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Observations on the rhinoceros cardiac receptor system

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(With 1 plate and 7 figures in the text)

First-time observations are submitted on the anatomy of the rhinoceros cardiac receptor apparatus. This is shown to comprise chemoreceptors in the form of canonical aortic and carotid glomera and mechanoreceptor areas essentially similar to those established for certain other mammalian forms. A description is given of the cardiac adventitial nerves (aortic nerves) which provide a guide to receptor areas. The structure of the rhinoceros aortic glomus is detailed.

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Introduction

In recent years the mammalian cardiac receptor system has been intensively investigated both histologically and experimentally towards elucidating the precise anatomical pathways involved in the conduction of the various cardiac reflexes. In such experimental animals as the cat, dog, rabbit, rat and pig special attention has been devoted to mechanoreceptor morphology and to the plotting of receptor areas (Hainsworth, Kidd & Linden, 1979). Of necessity receptor areas have been determined on histological grounds alone, since the proximate and certain anatomical guides thereto—the peripheral branches of the cardiac nerves—are impracticable of isolation by dissection in the small hearts of the usual experimental animals. Nevertheless such peripheral branches entering the wall of cardiac chamber or great vessel indicate the presence therein of receptor areas and their exposure by nice dissection renders unnecessary any histological search for mechanoreceptors in their territory of distribution. Such peripheral branches are patient of isolation by dissection in the large ungulate heart and those of the rhinoceros heart are described below under the designation of aortic nerves.

In subservience to haemodynamic requirements the mammal heart is equipped with an elaborate receptor apparatus comprising mechano- and chemoreceptors. Mechanoreceptors (pressor receptors, baroreceptors) monitor the status of the circulation (i.e. its volume and complex pressures) whilst chemoreceptors monitor changes in the blood

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chemistry. The former are the specialized endings of cardiac nerves and are chiefly situated below the endothelial lining of the cardiac chambers and annectant great vessels, where collectively they form receptor areas essential to the initiation of cardiac reflexes. The latter are macroscopic, vaso-epithelial structures (known variously as paraganglia, bodies or glomera) situated within the tunica adventitia of the aorta, the common carotid artery and (sometimes) the right subclavian artery.

Mammalian chemoreceptor organs have long enjoyed anatomical recognition though appreciation of their functional rôle is relatively recent. Thus the fairly obtrusive glomus caroticum has been well investigated in several mammalian species including some exotic forms (Adams, 1958). The more cryptic glomus aorticum, however, remains little known for mammals generally. For the Perissodactyla both the aortic and the carotid glomus remain virtually unknown, with the notable exception of the equid carotid glomus, first described by Mayer (1833) and subsequently well-studied by Sunder-Plassmann (1930), Aszodi & Paunz (1932), Argaud & de Boissezon (1936) and Meijling (1938) among others. For the Tapiridae the carotid glomus of *Tapirella bairdii* alone has been briefly noticed by Ask-Upmark (1935) as "a pea sized yellow lump" in the carotid bifurcation innervated by the glossopharyngeal, vagus and cervical sympathetic nerves. For the Rhinocerotidae nothing has been reported to date concerning either the aortic or the carotid glomus. Evidence is therefore presently submitted attesting the presence of both these chemoreceptor organs in at least two rhinoceros genera (*Diceros*, *Rhinoceros*) and strongly suggestive of the presence of a carotid glomus in a third genus (*Didermocerus*).

Material and methods

During the anatomization of the hearts of a young female African Black rhinoceros *Diceros bicornis* and an adult male Indian rhinoceros *Rhinoceros unicornis* the adventitial nerves were exposed by dissection and the aortico-pulmonary region was carefully explored. Both organs were uninjected and long preserved and the *Diceros* heart had suffered some necropsy destruction of the terminal pulmonary veins and left atrial wall. Glomus tissue was examined histologically by Professor F. R. Johnson, of the London Hospital Medical College, whose authoritative findings thereon are incorporated below. Examination was also made of the carotid vasculature of an adult female Sumatran rhinoceros *Didermocerus sumatrensis* for evidence of the presence of a glomus caroticum.

Observations

The glomus aorticum

An obtrusive glomus aorticum occupies the aortico-pulmonary recess of the *Diceros* heart. It takes the form of a discrete, encapsulated, purplish-coloured vascular mass of extremely soft consistency and of somewhat "granulated" surface. The mass is somewhat compressed and folded upon itself between the root of the ascending aorta on which it lies and that of the contiguous truncus pulmonis. It is triangular in outline and measures 25 mm in width, 15 mm in length and 2 mm in average thickness; it adheres largely to the anterior aortic sinus, its dextral extremity overlapping the origin therefrom of the right coronary artery. The mass is traversed by the terminal aortic and pulmonary branches of an adventitial anterior aortic nerve, from which it receives filaments during their passage through its substance. It receives also two exceedingly fine twigs directly from the truncus pulmonis but no comparable twigs from the ascending aorta (Fig. 1).

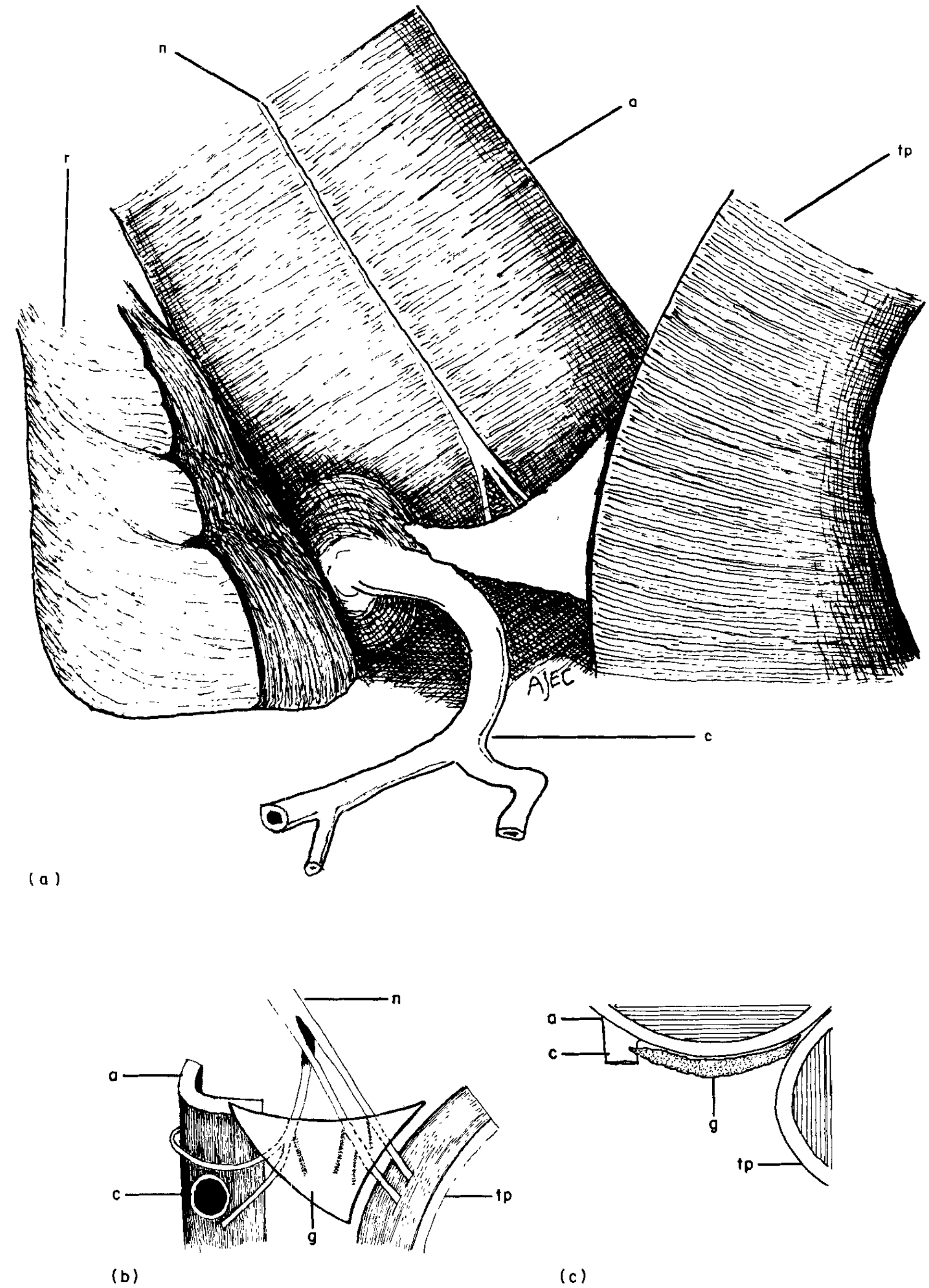

FIG. 1. Glomus aorticum of *Diceros*. Dissection sketches showing (a) the glomus *in situ*, (b) the glomus nerves, (c) the glomus in horizontal section. In (a) the truncus pulmonis is retracted somewhat sinistrally.

a, aorta; c, right coronary artery; g, glomus aorticum; n, anterior aortic nerve; r, right atrium of heart; tp, truncus pulmonis.

Microscopically the mass reveals structural features indicative of its chemoreceptor nature. Essentially it comprises an intricate interlacement of branching, blood-filled capillaries of differing diameters, embedded, together with some arterioles and venules, in an extremely loose matrix composed of very fine collagen and elastic fibres. In close approximation to the capillary walls lie many large (15–20 μm) cells, rendered epithelial-like in appearance by their abundance of cytoplasm; these cells possess round, centrally placed nuclei and exhibit occasional nucleoi and chromatin-granule inclusions. Connective tissue cells of various kinds are present in the matrix, inactive fibroblasts and small lymphoblasts being the most common. The mass is encapsulated by delicate connective tissue and its peripheral regions contain nerve fibres of apparently non-myelinated type (Plate I).

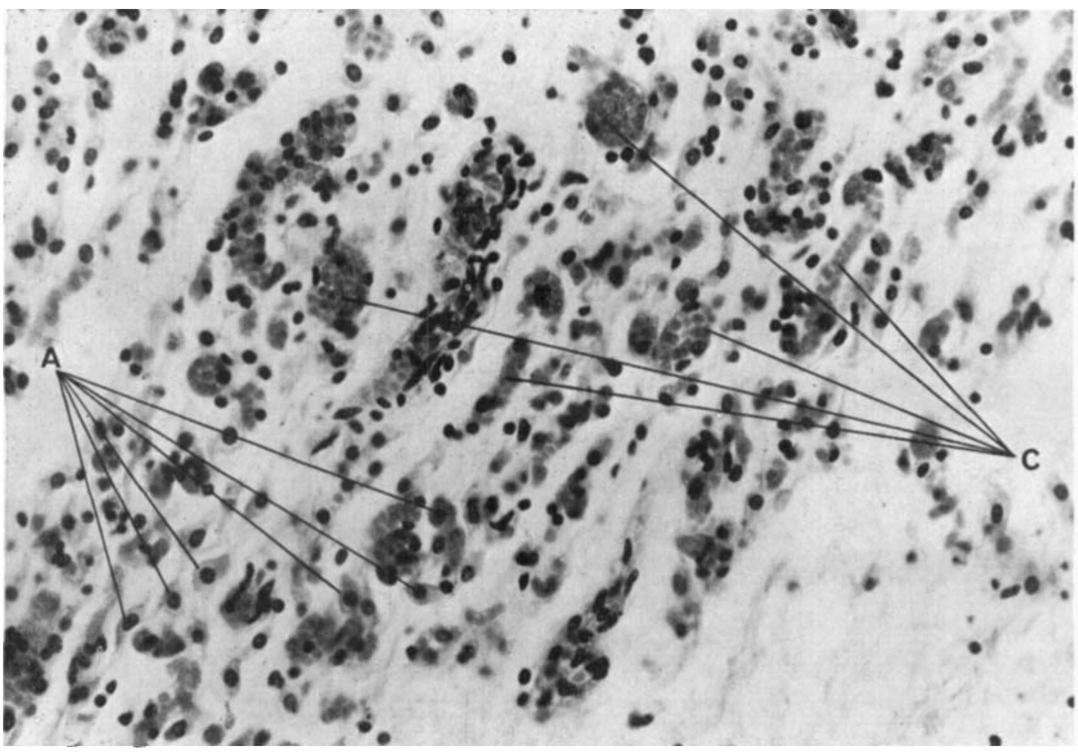

PLATE I. Rhinoceros (*Diceros*) glomus aorticum. Microphotograph of histological structure, showing epithelial-like cells (A) and capillaries (C). (Courtesy of Professor F. R. Johnson.)

The glomus aorticum of the *Rhinoceros* heart is represented by remnants only, its greater part having been inadvertently removed with the aortic adventitia during a prior dissection. These remnants comprise minute scattered islands of glomus tissue adherent to the aorta wall over a canonical glomus area. This area is of triangular outline, measures 40 × 30 × 30 mm and involves the anterior aortic sinus and the aorta wall sinistral thereof. Both within and without this glomus area remain small, discontinuous nerve-fragments which are clearly the remains of the terminal branches of an anterior aortic nerve and some of which are traceable directly into the walls of the ascending aorta and the truncus pulmonis (Fig. 2). These terminal nerve-branches had obviously traversed the substance of a well-developed aortic glomus en route to the vessel walls and had presumably provided filaments to its substance. The vascularization of the glomus is not determinable with certainty: since the most careful scrutiny fails to disclose any twigs to its area from the root of the aorta, the presumption is that glomus vascularization had been effected by the truncus pulmonis.

In all essential anatomical respects the *Diceros* and *Rhinoceros* aortic glomera show agreement.

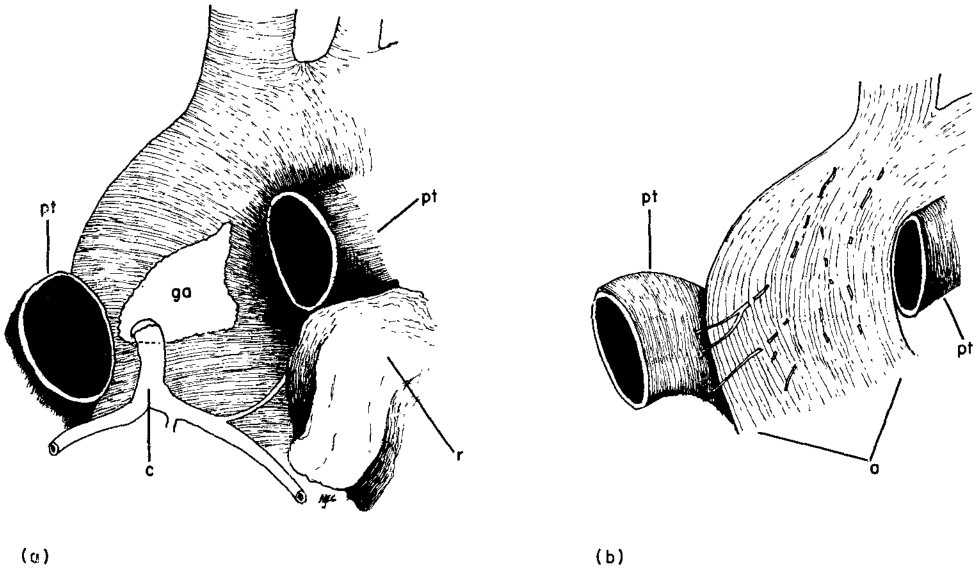

FIG. 2. Rhinoceros (*Rhinoceros unicornis*) glomus aorticum. Showing (a) the glomus area, (b) aortic nerve remnants in and about glomus area. The truncus pulmonis is divided and reflected.
a, aorta; c, right coronary artery; ga, glomus area; pt, truncus pulmonis; r, right atrium.

The glomus caroticum

The same *Rhinoceros* specimen displays a well-developed glomus caroticum in the angle formed by the divaricating terminal (occipital, internal and external carotid) branches of the common carotid artery (Fig. 3). This glomus is a compact, ovoid body, of pinkish colour, 14 mm long, 6 mm wide and 4·5 mm thick. (Aszodi & Paunz (1932) give the corresponding maximal dimensions of the equid glomus as 8 mm, 6 mm and 4 mm). The glomus lies wholly within the thick adventitia of the dilated initial portion of the entocarotid (the sinus caroticus), through which it extends to the tunica media; its non-capsulated surface merges into the surrounding connective tissue and two slender, parallel nerves ramify over its superficial aspect, descending thereto from a connexus of the glossopharyngeal, vagus and cervical sympathetic nerves. The glomus shows no sub-division but its cranial pole is distinctly cleft and admits filaments from the glomus nerves.

The caudal pole of the glomus is firmly anchored to the termination of the common carotid artery by a localized condensation of the carotid adventitia (the ligament of Mayer) within which an arterial twig of uncertain origin reaches the organ.

The carotid arteries of the *Didermocerus* specimen had been earlier denuded of their adventitial coat but strong presumptive evidence of the former presence of a carotid

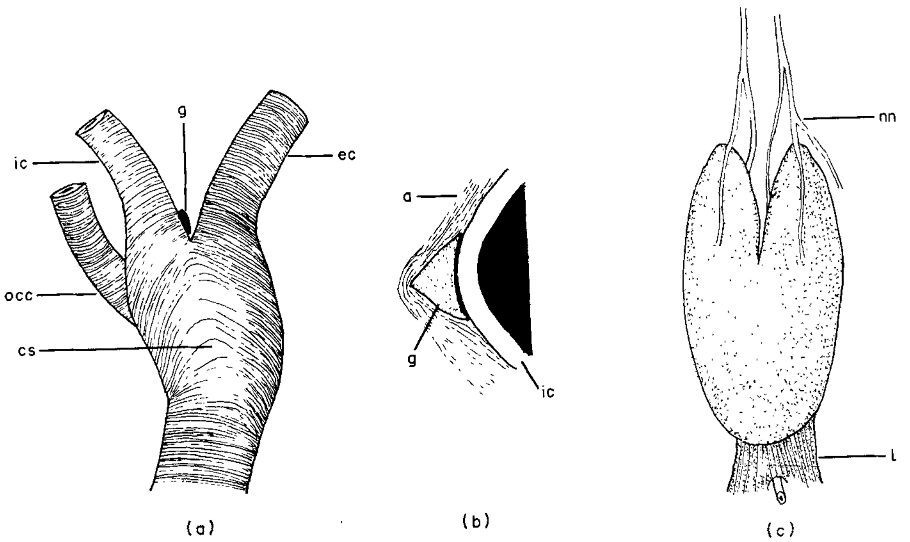

FIG. 3. Rhinoceros (*Rhinoceros unicornis*) glomus caroticum. Shown (a) *in situ*. (b) in horizontal section, (c) isolated. (About × 5 natural size.)

a, adventitia carotica; cs, carotid sinus; ec, ectocarotid; g, glomus caroticum; ic, entocarotid, l, ligament of Mayer and contained artery; nn, carotid nerves; occ, occipital artery.

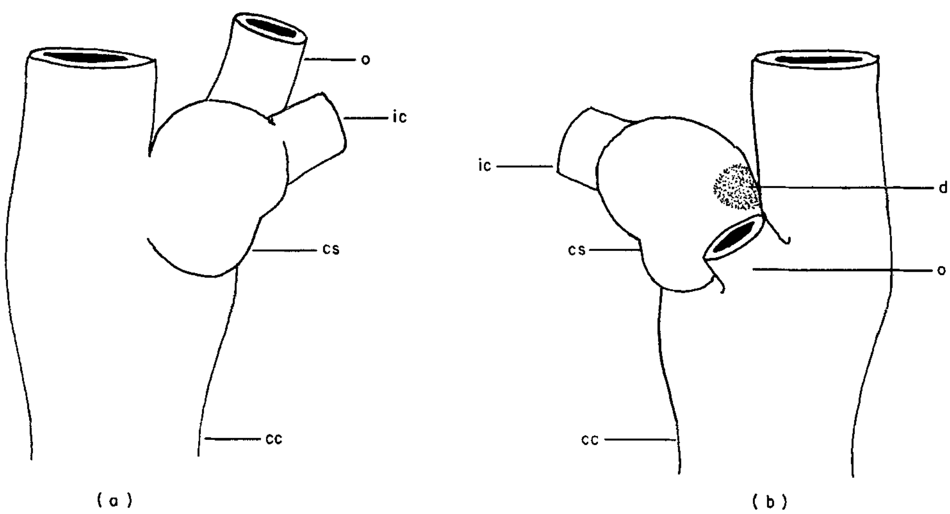

FIG. 4. Sumatran rhinoceros *Didermocerus sumatrensis*. Left carotid sinus seen from (a) the superficial and (b) the deep aspect.

cc, common carotid artery; cs, carotid sinus; d, glomus depression; ic, entocarotid, o, occipital artery.

glomus is provided by an indentation on the deep aspect of the obtrusive carotid sinus. The 15 mm wide common carotid artery attains a terminal width of 19 mm and trifurcates into 10 mm wide external carotid, 6 mm wide occipital and 6 mm wide internal carotid branches. The initial portion of the entocarotid is dilated into a 12 mm wide, flask-shaped carotid sinus. On its deep aspect, contiguous to the ectocarotid, this sinus manifests a well-defined and obviously permanent depression of rounded outline, which can have been produced by nothing other than a carotid glomus (Fig. 4).

The aortic nerves

These are the extremely fine peripheral branches of the main cardiac nerves which pursue a course within the cardiac adventitia to enter the walls of the cardiac chambers or annectant great vessels. They terminate intramurally in specialized (mechanoreceptor) endings which collectively constitute receptor areas and they are therefore an infallible guide to the localization of such areas.

In the *Diceros* heart two aortic nerves are developed, an anterior (ventral) and a posterior (dorsal). Between them they innervate both the glomus aorticum and the walls of the aorta, the truncus pulmonis and the terminal precava. Though direct evidence is wanting there is reason to suspect that *in vivo* these nerves innervated also the terminal pulmonary veins.

Directly or indirectly both aortic nerves arise from a pair of contiguous sympathetic ganglia (a major medial and a minor lateral) lying craniad of the aortic arch—and just possibly the separated portions of a common ganglionic mass. The major (? first thoracic) ganglion is long and fusiform, the minor ganglion is rounded and somewhat prismatic in shape: a short, horizontal connexion unites the ganglia cranially. From the caudal pole of each ganglion issues a substantial nerve bundle: that from the major ganglion descends alongside the right common carotid artery to loop ansa-wise around the first part of the right subclavian artery and to there give off the posterior aortic nerve: that from the minor ganglion is joined by an oblique bundle from the caudo-lateral aspect of the major ganglion to form the anterior aortic nerve (Fig. 5). The aortic nerves receive vagal fibres from an oblique branch of the vagus which subdivides into a shorter, horizontal branch to the major ganglion and a longer, descending branch to the subclavian ansa.

The anterior aortic nerve, some 140 mm long and initially 3 mm wide, proceeds caudalwards from its origin from the two sympathetic ganglia to the root of the ascending aorta. It first passes deep to the nerve-band from the major ganglion and then runs in the adventitia clothing the ventral aspect of the brachiocephalic artery and ascending aorta to the region of the anterior aortic sinus; here, craniad of the glomus aorticum, it divides into its dextral (aortic) and sinistral (pulmonary) terminal branches. Ventral to the brachiocephalic artery it gives off a considerable (55 mm long and 2 mm wide) collateral dextral branch: this supplies a recurrent sub-branch to the dorsum of that artery, then crosses the ascending aorta obliquely to gain its dorsum and there to terminate within the aorta wall (Fig. 5). The nerve's terminal branches traverse the aortic glomus and each supplies filaments to the glomus substance (Fig. 6). The aortic terminal branch, representing the intermediate fibres of the main nerve, is initially single; it supplies filaments to the glomus and thereafter divides into cranial and caudal sub-branches. These run dextrally through the glomus substance in relation to the origin of the right coronary artery; the cranial sub-branch courses above that origin on to the dorsum of the ascending aorta and there enters that vessel's wall: the caudal sub-branch courses caudo-dextrally to that origin and enters the ventral wall of the aorta root. The pulmonary terminal branch of the nerve is initially double: it comprises the lateral fibres of the main nerve in the form of two parallel and equal-sized nerves flanking the aortic terminal branch; these pulmonary branches traverse the glomus substance, individually supply filaments to it and thereafter terminate in the wall of the truncus pulmonis (Fig. 5).

The posterior aortic nerve is shorter than the anterior and arises directly from the ansa of the right subclavian artery. It descends thence caudo-sinistrally over the dorsal

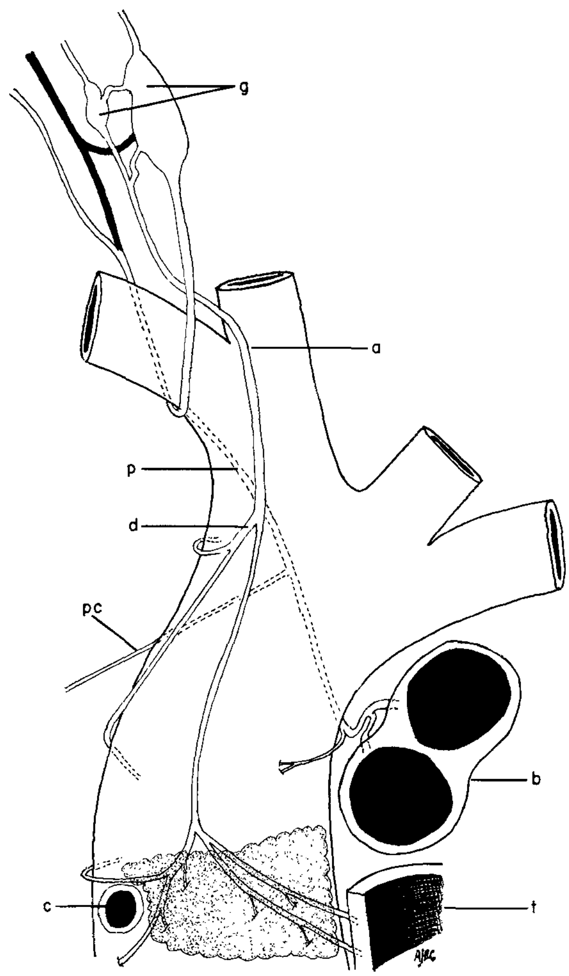

FIG. 5. Aortic nerve of rhinoceros (*Diceros*). Diagram showing origin and distribution. Contribution from vagus in black: glomus aorticum stippled: cranial end of specimen uppermost. Not to scale.

a, anterior aortic nerve; b, bifurcation of truncus pulmonis; c, right coronary artery; d, dextral branch of anterior aortic nerve; g, sympathetic ganglia; p, posterior aortic nerve; pc, precaval branch of posterior aortic nerve; t, segment of truncus pulmonis root.

aspect of brachiocephalic artery and ascending aorta to emerge below the aortic arch in close proximity to the bifurcation of the truncus pulmonis. Here it gives off a short, horizontal branchlet to the ventral wall of the ascending aorta and then divides into two equal-sized terminal branches, each of which enters the wall of the truncus where this vessel becomes continuous with one or other of the pulmonary arteries. Soon after gaining the aorta dorsum the nerve gives off a long, delicate, collateral branch which runs caudally between the aortic arch and the right atrium to terminate within the wall of the precava at its junction with that atrium (Figs 5, 7).

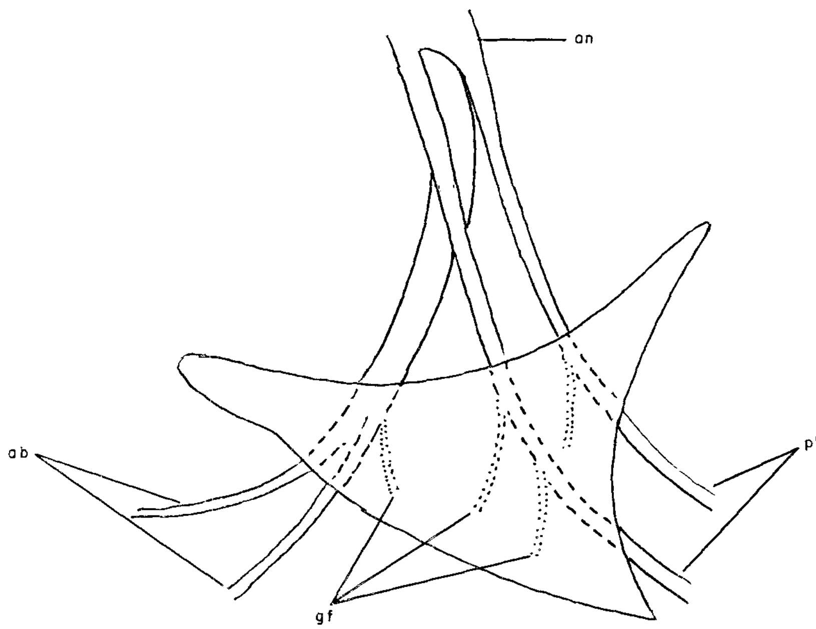

FIG. 6. Glomus aorticum of *Diceros*. Diagram showing division of anterior aortic nerve into superficial (pulmonary) and deep (aortic) moieties and mode of glomus innervation.

a, anterior aortic nerve; ab, aortic terminal branches; gf, nerve filaments to glomus; pb, pulmonary terminal branches.

Throughout its course the nerve lies craniad of the glomus aorticum and separated therefrom by the ascending aorta; it is thus precluded from participation in the innervation of the glomus (Fig. 5). It is most probable that *in vivo* this nerve provided branches also to the terminal pulmonary veins, though no such structures are identifiable in the mutilated left atrial region of the specimen.

In the *Rhinoceros* heart (as noted) the fragmentary remains of the terminal branches of an anterior aortic nerve are observable both within and alongside the triangular district originally occupied by a well-developed aortic glomus. The orientation of these nerve fragments proclaims clearly a terminal disposition of the *Rhinoceros* anterior aortic nerve exactly similar to that of the *Diceros* anterior aortic nerve.

The anatomical evidence indicates that in both *Diceros* and *Rhinoceros* the glomus aorticum is innervated by an anterior aortic nerve of mixed sympathetic and vagal composition, that this nerve constitutes the depressor nerve of the rhinoceros heart and that, most probably, a comparable relationship of nerve to glomus obtains in other rhinoceros genera.

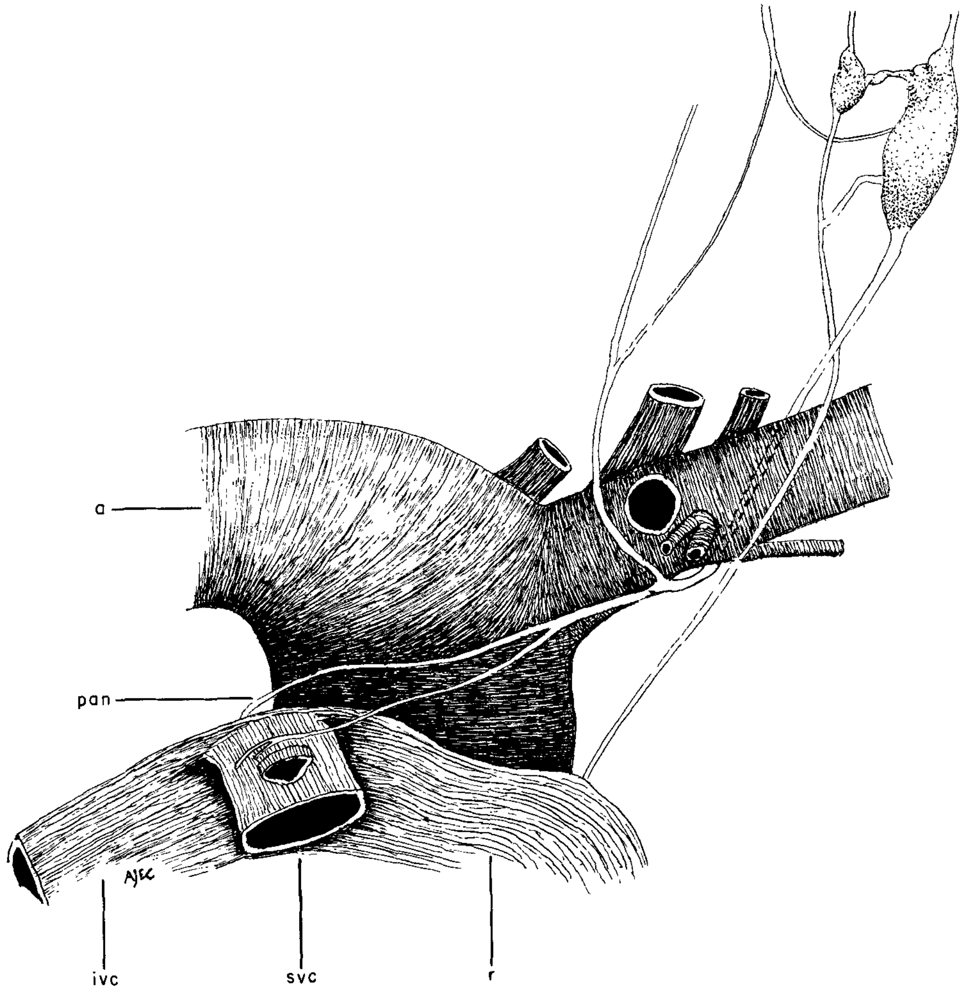

FIG. 7. Dissection of *Diceros* heart from the dextral aspect to show greater part of posterior aortic nerve and its branch to the (reflected) terminal precava.
a, aorta; ivc, terminal postcava; pan, posterior aortic nerve, r, right atrium; svc, terminal precava.

Commentary

Though of restricted numerical and taxonomic range, the anatomical evidence resulting from present enquiry suffices to establish the presence in the Rhinocerotidae of a cardiac receptor apparatus similar in arrangement to that determined in mammalian forms more closely investigated in this respect. Thus rhinoceros chemoreceptors are developed in the form of an aortic glomus (*Diceros*, *Rhinoceros*) and in that of a carotid glomus (*Rhinoceros* and, probably, *Didermocerus*). Baroreceptor areas are developed in the walls of (at least) the brachiocephalic artery, the aorta, the truncus pulmonis and the terminal precava and are probably even more topographically extensive, as the examination of further material may well show. Whilst aortic and carotid glomera are probably canonical features of rhinoceros morphology, a subclavian glomus appears not to be developed.

The vascularization of the *Diceros* aortic glomus from the truncus pulmonis recalls the similar mode of glomus vascularization reported for man and the cat by Palme (1934) and for the cat by Nonidez (1935). The detailed vascularization of the *Rhinoceros* carotid glomus awaits determination as does also its histological structure: the fine artery reaching the glomus through the ligament of Mayer, apparently from the common carotid artery, may well prove to be supplemented by vessels from other sources.

The adventitial (aortic) nerves of the rhinoceros heart are the peripheral portions of the anatomical pathways subserving those reflexes essential to harmonious haemodynamic activity. They afford dependable guidance to the localization of receptor areas since such areas are but the product of their intramural terminal ramifications. They demonstrate receptor areas to occur in the brachiocephalic artery, the ascending aorta, the truncus pulmonis and the terminal precava. It is noteworthy that such pulmonary trunk receptor areas are indicated as occurring both in the root of that vessel and in its bifurcation. The anterior aortic nerve, by virtue of its distribution both to the glomus aorticum and to the brachiocephalic, aortic and pulmonic walls, would appear to represent the "depressor nerve" of the rhinoceros heart. The presence of a dextral (precaval) branch from the posterior aortic nerve implies the presence of a (*Diceros*) precaval receptor area akin to that first noted in other mammals by Nonidez (1937); it is considered most probable that this nerve is distributed also to the terminal pulmonary veins, and much regretted that positive evidence concerning such suspected distribution is not forthcoming from the material presently examined.

Conclusions

The rhinoceros heart is equipped with a typically mammalian receptor apparatus which includes chemoreceptors in the form of canonical aortic and carotid glomera and baroreceptor areas, both arterial and venous.

The location of the cardiac receptor areas is indicated by the distribution of the aortic nerves, the anterior of which constitutes the physiological depressor nerve.

The anterior aortic nerve innervates the glomus aorticum, brachiocephalic artery, ascending aorta and pulmonary trunk root: the posterior aortic nerve innervates the aorta (minimally), the bifurcation of the truncus pulmonis and the terminal precava, and probably also the terminal pulmonary veins.

The glomus aorticum is vascularized by the truncus pulmonis, the glomus caroticum by the common carotid and/or some terminal branch thereof.

Gratitude is tendered to the Council of the Zoological Society of London for the donation of the *Rhinoceros* and *Diceros* material utilized in the present enquiry, and to Dr L. Forcart, of the Basel Naturhistorisches Museum, for the kind loan of *Didermocerus* material. Special acknowledgment is made of the generous assistance rendered by Professor F. R. Johnson, of the London Hospital Medical College, in undertaking the histologization, microphotography and examination of suspected glomus tissue and in providing authoritative opinion thereon.

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