auricles, arrived at a similar conclusion. He considered "The foramen ovale, a temporary arrangement to allow the rapid conversion of the reptilian to the mammalian heart," the "mixture of blood in the right auricle," and that "no artery in the fœtus contains arterial blood." The statement regarding the conversion of reptilian to mammalian heart is probably a slip in English—what he undoubtedly meant was a change from the type of reptilian circulation to that of the mammal. With no article published in its favor since 1835, the von Haller-Sabatier theory came into disrepute in the literature even if it still occupies its original prominence in the text books on anatomy, physiology, embryology and obstetrics, both human and comparative.

With Rüdinger's finding that the orifice of the inferior cava was divided on the limbus Vieussens as described by Wolff, Kilian and others, interest seemed to be reawakened in the course of the blood through the fetal heart. Preyer, although a champion for the Wolff theory, still inclined toward the idea that the head of the embryo received a better arterial supply and this he gained as follows: The circulation through the lungs he granted was free, and inasmuch as the fetal lung occasioned little waste, the return through the pulmonary veins would be of better quality than the return through the superior cava; now inasmuch as the blood of the inferior cava was passed in equal amounts to both ventricles, the left ventricle would contain a more arterial blood. The idea in a way offers a compromise between the Wolff and von Haller-Sabatier theories and is incorporated in the elaborate scheme of the fetal circulation in Preyer's book.

Ziegenspeck, working under Preyer, waived the question as to

the quality of blood and presented a unique scheme for the placental circulation. The heart was diagrammed as two hearts, in order to render evident the Wolff idea that the foramen ovale did not afford communication between the two auricles, and this in turn necessitated picturing the vena cava inferior as a forked vein. The scheme proved confusing and in his last article he has redrawn his figure which we present later.

In review, we find the following theories arranged in chronological order:

I. The theory of Galen-Harvey (300[?] and 1628). Foramen ovale affords communication between the two auricles. Passage of mixed blood from right to left.

II. The theory of Méry (1692). Passage of blood from the left auricle to the right ventricle through the foramen ovale.

III. The theory of Wolff (1775). Foramen ovale does not afford communication between the two auricles but connects with the left opening of the vena cava inferior. Right opening of that vein leads into the right auricle.

IV. The theory of von Haller-Sabatier (1779-91). Blood of the inferior cava passes over to left auricle through foramen ovale. Foramen ovale does not connect the two auricles.

V. The theory of Kilian (1826). Same as that of Wolff with this modification—division of vessels leaving the heart into Aorta cerebralis and Aorta abdominalis. Descending aortic arch conveys no blood during fetal life.

VI. The theory of Ziegenspeck (1881 and 1905). Same as that of Wolff with modification; that return to heart through superior cava equals return through pulmonary veins; that Pars communicans aortæ transmits the same amount of blood as ductus and that each carries one half of the contents of the left and the right ventricles respectively. "Gesetz der Halbierung des Blutes."

Méry's theory was refuted in the eighteenth century. Kilian's theory has not met with approval since 1835 and neither has the von Haller-Sabatier scheme. The latter one, however, demands some attention. We, therefore, consider it first, next the Wolff and Ziegenspeck contentions, and finally the theory of Galen-Harvey.

THE THEORY OF VON HALLER-SABATIER.

This theory may be interpreted in one of two ways: either the orifice of the inferior cava is placed in close relation to the foramen ovale and that all or practically all of its blood passes to the left; or, interpreted from the usual diagrams, the streams from the two cavæ cross in the chamber of the right auricle without mixing. The only difference between the former interpretation and the Wolff theory is one of degree and we, therefore, consider it later. We present our criticism to the latter reading taken from a preliminary article. "A critical examination of this theory shows it to be physically impossible, morphologically inaccurate, and developmentally unnecessary." We believe it is simple to show that it is physically impossible to preserve the identity of two currents when they cross within a distending chamber. Born has already pointed out the morphological inaccuracy of the scheme in that the condition is not to be found in the sauropsidian embryo. The scheme is developmentally unnecessary. It attempts to account for the more rapid growth of the head because that segment then obtains the better quality of blood. The head end of all vertebrates develops more rapidly than the tail end whether this alleged better arterial supply is present or not.

It is our opinion that the von Haller-Sabatier scheme of the fetal circulation should be eliminated from the text books except as a matter of historical interest, and we also believe that the investigators favoring the Wolff school will concur in this statement. This represents the neutral ground, and from here on we differ.

THE THEORY OF WOLFF, INCLUDING ZIEGENSPECK'S MODIFICATION.

This theory is based on the anatomical findings that the orifice of the inferior cava is placed dorsally on the auricular septum which is deficient at this point. The free edge of the septum constitutes the limbus Vieussens, and the current in the inferior cava is directed against it in such a manner that the blood is split into two streams; the left part of the current passes to the left of the limbus directly into the foramen ovale, while the right part passes to the right of

the limbus directly into the right auricle. The foramen ovale does not afford communication between the two auricles and inasmuch as the more arterial blood in the inferior cava is distributed to both ventricles, a mixing of bloods, arterial and venous, occurs in both ventricles. Ziegenspeck's work is the most scientific and recent and we, therefore, direct our attention to his article on the subject.

Ziegenspeck criticises both the von Haller-Sabatier and Galen-Harvey theories. We agree that the former is incorrect, but, inasmuch as we favor the latter, we present his views on the question.

Ziegenspeck claims that the Galen-Harvey theory is refuted; first, by the anatomical findings of Wolff which he substantiates, and second, "Wer kann bei Betrachtung der Abbildungen, . . . , es für wahrscheinlich oder möglich halten, dass während der Diastole beider Vorhöfe, *währendem doch beide aspirieren*, ein Blutstrom sich durch die rechte Mündung nach rechts, dann wieder durch dieselbe Mündung nach links ergiessen? Ist es nicht vielmehr ohne weiteres klar, dass sich jeder Vorhof aus der Vena cava inferior direct so viel Blut aspiriert, als zu seiner Füllung noch nötig ist?" We can answer the question quite frankly—it is not clear.

While we are tempted to agree with Ziegenspeck that the illustrations he presents seem to support the argument, and while these relations appear to hold in pig (the animal used in our experiments), we would hesitate before accepting these conditions to obtain necessarily in the living animal. Practically Born's criticism. Again we note that particular emphasis is laid upon an aspirating action of the auricles, a point also mentioned by Peaslee in his claim for a mixing of the blood. It must be remembered that the aspirating action of the auricles is by no means a certainty and that even if it be present, it is probably feeble and transient.

The physical data offered by Ziegenspeck are based on the following premise: if both ventricles expel the same amount of blood under the same pressure, then the vessels transmitting the blood must be of like caliber. Upon this assumption, therefore, if the ductus and Pars communicans aortæ (segment of aorta between left subclavian artery and ductus) are of like caliber, they carry equal quantities of blood. He tabulates 33 measurements; in 28

the two are of equal caliber; in 2, the ductus is larger, and in 3, the Pars communicans aortæ is larger. Allowing for variation, he deduces that the two structures transmit equal quantities of blood.

According to the laws of hydrodynamics, we should have a direct control as to the scientific value of these measurements, for we are able to compute the caliber of the Aorta descendens and compare it with the measured value. Caliber Aorta descendens =

$$\sqrt[2]{\text{caliber ductus}^3 + \text{caliber Pars. comm. aortæ}^3}.$$

The aggregate measurement in twenty-two cases, where the three measurements are to be found and in which ductus and Pars. comm. aortæ are equal (Table I), is as follows: Ductus = 2.97 —; Pars. comm. aortæ = 2.97 —, and Aorta descendens = 3.83 + mm. Computed the latter vessel should read 4.14 + mm. This error, while but 0.31 mm. in the linear caliber, is equal to 18.6 per cent in carrying capacity. In other words, according to Ziegenspeck's figures,

TABLE I.

NUMBER.	CALIBER DUCTUS.	CALIBER PARS. COMM. AORTÆ.	CALIBER AORTA DESCENDENS. Ziegenspeck.	CALIBER AORTA DESCENDENS. Calculated.	ERROR IN MM.	(CALIBER AORTA DESCENDENS.) ² Ziegenspeck.	(CALIBER AORTA DESCENDENS.) ² Calculated.	PERCENT CARRYING CAPACITY. Ziegenspeck.	ERROR IN CARRYING CAPACITY.
1	1.5	1.5	1.7	2.1	—0.4 +	2.89	4.50	64.22	—35.78
3	2.0	2.0	2.0	2.1	+0.1 —	9.00	8.00	112.50	+12.50
4	2.0	2.0	2.3	2.8	+0.2 +	6.76	8.00	84.50	—15.50
21	2.0	2.0	3.0	3.2	+0.2 —	9.00	8.00	112.50	+12.50
17	2.3	2.3	3.0	3.2	—0.2 +	9.00	10.58	85.06	—14.94
9	2.5	2.5	3.0	3.5	—0.5 +	9.00	12.50	72.00	—23.00
11	2.5	2.5	3.8	3.5	+0.2 +	14.44	12.50	115.50	+15.50
14	2.5	2.5	3.0	3.5	—0.5 +	9.00	12.50	72.00	—23.00
18	2.5	2.5	3.0	3.5	—0.5 +	9.00	12.50	72.00	—23.00
2	3.0	3.0	3.5	4.2	—0.7 +	12.25	18.00	68.05	—31.95
10	3.0	3.0	4.0	4.2	—0.2 +	16.00	18.00	88.88	—11.12
15	3.0	3.0	3.5	4.2	—0.7 +	12.25	18.00	68.05	—31.95
19	3.0	3.0	4.0	4.2	—0.2 +	16.00	18.00	88.88	—11.12
23	3.0	3.0	4.0	4.2	—0.2 +	16.00	18.00	88.88	—11.12
29	3.0	3.0	4.0	4.2	—0.2 +	16.00	18.00	88.88	—11.12
30	3.0	3.0	4.0	4.2	—0.2 +	16.00	18.00	88.88	—11.12
16	3.5	3.5	4.0	4.9	—0.9 +	16.00	24.50	65.30	—34.70
25	3.5	3.5	4.0	4.9	—0.9 +	16.00	24.50	65.30	—34.70
27	3.5	3.5	4.7	4.9	—0.2 +	22.09	24.50	90.16	—9.84
24	4.0	4.0	5.5	5.6	—0.1 +	30.25	32.00	94.53	—5.47
32	5.0	5.0	6.0	7.1	—1.1 +	36.00	50.00	72.00	—28.00
33	5.0	5.0	7.0	7.1	—0.1 +	49.00	50.00	98.00	—2.00
	2.97—	2.97—	3.83+	4.14+	—0.31			81.37	—18.63

the Aorta descendens can carry away but 82 per cent of the blood fed to it by the ductus and descending aortic arch—unless the resistance in the descending aorta is less than in the carotid-subclavian system and in the right and left pulmonary arteries. If the Aorta descendens actually carries away one half of the contents of both ventricles, as Ziegenspeck maintains, then it is also possible to compute the caliber of the aortic and pulmonary stems—measurements which he unfortunately does not give us.

Furthermore, much depends on the accuracy in calibration of small vessels. If we select certain of the measurements, we find that individual variations between the actual and computed value of the Aorta descendens are extreme. In No. 1, for example, the carrying capacity of the descending aorta is 35 per cent less than calculated. In only three cases does he obtain the vessel slightly larger; in ten, it is smaller; and in nine, it is too small by about 31 per cent.

To test the validity of these measurements we selected two pigs at random, taken from the same uterus and hardened by formalin injection. Ring segments were cut out of the vessels named in Table II; the rings split and carefully straightened to avoid stretching. A linear measurement on the intima when divided by 3.1416 ought to give a relatively accurate calibration if this method can be employed, and if the vessel lumina are circular. According to Ziegenspeck, the following equations obtain:

1. Caliber Aorta descendens² = caliber ductus² + caliber of Pars. comm. aortæ².
2. Caliber Pulmonary stem² = caliber ductus² + caliber right pulmonary² + caliber left pulmonary².
3. Caliber Aorta descendens² = caliber aortic stem² + caliber pulmonary stem².

2

TABLE II.

	A	B
Pulmonary stem	3.8 = 14.44 = 14.44	4.0 = 16.00 = 16.00
Ductus	2.6 = 7.76 } = 14.72	2.2 = 4.84 } = 9.89
Right pulmonary	2.1 = 4.40 }	1.9 = 3.61 }
Left pulmonary	1.6 = 2.56 }	1.2 = 1.44 }
Aortic stem	3.8 = 14.44 = 14.44	3.8 = 14.44 = 14.44
Pars comm. a.	3.0 = 9.00	3.0 = 9.00
Aorta descendens	4.1 = 16.81 = 16.81	3.8 = 14.44 = 14.44

Equation 1. In A. 16. 8 : 16.76. In B. 14.44 : 13.84.

Equation 2. In A. 14.44 : 14.72. In B. 16.00 : 9.89.

Equation 3. In A. 15.81 : 14.44. In B. 14.44 : 15.22.

Equation 1 conforms nicely in pig A; in B an error of 3 per cent carrying capacity. Equation 2 conforms nicely in pig A; in B an error of 38 per cent carrying capacity. Equation 3. In pig A, the Aorta descendens is 16 per cent larger than necessary (carrying capacity), and in B, it is 5 per cent smaller than necessary. In all of these measurements the coronary circulation has not been taken into account. In any event the results will show that measurements of this character are valueless for exact conclusions because we must grant that:

1. The vessel lumina are exactly circular.
2. The vessel elasticity must be equal.
3. The expansion of these vessels must be equal in all directions.
4. The intrinsic vessel resistance must be the same.
5. The capillary resistance in all vessels must be equal or known.
6. The quantity of blood expelled by the two sides of the heart must be the same and the pressure exerted equal.
7. The vessels must undergo no particular change after death and fixation.

When all these points have been established, there are still a number of factors to be considered before we can arrive at definite conclusions. We, therefore, raise the question of reasonable doubt to Ziegenspeck's major premise, and state in opposition that we believe we can show that the Aorta descendens carries away more than half of the contents of both ventricles, and further, that the ductus carries more blood than the Pars communicans aortæ.

DATA OBTAINED FROM INJECTION.

It would be difficult, indeed, to grant that the relations of the blood currents in the living fetal heart could be studied in the dead animal, and this is more true in Ziegenspeck's experiments, because only one vein was injected and no attempt made therefore to repro-

duce, as far as it was possible, the life-like conditions. We have seen that Trew, Roederer, Sénac and others found that injected material did pass through the foramen ovale; Reid found that material injected into the inferior cava in the human embryo passed over entire to the left, or at least he did in one case, even when a simultaneous injection was carried out in the superior cava; Ziegenspeck finds that material injected into the umbilical vein passes equally to the right and left ventricles. We do not object to this as a finding, but we do not see how of itself it proves anything for the living heart under entirely different conditions, and minus the factor of auricular and ventricular aspiration that Ziegenspeck himself uses as an argument against the theory of Galen-Harvey.

We now come to a critical examination of Ziegenspeck's contention: "Das Blut, welches in einem Herzrhythmus das Herz durchströmt, wird gevierteilt. Die Hälfte wird von der V. cava inf. geliefert und gleichmässig auf den linken und rechten Vorhof verteilt. Jedes Viertel der Gesamtmenge mischt sich links mit der gleichen Menge aus den Lungenvenen, rechts mit der gleichen aus der V. cava sup. Diese Mischung: $\frac{1}{2}$ Cava inf., $\frac{1}{2}$ Cava sup. geht zu $\frac{1}{2}$ durch die Lungenarterien nach links zu $\frac{1}{2}$ unverbraucht in die Aorta descendens (durch den Ductus arteriosus). Die Mischung links geht ebenso zu $\frac{1}{2}$ unverbraucht durch das Schaltstück in die Aorta descendens, zu $\frac{1}{2}$ in den Oberkörper. Auch das Blut der V. cava inf. wird somit gevierteilt."

To state this proposition in our own way, grant that the ventricular capacity, right and left, equals a volume of say 4.0 cc., then the matter can be expressed in the form of an equation:

$$\begin{array}{rcl}
 \text{R. V.} = 4 & \left\{ \begin{array}{l} \text{Lungs} = 2 \dots\dots\dots \text{Pulmonary return} = 2 \\ \text{Ductus} = 2 \end{array} \right. & \text{L. V.} = 4 \\
 & \qquad \qquad \qquad \text{Aorta descendens} = 4 = \text{Cava inf.} & \\
 \text{L. V.} = 4 & \left\{ \begin{array}{l} \text{Pars. comm. aortæ} = 2 \\ \text{Carotid} - \text{subclavian} = 2 \dots\dots\dots \text{Superior cava} = 2 \end{array} \right. & \text{R. V.} = 4
 \end{array}$$

Correlating this equation with Ziegenspeck's diagram (Fig. 1), we note that several important things have been omitted:

1. The coronary circulation—of the 4 cc. leaving the left ventricle a certain amount is returned to the right auricle but not through either inferior or superior cavæ. This, however, might be granted, practically speaking, in the return through the superior cava.

2. The azygos circulation—of the 4 cc. passing down the Aorta descendens a certain amount is not returned through the cava in-

FIG. 1.

ferior but through the azygos system either to the cava superior or to the coronary sinus (pig). Results in 4 cc. minus returned through the inferior cava.

3. The lymphatic return of the entire region supplied through the Aorta descendens is returned to the heart through the superior cava. Results in 4 cc. minus returned through the inferior cava.

Leaving out a consideration of the bronchial system, the objections would mean that according to Ziegenspeck's contention and diagram, the return through the superior cava is greater than through the pulmonary veins, and second, that the cava inferior returns less than the 4 cc. necessary to fill both ventricles one half.

The only way to make this scheme a tenable one would be (inasmuch as the foramen ovale does not afford communication between the two auricles—Wolff theory), to abandon the exact division of blood and to grant that more than one half of the return through the cava inferior passes to the left. Here, however, we read, "Dass die linke Mündung der Vena cava inf. enger ist als die rechte ändert daran nichts", which is far from reassuring; and further, "Das Herz wirkt als Saugpumpe und jeder Ventrikel aspiriert in der Diastole das zu seiner völligen Füllung noch nötige Quantum aus der V. cava inferior." Now even granting the marked suction action of the ventricles (which we do not believe) inasmuch as the beat of the two sides is synchronous, the only way for the left ventricle to fill itself through the narrower channel would be to aspirate more markedly. But here Ziegenspeck answers the question himself by presenting Table II with thirty-three measurements to show that the right and left ventricular walls are of equal thickness, and by his assumption in his major premise that both ventricles exert an equal pressure during systole.

We are not able to see how this proposition may be made a feasible one, and also for reasons presented as the result of our own investigations must oppose "Das Gesetz der Halbierung des Blutes im Foetal-kreislauf". Further we do not see wherein Ziegenspeck is justified in his claim that he has simplified the description of the placental circulation, or wherein the anatomical findings of the Wolff school can lead directly to the assumption that the foramen ovale does not afford communication between the two auricles.

PERSONAL FINDINGS.

It became evident from the varying results obtained through observation and injection of the dead fetus, that if any further work

was to be done on the course of the blood through the fetal heart, it must be undertaken in the living animal, and with the placental circulation intact. The fetal pig was chosen because of the accessibility and abundance of material and the several propositions demanding an answer through the experimental method were considered as follows:

- I. Is the ventricular capacity an equal one in the fetal heart?
- II. Is the pressure exerted by each ventricle equal?
- III. What is the course of the blood entering the heart through the cava inferior?
- IV. What is the course of the blood entering the heart through the cava superior?

I. The capacity of the two ventricles in the fetal mammal has always been considered equal (note the exception in the Méry theory) because that is the condition in the normal adult heart and because of the necessity of this condition at birth. There appears, however, to be no experimental evidence on the question. Accordingly, the pig embryo was opened (see later) and a ligature slipped around the heart at the auriculo-ventricular sulcus with the idea that if the ligature was tightened at the completion of auricular systole, the aortic-pulmonary and auriculo-ventricular orifices would be occluded and the contents of the ventricles isolated. The experiment proved successful in two out of ten trials. The heart was next removed from the body, washed, the contents of each ventricle bled into separate vials and the volumes compared. Comparison of the two vials showed equal capacity as nearly as this rather primitive method permitted in both cases. There being no valid objection to equal ventricular capacity (generally accepted), the point was considered as settled in the affirmative. The two ventricles in the living fetal pig contain or at least expel equal quantities of blood.

II. The pressure exerted by the right and left ventricles in the fetus has also been considered equal, because both ventricles expel blood into the Aorta descendens, and secondly by observation, nicely shown in Ziegenspeck's table, because the right and left ventricular walls are equally well developed until after birth when the left ventricle wall hypertrophies rapidly. Our later experiments required

the simultaneous recovery of blood under identical conditions and to this end the following technique was employed:

Pieces of glass tubing about 10 cm. in length were carefully drawn in the flame to a fine connecting piece of about 1 mm. in diameter; laid aside to cool and then carefully broken at the point indicated (Fig. 2). This procedure resulted in pipettes of the same

FIG. 2.

opening and, when fastened together with a small elastic band, permitted sufficient spreading to allow the pipettes to be passed one to either side of the ventricular septum and permitted their use as a single pipette. The opening in the pipettes was small enough to necessitate an actual pumping on the part of the ventricles, while the capillary attraction aided in holding the contained blood in place. This was further assisted by mouth pieces of rubber tubing which were pinched off on the withdrawal of the pipettes from the heart.

The beating heart was laid bare (see later) and the pipettes thrust one into each ventricle simultaneously. In all cases where the pipettes were properly introduced and where the heart continued to beat, the blood mounted progressively and evenly in both; proving to our satisfaction that the pressure exerted by the right and left sides is an equal one. Further there was little, if any, appreciable oscillation of the blood in the two pipettes which went to show that in the opened chest little aspirating action was manifested by the ventricles. The results, thus far, are in perfect harmony with what has been quite generally accepted and may be said to substantiate these views in an experimental way.

It was found that in the majority of pigs, the heart suffered but little inconvenience through the introduction of the pipettes and in some the heart beat quite rhythmically for many minutes even after they were withdrawn. Inasmuch as it was impossible to estimate how long it would take the blood to reach the heart from a given point, a requirement was set that the heart must beat at least five times after the introduction of the pipettes and that the blood

must mount evenly and progressively in both pipettes. Each pig used therefore directly controlled the point that the ventricles exerted an equal pressure.

Injection Experiments.

We have seen that the legitimate cry of artifact was raised by Born to the anatomical findings of Ziegenspeck, and that it may also be raised to all injection experiments on the dead animal even if the animal be used directly after death and all precautions taken to avoid undue pressure. The heart itself is no longer the active agent and there is no way of determining how much the contracture of the heart muscle may influence its normal intrinsic relations.

Technique. The following idea was carried out: to inject a non-irritant granular substance suspended in normal salt solution into a selected vein; to allow the blood current to propel these granules to the heart; to recover some of the blood from both beating ventricles under identical conditions; and to examine the blood recovered for the granules injected.

Stand was taken in the abattoir where the pig uteri were removed and dropped into a tank truck. The larger and uninjured uteri were selected and laid upon a table. Next a small incision was made into the uterine wall at some distance from the markedly vascular area and the incision widened by tearing to allow the escape of the pig. It was found that tearing through the uterine wall practically eliminated all hemorrhage and pigs were rejected if any amount of oozing occurred.

Injection was made only in those pigs in which the cord pulsation was strong. An ordinary hypodermic syringe was filled with corn-starch granules suspended in normal salt solution, the air expelled, and about one half of the syringe contents was injected slowly into the umbilical vein, some 5 cm. from the navel. The needle withdrawn, the pig was rapidly opened with a large blunt scissors by cutting through the length of the sternum and by a lateral cut through the abdominal wall just below the diaphragm. A blunt instrument was selected with the idea of tearing rather than cutting through the tissues and pigs were again rejected if anything further than

a slight oozing resulted from the incisions. Next the pericardium was incised and the paired pipettes thrust simultaneously into the two ventricles. An arbitrary requirement was established that the heart must beat at least five times after the introduction of the pipettes, giving a better chance of recovering the granules injected. The blood in the pipettes was immediately expelled into paired vials, marked right and left, containing a small quantity of half per cent acetic acid. The vials corked and shaken thoroughly. Later the vials were separated, and the contents diluted to an equal quantity with dilute acetic acid. Each was shaken a given number of times, and a small amount of fluid withdrawn by a pipette from the central area of the vials. Samples from the right and left sides were placed on one slide and compared under the microscope for the number of starch granules.

Objections.

1. The death of the mother. It is well known that pigs will live in the removed uterus for many hours after the death of the mother. In our experiments the time rarely exceeded half an hour and in some cases about fifteen minutes after the sow's death.

2. The contraction of the uterus. This was not marked but was present in some cases. We shall show later that this is not a serious objection to our results.

3. The artificial factors introduced in opening the chest and manipulating the heart. Granted present. The collapse of the lungs especially offers an abnormal condition which probably limits the pulmonary return.

4. The introduction of the pipettes. This is undoubtedly placing the heart under some disadvantage, but we do not consider the objection a serious one because only a small quantity of blood was withdrawn and because the heart showed no signs of interference for at least five beats.

5. The introduction of a foreign substance in the circulation. Cornstarch granules are non-irritant and non-toxic but are of sufficient size to plug the capillaries, hence the blood was obtained as soon as it reached the heart.

It will be seen from these objections to our method that it is practically impossible to reproduce the normal conditions in all details as they are found in the fetus in utero. All that we claim is that the artificial elements were avoided as far as facilities permitted, and that our procedure is an improvement on experiments made thus far. We at least allowed the blood stream to propel the granules through what appears to be the normal course of the blood in the fetal heart with a minimum of abnormal conditions imposed. The method can, therefore, not be called exact enough for definite proportions, and we make use of the term 'about equal' in this paper as a personal equation set within 10 per cent of difference in comparison of the two blood samples.

III. What is the course of the blood entering the heart through the cava inferior?

Injection of about one half of the contents of a hypodermic syringe filled with a suspension of cornstarch granules in normal salt solution was made into the umbilical vein about 5 cm. from the navel. The pig was opened immediately, and the blood recovered from the beating heart as in Experiment II. Seventeen paired samples were recovered which registered equal coloration on dilution to equal volumes, and these were examined. Five paired samples proved negative—no corn starch granules found in either ventricle and twelve paired samples were positive—starch granules present. In all twelve paired samples the number of granules proved to be 'about equal' on both sides.

The experiment proves beyond a doubt (as far as pig is concerned) that the von Haller-Sabatier theory is incorrect and that the objections of Williams, Peaslee and Macdonald were well taken. It seems to prove that the blood from the inferior cava is distributed about equally to the two ventricles, and is, therefore, in accordance with the Wolff theory or with the theory of Galen-Harvey. The former states that the blood from the inferior cava is split upon the limbus Vieussens and that the foramen ovale does not afford communication between the auricles; the latter assumes a small pulmonary return, a mixing of the blood of the two cavæ in the right auricle, and a passage of mixed blood through the foramen ovale.

It now remained to inject the superior cava—for if the granules did not pass through the foramen ovale, the Wolff theory was sustained; while if the granules were recovered from both ventricles, the theory of Galen-Harvey was substantiated.

IV. What is the course of the blood entering the heart through the cava superior?

This experiment was found more difficult than the preceding test. It was found almost impossible to open the chest the full length and expose the great veins at the root of the neck without injury to these structures. The insult offered proved to be greater and the death rate proportionately larger. Next only one or two drops could be injected into the superior cava to avoid undue pressure, and, when the needle was withdrawn, the unsupported vein tended to bleed freely. The time limit was reduced to one to two seconds from injection to introduction of the pipettes. Seven paired samples were finally obtained which registered equal coloration on dilution. One proved negative—no starch granules on either side, and six positive—starch granules present. In four, the number of granules on the right and left sides proved to be 'about equal;' in one, more were found on the left than on the right, and in one, more on one side than on the other (labels confused). In both of these samples the excess was easily 50 per cent.

The fact, however, that starch granules injected into the superior cava did pass through the foramen ovale in all cases where they were demonstrated at all showed conclusive evidence in favor of the theory of Galen-Harvey that the caval currents mix in the right auricle and that mixed blood passes from the right auricle into the left through the foramen ovale. Inasmuch as about ten seconds elapsed from the injection of the umbilical vein to the recovery of blood from the heart in Experiment III, and one to two seconds from the injection of the superior cava, it was thought possible to make a double injection in the same pig using colored granules in the one and colorless granules in the other injection. If both varieties of granules were found on both sides, the experiment would show that the currents mix in one and the same pig.

Pigs in this experiment were opened first and about ten seconds

allowed from the injection of the umbilical vein with colored granules (I-KI) to injection of the superior cava with colorless granules. Only six pigs lived through the requirements in two full mornings work, and of the six, three samples were lost owing to the hurry. Two paired samples were obtained and one from the left side (right pipette struck the septum). Superficial examination of these samples revealed the presence of both varieties of granules on both sides in the two and both varieties in the one from the left. There was of necessity a delay in counting, and when it was attempted some hours later, it was found that the iodine had diffused and colored a large proportion of the colorless granules so that a comparative count was impossible. The experiment, however, further substantiated the Galen-Harvey theory and opposed, therefore, all the more the Wolff theory.

The results from our experiment in the living embryo lead to the following statement: that the ventricular capacity and pressure is an equal one; that the foramen ovale does afford communication between the two auricles; that the blood of the two cavæ mixes in the right auricle; and that mixed blood passes through the foramen ovale. We agree, therefore, with the theory of Galen-Harvey and believe to have established it through experimental evidence.

It now remains to consider what objections may be raised to our results and wherein the evidence supports the Galen-Harvey theory as opposed to all other theories.

It will be seen from our results in the living pig embryo that about one half of the return through the superior and inferior cavæ passes through the foramen ovale into the left auricle. This fact might be interpreted in one of two ways if we grant, as we must, that the collapse of the lungs through opening the chest interferes with the pulmonary circulation—the passage of blood through other parts of the fetal body not necessarily being affected:

a. The pulmonary return is relatively free, as stated in the Wolff theory, and that the artificial factors (collapse of lungs and manipulation of the heart) are sufficient to practically prevent blood from passing through the lungs; or,

b. The lung circulation is relatively small in amount and that

the pulmonary return is reduced by the artificial conditions so that it might be well within the personal equation set in our experiments (10 per cent).

The first interpretation offers a serious objection to our results because those investigators favoring the Wolff theory will hold that if we interfere with a large pulmonary return (about one half [Wolff], exactly one half [Ziegenspeck] of the contents of the right ventricle), we also destroy the normal balance of return to the auricles through increase in flow through the cava inferior and through decrease in flow through the pulmonary veins. Hence, the normal position of limbus Vieussens to the orifice of the inferior cava and the function of the foramen ovale may be rendered false. This criticism we have foreseen and we, therefore, discuss the position of the Wolff theory rather fully.

The results of our first two experiments have confirmed the major premise of the Wolff theory that both ventricles expel the same amount of blood under the same pressure, and we now come to an examination of the physical laws underlying the flow of the blood through the arteries. Ziegenspeck based his measurements on the arguments that if the caliber of the ductus and Pars comm. aortæ was an equal one, they transmitted equal quantities of blood; that this quantity transmitted by each vessel was equal to one half of the contents of a ventricle; and that the Aorta descendens carried away one half of the contents of both ventricles. We stated in our objections to these propositions that we believed it might be shown that the ductus transmits more than the Pars comm. aortæ; and that both feed into the Aorta descendens more than one half of the contents of both ventricles.

If we can prove that the resistance to flow in the Pars comm. aortæ and in the ductus is less than in the branches of the aortic arch and in the right and left pulmonary arteries respectively, then we also prove that the Aorta descendens carries more blood than the caliber of its lumen would indicate, while the other branches convey relatively less. We believe we can substantiate the generally accepted idea that the placental area is the point of least resistance in the fetal circulation for the following reasons:

1. The two large umbilical arteries feed into one large umbilical vein—a proportion of lumina which would indicate that either the arteries are under lower pressure than usual, or the vein is under relatively higher pressure. In either case, it would present a low resistance in the placental capillaries.

2. The umbilical vein, practically of round lumen, transmits blood directly and indirectly into the intra-thoracic cava inferior without any marked increase in lumen of the latter vessel, showing that by far the larger proportion of blood passing down the Aorta descendens is returned through the umbilical vein.

3. The umbilical arteries and vein have a long and tortuous course through the jelly-like cord which probably offers little support to the vessel walls, and were not the placental resistance lower than the resistance in the vessels of the embryo body, little blood would pass through the umbilical vessels, whereas we know the reverse to be the case. It must be remembered that in human embryos the cord usually averages about 55 cm. at birth, and that the umbilical arteries may be reckoned on an average of 50 cm. longer than any other arteries in the fetal body, and the vein, while not proportionately long, is easily 40 cm. longer than any other vein. This distance of a little less than a metre represents an appreciable amount in terms of intrinsic vessel resistance.

4. There can be but little doubt that the contraction of the uterus must increase the resistance in the placental site and still the fetal heart is able to force the blood through the long course and quite freely. This is our answer to the objection that opening the uterus rendered false the circulatory condition in the fetal pig.

5. Taking Ziegenspeck's measurements at their face value if a 2.97—mm. ductus and Pars comm. aortæ feed into a 3.832 mm. Aorta descendens, then the resistance in the latter vessel must be considerably less than the resistance found in the lungs and carotid-subclavian vessels, for the lumen is too small to carry off the blood. It should read 4.14 + mm.

From these data we are able to assume with reasonable certainty that the resistance to flow in the placental area must be considerably less than in the fetal body, and that, therefore, until this resistance

is a known quantity, the lumen of the Aorta descendens is no criterion of its carrying capacity. We believe that the Aorta descendens carries more than one half of the contents of both ventricles, and believe this is not only a logical deduction but that it is confirmed by observation.

Conversely, if the circulation through the Aorta descendens is relatively free, then the blood flow through the carotid-subclavian and pulmonary arteries is relatively small. In other words, these two systems return less than one half of the contents of both ventricles. While this view is entirely contrary to Ziegenspeck's law of the equal division of blood, it is not entirely contrary to the Wolff theory of the splitting of the current of the inferior cava upon the limbus Vieussens. It will be necessary to substantiate our evidence from the injection experiments by an attempt to show clearly that the lung circulation is relatively smaller in amount than the circulation through the carotid-subclavian systems, or negatively, that the ductus carries more blood than the Pars comm. aortæ. The two points will be argued under separate headings, although they lead to the same result.

Evidence that the circulation through the lungs is relatively small in amount:

1. The histological appearance of the fetal lung, even when hardened in situ, does not substantiate the theory that large quantities of blood pass through the pulmonary circulation. The air sacs are collapsed, the capillaries are compressed and tortuous and possibly more numerous than elsewhere in the fetal body. Not only is the blood current interfered with directly in the capillary system, but the expansion of the vessels to the blood stream is limited.

2. The right and left pulmonary arteries are placed practically at right angles to the blood impact, while the blood wave passing around the aortic arch meets the carotid-subclavian vessels with their openings more nearly parallel to the current. Showing if the lumina of these vessels read alike, the carotid-subclavian arteries will receive a trifle more blood (the grain of truth in the Sabatier theory).

Evidence that the ductus conveys more blood than Pars comm. aortæ and that it carries more than one half of the contents of the right ventricle:

1. The laws governing the equal flow of fluid through pipes have certain limiting clauses; not only must be the 'head', the direct resistance at the pipe opening and the pipe lumen and character be the same, but the pipes must be of the same length and have the same course. Therefore, the Pars comm. aortæ will transmit less blood than the ductus, even if the caliber be circular and of the same diameter, because the course of the blood from the left ventricle is a longer one; because the course is curved as opposed to the relatively straight line to the ductus; and because the branches on the arch are more advantageously placed to interfere with the current.

2. If in our experiments we interfered with a large flow of blood through the lungs, then one of two things must have occurred:

- (a) We increased the pressure on the right side in order to force the excess of blood through the ductus, or
- (b) We decreased the amount of blood expelled by the right ventricle.

We have shown in our experiments that the pressure on the right and left side continued to remain the same, for the blood mounted progressively and equally in the pipettes when they were properly introduced and where the heart continued to beat. Inasmuch as no difference was observed in the character of the heart beat, we may infer that the ventricles continued to expel equal quantities of blood as demonstrated in Experiment I under the artificial conditions mentioned. If we grant that the lung circulation is free, the ductus carried away the excess without any appreciable effort on the part of the right ventricle; according to Ziegenspeck, the ductus would have to carry double the amount, and according to Wolff perhaps not quite double. If we grant that the circulation is relatively small, the ductus carried but little more than normally.

We, therefore, do not see any evidence that we interfered seriously with an alleged large amount of pulmonary return or that we oversupplied the vena cava inferior with blood. Further, waiving all this evidence aside, if we did increase the amount of return through the inferior cava, we also raised the pressure in that vein, and we still do not see why the limbus Vieussens should not divide the current in the manner demanded by the Wolff theory. If we inter-

ferred markedly with any of the return, it was that through the cava superior and this should if anything lessen the chances of that blood passing to the left.

If we now grant that the pulmonary return is relatively small in amount, then we can group the von Haller-Sabatier and the Wolff theories under one head, for in neither does the foramen ovale afford communication between the two auricles and in both the vena cava inferior must send an excess of blood to the left auricle to make up for the deficient pulmonary return. Against these theories we can present the view of Galen-Harvey that the foramen ovale does afford communication between the two auricles and that mixed blood in the right auricle passes through that opening to make up for the deficient pulmonary return. Which of these theories do the facts support?

Neither the von Haller-Sabatier nor the Wolff theory can account for the relatively good circulatory conditions found in embryos with bilocular and trilocular hearts; in the cases of incomplete separation of the ventral aortic stem into aorta and pulmonary artery; or in the anomalous cases where the lungs are supplied, in part, from the Aorta descendens. All of which conform to the Galen-Harvey theory.

For the Harvey theory, as opposed to all others, comes our evidence obtained in the living pig that in no case were cornstarch granules injected into the inferior or superior cavæ or both—not recovered from both sides of the heart. For the Harvey theory comes the simple explanation of a mixing of blood in the right auricle, and the passage of mixed blood through the foramen ovale to the left auricle. In this theory, we gain the point raised in the Wolff theory that no artery in the embryo contains arterial blood, without the extremely complicated and incorrect arrangement presented by that scheme.

We trust that this article carries conviction with it and that the coloring of diagrams of the fetal circulation to render the impossible theory of Sabatier clear to the student will hereafter be omitted. The arrows to indicate the course of the blood through the fetal heart may be replaced by the statement—the blood of the two caval

veins mixes in the right auricle, and mixed blood passes through the foramen ovale into the left auricle to make up for the deficient pulmonary return (the theory of Galen-Harvey).

PRELIMINARY NOTE ON THE REPTILIAN AND AMPHIBIAN
CIRCULATIONS.

Every article that has appeared since 1835 has been in favor of the proposition that no arteries in the mammalian embryo contain arterial blood. It would be fitting, therefore, to retrace our steps to the time of Harvey, Méry, Winslow and others. Here we find that the relations of the blood currents in the mammal were based largely on the turtle. In this animal, although the auricles are completely divided, the undivided ventricle lends itself to a similar scheme

FIG. 3.

of the crossing of currents, and diagrams illustrating this condition of affairs have been presented. We present the scheme taken from Parker and Haswell after Huxley (Fig. 3), together with the following description: "From the cavum pulmonale arise the pulmonary artery, and from the cavum venosum, the two aortic arches. When the auricles contract the cavum venosum becomes filled with venous blood from the right auricle, and the cavum arteriosum with arterial blood from the left auricle; the cavum pulmonale becomes filled with venous blood which flows into it past the edges of the incomplete septum. When the ventricle contracts, its walls come in contact with the edges of the septum, and the cavum pulmonale becomes cut off from the rest of the ventricle. The further contraction consequently results in the venous blood of the cavum pulmonale being driven out through the pulmonary artery to the lungs, while the blood

that remains in the remainder of the ventricle (arterial and mixed) is compelled to pass out through the aorta (ae)." Here, as in the mammal, we find anatomical observation correlated with inferred physiological necessity and no direct experimental evidence; and here again comes the question "Does this actually occur?"

We present a preliminary report of our findings in some twenty-five turtles of three species. We do not offer the data for anything more than its face value, or do we present it as an exact result. The method was somewhat primitive, but the evidence derived is suggestive.

The carapace was removed under precautions to eliminate hemorrhage, the heart laid bare and kept moist.² The experiment was divided into three parts: (1) injection of cornstarch granules in normal salt solution into the right auricle; (2) into the left auricle; and (3) double injection of colored and colorless granules into the two auricles.

The blood was recovered under identical conditions in the following way: A double ligature was placed around the three vessels at the transverse pericardial sinus; the cornstarch-salt solution was introduced into the auricle during its diastole; the auricle allowed to contract, giving time to have the distal ligature ready to tie; when the ventricular contraction was well under way, the distal ligature was tied and immediately the proximal ligature—thereby isolating a segment of the blood in each of the three vessels. The ligated part was then removed and washed to avoid any granules which might have been in the ventricle, and each vessel bled into separate watch glasses containing a quantity of $\frac{1}{2}$ per cent acetic acid. Washing between incisions to avoid any mixing. Comparison of the three glasses containing the blood recovered from right and left aortæ and from pulmonary artery respectively revealed that, whether cornstarch granules were injected into the right or left auricle or both, they were always recovered from all three vessels. Comparative count proved rather indefinite, although in one case equal quantities were counted in each vessel.

²The writer expresses his obligation to S. C. Murphy for the careful assistance rendered and for the use of his modification of Ringer's solution.

Further experiments on larger animals must be undertaken before the exact proportions can be established. The results show, however, decidedly in favor of the statement that in the turtle the arteries contain mixed blood.

It now remained to investigate the evidence presented in the amphibian, to which can offer as yet no personal experiments. The usual descriptions, however, are as follows: "When the auricles contract, the blood from the left auricle, which has come in from the pulmonary vein and is therefore oxygenated, is forced into the left side of the ventricle, while the impure blood from the right auricle, which comes through the sinus venosus, pours into the right side and middle portion of the ventricle. The blood from these different sources is prevented from becoming mixed by being received into slit-like chambers in the ventricular wall. During the contraction of the ventricle, the impure blood, lying near the opening of the bulbus, naturally passes out first, while the pure pulmonary blood from the left side is forced out only toward the close of the ventricular contraction. When the ventricle first contracts, the wall of the bulbus cordis is relaxed, and the impure blood flows freely over the edge of the spiral valve into the left compartment, when it is free to issue through the pulmo-cutaneous arches through their common opening. Now the blood is under less pressure in the pulmo-cutaneous arches than in the others, because its route is shorter and there are no impediments to its flow. The blood first issuing from the heart takes the line of least resistance, namely, the pulmo-cutaneous arches, and is forced through the first two pairs of arches only when it has no easier avenue of escape." (Holmes.)

Here are two definite statements, to which we may raise the plea of reasonable doubt: "Is the pulmo-cutaneous system really under less pressure and does it actually receive blood first?" With all preparations made to investigate this phase of the problem, we accidentally came across an article by Gompertz, who made simultaneous tracings from the two vessels and found that the curve in the aorta agreed with that in the pulmonary both for synchrony and for pressure. This statement again would sustain the objection made to the identity of currents in the amphibian circulation.

CONCLUSIONS.

1. The capacity of the right and left fetal ventricles is equal.
2. The pressure exerted by the right and left fetal ventricles is also an equal one.
3. The blood entering the heart through the superior and inferior cavæ mixes in the right auricle.
4. The foramen ovale affords communication between the two auricles.
5. Enough mixed blood passes from the right auricle into the left through the foramen ovale to make up for deficient pulmonary return.
6. The pulmonary return during fetal life is relatively small in amount, and probably does not exceed one fifth of the capacity of the ventricle.
7. The ductus carries more blood than the descending aortic arch; probably the proportion of 4-3 is not far from accurate.
8. The Aorta descendens, being under lower resistance, transmits more blood than the caliber of its lumen would indicate and the greater part of its blood passes out through the umbilical arteries.
9. No artery in the fetus contains pure arterial blood—all contain mixed blood.
10. We oppose the theory of von Haller-Sabatier and also the theory of Wolff and Ziegenspeck.
11. We substantiate the theory of Galen-Harvey.
12. We oppose the theory that the pulmonary artery in the turtle transmits only venous blood and hold for a mixture of blood in the common ventricle as opposed to Brücke's view.
13. We believe there is evidence for a mixing of blood in the amphibian ventricle or in the vessels or in both.
14. We believe that the closed circulation of an arterial and a venous blood is first found in the mammal and bird after birth; in the fetal mammal and bird; and in the reptile and amphibian we believe that the circulation is one of mixed blood. In the fetal mammal and bird, the mixing takes place in the right auricle; in the reptile, in the common ventricle or, where the ventricle is more completely divided, in the arterial orifices or in the foramen Panizzæ or in both;

in the amphibian, the mixing occurs in the common ventricle, in the vessels or in both.

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